

THE TAXONOMIC VALUE OF FRUIT WING TYPES IN THE ORDER APIALES¹

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This study shows that structural data, when carefully examined, can provide valuable characters for delimiting monophyletic groups and can complement DNA with observable features to recognize and circumscribe taxa. In the angiosperm order Apiales, traditional classification has relied heavily (often exclusively) on fruit characters. Recent molecular systematic studies, however, provided a radically different picture of relationships, calling into question the utility of fruit characters. We have studied fruit anatomy from 18 genera (*Annesorhiza*, *Asteriscium*, *Astrotricha*, *Choritaenia*, *Dasispermum*, *Elaeoselinum*, *Heptaptera*, *Hermas*, *Heteromorpha*, *Laretia*, *Molopospermum*, *Myodocarpus*, *Pachypleurum*, *Peucedanum*, *Polemanniopsis*, *Polylophium*, *Rouya*, and *Tordylium*) that represent all major taxonomic groups of Apiales characterized by winged fruits and the full range of wing types. Fruit anatomy closely corresponded with the phylogenetic position of these genera, as suggested by molecular studies. Fruit features of taxonomic importance include developmental origin of the wings, carpel shape, presence of vittae, woodiness of the endocarp, position of crystals, and type of carpophores. Despite the long history of recognizing umbellifers as a “natural group,” few studies have been able to provide structural characters to help circumscribe the clades identified by molecular data. The interpretations presented are an important step toward erecting a stable system of classification for this difficult family.

Key words: Apiaceae; Apiales; Araliaceae; classification; fruit anatomy; phylogeny; wings.

The union of Apiaceae and Araliaceae under the angiosperm order Apiales has its antecedents in taxonomic treatments dating back well over a century, but relationships within the order have vexed botanists for just as long. After major advancements in the 1960s and 1970s (e.g., Philipson, 1970; Eyde and Tseng, 1971; Heywood, 1971; Cauwet-Marc and Carbonnier, 1982), progress in deciphering phylogenetic relationships in Apiales subsided for several decades. Over the past few years, however, there has been a renewed surge in research focusing on relationships at all taxonomic levels in the order, from species circumscriptions to interfamilial relationships. In the most recent classification (Plunkett et al., 2004), Apiales were recircumscribed to include not only Apiaceae and Araliaceae, but also Myodocarpaceae (a segregate family of two genera formerly included in Araliaceae), Pittosporaceae, Torricelliaceae, Griselinaceae, and Pennantiaceae. This classification results from the advances of many recent studies, nearly all of which are based on molecular data (e.g., Plunkett et al., 1996a, b, 1997; Downie and Katz-Downie, 1999; Downie et al., 2001; Plunkett, 2001; Plunkett and Lowry, 2001; Valiejo-Roman et al., 2002; Lowry et al., 2004a; Plunkett et al., 2004). This reliance on DNA-based characters is due largely to the many difficulties, perceived and real, of using morphological

features in an order where parallelism and convergence have frustrated so many past generations of botanists. Despite these challenges, however, a few recent studies have made important contributions to the study of micromorphological and anatomical characters, particularly wood anatomy (e.g., Oskolski et al., 1997; Oskolski and Lowry, 2000, 2001; Oskolski, 2001) and fruit anatomy (e.g., Spalik et al., 2001; Liu et al., 2003a, b; Liu, 2004).

Traditional classification systems of the major apiacean families (e.g., Drude 1897–1898 for Apiaceae; Harms, 1894–1897 for Araliaceae) have relied heavily (and sometimes exclusively) on selected fruit characters such as carpel number (especially in Araliaceae), the direction and extent of carpel compression, and the development of wings (particularly in Apiaceae). However, these traditional systems have not compared favorably to the results of recent phylogenetic studies. Given these discrepancies, it is tempting to abandon morphology and focus exclusively on DNA (e.g., Downie et al., 2001). Before doing so, it should be noted that very few studies have attempted to follow up on the careful work by V. H. Heywood and his co-workers (e.g., Heywood and Dakshini, 1971; Saenz de Rivas et al., 1982), who showed that superficial studies of fruit morphology of the umbellifer tribe Caucalideae were fraught with problems, but demonstrated that careful anatomical studies could yield an abundance of new characters, many of which were strongly correlated to other micromorphological features, such as cytology, palynology, and phytodermology (see Saenz de Rivas et al., 1982).

In this study, we reconsider the taxonomic value of traditionally used fruit characters when carefully examined and evaluated in a phylogenetic context. Specifically, we have collected and analyzed data from a particular set of fruit characters, namely those associated with “winged” fruits, and we have evaluated their use in understanding relationships

¹ Manuscript received 20 September 2006; revision accepted 28 June 2006.

The authors thank the institutions listed and the following colleagues for providing important fruit samples: J.-P. Reduron, T. A. Ostroumova, A.-L. Anderberg, and G. T. Chandler. Support was provided to G.M.P. and P.P.L. by grants from the U.S. National Science Foundation (DEB-9981641) and the National Geographic Society (5793–96).

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within Apiales. Winged fruits involve a complex set of characters, generally restricted to bicarpellate taxa, usually including compression of the carpels (dorsally or laterally) and/or the elaboration of ribs into thin wing-like projections. No fewer than 80 apiaceous genera are characterized by winged fruits (see Theobald, 1971; Pimenov, 1980; Liu, 2004), including a number of well-known taxa such as *Anethum* L., *Angelica* L., *Cymopterus* Raf., *Ferula* L., *Heracleum* L., *Ligusticum* L., *Lomatium* Raf., *Pastinaca* L., and *Thapsia* L. Several additional genera with winged fruits can also be found among the other families of Apiales, listed in Table 1. *Astrotricha* DC. and *Myodocarpus* Brongn. & Gris., two woody genera with winged fruits, have traditionally been placed in Araliaceae (e.g., Willis, 1973). The Australian endemic *Astrotricha* has simple leaves (Gardner, 1952), a feature considered ancestral in Apiales (Plunkett et al., 1996a; Plunkett, 2001; Chandler and Plunkett, 2004). In molecular studies, this genus is placed among the earliest diverging lineages of Araliaceae, often as sister to the remaining members of that family (e.g., Plunkett, 2001). *Myodocarpus* is endemic to New Caledonia, and two of its 10 species also have simple leaves (Lowry, 1986b). Baumann (1946) regarded *Myodocarpus* as anomalous because it had a mixture of vegetative features typically found in Araliaceae combined with carpological characters usually restricted to Apiaceae. Lowry (1986a, b) examined selected fruit structures, such as the specialized oil vesicles in the endocarp, but did not attempt a comprehensive analysis. Oskolski et al. (1997, 2001), examining wood anatomy, observed that the stem structures of *Myodocarpus* and its close relatives (i.e., *Delarbrea* Vieill., into which the monotypic genus *Pseudosciadium* Baill. was recently transferred; see Lowry et al., 2004b) were sharply distinguished from all other Araliaceae. Concurrently, a series of molecular studies (Plunkett et al., 1996a, 1997; Plunkett, 2001; Plunkett and Lowry, 2001) showed that these genera should be removed from Araliaceae and placed in a new family, Myodocarpaceae, which represents one of the basally branching lineages within Apiales (see Plunkett et al., 2004).

In Apiaceae, Pimenov and Leonov (1993) recently placed *Asteriscium* Cham. & Schltdl. and *Laretia* Gillies & Hook. (two South American genera), along with *Hermas* L. and

Choritaenia Benth. (both from Africa), in Drude's subfamily Hydrocotyloideae Link, tribe Mulineae DC., subtribe Asteriscinae Drude, a group characterized by four-winged fruits (Drude, 1897–1898). With the discovery that Hydrocotyloideae are polyphyletic (its former members belong to no fewer than three distinct apialean groups), these four genera may now be placed in Apiaceae subfamily Azorelloideae Plunkett & Lowry (see Plunkett et al., 2004). They share many features, although the first three genera usually have simple and entire leaves, whereas *Choritaenia* has irregularly subternately dissected leaves (Drude, 1897–1898; Van Wyk, 2000). Some fruit characters of *Asteriscium*, *Hermas*, and *Laretia* were investigated by Mathias and Constance (1962) and Tseng (1967), but the fruit anatomy of *Choritaenia* remains unknown.

Polemanniopsis B. L. Burt is a woody African genus with deciduous leaves and dentate leaf margins, features shared with *Steganotaenia* Hochst. (Burt, 1988; Van Wyk, 2001), which is likewise African. Both genera have traditionally been placed in Apiaceae subfamily Apioideae, but similar leaf features are also found in members of subfamily Saniculoideae Burnett, which is generally characterized by toothed or spiny leaves (Drude, 1897–1898). Norman (1934) observed that the fruit anatomy of *Polemanniopsis* and *Steganotaenia* is very peculiar (in particular, the presence of large cavities in the wings), and recent molecular studies have confirmed that they are either sister to Saniculoideae or should be placed therein (Downie and Katz-Downie, 1999; Plunkett, 2001), a finding further supported by a detailed study of their fruits (Liu et al., 2003a).

Heteromorpha Cham. & Schltdl., a woody apioid genus endemic to Africa, has heteromorphic fruits and either simple or compound leaves (Winter et al., 1993; Winter and Van Wyk, 1996; Van Wyk, 2000). Cerceau-Larrival (1974) and Hilliard and Burt (1986) reported that *Heteromorpha*, *Anginon* Raf., and *Dracosciadium* Hilliard & B. L. Burt share oval pollen. Molecular data (Plunkett et al., 1996a, b; Downie and Katz-Downie, 1999; Downie et al., 2001) indicate that these three genera, together with two others that are endemic to Africa (*Glia* Sond. and *Polemanna* Eckl. & Zeyh.), are best recognized as a distinct tribe Heteromorphae Downie & Watson, which is sister to the remaining members of subfamily Apioideae.

TABLE 1. Genera of Araliaceae and Apiaceae with winged fruits used in this study. These genera were selected to represent the full range of major lineages in the order Apiales. Apiaceae genera are listed as in Pimenov and Leonov (1993).

Family	Subfamily	Tribe	Genus	Geographical distribution
Araliaceae Juss.			<i>Astrotricha</i> DC.	Australia
			<i>Myodocarpus</i> Brongn. & Gris	New Caledonia
Apiaceae Lindl.	Hydrocotyloideae Link	Mulineae DC.	<i>Asteriscium</i> Cham. & Schltdl.	South America
			<i>Choritaenia</i> Benth.	Africa
			<i>Hermas</i> L.	Africa
			<i>Laretia</i> Gillies & Hook.	South America
	Apioideae Drude	Smymieae Spreng.	<i>Heptaptera</i> Margot & Reut.	Europe, Asia
			<i>Molosperspermum</i> W.D.J. Koch	Europe
		Apieae Drude	<i>Annesorhiza</i> Cham. & Schltdl.	Africa
			<i>Dasispermum</i> Neck. ex Raf.	Africa
			<i>Heteromorpha</i> Cham. & Schltdl.	Africa, Asia
			<i>Pachypleurum</i> Ledeb.	Europe, Asia
		Peucedaneae Dumort.	<i>Peucedanum</i> L.	Europe, Asia, Africa, North America
		Tordylieae W.D.J. Koch	<i>Tordylium</i> L.	Europe, Asia, Africa, Oceania
		Laserpitieae Benth.	<i>Elaeoselinum</i> W.D.J. Koch ex DC.	Europe, Asia
			<i>Polylophium</i> Boiss.	Asia
			<i>Rouya</i> Coincy	Europe, Africa
		incertae sedis	<i>Polemanniopsis</i> B.L. Burt	Africa

TABLE 2. Voucher specimens used for anatomical study. Herbarium acronyms in parentheses follow Holmgren et al. (1990).

Species	Voucher or accession number	Geographic origin
<i>Annesorhiza macrocarpa</i> Eckl. & Zeyh.	<i>Rourke 1700</i> (NBG)	South Africa
<i>Asteriscium flexuosum</i> Hemsl.	<i>Werdermann 404</i> (U)	South America
<i>Astrotricha</i> cf. <i>cordata</i> A.R. Bean	<i>Coveny & Taylins 11333</i> (MO)	Australia
<i>Choritaenia capensis</i> Benth.	<i>Hanekom 1834</i> (PRE)	South Africa
<i>Dasispermum suffruticosum</i> (Berg.) B.L. Burtt	<i>Stirton 9601</i> (PRE)	South Africa
<i>Elaeoselinum asclepium</i> Bertol.	<i>Rerachem 207</i> (S)	Sweden
<i>Heptaptera colladonioides</i> Margot & Reut.	<i>Emanuelsson 1958</i> (S)	Greece
<i>Hermas villosa</i> (L.) Thunb.	<i>Compton 16844</i> (PRE)	South Africa
<i>Heteromorpha transvaalensis</i> H. Wolff	<i>Van Wyk 3651</i> (JRAU)	South Africa
<i>Laretia acaulis</i> (Cav.) Gillies & Hook.	<i>Werdermann 646</i> (U)	South America
<i>Molopospermum peloponessiacum</i> (L.) W.D.J. Koch	<i>Sennen 1926</i> (LD)	France
<i>Myodocarpus fraxinifolius</i> Brongn.	<i>MacKee 41344</i> (NOU)	New Caledonia
<i>Pachypleurum lhasanum</i> H.T. Chang & Shan	<i>PE 088245</i> (PE)	China
<i>Peucedanum natalense</i> (Sonder) Engler	<i>Gerstner 2648</i> (PRE)	South Africa
<i>Polemanniopsis marlothii</i> (H. Wolff) B.L. Burtt	<i>Taylor 11269</i> (PRE)	South Africa
<i>Polylophium panjutinii</i> Mandenova & Schischk.	<i>Ostroumova s.n.</i> (MW)	Russia
<i>Rouya polygama</i> (Desf.) Coincy	<i>Gysperger s.n.</i> (AMD)	France
<i>Tordylium maximum</i> L.	<i>PE 207887</i> (PE)	Romania

The African endemic *Annesorhiza* Cham. & Schtdl. also have winged fruits, along with pinnate leaves that typically develop only after flowering (Burtt, 1991; Van Wyk, 2000, 2001). The fruit anatomy of *Annesorhiza* has been studied previously, although not in great detail (Van Wyk and Tilney, 1994; Tilney and Van Wyk, 2001). The cladogram in Plunkett (2001) indicates that *Annesorhiza* may be closely related to *Heteromorpha*, and S. R. Downie (University of Illinois, personal observation) has suggested on the basis of molecular evidence that *Chamarea* Eckl. & Zeyh is nested within *Annesorhiza*. The monotypic European genus *Molopospermum* was placed in Apioideae tribe Smynnieae Spreng. by Pimenov and Leonov (1993), but S. R. Downie indicates that it is more likely a close relative of *Annesorhiza* and *Chamarea*.

Subfamily Apioideae includes many other genera with winged fruits, such as *Dasispermum* Neck. ex Raf., a monotypic genus endemic to South Africa, which has exceptionally polymorphic fruits (major morphological differences can be found among fruits collected from different plants; Tilney and Van Wyk, 1995). The fruits of the Eurasian genus *Heptaptera* Margot & Reut. also show great variability within and between populations (Herrnstadt and Heyn, 1971). *Pachypleurum* Ledeb., another genus found in Europe and Asia, has five-winged fruits (Shan and Sheh, 1979), whereas those of two wide-ranging genera, *Peucedanum* L. and *Tordylium* L., have marginal wings but have traditionally been placed in separate tribes (Pimenov and Leonov, 1993). *Elaeoselinum* W. D. J. Koch ex DC., *Polylophium* Boiss. and *Rouya* Coincy, placed in tribe Laserpitieae Benth. (Pimenov and Leonov, 1993), have two or four wings that develop from furrows (Drude, 1897–1898).

In this study we examine fruit morphology and anatomy in the 18 genera discussed, carefully selected from a broader survey of about 400 apialean genera (Liu, 2004, unpublished data) to represent the full range of basic types of winged fruits found in the order (Table 1). The results are then compared to recently proposed modifications and rearrangements of genera within Apiales to evaluate the utility of selected fruit characters for phylogenetic analyses and to gain new insights into the homology and taxonomic value of structural features of the fruit.

MATERIALS AND METHODS

Taxon sampling—Fruit anatomy was examined in 18 genera, representing all basic types of winged fruits in Apiales. From Apiaceae, these are *Annesorhiza*, *Asteriscium*, *Choritaenia*, *Dasispermum*, *Elaeoselinum*, *Heptaptera*, *Hermas*, *Heteromorpha*, *Laretia*, *Molopospermum*, *Pachypleurum*, *Peucedanum*, *Polemanniopsis*, *Polylophium*, *Rouya*, and *Tordylium*. Two additional genera with winged fruits from other families in Apiales (Table 1) were included. These are *Astrotricha* (Araliaceae) and *Myodocarpus* (Myodocarpaceae). The species sampled in each genus were chosen primarily based on availability of suitable material. One species per genus and at least two mature fruits per species were studied. Sources and voucher specimens are given in Table 2, together with author citations.

Anatomical studies—All fruits were rehydrated and placed in formalin-acetic acid-alcohol (FAA, 1:1:8) for a minimum of 24 h and then treated according to the method of Feder and O'Brien (1968) for embedding in glycol methacrylate (GMA), except that a minimum of 24 h was used for the first two infiltrations in GMA and a minimum of 5 d for the third infiltration. Capsules containing the fruit samples and GMA were placed in an oven at 60°C for 24 h. Medial transverse sections, about 3–5 µm thick, were cut using a Porter-Blum ultramicrotome. Samples were stained using the periodic acid-Schiff/toluidine blue staining method (Feder and O'Brien, 1968), and drawings were made using a camera lucida. Terminology is illustrated in Figs. 1–3.

RESULTS

A summary of the morphological and anatomical characters examined in this study is provided in Table 2. Variation in fruit structure is illustrated schematically in Figs. 1–3. The taxonomic implications of these characters are briefly discussed next.

Fruit shape and mericarp symmetry—All species studied have fruits comprising two schizocarpic mericarps, which are laterally compressed in *Astrotricha* cf. *cordata* and *Myodocarpus fraxinifolius* (Fig. 1A, B) and dorsally compressed in all other taxa examined. The fruits of *Polemanniopsis marlothii*, *Annesorhiza macrocarpa*, *Heteromorpha transvaalensis*, and *Molopospermum peloponessiacum* (Fig. 2A–C, E) are all heteromorphic, having a different number of wings on each of the two mericarps. *Heptaptera colladonioides* and *Dasispermum suffruticosum* (Figs. 2D and 3D) may have either

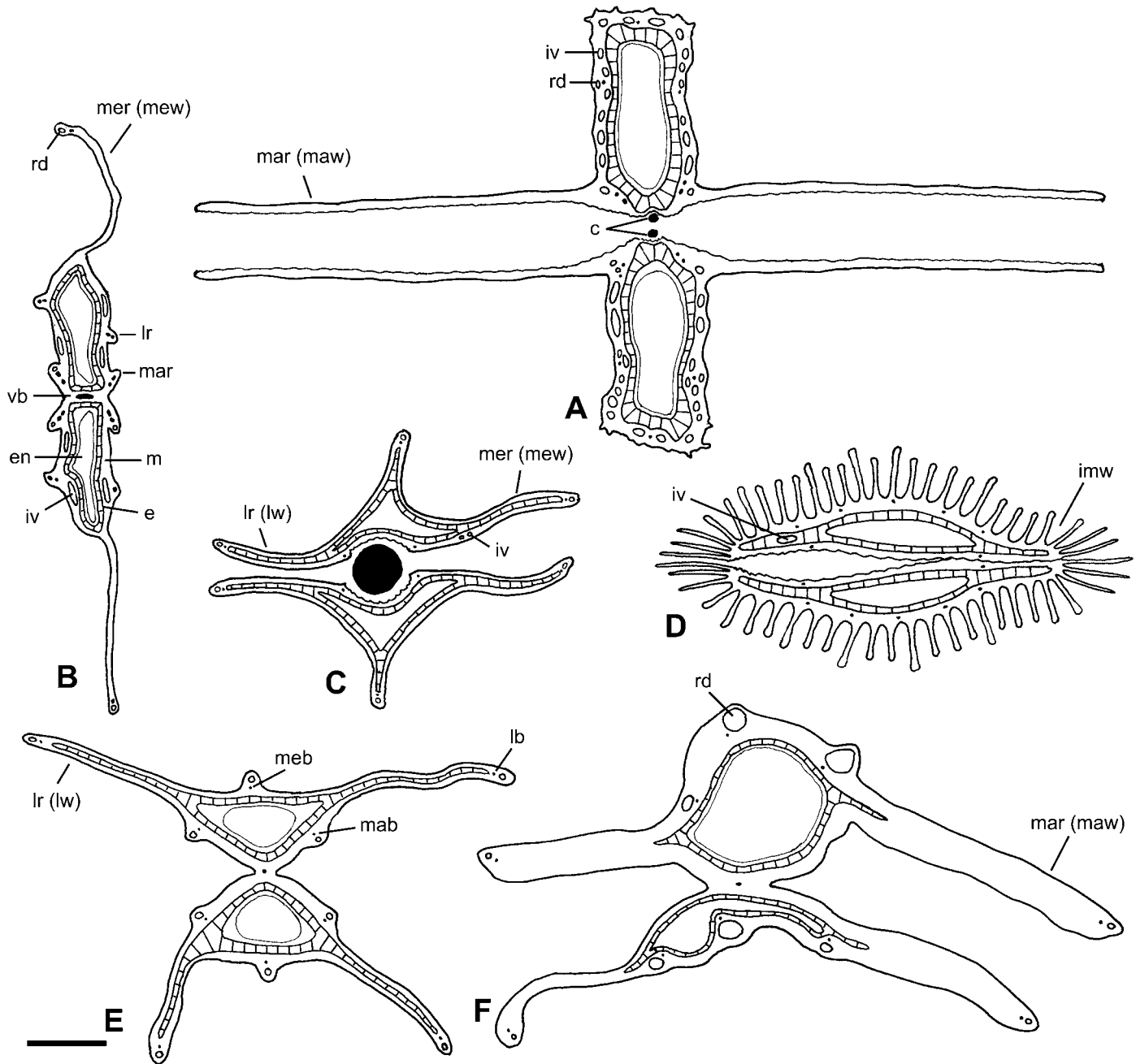


Fig. 1. Transverse sections showing variation in mericarp shape, wing type, secretory oil ducts, lignification of the endocarp, endosperm shape, commissural width, and presence or absence of a carpophore in the following species: (A) *Astrotricha* cf. *cordata*, (B) *Myodocarpus fraxinifolius*, (C) *Herma villosa*, (D) *Choritaenia capensis*, (E) *Asteriscium flexuosum*, (F) *Laretia acaulis*. Open circles: secretory oil ducts; filled circle: vascular bundles and carpophores; hatching: lignification. Abbreviations: c, carpophore; e, endocarp; en, endosperm; imw, inter-rib marginal wing; rd, rib duct; iv, irregular vitta; lr, lateral rib; lr (lw), lateral rib (lateral wing); lb, lateral bundle; m, mesocarp; mar, marginal rib; mar (maw), marginal rib (marginal wing); mab, marginal bundle; mer (mew), median rib (median wing); meb, median bundle; vb, ventral bundle. Bar = 1 mm.

heteromorphic or homomorphic mericarps. The mericarps of all other species are homomorphic.

Wings—Wings may develop from the primary ribs (typically including one median rib [Fig. 1B], two lateral ribs [Fig. 1E]), and two marginal ribs; see Fig. 1A), which form over the vascular bundles, or from the furrows (the intervals or valleculae between two ribs), or from both areas. Thus the

samples examined in this study may be divided into three groups on the basis of wing origin. (1) Wings developing from the main ribs. A median wing (without any other wings) is present in *Myodocarpus fraxinifolius* (Fig. 1B). The two lateral ribs develop into wings in *Herma villosa* (Fig. 1C) and in *Asteriscium flexuosum* (Fig. 1E); the former also has a median wing. In both genera, the median wing is situated at the base of the fruit only and does not reach the full length of the fruit.

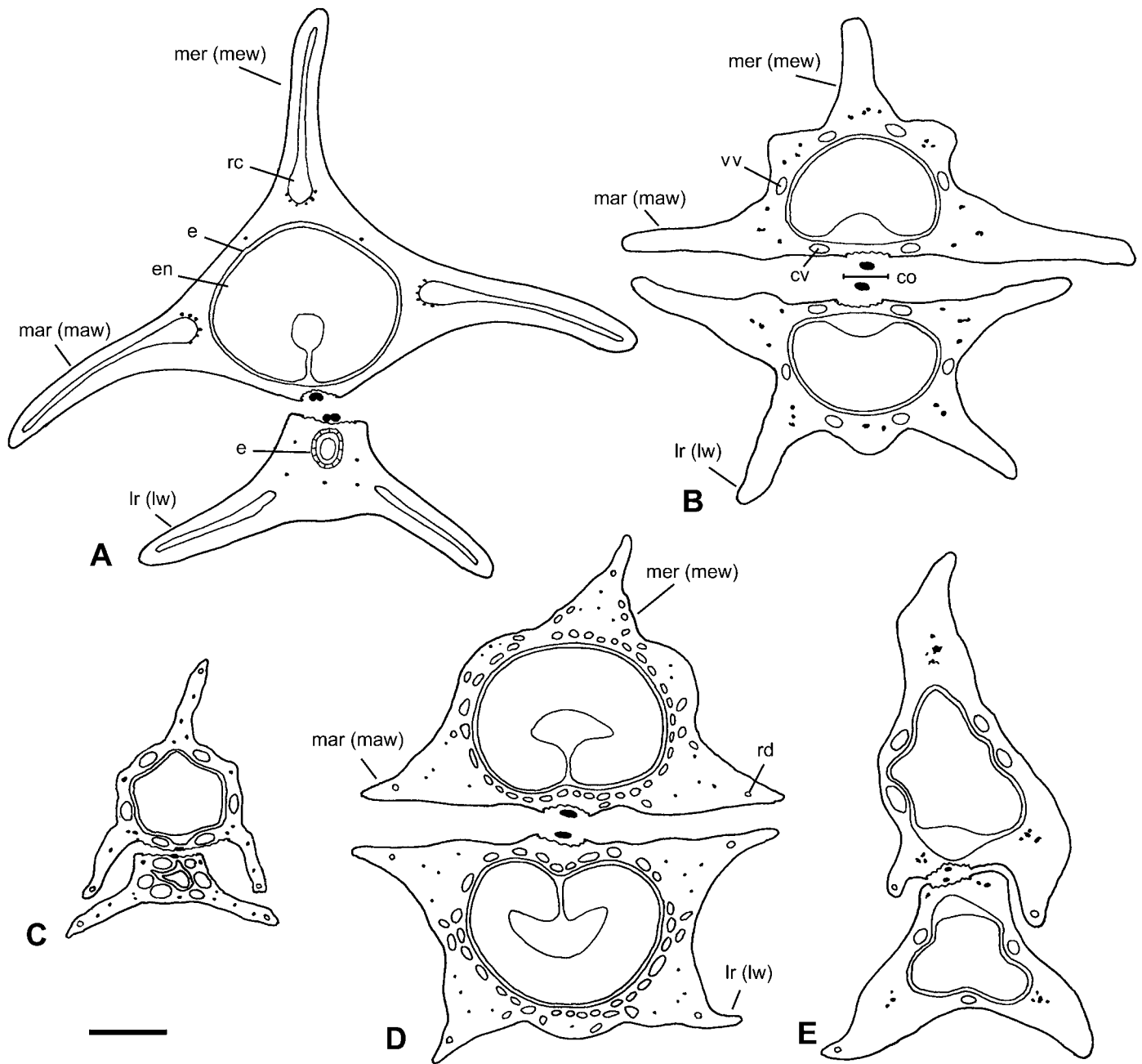


Fig. 2. Transverse sections showing variation in mericarp shape, wing type, secretory oil ducts, lignification of the endocarp, endosperm shape, commissural width, and presence or absence of a carpophore in the following species: (A) *Polemanniopsis marlothii*, (B) *Annesorhiza macrocarpa*, (C) *Heteromorpha transvaalensis*, (D) *Heptaptera colladonioides*, (E) *Molopospermum peloponessiacum*. Circles: secretory oil ducts; dots: vascular bundles and carpophores; hatching: lignification. Abbreviations: co, commissure; cv, commissural vitta; e, endocarp; en, endosperm; rc, rib cavity; rd, rib duct; lr (lw), lateral rib (lateral wing); mar (maw), marginal rib (marginal wing); mer (mew), median rib (median wing); vv, vallecular vitta. Bar = 1 mm.

Astrotricha cf. *cordata* (Fig. 1A), *Laretia acaulis* (Fig. 1F), *Peucedanum natalense*, and *Tordylium maximum* (Fig. 3A, B) all have two marginal wings, which are thickened distally in *Tordylium*. Among taxa with heteromorphic fruits, some genera have three wings (one median and two marginal) on one mericarp and two lateral wings on the other, as in *Polemanniopsis marlothii* (Fig. 2A), *Heteromorpha transvaalensis* (Fig. 2C), and *Molopospermum peloponessiacum* (Fig. 2E), whereas other species of *Molopospermum* have five

main ribs in one mericarp. *Annesorhiza macrocarpa* (Fig. 2B) is also heteromorphic, but has three wings (a median and two marginal wings) in one mericarp, and four wings (two lateral and two marginal) in the other, for a total of seven wings per fruit. The distribution of wings in *Heptaptera colladonioides* (Fig. 2D) is sometimes similar to *Annesorhiza macrocarpa*, but fruits with 10 unequal wings may also be present. Each mericarp of *Dasispermum suffruticosum* (Fig. 3D) has five wings; in one mericarp, the median and marginal wings are

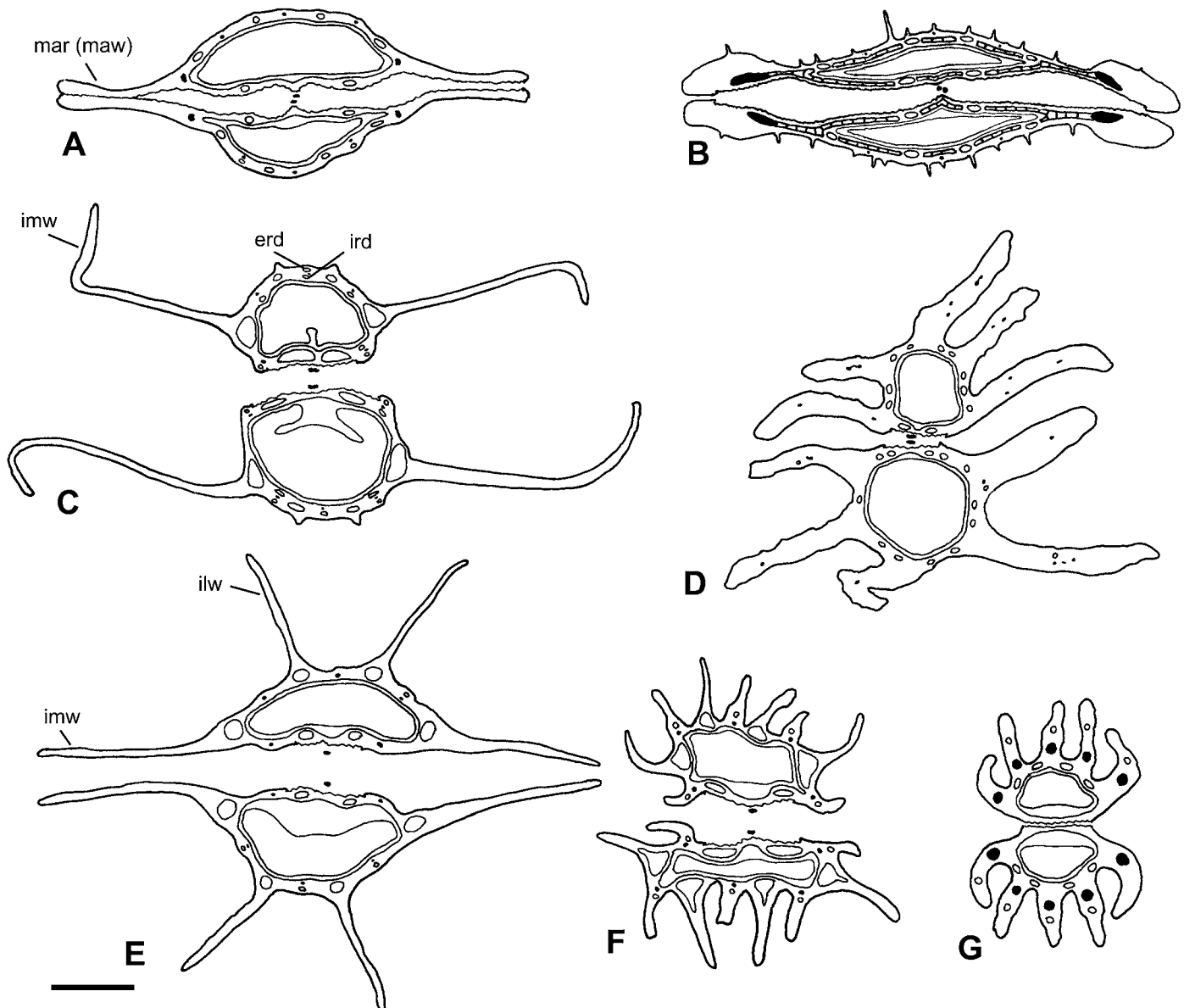


Fig. 3. Transverse sections showing variation in mericarp shape, wing type, secretory oil ducts, lignification of the endocarp, endosperm shape, commissural width and presence or absence of a carpophore in the following species: (A) *Peucedanum natalense*, (B) *Tordylium maximum*, (C) *Elaeoselinum asclepium*, (D) *Dasispermum suffruticosum*, (E) *Rouya polygama*, (F) *Polylophium panjutinii*, (G) *Pachypleurum lhasanum*. Circles: secretory oil ducts; dots: vascular bundles and carpophores; hatching: lignification. Abbreviations: erd, external rib ducts; ird, internal rib ducts; mar (maw), marginal rib (marginal wing); ilw, inter-rib lateral wing; imw, inter-rib marginal wing. Bar = 1 mm.

longer than the lateral wings, and in the other mericarp, the lateral wings are longer than the median and marginals (although wing structure can vary among fruits on an individual plant). *Pachypleurum lhasanum* likewise has five wings per mericarp, all developed from the main ribs (Fig. 3G). (2) Wings from furrows. *Choritaenia capensis* (Fig. 1D) has two "inter-rib" marginal wings, developing from the furrow or interval between the main ribs. *Elaeoselinum asclepium* and *Rouya polygama* (Fig. 3C, E) have two inter-rib marginal wings on each mericarp, as well as two inter-rib lateral wings. (3) Wings from both main ribs and furrows. *Polylophium panjutinii* (Fig. 3F) has mericarps with a total of nine wings each, five that develop from the main ribs, plus two inter-rib

lateral and two inter-rib marginal wings, where the inter-rib wings are longer than those of the main ribs.

Mericarp surface, mesocarp, and endocarp—The mericarp surface is smooth in all of the species examined except *Choritaenia capensis* (Fig. 1D) and *Tordylium maximum* (Fig. 3B), which have unicellular trichomes. The mesocarp is usually not lignified in *Astrotricha* cf. *cordata*, *Myodocarpus fraxinifolius*, *Hermas villosa*, *Choritaenia capensis*, *Asteriscium flexuosum*, and *Laretia acaulis* (Fig. 1A–F). *Tordylium maximum* likewise lacks a lignified mesocarp, although relatively thick-walled cells are found close to the endocarp (Fig. 3B), and their distribution is usually not continuous

(because the mesocarp cells closest to the vittae are not lignified). In several other species, the mesocarp is slightly lignified but with relatively thin-walled cells. A lignified endocarp characterized by two or more layers of relatively thick-walled cells is found in *Astrotricha* cf. *cordata*, *Myodocarpus fraxinifolius*, *Hermas villosa*, *Choritaenia capensis*, *Asteriscium flexuosum*, and *Laretia acaulis* (Fig. 1A–F). In *Polemanniopsis marlothii* (Fig. 2A), a single layer of endocarp cells is lignified in the two-winged mericarp, but is soft (parenchymatous) in the three-winged mericarp of the same sample. All other species studied have parenchymatous endocarps comprising only one layer of cells.

Ribs and vascular bundles in mericarps—All of the genera studied have five vascular bundles/ribs per mericarp (e.g., Fig. 1B) except *Choritaenia capensis* (Fig. 1D), which has seven, and *Molopospermum peloponessiacum* (Fig. 2E), which usually has three in one mericarp (but sometimes five) and four in the other. There are typically five vascular bundles per mericarp (e.g., Fig. 1E), with one bundle in each rib (one median, two laterals, and two marginals), although two bundles may occur in the marginal ribs of *Astrotricha* cf. *cordata* (Fig. 1A) and in both the lateral and marginal ribs of *Myodocarpus fraxinifolius* (Fig. 1B). Alternatively, the vascular tissue may be dispersed, not forming discrete bundles, or they may form groups of bundles, as in *Polemanniopsis marlothii*, *Annesorhiza macrocarpa*, *Heteromorpha transvaalensis*, *Heptaptera colladonioides*, *Molopospermum peloponessiacum* (Fig. 2A–E), and *Dasispermum suffruticosum* (Fig. 3D).

Vittae and rib ducts—The canals typically associated with the fruits of most members of Apioideae are referred to as regular vittae, which may be found either in the furrows (vallecular vittae) or in the commissure (commissural vittae). Among the wing-fruited umbellifers, both vallecular and commissural vittae are found in the fruits of *Annesorhiza macrocarpa* and *Heteromorpha transvaalensis* (Figs. 2B, C), as well as of *Peucedanum natalense*, *Tordylium maximum*, *Elaeoselinum asclepium*, *Dasispermum suffruticosum*, *Rouya polygama*, and *Polylophium panjutinii* (Fig. 3A–F). However, only vallecular vittae are present in *Molopospermum peloponessiacum* (Fig. 2E) and *Pachypleurum lhasanum* (Fig. 3G). In *Heptaptera colladonioides* (Fig. 2D), the vittae are arranged more or less continuously, forming a circle close to the endocarp, with additional vittae dispersed in the mesocarp at each furrow. The number of vittae varies among the taxa studied. In the heteromorphic fruits of *Molopospermum peloponessiacum* (Fig. 2E), there is one vitta per furrow in the four- and five-ribbed mericarps, but apparently two vittae in each furrow of the three-ribbed mericarp. *Dasispermum suffruticosum* (Fig. 3D) has one or two vittae in each furrow, and 2–4 vittae in the commissure. In the remaining species examined, there is always a single vitta in each furrow and two vittae in the commissure.

Rib oil ducts are similar to vittae but are always associated with the vascular bundles in the primary ribs. These were observed in all but three of the taxa sampled, *Choritaenia capensis* (Fig. 1D), *Annesorhiza macrocarpa* (Fig. 2B), and *Tordylium maximum* (Fig. 3B). In all but one of the remaining taxa, rib oil ducts are located in the mericarp, typically to the outside of the vascular bundles, whereas in *Elaeoselinum asclepium* (Fig. 3C) they were observed both to the inside and

the outside of the vascular bundles (the inner ones may also be vittae—this needs confirmation).

Finally, “irregular” vittae (either ducts or vesicles) may be found scattered in the mesocarp of some taxa, including *Astrotricha* cf. *cordata* (branched ducts), *Myodocarpus fraxinifolius* (vesicles), *Hermas villosa* (branched ducts), *Choritaenia capensis* (vesicles) (Fig. 1A–D), and *Heptaptera colladonioides* (ducts) (Fig. 2D). The irregular vittae of *Myodocarpus fraxinifolius* are scattered throughout the mesocarp (adjacent to the endocarp), but in *Choritaenia capensis* they are restricted to the wings.

Endosperm—The shape of the endosperm along the commissural face of each mericarp has played an important role in traditional classification systems, especially in Apiaceae (e.g., Drude, 1897–1898). In most genera of Apiales, the endosperm occupies more or less the entire inner space of the endocarp, but in some taxa its inner face may be pulled away from the endocarp wall. For example, the endosperm of *Polemanniopsis marlothii* (Fig. 2A), *Heptaptera colladonioides* (Fig. 2D), and *Elaeoselinum asclepium* (Fig. 3C) is marked by a deep commissural groove. In *Annesorhiza macrocarpa* (Fig. 2B) and *Rouya polygama* (Fig. 3E), the endosperm is more shallowly concave, and in *Heteromorpha transvaalensis* (Fig. 2C), *Molopospermum peloponessiacum* (Fig. 2E), *Peucedanum natalense* (Fig. 2A), *Tordylium maximum* (Fig. 2B), *Polylophium panjutinii* (Fig. 3F), and *Pachypleurum lhasanum* (Fig. 3G), it is flat. In *Hermas villosa*, the endosperm is also flat (not visible in Fig. 1C).

Commissure—The commissure is the area where a pair of mericarps is attached (e.g., see Fig. 2B). In *Astrotricha* cf. *cordata* (Fig. 1A), *Choritaenia capensis* (Fig. 1D), and *Peucedanum natalense* (Fig. 3A), the commissure occupies roughly the entire width of the fruit, but in some taxa it is much narrower. For example, in *Myodocarpus fraxinifolius* (Fig. 1B) and *Tordylium maximum* (Fig. 3B), it is greater than 50% (but less than 100%) of the fruit width, whereas in the remaining species examined it is less than 50% of the width.

Ventral bundles and carpophores—Ventral bundles are the vascular tissue associated with the commissure. In *Choritaenia capensis* (Fig. 1D) and *Pachypleurum lhasanum* (Fig. 3G), ventral bundles are absent. A single, fused ventral bundle is present in *Myodocarpus fraxinifolius* (Fig. 1B), whereas in *Hermas villosa* (Fig. 1C), *Asteriscium flexuosum* (Fig. 1E), and *Laretia acaulis* (Fig. 1F), the ventral bundles are fused into a single carpophore. In the remaining species examined, the ventral bundles are opposite one another and form two carpophores.

Crystals—As shown in Fig. 4, isolated crystals are present as a single layer in the outermost cells of the endocarp or the innermost layer of the mesocarp in *Astrotricha* cf. *cordata*, *Hermas villosa*, and *Asteriscium flexuosum* (and also in *Centella* of Mackinlayoideae; M. Liu, personal observations). Druse crystals, dispersed in the mesocarp, are known to occur in most members of Saniculoideae (Liu, 2004) and are also found in *Annesorhiza macrocarpa*, *Heteromorpha transvaalensis*, and *Molopospermum peloponessiacum* but not in any of the remaining species studied.

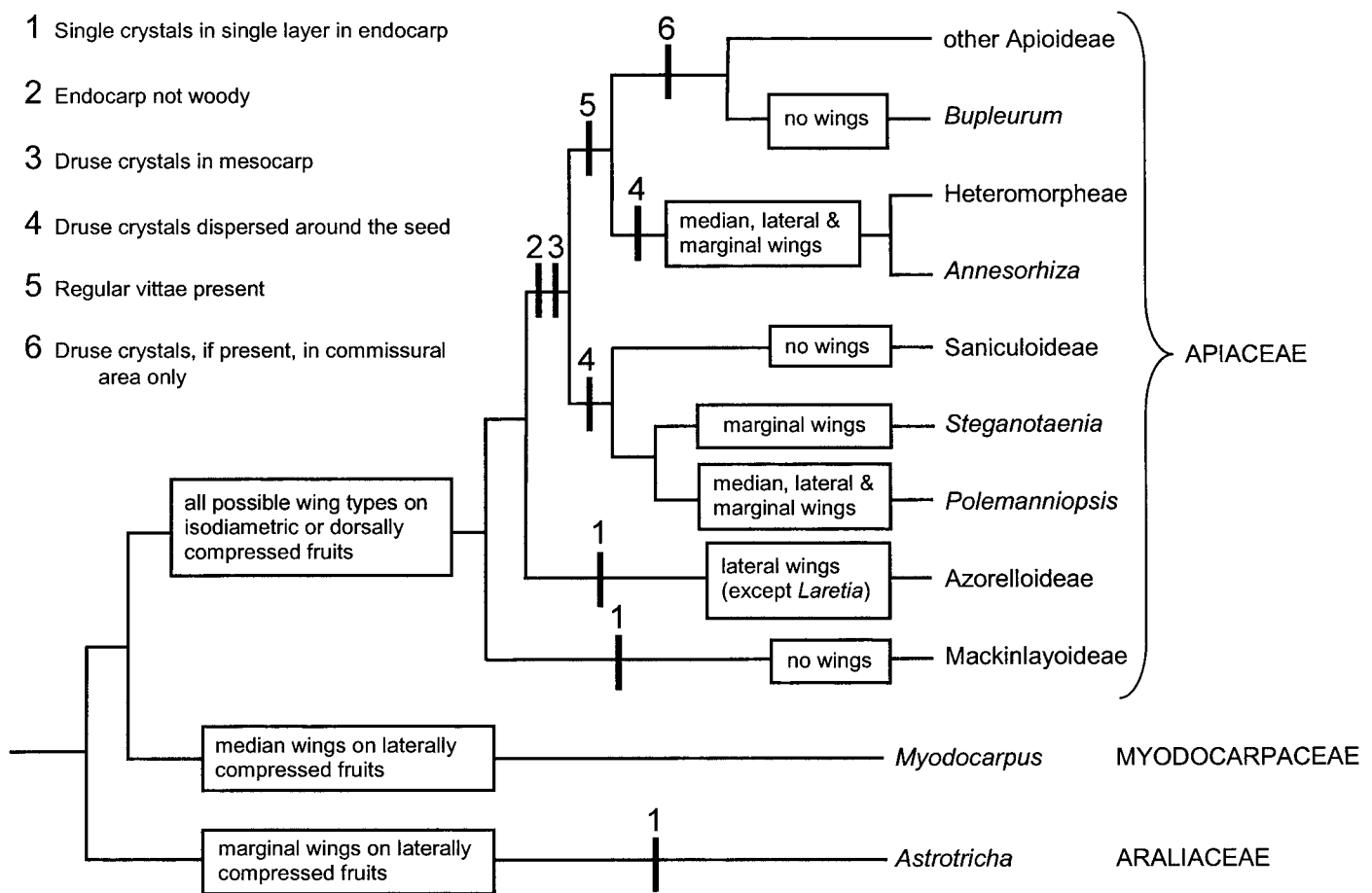


Fig. 4. Diagram of relationships amongst major lineages of the Apiales showing the distribution of fruit wing types in combination with other critical characters of the fruit. Adapted from the cladogram (fig. 3) in Plunkett et al. (2004).

DISCUSSION

Our results clearly show that fruit wing characters, if rigorously studied and properly interpreted, can provide deeper insights into phylogenetic relationships. While the taxonomy of much of Apiales (and nearly all of Apiaceae) was long based on fruit features, this “traditional” source of data, when carefully examined, must not be neglected. In fact, we have demonstrated that it can provide a host of diagnostic characters for novel taxonomic entities uncovered by molecular systematic studies.

Wings occur in the mericarps of more than 80 genera in the order Apiales. Based on the representative sample of taxa studied here, genera with winged fruits can be grouped into three developmental categories: (1) those with wings that form from the main ribs (observed in 12 genera), (2) those that develop from the furrows (three genera), and (3) those that form from both the main ribs and the furrows (one genus). The taxonomic value of these and other fruit features is discussed next, with reference to the phylogenetic placement of these taxa in Apiales. To help conceptualize and summarize the taxonomic value of wing types (together with crystals), the basic relationships and fruit patterns in the major lineages within the order are diagrammed in Fig. 4.

Genera of Araliaceae with winged fruits—Only two genera traditionally assigned to Araliaceae have winged schizocarpic

fruits, *Astrotricha* and *Myodocarpus* (Fig. 1A, B). The circumscription of this family has, however, been modified recently (see Plunkett et al., 2004) on the basis of phylogenetic studies using molecular data (notably Plunkett and Lowry, 2001; Chandler and Plunkett, 2004). *Myodocarpus*, along with the closely related genus *Delarbrea* (including *Pseudosciadium*), whose fleshy fruits lack wings, have been removed from Araliaceae and placed in the newly recognized family Myodocarpaceae (Plunkett et al., 2004). Carpological evidence supports the recognition of this family, which is characterized by a unique feature, the presence of large oil vesicles (= irregular vittae), either adjacent to (in *Myodocarpus*) or within (in *Delarbrea*) the woody endocarp (see also Lowry, 1986a). Smaller, irregular vittae may be present in some apiaceous genera belonging to subfamily Saniculoideae, but they have ducts with branches and have soft endocarps (see Liu et al., 2003a). The circumscription of Araliaceae has also been modified by the addition of several genera traditionally placed in the apiaceous subfamily Hydrocotyloideae (including *Trachymene* and *Hydrocotyle*). Within Araliaceae as now defined, *Astrotricha* is unique in having two-winged mericarps with free, bifurcating carpophores. Several other araliads have laterally compressed, bicarpellate fruits (including for example species of *Hydrocotyle*, *Metapanax* J. Wen & Frodin, *Panax* L., *Polyscias* J. R. Forst. & G. Forst., and *Trachymene*), but their structure is otherwise quite different from that of

TABLE 3. Summary of fruit characters in selected species of Apiales.

Species	Habit ^a	Mericarp shape ^b	Wing type(s)	Vallecular vittae	Rib ducts	Irregular vittae	Woody endocarp	Endosperm shape at commissure	Commissural width	Ventral bundles ^f or carpophore	Crystals
<i>Annesorhiza macrocarpa</i>	H	het	median, marginal & lateral, marginal	present	absent	absent	absent	concave	<50%	two carpophores	dispersed
<i>Asteriscium flexuosum</i>	H	hom	lateral	absent	present	absent	present	no groove	<50%	single carpophore	single layer
<i>Astrotricha cf. cordata</i>	W	hom	marginal	absent	present	duct	present	no groove	100%	two carpophores	single layer
<i>Choritaenia capensis</i>	H	hom	interrub marginal	absent	absent	vesicle	present	no groove	100%	absent	absent
<i>Dasispermum suffruticosum</i>	H	het ^c	10 unequal wings from ribs	present	present	absent	absent	no groove	<50%	two carpophores	absent
<i>Elaeoselinum asclepium</i>	H	hom	interrub marginal	present	present	absent	absent	groove	<50%	two carpophores	absent
<i>Heptaptera colladonioides</i>	H	het ^c	median, marginal & lateral, marginal	absent ^d	present	duct	absent	groove	<50%	two carpophores	absent
<i>Hermas villosa</i>	W	hom	median, lateral	absent	present	duct	present	not observed	<55%	single carpophore	single layer
<i>Heteromorpha transvaalensis</i>	W	het	median, marginal & lateral	present	present	absent	absent	no groove	<50%	two carpophores	dispersed
<i>Laretia acaulis</i>	H	hom	marginal	absent	present	absent	present	no groove	<50%	single carpophore	absent
<i>Molopospermum peloponnesiacum</i>	H	het	median, marginal & lateral	present	present	absent	absent	flat	<50%	two carpophores	dispersed
<i>Myodocarpus fraxinifolius</i>	W	hom	median	absent	present	vesicle	present	no groove	70%	single ventral bundle	absent
<i>Pachypleurum lhasanum</i>	H	hom	median, lateral, marginal	present	present	absent	absent	flat	<50%	absent	absent
<i>Peucedanum natalense</i>	H	hom	marginal	present	present	absent	absent	flat	100%	two carpophores	absent
<i>Polemanniopsis marlothii</i>	W	het	median, marginal & lateral	absent	present	absent	absent ^e	groove	<50%	two carpophores	dispersed
<i>Polyophium panjutinii</i>	H	hom	nine wings from all ribs and furrows	present	present	absent	absent	flat	<50%	two carpophores	absent
<i>Rouya polygama</i>	H	hom	interrub lateral & interrub marginal	present	present	absent	absent	concave	<50%	two carpophores	absent
<i>Tordylium maximum</i>	H	hom	marginal	present	absent	absent	absent	flat	<50%	two carpophores	absent

^a Habit: H = herbaceous; W = woody.

^b Mericarp shape: het = heteromorphic; hom = homomorphic.

^c Mericarps are sometimes heteromorphic.

^d Vittae are arranged in a circle close to the endocarp.

^e Lignified endocarp (one layer of cells) present in one mericarp.

^f Carpophore is used when the two mericarps separate at maturity; ventral bundle is used when the mericarps do not separate.

Astrotricha. For example, carpophores are completely lacking in all other Araliaceae (including *Hydrocotyle*) with the exception of *Trachymene* (which has laterally compressed but unwinged fruits). The molecular data indicate that *Hydrocotyle* and *Trachymene* occupy a basally divergent position in Araliaceae (Plunkett and Lowry, 2001; Chandler and Plunkett, 2004), and in most analyses *Astrotricha* is among the next most basally branching lineages. This interpretation is supported by the fact that the pattern of crystal distribution is similar in the fruits of *Hydrocotyle* and *Astrotricha* (in the outermost layer of the endocarp), a feature shared with some taxa outside Araliaceae, such as *Centella* L. (Apiaceae, Mackinlayoideae; discussed next) and *Asteriscium* (placement uncertain, possibly Apiaceae, Azorelloideae).

Genera of Apiaceae with woody endocarps and lateral wings—In Apiaceae, woody endocarps are restricted to taxa that have traditionally been placed in subfamily Hydrocotyloideae. Molecular data, however, have clearly demonstrated the polyphyly of this subfamily (Plunkett et al., 1997; Plunkett and Lowry, 2001; Chandler and Plunkett, 2004). In a recently revised classification of Apiales (Plunkett et al., 2004), the former “hydrocotyloids” were assigned to three groups: Araliaceae (discussed earlier), and two apiaceae subfamilies, Mackinlayoideae (which also includes two former araliads, *Mackinlaya* and *Apiopetalum*), and Azorelloideae (which most closely approximates the former Hydrocotyloi-

deae in circumscription and placement, but does not include *Hydrocotyle* itself). Among the former “hydrocotyloids” studied here, *Hermas* and *Asteriscium* (Fig. 1C, E) have both woody endocarps and lateral wings, features shared with three other members of the subfamily, *Diposis* DC., *Gymnophyton* (Hook. f.) Gay, and *Mulinum* Pers. These five genera also share several other characters, including fruits with a very narrow commissure, a single carpophore, and (with the exception of *Diposis*) crystals in the outermost layer of the endocarp adjacent to the mesocarp (Liu, 2004; M. Liu, personal observations). In Drude’s traditional classification (1897–1898), these five genera were placed together in Hydrocotyloideae subtribe Asteriscinae, and a close relationship among them was supported by the studies of Tseng (1967) and Henwood and Hart (2001). Molecular analysis (Chandler and Plunkett, 2004) placed *Mulinum* and *Gymnophyton* in the larger “Azorella group” (= Azorelloideae), but sequence data are not yet available for the three remaining genera. The two other members of Drude’s subtribe Asteriscinae, *Choritaenia* and *Laretia* (Fig. 1D, F), are also included in the present study but their winged fruits are not similar to those of *Asteriscium*, and Henwood and Hart (2001) have suggested instead that *Laretia* is more closely related to *Schizeilema* Hook. f. (traditionally placed in subtribe Azorellinae). Fruit characters clearly indicate that *Choritaenia* and *Laretia* differ from the genera of Asteriscinae, which have laterally winged fruits, but future phylogenetic studies are needed to clarify their position.

Genera with heteromorphic mericarps—Lateral wings may be combined with wings occupying other positions to form the unusual heteromorphic fruits that characterize *Polemanniopsis* (Fig. 2A), *Annesorhiza* (Fig. 2B), *Heteromorpha* (Fig. 2C), and *Molopospermum* (Fig. 2E). The fruits of *Polemanniopsis* in some ways resemble those seen in taxa belonging to subfamily Apioideae (e.g., by the presence of two carpophores), but are characterized by having large rib cavities and lacking vallecular and commissural vittae, features shared with members of subfamily Saniculoideae and *Arctopus* L. (Liu et al., 2003a). Phylogenetic studies based on molecular data support a close relationship of *Polemanniopsis* and *Steganotaenia* (which has similar fruit features) to Saniculoideae (Downie and Katz-Downie, 1999; see also Plunkett, 2001).

The heteromorphic fruits of *Heteromorpha*, *Annesorhiza*, and *Molopospermum* differ strikingly from those of *Polemanniopsis*, exhibiting both vittae and carpophores, features that suggest a relationship to Apioideae. However, the distribution of crystals in the fruits of these three genera (dispersed in the mesocarp around the seed) is similar to Saniculoideae and not to other Apioideae, where crystals, if present at all, are restricted to the commissure and sometimes the area around the carpophore (see Burt, 1991). This unusual mixture of apioid and saniculoid features makes it difficult to place these genera based on fruit morphology and anatomy, and future studies incorporating molecular data will likely be needed to clarify their relationships and interpret the evolution of fruit characters. S. R. Downie (University of Illinois, personal communication) has suggested a close relationship among *Heteromorpha*, *Annesorhiza*, and *Molopospermum* based on ITS sequence data. Some species of *Annesorhiza* have a lignified hypodermis, a feature known from only one other apioid, *Chamarea* (N. Vessio and M. Liu, personal observations), which likewise shares an unusual life history trait where the leaves develop only after the inflorescences have withered (see Van Wyk, 2000). Finally, *Molopospermum* has four groups of vascular bundles in one of its two mericarps, a feature unknown in any other genus of Apiales.

Genera exhibiting fruits with labile wing development—Within the main clade of Apioideae (excluding the woody, basally branching lineages), lateral wings are found only in *Dasispermum* (Fig. 3D) and *Heptaptera* (Fig. 2D). The fruits of these two genera, however, differ from those of *Annesorhiza*, *Heteromorpha*, and *Molopospermum* in having wings whose development is highly labile, producing almost every possible combination of wing structure, sometimes within a single population and even on the same plant (Herrnstadt and Heyn, 1971; Tilney and Van Wyk, 1995). Heteromorphy involving the lateral wings represents just one of many possible variants in these taxa. Tilney and Van Wyk (1995) have shown that variation in the fruit structure of *Dasispermum* does not appear to be correlated with geographic or taxonomic patterns. The phylogenetic position of these genera has not yet been confirmed by molecular study (see Downie et al., 2001). Apart from the heteromorphic fruits that characterize some individuals of *Heptaptera*, all other fruit features (e.g., vittae and endosperm) suggest a close relationship to *Smyrniium* L., which was placed in tribe Smyrnieae Spreng. in both of the principal traditional classifications (Drude, 1897–1898; Pimenov and Leonov, 1993) and in the system based on molecular data (Downie et al., 2001). Therefore, we suggest placing *Heptaptera* in the same tribe. Our study also shows that

Dasispermum differs from *Annesorhiza*, *Heteromorpha*, and *Molopospermum* in that it lacks crystals in its fruits, a feature that characterizes Drude's Apioideae. Molecular analyses are likewise needed to confirm the placement of *Dasispermum*.

Genera with five-winged mericarps—In *Pachypleurum*, both mericarps have five wings (Fig. 3G), a character that can also be found in several other genera of Apioideae, including *Cnidium* Cusson ex Jussieu, *Conioselinum* Hoffm., *Coristospermum* Bertol., *Cortia* DC., *Haplosphaera* Hand.-Mazz., *Notopterygium* H. Boissieu, *Scandia* J. W. Dawson, *Seselopsis* Schischk., and *Todaroa* Parl (Liu, 2004; M. Liu, personal observations). These genera were all traditionally placed in tribe Apieae, but phylogenetic studies have demonstrated that this is not a monophyletic group (e.g., Plunkett et al., 1996a; Downie et al., 2001). Unfortunately, with the exception of *Notopterygium* (which is part of the *Angelica* clade) and *Todaroa* (belonging to tribe Scandiceae), the positions of the remaining genera have not yet been assessed using molecular data (see Downie et al., 2001). *Polyophium* (Fig. 3F), whose mericarps not only have five wings that develop from the main ribs but also have additional wings (developing from the furrows), is discussed later.

Genera having fruits with marginal wings—Pimenov and Leonov (1993) included all genera with fruits that have marginal wings in one of three tribes: Angeliceae W. D. J. Koch, Peucedaneae Dumort., and Tordylieae W. D. J. Koch. *Peucedanum* (Fig. 3G) and *Angelica* have very similar fruits, marked by strong dorsal compression of the two mericarps, prominent marginal wings, mesocarps that are not lignified or only slightly so (with thinner cell walls), and free carpophores. Theobald (1971) noted that fruit development in *Peucedanum* is apparently similar to *Lomatium* (which Pimenov and Leonov, 1993, place in Peucedaneae), but differs from that of *Angelica*. For example, he noted differences in fruit development between *Lomatium dasycarpum* (Torr. & A. Gray.) J. M. Coult. & Rose and *Angelica triquinata* Michx. In *L. dasycarpum*, there is a single trace in the "lateral" (= marginal) ribs that supply both the sepals and petals, whereas in *A. triquinata* two traces are usually evident in the marginal ribs, although sometimes there is only a single bundle. In fact, examination of transverse sections of mature fruits representing 25 species of *Angelica*, 23 species of *Peucedanum*, and two species of *Lomatium* (M. Liu, unpublished data) has shown both character states in all three genera (as currently defined), with species in each genus having either one or two bundles in each marginal rib. However, *A. triquinata* has a very narrow commissure, whereas both *L. dasycarpum* and the species of *Peucedanum* have very wide commissures. Overall, very broad commissures (e.g., Fig. 3A) characterize most species of *Peucedanum* and *Lomatium*, whereas much narrower commissures are found in most (but not all) species of *Angelica*. For example, *A. pubescens* Maxim. has a relatively wide commissure (92% of the mericarp width), similar to that of *P. praeruptorum* Dunn. In *Tordylium* (Fig. 3B), the marginal wings become thickened, a feature also found in *Heracleum* and *Pastinaca*. These three genera further share what Theobald (1971) called "woody endocarps," but which we here describe more correctly as heavily lignified mesocarps with very thick cell walls. Phylogenetic analysis (Downie et al., 2001) and fruit anatomical study (Spalik et al., 2001) place *Peucedanum*, *Lomatium*, and *Angelica* in the *Angelica* clade, separate from

Tordylium and *Pastinaca*, which belong to the *Heracleum* clade. The present study provides additional support for these groups. Fruits with marginal wings have also been observed in many other genera of Apiaceae (Liu, 2004). *Zosima* Hoffm., like *Tordylium* (both members of Tordylieae), has fruits with distally thickened marginal wings and a heavily lignified mesocarp, but in *Cymopterus*, *Glehnia* Fr. Schmidt ex Miq., *Pteryxia* (Nutt. ex Torr. & A. Gray) J. M. Coult. (Angeliceae), and *Imperatoria* L. (Peucedaneae), the fruits have marginal wings without distal thickenings, and the mesocarp is not lignified (or only slightly so). Molecular data (Downie et al., 2001) place *Zosima* in the *Heracleum* clade, whereas *Cymopterus*, *Glehnia*, *Imperatoria*, and *Pteryxia* belong to the *Angelica* clade.

Genera with fruits whose wings develop from secondary ribs—Drude (1897–1898) recognized tribe Laserpitieae Benth. based on the presence of both primary ribs, which develop over the vascular bundles, and secondary ribs, which develop from the furrows or valliculae between each primary rib. In *Elaeoselinum* (Fig. 3C), *Rouya* (Fig. 3E), and *Polylophium* (Fig. 3F), these secondary ribs develop into wings. The same type of development characterizes the winged fruits of *Laserpitium* L., *Melanoselinum* Hoffm., *Monizia* Lowe, and *Thapsia* (Liu, 2004; M. Liu, personal observations). Secondary ribs are also found among the members of tribe Caucalideae Spreng., [e.g., *Agrocharis* Hochst., *Ammodaucus* Coss. & Durieu ex Coss., *Cuminum* L., *Daucus* L., *Orlaya* Hoffm., and *Pseudorlaya* (Murb.) Murb.], but these genera were separated from Laserpitieae in traditional systems (e.g., Drude, 1897–1898) because their secondary ribs are generally more prominent than the primary ribs, never develop into wings, and often bear bristles or barbs. Molecular evidence (see Downie et al., 2001), however, indicates that all taxa with secondary ribs, whether winged or unwinged (i.e., Laserpitieae and Caucalideae), are closely related and are best placed in a single subtribe, Daucinae Dumort., of tribe Scandiceae. Fruit anatomical evidence thus provides strong confirmation of this interpretation (see also Lee et al., 2001).

A summary of the overall pattern of important fruit characters is presented in Fig. 4, which is adapted from the system of Plunkett et al. (2004). Fruit wing type and wing configuration can be useful in characterizing major lineages, especially when combined with other characters such as fruit shape (laterally or dorsally compressed), endocarp lignification, crystals (presence, type and distribution), and regular vittae (in the furrows).

Conclusion—Our study shows that structural data, such as fruit anatomy and micromorphology, when examined rigorously and in a phylogenetic context, offer an invaluable source of characters to recognize and delimit monophyletic taxa in complex groups of organisms. In Apiales over the past decade, we have witnessed the dismantling of traditional classification systems throughout the order, largely through the advancement of cladistic studies using molecular data. Because these traditional systems were based almost solely on carpological characters (especially in Apiaceae), there has (perhaps understandably) been a temptation to treat fruit features as wholly unreliable and fraught with excessive levels of convergence. DNA-based markers are undeniably useful in estimating phylogenies, but they offer few practical characters upon which to erect systems of classification and are almost useless

for identifying plants. In the present study, we have identified many examples of carpological synapomorphies that can be used to characterize taxa and circumscribe groups previously identified on the basis of molecular data. This is especially important at deeper levels of phylogeny, where many features traditionally used to define angiosperm groups have often been difficult to interpret, a situation that certainly applies to Apiales. The correlation observed between molecular data and fruit anatomical features further suggests that carpological characters may have a strong predictive value for resolving many of the remaining problems involving the phylogeny and classification of Apiales. For example, many former “hydrocotyloids” remain unsampled in molecular studies, largely because they are restricted to remote areas (making it difficult to collect fresh leaf material). Fruit anatomical studies, however, can be conducted using existing herbarium collections and may provide reliable indications of relationship. More generally, fruit anatomy, if studied carefully, can provide an excellent source of characters to test, support, and supplement findings based on molecular evidence. It is our hope that the enthusiasm for these features, championed by V. H. Heywood, W. L. Theobald, and their colleagues almost 35 years ago, will be rekindled as we move toward producing comprehensive infrafamilial classification systems within Apiales.

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