

# **A WORLDWIDE MONOGRAPH OF GENTIANA**

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# Introduction

*Gentiana* represents the largest genus of the family Gentianaceae. It comprises about 362 species and has subcosmopolitan distribution. The center of the highest concentration of species occurs in the mountain regions of the southwestern China and adjacent northeastern Myanmar, where more than half of all species are found. Gentians are very beautiful and highly attractive. They, the real aristocrats in the plant kingdom, are one of the most beautiful and popular decorative plants. Its dominantly alpine habit makes it a model of alpine plants and is called as “one of three most beautiful flowers of alpine mountains” in China. Gentians are very useful. They have been widely used as a medicine in China, India, Nepal and Kashmir regions, especially as a traditional Chinese and Tibetan medicines in China.

The genus *Gentiana* has been studied by many botanists since it was formally established by Linnaeus. These botanists published numbers of new species and papers as well as various regional and continental floras. They also treated the genus in a wide variety of ways. However, the generic circumscription, relationships with related genera, its infrageneric classification and phylogeny have not very well been understood, or have been subjected to great controversies. With a large number of new species to discover and result in an alarming accumulation of names, these subjects have come into annoying difficulty with botanists. The fundamental data, e.g. on cytology, embryology and palynology, still are lacking or even nothing. Only there are piecemeal works on these subjects.

We have been continuously working on Gentianaceae for more than 30 years. As a result the present book is a worldwide monograph of systematic botany for the genus *Gentiana*. The text is in nine parts. It expounds taxonomy, morphology and anatomy, embryology, chromosomology, palynology, phylogenetics and phytogeography of this genus. On the basis of nomenclature types, an enormous and confused species and names, 2048 in all, have been revised. 362 species and 68 varieties (subspecies) of *Gentiana* are now recognized, but 911 names are brought under synonyms. However, 708 names, which originally were placed in *Gentiana*, are now transferred to other genera. The names excluded from *Gentiana* and two lists of cited specimens in different arrangements are presented as an aid to understanding these species. We examined about 20,000 herbarium specimens and the types for most relevant names from the major herbaria of Europe, Asia and North America and from the Chinese national and various regional herbaria. We have taken part in many botanic expeditions in Qinghai, Xizang, Yunnan and Sichuan provinces of China, collected a large number of specimens, and observed most Chinese species of alpine plants in their native habitat. From our own detailed field observations, a dynamic morphology and variant range in some species have been more deeply understood, and some important diagnostic characters, which were neglected before, have been paid attention to. Living collections of some species in domestic and abroad were grown in the gardens for detailed morphological observations, and cytological and embryological studies.

The phylogenetic relationships among taxa and evolutionary lines have been expounded, using some principles and methods of synthetic classification and cladistics. A natural system of infrageneric classifications has been established. The genus *Gentiana* is divided into 15 sections, of which 5 further into 22

series. Firstly comprehensively systematic investigations on embryology, morphology, anatomy and palynology were made to full in the gaps and insufficiency in these respects.

Today, there is an increased interest in *Gentiana* and more and more appearing in scientific studies, medicines and horticulture. We hope that this book, as a review of current knowledge of *Gentiana*, has more worth of making a better understanding of its taxonomy and systematics and of promoting the interactive studies of multidisciplinary approaches. We also hope that it will be more useful for horticulturists and material mediciners.

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# 1. Historical survey

The name *Gentiana* in its modern sense is generally accredited to Tournefort, who was first described this genus in 1700: “*Gentiana* est plantae genus, flore monopetalo campaniformi vel patente, vel tubulato et multifido; ex cujus calyce surgit pistillum, quod infimam floris partem perfodit, abique deinde in fructum membranaceum, ovato-acuminatum, bivalvem, unicapsularem, seminibus foetum plerumque planis, orbiculatis et marginatis. *Gentiana* ut refert Dioscorides primum inventa creditur a Gentio Illyriorum Rege, a quo etiam cognomentum habuit”.

In 1718 and 1745 Ruppium divided *Gentiana* into two genera (*Gentiana* and *Gentianella*), which were within the modern *Gentiana* sensu lato.

In 1737 Linnaeus took up Tournefort's *Gentiana* in “Genera Plantarum” and gave the following description: “Cal. Perianthium quinquepartitum, acutum; laciniis oblongis, persistentibus. -Coro. Petalum unicum, inferne tubulatum, imperforatum, superne quinquefidum, planum, marcescens, figura varia, -Stam. Filamenta quinque, subulata, corolla breviora. Antherae simplices. -Pist. Germen oblongum, cylindraceum, longitudine staminum. Styli nulli. Stigmata duo, simplicia. -Per. Capsula oblonga, teres, acuminata, apice leviter bifida, unilocularis, bivalvis. - Sem. numerosa parva. Receptacula duo singulae valvulae longitudinaliter adnata. - Obs. Fructus figura constans est. Floris autem numerus et figura valde variat in diversis speciebus”. Linnaeus also united *Centaurium minus* Tournefort with *Gentiana* and divided this genus into seven groups: 1) species alia corollae collo patente; 2) alia collo villis clauso; 3) alia laciniis corollae ciliatis; 4) alia limbo campanulato, erecto, plicato; 5) alia limbo stellato, lacinulis laciniis interjectis; 6) alia campanulata; 7) alia infundibuliformi gaudet corolla. The fifth edition of Linnaeus' “Genera Plantarum” was reprinted in 1754.

In 1753 Linnaeus redivided *Gentiana* less successfully into three unnamed groups, describing 23 species, of which the first, *G. lutea* L., was taken as the type species of *Gentiana* by later authors:

\* Corollis quinquefidis subcampaniformibus. This group included *G. lutea*, *G. purpurea*, *G. punctata*, *G. asclepiadea*, *G. pneumonanthe*, *G. saponaria*, *G. villosa*, and *G. acaulis*.

\*\* Corollis quinquefidis infundibuliformibus. This group included *G. verna*, *G. bavarica*, *G. nivalis*, *G. aquatica*, *G. utriculosa*, *G. centaurium*, *G. spicata*, *G. quinquefolia*, and *G. amarella*.

\*\*\* Corollis non quinquefidis. This group included *G. campestris*, *G. ciliata*, *G. cruciata*, *G. sessilis*, *G. filiformis*, and *G. perfoliata*.

In 1790 Necker included most of the Gentianoideae in one of his all-inclusive “genera”. His genus *Darinyphytum* included not only most of the Gentianoideae but also a great variety of incongruous groups from a number of modern families. Within this “genus” he recognized a number of “species”, of which some were equivalent in extent to modern genera or sections (*Pneumonanthe* = *Gentiana* sect. *Pneumonanthe*, *Anthopogon* = *Gentianopsis*, and *Spiragyne* = *Gentianella*). In most cases his descriptions are so inadequate that these “species” cannot be identified readily with modern taxa. Plates published in his “Elmenta Botanica” demonstrate characters used in the diagnosis of his super-genera. This ambiguity of description, failure to include names on which his “species” were based, and his usage of a species concept quite at variance with either modern practice or that of other authors of his day, makes these names nomina invalida. Significantly, thorough examination of the 1950 International Code reveals that 57 Neckerian names were rejected for one reason or another, and 6 were conserved in addition to three proposed for conservation.

In 1794 Moench segregated the genus *Gentianella* from Linnaean *Gentiana*, based on *Gentiana*

*campestris* L. which he renamed *Gentianella tetrandra* Moench.

In 1796 Schmidt divided Linnaeus' *Gentiana* into six segregate genera: *Chironia*, *Gentiana*, *Swertia*, *Chlora*, *Pneumonanthe* and *Hippion*. Currently the first four genera are still recognized as separate genera, but his *Pneumonanthe* is mainly included in sections (*Gentiana*, *Pneumonanthe*, *Calathianae*, *Chondrophyllae*, *Calathianae*, and *Ciminalis*) of *Gentiana* sensu stricto, and *Hippion* mainly in *Gentianella*, *Gentianopsis* or other genera excluded from the subtribe Gentianeae.

Borkhausen, in a paper following Schmidt in the same publication, divided Linnaeus' *Gentiana* into 13 genera. Among them *Gentiana* (p. p.), *Asterias*, *Coilantha*, *Dasystephana*, *Hippion*, *Ciminalis*, and *Ericoila* have been included in the modern *Gentiana* sensu stricto. *Gentiana* (p. p.) and *Erythalia* are within the modern genus *Gentianella*. His *Gentianella* corresponds to the modern *Gentianopsis*, *Centaurium* to *Canscora* and *Erythraea* to *Centaurium*. Only his *Swertia*, *Halenia* and *Chlora* remain as segregate genera in the modern classification of Gentianeae.

In 1796 Froelich monographed *Gentiana* for the first time (Table 1. 1), describing 47 species in four groups of uncertain ranks, of which two belonged to *Gentiana* sensu stricto and the other two belonged to *Gentianella*. Froelich's system was the most successful until his time. This system may be summarized as follows:

\* *Coelanthae*. Corollis campanulatis, 5–9-fidis. This group included 21 species, but it has been treated as a synonym of sect. *Gentiana* because it contains *G. lutea* L., the type species of the latter (Pringle 1978).

\*\* *Calathianae*. Corollis infundibuliformis, nudis, quinque- v. decemfidis. This group included 11 species. It has been included as a formal section in the genus *Gentiana*, and *G. nivalis* L. was designated as the type species by latter authors.

\*\*\* *Endotrichae*. Corollis fauce squamis capillaceo-multifidis auctis, quinque- v. quadrifidis. This group contained 10 species. As *Endotrichae* circumscribed by Froelich included *Gentiana campestris* L., the type species of the genus *Gentianella*, so it was treated as a synonym of the latter.

\*\*\*\* *Crossopetalae*. Corollis quadrifidis hypocrateriformibus fauce nudis. This group included 5 species, but it has been treated as a section of *Gentiana* sensu lato or as a genus (*Gentianopsis*) by latter authors.

In 1821 Link recognized Linnaeus' circumscription and divided *Gentiana* into three sections (*Gentiana*, *Pneumonanthe* and *Amarella*). In 1829 Link redivided it into two genera (*Gentiana* and *Gentianella*) and subdivided the former into five sections (*Gentiana*, *Ericoila*, *Pneumonanthe*, *Hippion*, and *Gentianella*).

In 1824 Bunge maintained a classification somewhat influenced by Froelich and Borkhausen but described 80 species, which were nearly twice as many species as recognized by Froelich. He divided *Gentiana* into nine sections, among which six still belonged to *Gentiana* sensu lato but the other three belonged to *Gentianella*, *Gentianopsis*, or *Lomatogonium*. Bunge's classification is as follows:

I. Sect. *Asterias*. Corollis fauce nudis rotatis. This section consisted of two species.

II. Sect. *Coelanthae* Bunge. Corollis fauce nudis campanulatis. This section contained 18 species, but it has been treated as a synonym of *Gentiana* sect. *Gentiana*.

III. Sect. *Pneumonanthe*. Corollis fauce nudis infundibuliformibus. This section included 6 species.

IV. Sect. *Crossopetalae*. Corollis fauce nudis hypocrateriformibus, quadrifidis, laciniis ciliatis. This section included 6 species.

V. Sect. *Calathianae*. Corollis fauce nudis hypocrateriformibus, quinquefidis. This section consisted of 15 species.

VI. Sect. *Chondrophyllae* Bunge. Corollis fauce nudis hypocrateriformibus, subdecemfidis. This section



included 6 species, and it was recognized as a formal section, in which *Gentiana aquatica* L. was designated as the type species by latter authors.

VII. Sect. *Erythaliae* Bunge. Corollis fauce nudis tubulosis. It included 9 species. Because the section *Erythaliae* circumscribed by Bunge included *Gentiana cruciata* L., the type species of *Gentiana* sect. *Cruciatata* Gaudin, it was treated as a synonym of the latter.

VIII. Sect. *Endotrichae*. Corollis fauce barbatis. This section included 14 species.

IX. Sect. *Trochanthae* Bunge. Corollis fundo squamosis rotatis. This section included four species. However, one species should belong to the genus *Swertia* and the other three belong to the genus *Lomatogonium*, in which *L. carinthiacum* (Wulfen) Reichenbach (= *Gentiana carinthiaca* Froelich) is the type species.

In 1836 Endlicher essentially adopted Bunge's system in his "Genera Plantarum" but changed the orthography of some names.

In two publications in 1837 D. Don and G. Don did not recognize Linnaeus' circumscription but divided *Gentiana* into small genera. In "Descriptions of Indian Gentianeae" D. Don divided *Gentiana* into four genera (*Gentiana* Borkhausen, *Pneumonanthe* Schmidt, *Ericala* Renealmi, and *Eurythalia* Renealmi). Among them the first three genera belong to *Gentiana* sensu stricto. In "A General System of Dichlamydeous Plants", G. Don included 29 genera in the subtribe Gentianineae, of which four genera (9 *Asterias*, 10 *Coilantha*, 13 *Ericala*, and 14 *Pneumonanthe*) belonged to *Gentiana* sensu stricto.

Grisebach's monographic study of Gentianaceae is a landmark among works on the family. In "Genera et Species Gentianaceae" (1838) he divided the 125 species of *Gentiana* into seven sections. In his 1845 of treatment of Gentianaceae in De Candolle's "Prodromus" he redivided *Gentiana* into 15 sections, of which seven (*Asterias*, *Coelanthae*, *Pneumonanthe*, *Tretorrhiza*, *Chondrophyllae*, *Thylacites*, *Cyclostigma*, and *Eurythalia*) belonged to *Gentiana* sensu stricto, and the number of species increased to 153. His system is as follows:

I. Sect. *Asterias* Renealmi. Calyx obliterated, spathaceo-dimidiatus. Corolla rotata, nuda, plicis destituta, 5-6-partita. Antherae erectae, liberae. Stylus nullus, stigmatibus 2 distinctis. Capsula sessilis. Testa alata, ala concolori. Herba perennis. This section included one species, *Gentiana lutea* L.

II. Sect. *Andicola* Grisebach. Calyx integer, basi in tubum connexus. Corolla rotata vel hypocraterimorpha, plicis glandulisque destituta; hinc inter filamentorum basim barbata nuda vel rarius fimbriis coronata. Antherae versatiles, liberae. Stylus subnullus, stigmatibus 2 distinctis. Capsula sessilis. Testa exalata. Herba perennis. This section contained 46 species, but it has been transferred to the genus *Gentianella* as a separate section with the type species *G. diffusa* (Humboldt, Bonpland & Kunth) Fabris by Holub (1967).

III. Sect. *Imaicola* Grisebach. Calyx integer, basi in tubum connexus. Corolla infundibuliformis, plicis glandulisque destituta, imberbis. Antherae versatiles, liberae. Stylus nullus, stigmatibus 2 distinctis. Capsula sessilis. Testa exalata. Herba annua. This section included 2 species. However, one species (*Gentiana contorta* Royle) has been transferred to the genus *Gentianopsis* and another species (*G. oligosperma* Griseb.) to the genus *Jaeschkea* (= *J. gentianoides* Kurz).

IV. Sect. *Amarella* Grisebach. Calyx integer, in tubum connexus. Corolla hypocraterimorpha, plicis glandulisque destituta, saepius fimbriis e basi limbi ortis coronata. Antherae versatiles, liberae. Stylus nullus, stigmatibus 2 distinctis. Capsula plerumque sessilis. Testa exalata. Testa exalata. Herba annua. This section contained 14 species. Because Grisebach's section *Amarella* included *G. campestris* L., the type species of the earlier section, *Gentianella* sect. *Gentianella*, it has been treated as a synonym of the latter.

V. Sect. *Antarctophila* Grisebach. Calyx integer, in brevem tubum connexus. Corolla rotata, plicis glandulisque destituta, imberbis. Antherae versatiles, liberae. Stylus nullus, stigmatibus 2 distinctis. Capsula

sessilis. Testa exalata. Herba annua. This section includes 4 species. It has been transferred to the genus *Gentianella* as a separate section and *Gentianella montana* (Forst.) Holub (= *Gentiana montana* Forst.) was designated as the type species by Holub (1967).

VI. Sect. *Arctophila* Grisebach. Calyx integer, basi in tubum connexus. Corolla infundibuliformis vel hypocraterimorpha, plicis destituta, inter basim filamentorum glandulifera, non coronata, in loborum margine hinc inde setulis subsolitariis instructa. Antherae versatiles, liberae. Stylus nullus, stigmatibus 2 distinctis. Capsula sessilis. Testa exalata. Herba annua. This section included 7 species. It has been transferred to *Gentianella* as a separate section and *Gentiana aurea* (L.) Harry Smith ex Hylander is the type species.

VII. Sect. *Crossopetalae* Froelich. Calyx integer, in tubum connexus. Corolla infundibuliformis vel hypocraterimorpha, plicis destituta, inter basim filamentorum glandulifera, non coronata, in margine loborum plerumque fimbriata vel crenata. Antherae plerumque versatiles, liberae. Stylus nullus vel distinctus, stigmatibus 2 distinctis, orbiculatis vel in una specie contiguus. Capsula sessilis vel stipitata. Testa patula, sive squamulosa, sive apicibus subalata. Herba annua vel perennis. This section contained 7 species.

VIII. Sect. *Cyclostigma* Grisebach. Calyx integer, ope epidermidis in tubum connexus. Corolla hypocraterimorpha vel infundibuliformis, tubo cylindrico, plicis rotundatis vel bifidis aucta, glandulis destituta, non coronata, margine hinc crenata. Antherae erectae, liberae. Stylus distinctus, stigmatibus contiguus, orbiculato-infundibularibus, margine horizontali plerumque crenato-fimbriatis. Capsula sessilis vel breviter stipitata. Testa appressa, reticulata, in una specie alata. Herba annua vel perennis. This section contained 7 species. Because Grisebach's section *Cyclostigma* included *Gentiana nivalis* L., the type species of the earlier section *Calathianae* Froelich, it has been treated as a synonym of the latter.

IX. Sect. *Chondrophyllae* Bunge. Calyx integer, ope epidermidis in tubum connexus. Corolla infundibuliformis vel hypocraterimorpha, plicis aucta, glandulis destituta, non coronata. Antherae erectae, liberae. Stylus nullus aut distinctus, stigmatibus binis distinctis oblongis demum revolutis. Capsula demum longissime stipitata. Semina oblonga, testa appressa exalata, laevis. Herba annua vel perennis. This section included 22 species.

X. Sect. *Eurythalia* Grisebach. Calyx integer, ope epidermidis in tubum connexus. Corolla infundibuliformis, plicis aucta, glandulis destituta, fimbriis coronata. Antherae demum versatiles, liberae. Stylus distinctus, stigmatibus binis oblongis. Capsula stipitata. Testa alata. Herba annua. This section was of 3 species. The name of this section is illegitimate and thus the section has been renamed as sect. *Fimbricorona* T. N. Ho with the type species *Gentiana coronata* Royle.

XI. Sect. *Pneumonanthe* Necker. Calyx integer, ope epidermidis in tubum connexus, vel rarius spathaceo-dimidiatus. Corolla plicis aucta, glandulis destituta, non coronata, lobis cum tubo continuis, clavata, obconica vel campanulata. Antherae plerumque erectae, liberae aut connatae, loculis tum extrorsum apertis. Stylus brevis vel saepius nullus, stigmatibus binis distinctis oblongis integerrimis demum revolutis. Capsula demum stipitata. Testa saepissime ala discolori cincta, quibusdam exalata. Herba perennis. This section contained 30 species.

XII. Sect. *Thylacites* Reenalmi. Calyx integer, ope epidermidis in tubum connexus. Corolla plicis aucta, glandulis destituta, non coronata, lobis brevibus subpatulis infundibuliformi-campanulata. Antherae erectae, connatae, hinc lusu liberae. Stylus brevis, stigmatibus subcontiguus dilatatis connato-fimbriatis horizontalibus, demum distinctis. Capsula basi attenuata. Testa exalata, cum albumine rugosa. Herba perennis. This section only included one species, *Gentiana acaulis* L. However, this species is the type species of the earlier section *Ciminalis* (Adanson) Dumort., so the section has been treated as a synonym of the latter.

XIII. Sect. *Coelanthae* Reenalmi. Calyx integer, ope epidermidis in tubum connexus, aut spathaceo-

dimidiatus. Corolla plicis aucta, glandulis destituta, non coronata, lobis cum tubo continuis, obconica vel campanulata. Antherae erectae, connatae, extrorsum dehiscentes. Stylus distinctus, stigmatibus binis oblongis revolutis integerrimis. Capsula sessilis. Testa ala concolori cincta. Herba perennis. This section included 4 species.

XIV. Sect. *Dasystephana* Grisebach. Calyx integer in tubum connexus. Corolla plicis glandulisque destituta, non coronata, lobis erectiusculis campanulato-hypocraterimorpha. Antherae erectae liberae. Stylus subnullus, stigmatibus binis latis. Capsula sessilis. Testa exalata. Herba perennis. This section only included one species, *Gentiana thyrsoides* Hooker which belonged to the genus *Gentianella*.

XV. Sect. *Tretorrhiza* Renealmi. Calyx integer, ope epidermidis in tubum connexus. Corolla plicis bifidis aucta, glandulis destituta, non coronata, hypocraterimorpha. Antherae erectae vel incumbentes, liberae. Stylus plerumque nullus, stigmatibus binis oblongis revolutis integerrimis. Capsula sessilis. Testa exalata. Herba perennis vel annua. This section consisted of 4 species. The sectional name is illegitimate because it includes the type species (*Gentiana cruciata* L.) of the earlier section *Cruciata* Gaudin, so it has been treated as a synonym of the latter.

In addition, in 1838 Grisebach also separately treated the then known 23 species of North American species in Hooker's "Flora Boreali-Americana".

Most 19<sup>th</sup> century botanists working on the Gentianaceae followed Grisebach's system, e.g., Turczaninow in his "Mongraphische Beschreibung der Enzianen" (1860) and Bentham and Hooker in "Genera Plantarum" (1875).

In 1841 Reichenbach divided Linnaeus' *Gentiana* into two groups (*Gentiana* and *Gentianella*), and he further divided the former into six sections (*Ericala* Renealmi, *Pneumonanthe* Cordus., *Tretorrhiza* Renealmi, *Chondrophyllae* Bunge, *Coilantha* Renealmi, and *Gentiana* L.).

In 1875 Clarke treated the Indian species of *Gentiana* in J.D. Hooker's "Flora of British India". Not only did he discover many new species but also establish a new section *Kurroo*, which was misplaced in sect. *Pneumonanthe* by Grisebach (1845). In 1883 Clarke revised the Indian *Gentiana* and established another new section *Stylophora*, based on *Gentiana stylophora* C. B. Clarke. A few years later, Hemsley (1890) also established a section *Megacodon* Hemsl., which corresponded in extent to sect. *Stylophora*, but based it on a different species, *Gentiana venosa* Hemsl. In 1936 Smith raised Hemsley's section *Megacodon* to generic rank, but in 1965 Toyokuni replaced it in *Gentiana* as a subgenus.

In 1878 Asa Gray divided the American species of *Gentiana* into two parts: *Pneumonanthe* with a plicate corolla and *Gentianella* with a non-plicate corolla.

In 1888 Huxley suggested a rearrangement of the family Gentianaceae based on the position of corolla nectaries. His *Mesomelitae* included the plants having glands at the base of ovary, while *Perimelitae* included those with epipetalous glands.

Kusnezow's monograph of *Gentiana* subgenus *Eugentiana* (1894) and his treatment of *Gentiana* in Engler & Prantl's "Die natürlichen Pflanzenfamilien" (1895) provided a generally accepted basis for the division of *Gentiana* into sections. His subgen. *Eugentiana* corresponded to *Gentiana* sensu stricto as a genus, and was divided into 10 sections (*Coelanthae*, *Pneumonanthe*, *Stenogyne*, *Frigidae*, *Aptera*, *Chondrophyllae*, *Otophora*, *Isomeria*, *Thylacites*, and *Cyclostigma*), with 162 species. Kusnezow's system can be summarized as follows:

I. Sect. *Coelanthae* Renealmi. Radix perennis. Caules erecti, solitarii, vegetiores; folia lata, ima petiolata, connato-vaginata, radicalia fasciculata, margine non cartilaginea. Flores speciosi 5—6—7—meri, flavi v. purpurascens, saepius punctati, pedicellati v. sessiles, axillares terminalesque aggregati. Calyx integer et

membrana intracalycina in tubum connexus v. obliteratedus, membrana intracalycina vaginali dimidiata. Corolla rotata, plica intermedia destituta, v. campanulata, plica parva asymmetrica aucta, fimbriis destituta, lobis cum tubo continuis. Antherae connatae v. liberae; filamenta gracillima, exalata. Stigmata distincta, oblonga, integerrima, demum revoluta; stylus distinctus; capsula sessilis v. (in *G. pannonica* Scop.) breviter stipitata. Testa ala lata concolori cincta. Herba perennis. This section included 5 species and 6 hybrid forms.

II. Sect. *Pneumonanthe* Necker. Radix perennis. Caules erecti, adscendentes v. procumbentes, solitarii v. plures, foliosi; folia in plurimis margine non cartilaginea, radicalia desunt (excl. *G. newberryi* Gray), omnia caulina, ima squamiformia, cetera foliosa, lata v. angusta, plerumque sessilis. Flores plures, rarius solitarii, terminales v. axillares, sessiles, rarius pedicellati. Calyx integer et membrana intracalycina in tubum connexus, rarius obliteratedus, membrana intracalycina vaginali dimidiata. Corolla plica aucta, fimbriis destituta, clavata, obconica v. campanulata, lobis cum tubo continuis, saepe punctata v. vittata, plerumque cyanea, rarius alba, flava v. purpurea; plica parva v. magna asymmetrica, rarius symmetrica, integra v. bifida. Antherae connatae v. liberae; filamenta plus minus alata, rarius exalata. Stigmata distincta, oblonga, integerrima, demum revoluta; stylus brevis v. distinctus, rarius subnullus; capsula stipitata. Testa saepissime ala discoroli cincta, quibusdam exalata. Herba perennis. This section contained 41 species.

III. Sect. *Otophora* Kusnezow. Radix perennis. Caules adscendentes; folia margine non cartilaginea, radicalia fasciculata petiolata. Flores plures, dense fasciculati, pedicellati. Calyx integer v. subinteger et membrana intracalycina in tubum connexus. Corolla fere ad basin usque 5-loba, campanulata v. subrotata, plica asymmetrica parva aucta, fimbriis destituta, tubo brevissimo. Antherae liberae, versatiles. Stigmata distincta, oblonga, integerrima, demum revoluta; stylus brevis; capsula breviter stipitata. Testa alata, reticulata. Herba perennis. This section included one species, *Gentiana otophora* Franchet, and was described as new.

IV. Sect. *Stenogyne* Franchet. Radix perennis v. annua. Caules erecti v. procumbentes, quadranguli, foliosi, valde ramosi, ramis unifloris; folia firma, plerumque ovato-cordata, margine cartilaginea, scabra v. crispa. Flores 5-meri, speciosi, plerumque inter foliorum par supremum sessiles, rarius brevissime pedunculati. Calyx integer et membrana intracalycina in tubum connexus, plerumque alatus. Corolla plica aucta, fimbriis destituta, campanulata, lobis cum tubo continuis, v. hypocraterimorpha tubo angusto; plica magna, asymmetrica, integra, saepius quadrata. Antherae liberae, filamenta alata v. exalata filiformia, apice recurva v. erecta. Stigmata distincta, anguste linearia, elongata, integerrima, demum revoluta; stylus longissimus longitudine capsulam aequans; capsula elongata, sessilis v. longe stipitata. Semina rotundata v. triquetra, alata v. rarius exalata. Herba perennis v. annua. This section included 6 species.

V. Sect. *Frigidae* Kusnezow. Radix perennis v. annua. Caules plerumque caespitiosi, procumbentes v. adscendentes, rarius erecti; folia saepius margine cartilaginea, ima rosulata v. fasciculata, rarius radicalia desunt. Flores plerumque speciosi plures v. solitarii. Calyx integer et membrana intracalycina in tubum connexus, rarius membrana intracalycina vaginali dimidiata. Corolla plica aucta, fimbriis destituta, clavata, obconica v. campanulata, lobis cum tubo continuis, saepe punctata v. vittata; plica asymmetrica, saepe uno latere auriculata. Antherae liberae, rarius connatae. Stigmata distincta, oblonga, linearia, demum revoluta, v. apice aucta, v. orbiculata horizontalia; capsula longe stipitata e corolla exserta v. inclusa, apice in stylum brevem v. longum attenuata v. stylo nullo. Testa lamellosa-rugosa, lamellis albis areolas hexagonas formantibus, rarius testa utriculato-alveolata v. longitudinaliter lamellis crispis alaeformibus oblecta. Herba perennis v. annua. This section was of three groups.

A. *Typicae*. Testa lamellosa-rugosa, lamellis albis areolas hexagonas formantibus. Group A was further divided into two unnamed series; series I with 6 species and series II with 17 species.

B. *Phyllocalyx*. Testa longitudinaliter lamellis crispis alaeformibus obtecta. Stigmata orbiculata, horizontalia. This group included one species (*Gentiana phyllocalyx* C.B. Clarke).

C. *Froelichii*. Testa longitudinaliter lamellis crispis alaeformibus obtecta. Stigmata linearia, demum revoluta. This group included one species (*Gentiana froelichii* Jan ex Reichenbach).

VI. Sect. *Aptera* Kusnezow. Radix perennis. Rhizomatis collum filamentoso-comosum. Caules erecti, adscendentes v. procumbentes, solitarii v. plures, rarius acaulis (*G. biflora* Rgl.); folia margine vix cartilaginea, radicalia fasciculata, omnia plerumque linearia v. lineari-lanceolata, basi vaginato-connata. Flores plures, rarius subsolitarii, terminales v. axillares, sessiles v. pedicellati. Calyx integer et membrana intracalycina in tubum connexus v. obliterated, membrana intracalycina vaginali dimidiata. Corolla plica aucta, fimbriis destituta, campanulata v. tubulosa, tubo cum limbo continuo, v. subhypocraterimorpha tubo a limbo distincto, cyanea v. lutea; plica magna plerumque symmetrica bifida, rarius asymmetrica v. integra. Antherae liberae, filamenta plerumque anguste alata. Stigmata distincta, oblonga, linearia, demum revoluta; stylus brevis v. distinctus, rarius subnullus; capsula sessilis v. stipitata. Testa oblonga appressa exalata reticulata v. laevis, rarius uno latere alata. Herba perennis. This section contained 17 species. Sect. *Aptera* was established by Kusnezow in 1893 and included two species (*Gentiana kaufmanniana* Regel & Schmalhausen var. *afghanica* Kusnezow and *G. biflora* Regel ex Kusnezow). The following year, Kusnezow (1894) indicated the full scope of the section and included *G. cruciata* L., the type species of the earlier section *Cruciata*. Thus, the sectional name *Aptera* is clearly superfluous.

VII. Sect. *Isomeria* Kusnezow. Radix perennis v. annua. Caules caespitiosi; folia margine cartilaginea v. non cartilaginea, ima rosulata v. radicalia desunt. Flores speciosi, solitarii v. plures. Calyx integer et membrana intracalycina in tubum connexus. Corolla plica aucta, fimbriis destituta, obconica v. campanulata, lobis cum tubo continuis, plerumque vittata; plica magna, symmetrica. Antherae liberae. Stigmata distincta, oblonga, linearia, demum revoluta; capsula elongata, basi plerumque obtusa, longe stipitata, e corolla exserta, v. breviter stipitata, inclusa, apice acuta, in stylum brevem v. longum attenuata. Testa oblonga, appressa, exalata. Herba perennis v. annua. This section included 5 species.

VIII. Sect. *Chondrophyllae* Bunge. Radix perennis v. annua. Caules plerumque caespitiosi, procumbentes v. adscendentes, rarius erecti. Folia margine plus minus cartilaginea, plerumque minuta, saepius ima rosulata, rarius radicalia desunt. Calyx integer et membrana intracalycina in tubum connexus. Corolla infundibuliformis v. hypocraterimorpha, plicis aucta, plerumque non coronata, rarius fimbriis coronata, saepe punctata v. vittata; plica symmetrica, magna. Antherae erectae v. demum versatiles liberae. Stylus distinctus v. nullus, stigmatibus binis distinctis oblongis demum revolutis, rarius apice dilatatis. Capsula plerumque brevis, late obovata, apice rotundata, plus minus cristata, basi attenuata, demum longissime stipitata, e corolla exserta v. inclusa, rarius capsula obovata sessilis v. oblongo-linearis basi supra stipitem longum rotundata. Semina oblonga, testa appressa exalata laevis. Herba perennis v. annua. It contained 54 species. The section was divided into two groups: A. Perennes with 6 species; B. Annuae with 48 species.

IX. Sect. *Thylacites* Reichenbach. Radix perennis. Caules caespitiosi. Folia margine non cartilaginea, ima rosulata. Flores solitarii, terminales. Calyx integer et membrana intracalycina hinc rupta connexus. Corolla cyanea, punctata, infundibuliformis, plica aucta, fimbriis destituta, lobis brevibus cum tubo continuis; plica asymmetrica. Antherae erectae, connatae, hinc lusu liberae. Stigmata dilatata, crenato-fimbriata, horizontalia, subcontigua, demum distincta; capsula basi attenuata. Testa exalata, appressa, cum albumine rugosa. Herba perennis. This section included one species (*Gentiana acaulis* L.) and four subspecies.

X. Sect. *Cyclostigma* Grisebach. Radix annua v. perennis. Caules plerumque caespitiosi. Folia margine non v. paulo cartilaginea. Calyx integer et membrana intracalycina in tubum connexus. Corolla hypocrateri-

morpha v. *infundibuliformis*, plerumque pulchre cyanea, rarius lutea tubo cylindrico, plicis symmetricis rotundatis v. bifidis, saepius albis aucta, fimbriis destituta, margine hinc crenata. Antherae erectae, liberae. Stylus distinctus, sigmatibus contiguus orbiculato-infundibularibus, margine horizontali plerumque crenato—fimbriatis; capsula sessilis v. breviter stipitata. Testa appressa, reticulata, exalata. Herba perennis v. annua. This section included 6 species, which sorted out two groups (*Perennes* and *Annuae*).

Kusnezow made no attempt to revise subgenus *Gentianella* beyond establishing characters to distinguish it. Although *Gentianella* was separated from *Gentiana* as a distinct genus as early as 1794 by Moench. Kusnezow (1895) still treated this group as a subgenus. It was until Gillett (1957) that the segregation of *Gentianella* from *Gentiana* was generally accepted.

In 1896 Wettstein established a new section, *Comastoma*, distinguished by the corolla bearing two evascular fimbriate scales at the throat of each lobe. Sixty-five years later (1961) Toyokuni raised this section to generic rank and designated *Comastoma tenellum* (Rottboell) Toyokuni as the type species, and the following year he further discussed the relationships with its allies.

Marquand published several papers from 1928 to 1937, notably his revision of Chinese species of *Gentiana* (1937). The genus included 163 species, of which 34 were endemic to China (more than the numbers of species that Kusnezow (1894) described for the whole world). He adopted mainly the infrageneric classification of Kusnezow's subgenus *Eugentiana*, but combined the genera *Crawfordia* and *Tripterospermum* with *Gentiana* as two additional sections and relegated *Pterygocalyx* to *Gentianella*, which had been excluded from *Gentiana* by him in an earlier paper (1931). He also subdivided sections into some series. Certainly these series are very useful, especially for the large section *Chondrophyllae* which includes about 40% species of the whole genus. Marquand's system of 1937 is as follows:

I. Sect. *Otophora* Kusnezow.

i. Ser. *Otophorae* Marquand. Plantae dense caespitosae; folia caulina numerosa. This series included 4 species.

ii. Ser. *Decoratae* Marquand. Plantae haud caespitosae; folia caulina pauca. This series included 3 species.

II. Sect. *Stenogyne* Franchet ex kusnezow. This section contained 14 species and one variety.

III. Sect. *Dipterospermum* (C. B. Clarke) Marquand. This section included 19 species.

IV. Sect. *Tripterospermum* (Blume) Marquand. This section contained 2 species and 1 variety.

V. Sect. *Frigidae* Kusnezow.

i. Ser. *Verticillatae* Marquand. Perennes; folia verticillata, 3–7-nata, angusta; flores magni, terminales, solitarii. This series was of 9 species and 2 varieties.

ii. Ser. *Ornatae* Marquand. Perennes; folia opposita, angusta; flores magni, terminales, solitarii. This series included 6 species and 2 varieties.

iii. Ser. *Suborbisepalae* Marquand. Perennes; folia opposita, laxa; flores solitarii, terminales; calycis lobi suborbiculares vel spatulati; corollae tubus fauce constrictus. This series consisted of 3 species.

iv. Ser. *Confertifoliae* Marquand. Perennes; folia opposita, imbricata, latoria, margine cartilagineo; flores solitarii, terminales; corollae tubus fauce haud constrictus. This series included 4 species.

v. Ser. *Uniflorae* Marquand. Perennes; caudex crassus; folia opposita, imbricata, latoria; calycis lobi haud in basin attenuati; flores solitarii, terminales; corollae tubus fauce haud constrictus sed leviter expansus. This series included 5 species.

vi. Ser. *Sikkimenses* Marquand. Perennes; flores numerosi, ± congesti; folia radicalia conspicua; folia caulina opposita. This series included 4 species.

vii. Ser. *Multiflorae* Marquand. Perennes; flores numerosi; folia radicalia nulla. This series contained 17 species and 2 varieties.

viii. Ser. *Annuae* Marquand. Plantae annuae.

1. Subser. *Tetramerae* Marquand. Calyx 4-lobatus. This subseries contained 2 species.

2. Subser. *Pentamerae* Marquand. Calyx 5-lobatus. This subseries contained 3 species and 1 variety.

VI. Sect. *Aptera* Kusnezow. This section included 12 species and 1 variety.

VII. Sect. *Pneumonanthe* (Necker) Link. This section included 1 species and 1 variety.

VIII. Sect. *Isomeria* Kusnezow. This section comprised 1 Chinese species.

IX. Sect. *Chondrophyllae* Bunge.

i. Ser. *Pubigerae* Marquand. Caulis, folia et calyx pubescentia. This series consisted of 1 species and 1 variety.

ii. Ser. *Fimbriatae* Marquand. Plicae fimbriatae. This series contained 8 species.

iii. Ser. *Orbiculatae* Marquand. Calycis lobi ovato-lanceolati, recurvati. This series comprised 6 species.

iv. Ser. *Linearifoliae* Marquand. Folia caulina linearia vel subulata, elongata, angustissima. This series included 7 species and 1 variety.

v. Ser. *Rubicundae* Marquand. Flores magni (usque ad 5 cm. longi), carmesini. This series included 3 species and 2 varieties.

vi. Ser. *Humiles* Marquand. Flores parvi, caerulei vel albi. This series comprised 49 species and 3 varieties.

In 1936, Smith treated the subgenus *Gentianella* of Kusnezow (1895) as a distinct genus from *Gentiana* and almost 30 years later (1965) he reinstated *Crawfurdia* and *Tripterospermum* as two independent genera. In 1961, when Smith studied the *Gentiana cachemirica* Decne group he combined section *Frigidae* with section *Isomeria* and redivided section *Isomeria* into two subsections; *Monopodiae* and *Sympodiae*, based on the difference in branching types which were very important character in perennial *Gentiana*.

In 1951 Ma segregated sect. *Crossopetalae* from *Gentiana* as a distinct genus, *Gentianopsis* and designated *G. barbata* (Froelich) Ma as the type species.

In a series of papers published between 1967 and 1979, Pringle monographed sect. *Pneumonanthe* and sect. *Chondrophyllae* of the eastern North America, Central America, and Mexico and made a careful and clear revision of sectional and subsectional names.

In 1985 and 1988 Ho & Liu monographed the Gentianaceae with 427 species from China, of which 247 belonged to *Gentiana*. In 1990 they studied the genus *Gentiana* for the whole world and presented an infrageneric classification with 15 sections, of which 5 sections were subdivided into 22 series. In both their works *Gentiana* clearly corresponded to subgen. *Eugentiana* Kusnezow, as a genus.

In 1988 Halbmayr monographed the genus *Gentiana*. He included morphology as well as illustrations, chromosome numbers and anatomy of some species.

The most recent work on *Gentiana* is that of Haldas'. In 1995 he published "A synopsis of the new system of the genus *Gentiana*" and next year (1996) he monographed an illustrated book "The genus *Gentiana*". In both works he replaced *Stylophora* in *Gentiana* as a subgenus which had been excluded from *Gentiana* by most recent authors. He also raised almost all sections and series, which had been recognized by most recent authors, to subgeneric and sectional ranks respectively. In addition, he reduced some species to subspecies or varieties but no plain explanation of the new diagnostic characters he was using. However, the excellent illustrations in this book are very useful.

In the last thirty years some authors (Löve. & Löve 1972, 1975, 1976, 1978, 1986, Holub 1973, Lá nz 1976 and Weber 1985, Omer 1985, Omer & Qaiser 1992, Zuyev 1985, 1990, etc.) suggested that the genus *Gentiana* should be divided into many small genera, 15 genera in all. Among them, Löve. & Löve (1972, 1975), Holub (1973) and Lá nz (1976) suggested four new genera (*Favargeria*, *Gentianodes*, *Kuepferella* and *Holubogentia* = *Holubia*) for *Gentiana*, based on the basic chromosome number. In 1975 they further divided *Gentiana* into what they called monobasic chromosome genera. Thus, in this scheme the genus *Gentiana* was restricted to the five European species treated by Tutin (1972) as sect. *Gentiana*.

When Zuev (1985, 1990) studied Siberian species of *Gentiana*, he reinstated *Calathiana*, *Ciminalis*, *Pneumonanthe*, and *Dasystephana* as separate genera, and divided *Ciminalis* into 2 sections (*Speciosae*, *Chondrophyllae*) whereas *Dasystephana* was divided into 4 sections (*Dasystephana*, *Tretorrhiza*, *Aptera*, and *Frigidae*).

In 1988, 1989, 1991, and 1992 Omer and Qaiser dealt with the Gentianaceae in Pakistan and Kashmir. They recognized twelve genera, of which four (*Kurramiana*, *Aloitis*, *Aliopsis* and *Qaisera*) were described as new and three (*Qaisera*, *Ciminalis*, and *Gentianodes*) should belong to *Gentiana* sensu stricto.

In 1993 Tzvelev made a synopsis of Gentianaceae from the Caucasus. He recognized 22 species in the genus *Gentiana* and divided them into 3 subgenera, of which subgenera *Calathianae* and *Diploma* were combined as new. He also further divided these subgenera into 9 sections (subgen. *Pneumonanthe* into 5 sections with 15 species, subgen. *Calathianae* into 2 sections with 4 species and subgen. *Diploma* into 2 sections with 3 species).

Some 40 botanists have studied *Gentiana* intensively since Linnaeus formally established the genus. They not only discovered large numbers of new species, but they have also treated the genus in a wide variety of ways. More important infrageneric classifications of *Gentiana* treated by different authors are listed in Table 1.1.



**Table 1.1 The circumscription and infrageneric classification of *Gentiana* treated by different authors.**

CG	Ho(present book)	Halda(1996)	Ho (1990)	Marquand (1937)	Kusnezow (1894)	Grisebach(1845)	Bunge(1824)	Frolich (1796)
<i>Gentiana</i>	sect. <i>Gentiana</i> (5)	subgen. <i>Gentiana</i> (5) sect. <i>Gentiana</i> sect. <i>Coilantha</i> ser. <i>Coilantha</i> ser. <i>Spathaceae</i>	sect. <i>Gentiana</i> (5)		subgen. <i>Eugentiana</i> sect. <i>Coelanthae</i> (5)	sect. <i>Asterias</i> (1)  sect. <i>Coelanthae</i> (4)	sect. <i>Asterias</i> (2)  sect. <i>Coelanthae</i> (18)	* <i>Coelanthae</i> (21)
	sect. <i>Pneumonanthe</i> (42)	subgen. <i>Pneumonanthe</i> (76)  sect. <i>Pneumonanthe</i> ser. <i>Pneumonanthe</i> ser. <i>Triflorae</i> ser. <i>Angustifoliae</i> ser. <i>Spathaceae</i> sect. <i>Caliculatae</i> sect. <i>Septemfidae</i> sect. <i>Paradoxae</i> subgen. <i>Newberryi</i> (2)	sect. <i>Pneumonanthe</i> (38)	sect. <i>Pneumonanthe</i> (1)	sect. <i>Pneumonanthe</i> (41)	sect. <i>Pneumonanthe</i> (30)	sect. <i>Pneumonanthe</i> (6)	
	sect. <i>Frigidae</i> (18)	subgen. <i>Frigidae</i> (13) sect. <i>Frigidae</i> sect. <i>Glaucæ</i>	sect. <i>Frigidae</i> (18)	sect. <i>Frigidae</i> (53)	sect. <i>Frigidae</i> (25)			
	sect. <i>Monopodiae</i> (10)	subgen. <i>Monopodiae</i> (34) sect. <i>Apteroideae</i>	sect. <i>Monopodiae</i> (37) ser. <i>Apteroideae</i>	ser. <i>Multiflorae</i>				
	sect. <i>Kudoa</i> (28) ser. <i>Verticillatae</i> ser. <i>Ornatae</i> ser. <i>Monanthae</i>	sect. <i>Kudoa</i> sect. <i>Verticillatae</i> sect. <i>Ornatae</i> sect. <i>Monopodiae</i>	ser. <i>Verticillatae</i> ser. <i>Ornatae</i> ser. <i>Monanthae</i>	ser. <i>Verticillatae</i> ser. <i>Ornatae</i>				
	sect. <i>Phyllocalyx</i> (1)	subgen. <i>Phyllocalyx</i> (1)	sect. <i>Phyllocalyx</i> (1)					
	sect. <i>Isomeria</i> (18) ser. <i>Confertifoliae</i> ser. <i>Uniflorae</i> ser. <i>Stragulatae</i>	subgen. <i>Isomeria</i> (16) sect. <i>Depressae</i> sect. <i>Uniflorae</i> sect. <i>Stragulatae</i>	sect. <i>Isomeria</i> (18) ser. <i>Depressae</i> ser. <i>Uniflorae</i> ser. <i>Stragulatae</i>	ser. <i>Confertifoliae</i> ser. <i>Uniflorae</i>	sect. <i>Isomeria</i> (5)			

CG	Ho(present book)	Halda(1996)	Ho (1990)	Marquand (1937)	Kusnezow (1894)	Grisebach(1845)	Bunge(1824)	Frolich (1796)
Gentiana	ser. <i>Sikkimenses</i>	sect. <i>Sikkimenses</i>	ser. <i>Sikkimenses</i>	ser. <i>Sikkimenses</i>				
	sect. <i>Microsperma</i> (10)	subgen. <i>Microsperma</i> (8)	sect. <i>Microsperma</i> (10)					
	ser. <i>Tetramerae</i>	sect. <i>Tetramerae</i>	ser. <i>Tetramerae</i>					
	ser. <i>Suborbisepalae</i>	sect. <i>Suborbisepalae</i>	ser. <i>Suborbisepalae</i>	ser. <i>Suborbisepalae</i>				
	ser. <i>Annuae</i>	sect. <i>Annuae</i>	ser. <i>Annuae</i>	ser. <i>Annuae</i> & sect. <i>Isomeria</i>				
	sect. <i>Cruciata</i> (21)	subgen. <i>Cruciata</i> (40) sect. <i>Cruciata</i> ser. <i>Cruciatae</i> ser. <i>Olivierianae</i> ser. <i>Kaufmannianae</i> sect. <i>Decumbentes</i> ser. <i>Decumbentes</i> ser. <i>Siphonanthae</i>	sect. <i>Cruciata</i> (21)	sect. <i>Aptera</i> (12)	sect. <i>Aptera</i> (17)	sect. <i>Tretorrhiza</i> (4)	sect. <i>Erythaliae</i> (9)	
	sect. <i>Otophora</i> (12)	subgen. <i>Otophora</i> (7) sect. <i>Otophora</i>	sect. <i>Otophora</i> (12)	sect. <i>Otophora</i> (7)	sect. <i>Otophora</i> (1)			
	ser. <i>Otophorae</i>	sect. <i>Otophora</i>		ser. <i>Otophorae</i>				
	ser. <i>Decoratae</i>	sect. <i>Decoratae</i>		ser. <i>Decoratae</i>				
	sect. <i>Calathianae</i> (8)	subgen. <i>Calathianae</i> (12) sect. <i>Calathianae</i> sect. <i>Vernae</i>	sect. <i>Calathianae</i> (8)		sect. <i>Cyclostigma</i> (7)	sect. <i>Calathianae</i> (15)	sect. <i>Calathianae</i> (15)	
	sect. <i>Ciminalis</i> (7)	subgen. <i>Ciminalis</i> (7)	sect. <i>Ciminalis</i> (5)		sect. <i>Thylacites</i> (1)	sect. <i>Thylacites</i> (1)		
	sect. <i>Dolichocarpa</i> (14)	subgen. <i>Dolichocarpa</i> (12)	sect. <i>Dolichocarpa</i> (14)					
	sect. <i>Chondrophyllae</i> (163)	subgen. <i>Chonerophyllae</i> (122) sect. <i>Chondrophyllae</i>	sect. <i>Chondrophyllae</i> (158)	sect. <i>Chondrophyllae</i> (75)	sect. <i>Chondrophyllae</i> (54)	sect. <i>Chondrophyllae</i> (22)	sect. <i>Chondrophyllae</i> (6)	
ser. <i>Fimbriatae</i>	ser. <i>Fimbriatae</i>	ser. <i>Fimbriatae</i>	ser. <i>Fimbriatae</i>					
ser. <i>Rubicundae</i>	ser. <i>Rubicundae</i>	ser. <i>Rubicundae</i>	ser. <i>Rubicundae</i>					
ser. <i>Humiles</i>	ser. <i>Humiles</i> ser. <i>Linearifoliae</i>	ser. <i>Humiles</i> ser. <i>Linearifoliae</i>	ser. <i>Humiles</i> ser. <i>Linearifoliae</i>	ser. <i>Humiles</i> ser. <i>Linearifoliae</i> ser. <i>Pubigerae</i>				

CG	Ho(present book)	Halda(1996)	Ho (1990)	Marquand (1937)	Kusnezow (1894)	Grisebach(1845)	Bunge(1824)	Frolich (1796)
	ser. <i>Fastigiatae</i> ser. <i>Capitatae</i> ser. <i>Napuliferae</i> ser. <i>Grandiflorae</i>  ser. <i>Coriaceae</i>  ser. <i>Orbiculatae</i> ser. <i>Piasezkianae</i> sect. <i>Fimbricorona</i> total numbers(362)	ser. <i>Fastigiatae</i> ser. <i>Capitatae</i> sect. <i>Napuliferae</i> sect. <i>Pyrenaicae</i> ser. <i>Pyrenaicae</i> ser. <i>Coriaceae</i> ser. <i>Nipponicae</i> sect. <i>Orbiculatae</i> sect. <i>Piasezkianae</i> sect. <i>Fimbricorona</i>	ser. <i>Fastigiatae</i> ser. <i>Capitatae</i> ser. <i>Napuliferae</i> ser. <i>Grandiflorae</i>  ser. <i>Coriaceae</i>  ser. <i>Orbiculatae</i> ser. <i>Piasezkianae</i> sect. <i>Fimbricorona</i> (5)					
	<i>Metagentiana</i>	subgen. <i>Stenogyne</i> (10)	sect. <i>Stenogyne</i> (14) total numbers(361)	sect. <i>Stenogyne</i> (14) total numbers(163.)	sect. <i>Stenogyne</i> (6) total numbers(162)	total numbers(72)	total number(56)	total numbers(32)
excluded from <i>Gentiana</i>	<i>Megacodon</i>	subgen. <i>Stylophora</i> (2) total numbers(364)	<i>Megacodon</i>					
	<i>Gentianella</i>		<i>Gentianella</i>		subgen. <i>Gentianella</i>		sect. <i>Endotrichae</i> (14)	*** <i>Endotrichae</i> (10)
	sect. <i>Gentianella</i> sect. <i>Andicola</i> sect. <i>Antarctophila</i>		sect. <i>Gentianella</i> sect. <i>Andicola</i> sect. <i>Antarctophila</i>			sect. <i>Amarella</i> (14) sect. <i>Andicola</i> (46) sect. <i>Antarctophila</i> (4) sect. <i>Arctophila</i> (7) sect. <i>Dasystephana</i> (1) sect. <i>Crossopetalae</i> (7)		
	sect. <i>Arctophila</i>		sect. <i>Arctophila</i>					
	<i>Gentianopsis</i>		<i>Gentianopsis</i>			sect. <i>Imaicola</i> (2)	sect. <i>Crossopetalae</i> (6)	**** <i>Crossopetalae</i> (5)
	<i>Crawfurdia</i>		<i>Crawfurdia</i>	sect. <i>Dipterospermum</i> (19)				
	<i>Tripterospermum</i>		<i>Tripterospermum</i>	sect. <i>Tripterospermum</i> (2)				
	<i>Lomatogonium</i>		<i>Lomatogonium</i>				sect. <i>Trochanthae</i> (4)	

Notes: the numbers in parentheses = species numbers; CG=the circumscription of *Gentiana*.

## 2. Generic circumscription and systematic position

As indicated in the historical survey, there have been three different viewpoints in the concept of *Gentiana*. *Gentiana* sensu lato (broadest sense), as traditionally circumscribed by Necker (1790), Froelich (1796), Bunge (1829), Grisebach (1838, 1845), Clarke (1883), Grossheim (1952), etc., is a very heterogeneous assemblage of morphologically diverse groups, including most genera of subtribe Gentianinae (*Gentiana*, *Gentianella*, *Comastoma*, *Gentianopsis*, *Tripterospermum*, *Crawfurdia*, *Pterygocalyx*, and *Megacodon*) and some genera of the other subtribes (*Erythraea*, *Canscora*, *Chironia* and *Chlora*) which are now treated as distinct genera by most authors. In contrast to *Gentiana* sensu lato, *Gentiana* circumscribed by Schmidt (1796), Borkhausen (1796), D. Don (1837), G. Don (1837), Asa Gray (1878), Löve & Löve (1972, 1975, 1976, 1986), Holub (1973), Lainz (1976), Weber (1985), Omer, Ali & Qaiser (1988), Omer (1989), Omer & Qaiser (1992), Zuev (1985, 1990), etc. is extremely narrow (narrowest strict sense). They did not recognize Linnaeus' concept of *Gentiana* but segregated it into more small genera, which were equivalent in extent to the sections of most current authors. At least 15 genera (*Kurramiana*, *Aloitis*, *Aliopsis*, *Qaisera*, *Qaisera*, *Ciminalis*, *Gentianodes*, *Calathiana*, *Chondrophyllae*, *Dasystephana*, *Favargera*, *Holubogentia*, *Kuepferella*, *Pneumonanthe* and *Tretorrhiza*) have been created by these authors. Thus, the circumscription of *Gentiana* was only restricted to five European species treated by Tutin (1972) as sect. *Gentiana*. These segregates, however, have not been widely accepted by most authors. The third standpoint is sensu stricto (strict sense), of which the generic circumscription of *Gentiana* corresponds to Kusnezow's subgen. *Eugentiana* (1894), namely excluding 11 genera of *Gentiana* sensu lato (*Gentianella*, *Gentianopsis*, *Comastoma*, *Tripterospermum*, *Crawfurdia*, *Pterygocalyx*, *Megacodon*, *Erythraea*, *Canscora*, *Chironia*, and *Chlora*) but still including all the new genera split by Holub, Löve & Löve, Omer & Qaiser, and Zuev within *Gentiana*. This circumscription is narrower than *Gentiana* s. l. (sensu lato), but much wider than *Gentiana* s. n. s. (narrowest strict sense) and thus, this circumscription of *Gentiana* is more natural and homogeneous. This viewpoint has been widely adopted by most authors working on Gentianaceae in the 20<sup>th</sup> century, e.g., Smith (1936, 1965), Tutin (1972, 1981), Czerepanov (1973), Pringle (1967–1979), and Ho & Liu (1985, 1988, 1990). We are also following this circumscription but exclude sect. *Stenogyne* (see details below).

According to Gilg's comprehensive survey of the family (1895), *Gentiana* is included in subfamily Gentianoideae, tribe Gentianeae, subtribe Gentianinae. However, since Maheswari Devi (1962) strongly supported the Menyanthaceae to separate from Gentianaceae on the basis of embryological characters. Many systematists have adopted this segregation in their systems, e.g., Engler system of Melchior (1964), Young system (1982), Thorne system (1983), Dahlgren system (1983) and Takhtajan system (1987). We also follow this separation here. The subtribe Gentianinae circumscribed by most modern authors comprises 16 genera, i. e., *Gentiana*, *Crawfurdia*, *Tripterospermum*, *Megacodon*, *Latouchea*, *Ixanthus*, *Gentianella*, *Comastoma*, *Gentianopsis*, *Pterygocalyx*, *Lomatogonium*, *Lomatogoniopsis*, *Swertia*, *Veratrilla*, *Jaeschkea*, and *Halenia*. Recently, we have segregated sect. *Stenogyne* from *Gentiana* as a distinct genus (*Metagentiana*). Thus, subtribe Gentianinae comprises 17 genera in all. These genera may be split into two artificial groups—the *Gentiana* group and the *Gentianella* group. The two groups can be clearly distinguished on the basis of the position of floral glands; the *Gentiana* group (including *Gentiana*, *Metagentiana*, *Crawfurdia*, *Tripterospermum*, *Megacodon*, *Latouchea*, and *Ixanthus*) has gynoeceal glands at the base of

the ovary while the *Gentianella* group (including *Gentianella*, *Comastoma*, *Gentianopsis*, *Pterygocalyx*, *Lomatogonium*, *Lomatogoniopsis*, *Swertia*, *Veratrilla*, *Jaeschkea*, and *Halenia*) has glands in foveae or spots borne on the surface of the corolla (epipetalous nectaries) alternating with the stamens. Within the *Gentiana* group, four genera (*Gentiana*, *Metagentiana*, *Crawfordia*, and *Tripterospermum*) form a plicate corolla group and are easily distinguish from *Megacodon*, *Latouchea*, and *Ixanthus* as well as from the *Gentianella* group. Their corolla bears plicae or folds between lobes (except *Gentiana lutea* is often without plicae) and the calyx has a membrane or rim extending completely around the interior of the tube (a continuous intracalycular membrane, but sometimes it is obsolete in some sections of *Gentiana*). In the *Gentianella* group and in three genera (*Megacodon*, *Latouchea*, and *Ixanthus*) of the *Gentiana* group, no plicae or folds occur between the corolla lobes and no a continuous intracalycular membrane exists. Only *Gentianopsis* has a discontinuous, triangular and pocket-shaped intracalycular membrane which is restricted to the sinuses of the calyx lobes. The genus *Gentiana* may be further distinguish from *Tripterospermum* and *Crawfordia* by having erect to ascending stems, no or shortened rhizomes, and developed (long and broad) corolla plicae, from *Metagentiana* and *Tripterospermum* by having straight and equal stamens, and from three genera (*Metagentiana*, *Tripterospermum*, and *Crawfordia*) by having linear to cylindrical style which is much shorter than ovary, ovoid, ellipsoid to global but triquetrous seeds, and by no bracts at the base of flowers in most species.

By character analysis of external morphology, the intergeneric relationships in subtribe Gentianinae show two essential evolutionary lines — the *Gentiana* evolutionary line (i. e., plicate corolla line, including *Gentiana*, *Metagentiana*, *Tripterospermum*, and *Crawfordia*) and *Gentianella* evolutionary line (i. e., epipetalous nectary line, including *Gentianella*, *Gentianopsis*, *Pterygocalyx*, *Lomatogonium*, *Lomatogoniopsis*, *Swertia*, *Veratrilla*, *Jaeschkea*, and *Halenia*). In the *Gentiana* evolutionary line the evolution is through a development series of characters: the flower bracts from the existence to disappearance, corolla plicae from small to large, stamens from straight and equal to decurved and unequal, style from the middle in length either to very short or to very long, and stems from erect or ascending to twining and trailing, etc. In this evolutionary line *Metagentiana*, *Tripterospermum*, and *Crawfordia* seem to be rather closely related to one another, and *Gentiana* stands in an isolated position. In the *Gentianella* evolutionary line the evolution is through a development series of nectaries: the structure of nectaries changes from simple and naked nectaries to foveae accompanied by squamellae and development of the squamellae themselves, to the final development of spurs. *Megacodon* has gynoeceal nectaries of the *Gentiana* group, but it does not have any plicae or folds between corolla lobes which suggests a closer relationship with the *Gentianella* group and thus it shows the intermediate and ambiguous position. However, the pollen morphology (see below) and ITS phylogeny (Yuan et al. 1996) suggests that it belong to the epipetalous nectary line as a basal clade and it does shed light on a link between the two evolutionary lines through the position of nectaries from the base of the ovary to the corolla tube. *Latouchea* has gynoeceal nectaries and no plicae or folds between corolla lobes and an incomplete bilocular ovary which also occurs in the subtribe Erythraeinae. *Latouchea* may be a very primitive genus which is located at the base of two evolutionary groups. The final genus *Ixanthus*, like *Latouchea*, has no plicae or folds between the corolla lobes, incomplete bilocular ovary, and perhaps no nectary at all (at least on dry specimens). However this genus, which is restricted to the Canary islands, is undoubtedly a very isolate and specialized one.

#### **Key to genera in subtribe Gentianinae**

1a. Corolla with plicae extending between lobes (except *G. lutea* L.):

2a. Flowers ebracteate at base (except few species in sections *Pneumonanthe* and *Gentiana*); style linear to

- cylindrical, shorter than ovary; seeds ellipsoid, ovoid to global, not triquetrous; calyx tube with 15 vascular bundles ..... *Gentiana* L.
- 2b. Flowers bracteate at base; style filiform, as long as to longer than ovary; seeds triquetrous to compressed, with three edges; calyx tube with 5–12 vascular bundles:
- 3a. Stems striate-angled, erect, neither twining nor trailing; flowers sessile, solitary and terminal at branches; bracts of flowers as large as to larger than stem leaves; fruits included in persistent corolla; seeds triquetrous with narrow wings on edges, three edges forming three equal faces; annuals, rarely perennials with stout and extremely shortened disclike-rhizome .....  
..... *Metagentiana* T. N. Ho & S. W. Liu
- 3b. Stems terete, twining or trailing; flowers 1–5, pedicellate, in terminal and axillary cymes; bracts of flowers much smaller than stem leaves; fruits exserted from persistent corolla; seeds compressed with discoid wings on edges, rarely triquetrous to compressed with narrow wings, three seed edges forming three extremely unequal faces; perennials with stout, long and branched rhizomes;
- 4a. Nectaries conspicuously developed, forming a collarlike disc around gynophore; stamens, unequal, apically decurved; fruit a capsule or berry; calyx tube with 5 vascular bundles .....  
..... *Tripterospermum* Blume
- 4b. Nectaries small, on gynophore; stamens symmetrical, equal, straight; fruits a capsule; calyx tube with 10 vascular bundles ..... *Crawfordia* Wallich
- 1b. Corolla without plicae between lobes;
- 5a. Corolla with 4 distinct spurs near base of corolla tube, rarely spurless; glands prolonged into spurs ..... *Halenia* Borkhausen
- 5b. Corolla without spurs; foveae on corolla tube or lobes:
- 6a. Corolla rotate, lobed nearly to base, tube very short, indistinct, much shorter than lobes;
- 7a. Plants dioecious, with unisexual flowers; seeds discoid-winged ... *Veratrilla* Baillon ex Franchet
- 7b. Plants with perfect flowers; seeds wingless;
- 8a. Stigma elevated above ovary, not decurrent; corolla lobes concolorous;
- 9a. Nectaries simple and naked, not surrounded by fringes or appendages .....  
..... *Gentianella* Moench
- 9b. Nectaries complex and various, often surrounded by fringed or tubular appendages .....  
..... *Swertia* L.
- 8b. Stigma decurrent along ventral suture of ovary; corolla lobes conspicuously bicolorous, half pale and half dark;
- 10a. Corolla lobe with 2 foveae each in a conspicuous pit; corolla tissue associated with nectary and pit sometimes basally connate, apically lobulate or lamellate .....  
..... *Lomatogonium* A. Braun
- 10b. Corolla lobe with 1 fovea not in a conspicuous pit; corolla tissue associated with nectary lamellate or galeate appendaged, margin entire or erose .....  
..... *Lomatogoniopsis* T. N. Ho & S. W. Liu
- 6b. Corolla tubular to campanulate, tube distinct, longer than lobes, less often tube shorter than, or as long as, lobes;
- 11a. Stems twining; calyx strongly 4-winged; seeds discoid-winged ..... *Pterygocalyx* Maximowicz
- 11b. Stems not twining; calyx unwinged; seeds unwinged;
- 12a. Stamens inserted at or very near sinuses of corolla lobes;

- 13a. Ovary unilocular, ovules restricted to the sutures and with an additional row between them; corolla lobes valvate in bud at least toward base; seeds few per capsule ..... *Jaeschkea* Kurz.
- 13b. Ovary incomplete bilocular, with a lamellate intrusion of the placenta into the locular cavity; corolla lobes contorted in bud; seeds generally numerous per capsule:
- 14a. Capsule distinctly curved, valves with bent or twisted tips; calyx lobes free; seed coat longitudinally rugose ..... *Latouchea* Franchet
- 14b. Capsule straight, valves without bent or twisted tips; calyx lobes united; seed coat alveolate, with simple and shallow hexagonal pits ..... *Ixanthus* Grisebach
- 12b. Stamens inserted on corolla tube distinctly below sinuses;
- 15a. Nectaries on gynophore; flowers over 5 cm ..... *Megacodon* (Hemsley) H. Smith
- 15b. Nectaries on corolla; flowers less than 5 cm if longer than 4-lobed:
- 16a. Alabastrum large, slightly flattened, 4-angled; pairs of calyx lobes dissimilar, 2 outer lobes narrower than and basally overlapping 2 inner lobes; corolla frequently fringed or toothed; seeds angular-papillate; discontinuous intracalycular membranes present ..... *Gentianopsis* Y. C. Ma
- 16b. Alabastrum small, not flattened; calyx lobes equal or nearly so, not overlapping nor in 2 distinct pairs; corolla not fringed; seeds almost smooth; intracalycular membranes absent;
- 17a. Corolla with 1 or 2 nonvascularized fringed scales at base of each lobe ..... *Comastoma* (Wettstein) Toyokuni
- 17b. Corolla either without appendages or with a single vascularized fringed scale at base of each lobe ..... *Gentianella* Moench

The floral anatomical characters of *Gentiana* are comparatively simple and essentially conform to those of subtribe *Gentianinae* (Table 2. 1). The sepals (calyx), petals (corolla) and stamens each receive one bundle trace. As the traces diverge, each sepal trace divides into three bundles, one median and two laterals, and thus the calyx tube has fifteen bundles. As a rule, the five petal traces each divide into three bundles, one median and two laterals. The laterals of the two adjacent lobes are the first to fuse in pairs, and then separate again and thus the corolla has fifteen bundles. The corolla plicae arise between secondary bundles, and they consist of the parenchyma without vascular bundles. Each stamen has a single bundle. The ovary is bicarpellate and unilocular. Each carpel receives three traces, one dorsal and two ventral. Later, the ventral bundles may divide into 2 or 3 branches. The nectaries consist of the secretory epidermic and nectarous tissue without vascular bundles.

The floral anatomical characters of *Gentiana* are similar to those of *Metagentiana*, *Tripterospermum*, and *Crarwurdia*, but differ from them by having 15 sepal bundles and nectaries without vascular bundles. The last three genera all have vascular nectaries and the vascular tissue is weak in *Metagentiana* and *Crawfordia* but distinctly developed in *Tripterospermum*. The sepal vascular bundles are 5 in *Tripterospermum*, 10 in *Crarwurdia*, and 12 in *Metagentiana*. Some authors, such as Liang (1986), Davis (1966), Eames (1961), Lindsey (1940), considered the fusion and simplification of the floral vascular bundles as more advanced characters. Den (1995) also suggested that the evolution of floral nectaries should be from the absence of vascular tissue to existence. Therefore, the characters of the floral anatomy of *Gentiana* are more primitive than those of *Metagentiana*, *Tripterospermum* and *Crawfordia*.

**Table 2.1 A floral anatomic comparison of *Gentiana* with *Metagentiana*, *Tripterospermum* and *Crawfurdia*.**

Characters	<i>Gentiana</i>	<i>Metagentiana</i>	<i>Tripterospermum</i>	<i>Crawfurdia</i>
Numbers of vascular bundles				
in calyx tube	15	12	5	10
in corolla tube	15	15	15	15
in stemens	5	5	5	5
at base of ovary	6	6	6	6
Structurs of nectaries				
Epidermis	present	present	present	present
Secretory tissue	present	present	present	present
Vascular tissue	absent	weak	development	weak

The embryological characters of *Gentiana* conform to the following framework of subtribe Gentianinae: tetrasporangiate anthers, dicotyledonous type of microsporangial development, normal endothecium (fibrous thickenings), secretory tapetum, simultaneous cytokinesis in meiosis of microsporocytes, dominant tetrahedral microspore tetrads, three- or two-celled pollen grains at the time of anther dehiscence, parietal placentation, unitegmic, tenuinucellate ovules, Polygonum type of megagametophyte, porogamous fertilization, endosperm of nuclear type, Solanad type of embryogeny and endospermic seeds. A comparison of embryological characters of some genera in subtribe Gentianinae is given in Table 2. 2.

*Gentiana* has some other embryological characters which are only restricted in a few genera of subtribe Gentianinae. For example, the middle layer is 2-celled layers; the origin of the tapetum is dual; tapetal cells have 2 to more nuclei and these cells divide, elongate and protrude into the anther locule to form “Trabeculae” and “Placentoids” which separate this locule into several chambers of varying sizes; the placentation is of superficial placenta with anatropous ovules arranged in columns of 10–30; the synergids have distinct filiform apparatus; antipodal cells with uninucleus are 3 in number and non-enlarged; the embryogeny corresponds to the Solanad type variety Physalis II subtype.

Thus, the embryological characters of *Gentiana* are more similar to those of *Metagentiana*, *Tripterospermum*, and *Crawfurdia* than to those of *Gentianella*, *Comastoma*, *Lomatogonium*, *Swertia*, *Halenia*, etc. With the former it shares the same Solanad type variety Physalis II subtype of embryogeny and 3 non-enlarged antipodal cells with 1(2) nuclei but the former has unitary original tapetum which does not or weakly protrudes into the anther locule to form “Placentoids”, typically parietal placenta with ovules arranged in columns of 8 (rarely 4 or 12).

The formation and differentiation of the anther walls, and the evolutionary trend of ovule and placenta types were studied by Johri et al. (1992, 1984), Tobe (1989), Gopal et al. (1992), and Lindsey (1940). They considered that the fibrous thickenings of the endothicium, uninucleate tapetal cells, unitary original tapetum which does not protrude into the anther locule to form “Trabeculae” and “Placentoids”, etc. are more primitive characters; the evolutionary trend of the ovule types is from anatropous to hypertropous; and both reduced or superficial parietal placenta to be two extremes arising from the typical parietal placenta. According to these suggestions the embryological characters of *Gentiana* are more advanced than those of *Metagentiana*, *Tripterospermum*, and *Crawfurdia*.

Chromosome numbers in the subtribe Gentianinae have been reported for 14 genera. Three gen-



Table 2.2 A comparison of embryological characters in some genera of the subtribe Gentianinae.

Characters	<i>Gentiana</i>	<i>Metagentiana</i>	<i>Craufurdia</i>	<i>Tripterosperrum</i>	<i>Pterygocalyx</i>	<i>Gentianopsis</i>	<i>Gentianella</i>	<i>Comastoma</i>	<i>Sveertia</i>	<i>Lomatogonium</i>	<i>Halenia</i>
Developed type of anther wall	dicotyledonous	dicotyledonous	dicotyledonous	dicotyledonous	dicotyledonous	dicotyledonous	dicotyledonous	dicotyledonous	dicotyledonous	dicotyledonous	dicotyledonous
Epidermis	do	do	do	do	do	do	do	do	do	do	do
persistent fibrous thickenings	no	do	do	no	do	do	do	do	no (do)	no	no
Endothecium	do	do	do	do	do	weak	weak	weak	do	do	do
fibrous thickenings	2	1	1	1 or 2	1	2	2	1	1—3	1	2
Middle layers											
Tapetum	dual	unitary	unitary	unitary	dual	dual	unitary	unitary	dual	dual	dual
origin	secretory	secretory	secretory	secretory	secretory	secretory	secretory	secretory	secretory	secretory	secretory
type	formed	no	no	weak	formed	formed	no	no	formed	formed	no
trabecular & placentoids											
number of nuclei in cell	2 or more	1	1	1	2(1)	2(1)	1(2)	2(1)	2(1)	1(2)	2
Microsporogenesis											
cytokinesis type	simultaneous	simultaneous	simultaneous	simultaneous	simultaneous	simultaneous	simultaneous	simultaneous	simultaneous	simultaneous	simultaneous
main tetrad shape	tetrahedral	tetrahedral	tetrahedral	tetrahedral	tetrahedral	tetrahedral	tetrahedral	tetrahedral	tetrahedral	tetrahedral	tetrahedral
mature pollen at shedding	2- or 3-celled	3-celled	3-celled	3-celled	3-celled	3-celled	3-celled	3-celled	3(2)-celled	3-celled	3-celled
Megasporangium ( ovule)											
type	anatropous	hypertropous	hypertropous	hypertropous or anatropous	anatropous	anatropous	hemiana-tropous	anatropous	anatropous or orthotropous	campylotropous	orthotropous
column numbers	10—30	8(4 or 12)	8(4 or 12)	8(4 or 12)	25—40	20—30	4	8	4, 8 or 16	12	4
placenta											
intrusion	no	no	no	no	no	no	no	no	no(very)	no	very
type	superficial	typical	typical	typical	superficial	superficial	reduced	typical	typical	typical	reduced
integument type	parietal	parietal	parietal	parietal	parietal	parietal	parietal	parietal	parietal	parietal	parietal
nucellus type	unitegmic	unitegmic	unitegmic	unitegmic	unitegmic	unitegmic	unitegmic	unitegmic	unitegmic	unitegmic	unitegmic
	tenuinucellate	tenuinucellate	tenuinucellate	tenuinucellate	tenuinucellate	tenuinucellate	tenuinucellate	tenuinucellate	tenuinucellate	tenuinucellate	tenuinucellate

Characters	<i>Gentiana</i>	<i>Metagentiana</i>	<i>Craufurdia</i>	<i>Tripterospermum</i>	<i>Pterygocalyx</i>	<i>Gentianopsis</i>	<i>Gentianella</i>	<i>Cornustoma</i>	<i>Suertia</i>	<i>Lomatogonium</i>	<i>Haleria</i>
epistase	no	no	no	no	no	formed	formed	no	no		formed
hypostase	no	no	no	no	no	no	no	no	no (formed)		
Megasporogenesis											
archesporium	1	1	1	1	1	1	1	1	1	1	
functional megaspore	first (second to fourth) chalazal	first chalazal	first chalazal	first chalazal	first chalazal	first chalazal	first chalazal	first chalazal	first chalazal	first chalazal	first chalazal
tetrad shape	Linear	linear	linear	linear	linear	linear	linear	linear	linear	linear	linear
Female gametophyte (embryo sac)											
formation type	Polygonum	Polygonum	Polygonum	Polygonum	Polygonum	Polygonum	Polygonum	Polygonum	Polygonum	Polygonum	Polygonum
shape	ellipsoid	ellipsoid	ellipsoid	ellipsoid	ellipsoid	ellipsoid	ellipsoid	ellipsoid	ellipsoid (ovoid)	ellipsoid	ellipsoid
synergids' filiform apparatus	distinct	distinct	distinct	distinct or indistinct	indistinct	distinct	indistinct	indistinct	indistinct	indistinct	indistinct
antipods											
cell numbers	3(4—8)	3	3	3(4)	3	3—5	8—12	8—12	3, 5—8	8—12	3(5)
cell enlarged	no (weak)	no (enlarged)	no (enlarged)	no (enlarged)	enlarged	enlarged	enlarged	enlarged	enlarged	enlarged	enlarged
nucleus	1(2)	1(2)	1(2)	1(2)	3—4	more	3—4	more	more	do	2 (or more)
endopolyploid	no	no	no	no	do	do	do	do	do	do	no
haustorium	no	no	no	no	do	weak	well developed	well developed	not or well developed	well developed	distinct
Fertilization											
pollen tube path	A(B & A)	B	B	porogamy	porogamy	A	B	A	porogamy	porogamy	porogamy
fertilization mode	porogamy	porogamy	porogamy	porogamy	porogamy	porogamy	porogamy	porogamy	porogamy	porogamy	porogamy
Endosperm											
formation type	nuclear	nuclear	nuclear	nuclear	nuclear	nuclear	nuclear	nuclear	nuclear	nuclear	nuclear
endosperm in mature seeds	abundant	abundant	abundant	abundant	abundant	abundant	abundant	abundant	abundant	abundant	abundant
Embryogeny type	Solanad type var. physalis II	Solanad type var. physalis II	Solanad type var. physalis II	Solanad type var. physalis II	Solanad type var. physalis II	Solanad type var. physalis I	Solanad type var. physalis I	Solanad type var. physalis I	Solanad type var. physalis I	Solanad type var. physalis I	Solanad type var. physalis I
References	Ho(1999)	Ho(2000)	Chen(2000)	Chen (1999, 2000)	Chen(1998)	Liu(1997)	Liu(1996b)	Liu(1996a)	Ho(1999); Liu(1998); Xue(1999)	Liu(in press)	Xue(1999)

Notes: A = the pollen tube destroys one of the synergids when it enters the embryo sac; B = the pollen tube enters the embryo sac between one synergid and the embryo sac wall.

era (*Veratrilla*, *Latouchea* and *Ixanthus*) have not been investigated cytologically. Among published works, most concentrate on the accumulation of chromosome numbers but few on karyology. The chromosome numbers of the subtribe Gentianinae are shown in Table 2.3, and the karyological data in Table 2.4. The chromosomes of *Gentiana* are characterized by having the great variation in number but the extremely similar and symmetrical karyotypes as well as the chromosome complement, with no bimodality. The chromosome numbers of  $2n=12, 14, 16, 18, 20, 22, 24, 26, 28, 30, 31, 32, 33, 36, 38, 40, 42, 44, 48, 52, 60, 72, 76$  and  $96-98$  have been reported for the genus and established a wide range of chromosome number variation which indicates a typical dysploidy series. The karyotypes consist mainly of median (m), a few submedian (sm), and/or less subterminal (st) chromosomes, but the terminal chromosome (t) is entirely absent. In the chromosome complement of relative length  $M_1$  and  $M_2$  are more than L and/or S, and the chromosomes show a gradual decrease from the longest to the shortest and thus the bimodality is indistinct. These chromosome characters are rather special in the subtribe Gentianinae. They are slightly more similar to *Megacodon*, *Metagentiana*, *Tripterospermum*, and *Crawfordia* than to *Gentianella*, *Comastoma*, *Lomatogonium*, etc. They all have more symmetrical karyotypes with a low intrachromosomal index ( $A_1=0.240-0.397$  in mean), a low interchromosomal index ( $A_2=0.15-0.23$  in mean), a low karyotype asymmetrical index  $As.k\%$  ( $52.69-61.46$  in mean), and no or indistinct bimodality. The differences between *Gentiana* and the other three genera are: *Gentiana* has very common dysploidy with the basic chromosome numbers from  $x=6$  to  $x=16$ , rarely  $x=19$  or  $21$  whereas *Tripterospermum*, *Crarwfurdia*, and *Metagentiana* have uniformly high and secondary basic chromosome numbers (the first two have  $x=23$  (10), the last one has  $x=17, 21$ , and  $23$ ). In the other genera of subtribe Gentianinae the karyotypes are more asymmetrical and the bimodality of chromosome complement is rather distinct (see Table 2.4). However, most genera of subtribe Gentianinae have polybasic chromosome numbers and a parallel development of the dysploid series is obvious involved in the chromosome evolution of these genera.

**Table 2.3** The available chromosome data in the subtribe Gentianinae.

Genera	Chromosome numbers		Karyotype types
	Recorded numbers ( $2n$ )	Suggested basic numbers ( $x$ )	
<i>Gentiana</i>	18, 20, 24, 26, 36, 40 (12, 14, 16, 22, 28, 30, 32, 38, 42, 44, 48, 52, 60, 72, 76, 96-98)	9, 10, 12, 13, 14, 15 (6, 7, 8, 11, 16, 19, 21)	1A, 2A (3A, 1B, 2B, 3B)
<i>Metagentiana</i>	46 (34, 42)	23 (17, 21)	3A, 2B (2A)
<i>Tripterospermum</i>	46 (20)	23 (10)	2B
<i>Crawfordia</i>	46	23	2B
<i>Pterygocalyx</i>	26 (24)	13 (12)	2A (3A)
<i>Gentianopsis</i>	26 (44, 52, 78)	13 (11)	2A (3A)
<i>Suertia</i>	20, 26 (14, 16, 18, 22, 24, 28, 52, 60, 78)	10, 13 (7, 8, 9, 11, 12, 14)	2B (2A, 3A)
<i>Gentianella</i>	36 (16, 18, 22, 26, 44, 48, 54)	9 (8, 11, 12, 13)	2B (3B, 2C)
<i>Comastoma</i>	18 (10, 12, 16, 20, 28, 30, 32, 36)	9 (5, 8, 10)	2B, 2C (3C)
<i>Lomatogonium</i>	16 (10, 18, 32, 40, 48)	8 (5?, 9)	
<i>Lomatogoniopsis</i>	12	6	1A
<i>Megacodon</i>	28	14	2A
<i>Halenia</i>	22	11	
<i>Jaeschkea</i>	16, 18, 20, 22	8, 9, 10, 11	1A
<i>Latouchea</i>	no count available		
<i>Veratrilla</i>	no count available		
<i>Ixanthus</i>	no count available		

Notes: the numbers in parentheses = rare numbers, infraspecific aneuploid numbers are not taken into account.

Table 2.4 The available karyotype data in some species of the subtribe Gentianinae.

Taxa & No.	Karyotype formulae & chromosome complement	Length ( $\mu\text{m}$ )		L/S	P>2	Karyotype asymmetry				References
		Range	Mean			Type	A <sub>1</sub>	A <sub>2</sub>	As. k%	
<i>Metagentiana</i>										
( <i>Gentiana souliei</i> )	$2n=46=34m+10sm+2st$ $=4L+14M_2+24M_1+4S$	1.76-4.03	2.57	2.29	0.22	2B	0.27	0.20	59.58	Ho et al. (2001)
( <i>G. expansa</i> )	$2n=34=10m(2SAT)+24sm$	1.7-2.8		1.69	0.29	2A	0.459	0.134		Yuan 1993
( <i>G. primuliflora</i> )	$2n=42=12m+24sm+6st$	1.4-1.9		1.40	0.71	3A	0.503	0.095		Yuan 1993
( <i>G. serra</i> )	$2n=34=12m+12sm+10st$ $=2L+12M_2+20M_1$	1.26-2.18	1.62	1.73	0.59	3A	0.50	0.160	68.07	Ho et al. (2001)
<i>Tripterospermum</i>										
<i>T. japonicum</i>	$2n=46=35m+9sm+2st$ $=4L+16M_2+21M_1$ $+5S$	2.20-4.90	3.60	2.23	0.15	2B	0.36	0.19	60.33	Shingenbu 1984
<i>T. chinense</i>	$2n=46=30m+14sm+2st$ $=6L+18m_2+14M_1+8S$	1.54-4.39	2.84	2.85	0.30	2B	0.34	0.24	60.26	Chen et al. (unpublished)
<i>T. cordatum</i>	$2n=46=40m+6sm$ $=22m_2+18M_1+6S$	1.21-3.71	2.18	2.23	0.09	2B	0.29	0.20	58.67	Chen et al. (unpublished)
<i>Craufurdia</i>										
<i>C. delavayi</i>	$2n=46=28m+16sm+2st$ $=8L+14m_2+16M_1+8S$	1.82-3.89	2.65	2.14	0.13	2B	0.36	0/23	61.46	Chen et al. (unpublished)
<i>Megacodon</i>										
<i>M. stylophorus</i>	$2n=28=24m+4sm$ $=12M_2+14M_1+2S$	2.46-4.95	3.37			2A	0.24	0.20	57.23	Liu et al. (2001)
<i>Gentianopsis</i>										
<i>G. paludosa</i>	$2n=26=10m+8sm+8st$ $=2L+8M_2+14M_1+2S$					2A	0.44	0.19	66.96	Liu et al. (unpublished)
<i>G. barbata</i>	$2n=26=8m+8sm+6st+4t$ $=2L+10M_2+14M_1$					2A	0.53	0.22	70.45	Liu et al. (unpublished)
var. <i>stenocalyx</i>	$2n=26=4m+6sm+16st$ $=22M+4S$					3A				Liu et al. (unpublished)
<i>Gentianella</i>										
<i>G. arenaria</i>	$2n=18=8m+8sm+2st$ $=2L+14M+2S$					2B				Liu et al. (unpublished)
<i>G. pygmaea</i>	$2n=18=12m+2sm+4st$ $=2L+14M+2S$					2B				Liu et al. (unpublished)
<i>G. azurea</i>	$2n=22=14m+4sm+2st+2B$ $=4L+14M+4S$					2B				Liu et al. (unpublished)
	$2n=44=24m+12sm+4st+4B$ $=4L+36M+4S$					2B				Liu et al. (unpublished)
	$2n=22=10m+6sm+6st$ $=2L+18M+2S$					3B				Liu et al. (unpublished)
	$2n=22=4m+6sm+6st+4t$ $2B=2L+18M+2S$					3B				Liu et al. (unpublished)
	$2n=22=10m+10sm+2B$ $=4L+12M+2S$					2C				Liu et al. (unpublished)

Taxa & No.	Karyotype formulae & chromosome complement	Length ( $\mu\text{m}$ )		L/S	P>2	Karyotype asymmetry				References
		Range	Mean			Type	A <sub>1</sub>	A <sub>2</sub>	As.k%	
<b>Comastoma</b>										
<i>C. pulmonarium</i>	$2n=18=6m+2sm+10st$ $=10L+2M+6S$					3C				Liu et al. (2001)
	$2n=18=6m+2sm+10st$ $=6L+6M+6S$					3C				Liu et al. (unpublished)
	$2n=18=6m+2sm+10st$ $=8L+2M+6S$					3C				Liu et al. (2001)
<i>(C. arrectum)</i>	$2n=18=10m+8st=8L+4M+6S$					2C				Liu et al. (2001)
	$2n=18=10m+8st=6L+6M+6S$					2C				Liu et al. (2001)
	$2n=18=8m+4sm+6st$ $=16M+2S$					2B				Liu et al. (2001)
<i>C. falcatum</i>	$2n=18=12m+2sm+4st$ $=4L+8M+6S$					2C				Liu (2001)
<i>C. chiuchense</i>	$2n=20=10m+4sm+6st$ $=8L+6M+6S$					2C				Liu et al. (2001)
<i>C. traillianum</i>	$2n=18=8m+4sm+6st=18M$					2B				Liu et al. (2001)
<i>(C. beesianum)</i>	$2n=18=14m(4SAT)+2sm+$ $2st=4L+10M+4S$					2B				Liu et al. (2001)
<i>C. pedunculatum</i>	$2n=16=6m+2sm+8st$ $=10L+2M+4S$					2C				Liu et al. (2001)
	$2n=32=12m+8sm(4SAT)+$ $12st=8L+16M+8S$					2B				Liu et al. (unpublished)
<i>C. polycladum</i>	$2n=16=6m+2sm+8st$ $=10L+2M+4S$					2C				Liu et al. (2001)
<b>Pterygocalyx</b>										
<i>P. volubilis</i>	$2n=26=18m+4sm+2st+2t$ $=4L+8M_2+14M_1$					2A	0.39	0.22	62.91	Chen et al. 1998
<b>Suertia</b>										
<i>S. bifolia</i>	$2n=28=14m+4sm+10st$ $=2L+14M_2+10M_1+$ $2S$	2.53-5.60	4.15			2B	0.53	0.27	68.34	Ho et al. et al. (1999)
<i>S. wolfgangiana</i>	$2n=12m+14sm+2st$ $=6L+8M_2+8M_1+6S$	1.93-5.40	3.44			2B	0.42	0.30	63.35	Ho et al. (1999)
<i>S. hickinii</i>	$2n=20=8m+4sm+8st$ $=8M_2+12M_1$	1.91-2.73	2.31			3A	0.50	0.12	67.45	Ho et al. (1999)
<i>S. franchetiana</i>	$2n=20=6m+12sm+2st$ $=8M_2+12M_1$	2.23-3.59	2.63			3A	0.46	0.14	65.34	Ho et al. (1999)
<i>S. tetraptera</i>	$2n=14=4m+8sm+2st$ $=2L+6M_2+4M_1+2S$	1.73-4.6	3.14			2B	0.45	0.29	66.46	Ho et al. (1999)
<b>Lomatogoniopsis</b>										
<i>L. alpina</i>	$2n=12=12m=6M_2+6M_1$	2.44-3.67	2.83			1A	0.18	0.16	55.59	Liu et al. (2001)
<b>Jaeschkea</b>										
<i>J. microspemu</i>	$2n=16=16m$	2.0-3.3	2.56			1A	0.278	0.172		Yuan et al. (1998)

Notes: L=length of the longest chromosome; S = length of the shortest chromosome; P>2 = proportion of chromosome with arm ratio>2; A<sub>1</sub>=the intrachromosomal asymmetry index defined by Romero Zarco (1986); A<sub>2</sub>=the interchromosomal asymmetry index defined by Romero Zarco (1986); As.k % = the karyotypic index defined by Hisao Arano (1963); m=median; sm=submedian; st=subterminal; t=terminal.

The pollen morphology in subtribe Gentianinae is extremely differentiated, especially in shape, size, and sexine ornamentation. A comparison of the pollen morphology of some genera in subtribe Gentianinae may be seen in Table 2.5. Pollen grains of *Gentiana* are spheroidal, subspheroidal to prolate, scarcely perprolate or rhomboid,  $22-48(-60) \times 20-35(-50) \mu\text{m}$ . The sexine ornamentation types are striate-imperforate, striate-perforate, striate-foveolate, striate-reticulate, rarely reticulate, and lirae often  $0.4-0.7 \mu\text{m}$  wide. On the columellate layer, the bacula are arranged in one, (occasionally two rows). Pollen morphology of *Gentiana* is very similar to *Tripterospermum*, *Crawfordia* and *Metagentiana*. The pollen grains of *Tripterospermum* (plate 3.19) and *Crawfordia* are spheroidal, subspheroidal, scarcely prolate,  $26-52 \times 23-40 \mu\text{m}$ . The sexine surface has striate-imperforate, striate-perforate to striate-reticulate ornamentation with wide to very wide lirae more than  $1 \mu\text{m}$  which are supported by bacula in two or more rows (occasionally in one). In *Metagentiana* (plate 3.4, plate 3.21) most species have a similar pollen morphology to that of *Gentiana* sect. *Otophora* (very narrow lirae and bacula lobed at tops and arranged in 1 row) but few species have that of *Tripterospermum* and *Crawfordia* (very wide lirae often more than  $1 \mu\text{m}$ , bacula in two rows). The pollen morphology of *Gentiana* differs from that of *Tripterospermum* and *Crawfordia* by often having narrower lirae and bacula in one (occasionally two) row on the columellate layer. Pollen grains of *Metagentiana* have intermediate characters between *Gentiana* and *Tripterospermum*. The pollen morphology of *Gentiana* is less similar to that of the other genera of subtribe Gentianinae. The pollen grains of *Veratrilla* are very small, ca.  $20 \times 20 \mu\text{m}$  and the exine ornamentation is striate-imperforate. The pollen grains of *Jaeschkea* and *Megacodon* are larger,  $38-52 \times 25-32 \mu\text{m}$  and the exine ornamentations are foveolate to reticulate in *Jaeschkea* and tuberculate to reticulate in *Megacodon*. The exine ornamentations of *Swertia* and *Lomatogonium* are heterogeneous; verrucate, echinate, four striate types (striate-imperforate, striate-perforate, striate-foveolate, striate-reticulate), and reticulate. *Gentianopsis*, *Pterygocalyx*, *Lomatogoniopsis*, and *Halenia* have typical reticulate ornamentation with heterobrochate lumina. *Gentianella* has reticulate and four striate types (striate-imperforate, striate-perforate, striate-foveolate, and striate-reticulate). *Comastoma* has smooth sexine which is rather special in subtribe Gentianinae and the ornamentation is perforate, foveolate to minutely and densely reticulate. Although some parallel and mosaic evolution occur in different genera, generally speaking, the two evolutionary lines in subtribe Gentianinae, which are based on the external morphology, are also supported by the pollen morphology—the *Gentiana* evolutionary line mainly has essentially striate exine ornamentation whereas the *Gentianella* evolutionary line has reticulate ornamentation. The *Gentiana* group seems to be more primitive than the *Gentianella* group because the allied subtribe Erythraeinae of subtribe Gentianinae has striate-imperforate and striate-perforate ornamentation.

After having analyzed characters of external morphology, floral anatomy, embryology cytology and pollen morphology, we conclude that the intergeneric relationships in the subtribe Gentianinae show two essential evolutionary lines—the *Gentiana* evolutionary line (including *Gentiana*, *Metagentiana*, *Tripterospermum*, and *Crawfordia*) and the *Gentianella* evolutionary line (including *Gentianella*, *Gentianopsis*, *Pterygocalyx*, *Lomatogonium*, *Lomatogoniopsis*, *Swertia*, *Veratrilla*, *Jaeschkea*, *Halenia*, and *Megacodon*). *Gentiana* is more closely related to the genera *Metagentiana*, *Tripterospermum*, and *Crawfordia* than to any other genus in subtribe Gentianinae. Four genera have formed a plicate corolla group and stand at a more primitive level in the subtribe Gentianinae. Characters of external morphology, pollen morphology, and embryology of *Gentiana* are more advanced but those of cytology and floral anatomy are more primitive.