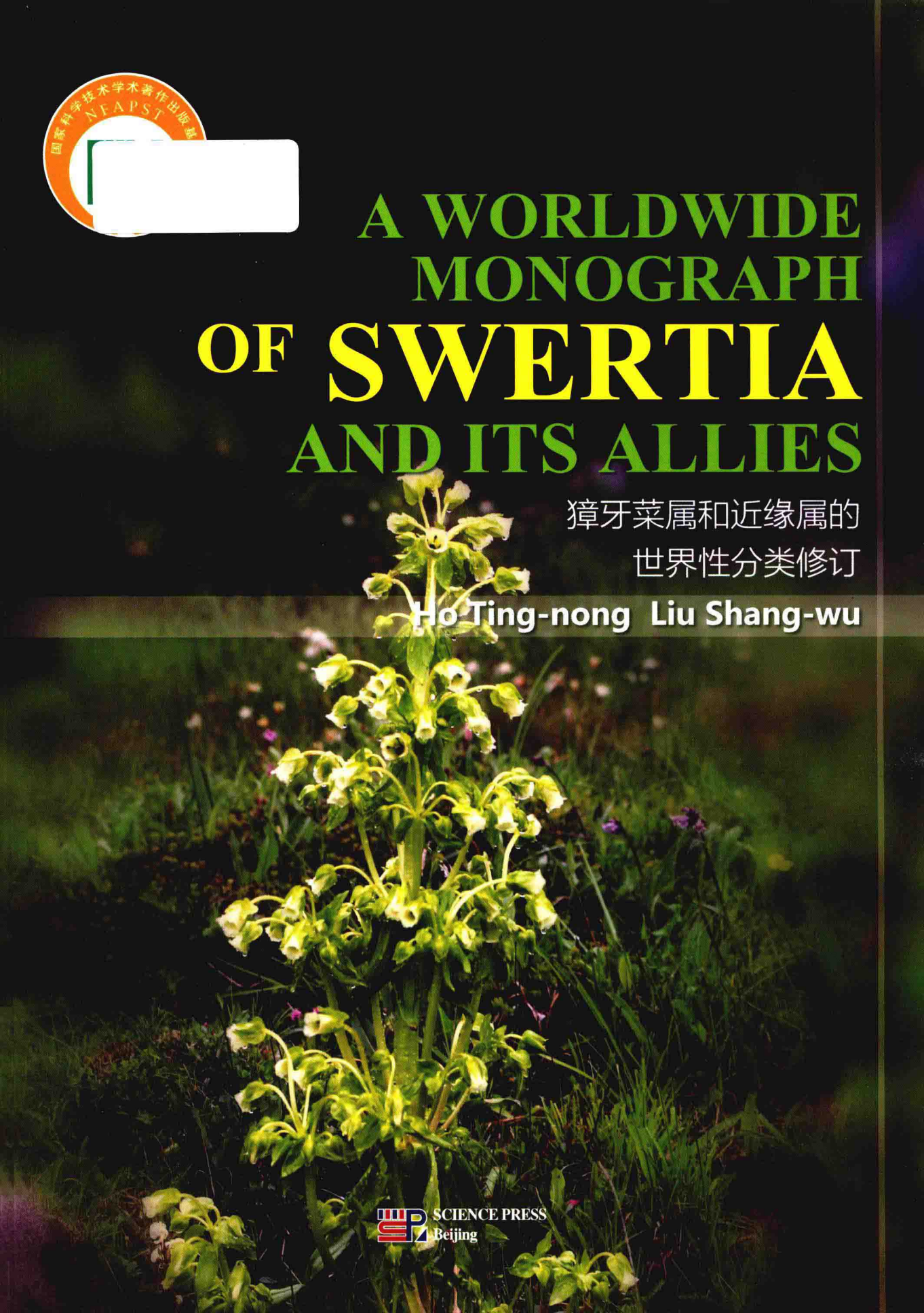
A WORLDWIDE MONOGRAPH OF SWERTIA AND ITS ALLIES

獐牙菜属和近缘属的世界性分类修订

Ho Ting-nong Liu Shang-wu



SCIENCE PRESS
Beijing

Supported by the National Fund for
Academic Publication in Science and Technology

A Worldwide Monograph of

Swertia and Its Allies

Ho Ting-nong Liu Shang-wu

Northwest Institute of Plateau Biology, Chinese Academy of Sciences

SCIENCE PRESS
Beijing

A Worldwide Monograph of Swertia and Its Allies

Ho Ting-nong
Liu Shang-wu

ISBN 978-7-03-042148-7
Science Press Beijing

Responsible Editors: Wang Jing, Luo Jing and Bu Xin

Contents

1 Inter-generic circumscription of *Swertia* and allies

1.1 An introduction to the tribe Gentianae

The tribe Gentianae circumscribed by Struwes and Albert (2002) comprises 17 genera in two subtribes. Subtribe Gentianinae contains *Gentiana*, *Crawfurdia*, *Tripterospermum*, while subtribe Swertiinae includes *Bartonia*, *Comastoma*, *Frasera*, *Gentianella*, *Gentianopsis*, *Halenia*, *Jaeschkea*, *Latouchea*, *Lomatogonium*, *Megacodon*, *Obolaria*, *Pterygocalyx*, *Swertia* and *Veratrilla*. Within the past three decades, we published three additional genera to be included in the Gentianae (*Lomatogoniopsis, Metagentiana* and *Sinoswertia*) (Ho and Liu, 1980; Ho et al., 2002; He et al., 2013b). Phylogenetic analyses constructed based on molecular evidence suggested that after erecting *Sinoswertia*, the genus *Swertia* sensu lato was still polyphyletic (Yuan and Küpfer 1995; Chassot et al., 2001; Liu et al., 2001; He et al., 2013b). However, a limited number of *Swertia* species were sampled. It remains elusive how many genera should be recognized within *Swertia* sensu lato. Here, we tentatively adopt the generic circumscriptions of most genera described by previous authors (for example, Struwes and Albert, 2002). In addition, we further place *Frasera* in *Swertia* sensu lato based on available morphological comparisons. Thus, the Gentianae should comprise 19 genera in total according to current taxonomic treatments. Both subtribes Gentianinae and Swertiinae can be easily distinguished by the presence or lack of corolla plicae and intracalycular membranes between lobes (Smith, 1936). The subtribe Swertiinae also may be subdivided into two groups: the Rotate group and the Tubular group (Smith, 1965). The former has a rotate corolla and calyx, with nectaries either naked or surrounded by fringed or tubular appendages, whereas the latter has a tubular corolla and calyx, with nectaries naked or absent (Ho and Liu, 2001). In the present book, we present a monograph of the rotate group comprising *Swertia*, *Sinoswertia*, *Lomatogoniopsis*, *Lomatogonium*, and *Veratrilla*.

1.2 Key to genera of the tribe Gentianae and subtribe Swertiinae

1a. Corolla with plicae extending between lobes (except in *G. lutea* L.); with an intracalycular membrane between lobes (except in ***Crawfurdia*** spp. and ***Tripterospermum*** spp.) (subtribe Gentianinae):

2a. Flowers ebracteate at base (except for a few species in sections *Pneumonanthe* and *Gentiana*); style linear to cylindrical, shorter than ovary; seeds ellipsoid, ovoid to global, not triquetrous; calyx tube with 15 vascular bundles..... ***Gentiana*** L.

2b. Flowers bracteate at base; style filiform, as long or longer than ovary; seeds

triquetrous to compressed, with three edges; calyx tube with 5–12 vascular bundles:

3a. Stems striate-angled, erect, neither twining nor trailing; flowers sessile, solitary and terminal at branches; bracts of flowers as large or larger than stem leaves; fruit included in persistent corolla; seeds triquetrous with narrow wings on edges, three edges forming three equal faces; annuals, rarely perennials with stout and extremely shortened disc-like rhizome ..... ***Metagentiana*** T. N. Ho and S. W. Liu

3b. Stems terete, twining or trailing; flowers 1–5, pedicellate, in terminal and axillary cymes; bracts of flowers much smaller than stem leaves; fruit exserted from persistent corolla; seeds compressed with discoid wings on edges, rarely triquetrous to compressed with narrow wings, three seed edges forming three extremely unequal faces; perennials with stout, long and branched rhizomes:

4a. Nectaries conspicuously developed, forming a collarlike disc around gynophore; stamens, unequal, apically decurved; fruit a capsule or berry; calyx tube with 5 vascular bundles ..... ***Tripterospermum*** Blume

4b. Nectaries small, on gynophore; stamens symmetrical, equal, straight; fruits a capsule; calyx tube with 10 vascular bundles..... ***Crawfurdia*** Wallich

1b. Corolla without plicae between lobes; without intracalycular membrane between lobes (except *Gentianopsis*) (subtribe Swertiinae):

5a. Corolla rotate, lobed nearly to base, tube very short, indistinct, much shorter than lobes; nectaries surrounded by fringed or tubular appendages or naked:

6a. Plants dioecious, with unisexual flowers; seeds discoid-winged ..... ***Veratrilla*** Baillon ex Franchet

6b. Plants with perfect flowers; seeds various:

7a. Nectaries not surrounded by fringes or appendages ..... ***Gentianella*** Moench

7b. Nectaries surrounded by fringed or tubular appendages:

8a. Both plants and flowers dimorphic: plants heterogeneous and homogeneous; the former with a distinct main stem and numerous weak branches at stem base, on main stem flowers larger and nectaries linear-oblong fringed, on weak branches flowers 1/4–1/3 as large as those of main stem and nectaries with broadly oblong entire elevated scales and indistinct flat gland patches; the latter with uniform stems and flowers, flowers are the same in shape, size and nectaries as those of large-sized flowers on heterogeneous plants ..... ***Sinoswertia*** T. N. Ho, S. W. Liu and J. Q. Liu

8b. Both plants and flowers uniform:

9a. Stigma elevated above ovary, not decurrent; corolla lobes concolorous..... ***Swertia*** L.

9b. Stigma decurrent along ventral suture of ovary; corolla lobes

conspicuously bicolored, half pale and half dark:

10a. Corolla lobe with 2 foveae each in a conspicuous pit; corolla tissue associated with nectary and pit sometimes basally connate, apically lobulate or lamellate..... ***Lomatogonium*** A. Braun

10b. Corolla lobe with 1 fovea not in a conspicuous pit; corolla tissue associated with nectary lamellate or galeate appendaged, margin entire or erose..... ***Lomatogoniopsis*** T. N. Ho and S. W. Liu

5b. Corolla tubular to campanulate, tube distinct, longer than lobes or less often shorter than or as long as lobes (corolla rarely rotate as in some species of ***Gentianella***); nectaries naked or absent:

11a. Plants mycotrophic:

12a. All leaves scale-like; flowers often single, ebracteate without bracts..... ***Bartonia*** Willd.

12b. Lower leaves scale-like, upper leaves spathulate; flowers usually in a cluster of 3 and subtended by two bracts..... ***Obolaria*** L.

11b. Plants autotrophic:

13a. Corolla with 4 distinct spurs near base of corolla tube, rarely spurless; glands prolonged into spurs..... ***Halenia*** Borkhausen

13b. Corolla without spurs; foveae on corolla tube or lobes:

14a. Stems twining; calyx strongly 4-winged; seeds discoid- winged..... ***Pterygocalyx*** Maximowicz

14b. Stems not twining; calyx unwinged; seeds unwinged:

15a. Stamens inserted at or very near sinuses of corolla lobes:

16a. Ovary unilocular, ovules restricted to the sutures and with an additional row between them; corolla lobes valvate in bud at least toward base; seeds few per capsule..... ***Jaeschkea*** Kurz.

16b. Ovary incompletely bilocular, with a lamellate intrusion of the placenta into the locular cavity; corolla lobes contorted in bud; seeds generally numerous per capsule..... ***Latouchea*** Franchet

15b. Stamens inserted on corolla tube distinctly below sinuses:

17a. Nectaries on gynophore; flowers over 5 cm in length..... ***Megacodon*** (Hemsley) H. Smith

17b. Nectaries on corolla; flowers less than 5 cm, but if longer then 4-lobed:

18a. Alabastrum large, slightly flattened, 4-angled; pairs of

calyx lobes dissimilar, 2 outer lobes narrower than and basally overlapping 2 inner lobes; corolla frequently fringed or toothed; seeds angular-papillate; discontinuous intracalycular membranes present..... ..... ***Gentianopsis*** Y. C. Ma

18b. Alabastrum small, not flattened; calyx lobes equal or nearly so, not overlapping nor in 2 distinct pairs; corolla not fringed; seeds almost smooth; intracalycular membranes absent:

19a. Corolla with 1 or 2 non-vascularized fringed scales at base of each lobe..... .....***Comastoma*** (Wettstein) Toyokuni

19b. Corolla either without appendages or with a single vascularized fringed scale at base of each lobe.....***Gentianella*** Moench

1.3 Morphological differentiation between the rotate and tubular genera

As mentioned before, allies of *Swertia* comprise four genera which together belong to the rotate group: these are *Sinoswertia*, *Lomatogoniopsis*, *Lomatogonium*, and *Veratrilla*. Here we summarize the possible links between *Swertia* and these other four genera based on different lines of evidence.

Embryology Embryological data are a critical prerequisite for a complete understanding of phylogenetic relationships of any taxon (Michael, 1991). The embryology of 12 species representing 6 sections of *Swertia* s.l. has been previously studied. Two other genera, *Sinoswertia* and *Lomatogonium*, have also been investigated embryologically, but embryological data are not available for *Lomatogoniopsis* and *Veratrilla*. The available results (Table 1.1) indicate that the basic embryological characters of *Swertia* s.l. are similar to those of the other genera in the subtribe Gentianinae. Thus it exhibits tetrasporangiate anthers, a dicotyledonous type of microsporangial development, a secretory tapetum, simultaneous cytokinesis in meiosis of the microsporocytes, dominant tetrahedral microspore tetrads, 3-celled pollen grains at anther dehiscence, a superior, bicarpellary, and unilocular ovary, an unitegmic, tenuinucellate ovule, a linear megaspore tetrad, a polygonum type of megagametophyte, porogamous fertilization, a nuclear type endosperm, and a Solanad type of embryogeny and endospermic seeds. In subtribe *Swertiinae*, *Swertia* s.l. shares more embryological characters with *Lomatogonium* and *Gentianopsis* than with other genera, by exhibiting a dual original tapetum, trabeculae and formed placentoids, typical parietal placentation with multiseriate ovules, fertilization involving destruction of

Table 1.1 Embryological characters of some genera in the subtribe *Swertiinae*

Characters	*Swertia*	*Sinoswertia*	*Halenia*	*Lomatogonium*	*Gentianopsis*	*Gentianella*	*Comastoma*
Developed type of	dicotyledonous	dicotyledonous	dicotyledonous	dicotyledonous	dicotyledonous	dicotyledonous	dicotyldonous
anther wall							
Epidermis							
persistent	do	do	do	do	do	do	do
cuticle	do	do	do	no	do	do	do
Endothecium							
fibrous thickenings	do (no)	do	do	do	weak	weak	weak
Middle layers	1–3	1	2	1–2	2	2	1
Tapetum							
origin	dual	dual	dual	dual	dual	unitary	unitary
type	secretory	secretory	secretory	secretory	secretory	secretory	secretory
trabeculae	formed	formed	no	formed	formed	no	no
placentoids	formed	formed	no	formed	formed	no	no
number of nuclei in cell	1(2)	2–3	2	1(2)	2(1)	1(2)	1(2)
Microsporogenesis							
cytokinesis type	simultaneous	simultaneous	simultaneous	simultaneous	simultaneous	simultaneous	simultaneous
main tetrad shape	tetrahedral	tetrahedral	tetrahedral	tetrahedral	tetrahedral	tetrahedral	tetrahedral
mature pollen at shedding	3(2)-celled	3-celled	3-celled	3-celled	3-celled	3-celled	3-celled
Megasporangium (ovule)							
type	anatropous (ana-campylotropous)	orthotropous	orthotropous	campylotropous	anatropous	hemianatropous	anatropous
column numbers	(8)12–16	4 (2)	4	12	20–30	4 or 6–8	8
placenta							
intrusion	no	strong	strong	no	No	no	no
type	typical parietal	reduced parietal	reduced parietal	typical parietal	superficial parietal	reduced or typical parietal	typical parietal

Continued

Characters	*Swertia*	*Sinoswertia*	*Halenia*	*Lomatogonium*	*Gentianopsis*	*Gentianella*	*Comastoma*
Developed type of	dicotyledonous	dicotyledonous	dicotyledonous	dicotyledonous	dicotyledonous	dicotyledonous	dicotyldonous
integument							
type	unitegumic	unitegumic	unitegumic	unitegumic	unitegumic	unitegumic	unitegumic
thickness (celled layers)	15–20			4–9	2–9	5–10	
nucellus type	tenuinucellate	tenuinucellate	tenuinucellate	tenuinucellate	tenuinucellate	tenuinucellate	tenuinucellate
epistase	no	no		no	No	formed	no
Hypostase (celled layers)	no (4–5)	4–6 or 8	developed	no	no or 2–3	no or formed	no
Megasporogenesis							
archesporium	1	1	1	1	1	1	
functional megaspore	first chalazal	first chalazal	first chalazal	first chalazal	First chalazal	first chalazal	first chalazal
tetrad shape	linear	linear	linear	linear	linear	linear	linear
Female gametophyte (embryo sac)							
formation type	polygonum	polygonum	polygonum	polygonum	polygonum	polygonum	polygonum
shape	ellipsoid (ovoid)	ellipsoid	ellipsoid		ellipsoid	ellipsoid	ellipsoid
synergids' filiform apparata	indistinct	indistinct	indistinct	indistinct	distinct	indistinct	indistinct
antipodal cells							
cell numbers	(2)3–8	3	3(5)	6–12	3(4–6)	8–12	8–12
cell enlarged	enlarged (no)	greatly enlarged	enlarged	enlarged	enlarged	enlarged	enlarged
nucleus	multinucleate (1, 2)		2 (multinucleate)	multinucleate	multinucleate	3–4	multinucleate
endopolyploid	do		no		do	do	do
haustorium	distinct (indistinct)	distinct	distinct	well developed	weak or not developed	well developed	well developed
Fertilization							
Endosperm							

Continued

Characters	*Swertia*	*Sinoswertia*	*Halenia*	*Lomatogonium*	*Gentianopsis*	*Gentianella*	*Comastoma*
Developed type of	dicotyledonous	dicotyledonous	dicotyledonous	dicotyledonous	dicotyledonous	dicotyledonous	dicotyldonous
formation type	nuclear	nuclear	nuclear	nuclear	nuclear	nuclear	nuclear
endosperm in mature seeds	abundant	abundant	abundant	abundant	abundant	abundant	abundant
Embryogeny							
type	solanad type	solanad type	solanad type	solanad type	solanad type	solanad type	solanad type
varieties	var. Physalis I	var. Physalis I	var. physalis I	var. physalis I	var. physalis I	var. physalis I	var. physalis I
divided direction of apical cell	transverse	transverse	transverse	transverse	transverse	transverse	transverse
cell arrangement at third cell generation	in eight tiers	in eight tiers	in eight tiers	in eight tiers	in eight tiers	in eight tiers	in eight tiers
References	Ho (1998, 1999)	Xue (1999)	Xue (1997)	Liu (in press)	Liu (1997)	Liu (1996)	Liu (1996)

one of the synergids by the pollen tube when it enters the embryo sac, and physalis I variety of solanad type in embryogeny Differences between these three genera involve *Swertia* s.l. having ovules that are anatropous (and rarely anatropous to ana-campylotropous), an indistinct filiform apparatus of synergids, and a well developed haustorium antipodal cell, (rarely not developed). In *Lomatogonium,* ovules are campylotropous, the filiform apparatus of synergids is also indistinct, and the haustorium antipodal cell is well developed, whereas in *Gentianopsis* ovules are anatropous, the filiform apparatus of synergids is distinct, and the haustorium antipodal cell is weakly developed or not formed.

Sinoswertia was originally placed in the genus *Swertia* as a section (*Swertia* sect. *Heteranthos*). However, its embryological characters are conspicuously different from *Swertia* s.l. in that it exhibits orthotropous ovules, a placenta that strongly intrudes into the locule cavity of the ovary, a reduced parietal placenta, and a developed hypostase. In addition, the monotypic species has two types of individuals with one type producing both large and small flowers (He et al., 2013). Most flowers of this species set seeds through a cleistogamous pollination mode. Because these characters are often used to circumscribe taxa above the generic rank, *Swertia* sect. *Heteranthos* is better treated as an independent genus, *Sinoswertia* (He et al., 2013b).

Lomatogonium is morphologically more similar and closely related to the rotate group than to the tubular group in subtribe *Swertiinae*, although previously it was considered to be closely related to the genus *Comastoma* by Löve (1953) and Toyokuni (1963). *Lomatogonium* shares more embryological characters with the rotate group (Table 1.2), in that it exhibits a dual original tapetum, trabeculae and placentoids formed, often typical parietal placentation, antipodal cells often 5–12 in number, enlarged, multinucleate, and distinct haustorim, and physalis I variety of solanad type in embryogeny. *Lomatogonium* is different from *Swertia* mainly in having campylotropous ovules and a decurrent stigma, which receives pollen grains during pollination. The embryological characters found in *Swertia* and allied genera are distinctly different from those found in the tubular group (for example, *Comastoma* and *Gentianopsis*) of subtribe Swertiinae.

Chromosomes Chromosome numbers in subtribe Swertiinae have been reported for 12 genera. No chromosomal data are available for *Veratrilla* (Table 1.2). Chromosomes of *Swertia* are characterized by showing less variation in number, asymmetrical karyotypes, and chromosome complements lacking distinct bimodality. Chromosome numbers of $2n$ = 16, 18, 20, 21, 22, 24, 26, 28, 36, 38, 39, 52, 60, 78 have been reported for the genus; $2n$ = 26 is relatively frequent in four perennial sections (sects. *Swertia*, *Apterae*, *Frasera*, *Montana*) and one annual or biennial section (*Ophelia*), while $2n = 20$ is frequent in three annual or biennial sections (sects. *Swertopsis*, *Platynema*, and *Echinulata*). The karyotypes reported for a few species predominantly consist of mainly median (m), a few submedian (sm), and fewer subterminal (st) and terminal chromosomes (t) (belonging to 2B, 1B, 2A, 3A and 1A types according to Stebbins' classification). *Sinoswertia* differs from *Swertia* in

having a base chromosome number of $2n = 2x = 14$, and a symmetrical karyotype [2B]. A chromosome count exists for only one species of *Lomatogoniopsis* ($2n = 2x = 12$), while counts for *Lomatogonium* vary as follows, $2n = 10, 16, 20, 24, 32, 48$, suggesting that $x = 5, 8, 10$, and 12. Although some chromosome numbers of these genera are the same as those occurring in other tubular genera of the Swertiinae, differences in basic numbers are evident to a degree.

Table 1.2 Available chromosome data for the tribe Gentianeae

Genus	Chromosome numbers		Karyotype types
	Recorded numbers ($2n$)	Suggested basic numbers (x)	
Swertia	20, 26 (16, 18, 21, 22, 24, 28, 36, 39, 52, 60, 78)	10, 13 (8, 9, 11, 12, 14, 18, 19, 39)	2B (1A, 2A, 3A, 1B)
Sinoswertia	14	7	2B
Lomatogoniopsis	12	6	1A
Lomatogonium	16 (10, 20, 24, 32, 48)	8 (5, 10, 12)	
Veratrilla	no count available		
Gentianopsis	26 (44, 52, 78)	13 (11)	2A (3A)
Gentianella	36 (16, 18, 22, 26, 44, 48, 54)	9 (8, 11, 12, 13)	2B (3B, 2C)
Comastoma	18 (10, 12, 16, 20, 28, 30, 32, 36)	9 (5, 8, 10)	2B, 2C (3C)
Pterygocalyx	26 (24)	13 (12)	2A (3A)
Halenia	22	11	
Jaeschkea	16, 18, 20, 22	8, 9, 10, 11	1A
Megacodon	28	14	2A
Latouchea	no count available		
Gentiana	18, 20, 24, 26, 36, 40 (12, 14, 16, 22, 28, 30, 32, 38, 42, 44, 48, 52, 60, 72, 76, 96-98)	9, 10, 12, 13, 14, 15 (6, 7, 8, 11, 16, 19, 21)	1A, 2A (3A, 1B, 2B, 3B)
Metagentiana	46 (34, 42)	23 (17, 21)	3A, 2B (2A)
Tripterospermum	46 (20)	23 (10)	2B
Crawfurdia	46	23	2B

Pollen Pollen morphology in subtribe Swertiinae is extremely variable, particularly with regard to shape, size, and sexine ornamentation (Table 1.3). In the rotate group of taxa, pollen grains of *Swertia* are mainly subspheroidal, less subprolate, prolate, rarely suboblate or spheroidal in equatorial view, circular, trilobate-circular, or obtuse-triangular in polar view. Pollen grain size ranges from 18–47 × 16–40 μm to 18–22 × 16–21 μm in small-sized pollen, to 22–29 × 21–29 μm in medium-sized pollen, and to 29–47 × 29–40 μm in large-sized grains. Pollen is 3-colporate, with colpi usually long, less often of medium length, and rarely short, with distinctly or rarely indistinctly thickened margins and granular colpus membranes. The exine stratification is distinct and 2–5 μm thick. Sexine is thicker than or rarely as thick as nexine. The exine surface can be individed into six different subtypes.

Table 1.3 Pollen characters of the tribe Gentianeae

Genus	Shape	Size(polar axis × equatorial axis μm)	Sexine characters	
			Ornamentation	Lira width (μm)
Swertia	Mainly subspheroidal, less subprolate, prolate, rarely suboblate or spheroidal	18–46 × 16–40	Striate-imperforate, striate-perforate, striate-microreticulate, striate-reticulate, microreticulate, rugulate, echinate or/and verrucate	0.17–0.80
Sinoswertia	Subprolate, less subspheroidal	25–27 × 15–23	Striate-perforate to irregularly striate-imperforate	0.25–0.33
Veratrilla	Subspheroidal or spheroidal	21–22 × 20–22	Striate-perforate	0.33–0.50
Lomatogonium	Spheroidal, prolate, oblate	20–42 × 17–40	Minutely verrucate or echinate, perforate, striate-perforate to -reculate	0.22–0.62
Lomatogoniopsis	Spheroidal or prolate	27–48 × 26–30	Echinate or reticulate	Absent or 0.29–0.53
Pterygocalyx	Subspheroidal	32 × 34	Reticulate	
Megacodon	Prolate	38–42 × 25–32	Reticulate, tuberculate-foveolate to reticulate	> 1
Jaeschkea	Spheroidal, prolate	48–52 × 27–32	Foveolate to reticulate	> 1
Gentianopsis	Prolate, oblate	29–55 × 20–52	Reticulate	> 1
Comastoma	Prolate, oblate, spheroidal	22–47 × 24–45	Minutely and densely reticulate (perforate, foveolate)	> 1
Gentianella	Spheroidal, prolate, oblate	21–52 × 22–40	Striate-perforate, -foveolate, -reticulate to reticulate	
Halenia	Prolate, rhomboid	30–32 × 25–27	Reticulate	
Gentiana	Spheroidal, subspheroidal, prolate (perprolate, rhomboid)	22–60 × 20–50	Striate-imperforate, -perforate, -foveolate, -reticulte to reticulate	(0.13–)0.4–0.7(–1)
Tripterospermum	Subspheroidal	26–52 × 23–40	Striate-imperforate to -reticulate	> 1 (< 0.6)
Crawfurdia	Subspheroidal, prolate	25–48 × 23–40	Striate-imperforate to -perforate	>1 (< 0.6)
Metagentiana	Subspheroidal	37–45 × 30–35	Striate-imperforate to -perforate	< 0.4 or > 1

Pollen grains of *Sinoswertia* are subprolate, rarely spheroidal with size ranging from 25–27 × 15–24 μm. They are 3-colporate, with colpi often of medium length. Exine ornamentation varies from a striate-perforate to an irregularly striate-imperforate type. Pollen grains of *Sinoswertia* are more similar to those of *Swertia* than to other genera in that they are subprolate rarely spheroidal, medium-sized, and have sexine ornamentation of the striate-perforate to irregularly striate-imperforate type.

Pollen grains of *Lomatogoniopsis* are spheroidal or prolate, often of large size (27–48 × 26–30 μm); they are 3-colporate, with long and narrow colpi that have distinctly or rarely indistinctly thickened margins and granular colpus membranes. Exine stratification is

distinct and 3–4 μm thick, and the exine surface is echinate or reticulate. Sexine is thicker than or rarely as thick as nexine.

Pollen grains of *Veratrilla* are subspheroidal or spheroidal, have a size range of 21–22 × 20–22 μm, and are 3-colporate with long and narrow colpi. Exine ornamentation is of the striate-perforate type.

Pollen grains of *Lomatogonium* are spheroidal, sometimes subprolate, but rarely subspheroidal or suboblate. Pollen grain size ranges from small to large (20–22 × 17–21 μm as small-size, 22–29 × 21–29 μm as medium-size, and 29–43 × 29-41 μm as large-size). Pollen is 3-colporate, with colpi normally short, and less often of medium length, but rarely long. Colpi have distinctly (or rarely indistinctly) thickened margins and granular colpus membranes. Exine stratification is distinct and 2–5 μm thick. The sexine is thicker than or rarely as thick as nexine. Sexine ornamentation is striate-microreticulate, echinate and perforate or echinate and verrucate, tubercular, less often striate-perforate or striate-reticulate. Generally speaking, *Swertia* and allied rotate genera have the striate (striate-imperforate, striate-perforate, striate-microreticulate, striate-reticulate, microreticulate, regulate) and echinate or verrucate exine ornamentation. However, in the tubular group of subtribe Swertiinae, pollen grains of *Jaeschkea* and *Megacodon* are larger, 38–52 × 25–32 μm, and exine ornamentation is foveolate to reticulate (in *Jaeschkea*) or tuberculate to reticulate (in *Megacodon*). *Gentianopsis*, *Pterygocalyx*, and *Halenia* have grains showing typical reticulate ornamentation with heterobrochate lumina, while *Gentianella* grains have reticulate ornamentation of four striate types (striate-imperforate, striate-perforate, striate-foveolate, and striate-reticulate). *Comastoma* pollen has a smooth sexine, which is rather special in subtribe Swertiinae, and ornamentation that is perforate, foveolate to minutely, and densely reticulate. Taken overall, rotate and tubular genera differ distinctly from each other in pollen ornamentation.

2 Swertia Linnaeus

2.1 Historical survey

Linnaeus first described the genus *Swertia* in "Amoenitates Academica" in 1751, and included five species, *S. perennis*, *S. difformis*, *S. rotata*, *S. corniculata* and *S. dichotoma*. *Swertia perennis* was taken as the type species of the genus by later authors. The genus was named after the Dutch horticulturalist Emanuel Sweert, author and editor of a book of plant illustrations "Florilegium" in 1612.

In 1753, Linnaeus described all five species in "Species Plantarum" and again in 1754 in "Genera Plantarum".

In 1775, Forsskahl described and illustrated an Ararian species of the genus as *Parnassia polynectaria*.

In 1788, Walter established the genus *Frasera* from the Carolina state of northern America in "Flora Carolina" with a single species *F. caroliensis*, naming it in honor of John Fraser, Scottish hosier, plant collector and traveler in North America.

In 1796, Borckahausen separated *S. corniculata* from other Linnean species on the basis of the spurred corolla and transferred it to a new genus *Halenia* where he placed it under *H. siberica*.

In 1831, Wallich published a catalogue of collections from the subcontinent of India during his services with the East India Company, and included 12 species of *Swertia*.

In January 1836, Don published his work on Royle's collections from the Himalaya with latin diagnoses for all species, including five species of *Swertia*, two species of *Agathotes* and six species of *Ophelia*. Among the *Swertia* species only three (*S. speciosa*, *S. petiolata*, and *S. cuneata*) were validly published for the first time; the other two species (*S. alternifolia* and *S. caerulea*) were old names. The two genera *Agathotes* and *Ophelia* were not formally characterized, and hence should be considered nomina nuda. Although species of these two genera were given diagnoses, they are invalid.

In 1836, Grisebach validly established the genera *Agathotes*, *Ophelia*, and *Anagallidium* with latin diagnoses in "Observationes Quaedam de Gentianearum Familiae Characteribus". Grisebach ascribed the first two genera to D. Don, so they may be treated as "*Agathotes* D. Don ex Grisebach and *Ophelia* D. Don ex Grisebach", respectively. Grisebach also separated *S. dichotoma* from the other Linnean species to establish *Anagallidium*.

In 1837, G. Don published "A general System of dichlamydeous Plants". In this work