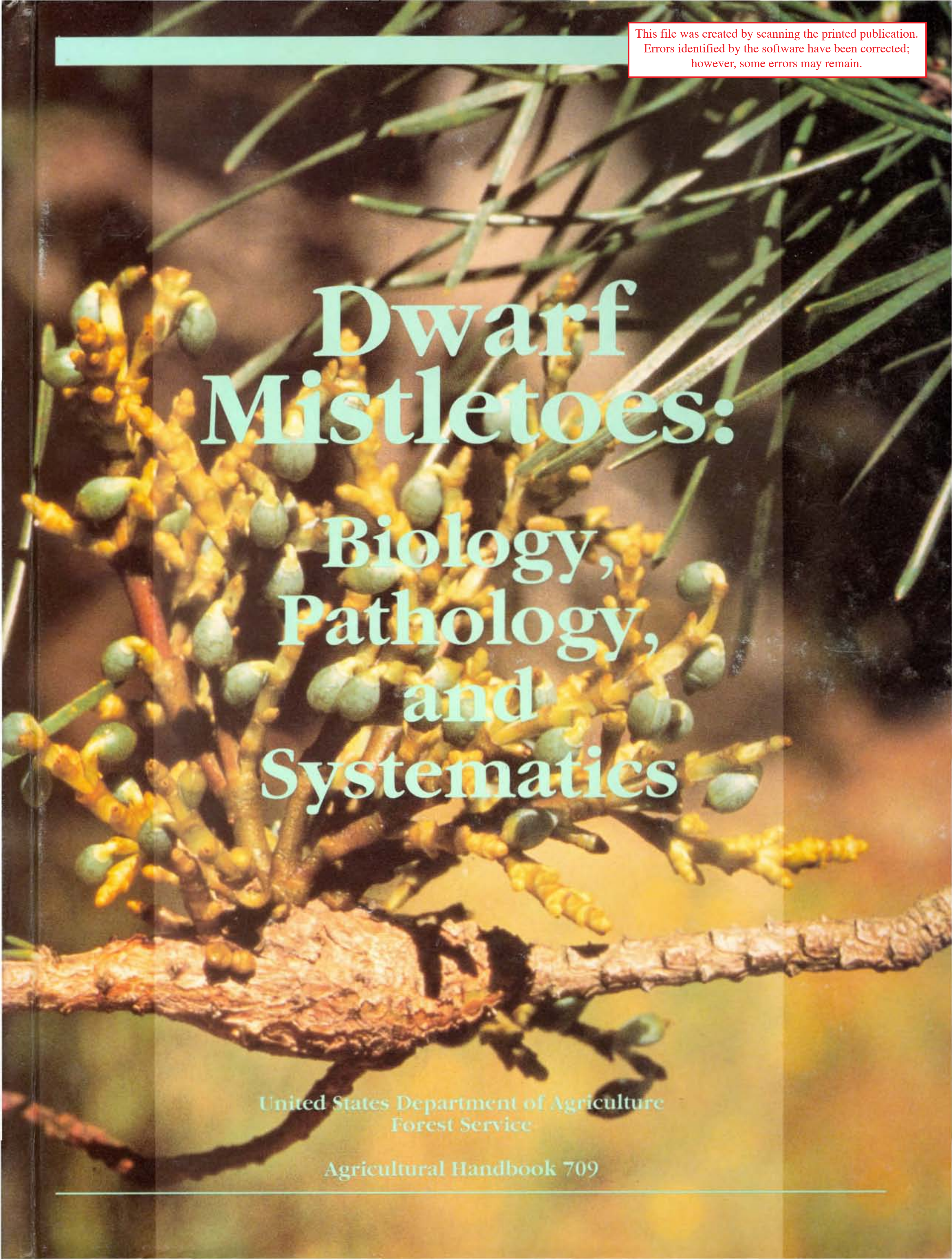

Dwarf Mistletoes:

Biology, Pathology, and Systematics

United States Department of Agriculture
Forest Service

Agricultural Handbook 709

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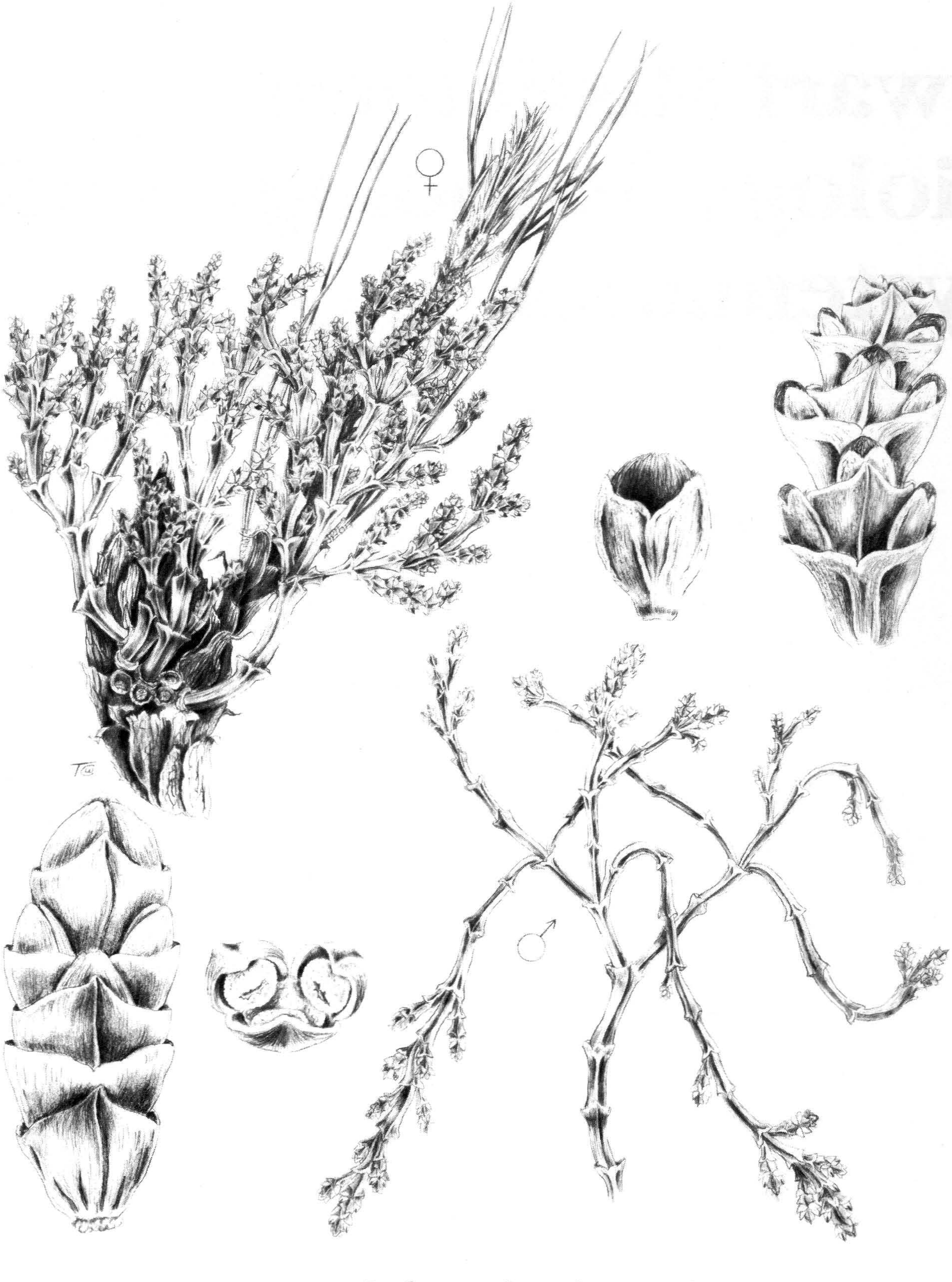

Arceuthobium hawksworthii

In Memory

Frank G. Hawksworth died on January 8, 1993, following heart surgery. He was known internationally as a forest pathologist, although his singular scientific passion was dwarf mistletoes. Frank's research spanned nearly four decades. He authored over 275 articles and reports, the majority of which concerned dwarf mistletoes. His enchantment with these fascinating plants never waned and his attention was not distracted.

Frank worked on this manuscript until the day he entered the hospital. He approached the study of mistletoes as a compositionist. He sought to understand the inter-relationships of species and thought of organisms as integral, functioning wholes. As an unusually acute observer, Frank possessed what taxonomists call "a good eye." His field studies were unrivaled and his comprehension of the literature was unsurpassed. Frank's outstanding knowledge, endless helpfulness, perennial good cheer, and his subdued but pervasive wit will be sorely missed. He is commemorated by *Arceuthobium hawksworthii* (a recently described species of dwarf mistletoe from Belize), *Phoradendron hawksworthii* (a mistletoe parasite of juniper in western Texas), and *Frankliniella hawksworthii* (a species of thrips associated exclusively with dwarf mistletoes).

Shortly before his death Frank sent me a reprint of a publication on the life of Lucy Bishop Millington, a nineteenth-century botanist of the Adirondack region of New York. In an accompanying note Frank commented "Shades of Durango in 1963?" He was referring to our discovery of five new species of *Arceuthobium* in a single day between Durango and El Salto, Mexico. He had marked a quote by Millington that described her emotions in 1871 when she realized that the decline and mortality of black spruce was caused by a then-undescribed mistletoe (now known as *A. pusillum*). Her reflections of that moment revealed a deep spiritual involvement with nature that elicited strong empathy in Frank. Perhaps her comments explain something of the fascination with discovery that motivates those with inquisitive minds. Few of us, however, would risk exposing the sensitivity necessary to acknowledge it.

> There is one day of my life marked with a white stone ... so few such days fall to the lot of man, that we do well to remember them. I drew nearer the secret heart of nature than ever before. I saw what human eyes had not seen before: I touched what none had touched before me. Though all the world may now look on, mine was the first delightful thrill of recognition ... in all one's lifetime scarce such a thing may happen again.
>
> Lucy Millington (1871a)

Del Wiens
Salt Lake City, Utah
June 1994

Dedication

For Peggy and Carol

Dwarf Mistletoes: Biology, Pathology, and Systematics

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Rocky Mountain Forest and Range Experiment Station
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and

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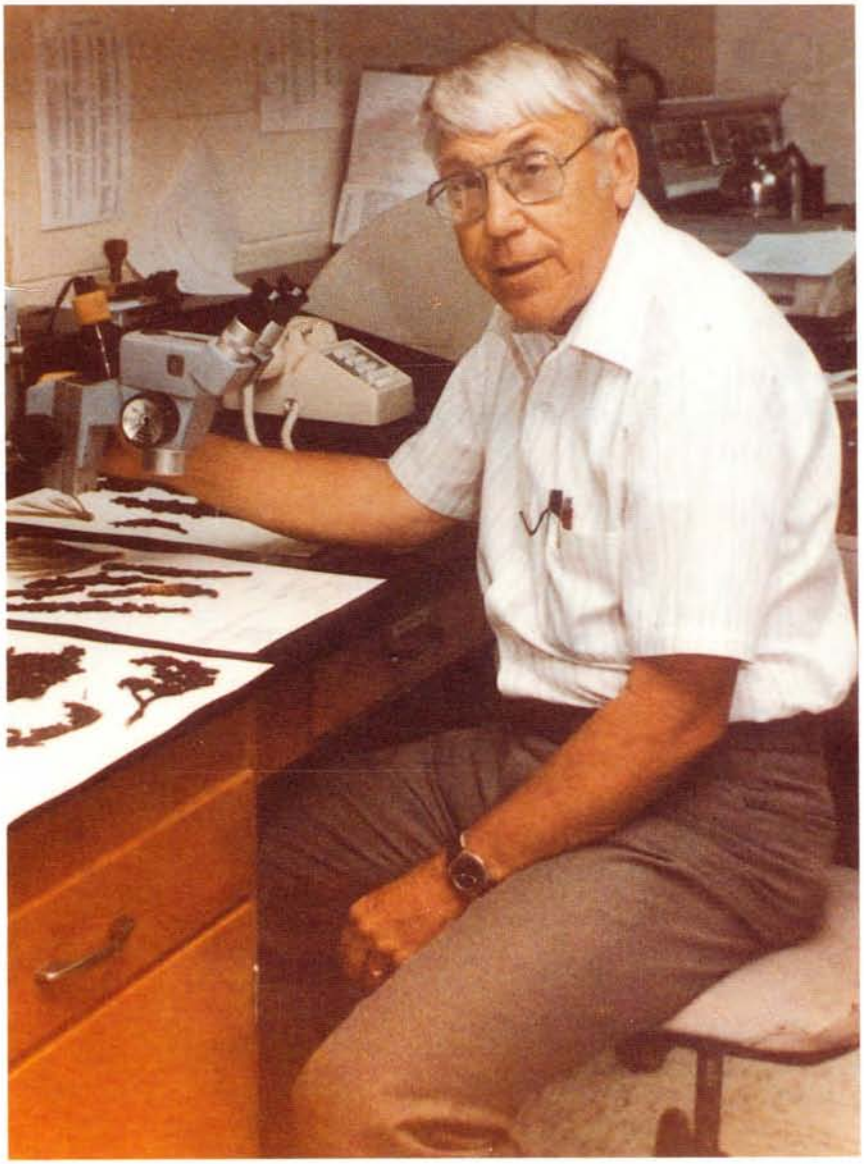

Frank Goode Hawksworth
1926–1993

Preface

"So much has already been written on this genus [*Arceuthobium*] of the Loranthaceae that many readers will no doubt be surprised that there should be anything new to be said on the subject" (Johnson 1888). However, since then there have been more than 4,200 publications involving *Arceuthobium*! Following the appearance of our monograph—*Biology and Classification of Dwarf Mistletoes* (Arceuthobium)—in 1972, over 2,200 publications concerning the group have appeared and 18 new taxa have been described. The dwarf mistletoes also have been the subject of two symposia: "Control Through Forest Management" in Berkeley, California (Scharpf and Parmeter 1978), and "Dwarf Mistletoe Biology" in Fort Collins, Colorado (Hawksworth and Scharpf 1984).

Because our 1972 monograph is out of print, and because of significant new research on the genus, we decided that a completely new publication was in order. This new study not only expands the topics covered in the earlier version, but it also includes several new aspects: reproductive biology, host–parasite physiology, ecological relationships, biotic associates, pathological effects on host trees, and control. Dr. Brian W. Geils contributed to the chapter "Biotic Associates" (chapter 8). Drs. Clyde L. Calvin and Carol A. Wilson, Portland State University and University of California, Berkeley, have contributed two chapters: "Anatomy of the Dwarf Mistletoe Shoot System" (chapter 10) and "Endophytic System of *Arceuthobium*" (chapter 11). Dr. Daniel L. Nickrent, Southern Illinois University, contributed the chapter "Molecular Systematics" (chapter 15).

Abstract

Arceuthobium (dwarf mistletoes), a well-defined but morphologically reduced genus of the family Viscaceae, is parasitic on Pinaceae in the Old and New Worlds and on Cupressaceae in the Old World. Although conifer forests in many parts of the Northern Hemisphere are infested with dwarf mistletoes, those most commonly infested are in western North America and Mexico. In North America, *Arceuthobium* ranges from central Canada and southeastern Alaska to Honduras. Only *A. pusillum* occurs in eastern North America, and only *A. juniperi-procerae* is found in the Southern Hemisphere. *Arceuthobium bicarinatum* and *A. azoricum* are restricted to islands (Hispaniola and the Azores, respectively).

In this taxonomic revision, the 46 recognized taxa comprise 42 species—4 with 2 subspecies each, and 1 with 2 *formae speciales*. Eight species are known in the Old World and thirty-four species occur in the New. Natural hybridization and polyploidy are unknown and have resulted in a relatively clear, dendritic line of evolution. The genus is probably of early Tertiary origin and its closest relative is the genus *Notothixos*, which has tropical Asian and Australasian distribution. *Arceuthobium* presumably migrated to the New World before the Miocene Epoch. Intensive adaptive radiation occurred into the Pinaceae. Some of the species of *Abies, Picea, Tsuga, Larix,* and *Pseudotsuga* and 95% of the species of the *Pinus* are parasitized.

The morphological characteristics that delimit species of *Arceuthobium* are often cryptic and may be apparent for only short periods of the life cycle. Species and subspecies nonetheless differ in a number of discontinuous variables. Most species are sympatric with other members of the genus somewhere in their distribution and flowering periods often overlap, but species appear to be isolated reproductively.

In addition to systematic and descriptive information for each species, we review ecological relationships, biotic associates, physiology, anatomy, pathogenic effects, and methods of control for the *Arceuthobium*. Color pictures, distribution maps, and a list of specimens examined are provided.

Disclaimers

The use of pesticides is mentioned in this monograph but only for general information and not as an endorsement. Because of frequent changes in pesticide registration and labeling, the reader should check with State and local forest pathologists, county agricultural specialists, or State extension specialists to be sure the intended use of a pesticide is still registered. Remember that pesticides can be harmful to humans, domestic animals, desirable plants, and fish and wildlife if they are not handled or applied properly. Use all pesticides selectively and carefully, following the label directions. Follow recommended practices for the disposal of surplus pesticides and pesticide containers.

Acknowledgments

The final preparation of this manuscript was completed with the generous assistance of many individuals. The following people read all or portions of the manuscript. Their keen insights and suggestions have enhanced the text significantly: C. L. Calvin, B. W. Geils, R. H. Hamre, J. G. Laut, E. J. King, R. L. Mathiasen, D. L. Nickrent, C. G. Shaw III, R. F. Scharpf, and R. O. Tinnin.

Following Frank Hawksworth's death, Charles (Terry) Shaw provided broad and generous support for all phases of the project. The assistance of Brian Geils was critical for completion of numerous technical details, especially editing tables, figures, and appendices. Bob Hamre's deft editorial pen benefitted the text enormously. Sheila Ames rose to the challenge of an enormous bibliographical task, and Bonnie Speir withstood requests for continual revisions with remarkably good cheer. Mai Dailey assisted with correspondence and indexing. Joyce Patterson, Bernadette Velick, and Tracy Wager, provided the skillful illustrations that occur throughout the text. John Sprackling made especially significant contributions by assisting with herbarium work, phenological analyses, and preparation of the distribution maps.

We thank the curators of the many herbaria in North America, Central America, Europe, Asia, and Africa who allowed us to examine dwarf mistletoe collections. Also, we acknowledge the assistance of the many colleagues who collected specimens, provided data, reviewed various aspects of the manuscript, supplied photographs or drawings, assisted with numerical analyses and laboratory work, and performed many other courtesies.

The more than 60 colleagues who provided information during the preparation of the 1972 monograph are listed in that work. Many of those associates and numerous others also aided us in the preparation of this revision. In addition, we are grateful to the following individuals for their assistance in various aspects of the study—

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Contents

CHAPTER 1

Introduction

Arceuthobium (Viscaceae) is a clearly defined group of small (generally less than 20 cm high), variously colored (yellow, brown, black, or red) flowering plants that are aerial parasites only on members of the Pinaceae and Cupressaceae. The dwarf mistletoes, as they are commonly known, are of unusual biological interest because they are the most evolutionarily specialized genus of the Viscaceae. Some of the features that make *Arceuthobium* unique among mistletoes include:

- Extreme reduction in size—*Arceuthobium minutissimum* with flowering shoots only several millimeters high is among the smallest of dicotyledonous plants.
- Evolution of species that regularly cause systemic patterns of witches' broom formation—*Arceuthobium douglasii, A. pusillum*, and *A. minutissimum.*
- Development of a highly effective mechanism of explosive seed dispersal (seeds of virtually all other aerial mistletoes are dispersed by birds).
- Occurrence of bicolored fruits.
- Stems with variant (anomalous) patterns of secondary growth.
- Sessile, ring-like anthers surrounded by a sterile central column that in *Arceuthobium americanum* and *A. pusillum* are capable of opening and closing in response to environmental changes.
- Geographical distribution that encompasses both the New and Old Worlds.

The dwarf mistletoes are of immense economic importance because they are the single-most destructive pathogen of commercially valuable coniferous timber trees in several regions of Mexico, western Canada, western United States, and parts of Asia (Bakshi and Puri 1971, Hawksworth and Shaw 1984, Zakaullah and Badshah 1977).

With the increasing recognition of dwarf mistletoes as destructive parasites on commercially important forest trees, the need for additional systematic and other biological studies on the group became apparent. Control of dwarf mistletoes in some areas has been hampered by inadequate knowledge of the identity of the parasite involved and the relationship to its host(s).

Arceuthobium has been classically included in the subfamily Viscoideae of the Loranthaceae. Van Tieghem (1895) considered *Arceuthobium* so distinct from related genera that he proposed its classification as a separate family positioned phylogenetically between the Viscaceae and the Santalaceae. This proposal, however, has never been followed. The subfamilies Loranthoideae and Viscoideae are now generally agreed to warrant family status (Barlow 1964, Thorne 1992). Members of these groups differ in floral morphology, floral anatomy, pollen characteristics, embryology, and chromosome size and numbers (Calder 1983). The previously supposed similarities between the two groups are largely the result of evolutionary convergence for the aerial parasitic habit and seed dispersal by birds, rather than the consequence of a common phyletic origin. We, therefore, accept full family status for both groups.

Engler and Krause (1935) classified *Arceuthobium* as a monogeneric tribe in the Viscoideae. They placed *Dendrophthora, Phoradendron,* and *Korthalsella* in the tribe *Phoradendreae* and separated *Korthalsella* in subtribe *Korthalsellinae* and *Phoradendron* in subtribe *Phoradendrinae.* Regardless of its relationship to other Viscaceae, *Arceuthobium* has clearly defined limits, and its generic status has never been questioned. Kuijt (1970) suggested that the genus is separable into two natural groups on the basis of branching habit (verticillate versus flabellate).

The New World has a greater number of species (34) than the Old World (8). In the Old World, two species are recently described from China (*Arceuthobium tibetense* and *A. sichuanense*). Another two species, *A. azoricum* and *A. juniperi-procerae,* have been segregated from the widely distributed species *A. oxycedri.* In the New World, dwarf mistletoes are found from southeastern Alaska, northern Canada, and Newfoundland through most of the western United States and Mexico to Central America (Honduras), with an extreme outlying population on the island of Hispaniola (see fig. 5.2).

Species diversity is greatest in northwestern Mexico and the western United States, where 28 of the 34 New World species occur. The six New World species outside this area are *Arceuthobium bicarinatum* on Hispaniola; *A. aureum, A. guatemalense, A. hawksworthii,* and *A. hondurense* in Central America; and *A. pusillum* in southeastern Canada, the Great Lakes region, and the northeastern United States. Twenty species occur in Mexico, and eight of these are found also in the western United States. Nineteen species occur in the United States, five of which also occur in Canada (*A. americanum, A. douglasii, A. laricis, A. pusillum,* and *A. tsugense*). *Arceuthobium douglasii* has the widest distribution in the New World. This mistletoe is distributed from southern British Columbia, Canada, southward throughout most of the western United States to southern Durango, Mexico.

Objectives and Scope

Our initial interest in *Arceuthobium* was to clarify the confusion surrounding the *A. campylopodum* complex (see Hitchcock and Cronquist 1964), which centered primarily around Gill's (1935) designation of host-forms in this group. However, when we discovered the rich dwarf mistletoe flora in Mexico (Hawksworth and Wiens 1965, 1977, 1980, 1989), we expanded our investigations to include a comprehensive treatment of the entire genus. We have since studied naturally occurring populations of all 38 known New World taxa, as well as 4 of the 8 known Old World species. Beginning in 1962, our field studies of *Arceuthobium* have taken us over 800,000 kilometers by foot, hoof, wheel, and wing throughout North America, Central America, the Caribbean, the Azores, Europe, North and East Africa, and the Himalayas.

The more than 3,000 dwarf mistletoe specimens we have collected in our field work, plus many early U.S. Department of Agriculture collections by J. R. Weir, G. G. Hedgcock, J. S. Boyce, and L. S. Gill, are filed at the USDA Forest Service's Mistletoe Herbarium at Fort Collins, Colorado. They provide the basis for our taxonomic understanding of the genus. Duplicates of our collections are deposited in various North American herbaria, particularly those of the University of Colorado (Boulder), Missouri Botanical Garden (St. Louis), U.S. National Museum (Washington, DC), and Instituto de Biologia of the Universidad Nacional Autonoma de Mexico, Escuela Nacional de Ciencias Biologias of the Instituto Politecnico Nacional, and Instituto Nacional de Investigaciones Forestales y Agropecuarias (Mexico City). In addition to our own collections, we have examined the specimens at the major herbaria in North America and Europe.

Our goal was to develop a natural and useful classification of dwarf mistletoes based on a broad eclectic approach involving morphology, ecology, physiology, biochemistry, and genetics. Other features of evolutionary interest included biogeography, paleobotany, reproduction, and life cycles. Finally, to provide utility for practicing foresters, discussions of pathological effects on host trees and control measures were included.

A glossary of some of the less familiar terms and special usages is included, as well as lists of scientific and common names of species mentioned in the text.

Taxonomic History

The first dwarf mistletoe described, *Arceuthobium oxycedri,* was originally included in *Viscum* (Clusius 1576). It was later segregated from *Viscum* by Hoffman (1808) as *Razoumofskya. Arceuthobium* was first proposed as a genus by Marschall von Bieberstein (1819), and it was generally used until the early 1900's. The Vienna Botanical Congress in 1905 conserved *Arceuthobium* over *Razoumofskya.* Because the American Code emphasized strict priority, however, most botanists in the United States continued to use *Razoumofskya. Arceuthobium* finally displaced *Razoumofskya* as a result of the 1930 Cambridge Botanical Congress and Gill's (1935) taxonomic revision of the species in the United States.

Humboldt and Bonpland's collection of a dwarf mistletoe on Cofre de Perote (Veracruz, Mexico, 1804) was apparently the first in the New World. This specimen was designated as the type for *Arceuthobium vaginatum* described in 1806 by Willdenow (as *Viscum vaginatum*). In 1826, David Douglas (1914) discovered two dwarf mistletoes on his botanical explorations of the Pacific Northwest: *A. campylopodum* (on *Pinus ponderosa*) and *A. americanum* (on *P. contorta*). William Hooker (1847) first discussed the taxonomy of *Arceuthobium* in North America north of Mexico and compared Douglas' specimens and another by Drummond (of *A. americanum*) with the European *A. oxycedri,* but he detected no differences except for color variations. George Engelmann was the first to publish (in Gray 1850) a formal description of a dwarf mistletoe found in the United States (*A. americanum*). As the taxonomic architect of the genus in North America, Engelmann (associated with the Missouri Botanical Garden) named most of the

American species of *Arceuthobium* during the latter half of the 19th century (Gray 1850, Watson 1880).

Between 1910 and 1920, G. G. Hedgcock and J. R. Weir of the Division of Forest Pathology (Department of Agriculture) independently initiated studies on the taxonomy and host relationships of *Arceuthobium* in the United States. Both published a number of articles on dwarf mistletoes, but for unknown reasons their taxonomic conclusions remained unpublished as manuscripts on file with the USDA Forest Service, Fort Collins, Colorado. This was unfortunate, because Hedgcock had a keen understanding of the genus. For example, he first recognized that the dwarf mistletoe on *Pinus lambertiana* (our *A. californicum*) was distinct from *A. cyanocarpum,* and that *A. campylopodum* was distinguishable from *A. occidentale.* Hedgcock (1915) published a host list of *Arceuthobium* for the United States and later reported some new hosts of *A. campylopodum* and *A. occidentale* resulting from artificial inoculations (Hedgcock and Hunt 1917).

Weir (1918a) artificially inoculated various hosts with several species of dwarf mistletoes in the Northwest under both field and greenhouse conditions, and he discussed the taxonomic implications of the results. He began a systematic treatise on American dwarf mistletoes but never completed the work. He did, however, publish observations of hosts associated with several dwarf mistletoes (Weir 1915a, 1915b, 1916c, 1917, 1918b).

Aven Nelson of the University of Wyoming described two new dwarf mistletoes: *Arceuthobium cyanocarpum* in Wyoming (Coulter and Nelson 1909) and *A. blumeri* in Arizona (Nelson 1913). Karl von Tubeuf (1919) published a review of the genus based on available literature, his extensive knowledge of *A. oxycedri,* and results of a brief trip in 1913 to the western United States. Unfortunately, this work did little to resolve taxonomic relationships. Heil (1923), another German worker, described *A. abietis-religiosae,* a parasite of *Abies* in central Mexico.

Following Nelson's and Tubeuf's studies, taxonomic understanding of the genus did not advance until a revision of the species in the United States was published in 1935 by L. S. Gill while employed by the U.S. Department of Agriculture. Gill re-evaluated Engelmann's taxonomic conclusions, recognized flowering periods as an important taxonomic character, and reduced the rank of several closely related species to host-forms of *Arceuthobium campylopodum* and *A. vaginatum.* Although Gill clearly established a taxonomic framework for the genus, he considered his work to be provisional "pending a complete revision of the genus based on further field and experimental evidence."

Job Kuijt (1955, 1960a, 1960b, 1963, 1964) rejected Gill's host-form concept for *Arceuthobium campylopodum* and *A. vaginatum* and considered each as a single variable species. He also concluded, as did Gill (1935), that *A. bicarinatum* of Hispaniola should be included in *A. campylopodum.*

Hawksworth and Graham (1963) first discussed the difficulties of applying Gill's host-form concept to the dwarf mistletoes that parasitize *Picea* in the western United States. They concluded that many of Gill's "forms" in the *Arceuthobium campylopodum* complex could be distinguished morphologically and should be accorded higher taxonomic rank.

Hawksworth and Wiens (1964) described a new species, *Arceuthobium gillii* (a parasite of *Pinus leiophylla* var. *chihuahuana* in southern Arizona and northern Mexico) that had been previously confused with the more widespread *A. vaginatum* subsp. *cryptopodum* (a parasite of *P. ponderosa*). Hawksworth and Wiens (1965) published the first comprehensive study of the genus in Mexico and described five additional taxa. Wiens (1968) analyzed the chromosome numbers in *Arceuthobium* and organized the species into distinct flowering groups. Next, Hawksworth and Wiens (1970a) published a subgeneric classification of the genus with descriptions of four new species and two new combinations from Mexico, Guatemala, and the United States. We then reviewed the biology and classification of the entire genus (Hawksworth and Wiens 1970b) and published our monograph on *Arceuthobium* 2 years later (Hawksworth and Wiens 1972).

Following the publication of our monograph, we segregated two species from the widely distributed *Arceuthobium oxycedri: A. azoricum* from the Azores and *A. juniperi-procerae* from East Africa (Hawksworth and Wiens 1976). Shortly thereafter, we described three additional taxa from Mexico and Guatemala (Hawksworth and Wiens 1977). This was followed by a study of the flavonoid chemistry of the genus (Crawford and Hawksworth 1979) and description of another new species (*A. pendens*) on pinyons from central Mexico (Hawksworth and Wiens 1980). Mark and Hawksworth (1981) analyzed the branching patterns in two California dwarf mistletoes. An update and review of the taxonomy of the genus was completed by Hawksworth and Wiens (1984). A re-evaluation of the classification of the dwarf mistletoes on *Tsuga* was then undertaken (Hawksworth 1987a), and the taxonomy and evolution of the genus was reviewed by Hawksworth (1987b). Clarification of the host relationships of three dwarf mistletoes that parasitize white pines in northern California and southern

Oregon was completed by Mathiasen and Hawksworth (1988). Two additional new species were described, and two new combinations were proposed for Mexican dwarf mistletoes by Hawksworth and Wiens (1989). Hawksworth (1991a) reviewed the genus in Mexico and Central America. Three species from California and southern Oregon were described, and the subspecies and host races of *Arceuthobium tsugense* were characterized by Hawksworth and others (1992b). Finally, differences between herbarium collections of *A. aureum* subsp. *aureum* from Guatemala and Belize lead us to the discovery of *A. hawksworthii* (Wiens and Shaw 1994).

Five dwarf mistletoes are now known from southwestern China (Kiu 1984b): *Arceuthobium chinense, A. oxycedri, A. pini, A. sichuanense,* and *A. tibetense.* Kiu and Ren (1982) described *A. tibetense*, a parasite of *Abies.* Kiu (1984a) described *A. pini* var. *sichuanense,* a parasite of *Picea;* and Hawksworth and Wiens (1993) raised it to specific rank.

The recent investigations of electrophoretic characteristics and DNA sequencing analyses of the genus by Daniel Nickrent and colleagues at the University of Illinois and Southern Illinois University (Nickrent 1986, 1987; Nickrent and Butler 1990; Nickrent and Stell 1990; Nickrent and others 1984; Schuette 1992; Schuette and Nickrent 1992) have provided exciting new insights into the evolutionary history of the group and the relationships among the various taxa (chapter 15).

Ethnobotanical and Medicinal Uses

An extensive folklore surrounds the European mistletoe, *Viscum album,* in northern Europe and England. As new lands were discovered and colonized by these Europeans, other Viscaceae such as *Phoradendron* were encountered that resembled *V. album.* Inevitably, the folklore associated with *V. album* was transferred to these plants (Calder 1983). Because of their relative inconspicuousness and general dissimilarity to *Viscum* and *Phoradendron,* little folklore, however, is associated with species of *Arceuthobium.* According to Fernald (1900), French and English women in northern Maine used spruce twigs infected with *A. pusillum* in their hair at the midwinter ball. He was unable to determine, however, if the plant had the traditional seasonal significance of the European mistletoe. Young women of the Okanogan-Colville tribe of British Columbia and Washington boiled branches from witches' brooms of Douglas-fir infected with *A. douglasii* to make a hair wash that they believed gave them long, thick hair (Turner and others 1980).

Mistletoes are utilized for medicinal purposes by aboriginal peoples in many parts of the world, and the dwarf mistletoes are no exception (Moerman 1977). California Indians prepared a decoction of *Arceuthobium occidentale* to treat stomach ache (Chestnut 1902). Indians in Butte County, California, used an undetermined species of dwarf mistletoe for treating hemorrhage of the lungs and mouth, tuberculosis, emaciation, stomach ache, cough, colds, and rheumatism (Taylor 1981). Bella Coola Indians of coastal British Columbia employed shoots of *A. tsugense* in the treatment of several of the same maladies (Smith 1928). Navajo Indians of New Mexico and Arizona used both *A. divaricatum* and *A. vaginatum* subsp. *cryptopodum* for unspecified medicinal purposes (Vestal 1952, Wyman and Harris 1941).

Dwarf mistletoes were utilized in the treatment of several ailments in Veracruz, Mexico (Cházaro and Oliva 1988), and Martínez (1959) reports that *Arceuthobium vaginatum* is used for the treatment of cough in Mexico. Sra. S. Gonzales of Villa Guerrero, Durango, Mexico (personal communication, 1987), informed us that indigenous peoples in the vicinity of Tepehuanes, Durango, used a decoction of *A. vaginatum* subsp. *vaginatum* for the treatment of rheumatism and lung disorders and that *A. globosum* subsp. *globosum* was utilized for the treatment of diarrhea and nervous, pulmonary, and rheumatic disorders. *Arceuthobium globosum* subsp. *globosum* is also burned as incense in religious ceremonies, but Sra. Gonzales did not know the basis for this practice.

Various mistletoes, especially *Viscum album,* have been studied for pharmaceutical purposes, but the dwarf mistletoes have received relatively little attention in this regard. Extracts of Old World *Arceuthobium oxycedri* have a hypotensive action similar to extracts of *V. album* (Livon 1913); constituents of *A. americanum* show some anti-tumor activity (Sealwry and others 1959). Toxic proteins in *V. album* and *Phoradendron* have been examined for cancer therapy (Luther and Becker 1987). Several dwarf mistletoes have also been tested for toxic proteins (*A. americanum, A. campylopodum, A. divaricatum* and *A. vaginatum* subsp. *cryptopodum*), but only *A. americanum* tested positive for toxic acetone precipitate. This indicates a moderate level of toxic proteins, but too low to be considered for commercial use (Samuelsson 1969). Recent tests for pharmacologically active lectins in several North American species of *Arceuthobium* taxa have all been negative (H. Fraanz, personal communication, 1988).

There are reports of minor uses of dwarf mistletoes as dye plants (Bliss 1980) and as pollen sources for honey bees in California (Coleman 1921) and Arizona (O'Neal and Waller 1984).

The juniper dwarf mistletoe, *Arceuthobium oxycedri,* is a preferred food of sheep and goats in Mediterranean countries, the Near East, and in the Himalayas (Acatay 1954, Zakaullah and Badshah 1977). Acatay (1954) expressed concern over the forest damage caused by cutting down juniper trees to provide dwarf mistletoe fodder for sheep and goats. Various mistletoes are utilized as food for domestic animals in different parts of the world, and both the Viscaceae and Loranthaceae appear to have few chemical defenses against predation (Barlow and Wiens 1977).

CHAPTER 2

Generalized Life Cycle

Differences between life cycles, particularly phenological shifts, constitute an important basis for taxonomic distinctions in *Arceuthobium*. Here we discuss the salient features of the dwarf mistletoe life cycle, excluding the more detailed aspects of sexual reproduction, which are treated separately in chapter 3. Shoots, flowers, and fruits of *Arceuthobium* are illustrated in figures 2.1–2.4. The critical features of the life cycle of a representative species (*A. americanum*) are shown in figure 2.5.

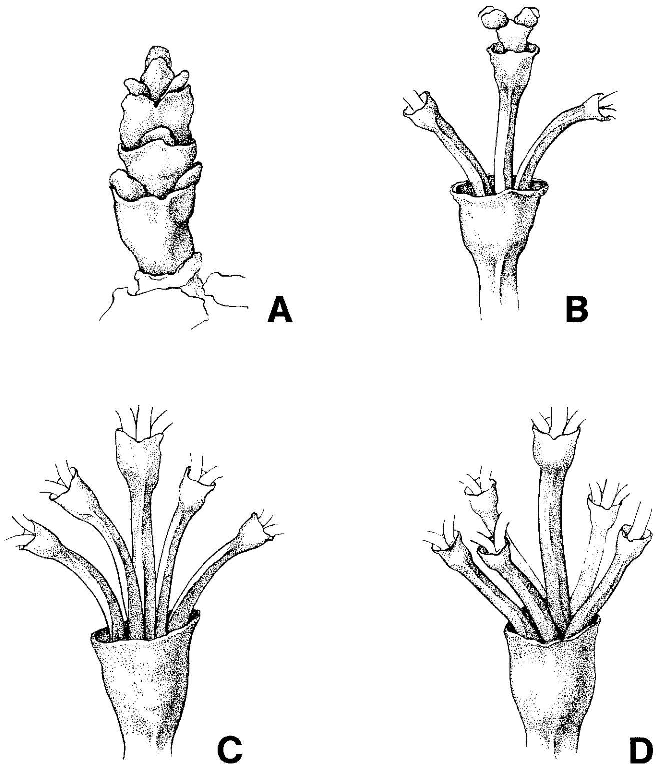

Figure 2.1 –Shoots of *Arceuthobium.* A: young shoots showing the decussate arrangement of the internodes; B: older shoots showing elongated internodes and branching; C: typical flabellate (fan-like) branching pattern of most New World species; D: verticillate (whorled) branching pattern of Old World and a few New World species. All species show the primary branching type (A and B), but most species also develop secondary branching, which may be either flabellate (C) or verticillate (D).

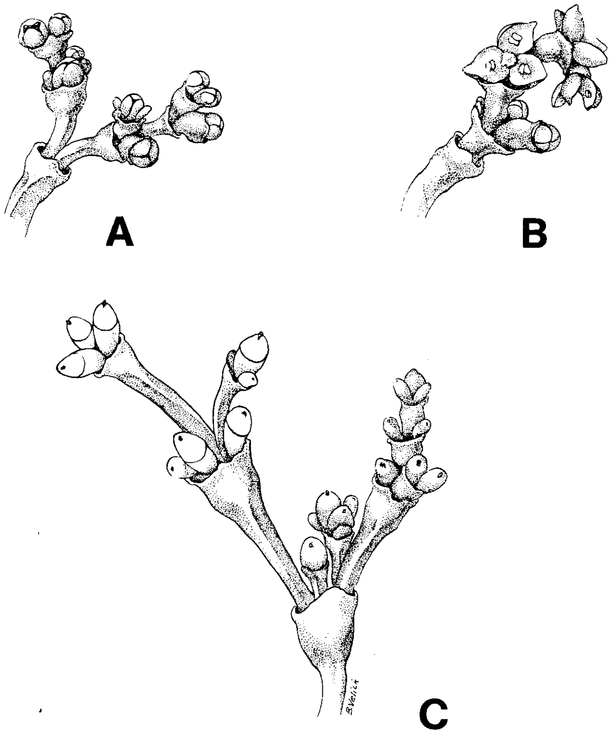

Figure 2.2 –Flowers and fruits of *Arceuthobium americanum.* A: terminal portion of staminate shoot showing mature flower buds; B: terminal portion of staminate shoot with open 3-merous flowers; C: terminal portion of pistillate shoot showing flowers shortly after pollination (upper portion of right branch) and developing fruits (left branch) that are about 1 year old and still require approximately 3 months to complete maturation and initial dispersal. (B. Velick).

The life cycles of the following species have been studied in some detail:

- *Arceuthobium abietinum*—Scharpf and Parmeter 1967, 1976, 1982.
- *Arceuthobium americanum*—Gilbert and Punter 1990, 1991; Hawksworth 1965b; Hawksworth and Johnson 1989a.
- *Arceuthobium campylopodum*—Roth 1959, Wagener 1962.
- *Arceuthobium chinense*—Tong and Ren 1980.
- *Arceuthobium douglasii*—Wicker 1965, 1967a.
- *Arceuthobium laricis*—Smith 1966a; Wicker 1965, 1967a.

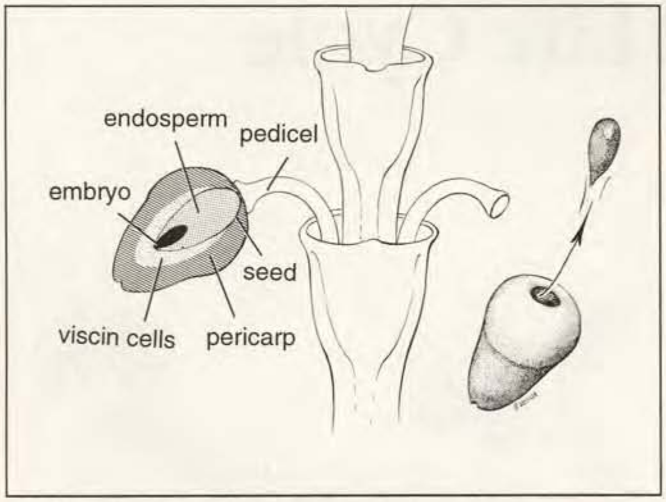

Figure 2.3 –Mature fruit and seed of *Arceuthobium.* Diagrammatic cross-section through a mature fruit (left) and fruit discharging its seed (right). (B. Velick)

Figure 2.4 –Explosive seed discharge in *Arceuthobium.* Seed is in flight immediately after discharge. (photograph taken at 5-millionths of a second, Hinds and others 1963)

- *Arceuthobium oxycedri*—Heinricher 1915a, 1915b, 1924; Rios Insua 1987.
- *Arceuthobium pusillum*—Baker 1981; Baker and French 1979, 1986; Baker and others 1981, 1985.
- *Arceuthobium tsugense*—Carpenter and others 1979; Shaw 1982b; Shaw and Loopstra 1991; Smith 1966a, 1966b, 1971.
- *Arceuthobium vaginatum* subsp. *cryptopodum*—Hawksworth 1961a, 1965b.

Various features of the life cycle are illustrated photographically: pistillate plant with mature fruit and characteristic swelling at the point of infection (fig. 2.6); mature staminate flowers at anthesis with moistened nectaries (fig. 2.7); pistillate flowers at anthesis with pollination droplets (fig. 2.8); mature fruit ready for dispersal (fig. 2.9); explosive dispersal of the seed (fig. 2.4); the dispersed seed sticking to a needle by means of its viscin coating (fig.2.10A); the dispersed seed sliding down the needle in the hygroscopically expanded viscin mass (fig. 2.10B); the seed and viscin at the base of a needle (fig. 2.10C); the germinated seed and elongated hypocotyl that has developed a holdfast from which infection can occur (fig. 2.11); the microscopic "penetration wedge" entering the host tissue (fig. 2.12); and young shoots emerging from the swollen tissue of a new infection (fig. 2.13).

Seed Dispersal and Interception

Our discussion of the dwarf mistletoe life cycle begins with the seed. The fruit normally contains a single seed with one embryo, but fruits may rarely contain two seeds or a single seed with two embryos (Weir 1914, Hawksworth 1961b). Dwarf mistletoes possess one of the most effective hydrostatically controlled, explosive mechanisms of seed dispersal known in flowering plants (fig. 2.4) (Hinds and others 1963, Hinds and others 1965; van der Pijl 1972). The only exception to this mode of dispersal among the dwarf mistletoes is exhibited by *Arceuthobium verticilliflorum,* which has the largest seeds in the genus (11 × 6 mm). In fact, these seeds are greater than twice the size of those of any other dwarf mistletoes. Fruits of *A. verticilliflorum* exhibit a weak explosive mechanism that accomplishes little more than removing the pericarp and exposing the seed. Seeds of *A. verticilliflorum* are undoubtedly dispersed primarily by birds.

Among temperate species of dwarf mistletoes, seeds are explosively discharged during late summer at velocities of about 27 m per second (Hinds and others 1963) (fig. 2.4). Maximum dispersal distance is about 16 m, but dispersal distances of 10 m or less are more typical. Most seeds are intercepted within 2 to 4 m by host needles. Seeds have a viscous coating (viscin) that readily adheres to any object they strike, especially conifer needles (fig. 2.10A) (Roth 1959, Hawksworth 1965b). Intercepted seeds usually remain on the needles until the first fall rain wets the hygroscopic viscin (fig. 2.10B). Gravity then pulls the well-lubricated seed to the base of an upright needle (fig. 2.10C). As the viscin dries, the seed is cemented to the shoot surface. Seeds intercepted by downward-pointing needles generally fall to lower branches or to the ground (Shaw and Loopstra 1991). To achieve infection, seeds must lodge on shoot segments usually less than 5 years old; only this portion of the host can be considered a "safe-site," i.e., a place where a seed can germinate and establish an infection.

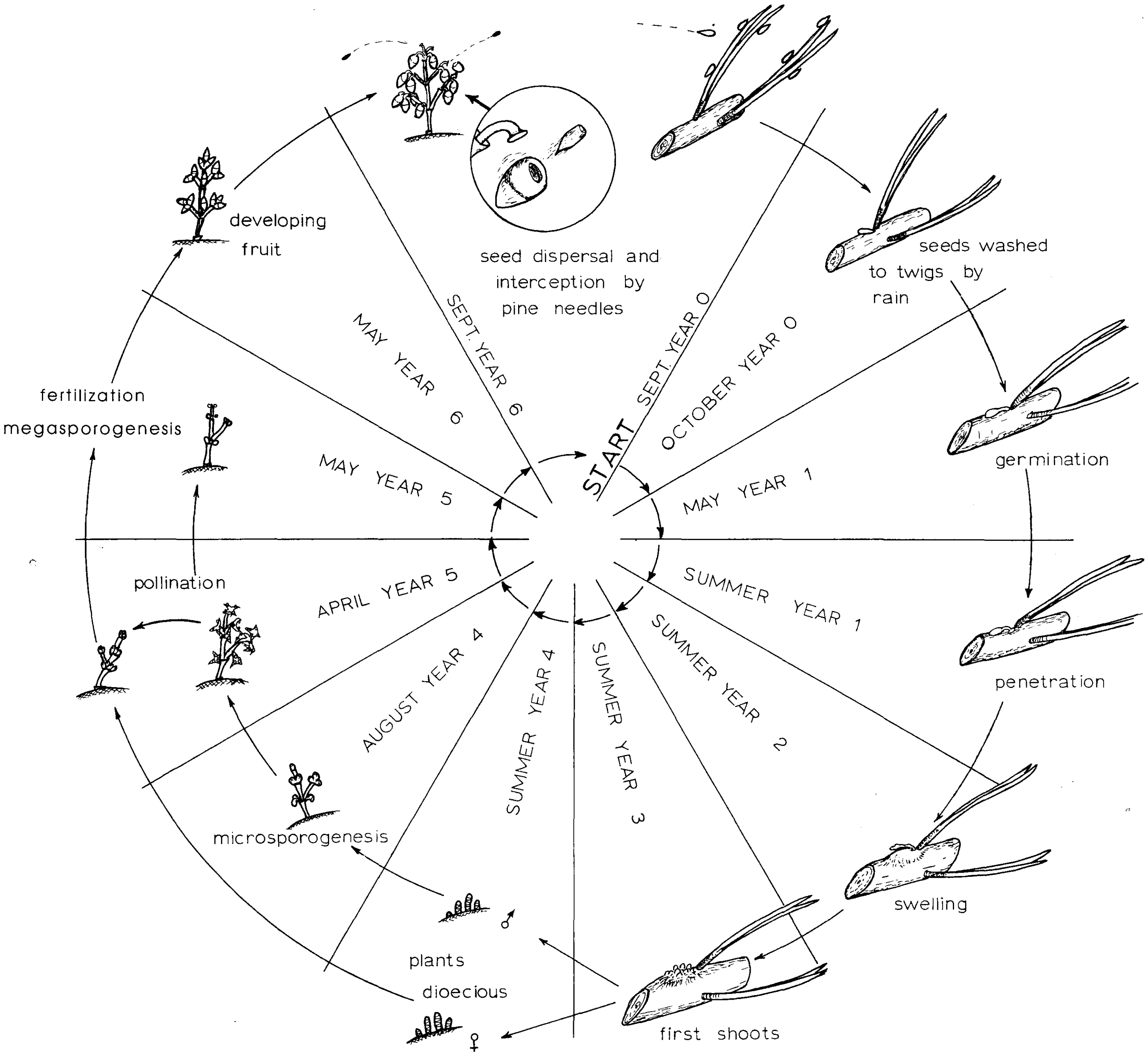

Figure 2.5–Generalized life cycle of dwarf mistletoe as exemplified by *Arceuthobium americanum* on *Pinus contorta*.

Studies of three species of dwarf mistletoes indicate that about 40% of dispersed seeds are intercepted by trees (Hawksworth 1965b, Smith 1985). Seed interception rates, however, are highly variable and depend on stand structure and composition, position of the dwarf mistletoe on the host, and needle characteristics of the host tree. For example, an adjoining tree within 2 to 3 m of an infected host will intercept about 90% of the seeds dispersed in its direction. From an infection site on the outer edge of a host crown, about 70% of discharged seeds will be dispersed outward, and the remaining seeds will be discharged inward. Only 40% of the outwardly dispersed seeds will escape from the host crown. Dwarf mistletoe shoots located closer to the interior of the crown will disperse only 20 to 30% of their seeds out of the crown (Smith 1985). Because few seeds escape the host crown, secondary infection is common, and intensification proceeds rapidly once a host tree becomes infected.

Many intercepted seeds are not deposited at safe-sites, and a high proportion of those that do arrive at safe-sites are lost to disease, predation, or removal by

Figure 2.6 –*Arceuthobium tsugense* subsp. *tsugense* on *Pinus contorta* var. *contorta.* Shoots of pistillate plant with mature fruit; note characteristic branch swelling at the point of infection. (D. L. Nickrent)

Figure 2.8 –Pistillate plant of *Arceuthobium cyanocarpum* at anthesis; note the pollination droplets at the tips of the flowers.

Figure 2.7 –Staminate flowers of *Arceuthobium americanum;* note the moist, glistening surfaces of the tripartite central nectary.

Figure 2.9 –Mature fruit of *Arceuthobium bicarinatum* ready for explosive seed discharge; note old sepals and stigma at the distal end of fruit.

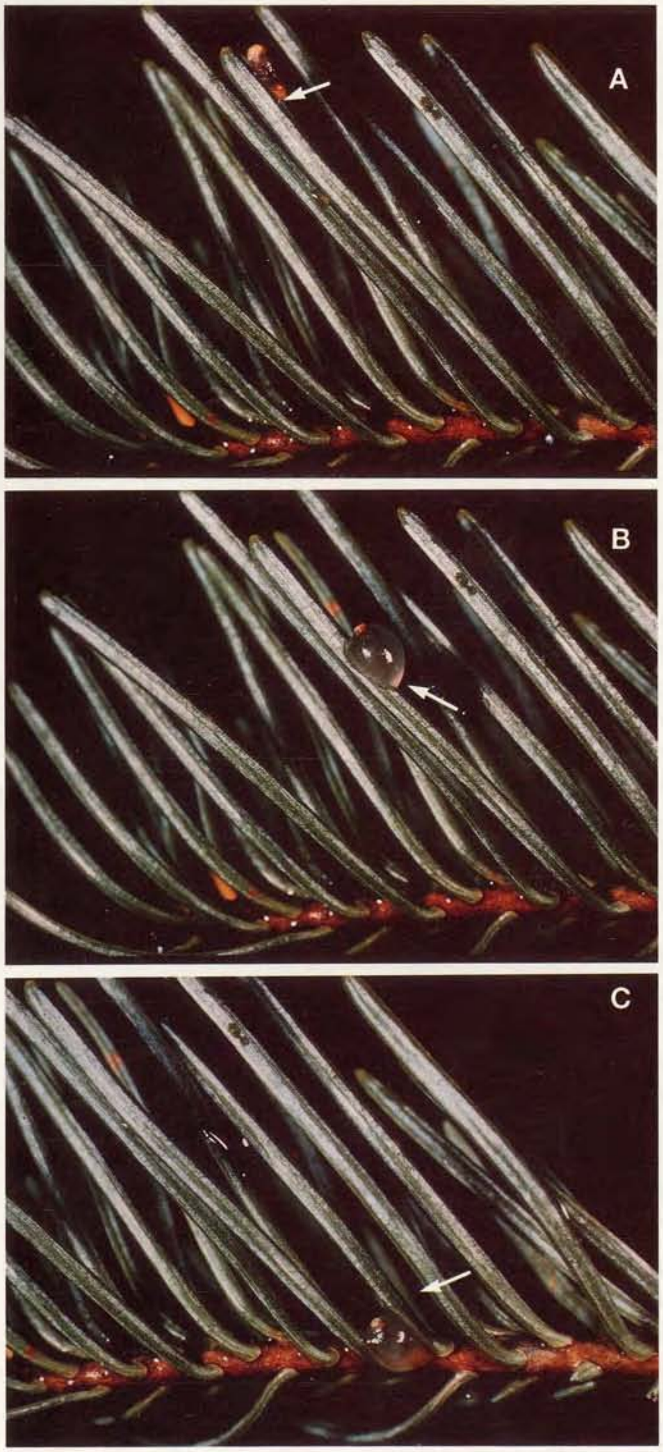

Figure 2.10–Capture and settlement of a seed of *Arceuthobium abietinum* on a shoot of *Abies* sp. A: Seed adhering to a needle by means of its dried viscin coating. B: seed sliding down needle in the hygroscopically swollen viscin mass. C: seed and hygroscopically enlarged viscin mass at the base of a needle where penetration of the host can occur. (R. F. Scharpf)

Figure 2.11–Germinated seed of *Arceuthobium abietinum* with extended radicle and terminal disc-like holdfast. (R. F. Scharpf)

Figure 2.12–Microphotograph of a penetration wedge of *Arceuthobium abietinum* entering host tissue from the holdfast to initiate infection. (R. F. Scharpf)

Figure 2.13 –Young shoots of *Arceuthobium abietis-religiosae* emerging from a swollen branch of *Abies religiosa.* (D. L. Nickrent)

rain. Less than 10% of seeds reach safe-sites (Hawksworth 1965b), and less than 5% of these establish new infections (Hawksworth 1961b, Wicker 1967a).

Within infested stands in Colorado, *Arceuthobium americanum* and *A. vaginatum* subsp. *cryptopodum* produce 0.9 to 1.3 million dwarf mistletoe seeds per hectare (Hawksworth 1965b). Smith (1973) estimated that a single *Tsuga heterophylla* tree infected by *A. tsugense* produced 73,000 dwarf mistletoe seeds annually, and Wicker (1967a) calculated that *A. campylopodum* on *Pinus ponderosa* produced an average of 32,000 (range 800 to 2.2 million) seeds per tree.

The large number of seeds produced compensates for the high proportional loss of seeds before infection. Consequently, explosive dispersal is a sufficiently effective mechanism for short distances so that dwarf mistletoes can spread rapidly within infested stands (Hawksworth 1965a). Beyond the explosive range of the dwarf mistletoe fruits, however, animal vectors are required for dispersal (chapter 8).

Germination

The seeds of most dwarf mistletoes have few characteristics that are typical for seeds of flowering plants. Because there are no true ovules in either the Viscaceae or Loranthaceae, there are no testa and consequently no true "seeds." The "seed" is an embryo embedded in a chlorophyllous endosperm surrounded by a layer of viscin. The embryo is green, rod-shaped, and only several millimeters long; and it possesses a meristematic radicular apex without a root cap. The cotyledons are vestigial.

Germination consists of little more than the initiation of meristematic activity at the radicular apex. The role of moisture in germination varies among species. Germination is virtually independent of humidity in *Arceuthobium abietinum* (Scharpf 1970), but free water greatly enhances embryo growth in *A. pusillum* (Bonga 1972). In temperate zones, seeds typically germinate with the onset of higher temperatures in the spring. Optimal embryo elongation occurs from 15 to 20° C (Gill and Hawksworth 1961, Scharpf 1970). Light significantly enhances germination of mistletoe seeds in general (Lamont 1983a) and that of several dwarf mistletoe species in particular (Scharpf 1970, Wicker 1974a).

Field germinability in excess of 90% is reported for *Arceuthobium americanum, A. vaginatum* subsp. *cryptopodum* (Hawksworth 1965a), and *A. abietinum* (Scharpf and Parmeter 1982). For other dwarf mistletoes, however, field germinability is apparently much lower: *A. pusillum*—7% (Baker and others 1979) to 25% (French 1968); *A. tsugense*—45% (Carpenter and others 1979), 3% (Smith 1965), 23% (Smith 1985), to 38% (Shaw and Loopstra 1991). Environmental factors undoubtedly play a strong role in germination. D. L. Nickrent (personal communication) indicates that mature seeds typically exhibit high percentages of germination under laboratory conditions.

The time of germination of many species is poorly known, but most temperate species germinate in the spring following fall dispersal. However, a few species (notably *Arceuthobium vaginatum* subsp. *cryptopodum* and *A. guatemalense*) germinate immediately after seed dispersal in the autumn. Seeds of some tropical Mexican and Central American species may also germinate soon after dispersal at the end of the wet season (late August to early September).

Dormancy in the traditional sense does not exist in dwarf mistletoes. Seeds stored under optimal conditions retained 58% germinability for 15 months (Knutson 1969, 1984); under laboratory conditions, some seeds remained viable up to 4 years (Beckman and Roth 1968). In the field, however, there is no evidence that seeds survive longer than the season following dispersal. Likewise, traditional "after-ripening" is not characteristic of dwarf mistletoe seeds (Scharpf 1970, Lamont 1983a), although varying periods of stratification did enhance germination for some species (Wicker 1965, Holmes and others 1968). Substrate appears to play no role in germination.

Perhaps the most unusual feature of all viscaceous seeds is the chlorophyllous endosperm. Although the embryo is also chlorophyllous, this condition is common for plant embryos. The growing hypocotyl possesses stomata, and the seed is photosynthetic (Tocher and others 1984). Lamont (1983a) suggests that simple sugars produced photosynthetically are a more efficient source of energy for radicular growth than the complex carbohydrates typical of storage endosperm. The autotrophic capability of germinating seeds of dwarf mistletoes undoubtedly increases their longevity beyond the availability of stored nutrients and, therefore, increases the likelihood of infection. Of course, growth of the hypocotyl is ultimately limited, and only those seeds that germinate within 5 mm of susceptible young shoots are likely to cause infection.

Infection and Initial Shoot Development

Infection is the equivalent of seedling establishment among terrestrial flowering plants. Successful infection by a dwarf mistletoe requires penetration of the host cortex by a growing embryo and development of an endophytic system. For most combinations of the host and dwarf mistletoe, infection can take place only through young stem tissues, usually a segment less than 5 years old. *Arceuthobium americanum,* however, can penetrate through the thin, chlorophyllous bark of *Pinus contorta* branches as old as 60 years (Hawksworth 1954).

The growing radicular apex has a unique combination of tropistic responses that promote infection. The radicular apex typically grows toward the low light intensities that characterize the surface of the host (negative phototropism), irrespective of the gravitational considerations (neutral geotropism). When the radicular apex encounters an obstruction such as a needle base, it responds (positive thigmotropism) by developing a rounded structure termed a "holdfast" (Bonga 1969b) (fig. 2.11).

The center of the holdfast then develops a region of intense meristematic activity known as a "penetration wedge" (fig. 2.12). The penetration wedge grows into the host cortex by exerting mechanical pressure (Scharpf 1963, Scharpf and Parmeter 1967). After the penetration wedge has entered the cortex, a rootlike endophytic system ramifies throughout the bark. Those portions of the endophytic system that subsequently become embedded in successive layers of xylem are described as "sinkers" (chapter 11).

Once infection is established, an incubation period of 2 to 5 years elapses before young shoots appear (fig. 2.13; see also 16.112 and table 2.1). A swelling at the point of infection usually precedes shoot production by a year or more. The incubation period or latency between infection and appearance of shoots (or swellings) varies by species of dwarf mistletoe, species of host, and various environmental factors. For example, in British Columbia, about half of the infections of *Arceuthobium tsugense* produced shoots in the second year after infection and an additional third produced shoots the following year (Smith 1971), whereas the incubation period extends 3 to 6 years in Alaska (Shaw and Loopstra 1991). The incubation period in other species lasts for 4 years—*A. pusillum* (Baker and

TABLE 2.1– Incubation times for 6 taxa of *Arceuthobium* from infection to production of the first shoot

	Percent of inoculations producing shoots											
Arceuthobium	1 yr	2 yrs	3 yrs	4 yrs	5 yrs	6 yrs	7 yrs	8 yrs	9 yrs	10 yrs	11 yrs	12 yrs
A. abietinum f. sp. *concoloris*	0	0	19	31	12	9	11	9	3	3	0	3
A. abietinum f. sp. *magnificae*	0	0	39	25	11	9	4	6	3	3	0	0
A. americanum	0	2	32	34	19	8	4	1	0	0	0	0
A. campylopodum	0	0	23	62	11	4	0	0	0	0	0	0
A. tsugense subsp. *tsugense*	0	51	33	6	6	6	0	0	0	0	0	0
A. varginatum subsp. *cryptopodum*	0	1	30	32	30	4	2	1	0	0	0	0

Note: Data for *A. abietinum* f. sp. *concoloris* and f. sp. *magnificae* from CA (Scharpf and Parmeter 1982), *A. americanum* from CO (Hawksworth and Johnson 1989), *A. campylopodum* from CA (Wagener 1962), *A. tsugense* subsp. *tsugense* from BC (Smith 1971), and *A. vaginatum* subsp. *crytopodum* from AZ (Hawksworth 1961a).

others 1981); for 6 years—*A. campylopodum* (Wagener 1962) and *A. tsugense* (Shaw and Loopstra 1991); for 8 years—*A. americanum* (Hawksworth and Johnson 1989a) and *A. vaginatum* subsp. *cryptopodum* (Hawksworth 1961a); for 10 years—*A. abietinum* f. sp. *magnificae* (Scharpf and Parmeter 1982); or as long as 12 years—*A. abietinum* f. sp. *concoloris* (Scharpf and Parmeter 1982). Dwarf mistletoe plants begin to flower 1 or 2 years after the initial shoots appear.

Dwarf mistletoes are typically parasites on branches or main stems of conifer trees, but they rarely occur on roots. Known instances of root parasitism include *Arceuthobium occidentale* on digger pine in California (reported by Scharpf in Kuijt 1969a), *A. globosum* subsp. *grandicaule* on pines in Guatemala (*Steyermark* MICH *36940* and our observations in central Mexico), *A. vaginatum* subsp. *vaginatum* on *Pinus hartwegii* in Mexico (Vasquez 1991), and *A. vaginatum* subsp. *cryptopodum* on ponderosa pine in Arizona (our observations) (fig. 2.14). These cases are abnormal, however, and result from vegetative growth into the roots from infections that originated on a main stem near the root collar. This phenomenon is not comparable to root parasitism in typical terrestrial mistletoes of the Loranthaceae (*Gaiadendron, Nuytsia, Atkinsonia*), where infection takes place initially through the roots (Kuijt 1969a).

Figure 2.14 –Arceuthobium vaginatum subsp. *crytopodum* infecting the roots of *Pinus ponderosa.*

Flower and Fruit Production

Meiosis may either occur immediately before flower production (direct flowering) or approximately 5 to 8 months before anthesis (indirect flowering) (Wiens 1968). Most species exhibit definite annual flowering periods, but a few tropical species (e.g., *Arceuthobium aureum* subsp. *aureum*) appear to flower continuously throughout the year. *Arceuthobium abietis-religiosae* and *A. nigrum* (both species found in Mexico) display two distinct flowering periods, and *A. hawksworthii* (found in Belize) may produce three flower crops annually (Wiens and Shaw 1994). *Arceuthobium juniperi-procerae* (found in East Africa) appears to produce several discrete flower crops annually. Flowering may occur as early as February or March (e.g., by *A. globosum*) or as late as November–January (e.g., by *A. occidentale*). For a given species and locality, flowering usually lasts 4 to 6 weeks, but most of the pollen is dispersed within a shorter, 2- to 3-week period.

The staminate flowers and terminal portions of the shoots are usually shed a few weeks after anthesis. However, the entire staminate flowering spikes of *Arceuthobium verticilliflorum* dehisce following anthesis. Individual shoots of most species produce crops of flowers over several successive years; *A. pusillum* produces a single crop. There were early reports that dwarf mistletoe shoots die after fruits mature (Peirce 1905, Korstian and Long 1922), but this is not typical of species other than the diminutive *A. pusillum* and perhaps *A. minutissimum*. Most shoots produce at least two successive crops of flowers. In Colorado, individual pistillate shoots of both *A. americanum* and *A. vaginatum* subsp. *cryptopodum* have produced successive fruit crops for 5 years (making these shoots at least 7 years old). Kuijt (1970) also reports that several species have relatively long-lived shoots.

The time required from pollination to fruit maturity varies considerably. *Arceuthobium pusillum* and perhaps some tropical species (e.g., *A. juniperi-procerae*) require about 5 months for fruit to develop. Fruit maturation may occur in about 4 months in *A. hawksworthii* from Belize. Most temperate species need one or more years for fruit to mature; *A. gillii* requires 19 months. The minimum time from infection to initial seed production averages 6 years for *A. americanum* (Hawksworth and Johnson 1989a) and 7 to 8 years for *A. vaginatum* subsp. *cryptopodum* (Hawksworth 1961a).

Sexual Reproductive Biology

Dwarf mistletoes reproduce only from seeds. The shoots occurring on widely divergent branch systems of large, systemic witches' brooms might be considered clonal ramets of the founder individual, but this represents only an increase in the size and reproductive output of the founder individual. New genets can only be established by seed.

Stages of sexual reproduction in seed plants can be conveniently divided into two categories:

1. Pre-dispersal events, beginning with pollination and culminating with viable seed production; these processes occur in the maternal environment but are primarily controlled by the genetic constitution of the zygotic genome.
2. Post-dispersal events, beginning with seed dispersal and culminating with successful reproduction of the progeny; these events occur in the ambient environment and are controlled by selective forces in the physical and biotic environments (Wiens and others 1987).

The pre-dispersal reproductive process includes several discontinuous phases: pollination; pollen germination and pollen tube growth; and fertilization and seed development (embryo and endosperm). Post-dispersal phases of dwarf mistletoe reproduction are discussed in chapter 2.

Pollination

Controversy has surrounded the pollination biology of *Arceuthobium* through much of this century because the genus exhibits floral characteristics typical of both insect–pollinated (entomophilous) and wind–pollinated (anemophilous) flowers. Interestingly, much the same controversy surrounds the mode of pollination in the European mistletoe, *Viscum album*. Heinricher (1915a) speculated that the floral characteristics of *Arceuthobium* favored entomophily, but he later modified his view after observing that greenhouse plants set seed in the absence of insects (Heinricher 1920).

Characteristics of *Arceuthobium* that favor entomophily include: (1) sessile anthers; (2) spined pollen; (3) clustered pollen bound together by mucous strands; (4) relatively low pollen production (over 11,000 grains per flower) in comparison to that of many wind-pollinated plants (cf. 50,000 grains per rye floret); (5) non-plumose stigma; (6) nectar production in staminate flowers and stigmatic exudate in pistillate flowers (figs. 2.7 and 2.8); and (7) faint odor production by both pistillate and staminate flowers.

Features indicating anemophily include: (1) exposed anthers; (2) pollen size in the general range of wind-pollinated species (10 to 60 µm, although pollen-clustering must upset this size and weight relationship); (3) long-distance transport of pollen (several kilometers) and its common occurrence in the fossil palynological record; (4) localized, dense population structure; (5) unisexual flowers; (6) single-"ovule" ovaries; (7) flowering periods temporally separated from those of their wind-pollinated hosts (the more abundant host pollen would likely saturate the mistletoe stigmas if they flowered simultaneously); (8) temporal partitioning of flowering periods when two dwarf mistletoe species co-occur in the same habitat (see discussion of sympatry in chapter 5); and (9) sexual dimorphism in which staminate plants are open and spreading (thereby favoring the release of pollen with minimum filtration effect from branches of the staminate plant) and pistillate plants are compact and densely branched (figs. 3.1 and 3.2). Other aspects of sexual dimorphism are discussed in chapter 14.

Pollination biology in *Arceuthobium americanum* has received greater study than other dwarf mistletoes (Coppola 1989; Gregor and others 1974; Penfield and others 1976; Stevens and Hawksworth 1984; Gilbert and Punter 1984, 1990, 1991). These studies generally indicated that both insects and wind contributed to pollination success, but Gregor and others (1974) suggested that entomophily predominated. Penfield and others (1976) reported that large numbers of generalist insects (over 200 species), especially various flies and ants, carried pollen and played a role in the pollination of three dwarf mistletoes in Colorado. For *A. americanum, Formica fusca* (silky ant) was considered the most important pollinator and *Philygria debilis* (a gnat)

Figure 3.1 –Staminate plant of *Arceuthobium nigrum* illustrating the typical pattern of sexual dimorphism, i.e., the open spreading branch habit of staminate plants.

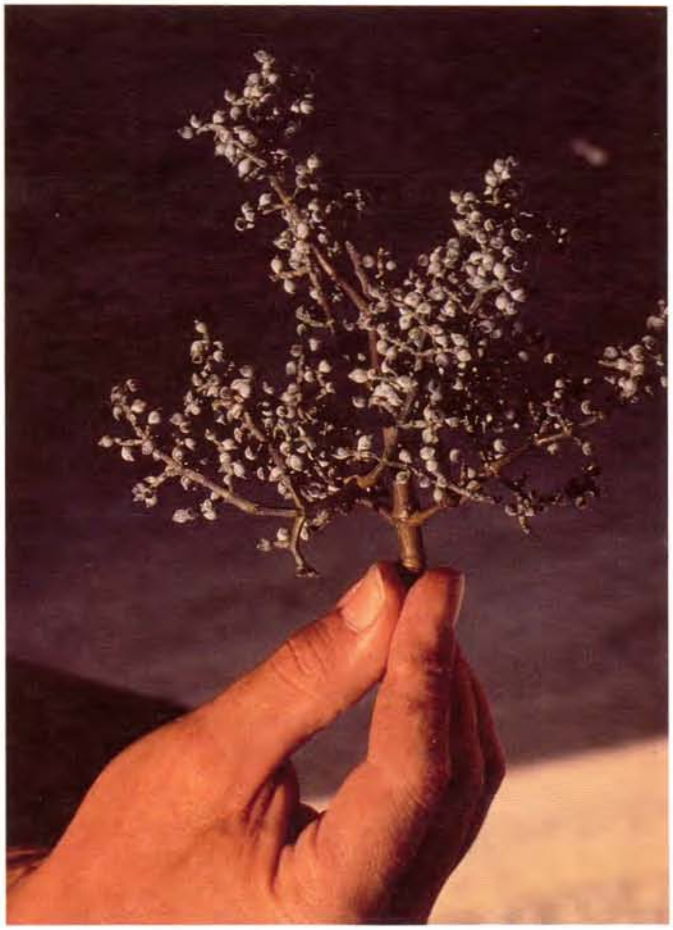

Figure 3.2 –Pistillate plant of *Arceuthobium nigrum* illustrating the typical pattern of sexual dimorphism, i.e., the compact and dense branch habit of pistillate plants.

second-most important. Other flies were involved in pollination at different stages of the flowering period. Penfield and others (1976) also noted that pollen was commonly transferred by wind to distances of 12 m and occasionally as far as 150 m. Coppola (1989) found that pollen in a Colorado population was wind-dispersed as far as 512 m; Gilbert and Punter (1984) in Manitoba observed a maximum distance of pollen dispersal of 400 m.

For *Arceuthobium vaginatum* subsp. *cryptopodum,* the parasitic wasp *Copidosoma bakeri* and the flea beetle *Phyllotreta lewisii* were judged to be the most important pollinators; the ants *Formica fusca* and *F. hemmorhoidalis* and flies of the genera *Bradysia* and *Hylemya* were also reported to be common pollinators (Penfield and others 1976). Vasquez (1991) studied pollination in *A. vaginatum* subsp. *vaginatum* in Mexico and concluded that anemophily predominated.

In *Arceuthobium cyanocarpum,* the primary pollinators were wasps (*Copidosoma bakeri*), flies (*Hylemya* spp.), and a beetle (*Hoppingiana* sp.). Ants were less important for pollination of *A. cyanocarpum* than for *A. americanum* and *A. vaginatum* subsp. *cryptopodum.*

Player (1979) studied the pollination biology of *Arceuthobium douglasii* in Utah and *A. strictum* in Durango, Mexico, and concluded that these species (and the genus as a whole) were fundamentally wind-pollinated. He based this conclusion primarily on the general lack of insect visitation and the abundance of airborne pollen from the populations of *A. douglasii* he studied.

Baker and others (1985), however, suggested that insects played the primary role in the pollination of *Arceuthobium pusillum.* They enclosed mistletoe plants with a relatively large mesh screen (4 mm) that should have reduced but not precluded insect visitation, yet only slightly interfered with transport of pollen by wind. Fruit set by these enclosed plants was significantly reduced. Airborne pollen was also much less prevalent in populations of *A. pusillum* than in *A. douglasii.*

Aspects of the pollination biology of dwarf mistletoes that deserve further comment include nectar production and anther movement. The flowers of dwarf mistletoes must be among the smallest that produce nectar. The staminate flowers (1 to 4 mm across) possess a nectary (the "central cushion" of earlier terminology), and the smaller pistillate flowers (0.5 to 1.5 mm across) produce a stigmatic exudate. The quantity of nectar secreted by staminate flowers is especially minute, and the nectary rarely produces more than a glistening moist layer over its surface (fig. 2.7). In contrast, the stigmatic exudate under conditions of high humidity forms large droplets that are many times the size of the stigma (fig. 2.8). In absolute terms, however, the quantity of stigmatic exudate is still minute. In *Arceuthobium abietinum,* the exudate is highly concentrated (58 to 92% solids) and comprised of 48% sucrose, 39% fructose, and 11% glucose (Brewer and others 1974). In *A. americanum* the stigmatic exudate is 50 to 65% sugars, but the staminate flowers produce significantly less concentrated nectar (19%) (Gilbert and Punter 1990). The importance of this difference, if any, is not readily apparent. Generally, nectar with a high sugar concentration is typical of fly-pollinated flowers (Faegri and van der Pijl 1966).

Pollen is likely deposited on the stigmatic exudate, and the exudate may therefore serve multiple functions: (1) pollinator attractant, (2) pollen adhesive, and (3) stimulant for pollen germination (Heinricher 1915a). Jones and Gordon (1965) and Hudson (1966) report that the pollen grains of *Arceuthobium americanum* and *A. douglasii* are held in place by the stigmatic secretions. They also comment that there was no marked increase in insect visitation during the period of exudate secretion. This observation offers strong support for wind pollination in *A. douglasii* as argued by Player (1979). As will be discussed later, the pollen of *A. americanum* requires an unusually high concentration of sucrose (20%) for optimal germination (Gilbert and Punter 1991). The high sugar content of the stigmatic exudate might, therefore, be important primarily as an aid to germination of the pollen grains and only of incidental importance as an attractant for opportunistic foraging insects. The large number of taxonomically diverse insects (over 200 species) known to visit dwarf mistletoe flowers exhibit no common characteristics to suggest that there are any coevolved features between themselves and the dwarf mistletoes that they may occasionally pollinate.

Gilbert and Punter (1990) discovered that the anthers of *Arceuthobium americanum* and to a lesser extent those of *A. pusillum* open in response to high temperatures and low humidity, and they close when the reverse conditions prevail. Although temperature increases would also stimulate insect activity, the lower humidity requirement argues against entomophilous pollination. The small insects (gnats, flies, wasps, and ants) that are commonly associated with dwarf mistletoe flowers should be particularly sensitive to low humidities. Small insects are able to forage at higher-than-optimal temperatures only if the humidity is also correspondingly high (D. Feener, personal communication). The combination of high temperatures and low humidity necessary for anther opening according to Gilbert and Punter (1990) are known to be the most favorable conditions for the airborne distribution of pollen (Whitehead 1969). Because of this dual requirement, it seems most probable that anther closing and opening enhance the possibilities of wind pollination. Such an apparently major structural modification would strengthen the case that at least these species of *Arceuthobium* are basically adapted for wind pollination. The occurrence of this character in other species has not yet been investigated, but inasmuch as the extent of anther opening and closing is variable between *A. americanum* and *A. pusillum,* this feature might serve as an indicator for anemophily or entomophily among other dwarf mistletoes.

Pollen Germination and Pollen Tube Growth

Pollen germination and subsequent pollen tube growth have received less study than any other phase of sexual reproduction in *Arceuthobium.* Pollen germination has been investigated only for *A. americanum* in Manitoba, Canada (Gilbert and Punter 1991). This species exhibited some unusual characteristics of pollen germination. The most noteworthy of these are the high concentrations of sucrose (20%) necessary for optimal germination and the failure of pollen to respond to known germination stimulants such as boric acid; salts of Ca, Mg, and K; and macerates of pistillate flowers. Optimal temperature for germination *in vitro* was 30°C. Germination percentages, however, were typically less than 30%. Germination of pollen originating from different dwarf mistletoe plants also varied significantly. In general, as the flowering season progressed, percent germination increased; presumably, this change was due to increased air temperatures. Thus, at least in this region, most fertilization likely occurs toward the end of the flowering period. As Gilbert and Punter (1991) point out, this also may explain why the anthers open and close in relation to temperature. Pollen in *A. americanum,* however, remains viable for long periods; it forms in August or September and is not dispersed until early spring.

Hudson (1966) observed pollen tubes in the stylar canals of *Arceuthobium americanum* in April, but he also reported that embryo sac meiosis (megasporogenesis) did not occur for almost 2 months (late May) and that fertilization was delayed until June. Thus, the pollen tube must grow for at least 2 months before it reaches and penetrates the embryo sac. Such an interval is inordinately long among flowering plants; the time between pollination and fertilization is usually about 48 hours. Hudson's (1966) observations disagree with Dowding's (1931a) earlier report that fertilization in *A. americanum* occurs within "a few days" of pollination. Hudson's (1966) assertions are also in marked contrast to observations for *A. douglasii* and *A. pusillum* that the interval between pollination and fertilization is "a few days" (Jones and Gordon 1965, Tainter 1968). The sperm of *A. oxycedri* (a fall-flowering species) are reported to overwinter in the pollen tube in contact with the embryo sac; they are released the following spring when growth is resumed and fertilization occurs (Johnson 1888).

Arceuthobium americanum, A. douglasii, and *A. pusillum* are all indirect flowering species—their flowers develop in the autumn and overwinter as mature buds. These mistletoes are among the earliest to initiate anthesis the following spring (March or April). Although pollen grain meiosis (microsporogenesis) occurs in the autumn, megasporogenesis is delayed until spring.

The reasons for the asynchrony in pollen grain and embryo sac development and the long period of pollen tube growth are not immediately evident. Interestingly, the conifer hosts of the dwarf mistletoes also require a year for their pollen tubes to reach the embryo sac. Furthermore, fruit development in dwarf mistletoes parallels that of conifers; both groups require about 12 to 18 months for seed maturation. Whether these unusual similarities in phenology between host and parasite are merely coincidental—or are evolutionarily significant—requires clarification.

Embryo Sac Development, Fertilization, and Fruit Maturation

Because all mistletoes lack ovules, technically they do not possess true "seeds" or "fruit." This anomaly has been the subject of considerable study since its discovery in the middle of the last century. For summations of our current understanding of this phenomenon, see Bhatnagar and Johri (1983) for Loranthaceae and Bhandari and Vohra (1983) for Eremolepidaceae and Viscaceae.

Embryo sacs in dwarf mistletoes arise from a mound of tissue at the base of the ovary, usually termed the ovarian papilla or mamelon (fig. 3.3A). The papilla has no integument and is not part of the mature fruit, having been crushed by the developing endosperm mass (fig. 3.3B-E). Two megasporocytes initiate development of the embryo sacs in the papilla. In *Arceuthobium americanum,* however, one megasporocyte is possibly arrested in development at the 4-nucleate stage (Hudson 1966; C. L. Calvin, unpublished data). In *A. douglasii,* after one megasporocyte is fertilized, the other degenerates, without being fertilized (Jones and Gordon 1965). The sequence of events in early embryo sac development requires further study.

Embryo sac development in *Arceuthobium* conforms to the *Allium* or bisporic type (Hudson 1966, Tainter 1968, Bhandari and Nanda 1968, Bhandari and Vohra 1983). In this system, only one of the two dyads produced by the first meiotic division survive. One degenerates rapidly, and the surviving, functional dyad completes meiosis and produces two haploid megaspore nuclei. These megaspore nuclei undergo two successive mitotic divisions that ultimately result in an 8-nucleate embryo sac. The *Allium*-type embryo sac is otherwise typical of the common *Polygonum* type at maturity, and the embryo sac is characterized by 3 antipodals, 2 polar nuclei, and 2 synergids surrounding the somewhat larger egg. Because the *Polygonum*-type of embryo sac has a monosporic origin, all cells are genetically identical, whereas bisporic embryo sacs should contain cells of two genetically distinct origins. The significance of this difference, if any, is not immediately apparent. Variant 7-nucleate embryo sacs are reported in *A. americanum* (Dowding 1931a) and in *A. campylopodum* (Cohen 1970), but these observations have not been confirmed (Bhandari and Vohra 1983).

Double fertilization and the formation of a triploid endosperm is common to all Viscaceae (Bhandari and Vohra 1983). There is apparently interspecific variation with respect to whether a primary diploid endosperm nucleus is formed or whether the two polar nuclei fuse with the sperm independently (Bhandari and Vohra 1983). Hudson (1966) reports an interesting anomaly in *Arceuthobium americanum* wherein the egg lies above and to the side of the synergids instead of between them, as is typical. If correct, this raises interesting questions as to the function of the synergids in dwarf mistletoes. Typically, sperm are released from the pollen tube, deposited into one of the adjacent synergids, and transferred to the egg by the synergid. The lack of juxtaposition in this case would appear to preclude this process. The role the

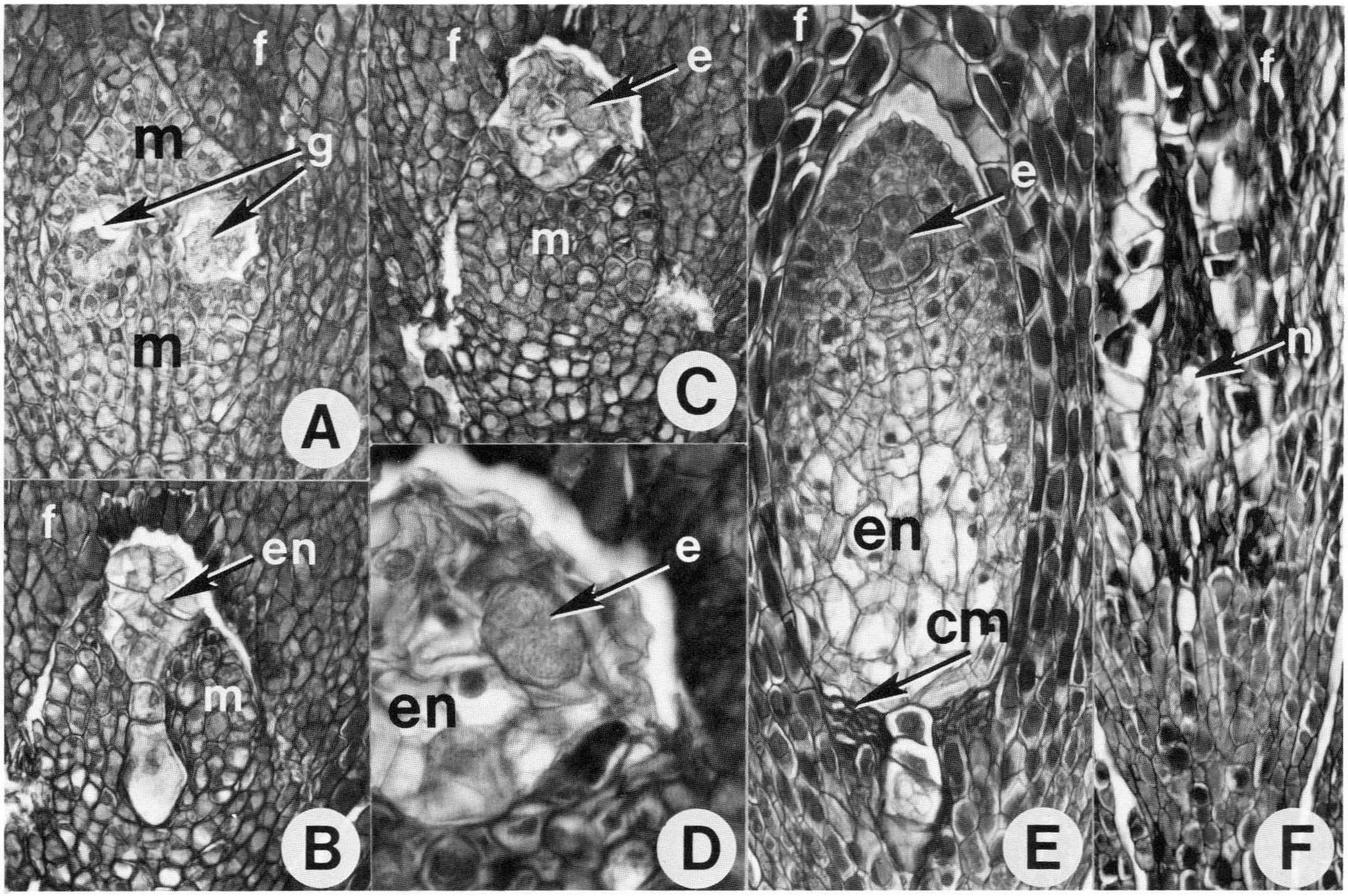

Figure 3.3 –Longitudinal sections through ovaries of flowers (A) and developing fruit (B-F) of *Arceuthobium cyanocarpum* (A-D) and *A. americanum* (E,F). A: mamelon (m) with 2 embryo sacs (g) and fruit wall (f), × 100. B: cellular endosperm (en) in mamelon (m), × 100. C: same specimen as B but at a different focal plane, embryo (e), mamelon (m), and fruit wall (f), × 100. D: enlarged view of specimen seen in C showing two-celled embryo (e) and endosperm (en), × 250. E: globular embryo (e) in endosperm (en), note crushed mamelon (cm), × 100. F: same development stage as E, but with necrotic, aborted embryo (n) surrounded by necrotic endosperm and fruit wall (f), × 100. (C. L. Calvin)

synergids in fertilization requires further study in dwarf mistletoes.

Endosperm formation is cellular in *Arceuthobium,* as is typical of plants with bisporic embryo sac development. Soon after fertilization, the embryo sac is separated transversely into two chambers; one includes the zygote and disintegrating synergids and the other contains the fertilized primary endosperm nucleus and degenerating antipodals. This latter portion of the separated embryo sac then develops a lateral extension or "haustorium" that elongates downward toward the base of the papilla, where it obtains nutrition from maternal tissue for the development of the endosperm. Endosperm production around the zygote continues for some time prior to the initiation of embryogenesis. No suspensors are formed, and embryonic development continues in the cellular endosperm until autumn. By then, however, embryogenesis has not progressed beyond the globular stage, and the embryo overwinters at this stage in the relatively massive endosperm. Fruit development is resumed the following spring; embryogenesis and endosperm formation are complete by middle to late summer of the year following fertilization. Knutson (1984) states that seeds approximately double in size from mid-July to mid-August.

The mature seed of dwarf mistletoes is a hypocotylar cylinder that has a highly meristematic radicular apex (without root cap) at one end and a pair of minute, vestigial cotyledons at the other. The mature fruit consists of a thick-walled pericarp with a layer of viscin cells and a parenchymatous zone surrounding the seed (see fig. 2.3 and fig. 10.9). With the exceptions of *Arceuthobium pusillum* and several tropical species (*A. abietis-religiosae, A. aureum* subsp. *aureum, A. hawksworthii, A. juniperi-procerae,* and *A. nigrum*), dwarf mistletoes typically require about 12 to 18 months to complete fruit development.

Pre-dispersal embryo survivorship in dwarf mistletoes averages around 50%, but the variance is high (Wiens, unpublished data). Typically, 80 to 90% of the fruits survive the first summer's growth, at which time the embryos are only at the globular stage of development. During the second summer's growth and prior to dispersal, an additional 30–40% of the embryos die (fig. 3.3F). These rates of first and second year survivorship have been confirmed in *Arceuthobium americanum* by Gilbert and Punter (1984) and Gilbert (1988).

Wiens and others (1987) attributed most of this loss to genetic lethals. Reduced seed set should not be due to resource limitations because dwarf mistletoe plants are resource sinks with relatively large reserves provided by the host.

Exceptional Characteristics of Fruits and Seeds

Several exceptional aspects of seed and fruit development in *Arceuthobium* are absence of true seeds, chlorophyllous endosperm and embryos, stomata on the growing hypocotyl, lack of a root cap, and occasional polyembryony. Virtually all of these characteristics are likely related, directly, or indirectly to the evolution of the parasitic habit.

Loss of the integument in *Arceuthobium* is perhaps the result of extreme evolutionary specialization of the seed for explosive dispersal. However, all other mistletoes also lack an integument and the majority of these are bird dispersed. Therefore, the ultimate evolutionary cause of integument loss is perhaps due to other factors. Another possible explanation is that the seed must be energetically self-sufficient for long periods before it infects the host. Thus, both the endosperm and embryo are chlorophyllous, and at least the hypocotyl possesses stomata. A testa would likely hinder the photosynthesis that occurs at low rates in the seedling (Tocher and others 1984).

Arceuthobium seeds have no innate dormancy systems. In temperate regions, growth of the hypocotyl is retarded through periods of unfavorable environments, but the radicular apex resumes growth whenever favorable conditions return.

The viscin coat may have importance beyond its adhesive qualities. It has a high water retention capacity, and it may play a role in reducing desiccation and infection by fungal pathogens (Knutson 1984).

The existence of multiple embryo sacs and the general occurrence of a single seed has prompted the assumption that there is competition for survival among embryo sacs or their developing embryos. Either one embryo sac may be arrested at the 4-nucleate stage (as in *Arceuthobium americanum*) or only one embryo sac may be fertilized and the other degenerates soon thereafter (as in *A. douglasii*). Because polyembryony does occur in dwarf mistletoes, limits on fertilization and development can not be absolute. In many species of *Viscum*, polyembryony is common, and the occurrence of 1 to 3 embryos per seed is the rule (Wiens, unpublished data). Therefore, competition among developing embryo sacs or embryos is possible.

Polyembryony in *Arceuthobium*, however, is rare. Hawksworth (1961b) reported that about 1% of the seeds of *Arceuthobium americanum* and *A. vaginatum* subsp. *cryptopodum* contained two embryos and two endosperms. Weir (1914) found somewhat higher levels of polyembryony in *A. vaginatum* subsp. *cryptopodum* (15%) and *A. douglasii* (13%), but his sample sizes were small. He also indicated that both germinating embryos in di-embryonic seeds grew "vigorously" upon germination and that infection should occur if penetration could be effected. The di-embryonic seeds were no smaller than the mono-embryonic seeds. Hawksworth (1961b) suggested that di-embryonic seeds provided a possible mechanism whereby new populations of a dioecious species could become established from a single seed, provided, of course, the embryos were of different sexes.

Sex Ratios

All dwarf mistletoes are obligately dioecious plants, and there is no evidence that bisexual flowers or unisexual flowers of the opposite sex occur in even low frequencies. Other than for *Arceuthobium tsugense*, sex ratios in *Arceuthobium* have not been extensively studied; table 3.1 summarizes available information. For those species of dwarf mistletoe (and other dioecious mistletoes) with a skewed sex ratio, the bias generally favors female plants. This is certainly the case for *A. tsugense* subsp. *tsugense*, which has a significantly female-biased sex ratio of approximately 3:2 in populations from Alaska, Washington, and Oregon (Wiens, Hawksworth, Shaw, and Hennon, unpublished data). Although fewer data are available, *A. tsugense* subsp. *mertensianae* in Washington and Oregon has a similar sex ratio.

Female-predominant sex ratios are typical of various African and European species of *Viscum* (Wiens and Barlow 1979), but *Arceuthobium tsugense* is the first clear example of a dwarf mistletoe characterized by a female-biased sex ratio over a broad geographical distribution. The sex ratios of other dwarf mistletoes should be examined.

TABLE 3.1—Sex ratios in *Arceuthobium*

Arceuthobium	Host	Sex ratio (female plants: male plants)	Location	Reference
A. abietinum	*Abies magnifica*	(62:55)	Sierra Nevada, CA	Scharpf and Parmeter 1982
	Abies concolor	(51:66)	Sierra Nevada, CA	Scharpf and Parmeter 1992
A. americanum	*Pinus contorta*	(210:246)*	3 areas near Banff, AB, Canada and their combined total	Muir 1966
		(258:183)**		
		(159:174)		
		(627:603)		
		(251:224)	CO (inoculation)	First report
		(254:246)	CO (natural infection)	First report
A. campylopodum	*Pinus ponderosa*	(53:47)	Spokane, WA	Wicker 1967b
A. globosum subsp. *globosum*	*Pinus cooperi*	(72:58)	Durango, Mexico	First report
	Pinus durangensis	(91:51)**	Durango, Mexico	First report
A. pusillum	*Picea mariana*	“Male plants most frequent”	NY	Parry 1872
		“Pistillate plants most numerous”	NY	Peck 1875
		(32:19)*	MN (inoculation)	Baker and others 1981
A. strictum	*Pinus leiophylla* var. *chihuahuana*	(47:32)*	Durango, Mexico	First report
A. tsugense	*Tsuga heterophylla*	(54:46)	BC, Canada (inoculation)	Smith 1971
		(1803:1254)**	AK, WA, OR	First report
A. vaginatum subsp. *cryptopodum*	*Pinus ponderosa*	(505:495)	Flagstaff, AZ	Hawksworth 1961a

* Significantly different from 1:1 based on χ^2 test, $P < 0.1$.

** Significantly different from 1:1 based on χ^2 test, $P < 0.01$.

CHAPTER 4

Mechanism and Trends of Evolution

Genetic System and Recombination Potential

Arceuthobium has a base chromosome number of $x = 14$ (i.e., the lowest extant haploid number), and polyploidy is unknown (Wiens 1968). The haploid chromosome number ($n = 14$) can also be considered as a tetraploid number on a base of 7, but there is little evidence for this. The lowest known haploid chromosome number in the Viscaceae is $n = 10$, and it is best interpreted as the lower end of a decreasing aneuploid series from 14 to 10 in *Viscum*. The base number of $x = 14$ also characterizes the other New World genera of Viscaceae (*Dendrophthora* and *Phoradendron*), as well as *Korthalsella*, a widely distributed genus occurring in East Africa, southern Asia, and Oceania as far east as Hawaii. (*Notothixos* is karyologically distinct with $n = 12$; and the chromosomes of *Ginalloa* are unstudied). Chromosome evolution in the Viscaceae is discussed in detail by Wiens and Barlow (1971) and Barlow (1983, 1984). If polyploidy were involved in the evolution of $x = 14$ as a base chromosome number in Viscaceae, then its origin was certainly ancient. Under any circumstances, however, the chromosome systems in *Arceuthobium* and other genera of Viscaceae clearly operate as functional diploids.

The genetic system in *Arceuthobium* is therefore sexual, diploid, and obligately outcrossing because of dioecy. Vegetative reproduction and agamospermy are unknown (Player 1979), and there is virtually no manifestation of the occasional bisexuality that often characterizes dioecious groups. In fact, the structures of the non-functional sex are either absent or vestigial. The relatively high diploid chromosome number, concomitantly large number of linkage groups, and relatively high chiasma frequency (averaging perhaps 2 to 3 per bivalent at late diakinesis–early metaphase I) result in high levels of genetic variability.

High levels of genetic variation in *Arceuthobium* have been verified by electrophoretic studies of enzyme polymorphisms (Nickrent 1984, Linhart 1984, Nickrent and others 1984). The maintenance of high levels of genetic variability may be especially important among parasites. If the host population is also recombining genetically and producing novel genotypes, then the dwarf mistletoe must respond similarly to remain adapted. Such situations are known among scale insects, which become adapted to certain populations and even individuals of *Pinus ponderosa* (Edmunds and Alstad 1978).

Linhart (1984) presented preliminary evidence showing significant interpopulational electrophoretic variability in *Arceuthobium vaginatum* subsp. *cryptopodum* in Colorado; high variability has also been demonstrated for the host *Pinus ponderosa* (Mitton and others 1977) and for pines in general (Hamrick and others 1981). This pattern of interpopulational genetic variation suggests that dwarf mistletoes may also be adapting to local populations of its host, just as are the scale insects mentioned above.

Adaptive Radiation

In addition to maintaining population adaptiveness on genetically variable host populations, a diploid genetic system with high recombination potential should also be theoretically well suited for rapid evolution. A large number of ecological niches (host species) became available for colonization by dwarf mistletoes following the extensive speciation in North American pines (especially in Mexico) during the Miocene Epoch (Mirov 1967). The high proportion of North American Pinaceae presently parasitized by *Arceuthobium* (chapter 6) indicates that such an adaptive radiation has, in fact, occurred. With the exception of the eastern pines of North America, most of the widely distributed species of Pinaceae are parasitized by *Arceuthobium* (chapter 5).

Arceuthobium is primarily a parasite of *Pinus*—33 of the 47 taxa occur principally on this genus (chapter 6). Of these 33 taxa, 23 parasitize *Diploxylon* and 9 *Haploxylon* pines. Mirov (1967) recognizes 73 *Diploxylon* and 32 *Haploxylon* pines, so about one-third of each group is parasitized. The oldest known pine fossils are from the Jurassic Period, and even then the pines had differentiated into the subgenera *Haploxylon* and *Diploxylon* (Mirov 1967).

In both the Old and New Worlds, *Pinus* (*Diploxylon* and *Haploxylon*), *Abies*, and *Picea* are hosts of *Arceuthobium*. However, 3 other genera that occur in both New and Old Worlds are parasitized only in the New World (*Larix*, *Pseudotsuga*, and

Tsuga). *Juniperus,* which is circumpolar, is a host for 3 of the 8 species of *Arceuthobium* found in the Old World; but junipers are not parasitized in the New World. The Old World genus *Keteleeria* is a host for dwarf mistletoe in southwestern China.

We originally suggested that the closest relative of *Arceuthobium* was *Korthalsella* (Hawksworth and Wiens 1972). Molecular data do not support such a relationship, but indicate that *Notothixos* is most closely allied to *Arceuthobium* (chapter 15). Resemblances between *Korthalsella* and *Arceuthobium* are no doubt the result of convergence. If the tropical Asian genus *Notothixos* and *Arceuthobium* had originated from a common ancestor, then *Arceuthobium* would have spread in the early Tertiary Period westward to the Mediterranean region (and possibly into North America), south into East Africa, and finally during the Miocene Epoch northeastward through Beringia into the New World (but see chapter 15). Thus *Arceuthobium* may have reached the New World in two migratory episodes—first in the early Tertiary Period by land connections with Europe (represented by *A. abietis-religiosae* and *A. verticilliflorum* as relict species) and second during the Miocene Epoch, which initiated the large radiation of species in Mexico and the western United States.

Generally, angiosperms in the Tertiary Period have evolved more rapidly than gymnosperms (Leopold 1967). Consistent with this trend, the dwarf mistletoes probably also evolved more rapidly than did their coniferous hosts.

Another factor in this adaptive radiation was the apparent lack of competition with other plants for these open niches (conifer hosts). With the possible exception of *Phoradendron pauciflorum,* which sometimes infects *Abies concolor* along with *Arceuthobium abietinum,* and a few tropical species of *Dendropemon, Psittacanthus,* and *Struthanthus,* no other extant mistletoe genera compete with *Arceuthobium.* Competition with epiphytes might be expected in certain tropical situations, but this does not appear to occur because only young shoots are susceptible to infection by dwarf mistletoes and dwarf mistletoes do not occur in moist tropical forests. Thus, newly emerging host shoots could perhaps be infected by dwarf mistletoes before epiphytes become established. Once the endophytic system is developed, the presence of epiphytes is likely immaterial so long as pollination and dispersal are not impeded.

Arceuthobium is likely the most highly specialized of all mistletoe genera. Within the genus, different species clearly exhibit various degrees of host, morphological, and physiological specialization. Because the majority of North American conifer species are parasitized by *Arceuthobium,* it appears that the basic, adaptive radiation has already taken place, and that current adaptive trends favor more specialized niches. The climax host species were perhaps colonized first by the more primitive species of dwarf mistletoes; then as those ecological niches (host species) were filled, further evolution necessitated the colonization of host species characteristic of pioneering or intermediate stages of the ecological succession. Thus, species (such as *A. americanum* and *A. douglasii*) with a relatively large number of derived characteristics—including the formation of systemic infections—parasitize trees that are intermediate in forest succession (*Pinus contorta* and *Pseudotsuga menziesii,* respectively).

Absence of Hybridization and Polyploidy

Two of the most significant factors in the evolution of vascular plants are natural hybridization and polyploidy (Grant 1981). So pervasive are these features that most groups of vascular plants appear to show some evidence of one or both of these phenomena.

In *Arceuthobium,* however, polyploidy is unknown. In our cumulative years of field experience and that of a number of knowledgeable colleagues, we have encountered no examples of natural hybridization, even though our studies of sympatry (chapter 5) led us to consciously search for such evidence. We have not found any mention of hybridization or polyploidy in the extensive literature on dwarf mistletoes, and experimental crosses between *A. apachecum* (male parent) and *A. blumeri* failed to set seed (R. L. Mathiasen, personal communication).

The near absence of hybridization is apparently typical of Loranthaceae and Viscaceae (Barlow and Wiens 1971, Wiens and Barlow 1971). In *Phoradendron,* a single clear instance of natural hybridization is known (*P. densum* x *P. juniperinum*), but the resulting hybrid was apparently sterile (Wiens 1962, Vasek 1966, Wiens and Dedecker 1972). Two examples of hybridization are also reported in Australian Loranthaceae, but these rare situations likewise have little evolutionary importance (Bernhardt 1983). The absence of natural hybridization in *Arceuthobium,* as well as other mistletoes, can be explained by the occurrence of strong, interspecific, isolating mechanisms, particularly seasonal isolation due to variation in flowering times among sympatric species (Wiens 1964, 1968).

Another factor that might explain the apparent absence of hybrids in *Arceuthobium* is the lack of suitable habitats for their establishment. Most dwarf mistletoes have a principal host that the species most commonly parasitizes. Because hybrids combine the genetic characteristics of two species, they are often best adapted to intermediate habitats. However, intermediate habitats for hybridized parasites theoretically could be produced only through hybridization of the two host species in question. In other words, "hybridization of the habitat," as Anderson (1948) expressed it, would literally be necessary. Where host pines hybridize, the hybridizing pine species are so closely related that they are usually already parasitized by the same dwarf mistletoe: e.g., *A. campylopodum* on *Pinus jeffreyi* x *P. ponderosa* in California, and *A. americanum* on *Pinus contorta* x *P. banksiana* in Alberta, Canada.

Whether hybrid establishment in dwarf mistletoes is precluded by strong pre-zygotic isolating mechanisms (as we suspect) or because hybrid seeds fail to become established, the result is the same. In either case, there should be strong selective pressures, especially among parasites, against gene combinations that permit hybridization (Dobzhansky 1951).

Absence of natural hybridization (or hybrid establishment) provides a theoretical explanation for the absence of polyploidy in *Arceuthobium* and other mistletoes (Wiens 1968, 1975). This is based on the assumption that most polyploids are of hybrid origin (alloploids) (Stebbins 1950). If hybridization does not occur, alloploidy is precluded. Autoploidy might still occur, but it is probably of limited evolutionary significance. Several cases of known polyploidy in *Viscum* might be of autoploid origin, but others are not (Wiens 1975).

Evolutionary Patterns

In the absence of hybridization and polyploidy, the various species of dwarf mistletoes have apparently maintained distinct phyletic lines that produce the dendritic patterns of evolution typical of animals. In vascular plants, however, reticulate evolution, the product of natural hybridization, is the rule. Alloploidy likely stabilizes natural hybrids, and they evolve into true-breeding species. Hybridization and polyploidy, therefore, result in combining and then stabilizing the characteristics of different evolutionary lines, thereby producing reticulate evolutionary patterns characteristic of vascular plants.

As previously mentioned, a dendritic evolutionary pattern appears to characterize *Arceuthobium*, but the situation is obscured by the extreme morphological reduction attendant with the parasitic habit. Most species of *Arceuthobium* are relatively distinct, but the characters separating them are often cryptic or discernible for only short periods of the life cycle. Even though particular characters are not always clearly evident, when the characters are analyzed in their totality, the taxa become well differentiated. This is evident from numerical analyses (Hawksworth and Wiens 1972), which show that all taxa have a relatively high degree of integrity and tend to be more distinct than in other groups where hybridization has played an important evolutionary role (Sokol and Sneath 1963).

The two subgenera or phyletic lines (flabellate or verticillate branching patterns) proposed by Kuijt (1970) are accepted here (see table 14.1 and 15.2) but the extreme reduction of shoots in some species (*Arceuthobium pusillum, A. chinense, A. sichuanense, A. tibetense,* and *A. minutissimum*) can obscure the branching patterns. In *Arceuthobium,* the evolutionary pattern can be generally characterized by three stages of evolutionary divergence that appear to be present in both the New and Old Worlds but are better developed in the former.

Because the evolutionary patterns are dendritic, these evolutionary stages generally correspond to ancestral (pleisiomorphic), intermediate, and highly derived (apomorphic) species groups (chapters 14 and 15). Some characteristics that appear to exhibit evolutionary trends in *Arceuthobium* are summarized below (adapted and revised from Gill 1935):

Characteristic	Pleisiomorphic	Apomorphic
Host specificity	Low	High
Shoot size	Large	Small
Fruit maturation period	Long	Short
Shoot longevity	Long	Short
Polymorphism	High	Low
Flowering group	Direct	Indirect
Branching type	Verticillate	Flabellate
Witches' brooms	Non-systemic	Systemic

By most of these criteria, *Arceuthobium americanum, A. douglasii, A. guatemalense,* and *A. pusillum* in the New World and *A. minutissimum* in the Old World are highly derived species. Conversely, *A. abietis-religiosae, A. globosum, A. verticilliflorum,* and *A. vaginatum* in the New World and *A. azoricum* and *A. pini* in the Old World are the least specialized, ancestral species. Intermediate species are well represented in section *Campylopoda* (chapters 14 and 15). These species groups are not cladistic alliances. They were picked solely to represent species with varying proportions of ancestral and derived characters.

Wiens (1968) studied the flowering characteristics of New World dwarf mistletoes. He hypothesized that the different flowering groups arose as the genus moved northward from Mexico (the present area of greatest species diversity) into latitudes of greater annual variation in photoperiod and temperature. He concluded that species with indirect, spring flowering (*Arceuthobium americanum, A. douglasii,* and *A. pusillum*) were derived from species with direct, summer flowering patterns, which in turn were derived from species with direct, spring periods of flowering.

Kuijt (1970) presents convincing evidence that the flabellate (fan-shaped) branching pattern, common in most North American taxa, is a derived character. The more ancestral, verticillate branching is present in all five of the Old World species in which this trait has been studied and in three New World species, *Arceuthobium abietis-religiosae, A. americanum,* and *A. verticilliflorum.*

The formation of systemic (isophasic) witches' brooms (see figs. 6.3 and 16.57) is a derived stage of evolution. Although systemic types of witches' brooms are occasionally induced by several dwarf mistletoes, they are consistently formed by only five species—*Arceuthobium pusillum, A. douglasii, A. guatemalense,* and *A. americanum* in the New World and *A. minutissimum* in the Himalayas. The type of witches' brooms formed by the other Old World species in the Himalayas is poorly documented, but apparently *A. tibetense* and *A. chinense* may also produce systemic witches' brooms (Kiu 1984b).

The host–parasite combinations where witches' brooms are not consistently formed may represent the original, ancestral state. These likely preceded nonsystemic, localized formation of witches' brooms (see fig 6.4), which may in turn have preceded systemic formation of witches' brooms. Systemic witches' brooms have adaptive significance because they increase reproductive output of the dwarf mistletoe. By the formation of systemic witches' brooms, the endophytic system from a single seed can ramify through hundreds of linear meters of host branches and produce a profusion of shoots, flowers, fruits, and seeds.

Most dwarf mistletoes eventually kill their hosts, but mortality occurs much sooner in some host–parasite combinations than in others. This factor, however, is apparently not related to the relative stage of evolutionary development as measured by the characters described above. Within the evolutionarily intermediate group, some species cause severe host mortality (e.g., *Arceuthobium laricis* on *Larix occidentalis* and see table 12.5), and other species cause relatively little host mortality (e.g., *A. divaricatum* on *Pinus edulis*).

CHAPTER 5

Biogeography and Paleogeographic History

Current Distribution

Distribution of the Genus and Species

Arceuthobium is widely distributed in the Northern Hemisphere (fig. 5.1). The 8 species in the Old World range from Spain and Morocco to the Himalayas of southwestern China, with outlying species on the Azores and in East Africa. In the New World, the genus is represented by 39 taxa concentrated primarily in Mexico and the western United States (fig. 5.2). The following two regions of North America show the greatest concentration of taxa:

- Sierra Madre Occidental in Durango, Mexico (11 taxa)—*Arceuthobium blumeri, A. douglasii, A. durangense, A. gillii, A. globosum* subsp. *globosum, A. nigrum, A. rubrum, A. vaginatum* subsp. *vaginatum, A. yecorense, A. verticilliflorum,* and *A. strictum;* the latter 2 species are endemic to Durango.
- Northern California (12 taxa)—*Arceuthobium abietinum* (f. sp. *concoloris* and f. sp. *magnificae*), *A. americanum, A. californicum, A. cyanocarpum, A. campylopodum, A. douglasii, A. littorum, A. monticola, A. occidentale, A. siskiyouense,* and *A. tsugense* (subsp. *tsugense* and subsp. *mertensianae*).

Of the 21 taxa in the United States, all but 1 are western (8 are endemic to the western states); 14 occur in California (3 of which are endemic), 11 in Oregon, and 8 in Arizona (table 5.1). A single species, *Arceuthobium pusillum,* occurs in the north-central and northeastern United States. Six taxa found in the United States also occur in Canada:

- *Arceuthobium americanum*—British Columbia, Alberta, Saskatchewan, and Manitoba (also formerly present in western Ontario but now presumably extirpated by wildfire, J. Laut, personal communication).
- *Arceuthobium douglasii*—British Columbia.
- *Arceuthobium laricis*—British Columbia.
- *Arceuthobium pusillum*—Saskatchewan, Manitoba, Ontario, Québec, Prince Edward Island, Nova Scotia, New Brunswick, and Newfoundland.
- *Arceuthobium tsugense* subsp. *tsugense*—British Columbia.
- *Arceuthobium tsugense* subsp. *mertensianae*—British Columbia.

There are 22 known taxa of *Arceuthobium* in Mexico (table 5.2). Although dwarf mistletoes are reported for 24 of the 32 states, actual distributions are poorly understood. Potential hosts occur in 5 of the states not reporting the occurrence of dwarf mistletoe (Aguascalientes, Baja California Sur, Colima, Morelos, and Quintana Roo); there are no indigenous Pinaceae in the remaining 3 states (Campeche, Tabasco, and Yucatán). Eight taxa are found in both Mexico and the United States (*A. abietinum* f. sp. *concoloris, A. apachecum, A. blumeri, A. campylopodum, A. divaricatum, A. douglasii, A. gillii,* and *A. vaginatum* subsp. *cryptopodum*). Guatemala has 4 known taxa; and Honduras, Belize, and Hispaniola each has a single endemic species. *Arceuthobium* has been reported from El Salvador on the basis of visual observations of witches' brooms, but no specimens are available.

In the Old World, *Arceuthobium* is represented by 8 species—*Arceuthobium azoricum, A. chinense, A. juniperi-procerae, A. minutissimum, A. oxycedri, A. pini, A. sichuanense,* and *A. tibetense.* The widely distributed *A. oxycedri* is found from China (Xizang), throughout the Mediterranean region, to Spain. This extensive east–west distribution (nearly 10,000 km) can be explained by its presence (and persistence) in latitudes relatively unaffected by Pleistocene glaciation. Distributions of the 6 species from central and eastern Asia are listed in table 5.3. *Arceuthobium minutissimum* is a markedly reduced species that parasitizes *Pinus wallichiana* in the Himalayas of Pakistan, India, Nepal, and Bhutan. Although it resembles *A. pusillum* and *A. douglasii* of the New World in diminutive size, systemic infection, and host specificity, we now believe the similarity to be the result of convergence rather than close phyletic relationship. Previously, we listed only 2 species in China—*A. chinense* on *Abies* and *Keteleeria,* and *A. pini* on *Pinus* (Hawksworth and Wiens 1972). Recent studies in China have revealed 3 additional species—*A. oxycedri* on *Juniperus, A. sichuanense* on *Picea,* and *A. tibetense* on *Abies* (Kiu 1984a).

Figure 5.1 –World distribution of *Arceuthobium*. The distribution is primarily in the Northern Hemisphere, crossing the Equator only in Kenya.

Relationship of Parasite to Host Distribution

The distribution of a dwarf mistletoe species is generally centered within the range of its principal host or hosts. There are only four exceptions to this "principle of central distribution." The explanation probably lies in the particular paleogeographic history of each species.

- *Arceuthobium pusillum* on *Picea mariana* and *P. glauca*—This dwarf mistletoe was perhaps centrally distributed within the range of its hosts prior to the Wisconsin glaciations, but now only the southern portions of spruce distribution are infested. *Picea mariana* and *P. glauca* may have migrated northward after the last glacial period faster than the dwarf mistletoe, but it is more likely that *A. pusillum* has simply reached the northern limit of its climatic tolerances.
- *Arceuthobium microcarpum* on *Picea engelmannii* and *P. pungens*—This dwarf mistletoe of western spruces occurs only in Arizona and New Mexico and is near the southern limits of its hosts' distribution. *Arceuthobium microcarpum* is confined to five general regions: (1) the north rim of the Grand Canyon, Arizona, (2) the San Francisco Peaks and nearby Kendrick Peak, Arizona, (3) the Pinaleno (Graham) Mountains, Arizona, (4) the White Mountains, Arizona, and adjacent Mogollon Mountains, New Mexico, and (5) the Sacramento Mountains, southern New Mexico (an extreme disjunct). The distribution of the hosts extends at least 3,000 km farther north than the parasite. *Pinus aristata* may have provided a bridge for the evolution of *A. microcarpum* from *A. cyanocarpum*. *Arceuthobium microcarpum* is common on *P. aristata* in the only population of this tree in Arizona (Mathiasen and Hawksworth 1980). *Arceuthobium cyanocarpum* does not now occur in the Southwest, but it does parasitize *P. aristata* and *P. flexilis* in southern Colorado and southern Utah and occurred on *P. flexilis* in northern Arizona during the Quaternary Period (Van Devender and Hawksworth 1986).

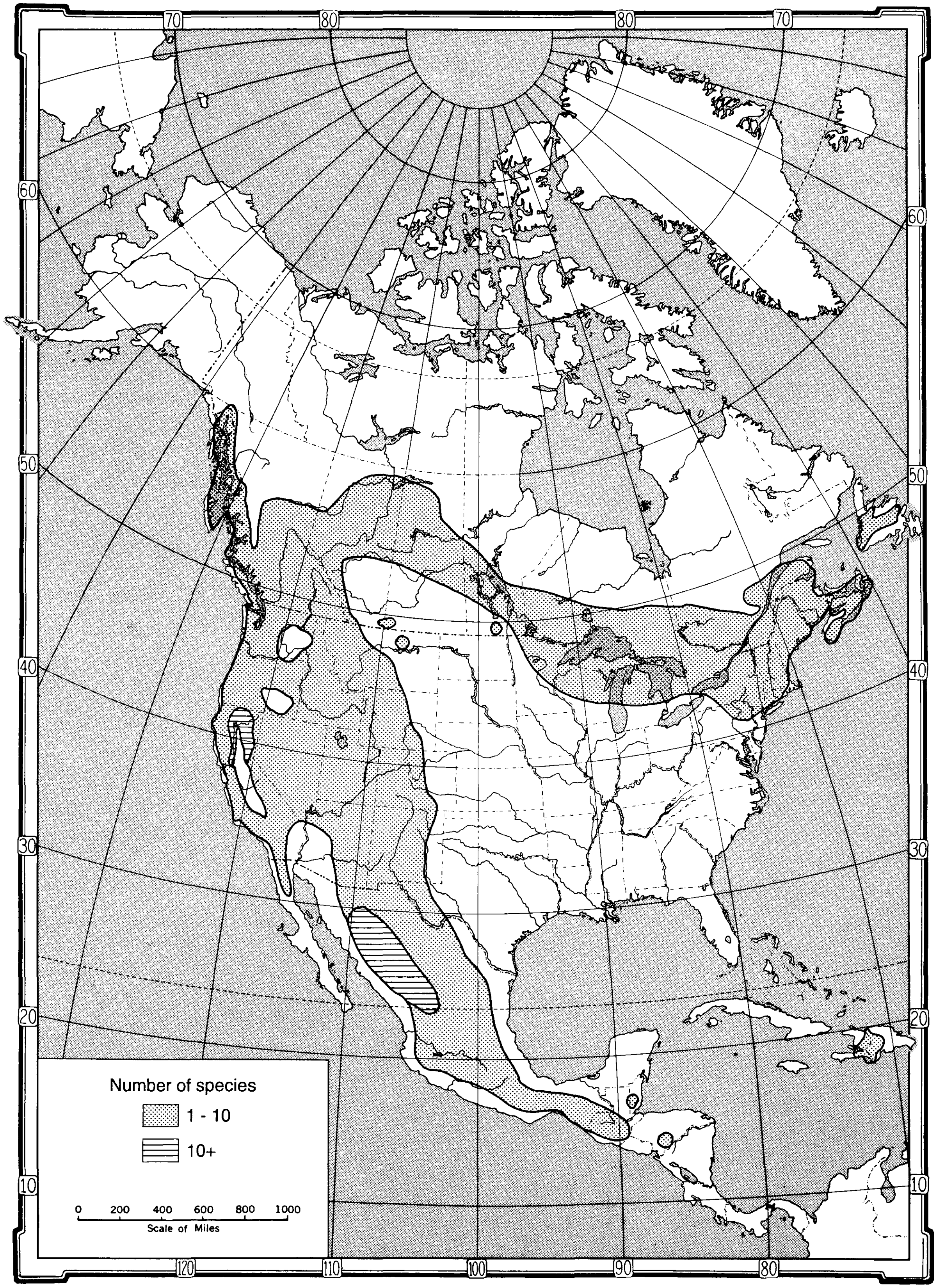

Figure 5.2 –Distribution of *Arceuthobium* in North America. There are 2 areas of high species concentrations: Sierra Madre Occidental in Chihuahua and Durango, Mexico (11 species) and northern California (11 species).

TABLE 5.1— Distribution of *Arceuthobium* in the western United States

Arceuthobium	AK	WA	OR	CA	NV	ID	MT	WY	UT	CO	AZ	NM	TX
A. abietinum													
f. sp. *concoloris*	—	X	X	X	X	—	—	—	X	—	X	—	—
f. sp. *magnificae*	—	—	X	X	RNC	—	—	—	—	—	—	—	—
A. americanum	—	X	X	X	RNC	X	X	X	X	X	—	—	—
A. apachecum	—	—	—	—	—	—	—	—	—	—	X	X	RNC
A. blumeri	—	—	—	—	—	—	—	—	—	—	X	—	—
A. californicum	—	—	—	X	—	—	—	—	—	—	—	—	—
A. campylopodum	—	X	X	X	X	X	—	—	—	—	—	—	—
A. cyanocarpum	—	—	X	X	X	X	X	X	X	X	—	—	—
A. divaricatum	—	—	—	X	X	RNC	—	—	X	X	X	X	X
A. douglasii	—	X	X	X	X	X	X	X	X	X	X	X	X
A. gillii	—	—	—	—	—	—	—	—	—	—	X	X	—
A. laricis	—	X	X	—	—	X	X	—	—	—	—	—	—
A. littorum	—	—	—	X	—	—	—	—	—	—	—	—	—
A. microcarpum	—	—	—	—	—	—	—	—	—	—	X	X	—
A. monticola	—	—	X	X	—	—	—	—	—	—	—	—	—
A. occidentale	—	—	—	X	—	—	—	—	—	—	—	—	—
A. siskiyouense	—	—	X	X	—	—	—	—	—	—	—	—	—
A. tsugense													
subsp. *tsugense*	X	X	X	X	—	—	—	—	—	—	—	—	—
subsp. *mertensianae*	—	X	X	X	—	—	—	—	—	—	—	—	—
A. vaginatum													
subsp. *cryptopodum*	—	—	—	—	—	—	—	—	X	X	X	X	X
Totals	1	7	11	14	5(7)	5	4	3	6	5	8	6	3(4)

RNC = Reported in state but not confirmed.

TABLE 5.2 – Distribution of *Arceuthobium* in Mexico

Arceuthobium	BC	CHA	CHI	COA	DF	DGO	GUA	GUE	HDG	JAL	MEX	MIC	NAY	NL	OAX	PUE	QUE	SLP	SIN	SON	TAM	TLX	VER	ZAC
A. abietinum																								
f. sp. *concoloris*	—	—	X	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
A. abietis-religiosae	—	—	—	—	X	—	—	—	X	X	X	X	—	X	—	X	—	—	—	—	X	X	—	—
A. apachecum	—	—	—	X	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
A. aureum																								
subsp. *petersonii*	—	X	—	—	—	—	—	—	—	—	—	—	—	—	X	—	—	—	—	—	—	—	—	—
A. blumeri	—	—	X	X	—	X	—	—	—	—	—	—	—	X	—	—	—	—	—	X	—	—	—	—
A. campylopodum	X	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
A. divaricatum	X	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
A. douglasii	—	—	X	X	—	X	—	—	—	—	—	—	—	X	—	—	—	—	—	—	—	—	—	—
A. durangense	—	—	—	—	—	X	—	—	—	X	—	—	—	—	—	—	—	—	X	—	—	—	—	—
A. gillii	—	—	X	—	—	X	—	—	—	—	—	—	—	—	—	—	—	—	X	X	—	—	—	—
A. globosum																								
subsp. *globosum*	—	—	X	—	—	X	—	—	—	X	—	—	—	—	—	—	—	—	—	X	—	—	—	—
subsp. *grandicaule*	—	—	—	—	X	—	—	X	X	X	X	X	—	—	X	X	—	—	—	—	—	X	X	—
A. guatemalense	—	X	—	—	—	—	—	—	—	—	—	—	—	—	X	—	—	—	—	—	—	—	—	—
A. nigrum	—	X	—	—	—	X	X	—	X	—	X	X	—	—	X	X	X	—	—	—	—	X	X	X
A. oaxacanum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	X	—	—	—	—	—	—	—	—	—
A. pendens	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	X	—	X	—	—	—	—	X	—
A. rubrum	—	—	—	—	—	X	—	—	—	—	—	—	—	—	—	—	—	—	X	—	—	—	—	—
A. strictum	—	—	—	—	—	X	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
A. vaginatum																								
subsp. *vaginatum*	—	—	X	X	X	X	—	—	X	X	X	—	X	X	X	X	X	—	X	—	X	X	X	X
subsp. *cryptopodum*	—	—	X	X	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	X	—	—	—	—
A. verticilliflorum	—	—	—	—	—	X	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
A. yecorense	—	—	X	—	—	X	—	—	—	—	—	—	—	—	—	—	—	—	—	X	—	—	—	—
Totals	2	3	8	5	3	11	1	1	4	5	4	3	1	4	6	5	2	1	4	5	2	4	4	2

Note: BC=Baja California, CHA=Chiapas, CHI=Chihuahua, COA=Coahuila, DF=Distrito Federal, DGO=Durango, GUA=Guanajuato, GUE=Guerrero, HDG=Hidalgo, JAL=Jalisco, Mex=Mexico, Mic=Michoacán, NAY=Nayarit, NL=Nuevo León, OAX=Oaxaca, PUE=Puebla, QUE=Querétaro, SLP=San Luis Potosí, SIN=Sinaloa, SON=Sonora, TAM=Tamaulipas, TLX=Tlaxcala, VER=Veracruz, ZAC=Zacatecas.

TABLE 5.3 — Distribution of *Arceuthobium* in central and eastern Asia

						China		
Arceuthobium	Afghanistan	Pakistan	India	Nepal	Bhutan	Xizang	Yünnan	Sichuan
A. chinense	—	—	—	—	—	—	X	X
A. minutissimum	—	X	X	X	X	—	—	—
A. oxycedri	PNC	X	X	—	—	X	—	—
A. pini	—	—	—	—	—	X	X	X
A. sichuanense	—	—	—	—	X	X	—	X
A. tibetense	—	—	PNC	—	—	X	—	—

PNC = Possible occurrence, but not confirmed.

- *Arceuthobium americanum* on *Pinus banksiana*—The distribution of *A. americanum* coincides closely with that of *P. contorta,* its major host. The parasite, however, is also common on *P. banksiana,* but only in the western portion of that host's distribution. *Pinus banksiana* extends for about 2,500 km east of the known limits of the dwarf mistletoe in western Ontario. Presumably, *A. americanum* evolved as a parasite of *P. contorta* and later spread to *P. banksiana* where the two species co-occur and hybridize in central Alberta. *Arceuthobium americanum* may still be spreading eastward on *P. banksiana* (see discussion for *A. americanum* in chapter 16).
- *Arceuthobium abietinum* f. sp. *concoloris* on *Abies concolor*—This dwarf mistletoe is most abundant in California and southern Oregon; however, the host species extends to Arizona and Utah, 800 km east of the range of the parasite. The spread of *A. abietinum* into these areas may have been prevented by the discontinuous distribution of *Abies concolor* in the Great Basin and southern Rocky Mountains.

Sympatry

The geographic co-occurrence of species, sympatry, is an important consideration in taxonomy. The rule of sympatry is that two genetically compatible taxa will hybridize if they have overlapping flowering periods, are in close proximity, and are pollinated by mutual agents.

Dwarf mistletoe plants within 30 m of each other are sufficiently close to be considered sympatric because that distance is well within the maximum range of pollen dispersal. In Manitoba, Canada, Gilbert and Punter (1984) trapped airborne pollen of *Arceuthobium americanum* 400 m from the closest pollen source; in Colorado, Coppola (1989) found *A. americanum* pollen 500 m from the closest pollen source. In New Mexico, Potter and Rowley (1960) discovered a single grain of *Arceuthobium* pollen 5 km from the nearest pollen source. In California, Leopold (1967) discovered dwarf mistletoe pollen in 8 of 11 pollen traps in a transect across the dry Searles Lake. The only dwarf mistletoe in the area was *A. divaricatum* and its nearest population was 16 km north on Argus Peak.

Most North American taxa of dwarf mistletoes are sympatric in some part of their distributions with at least one other species (fig. 5.3, tables 5.4 and 5.5). The allopatric taxa are *Arceuthobium aureum* subsp. *aureum, A. bicarinatum, A. guatemalense, A. hawksworthii, A. hondurense, A. littorum, A. oaxacanum,* and *A. pendens.*

Distributions of Old World species are too poorly known for determining which species are sympatric. *Arceuthobium minutissimum* and *A. oxycedri* are probably sympatric in the Indian Himalayas at elevations where host species overlap (Brandis 1907). The Chinese species, however, are probably separated by elevation and thus not sympatric (Kiu 1984b).

Sympatry between 2 species of *Arceuthobium* is not unusual (fig. 5.3), but we have observed only 10 instances (table 5.4) of sympatry among 3 species and 2 cases (table 5.5) of sympatry involving 4 species .

SYMPATRY ● Within 30 m. ○ Within 400 m. ★ Within 2 km.	A. yecorense	A. verticilliflorum	A. vaginatum ssp. cryptopodum	A. vaginatum ssp. vaginatum	A. tsugense ssp. mertensianae	A. tsugense ssp. tsugense (S. P. race)	A. tsugense ssp. tsugense (W. H race)	A. strictum	A. siskiyouense	A. rubrum	A. pusillum	A. oddicentale	A. nigrum	A. monticola	A. microcarpum	A. laricis	A. globosum ssp. grandicaule	A. globosum ssp. globosum	A. gillii	A. durangense	A. douglasii	A. divaricatum	A. cyanocarpum	A. campylopodum	A. californicum	A. blumeri	A. aureum ssp. petersonii	A. apachecum	A. americanum	A. abietis-religiosae	A. abietinum f. sp. magnificae	A. abietinum f. sp. concoloris
A. abietinum f. sp. concoloris			●		●		★					○			★	★					●	○	●	●	●				●		●	■
A. abietinum f. sp. magnificae					★																				○				●		■	
A. abietis-religiosae				●													●				●					●				■		
A. americanum			●		●						●					●					●		●	●					■			
A. apachecum			●												●						●	○						■				
A. aureum ssp. petersonii													●														■					
A. blumeri			●	●						★								●	●		●					■						
A. californicum																					○			★	■							
A. campylopodum									●			●		●		●					●	★	○	■								
A. cyanocarpum			●																		●		■									
A. divaricatum			●																		●	■										
A. douglasii			●	○	★		●			★					●	●		★			■											
A. durangense										●										■												
A. gillii	○		●	●															■													
A. globosum ssp. globosum	★		●	●						★			●					■														
A. globosum ssp. grandicaule				●													■															
A. laricis																■																
A. microcarpum			●												■																	
A. monticola									●					■																		
A. nigrum		★		●						★			■																			
A. occidentale												■																				
A. pusillum											■																					
A. rubrum		●		★						■																						
A. siskiyouense									■																							
A. strictum		●						■																								
A. tsugense ssp. tsugense (W. H. race)					★	●	■																									
A. tsugense ssp. tsugense (S. P. race)						■																										
A. tsugense ssp. mertensianae					■																											
A. vaginatum ssp. vaginatum	●	●		■																												
A. vaginatum ssp. cryptopodum	●		■																													
A. verticilliflorum		■																														
A. yecorense	■																															

Figure 5.3 –Sympatry among pairs of North American species of *Arceuthobium*.

An interesting but rare aspect of dwarf mistletoe parasitism is the occurrence of 2 different dwarf mistletoe species on a single host tree, "dual parasitism" (table 5.6 and fig. 5.4). The phenomenon is probably rare because of host competitive exclusion (chapter 6). Dwarf mistletoes also rarely parasitize trees already infected by other mistletoe genera; we know of only 5 such associations (table 5.7).

Figure 5.4 –Dual parasitism of *Pinus cooperi* by two species of dwarf mistletoe: *Arceuthobium vaginatum* subsp. *vaginatum* (left) and *A. globosum* subsp. *globosum* (right).

Paleobotany

Pollen

The oldest known fossil pollen of *Arceuthobium* is from the middle Eocene Epoch in eastern Germany. Identified as *Spinulaepollis arceuthobiodes* (Krutzsch

TABLE 5.4 – Sympathy of *Arceuthobium* as indicated by the co-occurrence of 3 different mistletoe species within a 30-m distance

Arceuthobium	Hosts	Location
A. abietinum f. sp. *concoloris* *A. douglasii* *A. vaginatum* subsp. *cryptopodum*	*Abies concolor* *Pseudotsuga menziesii* *Pinus ponderosa* var. *scopulorum*	Grand Canyon, AZ
A. cyanocarpum *A. douglasii* *A. vaginatum* subsp. *cryptopodum*	*Pinus flexilis* *Pseudotsuga menziesii* *Pinus ponderosa* var. *scopulorum*	Bryce Canyon, UT
A. apachecum *A. douglasii* *A. vaginatum* subsp. *cryptopodum*	*Pinus strobiformis* *Pseudotsuga menziesii* *Pinus ponderosa* var. *scopulorum*	Mogollon Mtns., NM, and Santa Catalina Mtns., AZ
A. apachecum *A. douglasii* *A. microcarpum*	*Pinus strobiformis* *Pseudotsuga menziesii* *Picea pungens*	Alpine, AZ
A. americanum *A. douglasii* *A. laricis*	*Pinus contorta* var. *latifolia* *Pseudotsuga menziesii* *Larix occidentalis*	Tieton Lake, WA and Flathead Res., MT
A. abietis-religiosae *A. blumeri* *A. vaginatum* subsp. *vaginatum*	*Abies vejari* *Pinus strobiformis* *Pinus arizonica* var. *arizonica*	Cerro Potosí, Nuevo Leon, Mexico
A. blumeri *A. globosum* subsp. *globosum* *A. vaginatum* subsp. *vaginatum*	*Pinus strobiformis* *Pinus cooperi* *Pinus cooperi*	El Salto, Durango, Mexico
A. blumeri *A. gillii* *A. vaginatum* subsp. *vaginatum*	*Pinus strobiformis* *Pinus leiophylla* *Pinus arizonica* var. *arizonica*	La Junta, Chihuahua, Mexico
A. blumeri *A. douglasii* *A. vaginatum* subsp. *cryptopodum*	*Pinus strobiformis* *Pseudotsuga menziesii* *Pinus ponderosa* var. *scopulorum*	Huachuca Mtns., AZ
A. americanum *A. campylopodum* *A. douglasii*	*Pinus contorta* var. *latifolia* *Pinus ponderosa* var. *ponderosa* *Pseudotsuga menziesii*	Unity, OR

TABLE 5.5 – Sympatry of *Arceuthobium* as indicated by the co-occurrence of 4 different mistletoe species within a 30-m distance

Arceuthobium	Hosts	Location
A. apachecum	*Pinus strobiformis*	Big Lake, AZ
A. douglasii	*Pseudotsuga menziesii*	
A. microcarpum	*Picea pungens*	
A. vaginatum subsp. *cryptopodum*	*Pinus ponderosa* var. *scopulorum*	
A. apachecum	*Pinus strobiformis*	San Mateo Mtns., NM
A. douglasii	*Pseudotsuga menziesii*	
A. divaricatum	*Pinus edulis*	
A. vaginatum subsp. *cryptopodum*	*Pinus ponderosa* var. *scopulorum*	

TABLE 5.6 – Dual parasitism of a common host by simultaneous infection with 2 *Arceuthobium* species

Arceuthobium	Host	Location	Reference
A. americanum *A. campylopodum*	*Pinus ponderosa*	ID	Weir 1916a
A. americanum *A. campylopodum*	*Pinus contorta*	ID	Weir 1916a
A. americanum *A. laricis*	*Pinus contorta*	BC, Canada WA MT	Kuijt 1954b Hawksworth and Wiens 1972 Hawksworth and Wiens 1972
A. americanum *A. laricis*	*Pinus sylvestris*	WA	Graham and Leaphart 1961
A. americanum *A. vaginatum* subsp. *cryptopodum*	*Pinus ponderosa*	CO	Hawksworth and Peterson 1959
A. americanum *A. vaginatum* subsp. *cryptopodum*	*Pinus contorta*	CO	Hawksworth and Wiens 1972
A. globosum subsp. *globosum* *A. vaginatum* subsp. *vaginatum*	*Pinus* spp.	Durango, Mexico	Hawksworth and Wiens 1965
A. rubrum *A. durangense*	*Pinus herrerai*	Durango, Mexico	Hawksworth and Wiens 1972
A. vaginatum subsp. *vaginatum* *A. verticilliflorum*	*Pinus arizonica*	Durango, Mexico	First report
A. globosum subsp. *globosum* *A. nigrum*	*Pinus cooperi*	Durango, Mexico	First report
A. aureum subsp. *petersonii* *A. nigrum*	*Pinus oocarpa*	Chiapas, Mexico	First report
A. douglasii *A. microcarpum*	*Abies lasiocarpa*	AZ	First report

TABLE 5.7 – Dual parasitism of a common host by simultaneous infection with an *Arceuthobium* and a mistletoe of another genus

Arceuthobium and mistletoe of another genus	Host	Location	Reference
A. abietinum f. sp. *concoloris* *Phoradendron pauciflorum*	*Abies concolor*	CA	Gill 1935 and our observations
A. bicarinatum *Dendropemon pycnophyllus*	*Pinus occidentalis*	Dominican Republic	Hawksworth and Wiens 1972
A. globosum subsp. *grandicaule* *Psittacanthus maracranthus*	*Pinus pseudostrobus*	Michoacán, Mexico	I. Vasquez (personal communication)
A. hawksworthii *Psittacanthus* sp.	*Pinus caribaea* var. *hondurensis* *Pinus oocarpa*	Belize	First report
A. vaginatum subsp. *vaginatum* *Psittacanthus maracranthus*	*Pinus engelmannii*	Durango, Mexico	First report

1962), it was found at more than 60 sites. Most pollen grains were found in strata from the upper Eocene to Miocene Epochs (extremes from middle Eocene to Pliocene Epochs). Stuchlik (1964) studied Miocene deposits in Poland and considered the pollen similar to, if not identical with, modern *A. oxycedri*. The northern limits of *A. oxycedri* are now about 800 km south of the German and Polish fossil pollen sites (table 5.8). Stuchlik also found a rare large-grained pollen, putatively belonging to a new subspecies *Spinulaepollis arceuthobiodes* subsp. *major*. Pollen grains of this subspecies ranged 24 to 30 µm in diameter, whereas other collections of the species ranged 20 to 24 µm. Although swelling caused by fossilization or laboratory preparation could have affected pollen size, our studies indicate that a range as great as 20 to 30 µm is unusual within a species (pollen of *A. oxycedri* is only 18 to 20 µm). Therefore, the large-grained collection may well represent an extinct taxon.

The fossil genus *Patzea* (Caspary 1872), which was considered by Engler and Krause (1935) and Nemejc (1975) to be synonymous with *Arceuthobium*, was described from Oligocene amber formations along the Baltic Coast. However, drawings published

TABLE 5.8 – Fossil pollen records of *Arceuthobium oxycedri*

Period	Epoch	Location	Reference
Quaternary	Holocene	Greece	Bottema 1974
Quaternary	Holocene	Yugoslavia	Brande 1973
Quaternary	Holocene	Poland	Stachurska and others 1973
Quaternary	Pleistocene–Holocene	Spain	Pons and Reille 1988
Quaternary	Pleistocene	Greece	Van der Weil and Wijmstra 1987
Tertiary	Pliocene	Germany	Menke 1975, 1976
Tertiary	Miocene	Poland	Oszast and Stuchlik 1977, Sadowska 1977, Stuchlik 1964

by Conwentz (1886) suggest to us and to Lancucka-Srodoniowa (1980) that *Patzea* is not congeneric with *Arceuthobium*.

Only 3 North American sites of the Miocene Epoch have yielded *Arceuthobium* pollen: (1) north flank of the Alaska Range, associated with *Pinus* and *Picea* pollen (Wahrhaftig and others 1969); (2) Troublesome Formation in north-central Colorado, associated predominantly with the pollen of *Picea, Pinus,* and *Abies* (Weber 1965); and (3) Split Rock, Carbon County, Wyoming (Leopold and Denton 1987).

Several reports of *Arceuthobium* pollen from the Quaternary Period in western North America and Mexico are listed in table 5.9. Pollen ages range from the present to about 30,000 years BP. A reasonable guess regarding the species of pollen can usually be made from the associated host's pollen and location of the site. Adam (1967) reported the irregular occurrence of *Arceuthobium* pollen over the last 10,000 years in the central Sierra Nevada of California. He noted that *Arceuthobium* pollen abundance peaked when pine populations were decreasing and suggested that *Arceuthobium* was more abundant during drier

TABLE 5.9 – Reports of *Arceuthobium* pollen of the Quaternary Period from western North America and Mexico

Arceuthobium	Location	Age (years BP)	Reference
Arceuthobium spp.	Sierra Nevada, CA	10,000	Adam 1967, 1973, 1974
Arceuthobium spp.	Elana Range, NV	30,400	Spaulding 1977
Arceuthobium spp.	Guadalupe Mts., TX	11,000	Spaulding and Martin 1979
Arceuthobium spp.	southwest WA	8,500	Barnosky 1985
Arceuthobium spp.	Sanpoil River, WA	3,000–4,000	Mack and others 1978
Arceuthobium spp.	Tlaxcala, Mexico	8,500–10,000	Ohngemach and Straka 1978, 1981, 1982
A. americanum	Peace River, AB, Canada	7,000–10,000	White and Mathewes 1986
A. americanum	Banff NP, AB, Canada	10,000	Macdonald 1989
A. americanum	central BC, Canada	age ? (1% pollen)	Donahue and Habgood 1974
A. americanum	Yoho NP, BC, Canada	6,000–10,000	Reasoner and Hickman 1989
A. americanum	Kootenai River, MT	5,000	Mack and others 1983
A. americanum	Sheep Mtn. Bog, MT	10,700	Mehringer 1985
A. americanum	Lost Trail Bog, MT	11,500	Mehringer and others 1977
A. americanum	Yellowstone, WY	13,000	Baker 1969, 1970, 1976; Baker and Richmond 1978; Waddington and Wright 1974
A. campylopodum?	Yosemite NP, CA	age ?	Anderson and Carpenter 1991
A. campylopodum	Harney Co., OR	5,000–5,500	Wigland 1987
A. cyanocarpum	Ny Co., NV	14,000 (trace)	Spaulding and others 1984
A. divaricatum	Searles Lake, CA	5,000–10,000	Leopold 1967
A. divaricatum	Chaco Canyon, NM	3,000	Betancourt 1984
A. divaricatum	Great Salt Lake, UT	4,000–6,500	Mehringer 1985
A. globosum	Tlaxcala, Mexico	age ? (2.5% pollen)	Heine and Ohngemach 1976; Ohngemach 1977;
A. globosum	Michoacán, Mexico	5,000	Watts and Bradbury 1982
A. littorum	central coast, CA	3,000–5,000	Adam 1975, Adam and others 1981
A. occidentale	Clear Lake, CA	age ?	Adam 1988
A. tsugense	Vancouver Is., BC, Canada	9,000–10,500	Hebda 1983
A. tsugense	SW coast, BC, Canada	10,500–11,500	Mathewes 1973, Mathewes and Rouse 1975
A. tsugense	Puget Sound, WA	7,000	Hansen and Easterbrook 1974
A. tsugense	Olympic Pen., WA	11,000–19,000	Heusser 1973a, 1973b, 1974, 1978, 1983; Peterson and others 1983
A. tsugense	Puyallup, WA	age ? (trace)	Heusser 1977
A. vaginatum	La Plata Mts., CO	2,500–10,000	Peterson and Mehringer 1976

periods. Certainly, dwarf mistletoe on *Pinus ponderosa* in California is now more abundant in drier regions. Janssen (1968) also noted that *A. pusillum* in Minnesota was more abundant when spruce populations were decreasing.

Arceuthobium pusillum has the most complete fossil pollen record within the genus. A number of pollen-bearing sites have been located both within and outside the modern distribution of the species (table 5.10). Pollen that is presumably *A. pusillum* has been found in the southeastern United States (North Carolina, Georgia, and Tennessee), 500 km south of its present southern limit in northern New Jersey. Recorded pollen ages range from 10,000 to nearly 40,000 years BP (table 5.10). Whitehead and Barghoorn (1962) suggest that this pollen may represent a species of dwarf mistletoe from the western United States or an extinct species. Most fossil pollen, however, is associated with spruce pollen and needles, and *A. pusillum* is the only species of dwarf mistletoe in eastern North America. It rarely parasitizes any host other than spruce, and no other species of dwarf mistletoe presently occurs within 2,000 km of the fossil sites. Therefore, it is likely that the pollen is either *A. pusillum* or a close extinct relative.

Spaulding and Martin (1979) identified pollen of *Arceuthobium* in 11,000-year-old ground sloth dung from the Guadalupe Mountains, Texas. Because pine pollen was also common in the dung, the species would likely be either *A. divaricatum* or *A. vaginatum* subsp. *cryptopodum,* both of which presently occur in the Guadalupe Mountains.

Macrofossils

The oldest macrofossils of *Arceuthobium* are known from the upper Miocene Epoch in Lower Silesia, Poland (Lancucka-Srodoniowa 1980). These collections include many well preserved plants with shoots, flowers, and fruits. Morphologically, the fossil plants resemble modern *A. oxycedri* except for the number of perianth segments. The frequency of 3- or 4-merous flowers in fossil plants is approximately equal; flowers of modern plants are mostly 3-merous (95%) (Hawksworth and Wiens 1976). Lancucka-Srodoniowa (1980) states that some fossil dwarf mistletoe plants are still attached to the host branches. Although the host is not identified, *Juniperus* is the only modern Old World host found west of the Himalayas.

Chaney and Mason (1930, 1933) and Mason (1934) discovered fossils of *Arceuthobium* in Pleistocene formations of coastal California. Axelrod (1966) dated the sites as late Pleistocene Epoch and obtained radiocarbon dates of 30,000 to 40,000 years BP. The sites were

TABLE 5.10 – Reports of *Arceuthobium pusillum* pollen of the Quaternary Period from within and outside modern distribution of the species

Location	Age (years BP)	Reference
Within modern distribution		
Isanti Co., MN	10,000–11,000	Cushing 1964
Stevens Pond, MN	Holocene Epoch (trace)	Janssen 1967
Koochiching Co., MN	9,000	Janssen 1968, 1973
Hubbard Co., MN	5,000 (trace)	McAndrews 1966
western Lake Superior, MN	age ?	Maher 1977
Franklin and Monroe Co., PA	11,000–13,000	Watts 1980
Outside modern distribution		
northwest GA	Pleistocene Epoch	Watts 1970, 1973, 1975
Lincoln Co., IN	age ? (1% pollen)	Whitehead and others 1982
NC	40,000 (1% pollen)	Whitehead 1963, 1964, 1965, 1967, 1981 Whitehead and Barghoorn 1962 Whitehead and Doyle 1969
TN	20,000 (trace)	Delacourt and others 1980
VI	10,000 (trace)	Craig 1969
Driftless area, SE WI	age ?	Hartley 1966

Carpinteria, Santa Cruz Island, and Tomales Bay (fossils were abundant at Santa Cruz and Tomales). The dwarf mistletoe was associated with *Pinus radiata* and *P. muricata* and was indistinguishable from modern *A. littorum* (reported as *A. campylopodum*), which presently parasitizes these pines. This species does not now occur at the Carpinteria or Santa Cruz sites, although *Pinus muricata* is still present on Santa Cruz Island. The closest populations of *A. littorum* are on *P. radiata* near Cambria, about 60 km north of Carpinteria, and on *P. muricata* at Inverness Ridge adjacent to Tomales Bay. Chaney and Mason (1934) note that the fossil plant had primarily 4-merous staminate flowers; although this character is variable, 4-merous flowers are most common in modern populations of *A. littorum.*

Fragments of *Arceuthobium* have been identified in packrat (*Neotoma* spp.) middens from the southwestern United States and adjacent Mexico (Van Devender and Hawksworth 1986). If a site is well protected under a rock ledge, material can remain identifiable for thousands of years (occasionally as long as 40,000 years). Because packrats collect vegetation only within 50 m of a den, these accumulations provide a natural herbarium specific to a small, local site (in contrast to pollen collections, which tend to be more regional). By radiocarbon dating various layers of the midden, it is possible to construct a nearly complete floristic history of the site (Van Devender and others 1977). At least two species (*A. divaricatum* and *A. cyanocarpum*) and possibly a third species (*A. abietinum*) have been detected in packrat middens. *Arceuthobium divaricatum,* a parasite of pinyon pines, has been found in middens from the following areas:

- Sheep Mountains, Clark County, Nevada, age 9,400 to 9,800 years BP (Spaulding 1977, 1980; Van Devender and Hawksworth 1986).
- Chaco Canyon, San Juan County, New Mexico, age 3,000 years BP (Betancourt 1984, Van Devender and Hawksworth 1986).
- Heuco Mountains, El Paso County, Texas, age 13,200 years BP (Van Devender and Hawksworth 1986).
- Chisos Mountains, Brewster County, Texas, age 11,200 to 21,000 years BP (Van Devender and Hawksworth 1986).

In all cases except the last, the host species is still present near the fossil site. The Chisos Mountains site is of particular interest because the dwarf mistletoe was associated with *Pinus remota,* a pinyon not now known to be parasitized by *Arceuthobium.* No dwarf mistletoe now occurs in the Chisos Mountains, but *P. cembroides* is present. *Pinus cembroides* is parasitized by *A. divaricatum* in the Davis Mountains, 190 km north of the Chisos.

Arceuthobium cyanocarpum, a parasite of *Pinus flexilis, P. longaeva,* and related pines, has been found in middens at 3 locations:

- Sheep Mountains, Clark County, Nevada, age 21,500 years BP (Spaulding 1977, Van Devender and Hawksworth 1986).
- Elana Range, Nye County, Nevada, age 14,100 years BP (Spaulding and others 1984).
- Grand Canyon, Coconino County Arizona, age 16,200 years BP (Van Devender and Hawksworth 1986).

In the latter area, the dwarf mistletoe was associated with *P. flexilis,* a species that no longer occurs in the Grand Canyon area, but *P. flexilis* is now parasitized by *A. cyanocarpum* near Navajo Lake in southern Utah, 190 km north.

Arceuthobium abietinum is perhaps the species reported from a 30,400-year-old midden in the Sheep Range, Nevada (Spaulding 1977). *Abies concolor* was the predominant associated conifer, and *Arceuthobium abietinum* still occurs on this host in the Sheep Range.

Paleogeography

Because dwarf mistletoes have not colonized eastern and southern pines, the occurrence of *Arceuthobium pusillum* on eastern spruces is perplexing. *Arceuthobium pusillum* could have evolved somewhere outside its present distribution, perhaps in northwestern North America. According to Mirov (1967), the pines in eastern and western North America have been essentially isolated since the Pliocene Epoch; hence, the dwarf mistletoes may not have had an opportunity to colonize the eastern pines.

Perhaps Pleistocene glaciations played a role in eliminating *Arceuthobium pusillum,* or its immediate ancestors, from the northern and western portions of the present distribution of spruces. The pollen of *Arceuthobium* occurred in the southern spruce refugia in the Appalachian Mountains of North Carolina, South Carolina, and Georgia and possibly also on the Gaspé Peninsula, Québec. During the Holocene Epoch, *A. pusillum* again moved northward but not as far as its spruce hosts had migrated. Both *Picea mariana* and *P. glauca* now occur as far northwestward as Alaska, but *A. pusillum* just enters eastern Saskatchewan.

Picea apparently migrated to North America from Asia in two or more waves (Gordon 1968, Wright

1955). The available information on dwarf mistletoe parasitism of *Picea* tends to confirm this. The species that arrived in the Cretaceous Period or earlier (relatives of *Picea breweriana, P. chihuahuana,* and possibly *P. sitchensis*) are not principal hosts for any dwarf mistletoes. Spruces that evolved later, in the early Tertiary Period (*P. pungens, P. engelmannii, P. mariana, P. rubens,* and *P. glauca*) are heavily parasitized (by *Arceuthobium microcarpum* and *A. pusillum*).

The three dwarf mistletoe taxa that presently have far northern distributions are *Arceuthobium americanum, A. pusillum,* and *A. tsugense* subsp. *tsugense.* Their presumed northward migrations of 500 to 1,500 km since the last Wisconsin glaciation are difficult to explain unless there were refugia within the glaciated areas where the host and parasite persisted, or there was significant long-distance dispersal by birds. Current rates of spread by explosive fruits average only 0.3 to 0.6 m per year through infested stands (Hawksworth 1958, 1961a); these rates are insufficient to account for the observed migrations.

The history of *Pinus contorta* in the late Quaternary Period was reviewed by Critchfield (1985). There is limited agreement that a refugium for *P. contorta* existed in the Yukon, but the evidence for an ice-free corridor along the eastern slope of the Rocky Mountains in Alberta is more debatable. Pollen evidence does not indicate that *Arceuthobium americanum* survived in the Yukon refugium, but there are records of 7,000- to 10,000-year-old pollen of this dwarf mistletoe as far as latitude 56°30′N in the Banff-Jasper and Peace River areas (White and Mathewes 1986, Macdonald 1989). This is within about 400 km of the present northern limits of *A. americanum,* which requires a 40-m/year rate of spread (2 orders of magnitude greater than spread by explosive fruits).

The higher rates of migration than explained by explosive fruits suggest that a supplemental means of dispersal, possibly by birds, may have been involved (Nicholls and others 1984). Several studies document the dispersal of dwarf mistletoes for distances up to 0.5 km (chapter 8). Definitive studies are needed on the possible role of birds in dispersal for longer distances. Because dwarf mistletoes are dioecious, establishment of a new population requires that least 2 seeds of different sex are transported to distant safe-sites near each other, and that these seeds germinate, cause infection, flower, and produce mature seeds. Although di-embryonic seeds occur in *Arceuthobium* (chapter 3), their frequency is so low it seems unlikely that polyembryony would play any role in long-distance dispersal. Because seeds mature in the autumn, long-distance bird migration would tend to disseminate seeds southward. Although the responsible dispersal mechanisms are unknown, at least 6 species of mistletoe have become established 10 to 200 km from the closest naturally infested stands (table. 5.11).

The widespread occurrence of *Arceuthobium tsugense* in the forests of southeastern Alaska, the Queen Charlotte Islands, and coastal British Columbia suggests that there were refugia where *Tsuga heterophylla* and its dwarf mistletoe survived well north of the southern limits of glaciation in British Columbia (Dillon 1956). This is approximately 1,600 km south of the present northern limits of distribution (latitude 60°N) of this dwarf mistletoe.

The disjunct distributions of two species on oceanic islands (*Arceuthobium bicarinatum* and *A. azoricum*) have special biogeographical interest. *Arceuthobium bicarinatum* likely reached Hispaniola during the Miocene Epoch when land connections may have existed between Caribbean islands and Central America (Mirov 1967). Although separated by 1,600 km, *A. bicarinatum* and *A. hondurense* (an endemic of Honduras) are morphologically similar and may be vicariants that were widespread during the Miocene Epoch (but see chapter 15). The distinctiveness of *A. azoricum* and its host *Juniperus brevifolia* suggests a long and isolated evolutionary history rather than recent introduction by long-distance dispersal as proposed by Ridley (1930) (also see chapter 16). These species are probably survivors from the early Tertiary Period as continental genera became restricted to recurrent volcanic islands along the mid-Atlantic ridge (McKenna 1972).

The lack of dwarf mistletoes on low-elevation Caribbean pines is difficult to explain. These trees were presumably exposed to parasitism by dwarf mistletoes during the evolution of *Arceuthobium bicarinatum* when there was a land bridge between Central America and Hispaniola. *Pinus occidentalis,* the host of *A. bicarinatum* is, however, a relatively high-elevation species. Although *A. hawksworthii* infests *P. caribaea* var. *hondurensis* in the uplands of Belize, no dwarf mistletoes occur on the extensive low-elevation stands of *P. caribaea* elsewhere in the Caribbean Basin. In fact, there are no species of *Arceuthobium* in any lowland, moist, tropical climate. *Arceuthobium tsugense* is widespread on *Tsuga heterophylla* in the temperate rain forests along the northwestern coast of North America, and *A. juniperi-procerae* occurs in moist, high-elevation forests in the Kenya highlands near the Equator. It appears that dwarf mistletoes, which presumably originated in temperate regions, are unable to adapt to warm, moist, low-elevation tropical environments (see chapters 15 and 16).

TABLE 5.11– Establishment of *Arceuthobium* species outside their natural range

Arceuthobium	Host	Location	Distance to closest known naturally infested stands	Reference
A. cyanocarpum	*Pinus flexilis*	Fort Collins, CO	35 km	First report
A. divaricatum	*Pinus edulis*	Fort Collins, CO	200 km	First report
		Albuquerque, NM	20 km	Hawksworth and Wiens 1972
A. littorum	*Pinus radiata*	Berkeley, CA	130 km	Offord 1964
		Stanford, CA	85 km	Peirce 1905
		Hillsborough, CA	100 km	Butler 1992
A. microcarpum	*Picea pungens*	Alpine, AZ	10 km	Hawksworth and Wiens 1972
		Springerville, AZ	10 km	First report
A. pusillum	*Picea glauca*	Fort Gary, MB Canada	10 km	Thomas 1954
A. vaginatum subsp. *cryptopodum*	*Pinus ponderosa*	Denver, CO	15 km	Hawksworth and Wiens 1972
		Pueblo, CO	30 km	J. Hoffman (personal communication)

CHAPTER 6

Host Relationships

Natural Hosts

The hosts of dwarf mistletoes are ranked as "principal," "secondary," "occasional," and "rare." Potential hosts that are not parasitized are designed as "immune". These susceptibility classifications are defined in table 6.1, and were devised by Hawksworth and Wiens (1972). They were based on an "infection index" defined by percentage classes of infected trees (for each host species) within 6 m of a heavily parasitized host. Infection indices are meaningful only in stands with trees older than 30 years.

The susceptibility classification (table 6.1) is not a measure of the frequency with which a host species may be infested over its geographical distribution. For example, *Pinus cembroides* is designated as a principal host of *Arceuthobium divaricatum*, even though the two species occur together only in the Davis Mountains of west Texas. In this region, however, *P. cembroides* is as susceptible as the other pinyons that act as principal hosts in other portions of this dwarf mistletoe's distribution.

Some variation in susceptibility is to be expected over the geographical distribution of a host species, as well as in certain habitats (see chapter 7). Such differences could reflect variation in the host, parasite, or environment (Wiens 1961). Nonetheless, the host relationships of each dwarf mistletoe species are sufficiently consistent to make the rankings meaningful.

The principal hosts of both New World and Old World dwarf mistletoes tend to be restricted to a single genus or for *Pinus* to a single subgenus (figs. 6.1 and 6.2). Only *Arceuthobium microcarpum, A. laricis,* and *A. tsugense* have principal hosts that belong to different genera (respectively, *Picea* and *Pinus; Larix* and *Tsuga;* and *Abies, Pinus,* and *Tsuga*).

The susceptibility of natural hosts is listed by *Arceuthobium* taxa in table 6.2 and by host taxa in table 6.3. Host susceptibility classification is usually based on direct field observations; for those cases where data are lacking, we classified taxa on the basis of our field experience. The absence of field studies precludes the preparation of a susceptibility classification for the Old World species.

The susceptibility classes were based on the most common situation encountered for a particular host–parasite combination. For example, in the San Bernardino Mountains near Snow Valley, California, *Arceuthobium campylopodum* severely parasitizes *Pinus coulteri;* at lower elevations, however, the mistletoe severely parasitizes *P. attenuata* and only occasionally infects *P. coulteri.* Therefore, even though *P. coulteri* is sometimes heavily infested by *A. campylopodum,* it is a secondary host in most situations and is classified as such. Fortunately, this kind of variation is rare, and most host taxa readily fall into a single susceptibility class for an associated dwarf mistletoe taxa.

TABLE 6.1 – Classes of host susceptibility to *Arceuthobium*

Class	Susceptibility	Infection level
I	Principal*	≥90%
II	Secondary	90–50%
III	Occasional	50–5%
IV	Rare	≤5%
V	Immune†	0%

*Except for young trees, infection levels usually approach 100% within 6 m of a seed source.
†Trees are not infected even where the dwarf mistletoe is common.

ARCEUTHOBIUM	*Abies*	*Larix*	*Picea*	*Pinus* (*Haploxylon*)	*Pinus* (*Diploxylon*)	*Pseudotsuga*	*Tsuga*
A. abietinum f. sp. *concoloris*	●						
A. abietinum f. sp. *magnificae*	●						
A. abietis-religiosae	●						
A. americanum					●		
A. apachecum				●			
A. aureum subsp. *aureum*					●		
A. aureum subsp. *petersonii*					●		
A. bicarinatum					●		
A. blumeri				●			
A. californicum				●			
A. campylopodum					●		
A. cyanocarpum				●			
A. divaricatum				●			
A. douglasii						●	
A. durangense					●		
A. gillii					●		
A. globosum subsp. *globsum*					●		
A. globosum subsp. *grandicaule*					●		
A. guatemalense				●			
A. hawksworthii					●		
A. hondurense					●		
A. laricis		●					
A. littorum					●		
A. microcarpum			●	●			
A. monticola				●			
A. nigrum					●		
A. oaxacanum					●		
A. occidentale					●		
A. pendens				●			
A. pusillum			●				
A. rubrum					●		
A. siskiyouense					●		
A. strictum					●		
A. tsugense subsp. *tsugense*	●				●		●
A. tsugense subsp. *mertensiana*	●						●
A. tsugense subsp. *vaginatum*					●		
A. tsugense subsp. *cryptopodum*					●		
A. verticilliflorum					●		
A. yecorense					●		

Figure 6.1 –Taxonomic affiliations of principal hosts of New World *Arceuthobium*.

ARCEUTHOBIUM	PINUS (HAPLOXYLON)	PINUS (DIPLOXYLON)	ABIES	PICEA	KETELEERIA	JUNIPERUS
A. azoricum						●
A. chinense					●	
A. juniperi-procerae						●
A. minutissimum	●					
A. oxycedri						●
A. pini		●				
A. sichuanense				●		
A. tibetense			●			

Figure 6.2 –Taxonomic affiliations of principal hosts of Old World *Arceuthobium*.

As shown in table 6.3, some host taxa are parasitized by a number of dwarf mistletoes: 9 taxa infect *Pinus durangensis*; 7 parasitize *P. cooperi, P contorta* var. *latifolia, P. engelmannii,* and *P. monticola;* and 6 infect *P. arizonica* var. *arizonica, P. teocote,* and *P. pseudostrobus.*

Some dwarf mistletoes are highly host specific—*Arceuthobium apachecum* is restricted to *Pinus strobiformis, A. bicarinatum* to *P. occidentalis,* and *A. guatemalense* to *P. ayacahuite.* Other dwarf mistletoes, however, have broader host ranges—*A. laricis,* which principally parasitizes *Larix occidentalis,* also occurs on *Abies, Picea, Pinus,* and *Tsuga. Arceuthobium douglasii* primarily parasitizes *Pseudotsuga menziesii* although it infects *Abies* and *Picea* rarely.

A number of species of *Arceuthobium* infect nearly all western true firs (*Abies*) to some extent. However, *Abies* is the principal host of only 3 dwarf mistletoe species—*A. abietinum* in the western United States and northern Mexico, *A. abietis-religiosae* in central Mexico, and *A. tsugense* in the coastal north Pacific region. There is a single collection by Weir (ILL) of an *Arceuthobium* on the rare bristlecone fir, *Abies bracteata,* of the Santa Lucia Mountains, California. The mistletoe species is most likely *A. occidentale,* which typically parasitizes *Pinus sabiniana,* but the specimen is poorly documented and so fragmented that positive identification is impossible.

All North American spruces—except the Mexican species *Picea chihuahuana* and *P. mexicana* (Martínez 1963) and the recently described *P. martinezii*—are hosts for *Arceuthobium.* Two dwarf mistletoe species are principal parasites of spruce: (1) *A. pusillum* on *Picea mariana, P. glauca,* and *P. rubens* in the Great Lakes region, New England, and eastern Canada; and (2) *A. microcarpum* on *Picea engelmannii* and *P. pungens* in Arizona and New Mexico. *Picea sitchensis* is rarely parasitized by *A. tsugense* subsp. *tsugense* (Laurent 1966, Mathiasen 1994).

Eight dwarf mistletoe species occur primarily on the North American white pines (subgenus *Haploxylon*) —*Arceuthobium apachecum* on *Pinus strobiformis; A. blumeri* on *P. ayacahuite* var. *brachyptera* and *P. strobiformis; A. californicum* on *P. lambertiana; A. cyanocarpum* on *P. albicaulis, P. aristata, P. flexilis,* and *P. longaeva; A. divaricatum* on numerous pinyons; *A. guatemalense* on *P. ayacahuite* var. *ayacahuite; A. monticola* on *P. monticola;* and *A. pendens* on several pinyons. *Pinus chiapensis,* a species indigenous to Guatemala and southern Mexico, is the only North American white pine not known to be parasitized by *Arceuthobium.*

The hard pines (subgenus *Diploxylon*) are by far the most common hosts of North American dwarf mistletoes. Twenty-three of the 39 North American taxa are primary parasites of these pines, and 6 other species occur at least rarely on them.

Usually a dwarf mistletoe species parasitizes 1, sometimes 2, or rarely 3 host species in the same stand. We have observed only 3 instances where a particular dwarf mistletoe species parasitized 4 different host species within a stand:

- *Arceuthobium microcarpum* on the San Francisco Peaks, Arizona—*Picea engelmannii* and *Pinus aristata* (principal hosts) and *Abies lasiocarpa* var. *arizonica* and *Pinus strobiformis* (rare hosts).
- *Arceuthobium nigrum* near Zacatlán, Puebla, Mexico—*Pinus leiophylla* var. *leiophylla, P. patula, Pinus teocote* (principal hosts), and *P. pseudostrobus* (occasional host).
- *Arceuthobium oaxacanum* south of Suchixtepec, Oaxaca, Mexico—*Pinus lawsonii, P. michoacana, P. pseudostrobus* (principal hosts), and *P. oaxacana* (occasional host).

Artificial Inoculations to Unnatural Hosts

Trees of various species have been inoculated with, and have occasionally become colonized by, dwarf mistletoe species that do not occur naturally within the range of the host species (extra-limital hosts). In some instances, trees co-occurring with a particular dwarf mistletoe are immune to natural infection but can be artificially inoculated. For example, Weir (1918a) inoculated and established *Arceuthobium campylopodum* on *Abies concolor.* Even though this species is frequently associated with *A. campylopodum* in nature, no natural infections have been found. Numerous examples of successful artificial inoculation are reported in table 6.4. Most such experiments have been conducted in unnatural environments, and life cycle data based on such artificial inoculations may be misleading. For example, when *Arceuthobium cyanocarpum* was grown on *Pinus strobiformis* in a greenhouse, dwarf mistletoe plants exhibited accelerated growth and produced shoots within 5 months and flowers within 7 months (Hawksworth, unpublished data). In nature, *A. cyanocarpum* does not produce shoots until 2 or 3 years following infection and flower production requires 4 or 5 years.

The susceptibility of a host species to natural infection by a dwarf mistletoe species with which it

TABLE 6.2 – Susceptibility of hosts for 39 North American taxa of *Arceuthobium* based on natural infection of native trees

Arceuthobium	Principal hosts	Secondary hosts	Occasional hosts	Rare hosts	Immune taxa
A. abietinum f. sp. *concoloris*	*Abies concolor* var. *concolor* var. *lowiana* *Abies durangensis* *Abies grandis*	*Picea breweriana*	*Abies lasiocarpa* var. *lasiocarpa*	*Abies amabilis* *Pinus ayacahuite* var. *brachyptera* *Pinus contorta* var. *murrayana* *Pinus lambertiana* *Pinus monticola*	*Abies magnifica* *Picea chihuahuana* *Picea engelmannii* *Picea pungens* *Pinus arizonica* *Pinus discolor* *Pinus flexilis?* *Pinus monophylla* *Pinus muricata* *Pinus ponderosa* var. *ponderosa* var. *scopulorum* *Pinus strobiformis* *Pinus washoensis* *Pseudotsuga menziesii* *Tsuga heterophylla*
A. abietinum f. sp. *magnificae*	*Abies magnifica*				
A. abietis-religiosae	*Abies religiosa* var. *religiosa* var. *emarginata* *Abies vejari*				*Pinus arizonica* *Pinus hartwegii* *Pinus leiophylla* var. *leiophylla* *Pinus montezumae* *Pinus rudis* *Pseudotsuga menziesii*
A. americanum	*Pinus banksiana* *Pinus contorta* var. *contorta?* var. *latifolia* var. *murrayana*	*Pinus ponderosa* var. *scopulorum*	*Pinus albicaulis* *Pinus flexilis* *Pinus jeffreyi* *Pinus ponderosa* var. *ponderosa*	*Picea engelmannii* *Picea glauca* *Picea mariana* *Picea pungens* *Pinus aristata* *Pinus attenuata?* *Pseudotsuga menziesii*	*Abies grandis* *Abies lasiocarpa* var. *lasiocarpa* *Abies magnifica* *Larix occidentalis* *Tsuga mertensiana*
A. apachecum	*Pinus strobiformis*				*Abies concolor* *Abies lasiocarpa* var. *arizonica* *Picea pungens* *Pinus arizonica* *Pinus edulis* *Pinus ponderosa* var. *scopulorum*
A. aureum subsp. *aureum*	*Pinus montezumae* *Pinus oaxacana* *Pinus oocarpa?* *Pinus pseudostrobus*				
A. aureum subsp. *petersonii*	*Pinus michoacana* *Pinus montezumae* *Pinus oaxacana* *Pinus oocarpa* *Pinus patula* *Pinus pseudostrobus*				
A. bicarinatum	*Pinus occidentalis*				

TABLE 6.2 – Susceptibility of hosts for 39 North American taxa of *Arceuthobium* based on natural infection of native trees (continued)

Arceuthobium	Principal hosts	Secondary hosts	Occasional hosts	Rare hosts	Immune taxa
A. blumeri	*Pinus ayacahuite* var. *brachyptera* *Pinus strobiformis* var. *strobiformis* var. *potosiensis*				*Abies concolor* *Abies durangensis* *Abies vejari* *Picea chihuahuana* *Pinus arizonica* *Pinus ponderosa* var. *scopulorum* *Pinus cooperi* *Pinus durangensis* *Pinus leiophylla* var. *leiophylla* *Pseudotsuga menziesii*
A. californicum	*Pinus lambertiana*	*Pinus monticola*			*Abies concolor* *Pinus attenuata* *Pinus coulteri* *Pinus jeffreyi* *Pinus ponderosa* var. *ponderosa*
A. campylopodum	*Pinus jeffreyi* *Pinus ponderosa* var. *ponderosa* var. *scopulorum*	*Pinus attenuata* *Pinus coulteri*	*Pinus contorta* var. *latifolia* var. *murrayana* *Pinus sabiniana*	*Pinus lambertiana*	*Abies concolor* *Abies grandis* *Pinus monophylla* *Pinus monticola* *Pseudotsuga menziesii*
A. cyanocarpum	*Pinus albicaulis* *Pinus aristata* *Pinus flexilis* *Pinus longaeva*	*Pinus monticola* *Tsuga mertensiana*	*Pinus balfouriana* subsp. *balfouriana?*	*Picea engelmannii?* *Pinus contorta* var. *latifolia* *Pinus ponderosa* var. *scopulorum*	*Abies concolor* *Abies lasiocarpa* var. *arizonica* *Abies magnifica* *Pinus edulis* *Pinus lambertiana* *Pinus ponderosa* var. *ponderosa* *Pseudotsuga menziesii*
A. divaricatum	*Pinus californiarum* subsp. *californiarum* subsp. *fallax* *Pinus cembroides* *Pinus discolor* *Pinus edulis* *Pinus monophylla* *Pinus quadrifolia*				*Pinus jeffreyi* *Pinus leiophylla* var. *chihuahuana* *Pinus ponderosa* var. *scopulorum* *Pseudotsuga menziesii*
A. douglasii	*Pseudotsuga menziesii* *var. menziesii* *var. glauca*		*Abies amabilis* *Abies lasiocarpa* *var. arizonica*	*Abies concolor* *Abies grandis* *Abies lasiocarpa* var. *lasiocarpa* *Picea engelmannii* *Picea pungens*	*Abies magnifica* *Abies vejari* *Larix occidentalis* *Pinus arizonica* *Pinus ayacahuite* *Pinus discolor* *Pinus edulis* *Pinus engelmannii* *Pinus flexilis?* *Pinus ponderosa* var. *ponderosa* var. *scopulorum* *Pinus strobiformis* *Tsuga heterophylla*

TABLE 6.2 – Susceptibility of hosts for 39 North American taxa of *Arceuthobium* based on natural infection of native trees (continued)

Arceuthobium	Principal hosts	Secondary hosts	Occasional hosts	Rare hosts	Immune taxa
A. durangense	*Pinus douglasiana* *Pinus durangensis* *Pinus michoacana* *Pinus montezuma* *Pinus pseudostrobus*	*Pinus herrerai*	*Pinus oocarpa?*		*Pinus leiophylla* var. *leiophylla* *Pinus lumholtzii* *Pinus teocote*
A. gillii	*Pinus herrerai* *Pinus leiophylla* var. *leiophylla* var. *chihuahuana* *Pinus lumholtzii*			*Pinus arizonica* var. *arizonica* *Pinus cooperi*	*Pinus cembroides* *Pinus discolor* *Pinus engelmannii* *Pinus ponderosa* var. *scopulorum* *Pinus strobiformis* *Pseudotsuga menziesii*
A. globosum subsp. *globosum*	*Pinus cooperi* *Pinus durangensis* *Pinus engelmannii* *Pinus rudis?*		*Pinus arizonica*	*Pinus teocote*	*Pinus ayacahuite* *Pinus leiophylla* var. *leiophylla*
A. globosum subsp. *grandicaule*	*Pinus douglasiana* *Pinus durangensis* *Pinus hartwegii* *Pinus lawsonii* *Pinus maximinoi* *Pinus michoacana* *Pinus montezumae* *Pinus patula* *Pinus pringlei* *Pinus pseudostrobus* *Pinus rudis* *Pinus teocote*			*Cupressus sp.?*	*Abies guatemalense* *Abies religiosa* *Pinus ayacahuite* *Pinus chiapensis* *Pinus leiophylla* var. *leiophylla*
A. guatemalense	*Pinus ayacahuite* var. *ayacahuite*				*Abies guatemalense* *Pinus pseudostrobus* *Pinus rudis*
A. hawksworthii	*Pinus caribaea* var. *hondurensis* *Pinus oocarpa?*				
A. hondurense	*Pinus maximinoi* *Pinus oocarpa*				
A. laricis	*Larix occidentalis* *Tsuga mertensiana*	*Pinus contorta* var. *latifolia*	*Abies lasiocarpa* var. *lasiocarpa* *Pinus ponderosa* var. *ponderosa*	*Abies grandis* *Picea engelmannii* *Pinus albicaulis* *Pinus monticola*	*Pseudotsuga menziesii* *Tsuga heterophylla*
A. littorum	*Pinus muricata* *Pinus radiata*		*Pinus contorta* var. *bolanderi*		*Abies grandis* *Pseudotsuga menziesii* *Tsuga heterophylla*
A. microcarpum	*Picea engelmannii* *Picea pungens* *Pinus aristata*			*Abies lasiocarpa* var. *arizonica* *Pinus strobiformis*	*Abies concolor* *Abies lasiocarpa* var. *lasiocarpa* *Pinus ponderosa* var. *scopulorum* *Pseudotsuga menziesii*

TABLE 6.2 – Susceptibility of hosts for 39 North American taxa of *Arceuthobium* based on natural infection of native trees (continued)

Arceuthobium	Principal hosts	Secondary hosts	Occasional hosts	Rare hosts	Immune taxa
A. monticola	*Pinus monticola*	*Pinus lambertiana*	*Picea breweriana*	*Pinus jeffreyi*	*Pinus attenuata* *Pinus ponderosa* var. *ponderosa*
A. nigrum	*Pinus lawsonii* *Pinus leiophylla* var. *leiophylla* var. *chihuahuana* *Pinus lumholtzii* *Pinus oaxacana* *Pinus patula* *Pinus teocote*		*Pinus montezumae* *Pinus pseudostrobus*	*Pinus arizonica* var. *arizonica* *Pinus cooperi*	*Pinus ayacahuite* *Pinus durangense* *Pinus engelmannii* *Pinus oocarpa*
A. oaxacanum	*Pinus lawsonii* *Pinus michoacana* *Pinus pseudostrobus*		*Pinus oaxacana*		
A. occidentale	*Pinus sabiniana*	*Pinus attenuata* *Pinus coulteri*	*Pinus jeffreyi* *Pinus ponderosa* var. *ponderosa*		
A. pendens	*Pinus discolor* *Pinus orizabensis*				*Pinus cembroides?*
A. pusillum	*Picea glauca* *Picea mariana* *Picea rubens*		*Larix laricina*	*Abies balsamea* *Pinus banksiana* *Pinus resinosa* *Pinus strobus*	*Pinus rigida?*
A. rubrum	*Pinus cooperi* *Pinus durangensis* *Pinus engelmannii* *Pinus herrerai* *Pinus teocote*				*Pinus ayacahuite*
A. siskiyouense	*Pinus attenuata*			*Pinus contorta* var. *contorta* *Pinus jeffreyi* *Pinus ponderosa* var. *ponderosa*	*Pinus lambertiana* *Pinus monticola*
A. strictum	*Pinus leiophylla* var. *chihuahuana*		*Pinus teocote*	*Pinus engelmannii*	*Pinus cembroides*
A. tsugense subsp. *tsugense*	*Abies amabilis?* *Abies lasiocarpa* var. *lasiocarpa?* *Abies procera?* *Pinus contorta* var. *contorta* *Tsuga heterophylla*		*Abies grandis?* *Pinus contorta* var. *latifolia*	*Picea engelmannii* *Picea sitchensis* *Pinus monticola* *Tsuga mertensiana* *Pseudotsuga menziesii*	*Pinus contorta* var. *murrayana*
A. tsugense subsp. *mertensianae*	*Abies amabilis* *Abies lasiocarpa* var. *lasiocarpa* *Abies procera* *Tsuga mertensiana*	*Pinus albicaulis*	*Pinus monticola*	*Picea breweriana* *Pinus contorta* var. *latifolia* *Tsuga heterophylla* *Abies grandis*	*Abies magnifica* *Pinus contorta* var. *murrayana* *Pseudotsuga menziesii*

TABLE 6.2 – Susceptibility of hosts for 39 North American taxa of *Arceuthobium* based on natural infection of native trees (continued)

Arceuthobium	Principal hosts	Secondary hosts	Occasional hosts	Rare hosts	Immune taxa
A. vaginatum subsp. *vaginatum*	*Pinus arizonica* var. *arizonica* var. *stormiae* *Pinus cooperi* *Pinus durangensis* *Pinus engelmannii* *Pinus hartwegii* *Pinus herrerai* *Pinus lawsonii* *Pinus montezumae* *Pinus patula* *Pinus rudis*	*Pinus teocote*		*Pinus culminicola*	*Abies religiosa* *Abies vejari* *Pinus ayacahuite* *Pinus leiophylla* var. *leiophylla* var. *chihuahuana* *Pinus lumholtzii* *Pinus pseudostrobus?* *Pseudotsuga menziesii*
A. vaginatum subsp. *cryptopodum*	*Pinus arizonica* var. *arizonica* var. *stormiae* *Pinus durangensis* *Pinus engelmannii* *Pinus ponderosa* var. *scopulorum*	*Pinus cooperi*	*Pinus aristata* *Pinus contorta* var. *latifolia*	*Pinus flexilis* *Pinus strobiformis*	*Abies concolor* *Abies lasiocarpa* var. *arizonica* *Picea pungens* *Pinus californiarum* subsp. *fallax* *Pinus cembroides* *Pinus edulis* *Pinus herrerai* *Pinus leiophylla* var. *leiophylla* var. *chihuahuana* *Pseudotsuga menziesii*
A. verticilliflorum	*Pinus arizonica* var. *arizonica* *Pinus cooperi* *Pinus durangensis* *Pinus engelmannii*				*Pinus ayacahuite* *Pinus cembroides* *Pinus leiophylla* var. *leiophylla* var. *chihuahuana* *Pinus teocote*
A. yecorense	*Pinus durangensis* *Pinus herrerai* *Pinus leiophylla* var. *chihuahuana* *Pinus lumholtzii*	*Pinus engelmannii*			*Pinus arizonica*

Note: a question mark indicates that we have not determined the appropriate susceptibility class or that the reported host–parasite combination has not been confirmed.

TABLE 6.3 – Host susceptibility of 85 taxa of North American Pinaceae to natural infection by *Arceuthobium*

Host	*Arceuthobium*	Susceptibility
True firs		
Abies amabilis	*A. abietinum* f. sp. *concoloris*	Rare
	A. douglasii	Occasional
	A. tsugense subsp. *tsugense*	Principal?
	A. tsugense subsp. *mertensianae*	Principal
Abies balsamea	*A. pusillum*	Rare
Abies concolor var. *concolor*	*A. abietinum* f. sp. *concoloris*	Principal
	A. douglasii	Rare
Abies concolor var. *lowiana*	*A. abietinum* f. sp. *concoloris*	Principal
Abies durangensis	*A. abietinum* f. sp. *concoloris*	Principal
Abies grandis	*A. abietinum* f. sp. *concoloris*	Principal
	A. douglasii	Rare
	A. laricis	Rare
	A. tsugense subsp. *tsugense*	Occasional?
	A. tsugense subsp. *mertensianae*	Rare
Abies lasiocarpa var. *lasiocarpa*	*A. abietinum* f. sp. *concoloris*	Occasional
	A. douglasii	Rare
	A. laricis	Occasional
	A. tsugense subsp. *tsugense*	Principal?
	A. tsugense subsp. *mertensianae*	Principal
Abies lasiocarpa var. *arizonica*	*A. douglasii*	Occasional
	A. microcarpum	Rare
Abies magnifica	*A. abietinum* f. sp. *magnificae*	Principal
Abies procera	*A. tsugense* subsp. *tsugense*	Principal?
	A. tsugense subsp. *mertensianae*	Principal
Abies religiosa var. *religiosa*	*A. abietis-religiosae*	Principal
Abies religiosa var. *emarginata*	*A. abietis-religiosae*	Principal
Abies vejari	*A. abietis-religiosae*	Principal
Larches		
Larix laricina	*A. pusillum*	Occasional
Larix occidentalis	*A. laricis*	Principal
	A. tsugense subsp. *tsugense*	Rare
Spruces		
Picea breweriana	*A. abietinum* f. sp. *concoloris*	Secondary
	A. monticola	Occasional
	A. tsugense subsp. *mertensianae*	Rare

TABLE 6.3 – Host susceptibility of 85 taxa of North American Pinaceae to natural infection by *Arceuthobium* (continued)

Host	*Arceuthobium*	Susceptibility
Spruces (continued)		
Picea engelmannii	*A. americanum*	Rare
	A. cyanocarpum	Rare?
	A. douglasii	Rare
	A. laricis	Rare
	A. microcarpum	Principal
	A. tsugense subsp. *tsugense*	Rare
Picea glauca	*A. americanum*	Rare
	A. pusillum	Principal
Picea mariana	*A. americanum*	Rare
	A. pusillum	Principal
Picea pungens	*A. americanum*	Rare
	A. douglasii	Rare
	A. microcarpum	Principal
Picea rubens	*A. pusillum*	Principal
Picea sitchensis	*A. tsugense* subsp. *tsugense*	Rare
Pines — Subgenus *Haploxylon*		
Pinus albicaulis	*A. americanum*	Occasional
	A. cyanocarpum	Principal
	A. laricis	Rare
	A. tsugense subsp. *mertensianae*	Secondary
Pinus aristata	*A. americanum*	Rare
	A. cyanocarpum	Principal
	A. microcarpum	Principal
	A. vaginatum subsp. *cryptopodum*	Occasional
Pinus ayacahuite var. *ayacahuite*	*A. guatemalense*	Principal
Pinus ayacahuite var. *brachyptera*	*A. abietinum* f. sp. *concoloris*	Rare
	A. blumeri	Principal
Pinus balfouriana subsp. *balfouriana*	*A. cyanocarpum*	Occasional?
Pinus californiarum subsp. *californiarum*	*A. divaricatum*	Principal
Pinus californiarum subsp. *fallax*	*A. divaricatum*	Principal
Pinus cembroides	*A. divaricatum*	Principal
Pinus orizabensis	*A. pendens*	Principal
Pinus culminicola	*A. vaginatum* subsp. *vaginatum*	Rare
Pinus discolor	*A. divaricatum*	Principal
	A. pendens	Principal

TABLE 6.3 — Host susceptibility of 85 taxa of North American Pinaceae to natural infection by *Arceuthobium* (continued)

Host	*Arceuthobium*	Susceptibility
Pines — Subgenus *Haploxylon* (continued)		
Pinus edulis	*A. divaricatum*	Principal
Pinus flexilis	*A. americanum*	Occasional
	A. cyanocarpum	Principal
	A. vaginatum subsp. *cryptopodum*	Rare
Pinus lambertiana	*A. abietinum* f. sp. *concoloris*	Rare
	A. californicum	Principal
	A. campylopodum	Rare
	A. monticola	Secondary
Pinus longaeva	*A. cyanocarpum*	Principal
Pinus monophylla	*A. divaricatum*	Principal
Pinus monticola	*A. abietinum* f. sp. *concoloris*	Rare
	A. californicum	Secondary
	A. cyanocarpum	Secondary
	A. laricis	Rare
	A. monticola	Principal
	A. tsugense subsp. *tsugense*	Rare
	A. tsugense subsp. *mertensianae*	Occasional
Pinus quadrifolia	*A. divaricatum*	Principal
Pinus strobiformis var. *strobiformis*	*A. apachecum*	Principal
	A. blumeri	Principal
	A. microcarpum	Rare
	A. vaginatum subsp. *cryptopodum*	Rare
Pinus strobiformis var. *potosiensis*	*A. blumeri*	Principal
Pinus strobus	*A. pusillum*	Rare
Pines — Subgenus *Diploxylon*		
Pinus arizonica var. *arizonica*	*A. gillii*	Rare
	A. globosum subsp. *globosum*	Occasional
	A. nigrum	Rare
	A. vaginatum subsp. *vaginatum*	Principal
	A. vaginatum subsp. *cryptopodum*	Principal
	A. verticilliflorum	Principal
Pinus arizonica var. *stormiae*	*A. vaginatum* subsp. *vaginatum*	Principal
	A. vaginatum subsp. *cryptopodum*	Principal

TABLE 6.3 – Host susceptibility of 85 taxa of North American Pinaceae to natural infection by *Arceuthobium* (continued)

Host	*Arceuthobium*	Susceptibility
Pines — Subgenus *Diploxylon* (continued)		
Pinus attenuata	*A. americanum*	Rare?
	A. campylopodum	Secondary
	A. occidentale	Secondary
	A. siskiyouense	Principal
Pinus banksiana	*A. americanum*	Principal
Pinus caribaea var. *hondurensis*	*A. hawksworthii*	Principal
Pinus contorta var. *contorta*	*A. siskiyouense*	Rare
	A. tsugense subsp. *tsugense*	Principal
Pinus contorta var. *bolanderi*	*A. littorum*	Occasional
Pinus contorta var. *latifolia*	*A. americanum*	Principal
	A. campylopodum	Occasional
	A. cyanocarpum	Rare
	A. laricis	Secondary
	A. tsugense subsp. *tsugense*	Occasional
	A. tsugense subsp. *mertensianae*	Rare
	A. vaginatum subsp. *cryptopodum*	Occasional
Pinus contorta var. *murrayana*	*A. abietinum* f. sp. *concoloris*	Rare
	A. americanum	Principal
	A. campylopodum	Occasional
Pinus cooperi	*A. gillii*	Rare
	A. globosum subsp. *globosum*	Principal
	A. nigrum	Rare
	A. rubrum	Principal
	A. vaginatum subsp. *vaginatum*	Principal
	A. vaginatum subsp. *cryptopodum*	Secondary
	A. verticilliflorum	Principal
Pinus coulteri	*A. campylopodum*	Secondary
	A. occidentale	Secondary
Pinus douglasiana	*A. durangense*	Principal
	A. globosum subsp. *grandicaule*	Principal
Pinus durangensis	*A. abietinum* f. sp. *concoloris*	Principal
	A. durangense	Principal
	A. globosum subsp. *globosum*	Principal
	A. globosum subsp. *grandicaule*	Principal
	A. rubrum	Principal
	A. vaginatum subsp. *vaginatum*	Principal
	A. vaginatum subsp. *cryptopodum*	Principal
	A. verticilliflorum	Principal
	A. yecorense	Principal

TABLE 6.3 — Host susceptibility of 85 taxa of North American Pinaceae to natural infection by *Arceuthobium* (continued)

Host	*Arceuthobium*	Susceptibility
Pines —Subgenus *Diploxylon* (continued)		
Pinus engelmannii	*A. globosum* subsp. *globosum*	Principal
	A. rubrum	Principal
	A. strictum	Rare
	A. vaginatum subsp. *vaginatum*	Principal
	A. vaginatum subsp. *cryptopodum*	Principal
	A. verticilliflorum	Principal
	A. yecorense	Secondary
Pinus hartwegii	*A. globosum* subsp. *grandicaule*	Principal
	A. vaginatum subsp. *vaginatum*	Principal
Pinus herrerai	*A. durangense*	Secondary
	A. gillii	Principal
	A. rubrum	Principal
	A. vaginatum subsp. *vaginatum*	Principal
	A. yecorense	Principal
Pinus jeffreyi	*A. americanum*	Occasional
	A. campylopodum	Principal
	A. monticola	Rare
	A. occidentale	Occasional
	A. siskiyouense	Rare
Pinus lawsonii	*A. globosum* subsp. *grandicaule*	Principal
	A. nigrum	Principal
	A. oaxacanum	Principal
	A. vaginatum subsp. *vaginatum*	Principal
Pinus leiophylla var. *leiophylla*	*A. gillii*	Principal
	A. nigrum	Principal
Pinus leiophylla var. *chihuahuana*	*A. gillii*	Principal
	A. nigrum	Principal
	A. strictum	Principal
	A. yecorense	Principal
Pinus lumholtzii	*A. gillii*	Principal
	A. nigrum	Principal
	A. yecorense	Principal
Pinus maximinoi	*A. globosum* subsp. *grandicaule*	Principal
	A. hondurense	Principal
Pinus michoacana	*A. aureum* subsp. *petersonii*	Principal
	A. durangense	Principal
	A. globosum subsp. *grandicaule*	Principal
	A. oaxacanum	Principal

TABLE 6.3 –Host susceptibility of 85 taxa of North American Pinaceae to natural infection by *Arceuthobium* (continued)

Host	*Arceuthobium*	Susceptibility
Pines—Subgenus *Diploxylon* (continued)		
Pinus montezumae	*A. aureum* subsp. *aureum*	Principal
	A. aureum subsp. *petersonii*	Principal
	A. durangense	Principal
	A. globosum subsp. *grandicaule*	Principal
	A. nigrum	Occasional
Pinus muricata	*A. littorum*	Principal
Pinus oaxacana	*A. aureum* subsp. *aureum*	Principal
	A. aureum subsp. *petersonii*	Principal
	A. nigrum	Principal
	A. oaxacanum	Occasional
Pinus occidentalis	*A. bicarinatum*	Principal
Pinus oocarpa	*A. aureum* subsp. *aureum*	Principal?
	A. aureum subsp. *petersonii*	Principal
	A. durangense	Occasional?
	A. hawksworthii	Principal?
	A. hondurense	Principal
Pinus patula	*A. aureum* subsp. *petersonii*	Principal
	A. globosum subsp. *grandicaule*	Principal
	A. nigrum	Principal
	A. vaginatum subsp. *vaginatum*	Principal
Pinus ponderosa var. *ponderosa*	*A. americanum*	Occasional
	A. campylopodum	Principal
	A. laricis	Occasional
	A. occidentale	Occasional
	A. siskiyouense	Rare
Pinus ponderosa var. *scopulorum*	*A. americanum*	Secondary
	A. campylopodum	Principal
	A. cyanocarpum	Rare
	A. vaginatum subsp. *cryptopodum*	Principal
Pinus pringlei	*A. globosum* subsp. *grandicaule*	Principal
Pinus pseudostrobus	*A. aureum* subsp. *aureum*	Principal
	A. aureum subsp. *petersonii*	Principal
	A. durangense	Principal
	A. globosum subsp. *grandicaule*	Principal
	A. nigrum	Occasional
	A. oaxacanum	Principal

TABLE 6.3 —Host susceptibility of 85 taxa of North American Pinaceae to natural infection by *Arceuthobium* (continued)

Host	*Arceuthobium*	Susceptibility
Pines—Subgenus *Diploxylon* (continued)		
Pinus radiata	*A. littorum*	Principal
Pinus resinosa	*A. pusillum*	Rare
Pinus rudis	*A. globosum* subsp. *globosum*	Principal?
	A. globosum subsp. *grandicaule*	Principal
	A. vaginatum subsp. *vaginatum*	Principal
Pinus sabiniana	*A. campylopodum*	Occasional
	A. occidentale	Principal
Pinus teocote	*A. globosum* subsp. *globosum*	Rare
	A. globosum subsp. *grandicaule*	Principal
	A. nigrum	Principal
	A. rubrum	Principal
	A. strictum	Occasional
	A. vaginatum subsp. *vaginatum*	Secondary
Douglas-fir		
Pseudotsuga menziesii	*A. americanum*	Rare
	A. douglasii	Principal
	A. tsugense subsp. *tsugense*	Rare
Hemlocks		
Tsuga heterophylla	*A. tsugense* subsp. *tsugense*	Principal
	A. tsugense subsp. *mertensianae*	Rare
Tsuga mertensiana	*A. cyanocarpum*	Secondary
	A. laricis	Principal
	A. tsugense subsp. *tsugense*	Rare
	A. tsugense subsp. *mertensianae*	Principal

Note: A question mark indicates that we have not determined the appropriate susceptibility class or that the reported host–parasite combination has not been confirmed.

does not naturally occur is sometimes economically important (table 6.5). For example, Graham and Leaphart (1961) reported that *Pinus sylvestris* cultivated in Washington was so severely parasitized by *Arceuthobium laricis* that they recommended this species should not be planted where *A. laricis* is present.

Nonhosts

Because dwarf mistletoes parasitize so many western conifer species, it is of interest to know which are not hosts. We list here the few members of the Pinaceae from the western United States and Mexico that have not been found to be naturally infected by *Arceuthobium*. Some of these species, however, could be hosts because many *Arceuthobium* collections from Mexico do not identify the host species. Of the 14 species of pine listed below, 6 are pinyons (indicated by asterisks).

True firs

- *Abies guatemalensis*
- *Abies hickelii*
- *Abies mexicana*
- *Abies oaxacana*

Spruces

- *Picea chihuahuana*
- *Picea martinezii*
- *Picea mexicana*

Pines

- *Pinus balfouriana* subsp. *austrina*
- *Pinus chiapensis*
- *Pinus greggii*
- *Pinus jaliscana*
- *Pinus johannis**
- *Pinus lagunae*
- *Pinus maximartinezii**
- *Pinus nelsonii**
- *Pinus pinceana**
- *Pinus praetermissa*
- *Pinus remota**
- *Pinus rzedowskii**
- *Pinus torreyana*
- *Pinus washoensis*

Douglas-fir

- *Pseudotsuga macrocarpa*

Host–Parasite Relationships

An interesting feature of parasitism by *Arceuthobium* is the existence of a kind of "competitive host exclusion" between different mistletoe species (Hawksworth 1969). If a species of *Arceuthobium* that typically infests a certain host species is present in an area, then other dwarf mistletoe species only rarely infest that host species; if the principal parasite of that host species is not present, however, then another dwarf mistletoe species present in the area is likely to infest the host species. Several examples of host exclusion are found in the Colorado Front Range, where *Pinus contorta* is typically the principal host of *A. americanum* and *P. ponderosa* is typically the principal host of *A. vaginatum* subsp. *cryptopodum*. Infection of *P. ponderosa* trees by *A. americanum* was only 13% in stands where both mistletoe species were present, but 64% in stands where *A. vaginatum* subsp. *cryptopodum* was absent (Hawksworth 1969). The converse situation also occurs with respect to infection of *P. contorta* trees by *A. vaginatum* subsp. *cryptopodum* and *A. americanum* (Hawksworth 1969). Other examples involve the combination of *A. americanum* (principal host *P. contorta*) with *A. cyanocarpum* (principal host *P. flexilis*) in Colorado (Hawksworth and Wiens 1972) and *A. occidentale* (principal host *P. sabiniana*) with *A. campylopodum* (principal hosts *P. ponderosa* and *P. jeffreyi*) in California. Wiens (1961) also noted such competitive host exclusion in mistletoes of the genus *Phoradendron* parasitizing junipers near Sedona, Arizona (*P. juniperinum* and *P. densum*). The mechanism that controls this phenomenon constitutes a fascinating subject for additional research.

If a host is rarely parasitized by a species of *Arceuthobium*, parasitism is often an "all or nothing" phenomenon: that is, most trees of a rare host species are immune, but trees that are infected tend to be heavily infected. For example, *Picea engelmannii* is a rare host (<1% of trees infected) of *A. americanum*, but those trees that are parasitized typically bear hundreds of infections (Hawksworth and Graham 1963).

Some species that are exceedingly rare appear to have little resistance to dwarf mistletoe infection. For example, *Pinus culminicola* has one of the most restricted distributions of all pinyons, yet it is readily parasitized by *Arceuthobium vaginatum* subsp. *vaginatum* on Cerro Potosí, Mexico. Also, *Picea breweriana* is often heavily infested by *A. abietinum* f. sp. *concoloris*, *A. monticola*, and *A. tsugense* subsp. *mertensianae* where the host occurs with these dwarf mistletoes. No dwarf mistletoe occurs within the limited distribution of *Pinus torreyana*, but Kuijt (1960a)

TABLE 6.4 –Extension of *Arceuthobium* host range for 27 Pinaceae taxa based on reports of successful artificial inoculation

Host	*Arceuthobium*	Reference
True firs		
Abies amabilis	*A. laricis*	Smith and Wass 1972b
	A. tsugense subsp. *tsugense* (shore pine race)	Smith 1974
Abies concolor	*A. campylopodum*	Weir 1918a
Abies grandis	*A. campylopodum*	Weir 1918a
	A. tsugense subsp. *tsugense* (shore pine race)	Smith 1974
Larches		
Larix decidua	*A. laricis*	Weir 1918a
Larix kaempferi	*A. laricis*	Weir 1918a
Larix occidentalis	*A. campylopodum*	Weir 1918a
	A. tsugense subsp. *tsugense* (shore pine and western hemlock races)	Smith 1970a
Spruces		
Picea abies	*A. campylopodum*	Weir 1918a
	A. laricis	Hawksworth and Wiens 1972
	A. tsugense subsp. *tsugense* (western hemlock race)	Smith 1965
Picea glauca	*A. laricis*	Smith 1974
	A. tsugense subsp. *tsugense* (western hemlock race)	Smith 1965
	A. tsugense subsp. *tsugense* (shore pine race)	Smith 1974
Picea engelmannii	*A. tsugense* subsp. *tsugense* (shore pine and western hemlock races)	Smith 1970b
Pines		
Pinus banksiana	*A. laricis*	Graham 1959a
	A. occidentale	Hedgcock and Hunt 1917
Pinus bungeana	*A. occidentale*	Hedgcock and Hunt 1917
Pinus caribaea	*A. occidentale*	Hedgcock and Hunt 1917
Pinus contorta var. *latifolia*	*A. tsugense* subsp. *tsugense* (shore pine and western hemlock races)	Smith 1974

TABLE 6.4 –Extension of *Arceuthobium* host range for 27 Pinaceae taxa based on reports of successful artificial inoculation (continued)

Host	*Arceuthobium*	Reference
Pines (continued)		
Pinus flexilis	*A. apachecum*	Mathiasen 1978
	A. blumeri	Mathiasen 1978
	A. microcarpum	Mathiasen 1978
Pinus mugo	*A. americanum*	Weir 1918a
	A. campylopodum	Weir 1918a
Pinus palustris	*A. occidentale*	Hedgcock and Hunt 1917
Pinus pinea	*A. occidentale*	Hedgcock and Hunt 1917
Pinus ponderosa	*A. laricis*	Smith 1974
	A. tsugense subsp. *tsugense* (shore pine and western hemlock races)	Smith and Craig 1968
Pinus radiata	*A. occidentale*	Scharpf 1969a
	A. tsugense subsp. *tsugense* (western hemlock race)	Smith and Craig 1968
Pinus resinosa	*A. campylopodum*	Weir 1918a
	A. laricis	Hawksworth and Wiens 1972
Pinus strobiformis	*A. cyanocarpum*	Hawksworth and Wiens 1972
Pinus strobus	*A. cyanocarpum*	Hawksworth and Wiens 1972
Pinus sylvestris	*A. campylopodum*	Weir 1918a
	A. laricis	Graham and Leaphart 1961
	A. tsugense subsp. *tsugense* (western hemlock race)	Smith and Craig 1968
Pinus torreyana	*A. occidentale*	Kuijt 1960a
Pinus virginiana	*A. occidentale*	Hedgcock and Hunt 1917
Douglas-fir		
Pseudotsuga menziesii	*A. tsugense* subsp. *tsugense* (shore pine and western hemlock races)	Smith and Wass 1972a
Hemlocks		
Tsuga canadensis	*A. tsugense* subsp. *tsugense* (western hemlock race)	Weir 1918a

TABLE 6.5 —Natural infection by *Arceuthobium* on extra-limital hosts

Host	*Arceuthobium*	Location	Reference
Cypress			
Cupressus arizonica	*A. oxycedri*	Spain	Rios Insua 1984b
	A. oxycedri	Russia	Isikov and Zakharenko 1988
Cupressus lusitanica	*A. oxycedri*	Russia	Isikov and Zakharenko 1988
Cupressus macrocarpa	*A. oxycedri*	Russia	Zefirov 1955, Isikov and Zakharenko 1988
Cupressus macnabiana	*A. oxycedri*	Russia	Isikov and Zakharenko 1988
Juniper			
Juniperus virginiana	*A. oxycedri*	Russia	Isikov and Zakharenko 1988
Larch			
Larix decidua	*A. tsugense* subsp. *tsugense* (western hemlock race)	BC, Canada	Kuijt 1964
Spruce			
Picea abies	*A. campylopodum*	WA	K. Russell (first report)
	A. laricis	ID	Hawksworth and Wiens 1972
Picea pungens	*A. pusillum*	MA	USDA 1960
	A. pusillum	Canada	Davis and Myren 1990
Pine			
Pinus banksiana	*A. laricis*	ID	Graham 1960
Pinus halepensis	*A. campylopodum*	CA	Scharpf and Hawksworth 1986
	A. occidentale	CA	Scharpf and Hawksworth 1986
Pinus pinaster	*A. campylopodum*	CA	Kuijt 1960b
	A. occidentale	CA	Scharpf and Hawksworth 1986
Pinus pinea	*A. occidentale*	CA	Scharpf and Hawksworth 1986
Pinus radiata	*A. occidentale*	CA	Hawksworth and Wiens 1972
Pinus resinosa	*A. laricis*	ID	Hawksworth and Wiens 1972
Pinus sylvestris	*A. americanum*	AB, Canada	Powell 1968
	A. americanum	WA	Graham and Leaphart 1961
	A. campylopodum	ID	Hawksworth and Wiens 1972
	A. laricis	WA	Graham and Leaphart 1961
	A. occidentale	CA	Scharpf and McCain 1988
	A. vaginatum subsp. *cryptopodum*	CO	Hawksworth and Laut 1981
	A. vaginatum subsp. *cryptopodum*	AZ	R. Celaya (personal communication 1992)
Pinus thunbergii	*A. occidentale*	CA	Scharpf and Hawksworth 1986
Platycladus			
Platycladus orientalis	*A. oxycedri*	Russia	Isikov and Zakharenko 1988

inoculated a tree of this species with *A. occidentale* and found it to be susceptible.

A number of inoculation experiments have shown that various species are not compatible hosts for particular dwarf mistletoes (table 6.6). Features of the dwarf mistletoe that often indicate host–parasite incompatibility are reduced (sometimes complete lack of) shoot development and unusually large swellings at the point of infection.

Host Reactions to Dwarf Mistletoe Infection

The first external symptom of dwarf mistletoe infection is usually a swelling of the host tissues. As an infection develops, swelling enlarges and eventually becomes fusiform. Typically, dwarf mistletoe infection leads to the production of the profusely branched, dense masses of distorted host branches called "witches' brooms." Two basic types of witches' brooms are formed (Kuijt 1960b, Hawksworth 1961a):

- **Systemic or isophasic** (fig. 6.3)—Growth of the endophytic system keeps pace with apical and cambial growth of the infected branch, and the dwarf mistletoe shoots are scattered along the host branch or concentrated at branch girdles.
- **Non-systemic or anisophasic** (fig. 6.4)—Shoots of the dwarf mistletoe remain localized near the original site of infection, and the endophytic system only keeps pace only with cambial growth.

Figure 6.3 –Arceuthobium pusillum on *Picea glauca;* note typical systemic (isophasic) infection: lack of host swelling and presence of sequentially more mature mistetoe shoots on older portion of host branch.

In general, the type of witches' broom formation is characteristic of the parasite species rather than the host species; therefore broom type is an important taxonomic character in *Arceuthobium.* Although a dwarf mistletoe species that typically forms non-systemic brooms will rarely induce formation of a systemic broom, there is never any question regarding the basic type of witches' broom produced.

Systemic witches' brooms are consistently formed by *Arceuthobium americanum, A. douglasii, A. guatemalense, A. minutissimum,* and *A. pusillum,* and apparently by the Asian species *A. chinense, A. sichuanense,* and *A. pini* (Hawksworth and Wiens

TABLE 6.6 –Incompatible relationships of *Arceuthobium* with potential hosts

Arceuthobium	Potential host	Reference
A. abietinum f. sp. *concoloris*	*Pinus ayacahuite*	First report
	Pinus contorta	Hawksworth and Wiens 1972
	Pinus lambertiana	Hawksworth and Wiens 1972
A. americanum	*Pinus albicaulis*	Weir 1918b
	Picea pungens	Hawksworth and Wiens 1972
	Pseudotsuga menziesii	Hawksworth and Wiens 1972
A. pusillum	*Larix laricina*	Tainter and French 1967
A. tsugense subsp. *tsugense*	*Larix decidua*	Kuijt 1964
	Larix occidentalis	Hawksworth and Wiens 1972
	Picea engelmannii	Hawksworth and Wiens 1972
	Picea sitchensis	Laurent 1966
A. vaginatum subsp. *cryptopodum*	*Pinus flexilis*	First report

Figure 6.4 –Arceuthobium vaginatum subsp. *crytopodum* on *Pinus ponderosa;* note typical local (anisophasic) infection: tight clustering of mistletoe shoots on a swollen branch.

Figure 6.5 –Arceuthobium aureum subsp. *aureum* on *Pinus pseudostrobus;* note the presence of local infections but lack of broom formation. (C. G. Shaw III)

1972, Kiu 1984b). Non-systemic witches' brooms are much more common among trees parasitized by North American dwarf mistletoes. At the type locality of *A. pendens,* only staminate plants appeared to produce systemic infections; this particular form of sexual dimorphism deserves further study.

A few dwarf mistletoe taxa do not induce witches' broom formation in their hosts—*Arceuthobium aureum* subsp. *aureum* (fig. 6.5) and *A. globosum* subsp. *globosum.* Although *A. occidentale* does not induce typical broom formation, it does promote some "broom-like" development in *Pinus sabiniana* (R. F. Scharpf, personal communication).

Arceuthobium americanum produces shoots only at the girdles and not on segments of *Pinus contorta* branches more than 5 years old (Kuijt 1960b). Similarly, our limited observations of systemic infections of *A. abietis-religiosae* on *Abies religiosa* suggest that here, also, the dwarf mistletoe shoots are produced only at girdles.

Within a particular host genus, the types of witches' broom formed by a dwarf mistletoe species are generally similar (Weir 1916c, Hawksworth 1956a, Kuijt 1960b). For example, the witches' brooms formed by *Arceuthobium americanum* on all pines are similar, but brooms on spruces are distinctly different from those on pines (Hawksworth and Graham 1963, Kuijt 1960b).

Although systemically infected branches are usually immune to additional infection, Muir (1968) reported several secondary infections of *Arceuthobium americanum* on a witches' broom of *Pinus banksiana.* In Oregon, R. Tinnin (personal communication) has also observed secondary infections on witches' brooms of *P. contorta* induced by *A. americanum.* Secondary infections are detectable by location of shoots, differences in shoot color, differences in sex, and the formation of swellings. We have also rarely observed secondary infections in the following parasite–host combinations:

- *Arceuthobium americanum* on *Pinus contorta* in Colorado.
- *Arceuthobium douglasii* on *Pseudotsuga menziesii* in Oregon.
- *Arceuthobium guatemalense* on *Pinus ayacahuite* in Guatemala.
- *Arceuthobium vaginatum* subsp. *cryptopodum* on *Pinus ponderosa* in Arizona.
- *Arceuthobium tsugense* on *Tsuga heterophylla* in Alaska (C. Shaw, personal communication)

Kuijt (1960b) reported that cones usually are not produced on witches' brooms, particularly on systemic brooms. We have frequently observed cone formation on witches' brooms of *Pseudotsuga menziesii* caused by *Arceuthobium douglasii,* however. Cones were about half normal size, and apparently contained viable seeds. Bonga (1964) noted fertile cones on an aberrant witches' broom in *Picea mariana* caused by *A. pusillum.* Schaffer and others (1983) observed cones on several systemic witches' brooms on *Pinus contorta* induced by *A. americanum,* but all the cones were sterile.

CHAPTER 7

Ecological Relationships

Stand history is the most significant factor affecting the distribution of populations of *Arceuthobium.* Stand disturbances such as fire (Alexander and Hawksworth 1975), volcanic activity (Hawksworth 1960a), long-term climatic change, and silvicultural practice can profoundly affect dwarf mistletoe distribution. Long-term climatic change has eliminated dwarf mistletoe species from some areas. For example, *Arceuthobium divaricatum* occurred in the Chisos Mountains, Texas, during the Pleistocene Epoch (Van Devender and Hawksworth 1986), but the nearest modern populations are now about 200 km north in the Davis Mountains. Climatic warming in the southwestern United States over the last few thousand years has greatly fragmented the surviving populations of various dwarf mistletoes. Some populations of *A. vaginatum* subsp. *cryptopodum* that were apparently once contiguous are now separated by distances as large as 80 km (Hawksworth 1969). In addition to these long-term changes, climatic, topographic, and site factors also influence the current distribution of dwarf mistletoe populations. Weir 1916(d) commented that "these parasites follow very distinct predilections as to type of stand, topography, and to a certain extent, climate, from which the zones of greatest mistletoe infection may be quite readily determined."

Climatic Factors

Quantitative effects of climate on the distribution of dwarf mistletoe species are little studied. Climatic factors, however, are probably responsible for the limited distributions of several species that do not occur throughout the range of their host.

Working in British Columbia, Smith and Wass (1979) inoculated the principal hosts of *Arceuthobium americanum* and *A. douglasii* at sites beyond the natural range of these species. Their results indicated that minimum temperature was probably the factor limiting mistletoe distribution. Temperatures less than −39°C were lethal to *A. americanum,* and temperatures less than −29°C were lethal to *A. douglasii.* Correspondingly, the latitudinal distribution of *A. americanum* is greater than *A. douglasii* (see chapter 16 for additional information).

The northern limits of *Arceuthobium vaginatum* subsp. *cryptopodum* are in northern Colorado, but its host, *Pinus ponderosa* var. *scopulorum,* extends more than 700 km farther north to central Montana. The northern limit of distribution for this mistletoe species is likely related to climatic factors. Inoculation tests of *P. ponderosa* seedlings from the Black Hills of South Dakota (350 km north of present mistletoe distribution) showed that these seedlings are as susceptible to infection as those from within the present distribution of the parasite (Hawksworth 1963). Mark and Hawksworth (unpublished data) compared temperatures for 93 weather stations at sites in *P. ponderosa* forests that were either within or outside the range of *A. vaginatum* subsp. *cryptopodum.* The mistletoe was absent at all sites where mean January temperature was less than 6°C.

Arceuthobium douglasii is distributed throughout most of the range of *Pseudotsuga menziesii,* with the following notable exceptions: (1) the mistletoe is absent from the northeastern range of the host species in Colorado, Wyoming, and Montana; (2) it generally does not occur west of the Cascade Crest in British Columbia, Washington, and Oregon; and (3) its northern limits in British Columbia are about 500 km south of the northern distribution of its host.

The absence of *Arceuthobium douglasii* in western Oregon and Washington has been the topic of several studies. Wicker (1969) successfully inoculated native *Pseudotsuga menziesii* with *A. douglasii* at Diamond Point and Wind River in western Washington. Wicker (1974b) suggested that physiographic processes, forest succession, and fire have prevented the immigration and establishment of this mistletoe in western Washington. Tinnin and Knutson (1973) found *A. douglasii* at 7 sites west of the Cascade Crest (Clackamas, Linn, and Lane Counties in northern Oregon), but these sites were all within 15 km of the Crest. Tinnin and others (1976) and Tinnin (1978) later reported 2 additional sites with *A. douglasii* in the same general area. They agreed with Wicker (1974b) that fire and other natural disturbances probably account for the species' limited distribution on the western slope of the Cascades. The Columbia River Gorge, with its continuous stands of *P. menziesii* through the Cascades, would seem to provide a natural corridor for the migration of *A. douglasii.* The mistletoe, however, does not occur in these low-elevation stands (<700 m), which may lie below the lower elevational limit of the parasite.

Topographic Factors

The most detailed information on distribution of dwarf mistletoe populations in relation to elevation, topographic position, steepness of slope, and aspect is based on research in Arizona and New Mexico.

Elevation

Hawksworth (1959a) surveyed *Arceuthobium vaginatum* subsp. *cryptopodum* on the Mescalero Apache Indian Reservation in southern New Mexico and collected information for 2,464 plots distributed over 560,000 ha. In that forest, the distribution of dwarf mistletoe was strongly related to elevation (fig. 7.1) and was most abundant within the mid-elevational range of *Pinus ponderosa* (2,350 to 2,400 m). In a broader survey of forests throughout Arizona and New Mexico, Andrews and Daniels (1960) concurred that mistletoe abundance was greater above 2,010 m (table 7.1). Gottfried and Embry (1977) studied mistletoe distribution in a high-elevation, mixed conifer watershed in eastern Arizona. They found that the incidence of mistletoe (percentage of host trees infected) was highest (79%) at elevations below 2,650 m, moderate (45%) within 2,650 to 2,750 m, and least (30%) at elevations above 2,750 m. Studies in southern New Mexico (Hawksworth 1961a) and along the Front Range in Colorado (Williams and others 1972) show that dwarf mistletoe is found to the upper limits of *P. ponderosa* but not to the lowest limits. In northern Colorado, the approximate upper limits of both the host and mistletoe are 2,800 m, but pine populations are found as low as 1,600 m, and mistletoe populations descend to 1,900 m. The absence of the mistletoe at the low elevations may be due to high summer temperatures (Williams and others 1972), moisture stress (Fisher 1975), or both these factors.

On the Mescalero Apache Indian Reservation, *Arceuthobium douglasii* was distributed about equally throughout the elevational range (2,315 to 2,530 m) of

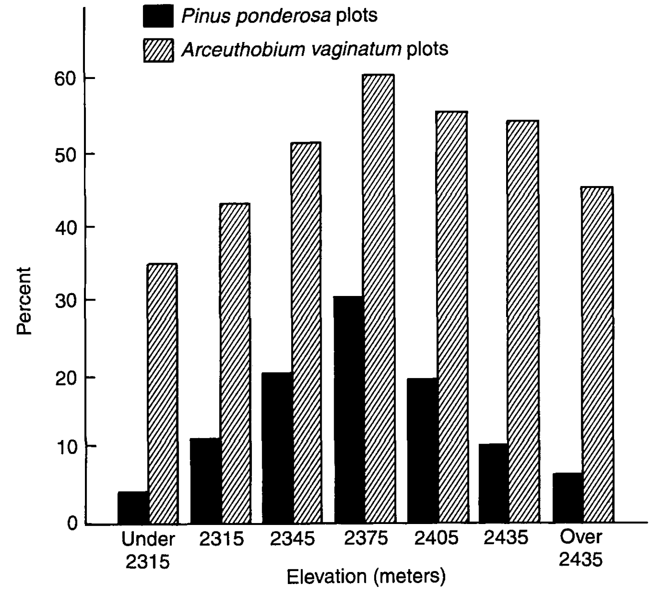

Figure 7.1–Relationship between elevation and abundance of *Arceuthobium vaginatum* subsp. *cryptopodum* and *Pinus ponderosa* on the Mescalero Apache Indian Reservation, New Mexico; based on 2,146 plots. (from Hawksworth 1959a).

TABLE 7.1 –Distribution by elevation of *Pinus ponderosa* and *Arceuthobium vaginatum* subsp. *cryptopodum* in Arizona and New Mexico

Elevation (meters)	Percent of plots in pine type	Percent of plots infested with dwarf mistletoe
1,400–1,700	6	17
1,700–2,000	12	17
2,000–2,300	28	36
2,300–2,600	46	41
over 2,600	8	50
Totals	100	36

Note: Percentages based on 2,164 plots (Andrews and Daniels 1960).

its host, *Pseudotsuga menziesii* (Hawksworth 1959a). Gottfried and Embry (1977) found a similar relationship in their high-elevation watershed (2,560 to 2,835 m). Throughout the southwestern United States, *A. douglasii* has an upper elevational limit at least 60 m below that of its host (unpublished data). In the Capitan Mountains, New Mexico the upper limit of the mistletoe is about 2,750 m, approximately 300 m below the upper limits of its host. In the Magdalena Mountains, New Mexico the upper limits for parasite and host are 2,900 m and 3,600 m, respectively.

Acciavatti and Weiss (1974) reported on the distribution of *Arceuthobium microcarpum* for the Fort Apache Indian Reservation, Arizona. Although *Picea engelmannii* was found at elevations from 2,750 m to over 3,350 m, *A. microcarpum* occurred only as high as 3,170 m and was abundant only below 2,900 m. On the San Francisco Peaks in central Arizona, the dwarf mistletoe's upper elevation limit is 3,140 m—even though the host reaches an elevation of 3,600 m (Mathiasen and Hawksworth 1980).

In the central Rocky Mountains, the upper elevational limit of *Arceuthobium americanum* is at least 185 m below that of its principal host, *Pinus contorta* (Hawksworth 1956b, Hawksworth and Johnson 1989a, Williams and others 1972). The elevation of this upper limit for mistletoe varies with latitude, and it ranges from 2,800 m in northern Wyoming to 3,350 m in central Colorado (fig. 7.2). The factors controlling for this limit are not known, but some information is available from an unpublished study conducted by Hawksworth and Laut in northern Colorado. They transplanted mistletoe-infected seedlings to a site about 120 m above the natural limits of the parasite. The mistletoe has survived for at least 20 years. Each year, the plants flowered, were pollinated, and initiated fruit development, but fruits failed to mature before the first killing frosts of autumn. A similar phenomenon may limit the northern distribution of *A. douglasii* (Smith 1972).

Arceuthobium tsugense has an upper distributional limit well below the upper limits of its host (*Tsuga heterophylla*) in southeast Alaska (Drummond and Hawksworth 1979). Although the host attains elevations in excess of 610 m, the dwarf mistletoe occurs to only 365 m and is rare above 150 m.

Observations along the Granite Cairn road and the Brunton trail northeast of Augustine, Belize, indicate a lower elevational limit of *Arceuthobium hawksworthii* on *Pinus caribaea* var. *hondurensis* near 700 m, but earlier collections place it as low as 520 m. Regardless of its actual lower altitudinal limit, *A. hawksworthii* is clearly absent from the lower elevational range of *P. caribaea* var. *hondurensis* in the Mountain Pine Ridge region! Given the tropical distribution of this dwarf mistletoe (latitude 17°N), its absence from the lower 300 m of the elevational distribution of *A. caribaea* var. *hondurensis* is an interesting ecological question.

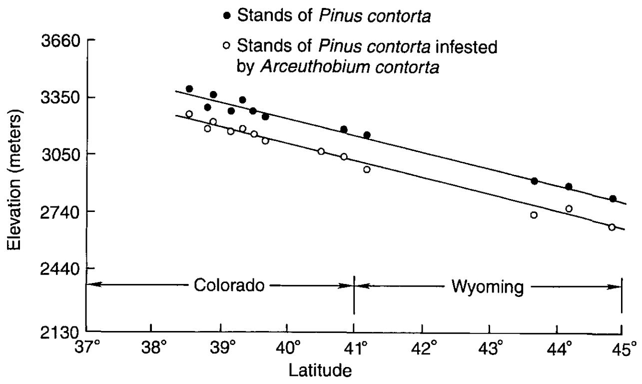

Figure 7.2–Upper elevation limits of *Arceuthobium americanum* and stands dominated by *Pinus contorta* in the central Rocky Mountains (from Hawksworth 1956b)

Topographic Position

Topographic position may affect the distribution of some dwarf mistletoe species. For example, several studies show that *Arceuthobium vaginatum* subsp. *cryptopodum* on *Pinus ponderosa* is most abundant on ridge tops, intermediate on slopes, and least common on bottom sites (table 7.2). Various other studies have also recorded high abundances of dwarf mistletoe species on ridge sites—*A. americanum* on *P. contorta* in the central Rocky Mountains (Hawksworth 1958), *A. americanum* on *P. banksiana* in Alberta (Dowding 1929), and *A. oxycedri* on *Juniperus* in Pakistan (Zakaullah 1977). An exception is *A. douglasii* on *Pseudotsuga menziesii* in New Mexico, which only showed weak correlation with topographic position (Hawksworth 1959a).

Some studies suggest that dwarf mistletoes are more abundant on middle slopes than on upper or lower slopes—*Arceuthobium douglasii* on *Pseudotsuga menziesii* and *A. vaginatum* subsp. *cryptopodum* on *Pinus ponderosa* in Arizona (Gottfried and Embry 1977). Other studies, however, report greater abundance on upper slopes for *A. vaginatum* subsp. *cryptopodum* on *P. ponderosa* in Colorado (Merrill and others 1987) and Arizona (Larson and others 1970). Obviously, the relationship of dwarf mistletoe distribution to topographic position is variable and requires further study.

TABLE 7.2 –Distribution by topographic position of *Pinus ponderosa* plots infested with *Arceuthobium vaginatum* subsp. *cryptopodum*

Percent of plots infested				
Ridge	Slope	Bottom	Location	Reference
67	53	37	Mescalero Apache Indian Reservation	Hawksworth 1959a
57	36	16	Arizona and New Mexico	Andrews and Daniels 1960
42	33	0	Colorado	Merrill and others 1987

Note: 2,464 plots were examined on Mescalero Apache Indian Reservation, 2,164 plots in Arizona and New Mexico survey, and 547 plots on Colorado survey.

Steepness of Slope

The incidence of dwarf mistletoe varies with respect to slope angle, categorized as gentle for slopes <10%, moderate for slopes 10 to 30%, and steep for slopes >30%. Hawksworth (1959a) found that incidence of *Arceuthobium vaginatum* subsp. *cryptopodum* on *Pinus ponderosa* in southern New Mexico was greater (57%) on gentle slopes than on steep slopes (45%). Incidence of *A. douglasii* on *Pseudotsuga menziesii* in the same area showed a similar but lower trend of 27% on gentle slopes and 3% on steep slopes. In a survey of *A. vaginatum* subsp. *cryptopodum* on *Pinus ponderosa* conducted throughout Arizona and New Mexico, Andrews and Daniels 1960 found that differences in mistletoe incidence were not statistically significant between moderate and steep slopes but were significantly different between gentle slopes and either moderate or steep slopes. In central Colorado, Hawksworth (1968b) observed a strong negative correlation between slope and incidence of *A. vaginatum* subsp. *cryptopodum*—gentle slopes, 87%; moderate slopes, 51%; and steep slopes, 34%. In contrast, Gottfried and Embry (1977) observed a positive correlation between slope and incidence on their high-elevation watershed—gentle slopes, 1%; moderate slopes, 25%; and steep slopes, 69%. In the same study area, the highest incidence of *A. douglasii* occurred on moderate slopes. Larson and others (1970) reported no correlation between slope and incidence of *A. vaginatum* subsp. *cryptopodum* near Flagstaff, Arizona. Working on the Pringle Falls Experimental Forest in central Oregon, Roth (1954) found the incidence of *A. campylopodum* on *P. ponderosa* was positively correlated with slope angle.

Aspect

Hawksworth (1959a) observed that *Arceuthobium vaginatum* subsp. *cryptopodum* on *Pinus ponderosa* in southern New Mexico was more abundant on west and southwest slopes and was less abundant on north and northeast slopes, but *A. douglasii* was most abundant on north aspects. Gottfried and Embry (1977), in contrast, reported that *A. vaginatum* subsp. *cryptopodum* was more abundant on east and south slopes and that *A. douglasii* was more abundant on south aspects. As with other site factors, the relation between aspect and mistletoe incidence is not definitive.

Soil Types

The effect of soil type on dwarf mistletoe abundance is poorly understood, and most available information is only anecdotal. Douglas (1914) in the journals of his 1826 expedition through eastern Washington, noted that dwarf mistletoe (presumably *Arceuthobium americanum* on *Pinus contorta*) was most common on dry, sandy soils. Loret (1859) observed that *A. oxycedri* in southern France was confined to *Juniperus* growing on sterile clay soils. Korstian (1924b) reported that *A. campylopodum* on *P. ponderosa* in the Payette National Forest, Idaho, was most abundant on basaltic soils.

Several quantitative studies involving soils and dwarf mistletoe distribution have been conducted for *Arceuthobium vaginatum* subsp. *cryptopodum* on *Pinus ponderosa*. On the Manitou Experimental Forest in central Colorado, Hawksworth (1968a) evaluated mistletoe abundance on 3 soil types: sandstone, granitic, and arkose. Although there were differences in mistletoe incidence by soil type, soil effects were confounded with steepness of slope—mistletoe was more abundant (59%) on sites with gentle slopes and arkose soils than on sites with steep slopes and granitic soils (32%). On the Beaver Creek Watershed south of Flagstaff, Arizona, Larson and others (1970) found mistletoe on 19% of plots in the Siesta–Sponseller soils group (derived from volcanic cinders and basalt) and 12% of plots in the less fertile Brolliar soils group (derived from basalt alone).

Habitat Types

Classification of potential vegetation by habitat types based on climax overstory and understory species is commonly used throughout the western United States (Daubenmire and Daubenmire 1968). The relationships between dwarf mistletoes and habitat types in western forests were summarized by Mathiasen and Blake (1984).

Most of the literature on dwarf mistletoe–habitat relationships is observational; few quantitative studies are available. One of the earliest reports was by Dowding (1929); she commented that *Arceuthobium americanum* on *Pinus banksiana* in Alberta was more common in the dry "pine-moss" habitat than in the mesic "pine-heath" habitats. The first detailed report of a relationship between dwarf mistletoe occurrence and habitat type was by Daubenmire (1961) for *A. campylopodum* on *P. ponderosa* in eastern Washington and northern Idaho. He recognized 7 habitat types in the *P. ponderosa* series but found dwarf mistletoe only in the driest types—*P. ponderosa / Agropyron spicatum* and *P. ponderosa / Purshia tridentata.* Later, Daubenmire and Daubenmire (1968) reported 2 other dry habitat types were also infested—*Pinus ponderosa / Festuca idahoensis* and *P. ponderosa / Stipa comata.*

Roe and Amman (1970) studied *Arceuthobium americanum* on *Pinus contorta* in southeastern Idaho and western Wyoming. They reported the parasite was most abundant in the *Abies lasiocarpa / Vaccinium scoparium* habitat type, intermediate in the *A. lasiocarpa / Pachystima myrsinites* habitat type, and least common in the *Pseudotsuga menziesii / Calamagrostis rubescens* habitat type.

Merrill and others (1987) studied abundance of *Arceuthobium vaginatum* subsp. *cryptopodum* on 3 national forests in Colorado and 8 habitat types in the *Pinus ponderosa* series. The greatest incidence and severity of dwarf mistletoe was found in the dry *P. ponderosa / Muhlenbergia montana* habitat type, and the lowest was on the more mesic *P. ponderosa / Quercus gambelii* habitat type in southwestern Colorado.

Mathiasen and Blake (1984) studied the effects of *Arceuthobium douglasii* on growth of *Pseudotsuga menziesii* in mixed conifer habitat types of Arizona and New Mexico. Dwarf mistletoe and its host occurred on 13 habitat types, and impacts on growth varied by habitat type. For example, reduction in 10-year radial increment for severely infested trees ranged from 20% in the *Abies concolor–P. menziesii / Quercus gambelii* habitat type to 75% in *A. concolor–P. menziesii / Berberis repens* habitat type.

Site Quality Factors

The relationship between site quality for host growth and dwarf mistletoe abundance is complex and has long been debated (Hawksworth 1969). Some mistletoe species are more abundant on poorer sites, whereas others show little relation to site quality (Parmeter 1978). Although the incidence of a particular dwarf mistletoe species in a stand may not be related to site quality, the effects of parasite on the growth and mortality of the host are strongly related to site quality (Hawksworth and Johnson 1989a, van der Kamp 1987). There is, however, a tendency to underestimate the importance of site quality as a factor influencing the abundance of dwarf mistletoes because of poor host growth and low tree densities typical of infested stands (Hawksworth 1961a, Childs and Wilcox 1966).

Korstian and Long (1922) suggested that *Arceuthobium vaginatum* subsp. *cryptopodum* is more abundant on "poorer" sites in the Southwest, but a region-wide survey by Andrews and Daniels (1960) found greater incidence on "better" sites. In a detailed inventory of the Beaver Creek Watershed with 1,412 plots, Larson and others (1970) observed the highest incidence on sites of intermediate quality (measured by potential dominant tree height, Meyer 1961):

Site class	Site index, (m at age 100)	Percent of trees infected
I	>22	5
II	17–22	28
III	<17	14

Merrill and others (1987) studied the relationship of dwarf mistletoe and site index in 3 national forests in Colorado and also found incidence levels were higher on intermediate sites than poor or good sites.

Daubenmire (1961) observed that *Arceuthobium campylopodum* was found only on the 2 "poorest" of the 7 *Pinus ponderosa* habitat types he recognized (see discussion above on habitat type). In California, Offord (1961) noted that dwarf mistletoe infestation was more serious on the "poorer" *P. ponderosa* sites in eastern and southern California than on the "better" sites along the western Sierra Nevada. However, Childs and Edgren (1967) found no correlation between dwarf mistletoe abundance and site quality near Chemault, Oregon.

Hadfield (1977) intensively surveyed stands in eastern Oregon and eastern Washington; he found incidence of *Arceuthobium americanum* varied with site index and was greatest in stands of intermediate site quality. Alexander (1975) reported that *A. americanum* in the Rocky Mountains is more abundant on "poor" than on "good" sites .

There are conflicting reports on the site relationships of *Arceuthobium americanum* on *Pinus banksiana*. Jameson (1961) reported that the dwarf mistletoe was most common on "poor" sites in Saskatchewan, but Muir and Robbins (1973) noted that the mistletoe is common on both "poor" and "good" sites in northern Alberta.

Buckland and Marples (1952) noted that in British Columbia *Arceuthobium tsugense* appears to be less abundant on "good" sites where mature stands of *Tsuga heterophylla* are open. However, in even-aged or climax stands, dwarf mistletoe infection is frequently severe, irrespective of the quality of the site.

Many reports agree that *Arceuthobium pusillum* is most abundant on "poor," boggy sites. For example, in Newfoundland, Singh (1982) indicated that the parasite was usually found on low-lying, moist to wet sites and did not occur on drier or upland sites. Magasi (1984) surveyed dwarf mistletoe on *Picea mariana* in the Maritime Provinces and found mistletoe on 20% of all sites but 44% of wet, boggy sites. The data for all sites and wet, boggy sites, respectively, were: 14% and 29% in New Brunswick, 25% and 72% in Nova Scotia, and 8% and 17% on Prince Edward Island.

Offord (1961) suggested that *Arceuthobium abietinum* on *Abies concolor* and *A. magnificae* in California showed weak correlation with site quality and that *Arceuthobium californicum* may be more common on the best sites. *Arceuthobium minutissimum* on *Pinus wallichiana* in Pakistan occurs in the dry zone but not in the mesic zone (Hawksworth and Zakaullah 1985).

Relationships With Fire

Historically, wildfires have been the most important single factor governing the distribution and abundance of dwarf mistletoes (Alexander and Hawksworth 1975, Wicker and Leaphart 1974). Most of the literature on dwarf mistletoe–fire relationships has been observational, but there have been some quantitative studies. Wildfires are frequently effective in limiting dwarf mistletoe populations because trees usually return to burned sites much faster than the parasite returns. In several situations, however, fire may ultimately increase mistletoe abundance and distribution. Spotty fires can leave scattered, live, infected trees that not only regenerate the stand but also re-infest it. Fire can also increase dwarf mistletoe populations by maintaining seral forest types composed of mistletoe-susceptible host species rather than permitting succession to climax species that are immune to mistletoe infection. A good example of this phenomena is found in the Rocky Mountains, where wildfires tend to re-establish seral *Pinus contorta* stands, which are highly susceptible to *Arceuthobium americanum,* and to limit development of climax species (*Picea* and *Abies*), which are not principle hosts of indigenous mistletoe species (Hawksworth 1975).

Roth (1966) suggested that fires may tend to eliminate any mistletoe-resistant *Pinus ponderosa* populations that happen to evolve. Infested stands typically contain large amounts of fuels due to the accumulation of dead witches' brooms, fallen trees, and live brooms in the lower crown. Because of these fuels, normally non-destructive fires become conflagrations that destroy not only infected trees but also any mistletoe-resistant individuals that may have become established.

Koonce and Roth (1980) studied the effects of prescribed burning on *Arceuthobium campylopodum* on *Pinus ponderosa* in central Oregon. Their results indicate that dwarf mistletoe can be partially sanitized from thinned or unthinned stands by prescribed understory fires. Scorch heights 30 to 60% of the crown length are required to reduce significantly dwarf mistletoe infestations. Koonce and Roth (1985) also studied the effects of mistletoe on fuel characteristics in sapling and pole-sized stands. Surface fuel loadings were correlated with stand density, and fuels in the lower crown were correlated with stand height and dwarf mistletoe intensity. Branches infected by dwarf mistletoe were larger, more resinous, and persisted longer than healthy branches. Infested stands had higher total fuel loadings.

A series of studies on the interrelationships of wildfires and prescribed burning in central Colorado was conducted in *Pinus contorta* stands infested with *Arceuthobium americanum* (Zimmerman 1990). In even-aged stands, 100 to 125 years old, the abundance of dwarf mistletoe was inversely proportional to fire frequencies during the period from the late 1800's to the 1980's (Zimmerman and Laven 1984). Nonmerchantable and unproductive infested stands could be eliminated (75 to 100% tree mortality) with prescribed burning. Although the method is cost-effective, it requires detailed planning and careful implementation under precise burning conditions (Zimmerman and others 1990).

The effects of fire and *Arceuthobium vaginatum* subsp. *cryptopodum* on mortality of old-growth *Pinus ponderosa* at Grand Canyon National Park were studied by Harrington and Hawksworth (1990). Dwarf mistletoe–infested trees were influenced by fire in several ways. Because infested trees have highly flammable witches' brooms and lower live crowns, a larger proportion of the crown of an infested tree was likely to be scorched than the crown of a healthy tree. With equal amounts of crown scorch in the 40 to 90% range, the probability of survival of heavily infested trees was less than half that of healthy trees.

The effects of smoke and heat on viability of dwarf mistletoe seeds was studied by Zimmerman and Laven (1987). Seeds of *Arceuthobium americanum*, *A. cyanocarpum*, and *A. vaginatum* subsp. *cryptopodum* were exposed to smoke from burning conifer needles and branch wood. Seed germination was inhibited for all mistletoe species exposed to smoke for 60 minutes or longer. Seeds of *A. americanum* were unaffected by 40-minute exposures to smoke from fuels with high moisture contents, but germination was enhanced after exposure for 30 minutes to smoke from dry fuels. The germination of seeds of *A. cyanocarpum* and *A. vaginatum* subsp. *cryptopodum* was little affected by exposure to smoke for 30 minutes.

CHAPTER 8

Biotic Associates

*Frank G. Hawksworth and Brian W. Geils**

Organisms associated with *Arceuthobium* include birds, mammals, insects, arachnids, and fungi. Most of the literature, however, is observational or anecdotal and widely scattered. Scientific names of birds and mammals mentioned here are listed in the appendix.

Birds

Except for the dwarf mistletoes (with their explosive fruits) and a few terrestrial root parasites, most mistletoe seeds are primarily dispersed by birds (Kuijt 1969a). Nicholls and others (1984) identified several types of bird–dwarf mistletoe associations: (1) long-distance dispersal of seeds, (2) use of shoots and fruits for food, (3) use of shoots and witches' brooms as foraging areas, and (4) use of witches' brooms for cover and nesting. Potential indirect effects of bird–dwarf mistletoe interactions are largely unstudied. Such effects include, for example, utilization of dwarf mistletoe–killed trees and those with dead tops by cavity–nesting birds, and openings in stand structure caused by dwarf mistletoe infestations.

Seed Dispersal

Birds have been implicated in long-distance dispersal of dwarf mistletoe seeds by several workers (Nicholls and others 1984, Weir 1916b, Zilka and Tinnin 1976). Kuijt (1963) discovered several isolated trees of *Pseudotsuga menziesii* infected by *Arceuthobium douglasii* in southern British Columbia that were about 80 km from the closest known source of infection. Weir (1916b) discovered seeds of *A. laricis* about 400 m from the closest infected larch trees. He surmised that the seeds were transmitted by high winds but mentioned that birds also may have been involved. Ireland (1926) found seeds of *A. occidentale* in an apple orchard about 1 km from the closest infested trees of *Pinus sabiniana.*

Only 3 studies quantify the frequency of isolated or "satellite" infection centers in otherwise mistletoe-free forests:

- Ostry (1978) studied *Arceuthobium pusillum* in 120-year-old *Picea mariana* stands in northern Minnesota and found 12 satellite infection centers in a 188-ha study area (0.06 centers/ha). The centers contained from 1 to >100 trees covering 0.51 ha; the most isolated infection center was 250 m from the nearest infection source.
- Hudler and others (1979) studied *Arceuthobium vaginatum* subsp. *cryptopodum* in 100- to 150-year-old *Pinus ponderosa* stands in Colorado and found 32 satellite infection centers in a 194-ha study area (0.16 centers/ha). Centers contained up to 175 trees covering 0.3 ha; the most isolated center was 450 m from the nearest infection source.
- Hawksworth and others (1987) studied *Arceuthobium americanum* in a 70-year-old *Pinus contorta* stand in Colorado and found 21 satellite infection centers in a 14.6-ha study area (1.4 centers/ha). Centers contained from 1 to 10 trees; the most isolated center was 65 m from the nearest infection source.

Although satellite centers are relatively scarce, the explosive mechanism of seed dispersal utilized by dwarf mistletoes enables them to intensify and spread rapidly from a newly established satellite center.

Nicholls and others (1984) made a thorough study of animal vectors of *Arceuthobium americanum* and reviewed the previous literature (table 8.1). They showed that animals, especially birds, act as long-distance dispersal agents of this dwarf mistletoe in Colorado. Unlike seeds of other mistletoes, those of *Arceuthobium* are destroyed if they are ingested (Hudler and others 1979). Thus, birds can only disperse seeds that accidentally adhere to their feathers and are subsequently deposited where infection is likely to occur (safe-site). Although such events are rare, a sufficient proportion of birds (27%) carried dwarf mistletoe seeds to make some such dispersal probable (Nicholls and others 1984). The gray jay was the most important seed vector for *A. americanum,* but other important resident species of birds were

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* Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.

TABLE 8.1 –Dispersal of seeds of *Arceuthobium* by birds

Arceuthobium	Location	Observation	Reference
A. americanum	CO	10 species of trapped birds had dwarf mistletoe seeds; gray jay was the most important vector	Hawksworth and others 1987 Nicholls and others 1989
A. americanum	MB, Canada	5 species of birds carried seeds	Punter and Gilbert 1989
A. pusillum	MN	7 species of trapped birds had dwarf mistletoe seeds; gray jay was the most important vector	Hudler and others 1974 Ostry and others 1983
A. pusillum	NFL, Canada	Gray jay was the most important vector	Singh 1982
A. tsugense	AK	Seeds found on feathers of Steller's jay	O'Clair and Armstrong 1985
A. vaginatum	CO	5 species of trapped birds had dwarf mistletoe seeds; pygmy nuthatch and mountain chickadee were the most important vectors	Hudler and others 1979
Arceuthobium spp.*	OR	4 species of birds carried seeds of 6 dwarf mistletoe species; Steller's jay was the most important vector	Zilka and Tinnin 1976

**A. abietinum, A. americanum, A. campylopodum, A. douglasii, A. laricis,* and *A. tsugense*

Steller's jay, mountain chickadee, and dark-eyed junco. Because dwarf mistletoe fruits mature in late summer, migratory birds such as warblers, robins, and hermit thrushes can also play a significant role in long-distance dispersal (Nicholls and others 1984).

Punter and Gilbert (1989) studied animal dispersal in *Arceuthobium americanum* on *Pinus banksiana* in southern Manitoba. They found no seeds on small mammals but observed seeds on 5% of the birds captured in mist-nets; gray jays and dark-eyed juncos were most common. A brown creeper, a red-breasted nuthatch, and a Swainson's thrush also carried dwarf mistletoe seeds.

Various bird species are implicated as dispersal agents for several dwarf mistletoe species. Gray jays are apparently the most important vectors for *Arceuthobium pusillum* in *Picea mariana* and for *A. americanum* in *Pinus contorta.* Steller's jays disperse several dwarf mistletoe species in the Pacific Northwest; nuthatches and chickadees are important for long-distance dispersal of *A. vaginatum* subsp. *cryptopodum* in Colorado (table 8.1). Birds, particularly the mistle thrush, have been suggested as long-distance vectors of *A. oxycedri* in France (Gerber and Cotte 1908) and Pakistan (Zakaullah and Badshah 1977), but quantitative data are lacking. Gorrie (1929) suggests that tits and finches are the primary long-distance dispersal agents of *A. minutissimum* in India.

Birds are very important for dispersal of dwarf mistletoe species that typically occur in isolated trees or in the tops of otherwise uninfected trees. This pattern is characteristic of the following dwarf mistletoes:

- *Arceuthobium minutissimum* on *Pinus wallichiana* in Pakistan (Hawksworth and Zakaullah 1985).
- *Arceuthobium occidentale* on *Pinus sabiniana* in California (unpublished data).
- *Arceuthobium cyanocarpum* on *Pinus flexilis* in the Rocky Mountains (Urban 1968, unpublished data).
- *Arceuthobium verticilliflorum* on *Pinus* spp. in Durango, Mexico (unpublished data).

Except for *Arceuthobium verticilliflorum,* seeds of these species are effectively dispersed by explosive fruit, although birds likely augment mistletoe spread. Because the large fruits of *A. verticilliflorum* are not explosively discharged, birds probably are the primary vectors of this species; their activity probably accounts for the widespread distribution of this mistletoe in the open-canopy stands where it commonly occurs. Dispersal agents for *A. verticilliflorum* have not been determined, but we suspect the gray silky-flycatcher because it feeds on the fruits of other mistletoes (particularly *Phoradendron* spp.) and is common in pine forests of the Sierra Madre Occidental (Sutton 1951).

Dwarf Mistletoes as Food

Birds in the United States that utilize dwarf mistletoes for food are summarized in table 8.2. Weir (1916b) noted house sparrows feeding on fruits of

TABLE 8.2 –Use by birds in the United States of *Arceuthobium* for food

Bird	*Arceuthobium*	Location	Reference
Blue grouse	*A. americanum*	WY	Skinner 1928
	A. campylopodum	WA	Boag 1963
	A. douglasii	AZ	Severson 1986, Lecount 1970
	A. douglasii?	OR	Crawford and others 1986
	A. douglasii	UT	Pekins and others 1987
	A. douglasii	WA	Standing 1960
	A. laricis	WA	Beer 1943
	A. sp.	?	Stewart 1944
	A. vaginatum	CO	Zwinger 1970
Ruffed grouse	*A.* spp.	ID	Wicker 1967a
	A. americanum	WY	Wagner 1968, Skinner 1928
Spruce grouse	*A. americanum*	WA	Zwickel and others 1974
"Grouse"	*A. douglasii*	MT	Weir 1916b
	A. laricis	MT	Weir 1916b
Phainopepla	*A. occidentale*	CA	First report
Black-capped chickadee	*A. americanum*	WY	Wagner 1968
House sparrow	*A. campylopodum*	ID	Weir 1916a
Mourning dove	*A. cyanocarpum*	ID	Urban 1968
Mountain bluebird	*A. cyanocarpum*	ID	Urban 1968
	A. vaginatum	CO	Evans and Evans 1991
Western bluebird	*A. vaginatum*	CO	Pinkowski 1981
Evening grosbeak	*A. vaginatum*	AZ	Hawksworth 1961a
American robin	*A. vaginatum*	CO	Zwinger 1970
Black-headed grosbeak	*A. vaginatum*	AZ?	Marshall 1957
Band-tailed pigeon	*A.* spp.	AZ, CA	Neff 1947

Note: A question mark indicates that species or location are unknown or inferred.

Arceuthobium campylopodum in Idaho, and Hawksworth (1961a) observed evening grosbeaks taking ripe fruits of *A. vaginatum* subsp. *cryptopodum* in Arizona. Phainopeplas feed on ripe fruits of *A. occidentale* in the Sierra Nevada foothills (W. J. Hawksworth, personal communication). The Antillean euphonia eats large quantities of *A. bicarinatum* fruits in the Dominican Republic (Etheridge 1971); tits and finches forage on fruits of *A. minutissimum* in India (Gorrie 1929). The song thrush ingests fruits of *A. oxycedri* in France (Gerber and Cotte 1908), and the mistle thrush feeds on this dwarf mistletoe in Pakistan (Zakaullah and Badshah 1977). In general, feeding on dwarf mistletoe shoots and fruits is uncommon for birds other than the euphonia in the Dominican Republic and the gray silky-flycatcher in Mexico.

A number of reports document feeding by grouse on dwarf mistletoes (table 8.2). Most of these reports are simply observational, but Severson (1986) notes that although blue grouse feed primarily on foliage of *Pseudotsuga menziesii,* 2 to 8% of the bird's diet is composed of *Arceuthobium douglasii.* The importance of such large birds as grouse for establishment of new mistletoe populations is unknown. Although ingested seeds would be rendered inviable, Zilka (1973) suggests that grouse roosting high in tree crowns would carry seeds externally that, once dislodged, would be washed down to young host shoots susceptible to infection.

Witches' Brooms as Nesting Sites and Cover

The dense and abnormally branched witches' brooms caused by dwarf mistletoe infection are commonly utilized by some birds for nesting sites. The often large systemic witches' brooms in *Pseudotsuga menziesii* that result from infection by *Arceuthobium douglasii* are often used as nesting platforms by several owls and accipiters (table 8.3). Approximately 25 to 30% of these raptors normally nest in witches' brooms. In eastern Oregon, however, 19 of 20 nests of long-eared owls were found in witches' brooms (Bull and others 1988). Ravens on the east side of the Cascades in Washington nest in witches' brooms (S. Martin, personal communication). Witches' brooms induced by *A. douglasii* are also commonly used for roosting cover by grouse (Martinka 1972, Stauffer and Peterson 1986, Weir 1916b). At least 10 passerine species have been found nesting in witches' brooms of various dwarf mistletoes (table 8.4).

TABLE 8.3 —Nesting by raptors in witches' brooms induced by *Arceuthobium*

Raptor	*Arceuthobium*	Location	Abundance*	Reference
Northern spotted owl	*A.* spp.	OR	3 of 18 nests in brooms	Forsman 1983
	A. spp.	OR	9 of 47 nests in brooms	Forsman and others 1984
	A. douglasii	WA	3 of 3 nests in brooms	Richards 1989
	A. douglasii	WA	11 of 29 nests in brooms	Irwin and others 1989
Mexican spotted owl	*A. douglasii*	NM	1 of 3 nests in brooms	Ligon 1926
	A. douglasii	NM	2 of 6 nests in brooms	Pederson 1989
	A. douglasii	AZ, NM	7 of 22 nests in brooms	Fletcher 1990
Great gray owl	*A. douglasii*	OR	10 of 49 nests in brooms	Bull and Henjum 1990
Long-eared owl	*A. douglasii*	OR	19 of 20 nests in brooms	Bull and others 1988
Great horned owl	*A. vaginatum*	CO	1 nest in broom	Reynolds, personal communication 1990
Cooper's hawk	*A.* spp.	OR	"common" in brooms	Reynolds 1979 Reynolds and others 1982
	A. douglasii	OR	20 of 31 nests in brooms	Moore and Henny 1983
	A. douglasii	OR	50–70% of nests in brooms	Moore and Henny 1984
Goshawk	*A. douglasii*	OR	5 of 34 nests in brooms	Moore and Henny 1983
Sharp-shinned hawk	*A. douglasii*	OR	3 of 25 nests in brooms	Moore and Henny 1983, 1984

*Relative abundance of nests for the raptor species that were found in witches' brooms.

TABLE 8.4 –Nesting by passerines in witches' brooms induced by *Arceuthobium*

Passerine	*Arceuthobium*	Location	Reference
American robin	*A. americanum*	CO	First report
	A. campylopodum	WA	First report
	A. vaginatum	CO	Bennetts and others 1992
	A. vaginatum	CO	Nicholls and others 1984
Gray jay	*A. pusillum*	MN	Warren 1899
Red crossbill	*A. vaginatum*	CO	Bailey and others 1953
House wren	*A. vaginatum*	AZ	Nicholls and others 1984
Mourning dove	*A. vaginatum*	CO	First report
Western tanager	*A. vaginatum*	CO	Bennetts and others 1992
Chipping sparrow	*A. vaginatum*	CO	Bennetts and others 1992
Hermit thrush	*A. vaginatum*	CO	Bennetts and others 1992
Cassin's finch	*A. vaginatum*	CO	Bennetts and others 1992
Pine siskin	*A.* spp.	OR	Zilka 1973

Dwarf Mistletoe Effects on Bird Habitat

Bennetts (1991) and Bennetts and Hawksworth (1992) studied relationships in central Colorado between infestations by *Arceuthobium vaginatum* subsp. *cryptopodum* in stands of *Pinus ponderosa* and the population dynamics of various bird species. The abundance of dwarf mistletoe in a stand was directly correlated with species diversity and bird density. They also demonstrated a strong positive correlation between incidence of dwarf mistletoe and the number of snags used by cavity-nesting birds. Severs and others (1991) reported a nearly three-fold increase in the density of cavity-nesting birds in stands severely infested by dwarf mistletoes over the density in comparable but uninfested stands.

Mammals

Literature involving mammal–dwarf mistletoe associations has been discussed in detail by Hawksworth (1975), Nicholls and others (1984), and Tinnin and others (1982).

Seed Dispersal

Red squirrels and flying squirrels are known to carry seeds of *Arceuthobium pusillum* in *Picea mariana* stands in Minnesota (Hudler and others 1974, Ostry and others 1983). In the first year of their studies, 20 seeds were found on mammals and birds—including 1 on a red squirrel and 10 on flying squirrels. In the following year, 25 seeds were found—all on red squirrels. Lemons (1978) studied the role of red squirrels as seed vectors of *A. campylopodum* in central Oregon. He found no seeds on squirrels in stands of *Pinus ponderosa* where dwarf mistletoe infestation was low, but about 50% of squirrels carried mistletoe seeds in severely infested stands. He observed that squirrels carried seeds for distances up to 150 m. Because squirrels groom seeds from their fur soon after becoming attached, he doubted they were important for establishment of new and distant infection centers.

The seed vectors of *Arceuthobium americanum* on *Pinus contorta* in Colorado were studied by Nicholls and others (1987b, 1989). Seeds were discovered on 4 species of mammals—least chipmunk (24 of 254 animals with seeds), golden-mantled ground squirrel (3 of 20 animals with seeds), red squirrel (1 of 15 animals with seed), and American marten (1 of 1 animal with seed). Although chipmunks and ground squirrels carried the most seeds, they are unlikely to initiate new infection centers because they spend most of their time on or near the ground and are therefore unlikely to deposit those seeds at infection safe-sites. Red squirrels are more effective animal vectors because they frequent tree crowns; but they have relatively small home ranges and are less likely than birds to effect long-distance dispersal.

Taylor (1935) studied porcupines in Arizona and discussed the possibility that they might disperse *Arceuthobium vaginatum* subsp. *cryptopodum.* Porcupines definitely feed on dwarf mistletoe shoots (see below), but we question the importance their role as an effective vector because (1) outer twigs with needles (safe-sites) are too small to support such large animals, and (2) resinous wounds on older tissues (where porcupines frequent) are unlikely infection courts (Hawksworth 1961a).

In Manitoba, Punter and Gilbert (1989) trapped 193 mammals in *Pinus banksiana* stands infested by *Arceuthobium americanum;* none of the animals (including least chipmunk, red-backed vole, deer mouse, and Franklin's ground squirrel) carried dwarf mistletoe seeds. Urban (1968) implicated various rodent species in the dispersal of *A. cyanocarpum* in the open stands of *P. flexilis* at Craters of the Moon National Monument in southern Idaho.

Dwarf Mistletoes as Food

Various mammals utilize dwarf mistletoe shoots as a dietary supplement, but none are dependent on them as a primary food source.

The red squirrel is the most thoroughly studied of all the mammals that forage on trees infected with dwarf mistletoe. It is most commonly associated with *Arceuthobium americanum* on *Pinus contorta* in British Columbia (Baranyay 1968, Wood and others 1985), Montana (U.S. Department of the Interior 1970), Wyoming (Wagner 1968), and Colorado (unpublished data). Small branches 6 to 13 mm in diameter are nipped off and the cortex consumed; in all areas observed, squirrels select mistletoe-infected twigs over uninfected twigs. In British Columbia, 90% of the mistletoe-infected branches over a 30-ha area were gnawed (Wood and others 1985). One of the earliest reports of dwarf mistletoes in North America mentions that this squirrel fed on *A. campylopodum* in the "Oregon Territory" (Hooker 1847). Rodents, presumably tree squirrels, in California feed on dwarf mistletoe cankers in true firs (Scharpf 1982).

Abert squirrels in northern Arizona feed nearly exclusively on the bark of young twigs of *Pinus ponderosa* (Keith 1965). Keith observed that these squirrels also feed on the inner bark of twigs infected by *Arceuthobium vaginatum* subsp. *cryptopodum* by removing the mistletoe shoots and outer bark, and consuming inner bark and associated endophytic system of dwarf mistletoe. Shaw and Hennon (1991) found that 22% of the infections caused by *A. tsugense* on young *Tsuga heterophylla* in southeast Alaska had been chewed by rodents. Wass (1976) reported rodent chewing on *A. tsugense* infections on *P. contorta* in British Columbia and noted their absence on similarly infected *T. heterophylla.* States and others (1988) found that foraging times of Abert squirrels on dwarf mistletoe and associated structures varied by season—1% in spring, 3% in summer, 5% in autumn, and 12% in winter. Stephenson (1975) reported that squirrels in Arizona consumed dwarf mistletoe shoots and fruits throughout the year, but mistletoe comprised less than 4% of the total diet. In southeastern Utah, however, dwarf mistletoe was rarely used for food (Patton and Vahle 1986).

Chipmunks eat the fruits and seeds of *Arceuthobium campylopodum* in Washington (Broadbooks 1958), those of an unidentified mistletoe in northern Idaho (Wicker 1967a), and those of *A. americanum* in Colorado (Nicholls and others 1984). Dwarf mistletoes, however, are probably not an important element in their overall diet.

Taylor (1935) commented that some porcupines in the Southwest are "excessively fond" of *Arceuthobium vaginatum* subsp. *cryptopodum* and prefer this plant to pine needles and inner bark during certain seasons. Winter foraging on dwarf mistletoe was restricted to only 20% of the porcupine population, but those individuals that did feed on mistletoe, did so extensively. In winter, spring, and summer, 20 to 25% of stomach contents was mistletoe shoots; in autumn, the amount rose to 65%. Certain trees of *Pinus ponderosa* in Colorado that are infested with *A. vaginatum* subsp. *cryptopodum* are also especially attractive to porcupines in winter; the ground under these trees is often littered with hundreds of porcupine fecal pellets comprised of fragments of dwarf mistletoe shoots. Johnson and Carey (1979) noted that, in one area of northern Colorado, dwarf mistletoe shoots made up about 25% of the porcupine fecal pellets. In the Pacific Northwest, *A. campylopodum* is such an attractive food for porcupines in autumn and winter that shoots of this dwarf mistletoe are used for bait to trap the animals (Hooven 1971, Lawrence 1957).

Deer forage opportunistically on dwarf mistletoes. Although shoots are high in nutritive value (Urness 1969), they are usually inaccessible. Shoots of *Arceuthobium vaginatum* subsp. *cryptopodum* have a digestibility ratio of about 50% and are high in nutrients—45 to 55% acid-detergent fiber, 0.15 to 0.25% phosphorus, and 5 to 7% crude protein (Urness 1969). Hawksworth (1961b) observed mule deer in northern Arizona feeding on shoots of *A. vaginatum* subsp. *cryptopodum* in green logging slash. Other observations of mule deer in several studies (Currie and others 1977) showed that this dwarf mistletoe contributed less than 1% to the total diet. Dried mistletoe shoots that had fallen to the ground were only eaten in April and constituted about 2.5% of that month's diet. Wright and Arrington (1950), in their study on mule deer of the northern Kaibab Plateau, reported that *A. vaginatum* subsp. *cryptopodum* contributed from a trace to 54% of the diet (overall average <1%). Leach (1956) and Leach and Hiele (1957) observed that *A. campylopodum* occurred in the stomach contents of California mule deer 10 to 25% of the time, but contributed only 1 to 2% of the volume consumed. Craighead and others (1973) report that *A. americanum* on *Pinus contorta* is an important, high-protein, winter food for elk in thermal areas of Yellowstone National Park.

Witches' Brooms as Nesting Sites and Cover

Farentinos (1972) found that, in Colorado, 10 of 40 nests of Abert squirrels were in witches' brooms of *Pinus ponderosa* induced by *Arceuthobium vaginatum* subsp. *cryptopodum*. Dwarf mistletoe was rare on the study site, and all large witches' brooms observed were utilized as nesting sites. Similar observations were reported near Allenspark, Colorado (Pollock 1981).

Red squirrels in Colorado nest in witches' brooms of *Pinus contorta* caused by *Arceuthobium americanum* (Hatt 1943). Patton and Vahle (1986) reported that 35% of red squirrel nests in an Arizona mixed conifer forest were found in witches' brooms. Nesting sites for red squirrels in eastern Oregon were found in brooms of *P. ponderosa* induced by *A. campylopodum* (Lemons 1978).

Witches' brooms of *Pinus contorta* induced by *Arceuthobium americanum* are frequently used by the American marten for nesting sites in California (Spencer 1987), Montana (Burnett 1981), and Wyoming (Campbell 1979, Hauptman 1979, Buskirk and others 1987). In northeastern Oregon, witches' brooms of *Pseudotsuga menziesii* caused by *A. douglasii* are often used by porcupines in winter for protection from snow and wind (Smith 1982). Flying squirrels on the east side of the Cascades in Washington also frequently utilize witches' brooms induced by *A. douglasii* for cover and nesting sites (S. Martin, personal communication). Lemons (1978) reports that witches' brooms of *Pinus ponderosa* caused by *A. campylopodum* are used as nesting sites by flying squirrels and bushy-tailed woodrats in eastern Oregon.

Dwarf Mistletoe Effects on Mammal Habitat

The indirect effects of dwarf mistletoe infection on stand opening—the production of dead branches and dying trees—have been studied in relation to abundance of mammals in *Pinus ponderosa* infested with *Arceuthobium vaginatum* subsp. *cryptopodum*. In certain years, dwarf mistletoe–infested stands in northern Arizona received significantly more use by mule deer than stands without dwarf mistletoe, but no long-term preferences were observed (Clary and Larson 1971). Both mule deer and elk in Colorado used infested stands more frequently than uninfested stands (Bennetts and others 1991).

Insects

The literature on insect–dwarf mistletoe associations was summarized by Stevens and Hawksworth (1970, 1984). They recognized 3 major types of association: (1) pollination (chapter 3), (2) predation of shoots, fruits, and seeds (this chapter), and (3) invasion of insects into trees weakened by dwarf mistletoe infection (chapter 12).

Predation of Shoots, Fruits, and Seeds

Many diverse species of insects feed on dwarf mistletoe shoots, fruits, and seeds (Stevens and Hawksworth 1970, 1984). Most are generalist feeders that only forage on dwarf mistletoes incidentally and opportunistically. For example, the grasshopper *Melanoplus devastator,* which usually feeds on herbaceous vegetation, destroyed more than 90% of the shoots of *Arceuthobium campylopodum* in a California plantation of *Pinus jeffreyi* (Scharpf and Koerber 1986). Also, the harvester ant, *Atta mexicana,* which is a generalist feeder, utilized shoots of *Arceuthobium durangense* in Sinaloa, Mexico (Nickrent 1988).

A number of insect species, including members of the Lepidoptera, Hemiptera, Coleoptera, and Thysanoptera, feed exclusively on dwarf mistletoes.

Lepidoptera

The thicket hairstreak butterfly, *Mitoura spinetorum* (Lycaenidae), is highly prized by butterfly collectors, and larvae are obligate feeders on dwarf mistletoe (fig. 8.1). The species occurs from southern British Columbia to central Mexico (Shields 1965). Larvae have been collected from 10 species of *Arceuthobium* (Stevens and Hawksworth 1970) and probably occur

Figure 8.1–Larvae of the thicket hairstreak butterfly, *Mitoura spinetorum*, feeding on a pistillate plant of *Arceuthobium americanum;* note how well late-instar larvae mimic mistletoe shoots.

on all North American species. Larvae are common enough in certain years to exert a minor degree of biological control but are usually too rare to significantly affect dwarf mistletoe populations. A related species, *M. johnsonii,* occurs on both subspecies of hemlock dwarf mistletoe—*A. tsugense* subsp. *mertensianae* in California and *A. tsugense* subsp. *tsugense* from Oregon to southern British Columbia (McCorkle 1962). McCorkle (Anonymous 1982) found in Oregon that 28 larvae completely destroyed 74% of 144 shoots of *A. tsugense* subsp. *tsugense.*

The most destructive larvae that feed on dwarf mistletoe are *Dasypyga alternosquamella* (Pyralidae) and *Filatima natalis* (Gelechidae) (Heinrich 1921). Little is known of the biology of these species, but both are apparently widespread in western North America and occur on several species of *Arceuthobium. Dasypyga alternosquamella* in British Columbia is extremely destructive to shoots of *A. americanum* (Reich 1992). Larvae of either species can destroy an entire crop of mistletoe shoots by mining larger shoots and consuming smaller shoots.

Hemiptera

The plant bug *Neoborella tumida* (Miridae) feeds on several species of dwarf mistletoes in the western United States and Mexico (Knight 1925, Stevens and Hawksworth 1970). *Neoborella tumida* is notable for its size and color mimicry of dwarf mistletoe fruits. Three other species of *Neoborella* that apparently also feed exclusively on dwarf mistletoes have been described from the western United States and Canada (Herring 1972, Kelton and Herring 1978). *Platylygus mexicanus* is reported from Durango, Mexico, on a "mistletoe" (presumably *Arceuthobium nigrum*) of *Pinus leiophylla* (Kelton and Knight 1970).

The spittle bug *Clastoptera distincta* (Cercopidae) is widespread on *Arceuthobium vaginatum* subsp. *cryptopodum* in Arizona, New Mexico, and southern Colorado, but it apparently does little damage. The spittle bug is also common in northern Arizona on *A. abietinum* f. sp. *concoloris.*

Coleoptera

The twig beetle *Pityophthorus arceuthobii* (Scolytidae) is apparently restricted to dwarf mistletoes in central Mexico. These beetles mine large shoots (frequently >3 cm at base) of both subspecies of *Arceuthobium globosum* (subsp. *globosum* and subsp. *grandicaule*) (Wood 1971, unpublished data). This twig beetle may also occur on other large-stemmed Mexican dwarf mistletoes such as *A. vaginatum* subsp. *vaginatum* and *A. durangense.*

Thysanoptera

Several species of thrips (Thripidae) are commonly associated with *Arceuthobium* (Stevens and Hawksworth 1970, 1984). Thrips are plant feeders, but the severity of their effects on dwarf mistletoe populations is not known. Most dwarf mistletoe–associated thrips have broad host ranges, but at least the species *Frankliniella hawksworthii* feeds exclusively on dwarf mistletoe (O'Neill 1970).

Mites and Spiders

Several species of mites (Mesostigmata and Trombiformes) occur on dwarf mistletoes (Stevens and Hawksworth 1970), but their effects are unknown. Most dwarf mistletoe–associated mites have broad host ranges, but at least 4 species appear to be exclusively associated with dwarf mistletoes—*Typhlodromus* *arceuthobius* (Pytoseiidae) on *Arceuthobium campylopodum* and *A. occidentale* in California (Kennett 1963); *T. pusillus* on *A. pusillum* in eastern Canada (Kennett 1963); *Paraphytopus arceuthobii* (Eriophiidae) on flowers of *A. campylopodum* and *A. occidentale* in California (Keifer 1952); and *Brevipalpus porca* (Tenuipalpidae) on several dwarf mistletoes in California, Arizona, Utah, and New Mexico (Pritchard and Baker 1958).

Spiders associated with dwarf mistletoes in northern Colorado were studied by Jennings and others (1989). They found 22 species in 18 genera associated with 3 species of dwarf mistletoe, but none was restricted to them. Of the 118 individuals collected, 65% were hunters and 35% were web spinners. The spider fauna varied considerably among *Arceuthobium americanum, A. cyanocarpum,* and *A. vaginatum* subsp. *cryptopodum,* but differences were apparently associated with their host trees (*Pinus contorta, P. flexilis,* and *P. ponderosa,* respectively) rather than with the dwarf mistletoe. Many of the spiders had *Arceuthobium* pollen adhering to their body setae, but it is unlikely that spiders are effective pollinators. Spiders may, in fact, hinder pollination by ensnaring pollen grains in their webs (Baker and others 1985, Jennings and others 1989) or by capturing pollinating insects.

Fungi

Many fungi are associated with dwarf mistletoes. They frequently kill shoots, fruits, and seeds directly; they may indirectly kill shoots by destroying the outer host cortex of a branch or by killing the entire branch. Heart rot fungi may also invade dwarf mistletoe swellings on the trunks of fir or hemlock trees (chapter 12).

Fungi on Shoots and Fruits

Several fungi infect shoots and fruits of *Arceuthobium* (Gilbert 1984, Kuijt 1963, Hawksworth and others 1977, Wicker and Shaw 1968). Many of these are saprophytic or weakly parasitic, but at least 8 species are parasitic and apparently restricted to *Arceuthobium* (table 8.5). Fungi that parasitize dwarf mistletoe-infected trees also may infect the dwarf mistletoe. For example, the brown felt blight fungus, *Herpotrichia juniperi,* which infects *Abies magnificae* in California, also parasitizes *A. abietinum* f. sp. *magnificae* (Scharpf 1986).

Sphaeria arceuthobii, long known as *Wallrothiella arceuthobii,* was recently transferred by Barr and others (1986) to *Caliciopsis. Sphaeria arceuthobii* was originally described by Peck (1875) as a parasite of *Arceuthobium pusillum* in New York and subsequently was found in northern Michigan (Wheeler 1900), but no additional records of the fungus on *A. pusillum* have been reported. The biology of *Caliciopsis* was studied by Weir (1915a), Dowding (1931b), Wicker and Shaw (1968), Kuijt (1969b), Parker (1970), and Knutson and Hutchins (1979). The fungus infects stigmas during anthesis; later, stigmas and apical portions of the fruit are replaced by a black mycelial stroma. Normal fruit development is prevented and infected fruits fail to produce seed (fig. 8.2).

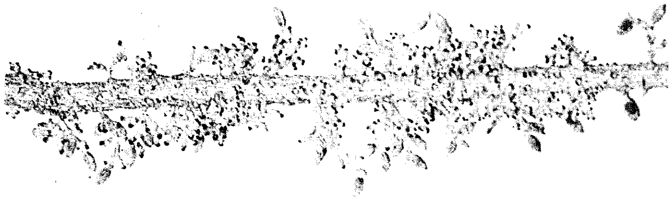

Figure 8.2 –Numerous aborted pistillate flowers of *Arceuthobium douglasii* infected by *Caliciopsis arceuthobii.* The fungus infects stigmas and apical portions of developing fruits, which are later aborted and transformed into prominent black mycelial stroma.

Caliciopsis arceuthobii is restricted to spring-flowering species of dwarf mistletoe (table 8.6) and is common on *Arceuthobium douglasii,* frequent on *A. americanum,* and rare on *A. vaginatum* subsp. *cryptopodum* (Hawksworth 1961b). In certain years, the fungus destroys more than 90% of the fruits of *A. douglasii* (Weir 1915c, Hawksworth and others 1977).

An 1,100-km disjunction (fig. 8.3) exists between populations of *Caliciopsis arceuthobii* in Oregon, Washington, and Idaho and those in Colorado, Arizona, New Mexico, and Mexico (Hawksworth and others 1977). We have been unsuccessful in spite of considerable effort over many years to collect the fungus within this distributional gap, and now believe it is a real discontinuity. Comparative studies on the biology and morphology of the northern and southern populations are needed. Wood (1986) gives a distribution map of *C. arceuthobii* in British Columbia.

TABLE 8.5 –Fungi parasitizing shoots of *Arceuthobium* in the New World*

Fungus	Location	Reference
Colletotrichum gloeosporioides (Melanconiales)	Canada, western US, & Mexico	Hawksworth and others 1968 Muir 1967, 1973a, 1977 Parmeter and others 1959 Scharpf 1964 Wicker 1967b Wicker and Shaw 1968 Wood 1986
Cylindrocarpon gillii (Melanconiales)	Canada, western US, & Mexico	Ellis 1939, 1946 Gill 1935 Kuijt 1963 Mielke 1959 Muir 1973a Wicker and Shaw 1968 Wood 1986
Cylindrocarpon sp. (Melanconiales)	southern Mexico	Hawksworth and others 1977
Caliciopsis arceuthobii (Sphaeriales)	Canada, US, & Mexico	Barr and others 1986 Dowding 1931 Hawksworth 1961 Hutchins 1974 Parker 1970 Peck 1875 Weir 1915 Wicker and Shaw 1968 Wood 1986
Alternaria alternata (Monilliales)	MB, Canada	Sutton 1973
Metasphaeria wheeleri (Sphaeriales)	CA	Linder 1938
Pestalotia maculiformans (Melanconiales)	WA	Wicker and Shaw 1968
Pestalotia heterocornis (Melanconiales)	Dominican Republic	Hawksworth and others 1977

*Updated from Hawksworth and others 1977.

TABLE 8.6 —Hosts and distribution of major fungal parasites of *Arceuthobium* in North America*

Arceuthobium	*Caliciopsis arceuthobii*	*Colletotrichum gloeosporioides*	*Cylindrocarpon gillii*
A. abietinum	US	US	
f. sp. *concoloris*	US	US	—
f. sp. *magnificae*	US	US	—
A. americanum	Canada, US	Canada, US	Canada, US
A. apachecum	US	US	—
A. blumeri	US	Mexico	—
A. californicum	US	US	—
A. campylopodum	US	US	—
A. cyanocarpum	—	US	—
A. divaricatum	US	US, Mexico	—
A. douglasii	Canada, US	Canada, US	Canada, US Mexico
A. laricis	US	US	—
A. microcarpum	US	US	—
A. monticola	—	US	—
A. occidentale	US	—	—
A. pusillum	—	—	Canada, US
A. siskiyouense	—	US	—
A. tsugense subsp. *tsugense*	Canada, US	Canada, US	—
A. tsugense subsp. *mertensianae*	US	US	—
A. vaginatum subsp. *cryptopodum*	—	—	US

*Updated from Hawksworth and others 1977.

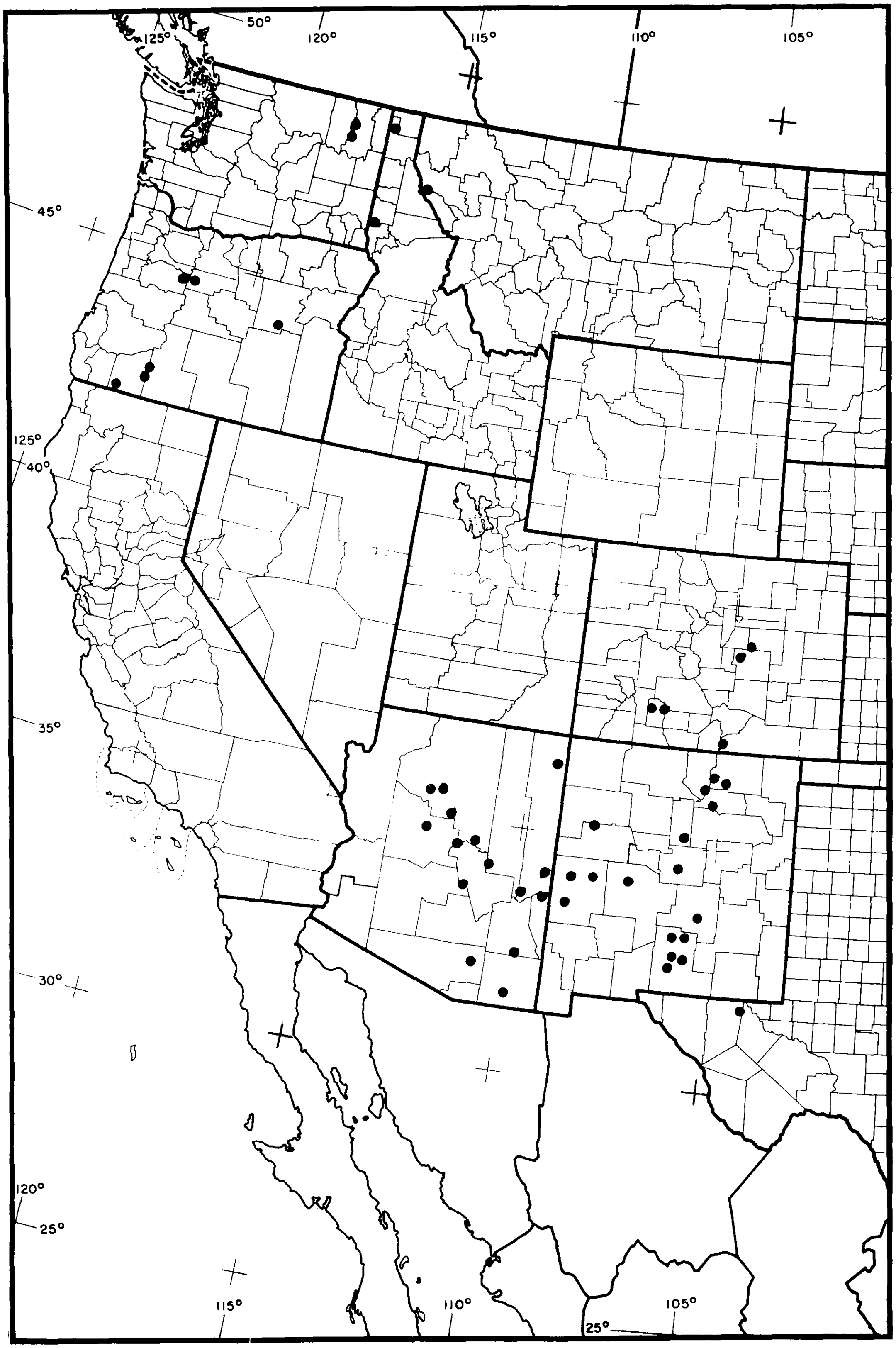

Figure 8.3 –Distribution of *Caliciopsis arceuthobii* on *Arceuthobium* in the western United States and Canada (updated from Hawksworth and others 1977 and Wood 1986).

Colletotrichum gloeosporioides is the most lethal and widespread pathogen of *Arceuthobium.* Weir recognized the fungus before 1920 as a serious parasite of dwarf mistletoes in the Pacific Northwest (Wicker and Shaw 1968). The biology and pathology of *C. gloeosporioides* were described in detail by Parmeter and others (1959). Infection first appears as small brown to black necrotic lesions on mistletoe shoots; lesions enlarge, coalesce, and ultimately cause dieback of shoots (fig. 8.4). The fungus affects most western species of dwarf mistletoe (table 8.6). Several observers report locating areas where a large portion of shoots have been killed by this pathogen. In California, Parmeter and others (1959) observed more than half of the shoots of *A. abietinum* killed; in Washington, Wicker (1967a) noted 24% of the shoots of *A. campylopodum* diseased; and in Alberta, Muir (1977) found more than half of the shoots of *A. americanum* affected. Muir (1967) and Wood (1986) describe the distribution of the fungus in western Canada; the distribution in the United States appears in figure 8.5.

Figure 8.4 –Dying shoots of *Arceuthobium abietinum* infected by *Colletotrichum gloeosporioides.* (R. F. Scharpf)

Cylindrocarpon gillii was studied in detail by Ellis (1946), but it was recognized as a serious shoot parasite of *Arceuthobium* by Weir before 1920 (Wicker and Shaw 1968). In fact, Weir described it as "*Fusarium campylopodii* sp. nov." in an unpublished manuscript. Ellis (1939) also originally thought that it was a *Fusarium,* but after detailed study he transferred it to *Septogloeum* (Ellis 1946). Muir (1973) classified it as *Cylindrocarpon.* Early infection of mistletoe shoots by *C. gillii* is characterized by small, yellowish white lesions. These lesions enlarge, coalesce, erupt through the epidermis, and expose conspicuous masses of white spores; shoot tissues distal to lesions die. The fungus is widespread and parasitizes most species of *Arceuthobium* in the western United States and western Canada (fig. 8.6 and table 8.6; Wood 1986). There are, however, few collections from Idaho, Montana, Nevada, or Wyoming. Mielke (1959) attempted to introduce the fungus on *A. americanum* in southern Idaho, but the population of the parasite became extinct within about 3 years.

Seed Fungi

Because seeds infected by mold will not germinate, molds can markedly effect populations of *Arceuthobium.* For example, Wicker (1967b) planted seeds of 6 dwarf mistletoe species and found that 32 to 60% of the seeds were killed by molds during the first winter (September to April) and an additional 6 to 11% in the following spring (April to June). Many species of fungi, yeasts, and bacteria were isolated from mistletoe seeds in the field (Wicker 1974a); the most common genera found were *Epicoccum, Stemphylium, Hormiscium, Phyllosticta,* and *Coniothyrium.* Carpenter and others (1979) and Shaw and Loopstra (1991) noted the loss to fungi of seeds of *A. tsugense* planted on *Tsuga heterophyll*a in the wet coastal environment.

Canker Fungi

Many fungi invade the already diseased inner bark of host branches infected by dwarf mistletoe (dwarf mistletoe cankers). Some of these kill infected branches or prevent shoot formation by the dwarf mistletoe.

The canker caused by *Cytospora abietis* is common on firs parasitized by *Arceuthobium abietinum* in California and Oregon (Wright 1942; Scharpf 1969c, 1980, 1983a, 1983b; Scharpf and Bynum 1975; Filip 1984, Filip and others 1979). The fungus kills infected branches, thereby giving trees a ragged appearance due to "flagging" of afflicted branches (see fig. 16.7).

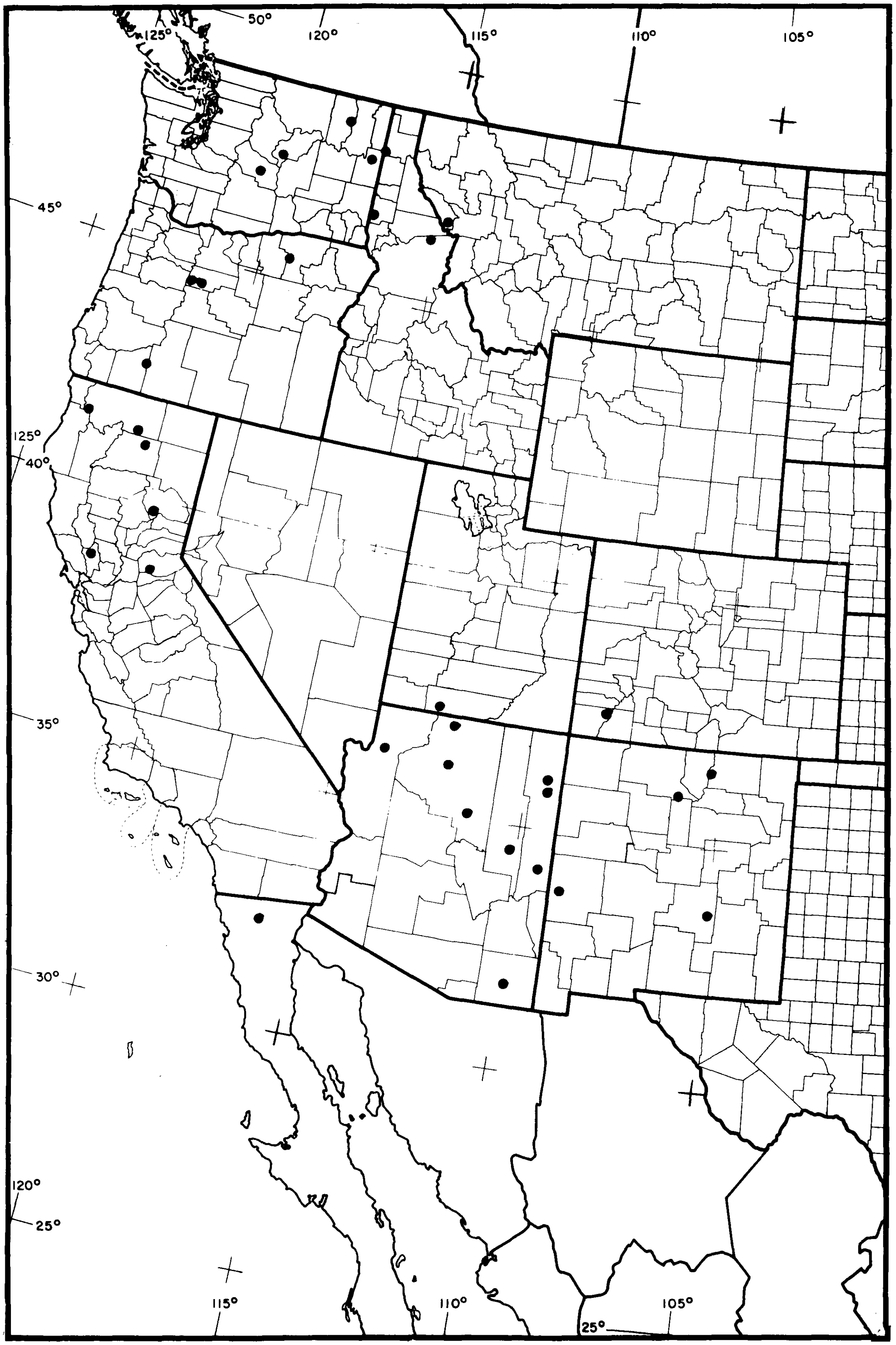

Figure 8.5–Distribution of *Colletotrichum gloeosporioides* on *Arceuthobium* in the United States and northern Mexico (updated from Hawksworth and others 1977).

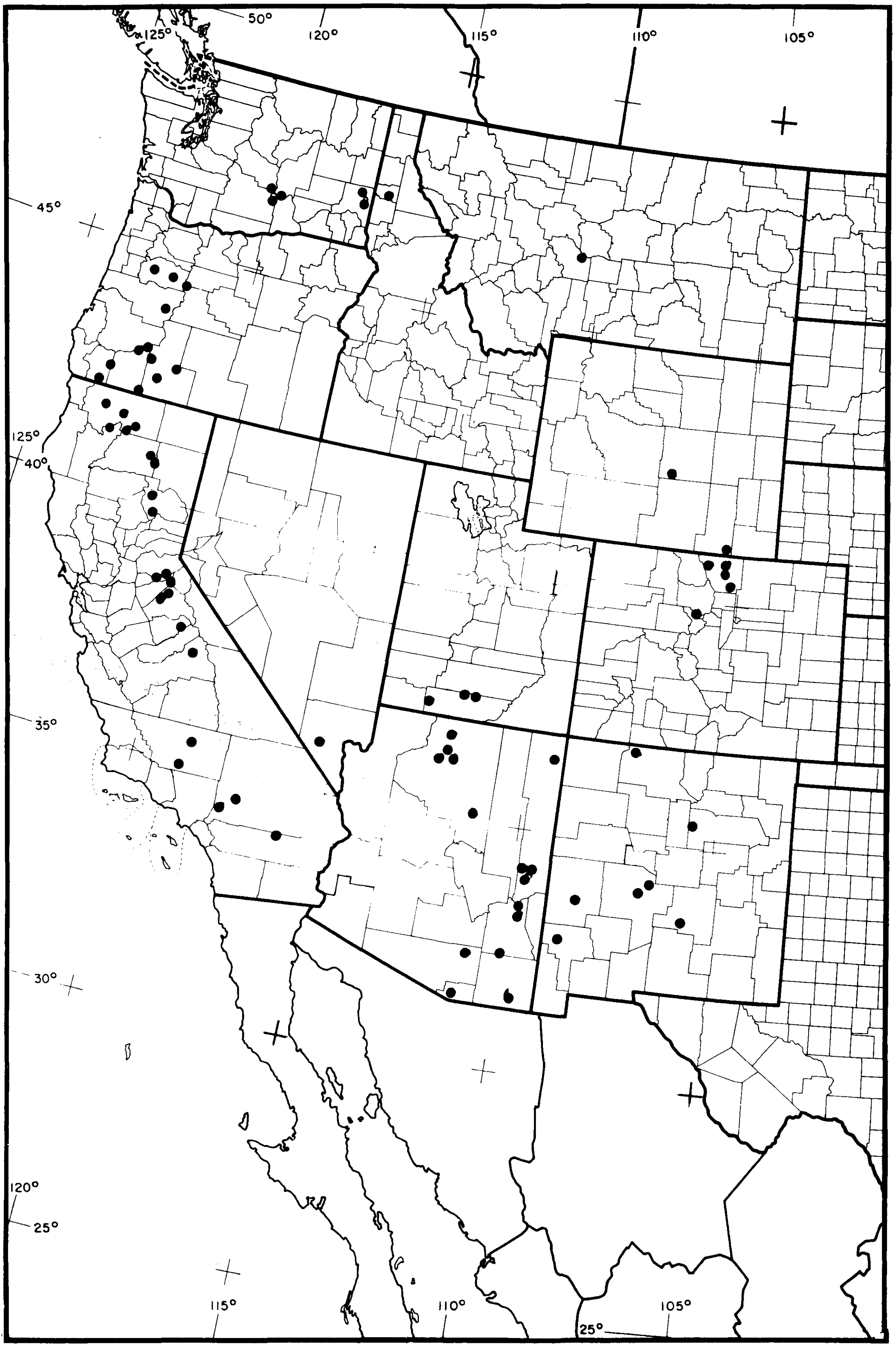

Figure 8.6–Distribution of *Cylindrocarpon gillii* on *Arceuthobium* in the western United States (updated from Hawksworth and others 1977).

Although the fungus is primarily associated with dwarf mistletoe-infected branches, it does occur on branches weakened from other causes as well. In California, 22% of mistletoe-infected branches were parasitized by the fungus, compared to only 4% of the non-mistletoe-infected branches (Scharpf 1969c).

More than 20 fungal species in coastal British Columbia are associated with the cankers caused by *Arceuthobium tsugense* infection of *Tsuga heterophylla* (Baranyay 1966; Funk 1973, 1979, 1981; Funk and Baranyay 1973; Funk and Smith 1981). The high incidence of fungi on this dwarf mistletoe is presumably due to the wet, cool climate characteristic of hemlock forests where the mistletoe is found. The most important of these fungi, *Nectria macrospora,* substantially reduces dwarf mistletoe shoot and fruit production (Funk and others 1973, Smith and Funk 1980).

A pathogenic syndrome termed "resin disease" is common throughout the central and northern Rocky Mountains on *Arceuthobium americanum* (Mark and others 1976). Several weakly parasitic fungi, primarily *Alternaria alternata* and *Aureobasidium pullans,* invade the outer cortex of the host tissue (*Pinus contorta*) adjacent to the dwarf mistletoe canker. A necrophylatic periderm layer develops, outer host tissue dies, and although the host branch remains alive, dwarf mistletoe shoot production ceases. The syndrome is occasionally abundant in some areas, usually killing nearly all mistletoe shoots.

A rust fungus, *Peridermium bethelii,* is associated with *Arceuthobium americanum* on *Pinus contorta* (fig. 8.7). It is common in the Rocky Mountains from southern Alberta to central Colorado, and is known from a single locality on the eastern slope of the California Sierra Nevada (fig. 8.8 and Hawksworth and others 1983). Hyphae infect not only the mistletoes' endophytic system but adjacent host tissues as well (Hawksworth and others 1983, Peterson 1966). Although the rust's life cycle has not been elucidated, observations of its patchy distribution within infested stands suggest that it does not have an alternate host but rather is transmitted directly from mistletoe canker to mistletoe canker. *Peridermium bethelii* kills mistletoe-infested branches but is too uncommon to exert significant biological control.

Several additional species of canker fungi are associated with dwarf mistletoe. *Nectria fuckeliana* is a pathogen in California of *Arceuthobium littorum* on *Pinus muricata* and of *A. abietinum* f. sp. *concoloris* on *Abies concolor* (Byler and Cobb 1972). Filip and others (1979) report that *Cytospora abietis, Cryptosporium pinicola,* and *Nectria macrospora* in Oregon are associated with cankers caused by *Arceuthobium abietinum* on *Abies grandis*. Funk (1984) observes that *Endothiella agregata* is associated with cankers on *Pinus contorta* induced by *Arceuthobium americanum* in British Columbia. *Sphaeropsis sapinea* in California causes necrosis and death of branches of *P. sabiniana* and *P. muricata* infected by *A. occidentale* and *A. littorum,* respectively (Hunt 1969).

Figure 8.7–A sporulating canker caused by *Peridermium bethelii* infecting *Arceuthobium americanum* on *Pinus contorta;* note white peridia and yellow spores erupting from a region of the branch within the already swollen mistletoe infection.

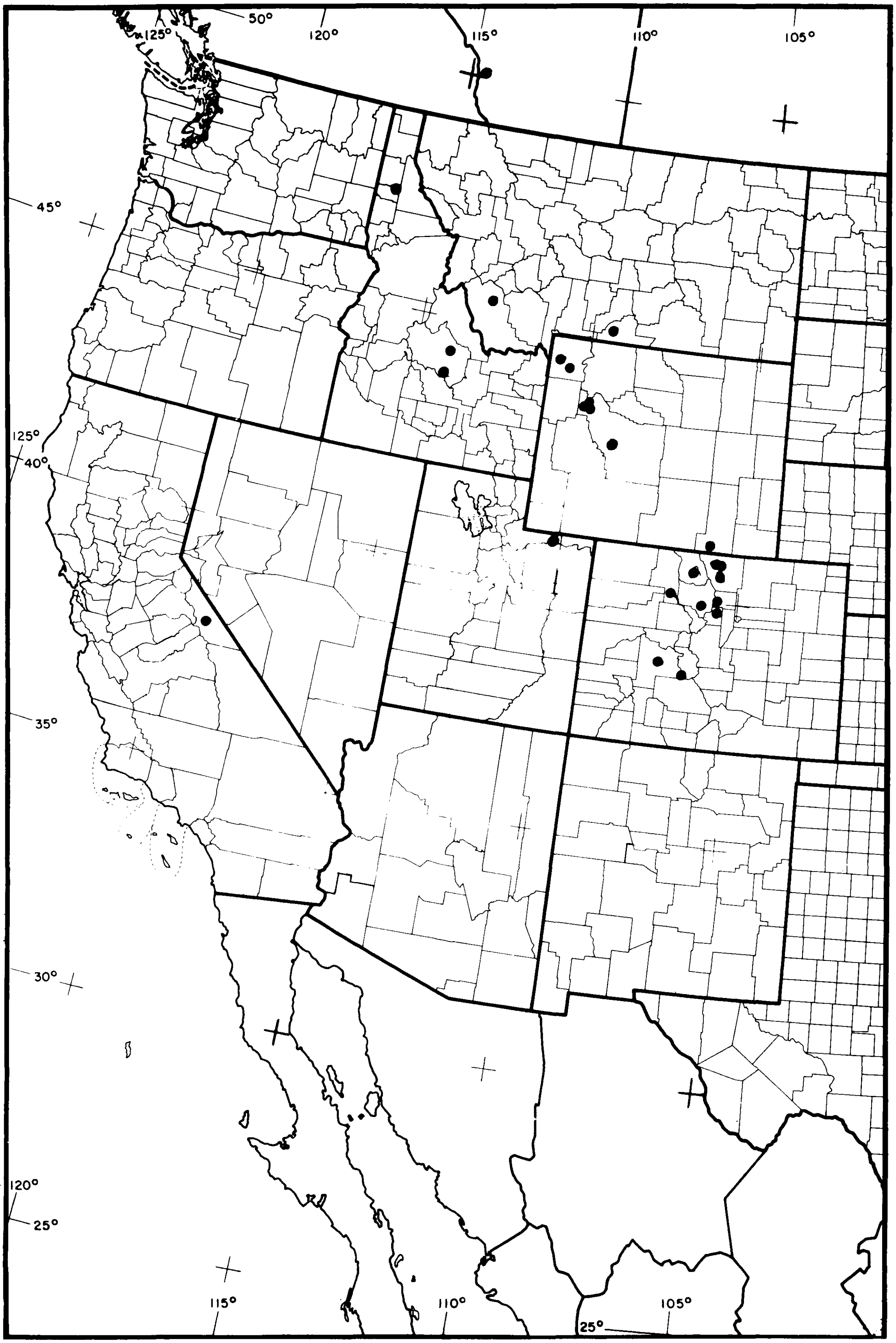

Figure 8.8 –Distribution of *Peridermium bethelii* in the western United States and Canada (updated from Hawksworth and others 1983).

Host–Parasite Physiology

Relatively few aspects of the relationship between the physiology of dwarf mistletoes and that of their hosts have been studied (Gill and Hawksworth 1961, Hawksworth 1958). The general physiology of mistletoes has been reviewed by Knutson (1979, 1983) and that of parasitic higher plants by Atsatt (1983). Although there are more than 200 publications on various aspects of dwarf mistletoe physiology, there have been no previous attempts to synthesize this scattered literature. Most studies of dwarf mistletoe physiology have dealt with water relations, photosynthesis, and carbon transport from host to parasite. A few attempts have been made to culture these parasites *in vitro*, and some recent research has focused on the role of growth regulators in the host–parasite interaction.

Water Relations

All mistletoes must move water and nutrients from the host to the parasite. The osmotic concentration of the parasite's cell sap must therefore be higher than that of the host (Fisher 1983, Hartel 1937). Some early physiological studies of the dwarf mistletoes compared osmotic concentrations of parasite and host: *Arceuthobium douglasii* on *Pseudotsuga menziesii* in Utah (Harris 1934, Korstian 1924a); *A. americanum* on *Pinus contorta* in Utah (Korstian 1924a); *A. cyanocarpum* on *P. flexilis* in Colorado (Harris 1934); and *A. vaginatum* subsp. *cryptopodum* on *P. ponderosa* in Arizona (Korstian 1924a) and Utah (Harris 1934). Average osmotic concentration of the mistletoes was −19.5 bars compared to −17.5 for the hosts. Even though differences between host and parasite are relatively small, osmotic concentration may limit the distribution of dwarf mistletoes in some parts of their hosts' range. For example, *A. vaginatum* subsp. *cryptopodum* is absent on *P. ponderosa* near its lower elevational limits in Colorado and the Southwest, where osmotic concentration differences are the least (Hawksworth 1959b). Mark and Reid (1971) reported that water potential gradients enabled *A. americanum* to obtain water from *Pinus contorta* in Colorado, even when the host was under considerable water stress. The average water potential of the parasite was −21.3 bars compared to −14.7 bars for the host.

The most intensive studies of water relations in dwarf mistletoes were by Fisher (1975, 1983) and Fisher and Reid (1976) for *Arceuthobium americanum* on *Pinus contorta* and *A. vaginatum* subsp. *cryptopodum* on *P. ponderosa* in Colorado. They used thermocouple psychrometers to monitor the airstream before and after it passed through cuvettes enclosing transpiring tissues. On a surface area basis, transpiration rates of the dwarf mistletoe were as much as 4 times the transpiration rates for the host. In other tests, infected pine seedlings were grown in cultures with solutions containing various concentrations of polyethylene glycol to obtain osmotic potentials from 0 to −15 bars. The dwarf mistletoes generally showed a lower water potential than the host, varying from −3 bars among well-watered hosts to −6 bars for hosts under the severest water stress.

Tocher and others (1984) studied the water relations of several dwarf mistletoe–infected seedlings: *Pinus contorta / Arceuthobium americanum, P. ponderosa / A. campylopodum,* and *Tsuga heterophylla / A. tsugense.* Transpiration rates for the mistletoes on pine were at least 8 times greater than that of their hosts under all conditions of moisture stress and darkness. The differences were greatest (up to 60 times), however, when the host was under the greatest water stress. Transpiration rates of host and parasite were comparable only for *T. heterophylla* growing under well-watered conditions. Quraishi and others (1977) observed that transpiration rates of *A. oxycedri* in Pakistan were about 4 times that of its host, *Juniperus excelsa.*

Kirkpatrick (1989) studied water relations of *Pinus contorta* infected by *Arceuthobium americanum* in central Oregon. Null-balance porometry was used to measure water vapor conductance of infected trees *in vivo.* Under optimal moisture conditions (May and June), conductance in the dwarf mistletoe was usually less than that in the host. Under summer drought conditions (August and September), however, conductance in the parasite was typically from 2 to 5 times that of the host.

Dwarf mistletoes, therefore, typically exhibit higher levels of transpiration than their hosts. If abundant moisture is available, then these differences are not great; but when the host is under moisture stress, the dwarf mistletoes maintained their high transpiration rates, thus greatly magnifying the differences. We suggest that the high transpiration rates observed in all mistletoes, in contrast to their hosts, increases mineral acquisition by mistletoes, which generally are considered to be nutrient sinks (Lamont 1983b).

Carbon Transport, Photosynthesis, and Respiration

One of the earliest studies to determine the direction of nutrient flow between host and parasite was by Weir (1916b). He removed all needles from small trees of *Pinus contorta* infected by *Arceuthobium americanum* and from comparable uninfected trees. After 2 years, uninfected trees were dead, but infected trees were still alive; these results perhaps suggest that there had been some translocation of nutrients from parasite to host.

Rediske and Shea (1961) noted that a significant proportion of radioactive photosynthate (mostly sucrose) produced by *Arceuthobium americanum* was translocated into its *Pinus contorta* host. These results, however, have not been confirmed by subsequent workers, and the present consensus is that there is little, if any, translocation of parasite-derived photosynthates from dwarf mistletoes to their host plants.

The most comprehensive studies of photosynthesis and carbon transport in *Arceuthobium* were by Hull and Leonard (1964a, 1964b) and Leonard and Hull (1965). They examined 8 species of dwarf mistletoes in California and concluded that mistletoes derived organic nutrition primarily from their hosts. The endophytic system and shoots accumulated labeled assimilates from their hosts at all seasons of the year. The dwarf mistletoes carried on limited photosynthesis, but no labeled carbon assimilates migrated through the endophytic system into the host. There was, however, limited translocation of labeled phosphorus from parasite to host, apparently through the apoplast.

Chlorophyll content of dwarf mistletoe seeds and shoots is on the order of 0.24 to 0.48 mg/g (Hull and Leonard 1964b, Tocher and others 1984), which is about 10 to 25% of the chlorophyll level of their hosts' foliage. The chlorophyll a/b ratio in *Arceuthobium* ranges from 1.3 to 2.8.

The growing hypocotyl of *Arceuthobium* is chlorophyllous, but the importance of photosynthesis in its establishment and early growth has been debated (Cohen 1963, Scharpf 1970). Muir (1975) reported that seeds of *A. occidentale* were photosynthetically able to fix small amounts of carbon dioxide, comparable to that of shoots (Hull and Leonard 1964b). Muir (1975) suggested that this source could provide significant levels of energy and carbohydrates during germination. Tocher and others (1984) and Gustafson and Tocher (1980) also concluded that *Arceuthobium* seeds fixed carbon dioxide.

How much of the photosynthate used by dwarf mistletoes is produced by the parasite and how much is derived from the host has been the subject of a few studies. You (1985) suggests that most of the photosynthates used by *Arceuthobium chinense* growing on *Keteleeria* in China are derived from the host. Hull and Leonard (1964b) reported that dwarf mistletoes produce about 30% of their needed photosynthates. Rey and others (1991) suggested that *A. oxycedri* parasitizing juniper in France produces about 50% of its needed photosynthate. However, this species has a deeper green color than any other (see fig. 16.126) and may, therefore, have a higher chlorophyll content and greater photosynthetic activity than other dwarf mistletoes. It appears unlikely that such exceedingly reduced species as *A. minutissimum* (see fig. 16.123, 16.124) or *A. pusillum* (see fig. 16.86) can contribute significant photosynthate to their extensive endophytic systems. These species are characterized by large, systemic infections and are exceedingly damaging to their hosts.

Rates of dark respiration for *Pinus contorta* shoots infected by *Arceuthobium americanum* were significantly lower than for comparable uninfected shoots (Wanner and Tinnin 1986), but dwarf mistletoe shoots exhibited higher respiration rates than host foliage.

Other Physiological Aspects

Minerals

Lamont (1983b) presented an excellent review of mineral nutrition in both mistletoe families. The dwarf mistletoes, as do mistletoes generally, selectively absorb minerals from their hosts and act as nutrient sinks. McDowell (1964) reported that concentrations of nitrogen, phosphorus, potassium, and magnesium were higher in *Arceuthobium campylopodum* than in its host, *Pinus ponderosa*. In contrast, calcium levels were lower in the mistletoe than in the host, which is consistent with parasitic phanerogams generally (Lamont 1983b).

Singh and Carew (1989) analyzed concentrations of a number of elements (N, P, K, Mg, Na, Ca, Fe, Zn, Mn, Cu, Al, and Ni) in the foliage, bark, and wood of uninfected *Picea mariana* trees as well as trees infected by *Arceuthobium pusillum.* They did not, however, detect meaningful differences in macronutrient or micronutrient concentrations for any of the plant parts analyzed.

Growth Substances

The dwarf mistletoes do not produce all the assimilates they need and thus must appropriate most of them from their hosts. This accumulation of assimilates, or "nutrient sink," is likely the result of changes in the host induced by growth substances, particularly cytokinins (Knutson 1979, Livingston and others 1984). Paquet (1979) studied the relative concentrations of cytokinins in *Arceuthobium douglasii* and its host, *Pseudotsuga menziesii* and in *A. tsugense* on *Tsuga heterophylla.* In general, concentrations of cytokinins were from 2 to 10 times higher in mistletoes than in their hosts. Zeatin riboside was the most common cytokinin, but zeatin and N6–adenosine were also present in smaller amounts.

Schaffer and others (1983) examined cytokinins in a dwarf mistletoe that induces witches' brooms, *Arceuthobium vaginatum* subsp. *cryptopodum* on *Pinus ponderosa,* and in one that does not, *A. occidentale* on *P. sabiniana.* Cytokinins were less concentrated in the species that does not induce witches' broom formation. Concentrations of cytokinins were highest in dwarf mistletoe shoots, less in mistletoe-infected branches, and not detectable in uninfected branches. Whether cytokinins in dwarf mistletoe shoots were produced by the parasite or whether they originated from infected branches was not determined.

Uninfected stem tissues from *Picea mariana* and tissues infected by *Arceuthobium pusillum* were assayed for abscisic acid (ABA), indole-3-acetic acid (IAA), zeatin, and zeatin riboside (Livingston and others 1984). Zeatin was not detected in the analysis, but concentrations of zeatin riboside and IAA were generally higher for infected tissues than for uninfected tissues tested from April to October. However, ABA levels were consistently lower for infected tissues throughout the test period. The authors concluded that increases in cytokinins and IAA, in conjunction with decreases in ABA, altered the growth substance composition and resulted in sink formation, stem swellings, and loss of apical dominance by infected branches.

Nitrogen and Nitrogen Metabolism

The concentration of nitrogen is generally higher in all mistletoes than in their hosts (Lamont 1983b). Knutson (1979) considered nitrogen a critical element in host–parasite physiology. The element is absorbed as ammonium and organic nitrogen rather than as nitrate. Greenham and Leonard (1965) made comparative host–parasite analyses of 22 amino acids in 6 mistletoes, including 4 dwarf mistletoes. Mistletoes generally had higher concentrations of both free and bound amino acids than their hosts, although the amino acid composition of the mistletoes closely resembled that of the host. *Arceuthobium abietinum* contained gamma aminobutyric acid, but its host, *Abies concolor,* did not. Shoots of all mistletoes tested contained asparagine, but most hosts did not. McDowell (1964) also found that *Arceuthobium campylopodum* had a similar amino acid composition to that of its host *(Pinus ponderosa),* except cysteic acid was present only in the dwarf mistletoe and glycine only in the host. Asparagine was the primary amino acid transferred from host to parasite in *A. oxycedri* (Rey and others 1991), and glutamine was present in the parasite only after periods of active growth (Evstigneeva and Aseeva 1967). *Arceuthobium oxycedri* was able to synthesize valine and isoleucine (Kagan and others 1964).

In Vitro Culture

Blakely (1959) unsuccessfully attempted *in vitro* propagation of seeds of *Arceuthobium douglasii* on callus-tissue cultures of *Pseudotsuga menziesii.* In a few cases, callus cultures of infected *P. menziesii* tissues were grown *in vitro,* but these were short-lived. Bonga (1968, 1972, 1974) attempted to culture *A. pusillum* on various media, but was unable to maintain cultures beyond seed germination and modified holdfast development.

Conclusions

The physiological processes causing reduced growth rates and eventual host mortality due to infection by dwarf mistletoes have not been adequately defined. The available information, however, allows us to speculate on some aspects of the interaction (Knutson 1979). The dwarf mistletoes initiate disease by penetrating the host and producing hormones (probably mostly cytokinins). These hormones cause increased translocation of nutrients to the dwarf mistletoe at the expense of the host's uninfected parts. This change is shown by the increased size of infected branches and increased ratio of branch to main stem biomass (Wanner and Tinnin 1986). The higher transpiration rates of dwarf mistletoe shoots and their higher cytoplasmic osmotic concentrations cause disproportionately higher rates of water and absorbed nutrient movement from the host to infected sites. This shift establishes a source–sink relationship. In addition, the concomitant loss of sugars, amino acids, and amines to the parasite also severely affects the host. As more and more nutrients are transferred from the host to infected branches and dwarf mistletoe shoots, main stem growth steadily declines. When there is insufficient foliage on a tree to sustain minimal photosynthetic capacity, growth ceases and death follows. Mortality is often hastened by secondary infestations of insects, such as bark beetles, when the tree is in decline.

The witches' brooms formed by most dwarf mistletoes cause greater losses of nutrients and water from the host than do the dwarf mistletoe plants themselves. This difference has been demonstrated by growth rates of broomed and non-broomed trees with the same infection ratings (Hawksworth 1961a); diameter growth rates of non-broomed trees was 4 to 6 times greater than that of comparable broomed hosts. Trees also recover vigor following broom removal, which is taken as further evidence of the debilitating effects of witches' brooms on tree growth and vitality (Hawksworth and Johnson 1989a, Lightle and Hawksworth 1973, Scharpf and others 1987).

Anatomy of the Dwarf Mistletoe Shoot System

Carol A. Wilson and Clyde L. Calvin *

In this chapter, we present an overview of the structure of the *Arceuthobium* shoot system. Anatomical examination reveals that dwarf mistletoes are indeed well adapted to a parasitic habit. An extensive endophytic system (see chapter 11) interacts physiologically with the host to obtain needed resources (water, minerals, and photosynthates); and the shoots provide regulatory and reproductive functions. Beyond specialization of their morphology (i.e., their leaves are reduced to scales), the dwarf mistletoes also show peculiarities of their structure that reflect their phylogenetic relationships with other mistletoes and illustrate a high degree of specialization for the parasitic habit. From *Arceuthobium globosum,* the largest described species with shoots 70 cm tall and 5 cm in diameter, to *A. douglasii,* a small species with shoots 3 cm tall and 0.3 cm in diameter, the anatomical features are consistent.

We have studied diverse species of *Arceuthobium,* including large primitive species and highly reduced specialized species. For this account, however, we concentrated on the shoots of *A. globosum* and *A. tsugense.* We chose these species for several reasons: (1) material on developmental stages was available; (2) *A. globosum* presumably represents a primitive member within the genus, whereas *A. tsugense* represents intermediate specialization; and (3) these species represent the two geographical areas of greatest speciation, central Mexico and northern California. Where appropriate, we compare features of *Arceuthobium* with the related genera *Korthalsella, Phoradendron,* and *Viscum.* These three genera share features with *Arceuthobium,* and *Korthalsella* had been proposed as a sister genus to *Arceuthobium* (Wiens and Barlow 1971, but see chapter 15).

In this chapter, we focus on leaf, stem, and fruit structure, and, wherever possible, attempt to relate structure to function. General morphology presents the best starting point for discussing the shoot system of *Arceuthobium.*

Morphology of Shoots

Arceuthobium does not produce shoots immediately after germination. The endophytic system first develops within the host branch. Oftentimes, the only evidence of infection is swelling of the tissues near the infection site (Scharpf 1967). After 1 to 3 years, the first shoots are produced (table 2.1). All shoots arise from the endophytic system and thus are root-borne shoots (Groff and Kaplan 1988). In emerging shoots, the leaves of adjacent nodes overlap and conceal the stem. As the internodes elongate, stem segments become visible; but the shoot apex remains tightly enclosed by newly developing leaf primordia (fig. 10.1A). Two oppositely arranged leaves, joined at their bases, occur at each node (fig. 10.1A–B). This decussate phyllotaxis characterizes the entire genus.

The mature, paired leaves form a boat-shaped structure that encircles the main stem and its branches at the node (fig. 10.1B–C). The merged leaf bases typically extend some distance into the internode below the attachment point (fig. 10.1D). This contributes to the much larger diameter of the internode below the point of attachment than above (fig. 10.1B). Generally, the mean diameter of the stem 1 to 2 mm below the node measures almost twice the diameter an equal distance above. The merger of leaf structure into the main axis results in a stem morphology in which internodes widen in an acropetal direction, particularly in the upper third of the internode. The functions of the widened upper portions of internodes are discussed more fully in a later section on the epidermis.

Several different branching patterns occur in *Arceuthobium* (fig. 2.1). The *A. tsugense* shoot (fig. 10.1B) displays decussate branching, a pattern common for shoots with decussate phyllotaxis. The evolutionary and systematic importance of these patterns was established by Kuijt (1970) and further refined by Hawksworth and Wiens (1972) and by Mark and Hawksworth (1981).

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* Department of Integrative Biology, University of California, Berkeley and Department of Biology, Portland State University, Portland, OR, respectively; contributed as Environmental Sciences and Resources Program Publication No. 242.

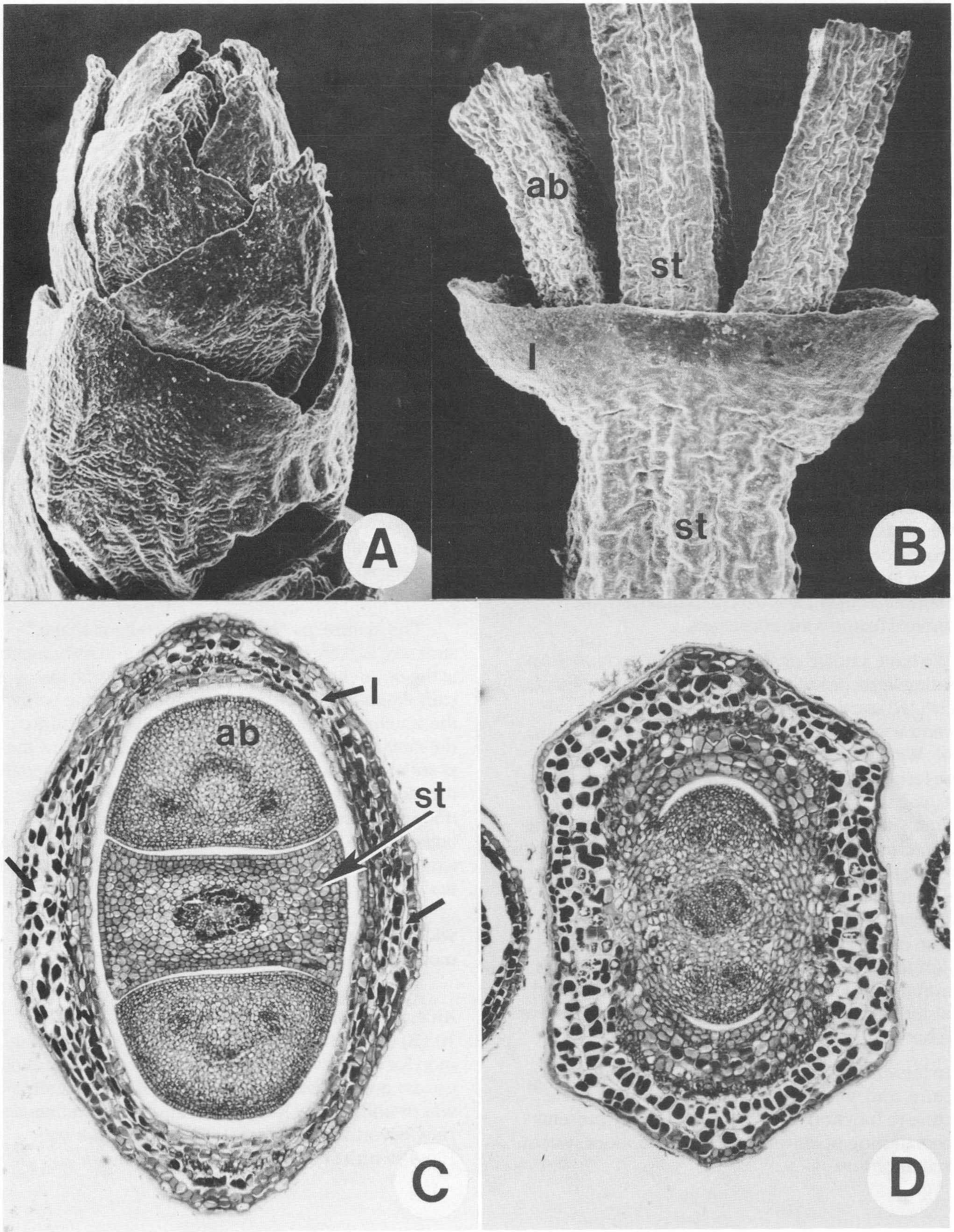

Figure 10.1 –Surface (A-B) and transectional views (C-D) of *Arceuthobium tsugense* shoots. A: shoot tip showing opposite, paired leaves and decussate phyllotaxis, ×60. B: nodal region showing stem (st), mature leaves (l) and axillary branches (ab), ×25. C: leaf 300 μm above point of attachement to stem, unlabeled arrows at points where leaf margins join, ×31. D: stem at point of leaf base fusion, ×31.

Shoot Apical Organization

In median longitudinal section, a shoot tip of *Arceuthobium* (fig. 10.2A) shows a highly stratified apex. Two stratified layers were present in all shoot apices that we examined. Although we did not analyze a large enough sample (Gifford 1954) to state authoritatively the number of tunica layers present, our observations suggest that the tunica is biseriate. A biseriate tunica has also been reported for *Phoradendron* (Cutter 1955). In the apices we examined, axillary buds were visible in the axils of the third leaf pair and were well developed in the axils of the fifth leaf pair. Studying several parasitic and "saprophytic" angiosperms, Cutter (1955) found no anomaly of shoot apical organization associated with these nutritional modes. Mauseth and others (1985) examined shoots of the mistletoe *Tristerix aphyllus* (Loranthaceae) and arrived at the same conclusion. Through our observations of *Arceuthobium* (fig. 10.2A–B), we concur.

Leaf Anatomy

Although *Arceuthobium* is described as "leafless," shoots are in fact squamate; that is, they bear simple, scale-like leaves. Leaves are initiated at the periphery of the shoot apex by periclinal divisions in the subsurface layer (fig. 10.2B). When leaves are initiated, primordia are more or less circular in transverse section, and each primordium is independent. As development continues, however, meristematic activity is limited to the lower leaf zone, so that by the third leaf pair the leaf bases are visible as a single unit due to congenital fusion. Leaf bases continue to expand and are tubular at maturity; but the upper leaf zone, which was prominent in early development (fig. 10.1A), becomes almost indistinguishable (fig. 10.1B).

Three stages of leaf development in *Arceuthobium tsugense* are shown in transverse sections in figure 10.2C–E. In figure 10.2C, a more or less continuous plate of procambial tissue occupies the center of the leaf, and one mature tracheary element is visible (at arrow). No other cells have matured from procambium at this level. At a slightly later developmental stage (fig. 10.2D), one mature tracheary element (at arrow), plus several adjacent cells in which secondary wall deposition is beginning, can be seen. In figure 10.2E, an older developmental stage, all procambial derivatives have matured. Several tracheary elements are present (at unlabeled arrows), but the majority of derivatives have matured as sclerified parenchyma cells, each with numerous, large, simple pits. Sclerified parenchyma cells abut directly against the tracheary elements (fig. 10.2E). No sieve elements were seen in any of the leaves we examined. In older leaves, sclerified parenchyma forms a mostly continuous plate of tissue that continues into the leaf base. This sclerified tissue is absent in the internode beneath the leaf base. Some of the cells contiguous with this sclerenchymatous layer contain rhomboidal (prismatic) crystals (fig. 10.2E). The sclerified parenchyma in *A. globosum* veins generally extends acropetally a greater distance than the tracheary elements; but in some cases, the two tissues appear to terminate at about the same level. Some tracheary elements at vein endings appeared to be tracheids. In more proximal positions, however, vessel members were present.

The ground tissue in leaves of *Arceuthobium tsugense* consists mainly of parenchyma, and only an occasional sclereid is present. As viewed basipetally in developing leaves (figs. 10.1C–D), chlorenchyma tissue begins as small groups of large cells in the midvein region and fused margins of the leaf. Moving basipetally, chlorenchyma becomes more abundant at the margins where the leaves are joined (at unlabeled arrows in fig. 10.1C). At a lower level where the leaf joins the stem, chlorenchyma occurs all the way around the sheathing leaf base (fig. 10.1D). This chlorenchyma layer is 3 to 5 cells thick around the entire stem (fig. 10.1D). No differentiation of the mesophyll into palisade and spongy tissue occurred in any of the species we examined, and intercellular space was minimal.

The leaf epidermis contains ordinary epidermal cells and stomatal complexes consisting of guard cells and subsidiary cells. No trichomes are present. Stomata are abundant in the abaxial epidermis but are sparse or absent in the adaxial epidermis. The abaxial stomata density on fully developed leaves reaches 38 per mm^2 (table 10.1). This value compares to those reported for leaves of numerous nonparasitic angiosperms (Meyer and Anderson 1952). As reported for many other members of Santalales (Butterfass 1987), stomata have a transverse orientation with respect to the plant axis. As viewed in transverse (fig. 10.3A) and longitudinal (fig. 10.3B) sections, guard cells are recessed beneath over-arching subsidiary cells. The subsidiary cells project above the surface and form a small crypt (fig. 10.3C) at the bottom of which occurs the stomatal aperture (fig. 10.3B). A small substomatal chamber is present (fig. 10.3B); but generally, cells of the stomatal complex have wall contacts with cells in the subepidermal layer (figs. 10.3A–B).

Epidermal cells are covered by a thick cuticular layer (fig. 10.3A) that may be waxy (fig. 10.3C). The

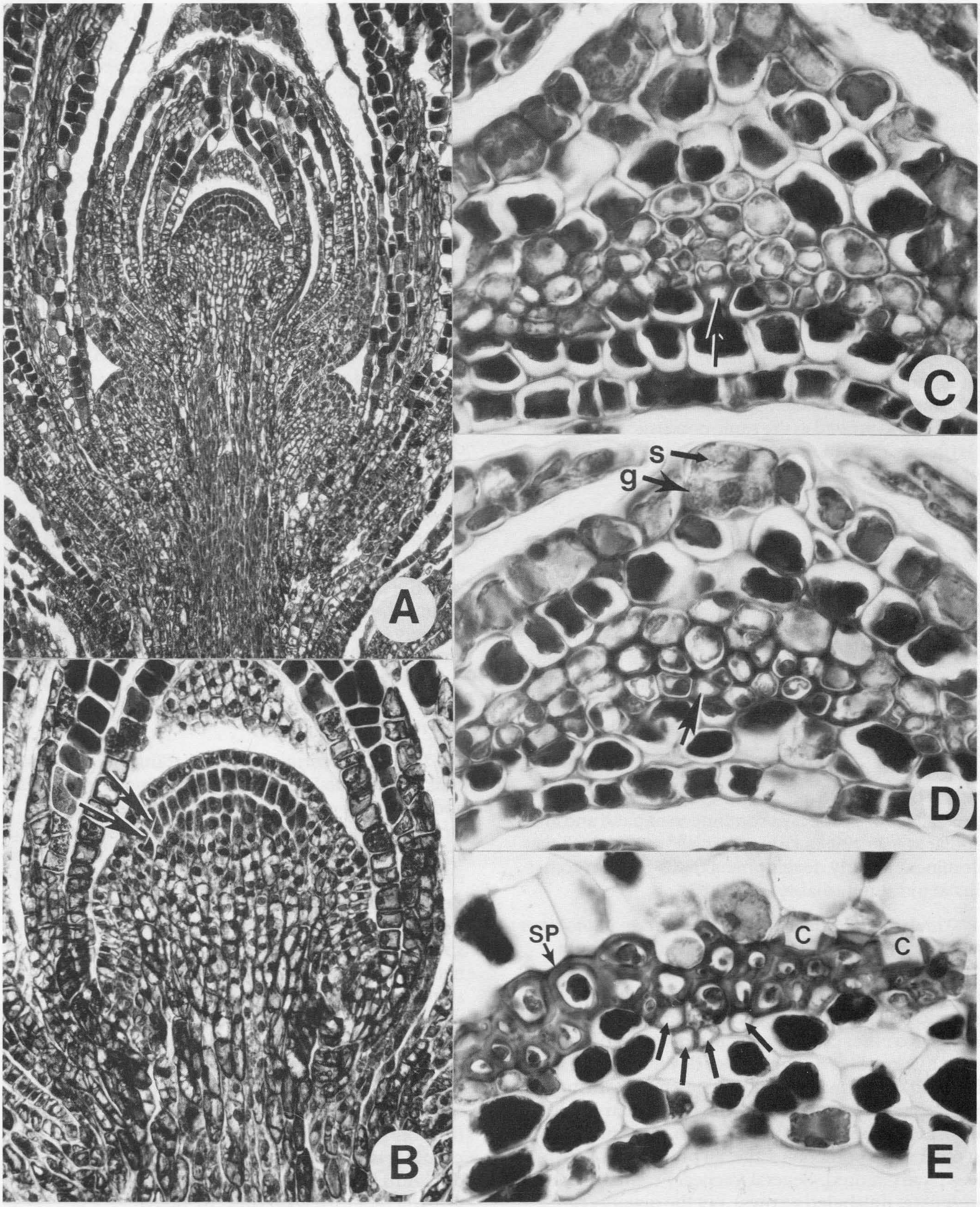

Figure 10.2–Longitudinal sections of stem tips of *Arceuthobium globosum* (A-B) and transverse sections of leaves of *A. tsugense* (C-E). A: shoot tip showing meristem and leaf primordia, ×40. B: apical meristem, periclinal divisions in subepidermal layer at unlabeled arrows, ×100. C-E: leaves at successive stages of maturation, showing xylem elements at unlabeled arrows, rhomboidal crystals (c), guard cells (g), subsidiary cell (s), and sclerified parenchyma (sp), ×250.

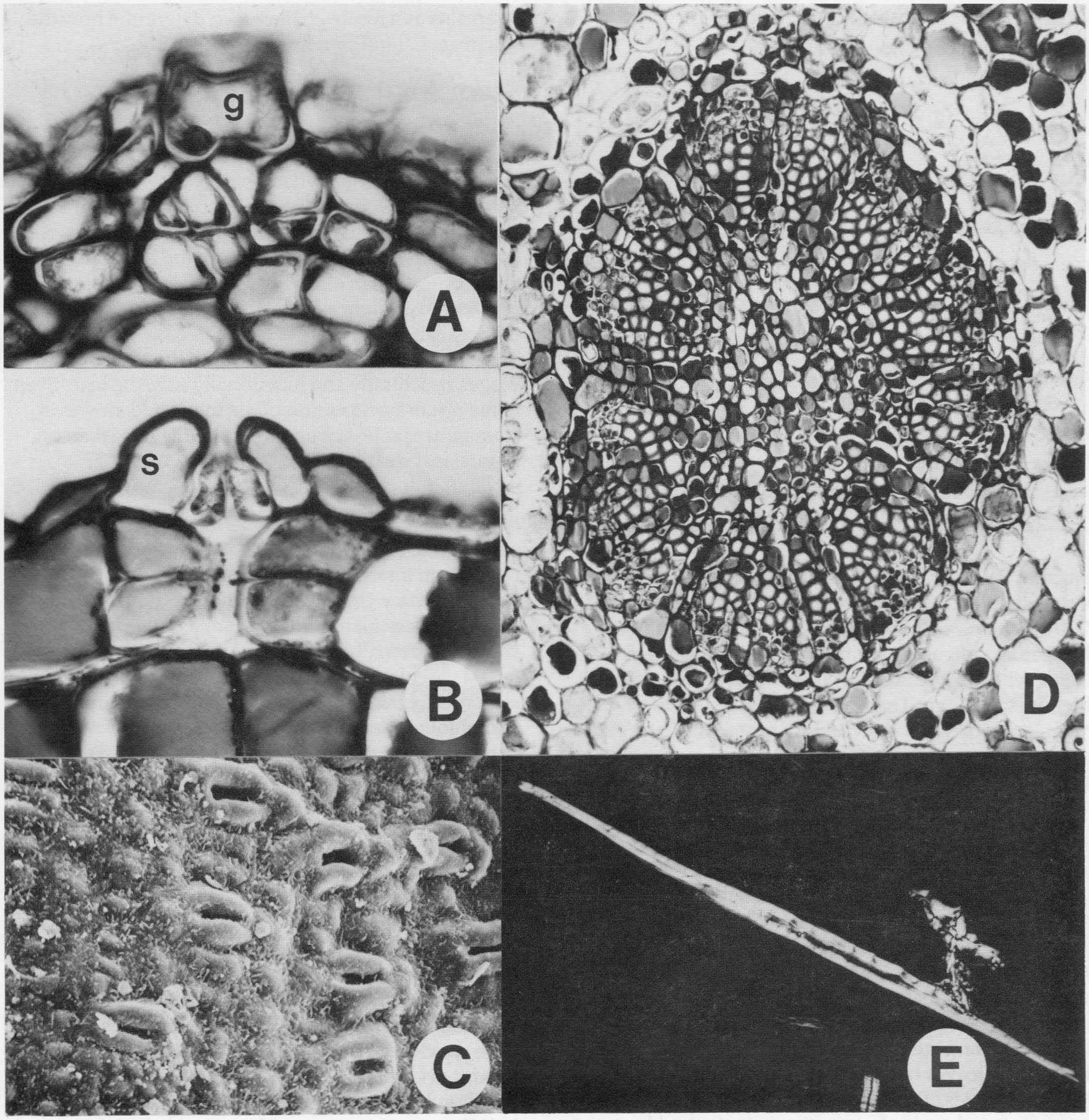

Figure 10.3 –Leaves in transverse (A), longitudinal (B), and suface view (C); stem in transverse view (D); and individual macerated cell (E), of *Arceuthobium tsugense* (A–D) and *A. durangense* (E). A: guard cell (g) ×300. B: subsidiary cell (s) and guard cells, ×300. C: SEM view showing emergent subsidiary cells, ×360; D: vascular cylinder, ×120. E: primary phloem fiber, ×48.

TABLE 10.1 – Stomatal distribution in *Arceuthobium americanum*

Plant part	Stomata (no./mm^2)
Leaf (N=9)	
abaxial surface	38.0 (3.0)
Internode (N=2)	
upper third	9.3 (0.2)
middle third	2.7 (0.0)
lower third	0.0
Fruit (N=9)	
distal portion	48.0 (3.5)
proximal portion	0.0

Source: unpublished data from L. Kirkpatrick. Values are mean and standard error in parentheses (N = sample size).

cuticular layer covering the abaxial epidermis is thicker than that on the adaxial surface. On the older (pair 7) *Arceuthobium tsugense* leaves that we examined, the abaxial cuticular layer had a mean thickness of 17 µm, whereas the adaxial cuticular layer had a mean thickness of 11 µm. Leaves occasionally develop a cuticular epithelium, a secondary protective layer that is well developed on stems (see discussion of epidermis).

Leaf reduction occurs in other genera of Viscaceae but not in all species. *Arceuthobium* and *Korthalsella* are entirely squamate, but only a few of the more than 150 *Phoradendron* species are squamate. Leaves of *Arceuthobium* undergo early development similar to other dicotyledons and possess certain features typical for autotrophic plants, such as a discontinuous pattern of xylem differentiation. At maturity, these leaves have a high density of stomata, a well-developed vascular system, and an extensive mesophyll. Leaf primordia and mature leaves have the dorsoventral symmetry typical of leaves. Development of the upper leaf zone stops at an early stage but continues in the basal zone. The presence of stomata and chlorenchyma suggests that these specialized leaves play important roles in gas exchange and photosynthesis. Also, young leaves of *Arceuthobium* protect the shoot apex during development, and mature leaves protect lateral branch primordia.

Although we know about some aspects of leaf reduction, interesting points remain unexplained. For example, while the squamate condition is common among Viscaceae, it is virtually absent in Loranthaceae. It remains as a future challenge to determine how the squamate habit serves the dwarf mistletoes.

Stem Anatomy

The shoot system of a plant consists of the stems and attached leaves. The division of the shoot into stem and leaf is somewhat arbitrary because the boundary between the two is often imprecise. This is particularly true in *Arceuthobium*. To illustrate, stomata are relatively more abundant on the distal third of the internode than elsewhere on the stem (table 10.1). The region of highest stomate density corresponds to the area where the leaf base extends down the stem. Thus, in the upper internode region the stem converges structurally and functionally with the leaf. Even in the uppermost portion of the internode, however, stomata are far less abundant (per unit area) than on abaxial leaf surfaces.

During primary growth, the stems of *Arceuthobium* have a structure similar to that of many terrestrial autotrophic dicotyledons. A transverse section through an internode of *A. tsugense* near the completion of primary growth shows that the stem bears a single ring of vascular bundles delimited internally by the pith and externally by the cortex (fig. 10.3D). The collateral vascular bundles contain, from inside to outside, protoxylem, metaxylem, residual procambium, and phloem tissue. The phloem may or may not contain sieve elements, but primary phloem fibers (fig. 10.3E), which in some species are only partially differentiated, and parenchyma cells are present (figs. 10.4A–B). As shown below, secondary growth complicates this otherwise typical stem anatomy.

Primary Growth

Primary growth forms the complete plant body; secondary growth only adds to this body. The extent of secondary growth in *Arceuthobium* varies greatly from species to species. Extensive secondary growth produces large plants such as *A. globosum*. An understanding of stem structure in *Arceuthobium,* particularly the vasculature, provides valuable insights into the physiology, evolution, and ecology of the genus.

The primary xylem contains tracheary elements and parenchyma. In the material we examined, all tracheary elements (where type could be determined) were vessel members with simple perforations (fig. 10.4C). Even in protoxylem elements with helical thickening, clearly delimited perforation plates were often visible. The presence of vessel members only agrees with Kuijt's (1960b) observation that in the four *Arceuthobium* species studied he had "yet to find a

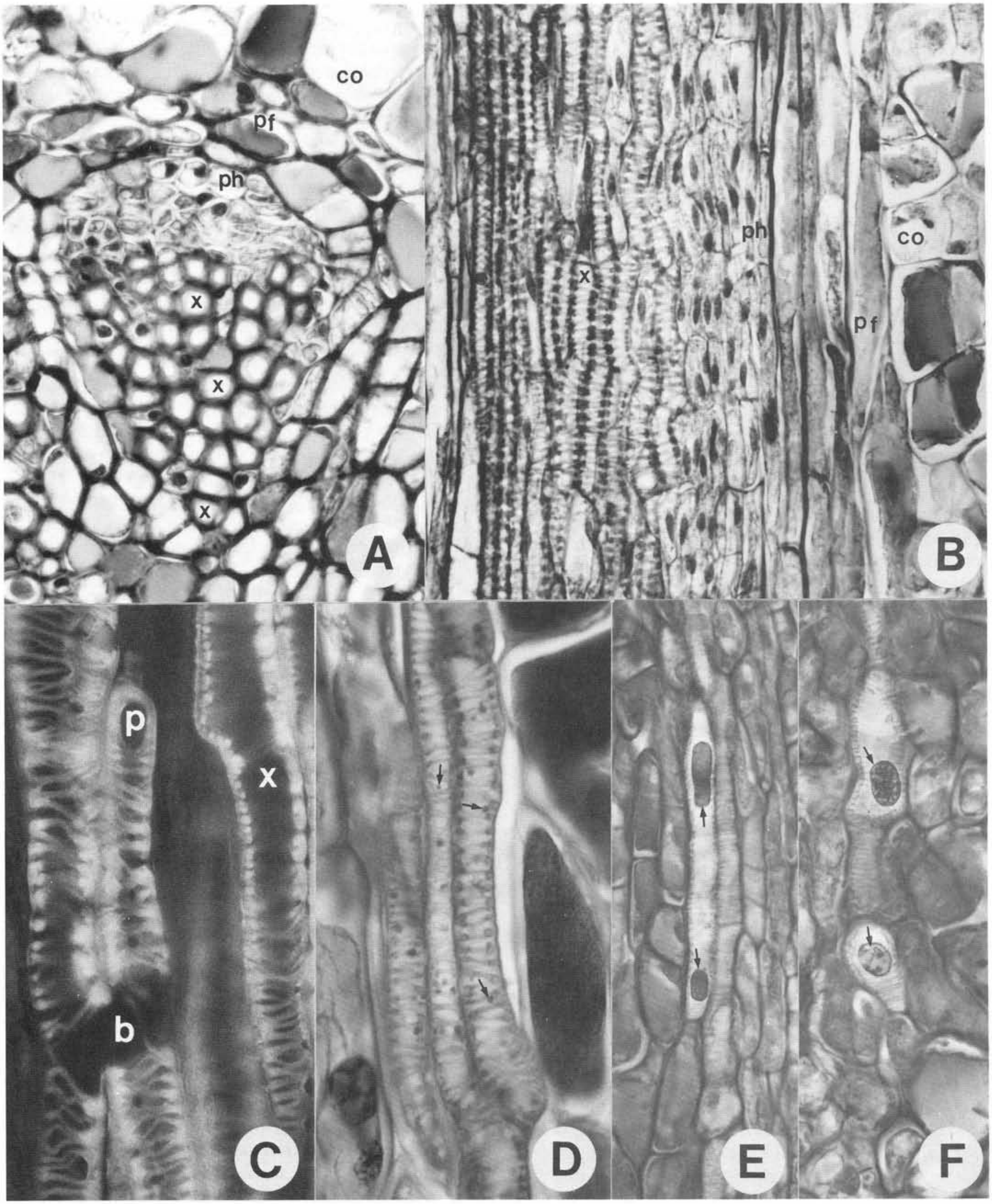

Figure 10.4 –Transverse (A) and longitudinal (B-F) sections of stems (A-C), leaf (D), and fruits (E-F) of *Arceuthobium tsugense* (A-B), *A. globosum* (C-D), and *A. cyanocarpum* (E-F). A: vascular bundle showing xylem (x), phloem parenchyma (ph), phloem fibers (pf), and cortex (co), ×100. B: vascular bundle, ×100. C: primary xylem (x) showing simple perforation (p) and breaks (b) in xylem continuity, ×480. D-F: graniferous tracheary elements, granules at unlabeled arrows (D, ×400; E-F, ×250).

xylem element without a perforation." Likewise, Calvin (1967a) reported only vessel members in stems of *Phoradendron*. Not all workers agree, however. Cohen (1954) interprets the tracheary elements in *A. campylopodum* to be tracheids, and Datta (1954) considers vessel members to be "completely absent" in the diminutive *A. minutissimum*. The observations of Cohen (1954) and Datta (1954) concerning the presence of tracheids need further confirmation.

In *Arceuthobium*, breaks in continuity occur between superimposed vessel members (fig. 10.4C). Similar breaks have been noted in *Phoradendron* (Calvin 1967a). In *Phoradendron*, we found that tyloses frequently were present in the breaks created by separation of vessel members. We did not find tyloses in *Arceuthobium* even though xylem parenchyma is abundant. Their absence indicates that the growth of the tyloses is not the cause of the discontinuities. These breaks likely occur when tracheary elements with non-extensible walls differentiate at levels where extension growth has not yet ceased.

Some parasitic plants have tracheary elements that contain granules or amorphous masses. These unusual cells have attracted attention because their function is not yet fully understood. Originally called "phloeotracheids," the cells were renamed "graniferous tracheary elements" by Fineran and others (1978). Fineran (1985) reviewed the historical and recent literature and also discussed the ontogeny, chemistry, and possible functions of these unusual xylem conducting cells.

Graniferous tracheary elements, which may be either tracheids or vessel members, have been observed most often in the haustoria of root-parasitic angiosperms. Fineran (1985) reported them in haustoria of selected members of Krameriaceae, Loranthaceae, Olacaceae, Opilaceae, Santalaceae, and Scrophulariaceae. Weber and Nietfeld (1984) confirmed these cells in *Arceuthobium oxycedri*, not only in haustoria but also in stems. We also have observed graniferous tracheary elements in *Arceuthobium*. They are present in leaves (fig. 10.4D), fruits (fig. 10.4E–F), stems, and haustoria. The graniferous tracheary elements may contain numerous small (fig. 10.4D) or one or more large granules (fig. 10.4E–F). The large granules may appear roughly amorphous (fig. 10.4E) or have a definite internal structure (fig. 10.4F). Both small and large granules may be present in a single tracheary element. With safranin-fast green, the small granules stain a dense bluish purple suggesting a proteinaceous content, whereas large granules have a translucent red appearance.

The primary xylem of *Arceuthobium* contains, in addition to tracheary elements, abundant parenchyma (Figs. 10.4A–B). These cells generally have large nuclei and appear rich in cytoplasmic contents. Some xylem parenchyma cells have large vacuoles that appear to contain phenolics. None of the parenchyma cells that we observed in primary xylem had secondary walls, and we found no fibers present in the primary xylem. Both *Phoradendron* (Calvin 1967a, see his figures 55 and 56) and *Viscum* (von Tubeuf 1923) have groups of primary xylem fibers, as well as sclerified parenchyma cells. In *Korthalsella*, Touw (1984) reports that intraxylary fibers occur and that these fibers may also occur interior to the xylem. It is not clear whether the intraxylary fibers of *Korthalsella* are of primary or secondary origin, but the fibers "central to the xylem" are interpreted to be equivalent to the primary xylem fibers of *Phoradendron*.

Primary phloem of the species we studied contains a variable number of cell types. Parenchyma cells and fibers are always present; sieve elements may be present, depending on the species. Parenchyma cells are enlarged, vacuolate cells located interior to the phloem fibers (figs. 10.4A–B). The parenchyma grades gradually into procambium within bundles. To the exterior, the parenchyma has a generally clear boundary with the phloem fibers (fig. 10.4B).

Protophloem fibers are present in all *Arceuthobium* species. In *A. tsugense* these fibers form a layer 2 to 5 cells thick (figs. 10.4A–B), whereas in woody species such as *A. globosum* fibers occur in bundles many cells thick. The cells are elongate with pointed ends and have intrusive growth (figs. 10.3E, 10.4B). Developing fibers are similar to those of *Phoradendron* (Calvin 1967a) in that they may have thickened primary walls. Secondary wall deposition in phloem fibers of *Arceuthobium* is variable. In *A. durangense* (fig. 10.3E) and *A. globosum* fibers may deposit secondary walls. We observed no secondary walls in *A. tsugense* (fig. 10.4B) or *A. americanum*. Mature fibers in the advanced species (*A. tsugense* and *A. americanum*) are morphologically similar to juvenile fibers in the more primitive species.

Sieve elements are absent or sparse in primary phloem. In *Arceuthobium tsugense* and *A. douglasii*, no cells were present in either the protophloem or metaphloem that could be positively identified as sieve elements. However, protophloem elements are naturally ephemeral and not easily observed or identified (Mauseth 1988). In *A. globosum*, we found no sieve elements that could be assigned with certainty to the protophloem, but sieve elements were present in the metaphloem. Using electron microscopy, Kuijt and Dong (1989) have confirmed the presence of sieve elements in *Korthalsella dacrydii*, a species that is significantly smaller than either *A. douglasii* or *A. tsug-*

ense. The reported absence of sieve elements in primary phloem of species such as *A. tsugense* and *A. douglasii* should be reevaluated utilizing electron microscopy.

Secondary Growth

The presence and extent of secondary growth varies greatly among the *Arceuthobium* species we studied. When the cambial state begins and how this state can be identified (Larson 1982) remain controversial. We limit our discussion of secondary vascular tissues to *A. globosum,* a species in which secondary growth is pronounced.

Secondary xylem of *Arceuthobium globosum* contains both parenchyma cells and tracheary elements (fig. 10.5A), but we observed no fibers. Parenchyma cells occur in both the axial and ray systems and may have thickened primary walls. Secondary walls were absent, however, even in woody stems exceeding 1 cm diameter. Contents of parenchyma cells vary. Most axial parenchyma cells are unspecialized. Their protoplasts stain a rich green with safranin-fast green (Jensen 1962) and contain prominent reddish nuclei. In our studies, a smaller percentage of cells stained a deep red, suggesting phenolic contents. Ray system cells were mainly of the latter type. We discovered no starch in parenchyma cells and no crystal-containing cells in the xylem.

Tracheary elements in *Arceuthobium globosum* occur as radial bands of cells, 1, 2, or occasionally 3 cells wide (fig. 10.5A). All tracheary elements we observed were vessel members with oblique to transverse simple perforations (fig. 10.5B). Perforations are small in diameter relative to cell width (fig. 10.5A at unlabelled arrows). Secondary wall thickening forms a reticulate pattern in cells, and bordered pits of lateral walls range from almost circular to strongly elliptical (fig. 10.5B). However, even the most "horizontally elongate" pit apertures do not exceed a wall face in width. Morphologically similar lateral-wall pitting has been reported for *Misodendron* (Carlquist 1985), the sole genus within the mistletoe family Misodendraceae. *Myoschilos* of the Santalaceae (Metcalfe and Chalk 1950) also displays this form of lateral-wall pitting. Carlquist (1988) noted a correlation between the presence of "horizontally elongate" pits and the abundance of axial parenchyma in wood. In *A. globosum,* virtually all tracheary elements contact parenchyma cells. Carlquist (1988) describes the horizontally elongate pits in *Misodendron* as scalariform-like, but he adds that such pits may not be relictual.

Secondary phloem of *Arceuthobium globosum* contains sieve elements and companion cells, plus axial and ray parenchyma (fig. 10.6). No fibers are present in secondary phloem, but groups of sclerified parenchyma cells and occasionally sclereids, probably

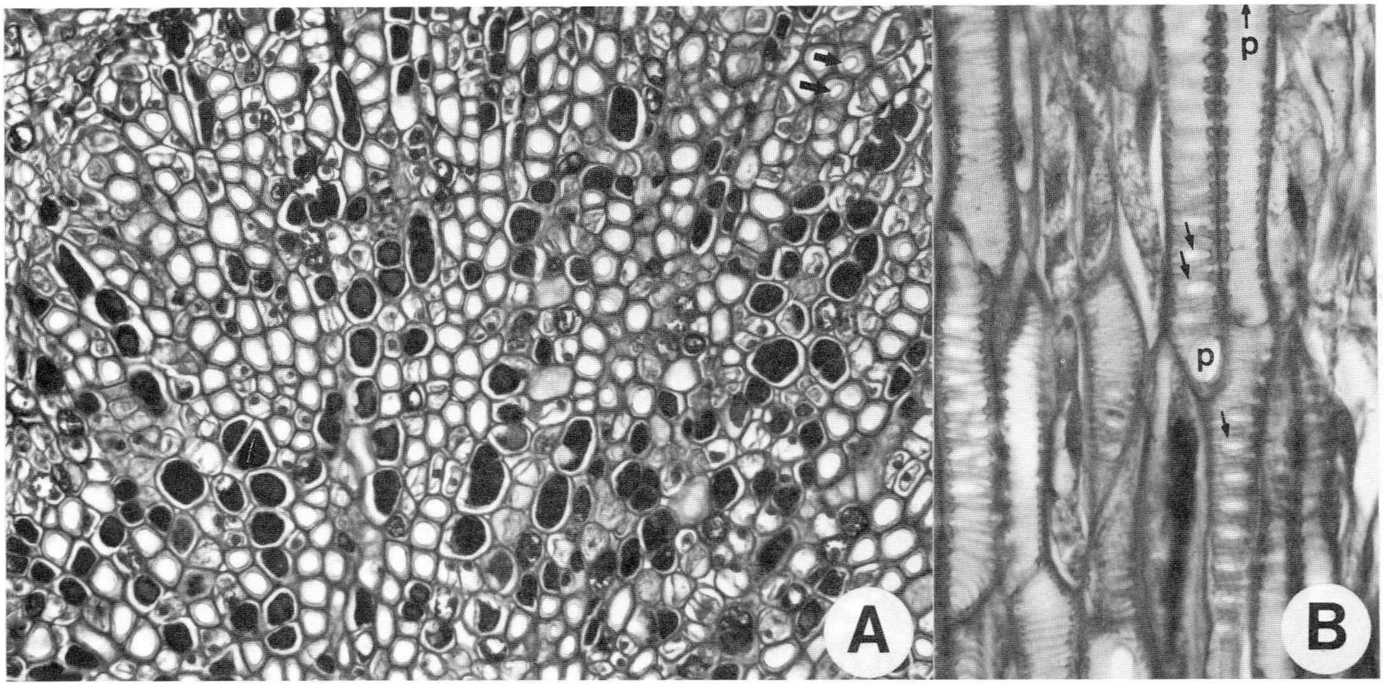

Figure 10.5–Transverse (A) and longitudinal (B) sections of *Arceuthobium globosum* wood. A: Simple perforations at unlabeled arrows in upper right corner, ×100. B: vessel members showing simple perforations (p) and lateral wall pitting (unlabeled arrows), ×250.

of secondary origin, do occur (fig. 10.7). Groups of sclerified cells are surrounded by short cells containing rhomboidal crystals. Walls of these crystal-containing cells also may sclerify. Rhomboidal crystals have been reported for some members of Loranthaceae, Misodendraceae, Santalaceae, and Viscaceae, as well as families not included within Santalales (Carlquist 1988). Within the Viscaceae, both *Viscum* (Fahn and others 1986) and *Phoradendron* contain rhomboidal crystals in their ray cells. Druses are also present in *Viscum* (Carlquist 1988) and *Phoradendron,* but we did not observe them in *Arceuthobium.*

Sieve elements of *Arceuthobium,* as described previously (Calvin and others 1984), have transverse to oblique, usually simple sieve plates (fig. 10.6B) and small but numerous diffuse lateral pores (fig. 10.6C–D). Sieve elements show a pattern of callose deposition and subsequent removal similar to that reported for other dicotyledons. As in *Phoradendron* (Calvin 1967b), companion cells are generally as large or larger in cross-section than accompanying sieve elements. Sieve elements do not appear to be particularly numerous in secondary phloem. Sieve tubes like those shown in figure 10.6 were difficult to find, even using sensitive fluorescence techniques to detect callose. Phloem parenchyma, in contrast, is abundant. Contents of axial parenchyma cells normally turn green with safranin-fast green stain, whereas protoplasts of ray cells often turn reddish, possibly due to phenolics.

Anomalous patterns of secondary growth, termed "cambial variants" by Carlquist (1988), occur in many plant families including the Loranthaceae and Misodendraceae. Successive cambia are formed in stems of the terrestrial mistletoe *Nuytsia* (Loranthaceae) and in *Misodendron,* subgenus *Angelopogon* (Carlquist 1988). However, the pattern of development is not identical. In *Nuytsia,* successive cambia form centrifugally; but they form centripetally in *Misodendron.* Reports of anomalous growth in *Arceuthobium* (Datta 1954, Metcalfe and Chalk 1950) and *Korthalsella* (Stevenson 1934) are problematic because they may refer to anomalous primary growth.

We observed anomalous secondary growth in *Arceuthobium.* For discussion here, we will exemplify the pattern by describing secondary growth for *A. globosum.* Cross sections of an older *A. globosum* stem (1 cm diameter) show discrete blocks of vascular tissue, and each block is separated by a broad band of

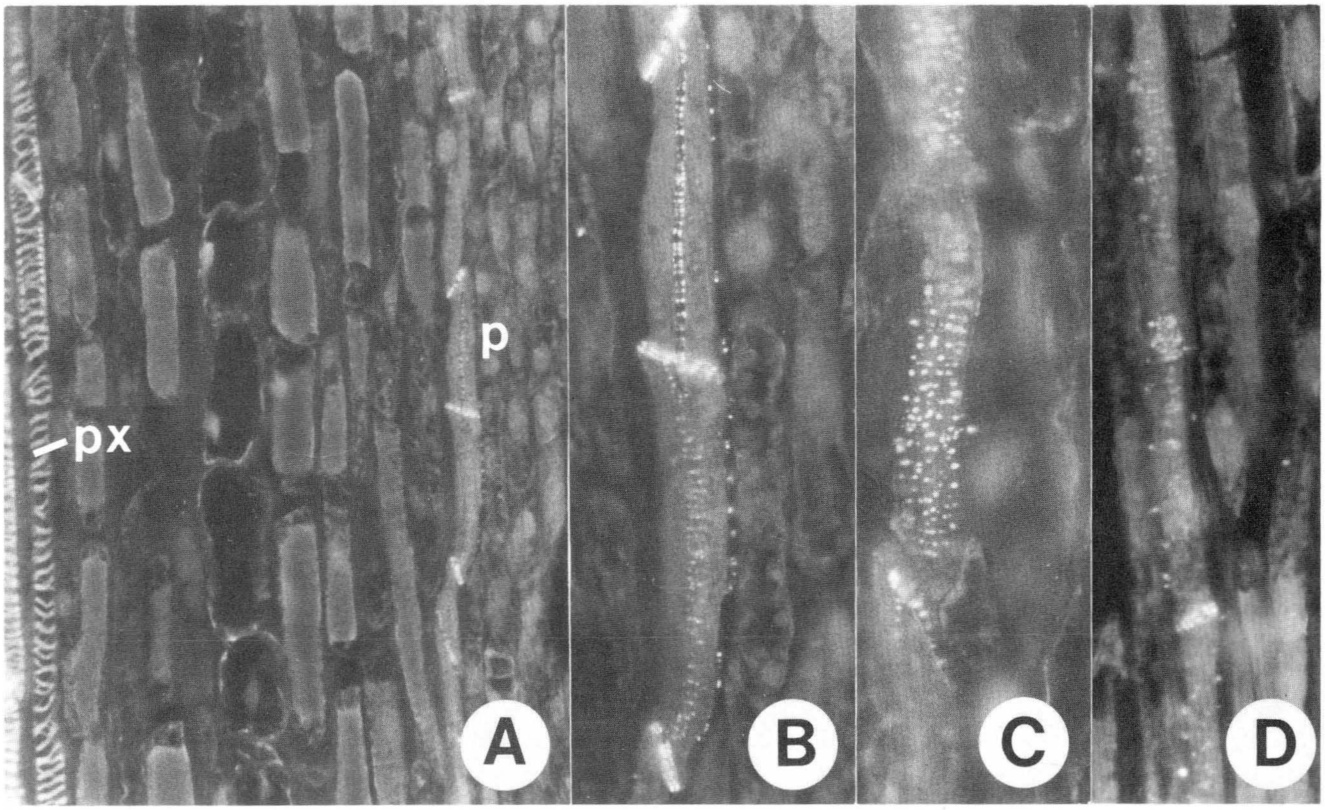

Figure 10.6–Longitudinal sections through secondary phloem of *Arceuthobium globosum.* A: sieve tube (p) and adjacent primary xylem (px), ×500. B: sieve tubes enlarged to show sieve plates and lateral sieve areas, ×1,250. C: lateral sieve areas in surface view, ×1,250. D: sieve tube showing oblique sieve plate and lateral sieve areas, ×960.

parenchyma (fig. 10.7A). In such blocks (fig. 10.7B), vascular cambium occurs not only centrifugal to secondary xylem but also extends radially along each flank of the block as far as the pith (fig. 10.7C). The extending cambial arms curve inward at this depth, initially towards each other, but gradually forming virtually a 180° turn (fig. 10.7D). At its inner limits, the cambial zone is interior to the protoxylem (fig. 10.7C–D). Due to the unusual configuration of the cambial zone within a vascular block, tracheary elements are differentiating in several directions. In secondary xylem (fig. 10.7D), for example, tracheary elements (at

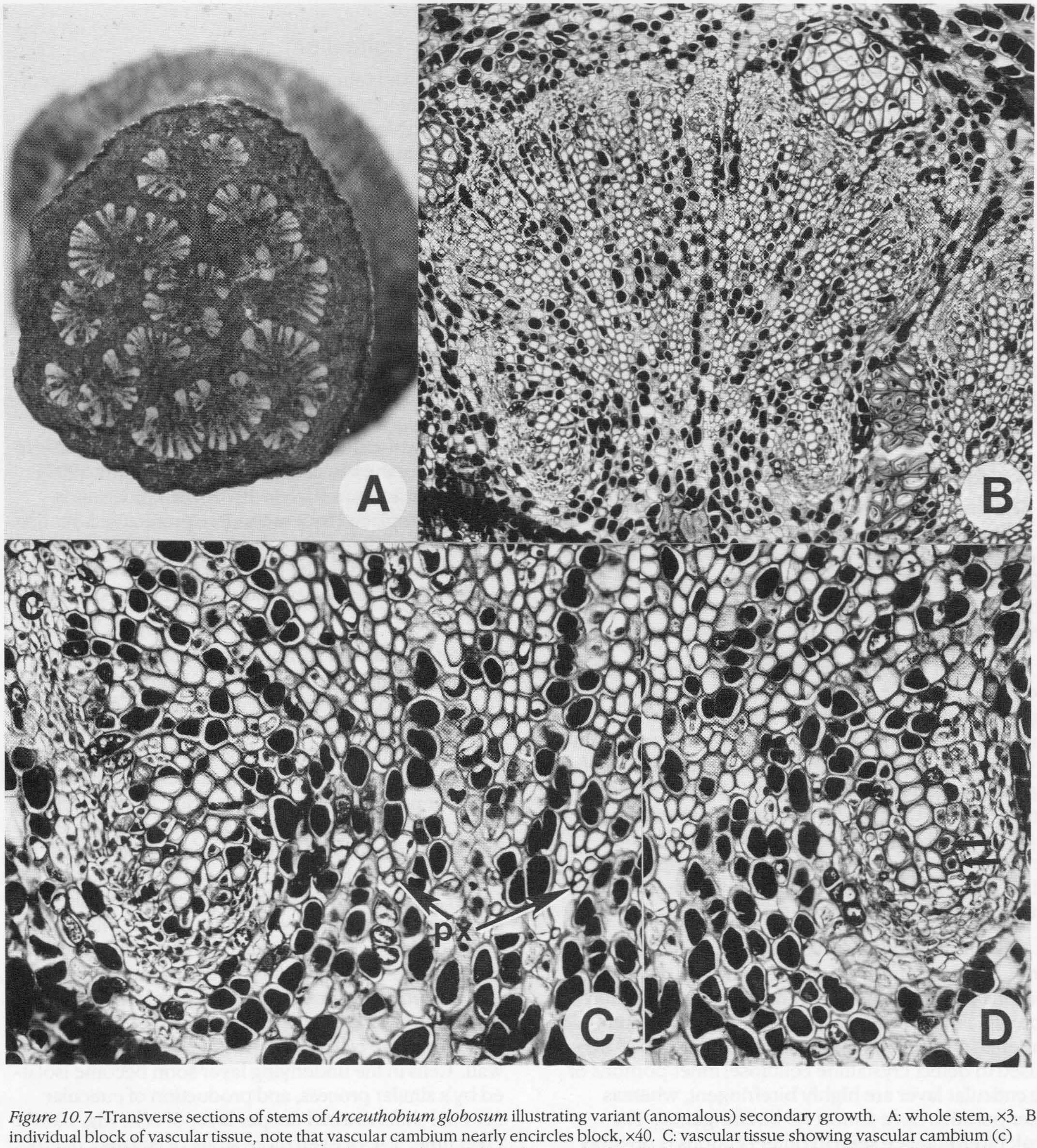

Figure 10.7–Transverse sections of stems of *Arceuthobium globosum* illustrating variant (anomalous) secondary growth. A: whole stem, ×3. B: individual block of vascular tissue, note that vascular cambium nearly encircles block, ×40. C: vascular tissue showing vascular cambium (c) along flank of block (see upper left corner) and groups of protoxylem elements (px), ×100. D: centrifugal direction of xylem differentiation at unlabeled arrows, note protoxylem at left of figure, ×100.

unlabeled arrows) are differentiating centripetally while at the outer limit of the block xylem differentiates centrifugally. Along the block flanks differentiation is outward along a tangent. Because of the unusual configuration of the vascular cambium, some recently formed secondary xylem (fig. 10.7C–D) and phloem (fig. 10.6A) may lie very near the earliest protoxylem elements.

In all of the *Arceuthobium* species we studied, the blocks of vascular tissue with secondary growth arose from 2 or more vascular bundles. We found 4 to 5 or more discrete regions of protoxylem inside each vascular block of *A. durangense.* The number of blocks of vascular tissue in a stem with secondary growth varies between and within species. In general, for a given species, greater stem diameter allows for more blocks of vascular tissue. This situation suggests that as secondary growth progresses, a block of vascular tissue (fig. 10.7A–B) may split into 2 or more blocks, possibly through expansion of rays present within the wood. We counted 10, and sometimes more, vascular blocks in older *A. globosum* stems (fig. 10.7A) but found only 2 blocks in the oldest *A. tsugense* stems.

Epidermis

The stem epidermis in *Arceuthobium* is composed of ordinary epidermal cells and stomatal complexes. Trichomes are absent. Each stomatal complex consists of 2 guard cells and over-arching subsidiary cells. Salient features of the stomatal complexes have been described above and need not be repeated here.

Species of *Arceuthobium* form an epidermis with a thick cuticular layer. Even on relatively young stems (fig. 10.8A), the cuticular layer is prominent, with a mean thickness of 17 µm. As stems age, this extracellular layer becomes remarkably thick, develops cuticular pegs, and acquires a definite morphological heterogeneity (figs. 10.8B–D). The layer's thickness at the stage shown in figures 10.8B–D averages 24 µm. Development of a thick cuticular layer decreases the ability of the epidermis to expand as the stem's circumference continues to increase (Calvin 1970).

Chemical composition of the cuticular layer also varies. Under primary fluorescence (fig. 10.8C), outer portions of the cuticular layer fluoresce considerably more than inner portions, suggesting a higher cutin content. In contrast, when polarized light (fig. 10.8D) is used to detect crystalline cellulose, inner portions of the cuticular layer are highly birefringent, whereas outer portions have almost no birefringence. The weak birefringence seen in outer portions is possibly due to some birefringent waxes embedded in the cutin. These observations agree with those of Sitte and Rennier (1963) that the cuticular layer is chemically variable with a substantial region composed similarly to that of the cuticle proper and an inner region with a major cellulose component. Cuticular pegs also appear to be high in cellulose (fig. 10.8D).

Cuticular Epithelium

Seed plants show striking differences in the extent to which their epidermis is modified during development. Many herbaceous dicotyledons complete their life cycles in a short time, have little or no secondary growth, and retain their epidermis with, at the most, only slight modification. At the other extreme are plants that increase greatly in circumference. The woody dicotyledons and gymnosperms are well known for this secondary growth. In these plants, the epidermis is commonly replaced at an early age by a protective tissue of secondary origin, the periderm. Between these extremes are many plants in which the epidermis remains active for a time, keeping pace with the increasing circumference of the enlarging organ. Generally, however, the epidermis eventually gives way to a well-defined periderm. Such is not the case in members of the Viscaceae. In *Viscum* (Damm 1902) and *Phoradendron* (Calvin 1970), the epidermis is gradually replaced by a secondary protective layer that is strikingly different than the periderm. This complex layer is characterized by many unique features (Calvin 1970) and was termed by Damm (1902) the "cuticular epithelium."

Developmental and structural features of the epidermis were outlined above (figs. 10.3A–C and 10.8A–D), and we noted that development of a thick cuticular layer decreased the ability of the epidermis to expand with the stem (Calvin 1970). With increasing stem enlargement and resulting tangential stresses, cuticular pegs (p in fig. 10.8E) develop between epidermal cells. As development continues, these pegs become wider and eventually begin to isolate epidermal cells from cortex cells (see cells at arrows, fig. 10.8E). Eventually, cells of the epidermis lose direct contact with underlying cells, and at about this time the underlying cells themselves begin to form a cuticular layer (fig. 10.8F). Calvin (1970) has shown that in *Phoradendron* some of the cuticular material produced by the underlying cells is deposited within the confines of the cell, not outside the outer periclinal wall. Cells in the underlying layer soon become isolated by a similar process, and production of cuticular material shifts to a still deeper layer of cells (fig. 10.8G). Over time, 3, 4, or even more strata of isolated, necrotic cells may be included within cuticular epithelium.

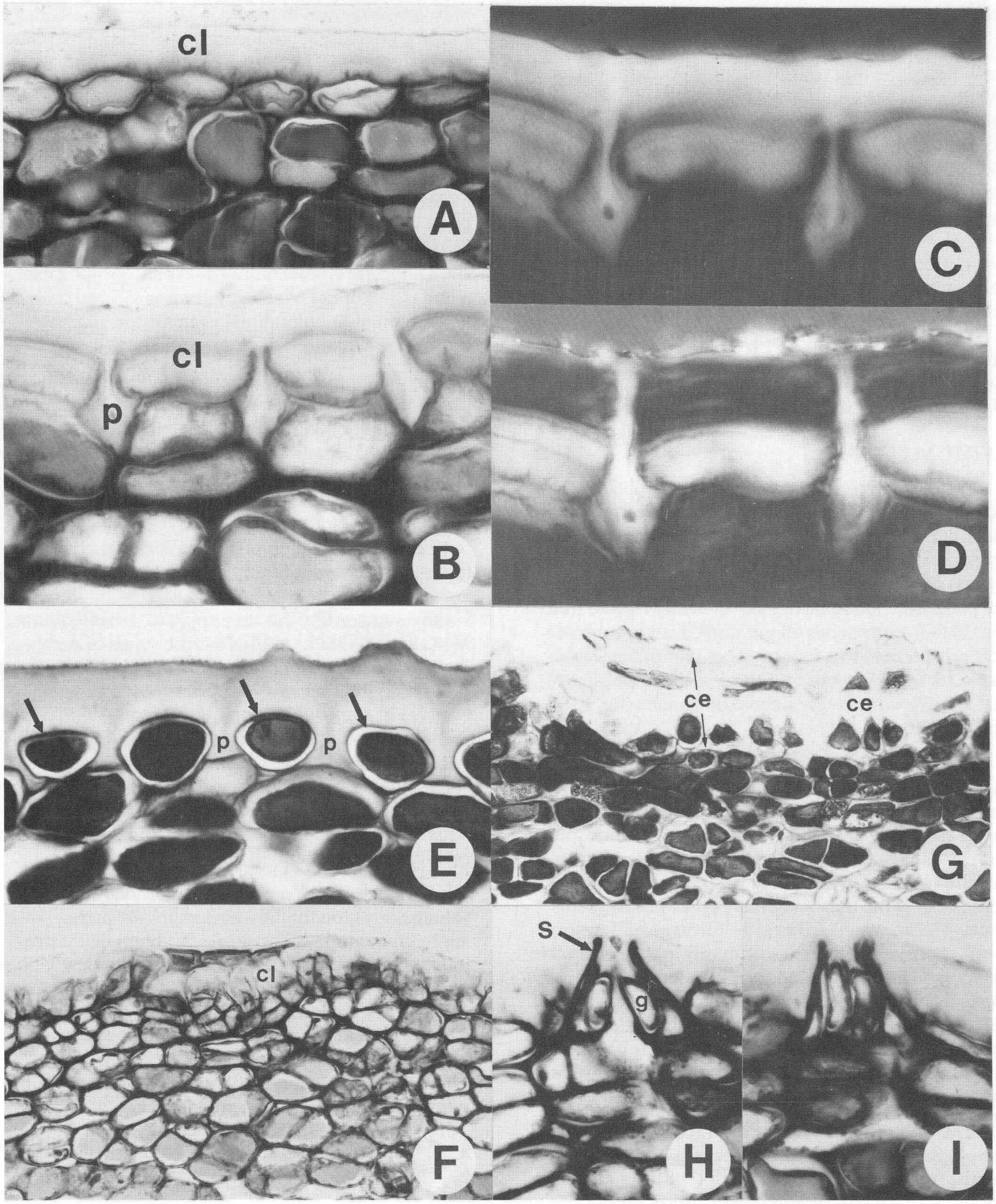

Figure 10.8 –Epidermis (A-E) and cuticular epithelium (F-I) of *Arceuthobium tsugense* (A-D, F, H-I) and *A. globosum* (E-G) stems as seen in transverse (A-G) and longitudinal (H-I) sections. A: cuticular layer (cl) of intermediate thickness, ×250. B-D: thick cuticular layer as seen using brightfield, fluorescence, and polarization optics, note cuticular pegs (p) between adjacent cells, ×400. E: individual epidermal cells becoming isolated (at arrows), ×250. F: cuticular layer formed by subepidermal cells, ×100. G: thick cuticular epithelium (ce), ×100. H-I: crushed stomata showing subsidiary (s) and guard (g) cells, note small substomatal chambers, ×250.

Ultimately, thickness of the cuticular epithelium may approach 100 µm.

The dramatic developmental changes leading to a cuticular epithelium disrupt stomata. As the cuticular layer covering the epidermal cells thickens, subsidiary cells collapse (fig. 10.8H–I), and the already small substomatal chambers (fig. 10.3B) almost disappear (fig. 10.8H–I). The guard cells degenerate. In older stems, remnants of the stomatal complex are still evident near the surface of the cuticular epithelium. On stems of this age, we could find no structures that could be interpreted as the functional equivalent of lenticels. Calvin (1970) listed several developmental features accompanying the formation of a cuticular epithelium in *Phoradendron*. Except for the loss of trichomes (trichomes are present in *Phoradendron*), developmental events in *Arceuthobium* mirror those in *Phoradendron* and in *Viscum* (Damm 1902).

Fruit Structure

Fruits of *Arceuthobium* (fig. 10.9) are divided into 2 distinct morphological zones. The upper one-third of the fruit is darker and attenuated distally (fig. 10.9A–B). Epidermis in this zone contain stomata (fig. 10.9C) that are, as elsewhere on the shoot, oriented tranverse to the plant axis. Stomatal density in nearly mature fruits (fig. 10.9C) approaches 48 per mm^2, a value considerably greater than that for any other part of the shoot (table 10.1). The lower two-thirds of the fruit (proximal zone) is completely devoid of stomata (fig. 10.9B and table 10.1).

A near-median, longitudinal section of a developing fruit of *Arceuthobium americanum* (fig. 10.9D) shows prominent structural features: (1) perianth segments (sepals), (2) stigma, (3) pericarp, (4) endosperm with globular embryo, (5) crushed remnants of mamelon, and (6) the flower stalk or pedicel. In the proximal zone, cells of the mesocarp have greatly thickened walls. Viscin, which arises at a later stage of development, reportedly originates primarily in the distal zone from tissue interior to the vascular tissue and ultimately forms a dome-shaped covering at the top of the "seed" (Bhandari and Vohra 1983). Tracheary elements comprising the vascular tissue are mainly of the graniferous type. The elongate open areas within the pericarp are presumably artifacts.

The fruit shown in figure 10.9D contains a single developing embryo, a feature characteristic of the genus. According to Hawksworth (1961b), however, about 1% of *Arceuthobium americanum* produce "abnormal fruits with 2 seeds and seeds with 2 embryos and endosperms." All 39 fruits that we examined had only a single embryo. Polyembryony is a common feature in *Viscum* (Sallé 1983). Other aspects of fruit biology are discussed in chapter 2 (life cycle), chapter 3 (sexual reproduction), and chapter 8 (biotic associates).

Discussion

The shoot system of *Arceuthobium* has a number of distinctive structural charateristics, including anomalous secondary growth, neotenic features in its vascular tissues, unusual orientation and distribution of stomata, a cuticular epithelium, and several xeromorphic features. An understanding of these structural characteristics provides important insights into plant function, reproductive biology, evolution, and ecology.

Arceuthobium clearly demonstrates anomalous secondary growth. Recent discussions of the topic include those of Carlquist (1988), Mauseth (1988), and Metcalfe (1979a). As far as is known, all *Arceuthobium* species display anomalous secondary growth. They may also display an anomalous or variant form of primary growth. Both Dobbins (1969, 1971, 1981) and van der Walt and others (1973) indicated that anomalous patterns of secondary growth were often directly correlated with the primary vascular tissue. Our observations suggest that this may apply to *Arceuthobium*. Metcalfe and Chalk (1950) describe stems of *A. oxycedri* as having "two opposite pairs of bundles." Datta (1954) observed a similar arrangement of vascular bundles in *A. minutissimum*. Stevenson (1934) noted that *Korthalsella* internodes are traversed by 2 main vascular bundles. In *A. tsugense*, we observed that some internodal regions have 2 separate sets of vascular bundles. We did not determine the relationship between this vascular arrangement and the variant secondary growth described below.

Carlquist (1988) reported that cambial variants (anomalous growth) fall into 3 main categories: (1) successive cambia, (2) a single cambium that yields interxylary phloem, and (3) cambia that typically begin as single, normal cambia that produce phloem externally and xylem internally and have or develop a conformation other than cylindrical. With the caveat that some *Arceuthobium* species produce little or no phloem (at least sieve elements), *Arceuthobium* falls within Carlquist's category three.

Carlquist (1988) commented that genera with cambial variants are specialized within families where most genera have normal cambial activity. This is certainly true within the Viscaceae. Besides *Arceuthobium*, anomalous secondary growth has also been reported but not described for *Korthalsella* (Stevenson 1934). Both genera are highly specialized members of

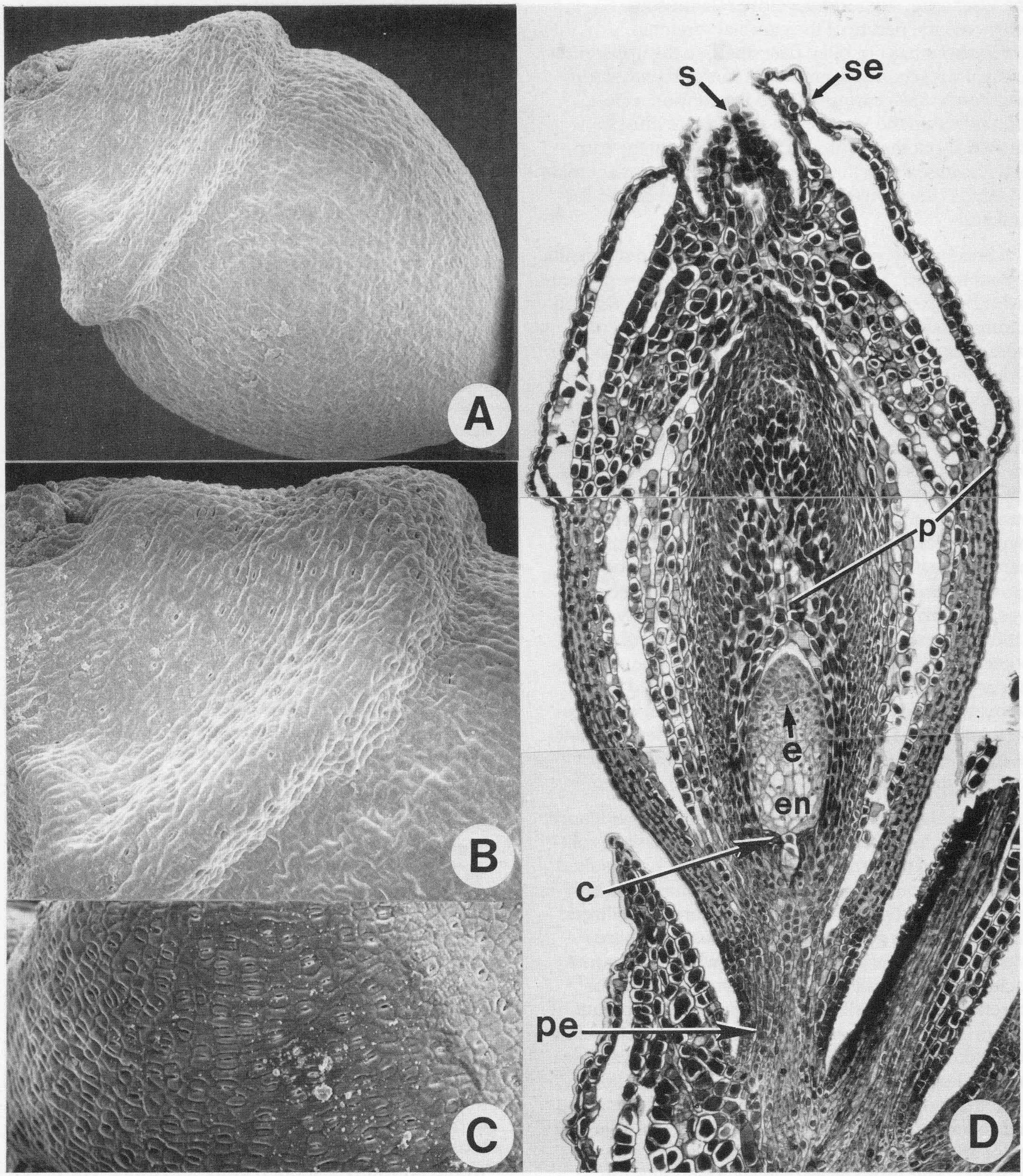

Figure 10.9 –Fruits of *Arceuthobium americanum* as seen in surface view SEM (A-C) and sectional view using brightfield microscopy (D). A: whole fruit showing distal and proximal zones, ×40. B: enlarged view showing juncture of zones, ×70. C: distal section showing dense concentration of stomata, ×80. D: longitudinal section of developing fruit showing crushed mamelon (c), embryo (e), endosperm (en), pericarp (p) pedicel (pe), remnants of stigma (s), and remnants of sepal (se), ×40.

the Viscaceae, suggesting a close relationship. However, the nature of the cambial variant in *Korthalsella* has not been described, so the apparent anomalous secondary growth in both *Arceuthobium* and *Korthalsella* cannot be used to support a close affinity within the Viscaceae. Much more must be known about the nature and distribution of the cambial variants within the family before evolutionary relationships based on this anatomical feature can be formulated.

Presumably, anomalous growth somehow benefits *Arceuthobium.* But how? Cambial variants are particularly abundant in lianas and vines (Carlquist 1988). An anomalous growth pattern also characterizes certain storage organs, such as those of beet and sweet potato. One feature that lianas, vines, and storage organs share is abundant parenchyma tissue in the variant organ. Anomalous growth in *Arceuthobium* also augments the already abundant parenchyma, especially between the blocks of vascular tissue. The added parenchyma has the effect of dispersing the individual blocks of vascular tissue. Carlquist (1988) presented several hypothetical advantages conferred by abundant parenchyma in lianas and vines with anomalous growth. Some of these generalizations have recently been confirmed experimentally. Fisher and Ewers (1989) experimentally injured stems of several lianas, some of which had an anomalous arrangement of secondary vascular tissues. Their results showed that stems with variant growth could heal damaged vascular tissues more rapidly, as well as limit xylem dysfunction. Whether or not these presumed advantages apply to *Arceuthobium* is unknown.

Carlquist (1962) called attention to the significance of neoteny in plants. Within *Arceuthobium* the evolutionary trend towards a herbaceous habit has resulted in the retention of numerous juvenile characteristics, which are most pronounced in the more specialized members of the genus. Examples illustrated here include (1) primary phloem fibers, which at maturity lack secondary walls; (2) parenchyma cells and/or parenchyma-like cells as the only axial components of xylem other than vessel members; and (3) wide, sclariform-like pits on the side walls of pitted tracheary elements. Regarding taxa he studied, Carlquist (1962) commented, "juvenile features are held to be retained in secondary xylem because these plants are adjusted to, or are tending toward, a habit other than truly woody." This trend characterizes *Arceuthobium.*

Stomata in *Arceuthobium* show unique orientation and distribution. They are dense on distal portions of fruits and are moderately abundant on abaxial leaf surfaces. A highly effective transpiring surface is essential to mistletoes because of their need to maintain negative water potentials relative to their hosts (Fisher 1983). Ehleringer and others (1985) have shown that stomata are the main pathway of evaporative water loss in mistletoes and that through stomatal action they can maintain a tight control over rates of water loss. Fisher (1983) proposed that *Arceuthobium* fruits, due to their abundant stomata and absence of a thick cuticular layer, must play an important role in evaporative water loss from shoots. We share this view, based on anatomical and reproductive features. *Arceuthobium* fruits have abundant xylem tissue. Further, this elaborate vascular network ends close to the area of greatest stomate density. Fruits of *Arceuthobium* have a long maturation period, with individual crops staying on the plant as long as 19 months in *A. gillii.* In *A. hawksworthii,* fruits may mature within about 4 months of fertilization. It would be interesting to know if tropical species such as this species have a standing crop of fruits in some stage of development throughout the year.

Even as one crop of fruits is discharged, a new crop is maturing; so at least one crop of fruit is always present on the plant. We suggest that the long period of fruit maturation in dwarf mistletoes is tied evolutionarily to maintaining the effective transpiring surface provided by fruits. If true, fruits serve not only in the traditional roles of protection and dispersal but also in a role normally assumed by leaves that is, transpiration. We speculate that this transfer of leaf function to fruits represents an interesting evolutionary advance. Transpiring surfaces can be controlled with fruit production and drop, and the separation of vegetative and reproductive roles is blurred. Even if this proves true, stomata are not the only adaptation for regulating water loss.

The presence of a cuticular epithelium in *Arceuthobium,* and other members of Viscaceae, also has important physiological ramifications. Opinions about transpiratory water losses by mistletoes have changed over time. The concept of uncontrolled water losses has given way to the concept of carefully regulated water losses (Ehleringer and others 1985). Results of our studies suggest that, on areas of stem where a cuticular epithelium is present, lenticels (or their functional equivalent) are absent. If this is the case, then transpiration water losses should be limited largely to those areas where an epidermis is present, which would be younger shoot regions and fruits. The development of a cuticular epithelium would give dwarf mistletoes the ability to regulate gas exchange more judiciously than occurs in woody plants in general, because gas exchange via stomata only is under tighter regulation than is gas exchange through stomata plus lenticels.

Alosi (1979) listed several modifications of *Arceuthobium* shoots that may reduce transpiration. These include (1) low external surface to volume ratio, (2) sunken guard cells, (3) small substomatal chambers, (4) lack of intercellular space in mesophyll tissue, and (5) thick cuticular layer. To this list should be added transversely oriented stomata, which are more often seen in xeromorphic species (Butterfass 1987). Alosi concludes that these seemingly xerophytic adaptations appear inconsistent with known high transpiration rates in *Arceuthobium.*

Metcalfe (1979b) discusses the distinction between xeromorphs and xerophytes. Accordingly, xeromorphs are plants that, based on their morphology and histology, give the impression that they would be found only in dry conditions. Xerophytes, on the other hand, are actually restricted to dry conditions. Is *Arceuthobium* a xerophyte, or does it simply display xeromorphic features? In a thought-provoking article, Niklas (1989) discusses the cellular mechanics of plants relative to ecology and evolution. In essence, in settings where water deprivation is unlikely, plants tend to utilize hydrostatic support mechanisms (turgidity of thin-walled cells) because they are "cheaper," whereas if water supply is unpredictable they tend to "invest" in thick-walled cells or water-insensitive tissues such as wood. Analysis of anatomy as related to evolution within *Arceuthobium* indicates that, with increasing specialization, species place greater emphasis on hydrostatic support mechanisms. Thus while *Arceuthobium* species display several xeromorphic features, they also display the mesomorphic feature of a loss of woodiness and the resulting reliance on hydrostatic support. We consider *Arceuthobium* to have xeromorphic features, but we do not consider it to be xerophytic.

Endophytic System

*Clyde L. Calvin and Carol A. Wilson**

The dwarf mistletoes, *Arceuthobium,* are widely recognized as the most highly specialized of the 7 genera comprising the family Viscaceae. Within the genus, evolutionary specialization has affected the haustorial system (endophytic system) and the shoot (ectophytic system) very differently. In general, the interface of the shoot with its environment has decreased over evolutionary time while that of the endophytic system has increased.

The specialized endophytic system of *Arceuthobium* is illustrated in several ways. First, the endophytic system is more highly developed than in related genera, and its haustorial processes more thoroughly permeate host tissues. To paraphrase Heinricher (1924), penetration power and efficiency of the absorbing system are superior to those of other Viscaceae. Second, individual sinkers do not retain their autonomy as in related genera but rather form a complex admixture of host and parasite cells (Alosi and Calvin 1984). This highly integrated unit produces a much more intimate association between parasite and host tissues. The unique character of this unit earns it the special name "infected ray" (Srivastava and Esau 1961b). Finally, dwarf mistletoes form not only localized infections but also systemic infections (Kuijt 1960b). Other mistletoes of the Viscaceae characteristically form only localized infections that show limited spread within the host branch. Systemic infections, in contrast, spread into the host's shoot apices and advance acropetally as host shoots elongate (Baranyay and others 1971).

Understanding the full character of the endophytic system of *Arceuthobium* requires basic familiarity with the infection process, bark strand and sinker morphology and anatomy, distinction of host and parasite cells, and discrete roles of host and parasite. The relationship begins when the parasite's seed contacts the host.

Infection Process

A generalized life cycle for *Arceuthobium* is shown in figure 2.5. To begin, seed are explosively discharged into the air (fig. 2.4). Seeds that strike host leaves adhere with viscin (fig. 2.10). Moistened viscin allows seeds to slide to leaf bases where they contact host branches and germinate. When the tip of a radicle contacts a host branch, a disk-like holdfast forms (fig. 2.11). As the holdfast enlarges, it becomes closely appressed to the branch. Sometimes, hyphae-like cells at the holdfast's margin elongate and penetrate a short distance into the host bark. These elongate cells do not reach living tissues of the host but presumably help anchor the holdfast to the branch. Beneath the holdfast, a penetration wedge develops (fig. 2.12). This wedge of parasite tissue is comprised of either just procambium (Cohen 1963) or procambium and ground meristem (Scharpf and Parmeter 1967). Primarily by mechanical force, the wedge of parasite tissue penetrates the outer, protective layers of the stem and enters the living host tissue (Scharpf and Parmeter 1967). Successfully establishing a nutritional link to the host concludes the most tenuous phase of the parasite's life cycle. (For more complete infection details, see Cohen 1963; Kuijt 1960b; Scharpf and Parmeter 1967.)

Once infection is accomplished, the holdfast and tissues distal to it wither and disappear. A gradual swelling at the site of infection provides the only early evidence that infection has occurred. Loss of aerial portions of the mistletoe seedling means that the first shoot does not develop from the plumular pole of the embryo. Instead, all shoots develop from endophytic portions of the plant. Using terminology Groff and Kaplan (1988) proposed, *Arceuthobium* can be described as forming only root-borne shoots. As far as is known, it is the only genus within Viscaceae that forms exclusively root-borne shoots. Developmental events in *Arceuthobium* are foreshadowed during embryogeny. The shoot apex of a mature embryo is poorly developed and vacuolate; cotyledons (usually 2) are minuscule. In contrast, the root pole of the embryo is enlarged, appears meristematic, and exhibits a complex pattern of zonation (Cohen 1963).

Endophytic System Morphology

During incubation within the host branch (table 2.1), the complex haustorial system of

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Arceuthobium grows and develops. Although events occurring in the early stages are not well understood, certain features are recognized.

First, a mass of tissue derived from the penetration wedge grows radially through host tissues to the vascular cambium and establishes a position within the cambial cylinder. This multicellular, radially oriented structure, which initiates a meristematic zone contiguous with that of the host cambium, is the primary haustorium (fig. 11.1A). Second, from the sides of the primary haustorium and from the initial penetration wedge, discrete strands are initiated. They grow acropetally, basipetally, and circumferentially (fig. 11.1A) within the host bark (Alosi and Calvin 1984, Sadik and others 1986a). Known as "bark strands" (also as "longitudinal strands" and "cortical strands"), they establish the basic framework for the endophytic system (Srivastava and Esau 1961b). Third, bark strands produce "sinkers" ("secondary haustoria") that grow radially to the vascular cambium (fig 11.1A). As a final stage of initial growth, the parasite differentiates into either a localized or a systemic infection type. A brief review of the salient features of localized and systemic infections will help clarify endophytic system morphology.

Localized infections, as the name implies, are contained within a limited section of host branch. The infected area usually develops a fusiform swelling (fig. 6.4) from hypertrophy and hyperplasia of host tissues and from the expanding parasite. The extent of branch swelling correlates with the extent of axial spread of the developing endophytic system (Shea 1957). In *Arceuthobium campylopodum,* the endophytic system was not observed in host tissue 3 cm beyond the area of swelling (Scharpf 1962). Generally, the basipetal spread of infections is about one-third greater than the acropetal spread (Hawksworth 1960b). A consistently greater basipetal spread of infections has also been observed in *Phoradendron* (Calvin and others 1991) and may be a general rule in localized infections. Production of shoots in localized infections is confined to swollen regions, and shoots occur in random tufts. All *Arceuthobium* species are capable of developing localized infections on appropriate hosts (Kuijt 1960b).

Systemic infections involve entire branches. Infections extend acropetally into regions of stem having only primary growth and even into buds (Thoday and Johnson 1930, Kuijt 1960b). The extent of basipetal spread of systemic infections remains problematic (Hawksworth 1960a,b); but it is generally considered to be somewhat less than acropetal spread (Kuijt 1960b). Typically, infected branches lack swelling and may be elongate and pendulous (fig. 6.3). Shoots in systemic infections (fig. 11.1B) generally emerge according to the age of the host stem (Kuijt 1960b). The ability to produce systemic infections is considered to be the evolutionarily advanced condition (see chapter 4) and is found consistently in only a few species of *Arceuthobium.* The systemic habit represents a radical departure from the growth pattern that characterizes localized infections, and it has required major changes in both ectophytic and endophytic systems.

Localized and systemic forms are stable morphological variations in *Arceuthobium,* but factors that determine which form develops in a particular situation are poorly understood. Important factors that have been identified include species of *Arceuthobium,* host, and site of the original infection (Kuijt 1960b). Some workers believe that the major factor in determining endophytic form is whether the parasite initially develops within primary or secondary tissues of the host branch (Alosi and Calvin 1984). Regardless of causes, the morphological differences between infection types are profound.

The region where bark strands grow within the host branch differ by infection type (endophytic form). In localized infections, strands grow mostly or exclusively in the outer part of the secondary phloem (Sadik and others 1986a). In systemic infections, strands initially grow in primary tissues and occur in inner cortex, phloem, and adjacent procambium (Alosi and Calvin 1984). Regardless of these early differences, strands of both infection types can initiate sinkers where they associate with secondary vascular tissue of the host. The sinkers, as indicated above, grow radially towards the host vascular cambium, displace host initials, and occupy positions within the cambial cylinder. With continued cambial activity of host and parasite, sinkers become embedded in the wood of the host (fig 11.1A). Because of sinker formation, mature regions of both infection types are similar structurally.

An endophytic network of bark strands within the host bark and radially oriented sinkers extending varying distances into host wood typifies *Arceuthobium* (figs. 11.1A and 11.2A); but similar systems occur in *Dendrophthora* (Thoday 1957), *Phoradendron* (Calvin 1967b), and *Viscum* (Sallé 1979a). *Korthalsella,* previously considered to be the genus most closely related to *Arceuthobium,* reportedly has a different endophytic plan (Thoday 1957; Fineran, personal communication). Its haustoria extend to the host wood and expand longitudinally and tangentially, thereby separating xylem from phloem. The tangentially spreading wedges may encircle the stem (Thoday 1957). Relationships between endophytic

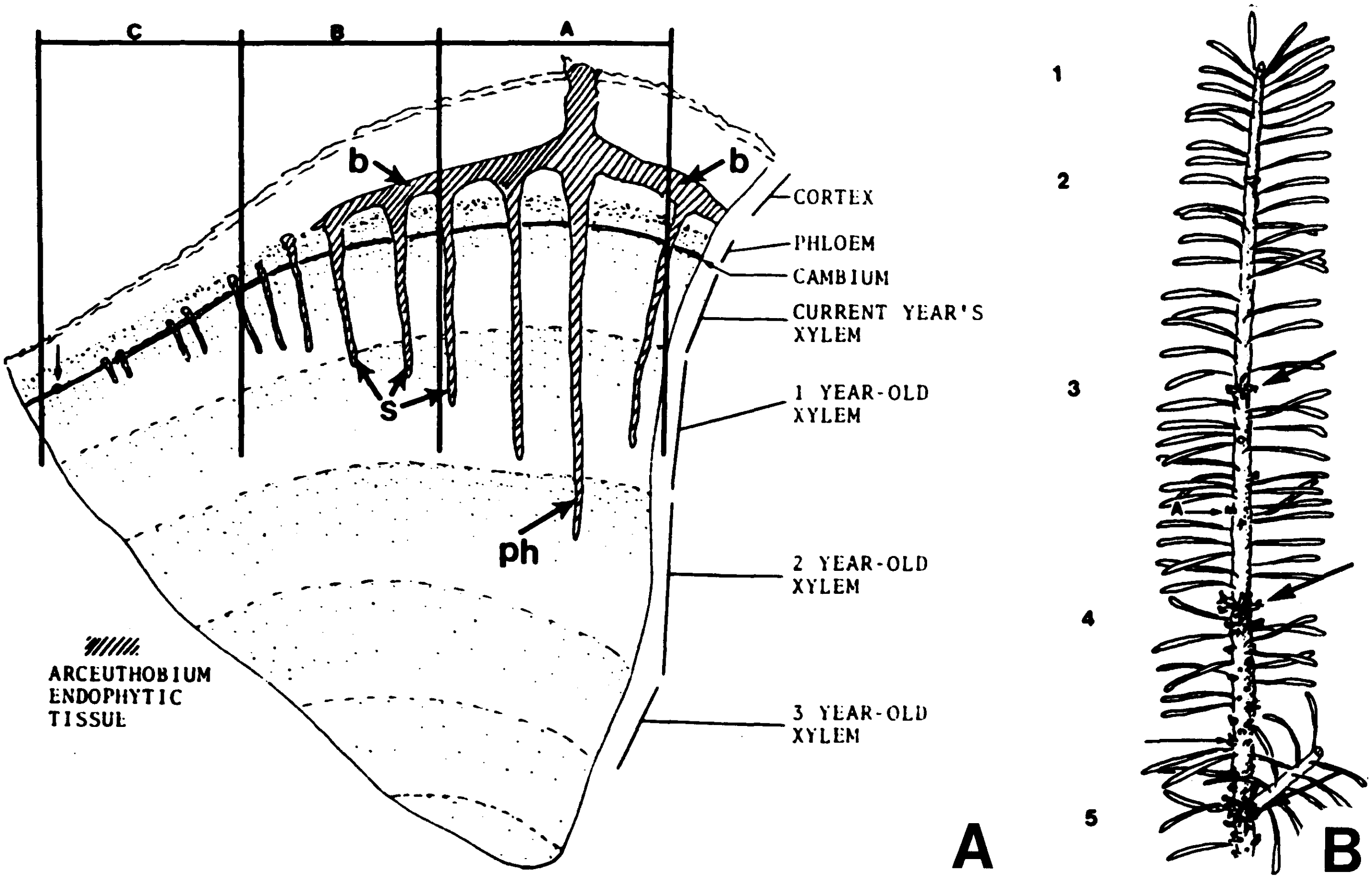


Figure 11.1 –A: diagram of *Arceuthobium occidentale* on *Pinus sabiniana.* The depth of individual sinkers (s) in host growth rings indicates the age of the infection in that specific area of the host stem. The oldest portion of the endophytic system shown is in section A, where the primary haustorium (ph) extends into 2-year-old xylem. The youngest portion is in section C, where the endophyte lies entirely within the cambial zone and the most recently produced phloem and xylem derivatives of the host. Sinkers are initiated from near the tips (unlabeled arrow in section C) of bark strands (b). B: diagram of a *Pseudotsuga menziesii* shoot infected with *Arceuthobium douglasii.* The bud scale regions or segment girdles (nos. 1-5) delimit annual growth increments. Although the endophytic system occupies the entire host branch, aerial shoots (A) do not erupt until the branch is 3 years old. Aerial shoots are particularly concentrated at bud scale regions (large arrows), 1×.

form and taxonomic affinity are uncertain. The reported endophytic differences between *Arceuthobium* and *Korthalsella,* if confirmed, would suggest that the two genera are not as closely related as once believed.

Though differences in endophytic systems generate interesting questions of evolutionary origins, generic divergence, and other issues, the task here remains to describe the character of the dwarf mistletoe. We now examine the anatomy behind the haustorial components.

Anatomy of the Endophytic System

Bark Strands

Dwarf mistletoe spreads within host branches by elongation of bark strands. A strand's growing tip is a simple, unicellular filament (Alosi and Calvin 1984, Bhandari and Nanda 1970, Kuijt 1960b). The constituent cells are 2 to 3 times longer than broad, are densely protoplasmic, and have large conspicuous nuclei (Thoday and Johnson 1930). Cells at the growing tips first elongate then divide transversely. The growing tips of *Viscum* are multicellular (Thoday 1951, Sallé 1979b). In *Viscum,* cells of the meristematic zone are elongate, are densely cytoplasmic, and have numerous dictyosomes plus a well-developed endoplasmic reticulum (Sallé 1979b). Bark strands of *Viscum* grow throughout the year (Sallé 1983), a feature that may also be true of *Arceuthobium.* Both mechanical and enzymatic action allow bark strands of *Viscum* to grow through host bark.

Behind the short, filamentous growing tips of *Arceuthobium* bark strands, cells divide longitudinally and the developing strands become multicellular. Such longitudinal divisions may take place in all subterminal cells, even the subapical cell (Kuijt 1960b). Continued enlargement of bark strands produces a

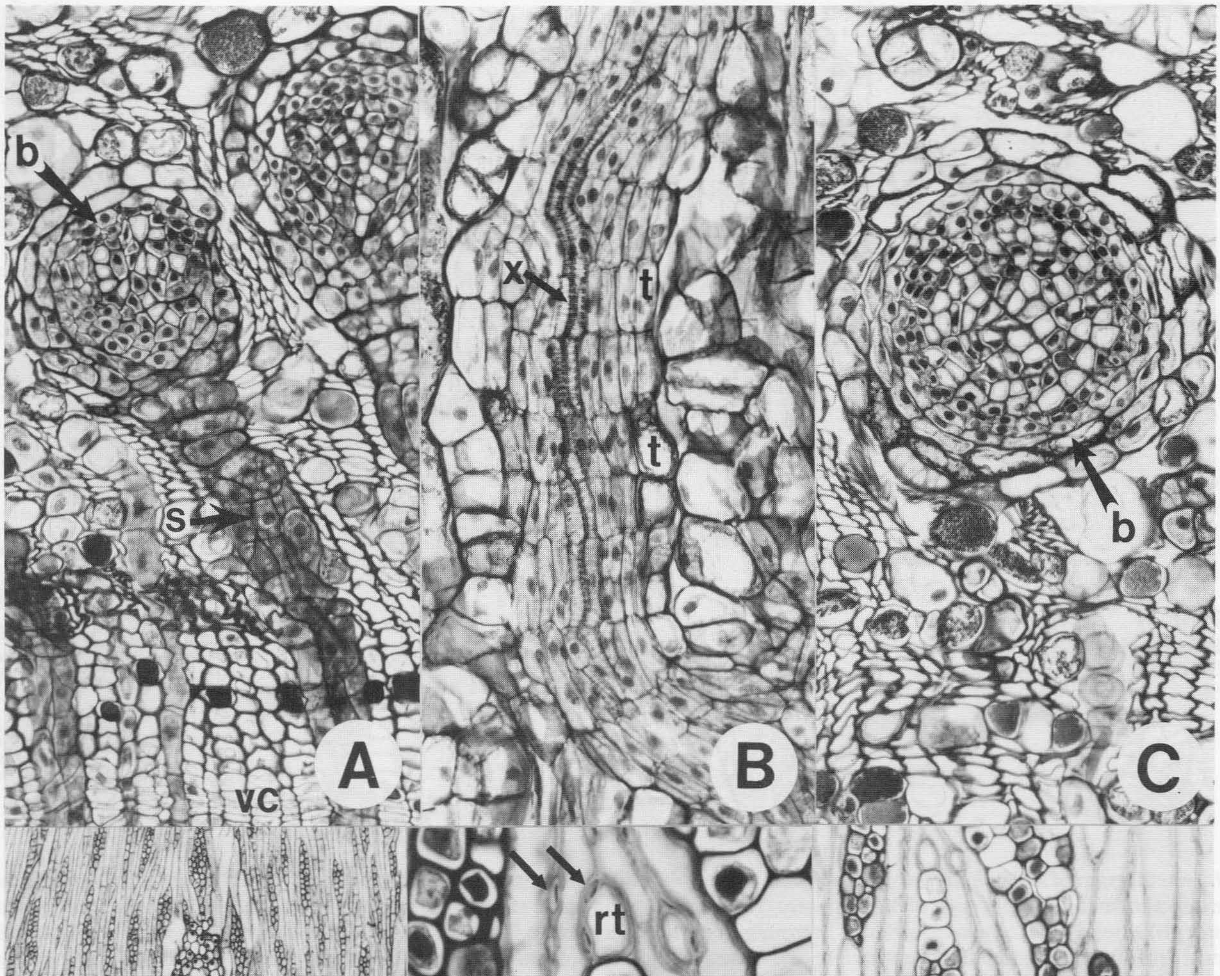


Figure 11.2 –Endophytic system of *Arceuthobium americanum* on *Pinus contorta* (A-C, E-F) and *Phoradendron macrophyllum* on *Juglans hindsii* (D); in transverse sections (A, C) or tangential section (B, D-F), through host bark (A-C) or wood (D-F). A: bark strand (b) with sinker (s), ×100. B: bark strand to show tiered arrangment (t) of cells, ×100. C: older bark strand showing secondary growth, ×100: D: sinker; compare size to host rays (r), ×40: E: infected ray showing host (h) and parasite (p) cells; pitting of axial and ray trachieds (rt) at unlabeled arrows, ×250. F: infected (ir) and uninfected (ur) rays in xylem (x), ×100.

core of smaller cells surrounded by larger parenchymatous cells (Bhandari and Nanda 1970). As development continues, some of the smaller diameter cells in the middle of the strand differentiate as tracheary elements and others as parenchyma (fig. 11.2A). Most, if not all, of the tracheary elements present within strands are vessel members (Kuijt 1960b). Phloem has not been observed in bark strands of the species examined to date. However, sieve elements are present in bark strands of *Phoradendron* (Calvin 1967b) and *Viscum* (Sallé 1979a).

Bark strands show a prominent tiered arrangement of cells when viewed in longitudinal section (fig. 11.2B). Even in older strands that have increased greatly in diameter, the tiered arrangement of cells may still be evident. The tiers become less distinct where sinkers merge with bark strands. Shoots, which originate on the outer side of bark strands, also alter the cell tiers (Kuijt 1960b).

Bark strands may undergo secondary growth. In localized infections of species such as *Arceuthobium americanum,* the amount of secondary growth may be modest (fig. 11.2C). In this species, the secondary vascular tissue laid down apparently consists only of additional tracheary elements and parenchyma. Fibers have not been observed in secondary vascular tissue of the species examined to date (Kuijt 1960b). However, bark strands of large, long-lived species such as *A. globosum* subsp. *grandicaule* are expected to show extensive secondary growth. Shoots of this Mexican species may exceed 70 cm in length with a 5-cm diameter at the base. Further, the stems contain a well-developed phloem, including sieve-tube members (Calvin and others 1984). Bark strands of *A. globosum* should have a well-defined vascular cambium that produces abundant secondary xylem and a typical secondary phloem like that found in shoots.

Sinkers

The term "sinker" was first used by Solms-Laubach in 1867 (Srivastava and Esau 1961a). In common usage, the term refers to a discrete, radially oriented strand with clearly defined boundaries. These strands extend through host phloem and cambium into xylem from a ramifying system of bark strands in the cortex or phloem.

The sinker of *Phoradendron* shown in figure 11.2D illustrates some of these features. The sinker is clearly delimited and shows little or no intermingling of host and parasite cells. Sinkers have the same orientation in host wood as do vascular rays. Thus, their tangential, vertical, and radial extent are measures of their width, height, and length, respectively (Srivastava and Esau 1961a). The "end" of a sinker is its most deeply embedded part; but this embedded "end" is, in reality, the sinker's initial part within the host xylem (Srivastava and Esau 1961a).

A sinker of *Arceuthobium* is shown in figure 11.2E. This structure differs from that of *Phoradendron* in significant ways. *Arceuthobium* sinkers lose much of their identity during development. The sinker shown is associated with host ray cells. Srivastava and Esau (1961b) proposed the name "infected ray" to describe this intergeneric, chimeral structure. Within infected rays, host cells occur in multiseriate groupings, whereas they occur as uniseriate panels in uninfected rays (fig. 11.2F). Infected rays may become large, aggregate structures through vertical and lateral fusion of individual infected rays (fig. 11.2F).

Sinkers originate as lateral emergences from bark strands and may be initiated from very young bark strands. Kuijt (1960b) illustrates a sinker arising near the tip of a bark strand by an oblique division of the single cell present at that level. Cohen (1954) asserts that sinkers arise endogenously only, but Kuijt (1960b) refutes this claim and data from Thoday and Johnson (1930) do not support it. In *Viscum,* sinkers arise exogenously (Sallé 1983) and grow radially in a centripetal direction.

Controversy persists as to the exact manner in which sinkers are initiated. Some workers claim that initiation occurs only when a bark strand contacts host vascular cambium. The initiation of at least some sinkers in *Phoradendron* does occur in this manner (Calvin 1967b). Others claim that sinkers originate from bark strands located in host phloem and grow centripetally towards the vascular cambium, possibly following the course of vascular rays. Kuijt (1960b) produced a convincing illustration of a sinker being initiated by a bark strand situated at the outer periphery of the secondary phloem. Whether one or both forms of sinker initiation occur in *Arceuthobium* remains problematic.

Regardless of how a sinker gets started, once it arrives at the vascular cambium it establishes a position within the cambial cylinder. The manner of the sinker's subsequent growth is also controversial. Some authors believe that an intercalary meristem forms in continuity with the host cambium and that with coordinated cambial activity the sinker becomes embedded in host wood (Thoday and Johnson 1930; Srivastava and Esau 1961a). Others have suggested that the intercalary meristem occurs at the "neck" of the sinker where the sinker joins with the bark strand (Cohen 1954, Kuijt 1960b). Parke (1951) suggested that two meristems occur: one at the juncture of bark strand and sinker and another contiguous with the host cambium. Alosi and Calvin (1984) observed a distinct intercalary meristem juxtaposed to the host cambium, but they also observed cell arrangements that suggested more diffuse meristematic activity at the juncture with bark strands. A sinker cambial zone contiguous with the host cambium has been shown convincingly for *Phoradendron* (Calvin 1967b) and *Viscum* (Sallé 1979a). Sallé has further shown that meristematic activity in sinkers of *Viscum,* in contrast to that of bark strands, does not occur in winter. The meristematic cells do not synthesize nuclear DNA nor do they divide. Instead, their activity coincides with that of the host vascular cambium.

The shape of individual sinkers varies with age and between genera. *Arceuthobium,* sinker ends may be only one cell wide, but many sinkers become wider with age (fig. 11.3A). Further, wide sinkers may be more or less dilated at the boundaries of xylem increments. Height of sinkers also may increase with age. The end of a sinker may be one or only a few cells high (Srivastava and Esau 1961a). Thus, sinkers increase in width and height with age and eventually appear wedge-shaped when viewed in both cross and radial sections of host branches. *Phoradendron* sinker ends are high, sometimes exceeding 1 cm (Calvin 1967b), but they actually may decrease in height over time. Also, some *Phoradendron* sinkers are displaced from the vascular cambium (Calvin 1967b). When this occurs, the sinker portion embedded in the xylem becomes isolated from the main body of the endophytic system. Loss of sinkers from the cambial zone possibly occurs in *Arceuthobium* too, but because most sinkers are intimately associated with host rays, the situation is more complex.

Distinguishing host from parasite tissues can be difficult, but several workers offer criteria for the task (Alosi and Calvin 1984, Srivastava and Esau 1961a). Several different cell types are found within infected rays. Alosi and Calvin (1984) identified 5 different kinds within infected rays of host phloem (fig. 11.3B–C):

- Host parenchyma
- Host Strasburger (albuminous) cells
- Parasite ground parenchyma
- Parasite xylem (elongate cells only)
- Parasite sheath cells

Within host xylem, infected rays may contain 4 kinds of cells (fig. 11.3A):

- Host parenchyma
- Host ray tracheids
- Parasite parenchyma
- Parasite xylem (both elongate cells and isodiametric cells)

Not all cell types identified above are necessarily present in a given infected ray. Some examples will illustrate this point. Srivastava and Esau (1961a) showed that sinkers may be initiated independently of host rays and may continue through an entire growth increment before they become associated with ray cells. Association with ray cells occurs through conversion of fusiform initials to ray initials adjacent to a parasite sinker (Alosi and Calvin 1984). Further, normally only a moderate percentage of infected rays contain parasite tracheary elements (see below). Finally, not all conifers have ray tracheids. Such cells occur only sporadically in *Abies* (Core and others 1979). Thus, infected rays within host xylem would be expected to lack ray tracheids.

A major focus of research on parasitic plants concerns the nature of vascular connections established between host and parasite (Sallé 1983). Because sieve elements are lacking in sinkers of *Arceuthobium* and because phloem tissue is difficult to study, many workers have focused on the question of xylem-to-xylem continuity between host and parasite. Direct xylem continuity (fig. 11.3A) has been shown to occur in many mistletoes (Kuijt 1977), including *Arceuthobium* (Kuijt 1960b, Srivastava and Esau 1961a, Thoday and Johnson 1930). Recently, however, several workers (Lamont 1983b, Pate and others 1990, Kuijt 1991) have questioned the importance of such connections in mistletoes and other parasitic plants. Thus, investigations of the nature and extent of xylem-to-xylem connections in *Arceuthobium* assume new importance.

The most detailed study of xylem-to-xylem contacts in *Arceuthobium* is that of Srivastava and Esau (1961b) for several species of *Arceuthobium* occurring on seven different coniferous hosts. Their study focused entirely on relationships of sinkers to host xylem and they reported the following salient findings:

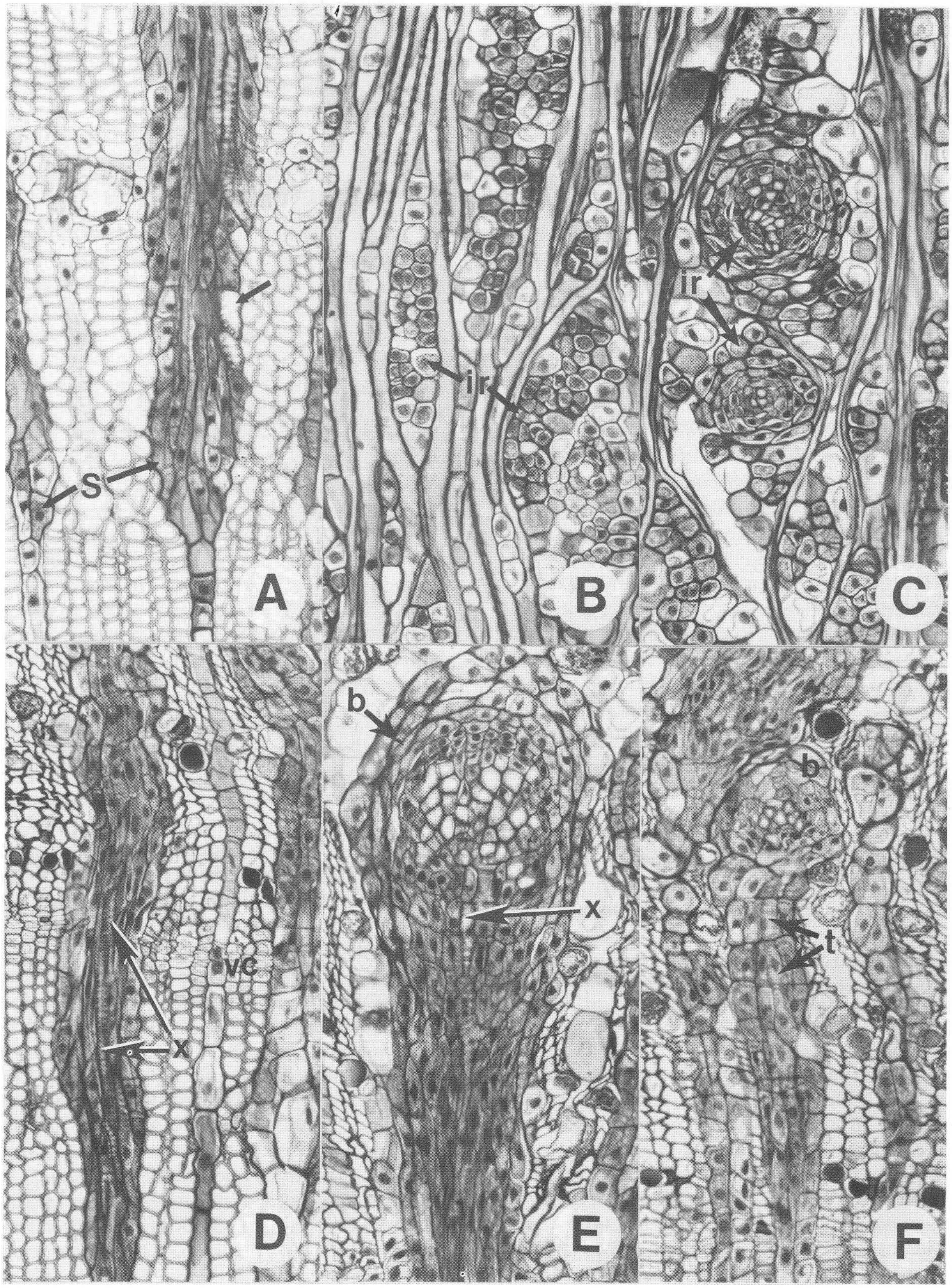


Figure 11.3 –Sinkers (A-F) and bark strands (E-F) of *Arceuthobium americanum* on *Pinus contorta;* in transverse section (A, D-F) or tangential sections (B-C). A: sinker (s) showing dilation at beginning of year's growth; xylem-to-xylem contact at unlabeled arrow, ×100. B-C: infected rays (ir) in host bark, ×100. D: xylem (x) of parasite extending across host cambial zone (vc), ×100. E: xylem leading to bark strand (b), ×100. F: tiered arrangement of cells (t) in sinker portion embedded in host bark, ×100.

- Only 915 of 5,971 sinkers (15.3%) studied had tracheary elements.
- About half (49.4%) of those sinkers with tracheary elements had direct contacts with either ray or axial host tracheids.
- In the area of contact between tracheary elements, a bordered pit of a host tracheid lies opposite the primary wall of the parasite xylem element.
- Many parasite tracheary elements are vessel members; a few elements are tracheids.
- Tracheary elements are most common in wide sinkers.
- In wide sinkers, a profuse differentiation of tracheary elements occurs at the boundaries of host xylem increments.
- The sinker end is usually parenchymatous.

The above observations suggest that dimorphism of sinkers may occur in *Arceuthobium.* Only about 15% of sinkers contain xylem, and of these slightly less than 50% have direct connections with host xylem. Thus, a large number of sinkers carry out their function without direct xylem connections, and even more do so with no tracheary elements at all. Finding that sinkers in *Arceuthobium* have different physiological roles would not be surprising. Schmid and Lindeman (1979) reported that *Phoradendron californicum* has dimorphic sinkers, of which uniseriate sinkers contain only parenchyma and multiseriate sinkers contain both tracheary elements and parenchyma. In their study, only about 2.5% of sinkers were multiseriate. Although the percentage of sinkers with xylem was lower in *Phoradendron* than in *Arceuthobium,* observations indicate that only a small percentage of vascularized sinkers is adequate to serve the needs of a parasite. Another suggestion that comes from these studies is that xylem-to-xylem connections are important. Srivastava and Esau (1961b) indicated that such connections between host and parasite were a consistent feature of all host–parasite combinations studied.

In sinkers with tracheary elements, parasite xylem is normally continuous from the wood across the cambium (fig. 11.3D) and secondary phloem to the bark strands (fig. 11.3E). This is true in *Arceuthobium* (Srivastava and Esau 1961a), as well as in other Viscaceae (Calvin 1967b, Sallé 1979a). It is therefore unusual that such xylem continuity did not occur in *A. campylopodum* growing on *Pinus sabiniana* (Srivastava and Esau 1961a). In this species, xylem was abundant in bark strands and in the sinker portion embedded in host wood but absent in sinker parts embedded in host cambium and phloem. A similar lack of continuity was noted by Parke (1951) for infections of *A. douglasii* on *Pseudotsuga menziesii.* Further studies are needed to determine if these absences in xylem continuity were related to sinker development or whether they characterize "mature" sinkers.

Ultrastructural Features

A major problem for investigations of host–parasite tissue relationships has been the ability to reliably discriminate between host and parasite cells. With light microscopy, cell determinations are difficult. At the ultrastructural level, however, distinctions between host and parasite can be made more easily (Alosi and Calvin 1985). Parenchyma cells of the parasite can be identified by an abundance of electron-dense lipid bodies, characteristic plastids and mitochondria, chromocentric nuclei, and distinctive cell wall features. For the ultrastructural details of the *Arceuthobium* endophytic system, see Alosi and Calvin (1985); Sadik and others (1986b); Tainter (1971); and Weber and Nietfeld (1984). Other Viscaceae investigated include *Korthalsella* (Fineran 1987; Coetzee and Fineran 1987, 1989) and *Viscum* (Sallé 1979b, 1983). Ultrastructural studies dealing with other parasitic angiosperms are numerous but not included here.

Most ultrastructural studies have focused on the interface between *Arceuthobium* and host tissues, particularly in the xylary portion of sinkers. A few observations, however, pertain to interface features in the region of the phloem. In *A. oxycedri,* a zone of crushed cells often occurs around large bark strands and around that part of the primary haustorium embedded in host phloem (Sadik and others 1986b). This layer of crushed cells is thought to be a barrier to transfer of materials between host and parasite. Where sinkers are embedded in host phloem, Alosi and Calvin (1985) observed one-sided, imperforate sieve areas of host sieve cells joining very thin-walled, pitted regions of parasite cells. In older sinkers, the portion embedded in host phloem may be enclosed in a layer of highly vacuolated sheath cells (fig. 11.3C) similar to that of bark strands (Srivastava and Esau 1961b). Where this occurs, the centrally located vascular tissue connecting the xylary portion of sinkers to bark strands is further separated from the conducting elements in host phloem. Older sinkers within host phloem (fig. 11.3F) may also show a tiered arrangement of cells much like that seen in bark strands.

In the xylary part of sinkers, various kinds of cell contacts occur. Host tracheids may abut sinker parenchyma (fig. 11.3A). Where this occurs, half-bordered pits of the host cell occur opposite portions of the parasite wall with very irregular surface features; as a consequence, the plasmalemma has a highly convoluted profile (Alosi and Calvin 1985). In adjacent cytoplasm, parallel arrays of endoplasmic reticulum are common. Viewed at high magnification, the irregular ingrowths of cell wall resemble the plasmatubule-like structures illustrated by Fineran (1987) for *Euphrasia* (Scrophulariaceae). Because living host and parasite cells are commonly contiguous (fig. 11.2E), some investigators question whether or not symplastic union occurs between host and parasite. Although Tainter (1971) reported the presence of plasmodesmata between cells of *Arceuthobium pusillum* and host needle trace phloem parenchyma, other observers (Alosi and Calvin 1985, Coetzee and Fineran 1987, Sallé 1979b) doubt the union of host and parasite cells is symplastic. The cell wall interface of host and parasite is fused and contains pits, but symplastic connections between parasite and host are now thought not to occur. However, workers occasionally see half-plasmodesmata at the host–parasite interface that appear to be aligned (Alosi and Calvin 1985). Parasite parenchyma cells typically have a smaller tangential diameter than host cells, prominently thickened, non-lignified walls, and abundant plasmodesmatal connections, indicating a high level of symplastic continuity.

Structural and Functional Relationships

Anatomical studies have shown that symplastic union does not occur between *Arceuthobium* and its coniferous hosts (Alosi and Calvin 1985; Sadik and others 1986b). Thus, the transfer of materials between host and parasite must occur via an apoplastic route (Alosi 1979). Direct tracheary element connections could facilitate transfer of materials between host and parasite. The presence of such connections in all *Arceuthobium* species studied by Srivastava and Esau (1986a), as well as in other Viscaceae (Calvin 1967b, Sallé 1979a), suggests they are an important part of the overall strategy of water and nutrient uptake. On the other hand, only a small percentage of sinkers appear to have direct xylary connections, and some of these sinkers lack xylem continuity across the vascular cambium and phloem to the vascular tissue of bark strands.

Another possible route for water and nutrient uptake is the apoplastic continuum provided by walls of adjacent host and parasite parenchyma cells. In an eloquent set of experiments, Coetzee and Fineran (1987, 1989) showed that in *Korthalsella* water and nutrients (including the amino acid, lysine) can be transferred from host to parasite parenchyma via this extensive pathway of adjoining parenchyma cell walls. Because so many *Arceuthobium* sinkers lack tracheary elements, the continuum demonstrated by Coetzee and Fineran is probably an important route for transfer of water and nutrients. The possession of plasmatubule-like ingrowths by interface parenchyma cells of both *Arceuthobium* (Alosi and Calvin 1985) and *Korthalsella* (Fineran 1987, Coetzee and Fineran 1987) lends further support to this view. Support for movement via the apoplastic continuum also comes from the work of Sadik and others (1986b). These workers have shown high levels of acid phosphatase and ATPase activity at the level of plasmalemma, plasmodesmata, and some small endocytotic and exocytotic vesicles in sinkers. They interpret such activity as a sign of intense, active transfer processes in the xylary part of sinkers. Although the relative importance of alternative pathways (symplastic and apoplastic) is problematic, evidence suggests that both pathways are involved in water and nutrient uptake. The latter pathway, the apoplastic continuum provided by walls of adjacent host and parasite parenchyma, should allow for selectivity in nutrient uptake. Finally, it also seems likely that dwarf mistletoe sinkers are dimorphic and thus differ not only in structure but also in function.

Graniferous tracheary elements have been found in the endophytic system of *Arceuthobium* (Fineran 1985, Weber and Nietfeld 1984), as well as in their stems, leaves, and fruits (chapter 10). After the bases of shoots are killed by steam, host-fixed carbon compounds are no longer transported into shoots even though transpiration continues (Hull and Leonard 1964b). Observations such as these must be considered in any hypotheses concerning water economy and nutrient transfer in *Arceuthobium.*

Srivastava and Esau (1961b) state, “the most pronounced abnormalities in the xylem anatomy of an infected host occur in the rays.” These abnormalities are especially evident in *Arceuthobium* because sinkers of dwarf mistletoes form almost exclusively within host rays. The significance of these highly complex, intergeneric structures (infected rays) as an evolutionary innovation becomes clear if one considers certain anatomical and physiological features of both host and parasite. Relevant features in *Pinus* (Zimmermann 1983) include

- Pitting almost entirely on radial walls of tracheids (fig. 11.2E at unlabeled arrows), thus facilitating the tangential movement of materials to rays.
- Ray tracheids facilitating the horizontal movement of materials within rays (fig. 11.2E).
- Rays that are highly efficient in horizontal transfer of water and nutrients (also true for host species in which ray tracheids are absent).

Important features of *Arceuthobium* (Srivastava and Esau 1961b) include both the reported ability to stimulate the production of additional host cells within infected rays and the ability to stimulate formation of new host rays. When these individual features are considered together, it becomes clear that infected rays provide the "ultimate" apoplastic continuum. This system is more extensive and dynamic in *Arceuthobium* than observed in other genera of Viscaceae. An appreciation of these features of infected rays gives new meaning to Heinricher's (1924) view that the penetration power and the efficiency of the absorbing system of *Arceuthobium* are superior to those of other Viscaceae.

CHAPTER 12

Pathogenic Effects

The dwarf mistletoes are serious pathogens of coniferous forest trees in many parts of the Northern Hemisphere, particularly in western North America. These widespread parasites retard growth of infected trees and cause extensive timber losses through direct and indirect mortality. In addition, the dwarf mistletoes reduce seed production and wood quality of the host plants, particularly in *Abies* and *Tsuga*. Infections by dwarf mistletoe also can provide entrance points for decay fungi.

Economic Impacts

In many parts of western North America, particularly in the central Rocky Mountains and the Southwest, the dwarf mistletoes are the most damaging pathogens of coniferous forest trees (Hawksworth and Shaw 1984). The extent of economic losses caused by dwarf mistletoes has been estimated at about 11.3 million cubic meters of wood annually (or about 3 billion board feet) in the western United States (Drummond 1982) and 3.8 million cubic meters in western Canada (Sterner and Davidson 1982). No information is available on losses in Latin America or Asia. It is difficult to calculate an actual dollar loss, but it is certainly several billion dollars annually.

The commercially important trees that are most seriously damaged in the western United States are *Pinus ponderosa, P. contorta, P. jeffreyi, Pseudotsuga menziesii, Abies magnificae, A. concolor, Larix occidentalis,* and *Tsuga heterophylla.* In parts of the Great Lakes region and New England, damage is severe on *Picea mariana, P. glauca,* and *P. rubens.* In Canada, the most seriously affected trees are *Pinus contorta, P. banksiana, Tsuga heterophylla, Larix occidentalis,* and *Picea mariana.*

Dwarf mistletoes also are the most serious parasites of conifers in Mexico, where at least 30 species of pines, as well as firs and Douglas-fir, are affected (Hawksworth 1991a). Although no economic data are available on losses outside the United States and Canada, dwarf mistletoes are known to have serious effects on forest production not only in Mexico, but also in Guatemala and Belize (our observations), the Dominican Republic (Etheridge 1971), India (Bagchee 1952, Bakshi and Puri 1971), Pakistan (Zakaullah 1988), and China (Tong and Ren 1980).

Pathogenic Effects on Host Plants

Dwarf mistletoe infections ultimately reduce a tree's growth rate in both height and diameter, but only after the upper half of the tree's crown is parasitized. Growth rate of the host then declines rapidly as the severity of infestation in the upper half of the crown increases (Hawksworth 1961a). Severe dwarf mistletoe infection will eventually kill the host. The time required for the parasite to kill a tree, however, varies considerably and depends on many factors, including

- Host–parasite combination
- Severity of infection
- Vigor of the host
- Ecological and climatic situation under which the host tree is growing
- Activity of secondary pests, particularly bark beetles (Scolytidae), which often attack and kill severely infected trees

Just how dwarf mistletoes affect the growth and physiology of their host trees is not fully understood (chapter 9). Presumably, they alter the tree's metabolic balance so that water, minerals, and various assimilates are appropriated by the parasite and infected parts of the lower crown at the expense of healthy parts of the crown. An infected branch thus becomes a nutrient sink. Radial growth of infected branches is greatly enhanced, as opposed to uninfected branches in the same whorl (Korstian and Long 1922, Hawksworth 1961a). Infected branches also tend to outlive adjacent uninfected branches. As progressively more nutrients are appropriated to infected branches, the vigor of the crown declines, and the tree ultimately dies.

Dwarf Mistletoe Infection Rating Systems

Several systems for quantifying the severity of dwarf mistletoe infestation have been proposed (Hawksworth 1977, Dooling 1978). Some of these systems have as few as 4 classes, and others have as many as 18. Most of the early systems used subjective, undefined ratings such as "light," "medium," or "heavy." In an attempt to develop a less subjective system that would be applicable to several host–parasite combinations, the 6-class dwarf mistletoe rating system (DMR) was developed in the early 1950's (Hawksworth and Lusher 1956, Hawksworth 1961a). Hawksworth (1977) gives details on the 6-class DMR system, including its uses and limitations.

In the 6-class system (fig. 12.1), the live crown is visually divided into thirds, and each third is rated as 0 for no mistletoe visible, 1 for light mistletoe infection (less than half of the branches infected), or 2 for heavy mistletoe infection (more than half of the branches infected). Ratings for each third are then added to obtain a total for the tree. For example, a tree heavily infected in the lower one-third of the crown, lightly infected in the middle one-third, and not infected in the upper third would be rated: 2 + 1 + 0 = class 3. A tree heavily infected in each third would be class 6. In this system, infections on the main stem are not considered, unless they are the only infections on the tree, which would be rated as class 1. An average stand or plot rating (stand DMR) is obtained by computing the mean rating of all live infected and noninfected host trees by species. This calculation may need adjustment depending on how trees are sampled (Filip and others 1993). Another statistic useful for describing infestation severity is the dwarf mistletoe index (DMI), the average DMR rating of live infected trees only (Geils and Mathiasen 1990). Because the 6-class system is easy to apply and ratings on the same tree by different observers are comparable, it has become the standard for quantifying the severity of dwarf mistletoe infection (Dooling 1978).

Host Vigor

Although effects of dwarf mistletoes on tree vigor (as exhibited by thin, off-color foliage) are obvious in most severely infested stands, they are difficult to quantify. The most comprehensive report is the now-

INSTRUCTIONS

STEP 1. Divide live crown into thirds.

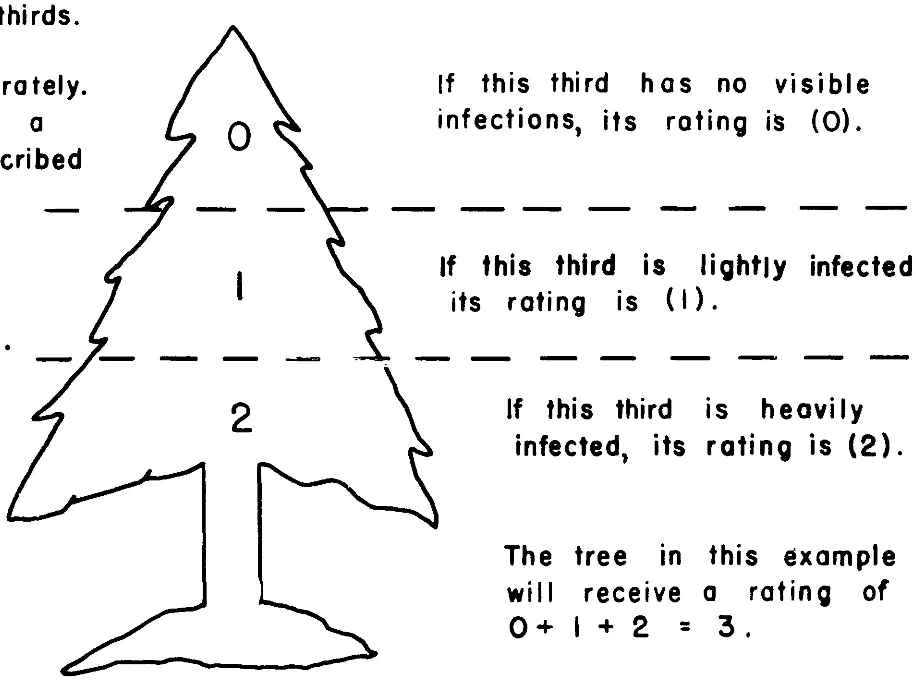
STEP 2. Rate each third separately. Each third should be given a rating of 0, 1 or 2 as described below.

(0) No visible infections.

(1) Light infection (1/2 or less of total number of branches in the third infected).

(2) Heavy infection (more than 1/2 of total number of branches in the third infected).

STEP 3. Finally, add ratings of thirds to obtain rating for total tree.



EXAMPLE

If this third has no visible infections, its rating is (0).

If this third is lightly infected, its rating is (1).

If this third is heavily infected, its rating is (2).

The tree in this example will receive a rating of 0 + 1 + 2 = 3.

Figure 12.1 –The 6-class dwarf mistletoe rating system (Hawksworth 1977).

classic study by Korstian and Long (1922) of *Arceuthobium vaginatum* subsp. *cryptopodum* on *Pinus ponderosa* in northern Arizona. They measured needle length, length of needle-bearing stems, number of needles, and photosynthetic surface on uninfected trees and comparable trees with various amounts of dwarf mistletoe infection (table 12.1). They found significant effects, particularly for heavily infected trees, in which average needle length was reduced by 30%, length of needle-bearing stems by 50%, leaf surface by 85%, and number of needles per tree by 80%. They also observed that infected trees had yellow-green foliage, whereas uninfected trees had olive-green foliage.

Andrade and Cibrián (1981) found a significant reduction in needle length on *Pinus hartwegii* heavily infected by *Arceuthobium globosum* subsp. *grandicaule* and *A. vaginatum* subsp. *vaginatum* in central Mexico—needles on uninfected trees averaged 14.8 cm long, whereas those of heavily infected trees averaged 9.4 cm, a reduction of 36%.

Weir (1918a) measured lateral and terminal buds of young *Pseudotsuga menziesii* trees in Montana that were uninfected or heavily infected with *Arceuthobium douglasii.* Terminal buds on uninfected trees averaged 12 x 4 mm compared with 8 x 3 mm for heavily infected trees. Uninfected trees had an average of 157 lateral buds (mean size 7 x 3 mm) compared to 108 (5 x 3 mm) for heavily infected trees.

Hawksworth (1961a) rated 1,600 *Pinus ponderosa* trees in southern New Mexico for crown vigor (on a 3-class scale) and severity of dwarf mistletoe infection (6-class DMR system). Vigor of the upper crown third was rated "good" for trees with normal needle color and density, "fair" for trees with intermediate needle color and density, or "poor" for trees with off-color needles and thin crowns. In a 55-year-old stand, 61% of the DMR class 6 trees were rated as poor, compared to 24% for DMR class 5 trees, and 2% for all other DMR infection classes, including noninfected trees. In a mature stand, 28% of the DMR class 6 trees were rated as poor, compared to 12% in DMR class 5 trees, and 3% for all other DMR infection classes.

Hawksworth and Johnson (1989a) conducted similar analyses for 2,600 mature *Pinus contorta* trees in Colorado and Wyoming infected by *Arceuthobium americanum*, but used Taylor's (1939) 4-class vigor rating system. This system rates trees as most vigorous (class A: crown dense, full, of good color, and pointed) to least vigorous (class D: crown thin, open, off-color, and rounded). Only 20% of the trees in DMR classes 0 to 3 were in vigor class D, but this increased to about 27% for DMR class 4 and 5 trees, and up to 66% for DMR class 6 trees.

Schaffer and others (1983a) measured pulsed electrical resistance of trunk sapwood for *Pinus contorta* trees in various DMR classes and rated crown vigor with a 3-class system (Hawksworth 1961a and

TABLE 12.1 – Effects of *Arceuthobium vaginatum* subsp. *cryptopodum* on foliage characteristics of mature ponderosa pine in northern Arizona

Degree of infection	Needle length (cm)	Length of needle-bearing twigs (cm)	Total leaf surface (cm^2)	Needles per tree (thousands)
None	13.7 (38)	25.9 (37)	6,555 (3)	539 (3)
Light	11.4 (15)	21.1 (15)	—	—
Medium	10.7 (18)	14.7 (15)	—	—
Heavy	9.9 (32)	12.2 (30)	1,361 (2)	83 (2)

Source: Adapted from Korstian and Long (1922). Number of trees in parentheses.

described above for *P. ponderosa* in New Mexico). Electrical resistance was found to be inversely correlated with crown vigor class:

"Good"	16.3 ± 0.4 k-ohms
"Fair"	21.9 ± 1.2 k-ohms
"Poor"	30.0 ± 3.6 k-ohms

However, only trees in DMR class 6 had a significantly higher electrical resistance than trees in other DMR classes (including class 0, uninfected).

Young Trees

Mortality rates of infected seedlings are high, particularly those with main-stem infections. Weir (1916b) studied a 0.4-ha stand of 480 young *Pinus ponderosa* trees near Spokane, Washington; 245 (51%) of these trees were infected by *Arceuthobium campylopodum* and 49 (10%) had been killed by dwarf mistletoe. Roth (1971), also studying *A. campylopodum,* observed about 50% mortality among infected seedlings after 12 years. The surviving but infected trees were only about half as tall as uninfected trees.

Weir (1918a) measured heights of 4- to 10-year-old *Pinus ponderosa* trees near Spokane, Washington, and found those infected with *Arceuthobium campylopodum* were 30 to 40% shorter than uninfected trees. Knutson and Toevs (1972) noted that 2-year-old seedlings infected with this dwarf mistletoe were reduced in height and had shorter roots and less root volume than comparable uninfected seedlings. Seedling infection can be especially high in some stands. For example, Scharpf and Vogler (1986) reported that in the Laguna Mountains of southern California, 77% of the *P. jeffreyi* seedlings about 15 years old were infected by *A. campylopodum,* mostly on the main stem.

Older Trees

There is considerable literature on the pathological effects of different dwarf mistletoes on various hosts, particularly with respect to mortality and growth in diameter, height, and volume. Pertinent literature for North America was summarized by Hawksworth and Shaw (1984) and Hawksworth and others (1992a). Only a few representative examples are provided here.

Diameter Growth

Reduction in diameter growth is related primarily to infection severity but is also a function of the host–parasite combination. Usually, the effect is not measurable until severity of infection reaches DMR class 3 (table 12.2). As infection increases above this threshold, growth rates decline rapidly. Generally, reduction measured as 10-year periodic diameter increment is 10% for class 4 trees, 30% for class 5 trees, and 50% or more for class 6 trees (Hawksworth and others 1992c, Wicker and Hawksworth 1988).

TABLE 12.2 – Relative rates of diameter growth in relation to intensity of infection by *Arceuthobium* as quantified with the 6-class dwarf mistletoe rating system (DMR)

		Percentage growth of infected trees					
Arceuthobium	Host	class 1	class 2	class 3	class 4	class 5	class 6
A. abietinum	*Abies concolor*	100	100	98	95	70	50
A. americanum	*Pinus contorta*	100	100	100	94	80	59
A. campylopodum	*Pinus ponderosa*	100	100	98	86	73	50
A. douglasii	*Pseudotsuga menziesii*	98	97	85	80	52	44
A. laricis	*Larix occidentalis*	94	92	88	84	58	54
A. vaginatum	*Pinus ponderosa*	100	100	98	86	73	50

Note: Diameter growth rates of uninfected trees taken as 100%. Percentages based on averages of several studies throughout the western United States (adapted from Hawksworth and others 1992c).

Height Growth

Information on height growth is more difficult to obtain than for diameter growth, and fewer data are available. In general, effects of dwarf mistletoes on height growth are similar to those for diameter growth, but height reductions are usually slightly greater and are detectable earlier. In *Pinus hartwegii* infected by two species of *Arceuthobium* near Chapingo, Mexico, diameter growth was reduced by 19% but height was reduced by 29% (Andrade and Cibrián 1981). Some studies quantifying effects of dwarf mistletoes on height growth are summarized in table 12.3.

Volume Growth

Reductions in stem volume reflect a combined effect of reduced growth in both diameter and height. Thus, losses in volume are proportionately greater than for those in diameter or height alone. Several studies show that severely infested stands produce only one-half to one-third the merchantable volume of timber expected from uninfected stands on comparable sites (Shubert and others 1993).

Mortality

Although volume growth losses in surviving trees are important for many host–parasite combinations, mortality is a more serious component of timber loss for other combinations. Increased mortality rates within dwarf mistletoe–infested stands were summarized by Hawksworth and others (1992c) (table 12.4). Some North American host–parasite combinations in which elevated tree mortality is particularly important are listed in table 12.5. In addition, *Arceuthobium minutissimum* increases mortality rates of *Pinus wallichiana* in the western Himalayas (Zakaullah 1988).

Mortality rates are significantly higher in multiple-age stands with trees less than 25 cm in diameter than in older stands with larger trees. This was demonstrated for stands of *Pinus ponderosa* infested by *Arceuthobium vaginatum* subsp. *cryptopodum* in Arizona (Hawksworth and Geils 1990) and stands of *Pseudotsuga menziesii* infested by *A. douglasii* in the Southwest (Mathiasen and others 1990).

Old-Growth Stands

Effects of dwarf mistletoes on old-growth stands have received relatively little study. Previously, emphasis has been primarily on harvesting old-growth stands and regenerating the areas with mistletoe-free stands. With an increasing emphasis toward preserving old-growth forests, however, information on the effects of pathogens in such stands is becoming more important. By inducing formation of witches' brooms and causing topkill and mortality of host trees, dwarf mistletoes affect the species composition, vertical crown structure, and spacing of trees within infested stands. These direct effects, in turn, have numerous

TABLE 12.3 – Relative rates of height growth in relation to intensity of infection by *Arceuthobium* as quantified with the 6-class dwarf mistletoe rating system (DMR)

		Percentage growth of infected trees					
Arceuthobium	Host	class 1	class 2	class 3	class 4	class 5	class 6
A. americanum	*Pinus contorta*	100	100	98	93	81	72
A. douglasii	*Pseudotsuga menziesii*	94	94	84	84	75	75
A. laricis	*Larix occidentalis*	99	99	87	87	83	83
A. vaginatum	*Pinus ponderosa**	100	100	96	92	89	85
	Pinus ponderosa†	100	100	94	92	87	79

Note: Height growth rates of uninfected trees taken as 100%. Data for *Pinus contorta* infected by *A. americanum* represent 10-year average stand growth (Myers and others 1971). Data for *Pseudotsuga menziesii* infected by *A. douglasii* and for *Larix occidentalis* infected by *A. laricis* are average annual growth rates for individual trees grouped into 3 infection classes: less than 1/3 of crown broomed (class 1-2), 1/3 to 2/3 of crown broomed (class 3-4), and more than 2/3 of crown broomed (class 5-6) (Pierce 1960). Data for *Pinus ponderosa* infected by *A. vaginatum* subsp. *crytopodum* given for two bases: *10-year average stand growth (Myers and others 1976) and †total height of 55-year-old trees (Hawksworth 1961a).

consequences on the physical structure and functioning of the ecosystem. For example, the brooms provide forage, nesting, and cover for birds and mammals, but also increase the likelihood of ground fires becoming crown fires. Canopy gaps caused by mistletoe-induced mortality increase within-stand diversity but also reduce the interior-forest area. These ecological effects are complex and provided a fascinating area for future research.

Roth (1954) made an intensive survey of *Arceuthobium campylopodum* in a 259-ha stand of old-growth *Pinus ponderosa* in central Oregon. Dwarf mistletoe occurred on 105 ha or 41% of the area surveyed. Within the infested area, infection level was rated as very light on 58% of the area, light on 29%, intermediate on 12%, and heavy to very heavy on only 1%. Dwarf mistletoes generally exhibited a patchy distribution as the result of many interacting factors, including steepness of slope, aspect, fire history, and stand structure.

Hawksworth and others (1992c) examined the distribution of *Arceuthobium americanum* and its effects on basal area growth and mortality in three 2.02-ha plots in 300-year-old *Pinus contorta* stands in Colorado. From 34 to 60% of the area was infested, and no isolated infection centers occurred. This pattern was in marked contrast to nearby 70-year-old stands, which had an average of 1.4 isolated infection centers per ha (Nicholls and others (1987a). Mortality levels on infested plots were 1.7 times greater than levels on uninfested plots. Basal area growth was significantly reduced (about 30%) only in the most heavily infected trees (DMR class 6). This reduction in basal area growth is considerably less than that in younger infested stands of *Pinus contorta:* 6% reduction for DMR class 4 trees, 20% for DMR class 5 trees, and 42% for DMR class 6 trees. The study suggests that old-growth *P. contorta* trees tolerate dwarf mistletoe infection with significantly less effect than do younger trees.

Cone and Seed Production

Cone and seed production of heavily infected trees are generally reduced, but there are few quantitative studies. Cone production on dwarf mistletoe witches' brooms is usually markedly reduced (Weir 1916b, Kuijt 1960b). However, Bonga (1964) noted mature cones with viable seeds on a witches' broom caused by *Arceuthobium pusillum* on *Picea mariana* in New Brunswick. We also have observed cones on systemic witches' brooms in *Pinus contorta* and *Pseudotsuga menziesii,* but these cones and seeds are smaller than normal.

Pearson (1912) studied seed germination of *Pinus ponderosa* trees in Arizona infected by *Arceuthobium vaginatum* subsp. *cryptopodum.* Germination of seed was 61% from infected trees and to 78% from uninfected trees. Korstian and Long (1922) studied these species in the same area and reported that production of viable seeds was not significantly reduced for lightly infected trees but was reduced by about 60% for moderately infected trees and 75% for heavily infected trees. Munns (1919) found that *P. jeffreyi* trees infected by *A. campylopodum* had seeds that were about half the normal weight, had a 20% lower germination rate, and produced less vigorous seedlings than those from uninfected trees. Reid and others (1991), however,

TABLE 12.4 – Increase in 10-year mortality rate within stands infested by *Arceuthobium*

		Additional mortality within infested stands					
Arceuthobium	Host	class 1	class 2	class 3	class 4	class 5	class 6
A. abietinum	*Abies concolor*	1	3	6	10	15	21
A. americanum	*Pinus contorta*	2	4	5	6	7	8
A. douglasii	*Pseudotsuga menziesii*	1	2	4	9	15	23
A. vaginatum	*Pinus ponderosa*	1	4	8	15	23	34

Note: Additional mortality within infested stands is the increase in 10-year mortality rate (percent of trees dying per decade) over the mortality rate expected within uninfested stands; severity of infestation is quantified as average 6 class dwarf mistletoe rating for all live host trees (stand DMR). Based on averages of several studies throughout the western United States (adapted from Hawksworth and others 1992c).

TABLE 12.5 – Combinations of North American taxa of *Arceuthobium* and their hosts in which host mortality rates are particularly high

Arceuthobium	Host	Location
A. abietinum f. sp. *magnificae*	*Abies magnifica*	CA
A. americanum	*Pinus contorta*	western US, Canada
	Pinus banksiana	MB, SK, and AB, Canada
A. blumeri	*Pinus* spp.	Chihuahua and Durango, Mexico
A. campylopodum	*Pinus ponderosa*	southern CA
A. cyanocarpum	*Pinus flexilis*	ID, UT, WY, CO
	Pinus albicaulis	northern CA
A. douglasii	*Pseudotsuga menziesii*	western North America
A. durangense	*Pinus* spp.	Jalisco, Mexico
A. gillii	*Pinus* spp.	Chihuahua and Durango, Mexico
A. guatemalense	*Pinus ayacahuite*	southern Mexico and Guatemala
A. laricis	*Larix occidentalis*	northwest US and BC, Canada
A. microcarpum	*Picea pungens*	AZ, NM
A. nigrum	*Pinus* spp.	Durango and Puebla, Mexico
A. occidentale	*Pinus sabiniana*	CA
A. pusillum	*Picea mariana* *Picea glauca*	eastern North America
A. strictum	*Pinus leiophylla*	Durango, Mexico
A. vaginatum subsp. *cryptopodum*	*Pinus ponderosa*	AZ, CO, NM, UT
	Pinus arizonica	Chihuahua, Mexico
A. verticilliflorum	*Pinus* spp.	Durango, Mexico

observed no effect on cone production on *Pinus rudis* infected by *A. vaginatum* subsp. *vaginatum*.

Schaffer and others (1983b), working in the Rocky Mountains, reported that cone size, seed size, and seed germination of *Pinus contorta* trees were negatively correlated with the severity of infestation by *Arceuthobium americanum*. In Oregon, Wanner (1986) reported that cone length, number of seeds per cone, seed weight, and calories per seed of *P. contorta* were significantly reduced from normal for moderately and heavily infected trees. However, he found no relationship between severity of dwarf mistletoe infection and seed viability. In fact, 1-year survival of seedlings was significantly higher in heavily infested stands; this increased survival was attributed to better seedbed conditions provided by the higher amounts of woody litter that negated effects of reduced seed production in heavily infested stands.

Picea mariana infected by *Arceuthobium pusillum* in Newfoundland showed 10 to 22% loss of cone production and 25% reductions in seed production (Singh 1981). Further studies by Singh and Carew (1989) showed that infected trees had 10 to 24 fewer cones per tree than uninfected trees, 8 to 30 fewer seeds per cone, 8 to 29% lighter seeds, and 18 to 63% lower germination rates.

Hawksworth and Zakaullah (1985) found a strong correlation between the severity of infection by *Arceuthobium minutissimum* and cone production of *Pinus wallichiana* in Pakistan. Cone production was rated on a 4-class scale: 0 for trees with no cone crop; 1 for trees with cone crop less than normal and restricted to less than half of the upper crown; 2 for trees with cone crop less than normal but distributed over more than half of the upper crown; and 3 for tree with a normal cone crop. The average ratings for trees in each DMR class were then determined:

6-class DMR system	Number of trees	Cone production rating
0	22	2.9
1	3	2.3
2	11	2.3
3	17	2.2
4	16	1.6
5	37	0.8
6	47	0.04

Trees in DMR class 6 produced practically no cones; trees in class 5 produced fewer and markedly smaller cones than those on uninfected and lightly infected trees.

Wood Quality

Infection by dwarf mistletoes also affects the merchantability of wood by producing larger knots, developing abnormal grain, and reducing strength. The anatomy of dwarf mistletoe–infected wood is characterized by shorter, distorted tracheids and increased ray volume (Srivastava and Esau 1961b, Piirto and others 1974, Cibrián and others 1980). In old-growth *Larix occidentalis,* distorted wood grain, heavy pitch infiltration, insect frass, and associated decay markedly reduce merchantability of wood around trunk burls (Weir 1916a).

Wellwood (1956a, 1956b) reported that sapwood of *Tsuga heterophylla* trees infested by *Arceuthobium tsugense* had a lower moisture content and lower specific gravity than comparable uninfected wood. However, Hawksworth (1961a) observed that sapwood of *Pinus ponderosa* infected by *A. vaginatum* subsp. *crytopodum* had a higher moisture content and higher specific gravity than uninfected wood from the same trees. Knutson (1970) studying stem wood of *P. ponderosa* infected by *A. campylopodum,* found no difference in moisture content or specific gravity of wood at the infection site or immediately above it. Below the infection site, however, there was significantly higher moisture content and lower specific gravity. He concluded that stem infections impede normal movement of water and metabolites through sapwood.

Piirto and others (1974) observed that wood of *Pinus contorta* infected by *Arceuthobium americanum* had a higher specific gravity, a higher percentage of alcohol-benzene extractives, greater longitudinal shrinkage, and a lower percentage of latewood than comparable uninfected wood. Furthermore, infected wood was weaker in all strength tests—modulus of elasticity, modulus of rupture, and work to proportional limit. Finally, not only was wood from infected zones lower in strength, but wood from other parts of an infected tree was also adversely affected.

Infection by *Arceuthobium vaginatum* subsp. *cryptopodum* had little effect on bolts of *Pinus ponderosa* that were used for posts and treated with preservatives. In fact, wood from infected trees had slightly greater preservative penetration and retention than uninfected wood, but the differences were not significant (USDA Forest Service 1954).

The cumulative effects of dwarf mistletoe infection on lumber or pulp quality are usually negligible on *Pinus contorta* in British Columbia (Dobie and Britneff 1975), *Abies concolor* in California (Wilcox and others 1973), and *Tsuga heterophylla* in British Columbia (Hunt 1971) and Washington (Hadfield 1981). Presumably, most of the mistletoe-infected wood is near the outside of the trunk and removed when the logs are squared for sawing into cants or lumber.

Predisposition to Infection by Decay Fungi

Dwarf mistletoe infections of the main trunk and adjacent limbs of fir, larch, or hemlock trees frequently provide infection courts for decay fungi. This is usually not the case, however, for pine, spruce, or Douglas-fir trees, presumably because of their more resinous nature. In *Tsuga heterophylla* from Oregon and Washington, Englerth (1942) reported that nearly a third of the decay entered through dwarf mistletoe stem infections and adjacent swollen limbs. Several decay fungi are associated with dwarf mistletoe cankers in *T. heterophylla* in British Columbia; the most common is *Fomitopsis pinicola* (Etheridge 1973).

Dwarf mistletoe stem cankers on fir trees generally provide entrance courts for decay fungi only if the bark has died and sloughed off and the wood is exposed (Aho 1982, Aho and Roth 1978, Kimmey and Bynum 1961). Living bark is not affected. Trunk decay in *Abies concolor* is essentially limited to the zone of the swelling (Aho 1982). Studies by Parmeter and Scharpf (1982) indicate that for well-managed, young-growth stands of true fir in California, decay associated with stem infections should not lead to serious timber losses.

Weir (1916b) examined 540 dwarf mistletoe–infected *Larix occidentalis* in northern Idaho and found that 278 of 600 (46%) dwarf mistletoe–induced burls were infected by wood decay fungi, primarily *Phellinus pini, Fomitopsis officinalis,* and *Laetiporus sulphureus.* However, Weir (1916a) observed little decay associated with dwarf mistletoe burls in *L. occidentalis* in eastern Oregon.

Relationship to Other Mortality Factors

Tree mortality may involve a complex of interacting pathological, entomological, and environmental factors. For example, Byler (1978) showed that interactions among several agents were involved in mortality of *Pinus coulteri* and *P. jeffreyi* in the Laguna Mountains of California: root pathogens alone were involved in 24% of the mortality, dwarf mistletoe alone in 32%, both pathogens jointly in another 28%, and other pest complexes in 16%.

Diseases

With the exception of infection by secondary fungi (chapter 8), there are surprisingly few studies on the interactions of dwarf mistletoes and other pathogens. Chorover and McBride (1987) reported a significant correlation between infection of *Pinus radiata* by *Arceuthobium littorum* and *Endocronartium harknessii* near Cambria, California. Singh and Carew (1989) observed that decay fungi infecting *Picea mariana* parasitized by *A. pusillum* were generally the same species as those on uninfected trees, but their frequency on mistletoe-infected trees increased by as much as 40%. Severe mortality occurs in many *P. banksiana* stands in southern Manitoba in which both *A. americanum* and *Armillaria* sp. (a root disease pathogen) are involved. The basis for the association and the role of each pathogen in the complex are now being investigated (Heberson and Baker 1994).

Insects

Whether or not infection by dwarf mistletoes alone can kill trees, severe infection can clearly weaken trees enough that they are readily killed by secondary infestations of insects. The interrelationships between dwarf mistletoes and Scolytidae (bark beetles) as causes of tree mortality have been long debated (Stevens and Hawksworth 1970, 1984). In some associations the susceptibility of mistletoe-infected trees to infestation by bark beetles increases, in others there is little or no effect, and in some instances mistletoe-infected trees may even be less susceptible. Associations where susceptibility of dwarf mistletoe-infected trees to insect infestation appears to be increased include:

- *Arceuthobium campylopodum* and *Melanophila californica* on *Pinus jeffreyi* in California (Swain and others 1974, Wood and others 1979).
- *Arceuthobium campylopodum* and *Dendroctonus brevicomis* on *Pinus ponderosa* in Oregon (Miller and Keen 1960).
- *Arceuthobium campylopodum* and *Dendroctonus valens* on *Pinus ponderosa* in California (Owen 1985).
- *Arceuthobium divaricatum* and *Ips* spp. on *Pinus edulis* in Colorado (James and Lister 1978) and *Ips confusus* in Arizona (Wilson and Tkacz 1992).
- *Arceuthobium douglasii* and *Melanophila drummondi* on *Pseudotsuga menziesii* in the Rocky Mountains and the Southwest (Stevens and Hawksworth 1984).
- *Arceuthobium* sp. and *Dendroctonus mexicanus* on *Pinus pseudostrobus* and *P. montezumae* in Jalisco, Mexico (unpublished data).
- *Arceuthobium vaginatum* and *Dendroctonus ponderosae* on *Pinus ponderosa* in Colorado (Johnson and others 1976, McCambridge and others 1982).
- *Arceuthobium vaginatum* and *Dendroctonus adjunctus* on *Pinus ponderosa* in New Mexico (Stevens and Flake 1974).
- *Arceuthobium vaginatum* and *Ips lecontei* on *Pinus ponderosa* in Arizona and New Mexico (Parker 1979).

Some associations where susceptibility of dwarf mistletoe–infected trees to bark beetle infestation is apparently little affected:

- *Arceuthobium douglasii* and *Dendroctonus pseudotsugae* on *Pseudotsuga menziesii* in the Rocky Mountains (Furniss and others 1981). However, Weir (1916b) suggests that in northern

Idaho this dwarf mistletoe does predispose the host to attack.

- *Arceuthobium microcarpum* and *Dendroctonus rufipennis* on *Picea engelmannii* in Arizona (Acciavatti and Weiss 1974).

An association where susceptibility of dwarf mistletoe–infected trees to bark beetles may be decreased:

- *Arceuthobium americanum* and *Dendroctonus ponderosae* on *Pinus contorta* in the Rocky Mountains (McGregor 1978).

The last association is not unexpected because *Pinus contorta* trees infected by dwarf mistletoe usually have thinner phloem than uninfected trees, and trees with thin phloem are less susceptible to bark beetle attack (Amman and McGregor 1985, Roe and Amman 1970). In Colorado, however, little correlation was observed between phloem thickness and severity of dwarf mistletoe infection (Hawksworth and others 1983).

Mortality in *Pinus ponderosa* in northern Arizona defoliated by *Coloradia pandora* (Saturniidae) was highest in trees most severely infected by *Arceuthobium vaginatum* subsp. *cryptopodum* (Wagner and Mathiasen 1985). Similarly, in British Columbia, *Tsuga heterophylla* trees free of dwarf mistletoe survived successive defoliations by *Lambdina fiscellaria* (Geometridae) much better than trees infected by *A. tsugense* (Buckland and Marples 1952). In the Pacific Northwest, Filip and others (1993) found that *A. douglasii* and *Choristoneura occidentalis* (Tortricidae) individually reduced diameter growth of *Pseudotsuga douglasii*, but no significant interactions were found.

Climatic Effects

Extremes in temperature and moisture can affect mortality rates of dwarf mistletoe–infected trees. Mortality rates are often highest following periods of drought, but there are few quantitative data. Childs (1960) noted that mortality of mistletoe-infected *Pinus ponderosa* branches was high following the severe drought of 1958–1959 in the Pacific Northwest. The most comprehensive studies of the interaction of drought and *Arceuthobium campylopodum* on mortality in *P. ponderosa* are by Page (1981) and Smith (1983) for the California drought of 1975–1977. After the drought, mortality of mistletoe-infected trees was more than four times higher than that of noninfected trees.

Air Pollution

Arceuthobium campylopodum is common on *Pinus ponderosa* and *P. jeffreyi* in the San Bernardino Mountains of southern California where oxidant injury is severe on conifers; however, no direct effects of oxidant injury on dwarf mistletoe plants have been observed (Miller and White 1977). Any indirect effects of oxidants on dwarf mistletoe, e.g., selective killing of diseased hosts, has not been assessed. De Bauer and others (1987) suggested that air pollution near Mexico City may predispose *P. hartwegii* to dwarf mistletoe damage. The most striking example of the effects of an air pollutant on dwarf mistletoe distribution is in the areas exposed to high levels of sulfur dioxide that surround the early copper smelter at Anaconda, Montana (Scheffer and Hedgcock 1955). Both *A. cyanocarpum* on *P. flexilis* and *A. americanum* on *P. contorta* had previously been common there but are now rare or absent. We have found no living *A. cyanocarpum* in that area, and the closest known *A. americanum* is at least 10 km from the smelter site.

Control

Because of the extensive timber loss caused by dwarf mistletoes in forests of western North America, considerable efforts have been made to control them. Some early forest pathologists in the West recognized that silvicultural controls were feasible and outlined suggestions for their implementation, notably Korstian and Long (1922) in the Southwest, Weir (1916c) in the Northwest, and Meinecke (1914) in California. Various alternative controls are applicable in different types of stands. Most emphasis, however, is given to silvicultural controls, as these are the only methods economically practical in most situations. Potentials for biological and chemical controls are also discussed, although their use is presently limited. Current efforts to develop dwarf mistletoe–resistant trees is also described.

Biological Control

In spite of the many organisms that are pathogens or predators of dwarf mistletoes (chapter 8), none have been sufficiently studied to consider developing them as biological controls (Hawksworth 1972). Insects (particularly various lepidopteran larvae) and some fungi are often highly destructive to dwarf mistletoes in some areas in certain years. However, these are indigenous organisms that have co-evolved with their hosts; their overall effects on dwarf mistletoe populations are probably negligible. Initial research has identified three destructive insect predators that are apparently endemic to Pakistan (Baloch and Ghani 1980), but no steps have been taken to test their applicability for introduction into North America. Other Asian dwarf mistletoes may also harbor candidates for biological control of New World dwarf mistletoes. The likelihood of developing insects or fungi as practical control agents in the near future, however, seems remote.

Chemical Control

The development of a selective herbicide to control dwarf mistletoes has been a primary, but elusive, goal for decades. Gill (1955) listed 260 tests that had been made by 7 investigators in the western United States and Canada. Nearly 60 different chemicals were tested (most were various formulations of 2,4-D or 2,4,5-T), but none were effective without also injuring the host tree. Furthermore, none of the chemicals tested affected the endophytic system of the dwarf mistletoe, and resprouting typically occurred. Gill's report was followed by additional studies (Quick 1962, Scharpf 1972). The results, however, were generally similar to those obtained in 1955, although Quick (1962) suggested that some formulations of 2,4,5-T showed promise as a practical control in high-value trees. Quick (1964) conducted extensive herbicide tests for dwarf mistletoes involving over 2,500 trees in California and concluded that the isooctyl ester of 2,4,5-T was the most effective in killing mistletoe shoots with the least damage to the host. In spite of its early promise, 2,4,5-T found little acceptance as an operational management tool for dwarf mistletoe control and is now banned because of concerns over environmental effects.

From 1970 to the early 1990's, Arthur Moinat (personal communication) tested *Arceuthobium vaginatum* subsp. *cryptopodum* in Colorado against many herbicides and growth regulators including 2,4-D (Dacamine), MCPA, 2,4-DB (Butyrac), oxyfluofen (Goal), MCPM (Thistrol), silvex (Weedone), (Emulsamine), GA-41065 (Prime), and ethephon (Florel). He obtained high mortality of dwarf mistletoe shoots and minimal host damage with most of these herbicides. None, however, affected the endophytic system and resprouting commonly occurred. His experiments with systemic chemicals that might also affect the endophytic system have been inconclusive to date.

The ethylene-releasing growth regulator Florel—active ingredient, ethephon (2-chloroethyl phosphoric acid)—is the most promising chemical for inducing dwarf mistletoe shoot abscission (Hawksworth and Johnson 1989b), and it is the only chemical approved by the Environmental Protection Agency for use on dwarf mistletoes in the United States. The success with ethephon for controlling *Arceuthobium pusillum* on *Picea mariana* in Minnesota renewed interest in testing this growth regulator on various western dwarf mistletoes (Livingston and Brenner 1983a, 1983b; Livingston and others 1985). Tests with *A. americanum* on *Pinus contorta* in Colorado showed that ground spraying of this chemical was effective in causing dwarf mistletoe shoot abscission (Nicholls and others 1987a, 1987b). However, applications by helicopter of ethephon to *P. contorta* in Colorado (Robbins and others 1989) and to *P. banksiana* in Manitoba, Canada (Baker and others 1989) were not effective. Presumably, adequate deposition on dwarf mistletoes shoots could not be achieved by aerial application. Ground spraying of ethephon for controlling *A. vaginatum* subsp. *cryptopodum* on *P. ponderosa* in Colorado was also effective (Nicholls and others 1987a, Johnson and others 1989). To date ethephon has been tested on 9 host–parasite combinations (Hawksworth and Johnson 1989b, Frankel and Adams 1989):

- *Arceuthobium americanum* on *Pinus banksiana* in Manitoba, Canada.
- *Arceuthobium americanum* on *Pinus contorta* in Colorado and California.
- *Arceuthobium campylopodum* on *Pinus ponderosa* in California and Idaho.
- *Arceuthobium campylopodum* on *Pinus jeffreyi* in California.
- *Arceuthobium divaricatum* on *Pinus edulis* in New Mexico.
- *Arceuthobium douglasii* on *Pseudotsuga menziesii* in Oregon.
- *Arceuthobium laricis* on *Larix occidentalis* in Oregon.
- *Arceuthobium pusillum* on *Picea mariana* in Minnesota.
- *Arceuthobium vaginatum* on *Pinus ponderosa* in Colorado and New Mexico.

Preliminary results from these tests are promising, yielding shoot abscission rates of 90 to 100% when coverage is thorough. However, rapid resprouting from the endophytic system in some species, e.g., *Arceuthobium campylopodum* (Parks and Hoffman 1991), may limit its effectiveness. Tests are currently underway to determine the extent of resprouting and the interval required to re-initiate flowering and fruit production. There has been limited, premature browning of older host needles in some tests, but in general there appear to be few serious side effects on the host (Nicholls and others 1987a). If resprouting is extensive following shoot abscission, then ethephon will not provide long-term dwarf mistletoe control. Seed production by the dwarf mistletoe, however, can be delayed by approximately 2 to 4 years, depending on the host–parasite combination and local environmental conditions.

Ethephon can reduce the rate of spread of dwarf mistletoe and protect understory trees beneath infected trees, but its use cannot cure infected trees as the endophytic system remains active. Spraying infested stands without an understory is not recommended, and application should be restricted to trees in high-value areas, such as recreational, residential, and commercial sites.

Control Through Genetic Resistance

Occasional evidence of host resistance to dwarf mistletoes has been noted in several host–parasite combinations:

- *Arceuthobium vaginatum* subsp. *cryptopodum* on *Pinus ponderosa* in Colorado (Bates 1927) and Arizona and New Mexico (Hawksworth 1961a).
- *Arceuthobium campylopodum* on *Pinus ponderosa* and *P. jeffreyi* in Oregon and California (Roth 1953, Scharpf 1984, Wagener 1965).
- *Arceuthobium americanum* on *Pinus contorta* in Colorado (unpublished data).
- *Arceuthobium tsugense* on *Tsuga heterophylla* (Smith and others 1993).
- *Arceuthobium chinense* on *Keteleeria evelyniana* in China (Tong and Ren 1980).

Information on the resistance of western conifers to dwarf mistletoes is reviewed by Roth (1978) and Scharpf (1984, 1987). Genetic resistance of *Pinus ponderosa* to infection by *Arceuthobium vaginatum* subsp. *cryptopodum* in Colorado was discussed by Roeser (1926) and Bates (1927). They observed a slow-growing form of *P. ponderosa* that exhibited less infection than most other trees in the area and attributed the resistance to "lack of succulence" in the bark. However, nearly 50 years after outplanting seedlings grown from seeds of "resistant" or "susceptible" trees, there were essentially no differences between the two groups with respect to either the incidence or severity of infection by the dwarf mistletoe (Hawksworth and Edminster 1981).

The most extensive studies of resistance are by Roth (1953, 1966, 1971, 1974a, 1974b) and Scharpf and Roth (1992) for *Arceuthobium campylopodum* on *Pinus ponderosa.* Roth (1966) noted that some *P. ponderosa* from western Oregon had "drooping" needles. He suspected that some resistance was imparted by this characteristic because dwarf mistletoe seeds would tend to slide off needles onto the ground, rather than onto safe-sites where infection could occur. However, grafts from these trees did not exhibit the drooping needle habit, and there was no evidence of resistance (Roth 1974a). Furthermore, some Mexican pines that are consistently characterized by drooping needles (notably *P. lumholtzii* and *P. patula*) are severely infected by dwarf mistletoes (Hawksworth 1991a).

Roth (1971, 1974a) showed that seedlings of *Pinus ponderosa* from less susceptible parents also were subject to less infection and exhibited faster growth rates than comparable seedlings from more susceptible parents. Roth (1974b) also observed that susceptibility to infection decreases with increasing tree age to 50 years. He further demonstrated that marked differences existed among trees with respect to both infection susceptibility and subsequent pathological effects.

In a test on the Pringle Butte Experimental Forest of central Oregon, small trees produced by grafting scions from dwarf mistletoe–resistant selections of *Pinus ponderosa* were planted in a heavily infested stand of *P. ponderosa*. After 20 years, high levels of resistance were found in grafts of several selections from the Ochoco and Deschutes National Forests (Scharpf and Roth 1992). Grafts and seedlings from susceptible selections showed no resistance.

An example of resistance to infection by *Arceuthobium campylopodum* was observed in low-elevation *Pinus jeffreyi* from Placer County, California (Scharpf 1987). Seedlings from the Placer County population that were planted near infected trees showed much lower levels of infection 13 years after planting than seedlings of *P. jeffreyi* from other sources:

Seed source	Mean elevation (m)	Percent of trees infected	Average 6-class rating (DMR)
Alpine	2,510	100	6.0
El Dorado	1,920	86	2.8
Ormsby	1,925	50	1.6
Placer	1,125	17	0.3

In a subsequent test, artificial inoculations were made on 7-year-old trees from the same *Pinus jeffreyi* seed sources. Again, the Placer County seed source showed higher levels of resistance (Scharpf and others 1992). Resistance in the Placer population is therefore heritable (Scharpf and others 1992), and outplantings from this seed source have been made in several state and national forest campgrounds in central and southern California.

Pinus contorta trees that are apparently resistant to mistletoe have been found in a small stand of fast-growing trees on the Colorado State Forest (G. Fechner personal communication). Preliminary inoculation tests on seedlings from this site and on seedlings from susceptible sources suggest that initial infection after 2–3 years is lower on the "resistant" source, but results are not yet conclusive (unpublished data).

Smith and others (1993) found significant differences in resistance between artificially inoculated trees propagated by grafting from selected "resistant" and "susceptible" *Tsuga heterophylla*. Resistance was considered to be operating "within rather than outside the host branch."

Silvicultural Control

Guidelines for silvicultural control of dwarf mistletoes were discussed by Baranyay and Smith (1972), Graham (1967), Hawksworth and Johnson (1989a), Hawksworth and Shaw (1984), Johnson and Hawksworth (1985), Kimmey (1957), Kimmey and Graham (1960), Scharpf and Parmeter (1978), Schwandt (1977), Weir (1977), and Wicker and Hawksworth (1988).

Various options exist for managing forests infested with dwarf mistletoes. Actual treatments of stands, however, must be decided on an individual basis. Dwarf mistletoes are most easily and economically controlled by sound silvicultural practices and not through separate management activities. Detailed guides have been developed for some of the more economically important dwarf mistletoes (Hawksworth and Scharpf 1978):

- *Arceuthobium abietinum* on *Abies* (Scharpf and Parmeter 1967).
- *Arceuthobium americanum* on *Pinus contorta* (Alexander 1986, Alexander and Edminster 1980, Baranyay and Smith 1972, Dooling and Brown 1976, Hawksworth and Johnson 1989a, Schmidt and Alexander 1985, van der Kamp and Hawksworth 1985).
- *Arceuthobium campylopodum* on *Pinus ponderosa* and *P. jeffreyi* (Childs 1963, Hawksworth and Shaw 1988, Scharpf and others 1988, Shea 1957).
- *Arceuthobium douglasii* on *Pseudotsuga menziesii* (Baranyay and Smith 1972, Jones 1974).
- *Arceuthobium laricis* on *Larix occidentalis* (Weir 1916a, Baranyay and Smith 1972).
- *Arceuthobium pusillum* on *Picea mariana* (Ostry and Nicholls 1979).
- *Arceuthobium tsugense* on *Tsuga heterophylla* (Hennon and Shaw 1988, Muir 1986, Shea and Stewart 1972, Shaw 1981).

- *Arceuthobium vaginatum* subsp. *cryptopodum* on *Pinus ponderosa* (Beatty 1983, Gill and Hawksworth 1954, Hawksworth 1961a, Hawksworth and Shaw 1988, Hawksworth and others 1989, Heidmann 1983, Korstian and Long 1922, Lightle and Hawksworth 1973, Lightle and Weiss 1974).

Management of stands infested by dwarf mistletoe involves detection, evaluation, prevention, and suppression of the pathogen. These activities must follow in a carefully planned sequence for successful reduction of disease. Several features of dwarf mistletoes make them ideal candidates for cultural management (Johnson and Hawksworth 1985):

- Dwarf mistletoes are obligate parasites that require a living host to survive. Once an infected tree or branch is cut, the mistletoe dies, and it is unnecessary to burn or destroy the slash.
- Dwarf mistletoes are generally confined to a single host species or a group of closely related species. Immune or rarely infected species can therefore often be favored during stand treatments.
- Dwarf mistletoes have relatively long life cycles and slow spread rates compared to other tree pathogens. Intensification increases at a slow enough rate that if a stand were properly treated, dwarf mistletoe would not be a serious problem in subsequent rotations.
- In open stands, most seeds are dispersed within 20 m of tall, isolated trees. In more dense, even-aged stands, spread averages only 0.3 to 0.6 m per year. Birds may effect rare long-distance dispersal of seeds, but this is of little practical significance from a control perspective.
- Dwarf mistletoe–infected trees are usually easy to detect because of the presence of witches' brooms. Trees in heavily infested stands show obvious signs of decline and mortality.

Several successful silvicultural strategies have been developed specifically for dwarf mistletoe control. However, these practices need to be integrated into management plans that also reduce susceptibility of stands to other pests. For example, outbreaks of *Dendroctonus ponderosae* (mountain pine beetle) may increase the proportion of trees infected by dwarf mistletoes by killing more uninfected trees, thus increasing spread and intensification of dwarf mistletoe in the remaining stand and ultimately increasing mortality from dwarf mistletoe. In this case, the management objective should be to reduce the incidence and severity of both dwarf mistletoe and insect, thereby creating a healthier, pest-resistant forest.

Infestations of dwarf mistletoes affect not only timber value but also recreation, aesthetics, fire hazard, wildlife habitat, and watershed. Depending upon stand age and management objectives, appropriate strategies should be designed to either suppress the dwarf mistletoes or prevent them from entering the stand. Priorities in control programs usually should be placed on prevention as it is much more effective than removing dwarf mistletoes after they have entered stands or than replanting severely damaged stands. The following actions should be considered:

- Design treatment units to take advantage of natural or constructed barriers (such as roads, streams, nonsusceptible forests, openings, or meadows) that prevent re-invasion from adjacent infested stands.
- Remove all infected trees before an area is planted or naturally regenerated with susceptible species.
- Use clearcuts to advantage for harvesting infested stands, if clearcutting is suited to the silvicultural regeneration of the featured tree species. In general, clearcutting with natural regeneration should be restricted to certain shade-intolerant species such as *Pinus contorta, P. banksiana,* and *Picea mariana.*
- Regenerate stands with the shelterwood method, retaining only mistletoe-free or lightly infected residual trees. If infected trees must be left, they should be removed before the regeneration stock is 1 m tall or 10 years old.
- Favor nonsusceptible tree species for regenerating a stand, making intermediate entries, or planting.

These strategies all reduce the likelihood of dwarf mistletoe spreading into subsequent stands. For stands that are already lightly infested, infected overstory and infected understory trees should be removed by sanitation thinning. Crop trees should be disease free; however, if necessary, lightly infected trees may be retained to meet minimum stocking guides. Replacing severely infested stands with healthy stands by clearcutting, roller chopping, or prescribed burning and regenerating may be required.

Effects of dwarf mistletoes on a stand depend on a combination of factors: intensity of infection, stand density, stand structure, and composition. For a given intensity of infection, effects are most pronounced in dense stands. For example, in 60-year-old stands of *Pinus contorta* with moderately heavy infestations (stand DMR of 2) estimated volume reduction is about 10, 20, or 30% for stands of growing stock level 12, 24, or 36 m^2/ha, respectively.

The techniques employed depend on individual situations, including stand age, structure, density, species composition, number of years to harvest, incidence and distribution of dwarf mistletoe, and length of time the stand has been infested. Tree, stand growth, and dwarf mistletoe infection models are available to assist the resource manager simulate yields of stands with infected trees (Demars and Barrett 1987, Edminster 1978, Edminster and others 1991, Hawksworth and others 1992c). Yields for a stand can be predicted under various management regimes and compared to no-treatment alternatives. By comparing outputs and economic analyses of control costs, foresters can determine the preferred management alternative for each infested stand.

Recently Harvested and Regenerated Stands

The opportunity to control dwarf mistletoe is greatest at the time of final harvest and, secondly, in recently regenerated stands, 5–15 years old. Sanitation is the primary emphasis of management in these young stands. The greatest dwarf mistletoe threat to regeneration exists where harvest of the previously infested stand was incomplete, and infected residual trees were left on site. Such residual trees are often left because they have no commercial value. Timber contracts should stipulate felling of diseased, nonmerchantable trees to prevent infection of the regeneration. Unfortunately, dwarf mistletoe control was not adequately addressed in many past timber sales, and remedial silvicultural management work is needed in such stands.

Infected residuals over 3 m tall should be felled. Shorter infected trees pose little threat, because infections will be located in the lower half of the crown and dwarf mistletoe seed dispersal will be minimal. Also, trunk infections on these trees will usually kill very small trees. All visibly infected trees, however, should be removed during subsequent precommercial stand entries.

Infected trees along the edges of openings should be felled back 20 m before the regeneration is 1 m tall or 10 years old. This will markedly reduce infection of the regeneration. If infected residuals have been present for more than 10 years, then regeneration is probably already infected and will require subsequent sanitation to prevent future losses. A survey of infection intensity in regeneration will indicate if sufficient stocking of noninfected and acceptable trees is available for future crop trees. If an infected residual stand has been present for 20 or more years and regeneration is heavily infested, then it may be necessary to clear and replant the site. Guidelines are available for stands of *Pinus contorta* based on stand age and average stand DMR (Hawksworth and Johnson 1989a).

Precommercial Stands

The appropriate control measure for precommercial stands should be based on survey data that include: (1) size and location of dwarf mistletoe–infested areas, (2) approximate number and location of infected residual trees, and (3) number of potential crop trees. In most precommercial stands, an intensive, systematic survey provides the best method of collecting these data. Data points (fixed or variable radius plots) should be arranged in a systematic grid over the entire area to insure adequate coverage. Spacing between plots should not exceed 200 m, and intervals of 100 m or less are recommended. The extent of dwarf mistletoe infestation should be noted when traversing from plot to plot.

Sanitation should be an integral part of all stand entries for thinning, especially in lightly infested precommercial stands from which all overstory or residual infected stems have been eliminated. Severity of infection, not strictly stand age, is the best criterion to decide whether sanitation is practical. Stands of *Pinus contorta* with more than 40% of the trees infected (or stand DMR ≥3) are too severely infested to attempt strict sanitation cutting (removal of all infected trees). The removal of this many trees would reduce stocking below minimal acceptable levels (Hawksworth 1978, Hawksworth and others 1977).

The highest priority for precommercial sanitation thinning should be for stands 10 to 20 years old with less than 40% of the trees infected. Potential crop trees should have no visible mistletoe infections. Stands should be thinned and sanitized only if evaluations indicate that a minimum acceptable stocking can be achieved with noninfected trees. Severely infested stands that lack acceptable stocking of potential crop trees should be harvested or destroyed (if no products can be salvaged), and the site regenerated. Simulation programs such as described by Edminster and others (1991) and Hawksworth and others (1992c) can be used to project growth of the stand to determine whether or not replacement is the best alternative. In stands where potential crop trees average ≥5 cm diameter at breast height (dbh), the order of priority for crop tree selection is:

1. Noninfected dominant and codominant trees.
2. Dominant and codominant trees with dwarf mistletoe confined to branches in the lower one-third of live crown (DMR <2).
3. Intermediate trees with no visible infection.
4. Dominant and codominant trees with mistletoe confined to less than one-half of the branches in the lower two-thirds of the live crown (DMR <3).

If acceptable stocking cannot be obtained within these guidelines, then perhaps the stand should not be thinned. Thinning crews must be able to recognize infected trees for sanitation treatments to be effective. Stands sanitized prior to harvesting should not need to be controlled for dwarf mistletoe again until they are entered for a commercial timber sale.

Commercial Stands

Survey information that includes the location and intensity of dwarf mistletoe infection is essential to determine the need for control. Yield projections for these stands are invaluable to determine whether infection levels are high enough to influence growth and yield. Sanitation thinning is recommended only where stand DMR is 3 or less and where removal of infected trees does not reduce stocking levels below accepted minima. Severely infested stands that lack acceptable stocking of potential crop trees should be harvested early, and the site regenerated. If nonsusceptible species are present, then those species should be favored during stand regeneration.

Mature stands that are infested and scheduled for harvest and regeneration offer the greatest opportunity for disease control by replacement with noninfected regeneration. Severely infested stands with sufficient cones may be clearcut, and the cone-bearing tops scattered to obtain natural regeneration. Alternatively, slash may be burned, and the site replanted. Clearcuts within infested stands should have as large an area-to-perimeter ratio as allowable to minimize re-invasion from infected trees along bordering stands. Narrow strips should be avoided, and cutting units should be no less than 8 ha to minimize edge effect (Dooling and Brown 1976). However, smaller cutting units may be needed where natural regeneration is desired for trees with nonserotinous cones and border trees provide the only seed (Alexander 1986a). Wherever possible, cutting boundaries should be located in noninfected stands, nonsusceptible timber types, and natural or artificial openings to prevent reinfection of the regenerated stand from adjacent infested stands.

In areas where retention of infected trees is needed to protect regeneration from adverse climatic conditions or where wildlife or aesthetic values require protection, a shelterwood prescription may be required. However, once the site has regenerated and a new stand is established (5 to 10 years), all infected trees should be felled or harvested to reduce infection in the regeneration. In Colorado, *Pinus ponderosa* trees rated as DMR class 3 or higher should not be left as seed trees (Alexander 1986b). In the Southwest, Heidmann (1983) recommends that 5 to 9 m^2/ha (20 to 40 ft^2/acre) of basal area in uninfected seed trees should be retained; if infected trees must be retained, then the basal area in seed trees should be doubled to provide an adequate seed source.

Developed and Recreational Sites

Suburban residential developments are now common in forested areas. These sites often are located in, or contain, stands that are infested by dwarf mistletoes. The object of dwarf mistletoe control in these sites is to retain tree cover by reducing the effects of infection on tree vigor and longevity and by preventing spread of dwarf mistletoe into areas not yet infested. Effects of dwarf mistletoes on tree growth rates are of minimal concern, except as they might eventually affect host vigor and mortality. Silvicultural techniques discussed earlier for commercial forests (clearcutting, sanitation thinning) are less acceptable alternatives in developed areas. Emphasis should therefore be placed on the introduction of nonsusceptible species into the understory and on favoring existing nonsusceptible species. Pruning of infected branches and witches' brooms and establishing buffers to prevent spread of dwarf mistletoe are additional options.

Pruning infected branches usually is not economical in large commercial stands because repeated treatments are often necessary to eliminate latent infections. Pruning may be practical, however, to save trees that are needed for stocking and to prolong the life of high-value trees in developed recreation, administrative, or home sites (Brown 1978, Hawksworth and Johnson 1993, Laut 1978, Lightle and Hawksworth 1973, Perry 1922, Weir 1923). Candidate trees for pruning should be infected only in the lower half of the crown, rate as DMR class 3 or less, and have no infections on or near a main stem less than 15 cm dbh. Because dwarf mistletoe infections on stems over 15 cm dbh have little impact on growth and produce few seeds, they are consequently of little management concern (Mark and Hawksworth 1974, Walters 1974).

To minimize the chances of pruning branches in which the dwarf mistletoe's endophytic system may already have entered the trunk of the tree, the following species-specific pruning guides have been developed:

- *Arceuthobium vaginatum* subsp. *cryptopodum* on *Pinus ponderosa* (Hawksworth and Andrews 1961)–for branches up to 3 cm diameter prune only if dwarf mistletoe shoots are at least 15 cm from the main stem; for each 2- to 3- cm increase in branch diameter, the distance should be increased by 5 cm.
- *Arceuthobium americanum* on *Pinus contorta* (Hawksworth and Johnson 1961)–prune branches only if mistletoe shoots are at least 10 cm from the trunk.

All live branches in the two whorls above the highest visibly infected branch, should be pruned if possible, but removal of more than one-half of the tree's live crown is not recommended. Pruning usually does not eliminate all the dwarf mistletoe because many small infections are overlooked or latent. Pruned trees should be re-examined 3 to 5 years later to see if additional branch removal is needed.

Pruning of witches' brooms may also be effective in prolonging the life of individual trees (Lightle and Hawksworth 1973), but all visibly infected branches need not be removed. Dramatic recovery has been demonstrated in crown vigor and tree longevity in broom-pruned *Pinus ponderosa* in Arizona (Lightle and Hawksworth 1973), *P. jeffreyi* in California (Scharpf and others 1987), and *P. contorta* in Colorado (Hawksworth and Johnson 1989a).

Some additional activities that should help mitigate effects of dwarf mistletoes in high-value stands include: (1) supplemental watering, (2) application of nitrogen fertilizer, (3) minimizing soil compaction by humans or machinery, and (4) protection of trees from bark wounding. In planning locations for new recreation sites, dwarf mistletoe–infested stands should be avoided when possible, or at least treated, before developmental activities are initiated.

With increased awareness of the complex interactions among dwarf mistletoes and other biotic associates (chapter 8) and heightened interest in biodiversity and forest health, mistletoe control assumes a new dimension. Dwarf mistletoes are no longer viewed as "pests" requiring eradication but as biotic agents of disturbance that can profoundly effect forest communities. From this perspective, emphasis is on remediation, and mistletoe control can be used to achieve non-traditional objectives with new management techniques. For example, *Pinus ponderosa* trees severely broomed by *Arceuthobium vaginatum* subsp. *cryptopodum* could be selectively killed by prescribed burning of individual trees to provide snags for cavity-nesting birds and roost trees for wild turkey while also reducing sources of infection to young trees (Conklin and others 1991). Because ecological effects of dwarf mistletoe infestation are very complex, attempts to use mistletoe as a natural disturbance tool in management will require continued monitoring of mistletoe distribution, abundance, and population trends.

Systematics: Philosophy, Problems, and Criteria for Classification

Taxonomic Considerations

Arceuthobium is considered a taxonomically difficult genus because of the extreme morphological reduction associated with the parasitic habit and the general morphological similarities among species. Many of the morphological features that are commonly used in classification of flowering plants, such as leaves and trichomes, are absent in *Arceuthobium.* Furthermore, flowers are small (2 to 4 mm across) and generally similar in form.

Danser (1950) stated that the function of taxonomy is to classify life cycles. He was a student of Old World mistletoes, and they no doubt influenced his views on plant taxonomy. The life cycle concept is particularly well suited to classification of Viscaceae, wherein reduction and convergence have obscured relationships among species. Danser's concept of classifying life cycles provides a useful model on which to base systematic studies in highly reduced, parasitic organisms or those with complex life histories, such as insects. As a corollary, discontinuities between life cycles and various morphological, physiological, and biochemical features have been utilized to determine taxonomic units in *Arceuthobium* and to construct a classification of the genus.

Taxonomic Criteria

Valid taxonomic criteria that are especially useful for classification of *Arceuthobium* include physiological and phenological characters such as time of meiosis, anthesis, period of seed dispersal, time of seed germination, host specificity, and host brooming response. These are measurable, show discontinuous variation, and are consistent within normal limits of variation. Quantitative and qualitative morphological, palynological, and cytogenetical characters are also utilized in classification. Even small-scale quantitative differences may be statistically and taxonomically significant. All phases of the life cycle are considered here as potentially valid taxonomic criteria. The first priorities are to determine basic features of the life cycle and to isolate discontinuities among species. The test of valid discontinuities rests on genetic control and consistency of occurrence.

Previous difficulties in classifying the genus result from the extreme reduction of the plants and especially the lack of detailed information on hosts, morphology, physiology, and life cycles. Taxonomic problems are further compounded by the proclivity of dried material to shatter, thereby destroying important characteristics of habit and size. In few other plant groups is a thorough knowledge of living populations so essential for their classification. Likewise, chemical and molecular data (see chapter 15) are potentially of greater value in *Arceuthobium* than in groups with a greater array of morphological characters available for classification.

At certain stages, some dwarf mistletoes are difficult to identify by life-cycle characters. The time of anthesis or seed dispersal might not be obvious on a herbarium specimen. Shoot color is reasonably consistent in living plants but may change with drying. Characteristics of habit that are obvious in living plants—such as the open spherical masses of *Arceuthobium globosum* subsp. *globosum*—may be completely obliterated by careless pressing or fragmentation. Furthermore, the aerial parasitic habit often makes dwarf mistletoes difficult to collect. This compounds the problem further because it results in their being typically undercollected.

The monographer's charge is to define taxa by whatever taxonomically valid characteristics are available. Whether these differences are easily discernible in a particular specimen in no way affects their intrinsic taxonomic value. The distinction between classification and ease of identification is sometimes confused. Because many dwarf mistletoes exhibit high levels of host specificity, knowledge of the host may provide a simple means of identification.

Natural hybrids are unknown in *Arceuthobium;* as a consequence, taxa are reasonably well defined, although distinctions are sometimes subtle and manifest only at particular stages of the life cycle. Even subspecific categories appear to be demarcated by relatively sharp discontinuities, albeit of lesser magnitude than those separating species. Variation within a taxon is of course present, as would be expected in any sexual, outcrossing group.

Subgeneric Classification

The first subgeneric classification of *Arceuthobium* was presented by Hawksworth and Wiens (1972) and revised approximately a decade later (Hawksworth and Wiens 1984). An update of this classification based primarily on traditional taxonomic characteristics (morphology, physiology, and phenology) has been prepared to include all 46 taxa currently recognized (table 14.1). An alternative classification that utilizes molecular techniques (isozyme analysis and DNA sequencing) in addition to the traditional characteristics is presented by Nickrent (see table 15.2). Nickrent's classification differs in a number of respects from that in table 14.1. Because of the general problem of character convergence and the extreme reduction that often accompanies the parasitic habit, molecular data are perhaps more useful in defining species relationships in *Arceuthobium* than in nonparasitic plants. The changes Nickrent proposes appear reasonable, and we accept these revisions. This attempt to assign relationships in subgenus *Arceuthobium* is particularly welcome because of the relictual nature of many species. Additional research will undoubtedly indicate further changes to our original designation of species relationships. We are pleased that the basic elements of the original classification have remained intact.

Species, Subspecies, Races, and Special Forms

Species are defined as population systems that exhibit suites of characteristics that remain constant within prescribed limits of variation, from generation to generation, on different hosts, and when they cooccur with other taxa. The distinctive features can be manifest at any stage of the life cycle.

Subspecies are similar to species, except that distinguishing differences are neither as numerous nor of the magnitude that separate species. In *Arceuthobium*, there is typically no gradation of characters between species or subspecies, as is typical of seed plants in general. Ultimately distinctions between species and subspecies is judgmental.

Races within a taxon of *Arceuthobium* constitute populations that are physiologically adapted primarily, but not exclusively, to one of the "normal" principal host species parasitized. There are no consistent morphological or other physiological features that distinguish them from other populations of the taxon. Where a race's principal host is sympatric with the principal hosts of other races, there is usually a low or rare frequency of cross infection. This situation is not to be confused with that in which a taxon may have more than one principal host or have secondary hosts (chapter 6). Only when a population of an otherwise uncommon host becomes heavily infected do we consider populations to be racially distinct. Currently, races are only known in *Arceuthobium tsugense* subsp. *tsugense* (see chapter 16). Races have no formal taxonomic status.

Special forms (*forma speciales*) are populations that are obligately restricted to a particular host species and cross infection with another host species is not possible. The absence of occasional cross infection distinguishes races from special forms. We have only used special forms in *Arceuthobium abietinum*. Special forms are designated primarily for host–specific fungi and are used here to avoid confusion with *forma* that carry morphological connotations. Special forms have no formal taxonomic status.

One might question why some dwarf mistletoes we recognize as species or subspecies should not be considered host ecotypes or races without formal taxonomic recognition. Ecotypes are usually defined as genetically distinct races that are physiologically adapted to localized habitats and sometimes differentiated morphologically by quantitative characters. The taxa we recognize as species maintain their morphological integrity on rare or occasional hosts and lack intermediate forms where they are sympatric. Ecotypes are typically not reproductively isolated and usually are not distributed as widely as the population systems to which we give formal taxonomic recognition. Although there are some exceptions, most dwarf mistletoes have reasonably broad geographic distributions. Conceivably, some taxa of dwarf mistletoes might correspond to regional ecotypes; but, as most taxonomists consider regional ecotypes to be comparable to subspecies, the systematic treatment would not differ greatly.

Problems in Classification

The Host–Form Concept

Gill (1935) segregated members of the *Arceuthobium campylopodum* and *A. vaginatum* complexes into host forms, "taxa delimited exclusively on the basis of the host relationships, without regard to biological parity." Although Gill's system provided an

TABLE 14.1 – Classification of *Arceuthobium* M. Bieb. based on morphology, physiology, and phenology

Subgenus *Arceuthobium* (no sectional classifications proposed)

New World species
1. *A. abietis-religiosae* Heil
2. *A. americanum* Nutt. ex Engelm.
3. *A. verticilliflorum* Engelm.

Old World species
4. *A. azoricum* Hawksw. & Wiens
5. *A. chinense* Lecomte
6. *A. juniperi-procerae* Chiovenda
7. *A. minutissimum* J. D. Hooker
8. *A. oxycedri* (DC.) M. Bieb.
9. *A. pini* Hawksw. & Wiens
10. *A. sichuanense* (H. S. Kiu) Hawksw. & Wiens
11. *A. tibetense* H. S. Kiu & W. Ren

Subgenus *Vaginata* Hawksw. & Wiens

Section *Vaginata*
12. *A. aureum* Hawksw. & Wiens subsp. *aureum*
13. *A. aureum* Hawksw. & Wiens subsp. *petersonii* Hawksw. & Wiens
14. *A. durangense* (Hawksw. & Wiens) Hawksw. & Wiens
15. *A. gillii* Hawksw. & Wiens
16. *A. globosum* Hawksw. & Wiens subsp. *globosum*
17. *A. globosum* Hawksw. & Wiens subsp. *grandicaule* Hawksw. & Wiens
18. *A. hawksworthii* Wiens & C. G. Shaw III
19. *A. nigrum* (Hawksw. & Wiens) Hawksw. & Wiens
20. *A. vaginatum* (Willd.) Presl subsp. *vaginatum*
21. *A. vaginatum* (Willd.) Presl subsp. *cryptopodum* (Engelm.) Hawksw. & Wiens
22. *A. yecorense* Hawksw. & Wiens

Section *Campylopoda* Hawksw. & Wiens
Series *Campylopoda*
23a. *A. abietinum* Engelm. ex Munz f. sp. *concoloris*
23b. *A. abietinum* Engelm. ex Munz f. sp. *magnificae*
24. *A. apachecum* Hawksw. & Wiens
25. *A. blumeri* A. Nelson
26. *A. californicum* Hawksw. & Wiens
27. *A. campylopodum* Engelm.
28. *A. cyanocarpum* (A. Nelson ex Rydberg) Coulter & Nelson
29. *A. divaricatum* Engelm.
30. *A. guatemalense* Hawksw. & Wiens
31. *A. laricis* (Piper) St. John
32. *A. littorum* Hawksw., Wiens & Nickrent
33. *A. microcarpum* (Engelm.) Hawksw. & Wiens
34. *A. monticola* Hawksw., Wiens & Nickrent
35. *A. occidentale* Engelm.
36. *A. pendens* Hawksw. & Wiens
37. *A. siskiyouense* Hawksw., Wiens & Nickrent
38. *A. tsugense* (Rosendahl) G.N. Jones subsp. *tsugense*
39. *A. tsugense* (Rosendahl) G.N. Jones subsp. *mertensianae* Hawksw. & Nickrent

TABLE 14.1 – Classification of *Arceuthobium* M. Bieb. based on morphology, physiology, and phenology (continued)

Subgenus *Vaginata* Hawksw. & Wiens (continued)

- Section *Campylopoda* Hawksw. & Wiens (continued)
  - Series *Rubra* Hawksw. & Wiens
    - 40. *A. bicarinatum* Urban
    - 41. *A. hondurense* Hawksw. & Wiens
    - 42. *A. oaxacanum* Hawksw. & Wiens
    - 43. *A. rubrum* Hawksw. & Wiens
  - Series *Stricta* Hawksw. & Wiens
    - 44. *A. strictum* Hawksw. & Wiens
  - Section *Minuta* Hawksw. & Wiens
    - 45. *A. douglasii* Engelm.
    - 46. *A. pusillum* Peck

Note: adapted from Hawksworth and Wiens (1984).

effective and facile method for naming dwarf mistletoes, it obscured systematic difficulties in the group. Gill realized his classification system was unnatural, but available data were too limited for a more natural treatment. Gill noted that

> ...the forms are not all of equal rank in the sense of being biologically distinct. Some are well developed strains showing a marked affinity for a limited group of host species, while others are admittedly artificial categories, into which infrequent or even accidental host relationships of the better defined forms have been cast.

Gill further stated that a system of forms based exclusively on hosts "though without good taxonomic precedent, should be tolerable as a temporary device, pending a complete revision of the genus based on further field and experimental evidence."

Our field and experimental studies indicate that Gill's (1935) host–forms of *Arceuthobium campylopodum* and *A. vaginatum* are distinct species or subspecies. When these dwarf mistletoes occur on trees other than their principal host, they maintain their morphological integrity and are readily identifiable. Such natural host crossovers from principal to secondary, occasional, or rare hosts have been observed for most New World species except *A. apachecum, A. blumeri, A. divaricatum, A. guatemalense, A. hawksworthii, A. hondurense,* and *A. pendens.*

Various examples illustrate difficulties with Gill's host–form concept. At McKenzie Pass, Oregon, *Arceuthobium tsugense* subsp. *mertensianae* occurs on *Pinus albicaulis, Abies lasiocarpa,* and *Tsuga mertensiana* (the principle host). On all three hosts, the parasite is clearly identifiable as the same subspecies. Under Gill's system, however, three different names (f. *cyanocarpum,* f. *abietinum,* and *f. tsugensis,* respectively) were assigned to these populations. At Priest River Experimental Forest in northern Idaho, *A. laricis* is common on *Larix occidentalis* (principal host), but it also occurs on *Pinus contorta* and on three introduced conifers (*P. banksiana, P. resinosa,* and *Picea abies*). Here, too, morphological integrity of the species is retained. The host–form concept is especially difficult to apply for dwarf mistletoes on introduced hosts because each form is restricted by definition to a specific host. Strict adherence to such an unnatural system requires that a different name be coined for each host–parasite combination. Furthermore, whenever more than one species parasitized the same host, all had the same name. For example, where *Arceuthobium campylopodum, A. laricis,* and *A. cyanocarpum* parasitized *Pinus ponderosa,* all three were classified as *A. campylopodum* f. *campylopodum.* Each dwarf mistletoe is, however, as morphologically distinct on *P. ponderosa* as it is on its principal and other hosts. In addition to morphological integrity, these dwarf mistletoes also exhibit clear host preferences, even though they may occasionally parasitize trees other than their principal hosts. Finally, whenever two or more of these species co-occur, we have no evidence of hybridization; thus, the rule of sympatry supports their classification as species.

The *Arceuthobium campylopodum* Complex

The most difficult taxonomic problems remain in the troublesome *Arceuthobium campylopodum* complex. Our field, inoculation, herbarium, and laboratory studies have shown this group to be more complex than we first believed (Hawksworth and Wiens 1972). Originally, we separated the group into 2 species—*A. campylopodum* and *A. occidentale.* The former was primarily parasitic on *Pinus ponderosa* and *P. jeffreyi,* but did not infect associated *P. sabiniana. Arceuthobium occidentale* was essentially limited to occurrence on *P. sabiniana* and not on associated *P. ponderosa* or *P. jeffreyi.* We have now concluded that the complex comprises 4 species that parasitize 6 species of pines in western North America:

- *Arceuthobium campylopodum* (*sensu stricto*) is parasitic principally on *Pinus ponderosa* and *P. jeffreyi* and is distributed from northern Idaho and northern Washington to northern Baja California, Mexico.
- *Arceuthobium littorum* principally infects *Pinus radiata* and *P. muricata* in coastal California.
- *Arceuthobium siskiyouense* is a parasite largely restricted to *Pinus attenuata* and is endemic to southwestern Oregon and northwestern California.
- *Arceuthobium occidentale* principally infects only *Pinus sabiniana* and occurs mostly in the low foothills surrounding the Central Valley of California.

Arceuthobium littorum is the most distinct. It is not sympatric with the three other taxa, and it is characterized by its dark, stout shoots and occurrence on *Pinus radiata* and *P. muricata* along the California coast from Fort Bragg to Cambria. Isozyme analyses also confirm its distinctiveness (Nickrent and Butler 1990). *Arceuthobium siskiyouense* is also reasonably well defined and readily distinguished by its small shoots and fruits, host preference, and allozyme characteristics (Nickrent and Butler 1991). It is sympatric with *A. campylopodum* in several areas.

The relationship between *Arceuthobium campylopodum* and *A. occidentale* is more nebulous. Although the species have differences in host preference, morphology, physiology, and phenology, they are obviously closely related and have similar isozyme patterns (Nickrent and Butler 1990).

Host ranges for both species are broader than we originally believed, and competitive host exclusion (chapter 6) appears to operate. Where these species are sympatric, *Arceuthobium campylopodum* does not parasitize *Pinus sabiniana,* and *A. occidentale* does not infect *P. ponderosa;* but in certain areas where the species are not sympatric cross infections do occur. In the southern Sierra Nevada at elevations 200 to 500 m above the upper limits of *A. occidentale, A. campylopodum* readily and severely parasitizes *P. sabiniana* trees associated with *P. ponderosa* or *P. jeffreyi.* Curiously, however, no witches' brooms are produced on *P. sabiniana* as is typical when this host is parasitized by *A. occidentale* elsewhere. This is unusual because the type of witches' broom formation is usually determined by the species of dwarf mistletoe and not by the host. Nevertheless, the two mistletoes maintain their distinctive shoot and fruit morphology and phenology in these situations. *Arceuthobium campylopodum* is apparently absent from the south Coastal Ranges of San Benito and Monterey Counties, California. In this area, *A. occidentale* is not only common on *P. sabiniana* but also infects associated *P. coulteri, P. jeffreyi,* and *P. ponderosa* (Griffin 1975).

Arceuthobium campylopodum and *A. occidentale* are distinguished by a number of morphological and physiological characteristics. Plants of *A. campylopodum* form rather open clusters of glaucous shoots and produce staminate inflorescences usually less than 10 mm long. Plants of *A. occidentale* typically develop dense, globose clusters; shoots are only lightly (if at all) glaucous, and staminate inflorescences usually exceed 10 mm in length. *Arceuthobium occidentale* does not induce formation of witches' brooms whereas *A. campylopodum* causes localized witches' brooms.

Arceuthobium campylopodum and *A. occidentale* also differ phenologically. Meiosis, flowering, and fruit dispersal peak about 1 month earlier in *A. campylopodum* than in *A. occidentale.* If the species' entire geographic distributions are considered, then pollination periods overlap; however, in specific locations where populations are sympatric, temporal isolation is apparently complete and the possibility of gene exchange is remote. Additional observations on this point, however, would be desirable. Seed dispersal in *A. occidentale* is not only generally later, but is protracted several months longer than in *A. campylopodum* (R. F. Scharpf, personal communication). Seeds of *A. campylopodum* require a period of after-ripening, whereas those of *A. occidentale* do not (Wicker 1965, Beckman and Roth 1968). Unfortunately, no data are available with respect to cross inoculation between principle hosts of *A. campylopodum* and *A. occidentale* (R. F. Scharpf, personal communication).

Arceuthobium occidentale gives every indication of being an incipient species in which morphological and isozyme differentiation has not progressed far, but temporal isolation has apparently precluded hybridization. Selected cross inoculations of these dwarf mistletoes onto their various hosts would be particularly revealing for elucidating both the nature of the taxa and the host exclusion phenomenon that characterizes them. The reason why *A. campylopodum* does not cause witches' brooms when it infects *Pinus sabiniana* would be interesting to determine. The sympatric distribution of the two populations favors species status, which we will maintain pending further study.

The *Arceuthobium blumeri* Complex

The taxon Gill (1935) recognized as *Arceuthobium campylopodum* f. *blumeri* is now divided into 4 species that are parasites of white pines (subgenus *Haploxylon*):

- *Arceuthobium apachecum* is a parasite of *Pinus strobiformis* in southern Arizona and central New Mexico, with an outlying population in the Sierra del Carmen in northern Coahuila, Mexico.
- *Arceuthobium blumeri* (*sensu stricto*) also parasitizes *Pinus strobiformis* in southern Arizona and other closely related pines in northern Mexico.
- *Arceuthobium californicum* infects principally *Pinus lambertiana* and is distributed from the Mt. Shasta area southward to the Cuyamaca Mountains in San Diego County.
- *Arceuthobium monticola* occurs principally on *Pinus monticola* and is endemic to the Sisykiyou and Klamath Mountains in northern California and southern Oregon, respectively.

None of these species are sympatric. *Arceuthobium californicum* and *A. monticola* are also reasonably well defined. *Arceuthobium apachecum* and *A. blumeri* appear to be closely related but are distinguished by several morphological characteristics (Mathiasen 1982) and differing isozymes patterns (Nickrent 1986). These species are unique in the genus because they both parasitize the same principal host, *Pinus strobiformis*. The two species are not sympatric but do occur within about 60 km of each other in southern Arizona. The morphological characteristics of each species remained constant when grown under greenhouse conditions (Hawksworth and Wiens 1972), thus supporting a genetic basis for the morphological differences. We maintain these taxa as species, but further research regarding their status is warranted.

Subspecific Classification

Subspecies in *Arceuthobium* do not conform to commonly accepted definitions. Four species of North American dwarf mistletoes show geographically associated morphological variation: *A. aureum, A. globosum, A. tsugense,* and *A. vaginatum*. In *Arceuthobium,* there usually is no gradation of characteristics or "shading-off" between population systems that constitute species and subspecies, as is common in many plant groups. The only exception is for *A. vaginatum*—subspecies *vaginatum* and *cryptopodum* exhibit a gradation of characters in a small zone of overlap in central Chihuahua, Mexico (see chapter 16).

The presence of discontinuous variation between population systems might suggest that they should be species, even though differences are small. This situation might be comparable to that in *Carex,* where the species are often based on small, yet apparently consistent, differences. We believe, however, that geographically restricted populations delimited by a few relatively small but consistent variations are best classified as subspecific units.

For *Arceuthobium tsugense* subsp. *tsugense,* we have used the term "race" to distinguish two host–forms. The typical and principal host throughout its extensive latitudinal distribution is *Tsuga heterophylla* (western hemlock). The other race predominantly infects a limited population of *Pinus contorta* var. *contorta* (shore pine). These "races" are similar to the *forma specialis* recognized in *A. abietinum,* except that there is usually some cross infection with the principal host, *Tsuga heterophylla.* Isozyme analyses of the western hemlock and shore pine races of *A. tsugense* subsp. *tsugense* indicate that they are similar and best retained as races of *A. tsugense* subsp. *tsugense* (Nickrent and Stell 1990).

In *Arceuthobium abietinum,* we have used the category of *forma specialis,* i.e., physiological races without morphological differences that will not infect another host. Scharpf and Parmeter (1967) have shown experimentally that populations of *A. abietinum* from *Abies magnifica* will not infect *A. concolor* and vice versa. However, the form on *A. concolor* will also infect *A. grandis* and *A. durangensis* (chapter 6). This obligate host specificity is confirmed from many field observations in stands containing a mixture of true fir species. If host races of *Arceuthobium abietinum* could parasitize any species of fir, then their presence would be expected in mixed stands where millions of dwarf mistletoe seeds from each species of fir are deposited annually on other fir species. Cross infection, however, has not been reported.

Morphological Characters

Plant Size and Habit

Shoot size varies enormously within the genus. Shoots of *Arceuthobium minutissimum,* a Himalayan species, are about 5 mm high and 1 mm wide, whereas those of *A. globosum* subsp. *grandicaule,* a Mexican species, are over 700 mm high and 50 mm wide. Thus, mature shoots may be nearly 150 times higher and 50 times wider in some species than in others. Hooker (1886) suggested that *A. minutissimum* was the smallest dicotyledonous plant; but *Pilostyles thurberi* (Rafflesiaceae), a parasite of leguminous trees in the Southwestern deserts, may be slightly smaller (Kuijt 1969a). *Viscum minimum* from South Africa is in the same size class (Wiens and Tölken 1979).

Within a taxon, shoots of dwarf mistletoes on systemic witches' brooms are somewhat smaller than those on non-systemic infections on the same host. Among those species that commonly produce systemic infections, shoots are more commonly associated with witches' brooms, and the dimensions of these shoots are used in the formal descriptions. Those species typically forming systemic witches' brooms include *Arceuthobium americanum, A. douglasii, A. guatemalense, A. minutissimum, A. pusillum, A. sichuanense,* and *A. tibetense.* Shoot measurements are taken from non-systemic infections for all other taxa. Also, shoot dimensions as given are for both pistillate and staminate plants. Plants of one sex (usually the pistillate plants) are occasionally larger than those of the other, but differences usually are not significant. We have also indicated the tallest shoots observed in a taxon.

Growth habit is a distinguishing character for some species. Shoots may form dense spherical masses (e.g., *Arceuthobium globosum* and *A. occidentale*), be scattered along the stem (as in most taxa), or become so dense that host branches are obscured (e.g., *A. cyanocarpum* and *A. apachecum*).

Most species exhibit sexual dimorphism. Staminate shoots are typically more open and spreading than pistillate shoots. This is particularly well-marked in *Arceuthobium gillii, A. hawksworthii,* and *A. nigrum* (figs. 3.1 and 3.2). In *A. strictum,* staminate shoots are not branched (see fig. 16.95), but pistillate shoots are densely branched. There are also color differences between pistillate and staminate plants in some species—*A. americanum, A. campylopodum, A. laricis, A. microcarpum, A. strictum,* and undoubtedly others. There is also some evidence that pistillate plants may be taller than staminate plants in some taxa. A detailed analysis of sexual dimorphism in the genus would be a useful contribution.

Shoots

Gill (1935) used branching as a major taxonomic character in classifying *Arceuthobium.* All species have decussate primary branching (Kuijt 1970), and in some taxa branching proceeds no further (*A. pusillum, A. minutissimum,* and *A. verticilliflorum*). In most taxa, however, secondary branching is apparent and is of two basic types—verticillate and flabellate (fig. 2.1). Kuijt (1970) considers the verticillate habit to be the primitive or ancestral state in all Old World taxa that have been studied, presumably including the highly reduced *A. minutissimum,* and in three New World species—*A. americanum, A. abietis-religiosae,* and *A. verticilliflorum.* The latter species does not actually exhibit secondary branching, but staminate flowers are verticillately arranged.

Other New World species exhibit flabellate secondary branching. *Arceuthobium pusillum* is so reduced, however, that branching type can only rarely be determined (Baker and French 1979). Some Mexican taxa, such as *A. rubrum* (flabellate) or *A. abietis-religiosae* (verticillate), show little secondary branching.

Internode dimensions distinguish several species. Length of the third internode and its standard deviation are given for many taxa because the basal and second internodes are frequently not consistently elongated. Dwarf mistletoe shoots have basal meristems similar to those of grasses, and individual shoot internodes may elongate for several years. For this reason, Kuijt (1970) questioned the validity of our use of internode dimensions as a taxonomic character. The overall mature internode dimensions among various species differ so significantly that internodal elongation does not negate the usefulness of the character in these cases. The length-to-width ratio is less variable than length. Internode length is probably correlated with total shoot height.

Species often can be readily distinguished by shoot color (see color photographs in chapter 16), even though it may vary within a taxon and between staminate and pistillate plants. Colors include black, purple, brown, red, orange, yellow, and green, to light gray. Specimens pressed soon after collection and dried quickly without application of intense artificial heat usually retain their original color; but regardless of treatment, the bright-red living shoots of *Arceu-*

thobium rubrum typically become dull brown upon drying.

Shoots are typically erect but may be somewhat pendant in larger individuals of the *Arceuthobium vaginatum* complex, as is also typical for staminate plants of *A. hawksworthii* and *A. pendens.*

Shoots in most species live approximately 5 to 7 years and produce several crops of flowers and fruits. Shoots of *Arceuthobium pusillum,* however, typically live for only one season. Rare perennial shoots, however, have been found in *A. pusillum* (Baker and French 1979). A single shoot axis typically originates from each basal cup, except for *A. minutissimum* that produces numerous shoots per cup. Shoots of *Arceuthobium minutissimum* arise from needles (usually within 2 mm of the base) or from stem tissues; shoots of all other taxa arise only from host stems.

Inflorescences

Various features of the inflorescence have taxonomic value. For example, size of staminate spikes before flowering is useful in separating some members of the *Arceuthobium campylopodum* complex. Furthermore, branching pattern of staminate spikes helps to distinguish various subspecies of *A. vaginatum.*

Buds and Flowers

Lateral staminate buds of *Arceuthobium aureum* subsp. *aureum, A. douglasii,* and *A. americanum* are spherical, but those of all other taxa are lenticular. Flowers are pedicellate in some taxa and sessile in others. Gill (1935) used the "pedicellate joint" of staminate flowers as a taxonomic feature in *A. americanum* and, to a lesser extent, in *A. douglasii.* Kuijt (1970) has shown that this "pedicellate joint" is, in fact, an annual dichasial unit. He also first reported pedicellate pistillate flowers on the main axis in some taxa. This feature is present in some groups (the *A. campylopodum* complex) and absent in others (*A. vaginatum, A. gillii,* and *A. globosum*).

Both staminate and pistillate flowers of *Arceuthobium* are small (several millimeters), structurally simple, and remarkably uniform throughout the genus (Cohen 1965, 1970). In spite of problems in scale, color, size, and number of perianth lobes of staminate flowers have useful taxonomic characters for most species. The inner surface of staminate flowers of most species is the same color as the shoots, but for *A. abietis-religiosae, A. bicarinatum, A. douglasii, A. hawksworthii, A. hondurense,* and sometimes *A. pusillum* inner staminate surfaces are usually dark red. Staminate flowers are about 2 to 3 mm in diameter for most species but average 4 mm across in *A. verticilliflorum.* Lateral staminate flowers are predominantly 3-merous except for *A. chinense, A. littorum,* and *A. verticilliflorum* (4-merous); *A. guatemalense* (2- to 3-merous); *A. blumeri* (4- to 6-merous); and *A. strictum* (3-to 7-merous). Terminal flowers are most frequently 4-merous, even among species that typically possess 3-merous flowers. Length and width of staminate perianth segments are closely related to overall flower size and are usually of little taxonomic value. Staminate flowers that do not fully expand are a unique feature of *A. rubrum.* A nectary ("central cushion" in older terminology) is present in the center of each staminate flower (Cohen 1968). We have not found any valid taxonomic features in the nectary (with the possible exception of *A. hondurense*), even though it is more prominent in some species than in others.

Anthers

Anthers are distinctive in a few species. Anther diameter may be as large as 1 mm in *Arceuthobium verticilliflorum* but is less than half this size in most species. Engelmann (in Watson 1880) used anther location on the perianth segment to demarcate some taxa, but we have not analysed this character thoroughly. Such differences might well be significant between species, but they would be minute (<1 mm).

Fruits

Mature fruits in most species are between 3 to 5 mm long but vary from 15 mm in *Arceuthobium verticilliflorum* to as little as 2 mm in *A. tibetense* (Kiu 1984b). All species have bicolored fruits separated by an equatorial line, and relative size of proximal and distal portions is a useful taxonomic character. The distal portion of the fruit may account for 45% of its total length in *A. gillii* but only 25% in *A. abietis-religiosae.* Fruits usually shrink 15 to 25% during drying. Because shrinkage is more pronounced in the distal portion (25 to 35%) than the proximal portion (10 to 20%), the proximal-to-distal ratio tends to be somewhat higher in dried plants.

The character of the fruit surface is also useful in taxonomy; and it may be either heavily glaucous (*Arceuthobium gillii* and *A. nigrum*), lightly glaucous (*A. aureum* subsp. *aureum*), nonglaucous and dull (most species), or nonglaucous and shiny (*A. oaxacanum* and *A. rubrum*). Seed size was not measured because it is directly correlated with fruit size. We have not analyzed seeds for taxonomic characteristics, but Nickrent (chapter 15) indicates that differences in seed shape and color distinguish the section *Campylopoda* from *Vaginata.*

Kuijt (1970) noted that some species typically have one or two sterile nodes just below the terminal fruit on the main axis of each pistillate shoot. This condition was evident in all populations of *Arceuthobium bicarinatum* we have studied.

In most species, the base of the mature fruit fuses smoothly into the receptacle at the terminus of the pedicel. In *Arceuthobium guatemalense* and *A. durangense,* however, the receptacle forms a characteristic ring at the base of the fruit.

Palynological Characters

Hawksworth and Wiens (1972) made the first comprehensive study of pollen of *Arceuthobium,* although a few species had been examined previously—*A. chinense* (Lecomte 1915), *A. minutissimum* (Bhandari and Nanda 1968), *A. oxycedri* (Erdtman 1952, Heinricher 1915a), and *A. pusillum* (Gill 1935, Pomerleau 1942, Whitehead 1963, Whitehead and Barghoorn 1962).

Hawksworth and Wiens (1972) examined all taxa of *Arceuthobium* then known, although there was a paucity of material available in some instances. We analyzed 1 to 8 collections of each species and measured at least 10 pollen grains in each collection. Our analyses were based primarily on dried pollen grains mounted in glycerin and examined under light microscopy. However, we utilized scanning electron microscopy (SEM) to study pollen of *A. pusillum* and *A. verticilliflorum.*

Pollen grains of *Arceuthobium* can easily be distinguished from other genera (Erdtman 1952). Grains measure approximately 20 to 30 µm in diameter and are roughly spherical in shape, but the equatorial diameter is 5 to 15% greater than the polar diameter (Hawksworth and Wiens 1972). Grains are divided into 6 alternating spined and smooth sections that converge at the poles. Grains are 3-colpate (grooved); and these colpae become deeply grooved as the pollen dries. Lying parallel to the colpae on the intervening walls are 3 pseudocolpae, or short grooves, that do not reach the poles but become more prominent with drying.

We have confirmed Gill's (1935) suggestion that pollen characteristics might be of taxonomic value, although we cannot confirm his report that *Arceuthobium pusillum* has larger pollen grains than other species. In our studies, pollen diameters ranged from a mean of 18 µm in *A. minutissimum* to 28 µm in *A. verticilliflorum.* Variation within a taxon is usually limited to within 1–2 µm of the mean. Another readily measured pollen feature of taxonomic value is the height of spines in relation to wall (exine and intine) thickness. In some species, spine height may be three times the wall thickness (*A. tsugense*), whereas in others wall thickness greatly exceeds spine height (*A. verticilliflorum*). These species and a few others are so distinct that they may be identified solely by their pollen.

Scanning electron micrographs of *Arceuthobium* reveal detail in pollen grain morphology that was not apparent with light microscopy (Hawksworth and Wiens 1972). For example, the wall of a pollen grain of *A. pusillum* is low and has widely spaced papillae; but the wall of *A. verticilliflorum* is uniformly rough. Spines of *A. pusillum* are larger and more abundant than spines of *A. verticilliflorum*; spines of *A. pusillum* are present in the grooves but absent from the grooves of *A. verticilliflorum.* Finally, the spine base in *A. pusillum* appears distinct and vertical in contrast to the spreading spine base of *A. verticilliflorum.*

Cytogenetic Characters

The chromosome number of all dwarf mistletoes studied is $n = 14$. In the New World, Dowding (1931) first reported $n = 14$ in *Arceuthobium americanum.* Wiens (1964) confirmed this result, and reported $n = 14$ for 5 additional species. Chromosome numbers for 10 additional species were presented by Wiens (1968) and for 12 more taxa by Hawksworth and Wiens (1972). Chromosome counts for 3 additional taxa are included in this study. Chromosome numbers for 28 of the New World taxa are now known. Taxa that have not yet been examined are *A. durangense, A. globosum* subsp. *globosum, A. guatemalense, A. oaxacanum, A. pendens, A. rubrum, A. siskiyouense, A. vaginatum* subsp. *vaginatum,* and *A. yecorense.* Chromosome counts are available for only 2 of the 8 Old World species. Pisek (1924) reported $n = 13$ for *A. oxycedri;* but Wiens (1964) suggested that it is more likely $n = 14$, as in all other species. *Arceuthobium juniperi-procerae* from Ethiopia, Eritrea, and Kenya is closely related to *A. oxycedri,* and its haploid chromosome number also is $n = 14$ (Wiens 1975).

Although chromosome numbers in *Arceuthobium* are consistently $n = 14$, other karyotypic differences distinguish among some species. For example, *A. douglasii* and *A. gillii* possess a bivalent (fig. 14.1) significantly smaller than other members of the genome. Both species undergo meiosis in late summer, but flower in late winter or early spring of the following year. Chromosomes of most species are roughly similar in length and possess metacentric or submetacentric centromeres. *Arceuthobium juniperi-procerae,* however, appears to have a considerable number of heteromorphic bivalents.

A detailed karyotypic study of the dwarf mistletoes would be a useful contribution to our knowledge of the genus. The difficulties of obtaining mitotic cells in large numbers, however, pose technical problems. For example, no root tips, in the usual sense, are available for study. Dwarf mistletoes possess basal meristems similar to grasses, but these are active primarily in spring and have not been examined as a potential source of mitotic cells. Mitosis was studied in dividing cells of the radicular apex of developing embryos and axillary buds, but their occurrence was too sporadic for effective karyotypic work (Wiens 1968). The radicular apex of germinating seeds might be a good source of mitotic cells, but it has not been examined for mitotic activity.

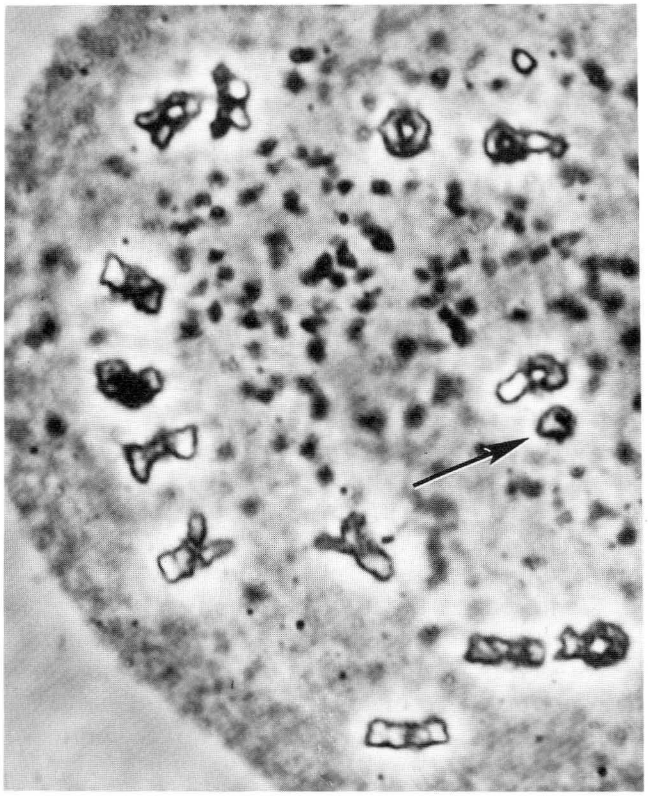


Figure 14.1 –Meiotic chromosomes of *Arceuthobium gillii* during early metaphase I; arrow depicts small bivalent, ×1,400.

Physiological Characters

Phenology

Gill (1935) used time of flowering (spring verses summer) as a principal taxonomic character. His "summer" flowering species (*Arceuthobium campylopodum* complex) contained some significant interspecific variation. For example, *A. occidentale* flowers as late as November or December and *A. californicum* as early as June.

A species generally flowers over a specific period each year, but timing among populations exhibit variation due to altitude, latitude, and weather. Flowering usually begins first at high elevation for those species that flower in summer or fall (Scharpf 1965). Among spring flowering species, however, anthesis typically begins at the lower elevations.

For our analyses of flowering and seed dispersal, we used a 5-point phenology rating system to classify individual populations:

0 = flowering (or seed dispersal) not yet begun

1 = flowering (or seed dispersal) begun but not at peak

2 = flowering (or seed dispersal) near peak

3 = flowering (or seed dispersal) passed peak

4 = flowering (or seed dispersal) over

The results were plotted at 2-week intervals and presented as phenology graphs (see chapter 16). First, a cumulative graph from 0 to 4 was prepared; then the curve beyond 2.0 was inverted to graphically enhance the timing of the flowering peak. We have prepared phenology graphs for most New World species for which we had at least 30 observations.

Whether meiosis occurs immediately before flowering or 5 to 8 months preceding anthesis is an important taxonomic criterion not previously utilized in this genus. Wiens (1968) established three basic flowering groups in *Arceuthobium:*

Group I = spring-flowering species that undergo meiosis directly preceding anthesis

Group II = mid or late summer-flowering species that undergo meiosis directly preceding anthesis

Group III = spring-flowering species that undergo staminate meiosis during the preceding late summer or early autumn

Group Ia was established for *Arceuthobium gillii* and *A. nigrum.* These species undergo meiosis in late summer and flower in late winter-early spring (characteristic of species in group III) but have other traits that place these species in a transitional position between groups I and II.

Time of seed dispersal is a useful taxonomic criterion. This period is relatively consistent for a given species but is much longer in some than in others. Peak seed dispersal may occur as early as July in *Arceuthobium globosum* or as late as November–January in *A. occidentale.* Fruits of *A. pusillum* develop in about 5 months, while those of most other taxa require at least 12 months; fruits of *A. gillii* require 19 months to reach maturity.

Too little information is available to attach taxonomic significance to time of seed germination and length of the incubation period (time from infection until initial shoot appearance). *Arceuthobium guatemalense, A. vaginatum* subsp. *cryptopodum,* and probably other Latin American species germinate in our autumm months, which coincide with the end of their rainy season, but all North American species in the temperate zone germinate in late winter or spring.

Hosts

The importance of hosts in the classification of dwarf mistletoes was discussed earlier (chapter 6). In most instances, a dwarf mistletoe is collected on its principal host. When a collection is made on a secondary host, it is important for identification to record the principal host. For example, the mistletoe usually found on *Pinus flexilis* is *Arceuthobium cyanocarpum;* but *A. americanum* may occasionally parasitize this host. Especially if the specimen were fragmented, the observation that the mistletoe was infrequent on *P. flexilis* and common on associated *P. contorta* would greatly assist in identification. Seldom are two species of dwarf mistletoe both common in a given stand and, in such cases, host crossovers are rare.

Witches' Broom Formation

The dwarf mistletoes cause two basic types of witches' brooms—systemic and non-systemic (chapter 6). The type of witches' broom formed is usually consistent with a particular host–parasite combination, and this taxonomic feature can be used in classification. The five species that consistently cause systemic witches' brooms are *Arceuthobium americanum, A. douglasii, A. guatemalense, A. minutissimum,* and *A. pusillum.* Most other taxa produce non-systemic types. *Arceuthobium globosum* subsp. *grandicaule* consistently forms witches' brooms, but subsp. *globosum* does not. Witches' brooms are not formed or are inconspicuous in the following host–parasite combinations: *A. aureum* subsp. *aureum* on *Pinus* spp., *A. divaricatum* on *P. monophylla, A. occidentale* on *P. sabiniana,* and *A. siskiyouense* on *P. attenuata.*

Chemical Characters

Amino Acids

Greenham and Leonard (1965) compared amino acids in three dwarf mistletoes—*Arceuthobium abietinum* f. sp. *concoloris* and f. sp. *magnificae* and *A. occidentale*—and their respective host trees. They reported some similarities in amino acid composition between host and parasite, but their results were inconclusive with respect to explaining host specificity.

Anthocyanins and Flavonols

Hawksworth and Wiens (1972) conducted the first comprehensive chemotaxonomic study of the genus. They studied the anthocyanins, flavonols, flavones, and cinnamic acid derivatives of all 28 New World taxa then known and 2 of the 4 known Old World species. Results were considered as preliminary because of the small number of individuals analyzed in some species and particularly because most of the compounds detected were not identified.

It was hypothesized that anthocyanin composition might have taxonomic value because dwarf mistletoes differ greatly by color. However, the anthocyanin compositions of most species were similar, and even species with black shoots (e.g., *Arceuthobium vaginatum* subsp. *vaginatum* and *A. nigrum*) had the same anthocyanins as those with lighter colored stems.

Although chromatographic data for anthocyanins and flavonols did not show discontinuous variation among all taxa, many species were distinct and could be readily identified. For example, *Arceuthobium bicarinatum* and *A. hondurense* (species that are morphologically similar) were distinct chromatographically. Although many species were mutually distinct chromatographically, none of these chemical features could be clearly associated with any subgeneric grouping.

Flavonoid chemistry of *Arceuthobium* was studied in more detail by Crawford and Hawksworth (1979) who analyzed all of the 32 New World taxa then known and 4 of the 6 known Old World species. Flavonoids were chosen because they have been shown to be of chemosystematic value in various groups of plants, and Mendelian mechanisms apparently govern their qualitative differences (Alston and others 1965). The results show that the genus is rather uniform and only produced 3-O-glycosides of the flavonoids quercitin and myricetin; glucosides and galactosides were particularly common; rhamnosides and arabinosides were occasional (table 14.2). There were no absolute differences in flavonoids among subgenera, sections, or series of the genus as defined in table 14.1 except that species of the subgenus *Arceuthobium* synthesized primarily glucosides whereas taxa of subgenus *Vaginata* produced galactosides more commonly. The taxonomic information provided by flavonols was, however, also limited.

The three species parasitizing junipers in the Old World (*Arceuthobium azoricum, A. juniperi-procerae,* and *A. oxycedri*) are generally similar (all had myricetin-3-O-glucoside); but they are distinct from *A. minutissimum,* a parasite of pines in the Himalayas.

TABLE 14.2 – Distribution of flavonoid compounds in *Arceuthobium*

Arceuthobium	A	B	C	D	E	F	G	H
A. abietinum	+			+				
A. abietis-religiosae		+	+		+		+	
A. americanum		+		+	+			
A. apachecum	+			+	+	+		
A. aureum subsp. *aureum*	+			+				+
A. aureum subsp. *petersonii*	+			+				+
A. azoricum		+			+			
A. bicarinatum	?	+		?	+			
A. blumeri	+			+				
A. californicum		+		+	+			
A. campylopodum	+			+				
A. cyanocarpum	+			+				
A. divaricatum	+			+				
A. douglasii		+		+	+	+		
A. durangense	+			+				+
A. gillii		+		+		?		
A. globosum subsp. *globosum*	+			+				+
A. globosum subsp. *grandicaule*	+			+				+
A. guatemalense		+			+			
A. hondurense	+	?		+	?		?	
A. juniperi-procerae		+						
A. laricis	+	+		+	+			
A. microcarpum	+	+	+	+	+		+	
A. minutissimum	+			+	+			
A. nigrum		+		+				
A. occidentale	+			+				
A. oxycedri		+						
A. pusillum		+		+				
A. rubrum		+			+			
A. strictum	+	+		+	+			
A. tsugense	+			+				
A. vaginatum subsp. *vaginatum*	+			+				+
A. vaginatum subsp. *cryptopodum*	+			+				+
A. verticilliflorum								

Note: a question mark denotes a compound only present in trace amount.
Key: A=myricetin-3-O-galactoside, B=myricetin-3-O-glucoside, C=myricetin-3-O-rhamnoside, D=quercitin-3-O-galactoside, E=quercitin-3-O-glucoside, F=quercitin-3-O-arabinoside, G=quercitin-3-O-rhamnoside, and H=quercitin-3-O-glycoside.
Adapted from: Crawford and Hawksworth (1979).

The three New World members of the subgenus *Arceuthobium* (*A. abietis-religiosae, A. americanum,* and *A. verticilliflorum*) are all distinct. *Arceuthobium verticilliflorum,* a primitive member of the subgenus and morphologically perhaps one of the most distinct species of *Arceuthobium,* was unique because it possessed no flavonoids.

No consistent differences were found among the three sections of subgenus *Vaginata* (table 14.1 and 14.2). However, 7 of the 9 taxa in section *Vaginata* contained quercetin-3-O-glycoside, a compound absent from all the other taxa studied. Some species that were previously considered to be a single species (e.g., *Arceuthobium apachecum, A. blumeri,* and A. *californicum*) were shown to be chemotaxonomically distinct. *Arceuthobium microcarpum* was unique because it possessed 6 flavonols. Several species had the same flavonoid pattern: *A. abietinum* (both *formae specialis*), *A. blumeri, A. campylopodum, A. divaricatum, A. occidentale,* and *A. tsugense. Arceuthobium bicarinatum* and *A. hondurense,* morphologically similar species, had similar flavonols, but these differed from those in *A. rubrum.* Flavonols of *A. douglasii* and *A. pusillum* were different, which suggests, along with phenological and other characteristics, that section *Minuta* is not a natural grouping (see chapter 15).

Conclusions

The taxa we proposed in 1972 have generally withstood the test of time and usage. We have, however, attempted to point out difficulties in the classification and where additional research would be useful.

In this traditional taxonomic treatment of *Arceuthobium,* we have considered various morphological, palynological, cytological, physiological, chemical, and molecular features. Some traits, such as branching and flowering season, are classical characters used by Engelmann and Gill. Other characters such as pollen, flowering group, and shoot pigments, were first employed by Hawksworth and Wiens (1972). Isozymes and DNA sequencing have been studied since the 1980's, and results are summarized by Nickrent in chapter 15.

Previously, we completed numerical analyses of the 28 New World taxa then known, based on 60 characters of shoots, flowers, fruits, phenology of flowering and seed dispersal, hosts and host reactions, and shoot pigments (Hawksworth and Wiens 1972). We have not reanalyzed these data to include the 14 New World taxa described since 1972, primarily because data are inadequate. For example, isozyme information is available for only 26 of the New World taxa and DNA data are available for only 23. For some taxa, even basic morphological or phenological data are lacking. For example, we have no fruiting or flowering specimens of *Arceuthobium yecorense,* and these data are also weak for several other species.

Molecular Systematics

*Daniel L. Nickrent**

Despite thousands of references to dwarf mistletoes, relatively little work has been conducted on the systematics or phylogenetics of the genus. Molecular analyses of intergeneric or interspecific relationships are even fewer. This chapter reviews previous studies that used macromolecular characters in systematic studies of *Arceuthobium,* presents new data, and summarizes those relationships that appear to be most strongly supported.

Macromolecular characters that have been examined within the dwarf mistletoes include isozymes and DNA sequences from nuclear ribosomal DNA and a plastid-encoded gene (*rbc*L). Using isozyme characters of triploid seed endosperms, interspecific relationships have been determined for 25 New World species, and the results are reviewed below. Subsequent work (Nickrent and Butler 1990, Nickrent and Stell 1990, Nickrent and Butler 1991) on species complexes within section *Campylopoda* utilized diploid shoot tissue, thereby allowing for the use of a wider array of population genetics statistics. The genetically variable internal transcribed spacer (ITS) regions have been sequenced for 22 species of New World and 1 species of Old World dwarf mistletoe (Schuette 1992, Schuette and Nickrent 1992, Nickrent and others 1994). Results of analysis of these sequences are compared with those derived from isozymes and other characters. Genetically conservative small subunit (18S) ribosomal DNA sequences for 3 species of *Arceuthobium* and representatives of the other 6 genera of Viscaceae have been determined. Intergeneric relationships are addressed using these 18S rDNA sequences and are compared to a similar study employing the chloroplast gene *rbc*L.

Isozyme Analyses of Interspecific Relationships

Isozyme electrophoresis has been extensively used to address questions of population genetics, breeding systems, and systematic relationships in plants (Soltis and Soltis 1989). Because of the extreme reduction associated with the parasitic habit and the resulting paucity of morphological characters, isozyme electrophoresis has proven especially valuable in providing useful data for examining species relationships in *Arceuthobium.* Nickrent and others (1984) and Nickrent (1986) first examined the isozymes of 19 North American taxa of *Arceuthobium.* From that study, it was learned that the genus has remarkably high levels of genetic diversity—67% of the loci were polymorphic and averaged 2.23 alleles per locus. This result was surprising given the relative homogeneity of the genus with regards to morphology and flavonoid composition (chapter 14).

Many of the results of that isozyme study were consistent with the taxonomic classifications of Hawksworth and Wiens (1972, 1984, and table 14.1), including the recognition of 2 subgenera (*Arceuthobium* and *Vaginata*), the close relationship among species of section *Campylopoda,* and the clustering of *A. gillii* (*sensu lato*) and *A. vaginatum* (*sensu lato*). Isozyme analysis did not, however, support placement of *A. douglasii* and *A. pusillum* together in section *Minuta.* An unexpected result of that study was the grouping of *A. douglasii,* a parasite of *Pseudotsuga menziesii,* with *A. divaricatum,* a parasite of pinyons. That isozyme analysis clearly raised as many questions as it resolved, hence further work was needed, especially on Mexican and Central American taxa.

The following portion of this chapter presents methodologies and results of an electrophoretic study of 36 dwarf mistletoe populations. The analysis incorporates genetic data on 13 populations of 7 Mexican taxa that were not included in the previous isozyme study (Nickrent 1986) but are pivotal for understanding species and sectional relationships. Some questions remained after the 1986 study:

- How is *Arceuthobium strictum,* the sole species within its series, related to other members of the genus?
- Given the discrepancy between Hawksworth and Wiens (1972) and Nickrent (1986) in sectional placement of *Arceuthobium divaricatum,* what is the relationship of *A. divaricatum* to *A. pendens,* the only other parasite of pinyons?

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- Given their high degree of genetic similarity, are members of the *Arceuthobium gillii* complex and the *A. vaginatum* complex best treated at specific or subspecific levels?
- With the inclusion of *Arceuthobium abietis-religiosae* and *A. verticilliflorum* in the study, will subgenus *Arceuthobium* remain monophyletic?

Methodologies

Electrophoretic methods are essentially as reported in Nickrent (1986). Briefly, seeds are germinated in H_2O_2; viscin is removed from the endosperm; and the endosperm is stored at −70°C. Endosperms are then homogenized in an extraction buffer; the buffer absorbed onto filter paper wicks; and the wicks inserted into horizontal starch gels. Enzyme separation is effected by electrophoresis, and the gel is sliced and stained for different enzymes (Wendel and Weeden 1989). The resulting banding patterns are used to infer genotypes. Results of gel electrophoresis for 14 individuals of 2 species of *Arceuthobium* stained for 6-phosphogluconate dehydrogenase appear in figure 15.1A. Relative intensities of the bands in one lane for heterozygotes (4:4:1 or 1:4:4) confirm the triploid nature of the endosperm tissue. In this study, 7 enzyme systems were used, representing 9 putative enzyme loci: 6-PGD, IDH, GPI, ADH-1, ADH-2, GDH, G-6-PDH, MDH-2, and MDH-3.

Genetic interpretation follows that reported in Nickrent (1986). Because the genotypes were not diploid, individual genotypes could not be entered directly into the statistical program BIOSYS-1 (Swofford and Selander 1981). Instead, allele frequencies were determined for all populations and loci, and these frequencies used as input data.

Isozyme data for 19 taxa (Nickrent 1986) were used in combination with new data for 13 populations of 7 additional taxa (*Arceuthobium abietis-religiosae, A. globosum* subsp. *grandicaule, A. nigrum, A. pendens, A. strictum, A. vaginatum* subsp. *vaginatum,* and *A. verticilliflorum*), yielding a total of 26 taxa (see the appendix "Specimens Examined" for additional data on host and collection locality).

Results and Discussion

Genetic variability statistics for the 36 dwarf mistletoe populations appear in table 15.1. The overall mean percentage of polymorphic loci is 48.7%, and the mean number of alleles per locus is 2.15. These values are lower than those reported in Nickrent (1986) because several populations of Mexican dwarf mistletoes with unusually low levels of polymorphism were included—*Arceuthobium abietis-religiosae, A. globosum* subsp. *grandicaule, A. pendens, A. rubrum, A. strictum,* and *A. verticilliflorum.* The mean number of alleles per locus for these 6 taxa (1.5) is lower than the overall mean for the genus (2.15); this reduction in allele frequency may be a consequence of their restricted distributions. However, two other Mexican taxa, *A. vaginatum* subsp. *vaginatum* and *A. durangense,* show high levels of polymorphism that are comparable to levels found in a related and more northern taxon, *A. vaginatum* subsp. *cryptopodum.* This contrast in species-to-species variation in polymorphism agrees with conclusions of Nickrent (1986) and Hawksworth and Wiens (1972) that section *Vaginata* (which includes *A. vaginatum* and *A. durangense*) is genetically and morphologically more variable than other sections in the genus. Although *A. globosum* subsp. *grandicaule* shows a low level of polymorphism and is also in section *Vaginata,* only 30 individuals from one population were examined electrophoretically, hence this sample may not be representative of the species' genetic diversity.

Interpopulational genetic differences were calculated using the chord distance of Cavalli-Sforza and Edwards (1967). These distances were then used for UPGMA (Sneath and Sokal 1973) phenogram construction (fig. 15.2). Values for several combinations are very nearly or equal to 1.0, indicating that few or no alleles are shared between the populations being compared. These large distance values generally resulted from comparisons among members of subgenus *Vaginata* section *Campylopoda* and subgenus *Arceuthobium.* This result is not unexpected because subgenus *Arceuthobium* contains 3 taxa (*A. abietis-religiosae, A. americanum,* and *A. verticilliflorum*) that are morphologically and genetically distinct from the rest of the genus.

Section *Campylopoda*

Eleven of the taxa examined are included within section *Campylopoda,* series *Campylopoda;* these taxa grouped together at a chord distance of 0.45 or less (fig. 15.2). Two additional taxa of section *Campylopoda* (as delimited in table 14.1) are newly analyzed—*Arceuthobium pendens* and *A. strictum.* Although they cluster together, the populations are linked at a genetic distance value of 0.54, hence their relationship is distant. The branch comprising these 2 taxa joins the 11 other taxa of section *Campylopoda* at the 0.65 level, indicating a significant amount of genetic differentiation. *Arceuthobium strictum* and *A. pendens* are 2 of

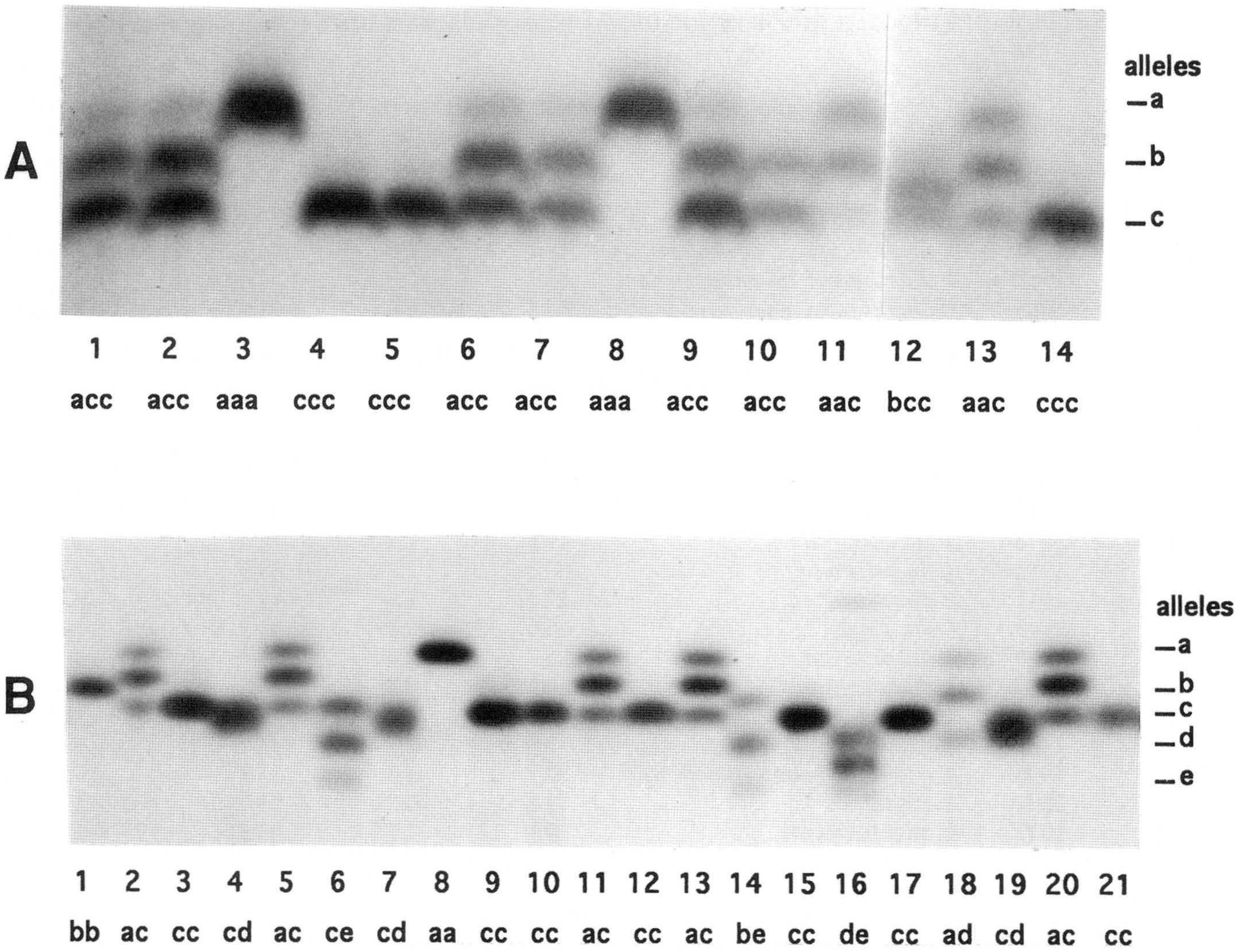

Figure 15.1 –Gel zymograms stained for 6-phosphogluconate dehydrogenase in *Arceuthobium*. Genotypes are given below each lane number. A: Banding patterns from triploid seed endosperms from *A. abietinum* f. sp. *magnificae* (No. 1910, lane 1-10) and *A. abietinum* f. sp. *concoloris* (No. 1917, lanes 11-14). Note the 1:4:4 or 4:4:1 dosage for heterozygotes. B: Banding patterns for 21 individuals of *A. campylopodum* (No. 2206) using diploid shoot tissue. Note the 1:2:1 dosage for heterozygotes.

the most unusual dwarf mistletoes found in Mexico and both have limited distributions: *A. strictum* is a parasite of *Pinus leiophylla* and *P. teocote* and is found only in the Sierra Madre Occidentale and in the state of Durango. *Arceuthobium pendens* is known only from Puebla, San Luis Potosí, and Veracruz and like *A. divaricatum* parasitizes pinyons. Although Hawksworth and Wiens (1980) placed both *A. pendens* and *A. divaricatum* in section *Campylopoda* series *Campylopoda,* several morphological features and flavonoid chemistry (fig. 14.2) gave preliminary evidence that *A. pendens* was quite distinct from *A. divaricatum*. This isozyme evidence is in agreement that these two parasites of pinyons are not closely related.

Placement of *Arceuthobium pendens* and *A. strictum* in a position intermediate between sections *Campylopoda* and *Vaginata* (fig. 15.2) indicates that a gradation of evolutionary divergence may exist. The extremes of this gradient are represented by the "strict" *Campylopoda* taxa of the western United States and the "strict" *Vaginata* taxa of Mexico. Interestingly, the most distant members of series *Campylopoda* are *A. apachecum* and *A. blumeri;* these species occur in the Southwest and northern Mexico. Whether this observation reflects a "genotypic cline" resulting from introgression or divergence from a common genotype is not known.

Arceuthobium divaricatum and *A. douglasii*

Arceuthobium douglasii is most closely allied (fig. 15.2 and Nickrent 1986) with *A. divaricatum,* not with *A. pusillum* (section *Minuta* of Hawksworth and Wiens 1972). This relationship is unexpected because the principle hosts of *A. douglasii* (*Pseudotsuga menziesii*) and *A. divaricatum* (pinyons) are not closely

TABLE 15.1 – Genetic variability at 9 isozyme loci in 36 populations of 26 taxa of *Arceuthobium*

Population number*	Collection number*	*Arceuthobium*	Mean sample size per locus	Mean no. of alleles per locus	Percent polymorphic loci†	Expected Hardy-Weinberg heterozygosity‡
1	1917	*A. abietinum* f. sp. *concoloris*	42.2	2.0	55.6	0.206
2	1906	*A. abietinum* f. sp. *magnificae*	54.7	2.3	44.4	0.183
3	1983	*A. abietis-religiosae*	34.3	2.0	55.6	0.250
4	2010	*A. abietis-religiosae*	61.6	1.4	33.3	0.109
5	1932	*A. americanum*	47.7	3.0	55.6	0.200
6	1929	*A. americanum*	35.8	3.8	77.8	0.351
7	1945	*A. apachecum*	61.7	2.0	44.4	0.210
8	1937	*A. blumeri*	35.1	2.0	22.2	0.133
9	1930	*A. californicum*	49.6	2.6	66.7	0.253
10	1924	*A. campylopodum*	28.8	2.1	55.6	0.211
11	1973	*A. cyanocarpum*	17.6	1.7	44.4	0.124
12	1953	*A. divaricatum*	80.3	2.7	55.6	0.209
13	1941	*A. douglasii*	27.7	2.1	44.4	0.228
14	1949	*A. douglasii*	44.6	2.4	33.3	0.192
15	1870	*A. durangense*	26.7	2.9	66.7	0.265
16	2049	*A. durangense*	9.3	2.3	66.7	0.299
17	2051	*A. durangense*	26.8	3.3	77.8	0.365
18	1938	*A. gillii*	77.8	2.8	44.4	0.198
19	1996	*A. globosum* subsp. *grandicaule*	27.2	1.6	11.1	0.092
20	1801	*A. laricis*	21.4	1.7	55.6	0.170
21	1947	*A. microcarpum*	19.1	1.7	33.3	0.154
22	2041	*A. nigrum*	31.7	2.4	66.7	0.269
23	1962	*A. occidentale*	37.8	2.0	55.6	0.184
24	1992	*A. pendens*	20.8	1.8	33.3	0.106
25	1970	*A. pusillum*	50.9	2.0	22.2	0.103
26	1971	*A. pusillum*	30.8	1.7	44.4	0.166
27	1853	*A. rubrum*	8.3	1.3	33.3	0.139
28	2061	*A. strictum*	24.2	1.1	11.1	0.039
29	1927	*A. tsugense* subsp. *mertensianae*	10.0	1.9	66.7	0.290
30	1876	*A. vaginatum* subsp. *cryptopodum*	53.0	2.7	44.4	0.172
31	1964	*A. vaginatum* subsp. *cryptopodum*	30.2	2.8	55.6	0.256
32	2059	*A. vaginatum* subsp. *vaginatum*	8.9	2.0	66.7	0.230
33	1980	*A. vaginatum* subsp. *vaginatum*	29.8	2.4	66.7	0.274
34	1981	*A. vaginatum* subsp. *vaginatum*	15.4	1.9	66.7	0.233
35	2001	*A. verticilliflorum*	12.8	1.7	44.4	0.175
36	2065	*A. verticilliflorum*	4.6	1.3	33.3	0.169
		Means	33.3	2.15	48.7	0.200

*See "Specimens Examined" for information on host and locality.

†A locus is considered polymorphic if the frequency of the most common allele does not exceed 0.95.

‡Unbiased estimate (Nei 1978). Direct count heterozygosity not possible given that the allelic data were derived from triploid genotypes.

related. These mistletoes are morphologically distinct, but *A. douglasii* is so morphologically reduced that association with any taxon is obscure. The concept of biochemical convergence between these species was discussed by Nickrent (1986) and dismissed in favor of a more parsimonious explanation of genetic and phylogenetic similarity. These species share 16 alleles across 6 loci, and both species are fixed for GDH^{66} (an isozyme absent in all other species). Both these mistletoes were included in section *Vaginata* by Nickrent (1986); however, addition of other Mexican taxa in the present analysis suggests that these species more likely form a transitional group between sections *Vaginata* and *Campylopoda*.

Evidence from flowering groups (Wiens 1968 and chapter 14) also supports the proposed relationship between *Arceuthobium douglasii* and members of section *Vaginata*.

Although some species of section *Vaginata* (e.g., *A. durangense, A. globosum,* and *A. vaginatum*) have direct spring-flowering, other species of section *Vaginata* (e.g., *A. gillii* and *A. nigrum*) and *A. douglasii* have indirect spring-flowering. Nickrent (1984) presents evidence supporting a derivation of indirect spring-flowering from direct spring-flowering as a response to exposure to cooler climates.

During these isozyme analyses, thousands of dwarf mistletoe seeds have been examined. Several seed features appear to be useful in differentiating between sections *Campylopoda* and *Vaginata*. Seeds of *Vaginata* species are often ellipsoid (versa pyriform to ovoid), have a slight protuberance at the chalazal end, have short viscin strands arranged more densely near the radicular end, and have endosperm epidermal cells pigmented with red (or purple/maroon) or variegated green and red (pinto). Because *Arceuthobium douglasii* seeds are ellipsoid and display the pinto phenotype (*A. pusillum* seeds are pyriform and entirely green), the species' affinity to section *Vaginata* is difficult to ignore.

Section *Vaginata*

The new taxa and populations of the predominantly Mexican section *Vaginata* included in this study are *Arceuthobium durangense, A. globosum* subsp. *grandicaule, A. nigrum,* and *A. vaginatum* subsp. *vaginatum*. Similarity averaging shows that section *Vaginata,* as defined here, is second only to subgenus *Arceuthobium* in terms of within-group heterogeneity (fig 15.2).

Arceuthobium globosum subsp. *grandicaule* emerges as the most distinct member of section *Vaginata,* as it had from previous morphological and physiological studies (Hawksworth and Wiens 1972, 1984). This taxon has the largest shoot diameter of the genus (reaching nearly 5 cm), parasitizes at least 12 host species, and ranges as far south as Guatemala. Samples from populations of *A. globosum* subsp. *globosum* (a more northern subspecies) are needed to determine levels of genetic similarity between the 2 taxa currently treated as suspecies.

The phylogenetic position of *Arceuthobium rubrum* remains somewhat enigmatic because this taxon clusters (distantly) with members of section *Campylopoda* based on phenetic analysis of morphological data (Hawksworth and Wiens 1972) but the taxon is clearly a component of the *Vaginata* group based on isozymes. *Arceuthobium rubrum* clusters at a genetic distance of 0.6 (fig. 15.2) with *A. gillii* and *A. nigrum* of section *Vaginata*. In a cladistic analysis of morphological and physiological features (Nickrent 1984), *A. rubrum* was identified as the most basal taxon of the *Campylopoda* clade; its morphological similarities to section *Campylopoda* may only be the result of convergence. Seeds of *A. rubrum* are ellipsoid and pigmented either green, maroon, or pinto, therefore geographic distribution, isozyme evidence, and seed characters support placement of *A. rubrum* in section *Vaginata*.

Arceuthobium gillii and *A. nigrum* were originally classified as sister subspecies (Hawksworth and Wiens 1972). In this study, they clustered together at a genetic distance of 0.553 and stand apart from the rest of section *Vaginata* (fig. 15.2). Although only two populations were analyzed, these taxa appear sufficiently differentiated to justify their elevation to specific status.

Clustering of taxa related to *Arceuthobium vaginatum* (*A. vaginatum* subsp. *vaginatum, A. vaginatum* subsp. *cryptopodum,* and *A. durangense*) corresponds to the existing taxonomy for some populations (e.g., populations 30, 31, 32, and 34) but appears genetically distinct for other populations (e.g., populations 15, 16, and 17). The lack of clustering for populations of *A. durangense* is partly due to the high number of alleles present at the GPI locus. Population 17 (Puerto Buenos Aires) has 8 alleles at this locus, whereas population 16 (El Madroño, only 7 km away) shows just 3 alleles at this locus. Although sample sizes for these populations differ, the results provide evidence for significant genetic differentiation over relatively small areas.

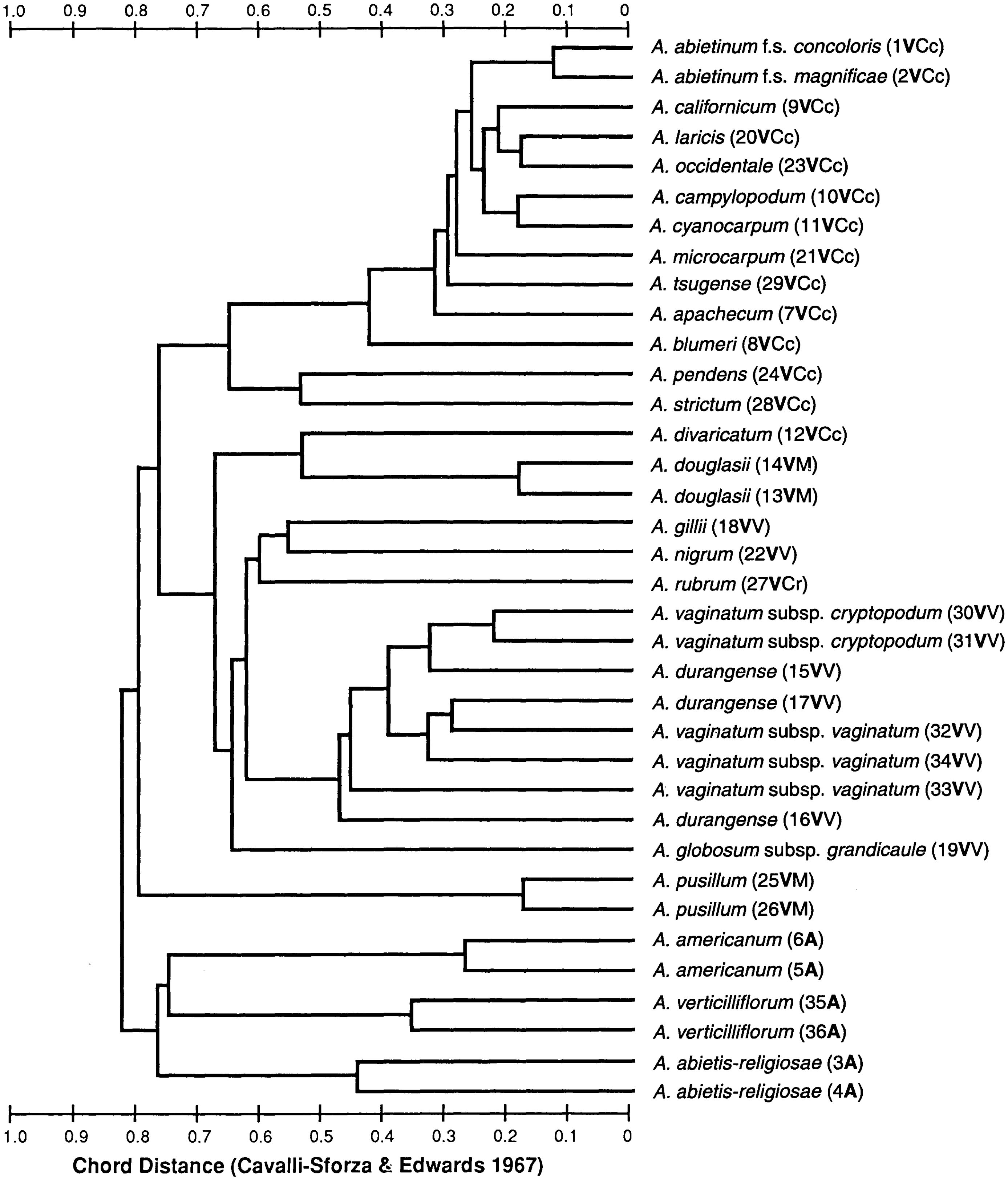

Figure 15.2 –The UPGMA phenogram resulting from isozyme analysis of 36 populations of *Arceuthobium*. Cophenetic correlation = 0.968, standard deviation 6.6%. Codes following species name indicate population number (table 15.1) and taxonomic affilation according to the classification of Hawksworth and Wiens (table 14.1 compare with table 15.2). Key: **A** = subgenus *Arceuthobium*, **V** = subgenus *Vaginata*, V = section *Vaginata*, C = section *Campylopoda*, M = section *Minuta*, c = series *Campylopoda*, r = series *Rubra*, s = series *Stricta*.

Arceuthobium pusillum

As reported in Nickrent (1986), isozyme evidence indicates that *Arceuthobium pusillum* is a distinct taxon in the genus that is placed midway between subgenus *Vaginata* and *Arceuthobium*. Isozyme analysis does not support a section *Minuta* composed of *A. pusillum* and *A. douglasii*. These results agree with those of Crawford and Hawksworth (1979 and see table 14.2), which show that these two species have different flavonoid patterns. Isozyme data also do not provide evidence that *A. pusillum* and *A. douglasii* are recent derivatives from section *Campylopoda* as suggested by Hawksworth and Wiens (1972, page 38). That these species share isophasic broom development and indirect spring-flowering must be interpreted as convergence.

Subgenus *Arceuthobium*

Only *Arceuthobium americanum* represented subgenus *Arceuthobium* in the earlier isozyme study (Nickrent 1986). With the inclusion of *A. abietis-religiosae* and *A. verticilliflorum*, all three New World members of the subgenus have been examined electrophoretically. These species share several isozymes (IDH^{136}, GPI^{200}, G-6-PGD^{100}, and MDH-3^{187}) and occupy the same branch of the phenogram (fig. 15.2). These results demonstrate that they are at least distantly related. A comparison of genetic distance values indicate that *A. americanum* is more closely related to *A. verticilliflorum* than it is to *A. abietis-religiosae*. The two populations of *A. abietis-religiosae* showed a genetic distance of 0.452; this relatively high value indicates that substantial genetic differentiation has occurred between populations separated by only 400 km. This genetic differentiation is further demonstrated by the fixation for different alleles at the IDH locus (IDH^{136} and IDH^{160}). According to similarity/distance measure averaging, subgenus *Arceuthobium* is the most heterogeneous of all the dwarf mistletoe groups examined, and *A. abietis-religiosae* occupies the most basal position among the species examined.

Conclusions

With the new isozyme evidence, questions raised in the introduction can now be answered. *Arceuthobium strictum* is distantly related to most other taxa in section *Campylopoda* and clusters with *A. rubrum*. These relationships are not totally in conflict with the classifications of Hawksworth and Wiens (1972 and table 14.1), in which these species were placed in their own series (*Stricta* and *Rubra*, respectively). It appears, however, that the majority of section *Campylopoda* species are found in the United States, where as section *Vaginata* species predominate in Mexico.

The two parasites of pinyons, *Arceuthobium divaricatum* and *A. pendens*, are not closely related. This conclusion is supported by the isozyme data, markedly different flavonoid chemistry, systemic broom formation in *A. pendens*, and different hosts (Hawksworth and Wiens 1980).

Arceuthobium gillii and *A. nigrum* are clearly related but cluster at a genetic distance value of 0.553, thus supporting their recognition as distinct species. The relatives of *A. vaginatum* have high levels of genetic diversity, and cluster analysis indicates a substantial genetic differentiation between populations. Further work is required to better understand apportionment of genetic variation in the *Arceuthobium vaginata* complex.

Subgenus *Arceuthobium* shows greater within-group heterogeneity than any of the other groups. Despite the variation, isozyme analysis places *Arceuthobium abietis-religiosae, A. americanum,* and *A. verticilliflorum* on a single branch that joins the remainder of the species at a genetic distance of 0.82. Thus, isozyme data support use of verticillate secondary branching (Mark and Hawksworth 1981) as a distinguishing character for the subgenus.

Species Relationships in the *Arceuthobium campylopodum* Complex

Additional isozyme analyses have been conducted on various members of the *Arceuthobium campylopodum* complex (Nickrent and Butler 1990, Nickrent and Stell 1990, Nickrent and Butler 1991). These studies utilized diploid shoot tissue as a source of isozymes, hence a larger number of population genetic analyses could be conducted. Enzyme banding patterns typical of diploid tissue are shown in fig. 15.1B. Based upon UPGMA cluster analysis, California coastal populations of *Arceuthobium* parasitic on *Pinus radiata* and *P. muricata* are genetically distinct from *A. campylopodum* (*sensu stricto*) and are segregated at the specific level as *A. littorum*. Examination of isozymes from allopatric and sympatric populations of *A. campylopodum* and *A. occidentale* did not reveal significant genetic differentiation, hence they could be considered a single biological species.

Nickrent and Butler (1991) examined genetic relationships among dwarf mistletoes related to *Arceuthobium campylopodum* that are parasitic on

Pinus attenuata and *P. monticola* of northwestern California and southwestern Oregon. The parasites of *P. attenuata* and *P. monticola* were genetically distinct from each other. These species were named, respectively, *A. siskiyouense* and *A. monticola* (Hawksworth and others 1992b). This result is in accordance with the observation that the Klamath-Siskiyou Mountain region contains a highly diverse and endemic flora. These dwarf mistletoes likely represent the most recent evolutionary lines to diverge from the *A. campylopodum* complex.

The results from electrophoretical examination of the three host-forms of *Arceuthobium tsugense* (mountain hemlock, western hemlock, and shore pine) indicate that the population infecting *Tsuga mertensiana* is genetically distinct and deserving of taxonomic recognition as *A. tsugense* subsp. *mertensianae* (Nickrent and Stell 1990, Hawksworth and others 1992b). *Arceuthobium tsugense* subsp. *tsugense* consists of two morphologically similar host races parasitic on *Tsuga heterophylla* (western hemlock race) and *Pinus contorta* var. *contorta* (shore pine race). Isozyme analysis failed to detect significant genetic differentiation between these two host-forms, hence they were retained within the same subspecies.

Species Relationships From Ribosomal DNA Spacer Sequences

Many studies addressing interspecific relationships in plants have been conducted using restriction site data from chloroplast DNA (see Soltis and others 1992). Few studies have used DNA sequences to examine interspecific relationships because a gene or segment of DNA that is of adequate size and that evolves at a sufficiently fast rate is required. Recently, the internal transcribed spacer (ITS) regions of the ribosomal DNA cistron have been shown to evolve at rates appropriate for examining more recently diverging lineages (Baldwin 1993). As shown in fig. 15.3, the rDNA cistron (transcriptional unit) comprises (from 5′ to 3′) an external transcribed spacer (ETS), the 18S rDNA, ITS-1, 5.8S rDNA, ITS-2, 26S rDNA, and a transcription termination site (TTS). This cistron is tandemly repeated several hundred to several thousand times in the nucleolar organizing region (Arnheim 1983).

The transcriptional units themselves are separated by a nontranscribed spacer (NTS). The NTS region has been used to study variation at the population or even individual level (May and Appels 1987). Although ribosomal cistrons occur in high copy number, the sequence of each repeat within a genome is conserved via unequal crossing over and other DNA turnover mechanisms. This phenomenon is referred to as "horizontal" or "concerted evolution" (Brown and others 1972, Arnheim and others 1980, Arnheim 1983). Within the cistron, ribosomal genes and spacers show markedly different tempos of evolution (Jorgansen and Cluster 1988), hence studies of closely related and distantly related organisms can be conducted using the appropriate region. The ITS regions and enclosed 5.8S rDNA were sequenced and analyzed in 22 species of *Arceuthobium* to allow a comparison with phylogenies generated from other methods.

Methodologies

Sequence analyses were conducted on samples from 24 populations of *Arceuthobium* that represented 22 taxa (see fifth appendix, "Specimens Examined"). Both shoot and seed materials were used as sources for DNA. Genomic DNA was obtained from shoots by grinding in liquid nitrogen and extracting in 2× CTAB (Doyle and Doyle 1987). Crude homogenates of seeds were made in a buffered protease solution (Schuette 1992, Nickrent and others 1994).

The polymerase chain reaction (PCR) was used to amplify the ITS region from the genomic DNA extract (Mullis and Faloona 1987). A number of conserved sites on both the 18S and 26S rDNA allow the construction of forward and reverse primers that bracket ITS-1, 5.8S rDNA, and ITS-2. A common primer combination employed the 18S 1830 forward and 26S 25 reverse (5′ AACAAGGTTTCCGTAGGTGA -3′ and 5′ TATGCTTAAAYTCAGCGGGT-3′ respectively), which yielded a 0.64-kb fragment upon symmetrical amplification. This fragment was used as a template for an asymmetrical PCR reaction (Gyllensten and Erlich 1988) that produces single-stranded DNA. In some cases, the double-stranded template was sequenced directly. Because *Arceuthobium abietis-religiosae* and *A. oxycedri* apparently had mutations at one or both of the above two priming sites, alternate internal 18S (forward) and 26S (reverse) primers were used. The PCR product was then gel purified for subsequent sequencing reactions (Nickrent 1994). These sequencing reactions were carried out using the terminal amplification primers or forward and reverse primers constructed for the conserved sites on the 5.8S rDNA (sites 32 to 52). Chain-termination sequencing reactions using dideoxynucleotides (Sanger and others 1977) were conducted using Sequenase® (U.S. Biochemical Corp.).

An autoradiogram with ITS sequences for three dwarf mistletoe species is shown in figure 15.4. Most mutations were base substitutions, thus allowing man-

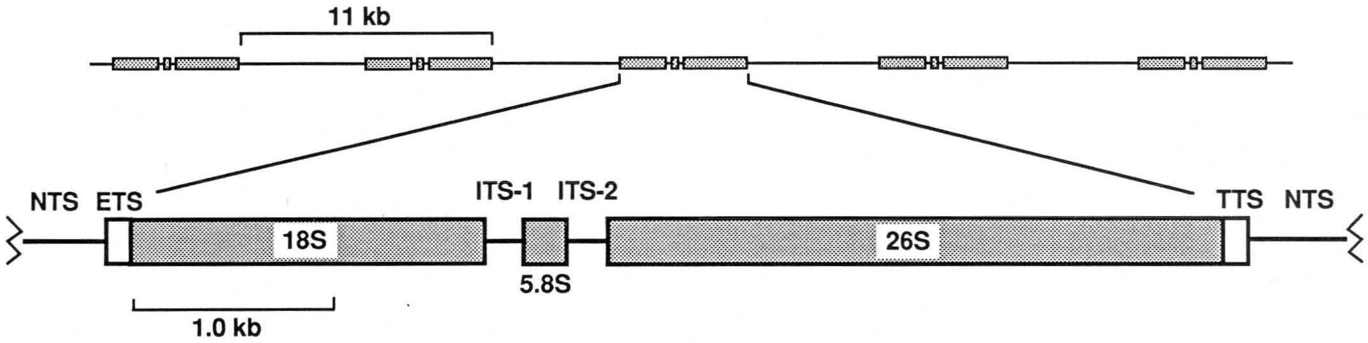

Figure 15.3 –The organization of higher plant ribosomal DNA cistron. NTS = nontranscribed spacer, ETS = external transcribed spacer, 18S = small-subunit rDNA, ITS-1 = first internal transcribed spacer, 5.8S = rDNA, ITS-2 = second internal transcribed spacer, 26S = large-subunit rDNA, TTS = transcription termination site. The rDNA cistron is tandemly repeated many times within the plant genome.

ual alignment using "Eyeball Sequence Editor" (Cabot and Beckenbach 1989). Minimum length trees and other analyses of the aligned sequences were conducted using PAUP version 3.1 (Swofford 1993).

Results and Discussion

Overall, little length variation occurs. ITS-1 sequences varied by less than 1% from the average length (208 base pairs); ITS-2 varied by less than 1.5% when compared to the average (226 bp). The 5.8S rDNA sequences were usually 167 bp in length, although the three members of subgenus *Arceuthobium* and *Arceuthobium divaricatum* had a 5.8S rDNA of length 166 bp. This is slightly larger than the common length (164 bp) seen in other angiosperms. The ITS sites can be classified according to their variability: 39% are monotypic, 33% are ditypic, 15% are tritypic, 2% are tetratypic, and 11% are insertions or deletions. These values were determined without the inclusion of *A. abietis-religiosae* and *A. oxycedri* because of their high sequence divergence compared with other taxa (see below). In *Arceuthobium,* ITS-1 is less variable than ITS-2 and is also smaller (which is the case for many other, mainly asterid, species). At 208 bp, dwarf mistletoe ITS-1 is within the range (194 to 265 bp) reported for other angiosperms (Baldwin 1993). In *Calycadenia* and other composites, as well as *Vicia* and *Sinapis,* ITS-1 is larger than ITS-2 (Baldwin 1993).

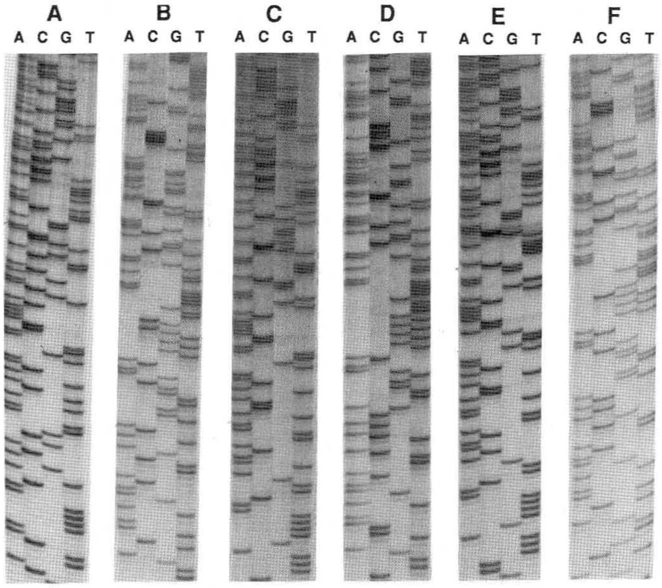

Figure 15.4 –Autoradiogram showing ITS sequences for three *Arceuthobium* species. Left set for each species utilized the 26S 25 reverse primer, right set the 18S 1830 forward. A and B: *A. apachecum* (No. 1945). C and D: *A. pusillum* (No. 1969). E and F: *A. vaginatum* subsp. *crytopodum* (no. 1978).

The alignment of ITS-1, 5.8S rDNA, and ITS-2 produced a matrix of 22 *Arceuthobium* species by 619 sites (a portion is shown in fig. 15.5). Of these sites, 388 (62.6%) were variable. Because *A. abietis-religiosae* and *A. oxycedri* had high sequence divergence compared with other taxa and could not be aligned beyond bp 470, these species are excluded from further variability calculations. Among the remaining 20 taxa, 304 variable sites were present. Of these, 174 were phylogenetically informative (i.e., a different nucleotide shared by at least 2 taxa). ITS-1 contained 71 sites (40.8% of total); 5.8S had 15 sites (8.6%); and ITS-2 had 88 sites (50.6%). When the number of phylogenetically informative sites is taken as a percentage of the number of variable positions, the following values were obtained: 53.7% (71/132) for ITS-1, 46.8% (15/32) for 5.8S, and 63.7% (88/138) for ITS-2.

To test for possible significant intraspecific variation, partial ITS sequences (100 bp) were determined for individuals from 3 populations of *Arceuthobium americanum* and 2 populations of *A. divaricatum.* A single change was detected in *A. americanum,* and no differences were seen in *A. divaricatum.* Several taxa have been sequenced twice from either the same genomic DNA sample or a second crude seed extract.

```
OXY GUA....U..G....G..G.......U..C......AUAAA..UU...G...U...CU.-.
ABR .-A....U..G....G..G.......G..C......AUAAA..UU...G...U...C..U.
AME UCGUGCUcUUAAAGAUGAAUGACAAAUAAUAAGUUACACU-AUCCUAGAUCGAUGAUCUAG 60
VER .......U.A..G...........G.C.C.....A.............UC.......
PEN ..A....U.C..............G...C.U..GU.C....UU.U....AU.......U
GUA ..A....U.C..............G...C.U..GUAC....UU.......AU.......U
PUS ..A.A..U...........CC...UGC.........AG...G.UU.......CU.....C.A
BIC ..A....U..........C-....UGC....-....AG...G.UU.........U.....C.A
GLO ..A.A..U................GC..C......AG....UU........U.......A
DIV .......UK.........G.....GC..A......AGAC...UU........C.......
DOU ..A....U................GC..A......AG....UU........U.......A
GIG ..A....U................GC.........AG...CUU........U......-A
NIG ..A...CU................GC....-....AG....UU........U.......A
RUB ..A....U..........U.....GC.......G.AG....UU...G...U......-A
VAC ..A...CU...G............GC.........AG....UU........U.......A
VAV ..A....U................GC.........AG....UU.....U.U.......A
DUR ..A....U................GC.........AG....UU........U.......A
STR ..A....U................GC...UG...GAG....UU........U.......A
ABM ..A.R..U............R...G...AG.....AU.....MU........U.......A
APA ..A....U................G...AG.....AU.....UU........U.......A
CAM ..A....U................G...AG.....AU.....UU........U.......A
MIC ..A....U................G...AG.....AU.....UU........U.......A

OYX ...-..U..GCG..UU.G..UU.CA.GCC.C...UG.CA..A.AU.U.UA.C....C.G.K
ABR ...-..U..GCG..UU.G..UU.CA.GCC.C...UG.CA..A.AU.U.UA.C....C.G.U
AME UAGGACAUUUGACACAUUGUCAGGGAAU-AUGUGCUCUCUUGUUCCAAAUAUAAAUUGACA 120
VER .G.........G...........U..-.......U..G......U.C.UA........G..
PEN CG.UG....C..U....G.CG..C.........AUGAGU.....U...U..C..U......
GUA C..AC....C..U.......G..CA..G.....AUGUGUG....U..UU........C.G..
PUS ...A.....CAU....CGA.UG.U...C......UGUGU.....UU..U...G...C.GU.
BIC .U.A.....CAU....CGA.UG.C...C.......UGUGU.....UU..U...G...C.GU.
GLO ...A.....C..U.......UG.U...C......UG--U.....UU..U...G...C.GU.
DIV .G.A.....C...........UG.U...C.......GUGU.....U...U...G..CC.GU.
DOU ...A.....CU.......G..UG.C...C......UGUGU.....UU..U...G...C.GU.
GIG ..UA....GC.......G..UG.C...C......UGUGU.....UG..U...G.U.C.GU.
NIG ...A.....C.......G..UG.C...C......UG.GU.....UU..U...G...C.GU.
RUB ..AA.Y...C..U....G..UG.C...C.......GAGU.....UU..UA..G.U.C.GU.
VAC ...A.....C.......G..UG.C...C......UG.GU.....UA..U...G...C.GU.
VAV ...A.....C.......G..UG.C......C...UG.GU.....UU..U...G...C.GU.
DUR ...A.....C.......G..UG.C...C......UG.GU.....UU..U...G...C.GU.
STR ..A......C.....G.G..UG.C...C......UG.GU.....UU..U...G...C.GU.
ABM ...A.....C..U....G..UG.C...C......UG.G......UU..U...G...C.GU.
APA ...A.....C..U....G..UG.C...C......UG.G......UU..U...G...C.GU.
CAM ...A.....C..U....G..UG.C...C......UG.G......UU..U...G...C.GU.
MIC ...A.....C..U....G..UG.C...C......UG.G......UU..U...G...C.GU.
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Figure 15.5 –Sequence alignment showing the first 120 bp of ITS-1 for 22 species of *Arceuthobium*. A dot indicates the same base as the reference (*A. americanum*). Ambiguous nucleotide designations follow IUPAC specifications (e.g., Y = C and T). Key: OXY = *A. oxycedri*, ABR = *A. abietis-religiosae*, AME = *A. americanum*, VER = *A. verticilliflorum*, PEN = *A. pendens*, GUA = *A. guatemalense*, PUS = *A. pusillum*, DIV = *A. divaricatum*, DOU = *A. douglasii*, GIG = *A. gillii*, NIG = *A. nigrum*, RUB = *A. rubrum*, VAC = *A. vaginatum* subsp. *cryptopodum*, VAV = *A. vaginatum* subsp. *vaginatum*, DUR = *A. durangense*, STR = *A. strictum*, ABM = *A. abietinum* f. sp *magnificae*, APA = *A. apachecum*, CAM = *A. campylopodum*, MIC = *A. microcarpum*.

Only very rarely were true polymorphisms detected, and these were subsequently coded in the matrix as ambiguous nucleotides.

The data matrix of 22 taxa by 619 sites produced 6 equally parsimonious trees of 735 steps. Bootstrap analysis with 200 replications was conducted to test the reliability of the resulting clades (fig. 15.6). As expected from their large sequence divergence, *Arceuthobium abietis-religiosae* and *A. oxycedri* form a clade well removed from the remainder of the genus. Removing these species from the analysis and substituting *A. americanum* and *A. verticilliflorum* as outgroups resulted in the same topologies. Specific relationships derived from this analysis are discussed below.

Section *Campylopoda*

As evidenced from the clustering and branch lengths, four members of section *Campylopoda* are genetically very similar—*A. abietinum* f. sp. *magnificae, A. apachecum, A. campylopodum*, and *A. microcarpum*. Sequences of *A. cyanocarpum, A. occidentale*, and *A. tsugense* were either very similar or identical to those of the above four taxa and therefore not included. The section *Campylopoda* clade, comparable to series *Campylopoda* (as delimited by Hawksworth and Wiens 1972, 1984, and table 14.1), occurs mainly in the United States and does not include Mexican and Caribbean species such as *A. guatemalense, A. pendens, A. rubrum, A. bicarinatum*, and *A. strictum*. The latter three of these species were previously segregated into series *Rubra* (*A. rubrum* and *A. bicarinatum*) and *Stricta* (*A. strictum*) (Hawksworth and Wiens 1972 and table 14.1), thus providing some indication of their differentiation from series *Campylopoda*. ITS sequence analysis does not support a close relationship among members of these three series; but rather, the analysis indicates various relationships to members of section *Vaginata*.

A strongly supported result of the ITS analysis (100% bootstrap) is the association of *Arceuthobium guatemalense* with *A. pendens*. This clade appears basal to all other members of subgenus *Vaginata*, not as a component of section *Campylopoda*, series *Campylopoda* (as delimited by Hawksworth and Wiens 1984 and table 14.1). *Arceuthobium guatemalense* is confined to the mountains of Guatemala and southern Mexico, where it parasitizes *Pinus ayacahuite* (of subgenus *Haploxylon*). *Arceuthobium pendens* is known only from Puebla, San Luis Potosí, and Veracruz, Mexico, and is parasitic on the *Haploxylon* pines, *P. discolor* and *P. orizabensis*. Both of these mistletoes and their hosts are narrow endemics. Given their position on the phylogram and their endemic distributions, these species could represent relictual taxa that diverged early during the migration and evolution of *Arceuthobium* in the New World.

Arceuthobium divaricatum and *A. douglasii*

Although classified into different sections by Hawksworth and Wiens (1972 and table 14.1), *Arceuthobium divaricatum* and *A. douglasii* cluster together according to isozyme analysis (Nickrent 1986). *Arceuthobium divaricatum* occurs near the base of section *Vaginata* and near *A. globosum* in the derived phylogram (fig. 15.6). When ITS-1 alone is analyzed (tree not shown), *A. divaricatum* and *A. douglasii* cluster together with a high bootstrap confidence. Examination of the alignment shows that

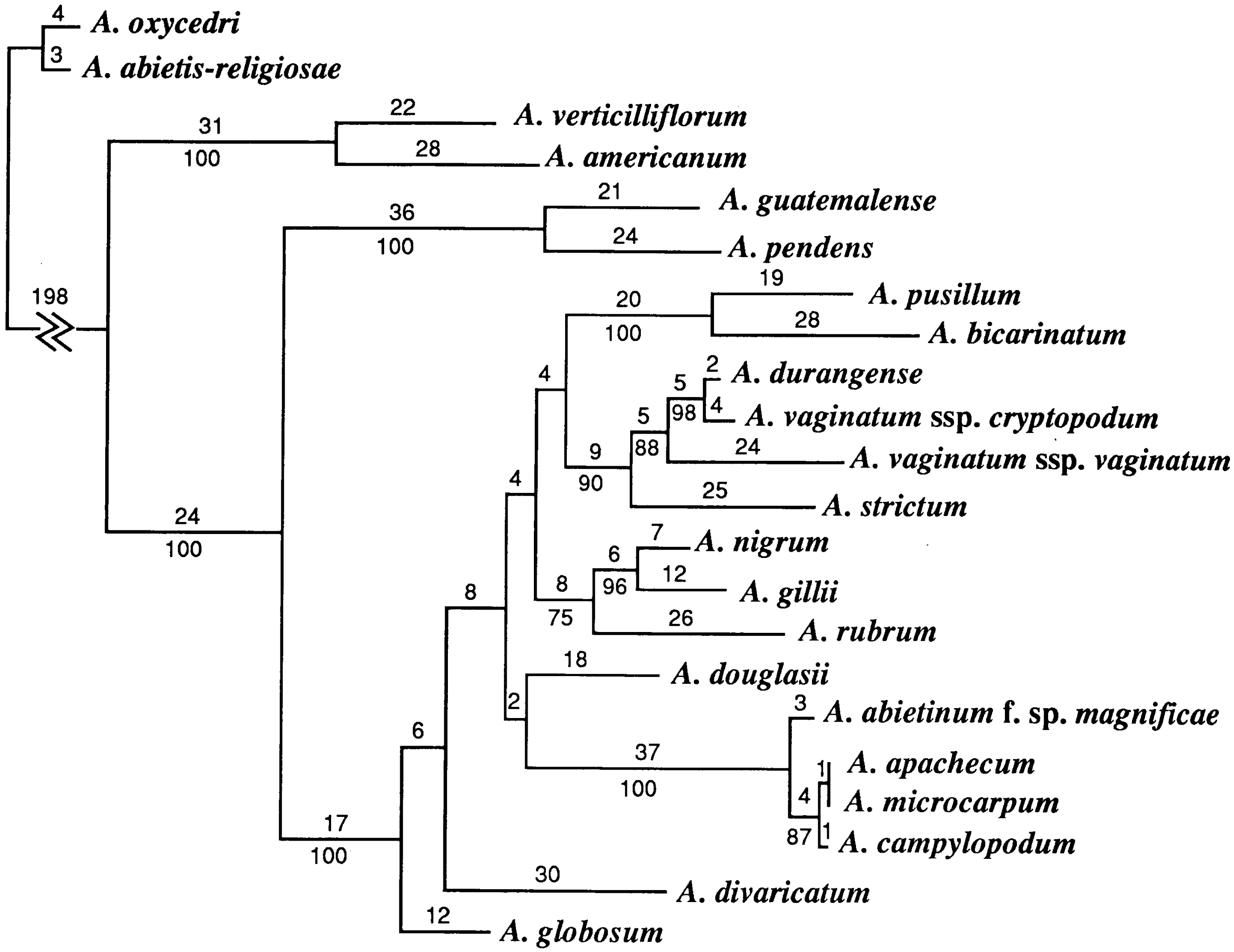

Figure 15.6–One of 6 equally parsimonious trees of length 738 derived from analysis of *Arceuthobium* ITS-1, -2, and 5.8S rDNA sequences. The numbers above the branches indicate number of nucleotide subsitutions and the numbers below the branches indicate percentage values from 200 replications derived from the bootstrap majority rule consensus tree. Clades with no bootstrap value indicated were not strongly supported (present in <50% of the trees). Consistency index = 0.755, homoplasy index = 0.286, retention index = 0.726.

A. divaricatum has a divergent ITS-2 sequence compared to other members of subgenus *Vaginata.* Taking the isozyme and ITS evidence together, a clade composed of *A. divaricatum* and *A. douglasii* is presently favored.

Section *Vaginata*

Two strongly supported clades representing section *Vaginata* are seen following bootstrap analysis (fig. 15.6). The first is composed of *Arceuthobium vaginatum* subsp. *vaginatum, A. vaginatum* subsp. *cryptopodum, A. durangense,* and *A. strictum.* Previous classifications (Hawksworth and Wiens 1972) and isozyme studies (Nickrent 1986 and this chapter) have shown relationships among the first three of these taxa. The addition of *A. strictum* is somewhat surprising, although isozyme analysis had shown genetic divergence between it and species in series *Campylopoda.* All four of these taxa parasitize pines of subgenus *Diploxylon* and their distributions range from the northern Sierra Madre Occidental (Durango through Chihuahua and Sonora) to the southwestern United States (Arizona, New Mexico).

The second clade is composed of *Arceuthobium rubrum, A. gillii,* and its recent segregate species, *A. nigrum.* The association of *A. gillii* with *A. nigrum* is strongly supported by ITS analysis (96% bootstrap). Bootstrap support is 75% for the entire clade containing *A. rubrum.* Because isozyme characters also indicated a grouping of these three species, their phyletic affinity is highly probable.

Arceuthobium pusillum and *A. bicarinatum*

A surprising but strongly supported clade (100% bootstrap) contains *Arceuthobium pusillum* and *A. bicarinatum.* The former species is a reduced parasite of spruce of the northern United States and Canada, and the latter is a relatively large parasite of *Pinus occidentalis* on the island of Hispaniola. Hawksworth and Wiens (1972) placed *A. pusillum* and *A. douglasii* in section *Minuta,* a placement not supported by isozyme analysis (Nickrent 1986). They also suggested that *A. bicarinatum* arrived in Hispaniola via a Central American land bridge that was connected to Honduras during the late Tertiary Period (see chapter 5). This route seemed plausible given the morphological similarity between *A. bicarinatum* and *A. hondurense.* The distance from Hispaniola to the nearest extant population of *A. pusillum* is about 2,300 km; *A. bicarinatum* and *A. hondurense* are presently separated by about 1,100 km.

Given these biogeographical distributions and the DNA sequence results, an alternate hypothesis regarding these two mistletoes is suggested. Several plant species found at high elevations in Hispaniola are known to have close relatives in the eastern United States, such as *Lyonia* (Judd 1981) and *Juniperus* (Adams 1989). Hawksworth and Wiens (1972) suggested that *Arceuthobium* arrived in the New World in the early Tertiary Period via a Beringian land bridge. If one accepts that the late Tertiary microthermal vegetation was largely derived from the preceding flora of that area (Wolfe 1975), then the ancestor to *A. bicarinatum* and *A. pusillum* was likely already present in eastern North America in the early Tertiary Period. *Arceuthobium* pollen (likely *A. pusillum*) is known from as far south as Georgia from the Pleistocene Epoch (Watts 1975 and table 5.10), hence dwarf mistletoes have occupied the eastern United States in past geological times. Evidence that some *Arceuthobium* species such as *A. oxycedri* were already well differentiated by the Miocene Epoch (Stuchlik 1964) also suggests evolution of the genus in the early or mid-Tertiary Period.

Configuration of the Caribbean region with respect to North and Central America during the Tertiary Period is an area of active research. In the later Paleocene to mid-Eocene Epochs, the Greater Antilles collided with the Bahama Platform (Pindell and Barrett 1990) and connected Cuba to the North American Plate. By the Miocene Epoch, Hispaniola was contiguous with the eastern part of Cuba, and northeastward displacement was occurring along the Oriental Fault. The connection between Honduras, Jamaica, and the Greater Antilles via the Nicaraguan Rise was likely severed during the middle Cenozoic Era by subsidence. This route to Hispaniola via Central America was proposed by Rosen (1975) as a "vicariance" pathway. But given the molecular evidence, entry into Hispaniola via eastern North America and Cuba is favored over the southwest track via Honduras.

The present lack of parasitism of low-elevation pines in Honduras, Belize, Cuba, Hispaniola, and the southeast United States indicates that an ancestral species was either already adapted to high-elevation hosts or that, subsequent to speciation, the low-elevation parasites became extinct. Even if *Arceuthobium bicarinatum* were found to be genetically similar to *A. hondurense,* this relationship would not favor one migration track over the other. These species would simply be a relictual taxon derived from the originally widespread ancestor. Given the overall climatic deterioration and the accompanying extinctions that occurred in eastern North America during the Oligocene Epoch (Tiffney 1985), this ancestral mistletoe is likely now extinct. The isolated position of *A. bicarinatum* on high-elevation pines of Hispaniola suggests that it is indeed a Tertiary relict.

Morphological differences between *Arceuthobium pusillum* and *A. bicarinatum* contrast with their high level of genetic similarity. High genetic variability as measured by isozymes and increased substitution rate at the nuclear ribosomal cistron suggests that *A. pusillum* is more genotypically variable than is outwardly apparent from its morphology. Sufficient diversity of pathogenicity genes apparently exists to allow this species to parasitize *Larix laricina, Pinus strobus, P. resinosa,* and *P. banksiana,* in addition to the spruces *Picea mariana, P. glauca,* and *P. rubens*, its three principal hosts. It is hypothesized that *A. pusillum* and *A. bicarinatum* represent morphologically divergent endpoints of lineages that have been shaped by quite different evolutionary forces.

The above genetic data on the modern species suggests that their ancestor likely possessed a large store of potential genetic variation that became manifest following diversifying selection. Increased fitness was attained by separate populations exploiting different environments and hosts. The reduction in shoot height, systemic broom formation, spring flowering, and rapid fruit maturation seen in *Arceuthobium pusillum* may represent adaptations to greater winter extremes, as occurred in other eastern North American plant species.

Subgenus *Arceuthobium*

Two of the most striking results of this study of ITS variation are the extreme divergence of *Arceuthobium* *abietis-religiosae* and *A. oxycedri* from the other taxa sampled and the similarity of these species to each other. These results require a modification of concepts regarding relationships among the three New World members of subgenus *Arceuthobium* as well as their relationship to Old World members of this subgenus.

Arceuthobium americanum and *A. verticilliflorum* are more closely related to each other than to any other species, as shown by 100% bootstrap confidence for their clade. This clade has more affinity with subgenus *Vaginata* than with *A. abietis-religiosae* and *A. oxycedri*—indicating a major divergence in the verticillately branched group during their evolution in the New World. Subgenus *Vaginata* was apparently derived from an ancestor shared with *A. americanum* and *A. verticilliflorum*. The extreme divergence of *A. abietis-religiosae* and *A. oxycedri* from the remaining species also could be interpreted as evidence of separate migrations into the New World. Further molecular work would greatly benefit from inclusion of additional Old World species, such as *A. azoricum, A. chinense, A. juniperi-procerae, A. minutissimum, A. pini*, and *A. tibetense*.

Intergeneric Relationships in the Viscaceae

Nickrent and Franchina (1990) published the first phylogenetic analysis of parasitic angiosperms using small-subunit 18S rRNA sequences. They showed that *Phoradendron serotinum* and *Dendrophthora domingensis* were apparently derived from the Santalaceae (represented by a sequence of *Buckleya*). Since that time, a large number of complete 18S rDNA sequences have been determined for representatives of all families of the Santalales (Nickrent 1992 and unpublished data). Over 1,000 angiosperm *rbc*L (ribulose bisphosphate carboxylase/oxygenase, large subunit) sequences exist, and their analysis has allowed unprecedented insight into the phylogeny of higher plants (Chase and others 1993).

Sequences of nuclear 18S rDNA and chloroplast *rbc*L genes representing all Viscaceae genera were determined to test the effect of phylogeny estimation given genes derived from different subcellular compartments and to allow integration into the immense *rbc*L database. Sequences used in this analysis were determined by direct sequencing of products generated via PCR, as discussed above for ITS sequencing. All *rbc*L sequencing primers were supplied by G. Zurawski (DNAX Research Institute, Palo Alto, CA). The sequence of *Phoradendron serotinum* was determined by Morgan and Soltis (1993). Discussion of these analyses provides insight into the phylogenetic position of *Arceuthobium* within the family.

18S rDNA and *rbc*L Sequence Analysis

The 18S rDNA sequences are approximately 1,805 bp in length and can be aligned manually given information on secondary structural features (Neefs and others 1990, Nickrent and Sargent 1991). On average, 1 to 5% of the sites are variable when comparisons are made among most flowering plants; higher rates of nucleotide substitution are observed in the parasitic angiosperm families Rafflesiaceae, Hydnoraceae, Balanophoraceae, and Viscaceae (Nickrent and Starr 1994). Given this higher evolutionary rate, parsimony analysis using PAUP (Swofford 1993) was employed to study relationships among *Arceuthobium oxycedri, A. pendens, A. verticilliflorum, Dendrophthora clavata, D. domingensis, Ginalloa arnotiana, Korthalsella complanata, K. lindsayii, Notothixos leiophyllus, N. subaureus, Phoradendron californicum, P. serotinum, Viscum album*, and *V. articulatum* (see "Species Examined" for host and collection data). In addition, the sequence of *Antidaphne viscoidea* (Eremolepidaceae) and *Santalum album* were used as outgroups. These species have been shown via global analysis of representatives of the entire order to be outside the Viscaceae.

For the 18S rDNA data, parsimony analysis using the branch and bound method yielded a tree of length 627. Five clades are present (fig. 15.7A, parts A to E). Clade A consists of the 3 *Arceuthobium* species; clade B, the 2 *Notothixos* species; clade C, *Korthalsella* and *Ginalloa*; clade D, *Dendrophthora* and *Phoradendron*; and clade E, the 2 *Viscum* species.

The relationship among *Arceuthobium, Notothixos*, and *Viscum* is unresolved. But with both *rbc*L and 18S rDNA sequences and high bootstrap values, *Korthalsella* forms a clade with *Ginalloa* and *Dendrophthora* forms a clade with *Phoradendron*.

Although components of these clades are stable, their relative topology is not. For example, all possible rearrangements of these clades add only one step to the tree, hence the topology is essentially a polytomy. This result is confirmed using bootstrap analysis.

The *rbc*L gene is consistently 1,428 bp in length (476 amino acids), hence manual alignment of the sequences is straightforward. The mean percentage of sites that differ between *Santalum* (the outgroup) and the 7 species of Viscaceae is 5.85% (from 5.39% for

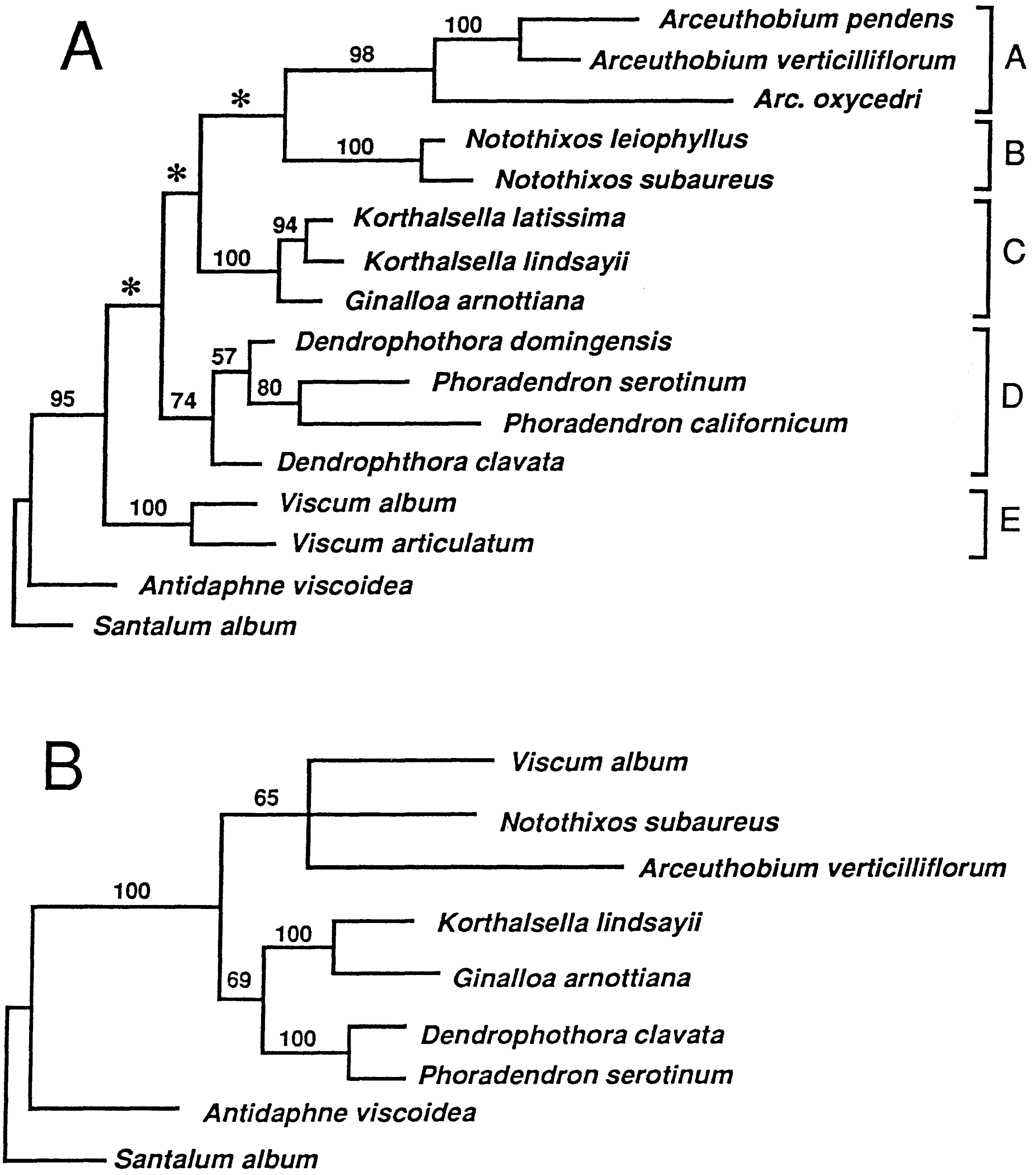

Figure 15.7 –Phylograms depicting relationships among genera of Viscaceae, rooted with *Antidaphne* (Eremolepidaceae) and *Santalum* (Santalaceae). A: single most parsimonious phylogram (627 steps) derived from anaylses of complete nuclear 18S rDNA. Nodes at asterisks are essentially unresolved, i.e. clades A-E can be rearranged at a cost of 1 step. B: strict consensus of 2 trees (305 steps) derived from analysis of chloroplast *rbc*L. Bootstrap values listed above the nodes.

Korthalsella to 7.3% for *Arceuthobium*). The accelerated evolutionary rate of *Arceuthobium* is seen by its having over twice as many substitutions as *Antidaphne* when compared to the outgroup. Figure 15.7B is the strict consensus of 2 trees of length 305 bp with bootstrap confidences indicated at the nodes. Although fewer species were sequenced for the *rbc*L gene than with 18S rDNA, several relationships are concordant. The relationship among *Arceuthobium*, *Notothixos*, and *Viscum* is unresolved; but with both *rbc*L and 18S rDNA sequences, *Korthalsella* forms a clade with *Ginalloa* and *Dendrophthora* a clade with *Phoradendron*, both with high bootstrap values. Less support exists for the positions of these major groupings as indicated by the bootstrap value of 65 and 69%. Greater resolution could possibly occur with continued sampling of *Arceuthobium, Notothixos,* and *Viscum,* but *rbc*L may not provide sufficient characters to distinguish genera within the Viscaceae. Alternative faster-rate molecules should be examined to resolve relationships among these genera.

Taken together, results of the 18S rDNA and *rbc*L analyses support the concept that *Phoradendron* and *Dendrophthora* are closely related and that *Viscum* is likely the most primitive member of the genus (Wiens and Barlow 1971). It does not appear, however, that *Korthalsella* is the sister taxon to *Arceuthobium* nor that *Ginalloa* and *Notothixos* are closely related. The topology of the phylogenetic tree suggested by Wiens and Barlow (1971) is as follows: (((*Ginalloa, Notothixos*) *Viscum*) ((*Korthalsella, Arceuthobium*) (*Phoradendron, Dendrophthora*))). This arrangement of genera, however, results in an 18S rDNA tree 29 steps longer than the minimum length, hence it is unlikely that this topology best represents the phylogeny. Chromosome size and number may not be as useful for inferring phylogenetic relationships in Viscaceae as in Loranthaceae.

The evidence for linking *Korthalsella* with *Arceuthobium* has been the reported presence of "mildly explosive" fruits in *Korthalsella.* However, these fruits may either not really be explosive (Molvray, personal communication; Nickrent, unpublished data) or may represent another case of convergence. The molecular analyses did not indicate which genus is the closest relative of *Arceuthobium.* Biogeographic evidence suggests *Notothixos* or *Viscum,* because both have centers of diversity (and presumably centers of origin) in Asia, as was also postulated for *Arceuthobium* (Hawksworth and Wiens 1972).

Wiens (personal communication) questioned whether *Arceuthobium verticilliflorum* should be segregated as a separate genus from *Arceuthobium* given its unusually large and non-explosive fruits. The 18S rDNA and ITS sequence data clearly indicate that this species is properly placed in *Arceuthobium.* The loss of explosive seed dehiscence therefore represents an evolutionary reversal.

Summary of Molecular Evidence on Phylogenetic Relationships

Morphology, life cycles, and molecular data must be integrated to best estimate the phylogeny of *Arceuthobium* species. The following conclusions can be synthesized from existing information.

The genus of Viscaceae most closely related to *Arceuthobium* remains unresolved despite analyses of 18S rDNA and *rbc*L sequences. Previous phyletic hypotheses that derived *Arceuthobium* from *Korthalsella* are not supported by molecular evidence. Division of the genus into two subgenera (*Arceuthobium* and *Vaginata*) is supported by all analyses.

From ITS sequence data, the New World members of subgenus *Arceuthobium* comprise two groups (fig. 15.6). The New World *Arceuthobium abietis-religiosae* is genetically very similar to the Old World *A. oxycedri* and included with *A. juniperi-procerae* in section *Arceuthobium* (table 15.2). *Arceuthobium abietis-religiosae* is genetically distinct from other New World members of the subgenus *Arceuthobium* (*A. americanum* and *A. verticilliflorum*) that comprise the newly proposed section *Americana* (table 15.2). This high amount of genetic differentiation is also seen between *A. oxycedri* and both *A. verticilliflorum* and *A. pendens* when the more conservative 18S rDNA sequences are compared. Further sampling of ITS variation in other Old World members of subgenus *Arceuthobium* is needed.

The reconstituted subgenus *Vaginata,* section *Vaginata* (table 15.2), includes taxa previously in section *Vaginata* (*Arceuthobium aureum, A. durangense, A. gillii, A. globosum, A. hawksworthii, A. nigrum, A. vaginata,* and *A. yecorense*) as well as several species previously placed in section *Campylopoda* (*A. divaricatum, A. oaxacanum, A. rubrum,* and *A. strictum*) and in section *Minuta* (*A. douglasii*).

Neither isozyme nor DNA analyses cluster *Arceuthobium douglasii* with *A. pusillum,* but the association of *A. douglasii* with *A. divaricatum* receives strong support from isozyme data and moderate support from ITS-1 sequence data. Section *Minuta* should be reconstituted as series *Minuta* composed of *A. douglasii* and *A. divaricatum* (table 15.2).

TABLE 15.2 – Classification of *Arceuthobium* M. Bieb. based on molecular systematics

Subgenus *Arceuthobium*

Section *Arceuthobium*

Caules cum frequentibus vel infrequentibus verticillatis ramis secundariis; surculi principales vulgo 3–16 cm alti et basi 1–10 mm diametro; flores staminati plerumque 3 meri; anthesis vernalis vel autumnalis. Type species: *A. oxycedri* (DC.) M. Bieb.

1. *A. abietis-religiosae* Heil
2. *A. juniperi-procerae* Chiovenda*
3. *A. oxycedri* (DC.) M. Bieb.

Section *Americana* Nickrent [Sec. Nov.]

Caules cum vel sine verticillatis ramis secundariis; surculi principales vulgo 6–7 cm alti et basi 1–5 mm diametro; flores staminati 3 vel 4 meri; anthesis vernalis; fructus autumno maturant plus quam 15 menses post pollinationem; parasiti praecipue in *Pinus*. Type species: *A. americanum* Nutt. ex Engelm.

4. *A. americanum* Nutt. ex Engelm.
5. *A. verticilliflorum* Engelm.

Section *Azorica* Nickrent [Sec. Nov.]

Caules cum infrequentibus verticillatis ramis secundariis; surculi principalis 7–14 cm alti et basi 5–9 mm diametro; flores staminati plerumque 4 meri; flores pistillatae verticillatis dispositae et cum bractea subtentae; in *Juniperus brevifolia* parasiticum. Type species: *A. azoricum* Hawksw. & Wiens

6. *A. azoricum* Hawksw. & Wiens*

Section *Chinense* Nickrent [Sec. Nov.]

Caules cum vel sine verticillatis ramis secundariis; surculi principales 0.5–22 cm alti et basi 1–3 mm diametro; flores staminati 3 vel 4 meri; anthesis vernalis vel autumnalis; efficiens infectus systemicos in *Keteleeria, Pinus, Picea* et *Abies*. Type species: *A. chinense* Lecomte

7. *A. chinense* Lecomte*
8. *A. minutissimum* J.D. Hooker
9. *A. pini* Hawksw. & Wiens*
10. *A. sichuanense* (H. S. Kiu) Hawksw. & Wiens*
11. *A. tibetense* H. S. Kiu & W. Ren*

Subgenus *Vaginata* Hawksw. & Wiens

Section *Penda* Nickrent [Sec. Nov.]

Caules flabellatim ramosi secundarii; surculi principales 1–22 cm alti et basi 1.5–3.5 mm diametro; flores staminati 2 vel 3 meri; anthesis mense Septembri; fructus Septembri maturant 12 menses post pollinationem; efficiens infectus systemicos in *Pinus*. Type species: *A. pendens* Hawksw. & Wiens

12. *A. guatemalense* Hawksw. & Wiens
13. *A. pendens* Hawksw. & Wiens

Section *Vaginata*

Series *Globosa* Nickrent [Ser. Nov.]

Caules flabellatim ramosi secundarii; surculi principales 10–22 cm alti et basi 3–48 mm diametro; flores staminati 3 vel 4 meri; tempora anthesis et fructificandi variabilia vel continua; parasiti praecipue in *Pinus*. Type species: *A. globosum* Hawksw. & Wiens

14. *A. aureum* Hawksw. & Wiens subsp. *aureum*†
15. *A. aureum* Hawksw. & Wiens subsp. *petersonii* Hawksw. & Wiens
16. *A. globosum* Hawksw. & Wiens subsp. *globosum*
17. *A. globosum* Hawksw. & Wiens subsp. *grandicaule* Hawksw. & Wiens

TABLE 15.2 – Classification of *Arceuthobium* M. Bieb. based on molecular systematics (continued)

Subgenus *Vaginata* Hawksw. & Wiens (continued)

Section *Vaginata* (continued)

Series *Rubra* Hawksw. & Wiens

18. *A. gillii* Hawksw. & Wiens
19. *A. nigrum* (Hawksw. & Wiens) Hawksw. & Wiens
20. *A. oaxacanum* Hawksw. & Wiens*
21. *A. rubrum* Hawksw. & Wiens

Series *Vaginata*

Syn. Series *Stricta* Hawksw. & Wiens (Brittonia 22:266, 1970)

22. *A. durangense* (Hawksw. & Wiens) Hawksw. & Wiens
23. *A. hawksworthii* Wiens & C. G. Shaw III†
24. *A. strictum* Hawksw. & Wiens
25. *A. vaginatum* (Willd.) Presl subsp. *vaginatum*
26. *A. vaginatum* (Willd.) Presl subsp. *cryptopodum* (Engelm.) Hawksw. & Wiens
27. *A. yecorense* Hawksw. & Wiens

Series *Minuta* Hawksw. & Wiens

28. *A. divaricatum* Engelm.
29. *A. douglasii* Engelm.

Section *Pusilla* Nickrent [Sec. Nov.]

Caules flabellatim ramosi secundarii si adsunt; surculi principales 1-21 cm alti et basi 1-9 mm diametro; flores staminati vulgo 3 meri, aliquando 2 vel 4 meri; lobi perianthii cum rubra interna superficie; anthesis vernalis vel autumnalis. Type species: *A. pusillum* Peck

30. *A. bicarinatum* Urban
31. *A. hondurense* Hawksw. & Wiens*
32. *A. pusillum* Peck

Section *Campylopoda* Hawksw. & Wiens

33a. *A. abietinum* Engelm. ex Munz f. sp. *concoloris*
33b. *A. abietinum* Engelm. ex Munz f. sp. *magnificae*
34. *A. apachecum* Hawksw. & Wiens
35. *A. blumeri* A. Nelson
36. *A. californicum* Hawksw. & Wiens
37. *A. campylopodum* Engelm.
38. *A. cyanocarpum* (A. Nelson ex Rydberg) Coulter & Nelson
39. *A. laricis* (Piper) St. John
40. *A. littorum* Hawksw., Wiens & Nickrent
41. *A. microcarpum* (Engelm.) Hawksw. & Wiens
42. *A. monticola* Hawksw., Wiens & Nickrent
43. *A. occidentale* Engelm.
44. *A. siskiyouense* Hawksw., Wiens & Nickrent
45. *A. tsugense* (Rosendahl) G. N. Jones subsp. *tsugense*
46. *A. tsugense* (Rosendahl) G. N. Jones subsp. *mertensianae* Hawksw. & Nickrent

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*Taxa not examined using molecular methods, hence placement is tentative.

†Recently obtained ITS and 5.8S rDNA sequences indicate that *A. aureum* subsp. *aureum* is closely related to *A. globosum* and that *A. hawksworthii* is related to *A. vaginatum*.

Arceuthobium pusillum is genetically very similar to *A. bicarinatum* but has developed a large number of morphological and physiological apomorphies such as reduced shoot size and systemic broom formation. These two species and *A. hondurense* are the likely survivors of an ancient lineage whose most recent common ancestor became extinct during the Tertiary Period. These species are recognized as members of section *Pusilla* (table 15.2).

Two additional segregates, *Arceuthobium pendens* and *A. guatemalense,* from the former section *Campylopoda* are deserving of placement in the new section *Penda.* These species are narrow endemics and are also likely relicts of a common Tertiary ancestor.

The remaining section *Campylopoda* now comprises 13 species mainly of the United States and with a high degree of morphological and genetic similarity. The reconstituted section includes *Arceuthobium abietinum, A. apachecum, A. blumeri, A. californicum, A. campylopodum, A. cyanocarpum, A. laricis, A. littorum, A. microcarpum, A. monticola, A. occidentale, A. siskiyouense,* and *A. tsugense.*

The observations made by Sytsma and Smith (1992) regarding concordance or discordance between morphological and molecular divergence in *Clarkia* and *Fuchsia* are applicable to dwarf mistletoes. Basically, four syndromes were described: low morphological and molecular divergence, high morphological and high DNA divergence, low morphological but high DNA divergence, and high morphological but low DNA divergence. *Clarkia ligulata* and *C. biloba* are given as examples for the first syndrome. In *Arceuthobium,* a similar situation occurs among members of section *Campylopoda.* The second syndrome was illustrated by comparing sections *Myxocarpa* and *Eucharidum* of *Clarkia* or the Old World section *Skinnera* with New World sections. In *Arceuthobium,* the most morphological divergence is seen between representatives of subgenera *Arceuthobium* and *Vaginata.* This distinction is strongly supported by molecular evidence. The third syndrome can be demonstrated by comparing *C. rostrata* with *C. lewisii* and *C. cylindrica.* In dwarf mistletoes, a low amount of morphological divergence is seen between *A. pendens* and *A. guatemalense* as compared with species in section *Campylopoda* (however, DNA evidence indicates these two groups are not closely related). Finally, the fourth syndrome can be seen in comparisons of *Clarkia rostrata* and *C. epilobioides* which differ in breeding system and floral morphology but are extremely similar genetically. Similarly, *Heterogaura heterandra* and *C. dudleyana* exhibit this type of discordance. For *Arceuthobium,* this syndrome is best shown by *A. pusillum* and *A. bicarinatum* or by *A. douglasii* and *A. divaricatum.*

The dwarf mistletoes continue to present a challenge to the systematist, as do all parasitic plants that follow reductional and/or convergent evolutionary paths. These plants provide the ultimate test of our abilities to reconstruct phylogenies, therefore alternate data sets for other genes must be assembled to confirm or support proposed relationships.

Formal Taxonomy

Generic Description

Arceuthobium M. Bieb. Dwarf Mistletoe

Razoumofskya Hoffman, Hortus Mosquensis, unpaged, 1808. *Arceuthobium* M. Bieb. Flora Taurico-Caucasica 3(IV) Supplement, p. 629, 1819. Nom. Cons. 2091. [Orthographic variants listed by Farr and others (1979) are: *Arcenthobium* Presl (1825), *Arceuthobion* Sprengel (1826), *Arceutholobium* Furnrohr (1850), *Arceutobium* Grenier & Gordon (1851), *Razumowskia* Presl (1825) and *Razoumoeskya* Jussieu (1826).]

Herbs or shrubs from 0.5 cm to approximately 70 cm high; parasitic on Pinaceae and Cupressaceae; plants glabrous, variously colored from greenish yellow to orange, reddish, or black; dioecious; stems with variant (anomalous) patterns of secondary growth; leaves reduced to minute, opposed, connate scales; internodes angled (at least when young); flowers generally decussate or rarely whorled on young shoots, 2–4 mm across; staminate flowers with a central nectary, perianth segments usually 3–4 (rarely 2 and up to 7) bearing a sessile, uniloculate, circular anther on each perianth segment; pollen spherical with 6 alternating spiny and smooth sections; pistillate flower manifestly epigynous with 1 style, perianth segments persistent, adnate to ovary, 2-merous; ovary 1-chambered; fruit an ovoid berry, 1-seeded, mucilaginous and bicolored (distal and basal portions of different shades), explosive at maturity; seeds without true integuments, usually 3–5 mm long, ovate-lanceolate, containing 1 (rarely 2) distal, cylindrical embryo, with copious endosperm. Basic chromosome number $n = 14$.

A genus of 42 species, mostly in the United States and Mexico; 8 species in the Old World.

Type species: *Arceuthobium oxycedri* (DC.) M. Bieb.

Artificial Key to the New World Species of *Arceuthobium*

1. Distributed in Mexico, Central America, or Hispaniola
  2. Hispaniola or Honduras
    3. Hispaniola; parasites of *Pinus occidentalis*............6. *A. bicarinatum*
    3. Honduras; parasites of *Pinus oocarpa*............18. *A. hondurense*
  2. Mexico, Guatemala, or Belize
    4. Parasites of *Abies* or *Pseudotsuga*
      5. Shoots 1–3 cm high; parasites of *Pseudotsuga*............12. *A. douglasii*
      5. Shoots more than 5 cm high; parasites of *Abies*
        6. Shoots less than 10 cm high, branching not verticillate, greenish; Chihuahua............1. *A. abietinum*
        6. Shoots 10–20 cm high, some branching verticillate, yellow; central Mexico............2. *A. abietis-religiosae*
    4. Parasites of *Pinus*
      7. Baja California
        8. Shoots olive green, ca. 1–2 mm in diameter; parasites of pinyons............11. *A. divaricatum*
        8. Shoots yellowish, ca. 2–4 mm in diameter; parasites of *Pinus jeffreyi* or *P. coulteri*............9. *A. campylopodum*
      7. Mainland Mexico or Central America
        9. Parasites of *Pinus* subgenus *Haploxylon* (pinyons and white pines)
          10. Parasites of pinyons............26. *A. pendens*
          10. Parasites of white or soft pines

11. Shoots greenish purple to purple; parasites of *Pinus ayacahuite* var. *ayacahuite*; Guatemala or southern Mexico .... 16. *A. guatemalense*
11. Shoots yellow or gray; parasites of *Pinus strobiformis* or *P. ayacahuite* var. *brachyptera;* northern Mexico
    12. Shoots yellowish, usually less than 4 cm high; northern Coahuila .... 4. *A. apachecum*
    12. Shoots gray, usually more than 6 cm high; Chihuahua, Durango, or Nuevo León .... 7. *A. blumeri*

9. Parasites of *Pinus* subgenus *Diploxylon* (yellow pines)
  13. Shoots dark, usually some shade of black, reddish (or dull brown when dried)
    14. Male and female plants similarly branched (little sexual dimorphism); fruits not glaucous
      15. Shoots usually more than 10 cm high and more than 1 cm diameter at base; fruits 4-5 mm long, not shiny .... 32a. *A. vaginatum* subsp. *vaginatum*
      15. Shoots usually less than 10 cm high and less than 1 cm diameter at base; fruits ca. 3 mm long, shiny .... 28. *A. rubrum*
    14. Male and female plants dissimilarly branched (sexually dimorphic); fruits markedly glaucous .... 23. *A. nigrum*
  13. Shoots yellow, brown, gray, or red
    16. Staminate flowers verticillate; spikes deciduous; mature fruits more than 10 mm long .... 33. *A. verticilliflorum*
    16. Staminate flowers not verticillate; spikes deciduous; mature fruits less than 6 mm long
      17. Plants of northern Mexico
        18. Male and female plants dissimilarly branched (sexually dimorphic)
          19. Male plants essentially non-branched and female plants densely branched; fruits not glaucous .... 30. *A. strictum*
          19. Male plants with very open branches and female plants densely branched ; fruits markedly glaucous .... 14. *A. gillii*
        18. Male and female plants similarly branched (little sexual dimorphism)
          20. Shoots yellow or yellow-brown
            21. Shoots bright yellow, in globose clusters, usually more than 10 cm high .... 15a. *A. globosum* subsp. *globosum*
            21. Shoots yellow or brown, not in globose clusters, usually less than 10 cm high .... 34. *A. yecorense*
          20. Shoots some shade of orange
            22. Shoots dark orange, usually more than 20 cm high; mature fruit 7 mm long; Durango or southward .... 13. *A. durangense*
            22. Shoots yellow-orange, usually less than 20 cm high; mature fruit 5 mm long; Chihuahua, Sonora, or Coahuila .... 32b. *A. vaginatum* subsp. *cryptopodum*
      17. Plants of southern Mexico (Chiapas and Oaxaca) or Central America
        23. Shoots reddish; Oaxaca .... 24. *A. oaxacanum*

23\. Shoots dark greenish yellow or orange; Oaxaca, Chiapas, Guatemala, or Belize

24\. Shoots yellow, often more than 2 cm in diameter at base; elevations above 2,700 m ....15b. *A. globosum* subsp. *grandicaule*

24\. Shoots dark, dull greenish yellow or yellow-orange, usually less than 2 cm in diameter at base; elevations below 2,400 m

25\. Shoots dark, greenish yellow; parasites of *Pinus caribaea* or *P. oocarpa*; elevations above 500 m; Belize.....17. *A. hawksworthii*

25\. Shoots yellow-orange; parasites of pine other than *P. caribaea* (sometimes on *P. oocarpa*); elevations 900–2,400 m; Oaxaca, Chiapas, or Guatemala..5. *A. aureum*

1\. Distributed in the United States or Canada

26\. Parasites principally of *Pinus*

27\. Parasites of *Pinus* subgenus *Haploxylon* (pinyons and white pines)

28\. Parasites of pinyons..11. *A. divaricatum*

28\. Parasites of white pines

29\. Parasites of *Pinus strobiformis*

30\. Shoots usually less than 4 cm high, yellow; southern Arizona or southern New Mexico ....4. *A. apachecum*

30\. Shoots usually more than 6 cm high, gray; Huachuca Mountains of Arizona...7. *A. blumeri*

29\. Parasites of white pines other than *Pinus strobiformis*

31\. Parasites of *Pinus aristata*; Arizona ....21. *A. microcarpum*

31\. Parasites of pines other than *Pinus aristata* or if parasite of *Pinus aristata* then not Arizona

32\. Shoots usually less than 6 cm high, densely clustered around the host branch; parasites of *Pinus flexilis, P. albicaulis, P. aristata*, or *P. longaeva*..10. *A. cyanocarpum*

32\. Shoots usually more than 6 cm high, not densely clustered around the host branch; parasites of *Pinus monticola* or *P. lambertiana*

33\. Shoots dark brown; parasites of *Pinus monticola*; southwestern Oregon or northwestern California ....22. *A. monticola*

33\. Shoots yellow to green; parasites of *Pinus lambertiana*; California ....8. *A. californicum*

27\. Parasites of *Pinus* subgenus *Diploxylon* (yellow pines)

34\. Shoots branching in whorls; parasites principally of *Pinus contorta* or *P. banksiana*..3. *A. americanum*

34\. Shoots (at least some) branching flabellately; parasites principally of pines other than *Pinus contorta* and *P. banksiana*

35\. Arizona, Utah, or eastward

36\. Fruits glaucous; male plants much more openly branched than female plants; parasites of *Pinus leiophylla* var. *chihuahuana*..14. *A. gillii*

        36. Fruits glabrous; male and female plants branch in similar manner; parasites of *Pinus ponderosa* var. *scopulorum, P. arizonica,* and *P. engelmannii* ....32b. *A. vaginatum* subsp. *cryptopodum*
    35. Pacific Coast States, Nevada, Idaho, or British Columbia
        37. Coastal areas (within ca. 10 km of the Pacific Ocean)
            38. Shoots usually less than 10 cm high; staminate flowers mostly 3-merous; parasites of *Pinus contorta* var. *contorta*; Orcas Island, Washington or British Columbia ....31a. *A. tsugense* subsp. *tsugense* (shore pine race)
            38. Shoots usually more than 10 cm high; staminate flowers mostly 4-merous; parasites of *Pinus radiata* or *P. muricata*; California ....20. *A. littorum*
        37. Inland areas
            39. Plants consistently forming witches' brooms; mature fruits ca. 6 mm long; shoots more than 3 mm in diameter at base; parasites principally of *Pinus ponderosa* var. *ponderosa, P. jeffreyi,* or *P. coulteri*; California, Oregon, Washington, Idaho, or Nevada ....9. *A. campylopodum*
            39. Plants not forming witches' brooms; mature fruits ca. 4 mm long; shoots less than 3 mm diameter at base; parasites principally of *Pinus sabiniana* or *P. attenuata*; California or southwestern Oregon
                40. Anthesis from late September to November; parasites principally of *Pinus sabiniana*; foothills surrounding Central Valley of California ....25. *A. occidentale*
                40. Anthesis in August; parasites of *Pinus attenuata*; southwestern Oregon or northwestern California ....29. *A. siskiyouense*

26. Parasites principally of *Tsuga, Larix, Pseudotsuga, Abies,* or *Picea*
    41. Parasites of *Tsuga, Larix,* or *Pseudotsuga*
        42. Shoots usually less than 4 cm high; parasites of *Pseudotsuga* ....12. *A. douglasii*
        42. Shoots usually more than 5 cm high; parasites of *Larix* or *Tsuga*
            43. Parasites principally of *Larix* ....19. *A. laricis*
            43. Parasites principally of *Tsuga*
                44. Parasites of *Tsuga heterophylla*; California to Alaska ....31a. *A. tsugense* subsp. *tsugense* (western hemlock race)
                44. Parasites of *Tsuga mertensiana*; California to Idaho and British Columbia
                    45. Host associated with infected *Larix occidentalis*; northern Idaho ....19. *A. laricis*
                    45. Host not associated with infected *Larix occidentalis*; central Sierra Nevada of California to southern British Columbia ....31b. *A. tsugense* subsp. *mertensianae*
    41. Parasites of *Abies* or *Picea*
        46. Parasites of *Abies*
            47. Shoots usually more than 10 cm high, yellowish; staminate buds same color as the subtending bracts; host not associated with infected *Tsuga*; Arizona, southern Utah, Nevada, California, Oregon, or Washington east of the Cascade Crest ....1. *A. abietinum*
            47. Shoots usually less than 6 cm high, green to purplish; staminate buds conspicuously lighter than the subtending purplish bracts; host associated with infected *Tsuga*; Oregon west of Cascade Crest to Alaska along Pacific Coast

- 48. Host associated with infected *Tsuga heterophylla* .... 31a. *A. tsugense* subsp. *tsugense* (western hemlock race)
- 48. Host associated with infected *Tsuga mertensiana* .... 31b. *A. tsugense* subsp. *mertensianae*

46. Parasites of *Picea*
- 49. Shoots less than 2 cm high; parasites of *Picea mariana, P. glauca*, or *P. rubens*; Saskatchewan and Great Lakes region eastward to New Jersey and Newfoundland .... 27. *A. pusillum*
- 49. Shoots usually more than 5 cm high; parasites on *Picea engelmannii* or *P. pungens*; Arizona or southern New Mexico .... 21. *A. microcarpum*

Artificial Key to the Old World Species of *Arceuthobium*

1. Parasites of *Juniperus*
    2. Shoots 5–9 mm in diameter at base; staminate flowers predominately 4-merous; parasites of *Juniperus brevifolia*; Azores .... 35. *A. azoricum*
    2. Shoots 1–3 mm in diameter at base; staminate flowers mostly 3-merous; parasites of junipers other than *J. brevifolia*; Africa, southern Europe, or Asia
        3. Branching rarely whorled (less then 5%); flowering and seed dispersal March to October (likely produces several fruit crops annually); shoots yellow-green; parasites of *Juniperus procera*; Ethiopia or Kenya .... 37. *A. juniperi-procerae*
        3. Branching commonly whorled (at least 30%); flowering and seed dispersal only September to November (produces 1 fruit crop annually); shoots green; parasites of junipers other than *J. procera*; Spain and Morocco eastward to the Himalayas of southwestern China .... 39. *A. oxycedri*
1. Parasites of *Abies, Keteleeria, Picea*, or *Pinus*
    4. Parasites of *Pinus*
        5. Shoots 0.5–1.0 cm high; parasites of *Pinus wallichiana*; Himalayas from Pakistan to Bhutan .... 38. *A. minutissimum*
        5. Shoots 5–20 cm high; parasites of *Pinus densata* or *P. yunnanensis*; Xizang, Yünnan, or Sichuan .... 40. *A. pini*
    4. Parasites of *Abies, Keteleeria*, or *Picea*
        6. Staminate flowers mostly 4-merous; parasites of *Keteleeria*; Yünnan or Sichuan .... 36. *A. chinense*
        6. Staminate flowers mostly 3-merous; parasites of *Abies* or *Picea*
            7. Shoots 1–2 cm high; parasites of *Abies*; Xizang .... 42. *A. tibetense*
            7. Shoots 2–6 cm high; parasites of *Picea*; Xizang, Sichuan, or Bhutan .... 41. *A. sichuanense*

New World Taxa

Arceuthobium abietinum
Fir Dwarf Mistletoe

1. *A. abietinum* Engelmann ex Munz, Manual Southern California Botany: 114, 1935. TYPE COLLECTION : CALIFORNIA: Sierra County: Sierra Valley, on *Abies concolor*, *Lemmon* in 1875 (Lectotype MO! Isotype GH). *A. abietinum* Engelm. in Gray, Proceedings American Academy of Arts and Sciences 8: 401, 1872, *nomen nudum*. *A. douglasii* Engelm. var. *abietinum* Engelm., in Watson, Botany of California 2: 107, 1880. *A. occidentale* Engelm. var. *abietinum* Engelm. in Watson, Botany of California 2: 107, 1880. *Razoumofskya douglasii* (Engelm.) Kuntze var. *abietina* (Engelm.) Howell, Flora Northwest America 1: 609, 1902. *Razoumofskya douglasii* (Engelm.) Kuntze var. *abietina* (Engelm.) Piper, Contributions U.S. National Herbarium 11: 223, 1906. *Razoumofskya abietina* (Engelm.) Tubeuf forma *parvula* Tubeuf. Naturwissenschaftliche Zeitschrift für Forst- und Landwirtschaft 17: 219, 1919, *nomen nudum*. *Razoumofskya abietina* (Engelm.) Tubeuf forma *magna* Tubeuf, loc. cit: 220, *nomen nudum*. *Razoumofskya abietina* (Engelm.) Abrams, Illustrated Flora Pacific Coast States 1: 530, 1923. *A. campylopodum* Engelm. forma *abietinum* (Engelm.) Gill, Transactions Connecticut Academy Arts and Sciences 32: 195, 1935. *A. abietinum* (Engelm.) Hawksworth & Wiens, Brittonia 22: 68, 1970.

Description: Mean shoot height ca. 8 (max. 22) cm. Shoots yellow green to yellow, flabellately branched (fig. 16.1). Basal diameter of dominant shoots 1.5–6.0 (mean 2) mm. Third internode 4–23 (mean 14) mm long, 1.5–4.0 mm (mean 2) mm wide; length/width ratio ca. 7:1 to 9:1. Staminate flowers ca. 2.5 mm across; perianth 3-merous, sometimes 4-merous, apex acute; same color as shoots; segments ca. 1.2 mm long, 1.0 mm wide. Mean anther diameter 0.4 mm, centered 0.7 mm from tip of segment. Pollen polar diameter 18–23 (mean 20) µm; equatorial diameter 19–25 (mean 22) µm; polar/equatorial diameter ratio 1:1.07; spine height ca. 1.5–2.0 × wall thickness (7 collections). Mature fruit ca. 4 × 2 mm; proximal portion ca. 2.5 mm long. Seeds 2.8 × 1.2 mm. $n = 14$.

Figure 16.1 –*Arceuthobium abietinum*, pistillate plant with maturing fruits, on *Abies grandis*.

Phenology: Meiosis in July. Anthesis usually August–September. Fruits mature in September or October of the year following pollination; maturation period averages 13–14 months.

Hosts: *Abies* spp.

Discussion: Parmeter and Scharpf (1963) first reported that, on the basis of field evidence and inoculation studies, the dwarf mistletoe on *Abies concolor* will not infect associated *A. magnifica*. Conversely, the parasite of *A. magnifica* will not parasitize associated *A. concolor*. Our observations in several mixed fir stands in the Sierra Nevada confirm Parmeter and Scharpf's conclusions. However, we have been unable to find morphological differences between the two mistletoes, and they are also similar phenologically. In the same locality, however, seed dispersal begins about 1 week earlier for the plants infecting *A. magnifica* (Scharpf and Parmeter 1967). Greenham and Leonard (1965) studied the amino acids of the two dwarf mistletoes and their respective hosts, and they concluded that amino acid composition probably could not explain the restriction of the two dwarf mistletoes to their respective hosts.

Munz and Keck (1959) report that there are up to 7 perianth segments in this species, but this is in error.

Because the host affinities of these two dwarf mistletoes are distinct, and inasmuch as they are of considerable importance in forest management, we have designated them as *formae speciales* in accordance with recommendation 4B of the International Code of Botanical Nomenclature.

Key to the *formae speciales*

1. Parasitic principally on *Abies concolor* or *A. grandis*; known in two areas in Chihuahua on *A. durangensis*. The primary distribution is from southern Washington southward through the Cascade and southern Coast Ranges in Oregon, and the North Coast and Cascade Ranges, Sierra Nevada to southern California. Isolated populations occur in southern Utah,

northern and southern Arizona, and Chihuahua, Mexico ....1a. *A. abietinum* f. sp. *concoloris.*

1. Parasitic principally on *Abies magnifica* from southwestern Oregon (Josephine County) to the southern Sierra Nevada, California ....1b. *A. abietinum* f. sp. *magnificae.*

Arceuthobium abietinum f. sp. *concoloris* White Fir Dwarf Mistletoe

1a. *A. abietinum* Engelmann ex Munz f. sp. *concoloris* Hawksworth & Wiens, Brittonia 22: 267, 1970.

Description: Mean shoot height ca. 10 (max. 22) cm. Basal diameter of dominant shoots 1.5–6.0 (mean 2) mm. Third internode 4–23 (mean 13.3 ± 3.8) mm long, 1.5–4.0 (mean 2.0) mm wide (15 collections), length/width ratio 6.7:1. Pollen polar diameter 18–23 (mean 20) µm; equatorial diameter 19–25 (mean 22) µm; polar/equatorial diameter ratio 1:1.07; spine height (ca. 1.5 µm) slightly greater than the wall thickness (ca. 1.1 µm) (5 collections). $n = 14$.

Phenology: Peak anthesis usually from mid-July to mid-August, with extremes from early July to late September (fig. 16.2). Fruits usually mature in September or October, with extremes from late August to early November; maturation period averages 13–14 months. Seeds germinate from February through June (Scharpf and Parmeter 1967).

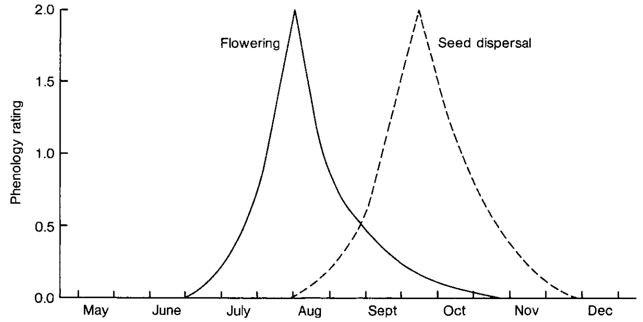

Figure 16.2 –Phenology of flowering and seed dispersal of *Arceuthobium abietinum* f. sp. *concoloris* (based on 112 observations).

Hosts: The principal hosts of this dwarf mistletoe are *Abies concolor, A. grandis*, and *A. durangensis. Abies concolor* var. *concolor* (Nevada, Utah, and Arizona) and var. *lowiana* (California) are about equally susceptible, although the dwarf mistletoe is much more widely distributed on the latter. The rare Brewer spruce, *Picea breweriana*, is associated with infected *Abies concolor* on Flat Top Mountain, west of Grants Pass, Oregon, and *Arceuthobium abietinum* produces heavy infections on Brewer spruce in this area (Hawksworth and others 1967). On the North Rim of Grand Canyon, Arizona, *Abies lasiocarpa* is occasionally parasitized where this tree grows in association with infected *A. concolor. Abies amabilis* is a rare host of this dwarf mistletoe; the only known instance of this host–parasite combination is in the vicinity of Crater Lake, Oregon. *Pinus lambertiana, P. monticola, P. ayacahuite* var. *brachyptera*, and *P. contorta* var. *murrayana* are rare hosts for *Arceuthobium abietinum* f. sp. *concoloris.*

Distribution: United States (Washington, Oregon, California, Nevada, Utah, and Arizona) (fig. 16.3), and Mexico (Chihuahua) (fig. 16.4). *Arceuthobium abietinum* f. sp. *concoloris* is widely distributed from southern Washington (Skamania, Wenatchee, and Klickitat Counties) south through the Cascade Range and Sierra Nevada to the San Bernardino Mountains of southern California. Reports of the dwarf mistletoe on Big Pine Mountain and Reyes Peak in Santa Barbara County have not been confirmed (Smith 1976). A single, probably relictual, population is known in the Willamette Valley of Oregon (at Helmick State Park, Polk County, on *Abies grandis*). It also occurs along the coast ranges from Mendocino County, California, to Curry County, Oregon. Three isolated populations are known in Nevada (Spring, Sheep, and Groom Mountains [= Bald Mountain of Beatley 1976]) and two in southwestern Utah (northwestern Kane County). The parasite has long been known in the Grand Canyon area of northern Arizona, and small populations have since been found some 400 km to the south in the Chiricahua Mountains (Cochise County) (Mathiasen 1976) and in the Santa Catalina Mountains (Pima County) (Mathiasen and Jones 1983). This dwarf mistletoe was recently found on *A. durangensis* in two localities in Chihuahua—near Tomochic in the central part of the state (Hawksworth and Wiens 1989) and at Cerro Mohinora in southern Chihuahua. The latter area is about 1,000 km south of the previously known southern limits of the taxon in southern Arizona.

This dwarf mistletoe occurs on *Abies concolor* throughout most of its range in California, Nevada, Arizona, and southern Oregon. *Abies grandis* is the principal host in central Oregon, southern Washington, and in the coastal ranges of Oregon and California. In the Siskiyou Mountains, Del Norte County, California, just south of the Oregon boundary, we found the parasite commonly infecting trees that exhibit characteristics of both *Abies concolor* and *A. grandis* in mixed stands, although *A. grandis* is not considered to be present in this area (Griffin and Critchfield 1972). This tree is an apparently undescribed taxon (R. S. Hunt, personal communication).

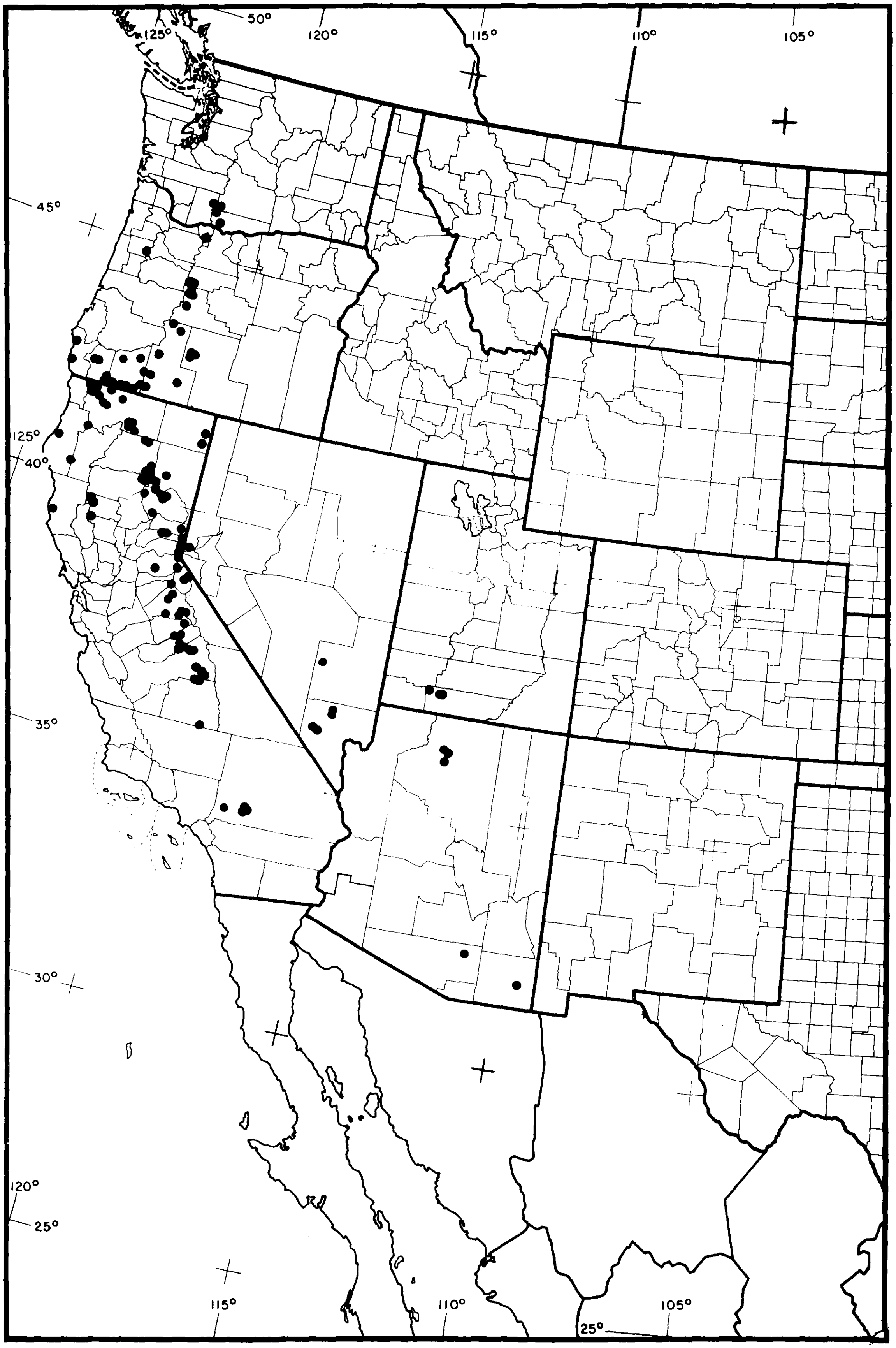

Figure 16.3 –Distribution of *Arceuthobium abietinum* f. sp. *concoloris* in the United States.

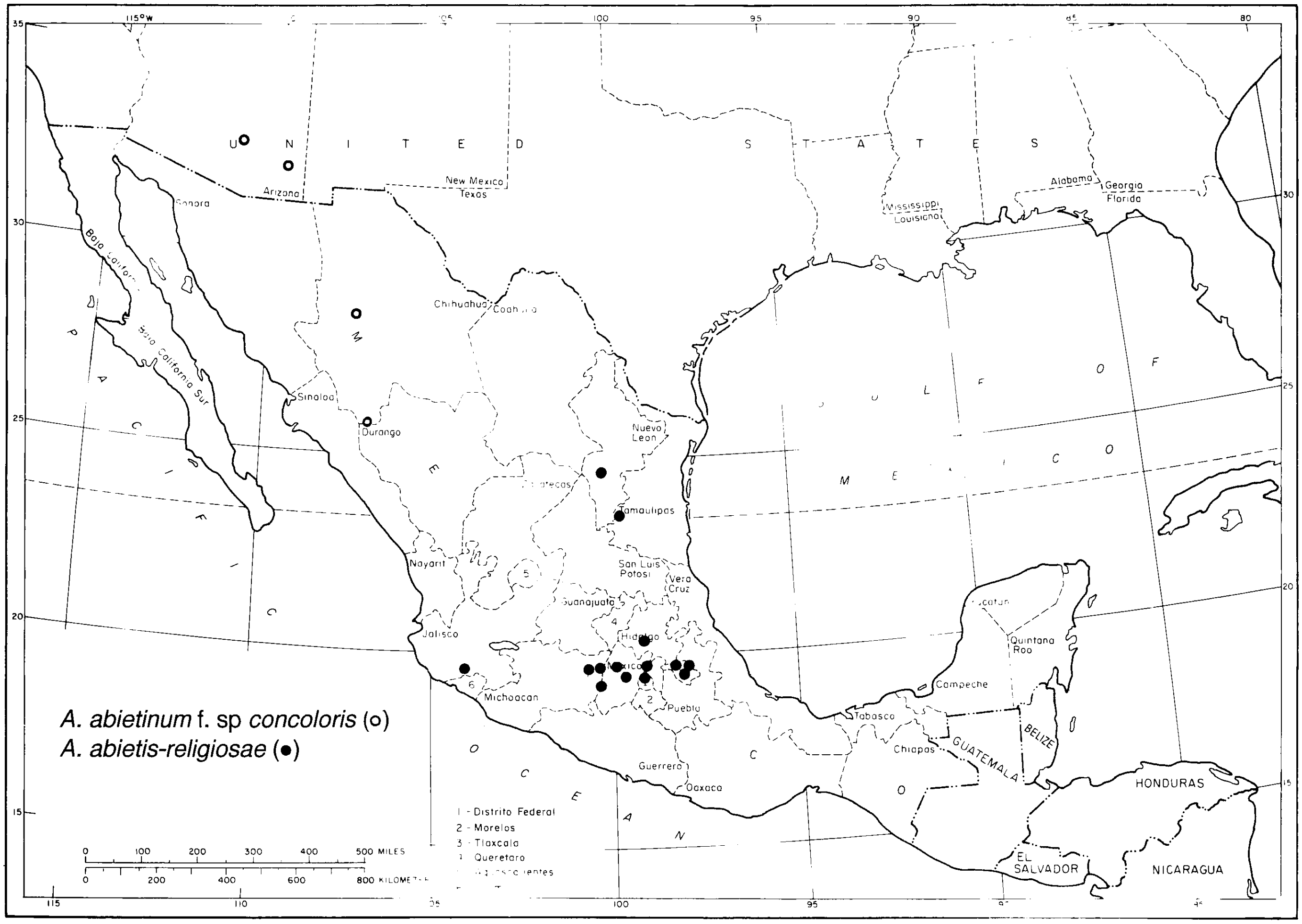

Figure 16.4 –Distribution of *Arceuthobium abietinum* f. sp. *concoloris* in Mexico and adjacent southeastern Arizona, and *A. abietis-religiosae* in Mexico.

Several localities for *Arceuthobium abietinum* recorded by Gill (1935) in other parts of the western United States have since been found to be based on the occasional parasitism of *Abies* by other species of *Arceuthobium*:

- Arizona: San Francisco Mountains (*Arceuthobium douglasii* on *Abies* sp.); Pinaleno (Graham) Mountains (*Arceuthobium douglasii* on *Abies lasiocarpa* var. *arizonica*).
- New Mexico: Mogollon Mountains (*Arceuthobium douglasii* on *Abies lasiocarpa* var. *arizonica*).
- Oregon: McKenzie Pass (*Arceuthobium tsugense* subsp. *mertensianae* on *Abies lasiocarpa*);
- Utah: Spring Lake and Charles Peak (*Arceuthobium douglasii* on *Abies concolor*).
- Washington: Longmire and Ellensburg (*Arceuthobium tsugense* subsp. *tsugense* on *Abies amabilis*).

Arceuthobium abietinum f. sp. *concoloris* occurs from near sea level along the coast of northern California and southern Oregon to over 2,650 m in the Spring (Charleston) Mountains of southern Nevada.

Discussion: In the Northwest, two other species of *Arceuthobium* occur on *Abies*: (1) *Arceuthobium tsugense* on *Abies amabilis*, *A. lasiocarpa*, and *A. grandis*, and (2) *Arceuthobium laricis* on *Abies lasiocarpa* and *A. grandis*. However, insofar as we are aware, neither of these dwarf mistletoes is sympatric with *Arceuthobium abietinum*, although *A. tsugense* occurs within about 0.5 km of *A. abietinum* on the east side of McKenzie Pass in central Oregon. *Arceuthobium laricis* and *A. tsugense* rarely infect pure stands of *Abies*, but they may parasitize *Abies* secondarily in stands where the principal hosts of these dwarf mistletoes are parasitized (for example *Larix* for *A. laricis* and *Tsuga* for *A. tsugense*). *Arceuthobium laricis* is readily distinguished from *A. abietinum* by its shorter, darker shoots (4 cm versus 10 cm) and shorter (in summer) staminate spikes (2–3 mm versus 5–7 mm). *Arceuthobium tsugense* differs from *A. abietinum* by its shorter (7 cm), green to purple shoots compared with the longer (10 cm), yellowish shoots of *A. abietinum.*

Dying branches (flagging) are one of the most conspicuous field symptoms of *Abies concolor* infected by dwarf mistletoe, particularly in California. Scharpf (1969c) has shown that flagging of dwarf mistletoe-infected fir branches is typically associated with the fungus *Cytospora abietis.*

Arceuthobium abietinum f. sp. magnificae Red Fir Dwarf Mistletoe

1b. *A. abietinum* Engelmann ex Munz f. sp. *magnificae* Hawksworth & Wiens, Brittonia 22: 268, 1970.

Description: Mean shoot height ca. 6 (max. 12) cm. Basal diameter of dominant shoots 1.5–3.0 (mean 2) mm. Third internode 10–22 (mean 15.0 ± 3.1) mm long, 1.5–2.0 (mean 1.7) mm wide (5 collections), length/width ratio 8.8:1. Pollen polar diameter 19–23 (mean 21) µm; equatorial diameter 19–24 (mean 22) µm; polar/equatorial diameter ratio 1:1.07; spine height (ca. 2 µm) approximately twice the wall thickness (ca. 1 µm) (2 collections). $n = 14$.

Phenology: Peak anthesis usually from early August to mid-September, with extremes from mid-July to late September (fig. 16.5). Fruits mature from early September to late October; maturation period averages 13–14 months.

Hosts: *Abies magnifica*

Distribution: United States (Oregon and California) (fig. 16.6). *Arceuthobium abietinum* f. sp. *magnificae* is distributed from Josephine County in southwestern Oregon south to Kern County in the southern Sierra Nevada in California. The reports of it on *Abies procera* in southern Oregon are probably the result of confusion with *Arceuthobium tsugense,* which occasionally parasitizes *Abies procera* in this region. We have not confirmed the presence of any populations of this dwarf mistletoe in Oregon outside of Josephine County, and we are unable to establish the basis for the reports of it in the vicinity of Crater Lake (Hawksworth and Wiens 1972, Weir 1917). It may occur on *Abies magnifica* in Nevada in the vicinity of Lake Tahoe (Kartesz 1988), and Guyon and Munson (1991) record it within 3 km of the Nevada border in Sierra County, California. Elevational range is 1,500–2,400 m.

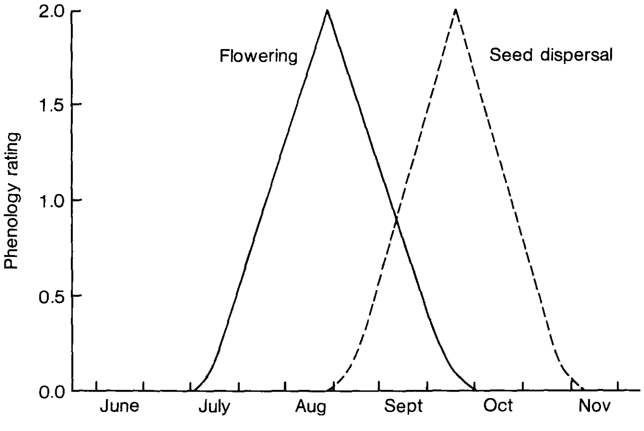

Figure 16.5 –Phenology of flowering and seed dispersal of *Arceuthobium abietinum* f. sp. *magnificae* (based on 58 observations).

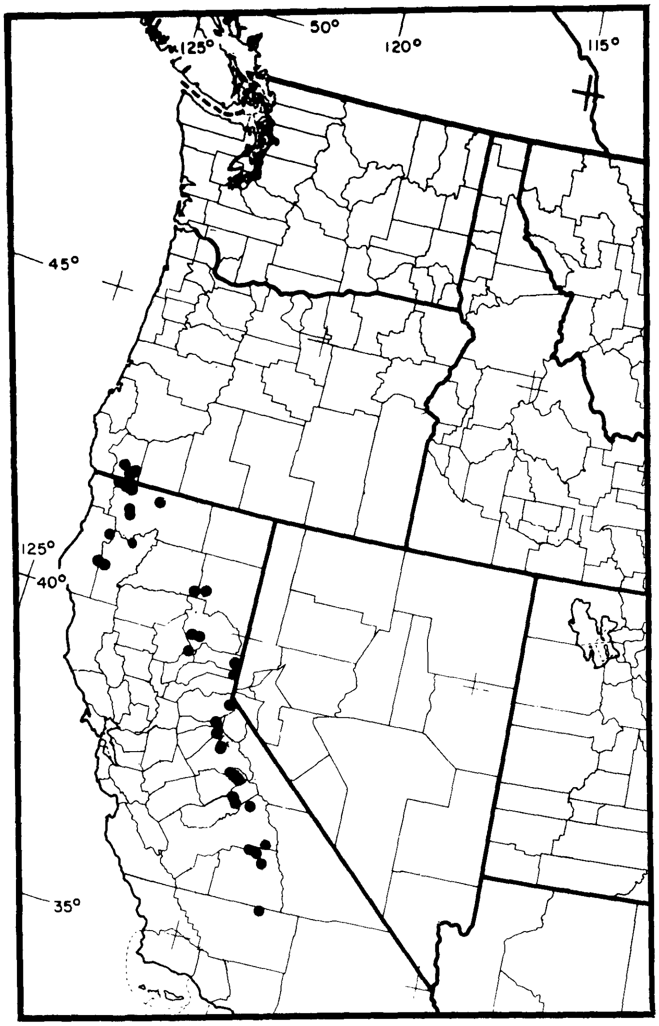

Figure 16.6 –Distribution of *Acreuthobium abietinum* f. sp. *magnificae.*

Discussion: *Arceuthobium abietinum* f. sp. *magnificae* is a very common and serious disease agent of the *Abies magnifica* forests of the Sierra Nevada. In a series of sample plots in California, this dwarf mistletoe was present on 46% of 103 *Abies magnifica* plots and on 36% of the trees (California Forest Pest Control Action Council 1968). Scharpf (1969b) discusses infection in young *Abies magnifica* stands and gives recommendations for control of the dwarf mistletoe.

Just as in *Arceuthobium abietinum* f. sp. *concoloris*, flagging is one of the most conspicuous field symptoms of *Abies magnifica* infected by dwarf mistletoe (fig. 16.7). Also as in f. sp. *concoloris*, such flagging is often associated with the fungus *Cytospora abietis* (Scharpf 1969c).

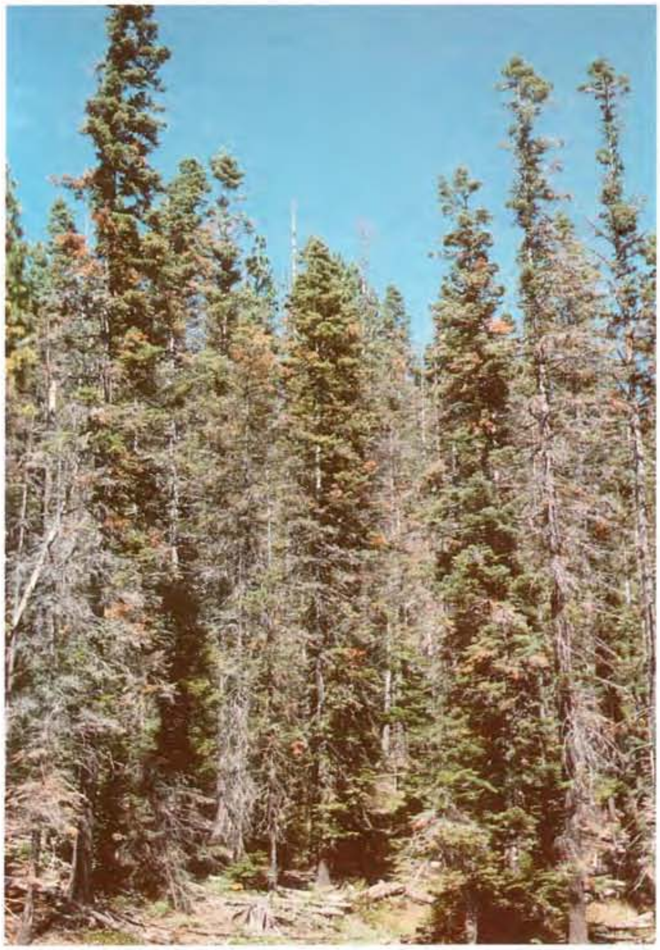

Figure 16.7 –Abies magnifica infected with *Arceuthobium abietinum;* note dead branches (flagging) that are typical of fir parasitized by this dwarf mistletoe.

Arceuthobium abietis-religiosae Mexican Fir Dwarf Mistletoe

2. *A. abietis-religiosae* Heil, Zentralblatt für Bakteriologie Abteilung 2: 28, 1923. TYPE COLLECTION: MEXICO: Mexico: Between Amecameca and Paso de Cortez, near km-78, below Popocatepetl and Ixtaccihuatl National Park, on *Abies religiosa, Hawksworth & Wiens 3339* in 1963 (NEOTYPE COLO! Isotypes: F, FPF, INIF, MEXU, MO, US). (See Hawksworth and Wiens, Brittonia 17: 231, 1965.)

Description: Mean shoot height ca. 10 (max. 16) cm. Shoots olive green, older shoots typically with black variegations, occasionally with verticillate branching (fig. 16.8). Basal diameter of dominant shoots 2–10 (mean 4) mm. Third internode 8–24 (mean 15.4 ± 5.3) mm long, 1–4 (mean 2.8) mm wide (3 collections), length/width ratio 5.5:1. Staminate buds 2–4 per node. Staminate flowers 2 mm long, 2–4 mm across; perianth mostly 3-merous, sometimes 4-merous; apex obtuse-acute; same color as shoots on outer surface, reddish on inner surface distal to anther; segments ca. 1.2 mm long, 0.9 mm wide. Mean anther diameter 0.4 mm, centered 0.8 mm from tip of segment. Pollen polar diameter 17–23 (mean 20) µm; equatorial diameter 22–26 (mean 24) µm; polar/equatorial diameter ratio 1:1.22; spine height approximately equal to wall thickness (1.5 µm) (2 collections). Pistillate flowers ca. 1.0 mm long, 0.5 mm across. Mature fruit 3.5 × 2 mm; proximal portion ca. 2.5 mm long. Seeds 2.2 × 1.0 mm. $n = 14$.

Figure 16.8 –Arceuthobium abietis-religiosae parasitizing *Abies religiosa;* note olive green color and black variegations on older shoots. (D.L. Nickrent)

Phenology: Meiosis in September. Anthesis poorly known but apparently exhibiting flowering periods in March–April and September–October. We have found that *Arceuthobium nigrum* also has two flowering periods, and *A. hawksworthii* may have three. Likewise, *A. juniperi-procerae* has multiple flowering periods in Kenya, and *A. aureum* subsp. *aureum* appears to flower continuously during the dry season in Guatemala. Heil (1923) stated that the fruits of *A. abietis-religiosae* mature in September. The fruits we observed in mid-September 1969, near Mexico City, however, were at least a month from maturity, and this discrepancy may be due to the two flowering periods. Fruits probably mature in October or November, but we have not determined when fruits pollinated from the two flowering periods are mature.

Hosts: Known only on *Abies* spp., and *A. religiosa* (including var. *emarginata*) is by far the most common host. In the Sierra Madre Oriental this dwarf mistletoe also frequently parasitizes *A. vejari*. It does not parasitize *Pinus* or *Pseudotsuga*, even where these trees are closely associated with infected firs. The parasite probably occurs on other Mexican and Guatemalan species of *Abies*. For example, an illustration of *A. guatemalensis* at Copainala, Chiapas, Mexico (Martínez 1963, p. 124) seems to exhibit witches' brooms that may be caused by this mistletoe.

Distribution: Mexico (Distrito Federal, Hidalgo, Jalisco, Mexico, Michoacán, Nuevo León, Puebla, Tamaulipas and Tlaxcala) (fig. 16.4). This dwarf mistletoe is common in the *Abies religiosa* forests of central Mexico (Madgiral 1967) and also occurs in the fir forests of the Sierra Madre Oriental. Elevational range is 2,500–3,350 m.

Discussion: The nomenclature of this distinctive Mexican dwarf mistletoe is discussed by Hawksworth and Wiens (1965). It is characterized by its large shoots, occasional verticillate branching (a feature shared in the New World only with *Arceuthobium americanum*), and exclusive parasitism of *Abies*. With the exception of the rare occurrence of *Arceuthobium abietinum* in Chihuahua, this is the only dwarf mistletoe that typically parasitizes *Abies* in Mexico.

Additional items of interest in *Arceuthobium abietis-religiosae* include the occurrence of systemic witches' brooms and verticillate staminate floral buds. Systemic infections are not common in this species, but on the few that we observed, the dwarf mistletoe shoots had formed only at the girdles of the host branches (fig. 2.13). The shoots on the systemic brooms are only about half as high as those on non-systemic infections. The staminate flowers are occasionally verticillate. The only other New World species with verticillate staminate flowers is *A. verticilliflorum*, in which the character is consistent and conspicuously developed.

Arceuthobium americanum
Lodgepole Pine Dwarf Mistletoe

3. *A. americanum* Nuttall ex Engelmann in Gray, Boston Journal Natural History 6: 214, 1850. TYPE COLLECTION: OREGON: Blue Mountains, on *Pinus contorta*, *Douglas* in 1826 (Lectotype MO!). *Razoumofskya americana* (Nutt. ex Engelm.) Kuntze, Revision of Genera of Plants 2: 587, 1891.

Description: Shoot height 5–9 (max. 30) cm. Shoots yellowish to olive green, with verticillate branching (fig. 16.9 and 16.10). Basal diameter of dominant shoots 1–3 (mean 1.5) mm. Third internode 6–23 (mean 12.1 ± 3.0) mm long, 1–2 (mean 1.2) mm wide (20 collections), length/width ratio 10.1:1. Staminate flowers borne on pedicel-like segments, ca. 2 mm long, 2.2 mm across; perianth mostly 3-merous, sometimes 4-merous; same color as the shoots; segments ca. 1.1 mm long, 1.0 mm wide. Mean anther diameter 0.6 mm, centered 0.7 mm from tip of segment. Pollen polar diameter 19–28 (mean 21) µm; equatorial diameter 23–30 (mean 25) µm; polar/equatorial diameter ratio 1:1.16; spine height (mean 1.8 µm) equal to or slightly greater than wall thickness (mean 1.5 µm) (8 collections). Pistillate flowers verticillate; ca. 1.5 mm long, 1.0 mm across; 2-merous. Mature fruit 3.5–4.5 (mean 4) mm long, 1.5–2.5 (mean 2) mm wide; proximal portion ca. 2.5 mm long. Seeds 2.4 × 1.1 mm. $n = 14$.


Figure 16.9 –Arceuthobium americanum, pistillate plant with mature fruits.


Figure 16.10 –Arceuthobium americanum, showing pattern of systemic infection; note verticillate branching of several shoots.

Phenology: Meiosis in August. Anthesis usually from early April to early June, with extremes from late March to late June (fig. 16.11). Fruits mature in late August or September of the year following pollination; maturation period averages ca. 16 months. Germination begins in May in Colorado.

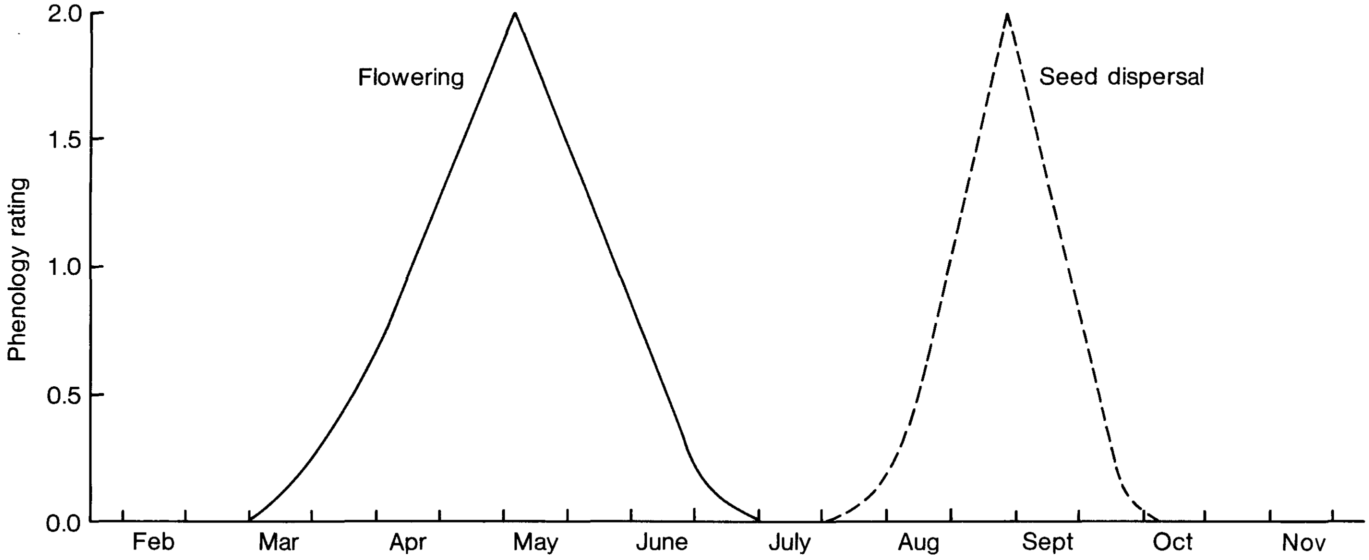

Figure 16.11–Phenology of flowering and seed dispersal of *Arceuthobium americanum* in the western United States (based on 294 observations).

Hosts: The principal hosts are *Pinus contorta* (var. *latifolia* and *murrayana*) and *P. banksiana*; all are about equally susceptible. *Pinus contorta* var. *contorta* is infected east of Squamish in southern coastal British Columbia, the only known area where this pine occurs within the range of *Arceuthobium americanum* (Smith and Wass 1979). *Pinus ponderosa* var. *scopulorum* is frequently parasitized in Colorado, Utah, and Wyoming, primarily where this tree is associated with infected *P. contorta*, but sometimes also in pure stands of *P. ponderosa* (Hawksworth 1968b). However, *P. ponderosa* var. *ponderosa* is less susceptible and is only occasionally infected (Kuijt 1953). Other occasional hosts for *A. americanum* include *P. albicaulis*, *P. flexilis*, and *P. jeffreyi*. Spruces are rare hosts—*Picea glauca* (Smith and others 1972), *P. mariana* (Baker and others 1988), *P. engelmannii* and *P. pungens* (Hawksworth and Graham 1963, Kuijt 1960b, Molnar and others 1968). When *P. mariana* and *P. pungens* are parasitized, witches' brooms are formed, but no dwarf mistletoe shoots have been observed. The presence of the dwarf mistletoe was confirmed by the occurrence of the endophytic system in the host branches.

Pinus aristata is a rare host in Colorado and *Pseudotsuga menziesii* is an extremely rare host in Alberta (Muir 1973b) and in northern Utah. In Utah, a *Pseudotsuga menziesii* with several small witches' brooms was observed in an infested *Pinus contorta* stand. The witches' brooms produced no dwarf mistletoe shoots, but dissection of infected twigs again revealed the presence of the endophytic system and confirmed infection by *Arceuthobium americanum*. Weir (1917) reported *A. americanum* on *Pinus attenuata* and *P. jeffreyi* near Oregon Mountain, Josephine County, Oregon. His specimens are unquestionably *A. americanum*, but we and others have visited this locality several times and have been unable to confirm the presence of *A. americanum*.

Weir (1918a) successfully inoculated seedlings of the European *Pinus mugo* (as *P. montana*) with *Arceuthobium americanum*, and this dwarf mistletoe has been found on planted *P. sylvestris* in Washington (Graham and Leaphart 1961) and in Alberta (Powell 1968).

Distribution: Canada (British Columbia, Alberta, Saskatchewan, Manitoba, and Ontario) (fig. 16.12 and 16.13) and the United States (Washington, Idaho, Montana, Oregon, California, Utah, Wyoming, and Colorado) (fig. 16.14). It probably occurs in Nevada in the vicinity of Lake Tahoe, but no specific locations are known (Kartesz 1988). *Arceuthobium americanum* has the most extensive distribution of any North American dwarf mistletoe (fig. 16.12). Its latitudinal range of about 2,800 km is exceeded only by *A. douglasii*. It occurs from Lake Athabasca in northern Saskatchewan south to the southern Sierra Nevada in California (Kern County) and to southern Colorado (Saguache County). Its longitudinal distribution of nearly 2,400 km extends from western Ontario to western British Columbia (Elliot and others 1967, Kuijt 1963, Larsen and Gross 1970, Zalasky 1956). *Arceuthobium americanum* extends to nearly latitude 60°N. *Arceuthobium tsugense* in Alaska and *Viscum album* in Sweden (Wallden 1961) reach similar latitudes, but both of these mistletoes occur in maritime environments that are much less extreme than the continental climate in which *A. americanum* is distributed.

Figure 16.12 –General distribution of *Arceuthobium americanum* in North America.

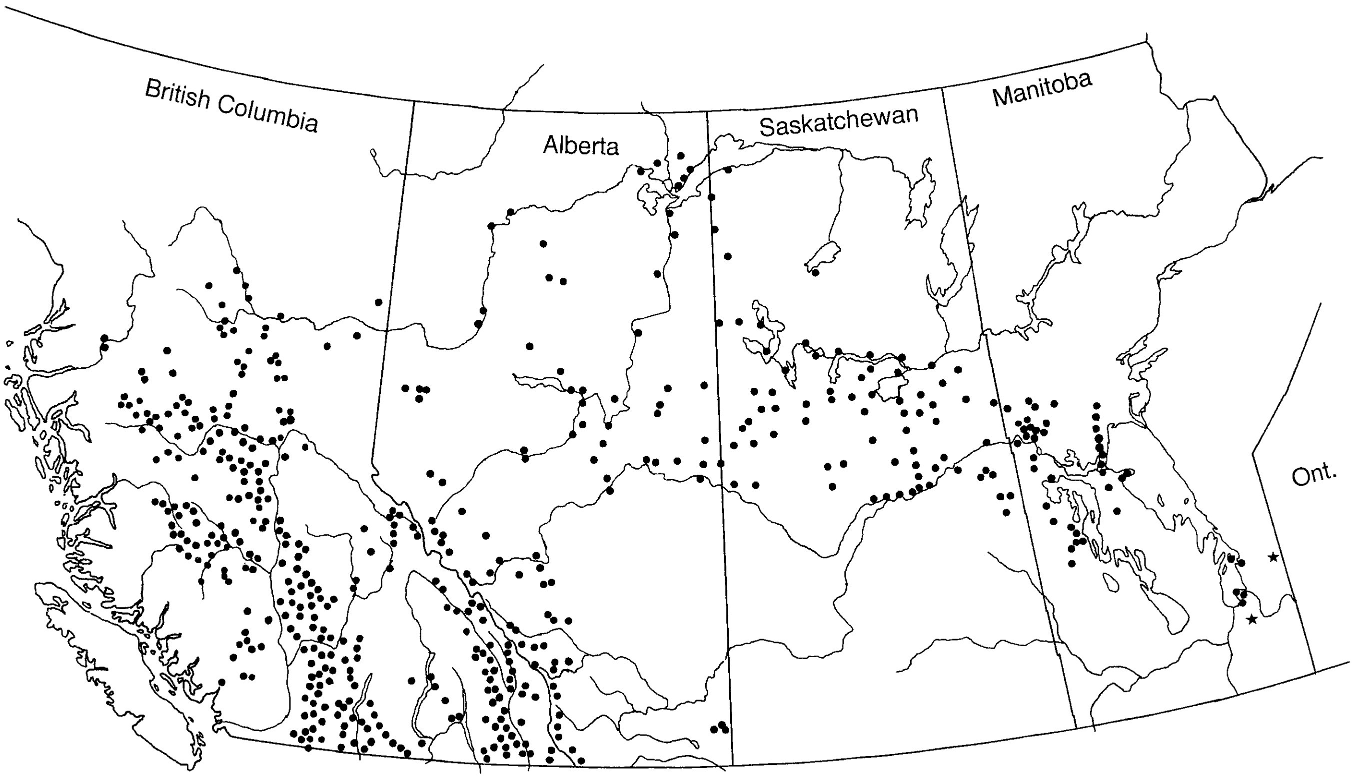

Figure 16.13 –Distribution of *Arceuthobium americanum* in Canada; the three locations in Ontario and extreme southeastern Manitoba where this dwarf mistletoe is now apparently extinct are shown by stars. (British Columbia records updated from Wood 1986).

There is one report of *Arceuthobium americanum* on *Pinus banksiana* in the Northwest Territories at about latitude 63°N, about 190 km north of Fort Providence (Moody and Cerezke 1985). However, this has not been confirmed (Y. Hiratsuka, personal communication and our observations). We observed brooming to be common in *P. banksiana* south of Fort Providence, but the brooms were not caused by dwarf mistletoe, and we suspect the report by Moody and Cerezke (1985) is in error.

The distribution of *Arceuthobium americanum* is centered within that of its principal host *Pinus contorta*, particularly varieties *latifolia* and *murrayana*. However, variety *murrayana* in southern California and Baja California is not infected. The latter is about 600 km south of the known range of the parasite in the southern Sierra Nevada.

Arceuthobium americanum rarely occurs within the distribution of *Pinus contorta* var. *contorta* (shore pine), but it has been observed on this host in coastal British Columbia (Smith and Wass 1979). As previously mentioned, Weir (1917) reported this variety as a host in the Oregon Mountains in southwestern Oregon, and he indicated it was associated with infected *P. jeffreyi* and *P. attenuata*. Although *P. contorta* var. *contorta* is common in this area, the only dwarf mistletoe occurring on it is *A. siskiyouense*, and then only rarely. Finding *A. americanum* in the Oregon Mountain area would extend the western limit of distribution by approximately 100 km from its known distribution in the Cascade Mountains.

Arceuthobium americanum occurs in outlying populations of *Pinus contorta* var. *latifolia* in the Cypress Hills of southeastern Alberta and several isolated mountain ranges in north central Montana (Dooling and Eder 1981)—the Little Rocky Mountains (Phillips County), Bearpaw Mountains (Hill County) (Dooling 1973), and Sweetgrass (Whitlash) Mountains (Liberty County) (Thompson and Kuijt 1976). Dooling and Eder (1981) report that this dwarf mistletoe is known from all the isolated *P. contorta* populations in central Montana, except those in the Highwood and Snowy Mountains.

In central and northern Alberta, *Arceuthobium americanum* occurs on *Pinus banksiana*, and it is common on this host in Saskatchewan and Manitoba. The reports of *A. americanum* at White Otter Lake in western Ontario (Hord and Quirke 1956) and near Sprague in extreme southeastern Manitoba (Zalasky 1956) are misidentifications based on a rare infection of *P. banksiana* by *A. pusillum* (Laut 1967, Sippell and others 1968).

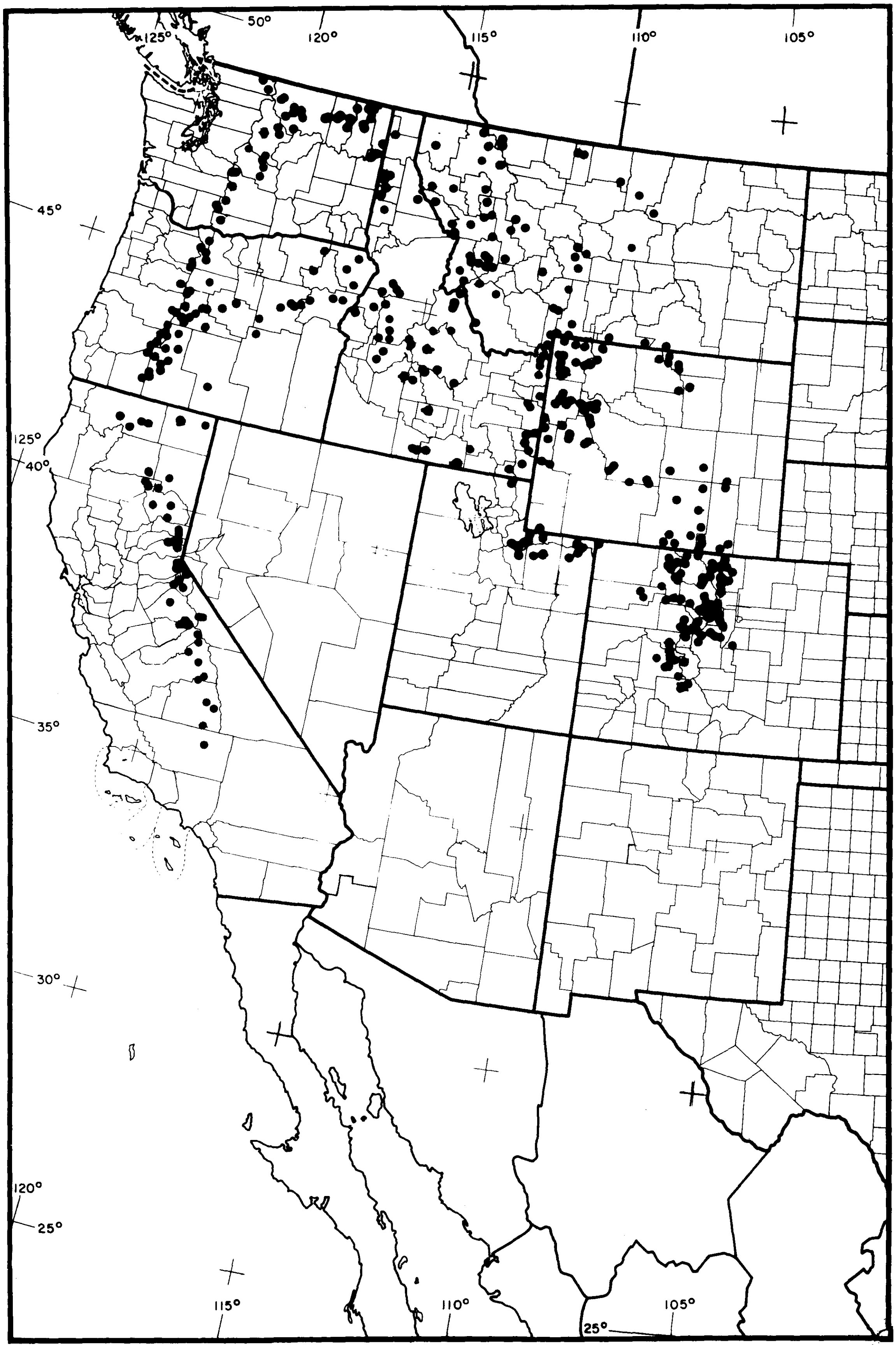

Figure 16.14 –Distribution of *Arceuthobium americanum* in the United States, which also approximates the range of its host, *Pinus contorta*

Arceuthobium americanum has been confirmed in Ontario (Larsen and Gross 1970) at the Sioux Lookout area (latitude 50°30' N, longitude 96°30' W), nearly 240 km east of the previously known eastern limits of the species near Belair at the south end of Lake Winnipeg, Manitoba. However, Sioux Lookout was severely burned by a wildfire in 1976, and the mistletoe was apparently eradicated (Myren and Gross 1977). The only other known populations in Manitoba south and east of Belair have also apparently been extirpated—Wallace Lake (latitude 49°50' N, longitude 95°30' W) by wildfire and Milner Ridge (latitude 50°N, longitude 96°10' W) by clearcutting (M. Slivitsky and T. Meyer, personal communication).

Arceuthobium americanum only occurs in the western part of the range of *Pinus banksiana*, so the spread of the parasite onto this tree has probably been relatively recent. *Arceuthobium americanum* likely evolved as a principal parasite of *P. contorta*, then spread to *P. banksiana* through central Alberta where these two species co-occur and frequently hybridize. Yeatman (1967) suggests that *P. banksiana* first became parasitized by *A. americanum* after the Wisconsin Glaciation, but available evidence indicates an earlier association (Zavarin and others 1969).

Arceuthobium americanum has been found on *Pinus contorta* × *banksiana* hybrids near Grand Prairie and Peace River, Alberta (Hawksworth and Wiens 1972). Also, *A. americanum* occurs on *P. contorta* that was planted in a naturally infested stand of *P. banksiana* at Prince Albert, Saskatchewan (Hawksworth and Wiens 1972).

In the central Rocky Mountains, *Arceuthobium americanum* occurs at the lower elevational limits of *Pinus contorta*, but its upper limits are usually about 200 m below the upper limit of stands dominated by *P. contorta* (Hawksworth 1956b and see fig. 7.2).

Arceuthobium americanum distribution maps have been published for western Canada (Kuijt 1963), Alberta (Baranyay 1970), British Columbia and adjacent southwestern Alberta (Baranyay 1975), British Columbia (Wood 1986), Manitoba and Saskatchewan (Zalasky 1956), Montana (Dooling and Eder 1981), Utah (Albee and others 1988), Colorado (Hawksworth 1987c), and California (Kuijt 1960a).

This dwarf mistletoe varies in elevation from 200 m near Lake Athabasca in northern Alberta and Saskatchewan to 3,350 m in central Colorado.

Discussion: Gill (1935) discusses the typification problem in *Arceuthobium americanum*. Engelmann believed that the specimen he was describing was collected by Nuttall, and it was designated as the type (Oregon, on *Pinus*). Gill states, however, that this specimen was actually collected by Douglas in the Blue Mountains of Oregon; we have designated this latter collection as the type specimen.

Despite the extensive geographic distribution of *Arceuthobium americanum*, we find no criteria for subspecific division. In general, the plants are larger in the Cascade Mountains of Oregon and in northern Idaho than elsewhere, but this is probably associated with the more vigorous host growth in these areas. *Arceuthobium americanum* induces characteristic systemic witches' brooms (fig. 16.15) on *Pinus contorta* (Kuijt 1960b) and produces the same type of broom formations on *P. ponderosa* (Hawksworth 1956a, Weir 1916c). The witches' brooms formed on *Picea engelmannii*, however, are non-systemic (Hawksworth and Graham 1963). Kuijt (1960a) noted that *A. americanum* cannot perpetuate itself for long periods of time on *Pinus jeffreyi* or *P. ponderosa* var. *ponderosa* in California. In northern Colorado and southern Wyoming, however, the parasite is aggressive in pure stands of *P. ponderosa* var. *scopulorum*, some of which are several kilometers from the nearest infection on *P. contorta*. Most areas where *A. americanum*

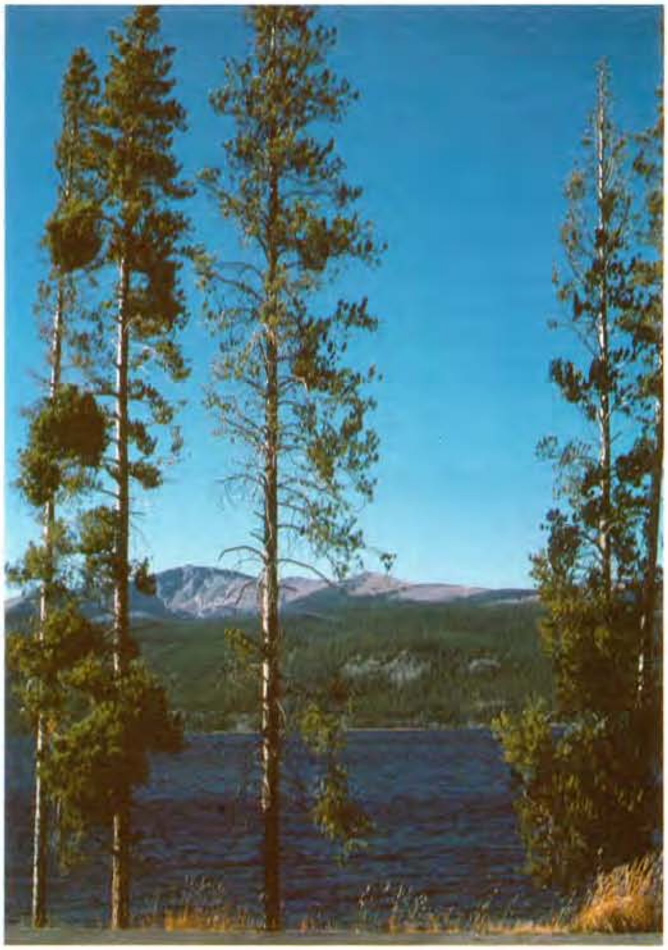

Figure 16.15–Pinus contorta var. *latifolia* showing witches' brooms induced by infection with *Arceuthobium americanum*.

occurs in pure stands of *P. ponderosa* are outside the range of *A. vaginatum* subsp. *cryptopodum*, which is the typical parasite on *P. ponderosa* in the Rocky Mountains (Hawksworth 1968b, 1969).

Arceuthobium apachecum
Apache Dwarf Mistletoe

4. *A. apachecum* Hawksworth & Wiens, Brittonia 22: 266, 1970. TYPE COLLECTION: ARIZONA: Pima County: Santa Catalina Mountains near the summit of Mt. Lemmon at 2,800 m, on *Pinus strobiformis*, *Hawksworth, Lightle, & Gilbertson 1110*, September 13, 1968. (Holotype US! Isotypes: ARIZ, COLO, DS, FPF, MO, RM, UC, UT.)

Description: Mean shoot height 3–4 (max. 9) cm. Shoots yellow, green, or reddish, flabellately branched and densely clustered (fig. 16.16). Basal diameter of dominant shoots 1–2 (mean 1.8) mm. Third internode 5–10 (mean 7.2 ± 2.0) mm long, 1–2 (mean 1.5) mm wide (12 collections), length/width ratio 4.8:1. Flowers axillary. Staminate flowers 2.7 mm across; perianth 3- to 4-merous; same color as shoots; segments ca. 1.3 mm long, 0.9 mm wide. Mean anther diameter 0.5 mm, centered 0.7 mm from tip of segment. Pollen polar diameter 16–23 (mean 19) µm; equatorial diameter 18–23 (mean 21) µm; polar/equatorial diameter ratio 1:1.11; spine height (1.5 µm), slightly greater than the wall thickness (ca. 1.1 µm) (4 collections). Mature fruit 4 mm long, long 2.5 mm wide; proximal portion ca. 2.5 mm long. Seeds 2.8 × 1.2 mm. $n = 14$.

Phenology: Meiosis in July. Anthesis from late July to mid-September, with a peak in mid-August (Mathiasen 1982) (fig. 16.17). Fruits mature from mid-August to mid-October with a peak in September (Mathiasen 1982); maturation period averages about 13 months.

Figure 16.16 –*Arceuthobium apachecum*, staminate plant parasitizing *Pinus strobiformis*; note short greenish shoots densely clustered around host branch. (D.L. Nickrent).

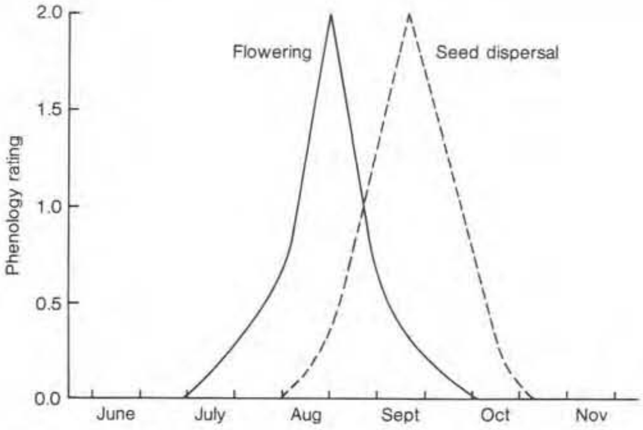

Figure 16.17 –Phenology of flowering and seed dispersal of *Arceuthobium apachecum* (based on 66 observations).

Host: Known only on *Pinus strobiformis*, the only member of subgenus *Haploxylon* (except pinyons) that occurs within its distribution.

Distribution: United States (Arizona and New Mexico) and Mexico (Coahuila) (fig. 16.18). This dwarf mistletoe has a limited distribution in southern Arizona and central New Mexico, with an outlier in the Sierra del Carmen in northern Coahuila, Mexico. In Arizona, it occurs in the White, Pinaleno, Santa Catalina, Santa Rita, and Chiricahua Mountains and in New Mexico in the Mangas, San Mateo, Magdalena, and Capitan Mountains. The report of a dwarf mistletoe on *Pinus strobiformis* on Mt. Livermore in the Davis Mountains of west Texas (Powell 1988) requires confirmation. The specimen on which the report was based (*Coleman s. n.* in 1936 at SRSC) is *Phoradendron juniperinum*, but there is no host material with the collection, and this mistletoe is not known to parasitize pines. A distribution map for *Arceuthobium apachecum* in New Mexico was published by Martin and Hutchins (1980). Elevational range is 2,000–3,000 m.

Discussion: We consider Gill's *Arceuthobium campylopodum* f. *blumeri* to comprise 4 allopatric species—*A. apachecum, A. blumeri, A. californicum*, and *A. monticola*, all of which parasitize pines of subgenus *Haploxylon*. These species differ in a number of characteristics including morphology, hosts, phenology, and distribution. Our previous numerical analyses support the classification of these population systems as species (Hawksworth and Wiens 1972), although they may exhibit superficial similarities.

The exclusive occurrence of two dwarf mistletoes (*Arceuthobium apachecum* and *A. blumeri*) on a single host species (*Pinus strobiformis*) is unique in *Arceuthobium*. Originally, we suspected these taxa

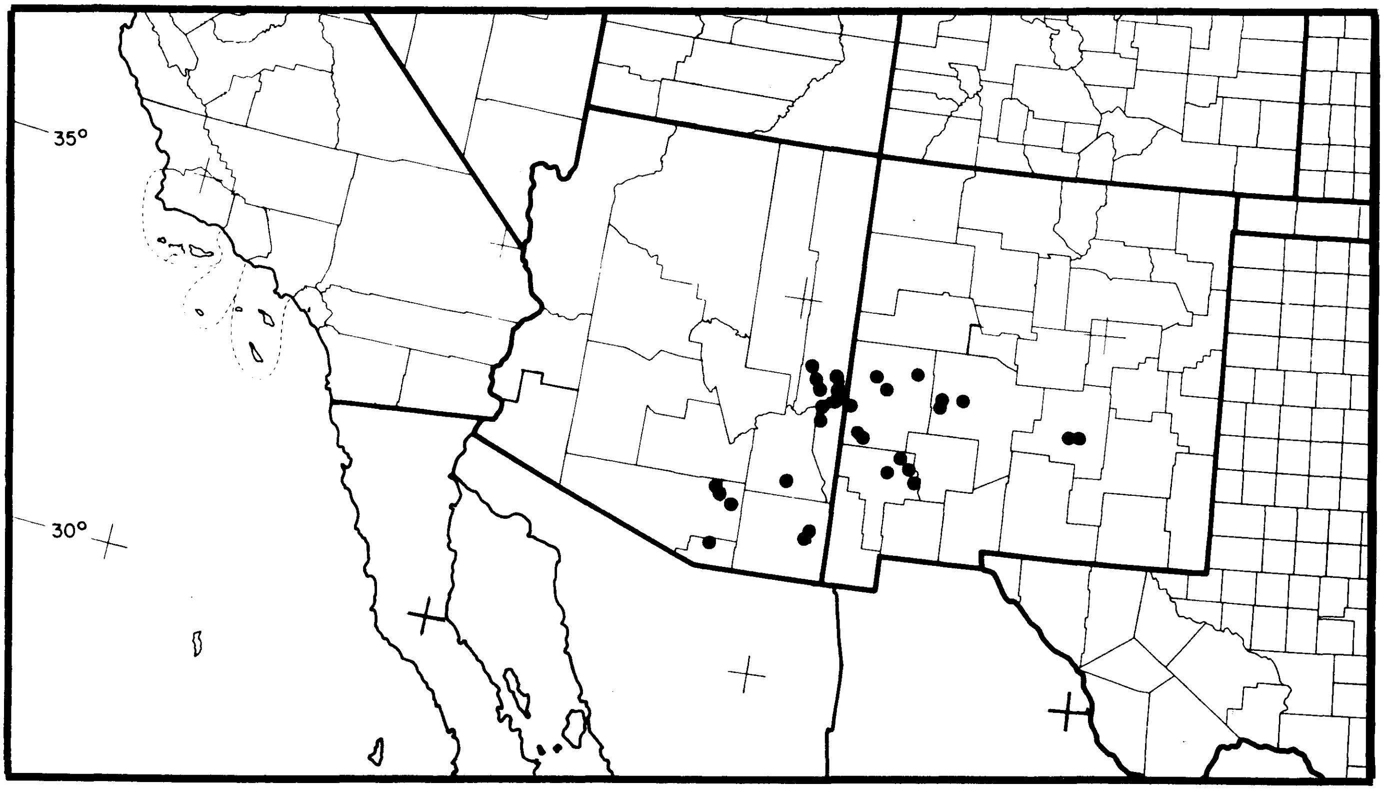

Figure 16.18 –Distribution of *Arceuthobium apachecum.*

TABLE 16.1–Comparison of *Arceuthobium apachecum* and *A. blumeri*

Character	*A. apachecum*	*A. blumeri*
Shoot height, mean (maximum)	4 (9) cm	7 (18) cm
Shoot color	Yellow-green to reddish	Gray to straw or light green
Shoot habit	Densely clustered around host branch	Not densely clustered around host branch
Lateral staminate spike length × width in summer	6 × 1 mm	11 × 2 mm
Staminate flowers	Usually 3- or 4-merous, rarely 5-merous	Usually 4-merous, occasionally 3- or 5-merous, rarely 6-merous
Color of staminate lobes compared to shoots	Same	Darker

Note: contributed by R. L. Mathiasen.

might represent a single, variable species. However, the occurrence of geographically consistent morphological differences (table 16.1) indicated that separate taxonomic status was warranted. This conclusion has been confirmed by Mathiasen (1982). The populations of *A. apachecum* in the Santa Rita Mountains tend to have taller shoots (up to 9 cm) than do those in other portions of its distribution.

When grown under common conditions in a greenhouse at Fort Collins, Colorado, the two species maintained morphological integrity. They are not sympatric, but they do approach to within about 60 km of each other in southern Arizona. *Arceuthobium apachecum* is abundant north and east of the Santa Rita and Chiricahua Mountains; *A. blumeri* occurs from the Huachuca Mountains south into Mexico. Unlike *A. blumeri, A. apachecum* frequently induces witches' brooms (fig. 16.19).

Figure 16.19 –Pinus strobiformis showing witches' broom induced by infection with *Arceuthobium apachecum.*

Arceuthobium aureum
Golden Dwarf Mistletoe

5\. *A. aureum* Hawksworth & Wiens, Brittonia 29: 414, 1977. TYPE COLLECTION: GUATEMALA: Alta Verapaz, 5 km west of San Cristóbal Verapaz, on Route 7W to Huehuetenango, on *Pinus pseudostrobus, Hawksworth, Wiens, & Player 1596*, in 1975 (Holotype US! Isotypes: ENCB, FPF, INIF, MO, UNAM, UT).

Description: Shoot height 12–40 cm yellow to golden brown, flabellately branched. Basal diameter of dominant shoots 3–24 mm. Third internode 16–35 mm long, 2–8 mm wide. Staminate flowers ca. 3 mm across, 3- or 4-merous. Mature fruits 4–5 mm long, 2.5 mm wide. Parasitic on pines of subgenus *Diploxylon*. $n = 14$.

Discussion: This taxon was originally considered to be part of the *Arceuthobium globosum* complex (Hawksworth and Wiens 1972), but further field studies in Mexico and Guatemala have shown that it is a distinct species (Hawksworth and Wiens 1977, see discussion under *A. globosum). Arceuthobium aureum* is comprised of two subspecies.

Key to the subspecies:

1. Shoots usually less than 20 cm tall, golden; dominant shoots usually less than 10 mm in diameter at base; mature fruits ca. 4 mm long; pedicels ca. 1.5 mm long; flowering and seed dispersal irregular throughout the year; witches' brooms not formed; below 2,000 m in Guatemala.........5a. *A. aureum* subsp. *aureum*
1. Shoots usually over 20 cm tall, golden brown; dominant shoots usually more than 10 mm diameter at base; mature fruits ca. 5 mm long, pedicels ca. 4 mm long; flowering in September; seed dispersal June–July; witches' brooms commonly produced; above 2,200 m in southern Mexico (Chiapas and Oaxaca)...... ....5b. *A. aureum* subsp. *petersonii*

Arceuthobium aureum subsp. *aureum*
Golden Dwarf Mistletoe

5a. *A. aureum* Hawksworth & Wiens subsp. *aureum.*

Description: Shoots 12–30 (mean 16) cm tall, golden, flabellately branched (fig. 16.20). Basal diameter of dominant shoots 3–14 (mean 5) mm. Third internode 16–30 (mean 20) mm long, 2–4 (mean 3) mm wide. Mature fruits ca. 4 mm long, lightly glaucous; pedicel ca. 1.5 mm long. $n = 14$.

Phenology: Anthesis and fruit maturity apparently continuous throughout the year, or at least in the dry season.

Figure 16.20 –Arceuthobium aureum subsp. *aureum* on *Pinus* sp.

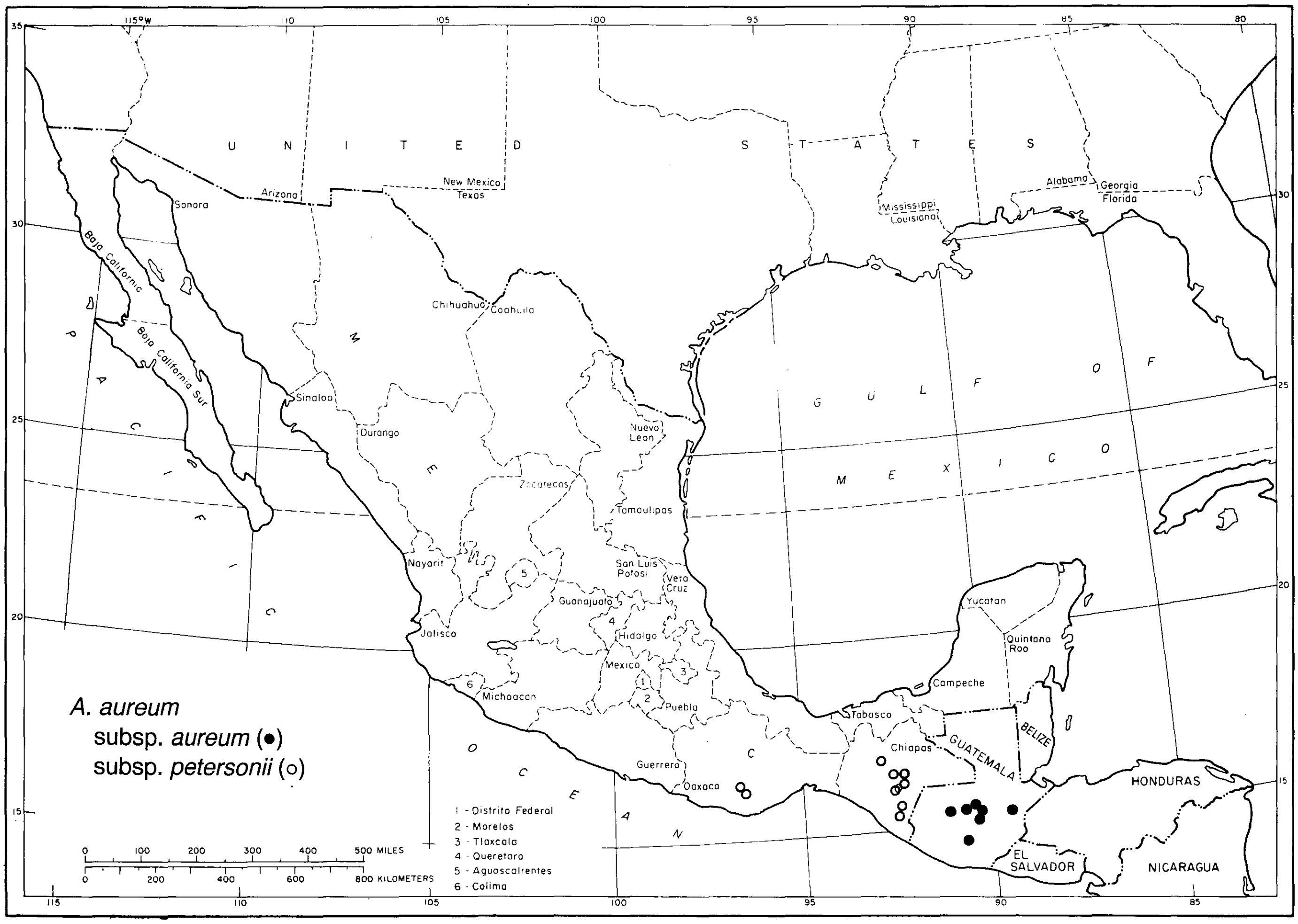

Figure 16.21 –Distribution of *Arceuthobium aureum* subsp. *aureum* and subsp. *petersonii.*

Hosts: *Pinus montezumae, P. oaxacana*, and *P. pseudostrobus.*

Distribution: Guatemala (fig. 16.21). A common taxon of the low-elevation pine forests in Guatemala. Elevational range is 900–2,000 m.

Discussion: This dwarf mistletoe was formerly considered to be part of the *Arceuthobium globosum* complex (Hawksworth and Wiens 1977) and is discussed under that species in greater detail.

Arceuthobium aureum subsp. *petersonii* Peterson's Dwarf Mistletoe

5b. *A. aureum* Hawksworth & Wiens subsp. *petersonii* Hawksworth & Wiens, Brittonia 29: 415, 1977. TYPE COLLECTION: MEXICO: Chiapas, near km-136 (52 km southeast of San Cristóbal de las Casas) on Panamerican Highway, 2,250 m, on *Pinus pseudostrobus, Hawksworth, Wiens, & Player 1598* in 1975 (Holotype US! Isotypes: ENCB, FPF, MO, UNAM, UT).

Description: Shoots 14–40 (mean 24) cm tall, golden to yellow-brown, flabellately branched. Basal diameter of dominant shoots 14–35 (mean 23) mm. Third internode 14–35 (mean 23) mm long, 2.5–8 (mean 5) mm wide. *n* = 14.

Phenology: Anthesis in September. Fruits mature June–July; maturation period of ca. 9–10 months. This is several months less than is common for many dwarf mistletoes.

Hosts: *Pinus michoacana, P. montezumae, P. oaxacana, P. oocarpa, P. patula,* and *P. pseudostrobus* are the principal hosts. *Pinus michoacana* is somewhat less susceptible and is infected only when it grows in association with the other principal hosts.

Distribution: Mexico (Oaxaca and Chiapas) (fig. 16.21). This dwarf mistletoe is common in Chiapas between San Cristóbal de las Casas and Teopisca. Its distribution in Oaxaca is poorly known, but there are a number of collections from the Miahuátlan- Suchixtepec area. Elevational range is 2,200–2,450 m.

Figure 16.22 –Witches' broom formation on *Pinus* sp. induced by infection with A. *aureum* subsp. *petersonii.*

Discussion: This subspecies is characterized primarily by its tall, slender, brown to golden shoots, slightly longer fruit (5 mm), long pedicels (4 mm), and general tendency to form witches' brooms (fig. 16.22). The subspecies is named for R. S. Peterson, who first discovered these populations.

Arceuthobium bicarinatum
Hispaniolan Dwarf Mistletoe

6. *A. bicarinatum* Urban, Symbolae Antillanae 7: 204, 1912. TYPE COLLECTION: DOMINICAN REPUBLIC: Constanza, on *Pinus occidentalis*, von Turckheim 3241 in 1910 (Holotype Z! Isotypes: BM, F, ILL, K, MO, NY, S, US). *Razoumofskya bicarinata* (Urban) Tubeuf, Naturwissenschaftliche Zeitschrift für Forst- und Landwirtschaft 17: 195, 1919.

Figure 16.23 –*Arceuthobium bicarinatum,* pistillate plant with mature fruits; note dark brownish red color of shoots and sterile node at tip of pistillate shoots.

Description: Mean shoot height ca. 10 (max. 17) cm, dark brownish red, terminal branches of living plants conspicuously glaucous (character lost after drying), shoots frequently twisted when dry, flabellately branched (fig. 16.23). Basal diameter of dominant shoots 2–4 (mean 3) mm. Third internode 6–14 (mean 10.5 ± 2.1) mm long, 1.5–4.0 (mean 2.0) mm wide (6 collections), length/width ratio 5.2:1. Staminate flowers ca. 3 mm across; perianth 3- or 4-merous, reddish, segments ca. 1.5 mm long, 1.0 mm wide, apex acute. Mean anther diameter 0.5 mm, centered 1.0 mm from tip of segment. Pollen polar diameter 21–25 (mean 23) µm; equatorial diameter 25–28 (mean 26) µm; polar/equatorial diameter ratio 1:1.14; spine height (ca. 3 µm) 3 × wall thickness (ca. 1 µm) (3 collections). Mature fruits ca. 4 × 2 mm; proximal portion ca. 2.5 mm long. Seeds 2.5 × 1.2 mm. $n = 14$.

Phenology: Meiosis in August. Anthesis usually in September. Fruits mature in late August or September of the year following pollination; maturation period averages ca. 12 months.

Hosts: Known only on *Pinus occidentalis*, the only native pine within its distribution.

Distribution: Dominican Republic and Haiti (fig. 16.24). *Arceuthobium bicarinatum* is common on the island of Hispaniola. In Haiti, this dwarf mistletoe is common in the Morne la Selle and the Morne des Commissaires, in the southeastern part of the country. In the Dominican Republic, *A. bicarinatum* occurs on

Figure 16.24 –Distribution of *Arceuthobium bicarinatum* on Hispaniola.

all three major mountain ranges where *Pinus occidentalis* is present—Cordillera Central, Sierra de Neiba, and Sierra de Bahoruco. More than half of the pine forests in the Dominican Republic are apparently infested by *A. bicarinatum*, and damage is particularly severe in Santiago and San Juan Provinces (Etheridge 1971). We commonly observed *A. bicarinatum* in La Vega Province between 1,000–2,600 m. Etheridge (1971) gives a distribution map for the species in the Dominican Republic. Thomas Zanoni of the Jardin Botánico Nacional, Santo Domingo, provided additional information on the distribution of this dwarf mistletoe in the Dominican Republic. Elevational range is 800–2,800 m (Darrow and Zanoni 1991, Etheridge 1971).

Discussion: This highly distinctive species is restricted to Hispaniola. Characteristic features are the dark brownish-red shoot color, sterile nodes near the tips of the pistillate shoots, and glaucous terminal internodes. Internodes on dried specimens often show a twist of about a quarter turn, but this trait is not discernible in living plants.

Figure 16.25 –*Pinus occidentalis* showing witches' broom induced by infection with *Arceuthobium bicarinatum*.

The witches' brooms caused by *Arceuthobium bicarinatum* are mostly non-systemic (as illustrated by Marie-Victorin 1943). Near Valle Nuevo in the Cordillera Central, however, some witches' brooms were anomalous. These brooms appeared to be systemic (fig. 16.25), but dwarf mistletoe shoots were not regularly produced on the infected branches, as is normally the case for systemic infections in other host–parasite combinations. Detailed studies are needed on the unusual witches' brooms induced by *A. bicarinatum*.

This is a serious parasite of *Pinus occidentalis* in the Dominican Republic, where from 15–85% of the trees in the northern Cordillera Central are infected (Darrow and Zanoni 1991). At higher elevations in Haiti and the Dominican Republic, a leafy mistletoe (*Dendropemon pycnophyllus*, Loranthaceae) is also common on *P. occidentalis* and frequently occurs on trees that are also infected by *Arceuthobium bicarinatum*.

Arceuthobium blumeri
Blumer's Dwarf Mistletoe

7. *A. blumeri* A. Nelson, Botanical Gazette 56: 65, 1913. TYPE COLLECTION: ARIZONA: Cochise County: Huachuca Mountains, on *Pinus strobiformis*, *Blumer* in October 1910 (Holotype RM No. 78604!). *Razoumofskya blumeri* Standley, Proceeding Biological Society Washington 29: 86, 1916. *A. campylopodum* Engelm. forma *blumeri* (Engelm.) Gill, Transactions Connecticut Academy Arts and Sciences 32: 207, 1935 (in part).

Description: Mean shoot height ca. 6–7 (max. 18) cm, gray to straw or light green, flabellately branched (fig. 16.26). Basal diameter of dominant shoots 1–3 (mean 2.1) mm. Third internode 5–14 (mean 9.1

Figure 16.26 –*Arceuthobium blumeri*, pistillate plant with mature fruits; note straw or yellow-green color of shoots.

± 2.5) mm long, 1–2 (mean 1.6) mm wide (8 collections), length/width ratio 5.5:1. Staminate flowers ca. 2.5 mm long, 2.5–3.0 mm across; perianth 3- to 6-merous (mostly 3- or 4-merous), segments ca. 1.3 mm long, 1.0 mm wide, apex acute. Mean anther diameter 0.6 mm, centered 0.4 mm from tip of segment. Pollen polar diameter ca. 19 µm and an equatorial diameter ca. 20 µm; spine height and wall thickness each ca. 1 µm (1 collection, few grains available). Mature fruit ca. 4 × 2.5 mm, proximal portion ca. 2.5 mm long. Seeds 2.7 × 1.0 mm. $n = 14$.

Phenology: Meiosis in July. Anthesis from mid-July to late-August, with a peak in early August (Mathiasen 1982). Fruits mature from late August to early October, with a peak in mid-September (Mathiasen 1982); maturation period averages 13–14 months.

Hosts: The host affinities of *Arceuthobium blumeri* are not clear because of the taxonomic confusion surrounding *Pinus strobiformis* and the closely related *P. ayacahuite* var. *brachyptera* in the Sierra Madre Occidental, Mexico (Eguiluz 1991, Hawksworth 1991b, Perry 1991). However, most host populations of this dwarf mistletoe in the Sierra Madre Occidental are best referred to the latter taxon. On Cerro Potosí in Nuevo León, it parasitizes a different white pine that has been called *"Pinus flexilis"* (Martínez 1948, Perry 1991), but is perhaps best classified as *P. strobiformis* var. *potosiensis* (Silba 1990).

Distribution: United States (Arizona) and Mexico (Sonora, Chihuahua, Durango, Nuevo León, and Coahuila) (fig. 16.27). This dwarf mistletoe extends southward from the Huachuca Mountains in southern Arizona through the Sierra Madre Occidental in Chihuahua and Sonora to southern Durango. In the Sierra Madre Oriental it is known only from Cerro Potosí, Nuevo León, and San Antonio de las Alazanas, Coahuila (Cibrián and others 1980), but it probably occurs elsewhere over this extensive distribution. Elevational range is 2,150–3,250 m.

Discussion: The parasitism of *Arceuthobium blumeri* and *A. apachecum* on *Pinus strobiformis* is discussed under *A. apachecum* and the two species are compared in table 16.1.

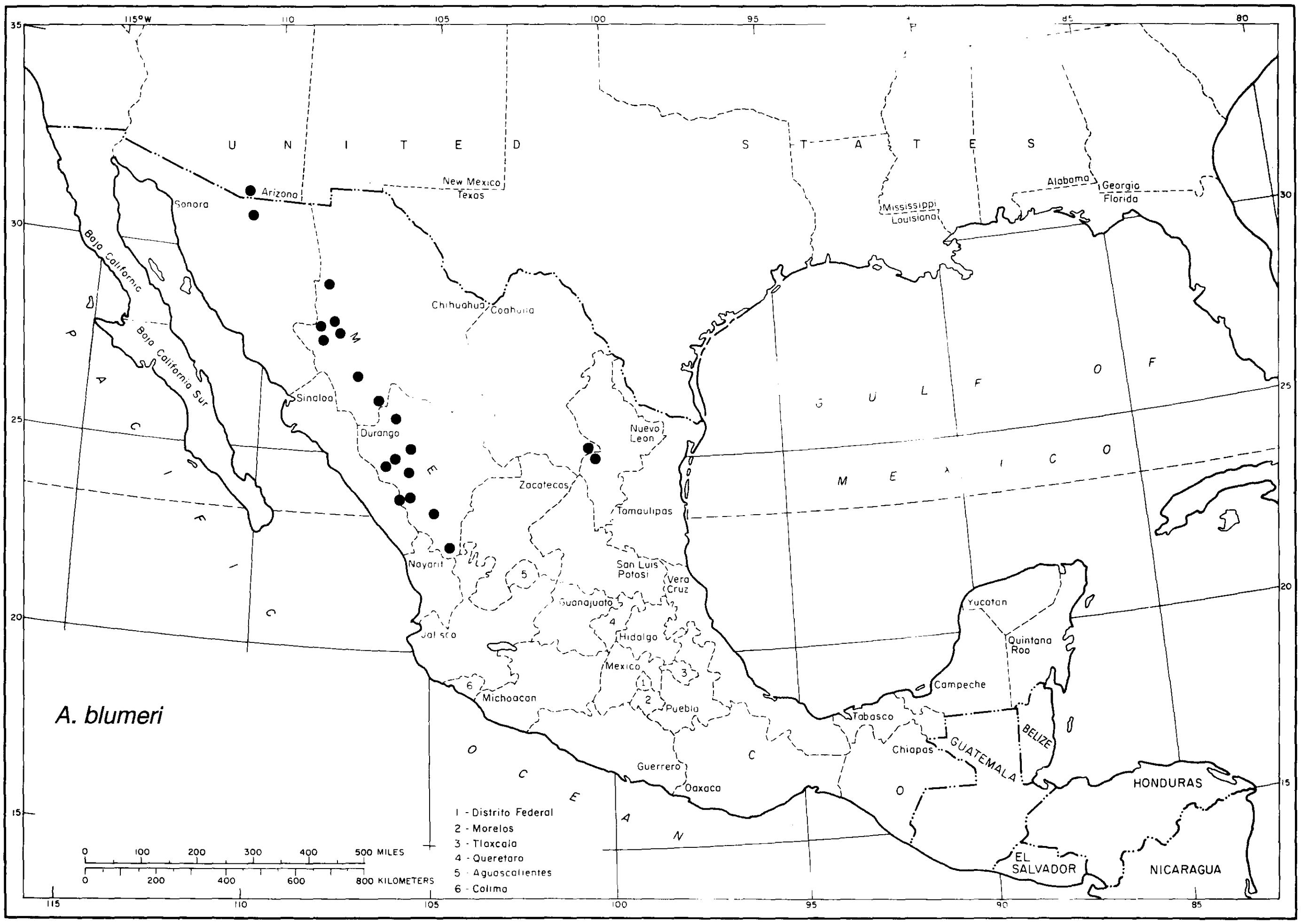

Figure 16.27–Distribution of *Arceuthobium blumeri* in Mexico and southeastern Arizona.

Mathiasen (1982) studied 13 populations in 3 areas of Arizona, Chihuahua, and Durango and found that the perianth segments of the staminate flowers were distributed as follows: 3 segments, 42%; 4 segments, 52%; 5 segments, 6%, and 6 segments, trace. The northern populations (Arizona) had the highest number of segments per flower: 3 segments, 30%; 4 segments, 53%; and 5 segments, 16%. The Durango population had the lowest: 3 segments, 55%; 4 segments, 44%; and 5 segments, 1%.

Distinctive features of *Arceuthobium blumeri* include its gray-colored shoots, 4- to 6-merous staminate flowers, and rare formation of witches' brooms. The populations in the southern portions of its distribution in Durango tend to have taller shoots (up to 18 cm).

Arceuthobium californicum
Sugar Pine Dwarf Mistletoe

8. *A. californicum* Hawksworth & Wiens, Brittonia 22: 266, 1970. TYPE COLLECTION: CALIFORNIA: Mariposa County, Fish Camp 0.4 km west of State Route 41 on Summit Camp Road, on *Pinus lambertiana, Hawksworth & Hawksworth 1147*, November 6, 1968 (Holotype US! Isotypes: ARIZ, COLO, DS, FPF, MO, RM, UC, UT). *A. campylopodum* Engelm. var. *cryptopodum* (Engelm.) Jepson, Manual of Flowering Plants of California 284. 1925.

Description: Mean shoot height ca. 8 cm (max. 12) cm, greenish to bright yellow, turning brown at base of older shoots, flabellately branched (fig. 16.28). Basal diameter of dominant shoots 1.5–4.0 (mean 2) mm. Third internode 6–16 (mean 10.5 ± 2.9) mm long, 1–2 (mean 1.5) mm wide (8 collections), length/width ratio 7.0:1. Flowers axillary. Staminate flowers 3.3 mm across; perianth 3- or 4-merous, segments ca. 1.5 mm long, 1.1 mm wide. Mean anther diameter 0.5 mm, centered 0.7 mm from tip of segment. Pollen polar diameter 18–23 (mean 20) µm; equatorial diameter 19–25 (mean 23) µm; polar/equatorial diameter ratio 1:1.12; spine height (ca. 1.6 µm), approximately 2 × wall thickness (ca. 0.8 µm) (4 collections). Mature fruit 4 × 2.5 mm; proximal portion ca. 2.0 mm long. Seeds 3.2 × 1.2 mm. $n = 14$.

Phenology: Meiosis in July. Anthesis usually in mid-July to mid-August, with extremes from early July to late August (fig. 16.29). Fruits mature from mid-September to mid-October, with extremes from late August to early November; maturation period averages ca. 13–14 months.

Hosts: The only principal host is sugar pine, *Pinus lambertiana*, but *P. monticola* is sometimes parasitized when it grows in association with infected *P. lambertiana*. This dwarf mistletoe induces large, compact witches' brooms in *P. lambertiana* (fig. 16.30).

Figure 16.28 –*Arceuthobium californicum,* pistillate plant with maturing fruits; note greenish-yellow color of shoots. (D.L. Nickrent)

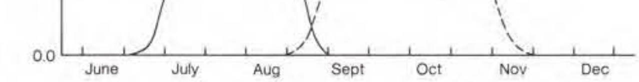

Figure 16.29 –Phenology of flowering and seed dispersal of *Arceuthobium californicum* (based on 28 observations).

Distribution: United States (California) (fig. 16.31). This species is distributed from Mt. Shasta southward through the North Coast Range and through the Cascade Range south to Lake County and the west side of the Sierra Nevada, ultimately reaching the Cuayamaca Mountains in San Diego County. Elevational range is 600–2,000 m.

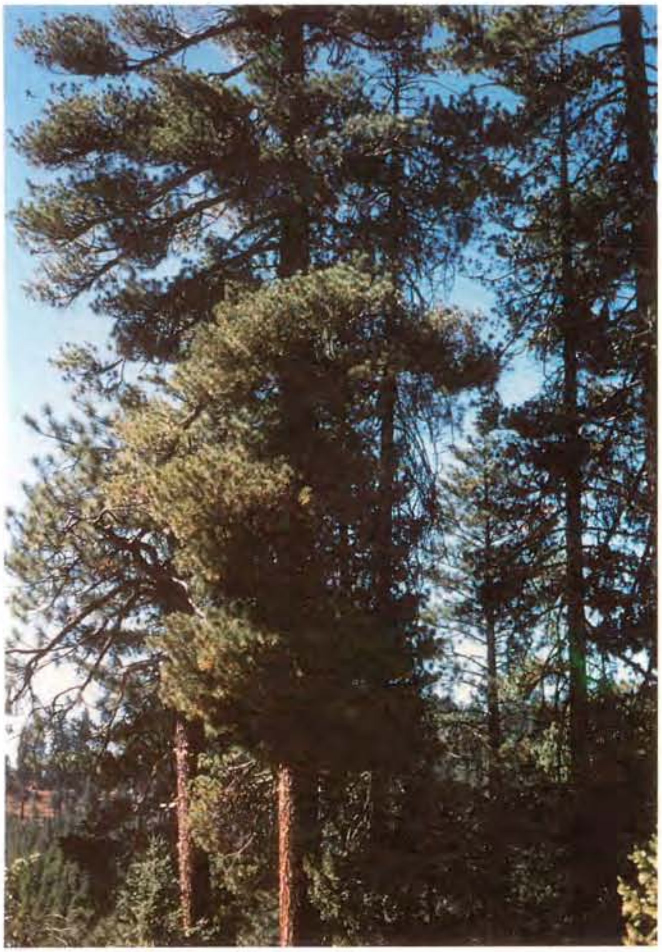

Figure 16.30 –*Pinus lambertiana* showing witches' brooms induced by infection with *Arceuthobium californicum.* (D.L. Nickrent)

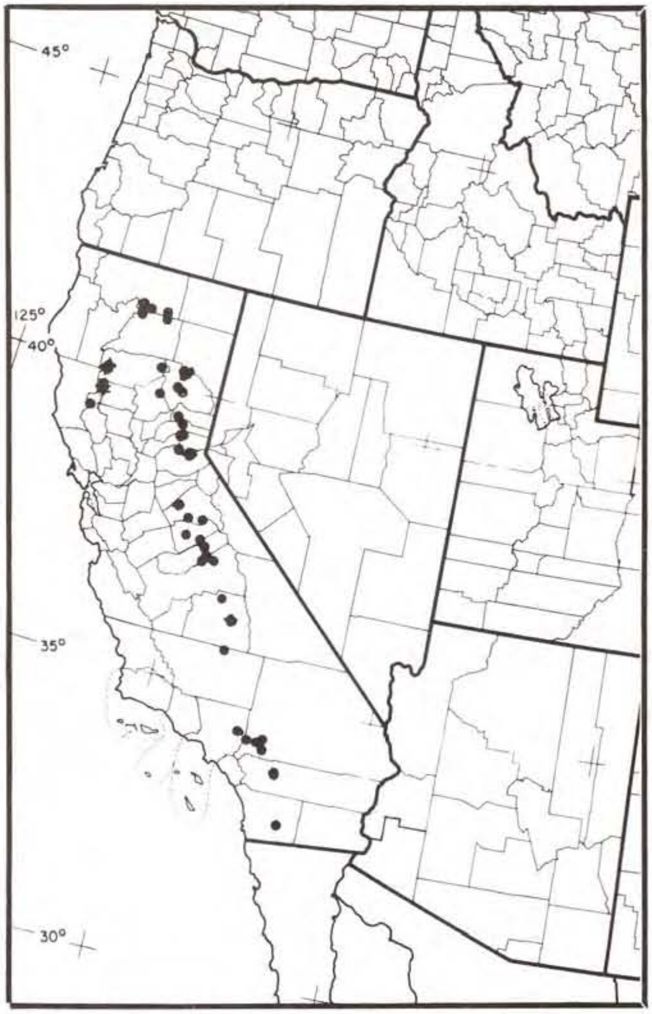

Figure 16.31 –Distribution of *Arceuthobium californicum.*

Discussion: Jepson's (1925) variety *cryptopodum*, which was intended to include parasites of *Pinus lambertiana* and *Abies grandis*, is based on a misapplied name, *Arceuthobium cryptopodum* Engelm., a Rocky Mountain parasite of *P. ponderosa*. As discussed under *Arceuthobium apachecum*, Gill's *A. campylopodum* f. *blumeri* includes four species—*A. apachecum, A. blumeri, A. californicum,* and *A. monticola.* A comparison of *A. californicum* and *A. monticola* is presented in table 16.2.

Concerning this dwarf mistletoe, Gill (1935) commented that "infected trees are infrequent and were found only in the presence of other infected species." Our studies do not support this observation. *Arceuthobium californicum* is common in many areas, rarely infects other species, and is a serious pathogen of *Pinus lambertiana* in California (Scharpf and Hawksworth 1968). Surveys found the parasite on 22% of 274 *P. lambertiana* plots in California (Anonymous 1968). In many instances *A. californicum* is the only dwarf mistletoe present in a stand, but it is sympatric with *A. campylopodum* or *A. abietinum* (this may have been the basis for Gill's statement).

Arceuthobium cyanocarpum did not parasitize *Pinus lambertiana* in the San Jacinto Mountains of southern California, the only instance we know of where *P. lambertiana* has been exposed to this dwarf mistletoe. These two dwarf mistletoes are morphologically distinct, and each is restricted to its respective host.

Arceuthobium campylopodum
Western Dwarf Mistletoe

9. *A. campylopodum* Engelmann in Gray, Boston Journal Natural History 6: 214, 1850. TYPE COLLECTION: "Oregon," on *Pinus ponderosa, Geyer 577* in 1843 (Lectotype GH! Isotype US). *A. campylopodum* Engelm. var. *macrarthron* Engelm., loc. cit. *Razoumofskya campylopoda* (Engelm.) Kuntze, Revision of Genera of Plants 2: 587, 1891. *A. campylopodum* Engelm. forma *typicum* Gill, Transactions Connecticut Academy Arts and Sciences 32: 185, 1935 (in part).

TABLE 16.2–Comparison of *Arceuthobium californicum* and *A. monticola*

Character	*A. californicum**	*A. monticola†*
Shoot height range (mean)	6–12 (8) cm	5–10 (7) cm
Shoot color	Yellow to greenish	Dark brown
Basal shoot diameter (mean)	1.5–4 (2) mm	2–4 (3) mm
Third internode length (mean) × width	5–16 (10) × 1.5 mm	8–15 (12) × 2 mm
Mature fruit length × width	4 × 2.5 mm	4 × 2 mm
Peak flowering period	July	July–August
Peak seed dispersal period	September	October–November
Parasitism of *Pinus lambertiana*	Common	Rare
Parasitism of *Pinus monticola*	Rare	Common

*Character values based on 8 collections.

†Character values based on 26 collections.

Description: Mean shoot height ca. 8 (max. 13) cm, olive green to yellow, flabellately branched (fig. 16.32). Staminate plants brownish, and pistillate plants greenish (particularly in northern populations). Basal diameter of dominant shoots 1.5–5.0 (mean 3) mm. Third internode 7–22 (mean 11.3 ± 3.8) mm long, 1.5–2.5 (mean 2.0) mm wide (27 collections), length/width ratio 5.6:1. Staminate flowers 3.0 mm across; perianth 3-merous (occasionally 4-merous), segments ca. 1.4 mm long, 1.0 mm wide. Mean anther diameter 0.5 mm, centered 0.8 mm from tip of segment. Pollen polar diameter 18–25 (mean 20) µm; equatorial diameter 20–27 (mean 24) µm; polar/equatorial diameter ratio 1:1.18; spine height (ca. 2.2 µm) about 2.5 times wall thickness (ca. 0.8 µm) (5 collections). Mature fruit 5.0 × 3.0 mm. $n = 14$.

Phenology: Meiosis in July. Peak anthesis usually from mid-August to early October, with extremes from early August to late October (fig. 16.33). Fruits usually mature from early September to mid-November, with extremes from late August to late November; maturation period averages ca. 13 months.

Hosts: The principal and most commonly infected hosts are *Pinus ponderosa* var. *ponderosa* and *P. jeffreyi*. According to Wagener (1965) and R. F. Scharpf (personal communication), *P. jeffreyi* is somewhat more susceptible than *P. ponderosa*, but both species incur considerable damage and are classed here as principal hosts. Other trees frequently infected, particularly when associated with the above hosts, are *P. coulteri* and *P. attenuata*. The three races of variety

Figure 16.32–*Arceuthobium campylopodum*, pistillate plant with mature fruits. (D. L. Nickrent)

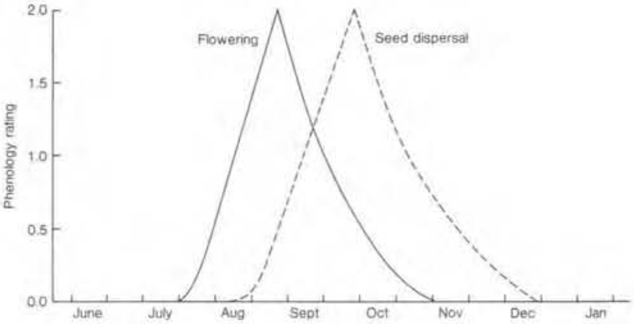

Figure 16.33–Phenology of flowering and seed dispersal of *Arceuthobium campylopodum* (based on 187 obervations).

ponderosa recognized by Conkle and Critchfield (1988)—North Plateau, Pacific, and Southern California—appear to be about equally susceptible. In the Spring (Charleston) Mountains of southern Nevada, *P. ponderosa* var. *scopulorum* is a common host, but this is the only known area where *Arceuthobium campylopodum* occurs naturally within the range of variety *scopulorum*. In Oregon, Roth (1967) inoculated varieties *scopulorum* and *ponderosa* and found them to be about equally susceptible to *A. campylopodum*. Occasional hosts for *A. campylopodum* are *P. contorta* vars. *latifolia* and *murrayana*. T. W. Childs (personal communication) informed us that *P. lambertiana* is very rarely infected by *A. campylopodum* in the vicinity of Hammer Butte in northern Klamath County, Oregon.

In certain areas in the southern Sierra Nevada where *Pinus sabiniana* occurs above the elevational range of *Arceuthobium occidentale, A. campylopodum* occasionally parasitizes *P. sabiniana* associated with infected *P. ponderosa* or *P. jeffreyi*. However, little or no cross-infection occurs in areas where the two dwarf mistletoes occur sympatrically (chapter 6 and 14).

Weir (1918a) successfully inoculated seedlings of *Pinus sylvestris, P. mugo* (as *P. montana*), *P. resinosa, Picea abies, Abies concolor, A. grandis,* and *Larix occidentalis* with *Arceuthobium campylopodum*. The latter three species are commonly associated with *Pinus ponderosa* when it is infected by *A. campylopodum*, but we have never observed the parasite on any of them. Kuijt (1960b) found the European *Pinus pinaster* infected naturally at the Institute of Forest Genetics Arboretum at Placerville, California, and J. R. Weir collected *A. campylopodum* on planted *P. sylvestris* near Hayden Lake, Idaho.

Pinus washoensis is probably susceptible to *Arceuthobium campylopodum*, but we know of no collections on this host. We found no infections on the extensive populations of this tree in the vicinity of Patterson Guard Station in the southern end of the Warner Mountains, Modoc County, California. Similarly, R. S. Peterson (personal communication) found no dwarf mistletoe in the type locality for *P. washoensis* on Mt. Rose, near Reno, Nevada.

Distribution: United States (Washington, Idaho, Oregon, California, and Nevada) and Mexico (Baja California Norte) (fig. 16.34). *Arceuthobium campylopodum* occurs from northern Washington and eastern Idaho, south through Oregon and California (but it is not known in the southern Coast Range) to the Sierra Juárez and Sierra de San Pedro Mártir in Baja California, Mexico. In Nevada, it occurs in the vicinity of Lake Tahoe and in the Spring (Charleston) Mountains of Clark County. *Arceuthobium campylopodum* is not known from British Columbia, but it occurs within about 30 km of the international boundary near Kettle Falls, Washington. Gill's (1935) report of this species in western Montana is based on occasional parasitism of *Pinus ponderosa* by the larch dwarf mistletoe, *A. laricis*.

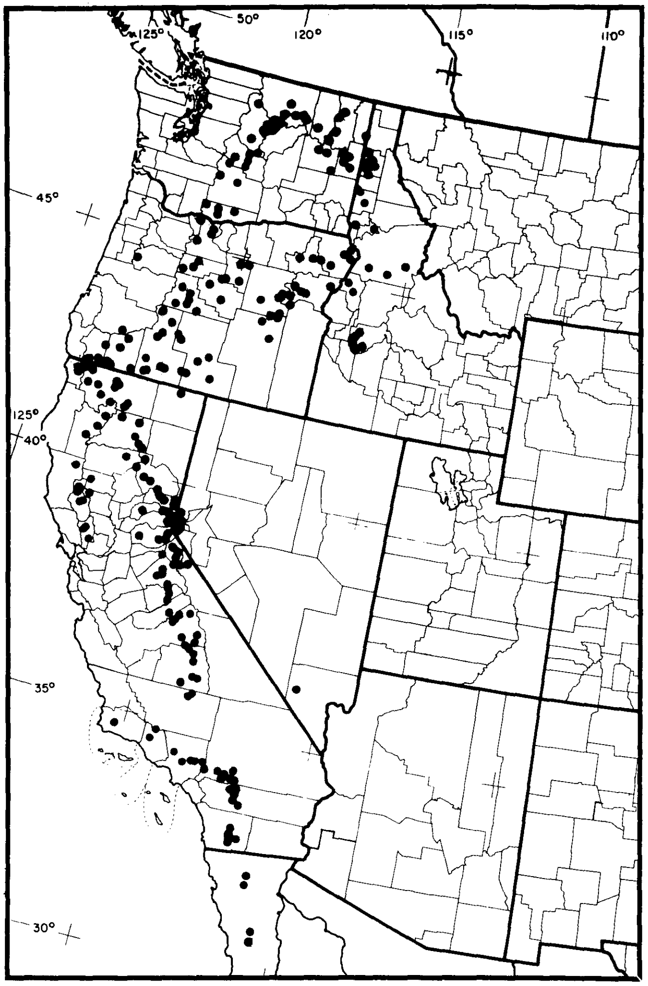

Figure 16.34 –Distribution of *Arceuthobium campylopodum*.

Arceuthobium campylopodum is distributed by elevation from 30 m along the Columbia River, near Hood River, Oregon, to 2,500 m in the Spring (Charleston) Mountains of southern Nevada.

Discussion: The type locality is listed as "Oregon," although Piper (1906) comments that the specimen must have come from northern Idaho or northeastern Washington, because Geyer did not collect in the area that is now Oregon.

G. G. Hedgcock (unpublished manuscript dated 1914) noted differences between *Arceuthobium campylopodum* and *A. occidentale* and suggested that they warranted separate taxonomic status. Gill's

(1935) *A. campylopodum* f. *typicum* is here considered to comprise four species—*A. campylopodum (sensu stricto)*, *A. occidentale, A. siskiyouense,* and *A. littorum* (Hawksworth and others 1992b). These are separable on the basis of phenology, morphology, geographic distribution, and host preference.

Arceuthobium campylopodum is a serious pathogen of *Pinus jeffreyi* and *P. ponderosa* (fig. 16.35). Our observations suggest that host damage is more severe in the southern parts of the distribution; the most severely infested stands occur in the Laguna Mountains in San Diego County, California. In the northern Sierra Nevada, pathogenic effects are more severe on the drier east-side forests than along the wetter west-side forests. Roth (1966) reports that drooping-needled races of *P. ponderosa* in Oregon are less frequently infected by the dwarf mistletoe than are populations with typical needles, but grafts from these trees showed no evidence of resistance (Roth 1974a and chapter 13). Recently, Scharpf (1987) has shown that some populations of *P. jeffreyi* show high resistance to infection by *A. campylopodum*.

Figure 16.35 –Extensive infection of *Pinus ponderosa* var. *ponderosa* by *Arceuthobium campylopodum*. (D. L. Nickrent)

Arceuthobium cyanocarpum
Limber Pine Dwarf Mistletoe

10. *A. cyanocarpum* (A. Nelson ex Rydberg) Coulter & Nelson, New Manual of Botany of the Central Rocky Mountains, p. 146, 1909. TYPE COLLECTION: WYOMING: Carbon County: Ferris Mountains, on *Pinus flexilis, Nelson 4959* in 1898 (Lectotype RM! Isotypes: NY, MO). *Razoumofskya cyanocarpa* A. Nelson in Rydberg, Colorado Agricultural Experiment Station Bulletin 100: 101, 1906. *A. cyanocarpum* (A. Nels.) Abrams, Illustrated Flora Pacific Coast States I: 531, 1923. *A. campylopodum* Engelm. forma *cyanocarpum* (A. Nels.) Gill, Transactions Connecticut Academy Arts and Sciences 32: 204, 1935.

Description: Mean shoot height ca. 3 (max. 7) cm, yellow green, flabellately branched, densely clustered (fig. 16.36). Basal diameter of dominant shoots 1–2 (mean 1.4) mm. Third internode 2–14 (mean 5.2 ± 2.0) mm long, 1.0–1.5 (mean 1.1) mm wide (15 collections); length/width ratio 4.7:1. Staminate flowers 3.0 mm across; perianth 3-merous (rarely 4-merous), same color as shoots; segments ca. 1.4 mm long, 1.0 mm wide, apex acute. Mean anther diameter 0.4 mm, centered 0.7 mm from tip of segment. Pollen polar diameter 15–21 (mean 19) µm; equatorial diameter 20–25 (mean 22) µm; polar/equatorial diameter ratio 1:1.19; spine height (ca. 1.5 µm) approximately 2 × wall thickness (ca. 0.8 µm) (6 collections). Mature fruit 3.5 × 2.0 mm; proximal portion ca. 2.0 mm long. Seeds 2.0 × 0.9 mm. $n = 14$.

Figure 16.36 –*Arceuthobium cyanocarpum,* staminate plant showing the typically short shoots densely clustered around the stem.

Phenology: Meiosis in July. Peak anthesis from mid-July to early September, with extremes from early July to mid-September (fig. 16.37). Fruits mature from mid-August to late September; maturation averages ca. 12 months. Seed germination mostly in June.

Hosts: *Pinus flexilis* is the most common host of this dwarf mistletoe throughout its extensive geographical distribution. However, *P. aristata, P. longaeva,* and *P. albicaulis* are also classed as principal hosts because, even though they are not as common within the range of *Arceuthobium cyanocarpum*, they appear to be about as susceptible as *P. flexilis*. Infection of *P. aristata* is known from only an area near La Veta Pass in southern Colorado where this mistletoe is also common on associated *P. flexilis*. *Pinus longaeva* is parasitized in many areas in Utah and Nevada, and *P. albicaulis* is infected in western Wyoming, northern Nevada, central Oregon, and northern California.

Pinus monticola in northern California and *Tsuga mertensiana* in central Oregon are secondary hosts of

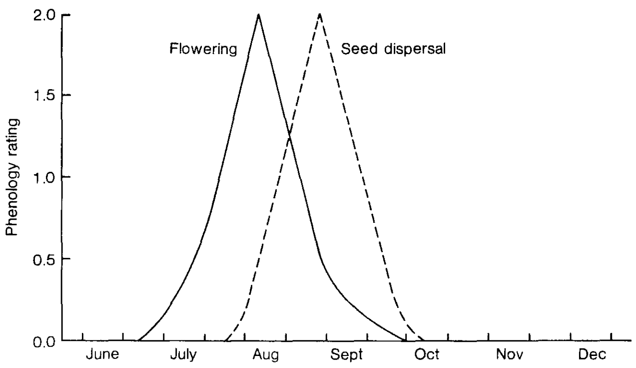

Figure 16.37–Phenology of flowering and seed dispersal of *Arceuthobium cyanocarpum* (based on 97 obervations).

this dwarf mistletoe (Mathiasen and Hawksworth 1988). *Pinus balfouriana* subsp. *balfouriana* is an infrequently but severely infected host in northern California (Miller and Bynum 1965, Mathiasen and Hawksworth 1988). No dwarf mistletoe has been found on the southern subspecies of foxtail pine, *P. balfouriana* subsp. *austrina,* in the southern Sierra Nevada in California. *Pinus ponderosa* var. *scopulorum* and *P. contorta* var. *latifolia* are rare hosts in the Rocky Mountains (Hawksworth and Peterson 1959). Von Tubeuf (1919) mentions a single collection of dwarf mistletoe on *Picea engelmannii* from Pikes Peak, Colorado, which Hawksworth and Graham (1963) surmised was *Arceuthobium cyanocarpum.*

Greenhouse inoculations of the seedlings of both *Pinus strobus* and *P. strobiformis* show that they are also susceptible to infection by *Arceuthobium cyanocarpum* (Hawksworth and Wiens 1972).

Distribution: United States (Idaho, Montana, Oregon, California, Nevada, Utah, Wyoming, and Colorado) (fig. 16.38). This dwarf mistletoe occurs from southern Montana (Brown 1970) and northern Wyoming south to southern Colorado and west to Oregon and California where it occurs on the east side of the Sierra Nevada, in the Panamint Mountains in Death Valley National Monument (Johnson 1976) and in the San Bernardino and San Jacinto Mountains of southern California.

Arceuthobium cyanocarpum occurs on many mountain ranges in Wyoming and Utah, including an isolated locality in the La Sal Mountains, near the Utah–Colorado border. *Arceuthobium cyanocarpum* is common in northern Colorado from near Idaho Springs to the Wyoming border, and it occurs in three other isolated localities in Colorado—Pikes Peak, Sangre de Cristo Mountains near Coaldale, and Silver Mountain near La Veta Pass. *Arceuthobium cyanocarpum* is presently known from only four localities in Idaho. The species is widely distributed in the mountain ranges of Nevada on *Pinus flexilis, P. longaeva, and P. albicaulis* (Mathiasen and Hawksworth 1990). The specimens listed by Gill (1935) as *A. campylopodum* f. *cyanocarpum* on *P. albicaulis* from the Crater Lake region of Oregon are referable to *A. tsugense* subsp. *mertensianae.* The only verified collection of *A. cyanocarpum* in Oregon is at Three Creek Lake, southwest of Sisters, on *P. albicaulis* and *Tsuga mertensiana* (Knutson and Tinnin 1981). We have tentatively listed a collection on *P. albicaulis* from "Obsidian Cliff," Oregon, as this species, but we have not been able to locate the site. We previously identified the dwarf mistletoe on *P. aristata* on the San Francisco Peaks, Arizona, as *A. cyanocarpum* (Hawksworth and Wiens 1972). That population, however, has since been transferred to *A. microcarpum* (Crawford and Hawksworth 1979, Mathiasen and Hawksworth 1980). *Arceuthobium cyanocarpum* apparently does not occur in Arizona.

Weir collected *Arceuthobium cyanocarpum* in 1913 and 1917 on *Pinus flexilis* in the vicinity of Anaconda, Montana. Several attempts to locate these populations were unsuccessful. Possibly sulfur dioxide fumes have resulted in its extirpation in this area. Scheffer and Hedgcock (1955), who studied the area in the late 1920's, noted that *P. flexilis* and *A. cyanocarpum* were relatively rare in the fume-damaged area.

Distribution maps for *Arceuthobium cyanocarpum* are available for Colorado (Hawksworth 1987c) and Nevada (Mathiasen and Hawksworth 1990). Elevational range is 1,600 m in southern Montana to nearly 3,050 m in central Colorado.

Discussion: Although Rydberg (1906) stated that he described no new species in that publication, Tiehm (1989) concluded that he did, in fact, validly describe several new species, including *Razoumofskya cyanocarpa.* We concur with Tiehm and accept Rydberg (1906) as having provided the first valid description of the species.

This dwarf mistletoe, which characteristically infects *Pinus flexilis* and associated high-altitude white pines, is easily recognized by its small, densely clustered shoots, especially the staminate plants (fig. 16.36). In many cases shoot mortality is very high (the cause is unknown but is probably associated with a secondary fungal pathogen).

Arceuthobium cyanocarpum causes heavy mortality in *Pinus flexilis* in many areas in the Rocky Mountains and in *P. albicaulis* on the north slopes of Mt. Shasta, California. In the latter locality, the high

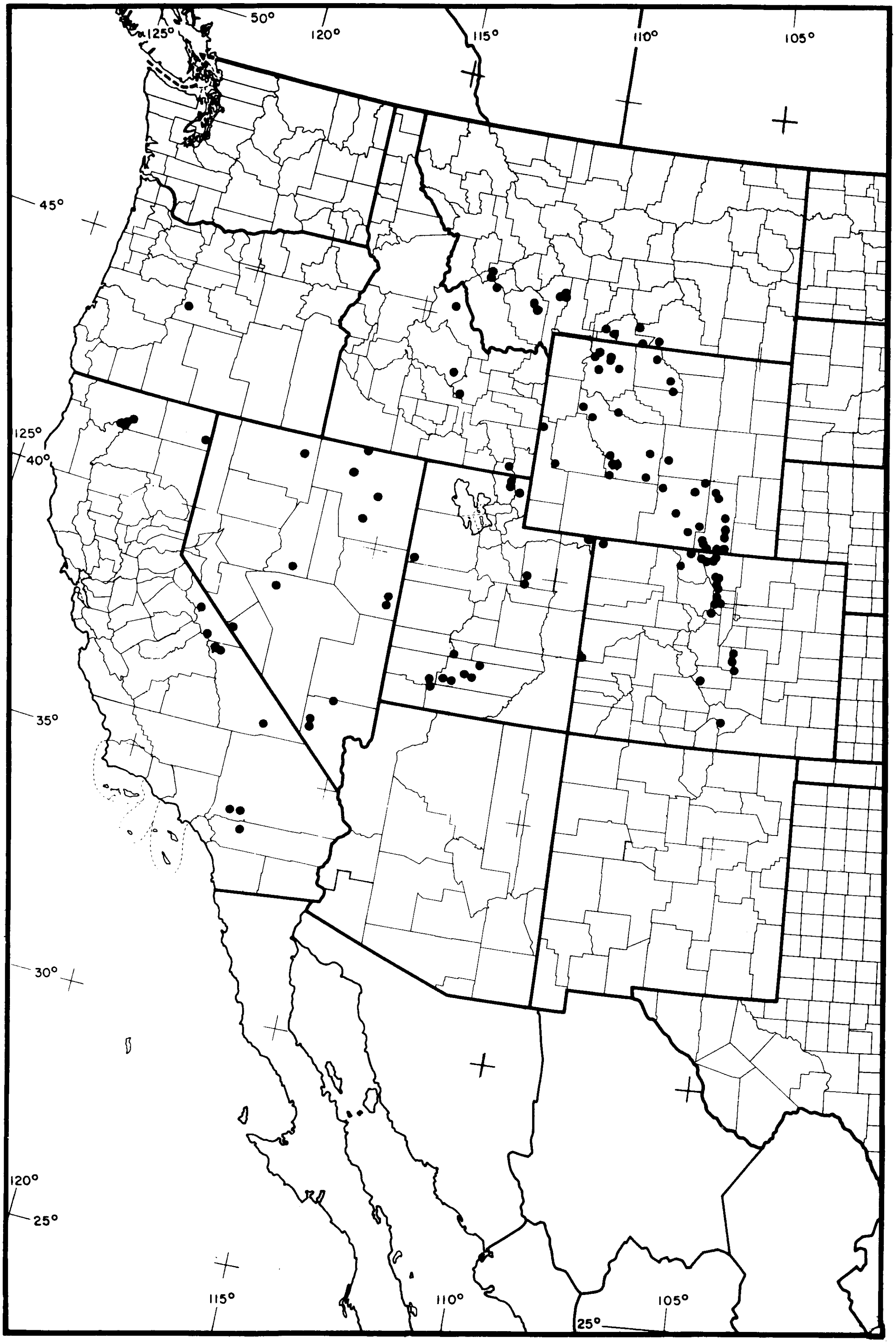

Figure 16.38 –Distribution of *Arceuthobium cyanocarpum.*

mortality caused by the dwarf mistletoe has resulted in large areas of "ghost forests" (Cooke 1955, Mathiasen and Hawksworth 1988).

Witches' brooms induced by *Arceuthobium cyanocarpum* are typically small and compact (fig. 16.39). In many instances, however, infection is general throughout the crown of the tree.

Figure 16.39 –Pinus albicaulis showing witches' brooms induced by infection with *Arceuthobium cyanocarpum.*

Arceuthobium divaricatum
Pinyon Dwarf Mistletoe

11. *A. divaricatum* Engelmann in U.S. Geographical Survey West of 100th Meridian (Wheeler Report) 6: 253, 1878. TYPE COLLECTION: ARIZONA: County unknown, Salt River Valley, on *Pinus edulis*, *Gilbert 116* in 1873 (Lectotype MO! Isotype US). *A. gracile* Engelmann in Gray, Memoires American Academy N.S. 4: 59, 1849, *nomen nudum. Razoumofskya divaricata* Coville, Contributions U.S. National Herbarium 4: 192, 1892. *A. campylopodum* Engelmann forma *divaricatum* (Engelm.) Gill, Transactions Connecticut Academy Arts and Sciences 32: 193, 1935.

Description: Mean shoot height ca. 8 (max. 13) cm, olive green to brown, flabellately branched (fig. 16.40). Basal diameter of dominant shoots 1.5–4.0 (mean 2) mm. Third internode 6–15 (mean 9.8 ± 2.4) mm long, 1–2 (mean 1.6) mm wide (19 collections), length/width ratio 6.1:1. Staminate flowers 2.5 mm across; perianth 3-merous; segments ca. 1.1 mm long, 0.9 mm wide. Mean anther diameter 0.5 mm, centered 0.5 mm from tip of segment. Pollen polar diameter 18–26 (mean 20) µm; equatorial diameter 21–30 mean 24 µm; polar/equatorial diameter ratio 1:1.17; spine height (1.6 µm) ca. 1.5 × the wall thickness (ca. 1.0 µm) (8 collections). Mature fruit 3.5 × 2.0 mm; proximal portion ca. 2.0 mm long. Seeds 2.0 × 0.9 mm. $n = 14$.

Figure 16.40 –Arceuthobium divaricatum parasitizing *Pinus edulis;* note olive green color of shoots.

Phenology: Meiosis in July. Peak anthesis usually from early August to late September (fig. 16.41). Fruits usually mature from early September to late October in the year following pollination; maturation period averages ca. 13 months.

Hosts: *Arceuthobium divaricatum* is restricted to pinyons. It is most common on *Pinus edulis* and *P. monophylla.* Other pinyons are also classed as principal hosts because they appear to be about equally susceptible to infection when the dwarf mistletoe is present—*P. quadrifolia, P. cembroides, P. discolor,* and *P. californiarum* subspecies *californiarum* and *fallax* (Bailey and Hawksworth 1988). *Arceuthobium divaricatum*, however, does not commonly occur within the distribution of the latter group of pinyons.

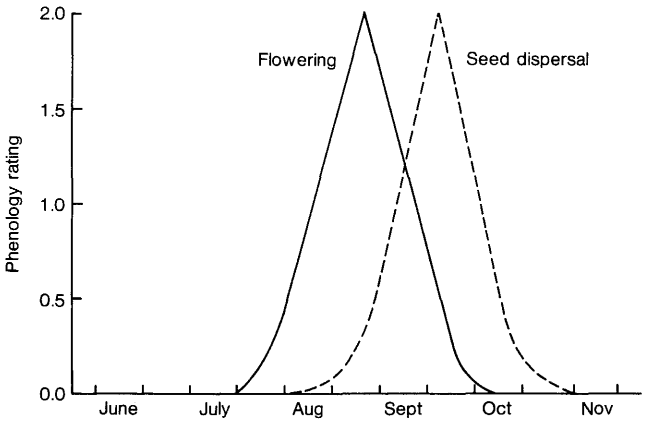

Figure 16.41 –Phenology of flowering and seed dispersal of *Arceuthobium divaricatum* (based on 104 obsevartions).

The principal host in California and Nevada is *Pinus monophylla*, but in Arizona, Colorado, New Mexico, Texas, and Utah the primary host is *P. edulis*. This dwarf mistletoe has been collected on *P. quadrifolia* only in the Sierra Juárez, Baja California (Hawksworth and others 1968), but it has been reported on this tree on the east slope of the Laguna Mountains in San Diego County, California (Beauchamp 1986), and in the Sierra San Pedro Mártir, Baja California (Hawksworth and others 1968). *Pinus cembroides* is parasitized only at the northern limits of its distribution in the Davis Mountains, Jeff Davis County, in west Texas. *Pinus discolor* is also parasitized only at its northern limits near Fort Bayard, and in the Mule Mountains, New Mexico, where this tree is associated with infected *P. edulis*. Infection is local on the two subspecies of *P. californiarum* it parasitizes—subsp. *californiarum* in several Mojave Desert ranges (New York Mountains, Providence Mountains, and in Joshua Tree National Monument) and subsp. *fallax* in southwestern Utah (Zion National Park), northwestern Arizona (Black Hole Mountains), and central Arizona near Prescott, Sedona, and Strawberry. Infected pinyons are not often associated with other pines, but where they are sympatric with *P. ponderosa* and *P. jeffreyi*, these trees were not parasitized by *Arceuthobium divaricatum*. No other dwarf mistletoe infects pinyon in the United States. *Arceuthobium pendens*, however, also parasitizes pinyons in Mexico.

Distribution: United States (California, Nevada, Utah, Colorado, Arizona, New Mexico, and Texas) and Mexico (Baja California) (fig. 16.42). *Arceuthobium divaricatum* occurs in eastern and southern California (the White and Inyo Mountains, the Mount Pinos area, the San Bernardino Mountains and the Mojave Desert Ranges), the southern three-fourths of Nevada and Utah, western Colorado, Arizona (except southwest), New Mexico (except northeast), and south to the Davis Mountains of western Texas. In Mexico it is known only in northern Baja California. J. R. Weir (unpublished manuscript, 1920) reported *A. divaricatum* on *Pinus monophylla* in Cassia County in southern Idaho, but we have not confirmed its presence there, nor do we know of any collections of this dwarf mistletoe from Idaho. The northernmost population of which we are aware is in the Pilot Range, western Box Elder County in northwestern Utah (latitude 44°30'N) (Albee and others 1988). *Arceuthobium divaricatum* has been reported on *P. discolor* (as *P. cembroides*) in the Santa Catalina Mountains in southern Arizona (G. G. Hedgcock, unpublished manuscript, 1914), but this has not been confirmed. We are aware of no collections from Arizona south of the Gila River.

Distribution maps have been published for *Arceuthobium divaricatum* in Colorado (Hawksworth 1987c), Utah (Albee and others 1988), and New Mexico (Martin and Hutchins 1980). Elevational range is from 1,200 m near Sedona, Arizona, to 3,000 m in the San Mateo Mountains of New Mexico.

Discussion: The type locality for *Arceuthobium divaricatum* is given by Gill (1935) as Salt "Run" Valley. The original label, however, is handwritten and scarcely legible, but it appears that Salt "River" Valley was the intended locality. Kuijt (1960a) points out the scattered distributions of this parasite in California. We suggest that *A. divaricatum* is probably more common than indicated by collections to date. The witches' brooms induced by this dwarf mistletoe are often poorly developed and not conspicuous because of the stunted habit of even healthy trees (fig. 16.43). Our observations suggest that witches' brooms are more consistent in *Pinus edulis* than in *P. monophylla*. Shoots of the mistletoe are often long, slender, and spreading, especially the staminate plants which also tend to have relatively few flowers per shoot.

Arceuthobium divaricatum is often associated with another mistletoe, *Phoradendron juniperinum*, a parasite of junipers, in the juniper–pinyon communities where both mistletoes may co-occur. The extent of their co-occurrence and the factors underlying their distribution could be a subject of considerable interest.

Arceuthobium douglasii Douglas-fir Dwarf Mistletoe

12. *A. douglasii* Engelmann in U.S. Geographical Survey West of 100th Meridian (Wheeler Report) 6: 253, 1878. TYPE COLLECTION: NEW MEXICO: Santa Fe County: Santa Fe River, on *Pseudotsuga menziesii*,

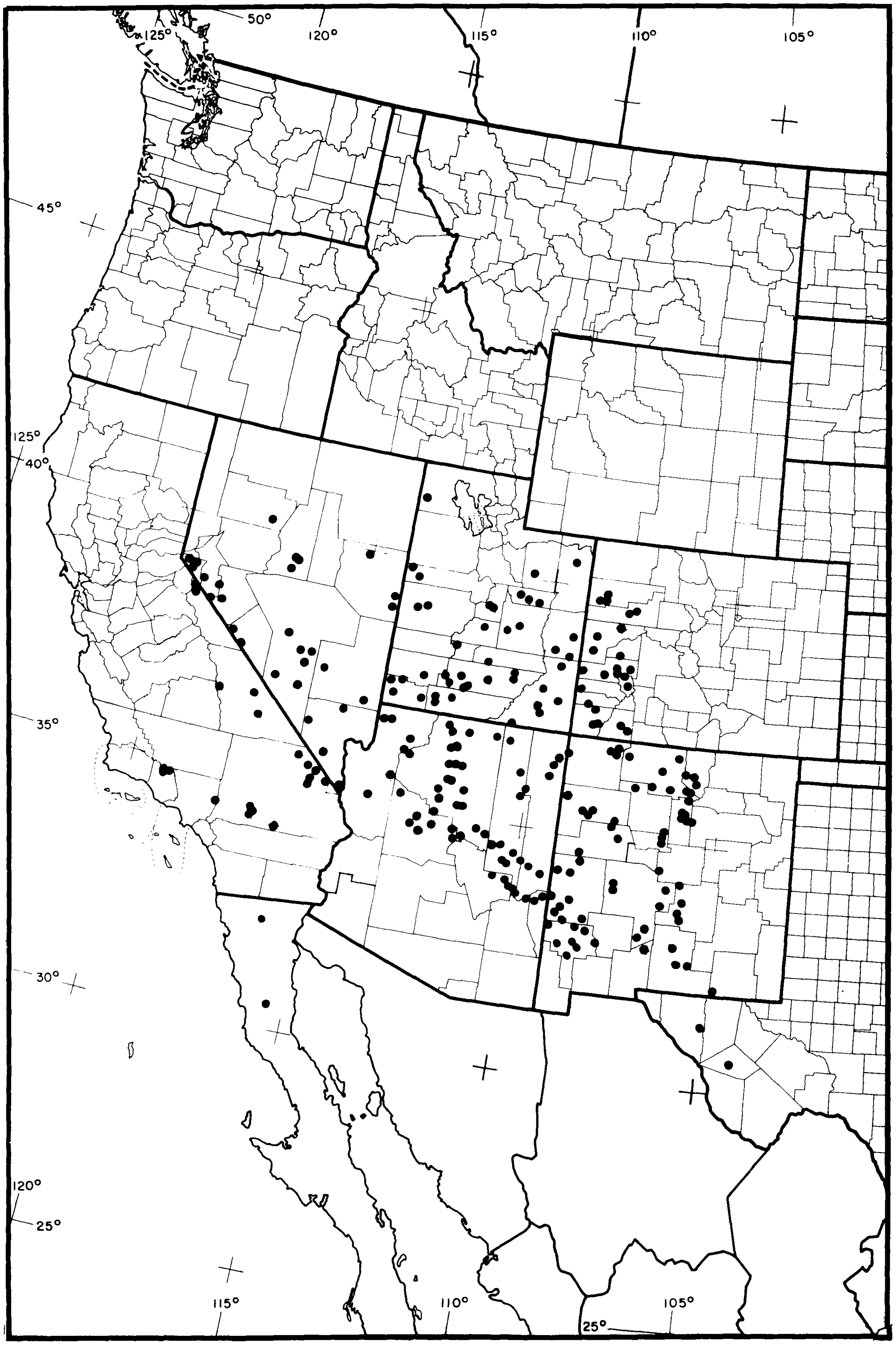

Figure 16.42–Distribution of *Arceuthobium divaricatum*. This also approximates the range of pinyon pines in the United States.

Figure 16.43 –*Pinus edulis,* probably killed as the result of infection with *Arceuthobium divaricatum;* note characteristic, small witches' brooms induced by this species.

Rothrock 69 in 1874 (Lectotype MO! Isotypes: F, US). *Razoumofskya douglasii* (Engelm.) Kuntze, Revision of Genera of Plants 2: 587, 1891.

Description: Mean shoot height ca. 2 (max. 8) cm, olive green, flabellately branched (fig. 16.44 and 16.45). Basal diameter of dominant shoots 1.0–1.5 (mean 1) mm. Third internode 2–6 (mean 3.6 ± 1.2) mm long, ca. 1.0 mm wide (29 collections), length/width ratio 3.6:1. Flowers usually axillary in pairs, occasionally borne on pedicel-like segments as in *Arceuthobium americanum*. Staminate flowers 2.0 mm long, 2.3 mm across; perianth mostly 3-merous (occasionally 4- or 2-merous); segments rounded at the apex, without a keel, inner surface reddish to purple, lower surface same color as shoots, ca. 1.0 mm long, 1.0 mm wide. Mean anther diameter 0.4 mm, centered 0.6 mm from tip of segment. Pollen polar diameter 16–25 (mean 21) µm; equatorial diameter 20–28 (mean 24) µm; polar/equatorial diameter ratio 1:1.16; spine height approximately equal to wall thickness (1.0–1.2 µm) (8 collections). Pistillate flowers ca. 1.5 mm long, 1.5 mm across. Mature fruit olive green 3.5–4.5 (mean 4) mm long, 1.5–2.0 mm wide, obovate; proximal portion ca. 2.5 mm long. Seeds 2.4 × 1.1 mm. $n = 14$.

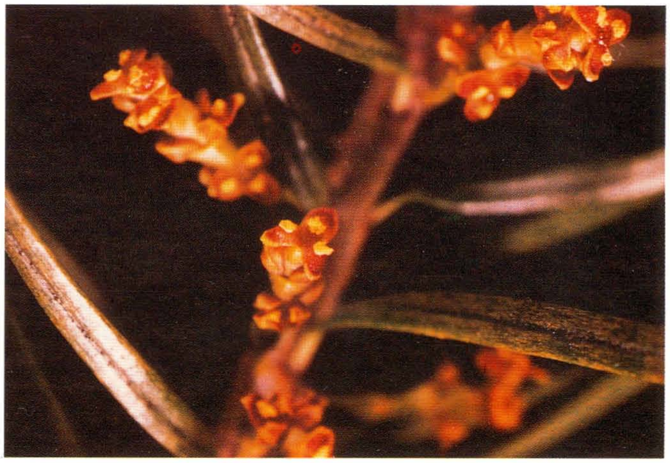

Figure 16.44 –*Arceuthobium douglasii,* staminate plant in flower. (E. F. Wicker)

Figure 16.45 –*Arceuthobium douglasii* showing the typical pattern of systemic infection.

Phenology: Staminate meiosis in September, pistillate meiosis in April (Jones and Gordon 1965). Peak anthesis is usually in April or May (fig. 16.46). However, this species exhibits a marked latitudinal variation in flowering—March in Mexico, late April to early May in Arizona and New Mexico, late May in

Colorado, Utah, Oregon, and early to mid-June in Washington, north Idaho, and Montana. In contrast, fruit maturity is more uniform and usually occurs from late August to late September throughout the distribution; maturation period averages 17–18 months. The seeds germinate in March (Wicker 1967a).

Hosts: The principal and only commonly infected host is *Pseudotsuga menziesii.* Both var. *menziesii* (Washington, Oregon, and California) and var. *glauca* (from British Columbia through the Rocky Mountains to central Mexico) are parasitized, although it is much more common on the inland variety. The following trees are occasional hosts when they are associated with infected *Pseudotsuga menziesii*: *Abies amabilis* in Oregon (Mathiasen and Loftis 1987) and *A. lasiocarpa* var. *arizonica* in Arizona and New Mexico (Mathiasen 1984). Rare hosts are *A. grandis* (Kuijt 1954a), *A. concolor* (Hawksworth 1952), *A. lasiocarpa* var. *lasiocarpa, Picea pungens,* and *P. engelmannii.* We concur with Kuijt (1960a) that reports of this dwarf mistletoe parasitizing *Pseudotsuga macrocarpa* (Jepson 1925, Munz 1935) are erroneous.

Distribution: Canada (British Columbia), United States (Washington, Idaho, Montana, Oregon, Wyoming, California, Nevada, Utah, Colorado, Arizona, New Mexico, and Texas) and Mexico (Chihuahua, Durango, Coahuila, and Nuevo León) (figs. 16.47, 16.48, and 16.49). *Arceuthobium douglasii* has the greatest latitudinal range (3,000 km) of any species in the genus (fig. 16.47). Its northernmost distribution is near Lytton and Sicamous in southern British Columbia, about 210 km north of the international boundary (Smith 1974, Wood 1986). This is somewhat north of the distribution given by Kuijt (1963). In Washington and Oregon, it occurs east of the Cascade Crest but is common on the Pacific slope from the Umpqua River drainage south to about latitude 40°N in northern California (California Forest Pest Council 1968). The report by Palmer and others (1983) of *A. douglasii* from the headwaters of the North Fork of the American River in Placer County, California, has not been confirmed and is probably in error. This dwarf mistletoe is common in eastern Washington, eastern Oregon, Idaho, western Montana, Idaho, Utah, Colorado, and New Mexico. It is rare in Nevada (Wheeler Peak, Hawksworth 1965c), Wyoming (Teton County, Hawksworth 1965c), and Texas (Guadalupe Mountains, Warnock 1974). The distribution of the dwarf mistletoe in Mexico is poorly known, and it is probably more widespread than the few available records in Chihuahua, Coahuila, Durango, and Nuevo León suggest (fig. 16.49).

The distribution of this species exhibits some interesting peculiarities. For further details refer to chapter 5.

Distribution maps of *Arceuthobium douglasii* have been published for British Columbia (Wood 1986), Montana (Dooling and Eder 1981), Utah (Albee and others 1988), Colorado (Hawksworth 1987c), New Mexico (Martin and Hutchins 1980), and California (Kuijt 1960a).

The altitudinal range of this dwarf mistletoe is correlated with latitude, and it occurs as low as 300 m near Lytton in southern British Columbia and as high as 3,250 m on Cerro Potosí in Nuevo León, Mexico.

Discussion: *Arceuthobium douglasii* is one of the most distinctive and stable species in the genus. In

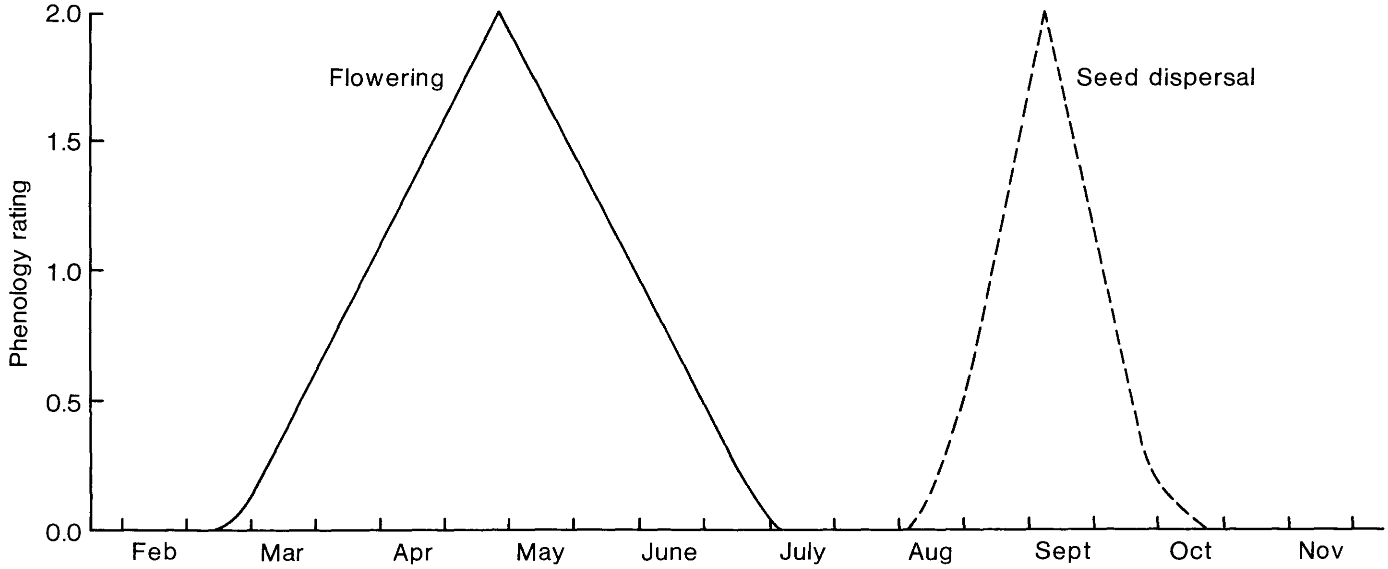

Figure 16.46–Phenology of flowering and seed dispersal of *Arceuthobium douglasii* in the western United States (based on 127 observations).

Figure 16.47 –General distribution of *Arceuthobium douglasii* in Canada, the United States, and Mexico.

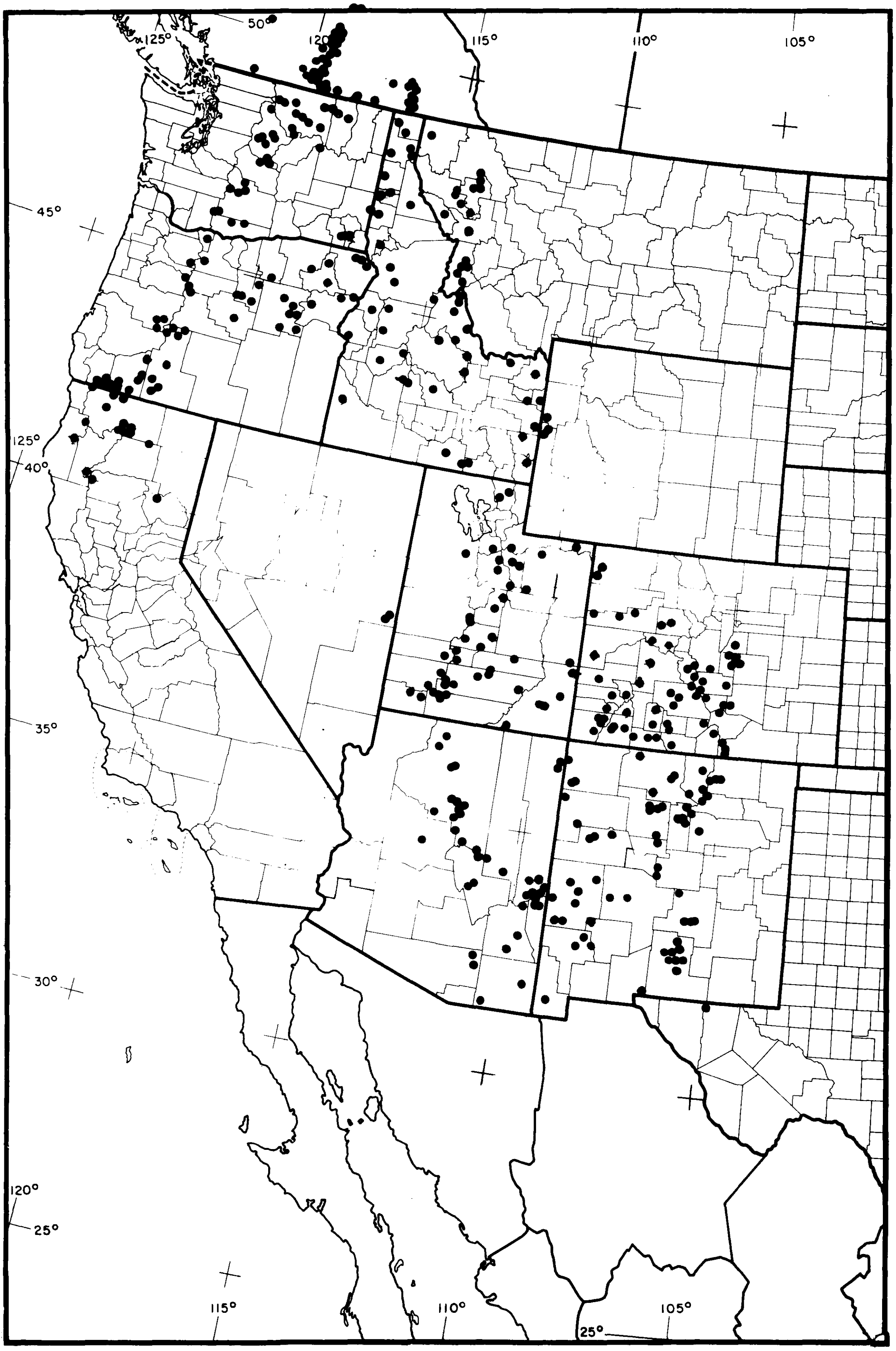

Figure 16.48–Distribution of *Arceuthobium douglasii* in the United States and southern British Columbia.

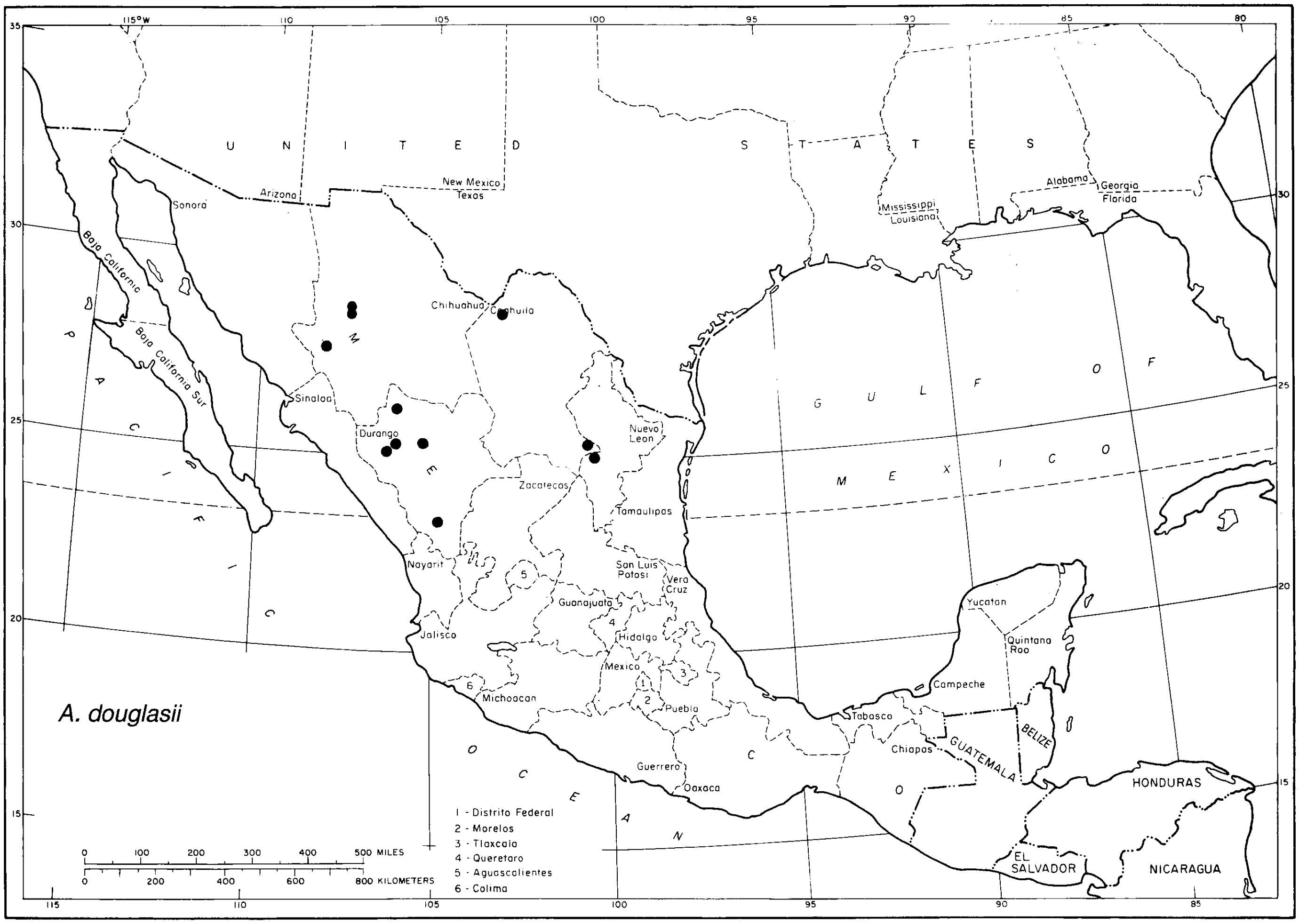

Figure 16.49 –Distribution of *Arceuthobium douglasii* in Mexico.

spite of its extensive latitudinal distribution, we find no characteristics that suggest subspecific separation. Much of the confusion in the literature on this species is due to its supposed affinities with various members of the *A. campylopodum* complex (Gill 1935). Weir (1918a) discussed the occurrence of "a small purple-flowered form on *Picea*" in the Inland Empire that he (and we) consider to be merely *A. douglasii* on an unusual host.

This dwarf mistletoe is the smallest in western North America, but its typically systemic mode of infection produces large witches' brooms (fig. 16.50) and causes severe growth loss and mortality in *Pseudotsuga menziesii.*

Arceuthobium durangense
Durangan Dwarf Mistletoe

13. *A. durangense* (Hawksworth & Wiens) Hawksworth & Wiens, Phytologia 66: 7, 1989. TYPE COLLECTION: MEXICO: Durango: 58 km west of El Salto on Route 40, on *Pinus durangensis, Hawksworth & Wiens 3507* in 1963 (Holotype COLO! Isotypes: DS, F, FPF, INIF, MEXU, MO, US). *A. vaginatum* subsp. *durangense* Hawksworth & Wiens, Brittonia 17: 230, 1965.

Description: Mean shoot height ca. 20–30 (max. 50) cm, bright orange; older shoots becoming pendulous (fig. 16.51). Basal diameter of dominant shoots 4–8 (mean 6) mm. Third internode 9–22 (mean 17.9 ± 4.1) mm long, 3.5–6.0 (mean 4.5) mm wide (3 collections), length/width ratio 3.3:1. Internodes often slightly swollen at base. Staminate flowers ca. 2.5 mm long, 2.5 mm across, segments ca. 1 mm long, 1 mm wide. Pollen polar diameter 18–19 (mean 18) µm; equatorial diameter 20–21 (mean 21) µm; polar/equatorial diameter ratio 1:1.15; spine height (1.5 µm) about 1.5 x wall thickness (1.0 µm) (1 collection). Mature fruit 7 x 3.5 mm; bluish; proximal portion ca. 4 mm long. Seeds 4 x 1.5 mm. $n = ?$

Phenology: Time of meiosis unknown (probably in February). Anthesis usually in April. Fruits mature

Figure 16.50 –Pseudotsuga menziesii showing systemic witches' brooms induced by infection with *Arceuthobium douglasii.*

Figure 16.51 –Arceuthobium durangense parasitizing *Pinus durangensis*; note pendulous older shoots and bright orange color.

from mid-July to September of the year following pollination; maturation period averages 15–18 months.

Hosts: *Pinus douglasiana, P. durangensis, P. montezumae, P. michoacana,* and *P. pseudostrobus* are the principal hosts. *Pinus herrerai* is secondarily parasitized when it occurs near infected principal hosts. *Pinus oocarpa* is reputed to be a host in Jalisco and southeastern Durango, but this requires confirmation. We have seen no collections from this tree. In the Sierra de Quilla, Jalisco, *P. oocarpa* growing with infected *P. montezumae* and *P. pseudostrobus* was not infected by *Arceuthobium durangensis.* The following pines have been observed growing near infected trees but were not themselves parasitized: *P. leiophylla* var. *leiophylla, P. lumholtzii,* and *P. teocote.*

Distribution: Mexico (Durango, Sinaloa, and Jalisco) (fig. 16.52). This rather local dwarf mistletoe occurs in extreme western Durango and adjacent Sinaloa on the western edge of the escarpment near the crest of the Sierra Madre Occidental and in the Sierra de Quilla in Jalisco. It probably occurs in other areas along the western slopes of the Sierra Madre Occidental, e.g., in Nayarit, but this region is difficult of access and little collected. Elevational range is 1,450–2,750 m.

Discussion: We originally classified this taxon as a subspecies in the *Arceuthobium vaginatum* complex, but our subsequent field studies have convinced us that it is a distinct species (Hawksworth and Wiens 1989). This dwarf mistletoe is not sympatric with either subspecies of *A. vaginatum*, and it differs from *A. vaginatum* subsp. *vaginatum* by its bright orange shoots and from *A. vaginatum* subsp. *cryptopodum* by its larger size, brighter color, branching pattern of the staminate spikes, larger fruit, and geographical distribution.

Arceuthobium gillii
Chihuahua Pine Dwarf Mistletoe

14. *A. gillii* Hawksworth & Wiens, Brittonia 16: 55, 1964. TYPE COLLECTION: ARIZONA: Cochise County: Huachuca Mountains, 0.8 km east of Reef, on *Pinus leiophylla* var. *chihuahuana, Hawksworth & Lightle 236*, in 1962 (Holotype COLO!, Isotypes: FPF, MO, ARIZ, DS).

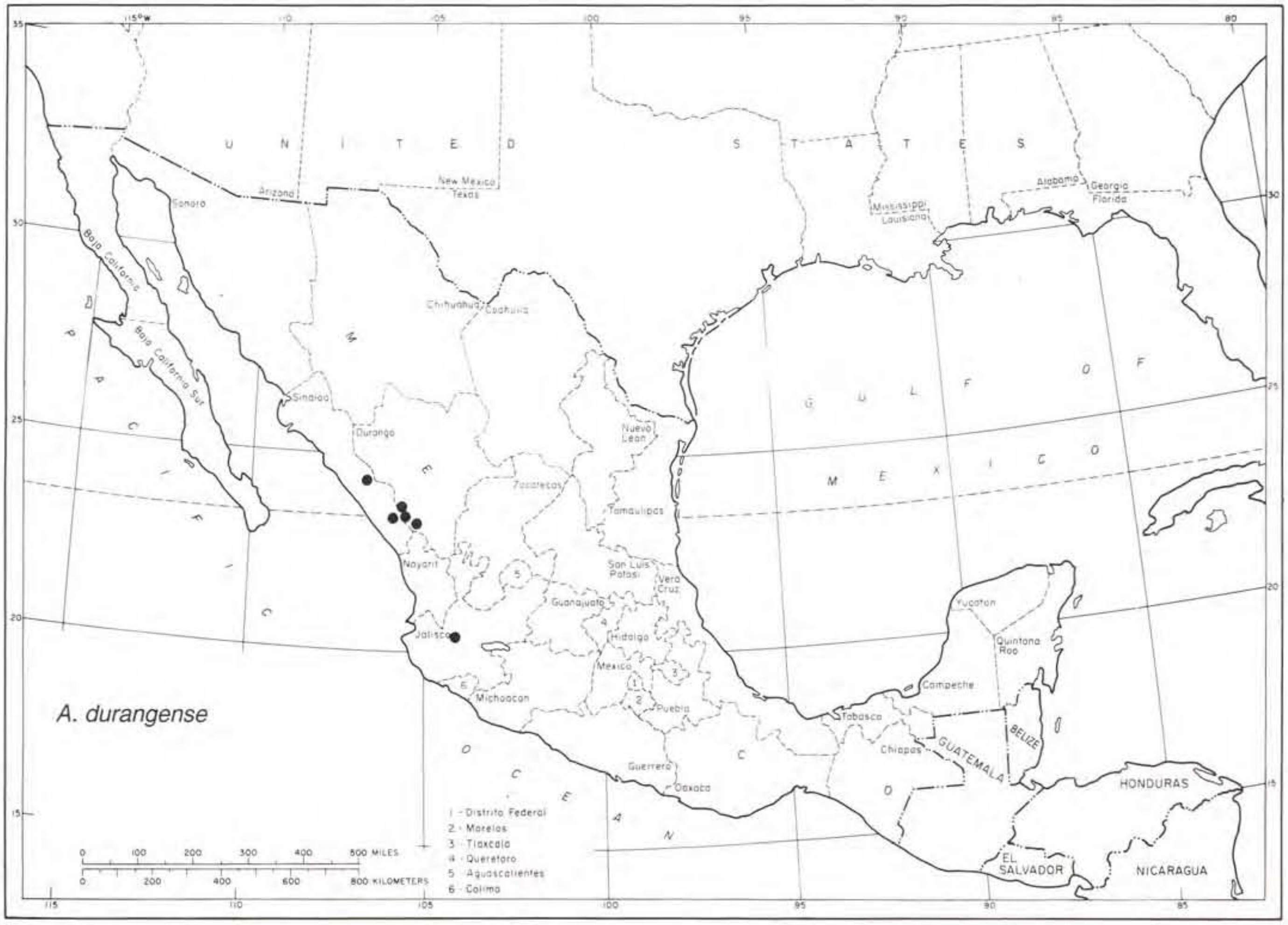

Figure 16.52–Distribution of *Arceuthobium durangense.*

Description: Mean shoot height ca. 8–15 (max. 25) cm, greenish brown, flabellately branched (fig. 16.53). Basal diameter of dominant shoots 2.5–8.0 (mean 4) mm. Third internode 5–18 (mean 10.7 ± 3.4) mm long, 2.0–4.5 (mean 2.8) mm wide (9 collections), length/width ratio 3.8:1. Staminate flowers 3.5 mm long, 2.5–4.0 (mean 3.2) mm across. Pollen polar diameter 19–25 (mean 22) µm; equatorial diameter 24–28 (mean 26) µm; polar/equatorial diameter ratio 1:1.19; spine height (1.7 µm) slightly greater than wall thickness (1.3 µm) (4 collections). Pistillate flowers ca. 1.5 mm long, 1 mm across. Mature fruit 4–5 mm long, 2–3 mm wide, the proximal portion of fruit conspicuously glaucous. Seeds 3.1 × 1.4 mm. $n = 14$.

Phenology: Meiosis in September. Anthesis usually in March and April. Fruits mature in October of the year following pollination; maturation period averages ca. 19 months, the longest in the genus. Seed germination begins in April (Chihuahua).

Hosts: The principal and only commonly infected hosts are *Pinus leiophylla* var. *chihuahuana,*

Figure 16.53 –*Arceuthobium gillii,* pistillate plant with mature fruits, parasitizing *Pinus leiophylla* var. *chihuahuana;* note the typical dense branching of pistillate plants and glaucous surface of the mature fruits.

P. lumholtzii, and *P. herrerai*. However, *P. leiophylla* var. *leiophylla* is about equally susceptible to the parasite but not common within the range of *Arceuthobium gillii*. In western Chihuahua, this dwarf mistletoe rarely parasitizes *P. cooperi* and *P. arizonica* var. *arizonica*. *Pinus ponderosa* var. *scopulorum* and *P. engelmannii* frequently occur in association with infected *Pinus leiophylla* var. *chihuahuana* in Arizona, but these two species are not parasitized.

Distribution: United States (Arizona and New Mexico) and Mexico (Chihuahua, Durango, Sinaloa, and Sonora) (fig. 16.54). This dwarf mistletoe occurs in southeastern Arizona (Santa Catalina, Rincon, Santa Rita, Huachuca, and Chiricahua Mountains) (Hawksworth and Wiens 1964) and the Animas Mountains in southwestern New Mexico (Hawksworth and Weiss 1975). It is most common in western Chihuahua but is also distributed in adjacent northern and eastern Sonora, northern Durango, and northeastern Sinaloa.

We have examined several additional populations of *Pinus leiophylla* var. *chihuahuana* in New Mexico (Bear Mountain near Silver City and in the Mule and Peloncillo Mountains) but *Arceuthobium gillii* was not found. Several localities in Arizona where *P. leiophylla* var. *chihuahuana* occurs have also been examined, but no *A. gillii* were observed in the Pinaleno (Mount Graham) and Pinal Mountains nor below the Mogollon Rim near Colcord Mountain, Gila County. Elevational range is from 1,700 m in southern Arizona to 2,650 m in southern Chihuahua.

Discussion: This dwarf mistletoe is named for Lake S. Gill. It had long been confused with *Arceuthobium vaginatum* subsp. *cryptopodum*, but it differs in host preference, phenology, and its conspicuously glaucous fruits (Hawksworth and Wiens 1964). These two dwarf mistletoes are usually separated by at least 300 m of elevation in Arizona and New Mexico. They co-occur, however, in several areas in central Chihuahua, but there was no evidence of hybridization.

A characteristic feature of *Arceuthobium gillii* is its strong sexual dimorphism—staminate plants are tall

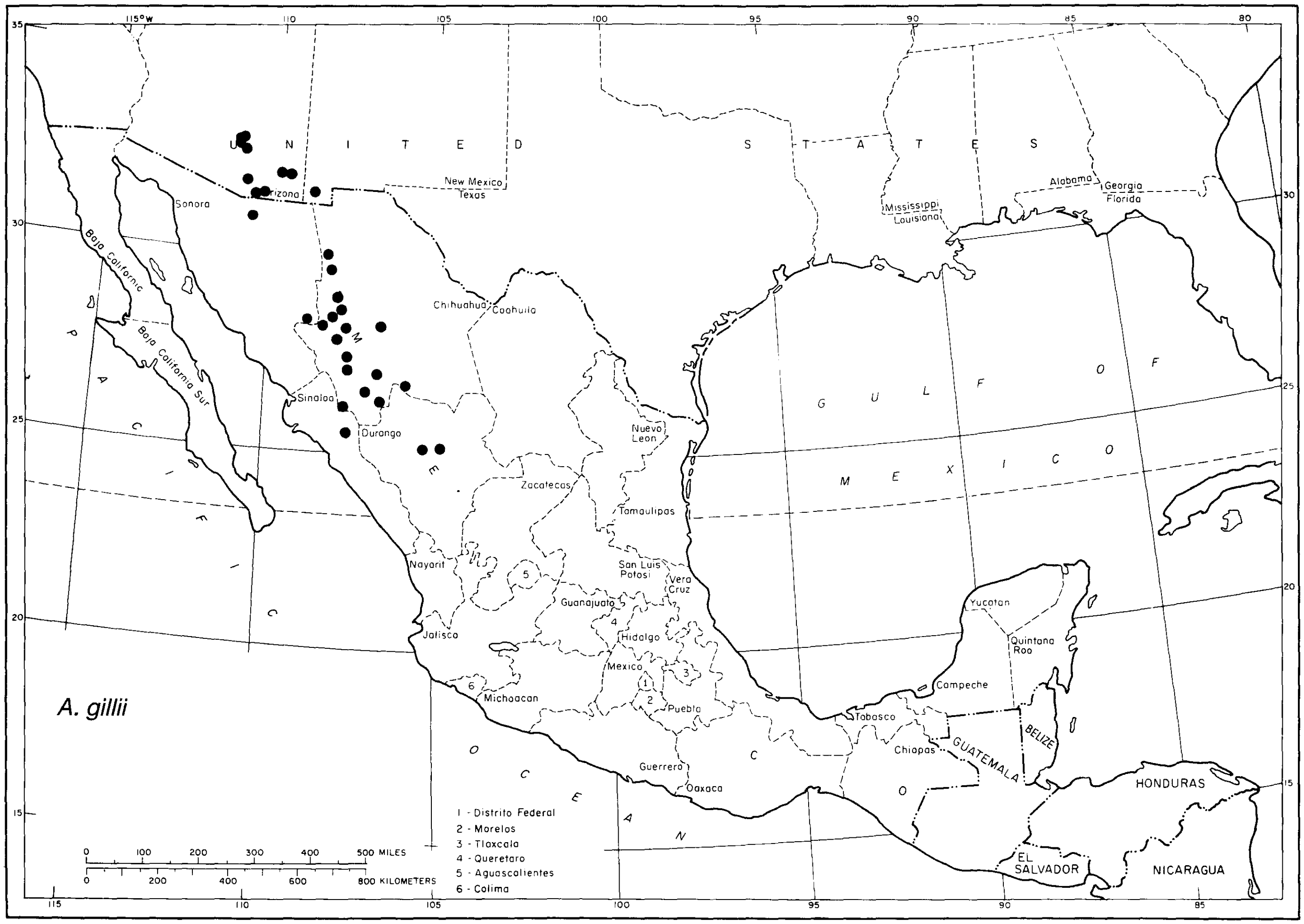

Figure 16.54 –Distribution of *Arceuthobium gillii* in Arizona, New Mexico, and Mexico.

and openly branched and the pistillate plants are small and densely branched.

This dwarf mistletoe causes open, non-systemic witches' brooms similar to those induced by *Arceuthobium nigrum*. It causes serious mortality in *Pinus leiophylla* var. *chihuahuana* and *P. lumholtzii* in Chihuahua, particularly on poor, rocky sites.

Arceuthobium globosum

15. *A. globosum* Hawksworth & Wiens, Brittonia 17: 223, 1965. TYPE COLLECTION: MEXICO: Durango: 2.4 km east of El Salto on Route 40, on *Pinus cooperi, Hawksworth & Wiens 3414* in 1963 (Holotype COLO! Isotypes: DS, F, FPF, INIF, MEXU, MO, US).

Description: Shoot height ca. 20–50 (max. 70) cm, yellow to greenish, flabellately branched. Basal diameter of dominant shoots 3–48 mm. Third internode 4–37 mm long, 2–24 mm wide. Staminate flowers ca. 3.5–5.0 mm long, 3.0–3.5 mm across; perianth 3- or 4-merous; same color as shoots; segments ca. 1.3 mm long, 1.0 mm wide. Mean anther diameter 0.6 mm, centered 0.9 mm from tip of segment. Pollen polar diameter 19–23 (mean 22) µm; equatorial diameter 24–28 (mean 26) µm; polar/equatorial diameter ratio 1:1.18; spine height (ca. 1.9 µm), ca. 2 × wall thickness (ca. 1.0 µm) (4 collections). Pistillate flowers ca. 1.5 mm long, 1.5 mm across. Mature fruit ca. 5–7 mm long, ca. 3–4 mm wide; proximal portion ca. 3.5 mm long, with pedicels 4.0–5.0 mm long. Seeds 5 × 2 mm. $n = 14$.

Hosts: Common on pines of subgenus *Diploxylon*.

Discussion: Previously, we (Hawksworth and Wiens 1972) noted that there was considerable variation within this dwarf mistletoe and that further field research was needed to determine whether the variation was sufficiently consistent to warrant the segregation of additional taxa. Subsequent studies in Mexico, Guatemala, and Belize have shown that the former *Arceuthobium globosum* (*sensu lato*) consists of five taxa (Hawksworth and Wiens 1977, Wiens and Shaw 1994):

- *Arceuthobium globosum* subsp. *globosum* (northwest Mexico)
- *Arceuthobium globosum* subsp. *grandicaule* (central Mexico and Guatemala)
- *Arceuthobium aureum* subsp. *aureum* (Guatemala)
- *Arceuthobium aureum* subsp. *petersonii* (southern Mexico)
- *Arceuthobium hawksworthii* (Belize)

Key to the subspecies:

1. Plants yellowish; shoots usually 15–20 (max. 50) cm tall, less than 1 cm in diameter at the base; witches' brooms not formed; shoots usually only on the host branches (not on trunk); northern Mexico .... 15a. *A. globosum* subsp. *globosum*

1. Plants greenish to yellow-green, typically dark at the base of older shoots; shoots usually 25–40 (max. 70) cm tall, greater than 1 cm in diameter at the base; witches' brooms usually induced; shoots on branches, but also frequently on the lower main trunks; central and southern Mexico to the highlands of western Guatemala .... 15b. *A. globosum* subsp. *grandicaule*.

Arceuthobium globosum subsp. *globosum*
Rounded Dwarf Mistletoe

15a. *A. globosum* Hawksworth & Wiens subsp. *globosum*

Description: Shoots 15–20 (max. 50) cm high, bright yellow, flabellately branched (fig. 16.55). Basal diameter of dominant shoots 3–10 (mean 7) mm. Third internode 19 mm long, 4 mm wide. Staminate flowers ca. 4 mm wide. Mature fruit 5 × 2.5 mm. Seeds 4 × 2 mm. $n = ?$

Phenology: Anthesis usually March–April. Fruits mature June–July; maturation period averages 15–16 months.

Hosts: The principal hosts are *Pinus cooperi, P. engelmannii*, and *P. durangensis*. *Pinus arizonica* is occasionally parasitized, but it appears to be less susceptible to infection than the three principal hosts.

Figure 16.55 –*Arceuthobium globosum* subsp. *globosum* parasitizing branches of *Pinus* sp.; note typical globular habit, bright yellow color, and lack of witches' broom formation.

Pinus teocote is a rare host. We have classified the host near the summit of Pico Candelaria (2,650 m) south of Chuchuichupa, Chihuahua, as *P. cooperi*, but the trees exhibit some characteristics of *P. rudis*.

Distribution: Mexico (Sonora, Chihuahua, Durango, and Jalisco) (fig. 16.56). This subspecies is widely distributed in the pine forests of the Sierra Madre Occidental from northwestern Chihuahua and adjacent Sonora, through Durango to northern Jalisco. Elevational range is 2,300–2,800 m.

Discussion: This dwarf mistletoe is characterized by its bright yellow, globose clusters and absence of witches' broom formation.

Arceuthobium globosum subsp. *grandicaule*
Large-Stemmed Dwarf Mistletoe

15b. *A. globosum* Hawksworth & Wiens subsp. *grandicaule* Hawksworth & Wiens, Brittonia 29: 413, 1977. TYPE COLLECTION: MEXICO: Mexico: km-59 on Highway 59, 35 km east of Zitácuaro, on *Pinus montezumae, Hawksworth & Player 1607* in 1975 (Holotype US! Isotypes: ENCB, FPF, INIF, MO, UNAM, UT).

Description: Shoots 18–50 (max. 70, mean 25) cm tall, yellow green, typically dark at the base of older shoots, flabellately branched. Basal diameter of dominant shoots 10–48 (mean 17) mm. Third internode 14–37 (mean 27) mm long, 3–20 (mean 7) mm wide. Staminate flowers ca. 5 mm wide, 4-merous. Mature fruits 6–7 mm long, 3.5 mm wide. Seeds 5 × 3 mm. $n = 14$.

Phenology: Meiosis in December. Anthesis from January–May, with peak March–April. Fruits maturing July–October. Detailed studies by Escudero and Cibrián (1985) in the Sierra Nevada between the states of Mexico and Puebla showed that seed dispersal lasted for 95 days from early July to early November, with a peak from mid-August to mid-September; maturation period averages 16–18 months.

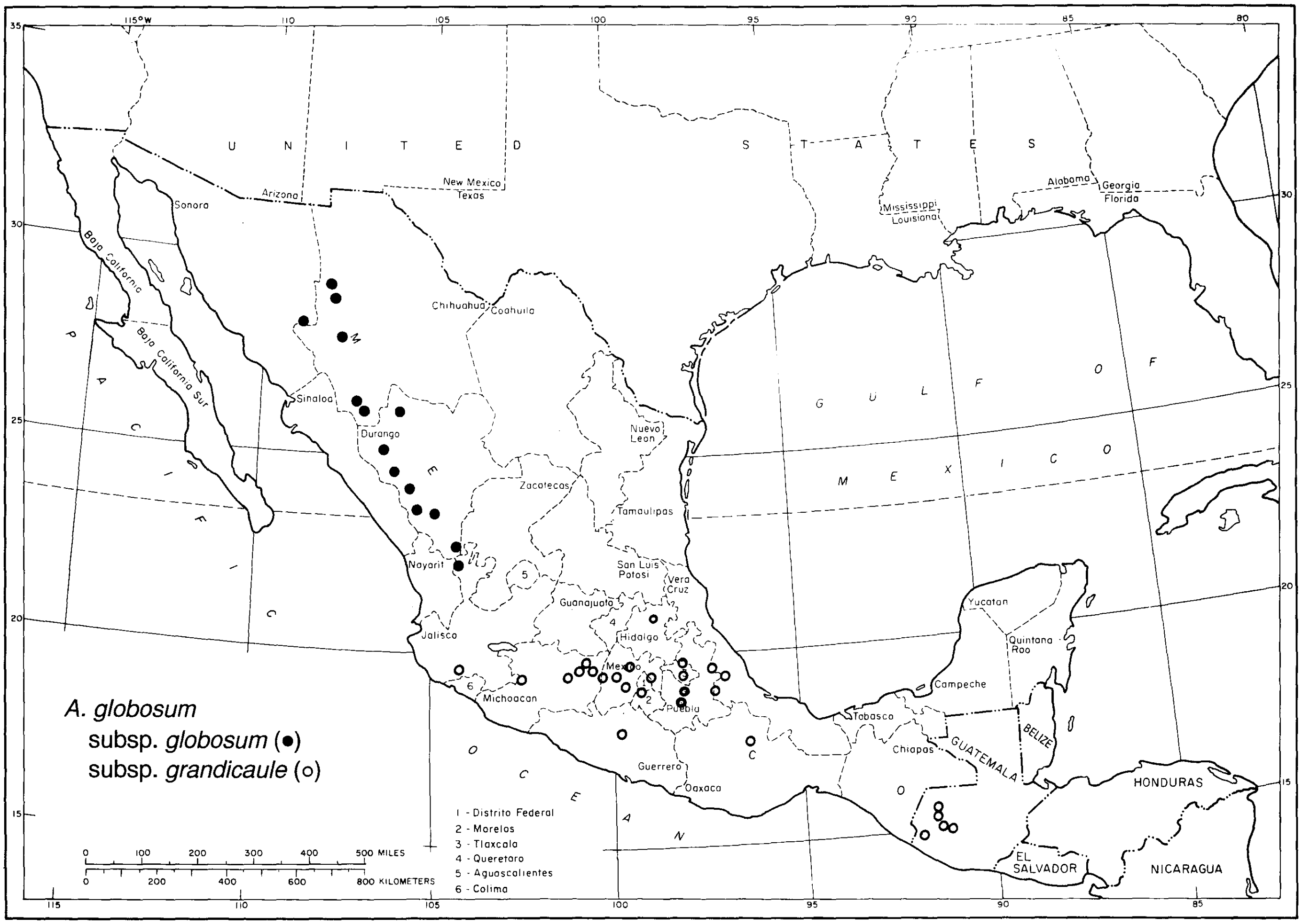

Figure 16.56 –Distribution of *Arceuthobium globosum* in Mexico and Guatemala.

Hosts: This subspecies has one of the broadest host ranges of any dwarf mistletoe. It infects at least 12 species of Mexican pines, all of which appear to be about equally susceptible: *Pinus douglasiana, P. durangensis, P. hartwegii, P. lawsonii, P. maximinoi, P. michoacana, P. montezumae, P. patula, P. pringlei, P. pseudostrobus, P. teocote,* and *P. rudis*. Valdivia (1964) studied the hosts of *Arceuthobium globosum* subsp. *grandicaule* in northeastern Michoacán, listing them in decreasing order of susceptibility: *P. maximinoi* (as *P. tenuifolia*), *P. pseudostrobus, P. pseudostrobus f. protuberans, P. montezumae, P. michoacana, P. durangensis, P. douglasiana, P. lawsonii, P. pringlei, P. teocote*, and *P. rudis. Pinus leiophylla* and *Abies religiosa* were recorded as immune.

The hosts of *Arceuthobium globosum* subsp. *grandicaule* in Guatemala are poorly known. However, *Pinus pseudostrobus, P. maximinoi, P. rudis,* and *Cupressus* sp. are reported to be infected there (Standley and Steyermark 1946). This report on *Cupressus* sp. is the only report of *Arceuthobium* on a host other than the Pinaceae in the Western Hemisphere and requires confirmation. The putative collection on *Cupressus* (*Steyermark 4904* in 1942 from the Sierra Cuchumatanes) has no host material. If the report were correct, the occurrence of *A. globosum* subsp. *grandicaule* on *Cupressus* would be rare. We did not observe any infections on *Cupressus* during our field studies in this region, even though the tree was common in many stands where *P. rudis* was heavily parasitized by *A. globosum* subsp. *grandicaule*.

Distribution: Mexico (Jalisco, Michoacán, Mexico, Hidalgo, Distrito Federal, Guerrero, Puebla, Tlaxcala, Veracruz, and Oaxaca) and Guatemala (Huehuetenango) (fig. 16.56). *Arceuthobium globosum* subsp. *grandicaule* is the most abundant dwarf mistletoe in central Mexico, and it is also locally common in the highlands of western Guatemala. Elevational range is 2,450–4,000 m (Hernandez and others 1992).

Discussion: This subspecies has the largest shoots in the genus, reaching a height of 70 cm and with a basal diameter of 5 cm.

Seed dispersal was studied by Escudero and Cibrián (1985). They showed that the maximum distance of seed dispersal was 15 m but that 91% of the seeds traveled less than 8.7 m. More than 7.3 million seeds per hectare landed on seed traps on the ground in stands of *Pinus hartwegii*. This number does not include the large proportion of seeds that were undoubtedly intercepted by the trees.

Valdivia (1964), who surveyed 400,000 ha of pine forest in northeastern Michoacán, reported that *Arceuthobium globosum* was present on nearly 40% of the forest area.

Arceuthobium guatemalense
Guatemalan Dwarf Mistletoe

16. *A. guatemalense* Hawksworth & Wiens, Brittonia 22: 267, 1970. TYPE COLLECTION: GUATEMALA: Department Huehuetenango, Sierra Cuchumatanes, on road from Huehuetenango to Santa Eulalia; 54 km north of Huehuetenango (10 km south of San Juan Ixcoy), on *Pinus ayacahuite, Hawksworth & Wiens 1221*, September 11, 1969. (Holotype US! Isotypes: COLO, DS, EAP, FPF, MO, UT).

Description: Mean shoot height ca. 1–3 cm on systemic witches' brooms, but shoots on non-systemic infections up to ca. 7 cm high; living shoots greenish to purple, yellow to brown when dried, flabellately branched (fig. 16.57). Basal diameter of dominant shoots 2.0–2.5 mm. Third internode 8–15 (mean 11.4 ± 2.8) mm long, 1.5–2.0 (mean 1.7) mm wide; length/width ratio 6.7:1 (3 collections). Staminate flowers ca. 2 mm across; perianth 2- or 3-merous, segments 0.9 mm long, 0.7 mm wide. Mean anther diameter 0.5 mm. Pollen polar diameter 21 µm and mean equatorial diameter 24 µm; polar/equatorial diameter ratio 1:1.14; spine height (ca. 1.5 µm), wall thickness (ca. 1.0 µm) (1 collection, few grains available). Mature fruit ca. 3.5–4.0 mm long, 1.5–2.0 mm wide; distal portion ca. 1.2 mm long; dark green, glabrous, with a slightly swollen ring at the base of the fruit where it joins the pedicel. Seeds 2.0 × 0.8 mm. $n = ?$

Phenology: Time of meiosis unknown. Anthesis apparently in August and early September. Fruits

Figure 16.57 –Arceuthobium guatemalense parasitizing *Pinus ayacahuite;* note typical pattern of systemic infection along host stem and the short, dark greenish to purple shoots.

mature in September; maturation period ca. 12–13 months. Seed germination in September.

Hosts: Known only on *Pinus ayacahuite* var. *ayacahuite*. The only other pine in subgenus *Haploxylon* that occurs within the range of *Arceuthobium guatemalense* is *P. chiapensis*. This tree, however, usually grows at lower elevations than *P. ayacahuite* (Martínez 1948). These two species, however, co-occur from about 2,700–2,800 m just north of the Continental Divide on Highway 175 north of Ixtlán, Oaxaca (Hawksworth and Wiens 1977), but *Arceuthobium guatemalense* was not present in these mixed stands.

Distribution: Mexico (Oaxaca and Chiapas) and Guatemala (Huehuetenango and Totonicapán) (fig. 16.58). This distinctive species is known only from the high mountains of western Guatemala and southern Mexico. It is common at the type locality in the vicinity of Santa Eulalia, in the Sierra Cuchumatanes in Guatemala. Elevational range is poorly known. Our collections were made between 2,450–3,100 m.

Discussion: The consistent formation of systemic witches' brooms is a distinctive characteristic of this species, and brooms sometimes measure 3–5 m across (fig. 16.59). An unusual feature of these witches' brooms is that the shoots of the dwarf mistletoe are consistently formed on 1-year-old host shoots and, in some cases, we found buds on the current year's growth (September). This species causes extensive damage and considerable mortality to *Pinus ayacahuite*.

Arceuthobium hawksworthii
Hawksworth's Dwarf Mistletoe

17. *A. hawksworthii* Wiens & C. G. Shaw III, Journal of Idaho Academy of Science 30 (1): 25–32. 1994. TYPE COLLECTION: BELIZE: Cayo District, Mountain Pine Ridge Region, 2.4 km south of Cooma Cairn Lookout, elevation 940 m, on *Pinus caribaea* var. *hondurensis*, *Wiens and Shaw 7768*, February 16, 1994 (Holotype US! Isotypes FPF, MO, UC).

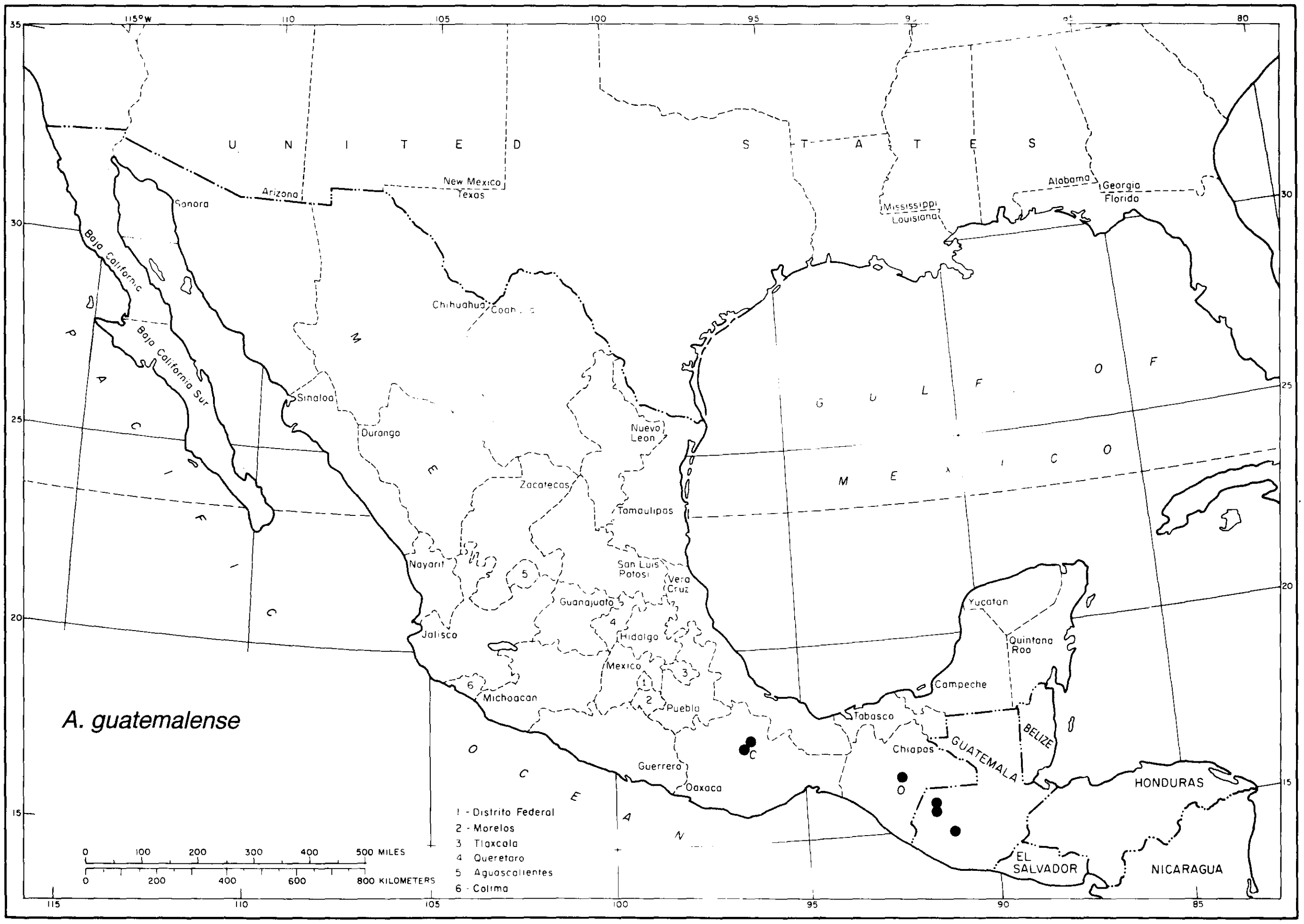

Figure 16.58 –Distribution of *Arceuthobium guatemalense.*

Figure 16.59 –*Pinus ayacahuite* showing witches' brooms induced by infection with *Arceuthobium guatemalense.*

Description: Shoot height 10–20 (max. 30) cm, pale yellow to light green, flabellately branched (fig. 16.60 and 16.61). Basal diameter of dominant shoots 3–5 mm. Third internode 10–19 (mean 14) mm long, 2–4 mm wide. Staminate flowers ca. 2.5 mm long, 3 mm across; perianth mostly 3-merous or occasionally 4-merous, adaxial surface dark red or purple, 1.2–1.5 mm long, 1.0–1.5 mm wide; anther diameter ca. 0.75 mm, sepals, stigma, and subtending bracts often dark brown to gray when flowering, giving the pistillate flowers a dark appearance. Mature (?) fruit 4.0 mm long, 1.5 mm wide, equatorial line approximately medial. $n = 14$.

Phenology: Meiosis probably in December and/or early January. Anthesis probably from mid-late January to early March, with a peak from mid-January to mid-February. Fruit dispersal was complete by late February, but a few fruits were present on previous collections (*Carty 3*) made sometime in June (exact date not specified). Fruit maturation therefore presumably requires about 3–4 months, the shortest period known for any dwarf mistletoe. If this is correct, then *Arceuthobium hawksworthii* likely has at least two flower and fruit crops annually and possibly a third (depending on whether it flowers during the wet season). This type of multiple, periodic pattern of

Figure 16.60 –*Arceuthobium hawksworthii,* pistillate plant on *Pinus* sp.

Figure 16.61 –*Arceuthobium hawksworthii,* staminate plant on *Pinus* sp.

flowering also occurs in other tropical species, e.g., *A. juniperi-procera*, *A. nigrum*, and *A. abietis-religiosae* (see discussion under those species). *Arceuthobium aureum* subsp. *aureum* produces new flowers continuously, at least during the dry season.

Hosts: The only known hosts are *Pinus caribaea* var. *hondurensis* and what appears to be *P. oocarpa* at higher elevations. Previous collections of *Arceuthobium hawksworthii* (*Carty 3A*) indicate these two pines may hybridize at higher elevations.

Distribution: Belize, known only from the Mountain Pine Ridge Region of Cayo District (fig. 16.62). *Arceuthobium hawksworthii* is not present in the coastal stands of *P. caribaea* south of Belize City. *Pinus caribaea* var. *hondurensis* also occurs at higher elevations in eastern Guatemala in the Poptún area, which is only about 75 km from the population in western Belize, and this area should be examined for the presence of *A. hawksworthii*. Elevational range is about 700–900 m. *Arceuthobium hawksworthii* does not occur in the lower 300 m of the elevational distribution of *P. caribaea* var. *hondurensis* in the Mountain Pine Ridge Region.

Discussion: This dwarf mistletoe commemorates Frank G. Hawksworth. The presence of a dwarf mistletoe in Belize has been known since 1957, but it was previously confused with *Arceuthobium aureum* subsp. *aureum* (table 16.3). The presence of red staminate flowers and its geographic distribution suggest affinities with the section *Campylopoda* series *Rubra*; but the lack of red pigment in the shoots, general stature, and presumed multiple flowering periods indicate a relationship with section *Vaginata* where it is placed provisionally (see tables 14.1 and 15.2).

Arceuthobium hondurense
Honduran Dwarf Mistletoe

18. *A. hondurense* Hawksworth & Wiens, Brittonia 22: 267, 1970. TYPE COLLECTION: HONDURAS: Department Francisco Morazán, Piedra

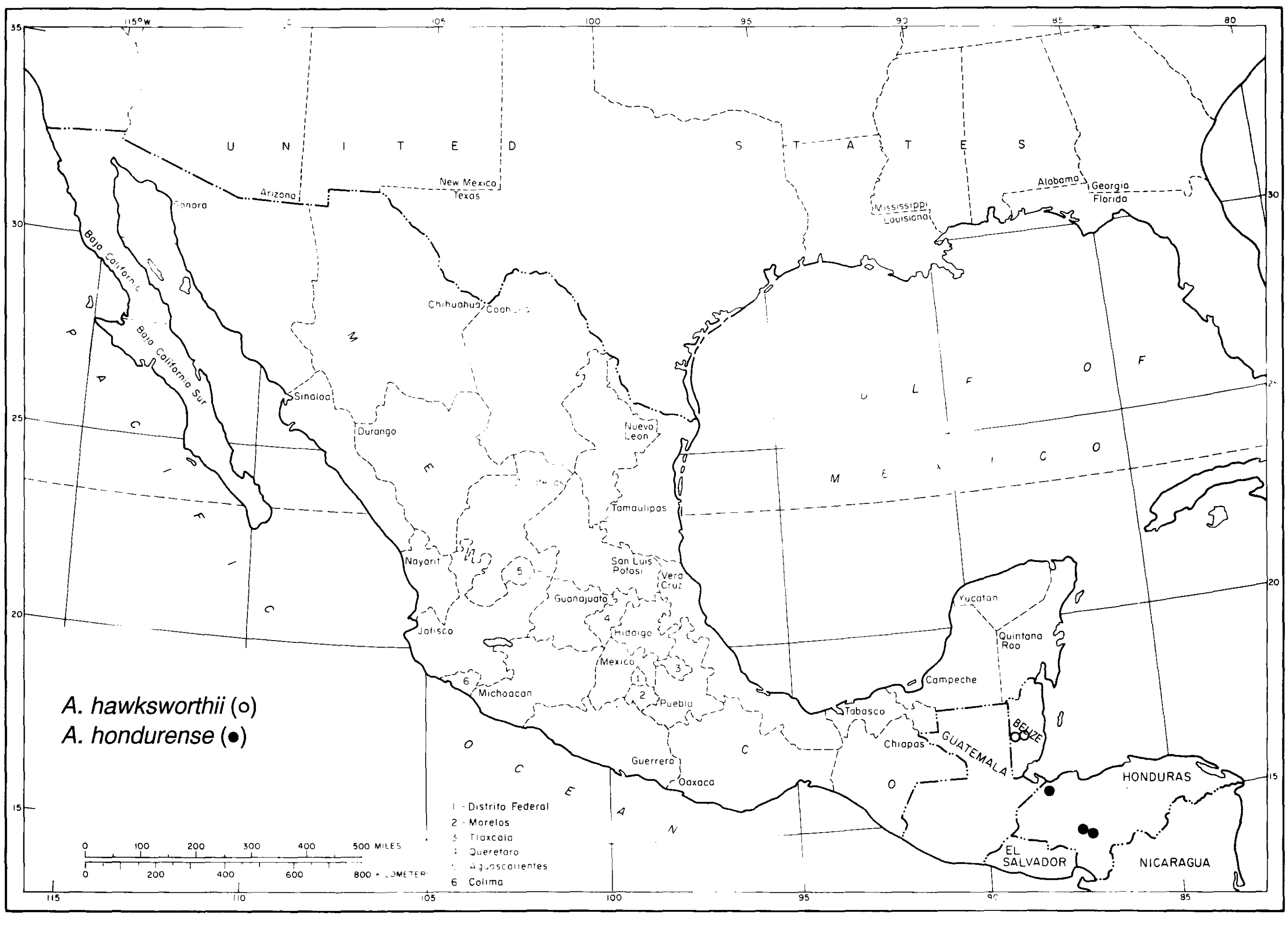

Figure 16.62 –Distribution of *Arceuthobium hawksworthii* in Belize and *A. houdurense* in Honduras.

TABLE 16.3—Comparison of *Arceuthobium hawksworthii* and *A. aureum* subsp. *aureum*

Character	*A. hawksworthii*	*A. aureum* subsp. *aureum*
Shoot color	Pistillate plants pale green; staminate plants becoming pale yellow with age	Both pistillate and staminate plants pale yellow to yellow-brown
Growth form	Shoots relatively tall, ca. 15–25 cm, few shoots arising from infection	Shoots relatively short, ca. 7–15 cm, numerous shoots arising from infection
Witches' brooms	Extensive	Absent
Inflorescence	Long and open, ca. 1.5–2.5 cm long, bearing 6–9 fertile nodes, pistillate inflorescence darkened	Short and densely clustered, ca. 1.0–1.3 cm long, bearing 2–4 fertile nodes, pistillate inflorescence pale yellow
Anthesis	Periodic: February and possibly June and October	Continuous (at least during dry season)
Sexual dimorphism	Extreme	Moderate
Staminate flower		
segment color	Vivid red inside, same as shoots outside	Both surfaces same as shoots
mature buds	Elongate, flattened, 3 mm long	Rounded, 1.5 mm long
diameter	3 mm	2 mm
lobe width	1.5 mm	1.0 mm
anther diameter	ca. 0.75 mm	ca. 0.5 mm
nectary	ca. 1.0 mm	ca. 0.5 mm
Pistillate flower		
stigma	Not exceeding length of perianth lobes	Exceeding perianth lobes by ca. 0.3 mm
color	Stigma, lobes, and bracts dark brown-gray	All flower parts and bracts same as shoots
Fruit		
equatorial line	Approximately medial	Approximately one-third below apex
surface	Not glaucous (?)	Light glaucous when living
shape and size	Narrowly elliptical, 4.0 × 1.5 mm	Broadly elliptical, 3.5 × 2.5 mm
Pedicel length at dispersal	2 mm	1 mm
Dispersal period	Periodic: May–June and possibly September and December	Continuous (at least during dry season)
Distribution	Highlands of west central Belize	Highlands of central Guatemala
Hosts	*Pinus caribaea* var. *hondurensis* *Pinus oocarpa*	*Pinus pseudostrobus* *Pinus montezuma*

Herrada, 22 km southeast of Tegucigalpa on road to Escuela Agricola Panamericana, on *Pinus oocarpa, Hawksworth, Wiens, & Molina 1203*, September 4, 1969 (Holotype US! Isotypes: EAP, COLO, DS, F, FPF, MO, UT).

Description: Mean shoot height ca. 14 (max. 21) cm, olive brown to grayish green, markedly glaucous; flabellately branched (fig. 16.63). Basal diameter of dominant shoots 3–9 (mean 5) mm; nodes of older shoots swollen; lateral branches of staminate plants at nearly right angles to the axis of the main shoot; third internode 7–12 (mean 9.1 ± 1.5) mm long, 2.5–4.0 (mean 3.2) mm wide; length/width ratio 6.1:1 (2 collections). Staminate flowers ca. 2.5 mm across; inner surface reddish, lower surface the same color as the shoots; perianth usually 3-merous (sometimes 2- or 4-merous), segments ca. 1.2 mm long, 0.8 mm wide; nectary with 2 large and 1 small lobe. Pollen polar diameter 18–23 (mean 20) µm, equatorial diameter 21–25 (mean 24) µm; polar/equatorial diameter ratio 1:1.21; spine height (ca. 2.5 µm) ca. 2 × wall thickness (1.1 µm) (2 collections). Pistillate flowers with stigmas

Figure 16.63 –Arceuthobium hondurense, staminate plant; note the divergent inflorescences, glaucous, gray color of shoots, and red color on inner surface of staminate flowers.

exserted ca. 0.5 mm, with copious stigmatic exudate at anthesis. Mature fruit 5.5 × 3.0 mm, greenish glaucous; proximal portion ca. 4.0 mm long; stigma exserted. Seeds ca. 3.1 × 1.5 mm. $n = 14$.

Phenology: Meiosis in August or early September. Anthesis and fruit maturity in September; maturation period averages ca. 12 months.

Hosts: The only known hosts are *Pinus oocarpa* and *P. maximinoi*.

Distribution: Honduras and possibly El Salvador (fig. 16.62). The distribution of this species is poorly known, but it is presently one of the rarest dwarf mistletoes in the New World with the possible exception of *Arceuthobium hawksworthii*. Only four collections are known, all from Honduras. Three are from the same general area near Piedra Herrada, southeast of Tegucigalpa on the road to Escuela Agricola Panamericana. The fourth population occurs 200 km to the northwest near Choloma. A roadside reconnaissance of 225 km through forests of *Pinus oocarpa* in the Departments of Francisco Morazán, El Paraiso, and Comayagua failed to uncover additional populations of *A. hondurense*. Recently, Jerry Beatty (personal communication) traveled extensively in the pine forests of Honduras and noted that this dwarf mistletoe was exceedingly rare and limited to the localities noted above. The indiscriminate cutting of the original forests has apparently reduced the populations of *A. hondurense* in these areas. These lands now have been either converted to agriculture or consist of second-growth forests. Unless *A. hondurense* has a broader distribution and occurs in areas less subject to deforestation, the species is in danger of extinction.

James Davis of the New Mexico State Forest Service (personal communication.) observed a dwarf mistletoe on pines in the Monte Cristo area (Santa Ana Province) of northeastern El Salvador near the Honduran border. This could be *Arceuthobium hondurense*, but unfortunately no collections of this dwarf mistletoe were obtained. Elevational range is poorly known. Our collections were made between 1,200 and 1650 m.

Discussion: Originally, we believed *Arceuthobium hondurense* might be conspecific with *A. bicarinatum*, a species endemic to Hispaniola. Observations of living plants of both dwarf mistletoes, however, demonstrated discontinuities in many characters. The species nonetheless appear closely related. *Arceuthobium hondurense* also exhibits some similarities with *A. rubrum* and *A. oaxacanum*. *Arceuthobium bicarinatum* and *A. hondurense* occupy the southern distribution limits of *Arceuthobium* in the New World.

Arceuthobium laricis
Larch Dwarf Mistletoe

19. *A. laricis* (Piper) St. John, Flora of Southeast Washington and Adjacent Idaho: 115, 1937. TYPE COLLECTION: WASHINGTON: Kittitas County: North of Ellensburg, on *Larix occidentalis, Brandegee 1071* in 1883 (Lectotype US! Isotypes: GH, PH, UC). *Razoumofskya douglasii* (Engelm.) Kuntze subsp. *laricis* Piper, Contributions U.S. National Herbarium 11: 223, 1906, *nomen nudum. A. douglasii* Engelm. var. *laricis* M. E. Jones, University of Montana Bulletin 61 (Biological Series 15): 25, 1910, *nomen nudum. Razoumofskya laricis* Piper, in Piper and Beattie, Flora Southeast Washington and Adjacent Idaho: 80, 1917. *A. campylopodum* Engelm. forma *laricis* (Piper) Gill, Transactions Connecticut Academy Arts and Sciences. 32: 202, 1935.

Description: Mean shoot height ca. 4 (max. 6) cm, mostly dark purple, flabellately branched (fig. 16.64). Basal diameter of dominant shoots 1.5–3.0 (mean 2) mm. Third internode 5–14 (mean 8.0 ± 2.0) mm long,

Figure 16.64 –Arceuthobium laricis, pistillate plants with maturing fruits.

1.0–2.5 (mean 1.3) mm wide (12 collections), length/width ratio 6.1:1. Staminate flowers 2.7 mm across; perianth mostly 3-merous (sometimes 4-merous); segments ca. 1.4 mm long, 1.1 mm wide. Mean anther diameter 0.5 mm, centered 0.5 mm from tip of segment. Pollen polar diameter 18–25 (mean 20) µm; equatorial diameter 21–27 (mean 23) µm; polar/equatorial diameter ratio 1:1.16; spine height (ca. 2 µm) about 2 × wall thickness (ca. 1.0 µm) (3 collections). Pistillate flowers ca. 1 mm long, 1 mm across. Mature fruit 4.5 × 2.5 mm; proximal portion ca. 2.5 mm long. $n = 14$.

Phenology: Meiosis in June. Peak anthesis from mid-July to late August, with extremes from early July to early September (fig. 16.65). Fruits usually mature in September, with extremes from early August to early October; maturation period averages 13–14 months.

Hosts: The principal and most commonly infected host is *Larix occidentalis*, but *Tsuga mertensiana* is also a principal host. *Pinus contorta* var. *latifolia* is a secondary host, and occasional hosts include *Abies lasiocarpa* and *Pinus ponderosa* var. *ponderosa*. Rare hosts are *Abies grandis* (Smith and others 1972), *Picea engelmannii* (Kuijt 1945b), *Pinus albicaulis* and *P. monticola* (Kuijt 1953, 1954b). *Larix lyallii* is no longer considered to be a natural host of *Arceuthobium laricis*. J. R. Weir's two fragmented collections from the Bitterroot and Cabinet Mountains of Montana are clearly *A. laricis*, but the host was misidentified as *L. lyallii*. Recent field studies in these areas have discovered numerous infected *L. occidentalis* at lower elevations but no infected *L. lyallii* at higher elevations (R. M. Mathiasen, personal communication).

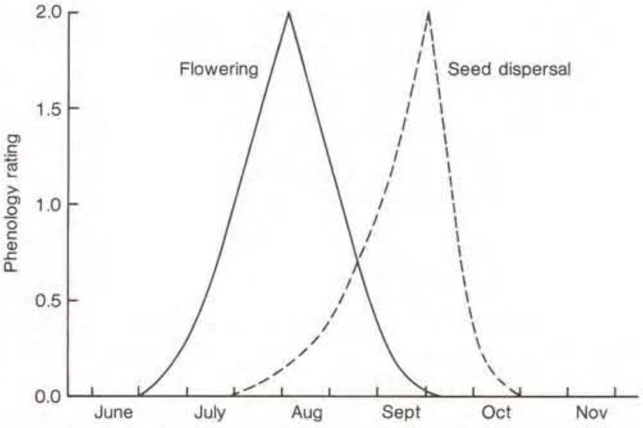

Figure 16.65 –Phenology of flowering and seed dispersal of *Arceuthobium laricis* (based on 67 observations).

Exotic trees infected naturally by *Arceuthobium laricis* include *Pinus banksiana* (Graham 1959a), *P. resinosa* (Hawksworth and Wiens 1972), *P. sylvestris* (Graham and Leaphart 1961), and *Picea abies* (Hawksworth and Wiens 1972). Weir (1918a) has shown that, on the basis of seedling inoculations, *Larix decidua* (as *L. europaea*) and *L. kaempferi* (as *L. leptolepis*), are susceptible to infection by this dwarf mistletoe.

The occurrence of *Arceuthobium laricis* on *Tsuga mertensiana* in Idaho and Montana is of interest because this dwarf mistletoe will not infect *T. heterophylla*. Our observations in many mixed *Larix–Tsuga* stands in Oregon, Washington, Idaho, and Montana confirm that *T. heterophylla* is not infected by *A. laricis*. In mixed *T. heterophylla–T. mertensiana* stands in the Coeur d'Alene National Forest, Idaho, only the latter was infected by *A. laricis*. It is unknown if *A. laricis* is associated with *T. mertensiana* in the Cascade Mountains of Oregon and Washington.

Distribution: Canada (British Columbia) and the United States (Washington, Oregon, Idaho, and Montana) (fig. 16.66). *Arceuthobium laricis* occurs generally throughout the range of its principal host, *Larix occidentalis,* in southern British Columbia, east of the Cascade Mountains in Washington and northern Oregon, north and central Idaho, and western Montana.

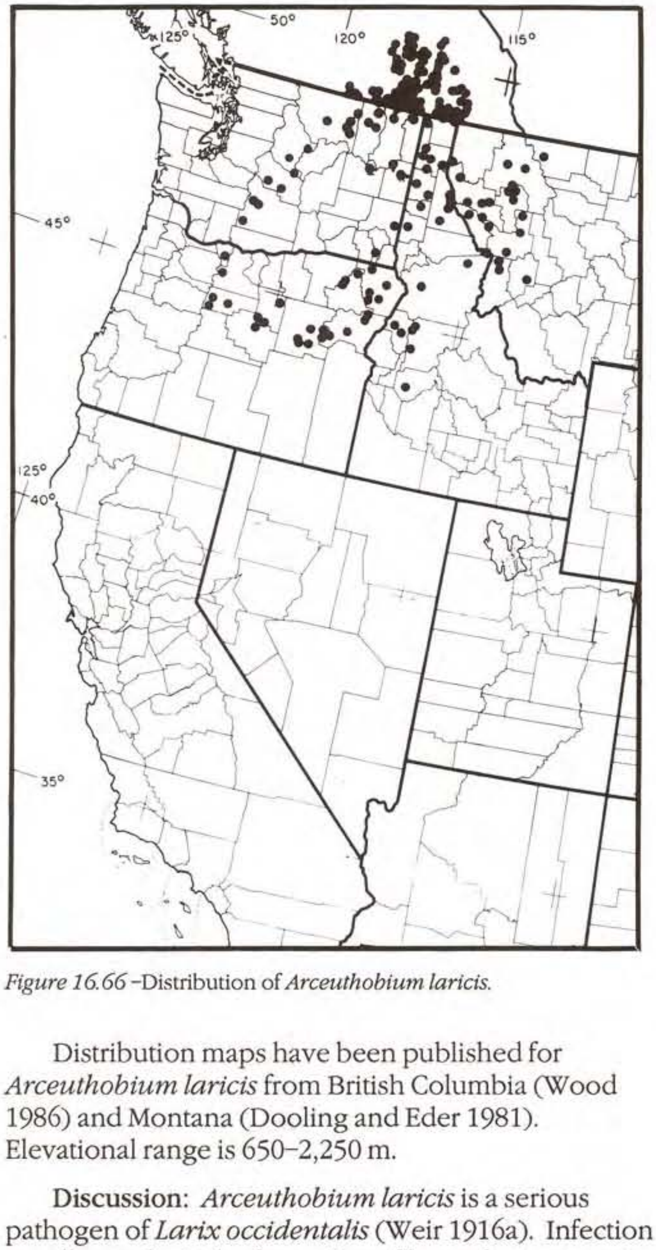

Figure 16.66 –Distribution of *Arceuthobium laricis.*

Distribution maps have been published for *Arceuthobium laricis* from British Columbia (Wood 1986) and Montana (Dooling and Eder 1981). Elevational range is 650–2,250 m.

Discussion: *Arceuthobium laricis* is a serious pathogen of *Larix occidentalis* (Weir 1916a). Infection usually results in the formation of heavy but compact brooms; because larch branches are brittle, larger brooms are readily broken off (fig. 16.67). Surveys show that about two-thirds of *L. occidentalis* stands are infested on the Coeur d'Alene National Forest, Idaho, and the Kootenai National Forest, Montana (Graham 1959b, 1959c). On the Colville National Forest and adjacent private lands in northeastern Washington, infestation was 86% (Graham and Frazier 1962).

Figure 16.67 –*Larix occidentalis* showing witches' brooms induced by infection with *Arceuthobium laricis.*

Arceuthobium littorum
Coastal Dwarf Mistletoe

20. *A. littorum* Hawksworth, Wiens & Nickrent, Novon 2: 206, 1992. TYPE COLLECTION: CALIFORNIA: Mendocino County: 4.8 km miles east of Novo on State Highway 20, on *Pinus muricata*, elevation 30 m, *R. L. Mathiasen 8940*, December 12, 1989. Holotype US! Isotypes: CAS, FPF, HSC, MO, UC).

Description: Shoots 8–20 (mean 12) cm, brown to yellow-brown, flabellately branched (fig. 16.68). Basal diameter of dominant shoots 2–5 (mean 3.5) mm. Third internode 10–20 (mean 15) mm long, 2–2.5 (mean 2.2) mm wide, mature fruits 4–5 mm long; staminate flowers mostly 4-merous. $n = 14$.

Phenology: The phenology is poorly known. Meiosis occurs in July, flowering begins in August, with peak anthesis probably occurring in September. Seed dispersal probably peaks in September or October.

Hosts: *Pinus radiata* and *P. muricata* are the primary hosts. It occasionally infects *P. contorta* var. *bolanderi* where this tree is associated with infected *P. muricata.*

Distribution: United States: (California: Mendocino, Sonoma, Marin, Monterey, and San Luis Obispo Counties) (fig. 16.69). *Arceuthobium littorum* is

Figure 16.68 –Arceuthobium littorum, pistillate plant with mature fruits; note brown to yellow-brown color of shoots.

Figure 16.69 –Distribution of *Arceuthobium littorum.*

restricted to within about 10 km of the Pacific Ocean from Fort Bragg south to the Point Reyes area on *Pinus muricata* and along the central coast at Monterey and Cambria on *P. radiata.* It also parasitizes the small population of *P. muricata* surrounded by infected *P. radiata* on Huckleberry Hill near Monterey.

This dwarf mistletoe has been established in at least three locations in the Bay Area, presumably by transplantation of infected *Pinus radiata:* Monterey–Stanford Arboretum (Peirce 1905), North Berkeley (Offord 1964a), and Hillsborough (Butler 1992). Elevational range is from sea level to ca. 250 m.

Discussion: Previously, we included *Arceuthobium littorum in A. occidentale* (Hawksworth and Wiens 1972, 1984). *Arceuthobium occidentale* is primarily a parasite of *Pinus sabiniana* in the foothills surrounding the Central Valley of California and is not sympatric with *A. littorum* near the coast. Electrophoretic studies support the segregation of *A. littorum* as a species distinct from other members of the *A. campylopodum–A. occidentale* complex (Nickrent and Butler 1989, 1990). A primary feature for distinguishing *A. littorum* from *A. occidentale* is the production of large, non-systemic witches' brooms by *A. littorum* (fig. 16.70); other differences between *A. littorum* and *A. occidentale* are presented in table 16.4.

Figure 16.70 –Pinus muricata showing witches' brooms induced by infection with *Arceuthobium littorum.*

TABLE 16.4–Comparison of *Arceuthobium littorum* and *A. occidentale*

Character	*A. littorum**	*A. occidentale*†
Shoot height (mean)	8–20 (12) cm	6–12 (8) cm
Shoot color	Dark brown to olive-green	Light green to straw
Shoot habit	Dense globose clusters	Loose, open clusters
Witches' brooms	Large, non-systemic	Uncommon
Basal shoot diameter (mean)	2–5 (3.5) mm	1.5–4 (2.3) mm
Third internode length × width	15 × 2.2 mm	12 × 2 mm
Staminate flowers	4-merous	3- or 4-merous
Mature fruit length	4–5 mm	3.5–4.5 mm
Peak flowering period	August–September	October–November
Seed dispersal period	September–October	October–December
Mean period of fruit maturation	14 months	13 months
Elevation range	Near sea level to 250 m	100 to 1,200 m

*Character values based on 8 collections, 24 observations of flowering, and 31 observations of seed dispersal.
†Character values based on 9 collections, 176 observations of flowering, and 187 observations of seed dispersal.

Arceuthobium microcarpum
Western Spruce Dwarf Mistletoe

21. *A. microcarpum* (Engelmann) Hawksworth & Wiens, Brittonia 22: 268, 1970. TYPE COLLECTION: ARIZONA: Apache County: Sierra Blanca, on *Picea engelmannii, Gilbert 112* in 1873 (Lectotype MO! Isotypes: ILL, US). *A. douglasii* Engelm. var.? *microcarpum* Engelm. in U.S. Geographical Survey West of 100th Meridian (Wheeler Report) 6: 253, 1878. *Razoumofskya microcarpa* (Engelm.) Wooton & Standley, Contributions U.S. National Herbarium 19: 179, 1915. *Razoumofskya douglasii* (Engelm.) Kuntze var. *microcarpa* (Engelm.) Tubeuf, Naturwissenschaftliche Zeitschrift für Forst- und Landwirtschaft 17: 216, 1919. *A. campylopodum* Engelm. forma *microcarpum* (Engelm.) Gill, Transactions Connecticut Academy Arts and Sciences. 32: 209, 1935.

Description: Mean shoot height ca. 5 (max. 11) cm, green to purple, flabellately branched (fig. 16.71). Basal diameter of dominant shoots 1.5–3.0 (mean 2) mm. Third internode 5–16 (mean 9.3 ± 2.2) mm long, 1–2 (mean 1.5) mm wide (9 collections), length/width ratio 6.2:1. Staminate flowers 2.3 mm across; perianth mostly 3-merous (rarely 4-merous); segments ca. 1.2 mm long, 1.0 mm wide. Mean anther diameter 0.4 mm, centered 0.6 mm from tip of segment. Pollen polar diameter 18–21 (mean 19) µm; equatorial diameter 21–23 (mean 22) µm; polar/equatorial diameter ratio 1:1.6; spine height (1.2 µm) approximately equal to the wall thickness (1.4 µm) (1 collection). Pistillate flowers ca. 1 mm long, 1 mm across. Mature fruit 3.5 × 2.0 mm; proximal portion ca. 2.5 mm long. Seeds 2.4 × 1.0 mm. $n = 14$.

Figure 16.71 –Arceuthobium microcarpum, staminate plant parasitizing *Picea pungens.*

Phenology: Meiosis in July. Anthesis in mid-August to early September, with extremes from late July to late September (fig. 16.72). Fruits mature in September, with extremes from late August to early October; maturation period averages 12–13 months.

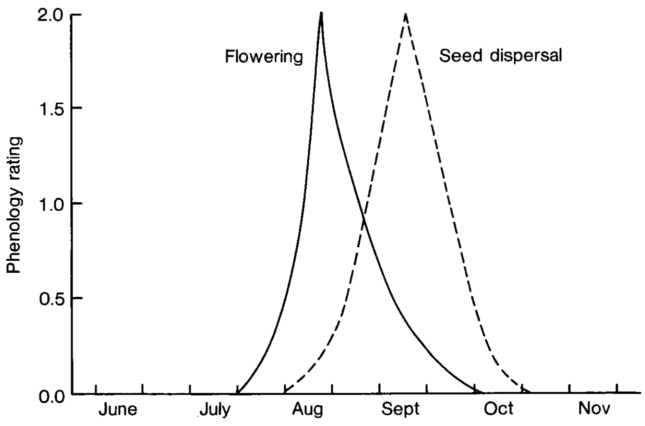

Figure 16.72 –Phenology of flowering and seed dispersal of *Arceuthobium microcarpum* (based on 62 observations).

Hosts: This dwarf mistletoe is a common and serious pathogen only on *Picea engelmannii* and *P. pungens*, but on the San Francisco Peaks (northern Arizona) it also parasitizes *Pinus aristata* (Mathiasen and Hawksworth 1980). *Pinus strobiformis* and *Abies lasiocarpa* var. *arizonica* are rarely infected, even where they are associated with infected *Picea* or *Pinus*.

Distribution: United States (Arizona and New Mexico) (fig. 16.73). *Arceuthobium microcarpum* has one of the more restricted distributions in the genus. In Arizona, the parasite occurs on the North Rim of the Grand Canyon, the San Francisco Peaks and nearby Kendrick Peak, White Mountains, and in the Pinaleno (Graham) Mountains, but not in the Chiricahua Mountains. In New Mexico, this dwarf mistletoe is present at several locations in the Mogollon Mountains, and it was discovered in the Sacramento Mountains, an outlier some 275 km from the closest known populations in the Mogollon Mountains (Mathiasen and Jones 1983).

A distribution map of *Arceuthobium microcarpum* in New Mexico was published by Martin and Hutchins (1980). Elevational range is 2,400–3,150 m (Acciavatti and Weiss 1974).

Discussion: The original specimens cited by Engelmann are *Gilbert 100* and *102*. The only specimen now at the Missouri Botanic Garden is *Gilbert 112*, which is labeled in Engelmann's handwriting as the type. The original label for specimen *100* is in the same packet. Presumably, *Gilbert 102* in the original citation should have been *112*. The collections are now combined, so *Gilbert 112* is our designate for a lectotype.

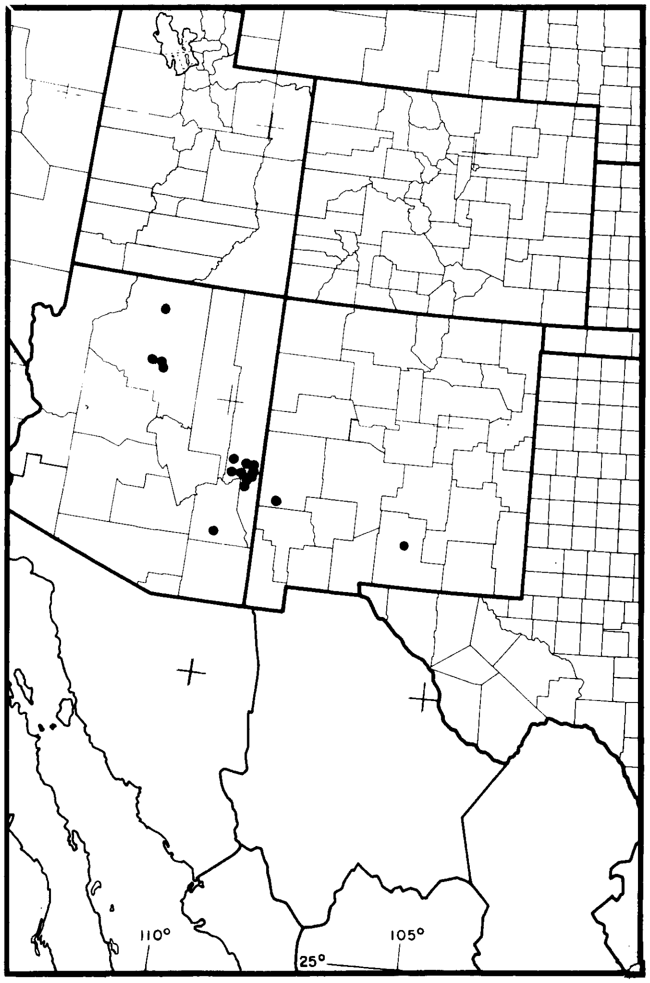

Figure 16.73 –Distribution of *Arceuthobium microcarpum.*

This localized species in Arizona and New Mexico is characterized by its near exclusive occurrence on *Picea*. Gill (1935) gave a much larger distribution for *Arceuthobium microcarpum* (to California, Idaho, and Montana). Hawksworth and Graham (1963) have shown, however, that Gill's records are based on rare parasitism of spruce by other dwarf mistletoes (*A. laricis, A. douglasii, A. americanum, A. tsugense,* and, possibly, *A. cyanocarpum*).

This species induces small, dense witches' brooms. Heavily infected trees may bear hundreds of such witches' brooms. This dwarf mistletoe causes heavy mortality in stands of *Picea pungens* and, to a lesser extent, of *P. engelmannii*. This dwarf mistletoe is not found in the principal range of *P. engelmannii* in the central or northern Rocky Mountains.

Arceuthobium monticola

Western White Pine Dwarf Mistletoe

22. *A. monticola* Hawksworth, Wiens & Nickrent, Novon 2: 205, 1992. TYPE COLLECTION: OREGON: Josephine County, 11 km south of O'Brien on Old Gasquet Toll Road (Oregon Mountain Road); parasite of *Pinus monticola*, T. 13 S., R. 9 W., Section 9; latitude 42°1' N, longitude 123°46' W, elevation 650 m, *D. Wiens 6575*, 20 July 1987. Holotype US! Isotypes: FPF, MO, ORE, OSC, UC).

Description: Shoots 5–10 (mean 7) cm tall, dark brown, flabellately branched (fig. 16.74). Basal diameter of dominant shoots 2–4 (mean 3) mm; third internode 8–15 (mean 12) mm long, 1.5–2.0 mm wide. Staminate flowers mostly 3-merous. Mature fruits 4.0–4.5 mm long, 2.0–2.5 mm wide. $n = 14$.

Figure 16.74 –Arceuthobium monticola, pistillate plant with mature fruits parasitizing *Pinus monticola.*

Phenology: The period of anthesis is poorly known but apparently occurs in late July–August. Fruits mature October–November; maturation period averages ca. 15 months.

Hosts: The principal and only commonly infected host is *Pinus monticola. Pinus lambertiana* is a secondary host, *Picea breweriana* an occasional host, and *Pinus jeffreyi* a rare host (only one case known).

Distribution: United States (Oregon and California) (fig. 16.75). *Arceuthobium monticola* is a local endemic in the Klamath Mountains of southwestern Oregon (Coos, Curry, and Josephine Counties) and the Siskiyou Mountains of adjacent northwestern California (Del Norte County and possibly in western Siskiyou County). Elevational range is 700–1,900 m.

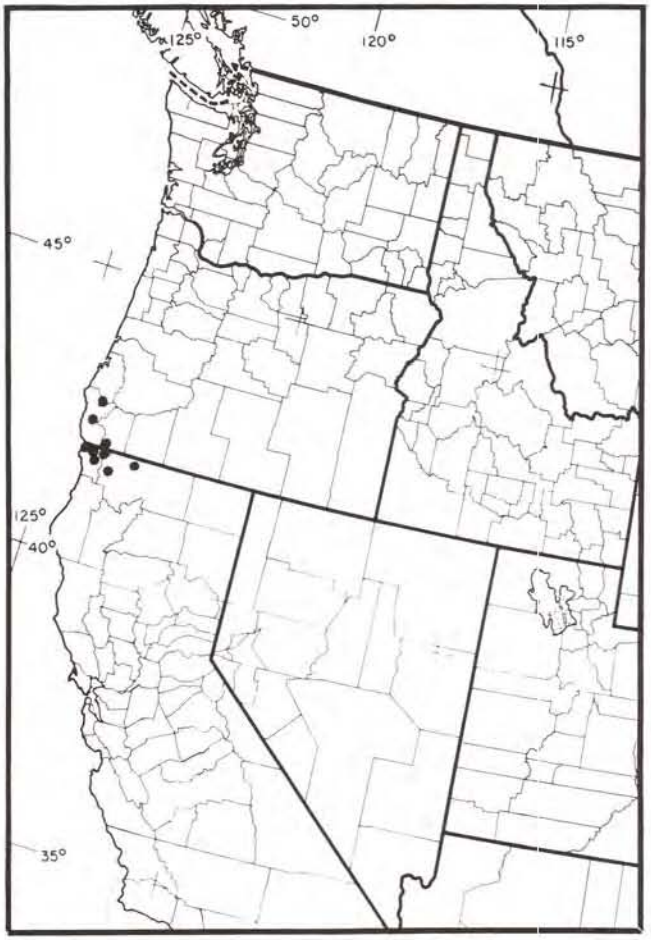

Figure 16.75 –Distribution of *Arceuthobium monticola.*

Discussion: Previously, we included this taxon under *Arceuthobium californicum* (Hawksworth and Wiens 1972). Subsequent field and laboratory studies have demonstrated that it is a distinct species and not apparently sympatric with *A. californicum*, a species restricted to California. *Arceuthobium monticola* differs from *A. californicum* in its much darker shoot color, later flowering and seed dispersal periods, and occurrence on *Pinus monticola*, as opposed to *P. lambertiana* (table 16.2).

Arceuthobium nigrum

Black Dwarf Mistletoe

23. *A. nigrum* (Hawksworth & Wiens) Hawksworth & Wiens, Phytologia 66: 9, 1989. TYPE COLLECTION: MEXICO: Durango, 51 km east of El Salto on Route 40, on *Pinus teocote, Hawksworth & Wiens 304* in 1963 (Holotype COLO! Isotypes: FPF, MEXU, MO, US). *A. gillii* subsp. *nigrum* Hawksworth & Wiens, Brittonia 17: 233, 1965.

Description: Mean shoot height ca. 15–35 (max. 45) cm, dark brown to black (fig. 16.76). Basal diameter of dominant shoots 3–8 (mean 5) mm. Third internode 5–19 (mean 10.8 ± 3.8) mm long, 2.5–6.0 (mean 3.7) mm wide (6 collections), length/width ratio 2.9:1. Staminate flowers ca. 3 mm long, 3.5 mm across. Pollen polar diameter ca. 20 μm, equatorial diameter ca. 23 μm; spine height (ca. 2.0 μm), ca. 2 × wall thickness (1.0 μm). Mature fruit 6–9 (mean 7) mm long, ca. 3.5 mm wide, proximal portion ca. 2–3 mm. Seeds 3.5 × 1.3 mm. $n = 14$.

Figure 16.76–Arceuthobium nigrum, pistillate plant, parasitizing *Pinus leiophylla;* note dark brown to black shoots and dense branching.

Phenology: This dwarf mistletoe is unusual in *Arceuthobium* because it has distinct flowering periods in March–April and September–October. We observed seed dispersal in September; presumably these fruits originated from the crop of flowers pollinated the previous September–October; however, when the seeds from the March–April pollinations are mature is unknown.

Hosts: This dwarf mistletoe is most common on pines of subsection *Leiophyllae* (*P. leiophylla* vars. *leiophylla* and *chihuahuana* and *P. lumholtzii*). However, *P. oaxacana, P. patula, P. teocote,* and *P. lawsonii* are also highly susceptible and are classed as principal hosts. *Pinus montezumae* and *P. pseudostrobus* are occasional hosts and *P. cooperi* and *P. arizonica* var. *arizonica* are rare hosts.

Distribution: Mexico (Durango, Zacatecas, Guanajuato, Querétaro, Hidalgo, Michoacán, Mexico, Tlaxcala, Puebla, Veracruz, Oaxaca, Chiapas) and possibly in western Guatemala (Hawksworth and Wiens 1977) (fig. 16.77). This mistletoe has been recently reported from the northeastern slope of Volcán la Malintzi (Malinche), Tlaxcala (Hernandez and others 1992). This species is common on pines in central and eastern Mexico. Elevational range is 1,800–2,800 m.

Discussion: *Arceuthobium nigrum* resembles *A. gillii*, a species occurring in Chihuahua, northern Durango, southeastern Arizona, and southwestern New Mexico. Both species possess markedly glaucous fruits, strong sexual dimorphism (open, divaricate branching in staminate plants versus densely branched in pistillate plants), and parasitize members of subsection *Leiophylla.* For these reasons, we originally classified *A. nigrum* as a subspecies of *A. gillii* (Hawksworth and Wiens 1965, 1972). Subsequent studies, however, have shown that they differ in a sufficient number of characters that specific status is warranted (Hawksworth and Wiens 1989).

Arceuthobium nigrum is a larger plant than *A. gillii* and has dark green to black shoots 15–35 (max. 45) cm high, whereas those of *A. gillii* are only 8–15 (max. 25) cm tall, and colored greenish brown. *Arceuthobium nigrum* also has the two flowering periods (March–April and September–October) compared to only one for *A. gillii* (March–April). To our knowledge, these species are not sympatric, although they occur in the same mountain range near Tepehuanes in northern Durango. Even there, however, they are separated both by elevation and by hosts. *Arceuthobium gillii* occurs at lower elevations (below 2,200 m) on *Pinus leiophylla* var. *chihuahuana* and *P. lumholtzii*, and *A. nigrum* occurs at higher elevations (over 2,600 m) on *P. teocote* and *P. leiophylla* var. *leiophylla*.

Arceuthobium oaxacanum
Oaxacan Dwarf Mistletoe

24. *A. oaxacanum* Hawksworth & Wiens, Phytologia 66: 7, 1989. TYPE COLLECTION: MEXICO: Oaxaca: Mpio. Tamazulapán, 13 km south of Mihuatlán (and 0.5 km south on side road) on Puerto Angel Road (Route 175), on *Pinus lawsonii, Wiens & Calvin 6003* in 1985 (Holotype US! Isotypes: ENCB, FPF, INIF, MO, UNAM).

Description: Shoots 8–20 (mean 12) cm tall, pale brown to reddish, flabellately branched (fig. 16.78). Basal diameter of dominant shoots 2–4 (mean 3) mm. Third internode 10–17 (mean 12) mm long and 2–3 mm wide (5 collections). $n = ?$

Phenology: Anthesis in July. Fruits mature in August of the following year; maturation period averages 13 months.

Hosts: *Pinus lawsonii, P. michoacana,* and *P. pseudostrobus* are principal hosts and are about equally susceptible; *P. oaxacana is* an occasional host.

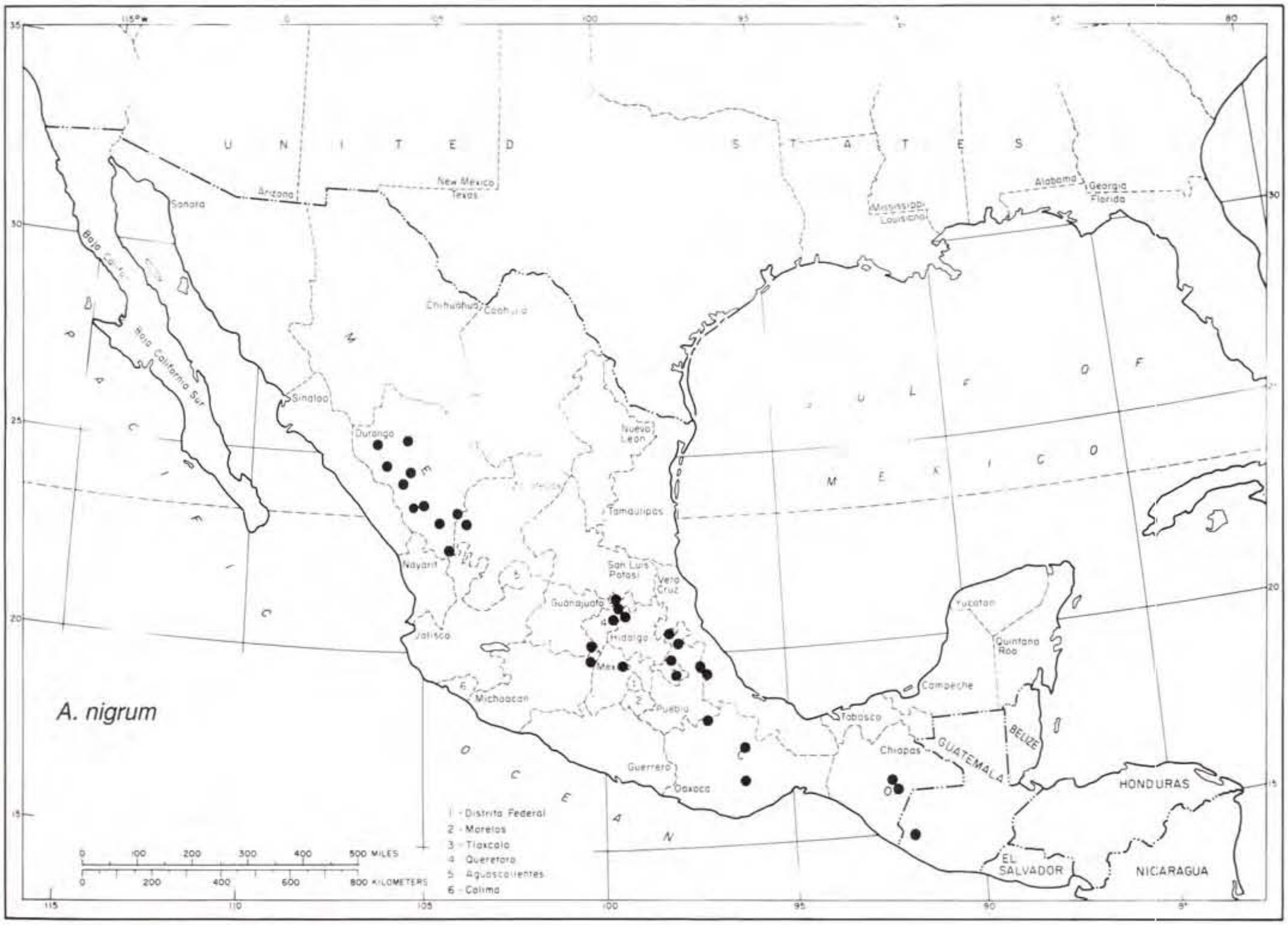

Figure 16.77 –Distribution of *Arceuthobium nigrum.*

Distribution: Mexico (Oaxaca) (fig. 16.79). This species is known from only three localities (two in southern Oaxaca south of Miahuatlán and another in northern Oaxaca near Ixtlán). Elevational range is 2,000–2,200 m.

Discussion: *Arceuthobium oaxacanum* was first discovered by R. S. Peterson in 1972 (Hawksworth and Wiens 1977). We originally classified it as an extreme disjunct (ca. 1200 km) of *A. rubrum*, but we noted that plants from Oaxaca were larger than those of *A. rubrum* from the Sierra Madre Occidental in Durango (Hawksworth and Wiens 1977). Subsequent studies of both taxa, however, indicate that they are distinct species (Hawksworth and Wiens 1989). Some characters of *A. oaxacanum* and *A. rubrum* are compared in table 16.5. In general, *A. oaxacanum* (fig. 16.78) is a larger, lighter colored, more openly branched plant and causes larger witches' brooms (fig. 16.80) than *A. rubrum*. *Arceuthobium oaxacanum* parasitizes principally *Pinus lawsonii, P. michoacana,* and *P. pseudostrobus*, and occasionally *P. oaxacana*; none of these pines occur within the range of *A. rubrum. Arceuthobium oaxacanum, A. rubrum,* and *A. bicarinatum* are the only species in the genus that have reddish shoots.

Figure 16.78 –*Arceuthobium oaxacanum;* note pale reddish brown shoots scattered along the stem.

Figure 16.79–Distribution of *Arceuthobium oaxacanum*.

Arceuthobium occidentale
Digger Pine Dwarf Mistletoe

25. *A. occidentale* Engelmann, U.S. Geographical Survey West of 100th Meridian (Wheeler Report) 6: 375, 1878 (see also Botany of California 2: 107, 1880). TYPE COLLECTION: CALIFORNIA: Kern County; Walker's Basin, on *Pinus sabiniana, Rothrock 429* in 1875 (Lectotype MO! Isotype US). *Razoumofskya occidentale* (Engelm.) Kuntze, Revision of Genera of Plants 2: 587, 1891.

Description: Mean shoot height ca. 8 (max. 17) cm, yellowish, glaucous, flabellately branched (fig. 16.81). Basal diameter of dominant shoots 1.5–5.0 (mean 2) mm. Third internode 7–18 (mean 12.7 ± 2.0) mm long, 1.5–3.5 (mean 1.8) mm wide (11 collections), length/width ratio 7.1:1. Staminate flowers 3.0 mm across; perianth 3- or 4-merous; segments ca. 1.5 mm long, 1.0 mm wide. Mean anther diameter 0.5 mm, centered 0.6 mm from tip of segment. Pollen polar diameter 18–23 (mean 20) µm; equatorial diameter 21–25 (mean 23) µm; polar/equatorial diameter ratio 1:1.16; spine height (ca. 2 µm) ca. 2 × wall thickness (1.1 µm) (3 collections). Mature fruit 4.5 × 3.0 mm; proximal portion ca. 3.0 mm long. Seeds 2.6 × 1.0 mm. $n = 14$.

Phenology: Meiosis in August. Peak anthesis from late September to late November, extremes from early September to early December (fig. 16.82). Most fruits mature from mid-October to mid-January, with extremes from late September to early February; maturation period averages ca. 13 months.

Hosts: *Pinus sabiniana* is the most common host. *Pinus coulteri* and *P. attenuata* are often parasitized where they are associated with infected *P. sabiniana. Pinus ponderosa* and *P. jeffreyi* may also be infected where they occur in areas outside the range of their typical parasite, *Arceuthobium campylopodum* (e.g., in the Coast Range of central California) and they are associated with infected *P. sabiniana. Arceuthobium occidentale*, however, infrequently infects *P. ponderosa* in the Sierra Nevada, even though this tree is

TABLE 16.5—Comparison of *Arceuthobium oaxacanum* and *A. rubrum*

Character	*A. oaxacanum**	*A. rubrum†*
Shoot height (mean)	8–20 (12) cm	8–18 (10) cm
Shoot color	Pale brownish to reddish	Dark red to blackish
Shoot habit–branching pattern	Spikes branch at nearly 90°to main shoot axis	Spikes usually branch at ca. 45°to axis
Shoot habit–cluster density	Shoot clusters open	Shoot clusters dense
Witches' brooms	Typically with systemic infections (shoots scattered 3–10 dm along branch)	Typically non-systemic infections (shoots in small clusters)
Basal shoot diameter (mean)	2–4 (3) mm	1–3 (2) mm
Third internode length (mean) × width	10–17 (12) × 2–3 mm	4–12 (7) × 2–3 mm
Pistillate spike length	1–1.5 mm	ca. 3 mm
Hosts	*Pinus lawsonii* *Pinus michoacana* *Pinus pseudostrobus* *Pinus oaxacana* (occasional)	*Pinus cooperi* *Pinus durangensis* *Pinus engelmannii* *Pinus teocote* *Pinus hennerai*
Distribution	Oaxaca, Mexico	Durango and Sinaloa, Mexico

*Character values based on 5 collections.
†Character values based on 17 collections.

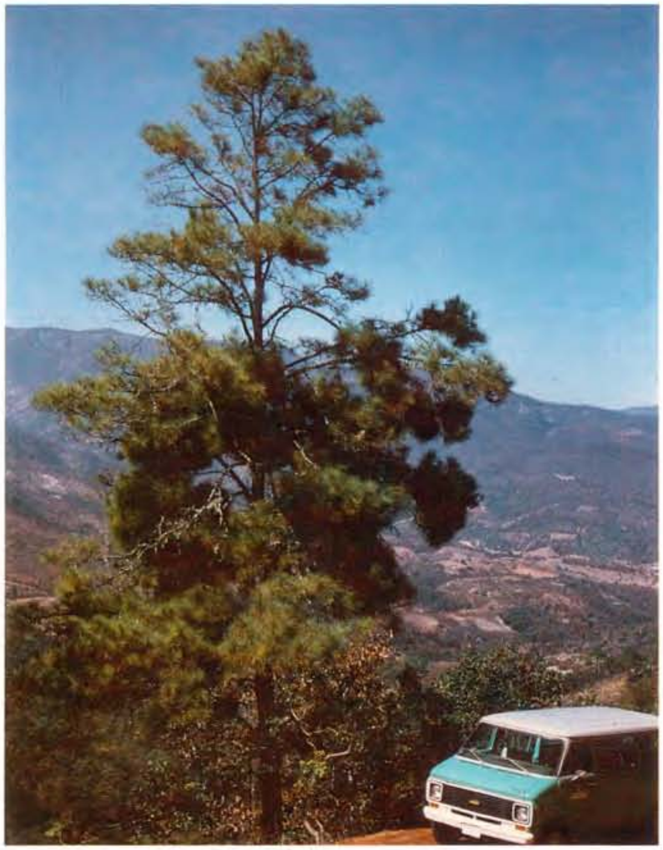

Figure 16.80–*Pinus* sp. showing witches' brooms induced by infection with *Arceuthobium oaxacanum.*

frequently associated with *P. sabiniana* infected by *A. occidentale.*

Hedgcock and Hunt (1917) successfully inoculated seedlings of *Pinus banksiana, P. bungeana, P. caribaea, P. pinea*, and *P. virginiana* with *Arceuthobium occidentale.* Kuijt (1960a) inoculated *P. torreyana* with this dwarf mistletoe, and Scharpf (1969a) also successfully inoculated *P. radiata* with *A. occidentale.* We have found this latter host–parasite combina-

Figure 16.81–*Arceuthobium occidentale* parasitizing *Pinus sabiniana;* note mistletoe plants typically form numerous rounded, yellow clusters but do not induce witches' broom formation.

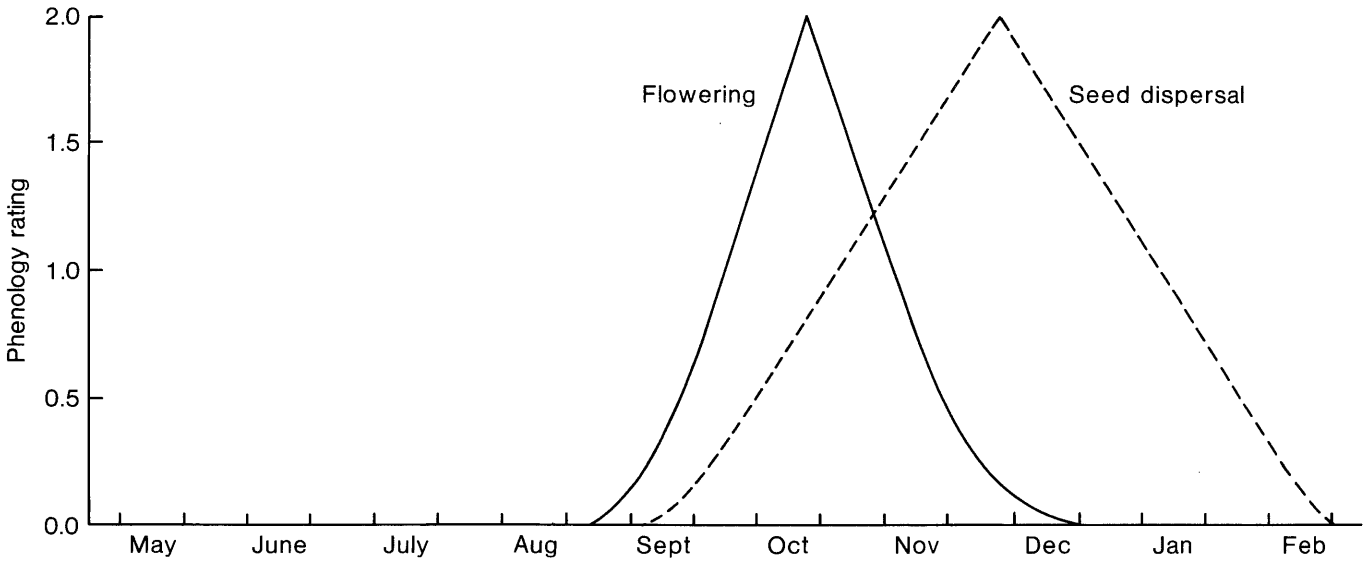

Figure 16.82 –Phenology of flowering and seed dispersal of *Arceuthobium occidentale* (based on 87 observations).

tion occurring spontaneously at Mt. Hamilton, California, where planted *P. radiata* was parasitized by *A. occidentale* when it grew near infected *P. sabiniana*. Some exotic pines recently found to be infected by this dwarf mistletoe in southern California are *P. halepensis*, *P. pinea*, and *P. thunbergii* (Scharpf and Hawksworth 1986).

Distribution: United States (California) (fig. 16.83). This dwarf mistletoe is a California endemic and commonly occurs on *Pinus sabiniana* throughout the foothills and low mountains surrounding the Central Valley of California and along the Coast Ranges from the Mt. Pinos area (Ventura County) north to Mendocino County. Elevational range is ca. 30–1,200 m (the higher elevations occurring in the southern Sierra Nevada).

Discussion: Engelmann's 1878 report specifically lists only the specimen *Rothrock 429* on *Pinus sabiniana*, but he also mentions that it occurs on *P. ponderosa*. No specimens are cited by Engelmann (1880) in his additional comments on the species. Engelmann thus apparently considered *Arceuthobium occidentale* to include both the parasite on *P. ponderosa* (our *A. campylopodum*) and *P. sabiniana* (our *A. occidentale sensu stricto*). Engelmann's writings are not clear as to what he considered to be the relationship of *A. occidentale* to his previously described *A. campylopodum* (in Gray 1850). Traditionally, the name *A. campylopodum* has been applied to the dwarf mistletoe associated with *Pinus ponderosa*. We maintain this usage.

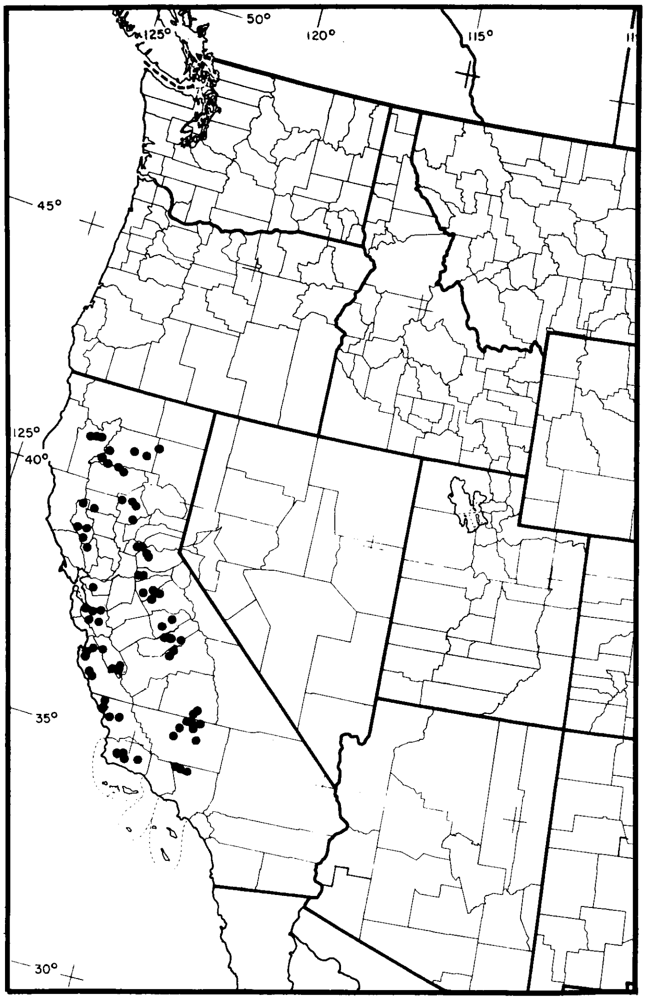

Figure 16.83 –Distribution of *Arceuthobium occidentale*.

Since the publication of our previous monograph (Hawksworth and Wiens 1972), we have continued our studies of the *Arceuthobium campylopodum*–*A. occidentale* complex (Hawksworth and others

1989). We now recognize four taxa in this complex (see also discussions under *A. campylopodum, A. littorum,* and *A. siskiyouense*).

Even though *Pinus sabiniana* typically occurs in open, savanna-like forests, *Arceuthobium occidentale* is widely distributed in these stands. Isolated, infected trees more than 100 m away from the closest infected trees are sometimes found, which suggests that bird vectors (possibly phainopepla) are involved in long-distance seed transport of this dwarf mistletoe. Studies of dispersal in *A. occidentale* would be a useful contribution to our knowledge of this species.

Arceuthobium pendens
Pendent Dwarf Mistletoe

26. *A. pendens* Hawksworth & Wiens, Brittonia 32: 348, 1980. TYPE COLLECTION: MEXICO: San Luis Potosí, Mpio. Villa de Reyes, Sierra San Miguelito, 5 km west of the village of Cerritos, on *Pinus discolor, Hawksworth, Wiens & Bailey 1877* in 1979 (Holotype US! Isotypes: ENCB, FPF, INIF, MO, UNAM, UT).

Description: Mean shoot height ca. 15 (max. 22) cm, light green, flabellately branched (fig. 16.84). Basal diameter of dominant shoots 1.5–3.5 (mean 2) mm. Third internode 12–20 (mean 16) mm long, 1–2 (mean 1.5) mm wide. Staminate flowers ca. 2.5 mm across, 3-merous. Pistillate flowers unknown. *n* = ?

Figure 16.84 –Arceuthobium pendens, staminate plant parasitic on *Pinus discolor;* note typical pendulous habit and open branching characteristic of the staminate plants.

Phenology: Time of meiosis unknown. Peak anthesis in September? Fruit maturity from June to September (Cházaro and Oliva 1987).

Hosts: Known only on pinyons—*Pinus discolor* in San Luis Potosí and *P. orizabensis* in Veracruz and Puebla. At the type locality in the Sierra San Miguelito (San Luis Potosí), this dwarf mistletoe parasitized *P. discolor* but did not infect associated *P. cembroides.*

Distribution: Mexico (San Luis Potosí, Veracruz, and Puebla) (fig. 16.85). The distribution of this dwarf mistletoe is poorly known. It has been collected in the areas mentioned above, i.e., the Sierra San Miguelito (San Luis Potosí) and the Frijol Colorado (Veracruz), and also on the nearby Cerro Pizzaro, Puebla (Cházaro and Oliva 1987). Elevational range is 2,250–2,700 m.

Discussion: This dwarf mistletoe likely occurs in other areas in Mexico and on other pinyons. The species exhibits striking sexual dimorphism—pistillate plants are densely branched and typically less than 8 cm tall and mature staminate plants are openly branched, and pendant, 15–20 cm long (fig. 16.84). A unique feature of this species, at least in the population at Sierra Miguelito, is that only the staminate plants appear to induce systemic witches' brooms.

Arceuthobium pusillum
Eastern Dwarf Mistletoe*

27. *Arceuthobium pusillum* Peck, Transactions Albany Institute 7: 191, 1872. TYPE COLLECTION: NEW YORK: Rensselaer County: Sandlake, on *Picea mariana, Peck* in 1871 (Isotype MO!). *Arceuthobium minutum* Engelmann, Bulletin of the Torrey Botany Club 2: 43, 1871, *nomen nudum. Arceuthobium oxycedri* (DC.) M. Bieb. var. *abigenium* Wood, American Botanist and Florist, p. 446, 1871. *Arceuthobium abigenium* Wood, Class-Book of Botany. p. 832, 1881. *Razoumofskya pusilla* (Peck) Kuntze, Revision of Genera of Plants. 2: 587, 1891. *Razoumofskya minuta* (Engelm.) Kuntze, Revision of Genera of Plants. 2: 587, 1891.

Description: Mean shoot height ca. 1 (max. 3) cm, green to brown, usually without secondary branching, but the rare branching that does occur is flabellate (fig. 16.86). Basal diameter of dominant shoots ca. 1.0 mm. Third internode 1–4 (mean 1.9 ± 0.8) mm long,

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* "In spite of Peck's efforts to see that [Lucy Bishop] Millington was remembered as the discoverer of this new species, her name has long been forgotten by present day investigators of *Arceuthobium*, if indeed they ever knew it" (Smith 1992).

Figure 16.85 –Distribution of *Arceuthobium pendens*.

Figure 16.86 –*Arceuthobium pusillum,* pistillate plant with mature fruits, parasitizing *Picea* sp. and showing the typical pattern of systemic infection along the stem. (J. Laut)

0.5–1.5 (mean 1.0) mm wide (17 collections), length/width ratio 1.9:1, often markedly wider at top than at base. Pistillate shoots often longer than the staminate. Staminate flowers 1.7–2.2 (mean 1.8 mm) across; perianth mostly 3-merous (sometimes 2- or 4-merous); segments ca. 0.8 mm long, 0.7 mm wide. Mean anther diameter 0.4 mm, centered 0.5 mm from tip of segment. Pollen polar diameter 19–25 (mean 22) µm; equatorial diameter 23–28 (mean 26) µm; polar/equatorial diameter ratio 1:1.16; spine height (2.2 µm) ca. 1.5 × wall thickness (1.4 µm) (4 collections). Mature fruit ca. 3.0 mm long, 1.25–1.75 mm wide (mean 1.5 mm); proximal portion ca. 2.0 mm long. Seeds 2.0 × 0.9 mm. $n = 14$.

Phenology: Staminate meiosis in September, pistillate meiosis in May (Tainter 1968). Anthesis usually in April or May, with extremes from late March to June (Fernald 1950, Tainter 1968). Fruits mature in September or early October of the same year as pollination (the only temperate North American species with this characteristic); maturation period averages ca. 5 months, one of the shortest in the genus, depending on the periods of fruit maturation ultimately determined in some of the tropical species, e.g., *Arceuthobium hawksworthii*. Seed germination mostly in May and June (Tainter 1968).

Hosts: *Arceuthobium pusillum* is most common and widely distributed on *Picea mariana*. *Picea glauca* and *P. rubens* appear to be about as susceptible as *P. mariana* and are also classed here as principal hosts, although the dwarf mistletoe is not so common on them. *Picea glauca* is commonly parasitized along the Maine Coast (Nash 1955), on the north shore of Lake Michigan, and near Glenboro, Manitoba (French and others 1981). Its occurrence on *P. rubens* was previously thought to be rare, but it is now known to be common on the old-growth stands in New York, Vermont, New Hampshire, and Maine (Hawksworth and Shigo 1980, Livingston and others 1991, Souto and Hawksworth 1988). *Larix laricina* is an occasional host in Québec (Pomerleau 1942), Wisconsin (Anderson and MacDonald 1976, Kliejunas 1969), and Minnesota (Tainter and French 1967, 1968). *Pinus banksiana* is a rare host in Québec (Pomerleau), Manitoba (Laut 1967), Ontario (Sippell and others 1968), and Minnesota (Baker and others 1978). *Pinus strobus is* also a rare host in New York (House 1935). *Abies balsamea* and *P. resinosa* are also rare hosts. *Picea pungens*, a western species, is infected when planted in Maine (U.S. Department of Agriculture 1960) and in Ontario (Davis and Myren 1990). We found a witches' broom on *Picea abies* in a plantation around naturally infected *P. rubens* near Hancock, Vermont. The tree was dead, but it was not possible to confirm that death was induced by infection with *A. pusillum*.

Distribution: Canada (Saskatchewan, Manitoba, Ontario, Québec, New Brunswick, Nova Scotia, Prince Edward Island, and Newfoundland) and United States (Minnesota, Wisconsin, Michigan, New York, Pennsylvania, New Jersey, Connecticut, Massachusetts, Vermont, New Hampshire, Rhode Island, and Maine) (figs. 16.87–16.89). *Arceuthobium pusillum* occurs in Canada from Hudson Bay, the Cumberland areas in eastern Saskatchewan to southern Manitoba, southern Ontario, Québec, and the Maritime Provinces including Newfoundland. Its northern limits in Ontario and Québec are poorly known. In the United States it occurs in the northern parts of Minnesota, Wisconsin, and Michigan, northeastern Pennsylvania, extreme northwestern New Jersey, and all of New England. It is rare near the limits of its southern distribution and is listed as an endangered plant in Rhode Island (Enser and Caljouw 1989), Connecticut (Dowhan and Craig 1976, Mehrhoff 1989), and New Jersey (Snyder and Vivian 1981) and a plant of "special concern" in Massachusetts (Anonymous 1989, Sorrie 1987).

Several distribution maps have been published for *Arceuthobium pusillum*:

- Canada—Nova Scotia (Catling and others 1985, Forbes and others 1968, Rolland and Smith 1969), and Prince Edward Island (Forbes and others 1968); New Brunswick (Forbes and others 1968, Hinds 1986); Manitoba (Gilbert 1984, Kuijt 1963); Saskatchewan (Kuijt 1963, Maher and Argus 1979, Zalasky 1956); Newfoundland (Carew 1986, Singh 1982); Ontario (Myren and Gross 1977); and Québec (Lavallée 1973, Rosseau 1974).
- United States—New England (Eaton 1931, Eaton and Dow 1940); Maine (Brower 1960, Livingston and others 1991); Minnesota (Tainter and French 1969); Michigan (Anderson and Mosher 1976, Mathiasen 1979, Voss 1985); National Forests in Minnesota, Wisconsin and Michigan (Anderson and Mosher 1976), Pennsylvania (Wherry and others 1979), and New Jersey (Hough 1983).

Elevational range is from sea level in Maine and the Maritime Provinces to ca. 800 m on Mt. Katahdin, Maine (Brower 1960).

Discussion: Wood's (1871) variety *abigenium* was based on Peck's specimen from Sandlake, New York. Because it was proposed as a variety, it cannot replace Peck's (1872) validly published specific name *pusillum*.

Thoreau (1858) provided an accurate description of the witches' brooms caused by *Arceuthobium pusillum* in spruce at Walden Pond, some 13 years before the species itself was described. The dwarf mistletoe is now extinct at Walden Pond (Eaton 1974). Smith (1992) presents an interesting account of the discovery of *A. pusillum* by Lucy B. Millington at Warrensburg, New York in 1871 and her correspondence with C. H. Peck about the new species (Millington 1871a, 1871b, 1872). This discovery triggered a flurry of activity that eventually showed the parasite to be widely distributed in the spruce forests of the Great Lakes region, New England, and southern Canada. The plant is now recognized as a damaging pathogen of spruce in many parts of its distribution. Mortality is severe in *Picea glauca* along the Maine Coast (Nash 1955), and the parasite is considered to be the most serious disease agent of *P. mariana* in the Great Lakes region (Beckwith and Anderson 1956).

Arceuthobium pusillum has the smallest shoots of any New World dwarf mistletoe (averaging about 1 cm high), but *A. minutissimum* in the Himalayas has even smaller shoots (averaging about 0.5 cm).

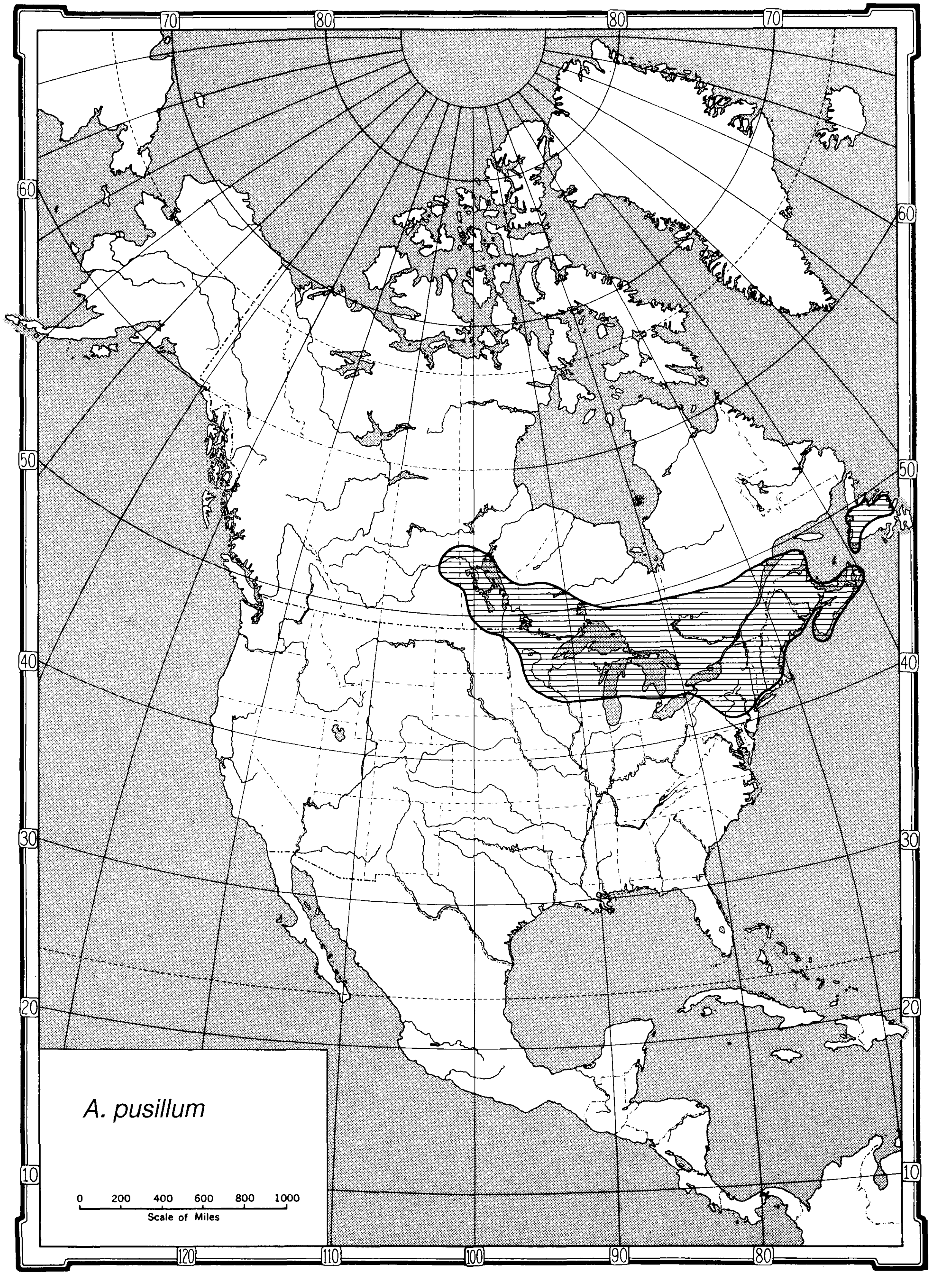

Figure 16.87 –General distribution of *Arceuthobium pusillum* in North America.

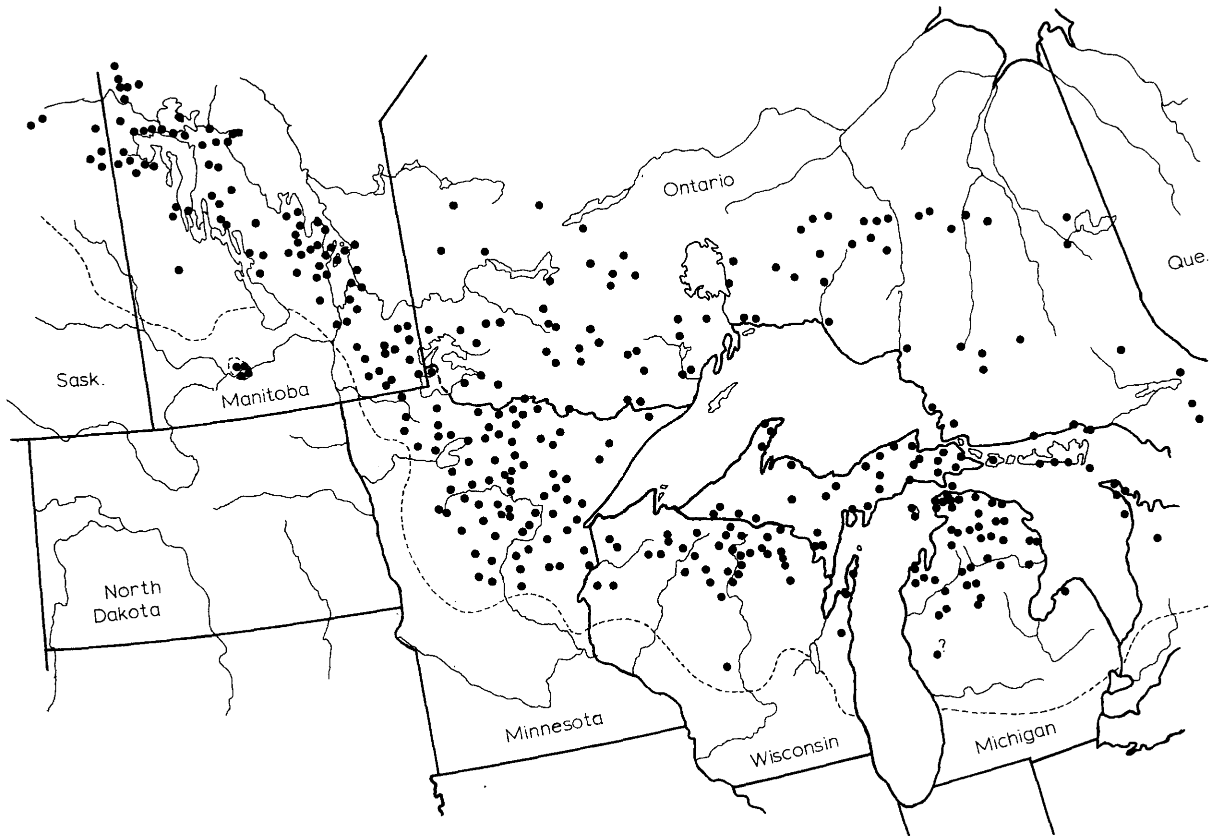

Figure 16.88 –Distribution of ***Arceuthobium pusillum*** in the western portion of its range.

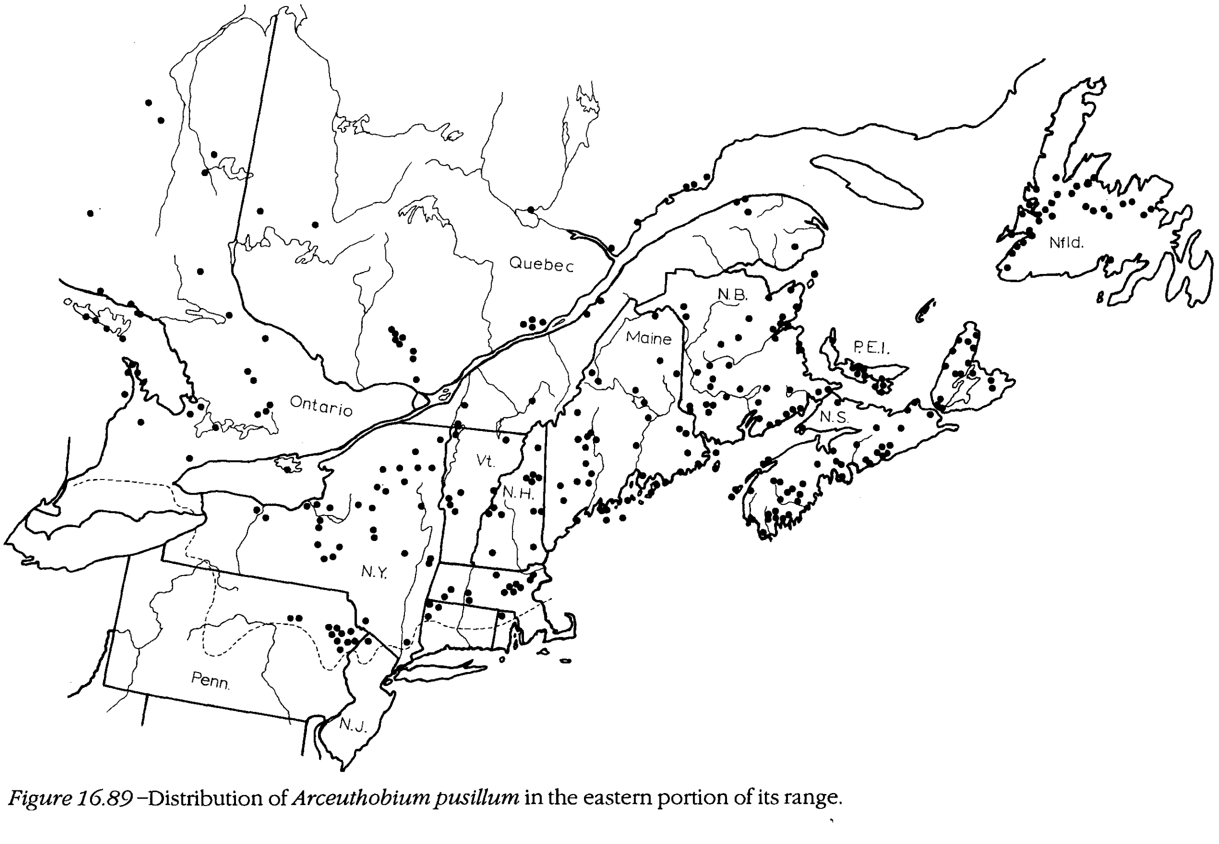

Figure 16.89 –Distribution of ***Arceuthobium pusillum*** in the eastern portion of its range.

The witches' brooms induced by *Arceuthobium pusillum* have been the subject of several investigations: von Schrenk (1900), Gill (1935), Pomerleau (1942), Anderson and Kaufert (1959), Kuijt (1960b), and Singh (1982). Witches' brooms appear to be mostly of the systemic type; thus shoot formation is regular and progressive. Shoots usually first appear in late summer or autumn as small eruptions in the bark of host branches 2 years old; the shoots mature during the third season; they flower the following spring, and the fruits mature by autumn. Thus, shoots with mature fruits usually occur only on 4-year-old host growth. Shoots usually fall after flowering or fruiting. Only rarely are the shoots perennial and produce a second crop of flowers (Baker and French 1979). This pattern of reproduction is unique among north temperate species of the genus.

Thomas (1954) stated that the witches' brooms formed on *Picea mariana* are dense and dark, whereas those on *P. glauca* are light and loose (fig. 16.90). The witches' brooms he observed possibly were in different stages of development, because Anderson and Kaufert (1959) demonstrated that in *P. mariana* the witches' brooms grew rapidly for the first 5–10 years and then abruptly declined in vigor. Large swellings on the main trunk are commonly induced by *Arceuthobium pusillum* in old-growth *P. rubens* in New England and New York (Hawksworth and Shigo 1980, Livingston and others 1991), but such swellings have not been reported on other spruces.

Figure 16.90–*Picea glauca* showing large and dense witches' brooms induced by infection with *Arceuthobium pusillum.*

Brower (1960) and Nash (1955) suggest that the dwarf mistletoe on *Picea glauca* along the Maine Coast is taxonomically distinct from the inland populations characteristically found in spruce bogs. However, our studies of both populations showed little evidence of morphological differences. Although *P. glauca* appears to be more severely infected along the Maine coast, the occurrence of *Arceuthobium pusillum* on this host is not unique to this area. It occurs commonly on *P. glauca* in the Mackinac Straits area of Michigan (Voss 1985) and in the Sprucewoods area of southwestern Manitoba (French and others 1981), and it is found sporadically on *P. glauca* throughout the range of the parasite.

Arceuthobium pusillum is common in spruce bogs, where it most frequently infects *Picea mariana*. In Québec, *A. pusillum* is apparently restricted to within 2 km of lakes or rivers (Bernard 1957). In Maine, it occurs on *P. glauca* only within ca. 300–400 m of the coast (Nash 1955). Bonga (1969a) suggests that *A. pusillum* in New Brunswick requires an uninterrupted period of high atmospheric humidity in the spring for normal growth. This might explain its presence in bogs and its absence from drier, upland sites farther inland.

Eaton (1931) reported a 130–160 km break in the distribution of *Arceuthobium pusillum* in southern New England. However, *A. pusillum* has since been reported from many locations within this supposed gap (fig. 16.89) (Eaton and Dow 1940).

Arceuthobium pusillum occurs on several islands that are isolated 30 km or more from the nearest known populations of the dwarf mistletoe—Mantinicus and Monhegan Islands off the Maine Coast and Beaver Island in Lake Michigan. *Arceuthobium pusillum* may occur on Isle Royale in Lake Superior, although a recent flora of the island does not list it (Slavick and Janke 1987). Also, the plant is not included in a flora of Anacosti Island in the Gulf of St. Lawrence, where it might be expected to occur (Marie-Victorin and Rolland-Germain 1969).

Arceuthobium rubrum
Ruby Dwarf Mistletoe

28. *A. rubrum* Hawksworth & Wiens, Brittonia 17: 233, 1965. TYPE COLLECTION: MEXICO: Durango: 47 km east of El Salto on Route 40, on *Pinus teocote, Hawksworth & Wiens 3490* in 1963 (Holotype COLO! Isotypes: FPF, INIF, MEXU, MO, US).

Description: Mean shoot height ca. 10 (max. 18) cm, dark red, brown to blackish, flabellately branched (fig. 16.91). Staminate plants usually taller than pistillate plants. Basal diameter of dominant shoots 2–3 (mean 2.4) mm. Third internode 4–12 (mean 6.9 ± 2.7) mm long, 2–3 (mean 2.3) mm wide (17 collections), length/width ratio 3.4:1. Staminate flowers 1.0–1.5 mm across; mostly 3-merous; segments ca. 0.6 mm long, 0.6 mm wide. Pollen polar diameter 23–26 (mean 24) µm; equatorial diameter ratio 1:1.05; spine height (ca. 1.0 µm) slightly greater than the wall thickness (0.8 µm) (1 collection). Mature fruit ca. 3.5 × 2.0 mm. Seeds 2.0 × 1.0 mm. *n* = ?

Figure 16.91 –*Arceuthobium rubrum* parasitizing *Pinus teocote;* note dark red color of shoots and shiny mature fruits in lower left corner. (D. L. Nickrent)

Figure 16.92 –Distribution of *Arceuthobium rubrum.*

Phenology: Meiosis probably in June. Anthesis usually in July. Fruits mature from mid-July to August of the year following pollination; maturation period averages 12–13 months.

Hosts: Principal hosts are *Pinus teocote, P. cooperi, P. engelmannii, P. herrerai*, and *P. durangensis*, all of which appear to be highly susceptible.

Distribution: Mexico (Durango and Sinaloa) (fig. 16.92). This species has a localized distribution in the Sierra Madre Occidental of western Mexico. Elevational range is 2,250–2,900 m.

Discussion: This distinctive, slender, reddish dwarf mistletoe is apparently widespread in the mountains of Durango. As the plants dry, the red color turns to dull brown, and the apical portion of each internode becomes golden yellow. This gives dried specimens a characteristic banded appearance. The shiny fruits, a character shared only with *Arceuthobium oaxacanum*, readily distinguish this species. The fruits remain shiny when dried, but the bright red turns to dark brown. Another distinctive characteristic of *A. rubrum* is the exceptionally small, scarcely opened staminate flowers. In all July collections examined, the staminate flowers were still not expanded, although they were past maturity and nearly all the pollen had been shed. The perianth segments formed a nearly closed cup with only a slight separation between the segments, and the flowers had to be examined closely to determine whether pollen was being dispersed. This species may possess an interesting mode of pollen dispersal that should be investigated further.

The populations in the Pueblo Altares area in northern Durango, about 150 km north of the populations around El Salto, have taller, darker, and stouter shoots. Superficially, they resemble *Arceuthobium vaginatum* subsp. *vaginatum*. These populations are almost black and have shoots up to 23 cm tall and up to 1 cm diameter at the base. However, they have small, shiny fruits typical of other populations of *A. rubrum*. Further studies may show that these populations warrant separate taxonomic status.

Arceuthobium rubrum exhibits a number of features similar to *A. oaxacanum* which occurs about 1,200 km to the south in Oaxaca. See discussion under *A. oaxacanum* and table 16.5.

Arceuthobium siskiyouense
Knobcone Pine Dwarf Mistletoe

29. *A. siskiyouense* Hawksworth, Wiens & Nickrent, Novon 2: 204, 1992. TYPE COLLECTION: OREGON: Josephine County, 9.6 km south of O'Brien on Old Gasquet Toll Road (Oregon Mountain Road), parasitic on *Pinus attenuata*, T. 13 S., R. 9 W., Section 9, latitude 42°1'N, longitude 123°46'W; elevation 650 m, *Wiens 6756*, 20 July, 1987 (Holotype US! Isotypes: FPF, MO, ORE, OSC, UC).

Description: Mean shoot height ca. 8 (max. 10) cm, dark brown, flabellately branched (fig. 16.93). Basal diameter of dominant shoots 2.0–2.5 mm across. Third internode 8–15 (mean 9) mm long, ca. 2 mm wide. Mature fruits 3.6 × 2.1 mm. $n = ?$

Phenology: Peak anthesis in August. Fruits at maturation not observed.

Hosts: *Pinus attenuata* is the principal and only common host of *Arceuthobium siskiyouense*. This dwarf mistletoe rarely parasitizes *P. ponderosa, P. jeffreyi*, and *P. contorta* var. *contorta* in areas where these trees grow in close association with infected *P. attenuata*.

Figure 16.93 –Arceuthobium siskiyouense parasitizing *Pinus attenuata;* note dark brown shoots. (D. L. Nickrent)

Distribution: United States (California and Oregon) (fig. 16.94). The distribution of *Arceuthobium siskiyouense* is restricted to the Klamath Mountains of southwestern Oregon (Curry and Josephine Counties) and the Siskiyou Mountains in adjacent northwestern California (Del Norte and Siskiyou Counties). Elevational range is 400–1,200 m.

Discussion: In our previous taxonomic treatments, this dwarf mistletoe was included in *Arceuthobium campylopodum* (Hawksworth and Wiens 1972, 1984). Subsequent studies, however, have demonstrated that it is a distinct species, but certainly closely related to *A. campylopodum.* Previously, we noted an anomalous situation near Gasquet, Del Norte County, California, where a dwarf mistletoe (then presumed to be *A. campylopodum*) was common on *Pinus attenuata* but rare on associated *P. ponderosa* (Hawksworth and Wiens 1972). This situation is now clarified—the population on *P. attenuata* is *A. siskiyouense.* The two species are sympatric in this and several other areas, yet both maintain their distinctive morphologies and host preferences, even though their flowering periods partially overlap (table 16.6). In marked contrast to the restricted distribution of *A. siskiyouense, A. campylopodum* has an extensive range and occurs from northern Idaho and northern Washington to Baja California. Furthermore, *A. siskiyouense* does not induce witches' brooms.

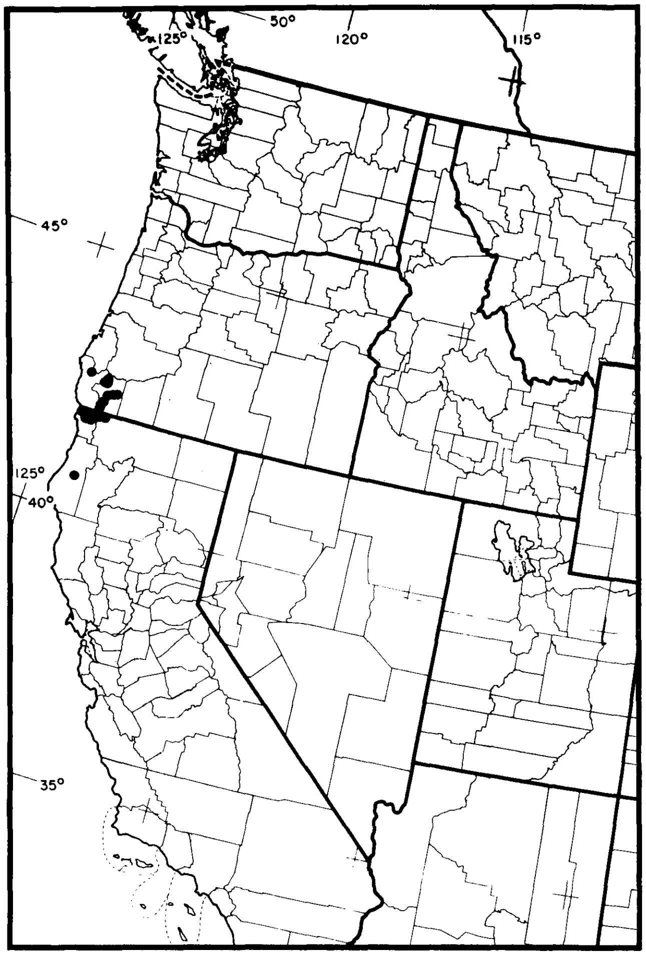

Figure 16.94 –Distribution of *Arceuthobium siskiyouense.*

TABLE 16.6—Comparison of *Arceuthobium siskiyouense* and *A. campylopodum* in the Siskiyou–Klamath Mountains

Character	*A. siskiyouense**	*A. campylopodum†*
Shoot height (mean)	6–10 (8) cm	10–14 (12) cm
Witches' brooms	None	Well developed
Basal shoot diameter	2–2.5 mm	3–6 mm
Third internode length (mean) x width	8–15 (9) x 2 mm	11–17 (14) x 3–3.5 mm
Mature fruit length (mean)	3.1–3.9 (3.6) mm	5.0–7.0 (5.6) mm
Mature fruit width (mean)	1.8–2.8 (2.1) mm	2.5–3.5 (3.0) mm
Peak flowering period	September	August
Seed dispersal period	September–October	September–October
Elevation range	400–1,200 m	50–2,400 m
Hosts	*Pinus attenuata* *Pinus jeffreyi*	*Pinus ponderosa*

*Character values based on 19 collections.

†Character values based on 17 collections.

Arceuthobium strictum
Unbranched Dwarf Mistletoe

30. *A. strictum* Hawksworth & Wiens, Brittonia 17: 234, 1965. TYPE COLLECTION: MEXICO: Durango: 26 km south of the city of Durango on road to La Flor, on *Pinus leiophylla* var. *chihuahuana, Hawksworth & Wiens 3465* in 1963 (Holotype COLO! Isotypes: DS, FPF,INIF, MEXU, MO, US).

Description: Mean shoot height ca. 7 (max. 13) cm, pistillate shoots generally greenish yellow brown, flabellately branched. Staminate plants brownish, rarely branching (fig. 16.95). Staminate plants usually taller than pistillate plants. Basal diameter of dominant shoots 2.5–4.0 (mean 3.1) mm. Third internode 1–8 (mean 3.6 ± 2.0) mm long, 1.5–3.5 (mean 2.3) mm wide (5 collections); length/width ratio 1.6:1. Staminate flowers ca. 3 mm across, perianth 3-, 4-, or 5-merous (rarely 6- or 7-merous), segments ca. 1.5 mm long, 1 mm wide. Pollen polar diameter 18–19 (mean 18) µm; equatorial diameter 20–25 (mean 22) µm; polar/equatorial diameter ratio 1:1.19; spine height (ca. 1 µm) approximately equal to the wall thickness (1 collection). Mature fruit ca. 4 × 2.5 mm. Seeds 2.5 mm × 1.0 mm. $n = 14$.

Figure 16.95–Arceuthobium strictum, staminate plant parasitizing *Pinus leiophylla* var. *chihuahuana;* note typical unbranched shoots of the male plants and numerous perianth segments.

Phenology: Meiosis in July. Anthesis late July–October, with peak in September. Fruits mature from mid-September to October of the year following pollination; maturation period averages ca. 13 months.

Hosts: *Pinus leiophylla* var. *chihuahuana* is the principal host; *P. teocote* is an occasional host; and *P. engelmannii* is a rare host. *Pinus cembroides* frequently grows in close association with heavily infected *P. leiophylla* var. *chihuahuana*, but no infections have been observed on this tree.

Distribution: Mexico (Durango) (fig. 16.96). This species is known only in the Sierra Madre Occidental south and west of the city of Durango. Elevational range is 2,200–2,500 m.

Discussion: The most distinctive feature of this dwarf mistletoe is the lack of branching in the staminate plants (Hawksworth and Wiens 1965, Kuijt 1970). The staminate shoots at anthesis become single spikes 6–13 cm long (fig. 16.95). The staminate flowers also possess a greater number of perianth segments (up to 7) than any other dwarf mistletoe (Kuijt 1970). The pistillate plants, however, have abundant secondary branching with dense clusters of small, yellow-green fruits. This dwarf mistletoe causes heavy mortality in its principal host, *Pinus leiophylla* var. *chihuahuana*.

Arceuthobium tsugense
Hemlock Dwarf Mistletoe

31. *A. tsugense* (Rosendahl) G. N. Jones, University of Washington Publications in Biology 5: 139, 1936 (as *A. tsugensis*). TYPE COLLECTION: CANADA: British Columbia: Vancouver Island, Port Renfrew on *Tsuga heterophylla, Rosendahl 826* in 1902, (Lectotype MIN, Isotypes: COLO!, DS, FPF!, K!, ILL!, MO!, RM!). *Razoumofskya tsugensis* Rosendahl, Minnesota Botanical Studies 3: 272, 1903. *Razoumofskya douglasii tsugensis* (Rosendahl) Piper, Contributions U.S. National Herbarium 11:222, 1906. *A. douglasii* Engelm. var. *tsugensis* (Rosendahl) M. E. Jones, University of Montana Bulletin 61 (Biology Series 15): 25, 1910. *A. campylopodum* Engelm. forma *tsugensis* (Rosendahl) Gill, Transactions Connecticut Academy Arts and Sciences. 32: 200, 1935.

Description: Shoot height ca. 5–7 (max. 13) cm, greenish to reddish, darker in winter, flabellately branched (fig. 16.97). Basal diameter of dominant shoots 1.5–4.0 (mean 2.0) mm. Third internode 4–16 (mean 9.2 ± 2.5) mm long, 1–2 (mean 1.5) mm wide (15 collections), length/width ratio 6.1:1. Staminate

Figure 16.96 –Distribution of *Arceuthobium strictum*.

Figure 16.97 –*Arceuthobium tsugense,* pistillate plant with mature fruits parasitizing *Abies procera;* note greenish to reddish shoots. (D. L. Nickrent)

flowers 2.8 mm across; perianth 3- or 4-merous, segments ca. 1.2 mm long, 1.0 mm wide. Mean anther diameter 0.5 mm, centered 0.6 mm from tip of segment. Pollen polar diameter 19–21 (mean 20) µm; equatorial diameter 23–25 (mean 24) µm; polar/equatorial diameter ratio 1:1.19; spine height (2.4 µm) 3 × wall thickness (0.8 µm) (4 collections). Pistillate flowers ca. 1 mm long, 1 mm across. Mature fruit 3 × 2 mm; proximal portion ca. 2.0 mm long. $n = 14$.

Discussion: This dwarf mistletoe has been variously treated as a distinct species or as allied to *Arceuthobium douglasii* or *A. campylopodum* (Gill 1935). Its phenology and general morphology, however, clearly align it with the A. *campylopodum* complex.

We commented previously on the unusually broad host range of *Arceuthobium tsugense*, which encompasses not only both western species of hemlock but also several species of fir, spruce, and pine (Hawksworth and Wiens 1972). Its occurrence on *Pinus contorta* var. *contorta* in British Columbia and the San Juan Islands of Washington also has long been known (Hawksworth and Wiens 1972; Smith 1971; Smith and Wass 1976, 1979; Wass 1976). The taxonomic status of these populations has now been re-evaluated. We separate *A. tsugense* into two subspecies (*tsugense* and *mertensianae*) and two physiologically differentiated host races (western hemlock and shore pine) that are not accorded formal taxonomic recognition (Hawksworth 1987a, Hawksworth and others 1992, Mathiasen and Hawksworth 1988).

Key to the subspecies:

1. Parasitic primarily on *Tsuga heterophylla* or *Pinus contorta* var. *contorta*; shoots 3–13 (mean 7) cm high .... *A. tsugense* subsp. *tsugense*
1. Parasitic primarily on *Tsuga mertensiana*; shoots 3–9 (mean 5) cm high... .... *A. tsugense* subsp. *mertensianae*

The subspecies are similar morphologically, but the shoots are about 30% taller in subsp. *tsugense* than in subsp. *mertensianae*. The differences are statistically highly significant ($P < 0.01$).

The phenology of flowering of the subspecies also differ somewhat. Flowering averages about 1–2 weeks earlier in subsp. *tsugense* (peak anthesis in August, with extremes from late July to late September, 56 observations; fig. 16.98) than for subsp. *mertensianae* (peak anthesis from mid-August to mid-September, 33 observations; fig. 16.99). In contrast to flowering, the seed dispersal period for subsp. *tsugense* (late September to early November, 57 observations) averaged about 2–4 weeks later than for subsp. *mertensianae* (mid-August, rarely to late October, 31 observations). Fruit maturation thus requires about 13–14 months for subsp. *tsugense* and approximately 12–13 months for subsp. *mertensianae*.

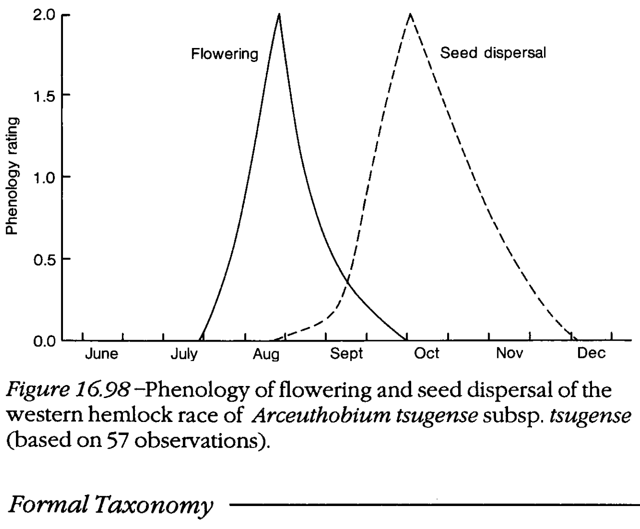

Figure 16.98–Phenology of flowering and seed dispersal of the western hemlock race of *Arceuthobium tsugense* subsp. *tsugense* (based on 57 observations).

Extensive field studies of these subspecies in the Cascade Mountains and Coast Range in Oregon and Washington during the last 2 weeks of September 1993 showed that by mid-September all the populations of subsp. *mertensianae* had completed dispersal, whereas subsp. *tsugense* did not initiate dispersal until about the last week of September. Peak dispersal in subsp. *tsugense* likely took place in early October. No overlap in dispersal was noted, even where the subspecies occurred in relatively close proximity, e.g., the populations of subsp. *tsugense* at Union Creek, Klamath County, Oregon, and those of subsp. *mertensianae* about 25 km farther north.

Arceuthobium tsugense subsp. *tsugense* Western Hemlock Dwarf Mistletoe

31a. *A. tsugense* (Rosendahl) G. N. Jones subsp. *tsugense*.

Description: As the species, but shoots vary from 3–13 cm high, mean ca. 7 cm. $n = 14$.

Phenology: Meiosis in July. Peak anthesis usually in August, with extremes from late July to late September (fig. 16.98) or even December in British Columbia (Baranyay 1962). Fruits mature from late September to early November (Smith 1966a); maturation period averages ca. 13–14 months. Seed germination is usually from February to May in British Columbia (Smith 1966b).

Hosts: *Tsuga heterophylla* is the common principal host. *Abies amabilis*, *A. lasiocarpa* var. *lasiocarpa*, and *A. procera* are reported as principal hosts (Mathiasen 1994), but classifications of these hosts are based on few observations and considered tentative. *Abies grandis* and *Pinus contorta* var. *latifolia* are

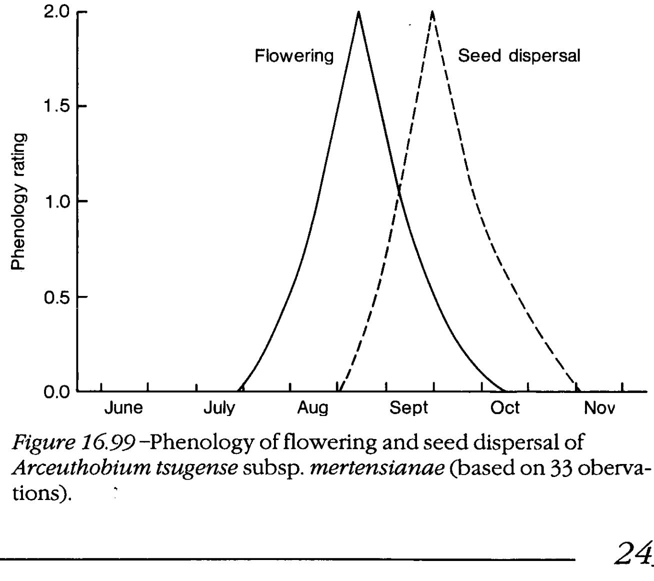

Figure 16.99–Phenology of flowering and seed dispersal of *Arceuthobium tsugense* subsp. *mertensianae* (based on 33 obervations).

occasional hosts (Mathiasen 1994). Rare hosts are *Picea engelmannii, P. sitchensis* (in Alaska, Laurent 1966; in British Columbia, Molnar and others 1968; and in Oregon), *Pinus monticola* (Gill 1935), *Pseudotsuga menziesii* (Hunt and Smith 1978), and *Tsuga mertensiana* (in Alaska, Shaw 1982a; and in Oregon, Mathiasen 1994). The status of *Pinus contorta* var. *contorta* as a host is discussed separately.

Seedlings of *Tsuga canadensis* were susceptible to inoculation with *Arceuthobium tsugense* (Weir 1918a). *Larix decidua* (cited as *L. europaea*) became infected when planted under *T. heterophylla* parasitized by *A. tsugense* on Vancouver Island (Kuijt 1964). Although swelling occurred, no shoots developed, and *L. decidua* was apparently not a compatible host. Smith (1965) successfully inoculated potted seedlings of the following trees originating beyond the natural distribution of *Tsuga heterophylla: Picea glauca* from interior British Columbia, *Pinus contorta* var. *latifolia* from Montana, and *Picea abies* from Europe. Smith (1970a,b) also successfully infected *Picea engelmannii* and, with difficulty, *Larix occidentalis*. In the latter host–parasite combination, most infections resulted only in swellings, but in one instance a few short-lived shoots were produced. We have examined several mixed *L. occidentalis–T. heterophylla* stands in the Oregon Cascade Mountains and *A. laricis* on *Larix* never infected associated *Tsuga*. Based on greenhouse and plantation inoculations in British Columbia, *Pinus ponderosa, P. radiata,* and *P. sylvestris* are also susceptible to infection by *A. tsugense* subsp. *tsugense* (Smith and Craig 1968).

Distribution: Canada (British Columbia) and the United States (Alaska, Washington, Oregon, and California) (figs. 16.100–16.103). *Arceuthobium tsugense* subsp. *tsugense* is distributed from near Haines, Alaska, to the vicinity of Mendocino in northwestern California. A general distribution map is given in fig. 16.100. The distribution in Alaska and British Columbia is presented in fig. 16.101, and that in Washington, Oregon, and California in fig. 16.102. The distribution of the populations infecting shore pine (*Pinus contorta* var. *contorta*) is illustrated in fig. 16.103. *Arceuthobium tsugense* subsp. *tsugense* occurs throughout the coastal *Tsuga heterophylla* forests of Alaska, British Columbia (Kuijt 1963), Oregon, and Washington. It has been collected rarely in northwestern California (Humboldt and Mendocino Counties). Hultén (1968) mentions that this dwarf mistletoe is "much overlooked" in Alaska, and this is emphasized by his distribution map for southeast Alaska, which shows only two localities.

Our field investigations have not confirmed the reports of *Arceuthobium tsugense* in Idaho (Weir 1916b). Weir reports and illustrates an infected hemlock on Marble Creek on the St. Joe National Forest, labeled as *Tsuga heterophylla*, but we suspect it is *T. mertensiana*. An intensive survey of dwarf mistletoe throughout northern Idaho, western Montana, and eastern Washington by D. P. Graham (1959b) found no infections on *T. heterophylla* in Marble Creek or elsewhere in this region. Graham (1959b) reports dwarf mistletoe on *T. mertensiana* on the Coeur d'Alene National Forest. Our studies there in 1966, however, identified the parasite as *A. laricis*, which typically infects *Larix occidentalis* and *T. mertensiana*, with which *Larix* is often associated. *Tsuga heterophylla* was not infected even though several individuals grew in close association with infected *T. mertensiana, L. occidentalis,* and *Abies lasiocarpa*. The specimens that Weir collected in Idaho, reportedly on *T. heterophylla* (see appendix), are so fragmentary that specific identification of the dwarf mistletoe is impossible. Thus, whether *A. tsugense* occurs in Idaho remains moot, but we consider it unlikely. Marble Creek and nearby areas have been extensively logged during the 75 years since Weir's report, and it is remotely possible that the parasite has been eradicated there. Although logging might be expected to reduce the amount of dwarf mistletoe in a stand (Stewart 1976), we know of no instances where it has eliminated *Arceuthobium* from an area. Elevational range is from sea level in Alaska, British Columbia, and Washington to about 1,250 m in Oregon.

Discussion: Many of the lower infections in *Tsuga heterophylla* produce few shoots of the dwarf mistletoe. Because dwarf mistletoes are sensitive to light, the absence of dwarf mistletoe shoots from the lower infections may be explained by the dense shade in the lower portions of coastal hemlock forests (Smith 1969). In such situations vigorous shoots are often found only along margins of stands, on young trees in openings, or in higher branches of older trees.

Arceuthobium tsugense subsp. *tsugense* has long been known to parasitize *Pinus contorta* var. *contorta* in southwestern British Columbia and the San Juan Islands, Washington (fig. 16.103). The populations of this dwarf mistletoe are distributed along the east coast of Vancouver Island, on the Channel Islands, and the mainland of British Columbia north of Vancouver. Two outlying populations have been reported about 250 km farther north at Port Clements on the Queen Charlotte Islands and at Terrace on the British Columbia mainland. Field studies are needed in these localities to determine whether they are populations

Figure 16.100–General distribution of *Arceuthobium tsugense* in the United States and Canada.

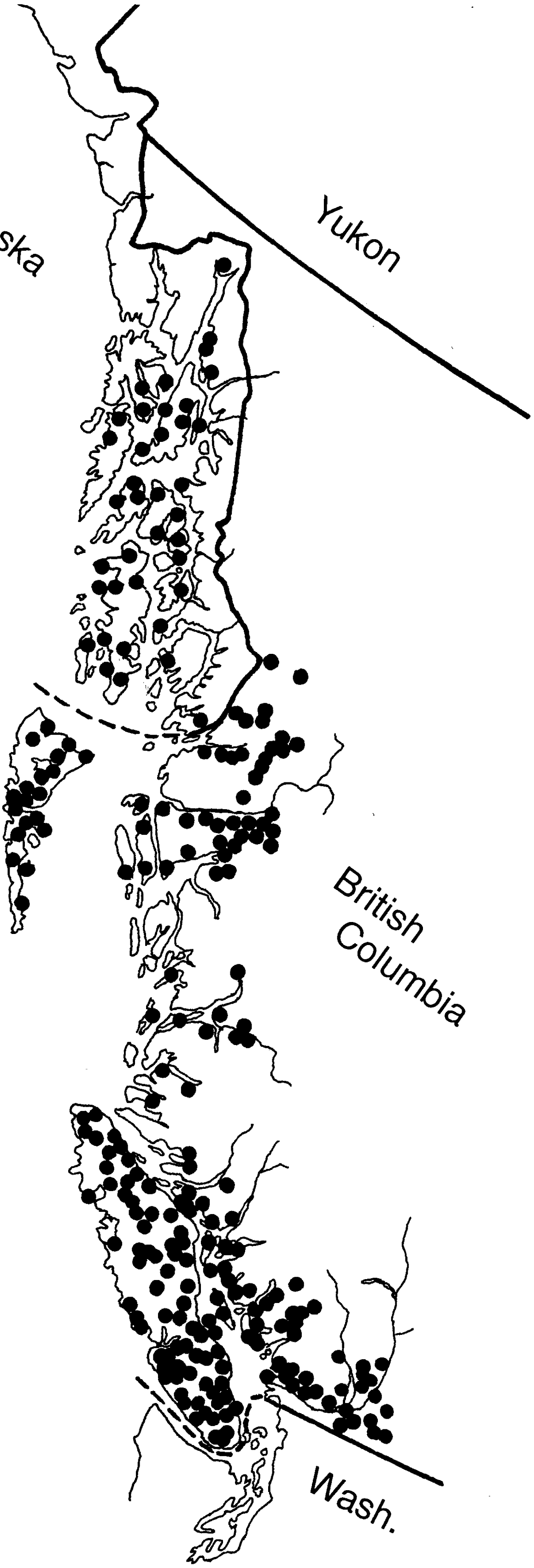

Figure 16.101 –Distribution of the western hemlock race of *Arceuthobium tsugense* subsp. *tsugense* in Alaska and British Columbia.

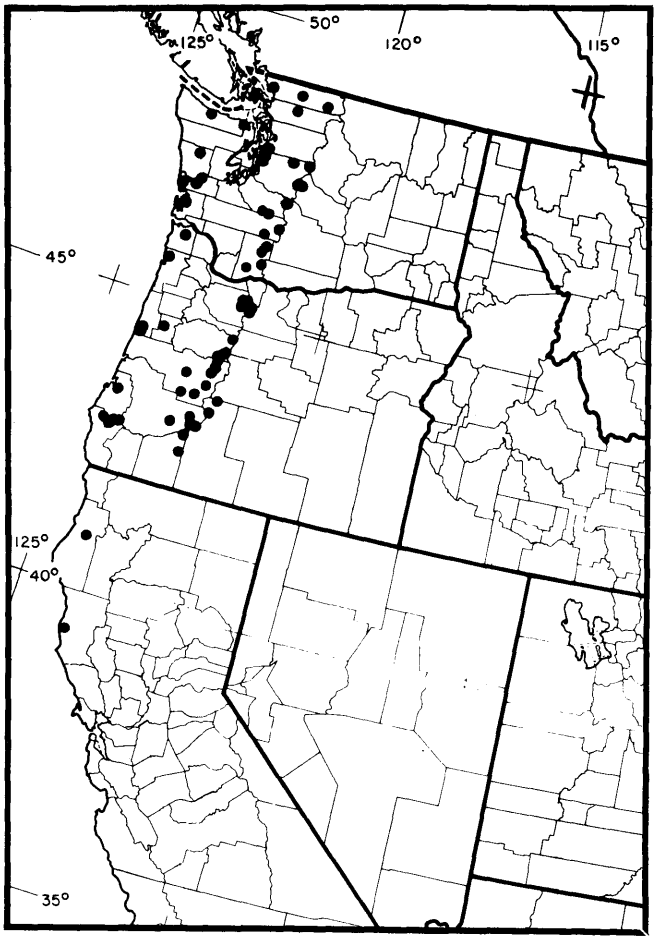

Figure 16.102 –Distribution of the western hemlock race of *Arceuthobium tsugense* subsp. *tsugense* in Washington, Oregon, and California.

of *A. tsugense* restricted to *P. contorta* var. *contorta* or rare crossovers from populations that also infect *Tsuga heterophylla.* In the United States, the only known populations occur on Orcas Island, San Juan Islands, Washington, where the mistletoe is common near the summit of Mt. Constitution and on Turtleback Mountain, about 7 km southwest of Mt. Constitution (K. Russell, personal communication). The elevational range is about 100–800 m.

The taxonomic status of the dwarf mistletoe populations on *Pinus contorta* var. *contorta* has been debated for several decades (Hawksworth and Wiens 1972; Hunt and Smith 1978; Kuijt 1956, 1963; Smith 1971, 1974; Smith and Wass 1976, 1979; Wass 1976). The western hemlock and shore pine races of subsp. *tsugense* are morphologically similar and appear to differ primarily in their host relationships (Smith 1971, 1974; Smith and Wass 1976, 1979; Wass 1976). Inoculation of *P. contorta* var. *contorta* with seeds from the western hemlock race produced low levels of

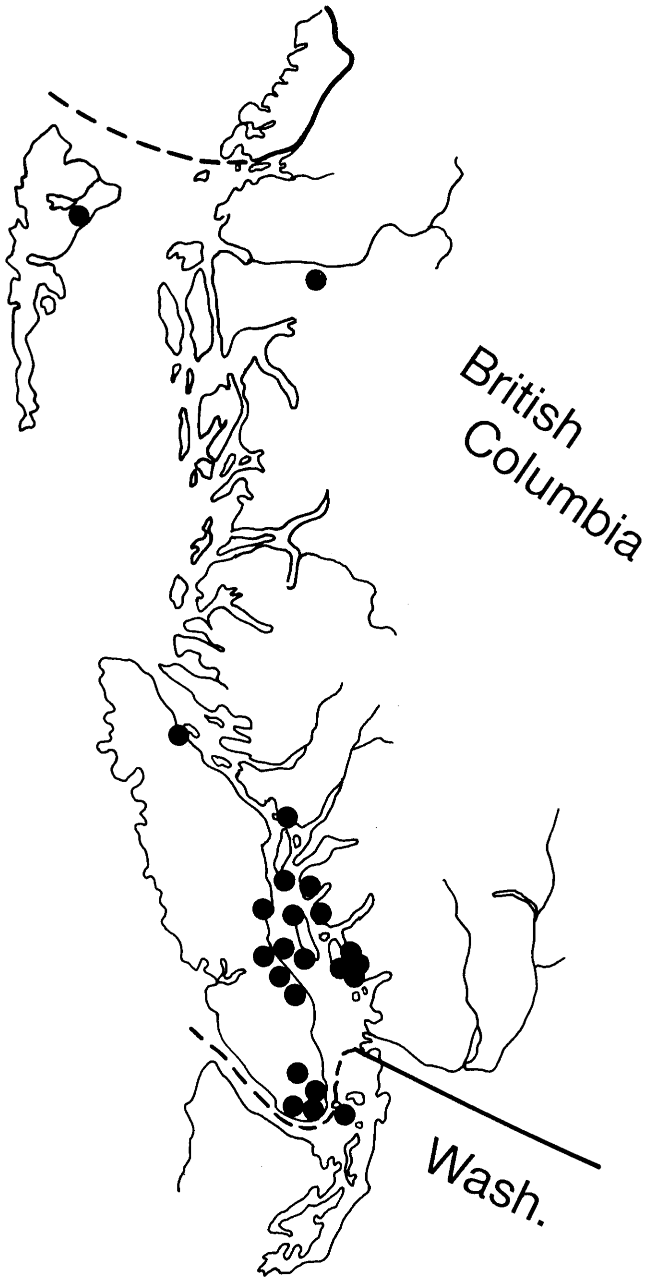

Figure 16.103 –Distribution of the shore pine race of *Arceuthobium tsugense* subsp. *tsugense* in British Columbia.

infection. The few successful infections, however, developed abundant aerial shoots. In contrast, seeds of the shore pine race produced moderate levels of infection on *Tsuga heterophylla*, but only a few of these infections produced shoots (Smith and Wass 1979). Maximum shoot height of the plants on *Tsuga heterophylla* was about 30% taller than shoots of the shore pine race (Smith 1971). Results of inoculation tests in areas where these two races are sympatric in British Columbia confirm their morphological similarity (E. Wass, personal communication). The only statistically significant difference that Wass obtained between the two populations was the occurrence of slightly larger fruits in the shore pine race. Anthesis and seed dispersal peaked about 10 days earlier in the shore pine race than in the western hemlock race on the same sites.

These populations show clear host affinities, but there is little else to warrant taxonomic recognition. In addition to their general morphological similarities, they are also similar in terms of their flavonoid composition (Crawford and Hawksworth 1979 and table 14.2) and their isozyme patterns (Nickrent and Stell 1990). Nickrent and Stell (1990) indicate the races are sympatric in some areas, but many of the populations on *Pinus contorta* var. *contorta* are isolated because this host is often confined to rocky outcrops, especially in the southern portions of Vancouver Island. Although the shore pine race of *A. tsugense* does not show sufficient differentiation to justify taxonomic recognition on the basis of the present data, further study of its systematic status is warranted.

The status of the dwarf mistletoe infecting *Abies procera* on Mary's Peak, west of Corvallis, Oregon, has long been uncertain. *Arceuthobium tsugense* subsp. *tsugense* is common in the area on *Tsuga heterophylla* at lower elevations. In some stands, however, it is common on both *T. heterophylla* and associated *Abies procera*; but near the summit of the mountain (1,250 m), it parasitizes *Abies procera* extensively and is rare on associated *T. heterophylla*. The populations on *Abies* are morphologically similar to populations infecting *Tsuga*, and isozyme studies indicate that the dwarf mistletoe population on Mary's Peak is subsp. *tsugense* (Nickrent and Stell 1990).

Arceuthobium tsugense subsp. *mertensianae* Mountain Hemlock Dwarf Mistletoe

31b. *A. tsugense* (Rosendahl) G. N. Jones subsp. *mertensianae* Hawksworth & Nickrent, Novon 2: 209, 1992. TYPE COLLECTION: OREGON: Douglas County: 26 km north of Union Creek on State Highway 230, on *Tsuga mertensiana*; elevation 1,500 m, *Mathiasen 9002*, January 2, 1990 (Holotype US! Isotypes: FPF, NO, ORE, OSC, UC, UWT).

Description: As the species, but shoots typically shorter (ca. 5 cm) than in subsp. *tsugense* (ca. 7 cm). *n* = 14.

Phenology: Peak anthesis from mid-August to mid-September (fig. 16.99). Seed dispersal from mid-August to early September (or rarely to October); maturation period averages ca. 12–13 months.

Hosts: The principal hosts of *Arceuthobium tsugense* subsp. *mertensiana* are *Tsuga mertensiana, Abies amabilis, A. lasiocarpa* var. *lasiocarpa,* and *A. procera. Pinus albicaulis* is a secondary host and *Pinus monticola* is an occasional host in areas where trees of these species are closely associated with infected principal hosts. *Picea breweriana* and recently *Abies grandis, Pinus contorta* var. *latifolia,* and *Tsuga heterophylla* are recognized as rare hosts (Mathiasen1994 and personal communication).

Distribution: Western Canada (southern British Columbia) and western United States (Washington, Oregon, and California) (fig. 16.104). The distribution of *Arceuthobium tsugense* subsp. *mertensianae* is still poorly known, but it extends from near Vancouver, British Columbia, through the Cascade Mountains of Washington and Oregon to the central Sierra Nevada in Alpine County, California.

A number of collections of dwarf mistletoe on *Tsuga mertensiana* from the east side of the Cascade Mountains (Chelan County, Washington) have not been studied in the field, but they are presumably this subspecies. *Arceuthobium tsugense* subsp. *mertensianae* was recently reported for the first time in the southern Olympic Mountains, Washington, (Henderson and others 1989) and confirmed by us. This is the first population of *A. tsugense* subsp. *mertensianae* to be discovered west of the Cascades in Washington or Oregon. This dwarf mistletoe is most common in the Cascade Mountains from central Oregon to central California. Elevational range is 1,200–2,500 m.

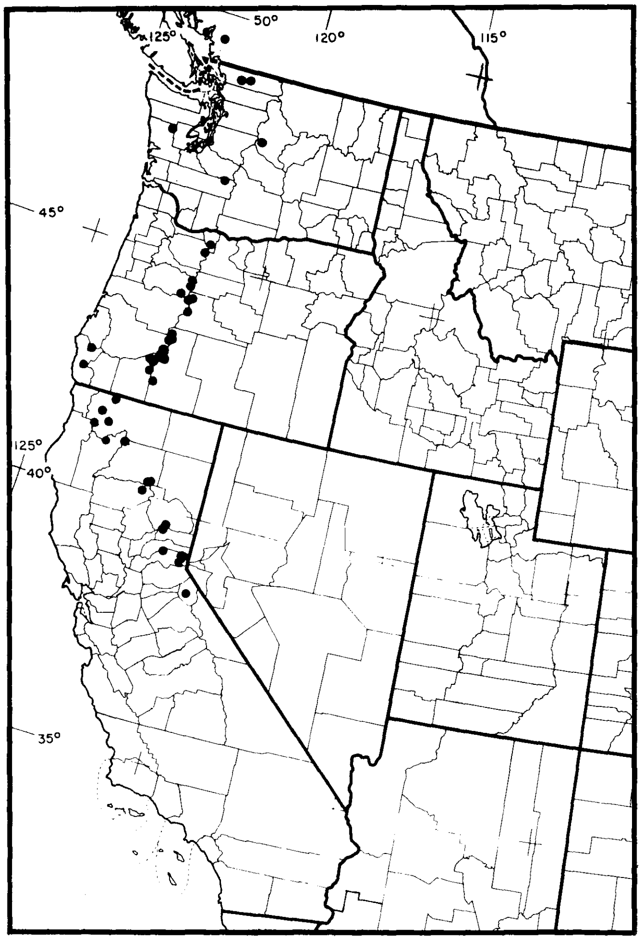

Figure 16.104 –Distribution of *Arceuthobium tsugense* subsp. *mertensianae.*

Discussion: Some populations of *Tsuga mertensiana* are exceptionally heavily infected by this dwarf mistletoe. Notable among such populations are those at Mt. Baker in the northern Cascade Mountains, and in the southwestern Olympic Mountains of Washington.

Arceuthobium vaginatum

32. *A. vaginatum* (Willdenow) Presl in Berchtold, O Přirozenosti Rostlin aneb Rostlinář 2: 28, 1825.

Description: Shoot height mostly from 20–30 (max. 5) cm, orange to dark brown, reddish, or black, usually densely branched and erect, but large older plants sometimes become pendulous; flabellately branched; basal diameter of dominant shoots ca.12–20 mm long, 0.2–0.4 cm wide. Staminate flower up to 3.5 mm long and up to 3.5 mm across, mostly 3-merous (sometimes 4-merous), segments up to 2.0 mm long and up to 1.5 mm wide, apex acute to obtuse. Pistillate flower up to 2.5 mm long, up to 1.5 mm across. Fruit 4–6 mm long, 2–3 mm wide, elliptical to obovate.

Phenology: Anthesis from approximately late March through May.

Hosts: Parasitic on pines of subgenus *Diploxylon.*

Discussion: Our studies in Mexico and the United States show that *Arceuthobium vaginatum* is comprised of two subspecies (*vaginatum* and *cryptopodum*) distinguishable by shoot color, shoot size, staminate flowers, fruit, time of anthesis, and geographic distribution (fig. 16.105). The taxon *durangense* that we originally included in *A. vaginatum* (Hawksworth and Wiens 1972) has since been raised to specific status (Hawksworth and Wiens 1989).

The distributions of the two subspecies overlap in the mountains of central Chihuahua (between latitudes 28°00' and 28°30' N), where intermediate characteristics are shown in some populations. Even here, however, there is a tendency to segregate by elevation, with subsp. *vaginatum* occurring at lower elevations

Figure 16.105–General distribution of *Arceuthobium vaginatum*.

and subsp. *cryptopodum* at higher elevations. The characteristics distinguishing these subspecies are perhaps greater than those distinguishing others, e.g., those in *Arceuthobium tsugense*. A case could be made for specific status, but we retain them as subspecies because they represent the only examples where we find intermediate populations between taxa of dwarf mistletoes.

Key to the subspecies:

1. Plants dark brown to black, usually over 20 cm tall; staminate flowers usually greater than 3 mm long and wide; anthesis March–April; Sierra Madre Occidental from central Chihuahua southward to the Central Cordillera, and in the Sierra Madre Oriental........31a. *A. vaginatum* subsp. *vaginatum*
1. Plants orange, usually less than 20 cm tall; staminate flowers usually less than 3 mm long and wide; anthesis May–June; Sierra Madre Occidental of central Chihuahua and Sonora and mountains of central Coahuila northward to central Utah and northern Colorado ....31b. *A. vaginatum* subsp. *cryptopodum*

Arceuthobium vaginatum subsp. *vaginatum* Mexican Dwarf Mistletoe

32a. *A. vaginatum* (Willdenow) Presl subsp. *vaginatum*, Berchtold, O Pŕírozenosti Rostlin aneb Rostlinár 2: 28, 1825. TYPE COLLECTION: MEXICO: Veracruz: Cofre de Perote, on *Pinus* sp., *Humboldt & Bonpland in 1804* (Lectotype B, Isotype MO!). *Viscum vaginatum* Willdenow, Sp. Pl. ed. 4, 4: 740, 1806. *Razoumofskya mexicana* Hoffman, Hortus Mosquensis (unpaged), 1808. *Viscum vaginatum* (Willd.) Kunth, Nov. Gen. et Spec. 3: 445, 1820. *A. vaginatum* (H.B.K.) Eichler, Mart. Fl. Bras. 5(2); 105, 1868. *Razoumofskya vaginata* (Willd.) Kuntze, Revision of Genera of Plants 2: 587, 1891.

Description: Mean shoot height ca. 20 (max. 55) cm, dark brown to black, rarely reddish (fig. 16.106). Basal diameter of dominant shoots 4–20 (mean 7) mm. Third internode 5–30 (mean 17.4 ± 6.0) mm long, 2.5–8.5 (mean 5.0) mm wide (11 collections), length/width ratio 2.9: 1. Staminate flower segments ca. 1.6 mm long, 1.1 mm wide. Mean anther diameter 0.6 mm centered 0.8 mm from tip of segment. Pollen polar diameter 19–23 (mean 21) μm; equatorial diameter 22–26 (mean 25) μm; polar/equatorial diameter ratio 1:1.17; spine height (1.7 μm) ca. 1.5 × wall thickness (1.2 μm) (3 collections). Mature fruit ca. 5.5 × 3.5 mm. $n = ?$


Figure 16.106–*Arceuthobium vaginatum* subsp. *vaginatum*, pistillate plant with maturing fruits parasitizing *Pinus* sp.; note dark brown shoots.

Phenology: Meiosis in February. Anthesis usually March–April. Fruits mature in August of the year following pollination; maturation period averages 16–17 months.

Hosts: *Arceuthobium vaginatum* subsp. *vaginatum* has the broadest known host range of any taxon in the genus. It has been collected on 13 species of Mexican pines and undoubtedly occurs on others. It is common on *Pinus montezumae, P. hartwegii, P. herrerai, P. lawsonii, P. rudis, P. cooperi, P. arizonica* vars. *arizonica* and *stormiae, P. durangensis, P. engelmannii,* and *P. patula,* all of which appear to be highly susceptible and are classed as principal hosts. *Pinus teocote* is a secondary host because it was parasitized only when it was associated with one of the infected principal hosts listed above. It rarely infects *Pinus culminicola* on Cerro Potosí, Nuevo León, where *P. culminicola* occurs in the understory of infested *P. rudis* forests (Hawksworth and Wiens 1965).

Distribution: Mexico (Chihuahua, Coahuila, Distrito Federal, Durango, Hidalgo, Jalisco, Mexico, Nayarit, Nuevo León, Oaxaca, Puebla, Querétaro, Sinaloa, Tamaulipas, Tlaxcala, Veracruz, and Zacatecas) (fig. 16.107). This is the most widely distributed dwarf mistletoe in Mexico, extending from the Sierra Madre Occidental in western Chihuahua south through Durango, Jalisco, and into the Central Cordillera of Mexico and Puebla and occurring in the Sierra Madre Oriental from Coahuila and Nuevo León to Oaxaca. Elevational range is from 2,100 m in Nuevo León to 3,900 m on Nevado de Toluca near Mexico City.

Discussion: The shoots of *A. vaginatum* subsp. *vaginatum* may exceed 55 cm in height in central Mexico. Only the shoots of *A. globosum* subsp. *grandicaule* are taller.

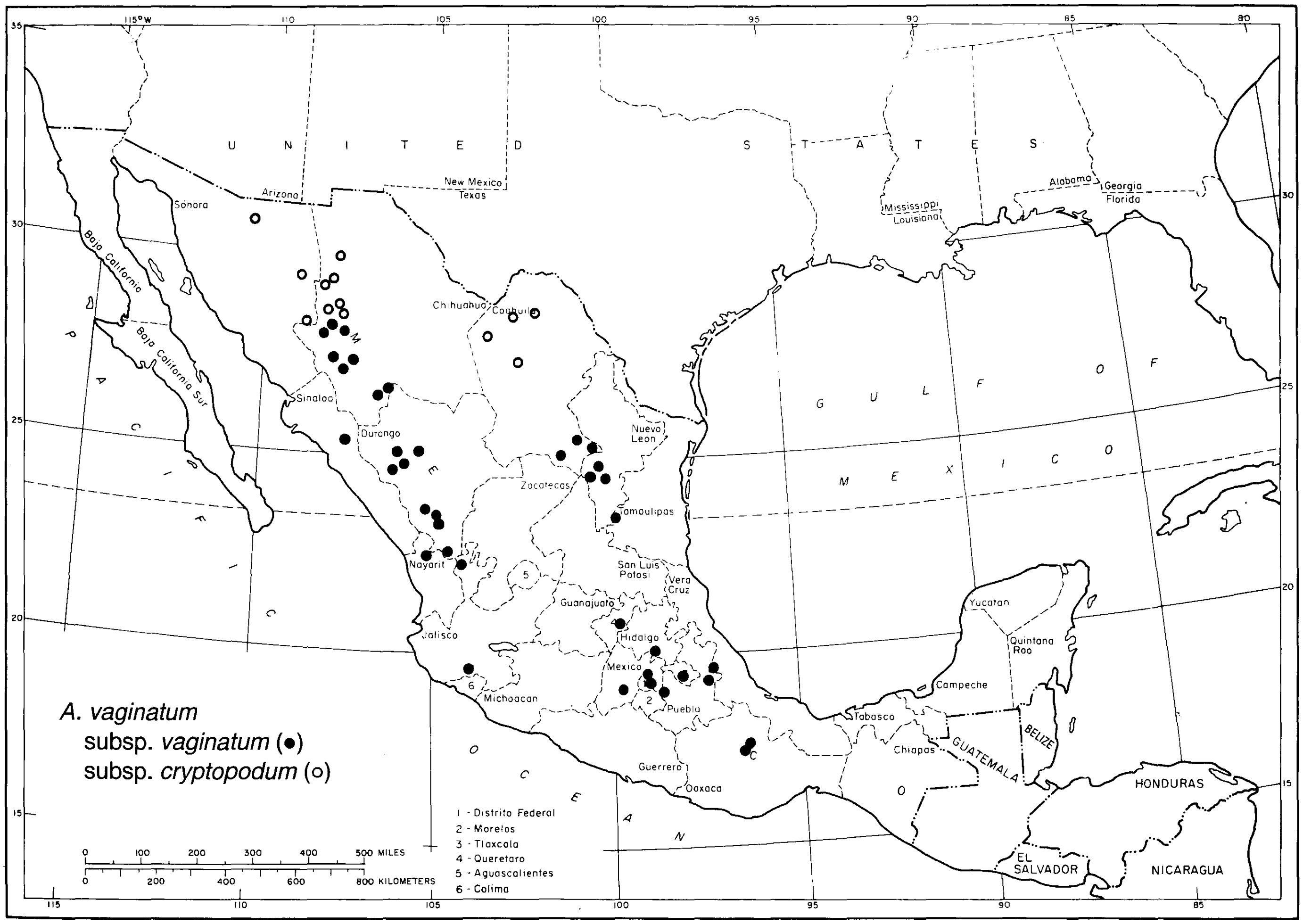

Figure 16.107 –Distribution of *Arceuthobium vaginatum* in Mexico.

The plants exhibit considerable sexual dimorphism. The staminate plants tend to be taller than the pistillate plants, but the character is variable. Vasquez (1981) studied this dwarf mistletoe near Texcoco, Mexico, and noted that the pistillate plants were short, erect, and dark, whereas staminate plants were long, pendulous, and reddish. Plants in some areas of the northern Sierra Madre Oriental (e.g., the Sierra de la Marta, Coahuila) are often reddish, but plants just 40 km to the south (Cerro Potosí, Nuevo León) are again typically black (Hawksworth and Cibrián 1985).

The hosts and ecological requirements of *Arceuthobium vaginatum* subsp. *vaginatum* and the two subspecies of *A. globosum* are similar, and they frequently co-occur, sometimes even on the same tree (Hawksworth and Wiens 1965) (fig. 5.4).

Arceuthobium vaginatum subsp. *cryptopodum*
Southwestern Dwarf Mistletoe

32b. *A. vaginatum* subsp. *cryptopodum* (Engelmann) Hawksworth & Wiens, Brittonia 17: 230, 1965. TYPE COLLECTION: NEW MEXICO: Santa Fe County, Santa Fe, on *Pinus ponderosa, Fendler 283* in 1847 (Lectotype GH! Isotypes: MO, K, NY). *A. robustum* Engelmann in Gray, Memoirs American Academy n. s. 4: 59, 1849, *nomen nudum. A. cryptopodum* Engelmann in Gray, Boston Journal Natural History 6: 214, 1850. *Razoumofskya robusta* (Engelm.) Kuntze, Revision of Genera of Plants 2: 587, 1891. *Razoumofskya cryptopoda* (Engelm.) Coville, Contributions U.S. National Herbarium 4:192, 1893. *A. vaginatum* (Willd.) Presl forma *cryptopodum* (Engelm.) Gill, Transactions Connecticut Academy Arts and Sciences. 32: 178, 1935.

Description: Mean shoot height ca. 10 cm (max. 27) cm, usually orange to reddish brown, sometimes dark to near black (fig. 16.108). Basal diameter of dominant shoots 2–10 (mean 4) mm. Third internode 4–16 (mean 7.8 ± 3.2) mm long, 2.0–4.5 (mean 3.1) mm wide (25 collections), length/width ratio 2.5:1. Staminate flowers 2.5–3.0 (mean 2.7) mm across; perianth segments ca. 1.3 mm long, 1.0 mm wide. Mean anther diameter 0.5 mm, centered 0.5 mm from tip of segment. Pollen polar diameter 18–28 (mean 22) µm; equatorial diameter 23–30 (mean 26) µm; polar/equatorial diameter ratio 1:1.15; spine height (ca. 1.5 µm) 1.5 × the wall thickness (1.0 µm) (5 collections). Mature fruit 4.5–5.5 (mean 5.0) mm long, 2.0–3.0 (mean 2.5) mm wide.; proximal portion ca. 3.5 mm long. Seeds 2.7 × 1.1 mm. *n* = 14.

Phenology: Meiosis in March or April. Anthesis usually in May–June, with extremes from late April to early July (fig. 16.109). Fruits mature in late July or early August, with extremes from early July to early September. Both anthesis and seed dispersal in Colorado occur 1–2 weeks later than in Arizona and New Mexico; maturation period averages 14–15 months. Seed germination from August to September, immediately following dispersal.

Figure 16.108 –*Arceuthobium vaginatum* subsp. *crytopodum*, pistillate plant (upper) with maturing fruits, staminate plant (lower), parasitizing *Pinus ponderosa* var. *scopulorum;* note flabellate branching and variation in color of the thick shoots from orange to reddish brown.

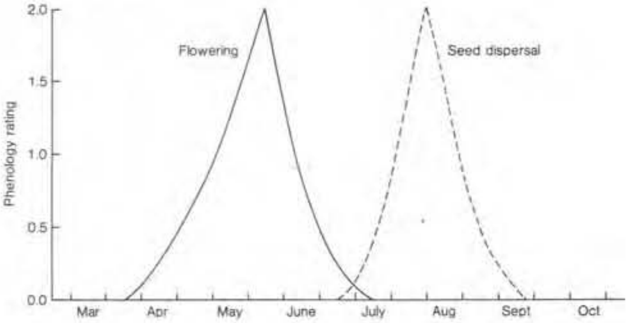

Figure 16.109 –Phenology of flowering and seed dispersal of *Arceuthobium vaginatum* subsp. *crytopodum* (based on 282 observations).

Hosts: *Pinus ponderosa* var. *scopulorum* is the most common host in Arizona, New Mexico, Colorado, Utah, and Texas. The two races of var. *scopulorum* recognized by Conkle and Critchfield (1988) (Rocky Mountain and southwestern) appear to be about equally susceptible, but most of the distribution of the Rocky Mountain race is primarily north of that of *Arceuthobium vaginatum* subsp. *cryptopodum*. Other principal hosts include *P. arizonica* var. *arizonica* (Arizona, New Mexico, Chihuahua, and Sonora) and var. *stormiae* (Coahuila), *P. engelmannii* (Arizona, Chihuahua, and Sonora), and *P. durangensis* (Chihuahua and Jalisco). *Pinus cooperi* is a secondary host. Occasional hosts are *P. contorta* var. *latifolia* in Colorado and Utah (Hawksworth 1956a) and *P. aristata* in Colorado and New Mexico (Hawksworth 1965a). Rare hosts are *P. flexilis* in Colorado (Hawksworth and Peterson 1959) and *P. strobiformis* in New Mexico.

Distribution: Northern Mexico (Sonora, Chihuahua, and Coahuila) (fig. 16.107) and United States (Utah, Arizona, Colorado, New Mexico, and Texas) (fig. 16.110). *Arceuthobium vaginatum* subsp. *cryptopodum* is widely distributed on *Pinus ponderosa* var *scopulorum* from central Utah (Sevier and Emery Counties) and northern Colorado (to latitude 40°52' N in Larimer County) to Arizona, New Mexico, west Texas (Guadalupe and Davis Mountains, but not the Chisos Mountains), at least as far south as the Sierra de la Madera in central Coahuila and the Sierra Madre Occidental in Sonora and Chihuahua. Confirmation is needed for the reports of *A. vaginatum* subsp. *cryptopodum* in southern Duchesne County and northwestern Emery County, Utah (Albee and others 1988). The Duchesne record is probably based on the infection of *P. ponderosa* by *A. cyanocarpum*.

Arceuthobium vaginatum subsp. *cryptopodum* occurs in nearly every mountain range where *P. ponderosa* var *scopulorum* grows, including some very isolated ranges such as the Virgin, Trumbull, and Hualapai Mountains in northwestern Arizona; the Ladron, Organ, Guadalupe, and San Andreas Mountains (Salinas Peak) in New Mexico; Navajo Mountain in southern Utah, and Mesa de Maya in southeastern Colorado. Andrews and Daniels (1960) recorded the parasite on 36% of about 3,000 plots scattered throughout the range of *P. ponderosa* var. *scopulorum* in Arizona and New Mexico.

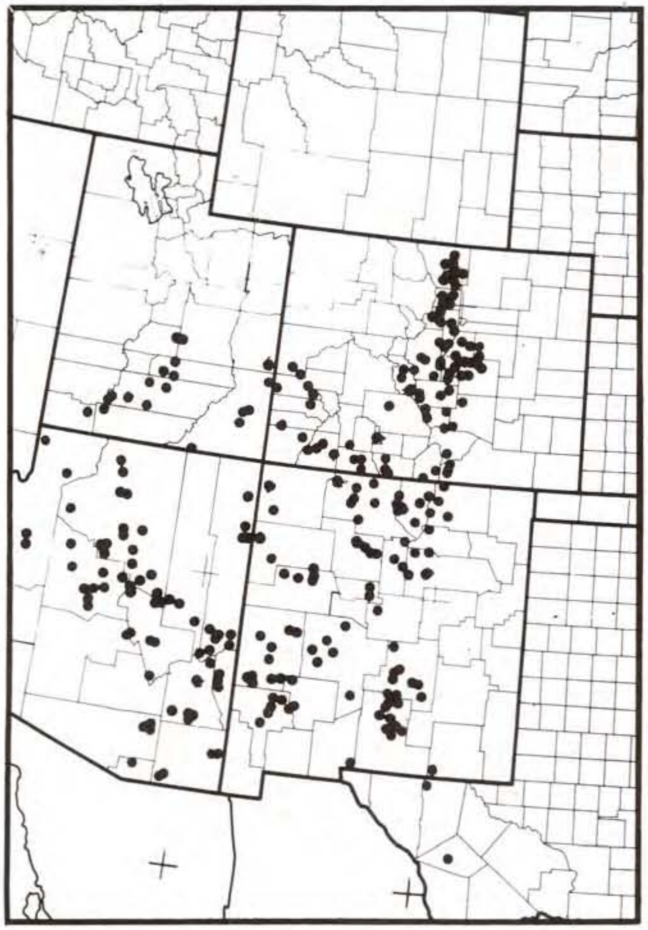

Figure 16.110 –Distribution of *Arceuthobium vaginatum* subsp. *crytopodum* in the western United States.

Arceuthobium vaginatum subsp. *cryptopodum* distribution maps have been published for Colorado (Hawksworth 1987c), Utah (Albee and others 1988), and New Mexico (Martin and Hutchins 1980). Elevational range is 1,700–3,000 m, although it is found primarily between 2,000 and 2,600 m in Arizona and New Mexico.

Discussion: *Arceuthobium vaginatum* subsp. *cryptopodum* is characterized by thick, orange-colored shoots, but certain populations show various gradations from yellow to red and rarely may be purple to nearly black. Dark plants are particularly common in the Black Forest northeast of Colorado Springs, Colorado. Plants growing in deep shade tend to be greenish, as do those on *Pinus contorta* var. *latifolia*.

This dwarf mistletoe is particularly damaging to *Pinus ponderosa* in the Sacramento Mountains in south central New Mexico (Lincoln National Forest and adjacent Mescalero Apache Indian Reservation), central Arizona, and along the Front Range in Colorado. For reasons yet to be explained, the parasite, although common, is less damaging to *P. ponderosa* var. *scopulorum* in southwestern Colorado and southeastern Utah than in other areas.

The witches' brooms induced by *Arceuthobium vaginatum* subsp. *cryptopodum* are similar on all hosts (fig. 16.111), except for *Pinus contorta* var. *latifolia* (Hawksworth 1961a). On this host the witches' brooms are small, but the swellings at the point of infection are much more pronounced than on *P. ponderosa* var. *scopulorum* (often 2–3 times the diameter of uninfected branches).

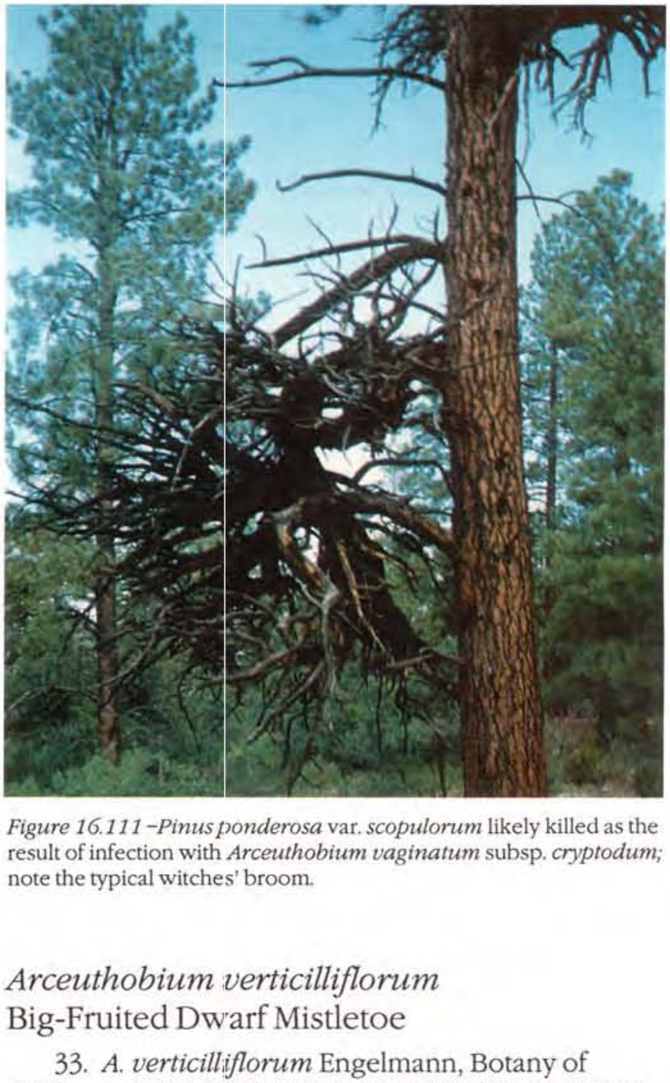

Figure 16.111 –*Pinus ponderosa* var. *scopulorum* likely killed as the result of infection with *Arceuthobium vaginatum* subsp. *cryptodum*; note the typical witches' broom.

Arceuthobium verticilliflorum
Big-Fruited Dwarf Mistletoe

33. *A. verticilliflorum* Engelmann, Botany of California 2:107, 1880. TYPE COLLECTION: MEXICO: Durango: Sierra Madre, (on *Pinus* sp.?), *Seemann 2138* in 1852 (Lectotype MO! Isotypes: K!, ILL!). *Razoumofskya verticillata* (Engelm.) Kuntze, Revision of Genera of Plants 2:587, 1891.

Description: Mean shoot height ca. 7 (max. 11) cm, mostly yellow to yellow-green to purplish, without secondary branching, lightly glaucous when young (fig. 16.112). Basal diameter of dominant shoots 2.5–5.0 (mean 3.6) mm. Third internode 2–7 (mean 3.0 ± 1.2) mm long, 2.5–4.5 (mean 3.2) mm wide (4 collections), length/width ratio 0.9:1. Staminate flowers 3.5–4.5 (mean 4.0) mm across; perianth mostly 4-merous (sometimes 3-merous); verticillate, with 5–10 flowers per whorl; segments 1.8 mm long, 1.2 mm wide. Mean anther diameter 1.0 mm, centered 0.8 mm from tip of segment. Pollen polar diameter 21–25 (mean 24) µm; equatorial diameter 26–30 (mean 28) µm; polar/equatorial diameter ratio 1:1.18; spine height ca. 1.0 µm or two-thirds wall thickness (1.5 µm) (2 collections). Mature fruit ca. 15 × 10 mm (figs. 16.113 and 16.114). Seeds ca. 11 × 6 mm; embryos 4 × 1 mm. $n = 14$.

Phenology: Meiosis September–October. Anthesis usually March–April. Fruits mature in September and October of the year following pollination; maturation period averages 18–19 months.

Hosts: This dwarf mistletoe parasitizes *Pinus engelmannii, P. cooperi, P. arizonica,* and *P. durangensis. Pinus leiophylla* vars. *leiophylla* and *chihuahuana,* and *P. teocote* are not parasitized even when they are associated with infected pines.

Figure 16.112 –Arceuthobium verticilliflorum, young shoots emerging from host. (D. L. Nickrent)

Figure 16.113 –Arceuthobium verticilliflorum, pistillate plant with young developing fruits (right) and mature fruits (left).

Figure 16.114 –Arceuthobium verticilliflorum, pistillate plant with mature fruits; note short, straight pedicles.

Distribution: Mexico (Durango) (fig. 16.115). This dwarf mistletoe is not as rare as we originally believed (Hawksworth and Wiens 1975). Several populations occur 11–54 km east of El Salto on the Durango–Mazatlán Highway. Recently populations have been discovered in the Sierra Candella, Sierra Huacol (Cibrián Tovar and others 1980), Sierra Guanacevi, and along the road from Santiago Papasquiaro to Altares. Elevational range is 2,000–2,750 m.

Discussion: This unusual species, although first described by Engelmann in 1880, was essentially ignored until we rediscovered the populations near El Salto (Hawksworth and Wiens 1965). The species is perhaps the most distinctive and primitive in the genus. The staminate shoots are characterized by thick spikes (4–6 mm) with verticillate 4-merous flowers, mostly 6 in a whorl; the entire spikes are deciduous after flowering. The species has fruits that are more than twice as large as any other dwarf mistletoe; they averaged 6 × 3 mm in March, 14 × 7 mm in July, and 15 × 10 mm in September when they were near maturity. A few fruits are probably dispersed in early September, but the peak period of seed dispersal is likely in October.

This is the only dwarf mistletoe in which the pedicels do not elongate and curve downward when the fruits mature (fig. 16.114), and the seeds are not explosively dispersed upward. In *Arceuthobium verticilliflorum* the pericarp appears to "ooze off" the top of the seed, which remains attached to the receptacle. There is no evidence of explosive discharge. This feature, plus apparent evidence of birds feeding among the fruits, suggests dispersal by birds. The primitive morphological features associated with this species indicate that birds are likely the original mode of dispersal and not a derived system. Its occurrence in very

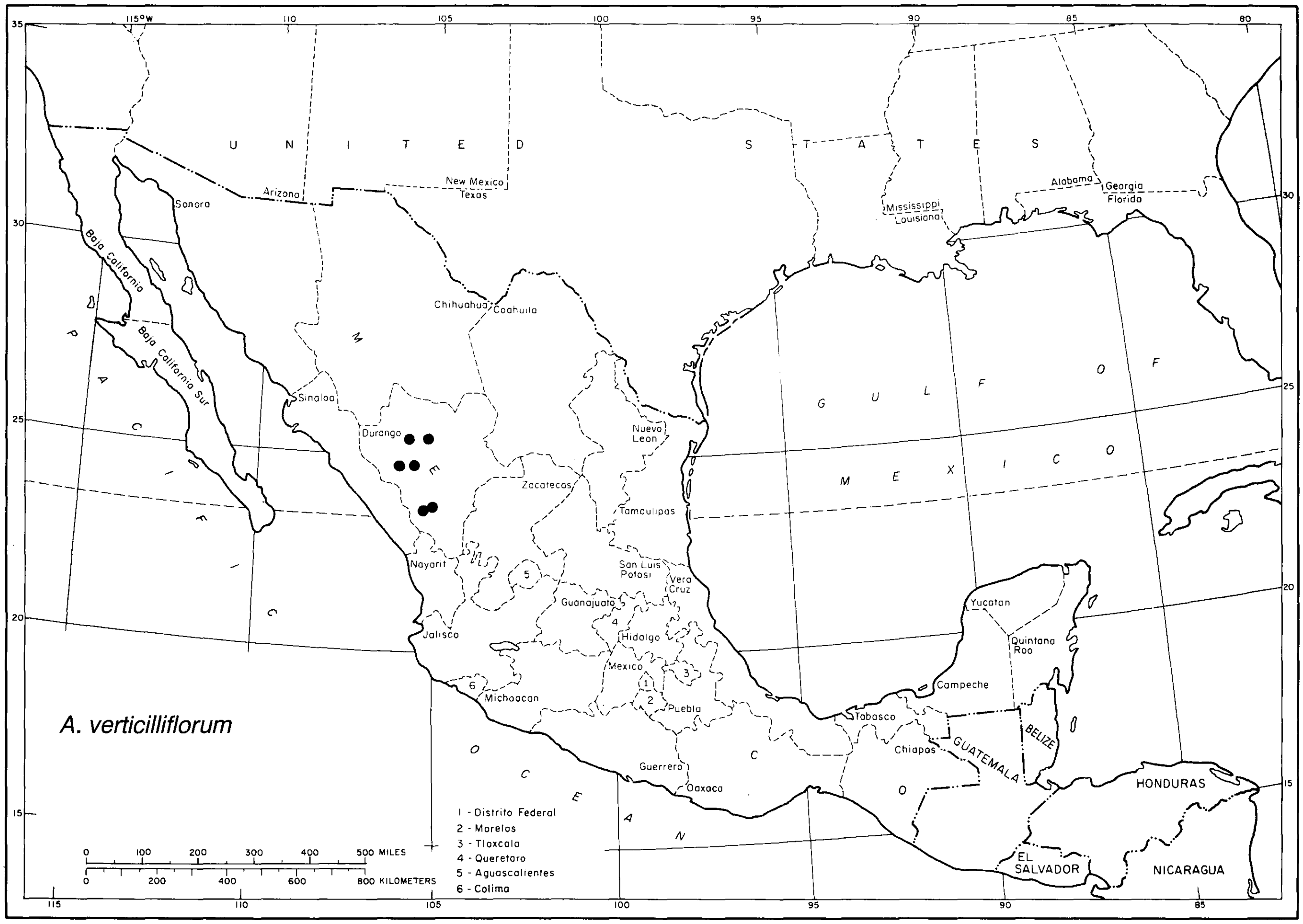

Figure 16.115–Distribution of *Arceuthobium verticilliflorum.*

open stands and the seemingly random distribution of the parasites within stands and trees suggests that dispersal by birds is common in this species (other species tend to occur in closed stands as pockets of trees more severely infected in lower crowns than in upper crowns).

Arceuthobium verticilliflorum is also chemically unique in the genus because it has no flavonoids (Crawford and Hawksworth 1979, see table 14.2). Another unique feature of *A. verticilliflorum* is the heaviness of the seeds (200–270 mg). This is about 100 x the weight of dwarf mistletoe seeds that are explosively dispersed (Hinds and others 1963, Knutson 1984). It is extremely unlikely that seeds weighing 200 mg could be effectively dispersed explosively.

Kuijt (1970) concluded that the branching pattern of *Arceuthobium verticilliflorum* is basically verticillate. This dwarf mistletoe causes massive witches' brooms, and the diameter of infected branches is sometimes greater than that of the trunk where the infected branch emerges. Infections on the main trunks of pines sometimes extend up to 3 m in length.

Arceuthobium yecorense
Yecoran Dwarf Mistletoe

34. *A. yecorense* Hawksworth & Wiens, Phytologia 66: 6, 1989. TYPE COLLECTION: MEXICO: Sonora: Mpio. Yecora: 2 km east-southeast of Yecora, on *Pinus herrerai*, latitude 28°22' N, longitude 108°54' W, elevation 1600 m, *Hawksworth 2168*, 7 May 1987 (Holotype US! Isotypes: ENCB, FPF, INIF, MO, UNAM, UC).

Description: Mean shoot height 12 (max. 17) cm, yellow-green to brown, flabellately branched (fig. 16.116). Basal diameter of dominant shoots 2–5 (mean 3) mm. Third internode 10–21 (mean 15) mm long, 2–4 (mean 2.4) mm wide. No flowers or mature fruits available for study. *n* = ?

Phenology: Anthesis has not been observed, but judging by the stage of development of the floral buds in early May, we suspect that it flowers in June. Time of fruit maturity is unknown, but it is presumably September–October.

Hosts: The principal hosts in the Yecora area of Sonora are *Pinus leiophylla* var. *chihuahuana* and *P. herrerai.* It occurs secondarily on *P. engelmannii,* and does not parasitize associated *P. arizonica.* In the Sierra Madre Occidental in western Durango, it occurs on *P. herrerai, P. lumholtzii, P. leiophylla* var. *chihuahuana, P. engelmannii,* and *P. durangensis.*

Distribution: Mexico (Sonora, Chihuahua, and Durango) (fig. 16.117). The distribution of this dwarf mistletoe is poorly known; it has been collected only in the Yecora area of southeastern Sonora and adjacent Chihuahua and about 100 km west of Santiago Papasquiaro in Durango. It is abundant at both locations. These populations are more than 400 km apart, so the dwarf mistletoe is to be expected in the intervening forest areas of western Chihuahua and northwestern Durango. Elevational range is 1,600–2,500 m.

Figure 16.116 –Arceuthobium yecorense on *Pinus* sp. (J. Beatty)

Discussion: This distinctive dwarf mistletoe was first collected in 1986 near Yecora, Sonora, by Ignacio Carbajal V. of Forestal Sanidad, SARH, Mexico City (Hawksworth and Wiens 1989). *Arceuthobium yecorense* is characterized by its slender, greenish yellow to brownish shoots and early summer flowering period. The plants are morphologically most similar to *A. aureum* subsp. *aureum* of the lowlands of Guatemala (Hawksworth and Wiens 1977). The populations in western Durango have more yellowish and slightly taller shoots than the Sonora populations, but otherwise they are similar. The Pueblo of Yecora is the primary pine-producing area of Sonora where this dwarf mistletoe is both common and damaging.

Old World Taxa

Arceuthobium azoricum
Azores Dwarf Mistletoe

35. *A. azoricum* Hawksworth & Wiens, Kew Bulletin 31:73, 1976. TYPE COLLECTION: AZORES: Faial, southeast slopes of the Caldiera, 900 m, on *Juniperus brevifolia, Wiens 4953,* October 1973 (Holotype US! Isotypes: FPF, K, LISU, UT).

Description: Plants 7–14 cm high, greenish-yellow; secondary branching is verticillate, but rare (figs. 16.118 and 16.119). Basal diameter of dominant shoots 5–9 mm. Third internode 8–15 (mean 12) mm long, 3–6 (mean 4) mm wide; length/width ratio 3:1; staminate flowers ca. 2.5 mm across, mostly 4-merous (97%), rarely 3-merous (3%). Pistillate flowers verticillate. Mature fruit is unknown. Pollen is unknown. $n = ?$

Phenology: Anthesis September–October, fruits mature in November.

Host: Exclusively on *Juniperus brevifolia* (the only juniper on the Azores).

Distribution: The species is endemic to the Azores and occurs on the islands of Terceira, San Jorge, Pico, and Faial. Because the endemic host, *Juniperus brevifolia,* occurs on several additional islands (Palhinha 1966, Sjogren 1973), the dwarf mistletoe may also have a wider distribution. Most of the islands are severely deforested, however. Elevational range is 600–1200 m.

Discussion: This dwarf mistletoe was not discovered until 1913 (Guppy 1914, 1917). An account of the early collections and distribution of *Arceuthobium azoricum* (as *A. oxycedri*) is given by Palhinha (1942). Recent descriptions of distribution are given by Palhinha (1966) and Sjogren (1973). The parasite had previously been considered to be an extreme outlier (ca. 1,600 km) of *A. oxycedri,* but *A. azoricum* is one of the most distinctive of all dwarf mistletoes (Hawksworth and Wiens 1977). The high frequency of 4-merous staminate flowers is unusual. The consistently whorled pistillate flowers subtended by minute bracts are unique in the genus, although *A. verticilliflorum* has consistently whorled staminate flowers. A comparison of *A. azoricum* with the other two Old World parasites of *Juniperus* (*A. oxycedri* and *A. juniperi-procerae*) is given in table 16.7.

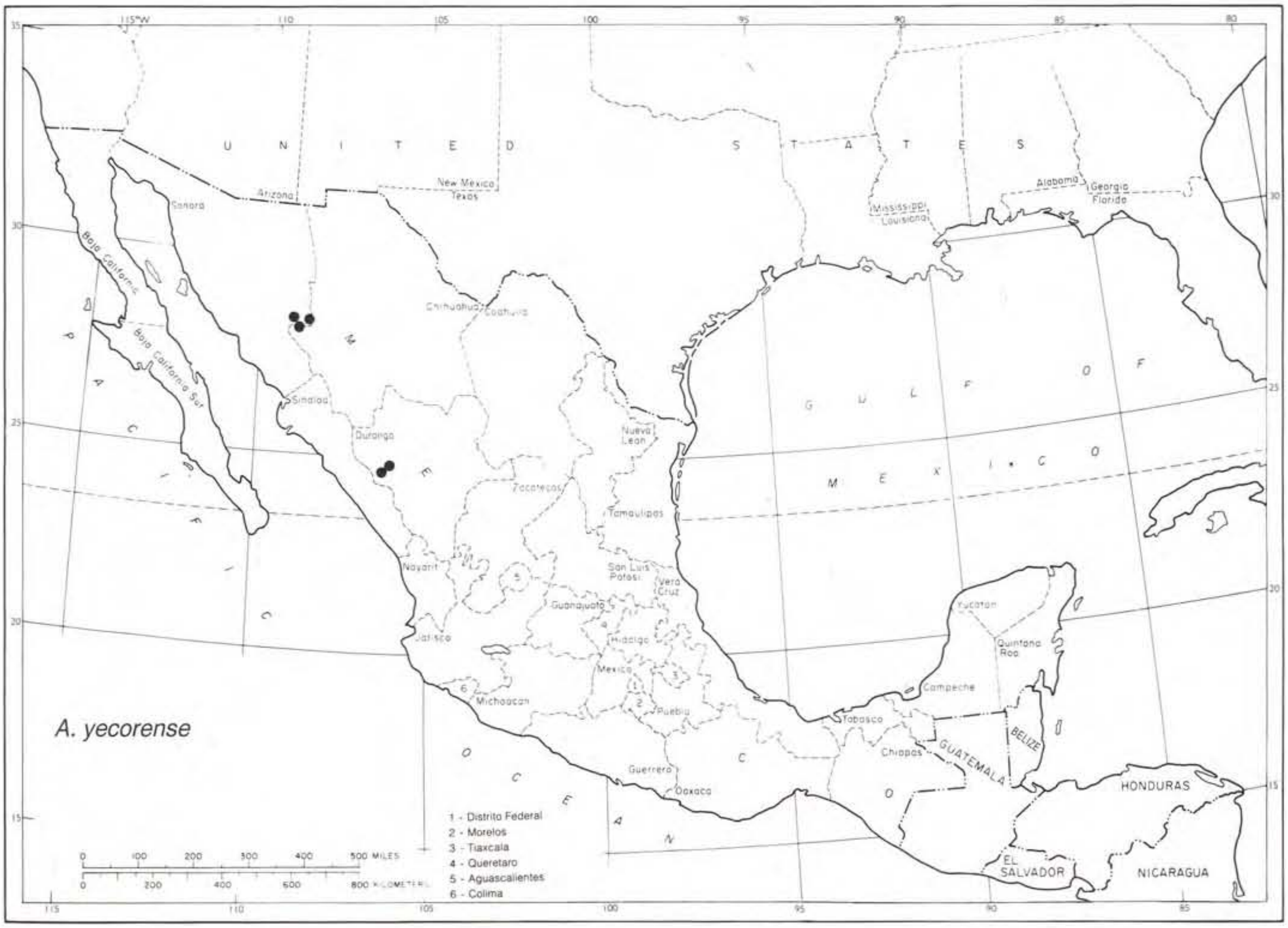

Figure 16.117 –Distribution of *Arceuthobium yecorense.*

Figure 16.118 –*Arceuthobium azoricum* parasitizing *Juniperus brevifolia;* no witches' brooms are induced by this species.

The basal internodes are unusually wide and approach 1 cm across. The shoots then taper gradually upward. This dwarf mistletoe typically occupies the distal ends of the host branch, where a gall up to about four times the size of the host branch is formed at the point of infection (fig. 16.119). The portions of the

Figure 16.119 –*Arceuthobium azoricum*; note the expanded, rounded basal swelling, wide base, and rapid taper of shoots.

host branch distal to the original point of the infection are killed and ultimately fall away. This host reaction is typical of many other genera of mistletoes, but is otherwise unknown in *Arceuthobium.*

Arceuthobium azoricum and *A. bicarinatum* (a Caribbean species) are the only dwarf mistletoes restricted to oceanic islands. *Arceuthobium azoricum* might be of exceptional interest from phylogenetic and biogeographical points of view. The distinctiveness of the species, as well as the host, suggests a long and isolated evolutionary history. Ridley (1930) specifically mentioned *A. azoricum* (as *A. oxycedri*) as an example of long-distance dispersal, and hence probably a recent immigrant to the islands. The necessity for seeds of both sexes to be distributed almost simultaneously and in close proximity, the ecological differences between the mainland and island habitats, and the general continental distribution of the genus argue strongly against long-distance dispersal. Also, the juniper host would not appear to be well adapted for long-distance dispersal. Hawksworth and Wiens (1976) suggested that *A. azoricum* and its host may be survivors of early Tertiary continental genera that became restricted to recurrent volcanic islands along the mid-Atlantic ridge (McKenna 1972).

Arceuthobium chinense
Keteleeria Dwarf Mistletoe

36. *A. chinense* Lecomte, Notulae Systematicae 3: 170, 1915. TYPE COLLECTION: CHINA: Yünnan: Bois audessus de Ta-pin-ze; *Delavay s. n.* in 1887 (Lectotype P, Isotype K!).

Description: Plants 2–12 (mean ca. 5) cm high, yellowish green, secondary branching verticillate. Basal diameter of dominant shoots 1–2 (mean 1.5) mm. Third internode 4–6 (mean 5) mm long, 1.0–1.5 (mean 1.1) mm wide (4 collections); length/width ratio 4.4:1. Staminate flowers ca. 2 mm across; 4-merous (rarely 3-

TABLE 16.7—Comparison of the three species of *Arceuthobium* on Old World junipers

Character	*A. azoricum**	*A. juniperi-procerae*†	*A. oxycedri*‡
Shoot height (mean)	7–14 (10) cm	4–14 (7) cm	3–14 (6) cm
Shoot color	Greenish yellow	Greenish yellow	Green
Glaucous shoots	None	Little or none	Conspicuous
Percent of nodes with branch whorls (mean)	3–5 (4)	1–7 (3)	32–55 (45)
Basal shoot diameter (mean)	5–9 (7) mm	1–3.5 (2) mm	1–3 (2) mm
Third internode length × width	12 × 4 mm	7 × 1 mm	7 × 1 mm
Staminate flower width (mean)	2.5 mm	1.8 mm	2.0 mm
Ratio of 3- to 4-merous staminate flowers	3:97	100:0	95:5
Mature fruit apex	Rounded	Shouldered	Rounded
Peak flowering period	September–October	March and later	September–October
Fruit maturation	November	March and later	October–November

*Character values based on 10 collections.

†Character values based on 14 collections, but only 1 collection with staminate flowers.

‡Character values based on 20 collections.

merous); segments ca. 1 mm long, 1 mm wide, tapered to tip, widest at base. Pollen polar diameter 14–18 (mean 16) µm; equatorial diameter 16–19 (mean 17) µm; polar/equatorial diameter ratio 1:1.09; spine height and wall thickness ca. 1.0 µm (2 collections). Mature fruit ca. 4–6 mm long, 3–4 mm wide, distal portion ca. 2 mm long, proximal portion yellowish green or glaucous. $n = ?$

Phenology: Time of meiosis unknown. Anthesis July–November, with a peak from mid-September to mid-October (Kiu 1984, Tong and Ren 1980), fruits mature in late-August to mid-October (Tong and Ren 1980); maturation period is 11–12 months.

Hosts: The only known host is *Keteleeria evelyniana*. The original description by Lecomte (1915), lists the host as *"Abies,"* but it was undoubtedly *Keteleeria*. Kiu (1984) also believes that the host was misidentified because *Abies* does not occur at the comparatively low elevation (2,500 m) reported for this species.

Distribution: China (Yünnan and Sichuan Provinces). Tong and Ren (1980) report that it occurs throughout the range of *Keteleeria evelyniana* in southwestern China. A distribution map is given by Kiu and Ren (1982). Elevational range is 1,500–2,700 m (Kiu 1984).

Discussion: The only information on this species is from the reports of Anonymous 1939, Danser 1936, Handel-Mazzetti 1929, Kiu 1984, Kiu and Ren 1982, Lecomte 1915, and Ton and Ren 1980. Some of these papers, however, do not distinguish between *Arceuthobium chinense* and *A. pini. Arceuthobium chinense* causes extensive damage in both pure and mixed stands of *Keteleeria evelyniana* (Tong and Ren 1980). Handel-Mazzetti (1929) reports a young stand of *Keteleeria* in Yünnan Province that was completely killed by this dwarf mistletoe, which apparently forms systemic witches' brooms (Kiu 1984b).

Arceuthobium juniperi-procerae
East African Dwarf Mistletoe

37. *A. juniperi-procerae* Chiovenda, Annali di Botanica, Roma 9:134, 1911. TYPE COLLECTION: ERITREA: Acchele Guzai, Ambra Debra, on *Juniperus procera, Pappi 355*, August 1902, and Mt. Mamahot, on *Juniperus procera, Pappi 1161*, August 1902 (Lectotype, *Pappi 1161* FT).

Description: Plants 4–14 (mean 7) cm high; greenish yellow; secondary branching verticillate, but rare (fig. 16.120). Basal diameter of dominant shoots 1.0–3.5 (mean 2) mm. Third internode averages 7 mm long, 1 mm wide. Staminate flowers 1.8 mm across, all 3-merous in the 1 collection studied. $n = 14$.

Phenology: Anthesis from November to March, probably having 2 distinct, or less likely, 1 extended flowering period(s) (Hawksworth and Wiens 1976). Fruit maturation period poorly known, mature fruits were present March–April (Hawksworth and Wiens 1976). Developing fruits observed in mid-December were approximately two-thirds of their mature size.

Host: Parasitic only on *Juniperus procera* (fig. 16.121).

Distribution: Eastern Africa (Kenya, Eritrea, and Ethiopia) (fig. 16.122). Elevation range is 2,000–3,000 m.

Figure 16.120–Arceuthobium juniperi-procerae, staminate plant.

Discussion: The earliest mention of a dwarf mistletoe from sub-Saharan Africa was by Chiovenda (1911) who described *Arceuthobium juniperi-procerae* from the northern highlands of Eritrea. With the exception of Cufodontis (1953), who cited *A. juniperi-procerae* in his checklist of Ethiopian plants, no one else has previously accepted this species as valid.

Arceuthobium juniperi-procerae is closely related to *A. oxycedri*. Consequently, it is useful to compare these species (table 16.7). Whorled branching is relatively common in *A. oxycedri* (45%), but uncommon to rare (3%) in *A. juniperi-procerae*. Occasionally, the staminate flowers occur in whorls in *A. juniperi-procerae*, a condition unknown in the other two species of dwarf mistletoes that parasitize junipers. The fruit of *A. juniperi-procerae* is also characterized by a distinctive shoulder below the perianth segments that is absent in *A. oxycedri*.

Figure 16.121 –*Juniperus procera* showing witches' brooms induced by infection with *Arceuthobium juniperi-procerae.*

The living plants of *Arceuthobium oxycedri* are often conspicuously glaucous, especially the apical portions of the shoots and the fruit. The glaucous character, however, tends to be lost on drying. *Arceuthobium juniperi-procerae* is only slightly glaucous. There is also a marked difference in coloration between *A. oxycedri* and *A. juniperi-procerae*. The former is a deep green and rather resembles the color of most *Viscum* and *Phoradendron* species, whereas *A. juniperi-procerae* is a yellowish green that is more typical of dwarf mistletoes.

The distribution of *Arceuthobium juniperi-procerae* is poorly known. It parasitizes only *Juniperus procera*, which is the only juniper occurring in sub-Saharan Africa. The only extensive highland areas in Kenya from which the parasite is not known are the Cherangani Hills and Mt. Elgon. Preliminary searches for the parasite in the southern Cherangani Hills failed to reveal its presence, but deforestation has reduced the populations of *J. procera* there. Only the eastern slopes of Mt. Elgon extend into Kenya, and juniper was not observed there. The western slopes of all the principal highland regions of Kenya are typically much drier than the eastern slopes, and this dwarf mistletoe seems to favor relatively dry areas. In addition to the western highlands of Kenya, *J. procera* is also known from several mountain ranges in the northern arid regions of Kenya that exceed 1,800 m (such as in the Maralal area); the dwarf mistletoe might also be expected to occur there. *Arceuthobium juniperi-procerae* may possibly be scattered from the principal highland regions of Kenya to Eritrea and northern Ethiopia wherever suitable host populations might occur. In southern Kenya, the Loita Hills should be favorable habitat for the dwarf mistletoe, as well as the interesting stand of comparatively low elevation junipers at the northern end of the Chyulu Hills.

Presently, *Arceuthobium juniperi-procerae* is unknown in East Africa outside Kenya. There might be favorable habitat, however, in Uganda and Tanzania, especially on the western slopes of Mt. Elgon and in some of the higher isolated northeastern mountain ranges in the Karamoja region. In Tanzania, the juniper stands at the northeastern base of Mt. Meru and the northwestern side of Mt. Kilimanjaro were examined for dwarf mistletoe, but none was observed. The juniper stand at Mt. Meru was not extensive, and the stands on the northwestern slopes of Mt. Kilimanjaro have been significantly reduced through deforestation. Several limited surveys of the northern portion of the western Usambara Mountains in northeastern Tanzania, where substantial stands of *Juniperus procera* occur, failed to reveal the presence of dwarf mistletoe. The highland areas around Ngorongoro Crater should also be explored for dwarf mistletoe, as well as regions around Loliondo, which is essentially an extension of the Loita Hills in southern Kenya.

The Kipengere Range in the southern Tanzanian highlands has a juniper stand in the Ndumbe forest. These trees are likely the largest individuals of *Juniperus procera* in Africa and are probably more than 30 m tall. A brief visit to this stand showed no evidence of dwarf mistletoe infection. This area, however, may be too moist for *Arceuthobium*.

Juniperus procera occurs in scattered localities as far south as Zimbabwe, but the stands have apparently not been examined for dwarf mistletoe, with the exception of those on the Nyika Plateau in northern Malawi. The Nyika stand, however, is also much reduced through deforestation, and the junipers consisted of only a few hectares of scattered trees; no evidence of dwarf mistletoe infection was observed.

In Ethiopia and Eritrea, *Arceuthobium juniperi-procerae* is known from only three localities, all in the north; two original collections of this species were from the Eritrean Highlands south of Asmara. We collected the dwarf mistletoe in the same general region, but south of the Tigre Provincial border northwest of Makale. Ethiopia and Eritrea are so badly deforested

Figure 16.122 –Distribution of *Arceuthobium juniperi-procerae* in Africa (open circles) and *A. oxycedri* in Europe, North Africa and Asia (solid circles).

that the original distribution of *A. juniperi-procerae* will likely never be known. Considering the degree of infection of *Juniperus procera* in the forest reserve northwest of Makale, where perhaps more than 90% of the trees were infected, one might suspect that *A. juniperi-procerae* originally had a rather widespread distribution in these countries, at least in the drier regions.

We suspect that *Arceuthobium juniperi-procerae* may also occur across the Red Sea in Yemen and adjoining areas.

Arceuthobium minutissimum
Himalayan Dwarf Mistletoe

38. *A. minutissimum* J. D. Hooker, Flora of British India 5: 227, 1886. TYPE COLLECTION: NEPAL: Kumaon Himalaya, 3,250 m, on *Pinus wallichiana* (as *Abies excelsa*), *Duthie s. n.* in 1884 (Lectotype K!).

Razoumofskya minutissima (Hook.) Tubeuf, Naturwissenschaftliche Zeitschrift für Forst- und Landwirstschaft 17: 195, 1919.

Description: Plants ca. 5 (max. 10) mm high; pistillate plants greenish (fig. 16.123), usually about twice as tall as the staminate plants; staminate plants yellow-green (fig. 16.124); primary branches multiple and arising from basal cups, but without secondary branching. Basal diameter of dominant shoots ca. 1 mm. Third internode 0.5–1.4 (mean 0.8 ± 0.3) mm long, 0.3–1.0 (mean 0.4) mm wide (3 collections); length/width ratio 1.5:1. Staminate flowers 2.0–2.5 mm across; perianth mostly 4-merous (sometimes 3-merous), segments ca. 0.8 mm long, 0.8 mm wide. Anther diameter ca. 0.5 mm, centered ca. 0.4 mm from tip of segment. Pollen polar diameter 16–19 (mean 18) µm; equatorial diameter 19–21 (mean 21) µm; polar/equatorial diameter ratio 1:1.16; spine height about the same as wall thickness (0.8 µm) (3 collections). Mature fruit 2.0–2.5 mm long, 1.0–1.5 mm wide. $n = ?$

Figure 16.123 –Arceuthobium minutissimum, pistillate plant with mature fruits; these plants are ca. 1 cm high, including fruits.

Figure 16.124 –Arceuthobium minutissimum, staminate plant at anthesis; note emergence of the inflorescences from just above the base of the fascicle.

Phenology: Time of meiosis unknown. Anthesis is reported August–October (Datta 1956), but all flowering specimens we have collected or examined in herbaria were obtained in September. Seed dispersal is also in September, so the fruit maturation period averages ca. 12 months.

Hosts: The principal and only commonly infected host is *Pinus wallichiana*. However, Zakaullah and Badshah (1984) found that *P. gerardiana* is sometimes infected in northern Pakistan in areas where this tree is associated with infected *P. wallichiana. Arceuthobium minutissimum* may occur on *Abies pindrow* in the Simla Hills of East Punjab, India (Rajagopaliengar 1955), but this requires confirmation. Similarly, Rechinger's (1976) report of it on *Cedrus deodara* in the Swat area of northwest Pakistan has not been verified. We, and several Pakistani forest pathologists, have found *A. minutissimum* to be common on *Pinus wallichiana* in this area, but it did not infect closely associated *Cedrus.* Gaur's (1981) report of *A. minutissimum* on *Debregeasia hypoleuca* (an angiosperm) at low elevations on the Gangetic Plain of northern in India is in error. The observation was based on a fungus that superficially resembled the fruit of a dwarf mistletoe.

Distribution: *Arceuthobium minutissimum* is known from the Himalayas in Pakistan, India, Nepal, and Bhutan. Bagchee (1952) reports that its distribution in India is associated with the dry zone of the Himalayas in Upper and Lower Bashahr in Himachal Pradesh, Kulu in East Punjab, and the four divisions of Kashmir. Several workers note that this dwarf mistletoe occurs in the dry zone of *Pinus wallichiana* forests in India and Pakistan, but not in the more mesic zones of the host's distribution (Bakshi and Puri 1971, Gorrie 1929, Hawksworth and Zakaullah (1985). Elevational range is 2,400–3,500 m (Brandis 1907).

Discussion: The type folder for *Arceuthobium minutissimum* at Kew contains 3 collections by Duthie from Nepal: *Duthie s. n.* in 1884, *Duthie 3359* in 1884 (2 sheets), *Duthie 5947* in 1886. Apparently *Duthie s. n.* in 1884 was intended as the type because the elevation of this collection agrees with the published description.

Hooker (1886) mentions that *Arceuthobium minutissimum* was perhaps the smallest dicotyledonous plant. The shoots are clearly the smallest of any dwarf mistletoe. Although the shoots (inflorescences) are usually less than 5 mm high, the "plant" is much more extensive if the endophytic system within the host tissues were included.

Several workers have questioned whether *Arceuthobium minutissimum* is dioecious, as are all the other members of the genus (Danser 1931, Datta 1951, and Hooker 1886). Our field observations indicate that the species is clearly dioecious. The suggestion of monoecism was likely based on the frequent occurrence of mixed pistillate and staminate infections. Datta (1951) described a single hermaphroditic flower in *A. minutissimum*, but this was undoubtedly a rare developmental aberration. Bhandari and Nanda (1968) discuss the embryology and morphology of *A. minutissimum*. The species is unique in the genus because the shoots emerge not only from the host cortex, but also from the needles, about 1–2 mm above the base of the fascicles.

Kuijt (1960b) suggested that the fruits of *Arceuthobium minutissimum* may mature in a single growing season (ca. 5 months) as in the North American species *A. pusillum*. However, our field studies in

Kashmir and Pakistan show that peak periods for both anthesis and seed dispersal occur in September. Thus, a seed maturation period of about 12 months is indicated or the species has two flowering periods, which is unlikely.

This dwarf mistletoe is a serious pathogen of *Pinus wallichiana* in India and Pakistan, particularly on the drier sites where it causes severe brooming (fig. 16.125) and mortality (Ciesla 1993, Gorrie 1929, Zakaullah 1988, Zakaullah and Badshah 1982). Severe host damage and mortality are often associated with dwarf mistletoes that induce systemic infections. Our field studies indicate this is certainly the case for *Arceuthobium minutissimum*, and so have others (Gorrie 1929, Kuijt 1960b).

Arceuthobium oxycedri
Juniper Dwarf Mistletoe

39. *A. oxycedri* (DC.) M. Bieb., Flora Taurico-Caucasica III: 629, 1819. TYPE COLLECTION: unknown but Komarov (1936) states it is at P. *Viscum oxycedri* DC., Fl. Fr. 4: 274, 1805. *Razoumofskya caucasica* Hoffman, Hortus Mosquensis (unpaged), 1808. *Razoumofskya oxycedri* (DC.) Schultz, ex Nym. Consp.: 320, 1853. *Viscum caucasicum* Steud. No. ed 1: 888, 1891. *A. juniperi* Bubani, Flora Pyrenacea: 131, 1897. *A. juniperorum* Reynier, Bull. Soc. Bot. Fr. 66: 97, 1919. *A. oxycedri* (DC.) M. Bieb. var. *cupressii* Zefirov, Akademi Nauk SSR. Bot. Inst. 17:110, 1955.

Figure 16.125–*Pinus wallichiana* showing witches' brooms induced by infection with *Arceuthobium minutissimum*.

Description: Shoots mostly 5–10 (max. 20) cm high, green; verticillate branching common (fig. 16.126). Basal shoots 1–4 (mean 2) mm across. Third internode 5–9 (mean 7) mm long, ca. 1 mm wide; shoots terete; internodes often markedly wider at the top than at the base. Staminate flowers 1.5–2.5 (mean 2.0) mm across, perianth mostly 3-merous (ca. 95%), occasionally 4-merous (ca. 5%), rarely 2-merous. Pollen polar diameter 17–19 (mean 18) µm, equatorial diameter 19–22 (mean 21) µm; polar/equatorial diameter ratio 1:1.17; spine height (1.5 µm) slightly greater than the wall thickness (1.0 µm) (2 collections). Mature fruit ca. 3 mm long, 1.5–2.0 mm wide. $n = 13–17$.

Phenology: Anthesis mostly September–October (August–September in China according to Kiu 1984b). Seed dispersal in October and November; maturation period about 13 months.

Hosts: Parasitic primarily on *Juniperus oxycedrus*, but also on several other native species of junipers and introduced *Juniperus, Cupressus, Chamaecyparis, Thuja,* and *Platycladus* (table 16.8). The most intensive studies of its hosts have been in Crimea, where Isikov and Zakharenko (1988) reported it on 18 species of trees including the native *Juniperus oxycedrus, J. excelsa, J. macropoda,* and *J. sabina;* but also on introduced *J. virginiana* (from the United States),

Figure 16.126–*Arceuthobium oxycedri,* staminate plant parasitizing *Juniperus;* note green color and frequent branching of the glaucous shoots.

J. thurifera (from the western Mediterranean region), *Cupressus macrocarpa* (3 varieties from California), *C. lusitanica* (2 varieties from Mexico), *C. arizonica* (3 varieties from Arizona), *C. macnabiana* (from California), *C. funebris* (from China), and *Platycladus orientalis* (2 varieties from China).

Distribution: Although described as "very local" in Europe (Tutin and others 1964), *Arceuthobium oxycedri* has the most extensive geographical distribution in the genus (fig. 16.122). Its range (table 16.9) extends over 100° of longitude or about 10,000 km from Spain and Morocco to the Himalayas of China (Hawksworth and Wiens 1976; Turrill 1920, 1926). The species probably occurs in Afghanistan, but we have no documentation. Tutin and others (1964) list its occurrence in Portugal as doubtful, and it is not listed in recent floras of that country.

Distribution maps for *Arceuthobium oxycedri* have been published by Hawksworth and Wiens (1976), for Spain (Bolos and Vigo 1990), for the Vaucluse Department in France (Girerd 1978), for Europe (Jalas and Souminen 1976), for the Mediterranean area (Markgraf 1934), for Himachal Pradesh, Jammu, and Kashmir States in India (Bakshi and Puri 1971), for the Upper Kanag Valley in Pakistan (Zakaullah and Badshah 1982), and for southwestern China (Kiu and Ren 1982). Elevational range is generally 1,000–2,500 m. It occurs as low as 550 m in northern Italy (Brilli-Cataerina and Gubellini 1983), as high as 2,700–3,100 m in Pakistan (Zakaullah and Badshah 1977), and up to 3,000–3,500 m in southwestern China (Kiu 1984b).

Discussion: Our field and laboratory studies (Hawksworth and Wiens (1976) have shown that *Arceuthobium oxycedri,* as originally interpreted, actually consists of three allopatric species: *A. oxycedri* (*sensu stricto*), *A. azoricum* from the Azores, and *A. juniperi-procerae* from Ethiopia and Kenya. All are parasitic on *Juniperus*. Some characteristics of these taxa are summarized in table 16.7 and discussed under the individual species.

Arceuthobium oxycedri is distinguished from the other species primarily by its deep green color, higher frequency of whorled branching, elongated internodes (especially in staminate plants), and more glaucous fruits. Zefirov (1955) described a new variety (var. *cupressi*) occurring on an introduced tree (*Cupressus macrocarpa*). This variety was distinguished from the typical form on *Juniperus* by its longer, thinner, greenish shoots. Giving formal taxonomic status to individuals or populations based on characters associated with plants occurring in unnatural habitats is unlikely to be accepted by most taxonomists. We place this variety into synonymy.

Arceuthobium oxycedri is reported to be damaging to juniper forests in many areas, but there are few quantitative reports of losses, except in Bluchistan, Pakistan, where this dwarf mistletoe caused 50% tree mortality in *Juniperus macropoda* (Jamal and Beg 1974).

Arceuthobium pini
Alpine Dwarf Mistletoe

40. *A. pini* Hawksworth & Wiens, Brittonia 22: 267, 1970. TYPE COLLECTION: CHINA: Yünnan Province, East flank of Lichiang Range, latitude 27°35' N, elevation 3,650 m, on *Pinus, Forrest 10169* in 1913 (Lectotype BM! Isotype K!).

Description: Plants 5–22 cm high, olive to dull green; with verticillate branching (fig. 16.127). Basal diameter of dominant shoots 1.5–3 mm. Third internode 5–14 (mean 12) mm long, 1.5–2.5 (mean 2) mm wide (5 collections); length/width ratio 6.2:1. Staminate flowers 2.0–2.5 mm across; perianth mostly 3-merous (rarely 4-merous); lobes 1.0–1.5 mm long, 1 mm wide, rounded. Pollen polar diameter 15–18 (mean 16) µm; equatorial diameter 16–18 (mean 18) µm; polar/equatorial diameter ratio 1:1.13; spine height 1.5 µm, wall thickness ca. 1.0 µm (3 collections). Mature fruit ca. 3.0–3.5 mm long, 2 mm wide, distal portion probably glaucous. $n = ?$

Phenology: Time of meiosis unknown. Anthesis usually April–June, but one specimen collected in July still had a few flowers with pollen. Fruit maturation time not precisely known, but apparently in August or

Figure 16.127 –Arceuthobium pini, staminate plant at anthesis. (C. Grey-Tulson)

TABLE 16.8—Hosts of *Arceuthobium oxycedri*

Host	Location	Reference
*Chamaecyparis thyoides**	Germany	Heinricher 1930
Cupressus arizonica†	Spain	Rios-Insua 1984a
Cupressus arizonica†	Ukraine	Isikov and Zakharenko 1988
Cupressus funebris†	Ukraine	Isikov and Zakharenko 1988
Cupressus lusitanica†	Ukraine	Isikov and Zakharenko 1988
Cupressus macrocarpa†	Ukraine	Zefirov 1955, Isikov and Zakharenko 1988
Juniperus communis	General	Turrill 1920
Juniperus drupacea	General	Turrill 1920
Juniperus excelsa	USSR	Komarov 1936
Juniperus foetidissima	USSR	Lazarev and Grigorov 1980
Juniperus formosana	USSR	Voronihin 1908
Juniperus icaina	USSR	Lazarev and Grigorov 1980
Juniperus macropoda	India	Brandis 1907
Juniperus macropoda	USSR	Komarov 1936
Juniperus oxycedrus	General	Turrill 1920
Juniperus oxycedrus	General	Turrill 1920
Juniperus phoenicia	France	Léveillé 1904
Juniperus pseudosabina	USSR	Lazarev and Grigorov 1980
Juniperus sabina	General	Turrill 1920
Juniperus semiglobosa	USSR	Komarov 1936
Juniperus thurifera†	Ukraine	Lazarev and Grigorov 1980
Juniperus tibetica	China	Kiu 1984b
Juniperus turcomanica	USSR	Komarov 1936
Juniperus virginiana†	Ukraine	Isikov and Zakharenko 1988
Juniperus wallichiana	China	Kiu 1984b
Platycladus orientalis†	Ukraine	Isikov and Zakharenko 1988
Platycladus orientalis‡	Germany	Beer 1951

*Greenhouse inoculation on North American tree.

†Natural infection on introduced tree.

‡Transmitted by graft from *Juniperus communis.*

TABLE 16.9—Distribution of *Arceuthobium oxycedri*

Country or region	Reference
EUROPE	
Albania	Turrill 1920
Bulgaria	Bondev and Lyubenova 1984
France (Corsica)	Turrill 1920, Pignatti 1982, Zangheri 1976
Greece	Polunin 1980, Turrill 1920
Italy	Brilli-Cattarini and Gubellini 1983
Hungary	Josifovic 1952
Russia	Kaupush and Tavasiev 1979
Spain	Smythies 1984
Ukraine	Isikov and Zakharenko 1988, Lazarev and Grigorov 1980
Croatia	Hayck 1924
Dalmatia	Hayck 1924
Bosnia	Hayck 1924
Macedonia	Hayck 1924, Perisic 1958
Montenegro	Mijuskovic 1972
Serbia	Josifovic 1973
AFRICA	
Algeria	Maire 1961, Quezel and Santa 1962
Morocco	Emberger and Maire 1941, Maire 1961
ASIA	
Afghanistan	?
Armenia	Turrill 1920
Azerbaijan	Fataliev 1987
Bhutan	First report
China (Xizang)	Cheng-Yih 1983, Kiu 1984b
Georgia	Komarov 1936
India (Kashmir)	Brandis 1907
Iraq	Rechinger 1976, Townsend 1980
Iran	Parsa 1949, Rechinger 1976
Kazakhstan	?
Kirghizstan	Komarov 1936
Lebanon	Mouterde 1966, Thiebaut 1953
Pakistan	Abdulla 1973, Rechinger 1976
Syria	Mouterde 1966
Tadzhikistan	Komarov 1936, Ovchinnikov 1968
Turkey	Czeczott 1939, Miller 1982
Turkmeniestan	Komarov 1936, Voronihin 1908
Uzbekistan	Botschantev 1953

September; maturation period presumably averages ca. 16 months.

Hosts: Known only from *Pinus densata* and *P. yunnanensis.*

Distribution: Southwest China (Yünnan, Sichuan, and Xizang). Distribution map given by Kiu and Ren (1982). Elevational range is 2,600–4,000 m (Kiu 1984b).

Discussion: This species was formerly included in *Arceuthobium chinense*; but it is easily distinguished by its much larger shoots (10–20 cm versus 3–5 cm) and its occurrence on *Pinus,* as opposed to *Keteleeria.* Kiu (1984b) suggests that the species does not induce witches' brooms, but the isotype at Kew clearly indicates systemic brooming (Hawksworth and Wiens 1972).

Arceuthobium sichuanense
Sichuan Dwarf Mistletoe

41. *A. sichuanense* (H. S. Kiu) Hawksworth & Wiens, Novon 3:156. 1993. TYPE COLLECTION: CHINA: Sichuan: Dawu, elevation 4,200 m; parasite of *Picea balfouriana* (as *P. likiangensis* var. *balfouriana*), *Wu & Gao 111629*; 23 May 1974 (Holotype CDBI). *A. pini* var. *sichuanense* Kiu, Acta Phytotaxonomica Sinica 22:205, 1984.

Description: Shoots 2–6 cm high, greenish yellow. Basal diameter of dominant shoots 1.0–1.5 mm. Flowers axillary or terminal on short lateral branches; staminate flowers 1.5–2.0 mm across; perianth 3-merous. Fruits 3–4 mm long, 1.5–2.0 mm wide. $n = ?$

Phenology: Anthesis June–July. Period of fruit maturation unknown.

Hosts: The known hosts are *Picea balfouriana* (= *P. likiangensis* var. *balfouriana*) (China and Bhutan) and *P. spinulosa* (Bhutan).

Distribution: Southwestern China (Sichuan and Xizang) and Bhutan. A distribution map of the species in Xizang is given by Kiu and Ren (1982). The species has been recently reported from Zong-lela in western Bhutan, where it is causing serious damage to *Picea balfouriana* and *P. spinulosa* (Naithan and Singh 1989). Elevational range is 2,800–4,200 m in southwestern China (Kiu 1984b) and 3,000–3,200 m in Bhutan (Naithan and Singh 1989; Rushforth, personal communication).

Discussion: This taxon was originally described as a variety of *Arceuthobium pini,* but we raised it to the specific level because it is a much smaller plant (2–6 cm versus 5–22 cm), has distinct host differences (*Picea* versus *Pinus*), and probable differences in witches' broom formation. The two species are allopatric. This dwarf mistletoe occurs at the highest elevation of any species in the genus (4,200 m). *Arceuthobium globosum* subsp. *grandicaule,* however, attains an elevation approaching this (4,100 m) in central Mexico. Kiu (1984) notes that *A. sichuanense* causes systemic witches' brooms.

Arceuthobium tibetense
Tibetan Dwarf Mistletoe

42. *A. tibetense* H. S. Kiu and W. Ren, Journal Yünnan Forestry College 1: 42, 1982. TYPE COLLECTION: CHINA: Xizang (Tibet): Mainling; elevation 3,400 m; parasite of *Abies forrestii* (= *A. georgei*); *Chao 14*, 21 May 1981 (Holotype, Herbarium of the Yünnan Forestry College, Kunming. Isotypes: SCBI, FPF!).

Description: Shoots 0.5–2.2 cm high, yellowish green, branching "opposite." Basal diameter of dominant shoots ca. 1.5 mm. Flowers terminal or axillary; staminate flower 2 mm across; perianth mainly 3-merous, rarely 4-merous, segments subtriangular, ca. 1.2 mm long. Fruit ca. 2 mm long, proximal portion glaucous. $n = ?$

Phenology: Anthesis May–June. Period of fruit maturation unknown.

Host: Known only on *Abies forrestii* (= *A. georgei*).

Distribution: Known only in the Mainling area in eastern Xizang (Tibet) at elevations of 3,200–3,400 m (Kiu and Ling 1988). A distribution map is given in Kiu and Ren (1982). The dwarf mistletoe reported on *Abies pindrow* in India may be this taxon (Rajagopaliengar 1955).

Discussion: This recently described species is characterized by its small size and exclusive occurrence on *Abies.* The species causes systemic witches' brooms (Kiu 1984). The fir forests in the Mainling area are severely damaged by this dwarf mistletoe, which occurs on about two-thirds of the trees (Kiu and Ren 1982).

Rejected Species

1. *Arceuthobium bonaniae* Grisebach, Cat. Plant. Cuben.: 121, 1866 = *Dendrophthora bonaniae* (Griseb.) Eichler, Flora Brasil. 5(2): 103, 1868.
2. *Arceuthobium cubense* Leiva & Bisse, Revue Jardin Botanic. Nac. Cuba 4: 60, 1983 = *Dendrophthora*

cupressoides (Macf.) Eichler, Flora Brasil. 5(2): 103, 1868. (Kuijt 1987) = *Dendrophthora podocarpicola* Leiva, Revue Jardin Botanic Nac. Cuba 7: 16, 1986.

3. *Arceuthobium cupressoides* (Macf.) Grisebach, Flora of British West Indies: 315, 1864 = *Razoumofskya cupressoides* (Macf.) Kuntze, Revision of Genera of Plants. 2: 587, 1891 = *Dendrophthora cupressoides* (Macf.) Eichler, Flora Brasil 5(2): 103, 1868.
4. *Arceuthobium dacrydii* Ridley, Journal of Fed. Malay States Museum 6: 170, 1915 = *Korthalsella dacrydii* (Ridley) Danser, Recueil des Travaux Botaniques Neerlandai 31: 759, 1934.
5. *Arceuthobium domingensis* (Spreng.) Grisebach, Cat. Plant. Cuben: 121, 1866 = *Dendrophthora domingensis* (Spreng.) Eichler, Flora Brasil. 5(2): 103, 1868.
6. *Arceuthobium epiviscum* Grisebach, Memoires American Academy of Arts and Sciences N.S., 8: 192, 1861 = *Dendrophthora epiviscum* (Griseb.) Eichler, Flora Brasil. 5(2): 103, 1868.
7. *Arceuthobium glauca* Grisebach, Cat. Plant. Cuben.: 121, 1866 = *Dendrophthora glauca* (Griseb.) Eichler, Flora Brasil. 5(2): 103, 1868.
8. *Arceuthobium gracile* (DC.) Grisebach, Flora British West Indies: 315, 1864 (non-Engelmann, Memoirs American Academy of Arts and Sciences, N.S., 4(4): 59, 1849). = *Razoumofskya gracilis* (DC.) Kuntze, Revision of Genera of Plants 2: 587, 1891 = *Dendrophthora flagelliformis* (Lam.) Krug & Urban, Berichte der Deutschen Botanischen Gesellschaft 14: 287, 1896.
9. *Arceuthobium mancinellae* Grisebach, Cat. Plant. Cuben.: 121, 1866 = *Dendrophthora mancinellae* (Griseb.) Eichler, Flora Brasil 5(2): 103, 1868.
10. *Arceuthobium opuntioides* (L.) Grisebach, Flora British West Indies: 315, 1864. = *Razoumofskya jamaicensis* Hoffman, Hortus Mosquensis (unpaged), 1808. = *Razoumofskya opuntioides* (L.) Kuntze, Revision of Genera of Plants 2: 587, 1891 = *Dendrophthora opuntioides* (L.) Eichler, Flora Brasil 5(2): 102, 1868.

Summary

Major Conclusions

1. *Arceuthobium* is a well-defined, but morphologically reduced, genus of the Viscaceae, parasitic on Cupressaceae and Pinaceae. The genus is probably of early Tertiary Period origin in Asia. Its closest relative is *Notothixos,* which has a tropical Asian and Australasian distribution.
2. *Arceuthobium* presumably migrated to the New World in the pre-Miocene times. An intensive adaptive radiation occurred into the Pinaceae of the New World, and western North America is now the center of species diversity. Forty-six taxa are recognized in this study, 38 of which are in the New World and 8 in the Old World.
3. Most of the Pinaceae of western North America and Mexico have been colonized by *Arceuthobium.* In the western United States, the hosts include at least some species of *Abies, Picea, Tsuga,* and *Larix,* about 95% of the species of *Pinus,* and one of the two species of the *Pseudotsuga.* The few conifers that are not known to be parasitized are primarily localized endemics.
4. *Arceuthobium* has a base chromosome number of $n = 14$. No natural hybridization or polyploidy is known in the genus. The absence of hybridization and polyploidy has apparently resulted in relatively clear, dendritic lines of evolution and well-defined species.
5. Most species are sympatric with other members of the genus somewhere over their geographic distribution and the flowering periods of co-occurring species often overlap. The species appear to be isolated reproductively.
6. The characteristics that delimit species, however, are often cryptic and may be apparent for only short periods of the life cycle. Species and subspecies differ only in the number of discontinuous variables, and with the exception of *Arceuthobium vaginatum* subspecies *vaginatum* and *cryptopodum* in one area in Chihuahua, even subspecies do not intergrade.

Suggestions for Further Research

1. The early studies of amino acid components of dwarf mistletoes and their hosts should be continued using contemporary molecular methods.
2. Ultrastructural studies of the host–parasite interface should be expanded to gain a better understanding of these interactions.
3. Efforts to effect *in vitro* culture of dwarf mistletoes should be continued.
4. The role of birds in long-distance dispersal is poorly understood and requires additional study, especially in *Arceuthobium occidentale* and *A. verticilliflorum.*
5. Experimental studies to determine the cause of competitive host exclusion discussed in chapter 6 should be a fascinating area for future study.
6. The effective distance and mode of pollen transport should be investigated experimentally; pollen dispersal in *Arceuthobium rubrum* should especially be examined.
7. Chromosome numbers should be determined for the species not yet studied: *Arceuthobium durangense, A. globosum* subsp. *globosum, A. guatemalense, A. rubrum, A. oaxacanum, A. pendens, A. siskiyouense, A. tsugense* (shore pine race), *A. vaginatum* subsp. *vaginatum,* and *A. yecorense* and all the Old World species (except *A. oxycedri* and *A. juniperi-procerae*). Detailed analysis of the karyotypes of related species groups, however, would be especially valuable.
8. The possibility that sex chromosomes might occur in *Arceuthobium douglasii* and *A. gillii* should be studied.
9. A thorough analysis of sexual dimorphism and sex ratio should be undertaken.
10. Crossing experiments should be carried out between closely related species, e.g., *Arceuthobium apachecum–A. blumeri* and *A. campylopodum–A. occidentale.*

11. Any aspects of the biology of the Asian species should be investigated.
12. The study of molecular systematics should be continued. This offers a powerful methodology to elucidate species relationships that are often unclear in highly reduced groups (chapter 15).
13. The relationships and taxonomic status of several Mexican and Central American taxa require clarification: (1) the small plants of *Arceuthobium globosum* subsp. *globosum* around El Salto, Durango, in comparison with the other populations of this subspecies in the Sierra Madre Occidental, (2) the "stocky" populations of *A. rubrum* in the vicinity of Altares, in northern Durango, (3) the occurrence of *A. aureum* subsp. *petersonii* in southern Oaxaca, (4) the identity of the dwarf mistletoe in El Salvador.
14. The northern limits of distribution for *Arceuthobium pusillum* in Ontario and Québec need to be established.
15. The unusual broom formation in species such as *Arceuthobium bicarinatum* should be studied.
16. The factors affecting the co-distribution of *Arceuthobium divaricatum* and *Phoradendron juniperinum* require investigation.
17. The ecological effects of dwarf mistletoe infestation on stand structure, fire behavior, and wildlife habitat should be studied.
18. The selection, testing, and development of genetic resistance should be expanded, both from the basic understanding of resistance to these parasites and as a practical ecological approach to control.
19. The number of flower crops produced by *Arceuthobium hawksworthii, A. abietis-religiosa,* and *A. juniperi-procerae* should be investigated, as well as the factors that limit the distribution of *A. hawksworthii* to the middle and upper altitudinal ranges of *Pinus caribaea* var. *hondurensis* in Belize.
20. Effort to develop chemical controls that will kill the endophytic system should continue.
21. The role of synergids in fertilization and early embryo development need to be examined.
22. The effects of heat, smoke, and light on reproduction by dwarf mistletoe should be further studied.

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Scientific and Common Names

Birds[1]

American robin	*Turdus migratorius* L.
Antillean euphonia	*Euphonia musica* (Gmelin)
Band-tailed pigeon	*Columba fasciata* Say
Black-capped chickadee	*Parus atricapillus* L.
Black-headed grosbeak	*Pheucticus melanocephalus* (Swainson)
Blue grouse	*Dendragapus obscurus* (Say)
Brown creeper	*Certhia americana* Bonaparte
Cassin's finch	*Carpodacus cassinii* Baird
Chipping sparrow	*Spizella passerina* (Bechstein)
Cooper's hawk	*Accipiter cooperi* (Bonoparte)
Dark-eyed junco	*Junco hyemalis* (L.)
Evening grosbeak	*Coccothraustes vespertinus* (Cooper)
Gray jay	*Perisoreus canadensis* (L.)
Gray silky-flycatcher	*Ptilogonys cinereus* Swainson
Great gray owl	*Strix nebulosa* Forster
Great horned owl	*Bubo virginianus* (Gmelin)
Hermit thrush	*Catharus guttatus* (Pallus)
House sparrow	*Passer domesticus* L.
House wren	*Troglodytes aedon* Vieilot
Long-eared owl	*Asio otis* (L.)
Mistle thrush	*Turdus viscivorus* L.
Mourning dove	*Zenaida macroura* (L.)
Mountain bluebird	*Sialia curruciodes* (Bechstein)
Mountain chickadee	*Parus gambeli* Ridgeway
Northern goshawk	*Accipiter gentilis* (L.)
Phainopepla	*Phainopepla nitens* (Swainson)
Pine siskin	*Carduelis pinus* (Wilson)
Pygmy nuthatch	*Sitta pugmaea* Vigors
Raven	*Corvus* spp.
Red-breasted nuthatch	*Sitta canadensis* L.
Red crossbill	*Loxia curvirostra* L.
Ruffed grouse	*Bonasa umbellus* (L.)
Sharp-shinned hawk	*Accipiter striatus* Viellot
Song thrush	*Turdus philomelos* Brehm
Northern spotted owl	*Strix occidentalis caurina*
Mexican spotted owl	*Strix occidentalis lucida*
Spruce grouse	*Dendragapus canadensis* (L.)
Steller's jay	*Cyanocitta stelleri* (Gmelin)
Swainson's thrush	*Catharus ustulatus* (Nuttall)
Turkey	*Meleagris gallopavo* L.
Western bluebird	*Sialia mexicana* Swainson
Western tanager	*Piranga ludoviciana* (Wilson)

Mammals[2]

Abert squirrel	*Sciurus aberti* Woodhouse
American marten	*Martes americana* (Turton)
Bushy-tailed woodrat	*Neotoma cinerea* (Ord)
Chipmunk	*Eutamius* spp.
Deer mouse	*Peromyscus maniculatus* (Wagner)
Elk	*Cervus canadensis* Erxleben
Golden-mantled ground squirrel	*Spermophilus lateralis* Cuvier
Flying squirrel	*Glaucomys sabrinus* (Shaw)
Franklin ground squirrel	*Spermophilus franklinii* (Sabine)
Least chipmunk	*Eutamius minimus* (Say)
Mule deer	*Odecoileus hemionus* (Rafinesque)
Packrat	*Neotoma* spp.
Porcupine	*Erethizon dorsatum* (L.)
Red-backed vole	*Clethrionomys gapperi* (Vigors)
Red squirrel	*Tamiasciurus hudsonicus* (Erxleben)

Insects and Mites[3]

Atta mexicana	harvester ant
Brevipalpus porca Pritchard & Baker	mite*
Choristoneura occidentalis Freeman	western spruce budworm†
Clastoptera distincta Doering	spittlebug‡
Coloradia pandora Blake	pandora moth†
Copidosoma bakeri (Howard)	wasp§
Dasypyga alternsquamella Heinrich	pyralid moth*
Dendroctonus adjunctus Blandford	roundheaded pine beetle†
Dendroctonus brevicomis LeConte	western pine beetle†
Dendroctonus mexicanus Hopkins	bark beetle¶
Dendroctonus ponderosae Hopkins	mountain pine beetle†
Dendroctonus pseudotsugae Hopkins	Douglas-fir beetle†
Dendroctonus rufipennis (Kirby)	spruce beetle†
Dendroctonus valens LeConte	red turpentine beetle†
Filatima natalis (Heinrich) *(= Gelechia natalis)*	gelechiid moth*
Formica fusca L.	silky ant#
Formica hemmorhoidalis Emery	ant
Frankliniella hawksworthii O'Neill	dwarf mistletoe thrips†
Ips confusus (LeConte)	pinon ips†
Ips lecontei Swain	Arizona fivespined ips†
Lambdina fiscellaria (Guenee)	hemlock looper†

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[1] Nomenclature follows the recommendations of the American Ornitholigists' Union (1983).

[2] Nomenclature follows the recommendations of Honacki and others (1982).

[3] Nomenclature follows the recommendations of these authors: *Stevens and Hawksworth (1970), †Furniss and Caroline (1977), ‡ Stevens and Hawksworth (1984), § Penfield and others (1976), ¶ Schowalter and Filip (1993), # Arnett (1985), || Gilbert and Punter (1984),** Wood (1971).

Melanophila californica Van Dyke	California flatheaded borer†
Melanophila drummondi (Kirby)	flatheaded fir borer†
Melanoplus devastator Scudder	devastating grasshopper†
Mitoura johnsonii (Skinner)	hairstreak butterfly#
Mitoura spinetorum (Hewitson)	thicket hairstreak butterfly#
(= *Callohrys spinetorum)*	
Neoborella tumida Knight	plant bug*
Paraphytopus arceuthobii Keifer	mite*
Philygria debilis L.	gnat||
Phyllotreta lewisii Crotch	flea beetle#
Pityophthorus arceuthobii S.L. Wood	twig beetle**
Platylygus mexicanus Kelton	plant bug‡
Typhlodromus arceuthobium Kennett	mite*
Typhlodromus pusillus Kennett	mite*

Trees[4]

Abies amabilis Douglas ex J. Forbes	Pacific silver fir*
Abies balsamea (L.) Miller	balsam fir*
Abies bracteata (D. Don) Poiteau	bristlecone fir*
Abies concolor (Gordon & Glendinning) Hildebrand	white fir*
var. *concolor*	Rocky Mountain white fir*
var. *lowiana* (Gordon) Lemmon	Sierra white fir*
Abies durangensis Martínez	Durango fir†
Abies forrestii C.C. Rogers	Forrest fir†
(= *Abies georgei)*	
Abies grandis (Douglas ex D. Don) Lindley	grand fir*
Abies guatemalensis Rehder	Guatemala fir†
Abies hickelii Flous & Gaussen	Hickel fir†
Abies lasiocarpa (Hooker) Nuttall	subalpine fir*
var. *lasiocarpa*	subalpine fir*
var. *arizonica* (Merriam) Lemmon	corkbark fir*
Abies magnifica A. Murray	red fir*
Abies mexicana Martínez	Mexican fir†
Abies oaxacana Martínez	Oaxacan fir†
Abies pindrow Royale	Pindrow fir†
Abies procera Rehder	noble fir*
Abies religiosa (H.B.K.) Schlechtendal & Chamisso	sacred fir†
var. *religiosa*	sacred fir†
var. *emarginata* Loock & Martínez	‡
Abies vejari Martínez	Vejar fir†
Cedrus deodora (Roxburgh) G. Don	Deodar cedar†
Chamaecyparis thyoides Britton, Sterns & Poggenburg	Atlantic white-cedar*
Cupressus arizonica Greene	Arizona cypress*
Cupressus funebris Endlicher	Chinese weeping cypress†
Cupressus lusitanica Miller	Mexican cypress†
Cupressus macnabiana A. Murray	Macnab cypress*
Cupressus macrocarpa Hartweg	Monterey cypress*
Debregeasia hypoleuca	
Juglans hindsii Jepson ex Smith	northern California walnut§
(= *Juglans californica* var. *hindsii)*	
Juniperus brevifolia (Seub.) Antoine	Azores juniper†
Juniperus communis L.	common juniper†
Juniperus drupacea Labillard	Syrian juniper†
Juniperus excelsa Bieb.	Grecian juniper†
Juniperus foetidissima Willdenow	stinking juniper†
Juniperus formosana Hayata	Formosan juniper§
(= *Juniperus oblonga* Knight & Perry)	
Juniperus icaina	juniper
Juniperus macropoda Boissier	Persian juniper†
(= *Juniperus serawschanica* Komarov)	
Juniperus oxycedrus L.	prickly juniper†
(= *Juniperus rufescens* Link)	
Juniperus phoenicia L.	Phoenician juniper†
Juniperus procera Hochstetter ex Endlicher	East African juniper†
Juniperus pseudosabina Fisher & Meyer	Xinjiang juniper†
(= *Juniperus turkestanica)*	
Juniperus sabina L.	savin†
Juniperus semiglobosa Regel	Russian juniper†
Juniperus thurifera L.	Spanish juniper†
Juniperus tibetica Komarov	Tibetan juniper†
Juniperus turcomanica B. Fedtsch	
Juniperus virginiana L.	eastern red-cedar*
Juniperus wallichiana Hooker f. & Thomas ex Parlatore	Wallich juniper†
Keteleeria evelyniana Masters	Evelyn keteleeria†
Larix decidua Miller	European larch†
(= *Larix europaea DC.)*	
Larix kaempferi (Lambert) Carrière	Japanese larch†
(= *Larix leptolepis* (Sieb. & Zuccarini) Gordon	
Larix laricina (Du Roi) K. Koch	tamarack*
Larix lyallii Parlatore	subalpine larch*
Larix occidentalis Nuttall	western larch*
Picea abies (L.) H. Karsten	Norway spruce*
Picea balfouriana Rehder & Wilson	Balfour spruce†
(= *Picea likiangensis* var. *balfouriana* (Franchet) Pritzel)	
Picea breweriana S. Watson	Brewer spruce*
Picea chihuahuana Martínez	Chihuahua spruce†
Picea engelmannii Parry ex Engelmann	Engelmann spruce*
Picea glauca (Moench) Voss	white spruce*
Picea mariana (Miller) Britton, Sterns & Poggenburg	black spruce*
Picea martinezii Patterson	Martínez spruce
Picea mexicana Martínez	Mexican spruce†
Picea pungens Engelmann	blue spruce*
Picea rubens Sargent	red spruce*
Picea sitchensis (Bongard) Carrière	Sitka spruce*
Picea spinulosa (Griffiths) Henry	Sikkim spruce†
Pinus albicaulis Engelmann	whitebark pine*
Pinus aristata Engelmann	Colorado bristlecone pine*
Pinus arizonica Engelmann	Arizona pine¶
var. *arizonica*	Arizona pine¶
var. *stormiae* Martínez	royal pine¶
Pinus attenuata Lemmon	knobcone pine*
Pinus ayacahuite Ehrenberg	Mexican white pine¶
var. *ayacahuite*	Mexican white pine¶
var. *brachyptera* Shaw	Mexican white pine¶

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[4] Nomenclature follows the recommendations of these authors: * Flora of North America Committee (1993), † Rushforth (1987), ‡ Liu (1971), ¶ Mirko (1991), § Perry (1991).

Pinus balfouriana Greville & Balfour	foxtail pine*
subsp. *balfouriana*	northern foxtail pine*
subsp. *austrina* R. Mastroguiseppe & J. Mastroguiseppe	southern foxtail pine*
Pinus banksiana Lambert	jack pine*
Pinus bungeana Zuccarini ex Endlicher	lacebark pine†
Pinus californiarum D.K. Bailey	California singleleaf pinyon
subsp. *californiarum*	California singleleaf pinyon
subsp. *fallax* (Little) D.K. Bailey	Arizona singleleaf pinyon
Pinus caribaea Morelet	Caribbean pine§
var. *hondurensis* (Sénécluse) Barr. & Golf.	Honduras Caribbean pine¶
Pinus cembroides Zuccarini	Mexican pinyon*
Pinus chiapensis (Martínez) Andresen	Chiapas white pine¶
Pinus contorta Douglas ex Loudon	lodgepole pine*
var. *contorta*	shore pine*
var. *bolanderi* (Lemmon) Critchfield	Bolander pine*
var. *murrayana* (Greville & Balfour) Engelmann	Sierra lodgepole pine*
var. *latifolia* Engelmann	Rocky Mountain lodgepole pine*
Pinus cooperi Blanco	Cooper pine¶
Pinus coulteri D. Don	Coulter pine*
Pinus culminicola Andresen & Beaman	Potosí pinyon
Pinus densata Masters	Gaoshan pine†
Pinus discolor D.K. Bailey & Hawksworth	border pinyon¶
Pinus douglasiana Martínez	Douglas pine¶
Pinus durangensis Martínez	Durango pine¶
Pinus edulis Engelmann	pinyon*
Pinus engelmannii Carrière	Apache pine¶
Pinus flexilis E. James	limber pine*
Pinus gerardiana Wallich ex D. Don	Chilgoza pine†
Pinus greggii Engelmann	Gregg pine¶
Pinus halepensis Miller	Aleppo pine†
Pinus hartwegii Lindley	Hartweg pine¶
Pinus herrerai Martínez	Herrera pine¶
Pinus jaliscana Perez de la Rosa	Jalisco pine¶
Pinus jeffreyi Greville & Balfour	Jeffrey pine*
Pinus johannis M.-F. Robert-Passini	Johannis pine¶
Pinus lagunae M.-F. Robert-Passini	Laguna pine¶
Pinus lambertiana Douglas	sugar pine*
Pinus lawsonii Roezl	Lawson pine¶
Pinus leiophylla Schiede & Deppe	smooth-leaf pine*
var. *leiophylla*	smooth-leaf pine*
var. *chihuahuana* (Engelmann) G.R. Shaw	Chihuahua pine*
Pinus longaeva D.K. Bailey	Intermountain bristlecone pine*
Pinus lumholtzii Robinson & Fern.	Lumholtz pine¶
Pinus maximartinezii Rzedowski	Martínez pinyon¶
Pinus maximinoi H.E. Moore	thinleaf pine¶
(=*Pinus tenuifolia* Bentham)	
Pinus michoacana Martínez	Michoácan pine¶
Pinus monophylla Torrey & Fremont	singleleaf pinyon*
Pinus montezumae Lambert	Montezuma pine¶
Pinus monticola Douglas ex D. Don	western white pine*
Pinus mugo Turra	dwarf mountain pine†
(=*Pinus montana* Miller)	
Pinus muricata D. Don	Bishop pine*
Pinus nelsonii Shaw	Nelson pinyon¶
Pinus oaxacana Mirov	Oaxacan pine¶
Pinus occidentalis Swartz	West Indian pine†
Pinus oocarpa Schiede	eggcone pine¶
Pinus orizabensis (D.K. Bailey) D.K. Bailey & Hawksworth	Orizaba pinyon
Pinus palustris Miller	longleaf pine*
Pinus patula Schlechtendal & Chamisso	Mexican weeping pine¶
Pinus pinaster Aiton	maritime pine†
Pinus pinceana Gordon	Pince pinyon†
Pinus pinea L.	stone pine†
Pinus ponderosa Douglas ex Lawson & C. Lawson	ponderosa pine*
var. *ponderosa*	ponderosa pine*
var. *scopulorum* Engelmann	Rocky Mountain ponderosa pine*
Pinus praetermissa Styles & McVaugh	
Pinus pringlei Shaw	Pringle pine¶
Pinus pseudostrobus Lindley	smooth-bark Mexican pine¶
Pinus quadrifolia Parlatore ex Sudworth	Parry pinyon*
Pinus radiata D. Don	Monterey pine*
Pinus remota (Little) D.K. Bailey & Hawksworth	papershell pinyon*
Pinus resinosa Aiton	red pine*
Pinus rigida Miller	pitch pine*
Pinus rudis Endlicher	Endlicher pine¶
Pinus rzedowskii Madrigal & Caballero	Rzedowski pine¶
Pinus sabiniana Douglas ex D. Don	digger pine*
Pinus strobiformis Engelmann	southwestern white pine*
var. *strobiformis*	southwestern white pine*
var. *potosiensis*	
Pinus strobus L.	eastern white pine*
Pinus sylvestris L.	Scotch pine*
Pinus tabuliformis Carrière	Chinese red pine†
Pinus teocote Schlechtendal & Chamisso	Teocote pine¶
Pinus thunbergii Parlatore	Japanese black pine†
Pinus torreyana Parry ex Carrière	Torrey pine*
Pinus virginiana Miller	Virginia pine*
Pinus yunnanensis Franchet	Yünnan pine‡
Pinus washoensis H. Mason & Stockwell	Washoe pine*
Pinus wallichiana Jackson	Himalayan blue pine†
(=*Pinus griffithii* McClelland)	
Platycladus orientalis (L. f.) Franco	biota (Oriental arborvitae)†
(=*Thuja orientalis* L.)	
Pseudotsuga macrocarpa (Vasey) Mayr	bigcone Douglas-fir*
Pseudotsuga menziesii (Mirbel) Franco	Douglas-fir*
var. *menziesii*	coast Douglas-fir*
var. *glauca* (Mayr) Franco	Rocky Mountain Douglas-fir*
Tsuga canadensis (L.) Carrière	eastern hemlock*
Tsuga heterophylla (Rafinesque) Sargent	western hemlock*
Tsuga mertensiana (Bongard) Carrière	mountain hemlock*

Fungi[5]

Alternaria alternata (Fr.) Keissler	Alternaria*
(=*Alternaria tenuis* Nees)	
Aureobasidium pullans (deBary) G. Arnaud	Aureobasidium†
Caliciopsis arceuthobii (Peck) Barr	Caliciopsis*
(=*Sphaeria arceuthobii* Peck)	
(=*Wallrothiella arceuthobii* (Peck) Sacc.)	
Colletotrichum gloeosporioides Penz.	Collectotricum*
Cryptosporium pinicola Linder	Cryptosporium‡
Cylindrocarpon gillii (D.E. Ellis) J.A. Muir	Cylindrocarpon†
(= *Septogloem gillii* D.E. Ellis)	
(= *Fusarium campylopodii* Weir)	
Cytospora abietis Fr.	Cytospora canker of true firs§
Endocronartium harknessii (J.P. Moore) Y. Hirat.	western gall rust§
Endothiella agregata Funk	Endothiella¶
Fomitopsis officinalis (Vill.:Fr.) Bond. & Sing.	brown trunk rot#
Fomitopsis pinicola (Swartz:Fr.) Karst	brown crumbly rot#
Herpotrichia juniperi (Duby) Petrak	brown felt fungus§
Laetiporus sulphureus (Bull.:Fr.) Murr.	brown cubical rot#
Metasphaeria wheeleri Linder	Metaspheria*
Nectria fuckeliana C. Booth	Nectria†
Nectria macrospora (Wr.) Ouellette	Nectria†
(Anamorph: *Cylindrocarpon cylindroides* Wr.)	
Peridermium bethelii Hedgc. & Long	mistletoe blister rust§
Pestalotia heterocornis Guba	Pestalotia*
Pestalotia maculiformans Guba & Zeller	Pestalotia*
Phellinus pini (Thore.:Fr.) A. Ames	red ring rot#
Sphaeropsis sapinea (Fr.) Dyko & Sutton	Diplodia blight§
(= *Diplodia pinea*)	

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[5] Nomenclature follows the recommendations of these authors: *Hawksworth and others (1977),† Farr and others (1989), ‡ Filip and others (1979), § Hawksworth and others, ¶ Funk (1984), # Gilbertson and Ryvarden (1987).

Collecting and Curating Techniques

Pressed specimens of *Arceuthobium* are easily broken or fragmented. The plants invariably fragment if a large host branch is pressed with an attached dwarf mistletoe. Relatively little fragmentation occurs, however, if individual shoots are pressed rather than the entire plant. The basal shoot internodes are sometimes taxonomically important, and thus dwarf mistletoe shoots should be cut from the host branch so that a small portion of the bark remains attached to each shoot. For smaller species such as *A. douglasii* or *A. pusillum*, the entire infected host branch can be pressed if it measures less than about 0.5 cm in diameter. Collection of both staminate and pistillate dwarf mistletoe plants is desirable. Also, it is critical to include sufficient host foliage to facilitate its identification.

The collection data on herbarium specimens are usually meager. Information that should be recorded when collecting dwarf mistletoes includes location, date, host (not only that of the specific collection but other associated infected trees as well), ecological data about the site, and shoot characters such as habit, size, sexual dimorphism, and original color. Also, the presence or absence of witches' brooms should be recorded. If more than one host species is involved, their relative susceptibility should be noted.

Mounted herbarium specimens were better preserved when we used a heavy grade herbarium paper and a heavy coat of adhesive applied to the back of each specimen before the plants became totally dry. Another satisfactory method is to use a cotton-backed envelope or Riker Mount. A modification of the latter is to place the dried specimen directly on Tomac, and file it in a large envelope with a transparent window so it can be observed with little handling.

Herbaria Consulted

The specimens we examined are tabulated with the following information: the host, location, collector, year of collection, and herbarium where the collection is housed. The herbarium in which specimens were examined or cited and their standard abbreviations are listed below. An asterisk indicates an abbreviation not in the 8th edition of Index Herbariorum (Holmgren and others 1990).

ARIZ	University of Arizona, Tucson
ASU	Arizona State University, Tempe
B	Botanisches Museum Dahlem, Berlin
BLH	Cranbrook Institute of Science, Bloomfield Hills, MI
BM	British Museum, London, England
CAS	California Academy of Sciences, San Francisco
CHAPA	Colegio de Postgraduados, Chapingo, Mexico
CIIDIR	Centro Interdisciplinario de Investigacion para el Desarrollo Integral de la Comunidad Rural, V. Guerrero, Durango, Mexico
COLO	University of Colorado, Boulder
CFB	Canadian Department of Forestry, Edmonton, AB
CS	Colorado State University, Fort Collins
DAVFP	Canadian Department of Forestry, Victoria, BC
DS	Dudley Herbarium, Stanford University (now at CAS)
E	Royal Botanic Garden, Edinburgh, Scotland
EA	National Museums of Kenya, Nairobi
EAP	Escuela Agricola Panamericana, Tegucigalpa, Honduras
ENCB	Escuela Nacional de Ciencias Biologicas, Mexico, DF
F	Field Museum of Natural History, Chicago, IL
FLAS	University of Florida, Gainesville
FPF	USDA Forest Service, Forest Pathology Herbarium, Fort Collins, CO
FPT*	Canadian Department of Forestry, Forest Pathology, Toronto, ON
FT	Erbario Tropicale di Firenze, Firenze, Italy
GH	Gray Herbarium, Harvard University, Cambridge, MA
IBUG	Institute of Botany, University of Guadalajara, Mexico
ID	University of Idaho, Moscow
IEB	Institute of Ecology, Patzcuaro, Michoacán, Mexico
ILL	University of Illinois, Urbana
INIF	Instituto Nacional de Investigaciones Forestales, Mexico, DF
JBSD	Jardin Botanical Nacional, Santo Domingo, Dominican Republic
JEPS	Jepson Herbarium, University of California, Berkeley
K	Royal Botanic Gardens, Kew, England
KUN	Botanical Institute, Academia Sinica, Kunming, China
MAINE	University of Maine, Orono
MEXU	Institute de Biologia, UNAM, Mexico, DF
MICH	University of Michigan, Ann Arbor
MIN	University of Minnesota, Minneapolis
MNA	Museum of Northern Arizona, Flagstaff
MO	Missouri Botanical Garden, St. Louis
MONT	Montana State University, Bozeman
MONTU	University of Montana, Missoula
MSC	Michigan State University, East Lansing
NMC	New Mexico State University, Las Cruces
NO	Tulane University, New Orleans, LA
NY	New York Botanical Garden, New York
OSC	Oregon State University, Corvallis
P	Museum National d'Histoire Naturalle, Paris, France
PE	Institute of Botany, Academia Sinica, Peking, China
PFRS	USDA Forest Service, Forest Pathology Herbarium, Berkeley, CA
PH	Academy of Natural Sciences, Philadelphia, PA
RAW	Pakistan Agricultural Research Council, Islamabad
RM	Rocky Mountain Herbarium, University of Wyoming, Laramie
RSA	Rancho Santa Ana, Claremont, CA

S	Swedish Museum of Natural History, Stockholm
SCBI*	South China Institute of Botany, Kwangchow, China
SD	Natural History Museum, Balboa Park, San Diego, CA
SRSC	Sul Ross State College, Alpine, TX
TEX	University of Texas, Austin
UC	University of California, Berkeley
UNM	University of New Mexico, Albuquerque
US	U.S. National Museum, Washington, DC
USFS	USDA Forest Service Herbarium (now incorporated into RM)
UT	University of Utah, Salt Lake City
UTC	Utah State University, Logan
VT	University of Vermont, Burlington
WINF	Canadian Department of Forestry, Winnipeg, MB (now at CFB)
WIS	University of Wisconsin, Madison
WS	Washington State University, Pullman
WSP	Washington State University, Mycological Herbarium, Pullman
WTU	University of Washington, Seattle
Z	Universität Zurich, Switzerland

Two collector abbreviations are used in the lists of specimens cited: *Hawksworth* = *H*, and *Wiens* = *W*. The following abbreviations are used in the collection citations (page 321).

canyon = cyn.
creek = cr.
collector unknown = col.?
County = Co.
east = E
Experimental = exp.
Forest = For.
junction = jct.
kilometer = km.
miles = mi.
Monument = Mon.
Mount = mt.
Mountain = mtn.
Mountains = mts.
National = Nat.
north = N
not dated = n.d.
range = R.
Reservation = Res.
Route = Rte.
road = rd.
Section = Sec.
Station = Sta.
south = S
township = T.
west = W

Specimens Examined

New World Taxa

1a. *Arceuthobium abietinum* f. sp. *concoloris*

All collections on *Abies concolor* except as noted.

MEXICO

CHIHUAHUA

Mpio. Temosachic, 18 km. N of Yahuirachi or 61 km. N of Tomochic, on *Abies durangensis, H 2185* in 1987 (FPF) and on *Pinus ayacahuite, H 2186* in 1987 (FPF); Mpio. Guadalupe y Calvo, Cerro Mohinora, on *Abies durangensis, Olivo & Velazco* in 1990 (FPF).

UNITED STATES

ARIZONA

COCHISE CO.: Chiricahua Mts., Mormon Cyn., Mormon Springs, *Mathiasen 7602* in 1976 (FPF) and *H & Mathiasen 1756* in 1976 (FPF). COCONINO CO.: Kaibab Plateau, *Richards* in 1938 (UC) and on *Abies lasiocarpa* var. *lasiocarpa, Richards* in 1938 (WTU); Grand Cyn. Nat. Park, North Rim: Cape Royal rd., *Gill FP 68297* in 1934 (FPF) and Cape Royal, *Gill & Ellis FP 89417* in 1939 (FPF); Fairview Point, *Peterson 37-61* in 1961 (FPF) and *H 252* in 1962 (FPF) and on *Abies lasiocarpa* var. *lasiocarpa, Peterson 39-61* in 1961 (FPF); Bright Angel Point, *H 254* in 1962 (FPF); Inspiration Point, *W 3180* in 1962 (COLO). Grand Cyn. Nat. Park, South Rim: 1 mi. E of Grandview Point, *H & Lightle 184* in 1962 (FPF) and *H & Scharpf 702* in 1964 (FPF). PIMA CO.: Santa Catalina Mts., Marshall Gulch, *Mathiasen 7901* in 1979 (FPF).

CALIFORNIA

ALPINE CO.: 8 mi. SW of Silver Cr. on Rte. 4, *H & Scharpf 667* in 1964 (FPF); 8 mi. SE of Markleeville, *H 1309* in 1970 (FPF). BUTTE CO.: Jonesville, *Copeland 414* in 1930 (ARIZ, CAS, MO, RM, RSA, UC, US, Z) and *Copeland* in 1929 (UC). CALAVERAS CO.: 12 mi. SW of Tamarack on Rte. 4, *H & Scharpf 662* in 1964 (FPF). COLUSA CO.: Trout Cr., SE side of Snow Mtn., *Heckard & Hickman 5733* in 1981 (UC). DEL NORTE CO.: 0.25 mi. S of Oregon boundary on O'Brien–Happy Camp rd., *H & Hinds 999* in 1966 (FPF) and on *Abies grandis, H & Hinds 998* in 1966 (FPF). ELDORADO CO.: US 50 near Camino, *Kuijt 1272* in 1957 (UC); Tahoma, *Kuijt 1340* in 1957 (UC) and on *Pinus contorta* (rare), *Kuijt 1341* in 1957 (UC); 6 mi. S of US 50 on Rte. 89, *H 2439* in 1991 (FPF). FRESNO CO.: 2 mi. S of summit on Shaver Lake-Dinkey Cr. rd., *Quick 53-27* in 1953 (CAS); Huntington Lake, *Wall* in 1919 (CAS); Bubbs Cr. and Charlotte Cr., *Howell 15674* in 1940 (CAS); Kings Cyn. Nat. Park, Roaring River Guard Sta., *Knutson* in 1981 (FPF); Huntington Lake, *H 2032* in 1982 (FPF). GLENN CO.: Bear Wallow rd. near Alder Springs, *Boyce 1906* in 1930 (FPF); Plaskett Ranger Sta., *Boyce 1905* in 1930 (FPF). HUMBOLDT Co.: Lasseck's Peak, *Kildare 2634* in 1926 (DS, UC); Humboldt Mill, vicinity of Eureka, on *Abies grandis, Tracy 1060* in 1901 (UC). LASSEN CO.: Crater Mtn., 15 mi. W of Eagle Lake, *Meinecke* in 1914 (FPF) and *Whitney 1703* in 1934 (UC). MADERA CO.: 1 mi. E of Fish Camp, *H 30* in 1954 (FPF) and *H* in 1963 (FPF); Bass Lake, *Gill & Wright FP 68161* in 1932 (FPF); Mile High Point, 27 mi. from North Fork on Mammoth Pool rd., *H 937* in 1966 (FPF); Ellis (now Benedict) Meadows, *Zieman* in 1917 (FPF). MARIPOSA CO.: Yosemite, *Hedgcock & Meinecke FP 4823* in 1910 (FPF); Fish Camp, *Hedgcock & Meinecke FP 4834* in 1910 (FPF); 1 mi. E of Fish Camp, *H* in 1963 (FPF). MENDOCINO CO.: Van Damme State Park, on *Abies grandis, Kuijt 1216* in 1957 (UC) and *H & Scharpf 855* in 1966 (FPF). MODOC CO.: Warner Mts.: Cedar Pass, *Alava* in 1957 (UC); 2.5 mi. W of Patterson Guard Sta., *H & Hinds 1002* in 1966 (FPF). NEVADA CO.: 2 mi. N of Truckee, *W 3228* in 1962 (COLO, FPF); Hobart Mills, *Boyce FP15981* in 1914 (FPF); Bear Valley, 6 mi. SE of Sierra City, *Jepson* in 1898 (JEPS); Gaston Ridge, 5 mi. N of Washington, *Howell 2459* n.d. (CAS). PLACER CO.: Trail to Mt. Ellis, above Homewood, *Schreiber 891* in 1933 (UC); Lake Tahoe, Carnelian Bay, *Blakely 3793* in 1960 (CAS). PLUMAS CO.: Chester, *Meinecke FP 10754* in 1914 (FPF); Bucks Lake, *Scharpf* in 1963 (FPF); Almanor, *Quick 53-76* in 1953 (CAS); 4 mi. SE of Almanor Jct. on US 89, *W 3232* in 1962 (COLO, FPF); 3 mi. SE of Almanor Jct. on US 89, *W 3233* in 1962 (COLO, FPF); Lassen Buttes, *Brown 675* in 1897 (MO, US); Taylorsville, *Clemens* in 1919 (CAS); near Prattville, *Howell 2115* in 1926 (CAS). SAN BERNARDINO CO.: San Bernardino Mts.: 10 mi. N of Big Bear Lake, *Gill & Wright FP68225* in 1931 (FPF); Barton Flat, 3 mi. E of Camp Angelus, *W 3210* in 1962 (COLO, FPF); Lost Cr., *Munz & Johnston 8576* in 1924 (RSA); Barton Flats, *Ross 1917* in 1937 (RSA); Inspiration Point, *Perkins* in 1917 (ILL); S fork of Santa Ana River, *Howe 1878* in 1948 (UC). SHASTA CO.: 22 mi. N of Lassen Nat. Park entrance on Rte. 89, *Kuijt 1365* in 1957 (UC); 4 mi. N of Lassen Nat. Park entrance on Rte. 89, *H & W 648* in 1964 (FPF); 0.5 mi. S of Siskiyou Co. line on Rte. 89, SE of Bartle, *W 6768* in 1987 (FPF); Rte. 89 at Ponderosa Jct., on *Pinus lambertiana, Kuijt 1369* in 1957 (UC). SIERRA CO.: Sierraville, *Meinecke & Boyce FP 17193* and *FP 17194* in 1915 (FPF) and *Boyce FP 15981* in 1914 (FPF). SISKIYOU CO.: Mt. Shasta, Sisson South Trail, *Cooke*

16132 in 1941 (COLO, MO, PH); Cyn. Cr., *Hedgcock FP 1858* in 1917 (FPF); N side Cascade Gulch, Mt. Shasta, *Cooke 17722* in 1947 (WS, WTU); Bartle-Whitehorse rd., *Newcomb 156* in 1957 (UC); Sisson South Trail, *Cooke 13574* n.d. (CAS); Shackelford Cr., 18 mi. W of Greenview, *Butler 270* in 1908 (UC); Joe Cr., 10 mi. S of Copper, Oregon, *H & W 635* in 1964 (FPF); 5 mi. E of US 99 on Mt. Shasta rd., *H & W 641* in 1964 (FPF); Along trail on N side of Black Butte, *H & W 643* in 1964 (FPF); side of Black Butte, on *Abies grandis, Dudley* in 1899 (FPF, CAS); Base of Mt. Shasta, *Engelmann* in 1880 (MO); Trestle rd. to Hilts, N of Oak Knoll Ranger Sta., *Quick 60-21* in 1960 (CAS); Happy Camp–O'Brien rd. at jct. with rd. to Kelly Lake, *Mathiasen 8625* in 1986 (FPF); Parks Cr. rd., 6 air mi. WSW of Weed, *H & Mathiasen 2422* in 1990 (FPF); Castle Lakes rd, 3.5 mi. S of Siskiyou Lake, *H & Mathiasen 2425* in 1990 (FPF); 5 air mi. WNW of Happy Camp, on *Picea breweriana, DeNitto* in 1990 (FPF). TEHAMA CO.: 2 mi. N of Hole-in-Ground Campground, S of Mineral, *Kuijt 1503* in 1958 (UC). TULARE CO.: Hollow Log Camp, near General Grant, *Dudley* in 1900 (DS); Sequoia Nat. Park, 1 mi. N of Lodgepole, *W 3613* in 1964 (FPF); Portuguese Pass, 7 mi. N of Summit Guard Sta., *W 3610* in 1964 (FPF). TUOLUMNE CO.: N of Mather, *Mason 1101* in 1924 (CAS); Cow Cr., *Gill FP 68060* in 1932 (FPF), *Quick* in 1966 (FPF) and on *Pinus lambertiana, Quick* in 1966 (FPF); Strawberry, *Wright FP 68052* in 1931 (FPF); Long Barn, *Wright FP 68115* and *FP 68116* in 1932 (FPF), *Gill FP 68085* and *FP 68096* in 1932 (FPF), and *Gill & Wright FP 68226* in 1932 (FPF); SE of Pinecrest, *Quick 50-40* in 1950 (CAS); Pinecrest, *Gill FP 68224* in 1932 (FPF) and on *Pinus lambertiana, Gill FP 68224* in 1932 (FPF); Tuolumne Grove, *Peterson 63-139* in 1963 (FPF); 7 mi. E of Long Barn, *W 3223* in 1962 (COLO, FPF); 5 mi. E of Long Barn, *Kuijt 1431* in 1957 (UC); 5.1 mi. E of Nat. For. boundary on Rte. 120, *Kuijt 1393* in 1957 (UC); Yosemite Nat. Park, Tuolumne Cyn., *Clemens* in 1919 (CAS); Gooseberry rd., Dodge Ridge Ski Area, *Scharpf* in 1978 (FPF); Yosemite Nat. Park, 1 mi. W of Tuolumne Grove, *W 6744* in 1987 (FPF).

NEVADA

CLARK CO.: Charleston Mts.: Little Falls, *Clokey 5433* in 1935 (CAS, FPF, RM, UC, US, WTU) and *5434* in 1935 (CAS, FPF, RM, US, WTU); Charleston Park, *W 3204* and *3033* in 1962(COLO, FPF); Deer Cr. Grade, 3 mi. E of Lee Cyn., *Train 2154* in 1918 (ARIZ, UC); Lee Cyn., *Heller 1160* in 1913 (CAS, MO, PH, UC) and *Peterson 64-142* in 1964 (FPF); Deer Cr. Campground, *Breedlove 1109* in 1961 (CAS); without locality, *Jaeger* in 1926 (RSA); Lee Cyn., 5 mi. W of Deer Cr. Jct., *H & Scharpf 674* in 1964 (FPF); Kyle Cyn., 2.5 mi. W of Ranger Sta., *H & Scharpf 676* in 1964 (FPF); Kyle Cyn., near end of highway, *Krebill 719* in 1968 (FPF); Kyle Cyn., 2 mi. W of ranger sta., *H & others 1176* in 1969 (FPF). Sheep Range: 0.25 mi. S of Hidden Forest Cabin, *Rockwell & Horn* in 1977 (FPF); Sawmill Cyn., *Haber* in 1978 (FPF). WASHOE CO.: Vicinity of Reno, *Hitchcock 559* in 1913 (US).

OREGON

(all Oregon collections on *Abies grandis*, except as noted).

CURRY CO.: S of Humbug Mtn., *Ferris 7828* in 1929 (DS); Grizzly Mtn., 0.5 mi. E of Gold Beach, *Theisen* in 1965 (FPF). DESCHUTES CO.: McKenzie Pass, *Gill FP 68186* in 1932 (FPF); 9 mi. W of Sisters, *W 3244* in 1962 (COLO, FPF); 7.5 mi. W of Sisters on Rte 242, *H & W 613* in 1964 (FPF) and *H & Hinds 990* in 1966 (FPF); 14 mi. NW of Sisters on US 126, *H & W 615* in 1964 (FPF); 8 mi. W of Sisters, *H 2346* in 1989 (FPF); 2 mi. W of Swampy Lake jct. on Mt. Bachelor rd., *H 2345* in 1989 (FPF). HOOD RIVER: [Obs., Badger Area, E slope of Mt. Hood, P. Zilka, 1973]. JACKSON CO.: 11 mi. E of Trail on Rte. 62, *H 2372* in 1989 (FPF); 10 mi. E of Butte Falls, *Graham* in 1964 (FPF); Long John Cr., SSW of Ashland, *Wheeler 3005* in 1934 (CAS, RSA, WTU); 11 mi. SW of Ashland on Copper rd., *H & W 637* in 1964 (FPF); Summit of Siskiyou Mts., near Siskiyou Sta., *Abrams 12130* in 1927 (DS); W Fork of Evans Cr., 18 mi. NE of Grants Pass, *Graham* in 1966 (FPF); 8 air mi. S of Ashland, *Graham* in 1965 (FPF); 18 air mi. E of Ashland, *Howard* in 1964 (FPF); Fish Lake rd., 12 mi. SE of Butte Falls, *Graham* in 1965 (FPF); 3.5 mi. S of Steamboat Mtn., *Knutson & Tinnin DM 78* in 1978; For. Service rd. 3780, 15 air mi. SE of Prospect, *H 2444* in 1991 (FPF). JEFFERSON CO.: 3 mi. E of Santiam Pass on US 20, *H & Scharpf 1257* in 1969 (FPF); Black Butte, near Deschutes Co. line, *Johnson 349* in 1960 (OSC); N slope of Black Butte, *Johnson 605a* in 1960 (OSC); Suttle Lake, *H 2351* in 1989 (FPF). JOSEPHINE CO.: Flat Top Mtn., 24 air mi. W of Grants Pass, *Graham* in 1963 (FPF), *H & W 632* in 1964 (FPF), and *Bynum* in 1967 (FPF); and on *Picea breweriana, Graham* in 1963 (FPF), *H & W 631* in 1965 (FPF), and *Bynum* in 1967 (FPF). Steve Cr., 15 mi. E of Takilma, *Knutson & Tinnin DM 75* in 1978 (FPF) and, on *Picea breweriana, Knutson & Tinnin DM 76* in 1978 (FPF); Thompson Cr., 8 mi. SSE of Williams, *Knutson & Tinnin DM 72* in 1978 (FPF). KLAMATH CO.: Hamner Butte, S of Davis Lake, *Childs 28* in 1939 (OSC) and *Englerth FP 91031* in 1939 (OSC); 9 mi. N of Fort Klamath on Rte. 62, *H & W 626* in 1964 (FPF); 9 mi. N of Ft. Klamath, near S entrance of Crater Lake Nat. Park, *H & others 1377* in 1971 (FPF); 31 mi. W of Klamath Falls on Rte. 66, *H & W 629* in 1964 (FPF); vicinity of Crater Lake, *Weir 2429* in 1916 (FPF, ILL) and on *Abies amabilis, Weir 2423* in 1916 (FPF, ILL); 1 mi. N of Bly Summit, 8 mi. SW of Beatty on Rte. 140, *H & W 874* in 1966 (FPF); 8 mi. SW of Lone Pine, *Knutson & Tinnin DM 68* in 1978 (FPF); Boundary Butte, 3 mi. ENE of Sun Pass, *H 2366* in 1989 (FPF); 4 air mi. N of Lake of the Woods, *H 2373* in 1989 (FPF). LAKE CO.: Silver Lake, *Jaenicke FP 21285* in 1916 (FPF); W Fork of Silver Cr., 12 mi. SW of Silver Lake, *Stewart* in 1968 (FPF); 8 mi. SE of Bear Butte, *Knutson & Tinnin DM 64* in 1978 (FPF). LANE CO.: W slope of Cascades, near Oakridge, on *Abies lasiocarpa, Cooper & Knutson* in 1979 (FPF). POLK CO.: Helmick State Park, 15 mi. N of Corvallis, *H 1750* in 1976 and *Hansen* in 1986 (FPF). COUNTY UNCERTAIN.: Willamette Valley, *Hall 458* in 1871 (PH).

UTAH

KANE CO.: 8 mi. S of Navajo Lake on Zion Park rd., *W 4122* in 1966 (FPF, UT); 5.2 mi. SE of W end of Navajo Lake *W 6678* in 1986 (FPF); near Navajo Lake, 1 mi. S of Nat. For. boundary, *H 2141* in 1986; Swapp Cyn., 6 air mi. E of Alton, *Rathdrum* in 1971 (FPF); 1 mi. S of Crawford Pass, 11 air mi. E of Alton, *Mathiasen 8936* in 1989 (FPF).

WASHINGTON

KLICKITAT CO.: Falcon Valley, on *Abies grandis, Suksdorf 2246* in 1893 (FPF, MO, UC, US, WS); Snowden, ca. 12 mi. NE of White Salmon, on *Abies grandis, Graham* in 1964 (FPF) and *H & W 592* in 1964 (FPF); 3.5 mi. N of Trout Lake on Randle rd., on *Abies grandis, H 2216* in 1987 (FPF); Bingen Mtn. near Bingen, on *Abies grandis, Suksdorf* in 1989 (WS). SKAMANIA CO.: 0.4 mi. E of For. Service rd. 880 on For. Service rd. 820 ("Big Tree Rd."), T. 7 N., R. 10 E., Sec. 26, on *Abies grandis, Mathiasen 92-02* in 1992 (FPF); "few" miles NE of Ice Caves, on *Abies grandis, Suksdorf* in 1900 (WS). YAKIMA CO.: 7 mi. NNE of Trout Lake on Bird Cr. Meadows rd., on *Abies grandis, H 2217* in 1987 (FPF).

1b. *Arceuthobium abietinum* f. sp. *magnificae*

All collections on *Abies magnifica* except as noted.

UNITED STATES

CALIFORNIA

AMADOR CO.: E of Lower Bear Res., *Quick 54-87* in 1954 (CAS). BUTTE CO.: Summit of Humboldt rd. near Jonesville, *Copeland* in 1928 (UC); "Big Summit," Jonesville, *Copeland* in 1931 (UC). CALAVERAS CO.: 10 mi. above Dorrington, *Wright FP 68050* in 1931 (FPF) and *FP 68123* in 1932 (FPF); 8 mi. SW of Tamarack on Rte. 4, *H & Scharpf 663* in 1964 (FPF). DEL NORTE CO.: 20 mi. NW of Happy Camp, *Knutson & Tinnin DM 80* in 1978 (FPF). EL DORADO CO.: S end of Echo Lake, *Howell 22902* in 1946 (CAS); Echo Summit, *Smith* in 1972 (UC); 0.5 mi. NW of Echo Summit on US 50, *H 2441* in 1991 (FPF). FRESNO CO.: Huntington Lake, *Miller FP98117* in 1965 (FPB); Roaring River, *Meinecke* in 1910 (FPB). HUMBOLDT CO.: Trinity Summit, E of Corral Prairie, *Tracy 10571* in 1932 (UC); South Fork Mtn., near Blake Lookout, *Tracy 8950* in 1930 (JEPS, WTU). KERN CO.: Greenhorn Mts., N side Sundry Peak, *Howell 38844* in 1962 (CAS). MADERA CO.: Haskell Meadow, *Miller FP 97956* in 1910 (FPB). MARIPOSA CO.: 5 mi. E of Fish Camp, *H* in 1963 (FPF). NEVADA CO.: Hobart Mills, *Boyce FP 15982* in 1914 (FPF, ILL); 5 mi. E of Hobart Mills, *Gill FP 68223* in 1931 (FPF). PLUMAS CO.: Grizzly Summit, SW of Bucks Lake, *Scharpf FP 98107* in 1964 (FPF); Claremont Peak near Quincy, *Weatherby 1674* in 1955 (CAS, RM, RSA). SHASTA CO.: Lassen Nat. Park on main rd., 10 mi. E of N entrance, *H & W 650* in 1964 (FPF). SISKIYOU CO.: near head of E Fork of Indian Cr., *Evans* in 1912 (FPF); 0.5 mi. E of Siskiyou Nat. For. boundary on Happy Camp-O'Brien rd., 14 air mi. NNW of Happy Camp, *H & Hinds 1000* in 1966 (FPF); Kidder Cr., ca. 11 mi. WSW of Greenview, *Gill & Sargent FP 68181* in 1932 (FPF); Happy Camp-O'Brien Rd. at divide, *Mathiasen 8626* in 1986 (FPF); 1.5 mi. W of White Mtn., *Mathiasen & Loftis 8632* in 1986 (FPF); Little Marble Valley, *Mathiasen 8622* in 1986 (FPF); Trinity Alps, Snowslide Lake, *Mathiasen 9015* in 1990 (FPF). TRINITY CO.: South Fork Mtn., near Hyampom, *Boyce 30* in 1914 (FPF); South Fork Mtn., *Parks & Tracy 11532* in 1941 (RM, RSA, UC, US, WTU). TULARE CO.: Bald Mtn., Kaweah River Valley, *Dudley 1395* in 1896 (DS); Mosquito Cr. near Mineral King, *Hopping* in 1913 (FPB); 17 mi. NW of Lodgepole, *W 3615* in 1964 (FPF). TUOLUMNE CO.: Pinecrest, *Scharpf* in 1963 (FPF); Yosemite Nat. Park, 7 mi. E of Crane Flat Jct. on Tioga Pass rd., *H 938* in 1966 (FPF). COUNTY UNCERTAIN: Lassen Nat. Park., *Boldenbeck* in 1910 (DS).

OREGON

JOSEPHINE CO.: Flat Top Mtn., ca. 24 air mi. W of Grants Pass, on *Abies procera; Bynum* in 1967 (FPF): Oregon Caves Nat. Mon., Sike Mtn. Trail, *Root & Gooding FP 68274* in 1932 (FPF); near Bolan Mtn., S of Oregon Caves, *Theisen* in 1966 (FPF).

2. *Arceuthobium abietis-religiosae*

All collections on *Abies religiosa,* except as noted.

MEXICO

JALISCO

NW slopes of Nevado de Colima, on *Abies* sp., *McVaugh & Wilber* 10130 in 1949 (MICH); 19 km. W of Fresnito on rd. to Nevado de Colima, *H & others 2313* in 1989 (IBUG, FPF); Volcán de Colima, on *Abies* sp., *Reich* in 1913 (MEXU); Mpio. Venustiano Carrenz, 8 km. from Puerto de Floripondio on rd. to Microondas Las Vibradores, *Chazaro & others 5902* in 1989 (FP, IBUG).

MEXICO

Ixtaccihuatl, *Purpus 6491* in 1912 (MO, UC, US); Popocatépetl, *Balls B4228* in 1938 (BM, K, UC, US); 17 km. E of Amecameca, *H & W 373* in 1963 and *1228* in 1969 (FPF), *Bailey 75-68* in 1975 (FPF) and *Nickrent 2010* in 1985 (FPF, ILL, MEXU); 12 km. E of Amecameca, *H & W 1227* in 1969 (FPF); District Temascaltepec, vicinity of Meson Viejo, *Hinton 3278* in 1933 (K, US); Sultepec rd. 10 mi. S of Nevado de Toluca Jct., *Peterson 68-91* in 1968 (FPF); 6 km. E of Michoacán-Mexico boundary on Angangueo-San Jose del Rincon rd., *Peterson 73-100* in 1973 (FPF); 8.7 mi. E of Angangueo, *H & Player 1540* in 1975 (FPF); Mpio. Texcoco; Cerro Tlaboc, 24 km., from Texcoco, *Garcia* in 1974 (INIF); 14 km. SE Teguesguinachuac, *Koch 788* in 1978 (ENCB, MEXU); Cerro Telapon, *Madrigal 988* in 1961 (INIF); Llano Grande, Cerro Telapon, *Paez* in 1964 (ENCB); Llano Grande, N of Volcán Nevades, *Luis* in 1964 (ENCB); Mpio. Chalco, Llano Grande, *Rzedowski 18411* in 1963 (ENCB); 2 km. NW of Santa Ana Jilotzingo, *Rzedowski 31644* in 1974 (ENCB); 3 km. S of Canjones, *Rzedowski 30724* in 1973 (ENCB); Mpio. Ixtalpaluca, 8 km. S of Rio Frio, *Mendoza 1169* in 1975 (MEXU).

MICHOACÁN

1 km. W of Mexico boundary on Angangueo-San Jose del Rincon rd., *Peterson 73-101* in 1973 (FPF); Chincua Monarch Butterfly Area, 3 km. N of Angangueo, *H 2111* in 1986 (FPF); 6 km. NE of Angangueo on rd. to San José del Rincon, *Rzedowski 38058b* in 1983 (ENCB, INIF).

NUEVO LEÓN

Cerro Potosí, on *Abies vejari, H & W 394* & *396* in 1963 (COLO, FPF), *H & others 1681* in 1975 (FPF), *Rzedowski 27162* in 1970 (ENCB), and *Nickrent 1983* in 1984 (FPF, ILL, MEXU); Mpio. de Derrumbadero, in moister cyns above Santa Elena, San Juanito to San Miguel and E as far as Los Toros, on *Abies* sp., *Mueller* in 1935 (MO).

PUEBLA

Mpio. Ixtacamaxitlan, La Caldera, 0.5 km. NE of Hidaldo, *Magana* in 1974 (ENCB, INIF).

TAMAULIPAS

Cerro El Borrado, 20 km. NE of Miqihana on *Abies* sp., *Rzedowski 3841* in 1961 (ENCB).

TLAXCALA

Malinche, 12 km. E of Ixtenco, *H 2108* in 1986 (FPF); Malinche, *Rzedowski 23752* in 1963 (ENCB).

3. *Arceuthobium americanum*

All collections on *Pinus contorta* except as noted. For these records the varieties *murrayana* and *latifolia* are not distinguished because these can be determined by the geographic area involved (Critchfield 1957).

CANADA

ALBERTA

N fork of N branch of Saskatchewan River, *Brown 795* in 1908 (PH); Kananaskis For. Exp. Sta., *Muir 64-327* in 1964 (FPF) and on *Pinus sylvestris, Powell* in 1968 (CFB, FPF); Banff Nat. Park: Bankhead, *Brown 794* in 1906 (MO,PH, US); 2 mi. E of Lake Louise, *H 90* in 1961 (FPF); 4 mi. W of Lake Louise, *Petty 64-568* in 1964 (FPF); Eisenhower Jct.; on *Picea glauca, H & Baranyay 92* in 1961 (FPF); 1.5 mi. E of Eisenhower Jct., *H 91* in 1961 (FPF); Cypress Hills, W of Spring Cr. Ranger Sta., *Breitung 5586* in 1947 (MO); Cypress Hills, Elkwater, *Lawrence* in 1967 (FPF, WINF); Jasper Nat. Park, Snaring River, on *Picea glauca, Bourchier* in 1954 (CFB, FPF); 7 mi. W of Cold Lake, on *Pinus banksiana, Wilkinson* in 1960 (CFB, FPF); 38 mi. SE of Conklin, on *Pinus banksiana, Wilkinson* in 1961 (CFB, FPF); 20 mi. NW of Slave Lake Town, on *Pinus banksiana, Smith* in 1962 (CFB, FPF); 2 mi. W of Fort Assiniboine, on *Pinus banksiana, Emond & Layton* in 1966 (CFB, FPF); 23 mi. SW of Clearwater Ranger Sta., *Smith* in 1966 (CFB, FPF); 3 mi. SW of Clearwater Ranger Sta., *Smith* in 1965 (CFB, FPF); 2 mi. N and 2 mi. E of St. Vincent, on *Pinus banksiana, Layton* in 1966 (CFB, FPF); 4 mi. NW of Rocky, *Smith* in 1966 (CFB, FPF); Highwood Valley, 62 mi. S of Trans. Can. Highway, *H & Laut 1301* in 1970 (FPF); Oldman Valley, 31 mi. N of Coleman, *H & Laut 1302* in 1970 (FPF); 13 mi. E of Smokey Lake on Rte. 28, *Oliver* in 1970 (FPF); 6 mi. N of town of Slave Lake, on *Pinus banksiana, W* in 1987 (FPF).

BRITISH COLUMBIA

Guichon Cr., 13 mi. S of Savona, *Hitchcock & Martin 7425* in 1941 (COLO, DS, MO, RM, RSA, UC, WTU); 10 mi. N of Clinton, *Calder & others 16644* in 1956 (COLO, US); Prince George, *Calder & others 14363* in 1954 (WTU); Kleena Kleen P. O., 50°57' N, 124°52' W, *Calder & others 19159* in 1956 (CAS, WTU); 3 mi. S of Ta Ta Cr., N of Cranbrook, *Calder & Savile 11374* in 1953 (UC, US); near Allenby, *McCallum* in 1940 (UC); Settlers rd., Kootenay Nat. Park, *Morf 64-86* in 1964 (FPF); 20 mi. NW of Kelowna, *Stewart* in 1965 (FPF); 2.5 mi. SW of Telkwa, *Calder & others 15273* in 1954 (US); Bonaparte River, *Macoun* in 1889 (US); Salmon Arm, *Weir 8444* in 1913 (ILL); 25 mi. SE of Kelowna, *Kuijt* in 1954 (DAVFP, FPF); Perry Cr., *Kuijt 598* in 1954 (DAVFP, FPF); Moyie River, *Kuijt* in 1954 (DAVFP, FPF); between Yahk and Moyie Lake, *Kuijt* in 1954 (DAVFP, FPF); 33 mi. N of Rock Cr., *Kuijt* in 1954 (DAVFP, FPF); 1 mi. S of Beaverdell, *Kuijt* in 1954 (DAVFP, FPF); Carmi, *Kuijt 591* and *592* in 1954 (DAVFP, FPF); McCulloch, *Kuijt 589* in 1954 (DAVFP, FPF); Thompson River, *Kuijt* in 1954 (DAVFP, FPF); 8 mi. N of Kimberly, *Kuijt 528* in 1953 (DAVFP, FPF); 45 mi. S of Radium, *Kuijt* in 1953 (DAVFP, FPF); Windermere, *Kuijt 535* in 1953 (DAVFP, FPF); Kootenay Park, *Kuijt* in 1954 (DAVFP, FPF); 12 mi. N. of Clinton, *Kuijt* in 1954 (DAVFP, FPF); Jesmond, *Kuijt* in 1954 (DAVFP, FPF); Pavilion Mtn., *Kuijt* in 1954 (DAVFP, FPF); Eholt, *Kuijt* in 1954 (DAVFP, FPF); Balfour, *Kuijt* in 1954 (DAVFP, FPF); Manning Park, 10 mi. E of Allison Summit, *Kuijt* in 1954 (DAVFP, FPF); Manning Park, 12 mi. E of Allison Summit, *H & Laut 1297* in 1967 (FPF); 10 mi. N of Sunday Summit, *Kuijt* in 1954, (DAVFP, FPF); Moyie Lake, *Kuijt* in 1954 (DAVFP, FPF); Mt. Robson Park, Fraser River, *Kuijt* in 1953 (DAVFP, FPF); Mt. Robson Park, Yellowhead, *Kuijt 536* in 1953 (DAVFP, FPF); 100-Mile House, *Simms* in 1955 (DAVFP, FPF); Manning Park, near E boundary, *Sugden* in 1960 (DAVFP, FPF); Alexis Cr., *Simms* in 1955 (DAVFP, FPF); 12 mi. W of Riske Cr., *H 1812* in 1977 (FPF); Yoho Nat. Park, 11 mi. SW of Fields on Trans Canada 1, *H & Laut 1300* in 1970 (FPF).

MANITOBA

Near Cowan, on *Pinus banksiana, Riley 47-208* in 1947 (MO, RM); Victoria Beach, on *Pinus banksiana, Jackson* in 1924 (ILL) and *Löve & Löve 5740* in 1953 (US); Belaire Provincial For., on *Pinus banksiana, Lawrence* in 1967 and 1968 (FPF, WINF), *Laut* in 1968 (FPF, WINF), and *H & others 1481* in 1973 (FPF); Wallace Lake, on *Pinus banksiana, Knowles* in 1982 (FPF); Iskwason Lake, on *Pinus banksiana, Laut* in 1968 (FPF, WINF); Black Island, Lake Winnipeg, on *Pinus banksiana, Lawrence* in 1968 (FPF, WINF).

ONTARIO

Kenora District, Vermillion Bay, on *Pinus banksiana, Thompson* in 1970 (FPF); Lac Seul, Scout Bay, on *Pinus banksiana, Laut & others* in 1970 (FPF).

SASKATCHEWAN

Prince Albert, on planted *Pinus contorta, Beveridge* in 1968 (FPF,WINF); MacDowall, on *Pinus banksiana, Blumer 5177* in 1913 (FPF); Lac la Ronge, on *Pinus banksiana, McLeod* in 1965 (FPF, WINF); 26 mi. SE of Cumberland House on *Pinus banksiana, Crawford* in 1967 (FPF, WINF); S shore of Lake Athabaska, on *Pinus banksiana, McLeod* in 1966 (FPF, WINF); Lac la Loche, on *Pinus banksiana, Rentz* in 1967 (FPF, WINF); Mile 10.7 on Cumberland rd., on *Pinus banksiana, Crawford* in 1968 (FPF, WINF); Mile 15 on Turner Lake rd., on *Pinus banksiana, Laut* in 1968 (FPF, WINF); Ile a'la Crosse, on *Pinus banksiana, Laut* in 1968 (FPF, WINF).

UNITED STATES

CALIFORNIA

ALPINE CO.: Sandy Flat, N Stanislaus River, 4 mi. NE of Alpine, *Stanford 629* in 1927 (RM); 5 mi. W of Alpine Co. boundary on Rte. 4, on *Pinus ponderosa, Kuijt 1411* in 1957 (UC); 0.5 mi. W of grade summit on Rte. 4, on *Pinus ponderosa, Kuijt 1412* in 1957 (UC). CALAVERAS CO. Rte. 4 near Alpine Co. boundary, *Peterson 63-134* in 1963 (FPF); Pacific Valley Campground on Rte. 4, *Scharpf* in 1970 (FPF); 3 mi. SW of Tamarack on Rte. 4, *H & Scharpf 664* in 1964 (FPF). EL DORADO CO.: US 50 at Pyramid Cr., *Kuijt 1513* in 1958 (UC); Lily Lake, Glen Alpine Cyn., *Abrams 12753* in 1903 (DS, MO, POM, UC); 16 mi. S of Tahoe City, on *Pinus ponderosa, Kuijt 1335* in 1957 (UC); 1.1 mi. N of Meyers on US 50, *H & W 838* in 1966 (FPF); 9 mi. E of Kyburz on US 50, *H & W 839* in 1966 (FPF); Just W of Luther Pass on Rte. 89, *H 2438* in 1991 (FPF). FRESNO CO.: Huntington Lake, *Solbrig 2420* in 1957 (UC), *Perkins* in 1920 (ILL), and *H 2031* in 1982; House Meadows, N fork of Kings River, 5 mi. W of Wishon Dam, *Hall & Chandler 426* in 1900 (UC); Vermillion Valley, *Quibell & Quibell 2641* in 1953 (RSA); Moraine Meadow, near Roaring River Guard Sta., *Knutson* in 1981 (FPF). KERN CO.: Havileah, 7 mi. S of Bodfish, *Coville & Funston 1073* in 1891 (FPF); Kern area, *Coville & Funston 1596* (US). LASSEN CO.: Bridge Cr., 7-8 mi. SW of Eagle Lake, *Whitney 1717* in 1934 (UC). MADERA CO.: Red's Meadow to Rainbow Falls, *Raven 3678* in 1951 (RSA); Devils Post Pile Nat. Mon., *H & Scharpf 670* in 1964 (FPF). MARIPOSA CO.: Tenaya Lake, *Root* in 1919 (FPF, ILL) and *H 939* in 1966 (FPF); Little Yosemite Valley, *Bolander 5095* in 1866 (MO, UC, US), *Rodin 877* in 1946 (UC); Merced Lake Trail, Yosemite, *Schreiber 1948* in 1935 (UC); Upper Yosemite Valley, *Lemmon* in 1878 (MO). MODOC CO.: Warner Mts., jct. of Davis Cr. and Harris Flat rds., *Mathiasen 8920* in 1989 (FPF). MONO CO.: 4.3 mi. W of jct. of Rts. 120 and 395, *Kuijt 1390* in 1957 (UC); 2 mi. W of Lee Vining, on *Pinus jeffreyi, Peterson 63-129* in 1963 (FPF); W of Lee Vining on Tioga Pass rd., *Krebill & Nelson 468* in 1967 (FPF). NEVADA CO.: 4 mi. from Truckee, *Wright FP 68107* in 1932 (FPF); Hobart Mills, *Gill FP 68063* in 1931 (FPF); Donner State Park, *H* in 1963 (FPF); Donner Lake, *Dudley* in 1893 (DS) and *Sonne* in 1898 (US); near Truckee, *Sonne* in 1898 (UC), *Wright FP 68048* in 1931 (FPF), *Gill FP 68227* in 1931 (FPF); Donner Summit on I-80, *H 2418* in 1990 (FPF). PLACER CO.: Near Cisco, *Boyce 40* in 1919 (FPF); 7 mi. W of Soda Springs, *W 3226* in 1962 (COLO, FPF); N Tahoe Meadow, Lake Tahoe, *Schreiber 776* in 1932 (UC); 3.5 mi. N of Tahoe City on Rte. 89, *Kuijt 1332* in 1957 (UC); 8.5 mi. W of Soda Springs, on *Pinus ponderosa, Kuijt 1330* in 1957 (UC); 10 mi. N of Tahoe City on Rte. 89, on *Pinus ponderosa, Kuijt 1331* in 1957 (UC); 9.2 mi. N of Tahoe City on Rte. 89, on *Pinus jeffreyi, Kuijt 1343* in 1957 (UC). PLUMAS CO.: Chester, *Meinecke FP 17053* in 1914 (FPF); 18 mi. N of Greenville, *Kuijt 1350* in 1957 (UC); Graegle Cr. near Lake Center Camp, *Mason 1079* in 1924 (JEPS, UC); Gold Lake, *Gill FP6 8046* in 1931 (FPF); Buck's Ranch, *Meinecke* in 1920 (FPF); Little Grizzly Valley, on *Pinus jeffreyi, Boyce* in 1915 (FPF). SHASTA CO.: Thousand Lake Basin, *Peirson 10136* in 1932 (RSA); Lassen Nat. Park on main rd. 10 mi. E of north entrance, *H & W 651* in 1964 (FPF); headwaters of Hat Cr., *Eggleston 7459* in 1911 (MO, US). SIERRA CO.: 8 mi. W of Rte. 89 on Webber Lake rd., *H & W 657* in 1964 (FPF); 9.5 mi. N of Truckee, *Kuijt 1344* in 1957 (UC); Webber Lake, *"Loran"*, n.d., (UC). SISKIYOU CO.: Military Pass, NE side Mt. Shasta, *Cooke 16034* in 1941 (DS, UC); Mt. Shasta, Sisson, *Pendleton* in 1919 (FPF, ILL); 3 mi. S of Tennant, *Boyce* in 1914 (FPF); N fork of Sacramento River, *Raven 10456* in 1959 (CAS); Parks Cr. rd, 9 air mi. SW of Weed, *H & Mathiasen 2420* in 1990 (FPF). TEHAMA CO.: Mineral, *Meinecke FP 97934* in 1911 (FPF); Mineral Campground, near Ranger Sta., *Kuijt 1358* in 1957 (UC); Deer Cr., 1.5 mi. S of jct. of Rts. 32 and 36, *Kuijt 1501* in 1958 (UC); Deer Cr., 1 mi. E of Rts. 89 and 36 on Rte. 32, *Waters 242* in 1958 (JEPS); 13 mi. W of Rts. 36 and 89 at Lake Almanor, on *Pinus ponderosa, Kuijt 1354 & 1355* in 1957 (UC); 7 mi. W of Rts. 36 and 89 at Lake Almanor, on *Pinus ponderosa, Kuijt 1352* in 1957 (UC). TULARE CO.: Kern River fork, *Coville & Funston 1596* in 1871 (FPF); Long Meadow, *Peterson 63-149* in 1963 (FPF); Bakeoven Meadows, S fork Kern River, *Howell 27038* in 1950 (DS, UC, US); Junction Meadows, Kern River, *Raven 8349* in 1955 (UC); 13 mi. NW of Lodgepole, *W 3614* in 1964 (FPF); Funston Camp, 11 mi. SE of Mineral King, *Peirson 1720* in 1919 (RSA); ridge between Monache and Bakeoven

Meadows, *Munz 15220* in 1950 (RSA); 3 mi. NW of Beach Meadow, *Howell & True* in 1967 (FPF). TUOLUMNE CO.: Pinecrest, *Wright FP 68114* in 1932 (FPF) and *Gill FP 68229* in 1931 (FPF). COUNTY UNCERTAIN: Summit, Tahoe Nat. For., *Meinecke* in 1917 (FPF); N California border, Salmon Nat. For., *Galbreath FP1691* in 1909 (FPF).

COLORADO

BOULDER CO.: 3 mi. S of Ward on Rte. 160, *H & Gill* in 1958 (FPF); 6 mi. N of Nederland, *H & Laut 1288* in 1970 (FPF); 1.5 mi. W of Rte. 160 on Brainard Lake rd., *H 418* in 1963 (FPF); Allenspark, *Johnston & Thompson FP24881* in 1917 (FPF); Niwot Hill, near Ward, *Schmoll 498* in 1922 (COLO); Pine Glade School, *Ramaley 3754* in 1907 (COLO); Ward, *Newman* in 1922 (COLO); near Nederland, *W 2966* in 1961 (COLO); Allenspark, on *Pinus ponderosa*, *H 828* in 1965 (FPF); 5 mi. S of Ward, on *Pinus flexilis*, *Peterson* in 1958 (FPF) and *H & Gill* in 1958 (FPF); 1 mi. N of Nederland, on *Pinus ponderosa*, *H 1793* in 1977 (FPF). CHAFFEE CO.: Alpine, *Brandegee* in 1880 (FPF); 8 mi. W of Buena Vista, *H 445* in 1963 (FPF); Forest City, *Brandegee 12201* in 1880 (MO). CLEAR CREEK CO.: Silver Plume, *Bethel FP 27111* in 1918 (FPF); 0.5 mi. SE of Alice, *H & W 283* in 1963 (FPF); 4.4 mi. E of Berthoud Pass, *Greene & Richter 112* in 1962 (COLO, FPF); Clear Cr. Valley, *Engelmann* in 1874 (MO, UC); Empire, *Patterson 297* in 1892 (MO, UC, US); 3 mi. W of Bergen Park, *H 566* in 1964 (FPF); above Empire, *Engelmann* in 1874 (MO); Bergen Park, *Greene* in 1873 (MO); Empire, *Torrey* in 1872 (MO); Georgetown, *Wootson 23* in 1873 (US); 1.5 mi. E of Berthoud Falls on Rte. 40, on *Pinus aristata*, *H 2303* in 1989 (FPF); 1.5 mi. E of Berthoud Falls, on *Pinus aristata*, *H 2303* in 1989 (FPF). DOUGLAS CO.: Rampart Range rd., 5 mi. S of Long Hollow Jct., *H 205* in 1962 (FPF); Rampart Range rd., 4 mi. N of El Paso Co., *H 1408* in 1972 (FPF); Rampart Range rd., 11 mi. N of Woodland Park, on *Pinus ponderosa*, *H 1493* in 1974 (FPF). EAGLE CO.: Mt. of the Holy Cross, *Coulter 7655* in 1873 (MO, PH, US) and *Hedgcock FP624* in 1909 (FPF): Red Cliff, *Gayman FP 26295* in 1917 (FPF); 5 mi. E of Vail on US 6, *H 947* in 1966 (FPF). GILPIN CO.: Rollinsville, *Wheeler 330* in 1901 (COLO, RM); Rollinsville, on *Pinus ponderosa*, *Hedgcock FP 22598* in 1916 (FPF); Tolland, *Bethel 317* in 1921 (CS), *Gayman & Hinson FP 26248* in 1917 (FPF), *Hedgcock FP 22592* in 1916 (FPF, UC); Lake Eldora, *Hedgcock FP 22549* in 1916 (FPF). GRAND CO.: Granby, *Bethel* in 1906 (CS), *Benson 4907* in 1933 (POM); Fraser, *Hedgcock & Johnston FP 26068* in 1917 (FPF); Idlewild, *Hedgcock FP 1649* in 1909 (FPF); 6 mi. W of Fraser, *H 81* in 1961 (FPF); 18 mi. S of Parshall on Leal rd., *Hinds & H* in 1960 (FPF); 8.3 mi. N of Fraser on US 40, *Greene & Richter 113* in 1962 (COLO, FPF); 11.3 mi. N of Granby on US 34, *Greene & Richter 114* in 1962 (COLO, FPF); Grand Lake, col.? in 1881 (MO) and *Shear & Bessey 5317* in 1898 (US); 3 mi. SW of Fraser, Byers Camp, *Gierisch 1247* in 1940 (USFS); Fraser Exp. For., 1 mi. N of headquarters, on *Picea engelmannii*, *H 2064* in 1984 (FPF). GUNNISON CO.: 5 mi. E of Taylor Park on Cottonwood Pass rd., *H 945* in 1966 (FPF); 2.5 mi. W of Monarch Pass on US 50, *Hinds 63-13* in 1963 (FPF); 3.5 mi. NE of Almont, *H & others 1503* in 1974 (FPF); 3 mi. W of Crested Butte, *H & Peterson 1866* (FPF); on Rocky Brook Cr. rd., 2.5 mi. E of jct. with Spring Cr. rd., *H 2043* in 1983 (FPF); 3 mi. NW of Dorchester Campground on Taylor River rd., *H 2044* in 1983 (FPF); 2 mi. NW of Dorchester Campground on Taylor River rd., *H 2045* in 1983 (FPF); 9 mi. NE of Almont, on *Pinus ponderosa*, *H & others 1504* in 1974 (FPF); One Mile Campground, on *Pinus ponderosa*, *Mathiasen 7825* in 1978 (FPF); Gunnison Nat. For., Rosy Lane Campground, on *Pseudotsuga menziesii*, *Mathiasen 7824* in 1978 (FPF). JACKSON CO.: North Park, *Barber* in 1874 (US); E side of Buffalo Pass, *H 414* in 1963 (FPF); Silver Cr., 4 mi. S of Gould, *H 415* in 1963 FPF); Silver Cr., 4 mi. SE of Gould, on *Picea engelmannii*, *H & others 934* in 1966 (FPF); 1 mi. N of Willow Cr. Pass, *H 416* in 1963 (FPF); Big Cr. Lake, *H 830* in 1965 (FPF); near Wyoming line on Rte. 127, *Davidson & Gill FP 89991* in 1952 (FPF); Camp Cr., ca. 9 mi. N of Cowdrey, *H 942* in 1966 (FPF); Silver Cr., ca. 3 mi. SE of Gould, *H 941* in 1966 (FPF); Rock Cr. drainage, ca. 6 mi. SW of Rand, *H 940* in 1966 (FPF); Just S of Colorado-Wyoming boundary on State Rte. 127, *H 1053* in 1967 (FPF); 2 mi. N of Gould, *H 1091* in 1968 (FPF); 16 air mi. W of Walden, *H 1695* in 1976 (FPF); 15 air mi. W of Walden, *H 1696* in 1976 (FPF). JEFFERSON CO.: Redskin Cr., *Hill FP 68279* in 1932 (FPF); 0.8 mi. E of Conifer on Deermont rd., *H 1863* in 1978 (FPF); 1 mi. S of Brook For., *H 2298* in 1989 (FPF); 4 mi. NW of Wellington Lake, *H 2299* in 1989 (FPF); 5 mi. NW of Conifer, *H 2298* in 1989 (FPF). LAKE CO.: Leadville, *Clokey 2684* in 1916 (DS, FPF, ILL, RM, UC, US) and *Schedin & Schedin*, n.d. (RM). LARIMER CO.: Longs Peak Inn, *Cooper 23* in 1908 (RM); 9.8 mi. W of Pingree Park rd. on Crown Point rd., *H 411* in 1963 (FPF); Rocky Mountain Nat. Park, Glacier Basin, *Smith* in 1937 (CS); 5 mi. W of Redfeather Lakes, *H 190* in 1961 (FPF); 4 mi. W of Redfeather Lakes, *H 407* in 1963 (FPF); Longs Peak Valley, *Kiener 5686* in 1937 (COLO); Buckhorn Mtn., Stove Prairie Summit, *H 553* in 1964 (FPF); 3 mi. NE of Cameron Pass on Chambers Lake rd., *H 1190* in 1969 (FPF); Stove Prairie Summit, 2 mi. E of Stove Prairie School, *H 1189* in 1969 (FPF); 2 mi. W of Buckhorn Ranger Sta., *H 560* in 1964 (FPF); Bear Gulch, 6 mi. W of Masonville, *H 711* in 1964 (FPF); 1 mi. N of Stub Cr. Ranger Sta., ca. 1 mi. S of Glendevy, *H 944* in 1966 (FPF); Twin Sisters Peak, near Estes Park, *Bailey 72-02* in 1972 (FPF); Stove Prairie Summit, on *Pinus ponderosa*, *H 192* in 1961 (FPF); 3 mi. E of Creedmore Lakes rd., on *Pinus ponderosa*, *H 261* in 1962 (FPF); Boulder Ridge, on *Pinus ponderosa*, *H 263* in 1962 (FPF); Tie Siding–Cherokee Park rd., on *Pinus ponderosa*, *H 286* in 1962 (FPF); 1 mi. W of Redfeather lakes, on *Pinus ponderosa*, *H 408* in 1963 (FPF); Devils Cr. on Sand Cr. Pass rd., on *Pinus ponderosa*, *Schacht* in 1962 (FPF); 0.5 mi. E of Buckhorn Ranger Sta., on *Pinus ponderosa*, *H 555* in 1963 (FPF); Pennock Cr., 3 mi. S of Pingree Park rd., on *Pinus ponderosa*, *H 563* in 1964 (FPF); Bear Gulch rd., 6 air mi. W of Masonville, on *Pinus ponderosa*, *H 712* in 1964 (FPF); Rawah Ranch, 10 mi. N of

Chambers Lake, on *Pinus ponderosa, H 1094* in 1968 (FPF); 4 mi. W of Redfeather Lakes, on *Pinus flexilis, H 258* in 1962 (FPF); 3 mi. W of Redfeather Lakes, on *Pinus flexilis, H & Hinds 409* in 1963 (FPF); 4.8 mi. W of Pingree rd. on Crown Point rd., on *Pinus flexilis, H 412* in 1963 (FPF); Pennock Cr. 2 mi. S of Pingree Park rd., on *Pinus flexilis, H 561* in 1964 (FPF); 5 mi. W of Redfeather Lakes, on *Picea engelmannii, H 189* in 1961 (FPF); 4 mi. W of Redfeather Lakes on *Picea engelmannii, H 406* in 1963 (FPF); SE of Chambers Lake, on *Picea engelmannii, Schacht* in 1962 (FPF); N Fork Poudre River, ca. 7 mi. W of Redfeather Lakes on *Picea engelmannii, H 559* in 1964 (FPF); 1 mi. E of Buckhorn Ranger Sta., on *Picea pungens, H 554* in 1964 (FPF). MOFFAT CO.: Cold Spring Mtn., 0.25 mi. E of Utah and 1.5 mi. S of Wyoming, *Brown* in 1965 (FPF). PARK CO.: Fairplay, *Gill FP 68140* in 1932 (FPF); 3 mi. NW of Fairplay, *H 447* in 1963 (FPF); Summit of Kenosha Pass on US 285, *H 448* in 1963 (FPF); 4 mi. NW of Wellington Lake on Estabrook rd., *H 2299* in 1989 (FPF); 6 mi. S of Boreas Pass, *Laut* in 1988 (FPF); 4.4 mi. N of Grant on Geneva Basin rd., *H 450* in 1963 (FPF) and on *Pinus aristata, H 449* in 1963 (FPF); 0.3 mi. E of Santa Maria, *H 451* in 1963 (FPF) and on *Pinus ponderosa, H 452* in 1963 (FPF); Payne Gulch, near Bailey, on *Pinus flexilis, Hill FP 68236* in 1932 (FPF). RIO BLANCO CO.: 1 mi. E of Wilson Park, *H & others 1385* in 1971 (FPF); 5 air mi. ENE of Buford, *H 1386* in 1971 (FPF). ROUTT CO.: Walton Cr. Campground, *Hinds 63-21* in 1963 (FPF); Steamboat Springs, *Galpin* in 1908 (FPF); Hahn's Peak, *Edmonston FP 188* in 1908 (FPF) and on *Picea engelmannii, Edmonston FP 199* in 1908 (ILL); near Trout Cr. Campground, 8 mi, W of Philipsburg, *H & others* in 1961 (FPF); 9 mi. E of Clark, *H 191* in 1961 (FPF); 4 mi. SE of Clark, *H 413* in 1963 (FPF); Seedhouse, E of Clark, *Weber 6725* in 1951 (COLO, WTU); 8 mi. E of Clark, *Weber 6093* in 1951 (COLO); near Steamboat Springs, *Greene & Richter 115* in 1962 (COLO); Lynx Pass Campground, *Laut* in 1970 (FPF). SAGUACHE CO.: 6 mi. E of Marshall Pass, *H 1485* in 1974 (FPF). SUMMIT CO.: Breckenridge, *Seay FP33403* in 1917 (FPF), *Mackenzie 78* in 1901 (MO, PH, RM, US); Dillon, *Shear 3764* in 1896 (RM); near Dillon, *W 3260* in 1962 (COLO); Dillon, *H 1640* in 1975 (FPF); Mt. Baldy near Breckenridge, *Henderson* in 1897-1909 (MO). COUNTY UNCERTAIN: Sawatch Range, *Brandegee* in 1880 (PH, UC); South Park, *Wolf & Rothrock 70* in 1873 (PH) and *Hall & Harbour 574* in 1862 (MO); Middle Park, *Patterson* in 1875 (PH) and *Torrey* in 1872 (MO); Latitude 39-41°, *Parry 574* in 1862 (US).

IDAHO

ADAMS CO.: Evergreen, *Hedgcock FP1908* in 1909 (FPF). BEAR LAKE CO.: 7 mi. NW of Liberty on Rte. 36, *H & Hinds 1007* in 1966 (FPF); 8.5 mi. NE of Georgetown in Georgetown Cyn., *H & others 1380* in 1971 (FPF). BENEWAH CO.: 1 mi. S of Emida, *Owenbey & Owenbey 2023* in 1940 (ARIZ, DS, MO, RSA, UC, US, WTU); S end of Coeur d'Alene Lake, col.? in 1891 (UC). BLAINE CO.: Near source of Wood River, *Henderson 3581* in 1895 (US); 17 mi. NW of Ketchum on Rte. 75, *H 1369* in 1971 (FPF). BOISE CO.: Idaho City, *Weir 8456* in 1917 (ILL); 21 mi. NE of Idaho City on Rte. 21, *H 1372* in 1971 (FPF). BONNER CO.: Priest Lake, *Hedgcock & Weir 8456* in 1917 (ILL); *Hedgcock & Weir FP 9489* in 1911 (FPF); and *Piper 3701* in 1901 (US). BONNEVILLE CO.: SW of Victor, *Peterson 62-14* in 1962 (FPF); 11 mi. NE of Swan Valley on Rte. 31, *H & Hinds 1120* in 1968 (FPF). CAMAS CO.: Boise River, 10 mi. NE of Elmore Co. boundary, *Peterson 62-51* in 1962 (FPF). CARIBOU CO.: Diamond Cr., 18 mi. NE of Soda Springs, *Mentz* in 1914 (ILL); 4 mi. W of Freedom, Wyoming on Rte. 34, *H & Hinds 1119* in 1968 (FPF). CASSIA CO.: 14 mi. W of Oakley on Rogerson rd., *H & Hinds 1005* in 1966 (FPF). CUSTER CO.: Redfish Lake, *Macbride & Payson 3654* in 1916 (MO, RM); Marsh Cr., 25 mi. NW of Stanley, *Cronquist 2829* in 1941 (MO); N fork of Big Lost River, about 15 mi. N of Ketchum, *Cusick 152* in 1928 (USFS) and ca. 18 mi. N of Ketchum, R-4 survey in 1979; Iron Bog Cyn., about 28 mi. W of Arco, *Jacobs 184* in 1931 (USFS); 8 mi. NW of Stanley on Rte. 21, *H 1370* in 1971 (FPF). FRANKLIN CO.: Franklin Basin, *Peterson 63-361* in 1963 (FPF) and *Holmgren 15554* in 1970 (OSC). FREMONT CO.: Eccles, near Pineview, *Hedgcock FP879* in 1909 (FPF); Big Springs, *Hedgcock FP 888* in 1909 (FPF); Buffalo For. Camp on Buffalo River, *Cronquist 1613* in 1929 (MO); 7 mi. N of Ashton on Rte. 20, *H 2275* in 1988 (FPF). IDAHO CO.: Warren Divide, 4 mi. from Warren, *Stillinger & Root* in 1920 (ILL); 14 mi. S of Salmon River on US 95, *Peterson 62-47* in 1962 (FPF); 7 mi. N of Burgdorf on Salmon River rd., *H 972* in 1966 (FPF). KOOTENAI CO.: Coeur d'Alene, *Weir FP17046* in 1914 (FPF), *Weir 8442* in 1917 (FPF, RM, US), and *Weir 9829* in 1918 (FPF, ILL), and on *Pinus ponderosa, Weir 2387*, n.d. (FPF, ILL); Twin Lakes, *Hubert (Weir 10821)* in 1919 (ILL); *Rathdrum & others 892* in 1892 (DS, US); Hayden Lake, *Weir 8440* in 1917 (FPF, ILL); without locality, *Sandberg 9358* in 1892 (MO, RM, WTU) and *Lieberg* in 1892 (PH). LATAH CO.: 7 mi. NE of Troy, *Helmers 9-39* in 1939 (ID). LEMHI CO.: Gibbonsville, *Wolpert* in 1917 (ILL); 4 mi. N of Gibbonsville on US 93, *H & Hinds 1124* in 1968 (FPF); 20-25 mi. N of Salmon on US 93, *Gill & Hinds FP 89981* in 1951 (FPF); Parker Mtn., ca. 18 mi. WNW of Challis, [listed as Custer Co.], *Macbride & Payson 3270* in 1916 (MO, RM, US); SW of Salmon, between Williams Cr. and Moccasin Cr., *Krebill 127* in 1964 (FPF); Morse Cr., about 9 mi. NE of May, *Cusick 74* in 1929 (USFS); 4 mi. E of Gibbonsville, on *Pinus ponderosa, Peterson 63-295* in 1963 (FPF); Ridge rd., 9 air mi. NW of Salmon, *H 2433* in 1990 (FPF). MADISON CO.: Hawley Ranger Sta., *Peterson 62-17* in 1962 (FPF). POWER CO.: Sublett Range, 4.5 mi. N of Sublett Guard Sta., *Mathiasen 8917* in 1989 (FPF). SHOSHONE CO.: St. Joe Nat. For., Fishook Cr., below Lick Cr. Lookout, *Gill FP 68200* in 1932 (FPF). TETON CO.: Packsaddle Cyn., W of Driggs, *Peterson 62-10* in 1962 (FPF). TWIN FALLS CO.: 15 mi. E of Rogerson on Oakley rd., *H & Hinds 1004* in 1966 (FPF); 30 mi. W of Oakley, *Benlow* in 1917 (FPF, ILL); about 13 air mi. E of

Rogerson, *Gierisch 800* n.d. (USFS). VALLEY CO.: Deadwood Basin, *Korstian* in 1918 (FPF, ILL); 3 mi. NW of McCall on shore of Payette Lake, *H 976* in 1966 (FPF); Smith Ferry, *Benlow* in 1917 (ILL); 13 mi. E of Cascade, on *Pinus ponderosa*, *Jones 5076* in 1934 (UC, WTU). COUNTY UNCERTAIN: Middle Fork of Salmon River, *Trey* in 1941 (US); Ross, *Weir 8389* in 1915 (ILL); Lemhi Nat. For., on *Pinus flexilis*, *Weir* in 1917 (ILL).

MONTANA

BEAVERHEAD CO.: Pioneer Mts., 11 mi. S of Dewey on Canyon Cr. rd., *H & Wicker 949* in 1966 (FPF); 2.5 mi. E of Lemhi Pass, *H & Hinds 1121* in 1968 (FPF); 9 mi. S of Wise River on Wise River rd., *H 2203* in 1987 (FPF). BROADWATER CO.: Elkhorn Mts., 15 mi. W of Townsend, *Booth* in 1958 (MONT). CARBON CO.: Woohoe Cr., near Red Lodge, *Langnor* in 1917 (ILL); Pryor Mts., *Corey & Flint* in 1978 (FPF). CASCADE CO.: Neilhart, *Langnor* n.d. (ILL). DEERLODGE CO.: 3 mi. N of US 10A on Warm Springs rd., *H & Wicker 951* in 1966 (FPF); Warm Springs Ranger Sta., *Peterson 62-18* in 1962 (FPF). FLATHEAD CO.: Glacier Nat. Park: Bowman Lake, *Jones* in 1910 (RSA) and McDonald Lake, *Standley 16335* in 1919 (US); Lake Cr. Trail ca. 12 air mi. S of Roosevelt Memorial, *Pierce 267* in 1926 (USFS); Hungry Horse Ranger Sta. on Rte. 2, *H 2198* in 1987. GALLATIN CO.: West Yellowstone, *Payson & Payson 1937* in 1920 (MO, RM) and *Hawkins 426* in 1922 (US); 1 mi. SW of West Yellowstone, *Whitman 952* in 1931 (USFS); Bridger Mts., 19 mi. N of Bozeman on Rte. 86, *H 2202* in 1987 (FPF); Hyalite Cyn., *Weber 1957* in 1941 (COLO); Shoefelt Ranger Sta., 9 mi. SE of Bozeman, *Hedgcock FP 4338* in 1910 (FPF); Ole Oleson Cyn., *Jameson 125* in 1944 (MONT); Specimen Cr., *Swingle* in 1933 (MONT); 5 mi. WNW of West Yellowstone, on *Pinus albicaulis*, *Dooling* in 1976 (FPF). GLACIER CO.: 7.8 mi. S of St. Mary on US 89, *H 89* in 1961 (FPF); 0.7 mi. S of Going-to-Sun Chalets, *Gill FP 68205* in 1932 (FPF); 3 mi. S of St. Mary on Rte. 89, *W 4363* in 1969 (FPF, UT). GRANITE CO.: Emerine Lookout rd., on *Pinus albicaulis*, *H & Wicker 952* in 1966 (FPF); Skalkaho Pass, *Peterson 62-60* in 1962 (FPF); Garnet, *Scheuber* in 1902 (UC, US) and *Schneider* in 1902 (MONT); Stumptown Cr. near Philipsburg, *Hughes* in 1917 (FPF, ILL); Georgetown, *Wolpert* in 1917 (FPF, ILL); 8 mi. NW of Phillipsburg, on *Pinus albicaulis*, *Wilkerson & Mayberry 7801* in 1978 (FPF). HILL CO.: Rocky Boy Indian Res., Rocky Boys Campground, *Dooling* in 1972 (FPF). JUDITH BASIN CO.: Little Belt Mts., about 24 mi. NE of White Sulfur Springs, *Petroni & Dooling* in 1982 (FPF). LAKE CO.: 38 mi. N of Seeley Lake on Rte. 83, *H 2199* in 1987 (FPF). LEWIS AND CLARK CO.: Flesher Pass on Rte. 279, *H 2201* in 1987 (FPF). LIBERTY CO.: Sweetgrass Hills, E Butte, Devils Chimney, *Kuijt 4920* in 1975 (FPF). LINCOLN CO.: Libby, *Smith* in 1915 (ILL). MEAGHER CO.: Little Belt Mts.; Sheep Cr. *Langnor* in 1918 (ILL); Adams Cr., 16 mi. N of White Sulfur Springs, *Gill FP89984* in 1948 (FPF); Castle Mts., *Corey & Mayberry* in 1978 (FPF); Castle Mts., on *Pinus albicaulis*, *Mayberry & Flint* in 1978 (FPF). MINERAL CO.: St. Regis, *Weir 7473* in 1918 (ILL); 6 mi. W of St. Regis on US 10, *H & Wicker 954* in 1966 (FPF); E of Savenac Nursery, near Haugan, *Hubert* in 1915 (ILL); De Borgia, *Hughes* in 1917 (FPF, ILL); Deer Park Range, head of Deer Cr., *Stickney 3670* in 1977 (MONT). MISSOULA CO.: Lolo Hot Springs, *Barkley & Barkley 3505* in 1938 (MO, UC, US); Seeley Lake *Weir 9780* in 1918 (ILL); 1 mi. SW of Lolo Hot Springs on Rte. 12, *H & Laut 1290* in 1970 (FPF); TV Mtn., 9 mi. N of Missoula, *Stickney 1323A* in 1966 (MONT); Lolo Hot Springs, on *Pinus ponderosa*, *Dooling* in 1982 (FPF); Lolo Nat. For., Seeley Lake Ranger District, on *Pinus ponderosa*, *Dooling* in 1985 (FPF). PARK CO.: Specimen Cr. *Swingle* in 1933 (CS, RM, WTU); Absoroka Range, 10 mi. S of Livingston, *Booth* in 1958 (MONT). PHILLIPS CO.: Little Rocky Mts., Midvale, *Umbach 594* in 1903 (ARIZ, DS, RM, US). POWELL CO.: 6 mi. W of Lincoln on Rte. 200, *H 2200* in 1987 (FPF); Near Rock Cr., W of Deer Lodge, *Trask 253* in 1962 (MONT). RAVALLI CO.: Lost Trail Pass, on *Pinus flexilis*, *Dooling* in 1982 (FPF); Darby, on *Pinus ponderosa*, *Weir 2382* in 1916 (ILL) and on *Pinus albicaulis*, *Weir 2379* in 1916 (ILL); Alta, *Jones* in 1909 (US); Skalkaho Trail, E of Hamilton, *Young 624* in 1926 (MONT); 19 mi. E of Darby, on *Pinus albicaulis*, *Filios* in 1976 (FPF); N fork of Willow Cr., 10 mi. E of Corvallis, on *Pinus ponderosa*, *Currey* in 1985 (FPF). SANDERS CO.: Thompson Falls, *Hedgcock & Weir FP9443* in 1911 (FPF); Lolo Nat. For. boundary, 2 mi. W of Hot Springs, *H & others 2262* in 1988 (FPF), and on *Pinus ponderosa*, *H 2263* in 1988 (FPF). SILVER BOW CO.: Highland Mts., 5 mi. SE of US 91 on Highland lookout rd., *H & Wicker 950* in 1966 (FPF). COUNTY UNCERTAIN: Big Adrian Gulch near Helena, *Starz* in 1893 (DS).

NEVADA

COUNTY UNCERTAIN: Without locality, Wheeler in 1872 (US).

OREGON

BAKER CO.: Jim Cr. fork of Eagle Cr., 30 mi. NE of Baker, *Graham* in 1965 (FPF); Horse Cr., 20 mi. W of Baker, *Graham* in 1965 (FPF). CLACKAMAS CO.: Lemiti Butte, SE corner of Co., *Thompson* in 1968 (FPF); 0.3 mi. E of jct. of Rts. 35 and 26 on Rte. 35, *H 2225* in 1987 (FPF). CROOK CO.: N Big Meadow, *Nelson 845* in 1905 (RM); Laidlow area, *Whited 3171* in 1906 (US). DESCHUTES CO.: 18 mi. W of Bend, *Ferris & Duthie 467* in 1919 (DS, RM); Head of Fall River, 9 mi. NW of La Pine, *Peck 14322* in 1925 (CAS, PH); 0.5 mi. E of Todd Lake, *H 2344* in 1989 (FPF); 3 mi. E of McKenzie Pass on Rte. 242, *H & others 2349* in 1989 (FPF); Pistol Butte, 9 mi. N of La Pine, *H & Scharpf 1260* in 1969 (FPF) and on *Pinus ponderosa*, *H & Scharpf 1261* in 1969 (FPF); China Hat rd. between East Lake and Arnold Ice Caves, *Knutson* in 1978 (FPF); 6 mi. N of Waldo Lake, *Knutson 99* in 1980 (FPF); China Hat, *Knutson* in 1978 (FPF) and on *Pinus ponderosa*, *Knutson* in 1978 (FPF); 10 mi. NW of Sisters on US 126, *H & W 614* in 1964 (FPF); 21 mi. S of Bend on US 97, *H & W 618* in 1964 (FPF); Pringle Butte, *H 988* in 1966 (FPF); 4 mi. E of

McKenzie Pass on Rte. 242, *H & Hinds 993* in 1966 (FPF); Three Cr. Lake, on *Pinus albicaulis*, *H 1926* in 1979 (FPF); 1/4 mi. E of Todd Lake, *H 2344* in 1989 (FPF); 3 mi. E of McKenzie Pass on Rte. 242, *H 2349* in 1989 (FPF). DOUGLAS CO.: Diamond Lake, *Henderson 11501* in 1929 (PH); 20 mi. NE of Union Cr. on Rte. 230, *H 1143* in 1968 (FPF); Lemolo Lake, *Knutson* in 1978 (FPF); 2 mi. W of Lemolo Lake Jct. on Rte. 138, *H 2338* in 1989 (FPF); 16 mi. N of Union Cr. on Rte. 230, *Mathiasen 8615* in 1986 (FPF). GRANT CO.: Whitman Nat. For., Bates, *Boyce FP 40120* in 1920 (OSC) and *Boyce 703* in 1920 (FPF); Dixie Butte rd., 5 mi. N of US 26, *H 979* in 1966 (FPF); 10 mi. N of John Day, *Graham* in 1964 (FPF); 15 mi. N of John Day, *Graham* in 1964 (FPF); John Day Exp. For., 9 mi. E of Bates, *Childs 245* in 1955 (OSC); Dixie Pass on Rte. 26, *H & W 581* in 1964 (FPF); Dry Meadow, ca. 24 air mi. E of Seneca, *H & Scharpf 1269* in 1969 (FPF). HARNEY CO.: [was Crook Co.], Black Butte, 27 mi. NW of Burns, *Cusick 2691* in 1901 (MO, RSA, RM, UC, US). HOOD RIVER CO.: Dufur Jct., 12 mi. S of Mt. Hood village, *H 2224* in 1987 (FPF); 0.8 mi. S of Clark Cr. on Rte. 35, *Mathiasen 9103* in 1991 (FPF). JACKSON CO.: 22 mi. E of Ashland on Lake of the Woods rd., *H & W 871* in 1966 (FPF); 5 mi. E of Union Cr. on Rte. 62, *H & others 1375* in 1971 (OSC). JEFFERSON CO.: Metolius area, *Gill FP68190* in 1932 (FPF). JOSEPHINE CO.: Waldo, on *Pinus jeffreyi*, *Weir 2384* in 1916 (FPF, ILL); Oregon Mtn., 14 mi. SW of Cave Jct., on *Pinus attenuata*, *Weir 2376* in 1916 (FPF, ILL) *and 2374* (ILL). KLAMATH CO.: Crater Lake Nat. Park, *Gill FP 68185* in 1932 (FPF); NE of Crescent Lake, *Overbay FP 68282* in 1932 (FPF); 15 mi. SW of Crescent Lake, *Childs 67* in 1937 (OSC); Crescent, *Peck 9594* in 1928 (CAS, MO, PH); Crescent, *Boyce FP 40198* in 1921 (OSC); 7 mi. S of Crescent, *Peck 21639* in 1943 (UC); 6 mi. S of Rte. 58 on Windigo Pass rd., *H & W 620* in 1964 (FPF); 0.5 mi. W of Rte. 97 opposite Silver Lake rd., *H 2365* in 1989 (FPF); 1 mi. S of Pelican Butte rd. on Cold Springs rd., *H 2374* in 1989 (FPF); 5 mi. W of US 97 on Rte. 230, *H & W 623* in 1964 (FPF); S of Sand Cr., 5 mi. N of Yamsey Ranger Sta., *Childs 14* in 1947 (OSC); Fort Klamath, *Walpole 234* and *323* in 1899 (US) and *Meinecke* in 1912 (FPF); Buck Lake, *Applegate 2478* in 1898 (US); 7 mi. N of Fort Klamath, *Meinecke* in 1913 (FPF); 6 mi. ESE of Sugar Pine Mtn., *Knutson & Tinnin DM59* in 1978 (FPF) and, on *Pinus ponderosa*, *Knutson & Tinnin DM60* in 1978 (FPF); 1.5 mi. SSW of Sugar Pine Mtn., *Knutson & Tinnin DM58* in 1978 (FPF); 4 mi. WSW of Sugar Pine Mtn., *Knutson & Tinnin DM55* in 1978 (FPF); Crater Lake, on *Pinus ponderosa*, *Dachnowski-Stokes* in 1913 (US); 0.5 mi. W of US 97, opposite Silver Lake rd., *H 2365* in 1989 (FPF); 1 mi. S of Pelican Butte rd. on Cold Springs rd., *H 2374* in 1989 (FPF). LAKE CO.: Dairy Cr. Guard Sta., 13 mi. NE of Quartz Pass, *Steward & Steward 7471* in 1958 (DS, US); NE edge of Sycan Marsh, 18 mi. S of Silver Lake, *Knutson & Tinnin DM 65* in 1978 (FPF). LANE CO.: 7 mi. N of Waldo Lake on Pacific Crest Trail, *Knutson* in 1980 (FPF). LINN CO.: 0.5 mi. W of Rte. 22 near jct. with Rte. 20, *Steward 6605* in 1953 (RSA, WTU); 5 mi. W of Santiam Pass at jct. of Rts. 22 and 20, *Tinnin* in 1979 (FPF) and *H 1374* in 1971 (FPF). MARION CO.: Lemiti Cr., 11 mi. NE of Breitenbush, *Knutson & Tinnin DM39* in 1977 (FPF). UMATILLA CO.: Langdon Lake, 20 mi. E of Weston on Rte. 204, *H & W 591* in 1964 (FPF). UNION CO.: 3 mi. SE of Kamela, *H & W 586* in 1964 (FPF). WALLOWA CO.: 6 mi. SE of Wallowa, *Sampson & Pearson 21* in 1907 (US); Billy Meadows, 30 mi. NNE of Enterprise, *Coville 2487, 2488, 2489, 2490,* and *2491* in 1907 (US); Target Springs, 6 mi. SE of Joseph, *Mason 7252* in 1965 (ASU); Ferguson Ridge, *Mason* in 1966 (ASU). WASCO CO.: Bear Springs, *Hansbrough FP68270* in 1931 (FPF); 20 mi. NW of Warm Springs on US 26, *H & W 612* in 1964 (FPF). COUNTY UNCERTAIN: Big Meadows, Deschutes River, *Leiberg 520* in 1894 (DS, MO, RSA, RM, US); Blue Mts., *Nuttall* n.d. (MO, PH).

UTAH

CACHE CO.:jct. of Rte. 89 and Beaver Mtn. rd., *Mielke* in 1952 (UC); 6.5 mi. N of Tony Grove jct. on Rte. 89, *H 2302* in 1989 (FPF). DAGGETT CO.: 45.5 mi. S of Manila on Rte. 44, *Greene & Richter 116* in 1962 (COLO, FPF); 19 mi. S of Manila on Rte. 44, *H 568* in 1964 (FPF) and on *Pinus ponderosa*, *H 569* in 1964 (FPF); Manila Ranger District, 1 mi. E of Leona Cr., on *Pinus ponderosa*, *Krebill 726* in 1968 (FPF). SUMMIT CO.: Kamas, *Hedgcock FP 9339* in 1911 (FPF) and *FP 22718* in 1916 (FPF); 8 mi. E of Kamas, on *Pinus ponderosa*, *Hedgcock FP22719* in 1916 (FPF, UC); 20 mi. E of Kamas on Rte. 150, *Peterson 62-4* in 1962 (FPF) and on *Pinus ponderosa*, *Peterson 62-5* in 1962 (FPF); Kamas Cyn. at Shingle Cr., *Peterson 65-90* in 1965 (FPF), on *Pseudotsuga menziesii*, *Peterson 65-88* in 1965 (FPF), and *Krebill* in 1969 (FPF), and on *Picea pungens*, *Peterson 65-89* in 1965 (FPF); Uinta Mts., 6 mi. S of Wyo. boundary on Rte. 150, *H 1188* in 1969 (FPF). COUNTY UNCERTAIN: Uinta Mts., *Greenman & Greenman 4650* in 1931 (MO); Little Bush Cr. Knob, Ashley Nat. For., [Uintah Co.?], *Harrison & Larson 7859* in 1936 (COLO).

WASHINGTON

CHELAN CO.: Washington For. Reserve, head of Twenty-Five-Mile Cr., W side of Chelan Lake near Stormy Mtn., *Gorman 576* in 1897 (US); 4 mi. N of Blewett Pass on Rte. 97, *W 4371* in 1969 (UT, FPF); 18 mi. NE of Telma, *Tinnin & Knutson* in 1976 (FPF). FERRY CO.: Sherman Cr. near Growden, *Wicker* in 1961 (WSP); Boulder Cr., *Eggleston 10599* in 1914 (US); 1.5 mi. W of Sherman Pass on Rte. 30, *H & others 1131* in 1968 (FPF). KITTITAS CO.: Ellensburg, *Brandegee 1069* in 1883 (US); Near Swauk Pass, on US 97, 18 mi. N of US 10, *Wicker* in 1966 (FPF); on Rte 97 S of Blewett Pass, 1.0 mi. N of jct. of USFS 2208, *Tinnin & Knutson* 1976 (FPF); N of Salmon la Sac, *Jacobsen 83* in 1983 (WS). KLICKITAT CO.: Falcon Valley, *Suksdorf* in 1883 (PH, US). OKANOGAN CO.: 8 mi. E of Methow, *Graham* in 1964 (FPF); Varden Cr., 6 mi. W of Mazama on Rte. 20, *Mathiasen 74-7* in 1974; 18.6 mi. W of jct. of Rts. 97 and 20 on Rte. 20, *Tinnin & Knutson* in 1976 (FPF); 2.9 mi. S of Okanogan Nat. For. boundary and 0.9 mi. N of Colville Indian Res. boundary, *Tinnin & Knutson* in 1976 (FPF) and on *Pinus ponderosa*, *Tinnin & Knutson* in 1976 (FPF); 10.7 air mi. NNE of Winthrop, *Tinnin & Knutson* in 1976 (FPF); 5.9 mi. E of Washington Pass on Rte. 20, *Tinnin & Knutson* in 1976 (FPF); 0.75 mi. W of Rte. 20 on Cutthroat Lake rd.. *Mathiasen 9004* in 1990 (FPF); 3 mi. E of Loup Pass on Rte. 20, *H 2209* in 1987 (FPF); Schneider Cr. rd., 6 air mi. W of Conconully, *H 2410* in 1990 (FPF); Middle Fork of Boulder Cr., 12 air mi. NE of Winthrop, *H 2411* in 1990 (FPF). PEND OREILLE CO.: 3 mi. SW of Newport on US 2, *H & Wicker 1126* in 1968 (FPF). SKAMANIA CO.: SW of Mt. Adams, col.? in 1915 (ILL). SPOKANE CO.: 21 mi. SW of Newport on US 2, *H & Wicker 1127* in 1968 (FPF); Little Spokane River, *Hedgcock FP67206* in 1934 (FPF); 5 mi. SE of Deer Park on US 395, *H & others 1128* in 1968 (FPF). STEVENS CO.: Northport, *Hedgcock FP 47157* and *FP 47756* in 1928 (FPF); 13 mi. E of Northport, *Hedgcock FP 49544* in 1929 (FPF); 12 mi. E of Northport, *Hedgcock FP 47529* in 1928 (FPF); Alladin, 15 mi. NE of Colville, *Hedgcock FP 54116* in 1931 (FPF); Colville, *Hedgcock FP 59245* in 1933 (FPF); 6.7 mi. from Colville, SW along extension of rd. 357, *Tinnin & Knutson* in 1976 (FPF). WHATCOM CO.: On Rte. 20 at trail head to Ross Lake and Ross Dam, *Tinnin & Knutson* in 1976 (FPF); 17 mi. E of Newhalem on Rte. 20 at Ross Dam trail head, *H 2210* in 1987 (FPF). YAKIMA CO.: Big Klickitat River, N of Mt. Adams, *Henderson 2539* in 1892 (WTU); 7 mi. E [as "W"] of Chinook Pass, *Thompson 15105* in 1940 (CAS, MO, PH, RSA, UC, US, WS, WTU); Tieton Cr., 2 mi. SW of Tieton Lake, *H & W 599* in 1964 (FPF); 1 mi. W of Rimrock, N of Tieton Lake, *Stewart* in 1968 (FPF); Lodgepole Campground, 19.9 mi. W of Cliffdell on Rte. 410, *Tinnin & Knutson* in 1976 (FPF); 8 mi. NE of Trout Lake on Bird Cr. Meadows rd., *H 2218* in 1987 (FPF). COUNTY UNCERTAIN: Cascade Mts., *Tweedy* in 1882 (MO).

WYOMING

ALBANY CO.: Medicine Bow Mts.: Centennial, *Hedgcock FP 15834* in 1914 (FPF, UC); Lake Cr., *Hedgcock FP 15849* in 1914 (FPF); Fox Park, *Hedgcock FP 15965* in 1914 (FPF, RSA, UC), *Hedgcock FP 15848* in 1914 (FPF, UC), *Evans FP 17832* in 1915 (FPF), *Hedgcock & Johnston FP 26425* in 1917 (FPF), *Evans FP 17843* in 1915 (FPF); Libby Lodge, *Ownbey 875* in 1935 (RM); Mountain Home, *Osterhout 2523* in 1897 (RM); 6 mi. W of Centennial on Rte. 130, *Greene & Richter 126* in 1962 (COLO, FPF); Libby Cr., *Williams 2402* in 1935 (MO, US). Laramie Mts.: E of Laramie, *Weir 9873* in 1918 (FPF, ILL) and, on *Pinus flexilis*, *Weir 9874* in 1918 (FPF); head of Pole Cr., *Nelson & Nelson 6833* in 1899 (RM); Sherman, *Letterman* in 1884 (PH); Boulder Ridge, 7 mi. SW of Tie Siding, *H 285* in 1962 (FPF); Pelton Cr., 5 air mi. W of Mountain Home, *H 1092* in 1968 (FPF); La Bonte Cyn., 17 mi. W of Estabrook, *Brown & Hoffman* in 1975 (FPF), and on *Pinus ponderosa*, *Brown & Hoffman* in 1975 (FPF); E of Laramie, on *Pinus ponderosa*, *Weir 9875* in 1918 (FPF, ILL). Laramie Mts., 5 mi. E of Interstate 80 on Happy Jack rd., *H & Bailey 1009* in 1966 (FPF) and, on *Pinus ponderosa*, *H & Bailey 1010* in 1966 (FPF). Pole Mtn.: on *Pinus ponderosa*, *Simmons* in 1917 (ILL); near Happy Jack, on *Pinus ponderosa*, *H 193* in 1960 (FPF) and *Porter 8756* in 1961 (RM). BIGHORN CO.: Bighorn Mtns., Meadowlark Lake, *H 265* in 1962 (FPF). CARBON CO.: Encampment, *Edmonston FP 51* in 1908 (FPF); 2 mi. E of Medicine Bow Lodge, *Greene & Richter 125* in 1962 (COLO, FPF); Wagonhound Cyn., 7 mi. SW of Arlington, *H & Mark 1336*, in 1971 (FPF); 3 mi. NW of Seminoe Dam, *H 1694* in 1976 (FPF); Sierra Madre Mts., 2.4 mi. W of Sandstone Ranger Sta. on Rte. 70, *H 1799* in 1977 (FPF), and 5 mi. N of Divide Peak, *H 1801* in 1977 (FPF); Shirley Mts., 0.3 mi. N of Cave Cr., *H 1803* in 1977 (FPF). CONVERSE CO.: Laramie Mts., Cold Springs, *Simmons* in 1917 (ILL). FREMONT CO.: Popo Agie Campground, ca. 17 air mi. SSW of Lander, *Stewart* in 1967 (FPF); Fossil Hill, ca. 12 air mi. SW of Lander, *Stewart* in 1967 (FPF): 5 mi. E of Togwotee Pass on US 287, *H 272* in 1962 (FPF); Horse Cr., 14 mi. NW of Dubois, *H 273* in 1962 (FPF); Wiggins Fork, 16 mi. N of Dubois, *H 275* in 1962 (FPF); Long Cr., 21 mi. WNW of Dubois, *H 276* in 1962 (FPF); 1 mi. SE of Sheridan Guard Sta., *H 278* in 1962 (FPF); T Cross Ranch, Dubois, *Cox FP 68228* in 1931 (FPF); South Pass, Slate Cr. area, 2 mi. N of Rte. 28 on Louis Lake rd., *H 1628* in 1975 (FPF); 12 air mi. SSE of Jeffery City, *H 1691* in 1976 (FPF); 0.25 mi. N of Cottonwood Campground, *H 1692* in 1976 (FPF); Green Mts., 10 air mi. SW of Jeffery City, *H 1693* in 1976 (FPF); Wiggins Fork, Shoshone Nat. For., on *Pinus flexilis*, *H 274* in 1962 (FPF); 18 mi. WNW of Dubois, on *Pinus flexilis*, *H 1631* in 1975 (FPF); 23 mi. WNW of Dubois, on *Pinus flexilis*, *Stewart* in 1964 (FPF); Snowshoe Cr., 11 air mi. W of Dubois, on *Pinus albicaulis*, *H 1634* in 1975. JOHNSON CO.: Bighorn Mts.: Duck Cr. Burn, ca. 20 mi. W of Buffalo on US 16, *H 264* in 1962 (FPF); 2 mi. E of Elgin Park, on *Pinus ponderosa*, *Stewart* in 1965 (FPF); Bighorn Nat. For., East Mesa area, on *Picea engelmannii*, *Cook* in 1977 (FPF). LINCOLN CO.: 28 mi. W of La Barge on La Barge Cyn. rd., *H & Hinds 1118* in 1968 (FPF); 7 mi. S of Smoot on Rte. 89, *H 948* in 1966 (FPF); Meadow Cr. Ranger Sta., ca. 9 air mi. E of Bedford, *McDonald 737* in 1927 (USFS); 13 mi. W of Hoback Jct. on Snake River, *W 4361* in 1969 (FPF, UT). NATRONA CO.: N Entrance Casper Mtn. Park, *Peterson 125-61* on 1961 (FPF); Casper Mtn. Park, *H 1635* in 1975 (FPF). PARK CO.: Cody Cyn. at Mormon Cr., *H 266* in 1962 (FPF); Cody Cyn., Pahaska Teepee, on *Pinus flexilis*, *Gill & Davidson* in 1954 (FPF); 6.5 mi. SW of Sunlight Ranger Sta. in Sunlight Cr. Cyn., *H 1861* in 1978 (FPF). SHERIDAN CO.: Bighorn Mts., Burgess Ranger Sta., 27 air mi. W of Sheridan, *Stewart* in 1966 (FPF); E fork of S Tongue River, 20 air mi. W of Big Horn, *Stewart* in 1966 (FPF). SUBLETTE CO.: 8.8 mi. N of Pinedale on Faler Cr. rd., *H 545* in 1963 (FPF); Pine Cr., near inlet to Fremont Lake, on *Pinus flexilis*, *Krebill 538* in 1967 (FPF); The Rim, 13.4 mi. SE of Bondurant on US 189, *H 546* in 1963 (FPF) and on *Pinus flexilis*, *H 547* in 1963 (FPF); 12.3 mi. E of US 89 on US 189, *H 548* in 1963 (FPF). TETON CO.: Jackson Hole, *Reed 1831* in 1948 (RM); Jackson Hole, Coulter Bay Jct., *H 271* in 1962 (FPF); 10.7 mi. NE of Jackson, *H 549* in 1963 (FPF); 4.9 mi. N of Moose, *H 550* in 1963 (FPF); 11.2 mi. W of Togwotee Pass on US 287, *H 551* in 1963

(FPF); 3 mi. S of Jenny Lake, *Greene & Richter 118* in 1962 (COLO, FPF); 1 mi. N of Teton Nat. Park on US 287, *Greene & Richter 119* in 1962 (COLO, FPF); Double Diamond Ranch near Moose, *Williams* in 1963 (RM); Teton Nat. Park, N of Jackson Lake Lodge, *Oswald 1202* in 1964 (MONT); 5.5 mi. E of Alta on Grand Targhee Ski Area rd., *H 2455* in 1992 (FPF). UINTA CO.: Black Fork Camp, SE of Evanston, *Haugl* in 1916 (ILL). YELLOWSTONE NAT. PARK: Fire Hole Basin, *Hayden Expedition* in 1872 (PH); Fountain Geyser, *Oleson 328* in 1904 (RM), and *Hawkins 417* in 1922 (MONT); Hayden Valley, *Hawkins* in 1925 (MONT); Upper Basin, *Cooper 106y* in 1906 (RM); Sylvan Pass, *H 267* in 1962 (FPF) and on *Pinus flexilis*, *H 268* in 1962 (FPF); Yellowstone Lake Lodge, *H 269* in 1962 (FPF); Lewis River, 7 mi. N of S entrance on US 287, *H 270* in 1962 (FPF); Upper Madison, *Rydberg & Bessey 3938* in 1897 (PH, RM, US); Madison River, *Nelson & Nelson 5515* in 1899 (RM, MO, UC, US); Mammoth Hot Springs, *Greene & Richter 121* in 1962 (COLO, FPF); 8 mi. W of Cyn., *Greene & Richter 122* in 1962 (COLO, FPF); 1 mi. E of Fishing Bridge, *Greene & Richter 124* in 1962 (COLO, FPF); 1 mi. N of Fishing Bridge, on *Pinus flexilis*, *Krebill & Hendrickson* in 1969 (FPF); Geyser Basin, Firehole River, *Jones 5372* in 1934 (WTU); Upper Geyser Basin, *Setchell* in 1905 (UC); Yellowstone Lake, *Hayden* in 1871 (PH); Cache Cr., *Tweedy 449* in 1885 (UC); Lake Fork, *Hayden* in 1860 (MO); Tower Falls, *W 4362* in 1969 (FPF, UT); (without locality) *Forwood* in 1882 (MO) and *Mearns 4513* in 1902 (US). COUNTY UNCERTAIN: Hebron, *Hedgcock & Johnston FP26433* in 1917 (FPF); near E entrance, Yellowstone Nat. Park, *Greene & Richter 123* in 1962 (COLO); Copperton, *Garrett* in 1918 (ILL); Copper City, *Garrett* n.d. (UT).

4. *Arceuthobium apachecum*

All collections on *Pinus strobiformis.*

MEXICO

COAHUILA

Sierra del Carmen, Ocampo, *H & others 1032* in 1967 (FPF).

UNITED STATES

ARIZONA

APACHE CO.: 4 mi. S of Eagar on Big Lake rd., *H & Lightle 210* in 1962 (FPF); Escudilla Mtn., *Andresen & Simpson 1787* in 1962 (FPF); 2 mi. E of Big Lake, *H 822* in 1965 (FPF); 2 mi. E of Green Peak, *H 1452* in 1973 (FPF) and *Mathiasen 7629* in 1976 (FPF); 3.7 mi. E of Rte. 666 on Apache Nat. For. rd. 56, *Mathiasen 7621* in 1976 (FPF); 6.0 mi. S of Alpine on Rte. 666, *Mathiasen 8117* in 1981 (FPF); Big Lake, *Mathiasen 7543* in 1975 (FPF). COCHISE CO.: Chiricahua Mts.: without locality, *Gill & Ellis FP 89432* in 1940 (FPF); Rustler Park, *Ellis & Gill FP 89404* in 1939 (FPF), *Ellis & Gill FP 89423* in 1939, and *Andresen & Niles 631* in 1960 (FPF); Onion Saddle, *Mielke & Ellis FP 89697* in 1944 (FPF), *Mielke & Ellis FP 89965* in 1944 (FPF), *Gilbertson* in 1968 (FPF), and *H & Lightle 156* in 1962 and *1107* in 1968 (FPF); Chiricahua Wilderness Area, *Mathiasen 75-2* in 1975 (FPF); Anita Peak, *Leithliter 105 & 368* in 1976 (ASU). GRAHAM CO.: Graham Mts.: *Ellis FP 89401* in 1939 (FPF), *Ellis FP 89415* in 1939 (FPF), and *Ellis FP 89431* in 1939 (FPF); Treasure Park, *Ellis FP 89429* in 1939 (FPF), *Stouffer & Gill FP 68292 and FP 68293* in 1934 (FPF), and *Gill FP 89313* in 1936 (FPF); 0.5 mi. E of Hospital Flat, *H & Lightle 228* in 1962 (FPF) and *1105* in 1968 (FPF). GREENLEE CO.: Blue Summit, *Gill FP 68306* in 1934 (FPF) and *Ellis FP 89413* in 1939 (FPF); 1 mi. S of Mogollon Rim on US 666, *Lightle 64-21* in 1964 (FPF); 4 mi. N of Reno Lookout, *H 1453* in 1973 (FPF); on For. Service rd. 37, 2.3 mi. NW of Rte. 666, *Mathiasen 7913* in 1979 (FPF). PIMA CO.: Santa Catalina Mts.: (without locality), *Hedgcock FP 9782* in 1911 (FPF, ILL) and *Shreeve* in 1908 (ARIZ); Mt. Lemmon, *Peterson 62-145* in 1962 (FPF) and *Weiss* in 1973 (FPF); Soldier Camp, *Goodding* in 1934 (RM), *Mielke & Ellis FP 89696* in 1944 (FPF), and *Gill FP 68128* in 1932 (FPF); head of Marshall Gulch, *Gill FP 68130* in 1932 (FPF); Bear Wallow, *H & Lightle 167* in 1962 (FPF), *Morrow 7501* in 1975 (FPF), and *Mathiasen 7633* in 1976 (FPF); near summit of Mt. Lemmon, *H & others 1110* in 1968 (FPF) and *Mathiasen 7558* in 1975 (FPF); Summit of Mt. Bigelow, *Pinkava and Lehto 6153* in 1966 (ASU). Rincon Mts., Mica Mtn., *Ela* in 1968 (FPF). SANTA CRUZ CO.: Santa Rita Mts.: *Mathiasen 74-26, 74-27, 74-28*, and *74-29*, in 1974 (FPF); 0.25 mi. N of Josephine Saddle on new trail to Madera Cyn., *H & Mathiasen 1759* in 1976 (FPF); Baldy Saddle, *Mathiasen 7556* in 1975 (FPF).

NEW MEXICO

CATRON CO.: 6 mi. S of Luna on US 260, *H & Lightle 212* in 1962 (FPF); 7 mi. E of Mogollon on Rte. 78, *H & Lightle 220* in 1962 (FPF); Mangas Mtn., *H & Scharpf 696* in 1964 (FPF); 1 mi. E of Fox Mtn., ca. 20 mi. N of Apache Cr., *H & Lightle 929* in 1966 (FPF); 8 mi. E of Mogollon, *Mathiasen 76-15* in 1976 (FPF) and *Pinkava 12576* in 1974 (ARIZ, ASU); Mogollon Mts., near Mogollon and White Water Baldy, *Hess 2210* in 1968 (ARIZ, NMSU); 11 mi. NNW of Datil, *Fletcher 1339* in 1976 (UNM); Gila Nat. For., Gila Wilderness Area, 0.6 mi. NW of Spruce Cr. Saddle on Trail No. 206, *Mathiasen 8104* (FPF); 1 mi. E of Silver Cr. Divide on Rte. 78, *Spaulding 78-7-36* in 1978 (ARIZ). GRANT CO.: Hillsboro Peak, *Metcalfe 1173* in 1904 (CAS, FPF, MO, RSA, UC, US); Emory Pass, *H & Lightle 121* in 1962 (FPF) and *1102* in 1968 (FPF); 24 mi. N of Mimbres on Rte. 61, *Lightle 65-40* in 1965 (FPF); Mimbres Valley and its E cyn. tributary, *Holzinger* in 1911 (US); 4 mi. E of Rte. 25 on Signal Peak rd., ca. 13 mi. N of Silver City, *H & Lightle 891* in 1966 (FPF); Just N of Rocky Cr. Campground on Rte. 61, *H & Lightle 892* in 1966 (FPF). LINCOLN CO.: Capitan Mts.: E side Capitan Peak, *Martin 902* in 1945 (WTU); Seven Cabins Cyn., *Gill & others FP89490* and *Ellis FP89492* in 1938 (FPF); 1-2 mi. E of Capitan Gap, *H & Lightle 105, 107 & 109* in 1962 (FPF) and *1098* in 1968 (FPF). SOCORRO CO.: San Mateo Mts.: Hughes Sawmill, 4 mi. SW of

Mt. Withington, *Long FP 21128* in 1915 (FPF); 12 mi. S of US 60 on Rte. 52, *Lightle 65-36* in 1965 (FPF); 13 mi. S of US 60 on Rte. 52, *H & Lightle 1117* in 1968 (FPF). Magdalena Mts.: North Baldy Mtn., *Lightle 66-19* in 1966 (FPF); 6 mi. above Water Cyn. Campground, *H & Bailey 1687* in 1975 (FPF).

5a. Arceuthobium aureum subsp. *aureum*

GUATEMALA

DEPARTMENT ALTA VERAPAZ

Cobán, on *Pinus pseudostrobus* (as *Pinus tenuifolia*), *von Turckheim II 1815* in 1907 (ILL, MO, NY, US); 4.5 mi. W of San Cristóbal Verapaz on Rte. 7-W, on *Pinus montezumae, Peterson 74-264* in 1974 (FPF); 3 mi. W of San Cristóbal Verapaz on Rte. 7-W, on *Pinus pseudostrobus, H & others 1696* in 1975 (FPF); Purulha, on *Pinus* sp., *Cook 7* in 1906 (FPF, ILL, US); 46.8 km. NW of El Rancho jct., Highway 17, on *Pinus pseudostrobus, W & C.G. Shaw III 7766* in 1994 (FPF); 8 mi. NW of Rte. C-9 on Cobán rd., on *Pinus pseudostrobus, H & others 1594* in 1975 (FPF).

DEPARTMENT CHEMALTENANGO

Between Tecpán and Encuentros, on *Pinus* sp., *Aguilar* in 1955 (EAP).

DEPARTMENT EL QUICHE

Just E of Uspantán on Rte. 7-W, on *Pinus pseudostrobus, H & others 1597* in 1975 (FPF).

DEPARTMENT ZACAPA

Sierra de las Minas, on *Pinus* sp., *Steyermark 29788* in 1939 (MICH) and *42524* in 1942 (MICH, NY).

5b. Arceuthobium aureum subsp. *petersonii*

MEXICO

CHIAPAS

On *Pinus* sp., *Seler 2190* in 1896 (US) near Siltepec, on *Pinus* sp., *Matuda 4408* in 1941 in (MEXU, MO, NY); Mt. Male, near Porvenir, on *Pinus* sp., *Matuda 4630* in 1941 (F, MEXU, NY) and on "oak tree" (probably in error; no host material with collection), *Matuda 4601* in 1941 (F, MO, NY, UC, US); between Cristóbal de las Casas and Buenavista on rd. to Tenejapa, on *Pinus* sp., *Langman 3712* in 1948 (EAP, PH, US); Trail to Pokolum, near Tenejapa Center, on *Pinus* sp., *Breedlove 6974* in 1964 (DS, FPF); E of San Cristóbal de las Casas on Rte. 190, on *Pinus pseudostrobus, Andresen & Steinhoff A2008* in 1962 (FPF); Valle cut SE of Las Casas, on *Pinus* sp., *Alexander 1199* in 1945 and *Blanco 367* in 1963 (COLO, FPF); 5 mi. W of San Cristóbal de las Casas on Rte. 190, on *Pinus oocarpa, H & others 1601* in 1975 (FPF); 32 mi. SE of San Cristóbal de las Casas on Rte. 190, on *Pinus pseudostrobus, H & others 1598* in 1975 (FPF); 12 km. SE of San Cristóbal de las Casas on Rte. 190., on *Pinus montezumae, Peterson 74-301* in 1974 (FPF); Between San Cristóbal de las Casas and Tuxtula Gutierrez, on *Pinus* sp., *Hermana* in 1969 (UNAM); San Cristóbal de las Casas, on *Pinus* sp., *Magana & others 1125* in 1983 (ENCB); 9 mi. SE of San Cristóbal de las Casas, on *Pinus* sp., *Laughlin 1165* in 1966 (MEXU); 10 mi. SE of Teopisca on Rte. 190, on *Pinus* sp., *Breedlove 9283* in 1965 (ENCB); Cerro Huitepec, W of San Cristóbal de las Casas, on *Pinus* sp., *Breedlove 26274* in 1972 (ENCB); Mpio. Huistan, on Huistan-Ocosingo rd., 32 km. from Rte. 190, on *Pinus montezumae, Peterson 74-338* in 1974 (FPF); Mpio. Jitotol, 3.5 km. S of Pueblo Nuevo Solistahuacan on Rte. 195, on *Pinus oocarpa, Peterson 74-335* in 1974 (FPF); Mpio. Chamula, on old rd. to Comitán from Mitziton, on *Pinus* sp., *Breedlove 8016* in 1964 (F, INIF).

OAXACA

10 km. SSW of Suchixtepec on Pochutla rd., on *Pinus* sp., *Rzedowski 21102* in 1965 (ENCB); El Moral, on *Pinus* sp., *Hagedora* in 1979 (MEXU); 14 km. S of San Pedro Teococuilco, on *Pinus pseudostrobus, Rzedowski 28919* in 1972 (ENCB); 8 mi. N of Suchixtepec on Rte. 175, on *Pinus michoacana, Peterson 68-105* in 1968 (FPF); 22 mi. S of Miahuatlán on Rte. 175, in *Pinus pseudostrobus, H & others 1566* in 1975 (FPF).

6. Arceuthobium bicarinatum

All collections on *Pinus occidentalis.*

DOMINICAN REPUBLIC

AZUA PROVINCE

Las Canitas, *Fuertes 1923* in 1912 (ILL, US, Z) and *Gasbarro* in 1963 (FPF); San José de Ocoa, Bejucal, *Ekman 12024* in 1929 (US).

BARAHONA PROVINCE

Between Pedernales and Aceital, *Howard & Howard 8129* in 1946 (BM, US).

LA VEGA PROVINCE

Constanza, *Allard 17432* in 1947 (US) and *H & W 1193* in 1969 (FPF); 26 km. S of Constanza on Valle Nueva rd., *H & W 1199* in 1969 (FPF); La Culeta de Constanza, *Zanoni & Mejia 12250* in 1981 (FPF, JBSD). Cordillera Central, Rio Grande, Constanza, *Liogier 19443* in 1973 (JBSD); between Bajito and Constanza, *Jimenez 6123* in 1973 (JBSD); Pico Duarte, *Zuill 1-12-86-2* in 1986 (JBSD) and *Zanoni & others 37595* in 1987 (JBSD); Rio Hojo Hondo. 5 km. NW of Constanza, *Proctor 39097* in 1982 (JBSD).

SAN JUAN PROVINCE

Sabana Nueva, *Howard & Howard 9125* in 1946 (US); 10 km. N of Hato Nueva, *Gasbarro* in 1963 (FPF).

SANTIAGO PROVINCE

Pico des Rubio, *Jiminez 1069* in 1946 (US).

PROVINCE UNCERTAIN

Sierra de Bahoruco: Aceitillar, N of Pedernales, *Liogier 19655* in 1973 (JDSD); Charco de la Paloma, 4-6 km. E of Villa Aida, *Zanoni & others 38000* in 1987 (JBSD); 15.6 km. S of Puerto Escondido on rd. to Aceitillar, *Zanoni & others 4054*, n.d. (JBSD); 40 km. from Cabo Rojo on the Alcoa Aluminum rd., *Fisher-Meerow 625* in 1981 (FLAS); 47 km. from Pedernales on rd. to Los Arroyos and Duverge, *Zanoni & others 20458* in 1982 (JBSD); "Isla", W of Hoyo de Pelempito, NE of Cabo Rojo, *Zanoni & others 10886* in 1981 (JBSD). Cordillera Central; 15–20 km. N of El Rio on rd. to Jarabacoa, *Zanoni & Mejia 7501* in 1980 (JBSD).

HAITI

DEPARTMENT DE L'OUEST

Vicinity of Furcy, *Leonard 4690* in 1920 (US); Massif de la Selle, *Ekman 1313* in 1924 (US) and *Proctor 10771 and 10772* in 1955 (US); Pic La Selle, *Adams 6441* in 1991 (FPF); near "Grand Ravine", 3 km. E of Seguin on rd. to Mare Rouge, *Zanoni & Mejia 24583* in 1982 (JBSD). Mormes des Commissiares, *Holdrige 1328* in 1942 (BM, F, MO, UC, US).

7. *Arceuthobium blumeri*

MEXICO

Hosts in Mexico are *Pinus strobiformis* or *Pinus ayacahuite* var. *brachyptera* (see text).

CHIHUAHUA

36 mi. SW of La Junta, *H & W 296* in 1983 (FPF); 13 mi. W of El Vergel, *H & W 314* in 1963 (FPF); 13 mi. SE of Mesa Huracan on Chico rd., *H & W 475* in 1963 (FPF); 65 mi. SW of Matachic on Ocampo rd., *H & W 493* in 1963 (FPF); "Sierra Madre", *Giguielat* in 1912 (ILL); 15 km. N of Yahuirichi, 59 km. N of Rte. 16, *H 2187* in 1987 (FPF); 25 km. SW of Chuhuichupa on rd to Pico Candelaria, *H & Cibrián 1954* in 1981 (FPF); 5 km. S of Magdalena, 67 km. W of La Junta, *H & Cibrián 1983* in 1981 (FPF); 18 km. W of San Juanito, *H & Cibrián 1977* in 1981 (FPF); 15 km. E of Guachochic, *H & Cibrián 1994* in 1981 (FPF); 20 mi. W of Tomochic on Rte. 16, *H & W 1650* in 1975 (FPF).

DURANGO

15 mi. W of El Salto on Rte. 40, *H & W 350* and *530* in 1963 (FPF); 16 mi. W of El Salto on Rte 40, *Mathiasen 7512* in 1975 (FPF); 34 mi. W of El Salto on Rte. 40, *H & others 1421* in 1972 (FPF) and *Mathiasen 7511* in 1975(FPF); 48 mi. S of Durango on La Flor rd., *H & W 516* in 1963 (FPF); 19 mi. SW of Santiago Papasquiero, *H & W 536* in 1963 (FPF); 22 mi. WNW of Santiago Papasquiero, 3.3 mi. W of crest on Topia rd., *Corral 705* and *Worthington 1145* in 1983 (FPF); Sierra de la Candela, 29 km. E of Tepehuanes, *H 2159* in 1987 (FPF); Sierra del Huacol, 28 km. W of Tepehuanes, *H 2166* in 1987 (FPF); Sierra del Papanton, 29 km. W of Rte. 26 on Topia rd., *H & others 2231* in 1987 (FPF); 8 km. SW of Pueblo Altares, *H & others 2243* in 1987 (FPF); 50 rd. mi. S of Rte. 12 on rd. to Cendradillas, *Peterson 72-169* in 1872 (FPF).

NUEVO LEÓN

Cerro Potosí, *Andresen & Steinhoff A2047* in 1962 (FPF) and *H & W 392* in 1963 (FPF).

SONORA

SW slope of Sierra de Ajos, *Mathiasen 7803* in 1978 (FPF).

UNITED STATES

All Arizona collections on *Pinus strobiformis.*

ARIZONA

COCHISE CO.: Huachuca Mts.: Carr Cyn., *Goodding 309* in 1909 (ARIZ); 1.2 mi. W of Reef, *H & Lightle 1109* in 1968 (FPF) and *Mathiasen 7551* in 1975 (FPF); 1.0 mi. w of Reef, *H & Lightle 235* in 1962 (FPF), *H 1283* in 1970 (FPF), *H & Mathiasen 1468* in 1973 (FPF), and *Mathiasen 7521* in 1975 (FPF); Miller Cyn., above Bathtub Springs, *Mathiasen 7553* in 1975 (FPF); Pat Scott Peak, *Mauk* in 1974 (FPF).

8. *Arceuthobium californicum*

All collections on *Pinus lambertiana,* except as noted.

UNITED STATES

CALIFORNIA

BUTTE CO.: Big Bar Mtn. Ridge, E of Pulga, *Quick 53-32* in 1953 (CAS). DEL NORTE CO.: 0.5 mi. N of Black Butte, *Mathiasen 8607* in 1986 (FPF). FRESNO CO.: Ely Meadow, between Shaver Lake and Big Cr., *H 2035* in 1982 (FPF). KERN CO.: Greenhorn Mts.: 4 mi. N of Summit Guard Sta., *W 3609* in 1964 (FPF); near Tiger Flat, *Howell 38805* in 1962 (CAS). LAKE CO.: 23.5 mi. N of Upper Lake on Pillsbury Lake rd., *H & W 862* in 1966 (FPF); 2 mi. SW of Scott Dam on Pillsbury Lake, *Nickrent 2714* in 1988 (FPF, ILL). LOS ANGELES CO.: Between Wrightwood and Kratka Ridge, *Embree* in 1956 (UC); 0.5 mi. E of Vincent Gulch Divide, *Krebill 247* in 1965 (FPF); Little Rock-Bear Cr. Divide, *Ewan 10110* in 1936 (MO). MADERA CO.: Ellis (now Benedict) Meadow, *Meinecke FP 17062* in 1914 (FPF); Fish Cr. on Rock Cr. rd., *H 9* in 1953 (FPF); Soquel-Bass Lake rd., *Gill & Wright FP 68160* (FPF) 5 mi. N of Bass Lake on Soquel rd., *H & H 1146* in 1968 (FPF); Vista Pt., 27 mi. from Northfork on Mammoth rd., *H 846* in 1966 (FPF); Willow Cr., *Hedgcock FP 4838* in 1911 (FPF). MARIPOSA CO.: Mariposa Grove, *Hedgcock & Meinecke FP 4822* in 1910 (FPF); Fish Cr. Camp, *Hedgcock & Meinecke FP 4833* in 1910 (FPF, ILL); Fish Camp, *Hedgcock & Meinecke FP 4827* in 1910 (FPF); 1 mi. E of Fish Camp, *H* in 1963 (FPF); 0.5 mi. SW of Fish Camp, *H 660* in 1964 (FPF). NEVADA CO.: Graniteville, *Boyce 32* in 1917 (FPF). PLUMAS CO.: Massack, *Gill & Wagener FP 68041* in 1931 (FPF); Silver Lake, near Quincy, *Scharpf* in 1963 (FPF); Slate Cr., 5.5 mi. W of Quincy, *W 3230* in 1962 (COLO, FPF) and *H & W 654* in 1964 (FPF); Meadow Valley, *Weatherby 1667* in 1955 (CAS, RM, RSA, UC); Feather River Exp. For. near Quincy, *Meinecke* n.d. (FPF). RIVERSIDE CO.: San Jacinto Mts., Idyllwild, *Meinecke FP 20151* in 1915 (FPF, ILL), *Cooper & Silva 923* in 1943 (ARIZ, RSA); 8 mi. N of Idyllwild, *H 740* in 1965 (FPF). SAN BERNARDINO CO.: San Antonio Mts., Coldwater Fork of Lytle Cr., *Johnston 1688* in 1917 (DS, UC). San Bernardino Mts.: Inspiration Point, *Perkins* in 1917 (ILL); Baldy Notch-Stockton Flat, *W 2808* in 1961 (COLO, FPF); W slope of Job Peak, *Ewan 3564* in 1929 (POM, UC); ridge E of Foxesee Cr., *Peirson 2818* in 1920 (RSA); 1 mi. E of Lake Gregory, *H 730* in 1965 (FPF). SAN DIEGO CO.: Cuyamaca Mts., Cuyamaca Peak, *Cox* in 1967 (FPF, UT). SHASTA CO.: 0.5 mi. S of Siskiyou Co. line on Rte. 89, *W 3238* in 1962 (COLO, FPF) and *W 6767* in 1987 (FPF); head of Tom Neal Cr., ca. 3 mi. SE of Castella, *Wyckoff & Randall* in 1920 (ILL); 3 air mi. E of Castella on Girard Ridge rd., *Nickrent & W 2710* in 1988 (FPF, ILL). SIERRA CO.: Between Downieville and Forest, *Boyce 31* in 1916 (FPF). SISKIYOU CO.: SE of Bartle on Rte. 89, *H & W 644* in 1964 (FPF); 8 mi. SW of McCloud, *W 6798-9* in 1978 (FPF); 5 mi. S of Siskiyou Lake on Castle Lakes rd., *H & Mathiasen 2430* in 1990 (FPF); 3.5 mi. S of Siskiyou Lake on Castle Lakes rd., *H & Mathiasen 2424* in 1990 (FPF); Castle Lakes Campground, 7 air mi. SW of the town of Mt. Shasta, on *Pinus monticola*, *H & Mathiasen 2426* and *2427* in 1990 (FPF). TEHAMA CO.: 2 mi. N of Hole-in-Ground Campground, S of Mineral, *Kuijt 1502* in 1958 (UC); 5 mi. E of Mineral on Rte. 89, jct. Lassen Nat. Park, *H 1738* in 1976 (FPF); 6 mi. E of Mineral on Rte. 89, *H 1737* in 1976 (FPF); on Rte. 89 1.2 mi. SE of jct. with Rte. 36, *Mathiasen 8512* in 1985 (FPF). TULARE CO.: Sequoia Nat. Park, Crystal Cave Jct., *W 3611* in 1964 (FPF). TUOLUMNE CO.: 5.1 mi. E of Nat. For. boundary on Rte. 120, *Kuijt 1394* in 1957 (UC); Yosemite Nat. Park, 5.1 mi. NW of Crane Flat Campground on Big Oak Flat rd., *W 6743* in 1987 (FPF).

9. Arceuthobium campylopodum

MEXICO

All Baja California collections on *Pinus jeffreyi.*

BAJA CALIFORNIA

Sierra de San Pedro Mártir: Low hills NW of La Encantada, *Wiggins & Demaree 5018* in 1930 (DS, F, RSA, US); without locality, on *Pinus* sp., probably *Pinus jeffreyi*, *Brandegee* in 1893 (UC); 0.25 mi. N of La Encantada, *H & Scharpf 765* in 1965 (FPF); La Grulla, *H & Scharpf 767* in 1965 (FPF). Sierra Juárez: *Moran 29300* in 1980 (SD), 30 mi. S of La Rumorosa on Laguna Hanson rd., *Lightle & Gill 64-35* in 1964 (FPF); 8 mi. W of Laguna Hanson, *H & Scharpf 783* in 1965 (FPF); El Rayo, *Moran 29240* in 1980 (SD), 3 mi. SW of San Pedro, *Moran 18520* in 1971 (SD).

UNITED STATES

All United States collections on *Pinus ponderosa* var. *ponderosa,* except as noted.

CALIFORNIA

ALPINE CO.: Silver Cr. Campground, E side of Ebbetts Pass, on *Pinus jeffreyi*, *Munz 21347* in 1955 (RSA); 5 mi. SW of Silver Cr. on Rte. 4, on *Pinus jeffreyi*, *H & Scharpf 668* in 1964 (FPF); Indian Cr., 1 mi. S of Markleeville, *H 1304* in 1970 and on *Pinus jeffreyi*, *H 1303* in 1970 (FPF); 1 mi. E of Wolf Cr. Meadows, on *Pinus jeffreyi*, *H 1308* in 1970 (FPF). BUTTE CO.: Jonesville, on *Pinus jeffreyi*, *Copeland* in 1931 (UC). CALAVERAS CO.: 15 mi. SW of Tamarack on Rte. 4, *H & Scharpf 661* in 1964 (FPF); Angels Camp, *Eggelston 9718* in 1913 (US). DEL NORTE CO.: Ship Mtn. trail, on *Pinus jeffreyi*, *Weir 3189* in 1916 (ILL). ELDORADO CO.: 3 mi. S of Meyers on U.S. 50, on *Pinus jeffreyi*, *Peterson 63-315* in 1963 (FPF); Kyburz, *Rossbach 237* in 1955 (UC); Lake Tahoe, Emerald Bay, *Boyce FP 97944* in 1913 (FPB); 8 mi. E of Kyburz on US 50, *H & W 840* in 1966 (FPF); 3 mi. NW of Placerville on Rte. 49, *H & W 842* in 1966 (FPF); Institute of For. Genetics, Placerville, on *Pinus jeffreyi*, *H 1319* in 1971 (FPF); Fallen Leaf Lake, on *Pinus contorta* subsp. *murrayana*, *Copeland 1425* in 1931 (RSA); Lily Lake, Glen Alpine Cyn., on *Pinus jeffreyi*, *Abrams 12752* in 1930 (UC); 9 mi. S of Camp Richardson on Fallen Leaf Lake rd., on *Pinus jeffreyi*, *Pickle 57-15* in 1957 (UC); 0.5 mi. S of Camp Richardson on Fallen Leaf rd., on *Pinus jeffreyi*, *Kuijt 1337* in 1957 (UC); between Camp Richarson and S end of Fallen Leaf Lake, *W 6722* in 1986 (FPF). FRESNO CO.: 1.3 mi. N of Mono Hot Springs, on *Pinus jeffreyi*, *H* in 1963 (FPF); between Brown Cone and Dualton rd., near Kaiser Diggings, on *Pinus jeffreyi*, *Quibell 280* in 1951 (DS, RSA); Camp 6, Big Cr., *Meinecke FP 97948* in 1917 (FPB). Kings Cyn. Nat. Park: Cedar Grove, on *Pinus jeffreyi*, *W 3616* in 1964 (FPF); Copper Cr. Cyn. Trail, on *Pinus jeffreyi*, *Howell 34204* in 1958 (CAS); 5 air mi. W of Shaver Lake, on *Pinus sabiniana*, *H 2266* in 1988 (FPF); Simpson Meadow, middle fork Kings River, *Howell 34093* in 1958 (CAS); Kings Cyn. Nat. Park, near Roaring River Guard Sta., *Knutson* in 1981 (FPF); 1 mi. NW of Big Cr. on Huntington Lake rd., *H 2034* in 1982 (FPF); Pine Ridge on Rte. 168, 1 mi. NE of Cressman, *H 2265* in 1988 (FPF); 2.2 mi. N of Stevenson Cr., *H 2267* in 1988 (FPF). GLENN CO.: 0.5 mi. above Long Pt. Lookout, Elk Cr. rd., on *Pinus attenuata*, *Newcomb 148* in 1957 (UC). HUMBOLDT CO.: NW of Scotia, on *Pinus attenuata*, *Miller FP 98033* in 1962 (FPB). KERN CO.: 6 mi. W of Summit Guard Sta., Glenville-Sierra Alta rd., *W 3606* in 1964 (FPF); 3 mi. N of Summit Guard Sta., on rd. to Tiger Flat, *W 3607* in 1964 (FPF); N of Tiger Flat, *Howell 38824* in 1962 (CAS); Indian Cr., on *Pinus jeffreyi*, *Root* in 1919 (ILL); rim of Kern Cyn., SW of Pine Flat, on *Pinus jeffreyi*, *Twisselmann 8681* in 1963 (CAS); Mt. Pinos region, on *Pinus jeffreyi*, *Wheeler* in 1931 (CAS). LAKE CO.: Elk Mtn., 8 mi. N of Upper Lake, *Tracy 2355* in 1905 (UC, US, WTU); Boggs Mtn. State For., *Scharpf* in 1965 (FPF); 16 mi. N of Upper Lake on Pillsbury Lake rd., *H & W 860* in 1966 (FPF); 20 mi. N of Upper Lake on Pillsbury Lake rd., on *Pinus attenuata*, *H & W 861* in 1966 (FPF); Upper Lake to Elk Mtn., on *Pinus attenuata*, *Mason 2590* in 1926 (UC); near Lucerne, on *Pinus attenuata, Sutliffe* in 1939 (CAS); Pine Mtn., 3 mi. NE of Lake Pillsbury, *Nickrent 2711* in 1988 (FPF, ILL); Pine area, 5 mi. NE of Potter Valley, on *Pinus attenuata, Nickrent 2712* in 1988 (FPF, ILL). LOS ANGELES CO.: San Gabriel Mts.: Chilao, *Peirson 2322* in 1921 (JEPS); Prairie Fork, San Gabriel River, *Johnston 1720* in 1917 (RSA, US, WTU); Pine Flat, *Wheeler 1115* in 1932 (UC) and on *Pinus coulteri, Sloan FP 97943* in 1914 (FPF); Crystal Lake Resort, *H & Scharpf 2079* in 1984 (FPF); Crystal Lake, *Martindale* in 1937 (RSA) Cedar Cyn. off Mescal Cr., *Ewan 9924* in 1936 (MO) Little Rock-Bear Cr. Divide, on *Pinus coulteri, Ewan 10111* in 1936 (MO); Barley Flat, on *Pinus coulteri, Perkins* in 1919 (ILL); 0.5 mi. W of Big Pine, on *Pinus jeffreyi, H 728* in 1965 (FPF) and on *Pinus jeffreyi, Krebill 244* in 1965 (FPF); near Crystal Lake, on *Pinus halepensis, Scharpf* in 1972 (FPF). MADERA CO.: Bass Lake, *Gill & Wright FP 68162* in 1932 (FPF); 2 mi. NW of North Fork, *H 659* in 1964 (FPF), *H* in 1964 (FPF), and *H & H 1145* in 1968 (FPF); 10 mi. SE of North Fork on Mammoth Pool rd., *H 848* in 1966 (FPF). MARIPOSA CO.: Yosemite, *Hedgcock & Meinecke FP 4788* and *FP 4789* in 1910 (FPF) and *Bolander 6380* in 1866 (US); Fish Camp, *Hedgcock FP 4835* in 1910 (FPF) and on *Pinus jeffreyi, Hedgcock & Meinecke FP 4836* in 1910 (FPF); Wawona, *Posey* in 1919 (ILL); Crane Flat, on *Pinus jeffreyi, Kuijt 1407* in 1957 (UC) and *Rose 60113* in 1960 (RSA); Snow Cr., on *Pinus jeffreyi, Hall* in 1911 (UC). MENDOCINO CO.: Without locality, on *Pinus jeffreyi, Brown 941* in 1898 (FPF, MO, US). MODOC CO.: 3 mi. N of Crowder Flat Guard Sta., *Peterson 64-100* in 1964 (FPF). MONO CO.: 3 mi. E of Sonora Pass, on *Pinus jeffreyi, Kuijt 1432* in 1957 (UC). NAPA CO.: Conn Valley, *Jepson* in 1893 (JEPS); near Pacific Union College, Angwin, *Boyce 1908* in 1930 (FPF); 2 mi. N of Angwin on Pope Valley rd., *H & W 858* in 1966 (FPF); 1.7 mi. E of Angwin on Howell Mtn. rd., *H 2270* in 1988 (FPF). Mt. St. Helena, on *Pinus attenuata, Wolf 1851* in 1928 (US, RSA); *Howell 2204* in 1926 (CAS); and *Sutliffe* in 1919 (CAS). NEVADA CO.: Between Truckee and Lake Tahoe, *Gill FP 68243* in 1931 (FPF) and on *Pinus jeffreyi, Gill FP 68237* in 1931 (FPF); 1 mi. N of Lake Tahoe, *W 3227* in 1962 (COLO, FPF); 5 mi. W of Truckee, on *Pinus jeffreyi, Wright FP 68109* in 1932 (FPF). PLACER CO.: 1.5 mi. E of Tahoe State Park on Rte. 28, on *Pinus jeffreyi, Kuijt 1339* in 1957 (UC); 1 mi. N of Tahoe City on Rte. 89, on *Pinus jeffreyi, Kuijt 1333* in 1957 (UC); Tahoe City, on *Pinus jeffreyi, Smith & Wilson* in 1972 (UC). PLUMAS CO.: Chester, on *Pinus jeffreyi, Boyce FP 15983* in 1914 (FPF); 1 mi. E of Rte. 89 on Rte. 40A, on *Pinus jeffreyi, H & W 656* in 1964 (FPF); Quincy Jct., *Gill & Wagener FP 68040* in 1931 (FPF); Quincy, Feather River Exp. For., *Boyce* in 1913 (FPF) and *Hunt FP 25071* in 1919 (FPF); Chester, *Meinecke FP 17100* in 1914 (FPF); Slate Cr., 5.5 mi. W of Quincy, *W 3231* in 1962 (COLO, FPF); 2 mi. SE of Cromberg, *W 3229* in 1962 (COLO, FPF); near Clio, *Meinecke* in 1915 (FPF); Quincy, *Boyce FP 97955* in 1913 (FPF); 21.5 mi. N of Sierraville, *Kuijt 1346* in 1957 (UC); 7.5 mi. W of Blairsden, *Kuijt 1347* in 1957 (UC); 6.5 mi. E of jct. of Rts. 40 & 89, near Indian Falls, *Kuijt l348* in 1957 (UC); 5 mi. W of Quincy, *H & W 655* in 1964 (FPF); 5 mi. W of Meadow Valley on *Pinus contorta* var. *murrayana, Gill & Wagener FP 68039* in 1931 (FPF). RIVERSIDE CO.: San Jacinto Mts.: *Spenser 1078* in 1919 (RSA); *Grant 1113* in 1901 (ARIZ, US); and on *Pinus coulteri, Munz & Johnston 8705* in 1924 (RSA); Idyllwild-Banning, *Clokey & Anderson 6574* in 1935 (RSA, RM, RSA, UC, WTU); Idyllwild, *Perkins* in 1916 (ILL); 8 mi. N of Idyllwild on Rte. 74, *H 739* in 1965 (FPF); 11 mi. N of Idyllwild on Rte. 74, on *Pinus coulteri, H 738* in 1965 (FPF); 2 mi. SE of Idyllwild, on *Pinus jeffreyi, H 742* in 1965 (FPF); Tahquitz Ridge, on *Pinus jeffreyi, Meyer 688* in 1929 (JEPS); Pine Cove, *Cooper 1547* in 1944 (RSA); Strawberry Valley, *Wheeler 242* in 1931 (CAS, RSA) and on *Pinus coulteri, Grand* n.d. (CAS); 0.6 mi. SE of Keen Camp Summit on Rte. 74, on *Pinus coulteri, Kuijt 1497* in 1958 (UC); Tripp Mill, on *Pinus coulteri, Meinecke FP 20152* in 1915 (FPF); Santa Rosa Mts., Peak rd. 9 mi. from Rte. 74, on *Pinus jeffreyi, H 745* in 1965 (FPF); San Jacinto Mts., Idyllwild, Wolf Cr. Trail, on *Pinus coulteri, Krebill (K-791)* in 1970 (FPF); Keen Summit on Rte. 74, 1.5 mi. SE Mtn. Center, on *Pinus coulteri, H 2287* in 1988 (FPF); Garner Valley, 5.5 mi. SE Mt. Center on Rte. 74, on *Pinus jeffreyi, H 2286* in 1988 (FPF). SAN BERNARDINO CO.: San Bernardino Mts.; *Engelmann* in 1880 (MO); on *Pinus coulteri, Parish* in 1892 (JEPS) and *Parish & Parish 966* in 1884 (MO, US); Big Bear Lake, *Gill & Wright FP 68240* in 1931 (FPF) and *W 2444* in 1959 (RSA, UC, US) and *2741* in 1960 (RSA); Camp Angelus, *W 3211* in 1962 (COLO, FPF); Wrightwood, *W 3212* in 1962 (COLO, FPF); S fork of Santa Ana River, *Munz 6260* in 1922 (RSA) and on *Pinus jeffreyi, Peirson 1721* in 1909 (RSA); 2 mi. E of Bluff Lake, *Munz 10566* in 1926 (RSA); Bear Valley, on *Pinus jeffreyi, Abrams 2818* in 1902 (FPF, MO, RSA, WTU, Z); 5 mi. W of Arrowbear, on *Pinus jeffreyi, Raven 16874* in 1961 (RM, RSA); Mill Cr. rd. near Big Bear, on *Pinus jeffreyi, Howell 386A* in 1927 (RSA); Snow Valley W of Big Bear, on *Pinus jeffreyi, H 731* in 1964 (FPF); 2 mi. W of Snow Valley, on *Pinus coulteri, H 734* in 1965 (FPF); 3 mi. SW of Running Springs on Rte. 30, on *Pinus coulteri, H 736* in 1965 (FPF) and, on *Pinus attenuata, H 735* in 1965 (FPF); City Cr. rd., on *Pinus attenuata, Johnston* in 1924 (RSA); San Bernardino Mts.: Barton Flats on Rte. 38, on *Pinus jeffreyi, H 2280* in 1988 (FPF) and Green Valley on *Pinus jeffreyi, H 2276* in 1988 (FPF). SAN DIEGO CO.: Without locality, on *Pinus coulteri, Weir* in 1913 (ILL); Julian, on *Pinus coulteri, Bethel FP 24449* in 1918 (FPF); Pine Hills near Julian, on Pinus coulteri, Brown in 1955 (SD); 4 mi. W of Julian, on *Pinus coulteri, Wiggins 2106* in 1926 (CAS, UC); 4.1 mi. S of Julian on Rte. 79, on *Pinus coulteri, Kuijt 1471* in 1958 (UC); 4 mi. SW of Julian, on *Pinus coulteri, H 751* in 1965 (FPF); Cuyamaca Rancho State Park, *H 2281* in 1988 (FPF) and, Middle Peak, *Beauchamp & others 2974* in 1971 (SD); 5 mi. SW of Pine Valley, *H & Scharpf 789* in 1965 (FPF). Cuyamaca Mts.: *Palmer* in 1875 (UC); Cuyamaca Lake, *Roos 1240* in 1937 (RSA) and *Gander 633* in 1936 (SD); North Peak, on *Pinus jeffreyi, Gander 2774* in 1936 (SD); top of

Middle Peak, on *Pinus* sp., *Gander 2809* in 1936 (SD); Base of Stonewall Peak, on *Pinus coulteri*, *Wiggins 2725* in 1926 (CAS, UC). Laguna Mts.: *Huey* in 1946 (RSA, SD); Laguna, *Schoenfeldt 3600* in 1894 (UC); Laguna Resort, on *Pinus jeffreyi*, *Gander 2842* in 1935 (SD); near Garnet Peak, on *Pinus jeffreyi*, *Gander* in 1935 (SD); 5 mi. N of Laguna Mtn. Lodge, on *Pinus jeffreyi*, *H 752* in 1965 (FPF); Laguna Campground, on *Pinus coulteri*, *Wiggins 2817* in 1927 (DS) and on *Pinus coulteri*, *Munz 8350* in 1924 (RSA); Yerba Buena Campground, *Scharpf* in 1977 (FPF), 0.5 mi. S of Pinyon Pt., on *Pinus jeffreyi*, *Bailey & Rockwell* in 1978 (FPF), and Garnet Information Center, on *Pinus jeffreyi*, *H 2282* in 1988 (FPF). SANTA BARBARA CO.: Los Olivos, on *Pinus jeffreyi*, *Hartley & Weir* in 1912 (ILL). SHASTA CO.: Fall Cr. rd. S of Castella, *W 6800* in 1987 (FPF); 3 mi. N of North entrance to Lassen Nat. Park on Rte. 89, *W 3236* in 1962 (COLO, FPF); Sisson Tavern Park, col.? *FP 97945* in 1913 (FPF); jct. of Rts. 89 and 299, *Kuijt 1366* in 1957 (UC); 12 mi. N of Rte. 299 on Rte. 89, *H & W 646* in 1964 (FPF); Lassen Nat. Park, 8 mi. E of N entrance, *H & W 649* in 1964 (FPF); Long Valley, SW of Burney Falls, on *Pinus jeffreyi*, *Scharpf FP 98114* in 1965 (FPF); between Oak Run and Whitmore, *Anderson* in 1949 (CAS); 15.2 mi. W of Platina on Rte. 36, *W 6751* in 1987 (FPF). SIERRA CO.: Sierraville, *Lemmon* in 1875 (MO); Lemon Cyn., Sierraville, on *Pinus jeffreyi*, *Meinecke & Boyce FP 17196* in 1915 (FPF); 20.5 mi. N of Truckee, on *Pinus jeffreyi*, *Kuijt 1345* in 1957 (UC); 2 mi. W of Bassetts, on *Pinus contorta* var. *murrayana*, *Peterson 63-166* in 1963 (FPF); 7 mi. NE of Manzanita Lake, on *Pinus jeffreyi*, *H 1739* in 1976 (FPF). SISKIYOU CO.: Rte. 3 between Ft. Jones and Yreka, *W 6755* in 1987 (FPF); Dillon Mtn. Rd., *W 6765* in 1987 (FPF); 1.5 mi. E of Callahan, *W 6775* in 1987 (FPF); Rte. 3 S of Callahan, *W 6753* in 1987 (FPF); Mt. Shasta, *Engelmann* in 1880 (FPF, MO); Yreka, *Hedgcock FP 1897* in 1909 (FPF); Scotts River, *Pond FP 193* n.d. (FPF); Mt. Shasta, *Brown 580* in 1897 (FPF, MO, US); Sisson, *Hedgcock & others FP 9668* in 1911 (FPF); Big Carmen Lake, Scott Mtn. rd., 6 mi. E of Callahan, *Barbe 314* in 1955 (RSA, UC); Mt. Shasta, Sisson South Trail, *Cooke 11593* in 1938 (DS, UC); Gravely Ridge, W of Craggy Mtn. NW of Yreka, *Ownbey & Brown 2428* in 1911 (UC); Cyn. Cr., ca. 12 mi. SSW of Hamburg, *Hedgcock FP 1873* in 1909 (FPF); 3 mi. NW of McCloud, *Scharpf & Miller* in 1965 (FPF), and on *Pinus attenuata*, *Scharpf & Miller* in 1965 (FPF); Russian Cr., on *Pinus attenuata*, *Butler 273* in 1908 (UC); 3 mi. N of Branch Guard Sta., N of Happy Camp, on *Pinus attenuata*, *Kuijt 1277* in 1957 (UC); Scott Mtn., on *Pinus jeffreyi*, *Engelmann* in 1880 (MO). TEHAMA CO.: Childs Meadow, 2 mi. W of Morgan Springs on Rte. 36, on *Pinus contorta* var. *murrayana*, *Scharpf FP 38026*, n.d. (FPF); 15 mi. W of Rte. 36 on Rte. 89, *Kuijt 1356* in 1957 (UC) and on *Pinus contorta* var. *murrayana*, *Kuijt 1357* in 1957 (UC). TRINITY CO.: 2 mi. E of Jct. City, *H 1743* in 1976 (FPF); 15.2 mi. W of Platina on Rte. 36, *W 6751* in 1987 (FPF); Trinity, *Munns FP 9440* in 1911 (FPF); Plummer Spring, [near Peanut?], *Meinecke* in 1912 (FPF); Trail to Granite Peak, *Baker 209* in 1926 (CAS); Scott Ranch, *Cantielow 1659* in 1936 (RSA); Trinity River at Betty May Mine, on *Pinus attenuata*, *Kildale 10275* in 1930 (CAS). TULARE CO.: Jordan Hot Springs, *Zeile* in 1924 (JEPS); Peppermint Valley, *Dudley 758* in 1895 (CAS); Whitaker For., *Benson 5705* in 1933 (RSA); Mineral King, on *Pinus jeffreyi*, *Coville & Funston 1460* in 1891 (CAS) and *1482* in 1891 (US); Sequoia Nat. Park, 1 mi. N of Lodgepole Campground, on *Pinus jeffreyi*, *W 3612* in 1964 (FPF); Mt. Sillman, ca. 3 mi. N of Lodgepole, on *Pinus jeffreyi*, *Hopping 391* in 1905 (UC); Little Kern River, between Lion Meadow and Trout River, on *Pinus jeffreyi*, *Dudley 1978* in 1897 (CAS); Sherman Pass Rd., 5 mi. from Kernville, Johnson Rd., on *Pinus jeffreyi*, *H & Scharpf 2091* in 1984 (FPF) and on *Pinus sabiniana*, *H & Scharpf 2090* in 1984 (FPF). TUOLUMNE CO.: Stanislaw Nat. For., 1 mi. W of Strawberry, *H & Scharpf 2039* in 1982 (FPF); Clark Fork of Tuolumne River, 1.5 mi. below Arnott Cr., on *Pinus jeffreyi*, *Wiggins 9322* in 1939 (CAS, RSA, UC, WTU); Crocker Sta., on *Pinus jeffreyi*, col.? *FP 97946* in 1915 (FPF); 2.8 mi. NE of Long Barn, on *Pinus jeffreyi*, *Thomas 10262* in 1963 (FPF, RSA); near Kennedy Meadows on Rte. 108, on *Pinus jeffreyi*, *Kuijt 1423* in 1957 (UC); Long Barn, *Gill FP 68087* and *FP 68097* in 1932 (FPF), *Wright FP 68117* in 1932 (FPF), and *Gill & Wright FP 68072* in 1932 (FPF); 6 mi. E of Long Barn, *W 3222* in 1962 (COLO, FPF); 1 mi. E of Twain Harte, *Kuijt 1428* in 1957 (UC); Cottonwood Meadows, E of Mather, *Clausen 1777* in 1939 (DS); Pate Valley, Yosemite, *Clemens* in 1919 (CAS). VENTURA CO.: Middle Fork, Mt. Pinos, *Hall 6642* in 1905 (UC); Mt. Pinos, *Rothrock 213* in 1875 (US); Mt. Reyes rd., 6 mi. E of Rte. 33, on *Pinus jeffreyi*, *H & Scharpf 2084* in 1985 (FPF). COUNTY UNCERTAIN.: Smith Fork Ranger Sta., on *Pinus attenuata*, *Lewis* in 1916 (RM, ILL); Mt. St. Helena, on *Pinus attenuata*, *Jepson* in 1893 (JEPS); 0.5 mi. toward Stony Ford below Old Mill Campground on Stony Fork–Upper Lake rd., on *Pinus attenuata*, *Newcomb 146* in 1957 (UC).

IDAHO

ADAMS CO.: Evergreen, *Hedgcock FP 1909* in 1909 (FPF); Bear, *Barr* in 1915 (ILL); 10 mi. N of Council on US 95, *H 978* in 1966 (FPF). BOISE CO.: S fork of Payette River, Garden Valley, *Miles FP 15108* in 1913 (FPF); Karney Cr., *Peterson 62-49* in 1962 (FPF). IDAHO CO.: N bank of Salmon River, 11 mi. E of Riggins, *H 970* in 1966 (FPF); MacKay Bar, on Salmon River 2 mi. E of jct. of S fork of Salmon River, *W 4127b* in 1966 (FPF, UT). KOOTENAI CO.: Without locality, *Sandberg* in 1892 (US); Coeur d'Alene Lake, *Wicker* in 1973 (FPF); Coeur d'Alene, *Weir FP 17047* in 1914 (FPF); Coeur d'Alene City Park, *Gill FP 68203* in 1932 (FPF); 5 mi. W of Coeur d'Alene, *W 3254* in 1962 (COLO, FPF); Spokane Bridge, *Heller 925* in 1892 (DS, MO); E side Coeur d'Alene Lake, 4 mi. N of inlet of Coeur d'Alene River, on *Pinus contorta* var. *latifolia*, *Krebill 154* in 1964 (FPF); Spirit Lake, on *Pinus contorta* var. *latifolia*, *Dodge* in 1916 (ILL); Fourth of July Cyn., on *Pinus contorta* var. *latifolia*, *Weir 8252* in 1914 (ILL); Fernan Lake, *H & Wicker 966* in 1966 (FPF) and on

Pinus contorta var. *latifolia*, *Weir 8243* in 1916 (ILL); Hayden Lake, on *Pinus sylvestris*, *Weir* in 1920 (ILL). LATAH CO. 4 mi. E of Troy, *Daubenmire* in 1945 (WTU). LEWIS CO.: Nezperce, *Anison* in 1914 (ILL).

NEVADA

CLARK CO. (all Clark Co. collections on *Pinus ponderosa* var. *scopulorum*): Charleston Mts: *Clokey 5431* in 1935 (CAS, FPF, JEPS, WTU) and *5432* in 1935 (CS, FPF, JEPS, WTU); Charleston Park, *W 3032* and *3205* in 1962 (COLO, FPF); Kyle Cyn., 2.5 mi. W of Ranger Sta., *H & Scharpf 675* in 1964 (FPF); Kyle Cyn., *Peterson 64-144* in 1964 (FPF), *Krebill 720* in 1968 (FPF), *H & others 1175* in 1969 (FPF). DOUGLAS CO.: Glenbrook, on *Pinus jeffreyi*, *Baker 1006* in 1902 (MO, RSA, UC); E of Spooner Jct. on US 50, on *Pinus jeffreyi*, *Peterson 65-403* in 1965 (FPF); 5 mi. E of Spooner Jct. on US 50, on *Pinus jeffreyi*, *H & W 836* in 1966 (FPF); Kingsbury rd. W of Minden, on *Pinus jeffreyi*, *W 6721* in 1986 (FPF); 4 mi. W of Daggett on Kingsbury rd., *H & H 2431* in 1990 (FPF). ORMSBY CO.: 2 mi. N of US 50 near Carson City, on *Pinus jeffreyi*, *Peterson* in 1960 (FPF). WASHOE CO.: Franktown, col? n.d. (PH); Hunter Cr. rd., *Kennedy* in 1907 (CAS); Incline Camp, N shore of Lake Tahoe, 3 mi. E of California boundary, on *Pinus jeffreyi*, *Wright FP 68111* in 1932 (FPF); Bowers Mansion, 26 mi. S of Reno, on *Pinus jeffreyi*, *Archer 6396* in 1938 (MO, UC); mts. W of Bowers, on *Pinus jeffreyi*, *Heller 10660* in 1912 (CAS, MO); N shore of Lake Tahoe, Crystal Bay, on *Pinus jeffreyi*, *Peterson 65-395* in 1965 (FPF); Sand Pt., NE shore of Lake Tahoe, on *Pinus jeffreyi*, *H 1339* in 1971 (FPF).

OREGON

BAKER CO.: 5 mi. NE of Halfway, near Mehlhorn Butte, *Knutson 103* in 1980 (FPF); on Rte. 26 NW of Unity, *H 1921* in 1979 (FPF); 7 mi. S of Baker, *Peterson 63-224* in 1963 (FPF); Dooley Mtn. area, 12 mi. S of Baker, *Graham* in 1965 (FPF); Sumpter, *Hedgcock FP 998* in 1909 (FPF) and on *Pinus contorta* var. *latifolia*, *Weir 3200* in 1913 (ILL); 23 mi. S of Baker on Rte. 7, *H & W 583* in 1964 (FPF); Buck Mtn., E Oregon [near Unity?], *Cusick 2701* in 1901 (MO, RSA, RM, UC, US); Halfway, *Miller* n.d. (ILL); Squaw Cr., 28 mi. ESE of Prairie City, *Graham* in 1965 (FPF). CROOK CO.: Maury Mts., *H 1923* in 1979 (FPF); Prineville, *Harvey FP 4159* in 1910 (FPF); Gerow Butte rd., Ochoco Nat. For., *Childs 52* in 1949 (OSC); Marks Cr. rd., Ochoco Nat. For., *Childs 61* in 1949 (OSC). CURRY CO.: Agness, *Mathiasen* in 1986 (FPF); 12 mi. NW of Agness, on *Pinus attenuata*, *Graham* in 1963 (FPF); 1.5 mi. S of Buckskin Peak, *Tinnin & Kirkpatrick 5* in 1981 (FPF); 9 mi. N of Agness on Powers rd., *H 2334* in 1989 (FPF). DESCHUTES CO.: 6 mi. SW of Sisters, *H & Scharpf 1259* in 1969 (FPF); top of Lava Butte, *Knutson & Tinnin* in 1975 (FPF); China Hat, *Knutson* in 1978 (FPF); 8 mi. W of China Hat, *Knutson* in 1978 (FPF); Deschutes River near Bend, *Nelson 866* in 1906 (RM); 10 mi. S of Sisters, *Henderson 14130* in 1931 (PH); Pringle Butte, [6 mi. NW of La Pine] *H 989* in 1966 (FPF) and *Steward & Sowder 6803* in 1954 (RSA); 9 mi. S of Bend on US 97, *H & W 617* in 1964 (FPF). DOUGLAS CO.: Big Camas Ranger Sta., *Kern* in 1915 (ILL). GRANT CO.: 25 air mi. ESE of Seneca, *H & Scharpf 1267* in 1969 (FPF); Strawberry Mts., Graham Cr., Blue Mtn. Hot Springs, 8 mi. SSE of Prairie City, *Ferris & Duthie 857* in 1919 (DS); 16 mi. S of John Day on Rte. 395, *H & W 577* in 1964 (FPF); 10 mi. NE of Prairie City on Rte. 26, *H & W 580* in 1964 (FPF). HARNEY CO.: 30 air mi. ESE of Burns, *Overbay FP 68281* in 1932 (FPF); Calamity Cr. near Van, *Griffith & Moore 803* in 1901 (US); Crow Flat Ranger Sta., ca. 18 mi. N of Burns, *Porter* in 1915 (ILL); Lee Cr., 25 air mi. ESE of Seneca, *H & Scharpf 1265* in 1969 (FPF). HOOD RIVER CO.: Hood River, *W 3245* in 1962 (COLO, FPF), *Gorman* in 1891 (WTU), and *Henderson 913* in 1884 (OSC); without locality, *Henderson 527* in 1923 (MO). JACKSON CO.: 18 mi. SW of Ashland, *Graham* in 1963 (FPF); Rogue Elk [near McLeod], *Stillinger* in 1919 (FPF, ILL, US); 12 mi. S of Ruch on Copper rd., *H & W 633* in 1964 (FPF); 7 mi. W of Klamath Co. on Rte. 66, *H 2377* in 1989 (FPF). JEFFERSON CO.: 5 mi. N of Camp Sherman, *Swedberg 260* in 1957 (OSC); Warm Springs Indian Res. *Childs FP 68272* in 1931 (FPF); Shuttle Lake, Metolius area, *Gill FP 68191* in 1932 (FPF); Montgomery Ranch, Lower Metolius River, 13 mi. W of Metolius, *Boyce 2121* in 1931 (FPF) and *Childs 68* in 1931 (OSC). JOSEPHINE CO.: 6.8 mi. SW of O'Brien, *W 6804* in 1987 (FPF); 3 mi. S of Cave Jct. on Rte 199, *H 2273* in 1988 (FPF); Waldo, 7 mi. S of Cave Jct., *Lewis* in 1917 (ILL), and on *Pinus jeffreyi*, *Lewis* in 1917 (FPF, ILL). Grants Pass, *Weir 3206* in 1916 (FPF, ILL); 5 mi. W of Grants Pass, on *Pinus jeffreyi*, *Graham* in 1964 (FPF); 5 mi. N of Grants Pass, *Abrams 8677* in 1922 (DS); 6.5 mi. SSW of O'Brien on Oregon Mtn. rd., *H & Hinds 996* in 1966 (FPF) and *H 2378* in 1989 (FPF); Oregon Mtn., *Weir 3194* in 1916 (ILL); 2 mi. E of Cave Jct., *Theisen* in 1965 (FPF); near Lookout Gap, 20 air mi. S of Galice, on *Pinus jeffreyi*, *Graham* in 1965 (FPF); Oregon Mtn., on *Pinus jeffreyi*, *Howard* in 1964 (FPF); Wonder, on *Pinus jeffreyi*, *Mitchell FP 68212* in 1932 (FPF); vicinity of Oregon Caves, *Weir 3193* in 1916 (ILL); 4 mi. E of Cave Jct, *H & W 869* in 1966 (FPF). KLAMATH CO.: 2 mi. W of Quartz Pass on Rte. 140, *H & others 1378* in 1971 (FPF); 2.5 mi. SW of Sugar Pine Mtn., *Tinnin & Knutson DM 56 & 57* in 1978 (FPF); 5 mi. ESE of Modoc Pt., *Knutson & Tinnin DM 69* in 1978 (FPF); Boundary Springs, near Cresent, *Knutson & Tinnin DM 84* in 1978 (FPF); 4 mi. SW of Lone Pine, *Knutson & Tinnin DM 66* in 1978 (FPF); 4 mi. SW of Bear Butte, *Knutson & Tinnin DM 61* in 1978 (FPF); near jct. of Rts. 230 and 97, *W 3239* in 1962 (COLO); Ringo Butte, *Childs 10* in 1946 (OSC); Brookside Ranch, Swan Lake Valley *"E.H." 3187* in 1904 (DS); Hamner Butte, *Bedwell & Childs FP 91033* and *FP 91034* in 1939 (OSC), *Childs 1* in 1939 (FPP), and on *Pinus contorta* var. *murrayana*, *Childs 22* in 1939 (OSC) and *Bedwell FP 91035* in 1939 (OSC); 11 mi. NW of Rte. 97 on Rte. 58, *H & W 619* in 1964 (FPF); 14 mi. W of Klamath Falls on Rte. 66, *H & W 627* in 1964 (FPF); Applegate Ranch, Swan Lake Valley, *Walpole*

417 in 1899 (US); 19 mi. NW of Klamath Falls on Rte. 140, *H & W 872* in 1966 (FPF); 14 mi. SW of Beatty on Rte. 140, *H & W 873* in 1966 (FPF); Little Odell Butte, 2 mi. S of Rte. 58, *H 2341* in 1989 (FPF); 3 mi. E of Rte. 58 on Davis Lake rd., *H 2342* in 1989 (FPF); S side of Boundary Butte, 3 mi. ENE of Sun Pass, *H 2367* in 1989 (FPF); 4 mi. W of Keno on Rte. 66, *H 2376* in 1989 (FPF). LAKE CO.: Winter Rock Mts. near Summer Lake, *Ferris & Duthie 422* in 1919 (CAS, RM); 6.7 mi. SE of Bear Butte, *Knutson & Tinnin DM 62* in 1978 (FPF); 30 mi. W of Lakeview on Rte. 130, *H & others 1328* in 1971 (FPF); Quartz Mtn. Pass, *Detting 4255* in 1940 (UC); Warner Mts., 1 mi. W of Warner Cyn. Ski Area on Rte. 140, *H & W 875* in 1966 (FPF); 8 mi. SE of Bear Butte, on *Pinus contorta* var. *murrayana*, *Knutson & Tinnin DM 63* in 1978 (FPF). LINN CO.: Peoria Ferry, *Roth* in 1942 (OSC). UNION CO.: Cove, *Mills* in 1924 (OSC). WALLOWA CO.: Wallowa Lake, *Mason* in 1964 (OSC), Wallowa Mts., between Bear Cr. and Minam River, *Sheldon 8845* in 1897 (MO, US). WASCO CO: Durfur, *Evinger* in 1928 (OSC); between Friend and head of Fifteen Mile Cr., *Milburge 1328* in 1936 (WTU); Friend, *Boyce FP 40179* in 1921 (OSC); Bear Springs, *H & W 611* in 1964 (FPF) and *Boyce 1907* in 1930 (FPF). WHEELER CO.: 1 mi. N of Nat. For. boundary on Derr Meadows rd., ca. 12 mi. SSE of Mitchell, *H 983* in 1966 (FPF); 1 mi. N of Ochoco Summit, 11 air mi. W of Mitchell, *H 987* in 1966 (FPF); 26 mi. S of Hardman on Rte. 207, *H & Scharpf 1271* in 1969 (FPF). COUNTY UNCERTAIN: Umpqua Mts., *Wilkes Expedition 1185* n.d. (US); mts. of eastern Oregon, *Cusick 2324* in 1899 (MO).

WASHINGTON

CHELAN CO.: 9.5 mi. N of Ardenvoir on rd. 371, *Tinnin & Knutson* in 1976 (FPF); 8 mi. NW of Chelan, *Hedgcock FP 48627* in 1929 (FPF); Rainbow Trail, 1 mi. from Stehekin River, *Ward 595* in 1946 (WTU); Peshastin, *Sandberg & Leiberg 593* in 1893 (MO, UC, US); Stehekin, Chelan Lake, *Jones* in 1911 (RSA, UC) and *Graham* in 1964 (FPF); Antwine Cr. [Antoine Cr.?, 8 mi. N of Chelan], *Harris FP 68283* in 1932 (FPF); Leavenworth, *Umbach* in 1901 (US) and *Otis 1011* and *1021* in 1920 (CAS, UC); Lake Chelan State Park, on *Picea abies*, *Russell 3848* in 1978 (FPF); Number Two Cyn. rd., 6 air mi. W of Wenatchee, *H 2380* in 1989 (FPF). FERRY CO.: 10 mi. E of Nespelem, *Peterson 63-225* in 1963 (FPF). KITTITAS CO.: 8 mi. N of Teanaway on US 97, *Wicker* in 1966 (FPF); 0.5 mi. W of Virden on US 97, *Staley* in 1973 (FPF); S of Blewett Pass, *Tinnin & Knutson* in 1976 (FPF); 2.4 mi. S of jct. of Rte. 90 and rd. from Ellensburg to Naches, *Tinnin & Knutson* in 1976 (FPF); 3 mi. W of Swauk Pass on Rte. 97, *H 2383* in 1989 (FPF). KLICKITAT CO.: 3 mi. E of Glenwood, *H 2220* in 1987 (FPF); Trout Lake, *W 3246* in 1962 (COLO, FPF); W Klickitat Co., *Suksdorf 1364* in 1892 (MO, UC, US); 1 mi. N of Satus Pass on Rte. 97, *H & W 594* in 1964 (FPF); Klickitat, *Howell 929* in 1881 (US); 3 mi. E of Glenwood on Goldendale rd., on *Pinus contorta* subsp. *latifolia*, *H 2221* in 1987 (FPF). LINCOLN CO.: 2 mi. E of Creston, *W 4369* in 1969 (FPF, UT); 6 mi. N of Davenport, *H 2061* in 1984 (FPF). OKANOGAN CO.: E of Omak, *Fiker 695* in 1932 (DS, MO, US, WTU); Squaw Cr., 5 mi. SW of Methow, *Graham* in 1964 (FPF); Pateros, *Mitchell* in 1915 (ILL); Colville Indian Res.: Disautel Summit, *Mathiasen 74-3* in 1974 (FPF); 7 mi. NW of Nespelem, *H 2207* in 1987 (FPF); 2 mi. NE of Disautel, *Tinnin & Knutson* in 1976 (FPF); Railroad Cr., *Elmer* in 1897 (WS). PEND ORIELLE CO.: Newport, on *Pinus contorta* var. *latifolia*, *Weir 3202* in 1916 (ILL). SPOKANE CO.: 15 mi. S of Spokane on US 195, *H & Laut 1293* in 1970 (FPF); 3 mi. N of Spangle, *Wicker* in 1962 (WSP); Spokane, *Weir 8475* in 1917 (FPF, RM, US) and *Weir FP 29660* in 1918 (FPF), *Sandberg 925* in 1892 (MO, US, WTU), and *Hubert FP 91292* in 1917 (OSC); 12 mi. S of Spokane, *Hansbrough & others FP 68273* in 1931 (FPF); Riverside State Park, NW of Spokane, *W 3253* in 1962 (COLO, FPF); near Spokane, *Milburge 253* in 1932 (WTU); Horseshoe Lake, NE part of Co., *Yocom* in 1947 (WTU); Tekoa Mtn., near Latah, *St. John 3051* in 1921 (UC); Medical Lake, *Elmer 1246* in 1898 (US); 9 mi. E of Reardon on US 2, *W 4368* in 1969 (FPF). STEVENS CO.: 11 mi. S of Fruitland on Rte. 25, *H 2062* in 1984 (FPF); 3.5 mi. S of Gifford, *Hedgcock FP 68059* in 1931 (FPF); 4 mi. S of Kettle Falls, *Hedgcock FP 49442* in 1929 (FPF); S of Gifford, *Hedgcock FP 54990* and *FP54991* in 1931 (FPF); N of Clark Lake, near Cedonia, *Dennis* in 1946 (WTU). YAKIMA CO.: Game Ridge Motel, Tieton River Cyn., *Wicker* in 1966 (FPF); N shore of Rimrock Lake, *Tinnin & Knutson* in 1976 (FPF); Upper Naches River region, *Grant* in 1938 (WTU); 23 mi. E of White Pass on Rte. 14, 2 mi. W of Nat. For. boundary, *H & W 595* in 1964 (FPF). COUNTY UNCERTAIN: Colville Indian Reservation, Sanpoil drainage, *Childs 53* in 1948 (OSC) and *FP 91575* in 1948 (OSC); Cascade Mts., *Tweedy* in 1882 (MO).

10. Arceuthobium cyanocarpum

All collections on *Pinus flexilis*, except as noted.

UNITED STATES

CALIFORNIA

INYO CO.: 17 mi. W of Bishop on Sabrina Lake rd., *H & Scharpf 671* in 1964 (FPF); Panamint Mts., *Johnson* in 1975 (FPF). MODOC CO.: Warner Mts., 0.8 mi. SW of Mosquito Lake, on *Pinus albicaulis*, *Mathiasen 8921* in 1989 (FPF). MONO CO.: Saddle above Convict Lake, *Kuijt 1415* in 1957 (UC): 2 mi. ESE of Lundy Lake, on *Pinus* sp., probably *Pinus flexilis*, *Hendrix 616* in 1937 (RSA, UC). RIVERSIDE CO.: San Jacinto Mts., Tahquitz Peak, *Andresen & Cochrane 1729* in 1962 (FPF); Saddle N of Tahquitz Peak, *W 3617* in 1964 (FPF, UT). SAN BERNARDINO CO.: 4 air mi. S of Tiptop Mtn., *Miller FP 98023* in 1962 (FPB); Fallsvale, Mt. San Gorgonio trail head parking lot, *Churchill 7691599* in 1976 (MSU). SISKIYOU CO.: Summit of Black Butte, on *Pinus albicaulis*, *Root & Goodding FP 68275* in 1932 (FPF), *Mielke & Zentmeyer FP 89238* in 1937 (FPF), *H & W 642* in 1964 (FPF), and *Mathiasen 8504* in 1985 (FPF); N fork of Molly Cr., on *Pinus* *albicaulis, Butler 272* in 1908 (UC); N slope of Mt. Shastina on *Pinus albicaulis, Cooke 11576* in 1938 (DS, UC); NW side of Mt. Shastina, *Cooke 16212* in 1941 (MO, PH, UC); Scott Mts., Toad Lake, 3 mi. S of Mt. Eddy, on *Pinus monticola, Engelmann* in 1880 (ILL) and *Mathiasen 8507* in 1985 (FPF); 4 mi. NW of Mt. Eddy, on *Pinus monticola, Mathiasen 8923* in 1989 (FPF); Whitney Cr., N side of Shastina, on *Pinus albicaulis, Mathiasen 8509* in 1985 (FPF) and *8924* in 1989 (FPF) and on *Pinus monticola, Mathiasen 8510* in 1985 (FPF) and *8925* in 1989 (FPF); Bolam Cr., NW slope of Shastina, on *Pinus albicaulis, Mathiasen 8620* in 1986 (FPF) and on *Pinus monticola, Mathiasen 8621* in 1986 (FPF); Klamath Nat. For., Lake Mtn., on *Pinus balfouriana, Bailey 72-39* in 1972 (FPF); Summit Divide between Bear Cr. and Toad Lake, on *Pinus balfouriana, Mathiasen 8508*, in 1985 (FPF); Parks Cr. rd., 9 air mi. SW of Weed, on *Pinus monticola, H & Mathiasen 2419* in 1990 (FPF). TRINITY CO.: High Camp Cr., 5 mi. WNW of Mt. Eddy: on *Pinus monticola, Miller & Bynum* in 1964 (FPF), *Scharpf & Miller* in 1965 (FPF), *Mathiasen 8506* in 1985 (FPF), and *Brown* in 1965 (FPF), on *Pinus balfouriana, Miller & Bynum* in 1964 (FPF), *Scharpf & Miller* in 1965 (FPF) and *Brown* in 1965 (FPF). COUNTY UNCERTAIN: Tenderfoot Lake, Siskiyou Nat. For., on *Pinus monticola, Lewis* in 1916 (ILL).

COLORADO

BOULDER CO.: 3 mi. S of Ward, *H & Gill 195* in 1958 (FPF); Brainard Lake rd. jct. at Ward, *H 417* in 1963 (FPF); Ward, *Bethel & others 4314* (MO) and *4315* in 1921 (CAS, CS, COLO, JEPS, MO, RSA, RM, UC, US, WTU), *Bethel* in 1921 (CS), and *W 2926* in 1961 (COLO); Allenspark, *Johnston & Thompson FP 24882* in 1917 (FPF); 1.3 mi. E of Eldora, *H 689* in 1964 (FPF); Sugarloaf Mtn., *H & Fisher 1495* in 1974 (FPF); Green Mtn. near Boulder, *Mathiasen* in 1973 (FPF) and on *Pinus ponderosa, Mathiasen* in 1973 (FPF); 3 mi. S of Ward on Rte. 160, on *Pinus contorta, H & Gill 194* in 1958 (FPF) and on *Pinus ponderosa, H & Gill 198* in 1958 (FPF) and *H & W 565* in 1964 (FPF); 2.2 mi. N of Boulder Cyn. on Four Mile rd., on *Pinus ponderosa, H & others 1344* in 1971 (FPF), *H & Laut 1429* in 1972 (FPF), and *H & Fisher 1494* in 1974 (FPF); at jct. of Rts. 7 and 72, on *Pinus ponderosa, H & others 1894* in 1979 (FPF); CLEAR CREEK CO.: Hamlin Gulch rd. 1.4 mi. from Fall River rd., ca. 7 air mi. NW of Idaho Springs, *H 1057* in 1967 (FPF), and on *Pinus ponderosa, H 1058* in 1967 (FPF). EL PASO CO.: Ridge rd., *Christ 1877* in 1935 (CS); Rock Cr., ca 0.5 mi. W of Cheyenne Mt. Zoo, *Hill FP 68276* in 1932 (FPF); 5 mi. S of Bruin Inn on Gold Camp rd., *H 540* in 1963 (FPF); Pikes Peak, Lake Moraine, *Ewan 15154* in 1943 (COLO); Pikes Peak, *Hedgcock FP 1614* in 1909 (FPF) and *FP 19185* in 1911 (FPF); *Macbride 2677* in 1913 (MO); Fremont Exp. For. (2 mi. W of Manitou Springs), *Hedgcock FP 22706* and *22707* in 1916 (FPF) and *Hedgcock & others FP 24852* in 1917 (FPF); Pikes Peak, Minnehaha, *Hedgcock FP 635* in 1909 (FPF); Pikes Peak For. Reserve, *Flintham* in 1903 (US); Pikes Peak, Halfway, *Hartley FP 1774* in 1909 (FPF) and *Hedgcock FP 15909* in 1914 (FPF, RSA); Rampart Range rd., 3 mi. SE of Woodland Park, *Schacht* in 1964 (FPF); 7 mi. NW of Manitou Springs, on Rampart Range rd., *H & Laut 1327* in 1971 (FPF); W of Monument, *Zimmerman* in 1981 (FPF); Crystal Park, *Gill FP 68235* in 1932 (FPF). FREMONT CO: Sangre de Cristo Range: 5-6 mi. SW of Coaldale, *Schacht* in 1969 (FPF); 8 mi. SW of Coaldale on Hayden Pass rd., *H & Laut 1317* in 1970 (FPF). GILPIN CO.: 1 mi. SW of Tolland, *H 827* in 1965 (FPF). HUERFANO CO.: Silver Mtn., 4 mi. E of La Veta Pass, *H & others 1498* in 1974 (FPF), and on *Pinus aristata, H & others 1497* in 1974 (FPF). JACKSON CO.: Red Cyn., 18 air mi. W of Walden, *H 1695* in 1976 (FPF). LARIMER CO.: Eaton Reservoir, *Douglass* in 1957 (CS); 4 mi. W of Eaton Reservoir, *Hinds* in 1962 (FPF); Estes Park, *Cooper 65* in 1904 (RM); Boulder Ridge, 0.5 mi. S of Sand Cr. rd., *H 82* in 1961 (FPF); 1.6 mi. E of Pingree Park on main rd., *H 1055* in 1967 (FPF), and on *Pinus contorta, H & others 1275* in 1970 (FPF); Rocky Mtn. Nat. Park, Gem Lake Trail, *Ashton 66* in 1930 (RMNP); Rocky Mtn. Nat. Park, Glacier Gorge, *Loll FP 11832* in 1924 (FPF); Boulder Ridge, *H 196* in 1961 (FPF); Boulder Ridge, 0.5 mi. S of Wyoming boundary, *H 84* in 1961 (FPF); 6.5 mi. S of Estes Park on Rte. 7, *H & Staley 288* in 1962 (FPF); Pennock Cr., 2 mi. S of Pingree Park rd., *H 562* in 1964 (FPF); Medicine Bow Mts., 4.3 mi. S of Wyoming boundary on Old Roach rd., *H 829* in 1965 (FPF). MOFFAT CO.: Cold Spring Mtn., Wiggins Hunting Camp, near O-Wi-Yu-Kit Spring, *Weber 14386* in 1970 (COLO). COUNTY UNCERTAIN: La Sal Mts., *Weir 8343* in 1915 (FPF, ILL).

IDAHO

BEAR LAKE CO.: Ridge S of Bloomington Lake, W of Bloomington, *Peterson 65-370* in 1965 (FPF). BUTTE CO.: Craters-of-the-Moon Nat. Mon., *Peterson 62-53* in 1962 (FPF), *Mahoney* in 1965 (FPF), and *H 1368* in 1971 (FPF). CUSTER CO.: Lost River Range, ridge NE of Birch Springs, on *Pinus albicaulis, Mathiasen 8914* in 1989 (FPF). LEMHI CO.: Near Salmon, *Wolpert* in 1917 (FPF, ILL).

MONTANA

BEAVERHEAD CO.: Big Hole Valley, on *Pinus albicaulis, Weir 3216* n.d. (FPF, ILL). BIG HORN CO.: Crow Indian Res., Bighorn Mts., Rotten Grass drainage, *Gregory* in 1969 (FPF); Pryor Mts., Sage Cr. rd., 1.4 mi. NW of Custer Nat. For. boundary, *Stickney 2670* in 1972 (MONT); CARBON CO.: Rock Cr. Ranger Sta., *Hedgcock FP 11147* in 1911 (FPF); 5 mi. W of Red Lodge on Rock Cr. rd., *W 3865* in 1965 (FPF, UT); Pryor Mts., Crooked Cr., *Brown* in 1969 (FPF). DEERLODGE CO.: French Gulch near Anaconda, *Weir 3246* in 1913 (FPF, ILL); Mt. Haggin near Anaconda, *Weir 3218* in 1914 (FPF, ILL); near Anaconda, *Weir 8254* in 1914 (ILL). GALLATIN CO.: Rocky Cyn., near Bozeman, *Blankinship 436* in 1905 (RSA, RM, US): 7 mi. E of Bozeman, *W 3257* in 1962 (COLO, FPF): Bozeman, *Brandegee* in 1883 (UC) and *Langohr* in 1917 (ILL); Mt. Bridger, *Henshall* in 1899 (MONT). MADISON CO.:

6 mi. N of McAlister on Rte. 287, *Mathiasen 9003* in 1990 (FPF). COUNTY UNCERTAIN: Mt. Powell, *Weir 8345* in 1914 (ILL).

NEVADA

CLARK CO.: Charleston Mts.: on *Pinus longaeva*, *Coville & Funston 311* in 1891 (US); head of Tractor Lane, Lee Cyn. *Train 2150* in 1938 (UC); Scout Cyn. rd., Lee Cyn., on *Pinus longaeva*, *Krebill 723* in 1968 (FPF); Peak Trail, *Clokey 5430* in 1935 (CAS, FPF, RM, RSA, UC, US, WTU), and on *Pinus longaeva*, *Clokey 5429* in 1935 (CAS, FPF, JEPS, UC, WTU) and *Clokey 5492* in 1935 (CAS, JEPS, RM, RSA, WTU); Sheep Range, Sawmill Cyn., on *Pinus longaeva*, *Haber* in 1978 (FPF). ELKO CO.: Ruby Mts.: *Grover* in 1958 (FPF), Lamoille Cyn., 12 mi. SE of Lamoille, *H & W 575* in 1964 (FPF), near top of Lemoille Cyn., *Mathiasen 8908* in 1989 (FPF); Copper Mts., 9 mi. S of Jarbridge, on *Pinus albicaulis*, *H & Mark 1379* in 1971 (FPF); E. Humboldt Mts., Angel Lake, *Bailey 75-93* in 1975 (FPF) and, on *Pinus albicaulis*, *Bailey 75-94* in 1975 (FPF); Bull Run Mts., NW slopes of Porter Peak, *Mathiasen 8929* in 1989 (FPF). ESMERALDA CO.: White Mts., 1.5 mi. SE of Boundary Peak, *Mathiasen 8913* in 1989 (FPF). HUMBOLDT CO.: Santa Rosa Range, 2.3 mi. S of Windy Gap, *Mathiasen 8919* in 1989 (FPF). LANDER CO.: Toiyabe Range; W slope of N Toiyabe Peak, *Mathiasen 8909* in 1989 (FPF); 0.5 mi. W of Big Cr. Campground, *Mathiasen 8910* in 1989 (FPF). NYE CO.: Toiyabe Range, 3 mi. N of Arc Dome, *Mathiasen 8911* in 1989 (FPF). WHITE PINE CO.: S Snake Range, Mt. Washington, on *Pinus longaeva*, *Bailey & Ellis 84-08* in 1984 (FPF), 2.5 mi. NE of Mt. Washington, *Mathiasen 8906* in 1989 (FPF) and, on *Pinus longaeva*, *Mathiasen 8907* in 1989 (FPF); N Snake Range, Mt. Moriah, 4.5 mi. NW of Hampton Cr. trailhead, *Mathiasen 8903* in 1989 (FPF) and, on *Pinus longaeva*, *Mathiasen 8904* in 1989 (FPF).

OREGON

DESCHUTES CO.: On ridge between Three Cr. Lake and Little Three Cr. Lake, on *Pinus albicaulis*, *H 1927* in 1979 (FPF) and *Mathiasen 8926* in 1989 (FPF) and on *Tsuga mertensiana*, *H 1928* in 1979 (FPF) and *Mathiasen 8927* in 1989 (FPF). COUNTY UNCERTAIN: Obsidian Cliff, on *Pinus albicaulis*, *Gorman 1753* in 1903 (US).

UTAH

CACHE CO.: Logan Cyn., near Jardine Juniper, *Krebill 454* in 1967 (FPF); Tony Grove Lake, *Maguire & Maguire 20377* in 1939 (RM, WTU) and *20378* in 1939 (RM); 0.25 mi. NW of Tony Grove Lake, *Peterson 62-75* in 1962 (FPF); Mt. Naomi, 1 mi. from Tony Grove, *Snell 1047* in 1938 (UC, WTU). DAGGETT CO.: 2 mi. W of Utah, Wyo., and Colo. corner on Loop rd. from Clay Basin, *Bleazard* in 1965 (FPF, UT). DUCHESNE CO.: Indian Cyn., 25.5 mi. SW of Duchesne on Rte. 33, *H 571* in 1964 (FPF). GARFIELD CO.: 10 mi. W of Bryce Cyn. Lodge, *Dorn* in 1947 (RSA); near Escalante, *Peterson 50-61* in 1961 (FPF) and on *Pinus longaeva*, *Peterson 52-61* in 1961 (FPF); Bryce Cyn. Nat. Park, 0.25 mi. W of Bryce Pt., on *Pinus longaeva*, *H 2103* in 1985 (FPF); Bryce Cyn. Nat. Park, Bryce Pt., *H 2102* in 1985 (FPF); Bryce Cyn. Nat. Park; Headquarters area, *Gill FP 68144* in 1932 (FPF) and on *Pinus longaeva*, *FP 68143* in 1932 (FPF); *Garrett FP 38107* in 1921 (FPF) and on *Pinus longaeva*, *FP 38106* in 1921 (FPF); *H 255* in 1962 (FPF) and on *Pinus longaeva*, *H 256* in 1962 (FPF); Bryce Point, *W 3034 and 3178* in 1962 (COLO, FPF), *Howell & Eastwood 7204* n.d. (CAS); Escalante Summit, *H & Geils 2144* in 1986 (FPF); 0.5 mi. N of Escalante Summit, *Mathiasen 8932* in 1989 (FPF) and on *Pinus longaeva*, *Mathiasen 8933* in 1989 (FPF); 3 mi. E of Pine Lake, *Mathiasen 8934* in 1989 (FPF) and on *Pinus longaeva*, *Mathiasen 8935* in 1989 (FPF). IRON CO.: 16.5 mi. E of Cedar City on Rte. 14, *H 679* in 1964 (FPF) and on *Pinus longaeva*, *H 680* in 1964 (FPF); 1 mi. W of Summit on Rte. 14, *W 4127* in 1966 (FPF, UT) and on *Pinus longaeva*, *W 4125* in 1966 (FPF, UT). KANE CO.: 1 mi. N of Navajo Lake on Rte. 14, *W 4124* in 1966 (FPF, UT); N shore of Navajo Lake, *H & Laut 1162* in 1969 (FPF). PIUTE CO.: 8 mi. S of Belknap Guard Sta., above Deep Cr., *Peterson 65-339* in 1965 (FPF). RICH CO.: 17.5 mi. W of Woodruff on Rte. 39, *H 2301* in 1989 (FPF). TOOELE CO.: Deep Creek Mts., *Bailey 74-07* in 1974 (FPF) and on *Pinus longaeva*, *Bailey 74-08* in 1974 (FPF). COUNTY UNCERTAIN: Charles Peak, southern part of state, *Siler* in 1879 (MO).

WYOMING

ALBANY CO.: 1 mi. N of Albany rd. on Cinnabar Park rd., *H & Hinds 197* in 1961 (FPF); Centennial Mtn., *Nelson* in 1915 (RM); Laramie Mts. *Nelson 8247* in 1901 (ARIZ, MO, RM, US); Pilot Knob, *Nelson* in 1905 (MO, RM); Boulder Ridge, 7 mi. SW of Tie Siding, *H 85* in 1961 (FPF); Sheep Mtn., *Nelson 3320* in 1897 (RM, US); Hermosa, *Garrett FP 38174* in 1921 (FPF); Centennial, Mullin Cr., *Hedgcock FP 15833* in 1914 (FPF); Dale Cr. Bridge near Sherman, col.? n.d. (MO); Laramie Mts., *Weir 9872* in 1918 (FPF, ILL); 3 mi. SW of Pilot Hill, *H & Bailey 1008* in 1966 (FPF); Boulder Ridge, 10 ft. N of Colorado boundary, 7 mi. SW of Tie Siding, on *Pinus ponderosa*, *H 284* in 1962 (FPF); Jelm Mtn., *H 1797* in 1977 (FPF); Laramie Mts., 10 air mi. E of Bosler, *Landis* in 1974 (FPF); Med. Bow Nat. For., col. ? *FP 89306* in 1935 (FPF). BIG HORN CO.: Big Horn Mts.: 3 mi. SW of Medicine Wheel, *Brown* in 1973 (FPF); 12 air mi. NNE of Tensleep, *Brown & Walters* in 1973 (FPF); Alkalai rd., 14 mi. N of Hyattville, *Nelson 3413* in 1979 (RM). CARBON CO.: Medicine Bow Mts.: 3 mi. S of Pennock Mtn., *Landgraf* in 1965 (FPF) and Cooper Cr., 12 air mi. N of Centennial, *Landgraf* in 1965 (FPF); Ferris Mts.: *Nelson 4959* in 1898 (MO, RM); NE slope of Whiskey Gap, *Dunder* in 1969 (FPF); Pete Cr. *Dorn 3698* in 1981 (RM) and *Lichvar 4608* in 1981 (RM); Shirley Mts., Lower Prior Flat, *Dunder* in 1969 (FPF); N side of Elk Mtn., Rattlesnake Cr., *Dunder* in 1969 (FPF); Shirley Mts., 2 mi. N of Cave Cr., *H 1802* in 1977 (FPF); Seminoe Mts., 3 mi. NW of Seminoe Dam, *H 1694* in 1976 (FPF). CONVERSE CO.:

Laramie Mts.: Cold Springs, *Simmons* in 1917 (ILL); Rock Cr., *Brown & Walters* in 1973 (FPF). FREMONT CO.: Slate Cr., SE Lander District, *Peterson* in 1960 (FPF); Fossil Hill, ca. 10 air mi. SW of Lander, *Stewart* in 1967 (FPF); W fork of Long Cr., 21 mi. WNW of Dubois, *H 277* in 1962 (FPF); 4 mi. WNW of South Pass City, *Landgraf & Davel* in 1965 (FPF); W side of South Pass on Rte. 28, *Krebill K-915B* in 1972 (FPF); 20 air mi. S of Lander, *H 1627* in 1975 (FPF); 7 air mi. SE of Dubois, *H 1632* in 1975 (FPF); 0.5 mi. W of Gas Hills, *H 1856* in 1978 (FPF); Louis Lake rd., on *Pinus albicaulis*, *H 1858* in 1978 (FPF); Rock Cr. Mtn., *Haines 6944* in 1986 (RM). Green Mts., Crook Gap, *H & Landgraf 279* in 1962 (FPF), 10 air mi. SSE of Jeffrey City, *H 1692* in 1976 (FPF); 10 air mi. SW of Jeffrey City, *H 1693* in 1976 (FPF). HOT SPRINGS CO.: Merrit Pass, 30 mi. N of Morton, *H 1860* in 1978 (FPF). LINCOLN CO.: Alpine, along Snake River, *Payson & Armstrong 3406* in 1923 (MO, PH, RM); E of Alpine, *Graham*, in 1965 (FPF). NATRONA CO.: Rattlesnake Mts., Garfield Peak, *Hartman 13016* in 1982 (RM). PARK CO.: "Cody," *Weir FP 91249* in 1918 (FPF, OSC, ILL); Cody Cyn., 44 mi. W of Cody on Rte. 20, *W 3258* in 1962 (COLO); Rattlesnake Cr., ca. 15 air mi. WNW of Cody, *Bailey* in 1966 (FPF); Dry Fork, ca. 19 air mi. NW of Cody, *Stewart* in 1967 (FPF); along switchbacks E of Dead Indian Campground, ca. 22 air mi. NW of Cody, *Stewart* in 1967 (FPF); Red Ridge, 18.5 mi. NW of Cody, *Nelson 13001* in 1985 (RM); Battleship Mtn., 2.5 mi. N of Dead Indian Pass, *Nelson 12587* in 1985 (RM); Heart Mtn., *Hartman 13059* in 1981 (RM); Rattlesnake Mtn., *Evert 4009* in 1982 (RM); Absaroka Range: 10-11 air mi. E of Sunlight Ranger Sta., *Hartman 22053* in 1985 (RM) and N Fork of Crandall Cr., *Hartman 21689* in 1985 (RM). SUBLETTE CO.: O.9 mi. N of LaBarge Cyn. rd. on Sheep Cr. rd., ca 17 air mi. WNW of LaBarge, *Mathiasen & LaMadeleine 8930* in 1989 (FPF). YELLOWSTONE NAT. PARK: "Yellowstone For. Reserve," *Hapeman* in 1906 (RM).

11. *Arceuthobium divaricatum*

All collections on *Pinus edulis*, except as noted.

MEXICO

BAJA CALIFORNIA

Sierra Juárez: 21 mi. S of La Rumorosa on rd. to Laguna Hanson, on *Pinus quadrifolia*, *Lightle & Gill 64-34* in 1964 (FPF); 16.5 mi. N of Laguna Hanson on La Rumorosa rd., on *Pinus quadrifolia*, *H & Scharpf 786* in 1965 (FPF).

UNITED STATES

ARIZONA

APACHE CO.: Carisso, *Brandegee 1226* in 1875 (PH, UC); 2 mi. S of Eagar, *H & Lightle 208* in 1962 (FPF); 17 mi. NW of Sawmill on Cyn. de Chelly rd., *Lightle & Weiss 66-45* in 1966 (FPF); 3 mi. E of Lukachukai, *Lightle & Weiss 66-47* in 1966 (FPF); 8 mi. SW of Red Rock on Lukachukai rd., *Lightle & Weiss 66-52* in 1966 (FPF); 5 mi. W of Window Rock on Rte. 264, *Lightle & Weiss 69-3* in 1969 (FPF); 19 mi. W of Maverick on White River rd., *H & Lightle 904* in 1966 (FPF); 15 mi. E of Keams Cyn. on Rte. 264, *H & Fisher 1354* in 1971 (FPF); 3 mi. N of US 60 on Rte. 61, *Lightle 69-1* in 1969 (FPF); Cyn. de Chelly Nat. Mon.: 6 mi. SE of Chinle, *Ferris 10158* in 1940 (UC); 5 mi. W of Tsalie Dam on N Rim of Cyn. del Muerto, *Lightle & others 65-54* in 1965 (FPF); Spider Rock Lookout, *Mathiasen & Ford 7912* in 1979 (FPF); Cyn. del Muerto, *Halse* in 1971 (ARIZ). COCONINO CO.: Grand Cyn. Nat. Park: South Rim: *Toumey* in 1894 (UC), *MacDougal 190* in 1898 (ARIZ, UC, US), *Knowlton 295* in 1889 (US), *Spaulding FP 303* in 1909 (FPF), *Hedgcock FP 4907* in 1910 (FPF), *Hitchcock 25* in 1913 (US), *Bartram 435* in 1920 (US), *Gill FP 68232 and FP 68233* in 1932 (FPF); El Tovar, *Eastwood* in 1917 (CAS); Rim at Bright Angel, *Eastwood 5903* in 1918 (CAS); Desert View: *Cronquist* in 1938 (RM), *Gill FP 68234* in 1932 (FPF), and *H & Scharpf 701* in 1964 (FPF); 1 mi. SW of Bright Angel Camp, *Gill FP 68132* in 1932 (FPF); Bright Angel Trail, *Gill FP 68230* in 1932 (FPF); Grandview, *Dachnowski-Stokes* in 1913 (US); El Tovar, *Setschell* in 1907 (UC); Duck-on-a-Rock, *H 35* in 1954 (FPF) and *H & Scharpf 703* in 1964 (FPF); near Roaring Springs, *Mathiasen 8119* in 1981 (FPF); Desert View, *H 1088* in 1967 (FPF). Flagstaff, *Jones 3973* in 1884 (ARIZ, DS, RSA, RM, UC); rim of Prospect Cyn., 14 mi. N of Frazier Well, *H & Lightle 187* in 1962 (FPF); 14 mi. SE of Rte. 64 on Rte. 180, *H 246* in 1962 (FPF); NE of Long Valley, *Ellis FP 89426* in 1939 (FPF); Sedona, *Hedgcock FP 4917* in 1910 (FPF); North Kaibab Plateau on US 89, *Gill FP 68300* in 1934 (FPF); 6 mi. E of Jacob Lake on US 89, *W 3185* in 1962 (COLO, FPF); Kaibab For., *Richards* in 1938 (WTU); Jacob Lake to Fredonia, *Kearney & Peebles 13761* in 1937 (ARIZ, US); 6 mi. N of Jacob Lake on Rte. 89, *H & Gill FP 89990* in 1952 (FPF); 10 mi. N of Jacob Lake on Rte. 89, *Mielke FP 89700* in 1944 (FPF); 30 mi. SW of Winslow on Rte. 87, *H & Lightle 915* in 1966 (FPF); 34 mi. S of Winslow on Chevlon rd., *H & Lightle 916* in 1966 (FPF); Walnut Cyn. Nat. Mon., *Lightle 66-22* in 1966 (FPF) and *H & Lightle 1355* in 1971 (FPF); Antelope Pass, 15 mi. S of Page on US 89, *Lightle & Weiss 69-4* in 1969 (FPF); Deadman Flat, about 8 air mi. NNW of Sunset Crater, *Little 4401* in 1937 (USFS); 23 mi. S of Williams on Perkinsville rd., *H & Lightle 1402* in 1972 (FPF); 10 mi. E of Jacob Lake, *Lightle & Weiss 69-5* in 1965 (FPF); 12.8 mi. W of Jacob Lake, *Moore & others 6756* in 1966 (ASU); 21 mi. S of Navajo Trading Post, *H & others 1390* in 1971 (FPF); 11 mi. N of I-40 on Rte. 64, *H 2399* in 1990 (FPF). GILA CO.: 6 mi. SE of Cedar Cr. on Rte. 73, *H & Lightle 906* in 1966 (FPF); 7 mi. ESE of Cibecue, *Granfelt 67-82* in 1967 (ASU). GRAHAM CO.: San Carlos Indian Res., 3 mi. W of Eagle Cr. on Malay Gap rd., *H & Lightle 1114* 1968 (FPF). GREENLEE CO.: Red Hill near Blue, *Ellis FP 89331* in 1939 (FPF); 32 mi. N of Clifton on US 666, *Mathiasen 74-18* in 1974 (FPF). MOHAVE CO.: Mt. Trumbull: on *Pinus californiarum* subsp. *fallax*, *Hevly* in 1959 (MNA) and col.? (MO); 5 mi. S of Nixon Spring, *H & others 1165* in 1969 (FPF); 3.8 mi. E of Nixon Spring, *Brown & Parfitt 716* in 1978 (ASU); 4 mi. E of Mt. Trumbull P. O., *H & Lightle 1168* in

1969 (FPF); 10 mi. W of Wolf Hole on Black Rock Mtn. rd., on *Pinus californiarum* subsp. *fallax*, *H & others 1171* in 1969 (FPF); Wolf Hole Mts., Little Wolf Hole Pass, on *Pinus californiarum* subsp. *fallax*, *H 2135* in 1986 (FPF); Hualapai Mts., ca. 7 mi. SE of Kingman on Hualapai Mtn rd., on *Pinus californiarum* subsp. *fallax*, *H 2401* in 1990 (FPF). NAVAJO CO.: 4.5 mi. S of Rte. 264 on Rte. 77, ca. 12 air mi. SE of Keams Cyn., *H & Lightle 1084* in 1967 (FPF), 15 mi. E of Heber, *Ellis FP 89337* in 1939 (FPF); 9 mi. E of Pinedale on Rte. 260, *Pinkava & others 4377* in 1969 (ASU); 2 mi. W of Heber, *Lightle 64-19* in 1964; 10 mi. E of Heber, *Lightle 69-2* in 1969 (FPF); between Snowflake and Show Low, *Hevly* in 1959 (MNA); 7 mi. W of US 60 on Mogollon Rim rd., *H & Lightle 922* in 1966 (FPF); Navajo Nat. Mon., Betatakin Cyn., *Wetherill 919/3149* in 1937 (ARIZ, MNA) and *Howell 24505* in 1948 (CAS); Pinon, *Whiting 854/2825* in 1937 (ARIZ, MNA); 4 mi. SE of Fort Apache on Maverick rd., *H & Lightle 905* in 1966 (FPF). YAVAPAI CO.: Mingus Mtn., 5 mi. W of Jerome on US 89, *H & Lightle 245* in 1962 (FPF); 17 mi. SE of Camp Verde, on *Pinus californiarum* subsp. *fallax* , *Weiss & Lucero* in 1974 (FPF); 5 mi. S of Sedona, *H 1786* in 1977 (FPF), and on *Pinus californiarum* subsp. *fallax*, *H 1785* in 1977 (FPF); Limestone Cyn., on For. Service rd. 573, 4.3 mi. W of Rte. 89, *Lightle* in 1984 (FPF); Rte. 6, 7 air mi. W of the village of Chino Valley, on *Pinus californiarum* subsp. *fallax*, *H 2398* in 1990 (FPF); Granite Mts., 12 mi. W of Seligman on I-40, on *Pinus californiarum* subsp. *fallax*, *H 2400* in 1990 (FPF). COUNTY UNCERTAIN: Mahogany Range, Point Daguerre, *Palmer 2* in 1869 (US); Salt Run [River?] Valley, *Gilbert 116* in 1873 (MO).

CALIFORNIA

All California collections on *Pinus monophylla*, except as noted.

INYO CO.: 8.5 mi. W of Lone Pine on Mt. Whitney Trail, *Gill & Wright FP 68061* in 1931 (FPF); 10 mi. "above" Lone Pine, *Schrieber 1017* in 1934 (UC); SE side of Mt. Whitney, *Armstrong 1024* in 1934 (UC); 3 mi. W of Lone Pine, *Kuijt 1389* in 1957 (UC); Inyo Mts., Whippoorwill Flats on Saline Valley rd., *W 2740* in 1960 (RSA). Death Valley Nat. Mon.: Wildrose Cyn., *Stewart* in 1935 (US); head of Death Valley Cyn., *Coville & Gilman 120* in 1931 (US); trail to Wildrose Summit, *Colville & Gilman 707* in 1931 (US); Thorndike Campground, Wildrose Cyn., *Bailey 77* (FPF). LOS ANGELES CO.: San Gabriel Mts.: Oak Springs Ranch, *Thorne & Tilforth 43085* in 1973 (ENCB); Mescal Cr., *Ewan 9941* in 1936 (MO); Swarthout Cyn., *Putnam* n.d., (ILL). MONO CO.: 6 mi. S of Coleville, *Wagener FP 89604* in 1936 (FPF) and *Kuijt 1413* in 1957 (UC); 0.5 mi. S of Coleville, *Peterson 63-131* in 1963 (FPF); 1.5 mi. S of Walker on Rte. 395, *W 6770* in 1987 (FPF); 6 mi. S of Walker on Rte. 395, *H 2437* in 1991 (FPF). SAN BERNARDINO CO.: San Bernardino Mts.: Johnson Grade, Little Bear Lake, *Gill FP 89420* in 1939 (FPF) and *Howe 1726* in 1947 (SD); Kingston Peak, 35 air mi. NNE of Baker, *Hendrickson 14051* in 1974 (SD); Big Bear Ranger Sta., *Gill & Wright FP 68239* in 1931 (FPF); Dobel Mine, Bear Lake, *Gill & Wright FP 68064* in 1931 (FPF); Arrastre Cr., 5 mi. E of Big Bear City, *Miller FP 98024* in 1962 (FPB); Arrastre Cr., 3 mi. SE of Baldwin Lake, *Jaeger* in 1938 (POM); NE slope San Bernardino Mts.: *Parish & Parish 1442* in 1882 (MO, UC, US); N side of Sugarloaf, *Munz 10771* in 1926 (RSA); 1 mi. N of Baldwin Lake, *H 733* in 1965 (FPF); Bear Valley, *Lieberg 3312* in 1898 (US). New York Mts.: 5 mi. SE of Ivanpah, *Gill & Wright FP 68238* in 1931 (FPF); Live Oak Cyn., *Johnston & others* in 1977 (FPF); 0.3 mi. NNW of Keystone Springs, *Bailey* in 1984 (FPF); 0.2 mi. S of Keystone Springs *Bailey* in 1984 (FPF); 1/4 mi. N of Keystone Springs, *Thorne & Tilforth 44475* in 1974 (ENCB); Live Oak Campground, on *Pinus edulis*, *Bailey & Rockwell* in 1978 (FPF); near head of Keystone Cyn., on *Pinus edulis*, *Johnston & others* in 1977 (FPF). Clark Mts.: 1.8 mi. up Coliseum Mine rd., *Thorne & Tilforth 44525* in 1976 (ENCB); S fork of Clark Mtn., *Bailey 78-78* in 1978 (FPF). Providence Mts.: *Brandegee* in 1902 (UC); S fork of N fork of Fountain Cyn., *Beal 660* in 1939 (JEPS); near Bonanza King Mine, *Munz & others* in 1920 (POM) and *Shields* in 1965 (FPF); Clark Mts., 0.5 mi. N of summit of Clark Mtn., *Johnson & others* in 1977 (FPF). VENTURA CO.: Mt. Pinos, Seymour Cr., *Peirson 3251* in 1922 (RSA); Mt. Pinos area, *W 3217* in 1962 (COLO, FPF); E edge of Fraser Mtn., *Putnam FP 98054* in 1919 (FPB); Fraser Mtn., *Root* in 1919 (ILL); about 13 mi. E of Rte. 33 on Lockwood Valley rd., *H & Scharpf 2082* in 1984 (FPF). COUNTY UNKNOWN: *Bigelow* in 1853-54 (US).

COLORADO

DELTA CO.: S of Delta, *Hedgcock FP 9299* in 1911 (FPF). DOLORES CO.: 4 air mi. E of Cahone, *Hinds 63-10* in 1963 (FPF); 13 mi. SE of Dove Cr., *H 1907* in 1979 (FPF). GARFIELD CO.: West Elk Guard Sta., N of Newcastle, *Hinds* in 1961 (FPF); 11 mi. NW of Rifle, *H & others 1383* in 1971 (FPF). LA PLATA CO.: without location, *Curran* in 1914 (US); Durango, *Tweedy 595* in 1896 (US); N of Durango, *Hunt & Bethel FP 24428* in 1917 (FPF); Bayfield, *Hedgcock & Bethel FP 24674* in 1917 (FPF); 5 mi. ENE of Ignacio, *Loughridge 484* in 1934 (USFS); 7 mi. SE of Bayfield, *Hinds* in 1975 (FPF) and *Ramalay* in 1985 (FPF); near Durango: ridge S of rd. up Smelter Mtn., ridge S of Horse Gulch, and Haflin Cr. Trail *Ramaley* in 1985 (FPF); 5 mi. NNE of Durango, *Ramaley* in 1985 (FPF). LARIMER CO.: transplanted tree in Ft. Collins, *H 1338* in 1971 (FPF). MESA CO.: Colorado Nat. Mon.: *Wilford* in 1961 (FPF); 2 mi. S of Fruita, *W 3168* in 1962 (COLO, FPF); 7 mi. SE of Palisade, *Hinds* in 1973 (FPF). MONTEZUMA CO.: Mancos: *Baker & others 94* in 1898 (CAS, MO, RSA, RM, US), *Tracy & others 388* in 1898 (CAS), and *Eastwood* in 1891 (COLO); 3 mi. S of Mancos, *Peterson 30-61* in 1961 (FPF); 1 mi. NE of Mancos, *Hinds* in 1965 (FPF). Mesa Verde Nat. Park: Wetherill Mesa, *Erdman 120* in 1959 (COLO, WTU), *Weber 6065* in 1951 (COLO), and *Bethel & Hunt FP29261* in 1918 (FPF), N entrance, *H & Scharpf 691* in 1964 (FPF), Spruce Tree House, *Mathias 652* in 1929 (MO); about 12 mi.

NE of Lewis, *Copple 99* in 1920 (USFS). MONTROSE CO.: 13 mi. SW of Montrose, *Hinds* in 1960 (FPF); 5 mi. W of Cimarron, *Hinds 63-14* in 1963 (FPF); 20 mi. N of Placerville, *Pesman* in 1960 (CS); 1 mi. E of Ute, *Hinds 63-17* in 1963 (FPF); 11 mi. E of Naturita on Rte. 90, *H 1087* in 1967 (FPF); 8 mi. W of Bedrock on Rte. 90, *H 713* in 1965 (FPF); Black Cyn. rd., 3.7 mi. N of US 50, *H & Laut 1433* in 1972 (FPF). OURAY CO.: 2 mi. SE of Ridgeway, *Payson FP 26016* in 1917 (FPF). RIO BLANCO CO.: 20 air mi. SSE of Rangely, *Snell* in 1974 (FPF); 13 air mi. SE of Rangely, *Snell* in 1974 (FPF); 8 air mi. NNW of Douglas Pass, *Landis* in 1975 (FPF). SAN MIGUEL CO.: 7 mi. N of Egnar on Rte. 141, *H & Mathiasen 1473* in 1973 (FPF).

NEVADA

All Nevada Collections on *Pinus monophylla*, except as noted.

CHURCHILL CO.: Carroll Summit, 10 mi. E of Eastgate on US 50; *H & W 835* in 1966 (FPF). CLARK CO.: Charleston Mts.: *Coville & Funston 308* in 1891 (US); Deer Cr. Campground, *W 3207* in 1962 (COLO, FPF); Kyle Cyn., *Clokey 8565* in 1939 (ARIZ, CAS, CS, MO, RM, RSA, UC, WTU); 2 mi. E of Nat. For. boundary on Rte. 158, *H & Scharpf 672* in 1964 (FPF); Lee Cyn., *Krebill 724* in 1968 (FPF); 1.8 mi. below Nat. For. boundary on Lee Cyn. rd., *Henderson 7310* in 1987 (ID). Sheep Mts.: Spring Cyn., *Johnson* in 1969 (FPF); 3 mi. W of Hidden Forest Cabin, *Rockwell & Horn* in 1987 (FPF); Sawmill Cyn., *Haber & others* in 1978 (FPF); Potosi Pass, *Bailey & Rockwell* in 1978 (FPF). Newberry Mts, 0.25 mi. E of Christmas Tree Pass, on *Pinus edulis*, *Bailey & Rockwell* in 1978 (FPF). DOUGLAS CO.: Pine Nuts Hills, S of Carson City, *Peterson* in 1960 (FPF); 9 mi. S of Gardnerville, *Wagener FP 89603* in 1936 (FPF); near Minden, *McKlevey 1464* in 1930 (US); ca. 7 mi. N of Topaz Lake on US 395, *Krebill & Nelson 467* in 1967 (FPF). ELKO CO.: Big Springs near Cave Cr. P. O., *Mason 4748* in 1928 (UC). ESMERALDA CO.: White Mts., *Roos 1028* in 1937 (RSA); White Mts., Mustang Cyn., *Morehead* in 1985 (ARIZ); Toiyabe Range, at boundary of Inyo. Nat. For., on Middle Cr. rd., *Mathiasen 8912* in 1989 (FPF). LANDER CO.: 10 mi. E of Austin on US 50, *H & W 833* in 1966 (FPF) and *W 6720* in 1986 (FPF); Austin, *Weir 3230* in 1916 (FPF, ILL, UC) and *Jones* in 1882 (RSA); Big Cr., *Linsdale & Linsdale 264* in 1931 (CAS); Toiyabe Range, 0.5 mi. E of Big Cr. Campground, *Mathiasen 8910* in 1989 (FPF). LINCOLN CO.: Deer Lodge, near Fay, *Train 2521* in 1938 (ARIZ, UC); Mormon Mts., *Haber* in 1978 (FPF). LYON CO.: Wassuk Range, Coal Valley, *Alexander & Kellogg 5328* in 1947 (UC, WTU); 6 mi. SE of Wellington, *McMillan 197* in 1941 (RSA, UT). MINERAL CO.: Alum Cr. S of Hawthorn, *Peterson 63-327* in 1963 (FPF); Masonic Mts., *Bailey & Rockwell* in 1978 (FPF). NYE CO.: Grant Range, Irwin Cyn. near Timber Mtn., *Peterson 63-329* in 1963 (FPF); E side of Pahute Mesa, *Bostick 5237* in 1967 (CAS, FPF); Saulsbury, *Dyreng 41* in 1933 (USFS); Belted Range, 1 mi, below Johnnie's Water, *Reveal 1330* in 1968 (FPF); S Shoshone Mtn., SE of Tiva Cyn., *Reveal 1384* in 1968 (FPF). PERSHING CO.: Fencemaker Mts., on rd. to microwave tower, *Bailey 86-03* in 1986 (FPF). WHITE PINE CO.: E of Lehman Caves Nat. Mon., *Peterson 63-338* in 1963 (FPF) and *Maguire & Becraft 2535a* in 1933 (UC); Mt. Moriah, 0.3 mi. W of Hampton Cr. Trailhead, *Mathiasen 8905* in 1989 (FPF).

NEW MEXICO

BERNALILLO CO.: Manzano Mts., Cedro Cyn., *Ellis FP 89502* in 1939 (FPF); Sandia Mts., 0.5 mi. W of Doc Long Campground, *H 36* in 1956 (FPF) and *Lightle* in 1962 (FPF). CATRON CO.: Mogollon, *Hedgcock & Long FP 9936* in 1911 (FPF); Mogollon Cr., *Metcalfe 288* in 1902 (ARIZ, DS, FPF, MO, RSA, UC, US); 2 mi. W of Mogollon, *H & Lightle 133* in 1962 (FPF); Adams Diggins, 18 mi. NW of Pie Town, *Lightle 65-5* in 1965 (FPF); 6.5 mi. S of Luna on Rte. 180, *H 817* in 1965 (FPF); Diamond Cr., 13 mi. S of Beaverhead on Rte. 61, *Lightle 65-41* in 1965 (FPF); 20 mi. N of Rte. 78 on Apache Springs rd. *Lightle 65-44* in 1965 (FPF); 11 mi. SE of Reserve on new rd. to Beaverhead, *H & Lightle 899* in 1966 (FPF); 1 mi. W of Red Hill on US 60, *H & Lightle 926* in 1966 (FPF); 11 mi. S of US 60 on Rte. 32, *H & Lightle 927* in 1966 (FPF); Cooney, Mogollon Mts., *Wooten* in 1900 (US). CIBOLA CO.: 2.3 mi. W of Cebolleta, *Lightle 65-6* in 1965 (FPF); 3 mi. NW of Trechado on Rte. 36, *Lightle 65-4* in 1965 (FPF); 10 mi. E of Grants on rd. to La Mosca Lookout, *Lightle 65-50* in 1965 (FPF); 11 mi. N of Grants, *Mathiasen* in 1976 (FPF). EDDY CO.: Guadelupe Mts., *H & Nicholls 2023* in 1982 (FPF). GRANT CO.: Telegraph Mts., *Wooton* in 1902 (RSA, RM, US); Walnut Cr., near Silver City, *Gill FP 68301* in 1934 (FPF); Fort Bayard, *Johnson FP 15106* in 1913 (FPF), *Hedrick FP 41* and *FP 286* in 1908 (FPF); Stephens Ranch, Fort Bayard Watershed, *Blumer 110* in 1905 (US); 5 mi. W of Mimbres River on Rte. 180, *H & Lightle 125* in 1962 (FPF); 21 mi. N of Mimbres on Rte. 61, *Lightle 65-38* in 1965 (FPF); Gila Hot Springs, *H & Bailey 1768* in 1977 (FPF); Silver City, *H & Bailey 1770*, in 1977 (FPF); Mule Mts., *H & Bailey 1781* in 1977 (FPF); Ft. Bayard, *H & Bailey 1783* in 1977 (FPF); Mule Mts., on *Pinus discolor*, *H & Bailey 1782* in 1977 (FPF); Ft. Bayard, on *Pinus discolor*, *H & Bailey 1784* in 1977 (FPF). LINCOLN CO.: 1 mi. S of Nogal on Rte. 37, *H & Lightle 101* in 1962 (FPF); 10.5 mi. E of Carrizozo on Rte. 380, *H 2395* in 1990 (FPF); Gallina Mts., SW of Corona, *Riffle* in 1964 (FPF) and *H & Lightle 1078* in 1967 (FPF); 3 mi. SE of Ancho, *Lightle 64-30* in 1964 (FPF). MCKINLEY CO.: Continental Divide, 25 mi. E of Gallup on US 66, *Ellis FP 89503* in 1939 (FPF) and *Lightle 64-12* in 1964 (FPF); 2 mi. NE of San Mateo, *Lightle 63-29* in 1963 (FPF); 0.5 mi. S of Old Fort Wingate, *Lightle 63-36* in 1963 (FPF); near Crown Pt., *H 1916* in 1979 (FPF). OTERO CO.: Pinon, *Wyman FP 18381* in 1914 (FPF); Box Cyn. near Highrolls, *Viereck* in 1902 (PH); 9.5 mi. S of High Rolls, *Worthington 6232* in 1980 (ARIZ, FPF); La Luz Cyn., 3 air mi. N of High Rolls, *H 2389* in 1989 (FPF); Ben Williams Cyn., 10 mi. W of Pinon on Timberon rd., *H 2404* in 1990 (FPF). RIO ARRIBA CO.: 5 mi. W of Coyote on US 96, *Lightle 63-18* in 1963 (FPF); 15 mi. NW of Espanola, *Lightle 63-16* in 1963 (FPF); 2.5 mi. W of Canjilon, *Lightle 63-6* in 1963 (FPF); near Gobernador, *Lightle 64-9* in 1964 (FPF); Carson Nat. For., La Jara Cr., on Rte. 17, *Lightle 64-11* in 1964 (FPF); 1 mi. S of Las Trampas on Rte. 76, *H 2254* in 1988 (FPF). SANDOVAL CO.: Sandia Mts., N side, *Gill & Long FP 68137* in 1932 (FPF) and *Ellis FP 89411* in 1939 (FPF); 14 mi. NW of Cuba on Rte. 44, *H & Scharpf 692* in 1964 (FPF). SAN JUAN CO.: Near Cedar Hill, *Standley 7979* in 1911 (US); Navajo Res., Tunitcha [Chuska] Mts., *Standley 7810* in 1911 (US); 5 mi. SW of Sheep Springs, *Lightle & Weiss 66-41* in 1966 (FPF); 15 mi. S of Ignacio, Colorado, on Rte. 511, *H 1636* in 1975 (FPF); Manzanares Mesa, ca. 10 mi. E of Blanco, *Wynoff 565* in 1974 (ASU); Cutter Cyn., E of Blanco, *Wynoff W565B* in 1974 (ASU). SAN MIGUEL CO.: 3 mi. N of Pecos on Rte. 63, *Lightle 65-30* in 1965 (FPF). SANTA FE CO.: Santa Fe, *Heller & Heller 3533* in 1897 (FPF, MO, US); Mesa NE of Santa Fe, *Hedgcock & Bethel FP 24730* in 1917 (FPF, ILL); Mts. E of Santa Fe, *Fendler 312* 1847 (MO); 20 mi. E of Espanola, *Lightle 63-13* in 1963 (FPF); near Rio en Media, *H & Hinds 1077* in 1967 (FPF); Canoncito, *Brandegee* in 1879 (UC); vicinity of Santa Fe, *Rose & Fitch 17765* in 1913 (US). SIERRA CO.: Rhodes Pass, 20 mi. E of Engle, *Cutler 2047* in 1938 (CAS, MNA, MO, UC); 2 mi. W of Kingston on Rte. 90, *H & Lightle 889* in 1966 (FPF); San Andreas Mts., 1.5 mi. N of Salinas Peak, *Lynch & others* in 1991 (FPF); 1 mi. N of Salina Peak, *Sprackling & others* in 1991 (FPF). SOCORRO CO.: San Mateo Mts., 10 mi. S of US 60 on Rte. 52, *Lightle 65-33* in 1965 (FPF); 5 mi. W of Magdalena on US 60, *Lightle 63-41* in 1963 (FPF); 25 mi. W of Carrizozo on US 380, *Lightle 65-1* in 1965 (FPF); 7.5 mi. W of Claunch, *Lightle 65-20* in 1965 (FPF). TAOS CO.: Taos, *Greene* in 1877 (MO); Penasco, *von Schrenk* in 1907 (MO); 19 mi. S of Tres Piedras on US 285, *Lightle 63-11* in 1963 (FPF); 11 mi. N of Taos on Rte. 3 at San Cristobal Jct., *Lightle 65-45* in 1965 (FPF); 12 mi. S of Tres Piedras on US 285, *H 1011* in 1967 (FPF). TORRANCE CO.: Manzano Mts., Priest Cyn., *Van Devender & Betancourt 84-334* in 1984 (FPF). COUNTY UNCERTAIN: Alamo Nat. For., *Long FP19634* in 1915 (FPF); Embudo to Rio Pueblo, *O'Bryne & Long FP18678* in 1914 (FPF).

TEXAS

HUDSPETH CO.: Sierra Diablo, 20 mi. N of Allamore, *H & others 1531*, in 1975 (FPF). JEFF DAVIS CO.: Davis Mts.: all on *Pinus cembroides*, *Young 63* in 1914 (MO); Mt. Livermore, *Andresen & Andresen 1824* in 1962 (FPF); Wood Cyn., Jones Ranch, *Hinckley* in 1936 (ARIZ); N slope of Sawtooth Mtn., *Little & Correll 19003* in 1963 (FPF); Mt. Livermore, Goat Cyn., *Hinckley* in 1935 (SRSC); H. O. Cyn., *Hinckley 3163* in 1944 (SRSC); H.O. Cyn., 1 mi. S of summit on Rte. 166, *H & others 1050* in 1967 (FPF) and *H & others 1523* in 1973 (FPF).

UTAH

BEAVER CO.: Southern end of Wah Wah Mts., *Bailey 80-29* in 1980 (FPF). CARBON CO.: Price, *Flowers* in 1934 (FPF, UT); Sunnyside, *Jones* in 1907 (RSA). DUCHESNE CO.: 11 mi. W of Duchesne on US 40, *H 1052* in 1967 (FPF). EMERY CO.: 44 mi. W of Green River on I-70, *H 1341* in 1971 (FPF); Huntington Cyn, *Krebill & Nelson K-771* in 1969 (FPF). GARFIELD CO.: 5 mi. SW of Panguitch, *Peterson 62-107* in 1962 (FPF); 2 mi. W of Tropic, *Buchanan 527* in 1959 (UT, WTU); SE of Table Cliffs, *Peterson 64-78* in 1964 (FPF); 21 mi. SW of Escalante on Rte. 54, *H 682* in 1964 (FPF); 4 mi. NW of Widtsoe, *Sparrow 292* in 1939 (USFS); 3.4 mi. S of Boulder, *Bailey & Voltmer 84-10* in 1984 (FPF); 1 mi. outside Dixie Nat. For. boundary on Rte. 14 between Henrieville and Escalante, *Bailey 77-17* in 1979 (FPF); Henry Mts., Coyote Benches, *H 2097* in 1985 (FPF); NW slope of Bull Mtn., *Harrison 11184* in 1947 (UC); W side of Bull Mtn., *H 2094* in 1985 (FPF); Pennell Cr. rd., *Mathiasen 8938* in 1989 (FPF). GRAND CO.: La Sal Mts., 3.5 mi. S of Castleton, *H & Mathiasen 1491* in 1974 (FPF); 0.5 mi. SE of Castleton Jct., *Bailey 79-16* in 1979 (FPF); 8.5 mi. N of Dead Horse Pt., *Bailey* in 1977 (FPF). IRON CO.: Near Cedar City, *Parry* in 1874 (MO). JUAB CO.: Deep Creek Range: Stewarts Cabin, on *Pinus monophylla*, *Holmgren 3745* in 1944 (UC, WTU); Trout Cr., on *Pinus monophylla*, *Johnson* in 1970 (FPF). KANE CO.: 0.5 mi. N of Glendale, *W3179* in 1962 (COLO, FPF); 4 mi. SE of Mt. Carmel on US 89, *H & Laut 1164* in 1969 (FPF). MILLARD CO.: House Mts., on *Pinus monophylla*, col.? in 1938 (UT); Confusion Mts., on *Pinus monophylla*, *Bailey* in 1977 (FPF). PIUTE CO.: 3 mi. SW of Marysvale, *W 4168* in 1967 (FPF, UT). SAN JUAN CO.: 5 mi. N of Blanding on Rte. 47, *Peterson 65-69* in 1965 (FPF); 8 mi. N of Blanding on Rte. 47, *H 1089* in 1967 (FPF); Navajo Mtn., 2 mi. W of Navajo Mtn. Trading Post, *H & others 1389* in 1971 (FPF); 14 mi. S of Rte. 95 on Rte. 261, *H & Mathiasen 1488* in 1974 (FPF); La Sal Mts.: 1.5 mi. NE of La Sal, *Taye 1803* in 1983 (RM); 16 mi. SE of Moab, *H & Mathiasen 1489* in 1974 (FPF); Abajo Mts., 3.1 mi. W of Rte. 275 on For. Service rd. 88, *Mathiasen 9008* in 1990 (FPF). SANPETE CO.: SE of Ephraim, *Hedgcock FP 8142* in 1912 (FPF); W of Ephraim, *Hedgcock FP 8135* and *FP 8139* in 1912 (FPF) and on *Pinus monophylla*, *Tidestrom 1300* in 1908 (US). SEVIER CO.: 8.5 mi. E of Salina, *Bailey 85-15* in 1985 (FPF). WASHINGTON CO.: Zion Nat. Park, on *Pinus californiarum* subsp. *fallax*, *Nelson & Nelson 2697* in 1938 (RM); 10 mi. N of Beaver Dam Summit, on *Pinus monophylla*, *W 3913* in 1966 (FPF, UT, WTU); 1 mi. N of Pine Park, ca. 16 air mi. W of Enterprise, *H & others 1174* in 1969 (FPF); ca. 2 mi. E of Pinto, *Bailey* in 1979 (FPF). WAYNE CO.: Aquarius Plateau, Head of Poison Cr., *Rydberg & Carlton 7371* in 1905 (RM, US); 2 mi. S of Grover, *W 3171* in 1962 (COLO, FPF). COUNTY UNCERTAIN: La Sal Mts., Little Springs on W slope, *Rydberg & Garrett 8542* in 1911 (RM, US).

12. *Arceuthobium douglasii*

All collections on *Pseudotsuga menziesii*, except as noted.

CANADA

BRITISH COLUMBIA

1 mi. S of Sirdar, N of Creston, *Calder & Savile 11413* in 1953 (WTU); Summerland Exp. Sta., *Calder & Savile 11536* in 1953 (UC, US); Similkameen River, *Macoun 79522* in 1905 (MO); 10 mi. SE of Kelowna, *Kuijt 588* in 1954 (DAVFP, FPF); Beaver Lake rd., near Wood Lake, *Kuijt 581* in 1954 (DAVFP, FPF); 10 mi. N of Sirdar, *Kuijt 650* in 1954 (DAVFP, FPF); 9 mi. E of Osoyoos on Rte. 3, *H & Laut 1296* in 1970 (FPF); 5 mi. E of Lytton on Rte. 1, *H & Laut 1299* in 1970 (FPF).

MEXICO

CHIHUAHUA

Mpio. Tomochic, 35 km. N of Tomochic-Basaseachic highway on rd. to Yahuirachi, 5 km. S of Yahuirachi, *H 2183* in 1987 (FPF); 55 km. N of Tomochic-Basaseachic Highway on rd. to Yahuirachi, 12 km. N of Yahuirachi, *H 2188* in 1987 (FPF).

COAHUILA

Sierra del Carmen, Ocampo, *H & others 1027* in 1967 (FPF); Sierra de la Martia, 16 mi. E of San Antonio de las Alazanas, *H & Cibrián 2000* in 1981 (FPF).

DURANGO

47 mi. S of Durango on La Flor rd., *H & W 514* in 1963 (FPF); Mpio. Santiago Papasquiaro: 29 km. W of Rte. 39 on Altares rd., *H & others 2230* in 1987 (FPF) and 8 km. SW of Altares, *H & others 2242* in 1987 (FPF); Mpio. Tepehuanes; 29 km. E of Tepehuanes on rd. to Sierra de la Candela, *H 2158* in 1987 (FPF). Mpio. Guanacevi, Bajio de Cochinos at 10 km. from El Cocino-Piedra rock and the Arroyo de las Piedras Guanacevi, *Najera & Gonzalez* in 1987 (FPF).

NUEVO LEÓN

Cerro Potosí: 11 mi. from village "18 de Marzo" on rd. to relay tower, *H & W 395* in 1963 (FPF), *Nickrent 1984* in 1984 (FPF, ILL, MEXU), and *H & others 1684* in 1975 (FPF).

UNITED STATES

ARIZONA

APACHE CO.: Hannagan Meadows, *Parfitt 3129* in 1983 (ASU); 4 mi. S of Eagar, *H & Lightle 209* in 1962 (FPF); Alpine, *Goodding FP 26737* in 1917 (FPF); 4.8 mi. SW of Alpine on Rte. 666, *H & Scharpf 699* in 1964 (FPF); Milk Cyn., 8 mi. E of Nutrioso, *Parker & McClintock 7585* in 1951 (ARIZ); 5 mi. E of Lukachukai on Red Rock rd., *Lightle & Weiss 66-48* in 1966 (FPF); 11 mi. SW of Red Rock on Lukachukai Rd. *Lightle & Weiss 66-50* in 1966 (FPF); 2 mi. E of Big Lake, *H 820* in 1965 (FPF); 3 mi. NW of Maverick on Fort Apache rd., *H & Lightle 902* in 1966 (FPF); 13 mi. E of McNary on Rte. 73, *H & Lightle 924* in 1966 (FPF); 14 mi. W of Eager, *H 1451* in 1973 (FPF); 5 mi. SW of Big Lake on Reservation Lake rd., *Mathiasen 7827* in 1978 (FPF); Fort Apache Indian Res., 7 mi. W of Maverick, *H 2197* in 1987 (FPF). COCHISE CO.: Chiricahua Mts.: Pinery Cyn. rd., *Gill & Ellis FP 89497* in 1939 (FPF); Pinery Cyn. rd., 7 mi. E of Nat. For. boundary, *H & Lightle 152* in 1962 (FPF); Rustler Park, *Gill FP 68056* in 1935 (FPF) and *Gill & Ellis FP 89408* in 1939 (FPF). Huachuca Mts., Carr Cyn., *Goodding FP 33284* in 1919 (FPF), *Goodding 2088* in 1915 (ARIZ), *H & Mathiasen 1469* in 1973 (FPF), and Miller Cyn., 4 mi. W of Rte. 92, *H 1622* in 1975 (FPF). COCONINO CO.: "Kaibab For.," *Richards* in 1938 (ARIZ, RM, WTU); San Francisco Peaks, *Knowlton 40* in 1889 (US); San Francisco Peaks, Interior Basin, *H & Lightle 251* in 1962 (FPF); Grand Cyn., South Rim, 1 mi. E of Grandview Point, *H 39* in 1954 (FPF) and *H & Lightle 183* in 1962 (FPF); Oak Cr. Cyn., *Ellis FP 89504* in 1939 (FPF); Jacob Lake, *Moberg & Gill FP 68299* in 1934 (FPF); Mt. Eldon, near Flagstaff, *Drake FP 15122* in 1913 (FPF); San Francisco Peaks, Spruce Cabin, *Gill FP 68134* in 1932 (FPF); Flagstaff, *Purpus* in 1900 (UC); N slope, Mt. Eldon, *Whiting 1053/5338* in 1941 (ARIZ, MNA); Grand Cyn., Grandview Trail, *Thornber & Hockdoerffer 2944* in 1907 (ARIZ); San Francisco Peaks, *Goodding* in 1917 (ARIZ); Baker Butte, *Andrews & others FP 89229* in 1937 (FPF); Rim rd., 5 mi. SE of W boundary of Sitgreaves Nat. For., *Lightle 64-16* in 1964 (FPF); 3 mi. E of Long Valley, *Lightle 64-14* in 1964 (FPF); North Kaibab Plateau, 7 mi. W of Kaibab Lodge, on *Picea pungens*, *Peterson 45-61* in 1961 (FPF); San Francisco Peaks, 7 mi. NE of Schultz Pass on Interior Basin rd., on *Abies lasiocarpa* var. *arizonica*, *H & Lightle 250* in 1962 (FPF); near Weimer Springs, W of Mormon Lake, *H & Lightle 913* in 1966 (FPF); 11 mi. S of Chevlon Ranger Sta., *H & Lightle 918* in 1966 (FPF); N Rim, Grand Cyn., on *Abies lasiocarpa*, *Kuijt* in 1960; N Rim, Kaibab Nat. For., on *Abies lasiocarpa*, *Mathiasen 8111* in 1981 (FPF); San Francisco Peaks, 0.5 mi. N of Schultz Pass, on *Abies lasiocarpa* var. *arizonica*, *H 1707* in 1976 (FPF); 4 mi. N of Rte. 89 on Snow Bowl rd., *H & others 1181* in 1969 (FPF); Kendrick Peak, *H & Mathiasen 1466* in 1973 (FPF); Dry Lake Hills near Flagstaff, *Lugenbuhl* in 1985 (MNA). GILA CO.: Sierra Ancha, Workman Cr., *H 44* in 1956 (FPF) and *Lightle & Lampi 65-15* in 1965 (FPF); 26 mi. E of Payson on Rte. 160, *Lightle 63-55* in 1963 (FPF); Sierra Ancha Exp. For., Parker Cr. Cyn., *Little 4190* in 1935 (USFS). GRAHAM CO.: Graham Mts.: 1 mi. above Arcadia Guard Sta., *H & Lightle 142* in 1962 (FPF); Hospital Flat, *H & Lightle 226* in 1962 (FPF); Turkey Flat, *Gill FP 68037* in 1936 (FPF); Treasure Park, *Mielke & Ellis FP 89694* and *FP 89698* in 1944 (FPF); between Turkey Flat and Ladybug, *Stouffer & Gill FP 68294* in 1934 (FPF), *Ellis FP 89403* in 1938 (FPF), and *FP 89427* in 1939 (FPF); San Carlos Indian Res., Anderson Flat Heliport, *H 2197* in 1987 (FPF); Grant Cr., on *Abies lasiocarpa* var. *arizonica*, *Stouffer FP 68289* in 1934 (FPF). GREENLEE CO.: 47 mi. S of Springerville on US 666, *Gill FP 68303* in 1934 (FPF); Blue Summit, *Gill FP 68307* in 1934 (FPF); 3 mi. S of Hannagan Meadows on Rte. 666, *Andrews* in 1963 (FPF); 5 mi. S of Alpine on Rte. 666, *Lightle 64-19* in 1964 (FPF); about 10 mi. SE of Maverick, on *Abies concolor*, *Mathiasen 7914* in 1979 (FPF). NAVAJO CO.: 6 mi. E of State Rte. 260 on Mogollon

Rim rd., *H & Lightle 920* in 1966 (FPF). PIMA CO.: Santa Catalina Mts., *Toumey* in 1896 (US); Soldier Camp, *Gill FP 68127* and *FP 68263* in 1932 (FPF); Bear Wallow Campground, *H & Lightle 166* in 1962 (FPF); Summerhaven, *Gilbertson* in 1985 (FPF); *Ellis FP 89425* in 1939 (FPF); *Gill & Ellis FP 89406* and *FP 89501* in 1939 (FPF). YAVAPAI CO.: Spruce Mtn., *Hedgcock FP 4856* and *FP 4871* in 1910 (FPF); 0.5 mi. N of Spruce Mtn., *H & Lightle 239* in 1962 (FPF).

CALIFORNIA

DEL NORTE CO.: 3 air mi. NW of Black Butte, *Tinnin & Kirkpatrick 2* in 1981 (FPF). PLUMAS CO.: Providence Hill ca. 4 mi. N of Twain, *Henson* in 1970 (FPF). SHASTA CO.: Near Pondosa Jct., *Kuijt 1367* in 1957 (UC); 2 mi. SW of Pondosa Jct., *H & W 645* in 1964 (FPF). SISKIYOU CO.: Sisson, *Hedgcock & others FP 9669* in 1911 (FPF); Dry Lake Lookout, Oak Knoll, 4 mi. SE of Cowdry Mtn., *Gill & Sargent FP 68179* in 1932 (FPF); N side Cascade Gulch, Mt. Shasta, *Cooke 17729* in 1947 (WTU); Upton, Mt. Shasta, *Hall & Babcock 4078* in 1903 (UC) and *Cooke 13920* in ? (DS); Joe Cr., 7 mi. S of Copper, Oregon, *H & W 634* in 1964 (FPF); W base of Black Butte, 5 mi. S of Weed on US 99, *H & W 639* in 1964 (FPF); Siskiyou Mts., W fork Cottonwood Cr., SW of Hilts, *Wheeler 2783* in 1934 (MO, POM, US, Z); rd. to Gumboot Lake, ca. 12 mi. W of Dunsmuir, *Smith & Bacigalupi* in 1957 (UC); 0.4 mi. N of White Mtn., *Mathiasen & Loftis 8630* in 1986 (FPF); 3 mi. SW of Scott River on rd. to Lovers Camp, *Mathiasen 8624* in 1986 (FPF); 3 mi. S and 20 mi. W of Hilt, on *Abies amabilis*, *Mathiasen & Loftis 8631* in 1986 (FPF); Parks Cr. rd, 8 air mi. WSW of Weed, *H & Mathiasen 2423* in 1990 (FPF); 5 mi. S of Siskiyou Lake on Castle Lake rd., *H & Mathiasen 2429* in 1990 (FPF). TRINITY CO.: S of Callahan on Rte. 3, *W 6752* in 1987 (FPF).

COLORADO

ALAMOSA CO.: La Mosca Cr., 1 mi. E of Sand Dunes Nat. Mon. headquarters, *H & others 1502* in 1974 (FPF). ARCHULETA CO.: Pagosa Springs, *Hedgcock & Bethel FP 24654* in 1917 (FPF); 3 mi. N of Piedra, *Hinds 63-6* in 1963 (FPF); 10 mi. E of Pagosa Springs, *H & others 2028* in 1982 (FPF). CHAFFEE CO.: 6.8 mi. S of US 285 on Bassam Park rd., *H 446* in 1963 (FPF); 6 mi. SW of Buena Vista, *H & Laut 1313* in 1970 (FPF); 6 mi. NE of Salida on Ute Trail rd., *H & Fisher 1364* in 1971 (FPF). CONEJOS CO.: 2 mi. SW of Conejos River on Rte. 17, *Lightle 63-2* in 1963 (FPF) and *Hinds 63-2* in 1963 (FPF). COSTILLA CO.: 15 mi. NE of Ft. Garland on Rte. 160, *H & others 1500* in 1974 (FPF). CUSTER CO.: 3.8 mi. NW of Isabel Lake on Rte. 165, *H 429* in 1963 (FPF) and on *Picea engelmannii*, *H 430* in 1963 (FPF); 4.7 mi. W of Hillside, *H 434* in 1963 (FPF). DOUGLAS CO.: 5.5 mi. W of Rte. 105 on Jackson Cr. rd., *H 206* in 1962 (FPF); Garber Cr., *Krieg* in 1980 (FPF). EAGLE CO.: 8 mi. SW of Gypsum on Cottonwood Pass rd., *H 946* in 1966 (FPF). EL PASO CO.: Palmer Lake, *Bethel* in 1912 (US) and in 1919 (CS); Clifton Park, *Hill FP 68280* in 1932 (FPF); Palmer Lake, *Hedgcock FP 15900* in 1914 (FPF, RSA, WTU); W of Palmer Lake, *Hedgcock & others FP 24901* in 1917 (FPF); 5 mi. W of Monument, *W 2984* in 1962 (COLO, FPF); 1.7 mi. above Cascade on Pikes Peak rd., *H & Hinds 425* in 1963 (FPF); 0.3 mi. E of Bruin Inn, N Cheyenne Cyn., *H 538* in 1963 (FPF); Air Force Academy, 0.5 mi. S of Cadet Area, *H 541* in 1963 (FPF); Crystal Park, *Gill FP 68141* in 1932 (FPF); Mt. Manitou, *Gill FP 68256* in 1932 (FPF); Halfway, Pikes Peak, *Hedgcock FP 905* in 1909 (FPF); Palmer Lake Reservoir, *Gill FP 68139* in 1932 (FPF); Manitou Springs, *Sheldon 577* in 1892 (US); 7 mi. NW of Manitou Springs, *H & Laut 1326* in 1971 (FPF); 0.5 mi. W of Manitou Springs, *H 1868* in 1978 (FPF). FREMONT CO.: Sangre de Cristo Mts., Hayden Pass rd. ca. 5 mi. SW of Coaldale, *Schacht* in 1969 (FPF); 8 mi. SW of Coaldale, *H & Laut 1316* in 1970 (FPF); Phantom Cyn., 13 mi. S of Victor, *H & Laut 1335* in 1971 (FPF); 10 mi. N of Cotopaxi, *Summerfelt* in 1982 (FPF). GARFIELD CO.: Douglas Pass on Rte. 139, *Mathiasen 9013* in 1990 (FPF); 0.5 mi. S of Douglas Pass, *H 686* in 1964 (FPF); 14 mi. NNE of Rifle, *Hinds* in 1965 (FPF); Rim of Parachute Cyn., 18 mi. WNW of Rifle, *H & others 1382* in 1971 (FPF). GUNNISON CO.: Elk Mts., Coal Cr. Cyn., *Brandegee* in 1881 (MO, PH, UC). HINSDALE CO.: Little Sand Cr., 21 air mi. NW of Pagosa Springs, *Landgraf* in 1965 (FPF). HUERFANO CO.: Williams Cr., ca. 10 mi. N of Gardner, *H 432* in 1963 (FPF); N of Black Mtn., ca. 10 mi. NNW of Gardner, *Stewart* in 1964 (FPF). LA PLATA CO.: Hills N of Durango, *Hunt & Bethel FP 24429* in 1917 (FPF); W of Trimble, *Hedgcock & Bethel FP 24639* and *FP 24689* in 1917 (FPF); Dry Fork Cr., 8 air mi. NW of Durango, *Landgraf* in 1965 (FPF); Vallecito Campground, *Mathiasen 7826* in 1978 (FPF). LAS ANIMAS CO.: Near Stonewall Gap, *Hedgcock & Johnston FP 24945* in 1917 (FPF); 12 mi. W of Gulinaire on Apishqua Pass Rd., *H 1427* in 1972 (FPF); 2 mi. S of Tercio, *H & Laut 1331* in 1971 (FPF) and on *Abies concolor*, *H & Laut 1332* in 1971 (FPF); S of Tercio, on *Abies concolor*, *Leatherman* in 1987 (FPF) and on *Picea engelmannii*, *Leatherman* in 1987 (FPF). MINERAL CO.: 4.2 mi. N of Archuleta Co. line on US 160, *Hinds 63-4* in 1963 (FPF). MOFFAT CO.: Dinosaur Nat. Mon., Cyn. Overlook, *W 4129* in 1967 (FPF, UT). MONTEZUMA CO.: W Mancos Cyn., *Baker & others 388* in 1898 (ARIZ, MO, RM, RSA, US); Priest Gulch, 8 mi. E of Stoner, *Landgraf* in 1965 (FPF); 14 mi. NE of Dolores on Rico rd., *Hinds 63-12* in 1963 (FPF); Aspen Guard Sta., 10 mi. NNE of Mancos, *Hinds* in 1965 (FPF); Mesa Verde Nat. Park, 8 mi. N of headquarters, *H & others 1431* in 1972 (FPF). MONTROSE CO.: Uncompahgre Plateau, Windy Point, *Peterson 57-61* in 1961 (FPF); 5.5 mi. N of Rte. 90 on Transfer rd., *Hinds 63-15* in 1963 (FPF); 4 mi. NE of Nucla, *Hinds 63-15* in 1963 (FPF). OURAY CO.: Ouray, *Gayman FP 26521* in 1917 (FPF) and *Hedgcock FP 15915* in 1914 (FPF). PARK CO.: 0.25 mi. W of Guffey, *H 1456* in 1973 (FPF). PITKIN CO.: near Marble, *W 3618* in 1964 (FPF, UT). PUEBLO CO.: Beulah, *Edmonston FP 295* in 1909 (FPF). RIO GRANDE CO.: Alamosa River Cyn. rd., *H 1917* in 1979 (FPF); 12 mi. SSW of Del Norte on Summitville rd., *H 1913* in 1979 (FPF). SAGUACHE CO.: 5 mi.

E of N Cochetopa Pass, *H 440* in 1963 (FPF); 2 mi. S of Poncha Pass on US 285, *H 444* in 1963 (FPF); 4 mi. SW of Rte. 114 on Dry Gulch rd., *H & Lightle 442* in 1963 (FPF); 8 mi. NNW of La Gorita, *Irvine* in 1976 (FPF); Sangre de Cristo Mts., 5.1 mi. E of Villa Grove on Hayden Pass rd., *H 1918* in 1979 (FPF), and on *Abies concolor*, *H 1919* in 1979 (FPF); near Cochetopa Pass, on *Picea engelmannii*, *Lightle & Schacht 63-26* in 1963 (FPF). SAN MIGUEL CO.: 7.9 mi. W of Dallas Divide on Rte. 62, *Hinds* in 1965 (FPF); 2 mi. W of Placerville, *Payson FP 26026* in 1917 (FPF). TELLER CO.: Hotel Gulch, 1.5 mi. E of Manitou Exp. For. headquarters, *H 260* in 1962 (FPF).

IDAHO

ADAMS CO.: Evergreen, *Hedgcock FP 988* in 1909 (FPF); 13 mi. N of Council on US 95, *H 977* in 1966 (FPF). BLAINE CO.: Bald Mtn. near Ketchum, *Mielke* in 1957 (FPF) and on *Abies lasiocarpa*, *Hoffman* in 1984 (FPF). BONNER CO.: Hope, *Sandberg & Lieberg 4443* in 1893 (MO, RSA, RM, US); Lake Pend Oreille, *Sandberg, MacDougal & Heller 744* in 1892 (MO, US, Z); Priest River *Weir 9995* in 1917 (ILL); Smiths Peak, Priest Lake, on *Abies lasiocarpa*, *Weir 2419* in 1913 (ILL). BOISE.: 25 mi. NE of Lowman on Rte. 21, *H 1371* in 1971 (FPF). BOUNDARY CO.: Pack River, on *Abies lasiocarpa*, *Weir 2415* n.d. (ILL). CAMAS CO.: Boise River, E of Featherville, 1 mi. E of Elmore Co. boundary, *Peterson 62-50* in 1962 (FPF). CLARK CO.: Spencer, *Hurtt FP 20583* in 1912 (FPF). CASSIA CO.: Albion Mts., jct. of Howell Cr. and For. Service rd. 549, *Mathiasen 8915* in 1989 (FPF); Black Pine Range, 0.5 mi. S of Pole Cyn. Spring on For. Ser. rd. 761, *Mathiasen 8918* in 1989 (FPF). CUSTER CO.: Challis, *Gill FP 68206* in 1932 (FPF); 8 mi. W of Challis, *Benlow* in 1917 (ILL); Garden Cr. near Challis, on *Abies lasiocarpa*, *Gill FP 68207* in 1932 (FPF). FRANKLIN CO.: Cub River near Franklin Basin, *Peterson 63-364* in 1963 (FPF). IDAHO CO.: 5 mi. S of Grangeville, *Krebill 159* in 1964 (FPF), and *H 968* in 1966 (FPF); 15 mi. N of Burgdorf on Salmon River rd., *H 971* in 1966 (FPF); Salmon River at Fern Cr., ca. 23 mi. W of Shoup, *W 4127a* in 1966 (FPF, UT). KOOTENAI CO.: Lakeside, col.? in 1889 (UC); Canfield Mtn., 4 mi. NW of Coeur d'Alene, *Weir 2412* in 1916 (ILL). LATAH CO.: 3 mi. E of Viola, *Wicker* in 1959 (WSP). LEMHI CO.: SW of Salmon on N fork of Williams Cr., *Krebill 126* in 1964 (FPF); 3 mi. N of Gibbonsville on US 93, *H & Hinds 1123* in 1968 (FPF); Wagonheimer, 3 mi. SE of North Fork, *Hedgcock FP 4457* in 1910 (FPF); 2.5 mi. E of Tendoy, *H & Hinds 1122* in 1968 (FPF); Salmon River Mts., 6 mi. W of Rte. 97 on Stormy Peak rd., *H 2432* in 1990 (FPF). LEWIS CO.: 3 mi. N of Winchester on US 95, *H 967* in 1966 (FPF). MADISON CO.: Hawley Ranger Sta., *Peterson 62-16* in 1962 (FPF). OWYHEE CO.: Owyhee Mts., 2 air mi. E of Silver City, *Hoffman* in 1986 (FPF). POWER CO.: Sublett Range, 2 mi. N of Sublett Guard Sta., *Mathiasen 8916* in 1989 (FPF). SHOSHONE CO.: Marble Mtn., on *Abies lasiocarpa*, *Weir 2418* in 1914 (ILL). TETON CO.: Near Driggs, *Peterson 62-11* in 1962 (FPF). VALLEY CO.: W of Cascade, *Thompson 13844* in 1937 (MO, UC, WTU); McCall, *Weir* in 1914 (ILL); 3 mi. NE of McCall, *H 975* in 1966 (FPF). WASHINGTON CO.: Weiser, *Oman* in 1912 (RM). COUNTY UNCERTAIN: St. Joe Nat. For., on *Abies lasiocarpa*, *Weir 2416* n.d. (ILL).

MONTANA

FLATHEAD CO.: Bigfork, *Jones 9308* in 1908 (MO, RSA). LAKE CO.: Flathead Lake: Yellow Bay, *Clemens* in 1908 (CAS); mainland opposite Bull Island, *Clemens* in 1908 (MO, PH); Bull Island, *Jones 9307* in 1908 (RSA, US); 12 mi. N of Polson on Rte. 35, *W 4364* in 1969 (FPF, UT); *Salisbury* in 1948 (DAVFP, FPF). LINCOLN CO.: Sylvanite, 18 mi. N of Troy, on *Picea engelmannii*, *Weir 2400* in 1916 (FPF, ILL). MISSOULA CO.: Norman Valley, *Barkley & Barkley 3504* in 1938 (ARIZ, COLO, MO, RSA, UC, US); Pattee Cr., near Missoula, *Weir FP 9777* in 1918 (FPF, OSC); "Paddy" Cyn., *Barkley 1999* in 1937 (RSA); Pattee Cyn., *Spaulding FP 15107* in 1913 (FPF) and *Hedgcock FP 4556* in 1910 (FPF); Missoula, *Weir 9986* in 1915 (ILL) and *7426* in 1917 (ILL); 8.5 mi. N of Missoula, *Stickney 1321A* in 1966 (USFS); SW slope of MacClay Mtn., *Lackschewitz 6434* in 1976 (WTU). RAVALLI CO.: Blogett Cr., W of Hamilton, *Hedgcock FP 9519* in 1911 (FPF); Spoon Cr. near Darby, *Hughes* in 1917 (FPF, ILL); 10 mi. E of Hamilton on Skalkaho Pass rd., *H & Wicker 953* in1966 (FPF); 5.5 mi. NW of Hamilton, *Stickney 617* in 1962 (USFS); 6 mi. N of Lost Cr. Pass on Rte. 93, *H 1644* in 1975 (FPF). SANDERS CO.: 11 mi. NW of Plains on Rte. 28, *W 4366* in 1969 (UT, FPF); Flathead Indian Res., 2 air mi. W of Hot Springs, *H & others 2260* in 1988 (FPF); 1.8 air mi. SE of Moiese, *Thomas 15286* in 1969 (FPF); 2.3 air mi. SE of Moiese, at Lake Co. boundary, *Thomas 15306* in 1969 (FPF).

NEVADA

WHITE PINE CO.: NE slope of Wheeler Peak, *Peterson 63-337* in 1963 (FPF); Wheeler Peak rd., on *Abies lasiocarpa*, *W* in 1985 (FPF); Snake Range, *Bailey 75-91* in 1975 (FPF); Snake Range, 2.5 mi. W of Hampton Cr. trailhead, *Mathiasen 8902* in 1989 (FPF).

NEW MEXICO

BERNALILLO CO.: Sandia Mts.: *Hedgcock FP 172*, *FP 185*, *FP 1538* and *FP 1539* in 1908 (FPF); *Ellis FP 89505* in 1939 (FPF); *Long & Seay FP 21275* in 1916 (FPF): La Luz, Juan Tabo Trail, *H 15* in 1954 (FPF); 2 mi. E of La Madera Ski Area, on *Abies concolor*, *H 56* in 1956 (FPF); Sandia Mts., on *Abies lasiocarpa* var. *arizonica*, *Walters* in 1977. CATRON CO.: 0.5 mi. W of Mogollon, *H & Lightle 131* in 1962 (FPF); 6 mi. S of Luna on US 260, *H & Lightle 213* in 1962 (FPF); Mangas Mts, *H & Scharpf 697* in 1964 (FPF); Tularosa Summit, 11.5 mi. N of Rte. 78 on Apache Springs rd., *Lightle 65-43* in 1965 (FPF); 7 mi. E of Mogollon, on *Abies lasiocarpa* var. *arizonica*, *Hedgcock & Long FP 9899* in 1911 (FPF) and *H & Lightle 216* in 1962 (FPF); 2 mi. E of Bursum Campground on Rte. 78, on *Abies lasiocarpa* var. *arizonica*, *H & Lightle 218* in 1962 (FPF); 1.5 mi. E of Bursum Campground on Rte. 78, on *Abies concolor*, *H & Lightle 217* in 1962 (FPF); 2 mi. W of Rte. 78 on

Bearwallow Lookout rd., *H & Lightle 898* in 1966 (FPF); 1 mi. E of Fox Mtn., *H & Lightle 928* in 1966 (FPF); 12 mi. N of Datil, *Fletcher 1625* in 1926 (UNM). CIBOLA CO.: Mt. Taylor, *Mathiasen 7612* in 1976 (FPF) and Marquez Cyn., *Lightle 63-31* in 1963 (FPF). Zuni Mts.: Redondo Campground, *Mathiasen 7628* in 1976 (FPF); Mt. Sedgwick, *Riffle 528* in 1968 (UNM) and *Lightle 65-7* in 1965 (FPF). COLFAX CO.: 8 mi. SE of Black Lake on Rte. 120, *Lightle 65-48* in 1965 (FPF); Carson Nat. For., Valle Vidal Unit, 16 mi. N of Ute Park, *H 2256* in 1988 (FPF); 1 mi. E of Eagle Nest Lake, *H FP 89958* in 1950 (FPF) and on *Abies concolor*, *H FP 89957* in 1951 (FPF); 9.5 mi. W of Cimarron on US 64, *Lightle 65-21* in 1965 (FPF); 0.5 mi. E of Idlewild, on *Abies lasiocarpa* var. *arizonica*, *Mathiasen 8007* in 1980 (FPF); Philmont Scout Ranch, French Henry Camp, *Hartman 1940* in 1968 (RM). GRANT CO.: Emory Pass, *H & Lightle 120* in 1962 (FPF); 2 mi. N of Redstone, *H & Lightle 127* in 1962 (FPF); 22 mi. N of Mimbres on Rte. 61, *Lightle 65-39* in 1965 (FPF). HIDALGO CO.: Animas Mts., Turkey Springs, 2 mi. N of Animas Peak, *H & others 1436* in 1972 (FPF). LINCOLN CO.: Capitan Mts.: 2 mi. E of Capitan Gap, *H & Lightle 106* in 1962 (FPF) and 1 mi. E of Capitan Gap, *H & Lightle 1099* in 1968 (FPF); W Capitan Mtn., *Lightle 66-20* in 1966 (FPF); Seven Cabins Cyn., *Ellis & others FP 89491* in 1938 (FPF); E side of Gallinas Peak, 10 mi. W of Corona, *Lightle & Riffle 63-43* in 1963 (FPF) and *H & Lightle 1079* in 1967 (FPF). LOS ALAMOS CO.: 1 mi. N of W gate to Los Alamos, *Lightle 65-31* in 1965 (FPF); 5 mi. W of Los Alamos on Rte. 4, *Lightle & Gill 65-24* in 1965 (FPF). McKINLEY CO.: Zuni Mts., Stinking Springs rd., *Lightle 63-34* in 1963 (FPF); Chuska Mts., 1 mi. S of Camp Ayassi, ca. 6 mi. S of Crystal, *Lightle 64-1* in 1964 (FPF). MORA CO.: 3 mi. NW of Holman on Rte. 3, *Lightle 65-49* in 1965 (FPF). OTERO CO.: Mescalero Apache Indian Res.: Summit Cyn., *H 26* in 1954 (FPF); Goat Cyn., *H FP 89992* in 1952 (FPF); Whitetail Well, *H 23* in 1954 (FPF); 1 mi. E of Apache Summit, *H & Scharpf 694* in 1964 (FPF); Silver Springs Cyn., 7.5 mi. NE of Cloudcroft, *H & Lightle 878* in 1966 (FPF); Curtis Cyn., 5 mi. W of State Rte. 130, W of Mayhill, *H & Lightle 880* in 1966 (FPF); 10 mi. S of Cloudcroft on Sacramento Peak rd., *H & Lightle 886* in 1966 (FPF); Sixteen Springs Cyn., 7 mi. E of Cloudcroft, *H & Lightle 1080* in 1967 (FPF); 6 air mi. S of Cloudcroft, on *Picea engelmannii*, *Mathiasen 8006* in 1980 (FPF); Mescalero Indian Res., Peso Cyn., on *Abies concolor*, *Mathiasen 8004* in 1980 (FPF); La Luz Cyn., Apache Cyn., 4 air mi. NW of Cloudcroft, *H 2388* in 1989 (FPF); 6 mi. N of Timberon on For. Service rd. 537, *H 2406* in 1990 (FPF). RIO ARRIBA CO.: 12.5 mi. E of Canjilon on Rte. 110, *Lightle 63-7* in 1963 (FPF); 6 mi. W of Vallecitos, *Lightle 63-8* in 1963 (FPF); 18 mi. W of Tres Piedras on Rte. 111, *H 1393* in 1971 (FPF). SANDOVAL CO.: 5 mi. SE of Fenton Lake *Lightle 63-22* in 1963 (FPF); N end Sandia Mts., *Gill & Long FP 68136* in 1932 (FPF); Placitas, *Hedgcock FP 650* n.d., (FPF); 2 mi. N of Sulphur Springs Jct. on Rte. 126, *Lightle & Gill 65-25* in 1965 (FPF); Tusas Mtn. *Trujillo* in 1990 (FPF), and on *Abies concolor*, *Trujillo* in 1990 (FPF). SAN JUAN CO.: 6.5 mi. SW of Sheep Springs, *Lightle & Weiss 66-43* in 1966 (FPF); Tunitcha [now Chuska] Mts., *Standley 7664* in 1911 (US). SAN MIGUEL CO.: 15 mi. E of Pecos, *Lightle 63-23* in 1963 (FPF); 4 mi. S of Cowles on Rte. 63, *Lightle 65-28* in 1965 (FPF); 1 mi. S of Cowles, *Lightle 65-29* in 1965 (FPF). SANTA FE CO.: Hyde State Park, *Lightle 63-39* in 963 (FPF); 8 mi. E of Chimayo, *Lightle 63-24* in 1963 (FPF); 9 mi. E of Santa Fe, *Heller & Heller 3527* in 1897 (ARIZ, DS, MO, US, Z); Santa Fe River, *Rothrock 69* in 1874 (MO). SOCORRO CO.: Magdalena Mts., 3 mi. above campground in Water Cyn., *W 2994* in 1962 (COLO, FPF); San Mateo Mts.: Hughes Sawmill, *Long FP 21126* in 1915 (FPF) and 11 mi. S of US 60 on Rte. 52, *Lightle 65-34* in 1965 (FPF); 13 mi. S of US 60 on State Rte. 52, *H & Mathiasen 1460* in 1973 (FPF); 6 mi. above Water Cyn. Campground, *H 1686* in 1975 (FPF). TAOS CO.: Penasco, near U.S. Hill, *Long FP 19340* in 1914 (FPF); 1 mi. W of Colfax Co. boundary on US 64, *Lightle 65-23* in 1965 (FPF); Cienega Ranger Sta., *Korstian FP 19276* in 1914 (FPF); 3 mi. E of Questa, *Lightle 65-46* in 1965 (FPF); Santa Barbara Cyn., on *Abies concolor*, *Thorne* in 1963 (FPF); Taos Cyn., 7 mi. E of Taos on US 64, *H 876* in 1966 (FPF); 10 air mi. SE of Taos, *Mathiasen 8008* in 1980 (FPF). TORRANCE CO.: Manzano Mts. 3 mi. NW of Manzano, *Riffle* in 1963 (FPF); Cibola Nat. For., Manzano Mts., Priest Cyn., Cottonwood Spring, *Van Devender & Betancourt 83-365* in 1984 (ARIZ, FPF). COUNTY UNCERTAIN: Front Cr. Basin, Gila Nat. For., *Hedgcock & Long FP 9847* in 1911 (FPF).

OREGON

BAKER CO.: Lily White Guard Sta., 7 mi. NE of Sparta, *Steward & Jackman 6499* in 1953 (WTU); 22 mi. S of Baker on Rte. 7, *H & W 584* in 1964 (FPF); 20 mi. NE of Halfway, *Knutson 102* in 1980 (FPF). CLACKAMAS CO.: Clackamas River, ca. 4 mi. W of the Cascade Crest, ca. 12 air mi. NE of Breitenbush, *Nicholson* in 1968 (FPF); W flank of Sisi Butte, *Knutson & Tinnin DM 40* in 1977 (FPF). CROOK CO.: Maury Mts., *H 1924* in 1979 (FPF). GRANT CO.: 20 mi. N of John Day, *Graham* in 1964 (FPF); Prairie City, Peebles Mill, *Boyce FP 40121* in 1920 (FPF); Dixie Butte, *H 980* in 1966 (FPF) and on *Abies lasiocarpa*, *H 982* in 1966 (FPF); 4 mi. S of Seneca on Rte. 395, *H & W 576* in 1964 (FPF); Skookum Cr., 25 air mi. ESE of Seneca, *H & Scharpf 1268* in 1969 (FPF); 13 mi. SE of Prairie City, *Knutson & Tinnin* in 1975 (FPF). HOOD RIVER CO.: 2.0 mi. S of Mt. Hood village on Rte. 35, *H 2223* in 1987 (FPF). JACKSON CO.: Yale Cr., ca. 14 mi. SSW of Medford, *Bedwell & Childs* in 1950 (FPF, OSC) and *Childs* in 1948 (OSC); 20 mi. SW of Ashland, *Graham* in 1963 (FPF); 10 mi. E of Butte Falls, *Graham* in 1964 (FPF); 11 mi. E of Ashland on Lake of the Woods rd., *H & W 870* in 1966 (FPF); 20 mi. W of Ashland, *H & W 636* in 1964 (FPF); Fish Lake rd., 12 mi. SE of Butte Falls, *Graham* in 1965 (FPF); Huckleberry Mtn., 9 mi. NE of Prospect, *Graham* in 1965 (FPF); Long John Cr., S of Ashland, *Quick 64-01* in 1964 (FPF, CAS); 3.5 mi. S of Steamboat Mtn., *Knutson & Tinnin DM 77* in 1978 (FPF). JEFFERSON CO.: Suttle Lake, *Gill FP 68192* in 1932 (FPF); 14

mi. NW of Sisters on US 126, *H & W 616* in 1964 (FPF). JOSEPHINE CO.: 16 mi. E of Cave Jct. on Oregon Caves rd., *H & W 868* in 1966 (FPF); 13 mi. E of O'Brien on Happy Camp rd., *H & Hinds 997* in 1966 (FPF); 15 mi. E & 2 mi. S of Takilma, *Knutson & Tinnin DM 74* in 1978 (FPF); 7 mi. S & 2 mi. E of Williams, *Knutson & Tinnin DM 73* in 1978 (FPF); 3 mi. S & 5 mi. E of Takilma, *Knutson & Tinnin DM 81* in 1978 (FPF); 3 mi. S & 4 mi. E of Takilma, *Knutson & Tinnin DM 82* in 1978 (FPF); 2 mi. S & 9 mi. E of Takilma, *Knutson & Tinnin DM 79* in 1978 (FPF); 6.8 mi. W of divide on Happy Camp–O'Brien Rd., *Mathiasen 8627* in 1986 (FPF). KLAMATH CO.: Odessa, Upper Klamath Lake, *Meinecke* in 1912 (FPF); Kirk, Pelican Bay Camp, *Boyce FP 40165* in 1921 (OSC); Pelican Bay, *Peck* in 1920 (PH); 20 mi. W of Klamath Falls on Rte. 66, *H & W 628* in 1964 (FPF); between Lake of the Woods and Pelican Bay, *Daniels* in 1914 (ILL); 6 air mi. SE of Crescent on Rte. 97, *Knutson & Tinnin* in 1975 (FPF); 13.5 air mi. NW of Crescent, *Knutson & Tinnin* (FPF); Crescent, Boundary Springs, *Knutson & Tinnin DM 85* in 1978 (FPF); 4 mi. SW of Lone Pine, *Knutson & Tinnin DM 67* in 1978 (FPF); 4 mi. N of Crescent rd. on Davis Lake rd., *H 2343* in 1989 (FPF); 3 mi. N of Klamath Jct., *H 2368* in 1989 (FPF). LANE CO.: Black Cr. Cyn., *Knutson & Tinnin DM 41* in 1977 (FPF); 2 mi. W & 19 mi. S of McCredie Springs, *Knutson & Tinnin DM 44* in 1977 (FPF); 3 mi. E & 12 mi. S of Oakridge, *Knutson & Tinnin DM 42* in 1977 (FPF). LINN CO.: 1.5 mi. ESE of Marion Forks, *Knutson & Tinnin DM 54* in 1978 (FPF). MORROW CO.: 35 mi. S of Heppner, *Steward & Stewart 7329* in 1957 (RSA, US). UMATILLA CO.: 1 mi. NE of Kamela, *H & W 587* in 1964 (FPF). UNION CO.: 4 mi. W of Elgin on Rte. 204, *H & W 590* in 1964 (FPF). WALLOWA CO.: 6 air mi. SW of jct. of Snake and Salmon Rivers, *Graham* in 1963 (FPF); Billy Meadows, 5 mi. E of Kirkland Spring, *Colville 2478a* in 1907 (PH); Kirkland area, 30 mi. N of Enterprise, *Graham* in 1965 (FPF). WASCO CO.: Bear Springs For. Campground, *Childs & Hansbrough FP 68261* in 1931 (FPF) and *Childs & Hansbrough, Childs 69* in 1931 (OSC); 3 mi. E of Bear Springs, *Childs 57* in 1948 (OSC); 4 mi. W of Bear Springs, *H & W 610* in 1964 (FPF). WHEELER CO.: 1 mi. N of Nat. For. boundary, on Derr Meadows rd., 12 mi. SSE of Mitchell, *H 984* in 1966 (FPF); 0.25 mi. N of Ochoco Divide on US 26, on *Abies grandis*, *H & Scharpf 1264* in 1969 (FPF); 1 mi. N of Ochoco Divide, 11 air mi. W of Mitchell, *H 986* in 1966 (FPF); 26 mi. S of Hardman on Rte. 207, *H & Scharpf 1272* in 1969 (FPF). COUNTY UNCERTAIN: White Pine, *Starker* in 1916 (FPF, ILL).

TEXAS

CULBERSON CO.: Guadalupe Mts. Nat. Park, The Bowl, *H & Bailey 1528* in 1975 (FPF,TEX).

UTAH

CACHE CO.: Logan Cyn., near Jardine Juniper, *Krebill 453* in 1967 (FPF). DAGGETT CO.: Big Springs outlet, 11 mi. SW of Manila on Rte. 44, *H 567* in 1964 (FPF); Sheep Cyn. SW of Manila, *W 4128* in 1966 (FPF, UT); Palisades Campground, *Peterson 64-217* in 1964 (FPF); Ridge just N of Long Park Reservoir, *Mathiasen 9014* in 1990 (FPF). DUCHESNE CO.: 24.5 mi. SW of Duchesne on Rte. 33, *H 570* in 1964 (FPF). GARFIELD CO.: S of Grover, near Wildcat Ranger Sta., *Peterson 64-92* in 1964 (FPF); 14 mi. SE of Panguitch, *Peterson 63-87* in 1963 (FPF); Bryce Nat. Park, 3 mi. N of Far View Point, *Buchanan 310* in 1957 (RSA); 23 mi. N of Boulder on Rte. 117, *H 685* in 1964 (FPF); Dixie Nat. For., Markegun Plateau, 4 mi. SW of Panguitch Lake, *H & Geils 2142* in 1986 (FPF); Henry Mts., Bull Cr. near Lonesome Beaver Picnic Ground, *H 2095* in 1985 (FPF) and *Mathiasen 9011* in 1990 (FPF) and on *Abies lasiocarpa*, *H 2096* in 1985 (FPF) and *Mathiasen 9012* in 1990 (FPF); 0.9 mi. N of Hells Backbone Bridge, *Mathiasen 8931* in 1989 (FPF). GRAND CO.: La Sal Mts., 7 mi. S of Castleton, *H & Mathiasen 1490* in 1974 (FPF). IRON CO.: 14 mi. N of Panguitch Lake, *Peterson 62-67* in 1962 (FPF); 12 mi. E of Cedar City on Rte. 14, *H 678* in 1964 (FPF); 13 mi. N of Panguitch Lake, on *Abies lasiocarpa*, *Peterson 62-28* in 1962 (FPF). KANE CO.: without locality, *Siler* in 1878 (MO); 10.4 mi. W of Rte. 89 on Rte. 14, *H 681* in 1964 (FPF); Panguitch Lake Jct. on Rte. 14, *W 4121* in 1967 (FPF, UT); 2 mi. above old Seegmiller Ranch on lower Kanab Cr., E of Alton, *W 4120* in 1967 (FPF, UT); 10 mi. W of US 89 on Rte. 14, *H & Laut 1163* in 1969 (FPF); Cougar Hollow, S end Bryce Cyn. Nat. Park, on *Picea pungens*, *Peterson 62-111* in 1962 (FPF); 1.3 mi. SW of Rte. 14 on Strawberry Point rd., on *Picea pungens*, *Mathiasen* 8937 in 1989 (FPF). MILLARD CO.: Willow Cr. rd., W of Salina, *Peterson 64-63* in 1964 (FPF) on *Abies concolor*, *Peterson 64-64* in 1964 (FPF). PIUTE CO.: 2 mi. W of Nat. For. boundary on Marysvale-Mt. Belknap rd., *W 3036* in 1962 (COLO); Puffer Lake rd., W of jct., *Peterson 64-83* in 1964 (FPF); Marysvale, Tote Mine, *Jones 5911c* in 1894 (POM, US); Marysvale, *Jones 5395* in 1894 (MO, RSA US). SALT LAKE CO.: Big Cottonwood Cyn., *Hartley FP 17865* in 1915 (FPF, ILL). SAN JUAN CO.: Abajo Mts., near Spring Cr., *Rydberg & Garrett 9864* in 1911 (RM, US); Elk Ridge, SW of Kigalia Guard Sta., *Peterson 65-76* in 1965 (FPF); N slope Abajo Mts., *Krebill 288* in 1964 (FPF); Abajo Mts. , 7.0 mi. from Dry Wash Res. on For. Service rd. 079, *Mathiasen 8901* in 1989 (FPF); Abajo Mts., top of White Cyn. just S of Bears Ears, *Mathiasen 9009* in 1990 (FPF); 6 mi. W of Navajo Mtn. Trading Post on Navajo Mtn. rd., *H & others 1388* in 1971 (FPF). SANPETE CO.: Ephraim Cyn., SE of Ephraim, *Hedgcock FP 8126* in 1912 (FPF); Great Basin Exp. Sta., *Gill FP 68262* in 1932 (FPF); 8.7 mi. E of Ephraim on Great Basin Exp. Sta. rd., *H 574* in 1964 (FPF). SEVIER CO.: 4 mi. NW of Joseph, *Harris* in 1914 (ILL); S end of Fish Lake, *H & Laut 1161* in 1969 (FPF). SUMMIT CO.: Kamas, *Hedgcock FP 9322* in 1911 (FPF). TOOELE CO.: Stansbury Mts., end of rd. in S Willow Cyn., *W 3865B* in 1965 (FPF, UT). UTAH CO.: 5 mi. SW of Rte. 50 on Skyline rd., *H 572* in 1964 (FPF); Spring Lake, *Parry* in 1875 (MO) and on *Abies concolor*, *Parry 86* in 1875 (MO, US). WASATCH CO.: on US 40 1 mi. N of Lodgepole Campground, *H 2189* in 1987 (FPF); near jct. of Layout Cr. and Current Cr., 9 mi. NW of US 40, *H 2190* in 1987 (FPF). COUNTY UNCERTAIN: Ephraim Plateau, *Harris C2770B* in 1927 (PH); central Utah, on *Abies concolor*, *Parry 10659* in 1875 (ILL, MO).

WASHINGTON

CHELAN CO.: 8 mi. NW of Leavenworth on US 2, *H & others 1136* in 1968 (FPF); Fish Lake, *Hanzlik FP 68257* in 1932 (FPF); Tip Top Mtn., 13 mi. W of Wenatchee, col.? in 1915 (ILL); Chelan Lake, *Weir 6162* in 1916 (ILL); Stehekin River at N end of Chelan Lake, *Graham* in 1964 (FPF); 14.3 mi. NW of Ardenoir on rd. 317, *Tinnin & Knutson* in 1976 (FPF); 4 mi. E & 16 mi. S of Lucerne, *Tinnin & Knutson* in 1976 (FPF); 8.5 mi. E of Stevens Pass on US 2, *H & others 1137* in 1968 (FPF); Tip Top Mtn., 13 mi. W of Wenatchee, col. ? in 1915 (ILL); Peavine Cyn., 7 air mi. WSW of Wenatchee, *H 2381* in 1989 (FPF). CLACKAMAS CO.: Clackamas River, ca. 12 air mi. NE of Breitenbush, *Nicholson* in 1968 (FPF). COLUMBIA CO.: Wolf Fork of Touchet River, *St. John 6936* in 1925 (UC); Tucanan Cr., *Knutson 69* in 1979 (OSC). FERRY CO.: Sherman Cr. near Growden, *Wicker* in 1963 (WSP); Republic, *Foster* in 1912 (MO). GRANT CO.: 0.5 mi. S of Grand Coulee Dam, *H 2205* in 1987 (FPF). KITITAS CO.: 1.0 mi. N of jct. of rd. 2208 and Rte. 97, S of Blewett Pass, *Tinnin & Knutson* in 1976 (FPF). KLICKITAT CO.: 2 mi. NW of Satus Pass, *H & W 593* in 1964 (FPF); 8 mi. E of Glenwood on Goldendale Rd., *H 2222* in 1987 (FPF). OKANOGAN CO.: Okanogan, *Weir*? in 1914 (ILL); 18 air mi. E of Tonasket, *Graham* in 1965 (FPF); 11 mi. NNW of Loomis, *Gregg* in 1969 (FPF); near Republic, *Knutson 75* in 1979 (OSC); 20 mi. E of Tonasket. *Knutson 76* in 1979 (OSC): 5 mi. SW of Methow, *Graham* in 1964 (FPF); 9 mi. W of Republic on Rte. 30, *H & others 1132* in 1968 (FPF); 12 mi. W of Okanogan on Rte. 20 *H & others 1135* in 1968 (FPF); Varder Cr., 6 mi. W of Mazama on Rte. 20, *Mathiasen 74-8* in 1974 (FPF); Disautel Summit on Rte. 155, *Mathiasen 74-5* in 1974 (FPF); 7.7 mi. from Colville SW along extension of rd. 357, *Tinnin & Knutson* in 1976 (FPF); 10.7 air mi. NNE of Winthrop, *Tinnin & Knutson* in 1976 (FPF); 10.8 mi. E of Rd. 153 on Rte. 20, *Tinnin & Knutson* in 1976 (FPF); 10 mi. N of Chelan, 0.25 mi. NW of Wells Dam, *Tinnin & Knutson* in 1976 (FPF); Colville Indian Res., 7 mi. NW of Nespelem on Rte. 155, *H 2206* in 1987 (FPF); 5.9 mi. E of Washington Pass on Rte. 20, on *Abies lasiocarpa*, *Tinnin & Knutson* in 1976 (FPF); 20 mi. NW of Winthrop on Rte. 20 at Klipchuck Campground, on *Abies lasiocarpa*, *Tinnin & Knutson* in 1976 (FPF); Conger Cr., 5 air mi. SW of Conconully, *H 2409* in 1990 (FPF); Middle Fork of Boulder Cr., 11 air mi. NNE of Winthrop, *H 2412* in 1990 (FPF). SKAMANIA CO.: White Salmon Cr., 9 mi. NNW of Trout Lake on Randle rd., *H 2215* in 1987 (FPF). WHITMAN CO.: Kamiak Butte, just N of Pullman, *Tinnin & Knutson* in 1979 (OSC). YAKIMA CO.: 23 mi. E of White Pass on Rte. 14, 2 mi. W of Nat. For. boundary, *H & W 596* in 1964 (FPF); Dog Lake, Tieton Cyn., *Wicker* in 1966 (FPF); 11.2 mi. W of jct. of Rte. 410 and Rte. 12, along Rte. 12, *Tinnin & Knutson* in 1976 (FPF); 3 mi. E of Dog Lake, Tieton Cyn., *Wicker 11* in 1966 (FPF); 6 mi. NE of Trout Lake on Bird Cr. Meadows Rd., *H 2219* in 1987 (FPF); Tieton Reservoir, *Wicker* in 1963 (WSP).

WYOMING

LINCOLN CO.: Wolf Cr. Campground on Snake River, Targhee Nat. For., *Peterson 62-64* in 1962 (FPF, RM); 18 mi. W of Hoback Jct., on Rte. 89, *W 4360* in 1969 (FPF, UT). TETON CO.: 4 mi. E of Idaho boundary on Teton Pass rd., *Peterson 62-12* in 1962 (FPF, RM); 7 mi. E of Alta on Grand Targhee Ski Area rd., *H 2455* in 1992 (FPF).

13. Arceuthobium durangense

MEXICO

DURANGO

59 km. W of El Salto on Rte. 40, on *Pinus durangensis*, *H & W 353* in 1963 (COLO, FPF); 72 km. W of El Salto on Rte. 40, on *Pinus michoacana*, *H & W 354* in 1963 (COLO, FPF) and *1237* in 1969 (FPF); 62 km. W of El Salto on Rte. 40, on *Pinus durangensis*, *H 1422* in 1972 (FPF); 61 mi. W of El Salto on Rte. 40, on *Pinus durangensis*, *H 2118* in 1985 (FPF); 1.6 km. W of El Madroño on Rte. 40, on *Pinus michoacana*, *Nickrent 2049* in 1985 (FPF, ILL).

JALISCO

Sierra de Quila: on *Pinus michoacana*, *H 2119* in 1986 (FPF) and *Carbajal* in 1985 (INIF); on *Pinus douglasiana*, *H 2220* in 1986 (FPF) and *Carbajal* in 1985 (INIF); on *Pinus* sp., *Chazaro & Guerrero 5713* in 1988 (FPF, IBUG); on *Pinus douglasiana*, *Guerrero 82* in 1989 (FPF, IBUG).

SINALOA

16 km. W of Durango boundary on Rte. 40, on *Pinus michoacana*, *Mathiasen 8120* in 1981 (FPF); 2 km. NE of Tropic of Cancer on Rte. 40, on *Pinus douglasiana*, *Worthington & others 9391* in 1983 (FPF, UTEP); 75 km. E of Rte. 15 on Rte. 40, on *Pinus michoacana*, *H & W 1234* in 1969 (FPF); 68 km. E of Rte. 15 on Rte. 40, on *Pinus* sp., *W 5975* in 1984 (FPF); 11 km. E of Cosala, on *Pinus michoacana*, *Mathiasen 8131* in 1981 (FPF).

14. Arceuthobium gillii

Specimens on *Pinus leiophylla* var. *chihuahuana* except as noted.

MEXICO

CHIHUAHUA

Continental Divide on Mexico NW Railroad on ridge between Rió Chico and Rió Caballo, on *Pinus leiophylla*, *Barlow* in 1911 (FPF); 1 km. S of Majalca, *Andresen & Andresen 1804* in 1961 (FPF); Majalca, *Sueur 599* in 1936 (UC); Mt. Mohinora, *Nelson 4887* in 1898 (F, US); 65 mi. E of Batopilas, *Goldman 184* in 1898 (F, US); 25 mi. SW of La

Junta, *H & W 292* in 1963 (FPF); 34 mi. SW of La Junta, *H & W 294* in 1963 (FPF) and on *Pinus arizonica* (rare), *H & W 293* in 1963 (FPF); 36 mi. SW of La Junta, *H & W 297* in 1963 (FPF); 14 mi. E of El Vergel, *H & W 307* in 1963 (FPF); 18 mi. W of El Vergel on Rte. 24, on *Pinus leiophylla* var. *leiophylla*, *H 1846* in 1978 (FPF); 22 mi. W of El Vergel on Rte. 24, on *Pinus lumholtzii*, *H 1849* in 1978 (FPF); 21 mi. S of Creel on La Bufa rd., on *Pinus lumholtzii*, *H & Cibrián 1983* in 1981 (FPF); 21 mi. W of Tomochic on Rte. 16, on *Pinus lumholtzii*, *H & others 1649* in 1975 (FPF); 26 mi. SW of Col. Juárez, *H & W 460* in 1963 (FPF); 12 mi. SE of Mesa Huracán on Chico rd., *H & W 474* in 1963 (FPF); 18 mi. S of Las Varas on Madera rd., *H & W 481* in 1963 (FPF); 48 mi. SW of Matachic on Ocampo rd., on *Pinus lumholtzii*, *H & W 487* in 1963 (FPF); 43 mi. SW of Matachic on Ocampo rd., *H & W 484* in 1963 (FPF) and on *Pinus cooperi*, *H & W 483* in 1963 (FPF); 29 mi. SW of Matachic on Ocampo rd., *H & W 497* in 1963 (FPF): 6 mi. W of Matachic on Ocampo rd., *H & W 499* in 1963 (FPF); 40 mi. WNW of Nuevo Casas Grandes, *Bailey 77-07* in 1977 (FPF); 21 mi. S of La Junta on Creel rd., *Reichenbacher & Toolin 1267* in 1981 (ARIZ); Basaseachic, on *Pinus lumholtzii*, *Van Devender & Van Devender 87-128* in 1987 (ARIZ, FPF) and *H 2180* in 1987 (FPF); 4 km. W of Yepachic on Maicova rd., on *Pinus lumholtzii*, *H 2179* in 1987 (FPF); 11 km. E of Sonora boundary on Yecora-Maicova rd., *H 2177* in 1987 (FPF); 9 km. N of Rte. 16 on Yahuirachi rd., *H 2181* in 1987 (FPF); Cascada Basaseachic overlook, *Spellenberg & others* in 1987 (FPF, NMC); 4 mi. N of El Vergel rd. on Balleza rd., *H & Cibrián 1997* in 1981 (FPF); 19 mi. W of La Junta on Rte. 16, *H & others 1945* in 1975 (FPF); 130 km. W of La Junta on Rte. 16, *H & Cibrián 1974* in 1981, and on *Pinus lumholtzii*, *H & Cibrián 1975* in 1981 (FPF); 8 mi. E of Guachochic on Balleza rd., on *Pinus lumholtzii*, *H & Cibrián 1991* in 1981 (FPF); 24 mi. S of La Bufa Jct. on Guachochic rd., on *Pinus lumholtzii*, *H & Cibrián 1989* in 1981 (FPF).

DURANGO

18 km. W of Tepehuanes on rd. to Sierra del Huacol, on *Pinus lumholtzii*, *H 2161* in 1987 (FPF); 10 km. E of Tepehuanes on rd. to Sierra de la Candela, *H 2153* in 1987 (FPF).

SINALOA

without locality, on *Pinus* sp., *Hartman 340* in 1890 (FPF); Mpio. Badiraguato, Sierra Surutato, on *Pinus lumholtzii*, *Breedlove & Thorne 18617* in 1970 (CAS).

SONORA

"Frosty Saddle," *Hartman 364* in 1890 (BM, F, ILL, K, NY, PH, UC, US); Sierra de Ajos, SW side of mts., *Mathiasen 7801* in 1978 (FPF); 15 km. SE of Yecora, on *Pinus herrerai*, *H 2174* in 1987 (FPF).

UNITED STATES

ARIZONA

COCHISE CO.: Chiricahua Mts.: Chiricahua Nat. Mon., Bonita Cyn., *Reeves R-1279* in 1974 (ASU); Pedestal Pass, *Blumer 1515* in 1906 (ARIZ, ILL, K, MO, RM, US, Z); Pine Cyn., *Blumer 2394* in 1907 (ARIZ, DS, RM, Z); 6 mi. from Faraway Ranch, Portal, *Gill FP 68036* in 1936 (FPF); Portal, near SW Research Sta., *H & Lightle 157* in 1962 (FPF); Rustler Park, *Ellis & Gill FP 89500* in 1939 (FPF); Parker Cyn. *Long FP 318* in 1909 (FPF); Pinery Cyn., *H & Lightle 153* in 1962 (FPF) and *H 806* in 1965 (FPF); Portal, *Long FP 15976* in 1914 (FPF, ILL); 0.8 mi. W of SW Research Sta., *H & others 1394* in 1972 (FPF); 0.5 mi. E of Reef, *H & Lightle 236* in 1962 (FPF, COLO, ARIZ, DS, US, MO) and *H & Mathiasen 1470* in 1973 (FPF); Pinery Cyn. at jct. of N and S forks, *Stone 201* in 1919 (PH). Huachuca Mts.: Reef, *Gill & Ellis FP 89496* in 1939 (FPF). PIMA CO.: Santa Catalina Mts.: General Hitchcock Campground, *H & Lightle 164* in 1962 (FPF) and *H & Scharpf 705* in 1964 (FPF); Oracle rd., *Peterson 62-148* in 1962 (FPF) and *H & Lightle 1111* in 1968 (FPF); Mt. Lemmon, *Peebles & others 2565* in 1926 (ARIZ, US): Mud Springs, *Harris C16354B* in 1916 (US). Rincon Mts., *Blumer 3362* in 1909 (ARIZ, MO, UC). SANTA CRUZ CO.: W side Huachuca Mts., T. 24 S, R. 18 E, *H & Lightle 161* in 1962 (FPF); Santa Rita Mts., SE side of Mt. Wrightson, 1 mi. up trail from end of Tunnel Springs rd., *Lightle 65-26* in 1965 (FPF). COUNTY UNCERTAIN: Santa Rita Mts., *Pringle 13876* in 1881 (FPF).

NEW MEXICO

HIDALGO CO.: Animas Mts., Indian Cr. Cyn., *H & others 1434* in 1972 (FPF).

15a. Arceuthobium globosum subsp. *globosum*

MEXICO

CHIHUAHUA

Mesa Colorado, on *Pinus* sp., *Gentry 587M* in 1933 (MICH); 19 mi. W of Mesa Huracán, on *Pinus arizonica*, *H & W 466* in 1963 (COLO, FPF), and on *Picea engelmannii*, *H & W 467* in 1963 (COLO, FPF); Llano Grande, Guadalupe y Calvo area, on *Picea engelmannii*, *Olivo* in 1987 (FPF); El Pinito, Guadalupe y Calvo area, on *Pinus* sp., *Olivo* in 1987 (FPF); Ejido Redondeado, near Guadalupe y Calvo, on *Pinus arizonica* and *Picea engelmannii*, *Olivo* in 1987 (FPF); Cerro Mohinora, on *Pinus arizonica*, *Conkle* in 1985 (FPF), *Olivo* in 1984 (INIF), and *Olivo* in 1987 (FPF); 15 km. S of Chuhuichupa on La Candelaria rd., on *Pinus durangensis*, *H & Cibrián 1952* in 1981 (FPF); Peak of La Candelaria, S of Chuhuichupa, on *Pinus rudis?*, *H & Cibrián 1956* in 1981 (FPF); Mpio. Madera, Ejido Tres Ojitos, on *Pinus durangensis*, *Flores* in 1984 (INIF); Mpio. Uriques, Ejido Piedras Verdes, on *Pinus durangensis*, *Olivo* in 1984 (INIF).

DURANGO

20 mi. W of El Salto on Rte. 40, on *Pinus* sp., *McVaugh 11518* in 1951 (MICH); N slopes of Cerro Huehueto, on *Pinus* sp.,

Maysilles 7260 in 1950 (MICH); San Luis del Rio, 51 mi. NW of Coyotes, on *Pinus* sp., *Maysilles 7977* in 1955 (NY); 1.5 mi. E of El Salto on Rte. 40, on *Pinus cooperi, H & W 344* and *524* in 1963 (COLO, FPF); 13 mi. W of El Salto on Rte. 40, on *Pinus cooperi, H & W 349* in 1963 (COLO, FPF); 24 mi. W of El Salto on Rte. 40, on *Pinus durangensis, H & W 351* in 1963 (COLO, FPF); 33 mi. W of El Salto on Rte. 40, on *Pinus durangensis, H & W 526* in 1963 (FPF); 34 mi. W of El Salto on Rte. 40, on *Pinus durangensis, H & others 1661* in 1975 (FPF); 35 mi. W of El Salto on Rte. 40, on *Pinus durangensis, H & W 1246* in 1969 (FPF); 2 mi. E of El Salto on Rte. 40, on *Pinus cooperi, H & others 1664* in 1975 (FPF); 3 mi. E of El Salto on Rte. 40, on *Pinus cooperi, H & others 1960* in 1975 (FPF); 21 mi. W of El Salto on Rte. 40, on *Pinus durangensis, H & others 1667* in 1975 (FPF); 19 mi. W of El Salto on Rte. 40, on *Pinus durangensis, H & others 1669* in 1975 (FPF); 12 km. SW of Altares, on *Pinus durangensis, H & others 2244* in 1987 (FPF); El Cocono, Guanacevi area, on *Pinus arizonica, Najera & Gonzales* in 1987 (FPF); Cienega de la Vaca, 40 km. WNW of El Zape, on *Pinus durangensis, Conkle* in 1985 (FPF); Mpio. Uruachi, Paraje Faledo Agua Negro, Eijdo Rocoroybo, on *Pinus durangensis, Rodriguez* in 1982 (INIF); Mpio. Guazapares, Paraje de Cordon Guazapares, on *Pinus durangensis* and on *Pinus engelmannii, Rodriguez* in 1982 (INIF).

JALISCO

Mpio. Mezquitic: 35 km. NW of Bolanos, on *Pinus* sp., *Flores & others 1603* in 1989 (FPF, IBUG); km. 50 on Bolanos-Tenzompa rd., NE of Pinos Altos, near Santa Catarina, on *Pinus durangensis, Villareal & Peraz la Rosa 3062* in 1988 (IBUG).

SONORA

"Pine Ridge Pass", on *Pinus* sp., *Hartman 340* in 1890 (ILL, K, NY, UC, US).

15b. *Arceuthobium globosum* subsp. *grandicaule*

GUATEMALA

DEPARTMENT CHEMALTENANGO

Between Tecpàn and Encuentros, on *Pinus* sp., *Aguilar* in 1955 (EAP).

DEPARTMENT HUEHUETENANGO

Sierra Cuchumatanes: Cerra Canana, between Nucapula and Canana, on *Cupressus* sp. (no host with collection), *Steyermark 49044* in 1942 (F); Chemal, on *Pinus* sp., *Johnston 1777* in 1940 (EAP, F); km. 36, Chemal, on *Pinus* sp., *Standley 81637* in 1940 (EAP, F, NY), *Standley 81642* in 1940 (F), *Standley 81683* in 1940 (F), and on *Pinus rudis, Clark & Paz* in 1972 (FPF); 3 km. S of Chemul, on *Pinus* sp., *Harmon & Fuentes 4845* in 1979 (ENCB); vicinity of Touquia, on *Pinus rudis, Steyermark 50130* in 1942 (MO, NY, US); between Paquix and San Miguel, on *Pinus pseudostrobus, Molina & others 16483* in 1966 (EAP, NY); 33 km. N of Huehuetenango near Chemal, on *Pinus rudis, H & W 1219* in 1969 (FPF); 10 km. N of Santa Eulalia on rd. to Barillas, on *Pinus rudis, H & W 1223* in 1969 (FPF); km. 123 on Barillas rd., on *Pinus rudis, Peterson 74-248* in 1974 (FPF); Todos Santos, on *Pinus rudis, Smith 969* in 1977 (FPF); San Mateo Ixtlán, on *Pinus* sp., *Breedlove 8646* in 1965 (DS, FPF); Chancol, on *Pinus rudis, Clark & Paz* in 1973 (FPF).

DEPARTMENT SAN MARCOS

Volcán Tajumulco, on *Pinus* sp., *Schmidt* in 1934 (F) and *Steyermark 36940* ("on pine roots and branches") in 1940 (MICH); Sibinal, on *Pinus pseudostrobus, Smith 540* in 1977 (FPF).

DEPARTMENT TOTONICIPÁN

Cerro Sajbachol, above Totonicipan, on *Pinus rudis, Clark & Paz* in 1972 (FPF) and *Smith & Clancy 568a* in 1977 (FPF).

MEXICO

DISTRITO FEDERAL

Desierto de los Leones, on *Pinus* sp., *Roldan* in 1919 (FPF, ILL); Cerro Santa Rosa, on *Pinus* sp., *Matuda* in 1952 (ENCB).

GUERRERO

Mpio. Tlacotepec, Cerro Teotepec, on *Pinus hartwegii, Rzedowski 16497* in 1963 (INIF).

HIDALGO

Mpio. Epazoyucán, 1 km. NE of Nopillo, on *Pinus hartwegii, Medina 1771* in 1976 (INIF, MEXU).

JALISCO

Juanacatlan, Tapala, on *Pinus michoacana, Daiz 7623* in 1975 (ENCB) and on *Pinus montezumae, Rzedowski 7869* in 1977 (INIF); Mpio. Tapalpa, near Ferreria de Tula, on *Pinus* sp., *Hernandez* n.d. (IBUG); Mamatlan, 15 mi. SSE of Autlan by way of Chante, on *Pinus* sp., *Wilbur & Wilbur 1837 and 1982* in 1949 (MICH); Mpio. Cuautitlan, Sierra Mammatlan, on *Pinus* sp., *Cueva & Guzman 2025* in 1987 (IBUG).

MEXICO

Ojos de Agua, Nevado de Toluca, on *Pinus* sp., *Balls B4089* in 1938 (BM, K, UC, US); 40 km. W of Toluca, on *Pinus* sp., *Frye & Frye 2590* in 1939 (ARIZ, DS, MO, NY, RSA, UC, WTU); Ixtacchiuatl, on *Pinus* sp., *Purpus 1778* in 1905 (F, ILL, MO, NY, UC, US); Mpio. Texcaltitlan, 1 km. S of Cajones, on *Pinus pseudostrobus, Rzedowski 32787* in 1975 (UNAM); Mpio. San Rafael, Nixcaulanco, on *Pinus hartwegii, Boyas 582* in 1974 (INIF); Amalacaxo, on *Pinus* sp., *Miranda 872* in 1940 (MEXU); Crucero Agua Blanco, Temascaltepec, on *Pinus* sp., *Hinton 8901* in 1936 (ARIZ, K, US); Valley of Mexico, on *Pinus* sp., *Borglav 1115* in 1866 (K, US); Nevado de Toluca, on *Pinus* sp., N slope, (4,120 m.), *Iltis & others 1701* in 1963 (WIS), on *Pinus hartwegii*, *Andresen & Steinhoff A2035* in 1962 (FPF), *Matuda* in 1952 (MEXU), *Rzedowski 15776* in 1962 (MEXU), and on *Pinus rudis*, *H & W 369* in 1963 (COLO, FPF); 6 mi. E of Michoacán boundary on Rte. 15, on *Pinus michoacana*, *H & W 368* in 1963 (COLO, FPF): 32 mi. W of Toluca on Rte. 15, on *Pinus montezumae*, *H 49* in 1956 (FPF); 3 mi. W of Rio Frio on Rte. 190, on *Pinus montezumae*, *H & W 371* in 1963 (COLO, FPF) and *H & others 1413* in 1972 (FPF); Rio Frio, on *Pinus* sp., *Matuda* in 1953 (MEXU); 1.5 mi. E of Michoacán boundary on Rte. 15, on *Pinus pseudostrobus*, *H & W 367* in 1963 (COLO, FPF); Mpio. Texcoco, NE slopes of Cerro Tlaaloc, on *Pinus hartwegii*, *Rzedowski 31535* in 1973 (ENCB); 8 km. NW of Presa Iturbidio, on *Pinus hartwegii*, *Rzedowski 27112* in 1970 (ENCB); Parque Nacional Bosencheve, on *Pinus montezumae*, *Madrigal 2479* in 1973 (INIF); E of Gauchupin, on *Pinus hartwegii*, *Hernandez 5-19* in 1972 (INIF); 11.4 mi. E of Angangueo on San José del Rincon rd., on *Pinus montezumae*, *H & Player 1539* in 1975 (FPF).

MICHOACÁN

Cerro Tancitaro, on *Pinus* sp., *Leavenworth 710* in 1940 (F, MO); and on *Pinus rudis*, *Leavenworth & Hoogstraal 1126* in 1941 (F, MO); 18 mi. S of Patzcuaro, on *Pinus* sp., *King & Soderstrom 5174* in 1961 (MICH, NY, UC, US); NW of Cuidad Hidalgo, on *Pinus* sp., *McVaugh 9952* in 1949 (MICH); San Alejo: on *Pinus lawsonii*, *Valdivia & Soloranzo 648* in 1963 (FPF); on *Pinus rudis*, *Valdivia & Soloranzo 649* in 1963 (FPF); on *Pinus michoacana*, *Valdivia & Soloranzo 650* in 1963 (FPF); on *Pinus montezumae*, *Valdivia & Soloranzo 646* in 1963 (FPF); and on *Pinus tenuifolia*, *Valdivia & Soloranzo 638, 640, 642, 643, 644,* and *654* in 1963 (FPF); 26 mi. E of Morelia on Rte. 15, on *Pinus pseudostrobus*, *H 51* in 1956 (FPF) and *H & W 361* in 1963 (COLO, FPF); 29 mi. E of Morelia, on *Pinus pseudostrobus*, *Valdivia & Soloranzo 634* in 1963 (FPF) and on *Pinus tenuifolia*, *Valdivia & Soloranzo 635* in 1963 (FPF); San Pedro Jacuaro, on *Pinus tenuifolia*, *Valdivia & Soloranzo 636* in 1963 (FPF); 32 mi. E of Morelia on Rte. 15, on *Pinus pseudostrobus*, *H & Player 1609* in 1975 (FPF); Mpio. Tangancicuaro, Mesa del Cerro Viejo, on *Pinus hartwegii*, *Takaki* in 1970 (INIF); Mpio. Charapán, San Isodoro, on *Pinus* sp., *Bello* in 1981 (INIF, MEXU); Mpio. Ciudad Hidalgo, Los Azufres, on *Pinus pseudostrobus*, *Rzedowski 27970* in 1970 (INIF); Mpio. Tancitaro, Rancho Nuevo, on *Pinus pseudostrobus* and *Pinus douglasiana*, *Bello* in 1981 (INIF); Mpio. Nahuatzen, Cerro Pilon, on *Pinus* sp., *Martínez 906* in 986 (ENCB, IEB); Mpio. Santa Clara de Cobre, Cerro del Burro, on *Pinus pseudostrobus*, *Rzedowski 43814* in 1987 (IEB); Mpio. Paracho, Cerro del Aguila, on *Pinus* sp., *Daiz & Zamudio* 3439 in 1986 (IEB); San Juan Nuevo, Agua Chiquita, on *Pinus pseudostrobus*, *Bello 12* in 1981 (MEXU); Angangueo, on *Pinus tenui-folia*, *Cibrián & others* in 1979 (MEXU); 11 km. SE of Apopepo, on *Pinus pseudostrobus*, *H 2115* in 1986 (FPF).

MORELOS

Mpio. Huitzialc, Parque Nacional Lagunas de Zempola, on *Pinus* sp., *Carduso 1245* in 1986 (MEXU).

OAXACA

Sierra de San Felipe, on *Pinus* sp., *Pringle 4727* in 1894 (BM, K, MEXU, MO, NY, PH, US, Z); 21 mi. S of Tuxtepec on rd. to Oaxaca de Juárez, on *Pinus rudis*, *Andresen & Steinhoff A1983* in 1962 (FPF); Macuiltianguis, on *Pinus hartwegii*, *Lucero 56* in 11980 (ENCB, MEXU); District Ixtlan, La Cumbre, on *Pinus* sp., *Garcia & others 1753* in 1985 (IBUG); 20 mi. N of Ixtlan and 0.8 mi. E of Rte. 175, on *Pinus rudis*, *H & others 1554* in 1975 (FPF); 32 km. N of Ixtlan on Rte. 175, on *Pinus rudis*, *W 6006* in 1985 (FPF); km. 160 on Rte. 175, near Atepec Jct., on *Pinus rudis*, *Peterson 74-80* in 1974 (FPF).

PUEBLA

Near Rio Frio, on *Pinus* sp., *Kenoyer* in 1938 (ARIZ); Campo Experimantal San Juan Tetla, on *Pinus hartwegii*, *Rodriguez* in 1974 (INIF); Mpio. Oyameles, Sierra de Mastoylan, NW of Numero, on *Pinus* sp., *Chazaro & Hernandez 5437* in 1988 (IBUG); Mpio. Vicente Guerrero, San Bernardino la Laguna, on *Pinus pseudostrobus*, *Lott & Wendt P-132* in 1987 (ENCB).

TLAXCALA

Manliche, 12 km. W of Ixtencio, on *Pinus montezumae*, *H 2107* in 1986 (FPF).

VERACRUZ

Mt. Orizaba, on *Pinus* sp., *Balls B4399* in 1938 (BM, K, UC, US); Cofre de Perote, on *Pinus hartwegii*, *Beaman 2214* in 1958 (RM, UC, US); Mpio. de Jalancingo, El Rincon, on *Pinus pseudostrobus*, *Cibrián T. & Chaboya P.* in 1988 (FPF).

16. Arceuthobium guatemalense

All collections on *Pinus ayacahuite* var. *ayacahuite*.

GUATEMALA

DEPARTMENT HUEHUETENANGO

Sierra Cuchumatanes: 2 km. N of Santa Eulalia on Barillas rd., *H & W 1222* in 1969 (FPF); 54 km. N of Huehuetenango on Santa Eulalia rd., *H & W 1221* in 1969 (COLO, DS, EAP, FPF, MO, US, UT).

DEPARTMENT TOTONICAPÁN

Near Km-170 on Pan American Highway, 15 km. W of Nahuala, *H & W 1226* in 1969 (FPF).

MEXICO

CHIAPAS

Mpio. Teopisca, 12 km. SE of San Cristóbal de las Casas, on ridge SW of Rte. 190, *Peterson 74-300* in 1974 (FPF).

OAXACA

29 mi. N of Ixtlán on Rte. 175, 0.5 mi. N of the Continental Divide, *H & others 1552* in 1975 (FPF) and *Nickrent 2039* in 1985 (ILL, MEXU); 54 mi. N of Oaxaca on Rte 175., *Peterson 72-93* in 1972 (FPF); 57 mi. N of Oaxaca on Rte. 175, *Peterson 72-98* in 1972 (FPF).

17. *Arceuthobium hawksworthii*

All collections on *Pinus caribaea* var. *hondurensis*, except as noted.

BELIZE

CAYO DISTRICT

Mtn. Pine Ridge: Granite Cairn rd., 6 mi. E of Augustine, ca. 30 mi. W of Stann Cr., *Hunt 286* in 1959 (US) (Host on sheet labeled as *Pinus* sp., but Hunt (1962) gives it as *Pinus caribaea*); Raspa rd., *Etheridge BFDS 26* in 1965 (DAVFP, FPF); on *Pinus* sp., *Whiteford 3104* in 1981 (MEXU); near Augustine, *Perry B-0-88* in 1988 (FPF); *Carty* in 1981 (FPF) and 1981 (FPF); Raspa-Brunton area, *Carty 2* in 1981 (FPF); Bokikine area, *Carty 5* in 1981 (FPF); on *Pinus oocarpa*, *Carty 7* in 1981 (FPF); Cow Trail area, on *Pinus oocarpa*, *Carty 6* in 1981 (FPF); Raspa-Brunton area, on *Pinus oocarpa x Pinus caribaea*, *Carty 3A* in 1981 (FPF); 5.2 mi. ESE of Georgeville-Augustine rd. on Granite Cairn rd., *W & C. G. Shaw III 7767* in 1994 (FPF); 2.7 mi. up Brunton rd. from Augustine-Carcol rd., *W & C. G. Shaw III 7769* in 1994 (FPF); 1.5 mi. S of Cooma Cairn Lookout, *W & C. G. Shaw III 7768* (on *Pinus caribea* var. *hondurensis*) (FPF, UC, MD, US).

18. *Arceuthobium hondurense*

HONDURAS

DEPARTMENT CORTES

Parque Nat. Cusuco, 20 km. W of Choloma on Cohdefor rd., on *Pinus maximinoi*, *Beatty* s. n. in 1991 (FCPF).

DEPARTMENT FRANCISCO MORAZÁN

Near Piedra Herrada: Rio Yeguare drainage, lat. 14°N, long. 87°W., on *Pinus oocarpa*, *Williams 15964* in 1969 (BM, EAP, F); 22 km. SE of Tegucigalpa on rd. to Escuela Agricola Panamericana, on *Pinus oocarpa*, *H, W & Molina 1203* in 1969 (COLO, EAP, CAS, F, FPF, MO, US, UT); 7 km. W of Zamorano on Tegucigalpa rd., on *Pinus oocarpa*, *H & W 1209* in 1969 (FPF).

19. *Arceuthobium laricis*

All collections on *Larix occidentalis*, except as noted.

CANADA

BRITISH COLUMBIA

Cascade, *Sugden* in 1955 (DAVFP FPF); Burton, *Kuijt 566* in 1953 DAVFP, FPF); Balfour, *Kuijt 563* in 1953 (DAVFP, FPF); Slocan Lake, *Kuijt* in 1953 (DAVFP, FPF); Christina Cr., *Kuijt 553* in 1953 (DAVFP, FPF); Grand Forks, *Kuijt 556* in 1953 (DAVFP, FPF); Salmo, *Kuijt 547* in 1953 (DAVFP, FPF); Castlegar, *Kuijt 546* in 1953 (DAVFP, FPF); Fruitvale, *Kuijt* in 1953 (DAVFP, FPF); Creston, *Kuijt* in 1953 (DAVFP, FPF); St. Mary's Lake, *Kuijt 544* in 1953 (DAVFP, FPF); St. Mary's River, *Kuijt* in 1953 (DAVFP, FPF); 3 mi. N of Moyie on Cranbrook rd., *Calder & Saville 11415* in 1953 (CAS, UC, WTU); 6 mi. W of jct. W of Rossland, *Calder & Saville 11465* in 1953 (US); Owens Lake, *Weir 8362* in 1913 (ILL); Salmon Arm, *Weir 8364* in 1913 (FPF, ILL).

UNITED STATES

IDAHO

ADAMS CO.: Evergreen, *Hedgcock FP 997* in 1909 (FPF); Payette Nat. For., Council Ranger District, about 12 air mi. E of Copperfield, *Hoffman* in 1988 (FPF). BENEWAH CO.: St. Maries, *Hedgcock FP 9526* in 1911 (FPF) and *Weir 659* in 1911 (ILL) and *Weir 663* in 1911 (FPF). BOISE CO.: Idaho City, *Weir 8371* in 1917 (ILL). BONNER CO.: Priest River, *Weir 8373* in 1917 (FPF, RM, US); Sandpoint, *Wehmeyer* in 1922 (US); 4 mi. N of Priest River on For. Exp. Sta. rd., *H & Wicker 961* in 1966 (FPF) and *H & Wicker 1125* in 1968 (FPF); Priest River Exp. For. Headquarters, on *Picea abies*, *H & Wicker 963* in 1966 (FPF); on *Pinus banksiana*, *Graham* in 1958 (FPF) and *H & Wicker 964* in 1966 (FPF), and on *Pinus resinosa*, *H & Wicker 965* in 1966 (FPF); 4 mi. N of Priest River on rd. to For. Exp. Sta., *H & Wicker 961* in 1966 (FPF) and on *Pinus contorta*, *H & Wicker 962* in 1966 (FPF); Coolin, on *Pinus contorta*, *Weir 8385* in 1917 (ILL) and on *Abies lasiocarpa*, *Weir 8391* in 1916 (ILL); Blue Lake, on *Abies grandis*, *Weir 8392* in 1917 (ILL); Priest River, on *Abies grandis*, *Weir 3252* in 1917 (ILL). BOUNDARY CO.: above Upper Priest Lake, *Boyce 1225* in 1924 (FPF, OSC). IDAHO CO.: 6 mi. S of Grangeville on Snow Haven rd., *H 969* in 1966 (FPF); 28 mi. W of Lolo Pass on Rte. 12, *H & Laut 1292* in 1970 (FPF). KOOTENAI CO.: Clark's Fork, Coeur d'Alene Mts., *Lieberg 1672* in 1895 (MO, RSA, RM, UC, US); 4th of July Summit, *W 3255* in 1962 (COLO, FPF); Granite Sta., *Sandberg, MacDougal & Heller 787* in 1892 (CAS, US); Coeur d'Alene, on *Pinus ponderosa*, *Weir 3271* in 1916 (ILL). LATAH CO.: Moscow Mtn., *Piper 1882* in 1894 (MO, RM) and *Weir 8368* (ILL). SHOSHONE CO.: Lich Cr. Lookout, ca. 6 mi. SSW of Avery, *Gill FP 68201* in 1932 (FPF) and on *Pinus monticola*, *Gill FP 68202* in 1932 (FPF); 3 mi. W of Montana boundary on US 10, *W 3256* in 1962 (COLO, FPF); 1/4 mi. W of Thompson Pass, on *Tsuga mertensiana*, *H & Wicker 957* in 1966 (FPF) and on *Abies lasiocarpa*, *H & Wicker 958* in 1966 (FPF); 1 mi. S of Jack Waite Mine on Woodchuck Pass rd., on *Tsuga mertensiana*, *H & Wicker 959* in 1966 (FPF); Marble Mtn., 9 mi. SW of Avery, col.? n.d. (*Weir 2458*) (FPF, ILL). VALLEY CO.: McCall, col.? in 1915 (ILL); 3 mi. NE of McCall on shore of Payette Lake, *H 973* in 1966 (FPF) and on *Abies lasiocarpa*, *H 974* in 1966 (FPF); Gold Fork River, 13 mi. W of Warm Lake, *Hoffman* in 1988 (FPF) and on *Pinus* *ponderosa*, *Hoffman* in 1988 (FPF). COUNTY UNCERTAIN: St. Joe Nat. For., *Weir 8472* in 1917 (ILL), and on *Pinus monticola*, *Weir 3245* in 1914 (ILL); Monumental Butte, St. Joe Nat. For., on *Pinus monticola*, *Weir* in 1914 (FPF, ILL).

MONTANA

FLATHEAD CO.: Somers, Flathead Lake, *Weir 3258* in 1916 (ILL); Big Fork, Flathead Lake, *Jones 9312* in 1908 (CAS, RSA) and *9309* in 1908 (RSA); Columbia Falls, *Williams 897* in 1892 (US). GLACIER CO.: E of St. Ignatius near St. Mary's Lake, *Krebill 133* in 1964 (FPF). GRANITE CO.: Phillipsburg, *Weir 8374* in 1917 (ILL). LAKE CO.: Yellow Bay, Flathead Lake, *Jones 9313* in 1908 (RSA) and *Butler 182* in 1908 (FPF); 4 mi. N of Dayton, *Krebill 136* in 1964 (FPF); 8 mi. N of Polson on Rte. 35, E side of Flathead Lake, *W 4365* in 1969 (FPF, UT). LINCOLN CO.: Cabinet Mts. near Scotchmans Peak, on *Larix occidentalis* (as *L. lyallii*) *Weir 3250* n.d. (FPF, ILL) and on *Tsuga mertensiana*, *Johns* in 1914 (FPF, ILL). MINERAL CO.: 7.5 mi. W of St. Regis, *Stickney 2220* in 1970 (MONT); 6 mi. W of St. Regis on US 10, *H & Wicker 956* in 1966 (FPF) and on *Pinus contorta*, *H & Wicker 955* in 1966 (FPF). MISSOULA CO.: Missoula, Pattee Cyn., *Weir FP 17048* in 1914 (FPF), and on *Pinus contorta*, *Paulson* in 1916 (FPF, ILL) and *Weir 3267* in 1916 (ILL); Blue Cr., 35 mi. NW of Missoula, on *Picea engelmannii*, *Toko & Pinney 65-34* in 1965 (FPF); Bitterroot Mts. near Lolo, on *Larix occidentalis* (as *Larix lyallii*) *Weir 8366* in 1914 (FPF, ILL); Lolo, on *Pinus ponderosa*, *Weir 8337* in 1916 (FPF, ILL); 3 mi. S of Lolo Hot Springs, on *Abies lasiocarpa*, *Dooling 3850* in 1979 (FPF). RAVALLI CO.: One Horse Cr. near Florence, col.? in 1915 (ILL); Victor: on *Picea engelmannii*, *Weir 8379* in 1917 (FPF); on *Pinus albicaulis*, *Weir 8334* in 1917 (ILL); on *Pinus contorta*, *Weir 8336* and *8384* in 1917 (ILL); and on *Abies lasiocarpa*, *Weir 8390* in 1917 (ILL); Bitterroot Nat. For., 5 mi. WNW of Stevensville, on *Abies lasiocarpa*, *Gates & Cornelisse* in 1984 (FPF). SANDERS CO.: Thompson Falls, *Hedgcock & Weir FP 9442* in 1911 (FPF), and on *Pinus ponderosa*, *Hedgcock & Weir FP 9444* in 1911 (FPF); 8 mi. N of Plains, on *Pinus ponderosa*, *Sieminski* in 1964 (FPF); 2 mi. E of Noxon on US 10A, *H & Wicker 960* in 1966 (FPF); 13 mi. E of Regis on Rte. 461, *W 4367* in 1969 (FPF, UT); 2 mi. W of Hot Springs, *H & others 2261* in 1988 (FPF).

OREGON

BAKER CO.: 6 mi. E of Medical Springs, *Peterson 63-236* in 1963 (FPF); 12 mi. S of Baker on Rte. 7, *H & W 585* in 1964 (FPF); Jim Cr. Fork of Eagle Cr., 30 mi. NE of Baker, *Graham* in 1965 (FPF) and, on *Pinus albicaulis*, *Graham* in 1965 (FPF); 9 mi. NW of Unity on Rte. 26, *H 1373* in 1971 (FPF); 1.6 mi. W of Wallowa-Whitman Nat. For. boundary on Rte. 26, NW of Unity, at jct. to Wetmore Campground, *H 1920* in 1979 (FPF). CROOK CO.: Ochoco, Cyn. Cr., *Donnelly* in 1920 (FPF). GRANT CO.: 16 mi. S of John Day on Rte. 395, *H & W 579* in 1964 (FPF) and on *Pinus ponderosa*, *H & W 578* in 1964 (FPF); 6 mi. E of Dixie Pass on US 26, *H & W 582* in 1964 (FPF); Elkhorn Spring rd., ca. 16 mi. E of Prairie City, *Childs 212* in 1952 (OSC); Dixie Butte, on *Abies grandis* (as *Abies concolor*), *Weir 2421* 1915 (FPF, ILL) and on *Abies lasiocarpa*, *Weir 2425* in 1916 (FPF, ILL); 4 mi. N of US 26 on Dixie Butte rd., on *Abies grandis*, *H 981* in 1966 (FPF); Big Cyn., 9 air mi. NE of Seneca, *H & Scharpf 1270* in 1969 (FPF). JEFFERSON CO.: Metolius area, *Gill FP 68189* in 1932 (FPF); Metolius River near Camp Sherman, *Graham* in 1964 (FPF); Camp Sherman, *Thompson & Stewart* in 1968 (FPF) and *H 2350* in 1989 (FPF); 2 mi. W of Camp Sherman, *H & Scharpf 1258* in 1969 (FPF). UMATILLA CO.: 13 mi. E of Kamela, *H & W 588* in 1964 (FPF); 12 mi. W of Elgin, *H & W 589* in 1964 (FPF); UNION CO.: 15 air mi. NNE of Elgin, *Orr* in 1968 (FPF). WALLOWA CO.: Minam Meadows, 12 mi. SW of Enterprise, *Sampson & Pearson 168* in 1907 (FPF, MO); Billy Meadows, 30 mi. NNE of Enterprise, *Coville 2459* in 1907 (US); Wallowa Mts., Bear Cr., *Coville 2363* in 1907 (US); W Morrain above Wallowa Lake, 4 mi. S of Joseph, *Mason 7199* in 1964 (ASU); Wallowa Mts. , Bear Cr. sheep trail, *Coville 2480* in 1907 (US); 8 mi. W of Troy, near Hoodoo Lookout, *Feddema 3509* in 1966 (USFS). WASCO CO.: Bear Springs Campground, Mt. Hood, *Childs & Hansbrough FP 68268* in 1931 (FPF) and *Childs 27* in 1940 (OSC); 5.7 mi. SE of Wapinita Pass on US 26, *H & W 609* in 1964 (FPF). WHEELER CO.: 3 mi. S of Nat. For. boundary on Derr Meadows rd., ca. 12 mi. SSE of Mitchell, *H 985* in 1966 (FPF); 21 mi. S of Hardman on Rte. 207, *H & Scharpf 1273* in 1969 (FPF); Ochoco Summit on US 26, *H & Scharpf 1262* in 1969 (FPF); Alder Cr., 35 mi. S of Heppner, *Steward & Steward 7328* in 1957 (CAS, RSA, US, WTU). COUNTY UNCERTAIN: Sumpter, *Hedgcock 1913* in 1909 (FPF).

WASHINGTON

CHELAN CO.: Chelan Lake, *Weir 8363* in 1916 (ILL); Leavenworth, *Bunder* n.d. (ILL); Beehive Mtn., 6 air mi. SW of Wenatchee, *H 2382* in 1989 (FPF). FERRY CO.: Growden, *Wicker* in 1963 (FPF); Fritz Cr. near Growden, *Wicker* in 1963 (FPF); 16 mi. E of Republic on Rte. 30, *H & others 1129* in 1968 (FPF) and on *Abies lasiocarpa*, *H & others 1130* in 1968 (FPF). GARFIELD CO.: 7 air mi. SSW of Peola, *Orr* in 1968 (FPF). KITTITAS CO.: N of Ellensburg, *Brandegee 1071* in 1883 (PH, US); Wenatchee Mts., *Coville 1181* in 1901 (US); Peoh Point, ca. 3 mi. S of Cle Elum, *Will* in 1968 (FPF). OKANOGAN CO.: 9 mi. W of Republic on Rte. 30, on *Pinus contorta*, *H & others 1133* in 1968 (FPF); Loup Cr., 12 mi. W of Okanogan on Rte. 20, *H & others 1134* in 1968 (FPF); Colville Indian Res., Disautel Summit on Rte. 155, *Mathiasen 74-4* in 1974 (FPF); 6.7 mi. from Colville Ind. Res. boundary along extension of rd. 357, *Tinnin & Knutson* in 1976 (FPF); 10 mi. SSW of Wauconda, *Tinnin & Knutson* in 1976 (FPF); 8 mi. NW of Nespelem on Rte. 155, *H 2208* in 1987 (FPF); Conger Cr., 5 air mi. SW of Conconully, *H 2408* in 1990 (FPF). PEND OREILLE CO.: Metaline Falls, *Weir 8365* in 1916 (FPF, ILL). STEVENS CO.: 3 mi. W of Park Rapids, *Krebill 147* in 1964 (FPF); 21 mi. S of Cheualah on Rte. 395, *H & Laut*

1294 in 1970 (FPF) and on *Pinus contorta*, *H & Laut 1295* in 1970 (FPF); 6 mi. NE of Bossburg on Rte. 25, *H 2063* in 1984 (FPF); WHITMAN CO.: N side of Kamiak Butte, *St. John 6359* in 1924 (MO, UC); Kamiak Butte Park, Kamiak Butte, 7 mi. N of Pullman, *Tinnin & Knutson* in 1979 (FPF). YAKIMA CO.: Havens Ranch, SE of Mt. Adams, *Henderson 2535* in 1892 (WTU); Tieton Basin, *Tweedy* in 1882 (DS); "Yakima Region," *Brandegee* in 1882 (UC); 2.5 mi. E of White Pass on Rte. 5, *H & W 597* in 1964 (FPF) and on *Pinus monticola*, *H & W 598* in 1964 (FPF); 6.5 mi. E of White Pass, on Rte. 5, *H & W 603* in 1964 (FPF); Tieton Cr., 2 mi. SW of Tieton Lake, on *Abies grandis*, *H & W 600* in 1964 (FPF); 7 mi. S of Tieton, *Graham* in 1966 (FPF); Dog Lake, Tieton Cyn., *Wicker 13* in 1966 (FPF); 4 mi. E of Dog Lake, *Wicker 8* in 1966 (FPF); 1 mi. W of Rimrock, *Stewart* in 1968 (FPF); 7.2 mi. E of White Pass on Rte. 12, *Tinnin & Knutson* in 1976 (FPF). COUNTY UNCERTAIN: Cascade Mts., *Tweedy* in 1882 (MO).

20. *Arceuthobium littorum*

UNITED STATES

CALIFORNIA

ALAMEDA CO.: Berkeley, on planted *Pinus radiata*, *Offord & Scharpf* in 1964 (FPF). MARIN CO.: Inverness Ridge, on *Pinus muricata*, *Howell 19686* in 1944 (CAS, UC); Mt. Vision rd., Inverness, on *Pinus muricata*, *Schreiber 853* in 1933 (UC); Point Reyes Nat. Seashore, 1.0 mi. NW of Inverness, on *Pinus muricata*, *Nickrent 2723* in 1988 (FPF, ILL). MENDOCINO CO.: Fort Bragg, on *Pinus muricata*, *Mason 5639* in 1930 (UC); mouth of Gualala River, on *Pinus muricata*, *Bacigalupi 1808* in 1921 (CAS); Van Damme State Park, on *Pinus muricata*, *Kuijt 1214* in 1957 (UC); Pine barrens near Fort Bragg, on *Pinus muricata*, *Johnson 1420* in 1929 (RSA); 3 mi. E of Fort Bragg, on *Pinus muricata*, *H & Scharpf 849* in 1966 (FPF); 2.7 mi. SE of Fort Bragg, on *Pinus muricata*, *Nickrent 2715* in 1988 (FPF, ILL); S of Van Damme State Park, on *Pinus muricata*, *Nickrent 2717* in 1988 (FPF, ILL); 2.9 mi. E of Point Arena, on *Pinus muricata*, *Nickrent 2719* in 1988 (FPF, ILL); 1.6 mi. E of Rte. 1 and Gualala, on *Pinus muricata*, *Nickrent 2721* in 1988 (FPF, ILL); Point Arena, on *Pinus contorta* var. *bolanderi*, *Mason 7168* in 1932 (UC); 2.9 mi. E of Point Arena, on *Pinus contorta* var. *bolanderi*, *Nickrent 2720* in 1988 (FPF, ILL); 2.7 mi. SE of Fort Bragg, on *Pinus contorta* var. *bolanderi*, *Nickrent 2716* in 1988 (FPF, ILL); Van Damme State Park, on *Pinus contorta* var. *bolanderi*, *Kuijt 1215* in 1957 (UC); just E of airport near Albion, on *Pinus contorta* var. *bolanderi*, *Peterson 65-116* in 1965 (FPF); White Sands near Mendocino City, on *Pinus muricata*, *Eastwood 18836* in 1912 (CAS); 4 mi. SE of Fort Bragg, on *Pinus contorta* var. *bolanderi*, *H & Scharpf 854* in 1966 (FPF); 3 mi. E of Noyo on Rte. 20 near Fort Bragg, on *Pinus muricata*, *H 2271* in 1988 (FPF); 2 mi. S of Anchor Cove, on *Pinus muricata*, *Wolf 1342* in 1927 (CAS). MONTEREY CO.: Carmel, Mission Trail Park, on *Pinus radiata*, *Nickrent 2724* in 1988 (FPF, ILL); Pebble Beach, Carmel, on *Pinus radiata*, *Boyce 33* in 1915 (FPF); between Pacific Grove and Carmel, on *Pinus radiata*, *Gill FP 68145* in 1932 (FPF); Carmel, on *Pinus radiata*, *von Schrenk* in 1920 (MO); Carmel highlands above Yankee Point, on *Pinus radiata*, *Balls 23608* in 1958 (WTU); Point Lobos State Park, on *Pinus radiata*, *Lee & Mason 9153* in 1935 (UC); Point Lobos, on *Pinus radiata*, *Kuijt 1213* in 1957 (UC); near Point Pinos, on *Pinus radiata*, *Dudley* in 1893 (FPF, CAS); Gibson Cr., on *Pinus radiata*, *Wheeler 4452* in 1936 (RSA). Monterey: on *Pinus radiata*, *Parry* in 1850 (MO), *Brewer 700* in 1861 (US), *Engelmann* in 1880 (MO), *Meehan* in 1883 (PH), *Elmer 4031* in 1902 (RSA), *Meinecke FP 9059* in 1910 (FPF, ILL), *Bethel FP 26279* in 1918 (FPF, ILL), *H & Scharpf 1151* in 1968 (FPF), and *H & Scharpf 1617* in 1975 (FPF). Pacific Grove: on *Pinus radiata*, *Davy 7064* in 1900 (UC), *Heller 6776* in 1903 (COLO, MO, RM, UC, US), *Smith 955* in 1905 (MICH), *Condit* in 1909 (UC), *Beattie 5281* in 1916 (FPF), *Guppy FP 97959* in 1924 (FPF), *Gill FP 68076*, *FP 68093* and *FP 68103* in 1932 (FPF), *W 3220* in 1962 (COLO, FPF), and *Peterson 63-156* in 1963 (FPF); Cypress Point, on *Pinus radiata*, *Abrams 7660* in 1920 (RM, US), and *Mason 3987* in 1927 (UC); between Monterey and Carmel, on *Pinus muricata*, *Mason 5888* in 1931 (UC); Huckleberry Hill, Carmel, on *Pinus muricata*, *Mason 5515* in 1929 (UC) and *Wheeler 4428* in 1936 (RSA); Huckleberry Hill, on *Pinus radiata*, *Howell 3028* in 1927 (CAS); Pacific Grove, on *Pinus radiata*, *Evermann* in 1914 (CAS); Carmel Highlands, Fern Cyn., *H 2435* in 1991 (FPF). SAN LUIS OBISPO CO.: Cambria, on *Pinus radiata*, *Gill FP 68079* and *FP 68253* in 1932 (FPF), *Hoover 6448* in 1946 (CAS), and *H & Scharpf 1159* in 1968 (FPF); just N of Cambria to Cambria Ranch, on *Pinus radiata*, *Nickrent 2725* in 1988 (FPF, ILL); between Cambria and Cambria Pines on Roberts Rd., on *Pinus radiata*, *H 2264* in 1988 (FPF). SONOMA CO.: Fort Ross, on *Pinus muricata*, *Mason 4285* in 1928 (UC); Kruse Rhododendron State Park on US 1, near Plantation, on *Pinus muricata*, *Nickrent 2722* in 1988 (FPF, ILL).

21. *Arceuthobium microcarpum*

All collections on *Picea engelmannii*, except as noted.

UNITED STATES

ARIZONA

APACHE CO. Mt. Baldy, *Woolsy FP 12566* in 1914 (FPF) and *Metcalfe 493* in 18?? (ARIZ); Sierra Blanca, *Gilbert 112* in 1873 (ILL, MO); Ft. Apache Indian Reservation, 7 mi. NW of Maverick, *H 2195* in 1987 (FPF); 20 mi. W of Eagar on Rte. 73, *H & Lightle 207* in 1962 (FPF); 4.7 mi. SW of Alpine on US 666, on *Picea pungens*, *H & Scharpf 700* in 1964 FPF); 1 mi. S of Horseshoe Cienega, 10 mi. E of McNary, on *Picea pungens*, *H & Gilbertson 1083* in 1967 (FPF); 6 mi. NE of Maverick, on *Picea pungens*, *H & Lightle 900* in 1966 (FPF); 5

mi. SW of Rte. 373 on Big Lake rd., 2 air mi. SW of Greer, on *Picea pungens*, *H & Lightle 925* in 1966 (FPF); 2 mi. E of Big Lake, on *Picea pungens*, *H 819* in 1965 (FPF); 3 mi. NE of Big Lake, on *Abies lasiocarpa* var. *arizonica*, *Mathiasen & Conklin 8103* in 1981 (FPF); 1 mi. E of Big Lake, on *Abies lasiocarpa* var. *arizonica*, *Mathiasen & Conklin 8101* in 1981 (FPF); 2 mi. SE of Big Lake, on *Abies lasiocarpa* var. *arizonica*, *Mathiasen & Conklin 8102* in 1981 (FPF); 4 mi. N of Big Lake, on *Abies lasiocarpa* var. *arizonica*, *H & Mathiasen 7910* in 1979 (FPF); Big Lake, *Mathiasen 7570* in 1975 (FPF) and *Mathiasen 7571* in 1975 (FPF); US 666, N of Gobbler Pt. rd., *Peterson 62-165* in 1962 (FPF); Ft. Apache Indian Res., Hawley Lake, on *Picea pungens*, *H & Mathiasen 1486* in 1974 (FPF); 6.0 mi. S of Alpine on Rte. 666, 0.4 mi. NE of Greenlee-Apache Co. line, on *Picea pungens*, *Mathiasen 8115* in 1981 (FPF); Sunrise Campground, 10 mi. SW of Greer, *Mathiasen 7568* in 1975 (FPF). COCONINO CO.: "Kaibab For.," *Richards* in 1938 (RM, UC, WTU); San Francisco Peaks on *Pinus aristata*, *Leiberg 5884* in 1901 (US); Interior Basin, *Long FP 21671* in 1916 (FPF); *H & Lightle 249* in 1962 (FPF); *H & Mathiasen 1487* in 1974 (FPF); *Mathiasen 7534* in 1975 (FPF), and on *Pinus aristata*, *Mathiasen 7535* in 1975 (FPF) and *Mathiasen 7537* in 1975 (FPF); Weatherford rd. to Fremont Pass, *H 1358* in 1971 (FPF), *H & lightle 1281* in 1970 (FPF), and *H & Lightle 1359* in 1971 (FPF); on *Abies lasiocarpa* var. *arizonica*, *H & others 1282* in 1970 (FPF) and *H & others 1360* in 1971 (FPF); on *Pinus aristata*, *H & Lightle 247* in 1962 (FPF), *H & others 1279* in 1970 (FPF), *H & Lightle 1357* in 1971 (FPF), *H & Lightle 1404* in 1972 (FPF), *Jones* in 1974 (FPF); and on *Pinus strobiformis*, *H & others 1280* in 1970 (FPF) and *H & Lightle 1361* in 1971 (FPF); Schultz Peak, *Mathiasen 7527* in 1975 (FPF) and *Mathiasen 7583* in 1975 (FPF); on *Abies lasiocarpa* var. *arizonica*, *Mathiasen 7529* in 1979 (FPF); on *Pinus aristata*, *H & Mathiasen 1462* in 1973 (FPF); on *Pinus strobiformis*, *H & Mathiasen 1464* in 1973 (FPF), *Mathiasen 7513* in 1975 (FPF) and *Mathiasen 7510* in 1975 (FPF); Kendrick Peak, *H & Mathiasen 1465* in 1973 (FPF) and *Mathiasen 7532* in 1975 (FPF) and *Mathiasen 7575* in 1975 (FPF). Grand Cyn. Nat. Park, North Rim, *Gill & Andrews FP 89301* in 1935 (FPF) and *Gill & Ellis FP 89418* in 1939 (FPF); near entrance, *Gill FP 68298* in 1934 (FPF); 2.0 mi. E of Rte. 64, on Point Imperial rd., *H 253* in 1962 (FPF) and *Mathiasen 7564* in 1975 (FPF); Telephone Cyn., *W 3183* in 1962 (COLO); 2.4 mi. E of Rte. 64 on Point Royal rd., on *Picea pungens*, *Peterson 43-61* in 1961 (FPF). GRAHAM CO.: Graham (Pinaleno) Mts. *Kearney & Peebles 9971* in 1934 (ARIZ, US), *Ellis FP 89414* in 1939 (FPF), *Ellis FP 89402* in 1939 (FPF), *Ellis FP 89433* in 1939 (FPF), and *Ellis FP 89430* in 1939 (FPF); Hospital Flat, *Gill FP 68310* in 1934 (FPF), *Mathiasen 7591* in 1975 (FPF), and *Kearney & Peebles 14135* in 1938 (ARIZ); Columbine, *Gill FP 68290* in 1934 (FPF), *Ellis FP 89428* in 1939 (FPF), *Maynard* in 1963 (FPF), *Mathiasen 7590* in 1975 (FPF), and on *Abies lasiocarpa* var. *arizonica*, *Stouffer & Gill FP 68291* in 1934 (FPF); High Peak rd., 3 mi. N of main rd., *H & Lightle 224* in 1962 (FPF) and *Mathiasen 7594* in 1975 (FPF); Soldier Cr. Campground, *H & Lightle 225* in 1962 (FPF) and on *Picea pungens*, *H & Lightle 1106* in 1968 (FPF); Webb Peak, *Darrow & others 1173* in 1944 (ARIZ) and *Mathiasen 7588* in 1975 (FPF). GREENLEE CO.: Blue Summit, *Ellis FP 89412* in 1939 (FPF); 1 mi. S of Blue Summit on US 666, *Gill FP 68302* and *FP 68305* in 1934 (FPF); 2 mi. N of Hannagan Meadows on Rte. 666, *Mathiasen 7541* in 1975 (FPF); 3 mi. N of Hannagan Meadows on US 666, *Andrews* in 1963 (FPF) and *Lightle 64-20* in 1964 (FPF); Hannagan Cr. N of Hannagan Meadows on US 666, on *Picea pungens*, *H 1082* in 1967 (FPF); 2.4 mi. ENE of Hannagan Meadows on US 666, on *Abies lasiocarpa* var. *arizonica*, *Mathiasen & Conklin 8108* in 1981 (FPF); 0.2 mi. N of US 666 on Apache Nat. For. rd. 25, on *Abies lasiocarpa* var. *arizonica*, *Mathiasen & English 7909* in 1979 (FPF); 3 mi. N of KP Cienega Campground, on *Abies lasiocarpa* var. *arizonica*, *Mathiasen* in 1979 (FPF); 8 mi. NW of Blue, on *Pinus strobiformis*, *Mathiasen & Conklin 8107* in 1981 (FPF).

NEW MEXICO

CATRON CO.: Mogollon Mts., on or near W fork of Gila River, *Metcalfe 493* in 1903 (ARIZ, FPF, ILL, MO, RSA, UC, US); Willow Cr. Campground, on *Picea pungens*, *H & L 219* in 1962 (FPF); 4 mi. W of Rte. 78 on Bearwallow Lookout rd., *H & Lightle 897* in 1966 (FPF); 13 mi. E of Glenwood, *Mathiasen 8105* in 1981 (FPF) and on *Abies lasiocarpa* var. *arizonica*, *Mathiasen 8106* in 1981 (FPF). OTERO CO.: Lincoln Nat. For., Hay Cyn., *Mathiasen 8005* in 1980 (FPF) and *H & Nicholls 2020* in 1982 (FPF).

22. *Arceuthobium monticola*

All collections on *Pinus monticola*, except as noted.

UNITED STATES

CALIFORNIA

DEL NORTE CO.: 0.5 mi. E of Sourdough Jct., ca. 10 air mi. N of Gasquet, *Miller* in 1969 (FPF); Black Butte, *Theisen & Bynum* in 1968 (FPF) and *Mathiasen 8608* in 1986 (FPF); and on *Picea breweriana*, *Mathiasen 8609* in 1986 (FPF); 2.4 mi. W of Smith River near Lee Brown Crossing, *Mathiasen 8606* in 1986 (FPF); 0.6 mi. N of Ship Mtn. Lookout on Little Jones Cr. rd., *Mathiasen 8502* in 1985 (FPF); 0.5 mi. N of Black Butte, *Mathiasen 8607* in 1986 (FPF); near Black Butte, 3 mi. E of Sanger Pk., *Nickrent & W 2709* in 1988 (FPF, ILL); 3.0 mi. E of Smith River bridge, 10 mi. N of Gasquet, *Nickrent & W 2705* in 1988 (FPF, ILL); Lower Coon Mtn., 1 mi. SW of Camp 6 Lookout, *Mastroguiseppe & Mastroguiseppe 153* in 1974 (WS). SISKIYOU CO.: Dillon Mtn. rd., 12 mi. N of Somes Bar, on *Pinus lambertiana*, *Miller FP 98034* in 1962 (FPF).

OREGON

COOS CO.: 13 air mi. S of Powers, *Mathiasen 8610* in 1986 (FPF). CURRY CO.: Saddle Mtn., ca. 15 air mi. ESE of Gold Beach, *Bynum* in 1967 and 1968 (FPF) and on *Picea breweri-*

ana, Bynum in 1967 and 1968 (FPF); 0.2 mi. N of Snow Camp Fire Lookout, *Mathiasen 8601* in 1986 (FPF), and on *Pinus jeffreyi, Mathiasen 8602* in 1986 (FPF); Snow Camp Mtn., *Nickrent & W 2701* in 1988 (FPF, ILL); 14 mi. ESE of Gold Beach, *W 6793* in 1987 (FPF); Windy Cr., N of Loeb State Park, *W 6794* in 1987 (FPF); 22.6 mi. SW of O'Brien, *W 6761* in 1987 (FPF). JOSEPHINE CO.: Oregon Mt., 14 mi. SW of Cave Jct., on *Pinus lambertiana, Weir 3191* in 1916 (FPF, ILL) and *Weir 3240* in 1916 (FPF, ILL) and *Theisen* in 1964 (FPF); ca. 6 mi. SSW of O'Brien on Oregon Mtn. rd., *H & Hinds 994* in 1966 (FPF), *Mathiasen 8503* in 1985 (FPF), *Mathiasen 8603* in 1986 (FPF), *Mathiasen 8604* in 1986 (FPF), *W 6803* in 1987 (FPF), *Nickrent & W 2708* in 1988 (FPF, ILL) and *H 2379* in 1989 (FPF); 7.6 mi. SW of O'Brien on Oregon Mtn. rd., *W 6781* in 1987 (FPF).

23. *Arceuthobium nigrum*

MEXICO

CHIAPAS

Mpio. Zinacantán, 8 km. W of San Cristóbal de las Casas on Rte. 190, on *Pinus oocarpa* var. *ochoterenai, Peterson 74-326* in 1974 (FPF); 0.5 mi. E of Zinacantán, on *Pinus teocote?, Peterson 72-113* in 1972 (FPF); 5 mi. W of San Cristóbal de las Casas, on *Pinus oaxacana, H & others 1600* in 1975 (FPF); Mpio. Teopisca, 3.1 mi. on left fork of Dolores (Belem) rd. that leaves Rte. 190 at Km-105, on *Pinus oocarpa* var. *ochoterenai, Peterson 74-314* in 1974 (FPF).

DURANGO

51.5 km. W of Durango on Rte. 40, on *Pinus teocote, H & Macias 2227* in 1987 (FPF); 30 mi. E of El Salto on Rte. 40, on *Pinus leiophylla* var. *chihuahuana, H & W 337* in 1963 (FPF) and *519* in 1963 (COLO, FPF), on *Pinus lumholtzii, H & W 336* in 1963 (COLO, FPF), and on *Pinus teocote, H & W 520* in 1963 (COLO, FPF); 32 mi. E of El Salto on Rte. 40, on *Pinus teocote, H & W 334* in 1963 (COLO, FPF): 5 mi. E of El Salto on Rte. 40, on *Pinus leiophylla, H & W 1244* in 1969 (FPF); 2 mi. E of El Salto on Rte. 40, on *Pinus leiophylla, H & W 343* in 1963 (FPF), *H & W 525* in 1963 (COLO, FPF), and *H 1424* in 1972 (FPF); 2 km. W of El Salto on Rte. 40, on *Pinus leiophylla, H & Macias 2226* in 1987 (FPF); 33 mi. S of Durango on La Flor rd., on *Pinus leiophylla* var. *chihuahuana, H & W 510* in 1963 (COLO, FPF), on *Pinus lumholtzii, H & W 509* in 1963 (COLO, FPF), and on *Pinus teocote, H & W 508* in 1963 (COLO, FPF); Mpio. Otaez, 55 km. S of Pueblo Altares on Banome rd., on *Pinus lumholtzii, H & others 2253* in 1987 (FPF), Mpio. Santiago Papasquiaro: 15 mi. W of Santiago Papasquiaro, on *Pinus leiophylla* var. *chihuahuana, H & W 533* in 1963 (COLO, FPF) and on *Pinus lumholtzii, H & W 534* in 1963 (COLO, FPF); 18 mi. W of Santiago Papasquiaro, on *Pinus leiophylla, H & W 535* in 1963 (COLO, FPF); 32 km. W of Rte. 39 on Altares rd., on *Pinus teocote, H & others 2232* in 1987 (FPF); 38 km. W of Rte. 39 on Altares rd., on *Pinus cooperi, H & others 2235* in 1987 (FPF); 73 km. W of Rte. 39 on Altares rd., on *Pinus lumholtzii, H & others 2236* in 1987 (FPF); 4 km. SW of Altares, on *Pinus leiophylla* var. *chihuahuana, H & others 2240* in 1987 (FPF); 12 km. SW of Altares, on *Pinus leiophylla, H & others 2245* in 1987 (FPF); Mpio. Tepehuanes, 29 km. W of Tepehuanes on rd. to Sierra del Huacol, on *Pinus teocote, H 2164* in 1987 (FPF).

GUANAJUATO

Mpio. Jerecurro, Cerro Puruaqua, on *Pinus teocote, Rzedowski 45491* in 1987 (IEB).

HIDALGO

20 mi. N of Zimapan on Rte. 85, on *Pinus teocote, H & W 385* in 1963 (COLO, FPF) and on *Pinus montezumae, H & W 386* in 1963 (COLO, FPF); 4 km. NE of La Hacienda de Apluco, on *Pinus teocote, Gimate 605* in 1972 (ASU, ENCB); 8 km. NE of Metepec on rd. to Tenango de Doria, on *Pinus teocote, H & others 1876* in 1979 (FPF).

MICHOACÁN

Mpio. Senguio, 3 km. NE of Senguio, on *Pinus teocote, Peterson 73-80* in 1973 (FPF).

OAXACA

District de Teotitlán, Camino de Huaulla, on *Pinus* sp., *Conzatti 4123* in 1921 (US); 15 km. E of Oaxaca on Rte. 175, on *Pinus lawsonii, W 6007* in 1985 (FPF); 1 mi. N of Suchixtepec on Rte. 175, on *Pinus lawsonii, Peterson 68-106* in 1968 (FPF); 9 mi. N of Rte. 190 on Rte. 175, on *Pinus lawsonii, H & others 1550* in 1975 (FPF).

PUEBLA

Tetla de Ocampo, on *Pinus patula, Sandoval 15* in 1979 (ENCB); Mpio. Oyameles, Sierra Mastaluyan, 3 km. NE of Los Humeros, on *Pinus teocote, Chazaro & Hernandez 5436* in 1988 (IBUG); Mpio. Vicente Guerro, San Bernardino la Laguna, on *Pinus pseudostrobus, Lott & Wendt P-132* in 1982 (CHAPA, FPF); 6 km. NE of Zacatlán, on *Pinus pseudostrobus, H 2105* in 1986 (FPF); 28 mi. N of Apizaco on Rte. 119, on *Pinus teocote, H & others 1606* in 1975 (FPF).

VERACRUZ

Cofre de Perote, 3 mi. SE of Perote, on *Pinus teocote, H & W 382* in 1963 (COLO, FPF) and on *Pinus* sp., probably *Pinus teocote, W 2574* in 1959 (FPF, RSA); Mpio. de Jalancingo, El Rincon, on *Pinus teocote, Cibrián & Chaboya* in 1989 (FPF); Mpio. Huayacotla, Sierra Huaycoctla, on *Pinus teocote, Chazaro & Hernandez Hor-83* in 1982 (IBUG).

ZACATECAS

Paraje de los Amoles, on *Pinus leiophylla* var. *chihuahuana, Cibrián & others 14* in 1979 (ENCB, IEB).

24. *Arceuthobium oaxacanum*

MEXICO

OAXACA

13 km. S of Miahuatlán near Puerto Angel rd. (Rte. 175), on *Pinus pseudostrobus, Peterson 72-110* in 1972 (FPF); on *Pinus lawsonii, H & others 1557* in 1975 (FPF); on *Pinus michoacana, H & others 1561* in 1975 (FPF); and on *Pinus lawsonii, W 5981* in 1984 (FPF); 7 km. S of Rte. 175 on dirt rd. leaving highway 6 km. S of Miahuatlán, lat. 16°11' N, long. 96°34' W, on *Pinus lawsonii?, Nickrent & Keller 2035* in 1985 (ILL); Mpio. Comaltepec, Distrito de Ixtlán, 5 km. S of Yolox on Rte. 175, on *Pinus pseudostrobus, Martin 388* in 1981 (MEXU).

25. *Arceuthobium occidentale*

All collections on *Pinus sabiniana*, except as noted.

UNITED STATES

CALIFORNIA

AMADOR CO.: 6 mi. E of Jackson, *Gill FP 68255* in 1932 (FPF); 1 mi. S of Jackson, *W 3224* in 1962 (COLO, FPF); near Ione, *Braunton* in 1904 (MO); 1 mi. S of Ione, *Kuijt 1208* in 1956 (UC); Pine Grove, *Hanson 718* in 1895 (MO, US); Bennett Ranch, 6 mi. E of Jackson, on *Pinus sylvestris, Scharpf* in 1988 (FPF). BUTTE CO.: Big Chico Cr. E of Chico, *Heller 11144* in 1913 (CAS, MO, PH, US); Magalia, *Howell 37436* in 1962 (CAS) and *Roderick* in 1983 (UC); near Magalia *W 2728* in 1960 (RSA); Chico, *Griffiths* in 1912 (MO); Paradise, *Wall* in 1935 (CAS); Bangor, *Rose* in 1931 (CAS); 17 mi. NE of Oroville on Rte. 70, *H 1733* in 1976 (FPF). CALAVERAS CO.: 1.5 mi. E of Copperopolis on Rte. 4, *Kuijt 1410* in 1957 (UC); rd. from Vallecito to Columbia, *Quick 53-141* in 1953 (CAS); locality unknown, col. ?, in 1922 (MO). CONTRA COSTA CO.: Mt. Diablo *Bethel FP 26266* in 1918 (FPF, ILL); *Scharpf* in 1963 (FPF); N slope, *Hicks 110* in 1917 (UC); Mitchell Cyn., *Jepson* in 1898 (JEPS, MO) and on *Pinus coulteri, Bacigalupi* in 1922 (CAS); Little Rock City, *Kuijt 1444* in 1958 (UC); Rock City, *Kuijt 1425a* in 1957 (UC); Ranger Headquarters near S entrance, *H & Scharpf 856* in 1966 (FPF) and on *Pinus coulteri, H & Scharpf 857* in 1966 (FPF). EL DORADO CO.: Smith Flat, *Benson 47* in 1924 (CAS); Placerville, *W 2335* in 1962 (COLO, FPF); 2-3 mi. E of Placerville on Rte. 550, *Robbins 1403* in 1943 (UC); 1.7 mi. SW of Garden Valley, *Kuijt 1257* in 1957 (UC); 3 mi. NW of Placerville on Rte. 49, *H & W 841* in 1966 (FPF); S fork of American River, N of Placerville, *Kuijt 1274* in 1957 (UC). FRESNO CO.: Auberry, *Stillinger* in 1920 (FPF, ILL) and *Trojan* in 1980 (FPF); 10 mi. SW of Auberry on Friant rd., *H 843* in 1966 (FPF); 5 mi. N of Auberry on North Fork rd., *H 844* in 1966 (FPF); old railroad grade, 3 air mi. W of Shaver Lake dam, *H 2268* in 1988 (FPF). GLENN CO.: 2.1 mi. N of Stonyford, *Kuijt 1506* in 1958 (UC). KERN CO.: Walker Basin, *Rothrock 429* in 1875 (MO, US); Caliente Cr., between Loraine and Twin Oak, *Tilforth & Dourly* in 1975 (UC); Caliente, *Gill FP 68089* in 1932 (FPF); Havilah, *Coville & Funston 1073* in 1891 (CAS, FPF, US); Greenhorn Pass, 4 mi. W of Kernville, *Gould 1010* in 1940 (CAS, MO, UC, US); 1 mi. E of Isabella Reservoir on Rte. 178, *Kuijt 1437* in 1957 (UC); head of Tejon Cr., *Twisselmann 8832* in 1963 (CAS); between Glenville and Sierra Alta, 7 mi. W of Summit Guard Sta., *W 3605* in 1964 (FPF); Kernville, *Kerr* in 1938 (CAS), and on *Pinus halepensis, Scharpf* in 1984 (FPF); Tehachapi Mts., Upper Cottonwood Cr., W of White Oak Lodge, *Tucker 3444* in 1938 (ARIZ); 2.5 mi. W of Wofford, *Howell 38710* in 1962 (CAS). LAKE CO.: Without locality, *Bolander 2671* in 1863 (UC, US); near jct. of Rts. 53 and 20, SE of Clear Lake, *Rossbach 236* in 1955 (UC); Siegler Springs, *Blankinship* in 1924 (CAS); Lakeside, Clear Lake, *Abrams 6297* in 1916 (CAS); Kelseyville, *Blankinship* in 1924 (RSA) and *Jussel* in 1931 (CAS); Kelseyville, Rincon School, *Benson 726* in 1928 (RSA); Mt. Konocti, *Blankinship* in 1923 (MO); 3 mi. N of Middletown on Rte. 29, *Scharpf* in 1965 (FPF); Bloody Rock Wildlife Management Area, *Nickrent 2713* in 1988 (FPF, ILL). LASSEN CO.: 10 mi. S of Pittville, *Wagener FP 97951* in 1928 (FPF). LOS ANGELES CO.: Liebre Mts.: Elizabeth Lake Cyn., *Dudley & Lamb 4411* in 1896 (CAS); Collins Ranch, *Peirson 4302* in 1921 (RSA); Sandbergs, *Munz 4423* in 1921 (RSA); Lake Hughes, *H & Scharpf 2080* in 1984 (FPF), and on *Pinus pinea, H & Scharpf 2081* in 1984 (FPF). MADERA CO.: Raymond, *Hedgcock FP 4837* in 1910 (FPF, ILL); 9 mi. W of Oakhurst, *Kuijt 1254* in 1957 (UC); 18 mi. N of Pinedale on Rte. 41, *H 1144* in 1968 (FPF); 1 mi. W of North Fork, *H 2* in 1954 (FPF), *H 658* in 1964 (FPF) and *H 1160* in 1968 (FPF); Hogue Ranch, 16 mi. from North Fork on Mammoth rd., *H 847* in 1966 (FPF); 1.5 mi. N of Oakhurst, *Howell 41197* in 1965 (CAS); Peckinpah Cr., *Howell & Barneby 29387* in 1954 (CAS); San Joaquin Exp. Range, *Green 37* in 1953 (USFS). MARIPOSA CO.: Bear Valley Mtn., *Ward 51* in 1895 (US); El Portal, *Posey* in 1919 (ILL); 3 mi. W of Mt. Bullion, *Kuijt 1253* in 1957 (UC); near Bootjack, *Howell 8135* in 1931 (CAS, US); Mariposa, *Congdon* in 1903 (MO, US). MONTEREY CO.: 7.2 mi. NE of Gonzales, *W 3219* in 1962 (COLO, FPF); Santa Lucia Mts.; San Antonio River, *Brewer 582* in 1861 (US); Pine Cyn., *Duncan 90* in 1920 (CAS, RSA); Miller Cyn., on *Pinus coulteri, Ferris 12158* in 1929 (CAS, RM, RSA, WTU); Miller Cyn., Chews Ridge, on *Pinus coulteri, Ray 1565* in 1949 (US); Tassajara rd. at Chews Ridge Lookout Jct., on *Pinus coulteri, Kuijt 1401* in 1957 (UC) and *H & Scharpf 1152* in 1968 (FPF); Marble Peak, 0.5 mi. NW of Anderson Peak, on *Pinus coulteri, Offord FP 98091* in 1963 (FPF); Junipero Serra Peak, on *Pinus coulteri, Howell 30162* in 1955 (CAS); near Cone Peak, on *Pinus coulteri, Ferris 3649* in 1923 (CAS, RSA) and *H & Scharpf 1158* in 1968 (FPF); Monterey For. Reserve, on *Pinus coulteri, von Schrenk* in 1920 (MO); 5 mi. W of Jolon on Nacimiento rd., *H & Scharpf 1153* in 1968 (FPF); Los Padres Nat. For., Santa Lucia Mts., on *Pinus coulteri, Griffin 3863* and *3859* (FPF), *H 1616* in 1975 (FPF), and *Cheatham* in 1980 (FPF); Santa Lucia Mts., on *Pinus ponderosa, Griffin 3223a* and *3223b* in 1972 (FPF), *Griffin 3861* and *3865* in 1973 (FPF), and *H 1615* in 1975 (FPF), and on *Abies bracteata*?, *Raymond* in 1915 (FPF). NAPA CO.: Conn Valley, *Jepson* in 1895 (JEPS, US) and *Raven 3928* in 1951 (CAS); Moore Cr., Howell Mtn., col.? in 1902 (UC); 3 mi. from Aetna Springs on Middletown rd., *Howell 5618* in 1930 (CAS); 14 mi. SE of Middletown on Aetna Springs rd., *H & W 859* in 1966 (FPF); Butz Cyn. rd., 6 mi. N of Pope Valley, *Wilken & Donahue 12699* in 1976 (FPF). PLACER CO.: Auburn, *Loran* in 1886 (UC) and *Englemann* in 1880 (ILL, MO); 1 mi. S of Auburn on Rte. 49, *H 2269* in 1988 (FPF). SAN BENITO CO.: Pinnacles Nat. Mon., *W 3218* in 1962 (COLO, FPF) and *Gill FP 68078* in 1932 (FPF); 20 mi. S (E?) of Bitterwater on New Idria rd., *Kuijt 1313* in 1957 (UC); rd. to New Idria, 4.5 mi. S of jct. N of Bitterwater, *Kuijt 1300* in 1957 (UC); San Benito Mtn., S fork of Clear Cr., *H & others 2071* in 1984 (FPF); near New Idria, on *Pinus coulteri*, *Quibell 1658a* in 1953 (RSA) and *Kuijt 1310* in 1957 (UC); San Benito Mtn., 19 mi. E of Bitterwater, on *Pinus coulteri*, *H & others 2073* in 1984 (FPF); Clear Cr., on *Pinus jeffreyi* and *Pinus ponderosa*, *Twisselmann 12862* in 1966 (FPF), *Thomas & others 6069* in 1956 (FPF); South Fork, Clear Cr. area, on *Pinus jeffreyi*, *Griffin 3878* in 1974 (FPF), *H & others 2072* in 1984 (FPF); no locality, on *Pinus coulteri*, *McGuire FP 97950* in 1940 (FPF). SAN LUIS OBISPO CO.: Paso de Robles, *Summers 926* in 1886 (UC); Santa Margarita, *Mason 525* in 1923 (UC); Mariana Cr., E side La Panza Range, *Hoover 6310* in 1946 (CAS). SANTA BARBARA CO.: San Rafael Mts., Yellow Gate, *Meinecke FP 97947 (FPF)* and *FP 17026* (FPF, ILL) in 1914; Pine Cyn., Roosevelt, *Hunt FP 97958* in 1912 (FPB); Figueroa Mtn., *Pollard* in 1950 (CAS) and 1956 (CAS); 8 mi. E of Los Olivos on Figueroa Mtn. rd., *H 935* in 1966 (FPF); 12 mi. E of Los Olivos on Figueroa Mtn. rd., on *Pinus coulteri*, *H 936* in 1966 (FPF); Zaca Lake For. Res., 9 mi. NNE of Los Olivos, on *Pinus coulteri*, *Eastwood* in 1906 (CAS); 0.25 mi. E of Figueroa Fire Sta. on Figueroa Mtn. rd., 12 mi. E of Los Olivos, *H & others 2076* in 1984 (FPF), and on *Pinus coulteri*, *H & others 2077* in 1984 (FPF). SANTA CLARA CO.: Mt. Hamilton Range; E slope of Mt. Hamilton, *Beane 225* in 1949 (RM); Mt. Hamilton, *Chanser 6022* in 1906 (UC); Long Branch Cr., Mt. Day, *Sharsmith 3848b* in 1936 (DS, UC); E slope of Mt. Hamilton, *Beane & James 2079* in 1949 (DS, RSA, WTU); 1 mi. above Alum Rock, Mt. Hamilton, *Dutton* in 1899 (DS); 2 mi. below summit of Mt. Hamilton, *Solbrig* in 1957 (UC); 2 mi. E of Mt. Hamilton on Livermore rd., *H & Scharpf 1149* in 1968 (FPF) and on *Pinus coulteri*, *H & Scharpf 1148* in 1968 (FPF); near Mt. Hamilton Observatory, on planted *Pinus radiata*, *H & Scharpf 1150* in 1968 (FPF); Summit Copernicus Peak, *Sharsmith 1406a* and *1406b* in 1934 (UC); Mt. Umunhum, *Thomas 3977* in 1954 (FPF) and *Thomas 5519* in 1956 (CAS, FPF, RSA); Loma Prieta, on *Pinus attenuata*, *Dudley* in 1895 (CAS); Stanford Arboretum, on planted *Pinus radiata*, *Wight 47* in 1900 (US). SHASTA CO.: Morleys, *Baker* in 1898 (UC); 2.5 mi. W of Round Mtn., *Kuijt 1374* in 1957 (UC); Black Butte, *Anderson* in 1949 (CAS); 0.5 mi. N of Hat Cr. Work Center, *H 1740* in 1976 (FPF); 6 mi. W of Platina on Rte. 36, *W 6749* in 1987 (FPF); 4 mi. W of Platina, on *Pinus ponderosa*, *W 6748* in 1987 (FPF); 0.6 mi. W of Platina, on *Pinus ponderosa*, *W 6747* in 1987 (FPF); 13 mi. W of Redding on Rte. 299, on *Pinus attenuata*, *H 1742* in 1976 (FPF). TEHAMA CO.: Manton, *Kuijt 1362* in 1957 (UC) and *Root* in 1919 (ILL); 12 mi. W of Mineral, *Kuijt 1361* in 1957 (UC); 0.2 mi. S of Beegum Cr. on Rte. 36, just S of Shasta Co. line, *W 6746* in 1987 (FPF). TRINITY CO.: Trinity River near Swede Cr., ca. 6 mi. W of Big Bar, *Tracy 6912* in 1924 (UC); near Weaverville, *Kleeberger* in 1879 (CAS); 9.5 mi. E of Big Bar on Rte. 299, *H 1744* in 1976 (FPF); S of Weaverville on Rte. 3, *Bailey 72-4* in 1974 (FPF). TULARE CO.: 6 mi. E of Roads End P. O., *Howell 33147* in 1958 (CAS); Kern River Cyn., 7.6 mi. N of Kernville, *Twisselmann* n.d. (CAS). TUOLUMNE CO.: 5 mi. E of Sonora, *Wright FP 68054* in 1931 (FPF); 2 mi. E of Sonora, *W 3221* in 1962 (COLO, FPF); E side Sonora, *Gill & Wright FP 68066* in 1932 (FPF); 1 mi. W of Columbia, *Peterson 63-136* in 1963 (FPF); Long Barn, *Gill FP 68080* and *FP 68099* in 1932 (FPF) and *Wright FP 68119* in 1932 (FPF); Confidence, *Boyce FP 97953* in 1915 (FPB); 2 mi. W of Rte. 49 jct. on Rte. 120, *Kuijt 1427* in 1957 (UC); 4 mi. NE of Columbia, *Smith* in 1956 (UC); Sonora, *Bigelow 4* in 1854 (MO); 1 mi. N of Columbia on Vallecito Rd., *H & Scharpf 2037* in 1982 (FPF).

26. Arceuthobium pendens

MEXICO

PUEBLA

Mpio. Tapeyahualcos, Volcán al Pizzaro, on *Pinus orizabensis*, *Calzado & others* in 1978 (IEB).

SAN LUIS POTOSÍ

Mpio. Villa de Reyes, Sierra San Miguelito, 3 km. W of village of Villa de Reyes, on *Pinus discolor*, *Robert 1059* in 1971 (ENCB) and 5 km. W on *Pinus discolor*, *H & others 1877* in 1979 (ENCB, FPF, INIF, MO, MEXU, US, UT).

VERACRUZ

Mpio. Perote, 3 km. W of Frijol Colorado, on *Pinus orizabensis*, *Bailey 80-08*, *Wendt 2496* in 1980 (ENCB, FPF, INIF, MO, MEXU, UT), *Nickrent 1992* in 1984 (ILL, MEXU), *Nickrent 2014* in 1985 (ILL, MEXU), and *Chazaro & Hernandez 4321* in 1988 (IBUG).

27. Arceuthobium pusillum

All collections on *Picea mariana*, except as noted.

CANADA

MANITOBA

Freshford, *Laut* in 1968 (FPF, WINF) and on *Pinus banksiana*, *Laut* in 1968 (FPF, WINF); Dawson Cabin, on *Pinus banksiana*, *Laut 10267* in 1968 (WINF, FPF); Belaire Provincial For., *Lawrence* in 1967 & 1968 (FPF, WINF) and *H*

& Laut 1482 in 1973 (FPF); Amana Bay, 40 mi. E of Gypsumville, on *Picea glauca*, *Lawrence* in 1967 (FPF, WINF); Sandilands For. Reserve, *Campbell* in 1966 (FPF, WINF), *H & Laut 1480* in 1973 (FPF), and on *Pinus banksiana*, *Laut* in 1967 (FPF, WINF) and in 1968 (WINF, FPF), and *MacDowall* in 1968 (WINF, FPF); Glenboro, on *Picea glauca*, *Campbell* in 1965 (FPF, WINF); E Braintree, on *Picea glauca*, *Campbell* in 1966 and *Lawrence* in 1967 (FPF, WINF); Long Point, SE of Grand Rapids, *Shepherd* in 1968 (FPF, WINF); Sprucewoods For. Reserve, near Glenboro, on *Picea glauca*, *Laut* in 1968 (WINF, FPF), *H & Laut 1481* and *1483* in 1973 (FPF), and *Lawrence* in 1968 (FPF, WINF); Birds Hill Provincial Park, near Lockport, on *Larix laricina*, *Laut 69-3641* in 1969 (WINF, FPF); Lockport River, on *Picea glauca*, *Laut 69-3639* in 1969 (WINF, FPF); 9.8 mi. W of Rennie, on *Picea glauca*, *Lawrence* in 1968 (FPF, WINF); Anama Bay, 40.3 mi. E of Gypsumville, on *Picea glauca*, *Shepherd* in 1967 (FPF, WINF).

NEW BRUNSWICK

Grand Mann, *Weatherby & Weatherby 5770* in 1927 (UC, US) and *6685* in 1934 (US); 10 mi. W of Napadogan, *Bonga* in 1964 (FPF); Acadia For. Exp. Sta., *Bonga* in 1965 (FPF); Deer Island, near Johnson Lake, on *Picea* sp., *Malte 731/29* in 1929 (US, WTU).

NEWFOUNDLAND

Wild Cover, near Humbermouth, White Cliff, Humber District, *Rouleau 612* in 1950 (RM, UC, US); Bay of Islands, *Howe & Lang 1141* in 1901 (GH); Deer Arm, Bonne Bay, McIver's Cove, *Fernald & others 1655* in 1929 (GH, PH); Deer Brook, *Fernald & others 1656* in 1929 (GH, PH), and Main River, *Fernald & others 1657* in 1929 (PH, US); Port a Port, on *Picea* sp., *Fernald & St. John 10830* in 1914 (GH).

NOVA SCOTIA

Cape Breton Island: Creignish, *Bonga* in 1965 (FPF); 2 mi. E of Margaree For., *von Schrenk* in 1928 (MO, PH, RSA, UC); Ingonish, on *Picea* sp., *Pease 20948* in 1929 (GH). Lower Argyle,*Fernald & others 21045* in 1920 (MO, UC, US); Gold Lake, Birchton Branch, *Fernald & Long 23788* in 1921 (GH, NY, PH); Hectanooga, *Fernald & Pease 21041* in 1920 (GH, PH); Pictou, *Howe & Lang* (GH,NY, PH, RM) and on *Picea glauca*, *von Schrenk* in 1929 (MO); Tefry's Lake, Arcadia, *Fernald & Pease 21043* in 1920 (GH); E Jordan, *Fernald & Pease 23787* in 1921 (GH); Mt. Uniache,*Jack 3225* in 1924 (GH); Woliamakeh Beach, Port Mouton,*Jack 3473* in 1924 (GH). Yarmouth Co.: Tusket, on *Picea glauca*,*Jack 3759* in 1924 (UC) and *Long & Fernald 21042* in 1920 (GH, PH); Eel Lake, on *Picea glauca*, *Fernald & others 21044* in 1920 (GH, PH). Shelburne Co.:*Jack 3468* in 1924 (US).

ONTARIO

Snelgrove, *White* in 1918 (FPF, ILL); 12 mi. S of Rte. 17 on Rte. 71, *H & others 1479* in 1973 (FPF); 7 mi. SW of Killarney, Georgian Bay, on *Picea glauca*, *Coville* in 1915 (US); near Cloche, McGregor Bay, N side Georgian Bay, on *Picea glauca*, *Coville* in 1915 (US); Bruce Peninsula, Stokes Bay, on *Larix laricina*, *Hamai* in 1964 (FPF); White Otter Lake, on *Pinus banksiana*, *McPhee & Miller*, in 1955 (FPF, FPT, WINF); Temagami For. Reserve, *Watson 6762* in 1922 (WIS).

PRINCE EDWARD ISLAND

Tracadie Beach, *Churchill* in 1901 (MO, PH): Tignish, *Fernald & others 7327* in 1912 (NY, PH, UC, US).

QUÉBEC

Richelieu, *Rouleau* in 1945 (UC, WIS); Lac-Aux-Atocas, Parc de Mont Tremblant, *Rolland-Germain* 220 in 1956 (UC, US); Riv. Ste. Anne des Monts, *Fernald & Collins 218* in 1906 (US, VT); St. Adolphe, Comte d' Argenteuil, Riv. du Lac. St. Joseph, on *Picea* sp., *Rolland-Germain 7512* in 1949 (CAS); Cap Chat River, below Pirian River, Matane Co., on *Picea* sp., *Fernald & Pease 25031* in 1922 (GH); St. Adolphe, Argentuc, on *Picea glauca*, *Rolland-Germain 3061* in 1949 (RM); Ste. Anne de la Pocatiere, on *Picea glauca*, *Marie-Victorin 28456* in 1928 (RM, US, WIS) and *Campagna 34173* in 1930 (GH), and on *Picea* sp., *Cody & others 676* in 1947 (MO); near Lake Ouimet, Tierbonne Co., *Pease 19055* in 1922 (GH); Lac Monroe, on *Picea* sp. *Rolland-Germain 361* in 1957 (US); Mont Tremblant, on *Picea* sp., *Louis-Alphonse* in 1952 (MO, US).

SASKATCHEWAN

Otosquen, *Crawford* in 1967 (FPF, WINF); and *Pratt* in 1957 (FPF, WINF): Mi-30 on Cumberland rd., on *Picea glauca*, *McLeod* in 1968(FPF, WINF); on Highway 123, on *Picea glauca* at Mi-20 *McLeod* in 1968 (FPF, WINF) and Mi-37, *McLeod* in 1968 (FPF, WINF); 41.6 mi. N of Hudson Bay on Rte. 109, *Devlin* in 1966 (FPF, WINF).

UNITED STATES

CONNECTICUT

LITCHFIELD CO.: N side Bear Mtn., *Greenman 2492* in 1910 (GH, MO); Bingham Pond, near Salisbury, *Mann* in 1906 (US); S Spectacle Pond, near Kent, *Gill & others FP 68284* in 1933 (FPF) and *Harger 45859a* in 1909 (PH), and on *Larix laricina*, *Gill & others FP 68285* in 1933 (FPF); Norfolk, *Weatherby 3906* in 1916 (PH, US) and *Bissell* in 1904 (GH).

MAINE

AROOSTOOK CO.: Fort Kent, *Fernald* in 1899 (UC); Monticello, *Fernald & Long 13521* in 1916 (PH); Fort Kent, host ?, *Williams* in 1901 (VT). CUMBERLAND CO.: Great Chebeague Island, on *Picea* sp., *Fernald 1741* in 1909 (GH). FRANKLIN CO.: New Sharon, *Knowlton* in 1903 (GH) and *Knowlton 23525* in 1905 (WIS). HANCOCK CO.: Mt. Desert Island, Great Head, on *Picea glauca*, *Rand* in 1906 (UC); Acadia Nat. Park, *Cottam 11561* in 1938 (FPF, UT): Gouldsboro, *Nortan* in 1922 (WIS). KENNEBEC CO.: Belgrade, *Fassett 2527* in 1925 (GH, WIS). KNOX CO.: Isle au Haut, on *Picea glauca*, *Arthur* in 1900 (GH); Matinicus Island, on *Picea glauca*, *Norton & Chamberlain* in 1916 (GH). LINCOLN CO.: Bristol, on *Picea glauca*, *Churchill 351* in 1903 (MO); Squirrel Island, Boothbay Harbor, on *Picea glauca*, *Welch* in 1958 (FPF); Monhegan Island, on *Picea glauca*, *von Schrenk* in 1899 (MO) and *Fernald* in 1933 (PH, US); Linekin, on *Picea glauca*, *von Schrenk* in 1899 (MO); Georgetown, on *Picea* sp., *Morton 2063* in 1921 (WTU); Lighthouse Hill, host?, *Churchill* in 1921 (WIS); White Island, host?, *Fassett 2185* in 1925 (WIS); Ocean Point, *Fassett 3923* in 1922 (WIS); Pemaquid Point, on *Picea glauca*, *H 1932* in 1979 (FPF). OXFORD CO.: Norway, *Bean 2241* in 1907 (GH). PENOBSCOT CO.: Alton, *Fernald 23322* in 1900 (GH, WIS); Penobscot Exp. For., 2-5 mi. SE of Orono, *Little & others 22260* in 1967 (USFS), and *H & Campana 1933* in 1979 (FPF). SAGADAHOC CO.: Reid State Park, 4.2 mi. S of Georgetown, on *Picea glauca*, *H 1931* in 1979 (FPF). SOMERSET CO.: Baker Brook, Headwaters St. John River, *St. John & Nichols 2281* in 1917 (US); Pleasant Ridge, *Murdoch 2010* in 1906 (F); Palmer Pond, *Fassett 14308* in 1931 (WIS). WASHINGTON CO.: Indian Township, Grand Lake Stream rd., *Gill FP 68313* in 1934 (FPF). COUNTY UNCERTAIN: Middle Cary Pond, *Spaulding & Collins* in 1920 (ILL); Deer River, *Weir 2394* n.d. (ILL); Christmas Cove, on *Picea glauca*, Hill in 1971 (VT).

MASSACHUSETTS

BERKSHIRE CO.: Becket, *Hoffmann* in 1904 (GH) and 1907 (MO). ESSEX CO.: Andover, *Pease 406* in 1902 (GH). HAMPDEN CO.: Springfield, *Clark & Seymour G586* in 1928 (WIS). MIDDLESEX CO.: Wilmington, *Moore 634* in 1903 (UC); Concord, *Eaton* in 1930 (RSA); Acton, on *Picea* sp., *Jack* in 1898 (GH). WORCESTER CO.: Ashburnham, *Murdoch 5301* in 1914 (F); Lancaster, *Fassett 2345* in 1924 (GH); Clinton, on *Picea glauca*, *Jack* in 1898 (F); Boylston, *Jack* in 1898 (MO) and on *Picea glauca*, *Jack* in 1898 (F, MO). B. Sorrie (personal communication 1990) reports the following current populations in Massachusetts: Berkshire Co. (New Marlboro, Otis, and Peru Townships), Franklin Co. (Ashfield and Hawley Townships), Hampden Co. (Palmer Township), Middlesex Co. (Hopkinton Township), and Worcester Co. (Ashburnham, Gardner City, Holden, Petersham, and Rutland Townships).

MICHIGAN

(Note: Information on the *Arceuthobium pusillum* collections at the University of Michigan (MICH) and the Cranbrook Institute of Science (BLH) provided by Dr. E. G. Voss and at Michigan State University (MSC) by Dr. J. H. Hart.)

ALCONA CO.: N end of Milikin Lake, *Voss 4581* in 1957 (MICH). ALGER CO.: Chatham, on *Picea* sp., col.? in 1901 (NY, US) and *Wheeler* in 1900 (MSC); Rock River, *Kauffman* in 1927 (MICH). ANTRIM CO.: 0.5 mi. S of Graves Crossing, *Perl 7803* (FPF). BENZIE CO.: Homstead Township, N Branch of Platte River, *Frohlich 61* in 1968 (MICH); T. 26 N, R. 14 W, Sec. 6, *Perl 7807* (FPF). CHARLEVOIX CO.: Beaver Island, Egg Lake, *Voss 7009* in 1958 (MICH); 2.5 mi. S of Wallon Lake, *Mathiasen 7816* (FPF); Green Bay, on *Picea glauca*, *Voss 3935* in 1957 (MICH); and Donegal Bay, on *Picea glauca*, *Voss 6986* in 1958 (MICH). CHEBOYGAN CO.: Little Lake 16, near Cheboygan, *Cutler* in 1937 (MO, US), *Voss 1539* in 1953 (MICH), and *Ehlers 6127* in 1936 (MICH); Mud Lake bog, *Gates & Gates 10682* in 1917 (RM), *Gates 14886* in 1927 (MO, UC), *Gates* in 1924 (VT), and *Erlanson 484* in 1924 (MICH); Douglas Lake, *Ehlers 1120* in 1920 (MICH, WIS); Bryans Bog, University of Michigan Biological. Sta., *Gates 11116* in 1919 (WTU); 3.2 mi. W of Tower on Rte. M-68, *Perl 7802* (FPF). CHIPPEWA CO.: 2.5 mi. N of Eckermann, *McVaugh 9781* in 1948 (BLH, MICH, MO); Munuskong Bay State Park, *Bessey* in 1927 (MSC); 3 mi. E of W border of co. on Rte. M-28, *Bourdo* in 1961 (MSC); Whitefish Township at mouth of Toquamonon River, *Churchill* in 1957 (MSC); Drummond Island, Warners Cove, on *Picea glauca*, *Voss 12239* in 1966 (MICH). CLARE CO.: Summerfield Township, Sec. 23, *Mathiasen 7812* (FPF). CRAWFORD CO.: T. 27 N, R. 1 W, Sec. 27, *Mathiasen 7819* (FPF); NW side of Lake Marquette, *Mathiasen 7808* (FPF). EMMET CO.: Bliss Township, Waugoschance Point, on *Picea glauca*, *Churchill* in 1955 (MSC) and *Voss 1048* in 1951 (MICH); Bliss Township, Sec. 18, on *Picea glauca*, *Marshall 809* in 1949 (MSC); Galloway Lake, 1 mi. N of Levering, *Wood, Clover & Voss 8118* in 1953 (MICH) and *Voss 12076* in 1966 (MICH); jct. of Rte. C-81 and Robinson rd., *Mathiasen 7806* in 1978 (FPF); 1.75 mi. W of Wilderness State Park boundary, *Mathiasen 7805* in 1978 (FPF). GOGEBIC CO.: Near Imp Lake, *Gillis 3007* in 1959 (MSC) and *Voss 7854* in 1958 (MICH); Banks Lake, *Voss 12467* in 1967 (MICH); Mud Lake, *Darlington 2749* in 1919 (MICH); Sylvania Recreation Area, *Voss 12712* in 1968 (MICH). GRAND TRAVERSE CO.: 2.5 mi. SE of jct. of River Rd. and Sleights Rd. on River Rd., *Mathiasen & English 7811* (FPF); 2.5 mi. S of jct. of Long Lake Rd. and Co. Rd. 610 on Long Lake Rd., *Mathiasen & English 7810* (FPF). HAMILTON CO.: Raquette Lake Village, *von Schrenk* in 1932 (VT). HURON CO.: Island in Rush Lake, *Dodge* in 1908 (MICH, MSC). IOSCO CO.: T. 24 N, R. 6 E, Sec. 4, *Perl 7810* (FPF). IRON CO.: Basswood Pond, ca. 3 mi. SE of Elmwood, *Voss 8602* in 1959 (MICH). KALISKA CO.: Oliver Township, Sec. 15, on *Picea glauca*, *Mathiasen 7815* in 1978 (FPF). KEWEENAW CO.: 1.5 mi. W of Eagle Harbor, *Voss 11870* in 1965 (MICH). LEELANAU CO.: Glenn Arbor Township, Sec. 13, bog near Crystal River, *Thompson L-1128* in 1948 (BLH). LUCE CO.: Barclay Lake, 9 mi. SW of Crisp Point on Lake Superior, *Voss 3169* in 1956 (MICH). MACKINAC CO.: 7 mi. E of Naubinway on US 2, on *Picea glauca*, *H 687* in 1964 (FPF); Bois Blaiic Island, on *Picea glauca*, *Dodge* in 1913 (MICH, MSC) and *Ehlers 5144* in 1932 (MICH). MARQUETTE CO.: Turin, *Barlow 145* in 1901 (MSC, UC); Conway Lake, *Stoutamire 3013* in 1959 (BLH). MENOMINEE CO.: Bog NE of Wireglass Lake, ca. 5.5 mi. WSW of Carney, *Voss 12696* in 1968 (MICH, MSC). MISSAUKEE CO.: 3.5 mi. N of Star City, *Mathiasen 7813* (FPF). MONTMORENCY CO.: Ess

Lake, 5 mi. N of Hillman, *Stewart* in 1966 (FPF); Lake 22 (Gaylanta Lake), *Case* in 1955 (MICH); 1.4 mi. W of M-33 on Co. Rd. 612, *Perl 7809* (FPF). OSCODA CO.: T. 25 N, R. 1 E, Sec. 6, *Mathiasen 7818* (FPF). OTSEGO CO.: 1 mi. NE of Pickerel Lake, *Mathiasen 7820* (FPF); 1.75 mi. W of Sparr Rd., Sparr Township, Sec. 30, *Mathiasen 7817* (FPF); 0.25 mi. S of Alexander Rd. near Vanderbilt, *Mathiasen 7807* (FPF). PRESQUE ISLE CO.: T. 34 N, R. 7 E, Sec. 23, *Perl 7806* (FPF); 1.7 mi. N of Rogers City on Rte. 23, *Perl 7805* (FPF); Ray Rd. near U. S. Lamprey Exp. Sta., *Perl 7804* (FPF). ROSCOMMON CO.: 1.5 mi. N of Clare Co. line on I-27, *Mathiasen 7809* (FPF). SCHOOLCRAFT CO.: Long Lake, ca. 5.5 mi. NE of Melstrand, *Voss 2660* in 1955 (MICH). WEXFORD CO.: Greenwood Township, Sec. 19, *Mathiasen 7814* (FPF).

MINNESOTA

AITKIN CO.: 6 mi. S of Aitkin, *Gill FP 68209* in 1932 (FPF); S of McGregor, *Rosendahl 4450* in 1924 (PH). BELTRAMI CO.: Waskish, *Anderson* in 1965 (FPF); W of Upper Red Lake, T. 153 N, R. 30 E, Sec. 5, *Anderson* in 1967 (FPF). CARLTON CO.: Fond du Lac State For., *H & others 1478* in 1973 (FPF). CASS CO.: Cass Lake, *Weir* in 1916 (ILL, RM, UC), *Weir 2402* in 1919 (FPF), and on *Larix laricina*, *Weir* in 1916 (FPF, ILL). CHISAGO CO.: T. 37 N, R. 22 W, *Gill FP 68208* in 1932 (FPF). CLEARWATER CO.: Itasca State Park, *Green 9* in 1947 (WIS) and on *Larix laricina*, *French & Tainter* in 1967 (FPF); 2 mi. NW of Mississippi River headwaters, *Thorne 19860* in 1958 (RSA); Lake Itasca, on *Picea glauca*, *Hedgcock & Freeman FP 4145* in 1910 (FPF); Lake Itasca, Floating Bog Bay, on *Picea glauca*, *Thorne* in 1962 (RSA). COOK CO.: Superior Nat. For., T. 64 N, R. 1 W, Sec. 6, on Rte. 12 ca. 24 air mi. NNW of Grand Marais, *Skilling* in 1964 (FPF). HUBBARD CO.: Itasca Park, SE of Mary Lake, *Grant 3197* in 1929 (GH, MO, PH, WTU, US, VT). LAKE CO.: Superior Nat. For., T. 60 N, R. 75 W, Sec. 5, on *Pinus banksiana*, *French & Nichols* 1977 (FPF). ST. LOUIS CO.: 16 mi. N of Duluth, *Lakela 4503* in 1941 (MO); Floodwood, *Lakela 18527* in 1954 (US); Duluth, Normanna Township, *Lakela 15555* in 1952 (WIS). COUNTY UNCERTAIN: Gnesen Township, N of Duluth, *Lakela 7912* in 1948 (RM).

NEW HAMPSHIRE

CARROL CO.: Ossipee, on *Picea* sp., *Grover* in 1896 (GH); White Mts. , Bear Notch, ca. 4 mi. SW of Bartlett, on *Picea rubens*, *H 2127* in 1986 (FPF); White Mtn. Nat. For., ca. 12 air mi. W of Conway, on *Picea rubens*, *H & Shigo 1934* in 1979 (FPF); White Mtn. Nat. For., ca. 3 air mi. SSW of Bartlett on summit, on *Picea rubens*, *H & Shigo 1935* in 1979 (FPF). COOS CO.: "White Trail," Shelburne, host ?, *von Schrenk* in 1938 (MO), and in 1894 (VT); Randolph, Brook Bank, *Pease 3258* in 1903 (UC); Round Pond, Errol, *Pease 32509* in 1946 (RSA); Fernway Region, Randolph, on *Picea rubens*, *Moore 143* in 1901 (RSA, UC). CHESHIRE CO.: Nelson, on *Picea* sp., *Batchelder* in 1931 (MO). GRAFTON CO.: Hanover, *Jesup & Eggelston* in 1893 (CAS, PH, US, VT) and on *Picea* sp., *Eggelston* in 1893 (PH, RM); Lebanon, *Jesup* in 1891 (MO); Hubbard Brook Exp. For., Zig Zag Brook, on *Picea rubens*, *H & Shigo 1930* in 1979 (FPF). ROCKINGHAM CO.: Nottingham, on *Picea* sp., *Eaton 443* in 1900 (GH). COUNTY UNCERTAIN: White Mtn. Nat. For., SE of Blue Brook Ranger Sta., *Hedgcock FP 8640* in 1913 (FPF, ILL).

NEW JERSEY

SUSSEX CO.: Pine Swamp, Lake Mashipscong, *MacKenzie* in 1920 (PH) and *Cain & Svenson 6597* in 1935 (UC, WIS).

NEW YORK

CHENANGO CO.: Newcomb, *Hansbrough & Spaulding FP 68210* in 1932 (FPF); Plymouth, *Coville* in 1887 (US); Preston, *Coville* in 1885 (US). CLINTON CO.: Platsburg, Hotel Champlain, on *Picea glauca*, *Schwartz FP 68288* in 1934 (FPF). COLUMBIA CO.: 1.5 mi. NW of Niverville, on *Picea* sp., *Wherry* in 1934 (UC). CORTLAND CO.: Labrador Swamp, *Wiegland* in 1893 (MO); Truxton, on *Picea* sp., *Wiegland* in 1894 (UC). ESSEX CO.: Newcomb, on *Picea glauca*, *House 7186* in 1920 (UC). FRANKLIN CO.: Saranac Inn, *Spaulding FP 34543* in 1909 (FPF); Adirondack Mts., 0.6 mi. S of Paul Smith's, *H & others 2129* in 1986 (FPF). HAMILTON CO.: Raquette Lake Village, *von Schrenk* in 1932 (PH, RSA, RM, UC); Whitney Park, Sabattis, on *Picea rubens*, *Spaulding & Eno FP 68312* in 1934 (FPF); Adirondack Mts., 5.3 mi. W of Blue Mtn. Lake, on *Picea rubens*, *H 2130* in 1986 (FPF). HERKIMER CO.: Without locality, on *Picea* sp., *Haberer* n.d. (UC); Graefender Swamp, *Haberer* in 1881 (PH); Frankfort Hill, *Haberer 188* in 1892 (DS); Litchfield, *Haberer* in 1881 (GH); Big Moose Lake, on *Picea rubens*, *von Schrenk* in 1932 (MO, RSA, UC). MONROE CO.: Mendon, *Baxter* in 1908 (UC) and *Killip* in 1917 (ARIZ, RSA). ONEIDA CO.: Frankfort Hills, Utica, col.? in 1881 (MO). ONONDAGA CO.: Cicero, *Wiegland 6344* in 1916 (GH, MO); Syracuse, *Pennington* n.d. (ILL) and on *Larix laricina*, *Pennington* n.d. (ILL). OSWEGO CO.: Oswego, *Wibbe 11532* in 1878 (MO) *Killip 7816* in 1921 (US) and on *Picea glauca*, *Sheldon 439* in 1881 (US); S New Haven, *Mathews 2663* in 1927 (RM); New Haven, *Rowlee* in 1891 (MO). RENSSELAER CO.: Without locality, *Wibbe* in 1891 (ARIZ, CS, RM, UC, US, WIS); Sand Lake, *Peck* in 1871 (MO). SCHENECTADY CO.: Schenectady, *Wibbe* in 1891 (F, US). ST. LAWRENCE CO.: Bean Pond, Wanakena, *Benedict* in 1918 (ILL). SULLIVAN CO.: Forestburg, *Peck* in 1873 (MO). THOMPKINS CO.: Franklin Hills, *Haberer* in 1882 (GH). WARREN CO.: E Lake George Marsh, Brayton, *Burnham* in 1897 (PH); Warrensburgh, *Millington* in 1912 (MO). WESTCHESTER CO.: Peekskill, on *Picea* sp., *LeRoy* n.d. (NY).

PENNSYLVANIA

LACKAWANA CO.: Moosic Mtn., NE of Scranton, col.? in 1886 (PH); Little Roaring Brook, Scranton, *Dudley* in 1886 (CAS). MONROE CO.: Tannersville, *Williamson* in 1908 (PH); Cranberry Marsh near Tannersville, *Batram & Long* in 1907 (PH); 5 mi. NE of Dresser, *Haas* in 1951 (PH). PIKE CO.: Pine

Lake, Greentown, *Olday 240* in 1961 (FPF); Spruce Pond, *Brown & Saunders* in 1899 (PH). SULLIVAN CO.: Shadynook, *Brown* in 1901 (MO, PH); near Lopez, *Williamson* in 1908 (GH, PH). WAYNE CO.: 1.5 mi. E of Hamlin, *Glowenke 2468* in 1938 (WTU).

RHODE ISLAND

PROVIDENCE CO.: Bowdish Reservoir, Glouchester, *Collins* in 1904 (PH, UC), in 1919 (US) and in 1927 (MO).

VERMONT

ADDISON CO.: Green Mts., 4.6 mi. W of Rte. 10 (Hancock) on Middleberry Gap (Ripton) Rd., on *Picea rubens, H & others 2128* in 1986 (FPF, VT); Ripton, Beaver Meadow, on *Larix laricina, Brainerd* in 1899 (VT). CHITTENDEN CO.: near Burlington, on *Larix laricina, von Schrenk* in 1899 (MO); Colchester, *Jones* in 1908 (VT). GRAFTON CO.: Hanover, *Jessip & Eggleston* in 1893 (VT); Lebanon, *Balch* in 1894 (VT); Hanover, *Eggleston* in 1898 (VT). GRAND ISLE CO.: Alberg, *Jones*, in 1899 (GH, VT); Isle La Motte, *Jones* in 1899 (VT); Alberg Peninsula, on *Larix laricina, Jones* in 1899 (VT). LAMOILLE CO.: Wolcott, *Zika* in 1980 (VT). ORANGE CO.: E Corinth, on *Picea glauca, Jones* in 1900 (VT). ORLEANS CO.: Morgan, on *Larix laricina, Hand* in 1967 (VT). RUTLAND CO.: Pittsford, on *Picea* sp., *Eggelston 1561* in 1899 (US); Mendon, on *Picea* sp., *Eggelston 1562* in 1899 (GH); Brandon, *Dutton* in 1911 (MO, VT); Pittsford, Noyes Swamp, on *Larix laricina, Eggleston* in 1899 (VT); Mendon, Bald Mtn. Bog, on *Larix laricina, Eggleston* in 1899 (VT). WINDHAM CO.: Dover, on *Picea rubens, Grout* in 1903 (VT). WASHINGTON CO.: Groton, on *Picea rubens, Jones* in 1900 (VT).

WISCONSIN

(Information on the *Arceuthobium pusillum* collections at the University of Wisconsin (WIS) provided by Dr. H. H. Iltis, 1969.)

ASHLAND CO.: Mellen, *Fassett 10093* in 1927 (WIS). BURNETT CO.: W Sweden, *Ninman & Thompson FP 38713* in 1922 (FPF); Gaslyn, *Davis* in 1911 (WIS). DOOR CO.: Sturgeon Bay, *Davis* in 1913 and 1929 (WIS). Baileys Harbor; *Davis* in 1918 and 1929 (WIS), and *Fassett & Sieker 14703* in 1932 (WIS) and on *Picea glauca, von Schrenk* in 1934 (FPF, WIS), *Pohl 1145* in 1938 (WIS), and *Iltis 17558* in 1961 (WIS). DOUGLAS CO.: Gordon, *Wadmond 271* in 1907 (GH, WIS); Solon Springs, *Fassett 22395* in 1934 (WIS). FLORENCE CO.: Boot Lake, *Iltis & others 22225* in 1964 (WIS); Long Lake, *Davis* in 1915 (WIS). FOREST CO.: Laona, *Davis* in 1915 (WIS). IRON CO.: Mercer, *Davis* in 1919 (WIS). JACKSON CO.: Glacial Lake, *Hartley 3991* in 1958 (WIS). LANGLADE CO.: Phlox, *Davis* in 1914 (WIS). LINCOLN CO.: Lost Lake, *Seymour 11906* in 1950 (WIS); Gerbig Lake, *Seymour 15104* in 1952 (WIS); Corning, *Seymour 14645* in 1952 (WIS) and *Schlising 124* in 1952 (WIS); Twin Lake, *Seymour* in 1950 (VT). MANITOWOC CO.: W of Kellnersville, *Fassett & others 18265* in 1934 (WIS). ONEIDA CO.: Rhinelander, *Anderson* in 1963 (FPF); 9 mi. W of Crandon on US 8, *H 688* in 1964 (FPF); W of Woodruff on Rte. 70, *Anderson* in 1965 (FPF); Rhinelander, on *Larix laricina, Ostry* in 1975 (FPF). PRICE CO.: Camp Merrill, *Davis* in 1911 (WIS); Butternut Lake, *Davis* in 1911 (WIS). RUSK CO.: Hawkins, *Davis* in 1918 (FPF, ILL, WIS). SAWYER CO.: Hayward, *Davis* in 1924 (WIS) and *Gilbert & Davis* in 1932 (WIS). TAYLOR CO.: 3.5 mi. N of Rib Lake, *Anderson 265* in 1947 (WIS). VILAS CO.: Trout Lake, *Spaulding FP 2693* in 1915 (FPF), *Fassett 8996* in 1929 (WIS), and *Fassett 13767* in 1932 (WIS); Lake Louise, 5 mi. E of Boulder Jct., *Wilson & Wilson 3067* in 1932 (RSA, WIS). WASHBURN CO.: Spooner, *Davis* in 1911 (WIS).

28. Arceuthobium rubrum

MEXICO

DURANGO

29 mi. E of El Salto on Rte. 40, on *Pinus teocote, H & W 338* and *521* in 1963 (COLO, FPF); on *Pinus engelmannii, H & W 339* in 1963 (COLO, FPF); and on *Pinus cooperi, H & W 340* in 1963 (COLO, FPF); 24 mi. E of El Salto on Rte. 40, on *Pinus teocote, H & W 1243* in 1969 (FPF); 2 mi. W of El Salto on Rte. 40, on *Pinus teocote, H & W 345* in 1963 (COLO, FPF), on *Pinus durangensis, H & W 346* in 1963 (COLO, FPF), on *Pinus* sp., *W 5987* in 1984 (FPF) and *W 6002* in 1985 (FPF); 30 mi. W of Durango on Rte. 40, on *Pinus teocote, H & others 1418* in 1972 (FPF); 35 mi. S of Durango on La Flor rd., on *Pinus teocote, H & W 511* in 1963 (COLO, FPF), on *Pinus engelmannii, H & W 513* in 1963 (COLO, FPF), and on *Pinus cooperi, H & W 512* in 1963 (COLO, FPF); 49 mi. W of El Salto on Rte 40, on *Pinus herrerai, H & W 1248* in 1969 (FPF); 30 mi. NW of Santiago Papasquiaro, on *Pinus teocote, Straw & Forman 1777* in 1959 (RSA); 35 mi. W of Durango on Rte. 40, on *Pinus teocote, Nickrent 1846* in 1982 (ILL, MEXU); 1 mi. W of El Salto, on *Pinus teocote, Nickrent 1853* in 1982 (ILL, MEXU); Mpio. Suchil, Reserva la Michilia, on *Pinus* sp., *Gonzales 2805* in 1986 (CIIDIR, FPF). Mpio. Santiago Papasquiaro: 6 km. SW of Pueblo Altares, on *Pinus arizonica, H & others 2241* in 1987 (FPF); Pueblo Altares, on *Pinus cooperi, H & others 2238* in 1987 (FPF); 43 km. SW of Pueblo Altares on Banome rd., on *Pinus cooperi, H & others 2248* in 1987 (FPF).

SINALOA

Without locality or host, Comision Catastral y de Estudio de los Recursos Naturales del Estado, *Gonzales 1717* in 1920 (K, US).

29. Arceuthobium siskiyouense

All collections on *Pinus attenuata,* except as noted.

UNITED STATES

CALIFORNIA

DEL NORTE CO.: Gasquet, *Tracy 16464* in 1939 (CAS, JEPS, UC, US, WTU); Smith River, between bridges 1 and 2, *Kildare 10484* in 1931 (CAS); Gordon Mtn., on rd. from Gasquet to Big Bar, *Newcomb 165* in 1957 (UC); Grassy Flat Guard Sta., 5 mi. E of Gasquet, *Wright FP 91563* in 1947 (OSC); Bear Wallows, 2 mi. N of Sanger Peak, *Kildare 8785* in 1929 (DS); Gasquet Mtn., *Eastwood 12138* in 1923 (CAS); 1 mi. N of Gasquet, on *Pinus ponderosa, Mathiasen* in 1985 (FPF); 0.1 mi. NE of Gasquet on old toll rd., on *Pinus ponderosa, W 6796* in 1987 (FPF); 0.5 mi. N of Gasquet, *H & W 863* in 1966 (FPF); 4 mi. NE of Gasquet on old toll rd., *H & W 865* in 1966 (FPF); 6 mi. NE of Gasquet on old toll rd., on *Pinus ponderosa, H & W 867* in 1966 (FPF) and on *Pinus contorta* var. *contorta, H & W 866* in 1966 (FPF); Ship Mtn. trail, on *Pinus jeffreyi, Weir 3189* in 1916 (ILL); 18 Mile Cr. Cyn., Elk Camp Ridge, on *Pinus contorta* var. *contorta, Parks & Parks 24063* in 1930 (UC); 2.5 mi. NW of Black Butte, *Tinnin & Kirkpatrick 1A* in 1981 (FPF); 5 mi. SE of the town of Smith River, on *Pinus attenuata* and *Pinus jeffreyi, Nickrent & W 2703* in 1988 (ILL, FPF); 9 mi. N of Gasquet, *Nickrent & W 2704* in 1988 (ILL, FPF); 4.0 mi. E of Gasquet, *Nickrent & W 2706* in 1988 (ILL, FPF); E of Gasquet at beginning of for. rd. 314, on *Pinus jeffreyi, Nickrent & W 2707* in 1988 (ILL, FPF); Oregon Mtn. rd., 2 mi. S of Hazelview Summit on Rte. 199 and 0.25 mi. W, *H 2272* in 1988 (FPF). SISKIYOU CO.: Russian Cr., 5 mi. E of Sawers Bar, *Butler 273* in 1908 (UC); 3 mi. N of Branch Guard Sta., N of Happy Camp, *Kuijt 1277* in 1957 (UC); 16 mi. N of Happy Camp, on O'Brien rd., *H & Hinds 1001* in 1966 (FPF).

OREGON

CURRY CO.: 1.5 mi. S of Buckskin Peak, *Tinnin & Kirkpatrick* in 1981 (FPF); 12 mi. NNW of Agness, *Graham* in 1963 (FPF); 19.6 mi. SW of O'Brien, *W 6760* in 1987 (FPF); W side of Vulcan Pk., *Denton 3689* in 1975 (WTU); SW slope of Iron Mtn., *Baker 3100* in 1946 (ID). JOSEPHINE CO.: O'Brien, *Lewis* in 1917 (ILL); on *Pinus contorta* var. *contorta, Weir 187* in 1916 (ILL); and on *Pinus jeffreyi, Lewis* in 1917 (FPF, ILL). Grants Pass, on *Pinus ponderosa, Weir 3206* in 1916 (FPF, ILL) and *Weir 9868* in 1916 (FPF, ILL); 5 mi. W of Grants Pass, on *Pinus jeffreyi, Graham* in 1964 (FPF); 6.5 mi. SSW of O'Brien on Oregon Mtn. rd., *H & Hinds 995* in 1966 (FPF), and on *Pinus ponderosa, H & Hinds 996* in 1966 (FPF); Oregon Mtn., 14 mi. SW of Cave Jct., *Weir 3194* in 1916 (ILL), on *Pinus contorta* var. *contorta, Theisen* in 1965 (FPF), and *Weir 3185* in 1916 (FPF, ILL) and *Bynum* in 1967 (FPF); 1.6 mi. N of Bain Sta. on For. Service rd. 112, on *Pinus contorta* var. *contorta, Mathiasen 8605* in 1986 (FPF); 2 mi. E of Cave Jct., *Theisen* in 1965 (FPF); near Lookout Gap, 20 air mi. S of Galice, on *Pinus jeffreyi, Graham* in 1965 (FPF); Hobson Horn Lookout, 25 air mi. N W of Grants Pass, *Graham* in 1965 (FPF); 0.5 mi. S of Galice-Agness rd. on Hobson Horn rd., *H 2333* in 1989 (FPF); Bain Sta., 2 mi. W of Oregon Mtn., *Howard* in 1964 (FPF); Oregon Mtn., on *Pinus jeffreyi, Howard* in 1964 (FPF); Wonder, on *Pinus jeffreyi, Mitchell FP 68212* in 1932 (FPF); Mt. Peavine, near Galice, *Childs FP 91615* in 1950 (OSC); Crescent City-Grant Pass rd., *Goodding & Root* in 1932 (UC); 7 mi. S of O'Brien on Lone Mtn. rd., *W 6756* in 1987 (FPF) and *W 6782* in 1987 (FPF); 1 mi. S of Buckskin Peak, on *Pinus contorta* var. *contorta, Tinnin & Kirkpatrick* in 1981 (FPF).

30. Arceuthobium strictum

All collections on *Pinus leiophylla* var. *chihuahuana*, except as noted.

MEXICO

DURANGO

City of Durango and vicinity, *Palmer 774* in 1896 (BM, F, ILL, MO, NY, UC, US); 38 mi. E of El Salto on Rte. 40, *H & W 329* in 1963 (COLO, FPF); 36 mi. E of El Salto on Rte. 49, *H & W 1242* in 1969 (FPF) and on *Pinus teocote, H & W 518* in 1963 (COLO, FPF); 25 mi. W of Durango on Rte. 40, *H & others 1416a* in 1972 (FPF); 16 mi. S of Durango on La Flor rd., *H & W 500* in 1963 (FPF); 24 mi. S of Durango on La Flor rd., on *Pinus teocote, H & W 505* in 1963 (COLO, FPF) and, on *Pinus engelmannii, H & W 506* in 1963 (COLO, FPF); 22 mi. W of Durango on Rte. 40, *Nickrent 1837* in 1982 (ILL, MEXU); 26 mi. W of Durango on Rte. 40, *Nickrent 1841* in 1982 (ILL, MEXU); 6 km from jct. to Otimpa, *Passini & Robert 3799* in 1974 (ENCB)

31a. Arceuthobium tsugense subsp. *tsugense*

All collections on *Tsuga heterophylla*, except as noted.

CANADA

BRITISH COLUMBIA

Vancouver Island: *Rosendahl & Brandegee 136* in 1901 (COLO, MO); Ucuelet, *Henry 1822* and *1881* in 1917 (RM); Pender Harbour, *Spaulding FP 41633* in 1923 (FPF); Minnesota Seaside Sta., *Rosendahl 826* in 1902 (MO, ILL, DS, COLO, RM, FPF); Sproat Lake, *Rosendahl 1958* in 1907 (UC); 6 mi. W of Duncan Jct., *Kuijt* in 1954 (DAVFP, FPF); 6 mi. W of Nanaimo Lakes Jct., *Kuijt* in 1954 (DAVFP, FPF); Cowichan Lake, *Kuijt* in 1954 (DAVFP, FPF), *Smith* in 1964 (DAVFP, FPF), *Smith* in 1969 (FPF), and *Nickrent 2661* in 1987 (ILL); Robertson River Valley, *Kuijt* in 1954 (DAVFP, FPF); 8 mi. W of Sooke, *Kuijt* in 1954 (DAVFP, FPF); Chemainus, *Porter* in 1954 (DAVFP, FPF); Horne Lake, *H 1815* in 1977 (FPF) and *Nickrent 2663* in 1987 (ILL); Sechelt, *Kuijt 618* in 1954 (DAVFP, FPF). Vancouver, Stanley Park, *Hopping FP 97939* in 1928 (FPB), *Kuijt* in 1954 (DAVFP, FPF), and *H & Laut 1298* in 1979 (FPF); Nanoose Bay, V. I., *Kuijt* in 1954 (DAVFP, FPF).; Vancouver, Univ. of British Columbia Botanic Gardens, *Kuijt* in 1954 (DAVFP, FPF); Agassiz, *Weir 2449*, n.d. (ILL); Mesachie Lake, V. I., *Thomas* in 1951 (FPF, DAVFP); Daisy Lake, ca. 30 mi. N of Squamish, *Boyce 2122* in 1931 (FPF).

UNITED STATES

ALASKA

Juneau, *Anderson 6406* in 1941 (PH, RM) and *Hennon & Loopstra* in 1986 (ILL); Eagle River, 25 mi. N of Juneau, *Laurent* in 1965 (FPF); 37 mi. N of Juneau, Veteran's Memorial Highway, *H & others 2448* in 1991 (FPF); Lena Point, 14 mi. N of Juneau, *H & others 2451* in 1991 (FPF); near Homeshore, about 24 air mi. W of Juneau, on *Tsuga mertensiana, Shaw* in 1981 (FPF); Chicagof Island, Basket Bay, *Laurent & Labue* in 1965 (FPF); Kupreanof Island, 15 mi. SW of Petersburg, *Graham* in 1966 (FPF); 1 mi. S of Little Basket Bay, on *Picea sitchensis, Laurent* in 1965 (FPF); Kosciusco Island, E Edna Bay, on *Picea sitchensis, Shaw* in 1978 (FPF) and *McWilliams & Nathenson 3849* in 1979 (FPF); near Sitka, on *Tsuga mertensiana, Weir* in 1913 (FPF, ILL). Revillagigedo Island, near Ketchikan, *Weir* in 1915 (ILL) and *Drake* in 1917 (FPF, ILL); Whittman Cr., 9 mi. SE of Ketchikan, *H and others 2446* in 1991 (FPF); Refuge Bay, 10 mi. N of Ketchikan, *H & others 2445* in 1991 (FPF). Mt. Verstovia, Sitka, *Coville & Kearney 916* in 1899 (US); Sitka, *Anderson 232* in 1915 (US); Auke Bay, 13 mi. N of Juneau, *H 2150* in 1986 (FPF) and *H & others 2450* in 1991 (FPF); S end of Chilkoot Lake, about 10 mi. N of Haines, *H 1903* in 1979 (FPF); 5.5 mi. S of Haines, *H 1902* in 1979 (FPF); Haines Dump, 2 mi. S of Haines, *H & others* in 1991 (FPF); Cleveland Peninsula, 3 Island Point, about 50 mi. NW of Ketchikan, *H 1896* in 1979 (FPF); Kupreanof Island, Hamilton Bay, about 7 mi. SE of Kake, *H 1898* in 1979 (FPF); Kupreanof Island, T. 57 S, R. 73 E, Sec. 20, *H 1899* in 1979 (FPF); Baranof Island: 10 air mi. S of Sitka, *H 1900* in 1979 (FPF), and 2.5 mi. SE of Sitka, *H 1901* in 1979 (FPF); Sitka Airport, *H & others 2447* in 1991(FPF). Kuiu Island, Halleck Harbor, on *Picea sitchensis, Hennon & others* in 1990 (FPF). Douglas Island, 12 mi. NW of Juneau, *H & others 1448* in 1991 (FPF).

CALIFORNIA

HUMBOLDT CO.: 18 mi. E of Rte. 101 on Rte. 299, *H 1746* in 1976 (FPF). MENDOCINO CO.: 3 mi. E of Mendocino, *H & Scharpf 850* in 1966 (FPF). COUNTY UNCERTAIN: Bald Mtn., *Hubert* in 1918 (ILL).

IDAHO

These Idaho records on *Tsuga heterophylla* are tentatively listed here pending confirmation. They are probably *Arceuthobium laricis* on *Tsuga mertensiana* (see text). LATAH CO.: Boville, *Weir* in 1918 (FPF, ILL). COUNTY UNCERTAIN: St. Joe Nat. For., *Weir 2452* in 1914 (ILL) and *Weir 6838* (?) in 1916 (FPF, ILL).

OREGON

BENTON CO.: Mary's Peak, *Knutson* in 1975 (FPF), and on *Abies procera, Shea* in 1968 (FPF), *Knutson* in 1975 (FPF), and *Hansen* in 1986 (FPF). CLACKAMAS CO.: Still Cr. Trail near Rhododendron, *Gill FP 68193* in 1932 (FPF), and on *Pinus monticola, Gill (FP 68194)* in 1932 (FPF); *Faull & others FP 68266* in 1931 (FPF), and on *Pinus monticola, Langley & Goodding* in 1931 (RM); 4 mi. E of Rhododendron, *Mielke FP 58275* in 1930 (OSC); 2 mi. W of Government Camp on US 26, *H & W 605* in 1964 (FPF) and on *Abies amabilis, H & W 606* in 1964 (FPF); Twin Bridges, 5 mi. W of Government Camp on US 26, *Thompson 4922* in 1928 (DS, MO); 2.9 mi. S of Rte. 35 on Rte. 26, on *Abies amabilis, Knutson & Tinnin* in 1975 (FPF); 7 mi. E and 2 mi. S of Three Lynx, *Knutson & Tinnin DM45* in 1977 (FPF); 1.3 mi. W of Government Camp on Highway 26, *Mathiasen 8644* in 1986 (FPF); near Frog Lake, Wapinita Pass, *Mathiasen 8642* in 1986 (FPF); 7 mi. E and 2 mi. S of Three Lynx, on *Abies procera, Knutson & Tinnin DM46* in 1977 (FPF). CLATSOP CO.: 10 mi. E of Seaside, *Knutson 4* in 1978 (FPF). COOS CO.: 14 mi. S of Powers, 2 mi. NE of Iron Mtn., *Mathiasen 8611* in 1986 (FPF); Near S fork of Coos River, 38 air mi. W of Roseburg, *Stewart* in 1968 (FPF); Iron Mtn., *Baker* in 1946 (OSC); 10 mi. E of Powers-Agness rd, on Glendale rd., *H 2335* in 1989 (FPF); Eden Valley, near Fuller Cr. on Glendale rd., *H 2336* in 1989 (FPF); 10 air mi. NNE of Agness, *Graham* in 1965 (FPF). CURRY CO.: 11 mi. W of Powers, *H 1743* in 1976 (FPF). DOUGLAS CO.: Myrtle Cr., Deadman Cr. Divide, ca. 11 air mi. N of Tiller, *Graham* in 1964 (FPF); 8 mi. W of Lemolo Lake jct. on Rte. 138, *H 2337* in 1989 (FPF); 16 mi. N of Union Cr. on Rte. 230, *Mathiasen 8613* in 1986 (FPF). JACKSON CO.: 6 mi. N of Union Cr. on Rte. 230, *Knutson & Tinnin DM 53* in 1977 (FPF); 5 mi. N of Union Cr. on Rte. 230, *Mathiasen 8612* in 1986 (FPF); 3 mi. NE of Union Cr., *Graham* in 1963 (FPF); 8 mi. NW of W entrance to Crater Lake Nat. Park, *Graham* in 1963 (FPF); 4 mi. E of Diamond Lake jct. on Rte. 230, *H 2370* in 1989 (FPF); Imnaha Campground, 10 air mi. SE of Prospect, *H 2442* in 1991 (FPF). KLAMATH CO.: 15 mi. SW of Crescent Lake, *Childs 65* in 1937 (OSC); 13.5 air mi. NW of Crescent, on *Abies amabilis, Knutson & Tinnin 5* in 1975 (FPF); 14 air mi. SW of Prospect on For. Service rd. 3780, *H 2443* in 1991 (FPF). LANE CO.: E Fork of S Fork of McKenzie River, 8 mi. S of McKenzie Bridge, *Stewart & Orr* in 1968 (FPF); Buck Cr. Cyn., 6 mi. E and 14 mi. S of Oakridge, *Knutson & Tinnin DM 43* in 1977 (FPF); near head of Mosquito Cr., on *Abies amabilis, Stewart & Orr* in 1968 (FPF); head of Olallie Cr., on *Abies amabilis, Abies grandis,* and *Abies lasiocarpa, Stewart & Orr* in 1968 (FPF); 19 mi. E of Oakridge on Rte. 58, *H 1140* in 1968 (FPF); near Foley Springs, on *Abies* sp., *Coville & Applegate 1090* and *1091* in 1898 (US); Brice Cr., 20 air mi. SE of Cottage Grove, *Graham* in 1964 (FPF); H. J. Andrews Exp. For., 1 mi. E of McRae Cr., *H 2362* in 1989 (FPF); Rebel Cr., 14 mi. S of US 126 S of Cougar Reservoir, *H 2363* in 1989 (FPF); Constitution Grove, 7 mi. E of Kiahane Campground, *H 2364* in 1989 (FPF). LINCOLN CO.: Eckman Cr., 4 mi. SSE of Waldport, *H & Scharpf 1253* in 1969 (FPF); 3 mi. E of Yachats, *Graham* in 1966 (FPF); Dicks Fork Cr., 4 mi. S of Waldport, *H 1252* in 1969 (FPF); ca. 3 air mi. SE of Yachats on *Picea sitchensis, Ferguson* in 1969 (FPF). LINN CO.: S side of Marion Lake, *Mathiasen 8639* in 1986 (FPF); 12 mi. W of Santiam Pass on US 20, *H & Scharpf 1254* in 1969 (FPF), on *Abies amabilis, H & Scharpf 1255* in 1969 (FPF), and on *Picea engelmannii, H & Scharpf 1256* in 1969 (FPF); on *Abies amabilis*: 2.3 mi. W of Santiam Pass on Rte. 20, *Mathiasen 8636* in 1986 (FPF); Trail to Blue Lake S of Marion Lake, *Mathiasen 8638* in 1986 (FPF); S side of Marion Lake, *Mathiasen 8640* in 1986 (FPF); H. J. Andrews Exp. For., Carpenter Mtn., on *Abies procera, Lattin* in 1978 (FPF); 2.3 mi. W of Santiam Pass on Rte. 20, *Mathiasen 8635* in 1986 (FPF); Trail to Blue Lake S of Marion Lake, *Mathiasen 8637* in 1986 (FPF); S shore of Big Lake, near Santiam Pass, *Knutson* in 1981 (FPF); 0.5 mi. W of Rte. 126 on Rte. 20, *H 2552* in 1989 (FPF); 1 mi. E of Lost Prairie on Rte. 20, *H 2353* in 1989 (FPF), and on *Abies amabilis, H 2354* in 1989 (FPF). TILLAMOOK CO.: near Nehalem, *Childs FP 40545* in 1930 (OSC). WASCO CO.: 5.7 mi. SE of Government Camp on US 26, *H & W 607* in 1964 (FPF), and on *Abies amabilis, H & W 608* in 1964 (FPF); 2 mi. S of Wapinita Pass on US 26, *H 2386* in 1989 (FPF).

WASHINGTON

CHELAN CO.: Chelan Lake, *Weir* n.d. (FPF). CLALLAM CO.: Lake Crescent, on *Tsuga* sp., *Jones 3439* n.d. (WTU); Piedmont, Crescent Lake, *Boyce 608* in 1920 (FPF) and *FP 40065* in 1920 (OSC); near Blyn, *W 3250* in 1962 (COLO); Crescent Lake, *W* in 1991 (FPF). GRAYS HARBOR CO.: Westport, *Gill FP 68195* in 1932 (FPF); 3.5 mi. NW of Montesano, *H 1250* in 1969 (FPF); 9.5 mi. N of Humptulip on Rte. 101 and 4.2 mi. S of Neilton, *Tinnin & Knutson* in 1976 (FPF); 1.6 mi. S of Cosmopolis on Rte. 101, *Tinnin & Knutson* in 1976 (FPF). KING CO.: Seattle, *Piper* in 1889 (PH), and on *Tsuga mertensiana?, Piper 663* in 1892 (CAS, MO, US, WTU); Seattle, Interlaken Park, *Jacobsen* in 1983 (WTU); Berlin, 5 mi. WNW of Skykomish, *Hedgcock FP 4765* in 1910 (FPF); Silver Lake near Seattle, *Meinecke* in 1917 (FPF); Ronald Bog, N of Seattle, *Gunther* in 1930 (WTU); Corea, *Otis 1036* in 1920 (US); 4 mi. W of Stevens Pass on US 2, *H & others 1138* in 1968 (FPF) and on *Abies amabilis, 1139* in 1968 (FPF). KITSAP CO.: Mountaineer's Cabin, on *Tsuga* sp., *Jones 4299* in 1931 (WTU). KITTITAS CO.: Near Ellensburg, *Brandegee 1070* in 1883 (PH, US), and on *Abies amabilis, Brandegee* in 1883 (US); E side Snoqualmie Pass, *W 3252* in 1962 (COLO) and on *Abies amabilis, W 3251* in 1962 (COLO); on I-90 near Keechelus Lake, about 10 mi. E of the Cascade crest, *H 2384* in 1989 (FPF), and on *Abies amabilis, H 2385* in 1989 (FPF). LEWIS CO.: 4 mi. W of White Pass on Rte. 12, *Wicker* in 1966 (FPF), and on *Abies amabilis, Wicker* in 1961 (WSP) and 1966 (FPF), and *Tinnin & Knutson* in 1976 (FPF); 3.3 mi. W of White Pass on Rte. 12, *Tinnin & Knutson* in 1976 (FPF); 12 mi. SE of Randle on Trout Lake Rd., *H 2212* in 1987 (FPF). PACIFIC CO.: 3 mi. N of Nemah on Rte. 101, *H & W 604* in 1964 (FPF) and *H & Scharpf 1251* in 1969 (FPF); Nemah, *Nickrent 2667* in 1987 (ILL). PIERCE CO.: 5 mi. N of Cayuse Pass on Rte. 410, on *Abies grandis, H & W 602* in 1964 (FPF); Mt. Rainier Nat. Park: Longmire: *Gill & Warren FP 68198* in 1932 (FPF), *Gill & Warren FP 68199* in 1932 (FPF), *Flett* in 1915 (ILL), *Bookman FP 68265* in 1931 (FPF), and on *Abies amabilis, Flett* in 1914 (ILL) and *Gill & Warren FP 68197* in 1932 (FPF); 5 mi. E of Longmire, *W 3248* in 1962 (COLO, FPF) and on *Abies amabilis, W 3249* in 1962 (COLO, FPF); White River Entrance, *Gill FP 68196* in 1932 (FPF). Silver Cr., just outside Mt. Rainier Nat. Park, *Nickrent 2670* in 1987 (ILL); Ashford, *Flett* in 1915 (FPF, ILL); Huckleberry Cr., 8 mi. S of Greenwater, *Stewart* in 1968 (FPF) and on *Abies amabilis, Stewart* in 1968 (FPF); Silver Springs, 32.5 mi. SE of Enumclaw on US 410, *H & W 601* in 1964 (FPF). SAN JUAN CO.: Orcas Island, Mt. Constitution, *Graham & Thompson* in 1965 (FPF) and *H & others 1443* in 1972. SKAGIT CO.: Near power dam on Skagit River, on *Tsuga* sp., col.? (WTU). SKAMANIA CO.: Tillicum Cr., 18 air mi. ESE of Spirit Lake, *Graham* in 1965 (FPF), and on *Abies amabilis, Graham* in 1965 (FPF); 24 mi. SE of Randle, *W 3247* in 1962 (COLO, FPF); Government Mineral Springs, Carson, *Boyce 596* in 1920 (FPF); Dry Cr., 20 air mi. N of Stevenson, *Graham* in 1965 (FPF); Lewis River Highway near jct. of For. Service rd. 88, ca. 11 air mi. W of Mt. Adams, *H 2213* in 1987 (FPF) and on *Abies amabilis, H 2214* in 1987 (FPF). SNOHOMISH CO.: 15 mi. N of Seattle, *Wittrock 5097* in 1927 (WTU). WHATCOM CO.: Black Hills, *Meyer 1685* in 1939 (MO); Colonial Cr. on US 29, 9 mi. NE of Newhalem, *H 2413* in 1990 (FPF); 6 mi. S of Silver Fir Campground on Mt. Baker Ski Area rd., *H 2417* in 1990 (FPF); 2.6 mi. above Silver Fir Campground on Mt. Baker Ski Area rd., *W* in 1991 (FPF); 4.7 mi. below Mt. Baker Ski Area on Rte. 542, *Mathiasen 9007* in 1990 (FPF). COUNTY UNCERTAIN.: Camp on Yakima Territory, *Brandegee* in 1882 (MO).

31a. Arceuthobium tsugense subsp. *tsugense* (shore pine race)

All collections on *Pinus contorta* var. *contorta*.

CANADA

BRITISH COLUMBIA

Vancouver Island: Sproat Lake, *Rosendahl & Butters 1092* in 1906 (WTU); Metchosin, *Kuijt 602* in 1954 (DAVFP, FPF); Horne Lake, *Kuijt* in 1954 (DAVFP, FPF), *Smith* in 1964 (FPF), *H 1814* in 1977 (FPF), and *Nickrent 2664* in 1987 (ILL); Courtnay, *Foster* in 1954 (FPF); Coldstream summit of Mt. Finlayson, *Ziller* in 1965 (DAVFP, FPF) and *Nickrent 2666* in 1987 (ILL); Sechelt, *Kuijt* in 1954 (DAVFP, FPF); Nanoose Bay, *Kuijt* in 1954 (DAVFP, FPF); Savary Island, *Davidson* in 1918 (FPF, ILL); Spider Lake, 6 km. S of Qualicum, *Nickrent 2665* in 1987 (ILL);

UNITED STATES

WASHINGTON

SAN JUAN CO.: Orcas Island: Mt. Constitution, *Foster* in 1907 (WTU), *Cowles 372* in 1907 (MO), *Rigg & Frye* in 1908

(WTU), *Wright* in 1914 (US), *Zeller & Zeller 1194* in 1917 (MO), *Beattie 5801* in 1921 (CAS, FPF), *Barker 254* in 1926 (CAS), *Graham & Thompsen* in 1965 (FPF), and *H & others 1442* in 1972 (FPF); Moran State Park, *H 2211* in 1987 (FPF, ILL).

31b. *Arceuthobium tsugense* subsp. *mertensianae*

All collections on *Tsuga mertensiana*, except as noted.

CANADA

BRITISH COLUMBIA

Cypress Bowl Park: Hollyburn rd., *Wood* in 1982 (DAVFP), *Morris & Van Sickle* in 1979 (DAVFP), and *H. & Macias 2414* in 1990 (FPF); Lost Lake, Brothers Cr., adjacent to Cypress Bowl Park, *Alexander* in 1972 (DAVFP).

UNITED STATES

CALIFORNIA

ALPINE CO.: Mosquito Lake, 11 mi. NE of Alpine, *H & Scharpf 665* in 1964 (FPF), *Mathiasen 8517* in 1985 (FPF), and *Nickrent 2216* in 1986 (ILL), and on *Pinus monticola*, *H & Scharpf 666* in 1964 (FPF), *Mathiasen 8516* in 1985 (FPF), and *Nickrent 2217* in 1986 (ILL). PLACER CO.: Emigrant Gap, *Jones* in 1881 (RSA); Alpine Meadows Ski Resort, *Nickrent 2212* in 1986 (ILL), and on *Pinus monticola*, *Nickrent 2213* in 1986 (ILL). PLUMAS CO.: Mt. Elwell, 6 mi. SW of Blairsden, *Lieberg 5363* in 1900 (ILL, US); 6 mi. SW of Graeagle, *Nickrent 2194* in 1986 (ILL), and on *Pinus monticola*, *Nickrent 2195* in 1986 (ILL). SHASTA CO.: Lassen Nat. Park: 2.5 mi. N of S entrance, *W 3235* in 1962 (COLO, FPF); 23 mi. SE of N entrance, on main rd., *H & W 652* in 1964 (FPF); 0.7 mi. E of Kings Cr. Picnic Ground on Rte. 89, *Mathiasen 8511* in 1985 (FPF); Hemlock Lake, *Nickrent 2187* in 1986 (ILL). SIERRA CO.: Hawlsey Lake, 3 mi. W of Gold Lake, on *Pinus monticola*, *Menzies* in 1961 (CAS) and *Mathiasen 8514* in 1985 (FPF), and on *Pinus monticola*, *Mathiasen 8513* in 1985 (FPF). SISKIYOU CO.: Marble Mts.: Kidder Cr., *Gill & Sargent FP 68180* in 1932 (FPF); Chimney Rock Lake, *Hemphill* in 1968 (FPF, UT) and on *Picea breweriana*, *Hemphill* in 1968 (FPF, UT); near Chimney Rock, on *Pinus monticola*, *Hemphill* in 1968 (FPF, UT); Little Marble Valley, *Mathiasen 8623* in 1986 (FPF). Siskiyou Mts.: Applegate Cr. Divide, *Meinecke FP 97938* in 1913 (FPF) and on *Picea breweriana*, *Meinecke FP 97941* in 1913 (FPF); N Slope of White Mtn., *Mathiasen & Loftis 8629* in 1986 (FPF), and on *Pinus monticola*, *Mathiasen & Loftis 8628* in 1986 (FPF); Trinity Alps, Snowslide Lake, *Mathiasen 9016* in 1990 (FPF). TEHAMA CO.: Mineral, *Lory FP 97940* in 1911 (FPF). TRINITY CO.: 1-2 mi. S of Helen Lake, *Scharpf FP 38027* n.d. (FPF).

OREGON

CLACKAMAS CO.: near Frog Lake, Wapinita Pass, *Mathiasen 8643* in 1986. COOS CO.: Siskiyou Nat. For., Iron Mtn., *Baker* in 1946 (OSC); 10 air mi. NNE of Agness, *Graham* in 1965 (FPF). CURRY CO.: Snow Camp Mtn., on *Pinus monticola*, *Nickrent & W 2701* in 1988 (FPF, ILL). DESCHUTES CO.: 11 mi. W of Sisters on McKenzie Pass rd., *H & Hinds 991* in 1966 (FPF) and on *Abies lasiocarpa*, *H & Hinds 992* in 1966 (FPF); 3 mi. E of McKenzie Pass on Rte. 242, *H 2347* in 1989 (FPF) and, on *Abies lasiocarpa*, *H 2348* in 1989 (FPF); 1 mi. W of Elk Lake near trail to Horse Lake, *Mathiasen 8645* in 1986 (FPF). DOUGLAS CO.: Just N of Crater Lake Nat. Park on Diamond Lake rd., *Graham* in 1964 (FPF); on Rte. 138 1.5 mi. N of Rte. 230, on *Pinus monticola*, *Mathiasen 8617* in 1986 (FPF); on Rte. 138 1.8 mi. N of Rte. 230, *Nickrent 2676* in 1987 (ILL); 15.5 mi. N of Union Cr., *Nickrent 2682* in 1987 (ILL), and on *Pinus monticola*, *Nickrent 2681* in 1987 (ILL); 16 mi. N of Union Cr. on Rte. 230, on *Pinus monticola*, *Mathiasen 8614* in 1986 (FPF); 20 mi. NE of Union Cr., on Rte. 230, *H 1141* in 1968 (FPF), and on *Pinus monticola*, *H 1142* in 1968 (FPF); 15 mi. SW of Crescent Lake, on *Pinus monticola*, *Childs 65* in 1937 (FPF); E side of Diamond Lake, 1 mi. N of jct. of Rts. 230 & 138 on 138, *Mathiasen 8616* in 1986 (FPF); 4 mi. SW of Windigo Pass on Lemolo Lake rd., *H 2339* in 1989 (FPF) and, on *Pinus monticola*, *H 2340* in 1989 (FPF); 15 mi. N of Rte. 62 on Rte. 230, *H 2371* in 1989 (FPF). HOOD RIVER CO.: State Rte. 35 at jct. of Mt. Hood Meadows Ski Area rd., *Mathiasen 9101* in 1991 (FPF), and on *Abies amabilis*, *Mathiasen 9102* in 1991 (FPF). JACKSON CO.: Union Cr., *Applegate 6038* in 1929 (DS); Huckleberry Mtn., 10 mi. NE of Prospect, *Graham* in 1965 (FPF); 12 mi. NE of Prospect, *Knutson & Tinnin DM 48-51* in 1977 (FPF); 11 mi. NE of Prospect, *Knutson & Tinnin DM 52* in 1977 (FPF); Thousand Springs Area, 3 mi. SE of Rte. 62 on For. Service rd. 800, *Nickrent 2679* in 1987 (ILL), and on *Abies lasiocarpa*, *Nickrent 2680* in 1987 (ILL). KLAMATH CO.: Crater Lake Nat. Park: Annie Springs Ranger Sta., *Gill FP 68184* in 1932 (FPF); Wineglass, on *Pinus albicaulis*, *Gill FP 68182* in 1932 (FPF); 0.5 mi. S of Wineglass, *Gill FP 68183* in 1932 (FPF); 5 mi. E of main rd. on N Rim of Crater Lake, *H & W 624* in 1964 (FPF) and on *Pinus albicaulis*, *H & W 625* in 1964 (FPF); Crater Lake, Palisades, *Coville 1478* in 1902 (US); Palisade Point, *Nickrent 2677* in 1987 (ILL), and on *Pinus albicaulis*, *Nickrent 2678* in 1987 (ILL); 6 mi. W of Annie Springs on Rte. 62, *H & others 1376* in 1971 (FPF); Crater Lake Nat. Park, 4 mi. SE of jcts. of Rts. 62 and 209, *Mathiasen 8618* in 1986 (FPF) and *H 2369* in 1989 (FPF), and on *Pinus monticola*, *Mathiasen 8619* in 1986 (FPF); 2 mi. N of Windigo Pass, *H & W 621* in 1964 (FPF) and on *Pinus monticola*, *H & W 622* in 1964 (FPF) and *Mathiasen 8634* in 1986 (FPF); 1.5 mi. NE of Windigo Pass, *Nickrent 2674* in 1987, and on *Pinus monticola*, *Nickrent 2675* in 1987 (ILL); 2.4 mi. N of Windigo Pass, *Mathiasen 8633* in 1986 (FPF); halfway between Crescent Lake and Summit Lake, *Knutson 100* in 1980 (FPF); 7 air mi. S of Crescent Lake on *Pinus monticola*, *Dolph* in 1969 (FPF); 8 air mi. N of Lake of the Woods on Cold Springs rd., *H 2375* in

1989 (FPF). LANE CO.: McKenzie Pass, on *Abies lasiocarpa*, *Childs FP 91561* in 1947 (FPP); on *Pinus albicaulis*, *Gill FP 68188* in 1932 (FPF), *Lachmund & Childs FP 68269* in 1930 (FPF), and *Childs FP 91560* in 1947 (OSC); *Gill FP 68187* in 1932 (FPF), *Childs FP 91562* in 1947 (OSC), and *Lachmund & Childs (FP 68264)* in 1930 (FPF); 1 mi. W of McKenzie Pass: *Boyce 2299* in 1930 (FPF) and *Boyce 2300* in 1930 (FPF), on *Abies lasiocarpa*, *Boyce 2298* in 1930 (FPF), and on *Pinus albicaulis*; 1.5 mi. W of McKenzie Pass: *W3242* in 1962 (COLO, FPF) and *Nickrent 2684* in 1987 (ILL), on *Abies lasiocarpa*, *W3241* in 1962 (COLO, FPF) and *Nickrent 2685* in 1987 (ILL), and on *Pinus albicaulis*, *W3243* in 1962 (COLO, FPF) and *Nickrent 2686* in 1987 (ILL); 15 mi. W of Sisters, on *Abies lasiocarpa*, *Lachmund & Childs FP 68260* in 1930 (FPF); H. J. Andrews Exp. For., near Frissell Point; *H 2359* in 1989 (FPF), on *Abies amabilis*, *H 2360* in 1989 (FPF), and on *Abies procera*, *H 2361* in 1989 (FPF). LINN CO.: Minto Mtn., *Mielke FP 40694* in 1931 (OSC); Marion Lake, *Coville & Applegate 1156*, in 1898 (US); S side of Marion Lake, *Mathiasen 8641* in 1986 (FPF) and 1978 (FPF); Wildcat Mtn.: *H 2358* in 1989 (FPF), on *Abies amabilis*, *H 2355* in 1989 (FPF) and *H 2357* in 1989 (FPF), and on *Abies procera*, *H 2356* in 1989 (FPF).

WASHINGTON

CHELAN CO.: Lyman Glacier W of Chelan Lake, *Weir 2456* in 1916 (ILL); Chelan Lake on *Tsuga heterophylla*, *Weir* n.d. (FPF, ILL) and on *Abies lasiocarpa*, *Weir 2417* in 1916 (ILL); N of Chelan Lake, on *Pinus albicaulis*, *Weir 3242* in 1916 (FPF, ILL). OKANOGAN CO.: 20 mi. NW of Winthrop on Rte. 20, on *Abies lasiocarpa*, *Tinnin & Knutson* in 1976 (FPF). PIERCE CO.: Upper Nesqually Valley, *Allen 303* in 1896 (CAS, MO, UC). WHATCOM CO.: Twin Sisters Range, 7 mi. SW of Mt. Baker, *Muenscher 10431* in 1939 (CAS); Bellingham to Mt. Baker, *Weir* in 1915 (ILL); 3.6 mi. below Mt. Baker Ski Area on Rte. 542, *Mathiasen 9006* in 1990 (FPF), *Mathiasen 9005* in 1990 (FPF) and *9006* in 1990 (FPF); 1 mi. E of Mt. Baker Ski Area on Rte. 542, *H 2416* in 1990 (FPF) and *W* in 1991 (FPF).

32a. Arceuthobium vaginatum subsp. *vaginatum*

MEXICO

CHIHUAHUA

Sierra Madre, on *Pinus* sp., *Nelson 6077* in 1899 (K, US); Sierra Madre near Guachochi, on *Pinus* sp., *Goldman 177* in 1898 (US); 36 mi. SW of La Junta, on *Pinus cooperi*, *H & W 295* in 1963 (COLO, FPF); 39 mi. SW of La Junta, on *Pinus cooperi*, *H & W 298* in 1963 (COLO, FPF); 6 mi. E of El Vergel, on *Pinus cooperi*, *H & W 310* in 1963 (COLO, FPF); 1 mi. W of El Vergel, on *Pinus arizonica*, *H & W 311* in 1963 (COLO, FPF); 18 mi. W of El Vergel on Rte. 24, on *Pinus cooperi*, *H 1848* in 1978 (FPF); 10 mi. W of El Vergel, on *Pinus arizonica*, *H & W 313* in 1963 (COLO, FPF): 10 mi. E of El Vergel, on *Pinus cooperi*, *H & W 308* in 1963 (COLO, FPF); on Ocampo rd. 48 mi., SW of Matachic, on *Pinus arizonica*, *H & W 486* in 1963 (COLO, FPF); 63 mi. *H & W 494* in 1963 (COLO, FPF); and at 69 mi. *H & W 491* in 1963 (COLO, FPF); Mpio. Urique, Ejido Piedras Verdes, on *Pinus herrerai*, *Olivo* in 1984 (INIF); Predio la Laja, San Juanito, Boycona, on *Pinus arizonica*, *Olivo* in 1984 (INIF); Mpio. Guadalupe y Calvo, Cerro Mohinora, on *Pinus arizonica*, *Olivo 10* in 1984 (INIF); Mpio. Creel, 7 km. SE of Creel, on *Pinus arizonica*, *Medina 2373a* in 1982 (ENCB); 5 km. S of Magdalena, ca. 80 km. W of La Junta, on *Pinus arizonica*, *H & Cibrián 1966* in 1981 (FPF); 26 mi. W of Tomochic on Rte. 16, on *Pinus arizonica*, *H & others 1648* in 1975 (FPF); 9 mi. S of La Bufa Jct. on Guachochic rd., on *Pinus durangensis*, *H & Cibrián 1988* in 1981 (FPF); 3.3 mi. S of Chorro de Agua, on Cuervo rd., on *Pinus* sp., *Van Devender & others 87-114* in 1987 (ARIZ, FPF).

COAHUILA

General Cepeda, *Pinus* sp., *Nelson 6730* in 1890 (US); Mpio. Arteaga, Sierra de la Martha, on *Pinus arizonica*, *Passini & Robert 4309* in 1975 (ENCB); 2 mi. W of La Siberia, on Rte. D16, on *Pinus rudis*, *H 1823* in 1978 (FPF); Sierra de Martha, 15 mi. E of San Antonio de las Anzanas, on *Pinus rudis*, *H & Cibrián* 1999 in 1981 (FPF); La Siberia, on planted *Pinus contorta*, *Bailey* in 1975 (FPF).

DISTRITO FEDERAL

Desierto de los Leones, on *Pinus* sp., *Alexander & Hernandez 2333* in 1945 (BM); Sierra del Ajusco, Montealegre, on *Pinus hartwegii*, *Nieto* in 1984 (INIF).

DURANGO

Cienega de Ibarra, on *Pinus* sp., *Martínez* in 1940 (F); 13 mi. W of El Salto on Rte. 40, on *Pinus cooperi*, *H & W 348* in 1963 (COLO, FPF) and *H & others 1665* in 1975 (FPF); 15 mi. W of El Salto on Rte. 40, on *Pinus cooperi*, *H & W 531* in 1963 (COLO, FPF); 18 mi. W of El Salto on Rte. 40, on *Pinus durangensis*, *H & W 1245* in 1969 (FPF); 23 mi. W of El Salto on Rte. 40, on *Pinus arizonica*, *Mathiasen 8126* in 1981 (FPF); 26 mi. S of Durango on La Flor rd., on *Pinus engelmannii*, *H & W 507* in 1963 (COLO, FPF); 47 mi. S of Durango on La Flor rd., on *Pinus cooperi*, *H & W 515* in 1963 (COLO, FPF); Mpio. Guanachevi, 5 km. S of la Ravela, on *Pinus* sp., *Perez 740* in 1980 (ENCB); Mpio. San Dimas, 10 km. SE of San Antonia de las Trudeas, on *Pinus* sp., *Perez 710* in 1980 (ENCB); 10 km. E of El Regocijo, on *Pinus cooperi*, *Perez 739* in 1980 (ENCB); Mpio. Tepehuanes, El Columpio, 70 km. W of Tepehuanes on Sierra del Huacal rd., on *Pinus engelmannii*, *H 2165* in 1987 (FPF); Mpio. Tepehuanes, 27 km. E of Tepehuanes on Sierra de la Candela rd., on *Pinus arizonica*, *H 2156* in 1987 (FPF); 32 km. W of Rte. 39 on Altares rd., on *Pinus durangensis*, *H & others 2233* in 1987 (FPF); Mpio.

Otaez, 49 km. SW of Altares on Banome rd., on *Pinus durangensis, H & others 2251* in 1987 (FPF).

HIDALGO

Real del Monte, on *Pinus* sp., *Coulter 17*, n.d. (GH, K). Mpio. Epazoyucán: 2 km. E of El Guajolote, on *Pinus rudis, Rzedowski 27145* in 1970 (ENCB) and 1 km. N of Nopalillo, on *Pinus montezumae, Medina 1683* in 1976 (ENCB).

JALISCO

Mpio. Mezquitic, 40 km. NW of Bolanos, on *Pinus durangensis, Flores & others 1608* in 1989 (FPF, IBUG). Nevado de Colima, on *Pinus* sp., *Jones 487* in 1892 (ILL, MO, RSA, US); *Pringle 4368* in 1893 (BM, ILL, K, MEXU, MO, NY, PH, UC, Z); *Reiche* in 1913 (MEXU); *McVaugh 10071* in 1949 (MICH) and *12916* in 1952 (MICH).

MEXICO

Nevado de Toluca, Ojos de Agua, on *Pinus* sp., *Balls B4086* in 1938 (BM, K, UC, US); Telapon Peak N of Rio Frio, on *Pinus* sp., *Miranda 114* in 1940 (MEXU) and on *Pinus hartwegii, Beaman 2441* in 1958 (UC); Ixtacchiuatl, on *Pinus* sp., *Purpus 3836* in 1905 (RSA); Rio Frio, on *Pinus* sp., *Hartley FP 89795* in 1947 (FPF); 3 mi. W of Rio Frio on Rte. 190, on *Pinus montezumae, H & others 1414* in 1972 (FPF); 6 mi. W of Rio Frio on Rte. 190, on *Pinus montezumae, H & W 370* in 1963 (COLO, FPF); Parque Nacional de Ixtaccihuatl, on *Pinus hartwegii, Madrigal* in 1960 (INIF); Mpio. Ixatpaluca, Llano Grande, on *Pinus* sp., *Ventura 460* in 1983 (ENCB), and on *Pinus hartwegii, Rzedowski 29293* in 1972 (ENCB); Mpio. Zinacantepec, NW slopes of Nevado de Toluca, on *Pinus hartwegii, Rzedowski 27276* in 1970 (ENCB); 2.2 mi. S of Raices on rd. to Neavdo de Toluca, on *Pinus hartwegii, Denton 1700* in 1970 (ENCB); 0.5 km. S of San Salvador, on *Pinus montezumae, Peterson 73-99* in 1973 (FPF); Desierto de los Leones, 1 km. W of Pico de San Miguel, on *Pinus hartwegii, H 2110* in 1986 (FPF).

NAYRIT

Sierra Madre, near Santa Teresa, on *Pinus* sp., *Rose 3460* in 1897 (US).

NUEVO LEÓN

Cerro Linadero, on *Pinus* sp., *Meyer & Rogers 2932* in 1948 (MO); 15 mi. SW of Galeana, on *Pinus* sp., *Mueller & Mueller 1013* in 1934 (F, MEXU, MICH); Galeana, Hacienda Pablilio, on *Pinus* sp., *Taylor 182* in 1936 (ARIZ, F, MEXU, MICH, RSA); Pablilio, 15 mi. S of Galeana, on *Pinus arizonica, Griffiths* in 1966 (FPF); 10 mi. E of San Roberto on Rte. 60, on *Pinus arizonica, H & Player 1535* in 1975 (FPF). Cerro Potosí: on *Pinus* sp., *Hinton & others 17023* in 1969 (ENCB) on *Pinus rudis, Andresen & Steinhoff A2050* in 1963 (FPF); 2 mi. from village "18 de Marzo" on rd. to relay tower, on *Pinus arizonica, H & W 393* in 1963 (COLO, FPF) and *Nickrent 1980* in 1984 (FPF, ILL); near relay tower, on *Pinus rudis, H & W 397* in 1963 (COLO, FPF), and on *Pinus culminicola, H & W 398* in 1963 (COLO, FPF), *Peterson 72-35* in 1972 (FPF), and *Bailey* in 1976 (FPF); 15 mi. from village "18 de Marzo" on rd. to relay tower, on *Pinus rudis, H & others 1693* in 1975 (FPF).

OAXACA

Sierra Juárez, Cerro Corral de Piedra, 12-14 km. W of La Cumbre, on *Pinus* sp., *Luteyn & Lebran-Luteyn 11660* in 1985 (MEXU). Mpio. Ixtlán: 20.9 mi. N of Ixtlán Jct. on Rte. 175, on *Pinus patula, Peterson 74-117*, in 1974 (FPF); near La Puerta, 64 mi. N of Oaxaca on Rte. 175, on *Pinus* sp., *Peterson 72-103* and *72-104* in 1972 (FPF); 12.8 mi. N of Ixtlán and 5.5 mi. into timber rd., on *Pinus rudis, Peterson 74-90* in 1974 (FPF) and on *Pinus patula, Peterson 74-87* in 1974 (FPF); 20 mi. N of Ixtlán on Rte. 175, on *Pinus teocote, H & others 1551* in 1975 (FPF).

PUEBLA

1.7 mi. E of Paso de Cortez, on *Pinus hartwegii, H & W 374* in 1963 (COLO, FPF); 4 km. E of Paso de Cortez, on *Pinus hartwegii, H & W 1229* in 1969 (FPF); Mpio. Guadalupe Victoria, rd. between Guadalupe Victoria and Tlalnalpa, on *Pinus hartwegii, Marquez & others 34* in 1982 (FPF, IBUG).

QUERÉTARO

Mpio. Cadereyta, 8 km. W of El Doctor, on *Pinus rudis, Rzedowski 43081* in 1987 (IEB).

SINALOA

Mpio. Badiraguato, Sierra Surutato, 3 mi. SE of Los Ornos, on *Pinus herrerai, Breedlove & Thorne 18535* in 1970 (CAS).

TAMAULIPAS

Rte. to Pena Nevada out of Hermosa, on *Pinus* sp., *Standord & others 495* in 1949 (CAS, UC, WTU); Cerro el Borrado, 20 km. NE of Miquihuana, on *Pinus* sp., *Gonzales 3853* in 1969 (ENCB).

VERACRUZ

Cofre de Perote: 6 mi. SE of Perote, on *Pinus montezumae, H & W 378* in 1963 (COLO, FPF), 5 mi. SE of Perote, on *Pinus montezumae, H & W 380* in 1963 (COLO, FPF), and 8 mi. SE of Perote, on *Pinus hartwegii, Cibrián & others 7* in 1979 (MEXU); Near Lagunas de San Bernardino, on *Pinus* sp., *Smith & Tejeda 4468*, date ? (INIF).

ZACATECAS

Sierra Madre, on *Pinus* sp., *Rose 3535* in 1897 (US).

32b. Arceuthobium vaginatum subsp. *cryptopodum*

All collections on *Pinus ponderosa* var. *scopulorum*, except as noted.

MEXICO

CHIHUAHUA

5 mi. S of Garcia on El Largo rd., on *Pinus arizonica*, *H & W 461* in 1963 (COLO, FPF); 17 mi. N of El Largo on Garcia rd., on *Pinus cooperi*, *H & W 462* in 1963 (COLO, FPF); 9 mi. N of El Largo on Garcia rd., on *Pinus engelmannii*, *H & W 464* in 1963 (COLO, FPF); 16 mi. W of Mesa Huracán on Ranch Rio Negra rd, on *Pinus cooperi*, *H & W 465* in 1963 (COLO, FPF); 7 mi. SE of Mesa Huracán on Chico rd., on *Pinus engelmannii*, *H & W 471* in 1963 (COLO, FPF); 13 mi. SE of Mesa Huracán on Chico rd., on *Pinus cooperi*, *H & W 476* in 1963 (COLO, FPF); 5 mi. W of Las Varas on Mesa Huracán rd., on *Pinus engelmannii*, *H & W 479* in 1963 (COLO, FPF); 18 mi. S of Las Varas on Madera rd., on *Pinus engelmannii*, *H & W 480* in 1963 (COLO, FPF); 45 mi. SW of Matachic on Ocampo rd., on *Pinus arizonica*, *H & W 485* in 1963 (COLO, FPF); 66 mi. SW of Matachic on Ocampo rd., on *Pinus arizonica*, *H & W 492* in 1963 (COLO, FPF); 14 km. N of Yahuirichi, 54 km. N of Rte. 16, on *Pinus arizonica*, *H 2184* in 1987 (FPF); 25 km. by air NNW of Mesa Huracán, on Nuevo Casas Grandes rd., on *Pinus arizonica*, *Bailey* in 1985 (FPF); 4 mi. NW of Las Varas on El Largo rd., on *Pinus engelmannii*, *H & Cibrián 1950* in 1981 (FPF); Candelaria Peak, 3 km. W of lookout, S of Chuhuichupa, on *Pinus cooperi*, *H & Cibrián 1958* in 1981 (FPF); 23 km. S of Chuhuichupa on rd. to Candelaria Peak, on *Pinus durangensis*, *H & Cibrián 1953* in 1981 (FPF); 6 mi. W of San Juanito, on *Pinus cooperi*, *H & Cibrián 1981* in 1981 (FPF); near Madera, on *Pinus cooperi*, *Peterson 68-14* in 1968 (FPF).

COAHUILA

Sierra del Carmen: 1 mi. W of Ocampo, on *Pinus arizonica*, *H & others 1023* in 1967 (FPF) and, on *Pinus arizonica* var. *stormiae*, *H & others 1024* in 1967 (FPF); 6 mi. W of Ocampo, on *Pinus arizonica*, *H & others 1026* in 1967 (FPF). Sierra del Pino, on *Pinus arizonica*, *Johnston & Mueller 591* in 1940 (GH) and on *Pinus arizonica* var. *stormiae*, *Bailey 83-04* in 1983 (FPF). Sierra de la Madera, Deciderio Cyn., on *Pinus arizonica*, *H & others 1511* in 1975 (FPF). Sierranias del Burro, El Bonito, on *Pinus arizonica*, *Riskind & others 1928* in 1976 (FPF,TEX).

SONORA

2.7 mi. N of La Mesa, on *Pinus engelmannii*, *Tucker 2563* in 1952 (ARIZ, UC); Canada Cabeza de Vaca, 15 air km. SE of Yecora, on *Pinus engelmannii*, *H 2175* in 1987 (FPF); Mesa la Plata, 6 km. SE of Yecora, on *Pinus engelmannii*, *H 2167* in 1987 (FPF); SW slopes of Sierra de Ajo, on *Pinus engelmannii*, *Mathiasen 7802* in 1978 (FPF).

UNITED STATES

ARIZONA

APACHE CO.: 6 mi. W of Window Rock, *H & Lightle 188* in 1962 (FPF); 4 mi. S of Eagar, *H & Lightle 211* in 1962 (FPF); 2 mi. E of Big Lake, *H 821* in 1965 (FPF); Lukachuikai Mts., *Goodman & Payson 2927* in 1936 (WTU); Fort Apache Indian Res., 5 mi. NW of Maverick, *H & Lightle 901* in 1966 (FPF); Fort Apache Indian Res., 14 mi. W of Maverick on Fort Apache rd., *H & Lightle 903* in 1966 (FPF); 8 mi. E of McNary on Rte. 73, *H & Lightle 923* in 1966 (FPF); 6 mi. S of Alpine on Rte. 666, 0.4 mi. NE of Greenlee-Apache Co. line, *Mathiasen 8118* in 1981 (FPF); Fort Apache Indian Res., 4 mi. W of Maverick, *H 2193* in 1987 (FPF); Ft. Apache Indian Res., 7 mi. W of Maverick, *H 2192* in 1987 (FPF); Navajo Indian Res: 6 mi. NW of Sawmill, *Lightle & Weiss 66-44* in 1966 (FPF); 6 mi. E of Lukachuikai on Red Rock rd., *Lightle & Weiss 66-49* in 1966 (FPF); 11 mi. SW of Red Rock on Lukachukai rd., *Lightle & Weiss 66-51* in 1966 (FPF); Lukachuki-Chuska Mts., headwaters of Aspen Spring Valley, *Mason & others 2657* in 1967 (ARIZ). COCHISE CO.: Chiricahua Mts., *Burrall 55* in 1908 (FPF) and *Raue 50* in 1956 (ARIZ); Rustler Park, *Gill FP 68047* in 1935 (FPF); 1 mi. S of Rustler Park, *H 808* in 1965 (FPF); Onion Saddle, on *Pinus arizonica*, *H & Lightle 154* in 1962 (FPF) and on *Picea engelmannii*, *H & Lightle 155* in 1962 (FPF); Barfoot Peak on *Pinus arizonica*, *Blumer 1452* in 1906 (ARIZ, FPF, ILL, RM, US); Rustler, on *Pinus arizonica*, *Ferris 9953* in 1940 (DS, RM, RSA, UC, WTU); Gulching rd., on *Picea engelmannii*, *Blumer 1557* in 1907 (ARIZ, FPF, ILL, RM, US, K); 10 mi. W of Portal, on *Picea engelmannii*, *Gill FP 68038* in 1936 (FPF); Huachuca Mts.: Carr Cyn., *Gill & others FP 89498* in 1939 (FPF) and *Goodding FP 33285* in 1919 (FPF); head of Carr Cyn., on *Pinus arizonica*, *Gill & others FP 89499* in 1939 (FPF); Miller Cyn., *Goodding* in 1909 (ARIZ); head of Ramsey Cyn., *Doherty FP 15240* in 1914 (FPF, ILL); 1.5 mi. W of Reef, on *Pinus arizonica*, *H & Lightle 233* in 1962 (FPF). COCONINO CO.: Jacob Lake, *Reed & Barkley 4381* in 1939 (POM); Flagstaff, *MacDougal 23* in 1898 (ARIZ, RM, UC); 15 mi. S of Williams, *Gill FP 68252* in 1932 (FPF); Williams, *Hedgcock & Bethel FP 24413* in 1917 (FPF); 2.5 mi. E of Fort Valley Exp. For., *Gill FP 68249* in 1932 (FPF); Fort Valley Exp. For., *Long FP 19724* in 1915 (FPF); Grand Cyn., S Rim, Grandview Point, *H & Lightle 185* in 1962 (FPF); 3 mi. N of Weimer Springs, W of Mormon Lake, *H & Lightle 912* in 1966 (FPF); 13 mi. NE of Clints Well on Rte. 65, *H & Lightle 914* in 1966 (FPF); 3 mi. S of Chevlon Ranger Sta., 43 mi. S of Winslow, *H & Lightle 917* in 1966 (FPF); Jacob Lake, *Gill FP 68296* in 1934 (FPF); Dry Park, NW of Kaibab Lodge, *Peterson 64-72* in 1964 (FPF); Kaibab Plateau, *Richards* in 1938 (UC); 4 mi. E of Grandview, Grand Cyn., *Newlon 856* in 1922 (JEPS); Museum of Northern Arizona, N of Flagstaff, *Heiser 848* in 1944 (WTU); Grand Cyn., *Toumey 8* in 1893 (UC); 5 mi. E of Woods Cyn. Lake, *Mason & others 2422* and *2422a* in 1964 (ARIZ); Oak Cr., *Goodding 17* in 1916 (ARIZ); Observatory Hill, Flagstaff, *Thornber* in 1930 (ARIZ); Hualapai Indian Res., ca. 5 mi. NW of Frazier's Well, *Truesdell* in 1965 (FPF); Coconino Rim rd., 1 mi. SE of Sitgreaves Nat. For. boundary, *Lightle 64-15* in 1964 (FPF) and 0.5 mi. N of jct. with Payson-Heber rd., *Lightle 64-17* in 1964 (FPF); 16 mi. S of Happy Jack, *Lightle 64-13* in 1964 (FPF); 14 mi. S of Williams on Perkinsville rd., *H & Lightle 1401* in 1972 (FPF); 5 mi. W of Rte. 87 on Camp Verde rd., *H & Lightle 1403* in 1972 (FPF); Kendrick Peak, at trailhead to lookout, *H &*

Mathiasen 1467 in 1973 (FPF); 2.5 mi. W of Williams on I-40, *H 1637* in 1975 (FPF); S of Williams at base of Bill Williams Mtn., *Gill FP 68133* in 1932 (FPF). GILA CO.: 21 mi. E of Payson, 3 mi. E of Indian Gardens, *Lightle 63-54* in 1963 (FPF); 2 mi. W of Pine, *W 2705* in 1960 (RSA); 17 mi. NE of Young, *Lightle & Lampi 65-16* in 1965 (FPF); Sierra Ancha: Aztec Peak, *Johnson* n.d. (ARIZ), *Pinkava & Lehto 5620* in 1965 (ASU), and *Mishler 1001* in 1965 (ASU); Sierra Ancha Summit, between Roosevelt and Pleasant Valley, *Harrison & others 5979* in 1929 (ARIZ, US); Baker Mtn., *Harrison 7868* in 1931 (ARIZ); Sierra Ancha, *Peebles & Smith 13264* in 1937 (ARIZ, US); Sierra Ancha, Workman Cr., *Lightle & Lampi 65-14* in 1965 (FPF); 4 Peaks, *Mullen 114* in 1968 (Davidson College). Pinal Mts.: Ice House Cyn., *Kirby & Long FP 18735* in 1914 (FPF) and *Kirby FP 12673* in 1914 (FPF); Bob Tail Ridge, *Gill FP 68295* in 1934 (FPF); 5 mi. above Sulphide del Rey, *Gill & Lightle 63-51* in 1963 (FPF). GRAHAM CO.: Graham Mts.: Pine Crest, *Maguire 12138* in 1935 (RM); 1 mi. above Arcadia Guard Sta., *H & Lightle 140b* in 1962 (FPF) and on *Pinus arizonica*, *H & Lightle 140a* in 1962 (FPF); 0.5 mi. above Arcadia Guard Sta., on *Pinus arizonica*, *H & Lightle 141* in 1962 (FPF); Tripp Cyn., 5 mi. S of Nat. For. boundary, *H & Lightle 146* in 1962 (FPF); Hospital Flat, *H & Lightle 227* in 1962 (FPF) and *Gill FP 68309* in 1934 (FPF); Columbine, *Shreve 5239* in 1917 (DS); Swift Trail, *Peebles 12981* in 1936 (ARIZ, US); Graham Mts., Riggs Flat Lake, *Van Devender & Van Devender 86-165* in 1986 (FPF); San Carlos Indian Res., Malay Gap, *H & Lightle 1115* in 1968 (FPF); San Carlos Indian Res., Anderson Flat Heliport, *H 2196* in 1987 (FPF); Galiuro Mts., Deer Cr. Cyn., *Mathiasen 7704* in 1977 (FPF), and on *Pinus arizonica*, *Mathiasen* in 1979 (FPF). GREENLEE CO.: 3 mi. N of Nat. For. boundary on US 666, 17 mi. N of Clifton, *H & Lightle 136* in 1962 (FPF); 47 mi. S of Springerville on US 666, *Gill FP 68304* in 1934 (FPF); 10 mi. S of Mogollon Rim on US 666, *Lightle 64-22* in 1964 (FPF). MARICOPA CO.: Mazatzal Mts., near 4 Peaks, *Krebill & Krebill* in 1981 (FPF) and *Krebill* in 1982 (FPF). MOHAVE CO.: Hualapai Mtn. Park, *Gill & Andrews* in 1959 (FPF), *W 3029* in 1962 (COLO), and *H 715* in 1965 (FPF); Hualapai Mtn., *Kearney & Peebles 12724* in 1935 (ARIZ, US) and *Gilbertson* in 1973 (FPF); Hualapai Mts., near summit of Waybayuma Peak, *Butterwick & Parfitt 5171* in 1979 (ASU); Hualapai Mtn. Park, NE side of Aspen Peak, *Parfitt 2595* in 1978 (ASU); Mt. Trumbull area, 2 air mi. E of Mt. Logan, *Davis* in 1986 (FPF); Virgin Mts., 2/3 mi. ENE of Mt. Bangs, *H & others 2137* in 1986 (FPF). NAVAJO CO.: 1 mi. W of Show Low on Rte. 60, *Lightle 63-45* in 1963 (FPF); 4 mi. E of Rte. 160 on Mogollon Rim rd., *H & Lightle 919* in 1966 (FPF); near Deer Springs, 26 mi. E of Rte. 160 on Mogollon Rim rd., *H & Lightle 921* in 1966 (FPF). PIMA CO.: Santa Catalina Mts.: *Loran* in 1881 (UC) and *Thornber* in 1930 (ARIZ); Soldier Camp, *Gill FP68129* and *FP68251* in 1932 (FPF), and on *Pinus arizonica*, *Hedgcock & Long FP 9759* in 1911 (FPF); Summerhaven, *Loomis & others 2179* in 1926 (ARIZ) and *H & Lightle 168* in 1962 (FPF); Mt. Lemmon, *Nichol* in 1925 (ARIZ); Palisade Ranger Sta., *H & Lightle 172* in 1962 (FPF) and on *Pinus arizonica*, *H & Lightle 171* in 1962 (FPF); Mt. Lemmon Ski Lodge, *H & Lightle 169* in 1962 (FPF); Summit of Marshall Cyn., *Gill FP 68131* in 1932 (FPF); 1 mi. S of Rose Lake Jct., on *Pinus arizonica*, *H & Lightle 165* in 1962 (FPF); Sabino Cyn., on *Pinus arizonica*, *Hedgcock & Long FP 9781* in 1911 (FPF, ILL). Rincon Mts., Mt. Oeboa, on *Pinus arizonica*, *Blumer 3563* in 1909 (ARIZ, DS, FPF, ILL); Mica Mtn., on *Pinus arizonica*, *Ela* in 1968 (FPF). SANTA CRUZ CO.: Santa Rita Mts., Mt. Wrightson trail, 4 mi. from end of rd., *H 795* in 1965 (FPF); 1.5 mi. from end of rd., on *Pinus arizonica*, *H 797* in 1965 (FPF); Santa Rita Mts., Baldy Saddle, on *Pinus arizonica*, *Mathiasen 74-30* in 1974 (FPF). YAVAPAI CO.: Groom Cr., *H & Lightle 177* in 1962 (FPF) and *Taylor FP 18641* in 1914 (FPF); Mingus Mtn., ca. 2 mi. S of US 89A, *H & Lightle 243* in 1962 (FPF); top of Mingus Mtn., *Wetherill* in 1959 (MNA); Beaver Cr. Ranger Sta., *Drake FP 15119* in 1914 (FPF); Crown King, *Ancona & Long 12829* in 1914 (FPF); Horsethief Basin, 7 mi. S of Crown King, *H & Laut 1180* in 1969 (FPF); Prescott, *Hedgcock FP 4856* in 1910 (FPF, ILL); near Prescott, *Hedgcock FP 4854* and *FP 4855* in 1910 (FPF); Copper Basin, *Toumey 292* in 1892 (ARIZ); Santa Maria Mts., 5 air mi. WNW of Camp Wood, *H & Laut 1179* in 1969 (FPF); Juniper Mts., *Weiss & Lucero* in 1973 (FPF); Lane Mts., Ft. Jackson Mine Area, *Blakely 284* in 1951 (ASU).

COLORADO

ARCHULETA CO.: Pagosa Springs, *Bethel* in 1897 (CS) and *Smith* in 1894 (PH); 20 mi. S of Pagosa Springs on US 84, *H & Lightle 1051* in 1967 (FPF); S of Pagosa Springs, *Hedgcock & Bethel FP 24656* in 1917 (FPF); 10 mi. W of Pagosa Springs, *Hinds 5-63* in 1963 (FPF). BOULDER CO.: Sugarloaf Mtn., *Ramaley & Robbins 1784* in 1906 (COLO, RM) and *H & Stevens 1289* in 1970 (FPF); between Sunset and Ward, *Tweedy 4973* in 1902 (RM); Mt. Alto, *Ramaley 824* in 1901 (COLO, RM); S Boulder Peak, *Ewan 12721* in 1941 (COLO); Tucker's Meadow, *Wolcott* n.d. (COLO); Lyons, *Thomson FP 26558* in 1917 (FPF); SW of Boulder, *Hedgcock FP 22571* in 1916 (FPF, UC); 1 mi. E of Rte. 160 on Left Hand Cyn. rd., *H 203* in 1962 (FPF) and on *Pinus contorta* var. *latifolia*, *H 204* in 1962 (FPF); Boulder, *Hedgcock & others FP 24755* in 1917 (FPF); near Boulder, *W 2802* in 1961 (COLO); between Nederland and Rollinsville, *Jones 23161* in 1962 (ILL); 5 mi. N of Nederland on Rte. 160, on *Pinus flexilis*, *H 202* in 1958 (FPF); Ridge S of Left Hand Cyn., 2 mi. SE of Ward, on *Pinus flexilis*, *Sprackling & Plumb* in 1966 (FPF); 1.1 mi. N of Nederland on Rte. 72, on *Pinus contorta* var. *latifolia*, *H & Linhart 2041* in 1983 (FPF), and on *Pinus flexilis*, *H & Linhart 2040* in 1983 (FPF); 2.1 mi. S of Science Lodge Jct. on Rte. 160, on *Pinus flexilis*, *H & others 1347* in 1971 (FPF); 2.2 mi. N of Boulder Cyn. on Salina rd., *H & others 1345* in 1971 (FPF); 1 mi. N of Nederland on Rte. 119, *H* in 1977 (FPF). CHAFFEE CO.: Mercury Cr., 4 mi. W of Buena Vista, *H & Laut 1312* in 1970 (FPF); Chalk Cr. Cyn., 3 mi. W of Mt. Princeton Hot Springs, *H & Laut 1314* in 1970 (FPF); 2 mi. S of Trout Cr. Pass on Rte. 285, *H & Laut 1412* in 1972 (FPF). CLEAR CREEK

CO.: Mill Cr., Brookvale, *Churchill* in 1918 (RM); 0.5 mi. S of divide between Idaho Springs and Central City, *H & Staley 280* in 1962 (FPF); Empire, *Weir 6163* in 1918 (ILL); Hamlin Gulch rd., 1.4 mi. from Fall River rd., 7 air mi. NW of Idaho Springs, *H 1056* in 1967 (FPF). CONEJOS CO.: River Springs Ranger Sta., ca. 15 mi. W of Antonito, *Hinds 63-3* in 1963 (FPF); 3.1 mi. W of Nat. For. boundary on Rte. 17, *Lightle 63-1* in 1963 (FPF); 4.4 mi. W of Terrace Reservoir, *Hinds 1* in 1963 (FPF). COSTILLA CO.: Costilla Estate at New Mexico boundary, *Edmonston FP 1511* in 1908 (FPF); Trinchera Estate, E side of San Luis Valley, *Edmonston FP 175* in 1908 (FPF); Culebra Cr., 10 mi. E of San Luis, *H & others 1501* in 1974 (FPF). CUSTER CO.: Greenwood, *Edmonston FP 561* in 1909 (FPF); Alvarado Campground, 9 mi. SW of Westcliffe, *H 433* in 1963 (FPF); 4.5 mi. W of Hillside, *H 435* in 1963 (FPF); 3.5 mi. SW of Hillside on Spruce Cr. rd., on *Pinus contorta* var. *latifolia*, *H 436* in 1963 (FPF); Westcliffe, Clay Ranger Sta., *Hedgcock & others FP 24828* in 1917 (FPF). DENVER CO.: Denver, transplanted trees at Case Golf Course, *H & Stewart 832* in 1965 (FPF). DOLORES CO.: Doe Springs rd., 12 mi. ESE of Dove Cr., *Hinds 11-63* in 1963 (FPF); Narraguinnep Cyn., 15 mi. ESE of Dove Cr., *H 1906* in 1979 (FPF). DOUGLAS CO.: 1.5 mi. E of Franktown on Rte. 86, *H 544* in 1963 (FPF); Missouri Ridge rd., Manitou Exp. For., *H 257* in 1962 (FPF); 4.0 mi. S of Rte. 64 on Rampart Range rd., *H 2257* in 1988 (FPF). ELBERT CO.: 5.5 mi. S of Elbert on Rte. 157, *H 420* in 1963 (FPF); 6 mi. W of Kiowa on Rte. 86, *H 543* in 1963 (FPF). EL PASO CO.: Cheyenne Cyn., *Christ 1864* in 1935 (CS); Colorado Springs, *Jones 801* in 1878 (ARIZ, RSA, RM); 14.5 mi. E of Monument, *H 419* in 1963 (FPF); 1.5 mi. E of Monument, *H 542* in 1963 (FPF); 1.7 mi. from Cascade on Pikes Peak rd., *H & Hinds 426* in 1963 (FPF); Bruin Inn, N Cheyenne Cyn., *H 539* in 1963 (FPF); Colorado Springs, *Saunders* in 1893 (RM); Pikes Peak, Halfway, *Hedgcock FP 903* in 1909 (FPF); Mt. Manitou, *Gill FP 68247* in 1932 (FPF); Palmer Park, Austin Bluff, *Gill FP 68248* in 1932 (FPF); NE of Manitou, *Hedgcock FP 22710* and *FP 22711* in 1916 (FPF); 5 mi. W of Monument, *W 2983* in 1962 (COLO, FPF); Monument, *Hedgcock FP 670* in 1909 (FPF), *Hartley FP 1613* in 1909 (FPF), *Hedgcock & Pierce FP 15951* in 1914 (FPF, ILL, RSA, UC, WTU), *Hedgcock FP 22550* in 1916 (FPF, UC), and *Hedgcock FP 24909* in 1917 (FPF); Fremont Exp. For., W of Manitou Springs, *Hedgcock FP 9174* and *FP 9175* in 1911 (FPF) and *FP 22704* and *FP 22705* in 1916 (FPF); Palmer Lake, *Hedgcock FP 15898* in 1914 (FPF, UC), *Hedgcock & others FP 24902* in 1917 (FPF), and *Gill FP 68244* in 1932 (FPF); Burgess Rd., 3 mi. ESE of Black Forest, *H 1642* in 1975 (FPF); 3 mi. N of Peyton, *H 1641* in 1975 (FPF): 2 mi. W of Manitou Springs, Fremont Exp. For., on *Pinus flexilis*, *H* in 1977 (FPF); U. S. Air Force Academy, Douglas Valley, on *Pinus sylvestris*, *H 1941* in 1981 (FPF). FREMONT CO.: "Canyon City," Sierra Majada, *Brandegee 11295* in 1877 (FPF, ILL); Stout Cr., 4 mi. S of Howard, *H & Laut 1315* in 1970 (FPF); Hayden Cr., 6 mi. SW of Coaldale, *H & Laut 1318* in 1970 (FPF); 11 mi. N of Rte. 50 on Phantom Cyn. rd., *H & Laut 1334* in 1971 (FPF). GILPIN CO.: Rollinsville, *Hedgcock FP 22599* in 1916 (FPF). HINSDALE CO.: Piedra River, ca. 15 air mi. NW of Pagosa Springs, *Peterson & Peterson 19-61* in 1961 (FPF). HUERFANO CO.: 10 mi. N of Gardner on Ophir Cr. rd., *H 431* in 1963 (FPF); La Veta, *Hedgcock & Thompson FP 24809* in 1917 (FPF). JEFFERSON CO.: Gunbarrel Cr., *Hill FP 68278* in 1932 (FPF); 10 mi. W of Deckers, *H 421* in 1963 (FPF); 8 mi. SW of Morrison on US 285, *H 453* in 1963 (FPF); Buffalo Cr., *Hill FP 68277* in 1932 (FPF); near Golden, *Weir 8958* in 1918 (ILL); Golden Gate Cyn. Park, 7 air mi. NW of Golden, *H & Laut 1444* in 1973 (FPF). LA PLATA CO.: Tacoma Power Plant, *Loughridge 273* in 1934 (CS); and on *Pinus flexilis*, *Loughridge 273* in 1934 (USFS, CS); W of Trimble, *Hedgcock & Bethel FP 24688* in 1917 (FPF, UC); 10 mi. W of Durango on US 160, *H & Scharpf 690* in 1964 (FPF). LARIMER CO.: Estes Park, *Cooper 243* in 1904 (ARIZ, RM); Prospect Mtn. near Estes Park, *Maize* in 1966 (FPF); "Ft. Collins," *Buffum 5690* in 1896 (RM); "mtns. of Larimer Co.," *Crandal* in 1889 (RM); 4 mi. SW of Log Cabin, *H 200* in 1960 (FPF); Rist Cyn. Picnic Ground, *H 201* in 1961 (FPF); near Cherokee Park, lat. 40°53' N, (northern limit?), *H 262* in 1962 (FPF); Poudre River 4 mi. E of Rustic, *H 410* in 1963 (FPF); Stove Prairie Hill, col.? *Plants of Colorado 2274* in 1896 (RM); Skyland Ranch, Rocky Mtn. Nat. Park, *Nelson 3205* in 1938 (RM); Rist Cyn., *Cameron, Plants of Colorado 2279* in 1897 (CS); Stove Prairie, col.? *Plants of Colorado 2277* in 1898 (FPF); 1 mi. SW of Glen Haven, *H & Staley 287* in 1962 (FPF); Association Camp, Rocky Mtn. Nat. Park, *Case FP 38702* in 1922 (FPF); Rattlesnake (Pinewood) Park, *H 87* in 1961 (FPF); Poudre River, Ft. Collins Mtn. Park, *H 1343* in 1971 (FPF); Rist Cyn., 7.2 mi. W of La Porte, *H 552* in 1964 (FPF); Rist Cyn., near Picnic Ground, on *Pinus contorta* subsp. *latifolia*, *H 199* in 1961 (FPF); Stove Prairie Hill, *Pennock*, on *Pinus contorta* var. *latifolia*, *Plants of Colorado. 899* in 1892 (CS); 1 mi. E of Pennock Pass, on *Pinus contorta* var. *latifolia*, *H & others 281* in 1962 (FPF) and *H 560* in 1964 (FPF); N of Stratton Park, 13 mi. WNW of Fort Collins, on *Pinus contorta* var. *latifolia*, *H 709* in 1962 (FPF); Bear Gulch, 5 mi. W of Masonville, on *Pinus contorta* var. *latifolia*, *H 710* in 1964 (FPF); 2 mi. W of entrance to Ben Delatour Scout Ranch, *H 1342* in 1971 (FPF); 2 mi. N of Horsetooth Mtn., *Staley* in 1968 (FPF); Rist Cyn., 15 mi. W of Bellvue, *H 1054* in 1967 (FPF); W of Arthur's Rock, *Laut* in 1972 (FPF). LAS ANIMAS CO.: Mesa de Maya, Green Cyn., *Rogers 6089* in 1948 (COLO, US); Stonewall Gap, *Hedgcock & Johnston FP24944* in 1917 (FPF); Monument Park, *H 1096* in 1968 (FPF); 5 mi. ENE of Apishipa Pass, on *Pinus aristata*, *Morey 78-267* in 1978 (FPF); head of Parras Cyn. N of Vigil, *Morey* in 1973 (FPF). MESA CO.: Sawmill Mesa rd., 20 mi. SW of Delta, *Hinds 19-63* in 1963 (FPF); 15 mi. SE of Rte. 141 on Divide Forks rd., *H & Mathiasen 1476* in 1973 (FPF). MONTEZUMA CO.: Water Cyn., ca. 10 mi. N of Mancos, *Hinds 8-63* in 1963 (FPF). MONTROSE CO.: 10 mi. W of Paradox, *Harrington 4392* in 1949 (CS); Hanks Valley rd., ca. 10 mi. NE of Norwood, *Hinds 16-63* in 1963 (FPF); 11 mi. NE of Nucla, *H*

& Mathiasen 1475 in 1973 (FPF). PARK CO.: 1.5 mi. NW of Bailey, *H 282* in 1962 (FPF); 1.7 mi. S of 11 Mi. Reservoir rd. on Blue Mtn. rd., near Lake George, *H 424* in 1963 (FPF); Nunatack rd., 4 mi. E of Tarryall rd., *H 1410* in 1972 (FPF); 3 mi. S of Guffey on Rte. 9, *H 1455* in 1973 (FPF); South Park, 3.5 mi. N of Hartsel on Rte. 15, *H 1864* in 1978 (FPF); South Park, about 7 mi. N of Hartsel, on *Pinus aristata*, *Sherman & Dzuba* in 1984 (FPF). PUEBLO CO.: 5 mi. W of Rye on Rte. 165, *H 427* in 1963 (FPF); 3 mi. E of Lake Isabel, *Lemon 25* in 1938 (USFS). SAGUACHE CO.: Spanish Cr., near N Cochetopa Pass, *H 438* in 1963 (FPF) and *Eggleston 570* in 1910 (USFS); E of N Cochetopa Pass, on *Pinus contorta* var. *latifolia*, *H 437* in 1963 (FPF) and on *Pinus aristata*, *H 439* in 1963 (FPF). SAN MIGUEL CO.: Iron Springs Mesa, 7 mi. NW of Placerville, *Payson FP26022* in 1917 (FPF). TELLER CO.: Florissant, *Ramaley 1333* in 1905 (RM); 6.2 mi. S of Divide on Rte. 67, *H & Hinds 423* in 1963 (FPF) and on *Pinus aristata*, *H & Hinds 422* in 1963 (FPF); Elkton, 2 mi. SE of Cripple Cr., *Hedgcock & Johnston FP26406* in 1917 (FPF); Woodland Park, *Gill FP 68138* and *FP 68246* in 1932 (FPF) and *Guthrie 53-G* in 1916 (USFS); 2.3 mi. NW of Cripple Cr. on Florissant rd., *H 1457* in 1973 (FPF); Aspen Valley, on *Pinus flexilis*, *Colorado State For. Service* in 1978 (FPF); Florissant Nat. Mon., 1 mi. NW of Headquarters, on *Pinus contorta*, *H & Bennetts 2332* in 1989 (FPF). COUNTY UNCERTAIN: Uncompahgre Divide, *Payson 396* in 1914 (COLO, RM); Rocky Ford, *Pool FP 20552* in 1912 (FPF).

NEW MEXICO

BERNALILLO CO.: Manzano Mts., 12 mi. S of US 66 on Rte. 10, *H 21* in 1954 (FPF); Sandia Mts., Doc Long Campground, *Gill & Long FP 68250* and *FP 68258* in 1932 (FPF) and *Muenscher & Muenscher 14562* in 1939 (MO, UC, WTU). CATRON CO.: Datil Mts., White House Cyn., 10.5 mi. NW of Datil on US 60, *H & Lightle 1116* in 1968 (FPF); 11 mi. N of Datil, *Fletcher 263* in 1976 (UNM); 10 mi. NNE of Datil, *Fletcher 1595* in 1976 (UNM); 1 mi. E of Mogollon, *H & Lightle 132* in 1962 (FPF); 7 mi. E of Mogollon, *H & Lightle 221* in 1962 (FPF); Mogollon Cr., *Woodrow & Long FP 18399* in 1914 (FPF); Mangas Mtn., *H & Scharpf 698* in 1964 (FPF); Tularosa Summit, 11.5 mi. N of Rte. 78 on Apache Springs rd., *Lightle 65-42* in 1965 (FPF); 5 mi. E of Beaverhead Ranger Sta. on Rte. 59, *H & Lightle 893* in 1966 (FPF); Cyn. Cr. Mts., 12 air mi. W of Beaverhead Ranger Sta., *H & Lightle 895* in 1966 (FPF); 1.5 mi. E of Rte. 78 on Loco Mtn. rd., *H & Lightle 896* in 1966 (FPF); 1 mi. E of Fox Mtn., 20 mi. N of Apache Cr., *H & Lightle 930* in 1966 (FPF). CIBOLA CO.: Ojo Redondo, *Lightle 63-38* in 1963 (FPF); S of San Mateo, Mt. Taylor, *Lightle 63-32* in 1963 (FPF); 14 mi. E of Grants on rd. to La Mosca Lookout, *Lightle 65-51* in 1965 (FPF); Zuni Mts., Redondo Campground, 12 mi. W of Grants, *Mathiasen 7627* in 1976 (FPF); Mt. Taylor, *Mathiasen 7613* in 1976 (FPF). COLFAX CO.: 1 mi. E of Taos Co. line on US 64, *Lightle 65-22* in 1965 (FPF); Tercio-Vermijo Park rd., 17 mi. S of Stonewall Gap at Colorado state line, *H & Laut 1330* in 1971 (FPF); Philmont Scout Ranch, Devils Wash Basin, *Hartman* in 1970 (RM). Valle Vidal, 1 km. NW of Shuree Lodge, on *Pinus aristata*, *H 2255* in 1988 (FPF), *Mathiasen 8311* in 1983 (FPF), and *Mathiasen 8401* in 1984 (FPF). DONA ANA CO.: Organ Mts., Fillmore Cyn., *Wooton* in 1903 (FPF). EDDY CO.: Guadalupe Mts.: *Johnson FP 18638* in 1914 (FPF); Dark Cyn., *H & Lightle 113* in 1962 (FPF) and *Higgins 7338* in 1973 (NMC); 11 mi. S of Rte. 137 on For. Service rd. 540, *H & Nicholls 2024* in 1982 (FPF). GRANT CO.: W side Emory Pass, *H & Lightle 119* in 1962 (FPF); 1 mi. NW of Redstone, *H & Lightle 126* in 1962 (FPF); Silver City, *Gaetz FP 182* in 1908 (FPF); N of Pinos Altos, *Hedgcock FP 813* in 1909 (FPF); 20 mi. N of Mimbres on Rte. 61, *Lightle 65-37* in 1965 (FPF); Burro Mts., near summit of Jack's Peak, *H & Lightle 1103* in 1968 (FPF); 7.5 mi. S of Gila Hot Springs on Rte. 15, *H & Bailey 1769* in 1977 (FPF); Redstone Cr., on *Pinus arizonica*, *Gill FP 68308* in 1934 (FPF); Snow cabin rd., 4 mi. W of Rte. 25, on *Pinus arizonica*, *H & Lightle 890* in 1966 (FPF). LINCOLN CO.: Ruidoso, *Fisher & Steyermark 38183* in 1938 (RM); Gallinas Peak, 10 mi. W of Corona, *Lightle & Riffle 63-42* in 1963 (FPF); White Mts., Valley of Carrizo, *Wickens 2403* in 1932 (PH); Jicarilla Mts., 7 mi. SE of Ancho on White Oaks rd., *Lightle 64-31* in 1964 (FPF); Tucson Mtn., NW of Capitan, *Lightle 64-32* in 1964 (FPF). Capitan Mts.: W Capitan Peak, *Lightle 66-21* in 1966 (FPF); ca. 12 mi. NE of Capitan, *Parks & Long FP 18383* in 1914 (FPF) and *Parks FP 18385* in 1914 (FPF); E slope of Capitan Peak at Pine Lodge, *Martin 883* in 1945 (WTU); Capitan Gap, *H & Lightle 104* and *108* in 1962 (FPF); S side of Capitan Mts., 15 mi. E of Lincoln, *H & Scharpf 695* in 1964 (FPF). LOS ALAMOS CO.: Bandelier Nat. Mon., *Lightle 65-55* in 1965 (FPF). MCKINLEY CO.: 2 mi. W of McGaffey, *Lightle 63-37* in 1963 (FPF). MORA CO.: 17 mi. N of Mora on Rte. 38, *Lightle 65-53* in 1965 (FPF). OTERO CO.: Avis, *Wyman FP 12815* in 1914 (FPF); Sierra Blanca Peak, *Wolf 2880* in 1928 (DS, RSA); Sacramento Mts., James Cyn., *Wickens 2199* in 1932 (PH); Cloudcroft, *H & W 454* in 1963 (FPF); above Ruidoso, *Hinckley* in 1963 (ARIZ); Sacramento Mts. , 2 mi. S of High Rolls, *Worthington 6095* in 1980 (FPF); 13 mi. SE of Cloudcroft on Rte. 24, *H & Lightle 879* in 1966 (FPF), Tall Pines Camp, 2 mi. NW of Weed, *H & Lightle 884* in 1966 (FPF); Upper Penasco Cyn., 13 mi. S of Cloudcroft, *H & Lightle 885* in 1966 (FPF); 0.5 mi. N of Timberon, *H 2405* in 1990 (FPF). Mescalero Apache Res.: Carrizo, *H & Lightle 103* in 1962 (FPF), Cow Camp Unit, *H* in 1952 (FPF), Paul's Cyn., *H 24* in 1954 (FPF), Goat Cyn., *H FP 98511* in 1952 (FPF); and Whitetail area, on *Pinus strobiformis*, *Lightle 64-2* in 1964 (FPF). RIO ARRIBA CO.: Chama, *Hedgcock & Bethel FP29454* in 1917 (FPF); 12 mi. NW of jct. of Lagunitas rd. and Rte. 285, *Lightle 63-13a* in 1963 (FPF); 24 mi. E of Canjilon, *Lightle 63-9* in 1963 (FPF); 2 mi. S of Tierra Amarilla, *Lightle 63-4* in 1963 (FPF); 3 mi. SW of Tres Piedras, *Lightle 63-25* in 1963 (FPF); 2.3 mi. N of Gallina, *Lightle 63-21* in 1963 (FPF); 2 mi. W of Tres Piedras, *W 2986* in 1962 (COLO, FPF); 1 mi. N of S Jicarilla Res. boundary on Rte. 95, *Lightle 64-7* in 1964

(FPF); 18 mi. E of co. boundary and 12 mi. S of Rte. 17, *Lightle 64-8* in 1964 (FPF); 9 mi. S of Dulce on Rte. 17, *H 1392* in 1971 (FPF). SANDOVAL CO.: E slope of Redondo Peak, *Osborn 1363* in 1963 (UNM); Horn Mesa, *Robertson 368* in 1964 (UNM). SAN JUAN CO.: Chuska Mts., 6 mi. SW of Sheep Springs, *Lightle & Weiss 66-42* in 1966 (FPF). SAN MIGUEL CO.: Windsor's Ranch, Pecos Nat. For., *Standley 4173* in 1908 (FPF); Glorieta Mesa, 3.5 mi. S of Rowe, *H 1097* in 1968 (FPF); 16 mi. N of Las Vegas on Rte. 3, 2 mi. S of Mora Co. line, *H 2068* in 1984 (FPF). SANTA FE CO.: Sante Fe, *Hedgcock & Bethel FP24712* in 1917 (FPF, ILL, UC); Borrega area E of Espanola, *Lightle 63-27* in 1963 (FPF); Canoncito, *Brandegee* in 1879 (UC); 4 mi. E of Santa Fe, *Heller 3608* in 1897 (ARIZ, Z); near Santa Fe, *W 2988* in 1962 (COLO). SIERRA CO.: Kingston, *Metcalfe 964* in 1904 (FPF, RSA, UC); near Boiler Peak on Rte. 59, 15 mi. E of Beaverhead Ranger Sta., *H & Lightle 894* in 1966 (FPF); E side of Emory Pass, *Zimmermann & Zimmermann 1405* in 1976 (ARIZ); San Andreas Mts., 0.7 mi. N of Salinas Pk., *Lynch & others* in 1991 (FPF). SOCORRO CO.: San Mateo Mts.: N side of San Juan Peak, *Lightle 65-32* in 1965 (FPF) and 11.5 mi. S of US 60 on Rte. 52, *Lightle 65-35* in 1965 (FPF); Ladron Peak, head of Canon del Norte, *Mantley 676* in 1975 (UNM). Magdalena Mts., 6 mi. above Water Cyn. Campground, *H 1688* in 1975 (FPF); Mouth of Hop Cyn., *Diehl 878* in 1903 (RSA). TAOS CO.: 4 mi. E of Questa on Rte. 38, *Lightle 65-47* in 1965 (FPF); 10 mi. S of Rancho de Taos on Rte. 3, *H 877* in 1966 (FPF); Bear Cyn. Camp near Red River, *Daggy 7354* in 1974 (Davidson College). TORRANCE CO.: 5 mi. N of Tajique, *Lightle & Riffle 63-56* in 1963 (FPF). COUNTY UNCERTAIN: Front Cr. Basin, Gila Nat. For., *Hedgcock & Long FP 9835* in 1911 (FPF); Gila Nat. For., *Munro FP 15114* in 1914 (FPF).

TEXAS

CULBERSON CO.: Guadalupe Mts.: *Johnston 3185* in 1958 (SRSC); ridge above McKittrick Cyn., *Moore & Steyemark 3470* in 1931 (DS, PH, UC, US); The Bowl, *Warnock & McVaugh 5452* in 1947 (SRSC) and *H & Bailey 1527* in 1975 (FPF); above Frijole, *McVaugh 8156* in 1947 (DS, SRSC). JEFF DAVIS CO.: Davis Mts.: Upper Madera Cyn., *Palmer 33429* in 1928 (PH); Mt. Livermore, *Hinckley* in 1937 (ARIZ, SRSC), *Hinckley 2650* in 1943 (SRSC) and *Warnock* in 1936 (SRSC): N slope of Mt. Livermore, *H & others 1046* in 1967 (FPF).

UTAH

GARFIELD CO.: Bryce Cyn. Nat. Park: Bryce Point, *W 3035* in 1962 (COLO, FPF) and Mistletoe Ridge, *Buchanan 99* in 1956 (ARIZ). Ruby's Inn, *Harris C2912813* in 1929 (UC); Aquarius Plateau, *Vickery 616* in 1960 (RSA, UT); 20 mi. N of Boulder on Rte. 117, *H 684* in 1964 (FPF); 13 air mi. S of Panguitch, *Crew 140* in 1936 (UTC); Dixie Nat. For., Markagun Plateau, 4 mi. SW of Panguitch Lake on Rte. 143, *H & Geils 2143* in 1986 (FPF). KANE CO.: N of Navajo Lake, *Peterson 49-61* in 1961 (FPF); 8 mi. S of Navajo Lake on Zion rd., *W 4123* in 1966 (FPF, UT); 5.2 mi. SE of W end of Navajo Lake, *W 6677* in 1986 (FPF). SAN JUAN CO.: Elk Mts.: *Rydberg & Garrett 9328* in 1911 (RM, US); Elk Ridge, 2 mi. E of Kigalia Guard Sta., *Peterson 65-74* in 1965 (FPF). La Sal Mts., Pine Ridge near Rte. 46, *Peterson 65-83* in 1965 (FPF); Abajo Mts., S side of Abajo Mtn., *Krebill 235* in 1965 (FPF). Navajo Mtn.: *Gentry & Davidse 1790* in 1967 (ARIZ, RM, WTU); on Navajo Mtn. rd. 4 mi. W of Navajo Mtn. Trading Post, *H & others 1387* in 1971 (FPF). SEVIER CO.: Wildcat Knolls, W of Emery, *Peterson 64-96* in 1964 (FPF); Emery, *Williams* in 1918 (FPF, ILL). WAYNE CO.: Near Grover, *Peterson 64-93* in 1964 (FPF); Wayne Wonderland, *Milner 7250a* in 1935 (UT). COUNTY UNCERTAIN: La Sal Mts., *Stithem* in 1960 (FPF); Muddy Watershed, Manti Nat. For., *Korstian* in 1918 (FPF, ILL, WTU).

33. Arceuthobium verticilliflorum

MEXICO

DURANGO

36 mi. E of El Salto on Rte. 40, on *Pinus engelmannii*, *H & W 331* and *517* in 1963 (COLO, FPF) and *1241* in 1969 (FPF); 24 mi. E of El Salto on Rte. 40, on *Pinus engelmannii*, *H & W 341* in 1963 (COLO, FPF); 7 mi. E of El Salto on Rte. 40, on *Pinus cooperi*, *H & W 342* in 1962 (COLO, FPF) and *W 5979* in 1984 (FPF, UT); 25 mi. W of Durango on Rte. 40, on *Pinus engelmannii*, *H & others 1417* in 1972 (FPF); Santa Barbara, 29 mi. W of Durango on Rte. 40, on *Pinus engelmannii*, *H & others 1659* in 1975 (FPF); 26.5 mi. W of Durango on Rte. 40, on *Pinus engelmannii*, *Nickrent 1843.5* in 1982 (ILL, MEXU); Cienega de la Vaca, 40 km. WNW of El Zape, on *Pinus durangensis*, *Conkle* in 1985 (FPF); 25 km. W of Tepehuanes on rd. to Sierra del Huacal, on *Pinus durangensis*, *H 2162* in 1987 (FPF); 26 km. W of Tepehuanes on rd. to Sierra del Huacal, on *Pinus arizonica*, *H 2163* in 1987 (FPF); Pueblo Altares, on *Pinus cooperi*, *H & others 2239* in 1987 (FPF); 27 km. E of Tepehuanes on rd. to Sierra de la Candella, on *Pinus arizonica*, *H 2157* in 1987 (FPF); 38 km. W of Rte. 39 on Altares rd., on *Pinus cooperi*, *H & others 2234* in 1987 (FPF).

34. Arceuthobium yecorense

MEXICO

CHIHUAHUA

4 km. E of Sonora boundary on Yecora-Maycava rd., on *Pinus leiophylla* var. *chihuahuana*, *H 2178* in 1987 (FPF).

DURANGO

Mpio. Otaez: Ojito del Caiman, 49 km. SW of Altares on rd. to Banome, on *Pinus herrerai*, *H & others 2249* in 1987 (FPF); same locality on *Pinus durangensis*, *H & others 2250* in 1987 (FPF); 63 km. SW of Altares on rd. to Banome, on *Pinus* *lumholtzii*, *H & others 2252* in 1987 (FPF); San José de la Laguna, 73 km. SW of Altares, on *Pinus herrerai*, *Hernandez* in 1987 (FPF).

SONORA

Mpio. Yecora: Predio Ejidal Mesa el Indio, on *Pinus herrerai*, *Carbajal* in 1986 (FPF,INIF); 6 km. W of Chihuahua boundary of Yecora-Maycava rd., on *Pinus leiophylla* var. *chihuahuana*, *H 2176* in 1987 (FPF); Canada Cabeza de Vaca, 9 km. SE of Yecora, on *Pinus herrerai*, *H 2170* in 1987 (FPF); same locality, on *Pinus engelmannii*, *H 2171* in 1987 (FPF); 2 km. ESE of Yecora, on *Pinus engelmannii*, *H 2169* in 1987 (FPF).

Old World Taxa

35. Arceuthobium azoricum

All collections on *Juniperus brevifolia*.

AZORES

TERCEIRA

Caldiera de Aqualva, *Palhinha & Sobrinho* in 1937 (LISU); Caldiera de Barbara, col.? in 1937 (LISU). S. Jorge: between Culpata and Topo, *Palhinha & Sobrinho* in 1937 (LISU); Ribiera dos Cedros, *da Cunha & Sobrinho* in 1938 (LISU); Ribiera do Salto, *da Cunha & Sobrinho* in 1938 (LISU); without locality or collector in 1937 (LISU).

FAIAL

Caldeira, *da Cunha & Sobrinho* in 1938 (LISU); on SE slopes of the Caldeira, *W 4953* in 1973 (US, FPF, K, LISU, UT). Pico: Mt. Pico, *Guppy* in 1913 (K) and in 1914 (FPF, K).

36. Arceuthobium chinense

All collections on *Keteleeria evelyniana*.

CHINA

YÜNNAN

W of von Fumin, vicinity of Yanggai and Dsolin-ho, *Handel-Mazzetti 4999* in 1914 (US); around Hoji between Hoching and Sunygueh, *Schneider 2951* in 1914 (K, US); W flank of Tali Range, lat. 25°40' N, on "conifers," *Forrest 15524* in 1917 (K); Yünnan City, *Kiu 266* and *267* in 1984 (FPF, SCBI); Yuxi Country, *Kui 258* and *259* (FPF, SCBI); Yipinglang For. Sta., Lufeng Co., *Kiu 210, 211, 215* and *216* in 1981 (FPF, SCBI); Kunming City, *Liou 16612* in 1946 (FPF, SCBI).

SICHUAN

Vicinity of Huei-li Hsien, *Yu 1558* in 1932 (GH); Jinyang Co., *Kiu & Jaing 247* in 1983 (FPF, SCBI).

37. Arceuthobium juniperi-procerae

All collections on *Juniperus procera*.

ETHIOPIA

TIGRE PROVINCE

Berhale Track from Makale to Danakil Depression, ca 26 km. E of Wokro Agula, *W & Gilbert 4578* in 1972 (FPF, K, UT) and *Gilbert & Getachew 2302* in 1972 (K); Berhale Track from Makale to Danakil Depression, ca. 32 km. E of Wokro Agula, *W & Gilbert 4580* in 1972 (FPF, K, UT); Bile A Region, 55 km. from Dodola on rd. to Dinshu, *Fries & others 3816* in 1984 (K); Dallel to Merkele, *Gilbert & Getachew 2308* in 1972 (K); Arssi Region, 1 km. E of Dodola on Shaohemane-Goba rd., *Gilbert & Bonnefille 3514* in 1974 (K).

KENYA

LAIKIPIA DISTRICT

Thompson Falls, *W 4466* in 1972 (EA, FPF, K, UT).

MERU DISTRICT

N slope of Mt. Kenya, 3 mi. above Timau, *Gilbert 6033* in 1981 (K); Mt. Kenya, *Hepper & Field* 4881 in 1975 (K).

NAROK DISTRICT

18 km. N of Narok on rd. up Mau Escarpment, *W 4581* in 1972 (EA, FPF, K, UT).

NORTH NYERI DISTRICT

14 km. S of Nanyuki on Nyeri rd., *W 4569* in 1972 (EA, FPF, K, UT); NE of Nanyuki, 4 km. above Mt. Kenya Nat. Park entrance, *W 4462* in 1971 (EA, FPF, K, UT); 5 km. below Mt. Kenya Nat. Park on Naro Moru track, *W 4456* in 1971 (EA, FPF, K, UT); 8 km. S of Nanyuki on Gathiwuru For. Reserve rd., 1971, *W 4460* (EA, FPF, K, UT); Mt. Kenya Safari Lodge-Nanyuki rd., *W 4910* in 1973 (FPF); 1 km. S of Sirimon River bridge, *Gilbert 20791* in 1975 (EA); 5 km. E of Nanyuki on Isiola rd., *W 4570* in 1972 (EA, FPF, K, UT); Timau-Nanyuki rd., 4-5 km. from Timau, *Faden & Faden 74/863* in 1974 (K).

NYANDARUA DISTRICT

NW side of Aberdare Escarpment, 8 km. E of Wanjonki, *W 4565* in 1972 (FPF, K, UT); NW slope of Aberdare Mts., *Dawson* in 1916 (K); For. Sta., Aberdare Mts., *Fries 520* in 1922 (K).

RAVINE DISTRICT

94 km. SE of Eldoret on Nairobi-Kampala Highway, *W 4494* in 1971 (EA, FPF, K, UT) and *W 4551* in 1972 (EA, FPF, K, UT).

38. Arceuthobium minutissimum

All collections on *Pinus wallichiana*, except as noted.

BHUTAN

PARO

Hillside below Taksang Monastery, *Rushforth 1058* in 1987 (E, FPF).

INDIA

KASHMIR

Baltal, *Stewart 7549* in 1922 (K, PH, RAW); Pahalagon, *Singh* in 1965 (FPF); Sonamarg, *Stewart* in 1921 (MO); Baltal to Sonamarg, *Stewart 21297* in 1940 (US); Kishenganga Valley, near Gurais, *Duthie* in 1892 (BM, K); Gurais Valley, *Duthie 14182* in 1893 (BM); Sonamarg in Sind Valley, *Duthie 11481* in 1892 (K); Kali River, Nabi, *Duthie 24933* in 1900 (K); Guohai Valley, Astor District, *Duthie 12292* in 1892 (K); 0.5 mi. S of Sonamarg, 59 mi. NE of Srinigar, *W & W 4358* in 1968 (FPF, UT); 0.5 mi. above Tangmarg, 24 mi. W of Srinigar, *W & W 4359* in 1968 (FPF, UT); above Sumbliali, *Duthie 11204* in 1892 (K).

HIMACHAL PRADESH

Sangwa-Rupin rd., *Parker* in 1928 (UC); Batakansh Kagan, *Duthie* in 1899 (K).

UTTAR PRADESH

Gangotri, *Dudgeon & Kenoyer 132-2-1* in 1920 (PH).

LOCALITY UNCERTAIN

Gangrinini, *Dudgeon & Kenoyer 561* in 1920 (MO).

NEPAL

Nampa Gadh, Western Nepal, *Duthie 5947* in 1886 (BM, K); Kali Valley near Kangua, Western Nepal, *Duthie 3359* in 1884 (BM, K); Near Tinkar, *Parker 2085* in 1923 (K); Kali Valley, 4-5 mi. above Sarbyang, *Duthie* n.d. (K).

PAKISTAN

HAZARA

Naran, *H & Zakaullah 2092* in 1985 (FPF).

SWAT

25 mi. above Bahrein, E of Kalam, *Rodin 5695* in 1952 (K, RAW, UC, US); 4 mi. W of Utrot, Kalam Agency, *Thatcher* in 1962 (FPF); above Utrot, *Stewart & Rahman 25213* in 1953 (BM, RAW); 3 mi. W of Kalam, *H & Beg 1448* in 1973 (FPF); between Kalam and Utrot, *Ahmead 7042* in 1973 (RAW); Hamya, *Nasir & Siddiq 1080* in 1962 (RAW); Kalam, *Stewart 24714* in 1952 (RAW); Utrot, *Nasir & Zoffar 4623* in 1966 (RAW).

NORTHWEST FRONTIER PROVINCE

Nanga Parbat, near Rama, *Webster & Nasir 6471* in 1955 (K, RAW, US);

39. Arceuthobium oxycedri

The specimens cited here represent only a small fraction of the hundreds of collections that have been made of this species, but they document its extensive distribution. The labels on many early collections are hand-written, often in languages unfamiliar to us, and scarcely legible, so we have no doubt included some creative spellings for place names and collectors. Also, the geographic boundary changes over the past century in eastern Europe and the near East and the more recent boundary changes in the former Soviet Union and Yugoslavia have made some of the names of localities obsolete in terms of political geography. *Arceuthobium oxycedri* is poorly represented in North American herbaria. The host of each collection cited is *Juniperus* sp., except as noted.

ALBANIA

NE of Lake Scutair, *Baldacci 45* in 1900 (K); Jamina District, between Paleschori and Syranoni, *Baldacci 185* in 1895 (K, MO); Bogdan, near Loussou, *Baldacci 225* in 1985 (K); below Kapinova, ascent of Tomor, *Alston & Sandwith 2423* in 1935 (K).

ALGERIA

Autour de Boghart, *Deseaux 238* in 1856 (B, CAS, US); slopes of the Atlas Range above Batna, *Harshberger 1149* in 1928 (US); Djebell-Tougour prope Batna, *Chevallier* in 1892 (MO); Environs de Bossuet Broussailes, *Faure* in 1929 (B, K); Provance Oronan, Coteaux a'Vaida, *Wariney* in 1871 (K); Gharroubau, *Veloren* n.d. (K).

BULGARIA

Causova Planina, hills above Backova, *Turrill 1163* in 1926 (K); Central Rodope, Karlik Dagh, *Turrill* in 1926 (K); Rhodopae Orientalis, Zlatograd, on *Juniperus communis, Stojanov & others* in 1953 (K).

CHINA

XIZANG

(Cited from Kiu 1984): Riwoge, *Tsoong 5319* in 1952 (PE); Bombi, *Ying & others* in 1984 (PE).

FRANCE

Basse Alpes, Chateau Amon, *Maillard* in 1854 (K); between Saint Aubon and Montfort, *Faure* in 1889 (K); Chateau-Arnaux pres Sisteron, *Maillard* in 1853 (CAS) and *Salan* in 1853 (CAS); Environs de Montfort, *Salan* in 1880 (CAS); Chateauneuf-Val, Saint Dowat, *Chatenier 5051* in 1903 (CAS); between Saint Aubon and Montfort, on *Juniperus communis* and *Juniperus oxycedrus, Chaboisseau* in 1880 (CAS); Bauden, on *Juniperus communis, Bouchard 849* in 1949 (K); Gran Candelo, on *Juniperus phoenicia, Delmaz* in 1905 (B). Corsica, without locality, on *Juniperus communis, Schultze 508* in 1850 (B, CAS).

GREECE

Mt. Oeta, on *Juniperus rufescens, Heldreich 408* in 1879 (CAS, K); Parnafsi Region, on *Juniperus rufescens, Guicciardi* in 1855 (K); Tonsenitza, *Balls & Gonslay* in 1957

(K); Phokis, Monte Parnassi Region, *Bornmuller 1374a* in 1926 (B); Pellis, Mt. Pinovon, *Strid & Papaniocolaou 15528* in 1979 (B).

HUNGARY

Lika-Krbava, Valle Senjska, on *Juniperus rufescens*, *Kummerle* in 1911 (B, K).

INDIA

KASHMIR

Lahaul, Sumdo, on *Juniperus polycarpos*, *Stewart* in 1913 (RAW); Tispa, on *Juniperus macropoda*, *Parker 3450* in 1939 (K);

IRAQ

Zaiska Gorge, on *Juniperus oxycedrus*, *Embezer & others* in 1956 (K); Swaratuka, on *Juniperus oxycedrus*, *Chapman 21470* in 1958 (K); Sezank, *Haines* in 1959 (K).

IRAN

Kurdistan, Groomah, *Turrill* in 1926 (K).

LEBANON

For. of Ehden, *Bornmuller & Bornmuller* in 1910 (B), and *Eig & Zohary* in 1931 (UC).

MOROCCO

Tandled, on *Juniperus oxycedrus*, *Balls 2615* in 1936 (K); 9 km. S of Iframe on Highway S 309, *W 4437* in 1971 (FPF).

PAKISTAN

BALUCHISTAN

Zirat, *Jamal 2028* in 1972 (RAW); Susnamana area, 5 air mi. N of Zirat, on *Juniperus polycarpos*, *H & Irshad 1450* in 1973 (FPF).

SPAIN

MADRID

Caberos, *Graells* in 1906 (K); Bolledo de Chavela, *Avila* in 1877 (K); Fuentenebro, Villalba, *Rivas-Martinez 8196* in 1977 (B); Mataelpino, on *Juniperus oxycedrus*, *Rios* in 1983 (FPF); Becem l'de la, on *Juniperus oxycedrus*, *Rios* in 1983 (FPF); Robeldo de Chavela, on *Juniperus oxycedrus*, *Fragoso* in 1917 (FPF); Sierra de Gredos, *W 4436* in 1971 (FPF).

SYRIA

Khotschbel, col.?, in 1889 (US).

TURKEY

CONSTANTINOPLE

Aznavour 4674 in 1904 (B, CAS); Bei Krucevic, *Reiser* in 1899 (US); A 8 Artvin, Coruh Gorge, on *Juniperus oxycedrus*, *Davis 47681* in 1966 (K).

ANTALYA

District Czebiz, Bostran Cuckur, on *Juniperus excelsa*, *Davis 15712* in 1949 (K); Insula Thasos, *Halacsy* in 1911 (B).

BOLU

Nordl Bolu, *Wagenitz & Beug 107* in 1957 (B): Bittyma, Dalmas, *Bornmuller 13453* in 1924 (B); Vol. Analya, Ridge between the villages of Gombe and Sutlegen, on *Juniperus oxycedrus*, *Frankis 89-42* and *89-43* in 1983 (FPF); Ridge between villages of Yayla Cavda and Sutegen, on *Juniperus oxycedrus*, *Frankis 89-44* and *89-53* in 1983 (FPF); S slopes of Ak Dag, 5 km. N of Yayla Cavda, on *Juniperus foetidissima*, *Frankis 89-56* in 1983 (FPF).

ANATOLIA

Sinkepass, on *Juniperus excelsa*, *Walter 944* in 1955 (B).

ARMENIA

Rossiea Siedlitz Riltzagazch, *Bunge* in 1855 (K).

TURKESTAN

Ispander Kul, *Komarov* in 1913 (US); Province Samarkand, Alpes Sarawschan, on *Juniperus semiglobosa*, *Bornmuller 232* in 1913 (B).

UKRAINE

CRIMEA

Yalta, *Davis 33084* in 1955 (K) and *Leonard 7106* in 1978 (K); Sudak, on *Juniperus marschallianus*, *Halacsy* in 1900 (K) and *Callier 621* in 1900 (B); Jskander, *Komarov* in 1893 (K); District Jaltensis, Charax, on *Juniperus rufescens*, *Zerov* in 1958 (K); Taura Mischoz, *Oxijuk* in 1925 (B).

YUGOSLAVIA

Tajashihe oberhalt Autostrasse bie Tadronova, *Walter 169* in 1966 (B).

CROATIA

Opposite Bakar, *Mayer* in 1964 (B); Bakarac, *Damin* in 1887 (B); Timme, Felsen be Ankrnica, *Mutchy* in 1882 (K).

FIUME

Between Buccariza and Porto Ree, *Noe 1234* in 1837 (K) and *Hirc* in 1881 (B).

BOSNIA AND HERCEGOVINA

Ad Urncenci im Valle Narontis, *Reisser* in 1899 (K).

ISTRIA

Carcauzze, on *Juniperus oxycedrus*, *Solla* in 1887 (B, K); between Brezzi and Puzzole, on *Juniperus communis*, *Fiore & others 786* in 1907 (K); Lussinpiccolo, Mt. Ossero, *Haracic* in 1902 (B).

MACEDONIA

3 mi. N of Ochoida, *Curtis* in 1953 (K).

40. *Arceuthobium pini*

CHINA

YÜNNAN

E flank of Lichiang Range, lat. 27°30' N, on *Pinus* sp., *Forrest 6672* in 1900 (K); Mekong-Salwin divide; Lat. 28°12'N, on *Pinus* sp., *Forrest 14194* in 1917 (K); Yulongxye Shan, Baushai Valley, on *Pinus yunnanensis*, *Cribb C72* in 1987 (K).

SICHUAN

Between Molien and Tialou beyond des Yalung, on *Pinus tabulaeformis*, *Handel-Mazzetti 2629* in 1914 (US).

XIZANG

Kongbo Province, Charko-Lilung, Valley of Lilung Chu, lat. 29°8' N, long. 93°54' E, on *Pinus* sp., *Ludlow & others 4465* in 1938 (BM); Tongyuk, on *Pinus* sp., *Kingdon-Ward 12089* in 1935 (BM); Mainling, on *Pinus densata*, *Yu 8310201* in 1983 (FPF, SCIB).

41. *Arceuthobium sichuanense*

BHUTAN

PARO

From Nat. Museum to Jele La dzong, on *Picea spinulosa*, *Rushforth 1044* in 1987 (E, FPF).

CHINA

SICHUAN

Dege, Korlondo, *De 7064* in 1974 (SCIB as cited by Kiu 1984); Heishu, Sangarpar, *Chaing & Chin 1047* in 1959 (PE as cited by Kiu 1984); Sundo, Daocheng, on *Picea likiangensis* var. *balfouriana*, *Dao 3847* in 1973 (FPF, SCIB).

XIZANG

Biru, *Tao 11287* in 1976 (KUN as cited by Kiu 1984).

42. *Arceuthobium tibetense*

CHINA

XIZANG

Mainling Co., on *Abies forrestii*, *Chao 14* in 1981 (FPF, SCIB).

Molecular Systematics

Isozyme Analysis

Host and locality information for 36 populations of *Arceuthobium* sampled for isozymes. Voucher specimens for all taxa are deposited with the following herbaria: MU, ILL, SIU and/or UNAM.

1. *Arceuthobium abietinum* f. sp. *concoloris* on *Abies concolor*. *Nickrent 1917*. For. Highway 7N09, T. 7 N R. 17 E Sec. 30 (SW) to T. 7 N R. 16 E Sec. 25, Calaveras Co., CA. September 19, 1982.
2. *Arceuthobium abietinum* f. sp. *magnificae* on *Abies magnifica*. *Nickrent 1906*. For. Highway 90, 8.9 km. N Greenhorn Summit Stn., turnoff GSA camp, T. 24 S R. 31 E Sec. 36, Tulare Co., CA. September 14, 1982.
3. *Arceuthobium abietis-religiosae* on *Abies vejari*. *Nickrent 1983*. 17.6 km. 18 de Marzo, rd. to Cerro Potosí, Nuevo León, Mexico. September 6, 1984.
4. *Arceuthobium abietis-religiosae* on *Abies religiosa*. *Nickrent 2010*. Km-17, E Amecameca, rd. to Popocatepetl, 19°10' N 98°45' W, Mexico. July 18, 1985.
5. *Arceuthobium americanum* on *Pinus contorta*. *Nickrent 1929*. Along Elwell Lodge–Mt. Elwell trail, Lakes Basin Group Campground, T. 21 N R. 12 E Sec. 7, Yuba Co., CA. September 22, 1982.
6. *Arceuthobium americanum* on *Pinus contorta*. *Nickrent 1932*. Haskins Valley PG & E, Bucks Lake, T. 23 N R. 7 E Sec. 3, Plumas Co., CA. September 25, 1982.
7. *Arceuthobium apachecum* on *Pinus strobiformis*. *Nickrent 1945*. Madera Cyn. trail to Josephine Saddle and Mt. Wrightson, Santa Rita Mts., Coronado Nat. For., Santa Cruz Co., AZ. October 3, 1982.
8. *Arceuthobium blumeri* on *Pinus strobiformis*. *Nickrent 1937*. Carr Cyn., Huachuca Mts., T. 23 S R. 19 E Sec. 1, Cochise Co., AZ. September 26, 1982. Col. by Robert Mathiasen.
9. *Arceuthobium californicum* on *Pinus lambertiana*. *Nickrent 1930*. E Claremont rd., off La Porte rd., ca. 4 km. SE of Quincy, T. 24 N R. 10 E Sec. 33, Plumas Co., CA. September 24, 1982.
10. *Arceuthobium campylopodum* on *Pinus ponderosa*. *Nickrent 1924*. Turnoff for Emerald Bay State Park, State Highway 89, SW shore Lake Tahoe, T. 13 N R. 17 E Sec. 22, El Dorado Co., CA. September 21, 1982.
11. *Arceuthobium cyanocarpum* on *Pinus flexilis*. *Nickrent 1973*. On rd. 2.6 km. E Pingree Park, T. 7 N R. 73 W Sec. 15, Larimer Co., CO. November 1, 1983. Col. by Tom Zimmerman.
12. *Arceuthobium divaricatum* on *Pinus edulis*. *Nickrent 1953*. For. Highway 567 ca. 9.6 km. E US 666/180 (Red Hill rd.), T. 4 N R. 31 E Sec. 22, Greenlee Co., AZ. October 7, 1982.
13. *Arceuthobium douglasii* on *Pseudotsuga menziesii*. *Nickrent 1941*. Bear Wallow Campground, Santa Catalina Mts., T. 12 S R. 16 E Sec. 5, Pima Co., AZ. October 2, 1982.
14. *Arceuthobium douglasii* on *Pseudotsuga menziesii*. *Nickrent 1949*. Near hairpin turns, along State Highway 366, W Turkey Flat, 25 km. S State Highway 666, Pinaleno Mts., T. 9 S R. 25 E Sec. 19–30, Graham Co., AZ. October 5, 1982.

15. *Arceuthobium durangense* on *Pinus durangensis. Nickrent 1870.* 1.6 km. E La Ermita turnoff (little settlement), 6.4 km. E Puerto Buenos Aires bridge on Rte. 40, Durango, Mexico. August 11, 1982.
16. *Arceuthobium durangense* on *Pinus montezumae. Nickrent 2049.* 1.6 km. W El Madroño on Highway 40, ca. 23°38' N 105°47' W, Durango, Mexico. August 19, 1985.
17. *Arceuthobium durangense* on *Pinus montezumae. Nickrent 2051.* Km-162 on Highway 40, ca. 1.6 km. E Puerto Buenos Aires bridge, Durango, Mexico. August 19, 1985.
18. *Arceuthobium gillii* on *Pinus leiophylla* var. *chihuahuana. Nickrent 1938.* Bear Cyn. Picnic Area, For. Highway 5, Santa Catalina Mts., T. 12 S R. 16 E Sec. 22, Pima Co., AZ. October 1, 1982.
19. *Arceuthobium globosum* subsp. *grandicaule* on *Pinus michoacana. Nickrent 1996.* Km-142 on Highway 195 from Oaxaca, 5.5 km. S Suchixtepec, Oaxaca, Mexico. September 25, 1984.
20. *Arceuthobium laricis* on *Larix occidentalis. Nickrent 1801.* Along US 395, 2 km. NE jct. For. Highway 1583, Grant Co. OR. October 3, 1981.
21. *Arceuthobium microcarpum* on *Picea engelmannii. Nickrent 1947.* Just NW Hospital Flat Campground, along logging rd. off State Highway 366, Pinaleno Mts., T. 9 S R. 24 E Sec. 3, Graham Co., AZ. October 5, 1982.
22. *Arceuthobium nigrum* on *Pinus lawsonii. Nickrent 2041.* Km-121 Highway 175, ca. 40 km. N Ixtlán, ca. 17°35' N 96°26' W, Oaxaca, Mexico. July 27, 1985.
23. *Arceuthobium occidentale* on *Pinus sabiniana. Nickrent 1962.* Near Placerville, El Dorado Co., CA. September 15, 1982. Col. by R. F. Scharpf.
24. *Arceuthobium pendens* on *Pinus orizabensis. Nickrent 1992.* 17 km. WNW Perote and jct. Highway 140, Veracruz, Mexico. September 17, 1984.
25. *Arceuthobium pusillum* on *Picea mariana. Nickrent 1970.* Nemadji State For., near Kerrick, T. 44 N R. 18 W, Pine Co., MN. September 25, 1983. Col. by Kathy Zuzek.
26. *Arceuthobium pusillum* on *Picea mariana. Nickrent 1971.* Fond du Lak State For., near Cromwell, T. 49 N R. 20 W, Carlton Co., MN. September 25, 1983. Col. by Kathy Zuzek.
27. *Arceuthobium rubrum* on *Pinus teocote. Nickrent 1853.* Along Rte. 40, ca. 1.6 km. W El Salto. August 10, 1982.
28. *Arceuthobium strictum* on *Pinus teocote. Nickrent 2061.* Along N side Highway 40 and W Ojo de Agua turnoff, 35 km. W Durango, Durango, Mexico. August 20, 1985.
29. *Arceuthobium tsugense* on *Pinus monticola. Nickrent 1927.* Along trail, Lakes Basin Group Campground to Mt. Elwell, ca. 9.6 km. SSW Graegle, T. 21 N R. 12 E Sec. 7, Yuba Co., CA. September 22, 1982.
30. *Arceuthobium vaginatum* subsp. *cryptopodum* on *Pinus ponderosa. Nickrent 1876.* Just N jct. State Highway 4 and For. Highway 776, Santa Fe Nat. For., T. 19 N R. 3 E Sec. 7, Sandoval Co., NM. August 19, 1982.
31. *Arceuthobium vaginatum* subsp. *cryptopodum* on *Pinus ponderosa. Nickrent 1964.* Pingree Park rd., Roosevelt Nat. For., Larimer Co., CO. August 28, 1983. Col. by F. G. Hawksworth (*2048*).
32. *Arceuthobium vaginatum* subsp. *vaginatum* on *Pinus arizonica. Nickrent 1980.* 3.2 km. 18 de Marzo, rd. to Cerro Potosí, Nuevo León, Mexico. September 6, 1984.
33. *Arceuthobium vaginatum* subsp. *vaginatum* on *Pinus arizonica. Nickrent 1981.* 17.6 km. 18 de Marzo, rd. to Cerro Potosí, Nuevo León, Mexico. September 6, 1984.
34. *Arceuthobium vaginatum* subsp. *vaginatum* on *Pinus cooperi. Nickrent 2059.* Km-122 on Highway 40, near Las Adjuntas, Durango, Mexico. August 19, 1985.
35. *Arceuthobium verticilliflorum* on *Pinus engelmannii. Nickrent 2001.* Near El Salto, Durango, Mexico. November 20, 1984. Col. by D. Wiens.
36. *Arceuthobium verticilliflorum* on *Pinus engelmannii. Nickrent 2065.* Along State Highway 40, ca. 42 km. W Durango, just before Los Mimbres Cyn., Durango, Mexico. August 20, 1985.

DNA Analysis

Host and locality information for taxa utilized for ITS and 18S rDNA/*rbc*L sequence analysis studies.

ITS Sequencing

Arceuthobium abietinum f. sp. *magnificae* on *Abies magnifica. Nickrent 1916.* jct. For. Highway 7N09 and State Highway 4, T. 7 N R. 17 E Sec. 32, 38°27' N 120°8' W, Calaveras Co., CA. September 18, 1982.

Arceuthobium abietis-religiosae on *Abies religiosa. Nickrent 2010.* Km-17, E Amecameca, rd. to Popocatepetl, 19°10' N 98°45' W, Mexico, Mexico. July 18, 1985.

Arceuthobium americanum on *Pinus contorta. Nickrent 1911.* Edges of sphagnum meadow, along SW side Upper Sky Ranch rd., W turnoff from Beasore rd., T. 6 S R. 23 E Sec. 7, 37°26' N 119°30' W, Madera Co., CA. September 16, 1982.

Arceuthobium americanum on *Pinus contorta. Nickrent 1925.* Along State Highway 89, 4.8 km. N entrance D. L. Bliss State Park, T. 14 N R. 17 E Sec. 29, 39°2' N 120°7' W, El Dorado Co., CA. September 21, 1982.

Arceuthobium apachecum on *Pinus strobiformis. Nickrent 1945.* Madera Cyn., on trail to Josephine Saddle and Mt. Wrightson, Santa Rita Mts., Coronado Nat. For., Santa Cruz Co., AZ. October 3, 1982.

Arceuthobium bicarinatum on *Pinus occidentalis*. *Nickrent 2750*. 19°10' N 70°30' W, Dominican Republic. Summer 1990. Col. by Sue Thompson (*7634*).

Arceuthobium campylopodum on *Pinus jeffreyi*. *Nickrent 2161*. 5.3 km. N Greenhorn Summit, For. Highway 90, 35°48' N 118°33' W, Kern Co., CA. September 13, 1985.

Arceuthobium divaricatum on *Pinus edulis*. *Nickrent 1953*. For. Highway 567, ca. 9.6 km. E US 666/180 (Red Hill rd.), T. 4 N R. 31 E Sec. 22, 33°55' N 109°15' W, Greenlee Co., AZ. October 7, 1982.

Arceuthobium divaricatum on *Pinus monophylla*. *Nickrent 2160*. 8.5 km. E Horseshoe Meadow on Horseshoe Meadow rd. from Lone Pine, T. 17 S R. 36 E Sec. 5, 36°29' N 118°7' W, Inyo Co., CA. September 13, 1985.

Arceuthobium douglasii on *Pseudotsuga menziesii*. *Nickrent 1955*. Mt. Withington, 22 km. S US 60, along State Highway 52, 33°55' N 107°32' W, Socorro Co., NM. October 8, 1982.

Arceuthobium durangense on *Pinus* sp. *Nickrent 2178*. At elevation 1780 m, 1.1 km. W Km-215 on Highway 40, W El Palmito, Sinaloa, Mexico. July 20, 1986.

Arceuthobium gillii on *Pinus leiophylla* var. *chihuahuana*. *Nickrent 1663*. Bear Cyn., Santa Catalina Mts., Pima Co., AZ. August 31, 1981.

Arceuthobium globosum subsp. *globosum* on *Pinus durangensis*. *Nickrent 2053*. At Km-155 on Highway 40, ca. 2.8 km. E Buenos Aires and La Ermita turnoff, 24°N 104°50' W, Durango, Mexico. August 19, 1985.

Arceuthobium guatemalense on *Pinus ayacahuite*. *Nickrent 2039*. Km-129 on Highway 175, ca. 46 km. N Ixtlan, 17°37' N 96°22' W, Oaxaca, Mexico. July 26, 1985.

Arceuthobium microcarpum on *Picea pungens*. *Nickrent 1950*. Three Forks Cr. and For. Highway 249, ca. 14 km. W Alpine, T. 5 N R. 29 E Sec. 6, Apache Co., AZ. October 6, 1982.

Arceuthobium nigrum on *Pinus lawsonii*. *Nickrent 2041*. Km-121 on Highway 175, ca. 40 km. N Ixtlán, 17°35' N 96°26' W, Oaxaca, Mexico. July 27, 1985.

Arceuthobium oxycedri on *Juniperus oxycedrus*. *Nickrent 2832*. Parke Regional Alta Manzanares, near Madrid, Spain. June 14, 1991. Col. by R. F. Scharpf.

Arceuthobium pendens on *Pinus orizabensis*. *Nickrent 2014*. Mountains, 3 km. NW El Frijol Colorado, ca. 16 km. NW Perote, 19°37' N 97°23' W, Veracruz, Mexico. July 21, 1985.

Arceuthobium pusillum on *Picea mariana*. *Nickrent 1969*. Pine Island State For., near Big Falls, 47°50' N 93°45' W, Koochiching Co., MN. September 25, 1983. Col. by Kathy Zuzek.

Arceuthobium rubrum on *Pinus durangensis*. *Nickrent 2071*. Along Highway 40, 1.6 km. W El Salto, 23°46' N 105°23' W, Durango, Mexico. August 20, 1985.

Arceuthobium strictum on *Pinus teocote*. *Nickrent 2061*. Along Highway 40 at turnoff W Ojo de Agua, 35 km. W Durango, Durango, Mexico. August 20, 1985.

Arceuthobium vaginatum subsp. *cryptopodum* on *Pinus ponderosa* var. *scopulorum*. *Nickrent 1978*. Just N jct. State Highway 4 and For. Highway 776 (rd. to San Antonio YCC Camp), T. 19 N R. 3 E Sec. 7, Sandoval Co., NM. August 10, 1984.

Arceuthobium vaginatum subsp. *vaginatum* on *Pinus teocote*. *Nickrent 2018*. Highway 140, 4 km. S Sierra de Aqua, 19°34' N 97°9' W, Veracruz, Mexico. July 21, 1985.

Arceuthobium verticilliflorum on *Pinus engelmannii*. *Nickrent 2065*. Along State Highway 40, ca. 42 km. W Durango, just before Los Mimbres Cyn., 23°56' N 104°55' W, Durango, Mexico. August 20, 1985.

18S rDNA and rbcL Sequence Analysis

Antidaphne viscoidea Poeppig & Endlicher (host not recorded). *Nickrent 2730*. Monteverde, Costa Rica. October 7, 1988. Col. by Sara Sargent (*s.n.*).

Dendrophthora clavata (Benth.) Kuntze (host unknown). *Nickrent 2182*. Cason de Mamarramos in Santuario de Iguqe, at elevation 2800 m, ca. 10 km. N Villa de Leyva, Department Boyaco, Columbia. July 22, 1986. Col. by Mike Melampy (*s.n.*)

Dendrophthora domingensis (Spreng.) Eichler (host unknown). *Nickrent 2698.5* Along Rte. 120, Reserva Forestal Maricao, Puerto Rico. July 7, 1988.

Ginalloa arnottiana Korth. (host unknown). *Nickrent 2982*. Ranau District, Lohan R. Sabah, Borneo. March 24, 1984. Col. by J. H. Beaman (*9074*).

Korthalsella complanata (Tiegh.) Engler on *Lanthium odoratum*. *Nickrent 1974*. At elevation 365 m, near 1972 burn on Mauumae Ridge, Oahu, Hawaii. April 28, 1984. Col. by Wayne Takeuchi (*Koolau-157*).

Korthalsella lindsayi (D. Oliv.) Engl. on *Melicope simplex*. *Nickrent 2740*. Peel For., South Canterbury, New Zealand. June 18, 1990. Col. by Dr. Brian Molloy (*286139*).

Notothixos leiophyllus Schumann, in Schumann & Lauterb. on *Grevillea robusta*. *Nickrent 2785*. Tree near farmhouse along Gillies Highway (Rte. 52), 17°16' S 145°32' E, Queensland, Australia. August 7, 1991.

Notothixos subaureus Oliver, hyperparasitic on *Lysiana spathulata* (*2791*) which was parasitic on *Alocasuarina littoralis*. *Nickrent 2790*. 0.8 km. S Lake Tinaroo Falls Dam, 17°10' S 145°32' E, Queensland, Australia. August 9, 1991.

Phoradendron californicum Nutt. on *Prosopis* sp. *Nickrent 2689*. Foot Sabino Cyn., Tucson, Pima Co. Arizona. December 16, 1987. Col. by Jack Paxton (*s.n.*).

Phoradendron serotinum (Raf.) M. C. Johnston on *Ulmus americana*. *Nickrent 2076*. Rte. 3, 1.6 km. E jct. 127, Pulaski Co., IL. November 1985.

Santalum album L. (host unknown). *Nickrent 2734*. Bangalore, India. March 22, 1990. Col. by R. Narayana.

Viscum album L. on *Populus* x *canadensis* (= *Populus nigra x deltoides*). *Nickrent 2145*. Along Rhine, Herrlisheim, France. January, 1986. Col. by Alain Obriot.

Viscum articulatum Burman on *Eucalyptus*. *Nickrent 2782*. Near mall along Fitzroy River, Rockhampton, 23°25' S 150°33' E, Queensland, Australia. August 4, 1991.

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Alexander & Hernandez 2333(32a).
Alexander & Kellogg 5328(11).
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Glossary

Abundance. See incidence.

Adaptive radiation.
The evolution of species into a diversity of previously unoccupied ecological niches.

Albuminous cell. See Strasburger cell.

Apomorphic.
Having species traits that are highly derived or specialized, in contrast to pleisiomorphic or ancestral traits.

Autoploid. See polyploidy.

Apoplast.
The cell wall continuum of a plant or organ; the movement of substances via cell walls is called **apoplastic** movement or transport.

Base chromosome number.
The lowest haploid chromosome component for a group; typically 14 for *Arceuthobium.*

Bark strand.
A structure that ramifies throughout the inner bark of the host and from which shoots and sinkers of the mistletoe are derived.

Bivalent.
An homologous pair of chromosomes in the synapsed, or paired, state during prophase of the first meiotic division.

Bordered pit.
A pit in which the aperture is considerably smaller than the pit margin or outline, the secondary wall forming a border or rim extending over the pit chamber. See also pit aperture.

Branch girdle, segment.
Girdle refers to a region on a vegetative branch or main stem of a conifer between two annual growth segments; **segment** refers to a single year's growth of a vegetative branch or main stem.

Callose.
A polysaccharide that is a common wall constituent in the sieve areas of sieve elements.

Canker, mistletoe canker.
The structure and malformation of a host stem or branch caused by a disruption of the cambium and bark as a result of dwarf mistletoe infection.

Centers of taxonomic diversity.
For many genera, the region of greatest taxonomic diversity is also the region in which the group originally evolved, but some genera, *Arceuthobium* for example, have migrated beyond their region of origin (Asia) and undergone adaptive radiation in new habitats.

Clade.
In biological systematics, a **clade** is a monophyletic grouping of taxa where all members share a common ancestor; the clade is defined by the presence of one or more derived features shared by the members (synapomorphies).

Climax. See habitat type.

Congenital fusion.
Fusion that occurs during initiation and early development of an organ.

Competitive host exclusion.
The condition wherein parasitism of a secondary host species by a mistletoe is rare in stands where the host's principal parasite is present but common where the other dwarf mistletoe is absent (see chapter 6).

Cortex.
Ground-tissue region of a stem or root bounded externally by epidermis and internally by the vascular system; a primary-tissue region.

Crystal, druse and rhomboidal.
A body that is formed by the solidification of a chemical element, compound, or mixture, usually calcium oxalate. A **druse** is globular and compound with numerous crystals projecting from its surface. A **rhomboidal** crystal is simple with a rhomboidal shape.

Disjunct.
Pertaining to a discontinuous range having two or more potentially interbreeding populations separated by a distance that precludes genetic exchange by pollination or dissemination.

Distribution. See incidence.

DNA sequencing.
A process, usually involving electrophoresis, that reveals the order of the four nucleotides in a fragment of DNA (deoxyribonucleic acid).

Druse. See crystal.

Dual parasitism.
Parasitism of an individual tree by two species of dwarf mistletoe (see fig. 5.4).

Ectophytic system.
The aerial parts of a dwarf mistletoe plant, consisting of shoots, flowers, and fruits.

Electrophoresis.
A process used to separate macromolecules; it relies on the differential migration of these molecules in an electric field based on their molecular weight and/or charge.

Embryo sac, allium-type, polygonum-type.
The female gametophyte of angiosperms, generally an eight-nucleate, seven-celled structure. The seven cells are the egg cell, two synergids and three antipodals (each with a single nucleus), and the central cell (with two nuclei). In the **polygonum- type**, megasporogenesis results in four well-defined megaspores, one of which gives rise to the embryo sac. Most commonly the megaspore farthest from the micropyle is functional. The definitive feature of the **allium-type** arises from abortion of one of the two dyad cells produced after the first meiotic division of the megasporocyte. The nucleus of the surviving dyad cell divides to form two haploid nuclei, which are interpreted as megaspore nuclei.

Embryo, radicle, plumule.
A young sporophytic plant, before the start of a period of rapid growth (germination in seed plants). The **radicle** is the embryonic root and the **plumule** is the first bud of an embryo, the portion of the young shoot above the cotyledons.

Endophytic system.
The root system parts of a dwarf mistletoe within host tissues. The endophytic system consists of bark strands within the inner bark and "sinkers" that are embedded in successively formed layers of xylem, referred to as haustorial root system or haustorium.

Endosperm.
A tissue, containing stored food, that develops from the union of a sperm nucleus and the polar nuclei of the central cell; it is digested by the growing sporophyte either before or after the maturation of the seed; found only in angiosperms.

Flabellate branching.
Fan shaped, a branching pattern produced by the continued development of superposed axillary buds (see fig. 2.1).

Flavonoid.
Any of a large group of plant substances that includes the anthocyanins, a class of pigments often associated with flowers.

Flowering, direct and indirect.
Indirect flowering is the result of an intervention of a rest period between initiation of a floral bud and anthesis, whereas **direct flowering** is the result of uninterrupted development of floral buds from initiation to anthesis.

Growth, primary and secondary.
The growth of shoots and roots from inception until completion of their expansion is **primary** growth. This growth is the result of apical meristems and their three primary derivative meristems (protoderm, ground meristem, and procambium). **Secondary** growth results from divisions of secondary meristems (typically the vascular cambium and phellogen) and adds circumference to the plant body.

Habitat type, climax, seral, series.
Habitat type describes units of land that are capable of producing similar plant associations if undisturbed. **Climax** refers to the final stage in a successional sere; its nature is determined largely by climate and soil in the region. **Seral** refers to a species or community that is demonstrably susceptible to replacement by another species or community. **Series** refers to a sequence of communities that follow one another in the same habitat and terminate in a particular kind of climax association.

Haustorium, primary and secondary.
The **primary haustorium** is a wedge-like projection, arising from the circular attachment disc of the radicle, which penetrates the outer bark extending to the host xylem. **Secondary haustoria** are "sinkers" produced by bark strands that grow radially to the vascular cambium.

Holdfast.
A disc-like swelling at the distal end of the radicle through which infection of the host occurs (see fig. 2.11).

Host, extra-limital.
Infection of a tree that does not occur within the natural range of a particular dwarf mistletoe. Susceptibility of such trees may be established either by inoculations or by introducing trees into areas where the dwarf mistletoe is endemic.

Host-form.
A taxon of dwarf mistletoe based exclusively on host relationship.

Host specificity.
The necessary presence of a specific host for the pathogen to complete its life cycle.

Host susceptibility.
A subjective classification system based on the percentage of trees of the host species in question that are infected by dwarf mistletoe within 6 m of a principal host heavily infected with the same species of dwarf mistletoe (see table 6.1).

Immune.
Refers to trees that are not infected, even in stands where the dwarf mistletoe in question is common.

Incubation period.
That period of time from infection to production of first shoots. See latency.

Incidence, abundance, distribution, severity.
Incidence refers to the frequency of which host trees in a given stand are infected by a given species of mistletoe (usually measured as percent of trees infected). **Abundance** refers to the relative quantity of mistletoe in a stand or on a host (not usually quantified). **Distribution** describes the spatial extant and pattern of a mistletoe species or population within a given area. **Severity** is a qualitative term describing the disease situation (see infection class); high incidence along with large abundance would result in a severe disease situation.

Infected ray.
A host ray in which mistletoe sinker tissue is present.

Infection, secondary infection, localized and systemic infections.
Infection refers to that process in which dwarf mistletoes successfully penetrate host tissue and initiate establishment of the endophytic system; infection also refers to the mistletoe plant and the associated diseased host tissues. **Secondary infection** is re-infection by dwarf mistletoe of already infected tissue. **Localized infections** (anisophasic) are those in which the endophytic system is generally restricted to within or near (e.g., a few centimeters) the swollen portion of the host, whereas **systemic infections** (isophasic) are those in which the endophytic system occurs within the host terminal bud and growth keeps pace with that of the host's shoot apices.

Infection center.
A distinct infestation of dwarf mistletoe, separated by some distance from other infestations, that is enlarging by tree-to-tree spread through time. The earliest infected trees are generally near the middle of such centers.

Infection class.
A measure (generally from 0-6) of the relative severity of dwarf mistletoe infection for individual trees (see fig. 12.1), in contrast to host susceptibility class (see table 6.1).

Infestation.
A condition in which one or more trees of a stand or group are infected.

Initial, fusiform and ray.
Cell in a meristem that by division gives rise to two cells, one of which remains in the meristem and the other is added to the plant body. **Fusiform** and **ray** initials comprise the vascular cambium, and give rise to cells of the axial and ray system, respectively.

Intensification, vertical intensification.
Increase in the number of dwarf mistletoe infections within a tree (see spread). **Vertical intensification** refers to the net result of dispersal of mistletoe seeds to higher portions of the host crown.

Internode. See node.

Isozyme analysis.
Isozyme electrophoresis typically identifies the enzyme variants (alleles) as well as the number and type of homozygote and heterozygote phenotypes among the individuals sampled. These data can be analyzed in a number of ways and for various purposes relating to breeding systems, population genetics, species determination, etc.

Isozyme electrophoresis.
The process of separating and identifying multiple molecular forms of an enzyme that are chemically distinct but functionally identical (see electrophoresis).

Klendusity.
The ability of a potential host to escape attack by a given pathogen when inoculum and environmental conditions are favorable for infection (e.g., tree size).

Latency.
Phenomena in which host tissues are infected by dwarf mistletoe but either visible symptoms of swelling or brooming are not apparent or shoots are not present. Infections are latent during the incubation period and when environmental conditions induce a cessation in production of shoots.

Mamelon (or ovarian papilla).
An undifferentiated mass of tissue in which the two embryo sacs of the female flower are embedded.

Mycelial stroma.
A mass of vegetative hyphae in or on which spores are produced.

Necrophylatic periderm.
Secondary protective tissue, consisting of phellem, phellogen, and phelloderm, that is formed in response to wounding.

Node, internode.
A region of the stem where a leaf or leaves diverge; the region inbetween nodes is an **internode**.

Parasite, parasitism.
A **parasite** is an organism, such as a mistletoe, that obtains sustenance from another organism, and also completes all, or at least some, of its life cycle on that host organism. **Parasitism** is the typical mode of existence or behavior of a parasite.

Penetration wedge.
A structure in dwarf mistletoes that develops from the holdfast and initiates the infection process (see fig. 2.12).

Periclinal.
Orientation of a cell wall or plane of cell division parallel with the circumference or the nearest surface of an organ.

Phloem, primary and secondary.
The principal food-conducting tissue of a plant composed mainly of sieve elements, various kinds of parenchyma cells, fibers and sclereids. **Primary** and **secondary phloem** are formed during primary and secondary growth, respectively.

Pit apertures, simple and bordered.
The narrowed opening in the cell from the pit chamber to the cell lumen in the bordered pit. If there is a pit canal there will be an inner aperture (adjacent to cell lumen) and an outer aperture (adjacent to pit chamber).

Pit chamber.
The cavity of a pit when a border is present.

Plasma membrane
Outer boundary of the protoplast, adjoining the cell wall.

Plasmatubule.
Wall ingrowths lined with a plasma membrane (plasmalemma) present in some living plant cells. These ingrowths greatly increase cell surface area thus facilitating exchange of materials between a cell and its apoplast.

Plasmodesmata.
The minute cytoplasmic threads that extend through openings in cell walls and connect protoplasts of adjacent living cells.

Pleisiomorphic.
Having species traits that are ancestral, in contrast to apomorphic.

Plumule. See embryo.

Polygonum-type. See embryo sac.

Polyploidy, alloploid, autoploid.
Polyploidy refers to an organism, tissue, or cell with more than two complete sets of chromosomes, **alloploid** refers to an individual of hybrid origin whose sets of chromosomes are derived from different parental species and **autoploid** refers to an individual that has one or more exact duplications of the diploid set of chromosomes.

Primary growth. See growth.

Radicle. See embryo.

Resistant.
Possessing qualities that hinder development of a given pathogen.

Rhomboidal crystal. See crystal.

Secondary haustorium. See haustorium.

Secondary infection. See infection.

Secondary growth. See growth.

Segments. See branch girdles.

Seral. See habitat type.

Series. See habitat type.

Severity. See incidence.

Simple pit.
A pit composed of a pit cavity and a pit membrane, but lacking a border, so that a pit chamber is absent.

Sinker.
A radially oriented structure, composed of tracheary and parenchymal elements, that originates from a dwarf mistletoe bark strand and grows centripetally to the cambium where it becomes embedded by successive layers of xylem.

Site index.
Refers to the average height of dominant and codominant trees at a specific reference age; a measure of site quality.

Source-sink.
In the context of the mistletoe–tree interaction, the tree is the source or supplier of water and nutrients to the mistletoe and the mistletoe plays the role of **sink** or depository of water and nutrients taken up by the host tree.

Spread.
Increase in the area of mistletoe infestation by infection of additional host trees.

Strasburger cell, albuminous cell.
Certain phloem parenchyma cells in gymnosperms that are spatially and functionally associated with sieve elements.

Subsidiary cells.
An epidermal cell associated with a stoma and morphologically distinct from other epidermal cells.

Sympatry.
The condition in which the distributions of two species overlap and hybridization between taxa would be possible if they were not reproductively isolated by factors other than spatial separation.

Symplast.
The interconnected protoplasts and their plasmodesmata.

Systemic infection (isophasic).
Infection in which growth of the endophytic system keeps pace with the growth of the infected host branch. See infection.

Taxon (plural, Taxa).
A taxonomic unit of any rank (order, family, genus, species, subspecies, etc.)

Tunica layer.
Peripheral layer or layers in an apical meristem of a shoot that has cells that divide in the anticlinal plane and contribute to the growth in surface of the meristem.

Tylose.
An outgrowth from a parenchyma cell through a pit membrane into a tracheary element.

Vector.
An organism, such as a bird, squirrel, or insect that carries pathogen propagules from one host to another.

Verticillate branching.
Whorled, a branch pattern produced by the continued development of superposed axillary buds (see fig. 2.1).

Vertical intensification. See intensification.

Viscin.
Mucilaginous material contained in the viscin cells of dwarf mistletoe fruit, which acts as the initial means of seed attachment to the host.

Witches' broom.
An abnormally profuse, dense mass of host branches. This is a common symptom induced by dwarf mistletoe infection, as well as other parasites and abiotic agents.

Index to Subjects and Species

Subjects

Page numbers for tables and figures are indicated in **boldface.**

Species

Page numbers for illustrations of mistletoe species are in **boldface.**

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