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Diversity in fruit and seed characters of *Chamaelirium* and *Chionographis* (Melanthiaceae)

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ABSTRACT: Phenotypic characters of fruits and seeds of two closely allied genera *Chamaelirium* and *Chionographis* (Melanthiaceae) are reexamined. The results show that the two genera differ mainly in the number of ovules per locule, the shape of seeds, and the arrangement of seeds within the locule and of a seed body within the testa. Evidence also shows that in *Chionographis* a Chinese species (*C. chinensis*) significantly differ from three species from Japan and Korea (e.g. *C. japonica*) chiefly by the seeds acutely beaked proximally and in the narrowly obovoid, proximally cuneate fruits (capsules) that ripen in May to June (vs. autumn) and have a carpo-gynophore and locules mutually free, acute, and indehiscent in the proximal part. Data obtained is discussed from taxonomical and evolutionary aspects.

KEY WORDS: Carpo-gynophore, *Chamaelirium, Chionographis*, Fruits, Diversity, Evolution, Melanthiaceae, Seeds, Taxonomy.

INTRODUCTION

Chionographis Maxim. (Melanthiaceae) is a genus of approximately eight species distributed in Vietnam, Laos, China, Japan and Korea (Tanaka, 2016a, b; Wu, 2016). It is regarded as most closely allied to a monotypic genus *Chamaelirium* Willd. of eastern North America (Miquel, 1866, 1867; Maximowicz, 1867; Hara, 1968; Kawano, 1976; Dahlgren *et al.*, 1985; Tanaka 1985, 2003; Takhtajan, 1997, 2009; Utech, 2002; Wu *et al.*, 2016). Recent analyses of the *mat*K gene region of chloroplast DNA in many genera of monocots support this view, showing that the two genera are sister groups in the monophyletic clade of the family Melanthiaceae (Fuse and Tamura, 2000). The closest group of the two genera was supposed to be *Helonias* L. and its closely allied genera (e.g. Tanaka, 1997; Tamura, 1998), which is also later supported by chloroplast DNA sequence data (Fuse and Tamura, 2000).

Chionographis is distinguished from *Chamaelirium* usually by its zygomorphic flowers (vs. actinomorphic flowers), unequal tepals (vs. equal tepals), fewer ovules per locule (2 vs. 6–12), fusiform seeds tailed at the ends (vs. oblong-elliptic seeds winged around), and hermaphroditic or gynodioecious populations (vs. dioecious populations) (Maximowicz, 1867; Baker, 1879; Bentham, 1883; Baillon, 1894; Krause, 1930; Hara, 1968; Tanaka, 1985, 2003, 2013, 2016a, b; Maki, 1993; Tamura, 1998; Utech, 2002; Wu et al., 2016).

Regarding their floral morphology, recent studies revealed that two species of *Chionographis*, *C. shiwandashanensis* Y.F. Huang et R.H. Jiang (Huang *et al.*, 2011) from southern China and *C. actinomorpha* Aver. et N. Tanaka (Averyanov and Tanaka, 2014) from Vietnam and Laos, have actinomorphic flowers with six equal tepals. This finding indicates that the two genera share the same floral trait as to symmetry and tepal length, and accordingly, they are taxonomically inseparable in this respect.

As for their fruits and seeds, the two genera reportedly differ in the number of ovules per locule and in the shape of seeds, as aforementioned. Previous reports also indicate that the size of capsules and the arrangement of a seed body within the testa differ between the two genera (Yatabe (1893) for *Chionographis*; Gleason (1952) for *Chamaelirium*; Hara (1968) for *Chionographis*). Further, Hara (1968) reported that the capsules and seeds of *Chionographis* are different in shape between species from China and species from Japan and Korea. Thus the information hitherto available implies that the two genera are not a little diversified in fruit and seed characters.

For the elucidation of taxonomic and evolutionary aspects of the two genera, it is necessary to accumulate sufficient data on various characters. Among others, having ample data on their fruits and seeds is crucial for achieving this purpose, because these characters are markedly diversified in them, according to previous reports. However, our knowledge on these characters still seems insufficient. For instance, we have no information on the arrangement of ovules (seeds) within the locule in *Chamaelirium*. To complement this insufficiency, the present work was undertaken.

In this study, fruits and seeds of the two genera are closely reexamined with the aim of clarifying their diversity. The results of comparative observations on them will be described here with illustrations, and discussed from taxonomical and evolutionary aspects.

MATERIALS AND METHODS

Plants examined in this study are *Chamaelirium luteum* (L.) A. Gray (distributed in U.S.A.) and four

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Table 1. Comparison of several characteristics (other than those of ovary-fruit and ovule-seed) in species of ***Chamaelirium*** and ***Chionographis.***

Character	***Cha. luteum*** (Range: USA)	***Chi. hisauchiana*** (Japan)	***Chi. japonica*** (Japan, Korea)	***Chi. koidzumiana*** (Japan)	***Chi. chinensis*** (China)
Inflorescence rachis					
Color [1] (sexual type)	white (male) or green (female)	white (all sexual types)	white (all sexual types)	green (all sexual types)[2]	white (all sexual types)
Flower					
Direction[1]	ascending	horizontal or sl. descending	sl. descending	sl. descending	sl. descending
Symmetry	actinomophic	zygomorphic	zygomorphic	zygomorphic	zygomorphic
Base	shortly pedicellate	sessile	sessile	sessile	sessile
Tepal					
Lower tepal (length)	as long as upper tepal	shorter than c.1/2 of upper tepal	vestigial or lacking	vestigial or lacking	shorter than c. 2/3 of upper tepal
Shape	spatulate	spatulate	spatulate	filiform	spatulate
Anther	bilocular	bilocular	bilocular	unilocular	bilocular

[1] At early and middle stages of flowering; [2] Other than female which is not found; Abbreviation: sl., slightly.

species of *Chionographis*, *C. chinensis* Krause (including *C. merrilliana* Hara; China), *C. hisauchiana* (Okuyama) N. Tanaka (Japan), *C. koidzumiana* Ohwi (Japan), and *C. japonica* (Willd.) Maxim. (Japan and Korea).

Living plants of *Chamaelirium* were introduced from U.S.A. through a botanical garden or nurseries, and those of *Chionographis* in Japan were collected myself in their habitats. They were/are cultivated at Hachioji, Tokyo, and studied from morphological and phenological aspects. Dried herbarium specimens kept at A, BM, GH, K, KYO, KANA, MAK, TI, TNS, UC and my own herbarium were also examined to grasp the range of variation in characters here concerned. Several representative specimens examined are cited at the end of this text. Obsevations and measurements of characters were made under a zoom stereomicroscope equipped with an eyepiece micrometer. Descriptions of characters are based on both living plants and herbarium specimens except *C. chinensis* of which the living plants were unavailable. Drawings were made from materials in List 1.

List 1. Sources of material used for drawing.

Chamaelirium luteum
L-1: U.S.A. West Virginia. Fruits harvested on 28 Sept. – 13 Dec. 2008 by Noriyuki Tanaka (s.n.).
L-2: U.S.A. Precise locality unknown. Fruits harvested on 19 Oct. 2015 by Noriyuki Tanaka (s.n.).
Chionographis chinensis
C-1: China. Guangdong. Tsengshing District, Naam Kwan Shan, 30 Apr. 1932, W. T. Tsang 20386 (UC).
Chionographis japonica
J-1: Japan. Toyama Pref., Uozu-shi, Kosuganuma, 19 July 1980, Noriyuki Tanaka s.n.; Infructescences harvested on 8 Nov. 2013 and 12 Nov. 2015 by Noriyuki Tanaka (s.n.).

Terms “carpophore”, “gynophore” or “carpopodium” followed the respective definitions in Harris and Harris (1994). The term “carpo-gynophore” used in the present paper refers to an elongate axis of receptacle that not only supports the carpels of a capsule but also centrally lies between the carpels.

RESULTS

Several characters of flowers and inflorescences are compared among five species of *Chamaelirium* and *Chionographis* in Table 1. As evident from this table, they are variable among the species, and the respective species are highly distinctive for their own features. The results of observations on their fruits, seeds and relevant floral characters (such as ovaries and ovules) are described below. Those characters which show variation among the species are outlined in Table 2.

1. Basic features in flowers, fruits and seeds of *Chamaelirium* and *Chionographis*.

All the species examined has a tricarpellary pistil with a superior, syncarpous (*Chamaelirium* and *Chionographis* excluding *C. chinensis*) or semicarpous (*C. chinensis*) ovary, and three, free, linear or ligulate, ventrally stigmatic styles. The styles, tepals and stamens are persistent in fruit (Fig. 4A). The ovaries develop into capsules that are antrorse, loculicidal and trivalvate (Figs. 1–4). Their pedicels are short and antrorse in fruit (Figs. 1–3, 4A).

Within an ovary, ovules are pendent from axile placentae, nearly hemitropous (*Chionographis*) or intermediate between anatropous and hemitropous (*Chamaelirium*), and have a negligibly short funicle at the adaxial middle (*Chionographis*) or middle to subdistal portion (*Chamaelirium*), a relatively large micropyle in the adaxial upper portion above the funicle, and a raphe situated along the adaxial lower portion of the nucellus. These features of ovules, as to the arrangement within an ovary and the relative position of a funicle, micropyle, raphe and nucellus, are more or less retained in mature seeds (Figs. 1–4). The body of a seed is (sub)ellipsoid, pale to medium brown, and clothed with a scarious testa (seed coat) (Figs. 1–4). A tiny, narrrowly ellipsoid embryo is embedded in copious albumen in the apical part of the body (Figs. 1E, 3G).

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Table 2. Variation in fruit and seed characters of ***Chamaelirium*** and ***Chionographis.***

Character	***Cha. luteum*** (Range: U.S.A.)	***Chi. hisauchiana*** (Japan)	***Chi. japonica*** (Japan, Korea)	***Chi. oidzumiana*** (Japan)	***Chi. chinensis*** (China)
Fruit (Capsule)					
Ripening	Oct. –Nov.	Oct. –Nov.	Oct. –Nov.	Oct. (–Nov.)	May–June
Shape	u. ellipsoid	ellipsoid(-ovoid)	ellipsoid(-ovoid)	ellipsoid(-ovoid)	obovoid, prox. cuneate
Carpels (ovary part)	syncarpous	syncarpous	syncarpous	syncarpous	semicarpous (prox. free)
Length (mm)	4.5–11.5	3.0–4.3	2.7–4.2	2.5–4.5	2.5–4.0(–4.8)[1] (carpels: 2.3–3.5)[2]
Breadth (mm)	3.0–6.0	2.0–2.8	1.5–2.8	1.6–2.3	1.5–2.0
Capsular locule breadth (mm)[3]	1.5–3.0	1.0–1.4	0.8–1.4	0.8–1.2	0.8–1.0
Pedicel length (mm)	0.2–3.5	0.3–0.5	0.3–1.5	0.5–1.0	0.2–0.6
Carpo-gynophore	absent	absent	absent	absent	present
Dorsal connation between adjoining carpels (along ventral sutures)	base to subdistal	base to apex	base to apex	base to apex	distal ca. 2/3–1/2
Shape of capsular locules at base	obtuse	obtuse	obtuse	obtuse	cuneately acute
Loculicidal dehiscence (along dorsal sutures)	apex to base	apex to base	apex to base	apex to base	distal ca. 3/4—1/2
Dehiscence among valves	distal ca. 1/3–1/4	distal 1/2	distal 1/2	distal 1/2	distal 1/2
Location of placentae on ventral sutures of carpels	middle to subdistal	middle	middle	middle	middle
Number of ovules per locule	6–11	2	2	2	2
Seed					
Arrangement in locule (to capsular axis)	oblique to parallel	parallel	parallel	parallel	parallel
Shape (incl. testa)	oblong or elliptic	subfusiform v. 1-(2-)winged	subfusiform v. 1-(2-)winged	subfusiform v. 1-(2-)winged	subfusiform v. 2-winged
Length (mm)	2.0–5.3	2.5–4.0	2.4–4.1	2.8–4.1	2.2–2.3
Breadth (mm)	1.0–1.8	0.7–1.0	0.6–1.0	0.7–1.1	0.6–0.7
Body					
Arrangement within testa	oblique	axial	axial	axial	axial
Shape	ellipsoid	sub-ellipsoid with a flat side	sub-ellipsoid with a flat side	sub-ellipsoid with a flat side	sub-ellipsoid with a flat side
Length (mm)	1.5–3.0	1.5–2.6	1.7–2.7	1.6–2.8	1.3–1.6
Width (mm)	0.6–1.3	0.6–1.0	0.5–0.9	0.5–1.0	0.5–0.7

[1] Length of fruit including both carpels and gynophore (carpopodium). [2] Length of carpels, excluding the gynophore. [3] Values obtained by halving the breadth of fruit (capsule). **Abbreviations**: prox., proximally; u, usually; v, vestigially.

2. Features of fruits and seeds of the respective species.

A. *Chamaelirium*

Chamaelirium luteum is highly variable in the size and shape of fruits and seeds. Living plants from two sources, L-1 (Fig. 1) and L-2 (Fig. 2), also markedly differ from each other. Compared with L-2, plants L-1 have larger oblong-ellipsoid capsules 6–10 mm long and 4.5–5 mm broad (vs. obovoid capsules 4.5–6 mm long and 3.5–4.8 mm broad) and larger seeds 4.2–5.3 mm long and 1.4–1.8 mm broad (vs. 2.0–2.5 mm long, 1.0–1.3 mm broad). Descriptions below are based on both the living plants and several herbarium specimens (some cited below).

Fruits (Figs. 1–2) ripen in autumn (usually October to November). Pedicels in fruit are usually 0.2–3.5 mm long. Capsules are oblong-ellipsoid, ellipsoid or obovoid, 4.5–11.5 mm long, 3.0–6.0 mm broad, bearing no carpophore nor gynophore (carpopodium). Adjoining carpels are connate dorsally along their ventral sutures (capsular axis) except the distal ca. 1/6–1/11 portion, forming septa (Figs. 1B, 2C, 5A), and each carpel dehisces to the base along the dorsal suture (Figs. 1A, 2B). Three valves of a capsule separate from one another in the distal 1/3 to 1/4 portion (Figs. 1B–C, 2B–D). Placentae occupy the middle to subdistal portion of the ventral sutures of carpels (Figs. 1B–C, 2C–D, 5A, 6A). Ovules count 6–11 per locule (6–12 in Bentham (1883)). Seeds (ovules) are obliquely or vertically pendent from the placentae (Figs. 1C, 2D, 6A), funiculate at the adaxial middle to subdistal portion (Figs. 1C–E, 2D–E, 6A), biseriate, imbricate, winged with a scarious, minutely alveolate testa around their body, oblong or (narrowly) elliptic, 2.0–5.3 mm long, 1.0–1.8 mm broad, and obtuse or subacute at the ends (Figs. 1C–E, 2D–E). The body of a seed is ellipsoid or ovoid, sometimes somewhat distorted, and obliquely set within the testa (Figs. 1C–E, 2D–E, 6A).

B. *Chionographis*

a) Four species from China, Japan and Korea

Pedicels are 0.2–1.5 mm long in fruit (Figs. 3–4). Adjoining carpels are connate dorsally along the ventral

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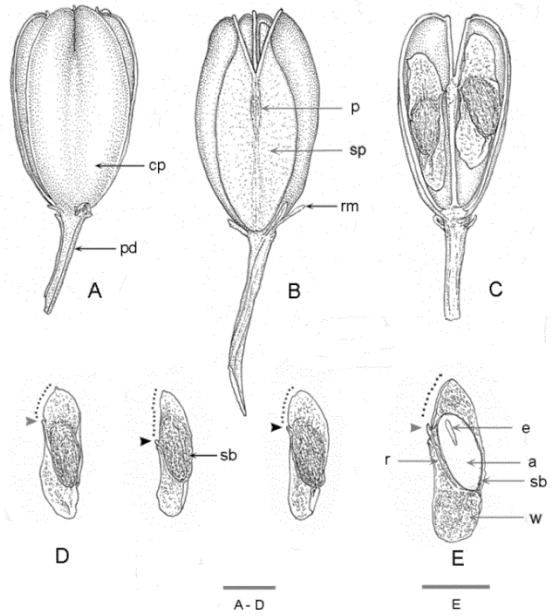


Fig. 1. Capsules and seeds of ***Chamaelirium luteum*** (material L-1). **A**: Dehisced capsule with seeds removed, side view. **B**: Dehisced capsule with free part of frontal carpel removed, leaving septa connate to adjoining carpels; most seeds removed. **C**: Dehisced capsule with frontal valve and several seeds removed; two seeds remain in locules. **D**: Three seeds. **E**: Seed with body longitudinally sectioned, showing embryo embedded in albumen. Position of funicle indicated by arrowhead, portion of micropyle by dotted line. a, albumen; cp, capsule; p, placentae; pd, pedicel; r, raphe; rm, remnants of tepals; sb, seed body; sp, septa; w, wing. Scale bars: 2 mm. Drawn by the author.

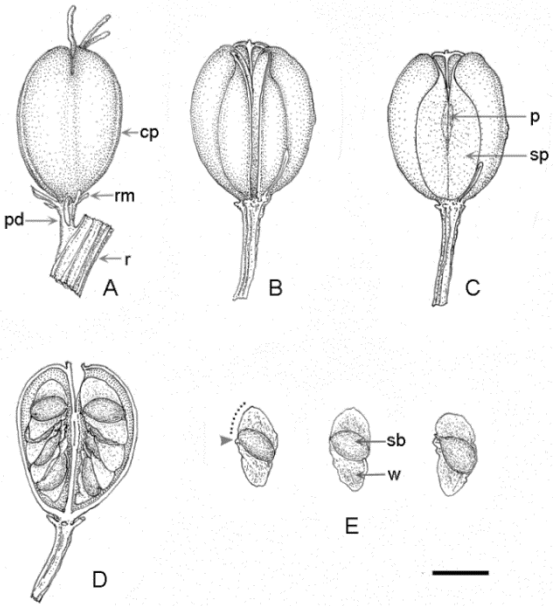


Fig. 2. Capsules and seeds of ***Chamaelirium luteum*** (L-2). **A**: Ripe capsule before dehiscence, side view. **B**: Dehisced capsule with seeds removed. **C**: Dehisced capsule with free part of frontal carpel removed, leaving septa connate to adjoining carpels. **D**: Dehisced capsule with frontal valve removed, showing arrangement of seeds in locules. **E**: Three seeds. Position of funicle indicated by arrowheaded, portion of micropyle by dotted line. cp, capsule; p, placentae; pd, pedicel; r, rachis; rm, remnants of tepals and stamens; sb, seed body; sp, septa; w, wing. Scale bar for A–E: 2 mm. Drawn by the author.

sutures at least for the distal ca. 2/3–1/2 portion, forming septa (Figs. 3C, 3E, 4C, 5B–C), although the connation in the apical portion is slight and sometimes indistinct (Figs. 3C, 4B–C, 5B–C). Placentae lie in the middle of the ventral sutures (Figs. 3C–D, 5B–C, 6B). Three valves of a capsule separate from one another in the distal half (Figs. 3B–D, 4C). Each locule of an ovary has up to two seeds (Fig. 3E). The seeds are (sub)fusiform with a flat side (nearly semicircular in cross section) (Figs. 3D–H, 4D–E), vertically pendent (parallel to the capsular axis) (Figs. 3D, 6B), funiculate at the adaxial middle (Figs. 3D, 3F–G, 4D, 6B), and collateral, lying with their flat sides face to face (Fig. 3E). Lateral wings are vestigial (Figs. 3D–H, 4D–E, 6B). The body of a seed is (sub)ellipsoid with a flat side, and axially set within the testa (parallel to the axis of the testa) (Figs. 3D–H, 4D–E, 6B).

b) Species from Japan and Korea

Chionographis japonica occurs in Japan and Korea, while *C. hisauchiana* and *C. koidzumiana* are endemic to Japan (Hara, 1968; Tanaka, 2003). These are called here "Japanese and Korean species".

Their fruits (capsules) (Fig. 3) ripen in autumn (usually October to November), ellipsoid or ovoid, 2.7–4.5 mm long, 1.5–2.8 mm broad, bearing no carpophore nor gynophore (carpopodium) (Figs. 3A–D, 5B). The carpels (capsular locules) are connate dorsally along the entire length of the ventral sutures, forming septa (Figs. 3C, 3E, 5B), and dehisce to the base along the dorsal sutures (Fig. 3A). The seeds (Figs. 3D–H, 6B) are 2.4–4.1 mm long, 0.6–1.1 mm broad, vestigially 1-(2-)winged (edged) laterally, shortly tailed at the proximal end, and acutely tailed at the distal end. The testa is minutely alveolate.

c) A Chinese species (*Chionographis chinensis*)

Fruits (capsules) (Fig. 4) ripen in May to June, and have a distinct carpo-gynophore 1.0–1.5(–2.0) mm long, reaching upward approximately to the middle of the carpels (Figs. 4A–C, 5C). Capsules are narrowly obovoid and cuneate toward the base, 2.5–4.0(–4.8) mm long including the gynophore (carpopodium), 1.5–2.0 mm broad. Carpels alone are 2.3–3.5 mm long, connate dorsally along the ventral sutures for the distal ca. 2/3–1/2 portion, forming septa (Figs. 4C, 5C), mutually separated proximally by the carpophore (the ovary is semicarpous, since its carpels are free proximally), acutely narrowed in the proximal ca. 1/3, and indehiscent for the proximal 1/4–1/2 (Figs. 4A–C, 5C). Seeds (Figs. 4D–E) are 2.2–2.3 mm long, 0.6–0.7 mm broad, acutely beaked at the proximal end, obtusely, more shortly winged at the distal end, and vestigially 2-winged longitudinally.

3. Comparison of *Chamaelirium* and *Chionographis*

A. Similarity

Besides the features common to both genera noted in the Result 1 (abbreviated as R-1 hereafter), *Chamaelirium*

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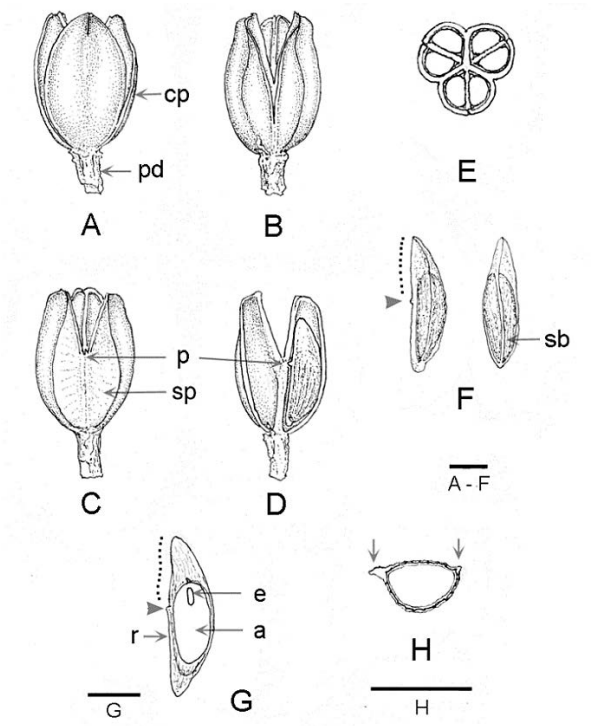


Fig. 3. Capsules and seeds of ***Chionographis japonica*** (J-1). **A** & **B**: Dehisced capsules in different side views. **C**: Dehisced capsule with free part of frontal carpel removed, leaving septa connate to adjoining carpels; seeds also removed. **D**: Dehisced capsule with frontal valve removed, leaving one seed in locule. **E**: Cross section of capsule with two seeds in each of three locules. **F**: Two seeds. **G**. Seed with body longitudinally sectioned, showing embryo embedded in albumen near apex of the body. **H**: Seed cross-sectioned; two reduced lateral wings arrowed. Funicle indicated by arrowhead, portion of micropyle by dotted line. a, albumen; cp, capsule; e, embryo; p, placentae; pd, pedicel; r, raphe; sb, seed body; sp, septa. Scale bars: 1 mm. Drawn by the author.

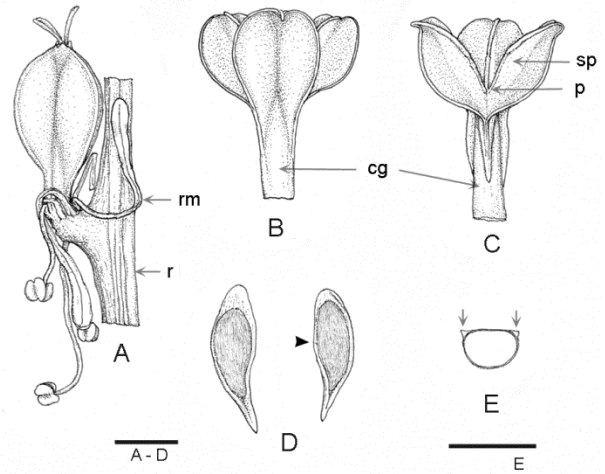


Fig. 4. Capsules and seeds of ***Chionographis chinensis*** (C-1). **A**: Capsule with persistent floral parts on short pedicel arising from rachis; a few tepals and stamens omitted to depict. **B** & **C**: Capsules in different side views. **D**: Two seeds; position of funicle indicated by arrowhead. **E**: Seed cross-sectioned; two reduced lateral wings arrowed. cg, carpo-gynophore; p, placentae; r, rachis; rm, remnants of tepals and stamens; sp, septa. Scale bars: 1mm. Drawn by the author.

(R-2A) is similar to the Japanese and Korean species of *Chionographis* (R-2Bb) in having ellipsoid capsules that ripen in autumn and have no carpo-gynophore, and capsular locules that are dorsally connate along the ventral sutures from the base at least to the subdistal portion, loculicidally dehiscent to the base, and obtuse at the base. In *Chamaelirium*, seeds borne on the distal part of the placentae tend to be obliquely pendent, while lower (proximal) ones tend to be more vertically pendent (Fig. 2D). The seeds vertically set (Fig. 1C) approach in posture to those of *Chionographis* (Fig. 3D).

B. Difference

Chamaelirium (R-2A) differs from *Chionographis* (R-2B) by the larger capsules, longer placentae occupying the middle to subdistal portion of the ventral sutures of carpels (capsular axis) (vs. middle portion), valves separating for the distal 1/3–1/4 portion (vs. distal half), more ovules per locule (6–11 vs. 2), often slightly larger seeds winged around (vs. vestigially winged along sides), without a particular flat side, and obliquely or vertically pendent from the placentae (vs. exclusively vertically pendent), and in the seed body obliquely set within the testa (vs. axially set).

Besides these differences, *Chamaelirium* is also distinct from *Chionographis chinensis* (R-2Bc) mainly by its fruits ripe in autumn (vs. May to June) and without a carpo-gynophore, and by the carpels dorsally connate along the ventral sutures except the distal short portion (vs. carpels mutually free proximally), loculicidally dehiscent to the base (vs. indehiscent proximally), and obtuse at the base (vs. acute).

4. Differences between the Japanese and Korean species and a Chinese species

The Japanese and Korean species of *Chionographis* (R-2B) differ from a Chinese species (*C. chinensis*; R-2Bc) chiefly by the ellipsoid or ovoid capsules (vs. narrowly obovoid, proximally cuneate capsules) ripe in autumn (vs. May to June) and without a carpo-gynophore, often slightly larger carpels (locules) dorsally connate along the full length of the ventral sutures (vs. carpels mutually free proximally), and loculicidally dehiscent to the base (vs. indehiscent proximally), and by the slightly larger seeds acute at the distal end (vs. acute at the proximal end).

DISCUSSION

1. Divergence in fruit and seed characters of *Chamaelirium* and *Chionographis* and its significance in taxonomy

While sharing similar features as noted in the Results 1 (abbreviated hereafter as R-1) and 3A (R-3A), *Chamaelirium* (R-2A) and *Chionographis* (R-2B) markedly differ in several characters (R-3B; Table 2). The species of *Chionographis* also share many similar

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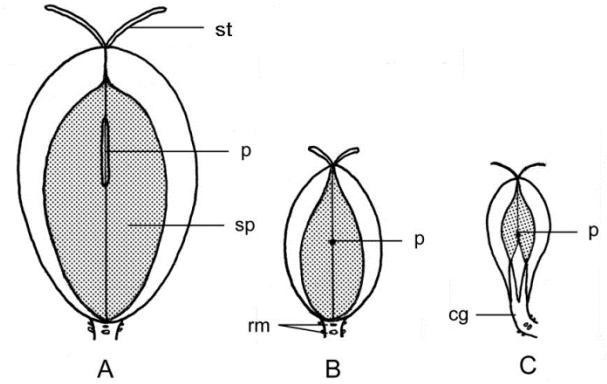


Fig. 5. Diagrams showing capsular structure of ***Chamaelirium*** and ***Chionographis***. Free part of frontal carpel removed, leaving septa connate to adjoining carpels (cf. Figs. 1B, 2C, 3C, 4C). One style not depicted. **A**: ***Cha. luteum***. **B**: ***Chi. japonica***. **C**: ***Chi. chinensis***. Carpellary septa shaded. cg, carpo-gynophore; p, placentae; rm, remnants of (vestigial) stamens and tepals; st, style; sp, septa. Drawn by the author.

features (R-2Ba), but a Chinese species, *C. chinensis* (R-2Bc), significantly differs from the Japanese and Korean species (R-2Bb) in many respects (R-4; Table 2). The characters examined are, accordingly, significantly divergent between the two genera and between the two species groups of *Chionographis*. The extent of divergence is obviously greater between the two genera. In this connection, it is noteworthy that these phenotypically divergent groups, *Chamaelirium* and *Chionographis*, and the two groups of *Chionographis*, are markedly disjunct in distribution, respectively (see Hara (1968) for the range of *Chionographis*; Utech (2002) for *Chamaelirium*). Evidently the geographical disjunction between the two genera (U.S.A. and Asia) is by far greater. The greater extent of divergence between the two genera may reflect the longer evolutionary history since they began to diverge.

In *Chionographis nanlingensis* L. Wu, Y. Tong & Q. R. Liu recently reported from southern China, capsules are described as subobovoid (Wu *et al.*, 2016), agreeing with those of *C. chinensis*. In *C. actinomorpha* and *C. shiwandashanensis*, there has been no report on ripe capsules. However, it is reported that *C. actinomorpha* has ellipsoid ovaries (Averyanov and Tanaka, 2014) and *C. shiwandashanensis* has subobovoid to subglobose ovaries (Huang et al., 2011, as capsules). In my observation of *C. chinensis*, the ovaries (at the flowering stage) are small (0.5–1.3 mm long) and ellipsoid or subglobose. They later become narrowly obovoid (at the fruiting stage). Therefore it is likely that the ellipsoid or subglobose ovaries observed in *C. actinomorpha* and *C. shiwandashanensis* also eventually develop into obovoid fruits, as in *C. chinensis*. In contrast, the ovaries of the Japanese and Korean species tend to be ovoid (e.g. Baker, 1879: Yatabe, 1893; Ohwi, 1930; Tanaka, 2016b). Accordingly, in the characters of ovary, *C. actinomorpha*, *C. nanlingensis*, *C. shiwandashanensis* and *C. chinensis* appear to be closer to one another than to the species from Japan and Korea.

Judging from the results of the present study, *Chamaelirium* and *Chionographis* may be regarded as congeneric, and ranked as subgenera or sections under one single genus *Chamaelirium*. The two species groups of *Chionographis* (the Japanese and Korean species and the Chinese and Indochinese species) may be ranked as subsections or series under the subgenus or section *Chionographis* of *Chamaelirium*. A recent phylogenetic analysis of chloroplast DNA sequences of *Cha. luteum*, *Chi. chinensis* and several taxa of Japanese species revealed that these three groups are independent sister groups (Maki, 2012). For a more conclusive taxonomic reevaluation of these groups, we still need to conduct a further integral study on various characters of them.

2. Factors underlying the arrangement of seeds within the locule and of a seed body within the testa

The following factors seem to have underlain the evolutionary development of the arrangement of seeds within the locule and of a seed body within the testa. Assuming that the longitudinal axis of the testa of a seed ('sl' in Fig. 6) is longer than the breadth of a capsular locule (the distance between the placenta and the opposite site of the capsular wall; 'lw' in Fig. 6), the seed (including the testa) cannot be strictly horizontal (vertical to the capsular axis), but would have to be either ascending or descending to be well set within the locule. Actually, in *Chamaelirium*, seeds are usually longer than the locular breadth (Figs. 1–2, Table 2), and obliquely or vertically pendent from the placentae (R-2A; Figs. 1C, 2D, 6A). In *Chiongraphis*, seeds are also longer than the locular breadth (Figs. 3–4, Table 2), and exclusively vertical within the locule (parallel to the capsular axis) (R-2Ba). The same can also be said for the arrangement of a seed body within the locule. If a seed body ('bl' in Fig. 6) is nearly as long as or longer than the locular breadth, it would tend to be ascending or descending within the locule. In fact, the seed bodies of *Chamaelirium* are slightly shorter to slightly longer than (on average nearly as long as) the locular breadth (Figs. 1–2, Table 2), and they tend to be obliquely or vertically descending (Figs. 1C, 2D, 6A). In *Chionographis*, seed bodies are longer than the locular breadth (Figs. 3–4, Table 2), and consisitently vertical (Figs. 3D, 6B). In general, it may safely be said that within a given, relatively narrow, limited locular space, the longer a testa or seed body is, the stronger it has to be descending or ascending. If a testa is fairly longer than the seed body, it would have to be more strongly descending or ascending than the body. This may explain the oblique arrangement of a seed body

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within the testa in *Chamaelirium* (R-2A). In *Chionographis*, both the testa and the seed body are much longer than the locular breadth (Figs. 3–4, Table 2), it is hence inevitable that they became vertical (R-2Ba). Further, the seeds of *Chionographis* are so tightly set within the narrow locules that they are likely to have eventually flattened their sides facing each other (R-2Ba) and reduced their wings especially on the sides (R-2Ba) in the evolutionary process.

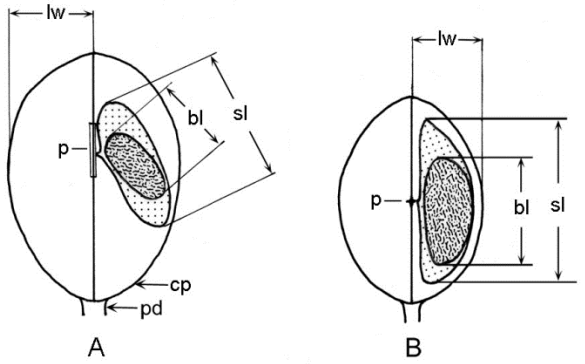


Fig. 6. Diagrams showing arrangement of seed within capsular locule and of seed body within testa of ***Chamaelirium*** and ***Chionographis***. **A**: ***Cha. luteum***. **B**: ***Chi. japonica***. cp, capsule; bl, length of seed body (densely dotted); lw, distance between placenta and opposite capsular wall; sl, length of seed (testa) (sparsely dotted); p, placenta; pd, pedicel. Drawn by the author.

3. Evolutionary aspects of morphological traits

Chamaelirium and *Chionographis* differ in various characters of fruits and seeds (R-3B), but there appear to be strong evolutionary relationships between the divergent character states. For instance, they differ in the number of ovules per locule (2 in *Chionographis* vs. 6–11 or 12 in *Chamaelirium*; R-2A, 2Ba, 3B), but the numbers seem to be closely correlated. In the tribe Heloniadeae to which the two genera belong together with two or three other genera such as *Helonias* and *Ypsilandra* (Hutchinson, 1934; Tamura, 1998), *Chionographis* has the fewest ovules per locule (Fig. 3E; for the ovule number of *Helonias*, *Heloniopsis* or *Ypsilandra* see Tanaka (1997)). To my knowledge, no other species of the Melanthiaceae have such a small number of ovules. Further, the seeds of *Chionographis* are acute at least at one end and flat on one side (R-2Ba; Figs. 3D–H, 4D–E, 6B). These features appear to be derived character states as compared to the seeds of *Chamaelirium* that are neither acute nor flattened on one side (Figs. 1C–E, 2D–E, 6A). It is therefore highly likely that the fewest ovules in *Chionographis* was derived from more ovules as possessed by *Chamaelirium* (Fig. 2D). With the reduction in ovule number, ovaries and placentae may have also reduced their size (R-3B). In such reduced locular space as possessed by *Chionographis*, changes in the arrangement and shape of seeds and even in the arrangement of a seed body within the testa (R-3B) also seem to have occurred in the evolutionary course (see the Disucssion 2 for underlying factors).

Of the species examined, only *Chionographis chinensis* has a carpo-gynophore (R-2Bc). Therefore, this feature appears to have developed specifically in *C. chinensis* in the evolutionary process. The development of this feature is also likely to have advanced additional features in carpels and seeds that surround the carpophore; e.g. capsular locules mutually free, acute, and indehiscent in the proximal part, and proximally sharply beaked seeds (R-2Bc, R-4).

Data on ripe fruits and seeds (ovules) of *Chionographis shiwandashanensis* and *C. actinomorpha* and seeds (ovules) of *C. nanlingensis* has unfortunately not been available. Making a close examination of them in the future is crucial to our understanding of the full picture of diversity and diversification of these characters. Molecular phylogenetic analyses of the two genera including the Chinese and Indochinese species may also provide significant data on the process of their diversification.

Representative specimens examined:

Chamaelirium luteum

U.S.A.: **Florida**: near Jacksonville, 28 Apr. & 2 Oct., 1894, *A. H. Curtiss 4781* (K); Lake Co., vicinity of Eustis, 16–31 July 1894, *G. V. Nash s.n.* (K). **Georgia**: Murray Co. Cohutta Wild Management Area, 7 June 1983, *N. C. Coile 3676* (BM). **Pennsylvania**: Yan, no date, *H. P. Sartwell s.n.* (K). **Tennessee**: Cocke Co., Cross mountain above Wolfe Creek Station, 5 June 1965, *E. W. Chester 751*(GH). **Virginia**: Bedford Co., June 1871, *A. H. Curtiss s.n.* (GH); Bath Co., Hot Springs, 1 July 1917, *F. W. Hunnewell, 2nd. 4685* (GH); Greensville Co., north of Emporia, 19 Sept. 1938, *Fernald & Long 9296* (GH).

Chionographis chinensis

CHINA: **Guangdong** (Kwangtung): Ts'ung-hwa (Tsung-fa) District, Ch'an Woh Tung Village, Sam Kok Shan, 1–25 May 1935, *W. T. Tsang 25214* (A); Tsengshing District, Naam Kwan Shan, 30 Apr. 1932, *W. T. Tsang 20386* (TI, TNS 653141). **Guangxi** (Kwangsi): precise locality unknown, no date, *C. Wang 39496* (A).

Chionographis hisauchiana

subsp. ***hisauchiana***

JAPAN: **Honshû**. Saitama Pref.: [Han'nô-shi] Musashi, Naguri-mura, Kawamata, 29 June 1941, *K. Hiyama* (TNS 59931). Tokyo Pref.: [Ôme-shi] Musashi, Osoki-mura, 23 Oct. 1949, *T. Sato 7495* (TI; TNS 130175).

subsp. ***minoensis*** (H. Hara) N. Tanaka

JAPAN: Honshû. Gifu Pref.: Mino, North of Kanbara, Yokokura-mura, 5 June 1961, *Hara & Kurosawa s.n.* (TI, holotype); Gujyô-gun, Gujyô-Hachiman, 17 Sept. 1967, *K. Inami s.n.* (TNS 184890).

subsp. ***kurohimensis*** (Ajima & Satomi) N. Tanaka

JAPAN: **Honshû.** Niigata Pref.: Mt. Kurohime, 21 June 1975, *T. Ajima 4546* (KANA 083861, holotype); Shibata, Mt. Ninôji, 28 July 1962, *F. Konta 688* (TNS 016272).

Chionographis japonica

JAPAN: **Honshû**. Shizuoka Pref.: Inasa-gun, Shibukawa, 23 Sept. 1959, *G. Murata* (KYO). Ishikawa Pref.: Ishikawa-gun, inter Hinomiko et Kuragatake, 13 Oct. 1953, *G. Masamune* (KANA 060010). Shiga Pref.: Hikone-shi, Sôgen-ji, 28 Oct. 1973, *N. Kurosaki 5893* (KYO). **Kyûshû**. Kagoshima Pref.: Aira-gun, Shinkawa-keikoku, 21 Oct. 1965, *N. Satomi 25408* (KANA 055197);

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Isl. Sakura, Nov. 1926, *T. Nakai* (TI). **Shikoku**. Kagawa Pref.: Isl. Syôdo-shima, 19 Nov. 1968, *M. Togashi* (TI). Kôchi Pref.: Takaoka-gun, Sakawa-chô, Nov. 1892, *T. Makino* (MAK 137199).

Chionographis koidzumiana

JAPAN: **Honshû**. Nachi-katsuura-chô, 2 Aug. 1900, *H. Nakajima* (MAK 137212); Tanabe-shi, Kurozô-tani, 11 Aug. 1971, *T. Iwasaki s.n.* (TNS 01000390). **Kyûshû**. Miyazaki Pref., Mt. Osuzu, 25 Aug. 1955, *S. Hirata 6* (TI). **Shikoku**. Kôchi Pref., [Shimanto-shi], Kurosonyama, 4 Aug. 1924, *S. Ogata* (KYO).

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