

tajan's and Cronquist's Asteridae into numerous superorders; removed Calyceraceae and Asteraaceae to Dipsacales and Asterales, respectively; and excluded Donatiaceae and Stylidiaceae from the order. Originally, he assigned these last two families to Cornales, between Columelliaceae and Hydrangeaceae. In a revision published posthumously by his wife (G. Dahlgren, 1989a, b), however, he removed them from that order, where he considered their terminal endosperm haustoria out of place, and segregated them as Stylidiales.

Dahlgren reduced Campanulales further by removing Brunoniaceae and Goodeniaceae to their own order Goodeniales. This action left Campanulales with only Campanulaceae, Pentaphragmataceae, Lobeliaceae, and Sphenocleaceae (included in Campanulaceae in the later versions). The disposition of the Cyphioideae was not explicitly stated.

Dahlgren's circumscription of Campanulales resembles that of Takhtajan (1987) in that it has become so narrow, its contents are identical to the family Campanulaceae of earlier workers (e.g., Schönland, 1889). It differs in the complete dissociation of Brunoniaceae, Calyceraceae, Donatiaceae, Goodeniaceae, and Stylidiaceae from any relationship with Campanulales and Asterales. This action was largely justified on chemical grounds; these five families produce iridoids, which were considered foreign to Campanulales and Asterales (Jensen et al., 1975; Dahlgren, 1977, 1983; Dahlgren et al., 1981). Their removal also narrowed the morphological description of the order by excluding families with involucrate capitulate inflorescences, hypogynous flowers, uniovulate ovaries, and stilar indusia.

Originally (Dahlgren, 1975a, 1977), the Campanulales were treated as the sole member of Campanulanae and were positioned near the likewise monofamilial Asteranae. In the subsequent versions, Campanulanae and Asteranae were merged as a single superorder under the latter name. The Cornales were assigned to Cornanae, Stylidiales to Ericanae, and Dipsacales and Goodeniales to the Gentiananae.

INCLUSION OF MENYANTHACEAE

No taxonomist working with morphological data has ever suggested that the Menyanthaceae were related to Campanulales. Most taxonomists, including Takhtajan and Thorne, put the family in Gentianales. Cronquist (1981), however, transferred it to Solanales, a move supported on chemical grounds by Gershenzon & Mabry (1983).

Dahlgren (1983) commented that neither placement was satisfactory and subsequently (G. Dahlgren, 1989a) removed Menyanthaceae to the already heterogeneous Cornales, between Viburnaceae and Adoxaceae.

Recently, however, molecular data (discussed below) have consistently placed Menyanthaceae among Asteraceae, Calyceraceae, Campanulaceae, Goodeniaceae, and Lobeliaceae, and at some distance from members of Gentianales and Solanales. Because molecular data are less prone to homoplasy than many other types of data (Jansen & Palmer, 1988; Palmer et al., 1988), and because they are supported by various chemical data (discussed below), it is prudent to include Menyanthaceae provisionally in this review of Campanulales.

SUMMARY

Twelve taxa are candidates for inclusion in the Campanulales (for uniformity, their names at familial rank are used pro tempore): Asteraceae, Brunoniaceae, Calyceraceae, Campanulaceae, Cyphiaceae, Donatiaceae, Goodeniaceae, Lobeliaceae, Menyanthaceae, Pentaphragmataceae, Sphenocleaceae, and Stylidiaceae. The common denominator of all classifications is the group comprising Campanulaceae, Cyphiaceae, Lobeliaceae, Pentaphragmataceae, and Sphenocleaceae. Surrounding this core are five satellites whose inclusion in the order is controversial: (1) Asteraceae, (2) Brunoniaceae and Goodeniaceae, (3) Calyceraceae, (4) Donatiaceae and Stylidiaceae, and (5) Menyanthaceae. The central problem of circumscription involves determining which, if any, of these satellites belong with the core group. The integrity of the core group and each of the bifamilial satellites cannot be assumed, however, and must also be examined.

DATA SETS

Traditionally, the circumscription of angiosperm orders has been based primarily upon a limited set of morphological data. An improved classification may be obtained by better reflecting the totality of similarities and differences among the taxa (Heywood, 1977; Kubitzki, 1977; Cronquist, 1987b; Stuessy, 1990). Among Campanulales, a significant body of data has accumulated from studies of their embryology, palynology, cytology, ultrastructure, chemistry, molecular biology, and paleontology. In the present review, I attempt to integrate these data, as a means of answering the questions posed at the beginning of this article. This synthetic approach should produce a revised classification of

the order that is maximally predictive (Stuessy, 1990).

However, it soon will be clear to the reader that the data base for Campanulales is not yet as complete as could be desired. The coverage is uneven, with a great deal known about certain families and certain types of data, but very little known about others (Hegnauer in Moeliono & Tuyn, 1960). Gibbs's (1974: 1190) lament regarding chemical data ("We obviously need much more information before we can help the taxonomists!") is equally true for other types of data, and Heywood's (1977) call for the accumulation of a better organized data base on angiosperm families is still appropriate today. For this reason, a formal revision of the classification of the order is delayed pending the conclusion of certain studies, described later, that are currently under way.

In this section, the data sets that pertain to the classification of the Campanulales are discussed. Most of this information was gleaned from the literature. The genera and species cited parenthetically are intended as examples of taxa with a given feature and not as an exhaustive list, unless otherwise indicated.

MORPHOLOGY

Morphology is the foundation upon which all taxonomy rests. In the following discussion, features considered important in previous classifications of Campanulales are described.

Habit and stems. Most species are iteroparous herbs with diverse perennating mechanisms, but nearly the entire range of habits among dicotyledons is represented, including annuals, biennials, shrubs and subshrubs, trees, pachycaul rosettes, twining vines (*Cyphia* Berg, Cyphiaceae; *Mikania* Willd., Asteraceae), leaf succulents (*Othonna* L., Asteraceae), stem succulents (*Brighamia* A. Gray, Lobeliaceae), and various types of hydrophytes, such as cabomboids (*Megalodonta* Greene, Asteraceae), isoetids (*Lobelia dortmanna* L., Lobeliaceae), and nymphaeoids (*Nymphoides* Seguiet, Menyanthaceae). In most cases, the woody species are believed to be derived from fundamentally herbaceous ancestors (Carlquist, 1962, 1969a, b), with the exception of Asteraceae, in which woodiness appears to be plesiomorphic (Carlquist, 1966; Stebbins, 1977; Jansen & Palmer, 1988). The small amount of secondary growth in some species of *Stylidium* Sw. ex Willd. (Stylidiaceae) is anomalous, as no cambial activity has been detected within the vascular bundles (Carlquist, 1981).

Campanulaceae, Cyphiaceae, Lobeliaceae, and

certain Asteraceae (most notably Lactuceae) accumulate latex, a viscous white or colored fluid that is produced in a network of articulated lactifers. Brunoniaceae, Calyceraceae, Donatiaceae, Goodeiaceae, Menyanthaceae, Pentaphragmataceae, Sphenocleaceae, and Stylidiaceae do not produce latex.

Leaves. Leaves typically are simple and correspond to the dillenid type of Hickey & Wolfe (1975). Deeply parted or compound leaves do occur, however (*Menyanthes trifoliata* L., Menyanthaceae; *Cyanea shipmanii* Rock, Lobeliaceae; *Bidens bipinnata* L., Asteraceae). An alternate arrangement of the leaves is most common, although opposite (*Eupatorium perfoliatum* L., Asteraceae) or whorled (*Ostrowskia* Regel, Campanulaceae) patterns also occur. The markedly asymmetric leaf base of Pentaphragmataceae is noteworthy. True stipules are lacking, although stipulelike processes occur in some Asteraceae (*Simsia* Pers.), and the winged petioles of Menyanthaceae have been called stipulelike. Stomates are anomocytic, except in Sphenocleaceae, where they are tetracytic, and in Brunoniaceae and Donatiaceae, where they are paracytic.

Inflorescences. In Donatiaceae and *Phyllachne* Forster & G. Forster (Stylidiaceae), there is a single sessile flower at the apex of the stem. Although solitary axillary flowers occur in some taxa (*Burmeistera* Triana, Lobeliaceae; *Cyphocarpus* Miers, Cyphiaceae), most have flowers aggregated into some sort of inflorescence, which may be terminal or less often axillary. Campanulaceae, Cyphiaceae, Goodeniaceae, Lobeliaceae, and Stylidiaceae have a diverse array of monotelic and polytelic inflorescences (Carolin, 1967). Pentaphragmataceae are characterized by a sympodial helicoid cyme, and Sphenocleaceae, by a dense terminal spike. In Asteraceae, Brunoniaceae, Calyceraceae, and some Campanulaceae (*Jasione* L.), the flowers are condensed into a tight capitulum subtended by an involucre, which often resembles an individual flower. These capitula may be aggregated into secondary groupings (synflorescences or capitulescences).

Flowers. Although the flowers are characteristically complete (tetracytic) and perfect, various types of structural and functional dicliny characterize certain taxa. Dioecious (*Lobelia dioica* R. Br.; *Pentaphragma tenuiflorum* Airy Shaw, Pentaphragmataceae) or gynodioecious (*Lobelia siphilitica* L.) species occur sporadically, while monosporangiate flowers are common components

of the capitula of Asteraceae. Many Menyanthaceae are heterostylous (*Villarsia capitata* Nees). Proterandry characterizes Brunoniaceae, Calyceraceae, Campanulaceae, Goodeniaceae, Lobeliaceae, and Stylidiaceae. This is correlated with their specialized mechanisms for the secondary presentation of pollen, discussed below.

The flowers of Lobeliaceae, with rare exceptions (*Downingia laeta* (Greene) Greene), and of some Stylidiaceae (*Stylidium petiolare* Sonder) are resupinate at anthesis, i.e., rotated 180° via torsion of the pedicel. As a result, the visually dorsal lobes of the perianth actually arise from the ventral portion of the floral primordium.

Calyx. The calyx is fundamentally pentamerous, although taxa and individuals with as few as two and as many as ten sepals are found in Calyceraceae, Campanulaceae, Donatiaceae, Goodeniaceae, and Stylidiaceae. The sepals are connate, with the exception of a few Menyanthaceae. In Brunoniaceae, some Goodeniaceae, and Menyanthaceae, this synsepalous calyx is free from the other floral organs. Otherwise, it is adnate to the corolla and androecium for some portion of their lengths, forming a hypanthium that is crowned by the distal portions of the sepals. With rare exceptions (*Cyananthus* Wallich ex Benth., Campanulaceae), this hypanthium is adnate to the ovary. In Pentaphragmataceae, however, it is connected only by five narrow longitudinal septa, which leave intervening lacunae or pits in which nectar is produced.

In many Asteraceae (*Chrysanthemum* L., *Xanthium* L.), nothing resembling a calyx lobe is evident, while in other genera of the family, various barbs, hairs, or scales are found where calyx lobes are expected. These structures, known collectively as the pappus, are presumed to be modified calyx lobes. The rigid persistent calyx lobes of Brunoniaceae and many Calyceraceae may represent an approach to this condition.

In Cyphiaceae and Lobeliaceae, the odd (unpaired) lobe originates in a ventral (anterior) position, a situation otherwise found only in *Logania* R. Br. (Loganiaceae) and some papilionoid legumes (Kaplan, 1967). However, in Lobeliaceae, this lobe is brought into a dorsal (posterior) position by the resupination of the flower (see above).

Corolla. The corolla is essentially pentamerous but with sporadic variation in taxa and individuals of some families. In *Stylidium* and *Levenhookia* R. Br. (Stylidiaceae), the odd (unpaired) petal is often so reduced as to give the impression

of a tetramerous corolla. Petals are connate in all but Donatiaceae and a few species of Pentaphragmataceae (*Pentaphragma decurrens* Airy Shaw).

Radial symmetry (actinomorphy) characterizes Brunoniaceae, Calyceraceae, Campanulaceae, Donatiaceae, Menyanthaceae, Pentaphragmataceae, and Sphenocleaceae. Actual shape of the corolla may be rotate, campanulate, urceolate, infundibular, tubular, or salverform. Bilateral symmetry (zygomorphy) characterizes Cyphiaceae, Goodeniaceae, and Lobeliaceae. The irregularity may be slight (*Cyphia brevifolia* Thulin, *Lobelia donanensis* van Royen), but is nonetheless perceptible. In Stylidiaceae, *Levenhookia* and *Stylidium* are zygomorphic, while *Forstera* L. f., *Phyllachne*, and *Oreostylidium* Berggren are actinomorphic. In Asteraceae, inflorescences may be composed of zygomorphic flowers only (ligulate capitula), actinomorphic flowers only (discoid capitula), or both (radiate capitula).

Zygomorphy among Campanulales involves several distinct patterns. In Goodeniaceae, the corolla typically is bilabiate with two dorsal and three ventral lobes, though unilabiate corollas with five ventral lobes are not uncommon (*Scaevola sericea* Vahl). In both types, the odd (unpaired) lobe is in a ventral position.

Three basic patterns are seen in Cyphiaceae and Lobeliaceae: (1) bilabiate with three dorsal and two ventral lobes (*Nemacladus* Nutt., Cyphiaceae; *Lobelia erinus* L.); (2) bilabiate with one dorsal and four ventral lobes (restricted to *Cyphocarpus*, Cyphiaceae); (3) unilabiate with five dorsal lobes (*Lobelia tupa* L.). At anthesis, the flowers of Lobeliaceae appear more similar to those of Goodeniaceae than to those of Cyphiaceae, because of their resupination. However, in both Cyphiaceae and Lobeliaceae, the odd (unpaired) lobe originates in a dorsal position, and their flower is thus fundamentally different from that of Goodeniaceae.

In Stylidiaceae (Erickson, 1958), the odd petal originates in a ventral position. In the zygomorphic genera, this takes the form of a highly reduced and modified labellum, which is irritable (pressure-sensitive) in *Levenhookia*. The remaining four lobes may be similar in size and shape or they may be heteromorphic. Most commonly, they are gathered into two pairs. Each pair may consist of a ventral and a dorsal lobe (*Stylidium diuroides* Lindley), or of like lobes (*S. emarginatum* Sonder). In others, the four major lobes may be cruciform (*S. xanthopis* Erickson & Willis) or unilabiate (*S. divaricatum* Sonder). The throat is often marked by a series of glandular appendages of diverse shape and size.

Among Asteraceae (Bremer, 1987), the zygomorphic flowers of most tribes are essentially unilabiate; those in ligulate capitula have five ventral lobes, while those in radiate capitula have but three. In Mutisieae, however, the zygomorphic flowers are bilabiate. Most genera have corollas with two dorsal and three ventral lobes, though in some Barnadesiinae, there are one dorsal and four ventral lobes.

Androecium. Anthers are tetrasporangiate (rarely bisporangiate in Asteraceae), basifixed, and dehiscent via longitudinal slits. The thecae are parallel, with the exception of Stylidiaceae, where they are divergent and sometimes (*Forstera*, *Phyllachne*) apically confluent. A single cycle of five is characteristic. Asteraceae with tetramerous disc corollas (*Oparanthus* Sherff, *Petrobium* R. Br., *Remya* Hillebrand) have four stamens, as do Campanulaceae with tetramerous corollas (*Phyteuma tetramerum* Schur). One species of Donatiaceae, *Donatia fascicularis*, has three stamens while the other, *D. novae-zelandiae* J. D. Hook., has two. Stylidiaceae likewise have two stamens.

The stamens are antisepalous (i.e., alternate with the corolla lobes) in all families. In Asteraceae, Calyceraceae, *Cyphocarpus*, Sphenocleaceae, and sympetalous Pentaphragmataceae, the stamens are epipetalous, i.e., inserted on the corolla tube at or above the middle. In Brunoniaceae, most Campanulaceae, most Cyphiaceae, Donatiaceae, Goodeniaceae, Lobeliaceae, Menyanthaceae, and polypetalous Pentaphragmataceae, the stamens are inserted at the base of the corolla tube, on the floral receptacle, or on the top of the inferior ovary. In *Cyananthus*, the stamens arise from the rim of the free hypanthium. In a few Lobeliaceae, the basally inserted filaments are adnate to the corolla tube, either dorsally (*Rollandia* Gaudich.) or completely (*Siphocampylus* Pohl sect. *Hemisiphocampylus* A. DC.). In Stylidiaceae, the two stamens are wholly adnate to the style, forming a gynandrium or gynostegium in which the divergent anther thecae flank the large stigma.

A distinctive feature of Asteraceae, Brunoniaceae, Calyceraceae, Campanulaceae, Goodeniaceae, and Lobeliaceae is their specialized pollination mechanisms. These involve the presentation of pollen to potential pollinators in or on certain structures associated with the style (Carolin, 1960a; Erbar & Leins, 1989; Leins & Erbar, 1990). Such flowers are proterandrous, with an introrse discharge of pollen onto stylar structures preceding the elongation of the style and maturation of the stigma.

A major structural aspect of these mechanisms is the gathering of the stamens around the style. Asteraceae, Brunoniaceae, Lobeliaceae, and some Goodeniaceae (*Dampiera* R. Br., *Leschenaultia* R. Br.) are syngenesious, i.e., the anthers are connate, forming a definite tube into which the pollen is shed. Lobeliaceae differ from the remaining syngenesious taxa in having the two ventral anthers shorter than the other three. In Lobeliaceae, the syngenesious Goodeniaceae, and some Asteraceae, the filaments are connate for part of their length. However, in Calyceraceae and certain Cyphiaceae (*Nemacladus*, *Parishiella* A. Gray, *Pseudonemacladus* McVaugh, and some species of *Cyphia*), the filaments are connate for part of their length, though the anthers are distinct. In *Nemacladus*, the two dorsal filaments bear small stipelike structures with one or more terminal transparent rod-shaped cells. These structures are unique and of unknown function.

In Campanulaceae and the remaining Goodeniaceae (*Scaevola* L., *Selliera* Cav.), the stamens are connivent around the style, separating once the pollen is shed onto the style. In many species of *Phyteuma* L. (Campanulaceae), the distal portions of the corolla lobes are connate, forming a tube that functions much like the anther tube of syngenesious taxa.

A second aspect of these mechanisms is the presence of various stylar structures that collect pollen from the anthers and present it to pollinators. In Asteraceae, Brunoniaceae, Campanulaceae, and Lobeliaceae, various sorts of hairs on the style and stigma perform this function. The stylar hairs of Campanulaceae are unique in their ability to invaginate as a means of dislodging pollen grains (Carolin, 1960a; Shetler, 1979; Erbar & Leins, 1989). Brunoniaceae and Goodeniaceae are unique among angiosperms in possessing an indusium, a cuplike structure subtending the stigma, into which pollen is shed.

The gynandrium or gynostegium of Stylidiaceae is structurally and functionally different from the mechanisms described above. The column is irritable (pressure-sensitive) in *Stylidium* and to a lesser degree in *Levenhookia* (Erickson, 1958). The movements of an insect on the flower cause the gynandrium to spring suddenly. Either the extrorse anther locules deposit pollen directly on the insect (if the proterandrous flower is in staminate phase), or the stigma picks up a load of pollen from the insect (if the flower is in carpellate phase). This structure cannot be derived evolutionarily from the typical campanulalean mechanisms, but must have had an independent origin from the apostemonous

condition (Carolin, 1960a; Erbar & Leins, 1989; Leins & Erbar, 1990).

Gynoecium. In Brunoniaceae and Menyanthaceae, the ovary is superior. The remaining families are characterized by an inferior ovary, though sporadic taxa have ovaries half-inferior (*Diastatea* Scheidw., Lobeliaceae) or superior (*Cyananthus*, Campanulaceae; *Velleia* Smith, Goodeniaceae). Epigyny in Campanulaceae is exclusively appendicular in origin, i.e., via the adnation of outer floral whorls to the ovary (Carolin, 1959, 1960b; Kaplan, 1967). Nonetheless, the hypanthia of Campanulaceae sens. lat. and Goodeniaceae are not strictly homologous in their formation (Carolin, 1978). In the former, coalescence of the outer whorls preceded their adnation to the ovary, while in the latter, the outer whorls became adnate to the ovary centrifugally.

The ovary is syncarpous. In most families, two or more fertile locules are evident. Bilocular ovaries characterize Cyphiaceae, Goodeniaceae, Lobeliaceae, Pentaphragmataceae, Sphenocleaceae, Stylidiaceae, and *Donatia novae-zelandiae*, while *D. fascicularis* is trilocular. Campanulaceae characteristically have three locules, though some have two (*Wahlenbergia linarioides* (Lam.) A. DC.) or five (*Campanula* L. subsect. *Quinqueloculares* Boiss., *Cyananthus*), and others appear to have more, due to intrusive partitions from the carpelary midribs (*Michauxia* L'Her., *Ostrowskia*). A few Goodeniaceae (*Scaevola porocarya* F. Muell.) have four locules.

Each locule typically contains several to many ovules attached to axile placentae, although this sometimes is reduced to one or two, in which case, placentation may be apical (*Catosperma* Benth., Goodeniaceae; *Siphocodon* Turcz., Campanulaceae).

In Asteraceae, Brunoniaceae, Calyceraceae, and Menyanthaceae, the ovary has one locule. In Menyanthaceae, this locule contains a pair of parietal placentae bearing numerous ovules; this condition is also found in some taxa of otherwise bilocular families (*Downingia yina* Applegate, Lobeliaceae). In the other three families, the single locule contains a solitary ovule, which is apical in Calyceraceae and basal in Asteraceae and Brunoniaceae. Unilocular ovaries with a single basal ovule also characterize certain genera in otherwise multilocular families (*Merciera* A. DC., Campanulaceae; *Unigenes* F. Wimmer, Lobeliaceae; *Verreauxia* Benth., Goodeniaceae).

Only the Donatiaceae are characterized by multiple styles: *Donatia fascicularis* has three and *D.*

novae-zelandiae, two. However, in *Calogyne* R. Br. (Goodeniaceae), the style divides into two, three, or four branches, each with its own indusium. In Brunoniaceae, Calyceraceae, a few Campanulaceae (*Cephalostigma* A. DC.), some Goodeniaceae, Pentaphragmataceae, Sphenocleaceae, and Stylidiaceae, the style terminates in a simple unlobed stigma. In most Campanulaceae, the number of stigmas or stigmatic branches equals the number of locules. Asteraceae, most Goodeniaceae, Lobeliaceae, Menyanthaceae, and most Cyphiaceae have a bifid stigma. *Cyphia* features a unique stigmatic cavity that is filled with fluid and communicates with the outer air via a lateral aperture (Thulin, 1978).

At maturity, multiovulate ovaries commonly form a capsule, which may be loculicidal or less often poricidal; that of Sphenocleaceae is circumscissile. In most, the seeds have no obvious adaptations for dispersal, though anemochorous (winged) seeds occur in some taxa (*Cyphia reducta* F. Wimmer; *Calogyne*, Goodeniaceae; *Trematolobelia* A. Zahlbr., Lobeliaceae). Baccate fruits, better adapted to zoochory, characterize Pentaphragmataceae and occur sporadically elsewhere (*Clermontia* Gaudich., Lobeliaceae; *Canarina* L., Campanulaceae; *Scaevola* sect. *Scaevola*, Goodeniaceae). The families with uniovulate ovaries form one-seeded indehiscent fruits: achenes in Brunoniaceae, cypselas in Asteraceae and Calyceraceae. Here, the calyx is often persistent and modified in ways that facilitate anemochory (plumose) or zoochory (barbate).

EMBRYOLOGY

Embryology is here defined broadly, so as to include all aspects of growth and development of the anther and ovule; only features of the mature pollen grain (palynology) are discussed separately. Data for angiosperms have been summarized by Davis (1966) and Palser (1975), and the following data are taken from these reviews, unless otherwise noted.

Anthers. The dicotyledonous type of anther wall development, producing a single middle layer, characterizes Asteraceae, Campanulaceae, Goodeniaceae, Lobeliaceae, Sphenocleaceae (Kausik & Subramanyam, 1946), and Stylidiaceae. The basic type, producing two middle layers, characterizes Pentaphragmataceae. Both patterns have been reported from Menyanthaceae. The endothecium contains fibrous thickenings in all these families as well as in Calyceraceae.

The tapetum functions in the nutrition of developing microsporocytes (Pacini et al., 1985). The

glandular or secretory type, in which the tapetal cells remain in their original position but discharge their contents, characterizes Calyceraceae, Campanulaceae, Goodeniaceae, Lobeliaceae, Menyanthaceae, Pentaphragmataceae (Kapil & Vijayaraghavan, 1965), Sphenocleaceae (Kausik & Subramanyam, 1946), Stylidiaceae, and some Asteraceae. The amoeboid or periplasmodial type, in which the protoplasts fuse to form a multinucleated periplasmodium, characterizes most Asteraceae. Tapetal cells are binucleate in Campanulaceae, Lobeliaceae, Pentaphragmataceae (Kapil & Vijayaraghavan, 1965), Sphenocleaceae (Kausik & Subramanyam, 1946), and Stylidiaceae, but multinucleate in Asteraceae, Goodeniaceae, and Menyanthaceae.

Ovules. The anatropous ovules are unitegmic and tenuinucellar, conditions that characterize virtually all Asteridae (Philipson, 1977). Embryo sac formation is monosporic (*Polygonum*-type), though bisporic (*Allium*-type) and various tetrasporic types occur in some Asteraceae. The inner layer of the integument develops as an endothelium (integumentary tapetum) upon coming in contact with the embryo sac. Embryogeny follows the Asterad pattern in Asteraceae and Menyanthaceae, and the Solanad pattern in the others. Endosperm formation characteristically is cellular ab initio, though nuclear endosperm development is found in some Asteraceae. Typically, copious endosperm forms, though it is absent or nearly so from mature seeds of Asteraceae, Brunoniaceae, and Sphenocleaceae. It is oily in most families, but starchy in Pentaphragmataceae and some Campanulaceae.

Terminal endosperm haustoria (i.e., with haustoria at both the chalazal and micropylar ends) characterize Campanulaceae, Lobeliaceae, Sphenocleaceae, and Stylidiaceae. In the first three families, the two ends are equally aggressive; in the last, the micropylar haustorium is more aggressive. In Pentaphragmataceae, a haustorium develops only at the micropylar end, while Asteraceae, Calyceraceae, Goodeniaceae, and Menyanthaceae lack them altogether.

PALYNOLOGY

Data on pollen morphology in angiosperms was summarized by Erdtman (1952). This review is supplemented by data presented in more recent papers (Chapman, 1966; Brewbaker, 1967; Dunbar, 1975a, b, 1978, 1981, 1984; Dunbar & Wallentinus, 1976; Skvarla et al., 1977). Typically, the grains are spheroidal or variously com-

pressed (oblate or prolate); those of Pentaphragmataceae are trilobate.

Apertures. Tricolporate pollen characterizes Asteraceae, Brunoniaceae, Calyceraceae, Cyphiaceae (6-colpate in *Parishella*), Donatiaceae, Goodeniaceae, Lobeliaceae, Menyanthaceae, Pentaphragmataceae, and Sphenocleaceae, though the pores are lacking from some Lobeliaceae, Menyanthaceae, and Pentaphragmataceae (i.e., the grain is tricolpate). Pollen grains of Stylidiaceae are 3-8-colpate. In most Campanulaceae, the grains are 3-4(-5)-porate (6-porate in *Githopsis* Nutt.). A few species of *Campanula* have 8-, 12-, or 14-20-pantoporate pollen, while other genera are characterized by pollen that is 3-6-colporate (*Platycodon* A. DC., *Canarina*) or 6-10-colpate (*Cyananthus*, *Ostrowskia*).

Surface. There is great variation in the sculpturing and ornamentation of the surface, with various types of ridges, reticulations, granulations, striae, pits, and protrusions noted. One such character is the presence or absence of spinules. These are all but ubiquitous among Campanulaceae with porate grains, but are largely reduced to verrucae in the colpate and colporate genera. Among Cyphiaceae, spinules characterize *Nemacladus* and *Parishella*, but are lacking in *Cyphia* and *Cyphocarpus*. Spinuliferous pollen is widespread in Asteraceae; notable exceptions are the relatively smooth grains of many Mutisieae. Grains of Brunoniaceae, Goodeniaceae, and Stylidiaceae are also spinuliferous, while spinules are lacking in Calyceraceae, Donatiaceae, Lobeliaceae, Menyanthaceae, Pentaphragmataceae, and Sphenocleaceae.

Nuclei. Pollen grains when shed may contain either two or three nuclei. The latter condition is clearly derived from the former, and in no instance is a reversal apparent (Brewbaker, 1967). Binucleate pollen characterizes Brunoniaceae, Calyceraceae, Goodeniaceae, and Pentaphragmataceae, while the pollen of Asteraceae, Sphenocleaceae, and Menyanthaceae is exclusively trinucleate. Taxa of Campanulaceae, Lobeliaceae, and Stylidiaceae may be binucleate or trinucleate. *Lobelia* is one of only ten angiosperm genera with both binucleate and trinucleate species, and in no case does a single species produce both types of pollen (Brewbaker, 1967).

Pollinators. Pollen grains are typically shed singly, though permanent tetrads occur in a few genera (*Leschenaultia*, Goodeniaceae; *Namacodon* Thulin, Campanulaceae). Dispersal typically

is zoophilous (Wagenitz, 1977). Generally speaking, taxa with actinomorphic flowers and pseudanthia are visited by a broad suite of generalized insects, including various bees, flies, wasps, butterflies, and settling moths. Taxa with zygomorphic flowers have a narrower range of more specialized, often vertebrate visitors. In Lobeliaceae, for example, ornithophily is well developed (Lammers & Freeman, 1986), involving hummingbirds and passerines, while chiropterophily reportedly occurs in *Burmeistera* (Vogel, 1969); a few genera with salverform corollas (*Brighamia*, *Hippobroma* G. Don) are sphingophilous (Lammers & Freeman, 1986).

CYTOLOGY

The chromosome numbers discussed below, unless otherwise indicated, were taken from the standard indices (Darlington & Wylie, 1955; Cave, 1958a, b, 1959a, b, 1960, 1961, 1962, 1963, 1964, 1965; Ornduff, 1967, 1968; Moore, 1973, 1974, 1977; Goldblatt, 1981, 1984, 1985, 1988; Goldblatt & Johnson, 1990). For convenience, all reports are presented as gametic (haploid or n) numbers. The ancestral base number (x), from which other numbers in the family have been derived via euploidy or aneuploidy, is of primary interest. In some cases, this is relatively easy to determine, while in others it remains controversial despite numerous counts. No chromosome numbers are known for any species of Pentaphragmataceae.

Asteraceae are well known cytologically; Solbrig (1977) summarized data on chromosome numbers from nearly 8,000 species. Numbers range from $n = 2$ to $n = 120$, though most lie in the range of $n = 4$ to $n = 18$, and high polyploids are very rare. The most common number is $n = 9$, found in more than 20% of the species. Solbrig cautiously suggested that this could be the ancestral base number for the family, a view accepted by Raven (1975). Although the Barnadesiinae are believed to be the most primitive extant Compositae (Jansen & Palmer, 1988; Palmer et al., 1988), this information is not particularly helpful in suggesting a base number for the family. Chromosome numbers known from these genera are $n = 8, 12, 24, 25, 27,$ and 54 , from which one could argue for $x = 8$ or 9 (or even $4, 5,$ or 6).

Campanulaceae also are well known, with more than 1,150 counts published. Numbers reported are $n = 6-21, 23-30, 32, 34-36, 40, 45, 48, 51,$ and 52 . By far, the commonest number is $n = 17$, with more than 480 (42%) of the published counts. Another 150 (13%) are presumably tet-

raploid ($n = 34$) and hexaploid ($n = 51$) derivatives of this number. However, a gametic chromosome number as large as 17 probably is derived from some smaller number via aneuploidy following polyploidization or via allopolyploidy.

Bocher (1964) and Contandriopoulos (1984) considered $x = 8$ to be the most likely base number for Campanulaceae. Raven (1975), however, suggested that Campanulaceae, like their apparent sister group the Lobeliaceae, have $x = 7$. Although species with $n = 7$ are rare among Campanulaceae (only 12 such counts have been reported), that number is found in both species of *Cyananthus* that have been examined (Kumar & Chauhan, 1975; Hong & Ma, 1991). *Cyananthus* is widely regarded as the most primitive extant genus in the family on morphological grounds (Hutchinson, 1969; Carolin, 1978; Takhtajan, 1980; Dunbar, 1984; Hong & Ma, 1991), and its possession of $n = 7$ supports the hypothesis of $x = 7$ for the Campanulaceae. Hong & Ma (1991) hypothesized that taxa with $n = 8$ and $n = 9$ are the result of ascending aneuploidy from $x = 7$, and that the numerous taxa with $n = 17$ are allopolyploids, derived from hybridization between taxa with these two numbers.

The Lobeliaceae clearly have $x = 7$ (Foster, 1972; Raven, 1975; Thulin, 1983; Lammers, 1987, 1988). More than 135 species have been counted; almost 75% have $n = 7, 14, 21,$ or 35 . The exceptions are largely members of genera that are morphologically quite specialized: *Downingia* Torrey and its allies *Porterella* Torrey and *Howellia* A. Gray, with an aneuploid series derived from $x = 11$ or 12 ; and *Lysipomia* Kunth, with $n = 10$ (Casas, 1981).

For Styliaceae, counts of $n = 5-16, 18, 26, 28,$ and 30 have been published. Unfortunately, nearly all are from the derived genus *Stylidium*; no counts are available for the less specialized genera *Phyllachne* and *Forstera*. Despite the presence of lower numbers, James (1979) believed 15 to be the base number of the family. As with Campanulaceae, one suspects that so high a base number may be derived via aneuploidy from some polyploid or via allopolyploidy. *Donatia fascicularis*, widely regarded as an even less specialized relative or member of Styliaceae, has $n = 24$ (Moore, 1983). From this, one might speculate $x = 6$ or 8 for both families.

The Goodeniaceae have $n = 7, 8, 9,$ and multiples thereof ($n = 16, 24, 32; 18, 27, 36, 45$). Peacock (1963) considered $n = 7$ to be derived via descending aneuploidy, because it occurred only in three species of *Goodenia* Smith, a genus oth-

erwise based on eight. He was unable to decide whether $x = 8$ or $x = 9$ was the ancestral base number. On the basis of correlations with morphology, the former, which also occurs in twice as many genera, would appear to be more likely (Carolin, 1978). Brunoniaceae clearly have $x = 9$, with counts of $n = 9, 18,$ and 36 reported.

Menyanthaceae clearly have $x = 9$. Over 90% of the reported counts are $n = 9, 18, 27,$ or 54 . The few reports of $n = 8, 20,$ and 28 are interpreted as aneuploid derivatives of these numbers.

Although few species of Cyphiaceae have been examined, they appear to have $x = 9$. This is based on counts of $n = 9$ from two species each of *Cyphia* and *Nemacladus*.

Few Calyceraceae have been examined, and the base number is uncertain. Counts reported are $n = 8, 15, 18,$ and 21 . From this, one could argue for $x = 7, 8,$ or 9 (Stebbins, 1977).

The base number of Sphenocleaceae is uncertain, because the five published counts for *Sphenoclea zeylanica* Gaertner each report a different number: $n = 12$ (Lewis et al., 1962), 16 (Bir & Sidhu, 1974), 20 (Larsen, 1966), 21 (Bhattacharyya, 1972), and 24 (Sidhu & Lata, 1984). While it is not unlikely that an invasive pantropical weed would exhibit intraspecific variation in ploidy level, alternative hypotheses must be considered. Misidentification of the material is scarcely credible for so distinctive a species. Miscounts also seem unlikely, at least in the reports by Lewis and Bhattacharyya, because of the details and figures presented. However, the number reported by Larsen could be erroneous, as he reported difficulties in counting discrete chromosomes due to their "sticky" nature. Even discounting this report, the ancestral base number could be $x = 6, 7,$ or 8 , none of which would be inconsistent with base numbers in related families.

ULTRASTRUCTURE

Protein intranuclear inclusions with a fibrillar structure are unique to Campanulaceae (Taler & Gailhoffer-Dengg, 1972; Bigazzi, 1986), where they are found in all 27 species of *Campanula*, *Edraianthus* A. DC., *Jasione*, *Phyteuma*, and *Trachelium* L. that have been examined. However, they are absent from the 11 species of *Asyneuma* Griseb. & Schenck., *Canarina*, *Legousia* Durand, *Petromarula* Vent., *Platycodon*, and *Wahlenbergia* Schrader ex Roth that have been examined, as well as from the seven species of Lobeliaceae examined in the genera *Downingia*, *Isotoma* (R.

Br.) Lindley, *Lobelia*, *Pratia* Gaudich., and *Solenopsis* C. Presl.

Sieve-element plastids have been examined in the phloem of over 300 species of Asteridae, representing 42 families and 280 genera (Behnke, 1981; Behnke & Barthlott, 1983). All, including representatives of Asteraceae, Campanulaceae, Goodeniaceae, Lobeliaceae, and Stylidiaceae, lack proteinaceous inclusions (i.e., they have S-type plastids).

CHEMISTRY

Various types of primary and secondary metabolites have played a significant role in the classification of Campanulales (Gershenzon & Mabry, 1983; Harborne & Turner, 1984). Unfortunately, virtually nothing is known of the chemistry of Brunoniaceae, Cyphiaceae, Donatiaceae, Pentaphragmataceae, and Sphenocleaceae (Gibbs, 1974; Wagenitz, 1977).

Oligosaccharides. Inulin, straight chain polymers of one to 40 fructose residues linked *alpha*(1-2) to a terminal sucrose molecule, replaces starch as a storage carbohydrate in some dicotyledons. Pollard & Amuti (1981) detected inulin in all examined samples (representing 96 species in 48 genera) of Asteraceae, Brunoniaceae, Calyceraceae, Campanulaceae, Goodeniaceae, Lobeliaceae, Menyanthaceae, and Stylidiaceae; it has been reported also from Cyphiaceae (Thulin, 1978) and Donatiaceae (Gibbs, 1974).

Iridoids. Iridoids are monoterpenoid cyclopentanoid lactones produced by the mevalonate pathway. They are found only in dicotyledons and apparently serve to deter herbivores and pathogens (Harborne & Turner, 1984). Analyses of numerous species of Asteraceae, Campanulaceae, and Lobeliaceae have yielded negative results (Jensen et al., 1975; Hegnauer, 1977; Kaplan & Gottlieb, 1982).

All species of Stylidiaceae examined produce carbocyclic iridoids, specifically 10-hydroxylated compounds similar to monotropein (Jensen et al., 1975; Kaplan & Gottlieb, 1982). All species of Calyceraceae, Goodeniaceae, and Menyanthaceae examined produce seco-loganin, a simple seco-iridoid (Jensen et al., 1975; Kaplan & Gottlieb, 1982). Some Menyanthaceae also produce sweroside, a gentiopicroside seco-iridoid. Furthermore, loganin, an iridoid precursor of both carbocyclic and seco-iridoids, occurs in some Menyanthaceae, as well as in many other families.

Sesquiterpene lactones. These bitter substances are 15-carbon terpenoids derived from the

mevalonate pathway, which may function as feeding deterrents (Hegnauer, 1977; Harborne & Turner, 1984). Though diverse, their distribution among angiosperms is extremely restricted (Herz, 1977; Gershenzon & Mabry, 1983). Of the 1,400 compounds known, approximately 90% have been isolated from Asteraceae, where they are either deposited in latex (Lactuceae) or associated with various glands (nonlactiferous tribes).

Polyacetylenes. These highly unsaturated hydrocarbons, containing 8–21 carbon atoms, are synthesized from oleic acid. Their function is uncertain, but they may serve to deter pathogens and herbivores (Harborne & Turner, 1984). They are best known as Asteraceae, where almost 700 compounds with 8–18 carbon atoms have been isolated; over 95% of the known polyacetylene-producing species are members of this family (Bohlmann et al., 1973; Sørensen, 1977; Ferreira & Gottlieb, 1982; Gershenzon & Mabry, 1983). Diverse species of Campanulaceae have yielded various 14-carbon polyacetylenes. Similar compounds have been reported from two species of Lobeliaceae, and a 13-carbon polyacetylene has been detected in a species of Goodeniaceae.

Alkaloids. Alkaloids are diverse compounds containing a basic group and one or more nitrogen-containing heterocyclic rings, synthesized primarily from protein amino acids (Hegnauer, 1966a; Harborne & Turner, 1984). Many alkaloids have significant physiological effects on higher vertebrates, and presumably function in deterrence of herbivores and pathogens. Among angiosperms, alkaloids are found in 15–20% of the species examined.

Pyridine alkaloids appear to be ubiquitous among Lobeliaceae, where they commonly accumulate in the latex (Willaman & Schubert, 1961; Raffauf, 1970; Vagujfalvi, 1971; Gibbs, 1974; Gomes & Gottlieb, 1980); many compounds (e.g., lobeline, lobinaline, siphocampiline) have been isolated from a diverse array of taxa. Various Asteraceae, primarily species of *Senecio* L., produce not only pyridine alkaloids, but pyrrolizidine, quinoline, and diterpenoid types as well (Willaman & Schubert, 1961; Gibbs, 1974). Alkaloids of an unspecified nature have also been detected in eight species of Goodeniaceae (Willaman & Schubert, 1961). Despite numerous assays, alkaloids are all but absent from Campanulaceae and Stylidiaceae, having been found in just a few species (Willaman & Schubert, 1961; Hegnauer, 1973), nor have any been detected in Cyphiaceae, Donatiaceae, or Pentaphragmataceae (Gibbs, 1974).

Phenolics. Various phenolic constituents appear to be of some taxonomic utility among Campanulales (Bate-Smith, 1962; Gornall et al., 1979). Most notably, caffeic acid occurs in Asteraceae, Calyceraceae, Campanulaceae, Goodeniaceae, Menyanthaceae, and Stylidiaceae, primarily as esters with quinic acid, notably chlorogenic acid. However, it is wholly lacking from Lobeliaceae, where it seems to be replaced by chelidonic acid (Hegnauer, 1966b; Mølgaard, 1985).

MOLECULAR BIOLOGY

Recently, analyses of chloroplast DNA restriction sites and *rbcL* sequences have contributed an entirely new set of data to studies of relationships among Campanulales. These studies have not yet incorporated representatives of all 12 candidate taxa, and as a result, the picture that emerges is only partially resolved.

The most important result is the discovery that all but a few Asteraceae share a unique inversion that is 22 kb in length (Jansen & Palmer, 1988; Palmer et al., 1988). The exceptions are members of the Barnadesiinae, in which the configuration of that region is colinear with that found in other vascular plants. This fact offers persuasive evidence that the Barnadesiinae are the most primitive Asteraceae extant.

Several attempts are underway to understand better phylogenetic relationships among Asteridae, using these techniques (Downie & Palmer, 1992; Olmstead & Palmer, 1992). Of the candidate taxa, only representatives of Asteraceae, Calyceraceae, Campanulaceae, Goodeniaceae, Lobeliaceae, and Menyanthaceae have been examined thus far. Extensive rearrangements of the chloroplast genome distinguish Campanulaceae and, to a lesser extent, Lobeliaceae; such rearrangements have not been noted in the other taxa (S. R. Downey, pers. comm.).

Cladistic analyses of these molecular data indicate the following phylogenetic relationships. Calyceraceae and Goodeniaceae form a clade that is the sister group of Asteraceae. Menyanthaceae form the sister group of these three families. The several representatives of Gentianales, to which Menyanthaceae supposedly belong, are quite distant, and the representatives of Solanales are even more so. This clade, comprising Asteraceae, Calyceraceae, Goodeniaceae, and Menyanthaceae, will be referred to as the "asterad" clade in the subsequent discussion. Campanulaceae and Lobeliaceae (the "campanulads") form the sister clade of the asterads. This asterad–campanulad major clade incorporates all candidate taxa that have been

examined to date. Adoxaceae, Caprifoliaceae, Dipsacaceae, Valerianaceae, and Viburnaceae form a clade (the "dipsacads") that is the sister group to Apiaceae and Araliaceae (the "apiads"). This apiad-dipsacad major clade is then the sister group to the asterad-campanulad major clade.

PALEONTOLOGY

Asteraceae are represented in the macrofossil record primarily by compressions assigned to the form-genera *Achaenites* Braun and *Cypselites* Heer (Turner, 1977). A compression supposed to represent a capitulum (*Viguiera cronquistii* Becker) may actually be an immature gymnosperm strobilus (Crepet & Stuessy, 1978). All are no older than Oligocene. Pollen unequivocally referable to Asteraceae also makes its first appearance in Oligocene rocks (Muller, 1981). The only other candidate taxon represented in the fossil record is Goodeniaceae. *Poluspissusites digitatus* Salard-Cheboldaef from the Oligocene of Cameroon is very similar to pollen of *Scaevola sericea* (Muller, 1981). Thus, there is no evidence at present for the existence of any Campanulales prior to the Oligocene, approximately 40 million years ago.

CIRCUMSCRIPTION

In this section, two aspects of circumscription will be addressed. First, what is the best circumscription of the order, i.e., which of the 12 candidate taxa should be included in Campanulales and which should be removed to other orders? Second, what is the best circumscription and rank for each of these taxa, e.g., should Campanulaceae include Lobeliaceae as a subfamily, or should the latter be recognized as a distinct family? The goal throughout is to delimit natural (i.e., monophyletic) groups. Ideally, these groups should be relatively homogeneous in their various features and sharply distinct from other such groups, due to pronounced gaps in the spectrum of variation and the possession of one or more uniquely derived character states (i.e., synapomorphies). This ideal may not always be attainable, given the present state of our knowledge.

The discussion will proceed in a stepwise manner. Rules of nomenclature dictate that Campanulaceae remain in the order as long as it is recognized, no matter what else is removed. For this reason, the first step is to examine relationships within the core group of families. Next, the relationships of each of the five satellites will be examined.

THE CORE GROUP

The traditional broad circumscription of Campanulaceae (Schönland, 1889; Takhtajan, 1980) results in a family that is heterogeneous and possibly not monophyletic. A more homogeneous group, with a greater likelihood of being monophyletic, results from a narrower circumscription (Kovanda, 1978; Shetler & Morin, 1986), in which the family includes only those genera encompassed by the following description.

Perennial herbs (less often annual or woody), with articulated lactifers, producing 14-carbon polyacetylenes and caffeic acid but no iridoids and few if any alkaloids, storing carbohydrate as inulin; sieve-elements with S-type plastids. Leaves exstipulate, commonly alternate and simple; stomates anomocytic. Inflorescences variously monotelic or polytelic, predominantly racemose, or flowers solitary and axillary. Flowers tetracyclic, commonly perfect, with a specialized method of proterandrous secondary pollen presentation. Calyx synsepalous, commonly pentamerous, the odd lobe dorsal. Corolla sympetalous, commonly pentamerous, actinomorphic, the lobes valvate. Stamens equaling the number of corolla lobes, antisepalous; filaments distinct, inserted atop the ovary (on the rim of the free hypanthium in *Cyananthus*); anthers tetrasporangiate, dithecal, basifixed, connivent, dehiscent introrsely via longitudinal slits, the wall development dicotyledonous; endothecium with fibrous thickenings; tapetum glandular, the cells binucleate; pollen spheroidal, oblate, or prolate, commonly triaperturate and spinuliferous, binucleate or trinucleate when shed. Ovary syncarpous, inferior and fully adnate to hypanthium (superior and free in *Cyananthus*), commonly 3-5-loculed; placentation commonly axile; ovules anatropous, unitegmic, tenuinucellar, commonly numerous; embryo sac *Polygonum*-type, with an integumentary tapetum; embryogeny Solanad; embryo dicotyledonous, straight; endosperm copious, commonly oily, with equally aggressive terminal haustoria, its development ab initio cellular; style 1, with a ring of invaginating hairs near the apex; stigmatic lobes typically equaling the locules in number; fruit a loculicidal or poricidal capsule, or a berry. Of these features, the unique invaginating styler hairs are the only evident synapomorphy for the family.

Approximately 46 genera, comprising some 950 species, match this description and are here included in Campanulaceae. Though nearly cosmopolitan in its distribution, the family is best developed in the temperate zones of the Old World:

over 60% of the species are native to Eurasia, and another 30% are African.

Lobeliaceae. This taxon, whatever its rank, is typically circumscribed (Wimmer, 1943, 1953; Wagenitz, 1964; Takhtajan, 1987) to include genera identical to Campanulaceae except for the following characters: plants producing chelidonic acid and pyridine alkaloids, but no caffeic acid; flowers resupinate, but the odd sepal ventral prior to resupination; corolla zygomorphic; filaments connate for at least part of their length; anthers connate; pollen never spinuliferous; ovary 2-loculed; stilar hairs noninvaginating. The resupinate flowers and connate anthers are evident synapomorphies uniting these genera.

This circumscription would encompass more than 1,200 species in 30 genera. The group is nearly cosmopolitan in its distribution but is most diverse in the tropics and subtropics (commonly at higher elevations): 55% of the species occur in Latin America and the Caribbean, 20% in Africa, and 10% in Polynesia (primarily the Hawaiian Islands).

A few authors (McVaugh, 1943; Hegnauer, 1966b; Hutchinson, 1973; Thulin, 1978; Thorne, 1983) have included one or more of the genera segregated here as Cyphiaceae in the Lobeliaceae at various ranks. These genera do share some features that differentiate Lobeliaceae from Campanulaceae: odd sepal ventral, corolla zygomorphic, ovary 2-loculed; some of the genera also have filaments connate for at least part of their length and most have a bilobed stigma. However, including these genera in Lobeliaceae disrupts the latter's homogeneity by introducing several novel character states: flowers nonresupinate, lacking a specialized pollen presentation mechanism; stamens epipetalous; filaments and anthers distinct; style topped by a laterally uniaferturate fluid-filled stigmatic cavity. These novel states rob the family of its defining synapomorphies. Furthermore, chromosome numbers in Lobeliaceae are clearly based on seven, while those of Cyphiaceae apparently are based on nine. For these reasons, the five genera of Cyphiaceae are excluded from this group.

The question of appropriate rank remains. No author has doubted that the Lobeliaceae are closely related to Campanulaceae. Among the numerous characters shared by both taxa, the presence of articulated lactifers, specialized proterandrous pollen presentation, equally aggressive terminal endosperm haustoria, and similar 14-carbon polyacetylenes are perhaps most indicative of a close relationship. Such a relationship is also supported by the molecular data. In all analyses performed

thus far, representatives of the Lobeliaceae and Campanulaceae consistently form a clade distinct from other clades, undoubtedly due to the extensive rearrangements found in the chloroplast genomes of both families.

However, Lobeliaceae also differs from Campanulaceae in a number of significant characters, listed above. These differences are similar in degree and kind to the differences that distinguish many other dicot families. Furthermore, the chloroplast genome of Lobeliaceae is not as extensively rearranged as that of Campanulaceae. For these reasons, it is appropriate to recognize Lobeliaceae as a family distinct from Campanulaceae, following Kovanda (1978), Takhtajan (1987), and others.

Cyphiaceae. Whatever its rank, this taxon in its broadest circumscription (Schönland, 1889; Wagenitz, 1964; Wimmer, 1968; Takhtajan, 1980) comprises five genera. All are poorly understood and little studied. *Cyphia* is the largest, with approximately 60 species in southern and tropical Africa. *Cyphocarpus* comprises three species endemic to northern Chile. *Nemacladus* includes 13 species, while both *Parishella* and *Pseudonemacladus* are monospecific. These last three genera, all endemic to western North America, are very closely related and could be treated as a single genus (Munz, 1924).

Although there is no question that the Cyphiaceae belong to Campanulales, there are questions regarding their precise relationships within the order. Most authors have considered them a link connecting plesiomorphic Campanulaceae to apomorphic Lobeliaceae (Cronquist, 1981). Indeed, they resemble both families overall, and the exceptions appear intermediate. With Lobeliaceae, they share a ventral odd sepal, zygomorphic corolla, connate filaments (some genera), bilocular ovary, and bilobed stigma (some genera); the unique sepal position may well be a synapomorphy uniting the two. Like Campanulaceae, they lack alkaloids and floral resupination, and the anthers are not connate. In common with both families, they produce latex; articulated lactifers probably are a synapomorphy uniting all three. However, there are additional characters not found in either family: the unique stigmatic cavity of *Cyphia* and the epipetalous stamens of *Cyphocarpus*. Furthermore, all five genera appear to lack specialized mechanisms for proterandrous pollen presentation.

There are also similarities between some of these genera and Goodeniaceae. The tricolporate pollen of Goodeniaceae, with its spinules lacking roots and its perforated tectum (Dunbar, 1975b), resembles

that of *Nemacladus*. *Cyphia*, *Nemacladus*, and Goodeniaceae have chromosome numbers based on nine. Goodeniaceae differ in the absence of latex, the dorsal origin of the odd sepal, and the presence of a stylar indusium; the latter, however, could be homologous to the stigmatic cavity of *Cyphia*.

Furthermore, there are fundamental questions regarding whether these five genera constitute a natural group (Bentham, 1875; Thulin, 1978; Dunbar, 1975b, 1984; Dunbar & Wallentinus, 1976). For example, Hutchinson (1973) included *Cyphocarpus* in Campanulaceae but placed the remaining four genera in Lobeliaceae. Similarly, Thorne (1983) segregated *Cyphia* as the sole member of Cyphioideae, but placed the others in Lobelioideae. Finally, Takhtajan (1987) divided the genera among three families: Cyphiaceae (*Cyphia*), Cyphocarpaceae (*Cyphocarpus*), and Nemacladaceae (the remaining three genera). Cyphiaceae and Nemacladaceae were positioned between Campanulaceae and Lobeliaceae, but Cyphocarpaceae followed Lobeliaceae.

Implicit in these classifications is the idea that one or more of the genera may not share an origin with the others. These five genera are indeed heterogeneous in various morphological features, more so than might be expected in so small a group. The corolla of *Cyphocarpus* has a four-lobed ventral lip with a gibbose palate and a one-lobed dorsal lip; the others have two ventral and three dorsal lobes and lack any sort of palate. The stamens are epipetalous in *Cyphocarpus*, but inserted atop the ovary in the others. The filaments are distinct in *Cyphocarpus* and some species of *Cyphia*, but connate in the remainder of the group. In *Cyphia*, the style is topped by a unique, laterally uniaperturate fluid-filled stigmatic cavity, while the others have a bilobed stigma.

These genera are likewise heterogeneous palynologically (Dunbar, 1975b, 1984; Dunbar & Wallentinus, 1976). *Parishella* has 6-colpate pollen, while the others are 3-colporate. In *Nemacladus*, the colpi are oriented obliquely at varying angles to the equatorial plane, while in others they are perpendicular to it. In both *Parishella* and *Nemacladus*, the sexine is covered with spinules 1 μm tall, lacking roots; the intervening tectum is pitted. No other genus has spinules or tectal pits. Pollen of *Cyphia* is nano-granulate, almost smooth, while that of *Cyphocarpus* is reticulate, with the muri in high relief and with protrusions in the lumina.

On the basis of morphology, palynology, and geography, the five genera fall into three apparently natural groups: African *Cyphia*, Chilean *Cy-*

phocarpus, and the three genera of western North America. Whether these three cyphioid groups can be tied together as a single taxon is an open question. As shown above, there are no obvious synapomorphies uniting them. Their characters are either shared with other families, or restricted to single genera. It is possible that all three groups should be recognized at familial rank, as Takhtajan (1987) has done.

Several questions regarding the three cyphioid groups must be answered before we can reach a conclusion on their relationships to other families and to each other. First, do they produce iridoids, particularly simple seco-iridoids such as seco-loganin? If so, it would support a relationship to Goodeniaceae. Second, are the tapetal cells binucleate or multinucleate? The former would favor Campanulaceae and Lobeliaceae, the latter Goodeniaceae. Third, do terminal haustoria form in the endosperm? Such structures would suggest a relationship to Campanulaceae and Lobeliaceae. Fourth, is there structural or developmental homology between the indusium of Goodeniaceae and the stigmatic cavity of *Cyphia*? Fifth, are fibrillar protein inclusions found within cell nuclei? Their presence could indicate a close relationship with certain Campanulaceae. If different genera were to yield different answers to any of these questions, this would be additional evidence that the five genera do not form a monophyletic group. Inclusion of all five genera in a phylogeny derived from molecular data could provide good evidence of their true affinities.

Based on our present knowledge, none of the three cyphioid groups can be assigned to Campanulaceae or Lobeliaceae without disrupting the naturalness and homogeneity of those families; none share the unique stylar hairs of Campanulaceae or the resupinate flowers and connate anthers of Lobeliaceae. I am unwilling to follow Takhtajan (1987) in elevating all three to familial rank, due to the conspicuous gaps in our knowledge of their embryology, chemistry, and molecular biology, and to their general phenetic similarity. For these reasons, I recommend that all five genera be recognized provisionally as members of a single, possibly unnatural family Cyphiaceae, as Kovanda (1978) has done. A final disposition can be proposed once the studies outlined above have been completed.

Sphenocleaceae. This taxon includes only *Sphenoclea* Gaertner, a genus of two species: pantropical *S. zeylanica* Gaertner and *S. pongatium* DC. of western Africa. These species differ from the description of Campanulaceae given above in

the following characters: annual herbs with abundant aerenchyma but no network of articulated lactifers; stomates tetracytic; inflorescence a dense terminal spike; flowers lacking a specialized method of pollen presentation; corolla lobes imbricate; filaments inserted on corolla tube; anthers distinct; pollen subprolate, never spinuliferous, trinucleate when shed; ovary 2-loculed; seeds exalbuminous; style glabrous; stigma unlobed; capsule circumscissile.

A close relationship between *Sphenoclea* and Campanulaceae has been widely recognized (Subramanyam, 1950; Bhattacharyya, 1972; Hutchinson, 1973; Monod, 1980; Takhtajan, 1980; Cronquist, 1981; Thorne, 1983). Only Airy Shaw (1948, 1973) seriously questioned it, calling such a relationship "illusory." On the basis of similarities in habit and unspecified anatomical characters, he suggested a close relationship to Phytolaccaceae (Caryophylliidae). However, the Phytolaccaceae and their allies differ from *Sphenoclea* in their anomalous secondary growth, sieve-element plastids with unique (P-III) protein inclusions, storage of carbohydrate as starch, betalain (vs. anthocyanin) pigments, bitegmic crassinucellar campylotropous ovules, lack of an integumentary tapetum, Caryophyllad or Onagrad embryogeny, curved embryo, and nuclear endosperm development (Rodman et al., 1984), as well as in the numerous floral features (e.g., distinct petals, superior ovary) noted previously (Hutchinson, 1969; Monod, 1980; Rosatti, 1986). Certainly the gap evident in this comparison is much wider than the one separating *Sphenoclea* from Campanulaceae.

Some authors (Schönland, 1889; Hutchinson, 1973; Takhtajan, 1980; Dahlgren, 1983; Thorne, 1983) have included *Sphenoclea* within Campanulaceae. Doing so, however, disrupts the homogeneity of that family. *Sphenoclea* lacks the unique styler hairs that help define Campanulaceae, as well as the articulated lactifers that unite Campanulaceae, Cyphiaceae, and Lobeliaceae into a clade. For this reason, it seems best to assign *Sphenoclea* to its own family Sphenocleaceae, following Wagenitz (1964), Cronquist (1981), and others.

Pentaphragmataceae. This taxon includes only *Pentaphragma* Wallich ex G. Don, a genus of approximately 30 species endemic to south-eastern Asia, the Malay Archipelago (excluding Java and Nusa Tenggara), and New Guinea. As with *Sphenoclea*, most authors (Schönland, 1889; Kapil & Vijayaraghavan, 1965; Hutchinson, 1973; Dunbar, 1978; Takhtajan 1980) have recognized a close relationship between *Pentaphragma* and

Campanulaceae. The following differences distinguish the former: stems never woody, often fleshy or succulent, without lactifers; leaves strongly asymmetric at base; inflorescence an axillary sympodial helicoid cyme; flowers lacking any specialized mechanism for proterandrous secondary pollen presentation; corolla polypetalous in some species; filaments inserted on corolla tube (atop ovary in polypetalous species); anthers distinct, the wall development basic; pollen trilobate, never spinuliferous, binucleate when shed; ovary adnate to the hypanthium only via 5 longitudinal septa, 2-loculed; endosperm with a micropylar haustorium only; style glabrous; stigma unlobed; fruit a berry. The asymmetric leaves, distinctive inflorescence, trilobate pollen, and unique hypanthium may serve as defining synapomorphies.

Only Airy Shaw (1942, 1954, 1973) questioned the presumed relationship with Campanulaceae, suggesting affinities with Begoniaceae (Dilleniidae). He cited the asymmetrical leaf base and unspecified anatomical characters as supporting his suggestion. However, such a relationship does not seem likely, as Begoniaceae differ from *Pentaphragma* in their bitegmic crassinucellar ovules, Onagrad embryogeny, and nuclear endosperm formation, as well as in numerous floral features noted previously (Kapil & Vijayaraghavan, 1965). Again, the gap separating *Pentaphragma* from Begoniaceae is much wider than the one that separates it from Campanulaceae.

Some authors (Schönland, 1889; Hutchinson, 1973; Takhtajan, 1980) have included *Pentaphragma* within Campanulaceae. As in the previous taxon, this disrupts the homogeneity of that family by introducing a significant number of new character states. *Pentaphragma* likewise lacks the distinctive invaginating styler hairs of Campanulaceae, and the articulated lactifers that serve as a synapomorphy for the clade comprising Campanulaceae, Cyphiaceae, and Lobeliaceae. Differences in details of the pollen also support exclusion of *Pentaphragma* from Campanulaceae (Dunbar, 1978). Although there are a few similarities to *Sphenoclea*, the more numerous differences and lack of any synapomorphies preclude assigning these two genera to one family. For these reasons, it seems best to assign *Pentaphragma* to its own family Pentaphragmataceae, following Wagenitz (1964), Cronquist (1981), and others.

BRUNONIACEAE AND GOODENIACEAE

The Goodeniaceae, excluding *Brunonia* Smith (Krause, 1912a, b; Wagenitz, 1964; Cronquist, 1981), comprise approximately 325 species in 16

genera. Over 95% of the species are endemic to Australia and Tasmania. Two species are widely dispersed on tropical shores of the Atlantic and Indian oceans, while the remainder extend north and east in the Pacific as far as China, the Philippines, the Hawaiian Islands, New Zealand, and Chile.

Goodeniaceae have been dissociated from Campanulales only by Dahlgren (1975a, 1977, 1980, 1983), primarily on chemical grounds. Dahlgren accepted the hypothesis that the ability to synthesize iridoids is a synapomorphy uniting many sympetalous dicots into a single clade, and that taxa unable to synthesize iridoids cannot be accommodated within this clade (Hegnauer, 1964; Bate-Smith & Swain, 1966; Frohne & Jensen, 1973; Jensen et al., 1975; Kaplan & Gottlieb, 1982; Gershenzon & Mabry, 1983). However, the ability to synthesize iridoids could have arisen more than once among Asteridae. Alternatively, their absence from certain taxa could be explained as a loss of the necessary biosynthetic pathways; a single point mutation affecting a critical enzyme could easily shut down iridoid production (Jensen et al., 1975; Cronquist, 1977; Gershenzon & Mabry, 1983).

Goodeniaceae differ from the core group of Campanulales in the following characters only: plants producing iridoids, tapetal cells multinucleate, endosperm lacking haustoria, and style with a cuplike indusium below the unlobed or bilobed stigma. The indusium is unique and serves as a synapomorphy for these genera. Furthermore, although polyacetylenes have been isolated from both, those in Campanulaceae and Lobeliaceae have 14 carbon atoms, while those of Goodeniaceae have 13. Overall, this gap does not seem sufficient to justify removal of the Goodeniaceae from the order. Furthermore, phylogenies reconstructed from molecular data consistently place Goodeniaceae in the sister group of the clade comprising Campanulaceae and Lobeliaceae. For these reasons, the Goodeniaceae are retained within Campanulales.

There remains the question of the affinities of *Brunonia*, a genus that has been variously included in or excluded from Goodeniaceae. It comprises a single species, *B. australis* Smith of Australia and Tasmania, that is distinguished by its involucrate capitulate inflorescence, actinomorphic corolla, connate anthers, superior ovary with a single ovule attached to the base of the single locule, and unlobed stigma. However, virtually all these features occur in various genera of Goodeniaceae, e.g., superior ovary in *Velleia*, connate anthers in *Dampiera*, solitary basal ovule in *Verreauxia*. The only thing unique about *Brunonia* is the co-occurrence of these traits in one genus.

Clearly, the phenetic gap separating *Brunonia* from Goodeniaceae is much smaller than those separating Campanulaceae from Lobeliaceae, Pentaphragmataceae, or Sphenocleaceae. In fact, Thorne (1976) commented that *Leschenaultia*, a genus unequivocally assigned to Goodeniaceae, is much more distinct than *Brunonia*. Furthermore, *Brunonia* possesses the unique styler indusium that defines Goodeniaceae, but lacks clear synapomorphies of its own. For these reasons, *Brunonia* is here retained within Goodeniaceae.

This conclusion may be tested by addressing several questions regarding the chemistry and embryology of *Brunonia*. First, does *Brunonia* produce iridoids (particularly simple seco-iridoids such as seco-loganin) and 13-carbon polyacetylenes? Second, is the tapetum glandular with multinucleate cells? Third, are the ovules anatropous, unitegmic, and tenuinucellar, with a *Polygonum*-type embryo sac and Solanad embryogeny? Fourth, is endosperm formation ab initio cellular, and are terminal haustoria lacking? Affirmative answers to any of these questions would support the proposed relationship with Goodeniaceae. Incorporating *Brunonia* in a phylogeny generated from molecular data should provide definitive evidence.

CALYCERACEAE

This distinctive family includes approximately 60 species in six genera endemic to temperate South America. The group has been little studied, and there are conspicuous gaps in our knowledge of its chemistry and embryology.

Although the Calyceraceae were assigned to Campanulales in traditional Englerian classifications (Höck, 1889; Wagenitz, 1964), most recent authors (Thorne, 1976; Dahlgren, 1980; Cronquist, 1981) have placed them in or near Dipsacales. However, that order differs in its storage of carbohydrate as starch, and in possessing glandular hairs, opposite leaves, centrifugal inflorescences, flowers with an epicalyx, imbricate corolla lobes, distinct stamens, amoeboid tapetum, trinucleate pollen, and Asterad embryogeny (Davis, 1966; Cronquist, 1981; Pollard & Amuti, 1981). Furthermore, molecular studies have placed representatives of Dipsacales at some distance from Calyceraceae.

From the core group, Calyceraceae differ primarily in the production of iridoids, possession of multinucleate tapetal cells, and lack of endosperm haustoria. Other characteristic features occur in certain genera, e.g., involucrate capitula of actinomorphic flowers in *Jasione* (Campanulaceae), connate filaments with free anthers in *Nemacladus*

(Cyphiaceae), uniovulate ovaries (though with basal placentation) in *Merciera* (Campanulaceae) and *Unigenes* (Lobeliaceae), and apical placentation in *Siphocodon* (Campanulaceae).

The Calyceraceae are even more similar to Goodeniaceae, differing primarily in their epipetalous stamens and lack of an indusium. Several characteristic features of the Calyceraceae occur sporadically among the Goodeniaceae: involucrate capitula of actinomorphic flowers (*Brunonia*), uniovulate ovary (*Brunonia*, *Verreauxia*), and apical placentation (*Catosperma*). Especially notable is the presence in both families of seco-loganin and specialized mechanisms for secondary presentation of pollen. Furthermore, molecular studies have placed Calyceraceae and Goodeniaceae together as a clade within the sister group of Campanulaceae and Lobeliaceae. These data support the traditional Englerian assignment of Calyceraceae to Campanulales.

MENYANTHACEAE

This family includes five genera and approximately 35 species of aquatic and wetland plants of scattered distribution throughout the world. As discussed earlier, recent authors have assigned it to Gentianales or Solanales. However, Gentianales differ in the production of L-(+)-bornesitol, flavones, C-glycoflavones, indole alkaloids, and cardenolides, but not simple seco-iridoids; storage of carbohydrate as starch; the possession of intraxylary phloem, opposite leaves, convolute or imbricate corolla lobes, and nuclear endosperm development; and the lack of an integumentary tapetum (Davis, 1966; Jensen et al., 1975; Schilling, 1976; Gornall et al., 1979; Cronquist, 1981; Pollard & Amuti, 1981; Gershenzon & Mabry, 1983). Furthermore, molecular data group Gentianaceae with Apocynaceae, Rubiaceae, and Spigeliaceae at a substantial distance from Menyanthaceae. Similarly, Solanales differ primarily in their lack of iridoids, storage of carbohydrate as starch (except Polemoniaceae), and intraxylary phloem (Jensen et al., 1975; Cronquist, 1981; Pollard & Amuti, 1981); once again, they lie at some distance from Menyanthaceae in the molecularly derived phylogenies. Of the two proposed assignments, Menyanthaceae are nearer overall to Solanales.

The family is closer yet to Campanulales, however. It differs from the core of that order only in its production of iridoids; possession of heterostyly, aposepalous calyx, multinucleate tapetal cells, and Asterad embryogeny; and lack of endosperm haustoria. Several distinctive features characteristic of

the Menyanthaceae are found sporadically among the core families, e.g., superior ovary (*Cyananthus*, Campanulaceae) and unilocular ovary with two parietal placentae (*Apetahia* Baillon, *Downingia*, Lobeliaceae).

Menyanthaceae differ from Goodeniaceae in their lack of an indusium and specialized mechanism of pollen presentation; possession of heterostyly, aposepalous calyx, actinomorphic corolla, distinct stamens, trinucleate pollen, parietal placentation, and Asterad embryogeny. The characteristic superior ovary occurs in some genera (*Brunonia*, *Velleia*).

From Calyceraceae, the Menyanthaceae differ in never having an involucrate capitulum; in possessing heterostyly, aposepalous calyx, distinct stamens, parietal placentation, and Asterad embryogeny; and in lacking a specialized method of proterandrous pollen presentation.

As can be seen, Calyceraceae, Goodeniaceae, and Menyanthaceae share many features. Especially suggestive of a close relationship among them are the production of seco-loganin, storage of carbohydrate as inulin, the possession of multinucleate tapetal cells, and the lack of endosperm haustoria. The chromosome numbers of all three are based on $x = 8$ or 9 . Most convincing are the molecular data, which place Menyanthaceae as the sister group of the clade that contains Asteraceae, Calyceraceae, and Goodeniaceae. For these reasons, it is recommended that Menyanthaceae be dissociated from Gentianales and Solanales, and assigned to Campanulales.

ASTERACEAE

The cosmopolitan Asteraceae are the largest family of dicotyledons, with membership estimated at more than 1,100 genera and 20,000 species (Cronquist, 1981). In the phylogenetic trees generated by molecular studies, Asteraceae are embedded firmly among campanulalean families, at a substantial distance from Apiales, Cornales, Dipsacales, Rubiales, and other supposed relatives. These molecular data are supported by the other data reviewed here. Asteraceae differ from the core group of Campanulales in the following characters: plants producing sesquiterpene lactones and a more diverse array of polyacetylenes; calyx reduced to a pappus or absent; tapetum often amoeboid, its cells multinucleate; embryo sac sometimes bisporic or tetrasporic; embryogeny Asterad; and endosperm lacking haustoria, its development sometimes nuclear. Several distinctive features characteristic of the Asteraceae occur sporadically among the core families: involucrate capitula (*Ja-*

sione, Campanulaceae); epipetalous stamens (poly-petalous Pentaphragmataceae, Sphenocleaceae); exalbuminous seeds (Sphenocleaceae); and uniovulate ovaries with basal placentation (*Merciera*, Campanulaceae; *Unigenes*, Lobeliaceae).

The molecular data suggest that Asteraceae are even closer to the group comprising Calyceraceae, Goodeniaceae, and Menyanthaceae. They form the sister group to the clade comprising Calyceraceae and Goodeniaceae; Menyanthaceae is then the sister group to this larger clade. From these three families, Asteraceae differ in producing sesquiterpene lactones and a more diverse array of polyacetylenes but no iridoids, and in having the calyx papose or absent. In particular, the Calyceraceae seem very similar by virtue of their involucrate capitula, specialized pollen presentation mechanism, epipetalous stamens, and uniovulate ovary; details of the pollen, particularly the presence of unusual intercolpar concavities in both Calyceraceae and Barnadesiinae, also support a close relationship (Skvarla et al., 1977). All these data support the Englerian assignment of Asteraceae to a position near Calyceraceae at the apex of Campanulales.

DONATIACEAE AND STYLIDIACEAE

The Stylidiaceae, excluding *Donatia* Forster & G. Forster (Carlquist, 1969c; Cronquist, 1981; Takhtajan, 1987), include five genera and approximately 175 species. Over 95% are restricted to Australia and Tasmania; the remainder are distributed to the north and east as far as Ceylon, southern China, the Philippines, New Guinea, New Zealand, and Tierra del Fuego.

Morphologically and chemically, the Stylidiaceae are the most discordant members of the Campanulales, bringing to that order a significant number of character states found nowhere else in the order: plants producing carbocyclic iridoids; secondary growth anomalous; flowers solitary and terminal; stamens 2, wholly adnate to the style, forming a gynandrium that is commonly irritable; anther thecae divergent and apically confluent. The unique gynandrium with its divergent thecae is clearly a synapomorphy uniting these five genera. Regrettably, the family has not yet been represented in a phylogenetic reconstruction based on molecular data.

Three characteristics of Stylidiaceae are of limited distribution among dicots, and thus may serve as an indication of their affinities. First, there is the storage of carbohydrate as inulin, a trait used to support their inclusion in Campanulales. Only a

handful of other families store inulin (Pollard & Amuti, 1981): Boraginaceae (Lamiales); Clethraceae, Monotropaceae, and Pyrolaceae (Ericales); and Polemoniaceae (Solanales).

Second, there is the production of iridoids, which might be used to support a relationship with Goodeniaceae, Calyceraceae, and Menyanthaceae. However, these families produce seco-iridoids, while Stylidiaceae produce monotropein, a carbocyclic iridoid. Monotropein has been detected in only a few other families (Jensen et al., 1975; Kaplan & Gottlieb, 1982): Altingiaceae (Hamamelidales); Cornaceae (Cornales); Ericaceae, Monotropaceae, and Pyrolaceae (Ericales); Globulariaceae (Scrophulariales); and Rubiaceae (Rubiales).

Third, there is the development of terminal endosperm haustoria, a feature that might suggest a relationship with Campanulaceae, Lobeliaceae, and Sphenocleaceae. However, terminal endosperm haustoria characterize several other dicots with ab initio cellular endosperm formation (Davis, 1966; Dahlgren, 1975b; G. Dahlgren, 1989a): Acanthaceae, Bignoniaceae, Gesneriaceae, Globulariaceae, Lentibulariaceae, Myoporaceae, Orobanchaceae, Pedaliaceae, and Scrophulariaceae (Scrophulariales); Bruniaceae (Rosales); Callitrichaceae (Callitrichales); Clethraceae, Cyrillaceae, Empetraceae, Epacridaceae, Ericaceae, Grubbiaceae, and Monotropaceae (Ericales); Lamiaceae and Verbenaceae (Lamiales); Loasaceae (Violales); and Plantaginaceae (Plantaginales).

The Ericales are the only order in which all three of these unusual character states are found; even the Campanulales share only two. Numerous other characteristics of Stylidiaceae are found in at least some members of Ericales: sieve-tubes with S-type plastids; leaves alternate, simple; stomates anomocytic; corolla sympetalous, zygomorphic (*Rhododendron* L., Ericaceae), the lobes valvate (*Kalmia* L., Ericaceae); stamens two (*Oligarrhena* R. Br., Epacridaceae); anthers tetrasporangiate, dehiscent via longitudinal slits (*Oxydendrum* DC., Ericaceae), development of the wall dicotyledonous, the endothecium with fibrous thickenings; tapetum glandular, the cells binucleate; ovary inferior, bicarpellate, with axile placentation, and crowned by an intrastaminal nectary disc; ovules numerous, anatropous, unitegmic, tenuinucellar, with an integumentary tapetum; embryo sac *Polygonum*-type; embryogeny Solanad; fruit capsular; endosperm copious, its development ab initio cellular. Even their ecology is suggestive. Carlquist (1969c: 15) hypothesized that Stylidiaceae are derived from "ancestors which prefer acidic or mineral-poor soils," a statement that fits more Ericales

than it does Campanulales. The bryoid or cushion-plant habit of many Stylidiaceae is likewise more common among Ericales than Campanulales.

A distinctive feature of many Ericales is their unusual anthers. Commonly, these are inverted during their development (i.e., the morphologically basal portion is uppermost at anthesis) and poricidal. The distinctive gynandrium of Stylidiaceae might be less out of place in Ericales, given this tendency toward structural modification and rearrangement of the anthers, than it is in Campanulales.

Some authors (Thorne, 1976; Dahlgren, 1980) have suggested a relationship with Hydrangeaceae and its allies in the Cornales-Saxifragales alliance. However, none of these plants stores inulin or develops terminal endosperm haustoria. Dahlgren later realized this, and transferred Stylidiaceae to its own order near Ericales in the Ericanae (G. Dahlgren, 1989a, b).

In summary, the only alternative placement of Stylidiaceae that seems credible is in or near Ericales. Aside from the unique gynandrium, the family has no features that could not be accommodated within that order as it is commonly circumscribed. At the very least, it would be no more out of place than among Campanulales, an order in which carbocyclic iridoids are totally foreign. Consequently, Stylidiaceae should be removed from Campanulales to a position in or near Ericales, pending further data from molecular phylogenetic studies.

There remains the question of the affinities of *Donatia*, a genus variously included in or excluded from the Stylidiaceae. The genus comprises two widely disjunct species, *D. novae-zelandiae* of Tasmania and New Zealand and *D. fascicularis* of Tierra del Fuego. Nothing is known of their embryology or chemistry, aside from the fact that inulin is stored. On morphological grounds, *Donatia* also should be removed from Campanulales. The solitary sessile terminal flower, dimerous or trimerous androecium, and distinct styles are unknown elsewhere in the order. The apopetalous corolla is matched by only a few species of Pentaphragmataceae, and paracytic stomates are otherwise found only in *Brunonia* (Goodeniaceae).

Most authors have considered *Donatia* to be closely related to Stylidiaceae; only Hutchinson (1969, 1973) has totally divorced the two. The perception of a relationship with Stylidiaceae is due primarily to the remarkable similarity of *Donatia* to *Phyllachne* in habit and ecology (Carlquist, 1969c). However, the habitual similarities are underlain by significant differences in vegetative anatomy, and may well represent parallelism or con-

vergence induced by the rigors of their antarctic cushion-bog habitat (Rapson, 1953).

Donatia differs from Stylidiaceae in its paracytic stomates, apopetalous corolla, free and distinct stamens, colinear anther thecae, smooth pollen, and free and distinct styles. Its inclusion in that family would not only increase the morphological heterogeneity of an already heterogeneous family, but would deprive that family of its defining synapomorphies. For these reasons, it is recommended to continue recognition of Donatiaceae as a family distinct from Stylidiaceae (Rapson, 1953; Hutchinson, 1973; Cronquist, 1981).

Is it possible that Donatiaceae still deserve a position somewhere near Stylidiaceae, or are they only distantly related? The distinct styles would seem to argue for the latter; this feature is as unknown among Ericales as it is among Campanulales. Carlquist (1969c) commented that there is no compelling evidence of a relationship, aside from the common occurrence of inulin. However, Carolin (1960b) found floral structure and anatomy to be quite similar, and expressed no hesitation in treating *Donatia* as the ancestor of the Stylidiaceae.

Several questions regarding chemistry and embryology must be answered before a conclusion on the relationship of *Donatia* to Stylidiaceae can be reached. First, does *Donatia* produce iridoids, particularly carbocyclic iridoids such as monotropein? Second, is the tapetum glandular with binucleate cells? Third, are the ovules anatropous, unitegmic, and tenuinucellar, with a *Polygonum*-type embryo sac and Solanad embryogeny? Fourth, is endosperm formation ab initio cellular, and do terminal haustoria form? Negative answers to any of these questions would weaken the case for a relationship with Stylidiaceae. The inclusion of *Donatia* in a phylogeny generated from molecular data should provide definitive evidence. Pending the results of such studies, it is recommended to maintain the status quo and consider Donatiaceae to be a more primitive relative of Stylidiaceae.

SUMMARY

The available data support the inclusion of the following candidate taxa at familial rank: Astera-ceae, Calyceraceae, Campanulaceae, Cyphiaceae, Goodeniaceae (including *Brunonia*), Lobeliaceae, Menyanthaceae, Pentaphragmataceae, and Sphenocleaceae. With this circumscription, the Campanulales comprise nine families, more than 1,200 genera, and approximately 21,650 species, distributed throughout the world. Donatiaceae and

Stylidiaceae are removed from the order and assigned provisionally to a position in or near Ericales.

The following description summarizes the character states found in the order. Perennial herbs (less often annual or woody), producing polyacetylenes, simple seco-iridoids, sesquiterpene lactones, or alkaloids (seldom with more than one class of compound in a given species), storing carbohydrate as inulin; sieve-elements with S-type plastids. Leaves exstipulate, commonly alternate and simple; stomates anomocytic (rarely paracytic or tetracytic). Inflorescences variously monotelic or polytelic, predominantly racemose, often condensed into a tight capitulum subtended by an involucre, or sometimes the flowers solitary and axillary. Flowers tetra-cyclic, perfect or imperfect, sometimes heterostylous, resupinate in Lobeliaceae, commonly with a specialized method of proterandrous secondary pollen presentation. Calyx synsepalous (rarely aposepalous), commonly pentamerous, papose or absent in Asteraceae. Corolla sympetalous (rarely polypetalous), commonly pentamerous, actinomorphic or variously zygomorphic, the lobes valvate (rarely imbricate). Stamens (4-)5, antisepalous; filaments distinct or connate, inserted atop the ovary or on the corolla tube (rarely on the rim of the free hypanthium or the floral receptacle); anthers tetrasporangiate (rarely bisporangiate), dithecal, basifixed, distinct, connivent or connate, dehiscent introrsely (less often extrorsely) via longitudinal slits, the wall development dicotyledonous (rarely basic); endothecium with fibrous thickenings; tapetum glandular (rarely amoeboid), the cells binucleate or multinucleate; pollen spheroidal, oblate, or prolate (rarely trilobate), commonly triaperturate, binucleate or trinucleate when shed. Ovary syncarpous, inferior (rarely superior), 1-5(-10)-loculed; placentation axile or basal (rarely parietal or apical); ovules 1-many, anatropous, unitegmic, tenuinucellar; embryo sac *Polygonum*-type (rarely *Allium*-type or variously tetrasporic) with an integumentary tapetum; embryony Solanad or Asterad; embryo dicotyledonous, straight; endosperm development ab initio cellular, with or without haustoria; style 1, often with a ring of hairs or cup subtending the unlobed or 2-5(-10)-lobed stigma; fruit a capsule, berry, achene, or cypsela. Chromosome numbers commonly $x = 7, 8, \text{ or } 9$.

Two facts are apparent from the above description. First, the Campanulales, despite their diversity, are relatively homogeneous when compared to other angiosperm orders. Second, while the order may be defined on the basis of a suite of correlated features, there are no evident nonmolecular synapomorphies that define it rigorously.

PHYLOGENY

Reconstructing the phylogeny of a group of families on the basis of morphology and other phenotypic data is rife with the potential for error, due to difficulties in correctly assessing homologies (Cronquist, 1987b; Stuessy, 1990). Missing data also reduce the confidence that can be placed in such phylogenetic trees. Fortunately, very low levels of such homoplasy characterize phylogenies inferred from the results of chloroplast DNA restriction fragment analysis and *rbcL* sequence data. Attempts are under way in various laboratories to incorporate all families of Asteridae into these molecular studies. Once such studies have been completed, as well as additional chemical and embryological investigations recommended above, it will be possible to examine phenotypic character state trends and changes in a more satisfactory manner, by integrating the data reviewed here into the framework provided by the molecular phylogeny. Then, a comprehensive understanding of phylogenetic relationships among Campanulales, as well as a sound revision of their classification, will be possible.

For these reasons, no diagram purporting to show phylogenetic relationships among the families of Campanulales is proffered at this time. Meanwhile, the following preliminary notes toward an integrated phylogeny of the order are appropriate. These may be considered hypotheses to be tested by the accumulation of additional data.

PHYLOGENETIC PATTERNS

The molecular phylogeny indicates that the Campanulales, as here circumscribed, are indeed a monophyletic group. Unfortunately, there are no evident nonmolecular synapomorphies to support this clade. The ability to store inulin, which occurs in but does not characterize three other orders, may be the closest approach to one. Note that if Asteraceae and/or Calyceraceae were to be segregated as discrete orders, the Campanulales that remained would clearly be paraphyletic.

The sparse fossil record suggests that the order arose no later than the Oligocene, some 40 million years ago. Given that the earliest fossils are of rather advanced families (Asteraceae, Goodeniaceae), origin earlier in the Tertiary or even in the late Cretaceous is not improbable (P. R. Crane, pers. comm.).

The molecular phylogeny shows the Campanulales dividing into two clades. This basal dichotomy is supported by three nonmolecular characters, none of them morphological. Taxonomically, the

two clades might be recognized as suborders; alternatively, it might be advantageous to recognize each at ordinal rank in a revised classification of Asteridae. Phylogenetic relationships within each clade are confused by the combination of plesiomorphic and apomorphic states in several of the families.

The asterad clade comprises Asteraceae, Calyceraceae, Goodeniaceae, and Menyanthaceae. These families have multinucleate tapetal cells, lack endosperm haustoria, and produce deterrent chemicals via the mevalonate pathway (either seco-iridoids or sesquiterpene lactones, but not both). Menyanthaceae might be the most primitive family in this clade (and perhaps in the order), judging by their greater diversity of iridoid compounds, lack of a specialized mechanism for secondary pollen presentation, free and often distinct sepals, actinomorphic corolla, and superior ovary. However, their heterostylous flowers, trinucleate pollen, and unilocular ovary with two parietal placentae would appear to be relatively advanced features. The Goodeniaceae seem relatively advanced in their zygomorphic corolla and stylar indusium, as do Calyceraceae by virtue of their involucrate capitula, epipetalous stamens, uniovulate ovaries, and apical placentation. Undeniably, Asteraceae are the most specialized group morphologically, both within the order, and within the Asteridae as a whole.

The campanulad clade comprises Campanulaceae, Cyphiaceae, Lobeliaceae, Pentaphragmataceae, and Sphenocleaceae. These families have binucleate tapetal cells, terminal endosperm haustoria, and apparently are unable to synthesize deterrent chemicals by the mevalonate pathway. The Campanulaceae would appear to be plesiomorphic, on the basis of their radially symmetric flowers and multilocular ovaries; in particular, *Cyananthus*, with its 5-locular ovary free from the hypanthium, has been suggested to be the most primitive extant genus in the family (Hutchinson, 1969; Carolin, 1978; Takhtajan, 1980; Dunbar, 1984). However, the production of latex and the specialized pollen presentation mechanism, including the unique invaginating stylar hairs, most likely are derived features.

The absence from Sphenocleaceae and Pentaphragmataceae of lactifers and any sort of specialized pollen presentation mechanism suggests that these families might be even more primitive than Campanulaceae. The sometimes polypetalous corolla, partially adnate hypanthium, and micropylar haustoria of the latter might be primitive features as well. However, these two families also exhibit

several apparently advanced characters, including the trinucleate pollen grains, circumscissile capsule, and exalbuminous seeds of the former; the asymmetric leaves, unique inflorescence, and trilobate pollen of the latter; and the epipetalous stamens and bilocular ovaries of both.

The Lobeliaceae clearly are more advanced than Campanulaceae, based on their resupinate flowers with the odd sepal ventral prior to resupination, zygomorphic corolla, connate heteromorphic anthers, and bilocular ovary. In as much as Cyphiaceae likewise have the odd sepal ventral and the corolla zygomorphic, they, too, seem to be more advanced than Campanulaceae. Their nonresupinate flowers and apparent lack of secondary pollen presentation mark them as less advanced than Lobeliaceae, however.

MORPHOLOGICAL TRENDS

This section examines the distribution of various morphological characters employed in the classification of Campanulales against the framework of this preliminary hypothetical phylogeny. For example, it is obvious that there has been an evolutionary reduction in the syncarpous gynoecium, involving both a reduction in the number of locules and in the number of ovules per locule. The two trends vary independently, as evidenced by the existence of several possible permutations, e.g., unilocular ovaries with numerous ovules and bilocular ovaries with a solitary ovule in each locule. The two trends converge at their respective culminations, producing a unilocular ovary with solitary ovule. Such ovaries occur among campanulads (*Merciera*, Campanulaceae; *Unigenes*, Lobeliaceae) and asterads (*Brunonia* and *Verreauxia*, Goodeniaceae; Calyceraceae; Asteraceae), suggesting that the uniovulate ovary has evolved more than once within Campanulales.

Epigyny likewise appears to have had multiple origins, because genera with superior ovaries are found among asterads and campanulads. Furthermore, there are significant differences in the non-epigynous flowers of these clades. In the putatively most primitive genus of the campanulad clade, *Cyananthus* (Campanulaceae), the flower is perigynous. The superior ovary is surrounded by (but free from) a cuplike hypanthium, upon which are inserted the corolla and filaments. By contrast, in the putatively most primitive members of the asterad line, the Menyanthaceae, the flower is hypogynous. There is no adnation among the floral whorls surrounding the superior ovary, all of which arise from the floral receptacle. These observations

correlate well with Carolin's (1959, 1960b, 1978) observations on anatomy and ontogeny in epigynous flowers of Campanulaceae and Goodeniaceae. These studies showed that in Campanulaceae, the outer floral whorls coalesced into a free hypanthium prior to adnation of the ovary, while the inferior ovary of Goodeniaceae formed by the sequential adnation of the outer floral whorls to the ovary. These facts suggest that inferior ovaries evolved independently in the asterad and campanulad clades.

Zygomorphy likewise appears to have arisen more than once and in different ways, because it occurs in derived taxa of both the campanulad (Cyphiaceae and Lobeliaceae) and the asterad (Asteraceae and Goodeniaceae) clades. As discussed previously, the bilabiate flowers of Goodeniaceae and Lobeliaceae may look very similar at anthesis, but are fundamentally different, due to differences in the position of the odd lobe and resupination. Even within a clade, zygomorphy may have multiple origins. Bremer (1987) considered the zygomorphic florets of Asteraceae to be derived from actinomorphic florets.

Even the distinctive mechanisms for secondary pollen presentation that characterize most members of the order also appear to have had multiple origins, as evidenced by detailed study of the structures involved (Carolin, 1960a; Erbar & Leins, 1989; Leins & Erbar, 1990) and their distribution among the families. Connate anthers occur among both campanulads (Lobeliaceae) and asterads (Asteraceae, some Goodeniaceae); likewise, connate filaments with distinct anthers occur in both clades (Cyphiaceae, Calyceraceae).

If these interpretations are correct, it means that any attempt to utilize these distinctive morphological features as synapomorphies in a cladistic analysis of Campanulales would be fraught with frustration. Assuming that a feature has evolved once when in fact it has had multiple origins would introduce considerable homoplasy to the phylogeny and indicate close relationships where none exist.

CHEMICAL TRENDS

The integrated phylogeny shows the sesquiterpene-producing Asteraceae to be derived from iridoid-producing families. The monoterpenoid structure of seco-iridoids is not very different from the basic skeleton of sesquiterpene lactones, and both classes of compounds are synthesized via the mevalonate pathway. From these observations, I hypothesize that mutations affecting one or more enzymes in the mevalonate pathway interrupted iridoid production in ancestral Asteraceae and that the

chemical precursors or intermediates were shunted into the production of sesquiterpene lactones. Such a hypothesis fits in with Cronquist's (1977) view that the evolutionary success of Asteraceae was due primarily to biochemical innovation.

This hypothesis also helps explain the oft-cited chemical similarity between Asteraceae and Apiaceae. These two families have been hypothesized to be closely related, because they are among the few angiosperms capable of producing sesquiterpene lactones (Hegnauer, 1964, 1977; Bate-Smith & Swain, 1966; Herz, 1977; Gershenzon & Mabry, 1983). However, the molecular data indicate that they are only distantly related. As discussed earlier, Apiaceae and Araliaceae form a clade, the apiads, that is the sister-group of the dipsacad clade. All dipsacads produce seco-iridoids; the apiads do not. Once again, it appears that a family rich in sesquiterpene lactones is related to iridoid producers. Apparently, there have been parallel mutations in the mevalonate pathways of Apiaceae and Asteraceae, shutting down the synthesis of seco-iridoids and initiating the production of sesquiterpene lactones in both families. Thus, the production of sesquiterpene lactones, while a derived character state, cannot be used as a synapomorphy to unite Apiaceae and Asteraceae.

From the above two cases, it might appear that the production of sesquiterpene lactones is the natural consequence of blockage of iridoid synthesis. However, it does not appear to be an obligate outcome, because Araliaceae, Campanulaceae, and Lobeliaceae produce neither iridoids nor sesquiterpene lactones. Rather, these families deter predators and pathogens with polyacetylenes and/or alkaloids, which are biogenetically unrelated to deterrents from the mevalonate pathway. Further study is needed to explain this pattern. The co-occurrence of polyacetylenes with sesquiterpene lactones in many Apiaceae and Asteraceae, and with seco-iridoids in some Goodeniaceae, may be significant in the elucidation of this problem.

RELATIONSHIPS TO OTHER ORDERS

Given the present state of our knowledge, it is difficult to draw any firm conclusions regarding the relationships of Campanulales to other orders. The difficulties with inferring phylogeny from morphological and chemical data, which cause such frustration for interfamilial comparisons, become even more insufferable at the ordinal level. It is expected that molecular studies will eventually resolve these problems, but at this time, not enough taxa have been included in these studies to permit a confident

conclusion. Until a more complete phylogeny is available, the following brief comment is offered.

As noted above, the molecular data indicate that the sister group of Campanulales is the apiad-dipsacad clade. The sister group of this combined clade includes Cornaceae and Philadelphaceae. These data support the hypothesis that the Campanulales ultimately take their origin very near the ancestry of the Asteridae, in the complex of families comprising the Cornales and woody Saxifragales (Thorne, 1976; Dahlgren, 1980). This complex is poorly understood, and much more study is required before a definitive statement can be made on its role in the ancestry of Campanulales.

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A NEW SUBFAMILY OF THE ASTERACEAE¹

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ABSTRACT

The Asteraceae are generally divided into two large subfamilies, the Cichorioideae (syn. Lactucoeae; tribes Mutisieae, Cardueae, Lactuceae, Vernoniaceae, Liabeae, Arctoteae) and the Asteroideae (Inuleae, Astereae, Anthemideae, Senecioneae, Calenduleae, Heliantheae, Eupatorieae). Recent phylogenetic analyses based on morphological and chloroplast DNA data show that the Mutisieae–Barnadesiinae are the sister group to the rest of the family. The Mutisieae–Barnadesiinae are here excluded from the Mutisieae and elevated to the new subfamily Barnadesioideae.

Until the 1970s the tribe Lactuceae was considered to be distinct from all other Asteraceae and it was classified in its own subfamily, the Liguliflorae. The other tribes were placed together in the Tubuliflorae (e.g., Hoffmann, 1890). During the 1970s there was a growing understanding that all the tribes, including the Lactuceae, could be arranged in two large groups (Robinson & Brettell, 1973; Carlquist, 1976; Wagenitz, 1976), foreshadowed by diagrams in Carlquist (1961) and Poljakov (1967). Carlquist (1976) treated these two groups as the subfamilies Cichorioideae and Asteroideae. Their precise circumscription was modified by later authors (Robinson, 1977, 1981, 1983; Thorne, 1983).

Since 1985 cladistic analyses of molecular and morphological data have clarified the phylogeny and classification of the Asteraceae. Jansen & Palmer (1987) reported the presence of a 22 kb cpDNA inversion in *Lactuca* and several other Asteraceae. The inversion was found to be absent in three genera of the Mutisieae–Barnadesiinae, suggesting a basal dichotomy between the Barnadesiinae and the rest of the family. Subsequently, Jansen & Palmer (1988) undertook an analysis of cpDNA restriction site data from 13 genera of the Mutisieae (including the Barnadesiinae) and 9 representatives from other tribes. Later Jansen et al. (1990, 1991a) sampled 57 genera from 15 tribes in an extended study of cpDNA restriction site data. These studies corroborated the sister-group relationship between the Barnadesiinae and the rest of the family. To date, Jansen et al. (1991b) have examined more than 250 Asteraceae genera for the cpDNA inversion, which has proved to be pres-

ent in all genera except those of the Barnadesiinae. The sister-group relationship between the Barnadesiinae and the rest of the family is supported also by analysis of *rbcL* sequences (Kim et al., 1992).

Simultaneously with Jansen & Palmer's cpDNA investigations, Bremer (1987) conducted a cladistic analysis of tribal interrelationships based on morphological data. The study included 27 tribes and subtribes and 47 phylogenetically informative characters, one of them being the cpDNA inversion. The sister-group relationship between the Mutisieae–Barnadesiinae and the rest of the family, revealed by the cpDNA inversion, was supported also by several morphological characters, such as presence of the typical Asteraceae twin hairs on the fruits and spiny pollen.

All available data sets strongly support the sister-group relationship between the Mutisieae–Barnadesiinae and the rest of the family (Jansen & Palmer, 1987, 1988; Bremer, 1987; Jansen et al., 1990, 1991a, b; Karis et al., 1992; Kim et al., 1992). The subtribe Barnadesiinae should now receive formal subfamilial status, as Barnadesioideae. It is a small subfamily of nine genera and nearly 90 species, distributed in South America mainly along the Andes. The Barnadesioideae genera share a number of morphological and molecular synapomorphies. Hence, the subfamily is a strongly supported monophyletic group. Its members are characterized by unique axillary spines and by a unique indumentum of long, unicellular, barnadesioid hairs on the corollas, cypselas, and pappus (Cabrera, 1959, 1961, 1977; Bremer, 1987).

The large subfamily Asteroideae is also a monophyletic group, with synapomorphies both in mor-

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phology and cpDNA. Members of the Asteroideae are characterized by shallowly lobed corollas, style branches with stigmatic areas separated in two parallel lines, and caveate pollen (Bremer, 1987). Among the molecular synapomorphies there is a length mutation at the 3' end of the *rbcL* gene involving a six bp repeat, which is repeated four times, in all examined Asteroideae taxa (Kim et al., 1992).

The status of the subfamily Cichorioideae (excluding Barnadesioideae) remains unresolved, and the interrelationships among its tribes are not clearly understood from our hitherto published analyses. The morphological and the cpDNA trees are incongruent in several of the groupings, especially if Bremer's (1987) tree is compared to those based on cpDNA. The more detailed analysis of Karis et al. (1992) has removed some of the conflicts, whereas others persist. Karis et al. propose that a large part of the Mutisieae form a monophyletic group, excluding a number of Mutisieae-Gochnatii-nae genera, which form a more or less unresolved paraphyletic grade at the base. Jansen et al. (1990, 1991a, b) suggested that the Mutisieae are monophyletic; all taxa sampled consistently group together. Further studies are necessary to evaluate the status of the subfamily Cichorioideae and to resolve tribal interrelationships within the two subfamilies Cichorioideae and Asteroideae.

Barnadesioideae (Bentham & Hooker) Bremer & Jansen, subfam. stat. nov. Barnadesieae (Bentham & Hooker) Bremer & Jansen, trib. stat. nov. Basionym: Mutisieae-Barnadesiinae Bentham & Hooker, Gen. Pl. 2: 168, 1873.
Type: *Barnadesia Mutis* ex L. f.

Spinae axillares frequenter presentes. Corollae, cypselae pappusque villosae pilis longis unicellularibus. Stylus breviter bilobus, glaber vel papillosus. Pollen laeve vel granulare, non spinosum.

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