

THE SPANISH GENTIANES

by

Askell LÖVE and Doris LÖVE

Dedicated to Prof. S. Rivas
Godoy on his 70th anniversary

Although the classification into a single genus of the more than 600 described species of gentians has long been recognized as being unduly artificial by those few botanists who have had an opportunity to study a considerable part of this vast assemblage, most flora manuals still maintain the wide concept of this group as a single cluster of numerous sections as proposed by the monographer KUSNETZOV (1895, 1896-1904), with only a few exceptions. In recent decades, some modification of this point of view has been observed, when the groups that according to KUSNETZOV (l. c.) constituted sections of the subgenus *Gentianella* have instead been given the status as sections under that name as a genus. However, even that concept leaves both the genera as heterogeneous taxa of several morphologically distinct and not closely related sections. The untenable logic of both these treatments has been made still more obvious in later years through increasing studies of the pollen grains (NILSSON, 1967) and of the seed coat as revealed by the scanning electron microscope (TOYOKUNI, unpubl.), though perhaps the strongest indication of the need for a thorough splitting of the group into several more clearly defined genera comes from investigations of the karyotype and basic chromosome numbers of the various sections. This latter observation was accentuated by D. LÖVE (1953) in a study of the North European members of the group. Her suggestion as to the need for a new system for the complex has later been substantiated by several authors, who have either resuscitated valid generic names long ignored or given new names to groups for which

no such epithets were available. A preliminary review of the situation and of the basis for the reclassification has recently been given by LÖVE & LÖVE (1975).

Since 1962 we have had several occasions to study the gentians of the Iberian Peninsula, first by aid of a generous NATO Science Grant No. 69 (cf. LÖVE & KJELLQVIST 1972, 1973, 1974a, b) and later with other and indirect support or during short visits as tourists. Because the cytological results are connected with the taxonomical conclusions on the generic designation of the groups in question, these are reported below under the valid nomenclatural combinations that we believe ought to replace older names based on the traditionally collective generic concept.

1. *Gentiana* L., s. str.

When the collective genus *Gentiana* is split up into more natural units, the Linnaean genus *Gentiana* must be restricted to the section *Coelanth*e of KUSNETZOV (l. c.). However, since this section is a somewhat heterogeneous assemblage of the type species *G. lutea* L. (cf. Hitchcock & Greene, in BRIQUET 1935) which automatically constitutes the section or subgenus *Gentiana* if the genus is so subdivided, and the other four or five species which differ from it in flower morphology and perhaps even in pollen type (NILSSON 1967), it was concluded by HOLUB (1970) that the latter ought to be placed in a distinct subgenus *Coilantha* (Borckh.) Holub. Hybrids between all the species of *Coilantha* so restricted seem to be common wherever these taxa meet and form hybrid swarms through backcrossing to either parent, so their reproductive isolation from each other is questionable. Furthermore, hybrids occur between *G. lutea* and the other species, as has been known for a considerable time (cf. FOCKE 1881), and these seem to be partially fertile. Therefore, we doubt the wisdom of separating these taxa in different sections or subgenera, whereas there seems to be a reason for wondering if they might not rather be reduced to sub-specific or varietal status within two species. The genus is characterized by its large 5-7-merous yellow or purple flowers with a rotate and deeply parted corolla, sometimes with plaits which then are small and asymmetrical. The seeds are broadly winged, and the plants are perennial with broad and petiolate leaves.

The genus *Gentiana* in the strict sense is cytologically characterized by the basic number $x = 5$; all the taxa are tetraploid with $2n = 40$ chromosomes, and their karyotype is similar, perhaps with a minor deviation in the frequency of exactly metacentric chromosomes in *G. lutea*. The following two species are represented in Spain:

Gentiana lutea L. $2n = 40$, determined on material of subsp. *lutea* from near Goñi in the Sierra de Andia west of Pamplona, voucher G-0411. This confirms previous reports by FAVARGER (1949, 1952).

Gentiana Burseri Lapeyr. $2n = 40$, determined on plants belonging to the subsp. *Burseri* from near Setcasas in the Sierra de la Fembra Morta in the Pyrenées, voucher G-0317, confirming previous reports by KÜPFER & FAVARGER (1967) and FAVARGER & KÜPFER (1968) also from the Pyrenées.

2. *Pneumonanthe* Gleditsch

Another group, which is well defined morphologically, palynologically and cytologically, is formed by the section *Pneumonanthe*, provided that the species *G. asclepiadea* L. and its close relative *G. schistocalyx* C. Koch are excluded as the separate genus *Dasystephana* Adans. (cf. D. LÖVE, 1953; NILSSON, 1967; LÖVE & LÖVE, 1974). The genus so restricted is characterized by its lack of a basal leaf rosette, small and scale-like lower leaves, a limbless corolla with erect lobes and well developed plaits, often connate anthers, and usually but not always winged seeds. It shares a similar pollen morphology, seed coat structure, and the basic number $x = 13$ with the following genus, of which it might therefore be regarded as a subgenus (LÖVE & LÖVE 1975). However, since we are not aware that the species of these two groups ever hybridize in nature or experimentally, despite our efforts including various taxa of both, we find it more logical to retain them as distinct genera, thus following the principle that it is wiser and evolutionarily more correct to separate taxa that may be similar than to unite those which are possibly distinct. The type species *G. pneumonanthe* L. was given a generic status as *Pneumonanthe* by Gleditsch (1764, cf. DANDY 1967). The only Spanish species of that genus so restricted is:

Pneumonanthe vulgaris F. W. Schmidt. $2n = 26$, determined on a collection from near Goñi in the Sierra de Andia west of Pamplona.

voucher G-0397. This confirms earlier reports by several authors (cf. LÖVE & LÖVE 1974).

3. *Tretorhiza* Adans.

This group, or the section *Cruciata* Gaudin, which KUSNETZOV (l. c.) renamed section *Aptera*, is similar to the last genus in its pollen morphology, seed coat structure and basic chromosome number, but it differs from it morphologically by its crown being enveloped in fibrillose sheaths of old leaves, and in that the lower leaves form a rosette; the corolla is limbless or obscurely limbed, the plaits are large and usually symmetrical and biparted, the anthers are free and the seeds are wingless. The only representative of this genus in Spain is the type species:

Tretorhiza cruciata (L.) Opiz. $2n = 52$, determined on material from near Sardenas in the Sierras de San Grao west of Figueras, voucher G-0413. The same chromosome number has been reported previously by several authors (cf. LÖVE & LÖVE 1974).

4. *Ciminalis* Adans.

The section *Megalanthe* Gaudin, or the section *Thylacites* Griseb. of most manuals, was tentatively united with the section *Chondrophylla* Bge. under the name *Ericoila* Ren. by LÖVE & LÖVE (1961a, b), accepting the validation of this pre-Linnaean name by BORCKHAUSEN (1796). This was premature, not only because the name *Ericoila* in the circumscription given to it by BORCKHAUSEN (l. c.) and even by GRAY (1821) under the corrected spelling *Ericala* S. F. Gray, must be rejected for various reasons (cf. HOLUB 1973), but also because the small group of perennial species of *Chondrophylla* with the basic chromosome number $x = 13$ is unrelated to the section *Megalantha* and to the large group of annual or biennial species with $x = 9$ traditionally included in the section *Chondrophylla*. The perennials of the section *Megalanthe* and the annual-biennial species of *Chondrophylla* are, however, morphologically closer and also known to be able to hybridize in nature and under experimental conditions. Therefore, we believe that they are correctly accommodated in a single genus, as concluded by LÖVE &

LÖVE (1961a, b), but its correct name is *Ciminalis* Adans. as typified by *Gentiana acaulis* L. (cf. HOLUB 1973). This genus so restricted is represented in Spain by the species:

Ciminalis acaulis (L.) Moench. $2n = 36$, determined on plants from near Goñi in the Sierra de Andia west of Pamplona. Voucher G-0408. This confirms earlier reports by FAVARGER (1949), RORK (1949) and LOVKA & alii (in LÖVE 1971).

Ciminalis alpina (Vill.) Holub. $2n = 36$, determined on plants from near Setcasas in the Sierra de la Fembra Morte in the Pyrenées. Voucher G-0311. This confirms earlier reports by FAVARGER (1949) and FAVARGER & KÜPFER (1968).

Ciminalis occidentalis (Jakowatz) Holub. $2n = 36$, determined on material from below the Pico Bassagoda west of Figueras in the eastern Pyrenées. Voucher G-0424. This confirms a previous report from the Pyrenées by FAVARGER & KÜPFER (1968) under the synonym *G. angustifolia* Vill.

5. *Holubia* Löve & Löve.

As mentioned in connection with the genus *Ciminalis*, the perennial species of the section *Chondrophylla* are morphologically, cytologically and even palynologically distinct from the annual species traditionally classified in this section, whereas the latter are congeneric with the taxa usually grouped in the section *Megalanthe* for which the correct generic name is *Ciminalis* Adans. For this small perennial group, LÖVE & LÖVE (1975) used provisionally the generic name *Ericala* S. F. Gray; however, that name must be regarded as being illegitimate or synonymous with *Ciminalis* and must, therefore, be rejected. Since that leaves the perennial species of section *Chondrophylla* without a legitimate name at the generic level, although they certainly constitute a natural and well-defined genus, a new name must be furnished to accomodate these about ten species of Eurasia, North and South America with the basic chromosome number $x = 13$, typified by the species *Gentiana pyrenai-ca* L. For this group we propose the name:

Holubia Löve & Löve, nov. gen.

Planta perennis, rhizomata repente ramoso caudiculis plurimis epigeis; caulibus firmis erectis 3-12 cm alt.; folia acuta, subobtusa vel mucronata, coriacea marginata; calyce campanulato non fisso quinque-dentato, corolla tubuloso-campanulata, tubuloso-clavata vel infundibulato-campanulata, ovario oblongo, stigmatibus ovatis. Chromosomata $x = 13$.

A perennial plant with creeping, branching and slender rootstock with numerous epigeous offshoots; stems firm and erect, 3-12 cm long; leaves acute, subobtuse or mucronate, coriaceous; calyx campanulate, unsplit, 5-toothed; corolla tubular-campanulate, tubular-clavate, or campanulate-infundibular; ovary oblong, styles ovate. Basic chromosome number $x = 13$.

Type species of the genus is *Holubia pyrenaica* (L.) Löve & Löve, comb. nov., based on *Gentiana pyrenaica* L., Mantissa (1767), 55.

The chromosome number $2n = 26$ has been determined for *Holubia pyrenaica* from the Sierra de la Caña north of Ribas de Freser in the eastern Pyrenées. Voucher G-0443. It confirms earlier reports by SOKOLOVSKAYA & STRELKOVA (1948), KÜPFER & FAVARGER (1967) and FAVARGER & KÜPFER (1968).

Another Spanish species of the genus is:

Holubia boryi (Boiss.) Löve & Löve, comb. nov., based on *Gentiana boryi* Boissier, Biblioth. Univ. Genève, ser. 2, 13 (1838), 410. Its chromosome number, which has not been previously reported, is $2n = 26$ as counted on material from near Pto. de la Bonaigua in the central Pyrenées. Voucher G-0522.

6. *Calathiana* Delarbr

The section *Cyclostigma* Griseb. or section *Calathianae* Froelich includes about ten perennial or rarely annual species with leaves that are sometimes in a rosette, and with short stems usually with a single terminal flower. The calyx is herbaceous, unsplit but with five teeth. The corolla-tube is almost cylindrical and plicate, but the corolla itself is blue and hypocrateriform with patent lobes and a small appendage in the sinus. The anthers are free, but the stigma-lobes are contiguous and fused into a circular and slightly concave disc with dentate-fimbriate

margins. The capsule is sessile and the seeds are not winged. The basic chromosome number seems to be $x = 7$ of which diploid, tetraploid and hexaploid multiples are known; the basic numbers $x = 8$ and 15 have also been reported. There seems to be no palynological or other indication of heterogeneity within the group, which is also characterized by a homogenous seed coat structure, so there is perhaps a reason to wonder if the chromosome number reports deviating from the basic number $x = 7$ might have been caused by the occurrence of B-chromosomes.

LÖVE & LÖVE (1961a, b) identified these plants of high-alpine and arctic regions in the boreal zone preliminarily with the genus *Hippion* F. W. Schmidt. Recent studies have, however, revealed that this name must be regarded as illegitimate and that the oldest correct name available for this taxon at the generic level is *Calathiana* Delarbre (HOLUB 1973), with the type species *C. nivalis* (L.) Delarbre. The genus is represented in Spain by the species:

Calathiana brachyphylla (Vill.) Holub. $2n = 28$, as counted on plants from north of Estahón in the Sierra de Campirme in the central Pyrenées. Voucher G-0429. This verifies earlier reports by FAVARGER & HUYNH (in LÖVE & SOLBRIG 1964) and FAVARGER (1965).

Calathiana delphinensis (Beauverd) Holub. $2n = 28$, counted on plants from near the Pico Bassagoda west of Figueras in the eastern Pyrenées. Voucher G-0429. This is a new number for this taxon of the SW Alps and the eastern Pyrenées, which FOURNIER (1938) regarded as a subspecies only of the otherwise eastern Alpique species *Gentiana pumila* Jacq. (= *Ciminalis pumila* (Jacq.) Holub). The eastern Alpique taxon was reported, by FAVARGER (1965), to have the chromosome number $2n = 20$, which may or may not have been determined on a hybrid individual ($2n = 21?$).

Calathiana nivalis (L.) Delarbre. $2n = 14$, determined on material from near Setcasas in the Sierra de la Fembre Morte in the Pyrenées. Voucher G-0309. This number has previously been reported from elsewhere in the Pyrenées by FAVARGER & KÜPPER (1968) and by several authors from other regions (cf. LÖVE & LÖVE 1974).

Calathiana verna (L.) Holub. $2n = 28$, determined on material originating from the slopes of Pico Bassagoda north of Sardenas in the eastern Pyrenées. Voucher G-0488. This confirms earlier counts by several authors (cf. LÖVE & LÖVE 1974).

7. *Comastoma* Toyokuni.

The section *Comastoma* Wettst. is often placed in the collective genus *Gentianella*, of which it has sometimes been assumed to be the most primitive species, although it is apparently not closely related to it but instead may be nearer to *Lomatogonium* A. Braun with which it shares certain morphological features, the basic chromosome number $x = 5$, and somewhat similar pollen morphology. LÖVE & LÖVE (1956) concluded from this resemblance observed already by WETTSTEIN (1896) that the section *Comastoma* ought to be transferred to *Lomatogonium*, whereas TOYOKUNI (1961, 1962) maintained that *Comastoma* is actually more correctly placed in a genus of its own. As such, this taxon includes less than twenty species, which are known to occur mainly in the eastern Asiatic mountains, although some taxa are also represented in Europe and North America and in the Arctic. The species are annuals or biennials usually with long-pedicelled flowers, a short calyx-tube, infundibular or campanulate corolla that is 4- or 5-merous and has one or two fimbriate scales at the base of each lobe; there is no style and only very short stigma, and the seeds are wingless. In Spair this genus is represented by the species:

Comastoma tenellum (Roth.) Toyokuni. $2n = 10$, as determined on material from near Pto. de la Bonaigua in the central Pyrenées. Voucher G-0519. This count confirms earlier reports by several authors from elsewhere (cf. LÖVE & LÖVE 1974).

8. *Gentianopsis* Ma.

Another section of *Gentiana* that some authors still include as a part of the genus *Gentianella*, is the section *Crossopetalum* Froel. It deviates considerably from all the other groups in general and floral morphology (LINDSAY 1940) but also in pollen morphology, seed coat structure and in cytological characteristics, as pointed out by D. LÖVE (1953) and NILSSON (1967). Morphologically, it is best characterized by its 4-merous flowers with an unsplit calyx and a tubular-infundibular corolla without a fringed ring in the throat, but the corolla lobes are frequently fringed or ciliate at the margin. The style is distinct and

oval or tubular, and the capsule is stipitate. The basic chromosome number is $x = 11$. The group includes about 70 annual or biennial species of mainly Asiatic and North American distribution, though it is also represented by a few species in alpine and subarctic-arctic Europe. At the generic level, the taxon has been given the invalid name *Anthopogon* Necker (cf. STAFLEU & alii 1972) and also the name *Crosso-petalum* Roth, which has an earlier homonym in the Celastraceae, whereas its valid name is *Gentianopsis*, as described by MA (1951). In Spain it is represented by a single species:

Gentianopsis ciliata (L.) Ma. $2n = 44$, as counted on material originating from north of Estahón in the Sierra de Campirme in the central Pyrenées. Voucher G-0427. This confirms previous reports by FAVARGER (1949, 1959), QUÉZEL (1957) and SKALINSKA (in SKALINSKA & alii 1959).

9. *Gentianella* Moench.

The genus *Gentianella* in its strict sense as typified by *Gentianella campestris* (L.) Börner includes the *Gentiana* sections *Endotricha* Froel. and *Arctophila* Griseb. of boreal mountains. It comprises about 100 annual or biennial species with 4-5-merous flowers, obconical or cylindrical corolla which is fimbriate in the throat and with erect or patent lobes, no style, but sessile and stipitate capsule. It has the basic chromosome number $x = 9$ and a polyploid series from the diploid to the hexaploid. In Spain, this genus so restricted is represented by two species:

Gentianella campestris (L.) Börner. $2n = 36$, determined on material collected on the north slopes of Pico Bassagoda in the eastern Pyrenées. Voucher G-0405. That verifies earlier reports by FAVARGER (1949) for the typical subspecies and by D. LÖVE (1953) and LÖVE & LÖVE (1956) for the subsp. *islandica*.

Gentianella hypericifolia (Murb.) Pritchard. $2n = 36$, counted on plants from the south slopes of Monte Adi north of Cilbeti in the western Pyrenées. Voucher G-0381. This confirms earlier reports by FAVARGER & HUYNH (in LÖVE & SOLBRIG 1964), KÜPPER & FAVARGER (1967) and FAVARGER & KÜPPER (1968).

RESUMEN

Al reclasificar las gencianas españolas en un sistema más natural que la agrupación tradicional, como secciones del género colectivo *Gentiana*, aquéllas pertenecen a los géneros restringidos *Gentiana* L., s. str., *Pneumonanthe* Gleditsch, *Tretorhiza* Adans., *Ciminalis* Adans., *Calathiana* Delarbre, *Comastoma* Toyokuni, *Gentianopsis* Ma, *Gentianella* Moench y *Holubia* Löve & Löve, describiéndose este último en el presente trabajo para incluir las especies perennes de la tradicionalmente delimitada sección *Chondrophylla*. También se relacionan las especies cuya presencia en España es conocida de forma natural, con indicación de los números cromosómicos determinados sobre material español.

ABSTRACT

When reclassified into a more natural system than the traditional grouping as sections only of the then very collective genus *Gentiana*, the Spanish gentians belong to the restricted genera *Gentiana* L., s. str., *Pneumonanthe* Gleditsch, *Tretorhiza* Adans., *Ciminalis* Adans., *Calathiana* Delarbre, *Comastoma* Toyokuni, *Gentianopsis* Ma, *Gentianella* Moench, and *Holubia* Löve & Löve, the last one being described in this paper to accommodate the perennial species of the traditionally delimited section *Chondrophylla*. The species known to occur naturally in Spain are the following, with chromosome numbers determined on Spanish material given in parentheses: *Gentiana lutea* L. subsp. *lutea* ($2n = 40$); *Gentiana Burseri* Lapeyr. subsp. *Burseri* ($2n = 40$); *Pneumonanthe vulgaris* F. W. Schmidt ($2n = 26$); *Tretorhiza cruciata* (L.) Opiz ($2n = 52$); *Ciminalis acaulis* (L.) Moench ($2n = 36$); *Ciminalis alpina* (Vill.) Holub ($2n = 36$); *Ciminalis occidentalis* (Jakowatz) Holub ($2n = 36$); *Holubia pyrenaica* (L.) Löve & Löve ($2n = 26$); *Holubia Boryi* (Boiss.) Löve & Löve ($2n = 26$); *Calathiana brachyphylla* (Vill.) Holub ($2n = 28$); *Calathiana delphinensis* (Beauverd) Holub ($2n = 28$); *Calathiana nivalis* (L.) Delarbre ($2n = 14$); *Calathiana verna* (L.) Holub ($2n = 28$); *Comastoma tenellum* (Rottb.) Toyokuni ($2n = 10$); *Gentianopsis ciliata* (L.) Ma ($2n = 44$); *Gentianella campestris* (L.) Börner ($2n = 36$); *Gentianella hypericifolia* (Murb.) Pritchard ($2n = 36$).

BIBLIOGRAPHY

- Borckhausen, D. B. M. — 1796 — Ueber Linnés Gattung *Gentiana* — Roemer: Arch. Bot., 1: 23-30.
- Briquet, J. — 1935 — International rules of botanical nomenclature — Jena.
- Dandy, J. E. — 1967 — Index of generic names of vascular plants 1753-1774 — *Regnum Vegetabile*, 51: 1-130.
- Favarger, C. — 1949 — Contribution à l'étude caryologique et biologique des Gentianacées — Ber. Schweiz. Bot. Ges., 59: 62-86.
- — 1952 — Contribution à l'étude caryologique et biologique des Gentianacées. II — Ber. Schweiz. Bot. Ges., 62: 244-257.
- — 1959 — Notes de caryologie Alpine. III — Bull. Soc. Neuchât. Sci. Nat., 82: 255-285.
- — 1965 — Notes de caryologie Alpine. IV — Bull. Soc. Neuchât. Sci. Nat., 88: 5-60.
- & Küpfer, P. — 1968 — Contribution à la cytotaxonomie de la flore alpine des Pyrénées. — *Collectanea Botanica*, 7: 325-357.
- Focke, W. O. — 1881 — Die Pflanzen-Mischlinge — Berlin.
- Fournier, P. — 1933 — Les quatres Flores de la France, Corse comprise — Poinson-les-Grancey, pp. 833-896.
- Gleditsch, J. G. — 1764 — *Systema naturum a staminum situ* — Berlin.
- Gray, S. F. — 1821 — A natural arrangement of British plants — London.
- Holub, J. — 1970 — New names in Phanerogamae. 1 — *Folia Geobot. Phytotax.*, 5: 435-441.
- — 1973 — New names in Phanerogamae. 2 — *Folia Geobot. Phytotax.*, 8: 155-179.
- Küpfer, P. & Favarger, C. — 1967 — Premières prospectus caryologiques dans la flore orophile des Pyrénées et de la Sierra Nevada — C. r. Acad. Sci. Paris, 264: 2463-2465.
- Kusnetzov, N. — 1895 — *Gentiana* Tournef. — Engler-Prantl: Nat. Pflanzenfam., 4 (2): 80-86.
- — 1896-1904 — Subgenus *Eugentiana* Kusnetz. generis *Gentiana* Tournef. — *Acta Horti Petrop.*, 15: 1-507.
- Lindsay, A. A. — 1940 — Floral anatomy in the Gentianaceae — *Amer. Journ. Bot.*, 27: 640-652.
- Löve, A. — 1971 — IOPB chromosome number reports XXXIV — *Taxon* 20: 808-821.
- & Kjellqvist, E. — 1972 — Cytotaxonomy of Spanish plants. I. Introduction. — *Pteridophyta and Gymnospermae* — *Lagascalia*, 2: 23-35.
- & Kjellqvist, E. — 1973 — Cytotaxonomy of Spanish plants. II. Monocotyledons — *Lagascalia*, 3: 147-182.
- & Kjellqvist, E. — 1974a — Cytotaxonomy of Spanish plants. III. Dicotyledons: Salicaceae-Rosaceae — *Lagascalia*, 4: 3-32.
- & Kjellqvist, E. — 1974b — Cytotaxonomy of Spanish plants. IV. Dicotyledons: Caesalpiniaceae-Asteraceae — *Lagascalia*, 4: 153-211.
- & Löve, D. — 1956 — Cytotaxonomical conspectus of the Icelandic flora — *Acta Horti Gotob.*, 20: 65-291.

- & Löve, D. — 1961a — Some nomenclatural changes in the European flora. I. Species and supraspecific categories — Bot. Notiser, 114: 33-47.
- & Löve, D. — 1961b — Chromosome numbers of Central and Northwest European plant species — Opera Botanica, 5: 1-581.
- & Löve, D. — 1974 — Cytotaxonomical atlas of the Slovenian flora — Lehre.
- & Löve, D. — 1975 — The natural genera of Gentianaceae — Recent Adv. in Botany, P. N. Mehra Jub., vol.: (in press).
- & SOLBRIG, O. T. — 1964 — IOPB chromosome number reports. II — Taxon, 13: 201-209.
- Löve, D. — 1953 — Cytotaxonomical remarks on the Gentianaceae — Hereditas, 39: 225-235.
- Ma, Y.-C. — 1951 — *Gentianopsis*: a new genus of Chinese Gentianaceae — Acta Phytotax. Sinica — 1: 5-19.
- Nilsson, S. — 1967 — Pollen morphological studies in the Gentianaceae-Gentianinae — Grana Palynologica, 7: 46-145.
- Quézel, P. — 1957 — Peuplement végétal des hautes montagnes de l'Afrique du Nord — Encyclop. Biogéogr. Ecol., 10: 1-445.
- Rork, C. L. — 1949 — Cytological studies in Gentianaceae — Amer. Journ. Bot., 36: 687-701.
- Skalińska, M., Czapik, R., Piotrowicz, M. & alii. — 1959 — Further studies in chromosome numbers of Polish angiosperms (dicotyledons) — Acta Soc. Bot. Polon., 28: 487-529.
- Sokolovskaya, A. P. & Strelkova, O. S. — 1948 — Geograficheskoe raspredelenie polyploidov. III. Issledovanie flory alpiyskoy oblasti tsentralnogo kavkazskogo khrebta — Uchen. Zap. Ped. F. A. Inst. Im. Gertsena, 66: 195-216.
- Stafleu, F. A. & alii — 1972 — International code of botanical nomenclature — Utrecht.
- Toyokuni, H. — 1961 — Séparation de *Comastoma*, genre nouveau, d'avec *Gentianella* — Bot. Mag. Tokyo, 74: 198.
- — 1962 — Further remarks on the genus *Comastoma* — Acta Phytotax. Geobot., 20: 136-138.
- Wettstein, R. v. — 1896 — Die Gattungszugehörigkeit und systematische Stellung der *Gentiana tenella* Rottb. und *G. nana* Wulf. — Österr. Bot. Zeitschr., 46: 172-176.

Institute of Alpine and Arctic Research
University of Colorado
Boulder, Colorado 80302, U. S. A.