

## 龙胆属的系统发育分析\*

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### A PHYLOGENETIC ANALYSIS OF *GENTIANA* (GENTIANACEAE)

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**Abstract** A cladistic study was undertaken to make the infrageneric classification and to evaluate the phylogenetic relationships in the genus *Gentiana*. As a monophyletic group, *Gentiana* is based on three synapomorphies and includes 23 series and 10 monotypic Sections. Two genera, *Tripterospermum* and *Crawfordia*, were selected as the outgroups. Most character complexes were surveyed and 61 informative characters from morphology, palynology and cytology were used for this study. The analysis resulted in 51 equally parsimonious cladograms and the one with the lowest f-value of 0.213 was selected as the base for discussing cladistic classification and making cladistic analysis. Results of the cladistic classification support most of the current systematic classification of *Gentiana*, with main differences in the circumscription of some sections (e. g., *Frigida*, *Isomeria* and *Chondrophylla*). In the cladogram, *Gentiana* was first split into two clades, the perennial clade and the annual clade. In the perennial clade, Sect. *Pneumonanthe* emerged earlier and is the most primitive taxon in this genus. Two subclades, the Asian subclade and the European subclade, came out after Sect. *Pneumonanthe*. The Asian subclade includes eight sections (*Cruciata*, *Otophora*, *Frigida*, *Microsperma*, *Monopodiae*, *Kudoa*, *Phyllocalyx* and *Isomeria*). The first two sections which form the *Cruciata*-branch diverged at a low level, especially Sect. *Cruciata* is also a primitive taxon of the genus *Gentiana*. The remaining sections which constitute the *Frigida*-branch are more advanced. The European subclade includes Sect. *Gentiana*, Sect. *Ciminalis* and Sect. *Calathianae*. This subclade is regarded as a relatively isolated and specialized one in *Gentiane*. The annual clade consists of two sections (*Dolichocarpa* and *Chondrophylla*), of which Sect. *Chondrophylla* is a more advanced taxon. In addition, Sect. *Stenogyne* was considered to be of a hybrid origin between the two genera *Tripterospermum* and *Gentiana* with some characters of its parents. A strict consensus tree summaries

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the points of agreement in all the 51 equally parsimonious trees. The phylogenetic relationships of the sections and series in the genus *Gentiana* are also strongly supported by this consensus tree.

**Key words** *Gentiana*; Phylogeny; Cladistic classification; Cladistic analysis

**摘要** 本文运用支序分类的原理和方法,对龙胆科龙胆属的属下等级进行了重新归类和系统发育分析。龙胆属是一个单系群,以3项近裔共性为归类依据。性状分析作了性状同源性和性状极性分析。性状极化主要以外类群比较、性状相关性及染色体资料为依据,其它方法,如生物重演律原则、地理递进原则以及孢粉形态等也被结合使用。分析结果,双蝴蝶属和蔓龙胆属被选择为外类群,71个性状被选择作为建立数据矩阵的基本资料。使用PAUP程序对矩阵进行了运算,得到4个最简约的谱系分支图,它们均具一致性系数0.637,支序长度为160步,f-比值范围为0.179~0.189,其中具最低f-比值的图被选作为类群归类和讨论亲缘关系的基础。在支序图上龙胆属归为15个组;其中5个组又划分为系,共包括23个系,其余组为单型组,故共有33个属下类群。一个严格的一致性谱系分支图总结了所有的一致点,从而支持了支序分析的结果。

**关键词** 龙胆属;系统发育;支序分类;支序分析

*Gentiana*, a large genus of about 361 species, is widely distributed all over the world except Africa. The majority of species are centred in Asia. A number of articles on its taxonomy have been published since the establishment of *Gentiana* by Linnaeus. However, only a few of them dealt with the evolutionary relationships among its infrageneric taxa, such as Kusnezow (1894). The present paper represents an attempt to make an infrageneric classification and to analyse the phylogenetic relationships of the infrageneric taxa, using the principles and methodologies of cladistics.

## 1 *Gentiana* as a monophyletic group

One of the essential principles of cladistics is the concept of strict monophyly. A monophyletic group must contain all the descendants derived from a common ancestor. Therefore, the erection of monophyletic groups is the starting point for cladistic analysis.

There have been different standpoints on the concept of *Gentiana*. *Gentiana* sensu lato, as traditionally circumscribed, is a very heterogeneous assemblage of morphologically diverse groups, including *Tripterospermum*, *Crawfordia*, *Megacodon* and *Gentianella* sensu lato. *Gentianella* sensu lato further consists of *Gentianella* sensu stricto, *Comastoma*, *Gentianopsis*, and *Pterygocalyx*. *Gentiana* is circumscribed in the present paper in the strict sense, as equivalent to subgenus *Eugentiana* Kusnezow (1894). This concept has been widely accepted by most 20th century authors on Gentianaceae, e. g., H. Smith (1965, 1936), Czerepanov (1973). It is narrower than *Gentiana* sensu lato mentioned above, but much broader than *Gentiana* as defined by Holub (1973) and Löve *et al.* (1975) who restricted *Gentiana* to the five European species treated by Tutin (1972) as Sect. *Gentiana*.

According to the synapomorphy principle in phylogenetic systematics, only strictly monophyletic taxa may be regarded as historical entities, and the only logical basis for infer-

ring monophyly is to show that the component taxa of a group possess one or more shared, derived character states, or synapomorphies. *Gentiana* is a monophyletic group separated from the other genera of Gentianaceae by the following three synapomorphies: (1) plants with quadrangular, erect or ascending stems; (2) well developed corolla plicae (folds) between the lobes (the plicae in Sect. *Gentiana*, Ser. *Otophorae* and Ser. *Decoratae* being very small and considered as a reduced and specialized result); and (3) seeds with various kinds of testa, such as reticulate, reticulately thickened, honeycomb-like, spongy, and sometimes with various wings.

As a monophyletic group, *Gentiana* includes 23 series and 10 monotypic sections (See Table 2) which were mostly recognized in a systematic revision of all the species of *Gentiana* by the present authors (Ho *et al.*, 1990).

## 2 Character analysis

The character analysis in the present paper focuses on homology analysis of characters and their polarization. Some essential principles and methods (e. g., outgroup comparison, character correlation, commonality principle, recapitulation law, geographical progression rule and irreversibility of chromosome polyploidy from low to high, etc.) were used to polarize the character states.

In subtribe Gentianinae, *Gentiana* is more closely related to *Tripterospermum* and *Crawfordia* than to the other genera. The three genera share two synapomorphies (corolla with plicae between the lobes; calyx with a continuous intracalycular membrane) and thus form a monophyletic group. Among them, *Tripterospermum* and *Crawfordia* are further closely related to each other and are more primitive. They were, therefore, selected as the outgroups. The relationships of the three genera is shown in Fig. 1.

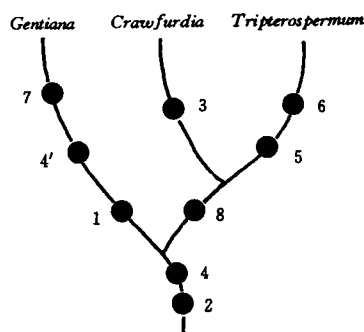


Fig. 1 Cladogram showing hypothesized relationships of the plicate-corolla group in Subtribe Gentianinae.

- 1 = stem quadrangular, erect or ascending
- 2 = calyx with a continuous intracalycular membrane
- 3 = calyx tube with 10 vascular bundles
- 4 = corolla with plicae between lobes
- 4' = plicae very developed
- 5 = stamens asymmetrical, and unequal in length, at the apex unilaterally and uniformly curved downwards
- 6 = glands turning a collar-like disc covering the base of the ovary
- 7 = seeds with reticulate, reticulately thickened, honeycomb-like to spongy pits and winged or unwinged
- 8 = seeds with reticulate pits, triquetrous in shape with unequal three ridges which form three unequal faces

The character information used in this analysis was taken to a great extent from our own studies on *Gentiana*, and sometimes also from the literature (e. g., some cytological information). 61 informative characters were used for this analysis and surveyed below (Table 1). All the characters are multiply coded, where number 0 represents the plesiomorphic state and numbers 1~4 represent apomorphic states. Number 9 indicates that the character

is unavailable or its information is lost. In some cases, a taxon has both plesiomorphic and apomorphic states, then this taxon was scored as the plesiomorphic state.

Table 1 Characters and character states used in the cladistic analysis of *Gentiana*

- 1 Herbs perennial (0); annual or biennial (1).
- 2 Roots arising from nodes of a rhizome (0); linear-cylindrical roots from collar (1); a fleshy stout taproot-like root (2); a fleshy stout taproot (3).
- 3 Roots arising from nodes of a rhizome (0); fibrous taproots (1).
- 4 Rhizome long and thick (0); short, slender and distinct (1); extremely shortened, thin and indistinct (2).
- 5 Rhizome long and thick (0); extremely shortened and thickened rhizome-disc-like(1).
- 6 Rhizome long and thick (0); poor stolon (1); developed stolon (2).
- 7 Rhizome long and thick (0); plant without rhizome or stolon (1); stem at lower nodes creeping and rooting (2).
- 8 Stem with sympodial branching of rhizome subtype (0); sympodial branching of stolon subtype (1).
- 9 Stem with sympodial branching of rhizome subtype (0); monopodial branching of perennial plant subtype with distinct plant axis and some weak branches (10); plant axis much shortened to retain almost only a terminal bud(2).
- 10 Stem with sympodial branching of rhizome subtype (0); monopodial branching of annual plant subtype with a distinct main stem (1); with fastigate branches (2); branches crowded in a head (3).
- 11 Stem with sympodial branching of rhizome subtype (0); monopodial branching of annual plant subtype with caespitose and dichotomous branches (1).
- 12 Basal vegetative rosette absent (0); rosette developed, with a terminal bud and many large leaves (1); rosette reduced, with few and small leaves (2).
- 13 Basal vegetative rosette absent (0); rosette developed, with a lateral bud and many large leaves (1).
- 14 Cauline leaves decreasing in size from the middle to both ends of stem (0); decreasing or increasing in size from base to top of stem (1).
- 15 Cauline leaves decreasing in size towards top of stem (0); increasing in size towards top of stem (1); crowded towards top of stem and the uppermost leaves surrounding inflorescence (2); the uppermost leaves similar to calyx lobes in shape (3).
- 16 Cauline leaves decreasing in size towards top of stem and widely separated (0); most of the leaves crowded at base of stem and much larger than the others (1).
- 17 Cauline leaves decreasing in size from the middle to both ends of stem (0); the whole plant with 1~2 pairs of basal leaves (1); basal leaves 2~4 pairs and large, sometimes in an involucre-like shape (2); all leaves closely spaced (3).
- 18 Inflorescence lax, axillary and terminal cymes with many flowers (0); a terminal inflorescence (cluster) with many flowers (1); several flowers (2); a single flower (3).
- 19 Inflorescence lax, axillary and terminal cymes (0); many cymes with 1~3 flowers arranged at ends of abundant branches (1).
- 20 Inflorescence lax, axillary and terminal cymes (0); flowers solitary and terminal unbranched flowering stem (1).
- 21 Inflorescence lax, axillary and terminal cymes (0); flowers solitary and terminal at ends of branches

- (1).
- 22 Bracts 4 (rarely 2) per flower (0); 2(1); disappearing (2).
  - 23 Flowers pedicellate or sometimes also cymes on peduncle-like branches (0); sessile (1).
  - 24 Flowers 5-merous (0); 6~9-merous (1).
  - 25 Flowers large-sized (4.1~7 cm long) (0); medium-sized (2.6~4 cm long) (1); small-sized (1.6~2.5 cm long) (2); very small (0.3~1.5 cm long) (3).
  - 26 Intracalycular membrane highly developed and calyx tube split along one side (0); intracalycular membrane reduced and calyx tube not split (1); intracalycular membrane considerably reduced and calyx tube always entire and tubular, sometimes angled or winged (2).
  - 27 Calyx lobes irregular and triangular or lanceolate (0); subequal and triangular to narrowly elliptic (1); equal and linear-spathulate, linear-lanceolate to linear (2).
  - 28 Calyx lobes irregular and triangular or lanceolate (0); subequal and triangular (1); narrowly triangular or ovate (2); spatulate (3); broadly oblong to flabelliform with keeled midveins (4).
  - 29 Calyx lobes irregular and triangular or lanceolate (0); unequal and suborbicular (1); equal and ovate-triangular with acuminate apex (2); oblanceolate (3).
  - 30 Calyx lobes irregular, triangular or lanceolate (0); equal, triangular, ovate-triangular or ovate with acute apex (1); filiform or subulate (2).
  - 31 Calyx lobes irregular, triangular or lanceolate and much shorter than tube (0); equal, acinular or linear, nearly as long as tube (1).
  - 32 Margins of calyx lobes not broadly membranous (0); very broadly membranous (1).
  - 33 Corolla infundibuliform (0); broadly tubular (1); urniform or tubular (2).
  - 34 Corolla infundibuliform, 3~4 times as long as calyx (0); tubular 2.5~3 times as long as calyx (1); ca. twice as long as calyx (2).
  - 35 Corolla infundibuliform, 3~4 times as long as calyx (0); tubular-infundibuliform, 2~2.5 times as long as calyx (1); campanulate, ca. twice as long as calyx (2); hypocrateriform (3).
  - 36 Corolla lobed to above the middle so tube much longer than lobes (0); deeply lobed to the middle or below so tube as long as to shorter than lobes (1).
  - 37 Corolla plicae poorly developed, short and narrow,  $1/4 \sim 1/3$  as long as and narrower than lobes (0); developed, longer but narrower, at least  $1/2$  as long as and narrower than lobes (1).
  - 38 Corolla plicae poorly developed, short and narrow,  $1/4 \sim 1/3$  as long as and narrower than lobes (0); well developed, large and symmetrical, at least  $1/2$  as long as and as wide as lobes, often entire (1); margins of plicae fimbriate (2).
  - 39 Corolla plicae asymmetrical, often obliquely truncate or triangular (0); symmetrical, narrowly triangular (1).
  - 40 Corolla plicae asymmetrical, often obliquely truncate or triangular (0); symmetrical, ovate-oblong with truncate apex (1).
  - 41 Corolla plicae asymmetrical, often obliquely truncate or triangular (0); reduced to a small tooth or auricle on side of lobe (1).
  - 42 Stigma-lobes free and recurved, oblong or linear (0); contiguous or connate, rounded and expanded into a small discoid or funnellform structure but free after anthesis (1); discoid or funnellform structure not free after anthesis (2).
  - 43 Gynophore long (0); sessile or subsessile (1).

- 44 Capsule cylindrical (0); narrowly ellipsoid or oblanceolate (1); obovoid or ellipsoid (2).
- 45 Capsule unwinged (0); winged along sutures towards apex (1).
- 46 Capsule large (often >15 mm long) (0); small-sized (often <10 mm long) (1).
- 47 Seeds triquetrous with three winged edges to form three unequal-sized faces (0); not triquetrous but winged with narrow wings (1); unwinged (2).
- 48 Seeds triquetrous with three narrow wings which form three unequal-sized faces (0); not triquetrous but few-angled with irregular spongy edges or winged with wing on one side or at one end of the body (1); neither angled nor winged (2).
- 49 Seed coat minutely and densely reticulate (0); reticulately thickened (1).
- 50 Seed coat minutely and densely reticulate (0); distinct reticulate (1); covered with membranous lamellae which form shallow, simple, honeycombed and hexagonal pits (2); membranous lamellae form deeply honeycombed pits (3); complex and spongy pits (4).
- 51 Seed coat minutely and densely reticulate (0); finely reticulate (1).
- 52 Seeds large (often >1.2 mm long) (0); small (often <1.2 mm long) (1).
- 53 Chromosome number  $x=7$ ,  $2n=2x$  (0); dominant chromosome numbers  $x=9$ ,  $10$ ,  $2n=2x$  (1); chromosome number  $x=13$ ,  $2n=2x=52$  (2).
- 54 Chromosome number  $x=7$ ,  $2n=2x$  (0); chromosome number series of  $x=15, 14, 13, 12, 11, 10, 9$ ,  $2n=2x$ , less often  $2n=4x$  (1).
- 55 Chromosome number  $x=13$ ,  $2n=2x$  (0); chromosome number  $x=12$ ,  $2n=2x$  (1).
- 56 Chromosome number  $x=13$ ,  $2n=2x$  (0); chromosome number  $x=10$ ,  $2n=2x$  (1); chromosome numbers  $x=10$ ,  $2n=4x=40$  or  $x=9$ ,  $2n=4x=39$  (2).
- 57 Pollen grains with striate-imperforate exine ornamentation with lirae very wide ( $0.6\sim 1\ \mu\text{m}$ ) (0); dominantly striate-foveolate or striate-reticulate with lirae lower and wide ( $0.4\sim 0.65\ \mu\text{m}$ ) (1).
- 58 Pollen grains with striate-imperforate exine ornamentation with lirae very wide ( $0.6\sim 1\ \mu\text{m}$ ) (0); striate-imperforate to striateless, perforate with lirae higher and wide ( $0.4\sim 0.65\ \mu\text{m}$ ) (1); typical striate-perforate (2); striate-foveolate (3); striate-reticulate or reticulate (4).
- 59 Pollen grains with striate-imperforate exine ornamentation with lirae very wide ( $0.6\sim 1\ \mu\text{m}$ ) (0); striate with lirae very thin ( $0.15\sim 0.3\ \mu\text{m}$ ) (1).
- 60 Bacula erect or slightly recurved (0); lobed at tops (1).
- 61 Sexine thicker than nexine (0); sexine as thick as nexine to nexine thicker than sexine (1).

**Growth habit** (character 1) All species of *Gentiana* are herbs, about half of which are annuals, belonging to 11 taxa (Ser. Suborbisepalae, Ser. Tetramerae, Ser. Annuae, Ser. Rubicundae, Ser. Orbiculatae, Ser. Humiles, Ser. Fastigiatae, Ser. Capitatae, Ser. Piaszkianae, Sect. Fimbricorona and Sect. Dolichocarpa); the other half species are perennials belonging to 20 taxa (Ser. Otopnoraе, Ser. Decoratae, Ser. Apteroideae, Ser. Monantnae, Ser. Ornatae, Ser. Verticillatae, Ser. Sikkimenses, Ser. Depressae, Ser. Stragulateae, Ser. Uniflorae, Sect. Cruciate, Sect. Frigida, Sect. Gentiana, Sect. Pneumonante, Sect. Phyllocalyx, Sect. Calathianae, Sect. Ciminalis, Ser. Napuliferae, Ser. Coriaceaе and Ser. Grandiflorae); in Ser. Fimbriatae and Sect. Stenogyne both perennials and annuals occur. The perennial habit is present in both outgroup genera and is therefore considered as a plesiomorphic state and the annual habit as apomorphic.

**Roots** (characters 2~3) Related to the growth habit and the branching of the stem, the roots of *Gentiana* are of five types: fibrous taproots, fleshy linear-cylindrical roots, fleshy stout taproot, fleshy twisted taproot-like root and rhizomes or stolons with adventitious roots. The first type: the roots of this type are fibrous or even woody. The primary root is rather small but slightly thickened, forming a slender taproot with a few secondary rootlets. This type is the commonest one in *Gentiana* and is typical in the annual plants. The second type: the plants of this type have several to many fleshy, linear-cylindrical roots arising from the collar, and belong to 4 series (Apteroideae, Monanthae, Ornatae, Verticillatae) and some species of Sect. Stenogyne. The third type is typical of two alpine series (Decoratae and Otophorae), of which the plant has a fleshy, stout, cylindrical or fusiform, persistent taproot and a few smaller secondary rootlets. The fourth type is characterized by 2~4 fleshy roots which are contiguous and twisted to form a stout taproot. It represents a conspicuous transition from the fleshy linear-cylindrical root type to the true stout taproot type and is only found in Sect. Cruciate. The last type, as the second and third, is always associated with the branching of stem, and the plants have rhizomes or stolons with adventitious roots from the nodes. This type is found in the majority of perennial taxa. Both outgroup genera have rhizomes with adventitious roots which is here considered as a plesiomorphic state. All other types were treated as apomorphic states.

**Rhizome and stolon** (Characters 4~7) All the perennial plants in *Gentiana* have a rhizome or stolon. There are four different rhizome types in *Gentiana*: long and thick (in Sect. *Gentiana* and some species of Sect. *Pneumonante*); short, slender and distinct (in Ser. *Apteroideae*, Ser. *Monanthae* and Sect. *Frigida*); extremely shortened, thin and indistinct in Ser. *Ornatae* and Ser. *Verticillatae*); extremely shortened and thickened, disc-like (in Sect. *Cruciate*, Ser. *Otophorae*, Ser. *Decoratae* and some species of Sect. *Stenogyne* and Sect. *Pneumonante*). The stolons occur in Ser. *Sikkimenses*, Ser. *Depressae*, Ser. *Stragulatae*, Ser. *Uniflorae*, Sect. *Phyllocalyx*, Sect. *Calathianae* and Sect. *Ciminalis*. However, in Ser. *Grandiflorae*, Ser. *Napuliferae*, Ser. *Coriaceae* and some species of Ser. *Fimbriatae*, the stems at the lower nodes are creeping and rooting, even forming stolons, this cases is considered as a secondary derivative. The annual plants have neither rhizome nor stolon. The long and thick rhizome type is present in both outgroup genera and thus is considered as a plesiomorphic state. The other rhizome or stolon types are coded as apomorphic states. The general evolutionary trends of the character states are from the reduction of the rhizome to its disappearance, and then to the occurrence of the stolon in annual plants.

**Stem and ramification** (characters 8~11) In *Gentiana* the stem is always erect or ascending, quadrangular with striae or angles, sometimes having a conspicuous caudex at the base. The ramification is a very constant and significant feature, and provides a reliable diagnostic character for the definition and grouping of sections and series. There are two main types and several subtypes of branching as follows:

(1) Monopodial branching. The terminal bud (growing point of the plant axis) of the plant is always present with great vitality and can grow continuously, lasting throughout the life of the plant. This type of branching falls into two subtypes:

A. Perennial plant subtype. The plant has a basal vegetative rosette with a terminal bud sunk in it. The flowering stems grow up each year from the axillary buds of the outer leaves of the basal rosette. They can grow continually and last for several years (in Ser. *Decoratae*) or only for one year. The plant axis is either more or less elongate, at least distinct (in Ser. *Apteroideae*, Ser. *Monanthae*, Sect. *Cruciata*, Ser. *Otophorae* and some species of Sect. *Stenogyne* and Sect. *Pneumonanthe*) or much shortened to retain only a terminal bud (in Ser. *Ornatae* and Ser. *Verticillatae*).

B. Annual plant subtype. The basal vegetative rosette is absent. The terminal bud is developed and forms a stem which is more or less branched. The main stem is relatively thick either with abundant branches (in Ser. *Suborbisepalae*, Ser. *Tetramerae*, Ser. *Annuae*, Ser. *Rubicundae* and some species of Sect. *Stenogyne*) or with fastigiate branches (in Ser. *Fastigiatae*) or many crowded ones (in Ser. *Capitatae* and Sect. *Fimbricorona*). However, sometimes the main stem is indistinct with caespitose and dichotomous branches (in Sect. *Dolichocarpa*, Ser. *Humiles*, Ser. *Orbiculatae*, Ser. *Piasezkianae*, Ser. *Fimbriatae*, Ser. *Napuliferae*, Ser. *Coriaceae* and Ser. *Grandiflorae*).

(2) Sympodial branching. In contrast to monopodial branching, the growing point in sympodial branching is lateral and constantly renewed. The plant without basal rosette has rhizomes or stolons which have nodes, internodes, buds and adventitious roots. The growth of the terminal bud slows down and stops after a period of time, then the lateral buds on the nodes grow up instead. The flowering shoots develop annually from the buds on the nodes of the rhizomes or stolons, as well as from the apex of the stolons. The sympodial branching of *Gentiana* exhibits two subtypes as follows:

A. Rhizome subtype. The plant has a rhizome. Adventitious roots and a lateral rosette arise first from a node and then buds in the axils of the outer leaves of the lateral rosette give rise to the flowering stems. This subtype is found in Sect. *Frigida*, Sect. *Gentiana* and some species of Sect. *Pneumonanthe*. However, most other species of Sect. *Pneumonanthe* are somewhat different from this model in that the plants have no rosette and the buds of the nodes give rise to the flowering stems directly.

B. Stolon subtype. This subtype is rather similar to the rhizome subtype but differs from it in having overground stolons and runners. The stolons produce runners from the nodes and these runners are ultimately terminated by a lateral rosette with a few small leaves. The central bud of this rosette in time produces the flowering stems. This subtype is found in Ser. *Sikkimensis*, Ser. *Stragulatae*, Ser. *Depressae*, Ser. *Uniflorae*, Sect. *Phyllocalyx*, Sect. *Ciminalis* and Sect. *Calathianae*.

The stem of both outgroup genera is quite different from that of the genus *Gentiana*. It



is single, terete, twining and twisted. However, the ramification of the stem in the outgroups is the same as that of Sect. *Gentiana* and some species of Sect. *Pneumonanthe* [(2), A]. This subtype is here considered as a plesiomorphic state whereas all other subtypes mentioned above as apomorphic states.

**Basal vegetative rosette** (characters 12~13) A basal vegetative rosette, which consists of a terminal bud or a lateral bud and a few basal rosette-leaves, is constantly present in some taxa and provides a diagnostic character. The evolutionary trend of the basal vegetative rosette with a terminal bud is always correlated with the shortening of the plant axis, so the developed rosette with large and abundant leaves has an elongated axis (in Ser. *Apteroideae*, Ser. *Monanthae*, Sect. *Cruciata*, Ser. *Otophorae* and some species of Sect. *Stenogyne* and Sect. *Pneumonanthe*) whereas the reduced rosette with a few small leaves always has very short axis (in Ser. *Decoratae*, Ser. *Verticillatae* and Ser. *Ornatae*), representing a reduction series. The basal vegetative rosette with a lateral bud occurs in Sect. *Gentiana* and Sect. *Frigida* and it is very like that of the outgroup *Tripterospermum* but having more pairs of basal leaves. *Tripterospermum* sometimes has a basal vegetative rosette with a lateral bud and two pairs of basal leaves. The other outgroup, the genus *Crawfordia* has not an rosette. In this cladistic analysis, the absence of the basal vegetative rosette is considered plesiomorphic.

**Arrangement of leaf size on stem** (characters 14~17) In *Gentiana* the arrangement of leaf size on stem is usually constant and certainly has taxonomic significance. By character analysis, this arrangement is correlated with the evolution of the inflorescence. In Sect. *Frigida*, Sect. *Gentiana*, Sect. *Gruciata* and Ser. *Otophorae*, the inflorescence is a complex cyme, so the cauline leaves are widely separated, and their size decreases towards the apex of the stem and the largest is at the lower part of the stem. This type is relatively primitive in *Gentiana*. With abbreviation, concentration and simplification of the inflorescence, the upper internodes of the stem are abbreviated and the upper cauline leaves become crowded and enlarged to surround the inflorescence. This type occurs in Ser. *Apteroideae*, Ser. *Monanthae*, Ser. *Ornatae*, Ser. *Verticillatae*, Ser. *Sikkimenses*, Ser. *Stragulatae*, Ser. *Depressae*, Ser. *Uniflorae*, Sect. *Phyllocalyx*, Ser. *Suborbisepalae*, Ser. *Tetramerae*, Ser. *Annuae* and some species of Sect. *Cruciata* and Sect. *Pneumonanthe*. Especially in Ser. *Monanthae*, Ser. *Ornatae* and Ser. *Verticillatae*, the inflorescence is reduced to a single flower and the leaves and calyx lobes further become narrow in shape. On the other hand, with the simplification of the inflorescence and abbreviation of the lower internodes of the stem, most of the leaves are crowded at the base of the stem and the basal leaves are much larger than the others. This type occurs in Sect. *Calathianae* and Sect. *Ciminalis*. In annual taxa, the cauline leaves are widely separated and the whole plant has only 1~2 pairs of large basal leaves (in Sect. *Dolichocarpa*) or these large basal leaves increase in number and sometimes form an involucre-like structure (in Ser. *Humiles*, Ser. *Rubicundae*, Ser. *Orbicu-*

latae, Ser. Fastigiatae, Ser. Capitatae, Ser. Napuliferae, Ser. Fimbriatae and Sect. Fimbricorona). The cauline leaves of Ser. Coriaceae and Ser. Grandiflorae are different from those of annual taxa in having closely spaced leaves. In Sect. Pneumonanthe, the lower cauline leaves are much reduced to become small membranous scale-like. The cauline leaves of *Tripterospermum*, *Crawfordia* and *Gentiana* Sect. Stenogyne are widely separated and their size decreases towards both ends of the stem. This state is here considered plesiomorphic.

**Inflorescence** (characters 18~23) The inflorescence in *Gentiana* is always a cyme. The cyme may be simple with 1~3 flowers or complex with a few to many flowers. However, there is a great deal of variation of the inflorescence with respect to the development of pedicel, rachis, bracts and flower numbers, etc. Since the complex cyme with pedicellate and bracteate flowers occupies almost throughout the stem and is present in both outgroup genera, this type of inflorescence is considered as a plesiomorphic state and all the others as apomorphies.

In Sect. Pneumonanthe the complex cyme is similar to that of the outgroups, but differs from it in the bracts of the flowers at the base which have been reduced to one pair, and in the inflorescence being concentrated at the upper part of the stem. In Sect. Frigida, Sect. Cruciate and Ser. Otophorae, with the disappearance of the bracts, the inflorescence with many flowers seems more advanced than that of Sect. Pneumonanthe, In Sect. *Gentiana*, with the abbreviation of the pedicels, the inflorescence becomes a verticillaster (the flowers being crowded in a terminal cluster and sometimes also in few-flowered axillary whorls). In Ser. Aptoideae, Ser. Monanthae, Ser. Ornatae, Ser. Verticillatae, Ser. Sikkimensis, Ser. Stragulatae, Ser. Uniflorae, Ser. Depressae and Sect. Phyllocalyx, the inflorescence with sessile flowers is concentrated at the top of the flowering stem and surrounded by more or less enlarged uppermost leaves, its flower numbers are reduced from many via several to a single, representing a reduction series. Another reduction series of inflorescence is present in Sect. Calathianae and Sect. Ciminalis. The inflorescence is strongly reduced to a solitary, terminal and pedicellate flower at the top of the flowering stem, but not surrounded by enlarged uppermost leaves. In Ser. Suborbisepalae, Ser. Tetramerae and Ser. Annuae, many cymes with 1~3 sessile flowers are arranged at the tops of abundant branches. The inflorescence of Sect. Dolichocarpa, Sect. Fimbricorona, Sect. Stenogyne and 10 series (Fimbriatae, Rubicudae, Piasezkianae, Orbiculatae, Humiles, Fastigiatae, Capitatae, Napuliferae, Coriaceae and Grandiflorae) rather similar to that of Ser. Suborbisepalae, Ser. Tetramerae and Ser. Annuae, but the simple cyme is always reduced to a single, smaller flower and the pedicels are more or less present.

**Merism of flower** (character 24) The flowers are generally 5-merous in *Gentiana*, but 6~9 merous flowers are found in Ser. Verticillatae and Sect. *Gentiana*, and 4-merous flowers in Ser. Tetramerae. The 5-merous flowers occur in both outgroup genera and repre-

sent a plesiomorphic state.

**Flower size** (character 25) *Tripterospemum* and *Crawfurdia* have large flowers, so the reduction of flower size in *Gentiana* must be seen as an apomorphy. By character analysis, the reduction trend of flower size is found consistent with that of the intracalycular membrane.

**Intracalycular membrane and calyx** (characters 26~32), **corolla** (characters 33~36) and **corolla plicae** (character 37~41) *Gentiana*, *Tripterospemum* and *Crawfurdia* in subtrib. Gentianinae are characterized by the calyx having a continuous intracalycular membrane and the corolla bearing plicae (or folds) between the lobes. By character analysis, the evolution of the calyx and the corolla is found closely correlated with that of the intracalycular membrane. In Sect. Pneumonanthe, Sect. Crucjata, Sect. Gentiana and Sect. Frigida, the intracalycular membrane is highly developed so that the calyx tube is split down one side (in some species the calyx tube is more deeply split even to form a spathe with small irregular teeth) and the corolla is much exserted from the calyx and enlarged to become 3~4 times as long as the calyx. The corolla is usually infundibuliform in shape and the corolla plicae are large and asymmetrical.

In Ser. Aptoeroideae, Ser. Monanthae, Ser. Ornatae, Ser. Verticillatae, Ser. Sikkimenses, Ser. Stragulatae, Ser. Uniflorae, Ser. Depressae, Sect. Phyllocalyx, Ser. Otophorae, Ser. Decorate, Ser. Suborbisepalae, Ser. Tetramerae, Ser. Annuae, Sect. Stenogyne and Sect. Ciminalis, along with the reduction of the intracalycular membrane, the calyx tube becomes narrow and not split so that the corolla is only limitedly exserted from the calyx and shortened to 2~3 times as long as the calyx (in Ser. Suborbisepalae, Ser. Tetramerae and Ser. Annuae), and its shape becomes tubular or urniform (in Ser. Sikkimenses, Ser. Stragulatae, Ser. Uniflorae, Ser. Depressae and Sect. Phyllocalyx). The corolla plicae are large and symmetrical or asymmetrical.

In Sect. Calathianae, Sect. Dolichocarpa, Sect. Fimbricorona and 10 series (Humiles, Rubicundae, Fimbriatae, Piasezkianae, Orbiculatae, Fastigiatae, Capitatae, Napuliferae, Coriaceae and Grandiflorae), the intracalycular membrane is often considerably reduced, therefore, the calyx tube is never split down one side (always entire, tubular) and the corolla is often campanulate, small-sized and twice as long as the calyx, scarcely large-sized and three times as long as the calyx. The corolla plicae are very large and symmetrical.

*Crawfurdia* of the outgroups has highly developed intracalycular membrane but *Tripterospemum* has only reduced one. In this analysis, the former is considered plesiomorphic.

In addition, while the intracalycular membrane is reduced, the calyx lobes also exhibit various shapes which provide a base for the definition and grouping of series (about 1/3 series are established based on calyx lobe shapes). The development of the intracalycular membrane, the calyx and the corolla are not only correlated with each other, but also with

that of the inflorescence. Along with the shortening and simplification of the inflorescence, the intracalycular membrane is usually reduced.

**Stigmas** (character 42) The oblong or linear, free and recurved stigma lobes occur in the majority of taxa of *Gentiana* and in both outgroup genera. Of 33 ingroups, three sections (Calathianae, Ciminalis and Phyllocalyx) depart from the norm. Their stigma lobes are contiguous or connate, rounded and expanded into a small disc or infundibuliform structure, either fimbriate on the surface and free after anthesis or almost smooth and free or not free after anthesis. The first condition is found in Sect. Ciminalis, the second in Sect. Phyllocalyx, and the third in Sect. Calathianae. These expanded stigmas are diagnostic in *Gentiana* and form the most important characters separating the three sections.

**Gynophore** (character 43) A gynophore is present in *Tripterospermum* and *Crawfordia* and in most taxa of *Gentiana*. This gynophore may elongate and become more apparent with age (it may be short in the young flower and elongate considerably as the capsule matures). However, of 33 taxa, 4 sections (Sect. Calathianae, Sect. *Gentiana*, Ser. Otophorae and Ser. Decoratae) have sessile or subsessile ovary. This character state is partially correlated with deeply lobed corolla (lobed to below the middle in Sect. *Gentiana*, Ser. Otophorae and Ser. Decoratae), but exhibits mosaic evolution with long style (in the first two taxa mentioned above).

**Capsule shape** (character 44~45) **and size** (character 46) The long, narrow, cylindrical and unwinged capsule is always regarded as a plesiomorphic state and is common in most taxa of *Gentiana* and also in both outgroup genera. Of 33 ingroups, Sect. Fimbricorona and 7 series (Humiles, Rubicundae, Fimbriatae, Orbiculatae, Fastigiatae, Capitatae and Napuliferae) have short, broad, obovoid or ellipsoid, strongly compressed and winged capsules. Their wings are rounded and broad at the apex but narrowed towards the base. The narrowly ellipsoid or oblanceolate and winged capsule is found in 3 series (Grandiflorae, Piasezkianae and Coriaceae) and represents a transition from cylindrical to obovoid capsule types.

Both outgroup genera and 21 ingroups have large capsules, but 12 ingroups (Ser. Humiles, Ser. Rubicundae, Ser. Fimbriatae, Ser. Orbiculatae, Ser. Fastigiatae, Ser. Napuliferae, Ser. Grandiflorae, Ser. Piasezkianae, Ser. Coriaceae, Sect. Fimbricorona and Sect. Dolichocarpa) have small-sized capsules.

**Seeds** (characters 47~52) The seed character is certainly diagnostically important in *Gentiana*. There is a great deal diversity of seed types.

(1) The seed has a relatively thickened testa, it is large-sized and winged with either a discoid wing which surrounds the convex lens-like body (in Sect. *Gentiana*) or a wing on one side or at one end of the body, rarely without a wing (in Sect. *Pneumonanthe* and Sect. Calathianae).

(2) The seeds vary from almost smooth to distinctly reticulate, they may be unwinged

and relatively large (in Sect. *Cruciata*, Ser. *Otophorae*, Ser. *Decoratae* and some species of Sect. *Stenogyne*) or small-sized (in Sect. *Fimbricorona*, most species of Sect. *Dolichocarpa*, and 10 series, such as *Fimbriatae*, *Humiles*, *Rubicundae*, *Orbiculatae*, *Fastigiatae*, *Capitatae*, *Piasezkianae*, *Napuliferae*, *Coriaceae* and *Grandiflorae*.)

(3) The seed is covered with membranous lamellae which form: a. shallow or deep, simple, honeycomb-like, hexagonal pits (in Ser. *Apteroideae*, Ser. *Monanthae*, Ser. *Ornatae*, Ser. *Verticillatae*, Ser. *Suborbisepalae*, Ser. *Tetramerae*, Ser. *Annuae*, Ser. *Depressae* and some species of Ser. *Sikkimenses* and Ser. *Uniflorae*); b. complex, spongy, hexagonal pits (in Sect. *Frigida*, Ser. *Stragulateae* and some species of Ser. *Sikkimenses* and Ser. *Uniflorae*).

(4) Like type (3) a, but the body of the seed is surrounded by a broad discoid wing (in Sect. *Phyllocalyx*).

(5) The seed has a densely and reticulately thickened testa and is rugose and unwinged (in Sect. *Ciminalis*).

(6) The seed is small-sized and angled with several irregular spongy ridges (in *G. nannobella* of Sect. *Dolichocarpa*) or with a wing on one side or at one end of the body (in a few species of Sect. *Dolichocarpa*).

(7) The seed has a minutely reticulate testa and is large-sized, triquetrous with three narrow wings on ridges which form three equal-sized faces (in some species of Sect. *Stenogyne*).

The seeds in *Tripterospermum* and *Crawfordia* are large-sized, reticulate, triquetrous with three narrow wings on ridges which form three extremely unequal-sized faces, rarely not triquetrous. This type is regarded as a plesiomorphic state.

Character analyses show that the evolutionary trends of the seed types of *Gentiana* are towards the decrease of the seed size and the development, reduction or even the disappearance of the seed wing, and then towards the development of membranous lamellae of the testa. With the development of membranous lamellae, the series of seed types form in which the testa changes from shallow, simple, honeycomb-like and hexagonal pits to spongy, complex, hexagonal pits. The occurrence of the seed type with shallow, simple, honeycomb-like pits and a discoid wing (type 4) obviously represents a secondary event. The evolutionary series of the seeds may be explained by the recapitulation law and the geographical progression rule. Although most species in Sect. *Dolichocarpa* have smaller, reticulate and unwinged seeds, the exceptions occur in a few species; for instance, *G. pudica* has a broad wing on one side of the body of the seed. *G. prostrata* has unwinged to narrowly winged seeds when young or mature, and the seeds of *G. nannobella* have several irregular spongy ridges, this type reminds one of the seed of *Megacodon stylophorus*, but of the later the seeds are rather large. Ser. *Otophorae* is mainly distributed in NW. Yunnan and has reticulate and unwinged seeds. The only exception in this group is *G. doxiongshanensis* which is

distributed in SE. Tibet, the northernmost margin of the distribution of this group, and has seeds with shallow honeycomb-like pits. According to the geographical progression rule, the more advanced seed type of *G. doxiongshanensis* might be derived from the primitive one of Ser. Otophorae.

**Chromosome analysis** (characters 53~56) According to our own work and previously reported data, the chromosomes in *Gentiana* are median or submedian and similar in size, so the karyotypes are rather symmetrical. Their chromosome number and ploidy, however, exhibit remarkable variations. The basic chromosome numbers range from  $x=7\sim 23$  with the commonest being  $x=9, 10, 12, 13, 14, 15$ . The most frequent ploidy level is diploidy ( $2n=2x$ ). *Gentiana* has the following chromosome number series;

(1) Both Sect. Pneumonanthe and Sect. Crucjata have the basic chromosome number  $x=13$ , and are mostly diploids ( $2n=2x=26$ ). However, tetraploids ( $2n=4x$ ) sometimes occur in high altitude or high latitude regions, for example, *G. straminea*, *G. tibetica*, *G. walujewii* and the European species *G. crucjata* and its subspecies, *G. crucjata* subsp. *phlogifolia*, are all tetraploids. Intraspecific chromosome number variation also occurs in some species, for example, *G. macrophylla* has chromosome numbers of  $2n=24, 26, 42$  and *G. asclepiadea*  $2n=32, 36, 44$ .

(2) The majority of species of the Asian perennial series (Apteroideae, Monanthae, Ornatae, Verticillatae, Suborbisepalae, Tetramerae, Annuae, Sikkimenses, Stragulateae, Depressae and Uniflorae, etc.) have the basic chromosome number of  $x=12$  and are usually diploids ( $2n=2x$ ), though there exist some exceptions, for instance, in alpine regions of central Asia. *G. yakushimensis* and *G. davidii* var. *formosana* in Taiwan of China and Japan have the basic chromosome number of  $x=13$  and both are diploids ( $2n=2x$ ); *G. lawrencei* var. *farreri* and *G. sino-ornata* in alpine regions of central Asia have the basic chromosome number of  $x=12$ , and both are tetraploids ( $2n=4x$ ); *G. frigida* distributed in Europe has the chromosome number of  $2n=42$ .

(3) In the three European sections, Sect. *Gentiana* has chromosome number of  $x=10$ ,  $2n=4x=40$ , Sect. *Ciminalis* has  $x=9$ ,  $2n=4x=36$ , (a), while Sect. *Calathianae* is rather different by having  $x=14, 15$ , less often  $7, 10, 11$ ;  $2n=2x$ , less often  $2n=4x$ . (b).

(4) The commonest chromosome numbers in Ser. *Fimbriatae*, Ser. *Rubicundae*, Ser. *Orbiculateae*, Ser. *Humiles*, Ser. *Fastigiatae*, Ser. *Capitatae*, Ser. *Piasezkianae*, Ser. *Napuliferae*, Ser. *Coriaceae*, Sect. *Fimbricoronae* and Sect. *Dolichocarpa*, etc. are  $x=9, 10$ ,  $2n=2x=18, 20$ . Exceptions often occur in a few widespread species, western Himalayan species and American species or European species, for example, *G. squarrosa* has the chromosome number  $x=9$ ,  $2n=4x=36$ , *G. coronata*  $x=10$ ,  $2n=2x=20$  or  $2n=4x=40$ , *G. scabrifolia*  $x=11$ ,  $2n=4x=44$ , both *G. aquatica* and *G. atlantica*  $x=12$ ,  $2n=4x=48$ , *G. pyrenaica*, *G. douglasiana* and *G. grandiflora* all  $x=13$ ,  $2n=4x=52$  (*G. grandiflora* sometimes with  $x=12$ ,  $2n=4x=48$ ).

(5) Sect. *Stenogyne* has very high basic chromosome numbers of  $x=23, 21, 17$ ,  $2n=2x=46, 42, 34$ .

Chromosome numbers of the outgroups have been reported only for three species in *Tripterospium*, which are  $x=10, 23$ ,  $2n=2x=20, 46$ , so the chromosome data are far from enough for making a comparison of the chromosome numbers of *Gentiana* with those of both outgroup genera. Since Subtrib. Gentaninae, to which *Tripterospium*, *Crawfordia* and *Gentiana* belong, is a primitive taxon in Gentianaceae and this family has the original basic chromosome number of  $x=7$  (Hong, 1990), the original basic chromosome number of *Gentiana* may also be  $x=7$ .

It is here supposed that the *Gentiana*-ancestor, perhaps a diploid with  $x=7$ , might have early diverged and formed two chromosome series with different chromosome numbers. The first one, represented by 12 taxa (type 4), has basic chromosome numbers  $x=9, 10$ , less frequently 8, 11, 12, 13, and usually comprises diploids ( $2n=2x$ ), less often tetraploids ( $2n=4x$ ). This chromosome series is considered being derived through ascending aneuploidy variations of the diploid *Gentiana*-ancestor. The second, represented by 21 taxa (types 1, 2, 3) is considered the result of an early tetraploidization event of the *Gentiana*-ancestor and of the subsequent descending aneuploidy variation. The detailed procedure can be further described as follows: initially the latter series might form the relatively primitive chromosome number of  $x=13$ ,  $2n=2x=24$  (type 1), then the chromosome complement underwent an aneuploidy drop and formed  $x=12$ ,  $2n=2x=26$  (type 2). On the other hand, the chromosome numbers  $x=14, 15$ , less often 11, 10, 7 and  $2n=2x$ , less often  $2n=4x$  in Sect. Calathianae (type 3. b) might be derived from  $x=13$ ,  $2n=2x=26$  of a *Pneumonanthe*-like ancestor, via the ascending (less often descending) aneuploidy variations and the chromosome complement being retained at diploidy level (less often being redoubled). The chromosome numbers of  $x=10, 9$ ,  $2n=4x=40$  and 36 (type 3. a) is considered being derived from an ancestor with the chromosome number of  $x=10$ ,  $2n=2x=20$  through an aneuploidy drop and redoubling. These evolutionary trends may be explained by the irreversibility of chromosome ploidy from low to high and the geographical progression rule. The infrageneric taxa (series and sections) or species which are distributed in the geographical distribution center of *Gentiana* (i. e., the mountains of SW. China, including NW. Yunnan, W. Sichuan and SE. Tibet) and grow in low altitude places often have lower basic chromosome numbers and are usually diploids in the chromosome series with ascending aneuploidy variations (type 4), while those in the chromosome series with descending aneuploidy variations have higher basic numbers (types 1, 2). On the contrary, the infrageneric taxa or species which are distributed outside the distribution center, often have higher basic chromosome number and are usually tetraploids in the chromosome series with ascending aneuploidy variations (type 3. b), while those in the chromosome series with descending aneuploidy variations (type 3. a) have lower basic number. The occurrence of high basic chromosome

numbers in Sect. *Stenogyne* might be a secondary event. This section might be derived through the hybridization between *Tripterospermum* and *Gentiana* after *Gentiana* had originated. The most primitive species of this section, *G. rhodantha*, which has the basic chromosome number of  $x=23$ , may be of an origin from a species with  $x=13$  and one with  $x=10$ .

**Pollen morphology** (characters 57~61) The pollen of *Gentiana* is spheroidal, prolate to perprolate, elliptical in equatorial view, trilobate-circular, scarcely triangular in polar view; the size ranges from  $22\sim48 \times 20\sim35 \mu\text{m}$ ; the aperture is 3-colporate, scarcely 4-colporate; the colpi are long, wide or narrow, with distinctly or indistinctly thickened margins; the ora is usually rounded, with lateral extension. The stratification of exine is distinct. The sexine is thicker than or as thick as the nexine, sometimes the nexine thicker than the sexine; the exine surface has striate-imperforate, striate-perforate, striate-foveolate, striate-reticulate, obscurely striate-reticulate and typically reticulate ornamentation, rarely rugulate-reticulate ornamentation; on the collumellate layer, the bacula are erect and scattered, sometimes lobed at tops and are arranged in one row, less often two rows.

Pollen grains of *Tripterospermum* and *Crawfordia* are morphologically similar to those of *Gentiana*. They are spheroidal or subspheroidal, scarcely prolate; the size ranges from  $26\sim52 \times 23\sim40 \mu\text{m}$ ; the aperture is 3-colporate; the colpi are long and wide, with distinct thickened margins. The sexine is thicker than the nexine; the exine surface has striate to striate-reticulate ornamentations; the lirae are low, slightly wide to wide, supported by bacula in two or more rows, less often one row.

By comparison with the outgroups, the general evolutionary trends of pollen grains in *Gentiana* are from striate-imperforate, striate-perforate, striate-foveolate to striate-reticulate or reticulate exine ornamentation; from long and wide colpi with distinctly thickened margins to short and narrow colpi with indistinct or nonthickened margins; and from spheroidal, prolate to perprolate. Although there are many sexine ornamentation types, the striate ornamentation is the basic pattern and the striate-imperforate type may be the most primitive pattern whereas the reticulate may be the most advanced one. All other types should belong to intermediates. It seems to exist three evolutionary steps from the striate-imperforate to the reticulate ornamentation type. First, the striate-imperforate exine produces a few perforations between the lirae in the two polar regions, then produces more perforations towards the equator at last forms striate-perforate ornamentation type. Second, the perforations of the striate-perforate ornamentation enlarge and fuse to form the striate-foveolate ornamentation type. There may be two different ways to form striate-foveolate ornamentation in *Gentiana*. In perennials (e. g., Ser. *Ornatae*, Ser. *Verticillatae* and Sect. *Ciminalis*), the perforations expand to different directions so that the foveolae are subequal and rounded, whereas in annuals (*G. microphyta*, *G. rubicunda* and *G. albicalyx*, etc.), the perforations enlarge and fuse along parallelly the lirae so that the foveolae exhibit ob-



long, elliptic to irregularly long shapes. Third, the striate-foveolate ornamentation further develops and forms striate-reticulate ornamentation, at last the muri disappear but the laminae enlarge and thus form typically reticulate ornamentation type.

Besides the characters mentioned above, there are some uninformative characters, i. e., those present in all ingroups (symplesiomorphies or autapomorphies for the whole genus) or in single taxon only (autapomorphies for single taxon), they have been excluded from the present analysis. They are:

**Caudex** The plant in Sect. *Cruciata* has a stout caudex sheathed by fibrous old petioles and that in Ser. *Monanthae* has a stout caudex sheathed by membranous petioles.

**Leaf texture** Leaves of Ser. *Coriaceae* are thick and subcoriaceous.

**Phyllotaxis** Leaves of Ser. *Verticillatae* are in whorles of 3~8, the uppermost surrounding the 5~8 merous flowers.

**Petiole** Petioles of Ser. *Sikkimenses* are broadened towards the top of the flowering stem.

**Corona of corolla** In Sect. *Fimbricorona* the Corolla bears a corona of multicellular hairs in the throat.

**Stamens** Anthers are contiguous in some species of Sect. *Pneumonanthe* and Sect. *Gentiana*; in Sect. *Stenogyne*, filaments are asymmetrical, unequal in length, at the apex unilaterally and uniformly curved downwards.

**Style** Styles in *Tripterospermum*, *Crawfordia* and *Gentiana* are variable. The styles in *Tripterospermum* and *Gentiana* Sect. *Stenogyne* are filiform and the long but those in *Crawfordia* and the other taxa of *Gentiana* are medium-length to short and linear.

### 3 Cladistic classification

A data matrix (Table 2) was constructed by 33 ingroups and 61 character states. The data matrix was computed with the PAUP (Phylogenetic Analysis Using Parsimony) program (Version 2.4.1, David L. Swofford, Ill. State Nat. Hist. Surv. Urbana 61820), in which the method of tree construction and search for equally parsimonious cladogram uses alternate swapping branch algorithm. An unusually large number of equally parsimonious trees (cladograms) were obtained (51 in total), all with a consistency index of 0.601 and 173 steps in length. The f-ratio (f-value) ranges from 0.213 to 0.231. Close examination of each of these most parsimonious trees shows that these trees are different from each other in the variation of the positions of 11 series (*Fimbriatae*, *Humiles*, *Rubicundae*, *Orbiculatae*, *Fastigiatae*, *Capitatae*, *Piasezkianae*, *Napuliferae*, *Coriaceae*, *Grandiflorae* and *Fimbricoroneae*) (Fig. 3). However, there is one tree with the lowest f-value of 0.213, which is reproduced in Fig. 2. It was selected as the base for discussing cladistic classification and making cladistic analysis.

In the cladogram (Fig. 2), 23 ingroup series are apparently grouped into five independent

Table 2 Data matrix of

	1									2									
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9
outgro	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Otopho	0	3	0	0	1	0	0	0	1	0	0	1	0	1	0	0	0	0	0
Decora	0	3	0	0	1	0	0	0	1	0	0	2	0	1	0	0	0	0	0
Crucia	0	2	0	0	1	0	0	0	1	0	0	1	0	1	0	0	0	0	0
Monant	0	1	0	1	0	0	0	0	1	0	0	1	0	1	3	0	0	3	0
Vertic	0	1	0	2	0	0	0	0	2	0	0	2	0	1	3	0	0	3	0
Ornata	0	1	0	2	0	0	0	0	2	0	0	2	0	1	3	0	0	3	0
Aptero	0	1	0	1	0	0	0	0	1	0	0	1	0	1	2	0	0	1	0
Frigid	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Gentia	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Pneumo	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phyllo	0	0	0	0	0	1	0	1	0	0	0	0	1	1	0	0	2	0	0
Calath	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	0	0	0	1
Cimina	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	0	0	0	1
Sikkim	0	0	0	0	0	2	0	1	0	0	0	0	1	2	0	0	1	0	0
Depres	0	0	0	0	0	2	0	1	0	0	0	0	1	2	0	0	2	0	0
Stragu	0	0	0	0	0	2	0	1	0	0	0	0	1	2	0	0	2	0	0
Uniflo	0	0	0	0	0	1	0	1	0	0	0	0	1	2	0	0	3	0	0
Suborb	1	0	1	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1
Tetram	1	0	1	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1
Annuae	1	0	1	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1
Stenog	0	1	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	1
Fimbri	0	0	0	0	0	0	2	0	0	0	0	1	0	0	0	0	2	0	0
Rubicu	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	2	0	0	0
Orbicu	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	2	0	0	0
Humile	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	2	0	0	0
Capita	1	0	1	0	0	0	1	0	0	3	0	0	0	0	0	2	0	0	0
Fastig	1	0	1	0	0	0	1	0	0	2	0	0	0	0	0	2	0	0	0
Napuli	0	0	0	0	0	0	2	0	0	0	1	0	0	0	0	2	0	0	0
Coriac	0	0	0	0	0	0	2	0	0	0	1	0	0	0	0	3	0	0	0
Grandi	0	0	0	0	0	0	2	0	0	0	1	0	0	0	0	3	0	0	0
Piasez	1	0	1	0	0	0	1	0	0	0	1	0	0	0	0	2	0	0	0
Fimcor	1	0	1	0	0	0	1	0	0	3	0	0	0	0	0	2	0	0	0
Dolich	1	0	1	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0

Abbreviation: 0=plesiomorphies; 1, 2, 3 or 4=apomorphies; 9=the character is unavailable or information is lost. outgro = outgroup. Otopho = Ser. Otophorae; Decora = Ser. Decoratae; Crucia = Sect. Crucata; Monant = Ser. Monanthae; Vertic = Ser. Verticillatae; Ornata = Ser. Ornatae; Aptero = Ser. Apteroideae; Frigid = Sect. Frigida; Gentia = Sect. Gentiana; Pneumo = Sect. Pneumonathe; Phyllo = Sect. Phyllocalyx; Calath = Sect. Calathianae; Cimina = Sect. Ciminialis; Sikkim = Ser. Sikkimenses; Depres = Ser. Derpressae; Stragu = Ser. Stragulateae; Uniflo = Ser. Uniflorae; sections based on more or less synapomorphies. Ser. Otophorae and Ser. Decoratae are grouped in Sect. Otophora by three synapomorphies (fleshy stout taproot; corolla deeply lobed to the middle or below, with very small, extremely asymmetrical and auriculate corolla

character states in *Gentiana*

3			4							5							6																									
0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9			
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
0	0	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0	2	0	0	1	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	1	1	0	0			
0	0	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0	2	0	0	1	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	1	1	0	0			
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0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	2	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0			
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0	0	0	2	0	0	0	1	0	0	0	0	0	0	0	0	2	0	0	3	0	0	0	1	1	0	0	0	1	1	0	0	2	0	0	0	2	0	0	0	0		
0	0	0	2	0	0	0	1	0	0	1	0	0	0	0	0	2	0	0	3	0	0	0	1	1	0	0	0	1	1	0	0	0	1	0	0	0	1	0	1	0		
0	0	0	2	0	0	0	1	0	0	1	0	0	0	0	0	2	0	0	4	0	0	0	1	1	0	0	0	1	1	0	0	0	1	0	0	0	1	0	1	0		
0	0	0	2	0	0	0	1	0	0	0	0	0	0	0	0	2	0	0	3	0	0	0	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0		
0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	2	0	0	2	0	1	0	1	1	0	0	1	1	0	0	1	0	0	0	1	0	0	0	0	0		
0	0	0	0	2	0	0	1	0	0	1	0	0	0	0	0	2	0	0	2	0	1	0	1	1	0	0	1	1	0	0	1	0	0	2	0	0	0	0	0	0		
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
1	0	0	0	0	1	0	0	2	0	0	0	0	0	2	1	1	0	2	0	0	1	1	1	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	
2	0	0	0	0	1	0	0	1	0	0	0	0	0	2	1	1	0	2	0	0	1	1	1	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	
1	0	0	0	0	2	0	0	1	0	0	0	0	0	2	1	1	0	2	0	0	1	1	1	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	
1	0	0	0	0	2	0	0	1	0	0	0	0	0	2	1	1	0	2	0	0	1	1	1	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	
1	0	1	0	0	2	0	0	1	0	0	0	0	0	2	1	1	0	2	0	0	1	1	1	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	
1	0	0	0	0	2	0	0	1	0	0	0	0	0	2	1	1	0	2	0	0	1	1	1	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	
1	0	0	0	0	2	0	0	1	0	0	0	0	0	2	1	1	0	2	0	0	1	1	1	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	
1	1	0	0	0	2	0	0	1	0	0	0	0	0	1	1	1	0	2	0	0	1	1	1	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	
1	1	0	0	0	1	0	0	1	0	0	0	0	0	1	1	1	0	2	0	0	1	1	2	0	0	0	1	1	2	0	0	0	1	0	0	0	0	0	0	0	0	
1	0	0	0	0	3	0	0	1	0	0	0	0	0	1	1	1	0	2	0	0	1	1	1	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	
1	0	1	0	0	2	0	0	1	0	0	0	0	0	2	1	1	0	2	0	0	1	1	1	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0
1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	1	0	0	1	1	1	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0

Suborb = Ser. Suborbisepalae; Tetram = Ser. Tetramae; Annuae = Ser. Annuae; Stenog = Sect. Stenogyne; Fimbri = Ser. Fimbriatae; Rubicu = Ser. Rubicundae; Orbicu = Ser. Orbicu = Ser. Orbiculatae; Humile = Ser. Humiles; Capita = Ser. Capitatae; Fastig = Ser. Fastigiatae; Napuli = Ser. Napuliferae; Coriac = Ser. Coriaceae; Grandi = Ser. Grandiflorae; Piasez = Ser. Piasezkianae; Fimcor = Ser. Fimbricoroneae; Dolich = Sect. Dolichocarpa.

plicae attached to one side of the lower part of each lobe; striate-imperforate exine ornamentation of pollen grains, with very thin lirae supported by bacula lobed at tops); Ser. Monanthae, Ser. Ornatae and Ser. Verticillatae are grouped in Sect. Kudoa by four synapomor-

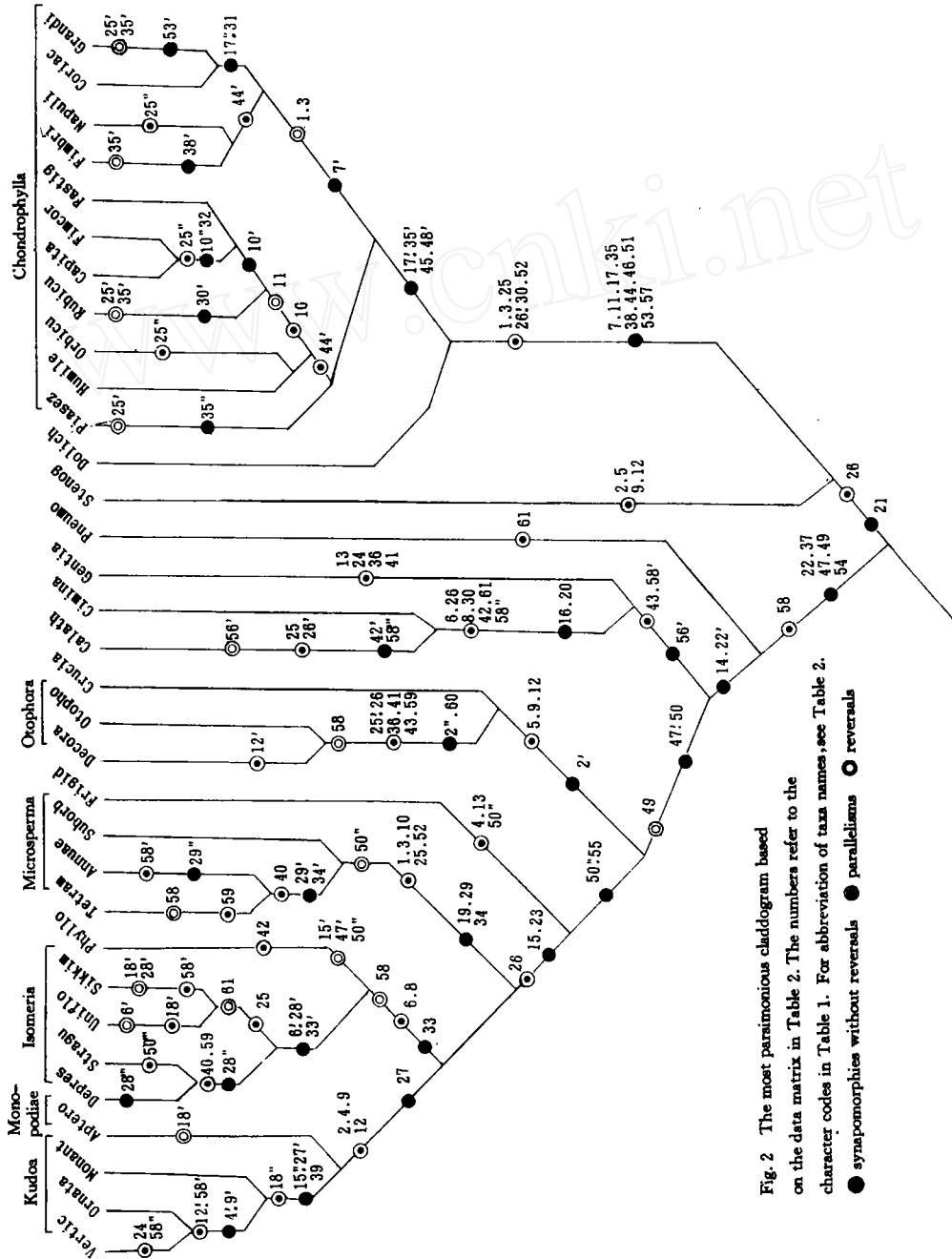


Fig. 2 The most parsimonious cladogram based on the data matrix in Table 2. The numbers refer to the character codes in Table 1. For abbreviation of taxa names, see Table 2.

● synapomorphies without reversals ● parallelisms ○ reversals

phies (flower solitary and terminal at the top of the flowering stem; regular, narrow, linear-lanceolate to linear calyx lobes and cauline leaves; large and regular corolla plicae); Ser. Sikkimenses, Ser. Strgulatae, Ser. Uniflorae and Ser. Depressae are grouped in Sect. Isomeria by three synapomorphies (subequal to equal, triangular to flabelliform calyx lobes; tubular to urniform corolla; developed stolons); Ser. Suborbisepalae, Ser. Tetramerae and

Ser. *Annuae* are grouped in Sect. *Microsperma* mainly by four synapomorphies (annual herbs; many cymes with 1~3 sessile flowers arranged at the ends of the abundant branches; corolla tubular, 2~3 times as long as calyx; small-sized seeds with shallow honeycomb-like pits); 11 series [*Fimbriatae*, *Rubicundae*, *Orbiculatae*, *Humiles*, *Fastigiatae*, *Capitatae*, *Piasezkianae*, *Napuliferae*, *Coriaceae*, *Grandiflorae* and *Fimbricoroneae* (=Sect. *Fimbricorona*)] are combined into Sect. *Chondrophylla* mainly by three synapomorphies (obovoid or narrowly ellipsoid, strongly compressed and winged capsule with a wing rounded and broad at the apex but narrowed towards the base; small-sized and unwinged seeds with reticulate testa; corolla tubular-infundibuliform to campanulate or hypocrateriform, 2~2.5 times as long as calyx). Because of these three synapomorphies just mentioned, it seems more reasonable to put Ser. *Grandiflorae* in Sect. *Chondrophylla* than in Sect. *Ciminalis*, although Ser. *Grandiflorae* is very similar to Sect. *Ciminalis* in growth habit and in that plants have stolons and large flowers. Besides the 23 series mentioned above, the remaining 10 ingroups are supported by this cladistic classification to be established as 10 monotypic sections, namely, *Pneumonanthe*, *Cruciata*, *Frigida*, *Monopodiae*, *Phyllocalyx*, *Stenogyne*, *Gentiana*, *Calathianae*, *Ciminalis* and *Dolichocarpa*. Thus, the 33 ingroups are combined into 15 sections. This result agrees essentially with the current infrageneric classification of *Gentiana* which is accepted by most authors on *Gentianaceae*, but differs from that mainly in the circumscription of some sections, such as *Frigida*, *Isomeria* and *Chondrophylla*. Sect. *Frigida* was widely circumscribed respectively by Kusnezow (1894), Marquand (1937) and H. Smith (1961), including almost the whole *Frigida*-branch but excluding some species in Sect. *Isomeria* or Sect. *Pneumonanthe*, both of which are independent and parallel to Sect. *Frigida*. From a cladistic point of view, this circumscription is wide but incomplete. Therefore, the Sect. *Frigida* defined by the above three authors is a paraphyletic or polyphyletic group because it does not accommodate all the descendants from a same ancestor. Similarly, the Sect. *Chondrophylla* circumscribed by Ho and Liu (1990) might be also a paraphyletic group because it does not contain Ser. *Fimbricoroneae* (=Sect. *Fimbricorona*). Thus, it seems relatively reasonable to treat the members in *Frigida*-branch of the cladogram as six independent sections, and to treat Sect. *Monopodiae* as monotypic, containing only the species of Ser. *Apteroideae*. But Ser. *Ornatae*, Ser. *Verticillatae* and Ser. *Monantha* should be still included in Sect. *Kudoa*.

#### 4 Cladistic analysis

As shown in the cladogram (Fig. 2), the *Gentiana* earliest split up into two clades, the perennial clade and the annual clade. In the perennial clade, Sect. *Pneumonanthe* emerges earlier and appears to occupy the most plesiomorphic node. This is an indication that this section is the extant taxon closest to the ancestral form. It has many plesiomorphic states (e. g., stout and long rhizome; retainment of one pair of bracts below the flower; calyx

tube split down one side with irregular teeth; highly developed intracalycular membrane; seeds with various wings; chromosome number of  $x=13$ ,  $2n=2x=26$ ).

Two subclades, the Asian subclade and the European subclade, come out after Sect. *Pneumonanthe*. The Asian subclade includes 8 sections (*Cruciata*, *Otophora*, *Frigida*, *Microsperma*, *Monopodiae*, *Kudoa*, *Phyllocalyx* and *Isomeria*). The first two sections, Sect. *Cruciata* and Sect. *Otophora*, which comprise the *Cruciata*-branch, diverge at a low level and have several plesiomorphies (e. g., large seeds with reticulate testa; complex cyme with many lax, pedicellate flowers). Especially Sect. *Cruciata*, with the same chromosome num-

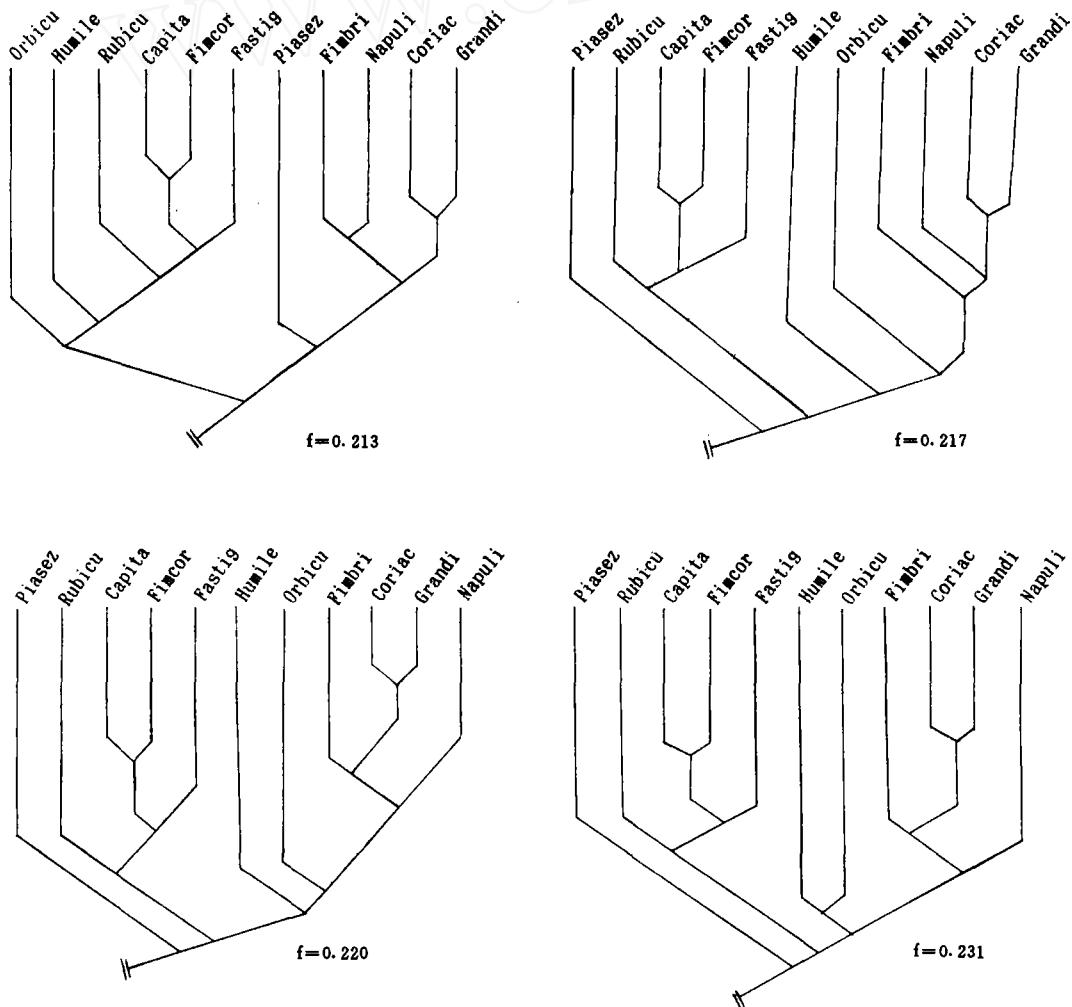


Fig. 3 Examples of some most parsimonious cladograms of *Gentiana* showing the variation of the positions of Ser. Rubicundae, Ser. Orbiculatae, Ser. Humiles, Ser. Fastigiatae, Ser. Capitatae, Ser. Piasezkianae, Ser. Fimbriatae, Ser. Napuliferae, Ser. Coriaceae, Ser. Grandiflorae and Ser. Fimbricoroneae. The remainders of the cladograms have been cut out.

ber of  $x=13$ ,  $2n=2x=26$  as Sect. *Pneumonanthe*, may be also a primitive taxon in this genus. Sect. *Otophora* was once regarded as the most primitive group of the genus *Gentiana* by Kusnezow (1894), in our opinion, however, this section might be a highly specialized

alpine group because it has some special apomorphies (for the detail, see the paragraph "Cladistic classification"). Sect. *Cruciata* and Sect. *Otophora* are connected mainly by two synapomorphies (a stout taproot-like root to a true fleshy taproot; extremely shortened and stout disc-like rhizome).

The *Frigida*-branch is the sister group of the *Cruciata*-branch, but it is more advanced than the latter and is defined by two synapomorphies (seeds covered with membranous lamellae which form honeycomb-like or spongy pits; chromosome number of  $x=12$ ,  $2n=2x=24$ ). Among the taxa in this branch, Sect. *Frigida* diverges earlier, having more plesiomorphies (highly developed intracalycular membrane; calyx tube split down one side with irregular teeth; complex cyme with many lax, pedicellate flowers; asymmetrical corolla plicae). On the other hand, however, this section has three apomorphies (shortened, slender and distinct rhizome; one to a few lateral vegetative rosettes with a few erect narrow leaves; seeds covered with membranous lamellae which form spongy hexagonal pits), indicating that it may be a relatively isolated group and distantly related to the other sections of this branch (i. e., *Monopodiae*, *Kudoa*, *Microsperma*, *Phyllocalyx* and *Isomeria*). Sect. *Microsperma* is the only annual taxon in this branch. It is linked with other sections by four synapomorphies (calyx tube not split; sessile flowers; the increase of leaf size towards the top of the stem). Sect. *Monopodiae* and Sect. *Kudoa* together form the sister group to Sect. *Phyllocalyx*. Sect. *Isomeria*, Sect. *Monopodiae* and Sect. *Kudoa* share four synapomorphies (plant with linear-cylindrical roots from the collar; stem with monopodial branching of perennial plant subtype; having a basal vegetative rosette with a terminal bud sunk in it; subequal to equal triangular to linear calyx lobes) whereas Sect. *Phyllocalyx* and Sect. *Isomeria* mainly share three synapomorphies (plants with stolons and runners creeping on the the surface; stem with sympodial branching of stolon subtype; tubular to urniform corolla). Sect. *Monopodiae* is a relatively primitive taxon by having some primitive characters, such as many-flowered inflorescence, irregular calyx lobes and corolla plicae, striate-imperforate to-perforate exine ornamentations of pollen grains. Sect. *Kudoa* is an alpine group in mountains of 3600~4600 m. It is characterized by four apomorphies (for the detail see the paragraph "cladistic classification"). Sect. *Phyllocalyx* and Sect. *Isomeria* are both advanced groups and can be distinguished from each other by the shapes of the corolla and of the calyx as well as by the features of the stigmas and seeds.

The European subclade includes Sect. *Gentiana*, Sect. *Ciminalis* and Sect. *Calathinae*, which are linked by three synapomorphies (subsessile or sessile ovary; chromosome numbers of  $x=10, 9$ ,  $2n=4x$  or  $x=15\sim 10$ ,  $2n=2x$ ; striate-perforate to reticulate exine ornamentation of pollen grains). In this subclade, Sect. *Gentiana* comes out earlier and is a highly specialized and rather isolated group. It is defined by three special apomorphies (spathaceous calyx tube with small teeth; very small auriculate corolla plicae attached to one side of upper part of each lobe; chromosome number of  $x=10$ ,  $2n=4x=40$ ). Sect. *Cimi-*

nalis and Sect. Calathianae are closely connected by several synapomorphies (e. g. , expanded stigma lobes contiguous or connate into a disc or a infundibuliform structure; most of the leaves crowded at the base of the stem and much larger than the others; flower solitary and terminal at the top of the unbranched flowering stem; striate-foveolate to typical reticulate

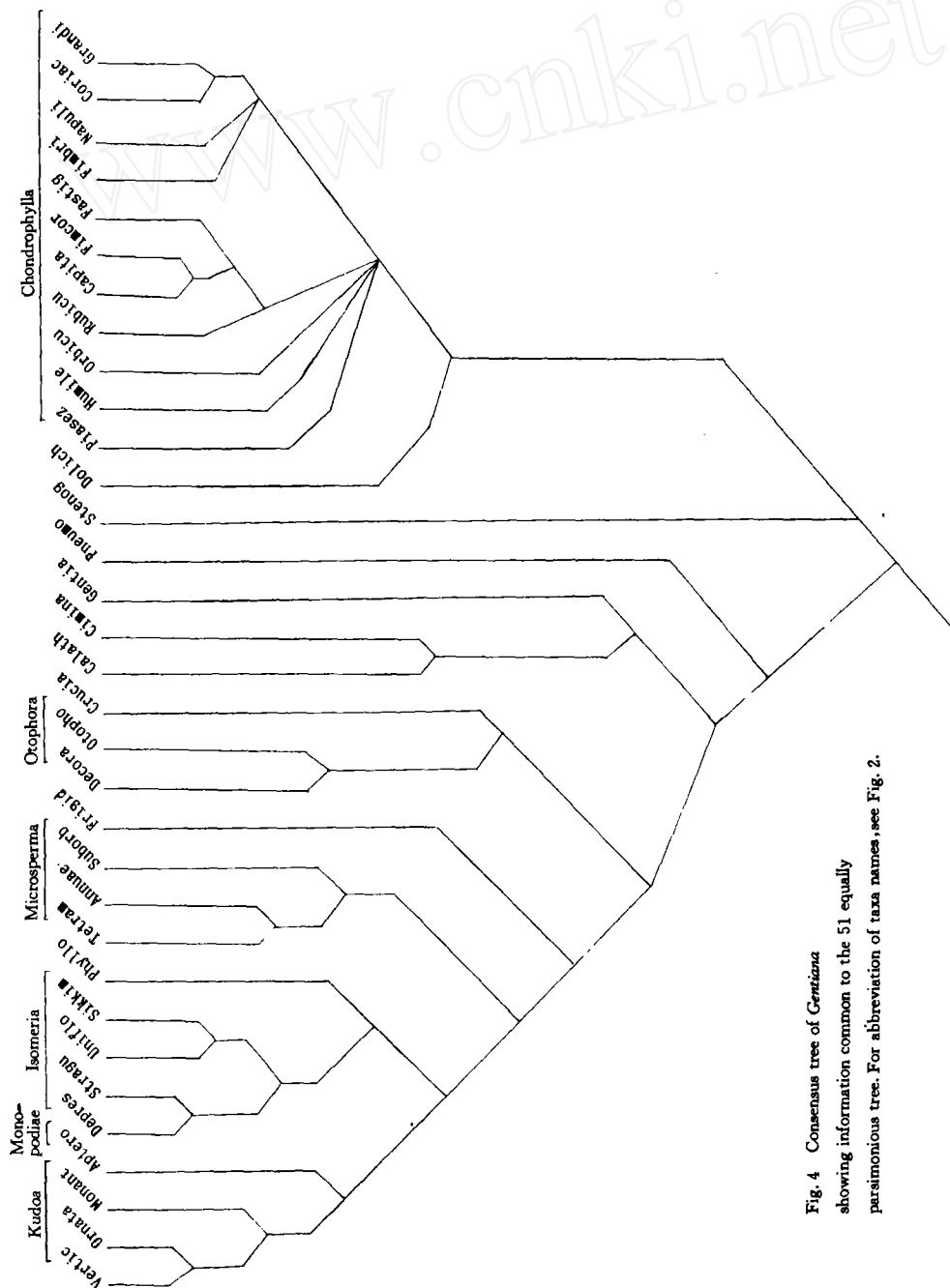


Fig. 4 Consensus tree of *Gentiana* showing information common to the 51 equally parsimonious trees. For abbreviation of taxa names, see Fig. 2.



exine ornamentations of pollen grains), both of them are advanced groups.

The annual clade is the sister group of the perennial clade, but more advanced than the latter. It includes two sections (*Dolichocarpa* and *Chondrophylla*) and shares a number of synapomorphies (e. g., solitary and terminal flowers at ends of branches; considerably reduced intracalycular membrane; calyx tube never split down one side and with equal lobes; large and symmetrical corolla plicae; small-sized capsule; chromosome numbers of  $x=9, 10$ , less often  $11\sim 13$ ,  $2n=2x$ ). Of the two sections in this clade, Sect. *Chondrophylla* is a large taxon with 2/5 species of the total *Gentiana* and seems more advanced by having three highly advanced autapomorphies (for the detail see the paragraph "Cladistic classification"). Kusnezow (1894) considered that Sect. *Chondrophylla* (sensu Kusnezow, including Sect. *Dolichocarpa*) was the most advanced taxon in *Gentiana* and originated from several lines. This opinion is not supported by our cladistic analysis.

Sect. *Stenogyne* was considered as a derivative from Sect. *Pneumonanthe* by Kusnezow (1894), or as an intermediate group between the two genera *Tripterosperrum* and *Gentiana* by H. Smith (1965). Our cladistic analysis suggests that it should be of a hybrid origin between *Tripterosperrum* and *Gentiana*. This result essentially agrees with H. Smith's opinion. In the cladogram, Sect. *Stenogyne* is situated at the outside of Sect. *Dolichocarpa* and Sect. *Chondrophylla*; gross-morphologically it exhibits the features of its parents. For example, Sect. *Stenogyne* is similar to *Tripterosperrum* in having the stamens unequal in length, unilaterally and uniformly curved downwards, the very long and filiform style (about as long as the ovary), the triquetrous seeds with three narrow wings which form three faces; it is similar to *Gentiana* in sharing some synapomorphies (quadrangular ascending stem; developed corolla plicae; flowers solitary and terminal at the ends of the branches). Nevertheless, Sect. *Stenogyne* has very high chromosome numbers of  $x=23, 21, 17$ ,  $2n=2x$ , suggesting its secondary nature in origin.

A strict consensus tree, as shown in Fig. 4, was obtained using the contree algorithm contained in PAUP program. It summarizes the points common to all the equally parsimonious trees. Our results of the phylogenetic relationships of the sections and series in *Gentiana* are also supported by this consensus tree.

### References

- De Beer G A. 1954. Archaeopteryx and evolution. *Advance Sci.* **42**: 1~11  
Czerepanov S K. 1973. Additamenta et corrigenda ad "Floram URSS" (Tomei I-XXX) [In Russian]. Leningrad: Science Press. 288~292.  
Holub J. 1973. New names in Phanerogamae 2. *Folia Geobot Phytotax.* **8**: 155~179  
Hong D Y. 1990. *Plant Cytotaxonomy*. Beijing: Science Press. 333  
Ho T N. Liu S W. 1988. Gentianaceae. In: *Flora Reipublicae Popularis Sinicae*. Beijing: Science press. **62**: 1~418  
Ho T N. Liu S W. 1990. The infrageneric classification of *Gentiana* (Gentianaceae). *Bull Br Mus Nat Hist (Bot)*. **20** (2): 169~192

- Ho T N, Liu S W, Xi Y Z *et al.*, 1994. Pollen morphology and phylogenetic analysis of *Gentiana*. *Cathaya*, **6**: 93~114
- Ho T N, Pringle J B. 1995. Gentianaceae. In: Wu Zheng-yi & Raven P H eds. *Flora of China*. Beijing: Science Press and St. Louis: Missouri Botanical Garden, **16**: 1~140
- Kusnezow N I. 1894. Subgenus *Eugentiana* of genus *Gentiana*. *Tourn Trudy Imp S-Petersb Estest.* **24** (2): 1~531. [1896~1904. Latin translation in *Acta Horti Petrop.* **15**: 1~507]
- Löve A, Löve D. 1975. The spanish Gentians. *Anales Inst Bot Cavanilles.* **32** (2): 221~232
- Marquand C V B. 1937. The gentians of China. *Bull Misc Inf R Bot Gdns Kew.* **1937**: 134~180.
- Nilsson S. 1967. Pollen morphological studies in the Gentianaceae-Gentianinae. *Grana Palynol.* **7**: 46~147
- Serebryakova T I. 1979. Models of shoot formation and some evolutionary trends in the genus *Gentiana* L. *Bull Moscou O-Va Ispyt prior OTD Biol.* **84** (6): 97~109. [in Russian]
- Shigenobu Y. 1984. Karyomorphological studies in some genera of Gentianaceae **I**. *Gentiana* and its allied four genera. *Bull Coll Develop Kochi Women's Univ.* **8**: 55~104
- Smith H. 1936. Gentianaceae. In: Handel-Mazzettii H ed. *Symbololae Sinicae.* Wien. **7**: 948~988
- Smith H. 1961. Problems relating to the *Gentiana cachemirica* of the "Flora of British India". *Kew Bull.* **15** (1): 43~65
- Smith H. 1965. Notes on Gentianaceae. *Notes R Bot Gard Edinb.* **26** (2): 237~258
- Stevens P F. 1980. Evolutionary polarity of character states. *Ann Rev Ecol Syst.* **11**: 333~358
- Tutin T G. 1972. *Gentiana*. In: Tutin T G, Heywood V H *et al.* eds. *Flora Europaea.* Cambridge: Cambridge University Press, **3**: 59~63
- Vasudevan K N. 1975. Contribution to the cytotaxonomy and cytogeography of the flora of the western Himalays (With an attempt to compare it with the flora of the Alps). part 1. *Ber Schweiz. Bot Ges.* **85**: 57~84
- Watrous L E, Wheeler Q D. 1981. The out-group comparison method of character analysis. *Sys Zool.* **30**: 1~11
- Wiley E O. 1981. *Phylogenetics, the Theory and Practice of Phylogenetic Systematics.* New York: J Wiley and Sons
- Yuan Y M. 1993. Karyological studies on *Gentiana* section *Cruciata* Gaudin (Gentianaceae) from China. *Caryologia.* **46** (2~3): 99~114
- Yuan Y M, Kupfer P. 1993. Karyological studies on *Gentiana* sect. *Frigida* s. l. and sect. *Stenogyne* (Gentianaceae) from China. *Bull Soc neuch Sci nat.* **116** (2): 65~78

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(F) **材料和方法** 材料,需指出其来源及凭证标本(说明采集地、采集人,采集号和标本存放地)。方法,人所共知的内容可从简,可指出所用方法的名称及其文献,其改进部分和独特处可重点简洁说明。

(G) **结果和讨论** 行文要条理清楚层次分明。要突出自己工作的创新内容。

实验结果和观察所得应如实列出,但不是全部,只写关键部分。强调科学、准确地表达实验结果,舍弃不必要部分。不要述中间的运算和变化过程。如果有图表,要精心挑选最必要的。注意图、表、文字不要重复,即用表或图表达的内容就不必再文字叙述,因图、表本身各自能单独表达一定的内容。图内尽量不标注文字解释和说明,必要时在图内标注代号,代号在图注中说明(关于图的要求见本刊1996年4期)。表格尽量不用或少用,只有必须列出具体数据和准确数字、不能用图表示的结果或用文字表达也极不方便时才用表格。图表中的文字要中、英文对照。

研究结果列出后应加以判断分析和讨论。对实验和观察结果经过判断、推理形成基本观点,以基本观点为轴心贯穿全文,用实验和观察结果说明观点,形成二者的统一。如发现异常现象又无法解释的,如不影响主要观点也应说明,留待后人研究。

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