

THE GENUS PHYLLOCLADUS (PHYLLOCLADACEAE)

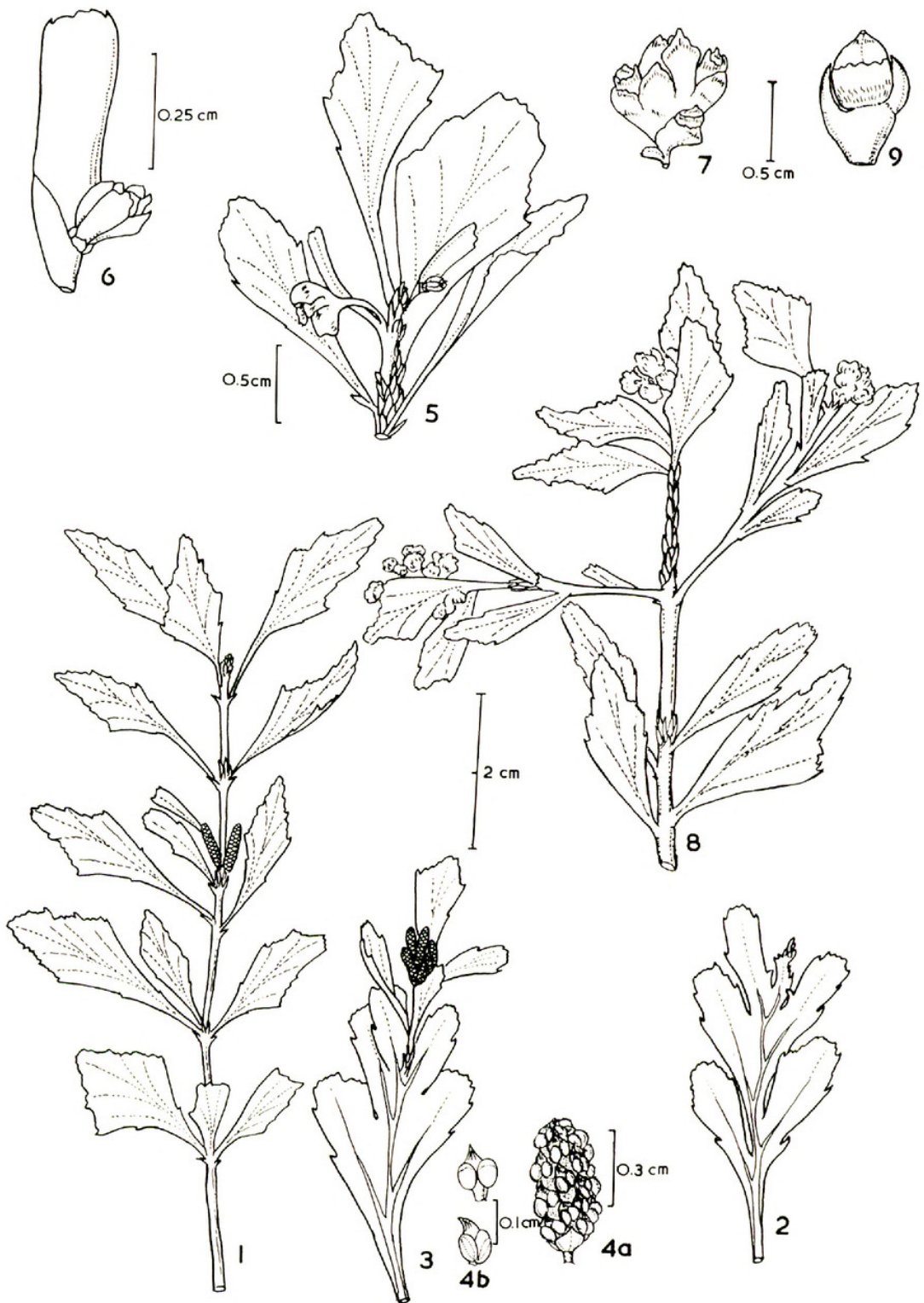
HSUAN KENG

THE CONIFEROUS GENUS *Phyllocladus* (Phyllocladaceae, formerly Podocarpaceae) was established by L. C. and A. Richard in 1826 based on the Tasmanian species *Phyllocladus rhomboidalis* L. C. & A. Rich., and is now known as *P. aspleniifolius* (Labill.) Hooker f. (FIGURES 1-9). This genus is noted particularly for the presence of large, celery-leaf-like photosynthetic organs (hence the common names "celery pine" or "celery-topped pine") which have been interpreted as phylloclades and from which the generic name is derived. The prevailing view of the origin and nature of the phylloclades is still dominated by the following statement made by Robertson (1906, p. 259) over half a century ago: "*Phyllocladus* is . . . characterized by the reduction of its true leaves to pointed scales, and the expansion of certain of its stem-branches into flattened leaf-like structures." This implies that the phylloclade is a highly specialized, and therefore an advanced, character.

My previous taxonomic and morphological studies on the genus were based mainly on a single Malesian species, *Phyllocladus hypophyllus* Hooker f. (Keng, 1963a, 1963b). From April to August, 1976, I visited Tasmania and New Zealand, and was able to examine living and preserved material and herbarium specimens of the other known species of *Phyllocladus*. In September and October, 1976, I also visited the Rijksherbarium, Leiden, the Netherlands, and examined a large number of herbarium specimens of *P. hypophyllus* collected from New Guinea and elsewhere in the Malesian regions. The main purpose of this extensive study tour was to re-examine my earlier suggestion (Keng, 1974) that the foliate phylloclade of this genus is a relict feature, possibly derived from or remotely related to the lateral branch systems of the recently established fossil taxon *Progymnospermae* (or *Progymnospermopsida*). This was discussed in a paper presented to an I.A.P.T. Symposium in September, 1976, in Hamburg, and has been published elsewhere (Keng, 1977). In this article, the morphology and taxonomy of the genus *Phyllocladus* are discussed, and brief notes on the evolutionary trends and the paleogeographic distribution of the genus are given.

MORPHOLOGY

HABIT. Species of the genus and, in some cases, plants of the same species, range from shrubs or small trees to large trees. *Phyllocladus aspleniifolius* var. *alpinus* (previously known as *P. alpinus*) is usually a bushy shrub at high altitudes. Its lowland form, however, may become a small tree, reaching 8-9 meters. *Phyllocladus glaucus* and *P. aspleniifolius* var. *aspleniifolius* are small to medium-sized trees; the former can attain about 12 meters,



FIGURES 1-9. *Phyllocladus aspleniifolius* var. *aspleniifolius*: 1, branch bearing whorled simple phylloclades and pollen cones; 2, pinnately lobed phylloclade with terminal bud; 3, young branch with simple phylloclades and pollen cones arising from tip of pinnately lobed phylloclade; 4a, pollen cone; 4b, microsporophyll bearing two pollen sacs (in two views); 5, portion of branch bearing ovulate cones; 6, ovulate cone on side of deformed simple phylloclade; 7, young seed cone; 8, branch bearing mature seed cones; 9, mature seed.

and the latter can reach approximately 18 meters under suitable conditions. The two remaining species, *P. trichomanoides* and *P. hypophyllus*, become lofty trees, reaching a height of approximately 25 and 30 meters, respectively. *Phyllocladus hypophyllus*, however, like most of the other species, becomes stunted in subalpine forests.

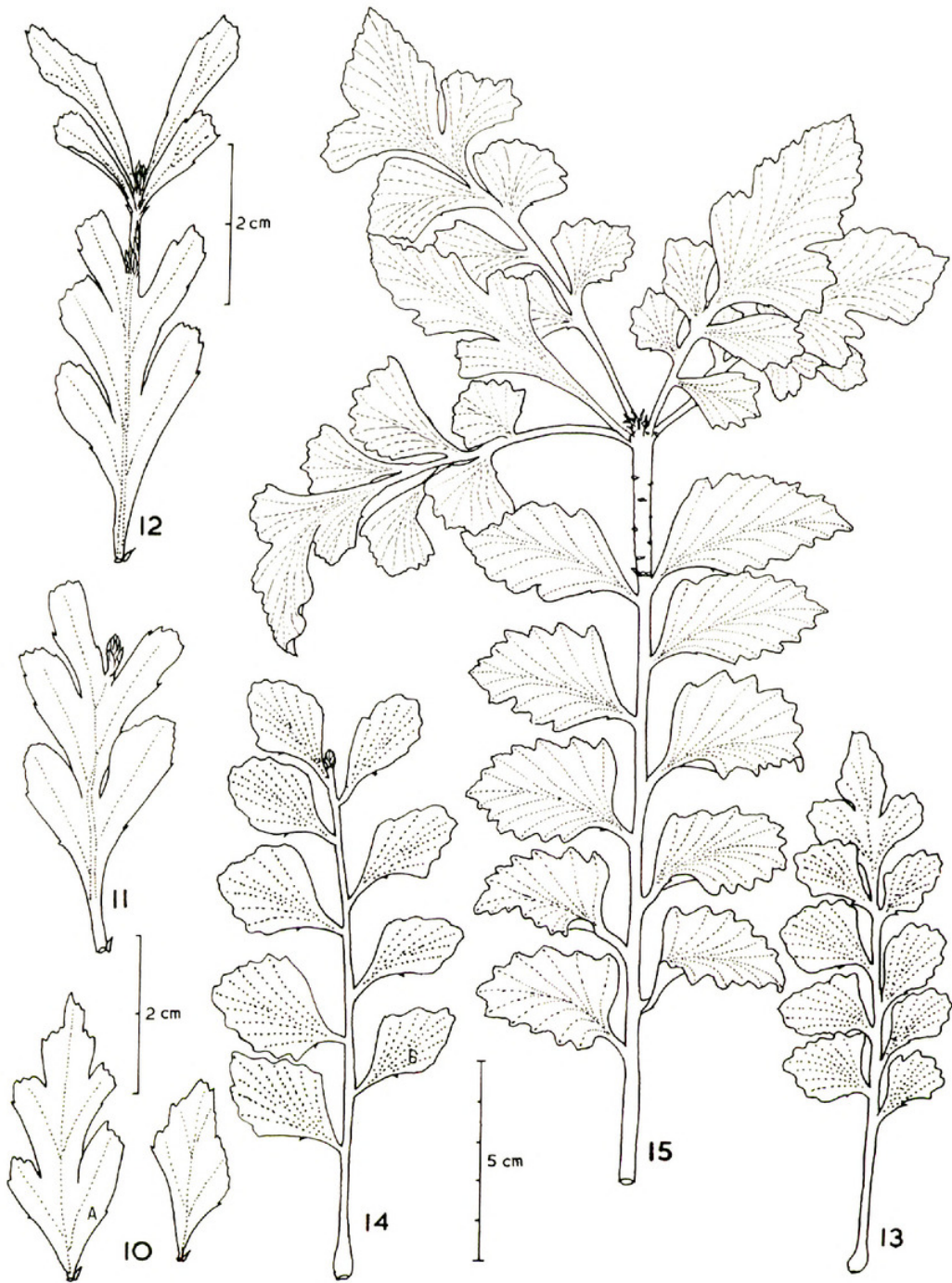
The bark of the species varies from greenish (*Phyllocladus trichomanoides*) to reddish brown (*P. hypophyllus*) or blackish (*P. aspleniiifolius* var. *aspleniiifolius*), and is yellowish or reddish and fibrous within. It is smooth (e.g., *P. trichomanoides*) or deeply fissured (e.g., *P. aspleniiifolius* var. *aspleniiifolius*), and is shed in large, thin flakes. Branches and branchlets are borne 3 to 5, rarely 8 or 9, in a false whorl. Trees of *Phyllocladus* can be readily identified in the field by their apparently whorled branches.

Species of *Phyllocladus*, especially *P. aspleniiifolius* var. *alpinus*, must be among the slowest growing conifers. A seven-year-old seedling of *P. aspleniiifolius* var. *alpinus* in its natural habitat was only 6 cm. tall. It was fully covered with linear juvenile leaves, and one of its two withered cotyledons still persisted. A seedling only 12 cm. tall was estimated to be 25 years old. Trunks of *P. aspleniiifolius* var. *alpinus* hardly exceed 30 cm. in diameter, yet may show up to 190 growth rings (Wardle, 1969).

A wild seedling of *P. aspleniiifolius* var. *aspleniiifolius* of unknown age was brought into cultivation at the Botany Department of the University of Tasmania and, after about 15 years (Prof. W. D. Jackson, University of Tasmania, pers. comm.) has reached a height of 1.1 meters and has begun to produce staminate cones. Displayed at the same department is a large disc of wood with a diameter of about 45 cm. (maximum radius 29 cm., minimum radius 20 cm.). This came from a tree that was cut in 1944 and was estimated by carefully counting the annual rings to be 389 years old.

PHYLLOCLADES (Cladodes). The unique "foliar" organ of the genus is a phylloclade or cladode, which emerges from the axil of an acicular leaf. Phylloclades are alternate, opposite, or more frequently in false whorls on stems and branches. They are thick and leathery, and are extremely variable in shape and size, apparently being easily modified by environmental changes; they can also be quite different in juvenile and adult plants. There are two types of phylloclades: simple phylloclades are found in *Phyllocladus aspleniiifolius* var. *aspleniiifolius* (FIGURE 10) and var. *alpinus*, while pinnately compound ones are characteristic of *P. glaucus* (FIGURES 13, 14), *P. hypophyllus*, and *P. trichomanoides*.

Simple phylloclades are 1–4 cm. long and are mostly rhombic in outline. Their margins are finely toothed or nearly entire, or sometimes shallowly to deeply 2- to 3-lobed on one or both sides in the lower part. They may also be pinnatifid, but are only very rarely pinnately compound. Some of the pinnatifid phylloclades bear a terminal bud which is covered with awl-shaped scales (FIGURE 11). These buds either remain dormant or give rise to a short shoot usually 1–4 cm. long. These short shoots are spirally covered with short, lanceolate, deciduous leaves, and terminate



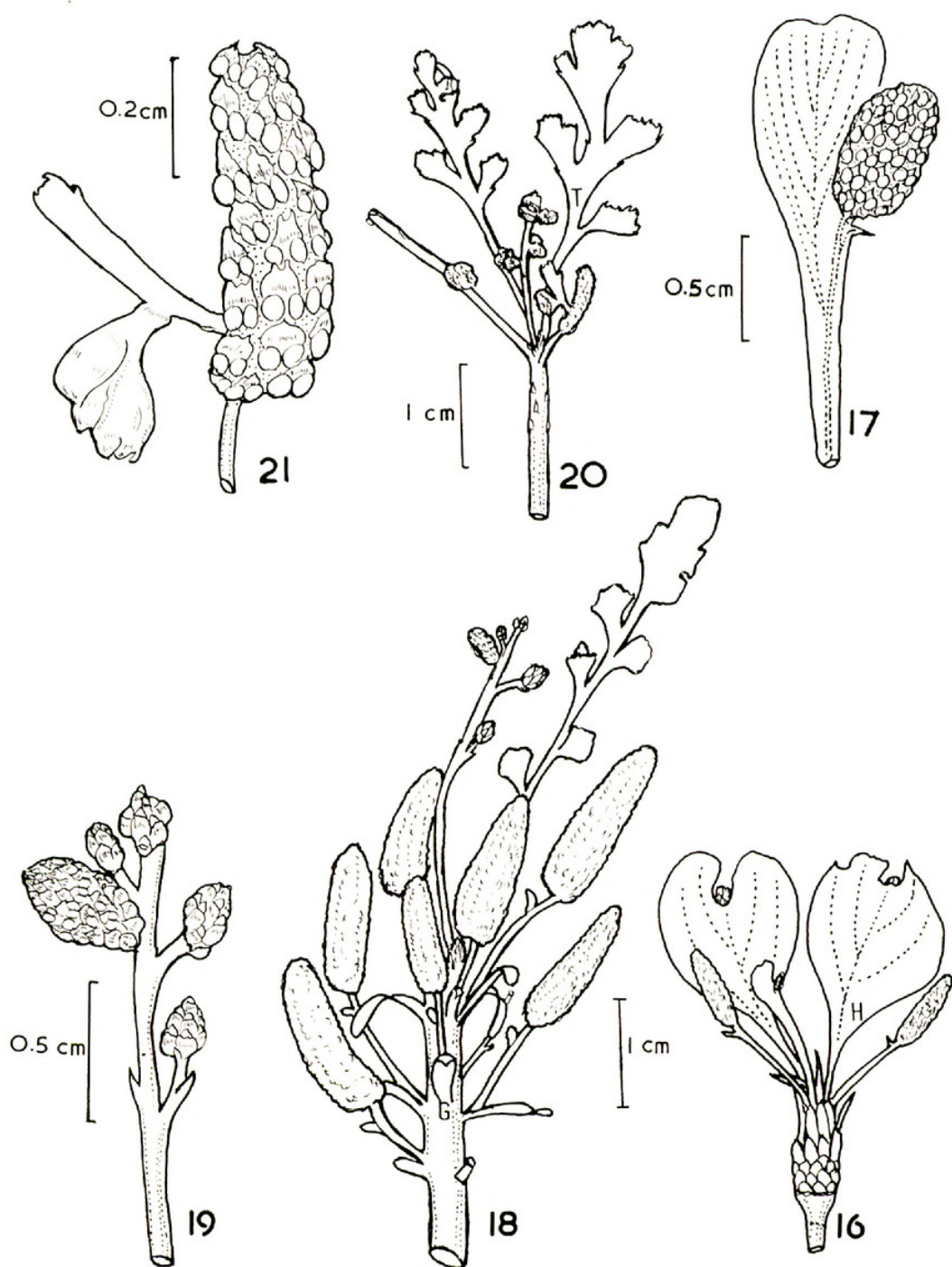
FIGURES 10-15. Simple and pinnately compound phylloclades. 10-12, *Phyllocladus aspleniifolius* var. *aspleniifolius*: 10, two simple phylloclades without terminal bud, one undivided, the other pinnately lobed; 11, simple pinnately lobed phylloclade with terminal bud; 12, short shoot arising from pinnately lobed phylloclade. 13-15, *P. glaucus*: 13, pinnate phylloclade with terminal lobe in place of terminal bud; 14, pinnate phylloclade with terminal bud; 15, short shoot with crown of pinnate phylloclades arising from tip of pinnate phylloclade.

in a group of 3 to 5 simple or occasionally pinnatifid phylloclades with a new terminal bud in the center (FIGURE 12).

The pinnately compound phylloclades can reach 10–15 cm. in length (in vigorous growth and especially in saplings they may be 30 cm. long), each of them consisting of 5 to 10 (to 12 or more) segments or pinnae distichously arranged in two rows along the rachis. In taxonomic literature these individual segments or pinnae have often been misleadingly called phylloclades or cladodes. The pinnate phylloclades, like the simple ones, may or may not possess a terminal bud (FIGURES 13, 14). In the former case, the terminal bud can develop into a short shoot 4–10 cm. (–15 cm. or more) long. This new short shoot is partly and sparsely covered with deciduous, linear-lanceolate scale leaves and is crowned with 3 to 5 (to 10) normally pinnately compound phylloclades, in addition to a terminal bud (FIGURE 15). In the latter case, there is always a large, prominent terminal segment in lieu of the terminal bud; this terminal segment is often partly lobed or partially fused with one or both lateral segments below it (FIGURE 13).

MONOECY AND DIOECY. In taxonomic literature, the same species of *Phyllocladus* has been described as monoecious or dioecious by different authors. For example, *P. asplenifolius* var. *alpinus* was generally considered as monoecious, but Wardle (1969), after careful observation, pointed out that dioecy is the usual condition. It is known that a *Phyllocladus* tree that normally produces pollen cones can occasionally produce a few ovulate cones, although the latter are often aborted to various degrees. Reduced ovulate cones have been found on the same branch with pollen cones in *P. hypophyllus* (Keng, 1962b) (FIGURE 16). Abnormal pollen cones of *P. asplenifolius* var. *alpinus*, each with an ovule at its base, were first reported by Robertson (1906) and again by Wardle (1969). During the present study (FIGURES 20, 21), a well-developed pollen cone was found on a branch of *P. trichomanoides* that bore predominantly ovulate cones. Preserved material of *P. glaucus* collected by Dr. A. E. Orchard from Cranwell Park, Auckland, New Zealand, shows a number of interesting abnormalities. There are 10 to 15 normal pollen cones spirally arranged on the axis of a dwarf shoot, and each is subtended by a lanceolate bract. At the top of the shoot, there are several pinnate phylloclades bearing reduced ovulate cones (FIGURE 18). Some of the pollen cones have reduced ovules at their bases. A most extraordinary teratological specimen from the same collection shows that some of these reduced ovules are in fact subtended by scales in turn bearing two minute pollen sacs.

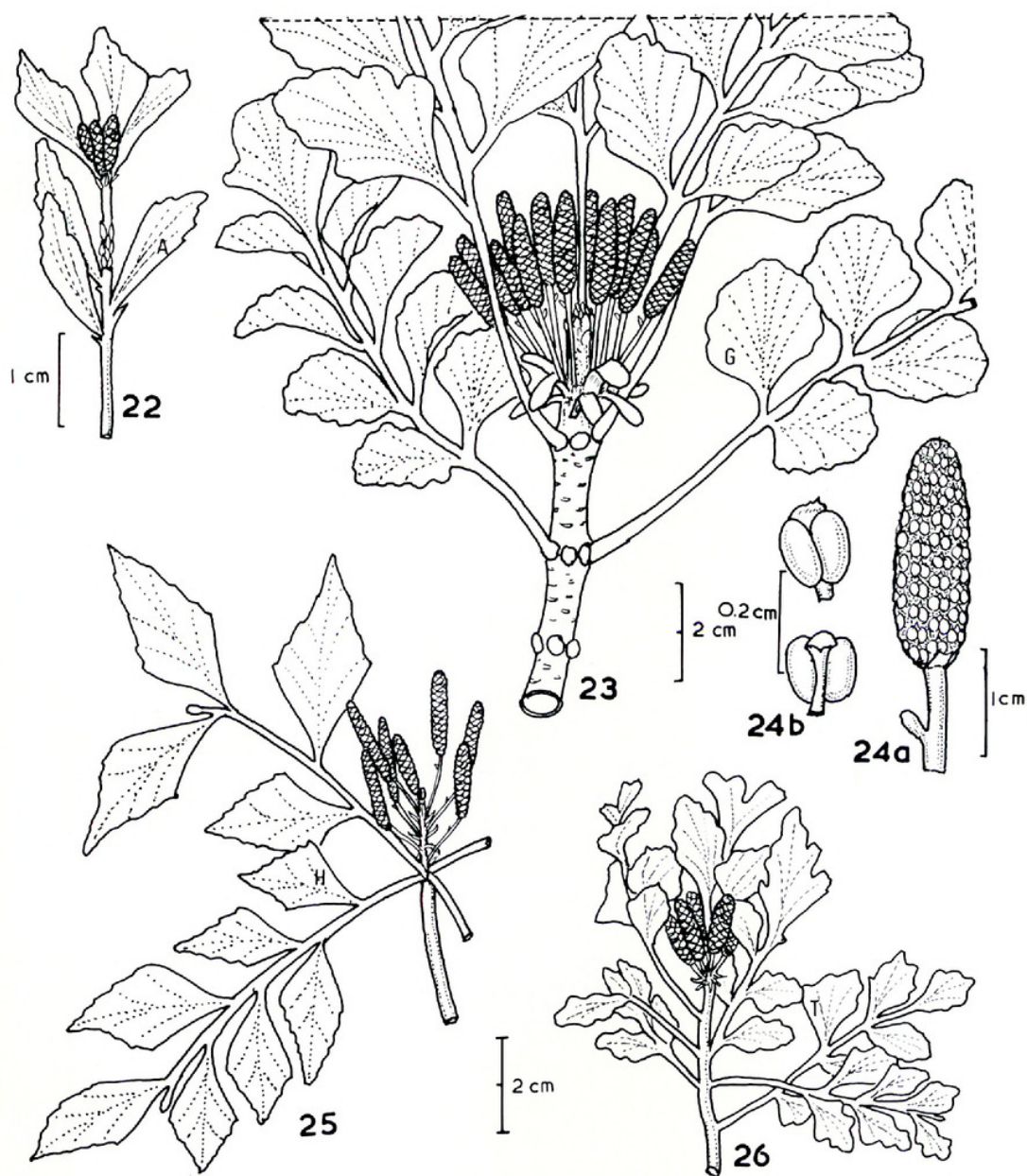
It appears that young trees of most species of *Phyllocladus*, with the possible exception of *P. glaucus*, bear either pollen or ovulate cones and thus are clearly dioecious. When the trees become older, the distinction is less clear. Dr. B. P. J. Molloy of the D.S.I.R., Lincoln, New Zealand, however, believes (pers. comm.) that sexuality of *Phyllocladus* gradually becomes more stable in older trees. Further observation is needed.



FIGURES 16-21. Some teratological specimens of *Phyllocladus*. 16, 17, *P. hypophyllus*: 16, pollen cones and underdeveloped ovulate cones arising from same branch; 17, pollen cone borne on partly deformed phylloclade. 18, 19, *P. glaucus*: 18, pollen cones spirally arranged on elongate short shoot, with partially reduced ovulate cones above; 19, reduced ovulate cones enlarged, the largest one with ovulate scales concealing aborted pollen sacs beneath. 20, 21, *P. trichomanoides*: 20, branch with ovulate cones and single pollen cone; 21, pollen cone, enlarged.

POLLEN CONES. The pollen cones are nearly sessile or short stalked and are usually crowded on the tip of an unfolding side branch. After the elongation of the new shoot from the tip of a side branch, it becomes apparent that these pollen cones are actually spirally arranged along the axis of the new shoot, and each cone is usually subtended by a bract. Old, dry pollen cones may remain on the tree for months or even years.

The young pollen cones are purplish pink to sulphur yellow in color. There are from 2 to 5 (as in *Phyllocladus aspleniifolius* var. *aspleniifolius*, FIGURE 22) up to about 20 (as in *P. glaucus*, FIGURE 23) cones together. The pollen cones are cylindrical, 1.5–2 (in *P. aspleniifolius*) to 3–4 (in



FIGURES 22–26. Branches of *Phyllocladus* with pollen cones: 22, *P. aspleniifolius* var. *aspleniifolius*; 23, 24, *P. glaucus* (after T. Kirk); 25, *P. hypophyllum*; 26, *P. trichomanoides*.

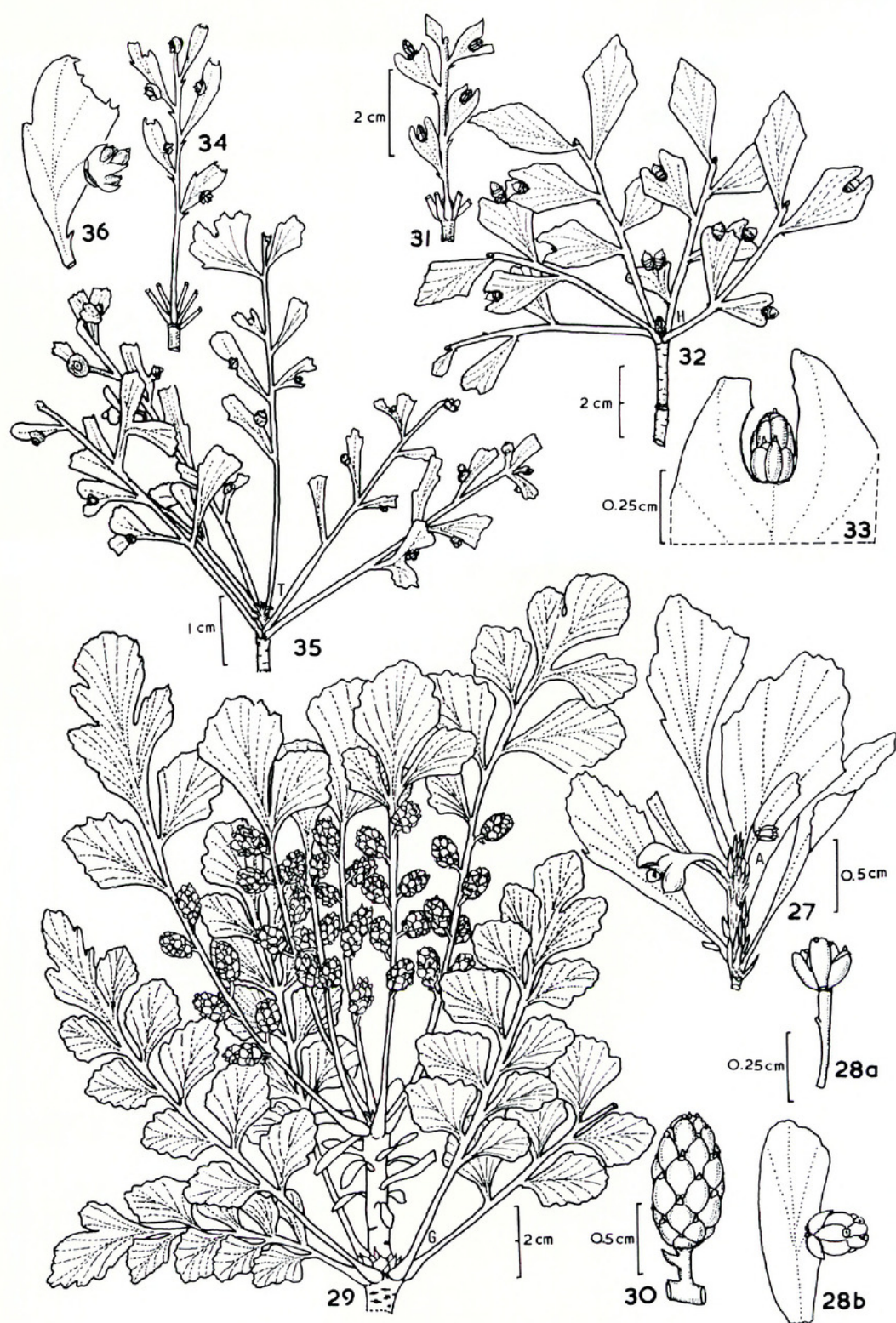
P. glaucus) cm. long, and consist of approximately 30 to 50 (to 60 to 70) cone scales spirally arranged along an axis. The cone scales are triangular in shape, often with a pointed tip and toothed upper margins. Each cone scale bears a pair of pollen sacs at its base (FIGURE 24). The pollen grains have two tiny bladder wings and are dispersed by wind.

The stalk of the pollen cone is always associated with a bractlike structure. From observation of teratological specimens of *Phyllocladus hypophyllus* (Keng, 1963b, 1974) (FIGURE 17) and other species, it was suggested that the bractlike structure on the stalk might represent a much-reduced simple phylloclade. It probably means that the pollen strobili were originally borne at the end of a simple phylloclade (or on the segments of a pinnate phylloclade). A similar situation still occurs in the ovulate strobili of modern species.

OVULATE CONES. In the species with simple phylloclades (i.e., *Phyllocladus asplenifolius* var. *asplenifolius* (FIGURE 27) and var. *alpinus*), the ovulate cones are single or borne 2 to 4 together. They arise below or on one side of a slightly deformed cladode (FIGURE 28, b), or are apparently terminal on a long stalk (FIGURE 28, a), the entire cladode being reduced. In species with pinnate phylloclades (*P. glaucus*, *P. hypophyllus*, and *P. trichomanoides*), the ovulate cones are either seated in the notch of a bilobed segment (e.g., *P. hypophyllus*) (FIGURES 31, 32) or attached to both sides of the rachis of a pinnate cladode, occupying the place of the lower lateral segments (e.g., *P. glaucus*) (FIGURE 29). Although these are the normal situations, there is considerable variation. For example, in *P. hypophyllus* the notched segments may be reduced to various degrees while the main axis of a pinnate cladode becomes enlarged and columnar; in *P. trichomanoides* (FIGURES 34, 35), on the other hand, the segments underneath the ovulate cones often become deformed or almost obsolete.

The ovulate cones are sessile (e.g., *Phyllocladus hypophyllus*) (FIGURE 33) or short stalked (e.g., *P. glaucus*) (FIGURE 30). They are usually ovoid in outline and consist of few to many, more or less spirally arranged cone scales. Some of these scales (usually 2 or 3, sometimes more) possess a single axillary ovule; most of the others, however, are barren. In most species, normally only one (rarely two or three) ovule in an ovulate cone develops into a seed, but in *P. glaucus* a fair number of seeds (5 to 10, sometimes up to 20) are produced in a single cone.

SEEDS. The seeds are oval in shape, slightly compressed dorsiventrally, and pointed above, often with a tiny, crooked tip. They are generally very small. Among the four species, *Phyllocladus trichomanoides* has the smallest seeds (2–3 mm. long), and *P. hypophyllus* the largest (6–8 mm. long). A conspicuous, cup-shaped aril protrudes beyond the ripe cone scales and envelops the lower half or two-thirds of the seed (FIGURE 9). The aril is more or less symmetrical, but the upper edge is often dentate or irregularly lobed. Mature cone scales are fleshy or leathery, and more or less fused. The cone scales form an amorphous mass known as the "receptacle" in the species with fewer cone scales; in *P. glaucus* the cone scales remain dis-



FIGURES 27-36. Branches of *Phyllocladus* with ovulate and seed cones. 27, 28, *P. aspleniifolius* var. *aspleniifolius*: 27, branch with both ovulate and young seed cones; 28, a, b, two ovulate cones, one subtended by phylloclade, the other appearing terminal. 29, 30, *P. glaucus*: 29, branch with seed cones borne on lower part of pinnate phylloclades (after T. Kirk); 30, ovulate cone. 31-33, *P. hypophyllus*: 31, ovulate cone in notches of pinnae of pinnate phylloclade; 32, branch with seed cones in notches of pinnae of pinnate phylloclades; 33, ovulate cone. 34-36, *P. trichomanoides*: 34, ovulate cones on one side of pinnae of pinnate phylloclade; 35, branch with seed cones; 36, ovulate cone.

tinguishable, and are more numerous (to about 20). Fully ripened scales usually turn bright red, in sharp contrast to the colors of the aril and seed, the former normally being white and the latter either chestnut brown (as in *P. hypophyllus*) or black (as in *P. aspleniiifolius* and others). The mature seeds fall from the arils to the ground close to the parent tree. However, due to the highly contrasting colors of the seed, the aril, and the receptacle, as well as the small size of the seed, it is conceivable that the seed of *Phyllocladus* might also be dispersed by birds as suggested by Preest (1963).

SEEDLINGS. The two cotyledons (FIGURE 37) are usually early deciduous but may last for two to several years before turning brown and withering away; they always leave a pair of inconspicuous scars on the lower part of the axis. They are linear-lanceolate in shape, double-nerved, 1.5–2 cm. long, and shallowly notched or bilobed at the apices. The juvenile leaves are linear and single-veined, varying between 0.5 and 1 cm. in length. They are spirally arranged on the axis. Their apices are acute or rounded and are often sharp pointed at the extremity. Later-produced leaves become successively smaller, finally being lanceolate or triangular scale leaves usually 2–3 mm. long; phylloclades or cladodes are present in the axils of some of these scale leaves. In *Phyllocladus aspleniiifolius* (FIGURE 38), the cladodes on seedlings are mostly simple, although toothed or crenate to various degrees in the margins. In *P. hypophyllus* (FIGURES 40, 41), the earlier-formed cladodes are simple; these are gradually replaced by the deeply lobed ones. The lobation then becomes more pronounced until, finally, almost all the cladodes are pinnately compound. In *P. glaucus* (FIGURE 39) and *P. trichomanoides* (FIGURES 42, 43), even the earlier-formed cladodes are pinnatifid. In the latter species, the cladodes of a fully grown seedling are distinctly pinnate and with the pinnae further shallowly or deeply lobed, thus approaching a bipinnate state (FIGURE 43).

The color of the seedlings varies from green (*Phyllocladus aspleniiifolius*), to grayish green (*P. glaucus*, *P. hypophyllus*), to purplish (*P. trichomanoides*), but this also depends on environmental conditions. Seedlings of nearly all species of *Phyllocladus*, especially those of *P. aspleniiifolius* var. *aspleniiifolius* and var. *alpinus*, are highly polymorphic with respect to the shape, size, and dentation of the early-formed cladodes. This probably suggests that they are not homogeneous genetically.

Dr. R. K. Crowden, of the University of Tasmania (pers. comm.), points out that in Tasmania, where forest fires are comparatively frequent, *Phyllocladus aspleniiifolius* var. *aspleniiifolius* is well adapted for survival. Seeds of this plant can probably remain in the forest soil for several years. After a forest fire, the vegetation is largely devastated, but a great number of seedlings of *Phyllocladus* often appear in the burned-over area. In contrast to this, seeds of the New Zealand species appear to be very short lived (Dr. B. P. J. Molloy, pers. comm.).

Seedlings of all the *Phyllocladus* species observed possess root nodules which contain symbiotic, nitrogen-fixing bacteria. These nodules are

especially well developed in the Tasmanian and New Zealand species. This is probably one of the attributes that enable the seedlings to survive in a rather unfavorable environment.

EVOLUTIONARY TRENDS

The following hypothetical evolutionary trends seem to occur within the genus *Phyllocladus*. In the trends listed, the simpler condition is considered to be the derived state; the more complex condition, the ancestral.

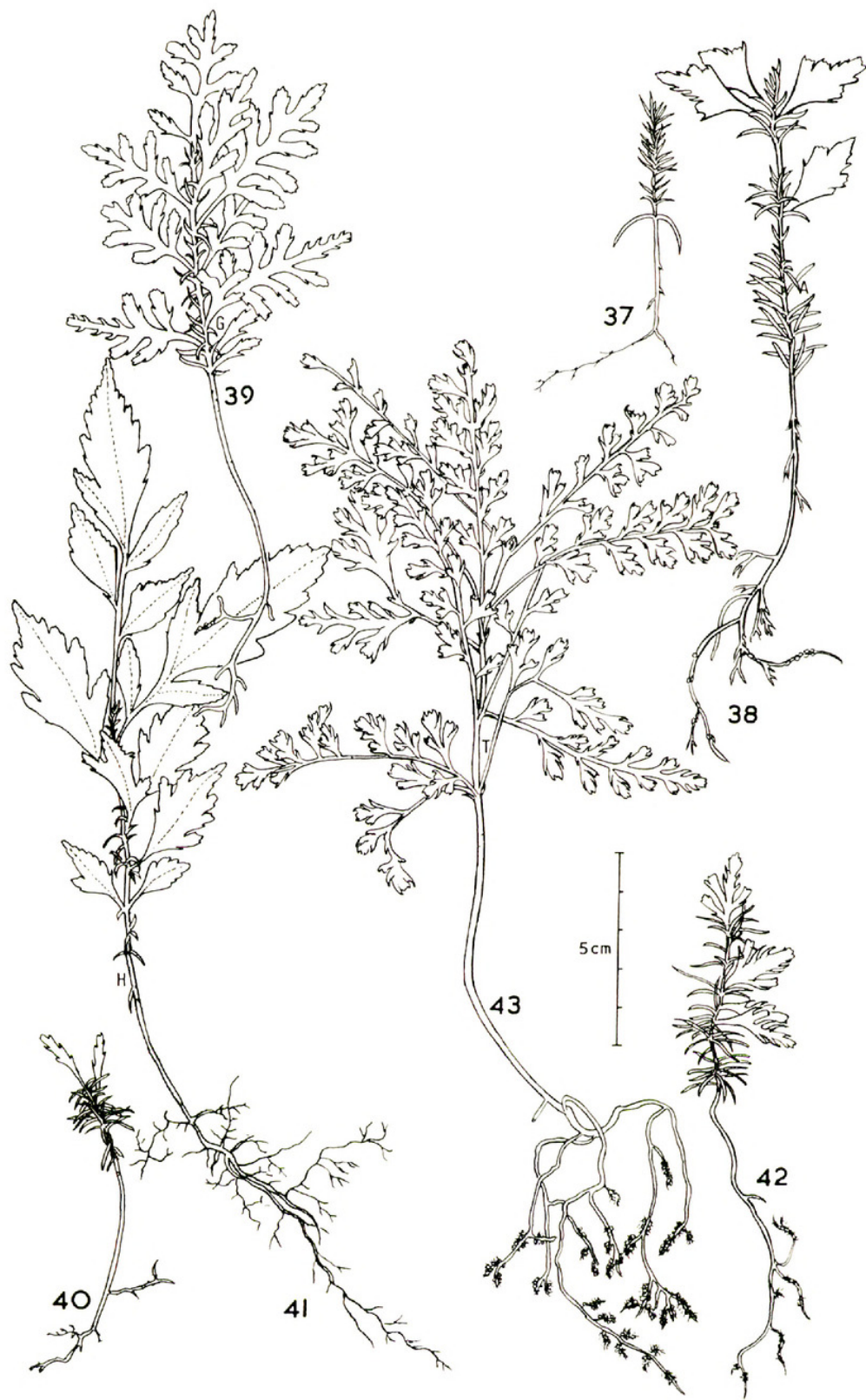
PHYLLOCLADES. The seemingly bipinnate phylloclades, as seen in the seedlings of *Phyllocladus trichomanoides* (FIGURE 43), likely represent the ancestral form from which simple pinnate, pinnatifid, and finally simple phylloclades (as in *P. asplenifolius*, FIGURE 10) were probably evolved.

POLLEN STROBILI. Each pollen strobilus was probably originally seated in the top notch of a simple phylloclade, as shown in a teratological specimen of *Phyllocladus hypophyllus* (FIGURE 17). These simple phylloclades are usually either reduced and bractlike (FIGURE 24, a) or obsolete. In *P. glaucus*, there are numerous (about 20) long-stalked, bracteate strobili, each composed of many (approximately 60 to 70) sporophylls. These strobili first appear to be crowded on the top of a short shoot and to surround the terminal bud (Figures 23, 26); later, after the activation of the terminal bud and the elongation of the new short shoot, it becomes clear that they are actually spirally arranged on the new short shoot (FIGURES 18, 25). In contrast, *P. asplenifolius* var. *asplenifolius* (FIGURES 1, 3, 4) has only 2 or 3 almost sessile strobili, with each strobilus composed of only 30 to 50 sporophylls. The latter probably represents the most highly evolved form.

OVULATE STROBILI. Each strobilus was probably originally seated in the notch of a pinna of a pinnate phylloclade, as shown in *Phyllocladus hypophyllus* (FIGURES 31, 33) and in some cases also in *P. trichomanoides* (FIGURE 35). These pinnate phylloclades thus remarkably and uniquely perform both vegetative and reproductive functions. There are 4 or 5 or more strobilus-bearing pinnate phylloclades together, arranged on the top of a short shoot in a false whorl. Each strobilus, presumably in the basic form, consists of a large number (to 20 or so) of fertile scales, as seen in *P. glaucus* (FIGURE 30).

DISTRIBUTION OF SEXES. The trend seems to be from monoecious to dioecious. Nearly every species of *Phyllocladus* shows a certain degree of monoecism. The ancestral form probably possessed a number of simple phylloclades spirally arranged on a short shoot, each of which bore a terminal staminate strobilus. On the tip of the same short shoot, there was a crown of pinnate phylloclades, each with an ovulate strobilus on its pinna (cf. FIGURE 18).

In short, among the four living species, it appears that *Phyllocladus glaucus* probably preserves more primitive traits than do the other species. This species is followed by *P. hypophyllus* and *P. trichomanoides*. Con-



FIGURES 37-43. Seedlings of *Phyllocladus*: 37, 38, *P. aspleniifolius* var. *aspleniifolius*; 39, *P. glaucus*; 40, 41, *P. hypophyllus*; 42, 43, *P. trichomanoides*.

versely, *P. aspleniifolius* var. *aspleniifolius* and var. *alpinus* in many respects possibly represent the much-reduced or the highly evolved form.

TAXONOMIC TREATMENT

Phyllocladus L. C. & A. Richard, Comment. Bot. Conif. Cycad. 129. t. 3, fig. 12. 1826.

Podocarpus Labill. Nov. Holl. Pl. Sp. 2: 71. t. 221. 1806, non L'Hérit. ex Pers.
Brownetera L. C. Rich. Ann. Mus. Hist. Nat. Paris 16: 299. 1810, *nomen nudum*.
Thalamia Sprengel, Anl. Kennt. Gewächse. ed. 2. 2: 218. 1817.

Shrubs or small to large trees. Juvenile leaves at first linear, changing gradually to subulate and scaly. Phylloclades simple, pinnatifid, or pinnately compound, variable in shape and size, usually 2 to 5 or more in a false whorl. Plants with unisexual strobili mostly dioecious, sometimes monoecious. Pollen cones 2 or 3 (up to 20), crowded in a cluster on the top of a short shoot, becoming spirally arranged along the new short shoot after its elongation; individual pollen cones consisting of 30 to 70 spirally arranged sporophylls, each bearing 2 pollen sacs; pollen grains winged. Ovulate cones terminal or marginal on fully grown or reduced simple phylloclades, or on the pinnae of a pinnate phylloclade, the phylloclades 2 to 5 or more in a false whorl on the top of a short shoot; individual ovulate cones consisting of few, several, or numerous scales, usually only one or few, sometimes many (as in *Phyllocladus glaucus*) of the scales being fertile; ovules erect, solitary in the axil of a scale. Seeds ovoid, dorsiventrally compressed, subtended by a cup-shaped, filmy aril and the often fused, succulent scales.

Four species, distributed in Tasmania, New Zealand, and Malesia (from New Guinea to Luzon and Borneo).

TYPE SPECIES: *Phyllocladus rhomboidalis* L. C. & A. Richard (= *Phyllocladus aspleniifolius* (Labill.) Hooker f.).

KEY TO THE SPECIES OF PHYLLOCLADUS

- A. Phylloclades of adult plants mostly simple, sometimes shallowly or deeply lobed, occasionally pinnatifid, very rarely truly pinnate. [Ovulate cones solitary or 2 to 4 on the margins and base of a modified (often much-reduced, with the cones thus seeming to be terminal) phylloclade, usually two or more such modified or reduced phylloclades together in a small cluster.] 1. *P. aspleniifolius*.
- A. Phylloclades of adult plants always pinnate, consisting of 5 or 6 to many (about 12) distinct segments.
 - B. Ovulate cones normally seated in the apical notch of a segment of the phylloclade, the segment varying from obcordate to oblanceolate, sometimes columnar, very rarely totally reduced; mature seeds 5–8 mm. long, mostly solitary, rarely in pairs, in an ovulate cone. 3. *P. hypophyllus*.
 - B. Ovulate cones usually on the margins and base of a segment which is often highly modified (the lower segments in a pinnate phylloclade sometimes

totally reduced, the ovulate cones thus appearing to be terminal on a side branch of the rachis); mature seeds 2–4 mm. long, 1 to many per cone.

C. Ovulate cones consisting of about 10 to 20 fertile scales; mature cones 1 or rarely 2 seeds; pollen cones 5 to 10 terminating a branchlet.

..... 2. *P. glaucus*.

C. Ovulate cones consisting of 2 or 3 fertile scales; mature cones with 1 or rarely 2 seeds; pollen cones 5 to 10 terminating a branchlet.

..... 4. *P. trichomanoides*.

1. *Phyllocladus aspleniifolius* (Labill.) Hooker f. in London Jour. Bot. 4: 151. 1845.

Podocarpus aspleniifolia Labill. Novae Holl. Pl. Sp. 2: 71. t. 221. 1806. TYPE: Tasmania, J.-J. H. de Labillardière (not seen).

Phyllocladus rhomboidalis L. C. & A. Rich. Comment. Bot. Conif. Cycad. 23. t. 3, fig. 2. 1826.

Phyllocladus billardieri L. C. Rich. ex Mirbel in Mém. Mus. Hist. Nat. Paris 13: 48. 1825, *nomen nudum*.

Thalamia aspleniifolia (Labill.) Sprengel, Anl. Kennt. Gewächse. ed. 2. 2: 218. 1817.

Shrub or small to medium-sized tree, 6–18 m. high. Bark brownish to dark brown, deeply furrowed in old trees. Juvenile leaves on seedlings linear, 0.7–1 cm. long. Scale leaves on seedlings and on the short branches of adult plants triangular or subulate, 0.1–0.3 cm. long. Phylloclades on seedlings usually linear-oblong to rhomboid, 1.5–2.5 cm. by 1–1.2 cm., shallowly or deeply lobed, sometimes pinnatifid; phylloclades on adult plants mostly simple, rhomboid, 2.5–8 cm. by 1.5–2 cm., the apex acute or blunt, the base cuneate, sessile or stalked, the margins irregularly lacerate or occasionally pinnatisect, very rarely pinnately compound. Plants usually dioecious. Pollen strobili usually 2 or 3 (to 5) together, terminating lateral branches, cylindrical, 0.3–0.5 (–1) cm. long, sulphur yellow, short stalked. Ovulate strobili solitary or several (2 to 4) at the side or base of a modified or highly deformed phylloclade, or sometimes the latter totally reduced, with 2 to 4 ovulate strobili together forming a seemingly terminal stalked cluster, each strobilus consisting of 2 or 3 (to 5) erect ovules each subtended by a pinkish red, fleshy scale. Seeds ovoid, about 0.5 cm. long, greenish black to black; aril white, irregularly lobed; receptacle purplish red and fleshy.

KEY TO THE VARIETIES OF *PHYLLOCLADUS ASPLENIIFOLIUS*

- A. Shrub or small to medium-sized tree, maximum height about 18 m.; scale leaves on short shoots of adult plants subulate, 0.2–0.3 cm. long. Confined to Tasmania. 1a. var. *aspleniifolius*.
- A. Shrub or small tree, maximum height about 9 m.; scale leaves on short shoots of adult plants triangular, less than 0.1 cm. long. Restricted to New Zealand. 1b. var. *alpinus*.

1a. *Phyllocladus aspleniifolius* (Labill.) Hooker f. var. *aspleniifolius*. FIGURES 1-9.

Phyllocladus aspleniifolius (Labill.) Hooker f. in London Jour. Bot. 4: 151. 1845; Henkel & Hochst. Synop. Nadelhölzer, 371. 1865; Pilger in Engler, Pflanzenr. 4(5): 97. 1903; Curtis in Stones, Endemic Fl. Tasmania 3: 106. pl. 60. 1971; Curtis & Morris, Stud. Fl. Tasmania. ed. 2. 1: 2. fig. 2. 1975.

Phyllocladus rhomboidalis L. C. & A. Rich. Comment. Bot. Conif. Cycad. 23. t. 3, fig. 2. 1826; Endlicher, Synop. Conif. 235. 1847; Hooker f. Fl. Tasmaniae (Bot. Antarctic Voy. pt. 3) 1: 358. 1859; Carrière, Traité Gén. Conif. ed. 2. 706. 1867; Parlatore in DC. Prodr. 16(2): 499. 1868; Curtis, Stud. Fl. Tasmania 1: 234. 1956.

Phyllocladus billardieri L. C. Rich. ex Mirbel in Mém. Mus. Hist. Nat. Paris 13: 48. 1825, *nomen nudum*.

Phyllocladus serratifolia Nois. ex Henkel & Hochst. Synop. Nadelhölzer, 372. 1865.

Podocarpus aspleniifolia Labill. Novae Holl. Pl. Sp. 2: 71. t. 221. 1806.

Thalamia aspleniifolia (Labill.) Sprengel, Anl. Kennt. Gewächse. ed. 2. 2: 218. 1817.

This variety is characterized by its taller stature (maximum height about 18 m.) and by its longer (about 0.2-0.3 cm.) subulate scale leaves on the short shoots of adult plants.

DISTRIBUTION. Endemic to Tasmania, Australia (MAP 1). In temperate rain and wet sclerophyll forests, from 500 to 800 meters, largely confined to the western or the moist parts, occasionally descending to sea level in wet coastal areas.

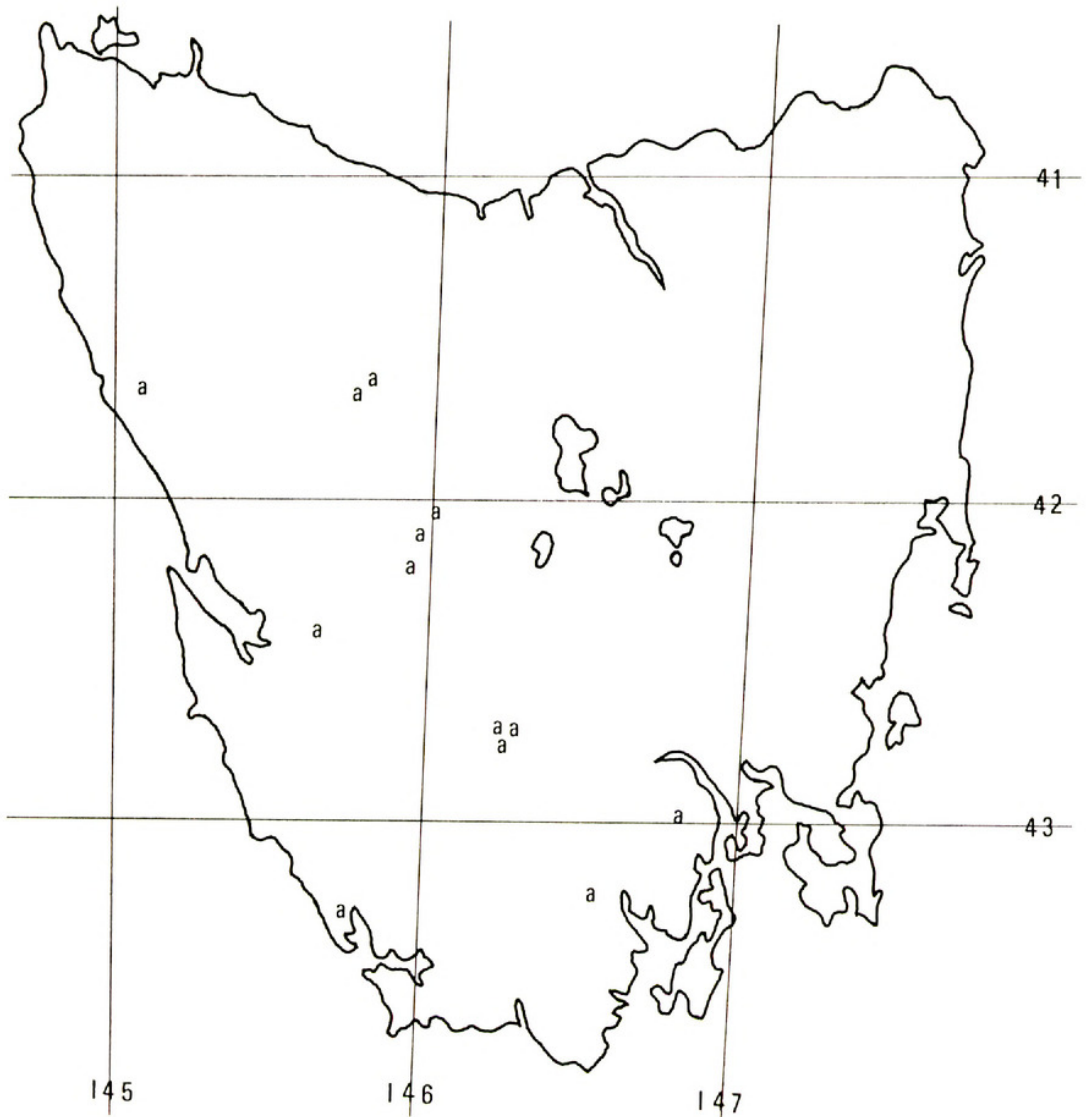
REPRESENTATIVE SPECIMENS. Australia. TASMANIA: Corinna, W. D. Jackson, J 146 (HO 2775); Cradle Mts., N. Sunderland (HO 2776); Lake St. Clair, below Mt. Ida, N. T. Burbidge (HO 2768); King William Range, E. Rodway 134 (HO 2767); Mt. Field Nat. Park, H. D. Gordon (HO 2756); W. M. Curtis (HO 2751); Wishing Well, Mt. Wellington, J. Somerville (HO 2766); Huon River, near Picton Hut, Somerville 288 (HO 2806); near Franklin Bridge, Lyell Highway, J. Townrow (HO 2782, 2801); Port Davey, D. H. Martin (HO 2777, 2778).

1b. *Phyllocladus aspleniifolius* (Labill.) Hooker f. var. *alpinus* (Hooker f.) H. Keng, comb. nov.

Phyllocladus alpinus Hooker f. Fl. Novae-Zeland. 1: 235. t. 53. 1853; Carrière, Traité Gén. Conif. ed. 2. 708. 1867; Kirk in Trans. New Zealand Inst. 10: 382. 1878, Forest Fl. New Zealand, 199. t. 100. 1889; Pilger in Engler, Pflanzenr. 4(5): 98. 1903; Cheeseman, Man. New Zealand Fl. 659. 1906, ed. 2. 120. 1925; Allan, Fl. New Zealand 1: 112. 1961; Wardle in New Zealand Jour. Bot. 7: 76. 1969. TYPE: New Zealand. North Island, Tongariro, Bidwill.

Phyllocladus trichomanoides D. Don var. *alpinus* (Hooker f.) Parl. in DC. Prodr. 16(2): 498. 1868.

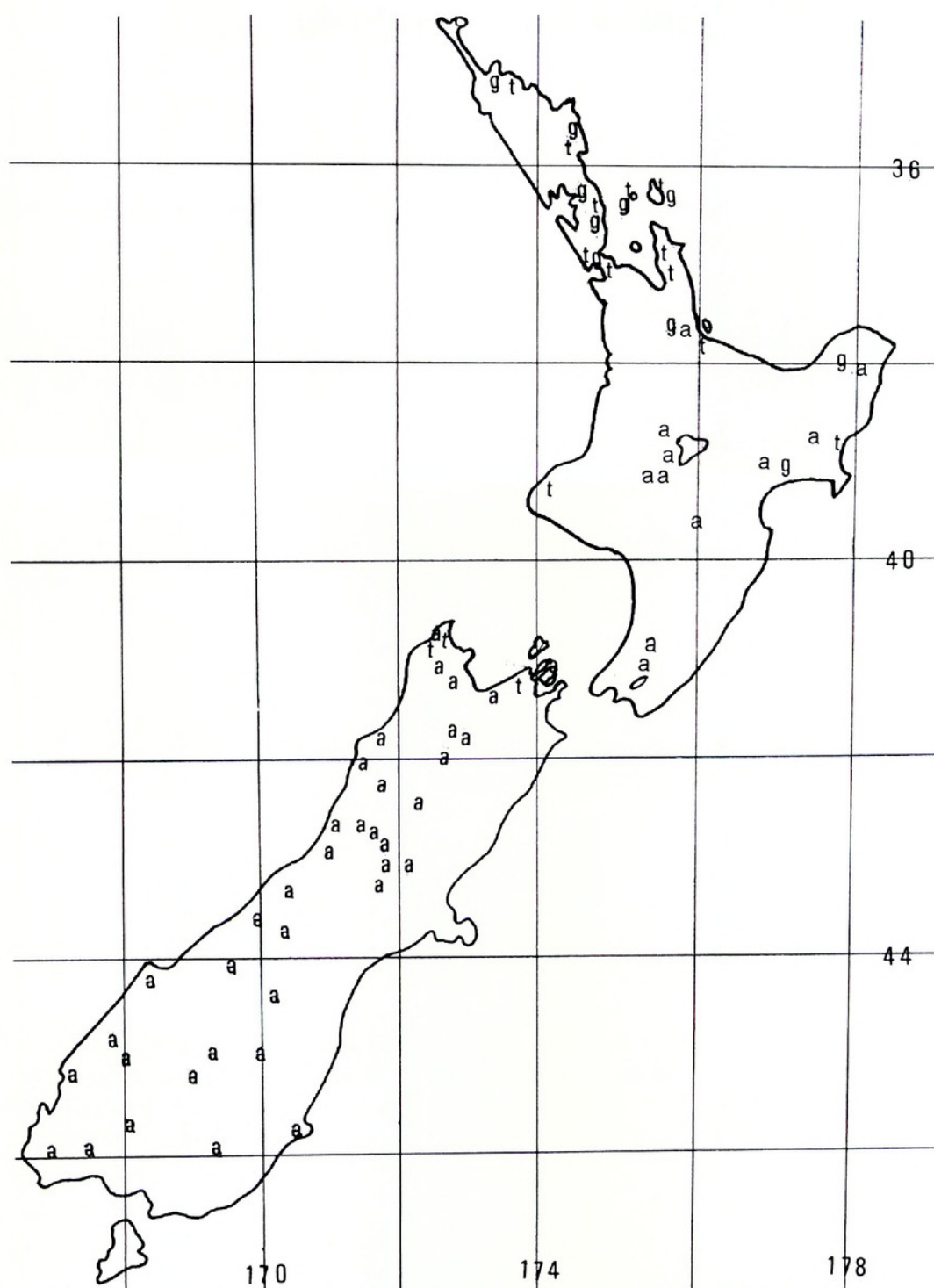
This variety differs from the typical form of the species in the lower stature (maximum height about 9 m.) and in the shorter (less than 0.1 cm.) triangular scale leaves on the short shoot in adult plants.



MAP 1. Distribution of *Phyllocladus aspleniifolius* var. *aspleniifolius* in Tasmania, Australia.

DISTRIBUTION. Endemic to New Zealand (MAP 2). In montane and subalpine forests and scrubs, usually at 500 to 1900 meters altitude on both North and South Islands, extending from approximately 37 degrees latitude to Foveaux Strait, but descending to sea level to the west of the coastal mountains of Nelson, the Southern Alps, and south of Southland.

REPRESENTATIVE SPECIMENS. **New Zealand.** **NORTH ISLAND:** King County, Pureora, *T. W. Rawson* (CHR 56455); Coromandel Peninsula, Moehau, *L. B. Moore* (CHR 40942, 40943); Raukumara Range, Hikurangi, *I. R. Fryer* (CHR 185456); Almateatua, Maungaha-rutu Range, *A. N. Druce* (CHR 216842); Volcanic Plateau, Puke-o-nake, *P. Wardle* (CHR 185468); Tongariro Nat. Park, Chateau, *R. Mason* (CHR 82609); Ruapehu Nat. Park, *A. Cook* (CHR 69111); Central Ruahine Range, near Waikanaka Hut, *Wardle* (CHR 185459); Ararua Range, *Druce* (CHR 190505, 190506); Wellington, Wilton's Bush, *Harrigan & Cook* (CHR 83778). **SOUTH ISLAND:** Nelson, Wanagapeka River, *B. H. MacMillan* (CHR 219942); Cobb Valley, Sylvester Stream, *Moore* (CHR 151027); near



MAP 2. Distribution of *Phyllocladus aspleniifolius* var. *alpinus* (a), *P. glaucus* (g), and *P. trichomanoides* (t) in New Zealand.

Nelson, Dun Saddle, *Wardle* (CHR 179033); Marlborough, Mt. Stokes, *J. G. Hay* (CHR 112278); Lewis Pass, Paradise Lake, *A. H. MacRae* (CHR 185463); near Agnes Bivouac, Clyde River, *D. R. Given* (CHR 178859); Arthur's Pass, *R. Melville* (CHR 130873); Mt. Cook, Hermitage, *H. E. Connor* (CHR 108109); Mt. Cockayne, Broken River, *E. M. Chapman* (CHR 258592); Karangama,

Westland Nat. Park, *Wardle* (CHR 179110); fiords, Stuart Mts., *W. H. Thomson* (CHR 88133); Expectation Stream, Caswell Sound, *V. D. Zotov* (CHR 71084); Fiordland, Lake Make, *M. J. A. Simpson* (CHR 115975); Southland, Nevis, *A. J. D. Barker* (CHR 20950); Matukituki, Otago, *J. A. Langbein* (CHR 167031); N. Otago, Omarama, *Moore* (CHR 71226); Lake Ohau, Dobson River, *Wardle* (CHR 185470).

In his *Flora Tasmaniae* (Vol. 1, p. 359), J. D. Hooker commented that the New Zealand alpine species (*Phyllocladus alpinus*) so closely resembles the Tasmanian species that he almost doubted "its being distinct." T. Kirk (in Trans. Proc. New Zealand Inst. 10: 382, 383. 1878) stated that "I have no doubt that it [*P. alpinus*] will ultimately prove identical with the Tasmanian *P. rhomboidalis*, . . . for although specimens from alpine habitats look very different to that plant, fruited specimens from low levels are undistinguishable." Recently, P. Wardle (1969) recognized two ecotypes (alpine and lowland) of this plant and observed that the lowland ecotype of *P. alpinus* is very similar to the Tasmanian plant. He also mentioned three characters that distinguish them: maximum height, bud scales in the adult plant, and seed clusters. The last character (seed clusters usually lateral at the base of the phylloclade in New Zealand species and usually terminal on the phylloclade in Tasmanian plants) does not stand, so varietal rank seems most appropriate.

2. *Phyllocladus glaucus* Carr. *Traité Gén. Conif.* 502. 1855, ed. 2. 707. 1867; Kirk in Trans. New Zealand Inst. 1: 149. 1868, *ibid.* 10: 380. 1878, *Forest Fl. New Zealand*, 195. *tt.* 98, 99. 1889; Pilger in Engler, *Pflanzenr.* 4(5): 95. 1903; Cheeseman, *Man. New Zealand Fl.* 658, 1906, ed. 2. 120. 1925; Allan, *Fl. New Zealand* 1: 113. 1961. TYPE: New Zealand. North Island, Maungatawhiri, *R. Mair*.

Phyllocladus trichomanoides D. Don var. *glaucus* (Carr.) Parl. in DC. *Prodr.* 16(2): 498. 1868.

Small tree, to 12 m. tall. Bark dark brownish, deeply fissured. Juvenile leaves on seedlings linear, obtuse or acute, sometimes falcate, 0.5–1 cm. long. Scale leaves on seedlings subulate, about 0.5 cm. long; those at the base of a young terminal shoot of adult plant linear-lanceolate, 1.5–2 cm. long, thin-membranaceous, caducous. Phylloclades on seedlings usually deeply pinnatifid, 3–5 cm. long; those on adult plants pinnately compound, 12–20(–30) cm. long, consisting of 5 to 10 (to 12) segments, the segments pale bluish green above and glaucous beneath when young, rhombic to ovate-flabellate, 2–5 cm. long, subsessile or stalked. Plants usually dioecious. Pollen strobili usually 10 to 20 crowded at the tips of the short branches, cylindrical, 1–2(–2.5) cm. long, stalked, the stalk stout, equaling or longer than the cone. Ovulate strobili 3 to 5, inserted on each side of the pinnate phylloclades at the tips of the short branchlets, occupying the place of the lower lateral segments; each strobilus ovoid, 0.5–0.8 cm. long, consisting of 10 to 20 spirally arranged fertile scales. Ripe seed cones pinkish red, 1–1.2 cm. long, with 8 to 20 seeds exerted beyond the

thickened scales. Seeds ovoid, compressed, black, 0.3 to 0.4 cm. long; aril cup-shaped, white, fleshy. Seed cone scales remaining integral; no receptacle formed.

DISTRIBUTION. Endemic to New Zealand (MAP 2). In lowland and montane forests from sea level to 850 meters, rarely to 1000 meters on some mountain peaks, in the northwestern parts of North Island.

REPRESENTATIVE SPECIMENS. New Zealand. NORTH ISLAND: Mangonui, Peria, Watts Bush, *H. Carse* 2343 (AK); near Whangarei, Mt. Maungatapere, *Carse* 641 (AK); Little Barrier Island, *L. Cockayne* 6296 (AK); Great Barrier Island, *T. Kirk* (WELT 37769); Auckland, Birkdale, *Carse* 2337 (AK); Coromandel Peninsula, *A. E. Wright* 700 (AK); Te Aroha Mts., *W. R. B. Oliver* (WELT 15267); Rotorua, Mt. Tarawera, *P. Hynes* 110361 (AK); Lake Waikare, Ani-waniwa Falls, *D. A. Crawford* (CHR 65355).

The following specimens are considered to be intermediate forms or hybrids: *WELT* 37791, collected by Thompson from Waitakere Range, New Zealand, is intermediate between *Phyllocladus glaucus* and *P. trichomanoides*; *CHR* 186617 and *CHR* 186618, collected by A. P. Druce from Hine River, west of Waikareti, in Urewere National Park, are between *P. glaucus* and *P. aspleniifolius* var. *alpinus*. Further examination is needed.

3. *Phyllocladus hypophyllus* Hooker f. *Ic. Pl. n.s.* 5: *t.* 889. 1852; Carrière, *Traité Gén. Conif.* ed. 2. 706. 1867; Parlatore in *DC. Prodr.* 16(2): 499. 1868; Stapf in *Trans. Linn. Soc. Bot.* 4: 249. 1894; Pilger in *Engler, Pflanzenr.* 4(5): 99. 1903; Merrill, *Enum. Philip. Fl. Pl.* 1: 5. 1925; H. Keng in *Gard. Bull. Sing.* 20: 123. fig. 1963; de Laubenfels in *Jour. Arnold Arb.* 50: 278. 1969. **TYPE:** Borneo. Mt. Kinabalu, alt. 8000 feet and upwards, *H. Low*.

Phyllocladus hypophyllus Hooker f. var. *protracta* Warb. *Monsunia* 1: 278. 1900. **TYPE:** Mindanao, *Warburg* 14722.

Phyllocladus protractus (Warb.) Pilger in *Engler, Pflanzenr.* 4(5): 99. 1903.

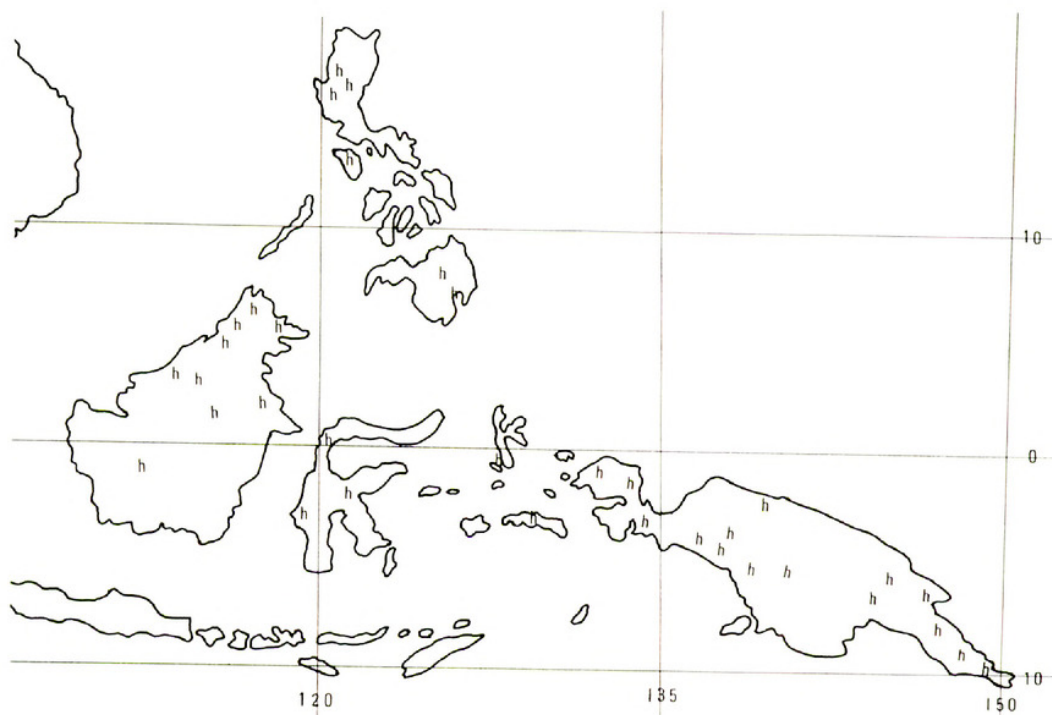
Phyllocladus major Pilger in *Bot. Jahrb.* 54: 211. 1916. **TYPE:** New Guinea, *Ledermann* 9872.

Small or large tree, up to 30 m. or more high. Bark reddish brown to dark brown, flaking, with hard, rough granules, breaking off in large scales. Juvenile leaves on seedlings linear, 0.5–0.8 cm. long. Scale leaves on the short branchlets of adult plant awl shaped, 0.2–0.3 cm. long. Phylloclades on seedlings spatulate to rhomboid, 2–8 cm. long, the apex acute or caudate, the base narrowly attenuate, the margin irregularly serrate, lacerate, or pinnatifid; phylloclades on adult plants pinnately compound, 10–15 cm. long, usually consisting of 5 to 10 segments, the segments oblanceolate, obovate to rhomboid, 1.5–4 cm. (–10 cm. in saplings) long, the upper surface dark green, the lower often glaucous. Plants usually dioecious. Pollen strobili often 2 or 3, sometimes to 15, in clusters on the tip of a short branchlet, sometimes mixed with sterile (but reduced) phylloclades or phylloclades bearing reduced ovulate strobili, yellowish brown, cylin-

drical, 1.2–1.5 cm. long, stalked. Ovulate strobili purplish, solitary or rarely 2 (or 3) together situated in the notch of a bilobed simple phylloclade, or in the notches of the bilobed segments of a compound phylloclade, sometimes these segments becoming columnar or obsolete; each ovulate strobilus ovoid or ellipsoid, consisting of about 15 coalescent scales of which only 2 or 3 are fertile, each bearing a simple, erect ovule. Seeds ovoid, chestnut brown, 5–8 mm. long, flattened, the aril whitish; receptacle yellowish brown, fleshy.

DISTRIBUTION. Endemic to Malesia (MAP 3), from Luzon and Borneo, through the Celebes and Moluccas, to New Guinea. Scattered in montane rain and subalpine forests, on ridges and summits, from 1500 to 3000 meters, and occasionally also from 900 to 4000 meters in some restricted areas.

REPRESENTATIVE SPECIMENS. **Philippines.** LUZON: Mt. Benguet, Panai, *E. D. Merrill* 4753 (L); Benguet, Mt. Singakalsa, *M. D. Sulit*, *PNH* 7669 (L). MINDANAO: Bukidnon, Mt. Katanglad, *Sulit*, *PNH* 10052 (L); Davao, Mt. Apo, *R. Robbins s.n.* (L). **Borneo.** SARAWAK: Baram, Mt. Mulu, *J. A. R. Anderson* 4544 (L); Melinau, Mt. Api, *P. Chai*, *S* 30366 (L); Mawas, Marigan Range, *E. F. Brunig*, *S* 9984 (L). BRUNEI: Mt. Ulak, *P. Ashton*, *BRUN* 1033 (L). SABAH: Mt. Kinabalu, *J. & M. S. Clemens* 29743 (L); Chew, Corner, & Stainton, *RSNB* 710 (L); Kudat, Trusmandi, *G. Mikil*, *SAN* 31784 (L). **KALIMANTAN:** Mt. Semedum, *H. Hallier* 697 (L); Banan, Bengkajang, *bb* 24777 (L). **Celebes:** Mt. Loemoet, Menado, *P. J. Eyma* 3621 (L); Enrekang, Sawito, collector unknown, *bb* 20782 (L); Labu, Malili, *A. Burhi*, *bb* 24089 (L). **Moluccas:** Batjan, *de Haan*, *bb* 23236 (L); Obi, *de Haan*, *bb* 23812 (L); Ceram, Mt. Sofia, *E. Stresemann*



MAP 3. Distribution of *Phyllocladus hypophyllus* in Malesia.

133 (L). Irian Jaya: Vogelkop Peninsula, Nettoti Range, *van Royen & Sleumer* 7403 (L); Kebar Valley, Neetjapaki Mts., *C. Kalkman*, BW 6373 (L); Wissel Lake, *Eyma* 4954 (L); Lake Habbema, *L. J. Brass* 10528 (L); Mt. Antares, Star Mts., *Kalkman* 4539 (L). Papua New Guinea. W. HIGHLANDS: Mt. Hagen, *Hoogland & Pullen* 5871 (L), Lake Inim, *J. R. Flenley*, ANU 2177 (L). MOROBE: Mannasat, Cromwell Mts., *R. D. Hoogland* 9482 (CANB, L); Mt. Kaindi, *Brass* 29692 (CANB, L). S. HIGHLANDS: Mt. Giluwe, *R. Schodde* 2014 (CANB, L). CENTRAL: Murray Pass to Woitape, *Forman & Wardle*, NGF 45587 (L).

4. *Phyllocladus trichomanoides* D. Don in Lambert, Descr. Genus *Pinus*. ed. 3. 2: 159. 1832. A. Cunningham in Ann. Nat. Hist. 1: 211. 1838; Hooker, Ic. Pl. n.s. 2: *tt.* 549–551. 1843; Endlicher, Synop. Conif. 235. 1847; Hooker f. Fl. Novae-Zeland. 1: 235. 1853; Carrière, Traité Gén. Conif. ed. 2. 705: 1867; Parlatore in DC. Prodr. 16(2): 498. excl. vars. 1868; Kirk in Trans. New Zealand Inst. 10: 381. 1878, Forest Fl. New Zealand, 9. *tt.* 6, 7. 1889; Pilger in Engler, Pflanzenr. 4(5): 97. 1903; Cheeseman, Man. New Zealand Fl. 658. 1906, ed. 2, 119. 1925, Illustr. New Zealand Fl. 2: *pl.* 190. 1914; Allan, Fl. New Zealand 1: 113. 1961. LECTOTYPE: New Zealand. North Island, Wangaroa, *A. Cunningham* (K).

Medium-sized to large tree, 20–23 m. tall. Bark smooth and thick, greenish to dark gray or blackish. Juvenile leaves linear, acute, 0.8–1 cm. long. Scale leaves at the base of young shoots subulate, 0.2–0.3 cm. long. Phylloclades on seedlings usually pinnatifid to pinnately compound, 5–7 cm. long, stalked; those on adult plants pinnately compound, 3–8(–12) cm. long, consisting of 6 to 10 (to 12) segments, the segments broadly rhomboid or ovate-flabellate, 1.2–2.5 cm. long, the margin varying from broadly toothed to deeply lacinate. Plants usually dioecious. Pollen strobili 5 to 10 in a terminal cluster, cylindric, 0.8–1 cm. long, stalked, the stalks 0.3–1 cm. long. Ovulate strobili usually borne on one side of the segments of the pinnate phylloclade, these segments often reduced in various degrees, sometimes merely stalklike; each strobilus irregularly ovoid or subglobose, 0.2–0.3 cm. long, usually consisting of 2 or 3 fertile scales, each possessing a single ovule. Seeds dark blue to black, ovoid, compressed, about 0.3 cm. long, solitary, exserted beyond the crenulate cupular aril and the succulent receptacle.

DISTRIBUTION. Endemic to New Zealand (MAP 2). In lowland and montane forests, from sea level to 800 meters, rarely to 1000 meters in restricted areas, on most parts of North Island (from North Cape to Taranaki and Hawke Bay) and on the northern tip of South Island.

REPRESENTATIVE SPECIMENS. New Zealand. NORTH ISLAND: North Cape, Kerr Point, *H. D. Gordon* 1993 (WELT); Mangonui, Kaitaia, Oinu, *H. B. Matthews* 2328 (AK); Bay of Islands, Russell State Forest, *A. E. Orchard* 3794 (AK); Whangarei, Mangakahia Valley, Twin Bridges, *R. Cooper* 120085 (AK); Little Barrier Island, *E. M. Smith* 109127 (AK); Great Barrier Island, *Cooper* (CHR 206941); Anawhata Valley, *L. B. Moore & L. M. Cranwell* 91345 (AK); Waite-

mata, Waitakere Range, *Orchard* 3372 (AK); Manukau, Hunua, *N. J. Pickett* 22156 (AK); Coromandel, Whitianga, *A. E. Wright* 666 (AK); Pakirarahi, Thames, *J. Adams* 14276 (AK); Tauranga, McLaren's Falls, *W. I. Simpson* (CHR 117400); Gisborne, Motu River, *E. M. Chapman* (CHR 258563); near New Plymouth, Barratt Lagoon, *A. N. Druce* s.n. (CHR 274998). SOUTH ISLAND: Marlborough, Okiwi Bay, *H. Talbot* (CHR 270096); near Nelson, Mai Tai Valley, *P. Wardle* (CHR 179034); S. E. of Cape Farewell, Puponga, *Druce* (CHR 273456).

ECONOMIC USES

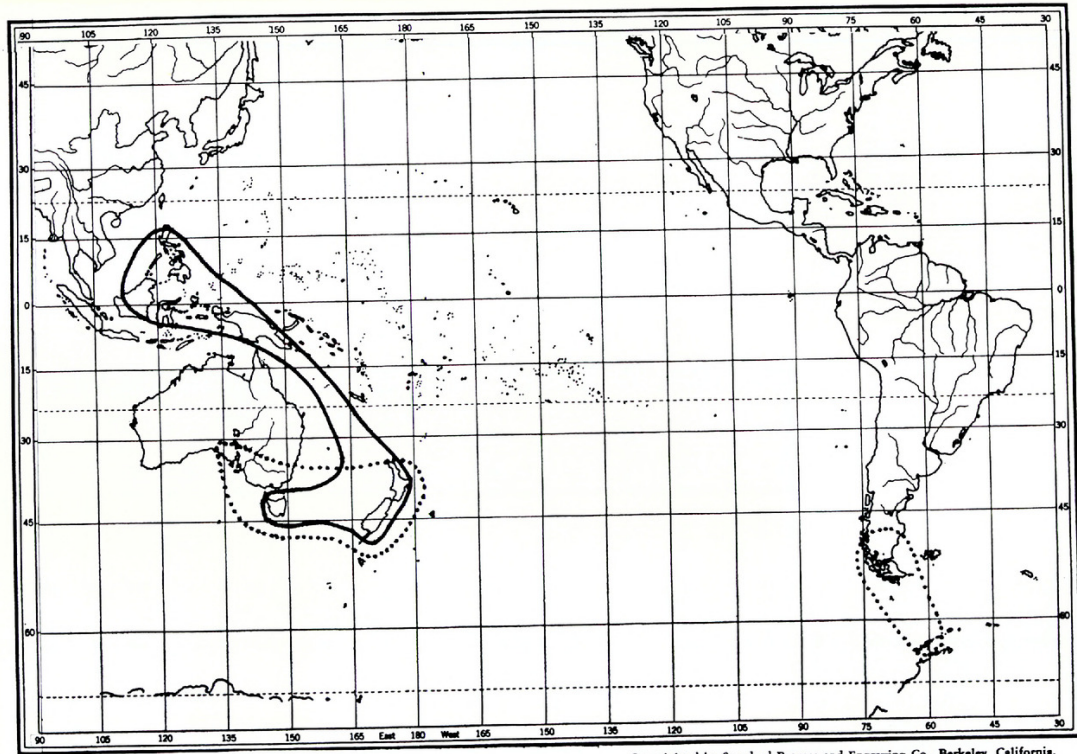
There is not enough timber from any of the four species of celery pine to be of commercial importance. Nevertheless, the wood is white and even grained, and shrinks very little on drying. It is valuable for flooring, boat decks, railway sleepers, mine props and piles, and occasionally for local building purposes and agricultural implements. The bark contains a high percentage (20 to 25%) of tannin, and once was considered to be of great value in tanning. According to Kirk (1889), the bark of two New Zealand species (*Phyllocladus glaucus* and *P. trichomanoides*) also yields a red dye which was formerly used by the Maoris for dyeing their cloaks.

PALEOGEOGRAPHIC DISTRIBUTION

Although *Phyllocladus* is now limited to Tasmania, New Zealand, and eastern Malesia, fossil records reveal its much wider distribution in geologic time. After enumerating and evaluating the paleobotanical data, Couper (1960) reached the following conclusions. (1) Macrofossils identified on the basis of cuticular structure and cladode morphology as *Phyllocladus* are recorded from the Oligocene of continental Australia and the Oligocene, late Tertiary, and Quaternary of New Zealand. (2) Microfossils (pollen grains) are found sporadically in Tertiary sediments in Australia, Tasmania, and New Zealand (MAP 4). In New Zealand they occur from the Oligocene onward, but in Australia they are found mainly in the Oligocene. They are also found in the lower Tertiary of Seymour Island in western Antarctica. (3) No fossils of *Phyllocladus* are known from the Cretaceous or Tertiary of northern South America, New Guinea, Borneo, or India. A phyllocladean affinity has been suggested for some fossil woods from southern South America, but these identifications are inconclusive.

Recent pollen studies by Dodson (1974a, 1974b) indicate that *Phyllocladus* grew in western Victoria and southeastern South Australia during the Quaternary and became extinct only a few thousand years ago. Also according to the same author (pers. comm.), *P. asplenifolius* var. *asplenifolius* was formerly present on Flinders Island in Bass Strait (between mainland Australia and Tasmania). It disappeared from the island at the beginning of this century as a result of an influx of settlers.

The absence of fossils in the tropics and in the Northern Hemisphere deserves special attention. It supports the view that the present extension



MAP 4. Distribution of *Phyllocladus*, present (solid line) and paleogeographic (dotted lines). (Paleobotanical data based on Couper, 1960.)

of *Phyllocladus* into eastern Malesia was a relatively recent development (Hair, 1963; de Laubenfels, 1969).

Among the fifty or so genera of extant conifers, about thirty of them are confined to the Northern and fourteen (including *Phyllocladus*) to the Southern Hemisphere. Li (1953) has summarized the present range of conifers and emphasized the clear differentiation into northern and southern groups. This separation, according to Li, has been shown by paleobotanical records to have existed since the Paleozoic. Nearly all of the considerable number of monotypic or oligotypic genera (including *Phyllocladus*) show restricted or disjunct ranges, grow best in a damp mesophytic habitat, and are practically all confined to lands bordering the Pacific Basin. This is considered by some botanists (including Li) to support the continental drift theory as modified by du Toit, who believed in two ancient land masses, Gondwana and Laurasia, separated by the Tethys Sea. Krassilov (1974), however, feels that the history of conifers has little bearing on the problem of continental drift and suggests that the southern and northern conifers have been more effectively separated by equatorial climatic conditions than by water barriers.

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LITERATURE CITED

- COUPER, R. A. 1960. Southern Hemisphere Mesozoic and Tertiary Podocarpaceae and Fagaceae and their palaeogeographic significance. *Proc. Roy. Soc. London B*, 152: 491-500.
- DE LAUBENFELS, D. J. 1969. A revision of the Malesian and Pacific rain forest conifers. I. Podocarpaceae, in part. *Jour. Arnold Arb.* 50: 274-369.
- DODSON, J. R. 1974a. Vegetation and climatic history near Lake Keilambete, West Victoria. *Austral. Jour. Bot.* 22: 709-717.
- . 1974b. Vegetation history and water fluctuations at Lake Leake, south-eastern South Australia. I. 10,000 B. P. to present. *Ibid.* 22: 719-741.
- HAIR, J. B. 1963. Cytogeographical relationships of the southern podocarps. Pp. 401-414 in J. L. GRESSITT, ed., *Pacific Basin biogeography*. Bishop Mus. Press, Honolulu.
- KENG, H. 1963a. *Phyllocladus hypophyllus* Hook. f. *Gard. Bull. Singapore* 20: 123-126.
- . 1963b. Aspects of morphology of *Phyllocladus hypophyllus*. *Ann. Bot. n.s.* 27: 69-78.
- . 1974. The phylloclade of *Phyllocladus* and its possible bearing on the branch systems of progymnosperms. *Ibid.* 38: 757-764.
- . 1977. *Phyllocladus* and its bearing on the systematics of conifers. Pp. 235-251 in K. KUBITZKI, ed., *Flowering plants: evolution and classification of higher categories*. Springer-Verlag, Wien & New York.
- KIRK, T. 1889. *The forest flora of New Zealand*. xv + 345 pp. George Didsbury, Wellington.
- KRASSILOV, V. A. 1974. *Podocarpus* from the Upper Cretaceous of eastern Asia and its bearing on the theory of conifer evolution. *Palaeontology* 17(2): 365-370.
- LI, H. L. 1953. Present distribution and habitats of the conifers and taxads. *Evolution* 7: 245-261.
- PREEST, D. S. 1963. A note on the dispersal characteristics of the seed of New Zealand podocarps and beeches and their biological significance. Pp. 415-424 in J. L. GRESSITT, ed., *Pacific Basin biogeography*. Bishop Mus. Press, Honolulu.
- ROBERTSON, A. 1906. Some points in the morphology of *Phyllocladus alpinus* Hook. *Ann. Bot.* 20: 259-265.
- WARDLE, P. 1969. Biological flora of New Zealand. 4. *Phyllocladus alpinus* Hook. f. (Podocarpaceae). Mountain toatoa, celery pine. *New Zealand Jour. Bot.* 7: 76-95.

DEPARTMENT OF BOTANY
UNIVERSITY OF SINGAPORE
BUKIT TIMAH ROAD
SINGAPORE 10



Keng, Hsuan. 1978. "The genus *Phyllocladus* (Phyllocladaceae)." *Journal of the Arnold Arboretum* 59(3), 249–273. <https://doi.org/10.5962/bhl.part.22773>.

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