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**PHYTOGEOGRAPHIC AND PHYLOGENETIC HISTORY
OF THE GENUS *NOTHOFAGUS* BL. (FAGACEAE)
IN THE SOUTHERN HEMISPHERE***

by

Toshimasa Tanai

(with 14 text-figures, 3 tables and 15 plates)

Abstract

The genus *Nothofagus* Bl. (Fagaceae) is one of the representative tree genera in the temperate forests of the southern hemisphere, and its phylogeographic history has been in controversy regarding the origin and dispersal route. Based on a recent collection from the Tertiary of southern Chile, all the previously-described species of *Nothofagus* or *Nothofagus*-like leaf fossils from South America and West Antarctica were reinvestigated, and compared with leaf architecture of nearly all the extant species of the genus in their phylogenetic relationships. The investigation of stratigraphic and areal distribution of fossils (leaves, wood and pollen) in South America reveals that *Nothofagus* gradually dispersed northward from the Antarctic region since Late Cretaceous to Miocene time. Leaves and pollen occur abundantly with various species in the Oligocene and the Lower Miocene of the Patagonia region, compared with paucity in the same horizons of northern region. This northward dispersal corresponds with the considerably decreasing temperature since Late Eocene age, which was suggested by oxygen isotope studies of sub-antarctic marine animal fossils.

The bibliographic survey of fossil records of *Nothofagus* leaves and pollen in other southern continents and deep-sea sediments further substantiated a conclusion that this genus seems to have been in southern origin during Late Cretaceous time. The comparison of leaf architecture with all the morphological characters of extant species allows that 36 extant species of *Nothofagus* are classified into five groups. A scheme of phylogenetic relationships of these extant species is proposed here, and it is consistent with breakup sequences of the Gondwanaland that is generally accepted by most workers.

Introduction

One of the representative tree genera in southern continents is the genus *Nothofagus* Bl. (Fagaceae), that is principally distributed in the temperate forests of Australia, New Zealand and southern South America, although some extend northward into New Guinea and New Caledonia. The modern distribution of *Nothofagus* is generally consistent with those of many land plants and invertebrate animals living in the cool-temperate regions of the southern hemisphere. Thus, the disjunctive distribution of *Nothofagus* has attracted attention as a key taxon to clarify the history of terrestrial life in southern continents. Discussion of the evolution and phylogeography of this genus have been, however, complicated by a number of authors. The phylogeographic interpretation especially has been in controversy with respect to the center of origin and dispersal route.

The past history of *Nothofagus* has been discussed mainly on the basis of pollen

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record by the biogeographers and palynologists. Although fossil leaves of *Nothofagus* or related leaf specimens have been described from the Tertiary of southern continents since the end of last century by several authors, they have been almost neglected in phytogeographic discussions. This may be mainly due to the fact that fossil pollen of *Nothofagus* is widely found with an accepted taxonomy through time and space in the southern hemisphere, and on the contrary that fossil leaves referred to *Nothofagus* have been lacking in taxonomic accuracy. During an investigation of Late Cretaceous and Tertiary floras of Chile during 1979—1980, a large collection of *Nothofagus* fossil leaves was obtained along with many other dicot fossils from the Tertiary of southern Chile. Based on the investigation of these fossil leaves in relationships with extant species, it has been possible to reinvestigate all the fossil species of *Nothofagus* that were previously described from South America and western Antarctica. The purpose of this paper is first to clarify the taxonomic relationships of fossil leaves with extant species, and to discuss the past distributional history of *Nothofagus* using a combination of the fossil records of pollen and wood. Further consideration of phylogenetic history of this genus in the southern hemisphere is discussed.

Modern Distribution of *Nothofagus*

The genus *Nothofagus* Bl. along with the genus *Fagus* L., belongs to the subfamily Fagoideae of the family Fagaceae. In striking contrast with *Fagus* which is confined to the northern hemisphere, *Nothofagus* is now distributed principally in the temperate regions of the southern hemisphere, and some taxa extend northward into the tropics. *Nothofagus* is composed of 36 extant species (Table 1), 10 of which are native to southern South America, 5 to New Zealand, 3 to southeastern Australia and Tasmania, 13 to New Guinea including the D'Entrecasteaux Islands and New Britain, and 5 to New Caledonia (Text-fig. 1).

Of the 10 species in southern South America most are deciduous except for the 3 evergreen species, *N. dombeyi*, *N. nitida*, and *N. betuloides*. Trees of *Nothofagus* form an almost continuous heavy forest on the top or along the western slopes of the Andes, distributed from central Chile (about 33°S. lat.) southward to southernmost part of this continent (about 56°S. lat.). *Nothofagus* is mixed with many broad-leaved trees in the north, while it forms frequently pure stands of single species in the south. The northern limit of *Nothofagus* distribution is probably due to aridity, and the southern limit is due to lack of vegetated land (McQueen, 1976). However, there is no *Nothofagus* in the Falkland Islands, east of the southern tip of South America.

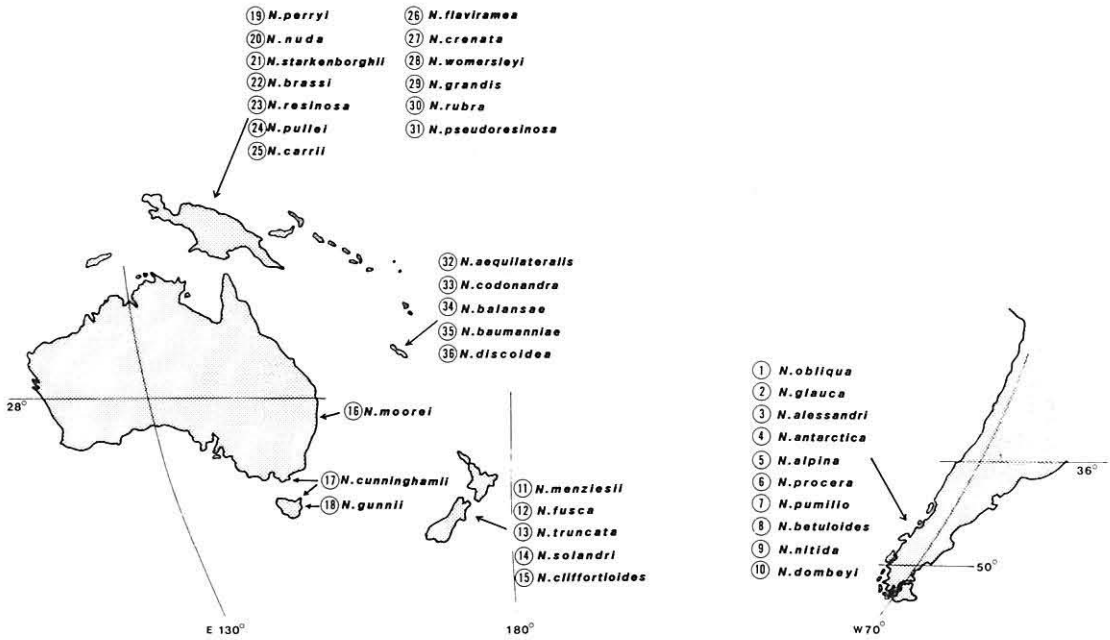
In New Zealand the heavy forest of *Nothofagus* is largely limited to the western side of South Island, but isolated tracts are widely scattered on both main islands, from near-coastal areas to the timberline (Wardle, 1971). However, this genus is absent in Stewart Island (about 47°S. lat.), situated south of South Island across the Foveaux Strait. All of the five species in New Zealand are evergreen trees.

Of three species in Tasmania and Australia, a deciduous species of *N. gunnii* is endemic to the highlands of Tasmania, forming dense forest. On the other hand, the

Table 1. Extant Species of the Genus *Nothofagus* Bl. and their Modern Distribution (Steenis, 1953, 1954, 1971; Soepadmo, 1972)

Specific Name	Modern Distribution
Sect. <i>Nothofagus</i>	
Subsect. <i>Antarcticae</i> Steen.	
<i>Nothofagus alessandri</i> Espinosa	South America
<i>Nothofagus alpina</i> (Poepp. & Endl.) Oerst.	South America
<i>Nothofagus antarctica</i> (Forst) Oerst.	South America
<i>Nothofagus glauca</i> (Phil.) Krasser	South America
<i>Nothofagus gunnii</i> (Hook. f.) Oerst.	Tasmania
<i>Nothofagus obliqua</i> (Mirb.) Oerst.	South America
<i>Nothofagus procera</i> (Peopp. & Endl.) Oerst.	South America
Subsect. <i>Pumiliae</i> Steen.	
<i>Nothofagus pumilio</i> (Poepp. & Endl.) Oerst.	South America
Sect. <i>Calusparassus</i> (Hombr. & Jacq.) Krasser	
Subsect. <i>Quadripartitae</i> Steen.	
<i>Nothofagus betuloides</i> (Mirb.) Oerst.	South America
<i>Nothofagus cunninghamii</i> (Hook. f.) Oerst.	Australia, Tasmania
<i>Nothofagus dombeyi</i> (Mirb.) Oerst.	South America
<i>Nothofagus fusca</i> (Hook. f.) Oerst.	New Zealand
<i>Nothofagus menziesii</i> (Hook. f.) Oerst.	New Zealand
<i>Nothofagus moorei</i> (F. v. Muell) Krasser	Australia
<i>Nothofagus nitida</i> (Phil.) Krasser	South America
<i>Nothofagus truncata</i> (Colenso) Cockayne	New Zealand
Subsect. <i>Tripartitae</i> Steen.	
<i>Nothofagus cliffortioides</i> (Hook. f.) Oerst.	New Zealand
<i>Nothofagus solandri</i> (Hook. f.) Oerst.	New Zealand
Subsect. <i>Bipartitae</i> Steen.	
<i>Nothofagus aequilateralis</i> (Baum.-Bod.) Steen.	New Caledonia
<i>Nothofagus balansae</i> (Baill.) Steen.	New Caledonia
<i>Nothofagus baumanniae</i> (Baum.-Bod.) Steen.	New Caledonia
<i>Nothofagus brassii</i> Steen.	New Guinea
<i>Nothofagus carrii</i> Steen.	New Guinea, D'Entrecasteaux Isl.
<i>Nothofagus crenata</i> Steen.	New Guinea
<i>Nothofagus codonandra</i> (Baill.) Steen.	New Caledonia
<i>Nothofagus discoidea</i> (Baum.-Bod.) Steen.	New Caledonia
<i>Nothofagus flaviramea</i> Steen.	New Guinea
<i>Nothofagus grandis</i> Steen.	New Guinea
<i>Nothofagus nuda</i> Steen.	New Guinea
<i>Nothofagus perryi</i> Steen.	New Guinea
<i>Nothofagus pseudoresinosa</i> Steen.	New Guinea, D'Entrecasteaux Isl.
<i>Nothofagus pullei</i> Steen.	New Guinea
<i>Nothofagus rubra</i> Steen.	New Guinea, D'Entrecasteaux Isl.
<i>Nothofagus resinosa</i> Steen.	New Guinea, New Britain
<i>Nothofagus starkenborghii</i> Steen.	New Guinea
<i>Nothofagus wormersleyi</i> Steen.	New Guinea

evergreen *N. cunninghamii* largely grows in the wet, heavy, southern temperate rain forest on the western side of Tasmania and southern Victoria (Howard, 1981). Another evergreen species, *N. moorei*, inhabits the wet, northern rain forest along the eastern coast of New South Wales; its northern limit is in the Macpherson range (about



Text-fig. 1 Distribution of Extant Species of the Genus *Nothofagus* Bl.

28°S. lat.) south of Brisbane (Webb & Tracey, 1981).

It is one of the remarkable features in *Nothofagus* that its modern distribution extends into the tropics or at least subtropics such as New Guinea and New Caledonia, although the trees grow largely on mountains. All the species in both regions are evergreen with leaves of thick texture. In New Guinea proper the extant trees of this genus are dominant members of the lower montane rain forest distributed at altitudes of 2000 to 3000m, and some species descend to 700–900m (Steenis, 1971). Several species common with New Guinea are found in the rain forest at altitudes of 600–2400m in D'Entrecasteaux Islands and New Britain, north of the eastern tip of New Guinea. There are 5 species in New Caledonia where the highest mountain is about 1640m in altitude. Trees of *Nothofagus* here are growing at lower elevation, ranging from 150 to 1350m (Dawson, 1966).

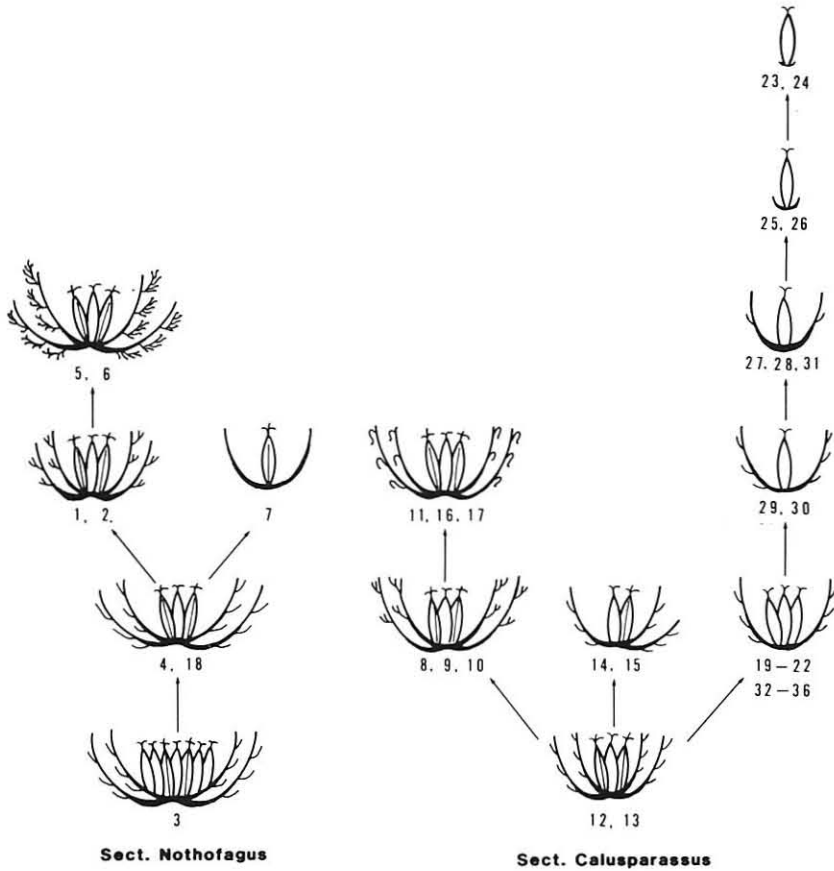
Nothofagus is widely distributed principally in the southern temperate regions, even in cooler areas such as in the southern tip of South America, or in the montane rain forest of New Guinea and New Caledonia. Their modern distribution is not ubiquitous but complicated and disjunctive in the southern continents, although seeds of *Nothofagus* are unsuitable for long-distance ocean dispersal. This fact has produced various interpretations for past distributional history.

Summary of the Previously-proposed Theories for Phylogeography

The evolution and phylogeography of *Nothofagus* have been discussed by a number of authors, because the disjunctive distribution of its extant species is conspicuous among the dicots of the southern hemisphere. The well-established taxonomy of this genus is due to the monographic studies of Steenis (1953, 1954). The phylogeographic history, however, has been controversial among biogeographers with respect to origin and dispersal route. The most conspicuous discrepancy in the previously proposed theories is in its place of origin. These include the northern origin theory represented by Darlington (1965) and Steenis (1971, 1972), and the southern origin theory represented by Couper (1960a), Cranwell (1963), Cracraft (1975) and Humphries (1980, 1983). Furthermore, the dispersal route has also been speculated upon by many authors (Steenis, 1962; Schuster, 1976; Axelrod & Raven, 1982; others). These various phylogeographic theories were summarized by Humphries (1981, 1983), dividing into narrative and analytical categories. All the previously described biogeography of *Nothofagus* is different in the interpretations that are based on several problems as below: (1) infrageneric relationships of extant species, (2) geologic history of the southern continents, (3) evaluation of paleobotanical record, especially for pollen, and (4) the center of origin of the Fagaceae.

Infrageneric Relationships of Extant Species

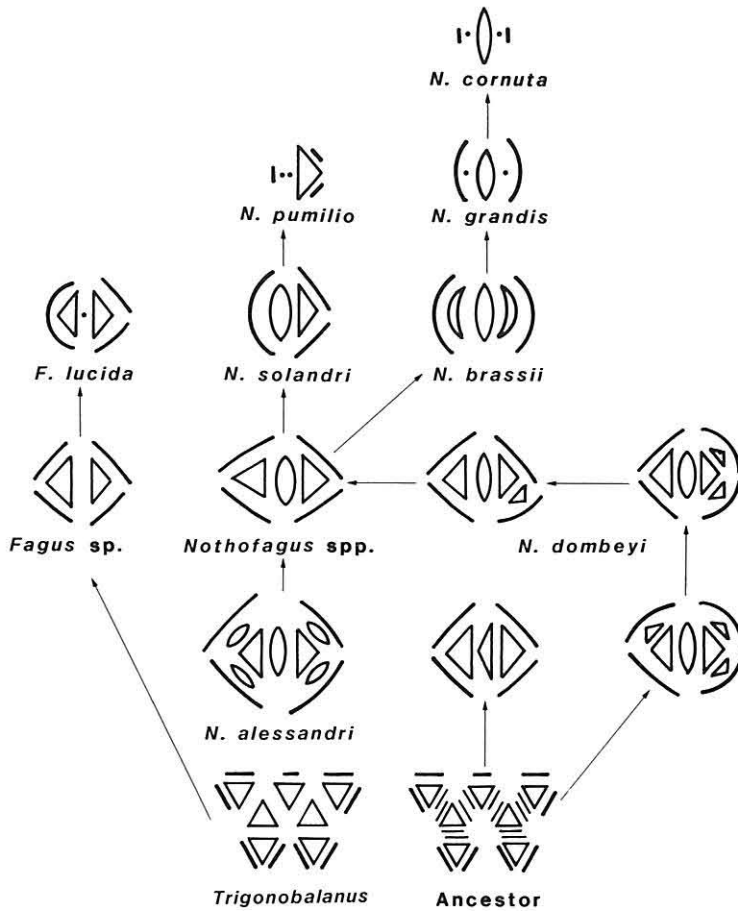
Phylogeographic interpretation is based fundamentally on the phylogenetic relationships of infrageneric taxa. The classification system of *Nothofagus* principally established by Steenis (1953) has been accepted by most botanists with minor changes (Soepadmo, 1972), and was based principally on floral anatomy and leaf structure. The genus *Nothofagus* is divided into two sections, *Nothofagus* and *Calusparassus*, based on leaf structure (e.g. deciduous vs. evergreen and flat or conduplicate in the bud stage). These two sections are further separated to several subsections and series, mainly based on fructification characters such as nutlet, parted cupule and lamellae. Considering a tendency toward reduction in cupule valves and flowers on one side and ornamentation of cupular lamellae on the other side, Steenis (1953) illustrated a phylogenetic scheme of the extant species (Text-fig. 2). As pointed out by Forman (1966), the original illustration includes some errors in *N. cliffortioides*, *N. solandri*, *N. pumilio* and *N. alessandri*, though Steenis (1953) correctly described them in text. Text-fig. 2 is correctly illustrated here to conform with his original description. The species which have a well-developed lamellar cupule containing three nutlets and male flowers in triads are reported to be morphologically more primitive than the species with an elamellate or even ecupular nutlet and solitary male flower. The older stock, however, is reported to be an extratropical species with four-valved cupule and three nutlets. Nevertheless, attaching importance to the records of fossil pollen, Steenis (1971) claimed that the center of origin was close to New Guinea and New Caledonia where species of the "primitive" category are still living. Thus, Steenis (1953, 1971)



Text-fig. 2 Scheme of the Morphological Interrelationships in the Cupular Structure of *Nothofagus* (Stenis, 1953). The numbers below each type correspond with those of the species that are shown in Text-fig. 1.

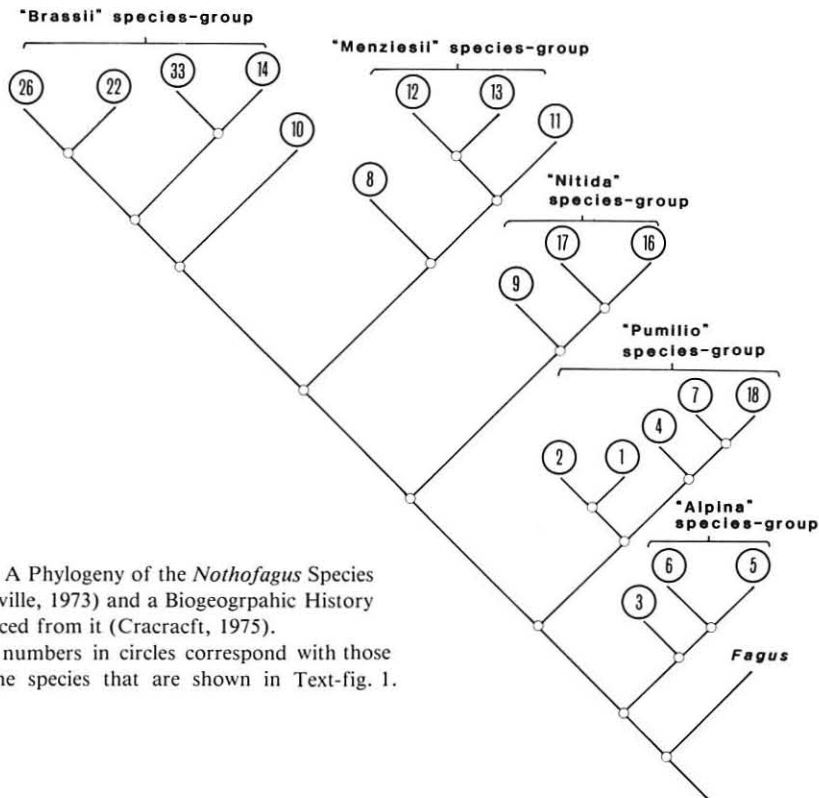
asserted that four-valved cupules including three nuts represent the basic form from which the various types of cupule that occur in *Nothofagus* can be derived.

Melville (1973, 1982) mostly followed Steenis' classification, but he proposed another phylogenetic scheme (Text-fig. 3) which is principally based on the evolutionary trend of reduction of dimerous and trimerous nutlets, and reduction of cupule lobes by fusion. Melville's scheme is based on Forman's (1966) interpretation that the genus *Trigonobalanus* which is disjunctively distributed in the Old World tropics of Southeast Asia and the Neotropics of Columbia, shows the most primitive female infructescence structure in the Fagaceae. Although variable in character toward maturity (Forman, 1964; Lozano-C. et al., 1982), the mature infructescence of *Trigonobalanus* has basically seven trimerous nutlets that are included in the nine-lobed cupule. As inferred by Hjelmqvist (1963) and Forman (1966), a South American species,



Text-fig. 3 Evolutionary progression in *Nothofagus* linked with Migration and Continental Drift (Melville, 1973).

Nothofagus alexandri that has seven nutlets (two trimerous and five dimerous) within the four-valved cupule seems to be most primitive in this genus. These authors advocated a general evolutionary trend, the reduction of a secondary flower from a trimerous to a dimerous condition that results in the fusion between corresponding pairs of valves (Forman, 1966). Melville (1973) illustrated an evolutionary progression in *Nothofagus*, that included the reduction from four via three to two cupule lobes as a continuous transformation, in which dimerous nutlets were gradually reduced from three to one in tropical species, accompanied by reduction of cupule lobes. Based on this phylogenetic scheme, he stated that the primitive form of *Nothofagus* originated in an area of Gondwanaland which included southern South America, western Antarctica and New Zealand. Later, Melville (1982) proposed an evolutionary scheme, involving relationships between leaf margin and venation among extant species, but this scheme is not consistent with data from infructescences.



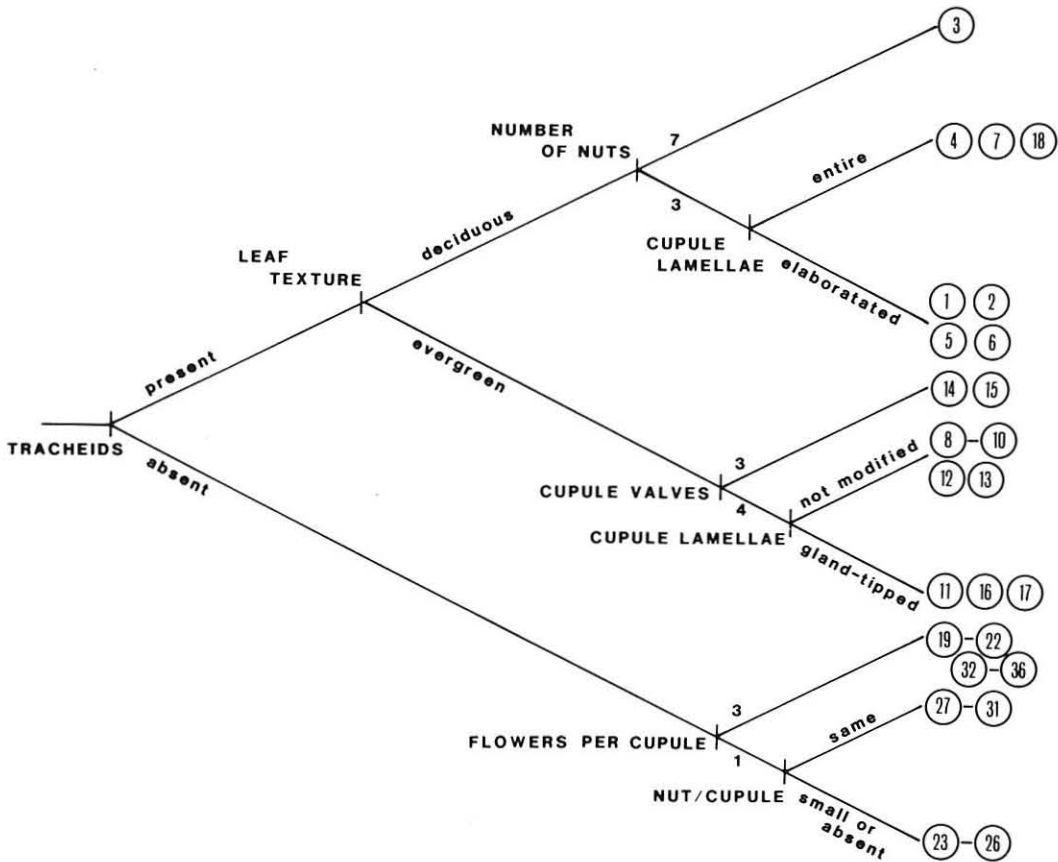
Text-fig. 4 A Phylogeny of the *Nothofagus* Species (Melville, 1973) and a Biogeographic History deduced from it (Cracraft, 1975). The numbers in circles correspond with those of the species that are shown in Text-fig. 1.

There have been recently many attempts to analyze the phylogenetic relationships of extant taxa by vicariance-cladistic method. Cladograms of taxa congruent with geological cladograms have been advocated to provide the most parsimonious explanation of biogeographic history (Croizat, 1952; Hennig, 1966). The first attempt for cladistic analysis of extant *Nothofagus* species was that of Melville (1973) in combination of geologic history. Although he did not give any detailed explanation of the cladogram, his phylogenetic relationships of the species followed Forman's interpretation and Steenis' classification. Using Melville's phylogeny, Cracraft (1975) proposed a reconstruction of the biogeographic history of *Nothofagus*; he attempted to locate the center of origin and direction of dispersal in five lineages that he recognized (Text-fig. 4). Using these five species-groups four separate trans-Antarctic relationships were shown in his cladograms. Although his model was discussed in combination with gradual fragmentation of southern continents to be parsimonious with Melville's cladogram, it is unsatisfactory for other characters excluding infructescence morphology. For instance, *Nothofagus dombeyi* of South America and *N. solandri* of New Zealand are included with all the tropical species of New Guinea and New Caledonia in the "*brassii* species" group*; but all of the tropical species are rather

* The selected specific names are conventionally given for five species groups by Cracraft (1975); however, the "*brassii* species group" is not related to the *brassii*-type group identified by pollen.

remote in wood anatomy from the extratropical species which have no tracheids and longer wood fibers (Dadswell & Ingle, 1954).

Recently Humphries (1981, 1983) discussed the biogeography of *Nothofagus* as one example of phylogenetic analysis in historical biogeography. Selecting 11 of the 22 morphological characters that are observed in the Fagaceae including *Nothofagus*, he presented a cladogram of this genus which was produced by Hennig's (1966) method whereby monophyletic groups are identified by synapomorphies. As shown in Text-fig. 5, his first dichotomy is based on the presence or absence of tracheids in wood, then followed in order by leaf structure, number of nutlets or cupule valves, cupule lamellae and others. Humphries' (1982) model of phylogenetic relationships of the extant species is considerably different from those of Melville and Cracraft, but still contains two trans-Antarctic relationships at the species level. This model was discussed in terms of the geological cladogram of the southern continents to account for the phylogenetic relationships (Humphries, 1981).



Text-fig. 5 A Cladistic Analysis of Extant Species of *Nothofagus* (Humphries, 1981).
The numbers in circles correspond with those of the species that are shown in Text-fig. 1.

Geologic History of the Southern Continents

Most phytogeographic discussions on disjunctively-distributed plants such as *Nothofagus* come to different conclusions, depending on the interpretation of geologic history of the now separated southern continents. Dispersal capabilities of *Nothofagus* are extremely restricted (Preest, 1963; Wardle, 1970): nutlets are too heavy to float on water, damaged in brine water, and rarely carried by birds. Furthermore, *Nothofagus* is genetically self-incompatible as are in most genera of the Fagaceae. It has been generally accepted that *Nothofagus* cannot disperse across a large water gap. Thus, theories of dispersal are divided into two types, depending on acceptance of either stable or mobile continents.

When stable continents are accepted, distribution of this genus is discussed with reference to long-distance overland dispersal (Darlington, 1965), by land bridge-isthmus links or oceanic island hopping (Steenis, 1962). Steenis (1962) and Darlington (1965) both claim that *Nothofagus* may have originated in Southeast Asia during Late Cretaceous time, and crossed the tropics to Australasia or New Zealand. The recent prevailed acceptance of the concepts of plate tectonics and continental rafting has resulted in various interpretations for the biogeography of *Nothofagus*, as well as that of other plants and animals. Emphasizing overland dispersal, although the mobile continents are accepted, many authors claim that the immediate ancestor of *Nothofagus* originated elsewhere of the assembled continents, and then migrated by long distance dispersal, in some cases in conjunction with continental rafting. Its center of origin and dispersal route, however, differ in these studies: for example, from Africa to South America and eventually to Australasia (Raven & Axelrod, 1972, 1974), and from North America to South America along the so-called Marsupial route, and further to Australasia via Antarctica (Schuster, 1976). In contrast with the above-mentioned northern origin theories, there have been southern origin theories that originate before the renewed interest in continental drift (Couper, 1960; Cranwell, 1963, and Moore 1971). These authors discussed a southern origin for *Nothofagus* in detail along with other austral-temperate plants. Even when continental drift is neither accepted nor rejected, most authors tried to determine the center of origin and dispersal route from modern and past (fossil) distribution of *Nothofagus*.

In contrast, another approach has been attempted on the basis of vicariance theory, which has been vigorously applied to discussions of biogeographic history during the last decade. Biotic distribution in this approach is considered as the result of vicariance of ancestral biotas rather than an origin in one region and dispersal to another, and that biotas have been carried on rafting crustal plates (Croizat et al., 1974; Rosen, 1978; Nelson & Platnik, 1981).

Although vicariance biogeography of *Nothofagus* was first attempted by Melville (1966) and Cracraft (1975), it was fully discussed by Humphries (1981) with cladistic analysis of phylogenetic relationships as already described. Humphries (1981) illustrated a fragmentation sequence of the *Nothofagus* distribution patterns as Gondwanaland was disrupted and split, compared with general patterns of area relationships for other plants and animals that are endemic to at least three of the areas occupied by

modern *Nothofagus*. On one hand, Melville (1981, 1982) assumed that the ancestor of *Nothofagus* originated in the hypothesized mid-Pacific continent, called "Pacifica", which included a peninsula of West Gondwana together with New Zealand and New Caledonia, and that early evolution of *Nothofagus* was complete before the disruption and rotation of Pacifica. A large, ancient continental mass in the paleo-Pacific was proposed independently by Nur & Ben-Avraham (1981), based on geological and geophysical interpretations; the speculated continent, however, has not been accepted by the majority of geologists (Tedford, 1981; Haugh, 1981). Even if the Pacifica hypothesis is true, the rise and diversification of *Nothofagus* occurred after the breakup of this continent, on the basis of much geological evidence. Thus, among those who accept mobile continental drift there has been a number of interpretations of *Nothofagus* biogeography, depending on the believed sequence of breakup and age of rafting.

Evaluation for Paleobotanical Record

Except for adherents of the recent vicariance theory, most biogeographers have generally regarded the fossil record as important in the history of biotas, especially in locating the center of origin and direction of dispersal, but also in phylogenetic analysis including time of appearance and extinction. Fossil leaves of *Nothofagus* have recently been used to investigate phylogenetic relationships on the basis of detailed venation or cuticular analyses (Hill, 1983, 1984; Tanai, 1984a,b). There were only a few classical works since the end of last century in southern South America (Dusén, 1899), West Antarctica (Dusén, 1909), Australia (Ettingshausen, 1888, 1891) and New Zealand (Ettingshausen, 1891). No fossil seeds have been recorded up to the present. In contrast, fossil pollen of *Nothofagus* in the Upper Cretaceous and Tertiary has been widely investigated by many workers in the southern continents since the 1940's. The fossil pollen record in time and space has significantly affected the phytogeographic discussion of *Nothofagus* among not only palynologists (Couper, 1960a; Cranwell, 1963, 1964) but most biogeographers (Darlington, 1965; Steenis, 1971, 1972; Raven & Axelrod, 1972, 1974; Schuster, 1976). Most of the phytogeographic discussions using the pollen record centers around two problems: first, whether or not *Nothofagus* fossil pollen reported from the northern hemisphere is *Nothofagus*, and second, how to consider phylogenetic relationships between extant and fossil pollen of the three type groups usually identified by palynologists.

After *Nothofagus* pollen reported in the Upper Cretaceous and Tertiary of the northern hemisphere was critically reviewed by Cranwell (1963), its pollen was described from India (Ramanujam, 1966), Hungary (Kedves, 1964) and North America (Elsik, 1974). Some of the identification of these pollen grains are still, however, controversial (Cranwell, 1963; Kuprianova, 1967; Steenis, 1971; Frederikson, 1980). Most biogeographers who discussed phytogeography of *Nothofagus* (Darlington, 1965; Couper, 1960a; Cranwell, 1963; Steenis, 1971) were not convinced of the existence of northern pollen; but some workers (Raven & Axelrod, 1972; Schuster, 1976; Hanks & Fairbrothers, 1976; Axelrod & Raven, 1982) discussed the migration route of

Nothofagus, using pollen occurrence in the northern hemisphere.

The three type groups of extant *Nothofagus* pollen have usually been used in discussing phylogenetic relationships of fossil pollen by most palynologists. As reviewed in a later chapter, fossil pollen referable to the *brassii* type group is older than that of the two other type groups in Australia, New Zealand, South America, and even in Antarctica. If fossils with the *brassii* type pollen are considered to be direct progenitors of the extant *brassii* group species now confined to New Guinea and New Caledonia, the northern origin may be concluded (Darlington, 1965; Steenis, 1971). On one hand, Hanks & Fairbrothers (1976) suggested that older fossil pollen of the *brassii* type may be not always directly related to the extant *brassii* type species: *Nothofagus* prototype differentiated into a *brassii* ancestral type, from which three types evolved along the independent lines of development.

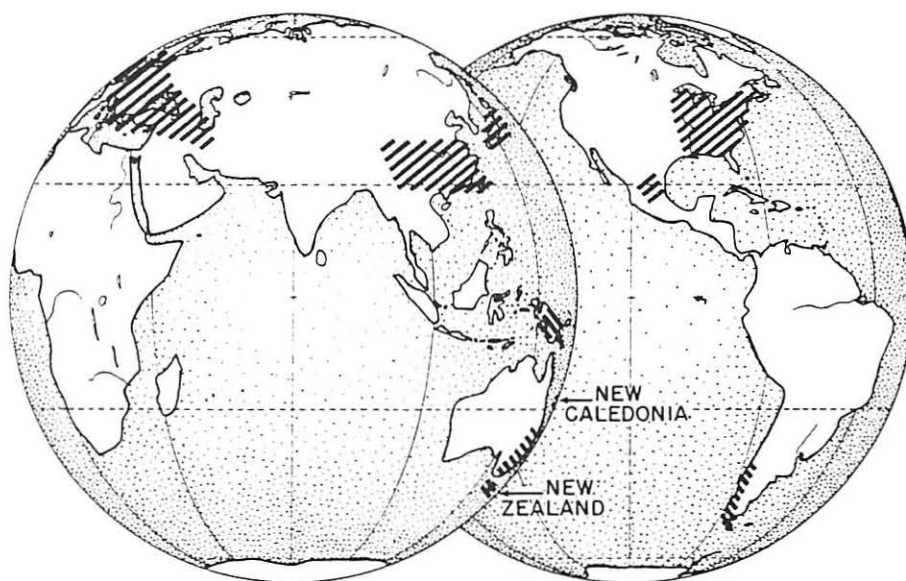
In contrast with the above theories, those who stress vicariance theory do not give any special role to fossil record of *Nothofagus* (Cracraft, 1975; Humphries, 1981, 1983), because they consider fossils too fragmentary and incomplete to be meaningful for phylogenetic and phytogeographic analysis.

In any case, since pollen of *Nothofagus* is easily recognized in older sediments, too much emphasis has been placed on pollen morphology for phytogeography and even for phylogeny of this genus.

Origin of the Fagoideae

Fagus and *Nothofagus*, included in the subfamily Fagoideae within the Fagaceae, share many common morphological characters. These two genera are bihemispheric in modern distribution, and they show a pattern of occurrence on both sides of the tropics (Text-fig. 6). Both *Fagus* and *Nothofagus* have been postulated as the ancestral types (prototypes) in the family. Most workers including taxonomists and biogeographers, have inferred that both have evolved from a common ancestor. Thus, interpreting the place of origin of this common ancestor and its segregation history to the northern and southern hemispheres is an inevitable problem in *Nothofagus* biogeography.

Since the primitive genera and even species of the Fagaceae are now well-concentrated in Southeast Asia, along with other many primitive genera of angiosperms, the Indo-Malaysian region between Yunnan and North Queensland was regarded as the original matrix area of the Fagaceae including the *Nothofagus* ancestor, from which there was southward dispersal to Australia and Antarctica (Takhtajan, 1969; Steenis, 1971, 1972). However, recent informations on plate tectonics in the Pacific reveals that the mid-Cretaceous ancestor would be too far removed geographically to cross from Southeast Asia to Australia during Cretaceous time (Smith & Briden, 1977; Owen, 1983). Accepting a Laurasian origin of the Fagaceae, Raven & Axelrod (1972, 1974) proposed that a mid-Cretaceous migration of the ancestral group occurred from Eurasia into Australasia via Africa-India. On the other hand, taking into account the two relict centers of the Fagaceae, Southeast Asia and North America, the immediate ancestor of *Nothofagus* was assumed to have migrated from North America into Gondwanaland by mid-Cretaceous time (Schuster, 1976).



Text-fig. 6 Distribution of Extant Species of the Fagoideae (*Fagus* and *Nothofagus*) in the World (Darlington, 1965).

Fagus is shown by diagonal lines with right-to-left direction, and *Nothofagus* is by those with left-to-right direction.

Melville (1982) who hypothesized the former Pacific continent with a west Gondwana peninsula claimed that disruption and drift or collision were explicable for the disjunction of most genera and species relationships of this family. The vicariists (Cracraft, 1975; Humphries, 1981) and some others (Hanks & Fairbrothers, 1976) postulated a large land mass such as Pangea containing an ancestor of the Fagaceae, especially *Fagus* and *Nothofagus*, but they did not designate any definite region as the center of origin.

Extant and Fossil Leaves of *Nothofagus*

Venation Characters of Extant Leaves

Steenis (1953) pointed out that the venation pattern of leaves is rather variable within the genus, and further suggested that relationships between the secondary vein termination and leaf margin may be useful in determining species group, illustrating many examples. His suggestion recently further advanced by Melville (1983), who elucidated an evolutionary scheme of leaf margin characters in the genera *Nothofagus* and *Fagus*. These investigations of leaf venation were, however, done directly from the herbarium specimens, and details of venation were not always correctly understood. Leaf architecture of *Nothofagus* was recently described in detail by Romero and coworker (Romero, 1980; Aguirre & Romero, 1982; Romero & Aguirre, 1982), using cleared leaves of nearly all the extant species. Keys were provided for the identification

of leaves to species level on each continent. However, they failed to give foliar evidence to enable discussion of interspecific relationships throughout the entire genus.

Fossil leaves show potential to play an important role in more precise estimation of phylogeny in *Nothofagus* than does fossil pollen. To accurately compare fossils and extant species, living leaves were collected from many regions, and are investigated here with respect to characters of leaf architecture. The venation of all extant species, except for the three New Guinean species whose leaves were unattainable, were investigated by clearing leaves. All *Nothofagus* leaves are characterized by the following features: the areolation generally irregular in size, irregularly branching ultimate veinlets (although most of them are once or twice branching), and the tertiary veins usually immersed in the reticulation. These venation features are effective to distinguish leaves of *Nothofagus* from those of *Fagus*. However, some leaves such as *N. alessandri* are somewhat similar to those of *Fagus* in shape and marginal character, as stated by Steenis (1953) and Melville (1983). On the other hand, the above-noted venation features of *Nothofagus* do not always provide a sufficient tool for distinction of infrageneric species.

Extant species of *Nothofagus* include evergreen and deciduous trees. Evergreen leaves are usually characterized by a distinct fimbrial vein or considerable thickening at the margin and thick-veined areoles, while deciduous leaves have no fimbrial vein and incomplete, thin-veined areoles. On one hand, deciduous leaves usually have toothed margins, variable from sharply-pointed to rounded at the tooth apex, while evergreen leaves contain both toothed and entire margins. The secondary veins are pinnate, and the feature of their termination are variable. The secondaries end in the tooth or sinus bottom, fork near the sinus or tooth, and form loops along the margin.

Examination of extant leaves indicates that all the *Nothofagus* species are assembled into five leaf groups by venation and margin characters. The genus *Nothofagus* is composed of two sections, *Nothofagus* and *Calusparassus*; the former section contains groups I and II, while the latter involves groups III to V. Leaves of these two sections are usually distinguishable by the presence of a fimbrial vein. Leaf venation characters of each group are summarized as below.

Group I

The secondary veins straightly enter the main teeth along the basal side of tooth, and give rise to 1 or 2 veins that end in subsidiary teeth. The tertiary veins are random percurrent or bifurcate on the way to the opposite secondary vein. The areoles composed of fourth- or fifth-ordered veins are four- or five-sided, irregularly-sized, and intruded irregularly by once to thrice branching veinlets. Species belonging to group I are *Nothofagus alessandri*, *N. alpina*, *N. glauca*, *N. obliqua* and *N. procera*, all of which are living in South America.

Group II

Leaves of group II are characterized by the serrate margin with rounded tips. The secondary veins fork near the sinus to embrace its bottom, and then both branches

enter the teeth without reaching the tooth apex. The tertiary veins are reticulate. The areoles composed of the fourth-order veins are irregularly-sized with quadrangular to pentagonal shape, and are intruded by thin, single to once branching veinlets. This group contains 3 species: *Nothofagus antarctica* and *N. pumilio* living in South America, and *N. gunnii* living in New Zealand.

Group III

Leaves of this group are considerably thick along the margin, although such thickening does not show the fimbrial vein. The secondary veins fork near the margin; the apical branch reaches the sinus bottom to form a plexus with the tertiary and quaternary veins, while the basal branch enters the glandular tooth apex centrally with flexuous course. The tertiary and quaternary veins are usually thick, and form the four- or five-sided areoles. The ultimate veinlets are generally thick, irregularly once to thrice branching, although sometimes lacking. This group is composed of 3 evergreen species, *Nothofagus betuloides*, *N. dombeyi*, and *N. nitida*, all of which are living in South America.

Group IV

Leaves of this group are characterized by a well-developed fimbrial vein at the margin, and thick secondary veins extending to or near the margin. The tertiary veins are usually thick, and form reticulations with thick quaternary veins. The areoles are irregular in size, and four- or five-sided with thick veins. The freely ending veinlets are thick, and branch variably from one to three times, although rarely lacking. Group IV is composed of six extant species living in New Zealand and Australia, and is further divided into three subgroups by secondary vein termination. The first subgroup (IV-a) is represented by *Nothofagus fusca* and *N. truncata* of New Zealand. In these leaves the secondary veins directly enter the principal teeth that exhibit glandular tips. Subgroup IV-b contains three extant species, *N. menziesii* of New Zealand and *N. cunninghamii* and *N. moorei* of Australia. In leaves of these three species the secondary veins terminate on the apical sides of a principal tooth or at the base of a main sinus. A strong branch that emerges basally near the margin also ends in the base of a subsidiary sinus or in the apical side of a subsidiary tooth. The marginal glands are present mostly on the apical side of the tooth. Subgroup IV-c is represented by *N. solandri* and *N. cliffortioides*, that are endemic to New Zealand. Except for the entire margin, leaves of these two New Zealand species are quite similar to those of *N. menziesii* and *N. cunninghamii* of the second subgroup (IV-b) in features of areolation and veinlets. However, the secondary veins bifurcate about two-thirds of way to the margin, and each branch has a variable ending. Forking secondary branches immerse in the intersecondary reticulation, or connect with other secondary and intersecondary veins to form irregular loops, and branches from the secondary form marginal areoles or terminate at a fimbrial vein.

Group V

This group includes all extant species of New Guinea (including New Britain) and New Caledonia, all of which bear evergreen leaves. Group V is characterized by stout venation, a marked fimbrial vein, and entire margin (rarely crenate) that is mostly revolute. The secondary veins arise along the margin to form large loops usually with a sinuous curve. The secondary loops enclose tertiary and quaternary arches, and quaternary or quinternary arches sometimes connect with the fimbrial vein. The tertiary veins are weakly percurrent, frequently connecting with the intersecondary vein. Thick quaternary or quinternary veins form small, four-sided areoles, that are intruded by thick, single to thrice branching veinlets. Group V is further divided into two subgroups by marginal characters. Subgroup V-a is usually represented by entire-margined leaves, while subgroup V-b is characterized by remotely crenate-margined leaves with glandular teeth in which a branch from the secondary loop ends. The former contains *N. brassii* and other 7 species from New Guinea, and *N. aequilateralis* and other 2 species from New Caledonia, while the latter contains *N. crenata*, *N. perryi*, *N. pseudoresinosa*, *N. resinosa* and *N. nuda* from New Guinea, and *N. discoidea* and *N. balansae* from New Caledonia.

Table 2. A Key for the Classification of Extant *Nothofagus* Leaves, based on Leaf Architecture.

- I. Fimbrial vein absent; areoles composed of thin veins; veinlets thin.
 - A. Secondary veins straightly entering teeth along the basal side of tooth; 1 or 2 branches emerging basally, and ending in subsidiary tooth apex I group
N. lessandri (SA), *N. alpina* (SA), *N. glauca* (SA), *N. obliqua* (SA), *N. procera* (SA).
 - B. Secondary veins forking near the sinus to embrace its bottom, and then the both branches entering teeth without reaching tooth apex II group
N. antarctica (SA), *N. gunnii* (NZ), *N. pumilio* (SA).
- II. Fimbrial vein present; areoles composed of thick veins; veinlets thick.
 - A. Secondary veins flexuous in course, forking near the margin; apical branch reaching the sinus bottom to form a plexus with tertiary veins, while basal one entering glandular tooth apex centrally..... III group
N. betuloides (SA), *N. dombeyi* (SA), *N. nitida* (SA).
 - B. Secondary veins nearly straight near the margin IV group
 - (1) Secondary veins entering glandular tooth apex centrally (IV-a subgroup)
N. fusca (NZ), *N. truncata* (NZ)
 - (2) Secondary veins ending in the sinus bottom or on the upper side of tooth; tooth tip rounded, glandular (IV-b subgroup)
N. cunninghamii (Aus, Tas), *N. menziesii* (NZ), *N. moorei* (Aus)
 - (3) Secondary veins forking at about two-third to the margin; the both branches irregularly looping or flexuously reaching the margin to join the fimbrial vein (IV-c subgroup)
N. cliffortioides (NZ), *N. solandri* (NZ)
 - C. Secondary veins arising along the margin to form sinuous loops, which enclose the tertiary and quaternary arches V group
 - (1) Margin usually entire (V-a subgroup)
N. aequilateralis (NC), *N. baumanniae* (NC), *N. brassii* (NG), *N. carrii* (NG), *N. codonandra* (NC), *N. flaviramea* (NG), *N. grandis* (NG), *N. pullei* (NG), *N. rubra* (NG), *N. starkerborghii* (NG), *N. wormersleyi* (NG)
 - (2) Margin remotely serrate with minute and obtuse teeth, which is glandular at apex; branches from the secondary loops enter directly the teeth (V-b subgroup)
N. balansae (NC), *N. crenata* (NG), *N. discoidea* (NC), *N. nuda* (NG), *N. perryi* (NG), *N. pseudoresinosa* (NG), *N. resinosa* (NG)

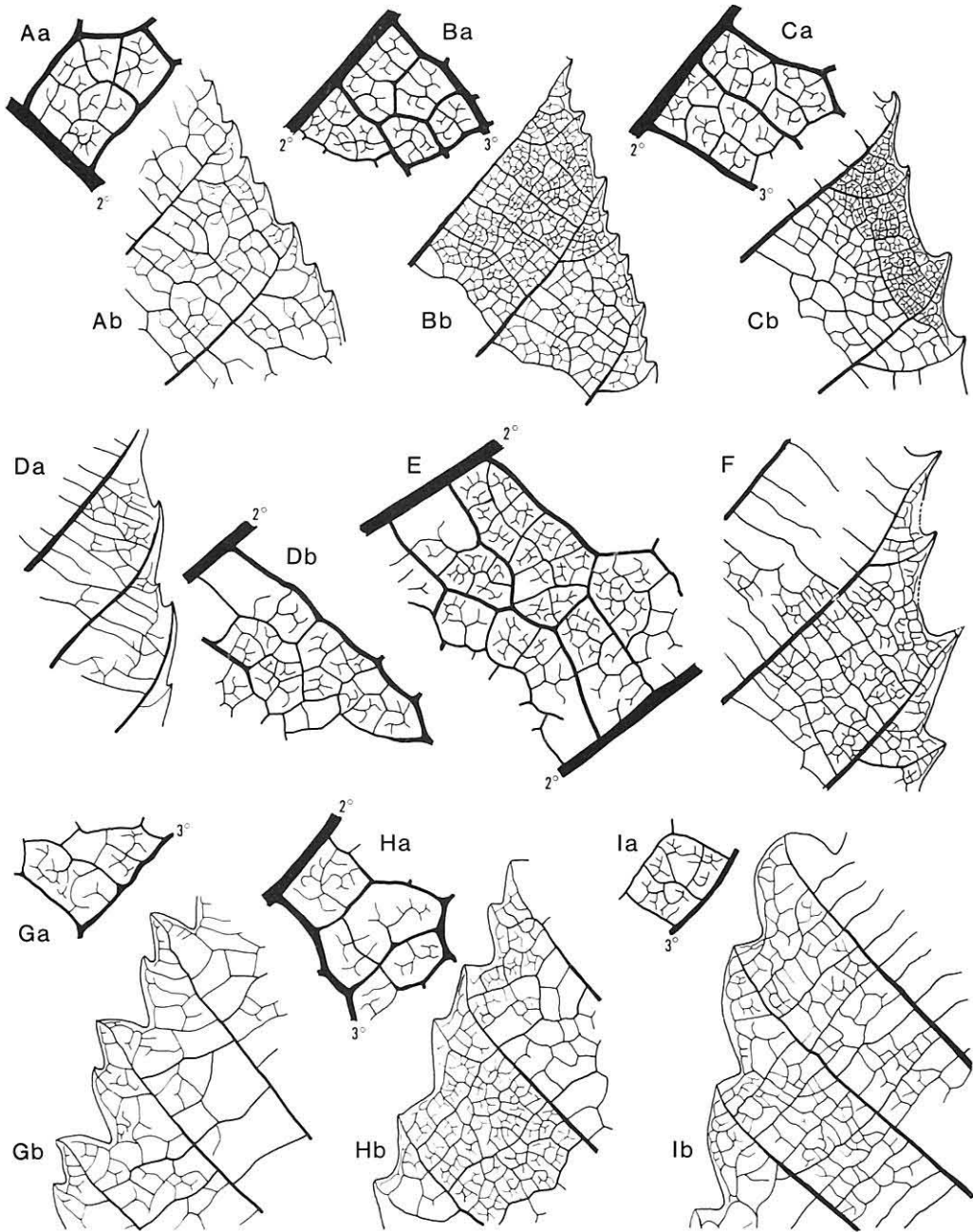
Considering the leaf architecture described above, groups I and II appear to be closely similar to each other in having poorly-organized high-order venation, no fimbrial vein and thin veinlets. Group IV is rather close to group V in a marked fimbrial vein, areolation bounded by thick higher-order veins and thick veinlets. Group III shows an intermediate venation pattern between groups I/II and IV/V. Venation group V has the sixth as the highest-order vein, while venation of the other four groups has the fourth or fifth. Based on investigations of venation characters, a key for the identification of the five groups of extant *Nothofagus* leaves is presented as shown in Table 2.

Fossil Leaves of *Nothofagus* from South America

The evolutionary history of *Nothofagus* in South America has been discussed principally on the basis of pollen (Doubinger, 1972, 1975; Archangelsky & Romero, 1974). Macro-fossils have been almost ignored, though leaf fossils that are referable or closely similar to this genus have been described from many localities by several authors since the end of last century. The first fossils of *Nothofagus* leaves were reported by Dusén (1899), who described nine well-illustrated species from the Tertiary of the Magellan region of southernmost South America. Despite of his keen eyes he could not convincingly separate *Nothofagus* leaves from those of northern beech, *Fagus* L.; he described three species of *Fagus* leaves along with *Nothofagus* from the Tertiary of same region. His taxonomy for *Nothofagus* or *Nothofagus*-like fossil leaves was followed by most of later workers until the 1940's; many leaves from several localities of the Argentine Patagonian region and West Antarctica were described with the addition of some new taxa (Berry, 1928—1938; Fiori, 1939, 1940; Frenguelli, 1941). Unfortunately, however, there has been less interest in fossil leaves since palynological work on *Nothofagus* has gradually attracted much attention since the 1950's in South America, Australia and New Zealand.

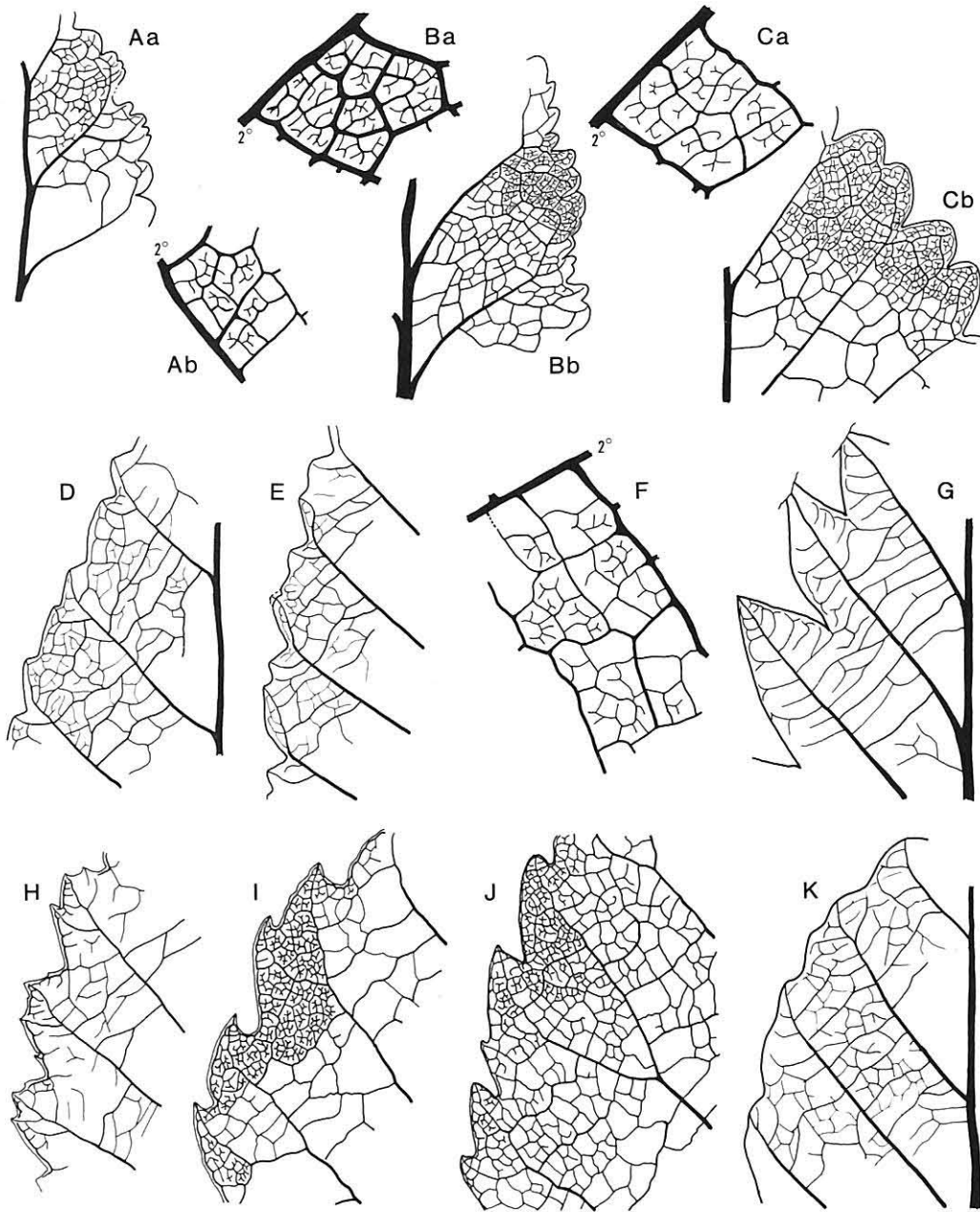
Through investigations of Late Cretaceous and Tertiary floras of Chile a large collection of fossils including a number of dicot leaves referable to *Nothofagus* has been studied. These fossil leaves of *Nothofagus* are not always well preserved, but they do allow close comparisons to those of modern species. Fossil leaves vary from very small (less than 1 cm in length) to medium-sized forms (about 9 cm) with rounded to acute marginal teeth, and a few to many secondary veins. Most specimens are represented by impressions, but are comparable with extant leaves in vein architecture. Some leaf specimens are represented by coalified compressions, and it is not possible to macerate them for cuticular analysis. The hair-base and stomata have been characterized, using an epifluorescence microscope. The lightly coalified compression of leaves are frequently excited to fluoresce, and epidermal features are easily observed without maceration (Friedrich & Schaarschmidt, 1977).

Based on investigations of collection from Chile, all the species of *Nothofagus* leaves that were previously described from South America and western Antarctica were reinvestigated. Corresponding with the above-noted leaf groups of this genus, nine



Text-fig. 7 Comparison of Leaf Architecture between Extant and Fossil Species — (1)

- A. *Nothofagus serrulata* Dusèn (HUMP no. 26280). a $\times 15$, b $\times 5$
 B. *Nothofagus alpina* (Poepp. & Endl.) Oerst. a $\times 15$, b $\times 5$
 C. *Nothofagus alessandri* Espinosa. a $\times 15$, b $\times 5$
 D. *Nothofagus subferruginea* (Dusèn) Tanai (HUMP no. 26293). a $\times 5$, b $\times 15$
 E. *Nothofagus subferruginea* (Dusèn) Tanai (HUMP no. 26296). $\times 15$
 F. *Nothofagus subferruginea* (Dusèn) Tanai (HUMP no. 26295). $\times 5$
 G. *Nothofagus magelhaenica* (Engelhardt) Dusèn (HUMP no. 26276). a $\times 15$, b $\times 5$
 H. *Nothofagus obliqua* (Mirb.) Oerst. a $\times 15$, b $\times 5$
 I. *Nothofagus simplicidens* Dusèn (HUMP no. 26286). a $\times 15$, b $\times 5$



Text-fig. 8 Comparison of Leaf Architecture between Extant and Fossil Species — (2)

- A. *Nothofagus crenulata* Dusén (HUMP no. 26250). a × 5, b × 15
- B. *Nothofagus antarctica* (Forst) Oerst. a × 15, b × 5
- C. *Nothofagus pumilio* (Poepp. & Endl.) Oerst. a × 15, b × 5
- A. *Nothofagus serrulata* Dusén (HUMP no. 26280). a × 15, b × 5
- D-F. *Nothofagus densinervosa* Dusén (HUMP nos. 26308, 26259, 26307). D × 5, E × 5, F × 15
- G. *Nothofagus dicksoni* (Dusén) Tanai (HUMP no. 26262). × 5
- H. *Nothofagus variabilis* Dusén (HUMP no. 26305). × 5
- I. *Nothofagus fusca* (Hook. f.) Oerst. × 5
- J. *Nothofagus truncata* (Colenso) Cockayne. × 5
- K. *Nothofagus gonzalezi* Tanai (HUMP no. 26267). × 5

species with some revisions are confirmed in the Tertiary of southern South America and Antarctica.

Group I

Nothofagus magelhaenica (Engelhardt) Dusén

Nothofagus serrulata Dusén

Nothofagus simplicidens Dusén

Nothofagus subferruginea (Dusén) Tanai

Group II

Nothofagus densinervosa Dusén

Nothofagus crenulata Dusén

Group IV

Nothofagus dicksoni (Dusén) Tanai

Nothofagus gonzalezi Tanai

Nothofagus variabilis Dusén

Of these nine species, six species of groups I and II show close similarities to extant species living in South America, while three species of group IV are related to the living species of New Zealand. It is noteworthy that no fossil leaves are similar to those of groups III and V so far, although leaves of group V are difficult to distinguish from entire-margined leaves of other families.

Systematic Descriptions and Revisions

As indicated in the descriptions that follow, most species of *Nothofagus* from the Tertiary of southern South America appear to have close relationships to extant species of South America and elsewhere in their leaf architecture. Terms of leaf architecture used in the description are mostly based on Hickey (1979). For accurate taxonomical description it was necessary to compare all specimens with Dusén's original material deposited in the Swedish Museum of Natural History in Stockholm. It was, however, regretfully impossible, because all the original specimens have been loaned abroad for study during these ten years.

All specimens cited here are deposited in the Museum of Paleontology, Hokkaido University (Abbreviation: HUMP) in Sapporo. Many duplicates are also stored in the National Science Museum (Paleontology Collection) in Tokyo.

Family Fagaceae

Genus *Nothofagus* Blume

Nothofagus crenulata Dusén

(Pl. 15, figs. 1-4, 6, 8; Text-fig. 8, A)

Nothofagus crenulata Dusén: 1899. Svensk. Exped. Magell. 1(4): 101. pl. 10. f. 3, 4

Type: Lectotype, Swed. Mus. Nat. Hist., Paleobot. Collection (Dusén, 1899: pl. 10, fig. 4); Rio Guillermo, north of Puerto Natales, Magallanes, Chile; the upper part of the Mina Chilena Formation (Early Miocene).

Supplementary Description: Leaves very small, oblong to ovate in general outline, 10.5

to 16 mm long and 5.5 to 12 mm wide; length/width ratio of leaves 1.3 to 2 (average 1.62 for 5 specimens); apex obtuse, not pointed; base obtuse to rounded, somewhat asymmetrical; margin irregularly crenulate; teeth irregular in size, rounded at tip; leaf texture chartaceous; petiole thick, but nearly missing. Midvein thick, somewhat sinuous; secondary veins slender, 3—5 opposite pairs, diverging from the midrib at acute angles, then slightly arcuate, forking once or twice near the margin and their branches forming loops or coarse reticulation; tertiary veins reticulate with fourth order veins; higher order vein fifth; areoles mostly quadrangular; ultimate veinlets thin, incompletely preserved but probably once or twice branching.

Discussion: Four small leaf impressions in my collection are identical in their venation and margin to *Nothofagus crenulata* which was described from the Rio Guillermo by Dusén (1899). The above description was supplemented on the basis of my specimens that are comparatively well preserved. Dusén (1899) compared *N. crenulata* with the extant *N. cunninghamii* (Hook. f.) Oerst. of New Zealand, while Frenguelli (1941) compared with the extant *N. betuloides* (Mirb.) Oerst. of South America. However, the margin and secondary vein termination indicate that *N. crenulata* belongs to the leaf group II, in special closely similar to the extant *N. antarctica* (Forst.) Oerst. of southern South America.

N. crenulata is rather uncommon member in the Tertiary of Magellan region, and it may be confined in occurrence to the upper part of the Loreto Formation and its equivalent.

Collection: Hypotypes, HUMP nos. 26250, 26251 (Rio Chico, west of San Sebastian, Fuego Island, Chile; the Brush Lake Formation, Early Miocene).

Other Occurrence: Rio Guillermo, north of Puerto Natales, Chile (Dusén, 1899); Rio Turbio, Santa Cruz, Argentina (Frenguelli, 1941).

Nothofagus densinervosa Dusén

(Pl. 12, figs. 1-12; Text-fig. 8, D-F)

Nothofagus densinervosa Dusén. 1899. Swed. Exped. Magell. 1(14): 99. pl. 9. f. 14-19.

Fiori. 1939. Giorn. Geol. [2]. 13: 49. pl. 1. f. 18.

Hünicken. 1966. Rev. Fac. Cienc. Exact. Fis. Nat., Univ. Nac. Cordoba, ser. Cienc. Nat. 27: 168. pl. 2. f. 7.

Fagus pulchra Dusén. 1908. Wiss. Ergeb. Schwed. Südpolar-Exped. 3(3): 10. pl. 1. f. 10, 12.

Type: Lectotype, Swed. Mus. Nat. Hist. Paleobot. Collection (Dusén, 1899: pl. 9, fig. 16); Rio Condor, Fuego Island, Chile (Rio Condor Formation, Miocene).

Supplementary Description: Leaves generally small, elliptic to oblong in shape, 1.1 to 4.2 cm long and 0.6 to 2.2 cm wide; length/width ratio of leaves 1.61 to 2.25 (average 1.85 for 18 specimens); apex acute; base obtuse to broadly acute, rarely rounded; margin compound-dentate with widely obtuse teeth whose apical and basal sides are nearly straight or slightly convex; leaf texture chartaceous; petiole thick but short, 2 to 2.5 mm long; midvein thick, nearly straight or somewhat sinuate in the upper part of blade; secondary veins stout, 8 to 11 pairs in most case, but rarely 12 to 15 pairs, diverging from the midvein at acute angles and nearly straight toward tooth sinus, then abruptly arising up along the basal side of tooth and entering tooth apex; a slender

subsecondary vein branching basally from the secondary, entering an intersecondary tooth; tertiary veins moderately thick, weakly percurrent and sinuate or forking in their course; the highest order veins sixth; the areolation irregular in size and shape, composed of fourth- or fifth-order veins; ultimate veinlets very thin, variable from once to two times branching, sometimes lacking.

Discussion: These specimens from the Fuego Island are characterized by the obtusely dentate teeth of margin and secondary vein termination near the marginal region; these features indicate that these leaves doubtlessly belong to the leaf Group II. These leaf specimens of my collection are referable in the above characters to *N. densinervosa* described by Dusén (1899), although most of the original specimens are smaller. Of three extant species of group II, *N. densinervosa* is closely related to *N. pumilio* (Poepp. et Endl.) Oerst. of South America in venation characters including areoles and veinlets; however, leaves of *N. pumilio* are crenate with smoothly rounded teeth in margin.

N. pulchura Dusén from Seymour Island in West Antarctica (Dusén, 1908) is closely similar to *N. densinervosa* in general outline, although it is represented by leaves of single-rounded toothed margin. My collection includes such type leaves, whose margin is broken as if the margin is single-toothed (pl. 12, figs. 5, 6, 9). Thus, *N. pulchura* probably represents leaves with incompletely preserved margin of *N. densinervosa*, but it needs to restudy the original specimens.

N. densinervosa is one of the common members in the Tertiary of southern South America, and is easily distinguishable from other species of *Nothofagus* by margin and secondary venation characters.

Collection: Hypotypes, HUMP nos. 26252-26254, 26255a (Rio Las Minas, west of Punta Arenas, Chile: Loreto Formation, Late Oligocene-Early Miocene); nos. 26256-26259 (Rio Chico, west of San Sebastian, Fuego Island, Chile; Brush Lake Formation, Early Miocene); nos. 26260, 26261 (Laguna Lynch, west of Punta Arenas, Chile; Loreto Formation, Oligocene-Early Miocene).

Other Occurrence: Rio Condor, Fuego Island, Chile (Dusén, 1899); Carmen Sylva and Rio Beta, Fuego Island, Argentina (Dusén, 1899); Rio Nirihua, Chubut, Argentina (Fiori, 1939); Rio Turbio, Santa Cruz, Argentina (Hünicken, 1966); Seymour Island, West Antarctica (Dusén, 1908).

Nothofagus dicksoni (Dusén) Tanai comb. nov.

(Pl. 13, figs. 4, 8, 13, 17; Text-fig. 8, G)

Fagus dicksoni Dusén. 1899. Svensk. Exped. Magell. 1(4): 95. pl. 8. f. 14-16.

Dusén. 1908. Wiss. Ergeb. Schwed. Südpolar-Exped. 3(3): pl. 1. f. 12.

Berry. 1937b. Johns Hopkins Univ. Stud. in Geol. (12): 93. pl. 18. f. 1.

Type: Lectotype, Swed. Mus. Nat. Hist. Paleobot. Collection (Dusén, 1899: pl. 8, fig. 14); Carmen Sylva, eastern coast of Fuego Island, Argentina; "Brush Lake" Formation (Early Miocene).

Emended Description: Leaves small to medium in size, elliptic to wide elliptic in general outline, 2.3 to 3.8 cm long and 1.2 to 2 cm wide; length/width ratio of leaves

1.47 to 2 (average 1.84 for 7 specimens); apex acute to slightly attenuate; base obtuse to rounded; margin deeply serrate or shallowly lobed with narrowly acute sinus; teeth large, elongate, gently convex on both sides, acute but not pointed at apex; leaf texture subcoriaceous; petiole nearly missing, rather slender. Midvein stout, nearly straight to the apex; secondary veins thick, 8 to 12 pairs, opposite to subopposite, diverging from the midvein at acute angles, nearly straight, entering centrally tooth apex; tertiary veins thin, weakly percurrent with about 0.5 to 0.7 mm distance; higher order veins not well preserved; thick fimbrial vein developing well along the serrate margin.

Discussion: These leaves are characterized by deeply serrate or shallowly lobed margin, and identical to *Fagus dicksoni* that was described from Fuego Island and near Punta Arenas by Dusén (1899). However, the large elongate teeth, secondary veins centrally entering teeth and a thick fimbrial vein along the margin indicate that these leaves are not related to *Fagus* but to some of the leaf group IV of *Nothofagus*. There are, however, no extant leaves which closely match these fossil leaves in all characters. *N. dicksoni* may be related to the extant *N. fusca* (Hook. f) Oerst. and *N. truncata* (Colenso) Cock. of New Zealand, but leaves of these extant species are smaller in size, less in number of secondary veins and less conspicuous in teeth than the fossil leaves.

N. dicksoni is somewhat variable in elongate shape of teeth; leaves with less prolonged teeth may be sometimes confusable with *N. simplicidens* in their general appearance, but they are easily distinguishable by the fimbrial vein.

Collection: Hypotypes, HUMP no. 26262 (Laguna Lynch, west of Punta Arenas, Chile), and nos. 26263, 26264 (Rio del Las Minas, west of Punta Arenas, Chile). Both from the Loreto Formation (Oligocene-Early Miocene).

Other Occurrence: Carmen Sylva, near the eastern coast of Fuego Island, Argentina (Dusén, 1899); Rio Turbio, Santa Cruz, Argentina (Berry, 1937b); Seymour Island, West Antarctica (Dusén, 1908).

Nothofagus gonzalezi Tanai sp. nov.

(Pl. 13, figs. 5, 9, 14, 16; Text-fig. 8, K)

Type: Holotype, HUMP no. 26265, paratypes no. 26266, 26267; Coastal cliff near Matanzas, southwest of Santiago, Chile (Matanzas Formation, Early Miocene).

Description: Leaves small, ovate to narrow ovate in general outline, 2.9 to 5 cm long and 1.85 to 2.6 cm wide; length/width ratio of leaves 1.56 to 2.15; apex acute to obtuse, not pointed; base somewhat asymmetrical, obtuse; margin crenate to double crenate; teeth large, rounded, separated by mostly obtuse sinus, sometimes accompanied by a small, rounded subsidiary tooth on basal side; both the apical and basal sides gently convex; leaf texture chartaceous; petiole thick, 3–4 mm long. Midvein stout, nearly straight; secondary veins thick, 7 to 11 pairs, opposite to subopposite, diverging from the midvein at acute angles, nearly straight near the margin, ending in apex or in apical side of principal tooth; a slender branch emerging basally from the secondary, ending in apex or in sinus bottom of a subsidiary tooth; tertiary veins rather thin, ill-preserved but reticulate with quaternary veins; the higher order veins not preserved; thick fimbrial vein developing well along the margin.

Discussion: These leaves from the Miocene of central Chile are characterized by crenate margin, thick fimbrial vein, and secondary vein terminating sometimes in apical side of tooth. Although ill-preserved in the higher order venation, the above-described characters show that these leaves belong to the leaf group IV. *N. gonzalezi* may be especially related to the extant *N. cunninghamii* (Hook. f.) Oerst. of Australia and *N. menziesii* (Hook. f.) Oerst. of New Zealand, both IV-b subgroup, but is distinctly different in having more than twice number of the secondary veins.

N. gonzalezi resembles *N. simplicidens* and *N. densinervosa* of the Magellan region at general appearance, but is distinguishable in a thick fimbrial vein and the secondary vein termination. This new species is named in the honor of Dr. Eduardo P. Gonzalez of Empresa Nacional del Petroleo of Chile, who kindly supported me to collect plant fossils in Chile.

Collection: HUMP holotype no. 26265, paratypes nos. 26266, 26267 (Coastal cliff near Matanzas, southwest of Santiago, Chile; Matanzas Formation, Early Miocene).

Nothofagus magelhaenica (Engelhardt) Dusén

(Pl. 10, figs. 1-12; pl. 11, fig. 1; Text-fig. 7, G)

Nothofagus magellanica (Engelhardt) Dusén. 1899. Svens. Exped. Magellans. 1(4): 97

Fagus magelhaenica Engelhardt. 1891 [part]. Senckenb. Naturf. Gesell. Abhandl. 16(4): 648. pl. 2. f. 18 (excluding f. 17. 19)

Nothofagus elongata auct. non Dusén. Berry. 1937b. Johns Hopkins Univ. Stud. in Geol. (12): 94. pl. 18. f. 7.

Type: Lectotype, Senckenberg Mus. Naturforschungs. Paleobot. Collection (Engelhardt, 1891: pl. 2, fig. 18); west of Punta Arenas, Chile (Loreto Formation, Oligocene-Early Miocene).

Supplementary Description: Leaves elliptic to narrow-elliptic in shape, acute to obtuse at base, acute to somewhat attenuate at apex, 2.9 to 4.5 cm long and 1.2 to 2.2 cm wide; length/width ratio of leaves 1.9 to 2.6; margin double serrate with acute, main teeth, whose sides are convex in the apical and slightly concave in the basal; main teeth in which the secondary veins end are usually accompanied with a small subsidiary tooth in their basal side; leaf texture chartaceous; petiole thick but incomplete, more than 5 mm long (7 mm long in the lectotype). Venation pinnate, craspedodromous; midvein thick in the lower half of blade, then suddenly becoming thin toward the apex, nearly straight or slightly arcuate; secondary veins moderate, 10 to 14 pairs, diverging from the midrib at acute angles, nearly straight, then somewhat flexuous within teeth areas, entering teeth apex; a branch from the secondary curving upward, then ending in subsidiary tooth; the tertiaries irregularly percurrent; the highest order vein probably sixth; the areolation irregular in size and shape; the ultimate veinlets very thin, more than twice branching.

Discussion: These leaves are generally similar to those of the extant *Nothofagus obliqua* (Mirbel) Oerst. in their venation and marginal characters, especially consistent in irregularly sized areoles and thin veinlets, although the extant leaves are somewhat more obtuse in the marginal teeth and less in number of the secondary veins.

Engelhardt (1891) described *Fagus magelhaenica* from the Tertiary near Punta

Arenas, based on three incomplete leaves which were considered to resemble leaves of the extant *N. obliqua* by him. *F. magelhaenica* was later transferred to *Nothofagus* by Dusén (1899), who supported its close similarity to *N. obliqua*. However, all the specimens illustrated by Dusén (1899) are different from *N. obliqua*, because they are single-toothed in margin. Considering marginal character, only one specimen (Engelhardt, 1891: pl. 2, f. 18) is confirmed to represent *N. magelhaenica*, which is here redesignated on the basis of the above-described foliar characters.

Collection: Hypotypes, HUMP nos. 26276, 26277 (Rio Chico, west of San Sebastian, Fuego Island, Chile; Brush Lake Formation, Early Miocene); nos. 26268-26275 (Rio del Las Minas, west of Punta Arenas, Chile; Loreto Formation, Oligocene-Early Miocene).

Other Occurrence: Rio Turbio, Santa Cruz, Argentina (Berry, 1937b).

Nothofagus serrulata Dusén

(Pl. 14, figs. 1, 2, 6, 7, 13; Text-fig. 7, A)

Nothofagus serrulata Dusén. 1899. Svens. Exped. Magell. 1(4): 96. pl. 9. f. 1-7.

Nothofagus cf. *serrulata* Dusén. Hünicken. 1966. Rev. Fac. Cienc. Exact. Fis. Nat., Univ. Nac. Cordoba, ser. Cienc. Nat. 27: 166, pl. 2. f. 1.

Type: Lectotype, Swed. Mus. Nat. Hist. Paleobot. Collection (Dusén: 1899: pl. 9, fig. 2). West of Punta Arenas, Chile (Loreto Formation, Oligocene-Early Miocene).

Discussion: These ovate to elliptic leaves are characterized by the following features: the margin is double-serrate except for basal entire part, with two or three smaller teeth between the principal teeth in which the secondary veins end; the tertiary veins are distinctly percurrent and sinuous or forked in course; a stout branch from the secondaries enters a smaller tooth just below the principal tooth; the secondary veins are 10 to 14 in number; the areoles are well-defined by thick fourth-order veins, and intruded by once to thrice branching veinlets.

These leaves with double-serrate margin in my collection are referable to *Nothofagus serrulata* Dusén, that was described from the Tertiary west of Punta Arenas by Dusén (1899). My specimens are closely similar in general features of venation and margin to leaves of the extant *N. alpina* (Poepp. et Endl.) Oerst. of South America, but they are different in obtuse marginal teeth and less secondary veins. Because of a close similarity between the under-secondary-order venation, *N. serrulata* seems a progenitor of the extant *N. alpina*, although most of fossil leaves are generally smaller than the modern ones.

Collection: Hypotypes, HUMP no. 26278 (Rio del Las Minas, west of Punta Arenas, Chile; Loreto Formation, Oligocene-Early Miocene); nos. 26279, 26280 (Rio Chico, west of Estacion San Sebastian, Fuego Island, Chile; Brush Lake Formation, Early Miocene).

Other Occurrence: Carmen Sylva, Fuego Island, Argentina (Dusén, 1899); Rio Turbio, Santa Cruz, Argentina (Hünicken, 1966).

Nothofagus simplicidens Dusén

(Pl. 13, figs. 1-3, 6, 7, 10-12; Text-fig. 7, 1)

Nothofagus simplicidens Dusén. 1899. Svens. Exped. Magell. 1(4): 100. pl. 9. f. 20-25.

Fiori. 1939. Giorn. Geol. [2]. 13: 48. pl. 1. f. 15-17.

Nothofagus magellanica (Engelhardt) Dusén. 1899. [part]. *ibid.* 1(4): 97. pl. 10. f. 8, 10, 11 (excluding f. 2, 7, 9).*Nothofagus australis* Dusén. 1899. *ibid.* 1(45): 100. pl. 8. f. 9, 10.

Fiori. 1939. Giorn. Geol. [2]. 13: 47. pl. 1. f. 14.

Nothofagus cf. *lanceolata* Dusén. Fiori. 1939. *ibid.* 13: 49. pl. 1. f. 19, 20.*Fagus magelhaenica* Engelhardt. 1891 [part]. Sencken. Naturf. Gesell. Abhandl. 16(4): 648. pl. 2. f. 19 (excluding f. 17, 18)? *Fagus* cf. *dicksoni* Dusén. Fiori. 1931. Gior. Geol. [2]. 6: 112. pl. 1. f. 13.**Type:** Lectotype, Swed. Mus. Nat. Hist. Paleobot. Collection (Dusén, 1899: pl. 9. f. 2.).

Supplementary Description: Leaves variable in shape and size, lanceolate oblong, sometimes broadly ovate in outline, 2.8 to 8.6 cm long and 1.4 to 3.2 cm wide; length/width ratio of leaves 1.5 to 2.6 (average 2.03 for 20 specimens); apex acute, sometimes acuminate; base obtuse to broadly rounded, rarely somewhat cordate; margin single-serrate with obtuse teeth which are separated by broadly-open sinuses; both apical and basal sides of teeth nearly straight or slightly convex; texture chartaceous; petiole stout, 5 to 7 mm long. Venation pinnate, simple-craspedodromous; midvein stout, nearly straight and rarely somewhat sinuate in the upper part of blade; secondary veins thick, 9 to 13 pairs, diverging from the midvein at acute angles, nearly straight, curving up near the margin, entering teeth along the basal side of tooth; tertiary veins thin but distinct, percurrent; highest order vein sixth; areolation composed of fourth- and fifth-order veins, quadrangular or pentagonal in shape; ultimate veinlets thin, several times branching.

Discussion: A number of single-serrate leaf specimens in my collection are referable to *Nothofagus simplicidens* described from the Tertiary of the Magellan region by Dusén (1899). These leaves closely resemble those of *N. magelhaenica* in general appearance, but they are distinguishable by single-serrate margin and regularly percurrent tertiary veins. *N. simplicidens* belongs to the leaf group I in the secondary vein termination and no fimbrial vein, and is related to the extant *N. obliqua* (Mirb.) Oerst. of South America, although usually single serrate in margin.

N. simplicidens is common in the Tertiary of southern South America. All the specimens listed in the synonymy are included in this species. *N. magelhaenica* described by Engelhardt (1891) and Dusén (1899) includes leaves with both single and double serrate margin; among these specimens the single serrate leaves should be included in *N. simplicidens*. *N. australis* Dusén from the Magellan Tertiary is also represented by single serrate leaves, and unseparable from *N. simplicidens*.

Collection: Hypotypes, HUMP nos. 26281-26287 (Rio Chico, west of Estacion San Sebastian, Fuego Island, Chile; Brush Lake Formation, Early Miocene); no. 26288 (Rio del Las Minas, west of Punta Arenas, Chile; Loreto Formation, Oligocene-Early Miocene).

Other Occurrence: Carmen Sylva and Rio Beta, Fuego Island, Argentina (Dusén,

1899); Rio Condor, Fuego Island, Chile (Dusén, 1899); Rio Guillermo, north of Puerto Natales, Chile (Dusén, 1899); Rio Nirihuau, Chubut, Argentina (Fiori, 1939); San Carlos de Bariloche, Rio Negro, Argentina (Fiori, 1931).

Nothofagus subferruginea (Dusén) Tanai comb. nov.

(Pl. 9, figs. 1-12; pl. 11, figs. 3, 5; Text-fig. 7, D-F)

Fagus subferruginea Dusén. 1899. Svensk. Exped. Magell., 1(4): 94. pl. 8. f. 1-8.

Berry. 1928. Proc. U.S. Nat. Mus. 73(22): 15.

Berry. 1937b. Johns Hopkins Univ. Stud. in Geol. (12): 93. pl. 18. f. 6.

Hünicken. 1966. Rev. Fac. Cienc. Exact. Fis. Nat., Univ. Nac. Cordoba, ser. Cienc. Nat. 27: 163. pl. 1. f. 12-18.

Fagus integrifolia Dusén. 1899. Svensk. Exped. Magell. 1(4): 95, pl. 8. f. 12.

Berry. 1937b. Johns Hopkins Univ., Stud. in Geol. (12): 94.

Fagus obscura Dusén. 1908. Wiss. Erdgeb. Schwed. Südpolar-Exped. 3(3): 9. pl. 1. f. 23.

Hünicken. 1966. Rev. Exact. Fis. Nat. Univ. Nac. Cordoba, Ser. Cienc. Nat. 27: 165. pl. 1. f. 19.

Fagus gortanii Fiori. 1940. Giorn. Geol. [2]. 14: 107. pl. 5. f. 5, 6.

Nothofagus cf. *engelhardtiana* Fiori. 1940. Giorn. Geol. [2]. 14: 108. pl. 5. f. 7.

Type: Lectotype, Swed. Mus. Nat. Hist. Paleobot. Collection (Dusén: 1899: pl. 8, f. 2); west of Punta Arenas, Magallanes, Chile (the Loreto Formation, Oligocene-Early Miocene).

Emended Description: Leaves generally medium in size, narrow ovate to lanceolate in shape, 4.2 to 8.2 cm long and 2.1 to 3.5 cm wide; length/width ratio of leaves 1.9 to 2.43 (average 2.14 for 10 specimens); apex acute to slightly attenuate; base obtuse to rounded, somewhat asymmetrical; margin mostly simple serrate with acute principal teeth which are generally apically pointed, acuminate at apical side and convex at basal side; sinus rounded; leaf texture chartaceous; petiole thick, incomplete, more than 2 mm long. Midvein thick, nearly straight but sometimes slightly sinuate in the upper part of the blade; secondary veins stout, 10 to 18 subopposite pairs, diverging from the midvein at acute angles, nearly straight toward the teeth, then abruptly arising up along the basal side of principal tooth and ending in tooth apex; a branch from the secondary entering a subsidiary tooth; tertiary veins rather thin in comparison with the secondaries, weakly percurrent with about 0.5 mm distance, sinuate or forking in their course; the highest order vein sixth; areolation somewhat irregular in size, fourth- or fifth-sided; ultimate veinlets very thin, once to twice branching.

Discussion: Several well-preserved specimens were collected from the river bank of Las Minas west of Punta Arenas, that is the locality of the lectotype; they are indistinguishable from *Fagus subferruginea* described by Dusén (1899). However, a subsidiary tooth between the principal teeth, the secondary veins directly entering teeth and once to thrice branching veinlets indicate that these leaves are not referable to the genus *Fagus* but to the genus *Nothofagus*. Especially, these fossil leaves are closely similar to the extant *N. alessandri* Espinosa of South America in their venation and margin characters, although they are frequently more prolonged in apex than extant leaves.

Leaves referable to *N. subferruginea* have been commonly reported from the Tertiary of southern South America, although some were not illustrated. All the specimens

listed in the above synonymy are included in this species. A single leaf described as *Fagus integrifolia* Dusén from Fuego Island is entire or serrate with minute teeth in the margin, and probably represents an incompletely leaf of *N. subferruginea*. A fragmentary single-toothed leaf from Seymour Island was described as *Fagus obscura* by Dusén (1809), along with a similar specimen of the Magellan region (Dusén 1899: pl. 8, fig. 4). These are, however, included in *Nothofagus subferruginea*, because leaves of *N. subferruginea* are sometimes simple toothed on the upper margin of blade as do in the extant *N. alessandri*. Leaves of *Fagus gortanii* Fiori and *F. cf. engelhardtiana* Fiori from the Tertiary near Lago Nahuel Huapi are unseparable from *N. subferruginea* in margin and foliar shape. Besides these specimens, there have been several leaf fossils similar or nearly identical to *N. subferruginea* from the Tertiary of western Antarctica, namely the King George Islands (Barton, 1963; Zastawniak, 1981; Zastawniak et al., 1985) and Seymour Island (Dusén, 1908). Especially, several specimens illustrated as *N. ulmifolia* (Ettings.) Oliver and *N. aff. alessandri* Espinosa from Point Hennequin of the King George Islands (Zastawniak et al., 1985) are probably referred to *N. subferruginea* in their marginal and venation characters.

Leaf specimens described as *Fagus novae-zealandica* Oliver and *F. australis* Oliver from the Upper Miocene of New Zealand (Oliver, 1936) are very similar to those of the extant *N. alessandri* in foliar shape and margin, and a further detailed comparison with the original specimens may confirm that these New Zealand species are closely related to *N. subferruginea*. This further confirmation provides an important evidence for the past phytogeographic history of *Nothofagus*.

Collection: Hypotypes, HUMP nos. 26289-26296 (Rio del Las Minas, west of Punta Arenas, Chile; Loreto Formation, Oligocene-Early Miocene); nos. 26297, 26298 (Rio Chico, west of Estacion San Sebastian, Fuego Island, Chile; Brush Lake Formation, Early Miocene); no. 26299 (Matanzas, southwest of Santiago, Chile; Matanzas Formation, Early Miocene).

Other Occurrence: Carmen Sylva, Fuego Island, Argentina (Dusén, 1899); Chenu-Niyeu, Chubut, Argentina (Fiori, 1940); Rio Barriloche, Chubut, Argentina (Berry, 1928); Rio Turbio, Santa Cruz, Argentina (Berry, 1937b; Frenguelli, 1941; Hünicken, 1966).

Nothofagus variabilis Dusén

(Pl. 14, figs. 3-5, 8-12, 14; Text-fig. 8, H)

Nothofagus variabilis Dusén. 1899. Svensk. Exped. Magell. 1(4): 96, pl. 9. f. 8-13.

Berry. 1937b. Johns Hopkins Univ., Stud. in Geol. (12): 94.

Nothofagus variabilis Dusén form. *microphylla* auct. non Dusén. Hünicken. 1966. Rev. Fac. Cienc. Exact. Fis. Nat. Univ. Nat. Cordova, ser. Cienc. Nat. 27: 167. pl. 2. f. 3-6.

Type: Lectotype, Swed. Mus. Nut. Hist. Paleobot. Collection (Dusén, 1899: pl. 9, fig. 11); Carmen Sylva, Fuego Island, Argentina ("Brush Lake" Formation, Early Miocene).

Supplementary Description: Leaves small, wide-ovate to suborbiculate in shape, 1.7 to 3.8 cm long and 1 to 2.7 cm wide; length/width ratio of leaves 1.3 to 1.8 (average 1.53

for 10 specimens); apex acute; base asymmetrical, rounded to broadly cordate; margin double-serrate with large teeth and angular sinus; principal teeth pointed and glandular at apex, straight or slightly acuminate at both sides; a small, acute subsidiary tooth on apical side and one or two small subsidiary teeth on basal side; leaf texture subcoriaceous; petiole medium, 5—6 mm long. Midvein medium, nearly straight or slightly sinuous; secondary veins slender, 6 to 10 pairs, opposite to subopposite, somewhat irregularly spaced, diverging from the midvein at acute angles, nearly straight or somewhat curving upward, craspedodromous; a slender tertiary vein branching abaxially, ending in a subsidiary tooth of basal side of principal tooth; tertiary veins thin, irregularly percurrent with more than 1 mm distance, sinuous or forking; the higher order venation not well preserved; thick fimbrial vein developing well along the margin.

Discussion: These leaves are characterized by the double serrate margin, well-developed fimbrial vein along the margin and the secondary veins entering centrally the principal teeth; these characters indicate that these leaves belong to the leaf subgroup IVa. *N. variabilis* is especially similar to the extant *N. fusca* (Hook. f.) Oerst. of New Zealand in the venation and general outline, but different in marginal serration. Although leaves of *N. variabilis* may be similar to those of the extant *N. betuloides* (Mirb.) Oerst. and *N. dombeyi* (Mirb.) Oerst. of South America in having fimbrial vein along the serrate margin, they are distinguishable from Chilean species in termination of the secondary veins. It is noteworthy for the *Nothofagus* history that *N. variabilis* is related not to extant species of South America but to those of New Zealand.

Leaves of *N. variabilis* are somewhat variable in their shape and size, and they were divided into three forms by Dusén (1899): forma *oblonga*, *subrotundata* and *microphylla*. However, these three forms are difficult to distinguish taxonomically as independent varieties, due to gradation of leaf forms. This species is one of common members in the Tertiary of the Magellan region.

Collection: Hypotypes, HUMP nos. 26300-26304 (Rio del Las Minas, west of Punta Arenas, Chile; Loreto Formation, Oligocene-Early Miocene); no. 26305 (Rio Chico, west of Estacion San Sebastian, Fuego Island, Chile; Brush Lake Formation, Early Miocene).

Other Collection: Carmen Sylva, Fuego Island, Argentina (Dusén, 1899); Rio Turbio, Santa Cruz, Argentina (Berry, 1937b; Frenguelli, 1941; Hünicken, 1966).

Doubtful Fagaceous Species

The following species were described as *Nothofagus* or its related fossils from the Tertiary of southern South America by some authors. However, these leaf specimens lack the definite character to be referable to the genus *Nothofagus* because of their ill-preservation, although some of them seem to resemble some leaves of the extant species.

Nothofagus elongata Dusén

Nothofagus elongata Dusén. 1899. Svensk. Exped. Magell. 1(4): 97. pl. 10. f. 12, 13.

Nothofagus cf. *elongata* Dusén. Hünicken. 1966. Rev. Exact. Fis. Nat., Univ. Nac. Cordoba, ser. Cienc. Nat. 27: 166, pl. 2. f. 1.

Nothofagus cf. *obliqua* auct non. Mirb. Dusén. 1899. Svensk. Exped. Magell. 1(4): 98. pl. 10. f. 1.

Discussion: Several leaves in my collection are referable to *N. elongata* that was originally described from Fuego Island (Carmen Sylva locality) by Dusén (1899). This species is represented by medium-sized and single-serrate margined leaves, whose large, obtuse teeth are separated by opened sinus and convex on the both sides. The secondary veins of 12 to 15 pairs enter nearly centrally tooth apex. These leaves including Dusén's specimens are questionable to be referable to the genus *Nothofagus*; they may correspond with some leaves of the leaf group IV (IV-a subgroup), but differ in no fimbrial vein and further more number of secondary veins.

Nothofagus engelhardtiana Fiori

Nothofagus engelhardtiana Fiori. 1939. Giorn. Geol. [2]. 13: 45. pl. 1. f. 13.

Discussion: Leaves described as *Nothofagus magellanica* from the Magellan region by Dusén (1899) include two types of leaf margin, as discussed in the preceding page. Fiori (1939) gave a new name of *N. engelhardtiana* to the single-serrate margined leaves of Dusén's specimens; however, these leaves are included in *N. simplicidens* in their all characters. A single leaf of *N. engelhardtiana* from Rio Nirihuau of Argentina (Fiori, 1939) is too fragmentary to determine its specific status.

Nothofagus lanceolata Dusén

Nothofagus lanceolata Dusén. 1899. Svensk. Exped. Magell. 1(4): 101. pl. 8. f. 13.

Discussion: Illustrating a lanceolate, double-serrate margined leaf, *N. lanceolata* was established by Dusén (1899), who considered it to be related to the extant *N. dombeyi* (Mirb.) Oerst. of South America. However, judging from Dusén's illustration, the original specimen seems to be different from *N. dombeyi* in the feature of the secondary vein termination: the secondary veins of *N. lanceolata* enter straightly marginal teeth, while those of *N. dombeyi* are flexuous in course and fork near the margin. No fossil leaves referable to *N. lanceolata* were collected by me in the Magellan region.

Nothofagus pulcherrima Fiori

Nothofagus pulcherrima Fiori. 1940. Giorn. Geol. [2]. 14: 109. pl. 5. f. 8.

Discussion: This species was described by Fiori on the basis of a double-serrate margined leaf from Rio Nirihuau of Argentina. It is difficult to judge only from his poor illustration whether or not this specimen is referable to the genus *Nothofagus*.

Fagophyllum duseni Berry

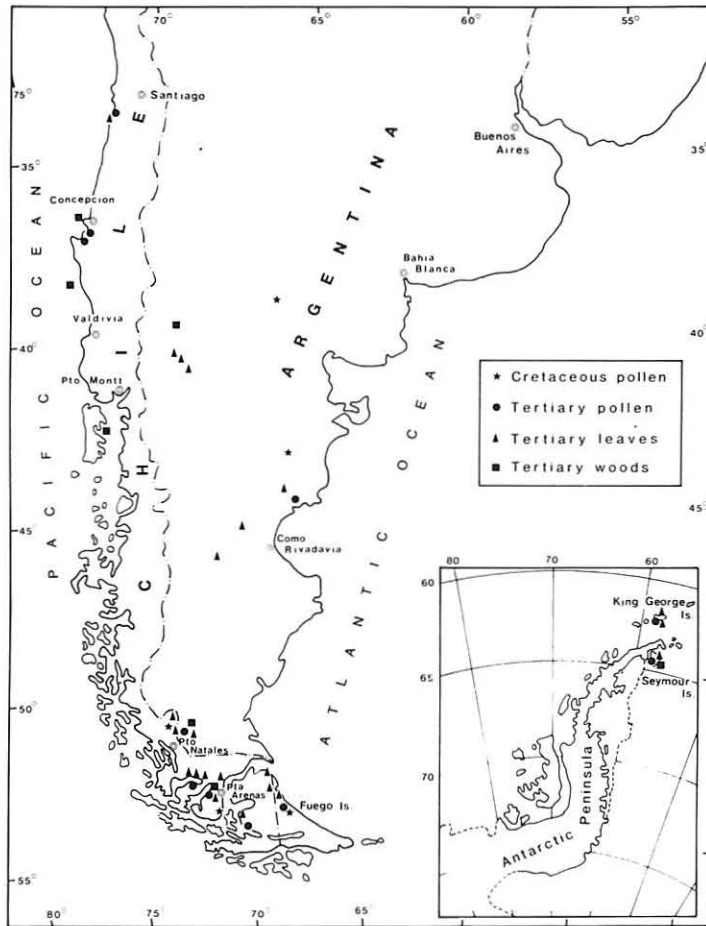
Fagophyllum duseni Berry. 1937a. Johns Hopkins Univ. Stud. in Geol. (12): 39. pl. 5. f. 1, 2.

This fagaceous species described from Cerro Funes, Chubut, Argentina (Berry, 1937a) may be similar to *Nothofagus simplicidens* in general features, as far as judged from the illustration of two leaves. However, the secondary vein termination is variable in

these illustration, although Berry described to be *craspedodromous*. A single leaf from Rio Turbio of Argentina was considered to be nearly identical with *F. duséni* by Hünicken (1966: pl. 2, f. 10). This incomplete leaf from Rio Turbio is probably referred to the genus *Cupania* by marginal character.

Stratigraphic and Past Areal Distribution of *Nothofagus* in South America and West Antarctica

A number of Late Cretaceous and Tertiary floras have been reported in South America and West Antarctica by various authors, based on pollen, leaves and wood. So far as is known, the fossil record of *Nothofagus* is limited to the south of about 35°S. lat., as shown in Text-fig. 9. Abundant occurrences in the Patagonian region are partly due to the fact that terrestrial sediments are well investigated due to coal and petroleum exploration.



Text-fig. 9 Localities of *Nothofagus* Fossils (pollen, leaves, and wood) in South America and Western Antarctica.

Central Region of Chile

Four principal Tertiary sedimentary basins, the San Antonio-Navidad, Arauco-Concepción, Temuco and Valdivia-Osorno (García, 1963), are known on the Upper Cretaceous or pre-Cretaceous rocks in central Chile. Leaves, wood and pollen of *Nothofagus* are known from the former two; however, no fossil leaves referable to this genus have yet been found from the latter two regions, although many dicot leaves have been collected from the Paleogene.

Matanzas Coastal Region southwest of Santiago

Oligocene-Miocene sediments (the Matanzas and Navidad Formations) are exposed well along the coastal cliff near Matanzas southwest of Santiago. The Matanzas Formation, though mostly of marine origin, yields well-preserved leaves of dicots and ferns in the middle part of the sequence exposed there. Fossil *Nothofagus* leaves, however, are rarely contained. Plant-bearing rocks yield also *Nothofagus* pollen, although very rare.

Arauco-Concepcion Region

Thick Tertiary sediments of continental and marine origin, are well developed mostly on the Paleozoic and partly on the Upper Cretaceous rocks in Arauco-Concepción region. The Tertiary sedimentary basin occupies an extensive area including offshore, from Tomé through the Arauco-Lebu coal field to Mocha Island, known from petroleum exploration. The Paleocene coal-bearing Cranilahue Formation occupying the basal part of the Tertiary, yields a number of well-preserved leaf fossils, which were described by Engelhardt (1891, 1905) and Berry (1922) and supplemented by Florin (1940) and Halle (1913, 1940). Many conifers and dicot leaves were also collected from the Lota coal mine in this area. This leaf flora shows a tropical aspect, including palms and many species of the Apocynaceae, Flacourtiaceae, Lauraceae, Leguminosae, Myrtaceae, Rubiaceae and Rutaceae. No fossil leaves of *Nothofagus* have been ever found in this leaf flora.

Recent palynological investigations on the Upper Cretaceous and Tertiary rocks have been reported by Martínez & Frutos (1968), Doubinger (1972), Doubinger & Chotin (1975) and Takahashi (1977a) for the Arauco-Lebu field, and by Takahashi (1977b) for Quiriquina Island off Concepcion. All these palynological investigations clearly indicate that *Nothofagus* pollen first appears in the Middle Eocene Trihueco Formation and later in the Upper Cretaceous and Tertiary sequence of the Arauco-Concepcion basin.

Some silicified woods of *Nothofagus* were recently described by Nishida (1984) from the basal part of the Tertiary in Quiriquina Island and the Tertiary of the southernmost end of Mocha Island southwest off Concepcion. All these wood-bearing formations are of marine origin, but an accurate age for them has not yet been determined.

Magellan Region

The Magellan region occupies the southern end of South America, including a number of large and small islands. In the Magellan sedimentary basin thick Cretaceous and Tertiary sediments overly Jurassic pyroclastic rocks. Some of these sediments have many intercalations of brown coals, while some of the Upper Cretaceous marine deposits contain oil-producing rocks. Cretaceous and Tertiary stratigraphy of this basin was comprehensively described by Feruglio (1945—1950) along with paleontological work, and recently summarized by Natland et al. (1974) with microfaunal divisions and by Empresa Nacional del Petroleo Chile (1978) with a compiled geologic map. Paleobotanical investigations of this region, although started first at the end of last century, have been slow to progress. Leaf floras from the Cretaceous and Tertiary are known from three horizons: the Maastrichtian Dorotea Formation, the Oligocene-Miocene Mina Chilena and Loreto Formations, and the Miocene Brush Lake Formation.

A Maastrichtian leaf flora has been described from the Dorotea Formation exposed on the top of Cerro Guido northwest of Puerto Natales, by Hauthal (1899), Kurtz (1902), Menendez (1972) and Hünicken (1971). Many fossil leaves were also collected in Cerro Guido with assistance of Dr. Nishida and others in 1979. The Cerro Guido flora consists of ferns, conifers and many dicot species, but contains no leaf remains of *Nothofagus*.

Oligocene-Miocene and Miocene plants are commonly found from the coal-bearing deposits, that are distributed principally along the strait of Magellan. Since these plants were first described by Engelhardt (1891) and Dusén (1899), there have been few further paleobotanical investigations except for those on palynomorphs. Many leaf fossils from several localities near Punta Arenas and in Tierra del Fuego were collected during this study. Earlier works and the present collection indicate that *Nothofagus* diversified with many species in the Magellan region during Oligocene to Miocene age. Leaf floras of the Loreto, Mina Chilena and Brush Lake Formations consist of many dicots species such as *Drimys*, *Laurelia*, *Lomatia*, *Maytenis*, *Nothofagus* and others. Of these dicots *Nothofagus* leaves are especially abundant, and they occupy more than 70 to 80 per cent of each collection in some localities. The flora including many leaves of *Nothofagus* was described from coal-bearing deposits of Rio Turbio, southern Santa Cruz, Argentina (Berry, 1937c; Frenguelli, 1941; Hünicken, 1966). These coal-bearing deposits seem to represent a northeastern extension of the Mina Chilena Formation, that develops in Ultima Esperanza, Chile. Actually the Rio Turbio flora is very similar to that of the Loreto Formation in its components.

Palynological investigations on the Cretaceous and Tertiary rocks in the Magellan region has recently been done by various authors although age determination and stratigraphic correlation are not always sufficient. Cretaceous pollen of *Nothofagus* was described from the Maastrichtian Dorotea Formation of Ultima Esperanza and the Maastrichtian Rocaloz (Rio Blanco) Formation of the Brunswick Peninsula (Romero, 1973; Archangelsky & Romero, 1974; Menendez & Filice, 1975), though frequency of occurrence is low. It is noteworthy that the Maastrichtian Dorotea Formation rarely

contains *Nothofagus* pollen, although no record of *Nothofagus* leaves exists. *Nothofagus* pollen, although uncommon, was recorded from the Early Eocene Agua Fresca Formation (Katz, 1961) and the Late Eocene Lena Dura Formation (Cookson & Cranwell, 1967), while it abundantly occurs in the Oligocene-Miocene Loreto Formation (Fasola, 1968) and its northern equivalents (Archangelsky & Romero, 1974; Romero, 1973), that also yield a number of *Nothofagus* leaves. Fossil woods of *Nothofagus* (*Nothofagoxylon*) were also described from the Loreto Formation and its equivalent (Kräusel, 1924; Boureau & Salad, 1960).

Northern and Central parts of the Argentine Patagonia Region

Except for the Magellan region and southern Santa Cruz province described above, Late Cretaceous and Tertiary floras have been reported from many localities of Rio Negro, Chubut and northern Santa Cruz provinces of Argentina. Most of these leaf floras were described by Berry (1925, 1928, 1932, 1937a-c, 1938) Frenguelli (1953) and Fiori (1931, 1939, 1940), based on specimens collected by Argentine geologists. The stratigraphical relationships of these leaf floras, however, have unfortunately not been well documented.

According to Fergulio's (1949) comprehensive work, these leaf floras in the Argentine Patagonia region were divided into three groups by floral composition. The first group is of Late Cretaceous time. Three floras were described in the region of central Santa Cruz between Rio Chico and Rio Santa Cruz (Berry, 1928, 1937; Frenguelli, 1953); though composed mainly of dicot leaves, they contain no *Nothofagus*. The second group contains fossils from the Riochican (Late Paleocene) to Colhuehuapian (Late Oligocene). The Cerro Mirador flora of Chubut (Berry, 1925) and Rio Pichileufu flora of Rio Negro (Berry, 1938) show a subtropical aspect, and contain no *Nothofagus* although dicot leaves are very abundant. These two floras are closely similar in composition and components to the Paleocene flora of the Arauco coal field of central Chile; they may be dated as Late Paleocene in age, although Menendez (1971) considered them to be of Eocene age. Besides these floras there are three others included in the second group by Fergulio: the Canadon Hondo (Berry, 1932) and Cerro Funes (Berry, 1937) near Rivadavia and a flora from the middle course of Rio Deseado (Fergulio, 1949) in Chubut. These three, though very poor in composition, contain *Nothofagus* leaves, and may be younger than the above two subtropical Paleocene floras. Fergulio's (1949) third group is composed of Late Oligocene to Miocene floras (Patagoian to Santacrucian in age), that are commonly known in southern Santa Cruz and Rio Negro provinces. Leaf floras from several localities near Lago Nahuel Huapi (Berry, 1928; Fiori, 1931, 1939, 1940) show a rather temperate aspect including *Nothofagus* leaves, and are probably contemporaneous with the *Nothofagus*-bearing floras of the Magellan and southern Santa Cruz regions. Fossil wood of *Nothofagus* is rare in Argentine Patagonia except for one report from the Upper Tertiary of Rio Negro (Cozzo, 1950a, b), although it was expected considering the common occurrence of pollen and leaves.

Late Cretaceous and Tertiary palynology of Argentine Patagonia has been investigated mainly by Archangelsky (1973a, b) and Archangelsky & Romero (1974a, b). The stratigraphical distribution of *Nothofagus* pollen in the Upper Cretaceous and Tertiary was summarized by Archangelsky & Romero (1974b), who reported *Nothofagus* pollen from Maastrichtian Jaguel Formation of Rio Negro, the Paleocene Salamanoca, Bororo and Rio Chico Formations of Chubut. Tertiary deposits of the Argentine Patagonia region excluding the Magellan region, are sporadically distributed in the wide Pampas area, and no continuous section has been confirmed. Stratigraphical relationships of the plant-bearing deposits need to be investigated further in combination with the mammalian faunal sequence, that has been well established recently with radiometric dating (Marshall et al., 1977, 1981).

The Falkland Plateau

The Falkland Plateau occupied an area west of the Scotia Arc that was presumed to be partly an archipelago or isthmus between the southern tip of South America and the Antarctic Peninsula by at least the Early Cretaceous (Dalziel & Elliot, 1973; Barker & Barrell, 1977). Recent works of the Deep Sea Drilling Project (Legs 25 and 71) indicated Upper Jurassic (Oxfordian) to Lower Tertiary (Eocene) sediments on the Falkland Plateau, west of the Falkland Islands. Pollen assemblages were found at three sites from the Neocomian-Upper Paleocene, site 327 and the Maastrichtian, site 328 (Harris, 1977), and from the Upper Eocene, site 511 (Bratzeva, 1983). In these three sections *Nothofagus* pollen of the *brassii* group was found from the Maastrichtian, and those of the *fusca* and *menziesii* groups from the Upper Eocene were found by Harris (1977) and Bratzeva (1983). Late Cretaceous palynomorphs are very similar to those from Australia, while Late Eocene palynomorphs are generally related to those of southern South America. Compared to Cretaceous rocks, Tertiary sediments contain increasingly abundant organic matters of terrestrial origin. This fact shows a shallowing sea or an increase in runoff from some land source during the early Tertiary (Harris, 1977).

West Antarctic Region

The geographical distribution of past plants and animals in Antarctica is increasingly exciting. What a role Antarctica did play in the past biogeographic history of the southern hemisphere? Western Antarctica is now most close to the vegetated land, the southern tip of South America, and it occupies an important position in reference to the above question. Thus, the fossil record of this region has attracted renewed interest in the biogeographic history of Antarctica and southern South America.

The first paleobotanical collections from western Antarctica were by the Swedish South-Polar Expedition (1901—1903) from Mesozoic (Jurassic) and Tertiary deposits of the Antarctic Peninsula and its neighbouring islands. Based on these collections, many Tertiary conifers and dicots were described from Seymour and Snow Hill Islands (Dusén, 1908; Gothan, 1908; Florin, 1940), and these fossil records have been important contributions to the knowledge of antarctic Tertiary vegetation. Recent

paleobotanical collections have come from the South Shetland Islands, principally from King George Island, by many scientific expeditions from Argentina, United Kingdom, the United States and Poland. These Tertiary dicot leaf fossils were described by Barton (1964), Orland (1964) and Zastawniak (1981), while pollen fossils were by Cranwell (1959) and Stuchlik (1981).

One Tertiary flora from Seymour Island (Dusén, 1908) is composed of conifers and various dicot leaves of the Aquifoliaceae, Cunoniaceae, Fagaceae, Lauraceae, Melastomaceae, Monimiaceae, Myricaceae, Proteaceae, Winteraceae and others. These dicot leaves include many characteristic South American genera such as *Caldcluvia*, *Drimys*, *Knightia*, *Laurelia*, *Lomatia* and *Nothofagus*. Judging their occurrence from Dusén's report, *Nothofagus* represented by four species seems to have been a rather uncommon member on this island at that time. Two types of *Nothofagus* pollen were reported from Dusén's rocks by Cranwell (1959), associated with conifer pollen of the Podocarpaceae and Araucariaceae, and many fern spores. Silicified wood of *Nothofagus* was also described from Seymour Island by Gothan (1908).

Tertiary leaf floras from King George Island are composed of ferns, conifers (Podocarpaceae and Araucariaceae) and several dicots (Anacardiaceae, Dilleniaceae, Fagaceae, Monimiaceae, Sapindaceae, Proteaceae and Sterculiaceae); these floras are generally similar to the Seymour flora in composition and component, although the plant fossils reported from several localities by Barton (1964), Orland (1964), and Zastawniak (1981) may not represent a flora of the same stratigraphic horizon. *Nothofagus* leaves are commonly found at Point Hennenquin (Barton, 1964; Zastawniak, 1981; Zastawniak et al., 1985), where the Point Hennenquin Group is exposed (Birkenmajer, 1980). On the other hand, the plants from Ardley Island (peninsula) do not include *Nothofagus* (Orlando, 1964). This plant-bearing rock, however, has uncertain stratigraphic relationships with the Point Hennenquin Group. Stuchlik (1981) described many pollen grains (the *fusca* and *brassii* types) of *Nothofagus*, associated with a number of fern spores, from the Ezcurra Inlet Group at Admiralty Bay. This group is older stratigraphically than the Point Hennenquin Group (Birkenmajer, 1980, 1981a, b).

The age of Tertiary leaf- and palynomorph-floras from western Antarctica have usually been discussed on the basis of comparison with those of South America, New Zealand and Australia, and especially the Patagonian region of South America. Because of uncertain stratigraphic relationships with marine or mammalian fossils, the plausible age assignment of these floras has been disputable. The Seymour flora was originally described as Middle Tertiary in age by Dusén (1908), and supported by Barton (1964), while it was considered to be of Early to Middle Miocene age by Orlando (1964) who compared with the Ardley flora. On the other hand, Cranwell (1959, 1963, 1964) maintained that the palynoflora of Seymour Tertiary rocks was, in all probability, of Early Tertiary age.

Recent geological and paleontological investigations by many authors have provided much information about the Late Cretaceous and Tertiary sequence in western Antarctica. A review by Zinsmeister (1982) on stratigraphy and by Woodburn &

Zinsmeister (1984) on age and correlation have been presented, although no new evidence of plant fossils, except for dinoflagellates (Hall, 1977), has been added to previous work. According to Elliot & Trautman (1982) and Woodburn & Zinsmeister (1984), Tertiary deposits overlying the Cretaceous are divided into two Formations, the La Meseta and the Cross Valley in descending order. Judging from the description of Woodburn & Zinsmeister (1984), the plant fossils described by Dusén (1908) were probably collected from the lower part of the La Meseta Formation, while the pollen-bearing samples investigated by Cranwell (1959) were collected from the Cross Valley Formation.

Evidence from various taxa of marine vertebrate, invertebrate and dinoflagellate fossils indicates that the La Meseta Formation is of Late Eocene age except for its uppermost part of the Earliest Oligocene and that the Cross Valley Formation is Paleocene in age (Woodburn & Zinsmeister, 1984). An unconformity observed between these two Formations may be consistent with a hiatus between the Paleocene and the Upper Eocene. Thus, we can conclude that the *Nothofagus* leaf-bearing flora of Seymour Island (Dusén, 1908) is probably of Late Eocene age, while *Nothofagus* pollen-bearing rocks (Cranwell, 1959) are of Paleocene age. Palynomorphs from the Cross Valley Formation include many fern spores that are presumed to be recycled specimens from the underlying Cretaceous (Senonian) rocks (Cranwell, 1959). Accordingly, some of *Nothofagus* pollen may be redeposited from the Upper Cretaceous. It is noteworthy that Hall (1977) described occurrences of *Nothofagus* pollen with microplankton of Late Cretaceous forms from the Upper Cretaceous deposits of limited exposure at the northern end of this island. This small exposure was tentatively correlated with the typical Sobral Formation of Maastrichtian age in lithology (Zinsmeister, 1982). A further palynological investigation is needed to confirm whether or not *Nothofagus* pollen is present in the Cretaceous sediments of Seymour Island.

Although extensively investigated by Argentine, British and Polish expeditions, Tertiary stratigraphy and correlation of King George Island have not yet been fully clarified. The *Nothofagus* leaf-bearing flora described by Zastawniak (1981) was found in the moraine of Admiralty Bay that comes from the Point Hennequin Formation, preliminary dated as Lower-Middle Miocene age (Birkenmajer, 1980). This leaf flora is very depauperate, and it is impossible to compare it with the leaf floras of Seymour Island and the Magellan region. *Nothofagus* pollen-bearing palynoflora of the Ezcurra Inlet Group was dated as Late Eocene-Early Oligocene age (Stuchlik, 1981). This is consistent with the fact that the Ezcurra Inlet Group is stratigraphically lower than the Point Hennequin.

Recycled pollen grains of *Nothofagus* were reported from seafloor sediments of the Weddell Sea, east of the Antarctic Peninsula (Truswell, 1983). This *Nothofagus* pollen is considered to be of Late Cretaceous or Paleocene in age, but the exposed source rock has not been confirmed.

Fossil angiosperm leaves were recently discovered from the presumed Tertiary volcanic sequence in the eastern Elgar Uplands (70° S. lat.) of northern Alexander

Island, that is west off the Antarctic Peninsula (Thomson & Burr, 1977). These fossil leaves are unfortunately too ill-preserved to identify with certainty. However, so far as is seen in illustrated figures (Thomson & Burr, 1977), some leaves appear to be similar to those of *Nothofagus* in marginal serration and secondary venation features. They are especially close to *N. subferruginea* that is redefined in this paper. If these are true *Nothofagus*, they represent the most southern record among the previously reported fossil leaves of *Nothofagus*.

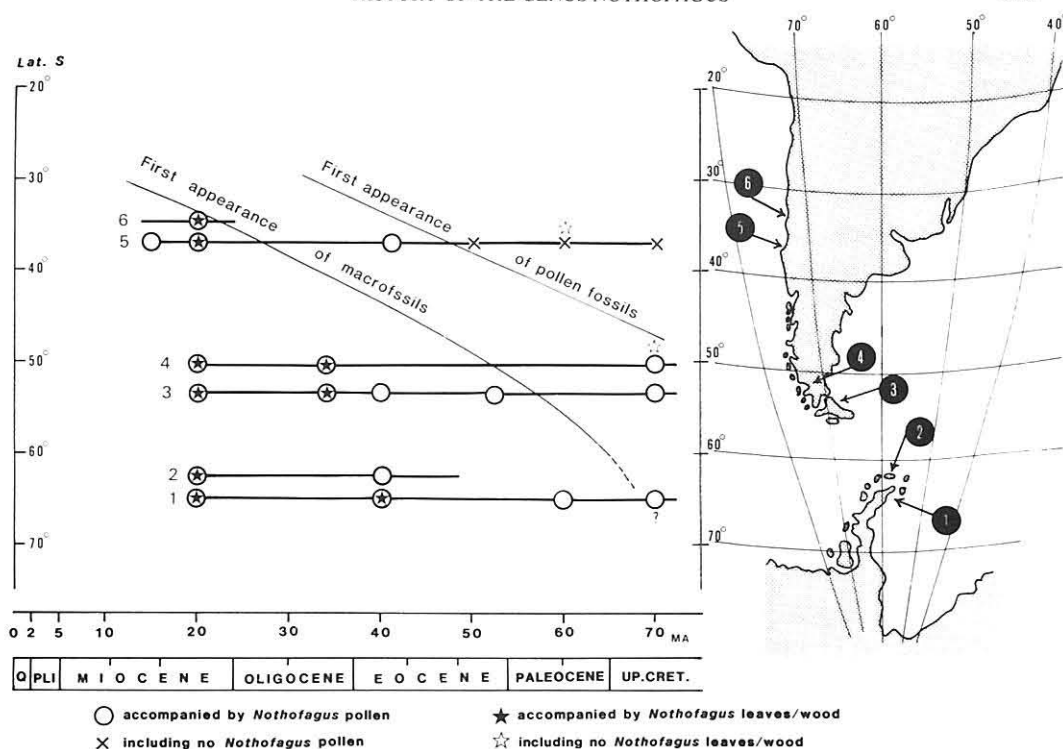
Considering paleobotanical investigations together with stratigraphy, *Nothofagus* in western Antarctica is concluded to be recorded from the Upper Eocene to Lower Miocene(?) by leaves, and from the Paleocene to Lower Oligocene(?) by pollen. A further investigation may confirm the presence of Late Cretaceous pollen of this genus in western Antarctica.

Distributional Relationships of *Nothofagus* in Time and Space

In order to understand the relationships of stratigraphic and latitudinal distribution, *Nothofagus* fossil localities and their sequential occurrence in southern South America and western Antarctica have been plotted in relation to time and space, as shown in Text-fig. 10. From this figure are excluded several localities of uncertain age or of no sequential occurrence in the Argentine Patagonian region, where *Nothofagus* leaves or pollen are recorded. Although the fossil record is not always complete, *Nothofagus* pollen is known from the Upper Cretaceous through the Miocene in the Magellan region and southward, while its leaves or wood are first known in the Upper Eocene or Lower Oligocene. On the other hand, in central Chile (about 40°S. lat.) *Nothofagus* pollen appears first in the Late Eocene and its macrofossils are first known in the Early Miocene. Such discrepancies of first occurrence of micro- and macrofossils in time and space are clearly shown in Text-fig. 10, suggesting that *Nothofagus* in South America dispersed northward from the southern region, probably from western Antarctica.

Accumulation of recent geological and geophysical evidence from both land and the ocean floor suggests a past land connection of South America and western Antarctica by Late Cretaceous time, although some different paleogeographic models have been proposed by many authors (Dalziel & Elliot, 1973; Barker & Barrell, 1977; Harrison et al., 1979; others). A marsupial mammal fossil (Polyplodidae) was very recently discovered from the Late Eocene La Meseta Formation of Seymour Island (Woodburn & Zinsmeister, 1982). This fossil evidence adds weight to the idea that the Antarctic Peninsula was connected to the southern tip of South America as the dispersal route of land mammals by the Early Tertiary (Woodburn & Zinsmeister, 1984). The Antarctic Peninsula might have been a long and narrow area such as a land bridge, that made it possible for *Nothofagus* to travel northward during Late Cretaceous to Early Tertiary time.

Text-fig. 10 points out another important problem; *i.e.*, that the first fossil records of macrofossils are later than those of pollen both in northern and southern regions. Such similar occurrence of *Nothofagus* leaves and pollen was pointed out in the Ter-



Text-fig. 10 Distributional Relationships of *Nothofagus* in Time and Space in South America and Western Antarctica.

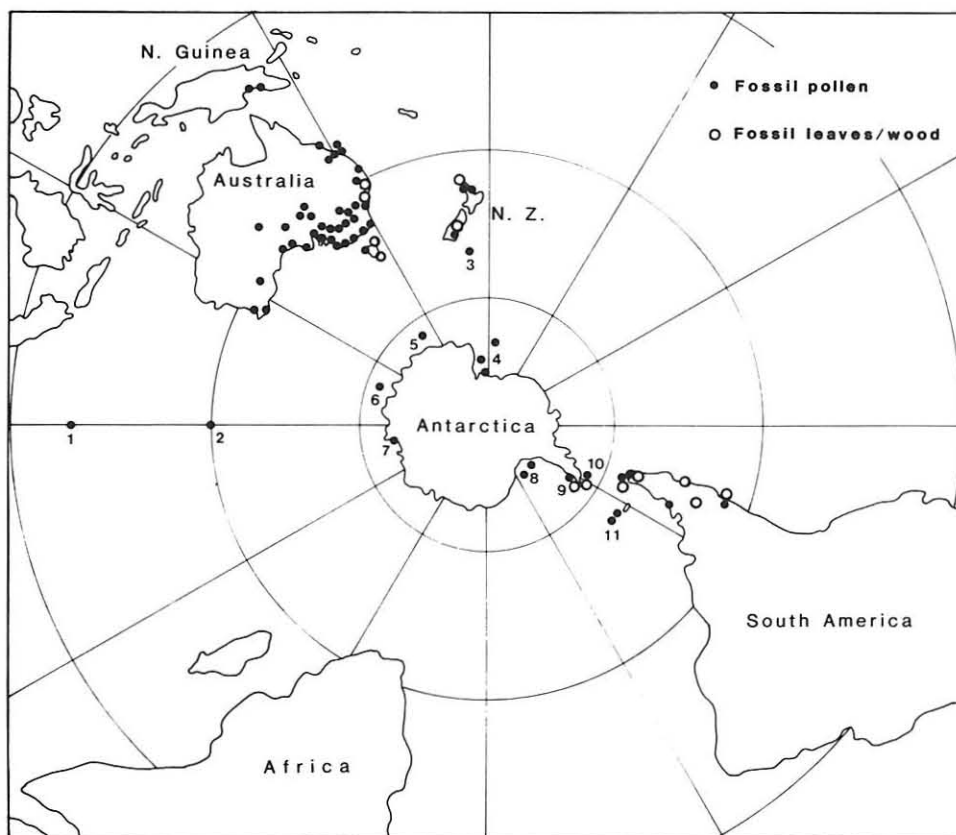
1. Seymour Island 2. King George Island 3. Fuego Island 4. Magellan region and southern Santa Cruz region 5. Concepcion-Arauco region in Chile 6. Matanzas coastal area in central Chile

tiary of Australia (Christophel, 1981; Hill, 1983). The usual reason given for this is that *Nothofagus* produces a prodigious amount of wind-dispersed pollen that can enter depositional sites over a great distance beyond the range of potential macrofossils (Dadson, 1976). Considering the latitudinal difference of distribution during Late Cretaceous and Early Tertiary time, northward dispersal of *Nothofagus* probably started by the Early Tertiary through the Antarctic Peninsula that consisted of a narrow range of mountains extending northward to the Andean mountain range. The lack of Late Cretaceous to Early Eocene megafossils in the Magellan region may indicate that *Nothofagus* inhabited the mountainous areas at that time. *Nothofagus* leaves in the Oligocene-Miocene of the Magellan region occupy more than 80 per cent of the total specimens in each locality along with specific diversity, while they are rather minor component in the Miocene of central Chile with only two species. These leaf-bearing deposits both in the Magellan and central Chilean regions are of neritic, even littoral origin, including many marine shells and frequent coal intercalations. These facts clearly show that *Nothofagus* dispersed northward since Late Eocene age, and that it gradually occupied the lowland adjacent to the sea, where plant remains such as leaf and wood easily entered the neritic sediments. The northward dispersal of *Nothofagus* is also consistent with the considerable cooling of temperatures since Late

Eocene time, as was indicated by subantarctic sea-water by Shackleton & Kennet (1975).

Past Distribution of *Nothofagus* in the Southern Hemisphere

Besides South America, *Nothofagus* fossils have been found from Australia and New Zealand, and a few from eastern Antarctica, New Guinea and Deep-Sea Drilling cores on the Ninetyeast Ridge and the Campbell Plateau. Most fossils are pollen, and, in contrast, leaf fossils are rare. Fossil pollen from the Upper Cretaceous and Tertiary deposits has been especially well investigated in Australia and New Zealand by various authors. Areal records of fossil *Nothofagus* in the southern hemisphere, including the above-discussed South America, are shown in Text-fig. 11.



Text-fig. 11 Distribution of *Nothofagus* Fossils in the Southern Hemisphere, based on Pollen, Leaves and Wood.

1. Ninetyeast Ridge (DSDP site 214) 2. Ninetyeast Ridge (DSDP site 254) 3. Campbell Plateau (DSDP site 275) 4. Ross Ice Shelf 5. Off George Land (DSDP site 269) 6. Off Wildes Land (DSDP site 268) 7. West Ice Shelf 8. Weddell Sea (recycled specimens) 9. Seymour Island 10. King George Island 11. Falkland Plateau (DSDP sites 327, 328, 511)

Pollen or leaf fragments of *Nothofagus* have sometimes been reported from the Upper Cretaceous or the Tertiary of the northern hemisphere as discussed in earlier. Most of them are, however, rejected or questioned by many later workers; all of the pollen of *Nothofagus* from the northern hemisphere is now excluded here.

Australia and Tasmania

Paleobotanical studies of the Tertiary are principally palynological for both surface and borehole rocks in Australia and Tasmania. These works that were pioneered by Cookson and her school, were reviewed in respect to Tertiary dicot pollen, associated with the location and age of the pollen-bearing sediments (Cookson & Pike, 1954). However, fossil pollen of *Nothofagus* was discussed in other papers (Cookson, 1946, 1959). Since the 1960's *Nothofagus*-bearing palynofloras from the Tertiary and the Upper Cretaceous have been published by many authors (Harris, 1965; Dettmann & Playford, 1969; Stover & Partridge, 1973; Hos, 1975; Martin, 1977; Tulip et al., 1982; and others). Martin (1978, 1982) especially reviewed the Tertiary palynofloral change of Australia, and described Tertiary *Nothofagus* that was widespread in eastern and southwestern Australia beyond its modern distribution, showing most abundant occurrence during Late Eocene to Early Oligocene age. Late Cretaceous *Nothofagus* pollen was confirmed in the Gippsland basin of southeastern Australia (Stover & Partridge, 1973; Dettmann & Playford, 1968, 1969). Of three groups of *Nothofagus* pollen grains, the *brassii* type pollen first appears in the Upper Cretaceous, the *fusca*-type appears in the Middle Paleocene and the *menziesii* type joined them in the lower Middle Eocene (Martin, 1982). Pollen grains of these three groups were dominant fossil forms in Early Oligocene to Early Miocene palynofloras, but those of the *brassii* type disappear in the Pliocene.

Compared with the common occurrence of pollen, leaves of *Nothofagus* have been scarcely known from the Tertiary of Australia. Ettingshausen (1888, 1891, 1895) claimed the presence of northern beech (*Fagus*) in the Tertiary and the Upper Cretaceous of New South Wales, although he compared some of his fossils with those of *Nothofagus*. Judging from his illustrated figures, most of these fagaceous leaves are doubtfully referred to the genus *Nothofagus*, and only two species described as *Fagus etheridgei* and *F. muelleri* from the Oligocene(?) of New South Wales may be probable *Nothofagus*. Following Ettingshausen's work there have been unfortunately few investigations of Tertiary leaves from Australia until the 1970's, and no fossil leaves of *Nothofagus* were recorded in the Eocene floras of southeastern Australia that are well studied (Christophel & Blackburn, 1978; Christophel, 1981; Hill, 1982). The first discovery of doubtless leaves of *Nothofagus* was from the Early Eocene-Oligocene to Miocene deposits of Tasmania by Hill (1983a, b; 1984). Based on anatomical comparisons, he believed that these Tertiary leaves are similar to the extant *Nothofagus fusca*, *N. moorei* and *N. cunninghamii*. Although the megafossil record is still incomplete, the first appearance of *Nothofagus* leaves in southeastern Australia is late than its pollen record that was dated as Late Cretaceous or Paleocene age.

New Zealand

Similar to the case of Australia, Cenophytic investigation in New Zealand has been mostly done by palynology which was pioneered by Cranwell. As reviewed by Cranwell (1963), Couper (1960a, b) and Mildenhall (1980), stratigraphic distribution of *Nothofagus* pollen was well known in New Zealand: the *brassii* and *fusca* type groups appear together in the Upper Cretaceous, and the *menziesii* type joined them in the Middle Oligocene. The *brassii* type pollen whose extant lineage trees are usually considered not to be native to New Zealand, was found there until the Pleistocene (Couper, 1960b).

Macrofossils of *Nothofagus* have been rarely found in New Zealand (Oliver, 1950). All the leaves described as *Fagus* from the Tertiary of North or South Islands by Unger (1864), Ettingshausen (1891a, b) and Pensler (1930), seem difficult to refer to either *Fagus* or *Nothofagus*, because the illustrated figures are too incomplete to compare with modern leaves. The first fossil record of *Nothofagus* leaves was reported from the Upper Miocene of Otago by Oliver (1936); only one species, *N. kairoraiensis*, which is represented by finely serrate margined leaves, is similar to leaves of the extant *N. alpina* and *N. glauca* of South America, but needs to be reinvestigated for venation characters. Several fagaceous leaves from same locality of Otago were described as *Fagus* and *Parafagus* by Oliver (1936); some of them are probably referable to *Nothofagus*. For instance, leaves of *Fagus novae-zealandica*, *F. australis* and *F. maorica* are closely similar to those of *Nothofagus alessandri* living in Chile, while some leaves of *Parafagus* appear to resemble those of *N. procera* living in Chile. However, the original specimens of these fagaceous leaves should be further reinvestigated for their generic relationships. Two leaves of *Nothofagus* with entire margins and looped secondary veins were reported from the Plio-Pleistocene of North Island (McQueen, 1954). These leaves may be similar to those of the extant *N. solandri* of New Zealand or some of the tropical species from New Guinea and New Caledonia, but they need to be further reinvestigated in detail.

Recently an important contribution was made to the macrofossils of *Nothofagus* in New Zealand. Four species were described from the Upper Miocene and Pliocene of Murchison, South Island (Holden, 1981). All the fossil leaves illustrated seem to show a close resemblance to those of the extant species of New Caledonia in margin and venation characters as discussed by Holden (1982). Leaves described as *Nothofagus novae-zealandica* by him, however, seem different from Oliver's specimens in number of secondary veins and marginal teeth, and may rather be included in *N. bidensis* Holden. It is noteworthy with respect to the phytogeographic history that some Late Tertiary macrofossils in New Zealand show a similarity to New Caledonian species such as *N. discoidea*, *N. balansae* and *N. aequilateralis*. No recent work has been published on the pre-Miocene megafossils, and further investigation is needed to trace *Nothofagus* leaves back to the Paleogene of New Zealand.

Eastern Antarctic Region

It is still not certain that Antarctica was the cradleland or corridor for dicots of the

present forests in southern continents which are now separated. The first dicot fossils from eastern Antarctica were found from the *Nothofagus* pollen bearing erratics in Mina Bluff, McMurdo Sound (Cranwell et al., 1960; Cranwell, 1964a), and later in Black Island, McMurdo Sound (McIntyre & Wilson, 1966; Wilson, 1968). Both localities are north of the Ross Ice Shelf. Here *Nothofagus* pollen is composed of the three groups: the *brassii*, *fusca* and *menziesii* types. These erratics including *Nothofagus* are of Late Eocene age, based on pollen floral composition and accompanying microplankton. Recycled *Nothofagus* pollen grains were also reported widely from the surface sediments of the Ross Sea (Wilson, 1968), and from glaciomarine sediments in the vicinity of the West Ice Shelf (Kemp, 1972). Recycled fossils are spores, pollen and microplankton, which were derived from erosion of the Permian, Cretaceous and Tertiary rocks. *Nothofagus* pollen was presumed to be derived from the Upper Eocene (Kemp, 1972). Recycled palynomorphs in the seafloor sediments of East Antarctica, from the Ross Ice Shelf via the Schackleton Ice Shelf to the West Ice Shelf, were recently reviewed by Truswell (1983). These pollen and spores are largely of Late Jurassic to Tertiary in age, and they include the three type pollen of *Nothofagus* in many sites.

The age of microfossil assemblage based on recycled specimens is not always easy to interpret accurately, unless most of specimens are concentrated in the known limited ranges. A Late Cretaceous to Early Tertiary palynomorph assemblage of the Ice Shelf described by Kemp (1972) is composed principally of Senonian-Late Eocene pollen and Eocene microplankton, and is derived largely from the Upper Eocene rocks as inferred by Kemp (1972). On one hand, this assemblage includes some older pollen such as *Proteacidites ambolesexinus* Dett. & Play. and *Gambierina edwardsii* (Cook. & Pike) Harris, that are limited to the Senonian to Paleocene in Australia and New Zealand (Stover & Partridge, 1973; Couper, 1960b). The assemblage of the Ice Shelf contains three of the groups of *Nothofagus* pollen, some of whose grains, especially the *brassii* and *fusca* types, are confirmed back to the Paleocene or even to the Upper Cretaceous in Australia and New Zealand. So far as can be judged from the assemblage that was described by Kemp (1972), *Nothofagus* pollen probably extends back to the Upper Cretaceous in the Ice Shelf.

The recent works of the Deep Sea Drilling Project (Leg 28) on bottom sediments of periglacial origin under the Ross Sea confirmed a Late Oligocene flora containing *Nothofagus* pollen, that seems likely to be *in situ* (Kemp & Barrett, 1975). This pollen assemblage is similar to those of the McMurdo Sound erratics. It is suggested that a *Nothofagus* forest appears to have persisted without any considerable change during Late Eocene to Late Oligocene time in eastern Antarctic region.

New Guinea

The fossil record in New Guinea should play an important role in the phytogeographic discussions of the genus *Nothofagus*, because all the extant species of this island have the *brassii*-type pollen that has been considered to be older than the other two types by palynologists. However, there have been unfortunately very few

paleobotanical investigations of the Upper Cretaceous and Tertiary of New Guinea. Fossil *Nothofagus* pollen of the *brassii*-type was first reported from the Pliocene and onward in this island by Couper (1960b). Recently abundant pollen grains of this genus, along with many tropical genera of dicots, were reported in borehole cores drilled in the Central Delta region of Papua (Khan, 1974, 1976). The *brassii*-type pollen commonly occurred there from the upper-Lower Miocene through the Pleistocene, and is especially abundant during the Lower Pliocene. A few grains of the *fusca*-type pollen were also found in the Pliocene; but it is probable that they derived by long-wind-dispersal from Australian trees at that time (Khan, 1974). No further investigation has been done for the pre-Miocene rocks in New Guinea.

Other Regions

Five species of *Nothofagus* are living in New Caledonia today, where a fossil record has naturally been expected, considering the geological history of this island. However, there have been no paleobotanical studies in New Caledonia up to the present.

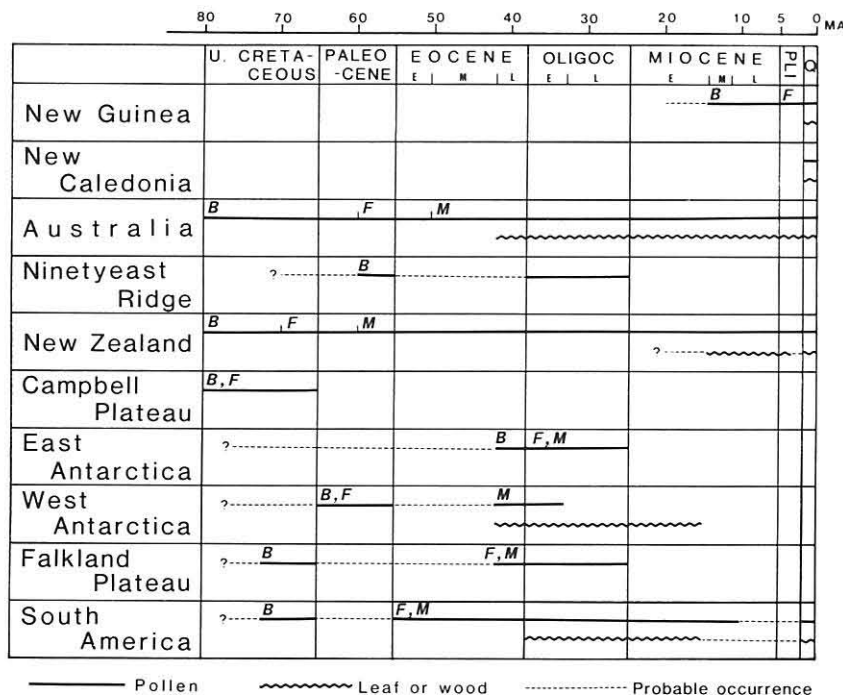
Recent works of the Deep Sea Drilling Project (Leg 22) confirmed the sediments of Paleocene through Pliocene age on the crest of the Ninetyeast Ridge. Pollen assemblages were found at two sites, from the Paleocene, site 214 (Kemp, 1974) and the Oligocene, site 254 (Harris, 1974). These two palynomorph assemblages include *Nothofagus* pollen, although extremely rare. Most of these palynomorphs are composed of ferns, conifers and angiosperms which are closely related to Tertiary elements of Australia or New Zealand. Indian or Indomalaysian Tertiary elements are very few. Considering this floristic composition together with recent geological and geophysical information, Kemp & Harris (1975) concluded that sites of the Ninetyeast Ridge were oceanic islands closer to a southern landmass during Early Tertiary time.

In another drilling site 275 on the southeastern Campbell Plateau *Nothofagus* pollen occurs from the Upper Cretaceous; and this pollen assemblage is very similar to assemblages of southern New Zealand (Wilson, 1975). Upper Cretaceous sediments of site 275 are of marine origin, but were deposited close to land since they contain much terrestrial plant debris.

On the Kerguelen Islands far south of the Indian Ocean (about 48°S. lat. and 68°E. long.) a leaf flora from the probable Lower Miocene lignite-bearing deposits have been reported. These plant remains include ferns, *Araucaria*, and fragmentary dicot leaves (Seward & Conway, 1934). No *Nothofagus* leaves have been confirmed. The palynomorph flora of the lignite also principally consists of fern spores, conifer pollen and a few angiosperm pollen grains (Mechkova, 1969). A single grain of *Nothofagus* pollen was recorded from two localities; however, it is questionable whether or not this grain was *in situ* in the islands.

Stratigraphic and Geographic Distribution in the Southern Hemisphere

The bibliographic survey that was reviewed above, summarizes the stratigraphic distribution of *Nothofagus* fossils in the southern hemisphere, as shown in Text-fig. 12. Similar to the case of South America discussed in an early section, fossil records of



Text-fig. 12 Stratigraphical Distribution of *Nothofagus* in the Southern Hemisphere.

The capital letters (B, F, M) show the first appearance age of each type pollen. B: *brassii*-type F: *fusca*-type, M: *menziesii*-type

Nothofagus pollen are known from the Upper Cretaceous through the Tertiary in Australia and New Zealand, while leaf fossils occurred first from the Eocene-Oligocene and upward. In eastern Antarctica only pollen from the Upper Oligocene rocks is presumed to be *in situ*. Furthermore, *Nothofagus* pollen is found widely from erratics and grab samples around the Ross Sea and the Ice Shelf, although these are confirmed to have been derived mainly from erosion of the Upper Eocene to Oligocene rocks. Its pollen is presumed to extend back to the Upper Cretaceous. Such palynological evidence in eastern Antarctica along with leaf and pollen fossils of western Antarctica suggests that a probable *Nothofagus*-bearing forest widely covered the Antarctica land-mass during Eocene-Oligocene time (Kemp, 1972; Kemp & Barrett, 1975), and that *Nothofagus* was likely native there even in Late Cretaceous time.

In contrast with the older occurrence and diversity of Australia, New Zealand and eastern Antarctica, pollen has only been known first in late-Early Miocene age with less diversity in New Guinea. Thus, the geographic and stratigraphic distribution of fossils from eastern Antarctica through Australia and New Zealand to New Guinea probably indicates that *Nothofagus* is southern in origin, and that it seems to have gradually dispersed northward, as in South America.

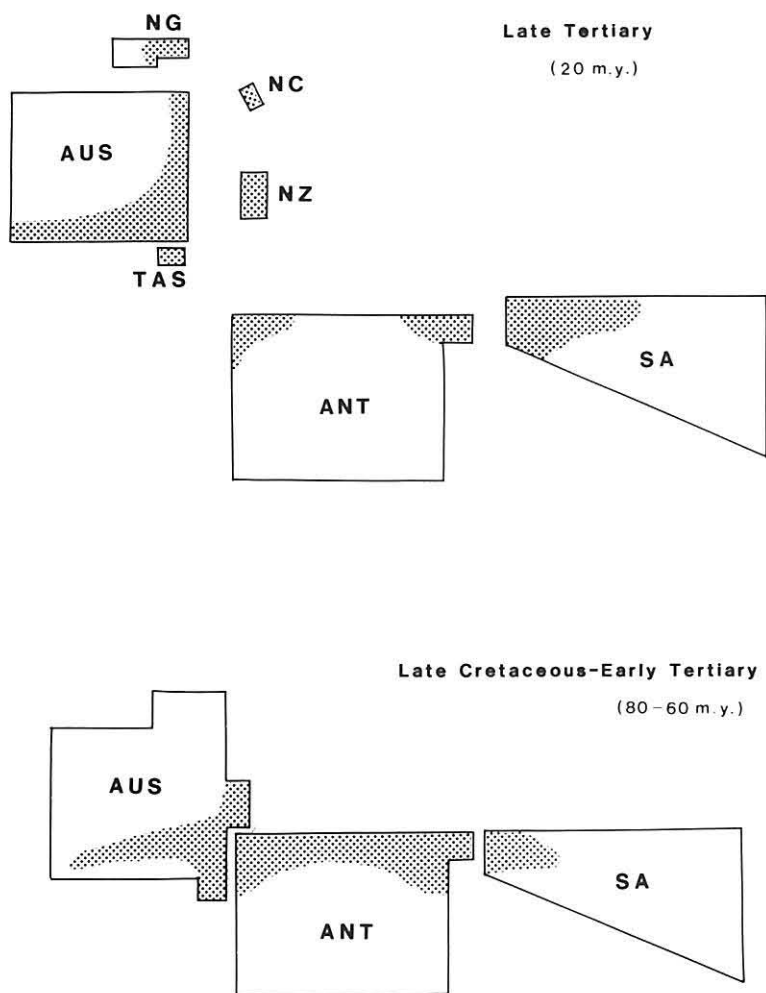
Both living and fossil pollen are divided into three types which have been considered to represent separate phylogenetic groups by palynologists. The *brassii* type pollen is produced from all the extant tropical species of New Guinea and New Caledonia, some of which are also believed to be primitive ones in cupule characters within this genus by Steenis (1954, 1971). It has been well shown through a number of palynological investigations that the first appearances of these three types were different on each continent or even within a continent. The northern origin theory of the genus *Nothofagus* well documented by Steenis (1971, 1972), was partly supported by the fact that the *brassii* type is usually older than the other two types in all regions of the southern hemisphere except for New Guinea. Such a fossil occurrence is consistent with the results of my bibliographic survey based on many recent paleobotanical information. Although paleobotanical investigation has been insufficient, the reason *Nothofagus* pollen has not been found from pre-Miocene rocks in New Guinea is unknown. Furthermore, it is puzzling that although fossil pollen of all the three types are widely recorded in Australia, New Zealand, Antarctica and southern South America, only the *brassii* type has been found since the Middle Tertiary of New Guinea. If Southeast Asia including New Guinea is the "cradle" of the genus *Nothofagus*, the above questions need to be answered through further investigation.

Age-determination of a pollen flora in geologically unknown region is based mainly on the correlation with the previously known range of pollen species. If the diversification or immigration rate of *Nothofagus* was different on each continent during the Tertiary, such methods for age assignment apt to produce unreliable conclusions. The age of all *Nothofagus*-bearing pollen floras have not always been cross-referenced by accompanying microfossils of other taxa. The fossil record shown in Text-fig. 12 suggests a differential development and migration within the genus *Nothofagus* in the southern hemisphere, although age determination of fossil floras has still been unsatisfactory in some regions. The *brassii* type appeared first in Late Cretaceous time was followed by the other two types in both Australia and South America. In New Zealand the *brassii* type was slightly older than the *fusca* type during Late Cretaceous time*, and was joined by the *menziesii* type in Early Oligocene time. The *brassii* type in both eastern and western Antarctica, is associated with the *fusca* type in first appearance, but this is probably due to lack of confirmed Late Cretaceous or early Tertiary sediments. The first appearance of the *fusca* type is in the Maastrichtian of New Zealand, and in the Paleocene or the Lower Eocene in other temperate regions except for eastern Antarctica where pre-Late Eocene rocks have not yet been confirmed. On one hand, the *menziesii* type is usually younger than the other two types in all regions, and its first appearance was different in age in each region. It is found in the Middle Paleocene of New Zealand, and in the Lower Eocene or Early Oligocene in most other regions. Furthermore, it is of interest to note that each pollen type is somewhat different in its occurrence even within Australia. In southeastern Australia the *fusca* type appears first in the Late Paleocene and the *menziesii* type appears in the Middle Eocene (Stover &

* According to Muller (1981), the *fusca* type pollen appears in the Maastrichtian, while the *brassii* type is recorded from the Campanian.

Partridge, 1973). On the other hand, the *fusca* type was recorded first from the Lower Eocene(?), but the *menziesii* type is absent through the Tertiary in southwestern Australia (Hos, 1975).

It is very significant that only the *brassii* type of *Nothofagus* pollen was found in the Paleocene (site 254) and Oligocene (site 214) on the Ninetyeast Ridge, which was formerly a group of oceanic islands situated further southward (Kemp & Harris, 1975). These palynofloras contain pollen grains of the Myrtaceae, Restionaceae, Proteaceae and others, all of which are not of a wind-dispersed origin. This fact suggests that *Nothofagus* migrated to the Ninetyeast Ridge region through a land-connection from a southern landmass during Late Cretaceous or Earlier Tertiary time. The post-



Text-fig. 13 Schematic Illustration of *Nothofagus* Distribution and Continental Rafting in the Past.
The dotted areas show probable distribution of *Nothofagus*, inferred from fossil record.

Paleocene sediments of southern site 254 and the post-late Oligocene of northern site 214 are composed entirely of calcareous ooze in contrast with the terrestrial or shallow sea sediments of Paleocene and Oligocene age of each section. The fossil record clearly indicates that the *fusca* and *menziesii* types did not occur on the Ninetyeast "oceanic islands" by Late Oligocene time, when the north-south trending ridge was whole submerged under the sea with a considerably northward shift.

By contrast, only the *brassii* type has been recorded from the post-Oligocene rocks in New Guinea, that is now nearly at same southern latitude as the Ninetyeast Ridge. Recent paleogeologic maps (Dow, 1977) show that the entire region of New Guinea is considered to have been under water during the Cretaceous, and that land areas appeared in the Late Eocene, separating northward from Australia. Thus, the absence of *Nothofagus* in New Guinea before Late Eocene age is consistent with the fossil record.

The accumulation of geological and geophysical evidence from both land and the ocean floor has postulated a renewed idea that the southern continents were once united into a major landmass, termed Gondwanaland, which subsequently fragmented into the present-day continents of the southern hemisphere, although the schemes presented by various authors are different in their age and position of displacement. The above discussion of the fossil record in the southern continents and on the ocean ridges and plateaus indicates that *Nothofagus* originated in the assembled southern continents, and then dispersal and diversification of *Nothofagus* progressed gradually northward (Text-fig. 13). Even considering the lack of an exact age for pollen floras, widespread *Nothofagus* is well represented in the pollen record with specific diversity in New Zealand, Australia, southern South America and even in Antarctica during Eocene to Early Oligocene time, where its diversification seems to have been different in time and space. It is noteworthy that the first record of leaf fossils in Tasmania, western Antarctica and South America corresponds with a time of considerable diversification shown by pollen. However, it should be further ascertained whether or not Cretaceous pollen referred to the *brassii* type is directly related to the extant tropical species of New Guinea and New Caledonia.

Morphological Relationships of Extant Species of *Nothofagus*

The distributional history of a certain genus of animals or plants must be compati-

Explanation of Plate 1

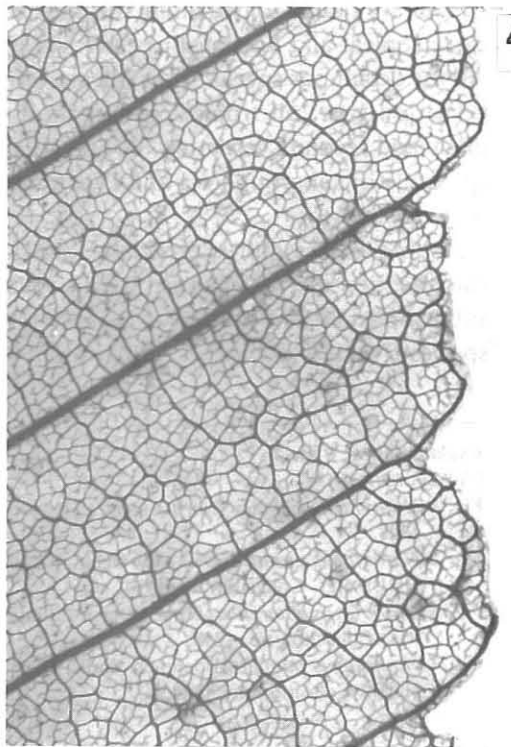
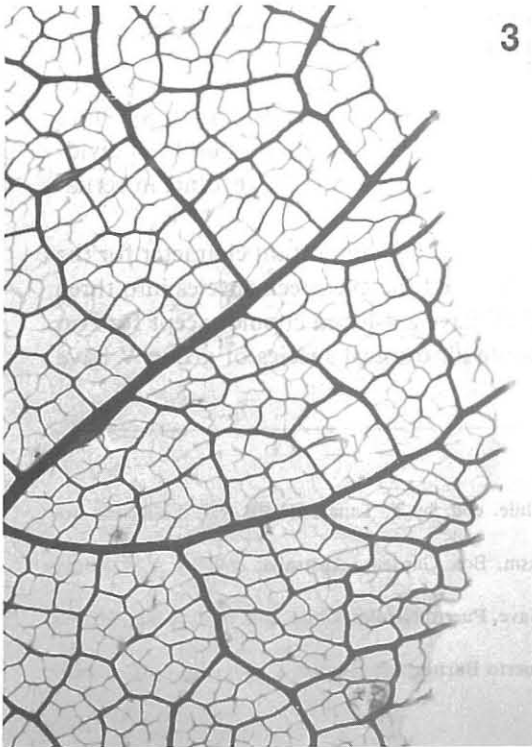
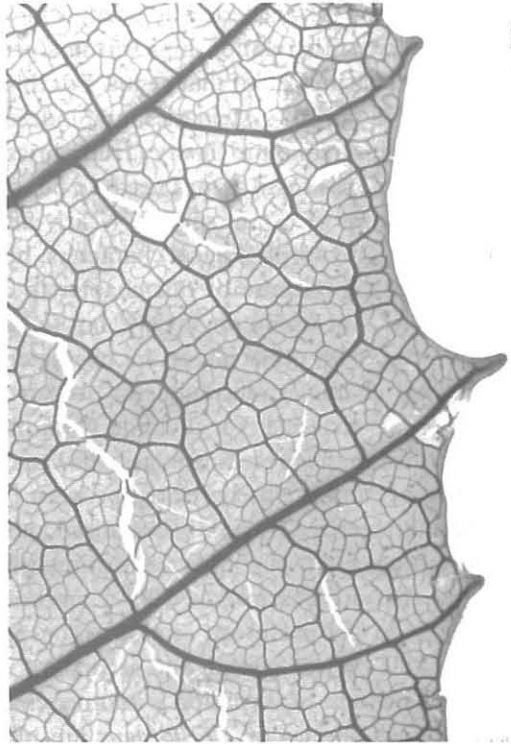
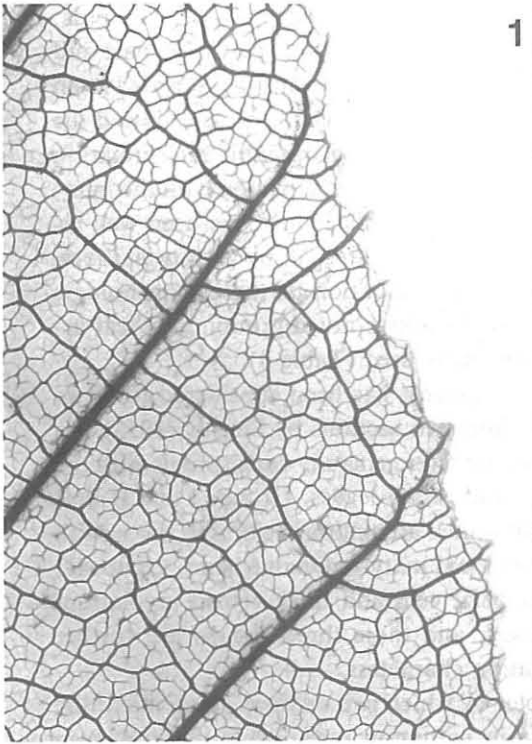
(All figures $\times 10$)

Fig. 1 *Nothofagus alpina* (Poepp. & Endl.) Oerst. Quilacoya, south of Concepcion, Chile. coll. by T. Tanai; HUPB Ref. Collection no. 1785.

Fig. 2 *Nothofagus alessandri* Espinosa. Emperado, Tapar, Chile. coll. by P. Gutierrez M. (MNHN Chile SGO 73603); HUPB Ref. Collection no. 2179.

Fig. 3 *Nothofagus glauca* (Phil.) Krasser. CONAF Arboretum, Cullen, Chile. coll. by T. Tanai; HUPB Ref. Collection no. 1986.

Fig. 4 *Nothofagus procera* (Poepp. & Endl.) Oerst. San Martin, Neuquen, Argentine. coll. by A. Bukart 26473 (NSM Herb. 272269); HUPB Ref. Collection no. 1967.



ble with the infrageneric phylogeny which is based on the taxonomy. In other words, the interspecific relationships within a genus should be well explained by the past and present distribution of that genus. For this reason biogeography must be regarded as an integrated part of systematics, and indeed changes in biogeography have followed the changes in taxonomic theory (Humphries, 1981). The phytogeographic interpretation of *Nothofagus* fossil record needs to be considered further in connection with the interrelationships of extant species. Nearly all the species of this genus have been well investigated in morphological characters, both internal and external, by various authors. It is not the purpose of this chapter to discuss the evaluation of these morphologic characters for use in phylogeny, but to compare the above-noted grouping by leaf architecture with other important characters previously used (Table 3).

Leaf character, deciduous or persistent (evergreen), has been considered to be an important character for dividing *Nothofagus* into two sections by Steenis (1953). As described in the preceding pages, the venation character generally corresponds with the leaf type, and is closely related between fossil and extant leaves. Groups I and II that are characterized by poorly organized and thin veined areolation, belong to the section *Nothofagus*, although they are distinguishable in leaf margin. On one hand, groups III to V that are characterized by a marked fimbrial vein and thick-veined areolation, belong to the evergreen section, *Calusparassus*, and these three groups are further separable by leaf margin and secondary venation characters.

The nature of venation is another character by which two sections are divided; the deciduous species of *Nothofagus* are plicate in venation type, while the evergreen species are flat or folded along the midrib (Steenis, 1953). Recently the venation of 15 extratropical and 8 tropical species was investigated by Philipson & Philipson (1979). All the deciduous species show plicate venation, but evergreen species are dissimilar in venation type: all tropical species (subsection *Quadripartitae* and *Tripartitae*) have plane and revolute venation. Group III shows plane venation, and group IV is divided into two: subgroup IV-a and IV-c are plane, and subgroup IV-b is revolute in venation.

Lobation of cupules, especially lobe number, is also an important character for the classification of *Nothofagus*; Steenis (1953) classified the evergreen species into three subsections. All the species of groups III and IV have a 4-lobed cupule except for two species (*N. solandri* and *N. cliffortioides*), while all tropical species of group V have

Explanation of Plate 2

(All figures $\times 10$)

Fig. 1 *Nothofagus obliqua* (Mirb.) Oerst. Temuco, Chile. coll. by T. Tanai; HUPB Ref. Collection no. 1808.

Fig. 2 *Nothofagus gunnii* (Hook. f.) Oerst. Royal Tasm. Bot. Gardens, Australia. coll. by A.M. Gray; HUPB Ref. Collection no. 1954.

Fig. 3 *Nothofagus antarctica* (Forst.) Oerst. Milodon Cave, Puerto Natales, Chile. coll. by T. Tanai; HUPB Ref. Collection no. 1958.

Fig. 4 *Nothofagus pumilio* (Poepp. & Endl.) Oerst. Fuerto Burnes, Magallanes, Chile. coll. by T. Tanai; HUPB Collection no. 1788.

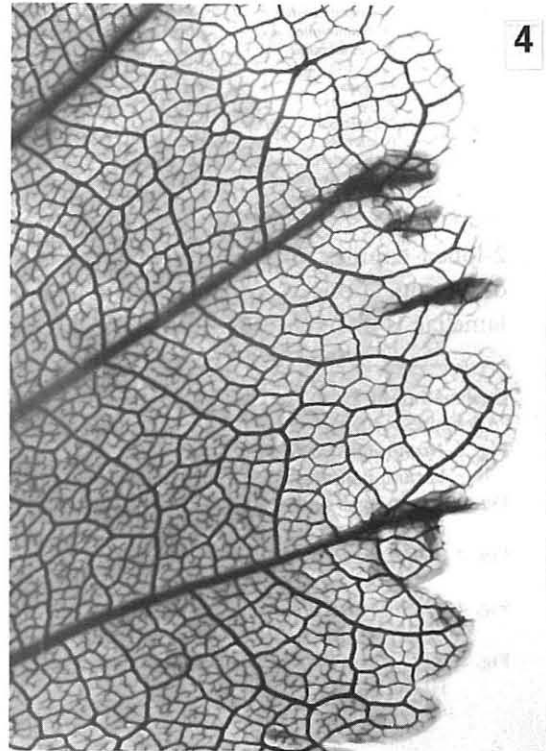
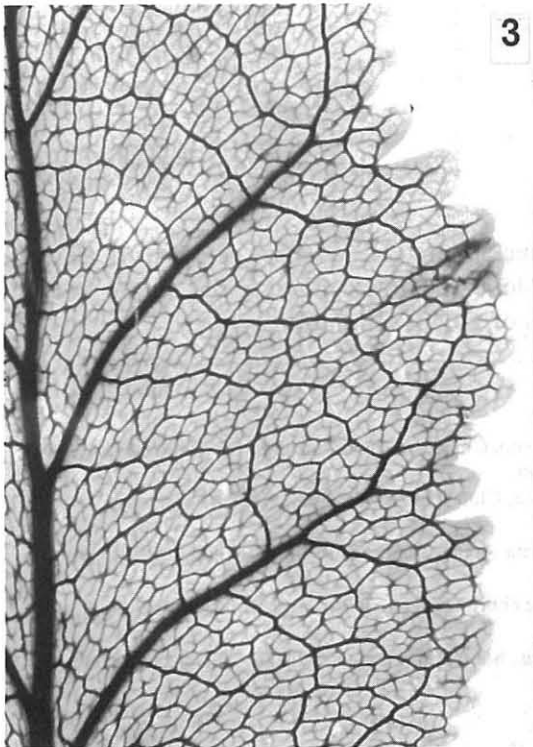
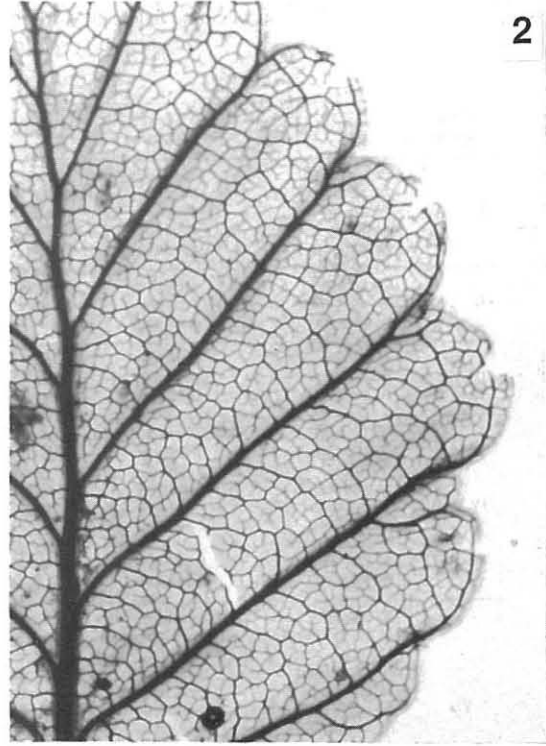
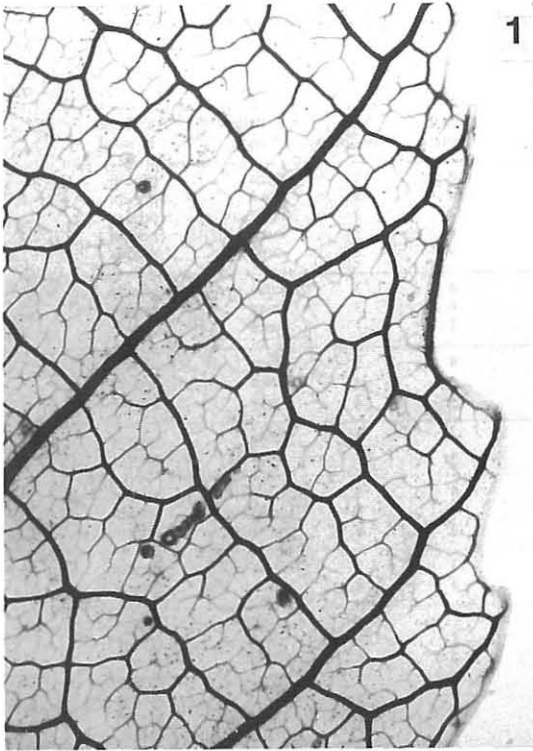


Table 3. Comparison of Some Selected Morphological Characters in Extant Species of the Genus *Nothofagus*

Lead group	Extant Species	Leaf abscission	Vernation	Cupule parts	Seed Number	Pollen type	Tracheid in wood
I	<i>N. alessandri</i>	deciduous	plicate	4	7	fusca	present
	<i>N. procera</i>	deciduous	plicate	4	3	fusca	present
	<i>N. alpina</i>	deciduous	plicate	4	3	menziesii	present
	<i>N. glauca</i>	deciduous	plicate	4	3	menziesii	present
	<i>N. obliqua</i>	deciduous	plicate	4	3	menziesii	present
II	<i>N. gunnii</i>	deciduous	plicate	4	3	fusca	present
	<i>N. antarctica</i>	deciduous	plicate	4	3	fusca	present
	<i>N. pumilio</i>	deciduous	plicate	2	1	fusca	present
III	<i>N. nitida</i>	persistent	plane	4	3	fusca	present
	<i>N. dombeyi</i>	persistent	plane	4	3-5	fusca	present
	<i>N. betuloides</i>	persistent	plane	4	3	fusca	present
IV-a	<i>N. fusca</i>	persistent	revolute	4	3	fusca	present
	<i>N. truncata</i>	persistent	revolute	4	3	fusca	present
IV IV-b	<i>N. menziesii</i>	persistent	plane	4	3	menziesii	present
	<i>N. cunninghamii</i>	persistent	plane	4	3	menziesii	present
	<i>N. moorei</i>	persistent	plane	4	3	menziesii	present
IV-c	<i>N. cliffortioides</i>	persistent	revolute	3	2	fusca	present
	<i>N. solandri</i>	persistent	revolute	3	2	fusca	present
V-a	<i>N. brassii</i>	persistent	conduplicate	2	3	brassii	absent
	<i>N. starkenborghii</i>	persistent	conduplicate	2	3	brassii	absent
	<i>N. carrii</i>	persistent	conduplicate	2	1	brassii	absent
	<i>N. flaviramea</i>	persistent	conduplicate	2	1	brassii	absent
	<i>N. grandis</i>	persistent	conduplicate	2	1	brassii	absent
	<i>N. rubra</i>	persistent	conduplicate	2	1	brassii	absent
	<i>N. wormsleyi</i>	persistent	conduplicate	2	1	brassii	absent
	<i>N. pullei</i>	persistent	conduplicate	2	1	brassii	absent
	<i>N. aequilateralis</i>	persistent	conduplicate	2	1	brassii	absent
	<i>N. baumanniae</i>	persistent	conduplicate	2	1	brassii	absent
V-b	<i>N. codonandra</i>	persistent	conduplicate	2	1	brassii	absent
	<i>N. nuda</i>	persistent	conduplicate	2	3	brassii	absent
	<i>N. perryi</i>	persistent	conduplicate	2	3	brassii	absent
	<i>N. balansae</i>	persistent	conduplicate	2	1	brassii	absent
	<i>N. crenata</i>	persistent	conduplicate	2	1	brassii	absent
	<i>N. discoidea</i>	persistent	conduplicate	2	1	brassii	absent
	<i>N. pseudoresinosa</i>	persistent	conduplicate	2	1	brassii	absent
	<i>N. resinosa</i>	persistent	conduplicate	ecupular	1	brassii	absent

2-lobed cupules. On one hand, except for one species (*N. pumilio*) of group II all deciduous species (groups I and II) have 4-lobed cupules, although the nature of lamellae is different from the 4-lobed cupules of groups III and IV.

Explanation of Plate 3

(All figures $\times 10$)

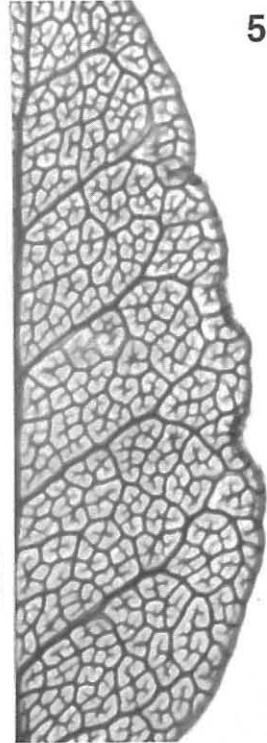
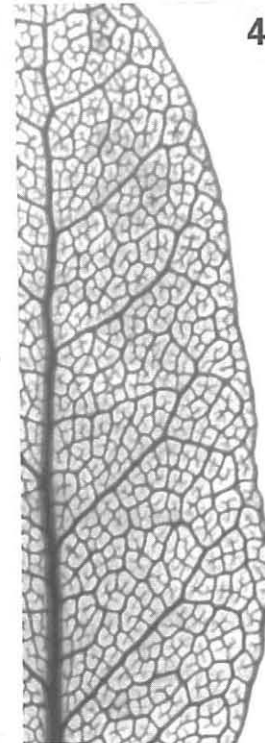
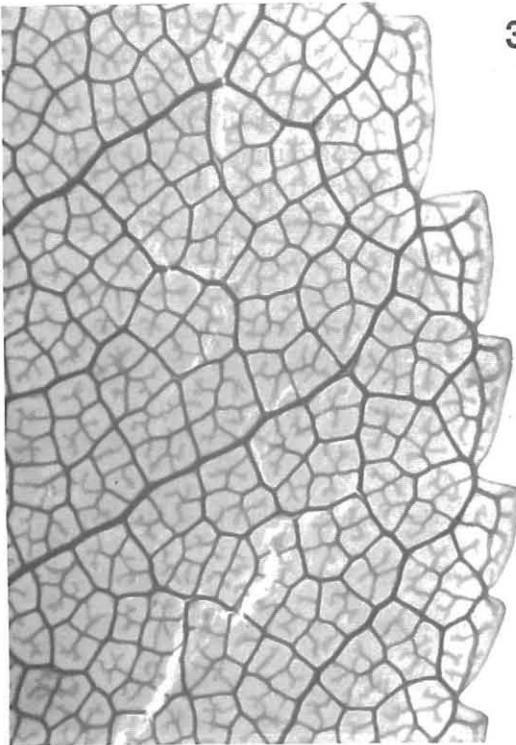
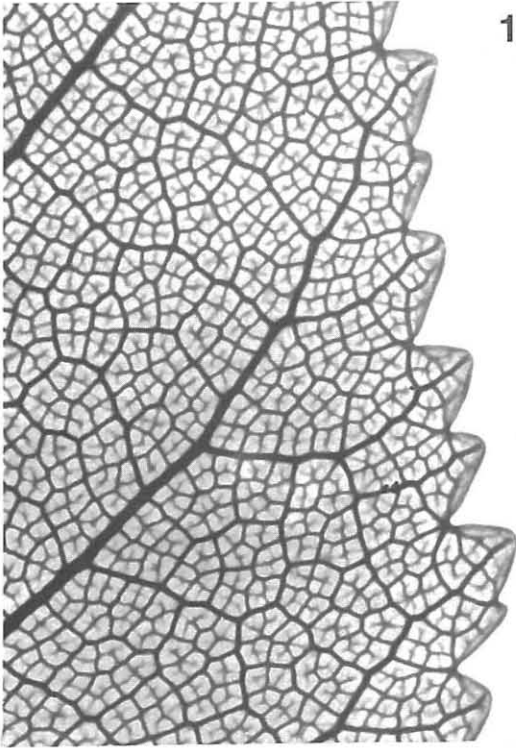
Fig. 1 *Nothofagus nitida* (Phil.) Krasser. Chiloe, Rio Yeleho, Chile. coll. by E. Bernath; MNHN Chile Herbarium collection; HUPB Ref. Collection no. 1766.

Fig. 2 *Nothofagus dombeyi* (Mirb.) Oerst. Lota Park, Lota, Chile. coll. by T. Tanai; HUPB Ref. Collection no. 1784.

Fig. 3 *Nothofagus betuloides* (Mirb.) Oerst. Loreto, Punta Arenas, Chile. coll. by T. Tanai; HUPB Ref. Collection no. 1787.

Fig. 4 *Nothofagus cliffortioides* (Hook. f.) Oerst. Craigieburn, South Island, New Zealand. coll. by A. Sakai; HUPB Ref. Collection no. 1858.

Fig. 5 *Nothofagus solandri* (Hook. f.) Oerst. Craigieburn, South Island, New Zealand. coll. by A. Sakai; HUPB Ref. Collection no. 1858.



The fructification of *Nothofagus* mostly has plural nutlets in a single cupule. Nutlets are dimerous or trimerous in shape. With a few exceptions (*N. alessandri*, *N. pumilio*, *N. dombeyi* and *N. solandri*) all the species of groups I to IV have three nutlets in a cupule, that are two trimerous and a single dimerous. All tropical species of Group V have only one dimerous nut in a single cupule, except for four species (*N. brassii*, *N. starckenborghii*, *N. nuda* and *N. perryi*), in which the cupule has three dimerous nutlets. An exceptional temperate species, *N. pumilio*, has a single nutlet in a cupule, but its nutlet is trimerous. An extratropical evergreen species, *N. solandri*, has two nutlets that are composed of a dimerous and trimerous shapes.

Nothofagus pollen, both living and fossil, is classified into three types. The species groups by pollen type are not always consistent with the infrageneric taxonomy of *Nothofagus*, that has been usually accepted by most taxonomists, although their division of pollen types is clearly identified. However, all tropical species (group V) have the *brassii* type pollen without exception. Groups II and III show the *fusca* type in pollen, while groups I and IV contain both the *fusca* and *menziesii* types.

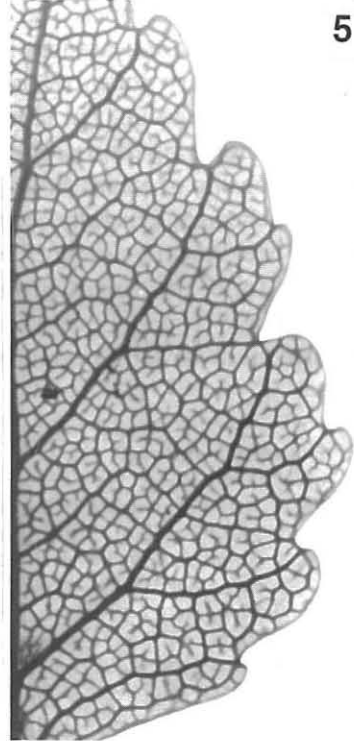
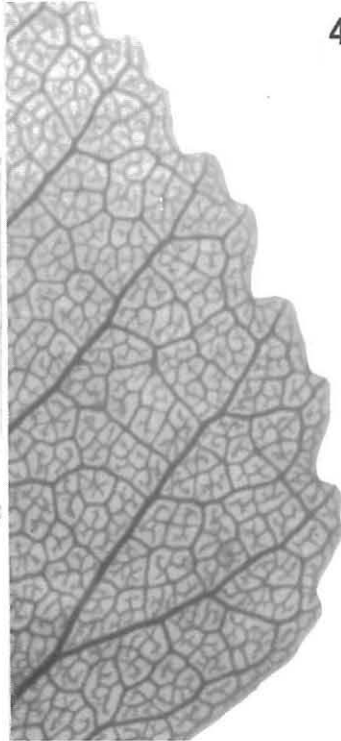
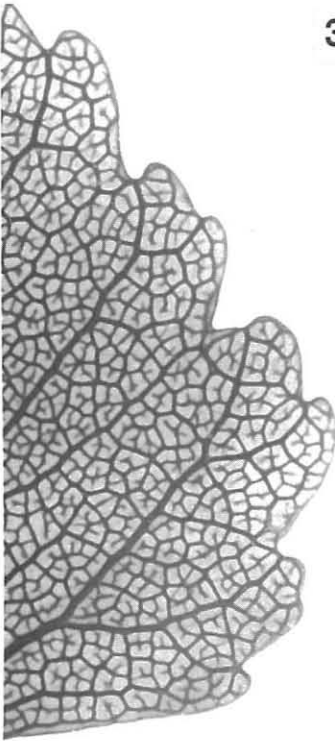
Investigating wood anatomy of 22 extant species of *Nothofagus*, Dadswell & Ingle (1954) showed that there is a marked difference between tropical and extratropical species. Wood of the former is usually distinguishable from that of the latter in having larger and fewer vessels, numerous irregularly spaced bands of parenchyma 2–6 cells wide, prominent crystals in parenchyma cells, and absence of tracheids. The difference between the tropical and extratropical groups is further observed by a fungi that is parasitic to *Nothofagus*. *Cyttaria* Berk., a fungal genus, consists of obligate parasites forming stem galls only on the twigs or branches of *Nothofagus*. It is noteworthy that *Cyttaria* is known to be restricted to extant extratropical species, and has not been known from tropical species (Korf, 1983).

The above-noted comparison of some important morphological characters of *Nothofagus* as summarized in Table 3, shows that the species grouping defined by leaf architecture is compatible with the distribution of various morphological characters among extant species, and that the tropical group from New Guinea and New Caledonia is pronouncedly different from the extratropical group as previously expressed by many workers. Hjelmqvist (1963) stressed that the tropical group belongs to a special line of development, quite separate from the extratropical group, based on comparative morphology of many organs. It is, however, rather difficult only by mor-

Explanation of Plate 4

(All figures $\times 10$)

- Fig. 1 *Nothofagus truncata* (Colenso) Cockayne. Christchurch, New Zealand. coll. by P. Wardle; HUPB Ref. Collection no. 1953.
- Fig. 2 *Nothofagus fusca* (Hook. f.) Oerst. Jackson, South Island, New Zealand. coll. by A. Sakai; HUPB Ref. Collection no. 1859.
- Fig. 3 *Nothofagus menziesii* (Hook. f.) Oerst. Christchurch, New Zealand. coll. by P. Wardle; HUPB Ref. Collection no. 1957.
- Figs. 4, 5 *Nothofagus cunninghamii* (Hook. f.) Oerst. Melba Gully Park, Victoria, Australia. coll. by T. Tanai; HUPB Ref. Collection no. 1956.



phological characters to determine definitely whether the extant tropical group is a living relict of the former widely-distributed *Nothofagus* or an advanced member derived from the extratropical one.

Concluding Remarks

Most phytogeographical considerations except vicariance-cladistic analysis have been concluded that the center of *Nothofagus* origin was in the tropics, from where *Nothofagus* diversified southward. This assumption has been partly supported by the fact that the *brassii* type pollen is usually older in fossil occurrence than the other two types in all regions of the southern hemisphere. However, the northern origin theory is inconsistent with paleobotanical and geological facts: the absence of pre-Miocene *brassii* type pollen in New Guinea, the recent knowledge of past geological and paleogeographical setting of New Guinea, and the lack of older records of fossil leaves similar to the tropical group in any region.

The evolutionary scheme of cupular and floral characters proposed by Steenis (1953) and Melville (1973) is plausible for infrageneric phylogeny of this genus, although they (Steenis, 1971; Melville, 1982) considered the tropical group as a relict member. Their scheme is acceptable as general evolutionary trend in the genus *Nothofagus* that reduction of a secondary flower from a trimerous to a dimerous condition resulted in fusion between the corresponding pair of valves (Forman, 1966). Paleobotanical and geological evidence as already discussed in detail, shows that the extratropical complex was widely distributed in the assembled southern continents, preceding the appearance of the tropical group. It is probable that Late Cretaceous and older Tertiary pollen referred to the *brassii* type is not related directly to the extant *brassii* type group, but represents pollen of an ancestral complex of *Nothofagus*.

Considering the morphologic characters together with fossil records, a phylogenetic relationship of extant *Nothofagus* species are proposed here. As shown in Text-fig. 14, this scheme is generally consistent with fragmentation of the southern continents that has been recently described by many authors (Smith & Briden, 1977; Owen, 1983). The ancestor of the tropical group was probably derived from the extratropical group during Early Tertiary time, when New Guinea and New Caledonia were once situated further southward. The extant tropical group (subsection *Bipartitae*) is probably a group

Explanation of Plate 5

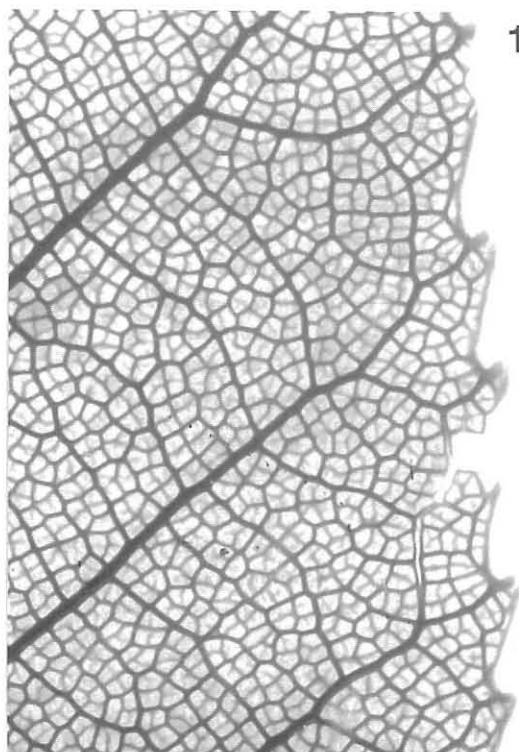
(All figures $\times 10$)

Fig. 1 *Nothofagus moorei* (F. Muell) Krasser. Springbrook, Southport, Q'ld, Australia. coll. by R. Schodde 5603 (Roy. Bot. Gard. Sydney Herb. collection); HUPB Ref. Collection no. 1955.

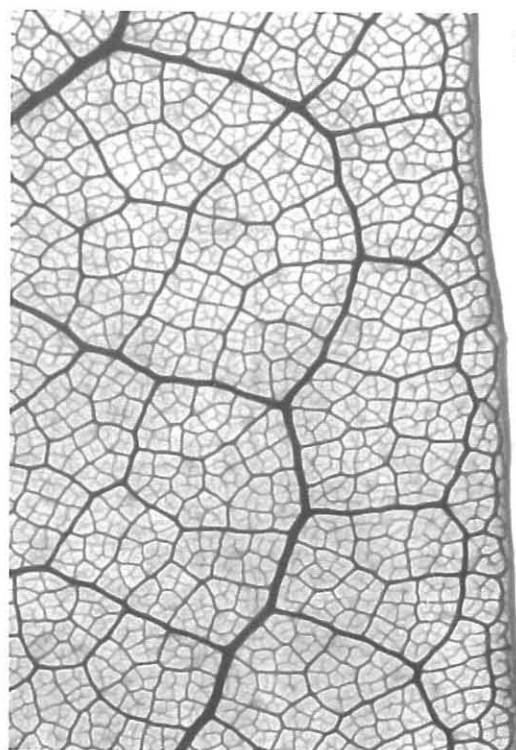
Fig. 2 *Nothofagus flaviramea* Steenis. Genofa Mts., New Guinea. coll. by C. Versteegh (BW 10253); HUPB Ref. Collection no. 2188.

Fig. 3 *Nothofagus brassii* Steenis. Chimbu, East Highlands, New Guinea. coll. by R.G. Robbins 659 (Lae Herb.); HUPB Ref. Collection no. 1959.

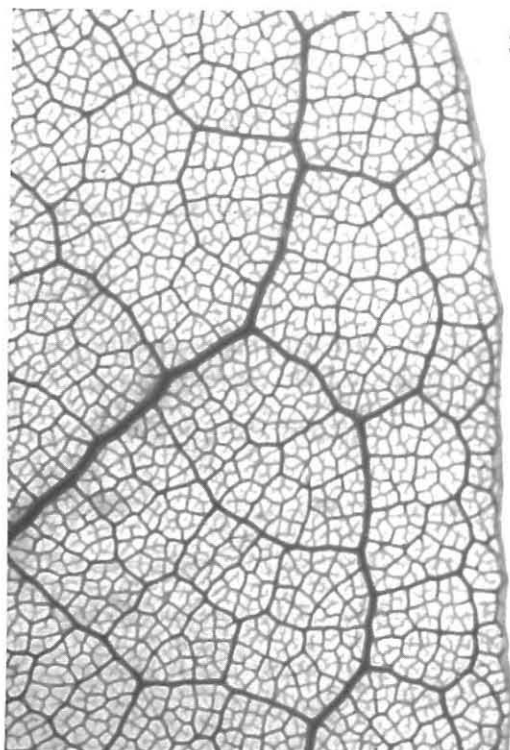
Fig. 4 *Nothofagus pullei* Steenis. Wabag, West Highlands, New Guinea. coll. by J.S. Womersley (NGF 15252); HUPB Ref. Collection no. 1960.



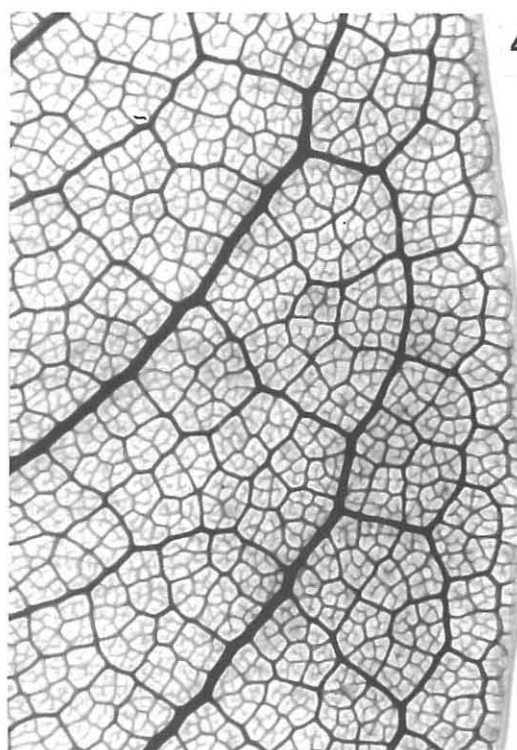
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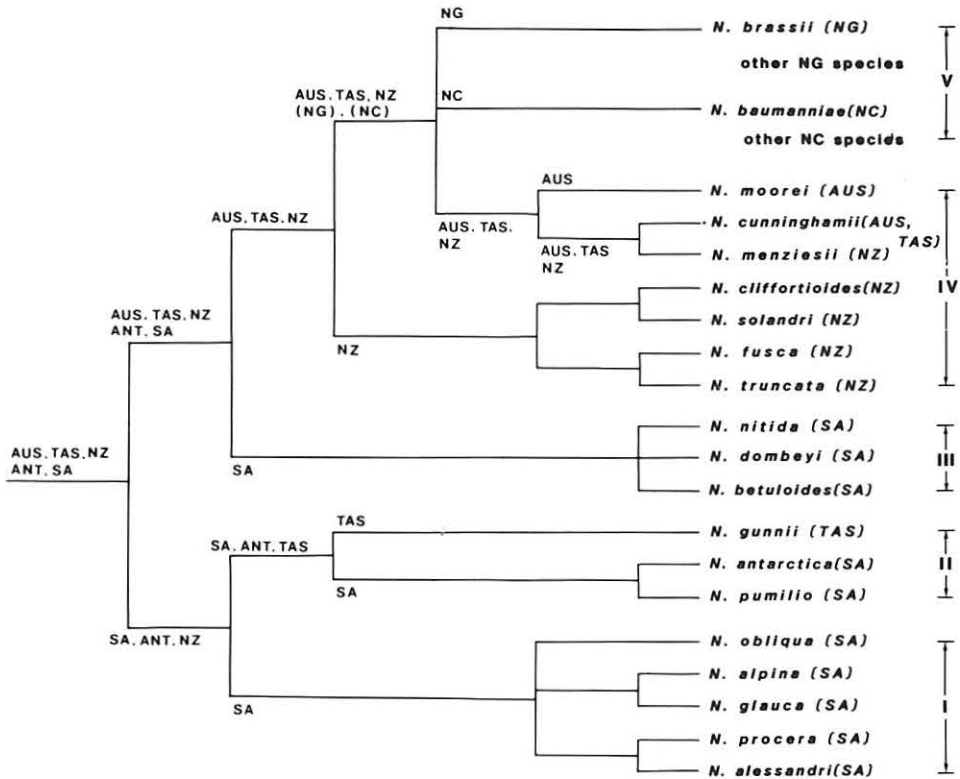
2



3



4



Text-fig. 14 A Biogeographic History and Phylogeny of the Genus *Nothofagus* proposed by the Author. Numbers of Greek letter correspond with the leaf groups designated by the author. SA: South America, ANT: Antarctica, AUS: Australia, TAS: Tasmania, NZ: New Zealand, NG: New Guinea, NC: New Caledonia

that adapted to warm and humid climate as the both islands shifted northward to their present position during Late Tertiary time.

Acknowledgements

I wish to express my cordial thank to contributors for their kind supports during staying in Chile in 1979—1980: Dr. Eduardo P. Gonzalez and Dr. Salvador Haran-

Explanation of Plate 6

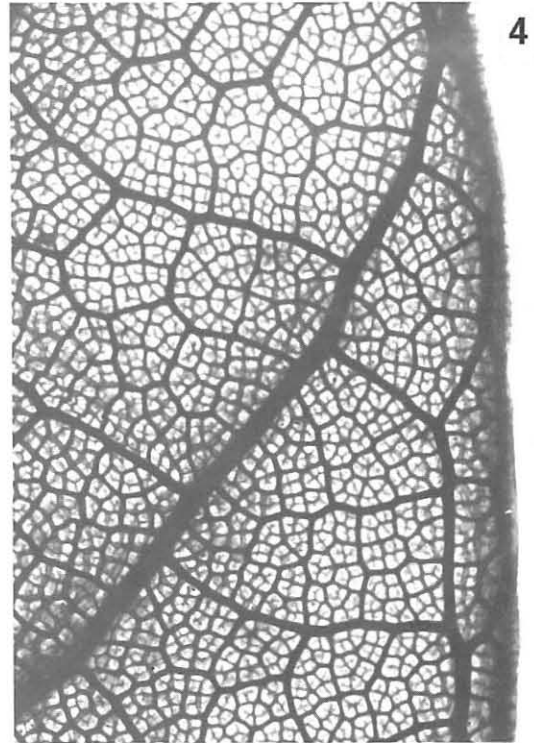
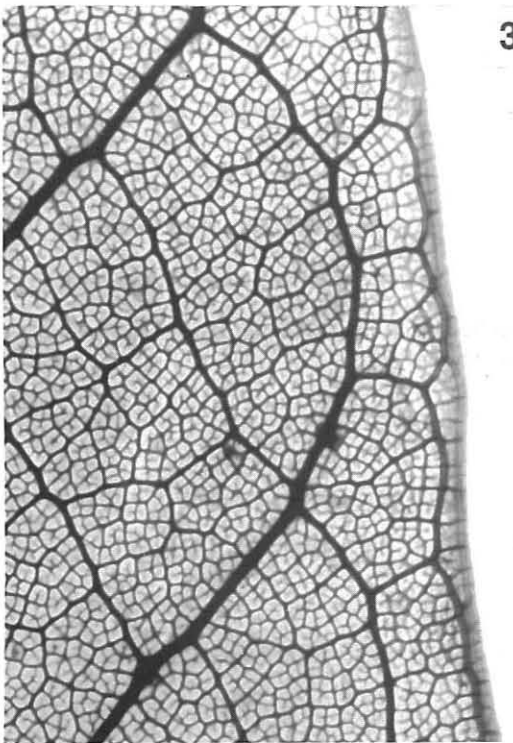
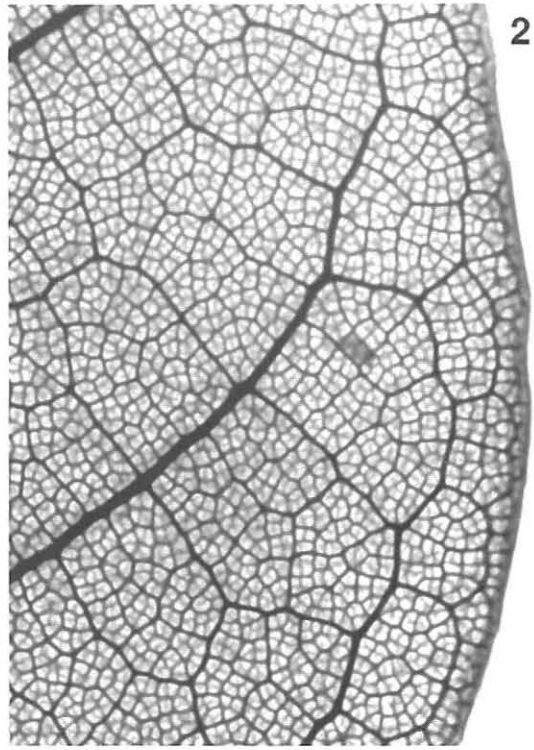
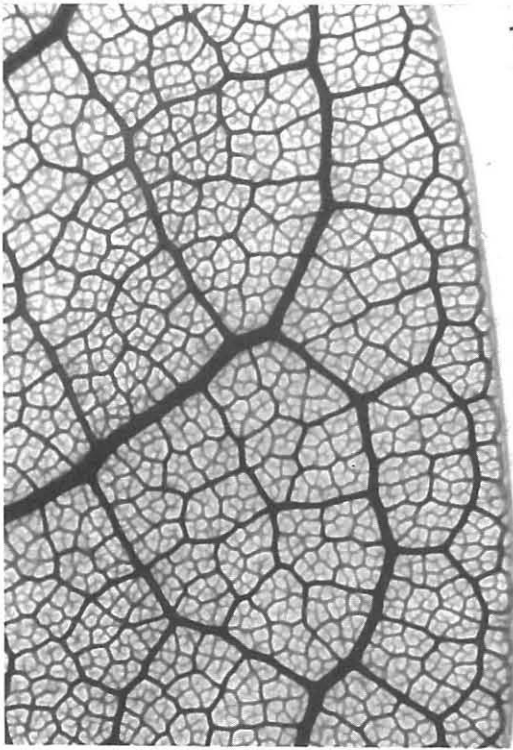
(All figures $\times 10$)

Fig. 1 *Nothofagus carrii* Steenis. Kebo, Wissel Lakes, New Guinea. coll. by C. Vinks & Schram. (BW 8920); HUPB Ref. Collection no. 1965.

Fig. 2 *Nothofagus rubra* Steenis. Mendi, South Highlands, New Guinea. coll. by P.J. Eddowes & M. Kumul (NGF 38122); HUPB Ref. Collection no. 1966.

Fig. 3 *Nothofagus aequilateralis* (Baum.-Bod.) Steenis. Laubenfels p. 516, New Caledonia. collector unknown (Rijks Herb. Leiden); HUPB Ref. Collection no. 2187.

Fig. 4 *Nothofagus codonandra* (Baill.) Steenis. Pic Bose. N. Cakedibea, New Caledonia. by M.G. Bauman-Bodenheim (Arn. Arb. Herb.); HUPB Ref. Collection no. 2413.



brous, Empresa Nacional del Petroleo of Chile, who offered me many facilities to trip and adequate geological informations to collect fossils; Mr. Sergio Cespedéz and Mr. Vicente Pérez D'Angello of same company for their generous guidance to the field trip. Heartily thanks are also due to the professors of the following botanical institutions to send me extant *Nothofagus* leaves or to allow to take the herbarium specimens for the venation study: Dr. G.L. Harden, Royal Botanic Gardens, Sydney, Australia; Dr. Alan M. Gray, Royal Tasmanian Botanic Gardens, Hobart, Australia; the Curator of Adelaide Botanic Gardens, Adelaide, Australia; Dr. Melica Munos Shick, Seccion Botanica, Museo Nacional de Historia Natural, Santiago, Chile; Dr. P. Wardle, Botanic Division, D.S.I.R., Christchurch, New Zealand; Dr. Heinar Streimann, Department of Forest, Papua New Guinea Forestry College, Bulolo, Papua New Guinea (now in National Botanic Garden, Canberra); Dr. Michael Galore, Division of Botany, Office of Forest, D.P.I., Lae, Papua New Guinea; the Director of Rijksherbarium, Leiden, the Netherland (through Dr. Ger van Vliet of the Botanic Garden, the University, Leiden); Dr. David C. Michener, the Arnold Arboretum, Harvard University, Cambridge, the United States.

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Explanation of Plate 7

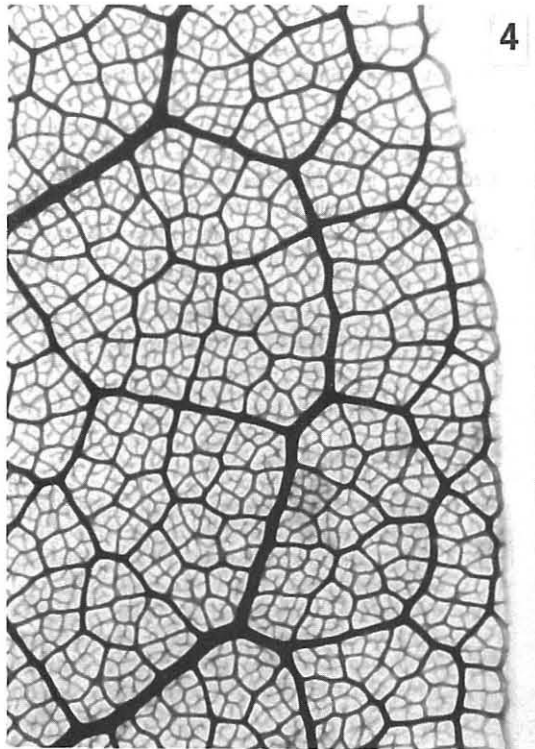
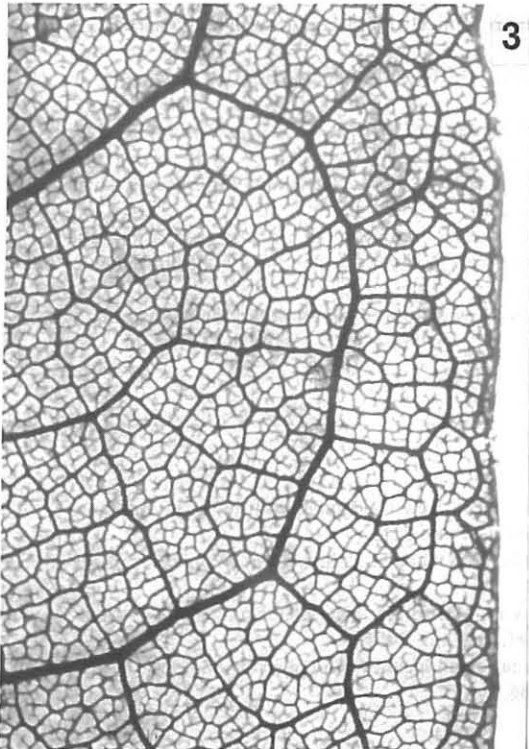
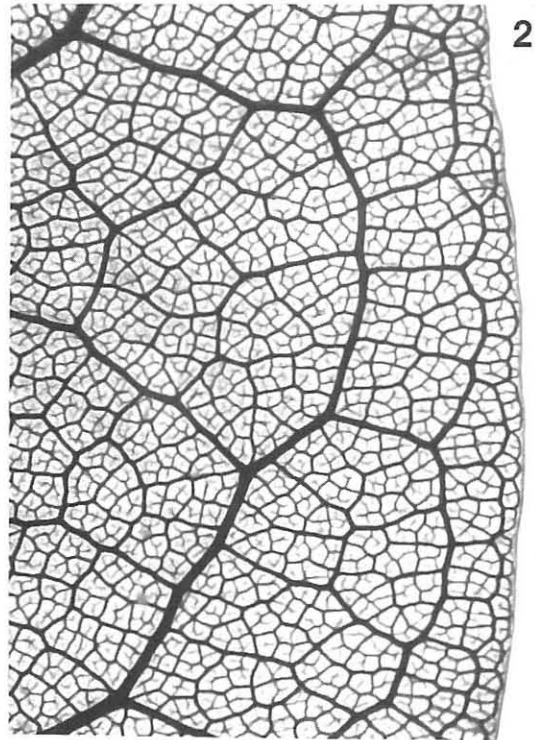
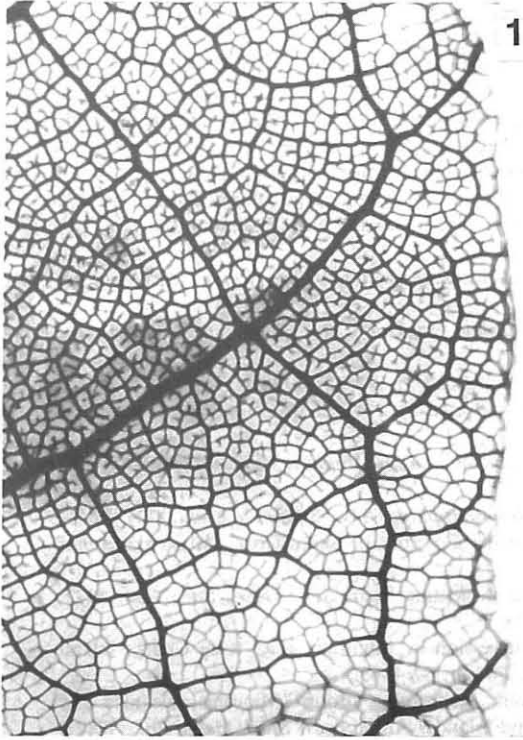
(All figures $\times 10$)

Fig. 1 *Nothofagus resinosa* Steenis. Nankai Plateau, Pomio, New Britain. Coll. by N. Clunie (DBDF Lae 63015); HUPB Ref. Collection no. 1964.

Fig. 2 *Nothofagus crenata* Steenis. New Guinea (16°32'S/143°54'E). coll. by N. Clunie et al. (DBDF Lae 63400); HUPB Ref. Collection no. 2184.

Fig. 3 *Nothofagus starkenborghii* Steenis. Kainantu, East Highlands, New Guinea. coll. by N. Clunie (DBDF Lae 63023); HUPB Ref. Collection no. 1963.

Fig. 4 *Nothofagus grandis* Steenis. Mt. Kindi, Morobe, New Guinea. coll. by D. Foreman & P. Wardle (NGF 45554); HUPB Ref. Collection no. 1961.



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Explanation of Plate 8

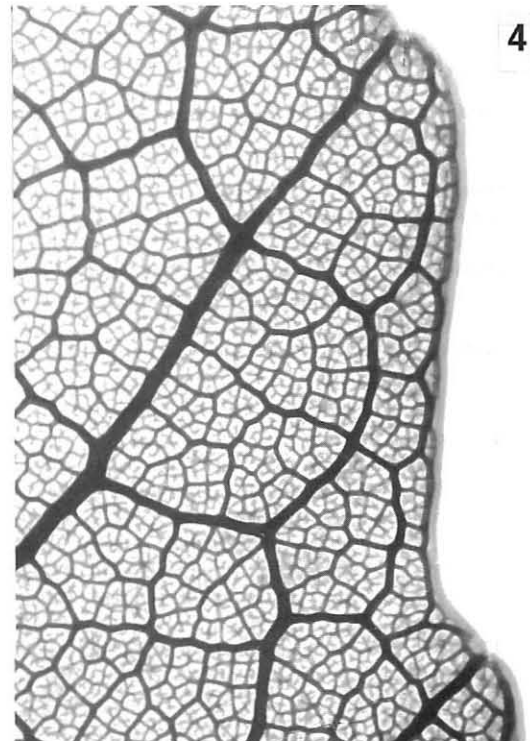
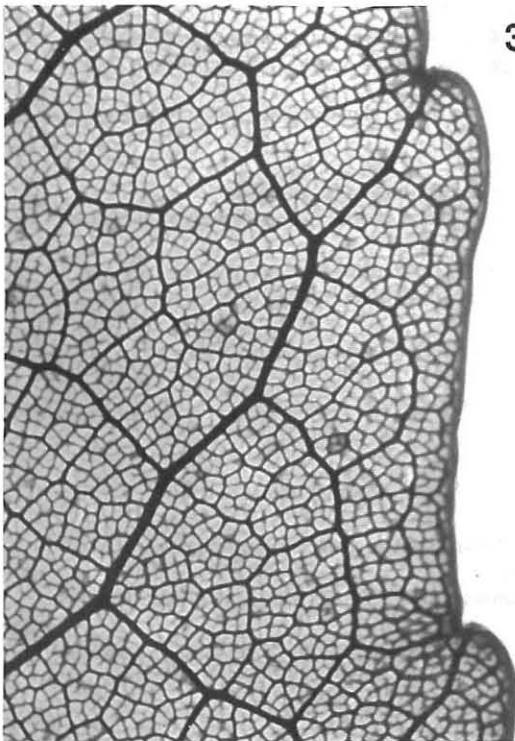
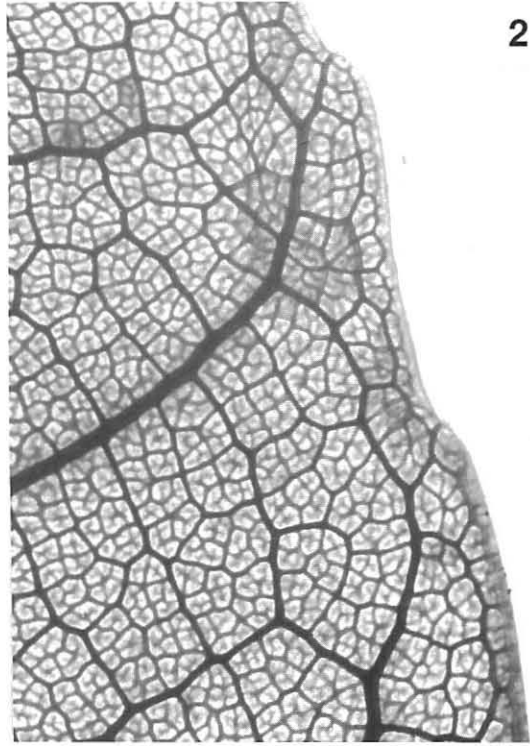
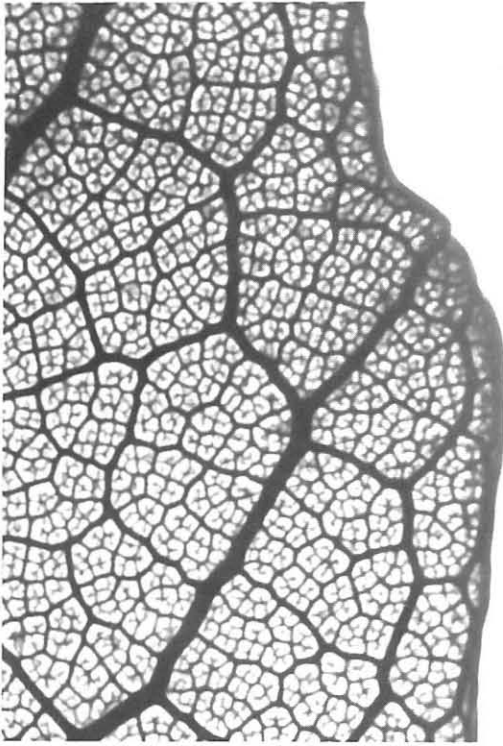
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Fig. 1 *Nothofagus baumanniae* (Baum.-Bod.) Steenis. Mt. Hou, New Caledonia. coll. by M.B. Bauman-Bodenheim (Univ. Tokyo Herb.); HUPB Ref. Collection no. 2219.

Fig. 2 *Nothofagus perryi* Steenis. Wabag, West Highlands, New Guinea. coll. by J.S. Womersley (NGF 15257); HUPB Ref. Collection no. 1962.

Fig. 3 *Nothofagus discoidea* (Baum.-Bod.) Steenis. Mois de Mai-forest, New Caledonia. coll. by M.G. Bauman-Bodenheim (Arn. Arb. Herb.); HUPB Ref. coll. no. 2414.

Fig. 4 *Nothofagus balansae* (Baill.) Steenis. New Caledonia, detail locality and collector unknown. (Herb. Mus. Paris 12973); HUPB Ref. Collection no. 2186.

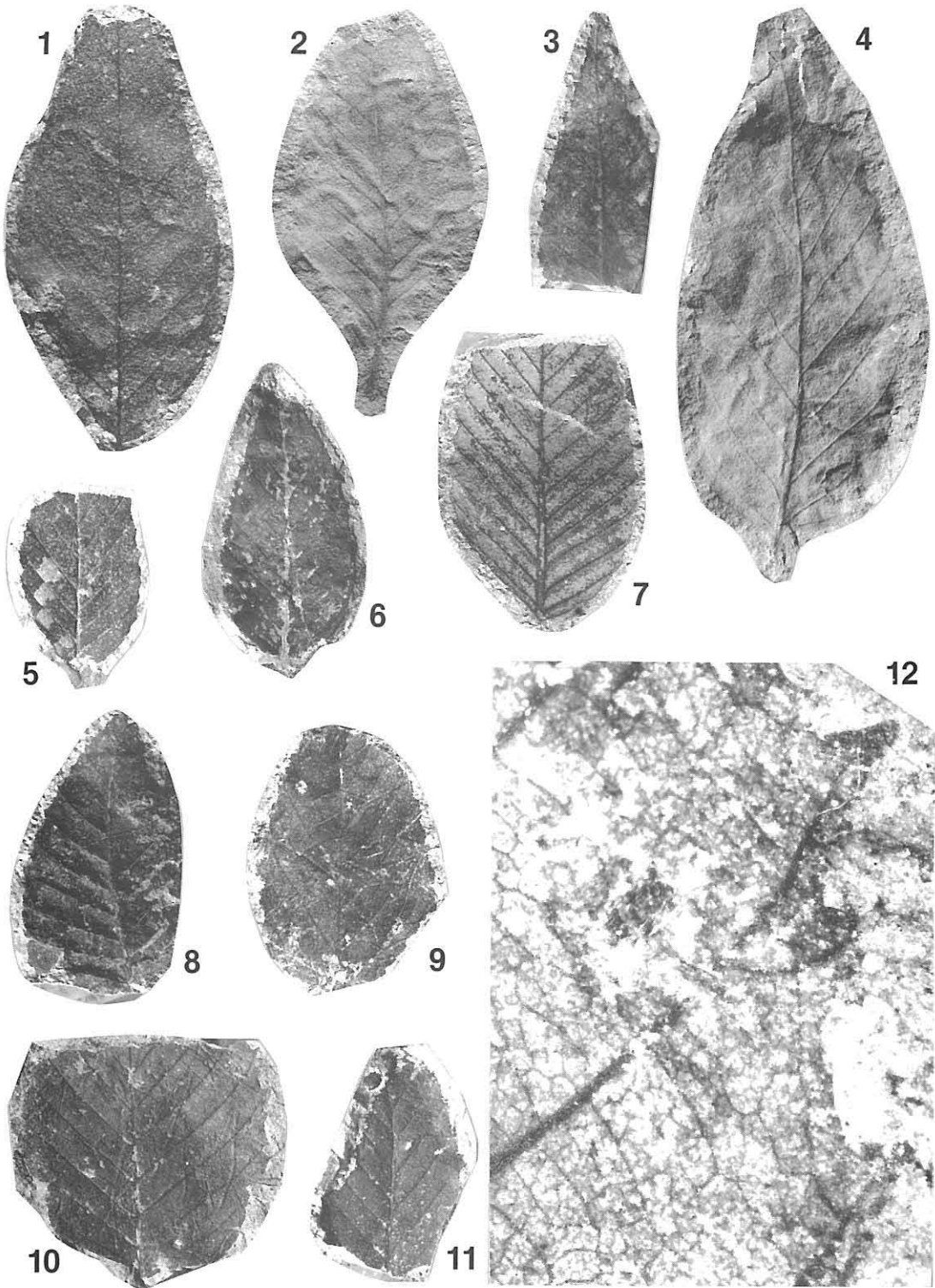


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Explanation of Plate 9

(All figures in natural size unless otherwise stated)

- Figs. 1, 3, 5-10** *Nothofagus subferruginea* (Dusén) Tanai. Las Minas, west of Punta Arenas, Magallanes, Chile. HUMP hypotypes nos. 26289-26296.
- Figs. 2, 4** *Nothofagus subferruginea* (Dusén) Tanai. Rio Chico, west of Estacion San Sebastian, Fuego Island, Chile. HUMP hypotypes nos. 26297, 26298.
- Fig. 11** *Nothofagus subferruginea* (Dusén) Tanai. Matanzas, southwest of Snatiago, Chile. HUMP hypotype no. 26299.
- Fig. 12** Showing the marginal serration and secondary vein termination of *Nothofagus subferruginea* (enlargement of fig. 10). ×10



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Explanation of Plate 10

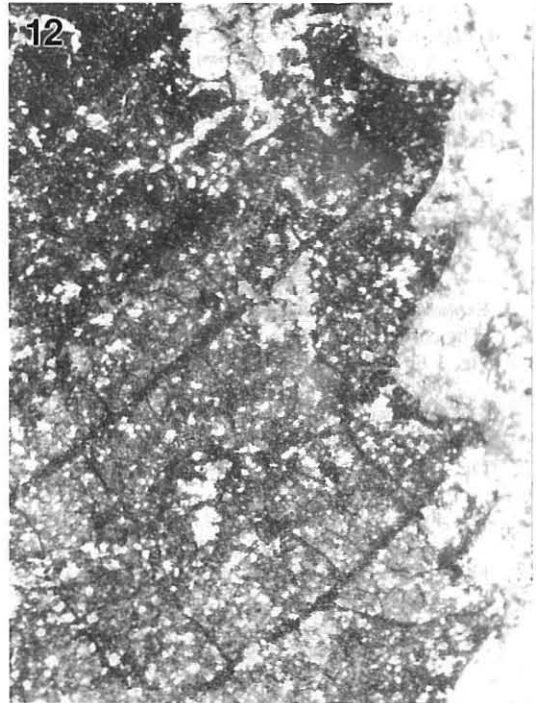
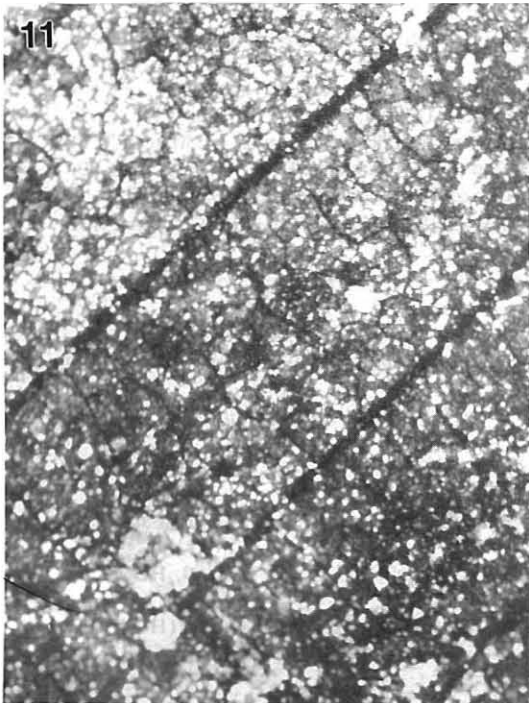
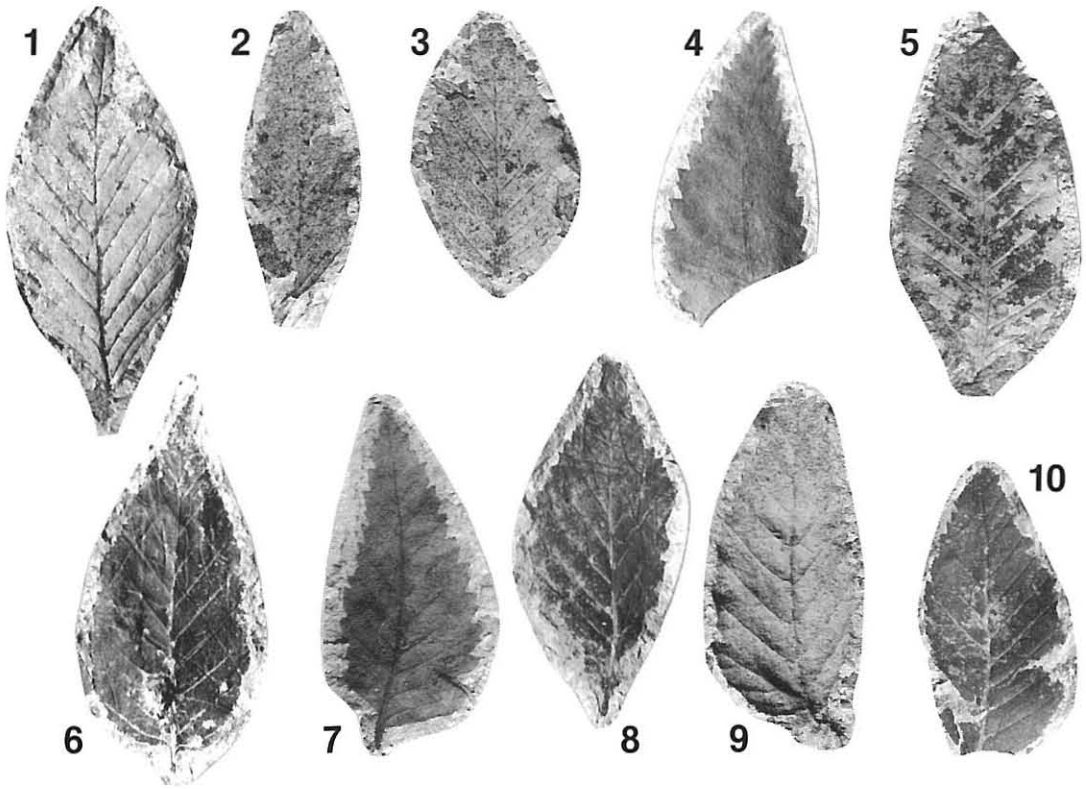
(All figures in natural size unless otherwise stated)

Figs. 1-3, 5, 6, 8-10 *Nothofagus magelhaenica* (Engelhardt) Dusén. Las Minas, west of Punta Arenas, Magallanes, Chile. HUMP hypotypes nos. 2655b, 26268-26274. Fig. 5 × 2

Figs. 4, 7 *Nothofagus magelhaenica* (Engelhardt) Dusén. Rio Chico, west of Estacion San Sebastian, Fuego Island, Chile. HUMP hypotypes nos. 26276, 26277.

Fig. 11 Showing the tertiary venation of *Nothofagus magelhaenica*. (HUMP no. 26275). × 10

Fig. 12 Showing the marginal serration and secondary vein termination of *Nothofagus magelhaenica*. (HUMP no. 26275). × 10

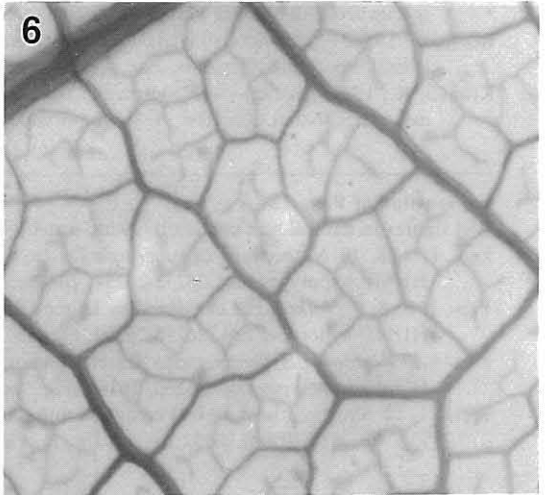
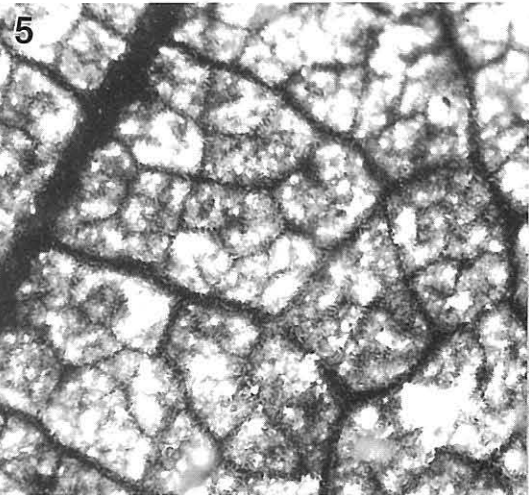
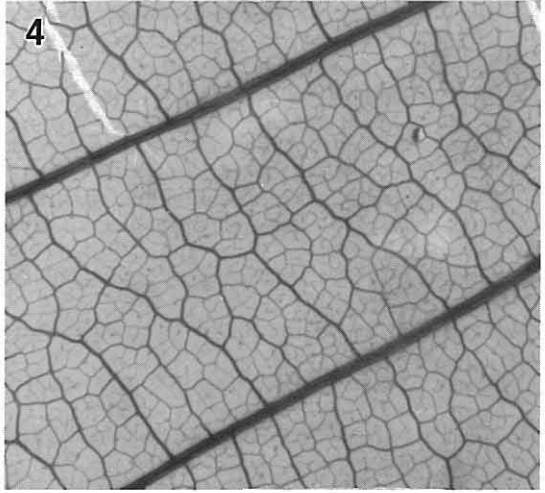
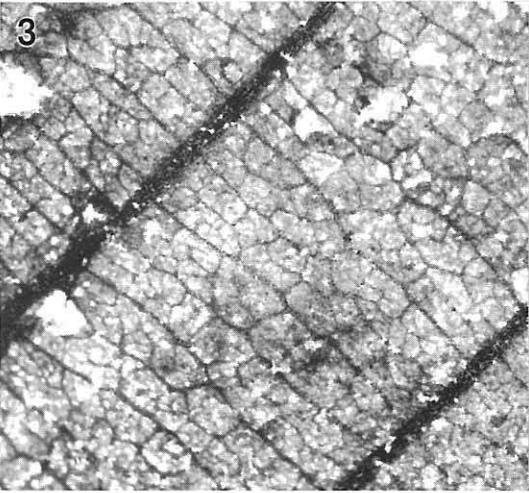
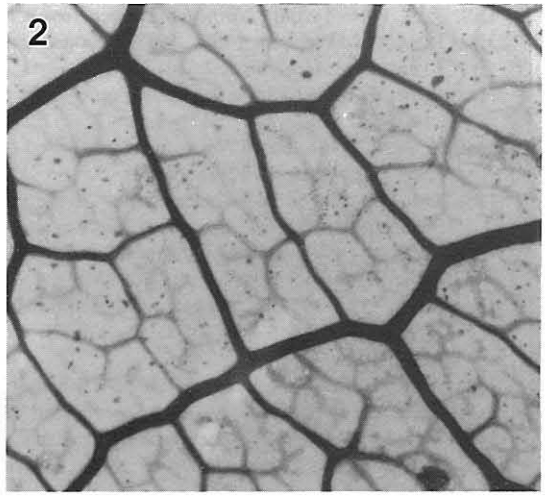
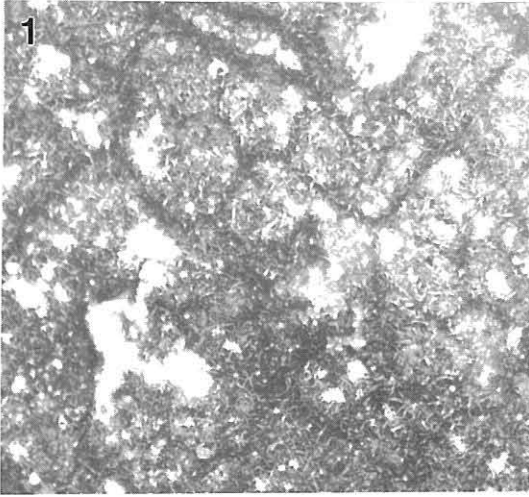


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Explanation of Plate 11

(The comparison of the venation details between fossil leaves and their modern equivalents)

- Fig. 1** Showing the areoles and ultimate veinlets of *Nothofagus magelhaenica* (Engelhardt) Dusén. (HUMP no. 26275). $\times 30$
- Fig. 2** Showing the areoles and the ultimate veinlets of the extant *Nothofagus obliqua* (Mirb.) Oerst. (HUPB Ref. Collection no. 1809). $\times 30$
- Fig. 3** Showing the tertiary and higher-order venation of *Nothofagus subferruginea* (pl. 9, fig. 9, HUMP no. 26295). $\times 10$
- Fig. 4** Showing the tertiary and higher-order venation of the extant *Nothofagus alessandri* Espinosa. (HUPB Ref. Collection no. 2179). $\times 10$
- Fig. 5** Showing the areoles and ultimate veinlets of *Nothofagus subferruginea* (pl. 9, fig. 9, HUMP no. 26295). $\times 30$
- Fig. 6** Showing the areoles and ultimate veinlets of the extant *Nothofagus alessandri* Espinosa. (HUPB Ref. Collection no. 2179). $\times 30$



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Explanation of Plate 12

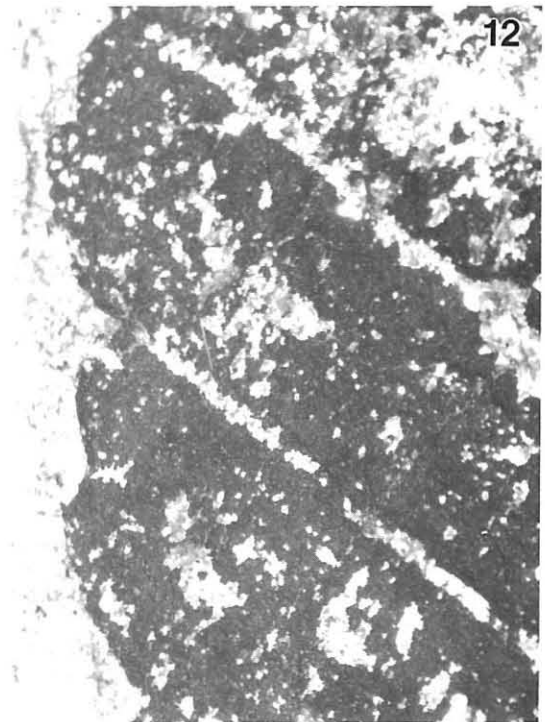
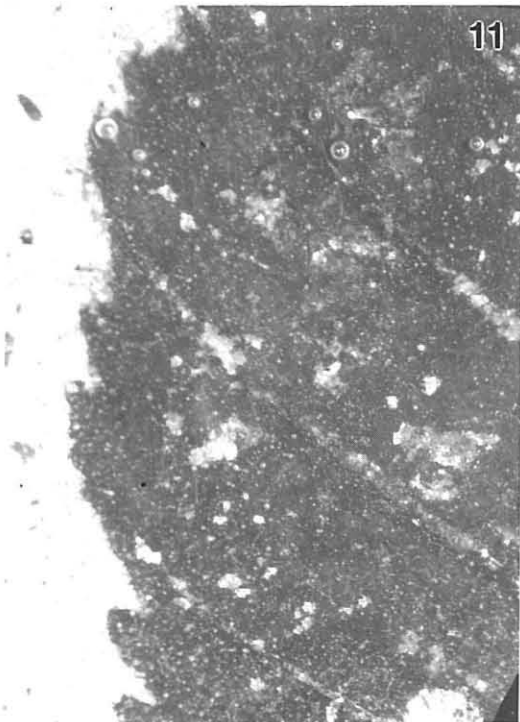
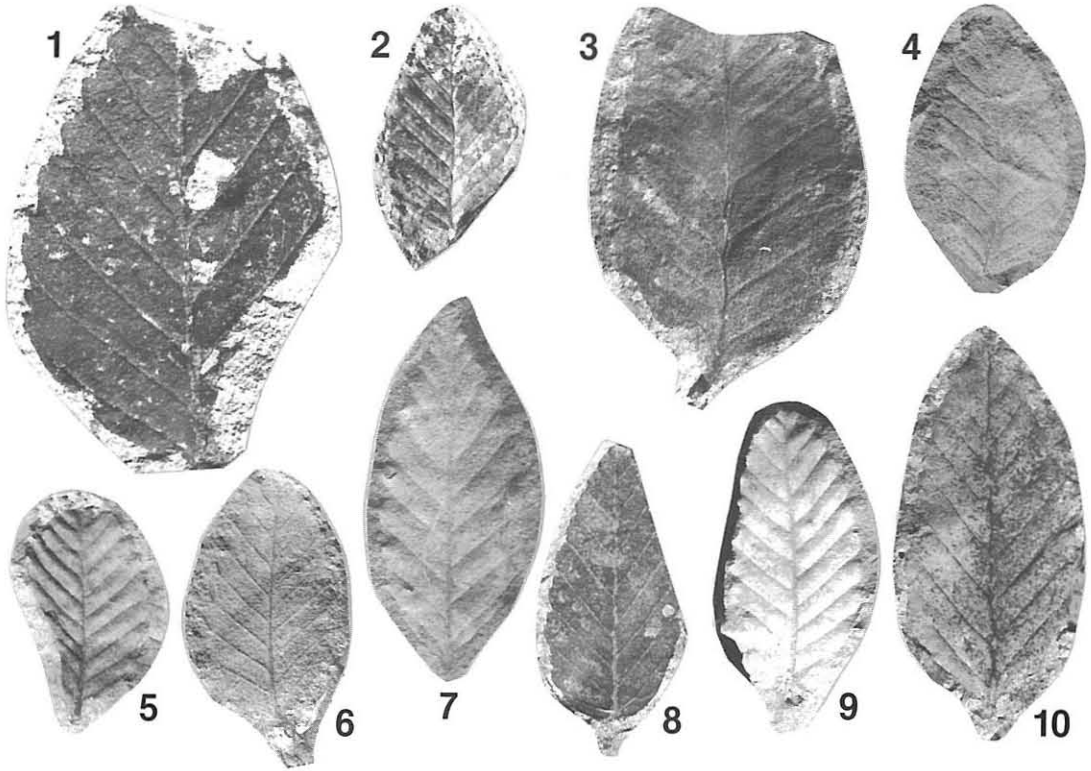
(All figures in natural size unless otherwise stated)

Figs. 1, 2, 8, 10 *Nothofagus densinervosa* Dusén. Las Minas, west of Punta Arenas, Magallanes, Chile. HUMP hypotypes nos. 26252-26254, 26255a. Fig. 1 × 2.5

Figs. 3, 5, 6, 9 *Nothofagus densinervosa* Dusén. Río Chico, west of San Sebastian, Fuego Island, Chile. HUMP hypotypes nos. 26256-26259. Fig. 3 × 2

Figs. 4, 7 *Nothofagus densinervosa* Dusén. Laguna Lynch, west of Punta Arenas, Magallanes, Chile. HUMP hypotypes nos. 26260, 26261. Fig. 7 × 1.5

Figs. 11, 12 Showing the marginal crenation and secondary vein termination of *Nothofagus densinervosa*. Fig. 11 (HUMP no. 26252; pl. 12, fig. 1), Fig. 12 (HUMP no. 26254; pl. 12, fig. 8). × 10

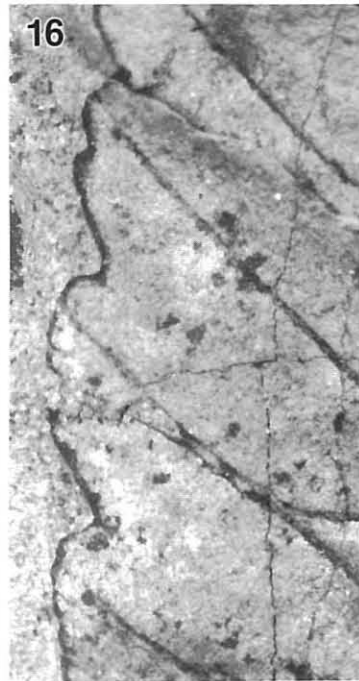
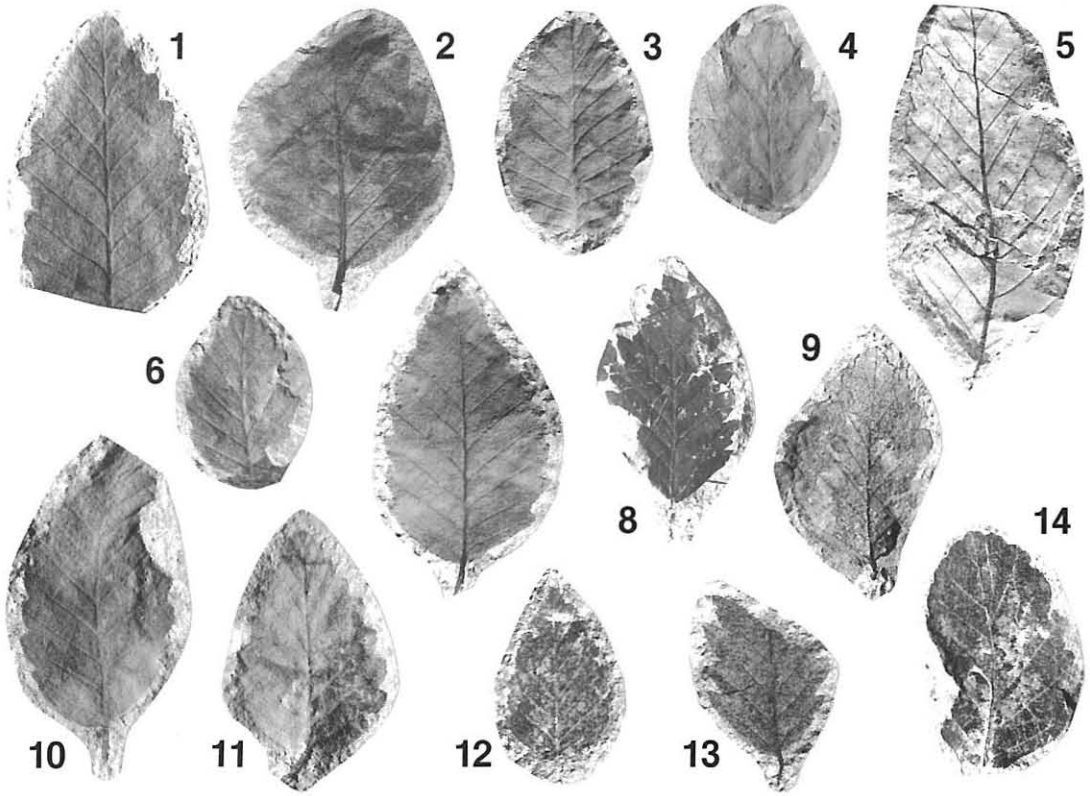


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Explanation of Plate 13

(All figures in natural size unless otherwise stated)

- Figs. 1-3, 6, 7, 10, 11** *Nothofagus simplicidens* Dusén. Rio Chico, west of Estacion San Sebastian, Fuego Island, Chile. HUMP hypotypes nos. 26281-26287.
- Fig. 4** *Nothofagus dicksoni* (Dusén) Tanai. Laguna Lynch, west of Punta Arenas, Magallanes, Chile. HUMP hypotype no. 26262.
- Figs. 5, 9, 14** *Nothofagus gonzalezi* Tanai. Matanzas, southwest of Santiago, Chile. HUMP holotype no. 25265 (Fig. 5), paratypes nos. 25266, 26267.
- Figs. 8, 13** *Nothofagus dicksoni* (Dusén) Tanai. Las Minas, west of Punta Arenas, Magallanes, Chile. HUMP hypotypes nos. 26263, 26264.
- Fig. 12** *Nothofagus simplicidens* Dusén. Las Minas, west of Punta Arenas, Magallanes, Chile. HUMP hypotype no. 26288.
- Fig. 15** Showing the marginal serration and tertiary venation of *Nothofagus simplicidens* (Enlargement of fig. 10). $\times 6.8$
- Fig. 16** Showing the marginal serration and the secondary vein termination of *Nothofagus gonzalezi* (Enlargement of fig. 5). $\times 6.8$
- Fig. 17** Showing the marginal serration and the secondary vein termination of *Nothofagus dicksoni* (Enlargement of fig. 4). $\times 6.8$

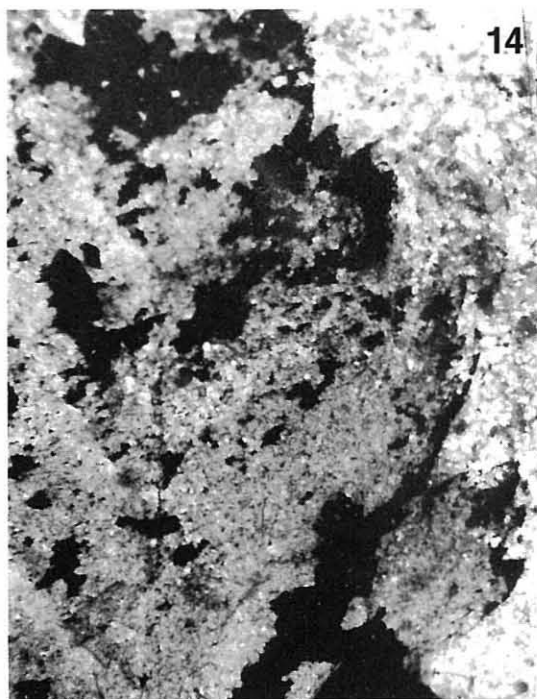
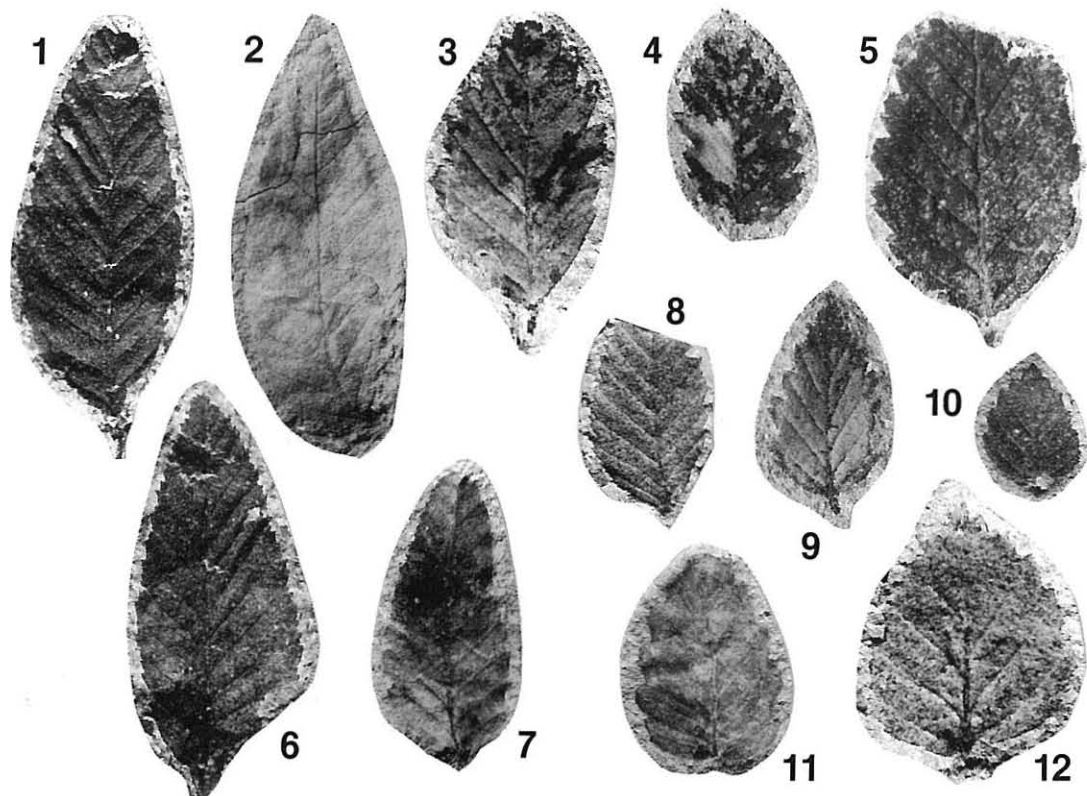


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Explanation of Plate 14

(All figures in natural size unless otherwise stated)

- Figs. 1, 6** *Nothofagus serrulata* Dusén. Las Minas, west of Punta Arenas, Magallanes, Chile. HUMP hypotype no. 26278a, b.
- Figs. 2, 7** *Nothofagus serrulata* Dusén. Rio Chico, west of Estacion San Sebastian, Fuego Island, Chile. HUMP hypotypes nos. 26279, 26280.
- Figs. 3-5, 8-10** *Nothofagus variabilis* Dusén. Las Minas, west of Punta Arenas, Magallanes, Chile. HUMP hypotypes, nos. 26300a, b, 26301-26304a, b. Fig. 3 × 2; Figs. 4, 5, 9 × 1.5
- Fig. 11** *Nothofagus variabilis* Dusén. Rio Chico, west of Estacion San Sebastian, Fuego Island, Chile. HUMP hypotype no. 26305. × 1.5
- Fig. 12** *Nothofagus variabilis* Dusén. the counterpart of fig. 10. HUMP no. 26300b. × 2
- Fig. 13** Showing the marginal serration and secondary vein termination of *Nothofagus serrulata* (enlargement of fig. 6). × 10
- Fig. 14** Showing the marginal serration and the secondary vein termination of *Nothofagus variabilis* (enlargement of fig. 4). × 10



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Explanation of Plate 15

(All figures in natural size unless otherwise stated)

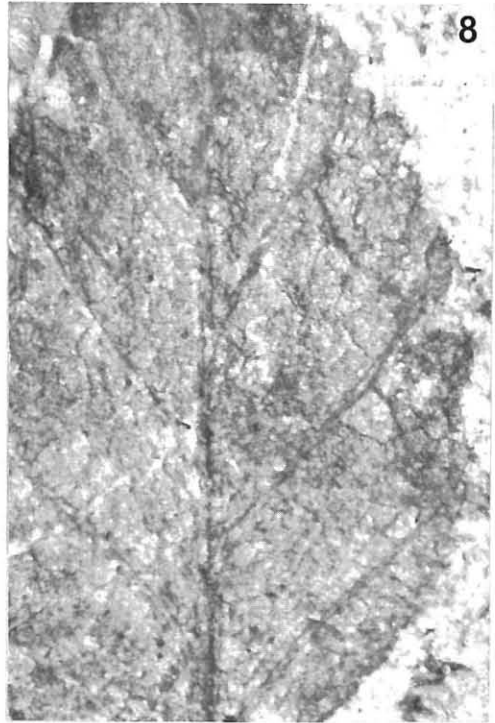
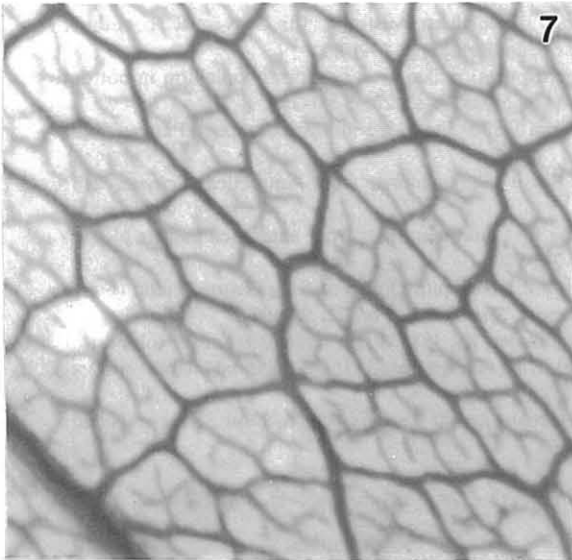
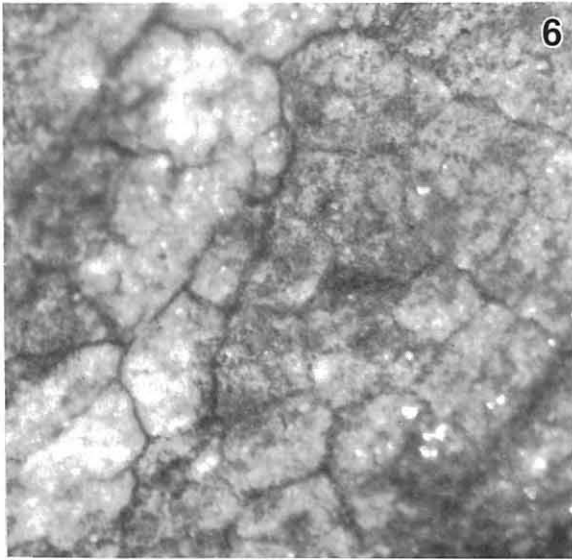
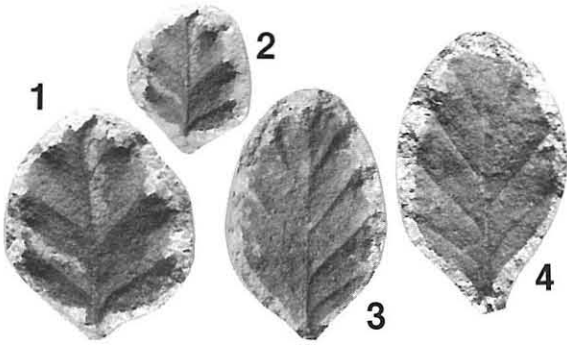
Figs. 1-4 *Nothofagus crenulata* Dusén. Rio Chico, west of San Sebastian, Fuego Island, Chile. HUMP hypotypes nos. 26250, 26251a, b. Figs. 1, 3, 4 × 2.5; Fig. 2 × 1.5; Fig. 4 (the counterpart of Fig. 3)

Fig. 5 Showing the marginal crenation and the secondary vein termination of *Nothofagus crenulata* (Enlargement of fig. 1). × 10

Fig. 6 Showing the areoles of *Nothofagus crenulata* (Enlargement of fig. 1). × 30

Fig. 7 Showing the areoles and ultimate veinlets of the extant *Nothofagus antarctica* (Forst.) Oerst. (HUPB Ref. Collection no. 1967) for comparison of *Nothofagus crenulata*. × 30

Fig. 8 Showing the marginal crenation and the secondary termination of *Nothofagus crenulata* (Enlargement of fig. 3) × 10



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