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ONTOGENY OF THE FRUITS OF TWO ANOMALOUS AFRICAN WOODY GENERA, *POLEMANNIOPSIS* AND *STEGANOTAENIA* (*APIACEAE*), AND THEIR PHYLOGENETIC RELATIONSHIP

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The fruits of two anomalous African woody *Apiaceae*, *Polemanniopsis marlothii* and *Steganotaenia araliacea*, differ in structure when mature though the ovaries are very similar, both being heteromorphic in young flower stage. This unexpected heteromorphism in *S. araliacea* has important implications for future studies of basal genera and the interpretation of fruit characters in general. Both taxa also have unique 'intrajugal cavities' in the ovaries and fruits, which supports the idea that the two genera are closely related, sharing some characters with the *Hydrocotyloideae*[1] and *Saniculoideae*. This provides morphological and anatomical evidence to support the previous hypotheses on their relationship with *Saniculoideae*. Their basal position is also supported by characters shared with other basal genera previously included in *Hydrocotyloideae*, such as the lateral wings and slightly lignified endocarp in *Polemanniopsis* and *Steganotaenia*.

Keywords. Anatomy, fruit, ontogeny, *Polemanniopsis*, *Steganotaenia*, *Umbelliferae*.

INTRODUCTION

There are only a few woody members of the *Apiaceae*, mainly in Africa, but they are very important in the classification of the family because some of their features are unique (Burtt, 1991). Until recently, these genera have remained relatively poorly known, and the significance of their peculiar morphology has started to emerge only recently (Lowry *et al*., 2001; Oskolski, 2001). Downie & Katz-Downie (1999) and Plunkett (2001) suggested that *Polemanniopsis* B.L. Burtt and *Steganotaenia* Hochst. are sister taxa and that they are closely associated with the *Saniculoideae*. In view of the typical 'Apioid' inflorescences in the two genera, this possible relationship with the *Saniculoideae* is surprising.

Polemanniopsis marlothii (H. Wolff) B.L. Burtt and *Steganotaenia araliacea* Hochst. are two of several woody *Apiaceae* in southern Africa, the former being a shrub and the latter a small tree (Norman, 1934). Some special characters of their vegetative organs have been observed, e.g. both have leaves with dentate margins (Burtt, 1988; Van Wyk, 2001), and their flowers commonly appear before the leaves

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[1] Subfamily *Hydrocotyloideae sensu* Drude (1898) is now known to be paraphyletic (e.g. Plunkett, 2001) but is used here for convenience.

though they sometimes appear together (Townsend, 1989; Glen & Onderstall, 1991). *Polemanniopsis marlothii* has heteromorphic fruits without vittae: both are very rare characters in the *Apiaceae* as a whole, and the combination of the two is unique in the family. *Steganotaenia araliacea* fruits have a very narrow commissure that is different from other members of the *Peucedanineae*, the subtribe in which this species has hitherto been placed (e.g. Wolff, 1921; Pimenov & Leonov, 1993). Norman (1934) observed in *Steganotaenia*, and Burtt (1988) in both genera, that the fruit anatomy has peculiar features, such as the presence of cavities in the wings. However, their relationships to each other and to other members of the subfamily were not very clear because some important morphological and anatomical details of the fruits had not been studied. Burtt (1988) concluded that 'little can be said about the hollow fruit-wings of *Polemanniopsis* until a thorough developmental study has been done'. In a cladistic analysis, Van Wyk (2001) used the cavities in the fruit wings as a synapomorphy without questioning the homology of this character in the two genera.

In the present study the ontogeny, morphology and anatomy of the fruits of *Polemanniopsis marlothii* and *Steganotaenia araliacea* were examined and interesting new information found that provides a more solid basis for a close phylogenetic relationship between the two taxa and their possible relationship with the *Saniculoideae*.

Materials and methods

Two mature fruits of each species were examined (*P. marlothii*: *Jacobsen* 2230, PRE; *S. araliacea*: *Taylor* 11269, PRE), as was FAA preserved material of ovaries in young and mature flowers, and immature fruits (*P. marlothii*: *Van Jaarsveld* s.n., 17 xii 1995, JRAU; *S. araliacea*: *Tilney* s.n., 18 x 1994, JRAU). At least three samples of each stage were taken. The mature fruits were rehydrated and placed in FAA for a minimum of 24 hours. Material was embedded in glycol methacrylate (GMA) according to Feder & O'Brien (1968) though a minimum of 24 hours was used for the first two infiltrations in GMA and a minimum of five days for the third infiltration. The material was then placed in an oven at 60°C for 24 hours. Transverse sections, about 5μm thick, were cut through the middle of the fruits using a Porter-Blum ultramicrotome. The periodic acid-Schiff/toluidine blue staining method was used. Photographs were taken using a Leitz Wetzlar microscope and Ilford Pan F film. Drawings were made using a camera lucida.

Results and discussion

The mature fruits of *P. marlothii* (Fig. 2, P4) are obovate-cordate in dorsal view and measure 11–12 × 6–7mm. The mericarps are heteromorphic, one having three wings (one median and two marginal), lateral ribs not visible; and the other two lateral wings, median and marginal ribs not visible. Most *Apiaceae* have homomorphic

(identical) mericarps, with marginal ribs or wings extending from opposite the commissural vascular bundles. Mericarps with lateral wings only, extending from the two dorsal vascular bundles on either side of the median vascular bundle, as in the two-winged mericarp of *Polemanniopsis*, are very rare and found mainly in Drude's (1898) *Hydrocotyloideae*. Each wing has a cavity surrounded by broken cells whose function may be secretory. Here we refer to them as 'intrajugal cavities'; they are described below. The mesocarp is slightly lignified. A parenchymatous endocarp is present in the three-winged mericarp whereas it is slightly lignified in the two-winged mericarp. The seed of the three-winged mericarp has a narrow commissural groove and is much larger than that of the two-winged mericarp. The carpophore is free and divided.

The mature fruits of *S. araliacea* (Fig. 2, S4) are ovate or obovate in dorsal view and measure 13–14 × 7–8mm. The two mericarps are strongly compressed dorsally, homomorphic and have marginal wings. Median and lateral ribs are not very prominent. Intrajugal cavities appear not only in the wings but also in the median and lateral ribs. Some small vittae containing yellow oil are scattered in the mesocarp. The mesocarp is non-lignified and the endocarp slightly lignified in both mericarps. Both seeds are concave on the commissural side and equal in size. The commissure is narrow and the carpophore is free and divided.

The young ovary of *P. marlothii* (Fig. 1, P1; Fig. 2, P1) is heteromorphic with a distinct median rib and two marginal ribs on one carpel, and two distinct lateral ribs on the other. Intrajugal cavities appear in the ribs, and are surrounded by what appear to be secretory cells. The ribs become more prominent and the cavities elongate in mature flowers (Fig. 1, P2; Fig. 2, P2). They both develop further in the immature fruits where the ribs form prominent wings and the cavities are large and more rounded (Fig. 2, P3).

The young ovary of *S. araliacea* (Fig. 1, S1; Fig. 2, S1) is, contrary to expectation, also heteromorphic. It has a distinct median rib and two marginal ribs on one carpel and two distinct lateral ribs on the other. Prominent cavities are associated with the distinct ribs and less-developed cavities with the other ribs (Fig. 1, S1; Fig. 2, S1). The marginal ribs and all cavities become larger in mature flowers. At this stage, some small vittae appear in the mesocarp, visible close to the endocarp in Fig. 1, S2, in addition to the intrajugal cavities that were present much earlier. The vittae become more numerous in the immature fruit (Fig. 2, S3).

The presence of lateral wings only (as opposed to marginal wings or other wing configurations) is characteristic of some *Hydrocotyloideae* genera, such as *Gymnophyton* (Hook.f.) Gay and *Mulinum* Pers. (Tseng, 1967). Two other African genera, *Annesorhiza* Cham. & Schltdl. and *Heteromorpha* Cham. & Schltdl., also have heteromorphic mericarps but they differ from each other and also from those of *P. marlothii*. One mericarp of certain *Annesorhiza* species, e.g. *A. nuda* (Ait.) B.L. Burtt, has a median wing, two marginal wings and two partially developed lateral wings, while the other mericarp has two lateral wings, two marginal wings and one

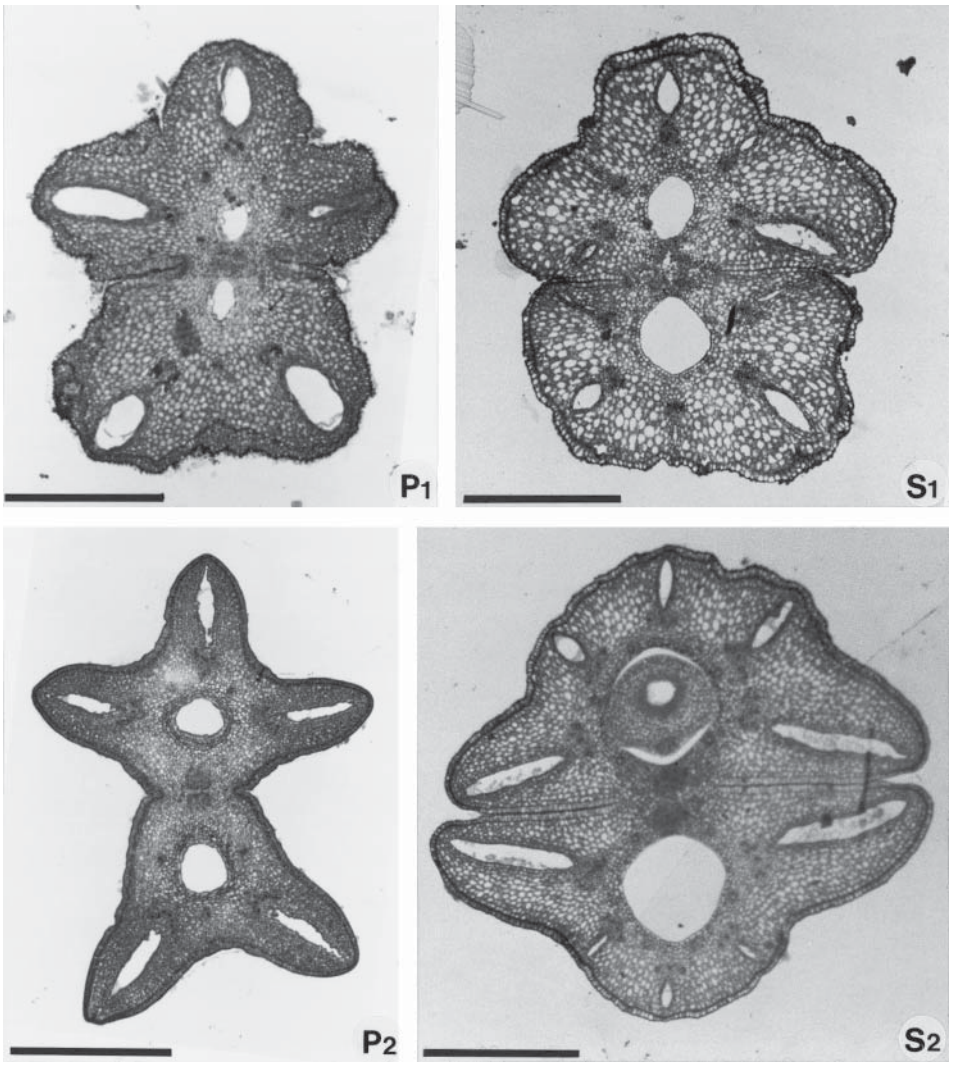

FIG. 1. Transverse section of ovaries of *Polemanniopsis marlothii* (P1 & P2) and *Steganotaenia araliacea* (S1 & S2). P1 & S1, young flower stage; P2 & S2, mature flower stage. Scale bar = 0.7mm.

partially developed median wing (Van Wyk & Tilney, 1994). In all *Heteromorpha* species, one mericarp has a median wing, two marginal wings and two partially developed lateral wings and the other has two lateral wings, one partially developed median wing and two partially developed marginal wings (Burtt, 1988). Lateral wings appear to be plesiomorphic for some *Hydrocotyloideae* genera and basal *Apioideae* with heteromorphic fruits (*Heteromorpha*, *Annesorhiza*). An important point, however, is that *Polemanniopsis* has no secondary ribs in the fruit as in other *Apioideae*; in this respect it is identical to *Hydrocotyloideae* genera.

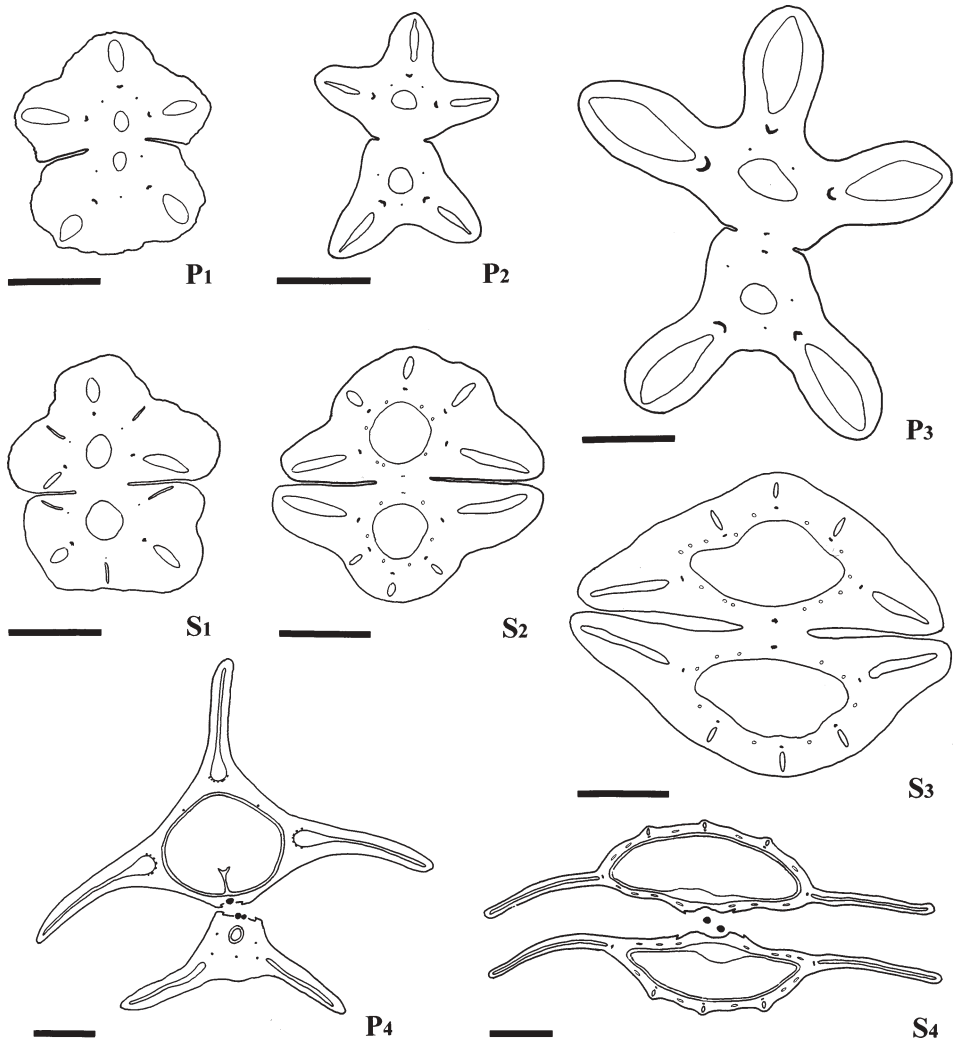

FIG. 2. Transverse section of ovary and fruit in *Polemanniopsis marlothii* (P1–P4) and *Steganotaenia araliacea* (S1–S4). P1 & S1, young flower stage; P2 & S2, mature flower stage; P3 & S3, immature fruit; P4 & S4, mature fruit. Scale bar = 0.7mm in P1–P3 & S1–S3; 1.5mm in P4 & S4.

Intrajugal cavities are present in the young flower stage of *P. marlothii* and *S. araliacea* towards the outside of the vascular bundles; these are surrounded by cells which appear similar to those of the secretory cells of the intrajugal vittae, but oil was not observed in them. These intrajugal cavities are characteristic of *P. marlothii* and *S. araliacea*. Cavities are known elsewhere in the family. *Bowlesia incana* Ruiz & Pav., for instance, has a large cavity under the median rib of the mericarp (Tseng, 1967) and *Myrrhis* Miller has cavities under all the ribs (Drude, 1898: 99, fig. 39). However, their structure and position are different from that in *P. marlothii* and

S. araliacea, and they are simply referred to as cavities or *vittae obsoletae* (e.g. Drude, 1898: 98) because they are clearly not homologous with the intrajugal cavities found in *Polemanniopsis* and *Steganotaenia*.

Some small vittae containing yellow oil are scattered in the mesocarp of *S. araliacea*. These look the same as those in the mesocarp of some species of the *Hydrocotyloideae* (such as *Dickinsia* Franch. and *Hermas* L.) and of the *Saniculoideae* (such as *Eryngium* L., *Hacquetia* Neck. ex DC. and *Sanicula* L.) but they are unlike the typical vallecular vittae found in most *Apioideae*.

The slightly lignified endocarp in the mature fruits of *S. araliacea* and *P. marlothii* (two-winged mericarp only) has not been reported before and also appears to support a basal position for the two genera. Lignified endocarps are highly characteristic for genera of the *Hydrocotyloideae*. Lignification occurs sporadically in the *Saniculoideae* and *Apioideae* but in these two groups it is the mesocarp and not the endocarp that is lignified.

Although the mature fruits of *P. marlothii* and *S. araliacea* are different, the young ovary of *S. araliacea*, surprisingly, shows a clear indication of heteromorphy (Fig. 1, S1; Fig. 2, S1). The early ontogeny of the ovary is similar to that of *P. marlothii* (Fig. 1, P1; Fig. 2, P1). Both have a distinct median rib, two marginal ribs on one carpel, and two distinct lateral ribs on the other. All the ovaries studied showed this structure. Our previous studies of *Apiaceae* fruits have consistently shown that ovaries have the same basic structure as mature fruits. It now appears that the early stage, before vittae are formed, may show presumably ancestral features that are lost before the flower matures. It would be interesting to make comparative studies, using ovaries dissected from very young flowers, at a stage before the vittae become evident. This may show the sequence of differential development of a homomorphic fruit from a heteromorphic ovary.

A summary of available evidence is given in Table 1. We can now more confidently interpret some of the morphological features described above as potential synapomorphies, not only between *P. marlothii* and *S. araliacea*, but also between them and the *Saniculoideae*. *Polemanniopsis marlothii* fruits have lateral wings similar to those in the *Hydrocotyloideae* and other basal groups (where the two wings are always opposite the lateral vascular bundles and not the marginal ones), and this character is here presumed to be a symplesiomorphy (Table 1). *Steganotaenia araliacea* has small vittae scattered in the mesocarp as in the *Hydrocotyloideae* and *Saniculoideae*. The lignification of the endocarp, the absence of secondary ribs and the dentate-aristate leaf margins (Van Wyk, 2001) all appear to support the phylogenetic hypothesis proposed by Downie & Katz-Downie (1999).

Conclusion

Although there are some differences between mature fruits in the woody African genera *Polemanniopsis* and *Steganotaenia*, with the mericarps of the former being

TABLE 1. Ovary and fruit characters in *Hydrocotyloideae*, *Polemanniopsis marlothii*, *Steganotaenia araliacea*, *Saniculoideae* and *Apioideae*

	Hydrocotyloideae	*Polemanniopsis marlothii*	*Steganotaenia araliacea*	*Saniculoideae*	*Apioideae*[a]
Young ovaries	Homomorphic	Heteromorphic	Heteromorphic	?	?
Mature ovaries	Homomorphic	Heteromorphic	Homomorphic	Homomorphic	Most homomorphic, a few heteromorphic[b]
Intrajugal cavities[1]	Absent	Present	Present	Absent	Absent
Scattered vittae[2]	Present in *Hermas* and *Dickinsia*	Absent	Present	Present in some genera[c]	Absent in most except e.g. *Bupleurum*
Endocarp lignification	Strongly lignified	Slightly lignified	Slightly lignified	Not lignified	Not lignified
Lateral wings[3]	Present in some genera[d]	Present	Absent	Absent	Present in some genera[e]
Secondary ribs	Absent	Absent	Present	Present	Present
Dentate-aristate leaf margins[4]	Absent?	Present	Present	Present	Absent

[a]Excluding *Polemanniopsis* and *Steganotaenia*.
[b]*Annesorhiza*, *Heptaptera* and *Heteromorpha*.
[c]*Eryngium*, *Hacquetia* and *Sanicula*.
[d]*Asteriscium*, *Gymnophyton*, *Hermas* and *Mulinum*.
[e]*Annesorhiza*, *Dasispermum*, *Heptaptera* and *Heteromorpha*.
[1]Present in intrajugal position, presumably homologous with intrajugal vittae.
[2]Small vittae present in mesocarp close to endocarp with no fixed position in relation to wings or furrows.
[3]Prominent ribs or wings developing above lateral vascular bundles of mericarp and not above marginal or dorsal vascular bundles of same mericarp.
[4]Prominently toothed, with slender tip.

heteromorphic and lacking vittae while those of the latter are homomorphic and possess vittae, the early developmental stage is heteromorphic in both taxa. Both have one carpel with a prominent median rib and two prominent marginal ribs and the other with two prominent lateral ribs. They also both have intrajugal cavities. It is therefore likely that these two genera were derived from a common ancestor with heteromorphic fruits and intrajugal cavities. They also share some characters with the *Hydrocotyloideae* and *Saniculoideae*. For example, *P. marlothii* has prominent lateral ribs, as present in certain *Hydrocotyloideae*, and *S. araliacea* has small vittae scattered in the mesocarp, as can be seen in some taxa of both subfamilies.

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An invited contribution to the Festschrift for B.L. Burtt's ninetieth birthday