

Cone and ovule ontogeny in *Phyllocladus* (Podocarpaceae)

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Received November 1987, accepted for publication December 1987

TOMLINSON, P. B., TAKASO, T. & RATTENBURY, J. A., 1989. **Cone and ovule ontogeny in *Phyllocladus* (Podocarpaceae)**. Cones are borne directly on phylloclades, usually in the position of basal segments or as segment appendages. Each cone consists of a series of spirally arranged bracts, of which the middle bracts each subtend a single, sessile ovule. There is no ovuliferous scale. Ovules arise as ovoid outgrowths; integument development involves periclinal divisions of hypodermal cells with the integument becoming bilobed and extended laterally. The mature ovule is flask-shaped. The integument includes an extensive middle region bounded by an inner and outer epidermis; the outer hypodermis is differentiated as two contrasted cell layers. An aril differentiates late by periclinal divisions of the outer hypodermal cells at the base of the ovule. The three outermost layers of the integument become differentiated in the mature seed as an epidermis, with thick, cutinized outer tangential walls, an outer hypodermal tanniniferous layer and a sclerotic inner layer. Each ovule is vascularized by two strands that diverge from the axial bundles delimiting the gap left by the departing bract trace.

ADDITIONAL KEY WORDS:—Conifers – development – aril – epimatium.

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INTRODUCTION

Phyllocladus L. C. & A. Rich. is unusual among conifers in its flattened branch complexes (phylloclades) that constitute its main photosynthetic surface

(Tomlinson, Takaso & Rattenbury, 1989). An additional unusual feature, shared with a few other conifers (*Microstrobis* (Podocarpaceae), *Taxus*, *Torreya* (Taxaceae) and possibly *Cephalotaxus* (Cephalotaxaceae)) is the absence of an ovule-supporting structure that can be homologized easily with the ovuliferous scale otherwise considered to be typical of conifers. Consequently in *Phyllocladus* the ovule can be described as axial. *Phyllocladus* develops a structure described as an aril and therefore bears comparison with Taxaceae (cf. Keng, 1963a; Singh, 1978). Hooker (1852) included *Phyllocladus* within his broad view of Taxaceae. However, the aril of *Phyllocladus* has also been homologized with the epimatium of other Podocarpaceae (Sinnott, 1913; Wilde, 1944), a structure which is itself considered to be the ovuliferous scale, whereas the aril of Taxaceae is considered an organ *sui generis* and is part of the evidence Florin (1951) uses in according ordinal status (as Taxales) to that group. Clearly information concerning the development of these structures is important in clarifying their homology and in establishing the systematic and evolutionary status of *Phyllocladus* (cf. Quinn, 1987).

We have described the development of the phylloclade of *Phyllocladus* in relation to the total architecture of the tree (Tomlinson, Takaso & Rattenbury, 1989). This information is relevant to the present article because cones are supported upon phylloclades. Here we describe aspects of cone and ovule ontogeny in an attempt to clarify some of their comparative aspects. Although a full understanding must await detailed ontogenetic study of related taxa, the information presented here is relevant to an overall understanding of coniferous cone morphology.

Cone and ovule anatomy in *Phyllocladus* has been studied to only a limited degree by previous workers and largely in relation to gametophyte and embryo development, following the early investigation of Baillon (1860). These include Robertson (1906), Kildahl (1908) and Buchholz (1941) on *P. aspleniifolius* (Labill.) Hook.f. var. *alpinus* (Hook.f.) H. Keng (as *P. alpinus* Hook.f.), Holloway (1937) on *P. aspleniifolius* var. *alpinus* and *P. glaucus* Carr., Keng (1963b) on *P. hypophyllus* Hook.f. and Young (1910) on an unidentified species, but probably *P. aspleniifolius* var. *alpinus* (see Buchholz, 1941). Quinn (1986) recently added information about *P. trichomanoides* D. Don and *P. aspleniifolius* var. *alpinus*, which shows that the genus is uniform in gametophyte and embryological details, and comparable to other representatives of the Podocarpaceae in these features (Quinn, 1987). All these observations seem to have been based on sectioned material without any attempt to document developmental features of intact ovules. Scanning electron microscopy greatly facilitates such documentation.

The vascular anatomy of the *Phyllocladus* cone has been reported on by Eichler (1881), Strasburger (1872), Young (1910), Sinnott (1913), Aase (1915) and Holloway (1937). All show that the ovule vascular supply arises directly from the stele of the cone axis.

MATERIAL AND METHODS

Our studies of ovule and cone ontogeny are restricted to *Phyllocladus glaucus* Carr., which is representative of the genus but shows fewer irregularities in cone position and organization than the other three species. Material, fixed in FAA, was obtained from several small trees along the Donald MacLean Walking track, near Huia, Waitakere Ranges, Auckland, New Zealand in November and

December of 1985 and 1986. The specimens collected were young phylloclades, with evident basal cones, projecting from within the expanded bud scales. From our knowledge of the phenology of bud development, earlier stages of cone initiation, likely to occur within expanding but unopened buds, might not be distinguished easily from young phylloclade segments and would therefore require extensive destructive sampling in order to locate them. Consequently we have only studied relatively late stages of cone development, but all stages of ovule development.

Cones were prepared for SEM by removal of some subtending bracts prior to dehydration in ethyl alcohol and critical point drying. They were coated with gold-palladium. Sections of cones at several stages of development were cut from material embedded in either paraffin or glycolmethacrylate after dehydration in either *t*- or *n*-butyl alcohol, respectively. Sections cut at 7 μm were stained in either safranin and fast green, Heidenhain's haematoxylin, or with PAS reagent. Vasculature was analysed from serial transverse sections.

For studies of seed development in *P. trichomanoides* D. Don young and mature seeds, fixed in FAA, were obtained from Kumeu, Auckland and processed for histological examination as described above. Comparable stages were not obtainable for *P. glaucus*.

RESULTS

Cone morphology

In the simplest condition, represented by *P. glaucus* (Fig. 1), cones are borne directly on phylloclades in the position of basal segments. The subtending bract is

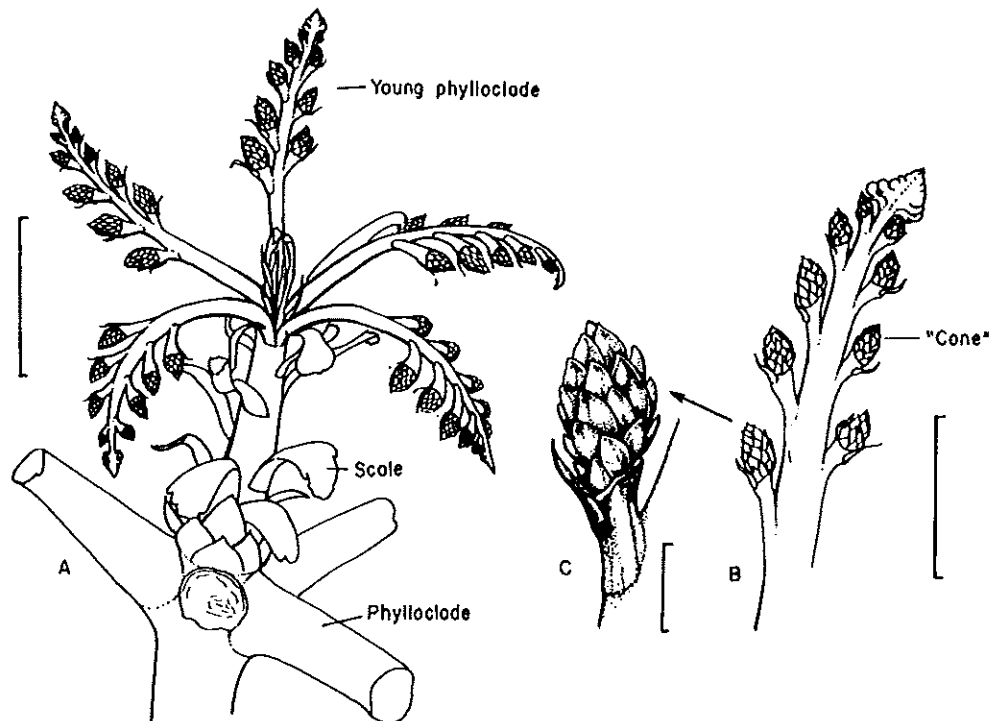


Figure 1. *Phyllocladus glaucus*. Cones on flushing shoot units. A. Extending shoot with young fertile phylloclades, three phylloclades of previous tier cut off above their insertion. Scale bar = 1 cm. B & C. Detail on one phylloclade and one cone, ovules totally enclosed by subtending bract, the bract subtending the cone itself is displaced onto the cone axis. Scale bars = 5 mm for B and 2 mm for C.

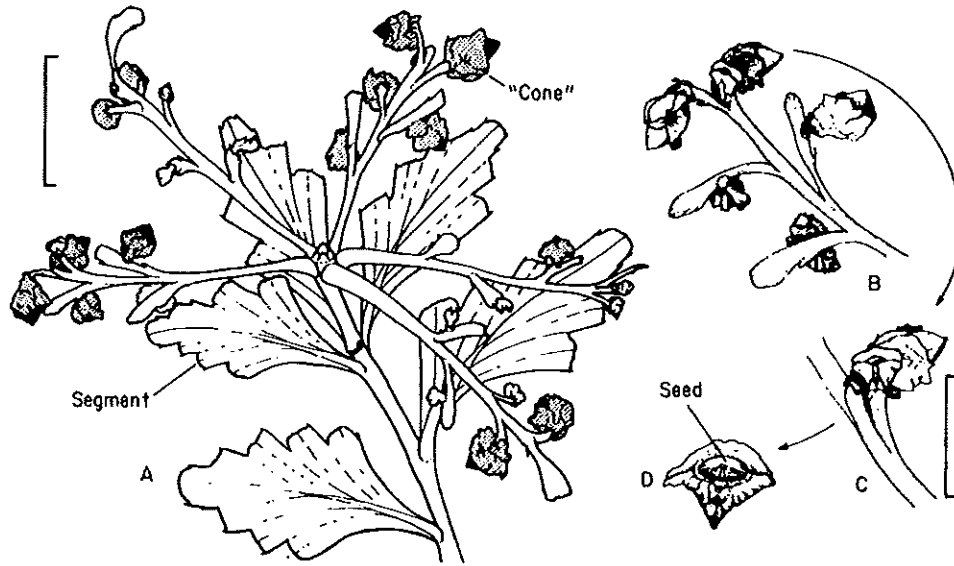
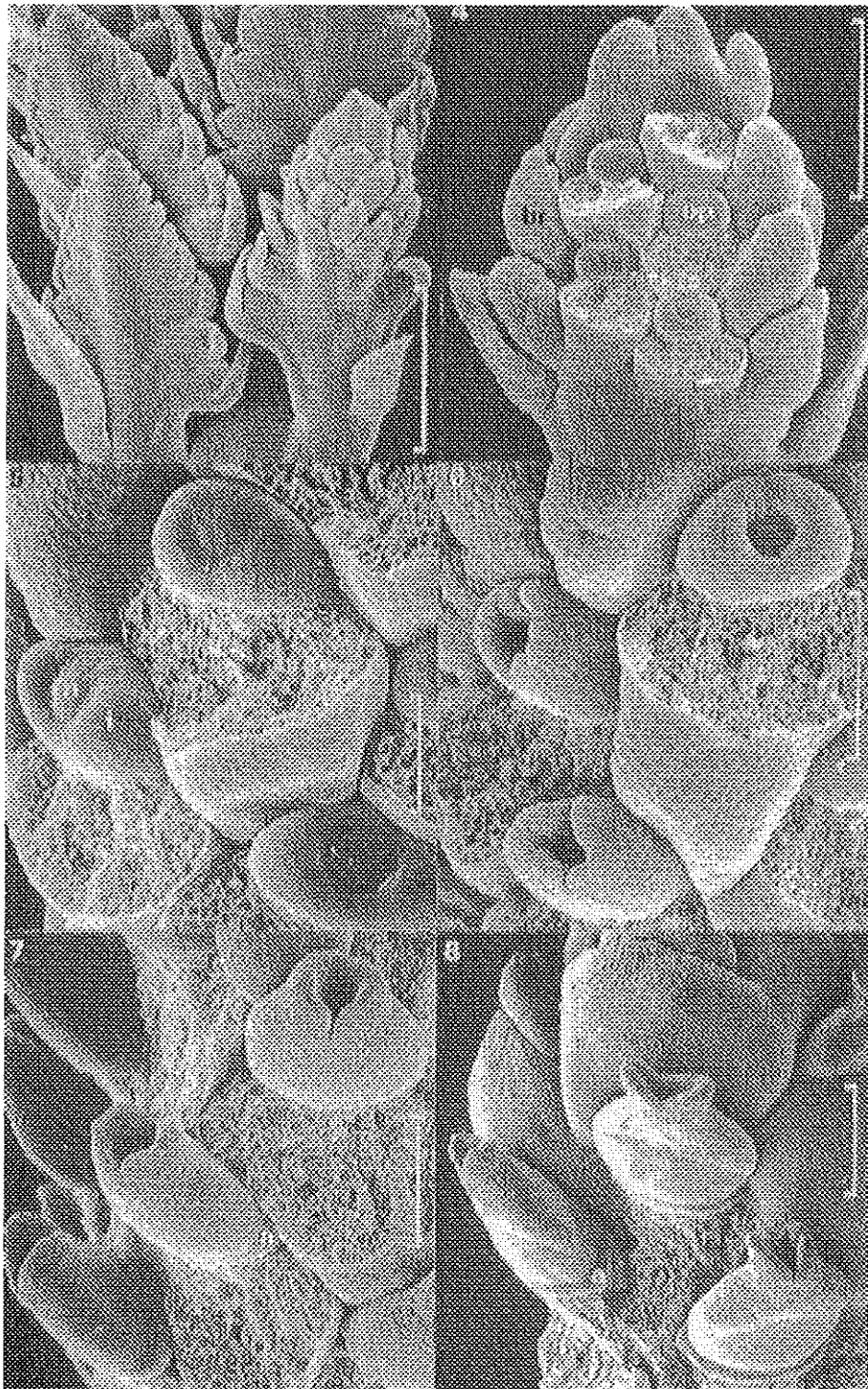


Figure 2. *Phyllocladus trichomanoides*. Mature shoots with seeds. A. Tier of fertile phylloclades and apex of previous indeterminate phylloclade. Mature fertile cones stippled, aborted cones unstippled. Scale bar = 10 mm. B. Detail of one phylloclade. C. Single cone. D. Seed from above, aril scarcely protruding; only one ovule per cone reaches maturity. Scale bar for B, C, D = 5 mm.

usually adnate to the cone axis and so carried above the level of cone insertion (Fig. 1B, C). Cones have radial symmetry and are quite comparable to the cones in some other Podocarpaceae like *Saxegothaea* and *Microstrobis*. However, transitions from dorsiventral segment morphology to radial cone morphology can occur, as shown in Fig. 3. *Phyllocladus trichomanoides* (Fig. 2) is representative of other species in that the cones are irregular and replace either a second-order axis, or are inserted on a vestigial segment as a third-order axis so that the fertile phylloclade is very distorted. Fertile phylloclades may make up an entire branch tier, as in Figs 1A and 2A, but on vigorous shoots there may be vegetative and fertile segments intermixed or even forming separate tiers within a single unit of extension. It is common for only a single seed per cone to mature (Fig. 2B–D). Irregularity in the position of cones was illustrated for *P. hypophyllus* by Hooker (1852). The change from dorsiventral (distichous) to radial (spiral) symmetry that is common in these irregular reproductive axes also occurs in the normal formation of an indeterminate phylloclade (Tomlinson, Takaso & Rattenbury, 1989).

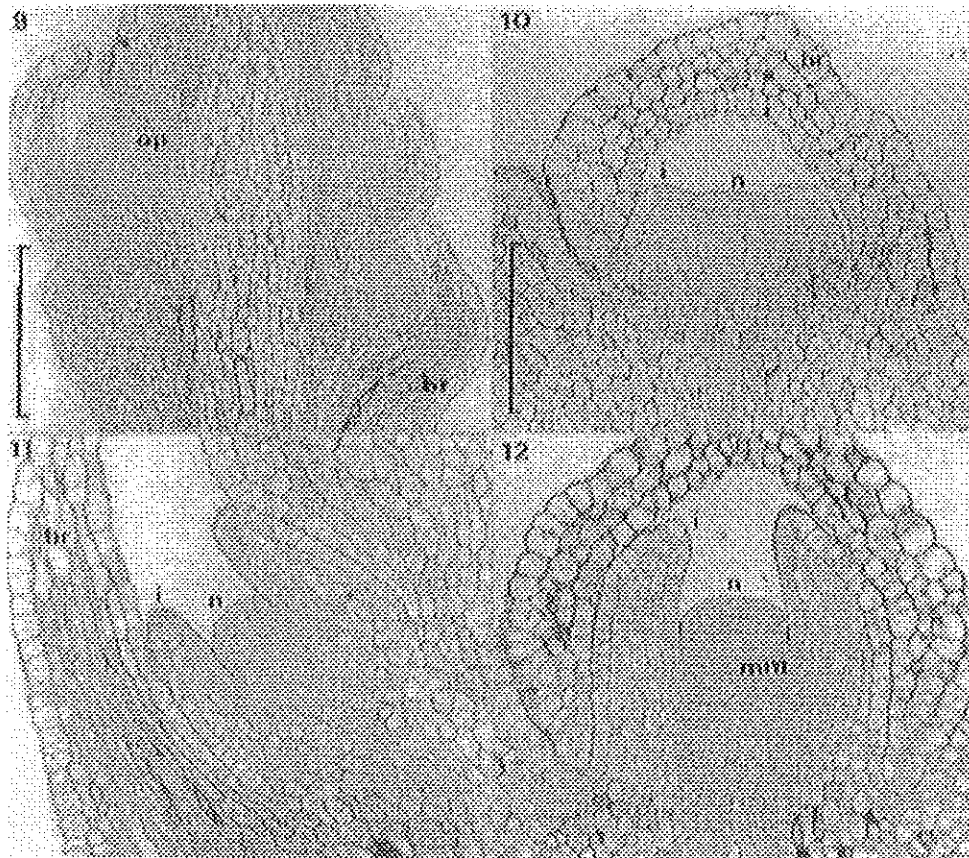
Figures 3–8. *Phyllocladus glaucus*. Scanning electron micrographs showing the development of the ovule and aril. Fig. 3. Young phylloclades, left, segments with dorsiventral symmetry; lower right, segment with transition from dorsiventral to radial symmetry of the cone, subtending scale removed. Fig. 4. Young female cone; ovule primordium directly inserted in the axil of the bract. Figs 5 & 6. Ovule primordia and young ovules; integument initiated in Fig. 5 and beginning to envelop the nucellus in Fig. 6. Figs 7 & 8. Maturing ovules, two stages showing bilobed integument apex; aril evident on the lateral margins at the base of the ovule in Fig. 7, more or less completely encircling in Fig. 8. (a, aril; br, bract; i, integument; n, nucellus; op, ovule primordium; some subtending bracts removed in Figs 4–8). Scale bars: Fig. 3 = 1 mm, Fig. 4 = 0.5 mm, Fig. 5 = 0.1 mm, Figs 6 & 7 = 0.2 mm, Fig. 8 = 0.4 mm.



Our detailed studies on *P. glaucus* refer to the more regular cones (Fig. 1C), which occur in two ranks (Fig. 1B, corresponding to the distichy of the phylloclade as a whole) but with varying numbers of cones in each rank. Since there is an acropetal order of development, a single phylloclade provides a range of stages. Each cone is subtended by a scale that may become adnate to the cone axis (Fig. 1C). From 12 to 24 spirally-arranged bracts were counted on the cones of the material available. Usually only the middle bracts subtend ovules. The range of ovules per cone varies from 8 to 21.

Ovule ontogeny (P. glaucus)

In the youngest stages available (Fig. 4) the ovule primordium is semi-ovoid in shape, tending to be horizontally flattened by the subtending bract or apically somewhat triangular by pressure of neighbouring bracts. In both surface aspect (Figs 4–8) and in sections (Figs 9–12) there is no evidence of any special ovule-



Figures 9–12. *Phyllocladus glaucus*. Early development of the ovule. Fig. 9. Part of a median longitudinal section of a cone; ovule primordium axillary in position; protodermal layer clearly uniseriate. Figs 10–12. Tangential (Figs 10, 12) and radial (Fig. 11) longitudinal sections of young ovules; integument develops initially due to periclinal and oblique divisions in hypodermal cells and anticlinal divisions in protodermal cells (cf. Fig. 14A–C). (br, bract; i, integument; mm, megaspore mother cell; n, nucellus; op, ovule primordium). Scale bars: Fig. 9 = 200 μ m, Fig. 10 = 100 μ m. Magnifications for Figs 11, 12 same as for Fig. 10.

supporting structure. The initiation of the integument as a circular swelling delimits the central mound of the future nucellus (Fig. 5). Growth of the integument is most active laterally, with the abaxial side initially somewhat higher than the adaxial. Increase in height of the integument is largely due to periclinal divisions in hypodermal cells, accompanied by anticlinal divisions in the protodermal layer (Figs 10 and 14A–C). The nucellus is initiated in the same manner, except for occasional periclinal divisions in the protodermal layer. In the later stages apically situated cells of the integument divide in various planes (Figs 11–12). Less frequent cell division in the dorsiventral plane of the ovule soon produces a bilobed integument. Further division, which results in the considerable extension of the integument, is the result of the production of cell files each seemingly derived from a hypodermal mother cell (Figs 11–12). There are also divisions that increase the thickness of the integument.

The nucellus also extends by repeated periclinal divisions of hypodermal cells, whereas the protodermal cells mainly divide anticlinally. A megasporocyte (megaspore mother cell) becomes recognizable towards the base of the nucellus by virtue of its large size and well-stained cell contents (Fig. 12).

Mature ovule (P. glaucus)

The mature ovule is flask-shaped, but considerably flattened (Fig. 8) and exceeded by the subtending bract after pollination. The mechanism of pollination is not known.

The integument, which is about 10 cell layers thick dorsally and ventrally but up to 20 layers thick laterally, becomes differentiated into five clear regions, an outer epidermis, two hypodermal layers, the extensive middle region and an inner epidermis (Fig. 13). The outer epidermal and two hypodermal layers are uniseriate. The outer two of these three layers are most pronounced in the micropylar region, the inner hypodermis is shallow and inconspicuous in early

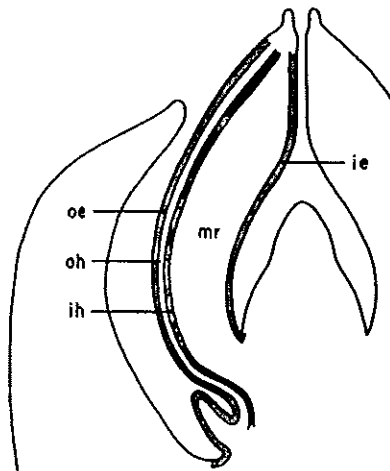


Figure 13. Diagram of the ovule showing positions of histological layers of integument described in the text (ie, inner epidermis; ih, inner hypodermis; mr, middle region; oe, outer epidermis; oh, outer hypodermis).

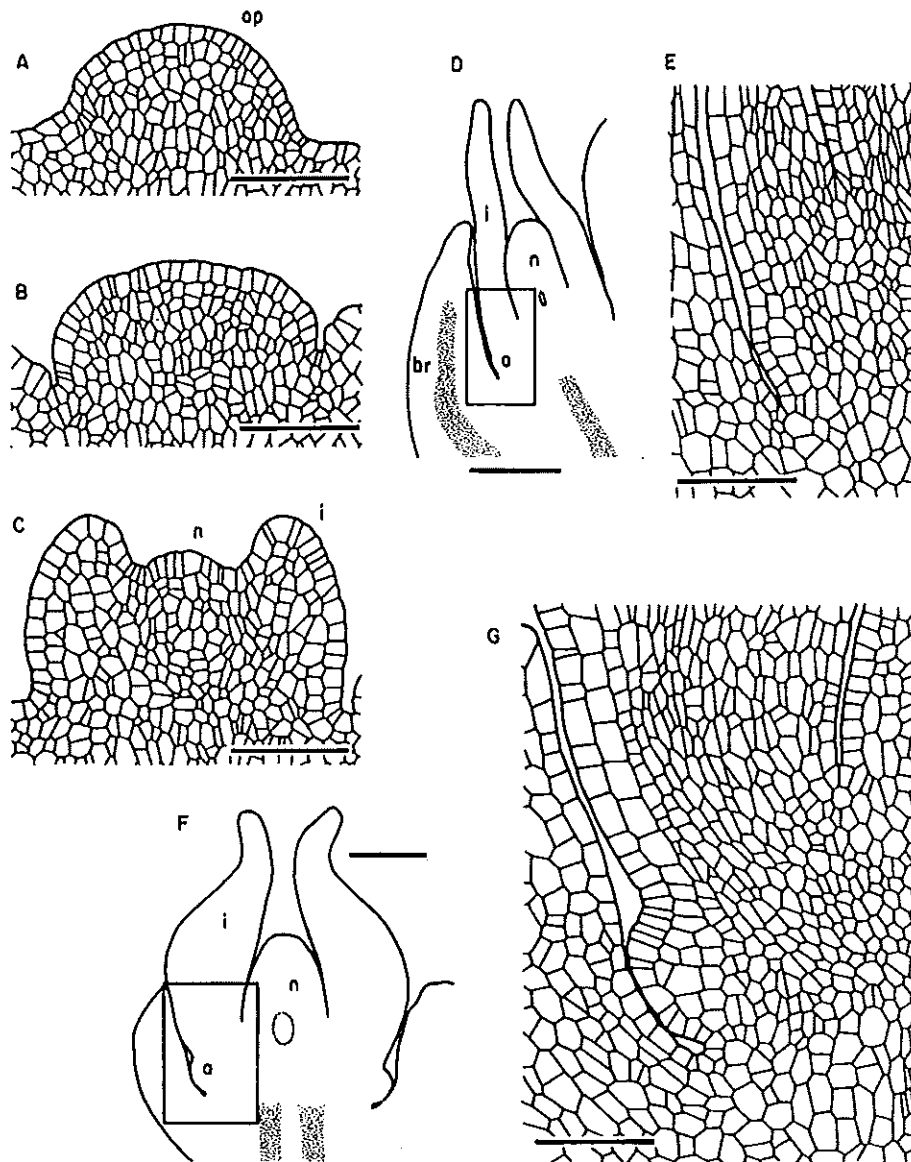


Figure 14. *Phyllocladus glaucus*. Initiation of the integument and aril. A–C. Tangential longitudinal sections of ovule primordia and a young ovule at three successive stages; noted active periclinal divisions in hypodermal cells. D. Radial longitudinal section of a mature ovule (*cf.* Fig. 7); see E for detail of rectangle a. F. Tangential longitudinal section of an ovule at a later stage (*cf.* Fig. 8); detail of a in G; aril initiated by periclinal divisions in outer hypodermal layer accompanied by anticlinal divisions in protodermal cells. Scale bars: A–C, E & G = 100 μ m. D & F = 250 μ m. (a, aril; br, bract; i, integument; n, nucellus, op, ovule primordium; bract and ovule traces stippled in D and E.)

stages (Fig. 15, *cf.* also Fig. 14G). Also the two outer layers become tanniferous in the lower part of the ovule, tannin deposition then extends acropetally (Fig. 15). The middle region consists of cells of varying shape and size although they are somewhat longitudinally extended in the lower part. The cells of the inner epidermis are small.

Nucellar cells above the female gametophyte become arranged in rows and extended. These cells are moderately stained (Fig. 15). The gametophyte is immediately surrounded by well-stained degenerated nucellar cells.

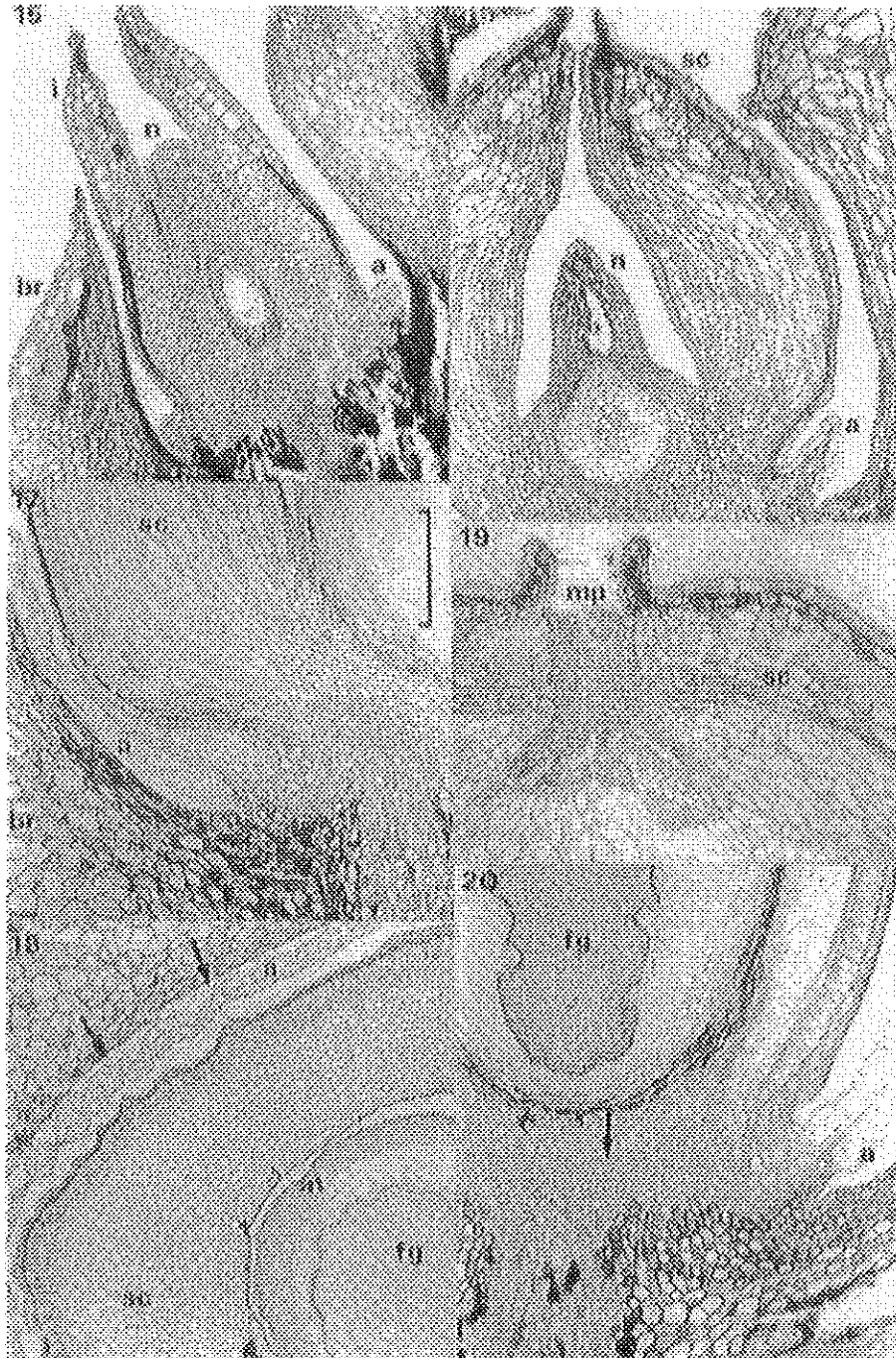
Aril (P. glaucus)

The aril is differentiated relatively late as an outgrowth at the base of the ovule, evident externally on the lateral margins (Fig. 7) but soon becoming a complete collar (Fig. 8). This involves periclinal divisions of the outer hypodermal cells and an increase in anticlinal divisions of the epidermal cells (Fig. 14D-G). Hypodermal cells may be tanniferous. The aril eventually becomes about 10 cells wide in part because of periclinal divisions in its outer and inner protodermal layers. The outer wall is thickened and well cutinized in its upper half. Further enlargement of the aril until it exceeds the subtending bract occurs as the embryo matures and is characterized by considerable cell division and extension. The apical part of the aril is lobed (Fig. 18, arrows).

Mature ovule and seed anatomy (P. trichomanoides)

The mature ovule of this species resembles that of *P. glaucus*, but it was also possible to study seed development because of the abundance of developmental stages. At maturity the seed, like the ovule, is ovoid but laterally flattened (Fig. 2D). Only its upper third is exposed, the rest is covered by the white aril that protrudes slightly from the cup-shaped structure consisting of the subtending bract and adjacent axis. At maturity the seed coat is 25-30 cells wide in the dorsiventral plane, but up to 35 cells wide laterally (Fig. 18). The three outer layers of the ovule undergo further differentiation. The epidermal cells become longitudinally extended, with a thick outer tangential wall, which is covered by a thick cuticle. Cells in the outer hypodermal layer are also elongated but densely tanniferous, especially in the micropylar region (Fig. 16). In the lower part of the seed cells of this layer locally may be more extended in a radial direction, producing slight longitudinal ridges (Fig. 18). At the very base, close to the aril, the corresponding layer is 2-3 cells thick (Fig. 20). The inner hypodermal layer becomes differentiated as radially extended cells with thick, lignified radial, inner tangential and occasionally outer tangential walls. Sclerification begins sub-apically (Fig. 16) and proceeds basipetally but with further acropetal development in the adaxial and abaxial regions. Some cells of this sclerotic layer contain a crystal at maturity. Within the sclerotic layer there is a part of the middle region two to five cells wide consisting of small, longitudinally extended cells that ultimately become compressed as the seed enlarges. This compressed layer is continuous into the subapical level of the ovule. Basally the bulk of the seed coat consists of the elongated cells of the middle region (Figs 16-18). Cells of the inner epidermis are also elongated and tanniferous.

The micropyle is closed by the proliferation through periclinal division of the inner epidermal layer and adjoining hypodermal cells of the nucellus (Figs 16, 19). Many cells near the micropyle become sclerotic. The nucellus is largely resorbed by the enlarged gametophyte, which shows the characteristic method of cell segmentation that results in radial files of cells, as seen in a transverse section (Fig. 18). Tanniferous cells are well developed at the base of



Figures 15–20. Development of the seed and aril (Fig. 15. *P. glaucus*; Figs 16–20. *P. trichomanoides*). Fig. 15. Radial longitudinal section of a mature ovule. Fig. 16. Radial longitudinal section of a young seed; cells of inner hypodermal layer of seed coat radially elongated in the upper half; this layer later becomes sclerotic (*cf.* Fig. 20). Fig. 17. Basal part of a tangential longitudinal section of a developed seed; aril increases its thickness mainly by basal periclinal cell divisions. Fig. 18. Part of a transverse section of a partly developed seed towards its base; outer three layers of seed coat highly differentiated; note apical lobes of the aril (arrows) and radial cell files in the female gametophyte. Fig. 19. Apical

the gametophyte, the cells further below form a distinct sclerified palisade that may be involved in seed abscission (Fig. 20). As a basal continuation of the axis of the ovule there is a dense region of small cells with sculptured walls that resemble those of tracheary elements.

Cone vasculature (P. glaucus)

In a transverse section of the cone axis about 11–14 strands form the vascular cylinder. This corresponds approximately to a $3/8$ phyllotaxis, with eight axial bundles and recently derived bract traces. Each bract is supplied by a single trace that diverges from an adjacent bundle either to the right or left. Above the level of bract trace departure two ovular traces diverge, one each from the axial bundles on either side of the parenchymatous gap left by the departing trace. The xylem of the opposed ovular traces usually faces each other, but rarely this is reversed, that is, with the phloem poles facing, a feature also noted by both Sinnott (1913) and Holloway (1937). The ovular traces remain discrete and end blindly at the base of the ovule and are seen as two separate strands only in a tangential plane (e.g. Fig. 14F). It is clear from this simple arrangement that there is no additional appendicular vascular system that might relate to an ovuliferous scale and that the aril has no vascular supply. Furthermore, the integument remains unvascularized.

DISCUSSION

Vegetative segments in the sterile phylloclades and cones in the fertile phylloclades can be considered as positional homologues. Since the former has been shown to correspond to a normal branch complex with axillary branching, the cone is simply an expression of the continuing branching complex at the second or higher order. The irregularity of the system, found in most species (e.g. Fig. 2) does not confound this interpretation, even though the cone has radial symmetry, since there is a strong tendency for a change from dorsiventral to radial symmetry in vegetative phylloclades. This change always occurs along the primary axis of an indeterminate phylloclade (Tomlinson, Takaso & Rattenbury, 1989), but less commonly on phylloclade segments of higher branch orders. The change in symmetry with an axis of second or higher order, as shown in Fig. 2, and in detail in Fig. 3, illustrates the morphogenetic integrity of fertile and vegetative shoot systems. This makes particularly cogent the interpretation of the ovule as an axial structure because it occupies the same axillary position as all branches in the system. This topographic consideration is further substantiated by the absence of any structural evidence for the existence of an ovule-supporting structure. It seems unlikely that the aril can be equated with this structure

part of a tangential longitudinal section of a mature seed; micropyle closed by periclinal divisions in the epidermal and hypodermal cells of adjacent seed coat (*cf.* Fig. 16), many of which become sclerotic. Fig. 20. Basal part of a radial longitudinal section of a mature seed; arrow indicates border between a sclerotic palisade and small cells with sculptured walls. (a, aril; br, bract; fg, female gametophyte; i, integument; mp, micropyle; n, nucellus; sc, seed coat). Scale bar: Fig. 17 = 400 μ m. Magnifications for Figs 15, 16, 18–20 same as for Fig. 17.

because of its late development and encircling origin. The direct vascular supply to the ovule as also reported by Eichler (1881), Strasburger (1872) and Young (1910), is unequivocal and further evidence for the axial nature of the ovule. Indeed, the vascular arrangement of two opposed traces departing from the axial system, one from each side of the bract gap, is that normally found for an axillary structure (e.g. a vegetative bud) in conifers.

The now unequivocal demonstration of the absence of an ovule-supporting scale in *Phyllocladus* raises the question of its relationship to other Podocarpaceae and the comparative morphology of their cones. As Quinn (1987) has pointed out, *Phyllocladus* is an acceptable member of the family, even though discussion of its affinities have often been overshadowed by its specialized vegetative morphology (cf. Hart, 1987). In particular it has a binucleate condition of the cells of the E tier, which is a suggested synapomorphy for the Podocarpaceae. The epimatium, characteristic of all podocarps except *Microstrobos* and *Phyllocladus*, is a problematical structure whose precise homologies are obscure. The conventional interpretation, largely following that of Sinnott (1913) and Wilde (1944), is that the epimatium is the much modified ovuliferous scale but eliminated by reduction in *Microstrobos* and *Phyllocladus*. This also accords with the interpretation of Florin (1951). There is, in fact, remarkable little objectively derived information to be brought to bear on this question. Sinnott provided evidence for his interpretation largely from vasculature, whereas Wilde and Florin mutually supported each others interpretation in a cyclic way, using Sinnott's data and a diagram of purely abstract derivation. Ovule orientation and the structure of the ovule-bearing complex in the Podocarpaceae is itself capable of varying structural interpretation (Quinn, 1987). If the ancestor of *Phyllocladus* had an epimatium, there seems no evidence for its existence now.

The Jurassic genus *Mehtaia*, assigned to the podocarps, has a single erect axillary ovule (Vishnu-Mittre, 1957). It has been compared to those living podocarps that have distinct cones, that is *Microcachrys*, *Microstrobos* (= *Phaeosphaeria*), *Phyllocladus* and *Saxegothaea*, but most specifically to *Microstrobos*. *Mehtaia* like *Microstrobos*, has no aril. The ovule is described as being borne terminally on a "very much reduced megasporophyll". Elsewhere, however, Vishnu-Mittre comments on the absence of "any sterile part to the flower". The vascular supply to the ovule is derived from the cone axis as a single strand that bifurcates. One branch becomes the trace to the ovule-subtending bract, the other supplies the ovule directly. This is quite unlike *Phyllocladus* and other podocarps according to Sinnott (1913).

Vishnu-Mittre proposed that the absence of an axillary ovule-supporting structure is ancestral to all podocarps and that the epimatium is an organ that originated *de novo* in those groups that possess it. Some evidence for this is the claimed post-ovular development of this structure in *Saxegothaea*. For a critical understanding of the family as a whole a comprehensive study of cone and ovule ontogeny is obviously necessary with scanning electron microscopy providing the objective documentation.

Our observations also confirm those of early workers, notably Holloway (1937), on the anatomy of the seed. His observations, on *P. asplenifolius* var. *alpinus*, that the stony layer originates basipetally from the inner hypodermal layer of the seed coat is confirmed for *P. trichomanoides*. He noted that thickening is confined to the radial and inner tangential wall of this layer and that each cell contains a crystal. Keng (1963b) reported that the outer hypodermal layer is resiniferous and that

the middle region (his inner layer) of the seed coat also contain resin cells. He also described the basipetal gradient in tissue differentiation.

The association of some fleshy, coloured structure with the seed is characteristic of most Podocarpaceae and clearly relates to animal dispersal although this remains incompletely documented (*cf.* Preest, 1963). In *Prumnopitys* the fleshy structure is the epimatium, which envelops the seed, and is the presumed homologue of the ovuliferous scale. In *Dacrydium*, *Lepidothamnus* and *Microcachrys* bracts become fleshy and brightly coloured. In *Dacrycarpus* and *Podocarpus* it is the axis supporting the seed that becomes fleshy. In *Halocarpus* it is a late proliferation of the epimatium. In *Phyllocladus* it is an aril. In all instances, even though the structure may be as much leathery as fleshy, there is some sharp colour contrast (e.g. red-black) that renders the structure conspicuous (Salmon, 1980). The aril never envelops the seed completely, as in *Taxus*, but forms a more or less conspicuous collar around the basal one-third or one-half of the seed. It may be white or yellow and it sets off the black or purplish seed. The assumption is that this arrangement is attractive to birds (Preest, 1963) but the details of dispersal are not known. In both *Phyllocladus* and *Taxus* the aril develops late and its homology with other appendages is quite unclear. There is every indication that the aril is an organ *sui generis* which has presumably evolved independently in these two genera. Further detailed documentation of ontogenetic processes involved in cone and ovule formation in Podocarpaceae will be provided as material becomes available.

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