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ORIGINAL ARTICLE

Evidence from fruit structure supports in general the circumscription of Apiaceae subfamily Azorelloideae

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Abstract The fruit anatomy of 51 species of Apiaceae, representing all 23 genera of the traditional tribe Mulineae (now recognized as Apiaceae subfamily Azorelloideae) and their putative relatives, was studied in detail. Most genera (*Asteriscium*, *Azorella*, *Bolax*, *Bowlesia*, *Dichosciadium*, *Dickinsia*, *Diplaspis*, *Diposis*, *Domeykoa*, *Drusa*, *Eremocharis*, *Gymnophyton*, *Hermas*, *Homalocarpus*, *Huanaca*, *Laretia*, *Mulinum*, *Oschatzia*, *Pozoa*, *Schizeilema* and *Spananthe*) have a combination of woody endocarps with the innermost layer of fibers arranged longitudinally and fruits that are either isodiametric or dorsally compressed (never laterally compressed), with lateral ribs or wings that are usually larger than all other ribs or wings. This combination of anatomical characters is unique to most of subfamily Azorelloideae. *Choritaenia*, and *Klotzschia*, however, lack prominent lateral ribs or wings, and also differ in other anatomical features, suggesting the exclusion of these taxa from the Azorelloideae. Carpological characters were found to be helpful in refining the circumscription of the subfamily.

Keywords Apiaceae · Umbelliferae · Apiales · Azorelloideae · Carpology · Fruit anatomy · Phylogeny

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Introduction

Recent phylogenetic studies based on molecular sequence data have shown that the family Apiaceae, as traditionally circumscribed, is not a monophyletic group (Plunkett et al. 1996, 1997, 2004; Downie and Katz-Downie 1999; Downie et al. 2001; Plunkett 2001; Valiejo-Roman et al. 2002; Chandler and Plunkett 2004). In particular, many of these studies have demonstrated that Drude's (1897–1898) subfamily Hydrocotyloideae is polyphyletic, with some members (including *Trachymene* Rudge and the subfamilial type *Hydrocotyle* L.) belonging to the closely related family Araliaceae. Other genera, including *Centella* L., *Micropleura* Lag., *Actinotus* Labill., *Platysace* Bunge, and two former araliads (*Mackinlaya* Hook.f. and *Apiopetalum* Baill.), were assigned to a newly described apiaceous subfamily, Mackinlayoideae (Plunkett et al. 2004). A second new subfamily, Azorelloideae, was described to accommodate most of the remaining hydrocotyloid genera, and is roughly equivalent to the hydrocotyloid tribe Mulineae as defined by Drude (1897–1898) and by Pimenov and Leonov (1993) (including *Azorella*, *Bolax*, *Bowlesia*, *Dickinsia*, *Dichosciadium*, *Diplaspis*, *Eremocharis*, *Huanaca*, *Mulinum*, *Schizeilema* and *Spananthe*; Plunkett et al. 2004). These realignments have substantially clarified relationships within Apiaceae, and provide a renewed framework for examining patterns of character evolution within the family and identifying potentially valuable diagnostic features for recircumscribed infra-familial groups.

Despite the consistent picture of relationships that has emerged in Apiaceae on the basis of molecular data (from a variety of markers and techniques), the complex patterns of morphological convergences and parallelisms in the family have made it difficult to identify structural characters that can be used to help define these clades. Fruit micromorphology and anatomy, however, have proved to be a major exception to this trend (e.g., see Liu et al. 2006). Thus, for the present paper, we investigated the fruit structure of genera previously assigned to tribe Mulineae to explore the taxonomic potential of these data to define clades and diagnose monophyletic groups. In this study, we examine fruit morphology and anatomy from all "hydrocotyloid" genera having a woody endocarp and isodiametric or dorsally compressed fruits. The results of this survey are then used to identify carpological features that support or refute the findings of molecular phylogenetic studies, and to predict the placement of several genera that were not sampled in previous DNA analyses (e.g., Plunkett 2001; Plunkett et al. 2004; Chandler and Plunkett 2004).

Materials and methods

Taxon sampling

Mature fruits of 51 species were studied in detail (Table 1), representing all 23 genera of tribe Mulineae (sensu Drude 1897–1898, Pimenov and Leonov 1993) and their putative relatives. *Mackinlaya confusa*, a member of Apiaceae subfamily Mackinlayoideae, was also examined for comparative analysis. Authorities for genus and species names, as well as voucher specimens, are given in Table 1 and are not repeated elsewhere.

Anatomical studies

After rehydration, fruits obtained from herbarium specimens were placed in FAA for a minimum of 24 h and then prepared for sectioning using the glycol methacrylate (GMA) method of Feder and O'Brien (1968), slightly modified by allowing a minimum of 5 days for the third infiltration. A Porter-Blüm ultramicrotome was used to prepare transverse sections ca. 5 μm thick. Samples were stained using the periodic acid-Schiff/toluidine blue method (Feder and O'Brien 1968). Drawings were made using a camera lucida. Terminology follows Kljuykov et al. (2004). The surface structures of the samples were observed.

Results

Variation in fruit structure, including fruit shape, mericarp surface, structure of the mesocarp and endocarp, fruit vasculature, secretory structures, structure of the commissure and carpophore, and type and arrangement of any crystals, was characterized and described for each of the 51 species (Figs. 1–26, 27–52, 53–64). A summary of the main characters examined is provided in Table 2.

Fruit shape

All taxa studied have dorsally compressed mericarps except *Mackinlaya confusa* (Fig. 1), a member of Apiaceae subfamily Mackinlayoideae, and *Oschatzia saxifraga* (Fig. 47). The mericarps may be strongly compressed dorsally (e.g., *Asteriscium chilense* and *Dickinsia hydrocotyloides*, Figs. 2, 16) or slightly compressed dorsally (e.g., *Bowlesia incana* and *Oschatzia cuneifolia*, Figs. 10, 46). Three groups of species can be distinguished based on the mericarp shape, the position of prominent fruit ribs/wings and features of the endocarp.

Group 1. Mericarps usually triangular, lateral ribs nearly always prominent or winged and endocarp with the innermost layer of fibers longitudinally arranged—The following taxa have mericarps which are more or less triangular and which have three dorsal ribs and two commissural ribs with the lateral ribs being more prominent than the others: all species of *Asteriscium* (Fig. 2), *Azorella* (Figs. 4, 6, 7) (except *Az. trifurcata*, *Az. compacta* and *Az. corymbosa*, whose mericarps have prominent marginal ribs or wings, Figs. 3, 5, 8), *Bolax* (Fig. 9), *Bowlesia* (Figs. 10, 11), *Dickinsia* (Fig. 16), *Dichosciadium* (Fig. 17), *Diplaspis* (Figs. 18, 19), *Diposis* (Figs. 20, 21), *Domeykoa* (Figs. 13, 14), *Drusa* (Fig. 15), *Eremocharis* (Figs. 22–24), *Gymnophyton* (Fig. 25–28), *Hermas* (Figs. 31–33), *Homalocarpus* (Figs. 29, 30), *Huanaca* (Figs. 34, 35), *Laretia* (Fig. 40) (except *Laretia acaulis*, whose mericarps have marginal wings, Fig. 39), *Mulinum* (Figs. 41–45), *Pozoa* (Figs. 48, 49), *Schizeilema* (Figs. 50, 51) and *Spananthe* (Fig. 52). Lateral wings (e.g., see Figs. 2, 20), are found in *Asteriscium*, *Drusa*, *Diposis*, *Gymnophyton*, *Hermas* (except *He. capitata*, Fig. 32) and *Mulinum* (Figs. 2, 15, 20, 21, 25–28, 31, 33, 41–45 (Table 2). A basal median wing is also present in *Hermas villosa* and *He. ciliata*. The height of sectioning is critical, so that the median wing will not be visible in transverse sections (see *He. ciliata*, Fig. 33) if they are made above the wing). In *Oschatzia* the two mericarps are not triangular

Table 1 List of taxa from Azorelloideae (and putative relatives) sampled for fruit anatomical studies, together with voucher specimen details

Species	Voucher specimens or accession number and herbarium	Origin
Asteriscium chilense Cham. & Schltdl.	Worth & Morrison 16376 (K)	Argentina
Azorella compacta Phil.	Hill 192 (K)	Peru
A. corymbosa Pers.	Ramsay & Merrow-Smith 376 (K)	Ecuador
A. incisa Wedd.	Constance & Sparre 3564 (K)	Chile
A. monantha Clos	Chandler & Bayer 1113 (PRE)	Argentina
A. multifida Pers.	Hutchison 1625 (F)	Peru
A. trifurcata Pers.	Pederser 14438 (F)	Argentina
Bolax gummifera (Lam.) Spreng.	Dollenza 147 (GH)	Argentina
Bowlesia incana Ruiz & Pav.	Dale Thones et al. 17972 (NY)	USA
B. tenera Spreng.	Pleijer s.n. (S)	Sweden
Choritaenia capensis Burtt Davy	Hanekom 1834 (PRE)	South Africa
Dichosciadium ranunculaceum (F.Muell.) Domin	Verdon 2678 (CBG)	Australia
Dickinsia hydrocotyloides Franch.	NAS 403956 (NAS)	China
Diplaspis hydrocotyle Hook.f.	Verdon 2671 (U)	Australia
D. nivis Van den Borre & Henwood	Jan 1954 (NE)	Australia
Diposis bulbocastanum DC.	Pirion 1741 (GH)	Chile
D. saniculifolia DC.	Gibert 426 (K)	Uruguay
Domeykoa amplexicaulis (H.Wolff) Mathias & Constance	Stafford 805 (K)	Peru
D. saniculifolia Mathias & Constance	Ellenberg 2730 (U)	Chile
Drusa oppositifolia DC.	Jahandiez 37712 (RAB)	Morocco
Eremocharis fruticosa Phil.	Johnston 5247 (GH)	Peru
E. longiramea I.M.Johnst.	Hutchison & Wright 3487 (U)	Peru
E. triradiata I.M.Johnst.	Solomon 3064 (F)	Peru
Gymnophyton flexuosum Clos	Looser 4259 (GH)	Chile
G. isatidicarpum (C.Presl ex DC.) Mathias & Constance	Schlegel 5867 (F)	Chile
G. polycephalum Clos	Werdermann 154 (U)	Chile
G. robustum Clos	Zollner 5128 (U)	Chile
Hermas capitata L.	Bolus 9111 (PRE)	South Africa
H. ciliata L.f.	Pillans 6742 (BOL)	South Africa
H. villosa Thunb.	Compton 16844 (PRE)	South Africa
Homalocarpus bowlesioides Hook. & Arn.	Philipps s.n. (K)	Chile
H. dichotomus (Poepp. ex DC.) Mathias & Constance	Mantero 308 (K)	Chile
Huanaca acaulis Cav.	Donat 128 (U)	Chile
H. andina Phil.	Werdermann 1340 (U)	Chile
Klotzschia brasiliensis Cham.	Iewin et al. 21900 (SP)	Brazil
K. glaziovii Urb.	Ratter & Bridgwate 7227 (K)	Brazil
K. rhizophylla Urb.	Anolusen et al. 36097 (SP)	Brazil
Laretia acaulis Gill & Hook.	Werdermann 646 (U)	Chile
L. yareta (Hamman) Mathias & Constance in R.L.Rodrig.	Venturi B161 (K)	Chile
Mulinum axilliflorum Griseb.	Fiebrig 2601 (PRE)	Argentina
M. echinus DC.	Constance 3832 (K)	Patagonia
M. leptactanthum Phil.	Elwre s.n. (K)	Chile–Argentina border
M. ovalleanum Phil.	Constance 3532 (K)	Chile
M. spinosum Pers.	Mutchison 3051 (NY)	Chile
Oschatzia cuneifolia (F.Muell.) Drude	Briggs 4782 (NSW)	Australia
O. saxifraga (Hook.f.) Walp.	Grof 10133 (CBG)	Australia
Pozoa coriacea Lag.	Werdermann 611 (U)	Chile
P. volcanica Mathias & Constance	Constance & Sparre 3578 (K)	Chile

Table 1 continued

Species	Voucher specimens or accession number and herbarium	Origin
Schizeilema colensoi Domin	CHR 286768 (CHR)	New Zealand
S. haastii Domin	CHR 330239 (CHR)	New Zealand
Spananthe paniculata Jacq.	Sagastegui 10524 (MO)	Peru
Mackinlaya confusa Hemsl.	Plunkett, Jensen & Oskolski 1549 (VCU)	Australia

The genus *Mackinlaya* (Apiaceae subfamily Mackinlayoideae) was included in the study for comparison
Herbarium acronyms follow Holmgren et al. (1990)

and are slightly dorsally compressed in *O. cuneifolia* (Fig. 46) and isodiametric in *O. saxifraga* (Fig. 47).

A woody endocarp, composed of several layers of fibers (e.g., see Figs. 58, 60, 62), which extends into the wings (e.g., see Fig. 61), is present in all of the above taxa. These layers of fibers are arranged longitudinally, transversely and obliquely, but the fibers of the innermost layer around the seed are all arranged longitudinally (e.g., Figs. 58, 62).

Group 2. Mericarps not triangular, wings marginal, endocarp with the innermost layer of fibres mainly transversely arranged—This group contains only a single species, *Choritaenia capensis*, and is characterized by the presence of mericarps that are markedly dorsally compressed, with apparently two marginal wings (Fig. 12) each developing from two marginal vascular bundles. However, although there are seven vascular bundles (see below) it is likely that the two marginal bundles near the base of each wing of a mericarp represent the marginal bundle that has split into two, thus resulting in a total of eight bundles in the marginal region of the entire fruit. The endocarp does not appear to extend into the wings—this is an important difference between this species and the other azorelloids. There are indications that a few of the innermost cells of the endocarp may sometimes remain non-lignified or are at least less prominently lignified than the adjoining layers (Fig. 63).

Group 3. Mericarps not triangular, ribs five and prominent, endocarp with the innermost layer of fibers arranged in different directions—This group comprises the three species of the genus *Klotzschia* (*K. brasiliensis*, *K. glaziovii*, and *K. rhizophylla*), which all have five prominent ribs per mericarp (Figs. 36–38), although the two marginal ribs may be larger than the other ribs, or slightly winged (Fig. 37). The woody endocarp in these three taxa is composed of longitudinal fibers, except for the innermost layer around the seed, where the orientation is variable (transverse, longitudinal and oblique) (Fig. 64).

Mericarp surface, mesocarp

All of the species examined have mericarps with a smooth surface except *Bolax gummifera* (Fig. 9), *Bowlesia* (*Bo. incana*, *Bo. tenera*, Figs. 10, 11), *Choritaenia capensis* (Fig. 12), *Drusa oppositifolia* (Figs. 15, 55), *Homalocarpus* (*H. bowlesioides*, *H. dichotomus*, Figs. 29, 30, 59), and *Klotzschia* (K. *brasiliensis*, *K. glaziovii*, and *K. rhizophylla*, Figs. 36–38, 54) (Table 2). Of these ten taxa, the mericarps of *Choritaenia capensis* are unique in having dense, unicellular trichomes (Figs. 12, 63) that are thick on the dorsal side and thin along the margins. The nine remaining taxa have multicellular stellate trichomes (e.g., Fig. 59) that are dense in each of the two species studied of *Bowlesia* and *Homalocarpus*, and *Klotzschia glaziovii*, but sparse in *Drusa oppositifolia* and two species of *Klotzschia* (*K. brasiliensis* and *K. rhizophylla*). In *Drusa*, multicellular stellate trichomes also occur at the tips of several peculiar, spine-like marginal appendages or bristles (Fig. 56). The multicellular stellate trichomes in *Klotzschia* (e.g., Fig. 54) are soft but hard in the other taxa. Multicellular stellate trichomes with long stalks were observed on the fruiting pedicel of *Dichosciadium ranunculaceum* (Fig. 53) but are not found on the epidermal surface of the fruit. None of the taxa studied here have a lignified mesocarp except *Bowlesia incana* (Fig. 10), whose entire fruit wall is lignified around a large air chamber, and *Choritaenia capensis* (Fig. 63), in which it appears that several layers of the mesocarp as well as at least part of the endocarp are woody. A ring of mesocarp cells containing rhomboidal crystals of calcium oxalate (e.g., see Fig. 58) is present adjacent to the endocarp (also in the wings) in all taxa studied except for *Choritaenia capensis* which completely lacks crystals.

Vascular bundles in mericarps

Mackinlaya confusa (Fig. 1) has branching vascular bundles that, in transverse section, appear as roughly seven strands in each carpel. *Choritaenia capensis* (Figs. 12, 63) has seven bundles in each mericarp, of which five are dorsal and two are commissural. However, as mentioned previously, it is likely that the marginal bundles split during fruit development. In all the other taxa examined, each mericarp has five vascular bundles (e.g., see Fig. 3), either three dorsal and two commissural (e.g., see Fig. 2) or all five on

Table 2 Summary of fruit characters of Azorelloideae (and putative relatives)

Species	Mericarps triangular	Mericarps dorsally compressed (or other)	Wing type (s) if present	Mericarp with five prominent ribs on dorsal side	Trichome type if present	Oil vesicles	Irregular vittae	Orientation of fibers (innermost layer of endocarp)	Groove in endosperm (if present)
Asteriscium chilense	+	++[a]	Lateral	–	–	–	–	Longitudinal	–
Azorella compacta	–	++	Marginal	–	–	–	–	Longitudinal	–
A. corymbosa	–	+[b]	–	–	–	–	–	Longitudinal	–
A. incisa	+	++	–	–	–	–	–	Longitudinal	–
A. monantha	+[c]	+	–	–	–	–	–	Longitudinal	–
A. multifida	+[c]	++	–	–	–	–	–	Longitudinal	–
A. trifurcata	–	++	–	–	–	–	–	Longitudinal	–
Bolax gummifera	+	++	–	–	Multicellular stellate	–	–	Longitudinal	–
Bowlesia incana[d]	+	+	–	–	Multicellular stellate	–	–	Longitudinal	–
B. tenera[d]	+	+	–	–	Multicellular stellate	–	–	Longitudinal	–
Choritaenia capensis	–	++	Marginal	–	Unicellular	+	–	Transverse	–
Dichosciadium ranunculaceum	+	++	–	–	Multicellular stellate	–	–	Longitudinal	–
Dickinsia hydrocotyloides	+	++	–	–	–	–	+	Longitudinal	–
Diplaspis hydrocotyle	+	++	–	–	–	–	–	Longitudinal	–
D. nivis	+	++	–	–	–	–	–	Longitudinal	–
Diposis bulbocastanum	+	++	Lateral	–	–	–	–	Longitudinal	–
D. saniculifolia	+	++	Lateral	–	–	–	–	Longitudinal	–
Domeykoa amplexicaulis	+	++	–	–	–	–	–	Longitudinal	Deep
D. saniculifolia	+	+	–	–	–	–	–	Longitudinal	Deep
Drusa oppositifolia	+	++	Lateral	–	Multicellular stellate	–	–	Longitudinal	–
Eremocharis fruticosa	+	+	–	–	–	–	–	Longitudinal	Deep
E. longiramea	+	+	–	–	–	–	–	Longitudinal	Deep
E. triradiata	+	+	–	–	–	–	–	Longitudinal	Deep
Gymnophyton flexuosum	+	++	Lateral	–	–	–	–	Longitudinal	–
G. isatidicarpum	+	++	Lateral	–	–	–	–	Longitudinal	Shallow
G. polycephalum	+	++	Lateral	–	–	–	–	Longitudinal	–
G. robustum	+	++	Lateral	–	–	–	–	Longitudinal	Shallow
Hermas capitata	+	+	–	–	–	–	+	Longitudinal	–
H. ciliata	+	++	Median, lateral	–	–	–	+	Longitudinal	–

Table 2 continued

Species	Mericarps triangular	Mericarps dorsally compressed (or other)	Wing type (s) if present	Mericarp with five prominent ribs on dorsal side	Trichome type if present	Oil vesicles	Irregular vittae	Orientation of fibers (innermost layer of endocarp)	Groove in endosperm (if present)
H. villosa	+	++	Median, lateral	–	–	–	+	Longitudinal	Shallow
Homalocarpus bowlesioides	+	++	–	–	Multicellular stellate	–	–	Longitudinal	–
H. dichotomus	+	+	–	–	Multicellular stellate	–	–	Longitudinal	–
Huanaca acaulis	+	++	–	–	–	–	–	Longitudinal	–
H. andina	+	++	–	–	–	–	–	Longitudinal	–
Klotzschia brasiliensis	–	++	–	+	Multicellular stellate	–	+	Different directions[e]	–
K. glaziovii	–	++	Marginal (narrow)	+	Multicellular stellate	–	+	Different directions	–
K. rhizophylla	–	++	–	+	Multicellular stellate	–	+	Different directions	–
Laretia acaulis	–	++	Marginal	–	–	–	–	Longitudinal	–
L. yareta	+	++	–	–	–	–	–	Longitudinal	–
Mulinum axilliflorum	+	++	Lateral	–	–	–	–	Longitudinal	–
M. echinus	+	++	Lateral	–	–	–	–	Longitudinal	–
M. leptactanthum	+	++	Lateral	–	–	–	–	Longitudinal	–
M. ovalleanum	+	++	Lateral	–	–	–	–	Longitudinal	–
M. spinosum	+	++	Lateral	–	–	–	–	Longitudinal	–
Oschatzia cuneifolia	–	+	–	–	–	–	–	Longitudinal	–
O. saxifraga	–	Isodiametric	–	–	–	–	–	Longitudinal	–
Pozoa coriacea	+	++	–	–	–	–	–	Longitudinal	–
P. volcanica	+	++	–	–	–	–	–	Longitudinal	–
Schizeilema colensoi	+	++	–	–	–	–	–	Longitudinal	–
S. haastii	+	+	–	–	–	–	–	Longitudinal	–
Spananthe paniculata	+	++	–	–	–	–	–	Longitudinal	–
Mackinlaya confusa	–	Laterally compressed	–	–	–	–	–	Different directions	–

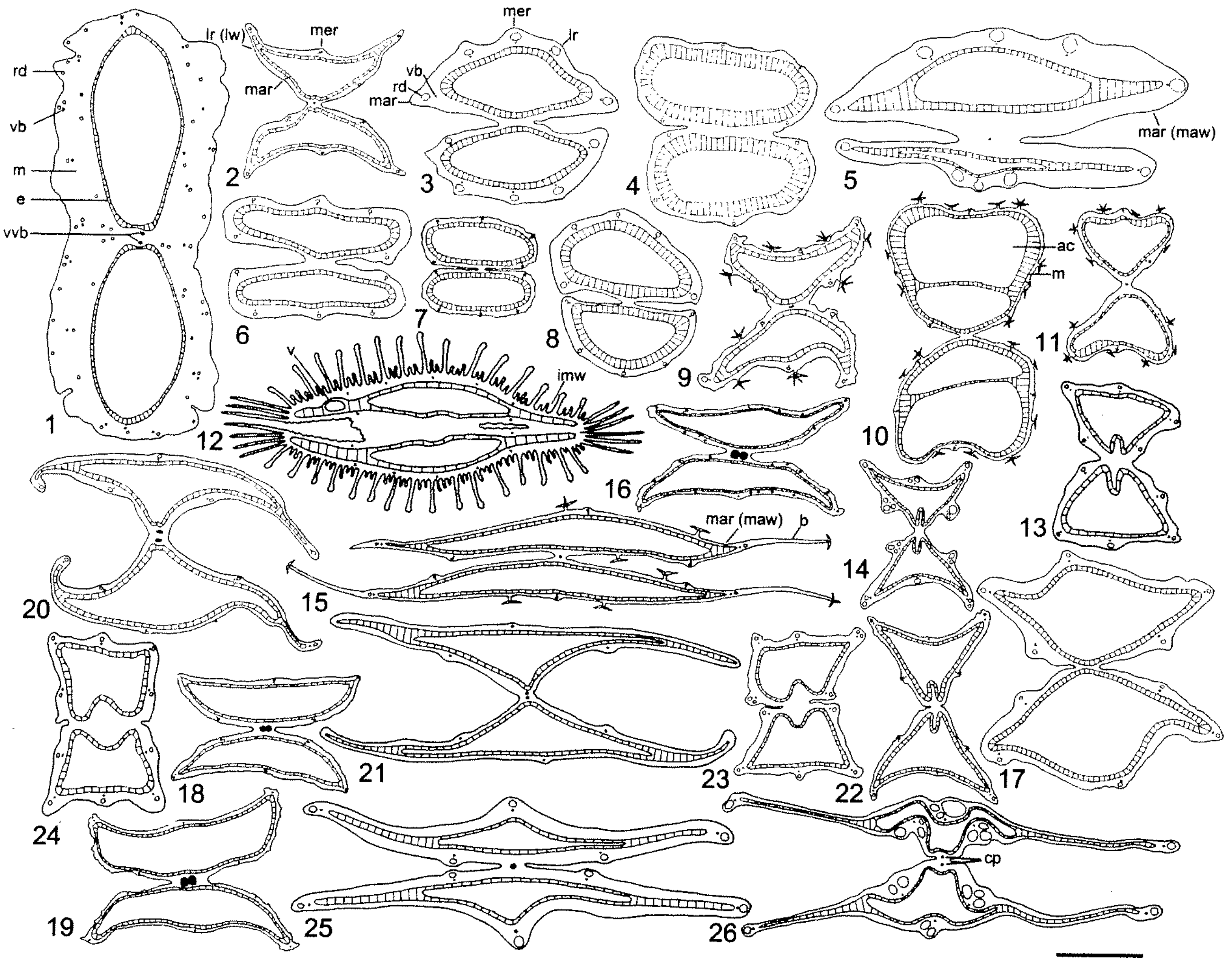
[a] Strongly dorsally compressed (dd): mericarp width is more than two times the mericarp thickness

[b] Slightly dorsally compressed (d): mericarp width is 1.3–2 times the mericarp thickness

[c] Although the triangular mericarps are not obvious in *Azorella monantha* and *A. multifida*, both taxa have three ribs on the dorsal side and two in the commissure

[d] According to Mathias and Constance (1965), *Bowlesia incana* and *B. tenera* are synonyms

[e] Different directions: fibers are arranged transversely, longitudinally and obliquely

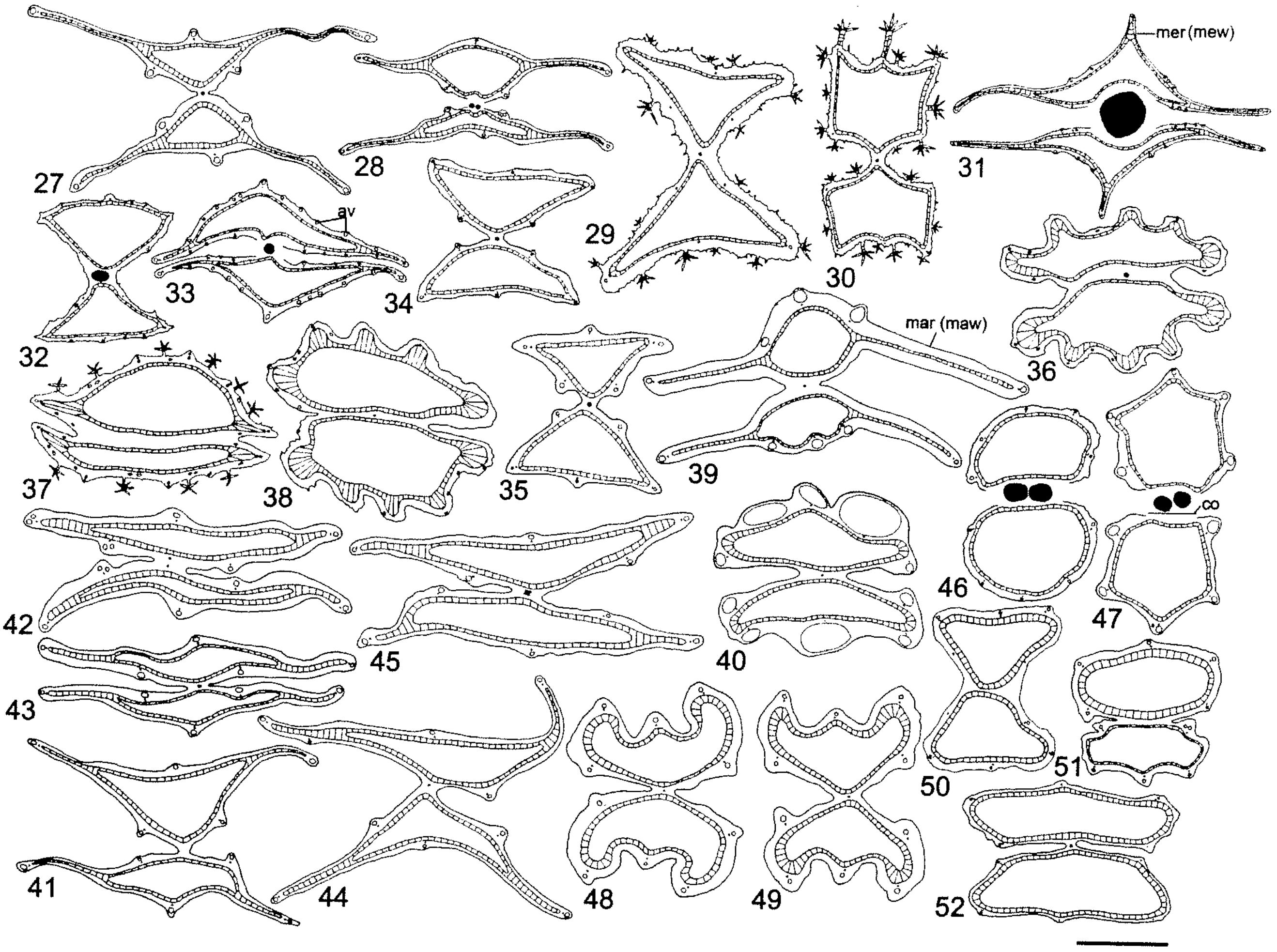


Figs. 1–26 Transverse sections of the fruits of *Mackinlaya confusa* (Apiaceae subfamily Mackinlayoideae) and members of subfamily Azorelloideae showing variation in mericarp shape, trichomes, wing types, secretory oil ducts, lignification of the mesocarp and endocarp, commissural width and features of the carpophore. *1 Mackinlaya confusa. 2 Asteriscium chilense. 3 Azorella trifurcata. 4 Azorella monantha. 5 Azorella compacta. 6 Azorella incisa. 7 Azorella multifida. 8 Azorella corymbosa. 9 Bolax gummifera. 10 Bowlesia incana. 11 Bowlesia tenera. 12 Choritaenia capensis. 13 Domeykoa amplexicaulis. 14 Domeykoa saniculifolia. 15 Drusa oppositifolia. 16 Dickinsia hydrocotyloides. 17 Dichosciadium ranunculaceum. 18 Diplaspis hydrocotyle. 19 Diplaspis nivis. 20 Diposis saniculifolia. 21 Diposis bulbocastanum. 22 Eremocharis fruticosa. 23 Eremocharis triradiata. 24 Eremocharis longiramea. 25 Gymnophyton polycephalum. 26 Gymnophyton robustum. open circles* secretory oil ducts and vesicle; *filled circles* vascular bundles and carpophore; *hatching* lignification; *ac* air chamber; *b* bristle; *cp* carpophore; *e* endocarp; *lr* lateral rib; *m* mesocarp; *lr* (*lw*) lateral rib (lateral wing); *mar* marginal rib; *mar* (maw) marginal rib (marginal wing); *mer* median rib, *rd* rib duct, *v* vesicle; *vb* vascular bundle; *vvb* ventral vascular bundle. *Scale bar* 0.7 mm in Fig. 1 and 1 mm in Figs. 2–26

the dorsal side (e.g., see Fig. 5). Vascular bundles are very small and comprise only a few cells (Figs. 58, 63), which are adjacent to the endocarp in *Diposis bulbocastanum*, *Gymnophyton isatidicarpum*, *Homalocarpus bowlesioides*, *Hermas capitata* (Figs. 21, 28, 29, 32), and the three species of *Klotzschia* (Figs. 36–38).

Secretory structures

Three types of secretory structures are present in the taxa studied, namely rib secretory ducts, irregular vittae and vesicles. Rib secretory ducts are typically located to the outside of the vascular bundles in each primary rib and are present in almost all of the species examined. Three ducts are found on the dorsal side and two on the commissure (e.g., Fig. 2), or five on the dorsal side (e.g., Fig. 3). Rib secretory ducts are absent in *Choritaenia capensis* (Fig. 12), indistinct in *Diposis bulbocastanum* (Fig. 21), *Diplaspis nivis* (Fig. 19), *Homalocarpus dichotomus* (Fig. 30), *Hermas capitata* (Fig. 32), *Klotzschia brasiliensis*, and *K. rhizophylla* (Figs. 36, 38). By contrast, these ducts are large in *Azorella trifurcata*, *Az. compacta* (Figs. 3, 5), *Gymnophyton*

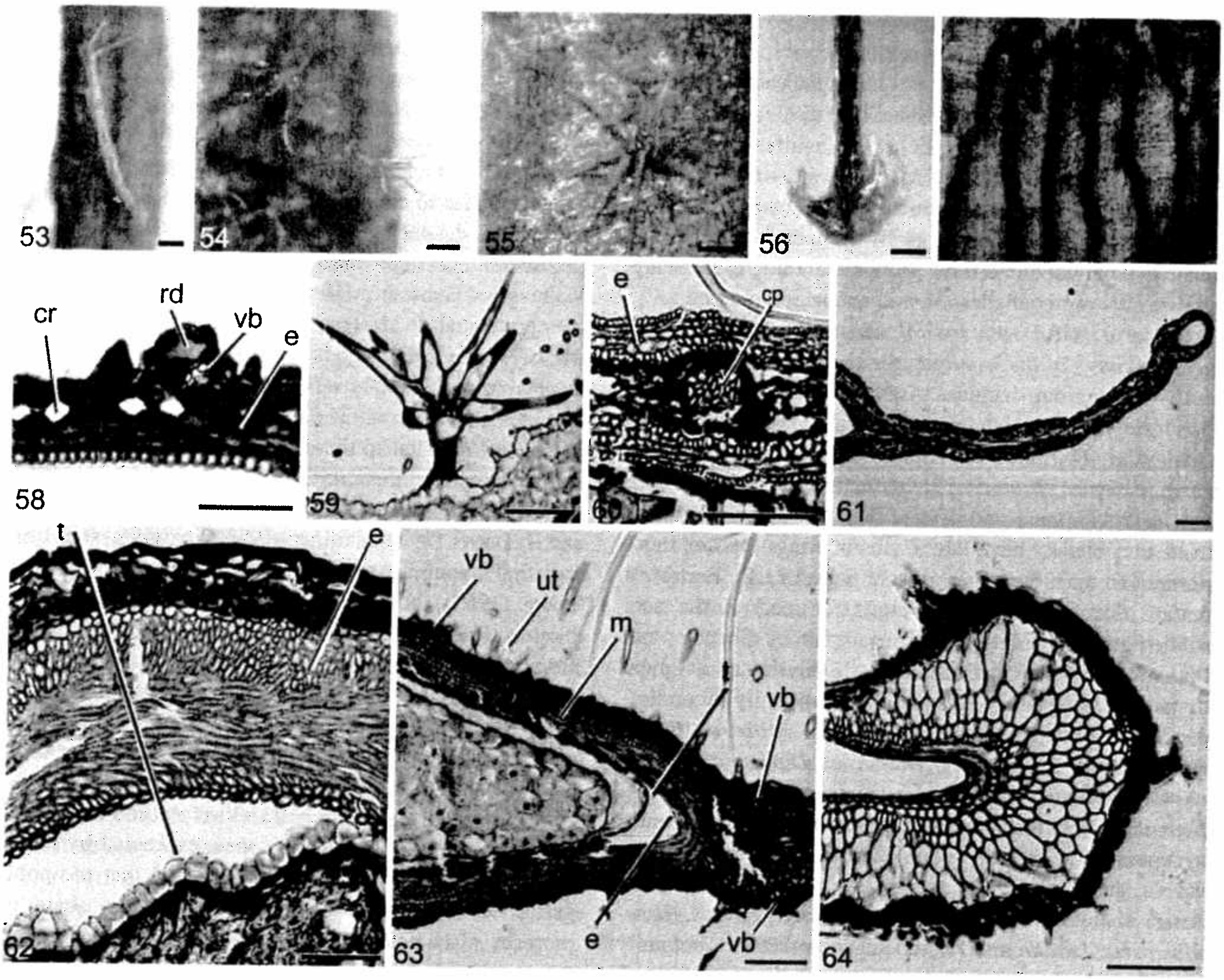


Figs. 27–52 Transverse sections of the fruits of members of Apiaceae subfamily Azorelloideae showing variation in mericarp shape, trichomes, wing type, secretory ducts, lignification of the endocarp, commissural width and features of the carpophore. *27 Gymnophyton flexuosus. 28 Gymnophyton isatidicarpum. 29 Homalocarpus bowlesioides. 30 Homalocarpus dichotomus. 31 Hermas villosa. 32 Hermas capitata. 33 Hermas ciliata. 34 Huanaca acaulis. 35 Huanaca andina. 36 Klotzschia brasiliensis. 37 Klotzschia glaziovii. 38 Klotzschia rhizophylla. 39 Laretia acaulis. 40 Laretia yareta. 41 Mulinum axilliflorum. 42 Mulinum echinus. 43 Mulinum spinosum. 44 Mulinum leptactanthum. 45 Mulinum ovalleanum. 46 Oschatzia cuneifolia. 47 Oschatzia saxifraga. 48 Pozoa coriacea. 49 Pozoa volcanica. 50 Schizeilema haastii. 51 Schizeilema colensoi. 52 Spananthe paniculata. open circles* secretory oil ducts; *filled circles* vascular bundles and carpophore; *hatching* lignification; *iv* irregular vittae; *co* commissure; *mar* (maw) marginal rib (marginal wing); *mer* (mew) median rib (median wing). *Scale bar* 1 mm

robustum (Fig. 26), *Laretia acaulis*, and *L. yareta* (Figs. 39, 40). Some of the ribs in the fruits of *Eremocharis fruticosa* (Fig. 22), *E. triradiata* (Fig. 23), *Gymnophyton robustum* (Fig. 26), *G. isatidicarpum* (Fig. 28) and *Oschatzia saxifraga* (Fig. 47) may have more than one duct. Irregular (branching and anastomosing) vittae are present in *Dickinsia hydrocotyloides* (Fig. 16), all species of *Hermas* (Figs. 31–33, 57), and *Klotzschia* (Figs. 36–38). Large oil vesicles (orbicular or disc-shaped hollows) are present in the woody mesocarp of the fruit wings of *Choritaenia capensis* (Fig. 12). *Mackinlaya confusa* does not have five rib ducts, but instead reticulate secretory ducts are observed, which are usually located to the outside of the vascular bundles (Fig. 1).

Commissure

The commissure is the area of attachment between the two mericarps (e.g., Fig. 47). Almost all of the taxa studied have a narrow commissure, varying from 2% (e.g., Fig. 2) to 20% of the total mericarp width (e.g., Fig. 5). A wide commissure (about 50% of the mericarp width) is present in *Azorella monantha* (Fig. 4), and three species of *Klotzschia* (Figs. 36–38). Two taxa, *Mackinlaya confusa* (Fig. 1) and *Choritaenia capensis* (Fig. 12), have very wide commissures, extending 90 and 100% of the mericarp width, respectively. Conspicuous grooves in the endosperm are visible at the commissural side in all taxa of *Domeykoa* (Figs. 13, 14) and *Eremocharis* (Figs. 22–24), whereas



Figs. 53–64 Multicellular stellate trichomes (53–56) occurring on the fruit stalk and fruit epidermal surfaces. *53 Dichosciadium ranunculaceum*. *54 Klotzschia glaziovii*. *55* and *56 Drusa oppositifolia*. *57* Irregular vittae in *Hermas ciliata*. Transverse sections (58–64) showing multicellular stellate trichome, unicellular trichomes, rib duct, vascular bundles, woody mesocarp, woody endocarp, carpophore and crystals. *58 Domeykoa saniculifolia*. *59 Homalocarpus dichotomus*. *60 Laretia yareta*. *61 Gymnophyton robustum*. *62 Azorella monantha*. *63 Choritaenia capensis*. *64 Klotzschia brasiliensis*. *cp* carpophore; *cr* crystal; *e* non-lignified cell of endocarp; *m* mesocarp; *rd* rib duct; *t* testa; *ut* unicellular trichome; *vb* vascular bundle. *Scale bar* 0.1 mm

shallower grooves are found in *Gymnophyton robustum*, *G. isatidicarpum* and *Hermas villosa* (Figs. 26, 28, 31).

Ventral vascular bundles and carpophore

The carpophore varies in the taxa studied. One entire carpophore is present in *Asteriscium chilense* (Fig. 2), *Azorella compacta* (Fig. 5), *Bolax gummifera* (Fig. 9), *Bowlesia tenera* (Fig. 11), *Choritaenia capensis* (the carpophore is very short and therefore not visible in median transverse section, Fig. 12), *Dickinsia hydrocotyloides* (Fig. 16), *Diplaspis hydrocotyle*, *D. nivis* (Figs. 18, 19), *Drusa oppositifolia* (Fig. 15), *Gymnophyton polycephalum*, *G. flexuosus* (Figs. 25, 27), and all species of *Homalocarpus* (Figs. 29, 30), *Hermas* (Figs. 31–33), *Huanaca* (Figs. 34, 35), *Klotzschia* (Figs. 36–38), *Laretia* (Figs. 39, 40), and *Pozoa* (Figs. 48, 49). A carpophore with two branches, which are arranged in a plane parallel to the mericarps, occurs in *Gymnophyton isatidicarpum*, *Oschatzia cuneifolia* and *O. saxifraga* (Figs. 28, 46, 47), whereas one carpophore with two branches arranged in a plane at right angles to the mericarps, is present in *Diposis saniculifolia*, *D. bulbocastanum* (Figs. 20, 21), *Gymnophyton robustum* (Fig. 26), *Mulinum echinus* and *M. ovalleanum* (Figs. 42, 45). The carpophore may be large, as in *Hermas* (Figs. 31–33) and *Oschatzia* (Figs. 46, 47), small, as in *Laretia yareta* (Fig. 40), or absent, as in all other taxa (e.g., Fig. 3). In *Mackinlaya confusa* a carpophore is absent, and the two ventral bundles are surrounded by parenchymatous cells (Fig. 1).

Discussion

All genera currently placed in Apiaceae subfamily Mackinlayoideae, including those historically assigned to subfamily Hydrocotyloideae, have laterally compressed mericarps, as exemplified by *Mackinlaya confusa* (Fig. 1). The remaining genera traditionally placed in Hydrocotyloideae have more or less dorsally compressed mericarps, and can be divided into three groups according to mericarp shape, rib/wing configuration and endocarp structure.

Group 1. Taxa with lateral wings and the innermost layer of fibers of the woody endocarp arranged longitudinally—This group includes *Asteriscium*, *Azorella*, *Bolax*, *Bowlesia*, *Dichosciadium*, *Dickinsia*, *Diplaspis*, *Diposis*, *Domeykoa*, *Drusa*, *Eremocharis*, *Gymnophyton*, *Hermas*, *Homalocarpus*, *Huanaca*, *Laretia*, *Mulinum*, *Oschatzia*, *Pozoa*, *Schizeilema* and *Spananthe*. The mericarps of all these taxa usually have lateral ribs or wings that are more prominent than the other ribs or wings (e.g., Fig. 2), a feature that appears to be unique for most of the taxa studied here, including all those sampled by Chandler and Plunkett (2004) for their molecular analysis and assigned to the newly established apiaceous subfamily Azorelloideae (Plunkett et al. 2004), namely *Azorella*, *Bolax*, *Bowlesia*, *Dichosciadium*, *Dickinsia*, *Diplaspis*, *Eremocharis*, *Gymnophyton*, *Huanaca*, *Mulinum*, *Schizeilema* and *Spananthe*. Prominent lateral wings may thus represent a synapomorphy for Azorelloideae, and their presence in several genera for which molecular data are lacking (viz., *Asteriscium*, *Diposis*, *Domeykoa*, *Drusa*, *Hermas*, *Homalocarpus*, *Laretia* and *Pozoa*) suggests that the subfamily should now be expanded to include them. Although *Oschatzia* does not have prominent lateral ribs (or wings), it is considered to be part of this group. Future molecular studies should target these taxa to confirm their placement in Azorelloideae.

Multicellular stellate trichomes occur in *Bolax* (Fig. 9), *Bowlesia* (Figs. 10, 11), *Drusa* (Fig. 15), *Homalocarpus* (Figs. 29, 30), *Klotzschia* (Figs. 36–38), and *Dichosciadium* (Fig. 53), but are not known in any other genera of Apiaceae. Mathias and Constance (1965) regarded *Drusa* and *Homalocarpus* as closely related. Hakansson (1952) confirmed the presence of bipolar embryo sacs in both *Bowlesia* and *Drusa*, and Henwood and Hart (2001) placed *Drusa* with *Homalocarpus* because they both have calyces forming an entire rim, stellate trichomes and opposite leaves; the latter two features are also present in *Bowlesia*. Elsewhere in the family, stellate trichomes occur only in *Marlothiella gummifera* H.Wolff., but these are unicellular (Liu et al. 2007b) and thus not homologous to the multicellar trichomes found in Azorelloideae. *Choritaenia* has many unicellular, simple trichomes (Burtt 1991), as do several other genera of Apioideae, such as *Ezosciadium* B.L. Burtt, *Magydaris* W.D.J.Koch ex DC., and *Tordylium* L. To date, uniseriate multicellular hairs have been found only in *Cannaboides betsileensis* (Humbert) B.-E. van Wyk and the forma of *Heteromorpha involucrata* Conrath previously known as *H. kassneri* H.Wolff (Liu et al. 2006).

Domeykoa and *Eremocharis* share several features, including a flat to concave surface on the dorsal side of the mericarp, and a deep groove on the commissural face of the endosperm. On the basis of morphological evidence, Mathias and Constance (1962) concluded that *Domeykoa* is closely related to *Asteriscium*, *Eremocharis* and *Pozoa*, while Tseng (1967) suggested a close relationship among *Domeykoa*, *Eremocharis*, *Asteriscium*, *Gymnophyton*, *Mulinum* and *Diposis*. The species of *Hermas* (Figs. 31–33) are also similar to these genera in their fruit anatomy, having triangular mericarps and prominent lateral ribs or wings. The large genus *Azorella* (c. 70 spp., see Pimenov and Leonov 1993; Martinez 1993b) exhibits significant variation among its species (Martinez 1989, 1993a, 1993b). Tseng (1967) showed that *Az. cryptantha* Clos and *Az. spinosa* (Ruiz & Pav.) Pers. have lateral ribs that are more prominent than the marginal ribs, precisely as in the sample of *Az. incisa* studied here (Fig. 6). Furthermore, the mericarps of *Az. cryptantha* and *Az. spinosa* are more or less triangular and are thus very similar in shape to those of the other genera listed above. Tseng (1967) suggested that *Schizeilema* and *Spananthe* are closely allied to *Azorella* and *Laretia*, echoing an earlier view expressed by Reiche (1901). Henwood and Hart (2001) stated that the pollen grains of *Azorella*, *Laretia* and *Schizeilema* share the presence of an ectoapertural bridge. Our results show that the mericarp shape of *Schizeilema* (Figs. 50, 51) and *Spananthe* (Fig. 52) is similar to that of some species of *Azorella* (Figs. 4, 6, 7) and *Laretia* (Fig. 40), but not to *Azorella trifurcata*, *Az. compacta*, *Az. corymbosa* (Figs. 3, 5, 8) and *Laretia acaulis* (Fig. 39). The diversity of wing types in *Azorella* and *Laretia* suggests that the two genera may not be monophyletic, a conclusion that was also reached by Chandler and Plunkett (2004) and Andersson et al. (2006) based on molecular sequence data, suggesting that a detailed phylogenetic study of *Azorella* and related genera may yield results of taxonomic significance. Henwood and Hart (2001) primarily used fruit morphological and anatomical characters in their preliminary phylogenetic study of Australian genera of "hydrocotyloids". Their results indicated that *Oschatzia* may be close to the *Bowlesia* clade, but our result showed that this genus may be close to *Gymnophyton* in carpophore structure.

Tseng (1967) showed that the arrangement of the innermost endocarp fibers varies in the different genera of Drude's Hydrocotyloideae. In all the above taxa, the cells of the innermost layer around the seed are invariably longitudinally orientated (e.g., Figs. 58, 62), which differs obviously from the other taxa below. Therefore, these genera are considered to be closely related and the fiber direction in the fruit may be of taxonomic significance.

Group 2. Taxa with marginal wings and an endocarp with the innermost layer of fibres mainly transversely arranged (*Choritaenia only*)—The combination of carpological features found in *Choritaenia* is unique for the genus (Liu et al. 2007a), including the presence of surface trichomes, marginal wings, a very broad commissure, oil vesicles, an endocarp not extending into the wings and a total absence of crystals. The mesocarp is partially woody, a state also found in some genera of subfamily Apioideae (e.g., *Coriandrum* L., *Krubera* Hoffm. and *Semenovia* Regel & Herder). In Apioideae splitting of vascular bundles in the marginal ribs of *Ducrosia* Boiss. and *Lomatium* Raf. (personal observation) is considered similar to that in *Choritaenia*. The fruits of *Choritaenia* clearly differ from those of all genera currently included in Azorelloideae. Future phylogenetic studies are needed to clarify its position.

Group 3. Taxa with the woody endocarp thickened in the ribs and an endocarp with the innermost layer of fibers arranged in different directions (*Klotzschia only*)—Shoup and Tseng (1977) studied the pollen of *Klotzschia* and reported similarities with several genera of Araliaceae (e.g., *Eleutherococcus* Maxim., *Reynoldsia* A.Gray, *Schefflera* J.R.Forst. & G.Forst., and *Tetraplasandra* A.Gray). The structure of the woody endocarp is the same in *Klotzschia* as in some members of Araliaceae, e.g., *Acanthopanax* Miq., *Eleutherococcus* and *Macropanax* Miq. The results of molecular systematic studies (reviewed in Plunkett 2001), however, have shown that *Klotzschia* forms a separate lineage between the apiaceous clades now recognized as subfamilies Mackinlayoideae and Azorelloideae, which prompted Plunkett et al. (2004) to exclude *Klotzschia* from Azorelloideae. This decision is supported by the fruit anatomy of *Klotzschia*, which is distinctly different from that of all other taxa examined here.

Other characters. *Rib secretory ducts, vittae and vesicles*

The presence and nature of secretory canals have played a prominent role in the phylogenetic speculations of Baumann (1946), Tikhomirov (1961), and Eyde and Tseng (1971). In the taxa studied here, rib secretory ducts are present in almost all genera (e.g., see Fig. 3), but they also characterize Araliaceae, and the apiaceous subfamilies Mackinlayoideae and Saniculoideae sensu lato, as well as some Apioideae. Eyde and Tseng (1971) suggested that "the gynoecia of ancestral Araliaceae were well supplied with scattered secretory canals, that the canals have been lost in a few of the derived taxa, and that they have been localized in others, including the Umbelliferae [=Apiaceae]." Secretory vesicles were found only in *Choritaenia*, *Bilacunaria* Pimenov & V.N.Tikhom. and *Smyrniopsis* Boiss. (subfamily Apioideae) (Tamamschan 1946; Liu 2004; Liu et al. 2007a). Elsewhere in Apiales, similar vesicles occur only in the genera of Myodocarpaceae (*Myodocarpus* and *Delarbrea*; personal observation, and see Lowry 1986a, b). Reticulate and irregular vittae are present in *Dickinsia* (Liu et al. 2002), *Hermas* and *Klotzschia* but this character also occurs in several species of the Apioideae and therefore seems to have arisen independently in different lineages.

Ventral bundles and carpophore

Ventral bundles are the vascular tissue associated with the commissure. Two ventral bundles, as exemplified by those of *Mackinlaya confusa* (Fig. 1), are widely present in members of subfamily Mackinlayoideae (e.g., *Centella* L. and *Micropleura* Lag.). An entire carpophore occurs commonly in subfamily Azorelloideae (e.g., Fig. 60). Most apioid taxa, however, have a carpophore splitting into two halves, as in *Bupleurum* and *Heteromorpha* Cham. & Schltdl., and this feature also characterizes the azorelloids (e.g., *Diposis saniculifolia*, *Gymnophyton robustum*, Figs. 20, 26). The type of carpophore characteristic of *Gymnophyton isatidicarpum* (Fig. 28), *Oschatzia cuneifolia* and *O. saxifraga* (Figs. 46, 47), is also found in *Astydamia canariensis* (Spreng.) DC. (subfamily Apioideae). A very short carpophore as in *Choritaenia capensis* has not been found in any other taxa of the family (Liu et al. 2007a). A carpophore is usually absent in Araliaceae (except in *Astrotricha* DC. and *Trachymene* Rudge) and in Apiaceae subfamilies Mackinlayoideae and Saniculoideae (except in *Alepidia* Delar.). A detailed study of carpophore structure in the Azorelloideae is currently underway.

Crystal type and distribution

Two main types of crystals are found in the Apiaceae and Araliaceae, namely rhomboidal crystals and druse crystals. Rhomboidal crystals (called cyclic crystals by Kljuykov et al. 2004) (Fig. 58) are present as individual structures in a single cell layer of the mesocarp and were observed in almost all of the genera studied. This type of crystal also characterizes Apiaceae subfamily Mackinlayoideae and some Araliaceae (e.g., *Hydrocotyle* and *Trachymene*) but they are totally absent from all taxa of the subfamilies Saniculoideae and Apioideae. Druse crystals are compound structures, more or less spherical in shape, that are typically dispersed throughout the mesocarp. The crystals are often dissolved during sample preparation, leaving characteristic "ghost cells". Druse crystals are absent from all the taxa studied in this paper. They are typically found in the subfamilies Saniculoideae and Apioideae. If present, they are usually amphi-seminal (scattered around the seed) (most Saniculoideae, e.g., *Sanicula* L. and *Eryngium* L.) or present only on the commissural side of the seed (some Apioideae, e.g., *Myrrhis odorata* (L.) Scop. and *Astrodaucus littoralis* Drude). Druse crystals are also found in Araliaceae (e.g., *Eleutherococcus brachypus* (Harms) Nakai and *Brassaiopsis chengkangensis* H. H. Hu).

Conclusions

A combination of carpological features, including the woody endocarp, the orientation of the innermost fiber layer of the endocarp and the usually triangular mericarps bearing prominent lateral ribs or wings, largely confirms the concept of Apiaceae subfamily Azorelloideae, as suggested previously by molecular analyses (Plunkett et al. 1996, 1997, 2004; Downie and Katz-Downie 1999; Downie et al. 1998, 2001; Plunkett 2001; Chandler and Plunkett 2004) and fruit anatomical studies (Liu 2004). On the basis of the DNA results, a new subfamily was formally recognized by Plunkett et al. (2004) as Azorelloideae Plunkett & Lowry. The fruit anatomical data presented here reinforce and expand the conclusions of these earlier studies by including a considerably broader sampling. Based on anatomical evidence, we suggest that all of the taxa placed in tribe Mulineae by Pimenov and Leonov (1993) should be included in Azorelloideae, with just two exceptions, *Choritaenia* and *Klotzschia*, which together comprise only four species. Regarding *Azorella* and *Laretia*, the broad morphological variability observed in the fruits of these genera appears to support the finding that both genera may not be monophyletic, as suggested by Chandler and Plunkett (2004) (see also Andersson et al. 2006). Recent taxonomic revisions are available for *Azorella* (Martinez 1993b) and *Mulinum* (Zech 1992), but Chandler and Plunkett (2004) found that *Azorella* was paraphyletic with respect to both *Mulinum* and *Huanaca*. It is clear, therefore, that these genera must be studied in the broader context of the entire subfamily, and future molecular studies should explore the phylogenetic positions of these and other azorelloid taxa. Perhaps most importantly, in the wake of the collapse of the traditional systems of classification of Apiaceae, which have proven inadequate when compared to findings based on molecular data, the present study and other recent analyses based on fruit anatomy (Liu 2004; Liu et al. 2003, 2006, and unpublished data) hold out the promise of identifying reliable features that can be used to erect a more stable classification of the entire family that reflects underlying evolutionary relationships, something that has eluded generations of botanists.

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References

Andersson L, Kocsis M, Eriksson R (2006) Relationships of the genus *Azorella* (Apiaceae) and other hydrocotyloids inferred from sequence variation in three plastid markers. Taxon 55:270–280

Baumann M (1946) *Myodocarpus* und die Phylogenie der Umbelliferenfrucht. Ber Schweiz Bot Ges 56:13–112

Burtt BL (1991) Umbelliferae of southern Africa: an introduction and annotated checklist. Edinb J Bot 48:135–275

Chandler GT, Plunkett GM (2004) Evolution in Apiales nuclear and chloroplast markers together in (almost) perfect harmony. Bot J Linn Soc 144:123–147

Downie SR, Katz-Downie DS (1999) Phylogenetic analysis of chloroplast *rps*16 intron sequences reveals relationships within the woody southern African Apiaceae subfamily Apioideae. Can J Bot 77:1120–1135

Downie SR, Ramanath S, Katz-Downie DS, Llanas E (1998) Molecular systematics of Apiaceae subfamily Apioideae: phylogenetic analyses of nuclear ribosomal DNA internal transcribed spacer and plastid *rpo*C1 intron sequences. Am J Bot 85:563–591

Downie SR, Plunkett GM, Watson MF, Spalik K, Katz-Downie DS, Valiejo-Roman CM, Terentieva EI, Troitsky AV, Lee BY, Lahham J, El-Oqlah A (2001) Tribes and clades within Apiaceae subfamily Apioideae: the contribution of molecular data. Edinb J Bot 58:301–330

Drude O (1897–1898) Umbelliferae, pp 63–150, 271. In: Engler A, Prantl K (eds) Die natürlichen Pflanzenfamilien, vol 3(8). Wilhelm Engelmann, Leipzig

Eyde RH, Tseng CC (1971) What is the primitive floral structure of Araliaceae? J Arnold Arboretum 52:205–239

Feder N, O'Brien TP (1968) Plant microtechnique: some principles and new methods. Am J Bot 55:123–142

Hakansson A (1952) Seed development in *Bowlesia tenera*. Bot Notiser 1:33–45

Henwood MJ, Hart JM (2001) Towards an understanding of the phylogenetic relationships of Australian Hydrocotyloideae (Apiaceae). Edinb J Bot 58:269–289

Holmgren PK, Holmgren NH, Barnett LC (1990) Index Herbariorum 1: the herbaria of the world, 8 edn. *Regnum Vegetabile* 120. New York Botanical Gardens, New York

Kljuykov EV, Liu M, Ostroumova TA, Pimenov MG, Tilney PM, Van Wyk B-E (2004) Towards a standardised terminology for taxonomically important morphological characters in the Umbelliferae. S Afr J Bot 70:488–496

Liu M (2004) A taxonomic evaluation of fruit structure in the family Apiaceae. Ph.D. thesis, Rand Afrikaans University, Johannesburg

Liu M, Van Wyk B-E, Tilney PM (2002) The taxonomic value of fruit structure in the Chinese endemic genus *Dickinsia* (Apiaceae). Nord J Bot 22:603–607

Liu M, Van Wyk B-E, Tilney PM (2003) The taxonomic value of fruit structure in the subfamily Saniculoideae and related African genera (Apiaceae). Taxon 52:261–270

Liu M, Plunkett GM, Lowry PP II, Van Wyk B-E, Tilney PM (2006) The taxonomic value of fruit wing types in the order Apiales. Am J Bot 93:1357–1368

Liu M, Van Wyk B-E, Tilney PM (2007a) A revision of the genus *Choritaenia* (Apiaceae). S Afr J Bot 73:184–189

Liu M, Van Wyk B-E, Tilney PM (2007b) A revision of the genus *Marlothiella* (Apiaceae). S Afr J Bot 73:208–213

Lowry PP II (1986) A systematic study of *Delarbrea* Vieill. (Araliaceae). Allertonia 4:169–201

Lowry II PP (1986a) A systematic study of three genera of Araliaceae endemic to or centered in New Caledonia: *Delarbrea*, *Myodocarpus* and *Pseudosciadium*. Ph.D. thesis, Washington University, St. Louis

Martinez S (1989) El gènero *Azorella* (Apiaceae, Hydrocotyloideae) en Argentina. Darwiniana (Buenos Aires) 29:139–178

Martinez S (1993a) Relaciones feneticas entre las especies del genero *Azorella* (Apiaceae, Hydrocotyloideae). Darwiniana (Buenos Aires) 32:159–170

Martinez S (1993b) Synopsis del genero *Azorella* (Apiaceae, Hydrocotyloideae). Darwiniana (Buenos Aires) 32:171–184

Mathias ME, Constance L (1962) A revision of *Asteriscium* and some related Hydrocotyloid Umbelliferae. Univ Calif Publs Bot 33:99–184

Mathias ME, Constance L (1965) A revision of the genus *Bowlesia* Ruiz. & Pav. (Umbelliferae—Hydrocotyleae) and its relatives. Univ Calif Publs Bot 38:1–73

Pimenov MG, Leonov MV (1993) The genera of the Umbelliferae: a nomenclator. Royal Botanic Gardens, Kew

Plunkett GM (2001) Relationship of the order Apiales to subclass Asteridae: a re-evaluation of morphological characters based on insights from molecular data. Edinb J Bot 58:183–200

Plunkett GM, Soltis DE, Soltis PS (1996) Evolutionary patterns in Apiaceae: inferences based on *mat*K sequence data. Syst Bot 21:477–495

Plunkett GM, Soltis DE, Soltis PS (1997) Clarification of the relationships between Apiaceae and Araliaceae based on *mat*K and *rbc*L sequence data. Am J Bot 84:565–580

Plunkett GM, Chandler GT, Lowry PPII, Pinney S, Sprenkle T (2004) Recent advances in understanding Apiales with a revised classification. S Afr J Bot 70:371–381

Reiche K (1901) Zur Kenntnis einiger chilenischer Umbelliferen-Gattungen. Bot Jahrb Syst 28:1–17

Shoup JR, Tseng CC (1977) Pollen of *Klotzschia* (Umbelliferae): a possible link to Araliaceae. Am J Bot 64:461–463

Tamamschan SG (1946) The genus *Hohenackeria* Fisch. et Mey. and its place in the Umbelliferae system (in Russ.). Sov Bot 14(4):219–238

Tikhomirov VN (1961) sistematicheskom polozhenii rodov *Hydrocotyle* L. i *Centella* L. emend. Bot Zhurn 46:584–586

Tseng CC (1967) Anatomical studies of flower and fruit in the Hydrocotyloideae (Umbelliferae). Univ Calif Publs Bot 42:1–58

Valiejo-Roman CM, Terentieva EI, Samigullin TH, Pimenov MG (2002) Relationships among genera in Saniculoideae and selected Apioideae (Umbelliferae) inferred from nrITS sequences. Taxon 51:91–101

Zech JC (1992) Systematics of the genus *Mulinum* (Apiaceae, Hydrocotyloideae, Mulineae). Ph.D. thesis. Ohio State University, Columbus