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The phylogenetic significance of the carpophore in Apiaceae

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- *Background and aims* Fruit structural characters have traditionally been important in the taxonomy of the family Apiaceae. Previous investigations using a limited number of taxa have shown that the carpophore may be especially useful in helping to circumscribe subfamily Azorelloideae. The present study examines, for the first time, carpophore structure in 92 species from 43 genera, representing all subfamilies of Apiaceae, and including all genera assigned to subfamily Azorelloideae. Phylogenetic interpretations are made for the first time, using all available information, and a standard terminology is proposed to describe the various character states found in carpophores.
- *Methods* Carpophore structure was studied in detail using light microscopy.
- *Key Results* Carpophores, when present, may be categorized into two main groups (B and C) based mainly on the arrangement of the vascular bundles in transverse section, and further divided into six sub-types according to the length of the carpophore (short in B1 and C1) and whether they are entire (B1–B3 and C1) or bifurcate (B4 and C2). Free carpophores are absent in subfamily Mackinlayoideae, and in tribes Lichtensteinieae and Phlyctidocarpeae, which have two opposite vascular bundles (Group A). Entire carpophores with one or two vascular bundles, or bifurcate carpophores with lateral vascular bundles (arranged side by side within the commissural plane), are the main types characterizing Azorelloideae. The short, hygroscopic carpophores found in *Choritaenia* are unique in Apiaceae and provide additional evidence for the exclusion of this genus from Azorelloideae. Carpophore type C2 is typical for most Apioideae *sensu lato* (exceptions are, for example, *Arctopus* and *Alepidea*, which have type B2).
- *Conclusions* A single carpophore and ventral vascular bundles not forming free carpophores are proposed to be the ancestral conditions in Apiaceae, while bifurcate carpophores with opposite vascular bundles are the derived state, present in most Apioideae. Secondary reductions seem to have occurred in several unrelated lineages in all major groups, e.g. many Azorelloideae, several protoapioids (including nearly all members of the tribe Saniculeae) and 29 euapioid genera (e.g. some Oenantheae).

Key words: Apiaceae, Apiales, Azorelloideae, carpophore, descriptive terminology, euapioids, phylogeny, protoapioids, Umbelliferae, vascular bundle.

INTRODUCTION

Apiaceae are a family comprising many useful plants, such as carrot, parsley, dill, coriander, fennel and caraway, all well known in the north-temperate zones of Eurasia and North America. These 'typical umbellifers' are all members of subfamily Apioideae, as defined in the traditional three-subfamily system proposed by Drude (1897–1898). Less well known are the genera of Drude's subfamily Hydrocotyloideae, which are better developed in the southern hemisphere. Despite the persistence of Drude's classification and its most recent update, that of Pimenov and Leonov (1993), this system is highly artificial, as demonstrated by numerous phylogenetic studies based on molecular sequence data, which have shown the polyphyly or paraphyly of nearly every traditional subfamily and tribe (e.g. 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). Plunkett *et al.* (2004) transferred the genus *Hydrocotyle* and several close relatives to Araliaceae, and described two new subfamilies, Azorelloideae and Mackinlayoideae, into which the other hydrocotyloid genera had historically been placed. In a more recent phylogenetic study, Nicolas and Plunkett (2009) expanded the sampling to include all but two of the former hydrocotyloid genera, placing nearly all of them within the updated classification system proposed by Plunkett *et al.* (2004). Their circumscription of Azorelloideae closely approximates Drude's Hydrocotyloideae tribe Mulinae (as updated by Pimenov and Leonov, 1993), with only four exceptions, notably the addition of *Stilbocarpa* (formerly placed in Araliaceae) and *Dickinsia* (formerly in tribe Hydrocotyleae), the removal of *Choritaenia* (transferred to subfamily Apioideae – see also Magee *et al.*, 2010), and the inclusion of *Hermas*, whose precise placement remains problematic (Nicolas and Plunkett, 2009). As such, subfamily Azorelloideae includes genera centred mostly in Andean South America (e.g.

Azorella, *Bolax*, *Asteriscium*, *Bowlesia*, *Eremocharis*, *Huanaca*, *Mulinum* and *Spanathe*), and Australia and New Zealand (e.g. *Dichosciadium*, *Diplaspis*, *Oschatizia* and *Schizeilema*), as well as several outliers (e.g. *Dickinsia* in China and *Drusa* in the Canary Islands). The updated classification system of Apioideae [representing an expanded Apioideae *sensu lato* (*s.l.*), including the Saniculoideae] includes the protoapioids, Annesorhizeae, Choritaenieae, Heteromorpheae, Lichtensteinieae, Marlothielleae, Phlyctidocarpeae, Saniculeae and Steganotaenieae, and the euapioids, such as Apieae (e.g. Downie *et al.*, 2001; Magee *et al.*, 2010).

The massive reconfiguration of subfamilies and tribes in Apiaceae has been based largely on phylogenetic analyses of molecular data, but several studies have demonstrated the utility of various fruit morphological characters in helping to delineate clades, including wing configuration, secretory structures, endocarp anatomy, and the presence and distribution of crystals (e.g. Henwood and Hart, 2001; Liu *et al.*, 2003, 2006, 2007*a*, *b*; Liu, 2004). Fruit features have been especially useful in helping to circumscribe subfamily Azorelloideae (Liu *et al.*, 2009), whose genera are united by the shared presence of similar (and presumably homologous) lateral ribs or wings, which are better developed than all other ribs or wings borne on the fruit. Some sub-clades within Azorelloideae are also united by fruit features, e.g. *Bolax*, *Bowlesia*, *Drusa*, *Dichosciadium* and *Homalocarpus*, which all have multicellular stellate trichomes on the fruits, while all other genera (e.g. *Gymnophyton* and *Mulinum*) have smooth surfaces (Liu *et al.*, 2002, 2009; Liu, 2004). Previous studies of a limited number of Azorelloideae, including those of Liu *et al.* (2009) and Nicolas and Plunkett (2009), suggested that the carpophore may also be rich in taxonomic information, an observation that has provided the motivation for the current study. In addition to examining the potential taxonomic value of carpophore features, we also hope to elucidate characters that may support the results based on molecular data (such as the exclusion of *Choritaenia* and the inclusion of *Dickinsia* and *Stilbocarpa*) and provide insights where molecular data remain equivocal (e.g. the placement of *Hermas*) or absent. The radical rearrangement of genera proposed over the last decade also provides a framework for re-interpreting the importance of the carpophore within Apiaceae and for assessing homology and patterns of evolution of this distinctive structure.

In Apiaceae, the carpophore has historically been referred to as an axis or axial structure (Lindley, 1853; Gray, 1879; Drude, 1897–1898; Hutchinson, 1926). It is a thin wiry stalk that supports each half (carpel) of the pendulous dehiscent fruit (Little and Jones, 1980). Jackson (1933) suggested that the carpophore was derived from four ventral vascular bundles of the two carpels, which have become modified to various degrees during floral and fruit development. Vascular bundles are present in members of subfamily Mackinlayoideae but they do not detach from the mericarps and do not form free carpophores, whereas in subfamilies Azorelloideae and Apioideae parts of the fruit including the vascular bundles, if present, usually form free carpophores (Drude, 1897–1898; Tseng, 1967; Henwood and Hart, 2001; Liu *et al.*, 2003; Liu, 2004).

In this study, we examine the carpophore in a wide range of Apiaceae, including subfamilies Mackinlayoideae, Azorelloideae and Apioideae, in order (1) to describe the structural details of the carpophore in a broad sampling of genera of Apiaceae (including near comprehensive sampling of Azorelloideae); (2) to compare any observed differences with the available phylogenies of the family; (3) to assess the level of homology of carpophore structures; (4) to identify characters that may be of value for identifying monophyletic groups and well circumscribed taxonomic entities; and (5) to clarify the confusion surrounding the definition of a carpophore and to propose a standard terminology for the structures derived from the ventral vascular bundles.

MATERIALS AND METHODS

Mature fruits from 99 samples were studied, representing 92 species from 43 genera, including four genera of Apiaceae subfamily Mackinlayoideae, all 24 genera of Azorelloideae (*sensu* Nicolas and Plunkett, 2009) and 15 genera of Apioideae *s.l.* representing all eight tribes of protoapioids (Annesorhizeae, Bupleureae, Heteromorpheae, Lichtensteinieae, Marlothielleae, Phlyctidocarpeae, Saniculeae and Steganotaenieae) and one tribe of euapioids (Apieae). Sample names and voucher information are provided in Appendix 1. Fruit anatomical details of a large number of genera of Apiaceae, as well as Myodocarpaceae and some Araliaceae, were available for comparison from previous studies (e.g. Liu, 2004; Liu *et al.*, 2006, 2009, 2010; pers. obs.), and the corresponding voucher specimens are not included herein (except when used in figures).

Fruits of each species were obtained from herbarium specimens, photographed to document the appearance of the carpophore, rehydrated and placed in FAA (formalin–acetic acid–alcohol) for a minimum of 24 h, and then prepared for sectioning using the glycol methacrylate (GMA) method of Feder and O'Brien (1968). A Leica Ultracut R microtome was used to prepare transverse sections about 5 μm thick. Samples were stained using the periodic acid–Schiff/toluidine blue method (Feder and O'Brien, 1968), and photographed using a Leitz Wetzlar compound microscope and JVC KY-F1030 digital camera. Carpophores of rehydrated fruits were also examined with a stereo-microscope to study their three-dimensional structure.

RESULTS

Carpophores, when present, vary in size, shape and three-dimensional structure (Fig. 1). This can be seen in transverse section, along with variation in the arrangement and size of the vascular bundles (Fig. 2). Sometimes carpophores are not formed (Group A). In these taxa, there is no rigid central structure supporting the mericarps. Two main types of carpophores were identified (Groups B and C), as described below, within which six sub-types were identified (B1–B4, C1 and C2). Their main characters are summarized in Appendix 2, where the genera and species are arranged in subfamilies and tribes according to the classification systems of Nicolas and Plunkett (2009) and Magee *et al.* (2010). Readers unfamiliar with the major suprageneric groups of Apiaceae may find this summary useful.

FIG. 1. Fruits of representatives of Apiaceae showing the shape and type of carpophore: in lateral view in A, B, C1 D1, E1, F1, G1, G2, H1, H2, I, M, N1, O, P, Q1, Q2, R, T1, U1, V, W1, X, Y, Z1, AA1, AA2, BB1, CC1–CC3 and DD–JJ, and in commissural view in C2, C3, R2, R3, S2, S3, W2, W3, BB2 and BB3. (A) *Mackinlaya confusa*. (B) *Asteriscium aemocarpon*. (C1–C3) *Azorella compacta*. (D) *Bolax gummifera*. (E1, E2) *Bowlesia incana*. (F) *Dichosciadium ranuculaceum*. (G1, G2) *Dickinsia hydrocotyloides*. (H1, H2) *Diplaspis hydrocotyle*. (I) *Diposis saniculaefolia*. (J) *Domeykoa amplexicaulis*. (K) *Drusa oppositifolia*. (L) *Eremocharis triradiata*. (M) *Gymnophyton polycephalum*. (N1–N3) *G. isatidicarpum*. (O) *G. robustum*. (P) *Homalocarpus dichotomus*. (Q1, Q2) *Huanaca acaulis*. (R1–R3) *Hermas villosa*. (S1–S3) *Klotzschia glaviozii*. (T1–T3) *Laretia acaulis*. (U1, U2) *Mulinum spinosum*. (V1–V3) *Oschatzia cuneifolia*. (W) *Pozoa volcanica*. (X) *Schizeilema ranunculus*. (Y1, Y2) *Spananthe paniculuta*. (Z1, Z2) *Stilbocarpa lyallii*. (AA1–AA3) *Arctopus echinatus*. (BB1–BB3) *Choritaenia capensis*. (CC) *Annesorhiza altiscapa*. (DD) *Bupleurum mundii*. (EE) *Diplolophium buchananii*. (FF) *Foeniculum vulgare*. (GG) *Heteromorpha involucrata*. (HH) *Lichtenisteinia trifida*. (II) *Phlyctidocarpa flava*. (JJ) *Polemanniopsis marlothii*. Abbreviations: cp, carpophore; pt, parenchyma tissue. Scale bars = 0·4 mm in V3, 3 mm in others.

Group A. Carpophore absent; ventral vascular bundles as long as mericarps, arranged on opposite sides of the commissural plane (Fig. 3A)

This group comprises all members of subfamily Mackinlayoideae studied, which have two vascular bundles arranged on opposite sides of the commissural plane, one in each mericarp, as represented by *Mackinlaya confusa*, both of which remain attached to the mericarps at maturity. This arrangement of the bundles (Fig. 3A, C1, C2) is hereafter referred to as opposite (in contrast to lateral, as in Fig. 3B2–B4). Each bundle shows in transverse section a small to moderate number of xylem elements (e.g. Fig. 2A). Some members of Azorelloideae, such as *Azorella biloba* and *Dichosciadium ranuculaceum*, lack ventral vascular bundles altogether (e.g. see Fig. 2F and Appendix 2) and the two mericarps of intact fruits are connected with parenchyma without any vascular tissue between them. In *Domeykoa* (e.g. see Fig. 2J) and *Eremocharis* (e.g. see Fig. 2L), a conspicuous groove is

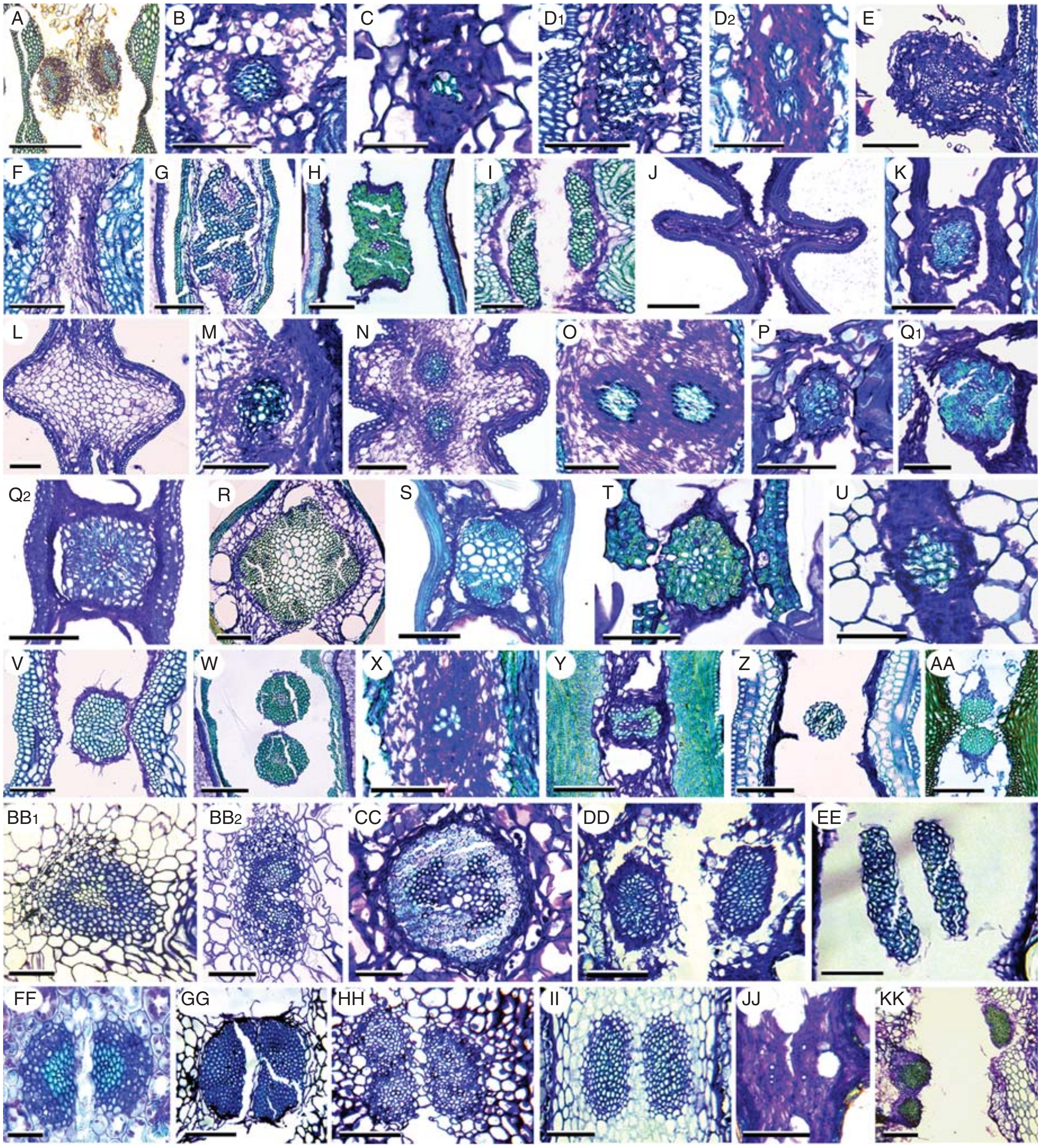

FIG 2. Transverse sections of the central portion of fruits of Apiaceae showing the ventral vascular bundles or vascular bundle(s) of the carpophore. The commissural plane is shown in the middle, with the mericarps on the left and right. (A) *Mackinlaya confusa*. (B) *Astericium aemocarpon*. (C) *Azorella compacta*. (D1) *Bolax gummifera* (Dollenza 147). (D2) *Bolax gummifera* (Moore 743). (E) *Bowlesia incana*. (F) *Dichosciadium ranuculaceum*. (G) *Dickinsia hydrocotyloides*. (H) *Diplaspis hydrocotyle*. (I) *Diposis saniculaefolia*. (J) *Domeykoa amplexicaulis*. (K) *Drusa oppositifolia*. (L) *Eremocharis triradiata*. (M) *Gymnophyton polycephalum*. (N) *G. isatidicarpum*. (O) *G. robustum*. (P) *Homalocarpus dichotomus*. (Q1) *Huanaca acaulis* (Donat 128). (Q2) *Huanaca acaulis* (Dusèa 5315). (R) *Hermas villosa*. (S) *Hermas ciliata*. (T) *Klotzschia glaviozii*. (U) *Laretia acaulis*. (V) *Mulinum spinosum*. (W) *Oschatzia cuneifolia*. (X) *Pozoa volcanica*. (Y) *Schizeilema ranunculus*. (Z) *Spananthe paniculuta*. (AA) *Stilbocarpa lyallii*. (BB1) *Arctopus echinatus* (Magee and Boatwright 6) (BB2) *Arctopus echinatus* (Van Wyk s.n., 14 Oct. 1993). (CC) *Choritaenia capensis*. (DD) *Annesorhiza altiscapa*. (EE) *Bupleurum mundii*. (FF) *Diplolophium buchananii*. (GG) *Foeniculum vulgare*. (HH) *Heteromorpha involucrata*. (II) *Lichtenisteinia trifida*. (JJ) *Phlyctidocarpa flava*. (KK) *Polemanniopsis marlothii*. Scale bar = 0·05 mm.

visible at the commissural face. Opposite vascular bundles (as found in Mackinlayoideae) are also present in *Lichtensteinia obscura* (tribe Lichtensteinieae) and *Phlyctidocarpa flava* (tribe Phlyctidocarpeae) of subfamily Apioideae (e.g. Figs 1II and 2JJ). The absence or partial absence of a free carpophore has been reported in generic descriptions for an additional 30 genera of Apioideae, including *Bifora*, *Bunium* (some species), *Chamaesciadium*, *Cortiella*, *Cymopterus* (some species), *Dimorphosciadium*, *Echinophora*, *Ergocarpon*, *Erigenia*, *Exoacantha*, *Grammosciadium*, *Hohenackeria*, *Hymenidium*

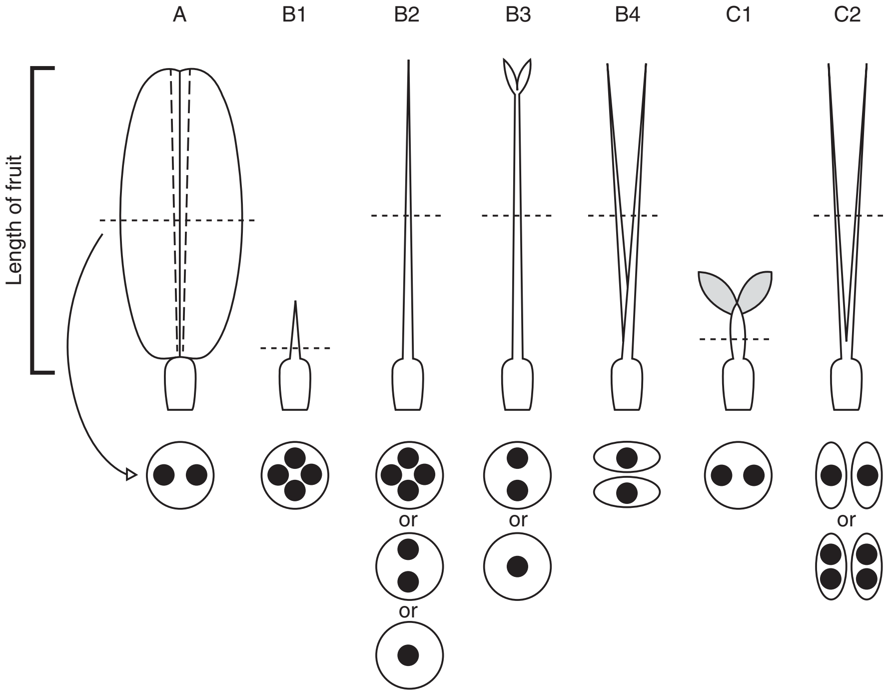

FIG. 3. Simplified diagrammatic illustrations of the ventral vascular bundles (A), the various types of carpophores identified (B1–B4 and C1–C2) and the arrangement of vascular bundles in transverse section. The ventral vascular bundles and carpophores are shown in lateral view, so that the commissural plane runs vertically through the middle of each transverse section.

(rarely), *Ledebouriella*, *Lilaeopsis*, *Lipskya*, *Marlothiella* (sometimes), *Naufraga*, *Oenanthe*, *Oreoxis*, *Orogenia*, *Pycnocycla* (some species), *Pyramidoptera*, *Rhysopterus*, *Sajanella*, *Shoshonea*, *Symphyoloma*, *Thaspium*, *Trachydium* and *Vanasushava*.

Group B. Carpophores mostly entire with vascular bundles single or, if more than one, then arranged side by side within the commissural plane

The carpophores in members of this group may be entire (i.e. completely undivided, cleft only at the tip, as in many of the genera studied) or bifurcate. It therefore differs from Group C mainly in the lateral arrangement of the vascular bundles (i.e. they are located within the commissural plane, as shown in Fig. 3B2–B4) (see also Fig. 2D2, G, H, N, W, AA, BB2. Four sub-groups are recognized within Group B (B1–B4).

(B1) Carpophores short and entire (Fig. 3B1). This type of carpophore, which is only about 30 % of the mericarp length, appears to be very rare, having been observed only in *Bowlesia incana* (Fig. 1E2). Because of its short length, it may not be visible in all median transverse sections. This type of carpophore contains four vascular bundles arranged in a cross between the two mericarps (Fig. 2E).

(B2) Carpophores as long as mericarps, with no obvious apical cleft (Fig. 3B2). A large number of taxa of subfamily Azorelloideae exhibit this type of carpophore (e.g. see Fig. 1B, C2, C3, D2, K, M, P, R2, R3, S2, S3, T2, T3, U2, AA2, AA3). In some species, the carpophore has thin tips that detach easily from the mericarps at maturity (e.g. Fig. 1C3, R3, S3, T3, AA3), whereas in others the tips tend to be somewhat swollen and remain attached to the mericarps (e.g. Fig. 1U2). In transverse section, the number and arrangement of vascular bundles may vary among closely related species. For example, *Hermas villosa* has four vascular bundles arranged in a cross (Fig. 2R), whereas *H. capitata* and *H. ciliata* have two lateral vascular bundles (arranged within the commissural plane, e.g. Fig. 2S). In *Bolax gummifera* (Moore 743, Fig. 2D2) and *Arctopus echinatus* (Van Wyk *et al.* s.n., Fig. 2BB2), there are two lateral vascular bundles, whereas in *B. gummifera* (Dollenza 147, Fig. 2D1), *Laretia acaulis* (Fig. 2U), *Arctopus echinatus* (Magee and Boatwright 6, Fig. 2BB1) and all other taxa studied there is only a single vascular bundle (e.g. Fig. 2B, C, K, M, P, T, V, X, Y). The presence of two lateral vascular bundles was also observed in *Alepidea amatymbica*, but only a single bundle was found in *A. natalensis.* In *Azorella*, *Laretia* and *Pozoa*, the carpophores are usually thin and contain only a few cells in transverse section (e.g. see Fig. 2C, U, X), but are relatively thick in the other taxa in sub-group B2. Fibres surrounding the vascular bundles were observed in the carpophores of *Hermas* and *Klotzschia* (e.g. Fig. 2R, S, T), but were not obvious in the other members of this subgroup.

(B3) Carpophores as long as mericarps, with an apical cleft (Fig. 3B3). This carpophore type was observed in species of five genera of Azorelloideae, i.e. *Dickinsia* (Fig. 1G1, G2), *Diplaspis* (e.g. see Fig. 1H1, H2), *Huanaca* (e.g. see Fig. 1Q1, Q2), *Spananthe* (Fig. 1Y1, Y2) and *Stilbocarpa* (Fig. 1Z2). When mature, the two mericarps become detached from the carpophore, except in *Stilbocarpa*, which has a small

cleft at the apical 10–20 % of the mericarp. Transverse sections made through the middle of the fruits showed two lateral vascular bundles in the carpophores of *Dickinsia hydrocotyloides* (Fig. 2G), *Huanaca andina*, *H. acaulis* (Duséa 5315, e.g. see Fig. 2Q1), both species of *Diplaspis* (e.g. see Fig. 2H) and *Stilbocarpa lyallii* (Fig. 2AA). In contrast, only a single vascular bundle was observed in *Spananthe paniculata* (Fig. 2Z) and in a second sample of *Huanaca acaulis* (Werdermann 1340) (Fig. 2Q2). In all of these taxa except *Spananthe paniculata*, conspicuous fibres surround the vascular bundle(s).

(B4) Carpophores as long as mericarps and bifurcate (Fig. 3B4). This type of carpophore occurs in some members of Azorelloideae, i.e. *Gymnophyton isatidicarpum* (Fig. 1N2, N3) and both species of *Oschatzia* (e.g. Fig. 1V2). As the fruits mature, the two mericarps become detached from the carpophore in *Oschatzia* but may remain attached in *Gymnophyton*. In *O. cuneifolia* each carpophore half has two or three projections from its tip (Fig. 1V3) that represent points of attachment to the stylopodium. In transverse section, the two carpophore halves are lateral (arranged within the commissural plane, e.g. Fig. 2N, W). In subfamily Apioideae this carpophore type has only been observed in *Astydamia canariensis*. Fibres surround the single vascular bundle in each carpophore half in both species of *Oschatzia* and in *Astydamia canariensis* (e.g. Fig. 2W).

Group C. Carpophores mostly bifurcate with bundles opposite the commissural plane, one (or two) in each mericarp (i.e. opposite bundles)

In some genera of Azorelloideae and most genera of Apioideae, the carpophore bifurcates to the base of the fruit at the point of attachment to the pedicel (type C2), but in *Choritaenia* (type C1) the carpophore is not bifurcate. Within Group C, two sub-groups are recognized.

(C1) Carpophores short, with bipartite parenchyma tissue (Fig. 3C1). Choritaenia capensis is the only taxon sampled that has this type of carpophore, which is very short (approx. 20 % of the mericarp length) and is topped by bipartite parenchyma tissue (Fig. 1BB2, BB3) that is hygroscopic and becomes markedly swollen when moistened, helping to separate the two mericarps (Fig. 1BB1). The entire carpophore is visible in transverse sections made in the lower portion of the fruit and contains two opposite vascular bundles (Fig. 2CC). These vascular bundles are surrounded by fibres.

(C2) Carpophores as long as mericarps, bifurcate with the halves on opposite sides of the commissural plane (Fig. 3C2). Within Azorelloideae this type of carpophore has only been observed in *Diposis saniculaefolia*, *D. bulbocastanum* (e.g. Fig. 2I) and *Gymnophyton robustum* (Fig. 2O), but it is the most common type in subfamily Apioideae (e.g. Fig. 1CC–HH, JJ). It is present in protoapioid taxa such as *Lichtensteinia trifida* (tribe Lichtensteinieae, Figs 1HH and 2II), *Polemanniopsis marlothii* (tribe Steganotaenieae, Figs 1JJ and 2KK), *Annesorhiza altiscapa* (tribe Annesorhizeae, Figs 1CC and 2DD), *Heteromorpha involucrata* (tribe Heteromorpheae, Figs 1GG and 2HH) and *Bupleurum mundii* (tribe Bupleureae, Figs 1DD and 2EE), as well as in euapioids such as *Diplolophium buchananii* (tribal placement uncertain, Figs 1EE and 2FF) and *Foeniculum vulgare* (tribe Apieae, Figs 1FF and 2GG). However, in *Heteromorpha involucrata* and *Polemanniopsis marlothii* (e.g. Fig. 2HH, KK), each carpophore half may be composed of two vascular bundles (Fig. 3C2).

DISCUSSION

The range of variation in carpophore types observed in this study (Fig. 3) provides sufficient insight to address the confusion surrounding the definition of a carpophore, and the disparate way this term is applied (e.g, the ‘carpophore absent’ of some authors may correspond to ‘ventral bundles forming a non-free carpophore’ of other authors). Our study has shown that ventral vascular bundles may be absent or present, and a carpophore may be absent or present. We propose here that a carpophore is absent when the ventral vascular bundles and surrounding elements do not form a central rigid supporting structure, and present when such a structure is visible. The ventral vascular bundles can be described by their number (0, 1, 2 or 4) and arrangement (opposite or lateral), regardless of whether they form a carpophore. Characterizing the number and arrangement of vascular bundles is an important first step towards understanding the homology among various carpophore types. It seems logical to us to reserve the term carpophore (i.e. ‘fruit carrier’) for structures where the vascular bundles form a definite supporting structure or ‘stalk’ to which the mericarps are attached in various ways. Depending on the degree of attachment (at the tip only or along its entire length), the carpophore can be described as free, partly free or non-free. The carpophore may be entire (not divided into two), bifid (cleft to various degrees) or bifurcate (split entirely into two parts down to the point of attachment). It may be useful to distinguish between various cleft carpophore types on the basis of the depth of the split (where this information is known and/or invariable); it may be apically cleft (split into two at the tip only), cleft (split for 1/4 to 1/2 of its length), parted (split for 1/2 to 3/4 of its length) or divided (split for more than 3/4 of its length but not entirely to the point of attachment).

Based on the results of our study, carpophores appear to be absent in Mackinlayoideae and in species of about 30 genera of Apioideae (e.g. *Lichtensteinia obscura* and *Phlyctidocarpa flava*) (Liu *et al.*, 2002; Liu, 2004), whereas they are present in a diverse range of structural types in Azorelloideae, exceeding the diversity found in any other suprageneric group of Apiaceae. The only members of Apioideae tribe Saniculeae known to have a carpophore are *Alepidea* and *Arctopus*, where it is entire. In the rest of Saniculeae, the two mericarps are connected with parenchyma cells and no vascular tissue is found between them. Elsewhere in other Apioideae, the carpophore usually bifurcates to the base of the fruit, with the vascular bundles opposite (pers. obs.).

The structure of the ventral vascular bundle found in members of subfamily Mackinlayoideae and the apioid tribes Lichtensteinieae and Phlyctidocarpeae (Group A) was also observed in *Panax ginseng*, a species of Araliaceae. Most species of Azorelloideae (Group B) have entire carpophores that vary in length, type of apex, and number and arrangement of vascular bundles, depending on the genus. Among our sample of azorelloids, carpophores corresponding to type B1 were found only in *Bowlesia incana.* In earlier studies by Mathias and Constance (1965) and Tseng (1967), no carpophore was observed in this species, probably because it does not reach the middle of the fruit where transverse sections are typically made. No carpophore was observed in the two other species of *Bowlesia* studied.

Type B2 carpophores are most common in Azorelloideae. Within this subfamily, the placement of *Klotzschia* and *Hermas* remains somewhat tenuous, although in the most recent and comprehensive survey of Apiales (Nicolas and Plunkett, 2009), *Klotzschia* was included in Azorelloideae as sister to all remaining genera of that subfamily, whereas *Hermas* was excluded from Azorelloideae altogether. The fruits of *Klotzschia*, with five prominent ribs on each mericarp, and those of *Hermas* (e.g. *H. capitata*, *H. ciliata* and *H. villosa*), that have a basal median wing accompanying two lateral wings, are distinctly different from those of all taxa of Azorelloideae (Liu *et al.*, 2009). Branching and anastomosing secretory canals like those seen in *Klotzschia* and *Hermas* (and also in *Dickinsia*, see below) also characterize some Araliaceae (e.g. *Cussonia kraussii*, *Dendropanax chevalieri* and *Oplopanax horridus*) and all members of Myodocarpaceae (*Delarbrea* and *Myodocarpus*) (Liu *et al.*, 2009, pers. obs.). In their morphological–cladistic study of hydrocotyloids (as classically defined), Henwood and Hart (2001) included *Drusa* with *Homalocarpus* because both have calyces that form an entire rim, stellate trichomes and opposite leaves. Stellate trichomes also occur in *Bolax* and *Bowlesia* (Tseng, 1967; Liu *et al.*, 2009), and many studies have suggested a close relationship among these four genera (Hakansson, 1952; Mathias and Constance, 1965; Henwood and Hart, 2001; Plunkett *et al.*, 2004; Nicolas and Plunkett, 2009). Molecular data support a close relationship between *Mulinum*, *Azorella* and *Laretia* (Nicolas and Plunkett, 2009). Our study shows that some species of *Azorella* (e.g. *A. incisa* and *A. multifida*) have prominent lateral ribs similar to those of the species of *Mulinum* studied (Liu *et al.*, 2009). Henwood and Hart (2001) suggested a close relationship between *Pozoa* and *Asteriscium* as both genera possess non-inflexed petal apices, and together with *Gymnophyton* they also formed a clade in the molecular study of Nicolas and Plunkett (2009), although species of *Gymnophyton* exhibit three different carpophore types (B2, B4 and C2).

Fruits with carpophore type B2 are also found in Myodocarpaceae (e.g. *Delarbrea collina*) as well as in the only two members of Apioideae tribe Saniculeae with carpophores (Liu *et al.*, 2010). This type of carpophore has not been found in any other species of subfamily Apioideae examined to date. The simplicity of type B2 carpophores, coupled with the placement of these taxa across many different lineages in Apiales, may indicate that it represents an early stage in the evolution of this structure. Similar carpophore-like structures are also found in some Araliaceae, where Baumann (1946) regarded the distinct, central, rod-like structure in the mature fruits of *Fatsia japonica* as morphologically homologous to the carpophores of Apiaceae. Our results appear to be consistent with this idea, as entire carpophores have also been observed in *Trachymene ornata*, another member of the Araliaceae.

Carpophore type B3 characterizes all species sampled of *Dickinsia*, *Diplaspis*, *Huanaca*, *Spananthe* and *Stilbocarpa*. A similar type of carpophore is also found in some Araliaceae (e.g. *Trachymene adenodes*) (pers. obs.). An earlier study of fruit anatomical features suggested a close relationship between *Dickinsia* and *Diplaspis* (Liu *et al.*, 2002), a result that was subsequently corroborated by molecular data (Nicolas and Plunkett, 2009). In the present study, we have found that the carpophores of *Huanaca acaulis* (Duséa 5315) and *H. andina* are very similar to those of *Dickinsia*, *Diplaspis* and *Stilbocarpa* in having apical clefts and two vascular bundles, but the latter feature is not found in *Spananthe*. Molecular analyses have placed all of these genera together with other taxa in the same large clade (referred to as the '*Azorella* clade' in Nicolas and Plunkett, 2009), although they do not form a single sub-clade within that group.

In some members of Azorelloideae, the carpophore bifurcates to the base (type B4) and the two carpophore halves are situated side by side in the commissural plane (vascular bundles lateral). *Gymnophyton* and *Oschatzia* were placed together in a clade on the basis of molecular data (the '*Gymnophyton* sub-clade' of Nicolas and Plunkett, 2009), albeit not sister to one another. Notwithstanding their similar carpophore structure, fruits from these two genera differ in overall shape (Fig. 1N1, V1): the two mericarps of *Gymnophyton isatidicarpum* are strongly dorsally compressed and have lateral wings, while those of *Oschatzia* are more or less isodiametric (Liu *et al.*, 2009). Outside Azorelloideae, a similar carpophore structure (i.e. with lateral vascular bundles) is only known in *Astydamia canariensis* (subfamily Apioideae), but two lateral bundles not forming a carpophore occur in *Delarbrea michieana* of Myodocarpaceae and many bicarpellate genera of Araliaceae (e.g. *Cussonia zuluensis*, *Eleutherococcus trifoliatus*, *Merrilliopanax listeri*, *Metapanax davidii*, *Polyscias sambucifolia* and *Tetrapanax papyrifer*).

The unusual carpophore (type C1) observed in *Choritaenia* appears to be unique within Apiaceae (Liu *et al.*, 2007*a*). The two vascular bundles present in the single carpophores are opposite, an arrangement similar to that in most Apiaceae, although in the latter the carpophores bifurcate to the base resulting in the vascular bundles becoming ultimately separated. The carpophore in *Choritaenia* is topped by hygroscopic parenchyma tissue that serves to separate the mericarps when wet and thereby presumably facilitates their dispersal. Features of the secretory vesicles in *Choritaenia* (Liu *et al.*, 2007*a*, 2009) resemble those found in *Smyrniopsis* and *Bilacunaria* of subfamily Apioideae (Liu, 2004; Liu *et al.*, 2007*a*) although in *Choritaenia* they are found in the fruit wings whereas in the two other genera they are dispersed in the mesocarp. The molecular studies of Nicolas and Plunkett (2009) and Magee *et al.* (2010) placed this genus in a clade with *Lichtensteinia*.

Carpophore type C2 is characteristic for most genera of subfamily Apioideae (pers. obs.) and is also seen in a few Azorelloideae (two species of *Diposis* and one of *Gymnophyton*). A close relationship between *Diposis* (*D. bulbocastanum* and *D. saniculifolia*) and *Gymnophyton*

(*G. flexuosum*, *G. isatidicarpum*, *G. polycephalum*, *G. robustum* and *G. spinosissimum*) was hypothesized by Tseng (1967) based on the shared presence of wings derived from the lateral ribs of the fruit, but these genera were placed far from one another in the molecular phylogenetic study of Nicolas and Plunkett (2009), suggesting that additional molecular phylogenetic study including all species of *Gymnophyton* is necessary to confirm whether it is monophyletic.

In Azorelloideae, vascular bundles are lacking altogether in most species sampled of *Azorella*, *Dichosciadium*, *Domeykoa* and *Eremocharis*, and in all species sampled of *Schizeilema* (except *S. ranunculus*). A close relationship between *Dichosciadium* and *Bolax* has been shown by molecular studies (Plunkett *et al.*, 2004; Nicolas and Plunkett, 2009). These genera are characterized by the presence of multicellular stellate trichomes, which are restricted to the pedicels of *Dichosciadium ranunculaceum* (Liu *et al.*, 2009) but occur on the fruit in *Bolax* and other members of the '*Bowlesia* clade' (which also includes *Bowlesia*, *Homalocarpus* and *Drusa*). *Domeykoa* and *Eremocharis*, which also lack ventral vascular bundles, share an intrusively sulcate endocarp on the commissural side of each mericarp (Mathias and Constance, 1965; Tseng, 1967) and are closely related to one another based on molecular data (Nicolas and Plunkett, 2009). Most samples of *Azorella* examined in our study also lack ventral vascular bundles (apart from *A. compacta*). This genus is marked by a diversity of wing types (Liu *et al.*, 2009), which is consistent with suggestions made in several molecular studies (Chandler and Plunkett, 2004; Andersson *et al.*, 2006; Nicolas and Plunkett, 2009) that *Azorella* may not be monophyletic. Nicolas and Plunkett (2009) also provided evidence for the polyphyly of *Schizeilema*, in particular with regard to the placement of *S. ranunculus*, a finding that is supported by our results, which show that vascular bundles are lacking in all species except *S. ranunculus*, where they are present and form a carpophore. Elsewhere in the family, the loss of a carpophore seems to have occurred several times in distinct lineages, namely in all members of subfamily Mackinlayoideae examined to date, and within Apioideae in species of about 30 genera, including all sampled genera of tribe Saniculeae (except *Alepidea* and *Arctopus*), members of tribes Lichtensteinieae, Phlyctidocarpeae and Oenantheae (although it should be noted that the fruits of Mackinlayoideae, Lichtensteinieae and Phlyctidocarpeae have ventral vascular bundles). A more detailed understanding of the phylogenetic structuring of carpophore loss within Apioideae will, however, require more comprehensive sampling from throughout the subfamily.

The recent fruit anatomical studies of Liu *et al.* (2009) suggested that almost all of the taxa placed in Drude's (1897–1898) tribe Mulineae by Pimenov and Leonov (1993) should be included in Azorelloideae, with the exception of *Choritaenia* and *Klotzschia*, whose fruits differ significantly from those of the other genera in their general morphology and anatomy. This finding was largely confirmed by Nicolas and Plunkett (2009), based on molecular data, with two notable exceptions. Their molecular analyses suggested that *Klotzschia* may arguably be treated as part of Azorelloideae, and that *Hermas* appears to be an early diverging lineage in Apioideae.

Among the remaining genera of Azorelloideae, our study has shown that carpophores are rich in taxonomically informative characters. Most azorelloid genera have entire carpophores with or without an apical cleft, and with one or two lateral vascular bundles (types B2 and B3). A similar structure is present in Araliaceae (e.g. *Trachymene adenodes* and *T. ornata*), Myodocarpaceae (e.g. *Delarbrea collina*, *D. longicarpa* and all species of *Myodocarpus*) and Apioideae tribe Saniculeae (*Alepidea* and *Arctopus*) (Liu *et al.*, 2010). Similarly structured carpophores are also found in the azorelloid taxa *Oschatzia* and *Gymnophyton isatidicarpum*, although they bifurcate into halves (type C1). In *Bolax* and *Laretia*, one or two vascular bundles appear in different fruits of the same species, as in *Myodocarpus fraxinifolius* (Myodocarpaceae), in which the two bundles that are often visible in young fruits seem to become merged in later developmental stages. Some other members of Azorelloideae (i.e. *Diposis* and *Gymnophyton robustum*) have two carpophore halves opposite rather than lateral, a situation also found in the majority of taxa in subfamily Apioideae, including both protoapioids (e.g. *Lichtensteinia* and *Polemanniopsis*) and euapioids (e.g. *Anethum* and *Angelica*).

Carpophore morphology and anatomy provide potentially useful synapomorphies for some clades of Azorelloideae, while in others there is a surprising diversity of forms where no obvious synapomorphies can be identified. Most species of *Azorella* sampled in our study lack carpophores altogether, with the notable exception of *A. compacta*, but this is perhaps not so surprising given that molecular data have shown this genus to be polyphyletic. Indeed, the type of carpophore found in *A. compacta* (type B2) also occurs in the monotypic genus *Laretia*, a finding that is consistent with the sister group relationship between these two taxa in the study of Nicolas and Plunkett (2009). Similarly, molecular data indicate that *Schizeilema* is polyphyletic (Nicolas and Plunkett, 2009), which is consistent with our finding that the single South American species (*S. ranunculus*) has type B2 carpophores whereas the species from New Zealand and Australia, which comprise a separate clade, all lack carpophores. Elsewhere in the broader '*Azorella* clade', as defined by Nicolas and Plunkett (2009), carpophore structure is quite diverse, but members of all the earliest diverging lineages (i.e. *Dickinsia*, *Diplaspis*, *Huanaca*, *Spananthe* and *Stilbocarpa*) have type B3 carpophores.

Nicolas and Plunkett (2009) also recognized two other major clades in Azorelloideae, the '*Asteriscium* clade' and the '*Bowlesia* clade'. In the *Asteriscium* clade, all samples of *Asteriscium* and *Gymnophyton* form a single clade, although the two genera are not strictly monophyletic. The samples of *Asteriscium* examined here all have entire (type B2) carpophores, as do two of the species of *Gymnophyton* (along with the two samples from the closely related genus *Pozoa*). However, two other *Gymnophyton* species have bifurcate carpophores (type B4 in *G. isatidicarpum* and C2 in *G. robustum*). Other members of the '*Asteriscium* clade' include *Oschatzia* (type B4) and the *Eremocharis*-*Domeykoa* sub-clade (carpophores lacking). In the *Bowlesia* clade, samples of *Bolax* and *Homalocarpus* examined here all have type B2 carpophores, whereas *Bowlesia incana* has type B1 carpophores, which are known from no other taxon examined to date. The remaining samples of *Bowlesia*, along with material of *Dichosciadium*, all lack carpophores.

Molecular data have proven indispensable in helping to sort out the complex phylogenetic relationships in Apiaceae, but structural characters are needed to support the recircumscription of the taxa into recognizable groups. Carpophore structure appears to be a potentially rich source of such characters in Azorelloideae and Apiales in general. The presence or absence of a free carpophore is of diagnostic value in several genera, but the arrangement of the vascular bundles is not yet known for most of them. It would be potentially valuable to compare more detailed anatomical results with phylogenetic hypotheses based on other sources of data, in particular molecular markers. The ecological significance of carpophores should also be taken into consideration as they function mainly as an aid to the dispersal of the mericarps by wind. Carpophores may be less prominent or absent in species with fruits dispersed by water or animals. It is clear that the presence of a carpophore has been lost (and perhaps also gained) multiple times in Apiaceae and that similar carpophore morphologies have evolved in parallel across various clades. Further insight into how the structures that comprise carpophores have evolved may require comparative developmental studies to evaluate whether apparently similar features represent homologies or are the result of convergence. Such a line of investigation would also help to identify those features that are most useful for defining and recognizing taxa at various ranks within the family.

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APPENDIX 1

Taxa of Apiaceae examined for ventral vascular bundle and carpophore features, together with voucher specimen details and geographic origin

Species	Voucher specimens or accession number and herbarium where deposited	Origin
Alepidea amatymbica Ecklon & Zeyh	Schelpe 97 (JRAU)	South Africa
A. natalensis J.M. Wood & M.S.Evans	De Castro 186 (JRAU)	South Africa
Annesorhiza grandiflora (Thunb.) Hiroe	Acocks 18611 (PRE)	South Africa
A. altiscapa Schltr. ex H.Wolff .	Van Wyk & Tilney s.n. (JRAU)	South Africa
A. lateriflora (Ecklon & Zeyh.) B.-E.van Wyk	Marloth 9694*b* (PRE)	South Africa
A. latifolia Adamson	Van Wyk 3674*b* (JRAU)	South Africa
Arctopus echinatus L.	Van Wyk s.n., 14 Oct. 1993 (JRAU)	South Africa
A. echinatus	Magee & Boatwright 6 (JRAU)	South Africa
A. dregei Sond.	Helme 2574 (NBG)	South Africa
A. monacanthus Carmich. ex Harv. & Sond.	Mauve & Hugo 49 (PRE)	South Africa
Asteriscium aemocarpon Clos	Moore 393A (K)	Chile
A. chilense Cham. & Schltdl.	Worth & Morrison 16376 (K)	Argentina
Astydamia canariensis DC.	Murray s.n. (K)	Canary Islands
Azorella biloba (Schltdt.) Wedd.	Hill 191 (K)	Peru
A. compacta Phil.	Venturi B161 (K)	Chile
A. corymbosa (Ruiz & Pav.) Pers.	Ramsay & Merrow-Smith 376 (K)	Ecuador
A. diapensioides A.Gray	Hugh & Iltis 1252 (K)	Peru
A. diversifolia Clos	Constance & Sparre 3564 (K)	Chile
A. filamentosa Lam.	Moore 1896 (K)	Argentina
A. monantha Clos	Chandler & Bayer 1113 (PRE)	Argentina
A. multifida (Ruiz & Pav.) Pers.	Hutchison 1625 (F)	Peru
A. pedunculata (Spreng.) Mathias & Constance	Grubb *et al.* 597 (K)	Ecuador
A. trifurcata (Gaertn.) Pers.	Pedersen 14438 (F)	Argentina
Bolax gummifera (Lam.) Spreng.	Dollenza 147 (GH)	Argentina
B. gummifera	Moore 743 (K)	Argentina
B. gummifera	Chandler 1122 (PRE)	Argentina
Bowlesia flabilis J.F.Macbr.	Pringle 1248 (K)	Mexico
B. incana Ruiz & Pav.	Dale Thones *et al.* 17972 (NY)	USA
B. tropaeolifolia Gillies & Hook.	Chandler 1895 (PRE)	Peru
Bupleurum exaltatum M.Bieb.	Axlubsole 27 (PE)	Russia
B. fruticosum L.	Vienue s.n. (PE)	France
B. gracillimum Klotzsch	Zhang 1538 (PE)	China
B. junceum L.	Halásesy s.n. (PE)	Hungary
B. mundtii Cham. & Schltdl.	Jacobsz 3089 (PRE)	South Africa
Centella linifolia Drude	Van Wyk s.n. (JRAU)	South Africa
C. pottebergensis Adamson	Adamson 4302 (PRE)	South Africa
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
Diplolophium buchananii C.Norman	De Castro 150 (JRAU)	Zimbabwe
Diposis bulbocastanum DC.	Pirion 1741 (GH)	Chile
D. saniculifolia DC.	Gilbert 426 (K)	Uruguay
Domeykoa amplexicaulis (H.Wolff) Mathias & Constance	Stafford 805 (K)	Peru
D. saniculifolia Mathias & Constance	Ellenberg 2730 (U)	Chile
Drusa glandulosa (Poir.) H.Wolff ex Engl.	Jahandiez 37712 (RAB)	Morocco
Eremocharis fruticosa Phil.	Johnston 5247 (GH)	Peru
E. longiramea (H.Wolff) I.M.Johnst.	Hutchison & Wright 3487 (U)	Peru
E. triradiata (H.Wolff) I.M.Johnst.	Solomon 3064 (F)	Peru
Eryngium foetidum L.	PE 00183 (PE)	Caribbean
Foeniculum vulgare L.	HANU 20258 (HANU)	China
Gymnophyton flexuosum Clos	Looser 4259 (GH)	Chile
G. isatidicarpum (C.Presl ex DC.) Mathias & Constance	Schlegel 5867 (F)	Chile
G. polycephalum (Gillies & Hook.) Clos	Werdermann 154 (U)	Chile
G. robustum Clos	Zollner 5128 (U)	Chile
Hermas capitata L.f.	Bolus 9111 (PRE)	South Africa
H. ciliata L.f.	Pillans 6742 (BOL)	South Africa
H. villosa Thunb.	Compton 16844 (PRE)	South Africa
Heteromorpha arborescens Cham. & Schltdl. var. *arborescens*	PRE 3264 (PRE)	South Africa
H. arborescens Cham. & Schltdl. var. *trifoliata* (Wendl.) Sond.	JRAU 89055 (JRAU)	South Africa

Continued

Appendix *Continued*

Species	Voucher specimens or accession number and herbarium where deposited	Origin
H. arborescens var. *trifoliata*	Winter 716 (JRAU)	South Africa
H. involucrata Conrath	Winter 3491 (JRAU)	South Africa
H. pubescens Burtt Davy	Winter 2837 (UNIN)	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. acaulis	Duséa 5315 (K)	Patagonia
H. andina (Phil.) Phil.	Werdermann 1340 (U)	Chile
Klotzschia brasiliensis Cham.	Irwin *et al.* 21900 (SP)	Brazil
K. glaziovii Urb.	Ratter & Bridgwate 7227 (K)	Brazil
K. rhizophylla Urb.	Anolusen *et al.* 36097 (SP)	Brazil
Laretia acaulis (Cav.) Gillies & Hook.	Werdermann 646 (U)	Chile
Lichtensteinia obscura (Spreng.) Koso-Pol.	Salter 8991 (NBG)	South Africa
L. trifida Cham. & Schltdl.	Van Wyk 4106 (JRAU)	South Africa
Mackinlaya confusa Hemsl.	Plunkett, Jensen & Oskolski 1549 (NY)	Australia
Marlothiella gummifera H.Wolff. fruit 1	Merxmueller 4957 (PRE)	Namibia
M. gummifera fruit 2	Merxmueller 4957 (PRE)	Namibia
Micropleura renifolia Laq.	Mc Vaugh 13003 (MICH)	USA
Mulinum albovaginatum Gillies & Hook.	Chandler & Bayer 1105 (PRE)	Argentina
M. echinus DC.	Constance 3832 (K)	Patagonia
M. hallei Skottsb.	Santesson 225 (K)	Argentina
M. leptactanthum Phil.	Elwre s.n. (K)	Chile-Argentina border
M. spinosum (Cav.) Pers.	Hutchison 3051 (NY)	Chile
Oschatzia cuneifolia (F.Muell.) Drude	Briggs 4782 (NSW)	Australia
O. saxifraga (Hook.f.) Walp.	Grof 10133 (CBG)	Australia
Phlyctidocarpa flava Cannon & Theobald	Giess *et al.* 6075 (PRE)	Namibia
Polemanniopsis marlothii (H.Wolff) B.L.Burtt	Jacobsen 2230 (PRE)	South Africa
Pozoa coriacea Lag.	Comber 1211 (K)	Chile
P. coriacea Lag.	Werdermann 1226 (U)	Chile
P. volcanica Mathias & Constance	Constance & Sparre 3578 (K)	Chile
Sanicula elata Buch.-Ham. ex D.Don	De Castro 197 (JRAU)	South Africa
Schizeilema colensoi Domin	CHR 286768 (CHR)	New Zealand
S. fragoseum (F.Muell.) Domin	Johnson 15875 (K)	Argentina
S. haastii (Hook.f.) Domin	Cheeseman 59 (K)	New Zealand
S. ranunculus Domin	Moore 2628 (K)	Argentina
Spananthe paniculata Jacq.	Sagastegui 10524 (MO)	Peru
Steganotaenia araliacea Hochst.	Tilney s.n. (JRAU)	South Africa
Stilbocarpa lyallii J.B.Armstr.	CHR 355324 (CHR)	New Zealand
Xanthosia pilosa Rudge	Canning 3919 (CBG)	Australia

Herbarium acronyms follow Holmgren *et al.* (1990).

APPENDIX 2

Summary of taxonomically important characters of the carpophore in various taxa of Apiaceae

Subfamilies, tribes, groups, genera and species	Carpophore characters				
	CT	CL	CS	VB	VA
Subfamily Mackinlayoideae:					
Centella linifolia	A	Long	Bifurcate	2	Opposite
C. pottebergensis	A	Long	Bifurcate	2	Opposite
Mackinlaya confusa	A	Long	Bifurcate	2	Opposite
Micropleura renifolia	A	Long	Bifurcate	2	Opposite
Xanthosia pilosa	A	Long	Bifurcate	2	Opposite
Subfamily Azorelloideae:					
Azorella clade:					
Azorella biloba	Ø	–	–	–	–
A. compacta	B2	Long	Entire	1	–
A. corymbosa	Ø	–	–	–	–

Continued

APPENDIX *Continued*

	Carpophore characters				
Subfamilies, tribes, groups, genera and species	CT	CL	CS	VB	VA
A. diapensioides	Ø	–	–	–	–
A. filamentosa	Ø	–	–	–	–
A. diversifolia	Ø	–	–	–	–
A. monantha	Ø	–	–	–	–
A. multifida	Ø	–	–	–	–
A. pedunculata	Ø	–	–	–	–
A. trifurcata	Ø	–	–	–	–
Dickinsia hydrocotyloides	B3	Long	Entire	2	Lateral
Diplaspis hydrocotyle	B3	Long	Entire	2	Lateral
D. nivis	B3	long	Entire	2	Lateral
Huanaca acaulis 1	B3	Long	Entire	1	–
H. acaulis 2	B3	Long	Entire	2	lateral
H. andina	B3	Long	Entire	1	–
Laretia acaulis	B2	Long	Entire	1	–
Mulinum albovaginatum	B2	Long	Entire	1	–
M. echinus	B2	Long	Entire	1	–
M. hallei	B2	Long	Entire	1	–
M. leptactanthum	B2	Long	Entire	1	–
M. spinosum	B2	Long	Entire	1	–
Schizeilema colensoi	Ø	–	–	–	–
S. fragosea	Ø	–	–	–	–
S. haastii	Ø	–	–	–	–
S. ranunculus	B2	Long	Entire	1	–
Spananthe paniculata	B3	Long	Entire	1	–
Stilbocarpa lyallii	B3	Long	Entire	2	Lateral
Asteriscium clade:					
Asteriscium aemocarpon	B2	Long	Entire	1	–
A. chilense	B2	Long	Entire	1	–
Domeykoa amplexicaulis	Ø	–	–	–	–
D. saniculifolia	Ø	–	–	–	–
Eremocharis fruticosa	Ø	–	–	–	–
E. longiramea	Ø	–	–	–	–
E. triradiata	Ø	–	–	–	–
Gymnophyton flexuosum	B2	Long	Entire	1	–
G. isatidicarpum	B4	Long	Bifurcate	2	Lateral
G. polycephalum	B2	Long	Entire	1	–
G. robustum	C2	Long	Bifurcate	2	Opposite
Oschatzia cuneifolia	B4	Long	Bifurcate	2	Lateral
O. saxifraga	B4	Long	Bifurcate	2	Lateral
Pozoa coriacea	B2	Long	Entire	1	–
P. volcanica	B2	Long	Entire	1	–
Bowlesia clade:					
Bolax gummifera 1	B2	Long	Entire	1	–
B. gummifera 2	B2	Long	Entire	2	Lateral
B. gummifera 3	B2	Long	Entire	1	–
Bowlesia flabilis	Ø	–	–	–	–
B. incana	B1	Short	Entire	4	Forming a cross
B. tropaeolifolia	Ø	–	–	–	–
Dichosciadium ranunculaceum	Ø	–	–	–	–
Drusa glandulosa	B2	Long	Entire	1	–
Homalocarpus bowlesioides	B2	Long	Entire	1	–
H. dichotomus	B2	Long	Entire	1	–
Diposis clade:					
Diposis bulbocastanum	C2	Long	Bifurcate	2	Opposite
D. saniculifolia	C2	Long	Bifurcate	2	Opposite
Incertae cedis:					
Hermas capitata	B2	Long	Entire	2	Lateral
H. ciliata	B2	Long	Entire	2	Lateral
H. villosa	B2	Long	Entire	4	Forming a cross
Klotzschia brasiliensis	B2	Long	Entire	1	–
K. glaziovii	B2	Long	Entire	1	–
K. rhizophylla	B2	Long	Entire	1	–
Subfamily Apioideae:					

Continued

Appendix *Continued*

	Carpophore characters				
Subfamilies, tribes, groups, genera and species	CT	CL	CS	VB	VA
Protoapioids:					
Tribe Saniculeae:					
Alepidea amatymbica	B2	Long	Entire	1	–
A. natalensis	B2	Long	Entire	1	–
Arctopus echinatus 1	B2	Long	Entire	2	Lateral
A. echinatus 2	B2	Long	Entire	1	–
A. dregei	B2	Long	Entire	1	–
A. monacanthus	B2	Long	Entire	1	–
Eryngium foetidum	Ø	–	–	–	–
Sanicula elata	Ø	–	–	–	–
Tribe Steganotaenieae:					
Polemanniopsis marlothii	C2	Long	Bifurcate	2 (4)	Opposite
Steganotaenia araliacea	C2	Long	Bifurcate	2 (4)	Opposite
Tribe Phlyctidocarpeae:					
Phlyctidocarpa flava	A	Long	Bifurcate	2	Opposite
Tribe Choritaenieae:					
Choritaenia capensis	C1	Short	Entire with bipartite parenchyma	2	Opposite
Tribe Lichtensteinieae:					
Lichtensteinia obscura	A	Long	Bifurcate	2	Opposite
L. trifida	C2	Long	Bifurcate	2	Opposite
Tribe Marlothielleae:					
Marlothiella gummifera 1	A	Long	Entire	1	–
M. gummifera 2	Ø	–	–	–	–
Tribe Heteromorpheae:					
Heteromorpha arborescens	C2	Long	Bifurcate	2	Opposite
H. arborescens var. *abyssinica*	C2	Long	Bifurcate	2	Opposite
H. involucrata	C2	Long	Bifurcate	2 (4)	Opposite
H. pubescens	C2	Long	Bifurcate	2	Opposite
H. trifoliata	C2	Long	Bifurcate	2	Opposite
Tribe Annesorhizeae:					
Annesorhiza grandiflora	C2	Long	Bifurcate	2	Opposite
A. altiscapa	C2	Long	Bifurcate	2	Opposite
A. lateriflora	C2	Long	Bifurcate	2	Opposite
A. latifolia	C2	Long	Bifurcate	2	Opposite
Astydamia canariensis	B4	Long	Bifurcate	2	Lateral
Euapioids:					
Tribe Bupleureae:					
Bupleurum exaltatum	C2	Long	Bifurcate	2	Opposite
B. fruticosum	C2	Long	Bifurcate	2	Opposite
B. gracillimum	C2	Long	Bifurcate	2	Opposite
B. junceum	C2	Long	Bifurcate	2	Opposite
B. mundii	C2	Long	Bifurcate	2	Opposite
Tribe Apieae:					
Foeniculum vulgare	C2	Long	Bifurcate	2	Opposite
Ungrouped:					
Diplolophium buchananii	C2	Long	Bifurcate	2	Opposite

Carpophore types (B1–B4 and C1–C2) refer to those described in the text (ventral vascular bundle type shown in A).

CT, carpophore type; CL, carpophore length; CS, carpophore shape; VB, number of vascular bundles in main portion of the carpophore(s); VA, vascular bundle arrangement in relation to the commissural plane (opposite = on either side of the commissural plane; lateral = side by side within the commissural plane); Ø, ventral vascular bundle lacking.