Jan J. Rybczyński · Michael R. Davey
Anna Mikuła *Editors*

The Gentianaceae - Volume 1: Characterization and Ecology

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Gentiana tibetica King. (Photograph A. Mikuła)

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ISBN 978-3-642-54009-7 ISBN 978-3-642-54010-3 (eBook)
DOI 10.1007/978-3-642-54010-3
Springer Heidelberg New York Dordrecht London

Library of Congress Control Number: 2014931384

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This volume is dedicated by the editors to their spouses

Preface

The Gentianaceae, or Gentian family, is worldwide in distribution with approximately 100 genera and about 1,800 species that include monocarpic and perennial herbs, shrubs, trees, and lianes, with terrestrial and epiphytic representatives. The plants are diverse in habit, the majority being herbaceous. The tropics are the main source of new species of the Gentianaceae. *Gentiana* (360 species), *Gentianella* (250 species), and *Swertia* (135 species) are the three largest genera; members of the family are protected by law. Several species are important pharmacologically because of their secondary metabolites, as some of the compounds have a broad spectrum of biological activity.

Initial contacts with Gentians often occur during childhood when skin is protected from bacterial infection by *Gencjana* (Polish) or *Violetum Gentianae* (Latin), while children suffering from chickenpox are also painted with *Violetum* to counteract infection by *Herpes virus varicellae*. The importance of Gentians escalated in the 1980s when several studies at the plant level focused on the vegetative propagation of species, such as *Gentiana lutea* and *G. cruciata*, following recognition of the secondary products synthesized by some members of this genus. Research into Gentians, especially in Poland, was stimulated further by publication of the “Red Book” of the Polish Flora. This volume included reference to numerous Gentians and Gentianellas, with the need for their multiplication and reintroduction into the wild because of destructive over-collection of wild material for pharmaceutical use, combined with loss of natural habitats. Some species are now rare and endangered. Variation in plant habit, especially flower morphology and pigmentation, also make members of the Gentianaceae attractive for outdoor and indoor cultivation. The establishment of the Web site “Gentiana.pl” supplemented the earlier reference site “Gentiana Research Network” established by Dr. Lena Struwe at Rutgers University, New Brunswick, USA. Much deliberation, contacts at the scientific level and discussions with colleagues at Springer, resulted in the compilation of these two volumes on Gentians. Volume 1 includes contributions on the characterization of this family of plants, while Volume 2 is devoted to aspects of biotechnology and their applications.

Volume 1: Characterization and Ecology

Volume 1, comprising 12 chapters, centers upon the characterization and ecology of the Gentianaceae, with some emphasis on the application of molecular and cytological approaches in relation to taxonomy. The first three chapters consider classification of this family of plants, with Chap. 2 reviewing research progress since the earlier revision of the Gentianaceae in 2002. This revision resulted in reclassification of some plants and the naming of new genera. Chapter 3 provides the most comprehensive report to date of the systematics of South American Neotropical woody members of the Gentians, with discussion of the use of cytological and molecular technologies to facilitate classification. Other reviews (Chaps. 4, 5) include details of the Gentianaceae in The Ukraine and Balkan Peninsula, with discussion of the taxonomy of representative species in these regions. Floral pigmentation in members of this family has been a topic of investigation for many years, with the key biochemical steps that result in the diversity of flower colors found in Gentians being summarized in Chap. 6. Other aspects of this diverse, interesting group of plants include the cytology of European species (Chap. 7), and a historical account of the importance of Gentians in herbal medicines, with links to evolution and classification (Chap. 8). Analysis of gene expression in overwintering buds is presented as an approach with which to study several aspects of plant taxonomy, phenotypic characteristics, phylogeography, and pedigree (Chap. 9). Two (Chaps. 10, 11) indicate the importance of Gentians in India in terms of their exploitation as herbal-based medicines, but emphasize the need for conservation to negate the loss of germplasm from natural habitats resulting from random harvesting. Finally, Chap. 12 presents evidence for the importance of fungi from the Phylum Glomeromycota in developing arbuscular mycorrhizal associations with the roots of members of the Gentianaceae. The role of such associations in plant growth and development is also discussed. Volume 1 of the Gentianaceae provides a general, broad-based foundation for more biotechnological approaches that are considered in Volume 2.

Volume 2: Biotechnology and Applications

The Gentianaceae includes species which are popular as ornamentals in the form of cut flowers and pot plants, with market demands necessitating improvement in flower quality, particularly characteristics such as inflorescence longevity. Micropropagation has become a routine procedure for multiplication of horticultural genera, including *Blakstonia*, *Centaurium*, *Genetiana*, *Gentianella*, and *Swertia*, with seedlings being the most common source of explants for plant propagation in vitro. Although organogenesis is the main route of plant regeneration, somatic embryogenesis is also a pathway in routine use for plant multiplication. These approaches are discussed in detail in Chaps. 1–6. Embryogenic cultures, such as cell suspensions, are an excellent source of protoplasts for gene transfer by somatic hybridization and cybridization. The relevance of the latter technologies (Chap. 7) is that they generate nuclear and cytoplasmic combinations normally unavailable to plant breeders through conventional sexual hybridization. Techniques presented in Volume 2 also include the generation of haploid and dihaploid plants from cultured anthers, and the genetic variation that may arise from tissue and organ culture (Chaps. 8, 9). Subsequent chapters discuss the molecular breeding of Gentians, particularly gene transfer by transformation, with associated genetic analyses (Chap. 10). Molecular markers facilitate breeding and cultivar identification. Vegetative propagation to generate genetically uniform populations and, conversely, manipulations to increase genetic variability, often rely upon cryopreservation as a common technology for long-term storage of relevant germplasm (Chap. 11). Other reviews consider the postharvest physiology of Gentian flowers (Chap. 12), and the biosynthesis of secondary metabolites, including antimalarial compounds (Chaps. 13–18). Modification of secondary metabolites has application in human health protection. Interestingly, the beauty of Gentian flowers and the pharmaceutical value of the plants have been the reasons for the special interest in the Gentianaceae since ancient times.

These two volumes should serve as key references for persons from a wide range of disciplines, including students and staff of universities and institutes, as well as professional gardeners and plant hobbyists.

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Contents

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Chapter 1
Morphological Characteristics of the Family Gentianaceae

James S. Pringle

Abstract The Gentianaceae or Gentian family is worldwide in distribution, with 1,800 or so species in about 100 genera. The plants are diverse in habit, although the majority are herbaceous. The leaves of most species are opposite, with the margins generally entire; stipules are absent in most genera. The perianths are biseriate, actinomorphic or somewhat zygomorphic, sympetalous, and usually synsepalous. The stamens are epipetalous, isomerous with the petals, and the pistil is solitary, bicarpellate, with a superior ovary containing several to many ovules.

1.1 Introduction

The plant family Gentianaceae comprises about 100 genera and 1,800 species, native to all continents except Antarctica. It is the type family of the order Gentianales, with morphological and molecular evidence indicating that it is most closely related to the Loganiaceae, Gelsemiaceae, and Apocynaceae (Struwe et al. 1994, 2002; Backlund et al. 2000; Stephens 2001; Albert and Struwe 2002; Mészáros et al. 2002). The tribal and subtribal classification accepted here follows that of Struwe et al. (2002). In the past, the genera constituting the subtribe Potaliinae were often placed in the Loganiaceae, but molecular evidence strongly supports their inclusion in the Gentianaceae (Struwe et al. 2002). The Menyanthaceae, formerly included in the Gentianaceae, are now generally recognized as a distinct family, and placed in the Asterales.

Species of the Gentianaceae occur in diverse vegetation zones and plant communities, including tropical forests and savannahs, temperate woodlands and prairies, and arctic and alpine regions, as well as in littoral and ruderal plant communities. Most grow in mesic habitats. Some are found in wetlands or on tidal flats, but none is

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J. J. Rybczyński et al. (eds.), *The Gentianaceae - Volume 1: Characterization and Ecology*, DOI: 10.1007/978-3-642-54010-3_1,

truly aquatic or marine. True desert species do not exist in the family, although that status is approached by some species in the tribe Chironieae, and many species grow in relatively dry savannahs or fell-fields. A few tropical species are epiphytes (Gilg 1895; Struwe et al. 2002). Many are cultivated as ornamentals.

The largest genus is *Gentiana* L., with about 400 species. This genus is nearly worldwide in distribution, but absent from low-altitude tropical regions and all but northernmost Africa and all but eastern Australia. It reaches its greatest diversity in China, where numerous species are present in the high mountains. The second-largest genus is *Gentianella* Moench, with about 300 species, similar in the extent of its distribution, but with its greatest diversity in the Andes of South America. Another large genus is *Sebaea* R. Br., with about 100 species in Asia, Africa, and Australasia. *Swertia* L., if widely circumscribed, includes 125–150 species, but its appropriate generic delimitation remains in question (Ho and Pringle 1996; Albert and Struwe 2002).

1.2 Habit

The majority of the species in the Gentianaceae are herbs or subshrubs, although many of the tropical species are shrubs or small to medium-sized trees (to ca. 10 m in most arborescent species, to 35 m in some species of the subtribe Potaliinae), and a few are lianas. The herbaceous species may be annual, winter-annual, biennial, pliestesial (long-lived but monocarpic), or perennial. Most are erect or decumbent, but a few are trailing or twining vines. Both sympodial and, less commonly, monopodial growth occurs among the perennial species. Most herbaceous perennial species develop an erect, often branched caudex. Some perennial and some otherwise monocarpic species produce new crowns from elongating rhizomes, spreading roots, or stems that root at proximal nodes, forming colonies. The plants of most species are glabrous; aside from axillary colleters, the indument of the vegetative parts, when present, consists of papillae or simple or rarely uniseriate, non-glandular or rarely glandular hairs, which may be present on the stems but absent from the leaves. Spiny stems occur only in some species of *Anthocleista* Afzel. ex R. Br. Phyllodia, bulbs, and highly modified, succulent stems do not occur in the family Gentianaceae (Wood and Weaver 1982; Struwe et al. 1994, 2002; Mészáros et al. 2002).

Persistent tap roots are common. Many perennial species produce secondary roots, which are often stout, and lack root hairs (Gilg 1895). Endomycorrhizae of the order Glomales (Zygomycotina) are generally present (Imhof 1999; Cameron and Bolin 2010). Most species are chlorophyllous, but several genera have greatly reduced leaves and root systems. *Voyria* Aubl., *Voyriella* (Miq.) Miq., and some species of *Exacum* L. (formerly segregated as *Cotylanthera* Blume) are completely mycoheterotrophic, lacking chlorophyll, with minute, scale-like leaves and coralline or “bird’s-nest” root systems (Imhof 1999).

1.3 Leaves

Phyllotaxy is opposite or less often whorled, or rarely with some or all leaves, alternate. Basal leaves are often present. The nodes are usually unilacunar or trilacunar, occasionally multilacunar. Leaves are simple and unlobed, sessile, or less often petiolate; distinctly petiolate leaves are common among the tropical, woody species, but are absent among species of the temperate and Arctic-alpine zones. Primary venation (except in species with narrowly linear or very small leaves) is usually basally or suprabasally acrodromous, or pinnate and camptodromous, especially in woody genera. Secondary venation is diverse, often more or less brochidodromous and sometimes with an intramarginal vein, or eucamptodromous. In nearly all species, the margins are entire (except for the projecting distal corners of marginal cell walls, which in some species form minute teeth or cilia); in the few exceptions the margins are shallowly crenulate or serrulate. Raised lines often connect the bases of the opposite or whorled leaves, but in many other species, sometimes within the same genus, such lines are absent, with the leaf margins often being decurrent as longitudinal ridges on the stems. In some species, the bases of the opposite or whorled leaves are connate and strongly ascending, forming a sheath around the stem. The blades of the distal or all leaf-pairs are perfoliate in some species in the tribe Chironieae. Other than lateral expansions of the petioles, which occur in several genera, stipules are absent except in the subtribe Potaliinae and some species of *Tachia* Aubl., in which they form low ocreae, and in *Macrocarpaea zophoflora* R. E. Weaver & J. R. Grant, in which they are interpetiolar and deciduous. Colleters are often present in the leaf axils (Gilg 1895; Metcalfe and Chalk 1950; Struwe et al. 1994, 2002; Mészáros et al. 2002).

The leaves are dorsiventral or, in a few small genera, isobilateral without a distinct palisade layer. The stomates are anomocytic or anisocytic, on the abaxial or less often both leaf surfaces. Some species of *Voyria* lack stomates. Kranz leaf anatomy does not occur in the family (Metcalfe and Chalk 1950; Struwe et al. 1994, 2002).

1.4 Inflorescences

The inflorescences are terminal and lateral. They are basically cymose, but many variations occur. The cymes range from dichasial to partly or wholly monochasial and, in some species, are racemoid, umbelloid, capitate, or grouped in thyrses or verticillasters, or the inflorescence may consist only of one flower. The flowers may be pedicellate or sessile, erect, horizontal, or nodding. They may or may not be subtended by paired bracts (Gilg 1895; Struwe et al. 1994, 2002; Mészáros et al. 2002).

1.5 Flowers

1.5.1 General

The flowers are hypogynous. In the majority of genera, the flower is actinomorphic, except often for some dorsal compression of the pistil. Slightly to moderately (but not strongly) zygomorphic flowers occur in some tropical and subtropical genera, mostly in the tribe Helieae. Zygomorphy in such flowers is usually more pronounced in the corolla than in the calyx, and most strongly expressed in the sexual parts (Gilg 1895; Wood and Weaver 1982; Struwe et al. 1994, 2002; Mészáros et al. 2002).

1.5.2 Perianths

The perianth, with the exception, presumably, in *Obolaria* L., is biseriate. In most genera, the perianth (or corolla) is tetramerous or pentamerous. Those of a few genera (or of sections, subsections, or individual species) are 6- to 16-merous; those of *Pycnosphaera* Gilg are trimerous. The sepals and petals are usually isomerous, but in a few genera, the lobes of the corolla are more numerous than those of the calyx.

The calyx is differentiated from the corolla, and is generally smaller, green and more or less leaf-like in texture, or occasionally coriaceous or nearly hyaline. Although usually inconspicuous, in a few genera the calyx forms a significant part of the floral display, notably in *Potalia* Aubl. in which, with the pedicels, it is yellow to orange, although not larger than the corolla. In *Prepusa* Mart., it is greenish yellow, rose-violet, or red and conceals much of the corolla. The corolla is usually actinomorphic, occasionally more or less irregular in its lobing, variably spathaceous, or slightly zygomorphic. In most genera the sepals are united proximally, but in a few genera they are completely separate. Aestivation of the calyx lobes is imbricate or valvate. In *Crawfurdia* Wall. and most sections of *Gentiana*, an adaxial invagination of the calyx tube forms an intracalycular membrane, so that the lobes appear to diverge abaxially from the tube slightly below its summit. *Obolaria* lacks a calyx (structures in that genus interpreted here as subtending bracts are sometimes regarded as a two-part calyx). Colleters, or less often paired scales or, mostly in woody species, discoid glands, are frequently present adaxially near the base of the calyx tube (Gilg 1895; Wood and Weaver 1982; Metcalfe and Chalk 1950; Struwe et al. 1994; Mészáros et al. 2002).

The corollas are petaloid and usually conspicuous, highly diverse in shape, with tubular, salverform, campanulate, and rotate corollas all being frequent. Corollas are also diverse in color, often with guidelines or "eyes," mostly in the tribe Chironieae and *Gentiana* section *Chondrophyllae* Bunge. In all species, the corolla is gamopetalous, although the depth of lobing varies greatly. Aestivation of the corolla is usually contorted, but is imbricate in a few genera, and proximally valvate in *Aripuana* (Struwe et al. 2002), *Jaeschkea* Kurz, and *Tachia schomburgkiana* Benth. In many species in the tribe Gentianeae, there is a fringe of vascularized or non-vascularized trichomes or a pair of deeply fimbriate scales near the base of each corolla lobe, or a more or less continuous fringe at or near the summit of the tube. In some genera in the subtribe Swertiinae, fringes of trichomes and/or tubular or scale-like prolongations of the rim surround the openings of discoid glands on the adaxial corolla surface (Gilg 1895; Wood and Weaver 1982; Struwe et al. 1994, 2002; Ho and Pringle 1996; Maas and Ruyters 1986; Mészáros et al. 2002).

1.5.3 Androecia, Gynoecia, and Nectaries

The stamens are in one cycle, isomerous and alternate with the corolla lobes, and are inserted either on the corolla tube or in the sinuses between the corolla lobes. Filaments are usually present; the anthers are sessile in some species of *Voyria* and nearly so in a few other genera. The filaments are mostly slender and often flattened; those of some genera or species are ± abruptly wider near the base. In most species, the stamens are equal, with the filaments straight or nearly so, forming an actinomorphic androecium. In some genera or species therein, mostly in the subtribe Chironiinae, all of the stamens are deflexed to one side, away from the stigma during the early floral stages, and later become erect. In some tropical species, mostly in the tribe Helieae, the stamens are declinate, forming a zygomorphic androecium, and are sometimes also coiled circinnately distally. In a few genera or individual species, also mostly tropical, especially in the subtribe Canscorinae, the stamens are unequal, and differ in filament length and/or level of insertion on the corolla tube. The anthers may differ in size, and one or two stamens may be reduced, having a sterile anther or lacking an anther. In most genera, the filaments are free above the level of insertion, but in some cases they are connected by a corona, which is often fringed between the filaments, or corona scales may be alternate with the filaments. The filaments are fused proximally forming a tube in the subtribe Potaliinae. The anthers are tetrasporangiate and dithecal, dorsifixed or basifixed, and free or more or less connate in some genera. In other genera, they are appendaged, sometimes with glands at the base or apex and in some cases they coil helically or circinnately upon dehiscence. Dehiscence is by longitudinal rimae, usually introrse, rarely latrorse or extrorse. In *Exacum*, dehiscence is restricted to the distal portion of the anther, forming one pore per anther in the chlorophyllous species, in which the thecae are fused distally, or two pores per anther in the achlorophyllous species (Gilg 1895; Lindsey 1940; Struwe et al. 1994, 2002; Stephens 2001).

Except in the achlorophyllous taxa, the pollen grains are small to medium-sized, 18–65 μm in the longest dimension, trinucleate in most genera, but binucleate in some. They are most often tricolporate, but in some genera are tetracolporate, pentacolporate, pericolporate, or triporate. The pores are round or nearly so. When shed in monads, as in the majority of genera, the pollen grains are usually prolate, occasionally spheroid. The pollen is shed in tetrads in most of the genera in the tribe Helieae and in several genera in other tribes, and in polyads in a few genera in the tribe Helieae. Except in some achlorophyllous species, both the exine and intine are well developed, the exine consisting of nexine and sexine, the sexine of endexine and ectexine. The sexine is striate, striato-reticulate, or reticulate in most genera, perforate in a few, and nearly smooth in *Halenia* Borkh.; projections of diverse forms occur in the tribe Helieae. The tectum is generally supported by columellae. Granules and/or other subtectal processes are sometimes also present. Pollen tends to be smaller in the achlorophyllous taxa. Pollen of most *Voyria* species is 11–15 μm in diameter, 1- or 2(-6)-porate, with the exine smooth and not distinctly stratified (Nilsson 2002).

The pistil is solitary, bicarpellate, and syncarpous at least below the distal portion of the style. A style may be present or absent. If present, it is solitary, usually not cleft below the stigmas or stigmatic lobes, but shallow to rather deeply bifid in some genera or species within some genera. The style is erect in most species, but in some species in the tribe Chironieae it is deflexed away from the stamens during the early stages of the flower, later becoming erect. It is usually declinate in species with more or less zygomorphic corollas and androecia. When the style is not bifid the stigmas may be solitary or paired. When solitary, they may be capitate, peltate, funnel-form, bilobed, or in *Sebaea*, bottle brush-like. They range when paired from orbicular to oblong or strap-shaped, and may become increasingly recurved as the flowers age. In genera with relatively long, narrow stigmas, the latter may remain straight or, along with the style branches, coil helically before and/or after receptivity. In most species of *Lomatogonium* A. Br. and to some extent in *Bartonia* Muhl. ex Willd., the stigmas are decurrent along the sutures of the ovary. The stigmatic surface is wet and usually papillate, sometimes nearly smooth. In genera with stout and/or poorly differentiated styles, the latter is generally persistent in the fruit; in species with slender styles, the style is often completely or partially deciduous (Gilg 1895; Wood and Weaver 1982; Bertin and Newman 1993; Struwe et al. 1994; Stephens 2001).

The ovary is superior. It may be sessile or stipitate; a stipe, when present often elongates in the fruit. Both carpels are ovuliferous. In most genera, the ovary is unilocular with parietal but often deeply inserted placentation. In some genera, the ovaries are proximally or completely bilocular with axile placentation, and in the achlorophyllous species of *Exacum* they are unilocular with partially free-central placentation. The ovules are few to very many, usually sessile and anatropous, tenuinucellate, and unitegmic, but ategmic in *Voyria* subgenus *Leiphaimos* (Schltdl. & Cham.) V. A. Albert & Struwe and the achlorophyllous species of *Exacum*. The embryo sac is of the *Polygonum* type (Gilg 1895; Wood and Weaver 1982; Struwe et al. 1994, 2002; Shamrov 1996; Stephens 2001; Bouman et al. 2002; Mészáros et al. 2002).

The flowers of most species produce nectar, except in many genera of the tribe Chironieae, and most also produce abundant pollen. The nectaries may be borne on the ovary or ovarian stipe, may form a ring at the base of the ovary, or may be epipetalous. When epipetalous, they may be on the adaxial corolla surface, in spurs in the majority of *Halenia* species, as clusters of nectariferous hairs in *Faroa* Welw., or in some genera of the subtribe Swertiinae, in pits within the corolline tissue. There may be one or two per corolla lobe, with the pits opening to the adaxial corolla surface immediately adaxial to the nectary or distal to it. In species in which the nectaries do not form a continuous ring, they are usually isomerous with or twice as many as the corolla lobes, but only two (if any), borne on the ovary, are present in *Voyria*. In *Orphium* E. Mey. and a few other genera, glandular discs between the calyx and corolla also appear to function as nectaries. Abaxial calycine and extrafloral nectaries are common in the tribe Helieae. In some species, mostly in the tribe Chironieae, pollen is the only "reward." Most species of *Exacum* L. produce "buzz flowers," in which pollen is released from the anthers by resonant vibration produced by the action of visiting bees (Wood and Weaver 1982; Struwe et al. 1994, 2002; Stephens 2001; Mészáros et al. 2002).

1.6 Pollination and Breeding Systems

Most species of the Gentianaceae are self-compatible, but pollination usually requires external agents. Most species in temperate regions are pollinated primarily by bees, although flies and other insects are also important, especially in *Sabatia* Adans., *Swertia*, and closely related genera. Butterflies, moths, hummingbirds, and bats are also important pollinators, especially among the tropical species. Wind-pollination does not occur in the family. Geitonogamous pollination is frequent, as the flowers of most species are long-lived and those on any one plant may open over a long period (Gilg 1895; Stephens 2001; Struwe et al. 2002).

Herkogamy, with the style being deflected to one side and the stamens deflected in the opposite direction, occurs in several genera. The style and stamens later become erect, allowing autogamy if xenogamous or geitonogamous pollination has not occurred previously (Bertin and Newman 1993).

In most species, the flowers are bisexual and monomorphic, usually protandrous and predominantly xenogamous. Most species in the tribe Saccifoliae and a few in *Sebaea*, although having all flowers bisexual, are heterostylous. *Veratrilla* (Baill.) Franch. is dioecious, and some species of *Gentianella* in the Southern Hemisphere are gynodioecious, andromonoecious, gynomonoecious, or trimonoecious. Species with obligately or usually autogamous flowers also occur mostly in the subtribe Chironiinae, and in many other species the flowers are facultatively autogamous, often with the stigma tardily coming into contact with the anthers. Agamospermy is believed to occur in achlorophyllous species of *Exacum* (Gilg 1895; Filippa and Barboza 2006; Freitas and Sagima 2009).

Fig. 1.1 The diversity of flowers of the species of the family Gentianaceae from North America. **a** *Frasera albicaulis* var. *nitida* (Benth.) C. L. Hitchc. in California, USA, showing nectary-pit openings and corona scales. *Photo* Norman Jensen: Copyright Allen L. Jensen with permission. **b** *Obolaria virginica* L., a strongly mycotrophic but chlorophyllous species, in Tennessee, USA. **c** *Gentiana andrewsii* Griseb., in Ontario, Canada, a species with permanently closed corollas. **d** *Gentiana newberryi* A. Gray var. *newberryi*. in Oregon, USA. *Photo* Tanya Harvey, with permission

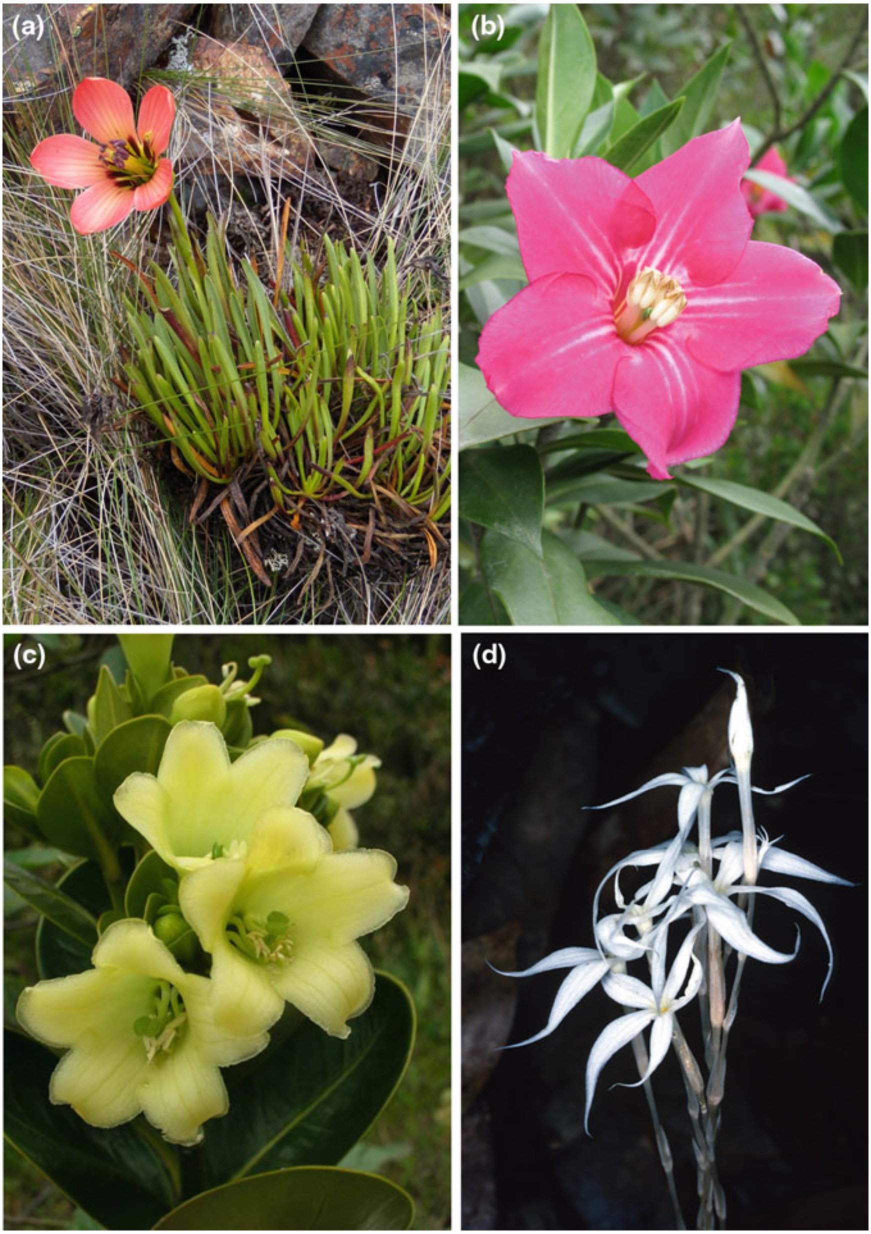

Fig. 1.2 The diversity of the species of the family Gentianaceae from South America. **a** *Gentianella gilgiana* (Reimers) Fabris ex J. S. Pringle. Peru. A species of high altitudes in the Andes. Note the actinomorphic flowers, isomerous calyx and corolla, gamopetalous but deeply lobed corolla, and epipetalous stamens alternating with the corolla lobes. Photo by Victor Villalobos, with permission. **b** *Symbolanthus mathewsii* (Griseb.) Gilg. Peru. A shrubby species with a slightly zygomorphic corolla. Photo by Jason R. Grant, with permission. **c** *Macrocarpaea subsessilis* Weaver & J. R. Grant. Ecuador. A shrubby species with slightly zygomorphous flowers with pale corollas that remain open at night, pollinated primarily by bats. Photo by Jason R. Grant, with permission. **d** *Voyria acuminata* Benth. French Guiana. Species is mycoheterotrophic, lacking chlorophyll. Photo by Carole Gracie; © 2013 Carol Gracie, with permission

1.6.1 Fruits

The calyx is persistent in fruit in all but two genera and some species in a third, usually not expanding, but in some tropical genera becoming indurate and/or accrescent. The corolla is marcescent in most genera. The fruits generally remain attached, but fall from the plants in a few tropical species. In most genera, the fruits are septicidal, bivalvate capsules, diverse in wall thickness, but in a few genera they are irregularly dehiscent or indehiscent capsules or berries (Gilg 1895).

1.6.2 Seeds and Dispersal

The seeds are diverse in shape, nonarillate, with the seed coat membranous or crustaceous. Seed-coat surfaces are diverse at maturity, often reticulate, sometimes winged or with papillose projections. In most genera, the seeds are small and light and, especially those with winged seed coats, are largely wind-dispersed. In some species in the tribe Gentianeae, elongation of the ovarian stipe elevates the capsule above the marcescent corolla and renders it more susceptible to breeze action. Rain-washed and melt-water from snowfields are also significant in seed dispersal, especially in alpine species of *Gentiana* and *Gentianella*. The capsules of some species of *Gentiana* section *Chondrophyllae* probably function as splash-cups. Rainwash is also significant in genera with indehiscent dry fruits, from which the seeds are released when the walls decay, and in species of *Curtia* Cham. & Schltdl. and *Voyria*, with fruits that dehisce after having fallen. *Gentianopsis detonsa* subsp. *victorinii* (Fernald) Lammers, and probably some other taxa, have seeds that float. Projections on the seed coats of some species may function in exozoochorous dispersal. The seeds are dispersed endozoochorically in the genera with baccate fruits. Most of the achlorophyllous species produce minute “dust seeds,” dispersed by wind or rain-wash. The embryo is small and cylindric or conical in the autotrophic species and minute or undifferentiated in the achlorophyllous species. The endosperm is copious, fleshy or oily, and nuclear in the autotrophic taxa, scant and in some species cellular in the achlorophyllous taxa. Detached vegetative disseminules such as bulblets do not occur in the family (Gilg 1895; Struwe et al. 1994, 2002; Stephens 2001; Bouman et al. 2002; Mészáros et al. 2002).

1.7 Conclusions

Morphological and molecular evidence indicates that the Gentianaceae is a natural group. Although many species are exceptional in one or more respects, the family is largely characterized morphologically by the combination of opposite, simple leaves with entire margins, a biseriate, an actinomorphic or nearly actinomorphic perianth, synsepalous and sympetalous and more or less persistent in fruit, epipetalous stamens, isomerous with the corolla lobes and alternating with them. There is a single bicarpelate pistil with a superior, unilocular ovary containing several to many ovules (Figs. 1.1, 1.2).

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Chapter 2
Classification and Evolution of the Family Gentianaceae

Lena Struwe

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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J. J. Rybczyński et al. (eds.), *The Gentianaceae - Volume 1: Characterization and Ecology*, DOI: 10.1007/978-3-642-54010-3_2,