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Developmental morphology of stipules and systematics of the Cunoniaceae and presumed allies.

I. Taxa with interpetiolar stipules

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Abstract

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The results of a survey of leaf and stipular development and mature architecture and nodal anatomy among those Cunoniaceae and allies with interpetiolar stipules are presented. The occurrence of interpetiolar (interfoliar) stipules that occupy a position between the insertion areas of opposite or whorled, often pinnately compound, leaves represent an important character complex in distinguishing the majority of Cunoniaceae. A similar combination of features is also present in the related genus *Eucryphia* (Eucryphiaceae). Within the Cunoniaceae, paired interpetiolar stipules generally arise simultaneously with, or slightly later than, the accompanying leaf primordia, and in some species soon overtop and enclose the young leaves. In species with whorled phyllotaxis, stipules arise as positionally equivalent primordia within the same node or whorl. Mature stipules are narrow or broad, entire or bifid, and in *Ceratopetalum*, *Schizomeria*, and *Eucryphia* possess elongate, adnate glandular ribs (adnate colleters) on the adaxial surface. It is concluded that the laterally positioned, nodal appendages of the Cunoniaceae are best called stipules and their spatial and partial vascular independence from the foliage leaves is documented. The Cunoniaceae provide additional evidence in support of the modified leaf-stipule concept, that regards stipules as more or less independent nodal outgrowths that are positionally associated with leaves but that follow divergent developmental pathways. The occurrence of a similar node-leaf-stipule complex in the legume genus *Platymiscium* is interpreted as a conspicuous example of convergent evolution.

Key words: Cunoniaceae, Eucryphiaceae, *Platymiscium*, stipules, nodal anatomy, colleters, development.

Introduction

The Cunoniaceae are a woody dicotyledonous family almost exclusively restricted to the Southern Hemisphere. The family is composed of between 19 and 26 genera, and

about 350 species, and generally appears as a basal group within the Rosidae, in or near the large saxifragaceous complex (Dickison 1980a). Close relationships with the Hamamelidae have also been stressed (Dickison 1989). In recent years the family has been the subject of intensive study. Hoogland (1960, 1979, 1981, 1987) has been involved in systematic studies on the family and aspects of the comparative morphology and anatomy have been discussed in a series of papers by Dickison (1975a, b, 1980a, b, 1984, 1989). Pollen morphology was described by Hideux & Ferguson (1976) and the results of a chemical survey were reported by Jay (1968). All of these investigations have found the family to be rather widely diverse both chemically and morphologically, and suggest that available family systematic treatments do not always accurately reflect evolutionary groupings within the assemblage.

One of the distinctive vegetative features that separates the family and its close allies from other members in the saxifragaceous complex is the occurrence of prominent interpetiolar (interfoliar) stipules in association with opposite or whorled, often pinnately compound leaves. Such stipules occupy a position between the insertion areas (petioles) of the leaves (see Rutishauser and Sattler 1986, Dickison 1980b) and are either narrowly or broadly inserted. Although this combination of features is uncommon in other dicotyledons, and is sometimes used as a distinguishing character for the Cunoniaceae, it is more complex and variable within the Cunoniaceae and allies when developmental data are considered (see Schrödinger 1927). This variability in stipular morphology further reinforces the view that the Cunoniaceae are unusually diverse morphologically and anatomically and that circumscription of the family as a natural (monophyletic) unit on the basis of one or a few uniquely derived character states is difficult.

Our observations on the structure and development of the stipules of the Cunoniaceae and presumed allies will be presented as two separate contributions. This initial contribution will deal with representatives of those genera having obvious interpetiolar stipules that arise united in pairs, viz., *Acrophyllum*, *Acsmithia*, *Caldcluvia*, *Callicoma*, *Ceratopetalum*, *Cunonia*, *Pancheria*, *Pullea*, *Schizomeria*, and *Weinmannia*. The apparently closely related genus *Eucryphia* (Eucryphiaceae) will also be described (see also Dickison 1978). Additional observations are presented on the leguminous genus *Platymiscium*, since it possesses a character combination strongly resembling many Cunoniaceae, viz., decussate or whorled phyllotaxis, interpetiolar stipules (partly covering the leaves of the same node), and pinnate leaf blades.

A subsequent contribution will present observations on those cunoniaceous and closely related genera that are without obvious interpetiolar stipules. For example, stipules are laterally positioned at the node (4 lateral stipules per leaf pair) in *Gillbeea adenopetala* (Cunoniaceae s.str.), *Bauera* (Baueraceae), and *Brunellia* (Brunelliaceae). In the cunoniaceous genus *Geissois* there are two modes of stipular origin observable: either axillary (two per leaf pair), or lateral (four per leaf pair) with the tendency to form strongly bifid mature interpetiolar stipules. The latter pattern can also be found in *Pseudoweinmannia* (Cunoniaceae). *Davidsonia* (Davidsoniaceae) is characterized by lateral stipules (two per leaf) combined with spiral phyllotaxis. Only colleters (glandular appendages) are observable in *Aphanopetalum* (Cunoniaceae), replacing obvious lateral stipules. The data presented in these two contributions will finally be compared with other characters of known taxonomic significance in the Cunoniaceae and allies in order to present a systematic analysis of the group.

Materials and methods

The material used for this study was fixed and preserved in formalin – acetic acid – ethyl alcohol (FAA). Hand and microtome sections were used to elucidate the nodal vascularization. For microtome sectioning the shoot tips were embedded in TissuePrep (melting point 61 °C) and were cut at 10 µm. The sections were stained with Astrablue and acid fuchsin, or with safranin and fast-green. For the scanning electron microscopy the dissected shoot tips were critical-point dried and sputter-coated (Au-Pd). The micrographs were taken with a Cambridge S4 scanning electron microscope at the University of Zürich and with a Jeol JSM 35 scanning electron microscope at the Université de Montréal. Twigs (including shoot tips and a few inflorescences) of twelve genera and seventeen species were examined. Voucher specimens are housed at CANB, NCU, NOU, P, Z. Species studied and collection numbers follow.

Cunoniaceae:

- Acrophyllum australe* (A. Cunn.) Hoogl., Australia: Dickison 201
- Acsmithia undulata* (Vieill.) Hoogl., Australia: Dickison 262
- Caldcluvia australiensis* (Schlechter) Hoogl., Australia: Dickison 208
- Callicoma serratifolia* H. C. Andrews, Australia: Kramer 9932
- Ceratopetalum apetalum* D. Don, Australia: Kramer s.n. (cult. Bot. Garden Perth)
- C. gummiferum* Sm., Australia: Dickison 191
- Cunonia capensis* L., S. Africa: Dickison s.n. (cult. Bot. Garden Sydney)
- C. lenormandii* Brongn. & Gris, New Caledonia: Endress 6096
- Pancheria confusa* Guillaumin, New Caledonia: Dickison 180
- P. elegans* Brongn. & Gris, New Caledonia: Dickison 161
- P. robusta* Guillaumin, New Caledonia: Endress 6263
- Pullea stutzeri* (F. Mueller) Gibbs, New Caledonia: Dickison 213
- Schizomeria whitei* Mattf., Australia: Endress 4209
- Weinmannia pinnata* L., Dominican Republic: Dickison 307
- W. trichosperma* Cav., Chile: Dickison s.n. (cult. Edinburgh Bot. Gard.)

Eucryphiaceae:

- Eucryphia milliganii* Hook. f., Australia: Hoogland 41731

Leguminosae:

- Platymiscium trinitatis* Benth., Northern S. America: Rutishauser s.n. (cult. Fairchild Tropical Gard., Miami)

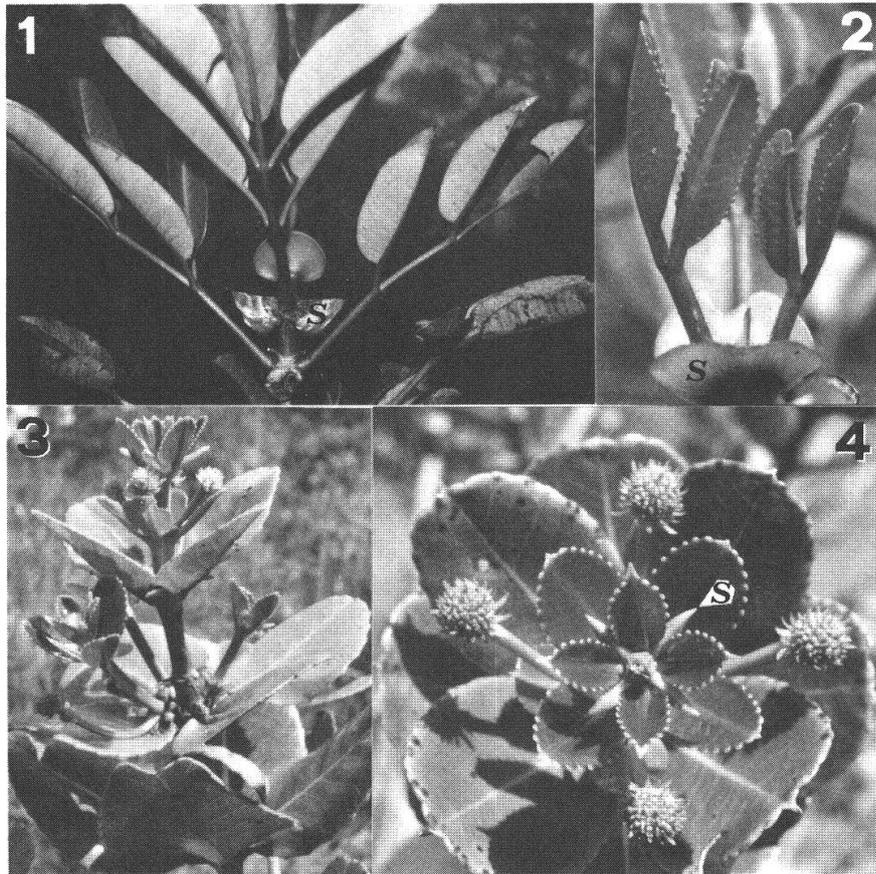
Observations

1. Development and mature structure of stipules of Cunoniaceae and allies

Cunonia L.

The genus *Cunonia* consists of about of 17 species of small- to medium-sized trees. With the exception of one species (*C. capensis*, from South Africa), all species are restricted to New Caledonia (Rao & Dickison 1985b).

The leaves are decussate, trifoliolate or imparipinnate (Fig. 1–2, 51). Very conspicuous flap-like interpetiolar stipules totally cover the leaf pair of the same node until the leaf blades start to expand. Both leaves and stipules are coriaceous. Despite their massive construction and rich vasculature, the stipules are shed soon after spreading of the leaf blades. The stipules are broadly inserted at the base, surrounding the node and ensheathing the associated leaf pair from behind (abaxial side). Glue-like mucilage is produced by the colleters, causing the stipular flaps to adhere together. Thus, it is difficult to open the bud without destroying the stipules. Some physiological properties of the copious mucilage and anatomical details of the colleters of *C. capensis* are described by Hanstein (1868: his Fig. 13–23). The colleters possess a palisade-like layer of secreting cells similar

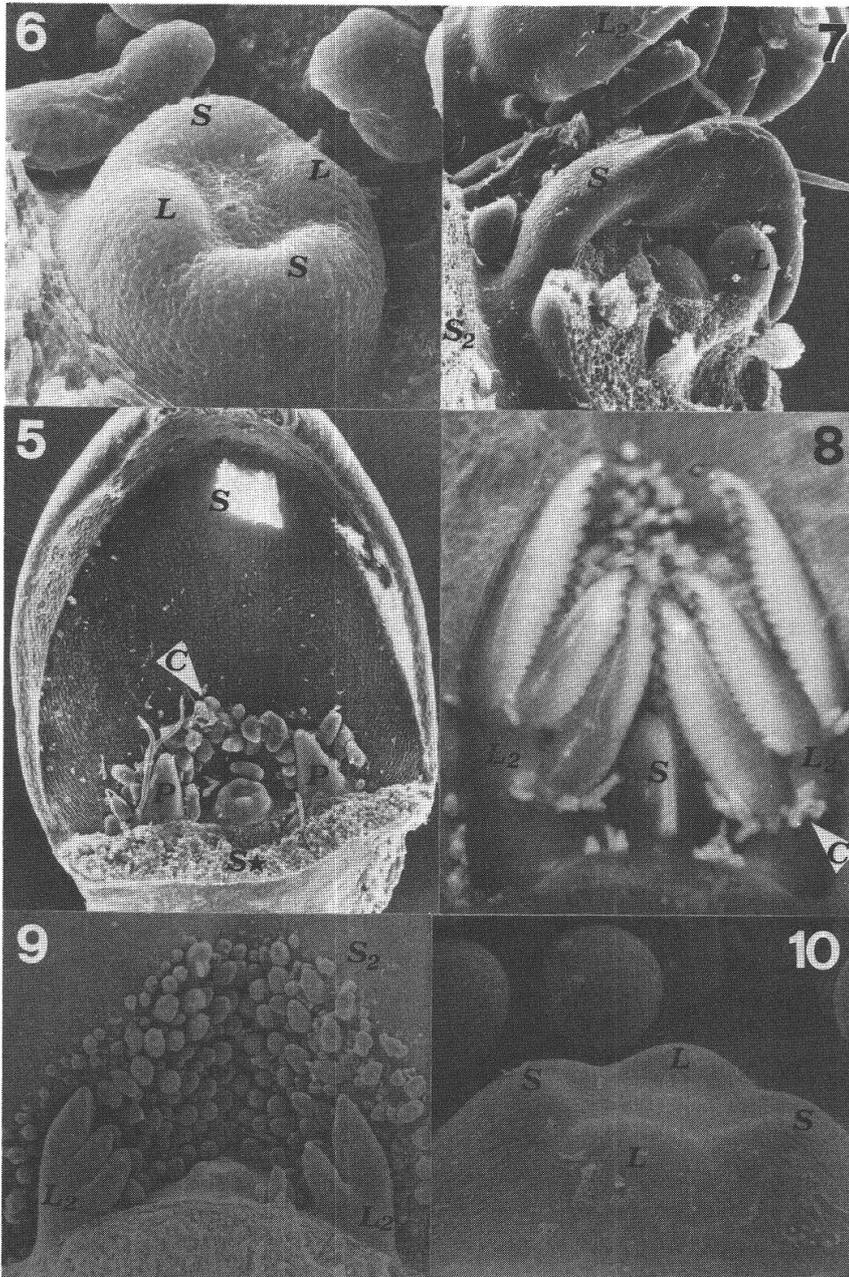


Figs. 1–2. *Cunonia macrophylla* (Endress s.n.): Young shoots with paired pinnate leaves and broad, massive and rather coriaceous stipules (S) in an interpetiolar position. Following the formation of a new leaf pair the associated stipular pair reflexes and drops off. (Photos by P. K. Endress).

Figs. 3–4. *Pancheria robusta* (Endress 6263): Flowering shoot with tetramerous leaf whorls, seen from the side and above. Each whorl is provided with narrow, interpetiolar stipules (S). The spherical, head-like inflorescences arise in leaf axils. (Photos by P. K. Endress).

to those observable in the Rubiaceae (Hanstein 1868, Rutishauser 1984). According to Hanstein (1868), secreting cells in *C. capensis* are not restricted to the colleters, but are also present, though less obvious, throughout the adaxial surface of the stipules.

Both leaf and stipular primordia belonging to the same node arise simultaneously around (or at) the shoot apex (Fig. 6: *C. capensis*, 10: *C. lenormandii*). Leaf primordia are initially circular in outline, whereas stipule primordia have a broadened insertion area from the beginning. Soon after initiation, the stipules begin to conspicuously overtop and enshath the associated leaf pair (Fig. 5, 7), whereas the leaves (blades) are developmentally retarded while still in the bud (Fig. 8–9). The colleters (glandular hairs) responsible for mucilage production are restricted to the lower adaxial stipular surface (Fig. 5, 9). Additional colleters also arise from the insertion areas of the pinnae along the leaf rachis (Fig. 8). Schrödinger (1927: Fig. 27–36) presented a detailed description of the leaf and stipule development in *C. capensis*. He is right in his view that the leaf and stipular primordia arise from the shoot apex as nearly independent units. He is incorrect, however, in the assumption that the stipular primordia are initiated earlier than the leaf primordia of the same node.



Figs. 5–8. *Cunonia capensis* (Dickison s.n.): 5, 6. Axillary bud with two leaf pairs and accompanying interpetiolar stipules. A prophyll pair (P) is overtopped by a flap-like stipule (S). One stipule of the pair has been removed (S*). Total stipule length is 1.7 mm. Note colleters (C) arising from the adaxial surface of the stipule. The primordia of the next youngest leaf pair (L) are rounded in outline whereas the associated stipular pair (S) form more elongated bulges ($32\times$, $220\times$). 7. A vegetative shoot tip with two leaf pairs (L–L₂, partly removed) and associated interpetiolar stipules (S–S₂, partly removed) ($80\times$). 8. Vegetative bud showing an older stage of leaf development: L₂=pair of pinnately compound leaves with colleters (C). S=stipular pair belonging to and protecting next youngest leaf pair ($16\times$).

Figs. 9–10. *Cunonia lenormandii* (Endress 6096): 9. Shoot tip with two leaf pairs. L₂=leaf pair with unequal, pinnately divided blades. S₂=interpetiolar stipule (length 9 mm) with numerous colleters on the adaxial surface in the vicinity of the young leaves and shoot apex ($32\times$). 10. The same shoot tip as viewed in Fig. 9. The youngest leaf pair (L) have rounded primordia whereas the associated pair of interpetiolar stipules (S) have a more extended outline ($220\times$).

The nodal anatomy of *Cunonia* ranges from trilacunar to pentalacunar (Fig. 50; Dickison, 1980 b). Stipules are typically supplied by veins branching from the lateral leaf traces. We did not observe pure stipular traces (i.e., traces that originate in the cauline vascular cylinder and that supply the stipules exclusively) as described by Mattfeld (1939).

Weinmannia L.

A genus of about 150–190 species of small- to medium-sized trees, widely ranging throughout the tropics including Central America northward to Mexico, the West Indies, Malesia, Melanesia, and Polynesia, as well as temperate New Zealand and Chile, the genus is absent in India, Australia, and mainland Africa (Rao & Dickison 1985 b).

The leaves are decussate and simple, trifoliolate, or imparipinnate (Fig. 54). The interpetiolar stipules (Fig. 55) may be tardily deciduous (i.e., remaining on the shoot 2–3 nodes behind the terminal bud). The structural and developmental patterns of the two species of *Weinmannia* included in our study, *W. pinnata* and *W. trichosperma*, closely resemble the related genus, *Cunonia*. Although stipular primordia arise from the shoot apex as early as the leaf primordia (Fig. 11), they soon begin to enclose the leaves of the same node, due to accelerated growth and broadening of the stipular insertion line (Fig. 12, 14). In contrast to *Cunonia*, the young leaves of *Weinmannia* are hairier and colleters are not evident on the stipular surface. The hairy seeds of *Weinmannia* are one of the key features distinguishing the genus from *Cunonia*, whose seeds are glabrous and winged (Dickison 1984).

The bracts of *Weinmannia* inflorescences are scale-like and each is topped by a single colleter. There are no associated stipular appendages observable with the bracts (Fig. 13).

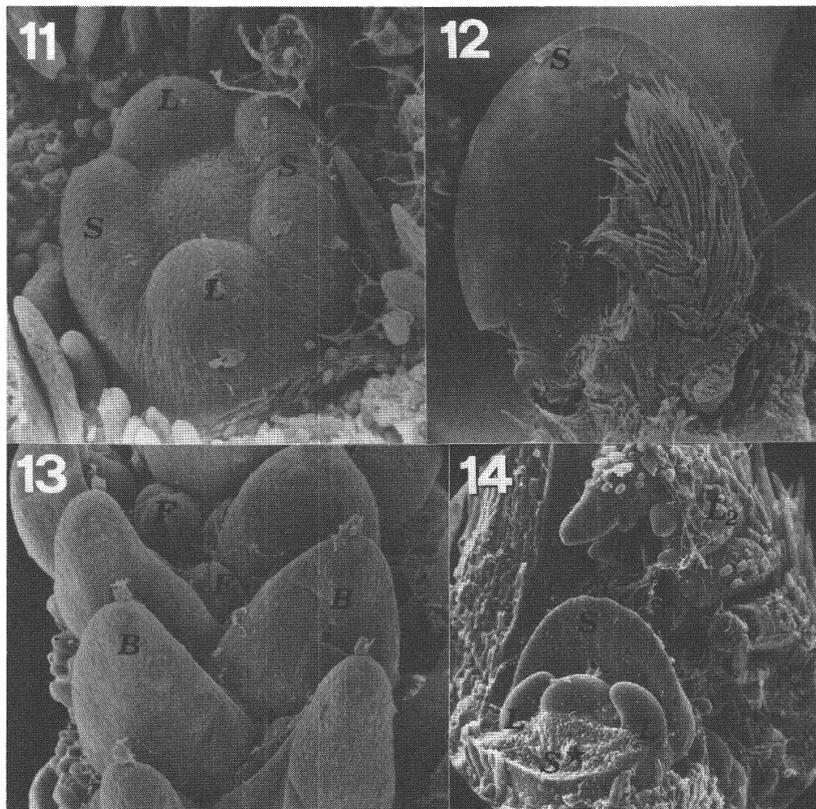
The nodal anatomy of *Weinmannia* is uniformly trilacunar, three-trace, with each stipule having a vascular connection to the two nearest lateral leaf traces (Fig. 53; Dickison, 1980 b).

Ceratopetalum Sm.

Ceratopetalum is composed of five species of trees or shrubs distributed in New Guinea and eastern Australia. Leaves are decussate and simple (unifoliolate) or trifoliolate (Fig. 57). The blade in the simple-leaved *C. apetalum* is attached to the leaf stalk by a joint or articulation (Floyd & Hayes 1961). The interpetiolar stipules are varnished, glabrous scales that are narrowed to an undivided tip (Fig. 58). Stipular primordia are initiated simultaneously with, or slightly later than, the associate leaf pair (Fig. 15). Unlike the situation in *Cunonia* and *Weinmannia*, the stipules never totally enclose and protect the associated leaf pair at the same node (see also, Schrödinger 1927: Fig. 17–20), although the two opposite stipules do surround the leaves and stipules of the next younger nodes (Fig. 58). In *Ceratopetalum*, the rate of growth of the stipules as compared to the associated leaves is less prominent than in *Cunonia* and *Weinmannia*. Furthermore, the stipular bases of *Ceratopetalum* never surround the node toward the abaxial side of the leaf insertion area (Fig. 18).

Mucilage production results from a system of parallel glandular ribs that are adnate to the adaxial surface of the stipule (Fig. 16). Each glandular rib (“adnate colleter”) consists of a multicellular base and an outer layer of glandular, radially elongated cells (Fig. 17).

The nodal anatomy of *Ceratopetalum* is normally trilacunar with three traces per leaf (Fig. 56; Dickison 1980 b: Fig. 1). The interpetiolar stipules are characteristically vascularized by strands arising from the lateral leaf traces. An additional pair of rather small



Figs. 11–13. *Weinmannia pinnata* (Dickison 307): 11. Axillary bud showing an early developmental stage of the paired leaf primordia (L) and interpetiolar stipules (S) (160 \times). 12. Vegetative tip illustrating a broad interpetiolar stipule (S) and an associated leaf blade (L) that is pinnate and hairy. A younger leaf pair is observable in the center of the bud (18 \times). 13. Part of young inflorescence (compound spike composed of 3–4 flowers per bract) with two rows of bracts covering floral buds (F). Note the prominent colleter at apex of each bract (B) (24 \times).

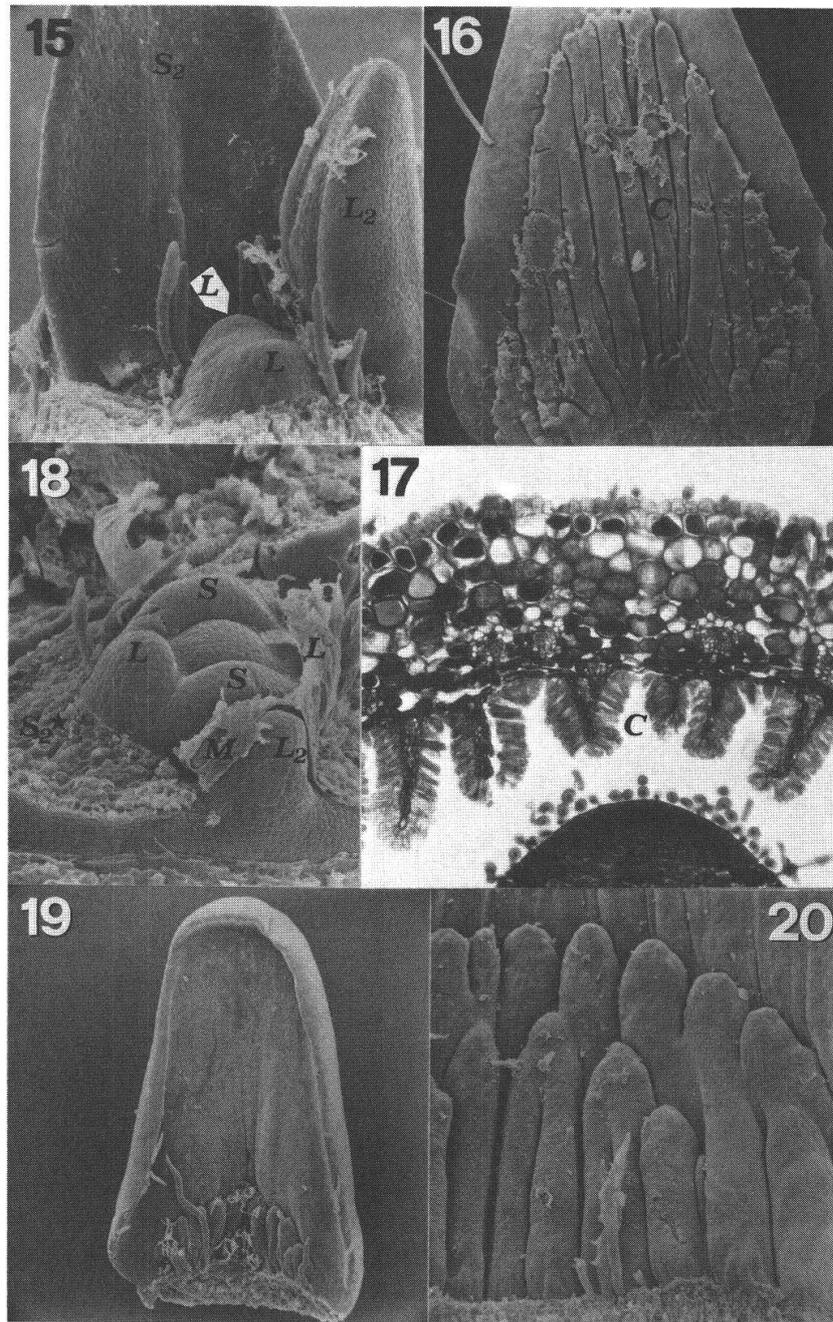
Fig. 14. *Weinmannia trichosperma* (Dickison s.n.): Vegetative tip illustrating shoot apex, youngest leaf pair (L), and interpetiolar stipules (S). One stipule of the pair has been removed (S*). The pinnately divided blade (L₂) of one of the next older leaf pair is evident (80 \times).

traces, however, may be found in some nodes and supply the stipules exclusively (Dickison 1980 b).

Schizomeria D. Don

A genus of about 15–18 species occurring as trees in Australia, New Guinea and Moluccas *Schizomeria* is apparently related to *Ceratopetalum* and is distinguished by the possession of fleshy drupes, whereas *Ceratopetalum* produces dry nuts (Dickison 1984). The leaves of *Schizomeria* are opposite and simple (Fig. 60), and there is no joint (articulation) observable between leaf stalk and blade (Floyd & Hayes 1961). The anatomical and developmental patterns observed for leaves and stipules of *Schizomeria* are similar to those described above for *Ceratopetalum* (Fig. 59, 61).

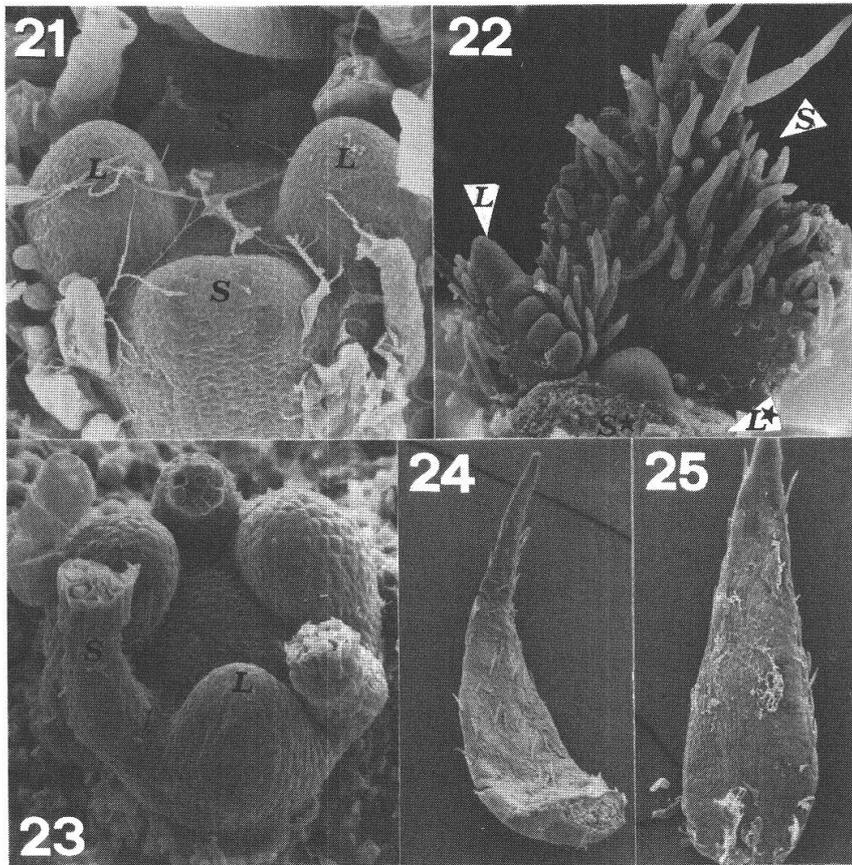
Stipules of *Schizomeria* possess adnate glandular ribs (adnate colleters) that are structurally similar to those occurring on *Ceratopetalum* (Fig. 17). In *S. whitei*, the glandular ribs are restricted to the lowermost part of the adaxial stipular surface (Fig. 19–20).



Figs. 15–16. *Ceratopetalum apetalum* (Kramer s.n.): 15. Vegetative tip showing shoot apex with newly initiated leaf pair (L) and the next older leaf pair (L_2) with overtopping interpetiolar stipule (S_2 , length 600 μm) (110 \times). 16. Adaxial surface of nearly mature stipule (length 4 mm) showing elongated and parallel secretory colleters (C) covered with mucilage (30 \times).

Fig. 17. *Ceratopetalum gummiferum* (Dickison 191): Transverse section through basal portion of mature stipule showing colleter ribs (C) arising from the adaxial surface. Each rib is composed of a multicellular base and an outer secretory cell layer (80 \times).

Figs. 18–20. *Schizomeria whitei* (Endress 4209): 18. Vegetative shoot tip showing the youngest leaf and stipular pairs, and parts of the next oldest leaf and stipular pair (* = removed parts): L/S = blade and stipular primordia of youngest pair, L_2/S_2 = leaf and stipular position of next older pair. M = mucilage (110 \times). 19. Adaxial view of older developmental stage of stipule (length 2 mm) illustrating secretory ribs confined to the stipular base (22 \times). 20. Enlarged view of mucilage producing ribs (110 \times).

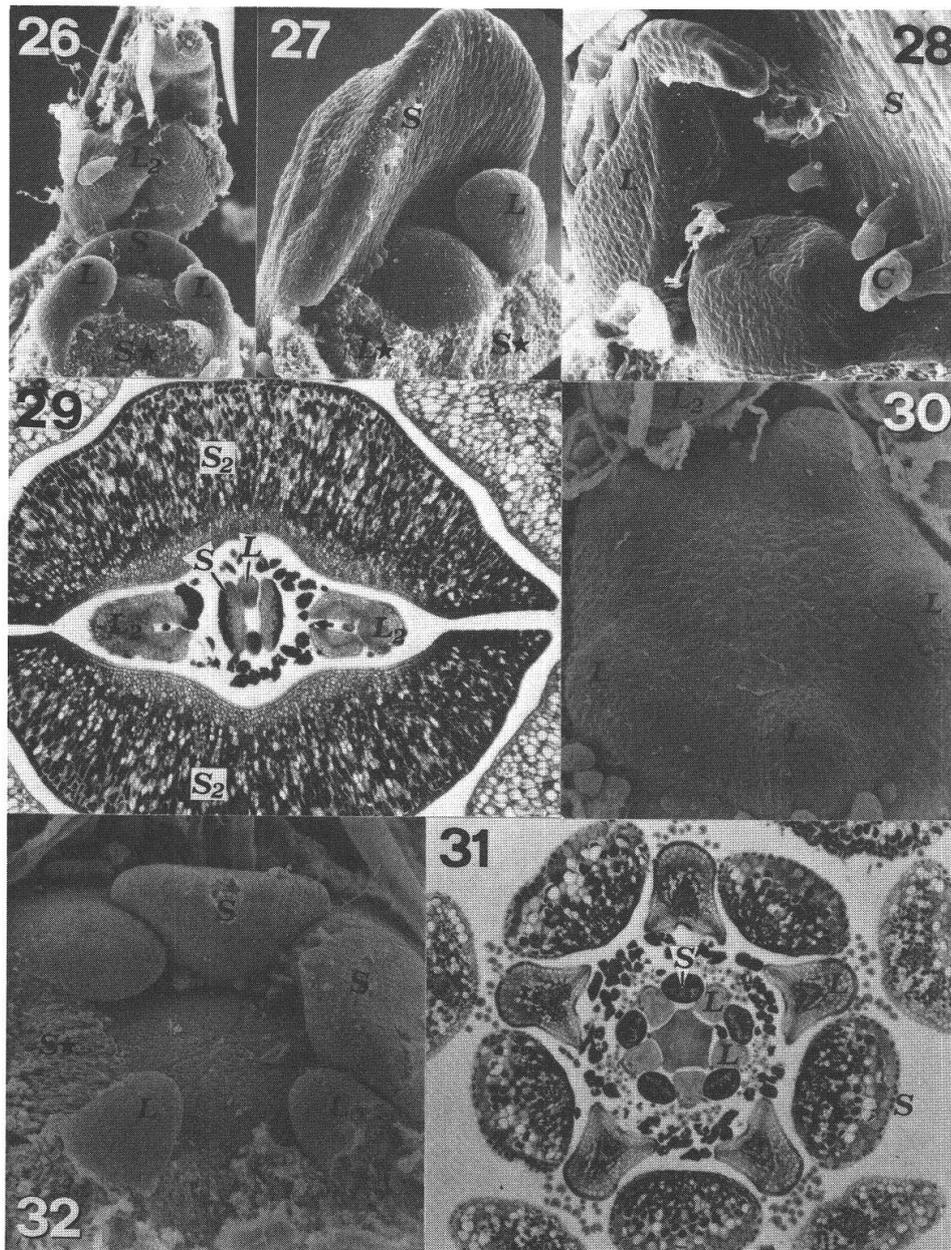


Figs. 21–22. *Caldcluvia australiensis* (Dickison 208): 21. Axillary bud with first leaf pair (L) and two associated interpetiolar stipules (S). Note slightly bifid condition of stipular primordia ($220\times$). 22. Vegetative shoot tip with a more developed pinnate leaf (L). The opposing leaf (L*) of the pair has been removed. A single bifid interpetiolar stipule (S) is present with the opposing stipule removed (S*) ($55\times$).

Figs. 23–25. *Acrophyllum australe* (Dickison 201): 23. Vegetative shoot tip with trimerous whorl of foliage leaves (L) and accompanying interpetiolar stipules (S) ($260\times$). 24, 25. Nearly mature stipule (5 mm long) as viewed adaxially ($10\times$).

Caldcluvia D. Don

Caldcluvia, as redefined by Hoogland (1979), includes *Ackama*, *Spiraeopsis*, and *Opocunonia*. *Caldcluvia* consists of 11 species of trees or shrubs mainly distributed in eastern Australia and New Zealand. With the notable exception of *C. paniculata* from southern S. America (Chile, Argentina), the genus is characterized by opposite, imparipinnate leaves with interpetiolar stipules (Fig. 22, 63). According to Hoogland (pers. comm.), the interpetiolar stipules of *C. nymanii* are frequently bifurcate, a situation intermediate between free lateral stipules (*C. paniculata*) and fused interpetiolar stipules typical for the remaining species. The stipules of *C. australiensis* are ovate, narrowly inserted, hairy on both sides, and provided with glandular teeth along the margin (Fig. 22, 64). The stipules are shed as the leaves expand. A pair of hemispherical leaf primordia are followed in early development by two slightly bilobed stipular bulges in an interpetiolar position (Fig. 21). Within the bud the stipules soon overtop the associated leaf blades (Fig. 22). The nodal anatomy of *Caldcluvia* is trilacunar, three-trace, with the stipules supplied by branches from the lateral leaf traces (Fig. 62).



Figs. 26–29. *Pancheria confusa* (Dickison 180): 26. Vegetative shoot tip with youngest leaf pair (L) and broad interpetiolar stipule (S). The opposing stipule has been removed (S*). One foliage leaf of the next older pair is present (L₂) whereas the opposing leaf has been removed (80 ×). 27. Another vegetative shoot tip with youngest leaf pair (L). One member has been removed (L*). One overtopping interpetiolar stipule (S) is present, the other member of the pair has been removed (S*) (180 ×). 28. Axillary bud with first leaf pair (L) and one of the totally ensheathing interpetiolar stipules (S). Prominent colleters (C) occur on the adaxial surface of the stipule. Note shoot apex (V) with initiation of next younger leaf pair in the *same* plane as the first leaf pair (180 ×). 29. Transverse section through vegetative shoot tip: L/S = youngest leaf pair and associated interpetiolar stipules, L₂/S₂ = next older leaf pair and associated stipules (32 ×).

Figs. 30–31. *Pancheria elegans* (Dickison 161): 30. Vegetative shoot tip showing simultaneous initiation of pentamerous leaf whorl. Stipular primordia are not yet observable. L = leaf primordia, L₂ = member of next older leaf whorl (260 ×). 31. Transverse section through vegetative shoot tip below apex showing two consecutive pentamerous whorls composed of 5 leaf blades (L) and 5 interpetiolar stipules (S) each (50 ×)

Fig. 32. *Pancheria robusta* (Endress 6263): Shoot tip with tetramerous leaf whorl (L) and broad interpetiolar stipules (S). Two stipular primordia (S*) removed (120 ×)

Acrophyllum Benth.

The monotypic genus, *Acrophyllum* (syn. *Calycomis*), is endemic to New South Wales, where it is typically restricted to moist rocks near waterfalls. *Acrophyllum australe* forms small subshrubs with simple, sessile, coarsely dentate leaves in trimerous whorls (Fig. 66). The interpetiolar stipules are lanceolate and tardily deciduous (Fig. 67). At early developmental stages the stipules appear as narrow, awl-like appendages with a terminal gland (Fig. 23). Except for a few widely distributed non-glandular hairs, the stipules are glabrous on both sides (Fig. 24–25).

The nodal anatomy of *Acrophyllum* is trilacunar, three-trace with split-lateral traces arising from a common gap (Fig. 65). "Split-lateral" traces, as defined by Howard (1970), were found by Dickison to be characteristic of nearly all Cunoniaceae with whorled leaves and interpetiolar stipules (see, e.g., Fig. 71).

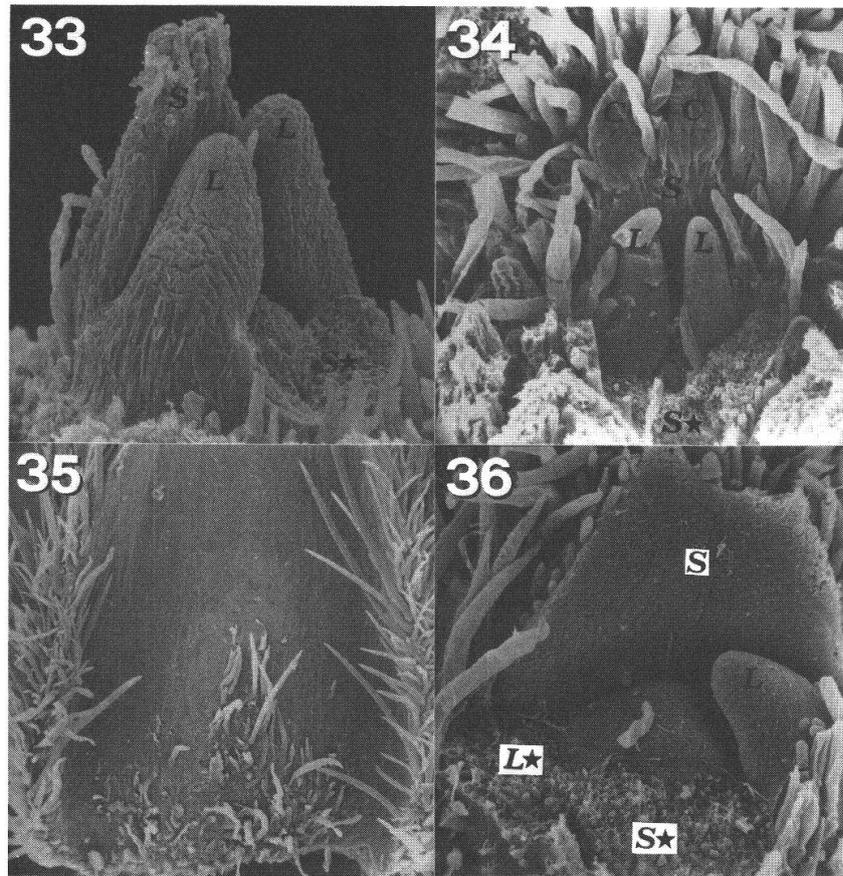
Pancheria Brongn. & Gris

Pancheria is a genus endemic to New Caledonia and composed of approximately 26–28 species forming small- to medium-sized shrubs or small trees (Rao & Dickison 1985 a). Leaves are simple, trifoliolate or, less commonly, imparipinnate, and are arranged in pairs (Fig. 26–29, 69) or trimerous to pentamerous whorls (Fig. 3–4, 30–32, 72).

Species with decussate phyllotaxis have prominent stipules similar to those of *Cunonia*, although *Pancheria* and *Cunonia* are thought to belong to different tribes within the family (Engler 1928). *Pancheria confusa* possesses rather massive ovate stipules that become reflexed and are shed soon after the leaf blades of the same node are expanded (Fig. 69–70). Within the bud the flap-like interpetiolar stipules protect the leaf pair of the same node as a result of a broad ensheathing stipular base surrounding even the abaxial side of the leaves (Fig. 27, 29). Leaf primordia and stipular primordia arise nearly simultaneously around the shoot apex (Fig. 26, 28). Soon afterward, the stipules grow much faster than the associated leaf primordia to become massive overtopping structures (Fig. 27, 29). Mucilage-producing colleters are observable on the basal portion of the adaxial stipular surface. In addition, a single colleter (gland) may be found at the apex of each young foliage leaf (Fig. 28).

The stipules of *Pancheria* species with tetramerous or pentamerous leaf whorls are narrow and tapering toward the apex (Fig. 72, 73 a–b). For example, the stipules of *P. elegans* are linear interpetiolar appendages up to 8 mm long and provided with a single median vein (Fig. 31). They are typically tardily deciduous, i.e., remaining on the shoot for 2–3 or even more nodes behind the terminal bud. In *P. elegans* the stipular primordia are clearly formed after the initiation of associated foliage leaves (Fig. 30). Nevertheless, as result of accelerated growth, the stipules soon overtop the leaves (Fig. 32).

The nodal anatomy of *Pancheria* is tri- to 5-lacunar, with an equal number of traces, with or without split-lateral traces. *Pancheria confusa*, with multiveined, broad stipules, may possess pure stipular traces that diverge directly from the cauline stele, in addition to the vascular branches that arise from the lateral leaf traces (Fig. 68, upper half). *Pancheria elegans* (Fig. 71), and other species with whorled phyllotaxis and relatively narrow stipular bases, have a consistent trilacunar nodal anatomy that is combined with the occurrence of split-lateral traces. In this respect these species are similar to the nodal anatomy of *Acrophyllum* (Fig. 65; Dickison 1980 b).



Figs. 33–35. *Callicoma serratifolia* (Kramer 9932): 33. Vegetative shoot tip with young leaf pair (L) and a single interpetiolar stipule (S). The opposing stipule has been removed (S*) (170 \times). 34. Axillary bud with first leaf pair (L) and overtopping interpetiolar stipule (S) having two prominent apically positioned colleter teeth (C). S* = removed stipule (120 \times). 35. Lower portion of nearly mature stipule (total length 3 mm), seen from adaxial side. No colleters are evident on adaxial surface of stipule (55 \times).

Fig. 36. *Pullea stutzeri* (Dickison 213): Axillary bud with first leaf (L) and interpetiolar stipular pair (S). One leaf (L*) and one stipule (S*) have been removed (120 \times).

Callicoma Andr.

This monotypic genus endemic to eastern Australia appears to be closely related to the New Caledonian genus *Pancheria* and is positioned in the tribe Pancherieae sensu Engler (1928). *Callicoma serratifolia* forms small trees with simple, coarsely dentate leaves arranged in pairs (Fig. 75; Cronquist 1981: his Fig. 53). The stipules are hairy, lanceolate, and vascularized by several parallel bundles. The stipules may or may not show bifid tips (Fig. 76 a–b, Melville 1972: Fig. 3 B). The bifid condition corresponds to developmental stages with two prominent apical glands (C = colleters) on the young stipules (S in Fig. 34). Stipules partially surround the associated leaf pair laterally, protecting the leaves to a minor degree (Fig. 33). No colleters are evident on the adaxial surface of the stipule (Fig. 35). The nodal anatomy of *Callicoma* is trilacunar, three-trace,

without split-lateral traces. Branches from the lateral leaf traces supply the stipules (Fig. 74; Dickison 1980 b).

Pullea Schlechter

A genus of three species of small- to medium-sized trees, occurring on Fiji, Queensland, Moluccas, and New Guinea (Hoogland 1979, Rao & Dickison 1985 b). The leaves are decussate and simple (Fig. 78). Stipules are interpetiolar and tardily deciduous, remaining on the shoot 4–5 nodes behind the terminal bud (Fig. 79). Both stipules and foliage leaves are hairy, especially on their abaxial surface. Obvious glandular hairs are lacking (Fig. 36). During early development the stipular primordia of *P. stutzeri* show a relatively broad insertion area (Fig. 36) whereas in more mature stages the stipules are blade-like with a tapering zone toward the base (Fig. 79). The nodal anatomy of *Pullea* is trilacunar, or even pentalacunar, with branches from the lateral leaf traces supplying the stipules (Fig. 77).

Acsmithia Hoogl.

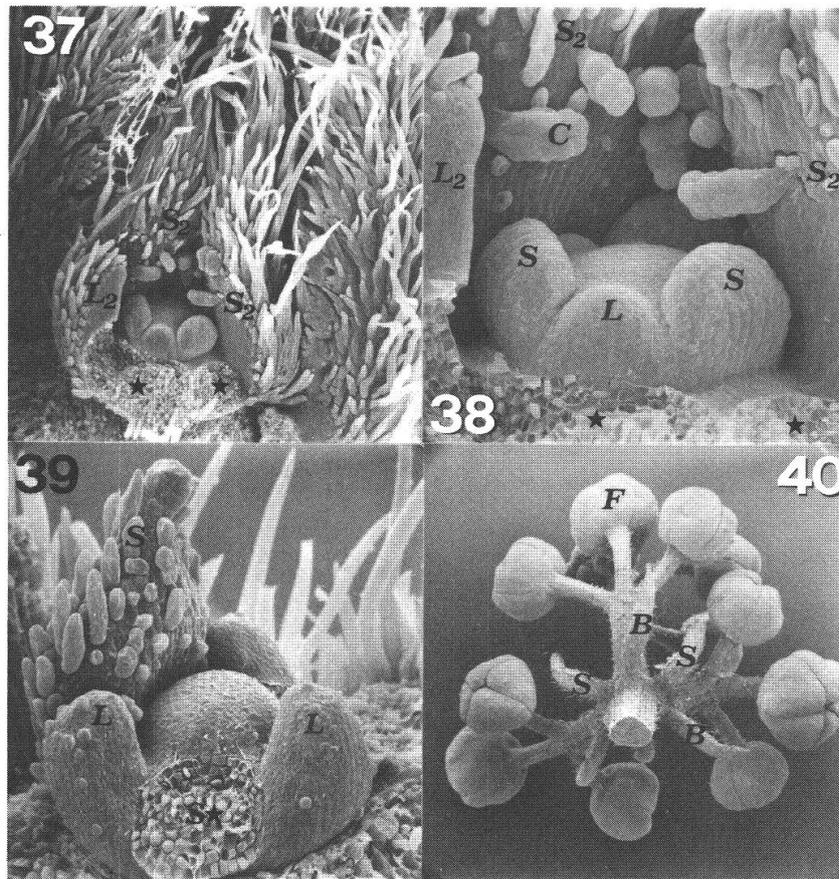
Acsmithia consists of 14 species of small- to medium-sized trees, distributed in Fiji, New Caledonia, Australia, New Guinea, and the Moluccas (Hoogland 1979, 1987, Rao & Dickison 1985 b). The genus was segregated from *Spiraeanthemum* by Hoogland (1979). *Acsmithia* and *Spiraeanthemum* are of particular interest as primitive members of the Cunoniaceae, as evidenced by the presence of apocarpy in both genera (Dickison 1984, 1989).

Leaves of *Acsmithia* are simple and either arranged in trimerous whorls (Fig. 81). The stipules are interpetiolar, narrowly triangular, and topped by a terminal gland in early stages (Fig. 39). Both leaf primordia (L) and stipular primordia (S) of the same whorl seem to arise simultaneously around the shoot apex (Fig. 38). Due to subsequent accelerated growth the stipules soon considerably overtop the leaf primordia (Fig. 39). Both leaves and stipules are covered by many non-glandular hairs (Fig. 37, 39). Only a few club-shaped spreading hairs (C, colleters) are present on the adaxial stipular surface just above the shoot apex (Fig. 38). *Acsmithia* possesses trilacunar nodes with split-lateral traces (Fig. 80, Dickison 1980 b). Unlike other Cunoniaceae, *Acsmithia* also forms prominent interpetiolar stipules in the reproductive region (Fig. 40). As seen in Fig. 40, three narrow, subulate bracts (B) can be distinguished from the three similar, interbracteal stipules because bracts subtend axillary cymes, whereas axils of the stipules are empty.

Eucryphia Cavanilles (Eucryphiaceae)

The genus *Eucryphia*, with five species, is traditionally accepted as a monogeneric family of its own (Bausch 1938). Anatomical data suggest a close relationship between Eucryphiaceae and the Cunoniaceae (Dickison 1978, 1989). The genus has a markedly disjunct southern distribution occurring in eastern Australia, Tasmania, and Chile. Our description is based upon *E. milliganii*, native to eastern Australia.

Eucryphia is characterized by decussate, simple or imparipinnate leaves (evergreen) and interpetiolar, tardily deciduous stipules (Fig. 84). The interpetiolar stipules arise as bilobed, U-shaped appendages completely surrounding and ensheating the shoot apex (Fig. 41–42: one-half of both interpetiolar stipules removed). Mature stipules are clearly bifid and show glandular ribs (i.e., more or less adnate colleters) on their adaxial surface (Fig. 43, 85). The prophylls of axillary shoots are also covered with adnate colleters on their adaxial side (Fig. 44) and strongly resemble stipules, although the apex is not bifid.



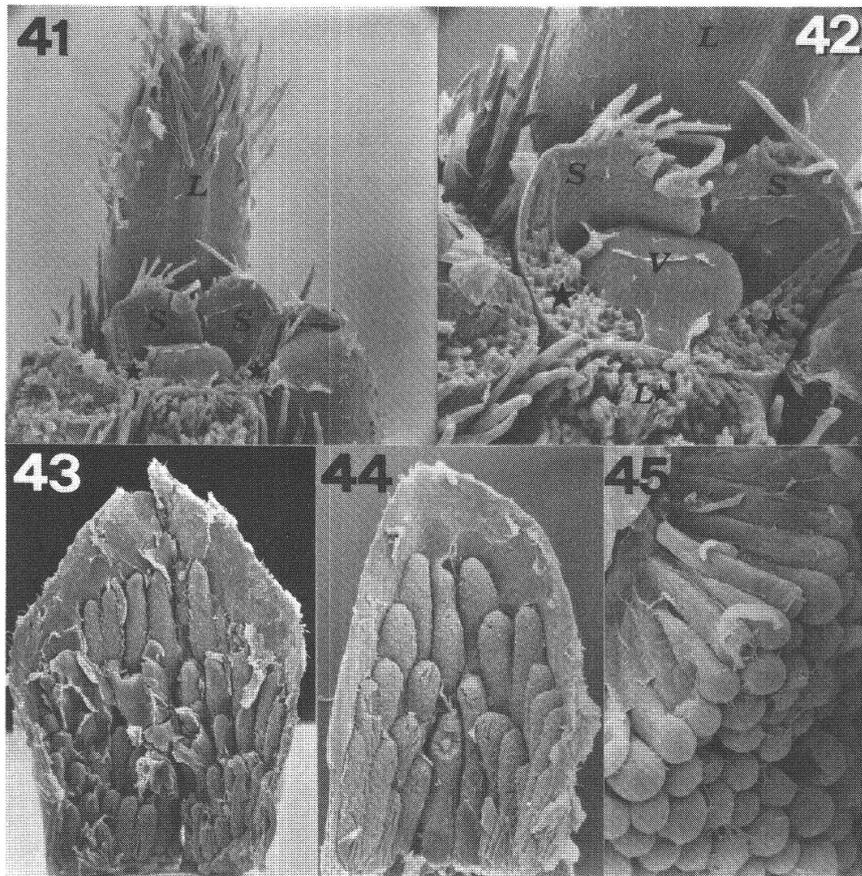
Figs. 37–40. *Acsmithia undulata* (Dickison 262): 37–38. Two magnifications of vegetative shoot tip, with newly initiated whorl of three leaf primordia (L) and three stipular primordia (S), surrounded by next older leaf whorl (L2), with overtopping, interpetiolar stipules (S2). * = removed parts of second whorl. Note colleters (C) arising from the adaxial surface of the stipules S2 (65 ×, 220 ×). 39. Another shoot tip with trimerous leaf whorl (L) and three overtopping, interpetiolar stipules (S), two of them (S*) removed (200 ×). 40. Portion of young inflorescence with trimerous bract whorl (B) accompanied by three bract-like interpetiolar stipules (S). Partial inflorescence (with about three flowers = F per cyme) in axils of the bracts (B) (13 ×).

Each colleter consists of a multicellular core (base) and an outer layer of radially elongated glandular cells (Fig. 45). In contrast to *Ceratophyllum* and *Schizomeria* (Fig. 17, 20), the colleters of *Eucryphia* are only partly adnate as glandular ribs; free colleters are circular in outline when viewed in transverse section (see Dickison 1978: his Fig. 18).

The nodal anatomy of *Eucryphia* in the region of foliage leaves is normally trilacunar with three traces to each leaf and branches of the lateral leaf traces supplying the stipules (Fig. 83: lower half). In *E. moorei*, however, additional trace(s) may arise directly from the stele supplying the stipules exclusively (Fig. 83: upper half, Dickison 1978).

2. Development and mature structure of stipules of *Platymiscium* (Leguminosae)

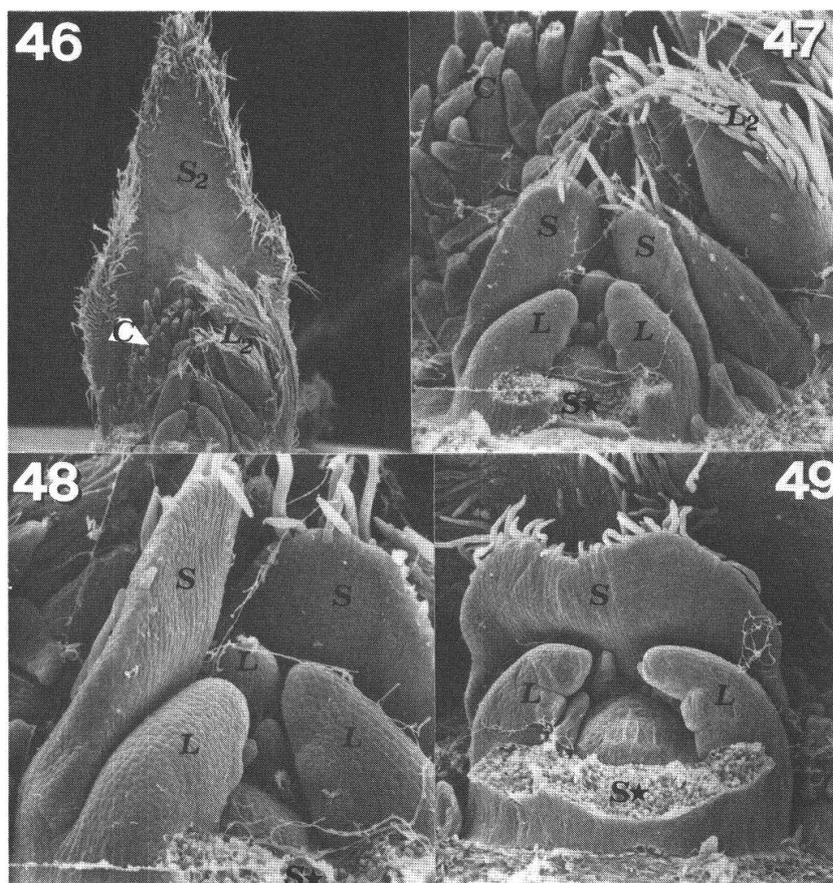
The leguminous genus *Platymiscium* Vogel contains about 20 species of trees and shrubs distributed throughout the West Indies, Central and South America. The genus



Figs. 41–45. *Eucryphia milliganii* (Eucryphiaceae, Hoogland 41731): 41–42. Two views of same vegetative shoot tip, with apex (V), youngest leaf pair (L, L*) with bilobed interpetiolar stipules (S). One half of each interpetiolar stipule removed (*) ($70\times$, $140\times$). 43. Adaxial view of mature bifid stipule (length 3 mm). Adaxial surface covered with parallel secretory ribs (partly adnate colleters) and mucilage ($15\times$). 44. Adaxial view of nearly mature prophyll, with secretory ribs similar to stipular surface ($30\times$). 45. Enlarged view of secretory rib portion, with radially elongated secreting cells ($580\times$).

is a member of the papilionoid tribe Dalbergieae (Melchior 1964, Polhill 1981), and is of particular interest since it combines several vegetative features typical of the Cunoniaceae. Leaves of *P. trinitatis* from northern South America are imparipinnate (often 3–5-foliolate) and are arranged in pairs or rarely trimerous whorls (Fig. 47, 49) (Amshoff 1939). Prominent, broadly-based stipules occur in an interpetiolar position and partly surround and protect the young leaves of the same whorl (Fig. 48). Like some Cunoniaceae, the lower half of the adaxial stipular surface is covered by glandular hairs of the colleter type (Fig. 46, 47). Preliminary hand sections show that the nodal anatomy of *P. trinitatis* is trilacunar, three-trace or pentalacunar, with or without split-lateral traces (i.e., a configuration similar to Fig. 77 and 83).

Platymiscium clearly represents an example of convergent evolution within the dicotyledonous subclass, Rosidae. Though not closely related to cunoniaceous stock, the development and mature structure of the node-leaf-stipular complex of *Platymiscium* is very similar to many Cunoniaceae.



Figs. 46–49. *Platymiscium trinitatis* (Leguminosae, Rutishauser s.n.): 46–48. Three views of vegetative shoot tip with trimerous leaf whorl (L) overtopped by interpetiolar flap-like stipules (S, one removed = S*). The youngest leaf primordia (L) with initiation of pinnae. Next older whorl with once-pinnate leaves (L2) and elongated triangular stipules (S2) partly covered with colleters (C) on adaxial surface. Two leaves and two stipules of whorl 2 removed (20 ×, 60 ×, 120 ×). 49. Axillary bud after removal of prophylls. Leaf pair (L) with early developmental stages of pinnae. Interpetiolar stipules (S) slightly bilobed (S* = removed opposite stipule) (80 ×).

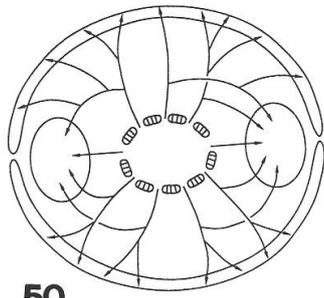


Figs. 50–52. *Cunonia capensis*. 50. Schematic reconstruction of nodal vascularization. 51. Shoot tip showing pinnately compound leaves and paired interpetiolar stipules enclosing the terminal bud (0.2 ×). 52. Interpetiolar stipule, abaxial view (1.5 ×).

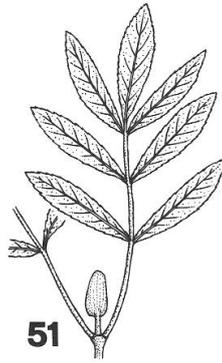
Figs. 53–55. *Weinmannia pinnata*. 53. Schematic reconstruction of nodal vascularization. 54. Shoot tip showing paired, pinnately compound leaves with winged rachis and prominent interpetiolar stipule (0.5 ×). 55. Interpetiolar stipule, abaxial view (3 ×).

Figs. 56–58. *Ceratopetalum apetalum*. 56. Schematic reconstruction of nodal vascularization. 57. Shoot tip showing paired simple leaves and terminal bud (0.25 ×). 58. Detail of terminal bud showing enclosing interpetiolar stipules (4 ×).

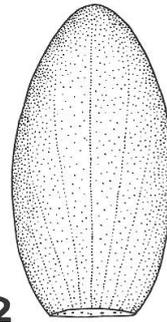
Figs. 59–61. *Schizomeria whitei*. 59. Schematic reconstruction of nodal vascularization. 60. Shoot tip showing paired interpetiolar stipules and simple leaves (0.25 ×). 61. Details of terminal bud illustrating opposing interpetiolar stipules. One leaf has been removed (3.3 ×).



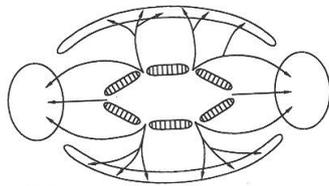
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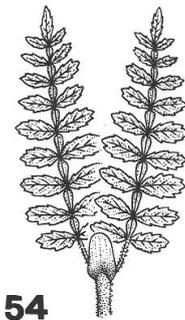
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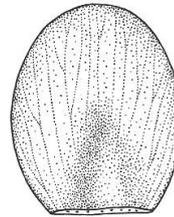
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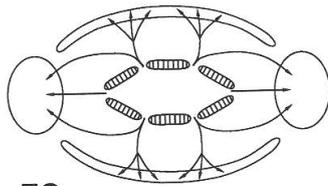
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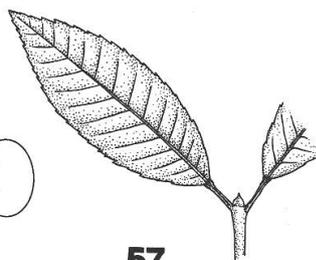
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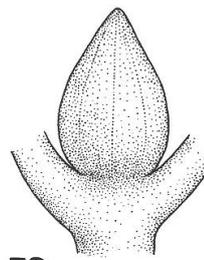
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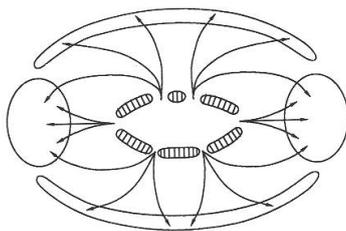
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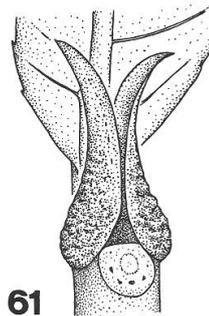
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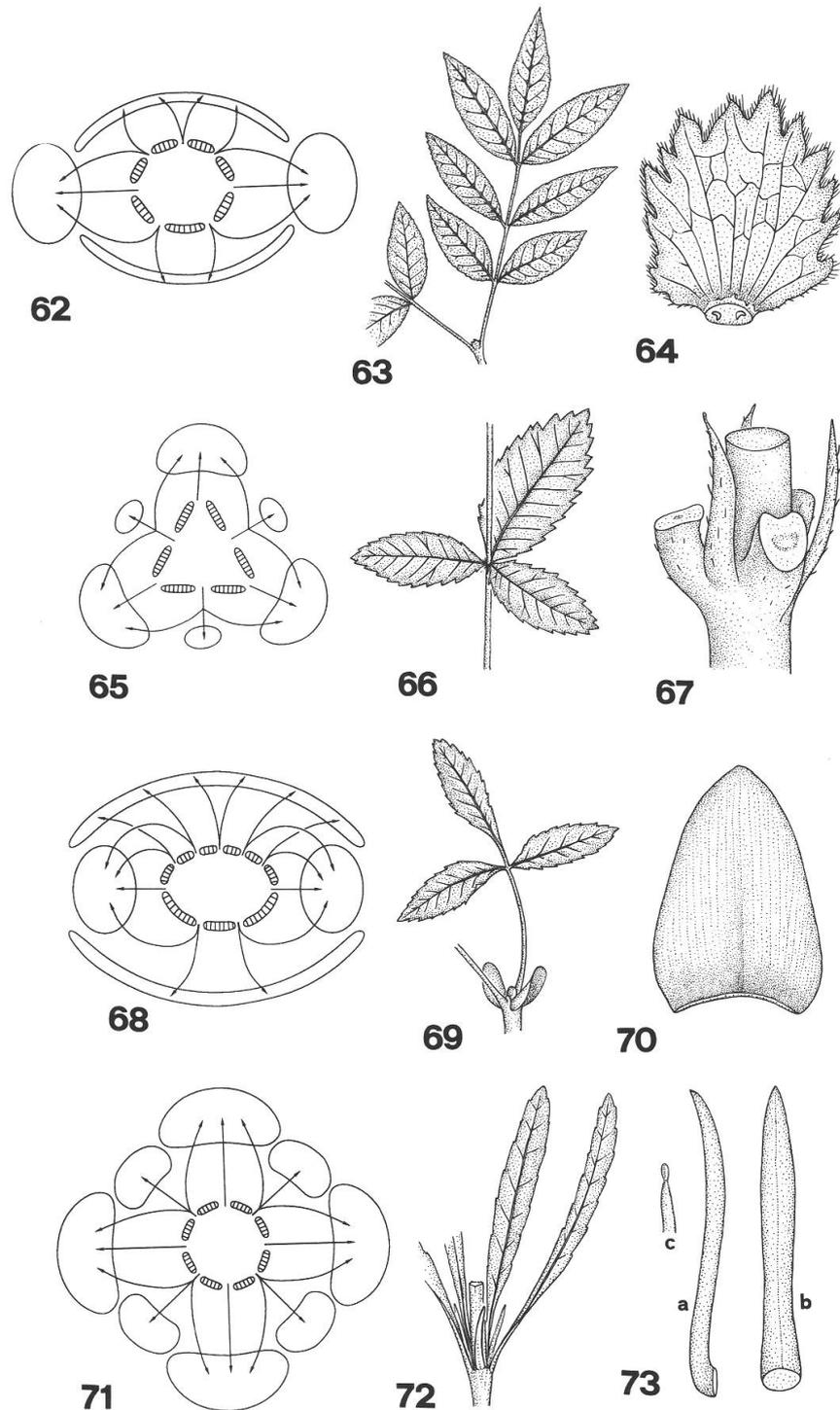
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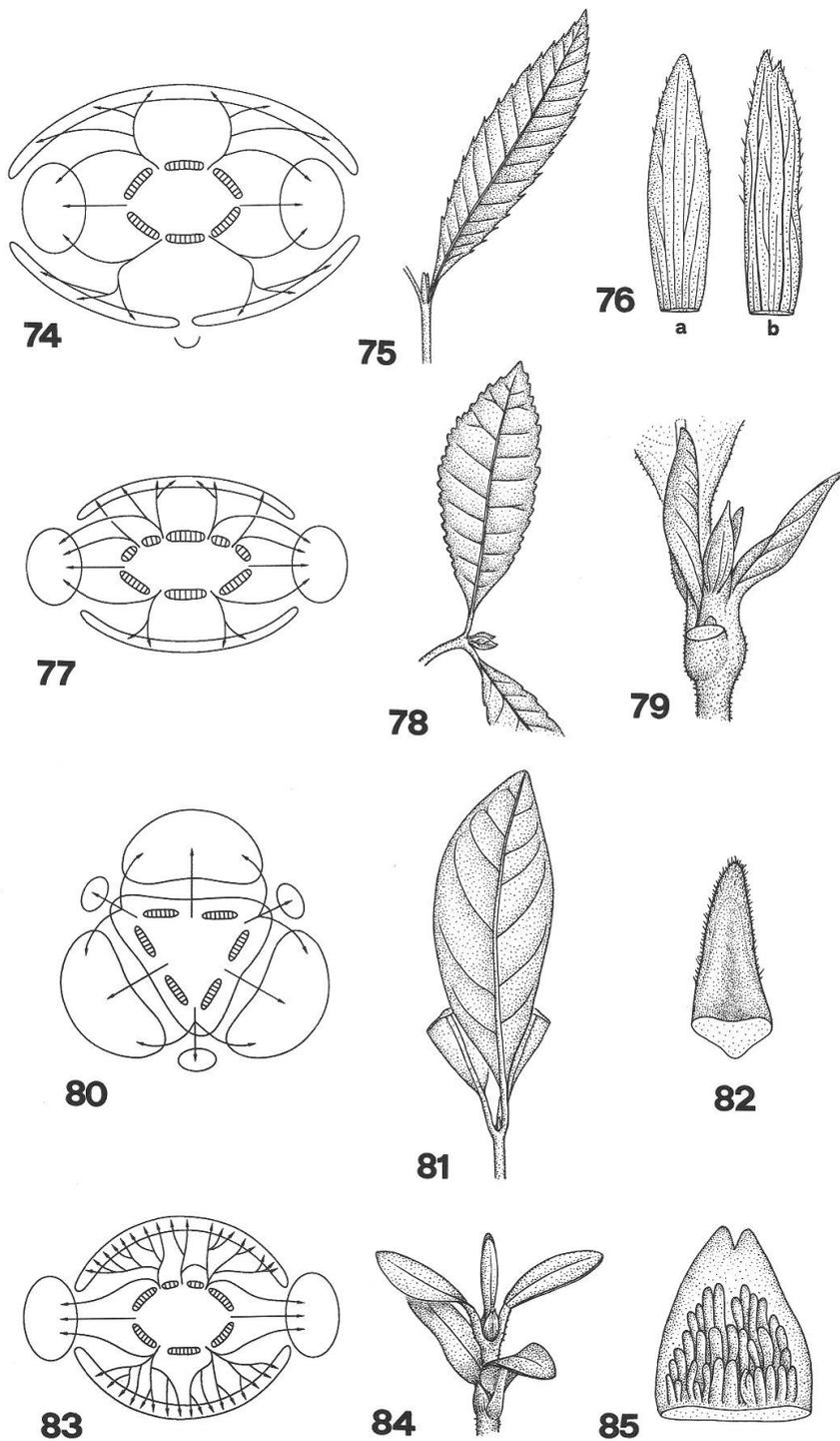


Figs. 62–64. *Caldcluvia australiensis*. 62. Schematic reconstruction of nodal vascularization. 63. Shoot tip showing opposite, compound leaves ($0.15\times$). 64. Stipule ($3.5\times$).

Figs. 65–67. *Acrophyllum australe*. 65. Schematic reconstruction of nodal vascularization showing split-lateral traces. 66. Stem with whorled phyllotaxis ($0.5\times$). 67. Detail of nodal region showing narrow, interpetiolar stipules ($6.5\times$).

Figs. 68–70. *Pancheria confusa*. 68. Schematic reconstruction of nodal vascularization. Note traces that vascularize the stipule directly. 69. Young shoot with paired trifoliate or pinnate leaves and prominent interpetiolar stipules ($0.4\times$). 70. Stipule ($2.5\times$).

Figs. 71–73. *Pancheria elegans*. 71. Schematic reconstruction of nodal vascularization illustrating split-lateral traces. 72. Detail of nodal region showing whorled leaf arrangement and narrow, interpetiolar stipules ($0.8\times$). 73 a–b. Stipule ($6\times$). 73 c. Bract with glandular apex ($6\times$).



Figs. 74–76. *Callicoma serratifolia*. 74. Schematic reconstruction of nodal vascularization. 75. Shoot tip with simple leaves and interpetiolar stipules (0.4 ×). 76. Stipules (3 ×).

Figs. 77–79. *Pullea stutzeri*. 77. Schematic reconstruction of nodal vascularization. 78. Shoot tip with opposite, simple leaves and interpetiolar stipules (0.2 ×). 79. Detail of shoot tip with interpetiolar stipules tapering toward the base (1.5 ×).

Figs. 80–82. *Acsmithia undulata*. 80. Reconstruction of nodal vascularization showing split-lateal traces. 81. Shoot tip (0.4 ×). 82. Stipule (6 ×).

Figs. 83–85. *Eucryphia milliganii*. 83. Reconstruction of nodal vascularization. 84. Shoot tip with interpetiolar stipules (0.9 ×). 85. Stipule showing elongated colleter ribs (7 ×).

Discussion

Stipules are leaf associated appendages, accompanying either one or two leaves, that have long served as an important vegetative character for the delimitation and subdivision of various dicotyledonous families (see, e.g., Weberling 1967, Cronquist 1981). The presence of prominent interpetiolar (interfoliar) stipules in association with opposite or whorled, often pinnately compound leaves is a distinguishing character of many Cunoniaceae. The study here presented deals with selected taxa of Cunoniaceae and allies with interpetiolar (connate) stipules, a character state that is herein regarded as a synapomorphy within the family. A second study to follow will describe the total diversity that exists within the family and allies with regards to the manner of stipular development and mature architecture including systematic and phylogenetic implications.

The present discussion will focus on the significance of stipules, particularly interpetiolar stipules, within the Cunoniaceae and related groups in relation to the morphological interpretation of stipular appendages in dicotyledons as-a-whole. Rutishauser & Sattler (1986) outlined 10 possible criteria for distinguishing vegetative leaves (especially foliage leaves) and stipules for descriptive purposes. Some of these criteria will be mentioned again:

1. Stipules typically are smaller than mature leaves although they may overarch the associated leaf primordia within the bud considerably.
2. Stipules are (by definition) neighbored by leaves, with insertion on the same node or on a common sheath together with the leaf or leaves, whereas leaves are often devoid of associated stipules.
3. Stipules normally are vascularized by branches of the foliar traces (if vascularized at all).
4. Stipules (especially when nonphotosynthetic) often drop off soon after unfolding of the associated leaf (leaves).
5. Stipules always have empty axils, whereas leaves may or may not subtend axillary buds.

Although the evolutionary origin and interpretation of stipules in dicotyledons are debatable, the same is also true for leaves or phyllomes. Historically, however, two opposing leaf-stipule concepts have been offered to explain the juxtaposition of stipules and leaves (as summarized by Rutishauser & Sattler 1986). The classical view, as defended by Eichler (1861) and Sinnott & Baily (1914), accepts stipules to be only the basal outgrowth (subunits) of the leaf itself. The modified leaf-stipule concept, on the other hand, envisions stipules as more or less independent nodal outgrowths (appendages) only positionally associated with leaves. This view was adhered to by such workers as Ponzo (1934), Croizat (1960), and Rutishauser (1984). According to the modified leaf-stipule concept the leaves (blades) and stipules of the same node are interpreted to be partially homologous with each other, i.e., as the result of divergent developmental pathways of positionally equivalent primordia within the same node or whorl. The Cunoniaceae provide additional evidence in support of this conclusion. Nevertheless, it must be remembered that the classical and modified leaf-stipule concepts are complementary rather than mutually exclusive, because both are based upon a number of common axioms (see Rutishauser & Sattler 1986, 1987). As long as the evolutionary origin of stipules and leaves is uncertain, as is the case for the Cunoniaceae, both concepts are acceptable as working hypotheses. A quite speculative variant of the modified leaf-stipule concept was proposed by Melville (1972) in order to understand the nature of the cunoniaceous stipule.

He interpreted the stipules of many (all?) Cunoniaceae as scale-like simple leaves (phylomes), that are directly comparable with the foliage leaves of extinct glossopterid gymnosperms. We have found no evidence in support of this concept.

Within the Cunoniaceae there is a considerable degree of stipular independence from the foliage leaves of the same whorl as evidenced by the following observations:

1. All Cunoniaceae examined for this initial contribution have interpetiolar (interfoliar) stipules that are detached, or free, from the adjacent leaves, although both arise from a common node.
2. The interpetiolar stipules of *Cunonia* spp., *Weinmannia* spp., and *Pancheria confusa* arise from the shoot apex *as early as* the associated leaf pair. We could not observe that the stipular primordia precede the initiation of the associated leaves as reported by Schrödinger (1927). Nevertheless, the simultaneous inception of leaves and stipules resembles the formation of a tetramerous whorl, two of the primordia becoming foliage leaves, and two of them becoming protective scales.
3. In contrast to the most common condition within the Cunoniaceae, in which stipular traces arise as branches from lateral leaf traces only, the pattern of nodal vascularization of certain species (e.g., *Pancheria confusa*) reveals the presence of pure stipular traces, that depart directly from the cauline stele and exclusively vascularize the stipules (see also Dickison 1980 b). This indicates a certain degree of vascular independence of the stipules.
4. Stipules and bracts or prophylls may resemble each other to a considerable degree, not only in *Acacia longipedunculata* (Rutishauser & Sattler 1986), but also in various Cunoniaceae. In *Schizomeria whitei*, for example, the stipules associated with a foliage leaf node and the prophylls located at the base of an axillary branch are morphologically similar in that both are scales with colleter ribs on the adaxial side. *Acsmithia undulata* possesses trimerous whorls of bracts (leaves) with axillary buds whereas the remaining three appendages, though morphologically similar to the bracts, may be called stipules because axillary buds are lacking.

The present study only covers genera with interpetiolar (interfoliar) stipules, although some of the species studied show bilobed interpetiolar appendages (e.g., *Caldcluvia*, *Callicoma*, *Eucryphia*). Bilobed stipules often start their development with two independent primordia that become confluent afterwards. Based on similar observations in other dicotyledons many botanists concluded that lateral stipules (four per leaf pair) are the primitive condition from which the interpetiolar stipules can be derived (e.g., Dickison 1980 b).

This view is especially tempting for adherents of the classical leaf-stipule concept. However, according to the modified leaf-stipule concept (see above) we may accept entire interpetiolar stipules as such without arguing about their origin by confluence ("congenital fusion") of lateral stipules. Moreover, not only stipules but also leaves of various dicotyledons tend to form bifid or twin structures (Rutishauser 1984).

There are two preconditions necessary for the appearance of interpetiolar stipules: 1) decussate or whorled phyllotaxis; 2) sufficient stipular size. These preconditions are regularly fulfilled in the Rubiaceae (Rutishauser 1984) and the Cunoniaceae included in the present study. Also certain Leguminosae (e.g., *Acacia* sect. *Lycopodiifoliae*, and *Platymiscium*) are characterized by interpetiolar stipules. In *Acacia longipedunculata* with 15–27 phyllodes and as many stipules per whorl the interpetiolar (interphyllodial) stipules resemble the uppermost portion of the associated phyllodes. Exceptionally there were also intermediates observable between stipules and phyllodes (Rutishauser & Sattler

1986). Certain legumes (especially *Platymiscium trinitatis*) share various vegetative features with typical Cunoniaceae. The appearance of interpetiolar stipules in the Leguminosae that are similar to the Cunoniaceae is an obvious case of convergent evolution.

To better understand the positional association of leaves and stipules in the Cunoniaceae and other dicotyledons we need more flexible concepts that encompass all possible ontogenetic and phylogenetic pathways (Rutishauser & Sattler 1986, 1987; Sattler 1988). For example, to ask the question, "What is a leaf or a stipule within a whorl?" may be ambiguous, or in some cases, even meaningless. In very general terms one can consider the node or shoot apical ring as a locus of meristematic activity capable of producing one or more than one appendage categories (compare Croizat 1960: 715, 915, his Fig. 114D; Howard 1974). Depending upon which criterion or criteria one uses or emphasizes for the definition of appendages, they must ultimately be regarded as leaves, stipules or something else. Computer simulations (as discussed in Rutishauser & Sattler 1987) may assist in understanding the physiological control mechanisms responsible for the inception of anisophyllous whorls or whorls consisting of leaves and foliose members called stipules.

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