Phylogeny of the *Asteridae* s. str. based on *rbcL* sequences, with particular reference to the *Dipsacales*

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**Abstract:** The *rbcL* gene of 15 taxa was sequenced and analyzed cladistically together with a large sample of genera representing all main clades of the subclass *Asteridae* in order to determine more precisely the delimitation of the order *Dipsacales* and to elucidate the phylogeny of the families within the order. The cladistic analyses show that the Dipsacales comprise the families Caprifoliaceae, Morinaceae, Dipsacaceae, and Valerianaceae including Triplostegia. The results also provide a basis for the exclusion of a number of taxa previously placed in the Dipsacales, such as Desfontainia, Columellia and Adoxaceae s. l. (including Sambucus and Viburnum). Ever since the order *Dipsacales* was first suggested by Dumortier (1829) and the similar *Caprifoliales* by Lindley (1833, 1836), there has been confusion concerning the circumscription of the order, the relations between the included families, their circumscriptions, and the position of the order in a larger context.

*Dipsacales* and *Rubiaceae.* The order *Dipsacales* is built up around a core of families, namely Dipsacaceae, Valerianaceae and Caprifoliaceae, all considered to be related. Due to the superficial morphological similarities between Caprifoliaceae (especially the formerly included genera Sambucus and Viburnum) on one hand and Rubiaceae on the other, early theories (Linnaeus 1738, Jussieu 1789, Bartling 1830) suggested a close relationship between those. This association was retained well into the 20th century (e.g., Tiegem 1909), until workers like Utzschneider (1947) and Wagenitz (1959) with more thorough anatomical and chemical analyses instead of suggested a connection between Rubiaceae and Gentianaceae leaving Dipsacales from them isolated.

*Dipsacales* and the *Cornales.* After the dispatch of the connections between Dipsacales and Rubiaceae a completely different theory of relationships emerged, also based on the inclusion of the genera Sambucus and Viburnum in the Caprifoliaceae, and leading to a number of problems. The most obvious one concerns the small and enigmatic genus Adoxa. Morphological studies had shown that Adoxa features a number of traits especially similar to Sambucus (Boll 1994). Adoxa earlier
had been considered a close relative of the family Saxifragaceae connected through Chrysosplenium. Furthermore, the superficial morphological similarities between Viburnum and Hydrangea (of the Hydrangeaceae in the Cornales) were regarded as an argument for close relations between Dipsacales and cornalean groups. The theory was further boosted by phytochemical studies, which were interpreted as strongly supportive of this view (DahlGren 1975, 1977, 1980).

**Dipsacaceae and Calyceraceae.** Parallel to the ideas described above, a third view advocated by Baillon (1880) among others suggested that the headlike inflorescences in Dipsacaceae and Calyceraceae are homologous, thus implying a close relationship between these families. This theory, and the impact on the sister-group relations of the Asteraceae to which Calyceraceae undoubtly are related, has been dealt with at length in a number of studies (Gustafsson & Bremer 1995, Gustafsson & al. 1996, and references therein). The similarities between Dipsacaceae and Calyceraceae now are regarded as merely superficial, and consequently, the position of the order Dipsacales remains an open question.

**Other suggested relatives.** Additional taxa that have been suggested to be closely related to the Dipsacales are the families Alseuosmiaceae (Airy-Shaw 1965a), Desfontainiaceae (Bremer & al. 1994), Bruniacaeae (Donoghue & al. 1992, Gustafsson & al. 1996), Apiaceae (Donoghue & al. 1992), and Columelliaceae (Jussieu 1848, Hallier 1901), all of which will be considered in the study presented here.

**Dipsacales and Columelliaceae.** The small monogeneric family Columelliaceae has been suggested to occupy positions in extremely diverse parts of the system. Suggestions of related taxa include: Gesneriaceae (Reichenbach 1828, Baillon 1888, Fritsch 1894, Macbride 1961), Saxifragaceae-Escallonioidaeae (Schnizlein 1849), particularly Argophyllum, Brexia and Roussea (Solereder 1899, Hallier 1910, Herzog 1915, Willis & Shaw 1966) or closer to Hydrangeaceae and Loganiaceae (Thornc 1968), or to Montinioidaeae in Saxifragaceae (Gentry 1993). Positions also have been suggested in Rubiales (actually in Cinchonales ≈ Rubiales; Lindley 1853), with the families Vacciniaeae, Onagraceae, and Cinchonaeae ≈ Rubiaeae very close to Caprifoliaceae (Jussieu 1848), or even nested between Caprifoliaceae and Valerianaceaee (Hallier 1901). Other taxonomic placements include: Oleaceae (Jussieu 1801, Reichenbach 1837), Scrophulariaceae (Kunth 1818, Bartling 1830, Hallier 1903), Ebenaceae (Endlicher 1839), Loganiaceae (Maout & Decaisne 1873, Hooker 1875), Lythraceae (Agardh 1858—due to the peculiar anthers which appear to be similar to the ones found in Cucurbitaceae, which Agardh considered closely related) and finally also in the assembly Pittosporaceae-Grossulariaceae but anyway “definitely in the order Rosales” (Cronquist 1968). Recently it was suggested that Columellia and Desfontainia might be related due to significant similarities in wood anatomy, features shared also by some members of “Saxifragaceae” s. l. (Carlquist 1992).

**Dipsacales and Alseuosmiaceae.** Another small genus—Alseuosmia—was formerly believed to be connected to the Caprifoliaceae (Fritsch 1897). Numerous systematic positions have since then been suggested for Alseuosmia, including Saxifragaceae (Stemins 1984; Dickson 1986, 1989), and Escalloniaceae-Loganiaceae (Airy-Shaw 1965b). The family Alseuosmiaceae consists of the three genera Alseuos-