Developmental shoot morphology in *Phyllocladus* (Podocarpaceae)

P. B. TOMLINSON, F.L.S., T. TAKASO

Harvard Forest, Harvard University, Petersham, MA 01366, U.S.A.

AND

J. A. RATTENBURY

Department of Botany, University of Auckland, Auckland, New Zealand

TOMLINSON, P. B., TAKASO, T. & RATTENBURY, J. A., 1989. **Developmental shoot morphology in *Phyllocladus* (Podocarpaceae).** Shoot architecture in the adult phase of *Phyllocladus* is established by a succession of units of extension that develop a system of permanent axes supporting photosynthetic units (phylloclades) each of which represents a branch complex with three branch orders. Seedlings have needle foliage leaves comparable to those of other conifers, but in adult plants all leaves are ephemeral, non-photosynthetic scales that for the most part subtend no axillary buds. Once rhythmic growth (usually seasonal) is established in the adult phase, each increment produces a whorl of phylloclades so that a regular tiered arrangement develops, with the tiers progressively reduced on outer units. In the resting terminal bud of permanent axes only scale primordia are present; with bud burst and beginning of extension of the unit the phylloclades are produced by syllepsis and complete the initiation and expansion of all axis orders in the short flushing cycle. Segments retain strict distichy throughout, but in a dorsiventral and not a lateral plane. Phylloclades may be either determinate, when the apex of the first-order axis develops as a terminal flattened segment, or indeterminate, when the apex retains radial symmetry and forms a resting bud that can continue axis extension as a permanent shoot in subsequent years. A phylloclade consequently only produces flattened lateral segments in its season of initiation. Reiteration from reserve buds is not possible, because none are produced in the adult phase, but is possible from detached meristems formed in the axils of needle leaves on juvenile shoots. Reiteration in the adult phase is thus possible only by axis dedifferentiation, that is, change from plagiotropy to orthoptropy. The distinctive massive vascular connection of the phylloclade is made possible by syllepsis. In this way the normal structural constraints of elaborate appendage development in conifers is fully overcome.

ADDITIONAL KEY WORDS:—Tree architecture – conifers – branching – reiteration.

CONTENTS

INTRODUCTION

Phyllocladus is unique in the Coniferales because its photosynthetic surface is provided primarily by flattened branch complexes (cladodes or phylloclades), which variously resemble simple or compound leaves. Despite extensive comparative study, much of it relating to speculative ideas of the relationship of this shoot type to extinct groups of plants, there still is no precise description of total organization which explains the growth limitations or advantages of the distinctive shoot morphology. This article describes the dynamic growth plan of the tree, initially in terms of the architectural models of Hallé, Oldeman & Tomlinson (1978) and adds details of phylloclade development. This information allows a comparison with existing seed plants and suggests that the shoot morphology may be of recent derivation and has parallels in other modern groups. No fundamentally unique features occur, with the possible exception of distichous phyllotaxis, which is rare and previously undocumented in gymnosperms. We account for this unique organization in terms of mechanisms that overcome the constraints of the coniferous vascular organization.

Phyllocladus is currently regarded as including five taxa (Keng, 1978, *cf.* Table 1), *P. aspleniifolius* (with two varieties, var. *aspleniifolius* in Tasmania and var. *alpinus* in New Zealand), *P. glaucus* (endemic to New Zealand), *P. hypophyllus* (with a wide Malesian distribution in Borneo, the Philippines, Sulawesi to New Guinea) and *P. trichomanoides* (endemic to New Zealand). The genus is most characteristic of montane or sub-montane habitats although *P. glaucus* and *P. trichomanoides* have a wide altitudinal range, from sea level to almost 1000 m. The fossil distribution includes a wider range in Australia, western Antarctica and possibly South America, based on macrofossils and pollen (Couper, 1960). The vegetative morphology of the genus has been studied most extensively by Keng (1963a, b, 1974, 1977) and there is a well documented account of the anatomy of phylloclades by R. S. L. Keng (1979) which establishes quite clearly the morphological nature of the shoot. Unfortunately, this important paper seems to have been entirely overlooked (*cf.* Quinn, 1987). Berggren (1980), using a diversity of techniques, has added information about the histology of the phylloclade, particularly the transfusion tissue. Kaussmann (1955) has presented limited information about primordial ontogeny and histogenesis. It is clear that

TABLE 1. Material of *Phyllocladus* studied

Name	Locality	Date & Collection No.
P. aspleniifolius (Labill.) Hook.f var. *alpinus* (Hook.f.) H. Keng	Lake Rotoaira New Zealand	27 xi 85
P. aspleniifolius (Labill.) Hook.f. var. *aspleniifolius*	Geeveston Tasmania	9 i 86, B, C
P. glaucus Carr.	Waitakere Ranges New Zealand	22 xi 85 & 6 xi 86
P. hypophyllus Hook.f.	Cultivated Royal Botanic Garden Edinburgh Scotland	29 iv 86
P. trichomanoides D. Don.	Waipoua New Zealand	24 x 85

the intrinsic nature of the phylloclade as a flattened branch complex has long been appreciated, for example, by Bertrand (1874), and especially Strasburger (1872). Seedling morphology and anatomy has been described most recently by Woltz & Rouane (1977). Reproductive morphology of the genus has been less well investigated and has largely been studied by Robertson (1906), Kildahl (1908), Young (1910), Sinnott (1913) and Holloway (1937), *cf.* Buchholz (1941).

On the basis of his understanding of the genus, Keng (1974, 1977, 1978, 1979, 1980) has proposed a morphological comparison with *Archaeopteris* (Progymnospermophyta) and suggested a direct telomic origin for the phyllocladic structures. Further, he suggests that *Phyllocladus* stands sufficiently apart from other Podocarpaceae in features of reproductive, as well as vegetative, morphology to merit recognition as a monotypic family Phyllocladaceae having affinities with the Taxales (Keng, 1973, 1975). Quinn (1987) reviews much of the evidence for and against these interpretations, both of which he rejects. The evolutionary comparison seems anomalous in view of the evidence provided by himself (Keng, 1963a, c) and his co-worker (R. S. L. Keng, 1979) for a more orthodox interpretation of the phylloclade as a branch complex quite comparable to that in related plants of much more recent derivation. Nevertheless, the opinions merit consideration, especially in relation to new information that can be brought to bear on the matter. An additional emphasis in this article is the plasticity of the trees in relation to environmental disturbance, since reiterative ability would, at first sight, seem limited by the highly deterministic shoot organization. A more direct explanation for phylloclade differentiation is also offered.

Detailed knowledge of phylloclade morphology is also important in interpreting seed supporting structures, since 'cones' appear as modified segments of phylloclades and the ovule has been reported as lacking a supporting structure comparable with the ovuliferous scale. Cone development is discussed in a later paper (Tomlinson, Takaso & Rattenbury, 1989).

MATERIAL AND METHODS

Material of all five taxa has been examined, all but one species from populations in natural environments (Table 1). In addition to notes taken from

living specimens, sections and bud dissections of material preserved in FAA have been used. The most detailed study has been of *P. glaucus* because of its relatively precise phylloclade organization, compared with other taxa. For a detailed study of bud morphology and phylloclade ontogeny in *P. glaucus* several additional bud collections of the same population cited in Table 1 were made at the initiation of the 1986–87 growing season. These were sufficient to show that there is a great deal of non-synchrony in shoot extension within an individual. Serial transverse and longitudinal paraffin sections of buds were made and stained in safranin and Alcian green. Dissected buds were examined with scanning electron microscopy (SEM) after critical point drying. Parts of young phylloclades embedded in paraffin or resin (glycomethacrylate) were also sectioned and stained either with Heidenhain's haematoxylin, safranin and fast green, or with PAS reagents. Vasculature of phylloclades was revealed by clearing material in 5% alcoholic NaOH, followed by washing in tap water and mounting in lactic acid. Some cleared specimens were stained in Harris's haematoxylin and mounted in Permount.

TERMINOLOGY

The use of the term 'phylloclade' needs clarification since its unrestricted application can lead to confusion. Troll (1937) in his discussion of flattened shoots (*Flachsprossen*) suggested that the term 'phylloclade' (Phyllocladien) be restricted to the simple structure with few internodes found in, for example, Asparagaceae and proposed the term 'platyclade' (Platycladien) for more elaborate flattened shoots, as in *Muehlenbeckia* (Polygonaceae) and *Phyllanthus* (Euphorbiaceae). Strictly the modified branch of *Phyllocladus* complex would also be a platyclade, but Troll himself emphasized that there were intermediate forms. In this account we retain the general term phylloclade and refer to the primary branch complex, produced during one cycle of development and subtended by a scale leaf borne on a permanent axis. This definition is comparable to that used, for example, by Keng (1977). For most individuals phylloclade production is probably a seasonal event. A more basic distinction is between phylloclades which are *determinate* (i.e. without a terminal bud), and those which are *indeterminate* by virtue of developing a resting terminal bud at the end of their first cycle of growth. Only indeterminate shoots can contribute to the permanent architecture of the tree. Wardle (1969) distinguished between these two types of phylloclade as "dwarf shoots" and "long shoots" noting also that only the latter are "capable of further growth". Keng (1977) used the term "short shoot" to decribe the shoot produced from the terminal bud of the indeterminate phylloclade, in its second year of growth. This is misleading because these shoots produce all first-and high-order axes of the tree and, when vigorous as on trunk axes, are very extended and make up the permanent framework of the tree. While many Pinaceae have axillary short shoots with indeterminate growth (e.g. *Larix*, *Cedrus* and *Pseudolarix*), no podocarp has short shoots in any morphological or developmental sense. Short shoots in conifers generally never branch unless they revert to the developmental morphology of a long shoot; phylloclades are intrinsically branched structures. In addition short shoots in conifers are usually proleptic in their development; phylloclades in *Phyllocladus* are sylleptic (Hallé, Oldeman & Tomlinson, 1978: 42).

R. S. L. Keng (1979) distinguished between "simple cladodes" (as in adult shoots of *P. aspleniifolius*) and "compound cladodes" (as in the remaining species) but indicated the morphological continuum between them (*cf.* Figs 7 & 6). In fact, all species of *Phyllocladus* have both "simple" and "compound" phylloclades, since the former occur at least in seedlings or saplings of all species, while the latter
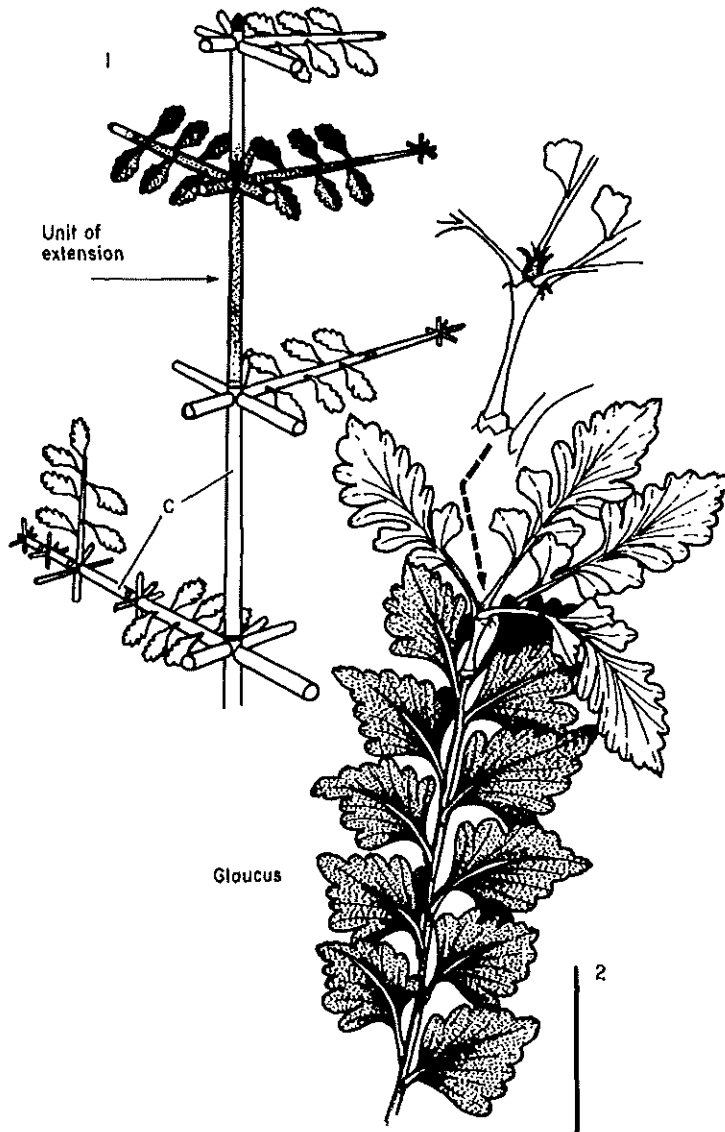

Figures 1, 2. *Phyllocladus glaucus*, adult shoot construction. Fig. 1. Architecture and shoot construction in dormant condition, semi-diagrammatic. Only one or two members of each branch tier are drawn, the rest are shown as if cut off. Note contemporaneous units of two orders are separated, as at C, the result of syllepsis. A unit of extension, the segment of the shoot system development during one (seasonal) growth increment is shown stippled. Fig. 2. Indeterminate and determinate phylloclades. Indeterminate phylloclade (stippled) with its terminal bud having produced a new unit of extension (unstippled) supporting four determinate phylloclades and a new resting terminal bud (inset detail). Scale bar = 2 cm.
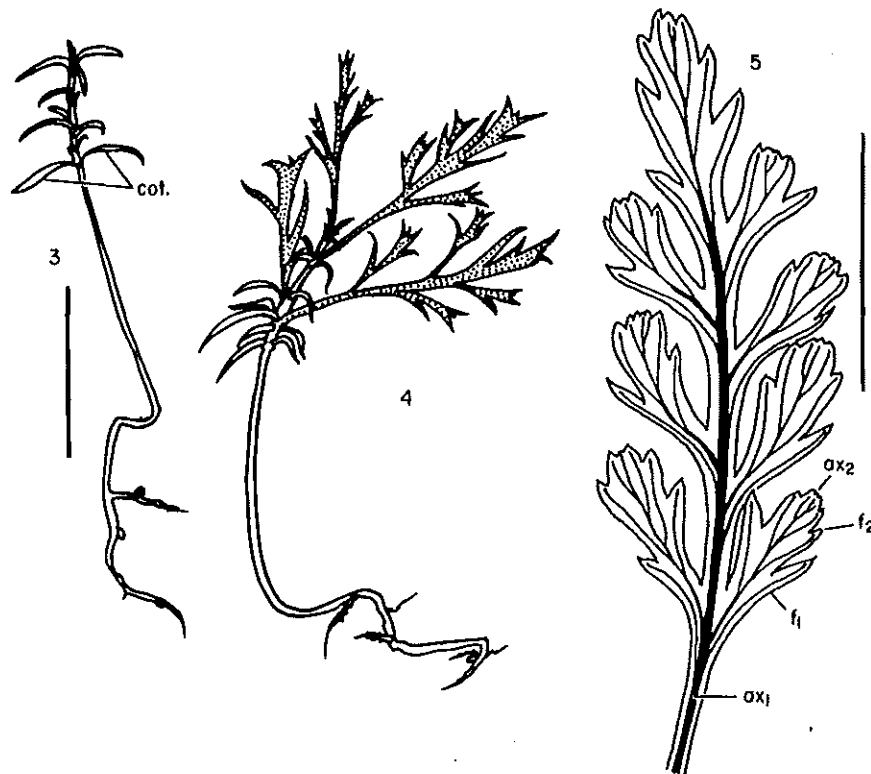
Figures 3–5. *Phyllocladus trichomanoides*, seedling morphology and 'juvenile' phylloclades. Fig. 3. Seedling with cotyledon pair (cot.); juvenile (needle) foliage alternating with scale leaves that represent presumed periods of bud dormancy. Fig. 4. Older seedling with first phylloclades (stippled), not produced in obvious tiers but each with clear planate morphology of a regular branch complex. Fig. 5. Juvenile phylloclade drawn from a cleared specimen. Relation of branch and leaf trace corresponds exactly to that of a planate shoot complex with distichous phyllotaxis; f_1–scale leaf of ax_1; f_2–scale leaf of ax_2; ax_2–subtended branch. Scale bar = 1 cm.

are essential for total shoot construction, even in *P. aspleniifolius*. Using the analogy of the angiosperm leaf, phylloclades run a gamut of shapes from simple leaves, through a range of pinnately lobed to pinnatifid forms to the ultimate pinnately compound type; the compound 'leaf' may be paripinnate (indeterminate) or imparipinnate (determinate). The range of form shown by a given species is still diagnostic for that species (Figs 2, 6–8).

In the precise morphological description of the phylloclade, which represents a flattened and planated branch complex, the terminology for a branching structure can be used (Tomlinson, 1987); if one designates the parent (initially seedling) axis as a "trunk" (ax_0), axes of higher orders can be designated by ordinal numbers, that is first (ax_1), second (ax_2), third (ax_3)...etc. order axis (Hallé, Oldeman & Tomlinson, 1978: 41). These correspond to "primary", "secondary", and "tertiary" branches of, for example, Keng (1977). Keng referred to the corresponding subtending structure as primary, secondary and tertiary "laminar appendage" whereas in the terminology of Hallé, Oldeman & Tomlinson (1978) a leaf belonging to one axis order subtends a branch of higher order for example f_1 subtends ax_2, a convention followed here (e.g. Fig. 9). For consistency, we use the term 'phylloclade' for the whole complex, with the
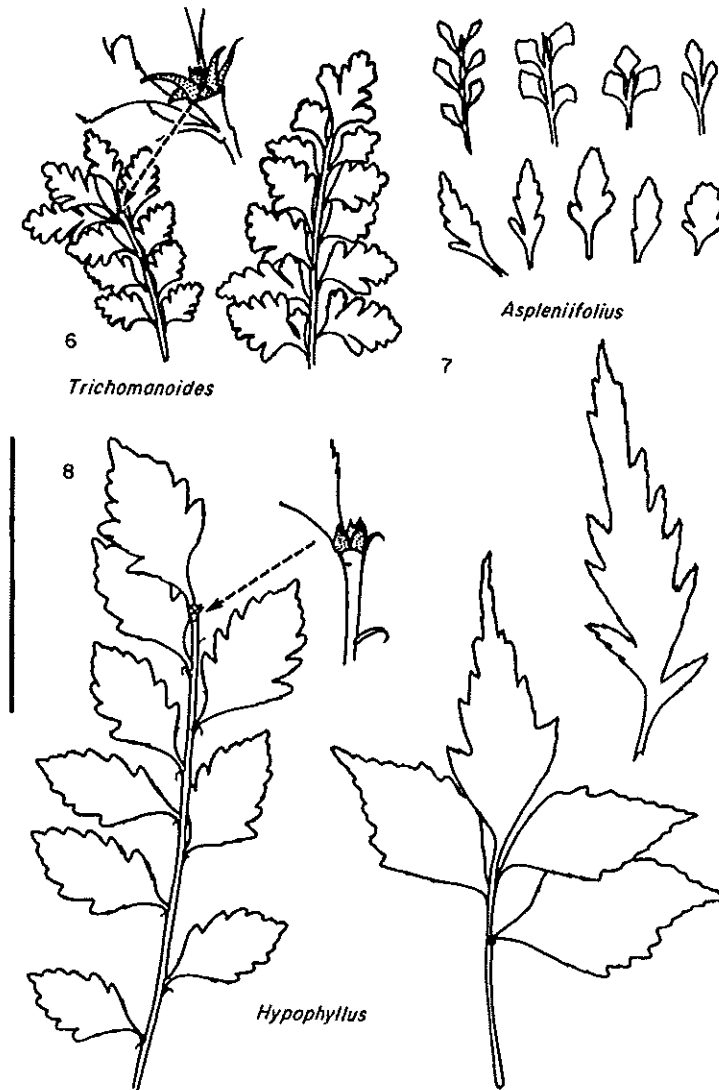
Figures 6–8. *Phyllocladus* species, morphology of phylloclades in three species to illustrate range and diagnostic features. Fig. 6. *P. trichomanoides:* an indeterminate (left) and determinate (right) phylloclade, the terminal bud of the former shown in inset. Fig. 7. *P. aspleniifolius:* range of phylloclades including either compound indeterminate (upper left) to simply lobed determinate (the rest). Fig. 8. *P. hypophyllus:* range from simple determinate (right), compound determinate (middle) to compound indeterminate (left-inset, terminal bud), all from a sapling *c.* 3 m tall. Scale bar = 10 cm.

ultimate flattened units as 'segments' (*cf.* Keng, 1977). Descriptively, it is still useful to distinguish 'simple' from 'compound' phylloclades, according to the range illustrated in Figs 6–8. However, in a strict morphological sense all phylloclades are compound because they include axes of at least two branch orders.

Kaussmann (1955) makes confused use of the term platyclade since it is not always clear whether he refers to segment or whole phylloclade. His account is suspect because he refers to shoot development in terms of northern hemisphere

••••••   Trace to f_1 ⊲—

●---------   Trace to f_2 ◄

○············   Trace to f_3 ⌒

▬▬▬▬▬   Axis trace (ox_2 and ox_3)

B

f_3

f_2

xy.

ph.

f_3

f_2

ox_3

A

ox_2

ox_1

f_1

ox_3

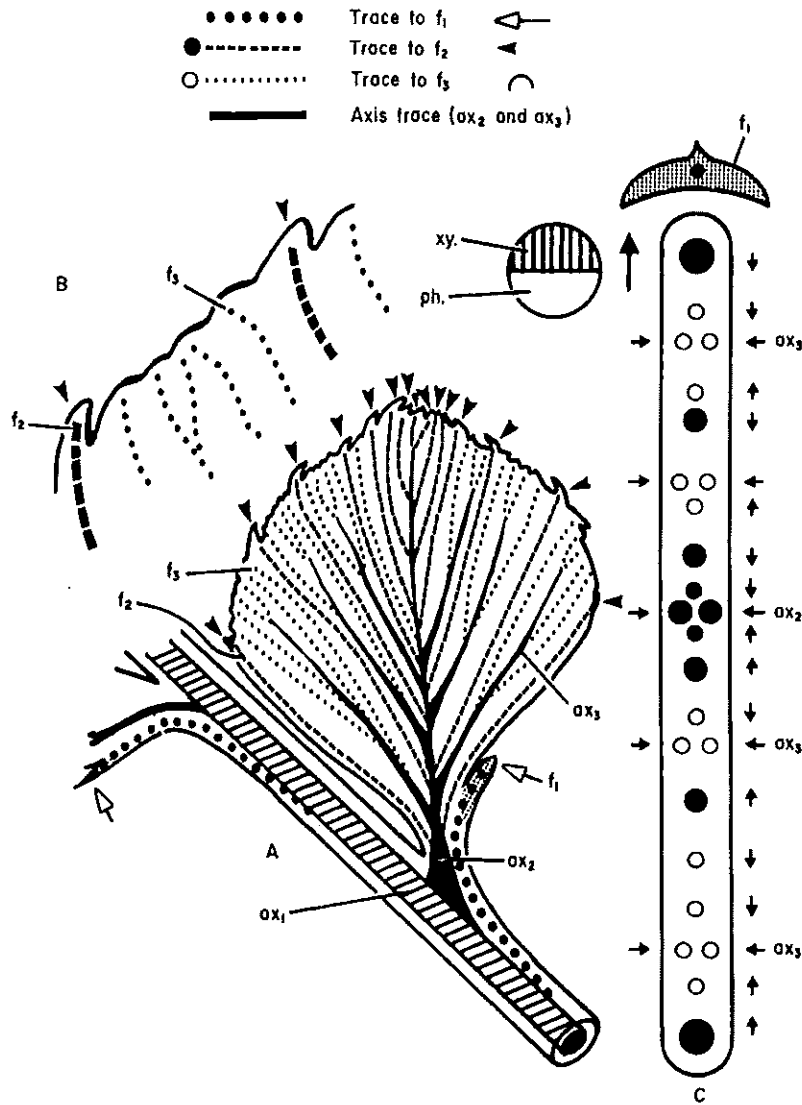ox_2

ox_3

ox_3

f_1

C

Figure 9. *Phyllocladus glaucus*, diagram of single segment (drawn from a cleared specimen) to illustrate vascular system. Sagittal orientation of segment as in nature, but morphologically rotated 90° from a transverse (dorsiventral) position. A. Segment with its vascular system diverging from the stele (shown solid and hatched) of the parent ax_1. B. Detail of margin to show relation between margin scales (f_3 = arrowheads) of ax_2 and f_3 of ax_3. C. Diagrammatic T. S. of segment just below insertion of lower pair of scales (f_2). Solid circles represent axis and leaf traces of ax_2, hollow circles axis and leaf traces of ax_3. Leaf traces are single, but axis traces are double (ax_3) or in fours (ax_2) representing a radially symmetrical reduced stele. Arrows show the orientation of the xylem (as in the key) of the leaf trace always toward the stele to which it is basally attached; the transition from one branch order to another is marked by a change in the orientation of the arrow.

growing seasons and implies that phylloclade primordia overwinter in bud. This phenology we have never observed.

The architecture of *Phyllocladus* remains relatively uncomplicated becuse all branching is monopodial, the only substitution of axes occurs with damage to the tree (see Discussion). In the normal architecture of the tree, production of permanent axes is progressively reduced in higher branch orders.

SHOOT MORPHOLOGY

Seedling
(Figs 3–5)

Germination is epigeal, the seedling producing two cotyledons (Fig. 3), each with two veins, as is characteristic of Podocarpaceae. The photosynthetic apparatus of the seedling axis is initially a series of juvenile needle leaves, each with a single vein. These are produced in discrete flushes, separated by a series of bud scales which protect the resting buds. This periodicity is not shown in the somewhat stylized diagrams of Woltz & Rouane (1977). The flushes appear to be annual and several are developed before the seedling initiates phylloclades. Seedlings may not produce phylloclades until their eighth year in *P. aspleniifolius* var. *alpinus*, according to Wardle (1969). Branching of seedlings occurs either deterministically, resulting in the production of the first phylloclades (Fig. 4), or opportunistically, resulting in the reiteration of the seedling axis. Phylloclades of seedlings differ from those of adult plants; they are subtended by the juvenile needle leaves, are always determinate and have a simpler morphology. Usually they are pinnately lobed and reveal the basic morphology of the phylloclade very clearly (Fig. 5). Seedling phylloclades are at first produced without apparent regularity in relation to the flushing cycle, but after one or more flushes they become restricted to the distal portion of the growth cycle and there is rapid transition to the kind of phylloclade produced in the adult tree. In the several cycles of the juvenile and transitional morphology, there is an increase in size and, to a certain extent, complexity of the phylloclades (e.g. Fig. 8 from right to left for *P. hypophyllus*).

Adult
(Figs 1, 2)

The adult morphology may arbitrarily be designated as beginning with the first development of indeterminate phylloclades, which add to the permanent axis system of the tree. Growth becomes rhythmic, resting buds with well-developed bud scales are formed during each period of dormancy, the juvenile needle leaves are wholly replaced by scales and permanent branch whorls are added. The transitional morphology occurs within one season or growth cycle. A unit of construction or extension that corresponds to the sequence of appendages developed by the axis during one cycle of growth can be recognized (Fig. 1). It includes a segment of the trunk axis and a tier of phylloclades.

In New Zealand, over-wintering resting buds consist of a series of up to 50 scarious bud-scales, each with a broad protective base and a narrow apiculus. Within is a series of immature primordia which enclose the dormant shoot apex. The time of development of phylloclade primordia appears to be at the beginning of the next growing season (October–December, depending on altitude), but within what is apparently a dormant bud. Each phylloclade is subtended by a single flattened scale; a series of such scales is associated with the pseudowhorl of from 5–10 phylloclades (e.g. Figs 31, 32), the number in each tier and the relative proportion of determinate and indeterminate phylloclades depending largely on the vigour of the shoot. In *Phyllocladus aspleniifolius* the phylloclades are often more dispersed so that the tiers tend be less discrete. Expansion of the preformed unit of

extension involves enlargement of the inner scales and internodal elongation followed by initiation and expansion of phylloclades, which complete their differentiation. The series of SEM photographs in Figs 10–15, 16–22 and 23–28 illustrate this process.

On the main (trunk) axis phylloclades are usually indeterminate so a tier of permanent branches is added with each cycle of growth (Fig. 1). On axes of higher order the proportion of determinate phylloclades is very high, permanent branch tiers are therefore added infrequently; usually only three permanent branch orders exist on young trees. Figure 2 illustrates a change from indeterminate to determinate construction. Determinate phylloclades persist for several years; Wardle (1969) quotes values of five to seven years for *P. aspleniifolius* var. *alpinus*, but greater ages may be achieved in very slow growing trees. Since growth rings are clear, such values can easily be established and destructive analysis could establish the entire previous history of a tree.

Permanent high order axes retain the radial symmetry of the trunk axis, plagiotropy then being determined primarily by branch orientation. Interaction between higher order branches is minimized because distal units produce few indeterminate phylloclades. Distal axes also show very limited extension, possibly the reason Keng (1977) referred to them as "short-shoots". In *P. aspleniifolius* var. *alpinus*, Wardle (1969) recorded annual increments of extension of 2–3 mm per year, with annual growth rings in the secondary xylem of 45–90 per cm in plants at timberline. In contrast, *P. hypophyllus* may extend one metre in each flush as a sapling.

Architecture
(Fig. 1)

Phyllocladus may be refered primarily to Massart's model (Hallé, Oldeman & Tomlinson, 1978; Edelin, 1984), which is defined as having an orthotropic monopodial trunk, with rhythmic growth, the branches (here indeterminate phylloclades), produced in regular tiers, are plagiotropic primarily by orientation (but in *Phyllocladus* by distichy in their first season of growth). Sexuality (i.e. cone production) does not influence architecture because pollen cones are added to a vegetative whorl in varying numbers and seed cones largely occupy the position of phylloclade segments. The distichous leaf arrangement of permanent branches in their first season of growth reverts within the same season to a spiral phyllotaxis, with consequent radial organization in subsequent years. Consequently, higher order branches lead to radial symmetry, which suggests Rauh's model. Elements of Roux's model can be found in the initial contrast between phyllotaxis of trunk axis (spiral) and branch axis (distichy), and of Cook's model in the development of scales, instead of foliage leaves, on the trunk (and on all higher order permanent axes). These two latter models differ from Massart's model in their continuous rather than rhythmic growth; the affinity between all three is suggested by their proximity in the Hallé–Oldeman typological scheme (Hallé, Oldeman & Tomlinson, 1978).

Shoot phenology and phyllotaxis
(Figs 1, 2)

Dissection of resting buds shows that there is limited preformation of appendages belonging to a subsequent growth increment. Buds are surrounded by

a close series of scarious scales, the lower (outer) each with a distinct mucro, which represents a leaf blade. Inner scales are narrower and longer, those close to the apex representing scales that become visible on the lower portion of the next growth increment. The shoot apex is a broad shallow dome (Figs 10, 11). Dimensions vary according to the size of the parent shoot, with a range from 290–420 µm. Resting apices seem to be sharply segregated anatomically from the proximal region by an abrupt transition to differentiated ground tissue, but we have sectioned too few apices to be certain of the uniformity of this feature. Active apices show continuous tissue differentiation (Fig. 36). There is non-synchrony of bud expansion on a single tree, which is most obvious when flushing growth starts sporadically in spring (September to November). This non-synchrony, combined with size variation of buds makes difficult an assessment of development processes that depend on a comparison of different apices by destructive sampling.

Phyllotaxis is usually spiral (Figs 10, 12–14), the most consistent value obtained from a series of SEM photographs of dissected apices was a fraction close to $\frac{3}{8}$ (3+5 parastichies). A high proportion of apices with bijugate phyllotaxis was observed (30% in one tree, 10% in another), with an angular divergence between successive leaf pairs of 66°, which approximated half the ideal Fibonacci angle of 137.5° (Fig. 11).

Phylloclade initiation
(Figs 10–15)

Phylloclades are clearly initiated during a cycle of extension and are not preformed since dormant buds do not include phylloclade primordia (30 apices examined as in Figs 10, 11). Phylloclade primordia only occur in shoots that are beginning to elongate (Figs 12–15). Phylloclades also have sylleptic morphology indicated by the absence of basal scales on them and the presence of an extended hypopodium, which develops relatively late in ontogeny (*cf.* Figs 14–15, 17–19 and Figs 20, 22, 23). They show a broad pith connection to the main axis (Fig. 37). During the synchronous development of parent axis and branch the scale subtending the phylloclade is often carried up onto the branch itself, a feature particularly noticeable in *P. glaucus*. The activity of the shoot apex, which marks the start of a new cycle of growth probably begins with the development of new scale primordia (Fig. 14). As we have commented, the absence of any obvious superficial articulation above each branch tier to mark the morphological boundary makes it impossible to distinguish between neo-formed and pre-formed appendages. An internal, anatomical boundary does not exist, since the original histological disjunction (Fig. 35) disappears as extension is renewed (Fig. 36). Changes in the size of shoot apices are also difficult to assess because of the inherent size variation among different shoots. The most obvious change associated with the newly extending shoot is the initiation of phylloclades, as axillary branches. The developing phylloclades are soon carried beyond the enveloping bud scales (Fig. 23). Vigorous shoots, as on saplings, may have growth increments averaging 50 cm long (especially in *P. hypophyllus*); distal shoots and those terminating higher order branches may have short increments less than 1 cm long. Shoot length is determined largely by the length of axis below the phylloclade tier.

Initiation of phylloclades is indicated by the appearance of a broad cushion of
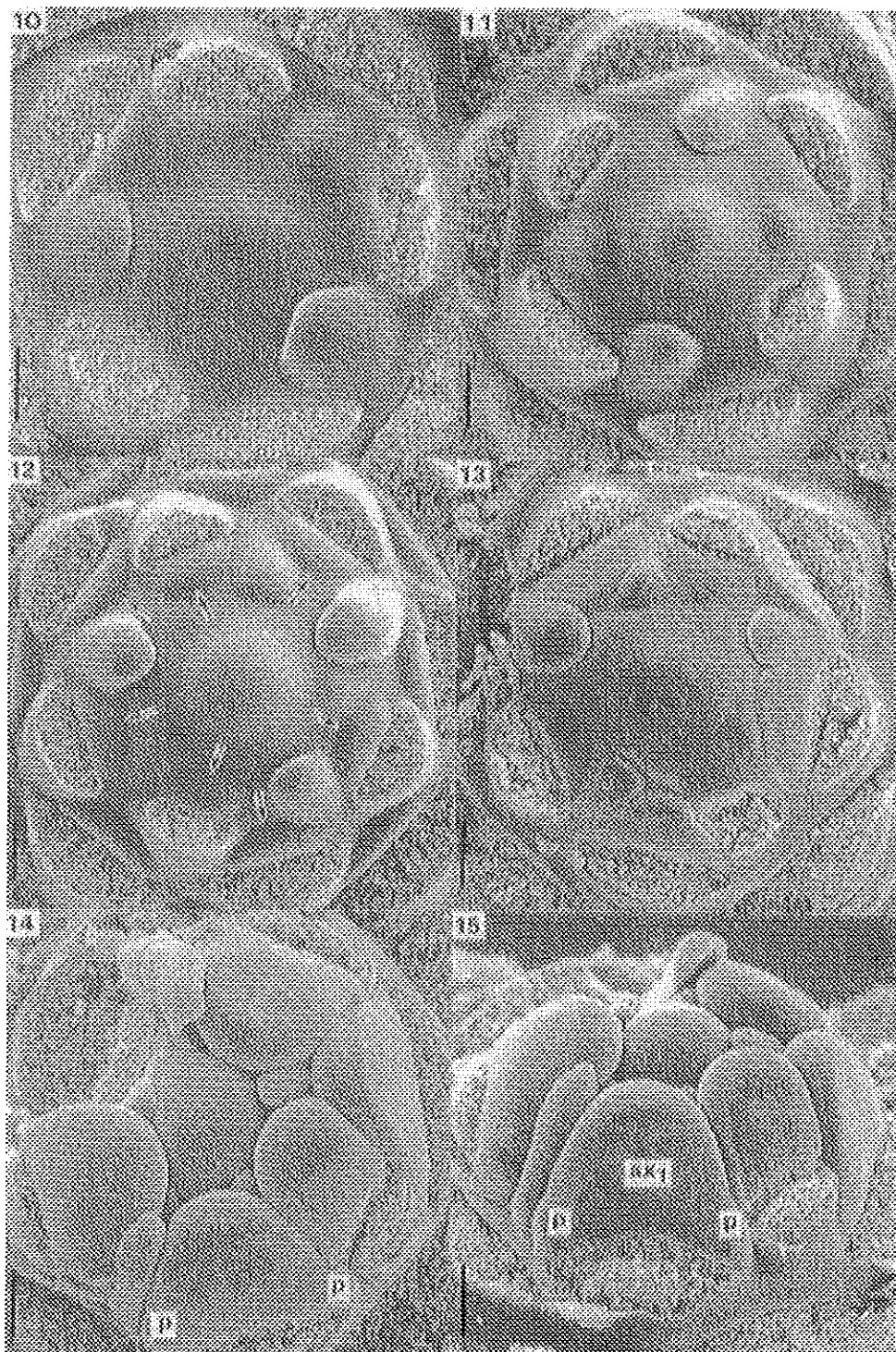
tissue in each axil of a series of scales that constitute a pseudowhorl (Figs 12 arrows, 13). Numbers vary from 5 to 10, depending on the vigour of the shoot. Phylloclade primordia are transversely flattened, dorsiventral structures from the start and soon become triangular (Figs 13–15). Flattening of the adaxial face of the phylloclade seems to be a result of pressure from the enveloping bud scales. The presence of these precocious branches also disrupts the regularity of adjacent younger primordia close to the phylloclade tier so that they are often displaced and spathulate (Fig. 13). As the phylloclades enlarge the shoot apex becomes narrower and more conical. We have not studied the further behaviour of the shoot apex at this stage of shoot development but it involves the production of the large numbers of bud-scales and those preformed scales that are found along the next unit of extension.

PHYLLOCLADE MORPHOLOGY AND ANATOMY

The interpretation of the phylloclade as a fused, planated branch system was provided as long ago as 1872 by Strasburger (*cf.* Richard, 1826; Bertrand, 1874). Its morphology and anatomy has been described by a number of authors (e.g. Robertson, 1906) but in most detail by R. S. L. Keng (1979) so that only a brief description is given here.

Seedling phylloclades
(Figs 4, 5)

Phylloclades on seedlings are always determinate. These are usually subtended by a juvenile needle leaf inserted on the seedling axis (ax_0). They have distichous phyllotaxis and dorsiventral symmetry with the plane of flattening horizontal as in a foliage leaf of most seed plants (Fig. 5). However, their first leaves (f_1) are alternate and not paired like prophylls. The axis of the phylloclade (ax_1) is flattened and supports a series of altenately arranged scale leaves (f_1) that are themselves flattened in the horizontal plane. These first-order leaves themselves subtend (at least in the proximal part) a branch to which they are often adnate. The branch axis (ax_2) is also flattened and toothed distally, the teeth representing second-order leaves (f_2). The first-order axis itself ends in a series of teeth, corresponding to the most distal first-order leaves. From this morphology it is clear that the lobes of pinnatifid phylloclades that are often described as 'simple', correspond to first-order branches. Sometimes in larger, more vigorous seedling phylloclades there are third-order axes (ax_3) subtended by a few of the proximal

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Figures 10–15. *Phyllocladus glaucus*, SEM photographs of shoot apex and phylloclade initials seen from above (Figs 10–14) or obliquely (Fig. 15). Fig. 10. Resting bud with spiral phyllotaxis (3+5, measured average angle of divergence = 137°), no evidence of phylloclade primordia. Fig. 11. Similar bud with bijugate phyllotaxis (4+6), average angular divergence between successive leaf pairs = 69°, no evidence of phylloclade primordia. Fig. 12. Possible initiation of phylloclade primordia (arrows) in axils of scale primordia P7–P13 to initiate a pseudowhorl (tier) of 7 branches. Scale primordia P1–P6 would then be the first primordia above the branch tier i.e. outer scales of the new terminal bud. Fig. 13. Later stage with evident phylloclade primordia in axils of P7–P12, note distortion of scale primordia (P1–P6) above branch tier. Fig. 14. Later stage with first leaf primordia (prophyll pair, p) at base of older phylloclade primordia, shoot apex reduced to a narrow cone. One phylloclade primordium (upper left) removed. Fig. 15. Same apex, note prophylls (p) at base of phylloclade primordium. ax_1–phylloclade axis. Scale bar for all figs = 200 µm.
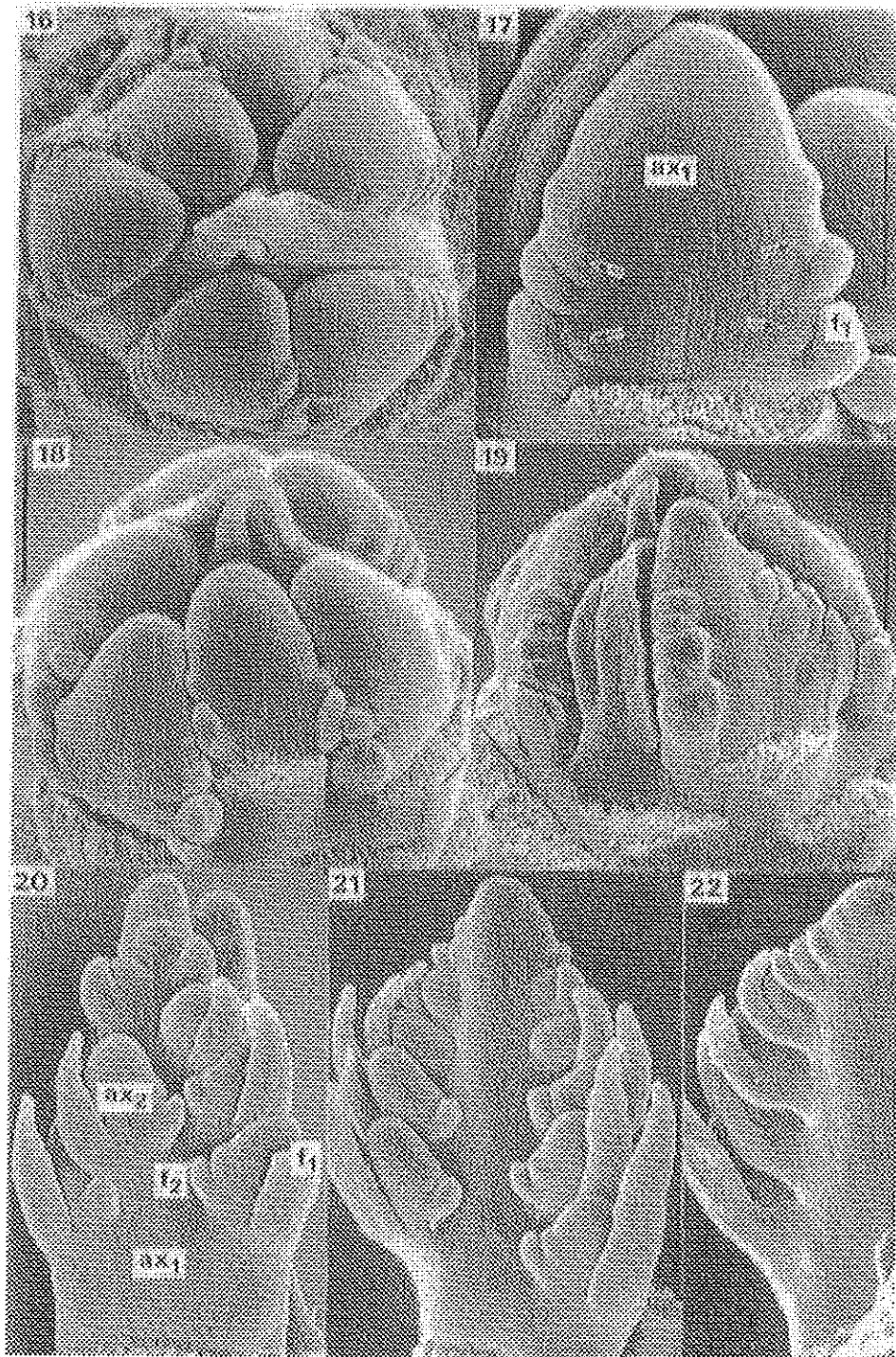
leaves of the second-order axis (ax_2) and recognized by the minute lobes corresponding to third-order leaves. This is a uniform feature of most adult leaves (*cf.* Figs 5, 9).

Vasculature is readily observed in cleared organs (Fig. 5). All leaves have a single trace that diverges from the vascular cylinder of the parent axis. The trace to adnate leaves diverges from the axial cylinder well below its departure into the leaf it supplies. Axis traces are intrinsically radially symmetrical but become progressively reduced in a distal direction along the phylloclade. This analysis shows that even the earliest phylloclades produced by a seedling can represent a branch complex with two or even three orders. There is much quantitative variation in the morphology of the youngest phylloclades but the transition series to the adult phylloclade is distinctive for each species.

### Determinate adult phylloclade
(Figs 2, 6–8, 9)

The initial description refers to the so-called 'compound' phylloclades of *P. glaucus*, *P. hypophyllus* and *P. trichomanoides*, which resemble a pinnately compound leaf with a terminal leaflet (Figs 6, 8). The first-order axis (ax_1) is internally radially symmetrical and supports the distichous series of lateral segments and a terminal segment. The scale leaf subtending the axis is either inserted directly on ax_1 (*P. hypophyllus*) or is adnate to it, as in *P. trichomanoides* and especially *P. glaucus*. The ultimate segments have the same morphology and vasculature as in the seedling phylloclade (Fig. 9). The range of forms for three taxa is shown in Figs 6–8.

Indeterminate adult phylloclade
(Figs 2, 6, 8)

These structures have the same intrinsic morphology of 'compound' determinate phylloclades but are distinguished by the development of a terminal bud (Figs 6 [inset], 8 [inset]). Figure 2 shows an indeterminate phylloclade in *P. glaucus* that has produced from its terminal bud a tier of four determinate phylloclades. The phylloclade usually appears like a paripinnate leaf, but sometimes the terminal bud is at the end of a reduced, but distinctly flattened segment. Occasionally an incipient terminal bud is formed at the apex of a lateral segment (i.e. one axis order higher), but these buds never seem to develop further. A terminal bud is established by an abrupt transition from distichous to spiral

Figures 16–22. *Phylloclades glaucus*, SEM photographs of shoot apex and phylloclade primordia. Fig. 16. Phylloclade tier from above, shoot apex obscured by scale appendages; phylloclades with first-order appendages. Fig. 17. Single phylloclade from same apex viewed from abaxial side, distichous series of scale leaves (f_1) evident, the lower with axillary primordia of next higher branch order (ax_2-arrows). Fig. 18. Same apex as Fig. 16 viewed obliquely to show lower appendages on ax_1 distorted by compression. Fig. 19. Later stage with further distortion of primordia f_1 and ax_2 because of close packing. Fig. 20. Abaxial view, single phylloclade, later stage with well developed scales f_1 subtending second-order axes (ax_2=segment axes) themselves developing appendages (f_2=leaves), note the transition to radial symmetry of the apex of ax_1 indicating an indeterminate phylloclade. Fig. 21. Abaxial view, single phylloclade from same tier as Fig. 20, later stage with f_1 exceeding the segment initial. Fig. 22. Adaxial view of different phylloclade but same tier as Fig. 20, showing how second-order axes twist about a sagittal plane. Scale bar=200μm in Fig. 17; =0.3 mm in Fig. 18; =0.5 mm in Fig. 19; magnification of Fig. 16 same as Fig. 18; magnification of Figs 20–22 same as Fig. 19.
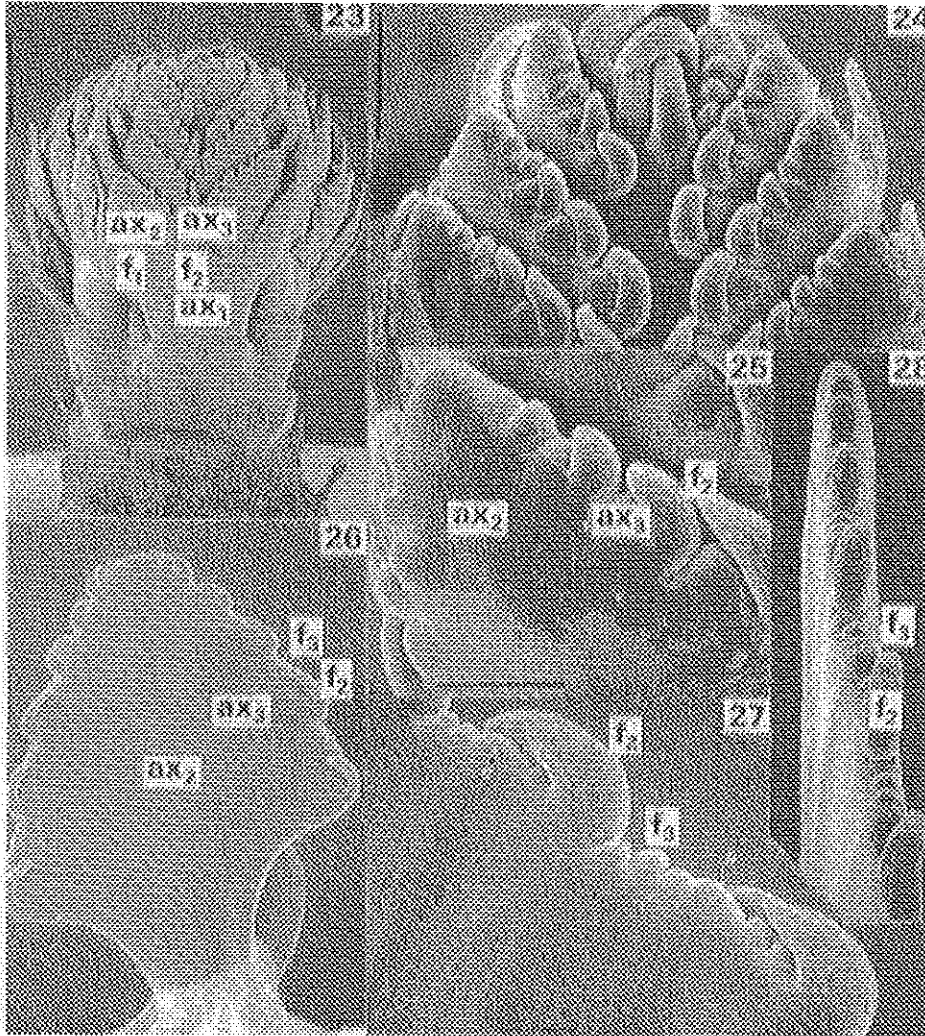
Figures 23–28. *Phylloclladus glaucus,* SEM photographs of late stage of phylloclade development. Fig. 23. Whole bud (with scales, removed) at stage when phylloclades become visible externally; older segment axes (ax$_2$) subtended by f, flattened against parent axis (ax$_1$), with f, and initials of ax$_3$. Fig. 24. Apex of phylloclade with distal scales arranged spirally to form the terminal bud of the indeterminate phylloclade. Distichy of segments pronounced, scales overarching initials of ax$_3$ (*cf.* Figs 39, 40). Fig. 25. Detail of segment (ax$_2$) tip, leaves (f$_1$) and axes (ax$_3$) appearing in regular acropetal order. Fig. 26. Maturing segment with almost all appendages initiated and planar growth well advanced, ultimate branches (ax$_3$) still initiating f$_3$. Fig. 27. Details (from Fig. 26) of apices (arrows) of ax$_3$. Fig. 28. Same segment view laterally to show pronounced distichy and planation, f, and f$_1$ clearly contrasted. Scale bar = 2 mm in Fig. 23; 1 mm in Fig. 24; 0.5 mm in Fig. 25; magnification of Fig. 26 same as Fig. 23; magnification of Fig. 27 same as Fig. 25; magnification of Fig. 28 same as Fig. 24.

phyllotaxis, the spirally arranged leaves becoming aggregated as bud-scales (Fig. 24).

Vasculature of indeterminate segments is identical with that of the determinate phylloclade except that in the former the vascular traces to appendages become spirally disposed distally as internal and external symmetry become coincident.
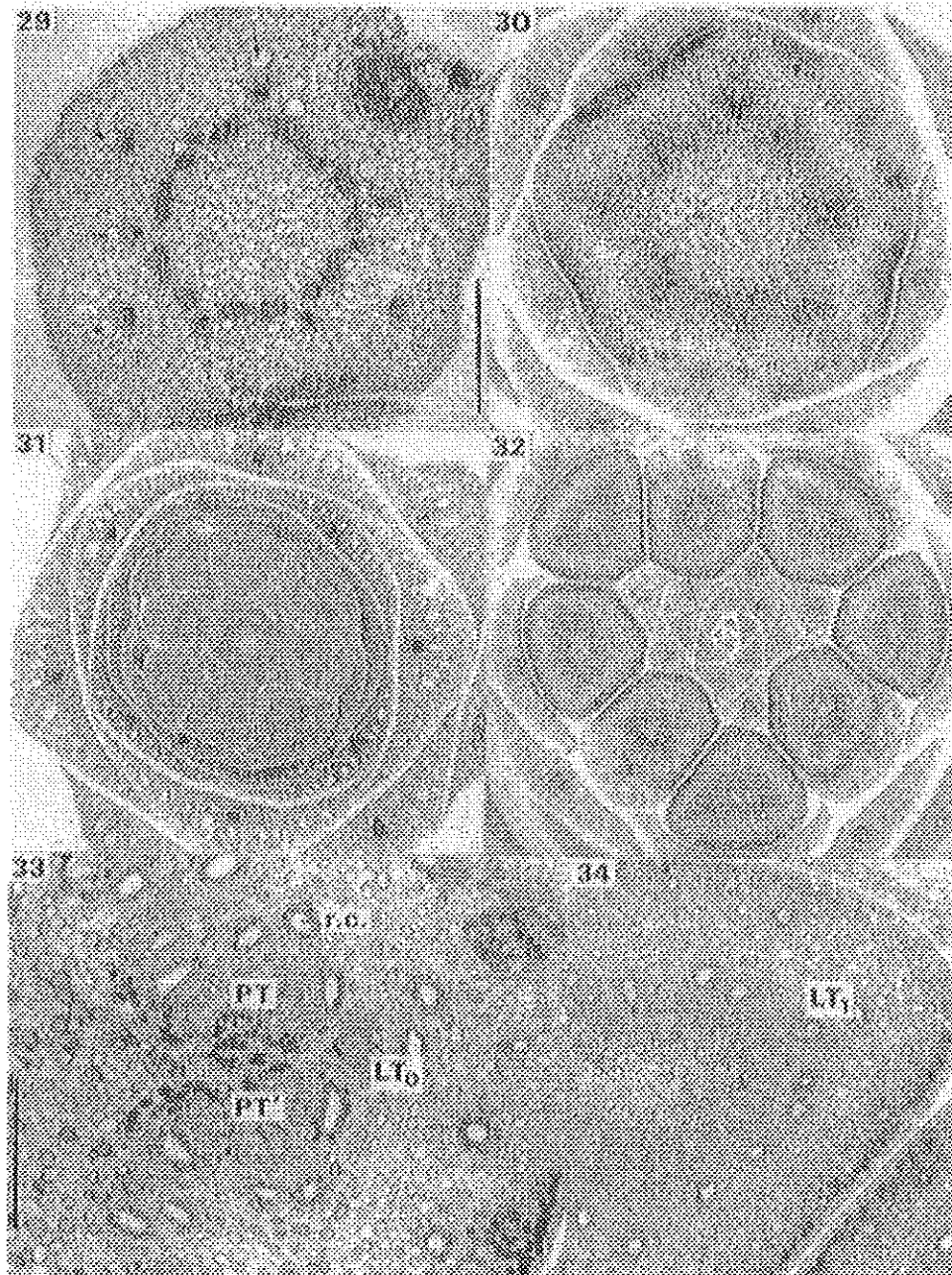
Figures 29–34. *Phyllocladus glaucus*, anatomy of phylloclade insertion, all T.S. Fig. 29. Main axis just below a tier of phylloclades, each leaf trace (e.g. arrows) associated with a resin canal; departing branch trace of a single phylloclade at top right. Fig. 30. Section at level of departure of trace system to eight phylloclades of one tier, each phylloclade trace disrupting the stele extensively (*cf.* Fig. 33 for detail of one branch complex). Fig. 31. Same tier at a level just below shoot apex, phylloclade axes distorted by mutual compression. Fig. 32. Same tier at a level above shoot apex, note close packing of scales forming the new terminal bud. Fig. 33. Detail of segment trace departing from stele of ax_0, trace to subtending scale ($f_0 = lt_0$) at right, note supernumerary (cortical) resin canals. Fig. 34. Part of vascular system of stele of phylloclade axis (ax_1) showing some dorsiventrality and scales diverging only laterally, reflecting the strict distichy of the phyllotaxis. lt_0–trace to scale leaf (f_0) subtending phylloclade; lt_1–trace to f_1 of phylloclade; pt and pt'–two halves of branch trace; rc–resin canal. Scale bar = 2 mm in Fig. 29; 0.5 mm in Fig. 33; magnification of Figs 30–32 same as Fig. 29; magnification of Fig. 34 same as Fig. 33.

Phylloclade anatomy
(Fig. 9)

The anatomy of a wide range of phylloclades illustrated by R. S. L. Keng (1979) shows the uniformity of organization in the genus (*cf.* Berggren, 1980). Phylloclades are dorsiventral, with distichous phyllotaxis throughout except in the distal transition to spiral phyllotaxis where this occurs. Stomata are more or less restricted to the lower (abaxial) surface of the phylloclade, emphasizing the leaf-like nature of the organ. There is a differentiation between central large-celled mesophyll and superficial palisade layers of smaller compact cells; that of the adaxial surface being most palisade-like. Sclerenchyma is largely restricted to bundle sheath fibers adjacent to the phloem of leaf and axis traces.

The vasculature reflects the organization of the complex as a distichously arranged system of axes and appendages with two (or more) branch orders, complicated by adnation of leaves and complete dorsiventrality (Fig. 9). Axis traces show radial symmetry, even though they usually include only two vascular bundles (paired circles in Fig. 9C). These have opposed orientation (opposed arrows in Fig. 9C) so that one bundle has an inverted arrangement of vascular tissue. Leaf traces, on the other hand, have an orientation perpendicular to axis traces (solitary circles in Fig. 9), since they relate directly to the trace system of the axis from which they diverge, in the manner of leaf trace to branch trace; that is with the xylem pole of the bundle toward the supporting axis (adaxial), the phloem pole away (abaxial). Orientation of branch and leaf traces is clearly perceived in the position of resin canals, since there is usually one immediately outside the strand of phloem fibers. *Phyllocladus glaucus* is exceptional, as reported by R. S. L. Keng (1979) in that there are commonly two resin canals instead of one associated with each leaf trace.

The vasculature can be confirmed, in principle, by superficial inspection, since the double bundle of the branch trace is translucent, as is most obvious in *P. glaucus,* presumably because the adaxial and abaxial resin canals approach the epidermis closely. In a transverse section of a phylloclade segment the internal morphological distinction between two ultimate order axes on the same side of the segment can be recognized because the two adjacent traces to leaves of different order have opposite orientation (i.e. are mirror images of each other, Fig. 9C). All these observations confirm those made by R. S. L. Keng (1979).

Axial anatomy
(Figs 29–34)

The axis of the phylloclade is initiated as a flattened structure, but it retains predominantly internal radial symmetry in its vascular cylinder. This can be seen in the distribution of inner cortical resin canals in Figs 32, 33 since each canal corresponds to an axial bundle. Dorsiventrality is indicated superficially by the somewhat flattened marginal wing along which the segments are inserted. The departure of traces to first order appendages in the dorsiventral plane is itself a direct reflection of the distichous phyllotaxis (Fig. 34) and represents a deviation from strict radial symmetry.

Departure of the trace system to the main axis of each phylloclade causes a major disruption of the vascular cylinder of the parent axis (*cf.* Figs 29–30) since a

branch 'gap' is produced as wide as the phylloclade trace (Fig. 33). Radial symmetry of the trace is established well below the morphological level of insertion of the phylloclade (Fig. 33), even though the branch trace is initiated laterally as branches from two adjacent axial bundles. The disruption of axial (ax_0) vasculature is major because of the departure of the traces to each member of the pseudowhorl of phylloclades at much the same level (Fig. 30).

A similar method of branch trace departure is seen in higher order axes within the phylloclade itself, but with a progressive trend towards dorsiventrality. In the ultimate branch order, represented in the segment vasculature, the axis trace is seen as a pair of bundles, one with inverted symmetry; the 'gap' between these two bundles representing the level of departure of the leaf traces (complexes of 3 and 4 circles in Fig. 9C). These features are illustrated in some detail for mature phylloclades by R. S. L. Keng (1979). A more detailed developmental analysis of the vascular system of *Phyllocladus* has not yet been attempted by us, although it is of obvious morphogenetic interest because a common vascular pattern is distributed among organs of contrasted symmetry.

PHYLLOCLADE DEVELOPMENT

Initiation of appendages
(Figs 14–28)

The first indication of appendages on the flattened phylloclade primordium are the basal leaves (Figs 14, 15; 16–18). Clearly their phyllotaxis is distichous and a regular acropetal series is produced. There is almost synchronous development of the apical meristems of branches of the next higher order that are the initials of the phylloclade segments with their subtending scales (Fig. 17, arrows *cf.* Fig. 19). The scale-like subtending leaf initially overtops the axillant branch, but eventually the segment becomes dominant. Distortion owing to the requirements of close packing is often pronounced at this stage and clearly results from the development of a structure which is intrinsically dorsiventral but enclosed in a cylindrical envelope. Displacement of phylloclade segments towards the abaxial face of the branch is common (*cf.* Figs 21, 22) and there is frequent distortion of segment primordia as they expand within the confines of the spaces between innermost bud scales. Ultimately they are all flattened in the same plane, the reorientation occurring quite early (Fig. 23).

Soon the symmetry of the ultimate segments is established. The apex is initially somewhat rounded (Figs 20, 21) but flattening becomes pronounced (Figs 23–25). Development of the segment involves the production of a further series of scale-like appendages of the next higher order (f_2) that in turn subtend the third order axis meristem (ax_3), also at first incipiently with a radial symmetry (Fig. 25). However, the axis (ax_2) at this stage has begun the planar growth that produces the flattened segment. The third (ultimate) order branch apices initiate the final series of scale appendages (f_3) as the segment as a whole broadens (Figs 25, 27). There can be up to 10 of these, persisting as minute bumps, before growth of superficial meristems and primordia ceases, even though some marginal activity brings the segment to its final size. The remains of the apex of the ultimate order persist as a somewhat enlarged median bump (Fig. 27, arrows). Phylloclade morphology is fully established and only growth in one plane is involved in further enlargement of the segment to produce its final flattened form (Figs 26, 28).
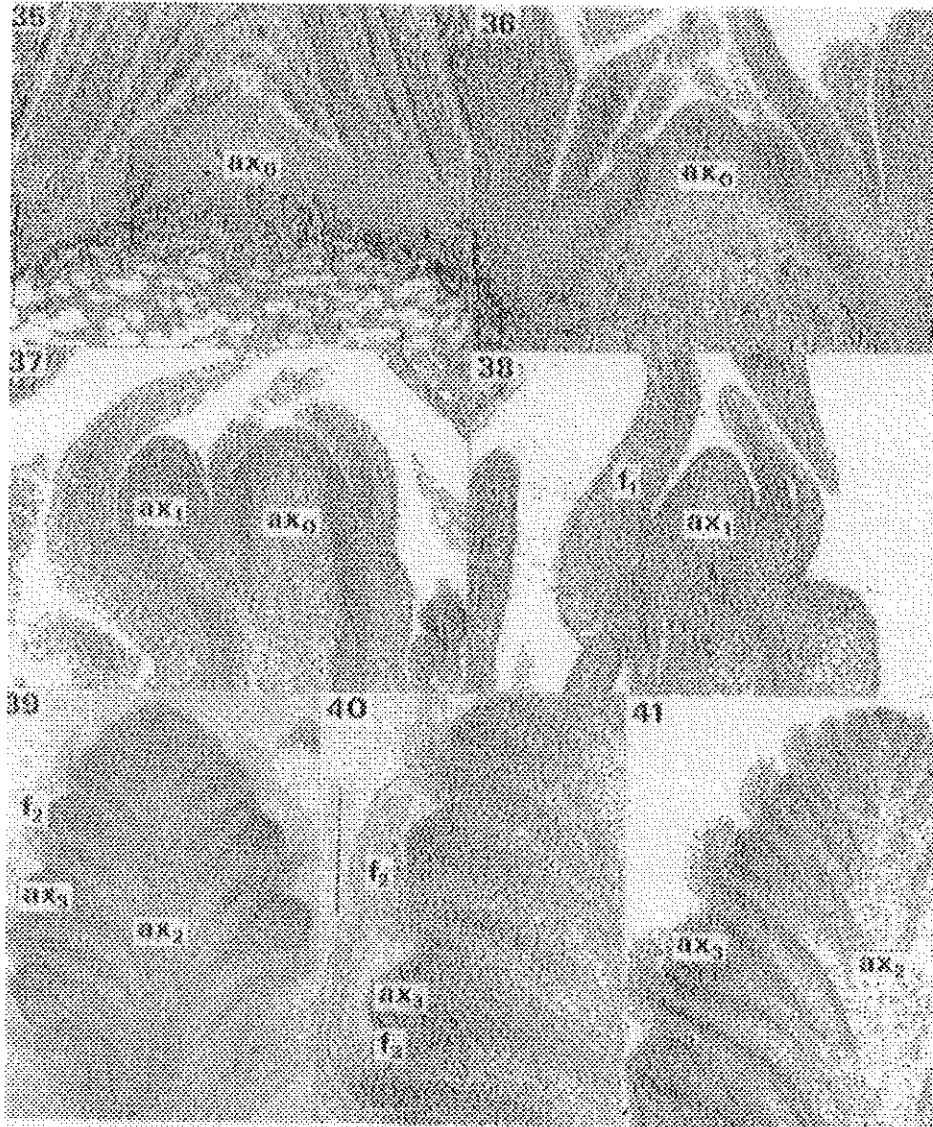
Figures 35–41. *Phyllocladus glaucus*, histology of apical and segment meristems, all L.S. Fig. 35. Dormant shoot apex of ax_0 with short meristematic region and abrupt transition to differentiated tissue. Fig. 36. Active apex of ax_0 at initiation of a new unit of extension, gradual transition to differentiated tissue via a rib meristem. Fig. 37. Shoot apex of elongating unit of extension (ax_0), to left an approximately median section through a developing phylloclade (ax_1) (*cf.* Fig. 14) showing broad pith connection characteristic of a sylleptic branch. Fig. 38. Median section of apex of an indeterminate phylloclade (ax_1) with the new apical meristem initiating scales (f_1) (*cf.* Figs 20 and 24). Fig. 39. Paradermal section of a young segment at about the stage of Fig. 25. Fig. 40. Detail of marginal meristematic region (*cf.* Fig. 25). Fig. 41. Somewhat older segment, the apical meristem of ax_1 initiating scales (f_1); contrast the stage of development of the scales (f_2) and the meristem complex each scale subtends. Scale bars = 0.5 mm for Figs 35, 37, 40; 1 mm for Fig. 39; magnification of Fig. 36 same as Fig. 35; magnification of Fig. 38 same as Fig. 37; magnification of Fig. 41 same as Fig. 39.

Determinate versus indeterminate phylloclades
(Figs 18–22, 24, 38)

In determinate phylloclades the apical region of ax_1 retains a distichous phyllotaxis throughout and the first-order axis becomes converted into a terminal segment, corresponding in all details of its development to the processes carried out in the higher order branch meristems of the lateral segments. This involves a flattening of the apex of the phylloclade axis (e.g. Fig. 22), even though the apex in early stages may have been somewhat cylindrical (Figs 18, 19). In contrast, indeterminate phylloclades show an abrupt change to radial symmetry, with the production of spirally-arranged scales (Figs 20, 24). Retention of radial symmetry, and the production of spirally-arranged scales frequently occurs with subsequent abortion of the apex so that a determinate phylloclade results without a terminal segment. The apical meristem of the indeterminate apex retains the same histology as parent apices, but is somewhat narrower (Fig. 38).

Segment histogenesis
(Figs 39–41)

We have studied segment histogenesis in only a limited way; primarily to determine location of meristems. The flattening of the segments, which are initiated as axillary shoots with an initially radially symmetrical shoot apex, is the result of activity becoming restricted to an extensive discontinuous marginal meristem (Figs 39–41). In paradermal section the whole margin is seen as an almost continuous meristem, with localized periclinal divisions producing the higher order branches that retain dorsiventral symmetry from the start. Discontinuities result from vacuolation of future ground tissue cells which blocks out the vascular system, consisting of axial and leaf traces (e.g. Fig. 40). Initially these strands remain densely cytoplasmic and with the constituent cells elongated, in the manner of procambial cells. Differentiation between ground tissue and vascular system proceeds in an acropetal direction (Fig. 41); there is no formation of an intercalary meristem. We have not seen very young stages; it is possible that the marginal meristem is initially continuous.

Cell division is complete at a stage when the phylloclade segment is about 2 mm long, all subsequent enlargement is the result of cell expansion. Protodermal cells continue division longest and mature last. The method of development by means of marginal growth as an organ complex ensures the determinate status of the segment, there is no retention of localized meristematic activity that could continue either extension of the segment axis or higher order branches. Segment scales (f_2) mature distally while their procambium is still immature basally (Fig. 41). In this sense, the segment is a good developmental homologue of a leaf.

DISCUSSION

Significance of shoot construction

Phyllocladus is shown to be highly deterministic in its architecture with simple qualitative 'rules of organization'. In the adult phase there are two types of shoot that are similar in their development but differ in their potential for further growth. Both these shoots are phylloclades and each is a flattened branch complex

with a distinction between a main axis and terminal or lateral segments that simulate leaflets. The simplest phylloclades resemble a simple leaf. In one kind of phylloclade (indeterminate) the main axis retains a potential for continued growth by forming a radially symmetrical terminal bud. These form the framework of the tree. In contrast the other kind of phylloclade (determinate) does not contribute to the main framework, although it may have an extended life span. Indeterminate phylloclades branch monopodially. Each higher branch order begins as a phylloclade; indeterminate phylloclades are initially dorsiventral but become radially symmetrical with the activation of the terminal bud.

Development of phylloclade segments involves adnation between appendages of ultimate branch orders brought about by limitation of cell division to submarginal regions that resemble the marginal meristem of leaves. Distichy is pronounced in all orders of branches at initiation, but there is a reversion to spiral phyllotaxis in the formation of a terminal bud in indeterminate phylloclades. It has been suggested that distichy may not occur in gymnosperms and this might be a growth limiting characteristic, especially of conifers (Tomlinson, 1982). *Phyllocladus* contradicts this generalization but the exceptional phyllotaxis is related to its highly specialized morphology.

Construction of a *Phyllocladus* tree is highly segmented with pronounced rhythmic (episodic) growth that is strongly seasonal, at least in temperate climates. There is a slight distinction between units of extension and units of development because of partial preformation of most, but not all, the appendages formed in the season of extension. The resting shoot apex is enclosed by an armour of numerous rigid scales, but includes the primordia of scales that expand as the shoot begins to extend. Bud break is characterized by enlargement of the shoot apex, initiation of new scale primordia and a series of branch meristems (the future phylloclades) that occupy approximately one phyllotactic cycle, that is one branch per orthostichy, constituting the pseudowhorl of a branch tier. Development is clearly sylleptic and reflected in the long hypopodium of the phylloclade. The shoot apex itself is considerably diminished by phylloclade production but its development is continued in the formation of the next series of bud scales, whose maturation ends the growth cycle, with the onset of bud dormancy.

The cycle of development is understood only in a very generalized way; no attempt has been made to follow the cycle of mitotic activity that would precisely establish the morphogenetic period (*cf.* Hallé & Martin, 1968 for *Hevea*). Similarly, the number of preformed scales has not been established with any precision. There are nevertheless two incremental limits between each unit; that established by the morphological boundary of the branch tier itself (which occupies the middle of a growth cycle) and that established by the tissue formed before and after bud-break, corresponding to a level just above the series of bud-scales (or their scars). The point to emphasize is that phylloclades are neo-formed so that all their development is incorporated in the early flush of growth following bud-break.

Construction with this degree of precision produces a highly model-conforming tree with elements of three or four closely related models in the system of Hallé, Oldeman & Tomlinson (1978). A feature of special interest is that once a regular rhythm of phylloclade development is established there are no reserve meristems.

Reiterative ability is then restricted to dedifferentiation of branches, as for example when a damaged leader is replaced by one (or more) of the uppermost tier of branches. Only in seedlings do reserve meristems play a part in shoot regeneration; this ability seems to be retained in some populations (e.g. in *P. aspleniifolius*) and may represent the effect of long-persistent reserve meristems. Some of these meristems are of the 'detached' type described by Fink (1984; Fink, personal communication). Contrast between seedlings and adults in leaf morphology is therefore complemented by the contrast between them in regeneration ability.

Evolutionary morphology

There is common agreement among most authors who have studied the genus that the phylloclade is a flattened branch complex. Indeed this interpretation can be said to have originated with Richard, who first described the genus. Although he refers to them as 'leaves', he commented on the way in which they could be considered analogues of the flattened appendages of 'Xylophyllae', probably referring to this section of the genus *Phyllanthus* (Euphorbiaceae), which has platycladistic morphology. Our observations provide further evidence in support of the interpretations of Strasburger (1872), Bertrand (1874), and all subsequent workers (e.g. Troll, 1937; Kaussmann, 1955), that the phylloclade is a branch complex. It originates as an axillary structure and shows a regular acropetal production of appendages that retain the standard relationship between leaf and subtended bud. The vasculature of the complex is exactly as one would observe in a branch system of three orders, with single leaf traces attached to the parent axis in a normal sequence. Branch traces diverge as paired strands from two adjacent axial bundles, as is usual in coniferous shoots. Our observation demonstrates that the planate morphology of segments is correlated with distichous phyllotaxis and the union of appendage primordia by a growth process resembling that of a discontinuous marginal meristem. Consequently a leaf blade is closely simulated. Histological features of a lamina include dorsiventrality, mesophyll and accessory transfusion tissue differentiation and a hypostomatic condition (R. S. L. Keng, 1979; Berggren, 1980). Nevertheless the segment vasculature continues the axis-appendage relationship of a shoot, albeit flattened in one plane. We find no evidence for ancestral telomic morphology, dichotomous branching and planation of radially symmetrical axes, as proposed by Keng (1974). We therefore support the position of Quinn (1987) concerning the morphology of *Phyllocladus* and find his arguments convincing for including the genus in the Podocarpaceae, rather than segregating it as a separate family.

To this discussion we now add a point of view that can account for the distinctive morphology in adaptive terms. A particular constraint imposed upon conifers is the unique presence of a single trace to all foliar appendages (except some cotyledons). To develop a large photosynthetic area within a single growing season requires either that a large number of needles be produced at one time or that branching be elaborated through several orders. The latter is achieved in many Cupressaceae in which the ultimate branch complexes are planated structures, with axes all inserted in one plane. Most of the complexes are 'determinate' in that they have a limited life span. Planation is usually the result of anisophylly by flattening of alternate leaf pairs, as shown to a marked degree by

Libocedrus, Thujopsis and *Platycladus.* A growth limitation, however, is that a broad branch insertion can only be established by secondary growth. *Agathis* and *Araucaria* species develop the largest leaves in conifers, the leaf trace is nevertheless a single structure, at least at its insertion.

Phyllocladus offers another alternative. It elaborates a *sylleptic* branch complex so that a broad branch trace insertion can be established by primary growth (e.g. Figs 34, 37). The system is entirely preformed (a feature that syllepsis favours) and most units function very much like compound leaves in being determinate and eventually abscissed. The same unit can be long-lived if it retains a terminal bud; it then adds to the permanent framework of the tree. Functionally the tree deploys a single appendage, but with an important morphogenetic switch from 'leaf' to 'branch'. These axes are comparable to those in *Agathis,* which are usually sylleptic in origin and show pronounced plagiotropy. Segments are here true leaves and the branch is morphologically indeterminate, but still with limited life span because they ultimately abscise (Licitis-Lindbergs, 1956).

Phylloclade ontogeny and dorsiventrality is dependent on distichy, otherwise unrecorded for conifers. (Where 'distichy' is used in description, as for *Prumnopitys* and *Dacrycarpus,* the dorsiventrality is secondary and imposed upon a spiral phyllotaxis.) Spiral phyllotaxis is favoured in conifers because of the needle leaves for which a 2-ranked arrangement is not very effective photosynthetically. However, distichy is not intrinsically difficult to derive because most coniferous shoots have a pair of opposite or sub-opposite lateral prophylls at the base of each branch; *Araucaria* is exceptional. Distichy could result from an extension of this 'juvenile' feature of each branch. However, a unique feature of *Phyllocladus* is the vertical (dorsiventral) plane of flattening of the ultimate branch orders of the phylloclade. A more complex morphogenetic transposition is thus involved. In comparison the phylloclades of Asparagaceae are typically flattened laterally, that is, horizontally (Cooney-Sovetts & Sattler, 1987). Distichy and planation in *Phyllocladus* segments are thus seen as complementary events.

It seems therefore that *Phyllocladus* can better be viewed as an example of extreme modification of the conventional coniferous shoot morphology and there is no need to invoke more remote connections as is proposed by Keng (1974), that are unlikely in a stratigraphic context. *Phyllocladus* does indeed have a morphology capable of explanation in terms of recent, rather than very ancient, groups of plants, even if one invokes homeosis and emphasizes the leaf-like features of the phylloclade segments (*cf.* Sattler, 1985; Rutishauser & Sattler, 1985). One can certainly introduce the concept of 'partial homology' in interpreting these structures, but preferably in morphogenetic rather than evolutionary terms (*cf.* Cooney-Sovetts & Sattler, 1987). The function of phylloclades in the architectural framework of the tree provides an element of biological understanding that is missing from more philosophical analysis. Planation is a morphogenetic process that has probably occurred repeatedly in the evolution of plants and its inception was undoubtedly important in the early evolution of leaf-like structures. However, one cannot draw homologues of organization on the basis of developmental processes alone. Systematic contexts have to be admitted (*cf.* Quinn, 1987). Ecological considerations are important. *Phyllocladus* seems to have sacrificed most of its regenerative ability in evolving phylloclades. However, the retention of dormant meristems, correlated with seedling morphology that must reflect an ancestral state shows that some plasticity can be retained.

The present account is preliminary and serves as a model for more detailed quantitative study. Clearly the morphogenetic cycle can be investigated more precisely. The precise histogenesis of the segment needs detailed investigation to substantiate the function of its marginal meristem. We have made only limited observations on stem vasculature—its disruption by the massive traces of sylleptic branches needs precise study. Since annual growth rings are present and seem to complement annual increments in length, it should be possible to reconstruct the chronology of development of a small tree quite precisely. This would lead to an understanding of meristem, shoot and phylloclade demography. Longevity of determinate phyllocades on different branch orders can be established precisely and the change in frequency of phylloclade type with branch order could be quantified. *Phyllocladus* also offers unique opportunities to quantify some reiterative events because only branch reorientation is involved, at least in adult trees.

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