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# THE ASTERIDAE: EVOLUTION OF A CONCEPT AND ITS PRESENT STATUS<sup>1</sup>

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## ABSTRACT

The concept of Asteridae can be traced back to the Monopetalae of Tournefort (1694) and de Jussieu (1789). This group, later better known as the Sympetalae, was essentially based on a single character, the united petals. A closer look at the floral morphology and the study of embryology (especially of the ovules) by Van Tieghem and Warming led to the exclusion of some families (e.g., the Cucurbitaceae). Moreover, it became clear that only the "Tetracyclae" (with one series of stamens alternating with the petals) may probably form a coherent group. Formal recognition of this group as a subclass was proposed by Takhtajan in 1964 and has been accepted by Cronquist (1968). Recent studies have emphasized chemical characters, although embryology is still important.

Because of a combination of characters, the following orders are good candidates for monophyletic groups: Gentianales (including Rubiaceae, but excluding Retziaceae, Buddlejaceae, and probably Menyanthaceae), Dipsacales, and Scrophulariales (including Plantaginaceae, Lamiales). Still controversial is the circumscription of the Solanales and Campanulales sens. lat. There have been some "imports" of families with strongly reduced flowers (mostly wind-pollinated water plants) formerly placed in orders outside the Asteridae: Hippuridaceae, Callitrichaceae, and Hydrostachyaceae. In these groups, flower morphology alone has been misleading in determining the proper taxonomic position. The position of the Dialypetalanthaceae and Loasaceae, with some characters pointing to an Asteridae affinity but with polyandry, is not clear. More important and much more controversial is the question of the nearest allies outside this group. Several orders in the Rosidae (Rosales, Geraniales, Cornales, Apiales) have been named as probable relatives for part of the Asteridae or for the whole group. However, the evidence is unequivocal neither from morphology nor from phytochemistry.

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At the beginning of scientific botany the flower was identified with the corolla as its most showy part. Botanists must have noted very early that in some groups this consisted of several separate parts, the petals, whereas in others it was shed as a whole and formed a single tube or funnel. Linnaeus (1751) called the botanists using criteria of the corolla for the primary division of the system "Corollistae," and the most important of these was Tournefort (1694, 1700). He maintained the old-fashioned division in *Arbores* and *Herbae*, and in each of these we find classes defined by the term "flore monopetalo." The Monopetalae were accepted as one of the main divisions of the Dicotyledones by de Jussieu (1789), who can rightly be named the father of the natural systems of the nineteenth century. His Monopetalae are nearly identical with the Sympetalae of later systems.

In 1813, A. P. de Candolle coined the new term

gamopetalous ("gamopétale"), which led to the replacement of Monopetalae by Gamopetalae. This meant that the corolla was seen as a product of the fusion of several petals. This is not an ontogenetically visible process and thus can be termed idealistic morphology, but it has in fact later been interpreted phylogenetically. Reichenbach (1828 in Mössler's *Handbuch der Gewächskunde*) seems to have been the first to use the alternative term Sympetalae ("Synpetalae") instead of Gamopetalae. In the systems of the nineteenth century, for example, by Bartling (1830), Endlicher (1836–1840), Bentham & Hooker (1873–1876), Eichler (1876), and Engler (1924), the Gamopetalae or Sympetalae can be found in nearly identical circumscription. An important step to the shaping of the Asteridae was the insight that two groups can be distinguished. A core group (the "Tetracyclae," a name first used by Warming in 1879) with

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invariably only one series of stamens alternating with the corolla lobes, and a more variable group (the "Heteromerae" of Bentham & Hooker, 1873–1876, or "Pentacycliae" of Warming, 1879) with two series of stamens or one with stamens superimposed to the lobes of the corolla. The Pentacycliae comprise the orders Ericales, Diapensiales, Ebenales, and Primulales of modern systems. These are placed in the Dilleniidae in the systems of Takhtajan and Cronquist.

The "Tetracycliae" are the immediate "ancestors" of the Asteridae. They can be found as a group without a name in Cronquist's (1957) system and were christened by Takhtajan in 1964.

This is the history of the formal concept of the Asteridae. Let us now look at the additional characters used for shaping the group, for the exclusion of some families and the addition of others, for the various attempts to subdivide the group into orders, and for tying the Asteridae to other subclasses. The molecular data that have recently become available have not influenced this overview.

#### SYSTEMATICS OF THE ASTERIDAE

Besides floral morphology, embryology and, in more recent times, phytochemistry have been of foremost importance in classifying groups. In the second half of the nineteenth century data on at least some embryological features accumulated. Very important was the distinction between ovules with one and two integuments and those with a massive or a very thin nucellus. The first to note this character was Warming in 1878. Van Tieghem (1897) even proposed to base a system on these characters. The Cucurbitaceae are a family that has been excluded at an early date from the Sympetalae by many authors based on this character (and the morphological similarities to families in the "Parietales"). Yamazaki (1974) created a system of the "Gamopetalae" using the embryogeny as the decisive character.

The characters shared by the Asteridae can be enumerated as follows: sympetalous corolla, stamens as many as or fewer than the corolla lobes and alternate with them, and unitegmic, tenuinucellate ovules. The sieve-element plastids are from the S-type (starch-containing), with the notable exception of part of the Acanthaceae (Behnke, 1986). Very characteristic is the constancy in the number of floral parts in most families in Asteridae as compared with other subclasses. This has been shown impressively in a publication by Endress (1990). According to Cronquist (1968), this subclass is "highly natural." The question is: are these

characters "shared-derived characters," i.e., are they synapomorphies in the sense of Hennig? We need not argue much about the status as derived characters; this is fairly evident, but it is not enough. Can we be reasonably sure that these characters are not due to parallel evolution originating from different phyletic lines? Of course we cannot be sure, and this is the point where the discussion begins. Before proceeding, however, I will address the larger groups (orders) within the Asteridae.

Good candidates for monophyletic groups are, in my opinion, the Gentianales, Dipsacales, Scrophulariales (including the Lamiales), and probably the Campanulales–Asterales.

The families of the Gentianales (Loganiaceae, Rubiaceae, Apocynaceae, Asclepiadaceae, Gentianaceae) are tied together by a combination of vegetative, floral, and phytochemical characters (Wagenitz, 1959). The group contains basically woody plants with opposite, entire leaves often with stipules (otherwise lacking in the Asteridae), and with colleters, a special type of multicellular glandular hair located on the stipules or the base of the leaves and even inside the calyx (other names for these structures in the calyx are: Intra-sepaldrüsen (Glück, 1919), squamellae (Woodson & Moore, 1938), and squamae intravaginales (Vijayaraghavan & Padmanaban, 1969)). An important anatomical character is the occurrence of internal phloem (lacking in the Rubiaceae). The flowers are nearly always regular with an isomerous androecium; contorted aestivation is widespread but is not a common character. Endosperm formation is nuclear with very few exceptions. Indolealkaloids of a special type occur in three families (although not in all genera): The Loganiaceae (excluding the Retziaceae and Buddlejaceae), Rubiaceae, and Apocynaceae constitute a coherent group on the basis of this character (Kisakürek, 1980). The Asclepiadaceae, which are morphologically close to the Apocynaceae, are linked to those Apocynaceae without alkaloids by the presence of cardenolides in both groups. Brewbaker (1967) and Mathew & Philip (1986) have stressed that all the families of Gentianales contain species with binucleate and trinucleate pollen, a fact difficult to evaluate. *Buddleja* and allied genera (Buddlejaceae) and the monotypic Retziaceae differ in many characters from the Loganiaceae and should be placed in the Scrophulariales sens. lat. (Bendre, 1973, 1975; Maldonado de Magnano, 1986a, b; Carlquist, 1986; Engell, 1987; Hegnauer, 1989). Still controversial is the position of the Menyanthaceae (Bohm et al., 1986; Vijayaraghavan & Padmanaban, 1969), which have been assigned to the Solanales (Cron-

quist, 1988), the Cornales (G. Dahlgren, 1989b), and the Asteranae (Yamazaki, 1974, because of the development of the embryo according to the Asterad type).

The Dipsacales (Caprifoliaceae, Valerianaceae, Triplostegiaceae, Morinaceae, Dipsacaceae) have a combination of the following characters: opposite leaves without stipules, inferior ovary, a strong tendency toward zygomorphy with reductions in the numbers of the stamens and carpels. Several families possess an epicalyx (Hofmann & Göttmann, 1990). The most distinctive character is the type of nectary consisting of a region of unicellular hairs on the corolla or sometimes on a massive structure at its base (Wagenitz & Laing, 1984). This character is not present in *Viburnum*, *Sambucus*, the Adoxaceae, and Calyceraceae, and their position in the order remains questionable, especially because there are other considerable differences (Donoghue, 1983; Troll & Weberling, 1966; Weberling, 1977; Weberling & Hildenbrand, 1982, 1986). Recently an interesting character has been worked out by Stabbetorp (1989) for *Sambucus*, which may connect the genus with the Caprifoliaceae sens. str.: the occurrence of sterile ovules in which megasporogenesis occurs. This should be reinvestigated in other genera. The presence of some special iridoids is a common character of *Sambucus*, *Viburnum*, and the Valerianaceae (Hegnauer, 1989).

It is more difficult to characterize the Scrophulariales, but the core families of this group are closely tied together by a common set of characters. Some of these characters may be lacking in some families but present in others. It has long been known that Scrophulariaceae, Orobanchaceae, Globulariaceae, Pedaliaceae, Martyniaceae, Lentibulariaceae, Gesneriaceae, Acanthaceae, Bignoniaceae, and Myoporaceae form a closely related group. In several cases there are genera or groups of genera that have been shifted from one family to another in this complex (e.g., *Paulownia* from Bignoniaceae to Scrophulariaceae (Armstrong, 1985; Raman, 1989) and *Charadrophila* from Gesneriaceae to Scrophulariaceae (Weber, 1989)). Some authors have included the Martyniaceae in the Pedaliaceae, but pollen morphology does not support this view (Bretting & Nilsson, 1988; cf. Ihlenfeldt, 1967). It is now generally accepted that Plantaginaceae, although rather different in habit and floral construction, belong to this group. Labiatae and Verbenaceae, two families notoriously difficult to delimit (see El-Gazzar & Watson, 1970; Raj, 1983; Hegnauer, 1989), are apparently close to this complex of families too (Cantino, 1982;

Dahlgren in G. Dahlgren (1989b) united Scrophulariales and Lamiales under the last-mentioned name). The close affinity between these families is also shown by the difficulties of the recent cladistic analysis by Lu (1990), the purpose of which is to resolve relationships in the group.

In the Scrophulariales flowers are nearly always zygomorphic, with a strong tendency toward reduction in the number of stamens, and with two carpels possessing numerous to few ovules. Endosperm formation is cellular, and endosperm haustoria are common (see Rauh & Jäger-Zürn (1966) and Di Fulvio (1979) for more detailed analyses of the embryological characters). Pollen tube callose (present in the Polemoniales) is absent (Prósperi & Cocucci, 1979; Cocucci, 1983). Occurrence of iridoid substances and the use of stachyose and other oligosaccharides as storing substances are characteristic (Hegnauer, 1989). A micro-morphological character that has been emphasized only recently (although basically known since at least 1893) is the occurrence of protein crystals in the nuclei. This is not a feature restricted to this group, but it is otherwise remarkably rare (Speta, 1977, 1979; Bigazzi, 1984, 1986, 1989a, b), and the different types of these inclusions may prove to be of similar interest to those in the sieve-tube plastids in other groups. The "placentoid" in the anthers (a parenchymatous outgrowth from the connective into the locule), present with few exceptions, is an interesting morphological feature connecting the Scrophulariales with part of the Solanales and should be investigated further (Warming, 1873; Hartl, 1964; Huber, 1980; Bernardello, 1987). It may occur outside these groups, for example, in part of the genus *Exacum* (Gentianaceae; Klackenberg, 1985) and in a few cases in the Rosidae (Endress & Stumpf, 1991), but remains a rather rare feature.

The Solanales-Boraginales-Polemoniales complex of families has many features in common with the Scrophulariales. Differences that I tabulated in my 1977 publication are still valid. A closer inspection reveals that most of the characters of the Solanales (sens. lat.) represent the plesiomorphic state, while the Scrophulariales show apomorphic character states. This makes the distinction less certain, and additional characters must be sought. The recent systems show a rather conspicuously different division of this group.

Asterales and Campanulales have long been connected on the basis of morphological characters and the similar pollen-presentation mechanism. The especially striking similarity in this respect between Lobeliaceae and Compositae is probably due to

parallelism, but the detailed investigations of the floral development in Goodeniaceae, Brunoniaceae, and Campanulaceae by Leins and Erbar (Erbar & Leins, 1988, 1989; Leins & Erbar, 1987, 1989) have revealed common characters and trends. Together with the occurrence of polyacetylenes in Goodeniaceae, Campanulaceae, and Compositae (Ferreira & Gottlieb, 1982), this speaks for the unity of this group. The screening of 210 dicotyledonous families by Pollard & Amuti (1981) found inulin alone to be the stored substance in all families of Campanulales in the broad sense, in the Asterales, the Calyceraceae, Boraginaceae, and Menyanthaceae. In view of other differences (especially the occurrence of iridoids in the Goodeniaceae and Stylidiaceae; Jensen et al., 1975), however, opinions are diverse about the delimitation of the Campanulales (Carolin, 1978). The Stylidiaceae have been put into the Rosales by Thorne (1983) and in a separate order near the Ericales by Dahlgren (in G. Dahlgren, 1989a, b), and the Goodeniaceae in a separate order Goodeniales near the Campanulales by Vijayaraghavan & Malik (1972).

#### ASTERIDAE WITH REDUCED FLOWERS

In this section we will look at some families or genera with very simple flowers, in which the perianth is reduced or lacking, that nevertheless have been considered to belong to the Asteridae because of a combination of embryological and phytochemical characters.

1. *Hippuris*. The embryology of this water plant was studied by Juel in 1911. It has unitegmic ovules with a reduced nucellus similar to those found in the Asteridae. Warming (1913) placed *Hippuris* near the Cornaceae (which can have the same type of ovule; see also Leins & Erbar, 1990), but the chemical data are clearly in line with a placement in or near the Scrophulariales (Hegnauer, 1969) as first proposed by Pulle (1938).

2. *Callitriche*. The single genus of this family has for a long time been placed near the Euphorbiaceae or the Haloragaceae, families with simple flowers. As in the case of *Hippuris*, embryological investigations (Samuelsson, 1913; Jørgensen, 1923, 1925) were decisive for the now prevailing opinion: The tenuinucellate and unitegmic ovule, formation of micropylar and chalazal haustoria, and cellular endosperm point to a position in the Scrophulariales-Lamiales complex. Taking into account the opposite leaves, the structure of the ovary, and the chemical characters, most modern systems include *Callitriche* in the Lamiales (or with these in the Scrophulariales).

3. *Hydrostachys*. This genus constitutes the family Hydrostachyaceae, which traditionally has been associated with the Rosales. Only in the 1960s did the painstaking studies by Jäger-Zürn (1965) and Rauh & Jäger-Zürn (1966, 1967) show that these reduced water plants seem to be derived from the Asteridae, especially the Scrophulariales. Embryological characters and the structure of the gynoecium were the characters showing this, while pollen morphology was not helpful in this respect (Straka, 1988). Recently, Leins & Erbar (1990) have shown that the male flowers can also be interpreted to conform with this view.

All these plants have some deviating character combinations besides the reduced flowers otherwise not known in the Scrophulariales: *Hippuris*: inferior, apparently monocarpellary gynoecium; *Callitriche*: transverse (not median) position of the carpels, free styles; *Hydrostachys*: transverse position of the carpels, median stipules, free styles.

Not many systematists follow Cronquist (1983) in uniting these diverse elements in one order. Although the cladistic analysis by Lu (1990) groups the three families together, the author himself considers the position of *Hydrostachys* uncertain. Additional evidence for the position of these genera is thus still welcome (Leins & Erbar, 1988, 1990).

#### POLYANDROUS ASTERIDAE

Another puzzle is posed by groups that show some connections with families of the Asteridae but are polyandrous. I will briefly discuss two of these: the Dialypetalanthaceae and Loasaceae. The genus *Dialypetalanthus* has been described as a member of Rubiaceae despite its polyandry, and most recent authors (Hutchinson, 1973; Takhtajan, 1959, 1987; Dahlgren & Thorne, 1985) have accepted a position in the order Rubiales. Others place the family in the Myrtales. The data base is clearly too limited, however. To my knowledge, the embryology and phytochemistry of the Dialypetalanthaceae are totally unknown. If living material is available, once these two types of study have been completed, deciding where to place this family should not be difficult. On the other hand, the Loasaceae have been rather extensively investigated. There are several characters pointing to placement in the Asteridae in embryology or phytochemistry, but these characters are not unequivocal, because they occur in some choripetalous groups too. The combination of an inferior ovary with polyandry (in most genera) makes it difficult to find a close alliance to any family of the Asteridae. Recently, Hufford (1990) has supported

Dahlgren's suggestion that "the family shares an ancestry with Cornales and woody saxifragales." As Cronquist (1988) remarked, this is surely a case where we are eagerly awaiting the results from molecular methods.

#### POSITION OF ASTERIDAE WITHIN ANGIOSPERMS

After a discussion of the circumscription of the Asteridae, the question remains: Where is the root (or the roots) of this group? In other words, can we find a sister group in the Choripetalae for the Asteridae as a whole or for their subgroups? Bessey (1897, 1915), Hallier (1912), and Wernham (1913) were the first to try an answer. In the earlier discussions of this problem the authors often tried to "derive" (German "ableiten") one recent group from another. This is especially clear from the graphic representations of the systems of Bessey and Hallier, although Cronquist and Takhtajan have used this model too. There are, however, problems with this system. In a strictly phylogenetic system, at least, no extant group can be the ancestor of another (special cases like allopolyploid species excepted); moreover, even if interpreted as meaning "derived from the ancestors of a present group," this is prone to misinterpretations. These difficulties have led many authors to another type of graphic representation: the famous "bubbles" of Dahlgren (1975; also Dahlgren, 1977, 1980; Dahlgren et al., 1981; G. Dahlgren, 1989a, b), which have forerunners in Linnaeus (in Giseke, 1792) and Pulle (1938). A similar scheme has been used by Stebbins (1974) and Thorne (1976, 1981, 1983). These taxonomists avoid discussing the derivation of one group from another, instead, they speak of a common origin or the relatively nearest group.

What is the result of the search for an ancestor or near relative among the nonsympetalous dicotyledons? We cannot go into details here, but I want to give some examples of the reasoning of different authors. Let us analyze how Wernham (1913) tackled the problem. In the search for an ancestor of the "Contortae" (Gentianales, not including the Rubiaceae), he looked for a group with the tendency to an isomerous androecium, a bicarpellate gynoecium, and without a tendency to epigyny. He found this in the Geraniales. From his "apocynal stock" he then derived the "Tubiflorae." Rubiaceae and Dipsacales were associated with the Umbelliferae mainly because of the common occurrence of an inferior ovary with two (or three) carpels and an "umbellifloral" inflorescence of Umbelliferae and Rubiaceae. At that time, presumed affinities rested solely on characters of floral

morphology. For us today these arguments alone are not convincing. In past decades embryology and phytochemistry have been used extensively as mentioned before, but difficulties remain.

Two groups of authors may be distinguished. Cronquist (1957-1988) and Takhtajan in his earlier systems (from 1959 to 1980) accepted the Asteridae as a monophyletic group and pointed to a "Rosalean" ancestry (Cronquist from 1981 onward). In the systems by Thorne and Dahlgren the Asteridae are not a monophyletic group (there are remarkable differences among the systems of Thorne from 1976 to 1982, which I cannot dwell upon), and in his most recent system Takhtajan (1987) has accepted a twofold origin too (splitting his old Asteridae into Asteridae and Lamiidae). For Dahlgren, who has been more explicit in his reasoning, chemical characters rank high. Two connections are supposed (see Kubitzki & Gottlieb, 1984):

1. The iridoid-containing groups Gentianales-Scrophulariales (sens. lat.) are linked with the Cornales in a broad sense (including the woody Saxifragales). Besides the chemical character, the occurrence of unitegmic-tenuinucellate ovules in several families of the Cornales can be regarded as a hint to some degree of affinity (Philipson, 1974).

2. The Asterales-Campanulales show several chemical correlations with the Apiales (and Rutales). The impressive list of chemical correspondences between the Compositae and Umbelliferae is tabulated by Hegnauer (1977), and it is interesting that butterflies of the genus *Papilio* feed exclusively on these two families (Richard & Guédès, 1983). Holub et al. (1987) have doubted that the sesquiterpenelactones must be accepted as a sign of a common ancestry because there are differences in the stereostructure (Holub & Buděšinský, 1986). To me, however, it seems improbable that all these different classes of substances (some of them rather rare in plants) have evolved totally independently, especially if other characters (e.g., floral development, Erbar, 1988) are taken into account. As stressed above, the circumscription of the Campanulales is still a problem.

The Solanales and Boraginales, which lack both iridoids and sesquiterpenelactones, are problematic. Most taxonomists place them rather close to the Scrophulariales complex.

Although there has been some convergence between the different systems published in recent times, there are many discrepancies, and admittedly some families are placed by the authors in an order without clear evidence only to dispose of

them. Even if we do not mention several families that are still poorly known, there remain a lot of questions, e.g., the placement and delimitation of the Solanales and Boraginales, the position of the Lennoaceae (Yatskievych & Mason, 1986), Hoplestigmataceae (Nowicke & Miller, 1989), Calyceraceae, and the Oleales. Furthermore, the idea of the connection of a larger part of the Asteridae with the "Cornales" or "Cornanae" is somewhat vague because authors differ widely in the circumscription of these groups.

Taxonomists will look at the forthcoming molecular data with great interest, although they will not expect a quick solution of all problems. Molecular taxonomists should bear in mind that without the work of many generations of botanists using classical methods, no one would know what the questions are, where the plants grow, and which of them are the most interesting to analyze.

Finally, it should be noted that the results of recent molecular investigations have deliberately not been taken into account. This should avoid any bias in comparing the different approaches.

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