

## THE MORPHOLOGY AND RELATIONSHIPS OF SEEMANNARALIA (ARALIACEAE)

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**ABSTRACT.** An account is given of the taxonomy, morphology and anatomy of the monotypic SE African genus *Seemannaralia* (Araliaceae). Contrary to previous descriptions the bicarpellate ovary is unilocular, the septum being complete only at the level of placentation; one seed matures and lies freely in the cavity of the laterally compressed fruit; the endosperm is shallowly ruminant. Vegetative anatomy is relatively primitive in the known range of the family, but the floral vascular system is advanced. The absence of septum in the fruit, and hence of any hint of procarpophore, shows that the resemblance to Umbelliferae-Hydrocotyloideae is superficial only. The bicarpellate fruit is functionally equivalent to a single mericarp of some Umbelliferae-Apioideae (e.g. *Heracleum*). The affinities of *Seemannaralia* within Araliaceae are uncertain: it is placed near *Cussonia* meantime.

This study originated with R. G. Strey, Curator of the Natal Herbarium, Durban. He made extensive collections of *Seemannaralia* while studying *Cussonia*, another genus of Araliaceae (Strey, 1973), and directed attention to the resemblance between the flat, laterally compressed fruits and those of some Umbelliferae-Hydrocotyloideae. Strey sent fruits to the Royal Botanic Garden, Edinburgh, and young plants have been successfully raised. He also supplied herbarium and wood specimens. The latter arrived in Edinburgh opportunely, just before a visit by W. C. Dickison; he promptly undertook the anatomical study and completed it on his return to America. The core of the paper is the result of this work: the drafting of taxonomy and morphology and the general discussion fell to Burtt.

### TAXONOMY AND MORPHOLOGY

*Seemannaralia* R. Viguier in Ann. Sci. Nat. sér. 9, 4:116, 118 (1906); Harms in Engler & Prantl, Natürl. Pflanzenfam., Nachtr. 4:219 (1914); Dyer in Kew Bull. 1932, 448; Henkel, Woody Pl. Natal & Zulu. 112 (1934); Phillips, Gen. S Afr. Fl. Pl. ed. 2, 545 (1951); Breitenbach, Indig. Trees S Africa 4:863 (1965) cum fig.; Hutchinson, Gen. Fl. Pl. 2:70 (1967); Pitman & Palmer, Trees S Africa 3:1705-1707 (1973) cum ill.; Bamps in Bull. Jard. Bot. Nat. Belg. 44:139 (1974) et in Distr. Pl. Afr. 8: carte 247 (1974).

*S. gerrardii* (Seem.) Harms in Engler & Prantl, Natürl. Pflanzenfam., Nachtr. 4:219 (1914).

Syn.: *Cussonia gerrardii* Seem. in Journ. Bot. 4:298 (1866); Oliver in Hook., Ic. Pl. 15: t. 1454 (1884); Burtt Davy, Fl. Pl. Transv. 2:514 (1932).

*Panax gerrardii* Harv. ex Hook. f. in Harv., Gen. S Afr. Pl. ed. 2:147 (1868); Wood, Handb. Fl. Natal 57 (1907); Sim, Fl. Trees & Shrubs S Afr. 180 (1919) et Native Trees S Afr. 95 (1921); Bews, Fl. Natal & Zulu. 150 (1921); Marloth, Fl. S Afr. 2, 2:234 (1925); Phillips, Gen. S Afr. Fl. Pl. 444 (1926); Erdtman, Pollen morph. & pl. tax. 60 (1970).

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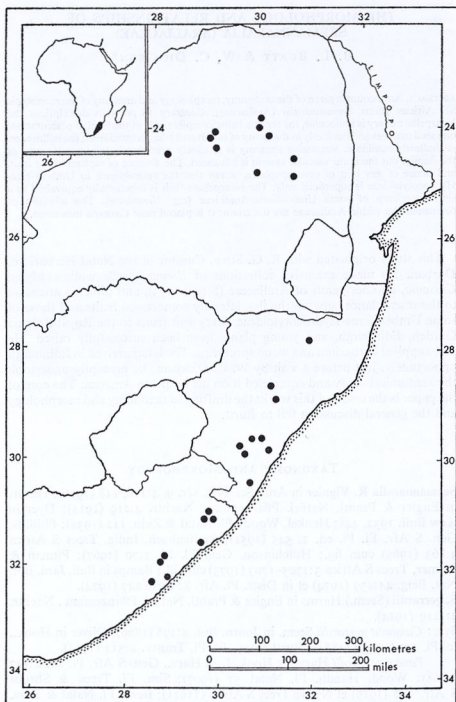


FIG. 1. Map of south-east Africa to show the distribution of *Seemannaralia gerrardii*.

**DISTRIBUTION.** From Willowvale in the Transkei (c. 32° 15' S) northward through the Natal midlands and to Ngome in N Zululand: the eastern escarpment of the Transvaal Drakensberg from Pilgrims Rest as far north as Woodbush (c. 23° 40' S) and reaching west to the Waterberg. At present there is a gap of some 200 miles between these two areas (cf. fig. 1).

**REVISED GENERIC DESCRIPTION.** A deciduous tree. Leaves alternate, exstipulate, petiolate; lamina palmately lobed; lobes acute sharply toothed. Inflorescence a compound panicle of umbels, its main axis terminal, the lateral components axillary to the uppermost leaves of the current year's growth. Flowers not articulated to pedicel, all hermaphrodite. Calyx of 5 triangular sepals c. 0.25 mm long. Petals c. 2 mm, ovate, imbricate. Stamens 5. Ovary bicarpellate but unilocular, the septum being incomplete except at level of placentation; disc conical; styles free, at length recurved. Fruit strongly compressed laterally, unilocular, usually 1-seeded (very rarely 2-seeded), falling with pedicel. Seed ovoid, much compressed, c.  $8.5 \times 3.5 \times 0.75$  mm; endosperm shallowly ruminant; embryo 1.5 mm.

*Additional descriptive notes.* The seedling has epigeal cotyledons, about  $15 \times 8$  mm soon after germination enlarging to nearly  $25 \times 15$  mm (cf. fig. 2) with 5 mm long petiole. The hypocotyl of the seedling becomes somewhat swollen, as do the base of the radicle and of the first-formed secondary roots.

The young leaves and stem are hairy. If trees are cut, coppice shoots are produced vigorously and these also have hairy leaves and stems: on the upper part of the tree they are glabrous. This was seen at Tabankulu Mt. in the Transkei [Hilliard & Burt 7283 (coppice), 7337 (adult)—both E, NU]. Here too the leaves on coppice shoots were more deeply cordate at the base than those on the upper part of the tree.

The tree is deciduous and the buds are protected by bud scales. A flowering shoot first produces about 7–8 fully formed foliage leaves, the upper ones being somewhat smaller and less lobed; finally there may be 1 or 2 much reduced leaves with a rhomboid-acuminate lamina. The shoot ends in an inflorescence axis and lateral axes are subtended by the upper foliage leaves and the reduced leaves, though one or more of these on the lower part of the main inflorescence may be sterile: similar sterile reduced leaves are borne on the lower part of the lateral axes. All axes bear a terminal umbel of flowers and below it several lateral shortly pedunculate umbels. The terminal umbel is the first to flower. At the base of each umbel is a whorl of 7–15 small deltoid caducous bracts. So far as can be seen in the herbarium, all flowers are hermaphrodite and potentially fertile.

The fruit is normally strongly compressed. Occasionally fruits with an additional median wing are found and dissection of these shows that the single seed grows to fill the more or less triangular fruit cavity, so that the endosperm itself is triangular in cross-section. Rarely, two-seeded fruits are found.

By the time the fruits have ripened all the leaves have fallen and the fruiting panicles stand out at the ends of the bare branches. Fruits fall individually as they mature, and eventually the whole of the fruiting part of

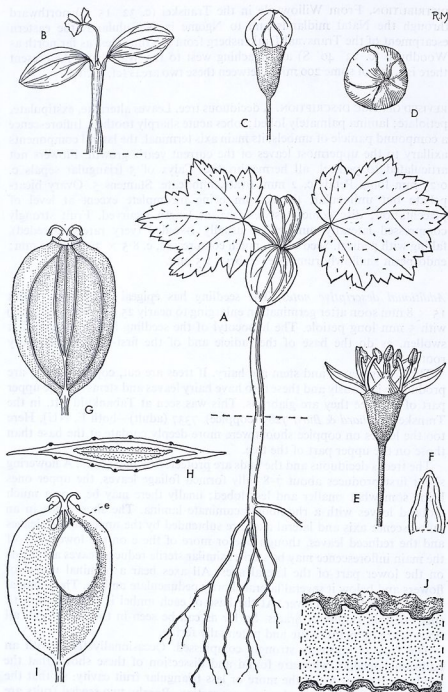


FIG. 2. *Seemannaralia gerrardii*: A, young seedling  $\times 1$ ; B, seedling at end of first season,  $\times 1$ ; C, flower bud  $\times 6$ ; D, flower bud, from above, showing aestivation,  $\times c.9$ ; E, flower, one petal removed,  $\times 6$ ; F, petal  $\times 6$ ; G, fruit  $\times 3$ ; H, fruit in T.S.  $\times 6$ ; I, fruit and seed in L.S. (e, embryo)  $\times 3$ ; J, part of seed in L.S.  $\times 32$ .

the shoot dies and falls. Growth is renewed from a vegetative bud axillary to one of the lower foliage leaves which did not subtend an inflorescence axis.

*Ecology.* *Seemannaralia* is characteristically a tree of forest and forest margins. Under these conditions it may reach a height of 15 m and has a smoothish bark with longitudinal fissures. It is also found on talus slopes where it is usually about 5 m high. Killick (1958, p. 34) found it dominant on the hotter drier talus slopes on Table Mountain, near Pietermaritzburg; with it are two taller trees *Sapium ellipticum* and *Trema guineensis*, but these are restricted to the less rocky spots. On the moister, cooler slopes the *Seemannaralia* consociation is also important, but less extensive than that of *Duvernoia adhatodoides*, one of the few woody members of the Acanthaceae and a plant with much the same distribution as *Seemannaralia*. *Duvernoia* is an evergreen and is absent from the hotter slopes. *Seemannaralia* is also present as understorey in the kloof forest on Table Mountain.

*Seemannaralia* is mentioned by Acocks (1953) as a component of two of his Veld types. Among the Coastal Tropical Forest types it is found in the forest of the Ngongoni Veld (p. 35). This covers areas, largely between 500 and 1000 m altitude, where forest destruction leads to sour grassveld dominated by the tussocky ngongoni (*Aristida junciformis*). It seems probable that most of the records from the Transkei and northward as far as Qudeni forest in Zululand fall in this belt or in its slightly more upland extension, the Natal Mistbelt Ngongoni Veld (p. 124). Further north, at Ngome in N Zululand and in the Transvaal, *Seemannaralia* is associated with one of the Inland Tropical Forest types which Acocks (p. 43) designates North-eastern Mountain Sourveld; the grassland that replaces forest in these areas being dominated by *Themeda triandra*. The original forest of these two types contains many of the same species, although their relative frequencies are rather different. The forests may be more closely related than the grasslands that follow. It will be noticed that the break between the Veld Types recognised by Acocks does not coincide with the apparent break in the geographical distribution of *Seemannaralia*.

Killick (1958) records that *Seemannaralia* frequently starts life as a lithophyte, but that its roots soon penetrate to soil between the rocks. The swollen hypocotyl and swollen roots probably act to conserve water and help to tide the plant over the period of early growth. A similarly swollen hypocotyl is found in *Cussonia* (Araliaceae) and in *Heteromorpha* (Umbelliferae—fide R. G. Strey). Edwards (1967, p. 176) notes that *Seemannaralia* may be epiphytic in its early stages in the Qudeni forests.

In parts of the Transvaal *Seemannaralia* also grows on rocky knolls on the hillsides in grassland. Here it is dwarfer than in the forest and the bark is much cracked and deeply corrugated (see illustration in Palmer & Pitman, 1973). This corrugated bark is presumably connected with the exposure of plants growing in such situations to intense sun and to fire.

**TAXONOMIC HISTORY.** The first specimens of *Seemannaralia gerrardii* were collected by W. T. Gerrard in Natal about 1860 and were studied simultaneously, but independently, by Berthold Seemann in London and by W. H. Harvey in Dublin. Seemann published *Cussonia gerrardii* in 1866, the year in which Harvey died. Harvey's own description of the plant as *Panax*

*gerrardii* was published after his death by J. D. Hooker in 1868. The two names were brought together, under *Cussonia*, by Oliver in 1884; but Oliver doubted whether the plant was a true *Cussonia*. He was the first author to deal at all with reproductive structures, and he lacked ripe fruit. Seemann and Harvey had both described only vegetative features.

Harms (1898) was aware of the anomalous position of this plant, for he keyed it out separately under the tribe Aralieae, although the rest of *Cussonia* belonged in his system to Schefflereae. The distinctive feature that necessitated this special treatment was the imbricate aestivation of the petals. Harms mentions this feature also when assigning the species to his new section *Neocussonia*, for it was still anomalous at sectional level. The other species of this section, which was raised to a genus by Hutchinson (1967, p. 70), are accommodated without strain in *Schefflera* according to recent authors (e.g. Bernardi, 1969, p. 92).

In 1906 R. Viguier published a paper on the systematic anatomy of Araliaceae and he raised *Cussonia gerrardii* to an independent genus, *Seemannaralia*. He was unable to place the genus precisely in his classification (he recognised ten tribes) because he did not know the seed characters. He said that if the endosperm proved, as he expected, to be smooth then *Seemannaralia* should be placed in tribe Schefflereae, if ruminant in tribe Hedereae. Viguier actually wrote his tribal names in subtribal form and in French: Schefflerinées and Hederinées: they may reasonably be brought into conformity with normal practice. Schefflereae, was a much more restricted concept in Viguier's work than in Harms (1898) and differed from Hedereae in its smooth, not ruminant, endosperm.

Viguier did not actually make the combination *Seemannaralia gerrardii*; that must be attributed to Harms, who adopted Viguier's genus in the *Nachträge* to the *Pflanzenfamilien* published in 1914. This however was in wartime and Harms's action largely escaped notice, as had Viguier's erection of the genus in his anatomical paper of 1906. Thus we find botanists using the names *Cussonia gerrardii* and *Panax gerrardii* (see citations above) until 1932, when R. A. Dyer rediscovered Viguier's work. Curiously enough Dyer himself was evidently unaware that *Seemannaralia* had been accepted by Harms.

Hutchinson (1967, p. 70) for some reason placed *Seemannaralia* in tribe Panaceae, which he characterised by valvate petals, although he correctly described those of *Seemannaralia* as imbricate. In Hutchinson's key the genus should be placed in Aralieae. It is divorced from *Cussonia* because Hutchinson created a new tribe for genera with spicate inflorescences, an arrangement which has been adversely criticized (Philipson, 1970). The generic descriptions given by Dyer and by Hutchinson still contain inaccuracies, as may be seen by comparison with that given above. Discussion of the affinities of the genus must now be based on the revised morphological data, particularly as it concerns the structure of ovary, fruit and seed, and the new anatomical information now presented.

#### THE ANATOMY OF SEEMANNARALIA

*Material and methods.* Dried stems, leaves and flowers were initially re-expanded in 5% hot NaOH before fixing in FAA and embedding in paraffin.



Sections were stained with safranin and fast green. Details of floral and leaf vasculature were revealed through the use of both cleared and sectioned materials. Wood was cut without embedding on a sliding microtome. Sections were stained with safranin or a safranin-haematoxylin combination. All statistical data relating to cell length were obtained by measuring fifty cells at random from macerations prepared with Jeffrey's macerating fluid. Anatomical terminology is that suggested by the Multilingual Glossary of Terms used in Wood Anatomy (1964). Comparative anatomical data were taken from Metcalfe & Chalk (1950) and Rodriguez (1957). The following collections of *Seemannaralia gerrardii* were studied—Natal: *H. Rudatis* 997 (E.); *R. G. Strey* 10844 (E), 10960 (E), 11004 (E), 8430 (E), 11009 (E).

*Juvenile stem* (diameter 5 mm). Epidermal cells are papillate and covered with a prominent cuticle. A phellogen is initiated immediately under the epidermis and produces 7–9 layers of thin-walled cork (in mature stems the periderm is very extensive). The cortex is differentiated into an outer region composed of 8–9 layers of angular collenchyma and an inner region composed of thick-walled parenchyma and secretory canals (plate 6A). Druses are numerous throughout the cortex. In older stems the cortex and nonfunctional phloem become sclerotic. Perivascular fibres are present as bundle caps and the primary vascular bundles are surrounded internally by fibrous sclerenchyma (plate 6A). Secondary phloem is well-developed and contains scattered secretory canals and druses. The xylem forms a continuous cylinder although in younger stems discrete vascular bundles are present. Vessel elements of the first-formed secondary xylem are distributed as solitary pores and radial multiples and clusters as seen on the transverse section. The pith is composed of thick-walled cells which are often conspicuously pitted and rounded in outline in transverse section (plate 6A). Secretory canals occur in the pith and tend to be confined to the vicinity of the primary bundles. In older stems the central pith cells break-down resulting in a central lacuna. Crystals are not present in the pith.

*Nodal anatomy.* The cotyledonary nodal anatomy is unilacunar, 2-trace. Two cotyledonary traces arise from the hypocotyl vascular system on opposite sides of the axis. Within the cotyledon the traces subsequently form five primary cotyledonary bundles that extend the length of the lamina. First-formed seedling foliage leaves receive three leaf traces which originate from widely separated regions in the cauline vascular system, i.e., the nodal structure is three-trace, three-gap. Nodes in more mature regions of the plant are multilacunar in that five traces arise from an equal number of gaps (plate 6A).

*Secondary xylem.* Wood is diffuse-porous. Pore distribution is 44 per cent solitary, 48 per cent radial multiples of 2–5 vessels, and 11 per cent clusters of 3–6 vessels (plate 7A). A few instances of vessels distributed in tangential rows up to 5 pores in length were observed. The number of pores per square millimetre ranges between 14–28 with an average of 20. Pores are mostly rounded in outline with an average tangential diameter of 92  $\mu\text{m}$  and a range of 59–130  $\mu\text{m}$ . Perforation plates are mostly simple (plate 7C), however,

occasional elements possess scalariform plates with 1-4(-5) non-bordered bars (plate 7D) or reticulate patterns including vestigial bars. The angle of the end wall varies from transverse to  $70^\circ$  (plate 7B). Ligules are present or absent from the ends of vessel elements. Average vessel wall thickness is  $5\text{ }\mu\text{m}$ . Intervascular pitting is crowded and varies from scalariform to transitional in some vessel elements (plate 7F) to opposite and alternate in other elements (plate 7E). The outline of the borders of intervacular pits is mostly rectangular to hexagonal in surface view, and they range in diameter between 10 and  $45\text{ }\mu\text{m}$ . Vessel-ray pitting is numerous and simple and does not form any recognizable pattern. Vessel elements range in length between 291-759  $\mu\text{m}$  with an average of 539  $\mu\text{m}$  based on 50 measurements.

Imperforate tracheary elements are libriform fibres, a large percentage of which are septate. Pits are numerous and typically have slit-like, crossed apertures. Fibre walls are thin, i.e. the lumen is greater than the thickness of the walls. Average fibre length is 760  $\mu\text{m}$  with a range of 412-1072  $\mu\text{m}$ .

Vascular rays (plate 7B) are uniseriate, biseriate, or multiseriate. Rays that are predominantly uniseriate may become biseriate at restricted locations along their length. Uniseriate rays range between 1-4 cells in height but average 2 cells high. Multiseriate rays range between 5-33 cells in height with an average of 14 cells, and 2-5 cells in width with an average of 3-4 cells. Rays are heterocellular with multiseriate rays composed of a body of procumbent cells accompanied by enlarged marginal cells and uniseriate, terminal extensions ("wings") of 1-3(-4) upright cells.

Axial parenchyma is always scanty with only occasional parenchyma cells in the vicinity of the pores (plate 7A).

*Leaf.* Leaves are dorsiventral. A thin cuticle with small, sharp, pointed projections occurs on both the adaxial and abaxial surfaces. Epidermal cells are elongated as viewed in transverse section and have sinuous anticlinal walls as seen in surface view. Epidermal cells of the adaxial surface are somewhat larger than those of the abaxial surface. Over the major veins surface cells are moderately papillate. Stomata are confined to the abaxial surface and are of the anomocytic type (*sensu* Metcalfe & Chalk, 1950). Guard cells average 30  $\mu\text{m}$  in length. Trichomes are simple (unbranched) and multiseriate. The mesophyll is bifacial, divided into a 2-3-layered palisade region and a spongy region with moderate inter-cellular spaces (plate 6D). A 1-layered, adaxial, thick-walled, and extensively pitted hypodermal layer is present (plate 6D). Lamina venation is actinodromous with the five primary veins originating basally. Venation development is perfect, i.e. ramification of the lateral actinodromous veins covers two-thirds of the blade area. Marginal teeth are supplied by both a secondary or tertiary vein and smaller veins representing fused marginal venation. Marginal ultimate venation is incomplete to incompletely looped. Areolation is perfect with veinlets either none, simple, or once or twice branched. Major veins are surrounded by thick-walled sheath cells. Subepidermal collenchyma is present in the vicinity of the primary veins. Outline of the primary veins assumes the configuration of an arc with incurved ends as viewed in transverse section (plate 6C). Druses are numerous in the mesophyll.

Petioles are supplied basally by five vascular bundles (first-formed seedling leaves receive three leaf traces) that divide and subsequently become



arranged in the form of a dissected arc with invaginated ends as viewed in transverse section (plate 6B). A prominent cuticle with many small, pointed projections covers the surface. The petiole epidermis is 1-layered and the cells are moderately papillate. Five to six layers of subepidermal collenchyma encircle the entire petiole. Remaining fundamental tissue in the petiole consists of thin-walled parenchyma with scattered secretory cavities and druses. Perivascular fibres form bundle caps at lower levels in the petiole but sclerenchyma is absent at the level of attachment of petiole and lamina.

*Root.* In older seedlings the entire hypocotyl, in addition to the bases of the primary and first-formed secondary roots, enlarges as a fleshy storage structure. The radicle alone does not enlarge to become a taproot. The young radicle and later formed secondary roots are initially diarch with two lateral patches of phloem. An endodermis is not evident nor is a well-differentiated endodermis present in older roots. Cambial activity is initiated very early and results in the production of large amounts of parenchyma scattered in the secondary xylem and phloem (plate 6E). Tracheary elements occur as isolated cells or strands of xylem cells embedded in parenchyma (plate 6E). Starch accumulates in great abundance in the xylem parenchyma but not in the cortical cells. Secretory canals occur on the periphery of the secondary phloem. Sclerenchyma or other thick-walled cells are absent. An extensive cortex is composed of uniformly thin-walled lacunate parenchyma in which cambium-like files of cells undergoing anticlinal division occur. No sloughing of the cortex was observed nor are crystals evident in root tissues. Phellogen activity produces 6-7 layers of external cork.

*Floral vasculature.* The floral venation of *Seemannaralia* conforms to the general pattern described for other members of the Araliaceae (Philipson, 1970). Following Philipson's terminology, the vasculature can be regarded as composed of three systems: (1) an outer system of peripheral bundles which supply the perianth parts and androecium; (2) a system of bundles supplying the carpels, and (3) a pair of ventral bundles supplying the ovules. The specific pattern of vasculature is similar to other araliaceous species that have three outer whorls of floral parts each with five members, e.g. *Pseudopanax anomalum* as described by Philipson (1970).

A system of ten bundles diverge at the top of the pedicel (plate 8A) and extend into the ovary wall. The two pairs of ventral bundles of the bicarpellate gynoecium are united in a heterocarpellous manner (sensu Eyde & Tseng, 1971), i.e., ventral bundles of adjacent carpels are connate (plate 8 B & C). Below the level of placentation the two loculi of the ovary are not separated by a septum, however, at the apex of the ovary near the level of ovular insertion a septum forms resulting in a two chambered gynoecium. At this level the ventral carpellary bundles become centrally located in the septum and almost appear to merge. Immediately, however, the two ventral strands become distinct and enter the placenta. Above the level of placentation the septum again opens. An outer system of ten peripheral bundles diverges from the major carpellary wall bundles near the base of the ovary (plate 8 B & C) and subsequently supplies the perianth parts and stamens. Each stamen and petal receives a single trace. Two outer peripheral bundles

which branch from the future dorsal bundles become distinct at a somewhat higher level. At the summit of the ovary two dorsal bundles become evident (plate 8D). Each dorsal bundle extends into a style accompanied by two additional styler bundles that represent the fused products of the variable number of wall bundles that occur at the base of the styles (plate 8E). The styler vasculature may eventually fuse (plate 8F) and always terminates short of the style apex.

Each anther contains four locules. Before dehiscence the partition between the two locules of the same theca breaks down, thus forming a single chamber. Each microsporangium has a well-developed fibrous endothecium and prominently enlarged epidermal cells. Thick walled lignified cells occur in the vicinity of the vein in the connective.

The adaxial epidermal cells of the corolla are enlarged whereas the epidermal cells of the gynoecium apex and styles are markedly papillate. Druses occur throughout the gynoecium and anther connective. Secretory canals are scattered in the carpel wall.

*Fruit anatomy.* The fruit is elliptic in outline in transverse section. At maturity a single seed occupies the central cavity of the ovary. A thin cuticle covers the rectangular-shaped, tanniniferous epidermal cells. Occasional epidermal cells become moderately papillate. The mesocarp is parenchymatous, one to four cells in thickness, and contains scattered druses. The endocarp ranges from two to five cells in thickness and is composed of thin-walled, lignified sclerenchyma in the form of fibres. The fibres are orientated with their long axes more or less parallel to the long axis of the fruit, those of the individual layers being somewhat oblique to one another. Four to six (often five) protruding rib bundles are located in the mesocarp on either side of the fruit. Secretory canals are absent from the material examined.

**ANATOMICAL DISCUSSION.** A summary of the salient vegetative anatomical features of *Seemannaralia* includes: unbranched, multiseriate hairs; anomocytic stomata; one-layered, adaxial hypodermis, vasculature of the petiole in the form of an arc of dissected bundles; subepidermal collenchyma in stem and leaf; nodal anatomy trilacunar in seedling leaves and multilacunar in the mature plant; secretory canals and druses common in the cortex, pith and phloem; vessels solitary and in radial multiples and clusters; vessel elements of medium length and with mostly simple perforation plates but occasionally scalariform plates with up to 4 bars; intervacular pitting scalariform or opposite, sometimes alternate; scanty axial parenchyma; heterocellular rays of both multiseriate and uniseriate types; and septate libriform fibres of very short length. Although most of the above characters are shared by members of both the Araliaceae and Umbelliferae, septate fibres are unknown in the Umbelliferae.

Araliaceae nodal anatomy is multilacunar or trilacunar with an apparent correlation between multilacunar nodes and clasping petioles and trilacunar nodes and nonclasping petioles (Philipson, 1970). The progression from trilacunar nodes in the first-formed seedling leaves to multilacunar nodes in the mature stem of *Seemannaralia* is similar to the transition described in many other dicotyledonous families. Anomocytic mature stomata are present

in *Seemannaralia* whereas paracytic stomata are reported for species of *Acanthopanax*, *Aralia*, *Astrotricha*, *Cheirodendron*, *Didymopanax*, *Oplopanax* (*Echinopanax*), *Eremopanax*, *Fatsia*, *Gastonia*, *Mackinalaya* and *Pseudopanax* ("Nothopanax").

Even though a much more thorough investigation of the xylem anatomy of the Araliaceae is needed, comparison with other genera in the family indicates *Seemannaralia* is at an intermediate to low level of evolutionary advancement as evidenced by the occurrence of vessel elements with predominantly simple perforation plates, although accompanied by occasional elements with scalariform plates with 1-4 bars. *Fatsia*, *Polyscias*, *Kalopanax*, *Pseudopanax* (incl. "Nothopanax"), and *Oreopanax* have advanced simple perforation plates exclusively or only rare vestiges of bars. *Pentapanax*, *Tetrapanax*, *Hedera*, *Aralia*, *Teighemopanax*, and *Tetraplasandra* are slightly less advanced having mostly simple perforations or simple perforations and a small proportion of double-barred scalariform plates. Genera such as *Didymopanax*, *Boerlagiodendron*, *Schefflera* and especially *Cussonia*, *Plerandra*, and *Myodocarpus*, represent lower levels of vessel element evolution by the occurrence of large percentages of scalariform perforation plates with frequently more than 4 bars. The mean vessel element length in *Seemannaralia* of 539  $\mu\text{m}$  is also intermediate between the extremes for the family of 324  $\mu\text{m}$  and 1252  $\mu\text{m}$ . The heterocellular nature of the rays is an unspecialized feature as compared to the homocellular condition in some araliaceous genera. Axial parenchyma is scanty throughout the family. The evolutionary significance of the presence or absence of spiral thickenings on the vessel wall and the occurrence of septate fibres is uncertain.

Vigui r (1906) tentatively suggested that *Seemannaralia* should be placed in the tribe Schefflereae near *Tetrapanax*, *Oplopanax* (*Echinopanax*) and *Didymopanax*. Wood anatomy is generally consistent with this position although Rodr guez (1957) pointed out that Schefflereae are rather heterogeneous anatomically and morphologically.

The wood of *Tetrapanax papyrifer* resembles *Seemannaralia* in vessel element length and diameter, and in the occurrence of vessels in clusters. Perforation plates are mostly simple with 1 or 2-barred scalariform plates occurring at a frequency of 1 per cent. Intervascular pitting is alternate. Rays are heterocellular or homocellular with uniseriate rays very scarce. Imperforate tracheary elements are non-septate.

Available data on the first-formed wood of *Oplopanax* shows a considerably shorter mean vessel element length (366  $\mu\text{m}$ ) than *Seemannaralia*, and a more extended ray height. Perforation plates are predominantly simple with an occasional scalariform plate of 1 or 2 bars. Intervascular pitting is scalariform and fibres are non-septate.

*Didymopanax* has vessel elements with a longer mean length (831  $\mu\text{m}$ ) than recorded for *Seemannaralia* although the vessels are distributed as solitary pores and radial multiples of 2 or 3. Intervascular pitting is transitional to opposite. Perforation plates are simple in 12 per cent of the vessels and scalariform in remaining elements. Scalariform plates have 1 to 3 bars with a high percentage of vestigial bars. Rays are heterocellular with both uniseriate and multiseriate present. Multiseriate rays have upright marginal cells. Imperforate tracheary elements are septate.

In contrast to the xylem, the floral morphology and anatomy of *Seemannaralia* is of an advanced type. Correlated with the occurrence of an advanced 2-carpellate gynoecium is a strong tendency towards fusion of the major floral bundles, a condition noted in the family as a whole by Eyde & Tseng (1971). The ventral bundles of adjacent carpels are fused (heterocarpellous union). At lower levels in the ovary the peripheral bundles and intermediate bundles are fused in a fashion very reminiscent of the Umbelliferae to form 10 major bundles in the gynoecium wall. The dorsal bundles remain united with the peripheral bundles until their departure at the apex of the locules. I could find no indication that the secretory canals in *Seemannaralia* have any constant distribution pattern.

#### GENERAL DISCUSSION

*Comparison with Umbelliferae.* In Umbelliferae fruits that are compressed laterally, that is in the same plane as those of *Seemannaralia*, are rare. They are restricted to subfamily Hydrocotyloideae and even there to the five genera that Tseng (1967) put together as Group I in his study of the flowers and fruits of this subfamily. These genera are *Hydrocotyle*, *Platysace*, *Xanthosia*, *Centella* and *Trachymene*. Some species of *Hydrocotyle* do lack commissural vasculature (except at the level of placentation), but there is never any sign of a breakdown of the septum and in all cases each individual loculus is completely surrounded by its sclerified endocarp. Where fruits are one-seeded (e.g. in species of *Trachymene*) it is always through the abortion of one carpel.

The situation on *Seemannaralia*, where there is a bicarpellate unilocular fruit lined by a common continuous sclerified endocarp, is not repeated in Hydrocotyloideae or elsewhere in Umbelliferae. The rumination of the seed and the anatomical character of septate fibres in the stem are also features unknown in Umbelliferae, and serve to emphasise the differences.

Functionally the fruit of *Seemannaralia* is equivalent to a mericarp of one of the Apioideae such as *Heracleum*. In both cases a symmetrical, single-seeded, much flattened but very narrowly winged diaspore has been formed: in *Seemannaralia* it is two fused carpels laterally compressed, in *Heracleum* it is one carpel dorsally compressed. As a contrast, where a dry winged mericarp has developed from a laterally compressed ovary in association with a procarpophore, it is necessarily asymmetrical; that of *Myodocarpus* is in effect a samara with a well developed wing outside the seed cavity. (On wing formation cf. Baumann, 1946; Theobald, 1972; Tseng, 1967.)

In discussing the union of Araliaceae and Umbelliferae, Rodriguez has pointed out that there are no direct transitional genera (Rodriguez 1957, p. 276; cf. also Thorne, 1972). This position is unaltered by our study of *Seemannaralia*. Both the winged mericarp of *Myodocarpus* and the unilocular fruit of *Seemannaralia* are, in fact, developments that might have been expected as derivatives of the situation now found in Hydrocotyloideae. They are certainly not transitional to it. The closest araliad approach to Umbelliferae is probably in *Mackinlaya*, with petals narrowed at the base and inflexed at the tip.

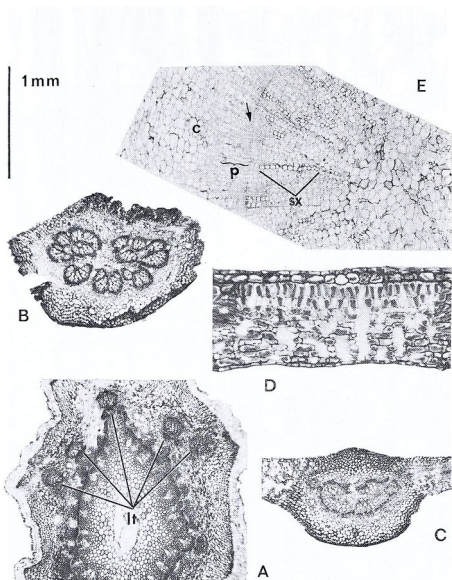


PLATE 6. Vegetative anatomy of *Seemannaralia*. A, transverse section of young stem at the level of a node showing departure of leaf traces (lt) (*Strey* 10844). B, transverse section of petiole at base of lamina showing pattern of vasculature (*Strey* 10844). C, transverse section of lamina in vicinity of a major vein (*Strey* 10844). D, transverse section of lamina (*Strey* 10844)  $\times 150$ . E, transverse section of storage root showing secondary xylem (sx), vascular cambium (arrow), secondary phloem (p), and cortex (c). Seedling grown from seed of *Strey* 11009.



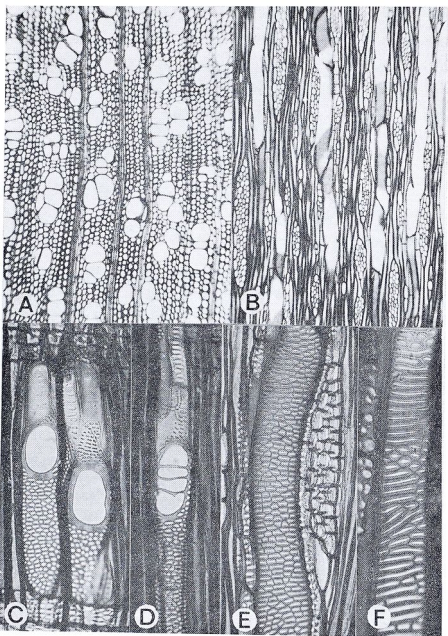


PLATE 7. Wood anatomy of *Seemannaralia* (Strey 11009). A, transverse section showing pore distribution,  $\times 45$ . B, tangential section showing heterocellular rays,  $\times 45$ . C, longitudinal section illustrating vessel elements with obliquely orientated, simple perforation plates,  $\times 300$ . D, longitudinal section illustrating vessel element with scalariform perforation plate,  $\times 300$ . E, longitudinal section showing vessel element with opposite to transitional intervascular pitting,  $\times 300$ . F, longitudinal section illustrating vessel element with predominantly scalariform intervascular pitting,  $\times 300$ .

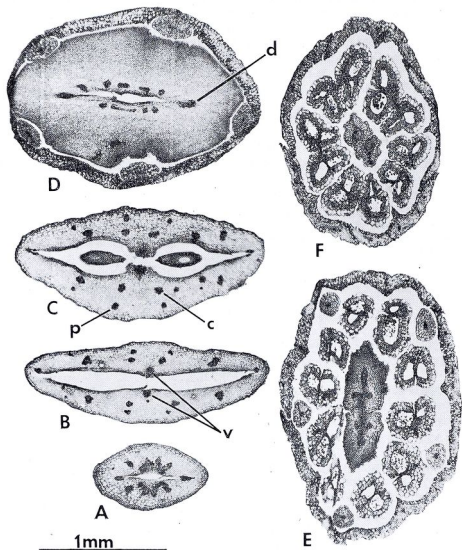


PLATE 8. A-F, serial transections of the flower of *Seemannaralia* from apex of pedicel to the top of the styles showing major vascular patterns (Strey 10844). c, carpellary bundle; d, dorsal bundle; p, peripheral bundle; v, ventral bundle.

*Affinities within Araliaceae.* Eyde & Tseng (1971) have cogently demonstrated that there is yet no reasonably satisfactory classification of Araliaceae. To discuss the relationship of a single genus at all critically is therefore impossible. Nevertheless a few brief notes may help to clarify the problems.

Harms (1897) based his 3 tribes on petal aestivation and form: broad-based, valvate (Schefflereae); broad-based, imbricate (Aralieae); narrow-based, inflexed tip, valvate (Mackinlayeae). Hutchinson (1967) relied successively on inflorescence, number of floral parts, aestivation and endosperm rumination: he recognised seven tribes. Neither of these authors laid stress on leaf-form. Eyde & Tseng (1971) have put forward the suggestion that the most natural primary division of Araliaceae would be into pinnate-leaved and palmate-(including digitate-) leaved groups, although they recognise that "*Panax* with palmately compound leaves and *Stilbocarpa* are closer to *Aralia* than they are to anything in the *Schefflera* alliance."

It may well be that, when detailed knowledge of the family is much more advanced, its classification will not start with an initial dichotomy. Nevertheless as a rough principle the suggestion made by Eyde & Tseng deserves further exploration. There is certainly no hint that *Seemannaralia* is closely allied to any genus with pinnate leaves.

It has been seen that the ovary and fruit of *Seemannaralia* are unique. This genus also differs from *Schefflera*, which forms the core of the palmate-leaved group, in having imbricate petals and ruminant endosperm. The enormous diversity of *Schefflera* does not, to our knowledge, include either of these characteristics.

Other palmate-leaved genera placed near *Seemannaralia* by Hutchinson (and by Viguier if the endosperm had proved to be smooth), are *Tetrapanax*, *Oplopanax* and *Didymopanax*. All have smooth endosperm and valvate petals; *Tetrapanax* also has well developed stipules (absent in *Seemannaralia*), *Oplopanax* is spiny and *Didymopanax* and *Tetrapanax* both have stellate indumentum.

The palmate-leaved genus with ruminant endosperm is *Cussonia*, in which *Seemannaralia* was once placed. *Cussonia* has the ultimate inflorescences spicate and the corolla lobes valvate. Hutchinson (1967) spoke of simple racemes and spikes in *Cussonia* and thought the genus primitive in Araliaceae. Philipson (1970) also thought racemes primitive in the family. This may be true (cf. Eyde & Tseng, 1971), but *Cussonia* does not have simple racemes or spikes. The inflorescences seem to be highly complex, the flowers open in anything but simple racemose order (Strey 1973), and herbarium specimens suggest that it is often the terminal group that opens first. In a panicle of umbels, which is the inflorescence-form of *Seemannaralia* and many other Araliaceae, it is the terminal umbel that opens first. The compact inflorescence of *Cussonia* could well be derived from a panicle of umbels. Although most species of *Cussonia* have digitately compound leaves, those of *C. natalensis* are simply palmatifid as in *Seemannaralia*.

The ruminant endosperm of *Hedera* was studied by Hegelmeier (1886, p. 591) and Periasamy (1966) has investigated the mature fruit of *Arthropphyllum*; but there is a sad lack of detailed information of the development of rumination in this family. Viguier (1906, p. 27) distinguished between rumination due to the physical impact (penetration) of an irregular endocarp surface on the seed (as in some species of *Polyscias*) and that due to

"digestion". The seed of *Seemannaralia* lies loosely in the fruit cavity and the endocarp wall is smooth. Its rumination clearly belongs to the second category, as does that of the genera grouped by Viguiér, and Hutchinson, in tribe *Hedereae*. Periasamy (1962), in a general review of ruminant endosperms, has recognised seven types and considers that the examples in Araliaceae probably have the *Spigelia*-type, originally described by Dahlgren (1922). In this, the rumination of the seed coat is originally formed over the nucellus while the endosperm is in a quiescent phase; subsequently the endosperm grows rapidly, absorbs the nucellus and comes to conform to the already existing ruminations of the seed coat. The grouping of most of the ruminant genera of Araliaceae into tribe *Hedereae* results in the close association of pinnate and palmate leaves. A comparison of the development of rumination in plants with these contrasting leaf-types would therefore be particularly valuable.

Bicarpellate ovaries are well-known in Araliaceae, but they either have two fertile loculi (e.g. *Didymopanax*, *Harmsiopanax*, *Myodocarpus*) or one loculus is fertile and the other aborted (e.g. *Mackinlaya*, including *Anomopanax*, Baumann 1955). A few Araliads have completely unilocular ovaries: Philipson (1970) interprets some (e.g. *Diplopanax*) as truly monocarpellate, but Baumann (1955) considered they were all pseudomonocarpellate. There is no trace of a second carpel in Philipson's figures and, as he says, there is no reason why carpel number should not be reduced to one. This is not, however, germane to our present study. What is important is that in none of the unilocular ovaries are the two carpel cavities fused. This condition appears to be unique to *Seemannaralia* and, being unique, of itself gives no taxonomic clues. There is, however, one anatomical feature that is important; namely the heterocarpellous union of the ventral bundles of the carpels. This is the pattern that Philipson illustrates for *Pseudopanax anomalum* (Philipson 1970, plate 1A); it leaves the lower part of the septum free of vasculature. The opposite condition, homocarpellous union, is found, for instance, in *Harmsiopanax* (Philipson 1970, p. 95, fig. 10); this results in vascular bundles running throughout the septum and might well interfere with the development of a unilocular ovary. Thus one would expect any close ally of *Seemannaralia* to show the heterocarpellous condition. Unfortunately the taxonomic value of this feature is very uncertain. Eyde & Tseng (1971, p. 277) record both heterocarpellous and homocarpellous fusion within the genus *Acanthopanax*, as well as the third possible state, a single central strand.

For *Cussonia* the same authors record heterocarpellous union in *C. paniculata* Eckl. & Zeyh., but *C. spicata* Thunb. and *C. arenicola* Strey both show a single central strand in the lower part of the ovary and this strand splits into two as the level of the placenta is reached. The heterocarpellous condition is the commoner in the sample of the family investigated by Eyde & Tseng (1970): homocarpellous fusion (or at least the presence of ventral bundles in the septum) seems to be a necessary prerequisite of carpophore formation and is found in *Myodocarpus* and *Harmsiopanax*, as well as in other genera.

*Seemannaralia* is distinctive amongst the arboreal Araliaceae of the southern hemisphere in being deciduous. Deciduous genera are also found in eastern Asia, *Kalopanax* being one with palmate leaves. There is, however, little likelihood of a close relationship: the deciduous habit has evidently

developed on both northern and southern borders of the main tropical range of the family.

As we have seen, a really close relationship between *Seemannaralia* and *Cussonia* is gainsaid by differences in inflorescence, aestivation and fruit structure. Also, vessel elements in *Cussonia* are generally longer than those of *Seemannaralia* and scalariform perforation plates with up to 10 bars predominate, whereas vessels with simple perforation plates are characteristic of *Seemannaralia*. Nevertheless, it is doubtful if any more probable affinity for *Seemannaralia* can be found at present. Pending a re-classification of the whole family, we do not have any trustworthy criteria to guide a decision whether the peculiarities of *Seemannaralia* merely justify the generic rank, or are enough to warrant subtribal or even higher status.

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