SYSTEMATIC BOTANY MONOGRAPHS

VOLUME 58

Monograph of Schisandra (Schisandraceae)

Richard M. K. Saunders

THE AMERICAN SOCIETY OF PLANT TAXONOMISTS
20 March 2000

SYSTEMATIC BOTANY MONOGRAPHS
ISSN 0737-8211

ISBN 0-912861-58-4

Printed in the United States of America

Schisandra propinqua subsp. *propinqua* (*S.* subg. *Schisandra* sect. *Sphaerostema*). A, flowering branch (male); B, androecial mass of fused stamens (longitudinal section); C, isolated stamen. Reproduced from Lindley (1834); photograph © Royal Botanic Gardens, Kew.

MONOGRAPH OF SCHISANDRA (SCHISANDRACEAE)

Richard M. K. Saunders
Department of Ecology and Biodiversity
The University of Hong Kong
Pokfulam Road
Hong Kong, China

ABSTRACT. *Schisandra* (Schisandraceae) comprises 23 species of scandent and twining woody vines. The floral characteristics of the genus are clearly indicative of its primitive status: although the flowers are unisexual, they have an elongated floral axis with generally spirally arranged organs, an indefinite number of tepals that show a gradual transition between outer chlorophyllous tepals and inner pigmented tepals, and free carpels that are poorly differentiated, without true stigmas and styles. The androecia are highly variable in the genus with four basic types, differing in the number, position, and extent of differentiation and fusion of stamens; previous interpretations of androecial structure are reappraised consonant with a study of floral ultrastructure and vasculature. The fruits are highly distinctive bacceta, consisting of fleshy red indehiscent apocarps that are separated on a greatly elongated torus. Various aspects relating to the genus are investigated and extensively reviewed and discussed in the present monograph, including: nomenclatural history; morphology and anatomy; reproductive biology (including sex expression, pollination systems, and mechanisms of fruit and seed dispersal); cytology; phytochemistry; ethnobotany (including medicinal uses); palaeobotany; and historical biogeography. A species level taxonomic revision is presented, adopting a phylogenetic species concept. Phylogenetic relationships are interpreted using techniques of parsimony cladistics, and the results used as the basis of a revised supraspecific classification of the genus. Three subgenera are recognized, viz. *Pleiostema* (4 species), *Sinoschisandra* (13 species), and *Schisandra* (6 species), with subg. *Schisandra* further subdivided into three sections, viz. *Schisandra* (3 species), *Sphaerostema* (2 species), and *Maximowiczia* (1 species). The genus is widely distributed in East Asia, with a center of diversity in southeastern and southcentral China; one species, *S. glabra*, is present in North America. Historical biogeographical interpretations based on occurrences of fossil species suggest that the Schisandraceae originated in the *Aquilapollenites* province (western North America-Asia) during the Upper Cretaceous, with subsequent retreat correlated with the post-Eocene climatic deterioration.

INTRODUCTION

The genus *Schisandra* Michx. (Schisandraceae) consists of 23 species of scandent woody vines. Most species grow in broad-leaved evergreen forests in temperate and subtropical regions, although some occur in humid montane tropical forests, and one species grows in northern deciduous and coniferous forests. The distribution of the genus is disjunct: one species, *S. glabra*, is indigenous to North America, whereas all other species occur in East Asia, from Hokkaido (Japan) and Far Eastern Siberia in the north-east, to Java and Bali in the south, and to Uttar Pradesh (India) in the west. The center of diversity lies in southeastern and south-central China.

Many of the characteristic features of *Schisandra* are indicative of its comparatively primitive phylogenetic position. The flowers are unisexual, with an elongated floral axis bearing essentially spirally arranged floral organs. The perianth consists of an indefinite number of tepals with a gradual transition from chlorophyllous sepal-like outer tepals to pigmented petal-like inner tepals. The female flowers bear numerous free carpels that are poorly differentiated and have a variably shaped "pseudostyle" rather than a distinct stigma and style. The androecium of male flowers is highly variable within the genus, with several different evolutionary lineages resulting in partial or complete synandry. In several species, the composite effect of androecial fusion and reduction in stamen number has resulted in an androecium that is superficially whorled in arrangement, although developmental studies have revealed that stamen formation is invariably spiral.

The fruits of *Schisandra* are bacceta (sensu Spjut 1994), consisting of fleshy scarlet or deep red indehiscent apocarps. The receptacle becomes highly elongated following fertilization, and the individual apocarps are consequently widely separated along the torus. This is in marked contrast to the closely related genus *Kadsura* Juss., in which the bacceta are aggregates of closely appressed apocarps, resulting from only minimal elongation of the receptacle after fertilization.

The first comprehensive taxonomic treatment of *Schisandra* was published by Smith (1947), who recognized 25 species. Smith's monograph was necessarily restricted by the limited number of collections available at the time; eleven species were accepted on the basis of fewer than ten specimens, and seven species were based on fewer than three specimens. Smith was furthermore unable to provide complete descriptions for many taxa, due to the lack of male flowers (four taxa), female flowers (six taxa), and fruits and seeds (six taxa). No comprehensive taxonomic treatment of *Schisandra* has been published since Smith's monograph, although several new names and new combinations have been published recently (Law 1983a; He 1988; Sun 1988; Zhou et al. 1994; Saunders 1997b).

The present monograph is based on the extensive examination of numerous herbarium specimens, supplemented with living collections. Phenetic and phylogenetic approaches have been adopted, enabling a revision of the supraspecific classification and an interpretation of the historical biogeography of the genus. Numerous journal articles have been published that contain information of relevance to the systematics of the genus, although they are not specifically taxonomic. The present monograph provides a broad synthesis of the available information, and includes discussions of the following aspects: morphology, ultrastructure and anatomy; ecology and reproductive biology; cytology; phytochemistry; ethnobotany (including medicinal uses); and palaeobotany. For comparative purposes, the format of this monograph is complementary to the author's earlier publication on the sister genus *Kadsura* (Saunders 1998).

MATERIALS AND METHODS

Plant Materials

Over 1,200 herbarium collections were examined from various international and regional herbaria (see Acknowledgments); characters were scored in detail (including flower or fruit dissections) from over 550 of these collections. FAA-preserved specimens of eight taxa were obtained for morphological, ultrastructural, and anatomical studies, viz.: *S. arisanensis* subsp. *arisanensis* (China. Taiwan: Meifeng, Nantou Co., 5 Apr 1988, *S.-M. Chaw 615*; idem, 5 Apr 1988, *S.-M. Chaw 616*; idem, Aug 1988, *S.-M. Chaw s.n.*); *S. arisanensis* subsp. *viridis* (China. Hunan: Hengshan [Nanyue Mt.], 13 May 1998, *Q. Lin 975*); *S. chinensis* (Cult.: Hortus Botanicus Wageningen, Netherlands, s.a., *P. Goetghebeur 8858* [*HBW 80.BG.20403*]; China. Liaoning: Gounaidian, ca. 35 km W of Qingyuan, 16 May 1998, *X. Li, H. Chang & Y. Wang s.n.*); *S. glabra* (Mexico. Hidalgo: Metztitlán, Sierra Madre Oriental, 13 Jun 1996, *J. L. Panero & I. Calzada 6563*); *S. henryi* subsp. *marginalis* (China. Hunan: Hengshan [Nanyue Mt.], 13 May 1998, *Q. Lin 974*; idem, 15 May 1998, *Q. Lin 977*); *S. propinqua* subsp. *sinensis* (Cult.: South China Botanical

Garden, Guangzhou, Guangdong, 22 May 1998, *R. M. K. Saunders 98/1*; idem, May 1998, *G. Hao 102*); *S. rubriflora* (Cult.: Hortus Botanicus Universitatis Gandavensis, Belgium, s.a., *P. Goetghebeur 8857* [*HBUG 87-0254*]); and *S. sphenanthera* (China. Hunan: Hengshan [Nanyue Mt.], 12 May 1998, *Q. Lin 973*; idem, 13 May 1998, *Q. Lin 976*). Voucher specimens of these collections have been deposited in HKU herbarium.

MORPHOLOGICAL AND ANATOMICAL METHODS

Gynoecial and androecial features and pollen ultrastructure were studied using scanning electron microscopy (SEM). Pollen grains were dusted onto the matte surface of photographic film attached to stubs, whereas larger specimens were attached directly to stubs with colloidal silver liquid or adhesive carbon tabs. Fresh material was critical point dried prior to mounting. Specimens were coated with gold and examined using a Cambridge Stereoscan 440 SEM at 10 kV. Seed anatomy was studied by hand sectioning seeds that had been immersed in 70% ethanol for several days and viewing with SEM.

Leaf vasculature was studied by autoclaving tissues in 80% ethanol at 15 psi for 15 minutes followed by treatment with sodium hypochlorite solution as required (O'Brien & Teichman 1974). Floral vasculature was examined by incubating FAA-fixed tissues in 2% unbuffered papain activated with sodium sulfide for several days (Rodin & Davis 1967), followed by clearing with 5% NaOH at 37°C (O'Brien & McCully 1981: 6.15–6.16). Cleared tissues were then stained with 1% safranin O in 50% ethanol.

MULTIVARIATE STATISTICAL METHODS

Multivariate statistical techniques were used for the ordination of data where taxonomic resolution was complex. Principal coordinate analysis (PCoA) was selected since it is a *Q*-mode analysis (designed for studying the relationships between individuals), whereas other ordination techniques, such as principal components analysis (PCA), are *R*-mode analyses (designed for studying the relationships between characters) (Reyment et al. 1984: 95). The data were standardized (producing a correlation rather than a covariance matrix) to eliminate the effects of different units of measurement used in the various characters analyzed. Gower's similarity coefficient (Gower 1971) was then used in the calculation of the similarity matrix, since the data sets consisted of mixed data types (quantitative, multiple qualitative, and binary). The statistical software package used was *MVSP* (Kovach 1995).

The following morphological characters were used: (1) petiole length (mm); (2) petiole width (mm); (3) lamina shape (0 = ovate; 1 = ovate-elliptic; 2 = elliptic; 3 = obovate-elliptic; 4 = obovate); (4) lamina length (cm); (5) lamina width (cm); (6) lamina length:width ratio; (7) lamina apex shape (0 = acute; 1 = short-acuminate; 2 = acuminate; 3 = long-acuminate); (8) number of lamina margin teeth; (9) angle of lamina margin teeth (0 = denticulate/dentate; 1 = serrulate/serrate); (10) secondary vein number (pairs per leaf). All measurements were based on an average of five counts per specimen where possible.

CLADISTIC METHODS

Parsimony cladistic methods were employed for the phylogenetic analysis of data, using *Hennig86* (Farris 1988). Three species of *Kadsura* were included in the analysis to investigate generic monophyly, with data abstracted from Saunders (1998). The *Kadsura* species were selected as representatives of the three supraspecific taxa within the genus, viz.: *K. coccinea* (Lem.) A. C. Sm. [subg. *Cosbaea* (Lem.) A. C. Sm.], *K. heteroclita* (Roxb.) Craib [subg. *Kadsura* sect. *Kadsura*], and *K. scandens* (Blume) Blume [subg. *Kadsura* sect. *Sarcocarpon* (Blume) A. C. Sm.]. Trees were rooted by out-group comparison (Watrous & Wheeler 1981) using the related species *Illicium dunnianum* Tutcher, with data obtained from Smith (1947) and personal observations based on living populations in Hong Kong. Cladograms were constructed using the "ie- bb" option in *Hennig86*, with consensus trees computed using the cluster methods available in *Component* (Page 1993). The stability of clades was assessed by calculating jackknife monophyly indices; this was achieved using the *Lanyon* program within *Random Cladistics* (Siddall 1997).

The following characters were used in the cladistic analysis: (1) growth of "short shoots": 0 = growth continuing in subsequent years, 1 = without subsequent growth; (2) shape of young branches: 0 = ± round, 1 = winged or angled; (3) perule/bud-scale persistence: 0 = ± fugaceous, 1 = ± persistent; (4) extent of hair covering: 0 = glabrous, 1 = restricted to main veins of abaxial leaf lamina, 2 = covering entire abaxial leaf lamina, petioles, peduncles, outer tepals, etc.; (5) type of hair covering: 0 = pubescent, 1 = tomentose; (6) glaucescence of abaxial leaf surface: 0 = not glaucescent, 1 = ± glaucescent; (7) presence of secondary flowers in axils of peduncle bracteoles: 0 = absent, 1 = present (at least occasionally); (8) size of outer tepal relative to largest tepal: 0 = slightly reduced (0.5–1.0 of length of largest), 1 = highly reduced (0.1–0.4 of length of largest); (9) presence of carnose base on innermost tepals: 0 = absent, 1 = present; (10) length:width ratio of largest tepal: 0 = broad [0.7–2.5 (–3.5)], 1 = narrow [6.5–10 (–11)]; (11) degree of development of apical stamens: 0 = complete, 1 = incomplete; (12) fusion of stamens: 0 = no fusion, 1 = fusion of filaments only, 2 = complete staminal fusion, forming true "synandrium"; (13) attachment of thecae: 0 = on connective, 1 = sessile; (14) angle of stamens: 0 = ± vertical, 1 = ± horizontal; (15) stamen number: 0 = < 7, 1 = 8–50, 2 = > 50; (16) connective shape: 0 = ± narrow, not extending far beyond top of thecae, 1 = broad, extending beyond top of thecae; (17) anther dehiscence: 0 = extrorse-lateral, 1 = introrse-lateral; (18) pollen type: 0 = tricolpate, 1 = hexacolpate; (19) lumina diameter: 0 = small (< 3.0 μm), 1 = medium (3.5–5.0 μm), 2 = large (> 6.0 μm); (20) receptacle shape in female flowers: 0 = obovoid, subclavate, or ellipsoid, 1 = cylindrical or conical-terete; (21) shape of pseudostyles: 0 = narrow, subulate, 1 = broad; (22) presence of pseudostigma: 0 = absent, 1 = present; (23) shape of fruiting torus: 0 = not elongated, 1 = elongated; (24) apocarp attachment: 0 = sessile, 1 = basally constricted; (25) seed testa ornamentation: 0 = ± smooth, 1 = rugulose to tuberculate. Characters 4, 12, 15 and 19 are multistate; the character states were treated as ordered in characters 4 and 15, and unordered in characters 12 and 19.

CRITERIA FOR THE DELIMITATION OF TAXA

Species are delimited in this monograph using the phylogenetic species concept (sensu Luckow, 1995, and references therein), in which the presence of at least one constant character state is interpreted as being indicative of the existence of a hierarchical relationship. Taxonomic relationships are reticulate below the species rank, however, and infraspecific taxa are accordingly recognized on the basis of differences in mean values of quantitative and overlapping characters. Du Rietz's (1930) recommendations for the use of infraspecific ranks have been adopted, in which subspecies are defined as regional facies of a species (geographically correlated, or allopatric), whereas varieties are local facies of a species (ecologically correlated, or sympatric). Supraspecific ranks are only applied to strictly monophyletic groups, as revealed by cladistic analysis.

TAXONOMIC HISTORY

André Michaux published the genus *Schisandra*, comprising the species *Schisandra coccinea*, in his book *Flora boreali-Americana* (1803). Rehder (1944) deduced that this book was probably published around 19 March 1803. This date is significant because John Brickell (1803) had already validly published the genus *Stellandria*, including only *Stellandria glabra*, for the same taxon sometime in late February or early March of that year (Rehder 1944). Although the name *Stellandria* consequently has nomenclatural priority over *Schisandra*, it was the latter name that was adopted in the early botanical literature, and *Stellandria* was not even listed as a synonym of *Schisandra* until it was included in *Index Kewensis* almost a century later (Hooker & Jackson 1895: 984). To prevent the loss of a widely used name, Rehder (1944) proposed conservation of the name *Schisandra*; the name of the type species *Schisandra coccinea* was not conserved, however, and the new combination, *Schisandra glabra* (Brickell) Rehder, was created accordingly.

Michaux (1803) explicitly stated that the name *Schisandra* was derived from the Greek words σχιςις (= division, splitting) and ανηρ (= man), in reference to the splitting of the androecium during dehiscence. Candolle (1818) misinterpreted the etymology of the name, however, and apparently assumed that it was derived from δχιζειν (= to split), which is more commonly transliterated as "schiz"; he accordingly misspelled the name as "*Schizandra*." This error was widely perpetuated in subsequent publications, and is still encountered in many contemporary papers. As noted by Rehder (1944), however, "*Schisandra*" is the correct spelling according to the etymological derivation explained by Michaux (1803), and is not an orthographic error.

Two other generic names now regarded as later synonyms of *Schisandra* were published in the 19th century, viz. *Sphaerostema* Blume (1825) and *Maximowiczia* Ruprecht (in Maximowicz 1856); both these names were subsequently adopted as basionyms for supraspecific taxa within *Schisandra* (discussed below).

Considerable confusion between *Schisandra* and the closely related genus *Kadsura* Juss. is apparent in the early botanical literature: several species of *Schisandra* were initially described in *Kadsura* (Wallich 1824; Turczaninow 1837), and conversely many species of *Kadsura* were published as species of *Schisandra* (Baillon 1868; Hemsley 1875; Parmentier 1896; Finet & Gagnepain 1907a; Gagnepain 1939). Many of the latter treatments were published by French taxonomists, who followed Baillon's (1868) approach of reducing *Kadsura* to a section within *Schisandra*, and therefore reflect different opinions regarding rank rather than confusion over generic delimitation.

Many names now referred to *Schisandra* were published during the 19th and early 20th centuries, viz.: two species described from North America (Brickell 1803; Michaux 1803); one species from far eastern Russia (Ruprecht in Maximowicz 1856); three species from Japan (Siebold & Zuccarini 1843; Gray 1859; Maximowicz 1872); two species from Korea (Mori 1922; Nakai 1933); 23 taxa from China (Turczaninow 1837; Maximowicz 1859; Franchet 1885; Oliver 1887; Diels 1900; Clarke 1905; Finet & Gagnepain 1905; Hemsley & Wilson 1906; Dunn 1908; Sprenger 1908; Léveillé 1911, 1916; Rehder & Wilson in Sargent 1913; Hayata 1915; Schneider 1917; Pax & Hoffmann in Pax 1922; Stapf 1928; Cheng 1932; Merrill & Chun 1934); two species from the Himalayas (Wallich

1824); and four species from Southeast Asia (Blume 1825, 1830; Gagnepain 1938). The first attempt at comprehensively revising these taxa was undertaken by Smith (1947) in his monograph of the families Illiciaceae and Schisandraceae. Smith recognized only 25 species (including six new species from China and one from Myanmar), although extensive infraspecific variation was described in four species. Many species were necessarily only tentatively delimited and often based on only the type specimen or very small sample sizes due to limited collections available. Comparatively little taxonomic research was conducted on *Schisandra* following Smith's monograph, although several new taxa have recently been described and new combinations proposed (Law 1983a; He 1988; Sun 1988; Huang & Zhou in Zhou et al. 1994; Saunders 1997b).

The earliest attempt at developing a supraspecific classification of the genus was undertaken by Nakai (1933: 101), who recognized three sections, viz. sect. *Eu-Schizandra* (=sect. *Schisandra*), sect. *Maximowiczia* (Rupr.) Nakai, and sect. *Sphaerostema* (Blume) Nakai. Nakai cited several diagnostic characters to support this classification, including the highly important androecial structure (discussed under "Androecium"). Nakai's treatment was essentially restricted to those species occurring in Korea, however, and his understanding of the delimitation of sect. *Sphaerostema* was confused since this taxon does not occur in the region. He indirectly included the two species described by Blume (1825) under the generic name *Sphaerostema*, which have fundamentally different androecial structures; these species were subsequently transferred to *Schisandra* as *S. axillaris* (Blume) Hook. f. & Thoms. and *S. elongata* (Blume) Baill. Smith (1947) resolved the problem of the delimitation of sect. *Sphaerostema* by transferring *S. elongata* to a new section, *Pleiostema* A. C. Sm. Section *Sphaerostema* was accordingly redefined very precisely as consisting only of species with a carnose androecium of fused stamens associated with shallow cavities, whereas sect. *Pleiostema* included those species with an androecium of essentially free stamens.

Smith's (1947) supraspecific treatment of *Schisandra* was therefore based on four sections (Table 1), largely defined by reference to androecial structures. The only alternative supraspecific classification to be suggested was published by Law (1996a). Law recommended three significant changes (Table 1): (1) the elevation of all sections to the subgeneric level; (2) the division of sect. *Pleiostema* into two subgenera, *Pleiostema* (A. C. Sm.) Y.-W. Law and *Sinoschisandra* Y.-W. Law, based on the presence or absence of connate apical stamens in male flowers; and (3) the division of sect. *Sphaerostema* sensu A. C. Smith into two subgenera, *Sphaerostema* (Blume) Y.-W. Law and *Plena* Y.-W. Law, based on the type of attachment of thecae to the carnose androecial mass. These supraspecific changes were not based on a phylogenetic interpretation of the data, however, and monophyly has not been demonstrated for any of the subgenera.

MORPHOLOGY AND ANATOMY

HABIT

All species of *Schisandra* are scandent or climbing woody vines; they lack tendrils or other specialized structures for climbing, but become entangled on supporting vegetation by spiral stem growth. Several species have been observed to produce roots from the nodes in prostrate stems, including *S. chinensis* (Komarova 1994) and *S. glabra* (Tucker 1994).

All species share an essentially similar growth pattern, with short lateral shoots that develop from the previous year's growth. Although most species therefore appear to have

TABLE 1. Comparison of supraspecific classifications of *Schisandra*, including revised proposals.

DIAGNOSTIC FEATURES	SMITH (1947)	LAW (1996a)	REVISED CLASSIFICATION
Androecium of numerous, ± free stamens, lacking fused stamens at apex; pollen tricolpate; testa smooth	sect. *Pleiostema*	subg. *Pleiostema*	subg. *Pleiostema*
Androecium of numerous, ± free stamens, with fused stamens at apex; pollen hexacolpate; testa ± rugulose		subg. *Sinoschisandra*	subg. *Sinoschisandra*
Androecium a pentamerous "shield" of sessile stamens attached to a broad torus apex; pollen hexacolpate; testa ± rugulose to tuberculate	sect. *Schisandra* (as "*Euschisandra*")	subg. *Schisandra*	subg. *Schisandra* sect. *Schisandra*
Androecium reduced to (4–) 5 (–6) apically free stamens with connate filaments; pollen hexacolpate; testa smooth	sect. *Maximowiczia*	subg. *Maximowiczia*	subg. *Schisandra* sect. *Maximowiczia*
Androecium a subglobose mass of fused stamens; thecae subsessile; pollen hexacolpate; testa smooth	sect. *Sphaerostema*	subg. *Sphaerostema*	subg. *Schisandra* sect. *Sphaerostema*
Androecium an elongate mass of fused stamens; thecae sessile; pollen hexacolpate; testa smooth		subg. *Plena*	

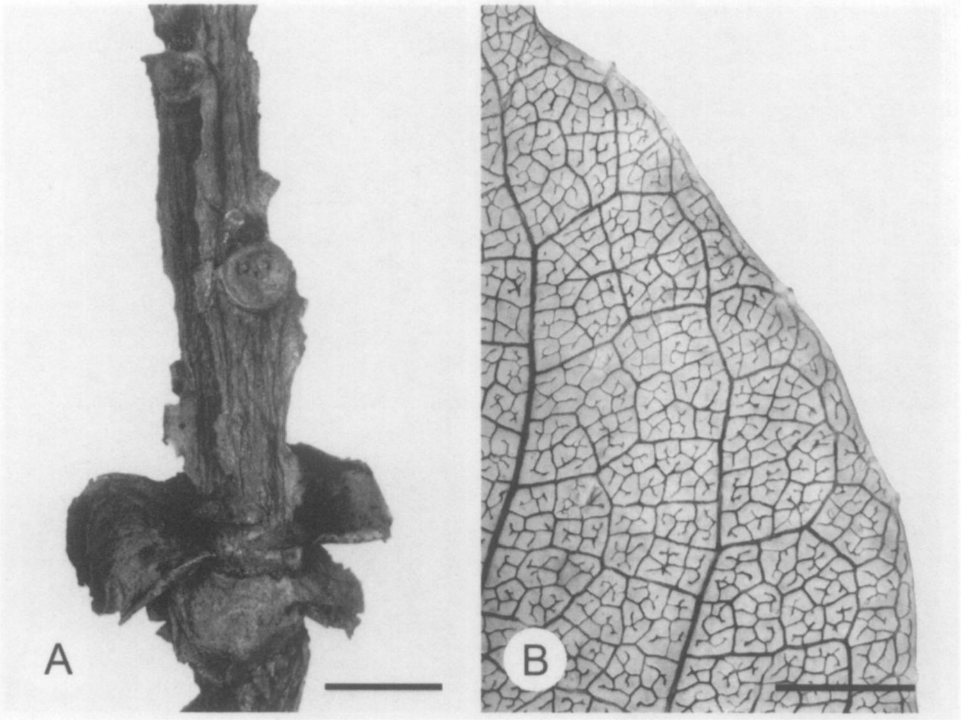


FIG. 1. Branch and leaf morphology in *Schisandra*. A, branch, showing large persistent perules and large lateral wings (*S. henryi* subsp. *henryi*). B, arrangement of veins at denticulate lamina margin (*S. arisanensis* subsp. *viridis*). Scale bars: 5 mm. (A, *D. E. Boufford et al. 24074*, A; B, *T. C. Chen 429*, MO.)

"short shoots" with clusters of leaves, the shoots generally continue growth later in the season. Bracts or perules occur at the base of these lateral shoots, and presumably act as bud-scales, protecting the vegetative shoot apex prior to shoot elongation; the bracts are generally small and fugaceous, although they are large and persistent in *S. perulata* and *S. henryi* (Fig. 1A). Although most species of *Schisandra* conform to the growth pattern outlined above, *S. repanda* and *S. bicolor* differ since the short lateral shoots do not usually continue growth after flower formation. These species therefore have true "short shoots," and typically have large closely positioned scars that result from the abscission of fruits from previous seasons.

STEMS AND BRANCHES

The stem anatomy of *Schisandra* has been extensively studied, although most research has inevitably been directed towards secondary structures. The cortex in young stems lacks a true endodermal layer (Jalan 1968b). Two regions are apparent, viz.: an outer layer 5–6 cells thick, composed of compactly arranged polygonal cells with slight angular thickening; and an inner layer 7–8 cells thick, composed of spongy cells devoid of tannins (Jalan 1968b). The central pith region consists of cells that are larger and more loosely arranged than those of the cortex (Metcalfe 1987).

The internodal regions are highly variable in primary xylem arrangement; both siphonostelic and eustelic arrangements occur (Bailey & Nast 1948; Ozenda 1949;

Benzing 1967; Jalan 1968b; Metcalfe 1987). The primary xylem of *S. chinensis* consists of protoxylem elements with annular thickening (early-formed cells) or helical thickening (later-formed cells), and metaxylem elements that possess scalariform and transitional bordered pits (Zamora 1966). The early-formed elements are tracheids, whereas later-formed elements are either tracheids or vessel members with long scalariform perforation plates.

The secondary xylem of young stems and branches has been described by Bailey and Nast (1948) and Metcalfe (1987), although most attention has been directed towards mature wood (Matsuda 1893; Groppler 1894; Garratt 1933; Lemesle 1933, 1945, 1946, 1953, 1956; McLaughlin 1933; Bailey & Nast 1948; Jalan 1968b; Soh & Park 1985; Takahashi 1985; Snezhkova 1986; Metcalfe 1987; Wang et al. 1989; Carlquist 1999). Bailey and Nast (1948) noted that the wood is structurally very variable, particularly with regard to the proportion of vessels and the thickness of the fiber-tracheid cell walls. In *S. chinensis*, for example, the cambium initially forms a narrow zone of almost vesselless xylem, which is succeeded by an abrupt transition to porous wood. Larger vessels have simple perforation plates, and the pits between vessels and parenchyma have large apertures with essentially vestigial borders; the perforation plates bear pit membrane remnants (Carlquist 1999), as in *Illicium* (Carlquist 1992). Intervascular pitting is rare but is scalariform or transitional to opposite where present. The parenchyma is scanty, diffuse, or abaxial paratracheal. Both uni- and multiseriate rays are present in the wood, with those of the early-formed wood prevailingly uniseriate; the wider rays are heterocellular.

The phloem consists of numerous contiguous sieve tubes accompanied by companion cells and scattered parenchyma (Bailey & Nast 1948; Metcalfe 1987). The sieve tube elements are long and narrow with elongate overlapping ends, and with numerous, sometimes widely spaced, sieve areas (Bailey & Nast 1948; Metcalfe 1987). The sieve elements contain "S-type" plastids that lack protein inclusions and store only starch (Behnke 1988). The phloem rays are uni- to triseriate and become slightly flared towards the periphery. Early stratification of the phloem into fibrous and non-fibrous zones is apparent in stems only 6 mm in diameter in *S. henryi* (Ozenda 1949). Cork formation has been variously described as subepidermal (Ozenda 1949) or superficial (Metcalfe 1987). *Schisandra henryi* has branches with lateral wings; these are particularly evident in subsp. *henryi*, where the wings can be as large as 7 mm wide (Fig. 1A).

LEAVES

The nodes are unilacunar, with three vascular traces that remain free in the petiole and basal region of the midrib (occasionally weakly associated), although they are reduced to a single arc with involute margins in the central and apical regions of the midrib (Vesque 1881; Bailey & Nast 1948; Ozenda 1949; Benzing 1967; Jalan 1968b, 1988; Metcalfe 1987). The foliar vascular bundles are sometimes observed to be heavily sheathed by pitted fibers (Metcalfe 1987).

Schisandra has alternately arranged, simple, petiolate, and exstipulate leaves; the laminar margins are generally denticulate or serrulate (rarely dentate or serrate). The epidermal cells can have undulating or sinuous anticlinal walls, particularly on the abaxial surface, although they are often straight (Rao 1939; Bailey & Nast 1948; Jalan 1962; Metcalfe 1987), and sometimes have cuticular striations (Matsuda 1893; Rao 1939; Bailey & Nast 1948). Several species (*S. glaucescens*, and *S. henryi* subspecies *henryi* and *marginalis*) have variably glaucescent abaxial lamina surfaces (Fig. 2A, B), consisting of irregular wax platelets (sensu Barthlott et al. 1998; see also Hennig et al. 1994).

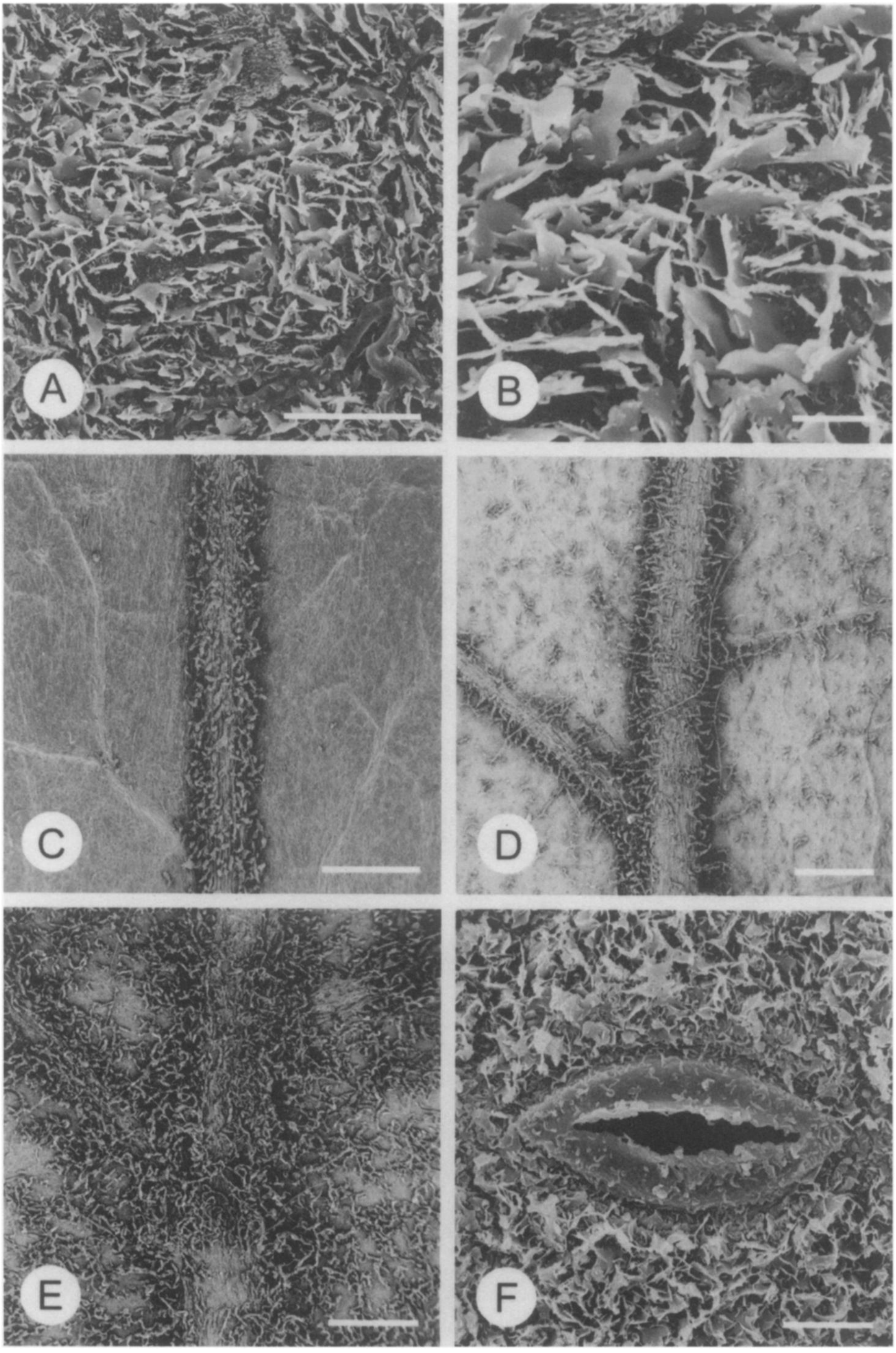


FIG. 2. Leaf indumentum and stoma in *Schisandra* (scanning electron micrographs). A, B, epicuticular wax platelets on abaxial lamina (*S. glaucescens*). C–E, various degrees of pubescence on abaxial lamina surface (C, *S. pubinervis*; D, *S. pubescens*; E, *S. tomentella*). F, stoma (*S. henryi* subsp. *henryi*). Scale bars: A, 20 µm; B, 5 µm; C–E, 1 mm; F, 10 µm. (A, B, *W. Y. Chun 3820*, A; C, *W. P. Fang 7765*, A; D, *W. P. Fang 7362*, A; E, *F. T. Wang 23052*, A; F, *H. C. Chow 12010*, A.)

The leaves of most species are entirely glabrous, although a small number of taxa have unbranched multicellular hairs on the abaxial lamina surface (*S. longipes*, *S. pubinervis*, *S. pubescens*, *S. tomentella*, and, to a lesser extent, *S. chinensis*). The degree of pubescence is variable, with hairs either restricted to the main veins (Fig. 2C) or else extending across the entire abaxial lamina surface (Fig. 2D, E). Similar pubescence has been reported in *Kadsura induta* A. C. Sm. (Saunders 1998: 54–55).

Stomata are irregularly and randomly distributed across the abaxial leaf lamina, but are absent from regions near the leaf margins and veins (Jalan 1962; Metcalfe 1987). Each stoma is elliptic and bounded by two reniform guard cells (Fig. 2F); a cuticular intrusion is apparent between both ends of the pair of guard cells (Bailey & Nast 1948; Metcalfe 1987). Variation in stomatal type is apparent, even within a single leaf (Bailey & Nast 1948): both paracytic and laterocytic types have been reported (Baranova 1981, 1983) with 2–7 subsidiary cells (Rao 1939; Jalan 1962; Baranova 1983), although there are also reports of anomocytic stomata (Bailey & Nast 1948; Jalan 1962). Jalan (1962) has described stomatal development in *S. grandiflora*, and has shown that the initial division of an epidermal cell gives rise to two unequally sized daughter cells; the guard cells are derived from the smaller of these cells, and the subsidiary cells are derived from adjacent protodermal cells. The developmental pattern is therefore perigenous, conforming to Florin's haplocheilic type (sensu Wilkinson 1979). These epidermal features have been interpreted as indicating a relationship with *Austrobaileya* (Baranova 1992). Stomatal features have been used extensively as diagnostic characters in the description of many fossil species in the genus; Jähnichen (1976), for example, has compared the stomata of several fossil *Schisandra* taxa with extant species.

Venation in the lamina is typically semicraspedodromous (sensu Hickey 1979) with most secondary (or lower order) veins merging near the margin, although the marginal teeth are associated with incomplete (freely ending) ultimate veinlets (Fig. 1B).

IDIOBLASTS

A variety of idioblastic cells have been reported in *Schisandra*, including crystalliferous sclereids, mucilage cells, and ethereal oil cells. Crystalliferous sclereids occur in roots, stems, petioles, and leaf laminas (Matsuda 1893; Solereder 1908; Bailey & Nast 1948; Jalan 1968a; Metcalfe 1987; Carlquist 1999). The sclereids in *S. grandiflora* and *S. neglecta* occur as either solitary cells or in groups of 2–5 cells, and are structurally diverse (both short or elongated, and branched or unbranched), and have asymmetrically thickened cell walls (Jalan 1968a). Different opinions have been expressed regarding the precise location of the crystals in the cells: Jalan (1968a) believed that they occur in the lumen, whereas Bailey and Nast (1948) believed that they are integrated in the secondary cell wall and become encysted in the outer surface of the cellulose adjacent to the protoplast. Similar crystalliferous sclereids occur in *Kadsura*, although they are absent from *Illicium*, and they therefore appear to be diagnostic for the Schisandraceae (Bailey & Nast 1948; Jalan 1968a).

Various types of secretory cells occur in *Schisandra* (Blenk 1884; Bailey & Nast 1948; Jalan 1963, 1965, 1975; Metcalfe 1987). Mucilage cells are present in the leaf epidermis, and in the phloem of the petiole and midrib, although occasionally external to the phloem (Jalan 1975; Metcalfe 1987) and in the carpel wall (Jalan 1975; Igersheim & Endress 1997). According to Jalan (1975), the young mucilage cells are spherical but later become irregular in shape, and this has previously resulted in their misinterpretation as

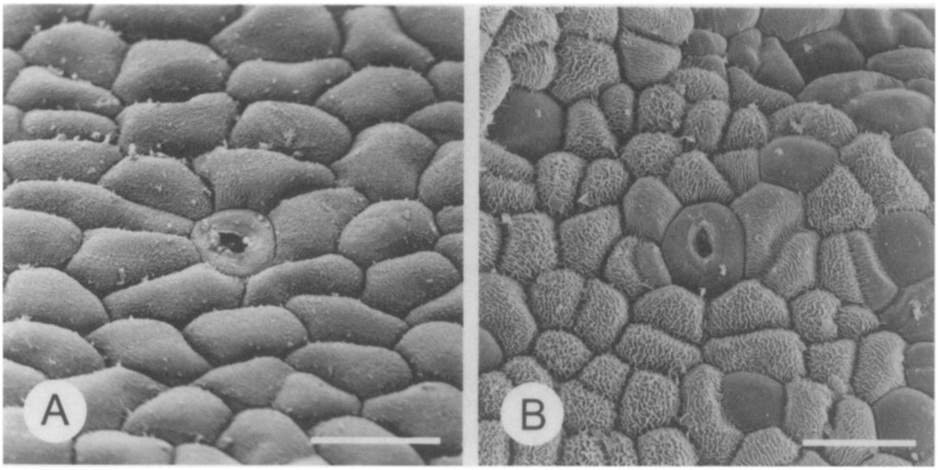


FIG. 3. Ethereal oil cells located on epidermis (scanning electron micrographs). A, stamen connective (*S. henryi* subsp. *marginalis*). B, carpel (*S. arisanensis* subsp. *arisanensis*). Scale bars: A, 50 µm; B, 25 µm. (A, *Q. Lin 977*, HKU; B, *S.-M. Chaw 616*, HKU.)

lysigenous ducts. Ethereal oil cells occur in the axial xylem of stems and epidermal or hypodermal layers of the stem, leaf, and petiole, as well as on stamen connectives (Fig. 3A) and carpel walls (Fig. 3B) (Bailey & Nast 1948; Jalan 1965; Carlquist 1999); they are spherical or polygonal, with suberized walls and a large lumen with granular content. The carpel walls also contain tanniferous cells and cells with oxalate druses and crystals (Jalan 1975; Igersheim & Endress 1997).

FLORAL ORGANIZATION

Although the arrangement of flowers in *Schisandra* is superficially simple, variation is apparent within the genus (Weberling 1988). Flowers commonly develop in the axils of basal bracts or perules (Fig. 4A, B), although later-forming flowers typically develop in leaf axils (Plate 5); this is particularly evident in more vigorously growing species, such as *S. henryi*, *S. longipes*, and *S. perulata*, and is presumably a reflection of the homology between perules and leaves. Some species (e.g., *S. propinqua*: frontispiece, Fig. 44) show an extreme adaptation of this condition; flowers appear to develop almost exclusively in the axils of leaves.

The flowers are solitary in most species, and are either ebracteolate or bear 1–3 bracteoles on the peduncle (Fig. 4C, D); the bracteoles closest to the apex of the peduncle often become integrated in the perianth since there is no marked distinction (Weberling 1988). In some species, however, including *S. propinqua* and *S. plena*, secondary flowers develop in the axils of the bracteoles, giving rise to clusters of flowers (Plate 5).

Flowers are unisexual, although *Schisandra* appears to be variably dioecious or monoecious (discussed under "Floral Reproductive Biology," below). Ueda (1988) reported the rare occurrence of small numbers of individuals in *S. chinensis*, which bear a few bisexual flowers; this has not been reported elsewhere and has not been confirmed by the present author.

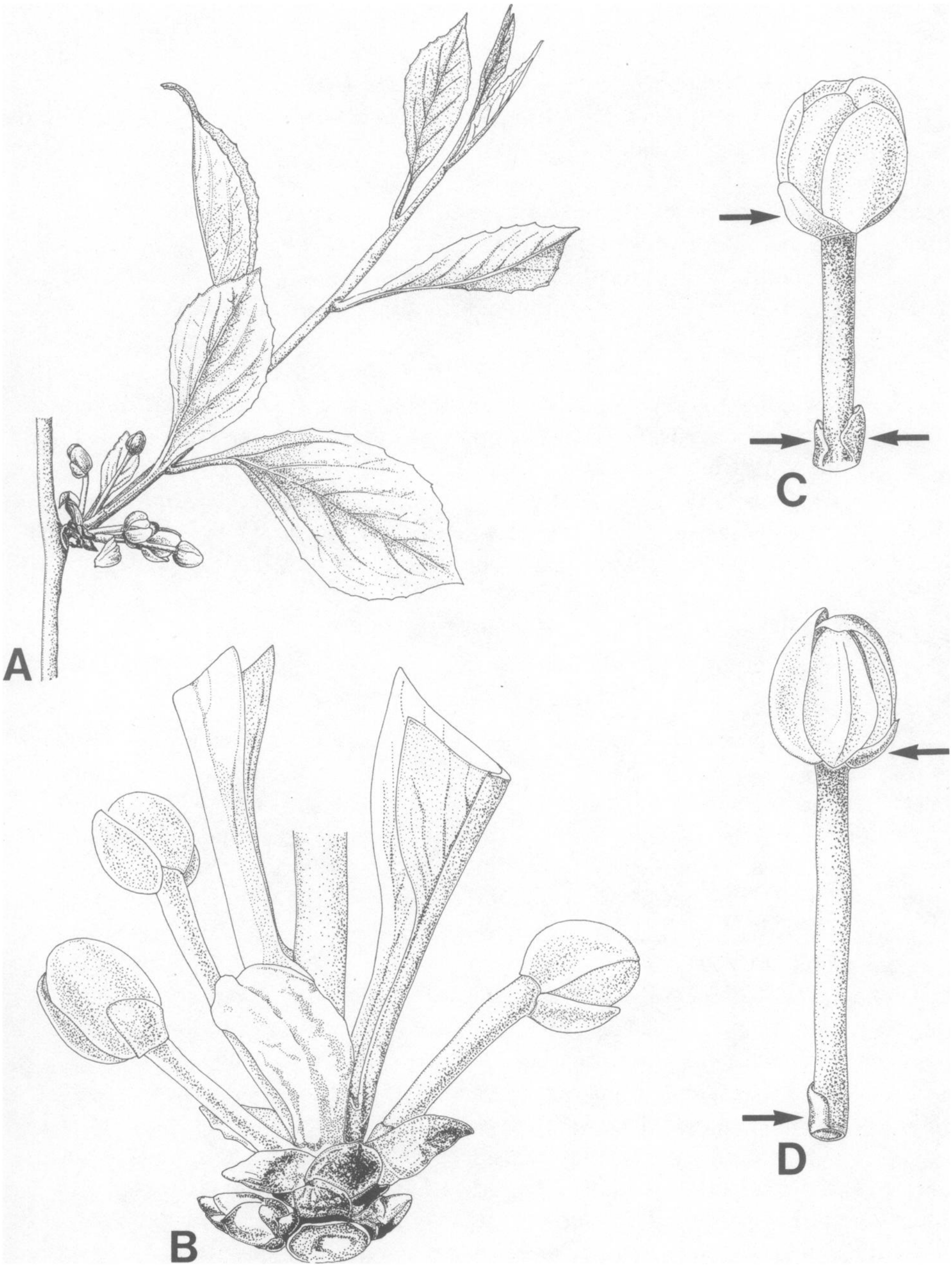


FIG. 4. Position of flower arrangement in *Schisandra*. A, B, arrangement of flowers at base of young growth, developing from the axils of fugaceous bracts (*S. chinensis*). C, D, solitary flowers, showing arrangement of bracts (arrows) (*S. chinensis*). (Redrawn from Weberling 1988: Fig. 7I-IV.) Drawing by S. J. Stanley.

PERIANTH

The perianth consists of 5–17 spirally arranged tepals; as in all flowers showing spiral phyllotaxis, aestivation of the tepals is imbricate. A transition is evident from outer chlorophyllous tepals to inner colored tepals, although there is no clear distinction between the two. Tepal pigmentation is variably cream, white, pink, red, orange, or yellow (frontispiece; Plates 1–5), and is often taxonomically useful at the species level. Several species, however, show infraspecific variation in tepal color, including *S. neglecta*, *S. lancifolia*, and *S. micrantha* (where pink, orange, and yellow flowers have been reported), and *S. sphaerandra* (with white, pink, and red forms). Pairs of otherwise closely related species are also observed to possess different flower pigmentation, viz.: *S. grandiflora* (white/cream) and *S. rubriflora* (red); and *S. repanda* (white/yellow) and *S. bicolor* (essentially red).

Taxonomically important variation is also evident in the shape and relative size of outer, mid, and inner tepals. Other characteristic features of the perianth include the ciliolate margin evident in the outermost tepals (Fig. 5A), consisting of multicellular hairs (Fig. 5B). The innermost tepals in species of sect. *Schisandra* (e.g., *S. glabra*) are basally thickened and carnose, occupying the space beneath the outwardly directed stamens. The epidermal cells of the tepals have marked cuticular striations (Fig. 5C, D).

ANDROECIUM

Considerable evolutionary diversification of the androecium is evident in *Schisandra*. Four basic androecial forms are recognized here.

Type "A," characterized by species of subg. *Pleiostema* and subg. *Sinoschisandra*, consists of 7–70 essentially free stamens that are spirally arranged around a slightly elongated floral axis (Fig. 6A). Each stamen is generally thick and carnose. The thecae show extrorse to introrse-lateral dehiscence, according to species. Each stamen typically has a single vascular trace, although this sometimes divides dichotomously (Fig. 8A; Ozenda 1946, 1949, 1952; Melville 1969; Jalan 1987). Jalan (1987) also noted that the staminal trace in *S. neglecta* is unusual, since the traces lead directly to the thecae rather than terminating within the connective.

Different evolutionary lineages are evident within the type "A" androecium, however, varying in the extent and manner in which adjacent stamens have become connate. The androecium of *S. sphaerandra* consists of a broad carnose axis, presumably derived by the fusion of the lower regions of filaments to the receptacle; the short upper regions of the filaments are free and bear thecae (Fig. 6B). In most species with the type "A" androecium, however, it is only the uppermost stamens that appear connate (Figs 7A–C, 8A): in addition to the numerous essentially free stamens, the receptacle is thick-carnose, and visible as a broad apical "shield" bearing a variable number of thecae on the margin (Fig. 7B). Although these apical stamens appear to be connate, they presumably represent stamens that are only partially differentiated at the apical growing point. The size of the carnose staminal mass is presumably dependent on the number of constituent stamens, and ranges in diameter from 1 mm or less (e.g., *S. glaucescens*, *S. tomentella*) to ca. 4.5 mm (*S. henryi*). Species that typically have smaller apical connate stamen masses are occasionally observed to lack them entirely, indicating that no clear distinction can be drawn between species on this basis. The staminal connectives in species with large apical "shields" are typically very broad, particularly in *S. henryi* and related species (Fig. 7D).

The type "B" androecium is observed in *S. bicolor*, *S. glabra*, and *S. repanda*, the

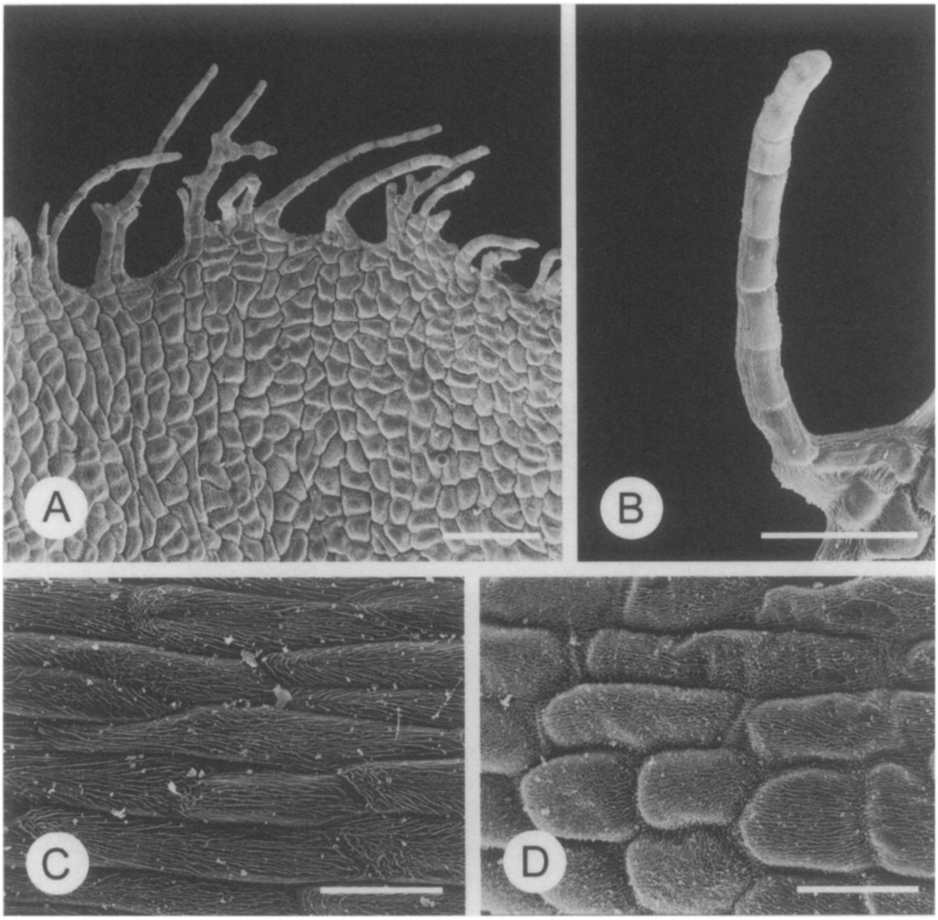


FIG. 5. Tepal morphology in *Schisandra* (scanning electron micrographs). A, B, ciliolate margin of outer tepal (*S. arisanensis* subsp. *viridis*). C, D, cuticular ornamentation on tepal epidermal cells (C, *S. chinensis*; D, *S. henryi* subsp. *marginalis*). Scale bars: A, 100 µm; B–D, 50 µm. (A, B, *Q. Lin 975*, HKU; C, *X. Li, H. Chang & Y. Wang s.n.*, HKU; D, *Q. Lin 977*, HKU.)

only members of subg. *Schisandra* sect. *Schisandra*. The androecium consists of a regular pentagonal "shield" of five stamens arranged around a broad floral apex (Fig. 9A). The stamens lack free filaments and are oriented perpendicularly to the floral axis in a radiating form. Each stamen has a very thick connective so that the thecae of adjacent stamens are contiguous (Fig. 9B, C), and contains a single vascular trace that divides dichotomously (Fig. 8B; Tucker & Bourland 1994). The lateral margin of the staminal "shield" (morphologically equivalent to the apex of the broad connectives) is often extended to form a narrow flange. Smith (1947: 90) believed that the type "B" androecium was derived by the fusion of filaments, although developmental studies by Tucker and Bourland (1994) suggest that the central region of the "shield" is derived from the floral apex rather than connate filaments. The presence of five staminal vascular traces in the stem of the androecium (Fig. 8B), however, suggests that it is at least partly composed of fused

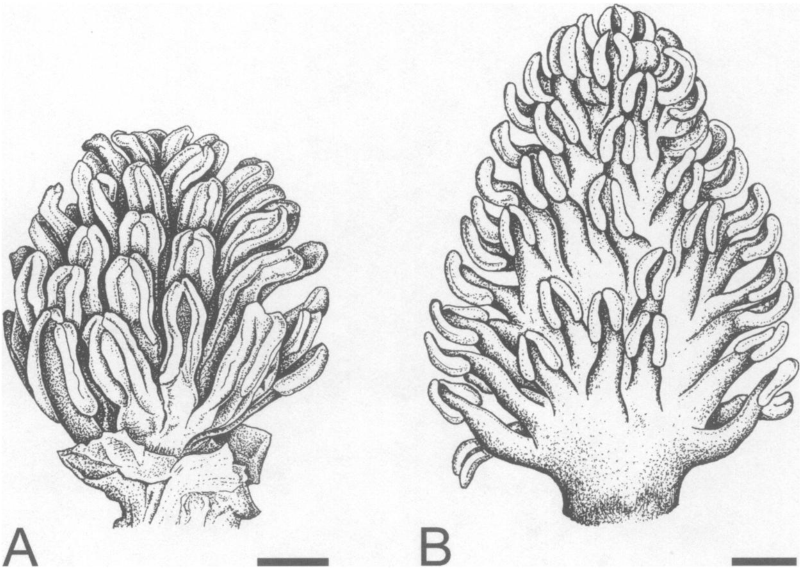


FIG. 6. Androecium type "A," occurring in *Schisandra* subg. *Pleiostema* (=sect. *Pleiostema* sensu Smith [1947], pro parte). A, *S. grandiflora*. B, *S. sphaerandra*. Scale bars: 1 mm. (A, *D. Chatterjee 230*, L; B, *F. K. Ward 20893*, A.) Drawing by H. L. Wilks.

filaments. Although the mature androecium consists of stamens that appear to be arranged in a whorl, development is actually spiral, with the stamen primordia derived from the same phyllotactic helix as the tepal primordia (Tucker & Bourland 1994). Occasionally, one or two additional stamens are observed, located either above or below the pentagonal shield (e.g., *S. glabra*: Tucker & Bourland 1994); if the supernumerary stamen is located above the shield it is often partially or fully sterile, whereas if it is located below the shield (Fig. 9D) it is generally transitional in form between a stamen and a tepal.

The type "C" androecium is observed in only *S. chinensis* (the sole member of subg. *Schisandra* sect. *Maximowiczia*). The number of stamens is reduced to only (4–) 5 (–6) (Fig. 10A, B), and each stamen appears to be basally connate, forming a staminal column that contains an equivalent number of vascular traces (Fig. 8C; Kozo-Poljanski 1946). The upper portion of each filament is free and bears extrorse-lateral thecae. The connective is often observed to extend slightly beyond the apex of the thecae, although this is highly variable. Occasionally, a central elongated receptacle is observed (Fig. 10A) and can extend beyond the height of the stamens. The development of the androecium in *S. chinensis* is described by Kolbasina (1967).

The most extreme degree of synandry in *Schisandra* occurs in *S. propinqua* and *S. plena* (sect. *Sphaerostema*). This form of androecium, designated type "D," consists of a subglobose or elongate carnose mass derived by the fusion of 4–18 stamens (Fig. 11A, D).

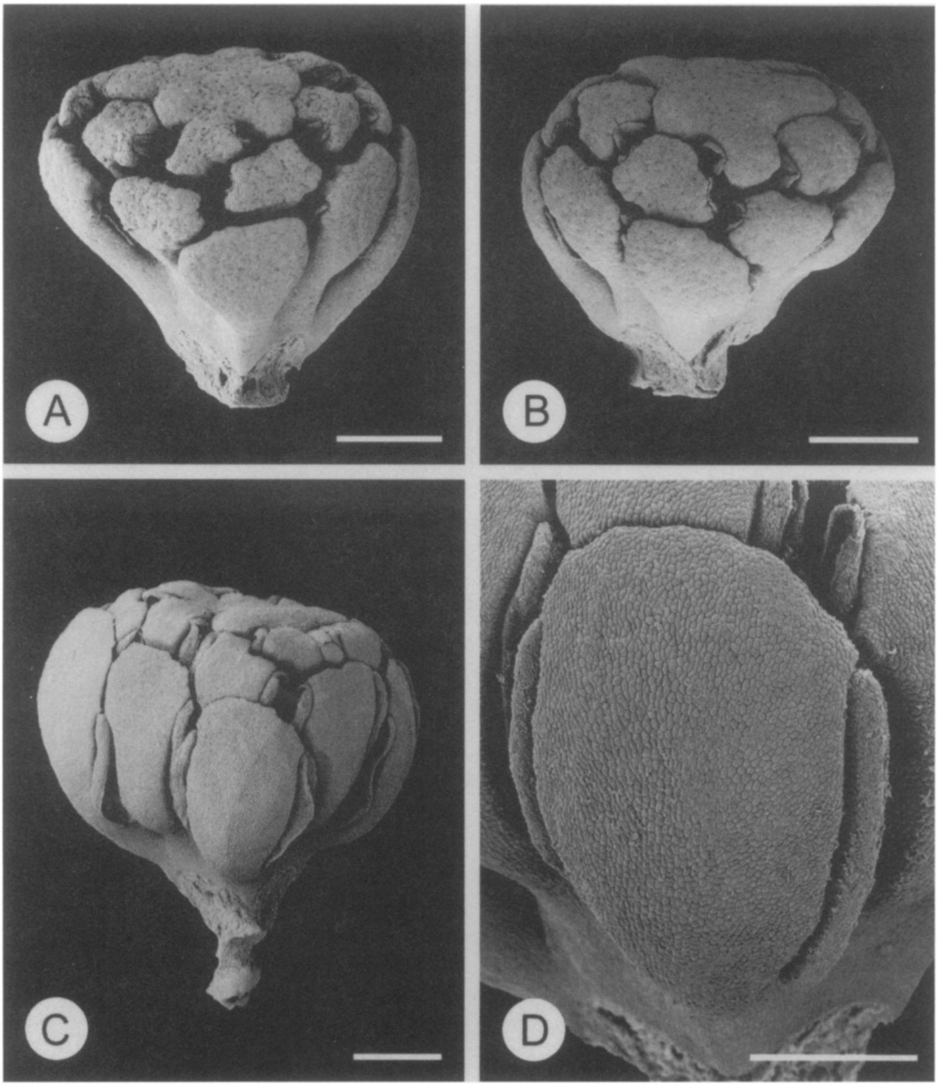


FIG. 7. Androecium type "A," occurring in *Schisandra* subg. *Sinoschisandra* (=sect. *Pleiostema* sensu Smith [1947], pro parte) (scanning electron micrographs). A, *S. arisanensis* subsp. *viridis*. B, *S. sphenanthera*. C, *S. henryi* subsp. *marginalis*. D, single stamen of *S. henryi* subsp. *marginalis*. Scale bars: 1 mm. (A, *Q. Lin 975*, HKU; B, *Q. Lin 973*, HKU; C, D, *Q. Lin 977*, HKU.)

In *S. propinqua*, the uppermost part of each stamen is free; the introrse thecae are borne on a connective that is adjacent to a small depression in the androecial mass (Fig. 11B, C). In contrast, the thecae of *S. plena* are sessile and are borne on opposing sides of a cavity in the androecial mass (Fig. 11E).

The phylogenetic relationships between the various androecial types are discussed in detail below under "Phylogeny and Supraspecific Classification."

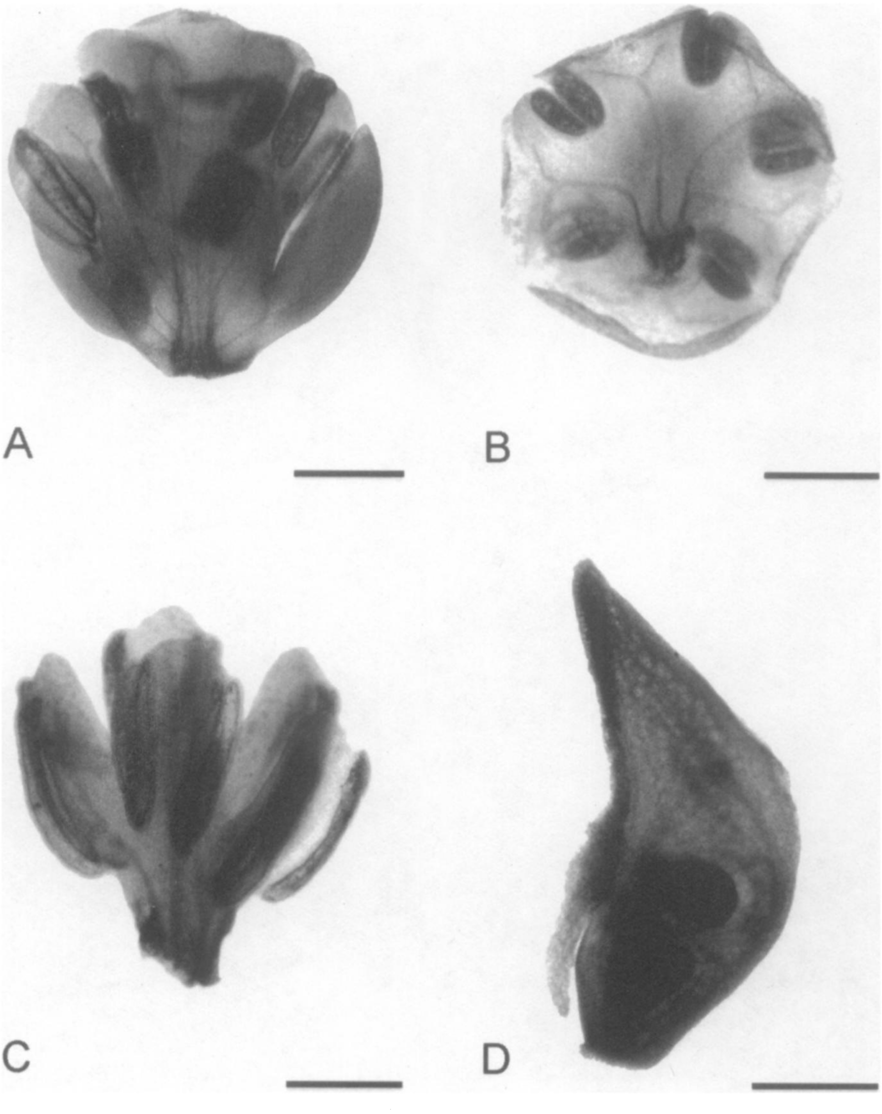


FIG. 8. Androecial and carpellary vascular systems in *Schisandra* (cleared specimens). A, androecium type "A" (*S. arisanensis* subsp. *viridis*). B, androecium type "B" (*S. glabra*). C, androecium type "C" (*S. chinensis*). D, carpel (*S. arisanensis* subsp. *arisanensis*). Scale bars: A–C, 1 mm; D, 0.5 mm. (A, *Q. Lin 975*, HKU; B, *J. L. Panero & I. Calzada 6563*, HKU; C, *X. Li, H. Chang & Y. Wang s.n.*, HKU; D, *S.-M. Chaw 616*, HKU.)

POLLEN AND MICROSPOROGENESIS

The most comprehensive study of *Schisandra* pollen was published by Praglowski (1976), involving a light and scanning electron microscope study of the internal and external structure of 19 species in the genus. Numerous other publications contain descriptions and illustrations of *Schisandra* pollen, including: Wodehouse (1936, 1959), Pokrovskaia (1950: 250–251), Erdtman (1952), Ikuse (1954, 1956), Hayashi (1960), Jalan and Kapil (1964), Kapil and Jalan (1964), Agababian (1966, 1968, 1973), Kuprianova

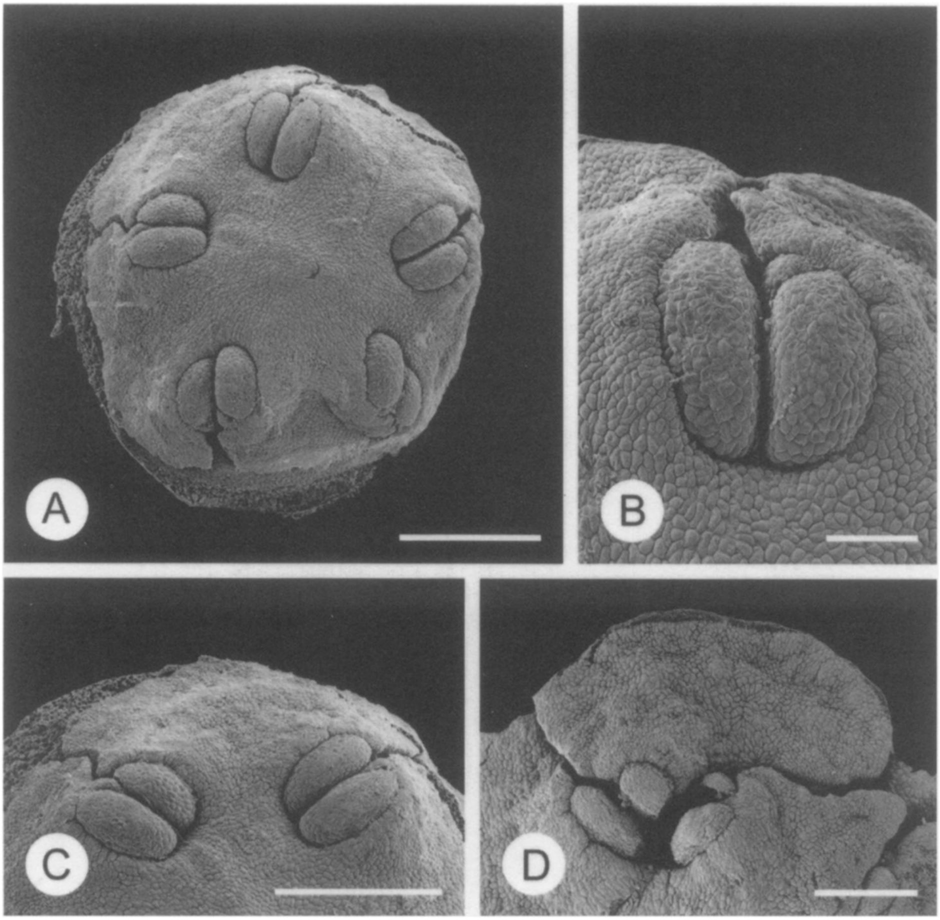


FIG. 9. Androecium type "B," occurring in *Schisandra* subg. *Schisandra* sect. *Schisandra* (scanning electron micrographs). A, adaxial surface of entire androecium (*S. glabra*). B, adjacent thecae of neighboring stamens (*S. glabra*). C, entire stamen (*S. glabra*). D, organ transitional between stamen and tepal, located below fertile stamens (*S. glabra*). Scale bars: A, 1 mm; B, 250 µm; C, 1 mm; D, 500 µm. (*J. L. Panero & I. Calzada 6563*, HKU.)

(1966), Huang (1967, 1972), Wang (1968), Mitroiu (1970), Roland (1971), Agababian and Zavarian (1974), Walker (1974a, 1974b, 1976a, 1976b), Walker and Doyle (1975), Huynh (1976), Jalan (1979), Lieux (1980), and Keng (1993: 590). The present monograph describes the pollen type in all species not previously studied.

Schisandra pollen is colpate, radially symmetrical, and heteropolar (Fig. 12A–E). Praglowski (1976) reported dimensions of 12–24 µm (polar) × 24–35 µm (equatorial) from glycerin jelly preparations. The pollen is generally plano-convex in lateral view (Fig. 12E), often with a slightly invaginated area (ca. 5–8 µm in diameter) at the proximal pole; the polar:equatorial ratios range from 0.44 to 0.78 (Praglowski 1976). The exine is of variable thickness, 1–2.5 µm (thinner towards the proximal pole), and has a reticulate structure composed of muri with a solid tectum and infratectal bacular part (Fig. 12F); occasionally isolated processes occur within the lumina (Praglowski 1976).

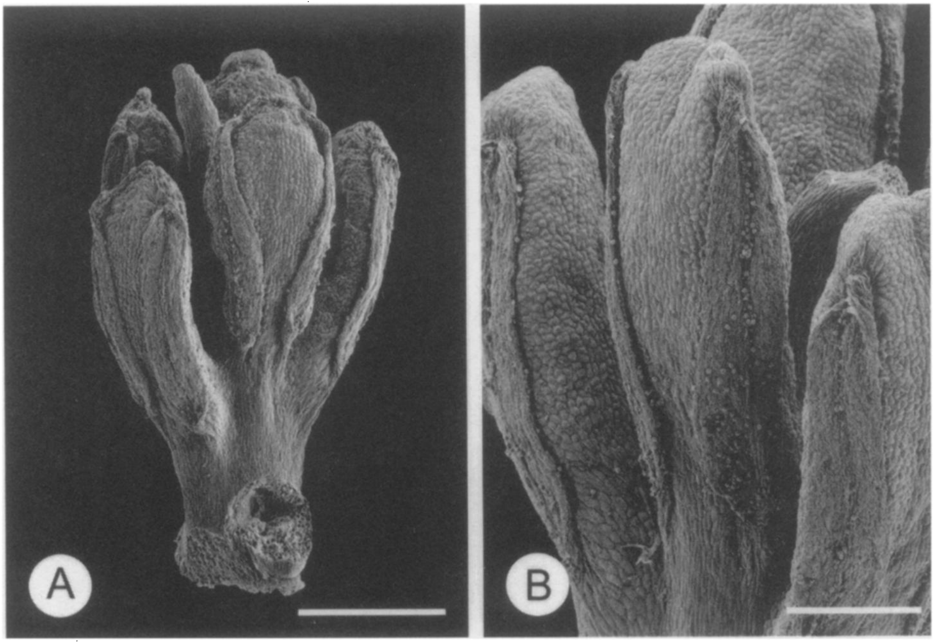


FIG. 10. Androecium type "C," occurring in *Schisandra* subg. *Schisandra* sect. *Maximowiczia* (scanning electron micrographs). A, entire androecium (*S. chinensis*), with elongate receptacle. B, solitary stamen (*S. chinensis*). Scale bars: A, 1 mm; B, 500 µm. (*X. Li, H. Chang & Y. Wang s.n.*, HKU.)

Although the genus is otherwise palynologically highly conservative, two major pollen types can be distinguished on the basis of aperture number and arrangement. Four species (*S. grandiflora*, *S. rubriflora*, *S. incarnata*, and *S. sphaerandra*) have tricolpate pollen (Fig. 12A, B); the colpi are 15–23 µm long and converge over the distal pole. The pollen of all other species in the genus is hexacolpate, with three long colpi (24–35 µm) converging at the distal pole and alternating with three shorter colpi (13–23 µm) that are not fused at either pole (Fig. 12C, D). Reports of hexacolpate pollen in *S. grandiflora* (Jalan & Kapil 1964; Kapil & Jalan 1964; Jalan 1979) are presumably due to incorrect taxonomic determinations. Several authors have reported abnormalities in aperture arrangement in *Schisandra*, including pollen with only one or two colpi, parasyncolpate pollen, and grains with a trischistoclasic arrangement of colpi (Erdtman 1952: 256–257; Jalan & Kapil 1964; Agababian 1966; Praglowski 1976).

An apocolpium (8–15 µm diameter) is delimited at the proximal pole by the apices of the colpi in the hexacolpate pollen type (Praglowski 1976); this region is thinner than other areas of the pollen wall, and presumably functions in enabling size and shape changes in response to the degree of hydration (harmomegathy). Pollen germination occurs by separation of the syncolpate apertures at the polar region, followed by protoplasmic extrusion and subsequently by pollen tube formation (Hayashi 1960; Kapil & Jalan 1964; Huynh 1976; Praglowski 1976).

Praglowski (1976) identified three pollen types within the species of *Schisandra* with hexacolpate pollen, differing with respect to the size of the lumina; two of these pollen

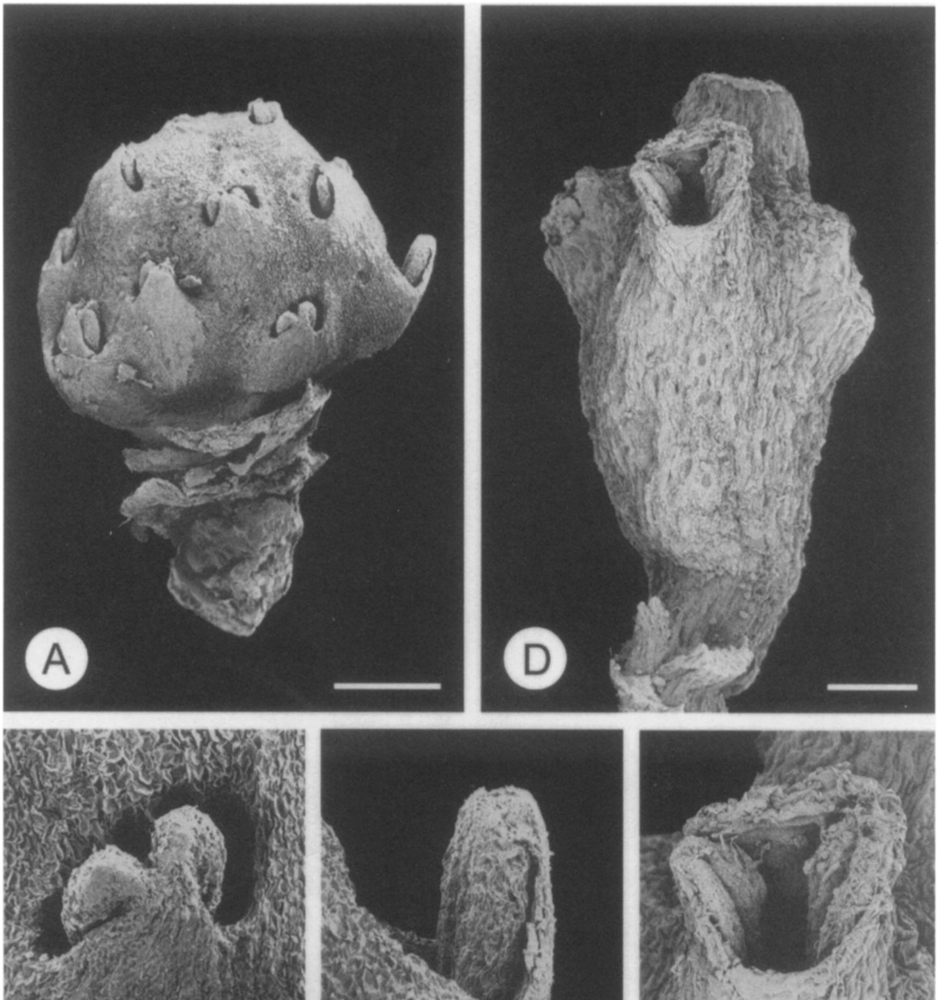


FIG. 11. Androecium type "D," occurring in *Schisandra* subg. *Schisandra* sect. *Sphaerostema* (scanning electron micrographs). A, androecium of *S. propinqua* subsp. *axillaris*. B, C, attachment of anthers in *S. propinqua* subsp. *axillaris* (B, abaxial view; C, lateral view). D, androecium of *S. plena*. E, attachment of anthers in *S. plena*. Scale bars: A, 1 mm; B–C, 250 µm; D, 500 µm; E, 250 µm. (A–C, *R. Brinkman 874a*, L; D, E, *A. Henry 11893*, A.) Reproduced from Saunders (1997b), © Cambridge University Press.

types were also reported from the related genus *Kadsura*, however, and the distinctions are therefore of comparatively minor phylogenetic significance.

Differing opinions have been expressed regarding the polarity of Schisandraceae pollen. Wodehouse (1936; subsequently supported by Jonker 1974) regarded the "convergent" pole as proximal, based on the proposed homology of the apocolpium with the

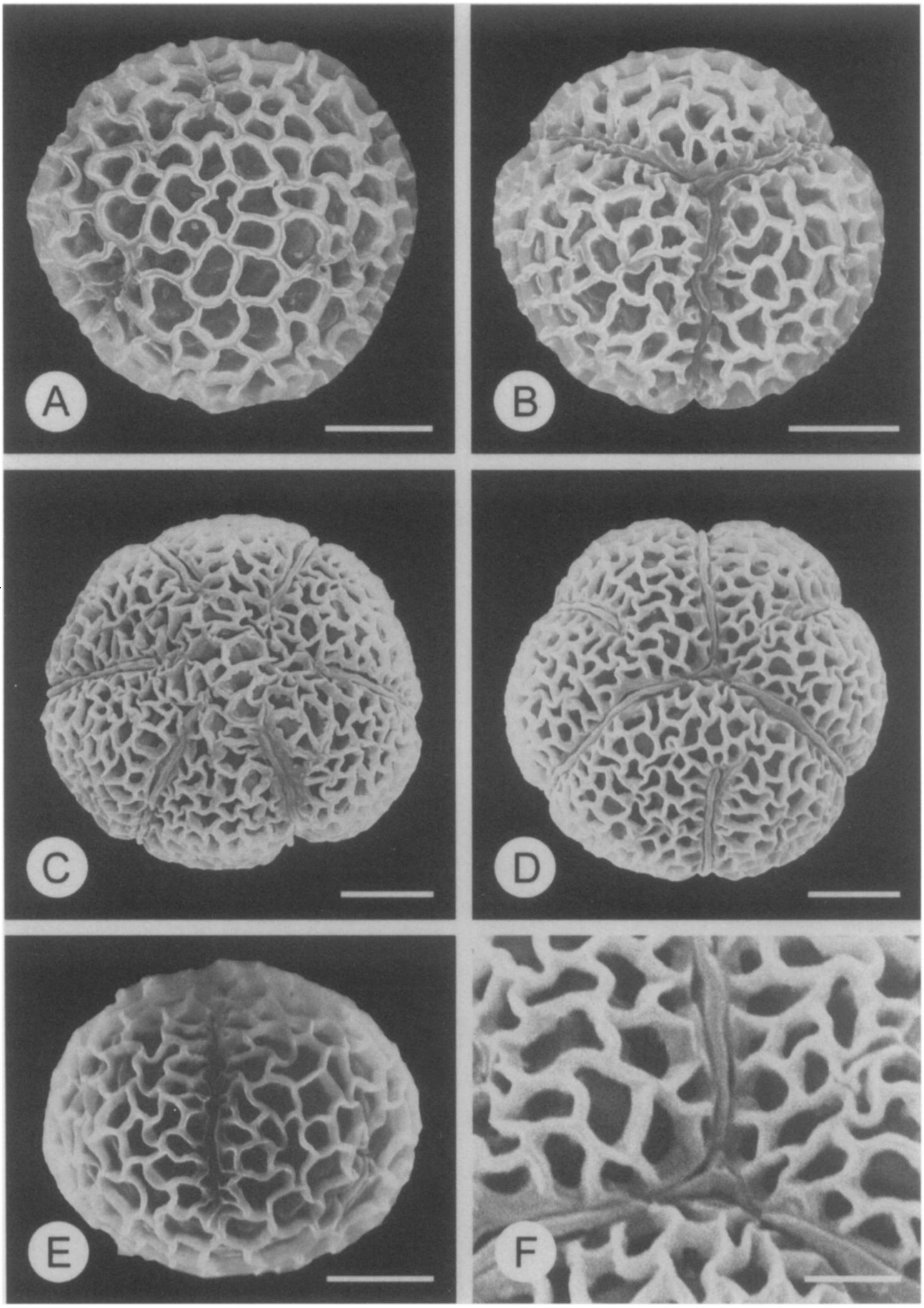


FIG. 12. Pollen morphology in *Schisandra* (scanning electron micrographs). A, B, tricolpate pollen of *S. grandiflora* (A, proximal pole; B, distal pole). C, D, hexacolpate pollen of *S. propinqua* subsp. *propinqua* (C, proximal pole; D, distal pole). E, lateral view of *S. grandiflora* pollen. F, colpus of *S. propinqua* subsp. *propinqua*. Scale bars: A–E, 5 µm; F, 2 µm. (A, B, E, *O. Polunin et al. 4131*, E; C, D, F, *A. D. Schilling & C. D. Sayers 558*, K.)

single aperture of *Drimys* (Winteraceae) pollen. Wodehouse proposed that the syncolpi were homologous with the trilete scar of pteridophyte spores (with apertures arranged so that three contiguous apertures occur at four points on the surface of the tetrad, in accordance with Garside's rule); he furthermore regarded the three shorter colpi of hexacolpate species as homologous with the colpi of ordinary tricolpate pollen grains.

Erdtman (1952: 255–258) proposed the opposing hypothesis in consideration of the frequency of variations at the convergent pole and the absence of any trilete tetrad scar in other Ranalean families. This view was subsequently supported by Muller (1970), who suggested that the syncolpi were homologous with distal trichotomosulcate apertures, and that the three shorter colpi originated de novo. This would imply that the convergent colpi are not "syncolpate," since they are derived from trichotomosulcate intermediates and are therefore not truly "fused." Significantly, the long colpi are therefore oriented according to Garside's rule, in contrast to most tricolpate pollen, which conforms to Fischer's rule.

The problem of pollen polarity in the Schisandraceae was ultimately resolved by direct observation of rare pollen tetrads in *Schisandra sphenanthera* and *S. incarnata* that had failed to separate into monads (Huynh 1976; Praglowski 1976). These studies confirmed Erdtman's (1952) and Muller's (1970) hypothesis that the colpi converge over the distal pole.

Recent cladistic analyses by Doyle et al. (1990) have corroborated this theory, and have indicated that the pollen of the Schisandraceae (and of the related family Illiciaceae) is phylogenetically derived from a form with a single distal aperture and united in tetrads, as in most extant Winteraceae. It can be concluded that colpate pollen originated independently in the Illiciales and other dicotyledons (Doyle et al. 1990).

Microsporogenesis has been described for two species of *Schisandra*, *S. repanda* (Hayashi 1960) and *S. grandiflora* (Kapil & Jalan 1964), although the taxonomic determination of the latter is in doubt since the authors describe the pollen as hexacolpate (discussed above). The tapetum is glandular and of parietal origin, and is reported to be a single layer in *S. repanda*, but irregularly bilayered in "*S. grandiflora*." The tapetal cells are either binucleate (*S. repanda*) or else initially uninucleate but subsequently becoming polyploid as a result of repeated nuclear divisions and fusions ("*S. grandiflora*"). Divisions of the microspore mother cells are simultaneous; both tetrahedral and decussate tetrads are formed in "*S. grandiflora*," but only tetrahedral types in *S. repanda*. The pollen grains are bicelled when the anthers dehisce. Microsporogenesis and the development of the male gametophyte in *Schisandra* is generally similar to that of *Kadsura* and *Illicium* (Hayashi 1960, 1965; Vijayaraghavan & Dhar 1975).

GYNOECIUM

Schisandra species have apocarpous gynoecia, with 12–120 ascidiate carpels spirally arranged around a cylindrical to conical receptacle (Fig. 13A–C). Individual carpels consist of a rounded ovarial region with a double stigmatic crest that is elongated into an unvascularised "pseudostyle" (sensu Smith 1947); the comparatively elaborate "pseudostigma" observed in *Kadsura* (Saunders 1998: 17, 18) is not evident in *Schisandra* (Fig. 13D). The stigmatic surface is unicellular-papillate and heavily secretory (Igersheim & Endress 1997). The carpel wall contains ethereal oil, tanniferous and mucilage cells, and cells with oxalate druses and crystals (Fig. 3B; Jalan 1965, 1975; Igersheim & Endress 1997). Although the vascular system in the carpel consists of the typical single dorsal trace and double ventral traces, it is unusual since it is either only the dorsal trace that provides

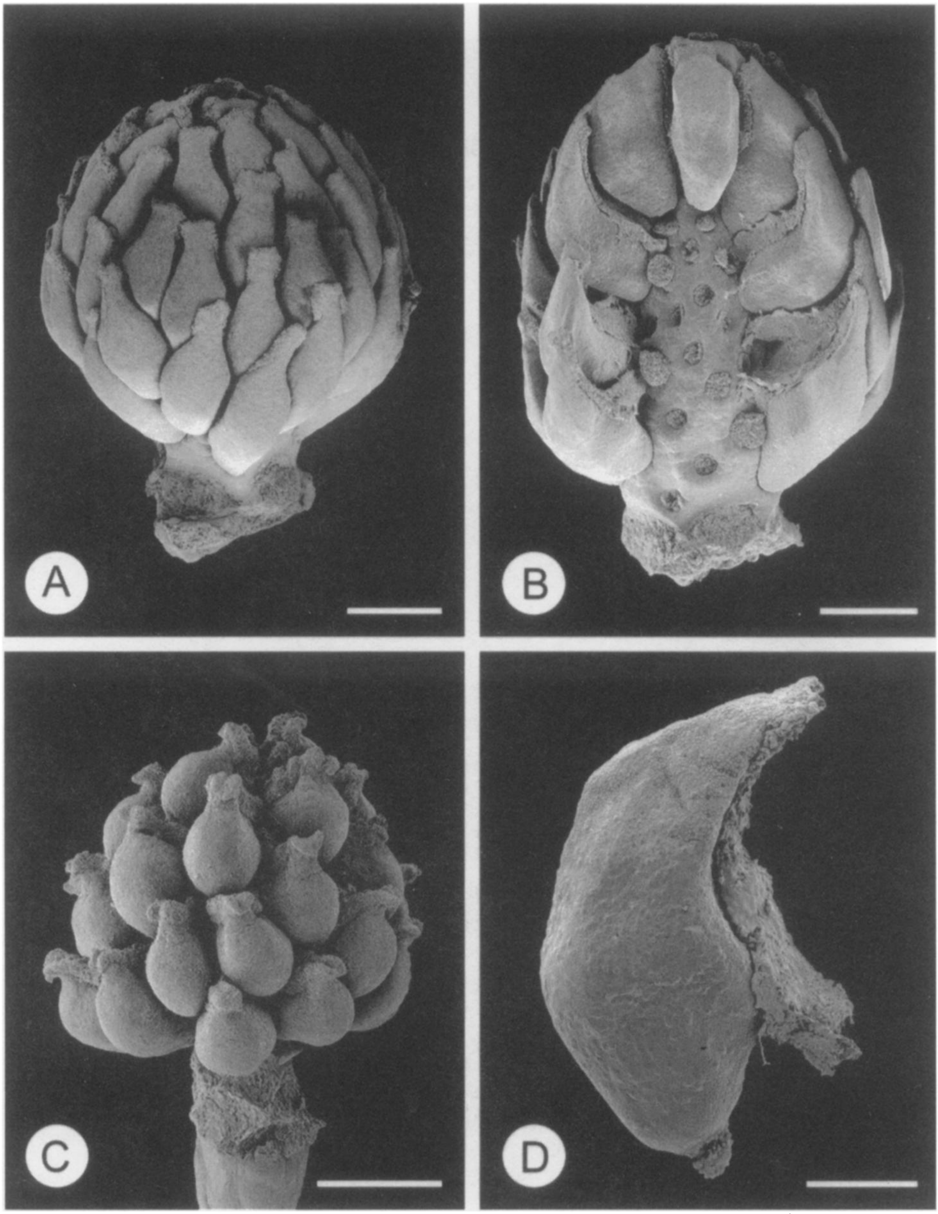


FIG. 13. Gynoecium and carpel structure in *Schisandra* (scanning electron micrographs). A, entire gynoecium (*S. arisanensis* subsp. *arisanensis*). B, gynoecium with proximal carpels removed, showing elongate receptacle (*S. arisanensis* subsp. *arisanensis*). C, entire gynoecium, shortly after fertilization (*S. chinensis*). D, solitary carpel, with pseudostyle (*S. arisanensis* subsp. *arisanensis*). Scale bars: A–C, 1 mm; D, 500 µm. (A, B, D, *S.-M. Chaw 616*, HKU; C, *X. Li, H. Chang & Y. Wang s.n.*, HKU.)

the vascular supply for the ovules (Jalan 1966; Melville 1969) or else both the dorsal and ventral traces (Ozenda 1946, 1949; Leinfellner 1966; Tucker & Bourland 1994). According to Bailey and Swamy (1951), the reduction of the ventral traces is correlated with the "adaxial deformation" of the carpel, resulting in a conspicuously arched dorsal side. Patterns of gynoecial development have been described for *S. chinensis* (Kolbasina 1967) and *S. glabra* (Tucker & Bourland 1994).

Intercarpellary spaces in the gynoecium are filled with a mucilaginous pectic secretion, which enables the transmission of pollen tubes between carpels; although *Schisandra* gynoecia are structurally apocarpous, they are therefore functionally syncarpous (Igersheim & Endress 1997). Similar "cryptic extragynoecial compita" are also reported in *Kadsura* (Igersheim & Endress 1997), *Illicium* (Williams et al. 1993) and *Austrobaileya* (Endress 1980), and support the putative phylogenetic relationship between these genera.

OVULES AND MEGASPOROGENESIS

Individual carpels of *Schisandra* contain 1–2 (–3) ovules with lateral-laminar placentation. The ovules are medium-sized, anatropous, crassinucellate, and bitegmic (Fig. 14A); the inner integument is typically 2–3 cells thick (Hayashi 1963b; Kapil & Jalan 1964; Igersheim & Endress 1997), whereas the outer integument has been reported to be 4–7 cells thick (Hayashi 1963b; Kapil & Jalan 1964; Igersheim & Endress 1997). The micropyle is variably formed by the inner integument (*S. sphenanthera*: Igersheim & Endress 1997), outer integument (*S. chinensis*: Yoshida 1962), or both integuments (*S. grandiflora*: Kapil & Jalan 1964). Jalan and Bhandari (1963) have reported rare teratologies of *S. grandiflora* in which extracarpellary ovules develop.

Detailed descriptions of ovule and embryo sac development have been published for three species: *S. chinensis* (Yoshida 1962; Swamy 1964); *S. repanda* (Hayashi 1963b); and *S. grandiflora* (Kapil & Jalan 1964). In most of these publications, an essentially similar pattern of development is described. A hypodermal archaesporial cell undergoes periclinal cell division to form a primary parietal cell and an underlying sporogenous cell; the former then produces 3–5 parietal cells, whilst the sporogenous cell acts as the megaspore mother cell (Yoshida 1962; Hayashi 1963b; Kapil & Jalan 1964). The first meiotic division of the megaspore mother cell results in two dyad cells. The larger (lower) dyad cell then either divides to produce a linear triad (Fig. 14B; *S. chinensis*: Yoshida 1962; *S. grandiflora*: Kapil & Jalan 1964), or else both dyad cells undergo division, producing a T-shaped tetrad (Fig. 14C; *S. repanda*: Hayashi 1963b). In both cases, the micropylar cells degenerate, and it is only the chalazal megaspore that develops further. The resultant embryo sac is seven-celled and eight-nucleate, of the *Polygonum*-type (Fig. 14E), with ephemeral antipodal cells (Yoshida 1962; Hayashi 1963b; Kapil & Jalan 1964).

Swamy (1964) has described two developmental patterns for *S. chinensis*, however, which differ from that described above. In the first pattern, the megaspore mother cell undergoes meiosis I (without cell wall formation), giving rise to binucleate dyad cells; the micropylar dyad cell degenerates, and the chalazal dyad cell undergoes nuclear division to form the embryo sac. This is therefore a bisporic tetranucleate embryo sac, of the *Allium*-type. In the second developmental pattern described by Swamy, meiosis II is accompanied by wall formation, resulting in a linear tetrad of megaspores (Fig. 14D); the three micropylar cells degenerate, whereas the chalazal cell undergoes two divisions, resulting in a monosporic tetranucleate embryo sac, of the *Oenothera*-type. Batygina and

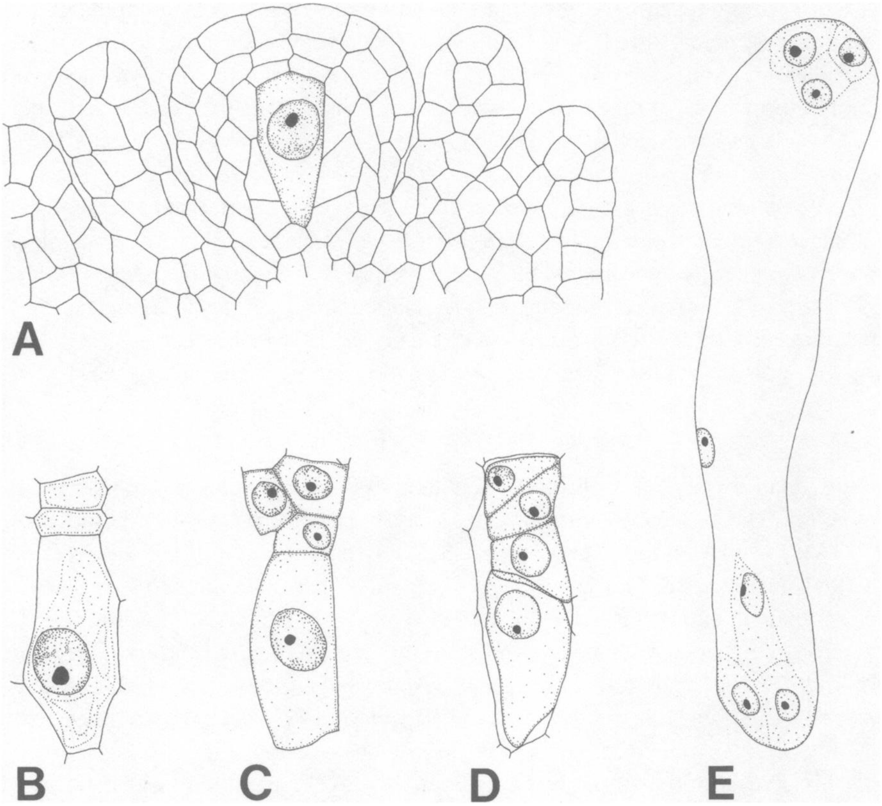


FIG. 14. Ovule anatomy in *Schisandra*. A, developing ovule, showing megaspore mother cell and two integuments (*S. chinensis*). B, linear triad of megaspores (*S. grandiflora*). C, T-shaped tetrad of megaspores (*S. repanda*). D, linear tetrad of megaspores (*S. chinensis*). E, mature embryo sac (*S. repanda*). (A, redrawn from Swamy, 1964: fig. 3; B, redrawn from Kapil & Jalan, 1964: fig. 4M; C, redrawn from Hayashi, 1963b: fig. 1.6; D, redrawn from Swamy, 1964: fig. 6; E, redrawn from Hayashi, 1963b: fig. 1.10.) Drawing by S. J. Stanley.

Vasilyeva (1995) have recently recognized a *Schisandra*-subtype of the *Oenothera*-type of embryo sac development.

Ovule development, megasporogenesis, and megagametogenesis in *Schisandra* is essentially similar to that of *Kadsura* (Hayashi 1963b; Vijayaraghavan & Dhar 1977) and *Illicium* (Hayashi 1963a). Although embryological data are widely interpreted as corroborating the close phylogenetic link between *Schisandra* and *Kadsura*, the relationship with *Illicium* is more controversial: Kapil and Jalan (1964) recommended that *Illicium* should be separated from *Schisandra* and *Kadsura* at the familial level, whereas Hayashi (1965) argued that they should be united.

SEEDS AND EMBRYOGENESIS

Schisandra seeds are small (2.4–6.0 × 2.6–7.5 mm) and flattened-reniform (rarely discoid or flattened-pyriform), with a lateral hilum (Fig. 15A–C). The external surface of the testa is either smooth (Fig. 15A, D; subg. *Pleiostema*, subg. *Schisandra* sect.

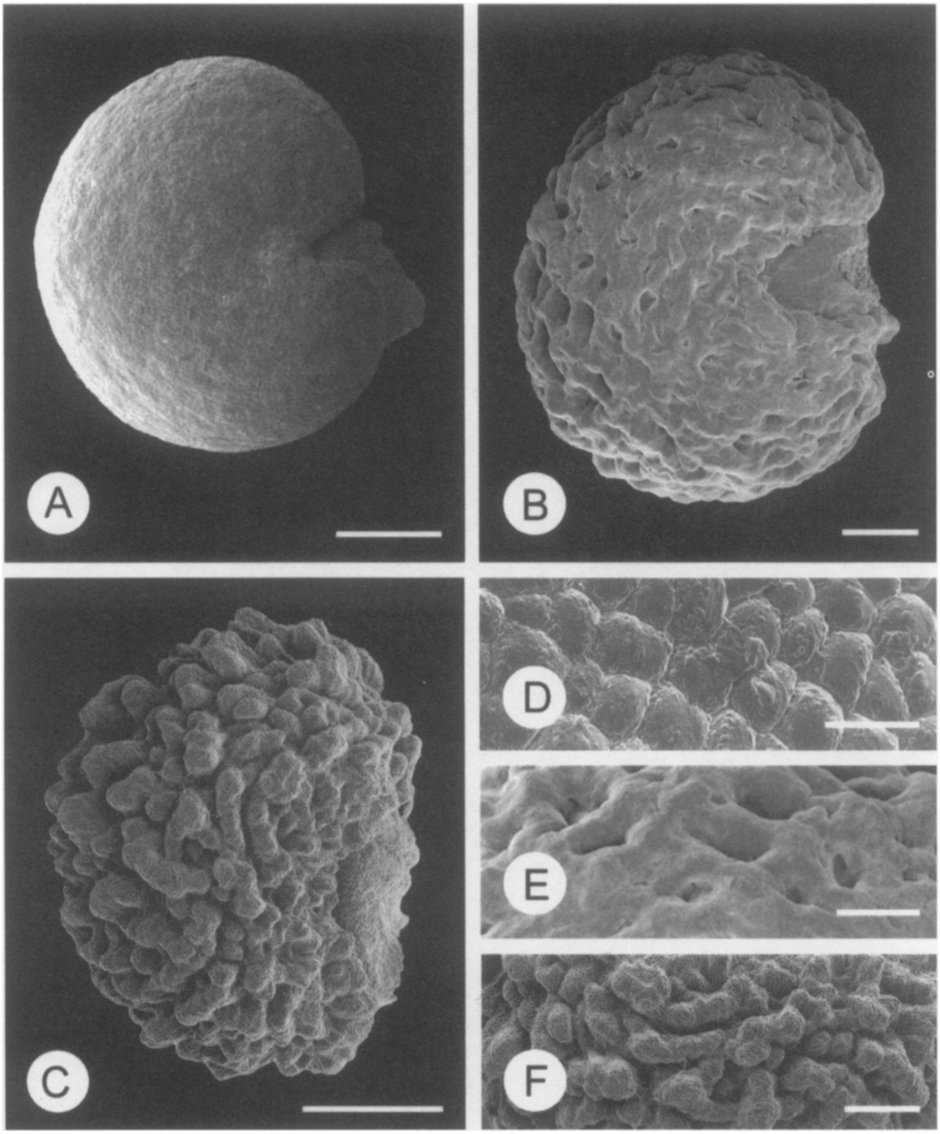


FIG. 15. Seed morphology in *Schisandra* (scanning electron micrographs). A, D, seed with smooth testa (*S. grandiflora*). B, E, seed with tuberculate testa (*S. bicolor*). C, F, seed with highly tuberculate testa (*S. longipes*). Scale bars: A–C, 1 mm; D, 25 μm; E, F, 500 μm. (A, D, *D. G. Long et al. 710*, E; B, E, *M. S. Huang 112217*, IBSC; C, F, *Yue-71 Expedition 543*, IBSC.)

Maximowiczia, and subg. *Schisandra* sect. *Sphaerostema*) or rugulose to tuberculate (Fig. 15B, C, E, F; subg. *Sinoschisandra*, and subg. *Schisandra* sect. *Schisandra*).

The internal anatomy of the seed has previously been described for only two species, viz. *S. chinensis* (Netolitzky 1926; Fujita 1929; Melikian 1988; Wang et al. 1992) and *S. grandiflora* (Kapil & Jalan 1964); anatomical descriptions of seeds of *S. rubriflora*, *S. neglecta*, and *S. repanda* are published here for the first time. The seeds of all species

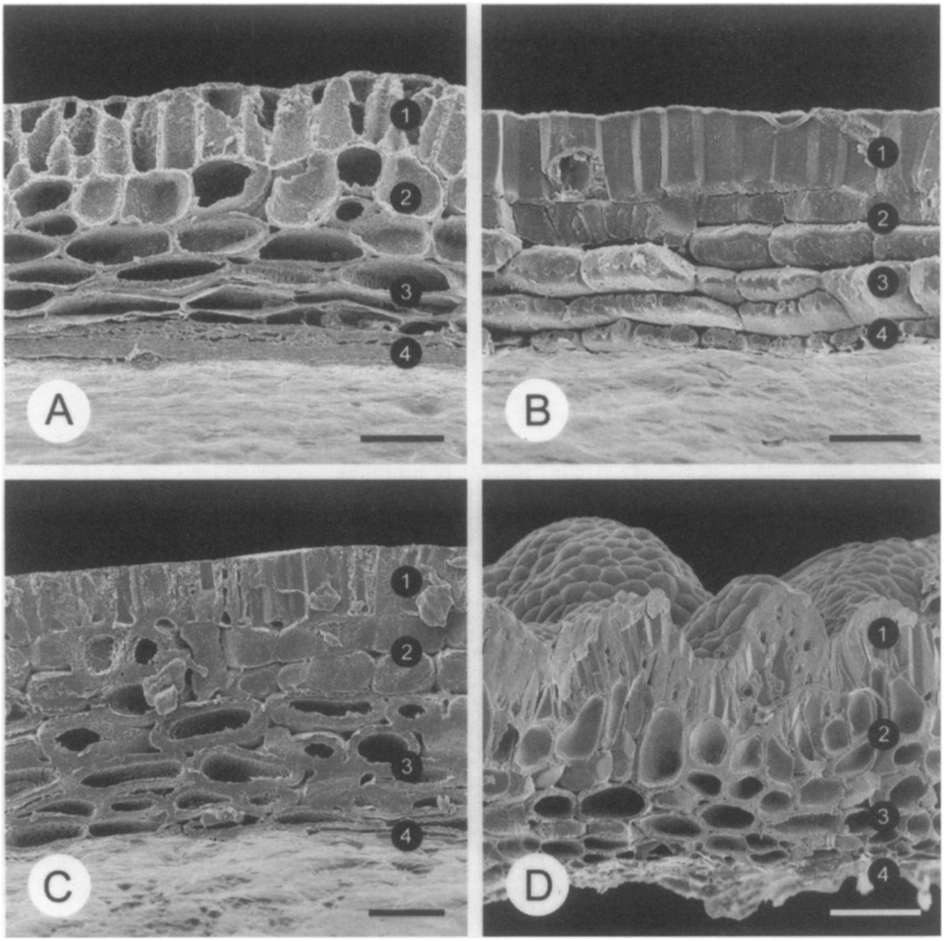


FIG. 16. Seed coat structure in *Schisandra*: transverse sections (scanning electron micrographs; 1 = outer epidermis of testa, 2 = outer hypodermis of testa, 3 = inner hypodermis of testa, 4 = inner epidermis of testa; tegmen not visible). A, *S. neglecta*. B, *S. rubriflora* (testa fractured between cells, illustrating cell shape). C, *S. chinensis*. D, *S. repanda*. Scale bars: A–C = 50 µm; D = 100 µm. (A, *K. M. Feng 2844*, A; B, *C. W. Wang 67966*, A; C, *A. P. Shklyaeva et al. s.n.*, UC; D, *H. Kanai 6350*, A.)

examined are structurally similar, with a seed coat consisting of two layers, the testa and tegmen, derived from the outer and inner ovular integuments respectively (sensu Corner 1976: 8). The testa is not multiplicative and consists of four distinct layers, viz. outer epidermis, outer hypodermis, inner hypodermis, and inner epidermis (Fujita 1929; Kapil & Jalan 1964; Melikian 1988; Wang et al. 1992). The outer epidermis of the testa (1 in Fig. 16A–D) is composed of a single layer of vertically oriented macrosclereids. The outer hypodermis (2 in Fig. 16A–D) is 2–4 cells thick and consists of irregularly shaped brachysclereids that are generally horizontally oriented. The inner hypodermis (3 in Fig. 16A–D) is a single layer of enlarged generally thin-walled cells, which ultimately become compressed. The inner epidermis (4 in Fig. 16A–D) is also a single layer of enlarged cells, although there is variation in the degree of wall thickening, with isolated sclerotic cells present; ethereal oil cells are particularly common in this layer (Fujita 1929; Wang et al. 1992). The tegmen, derived from the inner integument, does not undergo cell division and remains a minor component of the seed coat, ultimately becoming crushed. The primary mechanical layers in the seed coat are the outer epidermis and outer hypodermis of the testa. Seeds of *Schisandra* can therefore be classified as intermediate between exotestal and mesotestal seeds (sensu Corner 1976: 10), in contrast to seeds of *Kadsura* (Saunders 1998: 20–22), which are strictly exotestal. The rugulose or tuberculate ornamentation evident on seeds of several *Schisandra* species is the consequence of areas of thickened outer hypodermis (Fig. 16D).

Embryogenesis has been described in detail for two species, *S. repanda* (Hayashi 1963b) and *S. grandiflora* (Kapil & Jalan 1964). Following fertilization, the primary endosperm nucleus divides transversely to form two unequally sized cells; the smaller cell at the chalazal end (in *S. grandiflora*) or both cells (in *S. repanda*) subsequently divide to form a large cellular endosperm that occupies most of the content of the seed; the endosperm stores starch and oil.

Transverse division of the zygote results in a basal cell and a terminal cell; these cells subsequently divide to form a 4-celled proembryo, which consists of two juxtaposed cells derived from the terminal cell and two superposed cells derived from the basal cell. Subsequent divisions are generally simultaneous, and the embryo develops into an ovoid mass, later becoming heart-shaped. Half of the cells derived from the basal cell develop into a massive suspensor, whilst the remaining derivatives of the basal cell and those of the terminal cell develop into the embryo; the formation of the embryo is therefore of the Asterad-type. At the time of seed dispersal, the embryo of *S. repanda* is still heart-shaped and is not obviously dicotyledonous (Hayashi 1963b), although the embryo of *S. grandiflora* has small but distinct cotyledons (Kapil & Jalan 1964).

Embryogenesis in *Schisandra* is very similar to that in *Kadsura* (Hayashi 1963b) and *Illicium* (Hayashi 1963a). This has been interpreted as indicating a close taxonomic relationship (e.g., Hayashi 1965), although Kapil and Jalan (1964) argued that *Illicium* should be separated from *Schisandra* and *Kadsura* at the familial level.

The small embryo evident in mature *Schisandra* seeds is presumably correlated with the seed's capacity to remain dormant: *S. chinensis* seeds exhibit "morphophysiological" dormancy (a combination of both morphological and physiological mechanisms of dormancy) (Grushvitzky 1967; Nikolaeva 1969: 20), and have been found in persistent seed banks (Baskin & Baskin 1998: 147).

FRUITS

The receptacle in female flowers of *Schisandra* undergoes considerable post-fertilization development, resulting in a raceme-like aggregate fruit (Figs. 23E, 37F, 41G, 44E; Plate 1I). Individual carpels develop into fleshy indehiscent bacceta (sensu Spjut, 1994), which are typically bright red at maturity. The apocarps are small (2.5–16 × 2.5–16 mm) and widely separated on the torus of the fruit, and contain 1–2 (–3) seeds.

The anatomy of the pericarp has previously been studied in *S. chinensis* (Fujita 1929; Berger 1952; Wang et al. 1992) and *S. grandiflora* (Kapil & Jalan 1964). In these species, the pericarp consists of three distinct layers. The outermost layer, the exocarp (or epicarp), is a thin pigmented epidermal layer containing ethereal oil cells. The mesocarp forms the bulk of the fruit and is composed of unspecialized parenchyma cells with numerous ethereal oil cells. The innermost zone, the endocarp, is narrow.

DISTRIBUTION AND ECOLOGY

Of the 23 species of *Schisandra* recognized in the present monograph, 20 are indigenous to continental Asia (Fig. 17A–E). The center of diversity of the genus lies in central and southern China: 12 species occur in the Sikang-Yunnan Province of the Eastern Asiatic Region (sensu Takhtajan 1986), with eight species in the Central Chinese Province. *Schisandra elongata* (subg. *Sinoschisandra*) and *S. propinqua* subsp. *axillaris* (subg. *Schisandra* sect. *Sphaerostema*) are indigenous to Java. The only species indigenous to an area outside Asia is *S. glabra* (subg. *Schisandra* sect. *Schisandra*) from the North American Atlantic and Madrean Regions (sensu Takhtajan 1986). Possible explanations for these disjunct distributions are discussed below under "Historical Biogeography."

Schisandra species are scandent and scrambling woody vines, supporting themselves on rocks, shrubs, or trees; they generally grow near ridges, slopes, and ravines, and often near streams. Most species grow in broad-leaved forests (less commonly in open scrubland) in temperate or subtropical regions, although species from higher altitudes (e.g., *S. grandiflora*, *S. rubriflora*, *S. sphaerandra*) or higher latitudes (e.g., *S. chinensis*) frequently grow in coniferous or mixed forests. Where collection data is sufficiently detailed, the dominant genera in these forests are listed in the distributional data following the taxonomic account of individual species. *Schisandra* occupies a broad range of altitudes, from sea level (*S. glabra*) to 4000 m (*S. grandiflora*) (Fig. 18).

REPRODUCTIVE BIOLOGY

FLORAL REPRODUCTIVE BIOLOGY

Smith (1947), after examination of extensive herbarium material, described *Schisandra* as "dioecious or monoecious." Of the 25 species recognized by Smith, only five were observed to be monoecious; it is probable, however, that this is an under-estimate arising from the difficulty in assessing the sexuality of individual plants in herbarium specimens, which generally consist of only single branches. Ueda (1988) studied nearly 200 plants of *S. chinensis* in cultivation over an eight-year period. Sexuality was labile, with individuals changing among male, female, and monoecious states from year to year; these changes appeared to be correlated with overall plant size and soil sterility. Most individuals were dioecious within a single flowering season, suggesting that a greater proportion, if not all, *Schisandra* species are capable of monoecy, but appear to be dioecious due the infrequency of monoecy. This change in sex expression is not unusual (Schlessman 1988) and is known to be affected by various hormonal and environmental factors (Meagher 1988, and references therein). Male flowers appear to predominate in *Schisandra*; 73% of over 300 flowers dissected during the present study were staminate.

During his investigation of sex change in *S. chinensis*, Ueda (1988) discovered a small number of essentially male plants that apparently bore one or two bisexual flowers. These bisexual flowers were not illustrated or preserved, and the fertility of the stamens and carpels was not tested. If this report is correct, the rare bisexual flowers presumably represent teratologies; the present author failed to observe andromonoecy or floral hermaphroditism in the genus, and there are no other published reports of this.

Schisandra chinensis is the only species for which pollinators have been identified: Kozo-Poljanski (1946) recorded a wide variety of different insects visiting the flowers, including beetles, bees, and small moths. The most frequent and persistent visitors were

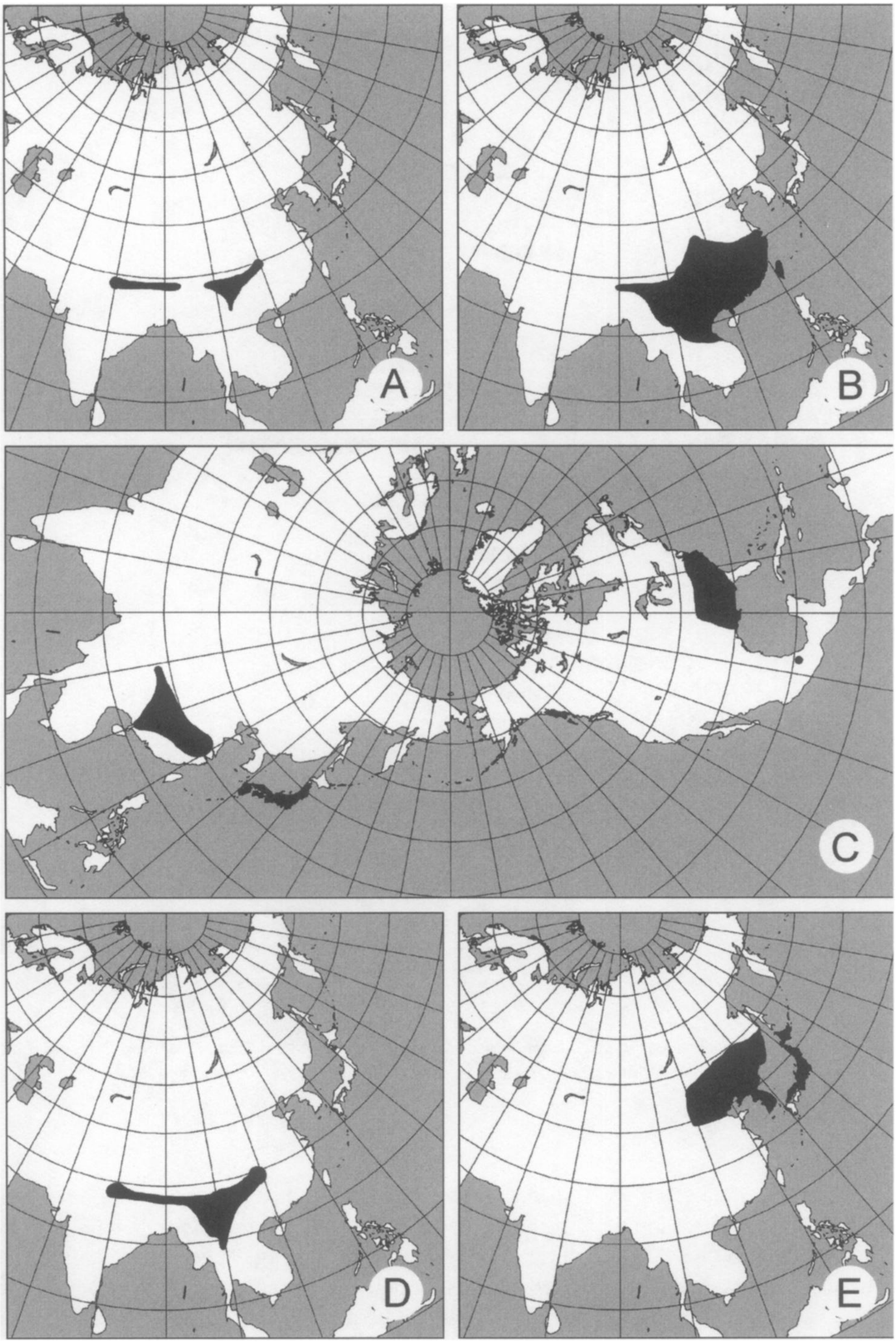


FIG. 17. Distribution of supraspecific taxa in *Schisandra*. A, *S.* subg. *Pleiostema*. B, *S.* subg. *Sinoschisandra* (also present in Java: Fig. 32). C, *S.* subg. *Schisandra* sect. *Schisandra*. D, *S.* subg. *Schisandra* sect. *Sphaerostema* (also present in Java: Fig. 45). E, *S.* subg. *Schisandra* sect. *Maximowiczia*.

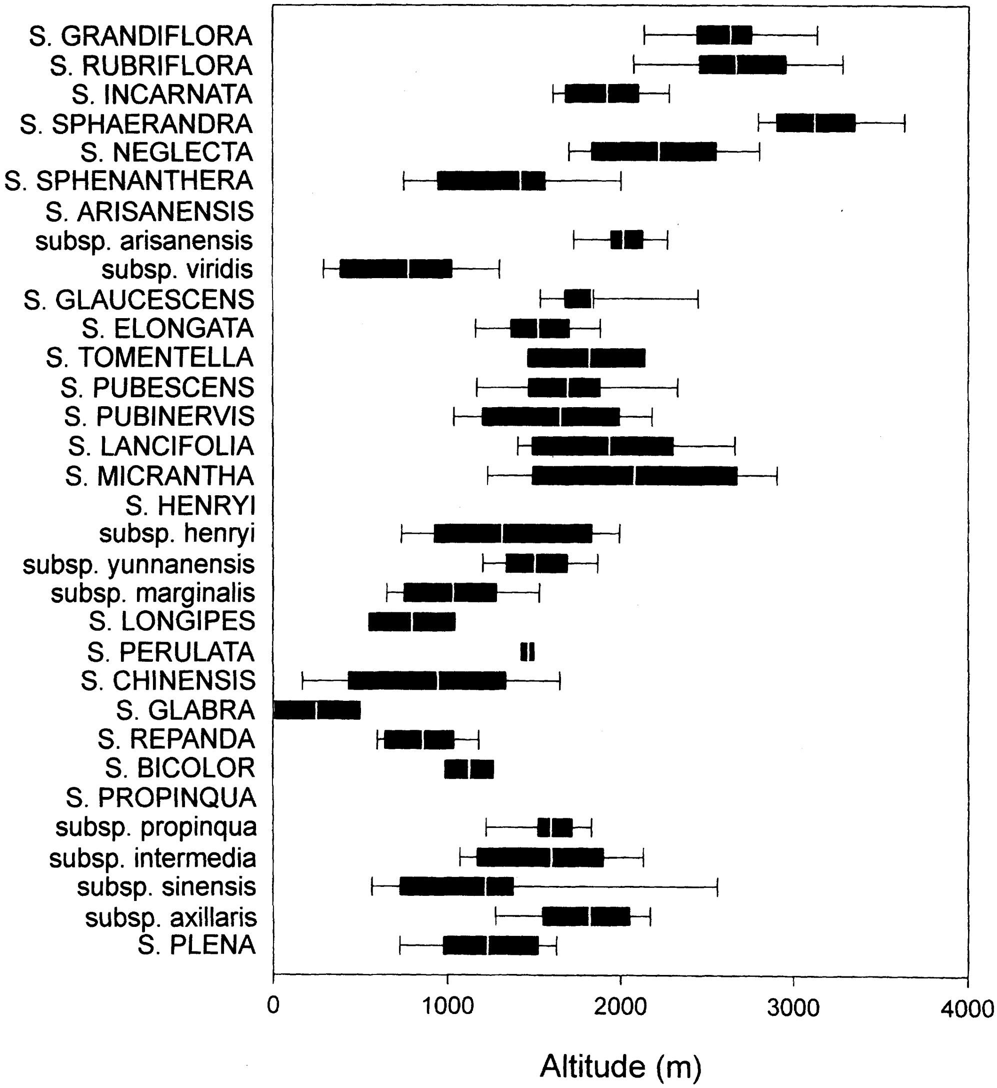


FIG. 18. Altitudinal ranges for species of *Schisandra*, with means and 5th/95th percentiles. Percentiles are omitted for species for which altitudinal records are insufficient. Species names are arranged in systematic order, as listed in the text.

Halictus bees, although Kozo-Poljanski noted that the frequency of visits was nevertheless low. Significantly, however, the plants under study were grown in cultivation in Alma-Ata, Kazakhstan, outside the natural distribution of the species. *Schisandra chinensis* is unusual within the genus, both in terms of its diminutive flower size with reduced stamen number and also in its high-latitude, cool-temperate distribution; these differences limit the extent to which extrapolations can be made regarding the pollination system in other species in the genus.

Willemstein (1987) drew general inferences on the pollination mechanism in the Schisandraceae based on floral morphology, concluding that they are successfully entomogamous and most probably cantharogamous (beetle-pollinated). Willemstein cited different attractants in flowers of different sexes, viz.: the stigmatic exudate of female flowers, and the carnose androecial mass of male flowers as a food source for beetles. As noted by Saunders (1998: 24), however, it seems unlikely that a pollination syndrome would have evolved that relies on different rewards being offered by flowers of different sexes to the same pollinator.

FRUIT AND SEED DISPERSAL

Fruit anatomy of *Schisandra* is generally indicative of bird dispersal and exhibits many of the characteristic features of ornithochory (Ridley 1930; Pijl 1982). Although the aggregate fruits can be quite large, they are composed of individual baccae that are generally only 2.5–16 mm in diameter. The baccae have a basal constriction at the point of attachment to the torus of the fruit and are widely separated from one another, enabling easy removal by birds. The apocarps are green and unpalatable when unripe, but turn deep red to scarlet (rarely blackish) at maturity. The pericarp is fleshy, without a hard exocarp, and lacks any significant odor. Each bacca typically contains only 1–2 (–3) seeds, measuring 2.4–6.0 × 2.6–7.5 mm, with a tough testa and capable of passing through the digestive tracts of many birds.

Although birds are probably the primary means of seed dispersal, fruits of an unspecified species of *Schisandra* have been shown to be an important food source for black gibbons (*Hylobates concolor*) during the wet season in Yunnan (Sheeran 1993); the significance of this report is limited, however, since primates are comparatively unspecialized feeders (Pijl 1982).

CYTOLOGY

Ten species of *Schisandra* have been examined cytologically (Appendix 1). Most reports are meiotic counts of n = 14 or corresponding mitotic counts of 2n = 28. Karyotypic formulae have been calculated for four species: *S. bicolor* (Wu & Huang 1995) and *S. glabra* (Stone 1968) are reported to have 14 pairs of metacentric chromosomes, whilst *S. repanda* (Okada 1975) and *S. chinensis* (Chen et al. 1993: 319–320) are reported to have 12 pairs of metacentric and 2 pairs of submetacentric chromosomes. X. Li et al. (1993) observed that one chromosome pair in *S. chinensis* has a satellite region, although this was not corroborated by Chen et al. (1993). In all cases the karyotype is described as symmetrical, with asymmetry indices of 57.11 (Chen et al. 1993: 319–320) and 55.02 (Wu & Huang 1995) calculated for *S. chinensis* and *S. bicolor*, respectively. All species of the related genus *Kadsura* that have been examined cytologically are reported to be 2n = 28 and to be generally symmetrical (reviewed in Saunders 1998: 25–26).

Although most chromosome counts indicate a base number of n = 14 for the genus, there are several reports of cytotypes of *S. grandiflora* with n = 7 (Appendix 1). These cytotypes appear to be naturally occurring in several localities (published reports are based on populations in Nepal and Himachal Pradesh, India), and there does not appear to be any significant reduction in pollen fertility (Sandhu et al. 1989). These results would suggest that the base chromosome number for the genus is n = 7, and that the widespread counts of 2n = 28 represent tetraploids; this is consistent with the hypothetical base chromosome number of n = 7 for primitive angiosperms, as proposed by Raven and Kyhos (1965).

There are two reported chromosome counts for *Schisandra*, however, which do not conform to the suggested base number of seven. Bostick (1965) reported n = 13 for *S. glabra* (under the synonym "*S. coccinea*"). This count may be erroneous, since it is based on the study of only one population, whereas subsequent reports based on several populations of the same species invariably indicate n = 14 and 2n = 28 (Stone in Anonymous 1965; Stone 1968); it is also possible, however, that the record of n = 13 represents a dysploid reduction from n = 14, as suggested by Ehrendorfer et al. (1968).

More recently, Solovyeva (1998) has reported a chromosome count of 2n = 24 for *S. chinensis*, with nine metacentric and three submetacentric chromosomes. This is in conflict with earlier reports of 2n = 28 (Darlington & Wylie 1955; Probatova & Sokolovskaya 1981; Probatova et al. 1989; Chen et al. 1993; Li et al. 1993), although Solovyeva (1998) reported the presence of satellites and secondary constrictions that could lead to erroneous counts. Curiously, most of the photographs of cytological preparations in Solovyeva's paper show 28 chromosomes.

PHYTOCHEMISTRY*

Schisandra has been extensively studied phytochemically, with reports for 15 of the 23 species in the genus. All the major supraspecific groups in the genus have been investigated, although the majority of studies have focused on *S. chinensis* because of its value in traditional Chinese medicine (discussed below, under "Ethnobotany"). Five significant classes of compounds have been reported (Table 2; Appendix 2), viz.: monoterpenes; sesquiterpenes (subdivided into the following biogenetic groups in the present study: sesquicaranes, chamigranes, cadinanes, and copaenes); lignans (subdivided into 8,8′-lignans and 8,8′,2,2′-cyclooctane lignans); triterpenes (subdivided into lanostanes, *seco*-lanostanes, cycloartanes, and *seco*-cycloartanes); and glycosides. Flavonoids have also been reported, but are not included in Table 2 or Appendix 2 since they are widespread in angiosperms; although flavonoid variation is very extensive, comparisons can only be made at the level of specific phytochemicals, and this is beyond the scope of this survey.

Lignans are the predominant phytochemical class in the genus: 8,8′-lignans have been reported in seven species, and 8,8′,2,2′-cyclooctane lignans in 13 species. They are presumably ubiquitous in the genus, and their apparent absence in some species probably reflects the failure of chemists to report the presence of compounds that are already known from other sources rather than their actual absence. Triterpenes are also very common in the genus and are again possibly more widespread than the results in Table 2 would suggest. The occurrence of lignans and triterpenes in *Schisandra* is therefore of comparatively little taxonomic significance.

In *Schisandra*, sesquiterpenes have only been reported from *S. repanda* (subg. *Schisandra* sect. *Schisandra*) and *S. chinensis* (subg. *Schisandra* sect. *Maximowiczia*); significantly, they have not been reported from any of the other supraspecific groups in the genus. This reflects the close phylogenetic affinities between these two species (described below, under "Phylogeny and Supraspecific Classification"). Glycosides are also only reported from *S. repanda* and *S. chinensis*, although this is of comparatively little taxonomic

---

* Geoffrey D. Brown, Department of Chemistry, The University of Hong Kong, Pokfulam Road, Hong Kong, China.

TABLE 2. Occurrence of major phytochemical groups in *Schisandra*, based on both observed (filled circles) and inferred (open circles) presence of biogenetic groups. Taxon codes used: GRAN = *S. grandiflora*; RUBR = *S. rubriflora*; INCA = *S. incarnata*; SPHA = *S. sphaerandra*; NEGL = *S. neglecta*; SPHE = *S. sphenanthera*; ARIV = *S. arisanensis* subsp. *viridis*; GLAU = *S. glaucescens*; PUBE = *S. pubescens*; LANC = *S. lancifolia*; HENR = *S. henryi*; REPA = *S. repanda*; CHIN = *S. chinensis*; PROP = *S. propinqua*; PLEN = *S. plena*. Supraspecific taxa indicated by superscript numbers: 1 = subg. *Pleiostema*; 2 = subg. *Sinoschisandra*; 3 = subg. *Schisandra* sect. *Maximowiczia*; 4 = subg. *Schisandra* sect. *Schisandra*; 5 = subg. *Schisandra* sect. *Sphaerostema*. A detailed list of phytochemical data with reference citations is given in Appendix 2.

	GRAN^1	RUBR^1	INCA^1	SPHA^1	NEGL^2	SPHE^2	ARIV^2	GLAU^2	PUBE^2	LANC^2	HENR^2	CHIN^3	REPA^4	PROP^5	PLEN^5
MENTHANE MONOTERPENES												●			
SESQUITERPENES															
Sesquicaranes												●			
Chamigranes												●			
Cadinanes													●		
Copaenes												●			
LIGNANS															
8,8′-lignans		●				●	●				●	●	●	●	
Dibenzylcyclooctanes		●	●		●	●	●	●	●	●	●	●	●	●	●
TRITERPENES															
Lanostanes						●							○	●	
seco-Lanostanes													●	●	
Cycloartanes	●			○		●							●		
seco-Cycloartanes				●											
GLYCOSIDES												●	●		

significance since they are widespread throughout the plant kingdom. The single report of menthane monoterpenes in *S. chinensis* (Hou et al. 1995) is also of little taxonomic significance, because individual compounds were not rigorously characterized in the original report. Compounds were determined as menthane monoterpenes solely on the basis of gas chromatography results.

Phytochemical data (Gottlieb et al. 1989; Sy et al. 1997) have recently been used to investigate phylogenetic relationships within the Magnoliidae. The Schisandraceae have been shown to be phytochemically distinct (Sy et al. 1997) since they contain lanostanes, *seco*-lanostanes, 8,8′-lignans and 8,8′,2,2′-cyclooctane lignans (dibenzylcyclooctanes), which are not found in *Illicium*. Gottlieb et al. (1989) furthermore noted that neolignans are absent from *Illicium* although present in the Schisandraceae; this evidence, however, was not based on the currently adopted definition of lignans and neolignans (Whiting 1985). Gottlieb et al. (1989) also suggested that there was a relationship between the Schisandraceae and Illiciaceae, since both apparently contain esters of angelic and tiglic acids; this was contradicted by Sy et al. (1997), who failed to find reports of such esters in *Illicium* during an extensive review of the phytochemical literature. Detailed investigation of the phytochemistry of *Illicium dunnianum* Tutcher by Sy et al. (1997) revealed the occurrence of cycloartanes and *seco*-cycloartanes for the first time in the genus; the presence of these chemical classes in both the Illiciaceae and Schisandraceae suggests a common phylogenetic origin.

ETHNOBOTANY

MEDICINAL USES

Schisandra has been used extensively in traditional Chinese herbal medicine since the later Han dynasty (AD 25–220). The various medicinal uses of different species of *Schisandra* were first described in 1596 by Li Shi Zhen in his *Compendium of Materia Medica*.

The fruits of *Schisandra chinensis* have been the most widely used. The Chinese name for the medicine, generally transliterated from the Chinese as "wu-wei-zi," means "five tastes plant," reflecting the different flavors of the seed and pericarp layers, and the belief that it contains the quintessence of the five elements. It is most commonly prescribed for the treatment of coughs, asthma, tuberculosis, and other lung conditions (Song & Xiao 1982; Song 1988; Lo 1994: 268), or as a digestive aid and in the treatment of diarrhea, enuresis, and kidney conditions (Song & Xiao 1982; Lo 1994: 268). *Schisandra chinensis* fruits have also been used in the treatment of hepatitis and other liver conditions, and recent research has confirmed that the fruits possess antihepatotoxic properties (Hikino 1985; Zhou 1985; Bi 1987). Other reported uses include the treatment of insomnia (Lo 1994: 268) and as an antipyretic (Mitsuhashi 1976).

Fruits of many other species of *Schisandra* are used in Chinese medicine for the treatment of similar conditions, viz.: *S. arisanensis* subsp. *arisanensis* (T.-S. Liu 1960: 83), *S. glaucescens* (Song & Xiao 1982; Song 1988; Yuan & Chao 1996), *S. henryi* (Song et al. 1977; Song & Xiao 1982; Yuan & Chao 1996), *S. incarnata* (Song 1990), *S. lancifolia* (Song & Xiao 1982), *S. neglecta* (Rao 1981), *S. propinqua* (Perry & Metzger 1980: 382; Song & Xiao 1982; Song 1988), *S. pubescens* (Song & Xiao 1982), *S. rubriflora* (Song & Xiao 1982), *S. sphaerandra* (Song & Xiao 1982), and *S. sphenanthera* (Song & Xiao

1982; Song 1988). They are generally prescribed as a substitute for *S. chinensis*, however, and are often reported to be less effective.

The stems and roots of many *Schisandra* species have also been used medicinally, primarily as an analgesic for rheumatism, arthritis, and traumatic injury, viz.: *S. bicolor* (Song 1990); *S. henryi* (Song et al. 1977; Song & Xiao 1982); *S. micrantha* (Song & Xiao 1982); *S. propinqua* (Cheo 1947; Song & Xiao 1982); *S. rubriflora* (Song & Xiao 1982); and *S. arisanensis* subsp. *viridis* (South China Institute of Botany 1982: 62). The stems and roots of *S. bicolor* (Song & Xiao 1982) and *S. glaucescens* (Song & Xiao 1982) have also been used as a general neurasthenic.

OTHER USES

The fruits of several species are reported to be eaten locally, although they are of no commercial value, viz.: *S. arisanensis* subspecies *arisanensis* (T.-S. Liu 1960: 83) and *viridis* (Zhang 1991: 112), *S. chinensis* (Gorokhova 1982; Crawford 1992: 10), *S. glaucescens* (Smith 1947: 124; Yuan & Chao 1996), *S. grandiflora* (Watt 1889–96; Arora & Pandey 1996: 150), *S. henryi* (Clarke 1905; Altschul 1973: 72; Zhang 1991: 112; Chen et al. 1999), *S. incarnata* (Law 1996a: 250), *S. lancifolia* (Yuan & Chao 1996), *S. propinqua* (Hooker 1851; Yuan & Chao 1996), *S. repanda* (Tanaka 1976: 668), and *S. sphenanthera* (Altschul 1973: 72; Yuan & Chao 1996). The seeds of *S. grandiflora* are used for their clove-like flavoring (Crawford 1992), and infusions of fruits of *S. repanda* and *S. chinensis* are drunk as tea in Japan (Tanaka 1976: 668) and Korea (Pemberton & Lee 1996). *Schisandra sphenanthera* fruits have been used in the preparation of wine and vinegar in China (Yuan & Chao 1996).

Various non-culinary uses have also been reported in the literature. Oils extracted from the fruits and seeds of *S. sphenanthera* have been used for the manufacture of soap and lubricants (Wang 1980: 802; Law 1983b: 534, 1996a: 260), and fibers from the stems of *S. chinensis* have been used in rope manufacture (Wang 1980: 800). Hooper (1929) reported that a viscid derivative of the fruit of *S. chinensis* was previously used in Japan as pomade.

Several species are cultivated as ornamental climbers, primarily for their foliage and fruits (Krüssmann 1986: 311–312; Cullen & Howe 1989), including *S. chinensis*, *S. glabra*, *S. glaucescens*, *S. grandiflora*, *S. henryi*, *S. propinqua*, *S. repanda*, *S. rubriflora*, *S. sphaerandra*, and *S. sphenanthera*.

PHYLOGENY AND SUPRASPECIFIC CLASSIFICATION

RELATIONSHIPS WITH OTHER TAXA

In the original description of *Schisandra*, Michaux (1803) suggested a relationship with the Menispermaceae. Although this approach was followed in several other early taxonomic publications (e.g., Wallich 1824), a close relationship between *Schisandra* and the Menispermaceae is not generally accepted in contemporary classifications systems. Significantly, however, some recent palynological publications have indicated similarities in pollen structure between the Schisandraceae and the menispermaceous genera *Parabaena* Miers and *Tinospora* Miers (Walker & Doyle 1975; Thanikaimoni 1984, 1986).

Blume (1825) was the first to recognize the similarity between *Schisandra* and *Kadsura* when he classified the two genera (under the synonyms *Sphaerostema* and

Sarcocarpon) in the Annonaceae, although he noted that the two genera were intermediate between the Annonaceae and Menispermaceae. Blume (1830) subsequently recognized the family Schisandraceae (as "Schizandreae"), consisting of *Schisandra* (as "*Sphaerostema*") and *Kadsura*. The close similarity between *Schisandra* and *Kadsura* has subsequently been universally accepted. Don (1831), for example, recognized the order "Schizandriaceae," in which he grouped *Schisandra*, "*Sphaerostemma*" (an orthographic variant of the synonym *Sphaerostema*), *Kadsura*, "*Sarcocarpum*" (an orthographic variant of the synonym *Sarcocarpon*), and *Mayna* Aubl. (now separated in the Flacourtiaceae).

Although the recognition of the close relationship between *Schisandra* and *Kadsura* became commonplace, most early authors regarded the two genera as members of the Magnoliaceae (e.g., Bentham & Hooker 1862; Baillon 1868; Dalla Torre & Harms 1900–07). The distinctions between the two genera and the rest of the Magnoliaceae was recognized by Dandy (1927), and supported by extensive anatomical investigations by Bailey and Nast (1948). This research, in association with the monographic revisions being conducted by Smith (1947), resulted in the revival of the familial name Schisandraceae.

Although *Schisandra* and *Kadsura* are closely related, cladistic analyses conducted during the present research indicate that the two genera are monophyletic; *Schisandra* possesses synapomorphies in the post-fertilization elongation of the torus, and in the presence of basal constrictions at the point of attachment of the apocarps in the fruit. The two genera are easily distinguished using the following identification keys:

KEY TO SCHISANDRA AND KADSURA
(for specimens with male flowers)

1\. Androecium composed of free stamens, not compressed into an androecial mass.
    2. Apex of androecium with variable number of staminodes (occasionally absent); pollen hexacolpate. *Kadsura.*
    2. Apex of androecium without staminodes; pollen tricolpate. *Schisandra.*
1\. Androecium composed of either connate or free but highly compressed stamens, forming an androecial mass.
    3. Androecium composed of free but highly compressed stamens. *Kadsura.*
    3. Androecium composed of connate stamens. *Schisandra.*

KEY TO SCHISANDRA AND KADSURA
(for specimens with female flowers or fruits)

1\. Floral receptacle obovoid, subclavate, or ellipsoid; aggregate fruits composed of apocarps attached to a ± ellipsoid receptacle; apocarps often closely appressed to form a spherical to ellipsoid mass. *Kadsura.*
1\. Floral receptacle cylindrical or conical-terete; aggregate fruits composed of apocarps attached to a greatly elongated receptacle; apocarps always separate, never appressed. *Schisandra.*

The anatomical research by Bailey and Nast (1948), which resulted in the revival of the family Schisandraceae, also led Smith (1947: 8–10) to publish the new familial name Illiciaceae for the genus *Illicium*. Taxonomic data from a broad range of sources indicate that the Illiciaceae and Schisandraceae are closely related, viz. general morphology and anatomy (Bailey & Nast 1948; Donoghue & Doyle 1989; Loconte & Stevenson 1991), embryology (Hayashi 1965), cytology (Ehrendorfer et al. 1968), DNA sequencing (Chase et al. 1993; Qiu et al. 1993; Soltis et al. 1997; Hoot et al. 1999), and phytochemistry (Sy et al. 1997). The most widely adopted system today is the isolation of the Illiciaceae and Schisandraceae as the sole members of the order Illiciales (e.g., Dahlgren 1980; Cronquist

1981; Takhtajan 1997), although Thorne (1992) recognizes the two families in the suborder Illiciineae within the Magnoliales.

Different opinions have been expressed regarding the phylogenetic affinities of the Illiciales as a whole. Cladistic analyses of morphological data typically indicate a relationship with the Winteraceae (Donoghue & Doyle 1989; Loconte & Stevenson 1991), whereas analyses of *rbc*L and 18S gene sequence data indicate a sister group relationship with the Austrobaileyaceae (Chase et al. 1993; Qiu et al. 1993; Soltis et al. 1997). A recent combined cladistic analysis using *rbc*L and morphological data (Nandi et al. 1998) confirms the latter relationship, both when the data sets are analyzed separately and when combined.

PHYLOGENETIC RECONSTRUCTION WITHIN SCHISANDRA

The cladistic character states for the 23 species of *Schisandra*, three representative species of *Kadsura*, and the outgroup taxon, *Illicium dunnianum*, are presented in Table 3 (cladistic characters listed under "Cladistic Methods" in the "Materials and Methods" chapter). Analysis of this data set resulted in the construction of only two equally parsimonious cladograms, one of which is presented as Fig. 19. These trees are 42 steps long, and have a consistency index (CI) value of 69 (indicating the level of homoplasy) and a retention index (RI) value of 85 (indicating the level of synapomorphy). Three of the 25 characters used are autapomorphies, which artificially inflate the CI value (Siebert 1992); exclusion of these characters from the analysis resulted in cladograms with only slightly reduced CI values of 66. The topology of the two cladograms is essentially similar, differing only in one node, which is reduced to a polytomy in one of the cladograms.

The minimal-length cladograms were reconciled by applying strict and semi-strict consensus methods (Fig. 20); differences are only apparent at one node, which is reduced to a polytomy in the strict consensus tree. Application of the jackknife monophyly index confirms the stability of all clades represented in Fig. 20.

Schisandra is shown to be monophyletic, with three main clades (numbered 1–3 in Fig. 20). Clade 1 consists of *S. grandiflora*, *S. rubriflora*, *S. incarnata*, and *S. sphaerandra*, and is defined by a synapomorphy of a broad pseudostyle. Other significant characters include extrorse-lateral anther dehiscence (although this character state is also shared with *Kadsura scandens*; Saunders 1998: 72–74), and tricolpate pollen (shared with the out-group *Illicium dunnianum*; Praglowski 1976).

Clade 2 (Fig. 20) includes all other species previously included in sect. *Pleiostema* by Smith (1947), and has a synapomorphy for the incomplete development of apical stamens (giving rise to stamens that appear fused towards the apex of the androecium). This clade is comparatively poorly resolved, reflecting the taxonomic complexity of the group and the paucity of phylogenetically significant characters used in the analysis. Two minor clades are well supported within clade 2, however, viz.: the *S. tomentella*-*S. pubescens*-*S. pubinervis* clade (with a synapomorphy in the distribution of hair); and the *S. henryi*-*S. longipes*-*S. perulata* clade (with a synapomorphy in the persistence of the bud-scales/perules). The latter clade is also characterized by angled or winged branches, although this is also apparent in the out-group taxon, *I. dunnianum* (Smith 1947: 71).

Clade 3 (Fig. 20) includes all remaining species in the genus, and is characterized by synapomorphies in the partial or complete fusion and reduced number of stamens. Clade 3 is fully resolved, with three important constituent clades evident (designated 3a–c in Fig. 20). Clade 3a consists of *S. glabra*, *S. repanda*, and *S. bicolor*, and is synapomorphic

TABLE 3. Data matrix of character states for cladistic characters studied. Taxon codes used: OUT = outgroup (*Illicium dunnianum*); KCOC = *Kadsura coccinea*; KHET = *K. heteroclita*; KSCA = *K. scandens*; GRAN = *Schisandra grandiflora*; RUBR = *S. rubriflora*; INCA = *S. incarnata*; SPHA = *S. sphaerandra*; NEGL = *S. neglecta*; SPHE = *S. sphenanthera*; ARIS = *S. arisanensis*; GLAU = *S. glaucescens*; ELON = *S. elongata*; TOME = *S. tomentella*; PUBE = *S. pubescens*; PUBI = *S. pubinervis*; LANC = *S. lancifolia*; MICR = *S. micrantha*; HENR = *S. henryi*; LONG = *S. longipes*; PERU = *S. perulata*; CHIN = *S. chinensis*; GLAB = *S. glabra*; REPA = *S. repanda*; BICO = *S. bicolor*; PROP = *S. propinqua*; and PLEN = *S. plena*.

	CHARACTERS																								
TAXA	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
OUT	0	1	0	0	–	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1	–	0	0	0	0
KCOC	0	0	0	0	–	0	0	1	0	0	0	0	0	0	2	0	1	1	1	0	0	0	0	0	0
KHET	0	0	0	0	–	0	1	1	0	0	0	0	0	0	2	0	1	1	1	0	0	1	0	0	0
KSCA	0	0	0	0	–	0	1	1	0	0	0	0	0	0	2	0	0	1	1	0	0	1	0	0	0
GRAN	0	0	0	0	–	0	0	0	0	0	0	0	0	0	2	0	0	0	1	1	1	0	1	1	0
RUBR	0	0	0	0	–	0	0	0	0	0	0	0	0	0	2	0	0	0	1	1	1	0	1	1	0
INCA	0	0	0	0	–	0	0	0	0	0	0	0	0	0	2	0	0	0	1	1	1	0	1	1	0
SPHA	0	0	0	0	–	0	0	0	0	0	0	0	0	0	2	0	0	0	1	1	1	0	1	1	1
NEGL	0	0	0	0	–	0	0	0	0	0	1	0	0	0	1	0	1	1	1	1	0	0	1	1	1
SPHE	0	0	0	0	–	0	0	0	0	0	1	0	0	0	1	0	1	1	1	1	0	0	1	1	1
ARIS	0	0	0	0	–	0	0	0	0	0	1	0	0	0	1	0	1	1	1	1	0	0	1	1	1
GLAU	0	0	0	0	–	1	0	0	0	0	1	0	0	0	1	0	1	1	1	1	0	0	1	1	0
ELON	0	0	0	0	–	0	0	1	0	0	1	0	0	0	1	0	1	1	1	1	0	0	1	1	1
TOME	0	0	0	2	1	0	0	0	0	0	1	0	0	0	1	0	1	1	1	1	0	0	1	1	?
PUBE	0	0	0	2	0	0	0	0	0	0	1	0	0	0	1	0	1	1	1	1	0	0	1	1	1
PUBI	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	1	1	1	1	0	0	1	1	1
LANC	0	0	0	0	–	0	0	0	0	0	1	0	0	0	1	0	1	1	1	1	0	0	1	1	1
MICR	0	0	0	0	–	0	0	0	0	0	1	0	0	0	1	0	1	1	1	1	0	0	1	1	1
HENR	0	1	1	0	–	1	0	0	0	0	1	0	0	0	1	1	1	1	1	1	0	0	1	1	1
LONG	0	1	1	1	0	1	0	0	0	0	1	0	0	0	1	1	1	1	1	1	0	0	1	1	1
PERU	0	1	1	0	–	0	0	0	0	0	1	0	0	0	1	1	1	1	1	1	0	0	1	1	1
CHIN	0	0	0	0	–	0	0	0	0	1	0	1	0	0	0	0	1	1	2	1	0	0	1	1	0
GLAB	0	0	0	0	–	0	0	1	1	0	0	1	0	1	0	1	1	1	0	1	0	0	1	1	1
REPA	1	0	0	0	–	0	0	1	1	0	0	1	0	1	0	1	1	1	0	1	0	0	1	1	1
BICO	1	0	0	0	–	0	0	0	1	0	0	1	0	1	0	1	1	1	0	1	0	0	1	1	1
PROP	0	0	0	0	–	0	1	1	0	0	0	2	0	0	0	0	1	1	0	1	0	0	1	1	0
PLEN	0	0	0	0	–	0	1	1	0	0	0	2	1	0	0	0	1	1	0	1	0	0	1	1	0

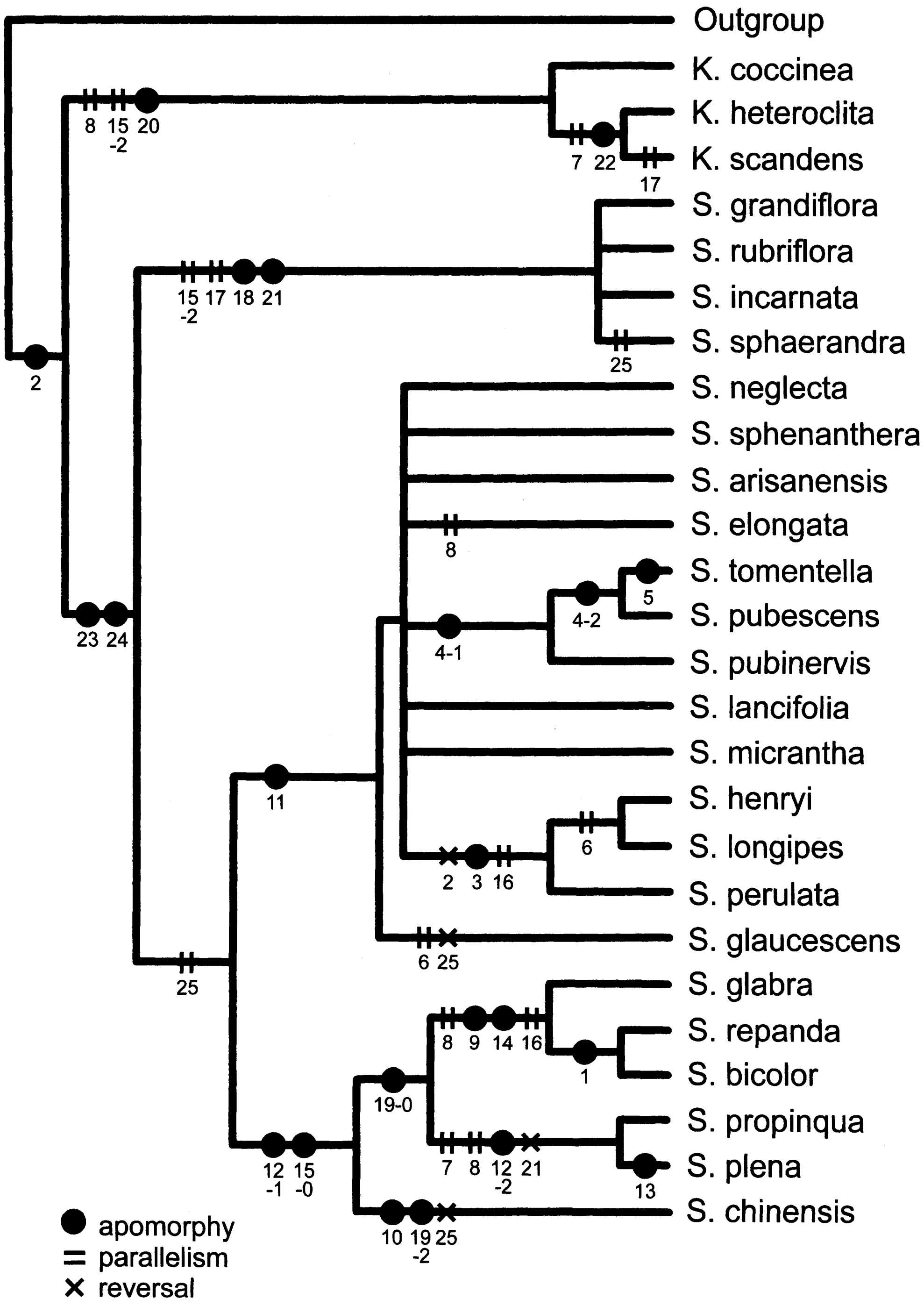


FIG. 19. One of two equally parsimonious cladograms for extant taxa of *Schisandra* and representative species of *Kadsura*. Numbers following hyphens indicate character states in multistate characters; the outgroup taxon is *Illicium dunnianum*.

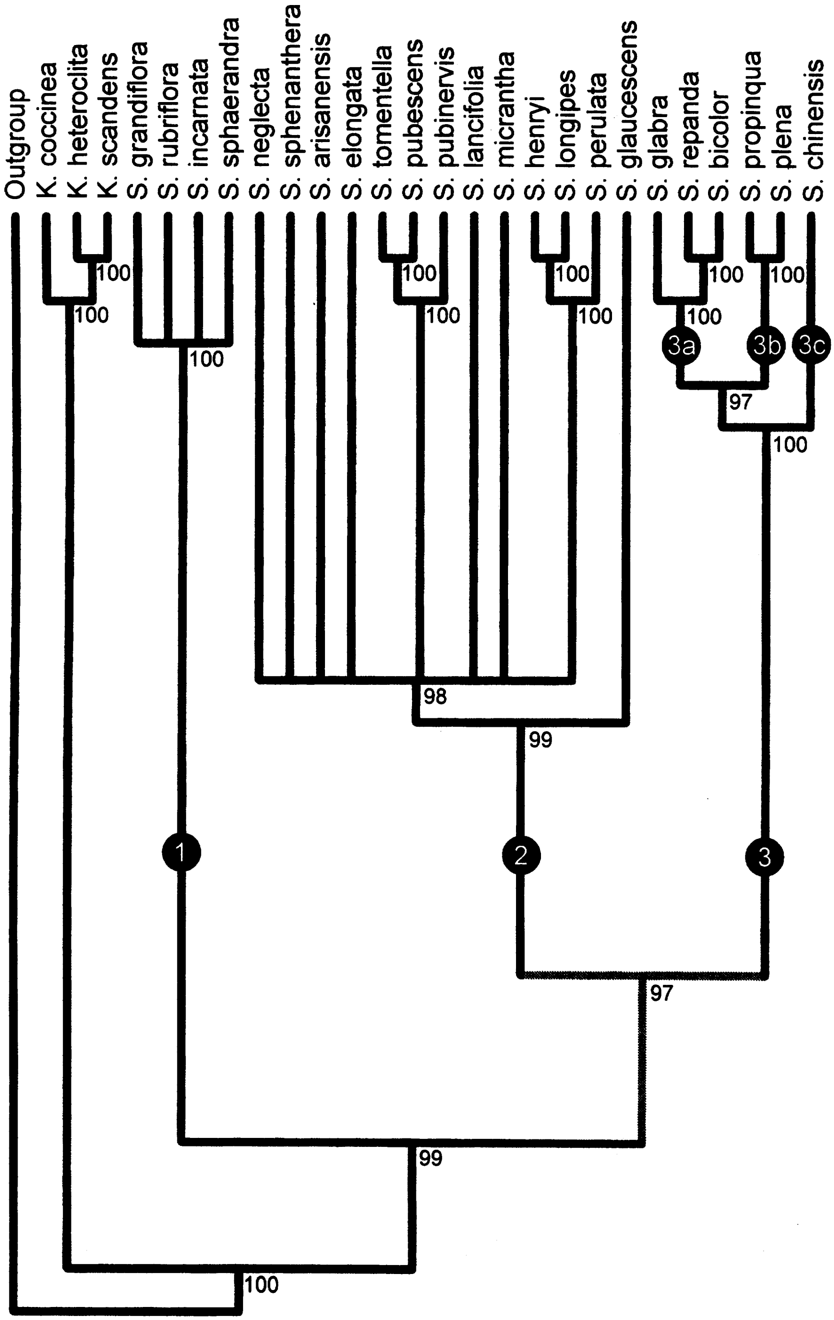


FIG. 20. Consensus tree, derived from the two equally parsimonious cladograms. Topology shows semistrict consensus tree; the gray node collapses in the strict consensus tree. Important clades are denoted by numbers and letters in black circles: 1 = *S.* subg. *Pleiostema*; 2 = *S.* subg. *Sinoschisandra*; 3 = *S.* subg. *Schisandra*; 3a = *S.* sect. *Schisandra*; 3b = *S.* sect. *Sphaerostema*; 3c = *S.* sect. *Maximowiczia*. The outgroup is *Illicium dunnianum*.

in the inner tepals with a thickened carnose base and in the horizontally oriented stamens. Clade 3b consists of *S. propinqua* (inclusive of *S. axillaris* sensu Smith, 1947) and *S. plena*, and is characterized by the complete fusion of stamens, forming a true synandrium. Clade 3c includes only one species, *S. chinensis*, and is sister to clades 3a and 3b collectively.

Smith (1947: 88–91) presented a hypothetical phylogeny for *Schisandra*, based largely on differences in androecial structure (Fig. 21). He hypothesized that the most primitive androecial form was the *S. grandiflora* type (designated A1 here). From this androecial type, Smith suggested that one lineage led to the *S. sphenanthera* androecial type (A2), and subsequently to both the *S. glabra* type (B) and the *S. chinensis* type (C). The second hypothesized lineage derived from the *S. grandiflora* androecial type (A1) led to the *S. sphaerandra* type (A3) and subsequently the *S. propinqua* type (D1) and the *S. plena* type (D2). The cladistic analysis presented here does not corroborate Smith's (1947) hypothesis, however. Smith believed that the *S. glabra* androecial type (B) represented a synandrium (which he called the "staminal shield") and was homologous with the "fused" apical stamens in the *S. sphenanthera* type (A2). Tucker and Bourland (1994), however, have shown that the center of the "staminal shield" in *S. glabra* represents the apex of the receptacle; the stem of the androecium is furthermore shown in the present monograph to be derived from connate stamens that are adnate to the receptacle. A second inconsistency between Smith's (1947) proposed phylogeny and the cladistic phylogeny presented here relates to the phylogenetic position of *S. propinqua* and *S. plena*; the synandrium present in these species (types D1 and D2) presumably represents an extension of the filament fusion evident in *S. glabra*, *S. repanda*, *S. bicolor*, and *S. chinensis*.

Current hypotheses regarding pollen evolution suggest that tri- and hexacolpate pollen is independently derived in the Illiciales, and is not homologous with superficially similar pollen in other angiosperm groups (Huynh 1976; Doyle et al. 1990). The cladistic analysis presented here indicates homoplasy in the evolution of tri- and hexacolpate pollen in the Schisandraceae, which suggests either that hexacolpate pollen has evolved in parallel in *Schisandra* and *Kadsura*, or that tricolpate pollen in *Schisandra* is secondarily derived. It is significant, however, that the homology between the tricolpate pollen in *Schisandra* and *Illicium* is in doubt. In some species of *Illicium*, the colpi fuse over both the distal and proximal poles (i.e., trisyncolpate), whereas in others the colpi do not fuse at all (i.e., trizonocolpate) (e.g., Saunders 1995); this contrasts with the tricolpate pollen in *Schisandra*, in which the colpi fuse over the distal pole only.

SUPRASPECIFIC TAXONOMY

The cladistic analyses presented here reveal three main monophyletic clades within *Schisandra* (designated 1–3 in Fig. 20); all three clades are well supported, with 100%, 99%, and 100% jackknife monophyly indices, respectively. It is furthermore possible that clades 2 and 3 are monophyletic and form a sister group to clade 1, although this is not reflected in the strict consensus tree (Fig. 20). The supraspecific classification proposed by Smith (1947: 88–97) is consequently only partially corroborated by the cladistic analyses presented here, since sect. *Pleiostema* (sensu Smith) consists of both clades 1 and 2, and is therefore paraphyletic. Section *Pleiostema* sensu Smith is accordingly divided into two monophyletic groups, subg. *Pleiostema* (clade 1) and subg. *Sinoschisandra* (clade 2). This treatment of Smith's sect. *Pleiostema* is in agreement with that presented by Law (1996a), although it is significant that Law did not use cladistic methodology to create his revised

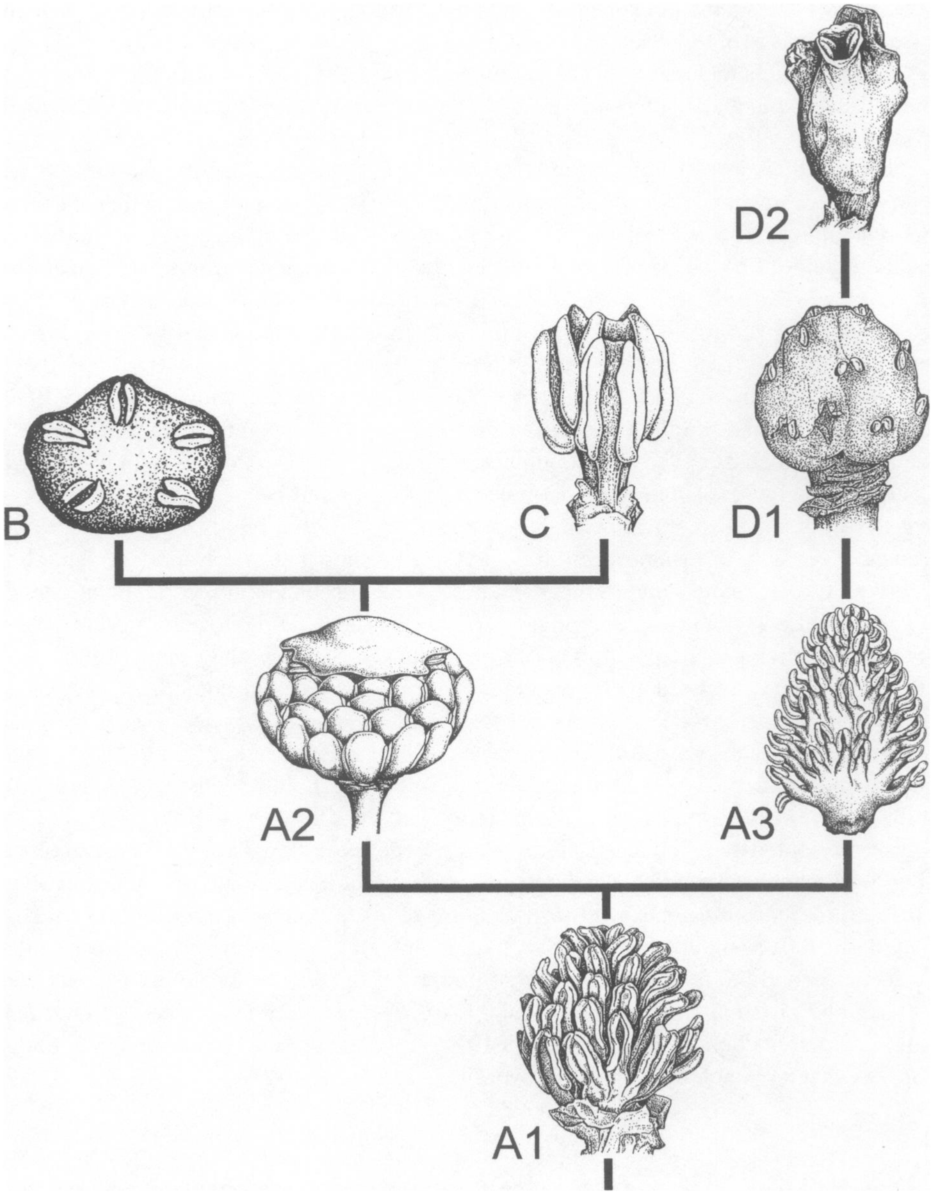


FIG. 21. Diagram illustrating Smith's (1947) hypothesised phylogeny for *Schisandra*. Letters A–D correspond to the four basic androecial morphologies described in the text: A1, *S. grandiflora*; A2, *S. henryi*; A3, *S. sphaerandra*; B, *S. bicolor*; C, *S. chinensis*; D1, *S. propinqua*; D2, *S. plena*. Androecia are not drawn to scale. (A1, *D. Chatterjee 230,* L; A2, redrawn from Law (1996a: fig. 73.6); A3, *F. K. Ward 20893*, A; B, *P. C. Tam 63323*, IBSC; C, *H. Takahashi 4079*, C; D1, *R. Brinkman 874a*, L; D2, *A. Henry 11893*, A.) Drawing by H. L. Wilks.

suprаspecific classification, nor was he apparently aware of the significant correlation with pollen morphology.

Clade 3 (Fig. 20) is regarded as a third supraspecific taxon in the genus (bearing the autonym *Schisandra*); subgeneric status has been adopted to reflect the equivalence with subgenera *Pleiostema* and *Sinoschisandra*. Within subg. *Schisandra*, three main clades are identified (designated 3a–c in Fig. 20); these correspond with three of the sections recognized by Smith, viz. sect. *Schisandra* (clade 3a), sect. *Sphaerostema* (clade 3b), and sect. *Maximowiczia* (clade 3c).

The relationship between the revised supraspecific classification presented here and the earlier systems published by Smith (1947) and Law (1996a) are summarized in Table 1.

PALAEOBOTANY

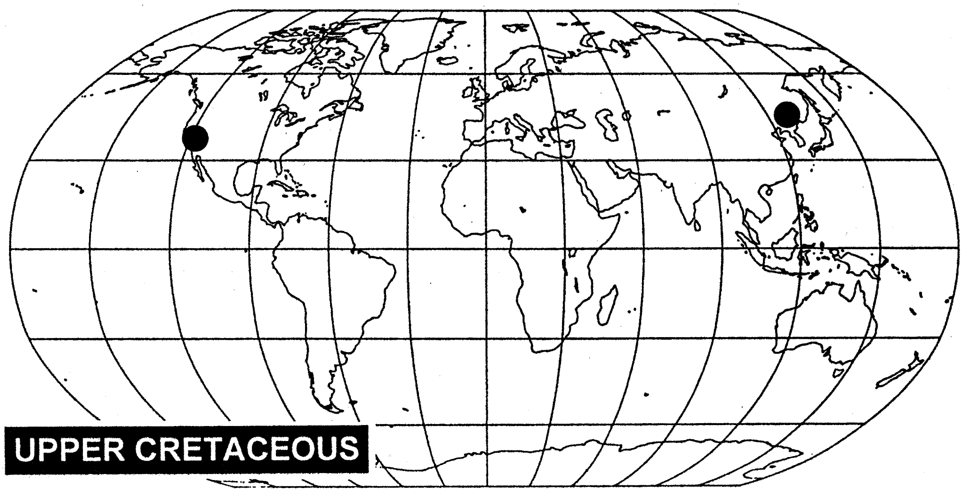
An extensive fossil record exists for *Schisandra*, with ten palaeontological species described (see "Fossil taxa"). Information on the geological occurrence of these records and the structures preserved is listed in Appendix 3, and their geographical locations are illustrated in Fig. 22. Most records are based on fossilized seeds and leaf fragments, and it should be noted that unambiguous taxonomic identity cannot always be achieved.

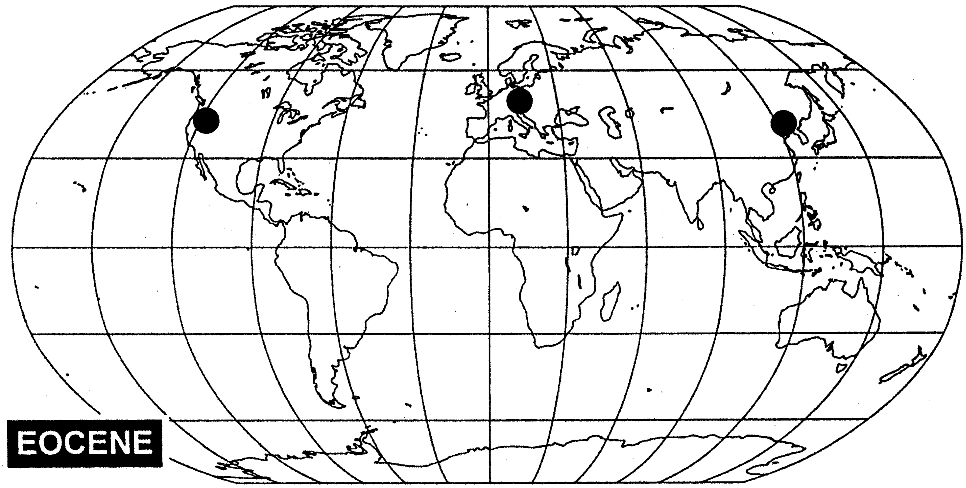
The earliest putative *Schisandra* fossils are leaves of *S. durbudensis* S. Guo (Guo 1984), which were discovered in Upper Cretaceous deposits in Heilongjiang Province in northern China (Appendix 3; Fig. 22). It is significant, however, that fossil pollen of a similar age and believed to belong to the Schisandraceae (without determination beyond the familial level) has also been reported from California (Chmura 1973). Subsequent reports from the Eocene include records of *Schisandra* in North America, Europe, and China (Appendix 3; Fig. 22). There is no post-Oligocene fossil record of *Schisandra* in North America: most subsequent records are restricted to Europe, central Asia, China, and Japan (Appendix 3; Fig. 22), although there is a report of *Schisandra* pollen from the Miocene of Borneo (Muller 1964, 1970).

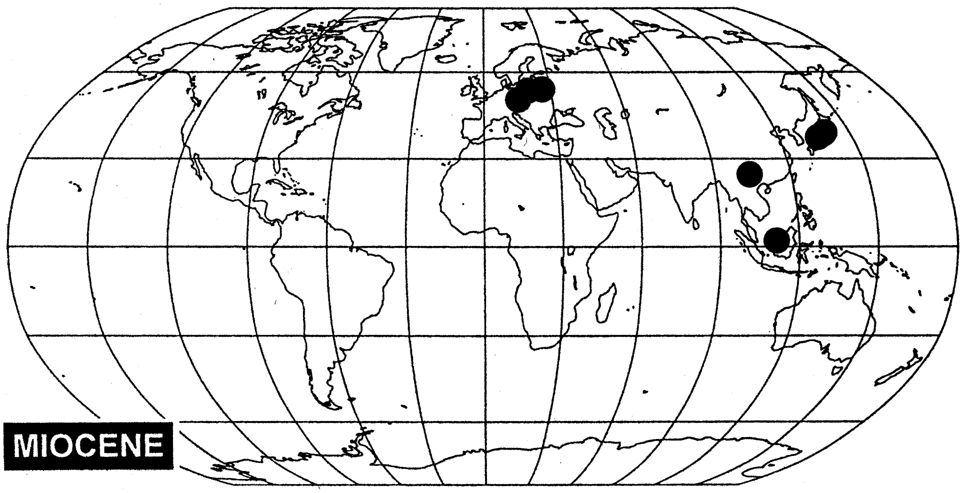
HISTORICAL BIOGEOGRAPHY

The historical biogeography of *Schisandra* is closely allied to that of numerous genera and families of primitive dicotyledons, including the close relative *Kadsura* (Saunders 1998: 35–38). The widespread occurrence of *Schisandra* fossils (Appendix 3; Fig. 22) clearly indicates that the genus now occupies a more restricted distribution, following near total extinction in North America, and complete extinction in Europe and central Asia. The geographical distributions of several extant species of *Schisandra*, including *S. glabra*, *S. propinqua*, and *S. plena*, exhibit disjunctions, suggesting that they were once more widespread and have subsequently undergone contraction.

The earliest fossil records of the Schisandraceae date from the Upper Cretaceous of both western North America (Chmura 1973) and northern China (Guo 1984). It is clear from the fossil assemblages that both these regions supported tropical or subtropical vegetation. During the Upper Cretaceous, two broad and almost mutually exclusive floral provinces developed in the Northern Hemisphere: the *Aquilapollenites* province in western North America-Asia and the *Normapolles* province in eastern North America-Europe


UPPER CRETACEOUS


EOCENE


MIOCENE

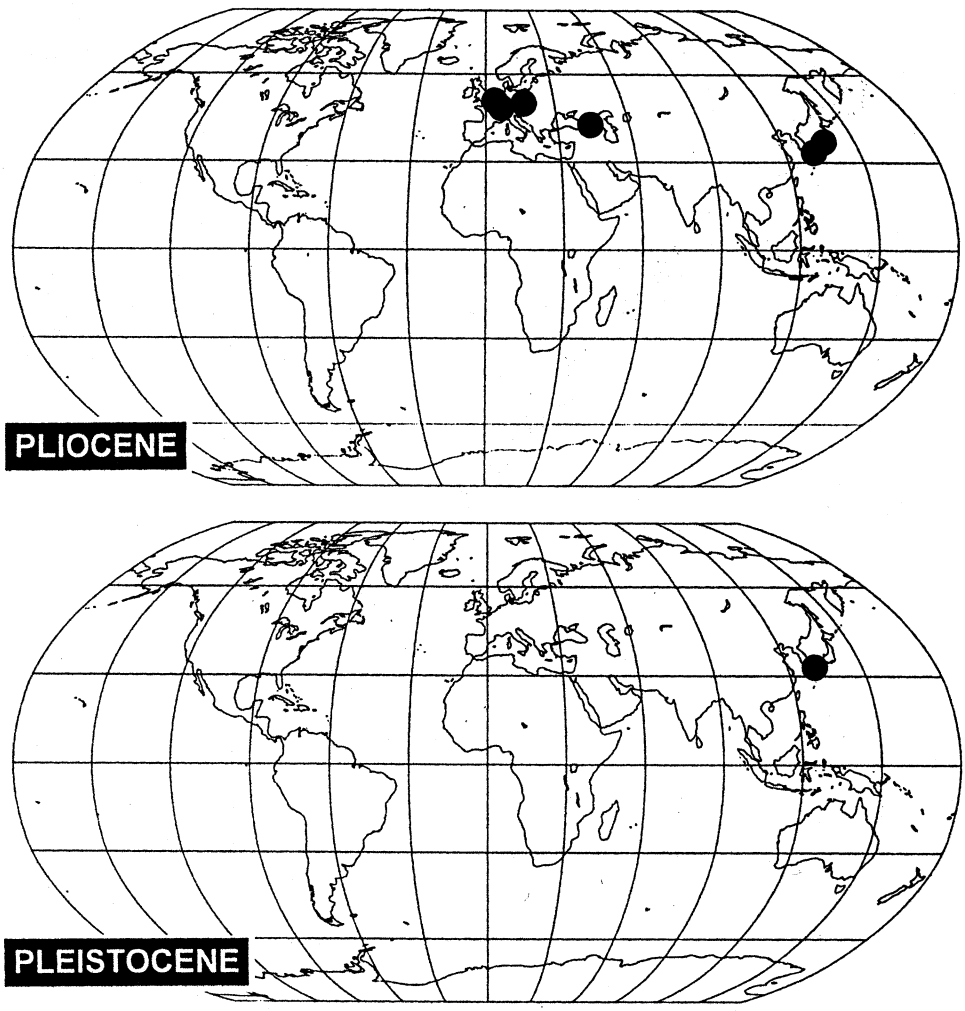


FIG. 22. Localities of fossil specimens of *Schisandra* (or Schisandraceae where determination is only to familial level) from the Upper Cretaceous, Eocene, Miocene, Pliocene, and Pleistocene. There are no records from the Paleocene or Oligocene. Symbols represent individual or multiple sites; information abstracted from the references cited in Appendix 3.

(Tschudy 1984). These provinces reflect the existence of two Northern Hemisphere continents, delimited by the Mid-Continental Sea and the Turgai Sea. The fossil evidence clearly indicates that the Schisandraceae originated in the *Aquilapollenites* province. It is possible that the family originated in Asia with subsequent dispersal to western North America via Beringia, since both *Kadsura* and *Schisandra* have Asian centers of diversity; alternatively, the current centers of diversity could have arisen as a result of near extinction in North America due to climatic changes.

The fall of eustatic sea levels that developed towards the end of the Cretaceous resulted in the disappearance of the Mid-Continental Sea; this possibly enabled dispersal of species of Schisandraceae from western to eastern North America, although there is no known fossil record of the family from the latter region. It would appear that *Schisandra* also dispersed into Europe as far as the Turgai Sea, since fossils of the genus exist in Europe from the Eocene to the Pliocene (Appendix 3; Fig. 22); such a dispersal process would need to have been completed before the early Eocene, when the North Atlantic connection between North America and Europe was broken (Tiffney 1985). This dispersal pattern would have been facilitated by the global warming that began in the late Palaeocene, reaching a thermal maximum in the early Eocene (Wolfe 1992). The extent of the migration of *Schisandra* from Europe eastwards into Asia is not clear; although trans-Beringian dispersal is generally given greatest attention in studies of the floristic similarities between east Asia and eastern North America, Tiffney (1985) believes that the North Atlantic connection was also a significant cause of the floristic affinity between the two continents.

There was a climatic deterioration throughout the Northern Hemisphere following the early Eocene thermal maximum, with reduced temperatures and precipitation levels (Collinson 1992; Wolfe 1992). This continued into the Pliocene (Potts & Behrensmeyer 1992), causing the retreat of the palaeotropical flora and the extinction of many taxa, particularly tropical species and those at higher latitudes. It is presumably during this period that *Schisandra* became largely extinct in North America and completely extinct in Europe and central Asia. The most recent fossil evidence of the Schisandraceae from North America is pollen from the Miocene (Gray 1964), although *Schisandra* extends into the Pliocene of Europe (Zagwijn 1959; Gregor 1981; Geissert & Gregor 1981) and central Asia (Kolakovskij 1957, 1964).

The North American-east Asian disjunction apparent in *Schisandra* is undoubtedly a consequence of this distributional contraction. The sole North American species in the genus, *S. glabra*, is shown in the present monograph to represent a phylogenetically comparatively advanced species, which is closely related to the east Asian species *S. bicolor* and *S. repanda*. Since long-distance dispersal is an unlikely explanation for the disjunction, it can be inferred that evolutionary diversification in *Schisandra* occurred at an early stage, and that many of the more recent evolutionary and biogeographical events in the genus represent extinctions and distribution contractions.

Panero and Aranda (1998) recently reported an important new range extension for *S. glabra* in the humid forests of the Sierra Madre Oriental in Hidalgo State, Mexico; this represents a significant disjunction from the previously known range for the species in the southeastern U.S.A. (Fig. 39). This disjunction is relatively common among plants, and again presumably reflects the contraction of a once wider distribution as a result of climatic change during the Tertiary (Miranda & Sharp 1950), with the increased aridity of northern Mexico and southern Texas.

Schisandra propinqua also shows a discontinuous distribution pattern; three subspecies (subspecies *propinqua, intermedia,* and *sinensis*) occur in continental Asia (Fig. 43) and one (subsp. *axillaris*) is restricted to Java and Bali (Fig. 45). This vicariant distribution pattern is mirrored by a disjunction in subg. *Sinoschisandra*: *S. elongata* is restricted to Java (Fig. 32) and discontinuous from all other members of the subgenus, which occur in continental Asia (Fig. 17E). Steenis (1979: 125–131, figs. 15–17) has shown that this disjunction is relatively common, listing over 100 Indo-Malesian widespread species that are absent from Sumatra, the Malay Peninsula, Borneo, northern Sulawesi, and the southern Philippines. Steenis (1979: 125) commented that these disjunctions are the result of climatic differences: north-western and eastern Java (together with the Lesser Sunda Islands and parts of southern Sulawesi) have seasonal droughts (Oldeman 1975), and therefore form a distinctly different climatic-vegetational region from more northern areas of Malesia, such as Sumatra, the Malay Peninsula, Borneo, northern Sulawesi, and the Philippines, which are generally tropical and perennially wet.

During the Pleistocene, western Malesia was emerged as the "Sunda shelf" due to lowered sea levels, estimated at between 100 m (Biswas 1973; Verstappen 1975) and 150 m (Chappel & Thom 1977) below the current level. Climatic conditions at the time were substantially cooler than at present, with lower precipitation levels and consonant periods of drought. Migration of Laurasian genera, such as *Schisandra,* south across the Sunda shelf therefore presumably occurred during this period, with subsequent extinction in northern Malesia following climatic change.

TAXONOMY

Schisandra Michaux, Fl. bor.-Amer. 2: 218, t. 47. 19 Mar 1803, nom. conserv. *Schisandra* sect. *Schisandra* Baillon, Hist. pl. 1: 189. 1868 (as "*Schizandra* sect. *Euschizandra*").—TYPE: *Schisandra coccinea* Michaux [=*Schisandra glabra* (Brickell) Rehder].

Stellandria Brickell, Med. Repos. 6(3): 327. Feb–Mar 1803.—TYPE: *Stellandria glabra* Brickell [=*Schisandra glabra* (Brickell) Rehder].

Sphaerostema Blume, Bijdr. fl. Ned. Ind. 22. 1825.—TYPE: *Sphaerostema axillare* Blume [=*Schisandra propinqua* subsp. *axillaris* (Blume) R. M. K. Saunders].

Maximowiczia Ruprecht in Maximowicz, Bull. Cl. Phys.-Math. Acad. Imp. Sci. Saint-Pétersbourg 15: 142. 1856, non *Maximowiczia* Cogniaux, 1881 (Cucurbitaceae).—TYPE: *Maximowiczia amurensis* Ruprecht [=*Schisandra chinensis* (Turczaninow) Baillon].

Woody vines; dioecious or monoecious. Lateral branches with fugaceous or (semi-) persistent perules at base. Leaves alternate (appearing clustered on short lateral shoots prior to elongation), exstipulate; lamina papyraceous to coriaceous, abaxial surface sometimes glaucous or pubescent, elliptic to ovate, apex acute to acuminate, base acute to obtuse, often attenuate, margins denticulate to entire, venation semicraspededromous; petioles with groove on adaxial surface, often red. Flowers axillary to bracts (giving appearance of clusters of flowers) or axillary to leaves; generally solitary, occasionally with secondary flower developing in axil of peduncle bract; tepals 5–20, imbricate at anthesis, outermost and innermost segments ± reduced, elliptic to suborbicular or obovate, outermost tepals with minutely ciliolate margin, white, (orange-) yellow, pink, or (purple-) red. Male flowers with androecium of few to numerous (4–60) stamens; stamens sometimes ± free but sometimes fused at base of filaments, apical stamens sometimes only partially differentiated to form carnose mass, entire androecium sometimes fused to form subglobose carnose mass with thecae embedded in cavities, stamens sometimes sessile and radiating horizontally from broad floral axis ("staminal shield"); pollen grains tri- or hexacolpate, distally syncolpate. Female flowers with gynoecium of numerous (12–120) carpels; receptacle cylindrical or conical, distinctly longer than wide; stigmatic crest forming subulate pseudostyle, lacking pseudostigma; ovary with 2 (–3) ventrally attached ovules. Fruit an aggregate of apocarps attached to elongated receptacle; apocarps ellipsoid to obovoid, ripening scarlet, deep red (rarely blackish); peduncle distally broader, not or slightly elongated in fruit. Seeds (1–) 2 (very rarely 3), smooth to rugulose, discoid to flattened-reniform, rarely flattened-pyriform, hilum generally lateral. Base chromosome number: x = 7.

KEY TO THE SUBGENERA, SECTIONS, SPECIES, AND SUBSPECIES OF SCHISANDRA

1\. Abaxial leaf lamina variably pubescent or tomentose (at least on primary and secondary veins).

  2\. Hairs on abaxial leaf lamina restricted to primary and secondary veins; petioles and peduncles glabrous.

    3\. Tepals narrow, largest tepal with length:width ratio 1.8–3.6 (–5.3); androecium of (4–) 5 (–7) stamens, apical stamens not connate; thecae extrorse-lateral; peduncles (6–) 11–20 (–28) mm long (male flowers), (7–) 25–35 mm long (female flowers). IIIa. *Schisandra* subg. *Schisandra* sect. *Maximowiczia*; 18. *S. chinensis*.

    3\. Tepals broad, largest tepal with length:width ratio 0.9–1.5; androecium of 14–28 stamens, apical stamens connate; thecae introrse-lateral; peduncles 23–52 mm long (male flowers), 50–71 mm long (female flowers). II. *Schisandra* subg. *Sinoschisandra* (pro parte).

      4\. Branches conspicuously angled or with narrow lateral wings; perules relatively large, (sub-) persistent; abaxial leaf lamina variably glaucescent; androecium of 18–28 stamens; seeds with (very) tuberculate testa. 16. *S. longipes*.

      4\. Branches not conspicuously angled, without lateral wings; perules small, fugaceous; abaxial leaf lamina not glaucescent; androecium of 14–19 stamens; seeds with smooth or slightly rugulose testa. 12. *S. pubinervis*.

  2\. Hairs on abaxial leaf lamina extending across entire surface; petioles and peduncles pubescent or tomentose. II. *Schisandra* subg. *Sinoschisandra* (pro parte).

    5\. Abaxial leaf lamina, petioles, and peduncles densely tomentose; perianth lacking red pigmentation; male flowers with ca. 5–6 tepals. 10. *S. tomentella*.

    5\. Abaxial leaf lamina, petiole, and peduncles variably pubescent; perianth sometimes with red pigmentation; male flowers with 7–8 tepals. 11. *S. pubescens*.

1\. Abaxial leaf lamina without hairs.

  6\. Flowers in axils of leaves on elongated shoots, or very rarely in axils of fugaceous bracts at base of young shoots; flowers sometimes solitary, but often with "secondary" flowers in axil of prophyll, occasionally in clusters; androecium of connate stamens. IIIc. *Schisandra* subg. *Schisandra* sect. *Sphaerostema*.

    7\. Leaf lamina with intricate tertiary and quaternary venation, prominent adaxially; androecium elongate; thecae sessile, located on opposing sides of cavities on the surface of the carnose androecium; fruiting torus 5–17 cm long; apocarps ca. 10 mm long, 12 mm wide; seeds 5.5–6 mm long, 7–7.5 mm wide. 23. *S. plena*.

    7\. Leaf lamina without prominent venation adaxially; androecium (sub-) globose; thecae introrse, borne on free connectives arising from cavities on the surface of the androecium; fruiting torus 2–6.5 cm long; apocarps 4.5–9 mm long, 4–8.5 mm wide; seeds (3.2–) 3.7–4.5 (–5.4) mm long, (3.5–) 4.2–4.9 (–5.5) mm wide.

      8\. Flowers solitary or in clusters; androecium ca. 1.8–2.4 mm in diameter, consisting of 4–11 stamens. 22c. *S. propinqua* subsp. *sinensis*.

      8\. Flowers solitary, rarely with secondary flower in axil of prophyll; androecium ca. 2.6–4.3 mm in diameter, consisting of 10–18 stamens.

        9\. Female flowers with 14–17 tepals. 22a. *S. propinqua* subsp. *propinqua*.

        9\. Female flowers with 9–14 tepals.

          10\. Leaves papyraceous; peduncles 4–12 mm long. 22b. *S. propinqua* subsp. *intermedia*.

          10\. Leaves generally coriaceous; peduncles (2–) 3–5 (–12) mm long. 22d. *S. propinqua* subsp. *axillaris*.

  6\. Flowers either in axils of leaves on elongated shoots or in axils of fugaceous bracts at base of young shoots; "secondary" flowers absent; androecium composed of essentially free stamens (apical stamens occasionally connate).

    11\. Androecium composed of 5 stamens radiating horizontally outwards from broad floral apex (forming pentamerous staminal "shield"). IIIb. *Schisandra* subg. *Schisandra* sect. *Schisandra*.

      12\. Perianth red; female flowers with (8–) 10–12 tepals. 19. *S. glabra*.

      12\. Perianth yellowish (at least outer tepals); female flowers with 6–10 tepals.

        13\. Leaf laminas (7–) 7.5–10.5 (–12) cm long; outermost tepal slightly reduced, 0.5–0.7 of length of largest tepal; gynoecium of 52–75 carpels; apocarps red, 10–16 mm long, 10–16 mm wide. 21. *S. bicolor*.

13. Leaf laminas (3.5–) 5–7 (–8.5) cm long; outermost tepal highly reduced, 0.2–0.4 of length of largest tepal; gynoecium of 12–17 carpels; apocarps black, 6–13 mm long, 6–11 mm wide. 20. *S. repanda.*

11. Androecium composed of (4–) 5–66 (–70) stamens, more or less spirally arranged around elongate floral axis.

14. Largest tepals (6–) 7.5–17 (–23) mm long; androecium of 22–66 (–70) stamens, apical stamens not connate; pollen tricolpate; gynoecium of (35–) 50–120 carpels; pseudostyle large and broad. I. *Schisandra* subg. *Pleiostema.*

15. Leaf laminas (3.5–) 4.5–8 (–12.5) cm long, 1.5–3 (–6.5) cm wide; stamens partially adnate with broad floral axis, only apically free with short filaments. 4. *S. sphaerandra.*

15. Leaf laminas (5.5–) 7–11.5 (–15) cm long, (2–) 2.5–5.5 (–7.5) cm wide; stamens free.

16. Perianth deep (purple-) red. 2. *S. rubriflora.*

16. Perianth cream, white, or flesh-pink.

17. Perianth cream or white; fruiting torus (13–) 16–18 (–25) cm long. 1. *S. grandiflora.*

17. Perianth flesh-pink; fruiting torus 5–7 (–11) cm long. 3. *S. incarnata.*

14. Largest tepals (3–) 3.5–10 (–13) mm long; androecium of (4–) 5–46 stamens, apical stamens sometimes connate; pollen hexacolpate; gynoecium of 14–65 carpels; pseudostyle small or narrow.

18. Branches with lateral wings; perules relatively large, (sub-) persistent. II. *Schisandra* subg. *Sinoschisandra* (pro parte).

19. Leaf lamina (10–) 12–14.5 (–16.5) cm long, translucent after drying; apocarps 9–12 mm long, 8.5–13 mm wide; seeds 3.5–4.5 mm long, 4–4.5 mm wide. 17. *S. perulata.*

19. Leaf lamina (5.5–) 7.5–11.5 (–14) cm long, rarely translucent after drying; apocarps 4.5–8.5 (–9.5) mm long, (3–) 3.5–6.5 (–7.5) mm wide; seeds (2.5–) 3–3.5 (–4) mm long, 3–4 (–4.5) mm wide.

20. Abaxial leaf lamina not glaucescent; perianth orange, or yellow and red; male flowers with 8–10 tepals. 15b. *S. henryi* subsp. *yunnanensis.*

20. Abaxial leaf lamina variably glaucescent; perianth yellow, without red pigmentation; male flowers with 6–7 (–8) tepals.

21. Branches conspicuously winged; androecium of 23–46 stamens; seed testa generally rugulose, rarely tuberculate. 15a. *S. henryi* subsp. *henryi.*

21. Branches narrowly winged; androecium of 12–19 stamens; seed testa rugulose to tuberculate. 15c. *S. henryi* subsp. *marginalis.*

18. Branches not conspicuously angled, without lateral wings; perules small, fugaceous.

22. Tepals narrow, largest tepal with length:width ratio 1.8–3.6 (–5.3); androecium of (4–) 5 (–7) stamens, apical stamens not connate; thecae extrorse-lateral. IIIa. *Schisandra* subg. *Schisandra* sect. *Maximowiczia*; 18. *S. chinensis.*

22. Tepals broad, largest tepal with length:width ratio 0.7–1.8 (–2.1); androecium of 7–35 (–40) stamens, apical stamens generally connate; thecae introrse-lateral or lateral. II. *Schisandra* subg. *Sinoschisandra* (pro parte).

23. Leaf laminas (3–) 4–8 (–10) cm long; petioles (3–) 6–15 (–22) mm long; flowers with largest tepal (3–) 3.5–6.5 mm long; gynoecium of 14–24 carpels.

24. Leaf lamina narrow, length:width ratio (2.0–) 2.4–3.4 (–3.7); fruiting torus 3–5 (–6.5) cm long. 13. *S. lancifolia.*

24. Leaf lamina broad, length:width ratio (1.0–) 1.2–1.9 (–2.5); fruiting torus 1.5–3.5 cm long. 14. *S. micrantha.*

23. Leaf laminas (4–) 5.5–12 (–15) cm long; petioles (7–) 11–27 (–46) mm long; flowers with largest tepal (4–) 5–9.5 (–12) mm long; gynoecium of 20–56 carpels.

25. Abaxial leaf lamina conspicuously glaucous. 8. *S. glaucescens.*

25. Abaxial leaf lamina not glaucous.

26. Secondary veins of leaf lamina strongly arcuate; female flowers with 9–10 tepals; outermost tepal 0.2–0.4 of length of largest. 9. *S. elongata.*

26. Secondary veins of leaf lamina (slightly) arcuate; female flowers with 5–9 tepals; outermost tepal 0.5–1.0 of length of largest.

27. Secondary and lower order veins of leaf lamina not prominent; seed testa smooth. 6. *S. sphenanthera.*
27. Secondary and lower order veins of leaf lamina slightly prominent abaxially and often adaxially; seed testa smooth or rugulose, rarely tuberculate.
    28. Leaf lamina venation appearing dark after drying; apocarps (3–) 5–7 (–8.5) mm long, (3–) 3.5–5.5 (–7.5) mm wide. 5. *S. neglecta.*
    28. Leaf lamina venation appearing pale after drying; apocarps (5–) 7–9.5 (–11) mm long, (3.5–) 5–6.5 (–7) mm wide.
        29. Gynoecium of 40–56 carpels. 7a. *S. arisanensis* subsp. *arisanensis.*
        29. Gynoecium of 22–29 carpels. 7b. *S. arisanensis* subsp. *viridis.*

I. Schisandra subgenus **Pleiostema** (A. C. Smith) Y.-W. Law, Fl. Reipubl. Popularis Sin. 30(1): 246, 272. 1996. *Schisandra* section *Pleiostema* A. C. Smith, Sargentia 7: 93. 1947.—TYPE: *Schisandra grandiflora* (Wallich) Hooker f. & Thomson.

Woody vines. Male flowers with androecium of 22–70 essentially free stamens (base of filaments sometimes partially adnate to receptacle), spirally arranged around floral axis, uppermost stamens not connate; thecae extrorse-lateral; pollen tricolpate. Female flowers with gynoecium of (35–) 50–120 free carpels; pseudostyles broad. Seed testa smooth.

Distribution (Fig. 17A). India (Himachal Pradesh, Uttar Pradesh, Sikkim, and northern West Bengal), Nepal, Bhutan, China (Hubei, Sichuan, Xizang [Tibet], and Yunnan).

1. Schisandra grandiflora (Wallich) Hooker f. & Thomson in Hooker f., Fl. Brit. Ind. 1: 44. 1872 (as "*Schizandra*"). *Kadsura grandiflora* Wallich, Tent. fl. Napal. 10. 1824. *Sphaerostema grandiflorum* (Wallich) Blume, Fl. Javae [Schizandreae] 17. 1830 (as "*S. grandifloro*").—TYPE: NEPAL. [Mt. Sheopore], 1821, *N. Wallich 4985* (lectotype, here designated: K!, photo: HKU!; isolectotypes: C! GH!, photo of GH lectotype: HKU!).

Woody vines, monoecious (often appearing dioecious). Lateral branches lacking wings, with fugaceous perules at base; branches continuing growth in subsequent years. Leaf laminas (6.5–) 7.5–11 (–13) cm long, (2–) 2.5–4 (–5) cm wide, length:width ratio (1.8–) 2.5–3.2 (–4.0), papyraceous, (40–) 50–60 (–70) μm thick, glabrous, generally elliptic; primary vein ± plane to slightly impressed above, (slightly) prominent below; secondary veins (4–) 5–6 (–8) pairs per leaf, (slightly) arcuate; base acute to attenuate, rarely obtuse; apex short to long-acuminate; margin denticulate, rarely subentire, (0–) 10–17 (–27) teeth per side of leaf; petioles glabrous, (9–) 11–22 (–30) mm long, (0.5–) 0.8–1.2 (–1.5) mm in diameter. Flowers borne in axils of fugaceous bracts at the base of young shoots, solitary; tepals 6–9 (male flowers), 6–8 (female flowers); tepals (cream-) white, outermost sometimes pink-tinged, glabrous; outermost tepal generally ovate, (8.0–) 9.0–11.5 (–14) mm long, 5.4–8.5 mm wide, length:width ratio 1.2–1.7; innermost tepal variably elliptic, ovate, or obovate, 6.8–12.0 mm long, 4.0–8.0 mm wide, length:width ratio (1.3–) 1.5–1.8 (–2.1); largest tepal variably elliptic, ovate, or obovate, (7.6–) 10.0–15.0 (–23.0) mm long, 7.4–15.0 mm wide, length:width ratio 1.0–1.7; outermost tepal slightly reduced to 0.7–1.0 of length of largest; innermost tepal slightly reduced to 0.6–1.0 of length of largest; peduncles glabrous, (12–) 14–25 (–36) mm long, 0.5–0.8 (–1.0) mm in diameter (male flowers), (20–) 35–47 mm long, 0.8–1.1 mm in diameter (female flowers). Male flowers with androecium of 30–50 essentially free stamens, spirally arranged around floral axis, uppermost stamens not connate; thecae extrorse-lateral; pollen tricolpate. Female flowers with gynoecium of 67–120 free carpels, gynoecium ca. 4.5–5 mm in diameter; carpels 1.1–1.9 mm long, 0.7–1.0 mm wide, length:width ratio 1.6–2.0; pseudostyle broad. Fruit peduncles glabrous, elongated, 4–7 cm long, (0.9–) 1.4–1.9 mm wide; torus (13–) 16–18 (–25) cm long, (3.2–) 3.7–4.0 (–4.7) mm wide; apocarps red, (4.5–) 5–8.5 (–10.5) mm long, (4–) 4.5–7.5 mm wide, length:width ratio 1.0–1.6. Seeds (1–) 2 per apocarp, discoid to flattened-reniform, (3.0–) 3.2–3.6 (–4.0) mm long, 3.6–4.0 mm wide, length:width ratio 0.8–1.0; testa smooth. Chromosome number: n = 7, 14 (see Appendix 1). Figs. 6A, 12A, B, 12E, 14B, 15A, D, 23.

Illustrations. Wallich (1824: fig. 14, as "*Kadsura grandiflora*"); King (1891: pl. 69A); Hutchinson (1969: fig. 10A–K); Law (1983b: fig. 185; 1996a: fig. 70); Grierson and Long (1984: fig. 22, l–o); Rao and Hajra (1993: fig. 29).

Phenology. Flowering from April to June; fruits maturing from June to October.

Distribution (Fig. 24). India (Himachal Pradesh, Uttar Pradesh, Sikkim, and northern West Bengal), Nepal, Bhutan, and southern Xizang [Tibet]; typically climbing on slopes, shrubs, and small trees, in broad-leaved, coniferous, or mixed forests dominated by *Abies*, *Picea*, *Pinus*, *Quercus*, *Rhododendron*, and *Tsuga*; (1800–) 2100–3300 (–4000) m.

Additional Specimens Examined. **Bhutan.** Ridge S of Dochu La, between Thimbu [Thimphu] and Wangdu Phodrang, *B. Bartholomew 158* (UC); Para valley, near Taksang Monastery, *B. Bartholomew & T. Y. Tse 1749A* (E, GH); Dochengla Pass, *Bigger 2852* (E); Tashiling, Tongsa, *R. E. Cooper 2061* (E); Gichla Punakha, *R. E. Cooper 2767* (E); Timpec, *R. E. Cooper 3003* (E); [precise locality not known], *R. E. Cooper 3310* (E); Dotena, *R. E. Cooper 3892* (E); Pumola area, *B. J. Gould 202, 202A* (K); Taba, Thimphu, 27°30′N, 89°39′E, *A. J. C. Grierson & D. G. Long 983* (E); Tongsa, 27°30′N, 90°30′E, *A. J. C. Grierson & D. G. Long 1155* (E, K); 2 km N of Byakar Dzong, Bumtang Chu, 27°34′N, 90°43′E, *A. J. C. Grierson & D. G. Long 1793* (E); Namning, SE of Sengor, 27°20′N, 91°01′E, *A. J. C. Grierson & D. G. Long 2555* (A, E, K); Drugye Dzong, Paro Chu, *F. Ludlow et al. 16188* (A, E). **China.** Xizang [Tibet]: Migyitun, Tsari Chu, *F. Ludlow & G. Sherriff 1704* (E); Nyam Jang Chu, *F. Ludlow et al. 12544* (E); between Tongyuk & Layoting, Pome, *F. Ludlow et al. 13006* (E); Chunyima, Rong Chu valley, Pome, *F. Ludlow et al. 13707* (E); Nambu La, Tongyuk River, Pome, *F. Ludlow et al. 13822* (E). **India.** Himachal Pradesh: Jaunsar Bahar, Derkan Range, May 1879, *Anonymous 1013* (K); Shilla, Bashahr State, Simla [Shimla] District, May 1908, *Anonymous s.n.* (A); Taprog, Bashahr State, Simla [Shimla] District, May 1908, *Anonymous s.n.* (A); Simla [Shimla], *R. Baksh 6290* (E); Pattarnala, Mt. Chur, *J. R. Drummond 3029* (E, K); between Mattiana [Matiana] and Narkanda, Simla [Shimla] District, *J. R. Drummond 8327* (K); Kidarkanta, *J. R. Drummond 14836* (E); Chepun, 18 May 1860, *E. Dubuc s.n.* (E); Narkanda, 8 Jun 1860, *E. Dubuc s.n.* (E); *J. F. Duthie 7244* (K); *J. S. Gamble 6094A* (K); Narkanda Forest, *J. H. Lace 57* (E); *J. H. Lace 2157* (E); Bashahr, May 1892, *J. H. Lace s.n.* (E); Taklech, Bashahr State, *M. V. Laurie 5372* (E); Jahan, Bashahr State, Simla [Shimla] District, *R. N. Parker 2799* (A); Bahli, Bashahr State, Simla [Shimla] District, *R. N. Parker 2827* (A); *R. N. Parker 3032* (A); Taprog, Bashahr State, Simla [Shimla] District, May 1908, *R. N. Parker s.n.* (A); Shilla, Bashahr State, Simla [Shimla] District, May 1908, *R. N. Parker s.n.* (A); Makasu, Simla [Shimla] Hills, *H. H. Rich 856* (K); Bagi, Magkanda, Simla [Shimla], *G. Watt 8312* (E).—Sikkim: Sinchul, *T. Anderson 7* (GH); Lachen, *K. Biswas 6642* (A); *K. Biswas 6887* (A); Lachen, Zemu and Lhonakh valleys, *G. H. Cave 117/47* (E); [precise locality not known], s.a., *J. D. Hooker s.n.* (GH, NY).—Uttar Pradesh: Chakrata, Siwalik & Jaunsar Divisions, *B. C. Datta 1* (A); Gurhwal [Garhwal], *H. Falconer 79* (C, GH, K); Gurhwal [Garhwal] & Kumaon [Kumaun], s.a., *Falconer s.n.* (K); Mundali, Jaunsar, *J. S. Gamble 26594* (K); Deolâ, Garhwal, *J. S. Gamble 26742* (K); Bhujkoti, Jaunsar, *K. Nand 108* (E); Mussoorie, Siwalik and Jaunsar, *M. L. Punj 3* (NY); Mundali, Jaunsar, *M. B. Raizada 7328* (E); Kumaon [Kumaun], *B. Ram 2324* (NY); N Garhwal-Buhna forest, *M. A. Rau 10212* (E); Banoi, Siwalik & Jaunsar Divisions, *C. S. Rawat 3* (A); Mundali, Siwalik & Jaunsar Districts, *S. Singh 2* (A); Kumaon [Kumaun], *R. Strachey & J. E. Winterbottom 1* (GH); Siwalik & Jaunsar, *N. K. Tripathi 3* (E).—West Bengal: Darjeeling [Darjiling], Sinchul, 5 Sep 1917, *G. H. Cave s.n.* (A, E); 3 May 1925, *G. H. Cave s.n.* (E); *C. B. Clarke 12217* (K); Darjeeling [Darjiling], *J. S. Gamble 8223* (K); *J. S. Gamble 28024* (K); Ming Nangi, *H. H. Haines 794* (K); Darjeeling [Darjiling], near Tonglu, *J. H. Lace 2280* (E); *J. H. Lace 2281* (E); Darjeeling [Darjiling], Tonglo, *R. Lepcha 1234* (E).—Precise locality not known: NW Himalaya, May 1881, *D. Brandis s.n.*

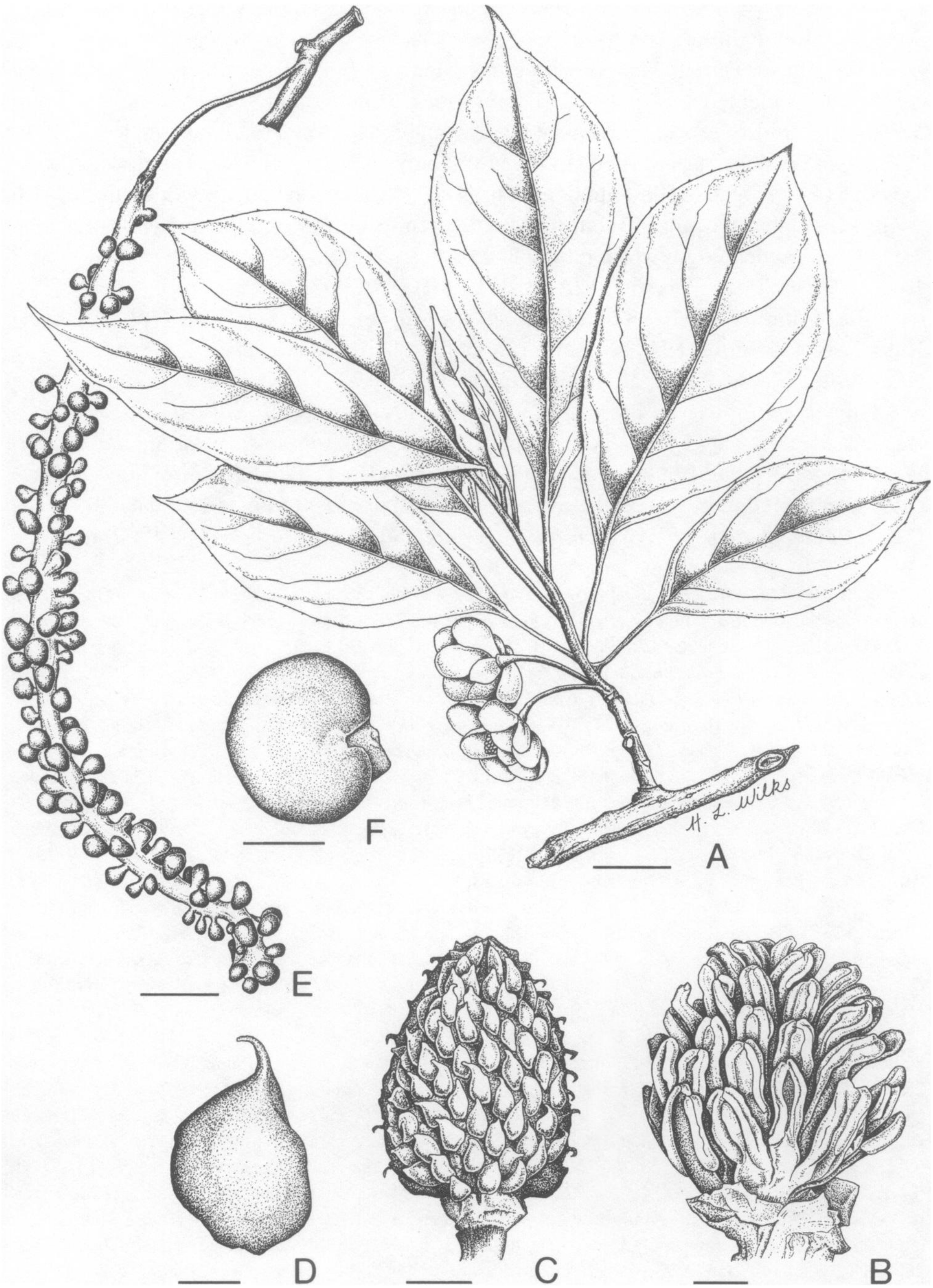


FIG. 23. *Schisandra grandiflora* (*S.* subg. *Pleiostema*). A, flowering branch. B, androecium. C, gynoecium. D, isolated carpel (lateral view). E, fruit (apocarps slightly immature). F, seed. Scale bars: A, E, 2 cm; B, F, 1 mm; C, 2 mm; D, 500 µm. (A, *J. H. Lace 57*, E; B, *D. Chatterjee 230*, L; C, D, *O. Polunin 434*, E; E, *A. J. C. Grierson & D. G. Long 2555*, E; F, *D. G. Long et al. 710*, E.) Drawing by H. L. Wilks.

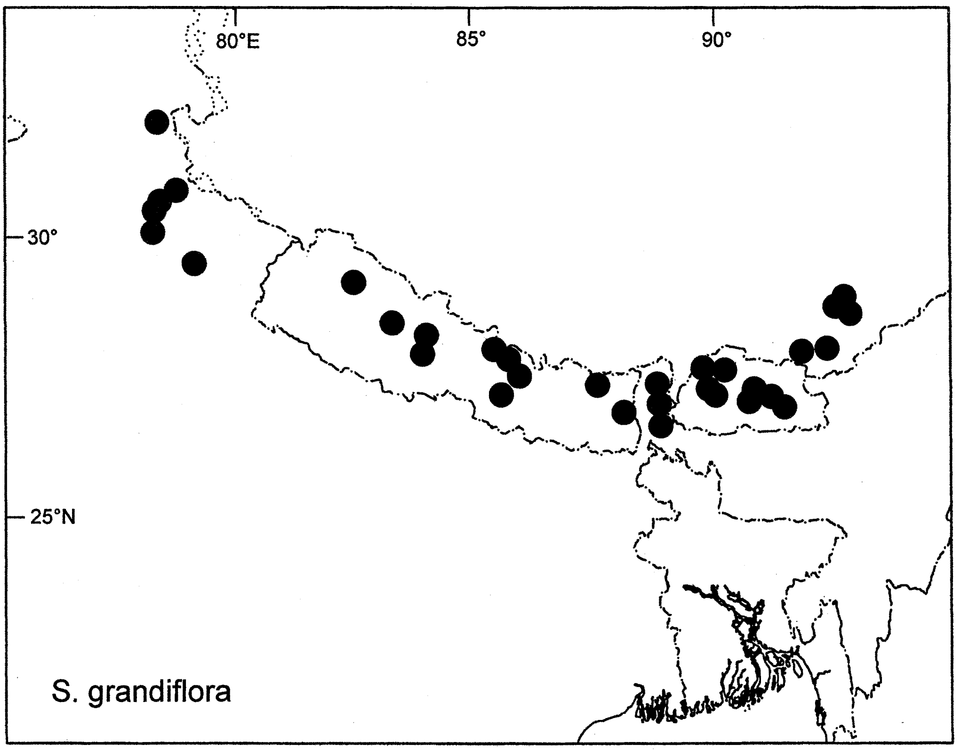


FIG. 24. Distribution of *Schisandra grandiflora.*

(A); Bowlee to Mogwee, s.a., *Cleghorn s.n.* (E); [locality illegible], *J. S. Gamble 699A* (K); NW Himalaya, *J. S. Gamble 23019* (K); "temperate," s.a., *J. D. Hooker s.n.* (L); Chowbhanjan, *Ribu & Rhomoo 6343* (E); NW Himalaya, s.a., *H. L. Royde s.n.* (K); NW Himalaya, *J. L. Stewart 73* (E); Madharee Pap, *R. Strachey & J. E. Winterbottom 103* (K); "temperate," *T. Thomson 37* (L); NW Himalaya, s.a., *T. Thomson s.n.* (GH). **Nepal.** Upper Saldim Khola, NW of Hatiya [Hatia], Sankhuwasabha District, 27°45′N, 87°17′E, *D. G. Long et al. 710* (E); Marsiandi valley, *D. G. Lowndes 906* (A, E); Langtang, *O. Polunin 434* (E); Khater Dara, Kawa, *O. Polunin et al. 866* (A, E); Bangthari, near Tibrikot, *O. Polunin et al. 2123* (A, E); between Darma and Chankheli Lagna, *O. Polunin et al. 4131* (E); Sheopuri, *D. Proud 126* (E); Tarke Gyang [Tarke Ghyang], *U. Søchting 71* (C); Ganesh Himal, Gatlang, 28°12′N, 85°16′E, *J. D. A. Stainton 3636* (E); Tarakholagaon, W of Beni, *J. D. A. Stainton et al. 175* (E); near Kuinekhani [Kulikhani], *J. D. A. Stainton et al. 2840* (A, E); Siklis, N of Pokhara, *J. D. A. Stainton et al. 4940* (A); Bhurungdi Khola, 28°22′N 83°45′E, *J. D. A. Stainton et al. 5401* (A, E); Lete, Kali Gandaki valley, *J. D. A. Stainton et al. 5598* (E); [precise locality not known], *N. Wallich 4905A* (L); [precise locality not known], *N. Wallich 4985A* (C, E, GH, K, L, NY; paratypes of *Kadsura grandiflora* Wall.); Chhintapu, 27°06′N, 87°56′E, *L. H. J. Williams 462* (E).

Schisandra grandiflora (Fig. 23) is one of the most attractive species in the genus, and is of commercial value as an ornamental due to both the large, waxy, strongly scented flowers and subsequently the fruits. The species was first collected by Wallich in 1821. Wallich's collections were numbered after study, with all specimens of a species receiving a single number; the type collection *Wallich 4985* is therefore a different collection from *Wallich 4985A*, duplicates of which are cited above as paratypes.

Schisandra grandiflora is most closely related to *S. rubriflora* and *S. incarnata*, which also have an androecium that consists of free stamens without any evidence of

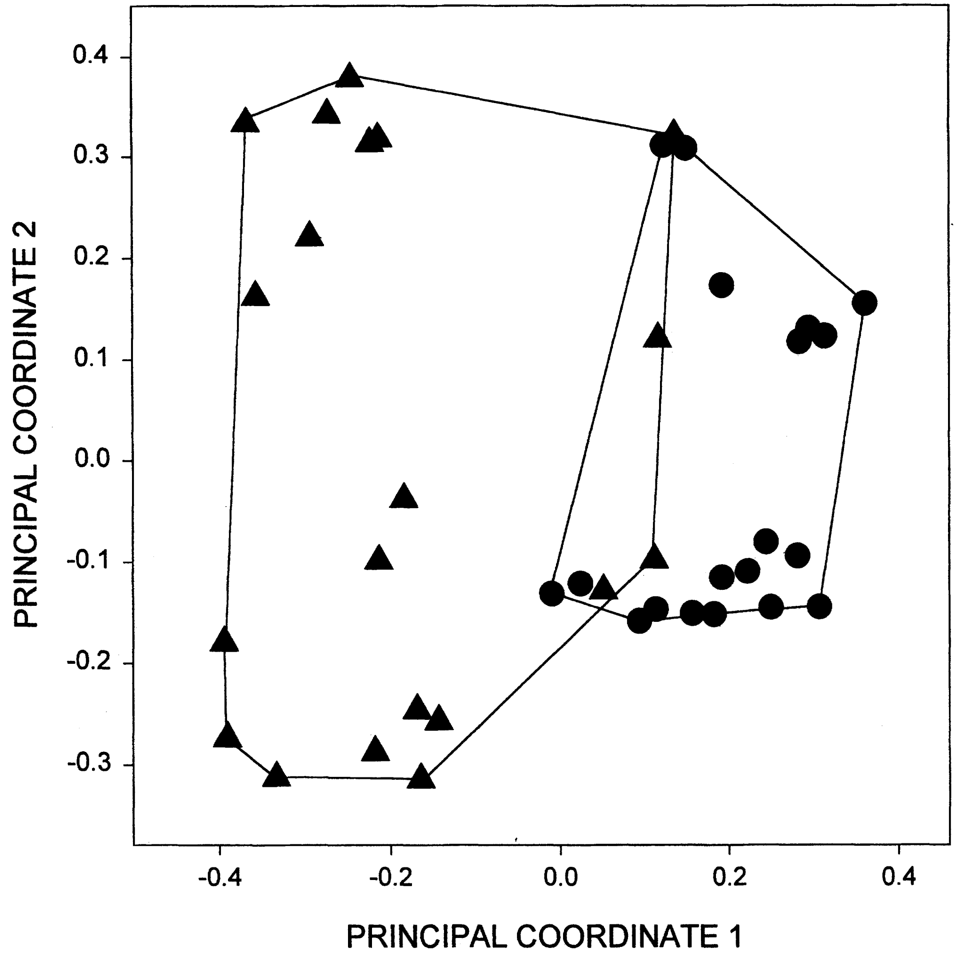


FIG. 25. Principal coordinates analysis (PCoA) of leaf variation in *Schisandra grandiflora* (circles) and *S. rubriflora* (triangles.)

fusion. They differ in several important respects. The most significant difference is flower color: the tepals of *S. grandiflora* are white or cream, whereas those of *S. rubriflora* are red and those of *S. incarnata* flesh-pink. Tepal pigmentation is shown elsewhere to be a generally poor taxonomic character in *Schisandra,* with color variation common within many species (e.g., *S. neglecta*, *S. lancifolia*, *S. micrantha*, and *S. sphaerandra*). It is significant, however, that the color variation evident in the *S. grandiflora-S. rubriflora-S. incarnata* group is strongly correlated with geographical distribution.

It is also noteworthy that the difference in flower color between *S. grandiflora* and *S. rubriflora* is correlated with differences in several leaf characters, as illustrated using PCoA (Fig. 25). The laminas of *S. grandiflora* are typically elliptic, with smaller marginal denticulations, whereas those of *S. rubriflora* are variably elliptic to obovate, with larger denticulations. Laminas of *S. rubriflora* are also generally broader, 2.5–5.5 (–7.5) cm, giving rise to lower length:width ratios of (1.4–) 1.7–2.5 (–3.3), than those of *S. grandiflora.*

As noted by Smith (1947: 102), numerous herbarium collections of *S. sphaerandra* from southern China have been misidentified as *S. grandiflora.* Although there are superficial similarities, *S. sphaerandra* can be distinguished on the basis of several important characteristics, viz.: smaller leaf laminas [(3.5–) 4.5–8 (–12.5) × 1.5–3 (–6.5) cm]; androecia with partial adnation of the filaments to the receptacle; and shorter fruiting tori [(2.5–) 6–10 (–15) cm]. *Schisandra sphaerandra* also shows greater variation in perianth color, often with distinct yellow pigmentation that is absent in *S. grandiflora.*

Potential confusion also exists with *S. neglecta,* although there are several obvious differences between the two species. *Schisandra neglecta* typically has: broader leaf laminas, with length:width ratios of (1.3–) 1.6–2.4 (–2.9); smaller flowers with only (12–) 20–35 (–40) stamens and 20–45 carpels; fusion of apical stamens; and smaller fruiting tori [(2–) 4–8 (–10.5) cm long, (0.8–) 1.0–2.0 mm wide].

Schisandra grandiflora is one of the most extensively studied of all species in the genus, and numerous structures and developmental processes have been described, including: idioblasts (Jalan 1963); ethereal oil cells (Jalan 1965); crystalliferous sclereids (Jalan 1968a); mucilage cells (Jalan 1975); leaf epidermis and stomatal ontogeny (Jalan 1962); petiole structure (Jalan 1988); nodal structure (Jalan 1968b); floral, carpellary, and ovular morphology (Kapil & Jalan 1964; Jalan 1966; Leinfellner 1966); extracarpellary ovules (Jalan & Bhandari 1963); micro- and megasporogenesis and embryology (Kapil & Jalan 1964; Batygina & Vasilyeva 1995); pollen structure (Erdtman 1952: 257; Agababian 1966, 1968; Walker 1974a, b, 1976a, b; Walker & Doyle 1975; Praglowski 1976); and fruit and seed structure (Kapil & Jalan 1964; Melikian 1988). The pollen descriptions in Jalan and Kapil (1964), Kapil and Jalan (1964), and Jalan (1979) are based on incorrectly determined material and do not refer to *S. grandiflora.*

2. Schisandra rubriflora Rehder & E. H. Wilson in Sargent, Pl. Wilson. 1: 412. 1913.—TYPE: CHINA. Western Szechuan [Sichuan]: Pan-lan Shan, W of Kuan Hsien, Niu-tou-shan, 20 Jun 1908, *E. H. Wilson 921b* (holotype: A!).

Woody vines, apparently dioecious (but probably monoecious). Lateral branches lacking wings, with fugaceous perules at base; branches continuing growth in subsequent years. Leaf laminas (5.5–) 7–11.5 (–15) cm long, 2.5–5.5 (–7.5) cm wide, length:width ratio (1.4–) 1.7–2.5 (–3.3), papyraceous, 40–90 μm thick, glabrous, elliptic to obovate-elliptic; primary vein ± plane to slightly impressed above, (slightly) prominent below; secondary veins (4–) 5–7 (–8) pairs per leaf, (slightly) arcuate; base acute to attenuate, rarely obtuse; apex (short-) acuminate; margin denticulate to serrulate, rarely sinuous-serrulate, (5–) 12–17 (–23) teeth per side of leaf; petioles glabrous, (10–) 12–26 (–30) mm long, (0.6–) 0.8–1.6 (–2.0) mm in diameter. Flowers borne in axils of fugaceous bracts at the base of young shoots, solitary; tepals 6–9 (male flowers), 6–7 (female flowers); tepals deep (purple-) red, glabrous; outermost tepal elliptic to ovate, ca. 10.9–12.0 mm long, 6.5–9.6 mm wide, length:width ratio ca. 1.2–1.7; innermost tepal variably elliptic, ovate, or obovate, ca. 6.9–13.5 mm long, 3.7–8.0 mm wide, length:width ratio ca. 0.7–2.0; largest tepal elliptic, ovate, or obovate, 7.5–15.7 mm long, 7.1–10.0 (–13.3) mm wide, length:width ratio 1.0–1.8; outermost tepal very slightly reduced to 0.9–1.0 of length of largest; innermost tepal slightly reduced to 0.7–1.0 of length of largest; peduncles glabrous, (10–) 18–32 (–50) mm long, 0.6–1.2 mm in diameter (male flowers), 18–32 mm long, 0.7–1.3 mm in diameter (female flowers). Male flowers with androecium of 34–66 essentially free stamens, spirally arranged around floral axis, uppermost stamens not connate; thecae extrorse to extrorse-lateral; pollen tricolpate. Female flowers with gynoecium of 50–70 free carpels; carpels 1.2–1.9 mm long, (0.5–) 0.8–1.0 mm wide, length:width ratio (1.5–) 1.8–2.4; pseudostyle broad. Fruit peduncles glabrous, elongated, (4–) 5–7 (–8) cm long, 0.7–2.1 mm wide; torus (6–) 9–12 (–15) cm long, (1.2–) 2–4 (–5) mm wide; apocarps dark (purple-) red, (4–) 5–8 (–11) mm long, (3–) 4–7 (–9) mm wide, length: width ratio 1.1–1.5. Seeds (1–) 2 per apocarp, discoid to flattened-reniform, 2.7–3.6 mm long, (3.1–) 3.4–4 (–4.5) mm wide, length:width ratio 0.8–0.9; testa smooth. Chromosome number: n = 14 (see Appendix 1). Fig. 16B; Plate 1.

Illustrations. Stapf (1928: fig. 9146); Law (1996a: fig. 71, 10–17).

Phenology. Flowering in May and June (rarely July); fruits maturing from July to October.

Distribution (Fig. 26). China (western Sichuan and northern Yunnan), northern Myanmar, and India (extreme eastern Assam); scandent or climbing in forests, rocky slopes, ravines; (1500–) 2500–3000 (–3600) m.

ADDITIONAL SPECIMENS EXAMINED. **China.** SICHUAN: near Ta Kwan, Ta Hsiang Ling, Sikong, *C. Y. Chiao 1628* (A); Mt. Omei [Emei Shan], *H.-C. Chow 7698* (A); Mt. Omei [Emei Shan], Paiyunssu, *H.-C. Chow 7920* (A); Mt. Omei [Emei Shan], *E. Faber 160* (K, NY); Nanchuan-hsien, *W. P. Fang 831* (A, NY), *893* (A); Ma-pien-hsien, *W. P. Fang 1585* (A, NY); Kuan-hsien, *W. P. Fang 2374* (A, NY); Omei-hsien [Emei Xian] *W. P. Fang 2788* (A); Hung-ya-hsien, *W. P. Fang 8270* (A, NY); Kangtin-hsien, Tachienlu [Kangding], *W. P. Fang 3650* (A); [precise locality not known], *A. Henry 8798* (K); near Tachienlu [Kangding], W Szechuan and Tibetan frontier, *A. E. Pratt 186* (K); Mt. Omei [Emei Shan], below Hsi-hsiang-chih, *S. C. Sun & K. Chang 150* (A); Mt. Omei [Emei Shan], Hsi-hsiang-chih, *S. C. Sun & K. Chang 926* (A); Mt. Omei [Emei Shan], Lei-tung-ping, *S. C. Sun & K. Chang 1031* (A), *1357* (A); Mt. Omei [Emei Shan], Chiu-lar-tung, *L. Y. Tai T.110* (A); W of Wen-chuan Hsien, *F. T. Wang 21001* (A); Wa-shan, Chui-Ting-Shan, SE of Tachien, *E. H. Wilson 921* (A, K); Wa-shan county, Wên Chuan Hsien, *E. H. Wilson 921a* (A); Pan-lan-shan, W of Kuan Hsien, *E. H. Wilson 4289* (A); O-pien Hsien, *T. T. Yü 864* (A); Juei-she Hsien, *T. T. Yü 949* (A).—YUNNAN: Pe-long-tsin, *E. E. Maire 3358* (UC); Fu Ch'uan Mt., *McLaren's collectors 77D* (A, K); Mt. Kenichunpo, Salwin and Irrawady divide, *J. F. Rock 22018* (A, K, NY, UC); Wei-se Hsien, *H. T. Tsai 57914* (A), *57985* (A); Wei-si Hsien, *C. W. Wang 63735* (A); Wei-si Hsien, Yeh-Chih, *C. W. Wang 67966* (A); [precise locality not known], *T. T. Yü 8307* (A); Atuntze, Mt. Kaakerpu, *T. T. Yü 8511* (A), *10319* (A), *10483* (A).—Precise locality not known: SW China, s.a., *P. Monbeig s.n.* (K, L); W China, *E. H. Wilson 3135* (K). **India.** ASSAM: Delei valley, 28°21′N, 96°37′E, *F. K. Ward 8210* (K); Delei valley, 28°15′N, 96°35′E, *F. K. Ward 8665* (K). **Myanmar [Burma].** Malikha-Salwin Divide, 26°30′N, *G. Forrest 29715* (E); Adung valley, 27°30′N, 97°30′E, *F. K. Ward 9530* (A); Adung valley, 28°20′N, 97°45′E, *F. K. Ward 9593* (A); Uring Bum, above Ahkail, *F. K. Ward 20893* (A, E).

Cultivated. Hortus Botanicus Universitatis Gandavensis, Belgium, *P. Goetghebeur 8857* [*HBUG 87-0254*] (HKU).

Schisandra rubriflora is closely related to *S. grandiflora*; the most significant taxonomic difference between the two species is the color of the perianth (deep red in *S. rubriflora*, cream in *S. grandiflora*), although there is also a range of minor vegetative differences (discussed under *S. grandiflora*, no. 1). The similarities between the two species have lead many taxonomists (e.g., Schneider 1917) to regard *S. rubriflora* as a variety of *S. grandiflora*. *Schisandra rubriflora* is also closely related to *S. incarnata*, again differing in perianth color (discussed under *S. incarnata*, no. 3).

Schisandra rubriflora is partially sympatric with two other species, *S. sphaerandra* and *S. neglecta*, which may cause taxonomic confusion. *Schisandra sphaerandra* often has red flowers and is superficially similar to *S. rubriflora*, although the distinction is obvious if male flowers are present due to differences in the degree of adnation of filaments to the receptacle. *Schisandra sphaerandra* also typically has: smaller and narrower leaf laminas [(3.5–) 4.5–8 (–12.5) × 1.5–3 (–6.5) cm], with length:width ratios of (1.6–)

PLATE 1. *Schisandra rubriflora* (*S.* subg. *Pleiostema*). A, flowering branch (female). B, male flower. C, D, stamens. E, receptacle of female flower, with carpels (longitudinal section). F, G, carpels. H, carpel (longitudinal section). I, fruit. J, K, seeds. Reproduced from Stapf (1928: pl. 9146); photograph © Royal Botanic Gardens, Kew.

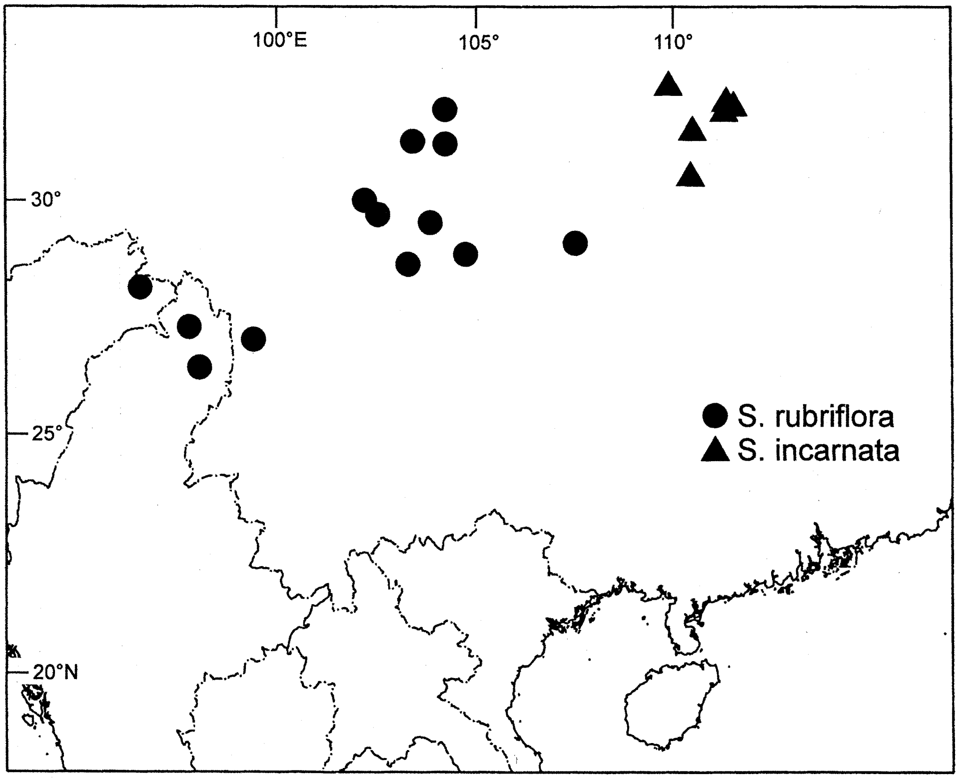


FIG. 26. Distribution of *Schisandra rubriflora* and *S. incarnata.*

2.2–3.2 (–3.8); only (1–) 5–10 (–27) lamina marginal denticulations; smaller flowers with only 22–42 (–70) stamens; and shorter male peduncles (5–24 mm).

Confusion is also possible with *S. neglecta*, although the following characters can be used to distinguish *S. neglecta*: leaf laminas that are commonly ovate, smaller [(5–) 5.5–9.5 (–11) × (2–) 3–4.5 (–6.5) cm], and with only (4–) 6–12 (–18) marginal denticulations; smaller male flowers, typically with fusion of apical stamens, (12–) 20–35 (–40) stamens, and introrse-lateral thecae; smaller female flowers with a greater number of tepals (7–9), and narrow pseudostyles; shorter fruiting tori [(2–) 4–8 (–10.5) cm]; and seeds with variably smooth to rugulose (rarely tuberculate) testa ornamentation.

The following structures have been studied in detail for *S. rubriflora*: leaf indumentum (Hennig et al. 1994; Metcalfe 1987), stomatal ontogeny (Metcalfe 1987), wood and bark anatomy (Carlquist 1999), and pollen structure (Praglowski 1976; Keng 1993).

3. Schisandra incarnata Stapf, Bot. Mag. 152: sub fig. 9146. 1928 (as "*Schizandra*").—Type: China. Hupeh [Hubei]: without locality, Jun 1907, *E. H. Wilson 2085* (lectotype, here designated: K!; isolectotypes: A! K! NY! US).

Woody vines, apparently dioecious (but probably monoecious). Lateral branches lacking wings, with fugaceous perules at base; branches continuing growth in subsequent years. Leaf laminas (7–) 8–11 (–12.5) cm long, (3.5–) 4–5.5 cm wide, length:width ratio (1.5–) 1.7–2.5 (–3.1), papyraceous, ca. 90–100 µm thick, glabrous, elliptic to obovate;

primary vein plane to slightly impressed above, slightly prominent below; secondary veins (4–) 5–6 (–7) pairs per leaf, slightly arcuate; base acute to attenuate; apex short- (rarely long-) acuminate; margin denticulate to serrulate, 10–19 teeth per side of leaf; petioles glabrous, (12–) 20–25 (–35) mm long, (0.7–) 0.9–1.2 (–1.5) mm in diameter. Flowers borne in axils of fugaceous bracts at the base of young shoots, solitary; tepals 7–8 (flowers of both sexes); tepals (deep) flesh-pink, glabrous; largest tepal elliptic to obovate, ca. 10–17 mm long, 6–12 mm wide, length:width ratio ca. 1.2–1.7; peduncles glabrous, 16–25 (–35) mm long, 0.6–0.8 (–1.3) mm in diameter (flowers of both sexes). Male flowers with androecium of ca. 28 essentially free stamens, spirally arranged around floral axis, uppermost stamens not connate; thecae extrorse-lateral; pollen tricolpate. Female flowers [fide Smith 1947: 106] with gynoecium of ca. 70 free carpels; carpels 1.8–2.2 mm long, 0.8–1.2 mm wide; pseudostyle broad. Fruit peduncles glabrous, elongated, 3.5–5 cm long, 0.6–1.0 mm wide; torus 5–7 (–11) cm long, 1.4–3.5 mm wide; apocarps red, 8–10.5 mm long, 5.5–8.5 mm wide, length:width ratio 1.0–1.4. Seeds 1–2 per apocarp, flattened-reniform, (3.0–) 3.2–3.7 mm long, (3.5–) 3.7–4.5 (–4.7) mm wide, length:width ratio 0.7–0.9; testa smooth. Chromosome number unknown.

Illustrations. Law (1996a: fig. 71, 1–9).

Phenology. Flowering in May and June; fruits maturing in August and September.

Distribution (Fig. 26). Endemic to China (western Hubei); scandent or climbing in thickets and forests dominated by *Fagus*, *Betula*, and *Pinus*; 1600–2300 m.

ADDITIONAL SPECIMENS EXAMINED. **China.** HUBEI: Shennongjia Forest District, along Qiaodonggou canyon W of the road between Jiuhuping Forest Farm and Bancang, 31°30′N 110°30′E, *Sino-American Expedition to Western Hubei Province 382* (A, UC); Shennongjia Forest District, between Qiujiaping & Mt. Laojun, 31°30′N, 110°30′E, *Sino-American Expedition to Western Hubei Province 645* (UC); Shennongjia Forest District, hillside above Qianjiaping, 31°30′N, 110°30′E, *Sino-American Expedition to Western Hubei Province 1389* (A, NY, UC); Hsing-shan Hsien, Wen Tsao Mt., *E. H. Wilson 263* (A, E, K, US; paratypes of *S. incarnata* Stapf); Fang Hsien, *E. H. Wilson 318* (A, K, US; paratypes of *S. incarnata* Stapf); Hsing-shan & Fang Hsien, *E. H. Wilson 4574* (A; paratype of *S. incarnata* Stapf).

Schisandra incarnata forms a coherent and well-supported clade with *S. grandiflora* and *S. rubriflora*. All three species are superficially similar, differing in a range of characters, the most significant of which is perianth color (flesh-pink in *S. incarnata*, deep red in *S. rubriflora*, and cream in *S. grandiflora*). *Schisandra grandiflora* has narrower leaf laminas than *S. incarnata* [(2–) 2.5–4 (–5) cm], resulting in a higher length:width ratios of (1.8–) 2.5–3.2 (–4.0), although *S. rubriflora* leaves are similar to those of *S. incarnata*. The fruiting torus is considerably shorter in *S. incarnata* than in either *S. grandiflora* [(13–) 16–18 (–25) cm] or *S. rubriflora* [(6–) 9–12 (–15) cm].

There are two partially sympatric species, *S. sphenanthera* and *S. glaucescens*, which may be confused with *S. incarnata*, although the distinctions are clearly evident if male flowers are present. In the absence of male flowers, taxonomic determination is possible by reference to the following characters: the presence of glaucescence on the abaxial leaf lamina surface (absent in *S. incarnata* and *S. sphenanthera*, present in *S. glaucescens*); the number of leaf lamina marginal denticulations [10–19 in *S. incarnata*, (0–) 5–11 (–15) in *S. sphenanthera*, and (4–) 6–12 (–13) in *S. glaucescens*]; carpel number (ca. 70 in *S. incarnata*, ca. 25–45 in *S. sphenanthera*, and ca. 42–50 in *S. glaucescens*); and pseudostyle shape (broad in *S. incarnata*, but narrow in both *S. sphenanthera* and *S. glaucescens*).

The pollen of *S. incarnata* has been described and illustrated by Praglowski (1976).

4. Schisandra sphaerandra Stapf, Bot. Mag. 152: sub fig. 9146. 1928 (as "*Schizandra*"). *Schisandra sphaerandra* forma *typica* A. C. Smith, Sargentia 7: 109. 1947.—TYPE: CHINA. NW Yunnan: eastern flank of Lichiang range, 27°12′N, May 1910, *G. Forrest 5663* (lectotype, here designated: K!; isolectotypes: E! US).

Schisandra grandiflora var. *cathayensis* C. K. Schneider, Bot. Gaz. 63: 522. 1917.—TYPE: CHINA. Szechuan [Sichuan]: Hua-li, Yalung, 28 May 1914, *C. K. Schneider 3936* (holotype: not located).

Schisandra sphaerandra forma *pallida* A. C. Smith, Sargentia 7: 109. 1947.—TYPE: CHINA. Yunnan: between Chien-chu'an plain and the Mekong drainage basin to La-chih-ming, May 1923, *J. F. Rock 8595* (holotype: A!; isotypes: NY! UC! US, photo of UC isotype: HKU!).

Woody vines, monoecious (often appearing dioecious). Lateral branches lacking wings, with fugaceous perules at base; branches continuing growth in subsequent years. Leaf laminas (3.5–) 4.5–8 (–12.5) cm long, 1.5–3 (–6.5) cm wide, length:width ratio (1.6–) 2.2–3.2 (–3.8), papyraceous (rarely subcoriaceous), 40–90 (–150) µm thick, glabrous, elliptic to obovate-elliptic (rarely ovate-elliptic); primary vein slightly impressed (rarely ± plane) above, slightly prominent below; secondary veins (4–) 5–7 (–9) pairs per leaf, (slightly) arcuate; base acute (rarely obtuse in older leaves); apex (short-) acuminate; margin denticulate to serrulate, (1–) 5–10 (–27) teeth per side of leaf; petioles glabrous, (6–) 9–20 (–33) mm long, 0.6–1.3 (–1.5) mm in diameter. Flowers borne in axils of fugaceous bracts at the base of young shoots, solitary; tepals (5–) 6–7 (–9) (male flowers), 6–8 (female flowers); tepals variably white, cream, yellowish, rose-pink, crimson, dark red, or purplish, glabrous; outermost tepal variably ovate, elliptic, or obovate, (3.4–) 6.6–10.0 (–16.0) mm long, (3.0–) 5.0–6.0 (–10.8) mm wide, length:width ratio (0.7–) 1.0–1.5 (–2.2); innermost tepal variably ovate, elliptic, or obovate, (3.0–) 6.0–9.2 (–10.0) mm long, (2.0–) 3.2–5.4 (–7.2) mm wide, length:width ratio 1.2–2.0; largest tepal variably ovate, elliptic, or obovate, (6.0–) 7.5–12.5 (–17.4) mm long, (4.3–) 6.0–11.0 mm wide, length:width ratio (1.0–) 1.2–1.7; outermost tepal slightly reduced, (0.4–) 0.9–1.0 of length of largest; innermost tepal (slightly) reduced, 0.4–0.9 of length of largest; peduncles glabrous, 5–24 mm long, (0.4–) 0.6–1.0 (–1.8) mm in diameter (male flowers), (6–) 10–25 (–44) mm long, (0.6–) 0.8–1.1 (–2.0) mm in diameter (female flowers). Male flowers with androecium of 22–42 (–70) stamens, spirally arranged around broad floral axis, basally adnate to receptacle, uppermost stamens not connate; thecae extrorse-lateral; pollen tricolpate. Female flowers with gynoecium of (35–) 70–100 free carpels; carpels (0.7–) 1.1–2.0 (–2.4) mm long, (0.5–) 0.6–1.2 mm wide, length:width ratio (1.1–) 1.3–2.2 (–2.5); pseudostyle generally broad. Fruit peduncles glabrous, elongated, (1.5–) 2.5–5.5 (–6.5) cm long, 1–1.6 mm wide; torus (2.5–) 6.5–10 (–15) cm long, (1.9–) 2.4–3.0 (–3.6) mm wide; apocarps ripening scarlet to deep red, 6–10.5 (–12) mm long, (4–) 5.5–7.5 (–9) mm wide, length:width ratio (1.1–) 1.2–1.6 (–1.7). Seeds (1–) 2 per apocarp, flattened-reniform (rarely discoid), (2.9–) 3.2–3.6 (–3.8) mm long, (3.6–) 3.7–4.1 (–4.3) mm wide, length:width ratio 0.8–0.9 (–1.0); testa ± smooth. Chromosome number unknown. Fig. 6B.

Illustrations. Smith (1947: fig. 17, l–n); Law (1996a: fig 72, 1–11).

Phenology. Flowering in May and June (rarely into August); fruits maturing in September and October (rarely from June on).

Distribution (Fig. 27). Endemic to China (southern Sichuan and northern Yunnan);

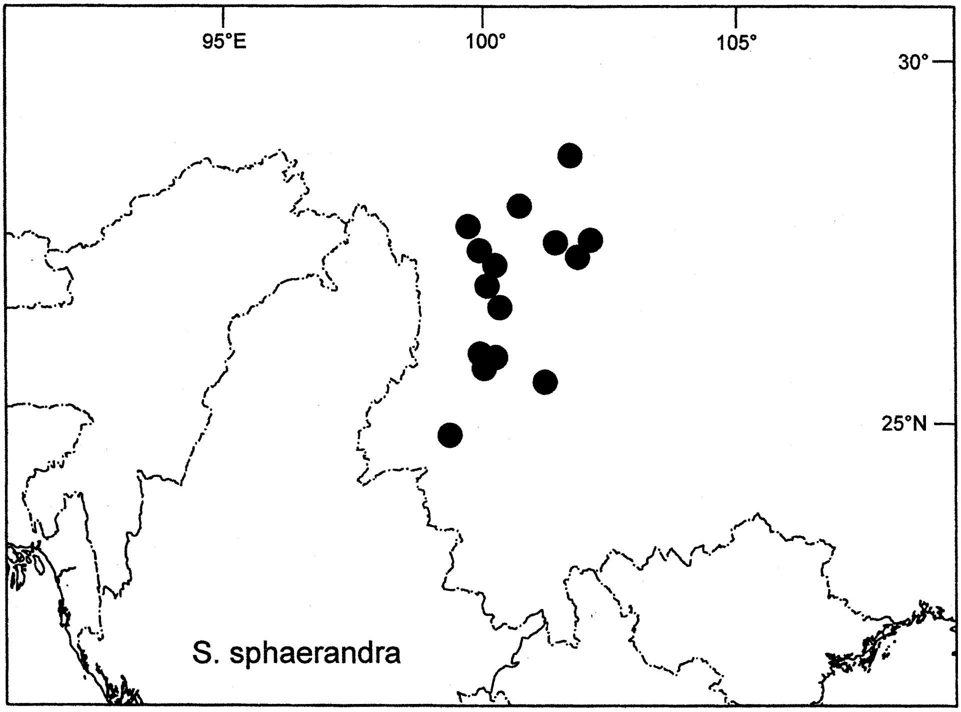


FIG. 27. Distribution of *Schisandra sphaerandra.*

scandent or climbing in open scrub and mixed and coniferous forests dominated by *Abies, Picea,* and *Pinus*; (1000–) 2700–3600 (–3800) m.

ADDITIONAL SPECIMENS EXAMINED. **China.** SICHUAN: 15 km S of Jiulong, near stream running to Jiulong River, *Expedition to Sichuan (SICH) 641* (K); Daörlbi, between Yenyüen & Yungning, 27°35′N, 101°12′E, *H. F. von Handel-Mazzetti 2962* (A, K; paratypes of *S. sphaerandra* Stapf); Kaushu shan, on trail to Leirong, SW of Muli, *J. F. Rock 24092* (A, NY, UC); between Kalapa & Linku, 27°40′N, 101°30′E, *C. K. Schneider 1276* (A, E, K; paratypes of *S. sphaerandra* Stapf and *Schisandra grandiflora* var. *cathayensis* C. K. Schneid.); Ta-hsiang-ling, *H. Smith 2031* (A).—YUNNAN: Lijiang Co., Yulong Shan, Gangheba, *D. Chamberlain et al. 28* (K); Tamichung, NW Likiang, *R. C. Ching 20572* (A); Isze-kow on Gangze, NW Likiang, *R. C. Ching 20644* (A); Si-fang-za, NW Likiang, *R. C. Ching 22003* (A); Bi Ye Go valley, N of Yangtze bridge at Lou Swang, *Chung-tien-Lijiang-Dali Expedition 599* (K); [precise locality illegible], 24 May 1889, *J. M. Delavay s.n.* (A); on the way to Anangu, SE Chungtien, *K. M. Feng 934* (A); N flank of Haba Snow Range, *K. M. Feng 1217* (A); Lamachang, near Ngerya, Muli, on the border of Chungtien, *K. M. Feng 2883* (A); E flank of Mt. Lichiang Range, 27°12′N, *G. Forrest 2122* (E, K; paratypes of *S. sphaerandra* Stapf); Tali Range, 25°40′N, *G. Forrest 4797* (A; paratype of *Schisandra grandiflora* var. *cathayensis* C. K. Schneid.); 25°40′N, *G. Forrest 7181* (K); Pe-long-tsin, *E. E. Maire 3359* (UC); Tali, *McLaren "C" collector 57* (A); E slopes of Linkiang Snow range, Likiang District, Yangtze watershed, *J. F. Rock 3399* (A, NY, UC); W of Talifu, Mekong watershed, en route to Youngchang and Tengyueh, *J. F. Rock 6825* (A); Mt. Shwe-Men-Kai, SE of Chung-tien, *J. F. Rock 17292* (A, NY); Chung-tien District, N of Chung-tien, Tonwa Territory, *J. F. Rock 24699* (A, K, NY, UC); N of Chung-tien, Tonwa Territory, *J. F. Rock 25273* (A, UC); Lichiang, *C. K. Schneider 3303* (A, GH; paratypes of *Schisandra grandiflora* var. *cathayensis* C. K. Schneid.); between Singguch & Tengchuan, *C. K. Schneider 2686* (A, GH; paratypes of *Schisandra grandiflora* var. *cathayensis* C. K. Schneid); Lizaiong, *C. K. Schneider 2807* (A; paratype of *Schisandra grandiflora* var. *cathayensis* C. K. Schneid.); Duanqing, above Yangbi, *Sino-British Expedition to Cangshan 137* (K); below Longquan, above Dali, *Sino-British Expedition to Cangshan 526* (A, K); by track from Longquan to Dali, *Sino-British Expedition to Cangshan 614* (A); Xiaohuadianba, N end of

Cangshan, *Sino-British Expedition to Cangshan 781* (A, K), *1017* (A, K); Wei-se Hsien, *H. T. Tsai 59793* (A), *59950* (A); Ta-li Hsien, *C. W. Wang 63163* (A); [precise locality not known], *T. T. Yü 5582* (A), *10075* (A), *11482* (A); Chungtien, Haba, *T. T. Yü 13497* (A); Mulii, Wachin, Yunnanpuh, *T. T. Yü 14506* (A); Lichiang Snow Range, *T. T. Yü 15108* (A).

This taxon was first recognized by Schneider (1917) as *S. grandiflora* var. *cathayensis*. Although the type specimen has not been located, numerous paratype specimens (listed above) have been examined and indicate that the name is undoubtedly synonymous with *S. sphaerandra*.

Specific rank was first applied by Stapf (1928), who commented that the "sessile or subsessile [anthers] on a semi-globose receptacle" were similar to those found in *S. propinqua*. Smith (1947: 108) subsequently elaborated on this, commenting that *S. sphaerandra* appeared to be transitional between the *S. grandiflora-S. rubriflora-S. incarnata* group and other species. The cladistic analysis presented in this monograph does not corroborate this hypothesis, however, since *S. sphaerandra* is a member of the *S. grandiflora-S. rubriflora-S. incarnata* clade, sister to all other taxa.

Stapf's (1928) concept of *S. sphaerandra* included specimens with two distinct perianth colors: either crimson to magenta, or white to pink. Smith (1947: 107–110) recognized these as forms (*typica* and *pallida*), although there are no correlated vegetative or reproductive characters, and specimens without flowers cannot be taxonomically determined below the species level. The two forms are furthermore fully sympatric and do not appear to occupy distinct ecological niches. Taxonomic recognition of the two forms does not appear warranted unless the existence of a breeding barrier can be found.

Schisandra sphaerandra is most closely related to the *S. grandiflora-S. rubriflora-S. incarnata* group, although it is sympatric with only *S. rubriflora*. *Schisandra sphaerandra* can easily be distinguished from *S. rubriflora* if male flowers are present, due to differences in the degree of adnation of filaments and receptacle (described under "Androecium"), or if the specimens of *S. sphaerandra* are pale-flowered. In the absence of these features, *S. rubriflora* can be distinguished on the basis of the following characters: larger leaf laminas [(5.5–) 7–11.5 (–15) × 2.5–5.5 (–7.5) cm]; and longer fruiting peduncles and tori [(4–) 5–7 (–8) cm and (6–) 9–12 (–15) cm, respectively].

It is also possible that *S. sphaerandra* could be confused with *S. neglecta*. *Schisandra neglecta*, however, typically has the following features: broader, elliptic to ovate leaf laminas [(2–) 3–4.5 (–6.5) cm wide], resulting in lower length:width ratios of (1.3–) 1.6–2.4 (–2.9); smaller flowers with the largest tepals measuring only 5.1–9.1 mm long; longer flower peduncles [(13–) 20–40 (–49) mm for male flowers, (21–) 25–65 mm for female flowers]; fewer stamens [(12–) 20–35 (–40)], with fusion of apical stamens; fewer carpels (20–45), with narrow pseudostyles; smaller apocarps [(3–) 5–7 (–8.5) × (3–) 3.5–5.5 (–7.5) mm]; and seeds that often have a rugulose (rarely tuberculate) testa ornamentation.

The pollen of *S. sphaerandra* has been described and illustrated by Praglowski (1976).

II. **Schisandra** subgenus **Sinoschisandra** Y.-W. Law, Fl. Reipubl. Popularis Sin. 30(1): 253, 272. 1996.—TYPE: *Schisandra henryi* Clarke.

Woody vines. Male flowers with androecium of 7–35 (–40) essentially free stamens, uppermost stamens generally only partially differentiated, appearing connate, forming a carnose mass with marginal thecae; thecae of free stamens introrse-lateral; pollen hexacolpate. Female flowers with gynoecium of 14–65 (–70) free carpels; pseudostyles small or narrow and subulate. Seed testa variably smooth, rugulose, or tuberculate.

Distribution (Fig. 17B). Nepal, India (Bengal, Sikkim, Manipur, Meghalaya), northern Myanmar [Burma], northern Thailand, northern Vietnam, China (Anhui, Fujian, Gansu, Guangdong, Guangxi, Guizhou, Henan, Hubei, Hunan, Jiangsu, Jiangxi, Shaanxi, Shanxi, Sichuan, Taiwan, Xizang [Tibet], Yunnan and Zhejiang), and Indonesia (Java).

5. **Schisandra neglecta** A. C. Smith, Sargentia 7: 127. 1947.—TYPE: CHINA. Yunnan: mountains of A-wa-lo, NE of Yeh-chih, E of the Mekong, Jun 1923, *J. F. Rock 8933* (holotype: A!; isotypes: UC! US).

? *S. lancifolia* var. *polycarpa* Z. He, J. S.-W. Agric. Univ. 10: 294. 1988.—SYNTYPES: CHINA. Sichuan: Xide Xian Lake commune, 19 May 1981, *G. H. Tang & J. M. Tan 11* (Herbarium, Sichuan Institute of Chinese Medicine, Chengdu, Sichuan); idem, 19 May 1981, *G. H. Tang & J. M. Tan 12* (Herbarium, Sichuan Institute of Chinese Medicine, Chengdu, Sichuan); CHINA. Sichuan: Xichang Xian, Luojishan, 21 Sep 1981, *J. M. Tan 22* (Herbarium, Sichuan Institute of Chinese Medicine, Chengdu, Sichuan).

Woody vines, apparently dioecious (but probably monoecious). Lateral branches lacking wings, with fugaceous perules at base; branches continuing growth in subsequent years. Leaf laminas (5–) 5.5–9.5 (–11) cm long, (2–) 3–4.5 (–6.5) cm wide, length:width ratio (1.3–) 1.6–2.4 (–2.9), papyraceous (rarely subcoriaceous), 40–50 (–80) μm thick, glabrous, elliptic to ovate; primary vein slightly impressed (rarely ± plane) above, (slightly) prominent below; secondary veins 4–7 pairs per leaf, (slightly) arcuate; base acute (younger leaves) to obtuse (older leaves); apex (short-) acuminate; margin denticulate to serrulate, (4–) 6–12 (–18) teeth per side of leaf; petioles glabrous, (7–) 11–20 (–30) mm long, 0.7–1.3 (–1.7) mm in diameter. Flowers borne in axils of fugaceous bracts at the base of young shoots or in axils of leaves, solitary; tepals 6–8 (–10) (male flowers), 7–9 (female flowers); tepals white, yellow, yellowish red, or pink, glabrous; outermost tepal elliptic to ovate, (4.6–) 6.4–7.6 mm long, 3.2–6.2 mm wide, length:width ratio 1.0–1.6 (–1.8); innermost tepal variably ovate, elliptic, or obovate, 4.0–6.3 mm long, (2.3–) 3.0–4.8 mm wide, length:width ratio 1.0–1.6; largest tepal variably ovate, elliptic, or obovate, 5.1–9.1 mm long, 4.5–7.4 mm wide, length:width ratio 0.8–1.4 (–1.8); outermost tepal slightly reduced, 0.8–1.0 of length of largest; innermost tepal (slightly) reduced, (0.4–) 0.6–0.9 of length of largest; peduncles glabrous, (13–) 20–40 (–49) mm long, (0.3–) 0.4–0.7 (–1.0) mm in diameter (male flowers), (21–) 25–65 mm long, (0.5–) 0.6–0.8 (–0.9) mm in diameter (female flowers). Male flowers with androecium of (12–) 20–35 (–40) essentially free stamens, uppermost stamens generally only partially differentiated, appearing connate, forming a carnose mass (0.6–) 1.5–2.5 mm in diameter, with marginal thecae; thecae of free stamens introrse-lateral; pollen hexacolpate. Female flowers with gynoecium of 20–45 free carpels; carpels (1.3–) 1.7–2.1 (–2.9) mm long, (0.5–) 0.6–1.0 mm wide, length:width ratio (1.7–) 2.1–3.3 (–4.0); pseudostyle narrow. Fruit peduncles glabrous, not elongated, (3.5–) 4.5–6 (–7.5) cm long, (0.4–) 0.5–0.8 (–1.0) mm wide; torus (2–) 4–8 (–10.5) cm long, (0.8–) 1.0–2.0 mm wide; apocarps red, (3–) 5–7 (–8.5) mm long, (3–) 3.5–5.5 (–7.5) mm wide, length:width ratio (0.9–) 1.1–1.5 (–1.8). Seeds 1–2 per apocarp, discoid to flattened-reniform, (2.7–) 2.8–3.4 (–3.6) mm long, (3.1–)

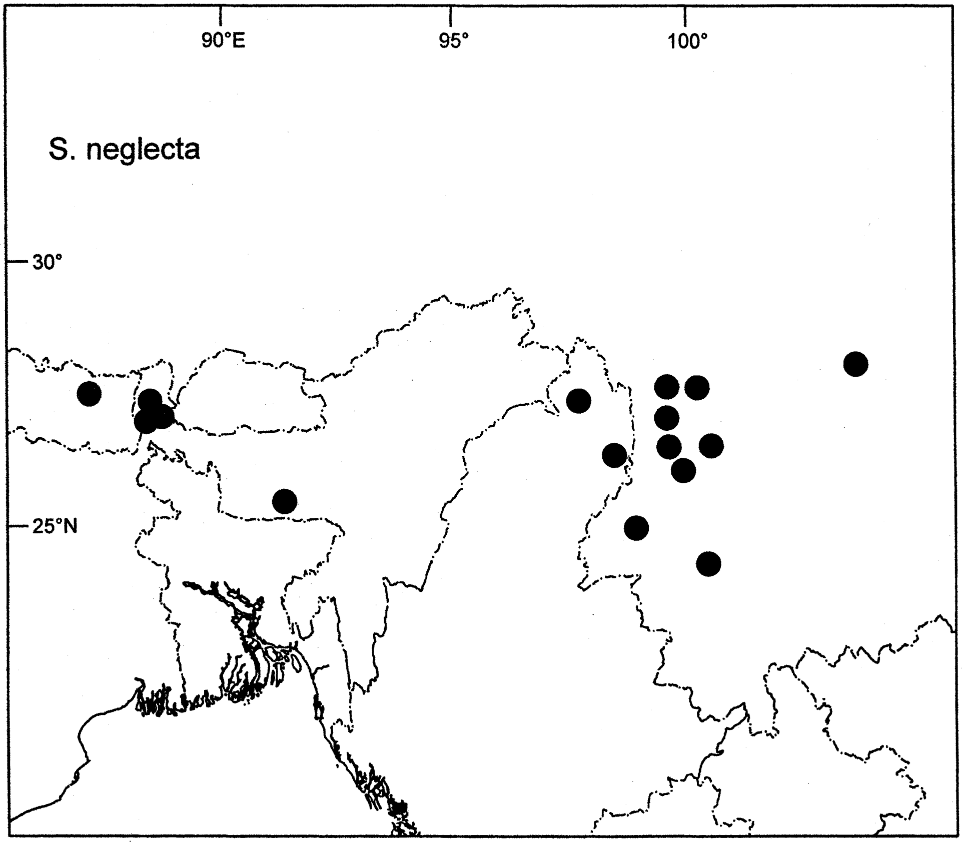


FIG. 28. Distribution of *Schisandra neglecta.*

3.3–3.9 (–4.2) mm wide, length:width ratio 0.8–0.9; testa ± smooth to rugulose (rarely ± tuberculate). Chromosome number unknown. Fig. 16A.

Illustrations. King (1891: pl. 69B, as "*Schizandra elongata*"); Smith (1947: fig. 17, g); Law (1996a: fig. 75, 11–20).

Phenology. Flowering from May to July (rarely from April); fruits maturing from July to November.

Distribution (Fig. 28). Nepal, north-east India (Bengal, Sikkim, Meghalaya), northern Myanmar, and China (Yunnan); scandent or climbing in thickets and mixed forests, often by streams and in ravines; (1300–) 1700–2900 (–3600) m.

ADDITIONAL SPECIMENS EXAMINED. **China.** YUNNAN: Tamichung, NW Likiang, *R. C. Ching 21484* (A); Wen-feng-tze, SW of Likiang valley, *R. C. Ching 21830* (A); Lamachang, Ngerya, on the border of Chungtien, Muli, *K. M. Feng 2844* (A); Chiao-tou, on Yangtze ba, *K. M. Feng 3149* (A); hills to the E of Tengyueh, 25°N, *G. Forrest 7622* (K, MO); [precise locality not known], *G. Forrest 15825* (K); between R. Djinscha-djiang (Yangtse) & Landsang-djiang (Mekong), *H. F. von Handel-Mazzetti 8820*, pro parte (A); S of Red River, *A. Henry 10697* (A, NY); [precise locality not known], *A. Henry 12022A*, pro parte (A); on hills above the mineral springs just W of Xiaguan at Wenqie, Dali Xian, *H. Li & V. Soukup 958* (A); [precise locality not known], s.a., *E. E. Maire s.n.* (UC); Yong-shan Hsien, *H. T. Tsai 51178* (A); Pin-chuan Hsien, *H. T. Tsai 52919* (A); Kien-shuei Hsien [= P'ing-pien Hsien], *H. T. Tsai 53052* (A); Lan-ping Hsien, *H. T. Tsai 54053* (A); [precise locality not known], *H. T. Tsai 57316* (A), *57585A* (A), *57594A* (A), *57681* (A); Wei-se Hsien, *H. T. Tsai 57875* (A), *59522* (A), *59827* (A), *59926* (A), *63107* (A); Ta Li Hsien, *C. W. Wang 63435* (A); Wei-si Hsien, *C. W. Wang 63549* (A), *63634* (A), *63997* (A), *64121* (A); Wei-si hsien, Yah-Chih, *C. W. Wang 68684* (A); Fo-Hai, *C. W. Wang 74223A* (A), *77299* (A); Shunning, Hoshaoshan, *T. T. Yü 16148* (A); Alulaka, Mekong-Salwin Divide, *T. T. Yü 19108* (A); Kiukiang, Chiengen, *T. T. Yü 19439* (A). **India.** BENGAL: Darjeeling, *C. B. Clarke 26715* (E); Darjeeling, *J. S. Gamble 26752B* (K); Darjeeling, *W. Griffith 76* (K); East Bengal, *W. Griffith 77* (C, GH, L); below Darjiling, Jun–Sep 1857, *T. Thomson s.n.* (K).—MEGHALAYA: "Khasia," s.a., *J. D. Hooker & T. Thomson s.n.* (GH, NY).—SIKKIM: Lebang, *T. Anderson 350* (GH); Kaliteshingpat, Lepcha, *J. S. Gamble 1891* (K); [precise locality not known], s.a., *J. D. Hooker s.n.* (GH, NY); Tonglo, s.a., *J. D. Hooker s.n.* (K). **Myanmar [Burma].** Near Kangfang, Myitkyina, *C. W. D. Kermode 17289* (K); N Adung valley, 27°30'N, 97°30'E, *F. K. Ward 9443* (A). **Nepal.** Hatiar, Arun valley, 87°–88°E, *J. D. A. Stainton 432* (A); [precise locality not known], s.a., *N. Wallich s.n.* (GH).

Schisandra neglecta was not described until 1947, despite its comparatively common and widespread distribution, extending from eastern Nepal to Yunnan. Numerous collections were made in the 19th century by collectors, such as C. B. Clarke, J. S. Gamble, W. Griffith, J. D. Hooker, T. Thomson, and N. Wallich, and the species is consequently well represented in herbaria. Most of these collections and early taxonomic treatments, however, referred to the species under the name "*Schisandra elongata*" or its synonym, "*Sphaerostema elongatum*" (see list of "Misapplied Names"). *Schisandra elongata* is endemic to Java and can be distinguished from *S. neglecta* by the following characters: the leaf laminas are larger [(7–) 9–12 (–15) × (3.5–) 4.5–7 (–8.5) cm] and typically thinner, with fewer leaf marginal denticulations [0–11 (–15)]; the secondary veins on the leaf laminas are strongly arcuate; the flowers have larger numbers of tepals (8–10 in male flowers, 9–10 in female flowers); and the outermost tepal is highly reduced to 0.2–0.4 of the length of the largest.

Within continental Asia, *S. neglecta* is closely related to two other species, *S. arisanensis* (inclusive of *S. viridis*) and *S. sphenanthera*; these species form a coherent group and pose significant problems in taxonomic determination. All three species are glabrous and have medium-sized flowers with an intermediate number of floral parts. Distinctions between the species can be made using the following characters: degree of prominence of secondary and lower order veins on the leaf laminas (slightly prominent abaxially, and often adaxially, in *S. neglecta* and *S. arisanensis*, but not prominent either abaxially and adaxially in *S. sphenanthera*); leaf lamina venation appearing dark (*S. neglecta*) or pale (*S. arisanensis* and *S. sphenanthera*) after drying; apocarps comparatively small in *S. neglecta* [(3–) 5–7 (–8.5) × (3–) 3.5–5.5 (–7.5) mm], but larger in *S. arisanensis* [(5–) 7–9.5 (–11) × (3.5–) 5–6.5 (–7.5) mm] and *S. sphenanthera* [(5.5–) 6.5–9 × 4–8 mm]; and seed testa variably smooth or rugulose (rarely tuberculate) in *S. neglecta* and *S. arisanensis*, but invariably smooth in *S. sphenanthera*. Smith (1947: 99) lists several other diagnostic characteristics, including leaf lamina shape and length, tepal shape, stamen and carpel number, and fruiting torus diameter; all these characters are highly variable and do not appear to be very useful.

The brief diagnosis that He (1988) provided for *S. lancifolia* var. *polycarpa* is insufficient for critically evaluating taxonomic affinities. The type specimens (syntypes and several paratypes) were deposited in an unregistered minor regional herbarium, apparently without depositing duplicate sheets in any other herbarium. Although it has not been possible to examine any of the types, the name is here reduced to synonymy on the basis of the tepal number (7–10) and carpel number [(19–) 21–29] mentioned in the protologue, both of which are too numerous for *S. lancifolia*. Some of the features in the illustration (He 1988: fig. 3) furthermore suggest *S. neglecta* rather than *S. lancifolia*: the female peduncles are ca. 50 mm long; the androecium has ca. 24 stamens; the gynoecium has ca. 44 carpels; and the fruiting torus is ca. 9 cm long.

Various structures and developmental processes have been studied in *S. neglecta*, including: idioblasts (Jalan 1963); ethereal oil cells (Jalan 1965); crystalliferous sclereids (Jalan 1968a); stomata (Rao 1939, as "*S. elongata*"); nodal structure (Jalan 1968b); floral vascular system (Jalan 1966, 1987); and pollen (Erdtman 1952: 257; Jalan & Kapil 1964; Praglowski 1976, as both *S. neglecta* and "*S. elongata*"). Other pollen descriptions (e.g., Agababian 1966, 1973) under the name "*S. elongata*" may refer to *S. neglecta*.

6. Schisandra sphenanthera Rehder & E. H. Wilson in Sargent, Pl. Wilson. 1: 414. 1913.—TYPE: CHINA. W Hupeh [Hubei]: Patung Hsien, May 1907, *E. H. Wilson 313*, pro parte (lectotype, here designated: A!; isolectotypes: E! K, US).

Schisandra chinensis var. *rubriflora* Franchet, Nouv. Arch. Mus. Hist. Nat., sér. 2, 8: 192. 1885 (as "*Schizandra*") [reprinted as Pl. David. 2: 10. 1888]. *Schisandra grandiflora* var. *rubriflora* (Franchet) C. K. Schneider, Bot. Gaz. 63: 523. 1917.—TYPE: CHINA. Sichuan: Moupin [Mupin/Baoxing], Jun 1869, *A. David s.n.* (lectotype, here designated: P!).

Schisandra flaccidiramosa C. R. Sun, Bull. Bot. Res., Harbin 8: 123. 1988.—TYPE: CHINA. Gansu: near Daheba Forestry Centre, Dangchang county, 17 May 1973, *Z. X. Peng 730053* (holotype: LZU).

Woody vines, apparently dioecious (but probably monoecious). Lateral branches lacking wings, with fugaceous perules at base; branches continuing growth in subsequent years. Leaf laminas (4–) 5.5–11 (–13.5) cm long, (2–) 2.5–6 (–8) cm wide, length:width ratio (1.1–) 1.4–2.7 (–3.1), papyraceous, 30–60 (–80) µm thick, glabrous, elliptic to ovate, rarely obovate; primary vein ± plane above, slightly prominent below; secondary veins (3–) 4–5 (–8) pairs per leaf, (slightly) arcuate; base acute (younger leaves) to obtuse or truncate (older leaves); apex short- to long-acuminate; margin (sinuous-) denticulate to (sinuous-) serrulate, rarely (sub-) entire, (0–) 5–11 (–15) teeth per side of leaf; petioles glabrous, 15–27 (–35) mm long, 0.8–1.3 (–1.7) mm in diameter. Flowers borne in axils of fugaceous bracts at the base of young shoots, solitary; tepals (5–) 6–8 (–9) (male flowers), 5–8 (female flowers); tepals variably yellow, orange, or red, often with outer tepals greenish yellow and inner tepals orange-red, glabrous; outermost tepal elliptic to ovate, 5.0–8.0 (–10.0) mm long, 2.5–5.0 (–6.3) mm wide, length:width ratio 1.2–1.6 (–2.0); innermost tepal variably ovate, elliptic, or obovate, 4.8–9.1 mm long, (2.9–) 3.5–5.9 mm wide, length:width ratio (0.9–) 1.4–2.0; largest tepal variably ovate, elliptic, or obovate, 6.0–9.5 (–11.3) mm long, (3.3–) 4.0–6.5 (–8.4) mm wide, length:width ratio (1.0–) 1.3–1.8 (–2.1); outermost tepal slightly reduced, (0.5–) 0.7–0.9 (–1.0) of length of largest; innermost tepal slightly reduced, (0.6–) 0.7–0.9 (–1.0) of length of largest; peduncles glabrous, (8–) 13–34 (–54) mm long, 0.2–0.8 (–1.2) mm in diameter (male flowers), (18–) 40–64 mm long, (0.4–) 0.6–0.8 (–1.0) mm in diameter (female flowers). Male flowers with androecium of (11–) 15–23 (–25) essentially free stamens, uppermost stamens generally only partially differentiated, appearing connate, forming a carnose mass (1.0–) 1.4–1.6 (–2.0) mm in diameter, with marginal thecae; thecae of free stamens introrse-lateral; pollen hexacolpate. Female flowers with gynoecium of ca. 25–45 free carpels; carpels (1.2–) 1.6–2.5 (–3.0) mm long, 0.6–1.0 (–1.1) mm wide, length:width ratio (1.7–) 2.3–3.3 (–4.0); pseudostyle small. Fruit peduncles glabrous, not elongated, (2–) 3–6.5 (–10) cm long, 0.6–1.1 (–1.4) mm wide; torus (2.5–) 4–14 (–22) cm long, (1.0–) 1.2–2.4 (–3.0) mm wide; apocarps red, (5.5–) 6.5–9 mm long, 4–8 mm wide, length:width ratio (1.1–) 1.2–1.8. Seeds 1–2 per apocarp, discoid to flattened-reniform, (2.6–) 3.0–3.5 (–3.9) mm long, (3.2–) 3.5–4.0 (–4.3) mm wide, length:width ratio (0.7–) 0.8–0.9 (–1.0); testa (±) smooth. Chromosome number: n = 14, 2n = 28 (see Appendix 1). Fig. 7B; Plate 2.

Illustrations. Dandy (1938: pl. 8921); Wang (1980: fig. 1603); Sun (1988: 125, as "*S. flaccidiramosa*"); M.-C. Liu (1992: fig. 447); Law (1996a: fig. 1–10).

Phenology. Flowering in May and June (rarely as early as March or as late as July); fruits maturing from June to October.

Distribution (Fig. 29). Widespread in central China (Anhui, Gansu, Guizhou, Henan, Hubei, Hunan, Jiangsu, Shaanxi, Shanxi, Sichuan, Yunnan, and Zhejiang); scandent and climbing on trees and shrubs in forests dominated by *Acer*, *Ailanthus*, *Broussonetia*, *Catalpa*, *Celtis*, *Cornus*, *Fortunearia*, *Juglans*, *Lindera*, *Morus*, *Pteroceltis*, *Quercus,* and *Ulmus*, commonly on hillsides and in ravines; (200–) 700–2000 (–5100) m.

Additional Specimens Examined. **China.** Anhui: Chu Hwa Shan, *R. C. Ching 2591* (A, UC); Whang Shan, *R. C. Ching 3008* (A); Lian Rui feng, Huangshan, *M. P. Dang & K. Yao 79107* (A, NY); Tien Chu Shan, Chien Shan Hsien, *C. S. Fan & Y. Y. Li 220* (A).—Gansu: Koan Ria Lo, SE Gansu, *E. Licent 5038* (K); Wu-dou, Wei-zi-gou Forestry Farm, *J. S. Ying, K. Y. Lang & Y. F. Li 851* (MO); Shanwangmiao, Bifenggou, Bikow, Wen Xian, *X. Wang 195* (MO).—Guizhou: Pin-fa, Yunnan-sen District, *J. Cavalerie 27* (K); Jiangkou Xian, Taiping River and along tributary streams, above the confluence with the Heiwan River, SE side of the Fanjing Shan mountain range, *Sino-American Guizhou Botanical Expedition 196* (A, NY).—Henan: Baotianman Nature Reserve, Yangchang Gou, Neixiang Xian, 33°23′N, 111°57′E, *D. E. Boufford, H. X. Cheng, B. D. Liu, C. Y. Xi, T. S. Ying, C. J. Zhang & X. L. Zhu 26074* (A), *26097* (A); Baotianman Nature Reserve, Pingfang, Neixiang Xian, 33°24′30″N, 111°53′30″E, *D. E. Boufford, B. D. Liu, T. S. Ying, C. J. Zhang & X. C. Zhang 26380* (A); Baotianman Nature Reserve, Yangchang Gou, Neixiang Xian, 33°24′N, 111°53′E, *D. E. Boufford, B. D. Liu, T. S. Ying & X. L. Zhu 26211* (A); Tumuai Pass, N of the city of Xiaguan; from the pass S to the highway along a footpath, Neixiang Xian, 33°20′N 112°00′E, *D. E. Boufford, T. S. Ying, C. J. Zhang & X. C. Zhang 26480* (A); Teng Feng Hsien, Yu Tai Shan, *J. Hers 243* (A); Yungning, Tsi Li Ping, *J. Hers 424* (A), *452* (A, K); Lushih, Hiung Eul Shan, *J. Hers 860* (A); Lushih, Lao Kiun Shan, *J. Hers 1220* (A); Sunhsien, Shih Tze Miao, *J. Hers 1246* (A); Yungning, Tsi Li Ping, *J. Hers 1335* (A).—Hubei: Hsing Shan Hsien, *Y. Chen 982* (UC); Patung Hsien, *H.-C. Chow 210* (A, NY), *689* (A, NY); Ichang and immediate neighbourhood, *A. Henry 3446* (GH, K); [precise locality not known], *A. Henry 3469* (GH); Ichang, Patung District, *A. Henry 4040* (K), *4059* (GH, K); Shennongjia, *Z. D. Jiang & G. F. Tao 228* (A); [precise locality not known], *E. H. Wilson 179a*, pro parte (A); Hsing-shan hsien, *E. H. Wilson 245* (A); Patung Hsien, Sep 1907, *E. H. Wilson 313*, pro parte (A, E); Changyang, *E. H. Wilson 675* (A, NY); [precise locality not known], *E. H. Wilson 779* (A, NY), *1036* (A); Wushan, *E. H. Wilson 1057* (K); [precise locality not known], *E. H. Wilson 1968* (A, NY); Hsing-shan Hsien, *E. H. Wilson 2553* (A), *2554* (A); [precise locality not known], s.a., *E. H. Wilson s.n.* (K); Shennongjia, *S.-X. Yang 256* (IBSC).—Hunan: Loudi, *H. F. von Handel-Mazzetti 595* [*11740*] (A); Hsikwangschan Hsinhwa, *H. F. von Handel-Mazzetti 784* [*11933*] (A, C); Xiang-xi-zi-zhi-qu, Da-yong County, Si-douping, Jiu-long-shan, *S. C. Lee 204818* (MO); Hengshan [Nanyue Mt.], *Q. Lin 973* (HKU), *976* (HKU); Zhi-jiang County, Wu-lang-qi, *P. X. Tan 62508* (MO); Yunschan, Wukang, *T. H. Wang 95* (A, C).—Jiangsu: Hai Wei, *R. C. Ching & C. L. Tso 498* (A).—Shaanxi: [precise locality not known], 4 Aug 1909, *G. Giraldi s.n.* (A); Huashan, *J. Hers 3089* (A); Paoki, *F. N. Meyer SPI 40025* (A); Tai-pu-shan, *W. Purdom 1037* (A); Fo-ping, Long-cao-ping, *J. S. Ying, K. Y. Lang & Y. F. Li 169* (MO), *182* (MO); Fo-ping, Yue-ba-xiang, left of Da-cheng-hao, *J. S. Ying, K. Y. Lang & Y. F. Li 242* (MO).—Shanxi: Feng-su, Xin-jia-shan Forestry Farm, *Q. H. He 2215* (MO); Shih-li-p'o-shan, Yuan ch'u district, *H. Smith 6577* (A).—Sichuan: vicinity of Sanwangmiao on Zhaogong Mt., Dujiangyan Municipality [Guan Xian], *D. E. Boufford, B. Bartholomew, G. Li & G. H. Zhu 24371* (A, NY); Longxi Forest Farm on Niang Ziling Mountain, Dujiangyan Municipality [Guan Xian], *D. E. Boufford, B. Bartholomew G. Li & G. H. Zhu 24403* (A, NY, MO); Moupin [Mupin/Baoxing], Apr–May 1869, *A. David s.n.* (P); Kuan-hsien, *W. P. Fang 2172* (A, NY), *2238* (A); [precise locality not known], *A. Henry 5527* (NY), *5527A* (A); Jingfushan, Nanchuan, *K. F. Lee 61431* (IBSC); Yi-xing, Long-di-shan, Dong-wu-ka, *S. H. Mao 170* (MO); near Tachienlu [Kangding], s.a., *A. E. Pratt s.n.* (K); between Hai-t'ang and Pin-yi-p'u, *H. Smith 1964* (A); S of Kuan Hsien, *F. T. Wang 20682* (A); W of Kuan Hsien, *F. T. Wang 20827* (A); W of Wen-chuan Hsien, *F. T. Wang 21043* (A); Na-pien Hsien, *F. T. Wang 23026* (A); Guan Xian, Masangping, *Z. T. Wang et al. 870242* (MO, NY); Guan Xian, Longchi, *Z. T. Wang et al.*

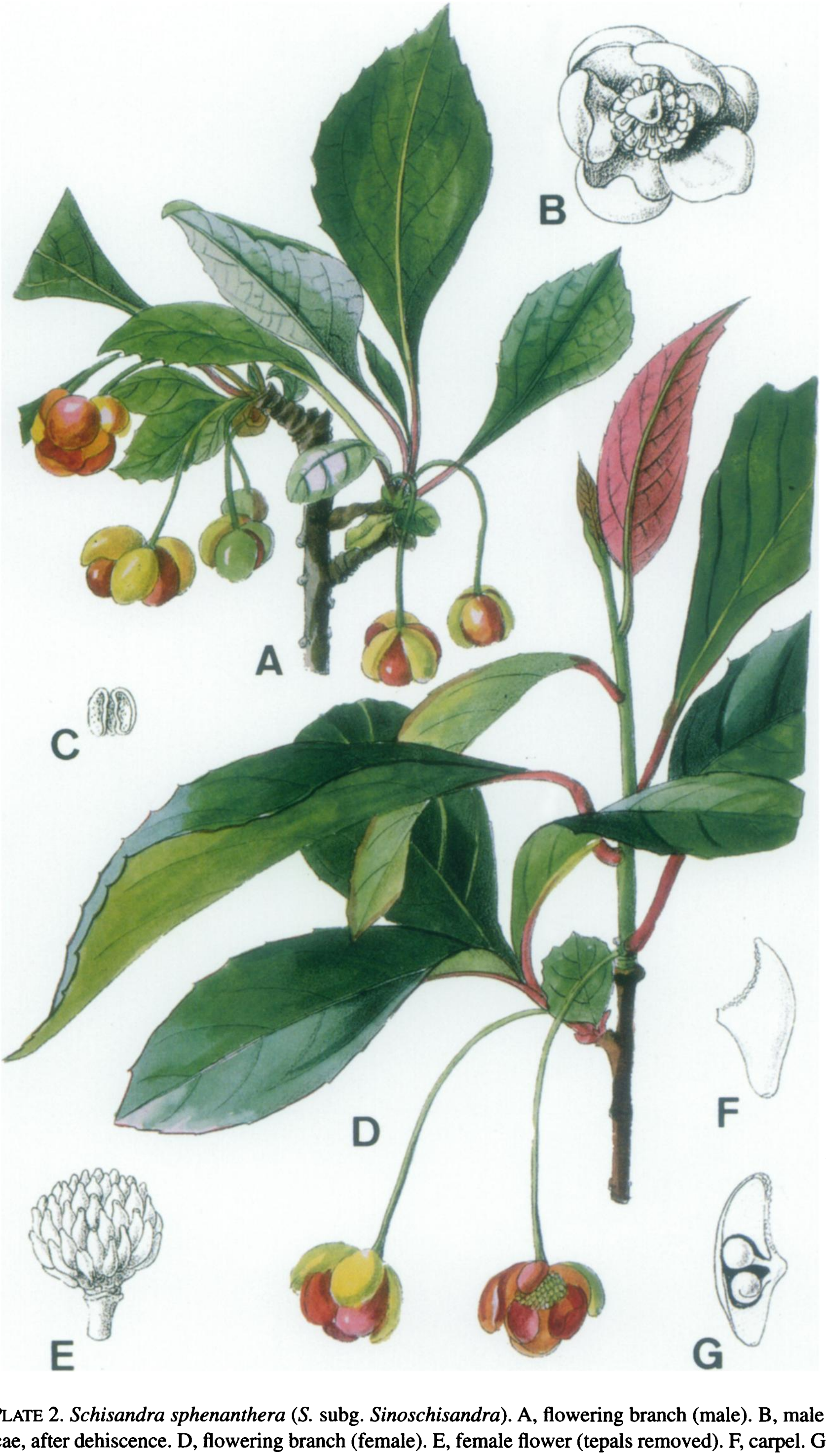


PLATE 2. *Schisandra sphenanthera* (*S.* subg. *Sinoschisandra*). A, flowering branch (male). B, male flower. C, thecae, after dehiscence. D, flowering branch (female). E, female flower (tepals removed). F, carpel. G, carpel (longitudinal section). Reproduced from Dandy (1938: pl. 8921); photograph © Royal Botanic Gardens, Kew.

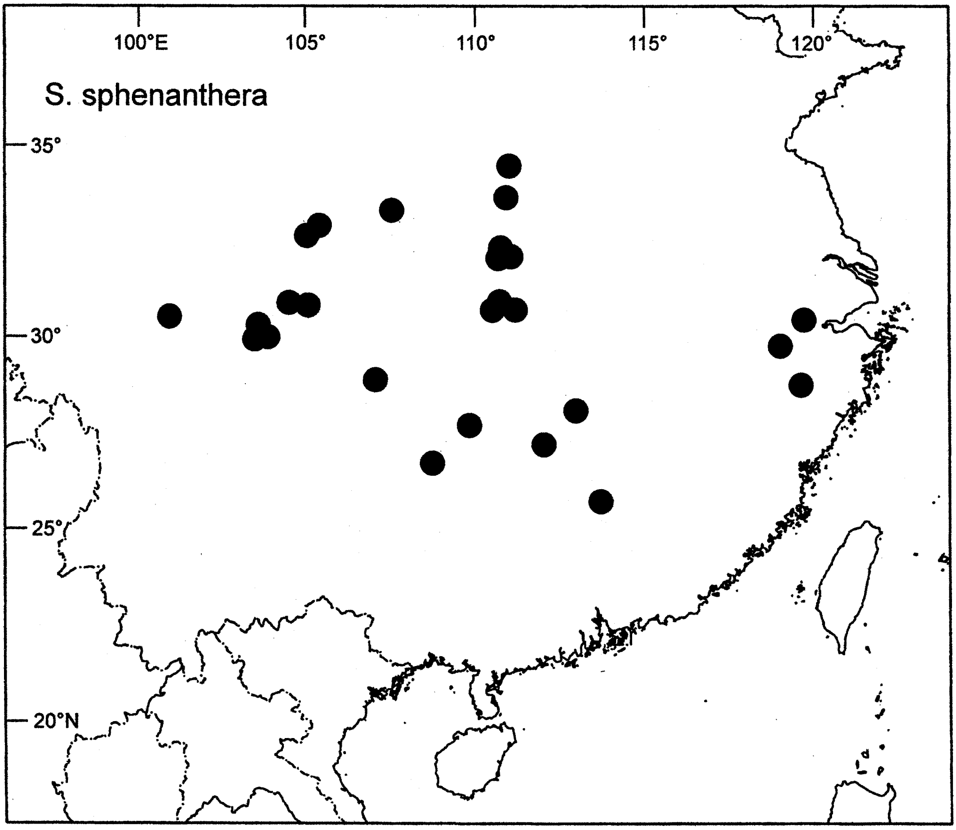


FIG. 29. Distribution of *Schisandra sphenanthera.*

870306 (HKU, MO, NY); Mupin, *E. H. Wilson 866*, pro parte (A); Wa-shan, *E. H. Wilson 866*, pro parte (A); near Maochan, *E. H. Wilson 866*, pro parte (A); Mupin, *E. H. Wilson 869* (A); Wen Chuan Hsien, Wa-sen county, *E. H. Wilson 869a* (A); Hung Yah hsien, *E. H. Wilson 897* (A); Mt. Omei [Emei Shan], *K. H. Yang 57314* (IBSC).—YUNNAN: Chao-tung Hsien, *H. T. Tsai 50888* (A).—ZHEJIANG: Long-quan, foot of Feng-yang-shan, *S. Y. Chang 4696* (MO); Tian-mu, San-li-ling, *P. L. Chiu 313* (MO); Xi-da-mu-shan, Heng-tang, *Zhang 417* (MO).

The original delimitation of *S. sphenanthera* by Rehder and Wilson (in Sargent 1913: 414–416) was very broad and included elements representing three other taxa recognized in the present monograph (*S. arisanensis* subsp. *viridis*, *S. pubinervis*, and *S. lancifolia*). Subsequent authors (see under "Misapplied Names") followed this broad circumscription. Merrill and Chun (1934) described a variety, var. *longipes*, which is here elevated to the rank of species (*S. longipes*, no. 16).

Rehder and Wilson (in Sargent 1913: 414) cited *Wilson 313* (A) as the type of *S. sphenanthera*; this collection number actually refers to two different collections, with both flowering material (dated May 1907) and fruiting material (dated September 1907). The flowering specimen in A is here chosen as the lectotype.

Schisandra sphenanthera forms a close alliance with *S. arisanensis* (inclusive of "*S. viridis*") and *S. neglecta*. The distinguishing characters between these three species are discussed following the treatment of *S. neglecta* (no. 5).

Several other species resemble *S. sphenanthera*, differing primarily on the basis of indument characters. *Schisandra glaucescens*, for example, is most easily distinguished by its generally highly glaucescent abaxial leaf laminas, although other differences include the absence of red tepal pigments and a larger number of carpels (ca. 42–50). *Schisandra pubinervis*, *S. pubescens*, and *S. tomentella* also bear a superficial resemblance to *S. sphenanthera*, although they all possess hairs on the abaxial surface of the leaves. As noted by Smith (1947: 126–127), sterile or fruiting specimens of *S. chinensis* often resemble *S. sphenanthera*, although their geographical distributions do not overlap. In the absence of flowering material, *S. chinensis* is most easily distinguished on the basis of the slight pubescence of the abaxial leaf laminas; shorter fruiting peduncles [2–4.5 (–7.5) cm]; and shorter fruiting tori [(1.5–) 2–6 (–9.5) cm].

Franchet (1885) described a variety of *S. chinensis*, var. *rubriflora*. Several later authors, without consulting the type, listed Franchet's name as a synonym of *S. rubriflora* (Sargent 1913; Stapf 1928; Smith, 1947: 102); however, examination of the type specimen during the present revision showed it belongs to *S. sphenanthera*. Schneider (1917) transferred Franchet's (1885) variety to *S. grandiflora* but erroneously cited *Wilson 921b* (the type of Rehder & Wilson's name *S. rubriflora*) as the type.

Although I was unable to examine the type specimen of *S. flaccidiramosa* Sun (1988), the detailed description and excellent illustration provided by Sun, and the collection localities of the type specimens (Gansu province, China), indicate that the name is a synonym of *S. sphenanthera*.

Various structures have been studied in *S. sphenanthera*, including wood and bark anatomy (Carlquist 1999), floral vascular anatomy (Ozenda 1946, 1949; Melville 1969), carpel and ovule anatomy (Igersheim & Endress 1997), and pollen structure (Huynh 1976; Praglowski 1976).

7. Schisandra arisanensis Hayata, Icon. pl. Formosan. 5: 1. 1915.—TYPE: CHINA. Formosa [Taiwan]: Mt. Arisan, between Funkiko and Taroyen, 25 Apr 1914, *B. Hayata s.n.* (lectotype, here designated: TI!; isolectotype: TI!).

Woody vines, monoecious (often appearing dioecious). Lateral branches lacking wings, with fugaceous perules at base; branches continuing growth in subsequent years. Leaf laminas (5–) 6.5–10.5 (–12.5) cm long, (2.5–) 3–5.5 (–7) cm wide, length:width ratio (1.3–) 1.5–2.5 (–2.8), papyraceous to subcoriaceous, 30–80 (–120) μm thick, glabrous, elliptic to ovate; primary vein ± plane to slightly impressed above, (slightly) prominent below; secondary veins 4–6 pairs per leaf, (slightly) arcuate; base acute (younger leaves) to obtuse (older leaves), often slightly attenuate; apex (long-) acuminate; margin (sinuous-) denticulate to (sinuous-) serrulate, (2–) 4–10 (–14) teeth per side of leaf; petioles glabrous, (10–) 13–27 (–34) mm long, (0.4–) 0.6–1.3 (–1.6) mm in diameter. Flowers borne in axils of fugaceous bracts at the base of young shoots or in axils of leaves, solitary; tepals (5–) 6–8 (–13) (male flowers), 7–8 (female flowers); tepals red, orange, or (white-) yellow, glabrous; outermost tepal elliptic, rarely ovate-elliptic or obovate, 2.2–11.5 mm long, (1.2–) 2.6–8.0 mm wide, length:width ratio (0.7–) 1.1–2.0 (–2.3); innermost tepal elliptic to obovate, (2.8–) 3.1–5.9 (–7.0) mm long, (1.4–) 2.3–4.2 (–5.3) mm wide, length:width ratio (0.9–) 1.2–1.7 (–2.4); largest tepal elliptic, rarely ovate or obovate, (3.9–) 5.0–9.7 (–12.0) mm long, (3.6–) 4.6–7.3 (–8.3) mm wide, length:width ratio (0.8–) 0.9–1.8 (–2.1); outermost tepal slightly reduced or not reduced, 0.5–1.2 of length of largest; innermost tepal (slightly) reduced, (0.4–) 0.6–0.7 (–1.0) of length of largest; peduncles glabrous, (18–) 22–37 (–45) mm long, (0.2–) 0.3–0.6 (–0.8) mm in diameter (male flowers), ca. 35–40 mm long, ca. 0.4–0.5 mm in diameter (female flowers). Male flowers with androecium of (8–) 12–23 (–30) essentially free stamens, uppermost stamens generally only partially differentiated, appearing connate, forming a carnose mass (0.8–) 1.8–2.5 (–3.4) mm in diameter, with marginal thecae; androecium 2.9–4.2 mm in diameter; thecae of free stamens introrse-lateral; pollen hexacolpate. Female flowers with gynoecium of ca. 22–56 free carpels; gynoecium ca. 4.0–5.8 mm in diameter; carpels (1.2–) 1.5–2.4 (–2.9) mm long, (0.6–) 0.7–1.0 (–1.3) mm wide, length:width ratio (1.4–) 1.7–3.0 (–3.3); pseudostyle short, narrow. Fruit peduncles glabrous, slightly elongated, (4–) 4.5–7 (–8) cm long, (0.5–) 0.6–1.0 mm wide; torus (3.5–) 5–10.5 (–15.5) cm long, (1.0–) 1.3–2.1 (–2.5) mm wide; apocarps red, (5–) 7–9.5 (–11) mm long, (3.5–) 5–6.5 (–7.5) mm wide, length:width ratio (1.0–) 1.1–1.8 (–2.2). Seeds 1–2 per apocarp, discoid to flattened-reniform, rarely flattened-pyriform, 3.0–3.8 (–4.0) mm long, (3.2–) 3.5–4.2 mm wide, length:width ratio 0.8–1.0 (–1.3); testa ± smooth to rugulose, rarely slightly tuberculate. Chromosome number unknown.

Schisandra arisanensis (inclusive of "*S. viridis*") shows close affinities with *S. sphenanthera* and *S. neglecta*; the diagnostic differences between the three species are described in detail in the discussion following *S. neglecta* (no. 5).

Smith (1947: 129–131) recognized "*S. viridis*" among specimens previously included in *S. sphenanthera*. Although the distinctions between *S. sphenanthera* and "*S. viridis*" are slight, the taxa warrant taxonomic recognition at the species level. The taxonomic distinctions between *S. arisanensis* sensu stricto and "*S. viridis*" are less convincing, and "*S. viridis*" is here reduced to a subspecies *S. arisanensis*. As Smith (1947) noted, there is a difference in carpel number, although this is not as large as Smith believed: *S. arisanensis* subsp. *arisanensis* has 40–56 carpels, whereas subsp. *viridis* has 22–29. Other differences include: tepal pigmentation (red pigments are more common in subsp. *arisanensis*, although specimens of subsp. *viridis* with red tepals have been collected in Guangxi); and outer tepal size (typically larger in subsp. *arisanensis*). Smith (1947: 131–132) was not able to examine seeds of *S. arisanensis* sensu stricto from Taiwan, and he relied on Hayata's (1915) description of the seeds as "muricate" to distinguish the species from "*S. viridis*," which has variably smooth to rugulose seeds. This distinction is not valid, however: seeds of subsp. *arisanensis* and subsp. *viridis* are identical.

The pollen of *S. arisanensis* subsp. *arisanensis* is described and illustrated by Erdtman (1952: 257), Huang (1967, 1972), Wang (1968), and Praglowski (1976).

7a. **Schisandra arisanensis** subspecies **arisanensis.**

Tepals reddish orange to yellow; outermost tepal 7.7–11.5 mm long, 5.0–8.0 mm wide, length:width ratio 1.1–2.0; outermost tepal not reduced, 0.9–1.2 of length of largest. Female flowers with gynoecium of ca. 40–56 free carpels. Seeds 3.0–3.4 mm long, 3.5–3.9 mm wide, length:width ratio 0.8–1.0. Figs. 3B, 8D, 13A, B, 13D.

Illustrations. Hayata (1915: pl. 1, as "*S. arisanensis*"); T.-S. Liu (1960: fig. 69, as "*S. arisanensis*"); H.-L. Li (1976: pl. 351, as "*S. arisanensis*"); Wang (1980: fig. 1601, as "*S. arisanensis*"); H.-L. Li and Chaw (1996: pl. 197, as "*S. arisanensis*").

Phenology. Flowering in April and May; fruits ripening in August and September.

Distribution (Fig. 30). Endemic to Taiwan; scandent or climbing in wet, deciduous forests, often on hillsides; 1600–2300 m.

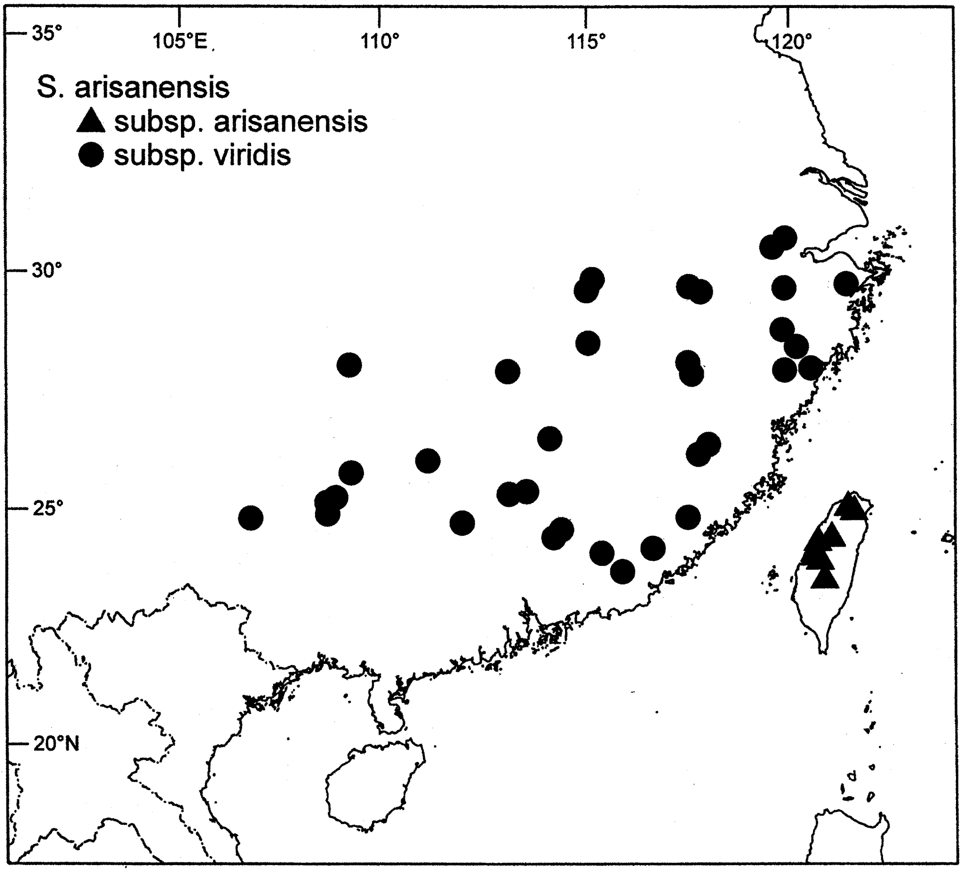


FIG. 30. Distribution of *Schisandra arisanensis* subsp. *arisanensis* and subsp. *viridis*.

Additional Specimens Examined. **China.** Taiwan: Meifeng, Nantou County, *S.-M. Chaw 615* (HKU), *616* (HKU); Meifeng, Nantou County, Aug 1988, *S.-M. Chaw s.n.* (HKU); Aridan, Arisan, *J. L. Gressitt 190* (A, K, L); from Tapachienshan hiking entrance to a low ridge, Sheipa National Park, Wufeng Hsiang, Hsinchu Hsien, 24°28′38″N, 121°11′52″E, *C. L. Huang, W. H. Hu & Y. Y. Lien 72* (A); Kuanwu, Sheipa National Park, Wufeng Hsiang, Hsinchu Hsien, 24°30′12″N, 121°6′50″E, *C. L. Huang, W. H. Hu & Y. Y. Lien 125* (MO); Mt. Lalashan, Yaoyuan, *M. T. Kao 10243* (A); en route from Tunyuan to Yunhai, Jenai Hsiang, Nantou Hsien, 24°03′00″N, 121°14′00″E, *C.-C. Liao, W. P. Leu, H.-L. Ho & T.-Y. Liu 1282* (E); Meilan Forest Road, Taoyuan Hsiang, Kaohsiung Hsien, *T.-Y. Liu, W.-H. Hu, Y.-R. Lin & S.-J. Liu 467* (E); May-fong, Taichung, *Ou & Kao 9322* (MO); Sanlinksea, Nantou County, *W. S. Tang 488* (A); mileage sign 13–17 km on Forest Road #100, Yuanyanghu, Chienshih Hsiang, Hsinchu Hsien, 24°34′40″N, 121°24′41″E, *C. C. Wang & D. S. Hsu 1335* (E, MO); mileage sign 126–127 km on Provincial Road #20, Kaosisung Hsien, Taoyuang Hsiang, *C. C. Wang, C. C. Liao & D. S. Hsu 1053* (A, MO); mileage sign 133–134 km on Provincial Road #20, Kaosisung Hsien, Taoyuang Hsiang, *C. C. Wang, C. C. Liao & D. S. Hsu 1060* (A); Tagi, Arisan Province, *E. H. Wilson 9826* (A).

7b. Schisandra arisanensis subpecies **viridis** (A. C. Smith) R. M. K. Saunders, comb. et stat. nov. *Schisandra viridis* A. C. Smith, Sargentia 7: 129. 1947.—Type: China. Kwangtung [Guangdong]: Nam Shan, Ts'ung-shue village, Ho-yuen district, 5–30 May 1938, *W. T. Tsang 28783* (holotype: A!; isotype: P).

Tepals (white-) yellow, rarely red; outermost tepal 2.2–6.4 mm long, (1.2–) 2.6–3.6 (–5.7) mm wide, length:width ratio (0.7–) 1.3–1.8 (–2.3); outermost tepal slightly reduced or not reduced, 0.5–1.0 (–1.1) of length of largest. Female flowers with gynoecium of ca. 22–29 free carpels. Seeds (3.0–) 3.2–3.8 (–4.0) mm long, (3.2–) 3.5–4.2 mm wide, length:width ratio (0.8–) 0.9–1.0 (–1.3). Figs. 1B, 5A, B, 7A, 8A.

Illustrations. Law (1983b: fig. 186, as "*S. viridis*"); Huang (1987: fig. 25, as "*S. viridis*").

Phenology. Flowering from April to June; fruits maturing from June to September.

Distribution (Fig. 30). Widespread in southern and eastern China (Anhui, Fujian, Guangdong, Guangxi, Guizhou, Hunan, and Jiangxi); scandent or climbing in shrubland and forest, often on wet, poor soil on hillsides and in valleys; (150–) 240–1300 m.

Additional Specimens Examined. **China.** Anhui: Li kan, W Chemen, *R. C. Ching 3166* (UC); Wang-shan, *K. S. Chow 91* (A, MO); Cha-wan forestry farm, Qi-men county, *X. Y. Dong & Y. N. Xiong 93291* (MO), *X. Y. Dong 93394* (A); Tien Chu Shan, Chien Shan Hsien, *C. S. Fan & Y. Y. Li 221* (A); Cha-wan, Qi-men, *K. Yao 10455* (NY).—Fujian: [precise locality not known], *S. T. Dunn 2330* (A); [near Buong Kang], Central Fukien [Fujian], *S. T. Dunn 2442* (A, HK, K; paratypes of *S. elongata* var. *longissima*); Nan-ping town, Mang-tang-shan, *G. S. He 4470* (MO); Chong-an, Xing-cun-gong-she, San-gang, *Wuyi Expedition 2274* (MO); Wu-yi-shan, mid-way from San-gang to Gao-qiao, *Wuyi Shan Team 80–0117* (MO); Wu-yi-shan, Huang-gang-shan, *Wuyi Shan Team 80-0243* (MO).—Guangdong: He-ping, Li-ming Forestry Farm, Zhang-shan-wuo, *G. C. Chang et al. 28* (MO); Le-chang, Tong-hang, *S. B. Guo 80700* (MO); Yu-yuen, *S. P. Ko 52691* (A), *52919* (A); Tsing Wan Shan, Wong Chuk I and vicinity, Wung Yuen District, *S. K. Lau 1993* (A); Wu-hua County, Long-cun Gong-she, Long-si-dian, *S. Y. Li 180617* (HKU, MO); Yaoshan, *S. S. Sin 9436* (NY); Yang-shan County, Cheng-jia-gong-she, water & electric power station, *P. X. Tan & X. X. Huang 365* (MO); Jiao-ling County, Shi-hu-xiang, Shi-hu Village, Da-feng-zhang, *L. Teng 4679* (MO); Shi-xing, Yao-zu-xiang, Zhong-ba-pian, Zhong-ba-shui, *L. Teng 6775* (MO); Lung T'au Mountain, right side of Iu Village, roadside of Ki ravine, *K. P. To, W. T. Ts'ang & U. K. Ts'ang 533* [*12532*] (UC); Yam Na Shan [Yit Nga Shan], Mei [Kaying] District, *W. T. Tsang 21423* (A, NY); Lok Chong, *C. L. Tso 20374* (A, NY); Yang shan and vicinity, S of Lin-chow, Yang Shan District, *T. M. Tsui 825* (A, NY); Wu-hua-shan, Qi-mu-zhang, *Y. J. Wang 59930* (MO), *60055* (MO); Nong-men, Nan-kun, Li-chang, *G. C. Zhang 5* (MO).—Guangxi: Da-miao-shan, San-fang-qu, Ben-gang-xiang, Jiu-wan-da-shan, *T. C. Chen 429* (MO); Luo-cheng County, Huang-jin-qu, Xi-pu-xiang, Jiu-wan-shan, Yu-xi, Ban-jiao-wan, *S. H. Chun 14953* (MO); Da-miao-shan, San-fang-qu, Ping-shi-xiang, Jiu-wan-shan, Jiu-yang River, *S. H. Chun 16580* (HKU, MO); Chuen Yuen, *Z. S. Chung 82002* (A); Chiu Tung, Lin Yuin Hsien, *A. N. Steward & H. C. Cheo 211* (A); Chiu Fong, Ling Yuin Hsien, *A. N. Steward & H. C. Cheo 213* (A, NY); Pai-yun-an & vicinity, Hwang-sha-ho, Ch'uan District, *W. T. Tsang 27641* (A); Pai-yun-an & vicinity, Hwang-sha-ho, Ch'uan District, *W. T. Tsang 27693* (A); Rong-shui, Xia-si-jian, *F. N. Wei 1386* (MO).—Guizhou: Wong-Kwan-Chou, Tsingchen, *S. W. Teng 90255* (A).—Hunan: Mang-shan, *G. Z. He 4799* (MO); Mang-shan, near Ping-hang, *M. X. Huang 112705* (MO); [precise locality not known], *Hunan Museum (comm. S. S. Sin) 238* (K); Ma-yang County, Xi-huang, Shan-shan, *S. C. Lee 203566* (MO); Heng-shan [Nanyue Mt.], *Q. Lin 975* (HKU).—Jiangxi: Lushan, *Cheng 168* (A, MO); [precise locality not known], *H. C. Cheo 126* (K); Lushan Mts., *H. H. Chung & S. C. Sun 732* (A, NY); Hong San, *J. L. Gressitt 1485* (A, MO); Lu-shan, Huang-long temple, *Hangchow University Taxonomy Team 2438* (MO); Hsin Feng Hsien, *H. H. Hu 1118* (A); Jing-gang-shan, Xing-zhou, *Jinggang Shan Team 661226* (MO); Huang Yai-Sz-Lin Shan, *A. N. Steward 1031* [*4653*] (UC); Taloushan, Fengcheng, *Y. Tsiang 10362* (A, NY); from Lienhuadong to Kul-ing, Lushan, *Y. Tsiang 10679* (NY); Kuling, *E. H. Wilson 1726* (A).—Zhejiang: Tai-shun, Wen-ping, *S. Y. Chang 3837* (MO); Tai-shun, Wen-feng, *S. Y. Chang 4990* (MO); Jing-ping, Da-jun, *S. Y. Chang 5207* (HKU, MO); Tai-shun, *S. Y. Chang 5675* (MO); Ping-yang, *S. Y. Chang 5891* (MO); [precise locality not known], *S. Chen 293* (A), *3258* (A); Chen Chiong, 40 mi S of Siachu, *R. C. Ching 1781* (A, K, UC); [precise locality not known], *R. C. Ching 4777* (A); Tien-mao-shan, *R. C. Ching 5132* (A); Long-quan, *Hangzhou Botanic Garden Herbarium 3009* (MO); Jian-de, Mo-ping-shan, *Hangzhou Botanic Garden Herbarium 3126* (MO); Ning-bo, Tian-tong, Er-tang, *Hangzhou Botanic Garden Herbarium 8251* (MO); [precise locality not known], *Y. Y. Ho 1138* (A), *1448* (A); E Tien-mu, *H. H. Hu 1584* (A, UC); W Tien-mu, *H. H. Hu 1693* (A, UC); Changhua Hsien, *Y. L. Keng 601* (A, UC); Tien-Mu shan, *K. Yao et al. 79263* (MO).

8. Schisandra glaucescens Diels, Bot. Jahrb. Syst. 29: 323. 1900 (as "*Schizandra*").—TYPE: CHINA. Setchuen [Sichuan]: Leichia-p'ing, Chinfu-shan, Nanch'uan, 29 Jul 1891, *C. Bock & A. von Rosthorn 131* [*2656*] (holotype: O!, photo: A!).

Woody vines, apparently dioecious (but probably monoecious). Lateral branches lacking wings, with fugaceous perules at base; branches continuing growth in subsequent years. Leaf laminas 6–8 (–9) cm long, 2.5–4 (–5) cm wide, length:width ratio (1.5–) 1.7–2.4 (–2.7), papyraceous, rarely subcoriaceous, 50–80 μm thick, abaxial surface conspicuously glaucous, elliptic to obovate; primary vein ± plane to impressed above, slightly prominent below; secondary veins 4–5 (–8) pairs per leaf, slightly arcuate; base acute (-attenuate) in younger leaves, obtuse (-attenuate) in older leaves; apex short-acuminate; margin (sinuous-) denticulate to serrulate, (4–) 6–12 (–13) teeth per side of leaf; petioles glabrous, (9–) 12–22 (–26) mm long, 0.7–1.2 (–1.6) mm in diameter. Flowers borne in axils of fugaceous bracts at the base of young shoots, solitary; tepals 6–8 (male flowers), ca. 7 (female flowers); tepals white to yellow, glabrous; outermost tepal ovate-elliptic, 8–13 mm long, 5–8 mm wide, length:width ratio ca. 1.6; innermost tepal elliptic to obovate, ca. 6 mm long, ca. 1.8 mm wide, length:width ratio ca. 3.3; largest tepal elliptic to ovate, 6.5–9.7 mm long, 4–7.7 mm wide, length:width ratio 1.2–1.7; outermost tepal slightly reduced, ca. 0.8 of length of largest; innermost tepal reduced, ca. 0.6 of length of largest; peduncles glabrous, 24–33 mm long, 0.6–0.8 mm in diameter (male flowers), ca. 37–40 mm long, ca. 0.5–0.6 mm in diameter (female flowers). Male flowers with androecium of 18–24 essentially free stamens, uppermost stamens generally only partially differentiated, appearing connate, forming a carnose mass ca. 1.0–2.5 mm in diameter, with marginal thecae; thecae of free stamens introrse-lateral to lateral; pollen hexacolpate. Female flowers with gynoecium of ca. 42–50 free carpels, gynoecium 4.5–7.0 mm in diameter; carpels 1.6–2.2 mm long, 0.5–0.9 mm wide, length:width ratio (1.8–) 2.4–3.5; pseudostyle small. Fruit peduncles glabrous, not elongated, 4.5–6 (–7) cm long, (0.5–) 0.8–1.2 (–1.5) mm wide; torus 3–12 cm long, 2.0–3.0 (–4.3) mm wide; apocarps red, (5–) 6–9 (–11) mm long, 4–6 (–8.5) mm wide, length:width ratio (0.5–) 0.7–1.4 (–1.6). Seeds 1–2 (–3) per apocarp, flattened-reniform, (2.6–) 2.9–3.7 mm long, (3.0–) 3.3–4.1 (–4.3) mm wide, length:width ratio 0.8–0.9; testa (±) smooth. Chromosome number: 2n = 28 (see Appendix 1). Fig. 2A, B.

Phenology. Flowering in May and June; fruits maturing from July to October.

Distribution (Fig. 31). Endemic to China (western Hubei and eastern Sichuan); scandent or climbing in woodlands, thickets, and over rocks; 1500–2600 m.

ADDITIONAL SPECIMENS EXAMINED. **China.** HUBEI: Gran-gia-gwan, *W. Y. Chun 3820* (A); [precise locality not known], *A. Henry 5378* (GH), *5478* (GH), *5931* (GH), *6292* (NY), *6383* (GH); Leibohan, Hexi, Enshi, *Y. J. Ma 287* (IBSC); Xiangdangping, Wufeng, *Y. J. Ma 375* (IBSC); Hsing-shan Hsien, 28 May 1907, *E. H. Wilson 164*, pro parte (A); Fang Hsien, 2 Jun 1907, *E. H. Wilson 164*, pro parte (A); Hsing-shan Hsien, Sep 1907, *E. H. Wilson 164*, pro parte (A); Fang Hsien, Oct 1907, *E. H. Wilson 164a* (A); W Hubei, Sep 1900, *E. H. Wilson 179a*, pro parte (K, NY); Changyang, Patung, *E. H. Wilson 883* (A, K, NY).—SICHUAN: Hanrui, Fengjie, *M. Y. Fang 24594* (IBSC); Nanchuan-hsien, *W. P. Fang 855* (A); [precise locality not known], *A. Henry 5725* (GH); Jingfushan, Nanchuan, *J. H. Xiong & Z. L. Zhou 91079* (IBSC).

Schisandra glaucescens has a very restricted geographical distribution in central China; although it is sympatric with several other species of *Schisandra*, only *S. sphenanthera* could be confused with it. The most significant difference is the degree of glaucescence of the abaxial leaf lamina. Differences also exist in leaf lamina shape (typically ovate to elliptic in *S. sphenanthera*, but obovate to elliptic in *S. glaucescens*) and perianth

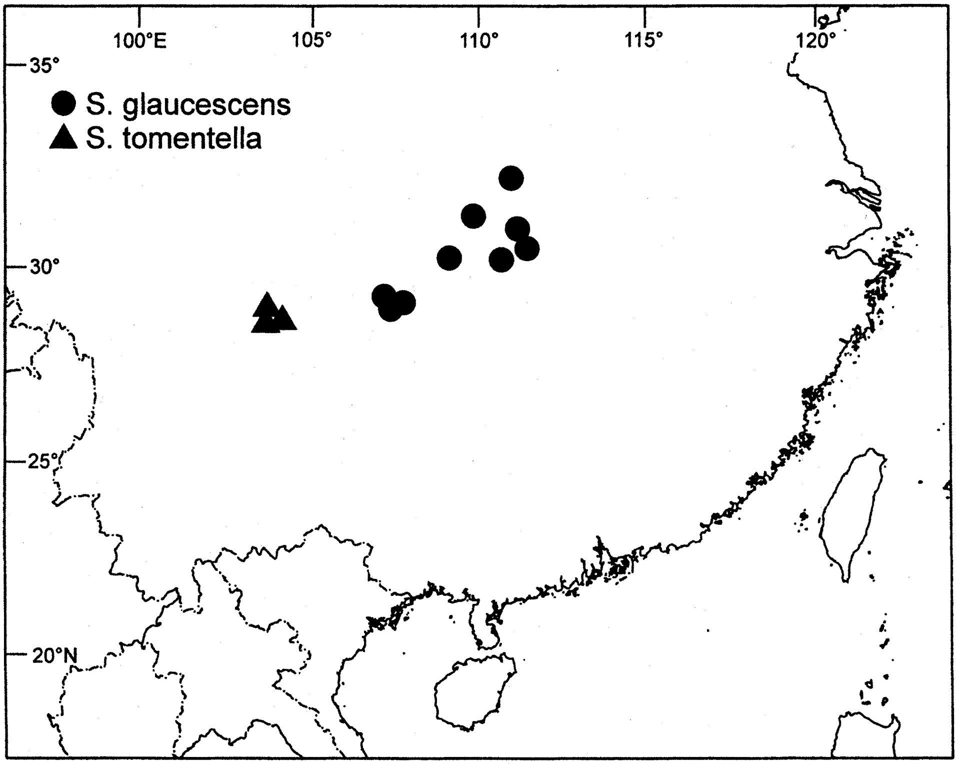


FIG. 31. Distribution of *Schisandra glaucescens* and *S. tomentella.*

color (the inner tepals in *S. sphenanthera* flowers are orange-red, but *S. glaucescens* flowers lack any red pigmentation). Smith (1947: 124) also commented on apparent differences in leaf lamina length:width ratios and the number of stamens, but these are not corroborated here.

The pollen of *S. glaucescens* is described by Praglowski (1976).

9. Schisandra elongata (Blume) Baillon, Hist. pl. 1: 148. 1868. *Sphaerostema elongatum* Blume, Bijdr. fl. Ned. Ind. 23. 1825 (as "*Sphaerostemma*").—TYPE: JAVA. "in altis montis Burangrang Provinciae Krawang," [date not known], *C. L. von Blume s.n.* (lectotype, designated by Saunders, 1997a: L!; isolectotype: K!).

Woody vines, apparently dioecious (but probably monoecious). Lateral branches lacking wings, with fugaceous perules at base; branches continuing growth in subsequent years. Leaf laminas (7–) 9–12 (–15) cm long, (35–) 4.5–7 (–8.5) cm wide, length:width ratio (1.5–) 1.7–2.1 (–2.5), (thin-) papyraceous, (35–) 50–100 μm thick, glabrous, ovate, occasionally elliptic; primary vein (slightly) impressed above, prominent below; secondary veins (3–) 4–5 pairs per leaf, highly arcuate; base obtuse to truncate (acute in younger leaves), often short-decurrent; apex acuminate; margin denticulate, occasionally entire, 0–11 (–15) teeth per side of leaf; petioles glabrous, (13–) 16–25 (–46) mm long, (0.6–) 0.7–1.1 (–1.5) mm in diameter. Flowers borne in axils of fugaceous bracts at the base of young shoots or in axils of leaves, solitary; tepals 8–10 (male flowers), 9–10 (female flowers); tepals yellow (outermost greenish), glabrous; outermost tepal ovate, ca. 1.5–3.2 mm long, 1.5–3.0 mm wide, length:width ratio ca. 0.6–1.2; innermost tepal ovate, round-elliptic, or obovate, ca. 2.4–5.2 mm long, 2.2–3.3 mm wide, length:width ratio ca. 1.1–2.0; largest tepal ovate, 7–8.2 mm long, 4.6–10.0 mm wide, length:width ratio 0.9–1.5; outermost tepal highly reduced, 0.2–0.4 of length of largest; innermost tepal (highly) reduced, 0.3–0.7 of length of largest; peduncles glabrous, 24–38 (–42) mm long, 0.2–0.7 mm in diameter (male flowers), (30–) 58–65 mm long, 0.3–0.6 mm in diameter (female flowers). Male flowers with androecium of ca. 27–30 essentially free stamens, uppermost stamens generally only partially differentiated, appearing connate, forming a carnose mass ca. 1.5–2.5 mm in diameter, with marginal thecae; androecium ca. 3.5 mm in diameter; thecae of free stamens lateral; pollen hexacolpate. Female flowers with gynoecium of 20–45 free carpels, gynoecium 3–3.4 mm in diameter; carpels 1.3–1.8 mm long, 0.6–0.7 (–0.8) mm wide, length:width ratio 2.0–3.0; pseudostyle narrow. Fruit peduncles glabrous, elongated, 4–6.5 cm long, 0.6–0.9 (–1.2) mm wide; torus 3–7.5 cm long, 1.3–1.8 (–2) mm wide; apocarps red, 7–8.5 mm long, 4.5–6.5 mm wide, length:width ratio (1.1–) 1.5–1.8. Seeds 2 per apocarp, discoid, 2.6–3.3 mm long, 2.8–3.3 mm wide, length:width ratio 0.9–1.0; testa rugulose. Chromosome number unknown. Plate 3.

Illustrations. Blume (1830: fig. 5); Koorders (1912: fig. 51, redrawn from Blume 1830: fig. 5); Steenis (1962: pl. 4.6, reproduced in Steenis 1972: fig. 2.10).

Phenology. Flowering and fruiting throughout much of the year: flowers reported from April to October; mature fruits reported from January to July.

Distribution (Fig. 32). Endemic to Java; submontane to montane humid forests; 1000–2000 m.

ADDITIONAL SPECIMENS EXAMINED. **Java.** G. Lembaeng, *C. A. Backer 12291* (L); [precise locality not known], *C. L. von Blume 1422* (L); [precise locality not known], s.a., *C. L. von Blume s.n.* (K, L); Tjibodas, s.a., *J. G. Boerlage s.n.* (L); [precise locality not known], *J. H. Coert 1002* (L); G. Lawoe, 26 Oct 1932, *J. H. Coert s.n.* (A); Madive, G. Lawae, Sarangan, *J. D. Dorgelo 137* (L); Pasoeroean, G. Tengga, *J. D. Dorgelo 1450* (L); SW Java, *H. O. Forbes 870* (L); Tjibodas, *J. G. Hallier 750* (L, NY); Kamodjan, *C. Holstvoogd 611* (L); Preanger, Tjibodas, *S. H. Koorders 31552b* (L); Ngadisari, *S. H. Koorders 37672b* (L); W Java, s.a., *H. Kuhl & J. C. van Hasselt s.n.* (L); Mt. Gedehu, Pampango, s.a., *H. Kuhl & J. C. van Hasselt s.n.* (L); [precise locality not known], *J. P. Mousset 964* (US); G. Larroe, Sarangan, *A. Rant 16* (L); Tosari, 29 Jan 1915, *H. N. Ridley s.n.* (K); Bandoeng, *J. J. Smith & A. Rant 408* (L); Batavia, G. Boender, *C. G. G. J. van Steenis 4032* (L); Res. Priangau, G. Papandajan (borem Tjisoeraepan), *C. G. G. J. van Steenis 4050* (L); Buitenzorg, Rarahan, beneden Bergtuin Tjibodas, *C. G. G. J. van Steenis 12272* (L).

Schisandra elongata is one of only two species in the genus occurring in Malesia. Both *S. elongata* and *S. propinqua* subsp. *axillaris* are endemic to Java, although there is little chance of taxonomic confusion, since they are very distinct and belong to different supraspecific groups. Sterile specimens of *S. propinqua* can easily be distinguished, since they typically have coriaceous leaves, with narrower laminas [length:width ratios of (2.0–) 2.3–3.2 (–3.5)], and lack the highly arcuate secondary veins typical of *S. elongata*.

Considerable nomenclatural confusion exists in the early botanical literature regarding use of the name "*S. elongata*." Although there are numerous reports of *S. elongata* from the Himalayas and Yunnan, Smith (1947) has shown that these refer to *S. neglecta* (see discussion following the latter species, no. 5). The "*S. elongata*" pollen described by Praglowski (1976) consequently represents *S. neglecta*, although the true taxonomic

PLATE 3. *Schisandra elongata* (*S.* subg. *Sinoschisandra*). A, flowering and fruiting branch. B, female flower (tepals removed). C, carpel. D, fruiting apocarp. E, fruiting apocarp (longitudinal section). F, seed. Reproduced from Blume (1830: fig. 5); photograph © Royal Botanic Gardens, Kew.

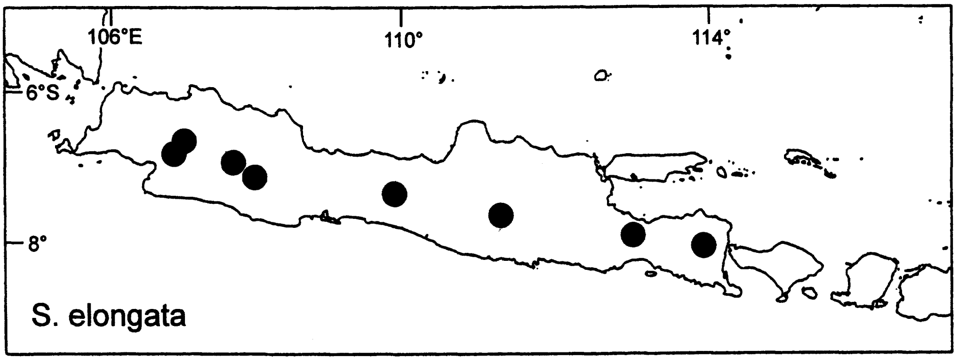


FIG. 32. Distribution of *Schisandra elongata*.

identities of other pollen descriptions identified as "*S. elongata*" are unclear (e.g., Agababian 1966).

Crystalliferous sclerenchyma cells of *S. elongata* are illustrated by Bailey and Nast (1948).

10. Schisandra tomentella A. C. Smith, Sargentia 7: 119. 1947.—TYPE: CHINA. Szechuan [Sichuan]: Ma-pien Hsien, 23 May 1930, *W. P. Fang 408* (holotype: A!; isotypes: E! K! NY! US).

Woody vines, monoecious (often appearing dioecious). Lateral branches lacking wings, with fugaceous perules at base; branches continuing growth in subsequent years. Leaf laminas (6–) 7–10 (–10.5) cm long, 4–5 (–6) cm wide, length:width ratio (1.2–) 1.6–2.5, papyraceous, 50–130 µm thick, abaxial surface densely tomentose, elliptic to obovate-elliptic; primary vein slightly impressed above, ± plane below; secondary veins (4–) 5 (–7) pairs per leaf, slightly arcuate; base acute-attenuate (younger leaves) to obtuse-attenuate (older leaves); apex short- to long-acuminate; margin denticulate, (5–) 8–15 teeth per side of leaf; petioles tomentose, (10–) 18–27 mm long, (0.6–) 0.8–1.2 (–1.3) mm in diameter. Flowers borne in axils of fugaceous bracts at the base of young shoots or in axils of leaves, solitary; tepals ca. 5–6 (male flowers), ca. 7 (female flowers); tepals yellow, outermost tomentose externally; outermost tepal round to elliptic, ca. 4.5–10 mm long, ca. 4–9 mm wide, length:width ratio ca. 1.1–1.2; innermost tepal ca. 4–8 mm long, ca. 3.5–10 mm wide, length:width ratio ca. 0.8–1.2; largest tepal elliptic to ovate, 5.4–10.0 mm long, 4.4–6.5 mm wide, length:width ratio 1.1–1.3; outermost tepal not reduced, ca. 0.8–1.0 of length of largest; innermost tepal slightly reduced, ca. 0.7–0.8 of length of largest; peduncles tomentose, 24–43 mm long, 0.3–1.2 mm in diameter (male flowers), ca. 20–45 mm long, ca. 2 mm in diameter (female flowers). Male flowers with androecium of 16–22 essentially free stamens, uppermost stamens generally only partially differentiated, appearing connate, forming a carnose mass ca. 0.9 mm in diameter, with marginal thecae; thecae of free stamens introrse-lateral; pollen hexacolpate. Female flowers with gynoecium of ca. 45 free carpels [ca. 70, fide Smith 1947: 120], gynoecium ca. 5.1 mm in diameter; carpels 1.6–1.8 (–2.0) mm long, 0.6–0.8 (–1.2) mm wide, length:width ratio 1.9–2.8; pseudostyle small. Fruit peduncles tomentose, not elongated, ca. 5.5 cm long, ca. 1.2–1.3 mm wide; torus ca. 4.5 cm long, ca. 2.8–3.2 mm wide; apocarps red, ca. 3–4 mm long, ca. 4–5 mm wide, length:width ratio ca. 1.2. Seeds 2 per apocarp, discoid, 2.7–3.1 mm long, 3.2–3.5 mm wide, length:width ratio 0.8–0.9; testa smooth. Chromosome number unknown. Fig. 2E.

Illustrations. Law (1996a: fig. 74, 1–8).

Phenology. Information is sparse due to the limited number of collections in herbaria; available information indicates that *S. tomentella* is in flower in May and in fruit in August.

Distribution (Fig. 31). Endemic to China (southern Sichuan); scandent and climbing in thickets and woodlands, on mountain slopes; 1300–2200 m.

ADDITIONAL SPECIMENS EXAMINED. **China.** SICHUAN: Ma-pien Hsien, *F. T. Wang 22845* (A; paratype of *S. tomentella* A. C. Sm.); Ma-pien Hsien, *F. T. Wang 23052* (A; paratype of *S. tomentella* A. C. Sm.); Leibo, Qinghexiang County, *Q.-S. Zhao 1341* (NY).

Schisandra tomentella is an exceptionally distinct species, most easily recognized by the dense mat of comparatively long hairs (Fig. 2E) on the abaxial leaf laminas, petioles, and peduncles (and, to a lesser extent, on the abaxial surface of the outer tepals). Contrary to the statement by Smith (1947: 120), the hairs are not branched.

The cladistic analysis reveals that *S. tomentella* is most closely related to *S. pubescens*, and these two species form a robust clade with *S. pubinervis* (Fig. 20). Differences exist, however, both in the type of hair present (considerably shorter in *S. pubescens* and *S. pubinervis*), and in the extent of hair coverage (restricted to the midrib and secondary veins on the abaxial leaf lamina in *S. pubinervis*). The leaves of *S. tomentella* are generally narrower and often more obovate than those of either *S. pubescens* or *S. pubinervis*, and the male flowers have fewer tepals (5–6 in *S. tomentella*; 7–8 in *S. pubescens* and *S. pubinervis*).

Schisandra tomentella is rare and locally restricted in southern Sichuan. Only four collections were available for study, three of which were previously examined by Smith during the preparation of his monograph (Smith 1947: 119–120).

11. Schisandra pubescens Hemsley & E. H. Wilson, Kew Bull. 1906: 150. 1906 (as "*Schizandra*"). *Schisandra pubescens* var. *typica* A. C. Smith, Sargentia 7: 118. 1947.—TYPE: CHINA. Hupeh [Hubei]: Changyang, Patung, Jun 1907, *E. H. Wilson 2234* (lectotype, here designated: K!; isolectotypes: A! E! NY!).

Schisandra vestita Pax & K. Hoffmann in Pax, Repert. Spec. Nov. Regni Veg. Beih. 12: 381. 1922 (as "*Schizandra*").—TYPE: CHINA. Szetschwan [Sichuan]: Yatschou fu, Tal des Ya ho bei Ming kan schan, 9 Jun 1914, *W. Limpricht 1572* (holotype: WRSL, photo: A! [plate no. 1379], fragment of holotype: A!).

Woody vines, apparently dioecious (but probably monoecious). Lateral branches lacking wings, with fugaceous perules at base; branches continuing growth in subsequent years. Leaf laminas (7–) 8–11 (–11.5) cm long, (3.5–) 4.5–7.5 (–8.5) cm wide, length:width ratio 1.1–1.7 (–2.6), papyraceous, 30–50 μm thick, abaxial surface sparsely pubescent, elliptic to ovate; primary vein ± plane to slightly impressed above, slightly prominent below; secondary veins (4–) 5–6 (–8) pairs per leaf, slightly arcuate; base obtuse to truncate; apex short- to long-acuminate; margin denticulate, (8–) 9–13 (–19) teeth per side of leaf; petioles pubescent, (15–) 22–35 (–43) mm long, (0.8–) 1.0–1.3 (–1.5) mm in diameter. Flowers borne in axils of fugaceous bracts at the base of young shoots, solitary; tepals 7–8 (flowers of both sexes); tepals variably cream, yellow, orange, or red, abaxial surface of outermost tepals pubescent; outermost tepal elliptic to ovate, 4–6 mm long, 2.5–6 mm wide, length:width ratio 1.6–2.2; innermost tepal elliptic to obovate, 5–8 mm long, 4–7 mm wide, length:width ratio 1.1–1.3; largest tepal elliptic to round-ovate, 6.9–10 mm long, 6.6–10 mm wide, length:width ratio 0.9–1.0; outermost tepal slightly reduced, ca. 0.8 of length of largest; innermost tepal slightly reduced, ca. 0.7–0.8 of length of largest; peduncles pubescent, 20–30 mm long, 0.4–1.2 mm in diameter (male flowers), 18–62 mm long, 0.6–0.8 mm in diameter (female flowers). Male flowers with androecium of 14–24 essentially free stamens, uppermost stamens generally only partially differentiated, appearing connate, forming a carnose mass ca. 1.8–2.0 mm in diameter, with marginal thecae; androecium ca. 7.5 mm in diameter; thecae of free stamens introrse-lateral; pollen hexacolpate. Female flowers with gynoecium of 40–62 free carpels; carpels (1.0–) 1.3–1.6 (–1.8) mm long, 0.5–1.0 (–1.2) mm wide, length:width ratio (1.4–) 1.8–2.2 (–2.8); pseudostyle narrow. Fruit peduncles pubescent, not elongated, 4–6 cm long, 0.9–1.1 (–1.2) mm wide; torus 5–11 cm long, (1.6–) 1.8–3.2 (–3.4) mm wide; apocarps red, 4.5–8 mm long, (3–) 3.5–6 (–7) mm wide, length:width ratio (1.1–) 1.3–1.4 (–1.6). Seeds 2 per apocarp, discoid to flattened-reniform, 2.5–3.1 mm long, 2.9–3.4 mm wide, length:width ratio 0.8–1.0; testa smooth. Chromosome number unknown. Fig. 2D.

Illustrations. Cheng (1944c: pl. 72); Law (1996a: fig. 74, 9–19).

Phenology. Flowering from May to July; fruits maturing from June to September.

Distribution (Fig. 33). Endemic to China (Hubei and Sichuan); scandent or climbing in thickets; 1000–1900 (–2400) m.

ADDITIONAL SPECIMENS EXAMINED. **China.** HUBEI: Ichang, Patung District, *A. Henry 1785* (K; paratype of *S. pubescens* and *S. henryi*); [precise locality not known], *A. Henry 5907* (GH, K, US; paratypes of *S. pubescens*); Patung Hsien, Wu-mei-tze, *E. H. Wilson 158* (A).—SICHUAN: Metasequoia Area, Hubei-Sichuan border, *W. C. Cheng & C. T. Hwa 823* (A, UC); Nanchuan-hsien, *W. P. Fang 1395* (A, NY; paratypes of *S. sphenanthera* var. *longipes*); Omei-hsien [Emei Xian], *W. P. Fang 2632* (A, NY); Ngo-pi-hsien, *W. P. Fang 7362* (A, IBSC); Nanchuan, *K. F. Lee 63001* (IBSC); [precise locality not known], *G. L. Qu 5822* (IBSC); Yibin, *C.-R. Sun 108* (IBSC); Erlangshan, Tianchuan, Sikang, *H. L. Tsiang 35162* (IBSC); Tiewashi temple, Jingfushan, Nanchuan, *J. H. Xiong & Z. L. Zhou 91648* (IBSC); Shancaicun, Xiaohe, Nanchuan, *J. H. Xiong & Z. L. Zhou 92143* (IBSC); Laizipo, Mt. Omei [Emei Shan], *G. H. Yang 55026* (IBSC); O-pien Hsien, *T. T. Yü 844* (A).

Schisandra pubescens forms a well-supported clade with *S. pubinervis* and *S. tomentella* (Fig. 20), sharing a synapomorphy for the presence of an indumentum of hairs; differences between the three species are described in detail in the discussion following *S. tomentella* (no. 10).

The protologue of *S. pubescens* (Hemsley & Wilson 1906) includes a detailed description of the "short, flattened curled appressed hairs" on the abaxial leaf lamina and petiole. Rehder and Wilson (in Sargent 1913: 415) subsequently described a new variety of *S. sphenanthera*, var. *pubinervis*; the authors recognized *S. pubescens* in the same publication and evidently did not regard the two taxa as closely related. Smith (1947: 116–119) recognized the affinity of the two taxa and adopted a broader definition of *S. pubescens* to include Rehder and Wilson's variety. This broad concept of *S. pubescens* has been accepted by all subsequent taxonomists (e.g., Cheng, 1944a, b; Law 1996a), but the two taxa are treated as distinct species in the present monograph. The species are undoubtedly close, but are easily distinguishable on the basis of several characters, particularly the extent and distribution of hairs. As noted in the description above, *S. pubescens* sensu stricto has hairs over the entire abaxial leaf lamina surface (with

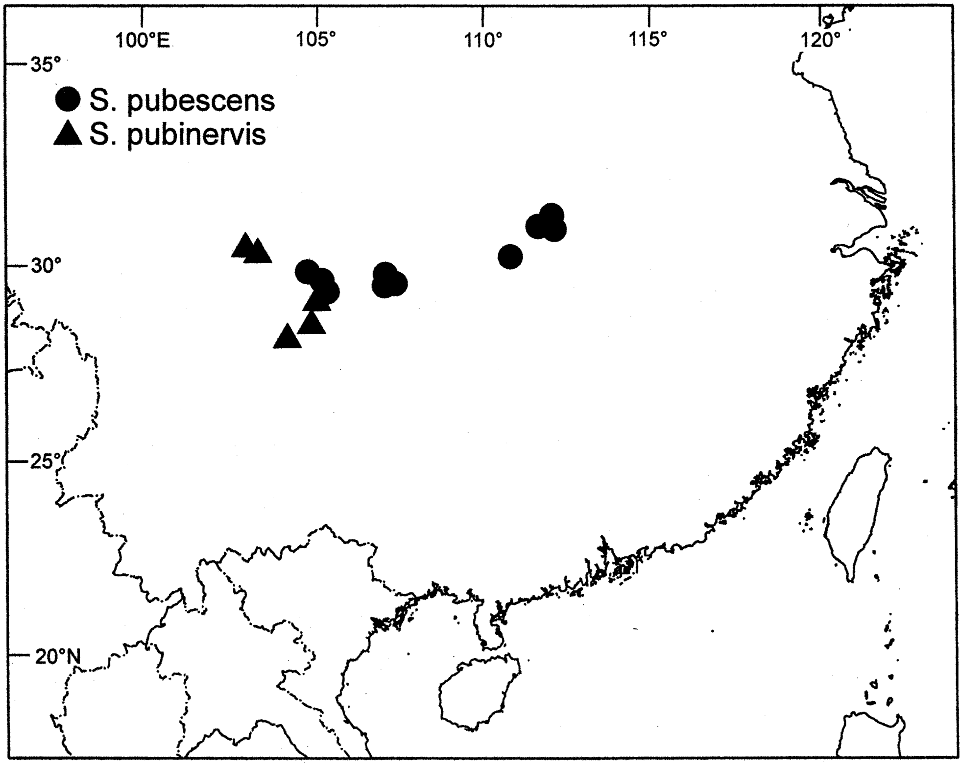


FIG. 33. Distribution of *Schisandra pubescens* and *S. pubinervis*.

greatest density over the midrib and secondary veins), as well as on the petioles, peduncles (of flowers of both sexes and of fruits), and on the outer surface of the outer tepals. In marked contrast, the abaxial surface of leaf laminas of *S. pubinervis* has the hairs restricted to the midrib and secondary veins. The lower order veins and the lamina surface between veins are glabrous; likewise, the petioles, peduncles, and outer tepals are uniformly glabrous. This distinction is absolute, and no intermediate specimens have been encountered. The laminas of *S. pubescens* also tend to be broader, with length:width ratios of 1.1–1.7 (–2.6), compared with (1.2–) 1.5–2.0 (–2.7) in *S. pubinervis*, and have a greater number of marginal denticulations [(8–) 9–13 (–19), compared with (5–) 6–10 (–13) in *S. pubinervis*]. The red perianth pigmentation occasionally noted in *S. pubescens* has never been observed in *S. pubinervis*. The female flowers of *S. pubinervis* typically have fewer carpels (36–50) than those of *S. pubescens* (40–62).

The holotype of *S. vestita* Pax & Hoffmann (in Pax 1922) was not available for study, but I examined a photograph and a leaf fragment of the type (deposited in A). The highly diagnostic pattern of pubescence clearly indicates that *S. vestita* is synonymous with *S. pubescens*.

The pollen of *S. pubescens* is described by Erdtman (1952: 257) and Praglowski (1976).

12. Schisandra pubinervis (Rehder & E. H. Wilson) R. M. K. Saunders, stat. et comb. nov. *Schisandra sphenanthera* var. *pubinervis* Rehder & E. H. Wilson in Sargent, Pl. Wilson. 1: 415. 1913. *Schisandra pubescens* var. *pubinervis* (Rehder & E. H. Wilson) A. C. Smith, Sargentia 7: 119. 1947.—TYPE: CHINA. W Szech'uan [W Sichuan]: near Monkong Ting, 19 Jun 1908, *E. H. Wilson 2551* (holotype: A!; isotypes: E! K! US).

Woody vines, apparently dioecious (but probably monoecious). Lateral branches lacking wings, with fugaceous perules at base; branches continuing growth in subsequent years. Leaf laminas (5–) 6.5–11 (–13.5) cm long, (3–) 3.5–6 (–7) cm wide, length:width ratio (1.2–) 1.5–2.0 (–2.7), papyraceous, 30–70 μm thick, abaxial lamina surface glabrous except for pubescent primary and secondary veins, elliptic to ovate; primary vein ± plane to slightly impressed above, slightly prominent below; secondary veins (3–) 4–5 (–6) pairs per leaf, (slightly) arcuate; base acute (younger leaves) to obtuse or truncate (older leaves); apex short- to long-acuminate; margin (sinuous-) denticulate to serrulate, (5–) 6–10 (–13) teeth per side of leaf; petioles glabrous, (10–) 15–30 (–40) mm long, (0.6–) 0.9–1.3 (–1.9) mm in diameter. Flowers borne in axils of fugaceous bracts at the base of young shoots or in axils of leaves, solitary; tepals 7–8 (male flowers), 8–10 (female flowers); tepals yellow, glabrous; outermost tepal elliptic to ovate, 4.6–7.4 mm long, 3.8–6.1 mm wide, length:width ratio 1.2–1.7; innermost tepal elliptic to obovate, 4.8–6.7 mm long, 3.0–5.6 mm wide, length:width ratio 1.1–1.6; largest tepal elliptic to ovate, 6.7–9.8 mm long, 6.4–8.8 mm wide, length:width ratio 1.0–1.3; outermost tepal not reduced or slightly reduced, 0.7–1.0 of length of largest; innermost tepal (slightly) reduced, 0.6–0.8 of length of largest; peduncles glabrous, 28–52 mm long, (0.3–) 0.4–0.6 (–0.8) mm in diameter (male flowers), 50–60 mm long (female flowers). Male flowers with androecium of 14–19 essentially free stamens, uppermost stamens generally only partially differentiated, appearing connate, forming a carnose mass, with marginal thecae; thecae of free stamens introrse-lateral; pollen hexacolpate. Female flowers with gynoecium of 36–50 free carpels, gynoecium ca. 4 mm in diameter; carpels 1.3–1.7 mm long, 0.8–1.0 mm wide, length:width ratio 1.4–2.1; pseudostyle narrow. Fruit peduncles glabrous, not elongated, (4.5–) 6–7.5 (–10) cm long, 0.7–1.1 (–1.4) mm wide; torus (2–) 4–10 (–15.5) cm long, 1.3–2.1 (–3.0) mm wide; apocarps red, 4–5 (–6) mm long, 3–4 (–5) mm wide, length:width ratio (0.9–) 1.1–1.3 (–1.5). Seeds (1–) 2 per apocarp, variably flattened-reniform, discoid or rarely flattened-pyriform, 2.4–3.0 (–3.6) mm long, (2.6–) 2.8–3.3 (–4.0) mm wide, length:width ratio 0.8–0.9 (–1.2); testa smooth to slightly rugulose. Chromosome number unknown. Fig. 2C.

Illustrations. Cheng (1944b: pl. 71, as "*Schizandra sphenanthera* var. *pubinervis*").

Phenology. Flowering in June and July; fruits maturing from July to August.

Distribution (Fig. 33). Endemic to China (Hubei and Sichuan); scandent or climbing in thickets and forests; 1000–2000 (–2600) m.

ADDITIONAL SPECIMENS EXAMINED. **China.** HUBEI: vicinity of Shui-sa-pa, *J. L. Gressitt 2444* (A); Hsing Shan, *A. Henry 6447* (A, K).—SICHUAN: Pao-hsing-hsien, *K. L. Chu 2962* (IBSC); Moupin [Mupin/Baoxing], 1870, *A. David s.n.* (P); Kuan-hsien, *W. P. Fang 2171* (A, NY); Omei-shan [Emei Shan], *W. P. Fang 7765* (A); Hung-ya-hsien, *W. P. Fang 8330* (K); Mt. Omei [Emei Shan], Chiu-lao-tung, *S. C. Sun & K. Chang 236* (A); Erlangshan, Tianchuan, Sikang, *H. L. Tsiang & Hsiung 34331* (IBSC), *34412* (IBSC); Mt. Omei [Emei Shan], *T. H. Tu 153* (IBSC); Mt. Omei [Emei Shan], Chiu-lar-tung, *L. Y. T. Tui 118* (A); Mt. Omei [Emei Shan], *F. T. Wang 23281* (A, IBSC); Mt. Emei [Emei Shan], *J. H. Xiong, X. S. Zhang, & X. H. Jiang 31566* (IBSC); Mt. Omei

[Emei Shan], *K. H. Yang 56238* (IBSC), *56707* (IBSC); Xining, Leibo County, *Q.-S. Zhao 1065* (A, NY); Nibashan Forest Farm, Rongjing County, *Q.-S. Zhao 1069* (A, NY, MO).

Although originally described as a variety of *S. sphenanthera*, this taxon is most closely related to *S. pubescens* and *S. tomentella*, with which it forms a well-supported clade. The diagnostic characters of *S. pubinervis*, and the reasons for elevating it to the specific level, are discussed under *S. pubescens* (no. 11).

Rehder and Wilson (in Sargent 1913: 415) cited a paratype, *A. Henry 6447* (A!), in the protologue for "*S. sphenanthera* var. *pubinervis*." Smith (1947: 119) discussed the identity of this specimen, commenting that "I do not believe that the Henry collection is referable to this variety, and possibly it does not even represent the species [*S. pubescens* sensu lato]; for the time being I cannot place it." The reasons given were that the fruiting peduncles were 8–11 cm long and the fruiting torus up to 18 cm long, far exceeding the other specimens measured by Smith. A broader range of specimens is now available, and although *A. Henry 6447* has large fruits, many other specimens have fruits only slightly smaller; this specimen has therefore been assigned to *S. pubinervis* here.

13. Schisandra lancifolia (Rehder & E. H. Wilson) A. C. Smith, Sargentia 7: 133. 1947. *Schisandra sphenanthera* var. *lancifolia* Rehder & E. H. Wilson in Sargent, Pl. Wilson. 1: 415. 1913.—TYPE: CHINA. Szech'uan [Sichuan]: Mupin, Jun 1908, *E. H. Wilson 2552* (holotype: A!; isotypes: K! US).

Woody vines, apparently dioecious (but probably monoecious). Lateral branches lacking wings, with fugaceous perules at base; branches continuing growth in subsequent years. Leaf laminas (3.5–) 4.5–7.5 (–10) cm long, 1.5–3 (–4) cm wide, length:width ratio (2.0–) 2.4–3.4 (–3.7), papyraceous, 50–60 (–100) μm thick, glabrous, elliptic to ovate; primary vein ± plane to slightly impressed above, slightly prominent below; secondary veins 4–6 (–7) pairs per leaf, (slightly) arcuate; base acute (younger leaves) to obtuse (older leaves); apex acute to (short-) acuminate; margin denticulate to serrulate, (4–) 5–9 (–17) teeth per side of leaf; petioles glabrous, (3–) 6–12 (–14.5) mm long, 0.6–1.1 (–1.5) mm in diameter. Flowers borne in axils of fugaceous bracts at the base of young shoots, solitary; tepals 6–8 (flowers of both sexes); tepals variably white, yellow, orange, red, or pink, glabrous; outermost tepal round or elliptic to ovate, 3.0–5.1 mm long, 2.5–4.0 (–5.4) mm wide, length:width ratio 0.9–1.2 (–1.8); innermost tepal variably elliptic, ovate, or obovate, 2.5–4.5 mm long, 1.5–2.7 (–3.8) mm wide, length:width ratio 0.9–2.4; largest tepal variably round or elliptic to ovate, rarely obovate, 3.7–5.2 (–6.1) mm long, (3.0–) 3.4–4.7 (–5.1) mm wide, length:width ratio (0.8–) 1.0–1.2 (–1.6); outermost tepal not reduced, 0.8–1.0 of length of largest; innermost tepal slightly reduced, 0.7–0.9 of length of largest; peduncles glabrous, (9–) 12–31 (–36) mm long, 0.2–0.5 (–0.7) mm in diameter (male flowers), (24–) 30–40 (–56) mm long, 0.5–0.8 mm in diameter (female flowers). Male flowers with androecium of 8–19 essentially free stamens, uppermost stamens generally only partially differentiated, appearing connate, forming a carnose mass ca. 1.5 mm in diameter, with marginal thecae; androecium ca. 2.5 mm in diameter; thecae of free stamens introrse-lateral; pollen hexacolpate. Female flowers with gynoecium of 14–24 free carpels; carpels (1.2–) 1.4–2.0 mm long, 0.5–0.9 mm wide, length:width ratio (1.3–) 2.0–3.0 (–3.4); pseudostyle narrow. Fruit peduncles glabrous, not elongated, 3–4.5 (–5.5) cm long, 0.3–0.5 mm wide; torus 3–5 (–6.5) cm long, (0.6–) 0.8–1.2 (–1.6) mm wide; apocarps red, (4.5–) 6.5–9.5 mm long, (4–) 4.5–7 mm wide, length:width ratio (1.0–)

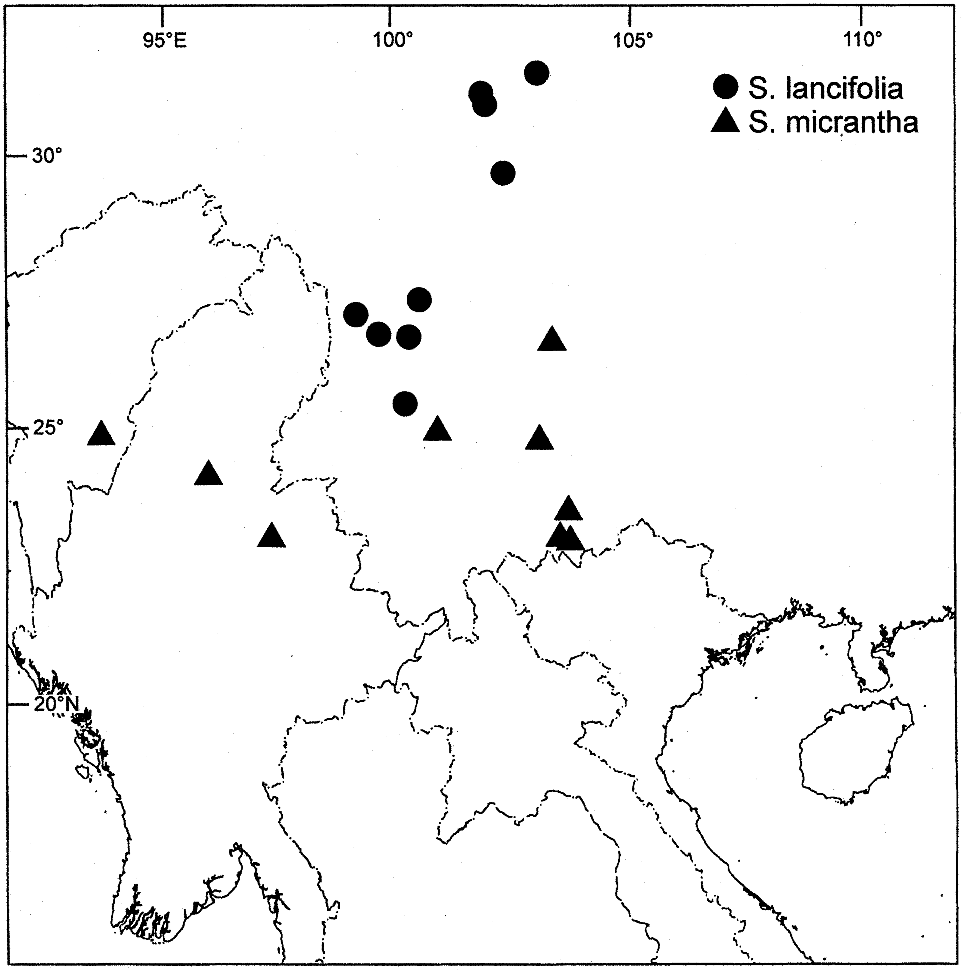


FIG. 34. Distribution of *Schisandra lancifolia* and *S. micrantha.*

1.2–1.5. Seeds (1–) 2 per apocarp, (discoid-) flattened-reniform, 2.9–3.3 mm long, 3.2–3.6 mm wide, length:width ratio 0.9 (–1.0); testa ± smooth to slightly rugulose. Chromosome number unknown.

Illustrations. Smith (1947: fig. 17a–c); Law (1996a: fig. 76, 10–17).

Phenology. Flowering from April to July; fruits maturing in October and November.

Distribution (Fig. 34). Endemic to China (Sichuan and Yunnan); scandent and climbing in thickets and woods, often on steep slopes and in ravines; 1350–2900 m.

ADDITIONAL SPECIMENS EXAMINED. **China.** SICHUAN: Ta Hsiang Ling, *C. Y. Chiao 1611* (A); Ssu queh, Chao kio, *C. K. Schneider 985* (A, K); "bei Tchao kio," *C. K. Schneider 999* (A, GH); Ta-tsien-lou [Kangding], *J. A. Soulié 453* (K); Tachien lu [Kangding], *E. H. Wilson 1268* (A; paratype of *S. sphenanthera* var. *lancifolia*); near Tachien lu [Kangding], *E. H. Wilson 1268a* (A; paratype of *S. sphenanthera* var. *lancifolia*); Mian-ning Hsien, *T. T. Yü 1771* (A).—YUNNAN: [precise locality not known], *G. Forrest 10197* (A), *16589* (A); Chien-chuan-Mekong divide, 26°40′N 99°40′E, *G. Forrest 21524* (A); Long Yu, Mt. Mung Hua, *McLaren's collector*

L106A (C, K, UC); eastern slopes of Likiang Snow Range, Prefectural District of Likiang, Yangtze watershed, *J. F. Rock 4299* (A, NY, UC); Mt. Lauchunshan, SE of the Yangtze bend at Shiku, *J. F. Rock 9602* (A, NY, UC); Mt. Lauchünshan, SW of the Yangtze bend at Shiku, *J. F. Rock 9603* (A, UC); Ta li Hsien, *C. W. Wang 63372* (A); Wei-si Hsien, *C. W. Wang 63595* (A); Li-kiang Hsien, *C. W. Wang 71297* (A); Juei-she Hsien, *T. T. Yü 1047* (A).—Precise locality not known: *E. H. Wilson 3134* (A; paratype of *S. sphenanthera* var. *lancifolia*).

Although *S. lancifolia* was originally described as a variety of Rehder and Wilson's broadly conceived *S. sphenanthera* (Sargent 1913: 414–416), the species is actually very distinct, and shows greater similarity with *S. micrantha*. Both *S. lancifolia* and *S. micrantha* have highly reduced flowers with fewer tepals, stamens, and carpels than flowers of *S. sphenanthera*, although it is not clear whether these similarities are truly homologous. The principal differences between *S. lancifolia* and *S. micrantha* include the following: leaf lamina shape [comparatively narrow in *S. lancifolia*, with length:width ratios of (2.0–) 2.4–3.4 (–3.7), but broad in *S. micrantha*, with ratios of (1.0–) 1.2–1.9 (–2.5)]; and the length of the fruiting torus [3–5 (–6.5) cm in *S. lancifolia*, but 1.5–3.5 cm in *S. micrantha*].

The narrow leaves in *S. lancifolia* may result in taxonomic confusion with *S. propinqua* subsp. *sinensis*, which has similarly shaped leaf laminas with length:width ratios of (2.2–) 2.5–5.0 (–5.7). Determination is easy if male flowers are present, since *S. propinqua* has a true fused synandrium, whereas the androecium in *S. lancifolia* is composed of essentially free stamens. Flowers of *S. lancifolia* are typically smaller and have fewer floral parts (6–8 tepals and 14–24 carpels), whereas flowers of *S. propinqua* have (7–) 8–15 tepals and 18–52 carpels. The difference in carpel number is furthermore reflected in fewer apocarps per fruit. Other valuable diagnostic characters include: the relative size of the outermost tepal [0.8–1.0 of the length of the largest tepal in *S. lancifolia*, but reduced to 0.1–0.4 (–0.7) in *S. propinqua*]; and the length of the flower peduncles [(9–) 12–31 (–36) mm and (24–) 30–40 (–56) mm long in male and female flowers of *S. lancifolia*, respectively, but 3–16 mm and 3–14 mm, respectively, in *S. propinqua*].

The pollen of *S. lancifolia* is described by Praglowski (1976).

14. Schisandra micrantha A. C. Smith, Sargentia 7: 135. 1947.—TYPE: CHINA. Yunnan: P'ing-pien Hsien, 17 May 1934, *H. T. Tsai 55161* (holotype: A!).

Schisandra elongata var. *dentata* Finet & Gagnepain, Bull. Soc. Bot. France 52: 49. 1905 (as "*Schizandra*") [reprinted as Contr. Fl. As. Or. 2: 49. 1907].—TYPE: CHINA. Yunnan: environs de Yunnan-sen, 9 Jun 1899, *F. Ducloux 585A* (lectotype, here designated: P!).

Schisandra gracilis A. C. Smith, Sargentia 7: 132. 1947.—TYPE: MYANMAR [BURMA]. Magok, Katha District, Sagaing, May 1934, *F. G. Dickason 5016* (holotype: A!, photo: HKU!).

Woody vines, apparently dioecious (but probably monoecious). Lateral branches lacking wings, with fugaceous perules at base; branches continuing growth in subsequent years. Leaf laminas (3–) 4–6.5 (–7.5) cm long, 2.5–4 (–6) cm wide, length:width ratio (1.0–) 1.2–1.9 (–2.5), thin papyraceous to subcoriaceous, (20–) 50–90 (–100) µm thick, glabrous, elliptic to ovate; primary vein ± plane to slightly impressed above, slightly prominent below; secondary veins (3–) 4–5 (–7) pairs per leaf, (slightly) arcuate; base acute (younger leaves) to obtuse or truncate (older leaves); apex acute or (short-) acuminate; margin (sinuous-) denticulate to (sinuous-) serrulate, (3–) 4–10 (–12) teeth per side of leaf; petioles glabrous, (5.5–) 7.5–15 (–22) mm long, (0.4–) 0.6–1.1 mm in diameter. Flowers borne in axils of fugaceous bracts at the base of young shoots, solitary; tepals 6–9 (male flowers), 5–8 (female flowers); tepals yellow, sometimes tinged pink or orange, glabrous; outermost tepal (round-) elliptic to ovate, rarely obovate, (1.9–) 2.5–5.3 mm long, 1.3–4.6 mm wide, length:width ratio 0.9–1.6 (–1.9); innermost tepal (round-) elliptic to obovate, 2.0–4.8 mm long, 1.7–4.3 mm wide, length:width ratio 0.9–1.7; largest tepal (round-) elliptic to ovate, (2.8–) 3.5–6.6 mm long, 3.1–6.0 (–6.5) mm wide, length:width ratio 0.8–1.1 (–1.5); outermost tepal (slightly) reduced or not reduced, 0.5–1.0 of length of largest; innermost tepal (slightly) reduced, 0.5–0.9 of length of largest; peduncles glabrous, (12–) 15–31 (–38) mm long, 0.2–0.7 mm in diameter (male flowers), (14–) 22–48 (–61) mm long, 0.4–0.7 (–0.9) mm in diameter (female flowers). Male flowers with androecium of 7–14 essentially free stamens, uppermost stamens generally only partially differentiated, appearing connate, forming a carnose mass 0.9–1.6 mm in diameter, with marginal thecae; androecium 2.0–2.3 mm in diameter; thecae of free stamens introrse-lateral; pollen hexacolpate. Female flowers with gynoecium of 14–22 free carpels, gynoecium 1.8–5.2 mm in diameter; carpels 1.2–2.8 (–3.4) mm long, (0.5–) 0.7–1.2 mm wide, length:width ratio (1.5–) 1.7–3.4 (–4.3); pseudostyle narrow. Fruit peduncles glabrous, not elongated, 3–5.5 cm long, 0.3–0.4 mm wide; torus 1.5–3.5 cm long, 0.7–1.4 mm wide; apocarps red, 4.5–7.5 mm long, 3.5–7 mm wide, length:width ratio 1.1–1.5. Seeds 1–2 per apocarp, discoid to flattened-reniform, 2.9–3.5 mm long, 3.5–4.0 mm wide, length:width ratio 0.8–1.0; testa slightly tuberculate. Chromosome number unknown.

Illustrations. Law (1996a: fig. 76, 1–9).

Phenology. Flowering from May to July; fruits maturing by August.

Distribution (Fig. 34). India (Manipur), northern Myanmar [Burma] and south-central China (Yunnan); scandent or climbing on slopes and in ravines, often near streams; 1200–2900 m.

ADDITIONAL SPECIMENS EXAMINED. **China.** YUNNAN: environs de Yunnan-sen, *F. Ducloux 585B* (P; paratype of *S. elongata* var. *dentata*); [precise locality not known], *F. Ducloux 735* (K); environs de Yunnan-sen, *F. Ducloux 2588* (P; paratype of *S. elongata* var. *dentata*); environs de Tou-dza, *F. Ducloux 2764* (P; paratype of *S. elongata* var. *dentata*); environs de Lawngy-tsin, *F. Ducloux 2765* (P; paratype of *S. elongata* var. *dentata*); Mengtse, *A. Henry 11211* (A, K, NY); La-Kou, *E. E. Maire 33* (A); Tché-hay, *E. E. Maire 177* (A); Tché-hai, *E. E. Maire 396* (A); Ping-pien Hsien, *H. T. Tsai 60136* (A); Huang-t'u-p'u, Cheng-kiang, *H. Wang 41426* (A). **India.** MANIPUR: Sirhoi, *F. K. Ward 17680* (A, NY). **Myanmar [Burma].** Htawgaw, Naung-chaung valley, Lashi County, *F. K. Ward 1594* (E).

Schisandra micrantha is closely related to *S. lancifolia*, with which it shares small flowers with reduced numbers of tepals, stamens, and carpels (see discussion following *S. lancifolia*, no. 13).

The earliest name referable to *S. micrantha* is *S. elongata* var. *dentata* (Finet & Gagnepain 1905), based on five syntypes (*F. Ducloux 585*, *2588*, *2764*, *2765*, and *F. J. Harmand 3321* ["in herb. Pierre"], all deposited in P). Smith (1947: 209) was unable to examine the type specimens, but mistakenly believed that *Harmand 3321* was the same specimen as *Pierre 3321*. Finet and Gagnepain (1907a: 85) included *Pierre 3321* among the syntypes for their *S. crassifolia* and used this collection for an illustration of the androecium (Finet & Gagnepain 1907b: fig. 8.1–2). Smith (1947: 187) and Saunders (1998: 47) both used this illustration and the original protologue to deduce that *S. crassifolia* is probably synonymous with *Kadsura heteroclita* (Roxb.) Craib; also, Smith (1947: 209) inferred that *S. elongata* var. *dentata* was also at least partly synonymous with *K. heteroclita*. All four *Ducloux* syntypes of *S. elongata* var. *dentata* have been examined during the present revision and found to be *S. micrantha*; *Harmand 3321* was not located. The best of the *Ducloux* specimens (*585A*) has been selected as the lectotype here, and *S. elongata* var. *dentata* is consequently referable to *S. micrantha*.

Smith (1947: 132–133) described *S. gracilis* based on a single specimen, *F. G. Dickason 5016* (A!). Smith believed that *S. gracilis* was similar to *S. micrantha*, but differed in having reduced outermost tepals, larger mid-tepals, and larger androecia. A larger number of specimens of *S. micrantha* than were available to Smith were examined during the preparation of the present monograph and allowed a clearer understanding of the patterns of phenotypic variation. The outermost and largest tepals in *Dickason 5016* were described by Smith as 1.5–4.0 mm and 5.5–7.5 mm long, respectively; these values lie within the range of variation evident in *S. micrantha* [(1.9–) 2.5–5.3 mm and (2.8–) 3.5–6.6 mm long]. The androecial diameter cited by Smith (4.5–5.0 mm) for *Dickason 5016* is larger than that of other specimens of *S. micrantha* (2.0–2.3 mm), but this is not regarded of sufficient importance for recognition of a distinct species.

15. Schisandra henryi Clarke, Gard. Chron. III 38: 162. 1905 (as "*Schizandra*") [reprinted in Repert. Spec. Nov. Regni Veg. 4: 172. 1907]. *Schisandra elongata* var. *longissima* Dunn, J. Linn. Soc., Bot. 38: 354. 1908 (as "*Schizandra*").—TYPE: CHINA. Yunnan: Meng-tzu, SE mountains, [date not known], *A. Henry 9193B* (lectotype: K!; isolectotype: A!). [The lectotype for *S. henryi* was designated by Smith (1947), that for *S. elongata* var. *longissima* is designated here.]

Woody vines, apparently dioecious (but probably monoecious). Lateral branches narrowly or conspicuously winged, with variably persistent perules at base; branches continuing growth in subsequent years. Leaf laminas (5.5–) 7.5–11.5 (–14) cm long, (3–) 4.5–7.5 (–9) cm wide, length:width ratio (1.1–) 1.4–2.2 (–2.8), (thin-) papyraceous, rarely subcoriaceous, (20–) 30–60 (–90) µm thick, abaxial surface glabrous or variably glaucous, elliptic to ovate; primary vein ± plane to slightly impressed above, ± plane to slightly prominent below; secondary veins 4–6 pairs per leaf, (slightly) arcuate; base acute (-attenuate) (younger leaves) to obtuse (-attenuate) or truncate (older leaves); apex (short-) acuminate, rarely long-acuminate; margin (sinuous-) denticulate to serrulate, rarely (sub-) entire, (0–) 4–11 (–16) teeth per side of leaf; petioles glabrous, (12–) 17–38 (–62) mm long, (0.6–) 0.8–1.6 (–2.2) mm in diameter. Flowers borne in axils of (semi-) persistent perules at the base of young shoots or in axils of leaves, solitary; tepals 6–10 (male flowers), 6–8 (female flowers); tepals yellow or orange, often with red inner tepals, glabrous; outermost tepal variably elliptic, ovate, or obovate, (4.4–) 5.1–7.0 (–9.0) mm long, (3.0–) 3.5–5.0 (–7.6) mm wide, length:width ratio (0.9–) 1.2–1.7 (–2.2); innermost tepal elliptic to obovate, rarely ovate, 4.6–5.5 mm long, 4.8–5.9 mm wide, length:width ratio 0.9–1.1; largest tepal (round-) elliptic to obovate, (5.4–) 6.8–10.0 (–12.8) mm long, (3.6–) 5.5–9.5 (–12.7) mm wide, length:width ratio (0.7–) 0.9–1.3 (–1.5); outermost tepal slightly reduced, 0.7–0.9 (–1.0) of length of largest; innermost tepal (slightly) reduced, (0.4–) 0.6–0.8 of length of largest; peduncles glabrous, (17–) 21–49 (–62) mm long, 0.4–0.8 (–1.1) mm in diameter (male flowers), 32–47 mm long, 0.4–0.9 mm in diameter (female flowers). Male flowers with androecium of 12–46 essentially free stamens, uppermost stamens generally only partially differentiated, appearing connate, forming a carnose mass 1.6–5.0 mm in diameter, with marginal thecae; androecium 4.4–7.0 mm in diameter;

thecae of free stamens introrse-lateral; pollen hexacolpate. Female flowers with gynoecium of 28–65 free carpels, gynoecium 4.3–6.3 mm in diameter; carpels (1.3–) 1.8–3.0 (–3.4) mm long, 0.6–1.2 (–1.5) mm wide, length:width ratio 1.6–3.5 (–4.2); pseudostyle narrow. Fruit peduncles glabrous, elongated, (3.5–) 6–10 (–14.5) cm long, (0.5–) 0.7–1.1 (–1.4) mm wide; torus (1.5–) 3.5–10.5 (–11) cm long, (1.0–) 1.3–2.4 (–3.6) mm wide; apocarps red, 4.5–8.5 (–9.5) mm long, (3–) 3.5–6.5 (–7.5) mm wide, length:width ratio (0.9–) 1.1–1.6 (–1.8). Seeds 1–2 per apocarp, discoid to flattened-reniform, rarely flattened-pyriform, (2.5–) 2.9–3.6 (–3.8) mm long, (2.9–) 3.2–3.9 (–4.6) mm wide, length:width ratio 0.8–1.0 (–1.3); testa variably rugulose to very tuberculate. Chromosome number unknown.

Although many of the species in subg. *Sinoschisandra* are difficult to distinguish, the *S. henryi*-*S. longipes*-*S. perulata* clade (Fig. 20) is clearly defined by conspicuous synapomorphies in the presence of angled or winged branches and large basal perules that are persistent (at least until fruits develop). *Schisandra longipes* is most easily distinguished from *S. henryi* by the presence of short hairs on the midrib and secondary veins of the abaxial leaf lamina; other diagnostic characters are listed in Table 4. *Schisandra perulata* is a highly distinct species, readily separated from *S. henryi* by several striking characters, viz.: rapidly elongating lateral shoots with consonantly long internode regions; larger leaf laminas [(10–) 12–14.5 (–16.5) × (4.5–) 6.5–8.5 (–10) cm] that are more commonly thin-papyraceous; longer fruiting tori [ca. 12–14 cm]; larger apocarps [ca. 9.0–12.0 × ca. 8.5–13.0 mm]; and larger seeds [ca. 3.7–4.5 × ca. 3.9–4.5 mm].

Smith (1947: 114–116) recognized several different infraspecific taxa within *S. henryi*, viz. varieties *henryi* (as "*typica*"), *marginalis*, *yunnanensis*, and *longipes*. The last is raised to specific status in the present monograph as *S. longipes*, since there are qualitative distinguishing characters that are consistent with the phylogenetic species concept adopted here (Table 4; see also the discussion following *S. longipes*, no. 16). The three other varieties recognized by Smith (1947) are all geographically correlated and are raised to subspecific status in the present monograph in compliance with Du Rietz's (1930) definition of subspecies as the "regional facies" of a species. The diagnostic characters for the three subspecies are listed in Table 4; all differences are essentially quantitative, and no single character can be used to identify specimens.

Schisandra henryi was first described by Clarke (1905), who listed two syntypes (*A. Henry 1785* and *9193B*). Smith (1947: 112) selected the K duplicate of *A. Henry 9193B* as the lectotype, since *A. Henry 1785* actually represents *S. pubescens*. Dunn (1908) cited four collections in the protologue of *S. elongata* var. *longissima*, viz. *A. Henry 9193A* (A! K!), *A. Henry 9193B* (A! K!, the latter designated as the lectotype here), *S. T. Dunn 2441* (not located), and *S. T. Dunn 2442* (A! HK! K!); *S. T. Dunn 2442* is referrable to *S. arisanensis* subsp. *viridis*.

Several important anatomical descriptions of *S. henryi* have been published, viz.: primary and secondary xylem and phloem structure, and the vascular arrangement (Lemesle 1946; Ozenda 1946, 1949; Metcalfe 1987; Carlquist 1999); floral anatomy (Ozenda 1946, 1949, 1952); and pollen morphology (Praglowski 1976).

15a. Schisandra henryi subspecies **henryi.** [*Schisandra henryi* var. *typica* A. C. Smith, Sargentia 7: 114. 1947.]

Schisandra hypoglauca H. Léveillé, Repert. Spec. Nov. Regni Veg. 9: 459. 1911 (as "*Schizandra*").—TYPE: CHINA. Kouy-Tchéou [Guizhou], 7 May 1904, *J. Esquirol 58* (holotype: E!; isotypes: A! K!).

TABLE 4. Variation in selected morphological characters of *Schisandra longipes* and subspecies of *S. henryi.*

	S. henryi subsp. *henryi*	*S. henryi* subsp. *yunnanensis*	*S. henryi* subsp. *marginalis*	*S. longipes*
Shape of young branches	conspicuously winged	angled or narrowly winged	angled or narrowly winged	angled or narrowly winged
Perule size and persistence	large, persistent (at least until fruiting stage)	medium sized, variably persistent	medium sized, variably persistent	medium sized, variably persistent
Leaf pubescence	glabrous	glabrous	glabrous	main veins on abaxial lamina slightly pubescent
Leaf glaucescence	variably glaucescent	not glaucescent	variably glaucescent	variably glaucescent
Flower color	yellow	yellow and red, or orange	yellow	yellow
Number of tepals (male flowers)	6–7 (–8)	8–10	6–7	6–7
Number of stamens	23–46	24–34	12–19	18–28
Structure of seed coat	rugulose, rarely tuberculate	rugulose to tuberculate	rugulose to very tuberculate	(very) tuberculate

Lateral branches conspicuously winged, with (semi-) persistent perules at base. Leaf laminas variably glaucescent on abaxial surface. Flowers with 6–7 (–8) tepals (male flowers); perianth yellow. Male flowers with androecium of 23–46 stamens. Seed testa rugulose, rarely tuberculate. Figs. 1A, 2F.

Illustrations. Cheng (1944a: pl. 70, as "*S. henryi*"); Law (1996a: fig. 73, 1–12, as "*S. henryi* var. *henryi*").

Phenology. Flowering from April to August; fruits maturing from August to October.

Distribution (Fig. 35). Widespread in central and southern China (Guangxi, Guizhou, Henan, Hubei, Hunan, Jiangxi, Sichuan, and Yunnan); scandent or climbing in thickets and mixed and evergreen forests, often in heavily shaded areas; (450–) 750–2100 m.

ADDITIONAL SPECIMENS EXAMINED. **China.** GUANGXI: Tsin Hung Shan, N Hin Yen, *R. C. Ching 6994* (A, NY, UC); Tsz Yuen District, *Z. S. Chung 83594* (A); Ling Wan District, *S. K. Lau 28461* (A); Ling Wun, *S. K. Lau 28629* (A); Damioashan [Jingxiu], *Q. H. Lu 2540* (IBSC); Yao Shan, Ping Nan, Luo-Yun, Luo-Yun-wei, *C. Wang 39328* (A, MO); [precise locality not known], *C. Wang 40988* (A).—GUIZHOU: between Kweiting [Guiding] & Tuyün [Duyun], *H. F. von Handel-Mazzetti 195* (A); Yinjiang Xian, Huguoshi, in valley above Zhangjiaba on the W side of the Fanjing Shan mountain range, *Sino-American Guizhou Botanical Expedition 1406* (A, NY, MO); Liang Feng Yah, *A. N. Steward, C. Y. Chiao & H. C. Cheo 132* (A, NY); Rsao-Feng-San, Tsingchen, *S. W. Teng 90618* (A, MO); Tungtze, *Y. Tsiang 5152* (NY, UC); Tuyun, along trail across ridge, *Y. Tsiang 5673* (NY).—HENAN: Ru-yuan County, Qing-qi-dong, Ji-gong-keng, *X. G. Liu 28955* (MO).—HUBEI: [precise locality not known], *A. Henry 1225* (A), *6226* (GH); Maoba, Xianen, *H. J. Li 2432* (IBSC); [precise locality not known], Jul 1905, *E. H. Wilson s.n.* (K).—HUNAN: Ling-ling, Yang-ming-shan, Tang-gong Temple, *S. H. Chun 574* (MO); Yang-Shan, Changning Hsien, *C. S. Fan & Y. Y. Li 280* (A, L); Yün-schan, Wukang, *H. F. von Handel-Mazzetti 735* [*12062*] (A).—JIANGXI: Wu Gong Shan, *X. M. Gao 1682* (MO); Dangshan, Fenyi city, *K. Yao 9514* (NY).—SICHUAN: Dujiangyan Municipality [Guan Xian], Lingyan Mt., *D. E. Boufford, B. Bartholomew,*

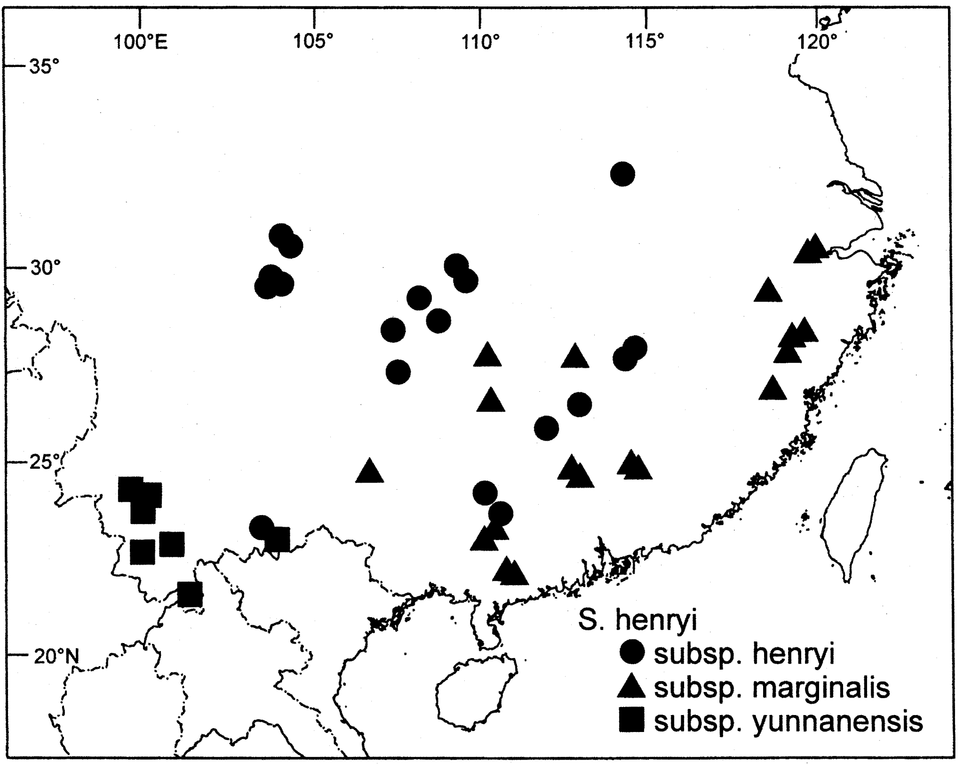


FIG. 35. Distribution of *Schisandra henryi* subsp. *henryi*, subsp. *yunnanensis,* and subsp. *marginalis.*

G. Li & G. H. Zhu 24074 (A, NY); Omei Shan [Emei Shan], *C. Y. Chiao & C. S. Fan 230* (A), *773* (A); Mt. Omei [Emei Shan], Hungchunp'ing, *H.-C. Chow 7522* (A); Mt. Omei [Emei Shan], Chutien, *H.-C. Chow 9932* (A); Mt. Omei [Emei Shan], *H.-C. Chow 11629* (A), *12010* (A); Chung Hsien, *W. P. Fang 429* (A); Nanchuan-hsien, *W. P. Fang 1116* (A), *1121* (A); Omei-hsien [Emei Xian], *W. P. Fang 16853* (A); Mt. Omei [Emei Shan], *F. T. Wang 23221* (A); Guan Xian, Lingyanshan, *Z. T. Wang et al. 870073* (MO, NY); Mt. Omei [Emei Shan], *E. H. Wilson 4722* (A, K).—YUNNAN: Megze [Mengzi], *A. Henry 9193* (A, K); S of Red River, from Manmei, *A. Henry 9193A* (A, K; paratypes of *S. elongata* var. *longissima*).

Cultivated. "Hort. Veitch, June 1911" [Hubei and Sichuan, fide Clarke 1905], *E. H. Wilson 710* (A, K; grown from type plant of *S. henryi* Clarke).

15b. Schisandra henryi subspecies **yunnanensis** (A. C. Smith) R. M. K. Saunders, stat. nov. *Schisandra henryi* var. *yunnanensis* A. C. Smith, Sargentia 7: 116. 1947.—TYPE: CHINA. Yunnan: mountains E of Szemao [Simao], southern Yünnan, 30 May [no year given], *A. Henry 12022* (holotype: A!; isotypes: NY! US).

Lateral branches narrowly winged, with variably persistent perules at base. Leaf laminas not glaucescent. Flowers with 8–10 tepals (male flowers); perianth yellow (outer tepals) and red (inner tepals), or orange. Male flowers with androecium of 24–34 stamens. Seed testa rugulose to tuberculate.

Illustrations. Law (1996a: fig. 73, 13–29, as "*S. henryi* var. *yunnanensis*").

Phenology. Flowering in May and June; fruits maturing from July to October.

Distribution (Fig. 35). Endemic to Yunnan, China; scandent or climbing in thickets and woods, generally in ravines and by streams; 1100–1800 (–2300) m.

ADDITIONAL SPECIMENS EXAMINED. **China.** YUNNAN: Szemao [Simao], *A. Henry 12022A*, pro parte (NY), *12022B* (A, K, NY); Kien-shuei Hsien [P'ing-pien Hsien], *H. T. Tsai 53321* (A), *55101* (A), *55188* (A), *55192* (A), *60058* (A), *60191* (A), *60230* (A), *60462* (A), *60597* (A), *60658* (A), *61106* (A), *61561* (A), *62241* (A); Mengla Xian, *Z. H. Tsi 91-225* (MO); Fo-Hai, *C. W. Wang 73810* (A); Lan-Tsang Hsien, *C. W. Wang 76484* (A), *76601* (A), *76756* (A); Meng-soong, Dah-meng-lung, Che-li Hsien, *C. W. Wang 77996* (A); Shunning, *T. T. Yü 16093* (A); Mienning, Wenpishan, *T. T. Yü 17763* (A); Mienning, Poshang, *T. T. Yü 18069* (A).

15c. Schisandra henryi subspecies **marginalis** (A. C. Smith) R. M. K. Saunders, stat. nov. *Schisandra henryi* var. *marginalis* A. C. Smith, Sargentia 7: 115. 1947.—TYPE: CHINA. Chekiang [Zhejiang]: 50 li north of Hsien-chü (Siachu), 22–25 May 1924, *R. C. Ching 1606* (holotype: A!; isotypes: E! UC! US).

Lateral branches narrowly winged, with variably persistent perules at base. Leaf laminas variably glaucescent on abaxial surface. Flowers with 6–7 tepals (male flowers); perianth yellow. Male flowers with androecium of 12–19 stamens. Seed testa rugulose to very tuberculate. Figs. 3A, 5D, 7C, D.

Phenology. Flowering in April and May; fruits maturing from July to October.

Distribution (Fig. 35). Widespread in southern and southeastern China (Fujian, Guangdong, Guangxi, Hunan, and Zhejiang); scandent or climbing in sparse woodland or shrubland; 650–1500 (–1800) m.

ADDITIONAL SPECIMENS EXAMINED. **China.** FUJIAN: Nan-ping city, Mang-dang-shan, *G. S. He 6270* (MO).—GUANGDONG: Zhu-tou-qiang, Nan-xiong, *S. P. Ko 50748* (MO); Xinyi County, *S. P. Ko 51301* (IBSC); Bai-mang-xiang, Ban-gou, Long-gui-zhai, Lian-nan County, *P. X. Tan 58965* (IBSC, MO); Nangxong County, *L. Tang 6171* (IBSC); Li-fu, Yang-shan County, 22 Jul 1936, *L. Teng s.n.* (MO); Da-yin-ding, Xin-yi County, *Z. M. Wu 218* (MO).—GUANGXI: San-fang-qu, Luo-gang-xiang, Jiu-wan-da-shan, Da-sha-tun, Da-miao-shan County, *T. C. Chen 658* (MO); N Luchen, Miu Shan, In-Tung, near border with Guizhou, *R. C. Ching 6236* (A, UC); Da-miao-shan, San-fang-qu, Chi-dong-xiang, Jiu-wan-shan, Yu-Long, *S. H. Chun 14631* (MO); Da-miao-shan, Gan-dong, Tong-lian-xiang, Jiu-wan-shan, Zhuan-lin, Jiang-shan, *S. H. Chun 15576* (MO).—HUNAN: Heng-shan, Nan-yue, Cang-jing-dian, *S. H. Chun 3305* (MO); Mang-shan, Jiu-zhu-hang, *M. X. Huang 111962* (MO); Hengshan [Nanyue Mt.], *Q. Lin 974* (HKU), *977* (HKU); Wu-lang-qi, Zhi-jiang County, *P. X. Tan 62490* (MO); Chengbu, *P. X. Tan 63656* (IBSC); Heng-shan, Nan-yue City to Ma-ji-si, *H. D. Zhang 3172* (MO).—ZHEJIANG: Long-quan, Feng-yang-shan, *S. Y. Chang 3300* (MO); Qing-yuan, Long-gong, *S. Y. Chang 3489* (MO); Rui-an, river to S of Shi-ping-keng, *S. Y. Chang 4468* (MO); [precise locality not known], *S. Chen 660* (A); Ping-tou-chuan, Kwang-wan, *R. C. Ching 2336* (A); Lin-an, Chang-hua, *P. L. Chiu 493* (MO); Kai-hua, Gu-tian-shan logging site, *P. L. Chiu 761* (MO); Lin-an, Chang-hua, *P. L. Chiu 809* (MO); Lin-au, *Hangzhou Botanic Garden Herbarium 26943* (MO); Tian-mu-shan, Heng-tang, *Hangzhou Botanic Garden Herbarium 30942* (MO); Feng Yang Mt., *H. Y. Zou 433* (A).

16. Schisandra longipes (Merrill & Chun) R. M. K. Saunders, stat. et comb. nov. *Schisandra sphenanthera* var. *longipes* Merrill & Chun, Sunyatsenia 2: 5. 1934. *Schisandra henryi* var. *longipes* (Merrill & Chun) A. C. Smith, Sargentia 7: 115. 1947.—TYPE: CHINA. Kwangtung [Guangdong]: Lochong/Lo-ch'ang, 14 Apr 1930, *C. L. Tso 20530* (lectotype, here designated: NY!; isolectotype: NY!).

Woody vines, apparently dioecious (but probably monoecious). Lateral branches conspicuously angled or narrowly winged, with variably persistent perules at base; branches continuing growth in subsequent years. Leaf laminas (7.5–) 8–11.5 (–13) cm long, (3.5–)

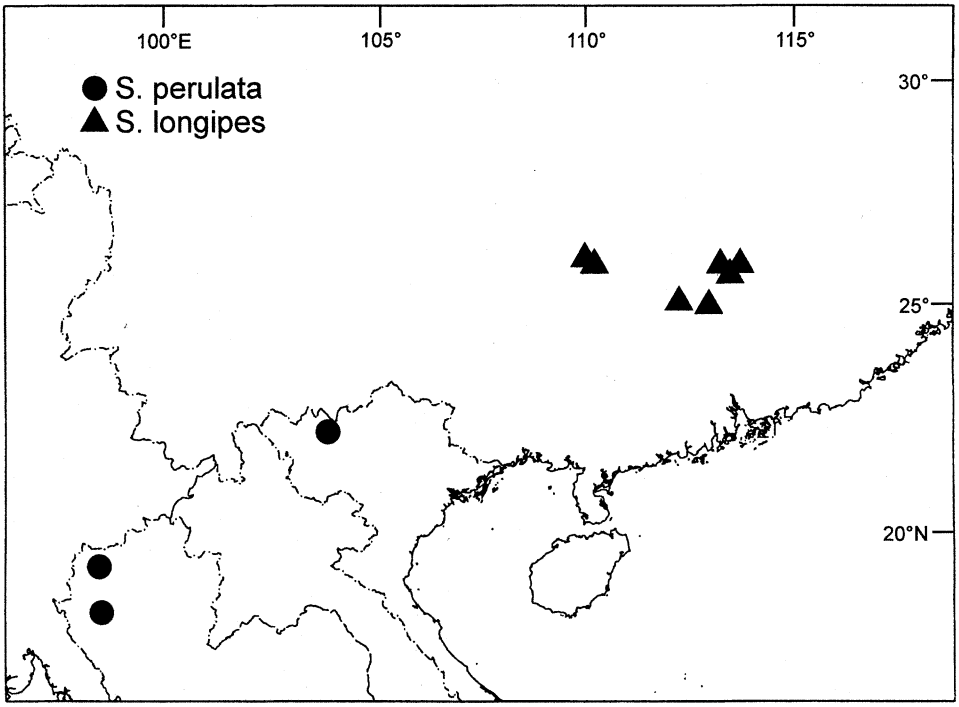


FIG. 36. Distribution of *Schisandra perulata* and *S. longipes*.

4.5–6.5 (–7.5) cm wide, length:width ratio 1.4–1.9 (–2.5), papyraceous, rarely thin-papyraceous or subcoriaceous, (20–) 40–50 (–80) µm thick, abaxial lamina surface glabrous except for pubescent primary and secondary veins, variably glaucescent, elliptic to ovate; primary vein ± plane to slightly impressed above, ± plane to slightly prominent below; secondary veins (4–) 5–6 (–7) pairs per leaf, (slightly) arcuate; base acute (younger leaves) to obtuse or truncate (older leaves); apex acuminate; margin (sinuous-) denticulate, 7–11 (–13) teeth per side of leaf; petioles glabrous, (19–) 24–41 (–59) mm long, (0.6–) 0.8–1.5 (–1.8) mm in diameter. Flowers borne in axils of (semi-) persistent perules at the base of young shoots or in axils of leaves, solitary; tepals 6–7 (male flowers), 6–8 (female flowers); tepals light yellow, glabrous; outermost tepal elliptic, 5.7–9.9 mm long, 3.2–7.5 mm wide, length:width ratio 1.1–1.8; innermost tepal (round-) elliptic to obovate, 4.7–7.9 mm long, 3.9–5.0 mm wide, length:width ratio 1.1–1.3; largest tepal round to elliptic, 7.6–10.8 mm long, 6.0–10.4 mm wide, length:width ratio 0.9–1.5; outermost tepal slightly reduced or not reduced, 0.7–1.0 of length of largest; innermost tepal (slightly) reduced, 0.4–0.8 of length of largest; peduncles glabrous, 23–48 mm long, 0.4–0.7 mm in diameter (male flowers), 54–71 mm long, 0.6–0.9 mm in diameter (female flowers). Male flowers with androecium of 18–28 essentially free stamens, uppermost stamens generally only partially differentiated, appearing connate, forming a carnose mass, with marginal thecae; thecae of free stamens introrse-lateral; pollen hexacolpate. Female flowers with gynoecium of 36–55 free carpels, gynoecium ca. 5.3–5.5 mm in diameter; carpels 1.4–2.8 mm long, 0.5–0.9 mm wide, length:width ratio (2.0–) 3.0–3.5; pseudostyle elongated, narrow. Fruit peduncles glabrous, elongated, 7.5–13.5 cm long, (0.3–) 0.7–1.0 mm wide; torus 7.5–10.5 cm long, 1.5–1.8 mm wide; apocarps red, 2.5–6 mm long, 2.5–4.5 mm wide, length:width ratio 1.0–1.9. Seeds 1–2 per apocarp, (discoid-) flattened-reniform, 3.1–3.5 mm long, 3.4–3.9 mm wide, length:width ratio ca. 0.9; testa (very) tuberculate. Chromosome number unknown. Figs. 15C, 15F.

Illustrations. Huang (1987: fig. 26, as "*S. henryi* var. *longipes*").

Phenology. Flowering in April and May; fruits maturing in July and August.

Distribution (Fig. 36). Endemic to China (northern Guangdong and northern Guangxi); scandent or climbing in dense or sparse woodlands, often near streams; 500–1400 m.

ADDITIONAL SPECIMENS EXAMINED. **China.** GUANGDONG: Ling-bei Gong-she, Cheng-su-chang-qiao, Lian-yang County, *Y. Q. Chen 170354* (MO); Le-chang, Jiu-zhao, *S. H. Chun 3142* (HKU, IBSC, MO); Dalingjiao, Ruyuan, *S. P. Ko 53043* (IBSC); Zhongshan, Dongxiang, Lechang, *S. P. Ko 54551* (IBSC); Luo-yang-xiang, Ban-feng-shan, Ru-wen County, *Y. G. Liu 596* (MO); Cheng-jia, Le-yu-chang, Jia-heng, San-cha-song, Yang-shan County, *P. X. Tang & X. X. Huang 354* (IBSC, MO); Lok Chong, Lechang County, *C. L. Tso 20679* (HK, NY; paratypes of *S. sphenanthera* var. *longipes*); Hong-qi-gong-she, Jiu-feng, Le-chang County, *S. Z. Wu 70033* (MO); Wuzhishan, Ruyuan, *Yue-71 Expedition 543* (IBSC).—GUANGXI: Long-sheng, Da-di-xiang, Yao-ren-chong, *Guang Fu Forest Team 231* (MO); Dadi, Longshen, *H. F. Qing & Z. T. Li 70010* (IBSC).

Schisandra longipes was first described by Merrill and Chun (1934) as a variety of Rehder and Wilson's broadly conceived species *S. sphenanthera*. Smith (1947: 115–116) correctly determined that the true affinities lay with *S. perulata* and *S. henryi*, however, and accordingly transferred it to *S. henryi* as a variety. The diagnostic characters distinguishing *S. longipes* from *S. henryi* sensu stricto include qualitative differences in indumentum: *S. longipes* has a dense covering of short hairs on the midrib and secondary veins on the abaxial leaf lamina, whereas *S. henryi* sensu stricto is entirely glabrous. This difference is absolute and easily determined, and no specimens with intermediate morphology have been observed. Recognition at the specific rank is consequently consistent with the phylogenetic species concept (sensu Luckow 1995). Other differences between the two species include peduncle length of female flowers (32–47 mm in *S. henryi*, 54–71 mm in *S. longipes*), and apocarp size [4.5–8.5 (–9.5) × (3.0–) 3.5–6.5 (–7.5) mm in *S. henryi*, 2.5–6.0 × 2.5–4.5 mm in *S. longipes*].

Merrill and Chun's (1934) circumscription of *S. sphenanthera* var. *longipes* was rather confused. They cited two paratype collections that do not represent *S. longipes*, viz. *W. P. Fang 1395* (A! NY!) and *2171* (A! NY!); these specimens have been determined as belonging to *S. pubescens* and *S. pubinervis*, respectively.

17. Schisandra perulata Gagnepain in Humbert, Fl. gén. Indo-Chine (suppl.) 1: 55. 1938.—TYPE: VIETNAM. Tonkin: Lo Lui Ho, near Cha Pa, Aug 1933, *A. Pételot 4788* (lectotype, here designated: P!; isolectotype: NY!, photo: HKU!).

Woody vines, apparently dioecious (but probably monoecious). Lateral branches conspicuously winged, with (semi-) persistent perules at base; branches with extensive growth in subsequent years, resulting in long internodes. Leaf laminas (10–) 12–14.5 (–16.5) cm long, (4.5–) 6.5–8.5 (–10) cm wide, length:width ratio 1.5–2.3, (thin-) papyraceous, 30–70 μm thick, glabrous, elliptic to ovate; primary vein ± plane above, slightly prominent below; secondary veins 4–6 (–7) pairs per leaf, (slightly) arcuate; base acute (younger leaves) to obtuse (older leaves); apex (short-) acuminate; margin (sub-) entire to denticulate or serrulate, 0–12 teeth per side of leaf; petioles glabrous, 16–40 mm long, 0.9–2.1 mm in diameter. Flowers borne in axils of fugaceous bracts at the base of young shoots or in axils of leaves, solitary; tepals 7–8 (male flowers); tepals yellow or red, glabrous; outermost tepal ovate, ca. 6.5 mm long, ca. 5.0 mm wide, length:width ratio ca. 1.3; innermost tepal obovate, ca. 5.3 mm long, ca. 3.5 mm wide, length:width ratio ca. 1.5; largest tepal ovate, ca. 8.4 mm long, ca. 5.3 mm wide, length:width ratio ca. 1.6; outermost tepal slightly reduced, ca. 0.8 of length of largest; innermost tepal reduced, ca. 0.6 of length of largest; peduncles glabrous, 26–66 (–88) mm long, 0.5–0.8 (–1.2) mm in diameter (male flowers). Male flowers with androecium of 22–30 essentially free stamens, uppermost stamens generally only partially differentiated, appearing connate, forming a carnose mass, with marginal thecae; androecium ca. 7–9 mm in diameter; thecae of free stamens introrse-lateral; pollen hexacolpate. Female flowers not seen. Fruit peduncles glabrous, ca. 12–14 cm long, ca. 1.2–1.6 mm wide; torus ca. 12–14 cm long, ca. 2.8–3.4 mm wide; apocarps red, ca. 9–12 mm long, ca. 8.5–13 mm wide, length:width ratio ca. 0.9–1.3. Seeds 1–3 per apocarp, discoid, ca. 3.7–4.5 mm long, ca. 3.9–4.5 mm wide, length:width ratio ca. 0.9–1.2; testa rugulose. Chromosome number unknown.

Illustrations. Gagnepain (1938: fig. 6, 3–4).

Phenology. Information is sparse due to the limited number of collections; available information indicates that *S. perulata* is in fruit in August.

Distribution (Fig. 36). Northern Thailand and northern Vietnam; scandent or climbing in evergreen forests; 1400–1500 m.

ADDITIONAL SPECIMENS EXAMINED. **Thailand.** Mae Soi ridge, Mae Soi Subdistrict, Jawa Tong District, Chiang Mai Province, *J. F. Maxwell 92-211* (E, GH); Nae Hong Son, Pai, near Doi Chang, *T. Santisuk 1108* (A). **Vietnam.** Chapa, Apr 1925, *A. Pételot s.n.* (A, P; paratypes of *S. perulata*).

Schisandra perulata is closely related to *S. henryi* and *S. longipes*, with which it forms a well-supported clade (Fig. 20), defined by the synapomorphic possession of large, persistent perules on lateral branches, and branches that are distinctly winged. *Schisandra perulata* and *S. henryi* can easily be distinguished, however, by reference to the following characters: leaf lamina size [(10–) 12–14.5 (–16.5) × (4.5–) 6.5–8.5 (–10) cm in *S. perulata*, (5.5–) 7.5–11.5 (–14) × (3–) 4.5–7.5 (–9) cm in *S. henryi*]; length of fruit peduncle [ca. 12–14 cm in *S. perulata*, (3.5–) 6–10 (–14.5) cm in *S. henryi*]; length of fruiting tori [ca. 12–14 cm in *S. perulata*, (1.5–) 3.5–10.5 (–11) cm in *S. henryi*]; and apocarp size [ca. 9.0–12.0 × ca. 8.5–13.0 mm in *S. perulata*, 4.5–8.5 (–9.5) × (3.0–) 3.5–6.5 (–7.5) mm in *S. henryi*]. *Schisandra perulata* leaves are also typically more thinly papyraceous and have a more intricate pattern of venation. *Schisandra perulata* is readily separated from *S. longipes* by the absence of hairs on the primary and secondary veins on the abaxial leaf surface.

The secondary xylem of *S. perulata* has been described and illustrated by Lemesle (1946, 1953, 1956) and the pollen by Praglowski (1976).

III. **Schisandra** subgenus **Schisandra.**

Woody vines. Male flowers with androecium of (4–) 5–18 stamens, with some degree of fusion, either restricted to base of filament or of entire stamens; thecae lateral; pollen hexacolpate. Female flowers with gynoecium of 12–75 free carpels; pseudostyles narrow and subulate, or slightly broadened. Seed testa rugulose or tuberculate.

Distribution (Fig. 17C–E). China (Guangxi, Hebei, Hunan, Jilin, Liaoning, Nei Mongol, Shanxi, Yunnan, and Zhejiang), Japan, Korea, Russia (Amurskaya Oblast', Khabarovskiy Kray, Primorskiy Kray, and Sakhalinskaya Oblast'), U.S.A. (Alabama, Arkansas, Florida, Georgia, Louisiana, Mississippi, North Carolina, South Carolina, and Tennessee), and Mexico (Hidalgo).

IIIa. Schisandra section **Maximowiczia** (Ruprecht) Nakai, Fl. sylv. Koreana 20: 101. 1933 (as "*Schizandra*"). *Maximowiczia* Ruprecht in Maximowicz, Bull. Cl. Phys.-Math. Acad. Imp. Sci. Saint-Pétersbourg 15: 142. 1856, non *Maximowiczia* Cogniaux, 1881 (Cucurbitaceae). *Schisandra* subg. *Maximowiczia* (Ruprecht) Y.-W. Law, Fl. Reipubl. Popularis Sin. 30(1): 250, 272. 1996.—TYPE: *Schisandra chinensis* (Turczaninow) Baillon.

Woody vines. Male flowers with androecium of (4–) 5 (–7) stamens, apparently free, although base of filaments probably ± connate; thecae extrorse-lateral; pollen hexacolpate. Female flowers with gynoecium of 14–40 free carpels; pseudostyles variably narrow and subulate to slightly broadened. Seed testa smooth.

Distribution (Fig. 17E). China (Hebei, Jilin, Liaoning, Nei Mongol, and Shanxi), Korea, Russia (Amurskaya Oblast', Khabarovskiy Kray, Primorskiy Kray, and Sakhalinskaya Oblast'), and Japan (Hokkaido and Honshu).

Various orthographic variants of the generic name *Maximowiczia* have been published, including *Maximovitzia*, *Maximowiczia,* and *Maximowitschia* (see Smith 1947: 136).

18. Schisandra chinensis (Turczaninow) Baillon, Hist. pl. 1: 148. 1868 (as "*Schizandra*"). *Kadsura chinensis* Turczaninow, Bull. Soc. Imp. Naturalistes Moscou 7: 149. 1837. *Maximowiczia chinensis* (Turczaninow) Ruprecht ex Maximowicz, Mém. Acad. Imp. Sci. Saint-Pétersbourg, ser. 6, Sci. Math., Seconde Pt. Sci. Nat. 9: 31. 1859. *Schisandra chinensis* var. *typica* Nakai, Fl. sylv. Koreana 20: 105. 1933 (as "*Schizandra*").—TYPE: CHINA. [precise locality not known], [date not known], *P. Y. Kirolov s.n.* (holotype: KW).

Maximowiczia amurensis Ruprecht in Maximowicz, Bull. Cl. Phys.-Math. Acad. Imp. Sci. Saint-Pétersbourg 15: 124. 1856 [reprinted in Mélanges Biol. Bull. Phys.-Math. Acad. Imp. Sci. Saint-Pétersbourg 2: 412. 1856].—TYPE: RUSSIA. "Am mittleren und südlichen Amur," [date not known], *C. J. Maximowicz s.n.* (holotype: LE; isotypes: GH, K! NY).

Sphaerostema japonicum A. Gray, Mem. Amer. Acad. Arts, n.s. 6: 380. 1859.—TYPE: JAPAN. Hakodate, Oshima, Jun 1855, *C. Wright s.n.* (holotype: GH; isotypes: K! L! NY, photo of L isotype: HKU!).

? *Maximowiczia sinensis* W. Robinson, Garden 6: 583. 1874.—TYPE: RUSSIA. Amur, [date not known], *M. O. Putz* s.n. (holotype: not located).

Schisandra chinensis var. *leucocarpa* P. H. Huang & L. H. Zhou in L. H. Zhou et al., Bull. Bot. Res., Harbin 14: 35. 1994.—TYPE: CHINA. Heilongjiang: Tieli Forestry Bureau, Jiu-lian Forest, 10 Aug 1993, *P.-H. Huang 93150* (holotype: not located).

Woody vines, monoecious (often appearing dioecious). Lateral branches lacking wings, with fugaceous perules at base; branches continuing growth in subsequent years.

Leaf laminas (4.5–) 5.5–8 (–10.5) cm long, (2.5–) 3.5–5 (–6.5) cm wide, length:width ratio (1.2–) 1.4–2.1 (–2.7), (thin-) papyraceous, 20–30 (–60) μm thick, glabrous or rarely sparsely pubescent on primary and secondary veins adaxially, elliptic to obovate; primary vein slightly impressed to ± plane above, slightly prominent to ± plane below; secondary veins (3–) 4–6 (–7) pairs per leaf, (slightly) arcuate; base acute to attenuate (occasionally obtuse in older leaves); apex short-acuminate; margin denticulate to (sinuous-) serrulate, (5–) 6–10 (–16) teeth per side of leaf; petioles glabrous, (9–) 11–23 (–40) mm long, (0.4–) 0.6–1.1 (–1.6) mm in diameter. Flowers borne in axils of fugaceous bracts at the base of young shoots, solitary; tepals (5–) 6–8 (–9) (male flowers), 7–9 (female flowers); tepals white to yellow, glabrous; outermost tepal narrowly elliptic, ovate, or obovate, 5.5–10.0 mm long, 2.2–4.2 mm wide, length:width ratio 1.4–3.9; innermost tepal narrowly elliptic or ovate, occasionally ± obovate-elliptic, 4.5–9.5 mm long, 1.1–3.1 mm wide, length:width ratio 2.2–4.9 (–7.8); largest tepal narrowly elliptic or ovate, occasionally ± obovate, 6.5–10.1 (–11.1) mm long, 2.1–4.8 mm wide, length:width ratio 1.8–3.6 (–5.3); outermost tepal (slightly) reduced, 0.6–1 of length of largest; innermost tepal slightly reduced, 0.6–1 of length of largest; peduncles glabrous, (6–) 11–20 (–28) mm long, (0.2–) 0.3–0.6 mm in diameter (male flowers), (7–) 25–35 mm long, 0.3–0.6 (–0.9) mm in diameter (female flowers). Male flowers with androecium of (4–) 5 (–7) stamens, apparently free, although base of filaments probably ± connate, stamens occasionally with connective extending beyond apex of thecae; thecae extrorse-lateral; pollen hexacolpate. Female flowers with gynoecium of 14–40 free carpels, gynoecium ca. 2.7–4 mm in diameter; carpels 1–1.8 mm long, 0.8–1 mm wide, length:width ratio 1.1–1.7; pseudostyle variably narrow to slightly broadened. Fruit peduncles glabrous, slightly elongated, 2–4.5 (–7.5) cm long, 0.5–0.8 mm wide; torus (1.5–) 2–6 (–9.5) cm long, 0.7–1.2 (–1.7) mm wide; apocarps (pinkish) red, 5–7.5 mm long, 4–5 (–6) mm wide, length:width ratio 1.1–1.4. Seeds 1–2 per apocarp, flattened-reniform, rarely round, (2.9–) 3.2–3.8 (–4) mm long, (3.6–) 4.4–4.8 (–5) mm wide, length:width ratio (0.6–) 0.7–0.8 (–0.9); testa smooth. Chromosome number: 2n = 24, 28 (see Appendix 1). Figs. 4A–D, 5C, 8C, 10A, B, 13C, 14A, 14D, 16C, 37.

Selected illustrations. Maximowicz (1859: fig. 1, as "*Maximowiczia chinensis*"); Nakai (1933: fig. 20, as "*Schizandra chinensis*"); Smith (1947: fig. 24); Wang (1980: fig. 1600); Law (1983b: fig. 187; 1996a: fig. 72, 12–20); Lo (1994: fig. 129).

Phenology. Flowering from May to July; fruits ripening in August and September (less commonly from July on) (see also Zhang et al. 1993).

Distribution (Fig. 38). North-eastern China (Hebei, Heilongjiang, Jilin, Liaoning, Nei Mongol, and Shanxi), Korea, far-eastern Russia (Amurskaya Oblast', Khabarovskiy Kray, Primorskiy Kray, and Sakhalinskaya Oblast'), and northern Japan (Hokkaido and Honshu); comparatively common in wet temperate, deciduous, coniferous and mixed forests, often growing with *Acer*, *Celastrus*, *Corylus*, *Fraxinus*, *Juglans*, *Pinus*, *Quercus*, *Rhus*; 100–1800 m.

ADDITIONAL SPECIMENS EXAMINED. **China.** BEIJING MUNICIPALITY: Xiaolongmen, Mentougou, *S. Y. He et al. 813030* (A); Beijing, 1843, *Kirilow s.n.* (UC); Xiao Long Men, Men Tou Gou Qu, *Z. T. Wang et al. 213* (MO, NY).—HEBEI: Hsiaowutaishan, *K. S. Chow 74266* (A, MO, NY); Siao Wu Tai Shan, Shui Shih Tao, *J. Hers 2154* (A); Hsiaowutaishan, Tienlinsze, Chark'ar, *H. W. Kung 79* (NY); [precise locality not known], *C. F. Li 11173* (NY); Hsiao Wu Tai Shan, T'ieh lin ssu, *J. C. Liu 1919* (UC); Hsiao Wu-tai-shan, *F. N. Meyer 1347* (MO, NY); Weichang, *W. Purdom 117* (A); Hsiaowutaishan, *C. W. Wang 61754* (A).—JILIN: [precise locality not known], *F. H. Chen 402* (A); Tong Hwa [Tonghua] Hsien, *F. H. Chen 618* (A); Hsiao Lin, *P. H. Dorsett & J. H. Dorsett 4098* (A, NY, UC); Tang-ho-ko, Sungari River, to Hui Fa River, May–Aug 1886, *H. E. M. James s.n.*

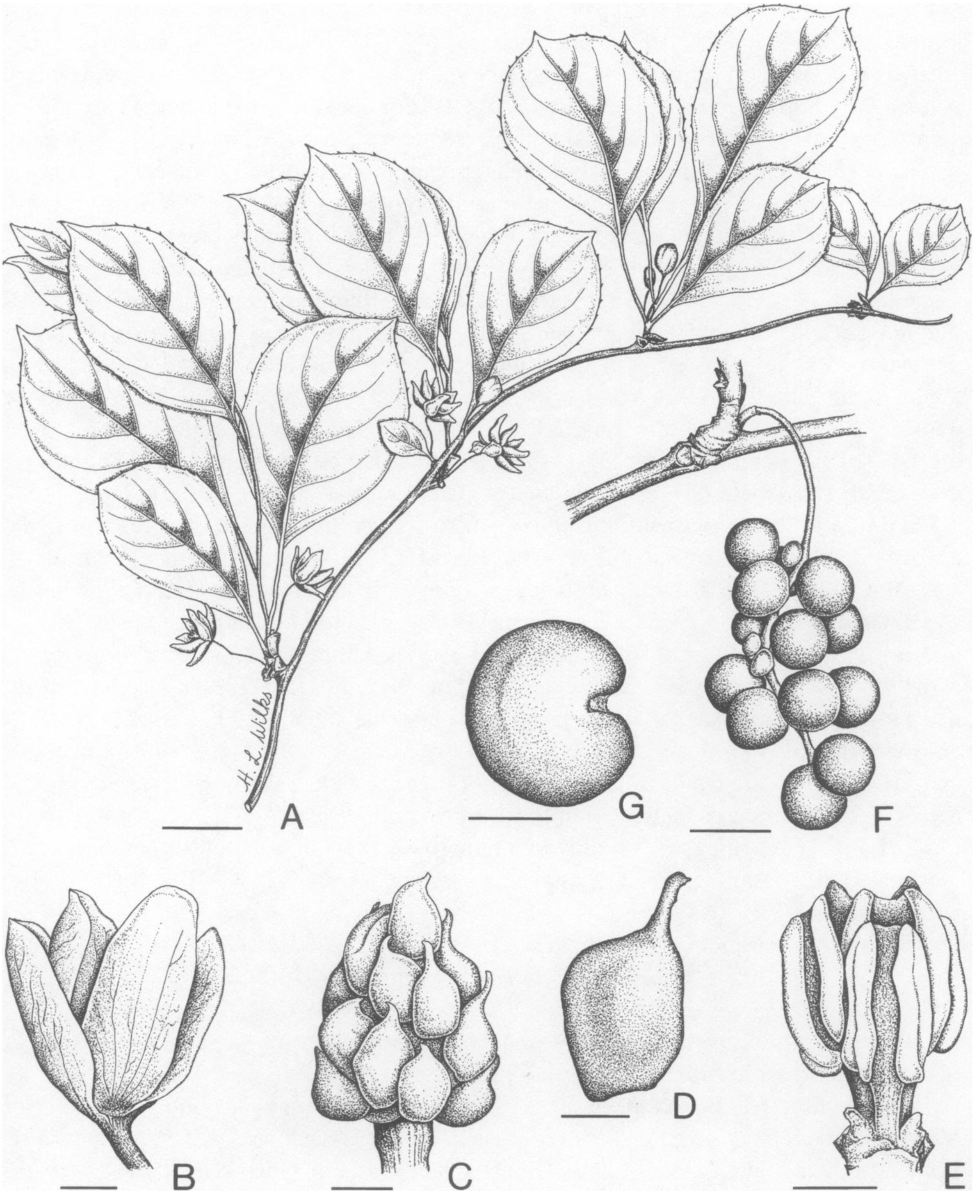


FIG. 37. *Schisandra chinensis* (*S.* subg. *Schisandra* sect. *Maximowiczia*). A, flowering branch. B, flower. C, gynoecium. D, isolated carpel (lateral view). E, androecium. F, fruit. G, seed. Scale bars: A, 2 cm; B, G, 2 mm; C, E, 1 mm; D, 500 μm; F, 1 cm. (A, *H. Takahashi 4079*, C; B, *H. Takahashi 1181*, C; C, D, *N. Palczevsky 3617*, C; E, *H. Takahashi 4079*, C; F, *H. Takahashi & O. Asahara 3716*, C; G, *J. Ohwi & K. Okamoto 1782*, C.) Drawing by H. L. Wilks.

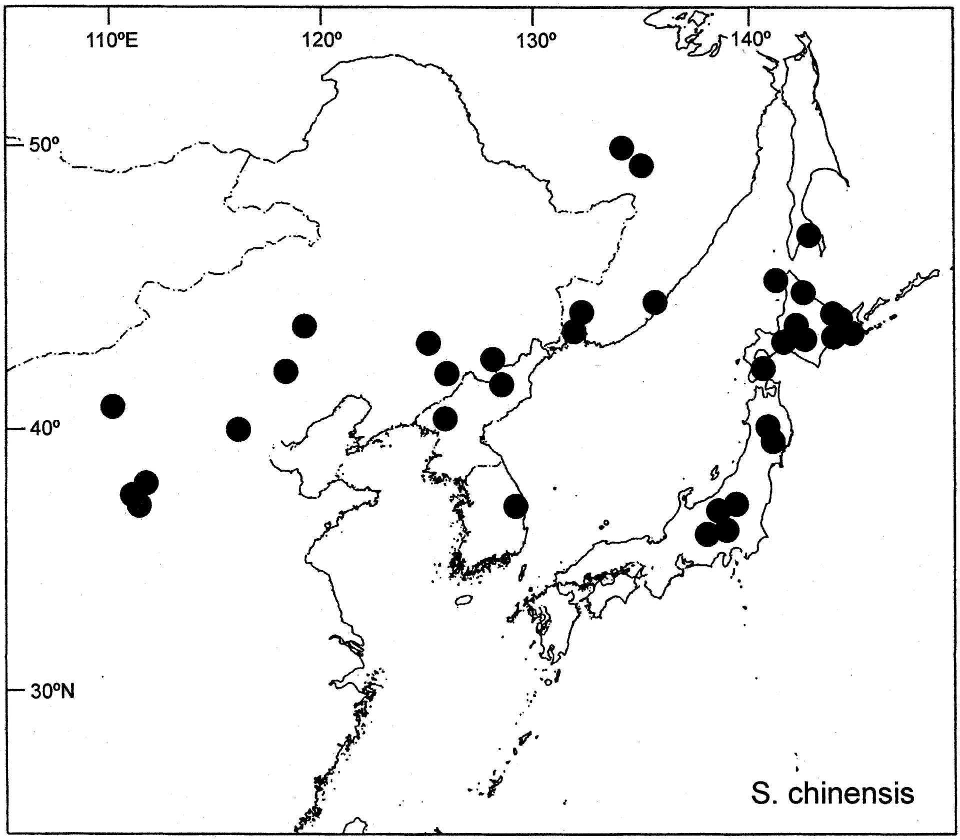


FIG. 38. Distribution of *Schisandra chinensis.*

(K); between Mukden and Tung-che-shien, May–Aug 1886, *H. E. M. James s.n.* (K); Lao-yeh Ling and other hills near Mukden, May–Aug 1886, *H. E. M. James s.n.* (K); Liao-tung pen, near Sta Vanfangoo, *D. Litvinov 1767* (NY); near Schitokhez Railroad Station, *D. Litvinov 2072* (A); Changbaishan, *B. B. Wan & K. S. Chow 81027* (MO, NY).—LIAONING: Gounaidian, ca. 35 km W of Qingyuan, *X. Li, H. Chang & Y. Wang s.n.* (HKU).—NEI MONGOL (INNER MONGOLIA): Jehol, *A. David 1839* (GH); Hu-he-hao, Da-qing-shan, *Q. R. Wu 78* (MO).—SHANXI: Si han, *E. Licent 2345* (K); Tsiliyü, Ho-schan, *E. Licent 12067* (A); Ch'o-mei-shan, Chieh-hsiu District, *H. Smith 5719* (A); Mien-shan, Lin-shih Hsien, *T. Tang 972* (A). **Japan.** HOKKAIDO: Sapporo, 11 Jun 1885, *Agricultural College, Sapporo s.n.* (A, NY); Jasankei [Jozankei], 21 Jul 1885, *Agricultural College, Sapporo s.n.* (A); Sapporo, Jun 1894, *Agricultural College, Sapporo s.n.* (A); near Hakodate, 1863, *Albrecht s.n.* (K, MO, NY; possible paratypes of *S. nigra*); [precise locality not known], 7 May 1903, *S. Arimoto s.n.* (GH); Sapporo, May 1903, *S. Arimoto s.n.* (GH); Jun 1903, *S. Arimoto s.n.* (MO); [precise locality not known], *W. P. Brooks 20* (UC); [precise locality not known], *W. P. Brooks 579* (UC); near Niniu, Shimukappu-mura, Yufutsu-gun, *K. Deguchi et al. 7524* (MO); Kiritappu, Hamanaka-cho, Atsukeshi-gun, *K. Deguchi 6454* (A, NY); Rishiri (NW of Hokkaido), *U. Faurie 3004* (UC); Biro, *U. Faurie 4774* (MO); Mt. Otara, *U. Faurie 6214* (UC); Hirowo-machi, mid-stream of Naka-hirowo-river, Tokachi Prov., *M. Furuse 6363* (MO); Itomuka-mine, Rubeshibe-choo, Tokoro-gun, Kitami Prov., *M. Furuse 6792* (MO); Moiwa, Satporo [Sapporo], 21 Jun 1908, *S. Itô s.n.* (K); 26 Sep 1904, *S. Itô s.n.* (K); Hakodate, 1861, *C. J. Maximowicz s.n.* (GH, K); Mt. Yubari, Minamifurano-cho, Sorachi-gun, *K. Mimoro & S. Tsugaru 4770* (A, MO); experimental forest of Tokyo University, Yamabe, Furano-shi, *K. Mimoro & S. Tsugaru 4836* (MO); Ohgawara, Miyagi Pref., *H. Muroi 4776* (A); Sapporo, Sep 1892, *C. S. Sargent s.n.* (A); Tokyo University Forest, Furano city, Yamabe, *K. Sohma & M. Takahashi 700* (A, MO); N side of Lake Onuma, Oshima Prov., *H. Takahashi 1181* (C); Tomakomai-shi, Tomakomaihigashi, Iburi Prov., *H. Takahashi 4079* (C); Tomakomai-shi, Numanohata, Iburi Prov., *H. Takahashi & O. Asahara 3716* (C); [precise locality not known], *T. Tanaka 294* (NY); Sapporo, Ishikari Prov., 23 Jun 1891, *Y. Tokubuchi s.n.* (MO); 28 Aug 1894, *Y. Tokubuchi s.n.* (UC); Senano & Nambu Prov., 1864–66, *Tschonoski s.n.* (GH, K); Mt. Bozu-yama, Hobetsu-cho, Yufutsugun, *S. Tsugaru 5080* (MO); Kitami Prov., *E. H. Wilson 7390* (A); Mt. Ooyama (Mombetsu-yama), Mometsu city, Abashiri Prov., *E. W. Wood & D. E. Boufford 3927* (A); Oshima, Hakodate, 1853–56, *C. Wright s.n.* (K).—HONSHU: near Oui-oshidashi-iwa, foot of Mt. Asaura, Nagano-ken, *R. K. Beattie & Y. Kurihara 10104* (A); between Kitakaruizawa and Kose, *P. H. Dorsett & W. J. Morse 874* (NY); Hayashino, *U. Faurie 6913* (A); Kita-koma-gun, Kiyosato-mura, Nenjho-ga-hara, Kai Prov., 7 Jun 1954, *M. Furuse s.n.* (A); Mikuni-tooge and Mikuni-tooge road, Azusayama Kawakami-mura Minami-saku-gun, Nagano Pref., Shinano Prov., 4 Sep 1960, *M. Furuse s.n.* (A); Minami-saku-gun, Kawakami-mura, Mt. Temgu, Nagano Pref., Shinano Prov., 22 May 1961, *M. Furuse s.n.* (A); Kakuma-tooge Osa-mura Chiisagata-gun, Shinano Prov., *M. Furuse 20507* (UC); Agatuma-gun, Rokurigahara, Gumma Pref., *K. Hasegawa 10393* (A); Minamiazumi-gun, Nagawa-mura, Kawaura, Shinano Prov., *H. Kanai 3927* (A); Agatuma-gun, Kita-karuizawa, Gumma Pref., *H. Kanai 8672* (A); Suwa-gun, N slope of Mt. Nyugase, Nagano Pref., *H. Kanai, H. Ohashi, K. Hasegawa & K. Okubo 9658* (A); above Inago Hot Spring, foot of Mt. Yatsugatake, Nagano Pref., *T. Koyama 8063* (A); Kutsukake-Kose, Shinano Prov., *M. Mizushima 10161* (A, MO); Morioka, Mt. Iwayama, Iwate Pref., *H. Muroi 4335* (A); Azusayama, Shinano Prov., *J. Ohwi 254* (A, C, MO, NY, UC); Kose Spa, Shinano Prov., *J. Ohwi & K. Okamoto 1782* (C, MO); Mt. Eboshidake, Chiisagata-gun, Nagano Pref., 36°25′N, 138°20′E, *S. Suzuki 280* (A); foot of Mt. Komagatake, *H. Takeda 209* (K); Chino-shi, Idzumino, Nagano Pref., *M. Togashi 9768* (A); Misaka pass, Kai Prov., *E. H. Wilson 6924* (A, K); Yatsuga-dake, Kai Prov., *E. H. Wilson 7535* (A); Agatsuma-gun, Tsumagoi-mura, Nidoage, Gumma Pref., *T. Yahara et al. 7082* (A); Kitasaku-gun, Karuizawa-cho, Sengataki, Nagano Pref., 2 Jun 1983, *T. Yahara et al. s.n.* (A); Suwa-gun, Fujimimura, Mt. Kamanashi, Nagano Pref., *T. Yamazaki 1044* (A).—Precise locality not known: Wada Ioge, *J. Bisset 1399* (E); [locality not known], *J. Bisset 4562* (E); [locality not known], *U. Faurie 6988* (K); [locality not known], *Saku 5897* (K). **Korea.** [locality not known], *K. S. Gilbert 22* (A, UC); Kangkai, 30 May 1911, *R. G. Mills s.n.* (UC); *R. G. Mills 68* (K); Kyongsang Pukto, Pong-hwa Gun, 37°03′50″N, 129°02′40″E, *Plant Exploration in the Republic of Korea 291* (MO); Ha-zan, near Suigen, Keiki, *E. H. Wilson 8479* (A); French Mine, Taiyudo, N Heian, Heihoku, *E. H. Wilson 8665* (A); Pukchin & Takkou, N Heian, *E. H. Wilson 8701* (A); Kankyo, *E. H. Wilson 8860* (A); Tumen-Yalu divide, Hankyo, *E. H. Wilson 9065* (A); Yutenji, Kongo-san, Kogen, *E. H. Wilson 10497* (A). **Russian Federation.** AMURSKAYA OBLAST': Amur, 8 Aug 1895, *V. Komaròv s.n.* (A); Amur River, s.a., *C. J. Maximowicz s.n.* (K); [precise locality not known], s.a., *G. Radde s.n.* (NY).—KHABAROVSKIY KRAY: Slavyanka, ca. 200 km NE of Khabarovsk, Amur River, 49°28′N, 136°54′E, *T. S. Elias & D. Murray 11050* (NY); between Bolon and Odshalense (Chabarowsk district), *I. W. Kusnezow 211* (C).—PRIMORSKIY KRAY: Suifun River, Liucze-chesa Valley, S Ussuri Prov., *V. Komaròv 652* (K); near Nikolsk-Ussuriysk, Sui-fun River, 43°48′N, 131°57′E, 12 Jun 1915, *I. Kozlov s.n.* (UC); Ussuri River, s.a., *R. Maak s.n.* (GH, K); near Vladivostok, 1860, *C. J. Maximowicz s.n.* (MO); 1902, *N. Palczevsky s.n.* (A); *N. Palczevsky 3617* (A, C, MO, NY); near Kharkovka, 29 Aug 1916, *A. P. Shklyaeva, A. P. Radchenko & I. Kozlov s.n.* (UC); Vladivostok and vicinity, *D. L. Topping 2090* (A); *D. L. Topping 2107* (A); *D. L. Topping 2496* (A); coast of Manchuria, 44°–45°N, *C. Wilford 1057* (GH, K).—SAKHALINSKAYA OBLAST': Odomari, *P. H. Dorsett & W. J. Morse 1330* (A); Korsakof, *U. Faurie 497* (A, P); *U. Faurie 498* (A, P); Ohdomari, Karafuto, *K. Uno 19902* (A, NY); Toyohara, *E. H. Wilson 7346* (A).—Precise locality not known: 20 Jul 1891, *S. Korshinsky s.n.* (GH); Amur River, 1855, *R. Maack s.n.* (GH).

Cultivated. Hortus Botanicus Wageningen, Netherlands, *P. Goetghebeur 8858* [*HBW 80.BG.20403*] (HKU).

Schisandra chinensis is a highly distinctive species, and since it is the sole member of subg. *Schisandra* sect. *Maximowiczia* all the characteristics diagnostic at the sectional level are also diagnostic for the species. The flowers are diminutive, with small white or yellow tepals that are markedly elongate and have a length:width ratio of 1.4–4.9 (–7.8). Consonant with the small size of the flowers, the androecium is reduced to only (4–) 5 (–7) stamens; although this reduction mirrors that observed in subg. *Schisandra* sect. *Schisandra*, the stamens are held vertically in *S. chinensis* rather than radiating outwards to form a pentagonal "shield," as observed in sect. *Schisandra*. Apical extensions of the connective beyond the top of the thecae are common, although this variation is not taxonomically significant.

Zhou et al. (1994) described *S. chinensis* var. *leucocarpa* on the basis of the unusual development of white rather than red fruits. This taxon is only known from three consecutively numbered collections from a single locality in Heilongjiang Province, China. Although it appears to be naturally occurring and could possibly be recognized at the taxonomic rank of form, no formal recognition is accorded in the present monograph. Attempts at locating the holotype have been unsuccessful: it appears that the specimen was not deposited in the herbarium of the North-Eastern Forestry University in Harbin, Heilongjiang, as stated in the protologue (Zhou et al. 1994). Cultivars with albino fruits are also recorded for *Kadsura japonica* (L.) Dunal (Saunders 1998: 28).

Smith (1947: 139) noted that some of the Japanese vernacular names for *S. chinensis* suggest a Korean origin for the species. Tanaka (1895) furthermore stated that *S. chinensis* was introduced to Japan from Korea around 1717. Although there is no evidence to confirm that this species is not native to Japan, it is possible that it was introduced from China and Korea as a result of its significant medicinal properties (discussed under "Ethnobotany"). It is perhaps noteworthy that Mitsuhashi (1976) discovered references to the medicinal uses of *S. chinensis* by the Japanese Ainu race in 18th or 19th century texts; the traditional pharmacopoeia of the Ainu is highly distinct from that of other Japanese, and would possibly suggest that *S. chinensis* was already used medicinally prior to the Japanese occupation of Hokkaido.

Schisandra chinensis is only partly sympatric with one other species in the genus, *S. repanda*. These two species have highly distinct flowers, but confusion is possible if the specimens are sterile or fruiting; the differences are discussed under *S. repanda* (no. 20).

Ueda (1988) has studied the occurrence of dicliny in *S. chinensis*: although the species is monoecious, it often appears to be dioecious (as observed, for example, by Kozo-Poljanski 1946) and has the capacity to change sex expression over several years of growth. Information on the floral mechanism and putative pollinators of *S. chinensis* is given by Kozo-Poljanski (1946). Various other aspects of the biology of *S. chinensis* have also received attention, viz.: age-related development (Komarova 1994); stem, leaf, and root anatomy (Matsuda 1893; Bailey & Nast 1948); axillary bud development (Garrison 1955); primary xylem structure (Zamora 1966); wood anatomy (Lemesle 1933; Soh & Park 1985; Snezhkova 1986; Wang et al. 1989); secondary phloem structure (Zahur 1959); stomatal anatomy (Baranova 1983; Jähnichen 1976); palynology (Wodehouse 1936, 1959: 339; Pokrovskaia 1950: 251; Erdtman 1952: 256–257; Ikuse 1954, 1956; Agababian 1966, 1973; Kuprianova 1966; Roland 1971; Agababian & Zavarian 1974; Praglowski 1976); floral organogenesis (Kolbasina 1967); megasporogenesis and embryology (Yoshida 1962; Swamy 1964; Batygina & Vasilyeva 1995); fruit anatomy and development (Fujita 1929; Wang et al. 1992; Zhang et al. 1993); and seed anatomy (Fujita 1929; Melikian 1988; Wang et al. 1992).

IIIb. Schisandra section **Schisandra.**

Woody vines. Male flowers with androecium of 5 sessile stamens, radiating horizontally from a broad floral axis; thecae lateral; pollen hexacolpate. Female flowers with gynoecium of 12–75 free carpels; pseudostyles narrow and subulate. Seed testa rugulose or tuberculate.

Distribution (Fig. 17C). China (Guangxi, Hunan, Yunnan and Zhejiang), southern Japan (Honshu, Kyushu, Shikoku), southern Korea (Cheju-do), U.S.A. (Alabama, Arkansas, Florida, Georgia, Louisiana, Mississippi, North Carolina, South Carolina, and Tennessee) and Mexico (Hidalgo).

19. Schisandra glabra (Brickell) Rehder, J. Arnold Arbor. 25: 131. 1944. *Stellandria glabra* Brickell, Med. Repos. 6(3): 327. Feb–Mar 1803.—TYPE: U.S.A. Georgia: Savannah, [date not known], *J. Brickell s.n.* (holotype: PH-Muhlenberg herbarium).

Schisandra coccinea Michaux, Fl. bor.-Amer. 2: 219. Mar 1803.—TYPE: Michaux's illustration (1803: fig. 47).

Woody vines, monoecious (often appearing dioecious). Lateral branches lacking wings, with fugaceous perules at base; branches continuing growth in subsequent years. Leaf laminas (6–) 8–11 (–13) cm long, (2.5–) 3.5–6.5 (–9) cm wide, length:width ratio (1.2–) 1.7–2.3 (–3.2), thin-papyraceous or membranaceous, glabrous, ovate to elliptic, rarely obovate-elliptic; primary vein ± plane to slightly impressed above, slightly prominent below; secondary veins 4–5 (–6) pairs per leaf, (slightly) arcuate, rarely highly arcuate; base acute (younger leaves) to obtuse, truncate or slightly cordate (older leaves); apex (short-) acuminate; margin subentire to denticulate, often lobed, (0–) 4–5 (–8) teeth per side of leaf; petioles glabrous, 17–45 (–50) mm long, (0.5–) 0.6–1.0 (–1.5) mm in diameter. Flowers borne in axils of fugaceous bracts at the base of young shoots or in the axils of leaves, solitary; tepals 9–14 (male flowers), (8–) 10–12 (female flowers); tepals red, glabrous; outermost tepal triangular to ovate, 0.9–2.5 mm long, 1.1–2.2 mm wide, length:width ratio 0.6–1.1; innermost tepal elliptic to obovate or round, rarely ovate, (1.7–) 3.0–4.7 (–6.4) mm long, (0.9–) 1.7–2.6 (–3.7) mm wide, length:width ratio (0.9–) 1.2–2.1 (–4.0); largest tepal elliptic to obovate-elliptic, rarely round, obovate, or ovate-elliptic, (3.5–) 4.8–6.2 (–6.7) mm long, (3.3–) 3.5–4.8 (–5.8) mm wide, length:width ratio (1.0–) 1.1–1.3 (–1.7); outermost tepal highly reduced, 0.2–0.3 of length of largest; innermost tepal reduced, 0.4–0.6 of length of largest; peduncles glabrous, (17–) 23–35 mm long, 0.2–0.4 (–0.5) mm in diameter (male flowers), 33–44 (–70) mm long, (0.2–) 0.3–0.4 (–0.6) mm in diameter (female flowers). Male flowers with androecium of 5 sessile stamens, radiating horizontally from a broad floral axis; androecium 3.0–4.0 mm in diameter; thecae lateral; pollen hexacolpate. Female flowers with gynoecium of (12–) 18–24 (–27) carpels; gynoecium (3.1–) 3.9–4.3 mm in diameter; carpels (1.2–) 1.5–1.9 (–2.7) mm long, (0.5–) 0.6–0.9 (–1.2) mm wide, length:width ratio (1.5–) 1.9–2.3 (–3.4); pseudostyle narrow. Fruit peduncles glabrous, not significantly elongated, 2.5–3.5 cm long, 0.3–0.5 mm wide; torus 2–4.5 cm long, 1.2–2.0 mm wide; apocarps red, 5–8 mm long, 4–6 mm wide, length:width ratio 1.0–1.5 (–1.8). Seeds (1–) 2 per apocarp, reniform, 3.4–3.9 (–4.1) mm long, 4.4–5.1 mm wide, length:width ratio ca. 0.8; testa ± rugulose. Chromosome number: n = 13, 14; 2n = 28 (see Appendix 1). Figs. 8B, 9A–D; Plate 4.

Selected illustrations. Michaux (1803: fig. 47, as "*Schisandra coccinea*"); Sims (1811: pl. 1413, as "*Schisandra coccinea*"); Baillon (1868: figs. 179–181, as "*Schizandra coccinea*"); Stone (1968: figs. 5–12); Godfrey (1988: fig. 328); Panero and Aranda (1998: fig. 1).

Phenology. Flowering in June and July; fruits maturing in August and September.

Distribution (Fig. 39). U.S.A. (Alabama, Arkansas, Florida, Georgia, Kentucky, Louisiana, Mississippi, North Carolina, South Carolina, and Tennessee) and Mexico (Hidalgo); growing in ravines and levees near streams, in the understory of forests dominated by *Acer*, *Alnus*, *Carya*, *Carpinus*, *Cornus*, *Fagus*, *Liriodendron*, *Magnolia*, *Ostrya*, *Pinus*,

PLATE 4. *Schisandra glabra* (*S.* subg. *Schisandra* sect. *Schisandra*). Reproduced from Sims (1811: pl. 1413); photograph © Royal Botanic Gardens, Kew.

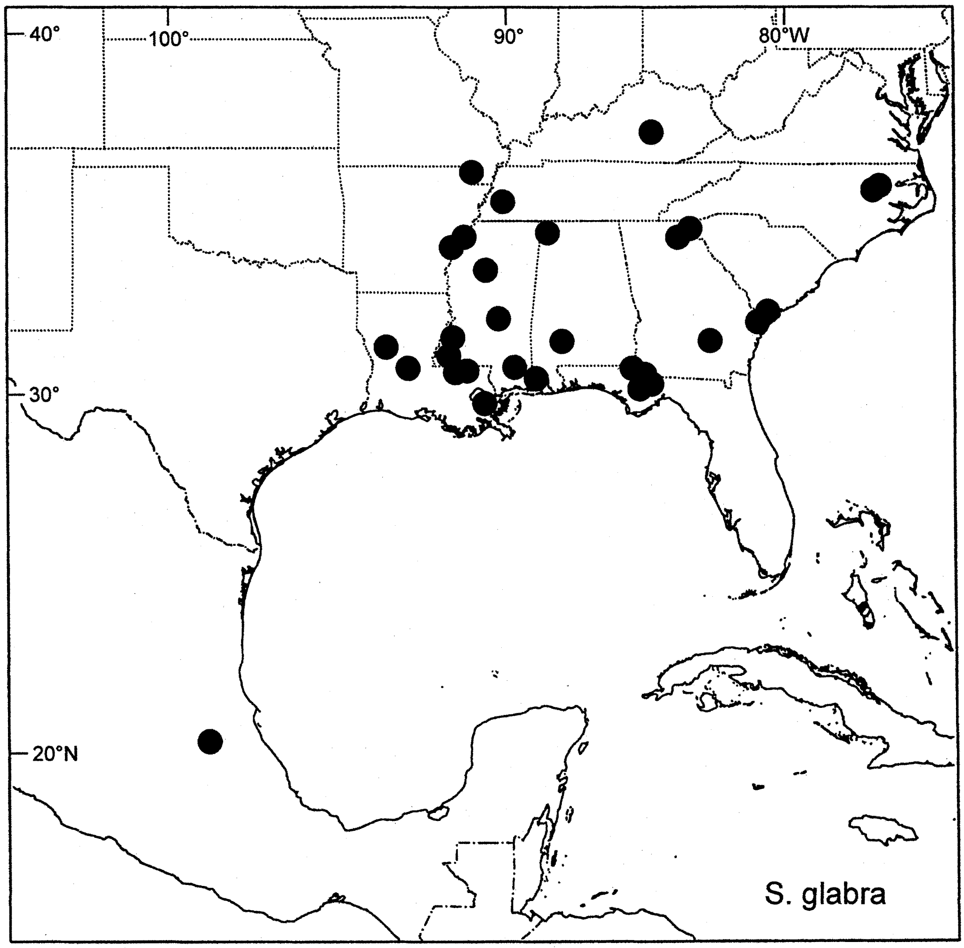


FIG. 39. Distribution of *Schisandra glabra.*

Quercus, *Symplocos*; sea level to 500 m (to 1800 m in the Sierra Madre of Mexico). Ettman (1980) provides a detailed analysis of the species associates of *S. glabra* in the southeastern U.S.A.

ADDITIONAL SPECIMENS EXAMINED. **Mexico.** HIDALGO: Metztitlán, 3.6 km al E de la carretera Pachuca–Zacualtipán–Tampico sobre la carretera a Tianguistenco, *J. L. Panero & I. Calzada 6562* (NY); Metztitlán, Sierra Madre Oriental, *J. L. Panero & I. Calzada 6563* (HKU, NY). **U.S.A.** ALABAMA: W slope of Salt Mountain, Clarke Co., *R. M. Harper 3377* (A, GH, MO, NY); Luthers Store, Marengo Co., 23 May 1893, *C. Mohr s.n.* (US), 2 Jul 1893, *C. Mohr s.n.* (US); Cherokee, s.a., *Stebbins s.n.* (NY).—ARKANSAS: Crowley's Ridge, near Helena, Phillips Co., *E. J. Palmer 25094* (A, MO), *26621* (A); W of Storm Creek Lake, N of West Helena, St. Francis National Forest, Phillips Co., *R. D. Thomas 131526* (NY); N of Madison on E edge of Crowley's Ridge, St. Francis Co., *R. D. Thomas & Arkansas Native Plant Society Group 131363* (NY).—FLORIDA: Aspalaga, s.a., *A. W. Chapman s.n.* (GH, MO, NY); [precise locality not known], 11 Jun 1849, *H. B. Croom 280* (NY); Apalachicola River, at Aspalaga, Liberty Co., *R. K. Godfrey 57050* (GH); Three Rivers State Park, W side of Lake Seminole, Jackson Co., *S. R. Hill & A. K. Gholson 19217* (NY); Lake Seminole, Three Rivers State Park, Jackson Co., *J. Wen & A. K. Gholson 945* (A).—GEORGIA: S side of Panther Creek, SW of Yonah Lake (Tugaloo River), Stephens Co., *D. E. Boufford & E. W. Wood 16697* (MO); Savannah, 1887, *M. Du Bois s.n.* (NY);

Hard Labor Creek, Morgan Co., *W. H. Duncan 11153* (GH); Phillip's Mill, Douglas Co., *N. C. Goldstein 62* (NY); S of Panther Creek, SW of Yonah Lake, N of Toccoa, Stephens Co., *J. Massey, D. E. Boufford & B. Katz 4705* (GH, NY); 1.3 mi SW of confluence of Panther Creek and Tugaloo River, along Panther Creek, *J. Solomon 1766* (MO); S side of Panther Creek, SW of Yonah Lake, N of Toccoa, Stephens Co., *E. W. Wood & D. E. Boufford 1675* (A).—LOUISIANA: 4 3/4 mi NW of Chipola, St. Helena Parish, *C. M. Allen 1950* (A); Feliciana, s.a., *W. M. Carpenter s.n.* (GH, NY), Sep [no year], *W. M. Carpenter s.n.* (NY); 2 mi W of Weyanoke P.O., West Feliciana Parish, *F. M. Givens 4524* (MO); [precise locality not known], s.a., *J. Hale s.n.* (GH, NY); New Orleans, s.a., *Ingalls s.n.* (NY); [precise locality not known], s.a., *C. W. Short s.n.* (GH, NY); Fluker's Bluff area, gorges E of Amite River, ca. 6 mi NW of Chipola, St. Helena Parish, *R. D. Thomas 42385* (GH, NY); W of Horseshoe Lake, Caldwell Parish, *R. D. Thomas & P. Marx 35972* (GH, MO); 2 mi W of Meeker, Rapides Parish, *R. D. Thomas & D. G. Rhodes 38808* (MO); Kisatchie Bayou, Kisatchie National Forest, Natchitoches Parish, *R. D. Thomas & C. Slaughter 103861* (MO, NY); NW of Chipola, Parish of St. Helena, *R. D. Thomas et al. 32751* (C).—MISSISSIPPI: [precise locality not known], 1850, *R. H. Brownne s.n.* (NY); 6 mi SW of Holcomb, Grenada Co., *C. T. Bryson & M. W. Morris 6496* (MO); 6 mi S of Woodville, Wilkinson Co., *J. Ewan 22399* (NY); 1 mi N of Doloroso, Adams Co., *J. D. Ray 6588* (GH); Ragland Hills, Forrest Co., *K. E. Rogers 8609* (GH, NY); Bluffs N of Wilkerson's Ferry, W bank of Pascagoula River, George Co., *K. E. Rogers 45154* (NY).—NORTH CAROLINA: Conoho Creek, ca. 4.5 mi NW of Williamston, Martin Co., *H. E. Ahles 53722* (C, GH, NY); Williamston, Martin Co., *D. E. Stone 1822* (NY); Williamston, Martin Co., *D. E. Stone, H. E. Ahles & R. Ornduff 1417* (GH).—SOUTH CAROLINA: Bluffton, Beaufort District, *J. H. Mellichamp 4300* (MO); Buckingham, *J. H. Mellichamp 10446* (A, NY); Bluffton, Beaufort District, Oct 1881, *J. H. Mellichamp s.n.* (GH), May 1882, *J. H. Mellichamp s.n.* (NY), Aug 1884, *J. H. Mellichamp s.n.* (NY), 1884, *J. H. Mellichamp s.n.* (GH, NY, US), 1884–85, *J. H. Mellichamp s.n.* (US), Spring 1885, *J. H. Mellichamp s.n.* (NY), Jul 1885, *J. H. Mellichamp s.n.* (NY), 1885, *J. H. Mellichamp s.n.* (GH), 1886, *J. H. Mellichamp s.n.* (NY), Aug 1887, *J. H. Mellichamp s.n.* (GH), May 1897, *J. H. Mellichamp s.n.* (NY), s.a., *J. H. Mellichamp s.n.* (NY).—TENNESSEE: near Covington, 27 Jun 1888, *J. Bryars s.n.* (US), 10 Jul 1888, *J. Bryars s.n.* (US); Covington, 1 May 1889, *J. Byars s.n.* (NY).

The almost simultaneous description of this species by Brickell (1803) and Michaux (1803) under the names *Stellandria glabra* and *Schisandra coccinea*, and the nomenclatural consequences, are described in the chapter "Taxonomic History."

Schisandra glabra is most closely related to two East Asian species, *S. repanda* and *S. bicolor* (Fig. 20), although there are substantial differences between them, viz. the inner tepals of *S. glabra* are red, whereas those of *S. repanda* and *S. bicolor* are yellow; *S. glabra* and *S. repanda* have 12–30 carpels in female flowers, whereas *S. bicolor* has 52–60; the fruiting torus is shorter in *S. glabra* (2–4.5 cm) than in either *S. repanda* (2.5–7 cm) or *S. bicolor* (3.5–15 cm); the fruiting apocarps are red at maturity in *S. glabra* and *S. bicolor*, but blackish in *S. repanda*; and the apocarps are typically smaller in *S. glabra* (5–8 × 4–6 mm) than in *S. bicolor* (10–16 × 10–16 mm), although *S. repanda* apocarps are intermediate in size (6–13 × 6–11 mm).

The degree of rarity of *S. glabra* is imperfectly known, due in part to potential confusion with the comparatively common species *Decumaria barbara* L. (Saxifragaceae), which has superficially similar foliage (Duncan 1967; Ettman 1980).

Wood and bark anatomy of *S. glabra* have been studied by Benzing (1967) and Carlquist (1999), and stomatal anatomy is illustrated by Jähnichen (1976). The pollen is described and illustrated by Erdtman (1952: 257), Wodehouse (1959: 339), Agababian (1966, 1973), Praglowski (1976), and Lieux (1980), often under the synonym *S. coccinea*. Floral ontogeny has been studied by Tucker and Bourland (1994).

20. Schisandra repanda (Siebold & Zuccarini) Radlkofer, Sitzungber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 16: 303. 1886. *Trochostigma repanda* Siebold & Zuccarini, Abh. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. 3: 728. 1843.—TYPE: JAPAN: [precise locality not known, date not known], *H. Bürger s.n.* (holotype: M; isotype: K!).

Schisandra nigra Maximowicz, Bull. Acad. Imp. Sci. Saint-Pétersbourg 17: 144. 1872 (as "*Schizandra*").—TYPE: JAPAN. Kundsho-san, Kiusiu [Kyushu], 1863, *C. J. Maximowicz s.n.* (lectotype, here designated: K!; isolectotype: GH!).

Schisandra discolor Nakai, Fl. sylv. Kor. 20: 103. 1933 (as "*Schizandra*").—TYPE: JAPAN. Miyajima, Aki, 9 Jul 1913, *B. Hayata s.n.* (holotype: TI!).

Woody vines, monoecious (often appearing dioecious). Lateral branches lacking wings, with fugaceous perules at base; branches without significant growth in subsequent years. Leaf laminas (3.5–) 5–7 (–8.5) cm long, (2.5–) 3–5.5 cm wide, length:width ratio (1.1–) 1.3–1.8 (–1.9), (thin-) papyraceous, rarely subcoriaceous, 30–60 (–90) µm thick, glabrous, elliptic to ovate; primary vein ± plane to slightly impressed above, ± plane to slightly prominent below; secondary veins (3–) 4–5 pairs per leaf, (slightly) arcuate; base acute (younger leaves) to obtuse or truncate (older leaves); apex (short-) acuminate; margin (sinuous-) denticulate to (sinuous-) serrulate, rarely subentire, (0–) 3–5 (–7) teeth per side of leaf; petioles glabrous, (13–) 15–32 (–57) mm long, 0.6–1.1 (–1.9) mm in diameter. Flowers borne in axils of fugaceous bracts at the base of young shoots, solitary; tepals 6–12 (male flowers), 6–10 (female flowers); tepals pale yellowish green, glabrous; outermost tepal elliptic to ovate or triangular, (1.0–) 1.6–4.0 mm long, (1.2–) 1.9–3.5 mm wide, length:width ratio 0.8–1.3; innermost tepal variably elliptic, ovate, or obovate, 2.6–6.0 mm long, 1.7–3.0 (–5.1) mm wide, length:width ratio 1.1–1.9 (–3.0); largest tepal variably elliptic, ovate, or obovate, 4.1–8.6 mm long, 3.6–6.4 mm wide, length:width ratio 0.9–1.4 (–1.8); outermost tepal highly reduced, 0.2–0.4 of length of largest; innermost tepal (slightly) reduced, 0.6–0.8 of length of largest; peduncles glabrous, (13–) 19–30 (–36) mm long, 0.3–0.6 (–1.0) mm in diameter (male flowers), 25–70 mm long, ca. 0.5 mm in diameter (female flowers). Male flowers with androecium of 5 sessile stamens, radiating horizontally from a broad floral axis; androecium 1.8–3.2 mm in diameter; thecae lateral; pollen hexacolpate. Female flowers with gynoecium of 12–17 free carpels, gynoecium 1.0–1.2 mm in diameter; carpels 1.6–2.2 mm long, 0.8–1.0 mm wide, length:width ratio 1.9–2.4; pseudostyle narrow. Fruit peduncles glabrous, not elongated, 3.5–8 cm long, 0.6–1.0 mm wide; torus 2.5–7 cm long, 1.2–2.1 (–2.9) mm wide; apocarps blackish, 6–13 mm long, 6–11 mm wide, length:width ratio 0.8–1.2 (–1.5). Seeds 1–2 per apocarp, flattened-reniform, (3.6–) 4.2–4.8 mm long, (4.7–) 5.0–5.8 (–6.0) mm wide, length:width ratio 0.7–0.9; testa rugulose to (very) tuberculate. Chromosome number: $2n = 28$ (see Appendix 1). Figs. 14C, E, 16D.

Illustrations. Smith (1947: fig. 27a–j).

Phenology. Flowering from May to July; fruits maturing from August to November.

Distribution (Fig. 40). Southern Japan (Honshu, Kyushu, Shikoku) and southern Korea (Cheju-do); scandent or climbing in woods or thickets; 600–1300 m.

ADDITIONAL SPECIMENS EXAMINED. **Japan.** HONSHU: Fukui, 10 Sep 1892, *[collector's name illegible] s.n.* (A); Jizogatake, *U. Faurie 5391* (A, UC); Kitakoma-gun, Seitetsu-mura, Prov. Kai, *M. Furuse 2792* (A); Torii-tooge, Seitetsu-mura, Kita-koma-gun, Prov. Kai, 22 Jun 1954, *M. Furuse s.n.* (A); Tsubakuro-iwa, Mt. Temso-zan, Nippara, Hikawa-machi, Nishi-tama-gun, Prov. Musashi, Tokyo-to, 15 Jul 1958, *M. Furuse s.n.* (A); foot of Mt. Surikogi, Ohdaira, Ihida-shi, Prov. Shinano, Pref. Nagano, 27 Jul 1961, *M. Furuse s.n.* (A); Higashi-iwai-gun, Okita-mura, Prov. Rikuchu, *K. Hosoi 2612* (A); Nojiri, Shinano, 6 Sep 1905, *J. G. Jack s.n.* (A); Nakaniikawa-gun, Kamiichi-machi ohiwa aso, Toyama Pref., *J. Jutila, H. Fugino & Yoshizaki 399* (NY); Minamitsuru-gun, between Mt. Mitsutooge and Takara copper mine, Yamanashi Pref., *H. Kanai 6350* (A); along the O-o-ma forest road in O-o-ma River valley, O-o-ma, Honkawane-cho, Haibara-gun, Shizuoka Pref., *F. Konta & S. Kusaka 119* (A); Fudzi-yama [Fuji-san], 1862, *C. J. Maximowicz s.n.* (NY; paratype of *Schisandra nigra*); Mt.

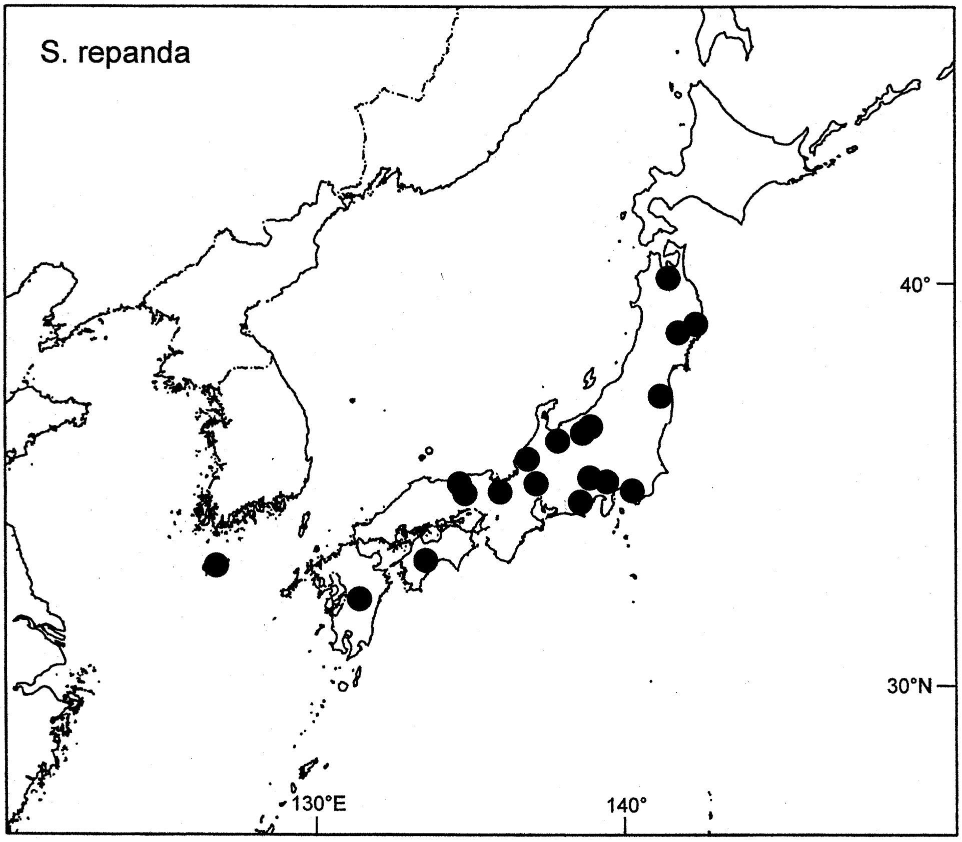


FIG. 40. Distribution of *Schisandra repanda.*

Atago, Musashi Prov., *M. Mizushima 516* (A); Nishichikuma-gun, Kaida-mura, Shinano Prov., *M. Mizushima 2401* (A); Mt. Hiei, Sakyoku, Kyoto-shi, Kyoto Pref., *G. Murata 44542* (A); Yasumiya, Aomori Pref., *H. Muroi 4534* (A); Mt. Hyonosen, Tottori Pref., *H. Muroi 5501* (A); Sekinomiya, Mikata-gun, Hyogo Pref., *H. Muroi 5685* (A); Kamaishi-shi, Kerobe, Iwate Pref., *H. Ohashi, B. H. Choi & J. Iketsu 22175* (IBSC); Fukushima, 28 [month illegible] 1892, *C. S. Sargent s.n.* (A); Mino Prov., *K. Shiota 4423* (A), *6494* (A); Prov. Senano, 1864, *Tschonoski s.n.* (A, C, K, NY); Mt. Choro, Kamiotomi, Wachi-cho, Funai-gun, Pref. Kyoto, *S. Tsugaru & T. Takahashi 17921* (MO); Fukui, 13 Sep 1892, *J. H. Veitch s.n.* (A); Tsukakarendake, Shinano Prov., *E. H. Wilson 7473* (A); Utake-gawa, Hondo, *E. H. Wilson 7744* (A); Yabu-gun, Sekino-miya-cho, en route from Fukusada to the NE foot of Mt. Hyonosen, Pref. Hyogo, *E. W. Wood & D. E. Boufford 3874* (A).—KYUSHU: Mt. Sibi, Prov. Satuma, *S. Hatusima 14036* (A).—SHIKOKU: Nanokawa, Tosa, 12 Jul 1889, *K. Watanabe s.n.* (GH).—Precise locality not known: Aug 1880, *Maries s.n.* (K); 1863. **Korea.** [Precise locality not known], *U. Faurie 1678* (A); Quelpaert Island [Cheju-do], *T. Taquet 940* (A, K); [precise locality not known], *T. Taquet 4108* (C); *T. Taquet 4109* (C); Quelpaert Island [Cheju-do], Monastery & over the top of Halla-san and down to Mushroom House, *E. H. Wilson 9446* (A).

Schisandra repanda is most closely related to *S. glabra* and *S. bicolor*, with which it forms a robust clade (Fig. 20). All three species have an essentially similar androecium of five horizontally oriented stamens. Although they are not sympatric, *S. repanda* and *S. bicolor* are superficially similar and taxonomic confusion is possible. Differences exist in the size of the leaf laminas [(3.5–) 5–7 (–8.5) × (2.5–) 3–5.5 cm in *S. repanda*, (7–)

7.5–10.5 (–12) × (3.5–) 4.5–7 (–8) cm in *S. bicolor*]; size of the outermost tepal relative to the largest (0.2–0.4 in *S. repanda*, ca. 0.5–0.7 in *S. bicolor*); carpel number (12–17 in *S. repanda*, 52–60 in *S. bicolor*); apocarp color (blackish in *S. repanda*, red in *S. bicolor*); and apocarp size (6–13 × 6–11 mm in *S. repanda*, 10–16 × 10–16 mm in *S. bicolor*).

Schisandra repanda is partly sympatric with *S. chinensis*, and although they are easily distinguished if flowering material is available, sterile or fruiting specimens can be confused. In the absence of flowers, the following characters are diagnostic: leaf lamina indumentum (glabrous in *S. repanda*, but often slightly pubescent and glaucescent abaxially in *S. chinensis*); number of leaf marginal denticulations [(0–) 3–5 (–7) in *S. repanda*, (5–) 6–10 (–16) in *S. chinensis*]; apocarp color (blackish in *S. repanda*, red in *S. chinensis*); apocarp size [6–13 × 6–11 mm in *S. repanda*, 5–7.5 × 4–5 (–6) in *S. chinensis*]; seed size [(3.6–) 4.2–4.8 × (4.7–) 5.0–5.8 (–6.0) mm in *S. repanda*, (2.9–) 3.2–3.8 (–4) × (3.6–) 4.4–4.8 (–5) mm in *S. chinensis*]; and seed testa ornamentation (rugulose to tuberculate in *S. repanda*, smooth in *S. chinensis*).

Smith (1947: 145) discussed the confused nomenclatural history of *S. repanda* in detail, including the synonymy of the names *Trochostigma repanda* and *S. nigra*. Smith correctly noted that the name *T. repanda* has nomenclatural priority and accordingly proposed the combination *Schisandra repanda*; however, he overlooked that Radlkofer had already published the combination (1886: 303). The correct name for this species should therefore be "*Schisandra repanda* (Siebold & Zuccarini) Radlkofer" and not the widely cited "*Schisandra repanda* (Siebold & Zuccarini) A. C. Smith."

The name *Schisandra nigra* was based on four unnumbered specimens (Maximowicz 1872), two of which were collected by Maximowicz (in Kundsho-san, Kiusiu [Kyushu], and Fudzi-yama [Fuji-san], Honshu), the others by Tschonoski (in Nambu Province) and Albrecht (in Yezo [Hokkaido]). As noted by Smith (1947: 145), the *Albrecht* specimen is referable to *S. chinensis*. Smith erroneously cited and annotated a *Tschonoski* specimen collected in "Prov. Senano" as one of the types; the actual *Tschonoski* type has not been located, and a lectotype has consequently been selected from one of the two *Maximowicz* collections available for study.

Various structural features and developmental processes have been described for *S. repanda* (often under the synonym *S. nigra*), viz.: stem, leaf, and root anatomy (Matsuda 1893); wood and bark anatomy (Soh & Park 1985; Takahashi 1985; Carlquist 1999); microsporogenesis and pollen morphology (Ikuse 1954, 1956; Hayashi 1960; Praglowski 1976); and megasporogenesis and embryology (Hayashi 1963b, 1965).

21. Schisandra bicolor W.-C. Cheng, Contr. Biol. Lab. Chin. Assoc. Advancem. Sci., Sect. Bot. 8: 137. 1932.—TYPE: CHINA. Chekiang [Zhejiang]: W Tienmu-Shan, near Sienting, 1 Jul 1932, *W.-C. Cheng 3656* (holotype: NAS!).

Schisandra wilsoniana A. C. Smith, Sargentia 7: 122. 1947.—TYPE: CHINA. Yunnan: mountains W of Hao-ch'ing, S of Li-chiang, 25–28 May 1922, *J. F. Rock 4039* (holotype: A!; isotypes: UC! US, photo of UC isotype: HKU!).

Schisandra tuberculata Y.-W. Law, Bull. Bot. Res., Harbin 3: 148. 1983. *Schisandra bicolor* var. *tuberculata* (Y.-W. Law) Y.-W. Law, Fl. Reipubl. Popularis Sin. 30(1): 269, 273. 1996.—TYPE: CHINA. Guangxi: Long Sheng, 28 Jun 1958, *Z.-Y. Chun 51104* (holotype: PE, on permanent loan to IBSC).

Woody vines, monoecious (often appearing dioecious). Lateral branches lacking wings, with fugaceous perules at base; branches without significant growth in subsequent years. Leaf laminas (7–) 7.5–10.5 (–12) cm long, (3.5–) 4.5–7 (–8) cm wide, length:width ratio 1.3–1.9 (–3.0), (thin-) papyraceous, rarely subcoriaceous, 20–60 (–80) µm thick, glabrous, variably elliptic, ovate-elliptic, or obovate-elliptic; primary vein ± plane to slightly impressed above, (slightly) prominent below; secondary veins 4–6 pairs per leaf, slightly arcuate; base acute (younger leaves) to obtuse (older leaves); apex short-acuminate; margin entire to (sinuous-) denticulate, 0–6 (–12) teeth per side of leaf; petioles glabrous, (13–) 20–50 (–67) mm long, (0.6–) 0.9–1.4 (–1.7) mm in diameter. Flowers borne in axils of fugaceous bracts at the base of young shoots, solitary; tepals 8–11 (male flowers), 6–7 (female flowers); tepals yellowish (outer), reddish purple (inner), glabrous; outermost tepal elliptic to obovate, ca. 2.8–4.4 mm long, ca. 2.1–4.0 mm wide, length:width ratio ca. 1.1–1.3; innermost tepal ovate, ca. 2.7–9.0 mm long, ca. 2.7–4.0 mm wide, length:width ratio ca. 1.7–2.3; largest tepal elliptic to ovate, 4.1–8.5 mm long, 3.6–6.2 mm wide, length:width ratio 0.8–1.4; outermost tepal (slightly) reduced, ca. 0.5–0.7 of length of largest; innermost tepal variably reduced, 0.5–1.0 of length of largest; peduncles glabrous, 17–42 mm long, 0.4–0.5 mm in diameter (male flowers), ca. 50–55 mm long, 0.2–0.5 mm in diameter (female flowers). Male flowers with androecium of 5 sessile stamens, radiating horizontally from a broad floral axis; androecium ca. 2.4–5.5 mm in diameter; thecae lateral; pollen hexacolpate. Female flowers with gynoecium of 52–75 free carpels; carpels ca. 1.7–2.0 mm long, ca. 0.5–0.6 mm wide, length:width ratio ca. 2.8–4.0; pseudostyle narrow. Fruit peduncles glabrous, not elongated, 2.5–6.5 cm long, 0.7–1.1 mm wide; torus 3.5–15 cm long, 1.0–1.6 mm wide; apocarps red, 10–16 mm long, 10–16 mm wide, length:width ratio 0.8–1.1. Seeds 1–2 per apocarp, (discoid-) flattened-reniform, (3.1–) 3.5–5.2 (–5.6) mm long, 3.9–6.5 (–7.3) mm wide, length:width ratio 0.7–0.9; testa tuberculate. Chromosome number: 2n = 28 (see Appendix 1). Figs. 15E, 41.

Illustrations. Law (1983a: 150, as "*S. tuberculata*"; 1983b: fig. 188; 1996a: fig. 78, 1–11, as "*S. bicolor* var. *tuberculata*," fig. 78, 12–24); M.-C. Liu (1992: fig. 446).

Phenology. Flowering from May to July; fruits maturing from August and November.

Distribution (Fig. 42). Endemic to China (Guangxi, Hunan, Yunnan, and Zhejiang; also reported from Jiangxi, fide Law 1996a: 269); scandent or climbing in sparse woodlands, often in river valleys; 750–1300 m.

ADDITIONAL SPECIMENS EXAMINED. **China.** GUANGXI: Long-sheng, Da-di-xiang, Cu-jiang, *Guang Fu Forest Team 872* (IBSC, MO); Longsheng, *H. F. Tan & S. L. Yu 700658* (IBSC; paratype of *S. tuberculata*).—HUNAN: Yizhang, *M. X. Huang 112217* (IBSC); Yizhang, *B. H. Liang & H. H. Hsue 85161* (IBSC, MO); Wugang, *L. U. Liou & K. C. Ho 16342* (IBSC); [precise locality not known], *P. C. Tam 63323* (IBSC); Men-ping, Ai-shang Village, Shu-chuang-shan, Cheng-bu County, *P. X. Tan 63781* (MO).—ZHEJIANG: Lin-an, Chang-hua Forestry Farm, *P. L. Chiu 20* (MO); Tian-mu-shan, Heng-tang, *P. L. Chiu 376* (MO).

Schisandra bicolor was first described by Cheng (1932) from a specimen collected in Zhejiang Province; this specimen was deposited in NAS herbarium and was not available to Smith (1947: 146–147) during the preparation of his monograph. Smith was furthermore unable to determine any specimens as belonging to *S. bicolor*, although he accepted the species as distinct on the basis of Cheng's excellent description and illustration. Smith's description was therefore based entirely on the information published by Cheng, and both accounts omit descriptions of the fruits and seeds.

Schisandra bicolor is closely related to *S. glabra* and *S. repanda* (Fig. 20); all three species have a distinctive androecium composed of five short stamens radiating horizontally from a broad floral axis. Although *S. bicolor* and *S. repanda* are allopatric, their

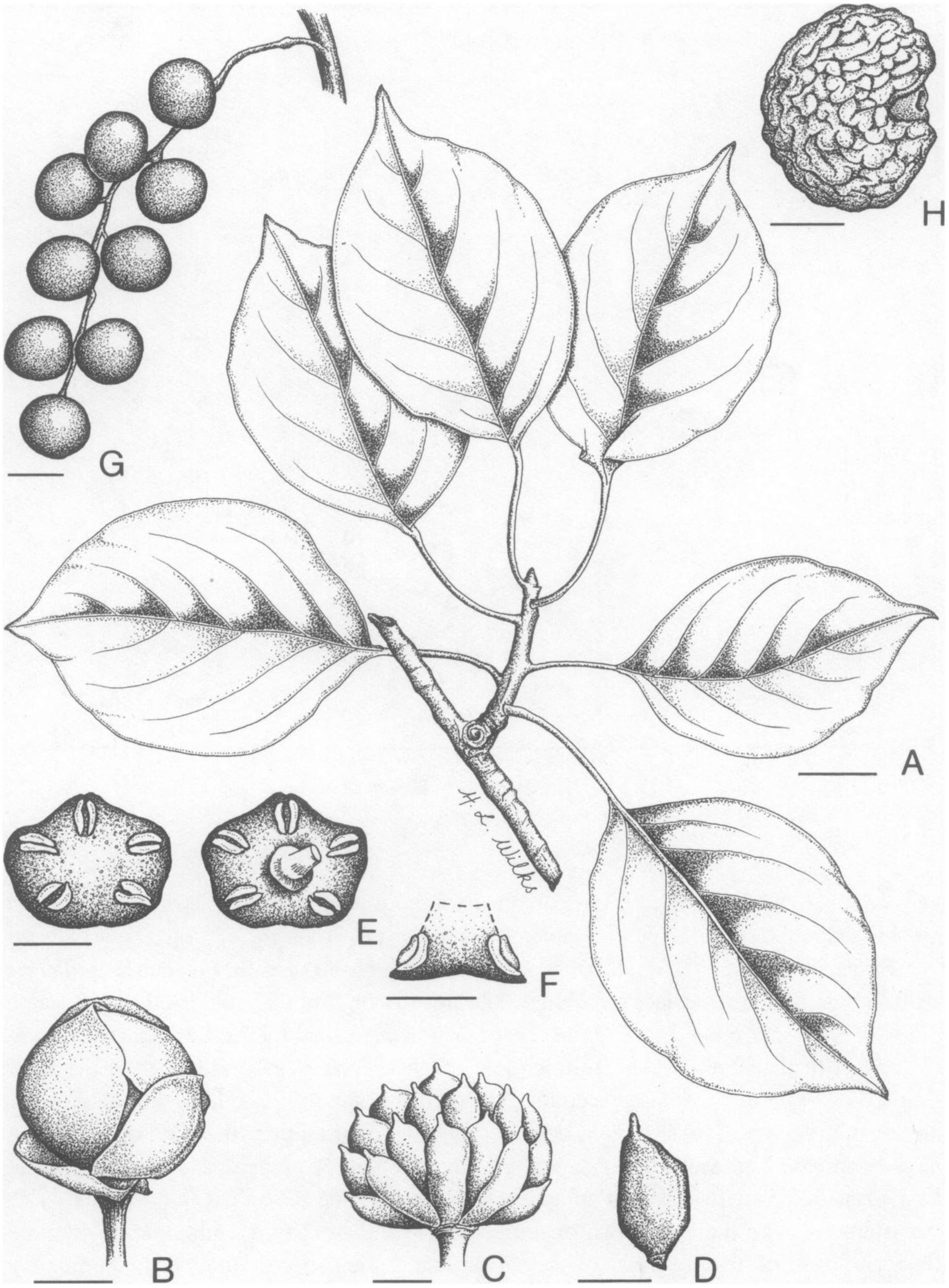


FIG. 41. *Schisandra bicolor* (*S.* subg. *Schisandra* sect. *Schisandra*). A, branch. B, flower. C, gynoecium. D, isolated carpel (lateral view). E, androecium (abaxial and adaxial views). F, isolated stamen, showing area of fusion (dotted line). G, fruit. H, seed. Scale bars: A, 2 cm; B, E, F, H, 2 mm; C, D, 1 mm; G, 1 cm. (A, *H. F. Tan & S. L. Tu 700658*, IBSC; B, *P. C. Tam 63323*, IBSC; C, redrawn from Law (1996a: fig. 78.16); D, *Guangfu Expedition 872*, IBSC; E, F, *P. C. Tam 63323*, IBSC; G, *P. H. Liang & H. H. Hsue 85161*, IBSC; H, *L. U. Liou & K. C. Ho 16342*, IBSC.) Drawing by H. L. Wilks.

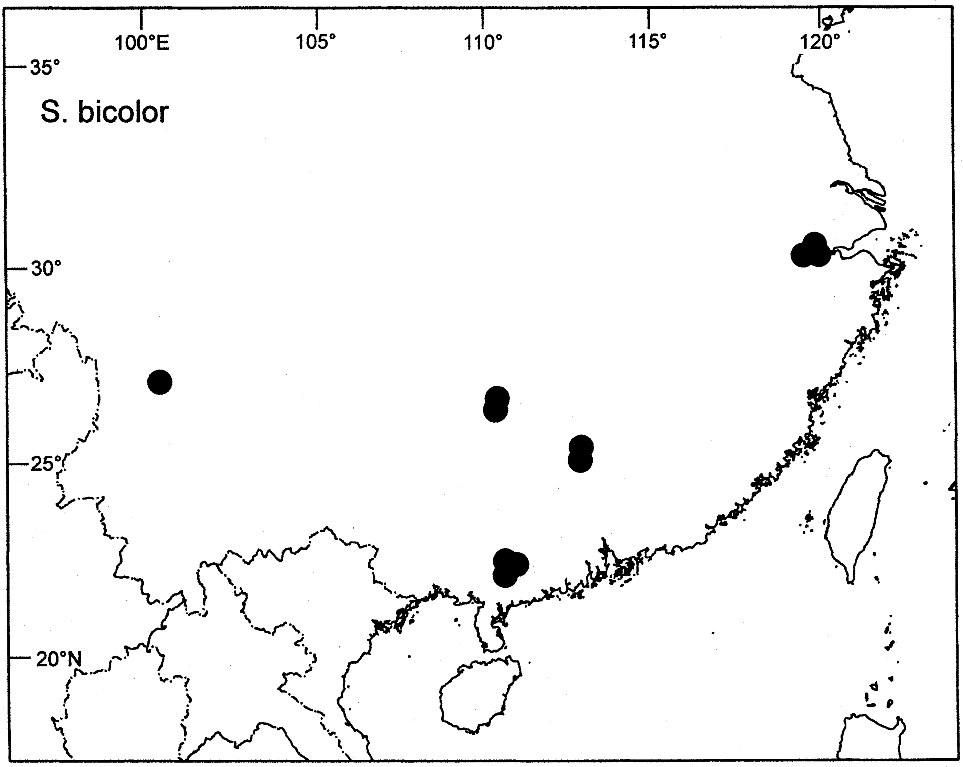


FIG. 42. Distribution of *Schisandra bicolor.*

geographical distributions are close, and taxonomic confusion is possible. The distinguishing characters are discussed under *S. repanda* (no. 20).

Smith (1947: 122–123) described *S. wilsoniana*, based on rather inadequate material with female flowers, but lacking either male flowers or fruits. He believed that *S. wilsoniana* was closely related to *S. glaucescens*, *S. neglecta,* and their allies. The only wide-ranging critical reappraisal of Smith's monograph to have been undertaken is the *Flora Reipublicae Popularis Sinicae* account published by Law (1996a). Law did not examine any of the types of *S. wilsoniana*, however, and his delimitation of the taxon appears to have been based on Smith's suggested relationship with *S. glaucescens* and *S. neglecta*: Law classified *S. wilsoniana* in subg. *Sinoschisandra*, and described it as having ca. 25 free stamens, with the apical two or three stamens adnate. My examination of the holotype and one of the isotypes of *S. wilsoniana* indicates that they are referrable to *S. bicolor*. The type specimens of *S. wilsoniana* have several characteristics of *S. bicolor* and *S. repanda*, including short lateral branches that do not significantly continue growth in subsequent years and bear the scars of fruiting peduncles from previous years. The numerous carpels (60–75) and the large pseudostyles noted by Smith (1947: 123) are furthermore typical of *S. bicolor*.

Law (1983a) described *S. tuberculata*, which he subsequently (Law 1996b) reduced to a variety of *S. bicolor*. The distinguishing characters cited by Law are relatively insignificant (tuberculate branches and rugulose seeds). Although the holotype has not been studied, examination of one of the paratypes (listed above), indicates that the name is synonymous with *S. bicolor.*

IIIc. Schisandra section **Sphaerostema** (Blume) Nakai, Fl. sylv. Kor. 20: 101. 1933 (as "*Schizandra*"). *Sphaerostema* Blume, Bijdr. fl. Ned. Ind. 22. 1825. *Schisandra* subg. *Sphaerostema* (Blume) Y.-W. Law, Fl. Reipubl. Popularis Sin. 30(1): 264, 272. 1996.—TYPE: *Schisandra propinqua* subsp. *axillaris* (Blume) R. M. K. Saunders.

Schisandra subg. *Plena* Y.-W. Law, Fl. Reipubl. Popularis Sin. 30(1): 272. 1996 (as "*Schisandra* subg. *Plenischisandra*" on p. 265, sphalm.).—TYPE: *Schisandra plena* A. C. Smith.

Woody vines. Male flowers with 4–18 stamens, fused into a carnose mass; anthers either sessile (*S. plena*) or on short free connectives (*S. propinqua*). Female flowers with 18–52 free carpels; pseudostyles narrow and subulate. Seed testa smooth.

Distribution (Fig. 17D). India (Uttar Pradesh, Arunachal Pradesh, Meghalaya, and Nagaland), Nepal, eastern Myanmar [Burma], northern Thailand, China (Gansu, Guizhou, Hubei, Hunan, Yunnan, Shanxi, Sichuan), and Indonesia (Java and Bali).

Although Law (1996b) validly published a new subgeneric name, subg. *Plena*, he apparently intended it to be published as "*Plenischisandra*"; the latter name is used in the main text of his *Flora Reipublicae Popularis Sinicae* account (Law 1996a: 265).

22. Schisandra propinqua (Wallich) Baillon, Hist. pl. 1: 148. 1868 (as "*Schizandra*"). *Kadsura propinqua* Wallich, Tent. fl. Napal. 11. 1824. *Sphaerostema propinqua* (Wallich) Blume, Fl. Javae [Schizandreae] 15. 1830 (as "*S. propinquo*").—TYPE: NEPAL. Mt. Sheopore, Sankoo [Sanku], [date not known], *N. Wallich 4986* (lectotype, designated by Saunders, 1997b: K-W; isolectotypes: C! K [2]!, photos of K lectotypes: HKU!).

Woody vines, monoecious (often appearing dioecious). Lateral branches lacking wings, with fugaceous perules at base; branches continuing growth in subsequent years. Leaf laminas (5–) 7–11.5 (–20) cm long, (1–) 2–4 (–8.5) cm wide, length:width ratio (1.8–) 2.5–4.0 (–5.7), variably papyraceous to coriaceous, (50–) 90–150 (–200) µm thick, glabrous, elliptic to ovate; primary vein plane to slightly impressed above, slightly to very prominent below; secondary veins (4–) 4.5–6.5 (–9) pairs per leaf, variably straight or arcuate; base obtuse to truncate (acute in younger leaves); apex short-acuminate; margin (sub-) entire to denticulate-serrulate, rarely serrate, 0–7 (–13) teeth per side of leaf; petioles glabrous, (4–) 8–16.5 (–27) mm long, (0.6–) 0.9–1.4 (–2.0) mm in diameter. Flowers borne in axils of fugaceous bracts at the base of young shoots or in axils of leaves, solitary, occasionally with secondary flower in axil of prophyll, or in clusters; tepals (7–) 8–10 (–12) (male flowers), (8–) 11–15 (–17) (female flowers); tepals cream, yellow, orange, pink, or flushed purplish, glabrous; outermost tepal ovate, (0.6–) 1.0–2.4 (–2.7) mm long, (0.8–) 1.1–2.4 (–3.0) mm wide, length:width ratio (0.5–) 0.6–1.5 (–1.8); innermost tepal elliptic to ovate (rarely obovate), (1.4–) 2.6–5.7 (–6.4) mm long, (0.9–) 1.7–3.5 (–4.0) mm wide, length:width ratio (0.7–) 1.1–2.4 (–3.6); largest tepal ovate or obovate, (3.1–) 5.0–9.0 (–12.5) mm long, (2.4–) 3.0–7.0 (–10.0) mm wide, length:width ratio 0.9–1.5

(–1.9); outermost tepal highly reduced, 0.1–0.4 (–0.7) of length of largest; innermost tepal (slightly) reduced, (0.4–) 0.5–0.9 of length of largest; peduncles glabrous, 2–17 mm long, 0.3–0.9 mm in diameter (male flowers), 3–14 mm long, 0.4–1.7 mm in diameter (female flowers). Male flowers with androecium of (4–) 8–18 stamens, fused into a carnose mass (1.8–) 2.4–3.5 (–4.3) mm in diameter, with anthers borne on free connectives, arising from cavities; thecae introrse; pollen hexacolpate. Female flowers with gynoecium of 18–52 free carpels, gynoecium 2.8–3.8 mm in diameter; carpels 1.1–2.0 mm long, 0.6–1.2 mm wide, length:width ratio (1.2–) 1.4–2.2 (–2.8); pseudostyle flat-subulate. Fruit peduncles glabrous, length variable, 0.5–3 cm long, 0.5–1.5 mm wide; torus 2–6.5 cm long, 0.8–1.7 mm wide; apocarps red to purple, 4.5–9 mm long, 4–8.5 mm wide, length:width ratio 0.8–1.2 (–1.4). Seeds 1–2 per apocarp, discoid, (3.2–) 3.7–4.5 (–5.4) mm long, (3.5–) 4.2–4.9 (–5.5) mm wide, length:width ratio (0.7–) 0.8–0.9 (–1.1); testa ± smooth. Chromosome number: $2n = 28$ (see Appendix 1).

Schisandra propinqua is most closely related to *S. plena* (Fig. 20), with which it shares the unusual feature of androecia that are composed of fused stamens, forming a carnose mass; differences are apparent, however, in the shape of the androecial mass, which is subglobose in *S. propinqua* and elongate in *S. plena*. In addition, the stamens in *S. propinqua* are apically free, with the thecae borne on short connectives; this contrasts with *S. plena*, in which the stamens are fully fused, so that the thecae are sessile.

A detailed multivariate statistical analysis of leaf variation in *S. propinqua*, using discriminant function and canonical variables analyses, was published by Saunders (1997b). The results essentially confirmed Smith's (1947) infraspecific classification of the species, although the varieties were elevated to subspecific level to reflect the correlation between the variation patterns and the distinct distributional ranges. Saunders (1997b) also reduced *S. axillaris* to a subspecies of *S. propinqua*. The primary characteristics used for distinguishing the four subspecies recognized are listed in Table 5. Distinguishing subspecies *propinqua* and *sinensis* is comparatively easy, since there are several excellent taxonomic characters, including size of the leaf margin teeth (larger, often serrate or dentate in subsp. *sinensis*), leaf length:width ratio, and male flower size (smaller in subsp. *sinensis*, correlated with fewer stamens). Although subspecies *propinqua* and *sinensis* can be distinguished quite easily, subsp. *intermedia* is more problematic. It is intermediate in all the characters diagnostic for subspecies *propinqua* and *sinensis* (Table 5). Subspecies *axillaris* is most similar to subsp. *intermedia*, although it can be distinguished on the basis of leaf thickness, peduncle length, and the number of tepals in male flowers (Table 5).

There has been considerable historical confusion over the use of the epithet "*axillaris*." The earliest described taxa referable to *S. propinqua* are *Kadsura propinqua* Wall. (=*S. propinqua* subsp. *propinqua*) from Nepal (Wallich 1824) and *Sphaerostema axillare* Blume (=*S. propinqua* subsp. *axillaris*) from Java (Blume 1825). Extensive collections were subsequently made in Assam and Myanmar [Burma], where a related taxon was recognized as being morphologically slightly distinct from "*Kadsura propinqua*." This taxon, now recognized as *S. propinqua* subsp. *intermedia*, was misleadingly referred to as *Schisandra axillaris*. The epithet "*axillaris*" has therefore been used in two different senses, and it should be noted that references in the literature to specimens of "*S. axillaris*" from continental Asia actually refer to *S. propinqua* subsp. *intermedia*.

Confusion is possible between vegetative specimens of *S. propinqua* subsp. *sinensis* and *S. lancifolia* (see discussion following *S. lancifolia*, no. 13).

Aspects of the secondary xylem of *S. propinqua* are described by Groppler (1894, as "*S. axillaris*," although probably referring to *S. propinqua* subsp. *intermedia*) and Lemesle

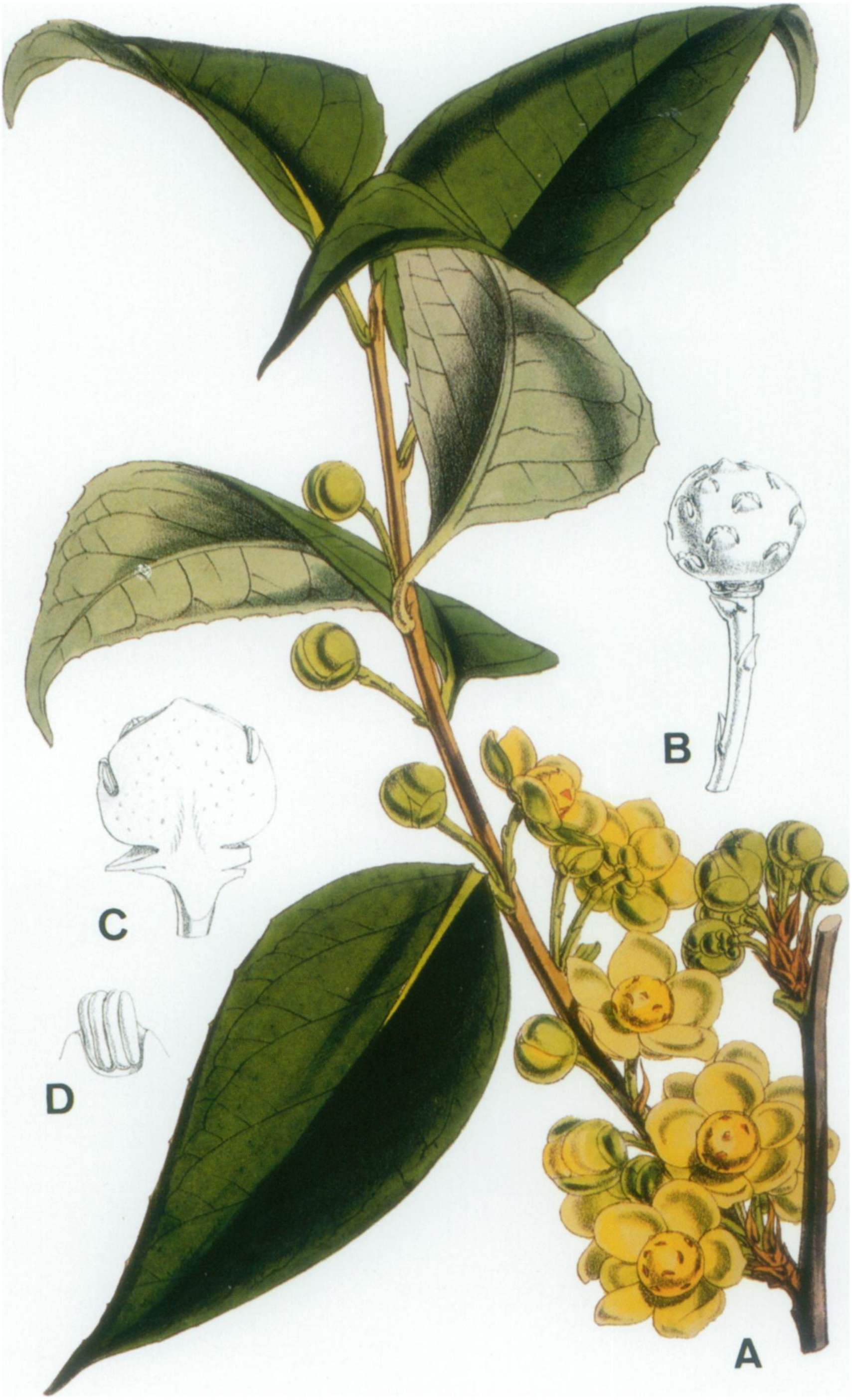


PLATE 5. *Schisandra propinqua* subsp. *propinqua* (*S.* subg. *Schisandra* sect. *Sphaerostema*). A, flowering branch (male). B, male flower (tepals removed). C, androecial mass of fused stamens (longitudinal section). D, thecae. Reproduced from Hooker (1851); photograph © Royal Botanic Gardens, Kew.

TABLE 5. Variation in selected morphological characters of *Schisandra propinqua.*

	S. propinqua subsp. *propinqua*	*S. propinqua* subsp. *intermedia*	*S. propinqua* subsp. *sinensis*	*S. propinqua* subsp. *axillaris*
Leaf thickness	generally papyraceous	generally papyraceous	papyraceous to subcoriaceous	generally coriaceous
Leaf length: width ratio	(2.1–) 2.5–2.9 (–3.3)	(1.8–) 2.4–4.0 (–5.4)	(2.2–) 2.5–5.0 (–5.7)	(2.0–) 2.3–3.2 (–3.5)
Arrangement of flowers	solitary, rarely with secondary flower	solitary, rarely with secondary flower	solitary or in clusters	solitary, rarely with secondary flower
Diameter of androecium	3.2–4.3 mm	2.6–2.8 mm	1.8–2.4 mm	2.8–3.9 mm
Number of stamens	10–18	10–12 (–16)	4–11	10–13 (–17)
Number of tepals (female flowers)	14–17	9–12	8–15	10–14
Peduncle length	4.5–12.5 mm	4–12 mm	3–16 mm	(2–) 3–5 (–12) mm

(1946, 1953), and crystalliferous sclerenchyma cells are illustrated by Bailey and Nast (1948). The stomatal anatomy of *S. propinqua* (including subspecies *propinqua* and *intermedia*) is described by Rao (1939). Pollen structure has been described and illustrated by Erdtman (1952: 257), Agababian (1966, 1973), Mitriou (1970), Walker (1974b, 1976b), and Praglowski (1976). References to "*S. axillaris*" in many of these publications presumably refer to *S. propinqua* subsp. *intermedia* rather than to subsp. *axillaris*, because specimens from continental Asia were studied; it should be noted that Mitriou (1970) did not cite vouchers.

22a. Schisandra propinqua subspecies propinqua. [*Schisandra propinqua* var. *typica* A. C. Smith, Sargentia 7: 151. 1947.]

Leaf laminas (6.0–) 8.5–10.5 (–13.0) cm long, (2.0–) 2.5–4.0 (–4.5) cm wide, length: width ratio (2.1–) 2.5–2.9 (–3.3), generally papyraceous; margin denticulate to serrulate, rarely (sub-) entire, (0–) 1–8 (–13) teeth per side of leaf. Flowers borne solitary in axil of leaf, rarely with secondary flower in axil of prophyll; peduncle 4.5–12.5 mm long. Male flowers comparatively large, largest tepals 3.5–7.2 mm long, 3.7–6.7 mm wide; androecium of 10–18 stamens, fused into a carnose mass 3.2–4.3 mm in diameter. Female flowers comparatively large, 14–17 tepals, largest tepals 7.2–12.5 mm long, 5.5–10.0 mm wide. Fruit peduncle short, up to ca. 10 mm long; apocarps ca. 7–8 mm long, 7–8 mm wide. Frontispiece; Figs. 12C, D, F; Plate 5.

Illustrations. Wallich (1824: fig. 15, as "*Kadsura propinqua*"); Lindley (1834: fig. 1688, as "*Sphaerostema propinquum*"); Hooker (1851: fig. 4614, as "*Sphaerostema propinquum*"); Baillon (1868: fig. 183–184, as "*Schizandra propinqua*"); King (1891: pl. 41A, as "*Schizandra propinqua*").

Phenology. Flowering from May to July; fruits maturing in October and November.

Distribution (Fig. 43). North-west India (northern Uttar Pradesh) and Nepal; open situations in scrublands and mixed woodlands; 1220–1830 m.

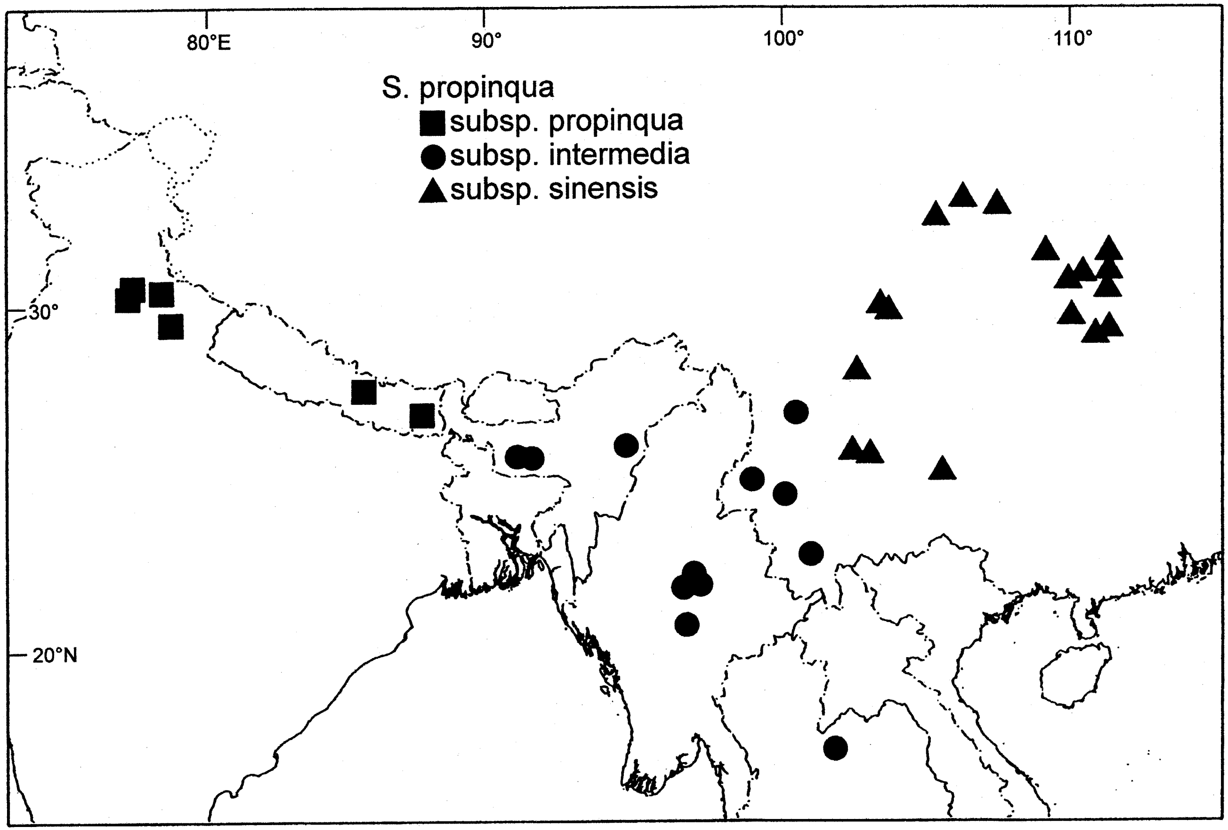


FIG. 43. Distribution of *Schisandra propinqua* subsp. *propinqua*, subsp. *intermedia,* and subsp. *sinensis*.

ADDITIONAL SPECIMENS EXAMINED. **India.** UTTAR PRADESH: Siwalik & Jaunsar Divisions, *C. S. Chand 2* (UC); Mandali, Siwalik & Jaunsar Divisions, *B. C. Datta 2* (A); Gurhwal, *H. Falconer 80* (A, C, GH, K, L); Korura forest, NWP, *U. Kanjilal 750* (K); Mussoorie, Siwalik & Jaunsar Divisions, *M. L. Punj 4* (NY); *C. S. Rawat 4* (A); Shaidevi, Kumaon, *R. Strachey & J. E. Winterbottom 2* (GH); Mussoorie, Siwalik & Jaunsar Divisions, *N. K. Tripathi 4* (E). **Nepal.** [precise locality not known], 1862, *C. E. Chardon s.n.* (P); Iladanda-Selap, E Nepal, *H. Kanai, G. Murata & M. Togashi 6303834* (A, K); Doti, *B. Ram 423* (A, NY); Godavari, Kathmandu valley, *A. D. Schilling & C. D. Sayers 558* (K); *A. D. Schilling & C. D. Sayers 561* (K); Pasgam, *J. D. A. Stainton, W. R. Sykes & L. H. J. Williams 5933* (E, L); [precise locality not known], *[N. Wallich] 1373* (C); [precise locality not known], *[N. Wallich] 1897* (C); [precise locality not known], s.a., *[N. Wallich] s.n.* (GH, K, L).

22b. Schisandra propinqua subspecies **intermedia** (A. C. Smith) R. M. K. Saunders, Edinb. J. Bot. 54: 278. 1997. *Schisandra propinqua* var. *intermedia* A. C. Smith, Sargentia 7: 152. 1947.—TYPE: CHINA. Yunnan: outskirts of lava bed W of T'eng-yüeh, 25°N, May 1912, *G. Forrest 7692* (holotype: A!, photo: HKU!; isotypes: E! K!, photo of K isotype: HKU!).

Leaf laminas (5.0–) 7.0–11.0 (–20.0) cm long, (1.0–) 2.0–4.5 (–8.5) cm wide, length: width ratio (1.8–) 2.4–4.0 (–5.4), generally papyraceous; margin entire to denticulate or serrulate, rarely serrate, 0–7 (–11) teeth per side of leaf. Flowers borne solitary in axil of leaf, rarely with secondary flower in axil of prophyll; peduncle 4–12 mm long. Male flowers comparatively large, largest tepals 4.0–7.4 mm long, 2.4–5.2 mm wide; androecium of 10–12 (–16) stamens, fused into a carnose mass ca. 2.6–2.8 mm in diameter. Female flowers with 9–12 tepals, largest tepals 6.3–10.9 mm long, 5.6–6.6 mm wide. Fruit peduncle short, 7–12 mm long; apocarps 6–9 mm long, 5.5–8.5 mm wide.

Illustrations. King (1891: pl. 74A, as "*Schizandra axillaris*"); Smith (1947: fig. 29, a–c, as "*Schisandra propinqua* var. *intermedia*"); Law (1983b: fig. 189, as "*Schisandra propinqua* var. *intermedia*").

Phenology. Flowering from May to July; fruits maturing by September.

Distribution (Fig. 43). North-east India (Meghalaya and Nagaland), eastern Myanmar [Burma], northern Thailand, and China (Yunnan); mixed woodlands and open scrublands, often near rocky areas; (820–) 1070–2130 m.

ADDITIONAL SPECIMENS EXAMINED. **China.** YUNNAN: Xundian, *Y. P. Chang 869* (IBSC); Yunnansen, Tchong chan, *F. Ducloux 468* (UC); Lijiang, *K. M. Feng 9303* (IBSC); [precise locality not known], *G. Forrest 7686* (A); Lengyueh, 25°N, *G. Forrest 11845* (A, UC); [precise locality not known], *G. Forrest 15860* (A); [precise locality not known], *G. Forrest 19125* (A, K); Chien-chuan-Mekong divide, 26°40'N, 99°40'E, *G. Forrest 21523* (A); *G. Forrest 22245* (A, K); between rivers Djinscha-djiang ("Yangtse") & Landsang-djiang (Mekong), *H. F. von Handel-Mazzetti 8820*, pro parte (K); Landsang-djiang (Mekong), *H. F. von Handel-Mazzetti 10017* (A); Mengyi, Mengtze, *A. Henry 10719* (A, K); Szemao [=Simao], *A. Henry 13023* (A, K); Yun-nan-sen, *E. E. Maire 196* (UC); Kou ty, Pe yen tsin, *S. Ten 296* (A); Tcheu-mo, *S. Ten 391* (A); Pe Yen Tsin, *S. Ten 540* (A); Shang-pa, *H. T. Tsai 54643* (A); [precise locality not known], *H. T. Tsai 57088* (A); Shunning, Wenkuankuai, *T. T. Yü 16315* (A); Salwin Valley, *T. T. Yü 22054* (A). **India.** MEGHALAYA: "Khasia," s.a., *J. D. Hooker & T. Thomson s.n.* (E, GH, K, NY); "temperate," s.a., *J. D. Hooker & T. Thomson s.n.* (L).—NAGALAND: between Pushing & Kangkoi, *F. K. Ward 17495* (A); Zakhoma, Naga Hills, *F. K. Ward 19035* (NY). **Myanmar [Burma].** Kalaw, *F. G. Dickason 5076* (A); Maymyo Plateau, *J. H. Lace 5432* (E, K); *J. H. Lace 5875* (E, K); Sakangyi Res., near Maymyo, *J. H. Lace 5919* (E); Wetwun, near Maymyo Plateau, 11 Jul 1913, *J. H. Lace s.n.* (E); Pa gan chaung, Maymyo, *C. G. Parkinson 3133* (K); Singaungle, Maymyo, *C. G. Parkinson 12176* (K); near Maymyo, *A. Rodger 610* (E) **Thailand.** Trail between Samhaek & Mangpae, Phu Kradung, Loei, NE Province, *N. Fukuoka T-63689 [508]* (A); near Langpae, Phu Kradung, Loei, NE Province, *H. Takahashi T-63507 [1314]* (A).

22c. Schisandra propinqua subspecies **sinensis** (Oliver) R. M. K. Saunders, Edinb. J. Bot. 54: 280. 1997. *Schisandra propinqua* var. *sinensis* Oliver, Hook. Ic. Pl. 18: pl. 1715. 1887 (as "*Schizandra*"). *Schisandra propinqua* var. *linearis* Finet & Gagnepain, Bull. Soc. Bot. France 52, Mém. 4: 51. 1905 (as "*Schizandra*"), [reprinted as Contr. Fl. As. Or. 2: 51. 1907].—TYPE: CHINA. Hupeh [Hubei]: Vicinity of I-ch'ang, 1885–88, *A. Henry 1544* (lectotype, designated by Saunders, 1997b: GH!, photo: HKU!; isolectotypes: E! GH! K!, photo of GH isolectotype: HKU!).

Embelia valbrayi H. Léveillé, Cat. pl. Yunnan 177. 1916.—TYPE: CHINA. Yunnan: La-kou, Jul [1912], *E. E. Maire s.n.* (lectotype, designated by Saunders, 1997b: E!; isolectotypes: A [2]).

Leaf laminas (5.5–) 7.0–11.0 (–12.5) cm long, (1.0–) 1.5–3.5 (–4.5) cm wide, length: width ratio (2.2–) 2.5–5.0 (–5.7), papyraceous to subcoriaceous; margin serrulate, occasionally denticulate, rarely (sub-) entire or serrate, (0–) 2–7 (–10) teeth per side of leaf. Flowers borne solitary or in clusters in axil of leaf; peduncle 3–16 mm long. Male flowers comparatively small, largest tepals 3.1–5.8 mm long, 2.4–3.5 mm wide; androecium of 4–11 stamens, fused into a carnose mass ca. 1.8–2.4 mm in diameter. Female flowers with 8–15 tepals, largest tepals 4.6–6.2 mm long, 3.6–5.1 mm wide. Fruit peduncle long, 14–30 mm long; apocarps 4.5–8.5 mm long, 4–8.5 mm wide.

Illustrations. Oliver (1887: pl. 1715, as "*Schisandra propinqua* var. *sinensis*"); Smith (1947: fig. 29, j–l, as "*Schisandra propinqua* var. *sinensis*"); Wang (1980: fig. 1602, as "*Schisandra propinqua* var. *sinensis*"); Law (1996a: fig. 77, 1–10, as "*Schisandra propinqua* var. *sinensis*").

Phenology. Flowering from May to September; fruits maturing from August to December.

Distribution (Fig. 43). Widespread in central and southcentral China (Gansu, Guizhou, Hubei, Hunan, Shanxi, Sichuan, and Yunnan); a small number of specimens also collected in Xizang [Tibet]; woods (generally broad-leaved), often near ridges, slopes, and ravines; 400–2600 (–3100) m.

ADDITIONAL SPECIMENS EXAMINED. **China.** GANSU: Wenxian, *J.-X. Yang 3643* (IBSC); *J.-X. Yang & Z. X. Hu 3570* (IBSC).—GUIZHOU: Huang tsao fa, *J. Esquirol 1555* (K); Anlong, *Guizhou Expedition 3960* (IBSC); *Guizhou Expedition 4336* (IBSC); Xingyi, *Guizhou Expedition 6958* (IBSC); Tschenning-Huang-tsauba-Yunnan, *H. F. von Handel-Mazzetti 119* (A).—HUBEI: Patung Hsien, *H.-C. Chow 567* (A); *H.-C. Chow 898* (A); Chienshih Hsien, *H.-C. Chow 1439* (A); Ichang, *W. Y. Chun & S. S. Chien 5127* [*8090*] (UC); Ichang, *A. Henry 1693* (K, US; paratypes of *S. propinqua* var. *sinensis*), *2028* (K; paratype of *S. propinqua* var. *sinensis* and *S. propinqua* var. *linearis*), *3243* (K, US; paratypes of *S. propinqua* var. *sinensis*), *3354* (K), *3699* (GH, K), *3961* (GH, NY; paratypes of *S. propinqua* var. *linearis*); [precise locality not known], *A. Henry 6219* (E, GH, K; paratypes of *S. propinqua* var. *linearis*); Xuan'an, *H. C. Li 2945* (IBSC); Xingshan, *M. H. Nieh & Q.-H. Li 264* (IBSC); Changyang Hsien, *E. H. Wilson 485* (A, GH); *E. H. Wilson 1304* (A, E, IBSC, K, NY; paratypes of *S. propinqua* var. *linearis*); [precise locality not known], *E. H. Wilson 1565* (K); Shennongjian, *S. X. Yang 537* (IBSC).—HUNAN: Souxiyu, Cili, *K. S. Chow et al. 120* (A); Yangshun, *Hunan Expedition 524* (IBSC); Dayong, *S. C. Lee 204722* (IBSC); *S. C. Lee 204799* (IBSC).—SHANXI: Lüeyang, *C. Y. Chang 17810* (IBSC); *C. Y. Chang 17994* (IBSC); Chenggu, *C. Y. Chang 18169* (IBSC); Shangyang, *T. P. Wang 16535* (IBSC).—SICHUAN: [precise locality not known], *Anonymous 1893* (IBSC); Dujiangyan municipality (Guan Xian), mountain opposite Longxi, by E side of Longxi River, *D. E. Boufford & B. Bartholomew 24908* (A); 5 mi from Yaan, *C. Y. Chiao 1163* (A); Fengjie, *H. C. Chow & H.-Y. Li 110710* (IBSC); Lu-shan-hsien, *K. L. Chu 4003* (IBSC); Chengkou, *T. L. Dai 103218* (IBSC); Ningyüen, Lu-schan mountains, *H. F. von Handel-Mazzetti 1943* (A); Chungking [Chongqing], *A. Henry 781* (K); Tienchuan-Lingkwan highway, Shikong, *S. Y. Hu 941* (A); [precise locality not known], *T. N. Liou & C. Wang 264* (IBSC); Xichang, *M.-G. Liu & J.-L. Liu 122* (IBSC); Tianquan, *D. Y. Peng 45343* (IBSC); Eastern Sichuan, *Sichuan University 108563* (IBSC); *Sichuan University 109051* (IBSC); Yu-ch'i-k'on, *H. Smith 2366* (A); Pao-hsin-hsien, Mupin, *T. P. Soong 39439* (IBSC); Tien-chuan-hsien, *F. C. Tai & C. M. Teng 5307* (IBSC); Cult. Ya-an, *T. H. Tsang 1.306* (IBSC); [precise locality not known], *H. L. Tsiang 35048* (IBSC); N of Cheng-tu Plain, *F. T. Wang 22166* (A); [locality illegible], *E. H. Wilson 1070* (A); Wa-shan, *E. H. Wilson 1268b* (A); Wushan, *K. H. Yang 58216* (IBSC).—XIZANG [TIBET]: Jilong, *Qingzang Expedition 4609* (IBSC).—YUNNAN: Ma-ch'ou, *E. E. Maire 91* (A); Sep 1910, *E. E. Maire s.n.* (NY, UC; possible paratypes of *Embelia valbrayi*); Sep [1912], *E. E. Maire s.n.* (E; paratype of *Embelia valbrayi*); [precise locality not known], *E. E. Maire 237* (IBSC); La-kou, *E. E. Maire 2923* (NY, UC; possible paratypes of *Embelia valbrayi*); Tong-tchouan, *E. E. Maire 3650* (UC); Luquan, *P. I. Mao 1934* (IBSC).

Cultivated. South China Botanical Garden, Guangzhou, Guangdong, *G. Hao 102* (HKU); *R. M. K. Saunders 98/1* (HKU).

22d. Schisandra propinqua subspecies **axillaris** (Blume) R. M. K. Saunders, Edinb. J. Bot. 54: 282. 1997. *Sphaerostema axillare* Blume, Bijdr. fl. Ned. Ind. 22. 1825 (as "*Sphaerostema axillaris*"). *Schisandra axillaris* (Blume) Hooker f. & Thomson in Hooker f., Fl. Brit. Ind. 1: 45. 1872 (as "*Schizandra*").—TYPE: JAVA. Goenoeng Tjareme, ["in sylvis altis montis Tjerimai Provinciae Cheribon"], [date not known], *C. L. von Blume 66* (lectotype, designated by Saunders, 1997b: BO, photo: HKU!).

Sphaerostema pyrifolium Blume, Fl. Javae [Schizandreae] 16. 1830.—TYPE: JAVA. Tjiandjoer, [date not known], *C. G. C. Reinwardt s.n.* (lectotype, designated by Saunders, 1997b: L!, photo: HKU!; isolectotypes: L [3]!, photos: HKU!).

Leaf laminas 6–11.5 cm long, 2.0–4.5 (–5.0) cm wide, length:width ratio (2.0–) 2.3–3.2 (–3.5), generally coriaceous; margin entire, occasionally denticulate, 0–6 (–8) teeth per side of leaf. Flowers borne solitary in axil of leaf; peduncle (2–) 3–5 (–12) mm long. Male flowers comparatively large, largest tepals 4.3–7.5 mm long, 4.1–7.0 mm wide; androecium of 10–13 (–17) stamens, fused into a carnose mass 2.8–3.9 mm in diameter. Female flowers with 10–14 tepals, largest tepals ca. 4.8–7.8 mm long, 5.0–6.0 mm wide. Fruit peduncle short, 3–8 mm long; apocarps 6.5–8.5 mm long, 6.5–8 mm wide. Figs. 11A–C, 44.

Illustrations. Blume (1830: figs. 3–4, former as "*Sphaerostema axillaris*," latter as "*Sphaerostema pyrifolium*"); Koorders (1912: fig. 52, as "*Schisandra axillaris*," redrawn from Blume, 1830: fig. 4); Steenis (1972: fig. 29.4, as "*Schisandra axillaris*"); Saunders (1997a: fig. 2, reproduced in Saunders, 1997b: fig. 10).

Phenology. Flowering from March to October (Backer & Bakhuizen van den Brink, 1963: 100).

Distribution (Fig. 45). Endemic to Java and Bali; submontane to montane forests; 1200–2200 m. Koorders (1912) reports "*S. axillaris*" growing at altitudes of only 400 m.

ADDITIONAL SPECIMENS EXAMINED. **Bali.** G. Batoekaoe, *Sarip 368* (L). **Java.** Mt. Ijen, E Java, *J. J. Afriastini 1484* (L); G. Imeroe, *C. A. Backer 3656* (L); [precise locality not known], s.a., *C. L. von Blume s.n.* (K, L, NY); Papandayang, *C. L. von Blume 750* (L); [precise locality not known], *C. L. von Blume 1601* (L); Kedoe, *R. Brinkman 874a* (L); G. Kendih, Lawae, *J. H. Coert 746* (L); Lawae Larangas, *J. H. Coert 944* (L); Wawar batjing, s.a., *F. W. Junghuhn s.n.* (L); Preanger, Tjibodas, *S. H. Koorders 25982b* (L); Lemarang, Telomojo, *S. H. Koorders 28047b* (L); Ngadisari, *S. H. Koorders 37670b* (L); *S. H. Koorders 37671b* (L); *S. H. Koorders 37673b* (L); [Tjiandjoer], s.a., *C. G. C. Reinwardt s.n.* (L); Talom Ridoel, Preanger, *Soegandiredjo 128* (L); [precise locality not known], 1859–60, *G. H. de Vriese & J. E. Teijsmann s.n.* (L); Medinie, s.a., *F. A. C. Waitz s.n.* (L).

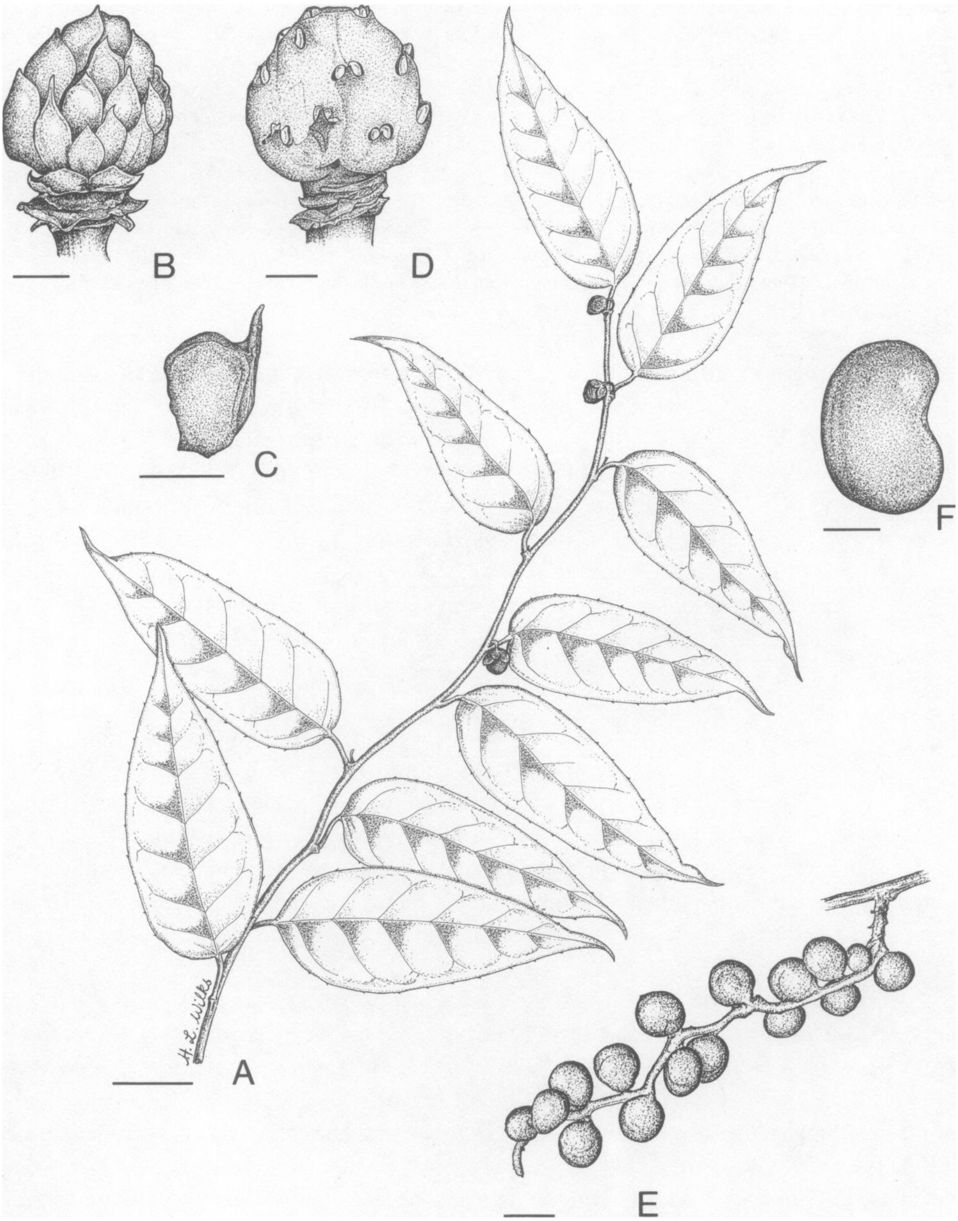


FIG. 44. *Schisandra propinqua* subsp. *axillaris* (*S.* subg. *Schisandra* sect. *Sphaerostema*). A, flowering branch. B, gynoecium. C, isolated carpel (lateral view). D, androecium. E, fruit. F, seed. Scale bars: A, 2 cm; B–D, 1 mm; E, 5 mm; F, 2 mm. (A, *C. L. Blume s.n.*, L; B, C, *J. H. Coert 944*, L; D, *R. Brinkman 874a*, L; E, F, *C. A. Backer 3656*, L.) Drawing by H. L. Wilks; reproduced from Saunders (1997a), © Rijksherbarium/ Hortus Botanicus, Leiden.

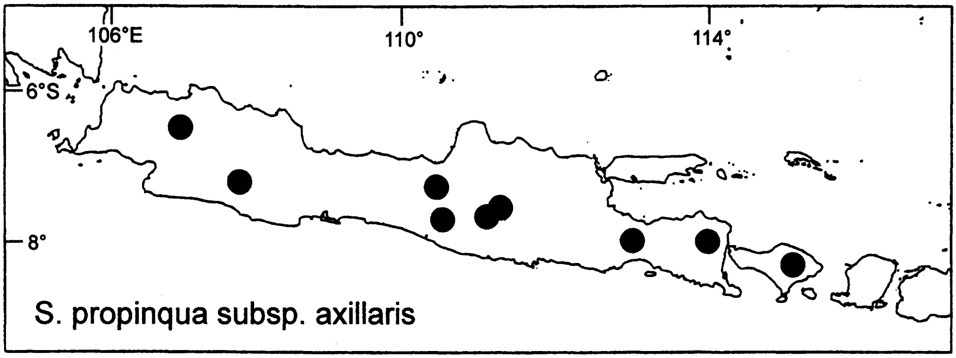


FIG. 45. Distribution of *Schisandra propinqua* subsp. *axillaris*.

23. Schisandra plena A. C. Smith, Sargentia 7: 154. 1947.—TYPE: CHINA. Yunnan: Ssumao/Sze-mao [Simao], 14 May [without year], *A. Henry 10854* (holotype: A!; isotypes: MO! NY! US, photo of NY isotype: HKU!).

Woody vines, apparently dioecious (but probably monoecious). Lateral branches lacking wings, with fugaceous perules at base; branches continuing growth in subsequent years. Leaf laminas (8–) 8.5–13.5 (–14) cm long, 3.5–5 cm wide, length:width ratio 1.8–3.0 (–3.3), papyraceous to subcoriaceous, glabrous, (ovate-) elliptic; primary vein (slightly) impressed above, prominent below; secondary veins 5–7 pairs per leaf, (slightly) arcuate; tertiary and quaternary venation very intricate and prominent above; base obtuse (acute in younger leaves); apex (short-) acuminate; margin entire; petioles glabrous, 13–16 (–19) mm long, 1.1–1.6 (–2.0) mm in diameter. Flowers borne axillary to leaves, solitary or in clusters; tepals 12–15 (–17) (male flowers), ca. 13 (female flowers); tepals white or pale yellow, red at base, glabrous; outermost tepal ovate, 0.8–1.0 mm long, 1.3–1.4 mm wide, length:width ratio 0.6–0.8; largest tepal ovate or obovate, 8.6–9.7 mm long, 4.0–4.2 mm wide, length:width ratio 2.1–2.4; outermost tepal highly reduced, ca. 0.1 of length of largest; innermost tepal often slightly reduced; peduncles glabrous, 7–15 mm long, ca. 0.6–0.7 mm in diameter (male flowers). Male flowers with androecium of ca. 8 stamens, fused into a carnose mass, 4.5–6 mm long, narrowing towards base, 3–4 mm wide, with sessile anthers; thecae on opposing sides of cavity, dehiscing towards each other; pollen hexacolpate. Female flowers with gynoecium of ca. 31 free carpels, gynoecium ca. 4 mm long, 4 mm wide; carpels ca. 1.2 mm long, 0.9 mm wide, length:width ratio ca. 1.3; pseudostyle subulate. Fruit peduncles glabrous, not significantly elongated, 1–1.5 cm long; torus 5–17 cm long [fide Smith, 1947: 156]; apocarps (orange-) red, ca. 10 mm long, ca. 12 mm wide, length:width ratio ca. 0.9. Seeds 1–2 per apocarp, flattened-elliptical, 5.5–6 mm long, 7–7.5 mm wide [fide Smith 1947: 156], testa ± smooth. Chromosome number unknown. Fig. 11D, E.

Illustrations. Smith (1947: fig. 29, d–i); Law (1996a: fig. 77, 11–15).

Phenology. Flowering in April and May; fruits maturing in August and September.

Distribution (Fig. 46). North-east India (Arunachal Pradesh) and China (Yunnan); dense woodlands; 600–1520 m.

ADDITIONAL SPECIMENS EXAMINED. **China.** YUNNAN: [precise locality not known], s.a., *Anonymous s.n.* (IBSC 174186); *A. Henry 11749* (A); *A. Henry 11893* (A, K); *A. Henry 12192* (A, K); Mengla, 12 Dec 1983,

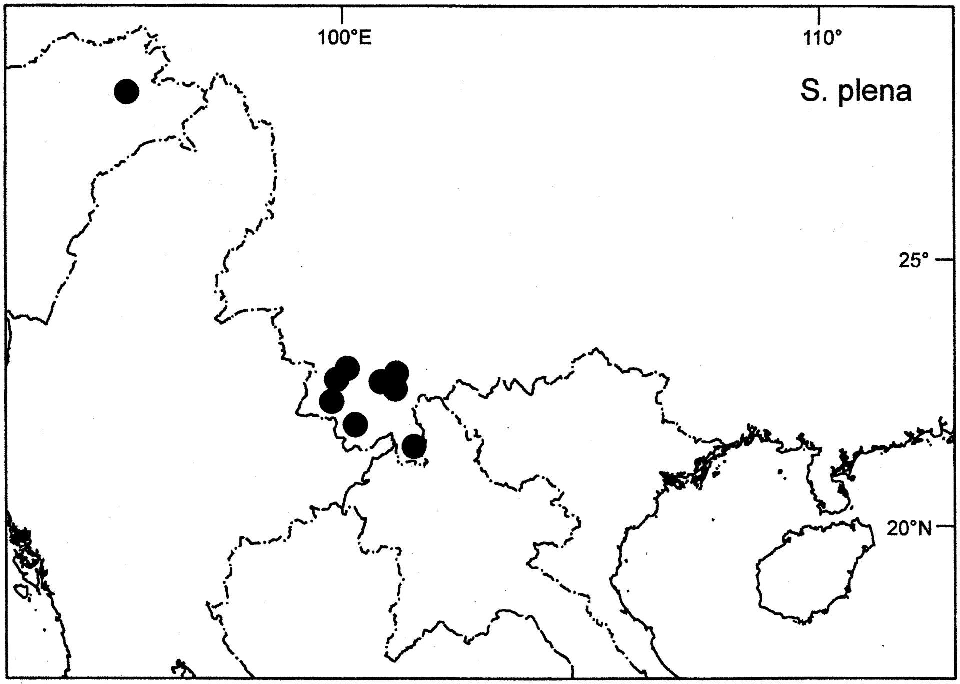


FIG. 46. Distribution of *Schisandra plena.*

C.-J. Liao s.n. (IBSC); Menghai Xian, *Z. H. Tsi 92–392* (A); Keng-Ma, *C. W. Wang 73145* (A); Maan-bang, Dahmeng-lung, Che-li Hsien, *C. W. Wang 76340* (A); Che-li Hsien, *C. W. Wang 78784* (A). **India.** ARUNACHAL PRADESH: Delei Valley, 28°05′N, 96°30′E, *F. K. Ward 8009* (K [photo]).

Male flowers of *S. plena* have a carnose androecial mass derived by the fusion of stamens. This feature is diagnostic for sect. *Sphaerostema*, and is consequently shared with only one other species, *S. propinqua*. The androecial mass is rather elongate in *S. plena*, with sessile thecae that are borne on the opposing sides of the associated cavity; in contrast, the androecial mass is subglobose in *S. propinqua*, and the thecae are borne on short free connectives adjacent to the androecial cavities. Differences are furthermore apparent in the number of tepals in male flowers of the two species: *S. plena* has 12–15 (–17) tepals, whereas *S. propinqua* has only (7–) 8–10 (–12).

The leaves of *S. plena* are also diagnostically important, since the laminas are comparatively large (8–14 × 3.5–5 cm) and have an intricate venation pattern, in which the secondary, tertiary, and quaternary veins are prominent adaxially.

Schisandra plena has a very restricted distribution (Fig. 46) in Yunnan, with one further collection from north-east India (Arunachal Pradesh state). Although it is over 50 years since Smith (1947) published his monograph, very few additional collections of this species have been made, and I was able to examine only three collections not previously studied by Smith.

Crystalliferous sclerenchyma cells are illustrated by Bailey and Nast (1948), and pollen morphology is described by Praglowski (1976).

FOSSIL TAXA

All species are listed as accepted taxa, without attempt at identifying synonyms. Information on the geological age of the taxa and the part of the plant fossilized is given in Appendix 3.

Schisandra durbudensis S. Guo, Acta Palaeontol. Sin. 23: 87. 1984.

Schisandra europaea H. Jähnichen, Abh. Zentr. Geol. Inst., Paläntol. Abh. 26: 151–155. 1976.

Schisandra florini T. Tanai, J. Fac. Sci., Hokkaido Univ., ser. 4, Geol. Mineral. 17: 308–310. 1976.
Schisandra chinensis (Turczaninow) Baillon sensu Florin, Kongl. Svenska Vetenskapsakad. Handl. 61: 31–32. 1920.

Schisandra fushuensis Li in Writing Group for Cenozoic Plants of China, Fossil plants from China 3: 29. 1978.

Schisandra geissertii H.-J. Gregor, Mitt. Bad. Landesvereins Naturk. Naturschutz Freiburg 12: 243–244. 1981.

Schisandra glandulosa Tao in Writing Group for Cenozoic Plants of China, Fossil plants from China 3: 29. 1978.

Schisandra grossheimi A. A. Kolakovskij, Trudy Suhumsk. Bot. Sada 10: 292–293. 1957.

Schisandra megasperma S. Miki, Jap. J. Bot. 11: 274. 1941.

Schisandra oregonensis S. R. Manchester, Palaeontogr. Amer. 58: 87–88. 1994.

Schisandra splendinervosa S. Guo, ined.—This name has not been formally published (Guo Shuang-xing, pers. comm.).

DOUBTFUL AND EXCLUDED NAMES

Maximowiczia japonica A. Gray ex K. Koch, Dendrologie 1: 386. 1869, pro syn. (as "*Maximowitschia*"). [*Schisandra chinensis* (Turczaninow) Baillon]

Schisandra subg. **Liberostema** Y.-W. Law, Rep. abstr. meeting 50th anniv. Bot. Soc. China 155. 1983, nomen nudum. [*Schisandra* section *Maximowiczia* (Ruprecht) Nakai]

Schisandra chinensis var. **glabrata** Nakai ex Mori, Enum. pl. Corea 166. 1922 (as "*Schizandra*"), nomen nudum. [Source of name: Korea. Mt. Unsan, Pyonganpuk Do, 10 Jun 1912, *T. Ishidoya s.n.* (TI!); *Schisandra chinensis* (Turczaninow) Baillon]

Schisandra chinensis var. **rubra** Sprenger, Mitt. Deutsch. Dendr. Ges. 16: 68. 1908 ("1907") (as "*Schizandra*").—TYPE: CHINA. Shen-si [Shaanxi], [date not known], *G. Giraldi* [collection number not known] (not located).—Giraldi's plant collections were deposited in FI (Holmgren et al. 1990: 190), and it is presumably from this herbarium that Sprenger (working in Naples) obtained the specimen that he used as the basis for his new variety. Sprenger's (1908: 68) description was very short ("Die Varietät hat kupferrote Blüten"), and his citation of the type specimen omitted a detailed collection locality, collection number, and date. Photographs of two of Giraldi's collections labelled "*S. chinensis*" were provided by FI, viz.: *Giraldi 452* (a flowering specimen collected on 20 May 1892 from Griu-ju-san, northern Shen-si [Shaanxi]); and *Giraldi 5481* (a fruiting specimen collected on 22 July1894 from Monte Si-ku-zui-san, Shen-si [Shaanxi]). Since the protologue refers to flower color, only *Giraldi 452* could possibly be original material; this specimen has not been annotated by Sprenger, however, and thus it is uncertain whether he actually examined it. Precise taxonomic determination of *Giraldi 452* is not possible, although it is clearly not *S. chinensis*. Smith (1947: 103), who was also unable to trace Sprenger's type, considered Sprenger's variety a putative synonym of *S. rubriflora*. The geographical origin of Giraldi's collections clearly indicate that this interpretation cannot be correct, and it is more probable that *S. chinensis* var. *rubra* refers to an extreme northern population of *S. sphenanthera*.

Schisandra crassifolia Pierre ex Finet & Gagnepain, Bull. Soc. Bot. France 54: 85. 1907 (as "*Schizandra*"). = ? *Kadsura heteroclita* (Roxburgh) Craib, Fl. Siam. 1: 28. 1925 ["1931"], pro parte (Schisandraceae); and ? *Kadsura verrucosa* (Gagnepain) A. C. Smith, Sargentia 7: 195–196. 1947, pro parte (Schisandraceae) [see discussion in Saunders (1998: 53–54)].

Schisandra elongata var. **marmorata** H. Hallier, Bull. Herb. Boissier 6: 214. 1898 [as "*Schizandra*"].—TYPE: Based on a sterile plant cultivated at the botanical garden in Buitenzorg [Bogor].—Application of this name is unclear. It does not apply to *Schisandra marmorata* (E. G. Henderson & A. Henderson) Hemsl. (basionym: *Sphaerostema marmoratum* E. G. Henderson & A. Henderson) [=*Kadsura marmorata* (E. G. Henderson & A. Henderson) A. C. Smith], as suggested by Hallier (1898).

Schisandra hanceana Baillon, Hist. pl. 1: 150. 1868 (as "*Schizandra*"). = *Kadsura coccinea* (Lemaire) A. C. Smith, Sargentia 7: 166. 1947 (Schisandraceae).

Schisandra japonica Siebold & Zuccarini ex A. Gray, Mem. Amer. Acad. Arts, n.s. 6: 380. 1859, pro syn. (as "*Schizandra*"). [*Schisandra chinensis* (Turczaninow) Baillon]

Schisandra marmorata (E. G. Henderson & A. Henderson) Hemsley, Garden 8: 271. 1875 (as "*Schizandra*"). = *Kadsura marmorata* (E. G. Henderson & A. Henderson) A. C. Smith, Sargentia 7: 196. 1947 (Schisandraceae).

Schisandra nigra var. **hypoleuca** Makino [cited in Ohwi 1965]. *Schisandra repanda* f. *hypoleuca* (Makino) J. Ohwi [cited in Ohwi 1965].—TYPE: unknown.—

Although Makino's name is presumably synonymous with *S. repanda*, no formal publication details have been discovered, and it is probably a nomen nudum.

Schisandra ovalifolia Parmentier, Bull. Sci. France Belgique 27: 237, 312. 1896 (as "*Schizandra*"). = *Kadsura scandens* (Blume) Blume, Fl. Javae [Schizandreae] 9. 1830 (Schisandraceae).

Schisandra verrucosa Gagnepain, Not. Syst. (Paris) 8: 66. 1939 (as "*Schizandra*"). = *Kadsura verrucosa* (Gagnepain) A. C. Smith, Sargentia 7: 195. 1947 (Schisandraceae).

Schizostigma axillare Hooker f. & Thomson ex Merrill, Enum. Philipp. fl. pl. 2: 153. 1923, sphalm. = *Schisandra propinqua* subsp. *axillaris* (Blume) R. M. K. Saunders.

Sphaerostema blumiana Griffith, Notul. pl. Asiat. 4: 714. 1854 (as "*Sphaerostemma*"). = *Kadsura heteroclita* (Roxburgh) Craib, Fl. Siam. 1: 28. 1925 ["1931"] (Schisandraceae).

Sphaerostema japonicum Siebold & Zuccarini, Abh. Bayer. Akad. Wiss., Math.-Naturwiss. Kl. 4: 188. 1845, nomen nudum. [reprinted in Fl. Jap. fam. nat. 1: 80. 1845.] (as "*Sphaerostemma japonica*"). [*Schisandra chinensis* (Turczaninow) Baillon]

Sphaerostema marmoratum E. G. Henderson & A. Henderson, Ill. bouquet 2: fig. 40. 1859–61. = *Kadsura marmorata* (E. G. Henderson & A. Henderson) A. C. Smith, Sargentia 7: 196. 1947 (Schisandraceae).

Sphaerostema pyrifolium var. **denticulatum** Blume ex Koorders, Exkursionsfl. Java 2: 243. 1912, pro syn. (as "*Sphaerostemma pirifolium*"). [*Schisandra propinqua* subsp. *axillaris* (Blume) R. M. K. Saunders]

Uvaria pyrifolia Reinwardt ex Blume, Fl. Javae [Schizandreae] 16. 1830, pro syn. [*Schisandra propinqua* subsp. *axillaris* (Blume) R. M. K. Saunders]

MISAPPLIED NAMES

Schisandra arisanensis subsp. **viridis** (A. C. Smith) R. M. K. Saunders.
Schisandra sphenanthera auctt. non Rehder & E. H. Wilson; Rehder & Wilson, J. Arnold Arbor. 8: 110. 1927; Merrill & Chun, Sunyatsenia 1: 57. 1930 (as "*Schizandra*"); W.-C. Cheng, Contr. Biol. Lab. Chin. Assoc. Advancem. Sci., Sect. Bot. 8: 138. 1932; W.-C. Cheng, Contr. Biol. Lab. Chin. Assoc. Advancem. Sci., Sect. Bot. 9: 283. 1934.

Schisandra bicolor W.-C. Cheng.
Schisandra elongata auct. non Baillon; Wilson, J. Arnold Arbor. 7: 238. 1926.

Schisandra chinensis (Turczaninow) Baillon.

Polycarpa maximowiczii auct. non Linden ex Carr.; Morren & de Vos, Ind. bibl. hort. Belg. 437. 1887, pro syn.

Idesia polycarpa auct. non Maximowicz; Morren & de Vos, Ind. bibl. hort. Belg. 437. 1887, pro syn.

Schisandra glaucescens Diels.

Schisandra elongata auctt. non Baillon; Diels, Bot. Jahrb. Syst. 29: 322. 1900; Finet & Gagnep., Bull. Soc. Bot. France 52, Mém. 4: 49. 1905 [reprinted as Contr. Fl. As. Or. 2: 49. 1907].

Schisandra henryi subsp. **marginalis** (A. C. Smith) R. M. K. Saunders.

Schisandra henryi auct. non Clarke; Cheng, Contr. Biol. Lab. Chin. Assoc. Advancem. Sci., Sect. Bot. 9: 284. 1934.

Schisandra incarnata Stapf.

Schisandra grandiflora auct. non Hooker f. & Thomson; Finet & Gagnepain, Bull. Soc. Bot. France 52, Mém. 4: 48. 1905, pro parte (as "*Schizandra*") [reprinted as Contr. Fl. As. Or. 2: 48. 1907]; Rehder & Wilson in Sargent, Pl. Wilson. 1: 411. 1913.

Schisandra lancifolia (Rehder & E. H. Wilson) A. C. Smith.

Schisandra sphenanthera auct. non Rehder & E. H. Wilson; Wilson, J. Arnold Arbor. 7: 237. 1926.

Schisandra neglecta A. C. Smith.

Sphaerostema elongatum auctt. non Blume; Hooker f. & Thomson, Fl. Ind. 1: 85. 1855; Walpers, Ann. Bot. 4: 79. 1857; Drury, Hand-book Ind. fl. 1: 648. 1864.

Schisandra elongata auctt. non Baillon; Hooker f. & Thomson in Hooker f., Fl. Brit. Ind. 1: 44. 1872 (as "*Schizandra*"); King, Ann. Bot. Gard. Calcutta 3: 220. 1891 (as "*Schizandra*"); Wilson, J. Arnold Arbor. 7: 238. 1926.

Schisandra propinqua auct. non Baillon; Handel-Mazzetti, Symb. Sin. 7: 245. 1931 (as "*Schizandra*").

Schisandra perulata Gagnepain.

Schisandra grandiflora auct. non Hooker f. & Thomson; Merrill, J. Arnold Arbor. 19: 28. 1938.

Schisandra plena A. C. Smith.

Schisandra propinqua auct. non Baillon; Rehder & Wilson in Sargent, Pl. Wilson. 1: 416. 1913.

Schisandra propinqua subsp. **intermedia** (A. C. Smith) R. M. K. Saunders.

Sphaerostema axillare auctt. non Blume; Hooker f. & Thomson, Fl. Ind. 1: 86. 1855; Drury, Hand-book Ind. fl. 1: 649. 1864; Walpers, Ann. Bot. 4: 79. 1857.

Schisandra axillaris sensu Hooker f. & Thomson, quoad specim. et descript., excl. basionym; Hooker f. & Thomson, Fl. Brit. Ind. 1: 45. 1872; King, Ann. Bot. Gard., Calcutta 3: 220. 1891.

Schisandra propinqua auct. non Baillon; Kanjilal et al., Fl. Assam 1(1): 28. 1934 (as "*Schizandra*").

Schisandra verrucosa auct. non Gagnepain; J. F. Maxwell, Nat. Hist. Bull. Siam Soc. 44: 11. 1996.

Schisandra rubriflora Rehder & E. H. Wilson.

Schisandra grandiflora auct. non Hooker f. & Thomson; Franchet, Bull. Soc. Bot. France 33: 385. 1886; Finet & Gagnepain, Bull. Soc. Bot. France 52, Mém. 4: 48. 1905.

Schisandra sphenanthera auct. non Rehder & E. H. Wilson; Kanjilal et al., Fl. Assam 1: 28. 1935 (as "*Schizandra*").

Schisandra sphaerandra Stapf.

Schisandra glaucescens auct. non Diels; Wilson, J. Arnold Arbor. 7: 237. 1926.

Schisandra grandiflora auct. non Hooker f. & Thomson; Handel-Mazzetti, Symb. Sin. 7: 244. 1931, pro parte (as "*Schizandra*").

Schisandra grandiflora var. *cathayensis* auct. non C. K. Schneider; Wilson, J. Arnold Arbor. 7: 238. 1926 (as "*Schizandra*").

Schisandra rubriflora auct. non Rehder & E. H. Wilson; Wilson, J. Arnold Arbor. 7: 238. 1926.

Schisandra sphenanthera Rehder & E. H. Wilson.

? *Schisandra chinensis* auctt. non Baillon; Maxim., Trudy Imp. S.-Petersburgsk. Bot. Sada 11: 39. 1889 (as "*Schizandra*"); Diels, Bot. Jahrb. Syst. 29: 322. 1900 (as "*Schizandra*").

? *Schisandra japonica* auct. non A. Gray; Hance, J. Bot. 18: 258. 1880 (as "*Schizandra*").

ACKNOWLEDGMENTS

Financial support for this project was provided by grant HKU 7247/97M from the Hong Kong Research Grants Council. I am grateful to the directors of the following herbaria for the loan of, or access to, their collections: A, BO, C, E, FI, GH, HK, IBSC, K, L, MO, NAS, NY, O, P, TI, UC, and US (acronyms acording to Holmgren et al. 1990). I am particularly grateful to Professor Hu Chi-ming and the staff at IBSC for their hospitality during several visits to Guangzhou. FAA-preserved material was kindly provided by: Dr. Chaw Shu-Miaw (Institute of Botany, Academia Sinica, Taipei, Taiwan); Dr. Paul Goetghebeur (University of Gent, Belgium); Dr. Lin Qi (South China Institute of Botany, Academia Sinica, Guangzhou, Guangdong); Dr. Jose L. Panero (University of Texas, Austin, Texas); and Dr. Zhang Yong-Yu (Shenyang Pharmaceutical University, Shenyang, Liaoning). I am indebted to Dr. G. D. Brown (Department of Chemistry, The University of Hong Kong) for contributing the chapter on phytochemistry, and Professor Guo Shuang-xing (Nanjing Institute of Geology and Palaeontology, Academia Sinica, Nanjing, Jiangsu) for information on fossil species of *Schisandra.* I also thank: Yvonne Su, Cecily Law, Sophie Chan, and Hilda Ho for general technical assistance; Hazel Wilks and Sue Stanley for the excellent line drawings; Hao Gang for translating numerous herbarium labels and for discussions on phylogeny; the staff of the Electron Microscope Unit at the University of Hong Kong; the interlibrary loans staff at the University of Hong Kong Library; and Christiane Anderson and two anonymous reviewers for their invaluable comments. Additional photographs (subsequently computer enhanced) were supplied by the library at K (Frontispiece, Plates 1–5). I am particularly grateful to my wife, Sue, for her patience and support, and my children, David and Arran, for their distractions.

LITERATURE CITED

Agababian, V. 1966. Pollen morphology of some primitive angiosperms. Biol. Zhurn. Armenii 19: 77–89. [In Russian]

______. 1968. Palynologia Magnolianae. 1. Palynomorfologia. Uconye zap. Jerevanskovo. Univ. 3: 151–167. [In Russian]

______. 1973. *Pollen of primitive angiosperms.* Bot. Inst. Akad. Nauk. Armenia, SSR. [In Russian]

Agababian, V., and E. L. Zavarian. 1974. Some peculiarities of sporoderm formation in angiosperms. Biol. Zhurn. Armenii 27: 21–25 + pl. 1–2. [In Russian]

Altschul, S. von Reis. 1973. *Drugs and foods from little-known plants.* Cambridge, Massachusetts: Harvard University Press.

Anonymous (ed.). 1965. Documented chromosome numbers of plants. Madroño 18: 122–126.

Arora, R. K., and A. Pandey. 1996. *Wild edible plants of India: diversity, conservation and use.* New Delhi: Indian Council of Agricultural Research.

Backer, C. A., and R. C. Bakhuizen van den Brink. 1963. *Flora of Java.* Vol. 1. Groningen: Noordhoff.

Bailey, I. W., and C. G. Nast. 1948. Morphology and relationships of *Illicium*, *Schisandra* and *Kadsura*. I. Stem and leaf. J. Arnold Arbor. 29: 77–89.

Bailey, I. W., and B. G. L. Swamy. 1951. The conduplicate carpel of dicotyledons and its initial trends of specialization. Amer. J. Bot. 38: 373–379.

Baillon, H. 1868. *Histoire des plantes.* Vol. 1. Paris: Hachette.

Bao, T.-T., G.-F. Xu, G.-T. Liu, R.-H. Sun, and Z.-Y. Song. 1979. Comparison of the pharmacological effects of seven constituents isolated from the fruit of Schizandrae. Acta Pharm. Sin. 14: 1–7. [In Chinese]

Baranova, M. A. 1981. On the laterocytic type of stomatal apparatus in Angiospermae. Bot. Zhurn. 66: 179–186. [In Russian]

______. 1983. On the laterocytic stomatotype in angiosperms. Brittonia 35: 93–102.

______. 1992. The epidermal structures and systematic position of the Austrobaileyaceae. Bot. Zhurn. 77: 1–17.

Barthlott, W., C. Neinhuis, D. Cutler, F. Ditsch, I. Meusel, I. Theisen, and H. Wilhelmi. 1998. Classification and terminology of plant epicuticular waxes. Bot. J. Linn. Soc. 126: 237–260.

Baskin, C. C., and J. M. Baskin. 1998. *Seeds: ecology, biogeography, and evolution of dormancy and germination.* San Diego: Academic Press.

Batygina, T. B., and V. E. Vasilyeva. 1995. *Oenothera*-type of embryo sac development in angiosperm plants. Bot. Zhurn. 80: 1–16. [In Russian]

Behnke, H.-D. 1988. Sieve-element plastids, phloem protein, and evolution of flowering plants: III. Magnoliidae. Taxon 37: 699–732.

Bentham, G., and J. D. Hooker. 1862. *Genera plantarum.* Vol. 1. London: A. Black.

Benzing, D. H. 1967. Developmental patterns in stem primary xylem of woody Ranales. I. Species with unilacunar nodes. Amer. J. Bot. 54: 805–813.

Berger, F. 1952. *Handbuch der Drogenkunde: Erkennung, Wertbestimmung und Anwendung.* Wien & Düsseldorf: Wilhelm Maudrich.

Bi, C. 1987. Wuweizi. In *Pharmacology and applications of Chinese materia medica.* Vol. 2, ed. H. M. Chang and P. P. H. But, 199–209. Singapore: World Scientific Publishing.

Bir, S. S. (ed.). 1988. SOCGI plant chromosome number reports VII. J. Cytol. Genet. 23: 219–228.

Bir, S. S., B. S. Gill, Y. S. Bedi, and V. K. Singhal. 1980. Evolutionary status of the woody taxa of Garhwal Himalaya. In *Improvement of forest biomass: symposium proceedings*, ed. P. K. Khosla, 81–96. Solan, India: Indian Council of Agricultural Research.

Biswas, B. 1973. Quaternary changes in sea-level in the South China Sea. Bull. Geol. Soc. Malaysia 6: 229–255.

Blenk, P. 1884. Ueber die durchsichtigen Punkte in den Blättern. Flora, n.s. 42: 49–57.

Blume, C. L. 1825. *Bijdragen tot de flora van Nederlandsch Indië.* Batavia: Lands Drukkerij.

______. 1830. *Flora Javae. [Schizandreae].* Brussels: J. Frank.

Bones, T. J. 1979. Atlas of fossil fruits and seeds from north central Oregon. Oregon Mus. Sci. Indust. Occas. Papers Nat. Sci. 1: 1–23.

Bostick, P. E. 1965. Documented plant chromosome numbers 65: 2. Sida 2: 165–168.

Brickell, J. 1803. Botanical intelligence. Med. Repos. 6: 327–328.

Buckingham, J. (ed.). 1997. *Dictionary of natural products on CD-ROM, version 7.1.* London: Chapman & Hall.

Bůžek, Č., F. Holý, and Z. Kvaček. 1996. Early Miocene flora of the Cypris Shale (western Bohemia). Acta Musei Nat. Pragae, ser. B, Hist. Nat. 52: 1–172.

Candolle, A. P. de. 1818 ["1817"]. *Regni vegetabilis systema naturale.* Vol. 1. Paris: Treuttel & Würtz.

→ Carlquist, S. 1992. Pit membrane remnants in perforation plates of primitive dicotyledons and their significance. Amer. J. Bot. 79: 660–672.

______. 1999. Wood and bark anatomy of Schisandraceae: implications for phylogeny, habit, and vessel evolution. Aliso 18: 45–55.

Chappell, J., and B. G. Thom. 1977. Sea levels and coasts. In *Sunda and Sahul: prehistoric studies in Southeast Asia, Melanesia and Australia*, ed. J. Allen, J. Golson, and R. Jones, 275–291. London: Academic Press.

→ Chase, M. W., D. E. Soltis, R. G. Olmstead, D. Morgan, D. H. Les, B. D. Mishler, M. R. Duvall, R. A. Price, H. G. Hills, Y.-L. Qiu, K. A. Kron, J. H. Rettig, E. Conti, J. D. Palmer, J. R. Manhart, K. J. Sytsma, H. J. Michaels, W. J. Kress, K. G. Karol, W. D. Clark, M. Hedrén, B. S. Gaut, R. K. Jansen, K.-J. Kim, C. F. Wimpee, J. F. Smith, G. R. Furnier, S. H. Strauss, Q.-Y. Xiang, G. M. Plunkett, P. S. Soltis, S. M. Swensen, S. E. Williams, P. A. Gadek, C. J. Quinn, L. E. Eguiarte, E. Golenberg, G. H. Learn Jr., S. W. Graham, S. C. H. Barrett, S. Dayanandan, and V. A. Albert. 1993. Phylogenetics of seed plants: an analysis of nucleotide sequences from the plastid gene *rbc*L. Ann. Missouri Bot. Gard. 80: 528–580.

Chen, C.-C., C.-C. Shen, Y.-Z. Shih, and T.-M. Pan. 1994. 6-*O*-Benzoylgomisin O, a new lignan from the fruits of *Schizandra chinensis*. J. Nat. Prod. 57: 1164–1165.

Chen, J., Y.-C. Su, G.-Q. Chen, and W.-D. Wang. 1999. Ethnobotanical studies on wild edible fruits in southern Yunnan: folk names; nutritional value and uses. Econ. Bot. 53: 2–14.

Chen, R.-Y., S.-H. Lin, W.-Q. Song, X.-L. Li, G.-L. Liang, and Z.-P. An. 1993. *Chromosome atlas of Chinese principal economic plants.* Vol. 1. Beijing: International Academic Publishers.

Chen, Y., J. Yue, and S. Hua. 1987. Analysis of the constituents of *Schisandra.* (II). Structure of a new constituent, ganwuweizic acid. Chem. J. Chin. Univ. 8: 447–448. [In Chinese]

Chen, Y.-Y., and L.-N. Li. 1977. Studies on fruit of *Schisandra.* Structure determination of wuweizi A and wuweizi ester B. Acta Chim. Sin. 34: 45–52. [In Chinese]

Chen, Y.-Y., Z.-B. Shu, and L.-N. Li. 1976. Studies on fructus Schizandrae. IV. Isolation and determination of the active compounds (in lowering high SGPT levels) of *Schizandra chinensis* Baill. Sci. Sin. 19: 276–290.

Chen, Y.-Y., and Y. Yang. 1982. Studies on the SGPT-lowering active component of the fruits of *Schisandra rubriflora* Rehd. et Wils. Acta Pharm. Sin. 17: 312–313. [In Chinese]

Cheng, C. Y. 1944a. *Schizandra henryi* Clarke. In *Icones plantarum Omeiensium.* Vol. 1(2), ed. W.-P. Fang, pl. 70. Chengdu, Sichuan: National Sichuan University.

______. 1944b. *Schizandra sphenanthera* Rehder et Wilson var. *pubinervis* Rehder et Wilson. In *Icones plantarum Omeiensium.* Vol. 1(2), ed. W.-P. Fang, pl. 71. Chengdu, Sichuan: National Sichuan University.

______. 1944c. *Schizandra pubescens* Hemsley et Wilson. In *Icones plantarum Omeiensium.* Vol. 1(2), ed. W.-P. Fang, pl. 72. Chengdu, Sichuan: National Sichuan University.

Cheng, W.-C. 1932. Plantae novae Chekiangenses. Contr. Biol. Lab. Chin. Assoc. Advancem. Sci., Sect. Bot. 8: 135–142.

Cheo, T.-Y. 1947. Medicinal plants of Omei-Shan. Bot. Bull. Acad. Sin. 1: 298–308.

Chinese Academy of Medical Sciences, X-ray Diffraction Group. 1977. The crystal structure of p-bromobenzoyloxy ester of schizandrin. Chin. Sci. Bull. 22: 504–506. [In Chinese]

Chmura, C. A. 1973. Upper Cretaceous (Campanian-Maastrichtian) angiosperm pollen from the western San Joaquin Valley, California, U.S.A. Palaeontographica Abt. B 141: 89–171.

Clarke, C. B. 1905. New or noteworthy plants. Gard. Chron. 38: 162–163.

Collinson, M. E. 1992. Vegetational and floristic changes around the Eocene/Oligocene boundary in western and central Europe. In *Eocene-Oligocene climatic and biotic evolution*, ed. D. R. Prothero and W. A. Berggren, 437–450. Princeton, New Jersey: Princeton University Press.

Corner, E. J. H. 1976. *The seeds of dicotyledons.* Vols. 1, 2. Cambridge: Cambridge University Press.

Crawford, M. 1992. *Useful plants for temperate climates.* Vol. 2. *Shrubs.* Torquay, Devon: Agroforestry Research Trust.

Cronquist, A. 1981. *An integrated system of classification of flowering plants.* New York: Columbia University Press.

Cullen, J., and J. Howe. 1989. *Schisandra* Michaux. In *The European garden flora.* Vol. 3. *Dicotyledons (Part 1)*, ed. S. M. Walters, J. C. M. Alexander, A. Brady, C. D. Brickell, J. Cullen, P. S. Green, V. H. Heywood, V. A. Matthews, N. K. B. Robson, P. F. Yeo, and S. G. Knees, 318. Cambridge: Cambridge University Press.

Dahlgren, R. M. T. 1980. A revised system of classification of the angiosperms. Bot. J. Linn. Soc. 80: 91–124.

Dalla Torre, C. G. de, and H. Harms. 1900–07. *Genera siphonogamarum ad systema Englerianum conscripta.* Leipzig: Wilhelm Engelmann.

Dandy, J. E. 1927. The genera of Magnoliaceae. Kew Bull. 1927: 257–264.

______. 1938. *Schisandra sphenanthera*. Bot. Mag. 34: pl. 8921.

Darlington, C. D., and A. P. Wylie. 1955. *Chromosome atlas of flowering plants*. London: George Allen & Unwin.

Diels, L. 1900. Die Flora von Central-China. Nach der vorhandenen Litteratur und neu mitgeteiltem Original-Materiale. Bot. Jahrb. Syst. 29: 169–659.

Don, G. 1831. *A general history of dichlamydeous plants*. Vol. 1. [Also published as *A general system of gardening and botany*]. London: J. G. & F. Rivington et al.

Donoghue, M. J., and J. A. Doyle. 1989. Phylogenetic analysis of angiosperms and the relationships of the Hamamelidae. In *Evolution, systematics, and fossil history of the Hamamelidae*. Vol. 1. *Introduction and "lower" Hamamelidae*, ed. P. R. Crane and S. Blackmore, 17–45. Oxford: Clarendon Press.

→ Doyle, J. A., C. L. Hotton, and J. V. Ward. 1990. Early Cretaceous tetrads, zonasulculate pollen, and Winteraceae. II. Cladistic analysis and implications. Amer. J. Bot. 77: 1558–1568.

Duncan, W. H. 1967. Woody vines of the Southeastern States. Sida 3: 1–76.

Dunn, S. T. 1908. A botanical expedition to central Fokien. J. Linn. Soc. 38: 350–373.

Du Rietz, G. E. 1930. The fundamental units of biological taxonomy. Svensk Bot. Tidskr. 24: 333–428.

→ Ehrendorfer, F., F. Krendl, E. Habeler, and W. Sauer. 1968. Chromosome numbers and evolution in primitive angiosperms. Taxon 17: 337–353.

Endress, P. K. 1980. The reproductive structures and systematic position of the Austrobaileyaceae. Bot. Jahrb. Syst. 101: 393–433.

Erdtman, G. 1952. *Pollen morphology and plant taxonomy. Angiosperms*. Stockholm: Almqvist & Wiksell.

Ettman, D. 1980. *A study of* Schisandra glabra *(Brickell) Rehder, a rare species endemic to the Southeastern United States*. Unpublished MSc thesis, Emory University, Atlanta, Georgia, USA.

Farris, J. S. 1988. *Hennig86, version 1.5*. [Computer program and documentation]. Port Jefferson Station, New York: published by the author.

Finet, A. E., and F. Gagnepain. 1905. Magnoliacées. In *Contributions à la flore de l'Asie orientale*. Bull. Soc. Bot. France 52: 23–54 + pl. 8.

______. 1907a. Additions à la flore de l'Asie orientale. Bull. Soc. Bot. France 54: 82–90.

______. 1907b. Magnoliaceae. In *Flore générale de l'Indo-Chine*. Vol. 1(1), ed. M. H. Lecomte, 29–42 + pl. 3. Paris: Masson.

Florin, R. 1920. Zur Kenntnis der jungtertiären Pflanzenwelt Japans. Kongl. Svenska Vetenskapsakad. Handl. 61: 1–71 + pl. 1–6.

Franchet, A. R. 1885. Plantae Davidianae ex Sinarum Imperio. Nouv. Arch. Mus. Hist. Nat., sér. 2, 8: 183–254 + pl. 2–10.

Fujita, N. 1929. Über die Früchte der *Schizandra chinensis* Bail. und *Kadsura japonica* Dun. Arch. Pharm. Ber. Deutsch. Pharm. Ges. 267: 532–540 + pl. 1–2.

Gagnepain, F. 1938. Magnoliaceae. In *Flore générale de l'Indochine (supplément)*. Vol. 1(1), ed. H. Humbert, 29–59. Paris: Masson.

______. 1939. Magnoliacées nouvelles ou litigieuses. Not. Syst. (Paris) 8: 63–66.

Garratt, G. A. 1933. Bearing of wood anatomy on the relationships of the Myristicaceae. Trop. Woods 36: 20–44.

→ Garrison, R. 1955. Studies in the development of axillary buds. Amer. J. Bot. 42: 257–266.

Geissert, F., and H.-J. Gregor. 1981. Eine neue elsässische Pliozän-Flora, die "Saugbagger-Flora" der Kiesgrube von Sessenheim (Bas-Rhin). Courier Forschungsinst. Senckenberg 50: 59–71.

Gill, B. S., S. S. Bir, and V. K. Singhal. 1984. Cytological studies in some western Himalayan woody species. II. Polypetalae. In *The vegetational wealth of the Himalayas*, ed. G. S. Paliwal, 497–515. Delhi: Puja.

Godfrey, R. K. 1988. *Trees, shrubs, and woody vines of northern Florida and adjacent Georgia and Alabama*. Athens & London: University of Georgia Press.

Gorokhova, G. I. 1982. Fruiting of far-eastern species of plants under conditions of the forest steppe zone of western Siberia. Sov. J. Ecol. 12: 219–222. [In Russian]

Gottlieb, O. R., M. A. C. Kaplan, K. Kubitzki, and J. R. Toledo Barros. 1989. Chemical dichotomies in the Magnolialean complex. Nord. J. Bot. 8: 437–444.

→ Gower, J. C. 1971. A general coefficient of similarities and some of its properties. Biometrics 27: 857–874.

Gray, A. 1859. Diagnostic characters of new species of phaenogamous plants, collected in Japan by Charles Wright, botanist of the U.S. North Pacific Exploring Expedition. With observations upon the relations of the Japanese flora to that of North America and of other parts of the Northern Temperate Zone. Mem. Amer. Acad. Arts, n.s. 6: 377–452.

Gray, J. 1964. Northwest American Tertiary palynology: the emerging picture. In *Ancient Pacific flora: the pollen story*, ed. L. M. Cranwell, 21–30. Hawaii: Hawaii University Press.

Gregor, H.-J. 1981. *Schizandra geissertii* nova spec. - ein exotisches Element im Elsässer Pliozän (Sessenheim, Brunssumien). Mitt. Bad. Landesvereins Naturk. Naturschutz Freiburg 12: 241–247.

Grierson, A. J. C., and D. G. Long. 1984. *Flora of Bhutan.* Vol. 1(2). Edinburgh: Royal Botanic Garden.

Groppler, R. 1894. Vergleichende Anatomie des Holzes der Magnoliaceen. Biblioth. Bot. 31: 1–51 + pl. 1–4.

Grushvitzky, I. V. 1967. After-ripening of seeds of primitive tribes of angiosperms, conditions and peculiarities. In *Physiologie, Ökologie und Biochemie der Keimung*, ed. H. Borriss, 329–336. Greifswald: Ernst-Moritz-Arndt-Universitat.

Guo, S. 1984. Late Cretaceous plants from the Sunghuajiang-Liaohe Basin, Northeast China. Acta Palaeont. Sin. 23: 85–90 + pl. 1. [In Chinese]

_____. 1988. The Palaeoenvironment in the Hengduan Mountain area since the Eocene. In *The palaeoenvironment of East Asia from the mid-Tertiary.* Vol. 1, ed. P. Whyte, J. S. Aigner, N. G. Jablonski, G. Taylor, D. Walker, P. Wang, and C.-L. So, 523–527. Hong Kong: Centre of Asian Studies, University of Hong Kong.

_____. 1990. A brief review on megafloral successions and climatic changes of the Cretaceous and early Tertiary in China. In *Proceedings of the symposium paleofloristic and paleoclimatic changes in the Cretaceous and Tertiary*, ed. E. Knobloch and Z. Kvaček, 23–38. Prague: Geological Survey Publisher.

Hallier, H. 1898. Neue und bemerkenswerte Pflanzen aus dem malaiisch-papuanischen Inselmeer. Bull. Herb. Boiss. 6: 213–220 + pl. 5–11.

Hayashi, Y. 1960. On the microsporogenesis and pollen morphology in the family Magnoliaceae. Sci. Rep. Tôhoku Imp. Univ., ser. IV (Biol.) 26: 45–52 + pl. 4–7.

_____. 1963a. The embryology of the family Magnoliaceae sens. lat. I. Megasporogenesis, female gametophyte and embryogeny of *Illicium anisatum* L. Sci. Rep. Tôhoku Imp. Univ., ser. IV (Biol.) 29: 27–33.

_____. 1963b. The embryology of the family Magnoliaceae sens. lat. II. Megasporogenesis, female gametophyte and embryology of *Schisandra repanda* Radlkofer and *Kadsura japonica* Dunal. Sci. Rep. Tôhoku Imp. Univ., ser. IV (Biol.) 29: 403–411.

_____. 1965. The comparative embryology of the Magnoliaceae (s.l.) in relation to the systematic consideration of the family. Sci. Rep. Tôhoku Imp. Univ., ser. IV (Biol.) 31: 29–44.

Hayata, B. 1915. *Icones plantarum Formosanarum.* Vol. 5. Taihoku: Government of Formosa.

He, X.-G., F.-X. Jiang, and Q.-R. Zhou. 1978. Application of high-speed liquid chromatography in phytochemistry. Acta Bot. Sin. 20: 76–83. [In Chinese]

He, Z. 1988. A new species and two new varieties of plants in Sichuan. J. S.-W. Agric. Univ. 10: 292–297. [In Chinese]

Hegnauer, R. 1990. *Chemotaxonomie der Pflanzen.* Vol. 9. Basel: Birkhäuser Verlag.

Hemsley, W. B. 1875. The Magnolias and their allies. Garden 8: 269–271.

Hemsley, W. B., and E. H. Wilson. 1906. Some new Chinese plants. Kew Bull. 1906: 147–163.

Hennig, S., W. Barthlott, I. Meusel, and I. Theisen. 1994. Mikromorphologie der Epicuticularwachse und die Systematik der Magnoliidae, Ranunculidae und Hamamelidae. Trop. Subtrop. Pflanzenwelt 90: 1–60.

Hickey, L. J. 1979. A revised classification of the architecture of dicotyledonous leaves. In *Anatomy of the dicotyledons.* 2nd ed. Vol. 1, ed. C. R. Metcalfe and L. Chalk, 25–39. Oxford: Clarendon Press.

Hikino, H. 1985. Chinese medicinal plants used against hepatitis. In *Advances in Chinese medicinal materials research*, ed. H. M. Chang, H. W. Yeung, W.-W. Tso, and A. Koo, 205–214. Singapore: World Scientific Publishing.

Hikino, H., K. Hosaka, Y. Ogawa, Y. Iketani, K. Kubota, and H. Taguchi. 1986. Chamigrenol derivatives as antihepatopathic agents. Jap. Kokai Tokkyo Koho JP 61 07,227. [Patent]

Hikino, H., Y. Kiso, H. Taguchi, and Y. Ikeya. 1984. Antihepatotoxic actions of lignoids from *Schizandra chinensis* fruits. Planta Med. 50: 213–218.

Holmgren, P. K., N. H. Holmgren, and L. C. Barnett. 1990. *Index herbariorum. Part I: the herbaria of the world.* New York: New York Botanical Garden.

Hooker, J. D., and B. D. Jackson. 1895. *Index Kewensis.* Vol. 2. Oxford: Clarendon Press.

Hooker, W. J. 1851. *Sphaerostema propinquum.* Bot. Mag. 77: fig. 4614.

Hooper, D. 1929. On Chinese medicine: drugs of Chinese pharmacies in Malaya. Gard. Bull., Straits Settlem. 6: 1–165.

→ Hoot, S. B., S. Magallón, and P. R. Crane. 1999. Phylogeny of basal eudicots based on three molecular data sets: *atp*B, *rbc*L, and 18S nuclear ribosomal DNA sequences. Ann. Missouri Bot. Gard. 86: 1–32.

Hou, D., W. Zhang, and R. Hui. 1995. Studies on the terpenoids in the volatile constituents of Liaoning *Schisandra chinensis* Baillon. Anal. Sci. Technol. 8: 505–509.

Hsu, C.-F., T.-H. Ho, K.-H. Pao, and C.-T. Cheng. 1980. Crystal structure of 4-bromoalcohol of *Schisandra chinensis.* Chin. Sci. Bull. 25: 1004–1006. [In Chinese]

Huang, M., J. Fan, and Y. Li. 1982a. Structure of En Shi Zhi Su, a new lignan from *Schisandra henryi* Clarke. Chin. Trad. Herb. Drugs 13: 22. [In Chinese]

Huang, M., S. Fang, and Y. Kao. 1982b. Studies on constituents of *Schisandra sphenanthera* Rehd. et Wils. III. Constituents of the lignan in different districts and the structure of d-epigalbacin. Acta Bot. Sin. 24: 451–455. [In Chinese]

Huang, T.-C. 1967. Pollen grains of Formosan plants (2). Taiwania 13: 15–110.

______. 1972. *Pollen flora of Taiwan.* Taipei: Botany Department Press, National Taiwan University.

Huang, W. F. 1987. Schisandraceae. In *Flora of Guangdong.* Vol. 1, ed. T. Wu, 22–26. Guangzhou: Guangdong Science & Technology Press. [In Chinese]

Hutchinson, J. 1969. *Evolution and phylogeny of flowering plants.* London: Academic Press.

Huynh, K.-L. 1976. L'arrangement du pollen du genre *Schisandra* (Schisandraceae) et sa signification phylogénique chez les Angiospermes. Beitr. Biol. Pflanzen. 52: 227–253.

Huzioka, K. 1964. The Aniai Flora of Akita Prefecture and the Aniai-type floras in Honshu, Japan. J. Min. Coll., Akita Univ., ser. A, Min. Geol. 3: 1–105 + pl. 1–18.

Igersheim, A., and P. K. Endress. 1997. Gynoecium diversity and systematics of the Magnoliales and winteroids. Bot. J. Linn. Soc. 124: 213–271.

Iketani, Y., S. Maeda, M. Yuda, H. Taguchi, and I. Yosioka. 1980. Isolation of gomisin N and use in antipyretic composition. Jap. Kokai Tokkyo Koho 80 22,612. [Patent]

Iketani, Y., H. Taguchi, H. Sasaki, and M. Yuda. 1989. New lignans from *Schizandra chinensis* as lipoxygenase inhibitors. Jap. Kokai Tokkyo Koho JP 01 42,448. [Patent]

Iketani, Y., J. Yamazaki, and R. Yoshida. 1996. Preparation of dibenzocyclooctane derivatives and their isolation from dry fruits of plants or as metabolites from animal bile. Jap. Kokai Tokkyo Koho JP 08,157,407. [Patent]

Iketani, Y., T. Yanagisawa, and H. Mihashi. 1990. 5-Lipoxygenase inhibitors containing lignans as inflammation inhibitors Jap. Kokai Tokkyo Koho JP 02,169,543. [Patent]

Ikeya, Y., H. Kanatani, K. Nakajima, and H. Mitsuhashi. 1990a. Process for extracting dibenzocyclooctadiene type lignan. PCT Int. Appl. WO 90 01, 487. [Patent]

Ikeya, Y., E. Miki, M. Okada, H. Mitsuhashi, and J. G. Chai. 1990b. Benzoylgomisin Q and benzyolgomisin P, two new lignans from *Schisandra sphenanthera* Rehd. et Wils. Chem. Pharm. Bull. 38: 1408–1411.

Ikeya Y., N. Ookawa, H. Taguchi, and I. Yosioka. 1982b. The constituents of *Schizandra chinensis* Baill. XI. The structures of three new lignans, angeloylgomisin O and angeloyl- and benzoylisogomisin O. Chem. Pharm. Bull. 30: 3202–3206.

Ikeya, Y., K. Sugama, M. Okada, and H. Mitsuhashi. 1991. Two new lignans from *Schisandra sphenanthera.* Phytochemistry 30: 975–980.

Ikeya, Y., H. Taguchi, H. Mitsuhashi, S. Takeda, Y. Kase, and M. Aburada. 1988. A lignan from *Schizandra chinensis.* Phytochemistry 27: 569–573.

Ikeya, Y., H. Taguchi, H. Sasaki, K. Nakajima, and I. Yosioka. 1980c. The constituents of *Schizandra chinensis* Baill. VI. Carbon–13 nuclear magnetic resonance spectroscopy of dibenzocyclooctadiene lignans. Chem. Pharm. Bull. 28: 2414–2421.

Ikeya, Y., H. Taguchi, and I. Yosioka. 1978a. The constituents of *Schizandra chinensis* Baill. The structures of two new lignans pre-gomisin and gomisin J. Chem. Pharm. Bull. 26: 682–684.

______. 1978b. The constituents of *Schizandra chinensis* Baill. The structures of three new lignans, angeloygomisin I, tigloylgomisin H and benzoylgomisin H and the absolute structure of schizandrin. Chem. Pharm. Bull. 26: 328–321.

______. 1979c. The constituents of *Schizandra chinensis* Baill. The cleavage of the methylenedioxy moiety with lead tetraacetate in benzene and the structure of angeloylgomisin Q. Chem. Pharm. Bull. 27: 2536–2538.

______. 1980b. The constituents of *Schizandra chinensis* Baill. VII. The structures of three new lignans, (-)-gomisin K_1 and (+)-gomisins K_2 and K_3. Chem. Pharm. Bull. 28: 2422–2427.

______. 1982a. The constituents of *Schizandra chinensis.* Baill. XII. Isolation and structure of a new lignan, gomisin R, the absolute structure of wuweisizu C and isolation of schisantherin D. Chem. Pharm. Bull. 30: 3207–3211.

______. 1982c. The constituents of *Schizandra chinensis* Baill. X. The structures of γ-schisandrin and four new lignans (-)-gomisins L_1 and L_2, (+/-)-gomisin M_1 and (+)-gomisin M_2. Chem. Pharm. Bull. 30: 132–139.

Ikeya, Y., H. Taguchi, I. Yosioka, Y. Itaka, and H. Kobayashi. 1979f. The constituents of *Schizandra chinensis* Baill. II. The structure of a new lignan, gomisin D. Chem. Pharm. Bull. 27: 1395–1401.

Ikeya,Y., H. Taguchi, I. Yosioka, and H. Kobayashi. 1978c. The constituents of *Schizandra chinensis* Baill. The structures of two new lignans, gomisin N and tigloylgomisin P. Chem. Pharm. Bull. 26: 3257–3260.

______. 1979a. The constituents of *Schizandra chinensis* Baill. V. The structures of four new lignans, gomisin N, gomisin O, epigomisin O and gomisin E, and transformation of gomisin N to deangeloylgomisin B. Chem. Pharm. Bull. 27: 2695–2709.

______. 1979b. The constituents of *Schizandra chinensis* Baill. I. Isolation and structure determination of five new lignans, gomisin A, B, C, F and G and absolute stereochemistry of schizandrin. Chem. Pharm. Bull. 27:1383–1394.

______. 1979d. The constituents of *Schizandra chinensis* Baill. III. The structures of four new lignans, gomisin H and its derivatives angeloyl-, tigloyl- and benzoyl-gomisin H. Chem. Pharm. Bull. 27: 1576–1582.

______. 1979e. The constituents of *Schizandra chinensis* Baill. IV. The structures of two new lignans, pregomisin and gomisin J. Chem. Pharm. Bull. 27: 1583–1588.

______. 1980a. The constituents of *Schizandra chinensis* Baill. VIII. The structure of two new lignans, tigloylgomisin P and angeloylgomisin P. Chem. Pharm. Bull. 28: 3357–3361.

Ikuse, M. 1954. Some minor problems of pollen grains. J. Jap. Bot. 29: 197–199.

______. 1956. *Pollen grains of Japan.* Tokyo: Hirokawa.

Jähnichen, H. 1976. Schisandraceae und Illiciaceae als holarktische und subtropische Florenelemente im mitteleuropäischen Alttertiär. Abh. Zentr. Geol. Inst., Paläntol. Abh. 26: 152–197 + pl. 8–18.

Jalan, S. 1962. The ontogeny of the stomata in *Schisandra grandiflora* Hook. f. & Thoms. Phytomorphology 12: 239–242.

______. 1963. Survey of the idioblasts in *Schisandra* Michaux together with discussion of its systematic position. In *Proceedings of the 50th Indian science congress. Part 3, abstracts. Section 4, botany*, 382.

______. 1965. Morphology and ontogeny of the ethereal oil cells in *Schisandra* Michaux. Curr. Sci. 18: 527–528.

______. 1966. Carpellary and ovular vascularization in two species of *Schisandra* Michaux. Sci. Cult. 32: 372–373.

______. 1968a. Observations on the crystalliferous sclereids of some Schisandraceae. Beitr. Biol. Pflanzen 44: 277–288.

______. 1968b. Contribution to the nodal structure of *Schisandra* Michaux. Bot. Jahrb. Syst. 88: 311–316.

______. 1975. The mucilage cells of *Schizandra grandiflora* Hook. f. & Th. J. Indian Bot. Soc. 54: 62–65.

______. 1979. The morphotaxonomic structure and value of pollen grains in *Schisandra* Michx. and *Kadsura* Kaempf. ex Juss. In *Proceedings of the IV international palynological conference, Lucknow, 1976–77.* Vol. 1, ed. Anonymous, 449–452. Lucknow: Birbal Sahni Institute of Palaeobotany.

______. 1987. A new type of staminal vasculature in *Schisandra neglecta.* J. Indian Bot. Soc. 66: 150.

______. 1988. Morpho-taxonomic structure and value of the petiole in *Schisandra grandiflora.* J. Ind. Bot. Soc. 67: 11–13.

Jalan, S., and N. N. Bhandari. 1963. Extracarpellary ovules in some Ranales. Curr. Sci. 32: 230–232.

Jalan, S., and R. N. Kapil. 1964. Pollen grains of *Schisandra* Michaux. Grana Palynol. 5: 216–221.

Jonker, F. P. 1974. Reflections on pollen evolution. Adv. Pollen-Spore Res. 1: 50–61.

Kapil, R. N., and S. Jalan. 1964. *Schisandra* Michaux - its embryology and systematic position. Bot. Notiser 117: 285–306.

Keng, H. 1993. Schisandraceae. In *The families and genera of vascular plants.* Vol. 2, ed. K. Kubitzki, J. G. Rohwer, and V. Bittrich, 589–592. Berlin: Springer-Verlag.

Kikuchi, M., and A. Yoshiokoshi. 1972. Nigranoic acid, a new A-*seco*-cycloartane triterpenoid. Chem. Lett. 1972: 725–728.

King, G. 1891. The Magnoliaceae of British India. Ann. Roy. Bot. Gard., Calcutta 3: 197–223 + pl. 38–74.

Kochetkov, N. K., A. Khorlin, and O. S. Chizhov. 1962. Deoxyschisandrin - structure and total synthesis. Tetrahedron Lett. 1962: 361–363.

Kochetkov, N. K., A. Khorlin, O. S. Chizhov, and V. I. Sheichenko. 1961. Schizandrin - lignan of unusual structure. Tetrahedron Lett. 1961: 730–734.

Kolakovskij, A. A. 1957. Pervoe dopolnenie k Kodorskoj pliocenovoj flore. Trudy Suhumsk. Bot. Sada 10: 235–318. [In Russian]

______. 1964. Pliocene flora of Kodori. Monogr. Suhumsk. Bot. Sada 1: 1–209 + pl. 1–56. [In Russian]

Kolbasina, E. I. 1967. The organogenesis of the flower of *Schizandra chinensis* (Turcz.) Baill. Bot. Zhurn. 52: 377–378. [In Russian]

Komarova, T. A. 1994. The age-related development of the bushy lianas *Schisandra chinensis* (Schisandraceae) and *Actinidia kolomikta* (Actinidiaceae). Bot. Zhurn. 79: 42–52. [In Russian]

Koorders, S. H. 1912. *Exkursionsflora von Java.* Vol. 2. Jena: Verlag von Gustav Fischer.

Kovach, W. L. 1995. *MVSP - A multivariate statistical package for IBM-PCs, version 2.2.* [Computer program and documentation]. Pentraeth, Wales: Kovach Computing Services.

Kozo-Poljanski, B. M. 1946. The floral mechanism of Woo-we-dzy *Schizandra chinensis* (Turcz.) Baill. Compt.-Rend. (Dokl.) Acad. Sci. URSS 53: 749–751.

Krüssmann, G. 1986. *Manual of cultivated broad-leaved trees and shrubs.* Vol. 3. Portland, Oregon: Timber Press.

Kryshtofowich, A. N., and T. N. Baikavskaja. 1965. *Sarmatian flora of Krynka.* Moscow & Leningrad.

Kuprianova, L. A. 1966. Apertures of the pollen grains of angiosperms and their evolution. In *The importance of palynological analysis for the stratigraphic and paleofloristic investigations*, ed. M. I. Nejshtadt, 7–14. Moscow: Nauca. [In Russian]

Law, Y.-W. 1983a. A new species of Schisandraceae from China. Bull. Bot. Res., Harbin 3: 148–150. [In Chinese]

______. 1983b. Schisandraceae. In *Sylva Sinica*, ed. W.-J. Zheng, 525–538. Beijing: China Forestry Publishers. [In Chinese]

______. 1996a. Magnoliaceae DC. trib. Schisandreae DC. In *Flora Reipublicae Popularis Sinicae.* Vol. 30(1), ed. Y.-W. Law, 231–269. Beijing: Science Press. [In Chinese]

______. 1996b. Addenda. In *Flora Reipublicae Popularis Sinicae.* Vol. 30(1), ed. Y.-W. Law, 270–273. Beijing: Science Press.

Lee, Y. W., R. D. Voyksner, T. W. Pack, C. E. Cook, Q. C. Fang, and Y. Ito. 1990. Application of countercurrent chromatography/thermospray mass spectrometry for the identification of bioactive lignans from plant natural products. Anal. Chem. 62: 244–248.

Leinfellner, W. 1966. Über die Karpelle verschiedener Magnoliales. III. *Schisandra* (Schisandraceae). Österr. Bot. Zeit. 113: 563–569.

Lemesle, R. 1933. De l'ancienneté des caractères anatomiques des Magnoliacées. Rev. Gén. Bot. 45: 341–354 + pl. 14–17.

______. 1945. Les ponctuations aréolées des fibres des genres *Schizandra* L., *Kadsura* J., *Illicium* L. et leurs rapports avec la phylogénie. Compt.-Rend. Hebd. Séances Mém. Soc. Biol. 221: 113–115.

______. 1946. Les divers types de fibres à ponctuations aréolées chez les dicotylédones apocarpiques les plus archaïques et leur rôle dans la phylogénie. Ann. Sci. Nat., Bot. Sér. 11, 7: 19–40.

______. 1953. Les caractéres histologiques du bois secondaire des Magnoliales. Phytomorphology 3: 430–446.

______. 1956. Les éléments du xylème dans les Angiospermes à caractères primitifs. Bull. Soc. Bot. France 103: 629–677.

Léveillé, H. 1911. Decades plantarum novarum. LIX–LXX. Repert. Spec. Nov. Regni Veg. 9: 441–463.

______. 1916. *Catalogue des plantes du Yunnan.* Le Mans: published by the author.

Li, H.-L. 1976. Schisandraceae. In *Flora of Taiwan.* Vol. 2, ed. Editorial Committee of the Flora of Taiwan, 399–402. Taipei: Epoch Publishing.

Li, H.-L., and S.-M. Chaw. 1996. Schisandraceae. In *Flora of Taiwan.* 2nd ed. Vol. 2, ed. Editorial Committee of the Flora of Taiwan, 423–426. Taipei: Editorial Committee of the Flora of Taiwan, Department of Botany, National Taiwan University.

Li, L.-N., and H. Xue. 1985. Schisandrone, a new 4-aryltetralone lignan from *Schisandra sphenanthera.* Planta Med. 51: 217–219.

______. 1986. Henricine, a new tetrahydrofuran lignan from *Schisandra henryi.* Planta Med. 52: 493–494.

Li, L.-N., C. Yang, H. Zhang, and X. Dai. 1995. Studies on the chemical constituents of *Schisandra propinqua* var. *intermedia.* J. Yunnan Univ., Nat. Sci. Ed. 17: 378–380. [In Chinese]

Li, X., W. Song, and R. Chen. 1993. Studies on karyotype of some berry plants in north China. J. Wuhan Bot. Res. 11: 289–292.

Li, Z., L.-N. Li, and H. Zhang. 1996. Studies on the chemical constituents of Zhongjian wuweizi. Chin. Trad. Herb. Drugs 27: 3–4. [In Chinese]

Lieux, M. H. 1980. An atlas of pollen of trees, shrubs, and woody vines of Louisiana and other southeastern states, part I. Ginkgoaceae to Lauraceae. Pollen Spores 22: 17–57.

Lin, Q. 1997. *Systematics and evolution of the family Illiciaceae.* Unpublished Ph.D. thesis, Forestry College, South China Agricultural University, Guangzhou, PRC. [In Chinese]

Lindley, J. 1834. *Sphaerostema propinquum.* Small-flowered *Sphaerostema.* Edward's Bot. Reg. 20: pl. 1688.

Liu, C.-S., S.-D. Fang, M.-F. Huang, Y.-L. Kao, and J.-S. Hsu. 1978a. Studies on the active principles of *Schisandra sphenanthera* Rehd. et Wils. The structures of schisantherin A, B, C, D and E and the related compounds. Sci. Sin. 21: 483–502.

Liu C.-S., M.-F. Huang, and Y.-L. Kao. 1978b. Studies on the constituents of Yi-Geng-Wu-Wei-Zi (*Schisandra henryi* Clarke). I. Structures of schisanhenol and deoxyschisandrin. Acta Chim. Sin. 36: 193–197. [In Chinese]

Liu, J.-S., S.-D. Fang, M.-F. Huang, Y.-L. Gao, and J.-S. Hsu. 1976. Studies on the constituents of Hua-Zhong-Wu-Wei-Zi (*Schizandra sphenanthera* Rehd. et Wils.). II. The structures of schisantherin A, B, C, D, E and related compounds. Acta Chim. Sin. 34: 229–240. [In Chinese]

Liu, J.-S., and M.-F. Huang. 1984. Constituents of *Schisandra sphenanthera* Rehd. et Wils. IV. Structures of anwuweizic acid and dl-anwulignan, and the absolute configurations of d-epigalbacin. Acta Chim. Sin. 42: 264–270. [In Chinese]

Liu, J.-S., M.-F. Huang, W. A. Ayer, and T. T. Nakashima. 1984. Structure of enshicine from *Schisandra henryi.* Phytochemistry 23: 1143–1145.

Liu, J.-S., M.-F. Huang, and Y. Tao. 1988a. Anwuweizonic acid and manwuweizic acid, the putative anticancer active principles of *Schisandra propinqua.* Can. J. Chem. 66: 414–415.

Liu, J.-S., Y. Ma, and M.-F. Huang. 1988b. Studies on the constituents of Schisandraceae plants in Shennongjia district. I. Constituents of *Schisandra propinqua* Hook. f. et Thoms. var. *sinensis* Oliv. Acta Chim. Sin. 46: 345–348. [In Chinese]

Liu, J.-S., Y. Tao, and M.-F. Huang. 1988c. Studies on the constituents of *Schisandra henryi.* V. Structures of wulignan A_1, A_2, epiwulignan A_1 and epischisandrone. Acta Chim. Sin. 46: 483–488. [In Chinese]

Liu, J.-S., W. Wang, and M.-F. Huang. 1990. Constituents of wuweizi from Lichuan (Hubei Province). Chin. Trad. Herb. Drugs 21: 294–295. [In Chinese]

Liu, M.-C. 1992. Magnoliaceae. In *Flora of Zhejiang.* Vol. 2, ed. J.-X. Wang, 327–346. Hangzhou: Zhejiang Science and Technology Publishing House. [In Chinese]

Liu, T.-S. 1960. *Illustrations of native and introduced ligneous plants of Taiwan.* Vol. 1. Taipei: National Taiwan University.

Liu, Y. G. 1986. Pharmaceutical composition, Pure San-Mai-sen, for cure and prevention of cardiovascular disease and for increasing the immune function. Eur. Pat. Appl. EP 200,169. [Patent]

______. 1990. Cardiovascular and immunity-enhancing composition containing ginsenolides, ophiopogonins, sesquicarene and chamigrene. Can. CA 1,266,236. [Patent]

Lo, H. S. 1994. *Coloured icones of Chinese medicine.* Vol. 3. Guangzhou: Guangdong Science & Technology Press. [In Chinese]

→ Loconte, H., and D. W. Stevenson. 1991. Cladistics of the Magnoliidae. Cladistics 7: 267–296.

Löve, Á. (ed.). 1977. IOPB chromosome number reports LVII. Taxon 26: 443–452.

→ ______. 1980. Chromosome number reports LXVII. Taxon 29: 347–367.

→ Luckow, M. 1995. Species concepts: assumptions, methods and applications. Syst. Bot. 20: 589–605.

Luo, G., and J. Liu. 1992. Studies on the constituents of *Schisandra viridis* A. C. Sm. in the northern Guangdong province. II. Acta Chim. Sin. 50: 515–520. [In Chinese]

Luo, G., J. Liu, and M.-F. Huang. 1992. Studies on the constituents of *Schisandra viridis* A. C. Sm. in the northern Guangdong province. I. Acta Chim. Sin. 50: 620–624. [In Chinese]

Macko, S. 1957. Lower Miocene pollen flora from the valley of Kłodnica near Gliwice (Upper Silesia). Prace Wrocławsk. Towarz. Nauk., ser. B 88: 5–309.

Mai, D. H., and H. Walther. 1985. Die obereozänen Floren des Weisselster-Beckens und seiner Randgebiete. Abh. Staatliches Mus. Mineral. Geol. Dresden 33: 1–60.

Manchester, S. R. 1990. Eocene to Oligocene floristic changes recorded in the Clarno and John Day formations, Oregon, U.S.A. In *Proceedings of the symposium paleofloristic and paleoclimatic changes in the Cretaceous and Tertiary*, ed. E. Knobloch and Z. Kvaček, 183–187. Prague: Geological Survey Publisher.

______. 1994. Fruits and seeds of the middle Eocene Nut Beds Flora, Clarno Formation, Oregon. Palaeontogr. Amer. 58: 1–205.

Matsuda, S. 1893. On the anatomy of Magnoliaceae. J. Coll. Sci., Tokyo 6: 115–149 + pl. 2–5.

Maximowicz, C. J. 1856. Ueber die wichtigeren Bäume und Sträucher des Amurlandes. In *Die ersten botanischen Nachrichten über das Amurland. Erste Abtheilung*, by F. J. F. Ruprecht. Bull. Cl. Phys.-Math. Acad. Imp. Sci. Saint-Pétersbourg 15: 120–144.

______. 1859. Primitiae florae Amurensis. Mém. Acad. Imp. Sci. Saint-Pétersbourg 9: 1–504 + pl. 1–10.

______. 1872. Diagnoses breves plantarum novarum Japoniae et Mandshuriae. X. Bull. Acad. Imp. Sci. Saint-Pétersbourg 17: 142–180.

McLaughlin, R. P. 1933. Systematic anatomy of the woods of the Magnoliales. Trop. Woods 34: 3–39.

Meagher, T. R. 1988. Sex determination in plants. In *Plant reproductive ecology: patterns and strategies*, ed. J. Lovett Doust and L. Lovett Doust, 125–138. Oxford: Oxford University Press.

Melikian, A. P. 1988. Illiciales. In *Comparative seed anatomy*, ed. A. Takhtajan, 48–50. Leningrad. [In Russian]

→ Melville, R. 1969. Studies in floral structure and evolution. I. The Magnoliales. Kew Bull. 23: 133–180.

Merrill, E. D., and W. Y. Chun. 1934. Contributions to our knowledge of the Kwangtung flora (2). Sunyatsenia 2: 3–22 + pl. 1–12 + fig. 1–3.

Metcalfe, C. R. 1987. *Anatomy of the dicotyledons.* 2nd ed. Vol. 3. Oxford: Clarendon Press.

Michaux, A. 1803. *Flora boreali-Americana.* Paris & Strasbourg: C. Crapelet.

Miki, S. 1941. On the change of flora in Eastern Asia since Tertiary period. I. The clay or lignite beds flora in Japan with special reference to the *Pinus trifolia* beds in Central Hondo. Jap. J. Bot. 11: 250–303 + pl. 4–7.

Miki, S., and S. Kokawa. 1962. Late Cenozoic floras of Kyushu, Japan. J. Biol., Osaka City Univ. 13: 65–86 + pl. 1–12.

→ Miranda, F., and A. J. Sharp. 1950. Characteristics of the vegetation in certain temperate regions of eastern Mexico. Ecology 31: 313–333.

Mitroiu, N. 1970. Études morphopolliniques et des aspects embryologiques sur les "Polycarpicae" et Helobiae, avec des considérations phylogénétiques. Lucr. Grad. Bot. Bucuresti [Acta Bot. Horti Bucurestiensis] 1969: 3–243.

Mitsuhashi, H. 1976. Medicinal plants of Ainu. Econ. Bot. 30: 209–217.

Mori, T. 1922. *Enumeration of plants hitherto known from Corea.* Seoul: Government of Chosen.

Motl, O., V. G. Bucharov, V. Herout, and F. Sorm. 1963. The structure of ylangene - a new type of tricyclic sesquiterpene. Chem. Ind. 1963: 1759–1760.

Muller, J. 1964. Palynological contributions to the history of Tertiary vegetation in N.W. Borneo. In *Abstracts of the Xth international botanical congress, Edinburgh*, ed. B. L. Burtt, 271. Edinburgh: International Botanical Congress.

______. 1970. Palynological evidence on early differentiation of angiosperms. Biol. Rev. 45: 417–450.

Nakai, T. 1933. *Flora sylvatica Koreana.* Vol. 20. Keijyo, Japan: Forestal Experimental Station.

Nakajima, K., H. Taguchi, Y. Ikeya, T. Endo, and I. Yosioka. 1983. The constituents of *Schizandra chinensis* Baill. XIII. Quantitative analysis of lignans in the fruits of *Schizandra chinensis* Baill. by high performance liquid chromatography. J. Pharm. Soc. Jap. 103: 743–749. [In Japanese]

→ Nandi, O. I., M. W. Chase, and P. K. Endress. 1998. A combined cladistic analysis of angiosperms using *rbc*L and non-molecular data sets. Ann. Missouri Bot. Gard. 85: 137–212.

Netolitzky, F. 1926. Anatomie der Angiospermen-Samen. In *Handbuch der Pflanzenanatomie.* Vol. 10, ed. K. Linsbauer. Berlin: Gebr. Borntraeger.

Nikolaeva, M. G. 1969. *Physiology of deep dormancy in seeds*, transl. Z. Shapiro. Jerusalem: Israel Program for Scientific Translations.

O'Brien, T. P., and M. E. McCully. 1981. *The study of plant structure: principles and selected methods.* Melbourne: Termarcarphi.

O'Brien, T. P., and I. von Teichman. 1974. Autoclaving as an aid in the clearing of plant specimens. Stain Techn. 49: 175–176.

Ohta, Y., and Y. Hirose. 1968a. Structure of sesquicarene. Tetrahedron Lett. 1968: 1251–1254.

______. 1968b. New sesquiterpenoids from *Schisandra chinensis.* Tetrahedron Lett. 1968: 2483–2485.

Ohwi, J. 1965. *Flora of Japan.* Washington, D.C.: Smithsonian Institution.

Okada, H. 1975. Karyomorphological studies of woody Polycarpicae. J. Sci. Hiroshima Univ., Ser. B, Div. 2, 15: 115–200.

Oldeman, L. R. 1975. An agro-climatic map of Java. Contrib. Centr. Res. Inst. Agric. Bogor (Indonesia) 17: 1–22 + map.

Oliver, D. 1887. *Schizandra propinqua.* Hooker's Icon. Pl. 18: pl. 1715.

Ozenda, P. 1946. Sur l'anatomie libéroligneuse des Schizandracées. Compt. Rend. Hebd. Séances Acad. Sci. 223: 207–209.

______. 1949. Recherches sur les Dicotylédones apocarpiques. Contribution a l'étude des Angiospermes dites primitives. Publ. Lab. École Norm. Supér. 2: i-viii + 1–183 + pl. 1–5.

______. 1952. Remarques sur quelques interprétations de l'étamine. Phytomorphology 2: 225–231.

Page, R. D. M. 1993. *Component, version 2.0.* [Computer program and documentation]. London: Natural History Museum.

→ Panero, J. L., and P. D. Aranda. 1998. The family Schisandraceae: a new record for the flora of Mexico. Brittonia 50: 87–90.

Parmentier, P. 1896. Histoire des Magnoliacées. Bull. Sci. France Belgique 27: 159–331 + pl. 1–27.

Pax, F. 1922. Aufzählung der von Dr. Limpricht in Ostasien gesammelten Pflanzen. In *Botanisches Reisen in den Hochgebirgen Chinas und Ost-Tibets*, by W. Limpricht. Repert. Spec. Nov. Regni Veg. 12: 298–515.

Pemberton, R. W., and N. S. Lee. 1996. Wild food plants in South Korea; market presence, new crops, and exports to the United States. Econ. Bot. 50: 57–70.

Perry, L. M., and J. Metzger. 1980. *Medicinal plants of East and Southest Asia: attributed properties and uses.* Cambridge, Massachussetts: MIT Press.

Pijl, L. van der. 1982. *Principles of dispersal in higher plants.* Berlin: Springer-Verlag.

Pokrovskaia, I. M. (ed.). 1950. *Pyclevoj analiz.* Moscow: Gos. Iz. Geol. Lit. [In Russian]

Potts, R., and A. K. Behrensmeyer. 1992. Late Cenozoic terrestrial ecosystems. In *Terrestrial ecosystems through time: evolutionary paleoecology of terrestrial plants and animals*, ed. A. K. Behrensmeyer, J. D. Damuth, W. A. DiMichele, R. Potts, H.-D. Sues, and S. L. Wing, 424–541. Chicago: University of Chicago Press.

Praglowski, J. 1976. Schisandraceae Bl. World Pollen Spore Fl. 5: 1–32.

Probatova, N. S., and A. P. Sokolovskaya. 1981. Kariologicheskoe issledovanie sosudistykh rastenij ostrovov Dal'nevostoenogo gosudarstvennogo morskogo sapovednika. In *Cvetkaye rastenija ostrovov Dalnevostochnogo morskogo sapovednika*, ed. IU. D. Chugunov, 92–114. Vladivostok: DVNTS an SSSR. [In Russian]

Probatova, N. S., A. P. Sokolovskaya, and E. G. Rudyka. 1989. Chromosome numbers in some species of vascular plants from Kunashir Island (the Kuril Islands). Bot. Zhurn. 74: 1675–1678. [In Russian]

Qiu, Y.-L., M. W. Chase, D. H. Les, and C. R. Parks. 1993. Molecular phylogenetics of the Magnoliidae: cladistic analyses of nucleotide sequences of the plastid gene rbcL. Ann. Missouri Bot. Gard. 80: 587–606.

Radlkofer, L. 1886. Neue Beobachtungen über Pflanzen mit durchsichtig punktierten Blättern und systematische Uebersicht solcher. Sitzungber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 16: 299–344.

Rao, H. S. 1939. Cuticular studies of Magnoliales. Proc. Ind. Acad. Sci., sect. B 9: 99–116 + pl. 4–21.

Rao, R. R. 1981. Ethnobotany of Meghalaya: medicinal plants used by Khasi and Garo tribes. Econ. Bot. 35: 4–9.

Rao, R. R., and P. K. Hajra. 1993. Schisandraceae. In *Flora of India.* Vol. 1, ed. B. D. Sharma, N. P. Balakrishnan, R. R. Rao, and P. K. Hajra, 188–196. Calcutta: Botanical Survey of India.

Ratter, J. A., and C. Milne. 1976. Chromosome counts in primitive angiosperms: II. Notes Roy. Bot. Gard., Edinb. 35: 143–145.

Raven, P. H., and D. W. Kyhos. 1965. New evidence concerning the original basic chromosome number of angiosperms. Evolution 19: 244–248.

Rehder, A. 1944. *Schisandra* Michaux, nomen genericum conservandum. J. Arnold Arbor. 25: 129–131.

Reyment, R. A., R. E. Blackith, and N. A. Campbell. 1984. *Multivariate morphometrics.* 2nd ed. London: Academic Press.

Ridley, H. N. 1930. *The dispersal of plants throughout the world.* Ashford, Kent: Reeve.

Rodin, R. J., and R. E. Davis. 1967. The use of papain in clearing plant tissues for whole mounts. Stain Technol. 42: 203–206.

Roland, F. 1971. Données évolutives résultant de l'étude ultrastructurale des apertures de pollens appartenant au groupe Ranales Centrospermales. Rev. Gén. Bot. 78: 329–338.

Samoylenko, L. I., and N. I. Suprunov. 1974. The contents of lignans in *Schizandra chinensis* (Turcz.) Baill. Rast. Resur. 10: 75–81.

Sandhu, P. S., S. K. Mann, and M. Kapil. 1989. A new record of diploid cytotype of *Schizandra grandiflora* Hook. f. & Thoms. from India. Curr. Sci. 58: 925–926.

Sargent, C. S. 1913. *Plantae Wilsonianae.* Vol. 1. Cambridge, Massachusetts: University Press.

Saunders, R. M. K. 1995. Systematics of the genus *Illicium* L. (Illiciaceae) in Malesia. Bot. J. Linn. Soc. 117: 333–352.

______. 1997a. Schisandraceae. Fl. Males., ser. I, 13: 185–207.

______. 1997b. A taxonomic revision of *Schisandra* section *Sphaerostema* (Schisandraceae). Edinb. J. Bot. 54: 265–287.

______. 1998. Monograph of *Kadsura* (Schisandraceae). Syst. Bot. Monogr. 54: 1–106 + 2 pl.

Schlessman, M. A. 1988. Gender diphasy ("sex choice"). In *Plant reproductive ecology: patterns and strategies*, ed. J. Lovett Doust and L. Lovett Doust, 139–153. Oxford: Oxford University Press.

Schneider, C. K. 1917. Arbores fruticesque chinenses novi. II. Bot. Gaz. 63: 516–523.

Shanghai Institute of Materia Medica. 1976. Studies on the transaminase-lowering principles of *Schisandra sphenanthera* Rehd. et Wils. Acta Biochim. Biophys. 8: 333–340. [In Chinese]

Sheeran, L. K. 1993. *A preliminary study of the behaviour and socio-ecology of black gibbons* (Hylobates concolor) *in Yunnan Province, People's Republic of China.* Unpublished Ph.D. thesis, Ohio State University.

Siddall, M. E. 1997. *Random cladistics, version 4.0.3.* [Computer program and documentation]. Toronto: Published by the author

Siebert, D. J. 1992. Tree statistics; trees and "confidence"; consensus trees; alternatives to parsimony; character weighting; character conflict and its resolution. In *Cladistics: a practical course in systematics*, ed. P. L. Forey, C. J. Humphries, I. J. Kitching, R. W. Scotland, D. J. Siebert, and D. M. Williams, 72–88. Oxford: Clarendon Press.

Siebold, P. F., and J. G. Zuccarini. 1843. Plantarum, quas in Japonia collegit Dr. Ph. Fr. De Siebold. Abh. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. 3: 719–749 + fig. 1–4.

Sims, J. 1811. *Schisandra coccinea*. Scarlet-flowered *Schisandra*. Bot. Mag. 34: pl. 1413.

Smith, A. C. 1947. The families Illiciaceae and Schisandraceae. Sargentia 7: 1–224.

Snezhkova, S. A. 1986. Wood structure in some lianes of the Far East. Bot. Zhurn. 71: 768–773. [In Russian]

Soh, W. Y., and S. J. Park. 1985. Systematic studies on some Korean woody plants. A comparative wood anatomy of Magnoliaceae, Winteraceae and Schizandraceae. Korean J. Bot. 28: 271–284. [In Korean]

Sohn, H. J., and J. Y. Bock. 1989. Identification of lignan compounds in fruits of *Schisandra chinensis* Baillon by gas chromatography/mass spectrometry. Han'guk Nonghwa Hakhoechi 32: 344–349. [In Korean]

Solereder, H. 1908. Systematic anatomy of the dicotyledons. Vols. 1–2, transl. L. A. Boodle, and F. E. Fritsch. Oxford: Clarendon Press.

Solovyeva, L. V. 1998. On the caryotype of *Schizandra chinensis* (Turcz.) Baill. Vestn. Mosk. Univ. Ser. XVI Biol. 1998: 35–41. [In Russian]

→ Soltis, D. E., P. S. Soltis, D. L. Nickrent, L. A. Johnson, W. J. Hahn, S. B. Hoot, J. A. Sweere, R. K. Kuzoff, K. A. Kron, M. W. Chase, S. M. Swensen, E. A. Zimmer, S.-M. Chaw, L. J. Gillespie, W. J. Kress, and K. J. Sytsma. 1997. Angiosperm phylogeny inferred from 18S ribosomal DNA sequences. Ann. Missouri Bot. Gard. 84: 1–49.

Song, W.-Z. 1988. Herbal studies on plants of the Schisandraceae. Bull. Chin. Mat. Med. 13: 3–6. [In Chinese]

______. 1990. Lignan compounds of Schisandraceae plant, biological activities and domestic resources. Nat. Prod. Res. Dev. 3: 68–80. [In Chinese]

Song, W.-Z., Y.-Z. Feng, S.-J. Lu, and Y.-Y. Tong. 1977. The uses of resources from *Schisandra*. Bull. Chin. Trad. Herb. Drugs 3: 34–40. [In Chinese]

Song, W.-Z., and Y.-Y. Tong. 1983. Occurrence and assay of some important lignans in Wu Wei Zi (*Schisandra chinensis*) and its allied species. Acta Pharm. Sin. 18: 138–143. [In Chinese]

Song, W.-Z., Y.-Y. Tong, and L. Cheng. 1990. Lignans of the genus *Schisandra* in China. Tianran Chanwu Yanjiu Yu Kaifa 2: 51–58. [In Chinese]

Song, W.-Z., and P.-G. Xiao. 1982. Medicinal uses of Schisandraceae plants in China and their lignan compounds. Chin. Trad. Herb. Drugs 13: 40–48. [In Chinese]

South China Institute of Botany. 1982. *A handbook of medicinal plants in Guangdong*. Guangzhou: South China Institute of Botany.

Spjut, R. W. 1994. A systematic treatment of fruit types. Mem. New York Bot. Gard. 70: 1–182.

Sprenger, C. 1908 ("1907"). Seltene Gehölze im Hortus botanicus vomerensis. Mitt. Deutsch. Dendr. Ges. 16: 65–69.

Stapf, O. 1928. *Schizandra rubriflora*. Bot. Mag. 152: pl. 9146.

Steenis, C. G. G. J. van. 1962. The mountain flora of the Malaysian tropics. Endeavour 21: 183–193 + pl. 1–4.

______. 1972. *The mountain flora of Java*. Leiden: Brill.

______. 1979. Plant-geography of east Malesia. Bot. J. Linn. Soc. 79: 97–178.

Stone, D. E. 1968. Cytological and morphological notes on the southeastern endemic *Schisandra glabra* (Schisandraceae). J. Elisha Mitchell Sci. Soc. 84: 351–356.

Suekawa, M., T. Shiga, H. Sone, and Y. Iketani. 1989. Gomisin H, J, N and G from *Schisandra* fruits and their uses as calcium antagonists with antihypertensive activity. Jap. Kokai Tokkyo Koho JP 01 42,421. [Patent]

Sun, C.-R. 1988. A new species of Schisandraceae. Bull. Bot. Res., Harbin 8: 123–125.

Sun, C.-R., and C.-B. Chen. 1999. Karyotype analysis in the family Schisandraceae and the preliminary evaluation on its systematic significance. In *XVI International Botanical Congress*; *abstracts*, p. 439. [Abstract]

Sun, H.-D., S.-X. Qiu, L.-Z. Lin, Z.-Y. Wang, Z.-W. Lin, T. Pengsuparp, J. M. Pezzutto, H. H. S. Fong, G. A. Cordell, and N. R. Farnsworth. 1996. Nigranoic acid, a triterpenoid from *Schisandra sphaerandra* that inhibits HIV-1 reverse transcriptase. J. Nat. Prod. 59: 525–527.

Swamy, B. G. L. 1964. Macrogametophytic ontogeny in *Schisandra chinensis*. J. Indian Bot. Soc. 43: 391–396.

Sy, L.-K., R. M. K. Saunders, and G. D. Brown. 1997. Phytochemistry of *Illicium dunnianum* and the systematic position of the Illiciaceae. Phytochemistry 44: 1099–1108.

Taguchi, H., and Y. Ikeya. 1975. The constituents of *Schizandra chinensis*. Baill. I. The structures of gomisin A, B and C. Chem. Pharm. Bull. 23: 3296–3298.

______. 1977. The constituents of *Schizandra chinensis* Baill. The structures of two new lignans gomisins F and G and the absolute structures of gomisins A, B and C. Chem. Pharm. Bull. 25: 364–366.

______. 1979. Gomisin J. Jap. Kokai. Tokkyo Koho 79 32,462. [Patent]

Taguchi, H., Y. Ikeya, and I. Yosioka. 1979. Structures and reactions of new dibenzocyclooctadiene lignans isolated from the fruits of *Schisandra chinensis* Baill. Koen Yoshishu-Tennen Yuki Kagobutsu Toronkai 22: 299–306. [In Japanese]

Takahashi, A. 1985. Wood anatomical studies of Polycarpicae. I. Magnoliales. Sci. Rep. Osaka Univ. 34: 29–83.

Takahashi, K., and M. Takani. 1975. Studies on constituents of medicinal plants. XIV. Constituents of *Schizandra nigra* Max. 1. Chem. Pharm. Bull. 23: 538–542.

______. 1976. Studies on constituents of medicinal plants. XVII. Constituents of *Schisandra nigra* Max. and their carbon-13 nuclear magnetic resonance spectra. Chem. Pharm. Bull. 24: 2000–2006.

Takani, M., M. Nakano, and K. Takahashi. 1977. Studies on constituents of medicinal plants. XIX. Constituents of *Schizandra nigra* Max. 3. Chem. Pharm. Bull. 25: 3388–3390.

Takani, M., K. Ohya, and K. Takahashi. 1979. Studies on constituents of medicinal plants XXII. Constituents of *Schizandra nigra* Max. 4. Chem. Pharm. Bull. 27: 1422–1425.

Takhtajan, A. 1986. *Floristic regions of the world.* Berkeley, California: University of California Press.

______. 1997. *Diversity and classification of flowering plants.* New York: Columbia University Press.

Talapatra, B., A. Basak, and S. K. Talapatra. 1982. Terpenoids and related compounds: Part XXII - schizandraflorin, a new tetracyclic triterpene dione from *Schizandra grandiflora* Hook. f. and Thom. Ind. J. Chem., Sect. B 21B: 76–78.

Tanai, T. 1976. The revision of the Pliocene Mogi flora, described by Nathorst (1883) and Florin (1920). J. Fac. Sci., Hokkaido Univ., ser. 4, Geol. Mineral. 17: 277–346.

Tanaka, T. 1976. *Tanaka's cyclopedia of edible plants of the world.* Tokyo: Keigaku.

Tanaka, Y. 1895. *Useful plants of Japan.* Tokyo: Agricultural Society of Japan.

Tao, Y., J. Liu, and M. Huang. 1991. Constituents of Henry magnoliavine (*Schisandra henryi*). VI. Isolation and identification of four lignan compounds. Chin. Trad. Herb. Drugs 22: 51–53. [In Chinese]

Thanikaimoni, G. 1984. Ménispermacées: palynologie et systématique. Trav. Sect. Sci. Tech. Inst. Fr. Pondichéry 18: 1–135.

______. 1986. Evolution of Menispermaceae. Can. J. Bot. 64: 3130–3133.

Thorne, R. F. 1992. Classification and geography of the flowering plants. Bot. Rev. 58: 225–348.

Tiffney, B. H. 1985. The Eocene North Atlantic land-bridge: its importance in Tertiary and modern phytogeography of the Northern Hemisphere. J. Arnold Arbor. 66: 243–273.

Toda, S., Y. Iketani, H. Taguchi, and H. Mihashi. 1989. Pharmaceuticals containing gomisin N as an antioxidant. Jap. Kokai Tokkyo Koho JP 01 16,721. [Patent]

Tong, Y., and W. Song. 1989. Determination of lignans in the fruits of *Schisandra chinensis* (Turcz.) Baill. and *S. sphenanthera* Rehd. et Wils. by HPLC and their chromatograms. Zhongguo Zhongyao Zazhi 14: 611–614. [In Chinese]

Tschudy, R. H. 1984. Palynological evidence for change in continental floras at the Cretaceous Tertiary boundary. In *Catastrophes and earth history*, ed. W. A. Berggren and J. A. Van Couvering, 315–337. Princeton, New Jersey: Princeton University Press.

Tucker, D. D. 1994. *Schisandra glabra* (Schisandraceae) new to Kentucky. Sida 16: 213–214.

Tucker, S. C., and J. A. Bourland. 1994. Ontogeny of staminate and carpellate flowers of *Schisandra glabra* (*Schisandraceae*). Pl. Syst. Evol. [Suppl.] 8: 137–158.

Turczaninow, N. 1837. Enumeratio plantarum quas in China boreali collegit et mecum benevole communicavit cl. Medicus Missionis Rossicae Porphyrius Kirilow. Bjull. Moskovsk. Obsc. Isp. Prir., Otd. Biol. 7: 148–158.

Ueda, K. 1988. Sex change in a woody vine species, *Schisandra chinensis*, a preliminary note. J. Jap. Bot. 63: 319–321.

Verstappen, H. T. 1975. On palaeo climates and landform development in Malesia. In *Modern Quaternary research in Southeast Asia*, ed. G.-J. Bartstra and W. A. Casparie, 3–35. Rotterdam: Balkema.

Vesque, J. 1881. De l'anatomie des tissus appliquée a la classification des plantes. Nouv. Arch. Mus. Hist. Nat., ser. 2, 4: 1–56 + pl. 1–2.

Vijayaraghavan, M. R., and U. Dhar. 1975. *Kadsura heteroclita* - microsporangium and pollen. J. Arnold Arbor. 56: 176–182.

______. 1977. Structure of the carpel with special reference to lysigenous cavities in *Kadsura Roxburghiana*. Bot. Jahrb. Syst. 98: 273–277.

→ Walker, J. W. 1974a. Evolution of exine structure in the pollen of primitive angiosperms. Amer. J. Bot. 61: 891–902.

→ ______. 1974b. Aperture evolution in the pollen of primitive angiosperms. Amer. J. Bot. 61: 1112–1136.

______. 1976a. Comparative pollen morphology and phylogeny of the Ranalean complex. In *Origin and early evolution of angiosperms*, ed. C. B. Beck, 241–299. New York: Columbia University Press.

______. 1976b. Evolutionary significance of the exine in the pollen of primitive angiosperms. In *The evolutionary significance of the exine*, ed. I. K. Ferguson and J. Muller, 251–308. [*Linnean Society symposium series 1*]. London: Academic Press.

→ Walker, J. W., and J. A. Doyle. 1975. The bases of angiosperm phylogeny: palynology. Ann. Missouri Bot. Gard. 62: 664–723.

Wallich, N. 1824. *Tentamen flora Napalensis illustratae.* Calcutta & Serampore.

Wang, H., and Y. Chen. 1985. Lignans from *Schisandra rubriflora* Rehd. et Wils. Acta Pharm. Sin. 20: 832–841. [In Chinese]

Wang, H., Y. Chen, and X. Liang. 1993. The structure of a new lignan diol. Chin. Chem. Lett. 4: 31–32.

Wang, H., F. Wang, D. Wang, and S. Wang. 1989. The anatomy of wood in *Schizandra chinensis* Baillon. Nat. Sci. J. Harbin Norm. Univ. 5: 74–77. [In Chinese]

Wang, J.-L. 1968. Morphological study on the pollen grains of Magnoliales of Taiwan. Bull. Taiwan Forest. Res. Inst. 159: 1–22.

Wang, L.-J., A.-G. Gu, G.-Z. Sheng, and Y.-M. Zhang. 1992. Studies on fruit anatomy of *Schisandra chinensis* Baillon. Bull. Bot. Res., Harbin 12: 383–388. [In Chinese]

Wang, M., and B. Li. 1983. High-performance liquid chromatographic analysis of active ingredients in the fruit of *Schizandra chinensis* Baill. Acta Pharm. Sin. 18: 209–214. [In Chinese]

Wang, W.-T. 1980. *Iconographia cormophytorum Sinicorum.* Vol. 1. Beijing: Science Press. [In Chinese]

→ Watrous, L. E., and Q. D. Wheeler. 1981. The out-group comparison method of character analysis. Syst. Zool. 30: 1–11.

Watt, G. 1889–96. *A dictionary of the economic products of India.* Vol. 6(2). Calcutta: Superintendant of Government Printing.

→ Weberling, F. 1988. Inflorescence structure in primitive angiosperms. Taxon 37: 657–690.

Whitaker, T. W. 1933. Chromosome number and relationship in the Magnoliales. J. Arnold Arbor. 14: 376–385 + pl. 80.

Whiting, D. A. 1985. Lignans and neolignans. Nat. Prod. Rep. 2: 191–211.

Wilkinson, H. P. 1979. The plant surface (mainly leaf). In *Anatomy of the dicotyledons.* 2nd ed. Vol. 1, ed. C. R. Metcalfe and L. Chalk, 97–165. Oxford: Clarendon Press.

Willemstein, S. C. 1987. *An evolutionary basis for pollination biology.* Leiden: E. J. Brill/Leiden University Press.

Williams, E. G., T. L. Sage, and L. B. Thien. 1993. Functional syncarpy by intercarpellary growth of pollen tubes in a primitive apocarpous angiosperm, *Illicium floridanum* (Illiciaceae). Amer. J. Bot. 80: 137–142.

Wodehouse, R. P. 1936. Evolution of pollen grains. Bot. Rev. 2: 67–84.

______. 1959. *Pollen grains. Their identification and significance in science and medicine.* 2nd ed. New York: Hafner.

Wolfe, J. A. 1992. Climatic, floristic and vegetational changes near the Eocene/Oligocene boundary in North America. In *Eocene-Oligocene climatic and biotic evolution*, ed. D. R. Prothero and W. A. Berggren, 421–436. Princeton, New Jersey: Princeton University Press.

Writing Group for Cenozoic Plants of China. 1978. *Fossil plants from China.* Vol. 3. *Cenozoic plants from China.* Beijing: Science Press.

Wu, Z., and C. Huang. 1995. Comparative studies on karyotypes of two taxa in Schisandraceae. Guihaia 15: 47–51. [In Chinese]

Yahara, S., C. Sakamoto, T. Nohara, Y. Niiho, Y. Nakajima, and H. Ito. 1993. Thymoquinol glucosides from schisandrae fructus. Jap. J. Pharm. 47: 420–422.

Yonemitsu, Y. 1989. Isolation of (+)-(6S,7S,R-biar)–5,6,7,8-tetrahydro–1,2,3,12-tetramethoxy–6,7-dimethyl–10,11-methylenedioxy–6-benzo[a,c]cyclooctenol from stems or roots of *Schisandra chinensis.* Jap. Kokai Tokkyo Koho JP 01,165,583. [Patent]

Yoshida, O. 1962. Embryologische Studien über *Schisandra chinensis* Bailley. J. Coll. Arts Sci., Chiba Univ. 3: 459–462 + pl. 1–4.

Yuan, S.-L., and W.-J. Chao. 1996. Germplasm resources of *Kadsura* Juss. and *Schisandra* Michx. in Qinling Bashan region. J. Pl. Resources Environ. 5: 35–37. [In Chinese]

Yue, J.-M., Y.-Z. Chen, S.-M. Hua, J.-L. Cheng, and Y.-X. Cui. 1989. Ganschisandrine, a lignan from *Schisandra sphenanthera.* Phytochemistry 28: 1774–1776.

Yue, J.-M., X. Jun, and Y.-Z. Chen. 1994. Triterpenoids of *Schisandra sphenanthera.* Phytochemistry 35: 1068–1069.

Zagwijn, W. 1959. Zur stratigraphischen und pollenanalytischen Gliederung der pliozänen Ablagerungen im Roertal-Graben und Venloer Graben der Niederlande. Fortschr. Geol. Rheinl. Westfalen 4: 5–26 + pl. 1.

Zahur, M. S. 1959. Comparative study of secondary phloem of 423 species of woody dicotyledons belonging to 85 families. Cornell Univ. Agric. Exp. Sta. Mem. 358: 1–160.

Zamora, P. M. 1966. Studies on the primary xylem elements in the order Ranales (sensu lato): a systematic survey. Philipp. Agric. 50: 391–623.

Zhang, B.-N. 1991. Schisandraceae. In *Flora of Guangxi,* ed. X. G. Li and F. Liang, 106–112. Nanning: Guangxi Science and Technology Publishing House. [In Chinese]

Zhang, Y.-Y., Y. Guo, K. Nakajima, Y. Ikeya, and H. Mitsuhashi. 1990. Quantitative analysis of lignans in *Schisandra chinensis* Baill. of different origins by HPLC. Yaowu Fenxi Zazhi 10: 146–148. [In Japanese]

Zhang, Y.-Y., K. Nakajima, E. Miki, Y. Ikeya, K. Hayashi, M. Okada, M. Maruno, Y.-Z. Guo, and H. Mitsuhashi. 1993. Developmental course of fruit of *Schisandra chinensis* (Turcz.) Baill. collected in Liaoning Province of China and seasonal variation of lignan contents in the fruitlets. Jap. J. Pharm. 47: 165–172. [In Japanese]

Zhou, L.-H., P.-H. Huang, W.-C. Jin, and C.-P. Yang. 1994. Varietas una nova *Schisandrae chinensis* (Turcz.) Baill. ex provincia Heilongjiang. Bull. Bot. Res., Harbin 14: 35–36.

Zhou, Q. 1985. Chinese medicinal herbs in the treatment of viral hepatitis. In *Advances in Chinese medicinal materials research,* ed. H. M. Chang, H. W. Yeung, W.-W. Tso, and A. Koo, 215–219. Singapore: World Scientific Publishing.

Zhu, Y., K. Yan, and G. Tu. 1988a. Chemical studies on Shengmai San. I. Quantitative determination of active ingredients of *Schizandra* in Shengmal San by TLC-densitometry. Yaowu Fenxi Zazhi 8: 71–73. [In Japanese]

Zhu, Y., K. Yan, J. Wu, and G. Tu. 1988b. Assay of lignans of *Schizandra chinensis* in Shengmai San by high performance liquid chromatography. J. Chromatogr. 438: 447–450.

APPENDIX 1

CHROMOSOME NUMBERS

S. arisanensis subsp. *viridis:* 2n = 28: Lin & Zhou (unpublished; cited in Lin 1997, as "*S. viridis*").

S. bicolor: 2n = 28: Wu & Huang 1995.

S. chinensis: 2n = 24: Solovyeva 1998; 2n = 28: Janaki-Ammal in Darlington & Wylie 1955, Probatova & Sokolovskaya 1981, Probatova et al. 1989, Chen et al. 1993, Li et al. 1993.

S. glabra: n = 13: Bostick 1965 (as "*S. coccinea*"); n = 14: Stone 1968; 2n = 28: Stone in Anonymous 1965, Stone 1968.

S. glaucescens: 2n = 28: Sun & Chen 1999.

S. grandiflora: n = 7: Malla et al. in Löve 1977, Sandhu & Mann in Bir 1988, Sandhu et al. 1989; n = 14: Bir et al. 1980, Singhal et al. in Löve 1980, Gill et al. 1984, Sandhu & Mann in Bir 1988, Sandhu et al. 1989.

S. propinqua subsp. *sinensis:* 2n = 28: Lin & Zhou (unpublished; cited in Lin 1997), Sun & Chen 1999.

S. repanda: 2n = 28: Okada 1975 (as "*S. nigra*").

S. rubriflora: n = 14: Ratter & Milne 1976.

S. sphenanthera: n = 14: Whitaker 1933; 2n = 28: Sun & Chen 1999.

APPENDIX 2

PHYTOCHEMICAL REPORTS

Reports of phytochemicals in *Schisandra,* arranged by biogenetic group (flavonoids excluded); only reports for named species are included. Data derived from Hegnauer (1990), Buckingham (1997), and *Chemical Abstracts.*

MONOTERPENES

Menthane monoterpenes. *S. chinensis*: Hou et al. 1995.

SESQUITERPENES

Sesquicaranes. *S. chinensis*: Y. G. Liu 1990; Ohta & Hirose 1968a.

Chamigranes. *S. chinensis*: Hikino et al. 1986; Y. G. Liu 1986, 1990; Ohta & Hirose 1968b; Motl et al. 1963.

Cadinanes. *S. repanda*: Takahashi & Takani 1976.

Copaenes. *S. chinensis*: Motl et al. 1963.

LIGNANS

8,8′-lignans. *S. arisanensis* subsp. *viridis*: Luo & Liu 1992. *S. chinensis*: Ikeya et al. 1978a, 1979e. *S. henryi*: Huang et al. 1982a; Li & Xue 1986. *S. propinqua*: J.-S. Liu et al. 1988b. *S. repanda*: Takani et al. 1979. *S. rubriflora*: Wang et al. 1993. *S. sphenanthera*: Huang et al. 1982b; Li & Xue 1985; Liu & Huang 1984; Yue et al. 1989.

8,8′,2,2′-cyclooctane lignans. *S. arisanensis* subsp. *viridis*: Luo et al. 1992; Luo & Liu 1992. *S. chinensis* (selected references only): Bao et al. 1979; Chen et al. 1976; Chen & Li 1977; Chen et al. 1994; Chinese Academy of Medical Sciences 1977; Hikino et al. 1984; Hsu et al. 1980; Iketani et al. 1980, 1989, 1996; Ikeya et al. 1978a, 1978b, 1978c, 1979a, 1979b, 1979c, 1979d, 1979e, 1979f, 1980a, 1980b, 1980c, 1982a, 1982b, 1982c, 1988, 1990a; Kochetkov et al. 1961, 1962; J.-S. Liu et al. 1990; Nakajima et al. 1983; Samoylenko & Suprunov 1974; Sohn & Bock 1989; Song & Tong 1983; Song & Xiao 1982; Song et al. 1990; Suekawa et al. 1989; Taguchi & Ikeya 1975, 1977, 1979; Taguchi et al. 1979; Toda et al. 1989; Tong & Song 1989; Wang & Li 1983; Yonemitsu 1989; Zhang et al. 1990; Zhu et al. 1988a, 1988b. *S. glaucescens*: Song et al. 1990. *S. henryi*: C.-S. Liu et al. 1978b; J.-S. Liu et al. 1984, 1988c; Tao et al. 1991. *S. incarnata*: Song et al. 1990. *S. lancifolia*: Song & Tong 1983. *S. neglecta*: Song et al. 1990. *S. plena*: Song et al. 1990. *S. propinqua*: L.-N. Li et al. 1995; Z. Li et al. 1996; J.-S. Liu et al. 1988b; Song et al. 1990. *S. pubescens*: Song et al. 1990. *S. repanda*: Iketani et al. 1996. *S. rubriflora*: Chen & Yang 1982; Ikeya et al. 1990a; Lee et al. 1990; Luo & Liu 1992; Song & Tong 1983; Wang & Chen 1985. *S. sphenanthera*: He et al. 1978; Iketani et al. 1990; Ikeya et al. 1990a, b, 1991; J.-S. Liu et al. 1976; C.-S. Liu et al. 1978a; Shanghai Institute of Materia Medica 1976; Song & Tong 1983; Song et al. 1990; Tong & Song 1989.

TRITERPENES

Lanostanes. *S. propinqua*: J.-S. Liu et al. 1988a. *S. sphenanthera*: J.-S. Liu & M.-F. Huang 1984; Yue et al. 1994.

Cycloartanes. *S. grandiflora*: Talapatra et al. 1982. *S. repanda*: Takahashi & Takani 1975, 1976. *S. sphenanthera*: Chen et al. 1987.

seco-Lanostanes. *S. propinqua*: J.-S. Liu et al. 1988a. *S. repanda*: Kikuchi & Yoshiokoshi 1972.

seco-Cycloartanes. *S. sphaerandra*: Sun et al. 1996.

GLYCOSIDES

S. chinensis: Yahara et al. 1993. *S. repanda*: Takani et al. 1977.

APPENDIX 3

FOSSIL RECORD

PLEISTOCENE (1.64 Ma–present)

S. repanda (Sieb. & Zucc.) Radlk.: Japan (leaves); Miki & Kokawa 1962 (as "*S. nigra* Maxim.").

PLIOCENE (5.2–1.64 Ma)

S. florini Tanai: Japan (leaves); Florin 1920 (as "*S. chinensis*"); Tanai 1976.

S. geissertii Gregor: Germany (seeds); Gregor 1981; Geissert & Gregor 1981.

S. grossheimi A. A. Kolakovskij: Georgia (leaves); Kolakovskij 1957, 1964.

S. megasperma Miki: Japan (seeds); Miki 1941.

Schisandra sp.: The Netherlands (seeds); Zagwijn 1959.

MIOCENE (23.3–5.2 Ma)

S. chinensis (Turcz.) Baill.: Poland (pollen); Macko 1957.

S. megasperma Miki: Japan (seeds); Miki 1941.

S. splendinervosa S. Guo [species not formally published]: Yunnan, China (leaves); Guo 1988; S. Guo, pers. comm., Oct 1996.

Schisandra sp.: Czech Republic (seeds); Bůžek et al. 1996.
Schisandra sp.: Japan (leaves); Huzioka 1964.
Schisandra sp.: Borneo (pollen); Muller 1964 (specified as Miocene in Muller 1970).
c.f. *Schisandra* sp.: Belorussia (leaves); Kryshtofowich & Baikavskaja 1965: 74.
Schisandraceae: Poland (seeds); Łańcucka-Środoniowa (cited in Jähnichen 1976).
Schisandraceae: Oregon, U.S.A. (pollen); Gray 1964.

OLIGOCENE (35.4–23.3 Ma): no records.

EOCENE (56.5–35.4 Ma)
S. europaea H. Jähnichen: Germany (leaves); Jähnichen 1976; Mai & Walther 1985.
S. fushuensis Li: Liaoning, China (leaves); Writing Group for Cenozoic Plants of China 1978; Guo 1990.
S. glandulosa Tao: Liaoning, China (leaves); Writing Group for Cenozoic Plants of China 1978; Guo 1990.
S. oregonensis S. R. Manchester: Oregon, U.S.A. (seeds); Manchester 1994.
Schisandra sp.: Oregon, U.S.A. (seeds); Manchester 1990.
Schisandraceae: Oregon, U.S.A. (seeds); Bones 1979.

PALEOCENE (65–56.5 Ma): no records.

UPPER CRETACEOUS (95–65 Ma)
S. durbudensis S. Guo: Heilongjiang, China (leaves); Guo 1984, 1990.
Schisandraceae: California, U.S.A. (pollen); Chmura 1973. Two pollen forms are described by Chmura: "Pollen Forma A" is identified as either Illiciaceae or Schisandraceae, whereas "Pollen Forma B" is determined as Schisandraceae.

NUMERICAL LIST OF SPECIES

1. *S. grandiflora*
2. *S. rubriflora*
3. *S. incarnata*
4. *S. sphaerandra*
5. *S. neglecta*
6. *S. sphenanthera*
7a. *S. arisanensis* subsp. *arisanensis*
7b. *S. arisanensis* subsp. *viridis*
8. *S. glaucescens*
9. *S. elongata*
10. *S. tomentella*
11. *S. pubescens*
12. *S. pubinervis*
13. *S. lancifolia*
14. *S. micrantha*
15a. *S. henryi* subsp. *henryi*
15b. *S. henryi* subsp. *yunnanensis*
15c. *S. henryi* subsp. *marginalis*
16. *S. longipes*
17. *S. perulata*
18. *S. chinensis*
19. *S. glabra*
20. *S. repanda*
21. *S. bicolor*
22a. *S. propinqua* subsp. *propinqua*
22b. *S. propinqua* subsp. *intermedia*
22c. *S. propinqua* subsp. *sinensis*
22d. *S. propinqua* subsp. *axillaris*
23. *S. plena*

INDEX TO NUMBERED COLLECTIONS EXAMINED

Numbers in parentheses refer to the corresponding species in the Numerical List of Species presented above. Chinese names are transliterated using the "pinyin" system, except for older names, which are given in their original transliteration and cross-referenced with the corresponding "pinyin" transliteration.

Bisset, J. 1399 (18), 4562 (18).
Biswas, K. 6642 (1), 6887 (1).
Blume, C. L. von 66 (22d), 750 (22d), 1422 (9), 1601 (22d).
Bock, C., & A. von Rosthorn 131 (8).
Boufford, D. E., & B. Bartholomew 24908 (22c).
Boufford, D. E., B. Bartholomew, G. Li, & G. H. Zhu 24074 (15a), 24371 (6), 24403 (6).
Boufford, D. E., H. X. Cheng, B. D. Liu, C. Y. Xi, T. S. Ying, C. J. Zhang, & X. L. Zhu 26074 (6), 26097 (6).
Boufford, D. E., B. D. Liu, T. S. Ying, C. J. Zhang, & X. C. Zhang 26380 (6).
Boufford, D. E., B. D. Liu, T. S. Ying, & X. L. Zhu 26211 (6).
Boufford, D. E., & E. W. Wood 16697 (19).
Boufford, D. E., T. S. Ying, C. J. Zhang, & X. C. Zhang 26480 (6).
Brinkman, R. 874a (22d).
Brooks, W. P. 20 (18), 579 (18).
Bryson, C. T., & M. W. Morris 6496 (19).
Cavalerie, J. 27 (6).
Cave, G. H. 117/47 (1).
Chamberlain, D., C. Grey-Wilson, Y. Li, R. McBeath, A. Schilling, T. Xu, & H. Yuan 28 (4).
Chand, C. S. 2 (22a).
Chang, C. Y. 17810 (22c), 17994 (22c), 18169 (22c).
Chang, G. C. 5 (7b).
Chang, G. C., et al. 28 (7b).
Chang, S. Y. 3300 (15c), 3489 (15c), 3837 (7b), 4468 (15c), 4696 (6), 4990 (7b), 5207 (7b), 5675 (7b), 5891 (7b).
Chang, Y. P. 869 (22b).
Chaw, S.-M. 615 (7a), 616 (7a).
Chen, D. Z. (see Chen, T. C.).
Chen, F. H. 402 (18), 618 (18).
Chen, S. 293 (7b), 660 (15c), 3258 (7b).
Chen, S. Q. (see Chun, S. H.).
Chen, T. C. 429 (7b), 658 (15c).
Chen, Y. 982 (6).
Chen, Y. Q. 170354 (16).
Cheng, W. C. 3656 (21).
Cheng, W. C., & C. T. Hwa 823 (11).
Cheng 168 (7b).
Cheo, H. C. 126 (7b).
Chiao, C. Y. 1163 (22c), 1611 (13), 1628 (2).
Chiao, C. Y., & C. S. Fan 230 (15a), 773 (15a).
Ching, R. C. 1606 (15c), 1781 (7b), 2336 (15c), 2591 (6), 3008 (6), 3166 (7b), 4777 (7b), 5132 (7b), 6236 (15c), 6994 (15a), 20572 (4), 20644 (4), 21484 (5), 21830 (5), 22003 (4).
Ching, R. C., & C. L. Tso 498 (6).
Chiu, P. L. 20 (21), 313 (6), 376 (21), 493 (15c), 761 (15c), 809 (15c).
Chow, H.-C. 210 (6), 567 (22c), 689 (6), 898 (22c), 1439 (22c), 7522 (15a), 7698 (2), 7920 (2), 9932 (15a), 11629 (15a), 12010 (15a).
Chow, H.-C., & H.-Y. Li 110710 (22c).
Chow, K. S. 91 (7b), 74266 (18).
Chow, K. S., et al. 120 (22c).
Chu, K. L. 2962 (12), 4003 (22c).
Chun, S. H. 574 (15a), 3142 (16), 3305 (15c), 14631 (15c), 14953 (7b), 15576 (15c), 16580 (7b).
Chun, W. Y. 3820 (8).
Chun, W. Y., & S. S. Chien 5127 [8090] (22c).
Chung, H. H., & S. C. Sun 732 (7b).
Chung, Z. S. 82002 (7b), 83594 (15a).
Chungtien-Lijiang-Dali Expedition 599 (4).
Clarke, C. B. 12217 (1), 26715 (5).
Coert, J. H. 746 (22d), 944 (22d), 1002 (9).
Cooper, R. E. 2061 (1), 2767 (1), 3003 (1), 3310 (1), 3892 (1).
Croom, H. B. 280 (19).
Dai, T. L. 103218 (22c).
Dang, M. P., & K. Yao 79107 (6).
Datta, B. C. 1 (1), 2 (22a).
David, A. 1839 (18).
Deguchi, K. 6454 (18).
Deguchi, K., et al. 7524 (18).
Deng, L. (see Teng, L.).
Deng, S. W. (see Teng, S. W.).
Dickason, F. G. 5016 (14), 5076 (22b).
Dong, X. Y. 93394 (7b).
Dong, X. Y., & Y. N. Xiong 93291 (7b).
Dorgelo, J. D. 137 (9), 1450 (9).
Dorsett, P. H., & J. H. Dorsett 4098 (18).
Dorsett, P. H., & W. J. Morse 874 (18), 1330 (18).
Drummond, J. R. 3029 (1), 8327 (1), 14836 (1).
Ducloux, F. 468 (22b), 585A (14), 585B (14), 735 (14), 2588 (14), 2764 (14), 2765 (14).
Duncan, W. H. 11153 (19).
Dunn, S. T. 2330 (7b), 2442 (7b).
Duthie, J. F. 7244 (1).
Elias, T. S., & D. Murray 11050 (18).
Esquirol, J. 58 (15a), 1555 (22c).
Ewan, J. 22399 (19).
Expedition to Sichuan (SICH) 641 (4).
Faber, E. 160 (2).
Falconer, H. 79 (1), 80 (22a).
Fan, C. S., & Y. Y. Li 220 (6), 221 (7b), 280 (15a).
Fang, M. Y. 24594 (8).
Fang, W. P. 408 (10), 429 (15a), 831 (2), 855 (8), 893 (2), 1116 (15a), 1121 (15a), 1395 (11), 1585 (2), 2171 (12), 2172 (6), 2238 (6), 2374 (2), 2632 (11), 2788 (2), 3650 (2), 7362 (11), 7765 (12), 8270 (2), 8330 (12), 16853 (15a).
Faurie, U. 497 (18), 498 (18), 1678 (20), 3004 (18), 4774 (18), 5391 (20), 6214 (18), 6913 (18), 6988 (18).
Feng, K. M. 934 (4), 1217 (4), 2844 (5), 2883 (4), 3149 (5), 9303 (22b).
Forbes, H. O. 870 (9).
Forrest, G. 2122 (4), 4797 (4), 5663 (4), 7181 (4), 7622 (5), 7686 (22b), 7692 (22b), 10197 (13),

11845 (22b), 15825 (5), 15860 (22b), 16589 (13), 19125 (22b), 21523 (22b), 21524 (13), 22245 (22b), 29715 (2).
Fukuoka, N. T-63689 [508] (22b).
Furuse, M. 2792 (20), 6363 (18), 6792 (18), 20507 (18).
Gamble, J. S. 699A (1), 1891 (5), 23019 (1), 26594 (1), 26742 (1), 26752B (5), 28024 (1), 6094A (1), 8223 (1).
Gao, X. M. 1682 (15a).
Gao, X. P. (see Ko, S. P.).
Gilbert, K. S. 22 (18).
Givens, F. M. 4524 (19).
Godfrey, R. K. 57050 (19).
Goetghebeur, P. 8857 [HBUG 87-0254] (2), 8858 [HBW 80.BG.20403] (18).
Goldstein, N. C. 62 (19).
Gould, B. J. 202 (1), 202A (1).
Gressitt, J. L. 190 (7a), 1485 (7b), 2444 (12).
Grierson, A. J. C., & D. G. Long 983 (1), 1155 (1), 1793 (1), 2555 (1).
Griffith, W. 76 (5), 77 (5).
Guang Fu Forest Team 231 (16), 872 (21).
Guizhou Expedition 3960 (22c), 4336 (22c), 6958 (22c).
Guo, S. B. 80700 (7b).
Haines, H. H. 794 (1).
Hallier, J. G. 750 (9).
Handel-Mazzetti, H. F. von 119 (22c), 195 (15a), 595 [11740] (6), 735 [12062] (15a), 784 [11933] (6), 1943 (22c), 2962 (4), 8820, pro parte (5), 8820, pro parte (22b), 10017 (22b).
Hangchow University Taxonomy Team 2438 (7b).
Hangzhou Botanic Garden Herbarium 3009 (7b), 3126 (7b), 8251 (7b), 26943 (15c), 30942 (15c).
Hao, G. 102 (22c).
Harper, R. M. 3377 (19).
Hasegawa, K. 10393 (18).
Hatusima, S. 14036 (20).
He, G. S. 4470 (7b), 4799 (7b), 6270 (15c).
He, G. Z. (see He, G. S.).
He, S. Y., et al. 813030 (18).
He, Q. H. 2215 (6).
Henry, A. 781 (22c), 1225 (15a), 1544 (22c), 1693 (22c), 1785 (11), 2028 (22c), 3243 (22c), 3354 (22c), 3446 (6), 3469 (6), 3699 (22c), 3961 (22c), 4040 (6), 4059 (6), 5378 (8), 5478 (8), 5527 (6), 5527A (6), 5725 (8), 5907 (11), 5931 (8), 6219 (22c), 6226 (15a), 6292 (8), 6383 (8), 6447 (12), 8798 (2), 9193 (15a), 9193A (15a), 9193B (15a), 10697 (5), 10719 (22b), 10854 (23), 11211 (14), 11749 (23), 11893 (23), 12022 (15b), 12022A, pro parte (5), 12022A, pro parte (15b), 12022B (15b), 12192 (23), 13023 (22b).
Hers, J. 243 (6), 424 (6), 452 (6), 860 (6), 1220 (6), 1246 (6), 1335 (6), 2154 (18), 3089 (6).
Hill, S. R., & A. K. Gholson 19217 (19).
Ho, Y. Y. 1138 (7b), 1448 (7b).
Holstvoogd, C. 611 (9).
Hosoi, K. 2612 (20).
Hu, H. H. 1118 (7b), 1584 (7b), 1693 (7b).
Hu, S. Y. 941 (22c).
Huang, C. L., W. H. Hu, & Y. Y. Lien 72 (7a), 125 (7a).
Huang, M. X. 111962 (15c), 112217 (21), 112705 (7b).
Huang, Z. (see Wang, C.).
Hunan Expedition 524 (22c).
Hunan Museum 238 (7b).
Jiang, Z. D., & G. F. Tao 228 (6).
Jinggang Shan Team 661226 (7b).
Jutila, J., H. Fugino & Yoshizaki 399 (20).
Kanai, H. 3927 (18), 6350 (20), 8672 (18).
Kanai, H., G. Murata, & M. Togashi 6303834 (22a).
Kanai, H., H. Ohashi, K. Hasegawa, & K. Okubo 9658 (18).
Kanjilal, U. 750 (22a).
Kao, M. T. 10243 (7a).
Keng, Y. L. 601 (7b).
Kermode, C. W. D. 17289 (5).
Ko, S. P. 50748 (15c), 51301 (15c), 52691 (7b), 52919 (7b), 53043 (16), 54551 (16).
Komaròv, V. 652 (18).
Konta, F., & S. Kusaka 119 (20).
Koorders, S. H. 25982b (22d), 28047b (22d), 31552b (9), 37670b (22d), 37671b (22d), 37672b (9), 37673b (22d).
Koyama, T. 8063 (18).
Kung, H. W. 79 (18).
Kusnezow, I. W. 211 (18).
Lace, J. H. 57 (1), 2157 (1), 2280 (1), 2281 (1), 5432 (22b), 5875 (22b), 5919 (22b).
Lau, S. K. 1993 (7b), 28461 (15a), 28629 (15a).
Laurie, M. V. 5372 (1).
Lee, K. F. 61431 (6), 63001 (11).
Lee, S. C. 203566 (7b), 204722 (22c), 204799 (22c), 204818 (6).
Lepcha, R. 1234 (1).
Li, C. F. 11173 (18).
Li, G. F. (see Lee, K. F.).
Li, H., & V. Soukup 958 (5).
Li, H. C. 2945 (22c).
Li, H. J. 2432 (15a).
Li, S. Y. 180617 (7b).
Li, X. G. (see Lee, S. C.).
Liang, B. H., & H. H. Hsue 85161 (21).
Liao, C.-C., W. P. Leu, H.-L. Ho, & T.-Y. Liu 1282 (7a).
Licent, E. 2345 (18), 5038 (6), 12067 (18).
Limpricht, W. 1572 (11).
Lin, Q. 973 (6), 974 (15c), 975 (7b), 976 (6), 977 (15c).
Liou, L. U., & K. C. Ho 16342 (21).
Liou, T. N., & C. Wang 264 (22c).

Litvinov, D. 1767 (18), 2072 (18).
Liu, J. C. 1919 (18).
Liu, M.-G., & J.-L. Liu 122 (22c).
Liu, T.-Y., W.-H. Hu, Y.-R. Lin, & S.-J. Liu 467 (7a).
Liu, X. G. 28955 (15a).
Liu, Y. G. 596 (16).
Long, D. G., R. J. D. McBeath, D. R. McKean, D. A. H. Rae, & N. P. Bhattarai 710 (1).
Lowndes, D. G. 906 (1).
Lu, Q. H. 2540 (15a).
Ludlow, F., & G. Sherriff 1704 (1).
Ludlow, F., G. Sherriff, & H. H. Elliot 12544 (1), 13006 (1), 13707 (1), 13822 (1).
Ludlow, F., G. Sherriff, & J. H. Hicks 16188 (1).
Ma, Y. J. 287 (8), 375 (8).
Maire, E. E. 33 (14), 91 (22c), 177 (14), 196 (22b), 237 (22c), 396 (14), 2923 (22c), 3358 (2), 3359 (4), 3650 (22c).
Mao, P. I. 1934 (22c).
Mao, S. H. 170 (6).
Massey, J., D. E. Boufford, & B. Katz 4705 (19).
Maxwell, J. F. 92-211 (17).
McLaren's collectors 77D (2), L106A (13).
McLaren "C" collector 57 (4).
Mellichamp, J. H. 4300 (19), 10446 (19).
Meyer, F. N. 1347 (18), SPI 40025 (6).
Mills, R. G. 68 (18).
Mimoro, K., & S. Tsugaru 4770 (18), 4836 (18).
Mizushima, M. 516 (20), 2401 (20), 10161 (18).
Mousset, J. P. 964 (9).
Murata, G. 44542 (20).
Muroi, H. 4335 (18), 4534 (20), 4776 (18), 5501 (20), 5685 (20).
Nand, K. 108 (1).
Nieh, M. H., & Q.-H. Li 264 (22c).
Ohashi, H., B. H. Choi & J. Iketsu 22175 (20).
Ohwi, J. 254 (18).
Ohwi, J., & K. Okamoto 1782 (18).
Ou, & Kao 9322 (7a).
Palczevsky, N. 3617 (18).
Palmer, E. J. 25094 (19), 26621 (19).
Panero, J. L., & I. Calzada 6562 (19), 6563 (19).
Parker, R. N. 2799 (1), 2827 (1), 3032 (1).
Parkinson, C. G. 3133 (22b), 12176 (22b).
Peng, D. Y. 45343 (22c).
Pételot, A. 4788 (17).
Plant Exploration in the Republic of Korea 291 (18).
Polunin, O. 434 (1).
Polunin, O., W. R. Sykes, & L. H. J. Williams 866 (1), 2123 (1), 4131 (1).
Pratt, A. E. 186 (2).
Proud, D. 126 (1).
Punj, M. L. 3 (1), 4 (22a).
Purdom, W. 117 (18), 1037 (6).
Qing, H. F., & Z. T. Li 70010 (16).
Qingzang Expedition 4609 (22c).
Qu, G. L. 5822 (11).
Raizada, M. B. 7328 (1).
Ram, B. 423 (22a), 2324 (1).
Rant, A. 16 (9).
Rau, M. A. 10212 (1).
Rawat, C. S. 3 (1), 4 (22a).
Ray, J. D. 6588 (19).
Ribu, & Rhomoo 6343 (1).
Rich, H. H. 856 (1).
Rock, J. F. 3399 (4), 4039 (21), 4299 (13), 6825 (4), 8595 (4), 8933 (5), 9602 (13), 9603 (13), 17292 (4), 22018 (2), 24092 (4), 24699 (4), 25273 (4).
Rodger, A. 610 (22b).
Rogers, K. E. 8609 (19), 45154 (19).
Saku 5897 (18).
Santisuk, T. 1108 (17).
Sarip 368 (22d).
Saunders, R. M. K. 98/1 (22c).
Schilling, A. D., & C. D. Sayers 558 (22a), 561 (22a).
Schneider, C. K. 985 (13), 999 (13), 1276 (4), 2686 (4), 2807 (4), 3303 (4).
Shiota, K. 4423 (20), 6494 (20).
Sichuan University 108563 (22c), 109051 (22c).
Sin, S. S. 9436 (7b).
Singh, S. 2[a] (1), 2[b] (1).
Sino-American Expedition to Western Hubei Province 382 (3), 645 (3), 1389 (3).
Sino-American Guizhou Botanical Expedition 196 (6), 1406 (15a).
Sino-British Expedition to Cangshan 137 (4), 526 (4), 614 (4), 781 (4), 1017 (4).
Smith, H. 1964 (6), 2031 (4), 2366 (22c), 5719 (18), 6577 (6).
Smith, J. J., & A. Rant 408 (9).
Søchting, U. 71 (1).
Soegandiredjo 128 (22d).
Sohma, K., & M. Takahashi 700 (18).
Solomon, J. 1766 (19).
Soong, T. P. 39439 (22c).
Soulié, J. A. 453 (13).
Stainton, J. D. A. 432 (5), 3636 (1).
Stainton, J. D. A., W. R. Sykes, & L. H. J. Williams 175 (1), 2840 (1), 4940 (1), 5401 (1), 5598 (1), 5933 (22a).
Steenis, C. G. G. J. van 4032 (9), 4050 (9), 12272 (9).
Steward, A. N. 1031 [4653] (7b).
Steward, A. N., & H. C. Cheo 211 (7b), 213 (7b).
Steward, A. N., C. Y. Chiao, & H. C. Cheo 132 (15a).
Stewart, J. L. 73 (1).
Stone, D. E. 1822 (19).
Stone, D. E., H. E. Ahles, & R. Ornduff 1417 (19).
Strachey, R., & J. E. Winterbottom 1 (1), 2 (22a), 103 (1).
Sun, C.-R. 108 (11).
Sun, S. C., & K. Chang 150 (2), 236 (12), 926 (2), 1031 (2), 1357 (2).
Suzuki, S. 280 (18).
Tai, F. C., & C. M. Teng 5307 (22c).

Tai, L. Y. T110 (2).
Takahashi, H. 1181 (18), 4079 (18), T-63507 [1314] (22b).
Takahashi, H., & O. Asahara 3716 (18).
Takeda, H. 209 (18).
Tam, P. C. (see Tan, P. X.).
Tan, H. F., & S. L. Yu 700658 (21).
Tan, P. X. 58965 (15c), 62490 (15c), 62508 (6), 63323 (21), 63656 (15c), 63781 (21).
Tan, P. X., & X. X. Huang 354 (16), 365 (7b).
Tanaka, T. 294 (18).
Tang, L. 6171 (15c).
Tang, P. X. (see Tan, P. X.).
Tang, T. 972 (18).
Tang, W. S. 488 (7a).
Taquet, T. 940 (20), 4108 (20), 4109 (20).
Ten, S. 296 (22b), 391 (22b), 540 (22b).
Teng, L. 4679 (7b), 6775 (7b).
Teng, S. W. 90255 (7b), 90618 (15a).
Thomas, R. D. 42385 (19), 131526 (19).
Thomas, R. D., & Arkansas Native Plant Society Group 131363 (19).
Thomas, R. D., & P. Marx 35972 (19).
Thomas, R. D., & D. G. Rhodes 38808 (19).
Thomas, R. D., & C. Slaughter 103861 (19).
Thomas, R. D., et al. 32751 (19).
Thomson, T. 37 (1).
To, K. P., W. T. Ts'ang, & U. K. Ts'ang 533 [12532] (7b).
Togashi, M. 9768 (18).
Tong, S. Y. (see Dong, X. Y.).
Topping, D. L. 2090 (18), 2107 (18), 2496 (18).
Tripathi, N. K. 3 (1), 4 (22a).
Tsai, H. T. 50888 (6), 51178 (5), 52919 (5), 53052 (5), 53321 (15b), 54053 (5), 54643 (22b), 55101 (15b), 55161 (14), 55188 (15b), 55192 (15b), 57088 (22b), 57316 (5), 57585A (5), 57594A (5), 57681 (5), 57875 (5), 57914 (2), 57985 (2), 59522 (5), 59793 (4), 59827 (5), 59926 (5), 59950 (4), 60058 (15b), 60136 (14), 60191 (15b), 60230 (15b), 60462 (15b), 60597 (15b), 60658 (15b), 61106 (15b), 61561 (15b), 62241 (15b), 63107 (5).
Tsang, T. H. 1.306 (22c).
Tsang, W. T. 21423 (7b), 27641 (7b), 27693 (7b), 28783 (7b).
Tsi, Z. H. 91-225 (15b), 92-392 (23).
Tsiang, H. L. 35048 (22c), 35162 (11).
Tsiang, H. L., & Hsiung 34331 (12), 34412 (12).
Tsiang, Y. 5152 (15a), 5673 (15a), 10362 (7b), 10679 (7b).
Tso, C. L. 20374 (7b), 20530 (16), 20679 (16).
Tsoong, T. S. (see Chung, Z. S.).
Tsugaru, S. 5080 (18).
Tsugaru, S., & T. Takahashi 17921 (20).
Tsui, T. M. 825 (7b).
Tu, T. H. 153 (12).
Tui, L. Y. T. 118 (12).
Uno, K. 19902 (18).
Wallich, N. 1373 (22a), 1897 (22a), 4905A (1), 4985 (1), 4985A (1), 4986 (22a).
Wan, B. B., & K. S. Chow 81027 (18).
Wang, C. 39328 (15a), 40988 (15a).
Wang, C. C., & D. S. Hsu 1335 (7a).
Wang, C. C., C. C. Liao, & D. S. Hsu 1053 (7a), 1060 (7a).
Wang, C. W. 61754 (18), 63163 (4), 63372 (13), 63435 (5), 63549 (5), 63595 (13), 63634 (5), 63735 (2), 63997 (5), 64121 (5), 67966 (2), 68684 (5), 71297 (13), 73145 (23), 73810 (15b), 74223A (5), 76340 (23), 76484 (15b), 76601 (15b), 76756 (15b), 77299 (5), 77996 (15b), 78784 (23).
Wang, F. T. 20682 (6), 20827 (6), 21001 (2), 21043 (6), 22166 (22c), 22845 (10), 23026 (6), 23052 (10), 23221 (15a), 23281 (12).
Wang, H. 41426 (14).
Wang, T. H. 95 (6).
Wang, T. P. 16535 (22c).
Wang, X. 195 (6).
Wang, Y. J. 59930 (7b), 60055 (7b).
Wang, Z. T., et al. 213 (18), 870073 (15a), 870242 (6), 870306 (6).
Ward, F. K. 1594 (14), 8009 (23), 8210 (2), 8665 (2), 9443 (5), 9530 (2), 9593 (2), 17495 (22b), 17680 (14), 19035 (22b), 20893 (2).
Watt, G. 8312 (1).
Wei, F. N. 1386 (7b).
Wen, J., & A. K. Gholson 945 (19).
Wilford, C. 1057 (18).
Williams, L. H. J. 462 (1).
Wilson, E. H. 158 (11), 164 (8), 164a (8), 179a, pro parte (6), 179a, pro parte (8), 245 (6), 263 (3), 313 (6), 318 (3), 485 (22c), 675 (6), 710 (15a), 779 (6), 866 (6), 869 (6), 869a (6), 883 (8), 897 (6), 921 (2), 921a (2), 921b (2), 1036 (6), 1057 (6), 1070 (22c), 1268 (13), 1268a (13), 1268b (22c), 1304 (22c), 1565 (22c), 1726 (7b), 1968 (6), 2085 (3), 2234 (11), 2551 (12), 2552 (13), 2553 (6), 2554 (6), 3134 (13), 3135 (2), 4289 (2), 4574 (3), 4722 (15a), 6924 (18), 7346 (18), 7390 (18), 7473 (20), 7535 (18), 7744 (20), 8479 (18), 8665 (18), 8701 (18), 8860 (18), 9065 (18), 9446 (20), 9826 (7a), 10497 (18).
Wood, E. W., & D. E. Boufford 1675 (19), 3874 (20), 3927 (18).
Wu, Q. R. 78 (18).
Wu, S. Z. 70033 (16).
Wu, Z. M. 218 (15c).
Wuyi Expedition 2274 (7b).
Wuyi Shan Team 80-0117 (7b), 80-0243 (7b).
Xiong, J. H., X. S. Zhang, & X. H. Jiang 31566 (12).
Xiong, J. H., & Z. L. Zhou 91079 (8), 91648 (11), 92143 (11).

INDEX TO SCIENTIFIC NAMES

Accepted names are in roman type; the principal entry for each is in **boldface**; synonyms are in *italics*. Orthographic errors, including incorrect specific epithet genders, are listed under their corrected form (e.g., "*Schizandra*" is listed under "*Schisandra*").