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# A NEW SHRUBBY GENUS OF AFRICAN UMBELLIFERAE

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ABSTRACT. *Polemannia? marlothii* H. Wolff, a shrub of western Cape Province, is shown to represent a new genus, described here as *Polemanniopsis*. It differs from *Polemannia* in its regularly toothed leaflets which lack an intramarginal nerve, in heteromorphic winged mericarps, and in the seed lying freely in the pericarp, having a commissural groove and being minutely ruminate. From *Heteromorpha* it differs in seed characters and in its constantly digitate leaves (not simple to pinnately 3–5(–7)-foliolate). Some features of the woody Umbelliferae of southern Africa are discussed in relation to the possible derivation of the family from Araliaceae.

Re-investigation of a problematic shrubby Umbellifer from the western Cape Province of South Africa, *Polemannia? marlothii* H. Wolff, became possible with the accession of flowering and fruiting material previously unknown. Wolff's type specimen was in leaf only, and he suspected that the plant might prove to represent a distinct genus when fruit became available. He was quite right, and it is described below as *Polemanniopsis*.

Woody members of Umbelliferae are few and of considerable interest, as the family is widely held to be derived from the same basic stock as the primarily woody Araliaceae. It is natural, therefore, to consider whether some of the peculiar features of these woody Umbelliferae can be regarded as primitive. The observations set down here are not intended to advocate any precise ideas on the phylogeny of the family. They are simply points that ought not to be forgotten when the problem is critically studied, and they are mentioned here because I have not found them brought together elsewhere. Africa has a relatively small representation of Umbelliferae, but it may be more important in the classification of the family than its size suggests.

The woody habit of *Polemannia? marlothii*, and a superficial resemblance of the leaves to those of *P. grossulariifolia* Ecklon & Zeyher were doubtless Wolff's justification for placing this plant in *Polemannia* Ecklon & Zeyher. However, the resemblance in the leaves does not stand up to closer examination. Those of *P. marlothii* lack the intramarginal vein that is characteristic of *Polemannia* (Hilliard & Burtt, 1986: 227, fig. 6E), also the cartilaginous margin is smooth and insignificant but the leaf-margin is regularly dentate (Fig. 1A), whereas in *Polemannia* there is a strong, usually rough, cartilaginous margin and the leaflets may be lobed but the margin is never regularly toothed.

The fruits of *Polemannia? marlothii* prove to be quite different from those of *Polemannia*. The mericarps are heteromorphic and strongly winged, one having three wings, the other two; the wings have an internal cavity which contains oil droplets in the young fruit. In *Polemannia* the mericarps are isomorphic and are not winged. Furthermore the commissural face of the seed is grooved in *P. marlothii* and the seed lies free in the ripe fruit: it is not united to the pericarp. Finally the endosperm is minutely ruminate. None of these features is found in *Polemannia* sensu stricto.

Another woody genus of the family found in southern Africa is *Heteromorpha* Cham. & Schlechtd., so named because of its heteromorphic mericarps (Chamisso & Schlechtendal, 1826: 385). These are built on the same pattern as those of *P. marlothii*, but *Heteromorpha* lacks the distinctive seed characters of that plant. Also *Heteromorpha* has simple or pinnately 3–5(–7)-foliolate leaves, whereas those of *P. marlothii* are digitately 3–5-foliolate.

Hiroe (1979: 674) reduced *Polemannia*, quite wrongly, to *Annesorhiza* Cham. & Schlechtd., and transferred *P. marlothii* to that genus. However all species of true *Annesorhiza* (i.e. excluding both *Stenosemis* Sonder and *Glia* Sonder) are herbs with the foliage leaves radical and those of the flowering stem reduced to sheath and rudimentary lamina. *Annesorhiza* lacks the seed-characters of *P. marlothii* and the pattern of heteromorphy shown by the mericarps is different (see further below). No close ally of *P. marlothii* has been found amongst tropical or southern Africa Umbelliferae, nor indeed amongst those from anywhere else. The conclusion that it represents a hitherto unrecognized genus is inescapable. It is described below as *Polemanniopsis* (p. 499) and that name will be used in the remainder of this discussion.

Heteromorphic mericarps are not infrequent in Umbelliferae, but the term is merely descriptive and covers examples that are unlike in both structure and function. Very often heteromorphy involves the abortion, or partial abortion, of one mericarp (see Baumann-Bodenheim (1955) for a wide treatment in Araliaceae and Umbelliferae, and Hedge & Lamond (1972) for its occurrence in the tribe Echinophoreae). Then, *Torilis nodosa* (L.) Gaertner has heteromorphic mericarps on the outer flowers of the umbellule, one mericarp being covered with short tubercles, the other by long hooked bristles. This, however, is a superficial difference affecting only the external ornamentation and obviously concerned with the provision of an alternative method of dispersal.

The pattern of heteromorphy found in *Polemanniopsis* and *Heteromorpha* (Fig. 1F) seems to be the result of structural conflict within a flower that has a pentamerous perianth and an inferior bicarpellate fruit splitting into two mericarps. Inevitably one mericarp carries two sepals, the other three. The fruit wings are developments of the ribs that carry the five vascular strands supplying the sepals: consequently one mericarp carries two wings, the other three. In *Polemanniopsis* the cross-section of the young fruit shows that the lateral wings on the mericarp with three wings are not strictly marginal (Fig. 1B) although they become so later (Fig. 1C).

Townsend (1985: 845, fig. 2D–F) has recently recorded some variation from the usual pattern of *Heteromorpha* in *H. involucrata* Conrath. In this species the normally unwinged ribs are much more strongly developed than in *H. trifoliata* (Wendl.) Ecklon & Zeyher and, as seen in the transverse sections drawn, might well be described as half-winged. However they never equal the wings on the sepaline ribs and the essential heteromorphy of the mericarps persists. It should be noted that *H. involucrata* is one of the subherbaceous species and in certain other features it shows somewhat exuberant growth tendencies, as evidenced by the foliaceous involucral bracts and the very large terminal umbel.

In *Annesorhiza* the heteromorphy of the mericarp is different. Each mericarp has both margins of the commissural face winged: these four wings are always present. In addition (as shown for *A. capensis*, Chamisso &

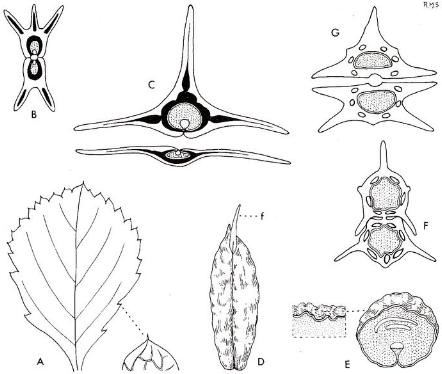

FIG. 1. A–E, *Polemanniopsis marlothii*: A, leaflet ×1; B, T.S. of young fruit ×8; C, T.S. of mature fruit ×8; D, seed ×6 (f = funicle); E, seed in T.S. ×10, with part of testa ×30. F, *Heteromorpha involucrata*: T.S. of mature fruit ×8; G, *Annesorhiza capensis*: T.S. of mature fruit ×8. (F & G adapted from Chamisso & Schlechtendal, 1826).

Schlechtendal, 1826, tab. 5 fig. 4; Fig. 1G) there is a median wing on one mericarp and two semi-lateral wings on the other; thus the whole fruit has seven wings. A similar pattern gives its name to the Mediterranean genus *Heptaptera* Margot & Reuter (1839).

In contrast to the invariably heteromorphic mericarps of *Polemanniopsis* and *Heteromorpha*, the patterns in *Annesorhiza* and *Heptaptera* are far less constant (Herrnstadt & Heyn, 1971). Isomorphy may be attained in these genera either by the winging of intermediate ribs so that each mericarp is 5-winged, or by the loss of all but the marginal (commissural) wings leading to a fruit with each mericarp having three dorsal ribs and two marginal wings, or by the loss of all the wings, so that each mericarp is 5-ribbed. In *Annesorhiza* one species, *A. macrocarpa* Ecklon & Zeyher, has particularly well developed wings: in addition to the 4 marginal wings there are 3 unequal dorsal wings on one mericarp two on the other. It is tempting to try to relate fruit wings to ribs carrying vascular supply to sepals and petals. In *Polemanniopsis* and *Heteromorpha* it is clearly only the sepaline ribs that are winged. The isomorphic *Heptaptera triquetra* (Vent.) Tutin has 5 wings on each mericarp, suggesting that both sepaline and petaline ribs are winged. The 7-winged *Heptaptera*-pattern is, however, less easily explained. Are two of the commissural wings sepaline and two petaline? Or are the commissural wings really just winged extensions of the commissure margin and not strictly associated with sepaline or petaline ribs? Theobald (1967: 259 & fig. 3) has pointed out that the commissural wing of *Lomatium dasycarpum* (Torrey & Gray) Coulter & Rose does not develop immediately above the lateral rib, but on the commissural side of it. This, however, is probably not a widespread condition. Detailed developmental studies of many more species are needed and the partially heteromorphic genera *Annesorhiza* and *Heptaptera* would be a good starting place.

It is the inconstancy of the *Heptaptera* type of heteromorphy that no doubt led Drude (1898: 94), quoting Eichler (1878: 409), to regard the possession of heteromorphic mericarps as of minor importance. The two different types were not distinguished. Similarly, Koso-Poljansky (1916: 117) grouped *Heteromorpha* and *Annesorhiza* together and said he could not really see any difference between them. Baumann (1946: 70) noted the two types of heteromorphy, but the condition was not of great interest in the context of his studies, probably because it seems that where a bicarpellate ovary has been developed in Araliaceae, the two halves are always isomorphic.

Despite the present lack of detailed anatomical and developmental information, I am inclined to think that the difference between the heteromorphy found in *Polemanniopsis* and *Heteromorpha* and that found in *Annesorhiza, Heptaptera* and elsewhere is fundamental. The important fact is that the *Heptaptera*-type is already adjusted to the isomorphic pattern by the equal development of the two marginal wings on each mericarp. It is noteworthy that the *Heptaptera*-type, which seems to be the more advanced, is found in typical Umbelliferous herbs with compoundly dissected leaves and an annual flowering stem. The pattern found in *Polemanniopsis* and *Heteromorpha* seems to be restricted to these two woody genera.

Little can be said about the hollow fruit-wings of *Polemanniopsis* until a thorough developmental study has been made. Such cavities are known elsewhere in the family, for instance in *Myrrhis* Miller (Drude, 1898: 99, fig. 39) and *Ferula* L. (Drude, 1898: 101, fig. 42B), but I do not know if these ever come to contain oil droplets (there are independent vittae in these genera). Another woody African genus of Umbelliferae, the pinnate-leaved *Steganotaenia* Hochst., has fruits whose marginal wings split internally when cut, even when fairly young. Norman (1934: 504) says that vittae are always absent, though later (p. 515) he says he has occasionally found rudimentary vittae that are 'clearly non-functional'. He cut numerous mericarps at various stages. In young fruits of *Dinter* 272 (E) there is certainly a very small vitta below each dorsal rib. However, there appeared to be no commissural vittae and no oil droplets were seen in the wing cavity.

Another interesting feature of *Polemanniopsis* is that the seed lies free in the carpel cavity and is easily extracted from the ripe fruit. This suggested *Eleutherospermum* as a generic name if it were not preoccupied. But it was: by another member of Umbelliferae! *Eleutherospermum* C. Koch is a typical umbelliferous herb with large dissected basal leaves and flowering stem without foliage leaves (Rechinger, 1987: 177); the mericarps lack the broad wings of *Polemanniopsis*, but the seed comes free from the fruit wall and, as in *Polemanniopsis*, is grooved on the inner face. However, there is no question of a close affinity between the two genera.

In an account of the Araliaceous *Seemannaralia* Viguier (Burtt & Dickison, 1975: 460) it was stated that seeds with ruminate endosperm were unknown in Umbelliferae. This must now be corrected. The seeds of *Polemanniopsis* are minutely ruminate (Fig. 1D, E). Rumination is fairly common in Araliaceae (see Harms, 1898), and characteristic of tribe Hedereae in some classifications. The degree of rumination in *Seemannaralia* is very slight (Burtt & Dickison, 1975, fig. 2J): as it is in *Polemanniopsis*. Nevertheless it might be regarded as a primitive character persisting from an Araliaceous-like ancestor. *Heteromorpha* does not have ruminate seeds.

There is another difference between these two genera. *Polemanniopsis* has strictly digitate leaves; *Heteromorpha* is very variable in leaf-form: leaves may be simple or trifoliolate or, especially on sucker shoots, definitely imparipinnate with 5 leaflets or the basal pair each with a subsidiary basiscopic leaflet (see e.g. *Hilliard & Burtt* 11217 (E) from near Creighton, Natal). Sucker shoots of *Polemannia montana* have large leaves, but they are still palmately divided (Hilliard & Burtt, 1986: 227, fig. 6E). Eyde & Tseng (1971: 222) have suggested that the most natural primary division of Araliaceae is into pinnate-leaved and palmate- (including digitate-) leaved groups. If the heteromorphic mericarps of *Heteromorpha* and *Polemanniopsis* are thought to indicate that these genera show some affinity to Araliaceae, then the fact that one has a pinnate and the other a palmate leaf-form is of added interest.

In considering the possibilities of relationships between the woody South African Umbelliferae and the family Araliaceae, the genus *Polemannia* must not be forgotten. This has leaves on a palmate-digitate pattern and isomorphic mericarps. There are three closely related species, *P. grossulariifolia* Ecklon & Zeyher (the type), *P. montana* Schlechter & Wolff, and *P. simplicior* Hilliard & Burtt; there is also an anomalous species, *P. verticillata* Sonder (Sonder, 1862), which is very poorly known and has not been collected since Drège found it over 150 years ago. It is of particular interest as the illustration (Engler 1921: 817, fig. 334; Wolff 1921: 229, fig. 1A) shows that the inflorescence in its lower part is a raceme of umbels, similar to the pattern that is frequent in Araliaceae, but decidedly unusual in Umbelliferae; however the inflorescence does appear to terminate in a compound umbel. Fruits are as yet unknown.

The woody *Steganotaenia* has been mentioned only in connection with its fruit structure. The other woody Umbelliferae in Africa are clearly leptocaul in habit: they have hard wood (some details of wood structure in *Heteromorpha* are given by Rodriquez, 1957: 223), and are much branched with thin branchlets. In contrast, *Steganotaenia* shows traces of a pachycaul affinity; it has a large pith, is little branched, and has relatively massive terminal buds and simply pinnate leaves. I have used here Corner's terms leptocaul and pachycaul (Corner, 1949); Mangenot (1969) described growth patterns according to the number of buds produced. The extreme pachycaul is, of course, monoblastic with a single terminal bud; oligoblastic applies to plants that may often be thought of as having had a pachycaul ancestry, though there is always the possibility that extreme pachycauly was derived. *Steganotaenia* would rank as oligoblastic. Leptocauls are clearly polyblastic, numerous buds leading to the much-branched habit.

Pachycauly, monoblastic in *Harmsiopanax* Warburg but more often oligoblastic, is common in Araliaceae. It is not unreasonable to regard the normal habit that we associate with Umbelliferae, radical leaves and a solitary, often massive, annual, flowering stem, as the herbaceous derivative of pachycauly. Any evidence of pachycauly in the family, as shown by *Steganotaenia*, is therefore important. *Heteromorpha* is leptocaul and suggests, through its simple-leaved representatives, an affinity with the genus *Bupleurum* L., especially with the shrubby evergreen and distinctly leptocaul *B. fruticosum* L. But *Heteromorpha* has 11 chromosomes in the haploid state, *Bupleurum fruticosum* has only 7; a difference which enjoins caution. However, *Bupleurum*, in its herbaceous species, does not show the characteristic habit of Umbelliferous herbs: is this because it has developed from a leptocaul, not pachycaul, stock? If attention is paid to habit, it is certainly incongruous to associate *Lichtensteinia* Cham. & Schlechtd. (with radical compound leaves and an annual flowering stem) with *Heteromorpha* and *Bupleurum*, as is done by Drude (1898: 176) and Wolff (1910). The affinity of *Lichtensteinia* needs to be re-examined: it may lie rather with *Annesorhiza* than with *Heteromorpha*.

Rodriguez (1957) made extensive studies of the wood-anatomy of Umbelliferae and allied families. He included *Heteromorpha* and *Steganotaenia* (but not *Polemannia*) in this work and concluded that on the characters studied (especially vessel-length and nature of perforation plates) *Heteromorpha* was the most primitive of the Umbelliferae examined, although it did show some specialized features (for example the whorled or helical tertiary thickenings of vessel walls).

The starting point of Rodriguez' work was the Central America genus *Myrrhidendron* Coulter & Rose, which he was able to study in the field. *M. donnell-smithii* Coulter & Rose grows as a small epiphytic or terrestrial tree up to 6m high with a trunk up to 7·5cm in diameter. In contrast to *Heteromorpha, Polemannia* and *Polemanniopsis, Myrrhidendron* has the large decompound leaves and strongly developed leaf sheath characteristic of the majority of herbaceous Umbelliferae. In fact the photographs published by Rodriquez (1957: 297, pl. 37, see also pp. 184–186, figs. 32–35) strongly suggest an herbaceous plant that has secondarily adopted an arborescent growth form: Rodriguez, however, says that there is no indication that the woody features of the plant are secondary. The fruit of *Myrrhidendron* has isomorphic mericarps with 5 small wings on each: a common pattern for herbaceous genera.

These varied observations all suggest that the woody African Umbelliferae have important roles to play in a reconsideration of the basic classification and evolution of the family. It is unfortunate that two international symposia, at Reading in 1970 (see Heywood, 1971) and at Perpignan in 1977 (see Cauwet-Marc & Carbonnier, 1978) have almost failed to recognize their existence. It is hoped that the establishment of *Polemanniopsis* will help to focus attention on them and will lead to more detailed and critical studies. The re-classification of Umbelliferae can scarcely be expected to make great headway when so much of the factual data necessary is unavailable.

**Polemanniopsis** B. L. Burtt **genus novum** adhuc in *Polemannia* Ecklon & Zeyher inclusum, sed foliolis nervo intramarginali carentibus, fructu valde 5-alato, mericarpiis heteromorphicis altero bialato altero trialato, seminibus ad commissuram sulcatis et in pericarpio liberis, endospermio minute ruminato longe recedit. *Polemanniopsis* fortasse *Heteromorphae* Cham. & Schlechtd. affinis, sed haec vittas valleculares et commissurales bene evolutas, semina a pericarpio haud libera et ad commissuram plana (nec sulcata), endospermium laeve (nec minute ruminatum), alas haud interne vacuas habet.

**Polemanniopsis marlothii** (H. Wolff) B. L. Burtt, **comb. nov.** Fig. 1A–E.
Type: W Cape Province, Clanwilliam, *Marloth* 2679 (B†; iso. PRE).
Syn.: *Polemannia (?) marlothii* H. Wolff in Bot. Jahrb. 57:228 (1921).
*Annesorhiza marlothii* (H. Wolff) Hiroe, Umbell. World 676 (1979)—non H. Wolff (1924).
[*Polemannia* sp. van Jaarsveld in Trees in S. Africa 32:79 (figs.), 83 (1980)].

Many-stemmed and much branched glabrous shrub up to 4m tall; flowering branchlets 1–2mm diam., lightly ribbed from leaf-bases, internodes c.2–3·5cm long, pith solid. *Leaves* glabrous, digitately 3–5-foliolate; leaflets up to 4 × 2cm, obovate, serrate especially in upper part, midvein raised below with 3–4 not very strong pinnately placed more or less alternating laterals on each side, veinlets reticulate; petiole up to 3cm long, expanded with thinner wings towards the base where it $\frac{3}{4}$ encircles the stem; on lower leaves up to a quarter the length of petiole is sheath, which may occasionally have slight auricles at top, on smaller upper leaves the petiole is almost wholly sheath. *Umbel* compound, usually solitary terminating a branch, sometimes with 2 or 3 just below it on short lateral branchlets, 7–8cm diam., c.12–15-rayed. *Involucre* apparently of a number of linear-lanceolate entire bracts c.8mm long, but already mostly fallen at flowering time. *Umbellules* on peduncles c.2·5cm long at flowering, lengthening to c.3cm in fruit; the occurrence of tertiary umbellules mixed with the individual flowers is not uncommon; flowers mixed hermaphrodite and male (i.e. plant andromonoecious). *Involucel* similar to involucre but bracts only c.4mm long, also withering early. *Pedicels* 4–7mm. *Sepals* deltoid, acute, 0·5mm long. *Petals* 2·5 × 1·25mm, ± ovate-acuminate, inrolled from just below the middle, the acuminate tip tucked in, free, light yellow. *Stamens* 5; filaments 1·5mm long; anthers 1 × 1mm, light yellow. *Disc* fleshy, c.2mm diam., slightly undulate on margin, dark coloured. *Male flower* with rudimentary styles barely 0·5mm long, and rudimentary ovary c.1mm long. *Female flower* with stylopodium and styles 1·5mm long, conical, style tapered to tip; ovary already 4mm long with wings 1mm wide at flowering, green. *Fruit* 12mm long, 5-winged, wings 3–4mm wide, cordate at top of fruit, slightly emarginate or truncate at base; mericarps heteromorphic, one 2-winged, the other 3-winged, wings associated with sepaline bundles, tawny yellow at maturity; carpophore slender. *Seed* with base 3–4mm above base of fruit and reaching to within 1·5mm of top, narrowly ellipsoid, acute at apex, narrowed to ± truncate base, 5 × 2mm, with well-developed groove on commissural face, lying loose within pericarp and easily removed from dry fruit; testa very shallowly rugose and green in the young fruit; endosperm minutely ruminate, white.

WESTERN CAPE. Clanwilliam div., 3128 BB, Pakhuis Pass, i 1976, *von Breitenbach* s.n. (K, NBG, PRE); *ibidem*, near Leipoldt's grave, 28 v 1976, *Moffett* 1104 (PRE); town commonage of Clanwilliam, along old Citrusdal-Clanwilliam road, 11 xi 1974, *von Breda* 4305 (K, PRE);

Warmhoek–Platberg, 5km S of Clanwilliam, c.350m, 5 i 1985 (flowers), *Taylor* 11232 (E, STE); Bushman Cave above Clanwilliam Dam before turnoff to Algeria, c.150m, 18 ii 1985 (fruit), *Taylor* 11269 (E, STE); Piekniekklippe, first TMS outcrop up Pakhuis Pass from Clanwilliam, c.500m, 8 ii 1985 (fruit), *Taylor* 11268 (E, STE); *ibidem*, 16 i 1987 (young fruit), *Taylor* 11729 (E, STE); *ibidem*, 13 x 1987 (leaves), *Taylor* 11817 (E, STE).

NORTHWESTERN CAPE. Richtersveld, 2817 AC, N foot of Rosyntjieberg, 650m, 30 viii 1977, *Thompson & le Roux* 192 (PRE); Bloubos, S side Ploegberg, ±30km S of Kubus, 2 xii 1975, *Moffett* 972 (K, PRE); 1km S of Kubus, *Jaarsveld & Drijhout* 5457 (PRE).

*Polemanniopsis marlothii*, as known at present, has a distinctly disjunct distribution, being found only in the Clanwilliam area and in the Richtersveld some 400km to the North. Taylor has emphasized that in the Clanwilliam area it is restricted to the Boulder Thicket community. In the Richtersveld, Moffett specified that it was found amongst pegmatite boulders; Thompson & le Roux record it in a steep dry rocky riverbed, while Jaarsveld & Drijhout mention a dry streambed in sandy soil. It is always recorded as a many-stemmed shrub between one and four metres high. It is deciduous in summer and the leaves have usually gone by the time the flowers are open. Taylor noted that these were being visited by numerous bees at mid-day.

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