

A commentary on the circumscription and evolution of the order Gentianales, with special emphasis on the position of the Rubiaceae

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Abstract. — Recently the inclusion of the Rubiaceae in a monophyletic Gentianalean group has been confirmed in several cladistic analyses of macromolecular as well as morphological data. These developments are discussed against an historical background and some comments are given on the evolution of our understanding of the position of the Rubiaceae within the angiosperms.

1 Introduction

This conference is focusing mainly on the intrafamilial relationships of the Rubiaceae. Within this large family, many genera need to be revised and many complex subfamilial and tribal classification problems remain unsettled. In comparison with the other large angiosperm families, the Rubiaceae still remain undertreated (Robbrecht 1993a), but the success of the first international Rubiaceae conference (Taylor 1995) and the size of this volume testify that the interest in Rubiaceae systematics is growing. Nevertheless, in this era of cladistics and macromolecular systematics, in which none of the subclasses of the angiosperms as defined by Cronquist (1981, 1988) are safe from drastic changes, one should not miss the opportunity to discuss the higher levels of the classification as well. Moreover, a quick look at the abstract book of this conference (Robbrecht et al. 1995) reveals several interesting contributions about the possible relatives of the Rubiaceae, and about taxa with a questionable taxonomical position within or near the Rubiaceae (cf. Robbrecht 1993b). With this in mind, it seems appropriate to present some comments on the history and recent developments of our understanding of the evolutionary position of the Rubiaceae within the angiosperms.

2 Historical background

During the previous century, hypotheses concerning the relationships of Rubiaceae stressed the strong affinity of this family with Caprifoliaceae, and hence with Adoxaceae, Dipsacaceae and Valerianaceae (Wagenitz 1959). Baillon (1880) even included Caprifoliaceae and Adoxaceae in the Rubiaceae. Affinities with Loganiaceae (cf. Wagenitz 1959: 31), Gentianaceae and Apocynaceae (e.g. Le Maout & Decaisne 1868: 159) were acknowledged, but in terms of formal classification these were mostly thought to be less important than the affinities with Caprifoliaceae. By the turn of the century, this general consensus was reflected in Engler's (1897b) *Reihe Rubiales*, containing Rubiaceae, Caprifoliaceae, Adoxaceae, Valerianaceae and Dipsacaceae (fig. 1).

Fig. 1. — The position of the Rubiaceae in Engler's system of 1897b (see text for discussion).

Reihe Contortae

Unterreihe Oleineae

Oleaceae
Salvadoraceae

Unterreihe Gentianineae

Loganiaceae
Gentianaceae (incl. Menyanthaceae)
Apocynaceae
Asclepiadaceae

Reihe Rubiales

Rubiaceae
Caprifoliaceae
Adoxaceae
Valerianaceae
Dipsacaceae

The main issue then was not the strong relationship between Rubiaceae and Caprifoliaceae, which was almost undisputed, but the wider relationships of the order Rubiales within the angiosperms. Engler's Reihen Rubiales and Contortae, including the Unterreihe Gentianeae (fig. 1) are not next to each other in the linear sequence of his classification, but nevertheless he did consider the possibility that Rubiales and Gentianeae were closely related, as is clear from his own comments (Engler 1897c: 370): "Es dürften somit die Loganiaceae einen älteren Typus repräsentieren, von dem sich die übrigen Familien der Gentianeae und vielleicht auch die Rubiales abgezweigt haben." In current terminology Engler's statement implies that he considered the possibility that Loganiaceae as well as Gentianeae were paraphyletic, while the group that consists of Gentianeae + Rubiales might be monophyletic. Bessey (1915: 116-118) had a different opinion. His orders Gentiales and Rubiales contain the same families as Engler's Contortae and Rubiales, but he did not consider them to be closely related at all: his Rubiales and Gentiales are representatives of two very distinct phyletic sequences, both with an origin in the Ranalean complex.

When Wagenitz (1959) was preparing the treatment of Gentiales and Rubiales for a new edition of Engler's syllabus (Wagenitz 1964), he was struck by the fact that, contrary to common belief, the Rubiaceae were much closer to Engler's Gentianeae than to the other families of the Rubiales. His extensive comparison of existing literature included morphological, anatomical, embryological as well as chemical evidence. The strong affinity between Rubiaceae and Caprifoliaceae, taken for granted for so long, was apparently based on two characteristics only: the presence of an inferior ovary and the absence of intraxylary phloem. It was probably the inferior ovary that made Engler conclude that Rubiales had reached a higher level of development than the Gentianeae, which in turn justified the recognition of a separate Reihe in his approach to classification (Engler 1897a; cf. also Barabé & Vieth 1990). Looking back, the overstatement of the progression to an inferior ovary may have hindered earlier recognition of the importance of the relationship between Loganiaceae and Rubiaceae.

Fig. 2. — Wagenitz' (1959) orders *Gentiales* and *Dipsacales* (see text for discussion).

Reihe Gentiales

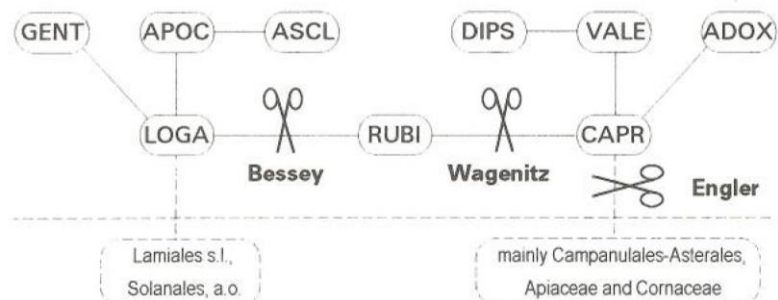
Loganiaceae
Rubiaceae
Gentianaceae
Menyanthaceae
Apocynaceae
Asclepiadaceae

Reihe Dipsacales

Caprifoliaceae
Adoxaceae
Valerianaceae
Dipsacaceae

Wagenitz (1959) proposed new circumscriptions for both orders (fig. 2). Compared to Engler's (1897b) classification (fig. 1), the major changes are the exclusion of the Oleineae from Gentiales, the transfer of the Rubiaceae to Gentiales, and the recognition of the subfamily Menyanthoideae of Gentianaceae as a separate family (because it proved to be very different from the subfamily Gentianoideae anatomically, embryologically as well as phytochemically; Wagenitz 1964). For the remaining families of Engler's Rubiales, Wagenitz proposed the name *Dipsacales*. He considered it highly improbable that *Dipsacales* were a derived group within *Gentiales*. From his discussion it is clear that he interpreted both orders to be monophyletic. He put forward several conjectures concerning the relationships of these orders, but seemed to be inclined to the idea that they had separate origins from within Chorisepalous orders. In comparison with Bessey's (1915) ideas, Wagenitz' treatment is a contribution toward a better

Fig. 3. — Simplified representation of the relationships around the Rubiaceae as perceived by the end of previous century (complete family names are given in fig. 2). When it came to phylogenetic interpretation, Engler (1897c: 370), Bessey (1915), and Wagenitz (1959) cut ties differently. See text for discussion.



understanding of the systematic position of the Rubiaceae, as the title of his paper implied. On the other hand, when confronted with Engler's conception of a monophyletic group consisting of Gentianineae + Rubiales, he actually raised the problem of the relationships of the Dipsacales (fig. 3). Indeed, both Bessey and Engler accepted the close phylogenetic relationship between Rubiaceae and Caprifoliaceae, but they differed in their opinion "which way up" evolution is (Stevens 1986).

In 1964, Wagenitz slightly changed his Gentianales: *Desfontainia*, a genus he had excluded from Loganiaceae and Gentianales in 1959, was now included in Gentianales as a monogeneric family. The circumscription of Dipsacales remained unchanged, and most recent systems of angiosperm classification (e.g. Takhtajan 1980, Cronquist 1981, 1988; Thorne 1992a, b) agree with the groups included (even though there is no unanimity about the familial delimitations within the order). The only notable exception is Dahlgren (1983; see also Dahlgren 1989), who transferred Caprifoliaceae, Viburnaceae and Adoxaceae to Cornales and included Calyceraceae in Dipsacales.

There has been less agreement concerning the delimitation of the Gentianales. The main points of discussion are:

1. Several groups with a long history of doubtful position within or near Loganiaceae, particularly *Buddleja* and related genera, and the genera *Desfontainia* and *Retzia* (see Bremer et al. 1994). Leeuwenberg & Leenhouts (1980) included these as the tribes Buddlejaceae, Desfontainieae and Retzieae in their broadly circumscribed Loganiaceae. Cronquist recognized *Retzia* as a monospecific family in Gentianales (Cronquist 1981) and later Solanales (Cronquist 1988), while Dahlgren (1983; see also Dahlgren 1989) and Thorne (1992a, b) stressed the relationship with the Stilbaceae; *Desfontainia* has been recognized as part of the Loganiaceae (Cronquist 1981, 1988; Takhtajan 1980), or as a separate family in Gentianales (Dahlgren 1983, see also Dahlgren 1989) or Hydrangeales (Thorne 1992 a, b). Buddlejaceae are unanimously excluded from Gentianales (Takhtajan 1980; Cronquist 1981, 1988; Dahlgren 1983; Dahlgren 1989; Thorne 1992a, b) and included in a variously circumscribed Scrophulariales (Bignoniales sensu Thorne 1992b; Lamiales sensu Dahlgren 1989).
2. The species *Dialypetalanthus fuscescens*, that was originally described and put in a new monospecific tribe Dialypetalantheae within the Rubiaceae by Kuhlmann (1925). Rizzini & Occhioni (1949) stressed the similarities with Myrtaceae and Melastomataceae. They raised *Dialypetalanthus* to family level and included it in Myrtales (see Piesschaert et al. 1996 for a more detailed account). Cronquist (1981, 1988), however, did not agree with a position in Rubiales or Myrtales and by lack of a better solution he included the family in his Rosales. Takhtajan (1980), Dahlgren (1983; not in his earlier systems: cf. also Dahlgren 1989) and Thorne (1992a) included the family in their Gentianales.
3. Menyanthaceae. This family is still included in Gentianales by Takhtajan (1980) and Dahlgren (1983), but transferred to Solanales by Cronquist (1981, 1988), to Campanulales by Thorne (1992a, b), and to Cornales by Dahlgren (1989).
4. Rubiaceae. Most authors agree with Wagenitz' inclusion of this family in Gentianales (Takhtajan 1980; Dahlgren 1983; Dahlgren 1989; Thorne 1992a, b); only Cronquist (1981, 1988) maintains an order Rubiales.

Apart from the problematic delimitation of the order, there are also different opinions concerning the familial delimitations within the order. An example is the species *Saccifolium bandeirae*, that was recently described by Maguire & Pires (1978). Takhtajan (1980) included it with some doubts in the Gentianaceae, while Cronquist (1981, 1988), Dahlgren (1983; see also Dahlgren 1989) and Thorne (1992a, b) recognize it as a monospecific family in their Gentianales. As for the Rubiaceae, familial delimitation problems are limited to the genus *Theligonum* (*Henriquezia* is included in the Rubiaceae in all systems mentioned). Thorne (1992a, b) is the only one to include *Theligonum* in the Rubiaceae. Takhtajan (1980) and Dahlgren (1983; see also Dahlgren 1989) recognized a monogeneric family Theligonaceae in the Gentianales, while Cronquist (1981, 1988) did the same in his Rubiales.

As stated above, Wagenitz' (1959) discussion of Gentianales implied monophyly of the order Gentianales. More recently he explicitly put forward the hypothesis that Gentianales, a group that is "tied together by a combination of vegetative, floral and phytochemical characters", may indeed be one of the larger monophyletic groups within the Asteridae (Wagenitz 1992: 210; the loganiaceous tribes Retzieae

and Buddlejaceae sensu Leeuwenberg & Leenhouts 1980 are excluded; the position of Menyanthaceae is called controversial). It is tempting to evaluate the characters of the order and its different delimitations as given by Takhtajan, Cronquist, Dahlgren or Thorne against this explicit hypothesis. These classifications are indeed often used as if they were cladistic, i.e. "as if the circumscription and the rank of taxa depended on the relative cladistic branching positions" (Stevens 1986: 330). It may not be overlooked, however, that neither the rank of taxa, which is mainly determined by phenetic distance, nor the "box-in-box structure" of these classifications are very meaningful phylogenetic components (Kubitzki 1977: 25). Rank and hierarchy are not intended to reflect cladistic relationships in these systems.

The same is true for the diagrams that are used by Takhtajan, Cronquist, Dahlgren and Thorne to illustrate their systems. Takhtajan (1980: 348) and Cronquist (1981: 853; 1988: 414) use treelike diagrams to depict the "putative relationships" among their orders. Even though the treelike appearance of these diagrams suggests cladistic branching patterns, they basically depict current relationships in terms of relative advancement and are interpreted wrongly when they are thought to express hypotheses of mono- or paraphyly of orders (cf. Heywood 1977: 6). Likewise, Cronquist's (1976: 520; 1988: 439, 445) comments on the origins of Rubiales, Dipsacales, Calycerales and Asterales and their relationship with Gentianales, pointing to close evolutionary relationships between these orders (contrary to Engler, Bessey as well as Wagenitz), are suggestive of a paraphyletic Gentianales, but they do not exclude the monophyly of this order. Dahlgren (1980: 107-109) and Thorne (1992b: 367-369), on the other hand, make use of a cross section through an imaginary evolutionary tree or hedge (Dahlgren) or phyletic shrub (Thorne). The positions of the orders and superorders in the plane of section imply nothing definite about the exact branching pattern below this plane. Hence the question of mono- or paraphyly of the orders is left open.

The differences between evolutionary classifications are often due to different interpretations of the evolutionary significance of characters (Stevens 1986: 327, Barabé 1984; for example, embryological and chemical characters are emphasized much more in Dahlgren's classification than in the system of Cronquist). Wagenitz (1977: 390) rightly pointed out that this was one of the major obstacles to further progress: "we often simply do not know which characters we can rely on as indicating phyletic affinity or only a certain level of evolution". Since then, cladistic analysis has become a major research tool to distinguish between homologous and homoplasious similarity. Besides this methodological advance, macromolecular research has recently started to provide a new class of data (Zurawski & Clegg 1993).

3 Current developments

Recently the inclusion of the Rubiaceae in a monophyletic Gentianales has been confirmed in several cladistic analyses of macromolecular as well as morphological and phytochemical data. With the exception of Downie & Palmer's (1992) study of restriction site variation of the chloroplast DNA inverted repeat, all the molecular analyses that are relevant to Gentianales are based on the same set of data, viz. the sequence of the *rbcL* gene (e.g. Chase et al. 1993; Olmstead et al. 1992, 1993; Bremer et al. 1994, 1995; see also Bremer, this volume). They differ in the choice and the number of species included, and in the sophistication of the parsimony analysis (cf. Soltis et al. 1993). With respect to Gentianales, one of the most interesting is Olmstead et al.'s (1993) thorough parsimony analysis of the Asteridae (fig. 4):

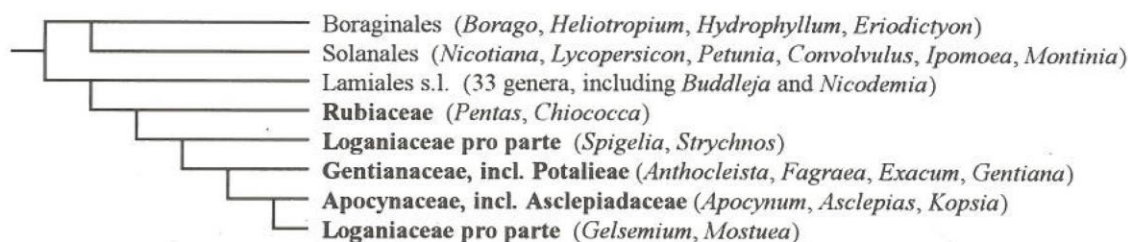


Fig. 4. — Condensed representation of part of fig. 5 of Olmstead et al. (1993). The position of Rubiaceae at the base of Gentianales and the exclusion of Menyanthaceae (not shown) is typical of *rbcL*-based studies.

it combines a relatively high number of species of Gentianales, spread over the order, with a wide range of possible relatives, including a.o. representatives of Dipsacales, Oleales, Cornales, Asterales and Campanulales. Other *rbcL*-based studies do not contradict Olmstead et al.'s main conclusions about Gentianales, which are always recognized as a monophyletic group when Menyanthaceae and part of Loganiaceae sensu Leeuwenberg & Leenhouts (1980) are excluded. Menyanthaceae are part of a Campanulales-Asterales clade (see also Chase et al. 1993, Olmstead et al. 1992; Cosner et al. 1994). This is not expected on the basis of gross floral and vegetative morphology of the family (Cronquist 1981), but restriction site variation of the chloroplast genome inverted repeat (Downie & Palmer 1992) and the presence of several primary and secondary metabolites (Lammers 1992) confirm this result. *Buddleja*, *Nicodemia* (Buddlejaceae), *Retzia* and *Desfontainia* (see Bremer et al. 1994 for *Retzia* and *Desfontainia*) are excluded from Loganiaceae sensu Leeuwenberg & Leenhouts (1980) and Gentianales; *Buddleja*, *Nicodemia* and *Retzia* are allied with Lamiales s.l., while *Desfontainia* is part of Dipsacales. The remaining genera of Loganiaceae that have been sequenced belong to the Gentianales, but they do not form a monophyletic group within the order. This had already been suggested on the basis of restriction site variation of the chloroplast DNA inverted repeat (Downie & Palmer 1992) and on the basis of morphological and phytochemical evidence (Bremer & Struwe 1992).

Struwe et al.'s (1994) cladistic analysis of morphological, anatomical, embryological and phytochemical data, the most extensive non-molecular analysis of Gentianales up to date, focuses particularly on the genera of Loganiaceae sensu Leeuwenberg & Leenhouts (1980). As in the macromolecular analyses, the Rubiaceae are part of a monophyletic Gentianales, and Loganiaceae are a highly unnatural group (fig. 5). The Rubiaceae are well nested within Gentianales, with the loganiaceous Gelsemieae as sister group. This is contradicted by the *rbcL*-sequence data as well as by the restriction site variation of the chloroplast DNA inverted repeat, where the Rubiaceae are the sister group of the remaining Gentianales. As suggested by Struwe et al. (1994), further study of non-macromolecular traits as well as further *rbcL* sequencing within Loganiaceae s.l. may help to clarify this issue.

Struwe et al.'s (1994) analysis confirms the exclusion of *Buddleja*, *Desfontainia* and *Retzia* from Loganiaceae and Gentianales, and adds the problematic genera *Plocosperma* and *Polypremum* to this list. Within Gentianales, the remaining genera of the Loganiaceae are scattered over five different monophyletic groups. Four of these are recognized as distinct families in the newly proposed familial classification of the order (fig. 5), while *Potalia*, *Fagraea* and *Anthocleista* (tribe Potalieae) are included in Gentianaceae. The presence of interpetiolar stipules or stipular lines, the presence of colleters, and the presence of vestured pits in the wood are discriminating characters for the order (Struwe et al. 1994).



Fig. 5. — Cladistics and classification of the Gentianales on the basis of morphological, anatomical, embryological, and phytochemical data (Struwe et al. 1994). The excluded taxa were included in Loganiaceae by Leeuwenberg & Leenhouts (1980).

Other characters are widespread in Gentianales, but there are more or less important exceptions: the opposite, entire leaves, the internal phloem, the regular flowers with an isomerous androecium, the contorted aestivation, the nuclear endosperm formation, and the presence of indole alkaloids belonging to the group of complex seco-iridoids (Wagenitz 1959, 1977, 1992, Jensen 1992).

4 Outlook

Formulating his guiding principles for making up a phylogenetic classification, Thorne (1976) also expressed some "strong convictions or concepts about classification." Taking into account that an approach that seeks a compromise between classifications of established authorities is still advocated nowadays (Nicholas & Baijnath 1994), his ninth conviction is worth quoting: "Phylogeny cannot be achieved by consensus. Although some botanists seem to think that a proper system of classification might be derived by popular vote and compromise among the modern phylogeneticists this is an unrealistic goal in view of our overwhelming lack of adequate knowledge of the angiosperms. One taxonomist may be right and ten other taxonomists may be wrong. Time and accumulation of more data will have to decide who, if any, was correct. A closer approach to unanimity of phylogenetic thought for the angiosperms should some day be possible, but no one should expect unanimity in our time".

Today, unanimity about the existence of a monophyletic Gentianalean group is almost reached, even though several details of its exact delineation and several important questions about its internal structure remain unsolved. This unanimity was not reached by a majority vote, as proposed by Nicholas & Baijnath (1994), but it is based on steadily accumulating data, provided by monographic work and the study of morphological and molecular characters, as anticipated by Thorne. However, at least as important has been the development of cladistics. Firstly cladistics has stimulated the development of a conceptual framework that enables us to think and talk in a clear way about phylogenetic relationships. In practice, all available data are evaluated simultaneously during cladogram construction; the resulting cladograms permit the distinction between homologous and homoplasious similarities, and between monophyletic groups and groups that reflect merely levels of advancement. Moreover, it would be almost impossible to interpret molecular data such as gene sequences without computerized analyses (other approaches besides cladistics have been developed for molecular data, see Darlu & Tassy 1993 for an overview).

The construction of a data matrix requires an explicit specification of all characters and character states that are used, and of their distribution over the analysed taxa. By this explicit emphasis on characters, it might have been expected that the rise of cladistics during the previous decades would have been accompanied by an increased interest in character research. However, the mere fact that a cladistic analysis is performed, does in itself not guarantee that the used characters are carefully circumscribed and well studied. Morphological and anatomical characters used in higher level systematics of angiosperms are a case in point. Indeed, the classical descriptive terminology was not developed with the intention to reflect topological correspondence (Rieppel 1988) or hypotheses of primary homology (de Pinna 1991), but nevertheless it is often taken for granted that it provides characters that can be used immediately in cladistic analyses. An example are the floral nectaries: e.g. a ring of nectariferous tissue in the flower is very often called a "nectary disk". However, ontogenetically some of these nectary disks are derived from gynoecial tissue, other from receptacular tissue and still other from androecial tissue. Therefore it is better to abandon the superficial similarity in adult morphology and position, and to homologise nectary disks that are derived from gynoecial (receptacular, androecial) tissue with other nectaries that are derived from gynoecial (receptacular, androecial) tissue, even though these can be very dissimilar when adult (Smets 1988, 1989, Smets & Cresens 1988). The gynoecium provides another illustration: Igersheim et al. (1994) recently showed that during early development the so-called superior ovary of *Gaertnera* (Rubiaceae) is basically inferior. Only during later stages the ovary deviates from the characteristic development in Rubiaceae, and it becomes secondarily superior. Clearly, much basic morphological work remains to be done in angiosperms, and continuing character research will certainly lead to improved homologisations, not only for relatively recently discovered ultrastruc-

tural features such as sieve-element plastids (Behnke & Barthlott 1983, Behnke 1991) or epicuticular waxes (Theisen & Barthlott 1994), but even for very familiar macromorphological features, as the above examples show.

In this way, it can be expected that, also for Gentianales, the quality of morphological data sets will steadily improve, and that the most interesting results indeed will be obtained when molecular and morphological data are confronted with each other (e.g. Sytsma 1990, Moritz & Hillis 1990, Donoghue & Sanderson 1992, Bremer & Struwe 1992, Patterson et al. 1993, Soltis et al. 1993, Bachmann 1995).

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