TOWARDS AN UNDERSTANDING OF THE PHYLOGENETIC RELATIONSHIPS OF AUSTRALIAN *HYDROCOTYLOIDEAE* (*APIACEAE*)

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Australian *Apiaceae*, dominated by *Hydrocotyloideae* Link, are characterized by a number of enigmatic genera, the phylogenetic relationships of which are obscure. A cladistic analysis using morphological and anatomical data indicated that *Apiaceae* are monophyletic and *Hydrocotyloideae* form a grade between a paraphyletic *Araliaceae* and a monophyletic *Apioideae* Drude + *Saniculoideae* Burnett. Beyond this, there was no support for past suprageneric arrangements within the order. *Hydrocotyleae* Spreng. and their constituent subtribes were polyphyletic, as were the subtribes of *Mulineae* DC. The relationships between Australian genera were not well resolved although the analysis did provide a good indication of broad generic affinities.

Keywords. Anatomy, *Apiales*, *Araliaceae*, *Hydrocotyleae*, morphology, *Mulineae*, *Umbelliferae.*

Introduction

Currently, 250 species in 46 genera are considered to comprise Australian *Apiaceae* (*Umbelliferae*) (Tables 1, 2). Of these, 80% of species and 27% of genera are endemic to Australia and its offshore islands. Each of Drude's (1898) three subfamilies is represented in Australia, but the diversity within *Hydrocotyloideae* Link. far outweighs that of *Apioideae* Drude and *Saniculoideae* Burnett. Australian *Apioideae* (see Table 1 for full list of genera and authorities) have much in common with those of New Zealand. *Aciphylla* (two species, both endemic) *Gingidia* (three species, one shared with New Zealand), *Anisotome* (one endemic species) and *Oreomyrrhis* (seven species, all endemic) are essentially New Zealand genera found at higher altitudes in Australia. Three species of *Lilaeopsis* occur at lower altitudes. However, most of the remaining genera (18 of the 27 apioid genera) are represented only by introduced species. *Saniculoideae* are represented only by *Eryngium*. Whilst this genus is in need of revision in Australia, it is conservatively thought to consist of about 15 species (Michael, 1999), 12 of which are endemic.

The highest levels of endemism are seen in the *Hydrocotyloideae* (Table 2). This subfamily accounts for 74% of Australian species of *Apiaceae*, and comprises 29% of the world's hydrocotyloid genera and 38% of the world's species (based on Pimenov & Leonov 1993). Of the 18 hydrocotyloid genera found in Australia, 12 are endemic and two (*Trachymene* and *Actinotus*) have about 90% of their species

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TABLE 1. Tribes of *Apioideae*, *Saniculoideae* present in Australia and territories. Genera represented only by introduced or naturalized taxa indicated by *

Subfamily and tribe	Genus	World	Australia
APIOIDEAE			
Apieae	*Aciphylla* J. R. Forst. & G. Forst.	40	2
	**Aegopodium* L.	7	1
	**Ammi* L.	3–4	2
	Anisotome Hook. f.	15	1
	Apium L.	25	4
	**Berula* W. D. J. Koch	2	1
	**Bupleurum* L.	180–191	3
	Carum L.	30	1
	**Crithmum* L.	1	1
	**Cyclospermum* Lag.	3	1
	**Foeniculum* Mill.	4–5	1
	Gingidia J. W. Dawson	10	3
	Lilaeopsis Greene	25	3
	Oenanthe L.	40	2
	**Petroselinum* Hill	2	1
Caucalideae	*Daucus* L.	22	2
	**Torilis* Adans.	15	1
Coriandreae	**Bifora* Hoffm.	3	1
	**Coriandrum* L.	2	1
Peucedaneae	**Anethum* L.	2	1
	**Ferula* L.	170	1
Scandiceae	**Anthriscus* (Pers.) Hoffm.	10–12	1
	**Scandix* L.	5–20	1
Smyrnieae	**Conium* L.	6	1
	Oreomyrrhis Endl.	25	7
Tordylieae	**Pastinaca* L.	14	1
	**Tordylium* L.	18	1
SANICULOIDEAE			
Saniculeae	*Eryngium* L.	230–250	15

restricted to the continent. However, with the exception of *Xanthosia* (20 species), *Platysace* (30 species), *Trachymene* (40 species) and *Actinotus* (20 species) most Australian endemic or near-endemic genera contain no more than three species. Generally, Australia's smaller genera represent segregates from larger, often non-Australian, genera. Thus, the generic diversity of Australian *Hydrocotyloideae* may be a reflection of the current state of taxonomic circumscriptions rather than phylogenetically meaningful taxa.

Arguably the most geographically widespread genus in the subfamily, *Hydrocotyle*, reaches a high level of diversity within Australia. Of the 130 species currently recognized at the world level (Pimenov & Leonov, 1993), c.60 are found in Australia,

TABLE 2. Tribes and subtribes of *Hydrocotyloideae* present in Australia and territories

Genus	World		Australia
HYDROCOTYLEAE			
Hydrocotylinae	*Brachyscias* J. M. Hart & Henwood	1	1
	Centella L.	40	2
	Chlaenosciadium C. Norman	1	1
	Homalosciadium Domin	1	1
	Hydrocotyle L.	130	c.60
	Neosciadium Domin	1	1
	Platysace Bunge	30	c.30
	Trachymene Rudge	45	40
	Uldinia J. M. Black	1	1
Xanthosiinae	*Actinotus* Labill.	21	20
	Pentapeltis Bunge	2	2
	Schoenolaena Bunge	1	1
	Xanthosia Rudge	20	20
MULINEAE			
Azorellinae	*Azorella* Lam.	70	2
	Dichosciadium Domin	1	1
	Diplaspis Hook. f.	3	3
	Oschatzia Walpers	2	2
	Schizeilema (Hook.f.) Domin	13	1

with c.58 of those considered to be endemic. Within the Australian region, *Hydrocotyle* express a range of life histories and habits not seen elsewhere in the genus. In particular, a cohort of annual species largely restricted to semi-arid regions of the country may warrant generic status (Eichler, 1987). In contrast, the predominantly South African *Centella* is poorly represented in Australia. Only one genus, *Azorella*, is common to Australia and South America whilst being absent from New Zealand and its territories. Australia's claim to two species of this predominantly Fuegian genus is merely an artefact of political boundaries for it is found on Australia's subantarctic islands: *A. macquariensis* Orchard, endemic to Macquarie Is., and the more widespread *A. selago* Hook.f. on Heard Is. and other subantarctic islands (Orchard, 1989). *Schizeilema*, on the other hand, is present in New Zealand (11 species; Dawson, 1971), the alpine regions of the Australian mainland (one species) and in South America (one species).

Hydrocotyloideae has traditionally accommodated species with 'woody' endocarps and fruit that lack vittae. Within *Hydrocotyloideae*, Drude recognized two tribes: *Hydrocotyleae* Spreng. (transversely compressed fruit) and *Mulineae* DC. (dorsoventrally compressed fruit). *Hydrocotyleae* was further divided into *Hydrocotylinae* W. D. J. Koch (calyces small or absent) and *Xanthosiinae* Tausch (calyces large). Similarly, Drude considered *Mulineae* to comprise several subtribes: species that

lacked winged fruit but had locelli in the fruit were assigned to *Bowlesiinae* Drude, whereas those that lacked both wings and locelli comprised *Azorellinae* Tausch; species with winged, non-locellate fruit were placed within *Asteriscinae* Drude. Of all Drude's subtribes of *Hydrocotyloideae*, *Xanthosiinae* is almost exclusively Australian. Of the 46 species in four genera assignable to this subtribe, only one species, *Actinotus novae-zelandiae* (Petrie) Petrie occurs outside Australia, in nearby New Zealand (Webb, 1980). In addition, the circumscription of the *Xanthosiinae* amply illustrates Drude's monothetic approach to classification, for *Xanthosiinae* was erected to accommodate taxa with laterally compressed fruit and 'large' calyx limbs. In doing so, all taxa with laterally compressed fruit and reduced or absent calyx limbs constituted his *Hydrocotylinae*.

One is left with the impression, then, that the Australian *Apiaceae* is characterized by relatively high levels of generic and specific endemism manifest in the *Hydrocotyloideae*. This may be either an artefact of taxonomic knowledge, reflect a relatively long period of isolation, or some combination of both.

Recent molecular investigations into the phylogenetic relationships of the *Apiales* have done much to adjust our perceptions of evolutionary affinity within the order (Plunkett *et al.*, 1996a; 1997; Downie *et al.*, 1998). From an Australian perspective, the most intriguing result of this recent wave of research has been the suggestion that that Drude's *Hydrocotyloideae* is polyphyletic (Plunkett *et al.*, 1996a; 1997; Downie *et al.*, 1998). Whilst the thrust of the recent molecular research has been the elucidation of the deeper branches within the order and lineages within *Apioideae*, one can only speculate what insights might be provided when such analyses use a larger sample of *Hydrocotyloideae*. We would certainly concur that the characters traditionally employed in the classification of *Apiales* are afflicted by homoplasy (Plunkett *et al.*, 1996a; Downie *et al.*, 1998; Katz-Downie *et al.*, 1999). Nevertheless, a number of molecular phylogenies have, to a certain extent, been able to successfully map morphological synapomorphies onto molecular trees (Plunkett *et al.*, 1996a; Katz-Downie *et al.*, 1999). So, whilst high levels of morphological homoplasy are common in the order, there appears to be some 'phylogenetic signal' present in the morphological and anatomical data. Part of the difficulty for any analysis of morphological and anatomical data – whether used as primary data or secondarily mapped onto trees – concerns the erection of homology hypotheses based upon (potentially) non-homologous data (e.g. parallel evolution of schizocarpous fruit in *Araliaceae* (*Astrotricha* DC. and *Harmsiopanax* Warb.) and *Apiaceae*). The situation is further compounded by relatively high amounts of missing and/or inapplicable data in some taxa.

More than any other of Drude's subfamilies, the *Hydrocotyloideae* have been surveyed across a range of organ systems at the generic level. We felt, therefore, that it would not be premature to undertake a morphological and anatomical phylogeny focussing on relationships within the subfamily. Our interest in initiating this exercise was primarily to investigate the broad generic affinities of the Australian genera of *Hydrocotyloideae* and, at the same time, to complement the phylogenetic conclusions drawn from molecular data sources.

Materials and Methods

Taxonomic sample

In the absence of comprehensive genus-level phylogenies and for the sake of simplicity, we have assumed that each genus is monophyletic and we used a single species to represent each genus. In view of Eichler's (1986) comments concerning the putative generic status of the annual species of *Hydrocotyle*, we have included a representative of each life-history form from this genus. In general, our selection of taxa was aimed at providing a representative sample of genera that have previously provided the 'backbone' of molecular phylogenies (Plunkett *et al.*, 1996a; 1997; Downie & Katz-Downie, 1999). However, given our focus on Australian genera, we were obliged to emphasize genera within Drude's (1898) *Hydrocotyloideae*. The choice of genera was influenced by the availability of comparative and (relatively) unambiguous morphological and anatomical data. Thus, four of the five hydrocotyloid genera listed as *incertae sedis* by Pimenov & Leonov (1993), plus *Dickinsia* Franch. and *Choritaenia* Benth., were excluded.

Our selection of non-hydrocotyloid taxa was similarly constrained. Representatives of *Pittosporaceae* were used as the outgroup following results of Plunkett *et al.* (1996a). Seventeen taxa of *Araliaceae* (*sensu* Harms, 1898) were included. In order to test the phylogenetic resolution in our data set we considered it appropriate to select genera that were indicative of the topologies derived from the molecular phylogenies of Plunkett *et al.* (1996a; 1997). However, only genera with a reasonable availability of data were eventually included. The inclusion of 10 genera from *Saniculoideae* and *Apioideae* were selected by applying the same criteria.

Character choice

Characters were chosen to reflect past (i.e. primarily those of Harms, 1898, and Drude, 1898; for a detailed discussion of the classificatory history of *Apiaceae* see Constance, 1971) as well as contemporary classificatory hypotheses for the order. In addition, we looked for data that were available for the majority of genera in our sample. In doing so, priority was given to data applicable to a large sample of hydrocotyloid genera. This often resulted in such data being unavailable or sparsely representative of non-hydrocotyloid genera.

When the results of different workers were in conflict on the interpretation of the same data source, we accepted the state distribution with the most explicit taxonomic scope. For example, Drude (1898) generalized the presence of a crystal layer surrounding the carpophore as the defining character of *Scandicineae* Tausch, but Tseng (1967) found no such layer in the five genera from this subtribe that he examined. Thus, following Tseng we scored *Torilis* and *Scandix* explicitly as not having crystals. This approach resulted in the exclusion of some data sources that previously formed the basis of alternative classifications within the order. Perhaps the most notable exclusion were the pollen and cotyledon data of Cerceau-Larrival (1962, 1971). The utility of these data has been discussed elsewhere (Tutin, 1968; Plunkett *et al.*, 1996b). However, whilst Cerceau-Larrival and her collaborators provided a broad taxonomic coverage of key genera in the *Apiaceae sensu stricto*, there is little or no comparable data available for *Araliaceae* and *Pittosporaceae*. Similarly, the somewhat patchy taxonomic coverage of phytochemical data rendered it inappropriate for inclusion in this study. The data matrix of 71 characters and 67 taxa (three *Pittosporaceae*, 17 *Araliaceae*, 36 *Hydrocotyloideae*, two *Saniculoideae*, 8 *Apioideae* and one *incertae sedis*) is shown in Fig. 1, and the character list and data sources are provided in the Appendix.

Apium prostratum	0100011000001111110011110 2????11????????0000010010??000100100211000000000
Bupleurum falcatum	0100000001001011110011110 2010?11????????1?0010?10??000100100220011000000
Daucus glochidiatus	0100011001001111110211110 2????11????????0100013?10??000100100 24?00101000
Donnellsmithia cordata	010001?10100111111001111 0(12)????11????????1?0010010??000100100 2????????00
Heteromorpha trifoliata	010001?10100111111001111 01010?110???????0?0010(23)10??000100100 2????????00
Lomatium dasycarpum	0100011001001111110211110 2????11????????0?0015110??000100100 2????????00
Scandix pecten veneris	0100011001001111110011110 2????11????????0?001??10000001001004400 0101000
Torilis nodosa	0200011001001111110011110 2????11????????0?001??10000001001000110 0100000
Acanthopanax trifoliatus	1031011010001011001100 0(01)0?(012)20?1101(01)1010001000?00???001100?0103000000000
Aralia spinulosa	0330010010001012001000010002111100010(01)0001000?00???001100?0103000000000
Arthrophyllum pinnatum	00310(01)1010001001001000000?2000110001000001010?00???001100?01?????????00
Astrotricha latifolia	1330011010001111 01(01)1000100022111110001000100010 0???000?00?01?3000000000
Delarbrea michieana	0330020011001011001000000?021?1101101001 0?000000?42000?00?01?3???????10
Fatsia japonica	1001011010001012001002010001011 1(01)1(01)1010001000?00???00?100?0103000000000
Hedera helix	1331011010001001001000010?01(01)011(01)1(01)1010001010?00???00?100?0103000000000
Mackinlaya macrosciadia	1140021011001111001100010 0????11????????0?00??00???000?00?01?????????0
Munroidendron racemosum	0041001010111003001002012?000?1100010110010 00?00??00?100?01?3100010100
Myodocarpus	0001020010001111010110 0(01)0??21?1100101001 0?010030?4200??00?01?????????10
Polyscias purpureus	0331001010001011001100010?1001110011010101000000 1??001100?0103000000000
Pseudopanax arboreus	1030011010001011001100010001001 1(01)1(01)1010001000000 1??00?100?0103000000000
Reynoldsia sandwicensis	0331001010111003001012000?000?1100000110010000 00???00?100?01?3100010000
Schefflera digitata	03310010100010(01)2001000000?(012)00?110(01)01010(01)01000000???001100?0103100000100
Tetrapanax papyrifer	1331001010001011001000000?02011101(01)1010001000000?1100?100?01???????100
Tetraplasandra hawaiiensis	0031011010021002001012010?0201110001011001000000?1100?100?01?3100010100
Tupidanthus calyptratus	1331011010121003001002000?200?1100010(01)010?000000?1100?100?01?010000?100
Centella asiatica	1100030011001111011100010(02)????11????????00101000022?00???00?50000000000?
Homalosciadium homalocarpum	1130030010001111010100 01??????11????????0?00?000???000????0?0????????0?
Neosciadium glochidiatum	113003?0000011110111000 1??????11????????0?00?300???000????0??????????0?
Chlaenosciadium gardneri	111003?10100111 1?1110001??????11????????0010?0000??000????0?1????????0?
Hydrocotyle pedicellosa	1330031010001111011100013 0????11????????0000000013200 00?00002000000000?
Hydrocotyle callicarpa	1130001010001111010100013?????11????????0000000013200 0??000020110000000
Micropleura renifolia	11(13)00100?1001111?1?10001?(02)????11????????0?1010000???00????0?1010000000?
Platysace stephensonii	1200010011001111011100 01(01)2??0?11????????0000010000320 00???00?30100000(01)0?
Trachymene incisa	1130010011001111010100011 2????11????????0100100012200010000021000100000

FIG. 1. Data matrix. See Appendix for character list and data sources.

Uldinia ceratocarpa	1130010011001111010100010 1????11????????0100131 0?22000????0??1100100 00?
Actinotus omnifertilis	1120021011001111017100032 ????11??????????100?2001320001 00?0010100000 00
Brachyscias verecundus	111003?10100111?1110?0???????11????????0?00?000???000????0??????????0?
Pentapeltis peltigera	11100210110011117111000 10?????11????????0?1010000??000???00?1????????0?
Schoenolaena juncea	?1000211010011110111000 10?????11????????0?00?000?32000????0?1????????0?
Xanthosia tridentata	11100211010011110111000 103????11????????0010?0000220001000001010000000 0
Laretia acaulis	??3001?0110011117112000 10?????11????????0000010200000 00???01??(03)010000000?
Eremocharis	101002?1010011117112000 102????11????????1000100003210 0???00?11?00000000?
Naufraga balearica	012001?0110011117101 0?1????????11????????0?00?00????000????0?1????????0?
Domeykoa amplexicaulis	10(013)00200(01)1001111?1120001 3?????11????????1000100003210 0???00??(01)00000000?
Pozoa	1020020011001111?112000????????11????????0?00?000???100???01?11000(01)0000?
Asteriscium closii	1020020001001111?1020001 0?????11????????0000100003210 0???01?1(01)100(01)0000?
Diposis saniculifolia	12000????001111?1020001 0?????11????????0000101000000 0???00??0000000000?
Hermas capitata	121002????001111?1120001 12????11????????0000010?0022000???00??1101100000?
Dichosciadium ranunculaceum	12000200?1001111?1120001??????11????????0?00?000???0?0????0??1????????0?
Huanaca andiana	1020010011001111?10200010????11????????0000100000000 0???00??0000(01)0000?
Diplaspis cordifolia	1230030011001111010200017 1????11????????0000100 0???000????0??0100000000?
Spananthe paniculata	1?1001?0010011117102000101????11????????0000100000000 10???00?3000000000?
Azorella spinosa	122001?0110011117102000101????11????????0000100000000001110003001 0000002
Bolax gummifera	122002?0110011117 1?20001??????11????????0?001000???0001???0??????????0?
Klotzschia braziliensis	13200????1001111?1?20001??????11?????????100???0???000????0??1000000000?
Mulinum chillanense	1200010011001111?10200010?????11????????0?0010100000000???0(01)?3(01)00000000?
Schizeilema fragoseum	1120010011001111?1120001 3?????11????????0?001000?00000????00??(03)010000000?
Oschatzia cuneifolia	1140010011001111?1020001??????11????????0?00?00????000????0??0100000000?
Bowlesia incana	12(34)0010011001111?1120001 32????11????????0000110003201011 10(01)030100000001
Homalocarpus bowlesioides	1010000011001111?10200010?????11????????0000110003201 0???00?3????????0?
Gymnophyton	1310010001001111?10200010???0?11????????0000101003210 0???00?1(01)10000000?
Drusa oppositifolia	1010000011001111?10200010?????11????????00001(13)100320101110 00?(01)000000001
Eryngium pinnatum	0030020101001111111211110 2??0?11????????0?0014010410001000003410000000?
Sanicula gregari	1020020101001111111211110 2????11????????0?0014010410001000003110000000?
Hymenosporum flavum	0210120010000000111010 0??00200000010???0?0000010??000300?0000000000000
Pittosporum undulatum	0210120010000000111010 0??00200000000???0?0000010??000300?0000000000000
Sollya heterophylla	0210120010000000101010 0??00200001000???0?0000010??000300?0000000000000

FIG. 1. (Continued.)

Analyses

The analyses used PAUP* (Version 4.0b4; Swofford, 1998) on a Power Macintosh computer with a MAXTREES setting of 40,000 trees due to memory limitations. All characters were assumed to be unordered and multistate taxa were treated as polymorphic. The heuristic search was run in two stages. Firstly, a heuristic search with MULTREES option, tree-bisection-reconnection (TBR) branch swapping and ACCTRAN optimization was run with 100 random addition sequence replicates, each limited to saving a maximum of 2000 trees. The minimal length trees from this search were then used as the starting trees for a second search with a single replicate limited to 40,000 trees (with all other options the same as the first analysis). Bootstrap values (Felsenstein, 1985) were calculated from 100 replicate analyses performed using a heuristic search strategy, random addition sequence of taxa and TBR branch swapping, with a limit of 400 trees per replicate.

Results and Discussion

A total of 14,000 trees (tree length = 334) were found from two replicates in the first stage of the heuristic search, from between one and seven islands. When these 14,000 trees were used as the starting trees for the second search, the maximum of 40,000 most parsimonious trees was reached and were swapped to completion. Each of the 40,000 trees had a length of 334 steps, consistency indices (CI) of 0.464, rescaled consistency indices (RC) of 0.342, and a retention index (RI) of 0.736. Comparison of strict consensus trees generated from the two sets of trees found them to be of identical topology, thus generating more trees of the minimal length obtained was considered unlikely to have any impact on our results. The strict consensus of these trees is illustrated in Fig. 2 and a majority rule consensus shown in Fig. 3.

Despite our relatively conservative approach to the inclusion of taxa and characters, the data set contained 26% missing information and, as a consequence, there is relatively low resolution in the strict consensus tree (Fig. 2) concomitant with low bootstrap support. Bootstrap support tends to be lowered by a number of factors including a low character/taxon ratio, high amounts of missing data and high homoplasy. Given the data at hand, no single factor can be identified as influencing bootstrap support.

With the possible exception of *Saniculoideae* and *Apioideae*, the strict consensus tree (Fig. 2) is not congruent with the classifications of either Harms (1898; *Araliaceae*) or with Drude (1898; *Apiaceae*). The topology does, however, agree broadly with trees obtained from sequence data in which *Araliaceae* constitutes a basal grade that merges with members of *Hydrocotyloideae* that in turn, grade into a monophyletic *Saniculoideae* and *Apioideae* (Plunkett *et al.*, 1996a). The latter two clades comprise a monophyletic group with 55% bootstrap support (Fig. 2). Given our emphasis on characters used in the traditional delimitation of the higher taxa of *Apiales*, it is surprising that we obtained little support for taxa commonly defined by such characters. One conclusion, then, might be that the extent of homoplasy within many of these characters is so high that their use obfuscates the actual relationships. We believe that homoplasy does not explain entirely the lack of congruence between our results and those of previous workers. What is more likely is that the

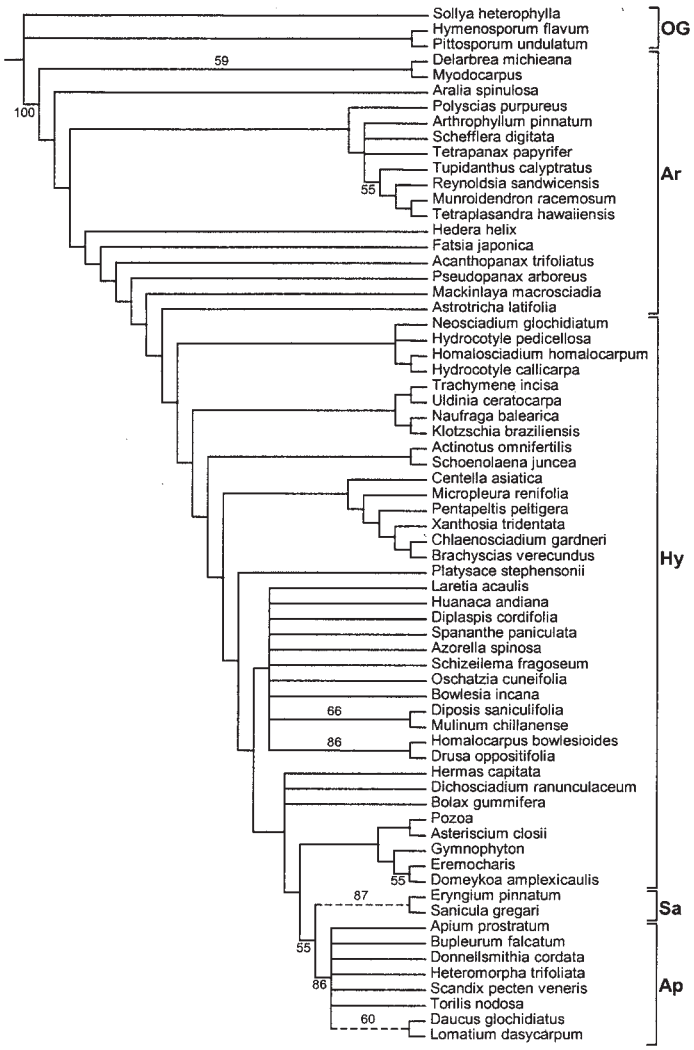

FIG. 2. Strict consensus tree of 40,000 trees. CI = 0.464, RC = 0.342, RI = 0.736. OG, Outgroup; Ar, *Araliaceae*; Hy, *Hydrocotyloideae*; Sa, *Saniculoideae*; Ap, *Apioideae*. Bootstrap values above 50% marked. Dashed branches indicate collapsed branches in the strict consensus for which bootstrap values above 50% were found.

combination of missing data and serially linked inapplicable data (such as characters 6 (calyx presence), and 31 (calyx aestivation) in this data set) serve to compound a relatively homoplastic data set.

Araliaceae

Our results were not congruent with any past classification of *Araliaceae*. In the case of the largely monothetic classifications of *Araliaceae* by Harms (1898), based on

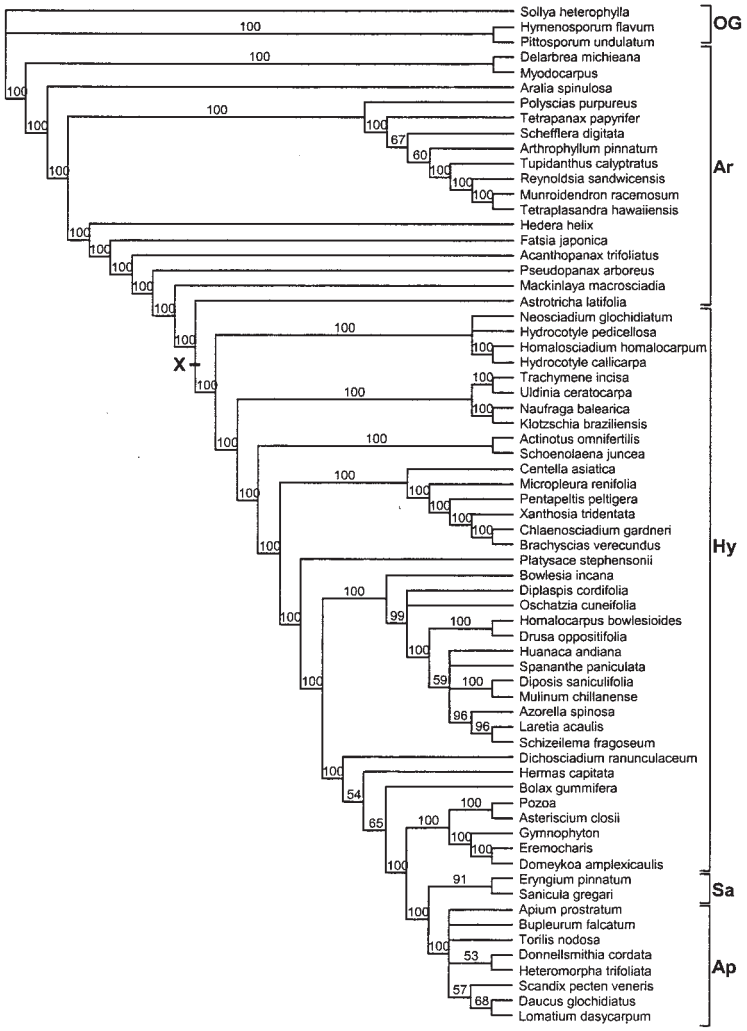

FIG. 3. Majority-rule consensus tree of 40,000 trees with percentage frequency indicated on branches. Groups indicated as in Fig. 2. The region above 'X' is expanded in Fig. 4.

petal aestivation, and by Eyde and Tseng (1971) who emphasized leaf morphology and fruit anatomy, this result is understandable. We could not provide any support for Eyde and Tseng's contention that mild polymery is plesiomorphic for the family, although the polymerous *Tupidanthus* Hook.f. & Thomson (palmate leaves) and *Reynoldsia* A.Gray and their relatives (pinnate leaves) do comprise a moderately well-resolved clade. The inclusion of *Reynoldsia*, *Munroidendron* Sherff. and *Tetraplasandra* A.Gray within a clade is further supported by the synapomorphies of sheathed multiseriate rays (character 39) and pollen with nexinous breaks (character 67).

There is broad agreement between our results and the family level phylogeny using *rbc*L and *mat*K sequence data of Plunkett *et al.* (1996a; 1997). Like Plunkett *et al.* (1996a, Fig. 3) we resolve *Araliaceae* as a basal grade between *Pittosporaceae* and *Apiaceae senso stricto*. The basal position of *Delarbrea* Viell. in our trees is consistent with results obtained using a combined data set of *rbc*L and *mat*K sequences (Plunkett *et al.*, 1997). Unlike the trees of Plunkett *et al.* (1997), however, we do not resolve *Araliaceae* as a distinct clade, nor do we see *Micropleura*, *Centella* and *Mackinlaya* nesting with *Delarbrea*. Furthermore, our results indicate that *Delarbrea* and *Myodocarpus* Brongn. & Gris. (the latter being absent from previous molecular analyses) form a sister relationship basal to the remainder of the order. *Delarbrea* and *Myodocarpus* share secretory cavities (Baumann, 1946; Lowry, 1986) and axial parenchyma (Oskolski, 1996). A close relationship between these genera has previously been suggested by Vieillard (1865) and by Viguier (1906).

Unlike Plunkett *et al.* (1996a) our results do not indicate a close relationship between *Delarbrea* and *Spananthe* Jacq. (*Hydrocotyloideae–Mulineae*), nor do we observe a close relationship between *Micropleura* Lag., *Centella* (both *Hydrocotyloideae–Hydrocotyleae*) and *Mackinlaya* F.Muell. (ancestral to core *Araliaceae* in Plunkett *et al.*, 1997). Our results indicate that *Mackinlaya*, along with the Australian endemic genus *Astrotricha*, are the two most derived taxa in our sample of *Araliaceae*. The derived nature of these genera has been suggested previously (Harms, 1898; Philipson, 1951), for both have incipient schizocarps, and in the case of *Mackinlaya*, clawed petals and stem-clasping leaf bases. Together, these characters have traditionally been used to distinguish typical *Araliaceae* from *Apiaceae* but may represent parallelisms.

The molecular phylogenies of Plunkett *et al.* (1996a; 1997) and Downie *et al.* (1998) resolved *Hydrocotyle* as being nested within *Araliaceae*. We could not confirm this with our morphological and anatomical data set, although *Hydrocotyle* and its segregates do form a clade that may well be transitional between typical *Araliaceae* and *Apiaceae*. Given that *Hydrocotyle* and their allies share a number of characters with at least some *Araliaceae* (a base chromosome number of $x = 12$, schizocarps that lack carpophores (with the exception of most annual *Hydrocotyle*) and sessile petal bases) we must admit that the eventual inclusion of *Hydrocotyle* and its relatives within 'core' *Araliaceae* is a possibility. If *Hydrocotyle* was to be included within *Araliaceae* it would appear that a base chromosome number of $x = 12$ may be the only synapomorphy for the family.

Hydrocotyloideae

Drude's (1898) tribes and, to a lesser extent, his subtribes, have been traditionally used as a means of organizing genera within *Hydrocotyloideae*. The artificial nature of Drude's subfamily and its constituent suprageneric taxa has been raised by a number of workers (Kondo *et al.*, 1996; Plunkett *et al.*, 1996a; 1997; Downie *et al.*, 1998; Katz-Downie *et al.*, 1999). As with *Araliaceae*, our analysis provided only

limited support for Drude's (1898) divisions of *Hydrocotyloideae*. *Hydrocotyleae* was depicted as being paraphyletic (see below), as was Drude's *Mulineae* (Figs 2–4). Two clades contain the majority of *Mulineae* (*Bowlesia* Ruiz & Pav. and *Pozoa* Lag. clades in Fig. 4). The Brazilian genus *Klotzschia* Cham. (Mulinae) is sister to *Naufraga* Constance & Cannon (*incertae sedis sensu* Pimenov & Leonov, 1993), which together are sister to the Australian genera *Trachymene* (*Hydrocotyleae*) and *Uldinia* (*Hydrocotyleae*). Very few data are available for *Uldinia*, *Klotzschia* and *Naufraga*, although, based upon pollen morphology, Shoup and Tseng (1977)

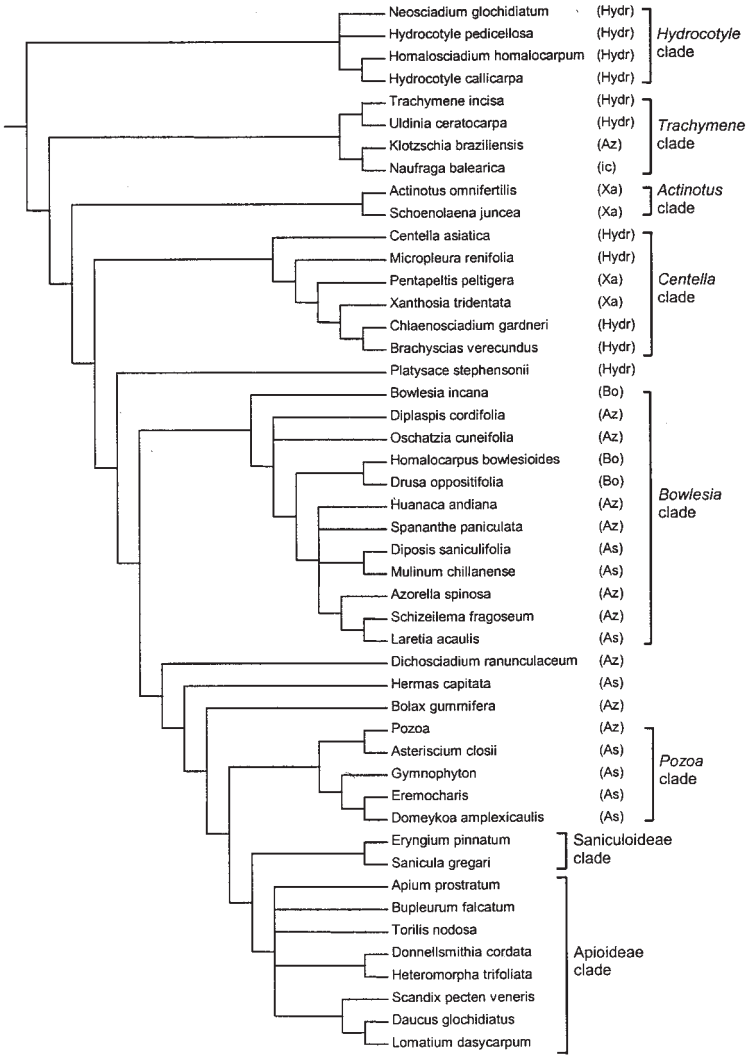

FIG. 4. *Apiaceae*, expanded beyond 'X' from Fig. 3. Subtribes of *Hydrocotyloideae* indicated by parenthetic abbreviations. *Hydrocotyleae*: Hydr, *Hydrocotylinae*; Xa, *Xanthosiinae*. *Mulinae*: Bo, *Bowlesiinae*; As, *Asteriscinae*; Az, *Azorellinae*. ic, *incertae sedis*.

suggested that *Klotzschia* formed a transition between *Araliaceae* and *Apiaceae*. Most of the remainder of *Mulineae* fall into two larger clades. The first (*Bowlesia* clade; Fig. 4) contains the Australian genera *Diplaspis*, *Oschatzia* and *Schizeilema* (shared with New Zealand and South America). This clade is supported by the presence of a tetrasporic, 16-celled embryo sac (characters 56 and 57) and the (homoplasious) presence of a carpophore (character 19): *Schizeilema ranunculus* (d'Urv.) Domin does, in fact, have a carpophore.

Relationships between various combinations of members of this clade have been postulated in the past. When emphasizing stipule and, somewhat equivocally, fruit morphology, Domin (1908) indicated an affinity between *Schizeilema*, *Huanaca* Cav., *Diplaspis, Bowlesia*, *Homalocarpus* Hook. & Arn. and *Drusa* DC. Given the difficulty of homologizing stipule morphology across the order, we could not include this potentially informative character in our data set. We did, however, include Tseng's (1967) fruit anatomy data and the pollen data of Ting *et al.* (1964). Tseng's grouping of *Schizeilema*, *Huanaca*, *Homalocarpus* and *Drusa* rested largely on the degree of development of certain fruit characters rather than upon the presence or absence of discrete character states. The palynological data of Ting *et al.* (1964) is similarly ambiguous, although we would agree that *Azorella*, *Laretia* and *Schizeilema* form a grouping based on the shared presence of an ectoapertural bridge. Mathias and Constance (1971) cogently outlined the problem concerning the relationships of *Diplaspis*, *Huanaca* and *Schizeilema*. We concur with them that revisiting the generic limits of these genera would be particularly rewarding, but we would add that *Azorella* and the Australian endemic, *Oschatzia* should also be considered if such a study is undertaken. Within this group, two moderately well-supported sister relationships are evident. One comprises *Homalocarpus* and *Drusa* whereas the other comprises *Diposis* DC. and *Mulinum* Pers. On the basis of fruit anatomy, Tseng (1967) considered *Mulinum* and *Diposis* to be transitional between his group III (*Eremocharis* Phil., *Asteriscium* Cham. & Schltdl. and relatives) and his group IV (*Azorella* and relatives) fruit-types. In our analysis, the sister relationship between *Diposis* and *Mulinum* is supported by the shared possession of wings derived from the lateral ribs (character 47), a character that has apparently arisen independently in *Drusa*, *Gymnophyton* Clos. and *Uldinia*.

A close relationship between *Drusa* and *Homalocarpus* was suggested by Mathias and Constance (1965). In the current analysis, the sister relationship between these genera is resolved only by the unique combination of a series of otherwise homoplasious character states: obvious calyx teeth (character 6), presence of stellate trichomes (character 46), and alternate leaves (character 53). *Drusa* and *Homalocarpus*, along with some species of *Bowlesia*, also have indumented petals (a character not used in this data set).

Pozoa, *Eremocharis*, *Domeykoa* Phil., *Asteriscium* and *Gymnophyton* constitute the second clade of *Mulineae* (*Pozoa* clade; Fig. 4). Members of this grouping were considered by Mathias and Constance (1962) to form a natural alliance. Our results indicate that this clade is separable from the taxa immediately basal to it (*Hermas*

L., *Dichosciadium* and *Bolax* Comm. ex Juss.) by the shared presence of a petal gland (character 52) and a base chromosome number of $x=5$ (character 61). In the case of the latter character, this appears to be derived from the more typical condition of $x=8$ for the *Mulineae*. The sister relationship between *Pozoa* and *Asteriscium* within the clade reflects their possession of the plesiomorphic state of non-inflexed petal apices (character 9).

Regardless of the eventual location of *Hydrocotyle* and its segregates *Neosciadium* and *Homalosciadium*, the *Hydrocotyleae* are clearly paraphyletic. Drude's *Xanthosiinae* is predominantly Australian with only *Actinotus novae-zelandiae* occurring outside the Australian plate in New Zealand. However, even this subtribe can not be upheld without some modification. In our results, *Xanthosiinae* can not be accepted without the inclusion of *Micropleura* Lag., *Chlaenosciadium*, *Brachyscias* and *Centella* (*Hydrocotylinae*) and the exclusion of *Actinotus* and *Schoenolaena*. The majority of this modified *Xanthosiinae* (*Centella* clade; Fig. 4) constitute a clade in our trees based on the shared possession of secondary ribs (fruit of *Brachyscias* is not available). The *Actinotus* clade are immediately basal to what might be considered as core *Xanthosiinae*. A close relationship between the predominantly South African genus *Centella* and the Australian endemic, *Xanthosia* is not novel. Tseng (1967) used fruit anatomy to postulate a close relationship, and recently Downie and Katz-Downie's (1999) phylogenetic analysis of chloroplast *rps*16 intron sequence data indicated a sister relationship between these genera.

Neither *Trachymene*, nor its sister, *Uldinia*, appear to be closely related to any other Australian genera. That *Trachymene* and *Uldinia* form a close relationship has been commented upon in the past (Theobald, 1967), and recently they have been treated as congeneric (Keighery & Rye, 1999). However, the genera can be distinguished by the form of the carpophore (although there is some debate about this feature, which is interpreted as a lignified extension of the pedicel by Theobald, 1967) and the position and form of the wings. The wings on the fruit of *Uldinia* develop from the apical portion of the lateral ribs, whereas in *Trachymene* the wings (when present) develop from the entire dorsal rib. Within the *Hydrocotyloideae*, wings arising from the lateral ribs are predominantly found in the *Mulineae*, whereas dorsal wings are apparently restricted to *Hydrocotylinae* and *Araliaceae* (*Myodocarpus*).

Naufraga is the only genus listed by Pimenov & Leonov (1993) as *incertae sedis* that was included in our data set. As indicated by our analysis, this genus forms a clade with *Trachymene*, *Uldinia* and *Klotzschia.* Constance & Cannon (1967) judiciously assigned *Naufraga* to *Hydrocotyloideae* on the possibility that its endocarps would become woody (fruit was not available to them), its apparently simple umbels and the absence of a carpophore. In their discussion of the new genus they indicated that the ovaries of *Naufraga* have vittae in the intercostal regions. This last character is one of only a few that apparently separates *Saniculoideae* and *Apioideae* from the remainder of the order. It should be noted that in our data set, woody endocarps do, in fact, segregate *Hydrocotyloideae* and *Araliaceae* from

Saniculoideae and *Apioideae*. In contrast with our results, Downie and colleagues (2000a) have indicated that *Naufraga* nests within *Apioideae*. Furthermore, Downie *et al.* (1998) placed *Klotzschia* as sister to *Saniculoideae* and *Apioideae* clades. Thus, we feel that it would be imprudent for us to attempt to sustain an argument for a relationship between *Trachymene*, *Uldinia*, *Naufraga* and *Klotzschia* on the basis of morphological and anatomical data.

The taxonomic affinities of *Platysace* have not received serious consideration apart from its inclusion by Drude within *Hydrocotylinae* and Tseng's assignment of it to his group I fruit-type (along with all other *Hydrocotyleae* in his sample). This is not surprising given the morphological diversity within the genus. The majority of *Platysace* are characterized by either simple lobed leaves with palmate venation or by entire leaves with parallel venation. The leaves of taxa with parallel venation are clearly derived from lobed leaves by the union of the lobes during the early development of the seedling leaves. Another group of species, mostly restricted to Western Australia, have dissected leaves with palmate venation which are frequently suppressed in the juvenile growth stage such that the adult plants are cladodenous. Whilst some species have strongly laterally compressed fruit others have terete mericarps or even weakly dorsally compressed mericarps (described by Tseng as rhomboid). This range of variation was not captured in the current analysis. The placement of *Platysace* between the *Centella* clade and the *Bowlesia* clade in our analyses is due to its base chromosome number of $x = 8$ (Keighery, 1982). This number is characteristic of *Mulineae* (Moore, 1971), but to our knowledge is unique within *Hydrocotyleae* (generally $x = 5$, 11 or 12). Given the small sample of *Platysace* used in our analysis it is premature to draw any conclusions as to the phylogenetic relationships of *Platysace*.

Apioideae *and* Saniculoideae

Apioideae and *Saniculoideae* together constitute a monophyletic group. *Saniculoideae* are not rendered as monophyletic in our analyses, possibly due to a small sample size (Fig. 2), but do form a sister relationship with the *Apioideae*.

Conclusions

If the success of this study is judged by our primary objective, the resolution of the phylogenetic affinities of Australian *Hydrocotyloideae*, then we must admit that we have taken only a small step forward. What is clear, though, is that if we are to truly understand the phylogenetic relationships within the *Apiales*, especially the relationships between *Araliaceae* and *Hydrocotyloideae*, then it is essential that we must focus more attention upon the taxa endemic to Australia. Much progress has been made in documenting the morphological and anatomical diversity within *Apiales*. The interpretation of future phylogenetic endeavours (regardless of the taxonomic sample used) will, however, continue to be compromised by a lack of

well-considered homology hypotheses for morphological and anatomical characters. Whilst hypotheses illustrating the extent of homoplasy within a character may be achieved by mapping character states on to a tree derived from an independent data source, such an approach can not necessarily determine the derivation of different states. Thus, whilst we admit that in some cases synapomorphies may not always be apparent, we endorse the approach of Downie *et al.* (2000b) in pursuing them in taxa that might otherwise be revealed only by molecular data. In particular, we would advocate the extension of Tseng's work on fruit anatomy in a comparative way throughout the order. Similarly, details of embryology may well prove to be informative in defining suprageneric taxa. Lastly, the resolving powers of data found to be useful in relatively small or diffuse taxonomic samples (e.g. data on stipule morphology, phytochemistry, palynological and seedlings) should also be extended.

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Appendix

Character list

1. *Leaf venation*
   0: pinnate
   1: palmate

2. *Inflorescence*
   0: umbellate
   1: cymose
   2: solitary
   3: paniculate

3. *Hermaphrodite flowers* (Froebe, 1979)
   0: pleiosciadioid
   1: heteropleiosciadioid
   2: symplesiosciadioid
   3: sciadioid
   4: einzelblute

4. *Pedicels*
   0: articulated
   1: not articulated

5. *Ovaries*
   0: inferior
   1: semi-inferior
   2: superior

6. *Calyx*
   0: an entire rim
   1: toothed
   2: ligulate
   3: absent

7. *Petals*
   0: imbricate
   1: valvate

8. *Petals*
   0: not apically cleft
   1: apically cleft

9. *Petals*
   0: inflexed
   1: not inflexed

10. *Petals*
    0: sessile
    1: tapering at the base

11. *Petals*
    0: typically 5
    1: typically >5

12. *Stamens*
    0: typically 5
    1: typically >5
    2: numerous

13. *Petal venation*
    0: many longitudinal veins
    1: one longitudinal vein

14. *Disks*
    0: not cleft
    1: cleft

15. *Styles*
    0: connate
    1: free

16. *Styles*
    0: 1
    1: 2–3
    2: 4–6
    3: 7+

17. *Stigma* (Heslop-Harrison & Shivanna, 1977)
    0: papillate
    1: smooth

18. *Fruit*
    0: fleshy
    1: dry

19. *Free carpophore*
    0: present
    1: absent

20. *Endocarp*
    0: not compressed
    1: laterally compressed
    2: dorsally compressed

21. *Endocarp*
    0: indurated to crustaceous
    1: chartaceous to membranous

22. *Gynoecial canals* (Tseng, 1967)
    0: associated with vascular bundles
    1: intercostal
    2: scattered

23. *Vittae* (Eyde and Tseng, 1971)
    0: absent
    1: present

24. *Dorsal bundles* (Eyde and Tseng, 1971)
    0: separate from peripheral bundles
    1: united with peripheral bundles

25. *Ventral bundles* (Eyde and Tseng, 1971)
    0: united
    1: separated
    2: anomalous
    3: absent

26. *Stomata* (Guyot, 1971)
    0: paracytic
    1: anomycitic
    2: anisocytic
    3: tetracytic

27. *Vessel element end wall* (Rodríguez, 1957)
    0: absent
    1: vestigial
    2: scalariform

28. *Intervascular pitting* (Rodríguez, 1957)
    0: scalariform
    1: opposite
    2: alternate

29. *Rays type* (Rodríguez, 1957)
0: heterogenous I II
1: homogenous I II
2: paedomorphic

30. *Vessel element bar number* (Rodríguez, 1957)
0: 0
1: 1–70

31. *Calyx*
0: imbricate
1: valvate

32. *Placentation*
0: parietal
1: apical

33. *Helical thickening* (Oskolski, 1996)
0: not thickened
1: thickened

34. *Vascular tracheids* (Oskolski, 1996)
0: absent
1: present

35. *Libriform fibre* (Oskolski, 1996)
0: thin
1: thick

36. *Septate fibres* (Oskolski, 1996)
0: absent
1: present

37. *Axial parenchyma* (Oskolski, 1996)
0: paratrachial
1: apotrachial

38. *Multiseriate rays* (Oskolski, 1996)
0: absent
1: present

39. *Sheaths on multiseriate ray cell* (Oskolski, 1996)
0: absent
1: present

40. *Radial canals* (Oskolski, 1996)
0: absent
1: present

41. *Commissural ingrowths*
0: absent
1: present

42. *Innermost endocarp layer* (Tseng, 1967)
0: longitudinal
1: transverse

43. *Secondary ribs on fruit* (Tseng, 1967)
0: absent
1: present

44. *Endocarp ruminate*
0: not ruminate
1: ruminate

45. *Ovules offset* (Tseng, 1967)
0: not offset
1: offset

46. *Fruit hair type*
0: glabrous
1: stellate
2: dendritic
3: barbs
4: glochids
5: unicellular

47. *Fruit wing position* (Tseng, 1967)
0: absent
1: lateral
2: marginal
3: dorsal

48. *Funicle length* (Håkansson, 1952)
0: short
1: long

49. *Hairs on funicle*
0: absent
1: present

50. *Crystals in mesocarp*
0: absent
1: scattered
2: discontinuous inner
3: continuous inner
4: septum

51. *Crystal type*
0: absent
1: druses
2: rhomboid

52. *Petal gland* (Mathias & Constance, 1962)
0: absent
1: present

53. *Leaf arrangement*
0: alternate
1: opposite

54. *Leaves* (Philipson, 1970)
0: not articulated with petiole
1: articulated with petiole

55. *Ovules in each mericarp*
0: one
1: two
2: more than two

56. *Embryo sac* (Håkansson, 1952)
0: monosporic
1: tetrasporic

57. *Nuclei in embryo sac* (Håkansson, 1952)
0: eight
1: sixteen

58. *Chromophilic substances* (Håkansson, 1952)
0: absent
1: present

59. *Dorsal surface of mericarp*
0: not concave
1: concave

60. *Nucellus* (Håkansson, 1952, Davis, 1966)
0: tenuinucellate
1: crassinucellate

61. *Base chromosome number* (Bell & Constance, 1957; 1960; 1966; Keighery, 1982)
    0: $x = 12$
    1: $x = 5$
    2: $x = 11$
    3: $x = 8$
    4: $x = 7$
    5: $x = 9$
62. *Pollen external outline* (Ting *et al.*, 1964)
    0: oblong
    1: elliptic
    2: rhomboid
    3: spheroid
    4: bone-shaped
63. *Aperture position* (Ting *et al.*, 1964)
    0: angles
    1: sides
64. *Pollen bridge without pore* (Ting *et al.*, 1964)
    0: absent
    1: present
65. Pollen bridge with pore (Ting *et al.*, 1964)
    0: absent
    1: present
66. Pollen rimmed (Ting *et al.*, 1964)
    0: absent
    1: present
67. *Nexine break* (Tseng, 1971)
    0: absent
    1: present
68. *Colpi length* (Ting *et al.*, 1964)
    0: long
    1: short
69. *Endoaperture width* (Ting *et al.*, 1964)
    0: broad
    1: narrow
70. *Secretory cavities* (Baumann, 1946)
    0: absent
    1: present
71. Embryo sac type
    0: polygonium
    1: drusa
    2: penea