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Cladistics of Gentianaceae: a morphological approach

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ABSTRACT

The infrafamilial relationships of the Gentianaceae are investigated by means of a cladistic analysis of 84 phenotypic characters, based mainly on data from the literature. The 41 genera that were selected for the analysis, including the formerly loganiaceous genera *Anthocleista* and *Fagraea* and the monotypic genus *Saccifolium*, are a fair representation of the character diversity in the family. The diverse genus *Gentiana* is represented by six of its sections. As outgroups we used *Strychnos* and *Geniostoma* (Loganiaceae), *Gelsemium* (Gelsemiaceae), and two genera each of Apocynaceae and Rubiaceae.

In the strict consensus cladogram of all most-parsimonious trees Gentianaceae has an unresolved basal trichotomy between *Saccifolium* (of tribe Saccifolieae), Potaliinae, and a major clade including all other genera. In this clade only tribe Gentianeae and subtribe Chironiinae of tribe Chironieae (*Ixanthus* excepted) are recognized as monophyletic groups. Within tribe Gentianeae, subtribe Gentianinae is nested in a paraphyletic subtribe Swertiinae. The relationships between the representatives of Exaceae, Canscorinae and Coutoubeinae (Chironieae), and Helieae are almost completely unresolved. An interesting exception is the sister-group relationship between *Exacum* and *Cotylanthera*.

Two complementary explanations for the lack of resolution in most parts of the cladogram are discussed: (1) the morphological characters of most tropical members of the family are insufficiently known, and (2) morphological characters are not well suited to resolve the more basal relationships in Gentianaceae.

Keywords: Gentianaceae, infrafamilial classification, morphology, phylogeny, phytochemistry.

INTRODUCTION

The family Gentianaceae is a (sub)cosmopolitan group of 87 genera and more than 1600 species (Struwe *et al.*, 2002 (Chapter 2, this volume)). There is strong evidence from cladistic analyses of both morphological and molecular data that its closest relatives are Apocynaceae *sensu lato*, Rubiaceae, and parts of the paraphyletic assemblage Loganiaceae *sensu lato* (e.g., Downie & Palmer, 1992; Olmstead *et al.*, 1993; Bremer *et al.*, 1994; Struwe *et al.*, 1994, 1998, 2002; Bremer, 1996; De Laet & Smets, 1996; Struwe & Albert, 1997). Compared with the classification of Gilg (1895), the most recent worldwide treatment of Gentianaceae, the delimitation of the family has been changed in two important ways: (1) Gilg's subfamily Menyanthoideae was raised to family level by Wagenitz (1964), and Menyanthaceae is now generally considered to be related to the Campanulales–Asterales complex (Downie & Palmer, 1992; Lammers, 1992; Olmstead *et al.*, 1992, 1993; Cosner *et al.*, 1994; Gustafsson *et al.*, 1996; Erbar, 1997), and (2) the loganiaceous tribe Potalieae (including *Potalia*, *Fagraea*, and *Anthocleista*) was transferred from Loganiaceae to Gentianaceae (Struwe & Albert in Struwe *et al.*, 1994, following Bureau, 1856; see also Fosberg & Sachet, 1980; Jensen, 1992). We also include *Saccifolium*, described as the monotypic family Saccifoliaceae (Maguire & Pires, 1978), in Gentianaceae (Thiv *et al.*, 1999a; Struwe *et al.*, 2002). Within Gentianales, Gentianaceae are characterized by the presence of internal phloem, contort corolla aestivation, superior ovary, and xanthones, and by the absence of laticifers, interpetiolar stipules, cardenolides, and indole alkaloids.

Other attempts at infrafamilial classification covering the whole family are Grisebach (1839, 1845) and Bentham (1876). Both Grisebach and Bentham based their classifications on a broader array of floral characters (mainly from anthers, styles, stigmas, and ovaries) than Gilg, who almost exclusively used pollen features. Even though Gilg's system has often been criticized (see Mészáros *et al.*, 1996, for details), it is the most used and best known of the three. Recent authors have used Gilg's classification (Ho *et al.*, 1988), partly returned to that of Bentham (Garg, 1987), or have not used any infrafamilial classification at all (e.g., Hutchinson, 1959; Wood & Weaver, 1982; Ho & Pringle, 1995). The different infrafamilial classifications are compared in Table 3.1, using Gilg's (1895) subfamily Gentianoideae as the point of reference. With some generalization, Grisebach's Lisyantheae and Bentham's subtribes Erythraeinae and Lisiantheae of tribe Chironieae correspond in outline to the ensemble of

Table 3.1. *Selected infrafamilial classifications of Gentianaceae: tribes (bold) and subtribes (not bold) of Gilg's (1895) subfamily Gentianoideae of Gentianaceae, and their (partial) correspondence to the (sub)tribes of Grisebach (1845), Bentham (1876), and Garg (1987)*

Gilg (1895)	Grisebach (1845)	Bentham (1876)	Garg (1987)
Gentianeae Exacinae	**Chironieae**	**Exaceae**	**Exaceae**
Gentianeae Erythraeinae	**Chloreae**	**Chironieae** Euchironieae Erythraeae **Swertieae**	**Chironieae**
Gentianeae Chironiinae	**Chironieae**	**Chironieae** Euchironieae	—[a]
Gentianeae Gentianinae	**Swertieae**	**Swertieae**	**Gentianeae** **Swertieae**
Gentianeae Tachiinae	**Lisyantheae**	**Chironieae** Euchironieae Lisiantheae	—
Rusbyantheae	**Lisyantheae**	**Chironieae** Lisiantheae	—
Helieae	**Lisyantheae**	**Chironieae** Erythraeae Lisiantheae	—
Voyrieae	**Lisyantheae**	**Chironieae** Euchironieae	—
Leiphaimeae	**Lisyantheae**	**Chironieae** Euchironieae	—

Note: [a] A dash indicates (sub)tribes that are absent from northwest Himalaya, the scope of Garg's regional treatment.

Gilg's subtribe Tachiinae of tribe Gentianeae and his tribes Rusbyantheae and Helieae. Considering that the only species of Gilg's tribe Rusbyantheae, *Rusbyanthus cinchonifolius*, is now included in *Macrocarpaea* (Weaver, 1974; Maas *et al.*, 1983), the main differences between Grisebach, Bentham, and Gilg center around the genera that are included in Gilg's much criticized neotropical (sub)tribes Helieae and Tachiinae; for example, Wood and Weaver (1982) proposed to merge Helieae and Tachiinae, thereby echoing Grisebach (1845). Gilg's tribe Rusbyantheae itself is a prime example of the artificial nature of a system that is too exclusively based on few characters.

Within Gentianaceae, several phylogenetic studies on the generic and tribal level have been published. Morphological cladistic analyses exist for *Exacum* (Klackenberg, 1985), *Tachiadenus* (Klackenberg, 1987), *Lomatogonium* (Liu & Ho, 1992), *Potalia* (L. Struwe & V. A. Albert, unpubl.), and *Voyria* (Albert & Struwe, 1997), while molecular studies have been published for part of *Lisianthius* (Sytsma & Schaal, 1985) and *Gentiana* (Gielly & Taberlet, 1996; Gielly *et al.*, 1996; Yuan *et al.*, 1996; Hungerer & Kadereit, 1997; Yuan & Küpfer, 1997). Studies at the tribal level cover Gentianinae (Yuan & Küpfer, 1995; Gutsche *et al.*, 1997), Erythraeinae (Thiv & Kadereit, 1997; Thiv *et al.*, 1999b), Helieae (Pihlar *et al.*, 1998; Struwe, 1999), and Potalieae (Struwe & Albert, 1997). Morphological cladistic analyses covering several tribes can be found in Mészáros (1994) and Mészáros *et al.* (1996). Lastly, cladistic studies of more than 150 *trn*L intron sequences and over 100 *mat*K sequences cover the whole family (Struwe *et al.*, 1998, 2002; Thiv *et al.*, 1999a) and form the basis of the infrafamilial classification that is proposed in Chapter 2 of this volume (Struwe *et al.*, 2002).

In this chapter we continue our principally morphological approach, broadening the scope from mainly temperate Gentianaceae (Mészáros *et al.*, 1996) to a more even sampling across the entire family. In order to contribute to an improved knowledge of the Gentianaceae, we aim to extend the documentation of character state distributions in the family and to present a cladistic analysis of the enlarged data set.

MATERIALS AND METHODS

Taxa

In Table 3.2 we present a survey of the genera of Gentianaceae, using Gilg's (1895) classification as a point of reference (but with Menyanthoideae excluded, Potalieae and Saccifoliaceae included, and Rusbyantheae reduced to Tachiinae), including the many new species and genera that have been described since Gilg presented his classification. We want to stress that the only purpose of the table is to provide a baseline against which new findings from phylogenetic analyses can be evaluated. Therefore, in compiling the table we followed Gilg (1895, 1897, 1908) for all the genera that were known to him, even though some transfers have subsequently been proposed (e.g., *Hockinia* to Erythraeinae (Maas & Ruyters, 1986), *Tachiadenus* to Exacinae (Klackenberg, 1987), *Eustoma* and *Coutoubea* to Erythraeinae (Kaouadji, 1990)); the remaining genera were accommodated using

Table 3.2. *Genera of Gentianaceae according to Gilg's (1895) classification. Accepted genera as in Struwe* et al. *(2002) except for* Xestaea *and* Frasera, *which are here included in* Schultesia *and* Swertia, *respectively. Figures in parentheses are number of species*

Genera included in the current data set	Genera not included in this study
Gentianeae-Exacinae	
Cotylanthera Blume (4)	*Microrphium* C. B. Clarke (2)[a1]
Exacum L. (65)	*Ornichia* Klack. (3)[1]
Sebaea Sol. ex R. Br. (60–100)	
Gentianeae-Erythraeinae	
Bartonia H. L. Mühl. ex Willd. (4)	*Bisgoeppertia* Kuntze (2)
Blackstonia Huds. (4)	*Cicendia* Adans. (2)
Canscora Lam. (9)	*Congolanthus* A. Raynal (1)[b2]
Centaurium Hill (50)	*Cracosna* Gagnep. (3)[c3]
Curtia Cham. & Schltdl. (6–10)	*Djaloniella* P. Taylor (1)[d4]
Enicostema Blume (3)	*Exaculum* Caruel (1)
Faroa Welw. (19)	*Geniostemon* Engelm. & A. Gray (5)
Hoppea Willd. (2)	*Karina* Boutique (1)[4]
Obolaria L. (1)	*Neurotheca* Salisb. ex Benth. (3)
Sabatia Adans. (20)	*Oreonesion* A. Raynal (1)
	Phyllocyclus Kurz. (5)[3]
	Pycnosphaera Gilg (1)
	Schinziella Gilg (2)
	Tapeinostemon Benth. (7)
	Urogentias Gilg & Gilg-Ben. (1)
Gentianeae-Chironiinae	
Chironia L. (15)	*Gentianothamnus* Humbert (1)[e5]
Orphium E. Mey. (2)	
Gentianeae-Gentianinae	
Crawfurdia Wall. (16–19)	*Comastoma* (Wettst.) Toyok. (7–25)[f6]
Gentiana L. (360)	*Jaeschkea* Kurz (4)
Gentianella Moench. (250)	*Latouchea* Franch. (1)
Gentianopsis Ma (16–24)[6]	*Megacodon* (Hemsl.) Harry Sm. (2)[6]
Halenia Borkh. (80)	*Pterygocalyx* Maxim. (1)
Ixanthus Griseb. (1)	*Veratrilla* Baill. ex Franch. (2)
Lomatogonium A. Braun (21)	
Swertia L. (150) (including *Frasera* Walter)	
Tripterospermum Blume (24)	
Gentianeae-Tachiinae	
Chorisepalum Gleason & Wodehouse (5)[g7]	*Hockinia* Gardn. (1)
Eustoma Salisb. (3)	*Zonanthus* Griseb. (1)
Lisianthius P. Browne (30)	*Zygostigma* Griseb. (2)
Macrocarpaea (Griseb.) Gilg (90)[h]	
Tachia Aubl. (10)	
Tachiadenus Griseb. (11)	

Table 3.2. (*cont.*)

Genera included in the current data set	Genera not included in this study
Helieae	
Celiantha Maguire (3)[7]	*Adenolisianthus* Gilg (1)
Coutoubea Aubl. (5)	*Aripuana* Struwe, Maas, & V. A. Albert (1)[7]
Deianira Cham. & Schltdl. (5)	*Calolisianthus* Gilg (6)
Irlbachia Mart. (9)	*Chelonanthus* Gilg (7)
Schultesia Mart. (16) (including *Xestaea* Griseb.)	*Helia* Mart. (2)
Symbolanthus G. Don (30)	*Lagenanthus* Gilg (1)
	Lehmanniella Gilg (2)
	Neblinantha Maguire (2)[7]
	Prepusa Mart. (5)
	Purdieanthus Gilg (1)
	Rogersonanthus Maguire & B. M. Boom (3)[7]
	Senaea Taub. (1)
	Sipapoantha Maguire & B. M. Boom (1)[7]
	Symphyllophyton Gilg (1)
	Tetrapollinia Maguire & B. M. Boom (1)[7]
	Wurdackanthus Maguire (2)[7]
Voyrieae	
Voyria Aubl. (19)	
Leiphaimeae	
Voyriella (Miq.) Miq. (1)	
Potalieae *sensu* Leeuwenberg & Leenhouts[i]	
Anthocleista R. Br. (14)	*Potalia* Aubl. (9)
Fagraea Thunb. (70)	
Saccifoliaceae *sensu* Maguire & Pires[j]	
Saccifolium Maguire & Pires (1)	

Notes:

[a] Genera not known or excluded by Gilg (1895) were classified on the basis of Gilg (1897, 1908) and Pilger and Krause (1915) and are marked with a superscript "1".

[b] Genera not known or excluded by Gilg (1895) were classified on the basis of Raynal (1968) and are marked with a superscript "2".

[c] Genera not known or excluded by Gilg (1895) were classified on the basis of Struwe *et al.* (2002) and are marked with a superscript "3".

[d] Genera not known or excluded by Gilg (1895) were classified on the basis of Taylor (1973; as relatives of *Faroa*) and are marked with a superscript "4".

[e] Genera not known or excluded by Gilg (1895) were classified on the basis of Humbert (1937) and are marked with a superscript "5".

[f] These genera were classified by the taxonomic position of the broader genus from which the new genus was segregated and are marked with a superscript "6".

[g] Genera not known or excluded by Gilg (1895) were classified on the basis of Gilg's (1895: 62) key (pollen in monads (=Tachiinae) vs. pollen in tetrads or polyads (=Helieae)) and Struwe and Albert (1998) and are marked with a superscript "7".

cont.

Notes to Table 3.2 (*cont.*)

[h] *Macrocarpaea* includes *Rusbyanthus*, the only genus of Gilg's tribe Rusbyantheae (Weaver, 1974).

[i] Potalieae *sensu* Leeuwenberg and Leenhouts (1980) are gentians (Bureau, 1856; Fosberg & Sachet, 1980; Jensen, 1992; Struwe *et al.*, 1994, 1998, 2002; Struwe & Albert, 1997; Thiv *et al.*, 1999a) but do not fit into Gilg's classification.

[j] Saccifoliaceae *sensu* Maguire and Pires (1978) are gentians (Thiv *et al.*, 1999a; Struwe *et al.*, 2002) but do not fit into Gilg's classification.

information from various sources, indicated by footnotes. Note that, unless indicated otherwise, we follow the classification of Struwe *et al.* (2002) in the remainder of the text.

Forty-one genera were selected for the current analysis (those in the left-hand column of Table 3.2; note that we include *Frasera* in *Swertia* and *Xestaea* in *Schultesia*). This amounts to about half of the total number of genera and over 90% of all species. These numbers are an indication of the covered diversity within the family rather than an assessment of the phylogenetic significance of the unsampled genera. To search for systematic affinities of the mycotrophic Gentianaceae (*Cotylanthera*, *Bartonia*, *Obolaria*, *Voyria*, and *Voyriella*), all these genera were included, and so was the enigmatic monotypic genus *Saccifolium* (Maguire & Pires, 1978). In order to reduce problems with polymorphism (Nixon & Davis, 1991), the diverse genus *Gentiana* was represented by six of its sections.

As outgroups we included *Geniostoma* and *Strychnos* (Loganiaceae), *Gelsemium* (Gelsemiaceae), *Plumeria* and *Rauwolfia* (Apocynaceae), and *Danais* and *Exostema* (Rubiaceae). In the selection of the outgroups we took into account the availability of recent cladistic studies (Bremer, 1996; Endress *et al.*, 1996), the availability of data from modern revisions (e.g., Conn, 1980; Buchner & Puff, 1993), and suggestions from B. Bremer (pers. comm.).

Characters

The data set (Table 3.3 and Appendix 3.1) contains 84 phenotypic characters, predominantly from morphology (including palynology and seed micromorphology) but supplemented with anatomical, embryological, karyological, and phytochemical characters. The data are mostly compiled from the literature, in some cases are supplemented with observations of herbarium (BP, BR, and DBN) and living plant material (*Centaurium*,

Table 3.3. *Characters and character states*

1. Heterotrophic syndrome: absent (0); present (1)
2. Life form: trees or shrubs (0); perennial herbs (1); biennial and annual herbs (2)
3. Cross-section of main stem: terete (0); quadrangular (1); winged (2)
4. Interxylary phloem in stem: absent (0); present (1)
5. Xylem rays: multi- and uniseriate (0); bi- and uniseriate (1); rayless (2)
6. Nodal anatomy: uni(tri)lacunar (0); multilacunar (1)
7. Stolons and runners: absent (0); present (1)
8. Stem: erect (0); twining (1)
9. Vessels: solitary (0); in chains or in clusters (1)
10. Vessel perforation plates: scalariform (0); simple (1)
11. Axial parenchyma: apotracheal (0); paratracheal (1)
12. Lacticifers in stems: absent (0); present (1)
13. Extrafloral nectaries: absent (0); present (1)
14. True interpetiolar stipules: absent (0); present (1)
15. Leaf venation: pinnate, brochidodromous (0); acrodromous (1)
16. Mesophyll anatomy: bifacial (heterogeneous) (0); homogeneous (1)
17. Mature stomata: anomocytic (0); paracytic (1); anisocytic (2); diacytic (3)
18. Calcium oxalate crystals in mesophyll: absent (0); present (1)
19. Inflorescence: dichasium (0); monochasium (1); flowers in clusters (2); solitary flowers (3)
20. Flower color: white, green, or yellow (0); pink, red, blue, lilac, or brown (1)
21. Calyx: polymerous (0); 5-merous (1); 4-merous (2); 2-merous (3)
22. Size of calyx lobes: equal (0); unequal (1)
23. Fusion of sepals: scarcely (0); half (1); almost completely (2)
24. Abaxial side of calyx lobes: smooth (0); keeled (1); winged (2)
25. Intracalycine membrane: absent (0); present (1)
26. Colleters or squamellae on adaxial side of calyx tube: absent (0); present (1)
27. Glandular area on top of calyx: absent (0); present (1)
28. Lateral traces of calyx: free (0); fused at origin (1); fused throughout (2)
29. Metaxylary fibers in calyx: absent (0); present (1)
30. Corolla aestivation: valvate (0); imbricate (1); contorted (2); plicate (3)
31. Corolla: polymerous (0); 5-merous (1); 4-merous (2)
32. Corolla shape: rotate (0); salver-shaped (hypocrateriform) (1); funnel-shaped (infundibular) (2); campanulate (3)
33. Petal fusion: scarcely (0); half (1); almost completely (2)
34. Nectar guide: absent (0); present (1)
35. Floral nectaries: none or rudimentary (0); on the corolla (1); gynoecial (2)
36. Anther shape: long, non-sagittate (0); long, sagittate (1); short (2)
37. Anther size: normal (0); enlarged (1)
38. Anther fixation: dorsifixed and non-versatile or basifixed (0); dorsifixed and versatile (1)
39. Anther dehiscence: longitudinal slits (0); apical pores (1)
40. Anther twisting after ripening: absent (0); present (1)
41. Anther cohesion: free (0); connate (in at least one floral type in heterostylous taxa) (1)
42. Anther abortion: none (0); 1–3 aborted stamina (1); one fertile stamen (2)
43. Anther appendix: absent (0); present (1)
44. Filament bases: not united (0); united by a membrane (1)

Table 3.3. (*cont.*)

45. Endothecium: fibrous (0); non-fibrous (1)
46. Heterostyly: absent (0); present (1)
47. Stamen insertion: near the base of the corolla (0); between the base and the mouth of the corolla (1); near the mouth of the corolla (2)
48. Ovary: superior (0); inferior (1)
49. Ovary: syncarpous (0); apocarpous (1)
50. Ovary shape: globular (0); oval (1); long, at least three times as long as wide (2)
51. Ovary position: sessile (0); stipitate (1)
52. Stigma: simple (0); capitate (1); lobed (2); decurrent (3); dichotomously lobed (4)
53. Carpel ventral traces: free (0); fused at origin (1); fused throughout (2)
54. Fruit dehiscence: septicidal (0); loculicidal (1); indehiscent (2); irregular (3)
55. Fruit type: capsule (0); baccate (1); drupe (2)
56. Ovule type: hemianatropous (0); anatropous (1); orthotropous (2); campylotropous (3)
57. Integuments: normal (0); absent or rudimentary (1)
58. Antipodal number: three (0); 8–12 (1)
59. Antipodials: ephemeral (0); persistent (1)
60. Antipodials: non-haustorial (0); haustorial (1)
61. Endosperm development: *ab initio* nuclear (0); *ab initio* cellular (1)
62. Embryo suspensor: uniseriate (0); 2–4-seriate (1)
63. Seed shape: angular or cubical (to irregular: e.g., *Schultesia* and *Celiantha*) (0); globular (1); oval (2); elongated (3)
64. Seed wing: absent (0); present (1)
65. Seed testa cell shape (away from hilum): not elongated (0); elongated (1)
66. Radial cell walls of seed testa cells: straight (to slightly undulated: e.g., *Celiantha*) (0); with clear undulations (1)
67. Inner tangential cell walls of seed testa cells: smooth (0); pitted (1); with papillae (2); with reticulum (3); multiply-pitted (*Sebaea*) (4)
68. Pollen germination: outside the thecae (0); within the thecae (1)
69. Pollen unit: monads (0); tetrads (1); polyads (2)
70. Pollen apertures: colpi (0); colpori (1); pori (2)
71. Exine structure: atectate (0); semitectate (1); tectate (2)
72. Supratectal processes: absent (0); present (1)
73. Haploid chromosome number *n*: below 15 (0); between 15 and 29 (1); 30 or above (2)
74. L-(+)-bornesitol (a cyclitol): absent (0); present (1)
75. Sugars: simple (glucose, primverose, rhamnose, galactose) (0); compound (gentianose, gentiobiose) (1)
76. End-product of secoiridoid biosynthesis: sweroside, including its derivatives (0); swertiamarin, including its derivatives (1); gentiopicroside (2); indole alkaloids (3)
77. Flavonoids: flavonols (O-glycosides) (0); flavone-O-glycosides (1); flavone-C-glycosides (2); flavonons (3)
78. Xanthones: absent (0); xanthone-C-glycosides (1); free xanthones and xanthone-O-glycosides (2)
79. Oxygenation of xanthone position C2: absent (0); present (1)
80. Oxygenation of xanthone position C4: absent (0); present (1)

Table 3.3. (*cont.*)

81. Oxygenation of xanthone position C5: absent (0); present (1)
82. Oxygenation of xanthone position C6: absent (0); present (1)
83. Oxygenation of xanthone position C7: absent (0); present (1)
84. Oxygenation of xanthone position C8: absent (0); present (1)

Eustoma, *Exacum*, *Gentiana*, *Ixanthus*, and *Plumeria*). The pollen characters and state distributions are mostly from personal observations of S. Nilsson; characters and character states of the seed characters are mostly from the work of V. Goethals. Of the cells in the data set, 24.4% are scored as question marks (designating either missing information or inapplicable characters); 9.8% of the data cells represent polymorphisms. Below we review the character state distributions and sources according to character groups.

Habit, duration of life cycle, and trophy

Gentianaceae cover a wide spectrum of habit and duration of the life cycle, from trees and shrubs to perennial, biennial, and annual herbs. Stebbins (1974) described some trends in the evolution of growth habits: (1) modern dicotyledonous trees have evolved from shrubby ancestors; (2) shrubs transformed to perennial herbs; and (3) annuals and biennials evolved from perennial herbs. In the first and second trend many examples of reversals are known, but the trend from perennial to monocarpic life cycle seems to be almost irreversible (Kremer & van Andel, 1995).

In our study, the outgroups are trees and shrubs but at the same time there are some indications for a reverse infrageneric trend in *Lisianthius*, *Exacum*, and *Tachiadenus* (Weaver, 1972; Klackenberg, 1985, 1987). Based on a comparison of families, Kremer and van Andel (1995) also argue that biennials emerged from annuals. Infrageneric data seem to contradict this trend; for example, within European species of *Centaurium* sect. *Centaurium* biennial species are diploids ($n = 10$) while annuals are the tetraploid ones ($n = 18, 20$; see Melderis, 1972). We therefore grouped biennials and annuals to one character state, as we did with trees and shrubs.

Another characteristic of Gentianaceae is a special type of arbuscular mycorrhiza, which differs from normal mycorrhizae in the structure of the endophyte and the way it spreads (Demuth, 1993). This type of mycorrhiza has also been reported for *Gelsemium* (Tiemann *et al.*, 1993), Rubiaceae (Rath, 1993), and Apocynaceae (Klahr, 1993), in the last case together with normal and transitional forms of arbuscular mycorrhizae. The family

Gentianaceae is also unusual in that, in tandem with the reduction in chlorophyll content, a phylogenetic transition from facultative to obligate mycotrophy has occurred. *Bartonia* and *Obolaria* have a low chlorophyll content while *Cotylanthera*, *Voyria*, and *Voyriella* seemingly have no chlorophyll at all, becoming endoparasites. Another conspicuous tendency in these genera is a reduction of the root system, changing to a coralloid or morning-star type (Furman & Trappe, 1971; Weber, 1992; Imhof *et al.*, 1994). The co-occurrence of these characteristics is coded as the presence of a heterotrophic syndrome.

Stem

When characterizing the stem of the Gentianaceae, anatomical characters related to secondary growth seem to have the most phylogenetic significance (note that according to Dickison, 1975, trends of specialization in the secondary xylem elements of dicotyledons tend to be paralleled, with an evolutionary lag, in the primary xylem). Wood anatomy of *Symbolanthus*, *Chelonanthus*, and *Ixanthus* was studied by Carlquist (1984), while the general anatomy of the family was described by Perrot (1897). In addition anatomical data for some genera can be found in Solereder (1885, 1899), Figdor (1897), Holm (1897, 1906), Metcalfe and Chalk (1950), Szujkó-Lacza and Sen (1979), Szujkó-Lacza and Gondar (1983), and ter Welle (1986).

Based on Carlquist (1984), general characteristics of the wood of Gentianaceae are absence of storied structures, absence of crystals, vessels round in transection and standing in radial chains, and presence of intraxylary (internal or medullary) phloem. The perforation plates of vessels are generally simple but the scalariform state is reported to occur in some of the outgroups (*Geniostoma* and *Rauwolfia*) and in *Saccifolium* (Maguire & Pires, 1978); both states co-occur in *Lisianthius* (Solereder, 1885), *Chironia*, *Coutoubea*, and *Orphium* (Solereder, 1899).

The imperforate tracheary elements are predominantly fiber-tracheids with bordered pits, but primitive tracheids occur in some of the outgroups (*Strychnos* and *Rauwolfia*). Libriform fibers with simple pits, considered the most advanced type, were reported for *Anthocleista*, *Fagraea* (Mennega, 1980), and *Ixanthus* (Carlquist, 1984).

In most of the outgroups and in *Symbolanthus* both multi- and uniseriate (heterogeneous) rays are present; the presence only of uniseriate (homogeneous) rays is characteristic for some other genera, and raylessness is reported for, or can be observed in, *Saccifolium* (Maguire & Pires, 1978) and in herbaceous genera: *Blackstonia*, *Centaurium*, and *Exacum* (Metcalfe & Chalk, 1950), *Schultesia* (Solereder, 1899), *Swertia* (Perrot, 1897), *Bartonia* and *Obolaria* (Holm, 1897, 1906), and *Gentiana* sect. *Gentiana* (*G. asclepiadea*; Szujkó-Lacza & Sen, 1979). Absence of interxylary (included) phloem is reported for *Anthocleista* and *Fagraea* (Mennega, 1980), and *Symbolanthus* and *Irlbachia* (Carlquist, 1984); its presence was documented for *Ixanthus* (Carlquist, 1984), *Chironia* (Vesque, 1875), *Orphium* (Solereder, 1885), *Crawfurdia*, *Schultesia*, *Swertia*, and *Tripterospermum* (Metcalfe & Chalk, 1950), and *Gentiana* sect. *Gentiana* (Szujkó-Lacza & Sen, 1979); furthermore it can be observed on Perrot's (1897) drawings of *Centaurium* and *Exacum*.

Leaves

In the autotrophic genera the leaves are simple, entire, and opposite (symplesiomorphies with other families of Gentianales), rarely verticillate (*Curtia*) or alternate (*Swertia*); in the heterotrophic genera they are reduced to scales. The principal venation pattern is acrodromous according to the terminology of Hickey (1979): two or more secondary veins run in convergent arches toward the leaf apex. This type is reported for *Canscora*, *Centaurium*, *Enicostema*, *Exacum*, and *Hoppea* by Mohan *et al.* (1989) and was observed in many other genera. Pinnate, brochidodromous venation (with a single primary midvein and secondaries joined together), characteristic for Gentianales (Hickey & Wolfe, 1975), occurs in some woody Gentianaceae (*Anthocleista*, *Fagraea*, *Macrocarpaea*, and some species of *Chorisepalum*). It is interesting to note that in the outgroup genus *Strychnos* both states exist (Leenhouts, 1962).

Types of mature stomata were reported in a series of papers (Pant & Kidway, 1969; Patel *et al.*, 1981; Trivedi & Upadhyay, 1983; Gill & Nyawuame, 1990). Two types dominate: the anomocytic (ranunculaceous) type, without subsidiary cells; and the paracytic (rubiaceous) one with two subsidiary cells beside the two guard cells (following the definitions of van Cotthem, 1970). The latter type occurs mainly in the genus *Gentiana*. Gill and Nyawuame (1990) tried to define the phylogenetic sequence of stomatal types based on the distribution of the types in 320 taxa of Bentham and Hooker's Bicarpellatae, and considered the anomocytic type to be the primitive one.

Calyx

The calyx in Gentianaceae is persistent, often gamosepalous and isomerous with the corolla lobes; in other respects it is very variable, resulting in seven characters for the analysis. We subdivided the considerable variation in the degree of sepal fusion into three states: scarcely, half, and almost completely. The state "scarcely" is found in the outgroups, in many tropical genera, in Gilg's (1895) tribe Exacinae and subtribe Erythraeinae, and in *Halenia*, *Lomatogonium*, and *Swertia* (polymorphic) of tribe Gentianeae. The other two states occur in the remaining part of the tribe Gentianeae as well as in some other genera (e.g., in *Canscora*, *Faroa*, and *Hoppea*). In addition to gamosepaly, the sepals of *Crawfurdia*, *Gentiana*, and *Gentianopsis* are connected by a "*membrana intracalycina*" (Grisebach, 1845). Kusnezow (1896–1904: 38–44) described the character in detail and found it in all species of *(Eu)Gentiana* that he investigated.

Vascular bundles to the calyx originate in whorls with one trace to each sepal; each of these traces then branches into three. According to Wood and Weaver (1982) specialization has tended toward fusion of the lateral traces of adjacent sepals. Lindsey (1940) demonstrated such fused calyx laterals in *Lisianthius* and in seven investigated genera of Gilg's Helieae. It occurs only sporadically in other parts of the family.

An interesting character is the squamellae or colleters that develop on the adaxial surface of the calyx tube and degenerate during anthesis. McCoy (1940) described the details of their structure in *Swertia (Frasera) carolinensis*, as did Vijayaraghavan and Padmanaban (1969) in *Centaurium ramosissimum*. The presence of this structure has been documented in many of the taxa included in our analysis; it is absent in, for example, *Gelsemium*, *Plumeria*, and *Rauwolfia* among the outgroups as well as in *Celiantha*, *Curtia*, *Coutoubea*, and *Lisianthius* within the ingroup; *Schultesia* and *Voyria* are polymorphic in this aspect.

Corolla

Corollas are sympetalous and generally actinomorphic or rarely slightly zygomorphic. Variable characters are aestivation, merosity, and corolla shape. Contort aestivation is reported to be characteristic for the family (including *Anthocleista* and *Fagraea*); imbricate aestivation, considered the most primitive by Takhtajan (1991), occurs in *Bartonia* and *Obolaria* (Wood & Weaver, 1982) and is also found in the outgroups *Exostema*, *Gelsemium*, and *Geniostoma*. Plicate aestivation, a special form of contort aestivation in which folds are alternating to lobes, is characteristic for *Crawfurdia*, *Gentiana*, and *Tripterospermum*.

Pentamery is the common and probably ancestral state for the family, but constant or occasional tetramery, presumably as a reduction, also occurs in many genera. More interesting are the cases exceeding pentamery: constant 6 in *Chorisepalum* (Maguire, 1981; with four sepals), 6–12 in *Blackstonia* (Tutin, 1972), 5–12 in *Sabatia* subsect. *Dodecandrae* (Wilbur, 1955), 8–16 in *Anthocleista* and *Potalia* (Leeuwenberg & Leenhouts, 1980; L. Struwe & V. A. Albert, unpubl.; with four sepals), and 5–9 in *Gentiana* sect. *Gentiana* (Tutin, 1972).

Main corolla shapes are rotate, salver-shaped (hypocrateriform), funnel-shaped (infundibular), and campanulate. Rotate flowers are characteristic for tribe Exacinae and Gilg's (1895) subtribe Erythraeinae, with some exceptions. In tribe Gentianeae the other three corolla forms predominate, but *Lomatogonium* and *Swertia* have rotate flowers. Variations are often infrageneric (e.g., *Gentiana* and *Gentianella*).

Based on our own observations there appear to be three mechanisms for constricting the corolla tube to form a nectar guide for pollinators with long probosces: (1) developing a salver-shaped corolla (typical for *Gentiana* sect. *Calathianae*), (2) growing fimbriae in the corolla throat (e.g., *Gentianella*), or (3) stamens adnating to the style, sometimes called "revolver-flowers" (*Gentiana* sects. *Gentiana*, *Ciminalis*, and *Pneumonanthe*).

Androecium

Stamens are generally isomerous, epipetalous, alternating with the corolla lobes, representing haplostemony according to the definition of Ronse Decraene & Smets (1995). Anthers are dithecal, tetrasporangiate, and mostly introrse. Reductions of the androecium shown to be typical for Asteridae (Ronse Decraene & Smets, 1995) are rare in Gentianaceae, occurring only in *Canscora*, *Hoppea*, and *Schinziella*.

Anthers are typically basifixed, the original configuration for the angiosperm stamen according to Baum and Leinfellner (1953). Dorsifixed and versatile anthers occur in *Gentiana* sect. *Otophora*, *Gentianella*, *Gentianopsis*, *Halenia*, and *Swertia*, as well as in *Bartonia* and *Obolaria*. This specialization is connected with a pollination mechanism where stamens rather than the stalk of the ovary are moving during anthesis (Philipson, 1972).

Another interesting specialization is twisting of anthers after ripening. This phenomenon is well known in *Centaurium* (drawn in Wagenitz, 1964) but it is also documented in *Orphium* (Gilg, 1895), *Chironia* (Schoch, 1903; Boutique, 1972; Paiva & Nogueira, 1990), *Sabatia* (Wood & Weaver, 1982), *Blackstonia* (Tutin, 1972), and *Bartonia* (Gillett, 1959), and was seen on living plants of *Eustoma*.

Several characters are found in only a few taxa. Anther appendices, called "Brown's bodies" by Schinz (1903), were observed in *Sebaea* (Marais & Verdoorn, 1963) and *Tachiadenus* (Klackenberg, 1987). Klackenberg (1985) considered non-fibrous (finely perforated) endothecium cell walls as a generic attribute of *Exacum*, but they are also characteristic for *Cotylanthera* (Figdor, 1897; Oehler, 1927).

Pollen

Pollen grains are generally radially symmetrical, tricolporate, two- or three-celled at the time of shedding, and with the longest axis varying from about 20 μm to 35 μm. Several states that are generally considered to be advanced occur mostly in neotropical genera: (1) pollen units are tetrads in *Coutoubea*, *Deianira*, *Schultesia*, and *Symbolanthus*, and polyads in *Celiantha* and *Irlbachia*; (2) besides the Rubiaceae outgroups, only *Celiantha* and *Irlbachia* have supratectal processes; and (3) porate ecto-apertures occur in the neotropical genera *Celiantha*, *Coutoubea*, *Irlbachia*, *Schultesia*, and *Voyria*, in the paleotropical genera *Anthocleista* and *Fagraea*, and in the outgroup *Geniostoma*. Exine sculpturing varies throughout the family, with some genera even being polymorphic.

Pollen characters and character states were established by S. Nilsson (see Nilsson, 1964, 1967a,b, 1968, 1970, 2002 (Chapter 4, this volume), and Nilsson and Skvarla, 1969, for documentation of these characters); data for several other neotropical genera are documented in Elias and Robyns (1975). Walker and Doyle (1975) and Punt (1978) discussed phylogenetic trends.

Pollination

Pollination syndromes in the family are rather diverse. Melittophily is considered as most common and probably ancestral. Chiropterophily was reported for several neotropical genera such as *Symbolanthus*, *Irlbachia*, *Lisianthius*, and *Macrocarpaea*, together with ornithophily (*Symbolanthus*) or melittophily and sphingophily (*Irlbachia*) for some species (Vogel, 1958, 1969). Pollen flowers, with pollen as the main reward, were observed in *Chironia*, *Exacum*, *Orphium*, *Sabatia* (Vogel, 1978), and *Eustoma* (Vogel, 1993) as well as in *Centaurium* and *Deianira* (S. Vogel, pers. comm.).

Several floral characteristics are correlated with the mode of pollination. Genera with pollen flowers are generally nectarless or have rudimentary nectaries; in other cases the flowers are nectariferous. The principal nectary type is a gynoecial nectary but another type, situated on the corolla, also frequently occurs (*Gentianella*, *Gentianopsis*, *Halenia*, *Lomatogonium*, and *Swertia*). All these genera have rotate flowers that supply free nectar for a large array of pollinators (Beattie *et al.*, 1973). The homology of the gynoecial glands of *Voyria* (Maas & Ruyters, 1986; see also Albert & Struwe, 1997) is difficult to interpret; we left the question open and coded *Voyria* as unknown for presence of floral nectaries.

The pollen flowers are of the *Solanum* type (Vogel, 1978): melittophilous, oligandrous, with shortened filaments and with enlarged anthers capable of producing excess pollen. In *Exacum*, *Cotylanthera*, and *Deianira* poricidal anther dehiscence has been reported (Figdor, 1897; Guimarães, 1977; Klackenberg, 1985), pointing to buzz pollination, which also occurs in Rubiaceae. Buzz-pollinated flowers probably developed secondarily from nectariferous flowers (Dukas & Dafni, 1990).

With the exception of *Gentianella* and *Veratrilla* (sometimes included in *Swertia*), where dioecy occurs, flowers in Gentianaceae are hermaphroditic. Protandry is the general form of dichogamy but other forms occur as well (e.g., approach herkogamy; Webb & Pearson, 1993). As these developments are infrageneric, characters of the breeding system could not be used for phylogenetic inference on the family level.

Gynoecium and fruit

The gynoecium is bicarpellate and syncarpous or paracarpous (Shamrov, 1996) with a superior ovary. Varying characters are shape, position, placentation of the ovary and number of locules, degree of fusion of carpel ventral traces, stigma morphology, and type of fruit dehiscence.

The ovary in Gentianaceae is unilocular or bilocular except in *Anthocleista*, where it seems to be 4-locular. The polarity of this character has been much discussed in the past (Lindsey, 1940; Krishna & Puri, 1962), but nowadays the bilocular condition, prevailing in six of the seven outgroups, is generally considered to be primitive in the family.

Axile placentation is associated with the bilocular state of the ovary. It prevails in the outgroups, in Gilg's tribe Exacinae, and in some woody neotropical genera. Parietal and superficial placentation (Krishna & Puri, 1962) are correlated with the unilocular ovary, the latter being characteristic for *Crawfurdia*, *Gentiana*, *Gentianella*, *Gentianopsis*, *Lomatogonium*, and *Tripterospermum*. Even if transitional states do occur, mainly for locule number (e.g., in *Lisianthius*), the distinction of ovary zones made by Leinfellner (1950) could not be used as characters because the detailed data required were available only for some neotropical genera (van Heusden, 1986; Struwe *et al.*, 1997).

The fruit is generally capsular, which is considered to be primitive in Gentianales. Berries are less widespread than in Rubiaceae; they are characteristic only for *Anthocleista* and *Fagraea* and occur only sporadically elsewhere (one section of *Tripterospermum* and one species of *Chironia* and

Symbolanthus). Septicidal fruit dehiscence is the common state for the ingroup; *Voyriella*, with an indehiscent fruit, and *Voyria*, with dehiscent, indehiscent, and transitional types, are the exceptions (Maas & Ruyters, 1986).

Embryology

Many embryological characters are constant throughout the family: microsporangial development is of the dicotyledonous type, ovules are unitegmic and tenuinucellar, megagametogenesis is of the *Polygonum* type, and embryogeny is of the Solanad type (Rao & Nagaraj, 1982). These character states constitute symplesiomorphies within the dicotyledons or only among some families of the Asteridae.

Characters varying within the family are ovule type and integument development, antipodal characteristics, endosperm development, and specializations of the nucellus and embryo. These characters are distinctive partly between autotrophic and heterotrophic genera, and partly between subtribe Gentianinae and the other (sub)tribes of the family.

Ovules are commonly anatropous. In monotypic *Voyriella* the ovule is orthotropous, and orthotropous ovules also occur in *Cotylanthera* and some *Voyria*; other ovule types were reported (Stolt, 1921; Oehler, 1927; Shamrov, 1988, 1991) for *Swertia* (campylotropous), *Halenia* (orthotropous), and *Gentianella* (hemitropous). *Voyriella* and *Voyria* also deviate from the common state of (nuclear) endosperm development: in *Voyriella* and *Voyria caerulea* (Oehler, 1927) endosperm development is *ab initio* cellular; in five other species of *Voyria* nuclear endosperm was recorded (Maas & Ruyters, 1986).

Antipodal variation is stated to be important within the family (Stolt, 1927; Rao & Chinnappa, 1983). Their number is generally three, but in *Swertia* and *Gentianella* there may be 8–12 antipodals. They may be haustorial or non-haustorial, and either ephemeral, degenerating before fertilization, or persistent. Rao and Nagaraj (1982) proposed a distinction between Gilg's (1895) subtribe Gentianinae and the other Gentianaceae, the latter characterized by three ephemeral, non-haustorial antipodal cells. This statement seems to be correct for *Cotylanthera, Exacum, Canscora, Hoppea, Voyria*, and *Voyriella*, but a wider variation has been reported for *Blackstonia*, and *Centaurium* and for the genera of subtribe Gentianinae (Stolt, 1927; Arekal, 1961; Vijayaraghavan & Padmanaban, 1969; Drexler & Hakki, 1979; Rao & Nagaraj, 1982; Shamrov, 1988).

Embryological reports are scarce (e.g., an integumentary tapetum – endothelium – has been reported only for *Exacum*; Maheswari Devi, 1962) or contradictory, as in reports of endosperm type and in the terminology of ovule types. It is also problematic that no reports exist for the neotropical autotrophic genera.

Seed

The seeds mostly develop from unitegmic and tenuinucellate ovules. The outer layer of the integument develops into a mechanical layer that gives the seed hardness and strength. Since only the outer layer of the integument contributes to the formation of the seed coat (Bouman & Schrier, 1979), the seeds are exotestal according to Corner's (1976) terminology. The remaining tissues of the testa are usually compressed or resorbed by the endosperm or the embryo. The seed coat fits tightly to the endosperm (when present).

Enlarged exotestal cells and secondary thickenings of radial (anticlinal) cell walls make up the reticulations of the mature seed coat, generally without intercellular gaps. These elaborations of the seed coat facilitate anemochory, or, in the case of tropical mycotrophs, ombrohydrochory (Bouman & Devente, 1986). The exotesta exhibits a great diversity in cell shape and especially in cell wall thickenings, as demonstrated by Guérin (1904). Varying characters are seed shape, presence or absence of seed wings, testa cell shape, anticlinal wall undulations, and inner tangential (periclinal) wall sculpturing (terminology as in Barthlott, 1981).

For seed shape we distinguished four types. The angular (cubical) type is best documented for *Exacum* (Klackenberg, 1985) but it seems to dominate among neotropical woody genera as well. The globular shape is typical for Gilg's subtribes Erythraeinae and Chironiinae. The transitional oval type occurs in tribe Gentianeae while long seed is typical for *Gentiana*, well documented in papers of Miège and Wüest (1984), Ho and Liu (1990), and Yuan (1993b).

In a number of taxa of tribe Gentianeae (sections *Gentiana, Otophora, Stenogyne*, and *Pneumonanthe* of *Gentiana, Crawfurdia, Tripterospermum*, the Asian species of *Swertia*, and some American species of *Frasera*) and in one genus of the Potalieae (*Urogentias*) the seeds have flat, marginal outgrowths of the seed coat, called seed wings. The presence of wings may be considered an advanced feature and it is seemingly correlated with seed size; the mentioned genera all have some of the largest seeds in Gentianaceae. The morphology of the seed wings is very diverse. They may be (1) regular and more or less equal all around the edge of the seed (e.g., *Gentiana, Swertia*, and *Frasera*), or (2) unequal or asymmetric (e.g., *Crawfurdia, Tripterospermum*, and *Urogentias*). In *Crawfurdia* and *Tripterospermum* the seeds have three wings. *Urogentias* has striate membranous wings that are extensions of the chalazal end of the seed coat.

The *Voyria aphylla* species group is characterized by fusiform to filiform seeds (Bouman & Devente, 1986) that are adapted to wind dispersal. In this group the seeds have long projections that show reticulate secondary thickenings on the radial and inner tangential cell walls and that are air-filled in the dry, mature state.

The outline of the exotestal cell can be isodiametric or elongated, the latter state being typical in *Gentiana*. The isodiametric state can be considered as primitive; it is interesting to note that African species of *Exacum* (Klackenberg, 1985) and the *Voyria truncata* species group, thought to be the most primitive in *Voyria* (Bouman & Devente, 1986; subgenus *Voyria* of Albert & Struwe, 1997), have isodiametric testa cells.

Straight anticlinal cell walls, the most common state, are thought to be plesiomorphic. Undulate (sinuated) anticlinal walls were shown for *Exacum* (Guérin, 1904; Klackenberg, 1985), *Irlbachia* (Cobb & Maas, 1983), *Curtia* (Grothe & Maas, 1984), *Tachiadenus* (Klackenberg, 1987), *Centaurium*, and *Faroa* (Goethals & Smets, 1995). The inner tangential cell walls of the exotesta often have sculpturings, as do sometimes the radial walls. The partial or reticulate thickenings of exotestal cell walls combine strength with low seed weight, thus advancing both seed dispersal and survival. We distinguished four types of inner tangential cell wall sculpturings: pitted, papillate, reticulate, and multiple pitted; some genera are polymorphic.

Cytology

Chromosome numbers are partially known for 36 of the 46 ingroup terminals (78.2%). There are genera with constant chromosome numbers, e.g., *Halenia* and *Lisianthius* (the latter documented for 10 species by Weaver, 1969), but in the majority of taxa chromosome numbers are variable because of euploidy, dysploidy, or aneuploidy. Infrageneric variation is best documented for *Centaurium* (Zeltner, 1970; Broome, 1978), *Sabatia* (Perry, 1971), *Swertia* (Khoshoo & Tandon, 1963; Shigenobu, 1983; Pringle, 1990), and *Gentiana* sect. *Calathianae* (Müller, 1982).

We used haploid chromosome number as a character in our analysis, even though it has a wide and almost continuous range from $n=5$ to $n=42$ in the family (the exceptions are $n=25$, 29, 35, and 37; in one variety of *Gentiana nipponica* even $n=48$ and 49 was observed; Shigenobu, 1984). However, on a generic level the distribution of haploid chromosome numbers is bimodal, with a local maximum at 9–11 and a global maximum at 18–21. We used $n=15$ as a demarcation between these two modi. Next, the distribution has a long right tail in which, among others, the woody genera *Anthocleista* ($n=30$), *Symbolanthus* ($n=40$), and *Fagraea* ($n=$ up to 42) are present. Considering the long right tail, $n=30$ was (arbitrarily) chosen as a second demarcation point. With maxima at $n=9$–11 and $n=$ 18–21 in the distribution of haploid chromosome numbers, $x=9$, 10, 11 may be frequent base numbers ($x=10$ or 11 is also found in many Apocynaceae and Rubiaceae). Zeltner (1970) documented different ploidy levels for *Centaurium* (based on $x=9$–11; see also Ubsdell, 1979) and *Blackstonia* ($x=10$). Different ploidy levels are also documented for *Swertia* ($x=10$, 13), *Gentianella* ($x=9$), *Gentianopsis* ($x=13$), and *Gentiana* sect. *Cruciata* ($x=13$) and sect. *Frigidae* ($x=12$) (Shigenobu, 1983; Yuan, 1993a; Yuan & Küpfer, 1993a,b). Therefore, ploidy levels are fairly well assessable based on $x=9$–13, at least for these genera.

Dysploidy or aneuploidy has been reported for *Sabatia* (Perry, 1971), *Swertia* (Vasudevan, 1975), the American species of *Centaurium* (Broome, 1978), and for *Gentiana* sect. *Calathianae* (Müller, 1982).

Chemistry

From the various biochemical compounds that are found in the family only iridoids, secoiridoids, xanthones, flavonoids, and carbohydrates are used as a source for characters in this analysis. Other interesting compounds, such as pseudo-alkaloids and triterpenes, do occur in the family, but there are insufficient data.

Regarding iridoids and secoiridoids, the biosynthetic route of mevalonate → loganin (loganic acid) → secologanin (secologanic acid) → sweroside → swertiamarin → gentiopicrine can be considered as proven (Hegnauer, 1989, based on experiments with different species of *Swertia* and *Gentiana*). Within this biosynthetic route there are several side branches; from this point of view secologanin and sweroside are the most interesting nodes. One route from secologanin leads to the complex indole alkaloids (route I of Jensen, 1992). These are found in other families of Gentianales, but genera of Gentianaceae (including Potalieae) are not able to synthesize them; instead they produce pseudo-alkaloids from swertiamarin or gentiopicrine. Sweroside is interesting because this compound is also present in some Apocynaceae (Hegnauer, 1989) and in *Desfontainia* (Jensen, 1992); swertiamarin and gentiopicrine, however, occur only in Gentianaceae. So presence of only sweroside seems to be a plesiomorphic state within Gentianaceae; it is observed in the neotropical Gentianaceae *Irlbachia* and *Lisianthius* (Hamburger *et al.*, 1990; Shiolara *et al.*, 1994; Jensen & Schripsema, 2002 (Chapter 6, this volume)).

Sources and coding of xanthone compounds are described in Mészáros (1994) and Mészáros *et al.* (1996). These data were supplemented with new data for *Halenia* (Rodriguez *et al.*, 1995), *Lomatogonium* (Khishgee & Pureb, 1993), *Schultesia* (Terreaux *et al.*, 1995), and *Gentiana* sect. *Frigidae* (Butayarov *et al.*, 1993). A new character was introduced to distinguish between taxa with no xanthones, taxa with only xanthone-C-glycosides (e.g., mangiferin), and taxa with also xanthone-O-glycosides. Data for flavonoids were also updated.

Massias *et al.* (1978) made a broad investigation of sugars. Simple sugars are widespread, but gentianose was found only in *Gentiana* and *Swertia*; it was not detected in nine other genera. Since that time another compound sugar, gentiobiose, has been documented for *Halenia* (Recio-Iglesias *et al.*, 1992) and *Lomatogonium* (Schaufelberger & Hostettmann, 1984). Schilling (1976) detected L-(+)-bornesitol, a special sugar, in 20 of 24 investigated genera of Gentianaceae; its absence is documented for *Curtia*, *Exacum*, *Irlbachia*, and *Sebaea*. L-(+)-bornesitol also occurs in *Anthocleista* and in some Apocynaceae and Rubiaceae (Plouvier, 1990).

Methods

The data set was analyzed using parsimony analysis (Farris, 1970, 1983; Fitch, 1971) with equal a priori character weights and unordered characters. The analyses were performed with the computer program NONA (Goloboff, 1993). In all analyses we used subset coding for polymorphisms (see Mészáros *et al.*, 1996, for some comments on polymorphisms and subset coding). Apart from the unordering of multistate characters and the total number of trees that can be stored in memory, all other default settings were retained in all analyses. By default, NONA collapses all branches that have no unambiguous synapomorphies (a character provides an unambiguous synapomorphy for a branch if a state transition occurs on that branch under every possible optimization of the character on the tree; Goloboff, 1993; see also Coddington & Scharff, 1994). The most-parsimonious cladograms and the cladograms that are one step longer were calculated using the instruction series "MULT*100; SUBOPTIMAL 1; MAX*". MULT*100 carries out 100 replications of randomizing the order of the taxa, creating a tree by means of stepwise addition, and submitting it to branch-swapping by means of tree bisection and reconnection. During each replicate a maximum of 20 trees was retained ("HOLD/20" setting, the default). The instruction "MAX*" is added to ensure full branch-swapping (i.e., unrestrained by the HOLD/20 setting) of the trees obtained with "MULT*100", also using tree bisection and reconnection. The "SUBOPTIMAL 1" command, issued before "MAX*", instructs the program to keep all trees that are one step longer than the most-parsimonious trees. As descriptive measures of the fit between data and trees we calculated consistency and retention indices (C and R; Kluge & Farris, 1969; Farris, 1989). All consistency indices are calculated with autapomorphies included (see Yeates, 1992).

In order to evaluate the relative support of clades, we calculated branch support, i.e., the number of extra steps needed to lose a branch in the strict consensus of near-most-parsimonious trees (Bremer, 1994; also called Bremer support and, using an unfortunate terminology, decay index; see Källersjö *et al.*, 1992). Because of the high number of near-most-parsimonious trees, we only calculated trees up to one step longer than the shortest. We also performed bootstrap (Felsenstein, 1985; but see Bremer, 1994) and jackknife analyses (Farris *et al.*, 1996). These were performed with the aid of macros that are distributed together with NONA (Goloboff, 1993). For the bootstrap and jackknife analyses we ran 100 replicates each; in each replicate the best trees were obtained with a "MULT*10" command. In the jackknife analyses, we followed Farris *et al.*'s (1996) suggestion and randomly deleted 36% of the characters in each replicate. In Fig. 3.1, the reported value for a given clade is the percentage of replicates that support that clade (only values exceeding 50% are shown). In the bootstrap analysis we considered a replicate as supporting a clade when that clade is present in at least one tree for that replicate. In the jackknife analysis we used a stricter interpretation and considered a replicate as supporting a clade only when that clade is present in all trees for that replicate.

RESULTS

Standard parsimony analysis resulted in 100 most-parsimonious trees of 366 steps, with consistency index $C = 0.34$ and retention index $R = 0.56$. In all these trees, *Plumeria* and *Danais* grouped together, as did *Gelsemium*, *Exostema*, and *Rauwolfia*. The failure to group together the two representatives each of Rubiaceae and Apocynaceae indicates a problem in our taxon and/or character sampling at the level of the outgroups. To investigate if this had an influence on the ingroup relationships we performed a second analysis in which both Apocynaceae and Rubiaceae were constrained to be monophyletic. This analysis resulted in 100 trees of length 367 (one step longer) that, apart from the constrained families Apocynaceae and Rubiaceae, were identical to the trees of the unconstrained analysis. The strict consensus tree, arbitrarily rooted between Apocynaceae and the rest, is shown in Fig. 3.1. To check if the outgroups influenced branching within Gentianaceae, we also performed an analysis of ingroup taxa only. This yielded 50 most-parsimonious trees of 311 steps ($C=0.37$, $R=0.56$). The strict consensus of these trees (oriented as indicated by the previous analyses) is exactly the same as in Fig. 3.1.

The large polytomy near the base of the family arises partly because of the variable position of *Celiantha* and *Irlbachia*; in all most-parsimonious trees of all analyses this polytomy resolves as a clade comprising *Chorisepalum*, *Macrocarpaea*, *Symbolanthus*, and *Tachia*, with *Irlbachia* and *Celiantha* occupying various positions (see Fig. 3.2). A third genus with variable position is *Deianira*: it groups either with *Coutoubea* or as the sister to *Cotylanthera–Exacum*. By excluding these three genera with variable positions, more resolution is retained in the strict consensus tree (Fig. 3.2).

In all three cases (unconstrained outgroups, constrained outgroups, ingroup only) all trees up to one step longer than most parsimonious were calculated (yielding 4520, 3900, and 2885 trees, respectively). Within Gentianaceae, the groups with branch support >1 were identical but for one case: the *Blackstonia–Centaurium–Chironia–Eustoma–Orphium–Sabatia* clade has branch support =1 in the ingroup-only analysis, but branch support >1 in the two other cases (branches with branch support >1 are indicated by double bars in Fig. 3.1). Bootstrap and jackknife analyses were performed only for the ingroup-only analysis. In Fig. 3.1, bootstrap and jackknife values that exceed 50% are indicated above branches.

DISCUSSION

Considering that the strict consensus tree (Fig. 3.1) is not well resolved and that most branches that are present have low branch support, bootstrap, and jackknife values, the results of the cladistic analysis should not be over-interpreted. Therefore we will concentrate only on the most salient features.

Our analysis fails to corroborate tribe Exaceae (*Sebaea* is unresolved close to tribe Gentianeae to *Cotylanthera–Exacum*, while *Tachiadenus* appears as sister to *Voyria–Voyriella*; see Fig. 3.2). Nevertheless, the sister-group relationship between *Cotylanthera* and *Exacum*, hypothesized and discussed by Klackenberg in Struwe *et al.* (2002), is supported by both the jackknife and the bootstrap analyses.

Voyria and *Voyriella* appear as the sister group of *Tachiadenus* but only a single unambiguous synapomorphy supports this relationship: the very similar corolla fusion, resulting in a long corolla tube; within this tube the

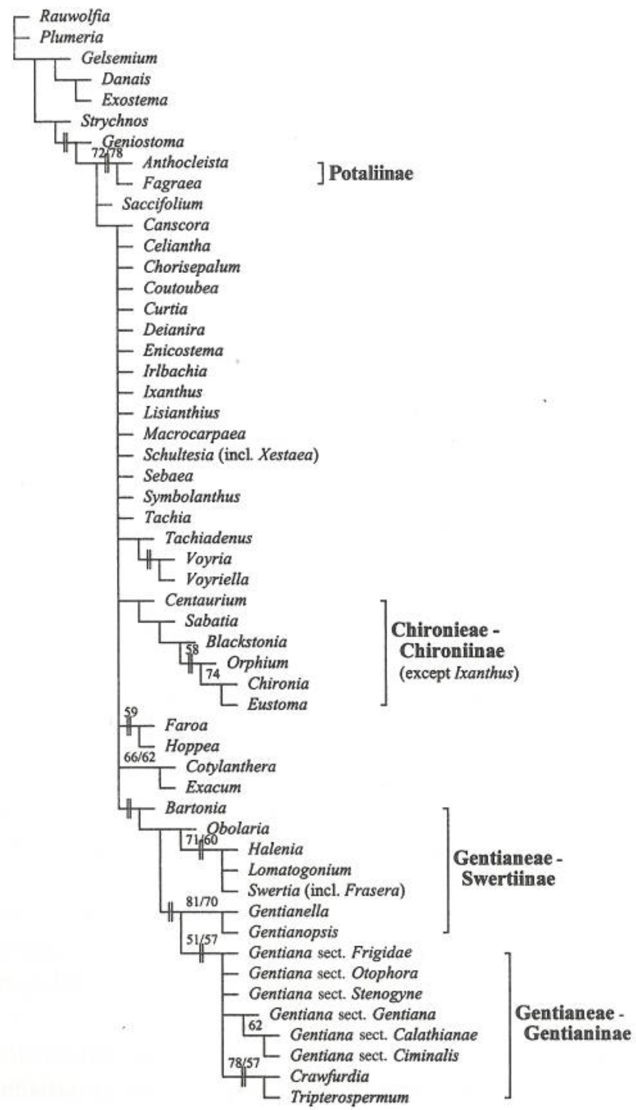

Figure 3.1. Summary of the parsimony analyses. Strict consensus tree of the 100 most-parsimonious trees that are obtained when Apocynaceae and Rubiaceae are both constrained to be monophyletic (367 steps, $C=0.34$, $R=0.56$), arbitrarily depicted with Apocynaceae basal. The strict consensus tree of the 100 trees of 366 steps that are obtained without constraints has identical relationships within Gentianaceae; the same result is also obtained with parsimony analysis of the ingroup only (50 trees of length 311, $C=0.37$, $R=0.56$). Double bars across branches indicate branches in Gentianaceae with branch support >1 (ingroup-only analysis); unmarked internal branches have branch support =1. Numbers above branches are bootstrap values (single numbers or numbers before slash) and jackknife values (numbers after slash) that exceed 50% (ingroup-only analysis).

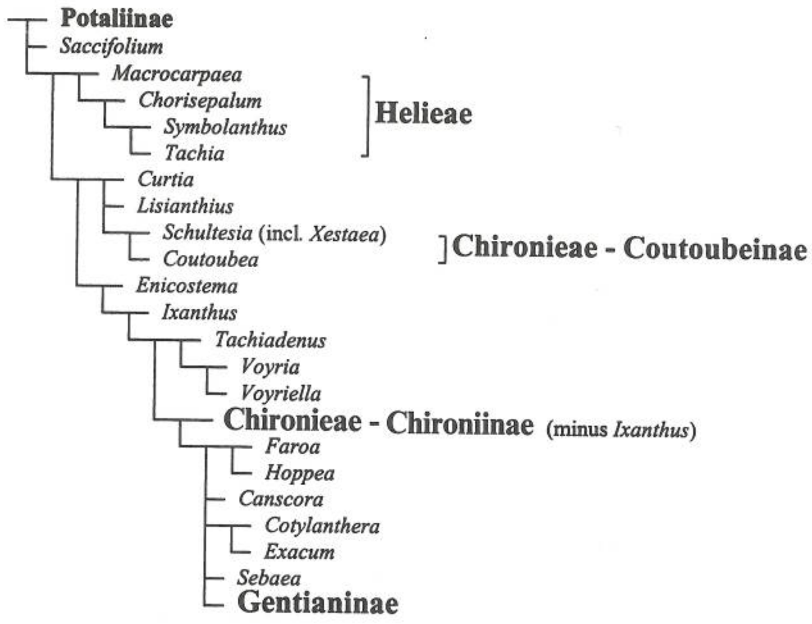

Figure 3.2. Strict consensus tree with exclusion of *Celiantha*, *Deianira*, and *Irlbachia*.

anthers, on very short filaments, are pressed against each other. Beside the characters that are related to the heterotrophic syndrome, *Voyria* and *Voyriella* share a very specific synapomorphy: pollen germination in thecae. However, this may also be the result of parallel evolution in the same tropical habitat. Molecular results, showing *Voyriella* to be closely related to *Curtia* and *Saccifolium* (Thiv *et al.*, 1999a; Struwe *et al.*, 2002), favor this latter interpretation.

Bartonia and *Obolaria* are nested within the monophyletic clade that represents tribe Gentianeae, which is in agreement with Grisebach's (1845) treatment of *Bartonia* and Holm's (1897) treatment of *Obolaria*; it is furthermore supported by the pollen morphological study of Nilsson and Skvarla (1969). However, contrary to the molecular analyses, subtribe Swertiinae, to which both *Bartonia* and *Obolaria* belong, is paraphyletic in our analysis. The monophyly of the Gentianeae clade, also obtained in Struwe *et al.*'s (2002) and Thiv *et al.*'s (1999a) analyses of more than 100 *mat*K sequences and over 150 *trn*L intron sequences of Gentianaceae and other Gentianales, confirms one of the results of our previous analysis (Mészáros *et al.*, 1996).

Another result of this previous study that is confirmed in the current analysis is the close relationship between *Blackstonia*, *Eustoma*, *Orphium*, *Chironia*, and *Centaurium*. *Sabatia*, not included in the earlier analysis, is now added to this Chironiinae clade. These relationships are also obtained in Struwe *et al.*'s and Thiv *et al.*'s molecular analyses, in which *Bisgoeppertia*, *Cicendia*, *Exaculum*, *Geniostemon*, and possibly *Zygostigma* are also added to Chironiinae.

Basal in Gentianaceae according to our results is the trichotomy between the woody genera *Anthocleista* and *Fagraea*, the shrubby genus *Saccifolium*, and the rest of the family (Fig. 3.1). Within this last clade, Helieae (with the possible exclusion of *Irlbachia* and/or *Celiantha*) are sister to the rest of the family (Fig. 3.2). At the base of Helieae are the three typical woody genera *Chorisepalum*, *Macrocarpaea*, and *Symbolanthus*. In combination, this suggests a woody and (pan)tropical origin of Gentianaceae, supporting Carlquist's (1984) conclusion that *Symbolanthus* is primarily woody while *Ixanthus*, nested deeper in the family, is secondarily so. Woody ancestry has been argued for Apocynaceae (Sennblad, 1997: 11) and Rubiaceae (Carlquist, 1992: 319) as well, and all of this is in agreement with the general dominance of the trend from a woody to a herbaceous habit in other families (Anderberg & Ståhl, 1995: 1719) and in dicotyledons (Kremer & van Andel, 1995: 472). However, cladistic analyses of *mat*K and *trn*L intron sequences in Gentianaceae and other Gentianales (Thiv *et al.*, 1999a; Struwe *et al.*, 2002) contradict these hypotheses. On the basis of these data, the first two splits in Gentianaceae set apart tribes Saccifolieae and Exaceae, respectively, while both Potalieae and Helieae are well nested within the remainder of the family. While these results do not exclude a woody origin of the family – the herbaceous or suffrutescent state might be plesiomorphous – they contradict the primary woodiness in Potalieae and Helieae.

This discrepancy between the current analysis and the broader analysis based on *trn*L intron and *mat*K sequences leads to the obvious question; which of the results has more strength? While in general neither type of data is intrinsically superior for purposes of phylogenetic reconstruction, it seems that in this case results from the molecular data are more robust than those from our analysis. The question could be addressed formally by doing a combined analysis of molecular and morphological data. However, our data set has been conceived from the start as a genus-level data set (with the exception of the sections in *Gentiana*), thereby implicitly assuming monophyly of these supraspecific groups. This severely complicates combination with the molecular data, which are basically sequences of exemplar specimens of different species within genera. We tend to find weak support for several (sub)tribes that are also obtained with the molecular data (Potalieae, Helieae, and other examples below). However, the relationships among these groups are almost completely unresolved, and the little resolution we get at this level is very poorly supported. The molecular data, in contrast, yield better-supported relationships at this level. Given these results, and the technical problems of combining the data sets in this case, a formal combination of the two sets would seem to be of little use.

Several factors likely contribute to the poor results obtained with our morphological data set compared with those obtained with *trn*L and *mat*K sequences (Thiv *et al.*, 1999a; Struwe *et al.*, 2002). A first issue is the combined effect of limited taxon sampling and a limited number of informative characters relative to the molecular analyses. This may well explain our inability to retrieve both Rubiaceae (*Danais* + *Exostema*) and Apocynaceae (*Plumeria*+ *Rauwolfia*) as monophyletic groups without imposing constraints upon the analysis. Next, there is a lack of good morphological studies for many tropical and subtropical representatives of Gentianaceae, which influences our data set in two ways. First, these taxa have a relatively high number of question marks, most simply representing missing information. Second, the lack of broader comparative studies often makes the primary homology statements that are expressed by the characters rather dubious. In contrast to this, the *mat*K and *trn*L sequences used by Struwe *et al.* (2002) and Thiv *et al.* (1999a) are both complete and easy to align, leading to higher information content and better hypotheses of primary homology. For these reasons, it could a priori be expected that the molecular data sets would give more and better-supported resolution, and this is precisely what is observed. An obvious way to proceed would be to increase research on poorly known characters (e.g., seed micromorphology and seed anatomy) and poorly known taxa, which often have ambiguous positions on different cladograms. At the same time, ontogenetic studies of flowers and inflorescences could help to detect pseudoconvergences (Kluge & Farris, 1969) in the floral region (see De Laet & Smets, 1996).

However, an additional problem for phylogenetic analysis of morphological data sets is posed by functional correlations among morphological traits. Given that only a limited number of morphological traits is available, this may well turn out to be a fundamental problem that is very difficult to overcome. In this particular case the heterotrophic genera provide a good example. As discussed above, they possess what we call the heterotrophic syndrome: co-occurrence of saprophytic or parasitic lifestyle, coralloid roots, reduced leaves, and loss of chlorophyll. It can be argued that within this syndrome the crucial characteristic is the capacity for a saprophytic or

parasitic lifestyle; once this capacity has evolved, the coralloid roots, the reduced leaves, and the loss of chlorophyll may be simple adaptations to this new mode of living. Coding all characteristics of the syndrome as separate independent characters may then potentially lead to grouping according to correlated convergence rather than according to common descent. The same effect may explain the above-discussed discrepancy between morphological and molecular analyses when it comes to evolution of woodiness in Gentianaceae. All the outgroups in our analysis are trees or shrubs, which may then force the woody (sub)tribes Potalieae, *Saccifolium*, and Helieae to the base of the family.

ACKNOWLEDGMENTS

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Appendix 3.1

Data matrices

Numbers of characters and character states refer to Table 3.3. Polymorphisms are shown in square brackets; "?" indicates missing values and inapplicable characters.

Character numbers:

1	2	3	4	5	6	7	8	9	10	11
12	13	14	15	16	17	18	19	20	21	22
23	24	25	26	27	28	29	30	31	32	33
34	35	36	37	38	39	40	41	42	43	44
45	46	47	48	49	50	51	52	53	54	55
56	57	58	59	60	61	62	63	64	65	66
67	68	69	70	71	72	73	74	75	76	77
78	79	80	81	82	83	84				

Outgroups:

Danais

0	0	?	?	0	?	0	1	0	1	?
0	0	1	?	0	1	?	0	[01]	1	?
0	?	0	?	0	?	?	0	1	2	?
?	2	0	?	0	0	0	0	0	0	?
?	0	2	1	0	?	?	2	?	1	0
1	0	?	?	?	?	?	1	1	[01]	0
?	0	0	1	?	[01]	?	?	?	?	?
0	?	?	?	?	?	?				

Exostema

0	0	0	?	1	?	0	0	0	1	?
0	0	1	0	0	[01]	1	[123]	[01]	[12]	0
?	?	0	?	0	?	?	1	[012]	[12]	1
?	2	0	?	0	0	0	0	0	0	1
?	0	0	1	0	?	?	0	?	[01]	0
?	?	?	?	?	?	?	[01]	[01]	?	?
1	0	0	1	1	1	0	?	?	?	?
0	?	?	?	?	?	?				

Gelsemium

0	0	0	0	0	0	?	[01]	0	1	?
0	0	0	0	0	1	?	[12]	0	1	0
0	0	0	1	0	?	?	1	1	[12]	2
?	2	1	0	0	0	0	0	0	0	0
?	0	0	0	0	1	0	4	?	0	0
?	?	?	?	?	?	?	2	[01]	?	?
3	0	0	1	1	0	0	?	0	3	?
0	?	?	?	?	?	?				

Geniostoma

0	0	0	0	0	0	0	0	1	[01]	1
0	0	0	0	0	0	?	0	0	1	0
1	0	0	0	0	?	?	[12]	1	[03]	1
0	2	2	0	0	0	0	0	0	0	0
?	0	1	0	0	[01]	0	1	?	0	0
0	0	?	?	?	?	?	0	0	?	?
2	0	0	2	2	0	1	?	?	?	?
0	?	?	?	?	?	?				

Plumeria

0	0	0	0	[01]	?	0	0	0	1	0
1	0	0	0	0	1	?	?	[01]	1	[01]
0	0	0	0	0	?	?	2	1	1	1
?	0	0	?	0	?	0	0	0	0	0
?	0	0	0	1	0	0	2	?	0	0
0	?	?	?	?	0	?	?	1	?	?
?	0	0	1	2	0	1	?	?	3	0
0	?	?	?	?	?	?				

Rauwolfia

0	0	[012]	?	0	?	0	0	0	[01]	?
1	0	0	0	0	1	?	0	0	1	0
[012]	0	0	1	0	0	?	2	1	[123]	[12]
?	2	[02]	0	0	?	0	0	0	0	0
0	0	2	0	1	[01]	0	1	0	?	2
0	0	0	1	0	0	0	?	0	?	?
?	0	0	1	2	0	[02]	?	?	3	0
0	?	?	?	?	?	?				

Strychnos

0	0	0	[01]	0	?	?	[01]	1	1	[01]
0	0	0	[01]	1	1	[01]	0	0	[12]	0
0	0	0	0	0	?	?	0	[12]	[012]	[012]
?	[02]	[02]	0	0	0	0	0	0	0	0
?	0	[12]	0	0	[01]	0	0	?	?	1
0	0	0	?	?	0	?	[12]	0	?	1
3	0	0	1	2	0	[012]	?	0	3	0
0	?	?	?	?	?	?				

Ingroups:

Anthocleista

0	0	0	0	1	1	0	0	1	1	1
0	1	0	0	0	0	?	0	[01]	2	0
0	0	0	0	0	?	?	2	0	1	2
0	?	1	0	0	0	0	0	0	0	1
0	0	2	0	0	1	0	1	?	2	1
?	?	?	?	?	?	?	[02]	[01]	0	?
?	0	0	2	2	0	2	1	?	1	?
2	0	0	0	[01]	[01]	1				

Bartonia

[01]	2	[012]	?	2	?	0	[01]	?	?	?
0	0	0	?	1	?	?	[03]	[01]	2	0
0	[01]	0	?	0	0	0	1	2	3	1
0	0	[02]	0	1	0	[01]	0	0	0	0
?	0	2	0	0	1	[01]	3	0	0	0
?	?	?	?	?	?	?	2	0	[01]	0
?	?	0	1	[12]	0	1	?	?	?	?
?	?	?	?	?	?	?				

Blackstonia

0	2	0	1	2	?	0	0	?	1	?
0	0	0	1	1	?	1	1	0	0	0
0	0	0	?	0	?	0	2	0	0	0
0	0	0	0	0	0	[01]	0	0	0	0
0	0	2	0	0	1	0	2	?	0	0
?	0	0	1	?	0	?	2	0	[01]	0
[23]	0	0	1	1	0	[12]	1	0	2	0
2	0	0	0	0	1	1				

Canscora

0	2	[12]	?	?	?	0	0	?	?	?
0	0	0	1	1	0	1	0	[01]	2	0
2	[02]	0	0	0	0	1	2	2	[12]	1
0	0	0	0	0	0	[01]	0	1	0	0
0	0	2	0	0	1	0	2	0	0	0
0	0	0	0	0	0	0	[01]	0	[01]	0
?	0	0	1	1	0	[12]	?	0	?	[23]
[12]	0	0	1	1	1	1				

Celiantha

0	1	[01]	?	?	?	0	0	?	?	?
0	0	0	1	?	?	?	[02]	[01]	[12]	0
2	0	0	1	0	?	?	2	[12]	2	2
0	?	0	0	0	0	0	0	0	0	0
0	0	1	0	0	1	0	2	?	0	0
?	?	?	?	?	?	?	0	0	[01]	0
?	0	2	2	[13]	1	?	?	?	?	?
?	?	?	?	?	?	?				

Centaurium

0	[12]	[012]	1	2	0	0	0	[01]	1	?
0	0	0	1	1	[01]	1	0	[01]	[12]	0
[01]	1	0	0	0	0	[01]	2	1	[12]	1
0	0	0	1	0	0	1	0	0	0	0
0	0	2	0	0	2	0	2	0	0	0
0	0	0	1	0	0	0	[12]	0	[01]	1
[12]	0	0	1	1	0	[012]	1	0	2	0
[02]	[01]	0	[01]	[01]	[01]	[01]				

Chironia

0	[012]	[12]	1	1	?	0	0	?	[01]	?
0	0	0	?	0	0	?	1	1	1	0
[01]	[01]	0	1	0	0	0	2	1	[03]	0
0	0	0	1	0	0	1	0	0	0	0
0	0	2	0	0	0	0	[012]	0	0	[01]
?	?	?	?	?	?	?	[12]	0	0	0
[21]	0	0	1	1	0	2	1	0	2	?
2	0	0	1	1	1	1				

Chorisepalum

0	0	1	?	?	?	?	0	?	?	?
0	0	0	[01]	?	?	?	[03]	[01]	2	1
0	[12]	0	0	1	?	?	2	0	[01]	2
0	2	0	0	0	0	0	0	0	0	0
0	0	0	0	0	2	0	2	?	[01]	0
?	?	?	?	?	?	?	?	0	0	0
3	0	0	1	1	0	?	?	?	?	?
?	?	?	?	?	?	?				

Cotylanthera

1	2	1	?	?	?	0	0	?	?	?
0	0	0	?	?	?	?	3	0	2	0
1	1	0	?	0	0	0	2	2	0	0
0	0	[01]	1	0	1	0	0	0	0	0
1	0	0	0	0	1	0	1	1	0	0
[02]	1	0	0	0	0	0	3	0	1	0
?	0	0	1	[12]	0	1	?	?	?	?
?	?	?	?	?	?	?				

Coutoubea

0	[12]	[01]	?	1	?	[01]	0	?	[01]	?
0	0	0	1	0	?	0	2	0	[01]	0
0	[01]	0	1	0	2	1	2	[01]	1	1
0	[02]	1	0	?	0	0	0	0	0	1
0	0	1	0	0	1	0	2	[12]	0	0
?	?	?	?	?	?	?	[01]	0	[01]	0
3	0	1	[12]	1	0	1	?	0	2	0
?	?	?	?	?	?	?				

Crawfurdia

0	1	0	1	?	?	0	1	?	?	?
0	0	0	1	?	?	1	[23]	[01]	1	0
2	0	1	?	0	0	0	3	1	2	2
?	2	?	0	?	0	0	0	0	0	0
0	0	1	0	0	2	1	2	0	0	0
?	?	?	?	?	?	?	[12]	1	?	?
?	0	0	1	1	0	?	?	?	?	?
?	?	?	?	?	?	?				

Curtia

?	2	1	?	?	?	0	0	?	?	?
0	0	0	1	0	?	1	0	[01]	[12]	0
0	1	0	1	0	?	0	2	[12]	[12]	2
0	?	[12]	0	0	0	0	0	0	0	0
0	1	1	0	0	1	0	1	?	0	0
?	?	?	?	?	?	?	[023]	0	[01]	[01]
0	?	0	1	[12]	[01]	?	0	?	2	?
?	?	?	?	?	?	?				

Deianira

0	1	0	?	1	?	0	0	?	?	?
0	0	0	[01]	0	[023]	1	2	1	2	0
[01]	[01]	0	?	0	2	0	2	2	1	1
0	2	0	1	0	1	0	0	0	0	0
?	0	2	0	0	1	0	2	[12]	0	0
?	?	?	?	?	?	?	[03]	0	0	0
?	0	1	[01]	1	0	0	?	?	?	?
?	?	?	?	?	?	?				

Enicostema

0	1	[012]	?	1	?	0	0	?	?	?
0	0	0	1	0	?	1	2	[01]	1	0
0	1	0	0	0	?	1	2	1	2	1
0	?	0	0	0	0	0	0	0	0	1
0	0	1	0	0	1	0	1	0	0	0
?	?	0	?	?	?	?	[12]	0	0	0
3	0	0	1	1	0	1	1	?	1	[12]
2	?	?	?	?	?	?				

Eustoma

0	[12]	?	?	?	?	0	0	?	?	?
0	0	0	1	0	?	1	1	[01]	1	0
0	1	0	?	0	0	0	2	1	3	0
0	0	0	1	1	0	1	0	0	0	0
0	0	2	0	0	1	0	1	0	0	0
0	0	0	?	?	0	?	1	0	0	0
[23]	0	0	1	1	0	2	?	0	2	0
2	0	0	1	1	1	1				

Exacum

0	[012]	[012]	1	2	?	0	0	?	1	?
0	0	0	1	1	[012]	1	0	[01]	[12]	0
[01]	2	0	0	0	2	0	2	[12]	0	0
0	0	[02]	1	0	1	0	0	0	0	[01]
1	0	2	0	0	0	0	[02]	1	0	0
0	0	0	[01]	0	0	0	0	0	0	[01]
?	0	0	1	[12]	0	[012]	0	?	2	1
0	?	?	?	?	?	?				

Fagraea

0	0	0	0	1	1	0	0	1	1	[01]
0	1	0	0	0	?	?	0	0	1	0
[12]	0	0	0	0	?	?	2	1	[12]	1
0	2	[01]	0	0	0	0	0	0	0	0
0	0	[01]	0	0	1	0	[12]	?	[12]	1
0	0	0	1	?	0	?	[023]	0	0	[01]
[23]	0	0	[12]	1	0	[02]	?	?	2	2
?	?	?	?	?	?	?				

Faroa

0	2	[012]	?	?	?	0	0	?	?	?
0	0	0	1	1	0	1	2	[01]	2	0
1	1	0	?	0	?	1	2	2	1	1
0	?	[12]	0	0	0	0	0	0	0	1
0	0	2	0	0	1	0	[012]	2	0	0
?	?	?	?	?	?	?	1	0	0	[01]
?	0	0	1	[12]	0	?	1	?	?	?
?	?	?	?	?	?	?				

Gentiana sect. *Calathianae*

0	[12]	1	?	2	0	1	0	?	?	?
0	0	0	1	[01]	1	0	3	[01]	1	0
2	[12]	1	?	0	0	0	3	1	1	1
0	2	0	0	0	0	0	0	0	0	0
0	0	0	0	0	2	1	2	0	0	0
?	?	?	0	?	?	?	3	0	1	0
3	0	0	1	1	0	[01]	1	1	2	2
[12]	0	0	0	0	1	1				

Gentiana sect. *Ciminalis*

0	1	1	?	2	0	1	0	?	?	?
0	0	0	1	?	1	1	3	1	1	0
1	0	1	?	0	0	0	3	1	2	2
1	2	0	0	0	0	0	1	0	0	0
0	0	0	0	0	2	1	2	0	0	0
?	?	?	?	?	?	?	3	0	1	0
?	0	0	1	1	0	1	1	1	2	2
2	0	0	0	0	1	1				

Gentiana sect. *Frigidae*

0	1	?	?	?	?	[01]	[01]	?	?	?
0	0	0	1	1	1	1	[23]	[01]	1	0
2	[02]	1	?	0	0	0	3	1	[23]	2
0	2	[02]	0	0	0	0	[01]	0	0	0
0	0	1	0	0	2	1	2	0	0	0
?	?	?	?	?	?	?	[23]	0	[01]	0
3	0	0	1	1	0	0	?	1	2	2
2	0	1	1	0	0	1				

Gentiana sect. *Gentiana*

0	1	2	1	2	1	0	0	?	1	0
0	0	0	1	1	0	1	2	[01]	1	[01]
2	0	1	?	0	0	0	3	1	[03]	2
1	2	0	0	0	0	0	[01]	0	0	0
0	0	0	0	0	1	1	2	0	0	0
0	0	0	0	1	0	1	2	1	[01]	0
[03]	0	0	1	1	0	1	1	1	2	[12]
[12]	[01]	0	0	0	1	0				

Gentiana sect. *Otophora*

0	1	1	?	?	?	0	0	?	?	?
0	0	0	1	0	?	1	[23]	[01]	1	0
1	0	1	?	0	0	0	3	1	0	[01]
0	2	0	0	1	0	0	0	0	0	0
0	0	[01]	0	0	2	1	2	0	0	0
?	?	?	?	?	?	?	2	1	?	?
?	0	0	1	1	0	?	?	?	?	?
?	?	?	?	?	?	?				

Gentiana sect. *Stenogyne*

0	1	1	?	?	?	0	0	?	?	?
0	0	0	1	?	?	1	3	[01]	1	0
[12]	[12]	1	?	0	0	0	3	1	2	2
?	2	0	0	?	0	0	0	0	0	0
0	0	[12]	0	0	2	1	2	0	0	0
?	?	?	?	?	?	?	[12]	[01]	0	0
?	0	0	1	1	0	1	?	?	2	?
?	?	?	?	?	?	?				

Gentianella

0	[12]	[012]	?	1	?	0	0	?	?	?
0	0	0	1	[01]	1	0	0	[01]	[12]	1
1	0	0	0	0	0	0	2	1	[02]	1
[01]	1	[12]	0	1	0	0	0	0	0	0
0	0	[012]	0	0	2	1	2	2	0	0
1	0	1	1	1	0	1	[12]	0	0	0
0	0	0	1	1	0	1	1	0	[02]	2
[12]	0	[01]	1	0	[01]	1				

Gentianopsis

0	[12]	?	0	?	?	0	0	?	?	?
0	0	0	1	1	1	0	1	1	2	1
1	[12]	1	0	0	2	0	2	2	2	1
0	1	1	0	1	0	0	0	0	0	0
0	0	1	0	0	2	1	2	1	0	0
0	0	0	1	1	0	1	[23]	0	0	0
?	0	0	[01]	1	0	[012]	?	0	2	[12]
[12]	0	0	0	0	1	1				

Halenia

0	[12]	1	?	?	?	0	0	?	1	?
0	0	0	1	0	?	[01]	1	[01]	2	0
0	0	0	0	0	0	0	2	2	3	0
0	1	[12]	0	1	0	0	0	0	0	0
0	0	[01]	0	0	[12]	0	2	0	0	0
2	0	0	1	1	0	1	[12]	0	0	0
0	0	0	1	1	0	0	1	[01]	?	1
2	1	1	1	0	1	0				

Hoppea

0	2	2	?	?	?	0	0	?	?	?
0	0	0	1	?	0	?	0	0	2	0
1	0	0	?	0	1	1	2	2	1	2
0	?	2	0	0	0	0	0	2	0	0
0	0	2	0	0	0	0	1	2	0	0
0	0	0	1	0	0	0	[01]	0	[01]	0
?	0	0	1	1	0	[01]	?	0	?	[23]
[12]	0	0	1	1	1	0				

Irlbachia

0	2	[012]	?	?	?	0	0	?	?	?
0	0	0	1	?	?	?	1	[01]	1	0
1	[01]	0	[10]	1	?	?	2	1	[123]	[12]
0	2	[01]	0	0	0	0	0	0	0	0
?	0	[01]	0	0	1	0	2	?	0	0
?	?	?	?	?	?	?	[01]	0	0	[01]
1	0	2	2	[12]	1	?	?	?	?	?
?	?	?	?	?	?	?				

Ixanthus

0	1	1	1	1	?	0	0	1	1	1
0	0	0	1	1	?	1	0	0	[12]	0
1	1	0	0	0	?	?	2	[12]	1	1
0	2	0	0	0	0	0	0	0	0	0
0	0	2	0	0	1	0	1	?	0	0
?	?	?	?	?	?	?	[12]	0	0	0
?	0	0	1	1	0	?	?	0	2	?
2	1	0	0	1	0	1				

Lisianthius

0	[012]	[01]	?	1	?	?	0	?	[01]	?
0	0	0	1	0	?	1	0	[01]	1	0
[01]	[012]	0	1	0	2	[01]	2	1	[12]	2
0	2	1	0	1	0	0	0	0	0	0
0	0	[012]	0	0	2	0	1	?	1	0
?	?	?	?	?	?	?	0	0	0	0
2	0	0	1	1	0	1	1	0	0	?
0	?	?	?	?	?	?				

Lomatogonium

0	[12]	[01]	?	?	?	0	0	?	?	?
0	0	0	1	0	?	0	[13]	[01]	[12]	0
0	0	0	?	0	?	0	2	[12]	0	0
0	1	2	0	?	0	0	0	0	0	0
0	0	0	0	0	1	0	3	?	0	0
?	0	?	?	?	?	?	[12]	0	0	0
?	0	0	1	1	[01]	0	[01]	[01]	1	[12]
2	0	0	1	0	1	1				

Macrocarpaea

0	[01]	[01]	?	1	?	0	0	?	?	?
0	0	0	[01]	0	?	1	0	[01]	1	0
[01]	0	0	[01]	1	0	0	2	1	[123]	2
0	2	0	0	0	0	0	0	0	0	0
0	0	1	0	0	1	0	2	?	0	0
?	?	?	?	?	?	?	[02]	0	[01]	0
3	0	0	1	1	[01]	1	1	?	?	?
2	1	0	0	1	1	1				

Obolaria

[01]	1	1	?	2	?	0	0	?	?	?
0	0	0	?	1	0	?	[023]	[01]	3	0
?	0	0	0	0	?	0	1	[12]	3	1
0	1	2	0	[01]	0	0	0	[01]	0	0
?	0	2	0	0	1	0	2	0	3	0
[02]	[01]	?	?	?	?	?	2	0	1	0
?	?	0	1	1	0	1	?	?	?	?
?	?	?	?	?	?	?				

Orphium

0	0	?	1	1	0	?	0	?	[01]	?
0	0	0	?	0	?	?	1	1	1	0
0	0	0	0	0	?	?	2	1	?	0
0	?	0	1	0	0	1	0	0	0	0
0	0	2	0	0	1	0	1	0	0	0
?	0	?	?	?	?	?	[12]	0	0	0
[21]	0	0	1	1	0	?	1	?	?	?
2	0	0	0	0	1	1				

Sabatia

0	[12]	[01]	?	?	?	[01]	0	?	?	?
0	0	0	1	1	?	1	0	[01]	[01]	0
0	0	0	?	0	?	0	2	[01]	0	0
0	0	0	1	0	0	1	0	0	0	0
0	0	2	0	0	1	0	2	?	0	0
?	?	?	?	?	?	?	1	0	0	0
[12]	0	0	1	[12]	0	[012]	1	?	2	?
?	?	?	?	?	?	?				

Saccifolium

0	0	0	0	2	?	0	0	1	0	?
0	0	0	1	0	2	0	3	0	1	0
0	0	0	1	0	0	?	1	1	?	2
0	0	1	0	0	0	0	0	0	0	0
?	?	1	0	0	0	0	1	?	?	0
0	0	?	?	?	?	?	0	0	0	0
?	?	0	1	2	0	?	?	?	?	?
?	?	?	?	?	?	?				

Schultesia–Xestaea

0	2	[01]	1	2	?	0	0	?	?	?
0	0	0	1	0	?	1	[03]	[01]	2	0
[012]	[12]	0	[10]	0	2	0	2	2	2	2
0	[02]	[01]	0	0	0	0	0	0	0	1
0	0	[01]	0	0	1	0	2	0	0	0
?	?	?	?	?	?	?	[01]	0	0	0
3	0	1	2	1	0	?	1	0	?	?
2	1	1	1	1	1	1				

Sebaea

0	[12]	[12]	?	?	?	0	0	?	?	?
0	0	0	?	1	0	1	[013]	[01]	[012]	0
0	[12]	0	0	0	0	0	2	[012]	[12]	[12]
0	?	[01]	0	0	0	0	0	0	1	0
0	0	[12]	0	0	[01]	0	[012]	[01]	0	0
?	0	?	?	?	?	?	2	0	[01]	0
4	0	0	1	1	0	0	0	?	?	?
?	?	?	?	?	?	?				

Swertia–Frasera

0	[12]	[012]	1	2	0	0	0	[01]	?	?
0	0	0	1	[01]	0	[01]	0	[01]	[012]	[01]
[01]	0	0	0	0	0	0	2	[012]	0	0
[01]	1	[012]	0	1	0	0	0	0	0	[01]
0	0	0	0	0	[01]	0	2	0	0	0
[03]	0	[01]	1	1	0	1	[12]	[01]	0	[01]
?	0	0	1	1	[01]	[012]	1	1	2	[012]
[12]	[01]	[01]	[01]	0	[01]	[01]				

Symbolanthus

0	0	[12]	0	0	?	?	0	1	1	1
0	0	0	[01]	?	?	?	[23]	[01]	1	0
0	[01]	0	0	1	?	?	2	1	2	2
0	2	[01]	0	0	0	0	0	0	0	1
0	0	0	0	0	1	0	2	?	0	[01]
?	?	?	?	?	?	?	0	0	?	?
?	0	1	1	1	0	2	1	?	?	?
?	?	?	?	?	?	?				

Tachia

0	1	[01]	?	?	?	0	0	?	?	?
0	0	0	[01]	?	?	?	3	0	1	0
[01]	[012]	0	0	1	?	?	2	1	2	2
0	2	[01]	0	0	0	0	0	0	0	0
0	0	0	0	0	1	0	2	?	0	0
?	?	?	?	?	?	?	[01]	0	0	0
1	0	0	1	[12]	1	?	1	?	[12]	?
?	?	?	?	?	?	?				

Tachiadenus

0	[012]	[012]	?	1	?	0	0	?	1	?
0	0	0	1	?	2	?	[01]	[01]	1	0
[01]	[02]	0	0	0	?	?	2	1	1	2
0	?	0	0	0	0	0	1	0	1	0
0	0	2	0	0	1	0	1	?	0	0
?	?	?	?	?	?	?	[01]	0	0	1
?	0	0	1	[12]	0	?	?	?	[12]	?
?	?	?	?	?	?	?				

Tripterospermum

0	1	0	1	?	?	0	1	?	?	?
0	0	0	1	0	?	1	[23]	[01]	1	0
1	[01]	?	?	0	0	?	3	1	[23]	2
?	2	?	0	?	0	0	0	0	0	0
0	0	[01]	0	0	2	1	2	0	0	[01]
?	?	?	?	?	?	?	[2]	1	[01]	0
?	0	0	1	[12]	0	1	?	0	?	?
[12]	[01]	[01]	[01]	1	1	[01]				

Voyria

1	1	0	?	?	?	0	0	?	?	?
0	0	0	?	?	0	?	[03]	[01]	1	0
[12]	0	0	[10]	0	?	?	2	1	[12]	2
0	?	[01]	0	0	0	0	[01]	0	0	0
0	0	[12]	0	0	[12]	[01]	1	?	[02]	0
[02]	[01]	0	0	0	[01]	1	[23]	0	[01]	[01]
2	1	0	2	0	0	1	?	?	?	?
?	?	?	?	?	?	?				

Voyriella

1	[12]	1	?	?	?	0	0	?	?	?
0	0	0	?	?	0	?	[02]	0	1	0
0	0	0	0	0	?	?	2	1	2	2
0	0	1	0	0	0	0	1	0	0	0
0	1	[02]	0	0	1	0	1	?	2	0
2	0	0	0	0	1	0	1	0	0	0
1	1	0	1	1	0	0	?	?	?	?
?	?	?	?	?	?	?				

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