

A PRELIMINARY ANALYSIS OF EVOLUTION OF AFRICAN AND MADAGASCAN *APIACEAE*

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A broad overview of the current state of taxonomic knowledge on the *Apiaceae* of Sub-Saharan Africa and Madagascar is presented. Sub-Saharan Africa has about 69 indigenous genera in the family, with 38 of them endemic, while Madagascar has at least 16 genera, of which six are endemic. Many taxa are poorly known and show unusual combinations of character states. Generic delimitations have not yet reached stability but monographic work, in which morphological, anatomical and some chemical characters are rigorously analysed, is contributing steadily to an improved understanding of generic relationships. A preliminary cladistic analysis of some genera is presented, based on characters such as woodiness, leaf persistence, leaf type, dentate-serrate leaf margins, heteromorphous fruits and the co-occurrence of intrajugal and vallecular vittae. Despite poor resolution, the results consistently show that several African and Madagascan genera are basal to the rest of the *Apiaceae*. The subfamily *Saniculoideae* Burnett always appears in a basal position, in close association with anomalous genera such as *Lichtensteinia* Cham. & Schldl., *Polemanniopsis* B. L. Burtt, *Steganoaenia* Hoscht. and *Pseudocarum* C. Norman. These genera are clearly central to a better understanding of the early evolution of the family and also to an ultimate improvement of Drude's (1898) classification system.

Keywords. *Apioideae*, morphology, phylogeny, relationships, *Saniculoideae*, *Umbelliferae*.

INTRODUCTION

The unique combinations of morphological characters and the isolated positions of African *Apiaceae* (*Umbelliferae*) were relatively poorly known until a review by Burtt (1991), in which the importance of the African taxa was highlighted. Generic delimitations have not reached stability, and several genera have only recently been discovered, described or properly circumscribed. Furthermore, the traditional concepts of the subfamilies *Apioideae* Drude and *Saniculoideae* Burnett (Drude, 1898) did not make provision for Madagascan genera (Van Wyk *et al.*, 1999) and the circumscription and monophyly of the subfamilies have not yet been demonstrated. This paper investigates the possible phylogenetic significance of unusual morphological characters in the *Apiaceae* of Sub-Saharan Africa and Madagascar. By focusing on the unique diversity in the two regions, it is hoped that future workers will include African and Madagascan taxa in comparative studies.

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CURRENT STATE OF KNOWLEDGE

In terms of the phylogeny of *Apiaceae*, the African and Madagascan component is of importance far beyond its relatively small size. About 80 indigenous genera are known from Sub-Saharan Africa and Madagascar (Pimenov & Leonov, 1993) but some of these are likely to be combined in future, while the delimitation of others (e.g. *Peucedanum* L.) may change. North African taxa have their affinities mainly with European counterparts and are therefore not considered here. There are a few exceptions – see Burttt (1989b) on *Stoibrax* Raf., and Pfisterer & Podlech (1986) on *Deverra* DC. Table 1 shows that there are 69 indigenous genera in Sub-Saharan Africa, of which 38 are endemic (refer to this table for author abbreviations unless given in the text). The corresponding numbers for Madagascar are 16 genera and six endemics. At least 20 genera are woody and therefore likely to be basal within the subfamily *Apioideae* (Oskolski, 2001). A significant percentage of genera are taxonomically isolated within the *Apioideae* and *Saniculoideae*, with no obvious relatives (Burttt, 1991). Madagascan *Apiaceae* have also remained practically unknown and interesting features in these genera, such as the co-occurrence of intrajugal and vallecular vitae, were only reported recently (Van Wyk *et al.*, 1999). African and Madagascan umbels have largely been ignored in previous international symposia on the family (Heywood, 1971; Cauwet-Marc & Carbonnier, 1982). Many taxa

TABLE 1. List of *Apiaceae* genera indigenous to Sub-Saharan Africa and Madagascar. For genera endemic to the two regions, the number of species is shown in brackets

SUB-SAHARAN AFRICA: *Aframmi* C. Norman (2), *Afrocarum* Rauschert (1), *Afroligusticum* C. Norman (1), *Afrosison* H. Wolff (3), *Agrocharis* Hochst. (4), *Alepidea* Delaroche (20), *Ammodaucus* Coss. (1), *Anginon* Raf. (12), *Angosesei* Chiov. (1), *Amnesorhiza* Cham. & Schldl. (12), *Anthriscus* Pers., *Apium* L., *Arctopus* L. (3), *Berula* W.D.J. Koch, *Bupleurum* L., *Capnophyllum* P. Gaertn. (1), *Carum* L., *Centella* L., *Chamarea* Eckl. & Zeyh. (5), *Choritaenia* Benth. (1), *Cyclospermum* Lag., *Cnidium* Jussieu, *Conium* L., *Cryptotaenia* DC., *Cuminum* L., *Dasispermum* Raf. (1), *Deverra* DC., *Diplolophium* Turcz., *Dracosciadium* Hilliard & Burttt (2), *Eryngium* L., *Erythroselinum* Chiov. (1), *Ezosciadium* B.L. Burttt (1), *Ferula* L., *Foeniculum* Hill., *Frommia* H. Wolff (1), *Glia* Sond. (3), *Haplosciadium* Hochst. (1), *Heracleum* L., *Hermas* L. (8), *Heteromorpha* Cham. & Schldl. (7), *Hydrocotyle* L., *Itasina* Raf. (1), *Lefebvrea* A. Rich. (6), *Lichtensteinia* Cham. & Schldl. (7), *Malabaila* Hoffm., *Marlothiella* H. Wolff. (1), *Nirarathamnos* Balf. f. (1), *Oenanthe* L., *Oreoschimperella* Rauschert, *Peucedanum* L., *Phlyctidocarpa* Cannon & Theobald (1), *Physotrichia* Hiern (10), *Pimpinella* L., *Polemanna* Eckl. & Zeyh. (3), *Polemanniopsis* B.L. Burttt (1), *Pseudocarum* C. Norman (2), *Pseudoselinum* C. Norman (1), *Pycnocyca* Lindl., *Sanicula* L., *Scandix* L., *Seseli* L., *Sium* L., *Sonderina* H. Wolff (4), *Spuriodaucus* C. Norman (3), *Steganotaenia* Hochst. (2), *Stenosemis* Harv. (2), *Stoibrax* Raf., *Torilis* Adans. and *Trachyspermum* Link.

MADAGASCAR: *Andriana* B-E. Van Wyk (3), *Anisopoda* Baker (1), *Apium* L., *Cannaboides* B-E. Van Wyk (2), *Carum* L., *Centella* L., *Diplolophium* Turcz., *Foeniculum* Hill., *Hydrocotyle* L., *Lilaeopsis* Greene, *Phellolophium* Baker (1), *Pimpinella* L., *Pseudocannaboides* B-E. Van Wyk (1), *Pseudocarum* C. Norman, *Sanicula* L. and *Tana* B-E. Van Wyk (1).

described by Cannon (1970, 1978) and Townsend (1989) have not yet been rigorously compared with other genera.

In ongoing taxonomic revisions (e.g. Cannon, 1978; Hilliard & Burt, 1985; Townsend, 1985, 1989; Burt, 1989a, 1991; Winter & Van Wyk, 1996; Allison & Van Wyk, 1997; Schubert & Van Wyk, 1997; Van Wyk *et al.*, 1999; Tilney & Van Wyk, 2001) some progress has been made in exploring the diversity and relationships of African taxa. There are still important gaps in our knowledge of character state distributions and much basic comparative work remains to be done. Burt (1991) noted the need for reliable data on seedling ontogeny, fruit anatomy, cytology and phytochemistry. The knowledge of African taxa has, however, now reached a stage where some speculation on generic relationships is possible. DNA sequence data has become a powerful tool to investigate phylogeny, and several recent papers (e.g. Downie & Katz-Downie, 1996, 1999; Plunkett *et al.*, 1997; Plunkett & Downie, 1999) confirmed the suspected basal position of some woody African taxa. Of particular interest is the paper by Downie & Katz-Downie (1999), in which chloroplast *rps16* intron sequences of several southern African taxa suggest that they have developed independently from the same ancestral stock as both the *Apioideae* and *Saniculoideae*.

MATERIAL AND METHODS

To explore the phylogenetic significance of some salient morphological features, 17 anomalous genera endemic to Sub-Saharan Africa and Madagascar were selected (Table 2). Other genera were not excluded, but are represented by place markers (see below). All of the chosen taxa have been studied in recent years, so that it was possible to make a rigorous comparison of 15 morphological characters (see below). The genera are presumed to form a monophyletic group because they share obvious *Apioideae* and *Saniculoideae* characters that are not present in the *Hydrocotyloideae* Link, such as the lack of a bony endocarp (present in *Centella* and other *Hydrocotyloideae*; character 8 in Table 2) and the symmetrical or dorsally compressed fruit (not laterally compressed as in *Centella* and other *Hydrocotyloideae*; character 14 in Table 2). *Centella*, *Diplophium* and *Alepidea* were chosen as place markers for the subfamilies *Hydrocotyloideae* (outgroup), *Apioideae* and *Saniculoideae* respectively. *Centella* was used as outgroup to determine the polarity of characters and character states as discussed below. The data were repeatedly analysed with the computer program HENNIG86. To explore the pattern of character state distributions in Table 2, various options were used, including the deletion, addition and successive weighting of characters. Only three results (cladograms) are included in Fig. 1. The result shown in A is a strict consensus tree of 18 equally parsimonious trees produced by the 'i.e.' option (tree length 29, consistency index 55). The tree shown in B is a strict consensus tree of 6 equally parsimonious trees produced by the 'i.e.' and 'successive weighting' options. The third tree (C) is a consensus tree of > 100 equally parsimonious trees produced by the 'i.e.' option, after intuitively assigning a weight of 2 to characters 1, 5, 9 and 11 in Table 2. Readers may want to generate their own trees and tree statistics (either manually, or using one of the several programs available for cladistic analysis), but the three trees in Fig. 1 can be recovered regardless of the computer program that is chosen. *Centella* (the outgroup) is by definition basal in all three trees, and is therefore not shown. The positions of *Diplophium* (place marker for the rest of the *Apioideae*) and *Alepidea* (place marker for the rest of the *Saniculoideae*) are respectively shown as '*Apioideae*' and '*Saniculoideae*' in Fig. 1.

TABLE 2. Polarization of characters and character states for selected genera of African and Madagascan *Apiaceae*. *Centella*, *Diplolophium* and *Alepidea* were selected as place markers for the subfamilies *Hydrocotyloideae*, *Apioideae* and *Saniculoideae*. When two states co-occur, the genus is scored for the plesiomorphic state

| Genera/groups | Characters | | | | | | | | | | | | | | |
|--|------------|---|---|---|---|---|---|---|---|----|----|----|----|----|----|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 |
| <i>Centella</i> (<i>Hydrocotyloideae</i>) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Diplolophium</i> (<i>Apioideae</i>) | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 |
| <i>Alepidea</i> (<i>Saniculoideae</i>) | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 |
| <i>Andriana</i> | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 |
| <i>Anginon</i> | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 |
| <i>Annesorhiza</i> | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 |
| <i>Arctopus</i> | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 |
| <i>Cannaboides</i> | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 |
| <i>Chamarea</i> | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 |
| <i>Dasispermum</i> | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 |
| <i>Dracosciadium</i> | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 |
| <i>Glia</i> | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 |
| <i>Heteromorpha</i> | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 |
| <i>Lichtensteinia</i> | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| <i>Polemanna</i> | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 |
| <i>Polemanniopsis</i> | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 |
| <i>Pseudocannaboides</i> | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 |
| <i>Pseudocarum</i> | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 |
| <i>Steganotaenia</i> | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 |
| <i>Tana</i> | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 |

Characters and polarization of character states

1. Growth form: herbaceous=0; woody=1.
2. Leaf persistence: leaves persistent=0; leaves hysteranthous or deciduous=1.
3. Leaf type: simple, digitate or palmate=0; pinnate=1.
4. Leaf lamina: broad, with dentate/serrate margin=0; dissected=1.
5. Leaf marginal setae (hair-like or thorny appendages): absent=0; present=1.
6. Inflorescences: not apioid (single or variously arranged, not umbellate)=0; apioid (umbellate)=1; saniculoid (congested)=2.
7. Fruit symmetry: homomorphic=0; heteromorphic=1.
8. Fruit wall: with bony endocarp=0; without bony endocarp=1.
9. Intrajugal vittae: present=0; absent=1.
10. Size of intrajugal vittae: small=0; very large=1.
11. Vallecular vittae: absent (rarely present in some fruits but then minute and inconspicuous)=0; present, large=1.
12. Fruit wings: absent=0; present=1.
13. Fruit surface structures: smooth or with hairs=0; with multicellular protuberances (warts, hooks or spines)=1.
14. Fruit shape: laterally compressed=0; fruit symmetrical or dorsally compressed.
15. Carpophore: undivided=0; divided=1.

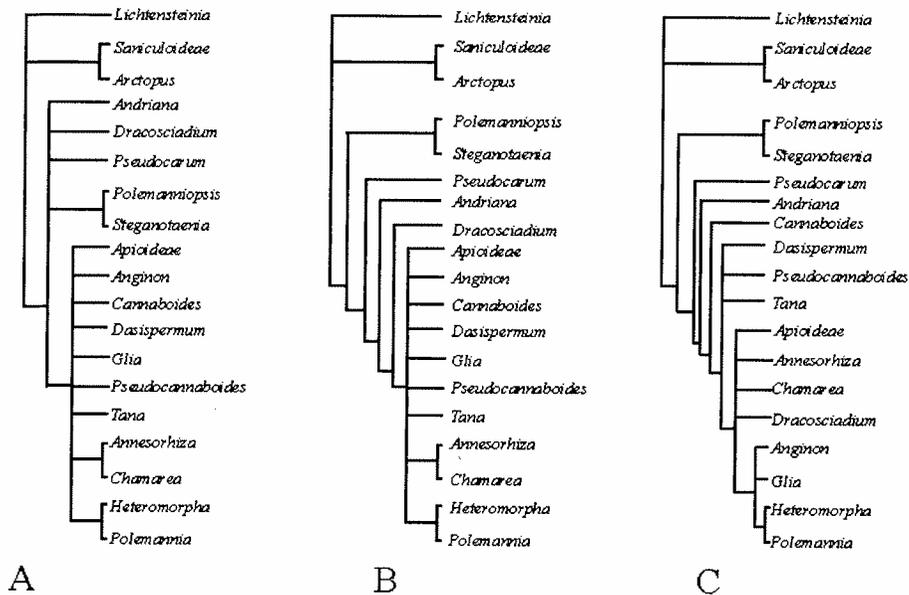


FIG. 1. Possible evolutionary relationships between some African and Madagascan genera of *Apiaceae* based on cladistic analyses of the data in Table 2, using the computer program HENNIG86. The result shown in A is a consensus tree of 18 equally parsimonious trees produced by the 'i.e.' option (tree length 29, consistency index 55). The tree shown in B is a consensus tree of 6 equally parsimonious trees produced by the 'i.e.' and 'successive weighting' options. The third tree (C) is a consensus tree of >100 equally parsimonious trees produced by the 'i.e.' option, after intuitively assigning a weight of 2 to characters 1, 5, 9 and 11 in Table 2.

CHARACTERS AND CHARACTER STATES

The presence of woody and herbaceous genera in both the *Araliaceae* and *Apiaceae* shows that the change from woody to herbaceous was not a single evolutionary change and it has been suggested that a secondary reversal to woodiness is possible (Rodríguez, 1957; Oskolski, 2001). Woody genera such as *Heteromorpha* and *Steganotaenia* are interesting, because they have several unusual features indicating that they may be relicts of a once much more diverse *Apiaceae* flora. Fossil wood from southern Ethiopia, dated to the early Pleistocene or earlier, was positively identified as that of *Steganotaenia* (Dechamps, 1982), but the early diversification of woody taxa must have happened much earlier. When using *Centella* or *Hydrocotyloideae* as outgroup, woodiness is interpreted as a derived character.

The leaves of several genera show interesting features. Hysteranthous or deciduous leaves provide some evidence for sister relationships between *Annesorhiza* and *Chamarea*, and between *Steganotaenia* and *Polemanniopsis*. Some species of *Peucedanum* also have deciduous leaves that wither in the dry season, and future

studies may show the need to reinstate the genus *Cynorhiza* Eckl. & Zeyh. to accommodate them (Van Wyk & Tilney, 2001). Leaf types and their ontogenetic development are poorly documented (Burt, 1991) and much can be learnt from seedling studies. Even in genera with pinnate mature leaves (such as *Anginon*), the first seedling leaves are simple or three-lobed, suggesting that this leaf type is primitive in *Apiaceae* (Van Wyk *et al.*, 1997). The use of *Centella* as outgroup leads to the same polarity decision. Leaves with broad laminas and dentate or serrulate margins are common in African genera and this leaf type is considered to be plesiomorphic. Hair-like or thorny appendages at the tips of marginal teeth is a well-known feature of genera of the *Saniculoideae*, and their presence in *Arctopus*, *Pseudocarum*, *Polemanniopsis* and *Steganotaenia* suggests that these genera have some relation with the *Saniculoideae*.

The inflorescence and fruit structure in *Apiaceae* have played a key role in the concept of the family (reflected in the name *Umbelliferae*) and its subfamilies (Drude, 1898). Congested umbels are typical of the *Saniculoideae* and this feature, together with sessile female flowers and kaurene type terpenoids, support a sister group relationship between *Arctopus* (hitherto ungrouped within the *Hydrocotyloideae* – see Pimenov & Leonov, 1993) and *Alepidea*. Heteromorphic fruits are present in *Polemanniopsis* (Burt, 1989a), *Heteromorpha* (Winter *et al.*, 1993; Winter & Van Wyk, 1996), some species *Annesorhiza* (Van Wyk & Tilney, 1994; Tilney & Van Wyk, 2001) and *Dasispermum* (Tilney & Van Wyk, 1995). These fruits usually have the five sepaline ribs expanded into wings, so that the homology of the character is more obvious than its interpretation from a phylogenetic point of view – is it a plesiomorphic relict or a synapomorphy? The vittae of the fruit are particularly interesting, and have been used for classification at subfamily level by Drude (1898). The presence of intrajugal vittae in *Centella* and other *Hydrocotyloideae* suggests that their loss in most *Apiaceae* is a derived condition. Vallecular vittae, on the other hand, seemed to have evolved later. The co-occurrence of these two types of vittae in the Madagascan genera (*Andriana*, *Cannaboides*, *Pseudocannaboides* and *Tana*) show that they are not homologous and should be interpreted as independent characters (Van Wyk *et al.*, 1999). Both these characters seem to agree with a basal position for *Lichtensteinia*, *Polemanniopsis* and *Steganotaenia*, as well as a basal position for *Pseudocarum* (and the Madagascan genera) relative to other *Apioideae*. The mericarps in the Madagascan genera (and in *Bupleurum* L.) are perfectly round in transverse section, devoid of any dorsal or lateral flattening (see figure in Van Wyk *et al.*, 1999). This perfect symmetry is here interpreted as characteristic for the most primitive fruit type in the *Apioideae*. The presence of enormously expanded intrajugal vittae, resulting in the ‘hollow’ fruit wings of *Polemanniopsis* and *Steganotaenia*, is an interesting but poorly investigated synapomorphy. Wings are quite common in the fruits of *Apiaceae* but their occurrence in several African genera does not provide convincing evidence of relationship. Multicellular surface protuberances, typical of *Saniculoideae* fruits, further support the proposed relationship between *Alepidea* (*Saniculoideae*) and *Arctopus* (currently *Hydrocotyloideae*). The carpophore in

Apiaceae is usually divided, so that the undivided carpophore of *Lichtensteinia* agrees with other anomalies (absence of vallecular vitae, R-shaped cotyledons) that point to a position near the *Saniculoideae*.

RESULTS AND DISCUSSION

The data in Table 2 were analysed using various options. Three results are shown in Fig. 1A–C. The ‘i.e.’ option of HENNIG86 resulted in poor resolution (more than 18 equally parsimonious trees) – the strict consensus tree is shown in Fig. 1A. The ‘successive weighting’ option produced six equally parsimonious trees, and the strict consensus tree is shown in Fig. 1B. In a third analysis, Characters 1, 5, 9 and 11 in Table 2 were arbitrarily assigned weights of 2 (double that of all other characters). These characters seem particularly interesting and could be polarized and scored for the investigated taxa with relative ease and accuracy. The analysis resulted in more than 100 trees, the consensus tree of which is shown in Fig. 1C. Despite the poor resolution, which was to be expected from the small number of characters and their obvious lack of congruence, the basic topology, and especially the basal part of the topology, remained unchanged. Fig. 1A–C shows that *Alepidea* (shown as ‘*Saniculoideae*’ in Fig. 1) is clearly sister to *Arctopus*, and close to *Lichtensteinia*. *Polemanniopsis* and *Steganotaenia* share several synapomorphies and they were invariably basal to the rest of the *Apioideae*. *Pseudocarum* and the Madagascan endemics formed a basal grade below the other African genera. The woody genera *Heteromorpha*, *Polemanna*, *Anginon* and *Glia* often formed a clade, and were sometimes sister to the herbaceous *Dracosciadium*, *Annesorhiza*, *Chamarea* and *Diplolophium* (representing the rest of the *Apioideae*, and shown as ‘*Apioideae*’ in Fig. 1).

The cladograms in Fig. 1, tentative as they may be, demonstrate several interesting points. They show that the present state of knowledge on character state distributions, even in relatively well-known genera, is not adequate to explore phylogenetic relationships with confidence. The topology of any morphology-based cladogram is likely to change drastically as new taxa and new characters are added, but some parts may be sufficiently rigorous to be taken seriously. Examples in the present study are those mentioned above, as reflected in the consensus trees in Fig. 1B,C. What is particularly encouraging, is the obvious agreement with recently published cladograms based on DNA sequence data, especially the study of Downie and Katz-Downie (1999). Note, for example, the sister group relationship between *Polemanniopsis* and *Steganotaenia*, and their basal position, as well as the basal position of the woody genera relative to other *Apioideae*. The lack of comparative data, lack of obvious congruence and inadequate sampling of genera have hampered phylogenetic studies in the past. It is likely that informative new morphological, chemical and cytological characters will be discovered in future, as more convincing ideas about relationships gradually begin to emerge. DNA sequence data will no

doubt play a major role in finding true affinities, and the evaluation and interpretation of such hypotheses from a morphological and chemical perspective is an exciting prospect for the future.

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