The morphology and development of the fruit of *Heteromorpha* (Apiaceae)

P.J.D. Winter, B.-E. van Wyk* and Patricia M. Tilney

Department of Botany, Rand Afrikaans University, P.O. Box 524, Auckland Park 2006, Johannesburg, Republic of South Africa

Received 26 January 1993; revised 2 March 1993

Fruits of the Apiaceae are generally bilaterally symmetric (disymmetric), i.e., the two mericarps are identical, so that they are symmetrical at the commissural plane. Some genera, however, have zygomorphic (monosymmetric) fruits, where the single plane of symmetry is perpendicular to the commissural plane. In the nine *Heteromorpha* species from the African mainland, the zygomorphy results from the expansion of all five sepaline ribs to form wing-like structures (the five petaline ribs never develop to the same extent). This peculiar wing symmetry is already evident at the flowering stage. The eight *Heteromorpha* species from Madagascar have disymmetric fruits and their inclusion within the genus is questionable. We suggest that the *Heteromorpha*-type wing configuration is an apomorphic condition which supports the monophyly of the mainland species.

Vrugte van die Apiaceae is oor die algemeen bilateraal simmetries (disimmetries), d.w.s., die twee vrughelftes is identies, sodat hulle simmetries is ten opsigte van die kommissurale vlak. Sommige genera het egter sigomorfe (monosimmetriese) vrugte, waar die enkele simmetrievlak loodreg op die kommissurale vlak is. In die nege *Heteromorpha* spesies van die Afrika-vasteland ontstaan die sigomorfie deurdat al vyf kelkriwwe vergroot om vlerkagtige strukture te vorm (die vyf kroonriwwe ontwikkel nooit tot dieselfde mate nie). Hierdie eienaardige vlerksimmetrie is reeds in die blomstadium vasgelê. Die agt *Heteromorpha* spesies van Madagaskar het disimmetriese vrugte en hulle insluiting in die genus kan bevraagteken word. Ons stel voor dat die *Heteromorpha*-tipe vlerkontwikkeling 'n apomorfe toestand is wat die monofilie van die vasteland-spesies ondersteun.

Keywords: Africa, Apiaceae, fruit symmetry, fruit wing configuration, *Heteromorpha*, Madagascar.

* To whom correspondence should be addressed.

Introduction

Fruits of the African mainland species of *Heteromorpha* Cham. & Schlechtd. display a rare wing configuration on which the generic name is based, having two wings on one mericarp and three on the other. This configuration seems to occur only in one other genus in Apiaceae, namely *Polemanniopsis* B.L. Burtt (Burtt 1988). Species with winged fruit of both genera are restricted to the African mainland, while eight species without winged fruit, geographically isolated in Madagascar, were included in *Heteromorpha* by Humbert (1955, 1956). Humbert (1956) thus broadened the generic concept to include non-winged fruit. The reason for the inclusion of the Madagascar species is not clear, but it involves similarity in fruit histology, namely the presence of calcium oxalate druses in the pericarp, a character studied by Drude in his classification (Burtt 1991).

Fruit-morphological characters have traditionally been used in tribal and generic delimitation in the Apiaceae, but in the interpretation of the symmetry, the relation to floral structure has usually been neglected. The occurrence of unequally winged mericarps has prompted the investigation of flower structure [and now raises the question of the respective roles of the receptacle and the perianth (hypanthium) in the development of the inferior ovary in different genera of Apiaceae]. In flowers of Apiaceae, there is a structural conflict due to the superimposition of a pentamerous perianth on an inferior, bicarpellate ovary (Burtt 1988). Ten perianth parts are divided equally between the two halves of the ovary which are later to become the mericarps, but since they comprise five sepals and five petals, the allocation of sepals and petals to each half is inevitably unequal.

The wing configuration of fruits of *Heteromorpha* was discussed as early as 1841 by Alexander Braun (Braun 1841), and recently by Burtt (1988) in relation to floral structure. This does not seem to have been integrated with the interpretation of wing configuration patterns in the family. Fruit development in the Peucedanieae has been studied by Theobald (1971), but this was not related to flower structure. This paper addresses the development of the heteromorphic fruit wing symmetry (hereinafter referred to as the *Heteromorpha*-type) and evaluates this character as important at the generic or even tribal level, specifically in comparing the species from Madagascar to the rest of the genus.

Materials and Methods

Flowers, young fruit and mature fruit were sampled from material preserved in FAA or from herbarium specimens. All 17 species of *Heteromorpha* were included in the sample. A complete list of voucher specimens is given in Table 1. Dried samples were rehydrated and embedded in glycol methacrylate (GMA) according to a modification (Tilney 1986) of the method of Feder and O'Brien (1968)

Table 1 List of *Heteromorpha* specimens examined

Species	Collector and number	Flowers	Young fruit	Mature fruit	FAA material
Africa species					
H. arborescens (Spreng.) Cham. & Schlechtd.	*Van Wyk 3313* (JRAU)	+			+
	Vlok 2633 (JRAU)			+	
H. gossweileri (Norman) Norman	*Quarré 5919* (PRE)	+	+		
H. involucrata Conrath					
typical form	*Winter 61* (JRAU)	+	+	+	+
'*kassneri*' form	*Brummit 9316* (PRE)	+			
	La Croix 3770 (PRE)		+		
'*stolzii*' form	*Jacobsen 2891* (PRE)	+			
	Torre & Paiva 11897 (PRE)		+		
	Stolz 24699 (PRE)			+	
H. papillosa C.C. Townsend	*Merxmüller & Giess 28004* (WIN)	+			
	Seydel 3948 (WIN)		+		
	Kers 149 (WIN)			+	
H. pubescens Burtt Davy	*Winter 66* (JRAU)	+	+	+	+
H. stenophylla Welw. ex Schinz	*Giess 15120* (WIN)	+			
	Giess 15169 (WIN)		+		
	De Winter 2914 (WIN)			+	
H. transvaalensis Schltr. & Wolff	*Winter 50* (JRAU)			+	+
	Winter 54 (JRAU)	+	+		+
H. trifoliata (Wendl.) Eckl. & Zeyh.	*Winter 56* (JRAU)	+			+
	Winter 71b (JRAU)		+	+	+
H. sp. nov.	*Winter 51* (JRAU)	+	+		+
	Winter 57a (JRAU)			+	
Madagascar species					
H. andohahelensis H. Humbert var. *andohahelensis*	*Humbert 13654* (P)	+			
	Humbert 6192 (P)		+		
H. andringitrensis H. Humbert	*Perrier de la Bathie 14430* (P)	+	+		
	Perrier de la Bathie 6809 (P)			+	
H. betsileensis H. Humbert	*Rarivo 11038* (P)	+			
	Perrier de la Bathie 6813 (P)		+	+	
H. bojeriana (Baker) H. Humbert	*Bojer s.n.* (P)	+			
	Baron 5185 (P)		+	+	
H. coursii H. Humbert	*Cours & Humbert 24702* (P)	+	+	+	
H. laxiflora (Baker) H. Humbert var. *laxiflora*	*Keraudren 266* (P)	+	+		
	Humbert & Capuron 25427 (P)			+	
H. marojejyensis H. Humbert	*Humbert 22710* (P)	+	+	+	
H. tsaratananensis H. Humbert	*Perrier de la Bathie 16411* (P)	+			
	Perrier de la Bathie 6806 (P)		+		
	Humbert 18374 (P)			+	

for sectioning on a Porter Blum MT-1 ultramicrotome. Mounted sections were stained according to the so-called Periodic Acid – Schiff / Toluidine Blue (PAS/TB) staining method and photographed using a Leitz Wetzlar compound light microscope with a 35-mm camera attachment using Ilford PAN F (ASA 50) film.

Results and Discussion

Basic morphology

In the fruits of all Apiaceae, ribs are generally associated with each vascular bundle supplying a perianth part (Burtt 1988). These ribs (Figure 1) can develop to varying degrees in the mature mericarp. The resultant pattern is thus one mericarp with three sepaline ribs and two petaline ribs, and the other with two sepaline ribs and three petaline ribs (Figure 2). These are collectively termed primary ribs.

We thus have a different (structurally based) terminology in addition to the traditional (positional) terms dorsal (or median), lateral (or marginal, commissural) and intermediate (or lateral) which were adequate to describe the disymmetric general type. These terms can be used in combination to describe more precisely the patterns in the family as a whole. Braun's (1841) structural terms based on his inter-

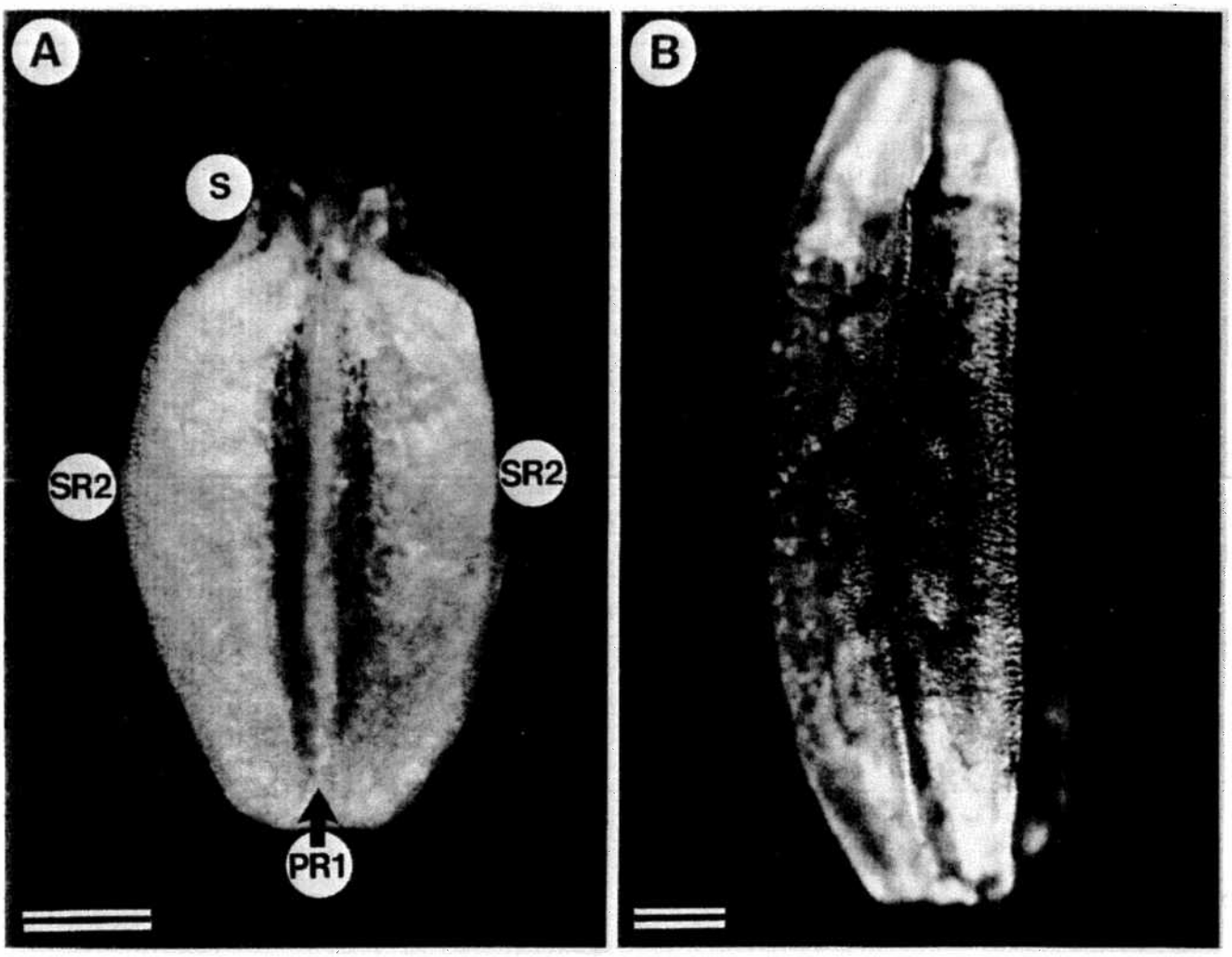

Figure 1 Fruit morphology of the African and Madagascar species of *Heteromorpha*. A. Dorsal view of mericarp of *H. involucrata* (Africa), showing sepals (S), prominently winged sepaline ribs (SR2) and unwinged petaline rib (PR1). B. Dorsal view of mericarp of *H. andringitrensis* (Madagascar), showing indistinct ribs with no expansion into wings. Scale bars: 1 mm.

pretation of the calyx (see below) can be compared to those proposed here.

In all the African mainland species of *Heteromorpha*, the fruit is zygomorphic (monosymmetric), i.e., the two mericarps are unequally winged and the single plane of symmetry is perpendicular to the commissural plane (Figure 2). The zygomorphy results from the expansion of all five sepaline ribs (Figures 1, 2A, 2B) to form wing-like structures. The five petaline ribs (Figures 1, 2A, 2B) never develop to the same extent. Corresponding positions (dorsal, intermediate and lateral/marginal) on opposing mericarps (Figure 2B) are thus differently occupied by wings or ribs in each mericarp. This results in an apparent irregularity which is in fact due to a highly regular wing development, as observed by Braun (1841). The orientation of the sepaline ribs (particularly the lateral two) adds to the zygomorphic appearance of the fruits (Figures 2A, 2B, 3A–C), although it is probably quite a natural configuration when the individual mericarps are considered, the angle between wings not departing much from the expected 120° (Figure 2B).

Continuing from the description of *Annesorhiza* in de Candolle's Prodromus, Braun (1841) interpreted the pattern in *Heteromorpha* (which he mistook for *Annesorhiza*) in terms of the appendicular theory of the nature of the inferior ovary. According to this theory, which was popular prior to the latter half of the nineteenth century (Eames 1961), only lateral appendages are involved in ovary wall formation, and not the receptacle. Braun (1841) regarded the external part of the ovary as a calyx tube — 'Kelchröhre' — comprising five 'carinal' ridges representing the dorsal midribs of the sepals, alternating with five 'commissural' ridges representing the adnate margins of adjacent sepals. Wolff (1910) used the terms carinal and sutural. This interpretation implies that the stamens and petals are in turn adnate to the calyx, so that the term 'hypanthium' is perhaps more appropriate than 'calyx tube'.

It may be noted that the only other genera with unequally winged (heteromorphic) mericarps in Apiaceae, *Annesorhiza* Cham. & Schlechtd. and *Heptaptera* Margot & Reuter, never exhibit the strict sepal–wing correlation and always retain the two pairs of marginal (commissural) wings (Burtt 1991). The pair on the one mericarp would be sepaline and that on the other petaline, according to the *Heteromorpha*-type interpretation. It seems more plausible that there are

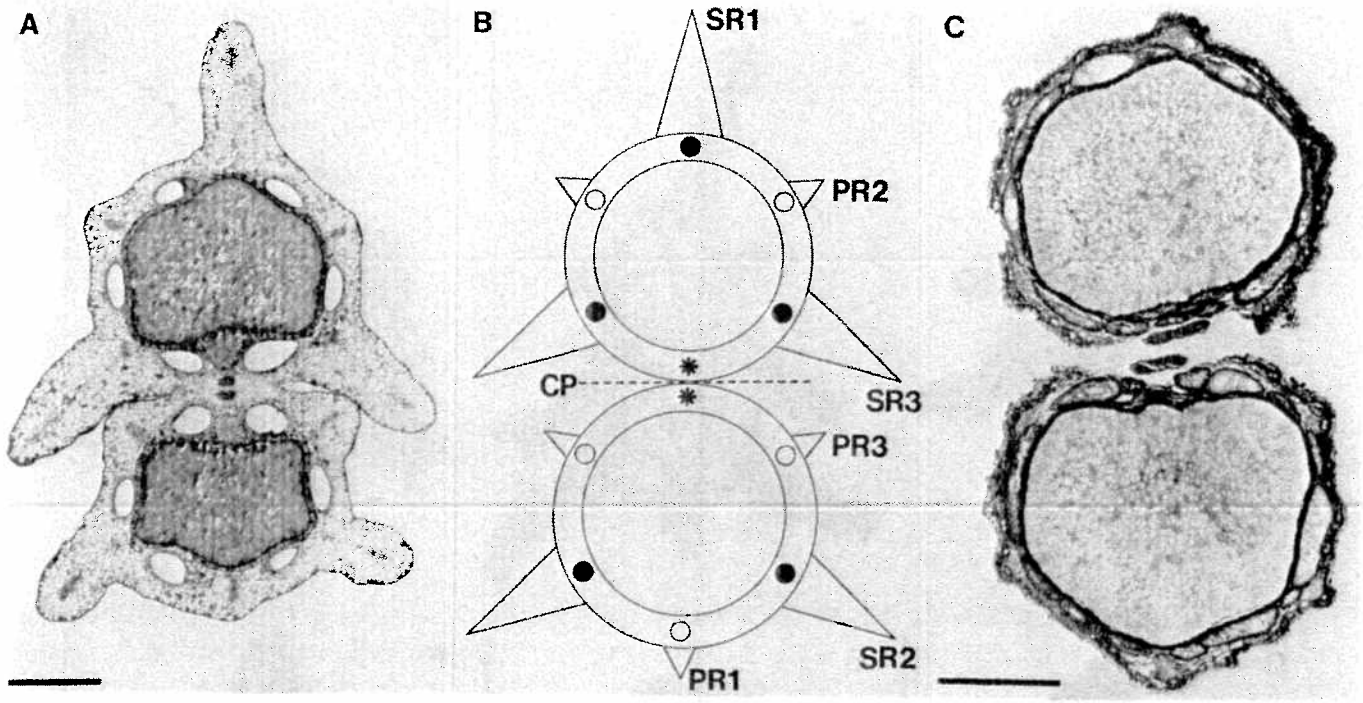

Figure 2 Fruit symmetry in the African and Madagascar species of *Heteromorpha*. A. Cremocarp (transverse section) of *H. involucrata* (Africa) showing single plane of symmetry, perpendicular to the commissural plane. B. Diagram showing ideal geometry with 120° wing angle per mericarp, and three sets of vascular bundles (○, petaline; ●, sepaline; ✱, carpophore) with their corresponding appendages (CP, commissural plane). Note the relation of sepaline ribs (SR) and petaline ribs (PR) to the dorsal (1), intermediate (2) and lateral (marginal) (3) positions normally used to describe disymmetric fruit. C. Cremocarp (transverse section) of *H. laxiflora* (Madagascar), showing no differentiation between petaline ribs and sepaline ribs. Scale bars: 0.5 mm.

two positional regulatory factors involved in these cases, the second being dependent on situation relative to the commissure irrespective of floral structure, as in *Peucedanum* (Theobald 1971). Burtt (1988) discussed this paradox and suggested detailed developmental studies. He noted that the apparent inconsistency in these genera was possibly the reason for underestimating the taxonomic value of wing configuration in the past.

The inclusion of several Madagascar species in *Heteromorpha* by Humbert (1955, 1956) is a good example of such disregard for this character. In all the Madagascar species, the fruit is bilaterally symmetric (disymmetric), i.e., the two mericarps are identical, so that they are symmetrical at the commissural plane as well (Figures 2C, 3D–F). The sepaline and petaline ribs may expand slightly, but they are invariably all similar in size and never form prominent wings (Figures 1B, 2C, 4F). The enormous vittae in the mature fruit (Figure 4F) are also characteristic of most of the Madagascar species (the African species have much smaller vittae).

Ontogeny

The developmental sequences from flower to fruit are shown in Figures 4A–C and 4D–F. In addition to symmetry, the *Heteromorpha*-type and *Peucedanum*-type of wing configuration also differ in their ontogeny. The peculiar wing symmetry of the African mainland species of *Heteromorpha* is already evident at the flowering stage (Figures 3C, 4A) and does not result from an early ontogenetic development. Fruits of *Heteromorpha* species thus have a congenital wing configuration, whereas the fruits of *Peucedanum* species exhibit an ontogenetic extension of the commissural margin, occurring relatively late during fruit expansion (Theobold 1971). The terms 'congenital' vs. 'ontogenetic' are here used as in Eames (1961). In fruits of *Heteromorpha* species there is a specific differential expansion of the prominent sepaline ribs (Figure 4C), which occurs only during the last stage of ripening. This final burst of growth is, however, phenotypically variable. It would be interesting to determine whether the wings occupying different positions in *Annesorhiza* and *Heptaptera* are formed at different stages of fruit set.

The fruits of all the Madagascar species of *Heteromorpha*, by contrast, are disymmetric at the flowering stage (Figures 3D, 3F) and remain so throughout their development (Figures 3E, 4E, 4F). The petaline and sepaline ribs are similar in size, shape and orientation, resulting in two identical mericarps.

Conclusions

Two fundamental wing extension types are identified in Apiaceae. These are the commissural ontogenetic type as in *Peucedanum*, and the sepaline congenital type as in *Heteromorpha* and *Polemanniopsis*.

The zygomorphy of the ovary and fruit is a useful diagnostic character for the African species of *Heteromorpha*.

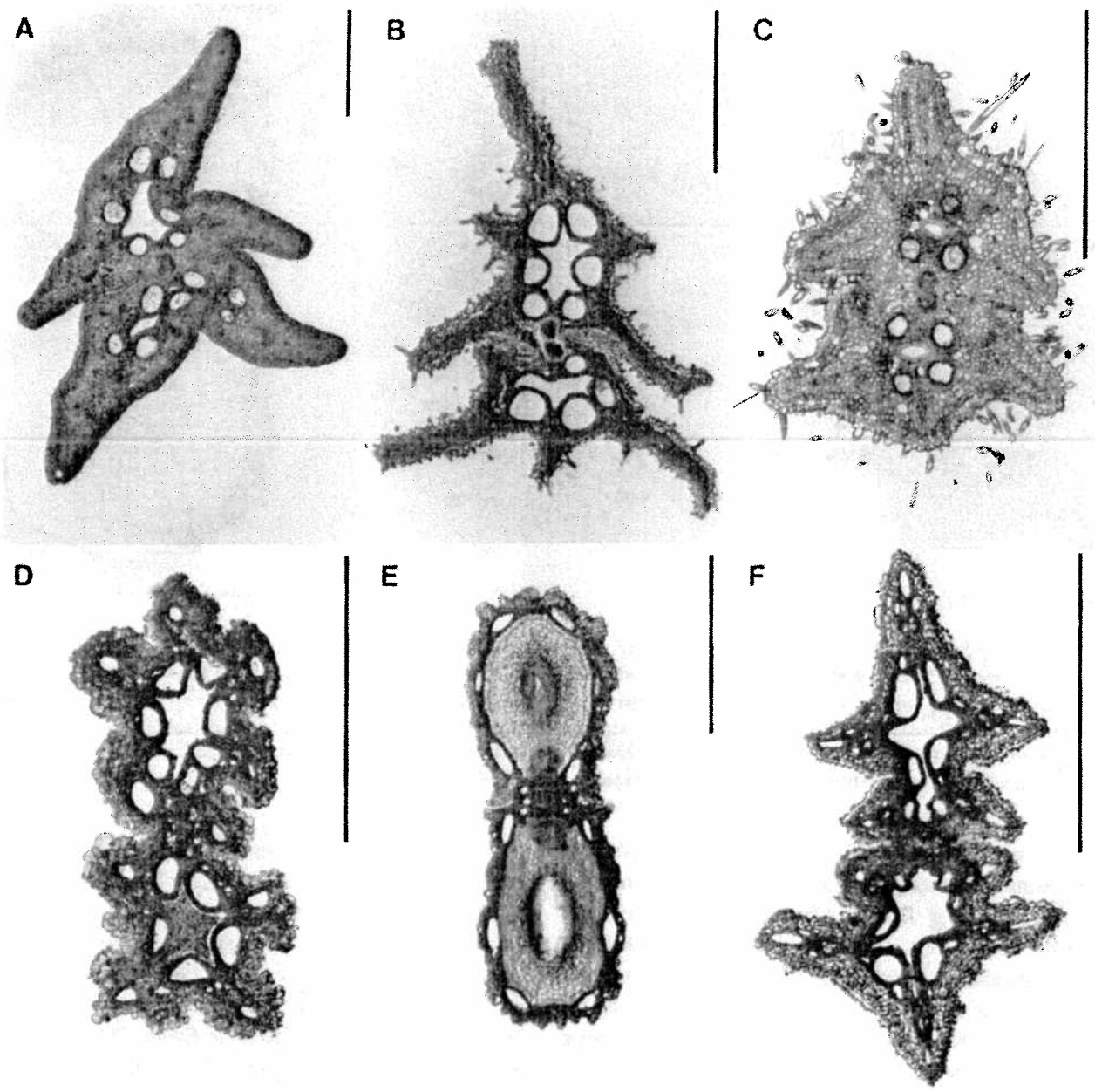

Figure 3 Young fruit of three African (A – C) and three Madagascar (D – F) species of *Heteromorpha*, showing the distinct differences in symmetry and wing configuration. A. *H.* sp. nov. (transverse section of young fruit). B. *H. papillosa* (transverse section of young fruit). C. *H. pubescens* (transverse section of ovary). D. *H. bojeriana* (transverse section of ovary). E. *H. laxiflora* (transverse section of young fruit). F. *H. coursii* (transverse section of ovary). Scale bars: 0.5 mm.

This type of wing development is unrelated to the *Peucedanum*-type of wing extension and appears to be an apomorphic condition which supports the monophyly of the mainland species.

The geographically isolated Madagascar species all have disymmetric fruits and their inclusion within the genus *Heteromorpha* is questionable. There are no convincing synapomorphies for the Madagascar group so that their generic delimitation and even their tribal placement within the woody Apiaceae should be investigated.

Acknowledgements

Financial support from the Foundation for Research Development is gratefully acknowledged.

References

BRAUN, A. 1841. Flora XXIV, 1: 337 – 340 (*Bot. Z.*) Table 2, Fig. B.

BURTT, B.L. 1988. A new shrubby genus of African Umbelliferae. *Notes RBG Edinb.* 45: 493 – 501.

BURTT, B.L. 1991. Umbelliferae of southern Africa: an introduction and annotated checklist. *Edinb. J. Bot.* 48: 133 – 282.

EAMES, A.J. 1961. Morphology of the Angiosperms, pp. 248 – 252. McGraw-Hill, New York.

FEDER, N. & O'BRIEN, T.P. 1968. Plant microtechnique: some principles and new methods. *Am. J. Bot.* 55: 123 – 142.

HUMBERT, H. 1955. Une Merveille de la Nature a Madagascar. Premiere Exploration Botanique du Massif du Marojejy et de ses satellites. *Mém. Inst. Sci. madag.*, Sér. 3,6: 1 – 210.

HUMBERT, H. 1956. Contributions à l'étude de la Flore de Madagascar et des Comores. Fascicle 5. *Not. Syst., Paris* 15:

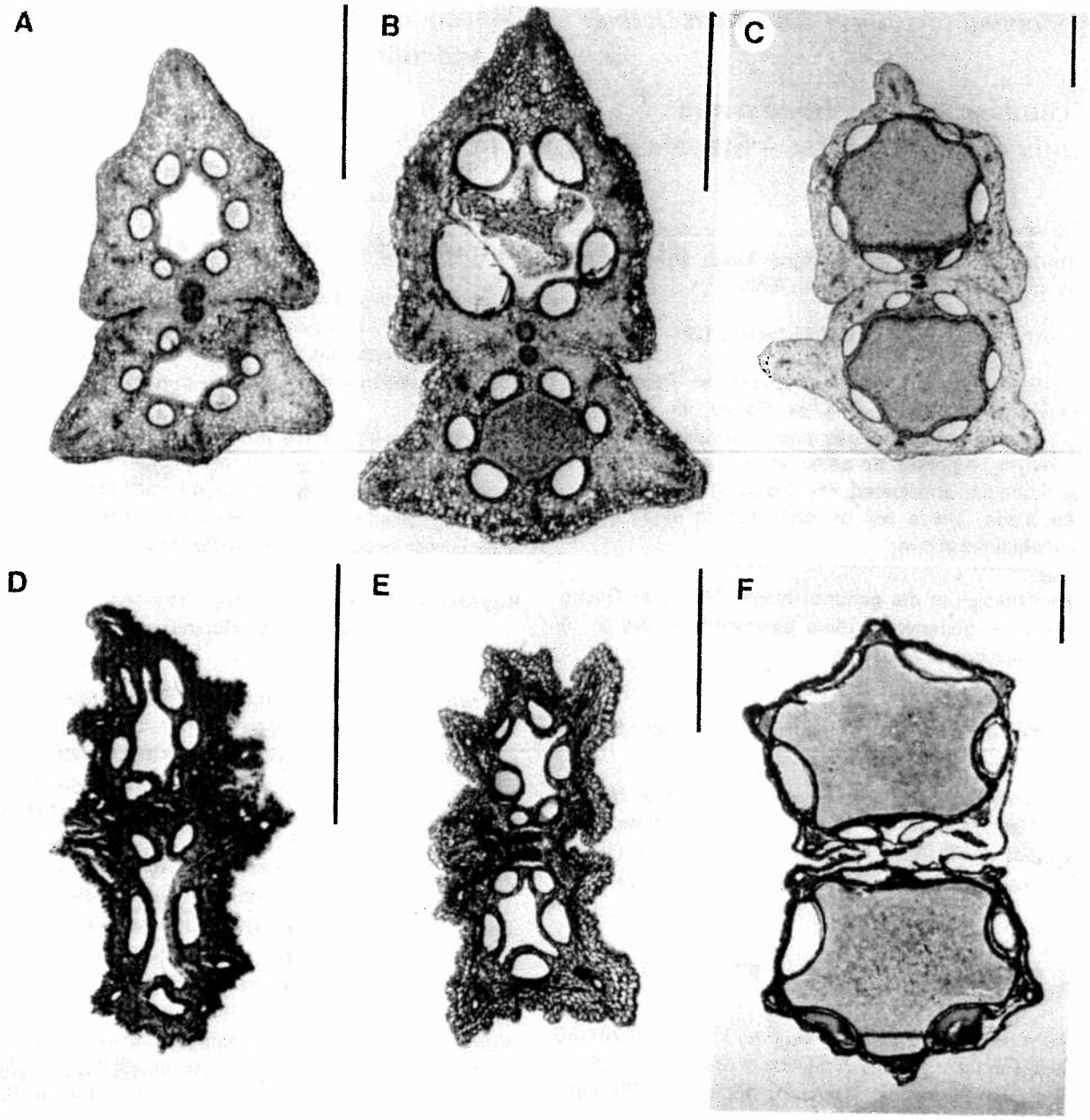

Figure 4 Fruit development in two species of *Heteromorpha* to show the difference in symmetry and wing configuration between the African and Madagascar species (all transverse sections). A. Ovary, B. young fruit, and C. mature fruit of *H. arborescens* (Africa). D. Ovary, E. young fruit, and F. mature fruit of *H. tsaratananensis* (Madagascar). Scale bars: 0.5 mm.

113 – 134.

THEOBALD, W.L. 1971. Comparative anatomical and developmental studies in the Umbelliferae. In: The biology and chemistry of the Umbelliferae, ed. V.H. Heywood, pp. 177 – 197 (Suppl. 1 to *Bot. J. Linn. Soc.* 64).

TILNEY, P.M. 1986. The taxonomic significance of anatomical and morphological characters in the southern African species of *Canthium* Lam. (Rubiaceae). Ph.D (Botany) thesis, University of Pretoria, Pretoria.

WOLFF, H. 1910. Umbelliferae–Apioideae–*Bupleurum, Trinia* et reliquae Amminiae heteroclitae. In: Das Pflanzenreich, ed. A. Engler, Heft 61. Engelmann, Leipzig.