

Chapter 2

Classification and Evolution of the Family Gentianaceae

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Abstract This chapter reviews research progress and resulting changes in classification in the Gentian family since the worldwide revision in 2002. Currently, the Gentianaceae includes 99 genera and approximately 1,736 species. The tribal classification still stands, but there have been some important changes of genus delimitations based on new evolutionary work. This includes reclassifications of poly- or paraphyletic genera (e.g., *Canscora*, *Centaurium*, *Fagraea*, *Sebaea*) that have led to the description of new or resurrected genera such as *Cyrtophyllum*, *Duplipetala*, *Exochaenium*, *Gyrandra*, *Lagenias*, *Limahlania*, *Klackenbergia*, *Phyllocyclus*, *Picrophloeus*, *Schenkia*, *Utania*, and *Zeltnera*. New genera have been discovered in South America, including *Roraimaea* and *Yanomamua*. Some genera were incorporated into others to preserve monophyly (*Cotylanthera* into *Exacum*, *Wurdackanthus* into *Symbolanthus*). *Bisgoeppertia* has been moved to the Potalieae. Unsolved generic delimitation problems remain in Gentianeae-Swertiinae and Helieae. The placement of the enigmatic mycoheterotroph *Voyria* is still uncertain, but it is likely an isolated, basally placed branch in the family. Recent biogeographic studies that address large-scale distribution patterns, vicariance events, and the significance of these new results are reviewed in this chapter, as are examples of evolutionary research progress within each tribe.

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2.1 Introduction

By the early 1990s, almost no phylogenetic family-level work had been done on gentians, which changed very quickly with the development of PCR, and rapid and efficient DNA sequencing, paired with computational advantages in speed, algorithms, and computer hardware. This revolution in evolutionary research occurred throughout all kingdoms, and for many plant families we had the first preliminary family-level phylogenies constructed by the late 1990s, gentians included. International collaborations sped up the process and, for the gentians, the primary laboratories involved in this early cladistic work were those of Joachim Kadereit and his students in Germany (Bernhard von Hagen, Mike Thiv), Philippe Küpfer's research group in Switzerland (Philippe Chassot, Jason Grant, Guilhem Mansion, Yong-Ming Yuan), and the work at The New York Botanical Garden in USA by myself and Victor Albert with Katherine (Gould) Mathews, Jason Grant, and other visiting gentian researchers.

About a decade ago, the book *Gentianaceae: Natural History and Systematics* was published (Struwe and Albert 2002). It was the first comprehensive volume on gentian systematics ever published in English, as well as the first detailed book in any language on this taxonomic topic since Grisebach's treatment in Latin about 150 years earlier (Grisebach 1839). There were 17 contributors to the book, and the main 290-page chapter was a new, multi-authored family-level classification and description of the Gentianaceae genera based on monophyly and new phylogenetic data (Struwe et al. 2002). Before then, Gilg's (1895) tribal and subtribal gentian classification was used mostly in taxonomy. The book also included important chapters, for example, on gentian pollen by palynologist Siwert Nilsson (who sadly passed away shortly after the book was published), seed anatomy and morphology, morphological cladistics, and phytochemistry (Bouman et al. 2002; Jensen and Shripsema 2002; Mészáros et al. 2002; Nilsson 2002).

This chapter outlines progress since the last book was published in 2002, so it primarily reviews and discusses papers published during 2001–2012. The number of scientists focusing their efforts on this not just beautiful, but incredibly exciting and interesting family, has increased steadily over the last decade and great strides have been made in understanding the evolution of the family both when it comes to phylogenetic and biogeographic relationships and changes in morphological, anatomical, and chemical diversity (the latter will be addressed in other chapters). In general, the tribal classification has held up, with only some changes for a few genera that earlier were placed tentatively based on non-DNA data, or necessary reclassifications of genera. There are still some taxonomic areas that need attention and a changed classification, and this will be discussed here at the end of this chapter.

2.2 Large-Scale Classification, Species Number Estimates, and Phylogenetic Progress

Based on molecular systematics research starting in the mid-1990s, the Gentianaceae is now known to have seven major monophyletic clades, corresponding to six tribes in the current classification, namely the Saccifolieae, Exaceae, Chironieae, Gentianeae, Helieae, and Potalieae (Fig. 2.1). The mycotrophic genus *Voyria* was placed as *incertae sedis* in 2002 and in this classification, but recent data indicates that it should be recognized as its own tribe (Merckx, “personal communication”). Three of the tribes have monophyletic subtribes. Chironieae includes the three subtribes Chironieae (mostly temperate or subtropical, cosmopolitan), Coutoubieinae (neotropical), and Canscorinae (paleotropical). Cosmopolitan and mostly temperate Gentianeae are divided into two subtribes, Swertiinae and Gentianinae. The tribe Potalieae has three subtribes, namely Faroinae (mostly tropical Africa), Lisianthiinae (neotropical), and Potaliinae (pantropical). Of the remaining tribes, Saccifolieae and Helieae are strictly neotropical, while Exaceae is strictly paleotropical. The mycoheterotrophic genus *Voyria* forms an early branch in the family, and might be classified soon as its own tribe (see discussion below).

The phylogenetic study that was the basis for the classification of Struwe et al. (2002) was published in the same book chapter as the classification. Since then no overarching family-level study has been published, but many tribal level phylogenies have been added and expanded our knowledge on relationships within tribes and subtribes. Major trends and results from these studies are discussed here, and new data are also reviewed under each tribe below.

The most basally positioned clade in the Gentianaceae is the tribe Saccifolieae (Fig. 2.1), which represents the first diverging lineage in the family and is also taxonomically the smallest one with only 5 genera and 18 species. All are restricted to continental South America (mostly on the Guayana and Brazilian Shields; Table 2.1). The next diverging clade in the phylogeny is the tribe Exaceae, with 184 (mostly) herbaceous species from Africa, Madagascar, and Southern Asia in 8 genera. Diverging above the Exaceae is the clade containing the tribe Chironieae, a morphologically variable group with 26 genera containing about 161 mostly herbaceous species.

Sister to the Chironieae in the family phylogeny is a large clade with the three most species-rich tribes; the Gentianeae (974 species; 56 % of species in the family), Helieae (218 species), and Potalieae (163 species; see Table 2.1 for statistics). These three tribes form a trichotomy in most phylogenetic studies (or Gentianeae is placed as the more basally positioned clade but with very low branch support; Struwe et al. 2002). Additional sequencing has not clarified these relationships further, despite the use of additional markers (Molina and Struwe, “unpublished”), so it is possible that the divergence of these three clades happened relatively suddenly, or that major lineages at the base of each clade might have become extinct and thereby have limited our possibilities to reconstruct the actual order of diversification events at that point in time.

Fig. 2.1 Overview of the major clades of the Gentianaceae. Each tribe and subtribe is supported as monophyletic by having substantial branch support in several phylogenetic analyses. The position of *Voyria* is uncertain, and it might form its own branch (and tribe) close to the base of the Gentianeae

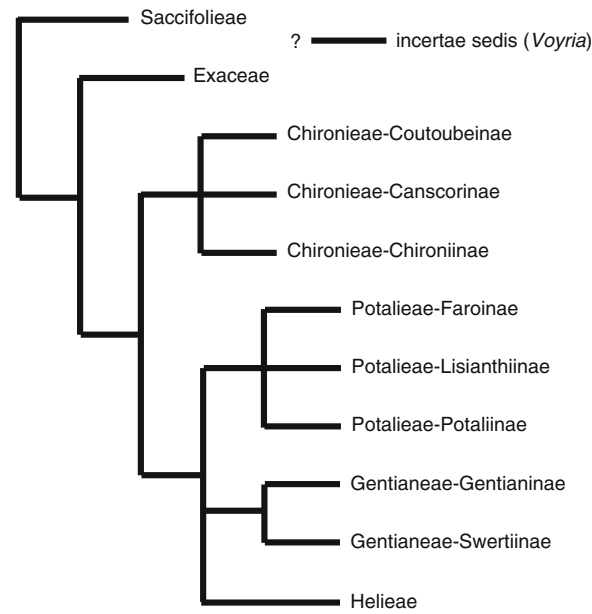


Table 2.1 Number and percentages of genera and species within each tribe (and *Voyria*) as part of the total in the Gentianaceae

	Number of species	% of species	Number of genera	% of genera
Saccifolieae	18	1	5	5
Exaceae	184	11	8	8
<i>Voyria</i>	18	1	1	1
Chironieae	161	9	26	26
Gentianeae	974	56	18	18
Potalieae	163	9	18	18
Helieae	218	13	23	23
Total Gentianaceae	1,736		99	

This pattern of more species in the relatively more recently diverged clades is not unusual, and can also be seen in clades such as the milkweeds (Apocynaceae-Asclepiadoideae). Some of the more species-rich genera most likely reflect relatively recent speciation influenced by mountain orogenies, island formation, and/or habitat fragmentation due to climate change, sea level changes, or tectonics (*Symbolanthus* and *Macrocarpaea* in the Andes; *Gentiana*, *Gentianella*, and *Swertia* in several mountain areas worldwide; *Fagraea* in Southeast Asia. Many of these diversification and biogeographic hypotheses still remain to be tested for gentians.

There are large discrepancies in the number of estimated species in many genera of the Gentianeae with, for example, *Gentianella* being estimated to have 150–275 species by current gentian researchers. *Gentiana* (with its estimated 360 species) most likely includes many Chinese species that are synonymous with

other Asian or European species. The lack of global revisions of these large, nearly cosmopolitan, genera hinders a full taxonomic and evolutionary understanding of these groups. Another example that has been resolved is *Halenia*, which was estimated to have 80–100 species, but only has 39 species recognized in its first global revision (Bernhard von Hagen, “personal communication”). In contrast to *Halenia*, estimates of species numbers in other genera have increased after new revisions, such as *Fagraea*, *Macrocarpaea*, and *Symbolanthus*, highlighting the historical tendency of lumping species together in these groups. In this discussion, estimates have been made of species numbers based on most recent information from current researchers. The synonymization of species within some genera has led to the fact that the estimated numbers of species in the family has been relatively stagnant, despite the discovery of new species. Such additions have been outweighed by recent revisions that resolved taxonomic inflation and included not just one country, but the total distribution.

2.3 New Generic Placements and Additions in the Classification

In general, the classification from 2002 has held up well, and the only required only changes needed are (1) para- or polyphyletic genera that have been divided into monophyletic units, (2) a few genera classified based on morphology that since have been sequenced and changed placement on their DNA-based result, and (3) two newly described genera for newly discovered taxa. The updated generic classification is outlined in Table 2.2. These are the generic taxonomic changes since the 2002 classification (see highlights below for discussion):

- The paraphyletic genus *Sebaea* (Exaceae) has been reclassified into four monophyletic genera, namely *Exochaenium*, *Klackenbergia*, *Lagenias* and *Sebaea* sensu stricto. *Klackenbergia* is a newly described genus.
- *Cotylanthera* (Exaceae) has been included in *Exacum*.
- *Centaurium* sensu lato (Chironieae-Chironiinae) was a paraphyletic clade and was therefore split into the four monophyletic genera *Centaurium* sensu stricto, *Gyrandra*, *Schenkia*, and *Zeltnera*. Of these, *Zeltnera* is a newly described genus.
- The genus *Duplipetala* was described as a segregate of the paraphyletic *Canscora* sensu lato in Chironieae-Canscoriinae, and *Canscora* sensu stricto is still accepted.
- The genus *Metagentiana* (Gentianeae-Gentianiinae) was described as a segregate from the largest genus in the family, *Gentiana*, but turned out to be polyphyletic.
- *Wurdackanthus* (Helieae) was included in *Symbolanthus*, since it formed a paraphyletic grade toward *Symbolanthus*.
- The genus *Roraimaea* (Helieae) was described from northern South America.

- The monotypic genus *Yanomamua* (Helieae) was described from Brazil.
- The genus *Bisgoeppertia* was moved from Chironieae-Chironiinae to Potalieae-Lisianthiinae based on new molecular data.
- The genus *Fagraea* sensu lato (Potalieae-Potaliinae) is now described as five distinct genera, i.e., *Fagraea* sensu stricto, *Cyrtophyllum*, *Limahlania*, *Picrophloeus* and *Utania* based on molecular and morphological data. *Limahlania* is a newly described monotypic genus.
- The genus *Voyria* forms an independent clade placed basally in the family, and will eventually be classified as a seventh tribe.

2.4 New Biogeographic and Age Findings

Tribes and subtribes of gentians are mostly restricted to the Neotropics or Palearctics or temperate areas worldwide, except for a few late dispersals into new territories. This pattern is even more obvious at the generic level, with very few genera present on more than one continent (Table 2.2). The center of diversity for the Gentianaceae can be measured in several ways. Species diversity reaches its maximum in East Asia, with Gentianaceae in the *Flora of China* listing 20 genera and more than 400 species just within China's borders (Ho and Pringle 1995), leading China to be probably the most species-rich country in the world with regards to gentians. However, nearly all of these species are in the tribe Gentianeae, and 248 of them are in the genus *Gentiana* (Ho and Pringle 1995).

In contrast to species diversity, the greatest evolutionary diversity occurs in South America, which is home to 47 genera (36 of which are endemic) and 5 of 6 tribes, as well as the unclassified genus *Voyria* (Albert and Struwe 2002). Saccifolieae, the most basally placed tribe in the phylogeny, is strictly from South and Central America, which supports the fact that South America is the ancestral, or at least part of the ancestral distribution, of the family. There is no strong support for China or a larger part of temperate Asia as part of the ancestral distribution of the gentian family.

Despite the high species diversity in China, many of the basal gentian clades are either absent from East Asia, or only have a few weedy, widespread species present such as *Exacum tetragonum* and *Sebaea microphylla*. This is a good example of how the number of species (i.e., 'center of species diversity') does not translate well into "center of origin" for a larger taxonomic group.

A family-wide biogeographic study analyzing the ancestral geographic origin for the gentians is still lacking, but progress has been made on biogeographical studies at tribal levels. Long distance dispersal of strongly disjunct taxa within transatlantic genera is the likely explanation for the presence of *Schultesia* on both sides of the Atlantic, but for potentially older genera, the case is less clear (*Neurotheca* and *Voyria*; Renner 2004).

Table 2.2 Updated tribal and subtribal classification of the Gentianaceae; list of genera with species numbers and general distribution**SACCIFOLIEAE***Curtia* Cham. & Schltld. (8; CA, SA)*Hockinia* Gardner (1; SA)*Saccifolium* Maguire & Pires (1; SA)*Tapeinostemon* Benth. (7; SA)*Voyriella* Miq. (1; CA, SA)**EXACEAE***Exacum* L. (69; AF, AS, AU)*Exochaenium* Griseb. * (22; AF)*Gentianothamnus* Humbert (1; AF)*Klackenbergia* Kissling * (2; AF)*Lagenias* E. Mey. * (1; AF)*Ornichia* Klack. (3; AF)*Sebaea* Sol. ex R. Br. * (75; AF, AS, AU)*Tachiadenus* Griseb. (11; AF)**CHIRONIEAE****Chironieae-Canscorinae***Canscora* Lam. (9; AF, AS, AU)*Cracosna* Gagnep. (3; AS)*Duplipetala* Thiv * (2; AS)*Hoppea* Willd. (2; AS)*Microrophium* C. B. Clarke (1; AS)*Phyllocyclus* Kurz (5; AS)*Schinzia* Gilg (1; AF)**Chironieae-Chironiinae***Blackstonia* Huds. (4; EU)*Centaurium* Hill. * (20; AF, AS, AU, CA, EU, NA, SA)*Chironia* L. (15; AF)*Cicendia* Adans. (2; AF, AU, EU, NA, SA)*Eustoma* Salisb. (3; CA, NA)*Exaculum* Caruel (1; EU)*Geniostemon* Engelm. & A. Gray (5; CA)*Gyrandra* Griseb. * (5; CA)*Ixanthus* Griseb. (1; AF)*Orphium* E. Mey. (2; AF)*Sabatia* Adans. (20; CA, NA)*Schenkia* Griseb. * (5; AF, AS, AU, EU, PA)*Zeltnera* Mansion * (25; CA, NA)*Zygostigma* Griseb. (1; SA)**Chironieae-Coutoubeinae***Coutoubea* Aubl. (5; CA, SA)*Deianira* Cham. & Schltld. (7; SA)*Schultesia* Mart. (15; CA, SA)*Symphyllphyton* Gilg (1; SA)*Xestaea* Griseb. (1; CA, SA)

(continued)

Table 2.2 (continued)**GENTIANEAE****Gentianeae-Gentianinae***Crawfordia* Wall. (18; AS)*Gentiana* L. (360; AF, AS, AU, CA, EU, NA, SA)*Metagentiana* T. N. Ho, S. L. Chen. & S. W. Liu* (14; AS)*Tripterospermum* Blume (33; AS)**Gentianeae-Swertiinae***Bartonia* H. L. Mühl. ex Willd. (3; NA)*Comastoma* (Wettst.) Toyok. (15; AS, EU, NA)*Frasera* Walter (15; NA)*Gentianella* Moench (275; AF, AS, AU, CA, EU, NA, SA)*Gentianopsis* Ma (24; AS, EU, NA)*Halenia* Borkh. (39; AS, CA, NA, SA)*Jaeschkea* Kurz (3; AS)*Latouchea* Franch. (1; AS)*Lomatogonium* A. Braun (18; AS, EU, NA)*Megacodon* (Hemsl.) Harry Sm. (2; AS)*Obolaria* L. (1; NA)*Pterygocalyx* Maxim. (1; AS)*Swertia* L. (150; AF, AS, EU, NA)*Veratrilla* Baill. ex Franch. (2; AS)**POTALIEAE****Potalieae-Faroinae***Congolanthus* A. Raynal (1; AF)*Djaloniella* P. Taylor (1; AF)*Enicostema* Bl. (3; AF, AS, EU, NA)*Faroa* Welw. (19; AF)*Karina* Boutique (1; AF)*Neurotheca* Salisb. ex Benth. (3; AF, SA)*Oreonesion* A. Raynal (1; AF)*Pycnosphaera* Gilg (1; AF)*Urogentias* Gilg & Gilg-Ben. (1; AF)**Potalieae-Lisianthiinae***Bisgoeppertia* Kuntze * (2; CA)*Lisianthus* P. Browne (30; CA)**Potalieae-Potaliinae***Anthocleista* R. Br. (14; AF)*Cyrtophyllum* Reinw. * (5; AS)*Fagraea* Thunb. * (55; AS, AU, PA)*Limahlania* K.M. Wong & Sugumaran (ined.) * (1; AS)*Picrophloeus* Blume * (4; AS)*Potalia* Aubl. (9; CA, SA)*Utania* G. Don * (15; AS)**HELIEAE***Adenolisanthus* (Progel) Gilg (1; SA)*Aripuana* Struwe, Maas, & V. A. Albert (1; SA)

(continued)

Table 2.2 (continued)

<i>Calolisianthus</i> Gilg (6; SA)
<i>Celiantha</i> Maguire (3; SA)
<i>Chelonanthus</i> Gilg (7; CA, SA)
<i>Chorisepalum</i> Gleason & Wodehouse (5; SA)
<i>Helia</i> Mart. (2; SA)
<i>Irlbachia</i> Mart. (9; SA)
<i>Lagenanthus</i> Gilg (1; SA)
<i>Lehmanniella</i> Gilg (2; SA)
<i>Macrocarpaea</i> (Griseb.) Gilg (112; CA, SA)
<i>Neblinantha</i> Maguire (2; SA)
<i>Prepusa</i> Mart. (5; SA)
<i>Purdieanthus</i> Gilg (1; SA)
<i>Rogersonanthus</i> Maguire & B. M. Boom (2; SA)
<i>Roraimaea</i> Struwe, Nilsson, & Albert * (2; SA)
<i>Senaea</i> Taub. (2; SA)
<i>Sipapoantha</i> Maguire & B. M. Boom (2; SA)
<i>Symbolanthus</i> G. Don * (37; CA, SA)
<i>Tachia</i> Aubl. (13; CA, SA)
<i>Tetrapollinia</i> Maguire & B. M. Boom (1; SA)
<i>Yanomamua</i> J. R. Grant, Maas & Struwe * (1; SA)
<i>Zonanthus</i> Griseb. (1; CA)
INCERTAE SEDIS
<i>Voyria</i> Aubl. (18; CA, NA, SA)

Generic changes since Struwe et al. (2002) are marked with * and discussed in the text. Estimated number of species are listed in parenthesis after each genus, as well as continental distribution (following abbreviations *AF* Africa (incl. Madagascar), *AS* Asia, *AU* Australia, *CA* Central America and Caribbean (incl. Mexico), *EU* Europe, *NA* North America (incl. Mexico), *PA* Pacific, *SA* South America. The distribution includes areas where non-native species have become naturalized

The crown-node age of the family and its major clades is not yet strongly supported, but molecular dating estimates have given some first indications. It should be remembered, however, that all dating exercises not strongly rooted in fossil records can be problematic. There are very few gentian fossils, and none from the basal clades, so calibration of internal nodes are difficult. Furthermore, fossils only provide minimum, not maximum, age estimates, so the actual ages of groups might be older, and much depends on what assumptions goes into the dating analyses.

The age of the Gentianaceae has been estimated to be about 50 million years (Yuan et al. 2003), 60 million years (Kissling 2007; Yuan et al. 2005), or in most recent estimates, slightly less than 100 million years, but with confidence intervals of 75–125 million years (Kissling, “personal communication”). In the older estimates, the family appeared to be younger than the Gondwanic continental breakup, which started about 120 million years ago, but recently the estimated family age has moved closer to a possible Gondwanic breakup of the family.

The age of the tribe Exaceae was estimated to be about 40 million years by Yuan et al. (2003) using one fossil calibration point and a nonparametric rate

smoothing (NPRS) method. Two years later, Yuan et al. (2005) did a new, improved dating analysis of the whole family and its major clades/tribes, using four calibration points [minimum age of Gentianales 60 million years (Muller 1984); minimum age of *Lisianthus* 40 million years based on pollen fossil from the Eocene (Graham 1984); inferred age of Gentianeae-Swertiinae 15 million years (von Hagen and Kadereit 2001, 2002); minimum age of *Gentiana* 5 million years, from fossil seeds (Mai and Walther 1988), and a molecular clock/smoothed, penalized likelihood analysis. This gave an age estimate for Exaceae of 29–32 million years. Older and younger ages were suggested when using fewer calibration points or other analytical techniques; total age range 12–54 million years]. The most recent analysis of the age and biogeography of the family is still unpublished, but supports the fact that the Gentianeae probably originated in the Neotropics (Merckx, “personal communication”), and that migration of tropical taxa through Laurasia during the Early Eocene may have played an important role in shaping the current global distribution patterns of the Gentianeae.

2.5 Highlights from Each Tribe

2.5.1 *Saccifolieae*

No generic changes have been made in the last ten years in the classification of the neotropical tribe Saccifolieae, the most basally positioned tribe of the gentians (Fig. 2.1). It still contains five morphologically very different genera and is the most species-poor of all the tribes (Table 2.1). During the last decade, research within this group has focused on alphataxonomy, pollen morphology, and the mycoheterotrophic attributes of the achlorophyllous *Voyriella*. Current understanding and hypotheses of generic relationships in the Saccifolieae are shown in Fig. 2.2a.

Crespo and Marcondes-Ferreira (2009) revised the genus *Curtia*, a much needed treatment that clarified many species complexes, and accepted eight species. The two species *C. tenella* and *C. tenuifolia* are separated once again as different species. The heterostyly of *Curtia* (some species at least) and *Hockinia* was confirmed by Crespo and Ferreira (2006), who also investigated the variation in pollen exine morphology.

Two genera of gentians include only achlorophyllous mycoheterotrophs, *Voyria* incertae sedis and *Voyriella* (Saccifolieae), but arbuscular mycorrhiza (AM) is common in many gentians. Bidartondo et al. (2002) investigated the AM in *Voyriella* and *Voyria* and showed a high fungal/mycorrhizal species specificity. The associated fungi were shown to link with surrounding trees, indicating that these mycoheterotrophic plant species obtain carbon from surrounding trees through shared AM fungi.

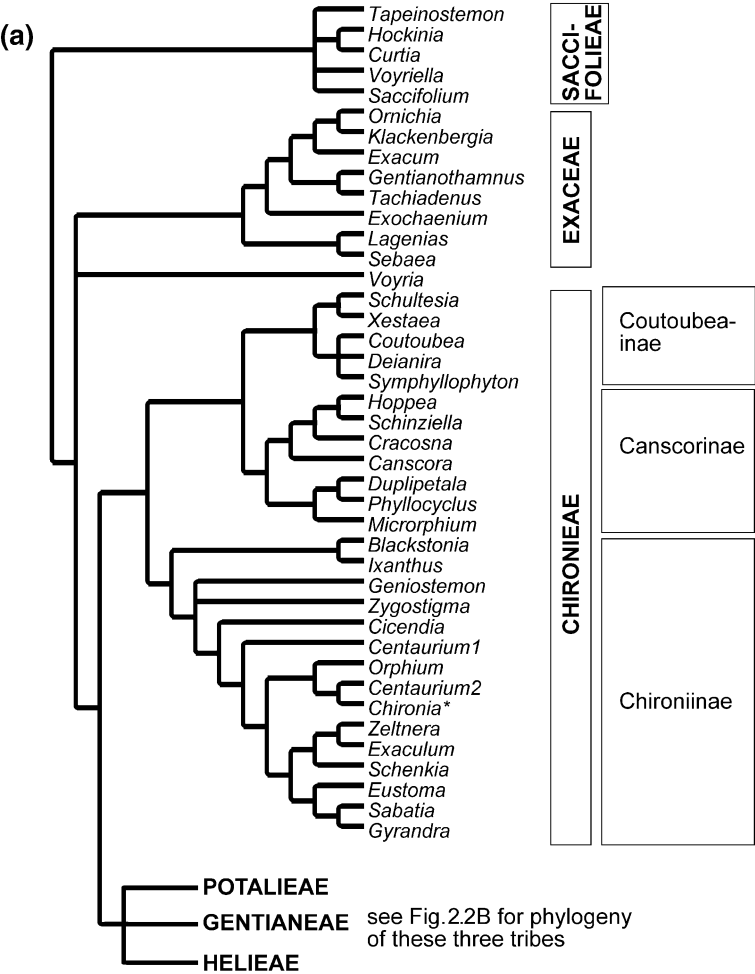


Fig. 2.2 Relationships among genera as currently understood based on studies reviewed in this chapter. This should be interpreted as a preliminary visual diagram summarizing many phylogenetic studies during the last ten years. Genera that have been shown as paraphyletic are indicated with ‘*’ and genera placed in several clades (i.e., polyphyletic or paraphyletic) have their subclades indicated with numbers. Additional details are in the text. **a** The basal clades of Gentianaceae (Saccifolieae, Exaceae, *Voyria*, and Chironieae). **b** The sister clade to tribe Chironieae (‘higher gentians’), a polytomy of tribes Helieae, Gentianeae, and Potalieae

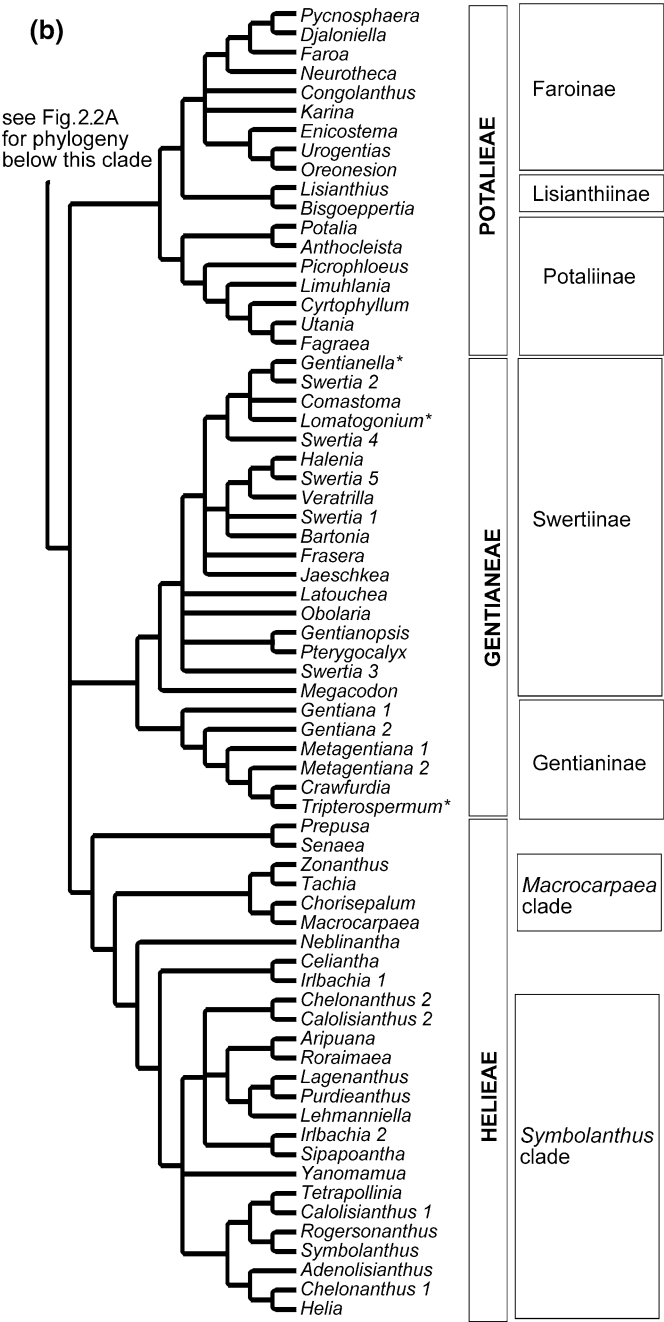


Fig. 2.2 continued

2.5.2 *Exaceae*

Extensive systematic work in the Exaceae in the last 10 years has strongly expanded taxon sampling in phylogenetic studies and clarified many species and generic relationships (Kissling et al. 2009b). The current understanding of the relationships among Exaceae genera, including the new generic circumscriptions, are shown in Fig. 2.2a, and for a generic list see Table 2.2. An updated key to all current genera of Exaceae were provided by Kissling (2012).

Sebaea turned out to be a polyphyletic genus in recent well-sampled studies (Kissling et al. 2009c; Yuan et al. 2003). This classification problem was quickly rectified through the description of a new genus, *Klackenbergia* (Kissling et al. 2009a), and the resurrection of the African genus *Exochaenium* (22 species) and the monotypic South African genus *Lagenias* (Kissling 2012). *Exochaenium* is more closely related to the *Exacum* subclade than to *Sebaea* sensu stricto, and *Exochaenium* and *Sebaea* also differ in seed testa cell anatomy. The seeds of *Exochaenium* have puzzle-shaped testa cells (as most Exaceae genera), while *Sebaea* have rectangular testa cell shapes (Kissling 2012). The rare feature of having two stigmas, one basal and one apical (diplostigmaty) in most *Sebaea* sensu stricto has also been investigated by Kissling et al. (2009c), and it was hypothesized to provide reproductive assurance.

Yuan et al. (2005) focused on the phylogeny of *Exacum*, and showed that the African *Exacum* species were nested inside a clade of Malagasy *Exacum* species, and that this African-Malagasy clade was sister to a clade formed from all Asian *Exacum* species, including one species also present in Australia. *Exacum* species from the Himalayas and Malaysia were nested inside groups present in Sri Lanka, India, Socotra, and the Arabian Peninsula, indicating a southwestern origin within Asia for this genus. It was also shown that the mycoheterotrophic genus *Cotylanthera* was a highly modified *Exacum*-clade (Yuan et al. 2005), so Klackenberg (2006) placed *Cotylanthera* and its four species into *Exacum*.

Cytological investigations of a large number of Exaceae species have shown that dysploidy and polyploidy are recurrent and common evolutionary phenomena within this tribe (Kissling et al. 2008).

2.5.3 *Chironieae*

The tribe Chironieae forms three monophyletic subclades, which are classified as subtribes Canscorinae (paleotropical), Chironiinae (world wide), and Coutoubeiinae (neotropical; Fig. 2.1). Detailed generic relationships of Chironieae are shown in Fig. 2.2a, and a list of all genera is provided in Table 2.2. In order to solve the problem with the paraphyletic *Canscora* in the subtribe Canscorinae, Thiv and Kadereit (2002) segregated out the new genus *Duplipetala* from *Canscora*. A new revision of all species in all seven genera in the subtribe was published by Thiv (2003).

It was already apparent in 2002 that the subtribe Chironiinae was suffering from the “large paraphyletic-genus” problem, with *Centaurium* occurring in several different clades. Updated phylogenetic hypothesis of the subtribe Chironiinae was presented by Mansion and Struwe (2004) and Mansion et al. (2005), confirming *Blackstonia* and *Ixanthus* as the most basally positioned genera in this clade, and providing good branch support for a new generic-level classification of *Centaurium*. Accordingly, Mansion (2004) resurrected two old genus names (*Gyrandra* and *Schenkia*) and named a *Centaurium* clade as the new genus *Zeltnera*, in honor of *Centaurium* specialist and cytologist Louis Zeltner and his wife Nicole Zeltner. *Gyrandra* contains five species distributed in Mexico and Central America. *Schenkia* also has five species, but the genus is highly disjunct between endemics of Australia, Hawaii and other Pacific islands, Eurasia, and northern Africa. *Zeltnera* is strictly New World in its distribution (Mexico and the US states of Texas and California) and includes about 25 species. Left in *Centaurium* sensu stricto are about 20 species centered around the Mediterranean, but with a few widespread weedy species worldwide (Mansion 2004).

The genus *Bisgoeppertia* was placed tentatively in Chironieae-Chironiinae based only on morphological data in the 2002 classification. Sequencing of newly collected material by Thiv showed that it was clearly affiliated with *Lisianthus* in Potalieae, so it has now been moved to the subtribe Lisianthiinae in the Potalieae (Molina and Struwe 2009; Thiv 2002).

The subtribe Coutoubeinae has the unusual characteristic of having pollen in tetrads (otherwise only known from a few Helieae genera and one Potalieae genus) and, curiously, all tetrad-bearing gentians are found in Latin America. Several studies have focused on the vegetative morphology (Delgado et al. 2009) and seed morphology (Guimarães et al. 2007) of this group, and also confirmed the presence of AM. *Schultesia* has also been under further taxonomic scrutiny and several new species have been discovered (Guimarães 2004; Guimarães and Fontella-Pereira 2001; Guimarães et al. 2003). It is remarkable how many new species are being described from South America in general, indicating that the biodiversity of this continent is still very poorly understood. Whether or not *Xestaea lisianthoides* should be separated from *Schultesia* as a monophyletic genus, as argued in Struwe et al. (2002), is still under discussion and needs further study.

2.5.4 *Gentianeae*

The widely distributed tribe Gentianeae has received considerable attention from researchers in the last decade. Current hypotheses of generic relationships are summarized in Fig. 2.2b, and Table 2.2 includes a list of all genera.

Large taxonomic problems have been associated with the para- and polyphyly of *Gentianella* and *Swertia* (subtribe Swertiinae), nested among smaller, more well-defined genera such as *Comastoma*, *Frasera*, *Gentianopsis*, and *Halenia* (Chassot et al. 2001). Neither *Gentianella* nor *Swertia* have been reclassified into

smaller monophyletic genera yet, so this is still a taxonomic problem to resolve when additional data is available on phylogenetic relationships and morphological character distributions supporting specific clades.

Kadereit and von Hagen (2003) and von Hagen and Kadereit (2003) showed that traditionally used floral characters show high homoplasy within the subtribe Swertiinae. Consequently, new characters would have to be sought as potential apomorphies for phylogenetically supported groups. The highly variable pollen morphology of *Swertia* was discussed by Chassot and von Hagen (2008) in a phylogenetic context, and showed that exine surface patterns might provide excellent characters for the definitions of several clades of *Swertia*. Seed coat morphology is also variable, as exemplified in *Gentianopsis* (Whitlock et al. 2010).

The highly diverse *Gentianella* of New Zealand, a monophyletic clade within the genus, was revised by Glenny (2004). During his revision of *Halenia* for *Flora Neotropica*, several new species were described by von Hagen (2007).

Bartonia and *Obolaria*, green but only barely so, are relatively basally positioned within Swertiinae, and their at least partially mycoheterotrophic status, long suspected and assumed, was confirmed recently by Cameron and Bolin (2010). The phylogenetic relationships of the initially four, now three, accepted *Bartonia* species were also investigated by Mathews et al. (2009), who provided a new key and species descriptions.

The subtribe Gentianinae contained the genera *Gentiana*, *Crawfurdia*, and *Tripterospermum* in 2002. No new genera or species have been moved into the subtribe, but the correct status and relationships among, and within, these genera are still unresolved (Chen et al. 2005; Favre et al. 2010; Zhang et al. 2009). *Gentiana* section *Stenogyne* was separated as the new genus *Metagentiana* by Ho and Chen (2002), and this genus is accepted by Asian contemporary botanists (Chen et al. 2008). There was new evidence that all four genera of the subtribe Gentianinae might be polyphyletic (Chen et al. 2005), which could soon lead to a large reclassification of many species and redefinition of generic boundaries. However, a recent phylogenetic study with larger taxon sampling by Favre et al. (2010) showed that *Tripterospermum* and *Crawfurdia* were definitely monophyletic, but *Metagentiana* was still found to be polyphyletic and positioned in three clades. There is also uncertainty about the correct phylogenetic position of *Gentiana* section *Otophora*. No new generic combinations and circumscriptions have been proposed to date.

2.5.5 *Helieae*

The phylogeny and molecular and morphological evolution of the genera *Helieae* were investigated in detail by Struwe et al. (2009a), which confirmed and expanded evolutionary patterns found in the 2002 analysis. A list of the current genera is shown in Table 2.2, and our current understanding of evolutionary relationships is shown Fig. 2.2b. Southeast Brazilian *Prepusa* and *Senaea* have

been placed consistently together as a clade sister to the rest of the Helieae (Struwe et al. 2009a). The remaining Helieae is informally divided into two major subclades, the *Macrocarpaea*-clade (*Chorisepalum*, *Macrocarpaea*, *Tachia*, and *Zonanthus*) and the *Symbolanthus*-clade (*Calolisianthus*, *Chelonanthus*, *Symbolanthus*). The phylogenetic positions of some genera (*Irlbachia* sensu stricto) are still unclear, and they might be positioned between the two subclades and the clade formed by *Prepusa* plus *Senaea* at the base.

Prepusa and *Senaea* were revised by Calió et al. (2008), and the biogeography and ecological vicariance patterns of *Prepusa* were investigated using the new method of spatial evolutionary and ecological vicariance analysis (SEEVA) by Struwe et al. (2011). The same method was also used to compare sister species patterns, biogeography, and speciation in Andean *Macrocarpaea* (Struwe et al. 2009b), highlighting ecological niche conservatism and dispersal. It was shown that long distance dispersal is a rather rare phenomenon in Andean *Macrocarpaea*.

No generic changes have been made in the *Macrocarpaea* subclade, but both *Tachia* and *Macrocarpaea* have been revised. Within *Tachia*, two new species were described and a revision is finished (Struwe et al. 2005; Struwe and Kinkade, 2014 (in press)). A trilingual field guide to *Tachia* was also published, and is freely available (Peters et al. 2004). Efforts with the taxonomy and phylogeny of the large genus *Macrocarpaea* continued with the publication of species, seed morphology and palynology (Grant 2004, 2005, 2007, 2009, 2011; Grant and Struwe 2003). The wood anatomy of *Macrocarpaea* showed interesting characters, suggesting a secondary derivation of woodiness within Gentianaceae (Carlquist and Grant 2005).

The *Symbolanthus* subclade has received considerable research attention, largely through the work of M. F. Calió at the University of São Paulo, and K. Lepis at Rutgers University. It was known already that a chaotic taxonomy was in use, especially related to species classified as *Calolisianthus*, *Chelonanthus*, *Helia*, *Rogersonanthus*, and *Wurdackanthus*. Through detailed alpha taxonomic and phylogenetic work, species and generic relationships have now been established (Lepis 2009; Struwe et al. 2009a). An update to the generic classification which identifies monophyletic clades as separate genera still has to be published, but is in the works (Calió et al., “personal communication”), and is incorporated into the phylogenetic relationships shown in Fig. 2.2b. There has also been new detailed anatomical work in this clade, as exemplified by studies of leaf anatomy by Delgado et al. (2011a, b) and self-pollination by Freitas and Sazima (2009).

Gould and Struwe (2004) showed that the genus *Wurdackanthus* (two species) formed a paraphyletic grade towards *Symbolanthus*, and it was therefore incorporated into *Symbolanthus* (Struwe and Gould 2004). A revision of *Symbolanthus* is ongoing, and will be published in geographically defined parts (Molina and Struwe 2008; Struwe 2003a, b). This includes the resurrection of many previously unaccepted species, as well as the description of many new morphologically well-defined species. In fact, the number of accepted species in this genus has increased from 3 to more than 30 in about 20 years.

Additionally, two new genera have been discovered in Helieae, both in the *Symbolanthus* subclade. The monotypic new genus *Yanomamua* from Brazil is a semi-woody species with very unusual lyrate leaves (Grant et al. 2006). The genus *Roraimaea* is based on a new orange-flowered Helieae species, and also includes the previously published *Roraimaea* (*Rogersonanthus*) *coccineus* (Struwe et al. 2008).

2.5.6 Potalieae

The pantropical tribe Potalieae and its three subtribes contain a fascinating diversity of habits (large timber trees to small, likely mycoheterotrophic herbs), corolla merosities (from 3 to 12-merous) and flower sizes (from a few mm to about 30 cm in diameter). A list of included, currently accepted genera is shown in Table 2.2, and a genus level estimate of phylogenetic relationships is shown in Fig. 2.2b.

Potalieae's phylogenetic relationships were investigated using internal transcriber spacer (ITS) data and the first DNA-alignment in the family based on secondary structure by Molina and Struwe (2009; for overall phylogeny see Fig. 2.2b). The study showed the conserved regions in the secondary structure of ITS and how these formed additional synapomorphies for certain clades within the Potalieae. The two subtribes, Lisianthiinae and Potaliinae, were well-sampled in this study and were supported as monophyletic, but the more poorly sampled subtribe Faroinae received no support for monophyly, possibly due to a long branch for *Neurotheca* (which would fit with it also being possibly mycoheterotrophic; Molina and Struwe 2009). Additional studies of the Faroinae, including all genera and many more species, are needed to fully understand evolution in this part of the Gentianaceae.

Potalia, the neotropical representative of the subtribe Potaliinae, was revised by Struwe and Albert (2004). This genus currently contains 11 species, of which nine were published in 2004. Its biogeographical history is very interesting, showing how lowland white sand areas are ancestral habitats within the genus, and that species on more recent, nutrient-rich and high-pH soils are derived from white sand-inhabiting ancestors (Frasier et al. 2008).

Also in the Potaliinae, the taxonomy of the species-rich and morphologically diverse genus *Fagraea* has been revised, leading to the resurrection of three genera, *Cyrtophyllum*, *Picrophloeus* and *Utania* for basally positioned clades in the genus, and the description of one new genus, *Limahlania* (Sugumaran and Wong 2012; Wong and Sugumaran 2012a, b). The revisions of *Fagraea* for peninsular Malaysia and Borneo have also led to the reacceptance of species previously considered as synonyms by Leenhouts (1962) in *Flora Malesiana*, and the discovery of many new species (Sugumaran 2010; Wong and Sugau 1996; Wong and Sugumaran 2012b). Motley (2004) also published the first treatment of the ancient and diverse ethnobotanical uses of *Fagraea* sensu lato.

As mentioned under the Chironieae, *Bisgoeppertia* was classified earlier in Chironieae-Chironiinae, but is now included in Potalieae-Lisianthiinae (Molina et al. 2009; Thiv 2002). More details on this rare taxon are found in Greuter and Rankin (2008).

2.5.7 *Incertae sedis* (*Voyria*)

The taxonomic and phylogenetic position of the enigmatic and beautiful genus *Voyria* has continued to baffle gentian taxonomists. New sequencing of nuclear and mitochondrial chloroplast genes have helped elucidate the correct evolutionary position, and recent multi-gene results suggest *Voyria* is a separate, monophyletic and isolated clade situated among the basal Exaceae and Saccifolieae tribes (Merckx et al. 2013). Its origin was likely in the Neotropics during the earlier part of the Eocene and it dispersed across the Atlantic to Africa at the end of the Oligocene.

Simultaneously, researchers have been investigating the mycoheterotrophic details of *Voyria* (Bidartondo et al. 2002; Courty et al. 2011; Franke 2002; Franke et al. 2006; Merckx et al. 2010). A pollen feature unique within the gentians has also been found in this genus. Pollen grains transported as one unit (through the presence of germinating pollen grains holding many grains together) was found in French Guianan *Voyria* species, as well as self-pollination and possible rodent dispersal of seeds (Hentrich et al. 2010).

2.6 Conclusions

As circumscribed here, the family Gentianaceae includes 99 genera and approximately 1,736 species distributed in seven tribes. There are still some uncertainties when it comes to some genera and their correct tribal or subtribal classification, but in general there is excellent knowledge of the overall phylogeny within the family and the tribal classification is expected to remain stable. As for genera, most appear to be monophyletic after some arranging in the last decade, but there should be reclassifications affecting poly- or paraphyletic genera such as *Chelonanthus*, *Gentiana* (in the broad sense), *Gentianella* and *Swertia*. The naming and identification of monophyletic clades within these genera will improve further the classification and make it both more practically useful in the field, as well as being more taxonomically and evolutionary correct. The next step in large-scale gentian pattern analysis will elucidate both the biogeography and the age of the family. Very little is known about this, and detailed and broad studies are needed urgently to explain not just how the different gentians are related, but where and when they evolved, why they have their current morphology, and how and when they moved to all continents. This will be an interesting challenge.

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