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390

## Taxonomy, evolution and phylogeography of the genus *Helonias* (Melanthiaceae) revisited

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## Abstract

This paper reviews the taxonomy, evolution and phylogeographic aspects of the genus *Helonias* L. sensu lato, including *Ypsilandra* and *Heloniopsis* (Melanthiaceae) that are basically similar in many morphological and ecological characters to *Helonias* sensu stricto. It includes three parts, I–III. In Part I, characters and their variation are examined to determine generic traits and diversity. In Part II, an attempt is made to taxonomically determine diversity among individuals. Taxonomic conclusions and revisions are principally the following: *Helonias* comprises 12 species, which are classified into two sections, *H.* sect. *Helonias* and *H.* sect. *Heloniopsis* comb. & stat. nov. *Helonias* sect. *Helonias* consists of *H. bullata* only; *H.* sect. *Heloniopsis* comprises two subsections, *H.* subsect. *Ypsilandra* comb. & stat. nov. and *H.* subsect. *Heloniopsis*. *Helonias* subsect. *Ypsilandra* is composed of five species previously published under the genus *Ypsilandra*. *Helonias* subsect. *Heloniopsis* consists of two series, *H.* ser. *Umbellatae* ser. nov., with three species from Taiwan and the Nansei Islands (incl. the Ryukyus), Japan, and *H.* ser. *Heloniopsis*, with three species from Japan, Korea and E. Russia (southern Sakhalin). *Helonias yunnanensis* var. *mesostyla* is described as a new variety from N Myanmar and SW China (NW Yunnan). The new combinations *Helonias koreana* (from Korea) and *H. parviflora* (from China) are proposed. Lectotypes for *Ypsilandra parviflora*, *Y. thibetica*, *Y. yunnanensis* var. *micrantha*, *Heloniopsis breviscapa* and *H. grandiflora* are designated. A revised typification for *Sugerokia japonica* is proposed, negating a previous lectotypification. *Heloniopsis tubiflora* is reduced to synonymy under *Helonias koreana*. In Part III, the evolutionary and phylogeographic aspects of *Helonias* are discussed, and a phylogram inferred from cladistic analysis of phenotypic characters is presented. In the phylogram, *Helonias* is monophyletic, while *H.* sect. *Helonias* and *H.* subsect. *Ypsilandra* are respectively paraphyletic, and *H.* subsect. *Heloniopsis* is monophyletic. Incongruence in results between morphological and DNA sequence analyses is briefly discussed.

**Key words:** character evolution, breeding system, floral structure, Heloniadeae, historical biogeography, infrageneric system, life history, phenology

## Introduction

*Helonias* (Melanthiaceae) was first described by Linnaeus (1753, 1754) with a single species *H. bullata* L. Several species, such as *H. asphodeloides* L. and *H. tenax* Pursh, and *H. lutea* (L.) Ker Gawl., were later added, but they were then transferred to genera such as *Xerophyllum* Michx. and *Chamaelirium* Willd., respectively. As a result, *Helonias* s.str. has been treated as monotypic by many botanists (e.g. Kunth 1843, Gray 1848, Baker 1879, Bentham 1883, Engler 1887, Baillon 1894, Krause 1930, Fernald 1950, Gleason 1952, Takhtajan 1997, Utech 2002).

Gray (1859) based the genus *Heloniopsis* on material from northern Hokkaidō, Japan. The specimen he examined, however, was an admixture with seeds of a species of *Luzula* DC. (Koidzumi 1930, 1934; Hara 1947), which Gray included in his description of *Heloniopsis*. In examining specimens from Japan, which are today regarded as equivalent to Gray's *Heloniopsis*, Miquel (1866, 1867a, b, 1870) noticed that his material differed in seed features from Gray's description of *Heloniopsis*, leading him to establish a new genus, *Sugerokia*. Franchet (1887–1888) created *Ypsilandra* based on *Y. thibetica* Franch. from eastern Tibet, since it has unilocular anthers. Tanaka (1997a–e) examined *Helonias* L. and its closely allied genera from various aspects, and found that they share many similar character-states, e.g., styles more or less connate along their length, thecae terminally confluent into one cell or vestigially confluent. Based on these similarities, he merged *Ypsilandra* Franch. and *Heloniopsis* A.Gray (*Sugerokia* Miq.) into *Helonias* (Tanaka 1998a, 2009). He showed (Tanaka 1997e) that *Helonias* s.lat. comprises three groups, *Helonias* (HA), *Ypsilandra* (YP) and *Heloniopsis* (HP), with *Heloniopsis* composed of two subgroups (HP-1, -2). He did not, however, formally create infrageneric taxa within *Helonias* (Tanaka 1998a) (for further remarks on the taxonomic history of *Helonias* s.lat., see Part II-1).

The present study was undertaken to more closely investigate *Helonias* s.lat. from various aspects using more samples than in my previous studies (Tanaka 1997a–e, 1998a, 2009).

This paper includes three parts. In Part I, various characters and their variations are examined with the aim of revealing generic traits and diversity. In Part II, an attempt is made to taxonomically grasp the diversity found among individuals. The results include a revised classification system for this plant group. In Part III, evolution and phylogeography of this group are discussed. A phylogram inferred from cladistic analyses of phenotypic characters is also presented.

## Materials and methods

Dried herbarium specimens or their digitized images of the *Helonias* species concerned were surveyed from morphological, phenological and phytogeographic aspects.

Living plants of *Helonias bullata*, *H. thibetica* (Franch.) N.Tanaka, and all the species of subsect. *Heloniopsis* (Part II) were examined. They were collected from their natural habitat (those used in my previous studies are listed in Tanaka 1997a, b) or obtained from cultivated sources. They are/were cultivated at Hachioji in Tokyo, Japan, and their morphological and phenological characters were observed. Habitats or sources of the living plants in the photographs of this paper are provided in List 1.

The basic logic, taxonomic methodology and species concept on which this research is based are given in Tanaka (1996, 1997f, 1998b). Cladistic analyses of phenotypic characters were made to construct a phylogenetic tree, where taxa are clustered by synapomorphies inferred from comparative survey of character-states (Hennig 1966, Wiley 1981).

Plant names in this paper are those accepted in Part II.

In the text, many of the specimens identified are cited with a code (often barcode) where a herbarium acronym is followed by a hyphen and a registration number given by the respective herbaria keeping the specimen, e.g. BM-001118054, GH-00293671. When only images were available, their specimen codes were asterisked, e.g. K-000400242\*, P-02101626\*.

Preliminary tests for the presence or absence of self-incompatibility in *Helonias thibetica* and *H. orientalis* (Thunb.) N.Tanaka were carried out. At least three individuals of *H. thibetica*, from two commercial sources were tested in 1987 and 2014. A total of 14 individuals of *H. orientalis* from three habitats in Niigata, Gifu and Mie prefectures (all in Honshû, Japan) were tested in 1987. The experiments were carried out mostly at the then Botanical Laboratory on the Hachioji Campus of Teikyo University in Tokyo. The plants were cultivated individually in pots. Shortly before opening, young scapes with flowers were covered with a thin (waxed) paper bag to prevent cross-pollination. The stigma of each flower in bloom was artificially self-pollinated and the scapes were immediately rebagged. The paper bags were removed from the scapes and the plants were returned to our experimental nursery after the pollinated stigmas faded. Seed set from artificial selfing was compared with open pollinated individuals and the soundness of the seeds was estimated externally.

In the text, terms “peduncle” and “inflorescence” are used following the definitions in Harris & Harris (1994) and Hickey & King (2000), and the term “flowering stem” refers to a structure consisting of both parts: a peduncle and the rachis of an inflorescence.

Photographs in Figs. 1A & 4 were taken by Jim Fowler, a photographer living in South Carolina, U.S.A., those in Fig. 7A & B by Yang Niu, a botanist of the Kunming Institute of Botany, Yunnan, China, and the original images of herbarium specimens in Figs. 7C–F, 8, 10 and 11 were availed from the websites of or directly provided by two herbaria keeping them (Royal Botanic Garden Edinburgh; Royal Botanic Gardens, Kew). All other photographs were taken by the author.

---

**LIST 1.** Sources of plants with photographs in the text (each source coded as Br-1, Ka-1).*Helonias breviscapa*

- Br-1: Japan. Honshû. Mie Pref., Taki-gun, Ôdai-chô, Tochihara.
- Br-2: Japan. Honshû. Nara Pref., Gojô-shi, Nishi-yoshino-machi, Momodani.
- Br-3: Japan. Shikoku. Tokushima Pref., Mima-gun, Tsurugi-chô, Sadamitsu, elev. ca. 540 m or slightly above.
- Br-4: Japan. Kyûshû. Fukuoka Pref., Kita-kyûshû-shi, Kokura-minami-ku, Michihara, Kagumeyoshi.
- Br-5: Japan. Kyûshû. Precise locality unknown, cultivated by Ôtsuka in Fukuoka Pref.

*Helonias bullata*

- Bu-1: U.S.A. South Carolina, Greenville Co., Watson-Cooper Heritage Preserve.
- Bu-2: U.S.A. Provided by Royal Botanic Gardens, Edinburgh, acc. no. 19694729 (Tanaka 1997a).

*Helonias kawanoi*

- Ka-1: Japan. Okinawa Pref., Ishigaki I. (as K-1 in Tanaka 1997b).
- Ka-2: Japan. Okinawa Pref., Iriomote I. (as K-3 in Tanaka 1997b).
- Ka-3: Japan. Okinawa Pref., precise locality unknown, from a nursery in Japan.

*Helonias koreana*

- Ko-1: Korea. Kangwon-do, Nyongol, Taepeksan, April 2008.
- Ko-2: Korea. Kangwon-do, Nyongol, Taepeksan, June 2014.

## White-flowered form

- Ko-w-1: Korea. Kangwon-do, Nyongol, Taepeksan, April 2008.

*Helonias leucantha*

- L-1: Japan. Okinawa Pref., Okinawa I., Nago-shi (as L-1 in Tanaka 1997b).
- L-2: Japan. Okinawa Pref., Okinawa I., Kunigami-gun.
- L-3: Japan. Okinawa Pref., Iriomote I. (as L-3 in Tanaka 1997b).
- L-4: Japan. Precise locality unknown, from a few nurseries in Japan.

*Helonias orientalis*

- O-1: Japan. Honshû. Yamagata Pref., foot of Mt. Chôkai.
- O-2: Japan. Honshû. Tochigi Pref., eastern part of Nikkô-shi.
- O-3: Japan. Honshû. Gifu Pref., Kamo-gun, Yaozu-chô, Ikitsushi.

## White-flowered form

- O-w-1: Japan. Honshû. Precise locality unknown, obtained from a nursery in Japan.

*Helonias thibetica*

- T-1: China. Precise locality unknown, from two nurseries in Japan.

*Helonias umbellata*

- U-1: Taiwan. Taipei Hsien, Chihsingshan (as U-1 in Tanaka 1997b).
- U-2: Taiwan. Taipei Hsien, Tatunshan (as U-2 in Tanaka 1997b).
- U-3: Taiwan. Ilan Hsien, Taipingshan, elev. ca. 1900–2000 m.
- U-4: Taiwan. Ilan Hsien, Taipingshan, elev. 2000–2200 m.

*Helonias yunnanensis* var. *yunnanensis*

- Y-1: China. Yunnan, Fugong county, Yaping Pass, elev. 3610 m.
- 

**Part I. Characters and variation**

Various characters and their variation are examined. Their evolutionary facets will be discussed mainly in Part III.

**1. Habitat preference**

*Helonias bullata* (*H.* sect. *Helonias*) indigenous to North America (Fig. 6) and the Asian species of *Helonias* (*H.* sect. *Heleniopsis* (A.Gray) N.Tanaka) (Fig. 32) are distributed mainly in temperate and subtropical regions with moderate temperature and precipitation (Fig. 31). *Helonias bullata* occurs in wetlands such as swamps or bogs (Fig. 4A; USFWS 1991, SCPCA 2017). An Asian species, *H. yunnanensis* (W.W.Sm. & Jeffery) N.Tanaka (Fig. 7), often grows in alpine wet boggy meadows which resemble the habitats of *H. bullata*. Another Asian species, *H. orientalis*, occurs in swamps

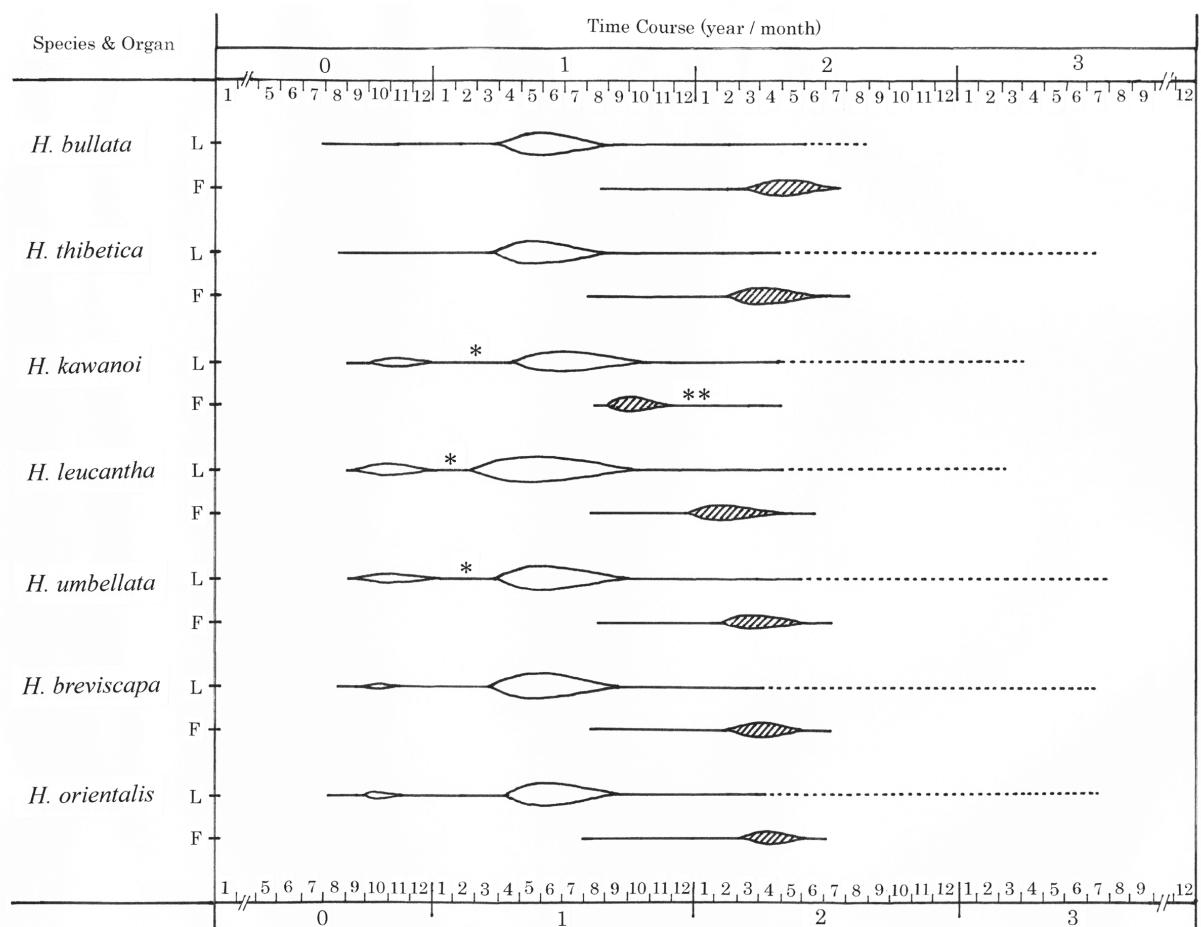
or sphagnum bogs like *H. bullata*, but it also often inhabits shady moist slopes or banks along streams, open mountain meadows, or moist forest floors as undergrowth, indicating that the habitats are more diverse than those of *H. bullata*. All Asian species prefer moist situations, but species such as *H. breviscapa* (Maxim.) N.Tanaka, *H. orientalis*, *H. thibetica* and *H. umbellata* (Baker) N.Tanaka often inhabit less moist locations in forests as well, implying that these species are somewhat more tolerable to dry conditions than *H. bullata*.

## 2. Habit and phenological characters

The species of *Helonias* are evergreen perennials with basal rosulate leaves that usually persist for 1 to 2 years (Figs. 1, 2).



**FIGURE 1.** Buds and their sprouting in *Helonias*. **A.** *H. bullata* (material Bu-1; photo on 5 April 2013). **B.** *H. orientalis* (O-3; 15 November 2014). **C, D.** *H. thibetica* (T-1; C on 19 February 2014, D on 2 March 2014). Flower buds or fresh flowering stem designated by *F*, leaf buds or sprouting leaves by *L*, rosulate leaves developed in previous years by *R*. In Fig. C, two of leaves developed in the preceding year marked with single white circle (dot); two of leaves developed the year before last marked with paired white circles (dots). Photo A by Jim Fowler at site of “Bu-1” in South Carolina; B–D by the author at Hachioji, Tokyo.



**FIGURE 2.** Diagram of phenology of rosette leaves and flowering stems (scapes) in *Helonias*. Phenological transition of rosette leaves (L) and flowering stem (F) in their lifetime (from bud formation to death) is schematized. Approximate magnitude of growth rate of two organs is expressed by line or shape of ellipse or lance (expanded portion). State of organs showing static, increasing or decreasing growth rate is represented respectively by line, or by expanding or narrowing (closing) portion of an ellipse or lance. Broken line represents period during which older leaves die, although their death is usually concentrated in growing season (April to July or August). In *H. bullata*, for example, leaf bud (see L-row) is initially formed in summer of year 0, it stays dormant until coming spring, and then develops rapidly in spring to summer (expanded open portion) of year 1. Mature leaves wither in growing season of following year (broken line in year 2). Flower bud of *H. bullata* (see F-row) is initially formed in fresh rosette (in L-row) in summer of year 1; like leaf bud it stays dormant until next spring, and then develops rapidly in spring (expanded shaded portion) of year 2. Flowering stem dies around summer of same year (closing shaded portion). Leaf bud (see L-row) of *H. kawanoi*, *H. leucantha* or *H. umbellata* after formed soon starts to sprout in late summer onwards (of year 0), although its growth appears more or less suppressed in subsequent cooler seasons (\*). Phenological progression of flowering stem of *H. kawanoi* (F-row) tends to be lagged (\*\*) when cultivated under lower temperature (in Tokyo) than in natural habitats.

Mature plants normally produce two kinds of buds in a rosette; a flower bud (an inflorescence bud) that develops into a flowering stem (F in Fig. 1), and leaf buds that develop basal leaves (L in Fig. 1). Flower buds develop slightly before leaf buds in the temperate vernal species such as *Helonias thibetica* (e.g. Fig. 1C, D), *H. orientalis* and *H. breviscapa* (Fig. 27D). In this respect the leaves are regarded as (slightly) hysteranthous.

Fresh rosulate leaves of the vernal species grow rapidly from spring to early summer. From July to September, when most leaves nearly complete their active growth, a flower bud (to sprout in the following year) is formed at the center of the fresh rosette (Figs. 13F, 25H). In this regard, the leaves are viewed as proteranthous, because the development of fresh leaves precedes the flowering stem (flower bud). The just formed flower bud remains dormant until spring in temperate vernal species (Figs. 1A, B, 2).

In *Helonias leucantha* (Koidz.) N.Tanaka (e.g. Fig. 18) of subtropical islands (Nansei Islands including the

Ryukyus), the flower bud starts to sprout somewhat earlier (usually late December to January) than in the temperate vernal species (usually late February to April in plants cultivated in Tokyo; Fig. 2). The dormant period of the flower bud of *H. leucantha* appears slightly shortened. In *H. kawanoi* (Koidz.) N.Tanaka (Figs. 2, 16), another subtropical species indigenous to the Nansei Islands, the flower bud starts to sprout shortly after development of most fresh leaves is nearly complete (usually in late summer to autumn; Fig. 16A, D, E). The dormancy of the flower bud of *H. kawanoi* is rather indistinct. The leaves of *H. kawanoi* are also considered to be proteranthous. *Helonias jinpingensis* may also be similar to *H. kawanoi* in the mode of development of the flowering stems and leaves.

Sprouting of the leaf bud of temperate vernal species is in the spring (Figs. 1C, D, 2), while sprouting in the subtropical *Helonias kawanoi* (Fig. 16A, D, E), *H. leucantha* (Fig. 18E) and *H. umbellata* is often earlier (around September onwards), although growth of new leaves appears suppressed to some extent during the subsequent cold season (Fig. 2). Dormancy of the leaf buds in these species appears somewhat indistinct.

### 3. Rhizome and roots

The rhizome is cylindrical, sometimes branched, (sub)annulate with many close scars, and persistent for many years. Asexual propagation by division of a branched rhizome appears rather rare under natural conditions.

The roots of *Helonias bullata* are pale orangish or pinkish brown (in dried herbarium specimens). In other species the roots are usually white. In many temperate species, such as *H. yunnanensis* and *H. parviflora* (F.T.Wang & Tang) N.Tanaka, the main, thick roots appear to be contractile.

### 4. Leaves and their adventitious plantlet formation

Leaf buds are initially formed in summer (around July to September; Fig. 2) in the central part of an existing fresh rosette.

A tuft of fresh rosulate leaves (developed from a leaf bud) arises from the center (when a flower bud is absent) or from a leaf axil (when a flower bud is present) near the center of the rosette developed in the preceding year in typical vernal species such as *Helonias orientalis* and *H. thibetica* (*L* in Fig. 1C, D) or in the current year (Fig. 16A, D, E, for *H. kawanoi*). The leaves are spatulate or oblanceolate, tapering to a petiole-like base (Figs. 13F, 23H, 25H, 27G), and mucronulate or apiculate at the apex (Fig. 23H). The apiculus of the leaf of ser. *Umbellatae* N.Tanaka appears slightly more prominent than in other species.

The leaves of *Helonias* are persistent for at least one year, and often for two years, if conditions permit (Fig. 2). The longevity of the leaves appears to be often affected by environmental factors. The development of fresh leaves and the withering of old leaves (one or two year old leaves) takes place almost concurrently during the growing season, usually from around late March to July in lowlands in temperate species. During the growing season when plants have both fresh and old leaves, a rosette usually consists of two (fresh and one year old leaves) or three (fresh, one and two year old leaves) consecutive age groups of leaves (Fig. 1C).

*Helonias orientalis* often produces one to a few tiny plantlets (ramets) usually at the tip of the leaf both in the wild (e.g. Nagano Pref., K. Asano & H. Asano 30185, MAK-317546) and in cultivation. Shaw (2008) reported (as *Ypsilandra yunnanensis* W.W.Sm. & Jeffrey var. *fansipanensis* Shaw) that *H. jinpingensis* (W.H.Chen, Y.M.Shui & Z.Y.Yu) N. Tanaka in cultivation can be propagated from leaf cuttings. *Helonias koreana* (Fuse, N.S.Lee & M.N.Tamura) N.Tanaka (material Ko-2) cultivated in my garden can also be propagated the same way, implying that the leaves of many species of *Helonias* are latently capable of producing plantlets in a similar way.

Kawano & Masuda (1980, as *Heloniopsis*) reported that the populations of *Helonias orientalis* in lowlands they surveyed are higher in the rate of adventitious plantlet formation by leaves and in the proportion of energy allocation to vegetative organs than in the subalpine or alpine zone. The habitats of the lowland populations are shady, moist forest floors, while those of the (sub)alpine populations are open meadows. Seedling establishment in the lowland populations is extremely low. The higher rate of foliar plantlet formation as well as the higher investment of photosynthetic products into vegetative organs in the lowland populations probably reflects habitat conditions in the forests and the low seedling establishment. Since seedling recruitment is extremely low, the plantlet formation by leaves must be effective in enhancing survivorship of the populations.

### 5. Flowering season

Many species of *Helonias* flower in the spring (usually March to April in lowlands, such as around Tokyo) (Figs.

23A–D, 25A–E, 27A–D), whereas *H. jinpingensis* flowers in September (data based on Chen *et al.* 2003, Shaw 2008), and *H. kawanoi* (Fig. 16) usually flowers in late summer to autumn. *Helonias leucantha* usually flowers from January through mid March (less commonly in late December; Fig. 18A–D), and *H. umbellata* usually flowers from February through early April (less commonly in late January; Fig. 21A–C).

## 6. Flowering stem

In vernal species, a flower bud (an inflorescence bud) is initially formed in July to August. In autumn flowering species, such as *Helonias kawanoi*, the buds are usually formed in August to September.

The flowering stem (scape) arises from the center of the rosette (Fig. 1) and bears scale-like leaves proximally and an inflorescence distally (e.g. Figs. 1C, D, 16A, 21A, B). The flowering stem of vernal species grows rapidly in the spring (Fig. 2), then dies usually within a month or so after dispersing the seeds. In cultivation in Tokyo, the stem of the vernal species usually dies by the end of June (Fig. 2). The approximate life span of the stem (from sprouting to death) is usually 3 to 4 months (stems with unfertilized flowers tend to fade earlier than those with fertilized flowers).

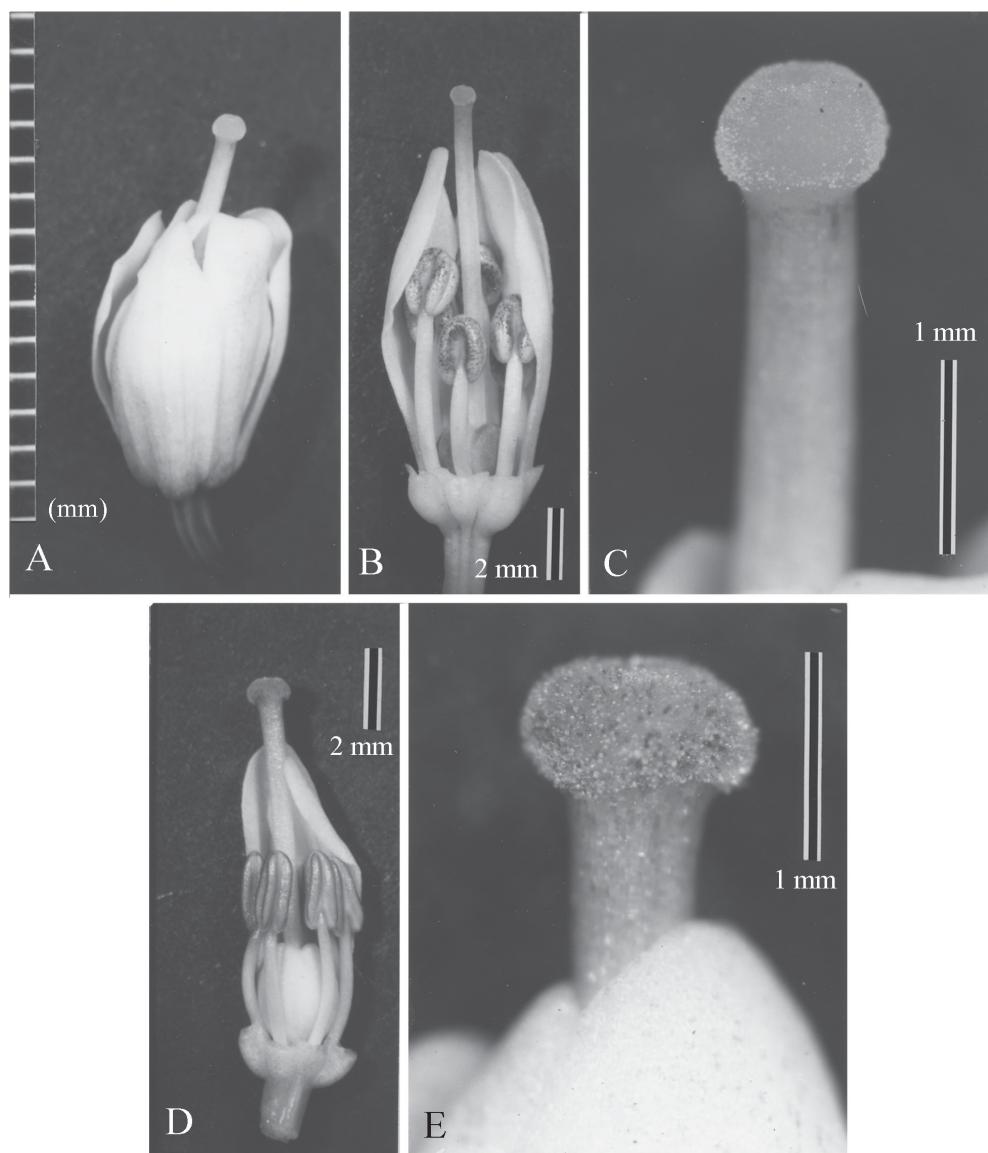
## 7. Inflorescence

Plants of *Helonias* sect. *Helonias* and *H.* subsect. *Ypsilandra* (Franch.) N.Tanaka have a typical raceme (e.g. Figs. 11, 13C; Tanaka 1997d). Those of *H.* ser. *Umbellatae* (*H.* subsect. *Heloniopsis*) have a raceme (e.g. Fig. 18A–D), subumbel or an umbel (e.g. Figs. 16A, B, 21A–C; Tanaka 1997d). The inflorescence of *H. leucantha* is a raceme, but often appears subumbellate, especially in early stages of flowering. *Helonias umbellata* usually produces an umbel (Fig. 21A–C; Tanaka 1997d), or rarely a raceme (Hsu *et al.* 2011). *Helonias kawanoi* has 1 or a few flowers borne in an umbel (Fig. 16A, B) or rarely a raceme. *Helonias* ser. *Heloniopsis* (*H.* subsect. *Heloniopsis*) has flowers in a subumbel or occasionally an umbel at anthesis (Figs. 23A–D, 2A–D, 27A–D; Tanaka 1997d).

## 8. Flowers

**Overall features including phenology:**—The floral parts of *Helonias* are arranged in five whorls of three (e.g. Figs. 20A, 22E, 26C). The flowers are pedicellate and ebracteate (e.g. Figs. 13, 18), except for *Helonias jinpingensis* and *H. kawanoi* (Fig. 16C) which have bracteate pedicels. The distal flowers tend to face upward, the middle ones sideward, and the proximal ones downward in *Helonias bullata* (Fig. 4D) and *H.* subsect. *Ypsilandra* (e.g. Figs. 8B, C, 11B, C), except in *H. thibetica*. The flowers of *H. thibetica* (Fig. 13C) and subsect. *Heloniopsis* (e.g. Figs. 16A, B, 18B, D) are often nodding at mid anthesis. Flowers in late anthesis consistently nod in all species (e.g. Fig. 23D, E). In contrast, fruiting pedicels are ascending and the capsules face upward (e.g. Figs. 4F, 13D, E, 18E, 25F, G, 27E, F). The pistil in *H.* sect. *Helonias* and *H.* subsect. *Ypsilandra*, except *H. thibetica*, is usually nearly as long as or shorter than the stamens (e.g. Figs. 5A–C, 9A, Table 6). *Helonias thibetica* (*H.* subsect. *Ypsilandra*) usually has a comparatively long pistil overtopping the stamens and the tepals (Figs. 13B, C, 14A, Table 6). Prior to full opening of the tepals, the stigmas emerge from the apical narrow slit of the flower bud or young flower (Figs. 3A–C, 13A), at which time they appear mature and receptive, since the surface is well papillulate (Fig. 3C). The anthers usually dehisce several days later after emergence of the stigmas (usually in February in plants cultivated in Tokyo; Fig. 13A, B), indicating that the flowers of *H. thibetica* are protogynous. As in *Helonias thibetica*, the well papillulate stigmas (Figs. 3E, 17B) of all species of *H.* subsect. *Heloniopsis* emerge from the apical slit of the flower bud or young flower before dehiscence of the anthers (e.g. Figs. 17A, 18C, 21A, 25A). Takahashi (1988, as *Heloniopsis*) confirmed experimentally that the stigmas of *Helonias orientalis* (as *Heloniopsis*) were already mature one day before anthesis. Flowers of all the species of *Helonias* are no doubt entomophilous. In *H. bullata*, *H. thibetica* and *H.* subsect. *Heloniopsis*, the flowers are often fragrant and bear a nectary at the adaxial base of the tepals (e.g. 5C, 14B–D, 20B, 22C–E). Those of *H. yunnanensis* are also fragrant, according to data on herbarium sheets. The tepals of *Helonias* are usually white, pink, bluish or violet, rarely chocolate (e.g. Figs. 4, 7, 18, 21, 23, 25, 27). Takahashi (1988) reported the flowers of *H. orientalis* to be pollinated by insects foraging for nectar and/or pollen (section 11). It is noteworthy that the functional duration of flowers of *Helonias* is comparatively long. In one plant of *H. bullata* once cultivated in Tokyo (material Bu-2, Tanaka 1997a), the flowering duration of the inflorescence was approximately 12 days. After opening of the tepals, the anthers remained indehiscent for two or three days (Fig. 5A), while the stigmatic segments were widely expanded. In both the cultivated plant (Fig. 5D) and plants in the field (e.g. B. Long 45636, GH!; Fig. 4E), the stigmatic segments of young flowers with dehiscing or dehisced anthers are markedly recurved and papillulate, looking mature and receptive. The

flowers are therefore viewed as (nearly) adichogamous. Similarly, in young flowers after opening of the tepals of *H. yunnanensis* var. *yunnanensis*, the anthers remain closed and the stigmatic segments are widely expanded (Fig. 7B). Since the stigmas and the anthers appear to become mature nearly simultaneously (e.g. *F. Ludlow et al.* 3651, BM-001118037!), the flowers of *H. yunnanensis* may also be (nearly) adichogamous. The flowering duration of this species is still unknown presently, but may not so largely deviate from that of *H. bullata*, judging from the overall similarity in their floral characteristics. Takahashi (1988) confirmed experimentally that the flowers of *Helonias orientalis* can be fertilized for at least 11 days, including one day before opening of the buds. Such a long duration may be required for the flowers to be pollinated by insects. *Helonias leucantha* cultivated in Tokyo flowers from winter to early spring (usually January through mid March). Duration of the flowers, including those with protruding pistils, is about two weeks. *Helonias orientalis* and *H. breviscapa* cultivated in Tokyo flower from mid March through early April. Duration of the flowers tends to be shorter, probably reflecting warmer conditions in mid spring.



**FIGURE 3.** Young slightly open flowers of *Helonias thibetica* (A–C; material T-1) and *H. umbellata* (D, E; U-1), showing protogyny. **A.** Flowers with precociously protruding pistil. **B, D.** Flowers similar in stage to A with frontal tepals removed to show indehiscent anthers. **C, E.** Closeup of densely papillulate mature stigma from flower in B and D, respectively.

**Tepals:**—There are six tepals in two whorls of three in *Helonias*. All six have a nectary at the base. The tepals of *H. bullata* (*H. sect. Helonias*) and subsect. *Ypsilandra* (*H. sect. Heloniopsis*) are adaxially nearly flat or only slightly canaliculate toward the base. The surface of the nectary is also nearly flat or slightly concave (e.g. Figs. 5C, E, 14B–D; Tanaka 1997a). In *H. ser. Umbellatae* (*H. subsect. Heloniopsis*), the tepals are slightly or moderately canaliculate toward the base (Tanaka 1997b). The proximal submarginal portions of the tepals are raised or ridged adaxially, and

the margins are slightly or moderately revolute proximally (Figs. 17D, 19D, E, 22D, E). The surface of the nectary is shallow in *H. kawanoi* (Fig. 17D, E), and moderately concave or saccate in *H. leucantha* (Figs. 19D, E) and *H. umbellata* (Figs. 22C–E) (Tanaka 1997b). In *H. umbellata*, the submarginal ridges of the tepals tend to be closely juxtaposed basally with those of adjoining tepals, and sometimes minutely connate with them (Figs. 22D, E; Tanaka 1997b). In *H.* ser. *Heloniopsis* (*H.* subsect. *Heloniopsis*), the tepals are usually prominently canaliculate toward the base and the proximal submarginal portions are narrowly winged (lamellate). The wings are not only connate basally with the wings of adjoining tepals, but also adnate to the stamen filaments to form a saccate or sheathed (tubular) nectary (Figs. 24B–E, 26A–C, 28B, C, E; Tanaka 1997b).

**Stamens:**—Each flower has six stamens, in two whorls of three. In *Helonias bullata* and *H.* subsect. *Ypsilandra*, the inner filaments are adnate basally to the base of the ovary (Figs. 5E, 14C; Tanaka 1997a). In fruit, the inner filaments are occasionally attached to the apical portion (contiguous with the base of the capsule) of a slightly elongate (gynophore-like) receptacle or floral axis in *H. thibetica* (Fig. 14F). The outer filaments are free from the ovary, but close to its base (Figs. 5E, 14C). The filaments are not adnate to their opposing tepals (Figs. 14B–D, F). In *H.* subsect. *Heloniopsis*, the filaments tend to be closer to the tepals and the inner filaments are not adnate to the ovary (Figs. 19B–E, 22B–E, 24B–E, 26A–C, 28B, C, E; Tanaka 1997b, c, e). In *H.* ser. *Umbellatae* the filaments are distinct to the base (e.g. Figs. 17D, E, 19B–E, 22C–E; Tanaka 1997b). The filaments of *H. kawanoi* (*H.* ser. *Umbellatae*) arise from the short floral axis (or receptacle) between opposing tepals and the base of the ovary (Fig. 17D, E). The base of the inner filaments is located close to the base of the ovary (Fig. 17E). The filaments of *H. leucantha* and *H. umbellata* are also free from their opposing tepals, but each of them arises from the adaxial rim of a concave nectary (Tanaka 1997b). In *H.* ser. *Heloniopsis* the filaments are adnate basally to the proximal submarginal wings of the opposing tepal, forming a sheathing (tubular) nectary at the base of the tepal (Figs. 24B–D, 26A–C, 28B, C, E; Tanaka 1997b).

The anthers of *Helonias bullata* (*H.* sect. *Helonias*) are adaxially basifixed, although they appear to be dorsifixed (Tanaka 1997a). In *H.* subsect. *Ypsilandra* they are abaxially basifixed (Fig. 14E; Tanaka 1997a). In ser. *Umbellatae* (*H.* subsect. *Heloniopsis*), the anthers are adaxially affixed at or close to the base of the connective (i.e. adaxially basifixed or nearly so; Figs. 20C, 22F; Tanaka 1997c). In ser. *Heloniopsis* (*H.* subsect. *Heloniopsis*) the anthers are usually adaxially affixed close to the connective base (i.e. (sub)dorsi-basifixed) (Figs. 24F). The anthers of *Helonias bullata* (*H.* sect. *Helonias*) and *H.* subsect. *Ypsilandra* are both unilocular (Figs. 4B, 5C, 14E; Tanaka 1997a). The anthers of *H. bullata* are longitudinally septate (furrowed) between sister thecae abaxially, but not adaxially, and are antorse-extrorse dehiscent (Fig. 5B; Tanaka 1997a). The anthers of *H.* subsect. *Ypsilandra* are not septate (furrowed) on either side (Fig. 14E; Tanaka 1997a), antorse-latrorse dehiscent, and peltate during early stages of dehiscence. The anthers of *H.* subsect. *Heloniopsis* are virtually bilocular, usually with a vestigial locular confluence at the apex (e.g. Figs. 17F, 20C, D, 24F, 28F; Tanaka 1997c). The anthers of *H.* ser. *Heloniopsis* (*H.* subsect. *Heloniopsis*), especially those of *H. koreana* (Fig. 24F) and *H. orientalis* (Fig. 25D–G; Tanaka 1997c), are often longer than those of *H.* sect. *Helonias* (Fig. 5A) and *H.* subsect. *Ypsilandra* (e.g. Fig. 14E; see also corresponding figures in Tanaka 1997a, c).

**Pistil:**—The pistil is tricarpellate and the ovary is syncarpous (e.g. Figs. 5D, 20A, 22E, 26C). The ovaries are globose and slightly trilobed distally (Figs. 5D, 9A, B, 12B, 22A, B). The ovules are borne on axile placentae (Figs. 20A, 22E, 26C). The ovules are anatropous, more or less narrowly ellipsoid-fusiform and mostly horizontal (i.e. perpendicular to the axis of placenta) (Figs. 22C, E, 24B, 26B, C, 28B, C). After fertilization, they gradually become more slender and assurgent (Fig. 14F). The number of ovules per locule (carpel) or ovary varies not only among species but also among individuals of the same species, and even among flowers of the same inflorescence. The ovules of *Helonias bullata* are significantly fewer than in other species (Table 1). Species such as *H. orientalis* (Utech 1978, Utech & Kawano 1981, as *Heloniopsis*), *H. breviscapa*, *H. koreana*, *H. umbellata*, and *H. thibetica* bear more numerous ovules (Table 1; Tanaka 1997c). There may be some correlation between the number of ovules and the size of the ovary or locule. In general, smaller flowers tend to bear fewer ovules (e.g., *H. kawanoi*), as the locules also tend to be smaller. In species such as *Helonias bullata* with comparatively few ovules, the ovules are biseriate on the placenta, while the more numerous ovules in species such as *H. thibetica*, *H. umbellata*, *H. leucantha*, and *H. orientalis* are multiseriate on the placenta (Figs. 22E, 26C; Utech 1978, Utech & Kawano 1981, for *H. bullata* and *Heloniopsis orientalis*).

The three carpels of *Helonias bullata* are often connate, forming a short column (Fig. 5D; Tanaka 1997a). The relative length of the style (to the stigmatic segments) varies among species (Tanaka 1997c, e). Except for *H. bullata*, *H. yunnanensis* var. *yunnanensis* has the shortest style (Fig. 7B, Table 6). *Helonias jinpingensis* has a slightly longer style (Table 6). *Helonias yunnanensis* var. *mesostyla* N.Tanaka (Fig. 9 A–C), *H. alpina* (F.T.Wang & Tang) N.Tanaka (Fig. 10E), *H. parviflora* (Fig. 12), *H. thibetica* (Figs. 13A–C, 14A), and all species of *H.* subsect. *Heloniopsis* (e.g. Figs. 17C, 22A, F) have a well developed style (Table 6 for *H.* subsect. *Ypsilandra*). The style of *H.* subsect. *Ypsilandra*

(except *H. thibetica*) is more or less trifurcate distally (e.g. Figs. 7B, 9A–C, Table 6), and the ventral surface of the distal segments is stigmatic with papillulae (Fig. 9A–C). The stigmatic portion is trisectioned to slightly trilobed (or nearly trigonal). *Helonias thibetica* (e.g. Fig. 3A–C) and *H. subsect. Heloniopsis* (e.g. Figs. 3D, E, 20D, 22A) share a discoid or subcapitate stigma, which is sometimes slightly trilobed except in *H. thibetica*. The stigmas of *Helonias bullata* (Figs. 4B, C, 5A–C, Tanaka 1997a, e) and subsect. *Ypsilandra* except *H. thibetica* are usually positioned lower than or as high as the anthers (Table 6). In contrast, the stigmas of *H. thibetica* (Figs. 13B, C, 14A, Table 6) and *H. subsect. Heloniopsis* (Figs. 16A, B, 19A, 22A, 25B, C, E, 27A–D, 28A) usually exceed the anthers.

**TABLE 1.** Number of ovules per locule in *Helonias* (Data in Tanaka 1997c, slightly modified).

Taxon	Number of ovules per locule	Total number of plants examined	Total number of locules examined
<i>H. bullata</i> *	6–18	3	24
<i>H. yunnanensis</i> var. <i>yunnanensis</i> *	18–79	5	6
<i>H. parviflora</i> **	ca. 55	1	1
<i>H. thibetica</i>	56–102	7	8
<i>H. kawanoi</i> *	23–78	6	11
<i>H. leucantha</i>	45–105	5	28
<i>H. umbellata</i>	59–113	17	44
<i>H. koreana</i> *	86–127	4	4
<i>H. orientalis</i> f. <i>orientalis</i>	68–189	14	20
<i>H. breviscapa</i>	50–175	36	54

\*Data added to Tanaka 1997c.

\*\* Cited as *Ypsilandra cavaleriei* in Tanaka 1997c.

## 9. Fruit

Fertilized ovaries develop into a trivalved loculicidal capsule. The capsule is oriented upward and dehisces into three divergent valves, exposing the seeds (Figs. 13E, 20E, 25F, G, 26E, F, 27E, F). In *Helonias* the dehiscence of ripe capsules usually occurs about 1.5–2.5 months from the beginning of flowering. The duration appears to vary to some degree, however, probably reflecting seasonal fluctuations and climatic factors like temperature.

## 10. Seeds and their dispersal

The (outer) testa of the seeds of *Helonias* is scarious and usually white (e.g. Figs. 5F, 20F). The seed itself is covered with a brownish (inner) testa. The most remarkable distinction in the size and shape of the seeds lies between *Helonias bullata* and other members of the genus. The seeds (including the testa) of *H. bullata* are somewhat flattened subfusiform (Fig. 5F), while those of other species are linear fusiform (Figs. 7G, 9D, 20F; Tanaka 1997c).

After sprouting, the flowering stems continue to elongate until their fruits become ripe. The ripe fruits (capsules) face upward (e.g. Figs. 13D, 25G, 27E). After dehiscence they expose their seeds on widely divergent capsular valves (e.g. Figs. 13E, 18E, 20E). These traits appear to be effective in seed dispersal by wind, for the seeds on the higher, upward capsules are likely to be dispersed farther than those on the lower, nodding ones.

According to Sutter (1984), seed dispersal of *Helonias bullata* is quite limited. In his experiment under natural conditions, no seed was found in traps located further than 20 cm from the nearest inflorescence. Without a strong wind, seeds rarely traveled farther than 40 cm. For *Helonias bullata*, which has a particular preference for swamps or bogs, such strongly limited seed dispersal may have an adaptive value, because seeds dispersed to distant drier locations may hardly survive.

## 11. Pollination and pollinators

According to Kawano & Masuda (1980), flowers of *Helonias orientalis* are visited by various insects such as *Andreana*, *Lasioglossum*, *Nomada* (Hymenoptera), *Bombylius major* (Diptera), and *Luehdorfia japonica* (Lepidoptera), among which large hymenopteran insects (*Andreana*, *Lasioglossum*, *Nomada*) are the most effective pollinators. Kawano *et al.* (2007) later added *Xylocopa appendiculata circumvolans*, several *Bombus* spp., and *Eristalomyia tenax* as pollinators for *H. orientalis*.

Takahashi (1988) reported that the flowers of *Helonias orientalis* are visited by various kinds of insects, such as Diptera, Hymenoptera and Lepidoptera. Some visitors forage only for pollen (e.g. one species of *Bombylius*, Diptera) or nectar (e.g. two species of *Bombus*, Hymenoptera), while others, such as the six species of Syrphidae (Diptera) and seven species of Andrenidae (Hymenoptera), forage for both nectar and pollen (Table 1 in Takahashi 1988). Most of the insects walk on the stamens and pistils and/or among them while foraging and very often touch the anthers and the stigmas, although the frequency of touching them is rather low for small insects.

As pollinators for *H. orientalis*, Tanaka (in Takahashi 1989) recognized three hymenopteran species; *Andrena hebes*, *Bombus diversus diversus*, *Tetralonia nippensis*, and two dipteran species; *Bombylius major*, *Eristalis cerealis*. He ranked *Bombus* as highly effective, *Andrena* and *Tetralonia* as effective, and the two dipterans as less effective.

Sutter (1984) reported that insect visitors representing many different orders were common in populations of *Helonias bullata*. In inflorescences emasculated without bagging, 81% of the flowers totally dependent on pollinators for cross-pollination set seed.

According to USFWS (1991), flowers of *Helonias bullata* are visited by beetles, black flies and a variety of other insects. SCPGA (2017) reported that various pollinators are attracted to the flowers, including a *Bombus* species (Fig. 4C, D), a Halictid species (Fig. 4E) and a butterfly species.

These data not only indicate that the flowers of both *Helonias bullata* and *H. orientalis* are structurally highly accessible for a wide range of insects, but also imply the possibility of some hymenopteran insects, such as Apidae (e.g. *Bombus*), Andrenidae (e.g. *Andrena*) and Halictidae (e.g. *Lasioglossum*) which are effective pollinators for *H. orientalis*, having been involved in the floral evolution of *Helonias*.

## 12. Self-compatibility, seed set, and seed germination

Sutter (1984) reported that *Helonias bullata* is highly self-compatible. In experiments, 100% of the flowers set seed in selfed treatments. The species is also highly cross-compatible, with 89% of the flowers setting seed in crossed treatments. Seed set per carpel for selfed and crossed treatments was almost identical, with 8 seeds produced per carpel and an average of 24.67 seeds per flower. There was no evidence for apomixis in this species.

Takahashi (1988) confirmed through experiments that *Helonias orientalis* is self-compatible. Flowers fruited by artificial selfing or crossing exceeded 91% in most flower-age groups and set viable seeds equally well. I also made preliminary experiments to examine self-compatibility in *H. orientalis* and *H. thibetica* (see "Materials and methods"). The two species set seeds well (Fig. 13D, E for *H. thibetica*), and the seeds appeared to be, at least externally, as sound as those produced naturally in the wild.

Takahashi (1988) confirmed in *Helonias orientalis* that the seeds from all capsules obtained through pollination experiments germinate very well (germination rates between 89.7 and 98.7%). The seed germination rate in *H. bullata* is also high (USFWS 1991).

## 13. Breeding system

Flowers of *Helonias bullata* are viewed as (nearly) adichogamous, for the stigmas and the anthers largely overlap in functional duration (section 8). Within the flowers the stigmas are positioned lower than the dehisced anthers (section 8), making it probable that the stigmas receive pollen mainly from the anthers of the same flower or from the same inflorescence when insects visit the flowers for pollen and/or nectar; i.e. the stigmas are likely to be self-pollinated. Since *H. bullata* is highly self-compatible (section 12), it is likely that the flowers (ovules) are self-fertilized. In fact, Sutter (1984) found that 77% of the flowers set seed by automatic self-pollination in the inflorescences bagged without emasculation. The possibility of self-fertilization in *H. bullata* is also supported by the data showing a comparatively low genetic diversity in populations of *H. bullata* (Godt *et al.* 1995). Flowers of *H. subsect. Ypsilandra* (except *H. thibetica*), such as *H. yunnanensis* (Fig. 7B, 9A) and *H. parviflora* (Fig. 12A), may also be self-pollinated to a large extent, since their stigmas are usually positioned below or as high as the anthers (Table 6).

In flowers of *Heloias bullata* and *H. subsect. Ypsilandra* (excluding *H. thibetica*), cross-fertilization may occur as well. For instance, in young open flowers with anthers not yet dehiscent of *H. bullata* and *H. yunnanensis*, the stigmas are already widely expanded (section 8; Figs. 4B,C, 5A, 7B). Even if the stigmas are still immature, pollen carried from other individuals and smeared on them by insects could germinate afterward when the stigmas have become mature.

Flowers of *Helonias thibetica* (Figs. 3A–C, 13A) and all species of *H. subsect. Heloniopsis* (Figs. 3D, E, 17A, B, 21A, 25A; Takahashi 1988 for *Heloniopsis orientalis*; Tanaka 1997d) are protogynous (section 8), although their stigmas and anthers largely overlap in functional duration (Takahashi 1988, Tanaka 1997d). In this respect, limited

protogyny appears to operate, and it must be effective to some degree in facilitating outcrossing. The stigmas exserted beyond the anthers (e.g. Figs. 14A, 16B, 21B, 25B, 27D) may also contribute to the promotion of outcrossing. *Helonias orientalis* has been reported to be self-compatible (Takahashi 1988) and my preliminary tests also suggest that *H. orientalis* and *H. thibetica* (Fig. 13D, E) are self-compatible (section 12). These species are therefore expected to produce seeds by both self- and cross-fertilization. The existence of interspecific hybrids between *H. orientalis* and *H. breviscapa* (section 14) (both belong to *H. ser. Heloniopsis*) verifies the occurrence of outcrossing and outbreeding in the parental species. The breeding system of other protogynous species of *H.* subsect. *Heloniopsis*, such as *H. umbellata* and *H. leucantha*, is probably similar to that of *H. thibetica* and *H. orientalis*, since they share similar floral morphology and phenology.

Thus, the flowers of *Helonias* appear to have evolved from those oriented to self-fertilization (*H. bullata* and *H.* subsect. *Ypsilandra* except *H. thibetica*) to those oriented to cross-fertilization (*H. thibetica* and *H.* subsect. *Heloniopsis*), although self-fertilization still operates as an essential breeding system even for the latter plant group.

#### 14. Hybridization

*Helonias orientalis* is widespread in Japan and southern Sakhalin, Russia, while *H. breviscapa* is confined to central and western Japan (Fig. 29; Fig. 1 in Kawano *et al.* 2007). The ranges of the two species overlap partly in Shikoku, and the Kinki and Chūgoku districts of western Honshū, Japan (Fig. 29). In two locations in the Kinki District, hybrid swarms between them were reported (Fuse & Tamura 2003). According to the report, the hybridization is introgressive toward *H. orientalis*, indicating that the hybrids are viable and sexually fertile and that postmating isolation is not in operation.

#### 15. Seedling establishment and growth rate of plants

In *Helonias bullata*, the number of seedlings that survive under experimental conditions as well as in the natural settings is very low and the growth rate of plants is very slow (USFWS 1991). Similarly, in plants of *H. orientalis* in the wild, seedling establishment is extremely low and the growth rate of plants is very slow. It is estimated to take at least several years for the seedlings of *H. orientalis* to reach sexual maturity (Kawano & Masuda 1980). Thus the two species are strikingly similar in seedling establishment and the growth rate of plants, both of which must be strongly related to the dynamics or maintenance of populations.

## Part II. Taxonomy

*Helonias* (s.str.) and its closely allied plants are examined taxonomically. Evolutionary aspects of the taxa recognized will be discussed mainly in Part III.

#### 1. Notes on the history

*Helonias*, with one species, *H. bullata*, was described by Linnaeus (1753, 1754) based on material from eastern North America, and classified under his Hexandria in accordance with the numerical characteristics of the sexual organs. *Helonias* was subsequently referred to Juncaceae, Liliaceae, Melanthiaceae, or Heloniadaceae (Table 2).

**TABLE 2.** Classifications of *Helonias* and allied taxa at suprageneric ranks.

Author and year of publication	Classification of <i>Helonias</i> and allied taxa <sup>1)</sup>
Linnaeus, C. 1753, 1754	Hexandria, Trigynia incl. <i>Helonias</i>
Thunberg, C.P. 1784	Hexandria, Monogynia incl. <i>Scilla japonica</i> , <i>S. bifolia</i> sensu Thunberg
Reichenbach, H.G.L. 1828	Juncaceae, Melantheae, Helonieae incl. <i>Helonias</i> , ‘Heleniae’
Endlicher, S. 1836–1841	Melanthiaceae, Veratraceae, Melantheae incl. <i>Helonias</i>
Gray, A. 1837	Melanthiaceae, Melantheae incl. <i>Helonias</i>
Miquel, F.A.W. 1867b	Melanthiaceae incl. <i>Sagerokia</i>
Watson, S. 1879	Liliaceae, Helonieae incl. <i>Helonias</i>
Baker, J.G. 1879	Liliaceae, Uvularieae incl. <i>Heloniopsis</i> ; Helonieae incl. <i>Helonias</i>
Bentham, G. 1883	Liliaceae, Narthecieae incl. <i>Helonias</i> , <i>Ypsilandra</i> , <i>Heloniopsis</i>
Engler, A. 1887	Liliaceae, Melanthioideae, Helonieae incl. <i>Helonias</i> , <i>Heloniopsis</i>

...continued on the next page

**TABLE 2.** (Continued)

Author and year of publication	Classification of <i>Heloniopsis</i> and allied taxa <sup>1)</sup>
Baillon, H. 1894	Liliaceae incl. <i>Heloniopsis</i> , <i>Heloniopsis</i> (incl. <i>Ypsilandra</i> )
Krause, K. 1930	Liliaceae, Melanthioideae, Heloniaceae incl. <i>Heloniopsis</i> , <i>Ypsilandra</i> , <i>Heloniopsis</i>
Hutchinson, J. 1934	Liliaceae, Heloniadeae incl. <i>Heloniopsis</i> , <i>Ypsilandra</i> ; Narthecieae incl. <i>Heloniopsis</i>
Dahlgren <i>et al.</i> 1985	Melanthiaceae, Narthecieae incl. <i>Heloniopsis</i> , <i>Heloniopsis</i>
Takhtajan, A. 1987	Melanthiaceae, Melanthioideae, Narthecieae incl. <i>Heloniopsis</i> , <i>Ypsilandra</i> , <i>Heloniopsis</i>
Takhtajan, A. 1997	Heloniadaceae incl. <i>Heloniopsis</i> , <i>Heloniopsis</i> , <i>Ypsilandra</i>
Tamura, M.N. 1998	Melanthiaceae, Heloniadeae incl. <i>Heloniopsis</i> , <i>Heloniopsis</i> , <i>Ypsilandra</i>
Takhtajan, A. 2009	Melanthiaceae, Heloniadeae incl. <i>Heloniopsis</i> , <i>Ypsilandra</i>
Tanaka, N. 2019 <sup>2)</sup>	Melanthiaceae, Heloniadeae incl. <i>Heloniopsis</i>

<sup>1)</sup>Author's original ending of names of taxa is retained, except for obvious typographic error.

<sup>2)</sup>This paper.

Gray (1859) described *Heloniopsis* based on material from Cape Romanzoff [Cape Sôya] in northern Hokkaidô, Japan. He found that it differs from *Helonias* of North America in having fewer flowers, a single slender style surmounted by a depressed capitate stigma, and seeds appendaged only at the hilum. As for the seeds he described, later studies revealed that they are actually of a species of *Luzula* mixed with the specimen of *Heloniopsis* (Koidzumi 1930, 1934, Hara 1947). According to Hara (1947), a small paper packet attached to the type specimen contained seeds, a capsule, and a flower of a species of *Luzula*, which was identified as *L. multiflora* Lejeune. It is suspected that Gray described the seeds of *Luzula* as being from *Heloniopsis*.

Not knowing that the seeds of Gray's *Heloniopsis* were based on a species of *Luzula*, Miquel (1866, 1867a, b, 1870) established *Sugerokia* as a new genus from Japan, since it differed markedly in seed characteristics from Gray's *Heloniopsis*. Maximowicz (1867), however, regarded *Sugerokia* as congeneric with *Heloniopsis*.

The differences in the number of flowers per scape and in the structure and shape of style and stigma between *Helonias bullata* and *Heloniopsis orientalis* were annihilated by the existence of transitional forms discovered later (Tanaka 1997c–e; 1998a). Accordingly, the grounds for separating *Helonias* and *Heloniopsis*, and *Heloniopsis* and *Sugerokia*, which were given by Gray (1859) and Miquel (1867a, b) respectively, are no more supportable.

Franchet (1887–1888, 1888) created *Ypsilandra* based on specimens from southeastern Tibet, since they differed from *Heloniopsis* in having unilocular anthers. Baillon (1894), however, viewed *Ypsilandra* as a section of *Heloniopsis*.

The anthers of *Helonias bullata* are also unilocular, and those of *Heloniopsis* (e.g. *H. leucantha*, *H. umbellata*) have traces of apical confluence between sister thecae (Tanaka 1997a, c). The styles of *H. bullata* are often connate at the base, forming a single short column which is equivalent to the column in *Ypsilandra* and *Heloniopsis* (Tanaka 1997a).

Tanaka (1998a, 2009) merged *Heloniopsis*, *Sugerokia*, and *Ypsilandra* into *Helonias*, because they are basically similar to one another in various characters. Kawano (1976; in Kawano & Masuda 1980) also suggested that *Helonias*, *Heloniopsis*, and *Ypsilandra* are congeneric, as they are so close to one another. Their close affinity has been confirmed by ultrastructural studies on the pollen grains of *Helonias*, *Ypsilandra*, and *Heloniopsis* (Takahashi & Kawano 1989), by the comparative vascular floral anatomy of *Helonias* and *Heloniopsis* (Utech 1978, Utech & Kawano 1981), by somatic karyotype analyses of *Helonias* and *Heloniopsis* (Utech 1980), and by analyses of plastid DNA sequences (Fuse & Tamura 2000, 2016, Fuse *et al.* 2004, Givnish *et al.* 2016, Kim *et al.* 2016).

From a survey on plastid DNA sequences (*matK* gene), Fuse & Tamura (2000) suggested that the inclusion of *Heloniopsis* and *Ypsilandra* in *Helonias* is unnecessary. However, in such molecular studies, independent clades (or clades unclustered with other related ones) do not necessarily represent "different genera". What they found is the presence of gaps in similarity between the three genera, which had been recognized in many previous morphological studies (e.g. Baillon 1894, Franchet 1887–1888, Tanaka 1997e). Their data do not contradict an attempt to classify the plants into infrageneric categories such as subgenus, section and subsection. A taxonomic category to apply to a plant group should be determined through an integral consideration of all the properties individuals possess (Tanaka 1996, 1997f, 1998b). Judging from the data so far accumulated, there appears to be no reasonable ground for treating each of the three groups as an independent genus.

Tanaka (1997e) presented a precursory phylogram of the *Helonias* group (including *Ypsilandra* and *Heloniopsis*) from cladistic analyses of phenotypic characters (Tanaka 1997a–d). The phylogram indicated that the *Helonias* group is monophyletic. At the same time, it was preliminarily demonstrated that the *Helonias* alliance comprises three groups, *Helonias*, *Ypsilandra* and *Heloniopsis*, with *Heloniopsis* consisting of two subgroups HP-1 and HP-2. The subgroup HP-1 includes three species from Taiwan and the Nansei Islands of Japan; the subgroup HP-2 includes two species

from Japan, Korea and southern Sakhalin, Russia. These infrageneric divisions are largely reflected in the new, revised taxonomic system proposed in the present paper (Table 3).

Studies of the phenology, life history, productive and reproductive biology (Kawano 1975, Kawano & Masuda 1980, 2004, as *Heloniopsis*; Kawano *et al.* 2007, as *Helonias*), and on the pollination and breeding system of *Helonias orientalis* (Takahashi 1988, as *Heloniopsis*) have been conducted. As for *H. bullata*, studies of reproductive biology including breeding system, conservation biology, and on the ecological and genetical aspects of the populations have been carried out (Sutter 1984, USFWS 1991, Godt *et al.* 1995). Data on these aspects in other species of the genus *Helonias* s.lat. is, however, still rather scanty. It is hence desirable that such studies also be carried out on them to more clearly elucidate the evolutionary aspect of *Helonias*.

## 2. *Helonias* as a genus including *Heloniopsis* and *Ypsilandra*

The members of *Helonias*, including *Heloniopsis* and *Ypsilandra*, are basically similar not only in habit but also in various characters such as the shape of the vegetative organs, floral structure (Utech 1978, Utech & Kawano 1981, Tanaka 1997a, b), pollen ultrastructure (Takahashi & Kawano 1989), capsular structure and dehiscence, seed morphology (Tanaka 1997c), and chromosome number (Utech 1980). Besides these features, they also share an ecological preference basically similar to one another. For instance, both the Asian and North American members inhabit mostly temperate regions at similar latitudes (Fig. 31) with moderate precipitation and temperature and prefer swampy or moist habitats. Their life history or seasonal growth patterns are also alike. As stated earlier, plastid DNA sequence data also support the monophyly of *Helonias* (s.lat.) (Fuse & Tamura 2000, 2016, Fuse *et al.* 2004, Givnish *et al.* 2016, Kim *et al.* 2016). Further, the data from cladistics analyses of phenotypic characters indicate paraphyly for both *Helonias* (s.str.) and *Ypsilandra* (Tanaka 1997e).

It is true that *Helonias* here circumscribed is not a little diversified, but considering the similarity in various characters of the members, the genus as a whole appears fairly uniform and is monophyletic (Fig. 30; Tanaka 1997e, Fuse & Tamura 2000, 2016, Fuse *et al.* 2004, Givnish *et al.* 2016, Kim *et al.* 2016). The degree of infrageneric diversity within *Helonias* appears much smaller than the intergeneric difference between *Helonias* and closely allied *Chamaelirium* s.lat. (including *Chionographis* Maxim., Tanaka 2017b). The generic delimitation of *Helonias* incorporating *Ypsilandra* and *Heloniopsis* proposed previously by Tanaka (1998a) is therefore followed in this paper.

## 3. Conspectus of a new infrageneric system for *Helonias*

From the results of this study a new classification system for *Helonias* is proposed (Table 3). More concrete, detailed taxonomic treatments are given in the following section (4).

**TABLE 3.** Conspectus of proposed infrageneric system for *Helonias*.

*Helonias* L.

Sect. 1. *Helonias*

1. *H. bullata* L.

Sect. 2. *Heloniopsis* (A.Gray) N.Tanaka\*

Subsect. 1. *Ypsilandra* (Franch.) N.Tanaka\*

2. *H. yunnanensis* (W.W.Sm. & Jeffrey) N.Tanaka

var. *yunnanensis*

var. *mesostyla* N.Tanaka\*

3. *H. jinpingensis* (W.H.Chen, Y.M.Shui & Z.Y.Yu) N.Tanaka

4. *H. alpina* (F.T.Wang & Tang) N.Tanaka

5. *H. parviflora* (F.T.Wang & Tang) N.Tanaka\*

6. *H. thibetica* (Franch.) N.Tanaka

Subsect. 2. *Heloniopsis*

Ser. 1. *Umbellatae* N.Tanaka\*

7. *H. kawanoi* (Koidz.) N.Tanaka

8. *H. leucantha* (Koidz.) N.Tanaka

9. *H. umbellata* (Baker) N.Tanaka

Ser. 2. *Heloniopsis*

10. *H. koreana* (Fuse, N.S.Lee & M.N.Tamura) N.Tanaka\*

11. *H. orientalis* (Thunb.) N.Tanaka

12. *H. breviscapa* (Maxim.) N.Tanaka

\* New names proposed are asterisked.

#### 4. Taxonomic treatment

Melanthiaceae, tribe Heloniadeae Reichenbach (1828: 63, as Helonieae).

- Helonias*** Linnaeus (1753: 342), p.p., excl. Plukenet & Morison; 1754: 159. Type:—*Helonias bullata* L.  
≡ *Abalum* Adanson (1763: 47, 511, ‘Abalon’), p.p., excl. *Ephemerum*.  
= *Hexonix* Rafinesque (1837, as ‘1836’: 13), nom. rejic. vs. *Heloniopsis* Gray (1859) (nom. cons.). ≡ *Kozola* Rafinesque (1837, as ‘1836’: 25), nom. rejic. vs. *Heloniopsis* Gray (1859) (nom. cons.). Basionym of types:—*Scilla japonica* Thunb.  
= *Sugerokia* Miquel (1866: 24; 1867a: 88; 1867b: 144). Type:—*Sugerokia japonica* Miq.  
= *Heloniopsis* Gray (1859: 416), nom. cons. Type: *H. pauciflora* A. Gray.  
= *Ypsilandra* Franchet (1887–1888: 93, t. 17; 1888: 131, t. 17). Type: *Y. thibetica* Franch.

**Japanese name:**—Shôjôbakama zoku (Tanaka 1998a: 114).

**Species included:**—12; *Helonias alpina*, *H. breviscapa*, *H. bullata*, *H. jinpingensis*, *H. kawanoi*, *H. koreana*, *H. leucantha*, *H. orientalis*, *H. parviflora*, *H. thibetica*, *H. umbellata*, *H. yunnanensis*.

**Description:**—Herbs glabrous, evergreen, polycarpic, hemicryptophytic, perennial. Rhizome cylindrical, sometimes nodose, vertical or ascending, closely subannulate with numerous scars, sometimes branched. Roots filiform, usually to 2 mm in diam., rame, white, rarely pale orangish or pinkish brown (in sicco), often contractile. Leaves hysteranthous, sometimes proteranthous, many, basal, rosulate at apex of rhizome, usually persistent for 1 or 2 years, spatulate or narrowly oblanceolate, gradually tapering to petiole-like base, margins entire or minutely undulate, apex mucronulate or apiculate, more or less chartaceous (thin to somewhat thick or firm), dull to glossy adaxially, veins parallel, converging near apex, rarely adventitiously producing plantlet (ramet) at apex. Flowering stem arising from center of basal rosette, erect or ascending, longitudinally ribbed, elongating with progression of anthesis, withering around May to June in vernal species, fistulose, bracteate; bracts (scale-like leaves) on peduncle 4–17(–24) (excl. basal ones), subulate, narrowly deltoid, (narrowly) lanceolate or narrowly oblong, apex acute or acuminate, (sub)membranous or herbaceous, sparser and smaller upward; inflorescence racemose, sub-umbellate or umbellate; pedicels terete, ribbed, ebracteate, rarely bracteate, ascending in fruit. Flowers spirally (in raceme) or subverticillately (in umbel) arranged, 1-many, actinomorphic, obconic, crateriform or sometimes campanulate, hermaphroditic, odorous or sometimes odorless, entomophilous, (nearly) adichogamous (homogamous) or dichogamous-protogynous; floral parts persistent after anthesis; flowers in raceme often erect (distal flowers), horizontal (middle ones) or reflexed (proximal ones), sometimes secund and pendulous at mid anthesis; flowers in subumbels and umbels often nodding at mid anthesis; flowers nodding toward end of anthesis. Tepals 6, in 2 whorls of 3, homomorphic, narrowly elliptic, oblong, oblanceolate or spatulate, apex rounded to acute, usually white, pink, purplish or sometimes bluish, turning green after anthesis, veins 3–7(–9), adaxially nearly flat or slightly to pronouncedly canaliculate toward base; proximal submarginal portions often raised (or ridged), sometimes winged (lamellate) inward, wings (lamellae) connate to wings of adjoining tepals, also adnate to opposite filaments forming a tubular nectary; abaxial basal portion usually slightly to markedly gibbous (directed downward); adaxial base secreting nectar, nectary nearly flat, saccate or tubular. Stamens 6, in 2 whorls; filaments subulate or filiform, sometimes complanate toward base, free or adnate basally to proximal submarginal wings of opposing tepals; inner filaments sometimes adnate basally to base of ovary; anthers ovoid, narrowly ovoid or hippocrepiform, unilocular or bilocular (usually) with rudimentary apical confluence between thecae, often purplish, positioned above or below stigmas; pollen usually whitish. Pistil 1, carpels 3; ovary syncarpous, superior, trilocular, adjoining locules dorsally connate partly along central axis (ventral suture), apex emarginate; styles 3, nearly free to base or connate into a single column; column distally trifurcate or simple; ventral surface of distal free part of style or of top of columnar style stigmatic; stigma trisepted to trilobed, discoid, capitate or depressed capitate, sometimes slightly trigonous, papillulate; ovules several to numerous per locule, biserrate to multiseriate on central axile placentae, subglobose or oblong at anthesis, anatropous, elongating after fertilization. Capsules antrorse, (broadly) obpyramidal, trifid or tripartite, apex depressed in center or sometimes (sub)truncate; lobes divergent, protruding subdistally, ovoid-subconic or subpyriform, apex rounded, ascending to nearly horizontal; loculicidal, trivalvate; valves cordiform, straw-colored. Seeds many, ascending, fusiform or linear-fusiform, often subfalcate, proximally linear-caudate, distally caudate to acicular; testa white or pale brownish, scarious, soft; body of seed brownish, narrowly oblong-fusiform, situated on one side in middle inside testa.

**Distribution:**—Eastern North America; eastern Asia (Bhutan, China, India, Japan, Korea, Myanmar, Nepal, Russia (S Sakhalin), Taiwan, Vietnam) (Fig. 31).

**Flowering:**—March–May, to July at higher elevations and latitudes; sometimes also August–October or late December–March.

**Fruit ripening:**—May–June, later at higher elevations and latitudes; rarely November–December or even later.

**Habitat:**—Open or shaded moist situations, such as swamps, meadows, banks along streams, forests and forest margins from cool temperate to subtropical regions.

**Remarks:**—*Helonias* makes up the tribe Heloniadeae with *Chamaelirium*. It consists of two sections, *H.* sect. *Helonias* and *H.* sect. *Heloniopsis* (Table 3). Their diagnostic characteristics are given in Table 4.

**TABLE 4.** Comparison of sections *Helonias* and *Heloniopsis*.

Character	Sect. <i>Helonias</i>	Sect. <i>Heloniopsis</i>
Inflorescence	raceme	raceme or (sub)umbel
Tepals		
Proximal adaxial surface	nearly flat or sl. canaliculate	nearly flat to prominently canaliculate
Basal connation between adjoining tepals	absent	absent or present
Nectary	almost flat	almost flat, sl. or mod. concave or (sub)tubular (sheathing)
Filaments		
Adnation to opposing tepal	absent	absent or present
Adnation between inner filament and ovary base	present	present or absent
Anthers		
Number of locules	1	1, or virtually 2
Attachment to filament	basifixed	basifixed or (sub)dorsi-basifixed
Style (columnar part)		
Length (mm)	ca. 0–0.6	ca. 0.2–22
Height of stigma vs anthers and tepals	lower	lower to higher
Maturation of stigmas and anthers	adichogamous	adichogamous or protogynous
Number of ovules per locule	6–18	18–189
Seeds (with testa)		
Shape	(sub)fusiform	linear-fusiform
Size (mm)	4.5–5.5 × 0.7–1.0	2.5–7.0 × 0.2–0.7

Abbreviations: mod.—moderately. sl.—slightly.

### Identification key to the sections of *Helonias*

1. Inflorescence racemose; flowers 30–72 per inflorescence, (nearly) adichogamous; tepals pink, adaxially slightly canaliculate toward base; anthers basifixed, antorse-extrorse, unilocular, septate (furrowed) medially on abaxial side; styles often connate at base and forming a column to 0.6 mm long, stigmatic segments 1.5–2(–2.5) mm long; ovules 8–18 per locule; seeds somewhat flattened subfusiform, 0.7–1 mm wide; testa of seeds whitish; eastern N. America ..... Sect. 1. *Helonias*
- Inflorescence racemose or sometimes (sub)umbellate; flowers 1–46 per inflorescence, adichogamous or protogynous; tepals white, pink, purplish or blue, adaxially slightly to markedly canaliculate toward base; anthers basifixed or (sub)dorsi-basifixed, antorse-latrorse or extrorse, unilocular or bilocular (usually) with vestigial apical confluence between thecae; styles connate at base and forming a column 0.2–22 mm long; stigma trisection to trilobed with segments to 1.5 mm long, or simply discoid or capitate; ovules 18–189 per locule; seeds linear-fusiform, 0.2–0.7 mm wide; testa whitish or pale brownish; eastern Asia .... Sect. 2. *Heloniopsis*

#### Sect. 1. *Helonias*

Section monotypic.

**Japanese name:**—Amerika (*America*)-shôjôbakama setsu.

**Distribution:**—Eastern North America (Figs. 6, 31-1).

1. *Helonias bullata* Linnaeus (1753: 342), p.p., excl. *Ephememerum phalangoides virginianum flosculis arbuteis bullatis aureis in spicam dispositis* in Plukenet (1692: t. 174, f. 5; 1696: 135) and in Morison (1699: 606, sect. 15, t. 2, f. 1). (Figs. 1A, 4, 5).

**Type** (lectotype designated by J.L. Reveal in Jarvis *et al.* 1993: 53):—U.S.A. Habitat in Pensylvaniae paludosis, *Pehr Kalm* s.n. (LINN No. 471.1\*!). Isolectotype: BM n.v.

≡ *Helonias latifolia* Michaux (1803: 212).

*Veratrum racemo simplicissimo, corollis patentibus, staminibus longioribus* Miller (1760: 181, t. 272).

*Veratrum scapo fistuloso squamoso, spica stricta* Ehret in Trew (1771: 41, t. 77, p.p., excl. A–C).

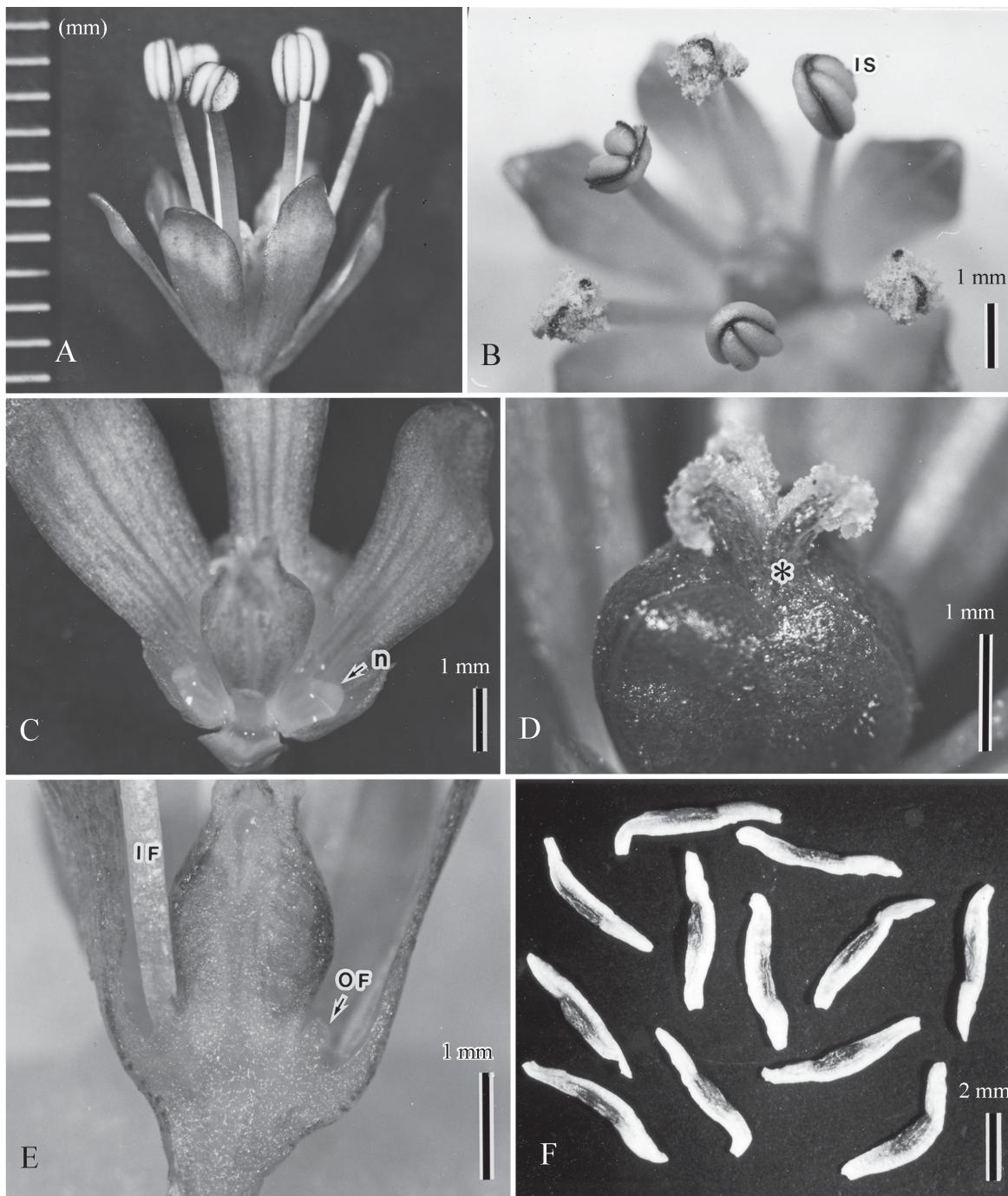
**Colloquial name:**—Swamp pink.

**Japanese name:** Amerika (*America*)-shôjôbakama (*nov.*).

**Description:**—Rhizome vertical or ascending, cylindrical, closely annulate with numerous scars, to 6 cm or longer, to 3 cm in diam. Roots filiform, some contractile, to 2 mm in diam., pale dull orangish (or pinkish) brown (or pale brick colored) when dry. Leaves slightly hysteranthous, main fresh rosette leaves 6–8(–13), usually persistent for 1 year, spatulate or oblanceolate, to 32 cm long, to 4 cm wide, tapering to cuneate base, margins entire, apex acute or acuminate, apiculus 0.5–0.8 mm long. Flowering stem 22–40 cm long at anthesis, to 72 cm long in fruit; peduncle



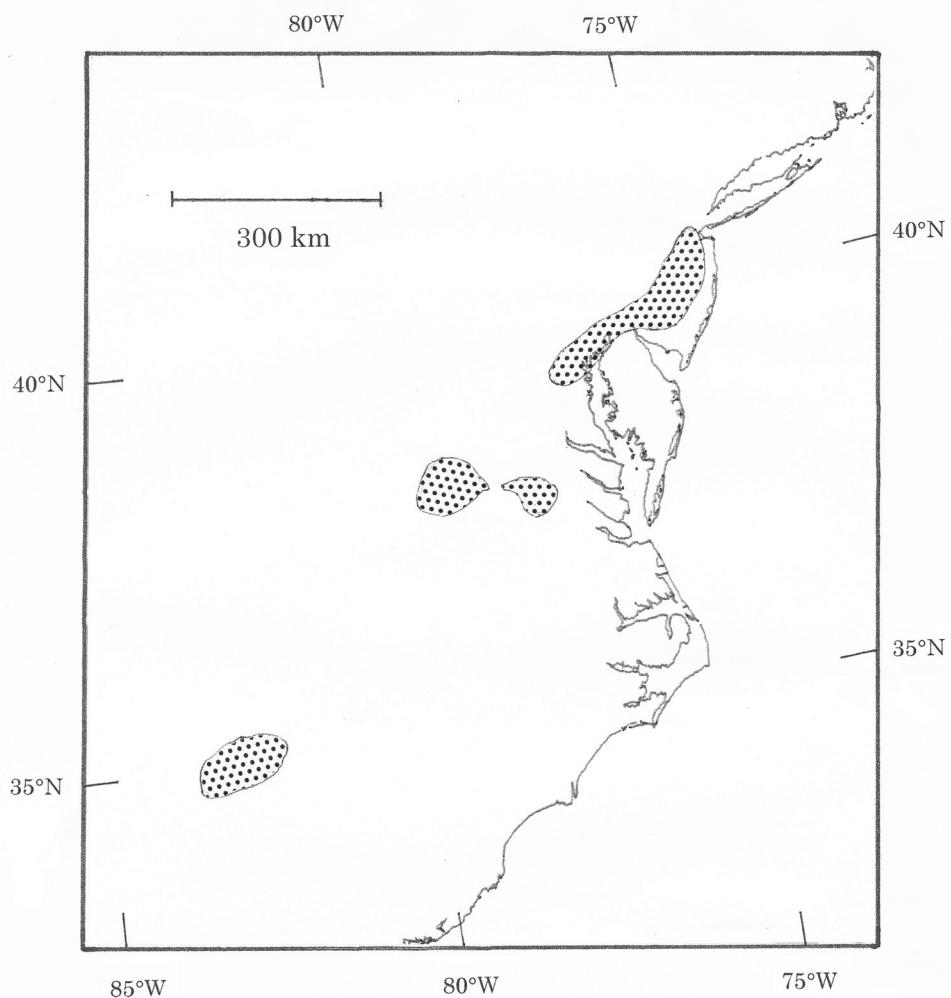
**FIGURE 4.** *Helonias bullata* (material Bu-1; photos A–E on 28 April 2014, F on 13 June 2002). A. Habit and boggy habitat. B. Young opening flowers with indehiscent anthers. C, D. Young flowers visited by a *Bombus* species sucking nectar. E. Flowers visited by a halictid bee. F. Fully dehisced, ascending capsules. All photos taken by Jim Fowler.



**FIGURE 5.** *Helonias bullata* (A–E; material Bu-2). **A.** Young flower with indehiscent anthers. **B.** Anthers seen from above. Three outer anthers dehisced earlier than three inner ones of which one marked with IS. **C.** Proximal interior of partial flower, showing nectar (n) secreted at adaxial bases of tepals. **D.** Pistil showing basal connation (\*) among three styles. **E.** Proximal portion of flower in vertical section. IF; inner filament. OF; outer filament. **F.** Seeds (Bot. Gard. Harvard Univ., year 1879, K). Photos A, C, E on 21 May 1996, B on 22 May 1996, D on 28 May 1996, all taken at Hachioji, Tokyo.

terete, 20–37 cm long at anthesis, elongating to 62 cm long in fruit; scale-like leaves on peduncle 9–11 (excl. basal ones), becoming shorter and laxer upward, ovate, oblong-ovate, lanceolate or narrowly deltoid, to 3.8 cm long, margins submembranous, apex acute or acuminate; inflorescence racemose, ovoid, narrowly ovoid or ellipsoid, 3–5 cm long, 2–2.5 cm in diam., rachis 2–4 cm long at anthesis, elongating to 12.5 cm in fruit; pedicels terete, 6-ribbed, pale pink, 2.5–6 mm long at anthesis, 5–10 mm long in fruit. Flowers 30–72 per inflorescence, spirally arranged, crateriform or funneliform, 7–10 mm across, facing upward (distal flowers), spreading horizontally (middle flowers) or downward (proximal flowers) at mid anthesis, fragrant, nearly adichogamous. Tepals ascending, pink, darker distally, slightly imbricate proximally, narrowly oblong or narrowly oblanceolate, 5–7 mm long, 1.5–2.1 mm wide, apex obtuse or

(sub)acute, veins 3 or 5, adaxial surface slightly canaliculate toward base; basal nectary almost flat, abaxial basal portion slightly inflated. Stamens 6; filaments ascending, pale pink, filiform-subulate, slightly complanate, 4.5–8 mm long, gradually widening toward base, apex subacute; inner filaments adnate to base of ovary; anthers extrorse (antrorse apically), adaxially basifix, ovoid-ellipsoid, base sagittate, unilocular, abaxial side longitudinally septate (furrowed) between thecae, adaxial side not septate nor furrowed, 1.5–2 mm long, whitish with blue tint, dark blue along suture of sacs, exserted beyond tepals. Pistil 1; ovary ovoid or ellipsoid, obtusely trigonous, apex emarginate, 2–3 mm long, 2–3 mm in diam., dark (greenish) purplish-pink; styles 3, often shortly connate basally into a single column to 0.6 mm long, free part of style ventrally stigmatic, papillulate, linear, 1.5–2(–2.5) mm long, recurved, white; ovules 6–18 per locule, biseriate on central axile placentae. Capsules antrorse, obpyramidal (obcordate laterally), 5–7 mm long, 10–12 mm broad, apex emarginate-sunken, trilobed; lobes ovoid-conic, rounded at apex, ascending. Seeds ascending within capsular cavity, with white testa, subfusiform, 4.5–5.5 mm long, 0.7–1 mm wide, slightly flattened, often somewhat falcate, subcaudate proximally, caudate distally; body of seed located on one side in middle within testa, fusiform, 1.1–1.8 mm long, 0.4–0.7 mm wide, brown.



**FIGURE 6.** Geographic range (dotted areas) of *Helonias bullata* in eastern North America (Data based principally on Utech 1978).

**Additional specimens examined:**—U.S.A. **Delaware:** New Castle Co., Belltown Run, NW of Glasgow Station, 21 April 1938, fl., R.R. Tatnall 3662 (GH); In paludosis civitatis, fl., Canby 15276 (BM-001118053); Farnhurst?, 13 May 1896, fr., A. Commons (GH); Swamps near Wilmington, Wm. M. Canby s.n. (K). **New Jersey:** Burlington Co., Buddtown, 30 April 1932, fl., H.M. Rusk & H.K. Svenson 6126 (P-02101625\*); Camden Co., cultivated from roots taken at Atco, May 1871, fl., J. H. Redfield s.n. (TI); swamps, near Atco, 3 May 1872, fl., J. H. Redfield s.n. (TI, 3 sheets); Middlesex Co., New Brunswick, 8 May 1932, M.A. Chrysler s.n. (P-02101626\*); Morris Co., Budd's Lake, 7 May 1905, fl. & fr., K. K. MacKenzie 1209 (E-00115524); Budd's Lake, 13 May 1906, 11 June 1905, fl. & fr., W.W. Eggleston s.n. (K, P-01879677\*); Salem Co., Whiglane, 14 April 1935, fl., B. Long 45636 (GH); Newfield, May 1900,

fl., H.E. Stone s.n. (BM-001118054). **North Carolina:** Transylvania Co., Pisgah National Forest, 7 May 2007, G. Kokubugata 6414 (TNS). ?**Pennsylvania:** Near Philadelphia, fl., Torrey s.n. (K). **Virginia:** Henrico Co., Whitecoak Swamp, west of Elko Station, 21 September 1938, fr., Fernald & Long 9295 (GH). **Cultivated material:** Botanic Gard. of Harvard Univ., 1879, fr., A. Gray (K); Hort. Edinburgh (Bot. Gard. Edinburgh), 14 May 1895, fl. (E-00115523).

**Distribution:**—U.S.A. Southern uplands of the Blue Ridge Mountains and on coastal plain northward; Delaware, Georgia, Maryland, New Jersey, New York, North Carolina, South Carolinas, Pennsylvania (not reported since the late 19th century), Virginia (Gleason 1952; Utech 1978, 2002). The population in New York is considered extirpated (USFWS 1988, 1991) (Figs. 6, 31-1).

**Habitat:**—Freshwater wetlands including spring seepages, swamps, bogs, meadows, and margins of small streams at elevations 0–1100 m (USFWS 1988, 1991, Utech 2002, Chafin 2007).

**Conservation status:**—*Helonias bullata* is threatened throughout the range (USFWS 1988, 1991). Threats to the species are outlined by Chafin (2007) as follows: Conversion of habitat to farmland and pasture, pollution runoff and sedimentation into wetlands, ditching and draining of wetlands, poaching, and encroachment by shrubs and trees. Conservation measures and recovery plans for threatened or endangered populations of this species are detailed in USFWS (1991). The populations vary extensively in size, stability, and quality of habitat conditions (USFWS 1991). While *H. bullata* is threatened, endangered or extirpated in several sites, it is locally abundant in New Jersey (Sutter 1984). It is noteworthy that a population in North Carolina contains over 100,000 rosettes, and the Blue Ridge populations in Virginia has a total of 15,000 plants (USFWS 1991). Having such large populations, *H. bullata* as a species is not assigned to any of the threatened categories CR, EN or VU, when assessed by the criterion D or D1 in the IUCN Red List Categories and Criteria (2001).

**Flowering:**—April–May.

**Ripening:**—June.

**Remarks:**—Although *Helonias bullata* was reported by Linnaeus as growing in a swamp in Pennsylvania, Gates (1918) stated that “the plant was originally discovered by Kalm near Philadelphia, probably on April 26, 1749, at Pennsneck, N[ew]. J[ersey]. It was formerly supposed to have occurred in eastern Pennsylvania, but this record was probably a mistake.” The persistence of its occurrence in that state has been doubted at least since the late 19th century (e.g. Britton & Brown 1896, 1913; Gates 1918; Utech 1978, 2002). I examined Torrey’s specimen, recorded as from ‘near Philadelphia’ (K, originally in Herbarium Hookerianum 1867). The specimen is cited under Pennsylvania in the list below, but it is uncertain whether it was actually collected in Pennsylvania or in nearby New Jersey. Gray (1848, 1868) included Pennsylvania within the range of *Helonias*. A detailed account of the distribution and habitat of *H. bullata* is provided in USFWS (1991).

## Sect. 2. *Heloniopsis* (A. Gray) N. Tanaka, *comb. & stat. nov.*

Type:—*Helonias orientalis* (Thunb.) N. Tanaka (≡ *Scilla orientalis* Thunb. = *Heloniopsis pauciflora* A. Gray).

≡ *Heloniopsis* Gray (1859: 416), excl. charact. seminum, *nom. cons.* Type:—*H. pauciflora* A. Gray.

= *Hexonix* Rafinesque (1837, as ‘1836’: 13), *nom. rejic.* vs. *Heloniopsis* Gray (1859) (*nom. cons.*). ≡ *Kozola* Rafinesque (1837, as ‘1836’: 25), *nom. rejic.* vs. *Heloniopsis* Gray (1859) (*nom. cons.*). Basionym of types:—*Scilla japonica* Thunb.

= *Sugerokia* Miquel (1866: 24; 1867a: 88; 1867b: 144). Type:—*Sugerokia japonica* Miq.

= *Ypsilandra* Franchet (1887–1888: 93, t. 17). Type:—*Y. thibetica* Franch.

**Japanese name:**—Shôjôbakama setsu.

**Species included:**—11; *Helonias alpina*, *H. breviscapa*, *H. jinpingensis*, *H. kawanoi*, *H. koreana*, *H. leucantha*, *H. orientalis*, *H. parviflora*, *H. thibetica*, *H. umbellata*, *H. yunnanensis*.

**Description:**—Leaves hysteranthous, sometimes proteranthous. Inflorescences racemose or (sub)umbellate. Flowers 1–many, adichogamous or protogynous. Tepals adaxially nearly flat or canaliculate toward base, distinct, or basally connate to adjoining tepals and adnate to opposing filaments. Nectary at base of tepal nearly flat, slightly or moderately concave or subtubular. Filaments distinct or adnate proximally to opposing tepals; inner filaments free or adnate basally to base of ovary. Anthers basifixied or (sub)dorsi-basifixied, unilocular or appearing bilocular. Style (fused columnar portion) 0.2–22 mm. Stigma trisectioned, trilobed, discoid or (sub)capitate. Seeds linear-fusiform.

**Distribution:**—Bhutan (NE), China (SW), India (NE), Korea, Japan, Myanmar (N), Nepal (Central, E), Russia (E: S Sakhalin), Taiwan, Vietnam (N) (Figs. 15, 29, 31-2–4, 32-2–4).

**Remarks:**—*Helonia* sect. *Heloniopsis* consists of two subsections, *H.* subsect. *Ypsilandra* and *H.* subsect. *Heloniopsis*. They are compared in Table 5, and a key to separate them is below.

**TABLE 5.** Comparison of subsections *Ypsilandra* and *Heloniopsis*.

Character	Subsect. <i>Ypsilandra</i>	Subsect. <i>Heloniopsis</i>
Inflorescence	racemose	racemose or (sub)umbellate
Tepals		
Adaxial surface in proximal part	nearly flat or sl. (or mod.) canaliculate	sl. to prominently canaliculate
Proximal submarginal portions	little or sl. raised	sl. or mod. raised (ridged), s. winged
Basal connation between adjoining tepals	absent	absent or present
Basal adnation to opposing filament	absent	absent or present
Inner filament		
Basal adnation to ovary base	present	absent
Anther		
Number of locules	1	virtually 2
Attachment to filament	basifixed	basifixed or (sub)dorsi-basifixed
Stigma	trisection, sl. trilobed, r. discoid or (sub)capitate	discoid, subcapitate, s. sl. trilobed
Maturation of stigmas and anthers	Adichogamous, or r. protogynous ( <i>H. thibetica</i> )	protogynous
Range in Asia	inland	insular or peninsular

Abbreviations: mod.—moderately. r.—rarely. s.—sometimes. sl.—slightly. u.—usually.

**Identification key to the subsections of *H. sect. Heloniopsis***

1. Inflorescence racemose; tepals distinct, adaxially nearly flat or slightly canaliculate toward base; nectaries nearly flat or slightly concave; inner filaments adnate basally to base of ovary; anthers unilocular, basifixed; stigma trisectioned or slightly trilobed, rarely discoid or (sub)capitate; Bhutan, China, India, Myanmar, Nepal, Vietnam. .... Subsect. 1. *Ypsilandra*
- Inflorescence racemose or (sub)umbellate; tepals distinct or connate, adaxially canaliculate toward base; nectaries slightly or moderately concave or tubular-saccate; inner filaments free from ovary; anthers appearing bilocular, basifixed or (sub)dorsi-basifixed; stigma discoid or (sub)capitate, sometimes slightly trilobed; Japan, Korea, Russia (S Sakhalin), Taiwan. .... Subsect. 2. *Heloniopsis*

**Subsect. 1. *Ypsilandra* (Franch.) N.Tanaka, *comb. & stat. nov.***

≡ *Ypsilandra* Franchet (1887–1888: 93, t. 17; 1888: 131, t. 17). Type:—*Helonias thibetica* (Franch.) N.Tanaka (≡ *Ypsilandra thibetica* Franch.).

**Japanese name:**—Chibetto (*Tibet*)-shôjôbakama asetsu.**Species included:**—5; *Helonias alpina*, *H. jinpingensis*, *H. parviflora*, *H. thibetica*, *H. yunnanensis*.

**Description:**—Leaves usually hysteranthous, rarely proteranthous. Inflorescence racemose. Flowers sometimes unilateral, usually adichogamous, rarely protogynous (*H. thibetica*). Tepals distinct, adaxially almost flat or slightly canaliculate toward base. Nectary at base of tepal nearly flat or slightly concave. Inner filaments adnate basally to base of ovary. Anthers basifixed, unilocular. Styles 3, connate proximally to almost entirely. Stigma trisectioned to slightly trilobed, rarely discoid or (sub)capitate. Flowering spring, rarely late summer to early autumn (*H. jinpingensis*).

**Distribution:**—Bhutan, China, India, Myanmar, Nepal, Vietnam (Figs. 15, 31-2, 32-2).

**Remarks:**—Subsection *Ypsilandra* and *Helonias bullata* of sect. *Helonias* are compared in Table 6. A key to the species of subsect. *Ypsilandra* is below.

**Identification key to the species of *H. subsect. Ypsilandra***

1. Stigma (sub)capitate or discoid ..... 6. *H. thibetica*
- Stigma trisectioned or slightly trilobed ..... 2
2. Leaves proteranthous; pedicels bracteate; flowering late August–September ..... 3. *H. jinpingensis*
- Leaves hysteranthous; pedicels usually ebracteate; flowering usually March–June (to July at high elevations) ..... 3
3. Stigma slightly trilobed (or nearly trigonal); tepals 3.8–4.5 mm long; style 1.2–1.5(–2.6) mm long ..... 5. *H. parviflora*
- Stigma trisectioned; tepals 2.5–10 mm long; style 0.2–6 mm long. .... 4

4. Flowers to 6 per scape; tepals narrowly oblong or narrowly oblong-ob lanceolate, 8–12 mm long; style 3.5–6 mm long ..... 4. *H. alpina*  
 - Flowers to ca. 28 per scape; tepals narrowly elliptic or narrowly elliptic-ob lanceolate, 2.5–5.5(–7.5) mm long; style 0.2–2.5 mm long ..... 2. *H. yunnanensis*

**2. *Helonias yunnanensis* (W.W.Sm. & Jeffrey) Tanaka (1998a: 105) (Figs. 7–9).**

= *Ypsilandra yunnanensis* Smith & Jeffrey (1916: 143). **Type** (lectotype designated in Lin *et al.* 2014: 414):—CHINA. Yunnan, shady situations in thickets on Shweli-Salween divide, lat. 25°20' N, elev. 9,000 ft, August 1913, G. Forrest 12055 (PE-00035459\*!). Isolectotypes: BM\*!, E-00115522!, K-000400240\*!, PE-00593975\*!, TI!

**Chinese name:**—Yunnan-yaruihua.

**Japanese name:**—Himaraya (*Himalaya*)-shôjôbakama (*nov.*).

**Distribution:**—Bhutan, China (Xizang, Yunnan), India (Assam), Myanmar, Nepal (Fig. 15-Yy, -Ym).

**Identification key to varieties of *Helonias yunnanensis***

1. Pistil usually 2–3 mm long (at anthesis); style column 0.2–1.2 mm long; stigmatic segments 0.7–1.5 mm long; stamens usually shorter than tepals ..... 2a. var. *yunnanensis*  
 - Pistil (2.5–)4–4.2 mm long (at anthesis); style column (1–)2–2.5 mm long; stigmatic segments (0.6–)0.8–1 mm long; stamens equaling or slightly exceeding tepals ..... 2b. var. *mesostyla*

**2a. *Helonias yunnanensis* var. *yunnanensis* (Fig. 7).**

= *Ypsilandra yunnanensis* var. *micrantha* Handel-Mazzetti (1923: 155). **Type** (lectotype, designated here):—CHINA. NW Yunnan. In regione frigide temperata jugi Nisselaka inter fluvios Mekong et Salween, 28°, s. micoschistaceo, ca. 4175 m, in palude, 18 June 1916, Handel-Mazzetti 8962 (WU-61254\*!).

= *Ypsilandra yunnanensis* var. *himalaica* H. Hara in Hara *et al.* (1978: 80). **Type:**—C. NEPAL. Rambrong, Lamjung Himal, 13,500 ft, 3 July 1954, Stainton, Sykes & Williams 6090 (Holotype: BM-521481\*! Isotype: E-00318414\*!; P-01724142\*! p.p.).

**Description:**—Rhizome cylindrical, vertical or ascending, nodose, 0.7–2.5(–4) cm long, 0.4–1.2 cm in diam. Roots filiform, to 1.8 mm in diam., whitish, often contractile. Leaves slightly hysteranthous, main fresh rosette leaves 5–13, persistent for ca. 1 year, spatulate or oblanceolate, 2.5–15(–22) cm long, 0.6–2.2 cm wide, tapering to cuneate base, margins sometimes revolute, apex acute, apiculate, apiculus 0.3–0.4(–1) mm long. Flowering stem 2–21 cm long at anthesis, elongating to 62 cm long in fruit; peduncle 1.5–18 cm long, elongating to 55.5 cm long in fruit; scale-like leaves on peduncle (excl. basal ones) few to several (or sometimes many), narrowly lanceolate, oblong-lanceolate, narrowly elliptic or oblanceolate, to 3.8 cm long; inflorescence racemose, ovoid or cylindrical-ovoid; rachis 0.3–4 cm long at anthesis, elongating to 2.8–7.5(–10) cm long in fruit; pedicels 0.3–2.5(–6) mm long at anthesis, becoming antrorse and 2–8 mm long in fruit, ebracteate, the lowermost rarely bracteate. Flowers 3–28, usually 3.5–8 mm across, facing upward, spreading horizontally or downward (depending on position on rachis), adichogamous, fragrant, nodding at late anthesis. Tepals 6, (narrowly) elliptic, oblanceolate, obtuse or subacute, 2.5–5.5(–7) mm long, 1.5–2.8 mm wide, white, pale to dark lilac, bluish, light violet purple, purple, veins (3 or) 5. Stamens 6, usually shorter than tepals, sometimes equaling or slightly exserted beyond tepals; filaments 1.5–4.5 mm long, apex short acuminate, white or purple; anthers reniform, basifixied, 0.5–1 mm long, dark purple or blue (sometimes darker along suture of sac). Pistil 1, 2–3 mm long, included in perianth, equaling or shorter than stamens; ovary globose, apex emarginate, trilobed, green or dark purplish green, 2–2.5 mm long, 2–2.3 mm across; style 0.2–1.2 mm long; stigma trisection, segments narrowly ligulate, 0.7–1.5 mm long, recurved, white or greenish white; ovules 18–79 per locule, multiseriate on central axile placentae. Capsules facing upward, broadly obpyramidal or obovoid (cordate in lateral view), apex usually depressed in center, tripartite, 4–5.5 mm long, 5–12 mm across, lobes ovoid-conic, apically rounded, ascending to horizontally divergent. Seeds many, with pale brownish testa, narrowly fusiform, 2.7–5 mm long, 0.4–0.6 mm broad, proximally sublinear, distally caudate or subulate; body of seed narrowly oblong, brown, 1.2–1.8 mm long, 0.3–0.5 mm wide.



**FIGURE 7.** *Helonias yunnanensis* var. *yunnanensis*. **A.** Habit and habitat (Y-1; photo on 24 May 2014). **B.** Closeup of inflorescence (Y-1 on 24 May 2014). **C–E.** Isolectotype (G. Forrest 12055, E-00115522). **C.** Habit. **D, E.** Closeup of inflorescence. **F.** Part of infructescence with dehisced capsules (G. Forrest 14961, E-00115516). **G.** Seeds (Gaoligongshan Biodiversity Survey 27019, GH-00293355). Photos A & B by Yang Niu.

**Additional specimens examined:**—BHUTAN. Me La, 14,000 ft, 15 September 1949, fr., *Ludlow et al.* 21189 (BM-001118031); Pang La, 11,000 ft, 9 July 1949, *Ludlow et al.* 20862 (E-00902974 \*, BM-001118030). CHINA. Xizang (S.E. Tibet): Kongbo Prov., Tum La, Nayü, Lat. N. 29°0', Long. E. 94°0', 12,000 ft, 7 July 1938, *Ludlow et al.* 5775 (BM-001118040); ibid., 11,000 ft, 9 July 1938, fr., *Ludlow et al.* 5798 (BM-001118034); Lusha Chu, 12,500 ft, 9 June 1938, fl., *Ludlow et al.* 4740 (BM-001118035); Pachakshiri Distr., Lo La, 9500 ft, 8 October 1938, F. *Ludlow* 6566 (BM-001118039); Lo La, 10,000 ft, 4 April 1938, fl., *Ludlow et al.* 3651 (BM-001118037); Ponu, above Trung, 13,000 ft, 26 June 1947, fl., *Ludlow et al.* 13210 (BM-001118036). Yunnan: Deqen Xian, Cizhong, 3650 m, 4 July

1940, *K.M. Feng* 5107 (PE-00593986); Deqen Xian, Cizhong, 3650–3700 m, 4 July 1940, *K.M. Feng* 5109 (PE-00593987\*, KUN); Fugong Xian, Gaoligongshan Region, 3560 m, 12 August 2005, fr., *Gaoligongshan Biodiversity Survey* 27019 (GH-00293355); Fugong Xian, Pi-he, elev. 3417 m, 15 May 2008, *X.H. Jin & T. Zhang* 054 (PE-01944105\*); Gongshan Xian, Cikai Zheng, 3400 m, 17 July 2000, *H. Li et al.* 12765 (GH); Gongshan, Bingzhongluo, 4270 m, 28 August 2006, fr., *Gaoligongshan Biodiversity Survey* 31512 (GH-00293671); Mekong-Salwin divide, 12,000 ft, September 1917, *G. Forest* 14961 (E-00115516); Salwen-Mekong divide, 13,000 ft, June 1911, *F. Kingdon-Ward* 163 (lectoparatype of *Ypsilandra yunnanensis*, E-00346116); Mekong-Salwin Divide, Londjrela, 3900 m, 9 October 1938, fr., *T.T. Yü* 22893 (A); ibid., Sila, 4000 m, 19 August 1938, fr., *T.T. Yü* 22420 (A); In regione frigide temperatae jugi Si-la inter fluvios Mekong et Salween, 28°, s. micoschistaceo, ca. 3900 m, in paludibus pascui Dotitong, 18 June 1916, *Handel-Mazzetti* 8949 (lectoparatype of *Ypsilandra yunnanensis* var. *micrantha*, WU-61254\*); Open pasture on the western flank of the Shweli-Salween divide, lat. 25°20' N, elev. 10,000–11,000 ft., August 1912, *G. Forrest* 8956 (lectoparatype of *Ypsilandra yunnanensis*, E-00346115\*, K-000400241\*); no detailed locality, no date, fl., *G. Forrest* 14158 (K); Mountains above Tseku and Tsehchung, Mekong-Salween watershed, June 1923, fl., *J.F. Rock* 9121 (P-01619474\*); Mountains above Tsehchung, 11,000 ft, July 1923, fl., *J.F. Rock* 10091 (E-00115517, GH); without detailed locality, 25°45' N, 98°40'E, 10,000 ft, Jun. 1924, *G. Forrest* 24438 (K, p.p., right plant only, left plant is *Theropogon*; PE-00593995\*). INDIA. Assam, Delei Valley, fl., *Kingdon-Ward* 8230 (K). MYANMAR. N. Burma. Tama Bum, 10,000–10,500 ft, 27 June 1953, *Kingdon-Ward* 21196 (BM-001118038); North and Upper region, 11,000 ft, June 1924, early fr., *G. Forrest* 24654 (K, PE-00593996\*); Ridge of Naung-Chaung-Nwai divide, Burmo-Chinese frontier, elev. 11,000–12,000 ft., 16 July 1914, *Kingdon-Ward* 1808 (lectoparatype of *Ypsilandra yunnanensis*, E-00318415\*); Upper Burma, 1924–25, *G. Forrest* 26906 (P-01619476\*). NEPAL. Kaski District, south of Annapurna. ca. 4300 m, 23 May 1972, fl., *R. G. Troth* 219 (TI); E. Nepal, Kasawa Khola, 14,000 ft, 1 June 1974, fl., *Stainton* 7063 (TI); Kasuwa Khola, 13,000 ft, 21 August 1975, fr., *L.W. Beer* 25356 (BM-001118029, TI); Koshi Zone, Sankhuwa Sabha Distr., 30 July 1988, fr., *M. Suzuki et al.* 8821028 (BM-001118033, TI); E. Nepal, Koshi Zone, Sankhuwasabha Distr., 3940 m, 27 August 1997, fr., *S. Noshiro et al.* (TI).

**Distribution:**—Bhutan, China (SE Xizang, NW Yunnan), India (Assam), Myanmar (northern border with China), Nepal (Central, E) (Fig. 15-Yy).

**Habitat:**—By streams, open moist alpine meadows, shady thickets at elevations ca. 2700–4300 m.

**Conservation status:**—The species is comparatively widespread, and may be assessed as LC according to the IUCN Red List Categories and Criteria (2001).

**Flowering:**—April–July.

**Ripening:**—June–October.

**Remarks:**—*Ypsilandra yunnanensis* var. *micrantha* or var. *himalaica*, a dwarf form in Bhutan, Nepal and Tibet passes into var. *yunnanensis* (Fig. 7) and hence is not distinguishable (Tanaka 1998a). The dwarf form appears to be an adaptation to harsh alpine environments. The stamens of *Helonias yunnanensis* var. *yunnanensis* are usually shorter than the tepals (Fig. 7B, D, E), but a form with stamens equaling or slightly exceeding the tepals and with somewhat longer pedicels, to ca. 6 mm long (e.g. *Ludlow et al.* 3651, 5775, 5798 at BM, cited below under China), is in southeastern Tibet. I regard this form as a local race, since it appears to gradually pass into var. *yunnanensis*.

## 2b. *Helonias yunnanensis* var. *mesostyla* N.Tanaka, var. nov. (Figs. 8, 9).

Differs from var. *yunnanensis* by the longer style with slightly shorter stigmatic segments, and stamens equaling or slightly exceeding (vs usually shorter than) tepals.

**Type:**—MYANMAR (BURMA). Myitkyina. Nr. Panwa Pass, alt. 7500 ft, 2 April 1938, Herb 4–5 inches high. Flowers pale blue-purple. Anthers purplish. Older flowers maroon. *C.W.D. Kermode* 17139 (Holotype, K-001235138!).

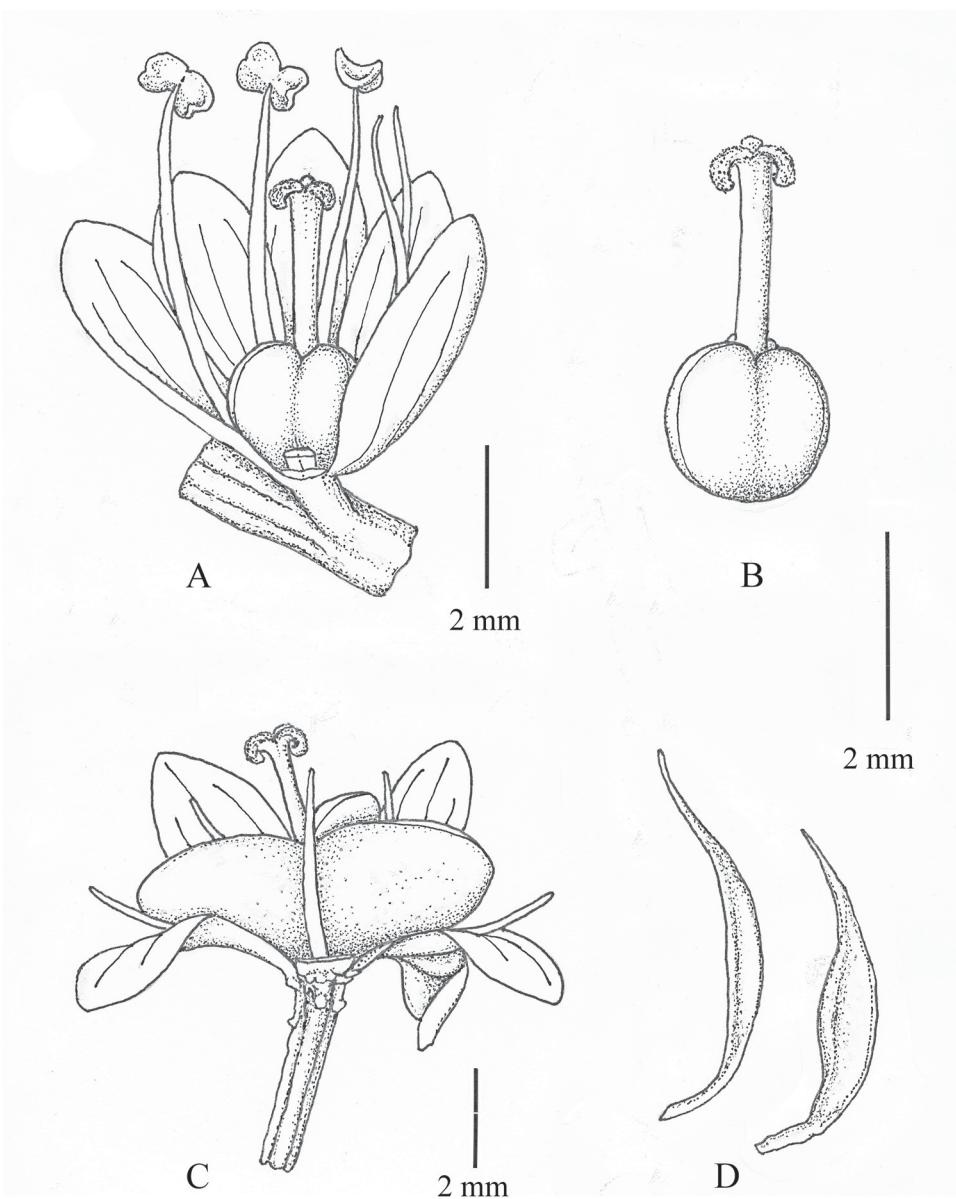
—*Ypsilandra alpina* auct. non Wang & Tang (1936: 81): Chen (1980: 18) p.p., Chen & Tamura (2000: 87) p.p.

Rhizome (sub)cylindrical, closely annulate with many scars, to 3 cm long, 1.4 cm in diam. Roots filiform, to ca. 2 mm in diam., contractile. Leaves slightly hysteranthous, main fresh rosette leaves 4–7, oblanceolate, to 13. 5 cm long, to 2.2 cm wide, tapering to base, apex apiculate. Flowering stem (4–)8–12.5 cm long incl. terminal raceme at anthesis, elongating to ca. 41 cm in fruit; peduncle to 11 cm long at anthesis, 33 cm long in fruit; scale-like leaves on peduncle several, becoming smaller and laxer upward, oblong-ovate or lanceolate, acute or acuminate, subherbaceous; inflorescence racemose, ovoid-ellipsoid, 2–2.5(–3) cm long, 1.2–1.5 cm in diam., becoming laxer with progression of anthesis due to elongation of rachis; rachis of inflorescence 0.5–1.5(–2.5) cm long at anthesis, to 8 cm long in fruit;

pedicels 0.5–2 mm long at anthesis, 1–3.5 mm long in fruit, ebracteate or lowermost sometimes bracteate. Flowers few to many, crateriform-funnelform, 5.5–9 mm across, spreading horizontally or slightly ascending, deliciously fragrant, adichogamous. Tepals narrowly elliptic or narrowly elliptic-ob lanceolate, 3.5–5.3(–7.5) mm long, (1.5–)1.8–2(–3) mm wide, subacute to obtuse, 3-veined, pale blue-purple, pale slaty violet, or white. Stamens equaling or slightly exceeding tepals, usually slightly longer than pistil; filaments (3–)4.5–5.5 mm long; anthers reniform, unilocular, (0.4–)0.7–0.8 mm long, purplish. Pistil 1, almost equaling or slightly shorter than tepals, (2.5–)4–4.2 mm long; ovary globose, trilobed, apex concave, 1.5–2.3 mm long, 1.5–2(–3.3) mm across; style terete, (1–)2–2.5 mm long; stigma trisection, segments oblong, (0.6–)0.8–1 mm long, recurved. Capsules erect, broadly obovate-pyramidal, tripartite, ca. 3 mm long, 6.5–7.8 mm across, apex depressed in center; lobes ovoid-conic, strongly divergent, apex obtuse. Seeds many, straw colored, narrowly fusiform, tailed at both ends, 4.2–4.8 mm long, 0.5–0.7 mm wide; body of seed narrowly oblong, 1.5–2.3 mm long, 0.5–0.6 mm wide, brownish.



**FIGURE 8.** *Helonias yunnanensis* var. *mesostyla* from N Myanmar (Kermode 17139, holotype, K-001235138). A. Habit. B, C. Closeup of inflorescence.



**FIGURE 9.** *Helonias yunnanensis* var. *mesostyla*. **A.** Flower with frontal tepal and stamen removed. **B.** Pistil. **C.** Fruit with persistent floral parts. One frontal tepal removed. **D.** Two seeds. A, B from N Myanmar (*Kermode* 17139, holotype, K-001235138). C, D from Yunnan, China (*Gaoligongshan Biodiversity Survey* 32015, GH-00292433). Scale on right corner for B and D. Drawn by Noriyuki Tanaka.

**Additional specimens examined (paratypes):**—CHINA. Yunnan. Gongshan. Cikai. Yipsaka Lake, 3500 m, 12 August 2006, fr., *Gaoligongshan Biodiversity Survey* 32015 (GH-00292433); Salwin-Kiukiang Divide, Newahlung, 2950 m, 9 July 1936, fr., T.T. Yü 19283 (A, PE-00035447\*, PE-00593847\*, PE-00593848\*); Salwin-Kiuking Divide, Tsukuei, 3850 m, 13 July 1938, fl., T.T. Yü 19337 (PE-00593985). MYANMAR. Adung Valley, 28°20'N, 97°40'E (Sources of the Irrawaddy), 8500–9000 ft, 27 May 1931, *Kingdon-Ward* 9557 (BM-001118041); ibid., 8500 ft, 23 May 1931, *Kingdon-Ward* 9522 (BM-001118042); Myanmar, opposite to Dazu in Gongshan County of China, 3100–3200 m, 30 July 2013, X.H. Jin et al. ST1434 (PE-02002621\*).

**Distribution:**—N Myanmar (border with China), SW China (NW Yunnan) (Fig. 15-Ym).

**Habitat:**—Alpine wet meadows and margin of thickets at elevations 2286–3850 m.

**Conservation status:**—This form is very local and the population size is supposedly small. Preliminarily assessed as DD according to the criteria set out in IUCN (2001).

**Flowering:**—March–May(–July).

**Ripening:**—Usually July–August.

**Etymology:**—The varietal epithet refers to the medium-long style.

**Remarks:**—Plants collected by T.T. Yü (*no. 19337, PE-00593985!*) on a high peak in NW Yunnan (3850 m) appear to be dwarf alpine forms of *Helonias yunnanensis* var. *mesostyla* with short leaves (to ca. 4 cm long, 1 cm wide), short flowering stems (2.5–4 cm long, including flower-bearing portion), few flowers (4 to 6 per scape), short tepals (3.5–4 mm long) and short styles 1–1.5 mm long, obviously reflecting the harsh alpine habitat. These plants may represent the smallest extreme in size within *H. yunnanensis* var. *mesostyla*. This variety appears to be closely allied to both *H. yunnanensis* var. *yunnanensis* (Fig. 7) and *H. alpina* (Fig. 10). It differs from *H. yunnanensis* var. *yunnanensis* by the longer style and usually slightly shorter stigmatic segments (Fig. 9A–C, Table 6). The anthers of *H. yunnanensis* var. *mesostyla* are usually slightly exserted beyond the tepals (Figs. 8, 9A), while those of *H. yunnanensis* var. *yunnanensis* are usually shorter than the tepals (Fig. 7B, D, E). *Helonias yunnanensis* var. *mesostyla* differs from *H. alpina* by its shorter, narrowly elliptic or elliptic oblanceolate (vs oblong or oblong-oblanceolate) tepals, and shorter styles and filaments. It is viewed as an intermediate form between *H. yunnanensis* var. *yunnanensis* and *H. alpina*. The geographic range of var. *mesostyla* (Fig. 15-Ym) partly overlaps with that of *H. yunnanensis* var. *yunnanensis* (Fig. 15-Yy) and is close to that of *H. alpina* (Fig. 15-A). *H. yunnanensis* var. *mesostyla* is also close to *Helonias jinpingensis*, but distinguishable by the slightly shorter, ebracteate pedicels, usually slightly longer style (Table 6) and vernal flowering.

**TABLE 6.** Comparison of *Helonias bullata* (*H.* sect. *Helonias*) and five species of *H.* subsect. *Ypsilandra* (*H.* sect. *Heloniopsis*).

Character	<i>Sect. Helonias</i>		<i>Sect. Heloniopsis – Subsect. Ypsilandra</i>				
	<i>H. bullata</i>	<i>H. yunnanensis</i> var. <i>yunnanensis</i>	<i>H. yunnanensis</i> var. <i>mesostyla</i>	<i>H. jinpingensis</i>	<i>H. alpina</i>	<i>H. parviflora</i>	<i>H. thibetica</i>
Leaves <sup>1)</sup>	hyst.	hyst.	hyst.	prot.	hyst.	hyst.	hyst.
Anthesis (month)	4–5	4–7	3–5(–7)	9	6–7	3–4	2–3
Height of pistil vs stamens	lower	lower	equaling or lower	lower	(sub)equaling	equaling or lower	u. higher
Style length <sup>2)</sup> (mm)	ca. 0–0.6	0.2–1.2	u. (1)–2–2.5	1.3–1.8	3.5–6	1.2–1.5(–2.6)	(5)–10–22
Stigma <sup>3)</sup>	u. trisected	trisected	trisected	trisected	trisected	sl. trilobed	capitate or s. discoid
Length of stigmatic segments (mm)	1.5–2(–2.5)	0.7–1.5	(0.6)–0.8–1	0.8–1	0.5–0.9	ca. 0.1–0.2	unlobed

<sup>1)</sup> Development of leaves vs flowering stems.

<sup>2)</sup> Columnar part.

<sup>3)</sup> Excluding columnar part of style.

Abbreviations: hyst.—hysteranthous. mod.—moderately. prot.—proteranthous. s.—sometimes. sl.—slightly. u.—usually.

### 3. *Helonias jinpingensis* (W.H.Chen, Y.M.Shui & Z.Y.Yu) Tanaka (2009: 190).

≡ *Ypsilandra jinpingensis* Chen *et al.* (July 2003: 267, fig. 1 on p. 268). **Type:**—CHINA. Yunnan: Jinping, Mt. Wutaishan, elev. 2660 m, 3 October 1996, S.G. Wu *et al.* 3742 (Holotype: KUN, n.v.).

= *Ypsilandra yunnanensis* W.W.Sm. & Jeffrey var. *fansipanensis* Shaw (2008: 41). **Type:** VIETNAM. Cultivated flowering plant pressed on 2 October 2007, originally collected from Vietnam, Lào Cai province, Mt. Fansipan, 2700 m, 1 December 2006, B. & S. Wynn-Jones 11839 (Holotype: WSY-0100773\*! Paratype?: Herb. B. Wynn-Jones, n.v.).

**Description:**—Description based on Chen *et al.* (2003) and Shaw (2008):—Rhizome vertical, ca. 1–2 cm long, ca. 7 mm in diam., brown, closely annulate with numerous scars. Roots to 30 cm long, 1–1.5 mm in diam., hirsute. Leaves proteranthous, main fresh rosette leaves 6–9(–ca. 22), oblanceolate, 7–21 cm long including petiole, 1.7–2.5 cm wide, gradually narrowed to petiole, chartaceous. Stem to ca. 45 cm long including terminal young infructescence (in fruit); peduncle 32–36 cm long (in fruit), grooved, with 10 or more narrowly oblong scale-like leaves 1.1–2.3 cm long, 0.2–0.6 cm wide; inflorescence racemose 8–9 cm long (in fruit); pedicels 5–12 mm long (incl. those in fruit), each subtended by narrowly oblong bracts 7–8 mm long, 1.0–1.2 mm wide. Flowers ca. 10 or more per scape; tepals narrowly oblanceolate or spatulate, 4.5–5.0 mm long, 1.6–2.0 mm wide, 3-veined, white or cream, turning yellowish green with age. Stamens 4.6–5 mm long, equaling or slightly exserted beyond tepals at anthesis, filaments 5–10 mm

long, white; anthers broadly oblong, 0.6–0.9 mm long, bright blue; pollen creamy-white. Ovary trilobed apically, trilocular, dark bluish black at anthesis; style 1.3–1.8 mm long; stigma trisepted, segments 0.8–1 mm long, recurved. Capsules broadly obovate-pyriform, apex depressed in center, tripartite, 4.5–5 mm long, ca. 2.2 mm across; lobes protruding obliquely upward. Seeds not seen.

**Distribution:**—SW China (SE Yunnan), N Vietnam (border with China) (Fig. 15-J).

**Habitat:**—Moist places in dense forests at elevations 2660–2910 m (fide Shui & Chen 2006, Shaw 2008).

**Conservation status:**—The range is narrow and the population size is supposedly small. Preliminarily assessed as DD according to the IUCN Red List Categories and Criteria (2001).

**Flowering:**—(late August–)September.

**Ripening:**—October–November.

**Remarks:**—*Helonias jinpingensis* appears to be closely allied to *H. yunnanensis* var. *yunnanensis*, but has a slightly longer style (Table 6). Judging from the drawings and description in Chen *et al.* (2003, as *Ypsilandra*), the type specimen of *Helonias jinpingensis* is already in fruit. A photograph of the young inflorescence is shown in Shaw (2008, as *Y. yunnanensis* var. *fansipanensis*). *Helonias jinpingensis* is unique in having bracteate pedicels. Supposedly, this character state is an apomorphy, since both *H. yunnanensis* var. *yunnanensis* and *H. bullata*, which are considered to be more primitive in the stylar characteristics, have no floral bracts. Because *H. jinpingensis* blooms in late summer to autumn (September, and probably also late August, judging from papers by Chen *et al.* 2003 and Shaw 2008), the leaves are regarded as proteranthous. This also implies that the dormancy of flower buds, which is seen in vernal species of *Helonias* (e.g. *H. thibetica*, *H. orientalis*), is lost. This feature may also be a derived character state acquired under subtropical or warm-temperate conditions.

#### 4. *Helonias alpina* (F.T.Wang & Tang) Tanaka (1998a: 106) (Fig. 10).

≡ *Ypsilandra alpina* Wang & Tang (1936: 81), ‘alpinia’\*. **Type:**—MYANMAR. Frontier of Tibet and Burma, Seingku-wang, 28°8' N, 97°24'E, 14,000 ft, on turf slopes on the exposed flanks of a limestone ridge, 9 July 1926, F. Kingdon-Ward 7084 (Holotype: K-000400242\*! Isotype: E-00115520!). \*The epithet ‘alpinia’ is obviously a printing error, for the specimen was annotated by the authors (December 1935) as *Y. alpina*.

**Description:**—Rhizome cylindrical, 1–1.3 cm long, 0.3–0.6 cm in diam. Roots filiform, to 1.5 mm in diam., whitish or pale brown (in sicco), contractile. Leaves slightly hysteranthous, main fresh rosette leaves 4–11, narrowly oblanceolate, to 6 cm long, to 1 cm wide, apex acute, minutely apiculate. Flowering stem to 6 cm long; peduncle to 5.5 cm long; scale-like leaves oblong-ovate to lanceolate, acute, imbricate, (sub)herbaceous; inflorescence racemose, compact, rachis 2–5 mm long; pedicels 0.5–2 mm long, ebracteate. Flowers 2 to 5 or 6 per inflorescence, mostly facing upward, few sideward, campanulate or funnelform, ca. 0.8–1.1 cm across, fragrant. Tepals narrowly oblong or narrowly oblong-oblanceolate, 8–12 mm long, (1.5–)2–3(–3.3) mm wide, apex rounded, 3–5(–6)-veined, violet or chocolate in color. Stamens slightly shorter than tepals and nearly equaling (or slightly shorter or higher than) pistil; filaments 6–9 mm long, straight; inner filaments adnate basally to ovary; anthers ovate-reniform, unilocular, basifix, 0.8–1 mm long, white. Pistil 1, 6.5–9 mm long; ovary globose, longitudinally trisulcate, 3 mm long and broad; style columnar, somewhat thick, 3.5–6 mm long; stigma trisepted, white, segments 0.5–0.9 mm long, recurved. Fruit and seeds not seen.

**Additional specimen examined:**—MYANMAR. Frontier of Tibet and Burma, Seingku-wang, 28°8' N, 97°24'E, 13,000 ft, 9 July 1926, fl., F. Kingdon-Ward 7083 (BM-001118047).

**Distribution:**—N Myanmar (Fig. 15-A).

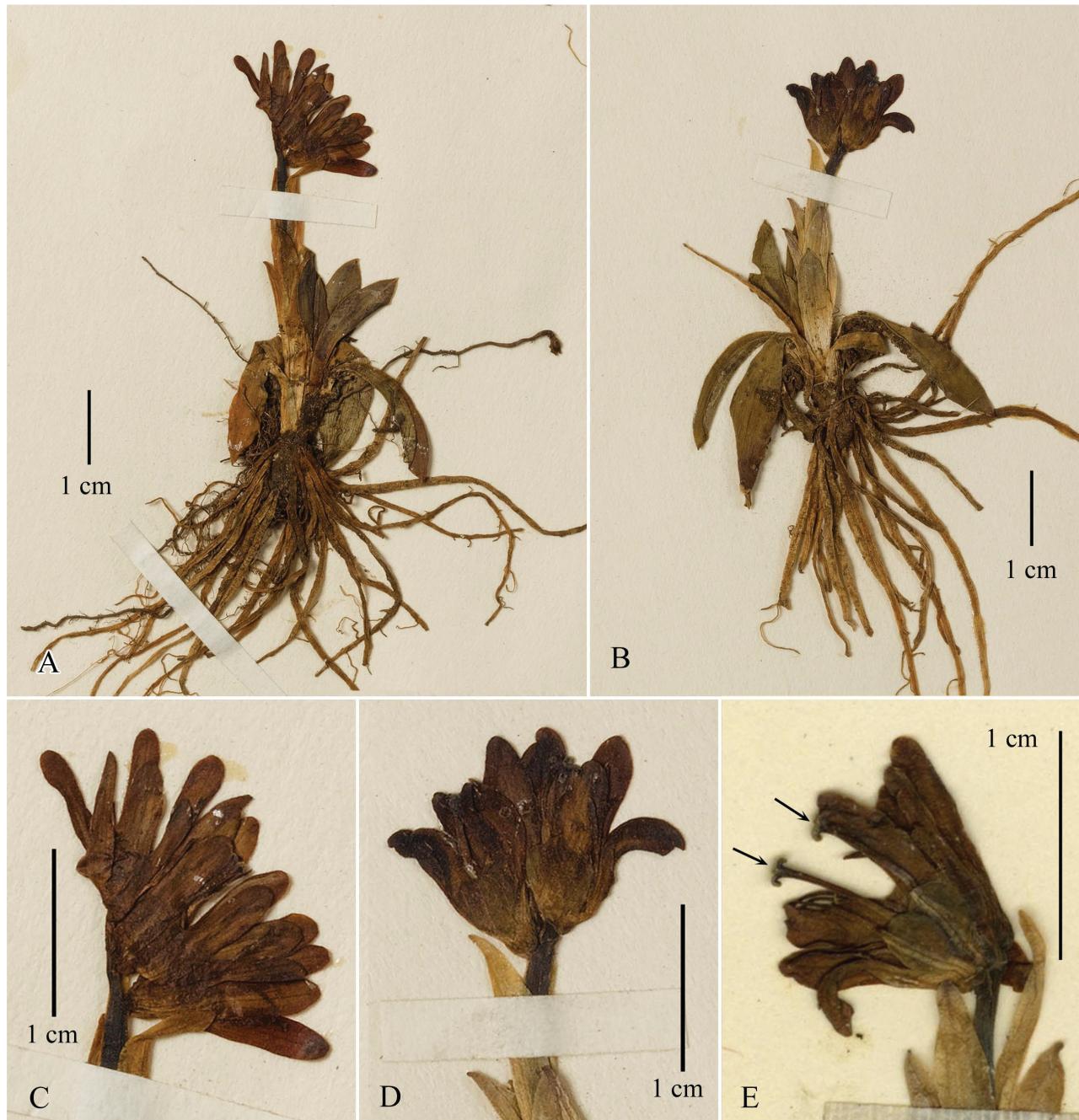
**Habitat:**—Turf slopes and level stretches of turf among boulder heaps in valleys at elevations 3962–4267 m (Kingdon-Ward 7083, BM; Kingdon-Ward 7084, E).

**Conservation status:**—The range is narrow and the population size is supposedly small. Preliminarily assessed as DD according to the IUCN Red List Categories and Criteria (2001).

**Flowering:**—June–July.

**Remarks:**—*Helonias alpina* appears to be most closely allied to *H. yunnanensis* var. *mesostyla* (Figs. 8, 9) in having comparatively long styles and short stigmatic segments. The ranges of *H. alpina* (Fig. 15-A) and *H. yunnanensis* var. *mesostyla* (Fig. 15-Ym) are close to each other, which may also suggest their close phyletic relationship. *Helonias alpina* is distinguishable from *H. yunnanensis* var. *mesostyla* by the larger flowers with longer oblong or oblong-oblanceolate tepals, and longer filaments and styles. The anthers of *H. alpina* are not exserted beyond the tepals (Fig. 10), while those of *H. yunnanensis* var. *mesostyla* are equaling or slightly exceed the tepals (Figs. 8, 9A). The stigmatic segments of the latter appear to be relatively slightly longer than those of *H. alpina* (Table 6). Chen (1980)

and Chen & Tamura (2000) reported *Ypsilandra alpina* from SE Xizang (Tibet) and NW Yunnan, China, but I have not yet confirmed its occurrence in the regions on a specimen basis. Chen identified specimens T.T. Yu 19283 (PE-00035447\*, PE-00593847\*, PE-00593848\*) from NW Yunnan as *H. alpina* (*Ypsilandra alpina*, ‘alpinia’) according to his annotations (dated May 1975) on the specimens. However, these belong to *H. yunnanensis* var. *mesostyla* in the present circumscription. Since the type specimens of *H. alpina* were collected in the frontier of Tibet and Burma (F. Kingdon-Ward 7084, E, K), there is a good possibility that it also occurs in SE Xizang and/or NW Yunnan. *Helonias alpina* is viewed as an alpine, (semi-)dwarf form with somewhat large flowers derived from *H. yunnanensis* var. *mesostyla*. To more clearly elucidate their relationship, it is necessary to conduct further surveys on the variation of the two taxa based on more samples.



**FIGURE 10.** *Helonias alpina* from SE Tibet (F. Kingdon-Ward 7084). **A, B.** Habit. **C–E.** Closeup of inflorescence. A–D: Holotype (K-000400242\*). E: Isotype (E-00115520). Stigmas arrowed in E.

5. *Helonias parviflora* (F.T.Wang & Tang) N.Tanaka, **comb. nov.** (Figs. 11, 12).

≡ *Ypsilandra parviflora* Wang & Tang (1943: 106). **Type** (lectotype, designated here):—CHINA. Kouy-Tcheou [Guizhou], Lou-tsong-kouan, 1450 m, Avril 1910, J. Esquirol 2013 (non 3012) (P-00730552\*!). Isolectotype: E-00115519!, K-000400239\*!

– *Ypsilandra cavaleriei* auct. non H. Lév. & Vaniot: Chen (1980: 17), p.p.; Chen & Tamura (2000: 87), p.p.; Tanaka (1997c: 222; 1997d: 286; 1997e: 329; 1998a: 106), p.p., as to *J. Esquirol 2013* (E-00115519!).



**FIGURE 11.** *Helonias parviflora* from China (*J. Esquirol 2013*, isolectotype, E-00115519). **A.** Habit. **B, C.** Closeup of inflorescence.

**Description:**—Rhizome cylindrical, to 1.5 cm long, 1.2 cm in diam. Roots filiform, to 2 mm in diam., white, contractile. Leaves slightly hysteranthous (vs. flowering in same year), main fresh rosette leaves usually 7–11, narrowly oblanceolate, to 17 cm long, to 1.8 cm wide, tapering to base, apex acute, with minute apiculus 0.6–1 mm long. Flowering stem terete, 11.5–27 cm long; peduncle ca. 10–25 cm long, scale-like leaves on peduncle narrowly (oblong-)lanceolate or narrowly deltoid, subherbaceous, smaller upward; pedicels 1–3 mm long, the lowermost sometimes bracteate; inflorescence racemose, narrowly ovoid or narrowly cylindrical, ca. 1.5–3 cm long, 1.2–1.5 cm in diam. Flowers 8–22, crateriform or funnelform, 4–7 mm across, facing upward or spreading horizontally, nodding at late anthesis. Tepals 6, narrowly oblong-elliptic or oblong-oblanceolate, 3.8–4.5 mm long, 1.2–1.6 mm wide, 3-veined, white, rose or red. Stamens 6, about equaling tepals; filaments 3–4 mm long; anthers unilocular, reniform, ca. 0.7–0.9 mm long. Pistil 1, 3–3.6 mm long, equaling or slightly shorter than stamens and tepals; ovary globose, 1.4–2 mm long, 1.8–2.3 mm across, trilobed, apex depressed in center; style 1.2–1.5(–2.6) mm long, slightly broadened distally; stigma

slightly trilobed, segments ca. 0.1–0.2 mm long, apex slightly depressed in center, 0.6–0.8 mm across. Fruit and seeds not seen.

**Additional specimens examined:**—CHINA. Guizhou. Lu-Tsoon-Kwan, Kweiyang [Guiyang], 15 April 1936, fl., S.W. Teng 90072 (A, IBK-139442\*, PE-00035449\*); Kouy-Tcheou [Guizhou], Pinfa, Kouy-yang, 8 Avril 1907, J. Cavalerie 3012 (lectotype of *Ypsilandra parviflora*, P-01724138\*).

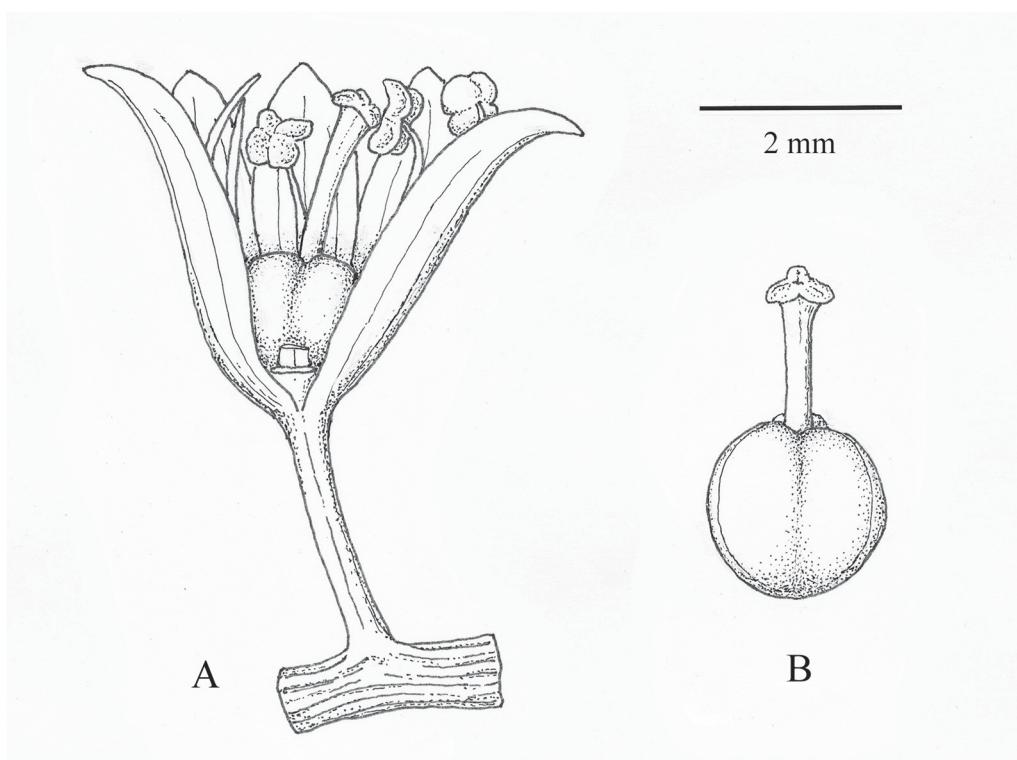
**Distribution:**—China (Guizhou) (Fig. 15-P).

**Habitat:**—Banks along streams at elevation 1450 m.

**Conservation status:**—The species is very local and the population size is supposedly small. Preliminarily assessed as DD according to the criteria set out in IUCN (2001).

**Flowering:**—March–April.

**Remarks:** Judging from the features of the style and stigma, *Helonias parviflora* appears to be most closely allied to *Ypsilandra cavaleriei* (Léveillé 1905), which was treated as a form with small flowers of *H. thibetica* (Tanaka 1998a: 106). *Helonias parviflora* (under the name of *Y. parviflora*) was once included in *Y. cavaleriei* (Chen 1980, Chen & Tamura 2000), but I recognize it as an independent species, in agreement with Wang & Tang (1943). *Helonias parviflora* is distinguishable from *Y. cavaleriei* by its smaller flowers with shorter tepals, stamens and pistils and by its shorter pedicels. In *H. parviflora* (Figs. 11, 12), both the pistil and the stamens are nearly as long as or slightly shorter than the tepals (i.e. not exserted beyond the tepals), and the stigma is 0.6–0.8 mm in diameter (S.W. Teng 90072, A) and slightly trilobed. In *Y. cavaleriei*, both the pistil and the stamens are normally exserted beyond the tepals at and after anthesis, and the stigma is smaller (ca. 0.3–0.45 mm in diameter) and discoid or subcapitate, not obviously trilobed. As far as images are examined, the following two specimens somewhat resemble *Helonias parviflora*. Details of the flowers (e.g. shape of the stigmas) are, however, unclear. Further closer (direct) examinations are needed to precisely identify the specimens: CHINA. **Guangxi.** Fong-tung, Yaoshan, elev. 1000–1200 m, 31 March 1930, S.S. Sin 9104 (PE-00035451\*!). **Hunan.** Xuan zhang, B.Q. Zhong 762 (PE-00593851\*!).



**FIGURE 12.** *Helonias parviflora* (S.W. Teng 90072, A). **A.** Pedicellate flower with frontal tepal and filament removed. **B.** Pistil. Drawn by Noriyuki Tanaka.

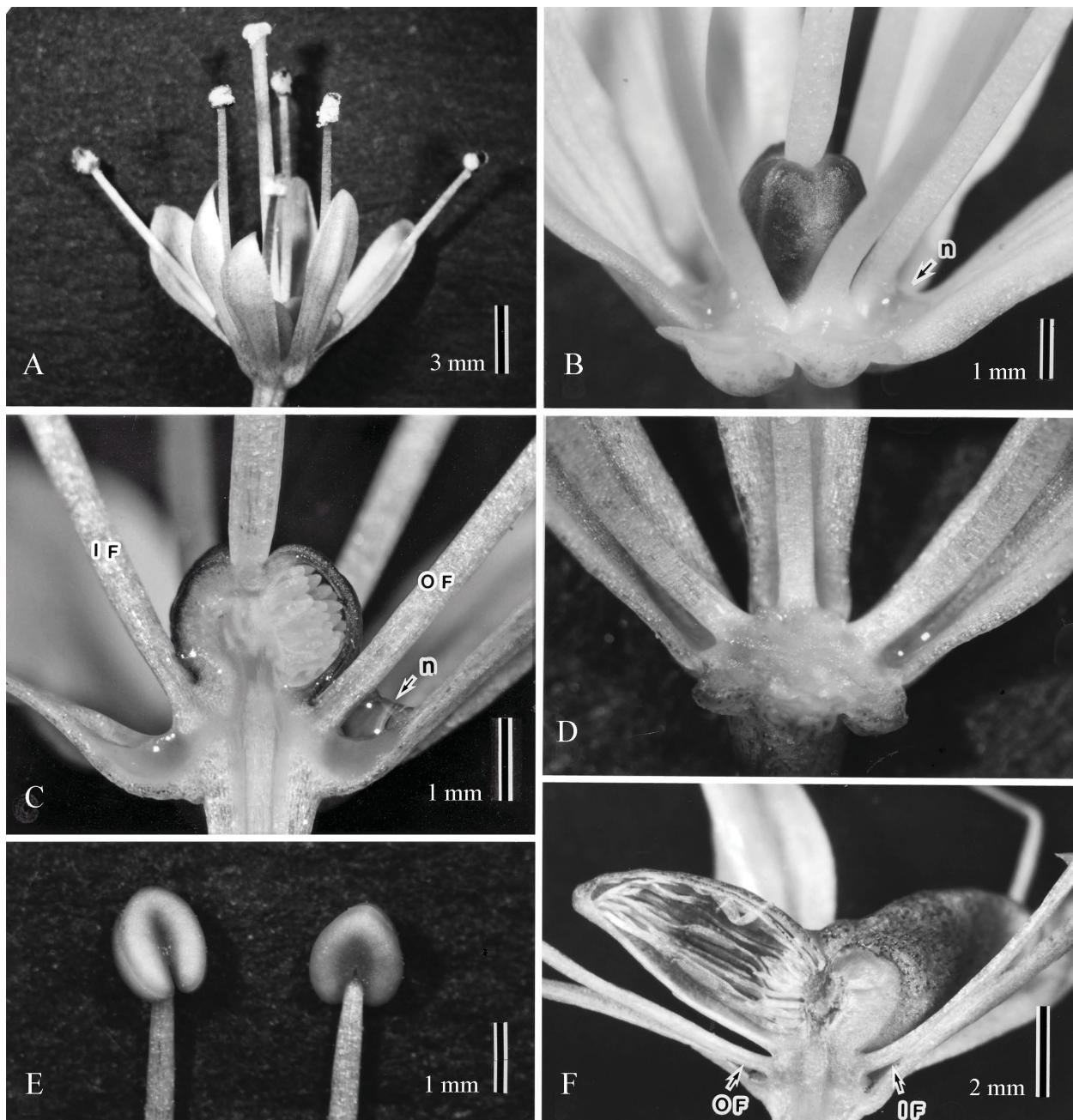
6. ***Helonias thibetica* (Franch.) Tanaka (1998a: 106)** (Figs. 1C, D, 3A–C, 13–14).

≡ *Ypsilandra thibetica* Franchet (1887–1888: 94, t. 17; 1888: 132, t. 17). **Type** (lectotype, designated here):—CHINA. Thibet Oriental [Sichuan]: Province de Moupin, Mars 1869, A. David s.n. (P-00282689\*!). Isolectotype: K-000400237\*!, P-00730550\*!, P-00730551\*!

- = *Ypsilandra cavaleriei* H.Lév. & Vaniot in Léveillé (1905: 375). **Type:**—CHINA. Kouy-Tchéou [Guizhou]: Environs de Tou-chan, dans la montagne, 3 Juin 1899, J. Cavalerie 2638 (Holotype: P-01724137\*! Isotype: E-00902989!, K-001235139!—both (in fruit) appear to be erroneously labeled as *Cavalerie 1291* that is in flower).
- = *Ypsilandra thibetica* Franch. var. *angustifolia* Wang & Tang (1943: 106). **Type:**—CHINA. Szechuan [Chongqing]: Su-tchuen oriental, Tchen-kéou-tin [Cheng-kou Xian], Juin, R.P. Farges 788 (non '188'). (Holotype: PE-00035458\*! Isotype: P-00730547-9\*!, P-00282693\*!, PE-00035457\*!, K-000400238\*!).
- =? *Ypsilandra kansuensis* Zhao & Peng (1987: 57, f. 1). **Type:**—CHINA. Gansu: Zhouqu Xian, Luojiayu, elev. 2060 m, 4 April 1980, Z.-J. Cao & R.-N. Zhao 550564 (Holotype Lzu n.v.). Paratype: CHINA. Gansu: Zhouqu Xian, Luojiayu, elev. 2000 m, 11 June 1982, R.N. Zhao 552501 (Lzu n.v.).



**FIGURE 13.** *Helonias thibetica* (material T-1). **A.** Young, slightly open flowers with protruding stigma (photo: 13 February 2014). **B.** Young flowers with anthers not yet dehiscent (19 February 2014). **C.** Flowers with dehiscent anthers and tepals turning creamy yellow (23 February 2014). **D.** Ripe fruits (5 April 2014). **E.** Same infructescence as D with dehiscing capsules exposing fertile seeds set by artificial selfing (3 May 2014). **F.** Rosette mostly of fresh leaves with young bud in center (14 August 2013). All photos taken at Hachioji, Tokyo.



**FIGURE 14.** *Helonias thibetica* (material T-1). **A.** Flower. **B.** Proximal part of flower with nectar (n) secreted from adaxial bases of tepals. Two frontal tepals removed. **C.** Vertical section of flower. **D.** Proximal interior of partial flower. **E.** Two anthers showing adaxial side (left) and abaxial side (right), respectively. **F.** Vertical section of capsule with persistent floral parts. IF; inner filament. OF; outer filament. n; nectar. Scale at C also for D.

**Chinese name:**—Yaruihua.

**Japanese name:**—Chibetto (*Tibet*)-shôjôbakama (*nov.*), Chûgoku-shôjôbakama (meaning Chinese *Helonias*).

**Description:**—Rhizome subcylindrical, closely annulate with many scars, to 7 cm long, to 1.7 cm in diam. Roots filiform, densely pubescent, to 1.5 mm in diam., white. Leaves hysteranthous, main fresh rosette leaves usually 6–13(–18), persistent for 1–2 years, spatulate, narrowly spatulate or oblanceolate, 7–20(–32) cm long, 0.7–2.5(–4) cm wide, tapering to linear petiole, apex acute or acuminate, apiculate, apiculus 0.3–1.3 mm long, moderately thick, soft, glossy (especially when young), entire, abaxial midvein raised. Flowering stem 6.3–21.5 cm long at anthesis, elongating to 52 cm in fruit; peduncle longitudinally ribbed, 4.5–7(–17) cm long at anthesis, to 36.3 cm long in fruit; scale-like leaves on peduncle several to many (to ca. 15; excl. basal ones), subulate, (narrowly) lanceolate, oblong or oblanceolate, to ca. 4 cm long, proximal scale-like leaves herbaceous, distal ones submembranous, apex acuminate or acute; inflorescence racemose, rachis 1.8–4.5 cm long at anthesis, becoming 5.8–15.7 cm long in fruit; pedicels

3.5–13 mm long at anthesis, 4–22 mm long in fruit, ebracteate, white, sometimes pale purplish, proximal few pedicels sometimes bracteate. Flowers 9–46, often secund, funnelform, ca. 0.8–2 cm across, strongly fragrant, protogynous. Tepals 6, ascending, spatulate, oblong-oblanceolate or narrowly elliptic, slightly canaliculate toward base, margins slightly revolute proximally, nectary at base slightly concave (or nearly flat), apex obtuse or subacute, 6.5–12 mm long, 1.6–3(–4.5) mm wide, 3–5(–7)-veined, white, sometimes pale cream or pinkish, turning yellowish to greenish at late and after anthesis; basal part slightly inflated abaxially. Stamens 6, usually exserted beyond tepals; filaments ascending, filiform, straight, (7)–11–15(–17.5) mm long, white; anthers basifix, ovate or elliptic-ovate, bilobed at base, rounded at apex, unilocular, white with purplish tint, grayish purple, or dark (bluish) purple, (0.8)–1.5–2.1 mm long, peltate at early stage of dehiscence; pollen (slightly purplish) white. Pistil 1, (8)–15–21 mm long, usually exceeding stamens and tepals; ovary globose or obovoid, trigonous, trisulcate, borne on short gynophore-like floral axis (receptacle), apex emarginate, depressed in center, 1.5–3 mm long, 1.5–3 mm across, (pale) green or pale brownish green; ovules numerous, usually 8- or 9-seriate on central axile placentae; style filiform, (5)–10–22 mm long, white or slightly purplish pink; stigma small, often only slightly broader than style, (depressed) capitate or discoid, unlobed, 0.3–1.2 mm across, white. Capsules broadly obpyramidal, broadly cordate laterally, tripartite, 3–6 mm in height, 5.5–14 mm across; lobes subconic or pyriform, obliquely or horizontally divergent, often slightly recurved distally. Seeds coated with whitish testa, narrowly fusiform, 4.5–7 mm long, 0.3–0.5 mm wide in middle, narrowly tailed at both ends; body of seed narrowly fusiform, light brown, 1–2 mm long, 0.3–0.4 mm wide.

**Additional specimens examined:**—CHINA. **Chongqing:** Nanchuan, elev. 2000 m, 9 May 1986, *Jinfoshan Kaocha-dui* 0127 (PE-01867400\*); Su-tchuen oriental, Tchen-kéou-tin, *R.P. Farges* s.n. (K-000400236\*). **Gansu:** *Bai-shui-jiang Caiji-dui* 4963 (PE-01823466\*); Dangchang Xian, elev. 3000 m, 25 July 1951, *T.P. Wang* 14561 (PE-00593854\*); Wen Xian, elev. 1600 m, 16 May 2007, *Bai-shui-jiang cajidui* 4963 (PE-01823466\*); locality unclear, 8500 ft, 16 May 1916, *R. Farrer & W. Purdom* 68 (E-00904006\*). **Guangdong:** Ruyuan, June 1933, fr., *X.P. Gao* 9117 (PE-00593853); Ruyuan, 29 April 1934, *S.P. Ko* 54199 (PE-00035448\*). **Guangxi:** Chuanhsien, 14 May, 1936, *Z.S. Chung* 81626 (PE-00593967\*); Rongshui Xian, elev. 1000 m, 2 May 1989, *Beijing dui* 892174 (PE-02018211\*); Xing'an Xian, 24 May 1979, *G.Z. Li* (IBK-188673\*). **Guizhou:** Jiangkou xian, 1100 m, 26 May 1964, *Zhang et al.* 400780 (PE-01318236\*); (Kouy-Tcheou) Pin-fa, montagnes, lieuz humides, 10 Mars 1909, fr., *J. Cavalerie* 1291 (E-00115518, E-00902989\*, P-00730553\*); (Kweichow) June 1905, *J. Esquirroll* 440 (E-00902988). **Hunan:** Hongjiang shi, 1954, *Li* 1723 (PE-00593855\*); Xinning Co., 1200 m, 6 April 1995, fl., *L.-B. Luo* 0601 (E-00071276\*, TNS); Xinning Xian, 800 m, March 1985, fl., *Luo* 2034 (PE-00593856). **Sichuan:** Leibo Xian, Zhongshan, 1400–1800 m, 9 June 1959, fr., *Z.T. Guan* 8432 (PE-00593934); Mt. Omi, *E.H. Wilson* 5221 (K); Omei-hsien, Mt. Omei, 2 May 1041, fr., *W.P. Fang* 16781 (A); ibid, 23 Mar. 1941, fl., *W.P. Fang* 18232 (A); ibid., 27 February 1940, fl., *W.P. Fang* 13849 (A-255367); Mt. Omei, Tachengssu, 2300 m, 19 May 1939, *H.C. Chow* 9825 (A); Tian-quan, 14 April 1953, *H.L. Tsiang* 33845 (PE-00593886); Tien-chuan-hsien, 2700 m, 25 May 1936, *K.L. Chun* 2649 (BM-001118046); Tien-chuan-hsien, 1360 m, 9 April 1936, *K.L. Chun* 2301 (BM-001118044, E-00904007\*); Western China. Limestone cliff, *E.H. Wilson* 4676 (K, TI); West Szechuen and Tibetan frontier, chiefly near Tachienlu, 9,000–13,500 ft, fl., *A.E. Pratt* 766 (BM-001118045; P-00282691\*). **Yunnan:** Ku-long-tchang, elev. 800 m, Fevrier, fl., *Maire* s.n. (L-1470205\*, P-01724143\*); Suijiang Xian, elev. 1600 m, *Z.H. Hu* 1351 (PE-18867402\*).

**Distribution:**—China: Chongqing, Gansu (S), Guangdong (NW), Guangxi (N, NE), Guizhou (Central, S), Hubei (SW), Hunan (S, W), Sichuan (Central, SE), Yunnan (NE) (some data based on literature) (Fig. 15-T).

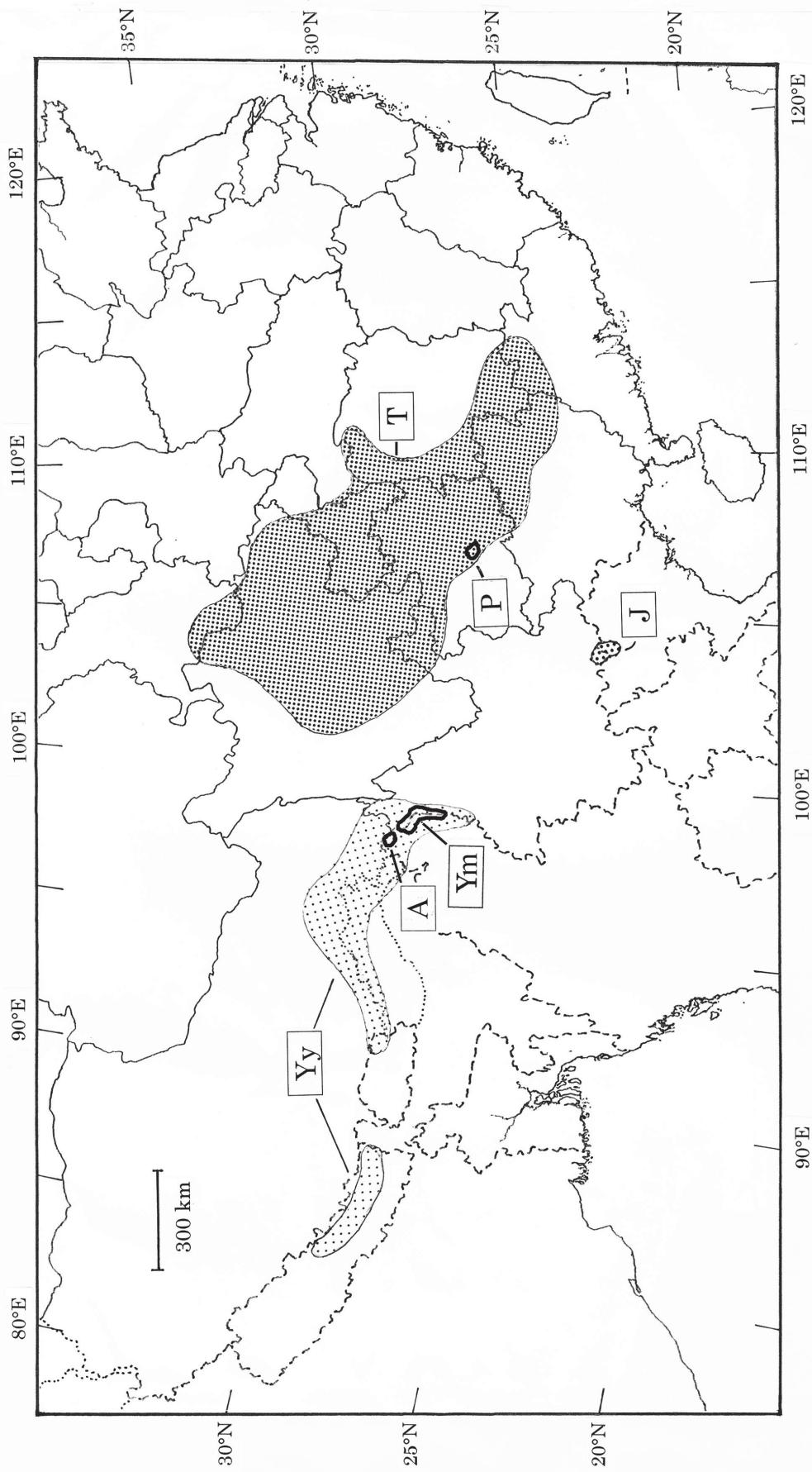
**Habitat:**—Shady moist slopes at elevations ca. 800–3000 m.

**Conservation status:**—The species is comparatively widespread, and assessed as LC according to the IUCN Red List Categories and Criteria (2001). However, local populations near human habitation may be more or less subject to disturbance and threats.

**Flowering:**—February–March.

**Ripening:**—May–June.

**Remarks:**—*Ypsilandra cavaleriei* was distinguished from *Y. thibetica* by Léveillé (1905), and this treatment was followed by Chen (1980) and Chen & Tamura (2000). In *Helonias thibetica*, specimens from the southern part of the range (Guizhou, Guangxi, Guangdong, and Hunan) tend to have somewhat smaller flowers than those from the northern part (Sichuan, including the type), and correspond to *Y. cavaleriei*. However, the specimens corresponding to *Y. cavaleriei* have no other particular difference from the typical form of *H. thibetica*. Chen (1980) and Chen & Tamura (2000) reported that the two species are distinguishable by the difference in the relative length of ovary lobes to the entire ovary. However, this proportion varies with the progression of flowering and fruiting, hence it seems inappropriate to apply this character for distinguishing them. Accordingly, it appears more reasonable to regard *Y. cavaleriei* as a local race of *H. thibetica*, as previously suggested in Tanaka (1998a). I have not yet seen any type



**FIGURE 15.** Approximate geographic ranges of five species of subsect. *Ypsilandra* in Asia. A. *H. alpina*. J. *H. jinpingensis*. P. *H. parviflora*. T. *H. thibetica*. Ym: *H. yunnanensis* var. *mesosyla*. Yy: *H. yunnanensis* var. *yunnanensis*.

material of *Ypsilandra kansuensis*, but a specimen collected by Farrer and Purdom (no. 68, E-00904006\*!) in Gansu province, China, may represent it. *Ypsilandra kansuensis* differs from *Helonias thibetica* by its stamens equaling (vs. exceeding) the tepals. There seem to be no other particular features characterizing it. To more clearly elucidate their relationship, it is desirable to study variation of their stamen length based on more samples especially from regions near the type locality of *Y. kansuensis*. The occurrence of *Helonias thibetica* in Taiwan was recently reported by Hsu *et al.* (2011, under the name of *Ypsilandra thibetica*). The plant is, however, not *H. thibetica*, but appears to be a form of *H. umbellata*. For further notes on this form see the remarks under *H. umbellata*.

**Subsect. 2. *Heloniopsis*.** Type:—*Helonias orientalis* (Thunb.) N.Tanaka (≡ *Scilla orientalis* Thunb., = *Heloniopsis pauciflora* A.Gray).

≡ *Hexonix* Rafinesque (1837, as ‘1836’: 13), *nom. rejic.* vs. *Heloniopsis* Gray (1859) (*nom. cons.*). ≡ *Kozola* Rafinesque (1837, as ‘1836’: 25), *nom. rejic.* vs. *Heloniopsis* Gray (1859) (*nom. cons.*). Basionym of types:—*Scilla japonica* Thunb.

= *Sugerokia* Miquel (1866: 24). Type:—*Sugerokia japonica* Miq.

= *Heloniopsis* Gray (1859: 416), excl. charact. seminum, *nom. cons.* Type:—*H. pauciflora* A.Gray.

**Japanese name:**—Shôjôbakama assetsu.

**Species included:**—6; *Helonias breviscapa*, *H. kawanoi*, *H. koreana*, *H. leucantha*, *H. orientalis*, *H. umbellata*.

**Description:**—Leaves persisting for 1 to 2 years. Inflorescences racemose or (sub)umbellate. Flowering usually in spring, rarely summer to autumn (*H. kawanoi*). Tepals pink, purplish pink, purple or white, distinct or connate basally to adjoining tepals, adaxial surface slightly to markedly canaliculate toward base, proximal submarginal portions more or less raised or ridged, sometimes winged (lamellate). Nectary at base of tepal slightly or moderately concave or tubular. Filaments distinct or adnate basally to opposing tepals. Inner filaments not adnate to ovary. Anthers adaxially affixed to filament at or close to base of connective (i.e. basifixated or [sub]dorsi-basifixated), extrorse, appearing bilocular, usually with vestigial apical confluence between thecae. Stigma discoid or (sub)capitate, sometimes slightly trilobed.

**Distribution:**—Japan, Korea, Russia (S Sakhalin), Taiwan (Figs. 29, 31-3-4, 32-3-4).

**Remarks:**—*Helonias* subsect. *Heloniopsis* consists of two series, *H. ser. Umbellatae* and *H. ser. Heloniopsis*. Several of their characters are compared in Table 7. A key to the series is below.

**TABLE 7.** Comparison of *H. series Umbellatae* and *Heloniopsis*.

Character	Ser. <i>Umbellatae</i>	Ser. <i>Heloniopsis</i>
Leaves		
Apical apiculus	somewhat prominent	moderate
Flowering	Jan.–Mar., or Aug.–Oct. ( <i>H. kawanoi</i> )	Mar.–May.
Inflorescence (at anthesis)	racemose or (sub)umbellate	(sub)umbellate
Proximal submarginal portions of tepal	raised or ridged	winged (lamellate) inward
Proximal adnation between tepal and opposing filament	absent	present
Basal connation between adjoining tepals	u. absent (s. present in <i>H. umbellata</i> )	present
Nectary	sl. or mod. concave	(sub)tubular-saccate

Abbreviations: mod.—moderately. s.—sometimes. sl.—slightly. u.—usually.

#### Identification key to the series of *H. subsect. Heloniopsis*

1. Proximal submarginal portion of tepals raised or ridged, not winged; tepals distinct, or rarely minutely connate at base with adjacent tepals, not adnate to opposing filament; nectary at base of tepal slightly or moderately depressed; Taiwan and Japan (Nansei Islands, incl. Ryukyus) ..... Ser. 1. *Umbellatae*
- Proximal submarginal portions of tepal winged; tepals connate basally, adnate to opposing filament to form a sheathing nectary; Japan, Korea, E Russia (S Sakhalin) ..... Ser. 2. *Heloniopsis*

#### Ser. 1. *Umbellatae* N.Tanaka, *ser. nov.*

Type:—*Helonias umbellata* (Baker) N.Tanaka (≡ *Heloniopsis umbellata* Baker).

**Japanese name:**—Hime-shôjôbakama retsu.

**Species included:**—3; *H. kawanoi*, *H. leucantha*, *H. umbellata*.

**Description:**—Leaves thin to moderately thick, persisting for 1 to 2 years, margins entire or sometimes minutely undulate, apex prominently apiculate. Inflorescences racemose or (sub)umbellate; pedicels ebracteate, or bracteate

(*H. kawanoi*). Flowers 1–many, funnelform or campanulate, nodding, or variously oriented, fragrant or sometimes odorless. Tepals pink or white, usually free to base, adaxial surface slightly to prominently canaliculate toward base, proximal submarginal portions more or less raised (or ridged), occasionally slightly connate with adjoining tepals (*H. umbellata*), nectary at adaxial base slightly or moderately concave, abaxial basal part slightly or moderately gibbous. Filaments free to base, positioned at or close to adaxial rim of nectary of opposing tepal. Anthers affixed adaxially to filament at or close to base of connective (i.e. basifixated or somewhat dorsi-basifixated), apparently bilocular with rudimentary apical confluence between thecae. Stigma discoid, sometimes slightly trilobed. Flowering January to March or late summer to autumn (*H. kawanoi*).

**Distribution:**—SW Japan (Nansei Isl., incl. Ryukyus), Taiwan (Fig. 29-Ka, -L, -U, 31-3, 32-3).

**Remarks:**—All the members of *Helonias* ser. *Umbellatae* are insular (e.g. Fig. 29), implying that they are relict descendants of ancestral populations that were once more widespread over land now under the sea. The seeds of *Helonias* can be dispersed by wind, but it is quite improbable that they disperse far beyond a vast sea or strait. Several characters of the three species of *H. ser. Umbellatae* are compared in Table 8; a key to distinguish the species is below.

**TABLE 8.** Comparison of three species of *H. ser. Umbellatae*.

Character	<i>H. kawanoi</i>	<i>H. leucantha</i>	<i>H. umbellata</i>
<b>Leaf</b>			
Length (cm)	2–7	10–31	7–16
Width (cm)	0.5–1	2–4	1–2.2
Adaxial surface	dull to subglossy	glossy	glossy
Thickness (texture)	thin	thick	thick
Flowering	u. l. Aug.–Oct.	u. l. Dec.–m. Mar.	u. l. Jan.–Mar.
Inflorescence	(sub)umbellate or (sub)racemose	(compact) racemose	u. umbellate, r. racemose
<b>Flower</b>			
Shape	funnelform	campanulate	funnelform
Tepal			
Length (mm)	4–8	9.5–16.5	8–12
Color	pink or white	white, s. pale lilac	u. pink, s. white
Basal connation between adjoining tepals	absent	absent	s. slightly present
Anter length (mm)	0.5–1.6	1.0–2.5(–3.3)	1.3–3.0
Seed (incl. testa) length (mm)	2.5–3.3	4.5–5.8	3.4–5.0

Abbreviations: e.—early. l.—late. m.—mid. r.—rarely. s.—sometimes. u.—usually.

### Identification key to the species of *H. ser. Umbellatae*

1. Leaves usually less than 7 cm long, 1 cm wide; flowering usually August to October; flowers 1–4(–9) per scape; tepals usually less than 8 mm long; seeds (incl. testa) 2.5–3.3 mm long ..... 7. *H. kawanoi*
- Leaves usually more than 7 cm long and 1 cm wide; flowering usually January to March; flowers usually more than 5 per scape; tepals usually more than 8 mm long; seeds (incl. testa) 3.4–5.8 mm long ..... 2
2. Leaves usually to 16 cm (sometimes to 31 cm long), 4 cm wide; inflorescence usually compactly racemose, often slightly drooping distally; flowers to ca. 36 per scape, narrowly campanulate, nodding, odorless or faintly fragrant; tepals narrowly elliptic or narrowly oblong-elliptic, acuminate or acute, white, sometimes pale purplish pink (or lilac), often turning pale pink at late anthesis, usually to 16.5 mm long, usually slightly imbricate proximally; seeds 4.5–5.8 mm long ..... 8. *H. leucantha*
- Leaves to 16 cm long, 2.2 cm wide; inflorescence (sub)umbellate, rarely racemose; flowers to ca. 21 per scape, facing various directions or often nodding, funnelform, strongly fragrant; tepals narrowly oblanceolate or oblong-oblanceolate, usually obtuse, pink or white, usually to 12 mm long, scarcely imbricate proximally; seeds 3.4–5 mm long ..... 9. *H. umbellata*

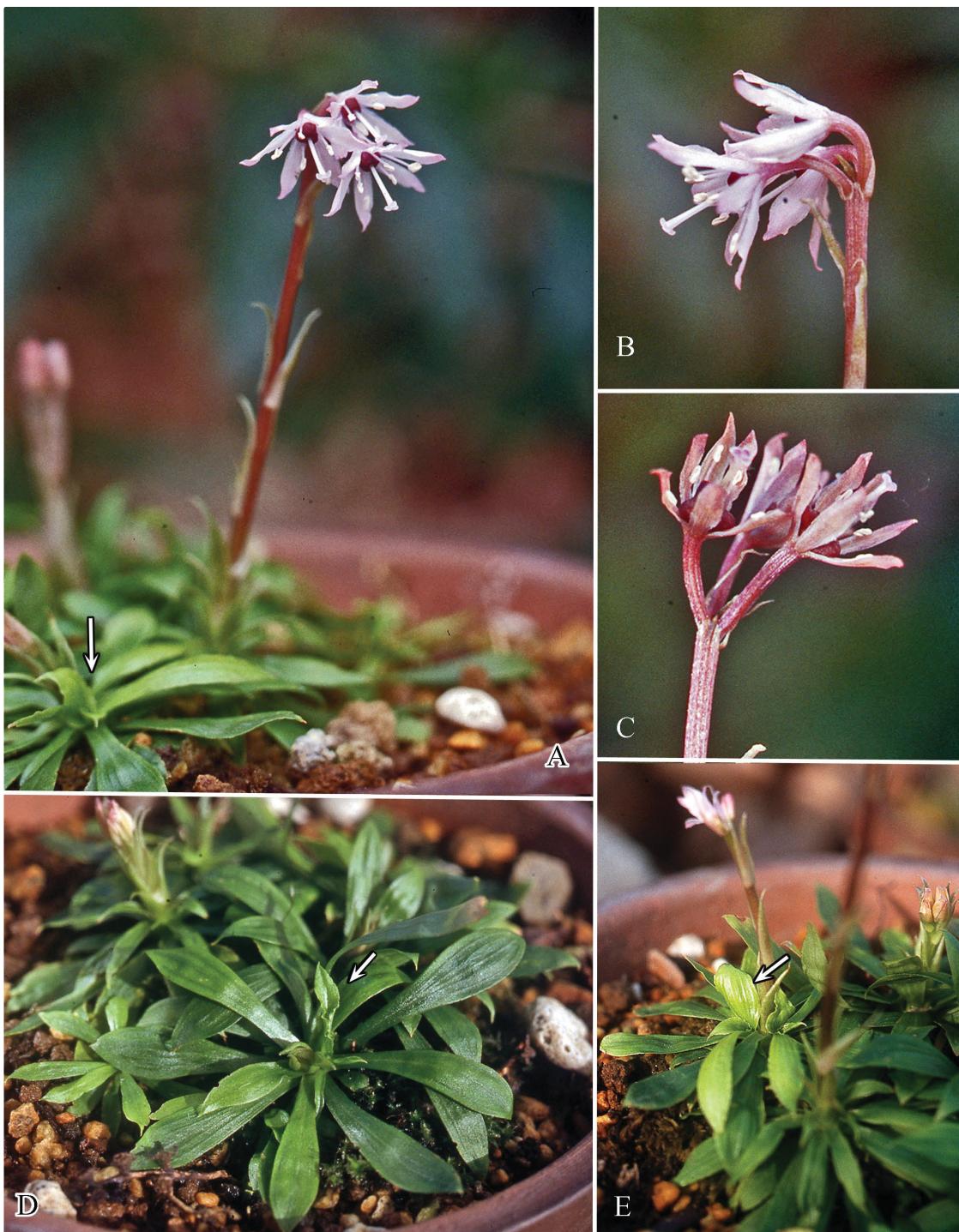
### 7. *Helonias kawanoi* (Koidz.) Tanaka (1998a: 109) (Figs. 16, 17).

≡ *Sugorokia kawanoi* Koidzumi (1937: 46). **Type:**—JAPAN. Loochoo [Ryūkyū, Okinawa Pref.]. Insula Irumti [Iriomote I.], ad Urautigawa, 6 Jun. 1923, G. Koidzumi s.n. (Holotype: KYO n.v.; photo in TNS!). ≡ *Heloniopsis kawanoi* Koidzumi (1937: 46). ≡ *Hexonix kawanoi* (Koidz.) Wang & Tang (1949: 113).

— *Heloniopsis orientalis* (Thunb.) Tanaka var. *yakusimensis* auct. non (Masam.) Ohwi: Masamune (1957: 103), p.p.

— *Heloniopsis umbellata* auct. non Baker: Hatusima (1971: 786; 1975: 786); Hatusima & Amano (1977: 198).

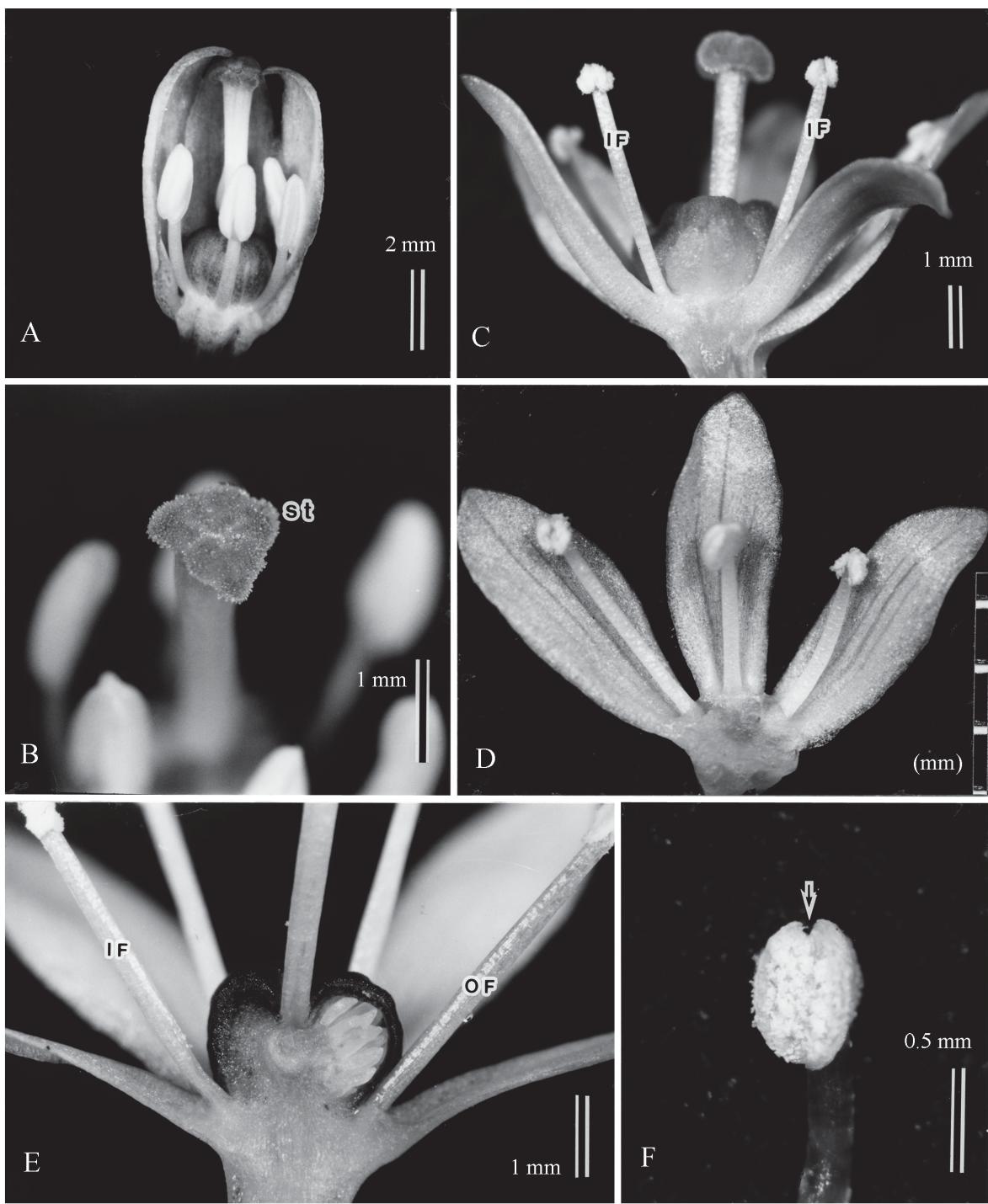
— *Heloniopsis kawanoana* Koidz. in Sakaguchi (1924: 86), nom. inval.



**FIGURE 16.** *Helonias kawanoi* (material Ka-3). A–C; one and same plant. A. Flowering plants with sprouting fresh leaves (arrowed) (photo: 3 December 2014). B. Umbellate flowers (4 December 2014). C. Ascending flowers after anthesis (19 December 2014). D, E. Rosettes with sprouting leaves (arrowed) and flowering stems (D on 15 November 2014; E on 19 December 2014). All photos taken at Hachioji, Tokyo.

**Japanese name:**—Ko-shôjôbakama (Koidzumi 1937), Okinawa-shôjôbakama (Sakaguchi 1924).

**Description:**—Rhizome subcylindrical, to 7 mm long, to 3 mm in diam. Roots filiform, ca. 0.5 mm in diam., ramose, white. Leaves many, narrowly oblanceolate or spatulate, 2–7 cm long, 0.5–1 cm wide, base narrowly cuneate, margin entire or occasionally slightly minutely undulate at margin, apex acute or short acuminate with apiculus at 0.8–1.5 mm long, light green, subglossy (when young) or dull, thin in texture, midvein and parallel veins usually slightly raised adaxially, persistent for 1–2 years. Flowering stem upright: peduncle usually 6–12 cm long at anthesis, elongating to 18.5 cm long (incl. plants in cultivation) in fruit, slender, 0.7–2.5 mm in diam. in middle, ribbed; scale-



**FIGURE 17.** *Helonias kawanoi* (A, B, E: material Ka-3. C, D, F: material Ka-1). A. Young slightly open flower with anthers not yet dehiscent. Three frontal tepals removed. B. Closeup of densely papillate stigma (st) of same flower as A. C. Flower with frontal tepal and stamen removed. D. Interior of partial flower. E. Vertical section of flower. F. Dehisced anther with apical confluence between thecae (arrowed), side view. IF; inner filament. OF; outer filament.

like leaves on peduncle 4–17(–24) (excl. basal ones), narrowly lanceolate or subulate, to 2 cm long, to 4 mm wide, acute or acuminate, membranous or subherbaceous, basal ones herbaceous; inflorescence (sub)umbellate or sometimes (sub)racemose; pedicels 3–12 mm long (incl. in fruit), ribbed, usually pale pink, bracteate at base. Flowers 1 to 4(–9) (incl. plants in cultivation), funnelform, 7.5–14 mm across, usually nodding, faintly fragrant, protogynous. Tepals 6, obliquely expanded, narrowly oblong-elliptic or (oblong-)oblanceolate, 4–8.4 mm long, 1.5–3 mm wide, apex acute to obtuse, sometimes recurved distally, veins (3 or) 5, white or pink, adaxially slightly canaliculate toward base, proximal submarginal portions slightly raised, margin slightly revolute, little or slightly imbricate with adjoining tepals

proximally, nectary on adaxial base slightly concave; abaxial base slightly gibbous; base of tepal affixed to receptacle (apex of pedicel) for ca. 0.5–0.6 mm in length. Stamens 6, subequaling tepals, obliquely expanded; filaments filiform, straight, 2–5.5 mm long, white or pink; anthers adaxially basifix, slightly exsert, ovoid, 0.5–1.6 mm long, base sagittate, bilocular with trace of apical confluence between thecae, white, pale cream or pale lilac; pollen white or pale cream. Pistil 1, 5–7.8 mm long, usually slightly exceeding, sometimes equaling or slightly shorter than tepals; ovary subglobose or obovoid, 1.3–3 mm long, 1.8–3.2 mm across, slightly trigonous, trisulcate, apex emarginate-concave, pale green, dull pink or dirty dark reddish brown; style erect, terete, often slightly broadened above, 2.1–5.2 mm long, white or pink; stigma discoid or slightly trilobed, 0.7–2 mm across, white, sometimes slightly tinged purple. Capsules obpyramidal (obcordate laterally), 3.5–4.5 mm long, 3.5–5 mm across, trifid or tripartite, apex emarginate-depressed in center; lobes subconic, ascending, apex obtuse. Seeds many, linear-fusiform, 2.5–3.3 mm long, 0.2–0.3 mm wide, testa whitish, proximally caudate-sublinear, distally acicular; body of seed narrowly oblong, 1–1.4 mm long, 0.2(–0.3) mm wide, brown.

**Additional specimens examined** (see also Tanaka 1998a):—JAPAN. **Kyūshū**. Kagoshima Pref., Amami-ōshima Isl.: Yuwandake, 20 May 1951, T. Amano 6500 (RYU-25059). **Okinawa**. Okinawa Pref., Miyako Isl.: 9 August 1894, T. Ito 1202 (TNS-60738). Okinawa Isl.: Kunigami, Aha, Tanaga-Gumui, elev. 100 m, 24 June 1955, fr., S. Hatusima 18309 (L-1455529\*, TI). Iriomote Isl.: 26 October 1973, fr., M. Furuse 4414 (MAK-141694, RYU-17010); near Nakaragawa Riv., 12 August 1894, T. Ito 1458 (TNS-60736, -60737); Gozadake, 250 m, 26 December 1963, fr., T. Yamazaki (TI, RYU-27147). Ishigaki Isl.: Omoto-dake, August 1922, fl., S. Sakaguchi 31 (MAK-138905).

**Distribution:**—SW Japan, Nansei Isl. (incl. Ryūkyū Isl.). Kagoshima Pref.: Amami-ōshima, and Tokunoshima Isl.. Okinawa Pref.: Okinawa, Miyako, Ishigaki, and Iriomote Isl. (Fig. 29-Ka).

**Habitat:**—Shady or semishady moist mossy rocks along streams in forests at elevations ca. 80–400 m.

**Conservation status:**—Assessed by the Environment Agency of Japan (2000) as VU on the basis of the criterion E in IUCN (1994). Deforestation and road construction are regarded as threats to the species.

**Flowering:**—Usually (late June–)August–November(–January). Sometimes also to February or even to March under cultivation.

**Ripening:**—Usually October–December(–February). Sometimes to June.

**Remarks:**—*Helonias kawanoi* is a small, highly specialized plant with small, somewhat thin leaves, 1 to few flowers (Fig. 16A–C) blooming in late summer to autumn (even in winter in cultivation in Tokyo), and bracteate pedicels and smaller (shorter) seeds. In many temperate vernal species, such as *H. bullata* (Fig. 1A), *H. orientalis* (Fig. 1B) and *H. thibetica*, newly formed flower buds remain dormant during cold weather (Fig. 2). In contrast, in *H. kawanoi* such dormancy appears to have been (nearly) lost, since flowering is principally in autumn (Fig. 2). This feature may have been acquired as an adaptation to warm climates. *Helonias kawanoi* shares some character states with *H. umbellata*. It often has an umbel of obconic or funnelform, white or pink flowers (Fig. 16A, B) like *H. umbellata* (Fig. 21A–C).

#### 8. *Helonias leucantha* (Koidz.) Tanaka (1998a: 107) (Figs. 18–20).

≡ *Sugorokia leucantha* Koidzumi (1937: 46). **Type:**—JAPAN. Loochoo [Ryūkyū, Okinawa Pref.]. Insula Utchina [Okinawa I.]; Kunchan, Hetona, Abagawa, Yonagawa, Katena, Taniwadake, Ajagawa, T. Sonohara (Syntype in KYO; photo of a syntype from Abagawa in TNS-320909!). ≡ *Heloniopsis leucantha* Koidzumi (1937: 46). ≡ *Hexonix leucantha* (Koidz.) Wang & Tang (1949: 114).

**Japanese name:**—Ô-shiro-shôjôbakama (Koidzumi 1937).

**Description:**—Rhizome subcylindrical, stout, to 2 cm long, 1.5 cm in diam. Roots filiform, ca. 1 mm in diam., white. Leaves persistent for 1–2 years, narrowly oblanceolate or spatulate, 10–31 cm long, 2–4 cm wide, base cuneate, apex acuminate or acute, with apiculus 0.7–2 mm long, somewhat thick in texture, glossy, abaxial midvein slightly raised, adaxially veins indistinct. Flowering stem to 27 cm long (incl. inflorescence); peduncle fistular, 5–25 cm long, 3–8 mm in diam. in middle, light green; scale-like leaves on peduncle usually 5–12 (excl. basal ones), narrowly lanceolate or subulate, to 3.8 cm long, becoming smaller upward, acute, involute, whitish or pale green, submembranous; inflorescence a short compact raceme, rachis to ca. 3.5 cm long, often slightly drooping distally; pedicels decurved at anthesis, 6-ribbed, to 11 mm long at anthesis, to 20 mm long in fruit, white, ebracteate. Flowers 4–36, often secund, nodding, (tubular-)campanulate, odorless or sometimes faintly fragrant, protogynous. Tepals 6, narrowly oblong or narrowly elliptic-oblong, 9.5–16.5 mm long, 2–6.5 mm wide, apex acute, recurved distally, silky white, sometimes pale lilaceous, turning pale pink with progression of anthesis, adaxially canaliculate toward base, proximal submarginal portions raised, proximal margins narrowly and slightly revolute, often slightly imbricate, basal nectary saccate adaxially; abaxial base slightly gibbous; base of tepal affixed to receptacle (apex of pedicel) for ca.



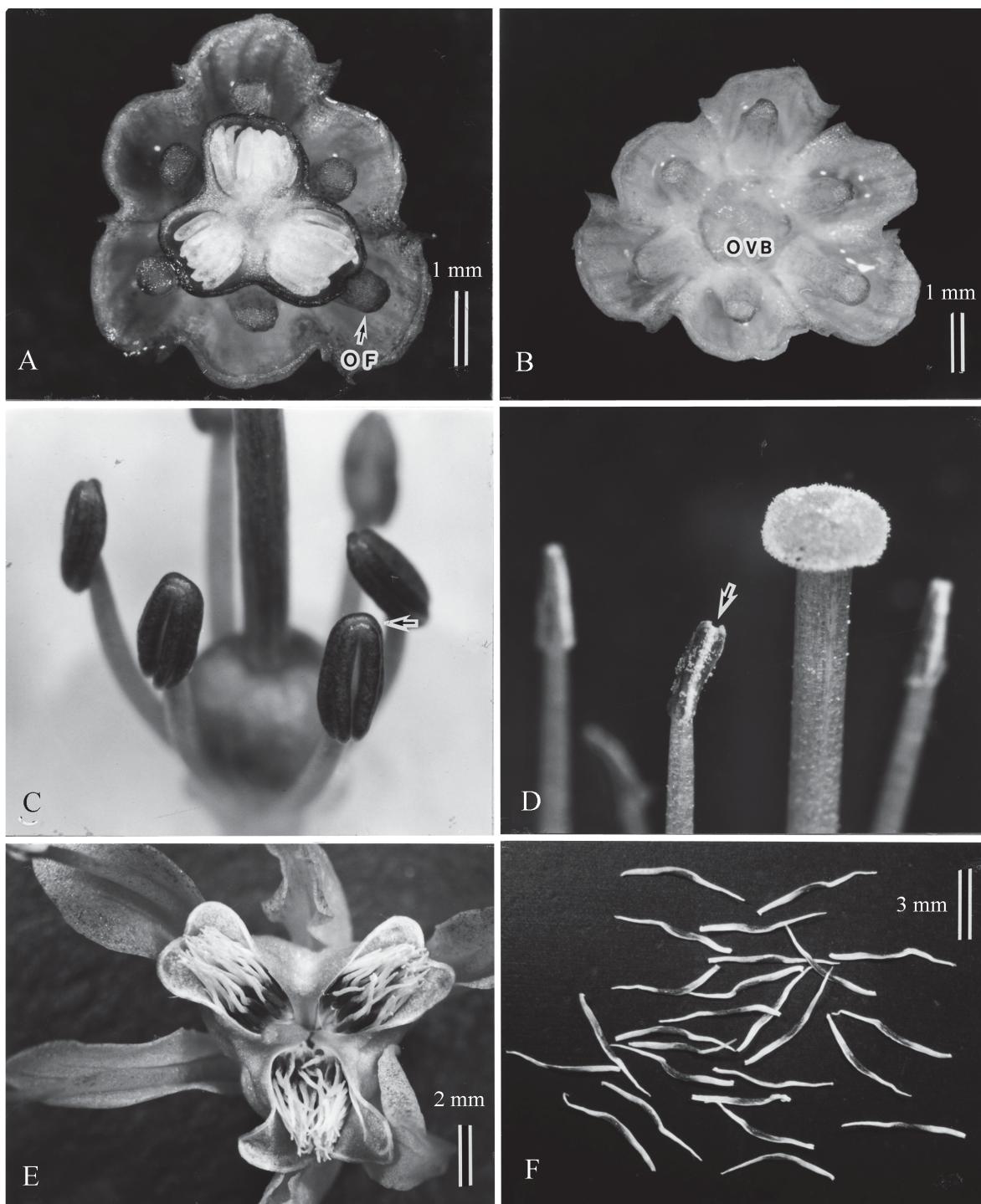
**FIGURE 18.** *Helonias leucantha*. A, B, E–G: material L-4. C, D: L-2. **A.** Flowering plant (photo on 24 January 2015). **B.** Raceme from plant in A (24 January 2015). **C.** Young slightly open flowers with protruding stigmas (21 January 2013). **D.** Raceme of pale purplish pink flowers (3 February 2013). **E.** Infructescence with dehiscing capsules (30 April 2012). **F.** Rosette with flower bud (long arrow) and sprouting small fresh leaves (short arrow) (19 December 2014). **G.** Plant with fresh green leaves and yellowish leaves developed in preceding year (arrowed) (14 August 2014). All photos at Hachioji, Tokyo.

1–1.2 mm in length. Stamens 6, usually exserted beyond tepals; filaments from adaxial rim of nectary of opposing tepal, filiform-subulate, 4.4–18.5 mm long, base slightly dilated and complanate, white or pale lilaceous; anthers narrowly ovoid or ellipsoid, 1–2.5(–3.3) mm long, base sagittate, apex obtuse, virtually bilocular, with vestigial apical confluence between thecae, basifixated adaxially, extrorse, pale to dark (bluish) purple; pollen whitish. Pistil 1, usually exceeding stamens and tepals; ovary globose or obovoid, slightly trilobed, 2.5–3 mm long, 3–3.7 mm across, apex emarginate-concave, yellowish green, dull dark purple, or dull dark purplish green, often with short stipe (gynophore)

to 0.6 mm long; style terete, strict, 4.5–14.5 mm long, pale purple or purplish pink; stigma densely papillulate, discoid, depressed capitate or hemispheric, often obtusely trigonous or slightly trilobed, 1.3–2.2 mm across, 0.7–1.2 mm thick, white, light purple or dark purplish pink; ovules numerous, multiseriate on central axile placentae. Capsules obpyramidal, obocordate in lateral aspect, apex depressed in center, tripartite, 8–9 mm long, 8–12 mm across, lobes mitriform, divergently protruding subdistally. Seeds sublinear or narrowly fusiform, testa whitish, proximally caudate, distally acicular, 4.5–5.8 mm long, 0.25–0.3 mm wide; body of seed oblong-fusiform, 1–1.5 mm long, 0.2 mm wide, (dark) brown.



**FIGURE 19.** *Helonias leucantha*. **A.** Flower (material L-1). **B.** Proximal interior of flower with frontal tepals and stamens removed (L-3). **C.** Vertical section of flower (L-1). **D.** Interior of partial flower (L-1). **E.** Proximal interior of partial flower (L-2). IF; inner filament. Scale at B also for C.



**FIGURE 20.** *Helonias leucantha*. **A.** Proximal part of flower, cross section (L-2). **B.** Proximal part of flower with ovary removed, cross section (L-2). **C.** Indehiscent anthers with rudimentary apical confluence between thecae (arrowed) (L-2). **D.** Distal part of pistil and dehisced anthers with rudimentary apical confluence between thecae (arrowed) (L-2). **E.** Dehiscing capsule with persistent floral parts (L-4). **F.** Seeds (L-4). OF; outer filament. OVB; base of ovary. Scale at A also for C and D.

**Additional specimens examined** (see also Tanaka 1998a):—JAPAN. Okinawa Pref. Okinawa Isl.: Kunigami-gun, Ôgimi-son, 16 August 1951, T. Amano 6331 (TNS-129705); Haneji-son, Makiya-ku, 29 November 1954, M. Nakamine 322 (RYU-41828; TNS-116547, 116548). Iriomote Isl.: Urauchi Riv., 150 m, 13 June 1971, T. Yamazaki (TI). Ishigaki Isl.: August 1958, Y. Niiro (RYU-19301).

**Distribution:**—SW Japan, Nansei Islands (incl. Ryûkyû Isl.). Kagoshima Pref.: Tokunoshima Isl. (Hatusima 1986). Okinawa Pref.: N Okinawa, Ishigaki, and Iriomote Isl. (Fig. 29-L).

**Habitat:**—Shady moist rocks and slopes near or along streams in forests at elevations 120–400 m.

**Conservation status:**—Assessed by the Environment Agency of Japan (2000) as EN on the basis of the criterion E in IUCN (1994). Deforestation and dam construction are regarded as main threats to the species.

**Flowering:**—Late December–mid March.

**Ripening:**—April–May.

**Remarks:**—*Helonias leucantha* is most closely allied to *H. umbellata* (e.g. Figs. 21, 22), from which it differs by its usually larger leaves (Fig. 18D), nodding tubular-campanulate flowers (Figs. 18A–D, 19A), narrowly oblong-elliptic tepals imbricate proximally (Figs. 19A, D), and somewhat smaller anthers (Fig. 19A, D). The tepals are usually white, but turn pale pink or purplish pink as flowering proceeds. Flowering of *Helonias leucantha* slightly precedes ser. *Heloniopsis*, and this may be due to the warm, maritime climate of the Nansei Islands where it occurs. Cernuous, campanulate, often scarcely fragrant flowers of *Helonias leucantha* are supposed to have originated in response to pollinators (Tanaka 1997d).

**9. *Helonias umbellata* (Baker) Tanaka (1998a: 108) (Figs. 3D, E, 21, 22).**

- = *Heloniopsis umbellata* Baker (1874: 278, ‘*Heleniopsis*’; 1879: 460). ≡ *Sugerokia umbellata* (Baker) Koidzumi (1930: 95). ≡ *Hexonix umbellata* (Baker) Wang & Tang (1949: 114). **Type:**—TAIWAN (Formosa). *R. Swinhoe s.n.* (Holotype: K-001045008\*!).
- = *Heloniopsis acutifolia* Hayata (1920: 144, f. 53). ≡ *Sugerokia acutifolia* (Hayata) Koidzumi (1930: 95). Japanese name: Taiwan-shōjōbakama (Koidzumi 1930). ≡ *Hexonix acutifolia* (Hayata) Wang & Tang (1949: 113, ‘*acutiflora*’). **Type:**—TAIWAN. [Ilan Hsien] Bonbonzan, 10 May 1917, B. Hayata & S. Sasaki (Holotype: TI!).
- = *Heloniopsis arisanensis* Hayata ex Honda (1938: 1679). ≡ *Sugerokia arisanensis* (Hayata ex Honda) Koidzumi (1939: 53). ≡ *Hexonix arisanensis* (Hayata ex Honda) Wang & Tang (1949: 114), (‘*Hayata*’). **Type:**—TAIWAN. [Chiayi Hsien] Arisan [Alishan], 2500 m, Junio 1914, U. Faurie 942 (Holotype: TI!. Isotype: BM-1118049!; P-01762777\*!).
- = *Heloniopsis taiwaniana* Ying (1980: 222, f. 108 on p.67). **Type:**—TAIWAN. Taipei Hsien, Urai, Mt. Tatungshan, 20 April 1976, S.S. Ying 3615 (Holotype: NTUF-F00008243\*!).
- *Heloniopsis orientalis* (Thunb.) Tanaka var. *yakusimensis* auct. non (Masam.) Ohwi: Masamune (1957: 103), p.p.
- *Ypsilandra thibetica* auct. non Franch.: Hsu *et al.* (2011: 99–104).

**Chinese name:**—(Taiwan) humahua.

**Japanese name:**—Hime-shōjōbakama (Hayata 1917), Arisan-shōjōbakama (Honda 1938), Shima-shōjōbakama (Kawakami 1910).

**Description:**—Rhizome subcylindrical, to 1.7 cm long, 1 cm in diam. Roots filiform, ca. 1 mm in diam. Leaves persistent for 1–2 year, narrowly spatulate or oblanceolate, 7–16 cm long, 1–2.2 cm wide, tapering to linear petiole to ca. 6 mm wide, margin entire (not undulate), apex short acuminate or obtuse, apiculus (0.5–)1–2 mm long, somewhat thick in texture, green, glossy, midvein raised abaxially. Flowering stem erect, fistulose, ca. 2–17 cm long at anthesis, elongating to ca. 29 cm long in fruit; peduncle 2–20(–28) cm long incl. in fruit, 1.5–5.5 mm in diam. in middle; scale-like leaves on peduncle 4–10 (excl. basal ones), narrowly elliptic or oblong, acuminate, to 23 mm long, submembranous; inflorescence umbellate or sub-umbellate, rarely racemose, rachis usually to 1.1 cm long (excl. raceme); pedicels ribbed, (3–)6–14(–18) mm long, whitish, sometimes tinged pink, ebracteate, 1 or a few proximal pedicels sometimes bracteate. Flowers 1–21, funnelform, often secund, strongly fragrant, protogynous. Tepals 6, oblong-oblanceolate or spatulate, 8–12 mm long, 2–3.7 mm wide, apex obtuse to acute, 3- or 5-veined, white or pale pink, not imbricate with adjoining tepals proximally, adaxially canaliculate toward base; proximal margins usually slightly revolute; proximal submarginal portions raised (ridged), sometimes minutely connate basally to adjoining tepals (connate portion to 0.3 mm in height); nectary at base concave adaxially; base of tepal affixed to receptacle (apex of pedicel) for ca. 1 mm in length. Stamens 6, equaling or slightly longer than tepals, obliquely divergent; filament arising from (adaxial) rim of nectary of opposing tepal, filiform, proximally scarcely dilated, (4–)6–14 mm long, white or pale (purplish) pink, not adnate to opposing tepals; anthers basifixated adaxially, slightly extrorse, white or pale (bluish) purple, narrowly ovoid, usually 1.3–3.1 mm long, base sagittate, apex obtuse, (sub)bilocular with vestigial apical confluence between thecae; pollen white or creamy. Pistil 1, exceeding stamens and tepals; ovary sessile or short stipitate, whitish, pale green or purplish pink, globose-ellipsoid or obovoid, obtusely trigonous, slightly trisulcate, 1.5–2.8 mm long, 1.8–3 mm across, apex emarginate-concave; ovules numerous, multiseriate on central axile placentae; style terete, often slightly broadened above, 5–19 mm long, white or purplish pink; stigma thick discoid, often slightly trigonous, 1.3–2.4 mm across, 0.5 mm thick, white or pale purple. Capsules broadly obpyramidal (obcordate or obdeltoid in lateral aspect), apex depressed in center, tripartite, 4–7 mm long, 6.5–10 mm across; lobes mitriform or ovoid-pyriform, divergently protruding. Seeds numerous, linear-fusiform, testa whitish, 3.4–5 mm long, 0.2–0.4 mm wide; body of seed narrowly fusiform, 1.2–1.8 mm long, 0.2–0.3 mm wide, brown.



**FIGURE 21.** *Helonias umbellata*. **A.** Young slightly open flowers with protruding pistils (material U-1; photo on 3 March 1989). **B.** Flowering plant (U-2; 14 March 1989). **C.** Umbel (U-1; 30 March 1992). **D.** Plant with fresh leaves (light green) and leaves developed in preceding year (darker green) grown in greenhouse during winter (U-3; 14 March 2015). All photos at Hachioji, Tokyo.

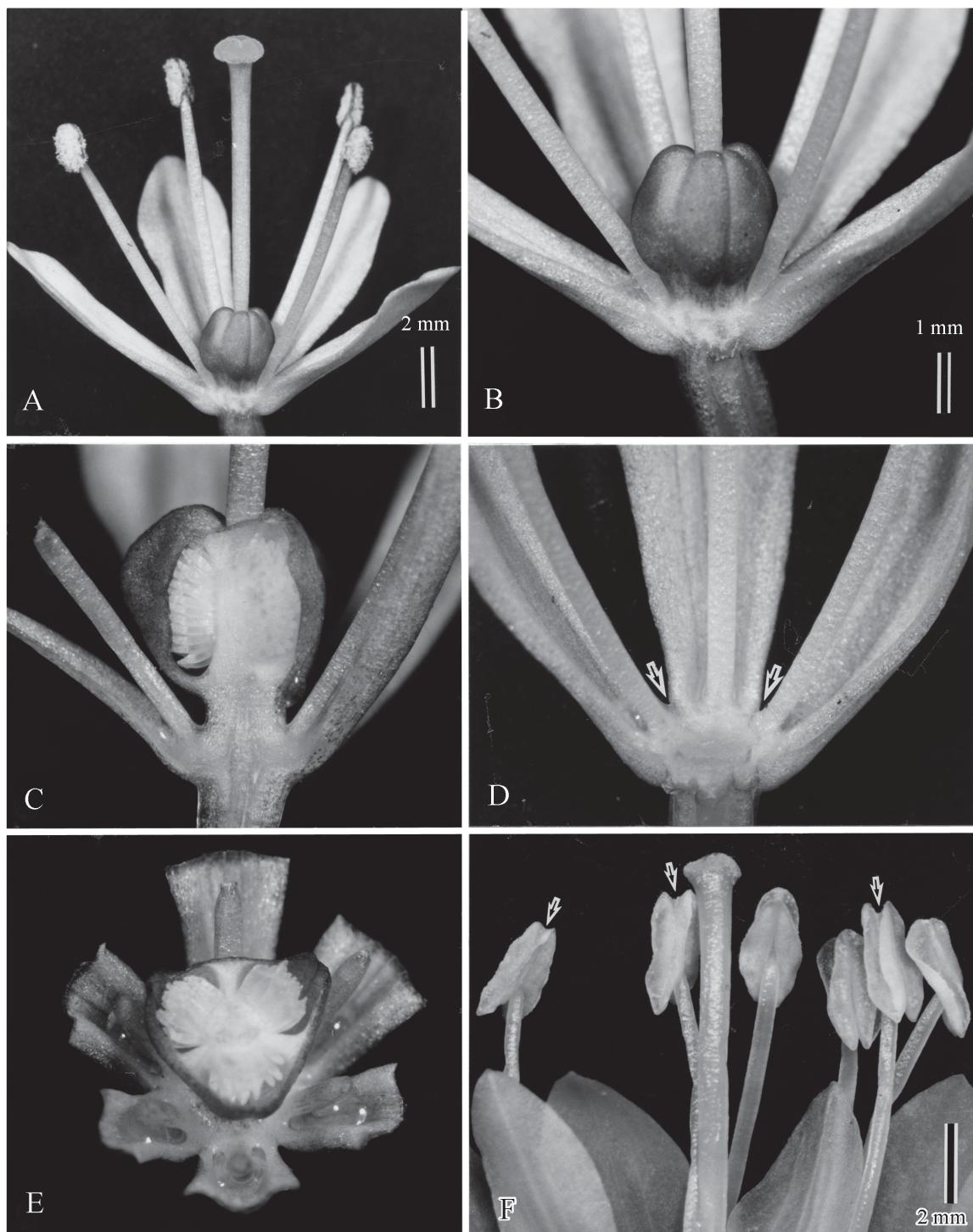
**Additional specimens examined** (see also Tanaka 1998a):—TAIWAN. **Hsinchu** Hsien: Chienshie Hsiang, ca. 2000 m, 20 February 2002, fl., Y.-Y. Huang 947 *et al.* (MAK-386385). **Iilan** Hsien: Mt. Taiping, 4 March 1967, fl., M.T. Kao 6796 (TI); *ibid.*, 1750m, 22 May 1949, fr., H. Keng 1217 (TAI-029039, PH-66762). **Miaoli** Hsien: Nanchuang Hsiang, Fengmeihsie, ca. 1500–1700 m, 7 January 1994, fl., T.Y. Liu *et al.* 358 (HAST-40520\*, BM-001118048). **Nantou** Hsien: Ching-shui-kou, 18 February 1959, Huang, Kou & Kao 938 (TAI-029016\*); Hsinyi Hsiang, ca. 1500 m, 12 February 2003, fl., C.-I. Peng 19224 (HAST-93318\*). **Taipei** Hsien: Shichiseizan (Mt. Chihsing), 3000 ft, 25 January 1932, fl., N. Fukuyama 3015 (TNS-59639); Shihting Hsiang, ca. 200–500 m, 17 February 2008, fl., P.-F. Lu 15304 (HAST-123134\*); in monte Taitun, ad 600 m, 7 mai 1903, U. Faurie 537 (MAK-137680, P-01762775); Yangminshan to Chihsing, 600–1100 m, 26 February 1961, fl., T. Shimizu 11117 (A, TI); Daitonzan (Mt. Tatun), 20 April 1932, fr., S. Sasaki (TNS-321209). **Taichung** Hsien: Leeshan, 20 April 1962, fr., C.S. Feung & M.T. Kao 4554 (TI); 710 logging tract, 1900–2000 m, 1 April 1993, fl., J.C. Wang *et al.* 8094 (HAST-27016). **Taitung** Hsien: Taito (Taitung), Sinsuie (Chinshuiying), 10 February 1925, fl., S. Sasaki (TNS 321217). **Taoyuan** Hsien: Fuhsing Hsiang,

ca. 1840 m, 11 Apr. 2002, fr., W.-C. Leong 2881 et al. (MAK-386590). **Pingtung** Hsien: Kosyun (Oluanpi), Garambi (Garambi), 29 March 1932, S. Sasaki 40061 (TAI-250118\*).

**Distribution:**—Taiwan (Fig. 29-U).

**Habitat:**—Shady and semishady moist rocks and slopes at elevations usually 200–2500 m.

**Conservation status:**—The species is comparatively widespread, and may be assessed as LC according to the IUCN Red List Categories and Criteria (2001).



**FIGURE 22.** *Helonias umbellata*. A–E: material U-1. F: U-4 (in spirit). **A.** Flower with two frontal tepals and stamens removed. **B.** Closeup of proximal interior of flower. **C.** Vertical section of flower with ovary shortly stipitate at base. **D.** Proximal interior of partial flower. Minutely connate portions between adjoining tepals arrowed. **E.** Proximal part of flower in cross section. **F.** Distal part of flower with anthers showing apical confluence between thecae (arrowed). Scale at B also for C–E.

**Flowering:**—Usually late January–March (to June at high elevations).

**Ripening:**—April–May(–June).

**Remarks:**—Hsu *et al.* (2011) reported *Ypsilandra thibetica* as being in Taiwan, but the plant on which the report is based appears to be a form of *Helonias umbellata* (see also the remarks under *H. thibetica*). Having a raceme, their plant may look like *H. thibetica*, but other characters such as anthers (e.g. Fig. 2E, H in their paper, appearing subbilocular) and stigmas (e.g. Fig. 2E, G in their paper, appearing slightly lobed or trigonal and slightly larger) agree with *H. umbellata*. Further, the karyotype in their paper (Fig. 4) does not agree with *H. thibetica* but rather with *H. umbellata* (N. Tanaka unpublished data). In *Helonias*, racemes are considered to be more primitive than umbels (Part III-2-2), so forms with racemes of *H. umbellata* may represent relict ancestors. It is also possible that racemose inflorescences were acquired secondarily from umbels. Further studies are needed to resolve this question. *Helonias umbellata* has tepals sometimes minutely connate to adjoining ones basally (Fig. 22D; Tanaka 1997b), suggesting a close relationship between *H. umbellata* and ser. *Heloniopsis*. *Helonias umbellata* occurs from hillsides to high peaks on Taiwan, and the habitats are not necessarily close to streams, indicating that the plant can tolerate diverse environmental conditions. *Helonias kawanoi* and *H. leucantha*, in contrast, are mostly confined to moist places along or near streams at low elevations on small, subtropical islands.

## Ser. 2. *Heloniopsis*

**Japanese name:**—Shôjôbakama retsu.

**Species included:**—3; *Helonias breviscapa*, *H. koreana*, *H. orientalis*.

**Description:**—Leaves hysteranthous, somewhat thin to thick in texture, dull to glossy, light (yellowish) green or green adaxially, minutely undulate or entire along margins, sometimes producing plantlet adventitiously at tip of leaf in the wild (*H. orientalis*). Inflorescence (sub)umbellate at anthesis, rachis often elongating with age. Flowers vernal, funnelform (obconic) or campanulate. Tepals adaxially canaliculate toward base, proximal submarginal portions winged (lamellate) inward, connate basally to adjoining tepals and also adnate to opposite filaments, forming a tubular nectary. Adnate portions between filament and opposing tepal and connate portions between adjoining tepals positioned higher than base of ovary (or apical surface of receptacle). Anthers affixed to filament adaxially at or close to base of connective (i.e. nearly basifixed or (sub)dorsi-basifixed), bilocular with vestigial apical confluence between thecae. Stigma thin to thick discoid or subcapitate, sometimes trilobed.

**Distribution:**—Japan, Korea, E Russia (S Sakhalin) (Figs. 29-B, -Ko, -O, 31-4, 32-4).

**Remarks:**—All members of this series are confined to islands and peninsulas of Far East Asia (Figs. 29), suggesting the past subsidence of land bridges (discussion in Part III-5). Several characters of the three species are compared in Table 9. A key to the species is below.

**TABLE 9.** Comparison of three species of ser. *Heloniopsis*.

Character	<i>H. koreana</i>	<i>H. breviscapa</i>	<i>H. orientalis</i>
Leaf			
Thickness (texture)	thin to moderate	thin to moderate	somewhat thick or firm
Glossiness (mature leaf)	dull	dull	glossy
Margin	u. min. undulate	u. min. undulate	entire
Ramets (plantlets) (in the wild)	absent	absent	s. present
Persistence (appr. duration in year)	1	1(–2)	1–2
Flower			
Shape	funnelform, campanulate or tubular	funnelform	funnelform
Tepal			
Color	u. bluish purple, purple or blue	white, s. proximally purplish pink	u. (purplish) pink, s. bluish
Height (length) <sup>1)</sup> of portion adnate to opposing filament (mm)	0.5–1.0(–1.5)	0.7–1.8	(0.8–)1.3–2.0
Filament			
Proximal part	sl. dilated, complanate	little dilated, sl. complanate	little dilated, little complanate

<sup>1)</sup> Height (or length) from base of ovary (or receptacle surface).

Abbreviations: appr.—approximate. min.—minutely. s.—sometimes. sl.—slightly u.—usually.

## Identification key to the species of *H. ser. Heloniopsis*

1. Leaves entire, comparatively thick or firm in texture, glossy, persistent for 1–2 years, sometimes with adventitious apical plantlets; flowers funneliform; nectaries lower than base of ovary; filaments proximally scarcely dilated and little complanate ..... 11. *H. orientalis*
- Leaves usually minutely undulate at margins, somewhat thin textured, (sub)dull, persistent for 1 (occasionally 2) year, not producing apical plantlets in the wild; flowers funneliform (obconic) or tubular-campanulate; nectaries positioned nearly as high as or lower than base of ovary; filaments slightly dilated and complanate, or not dilated and usually slightly complanate proximally ..... 2
2. Flowers funneliform to narrowly tubular-campanulate or campanulate; tepals usually (bluish) purple, purplish pink or blue; filaments slightly dilated, complanate, often slightly 2-edged or narrowly ancipital (2-winged) toward base; adnate portion between filament and opposing tepal often nearly as high as basal connate portion between adjoining tepals; nectaries lower than base of ovary ..... 10. *H. koreana*
- Flowers funneliform; tepals white, sometimes with proximal purplish pink tint; filaments not dilated, usually slightly complanate toward base; adnate portion between filament and opposing tepal higher than basal connate portions between adjoining tepals; nectaries nearly as high as base of ovary ..... 12. *H. breviscapa*

### 10. *Helonias koreana* (Fuse, N.S.Lee & M.N.Tamura) N.Tanaka, *comb. nov.* (Figs. 23, 24).

= *Heloniopsis koreana* Fuse, Lee & Tamura (2004: 956). **Type:**—KOREA. Gangwondo: Jeongseon-gun, Gohan, 1 May 1984, Y.N. Lee EWH-2324 (Holotype: EWH, n.v.).

= *Heloniopsis tubiflora* Fuse, Lee & Tamura (2004: 954), *syn. nov.* **Type:**—KOREA. Jeollabuk-do: Muju-gun, Seolchon-myeon, Mt. Deogyu, 1585 m, 6 May 2001, M.N.Tamura et al. 10333 (Holotype: KYO, n.v. Isotype: EWH, GH, HYO, OSA, TI, n.v.).

= *Heloniopsis orientalis* (Thunb.) Koidz. var. *purpurea* (Nakai) Nakai (1952: 146), p.p.?, as to Korean plants; Chong (1956: 961, t. 1922).

For further notes see the remarks under *Helonias orientalis* below.

– *Heloniopsis orientalis* auct. non (Thunb.) Tanaka: Lee (2002: 896), as to Korean plants.

– *Helonias orientalis* auct. non (Thunb.) N.Tanaka: Tanaka (1998a: 109), p.p., as regards Korean plants.

**Japanese name:**—Chōsen-shōjōbakama (*nov.*; meaning Korean *Helonias*).

**Korean name:**—Cheo-nyeo-chi-ma (Chong 1956, Lee 2006, Lee 2007).

**Description:**—Rhizome erect or ascending, subterete, nodose, closely annulate with many scars, to 25 mm long, to 13 mm in diam., pale brown. Roots filiform, to 1.5 mm in diam., white, contractile. Leaves hysteranthous, chartaceous (somewhat thin to moderately thick in texture), persistent usually for fully 1 year, spatulate or narrowly oblanceolate, to 16 cm long, 3.8 cm wide, tapering to linear petiole, margin usually minutely undulate, apex acuminate with apiculus 0.5–0.8 mm long, midvein keeled and main parallel veins slightly raised abaxially, adaxially dull (slightly glossy when young). Flowering stem upright; peduncle terete, 8–19 cm long; scale-like leaves ca. 6–10 (excl. basal ones), narrowly oblong-oblanceolate, narrowly oblong, lanceolate, linear or subulate, acute, sub-obtuse or obtuse, apex short mucronate, submembranous (or subherbaceous), pale green or white, multinerved; basal scales narrowly ovate, sharply pointed, whitish pale green; inflorescence compact, racemose or (sub-)umbellate; rachis 4–8(–18) mm long at anthesis, ribbed, usually slightly decurved; pedicels 3.5–10 mm long, often decurved, ribbed, pale purple. Flowers 4–10(–14), protogynous, often nodding, funneliform, (tubular-)campanulate or tubular, odorless. Tepals 6, blue, bluish purple, purple, purplish pink, often darker proximally, 5–7(–9)-veined, spatulate or oblong-oblanceolate, 11.5–16 mm long, 2.7–4 mm wide, base affixed to receptacle (apex of pedicel) for ca. 1.2 mm in length, abaxially slightly to markedly gibbous, apex obtuse or subobtuse, adaxially canaliculate toward base, proximal submarginal portions winged (lamellate) inward; wings connate basally to adjoining tepals for 0.4–0.8 mm in height, also adnate to opposite filaments for 0.5–1.0(–1.5) mm in height, forming a short sheath-like nectary. Stamens 6, exceeding tepals; filaments subulate, 14–20 mm long, pale purple or purplish pink, proximally slightly dilated, complanate, often slightly 2-edged or narrowly 2-winged, 0.7–0.9 mm wide, distal part terete, 0.5–0.6 mm in diam.; anther affixed to filament adaxially 0.3–1 mm above base of connective (i.e. [sub]dorsi-basifixied), bilocular with traces of apical confluence between thecae, dark grayish blue or bluish purple, narrowly ovoid or narrowly oblong-ellipsoid, 3–5.5 mm long, base sagittate, apex rounded; pollen cream. Pistil 1, exceeding tepals and usually also stamens; ovary globose, ellipsoid or obovoid, trilobed, sessile, emarginate-concave, 2.5–3.5 mm long, 3.5–4.5 mm across, pale dirty green or dark dirty purplish pink; style (sub)terete, often slightly 6-angulate or trisulcate, often up-curved distally in horizontal to nodding flowers, 11.5–20 mm long, pale purple or purplish pink; stigma (thinly) discoid, often obtusely trigonous, slightly concave in apical center, 1–1.5(–2.5) mm across, 0.5–0.7 mm thick, (dark) purple. Capsules broadly obovate-pyriform, tripartite, apex depressed in center; lobes ovoid-conic or pyriform, slightly flattened laterally, obliquely or almost horizontally divergent. Seeds numerous, testa whitish, narrowly fusiform or sublinear, narrowly tailed proximally and distally, 5–6.5 mm long, 0.3–0.5 mm wide; body of seed narrowly ellipsoid, 1.5–1.7 mm long, 0.2–0.3 mm wide, brown.



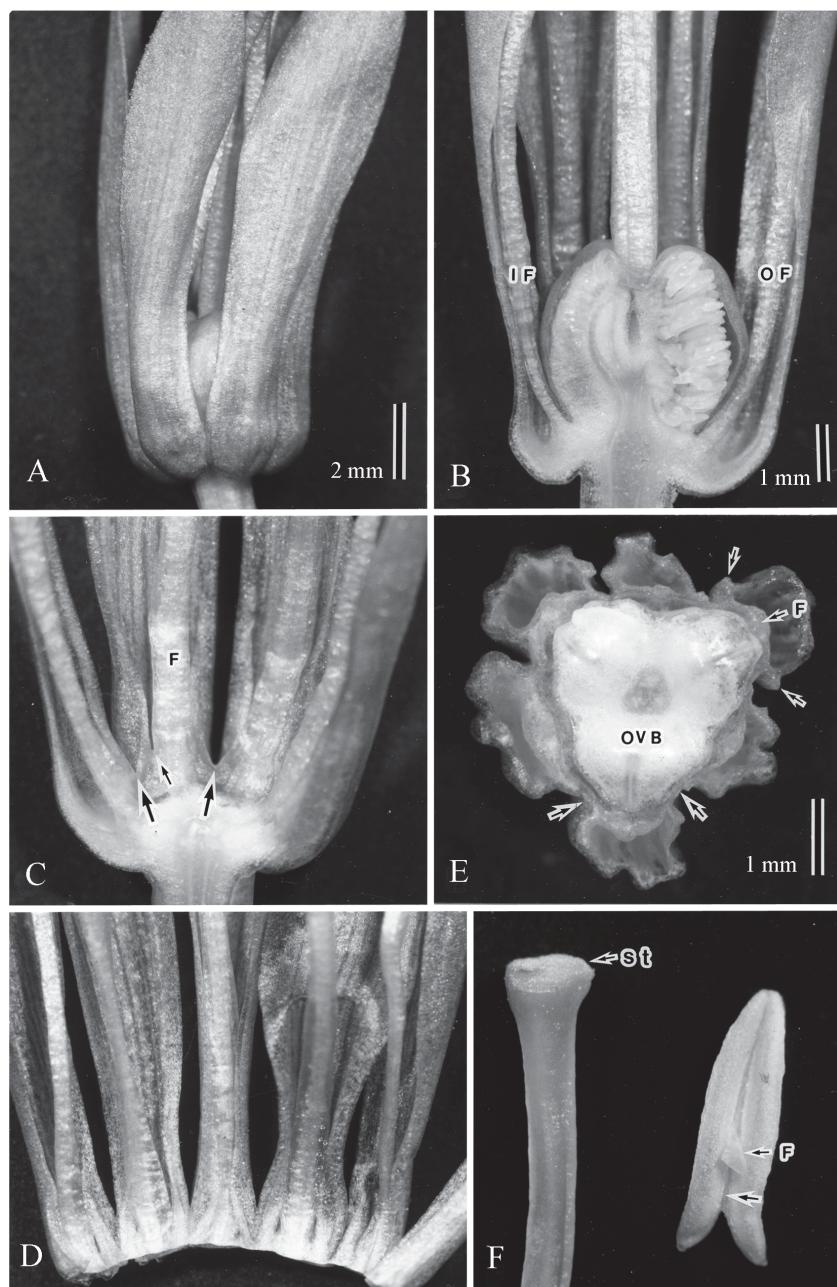
**FIGURE 23.** *Helonias koreana*. A–F: One and same umbel showing phenological transition of flowers (material Ko-2). **A.** Young flowers mostly with indehiscent anthers (photo on 8 March 2015). **B.** Flowers mostly with dehisced anthers at early to mid anthesis (9 March 2015). **C.** Flowers becoming nodding at mid to late anthesis (12 March 2015). **D.** Nodding flowers at late anthesis (14 March 2015). **E.** Nodding flowers after anthesis with persistent floral parts (26 March 2015). **F.** Slightly ascending young fruits (19 April 2015). **G.** Short raceme of white flowers at late anthesis (Ko-w-1; 15 April 2008). **H.** Fresh rosulate leaves minutely undulate along margins (Ko-2; 23 May 2015). All photos at Hachioji, Tokyo.

**Additional specimens examined:**—KOREA. **Chollanam-do:** Nogodan, Mt. Jiri, Toji-myeon, Gurye-gun, 1500 m, 7 May 2001, fl., M.N.Tamura et al. 10334 (isoparatotype of *Heloniopsis tubiflora*, TNS-774437\*). **Chungcheongbuk-do:** Goesan-gun, Mt. Sinseon-bong, 455 m, 28 April 2006, fl., H. J. Choi & J. E. Koh 60011 (MAK-372989, ex KH). **Gyeonggi-do:** Mt. Bukhan (Hokkanzan), 28 April 1912, fl., N. Okada s.n. (paratype of *Heloniopsis koreana*; TI); Pocheon-si, Gwanin-myeon, Mt. Jijang-bong, 17 April 2005, fl., H. J. Choi & G. H. Nam 50033 (TI ex KH); Kwangnung (Keiki-dô, Kôryô), 16 May 1948, fr., Chung I.-C. 4859 (TNS-151074). **Gyeongsangnam-do:** Mt. Jiri, 7 July 1913, fr., T. Nakai 622 (paratype of *Heloniopsis tubiflora*; TI!); en route from Seseog-cottage to Jangteomog-cottage in Mts. Chirisan, ca. 1600–1700 m in elev., 24 Jun. 1979, fr., K. Ueda et al. 1220 (paratype of *Heloniopsis tubiflora*, TI-1314994, TI-1313106). **Hamgyeongbuk-do:** Kyongsong (Kyôjô), 26 May 1930, fr., J. Ohwi 141 (TNS-231384). **Hamgyeongnam-do:** Seongjin (Zyôsin), 15 Junio 1909, T. Nakai s.n. (paratype of *Heloniopsis koreana*, TI);

Wonsan (Gensan), 9 Junio 1909, fr., T. Nakai s.n. (paratype of *Heloniopsis koreana*, TI). **Jeollanam-do:** Gurye-gun, around Sejeok Shelter in Jiri-san, 17 June 2003, fr., S. H. Park 31316 (TI, ex KH). **Pyeonganbuk-do:** Unsan, Mt. Hakuhekizan, 3 June 1945, without collector's name (TI). **Pyeongannam-do:** Yangdeok (Yōtoku), 15 June 1928, fr., T. Nakai 12487 (paratype of *Heloniopsis koreana*; TI). Gangwon-do: Mt. Keumgang (Kongōsan), 15 August 1916, T. Nakai 6026 (TI); Mt. Keumgang (Kongōsan), 31 July 1916, T. Nakai 5230 (paratype of *Heloniopsis koreana*, TI); In montes des diamants, Junio 1906, U. Faurie 266 (E-00904041\*).

**Distribution:**—Korea (Fig. 29-Ko).

**Habitat:**—Shady to open moist places on hillsides and high mountains at elevations 390–1700 m.



**FIGURE 24.** *Helonias koreana*. A–F: material Ko-1. **A.** Flower at late anthesis. **B.** Vertical section of flower at late anthesis. **C.** Proximal interior of flower, showing connate portions between adjoining tepals (long arrows) and adnate portion between tepal and opposing filament (short arrow). **D.** Perianth cut and opened, showing tepals connate basally by proximal submarginal lamellae. **E.** Proximal part of flower in cross section. Two larger arrows point connate portions between adjoining tepals, and two smaller arrows indicate margins of tepal. **F.** Stigma (st) and adaxial side of anther (in spirit). Portion of anther affixed to filament indicated with 'F'. Thecal connation below insertion point of filament indicated with arrow. F; filament. IF; inner filament. OF; outer filament. OVB; basal inside of ovary. Scale at B also for C, D and F.

**Conservation status:**—The species is comparatively widespread, and assessed as LC according to the IUCN Red List Categories and Criteria (2001). However, local populations near human habitation may be more or less subject to disturbance and threats.

**Flowering:**—Usually April–May.

**Ripening:**—May–July.

**Remarks:**—According to Fuse *et al.* (2004) and Lee (2007), *Heloniopsis koreana* and *H. tubiflora* differ in several characteristics. In *H. tubiflora*, the mature leaves are entire, but sometimes marginally minutely undulate when young, the perianth is basally tubular, and the tepals are saccate at the base. In *H. koreana*, the mature leaves are minutely undulate, the perianth is obconically expanded from the base, and the tepals are not or only slightly saccate. In living plants from Korea (mostly from Nyongol, Kangwon-do) that I examined, the leaf margins of some plants were like *H. tubiflora*, but others were consistently like *H. koreana* (Fig. 23H), indicating variation among them. The leaves are invariably minutely undulate at least when young. In early flowering stages, when the flowering stem is still short, the flowers are oriented in various directions and the perianth expands obconically from the base (Fig. 23A, B), as in *H. koreana*, but, the flowers of the same inflorescence gradually nod and the perianth also becomes tubular as anthesis progresses (Figs. 23C, D, 24A, B). The tepals are slightly or moderately gibbous at the base in early anthesis (Fig. 23A, B), but later the gibbous portion tends to become slightly more prominent, resembling *H. tubiflora* (Figs. 23C, D, 24A, B). The flowers in the early flowering stages (Fig. 23A, B) are like those of *H. koreana*, but in later stages they become more like *H. tubiflora* (Figs. 23C, D, 24A, B). All the diagnostic characteristics given by Fuse *et al.* (2004) and Lee (2007) for *Heloniopsis koreana* and *H. tubiflora* are rather quantitative. When typical forms are compared, the two species may appear to be somewhat distinct, but there appear to be no significant qualitative differences between them. The filaments of *Helonias koreana* here circumscribed (including *Heloniopsis tubiflora*) differ from those of *H. orientalis* and *H. breviscapa* in being slightly dilated and complanate toward the base (e.g. Fig. 24B–E). The proximal submarginal portions of the tepals of *H. koreana* are winged, connate to those of adjoining tepals, and also adnate to the opposing filament (Fig. 24C–E), as in *H. orientalis* (Fig. 26A; Tanaka 1997b) and *H. breviscapa* (Fig. 28E; Tanaka 1997b). It is notable, however, that adnation between tepals and filaments in *H. koreana* is less prominent (Fig. 24C, D) than in *H. orientalis* (Fig. 26A) and *H. breviscapa* (Fig. 28E). According to Fuse *et al.* (2004), the flanges of the base of the filament are adnate to the margin of the corresponding tepals in *Heloniopsis koreana*, *H. tubiflora*, *H. umbellata* and *H. leucantha*, but those of *H. orientalis* and *H. breviscapa* are adnate to the adaxial surface of the corresponding tepals. Their observations, however, are not consistent with mine. In my observations, in the three species of *Helonias* ser. *Heloniopsis*, *Helonias koreana*, *H. orientalis* and *H. breviscapa*, the filament is not adnate to the margins but to the proximal submarginal portions of the opposing tepal, as stated above. In the three species of *H. ser. Umbellatae*, *H. kawanoi* (Fig. 17D, E), *H. leucantha* (e.g. Figs. 19D, E), and *H. umbellata* (e.g. Fig. 22E), the filament is distinct and not adnate to the opposing tepal (Tanaka 1997b). *Helonias koreana* occasionally has white flowers (Fig. 23G). Photographs of the white-flowered forms of both *Heloniopsis koreana* and *H. tubiflora*, in the sense of Fuse *et al.* (2004), are shown in Lee (2006). The following names are invalid, since they were not accompanied by a Latin description and no type specimens were designated: *Heloniopsis koreana* forma *albiflora* Lee (2006: 406, f. 3290), *nom. inval.* *Heloniopsis tubiflora* forma *albiflora* Lee (2006: 406, f. 3292), *nom. inval.*

11. *Helonias orientalis* (Thunb.) Tanaka (1998a: 109) (Figs. 1B, 25, 26).

≡ *Scilla orientalis* Thunberg (1794: 334). ≡ *Heloniopsis orientalis* (Thunb.) Tanaka (September 1925: 2000). ≡ *Sugerokia orientalis* (Thunb.) Koidzumi (1930: 95). **Type:**—JAPAN. E Japonia, Thunberg (Holotype: UPS-THUNB 8327\*!). Note:—the type specimen was collected from Niphon [Honshû], Japan, according to the account of *Scilla bifolia* in Thunberg (1784: 138).

**Japanese name:**—Shôjôbakama (e.g. Itô 1829; Iinuma 1861, under *Scilla japonica* Thunb.; Tanaka & Ono in Iinuma 1875, under *Sugerokia japonica*).

**Distribution:**—Japan, Korea, E Russia (S Sakhalin) (Fig. 29-O).

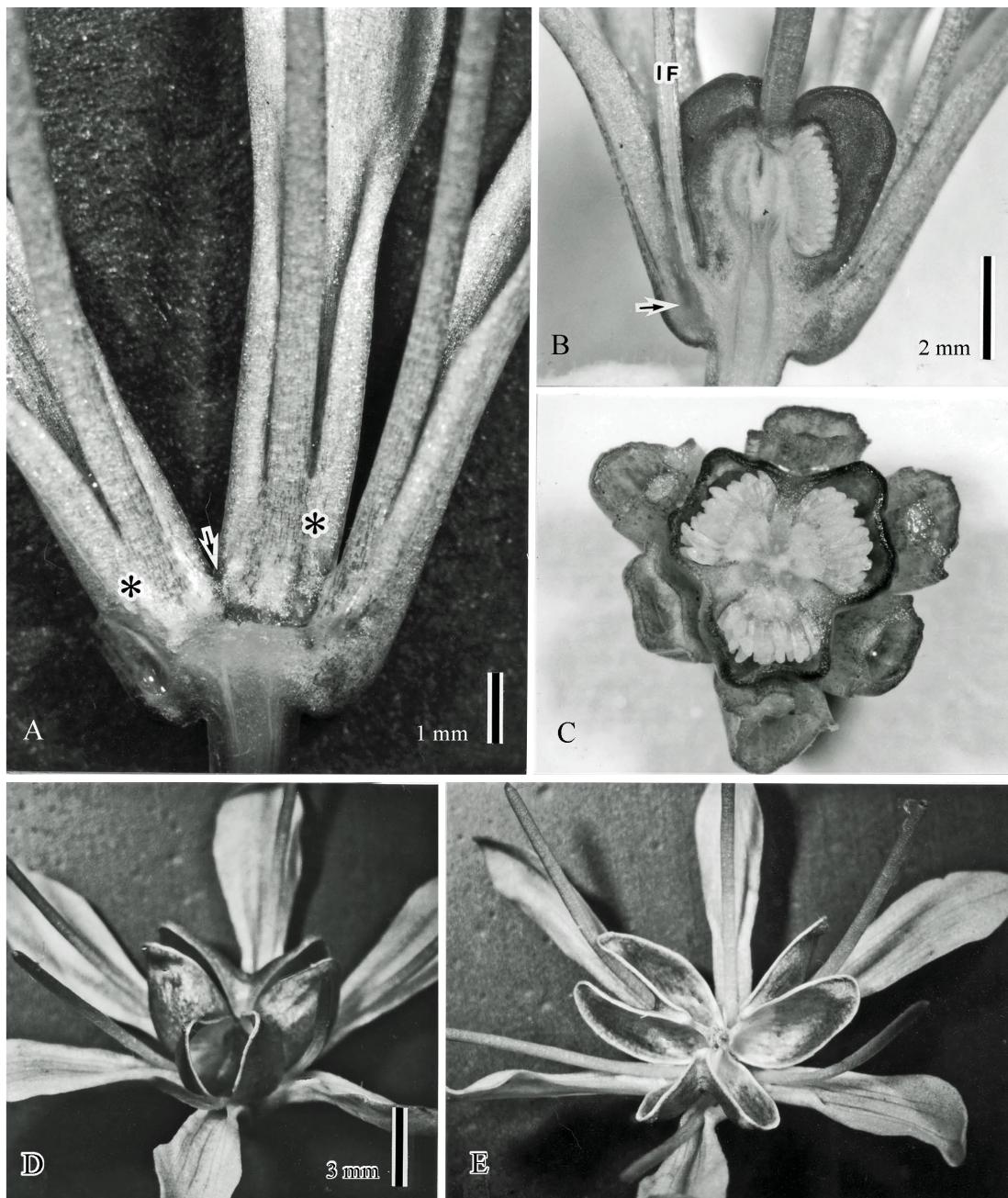
**Remarks:**—The floral color of *Helonias orientalis* is usually pink or purplish, but sometimes deviates from it. The plants are expediently grouped into the following three forms depending on their flower color: (11a) the form with flowers other than white or yellow (i.e. the most common form with pink or purplish is included here), (11b) the form with white flowers, and (11c) the form with yellow or yellowish flowers. Because of sporadic occurrence in populations of the form with pink or purplish flowers (11a), the forms 11b and 11c are not treated here as independent taxa. Names formerly given to or corresponding to them are listed in synonymy under the respective forms (11a–c).



**FIGURE 25.** *Helonias orientalis* (A–D, F; material O-2, G; O-1, H; O-3) and white flowered form (E; O-w-1). **A.** Young slightly open flowers with protruding pistil (photo: 25 March 2014). **B, C, D.** Sub-umbellate flowers (B on 31 March 2014; C on 29 March 2014; D on 5 April 2012). **E.** Compact raceme of white flowers (30 March 2012). **F.** Inflorescence (29 April 2014). **G.** Dehisced capsules (14 May 2014). **H.** Rosette with flower bud (arrow) in center (14 August 2014). All photos at Hachioji, Tokyo.

#### Identification key to the forms expediently grouped by their flower colors

1. Tepals (at anthesis) pink or purplish pink or sometimes brick-red, blood-red, purple or bluish ..... 11a.
- Tepals (at anthesis) white or yellowish ..... 2
2. Tepals white ..... 11b.
- Tepals yellowish ..... 11c.



**FIGURE 26.** *Helonias orientalis*. A–C; material O-3. D, E; O-2. A. Proximal interior of partial flower. Connate portion between adjoining tepals arrowed. Adnate portions between tepals and opposing filaments marked with asterisks (\*). B. Proximal portion of flower in vertical section. Surface of nectary arrowed. IF; inner filament. C. Proximal part of flower in cross section. D. Slightly dehisced capsule with persistent floral parts. E. Three valvate, dehisced capsule. Scale at A also for C; at D also for E.

11a. The form with flowers other than white or yellow (Figs. 1B, 25 excl. E, 26).

*Heloniopsis pauciflora* Gray (1859: 416). **Type:**—JAPAN [N Hokkaidô]. Cape Romanzoff [northwestern extremity of Jesso—presently Cape Noshappu in Wakkai-shi], 1853–1856, C. Wright s.n. (Holotype: GH-00029943\*, p.p., excl. admixed fragments of a *Luzula* vide Koidzumi (1930, 1934), Hara (1947). Isotype: US-00650433\*!).

*Sugerokia japonica* Miquel (1866, reprint: 24; 1867a: 88—publication February 1867 at latest, for the publication date see Stafleu 1966: 84; July 1867b: 145—publication date from Stafleu & Cowan 1981: 515); 1866–1867: 309; 1870: 92), p.p., excl. syn. ?*Scilla japonica* Thunb., *Heloniopsis breviscapa* Maxim., and specimens from Kiusiu [Kyûshû].  $\equiv$  *Heloniopsis japonica* Maximowicz (May 1867: 437). **Type:**—JAPAN (Japonia). *Botanicus japonicus* s.n. [no actual collector's name nor detailed locality in Japan is recorded on the sheet]. The following remark is made in the protologue: A Mizutani Sugerok probabiliter in Japonia boreali detecta. (Holotype: L 908. 106-1567, barcode L-00325576\*!). **Note on the typification of this taxon:**—Ohba et al. (2005) designated *Siebold* s.n. (L

908. 106-711; barcode L-0325582\*!) as the lectotype and several other specimens collected by Siebold, Bürger, or Keisuke ITO as syntypes for this taxon. However, in the protologue only one collection was cited by Miquel. Accordingly, their type designations are invalid. For more details see the remarks below.

*Sugerokia japonica* Miq. var. *racemosa* Miquel (July 1867b: 145; 1866–1867: 309). **Type:**—JAPAN. *Botanicus japonicus* s.n.. (“Legit bot. iaponicus, probabliter *Sugerok* [*Mizutani*]” in the protologue). (Holotype: L-0325576\*!). This specimen is regarded as the holotype for *S. japonica* Miq. *Sugerokia japonica* var. *racemosa* is therefore the homotypic synonym of *S. japonica*. For more details see the remarks below.

*Heloniopsis pauciflora* A.Gray var. *rubra* Koidzumi (1921: 15), cum descr. jap. **Type** (possible type collection needing further studies):—JAPAN. Hokkaidō. Kamifurano, 1916, *H. Koidzumi* (specimen collected by him in the same locality on 14 July 1917 is in TNS!). Nagano Pref.: Mt. Norikura, July 1920, *H. Koidzumi* (specimen collected on 10 July 1920 is in TNS!); Mt. Shirouma, August 1920, *H. Koidzumi* (specimen dated 20 July 1920 is in TNS!). Japanese name: Beni-shōjōbakama (Koidzumi 1921).

*Heloniopsis japonica* (Thunb.) Maxim. var. *purpurea* Nakai (1933: 243) p.p.? ≡ *Heloniopsis orientalis* (Thunb.) Koidz. var. *purpurea* (Nakai) Nakai (1952: 146). ≡ *Hexonix japonica* (Thunb.) Raf. var. *purpurea* (Nakai) Wang & Tang (1949: 113). **Type:**—Not designated. ‘Habitatio’ and ‘nomen japonicum’ given under this name by Nakai may not be for this taxon, but those for *Heloniopsis japonica* as a species, probably due to the erroneous insertion of the three lines of var. *purpurea* into the account of the latter. For further notes see the remarks below.

*Heloniopsis japonica* (Thunb.) Maxim. var. *sanguinea* Nakai (1933: 243). ≡ *Hexonix japonica* (Thunb.) Raf. var. *sanguinea* (Nakai) Wang & Tang (1949: 113). **Type:**—JAPAN. Hondo [Honshū]. No specimen designated. In TI, however, there is a specimen annotated with this name by Nakai, which is from the Konsei(tōge) Pass, Nikkō, 30 June 1923, fr., *Y. Yamamoto* s.n. Japanese name: Benibana-shōjōbakama (Nakai 1933).

*Heloniopsis japonica* Maxim. f. *lateritia* Nakai ex Honda (1938: 1679). **Type:**—JAPAN. Honshū. Prov. Tōtōmi [Shizuoka Pref.], Ogasa-gun, Mt. Ogasa, 3 April 1931, *G. Hashimoto* s.n. (Holotype: TI! Isotype: TNS-44182!). Japanese name:—Akabana-shōjōbakama (Honda 1938).

— *Scilla bifolia* auct. non L.: Thunberg (1784: 138).

— *Heloniopsis acutifolia* auct. non Hayata: Honda (1938: 1678).

— *Sugerokia acutifolia* auct. non (Hayata) Koidz.: Honda (1938: 1678).

— *Heloniopsis breviscapa* auct. non Maxim.: Makino (1891: 126); Matsumura (1905: 197), p.p.

— *Heloniopsis orientalis* (Thunb.) Tanaka var. *breviscapa* auct. non (Maxim.) Ohwi: Ohba et al. (2005: 127).

**Description:**—Rhizome subcylindrical, to 6.5 cm long, to 2.5 cm in diam., somewhat knobby, subannulate with many close scars, whitish or pale brownish. Roots filiform, to 2.5 mm in diam., white, contractile. Leaves persistent for 1–2 years, oblanceolate, spatulate or narrowly oblong, cuneate to petiole, 4–29 cm long, 1–4.5 cm wide, petiolar part to 1 cm wide, margin entire, apex short acuminate, apiculate, apiculus ca. 0.5 mm long, sometimes with adventitious plantlet (ramet) at apex, abaxial midvein raised, adaxially glossy, chartaceous (somewhat thick in texture). Flowering stem to ca. 17 cm long at anthesis, elongating in fruit; peduncle terete, 3.5–16 cm long at anthesis, to ca. 60 cm or more in fruit; base densely covered with acute or acuminate, ovate scale-like leaves; scale-like leaves on peduncle 7–12 (excl. basal ones), narrowly oblong(-elliptic), narrowly lanceolate or ovate, acute, to ca. 2.7 cm long; inflorescence subumbellate, sometimes umbellate, becoming racemose in fruit, rachis to 1 cm long at anthesis, 1.5–9.5 cm long in fruit; pedicels 6-ribbed, 0.4–2.8 cm long (incl. those in fruit), purplish pink. Flowers 2–10(–13), funnelliform, 1.2–2.5 cm across, usually slightly nodding, usually odorless, rarely slightly scented. Tepals 6, obliquely expanded, sometimes slightly recurved distally, usually pink or purplish pink (4–)5–7-veined, narrowly oblong-oblanceolate (or spatulate), 9.5–20 mm long, 2.4–5 mm wide, base affixed to receptacle (apex of pedicel) for ca. 1.2–1.5 mm in length, abaxially shortly gibbous, apex obtuse, adaxially canaliculate toward base, usually slightly revolute proximally at margin, scarcely imbricate with adjoining tepals, basal submarginal portions winged (lamellate) inward; wings extending over proximal ca. 1/4–1/3 of tepal, connate proximally to those of adjoining tepals for 0.4–0.5 mm in height, also adnate to opposite filament for (0.8–)1.3–2 mm in height, forming a sheathing nectary. Stamens 6, usually exceeding tepals; filaments obliquely expanded, purplish pink, filiform, 8–18 mm long, proximally scarcely dilated and complanate; anthers affixed to filament at adaxial portion ca. 0.2 mm above base of connective (i.e. [sub]dorsi-basifixied), extrorse, dark purple, narrowly ovate, oblong, or narrowly elliptic-oblong, 2.5–5.1 mm long, sagittate at base, rounded at apex, bilocular with vestigial apical confluence between thecae; pollen whitish or pale purplish. Pistil 1, usually exceeding stamens and tepals; ovary sessile, globose, obtusely trigonous, trisulcate, darkly purplish pink, 2–4 mm long, 2–3.8 mm across, apex emarginate-depressed in center; style terete, straight, or slightly up-curved distally in nodding flowers, 8–24 mm long, usually purplish pink; ovules numerous, multiseriate on central axile placentae (ca. 8–12-seriate in each ovarian locule); stigma discoid, often obtusely trigonous, sometimes trilobed or tricleft, slightly concave in center, 1–2.7 mm

across, (dark) purplish pink. Capsules obpyramidal, obcordate or obdeltoid in lateral aspect, triparted, 5–7 mm long, 9–12 mm across, apex depressed in center; lobes subpyriform, ascending to horizontal. Seeds numerous, coated with whitish testa, linear-fusiform, sublinear proximally, subulate distally, usually falcate, 3.5–6.6 mm long, 0.25–0.5 mm wide; body of seed narrowly oblong-fusiform, 1.1–1.6 mm long, 0.2–0.3 mm wide, (dark) brown.

**Additional specimens examined** (see also Tanaka 1998a):—JAPAN. **Hokkaidō**. Hidaka: Mt. Poroshiridake, 1600 m, 25 July 1971, fl., *H. Koyama et al.* 3808 (TNS-303241). Iwamizawa: Horomui, 29 June 1927, fr., *K. Kondo* 1630 (BM-001118050). Kamikawa: Asahikawa-shi, Kamuikotan, 27 April 1894, fl., *S. Ohwaki* (TNS-547312). Kamikawa-gun: Mt. Taisetsu, 18 July 1941, fl., *S. Okuyama* (TNS-69228). Oshima: Matsumae-gun, Mt. Daisengendake, 8 May 1907, fl., *Kudo* 20 (MAK-137595). Samani-gun: Hidaka, Mt. Apoi, 26 July 1941, fr., *S. Okuyama* (TNS-69229). Sorachi-gun: Mt. Yūbaridake, 27 July 1933, fr., *H. Iwamoto* (TNS-43155). **Honshū**. **Chūbu** Distr. Fukui Pref.: Takefu, Murakuniyama, 150 m, 26 March 1987, fl., *T. Yamazaki* (TI). Gifu Pref.: Kawai, 22 April 1960, fl., *S. Okuyama* 14149 (TNS-262517); Ohno-gun, Takane-mura, Dohgo-gawa, 1200 m, 7 May 1973, *H. Kanai* 731154 (BM-1118051). Nagano Pref.: Shimoina-gun, Etsutaro, Urugi-mura, 800 m, 16 September 2000, *K. Asano & H. Asano* 30185 (MAK-317546); Mt. Asama, 31 May 1937, fl., *H. Ito* (TI); Kita-azumi-gun, Mt. Shiroumadake, 27 August 1902, fl., *Y. Yabe* (TI); Kiso, Mt. Komagatake, 27 July 1925, fl., *H. Koidzumi* (TNS-315728). Niigata Pref.: Mt. Tairappyō, 21 June 1959, fl., *H. Hara* (TI); Nishikanbara-gun, Mt. Yahiko, 29 March 1987, fl., *K. Inoue* 4229 (TI); Isl. Sado, Nyūkawa-Tadaramine, 13 May 1954, fl., *S. Okuyama* 10886 (TNS-135230). Shizuoka Pref.: Abe-gun, Mt. Higashidake, 23 July 1924, fl. (TNS-315745); Hamana-gun, Kosai-chō, Bōse, April 1974, *H. Kanai & H. Koyama* (TNS-318330). Toyama Pref.: Yatsuo-chō, 27 May 1955, fl., *A. Kirino* 570 (TNS-122487). **Chūgoku** Distr. Okayama Pref.: Mt. Hirusen, 600 m, 4 May 1959, fl., *G. Murata* (TNS-186826). Tottori Pref.: Mt. Daisen, 6 June 1925, fr., *Y. Nishikado* (TNS-460543). Yamaguchi Pref.: Mt. Nameriyama, 14 October 1949, *T. Nakai & N. Maruyama* (TNS-83141). **Kantō** Distr. Chiba Pref.: (Sanmu-shi) Haniya, 14 April 1935, fl., *T. Makino s.n.* (MAK-137632). Gunma Pref.: Mt. Tanigawa, July 1956, fl., *K. Okamoto* (TNS-389529); Mt. Shibutsu, 20 June 1933, fl., *D. Hoshi* (TNS-315723). Tochigi Pref.: Mt. Takahara, 1400–1500 m, 25 May 1959, fl., *H. Kanai* (TNS-132582); Nikkō, Konsei-tōge, August 1883, fr., *H. Sakurai* (TNS-3844). Tokyo Pref.: Isl. Miyake, Mt. Oyama, 5 May 1938, fl., *Hayashi* (MAK-137631); Isl. Mikura, 9 August 1952, *H. Tsuyama* (TNS-102625); Isl. Kōzushima, 27 April 1887, fl., *K. Shirai* (TNS-54364). **Kinki** Distr. Hyōgo Pref.: Isl. Awajishima, Mt. Yuzuru-hayama, 5 May 1958, fr., *N. Satomi* (TI). Kyoto Pref.: Takeno-gun, Yasaka-chō, 300 m, 25 April 1970, fl., *G. Murata* 20968 (TNS-30409); Ōi-yama, 500 m, 28 April 1968, fl., *M. Togashi* (TNS-210893). Mie Pref.: Mt. Fujiwaradake, 5 April 1953, fl., *S. Okuyama* (TNS-102335, -102338). Ōsaka Pref.: Shinjyō-Nawate, 23 April 1933, fl., *Z. Yoshino* (TI). Shiga Pref.: Kōka-gun, Mt. Handōjisan, 22 April 1962, fl., *H. Koyama* 1196 (TNS-245904). **Tōhoku** Distr. Akita Pref.: Akita-shi, Mt. Tegata, 2 June 1929, fr., *H. Muramatsu* (TI); Senpoku-gun, Mt. Komagatake, 1300 m, 5 July 1975, *Y. Tateishi* 2123 (TI). Aomori Pref.: Mt. Iwaki, June 1941, fl., *D. Narita* (TNS 132383); Mt. Hakkō-dasan, 30 June 1964, fl., *K. Hasegawa* (TI). Fukushima Pref.: Aizu, Mt. Tashiro, 8 July 1959, fr., *S. Okuyama* 16611 (TNS-277605). Iwate Pref.: Hiraizumi-chō, Chūsonji Temple, 12 April 1932, fl., *K. Nemoto* (TNS-36033). Miyagi Pref.: Sendai, Dainohara, 5 April 1914, fl., *Y. Ogura* (TI); Shichikashuku-machi, Watase-fūketsu, 16 April 1978, fl., *R. Suzuki* (TNS-374850). Yamagata Pref.: Tsuruoka-shi, Mt. Yudonosan, 22 July 1887, *R. Yatabe* (TI); Mt. Chōkaisan, 28 July 1887, fl., *R. Yatabe* (TI). **Shikoku**. Ehime Pref.: Between Tsutsujōsan and Mt. Ishizuchiyama, 28 May 1956, fl., *G. Murata & T. Shimizu* (MAK-13149). Kōchi Pref.: Takaoka-gun, Sakawa-chō, June 1893, fr., *T. Makino* (MAK-137668). Tokushima Pref.: Mt. Kōtsusan, 18 April 1948, fl., *K. Abe* 12167 (TNS-132382).

**Distribution:**—Japan (Hokkaido, Honshū, Shikoku, N Kyūshū\*), E Russia (S Sakhalin—e.g. Miyabe & Kudo 1932, Sugawara 1937) (Fig. 29-O). \* The occurrence of *Helonias orientalis* in northern Kyūshū is recorded in Amakawa (1975), but the specimen has not yet been examined by the present author.

**Habitat:**—Shady moist banks along streams in forests, or sunny open mountain meadows or marshes, at elevations ca. 10–3000 m.

**Conservation status:**—This form is widespread, and assessed as LC according to the criteria set out in IUCN (2001). However, local populations near human habitation may be more or less subject to disturbance and threats.

**Flowering:**—Usually March–May. Delayed at high elevations and/or in northern regions.

**Ripening:**—Usually May. Delayed at high elevations and/or in northern regions.

**Remarks:**—On the nomenclature of two species of *Helonias* occurring in Japan, Hara (1947) made the following comment: “When Miquel (1866 in reprint, 1867a) first described *Sugerokia japonica* Miq., he did not cite *Scilla japonica* Thunb. (Thunberg 1784) as its basionym. It was in 1870 that he first cited *Scilla japonica* as the synonym for his species of *Sugerokia*. So the Miquel’s species at the time of publication is regarded as not based on the Thunberg’s species. On the other hand, *Heloniopsis japonica* published by Maximowicz (1867) is the combination not based on Thunberg’s *Scilla japonica* but on Miquel’s *Sugerokia japonica*”. Judging from the protologue by Miquel (1866,

1867a), the type of *Sugerokia japonica* appears to be equivalent with *Helonias orientalis* circumscribed in the present paper. Miquel's *Sugerokia japonica* is based on the specimen regarded by him as probably collected in northern Japan by [MIZUTANI] Sugerok [Sukeroku] (Miquel 1866). As no other collections were cited in the protologue, the specimen should be the holotype. On the other hand, Miquel (1867b) published *S. japonica* var. *racemosa* on a material regarded by him as probably collected by Sugerok. According to Yamaguchi *et al.* (2003: 295, as *Heloniopsis*), there is one specimen of *Helonias orientalis* collected by an anonymous Japanese (L 908. 106-1567, barcode L-0325576\*!). This specimen is evidently the holotype for var. *racemosa*. Yamaguchi *et al.* (2003) also indicates that there is no specimen of *Helonias* (*Heloniopsis*) at Leiden actually accompanying the name Sugerok as the collector. Accordingly it seems possible to view the specimen collected by an anonymous Japanese botanist (L-0325576) as the type of *S. japonica*. Judging from the description of *S. japonica* in the protologue (Miquel 1866), the specimen is at a fruiting stage. At this stage, *H. orientalis* usually has an elongate, racemose infructescence. This character is also consistent with the brief description of var. *racemosa* by Miquel (1867b). The name *S. japonica* var. *racemosa* is therefore the homotypic synonym for *S. japonica*. In Japan *Helonias orientalis* occurs mainly in snowy regions facing the Sea of Japan. Glossy, somewhat thick or firm leaves of this species seem closely related to a heavy snowfall in the habitats. Supposedly, their leaves have become durable to the heavy snowfall in the evolutionary process. The production of plantlets (ramets) by the leaves (Part I-4) might also be related to the heavy snowfall. Much snow accumulated during winter is likely to keep the leaves strongly appressed to the ground. This condition might have become a factor for the induction of such a plantlet production by leaves. If the habitats are kept moist during the growing season, the establishment of the plantlets may be favored. In contrast, in plants of *H. breviscapa* occurring in warmer, less snowy regions in Japan, the leaves are thinner, and adventitious plantlet formation by leaves is not seen. The authentic specimens for *Heloniopsis japonica* var. *purpurea* Nakai (1933) and *H. orientalis* var. *purpurea* (Nakai) Nakai (1952) (see the nomenclatural list above) are not known at present. Nakai (1952) applied the (latter) name to the Korean plants of *Helonias*, so *Helonias koreana* with purple flowers may represent the taxon. However, plants of *Helonias orientalis* with purple flowers also occur in northern Japan (Tōhoku and Hokkaidō), it is therefore possible that both Korean and Japanese plants were included in his original concept of the taxon. In *Helonias orientalis*, floral colors other than pink or purplish pink, such as brick-red, blood-red, blue, and blackish purple-blue, have also been known. Flowers with blue tepals of this species are often found in northern cool regions like Hokkaidō (Japan). Pink tepals often turn dirty brick-red after anthesis. Several variants in floral color were named previously as listed in the synonymy.

### 11b. The form with white flowers (Fig. 25E).

*Heloniopsis grandiflora* Franchet & Savatier (1877: 88, nom. nud.; 1878: 529), '*Helionopsis*'. ≡ *Heloniopsis japonica* (Thunb.) Maxim. var. *grandiflora* Nakai (1933: 243), p.p. Japanese name: Shirobana-shōjōbakama (Nakai 1933). ≡ *Hexonix breviscapa* (Maxim.) F.T.Wang & Tang var. *grandiflora* (Franch. & Sav.) Wang & Tang (1949: 113). **Type** (lectotype, designated here):—JAPAN. Honshū, in provincia Etchigo, circa Niigata, *Vidal* (Savatier 2726) (P-00730554\*!). Isotype: P-00730555\*!, P-00730556\*!.

**Japanese name:**—Yuki-shōjōbakama (*nov.*; meaning snowy white *Helonias*); Shiro-shōjōbakama (Hiyama 1939).

**Description:**—Tepals, filaments, styles and stigmas white. Anthers cream or purple. Similar in other character states to the form with pink or purplish flowers (11a).

**Additional specimens examined:**—JAPAN. **Honshū**. Shiga Pref. (Ômi): Hikone-shi, Surihari-tōge, 11 April 1902, *T. Makino* 960 (MAK-137679). Tōkyō Pref.: Izu, Isl. Kôzu-shima, Mt. Tenjō, in herbages, elev. 400 m, 14 April 1976, flowers white, only one plant has white flowers, others purplish pink (in Japanese), *T. Yamazaki* s.n. (TI). Yamagata Pref.: Mt. Zaô, 20 August 1928, fr., flowers are white, *C. Sto* 202 (TI). **Shikoku**. Kôchi Pref.: Hata-gun, Ôgata-mura, Komehara, 16 March 2003, fl., flowers white, *M. Tashiro* *et al.* (MBK-131864\*). The specimens listed below were recorded by collectors as having yellowish flowers, but there is a good possibility that their flowers were originally white and turned yellowish with the progression of anthesis, though the truth is unknown presently. The floral colors recorded on the herbarium sheets are varied from pale yellowish white to pale greenish yellow: JAPAN. Honshū. Prov. Iwashiro [Fukushima Pref.]: Fujita-tōge, 30 April 1929, flowers pale greenish yellow, *S. Saito* s.n. (TI). Nagano Pref.: Mt. Asama, Sekison-san, 9 April 1957, flowers pale yellowish white, *K. Kawamoto* (TNS-504635). Uzen [Yamagata Pref.]: Yonezawa, 2 May 1931, flowers pale yellow, *H. Koidzumi* (TNS-315689).

**Distribution:**—Japan (Honshū, Shikoku). Sporadically occurs.

**Flowering:**—Usually March–April.

**Remarks:**—Franchet & Savatier (1878 in 1877–1878) described the floral color of *Heloniopsis grandiflora* as white. This taxon is similar in other respects to *Helonias orientalis*. Hiyama (1939) quoted *Heloniopsis orientalis* f.

*albidula* H.Koidz. as a name for the white-flowered form. But unfortunately I have not been successful in tracing the original article with this name by Hideo Koidzumi.

### 11c. The form with yellow flowers.

*Heloniopsis orientalis* (Thunb.) Tanaka f. *lutea* Mochizuki (June 1978a: 14; November 1978b: 10). **Type:**—JAPAN. Honshū. Akita Pref., Nishi-senboku-machi, 24 May 1977, R. Mochizuki (Holotype: KANA-87335, n.v.).

**Japanese name:**—Kibana-shōjōbakama (Mochizuki 1978a, b).

**Description:**—This form has yellow tepals, and is similar in other respects to the form with pink or purplish pink flowers (11a).

**Specimen examined:**—JAPAN. Honshū. Nagano Pref.: Sarashina-gun, Shinonoi-cho, Shinbashi-yama, 30 April 1956, flowers clear yellow, *M. Minemura* 681 (MAK-6543).

**Distribution:**—Japan: Central and N Honshū (Chūbu and Tōhoku Districts).

**Remarks:**—Mochizuki (1978a, b) found an individual with yellow flowers among many individuals with purplish flowers. Minemura also collected a yellow-flowered form in Nagano Pref., central Honshū, Japan (MAK-6543!). She has left a record on the label that the flowers are clear yellow from a bud stage. One needs to be careful in recognizing a genuinely yellow-flowered form of *Helonias orientalis*, since white flowers of the same species consistently turn creamy yellow soon after the peak anthesis. In this connection, a few specimens recorded as having yellowish flowers are cited under the form with white flowers (11b).

### 12. *Helonias breviscapa* (Maxim.) Tanaka (1998a: 111) (Figs. 27, 28).

= *Heloniopsis breviscapa* Maximowicz (1867: 436). = *Heloniopsis japonica* (Thunb.) Maxim. var. *breviscapa* (Maxim.) Honda (1938: 1678). = *Hexonix breviscapa* (Maxim.) Wang & Tang (1949: 113). = *Heloniopsis orientalis* (Thunb.) Tanaka var. *breviscapa* (Maxim.) Ohwi (July 1953b: 68). = *Heloniopsis orientalis* (Thunb.) Tanaka subsp. *breviscapa* (Maxim.) Kitamura & Murata (1966: 72). **Type** (lectotype, designated here):—JAPAN. Kiusiu, in m. ignivomo Wunzen [Kyūshū, Nagasaki Pref., Mt. Unzen], medio Majo, 1863, C.J. Maximowicz s.n. (K-000901111\*!). Isolectotypes: NY-00319713\*-5\*!, P-00730557\*-9\*!, US-00650432\*!

?= *Scilla japonica* Thunberg (in Murray 1784 May–June: 329; August 1784: 137; 1802: t. 4). = *Hexonix japonica* (Thunb.) Rafinesque (1837: 13). **Type:**—JAPAN. Thunberg (Holotype: UPS-THUNB 8323\*!). Japanese name:—Kochō ('Kotjo' in Thunberg 1784); Shōjōbakama (Itō 1829, Iinuma 1861).

= *Sugerokia nipponica* Ohwi (1930: 566). = *Heloniopsis nipponica* (Ohwi) Nemoto (1936: 1058). **Type:**—JAPAN. Honshū. Prov. Yamato [Nara Pref.], Yoshino, between Kashiwagi and Obagamine, 19 May 1928, J. Ohwi (Holotype: KYO, photograph in TNS!). Japanese name:—Yamato-shōjōbakama (Nemoto 1936); Shirobana-shōjōbakama (Hiyama 1939: 79).

= *Heloniopsis japonica* (Thunb.) Maxim. var. *flavida* Nakai (1933: 243). Japanese name:—Kibana-shōjōbakama (Nakai 1933). = *Heloniopsis breviscapa* Maxim. var. *flavida* (Nakai) Hara (1947: 149). = *Hexonix breviscapa* (Maxim.) F.T.Wang & Tang var. *flavida* (Nakai) Wang & Tang (1949: 113). = *Heloniopsis orientalis* (Thunb.) Tanaka var. *flavida* (Nakai) Ohwi (July 1953b: 68). **Type:**—JAPAN. Honshū. Prov. Yamato [Nara Pref.]. Not designated. — *Heloniopsis japonica* (Thunb.) Maxim. var. *grandiflora* (Franch. & Sav.) Nakai (1933: 243), p.p., excl. syn.

= *Heloniopsis japonica* Maxim. var. *yakusimensis* Masamune (1934: 551). Japanese name:—Hime-shōjōbakama (Masamune 1934). = *Heloniopsis yakusimensis* (Masam.) Honda (1938: 1679). = *Sugerokia yakusimensis* (Masam.) Koidzumi (1939: 53). = *Heloniopsis breviscapa* Maxim. var. *yakusimensis* (Masam.) Hara (1947: 148). = *Hexonix breviscapa* (Maxim.) F.T.Wang & Tang var. *yakusimensis* (Masam.) Wang & Tang (1949: 113). = *Heloniopsis orientalis* (Thunb.) Tanaka var. *yakusimensis* (Masam.) Ohwi (July 1953b: 68). = *Heloniopsis yakusimensis* (Masam.) Masamune (1969: 11), isonym. **Type:**—JAPAN. Kyūshū. Kagoshima Pref.: Isl. Yakushima, ca. 1500 m, G. Masamune (from the protologue). The following specimen is possibly holotype, as it coincides well with the original description: Isl. Yakushima, 6 April 1927, G. Masamune (TI!).

= *Heloniopsis japonica* (Thunb.) Maxim. var. *albiflora* Honda (1938: 1678). = *Heloniopsis breviscapa* Maxim. var. *albiflora* (Honda) Hara (1947: 149). **Type:**—JAPAN. Honshū. Prov. Musasi [Tokyo Pref.], Sekido, [3 April] 1938, T. Sakai s.n. (Holotype: TI!). Paratypes cited in the additional specimens examined below. Japanese name:—Sirobana-shōjōbakama (Honda 1938).

= *Heloniopsis japonica* (Thunb.) Maxim. var. *tesselata* Nakai ex Honda (1938: 1679). **Type:**—JAPAN. Honshū. Prov. Awa [Chiba Pref.], Mt. Kiyozumi, April 1937, T. Nakai s.n. (Holotype: TI!). Japanese name:—Kiyozumi-shōjōbakama (Honda 1938).

— *Heloniopsis pauciflora* auct. non A.Gray: Miquel (1867: 146), as to specimens from Kiusiu by Maximowicz, '*Helionopsis*'.

— *Sugerokia japonica* Miquel (1870: 52), p.p., as to synonyms? *Scilla japonica*, *Heloniopsis breviscapa* Maxim., and specimens from Mt. Wunzen, Kiusiu [distributed under the name *Heloniopsis pauciflora* by Maximowicz with the date of 1865].

— *Heloniopsis japonica* auct. non Maxim.: Matsumura (1905: 197), p.p.; Honda (1938: 1677), p.p.

— *Sugerokia japonica* auct. non Miquel: Koidzumi (1930: 95).



**FIGURE 27.** *Helonias breviscapa*. A–D. Inflorescence and rosette turned brown in winter. A; material from Kyūshū Br-4 (Photo: 29 March 2014). B; Shikoku Br-3 (22 March 2014). C; Honshū Br-2 (19 March 2014). D; Honshū Br-1 (24 March 2014). E. Ripe fruits (Br-2; 12 May 2012). F. Dehiscing capsules (Br-2; 2 May 2014). G. Fresh rosulate leaves with minutely undulate margins (Br-1; 14 Aug. 2013). All photos at Hachioji, Tokyo.

**Japanese name:**—Kochō-shōjōbakama (Tanaka 1998, based on ‘Kojyo’ for *Scilla japonica* in Thunberg 1784: 137), Shirohana-shōjōbakama (e.g. Iwasaki 1824; Makino 1891, under *Heloniopsis japonica* Maxim., p.p.?; Koidzumi 1930), Tsukushi-shōjōbakama (Honda 1938), Yakushima-shōjōbakama (Honda 1938).

**Description:**—Rhizome cylindrical, subannulate with many close scars, to 5 cm long, to 1.5 cm in diam., pale brown. Roots filiform, to 1.5 mm in diam., white, some showing signs of contraction. Leaves hysteranthous, main fresh rosette leaves 7–15, persistent usually for fully 1 year (sometimes for ca. 2 years), spatulate or narrowly oblanceolate,

3.5–21.5 cm long, to 3.5 cm wide, often minutely undulate at margin, apex with apiculus 0.5–1 mm long, light (often yellowish) green, chartaceous (thin to moderately thick in texture), young fresh leaves somewhat glossy, mature leaves almost dull. Stem usually ca. 2–17 cm long at anthesis, becoming elongate toward fruiting stage; peduncle to 37 cm long in fruit; scale-like leaves 5–11 (excl. basal ones), linear-lanceolate, narrowly lanceolate, narrowly elliptic-oblong, to ca. 3.8 cm long, apex acute or acuminate; inflorescence compactly racemose or sub-umbellate, rachis to 1.7 cm long at anthesis, to 8 cm long in fruit; pedicels terete, 2–7 mm long at anthesis, to 23 mm long in fruit, 6-ribbed, ebracteate. Flowers 1–11, usually nodding at mid anthesis, funnelform, 1–1.9 cm across, scent or odorless. Tepals 6, obconically expanded, sometimes slightly recurved distally, 5–7(–9)-veined, white, often tinged (purplish) pink proximally, turning creamy yellow or sometimes pink with progression of anthesis, eventually green after anthesis, (oblong-)ob lanceolate or spatulate, 8.3–14 mm long, 1.8–5.2 mm wide, apex rounded to subacute; abaxial basal part scarcely to moderately gibbous; adaxially shallowly to moderately canaliculate toward base, proximal submarginal portions winged (lamellate) inward; wings extending over proximal ca. 1/4 of tepal, connate proximally to those of adjoining tepals for 0.25–1 mm in height, and also adnate to opposite filament for 0.7–1.8 mm in height, forming a sheathing nectary; surface of the nectary positioned nearly as high as base of ovary (or top of receptacle); base of tepal affixed to receptacle (apex of pedicel) for ca. 1.5 mm in length. Stamens 6, equaling or exceeding tepals; filaments filiform, 5–12.5(–15) mm long, 0.4–0.6 mm wide, nearly straight, scarcely dilated but slightly complanate toward base, white or pale purplish pink; anthers affixed to filament on adaxial portion close to base of connective (i.e. [sub]dorsi-basifixed), bilocular, (dark) purple, narrowly ovate or oblong-ovate, (1.5)–2–3.5(–4.5) mm long, base sagittate, apex scarcely confluent between thecae, sometimes minutely apiculate; pollen whitish. Pistil 1, 9–19.5 mm long, exceeding stamens and tepals; ovary globose, slightly trilobed, 2–4 mm long, 2–5 mm across, apex emarginate-concave, (pale yellowish) green or dark purplish pink, subdistal portion of carpel divergently protruding in fruit; ovules numerous, multiseriate (ca. 8-seriate) on central axile placentae; style terete, slightly narrowed proximally, straight or sometimes upcurved distally in nodding flowers, 6.7–13(–18.5) mm long, white or pale purplish pink; stigma discoid or depressed capitate, sometimes obtusely trigonous, or slightly trilobed to tricleft, 1.0–2.5(–3.3) mm across, white or pale purple. Capsules antorse, broadly obpyramidal, tripartite, subtriangular in frontal aspect, obcordate or broadly obdeltoid in lateral aspect, 5–8 mm long, 1–1.5 cm across; lobes mitriform (or ovoid-pyriform), ascending, strongly divergent. Seeds with white or pale brownish testa, linear-fusiform, usually falcate, 4.8–6.7 mm long, 0.3–0.5 mm wide, proximally sublinear, distally subulate; body of seed oblong-fusiform, 1.4–1.7 mm long, 0.3–0.4 mm wide, brown.

**Additional specimens examined** (see also Tanaka 1998a):—JAPAN. **Honshû. Chûbu** Distr. Shizuoka Pref.: Mt. Higaneyama, 10 April 1920, fl., *Ôsaka-fu Joshi Senmon-gakkô* (MAK-137590). **Chûgoku** Distr. Yamaguchi Pref.: Tokuyama-shi, Nakasu-kita, Datoko, 11 April 1971, fl., *H. Manabe* no. 3 (TNS); Abu-gun, Tokusa, Mt. Nodôyama, ca. 900 m, *N. Miake* no. 5 (TNS-285022). **Kantô** Distr. Chiba Pref.: Awa-gun, Mt. Kiyosumi, May 1938, fl., *S. Asano* (TNS-59232). Kanagawa Pref.: prov. Sagami, Mt. Hakone, [May] 1910, fl. yellow, *G. Koizumi* s.n. (paratype of *Heloniopsis japonica* var. *albiflora*, TI!); Mt. Tanzawa, April 1960, fr., *D. Yoshikawa* (TNS-140984). Tokyo Pref.: Tama-shi, Sekido 7 April 1952, fl., U. Mizushima (TI, TNS-02633). **Kinki** Distr. Hyôgo Pref.: Kôbe, Mt. Rokkô, 11 April 1948, fl., *C. Kataoka* (TNS-132386). Kyôto Pref.: prov. Yamashiro, Mt. Hiei, [29 March] 1911, fl.-albi, *T. Nakai* s.n. (paratype of *Heloniopsis japonica* var. *albiflora*, TI!). Mie Pref.: Ise, Rokusôdani, 24 March 1961, fl., *S. Okuyama* 13565 (TNS-261521). Nara Pref.: Yoshino-gun, Mt. Mikamiyama, May 1888, fr., *H. Sakurai* (TNS-3836). Ôsaka Pref.: Mt. Kongôsan, 25 April 1953, fl., *M. Togashi* 720 (BM-001118052, TNS-105921); Mt. Kongôsan, 5 May 1935, fr., *Z. Yoshino* (TI). Wakayama Pref.: Mt. Kôyasan, Yatake, 20 Mar., *G. Murata* 22166 (TNS-305431). **Kyûshû**. Fukuoka Pref.: Nogouchi-keikoku, 27 March 1932, fl., *H. Arao* (TNS-255640). Kagoshima Pref.: Mt. Takakuma, 20 March 1944, fl., *Y. Satake & S. Okuyama* (TNS-79936–79938); Isl. Sakurajima, April 1904, fl., *Y. Yoshise* (MAK-137580). Kumamoto Pref.: Mt. Aso, Akamizu, 500 m, 2 April 1954, fr., *Y. Shimada* (TNS-248995); Kami-mashiki-gun, Yabe-machi, 280 m, 1 April 1994, *T. Kawasaki* 1059 (TNS-605322). Miyazaki Pref.: Sakatani-mura, Inotani, 22 Mai 1942, fr., *S. Hattori* 760 (TNS-307327); Kawaminami-mura, 10 March 1950, fl., *M. Nagasawa* (TNS-98301). Nagasaki Pref.: Simabara in montibus, bot. *Japonicus* s.n. (LE-01011595\*); Mt. Unzendake, 29 March 1912, fl., *Z. Tashiro* (TNS-29965). Ôita Pref.: Mt. Kujuû, 24 April 1908, *Nakamura* 698 (TNS-79925). Saga Pref.: Ogi-gun, Mt. Hikodake, 22 April 1980, fr., *T. Hashimoto* (TI). **Shikoku**. Ehime Pref.: Shingû-mura, March 1889, fl., *T. Makino* (TNS-3838). Kôchi Pref.: Kami-gun, mononobe-mura, 3 March 1976, fl., *K. Suzuki* (MAK-270211); Nagaoka-gun, Ôtoyo-mura, Tatekawa, 5 May 1893, *T. Makino* (MAK-137567). Tokushima Pref.: Mt. Kôtsusan, 30 April 1903, *J. Nikai* (TNS-49296); Naka-gun, Aioi-chô, 300 m, 22 April 1983, fr., *M. Takahashi & K. Ueda* 1522 (TI); Mima-gun, Tsuzuro, 28 March 1940, fl., *T. Yoshinaga* (TI).

**Distribution:**—Japan: Honshû (southern Kantô District and westward to Chûgoku District), Shikoku, Kyûshû (Fig. 29-B).



**FIGURE 28.** *Helonias breviscapa*. **A.** Flower (material Br-5). **B, C.** Vertical section of flower (B; Br-5. C; Br-3). Surface of nectary arrowed. **D.** Proximal exterior of flower, side view (Br-1). **E.** Flower with pistil removed, front view (Br-2). Two connate portions between submarginal lamellae of adjoining tepals arrowed. **F.** Bilocular anthers with no apical confluence between thecae arrowed (Br-2). IF: inner filament. OF: outer filament.

**Habitat:**—Shady or semishady moist rocks or slopes usually along or near streams in forests at elevations ca. 150–900 m.

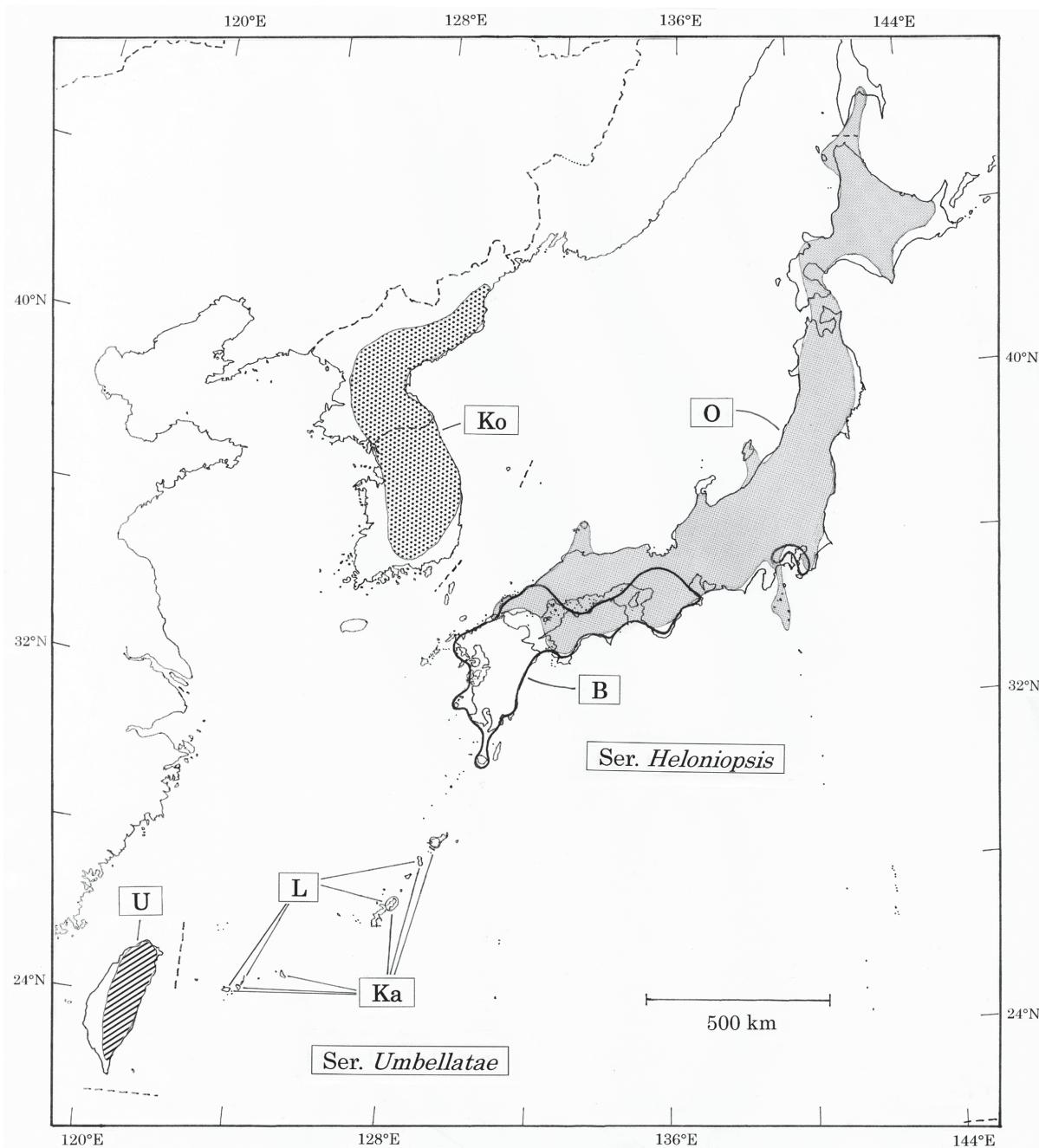
**Conservation status:**—The species is comparatively widespread, and assessed as LC according to the criteria set out in IUCN (2001). However, local populations near human habitation may be more or less subject to disturbance and threats.

**Flowering:**—March–April.

**Ripening:**—May.

**Remarks:**—Plants of *Helonias breviscapa* here circumscribed have often been treated as conspecific with *H. orientalis* (including its synonymous taxa) or as infraspecific taxa of the latter (Miquel 1870, Ohwi 1953a, b, 1965, Kitamura 1964, Kitamura & Murata 1966). The two species may look somewhat alike, but *H. breviscapa* differs from *H. orientalis* by the thinner, less glossy, somewhat lighter (yellowish) green leaves usually minutely undulate at the margin (Fig. 27G), usually smaller flowers, and white tepals of which the proximal submarginal wings are relatively shorter and the nectary is positioned nearly as high as the ovary base (Fig. 28B, C; Tanaka 1997b, 1998a). Compared with *H. orientalis*, *H. breviscapa* is usually in warmer regions with less snowfall in winter in Japan. Their geographic ranges overlap partly (Fig. 29-O, -B) (Tanaka 1997e, 1998a; Kawano *et al.* 2007). They were recognized as distinct by Maximowicz (1867), Hara (1947), and Tanaka (1998a). A few local forms of *Helonias breviscapa* have hitherto been recorded. For example, plants from Kyūshū (Figs. 27A, 28A, B), which were recognized as *Heloniopsis breviscapa* var. *breviscapa* (Hara 1947), usually have comparatively broad oblanceolate tepals which are abaxially often tinged (pinkish) purple and scarcely gibbous at the basal portion. Those from Isl. Yakushima, southern Kyūshū, which were distinguished as *H. breviscapa* var. *yakusimensis* (Hara 1947), are usually somewhat smaller in habit and have 1 or a few flowers and slightly thicker leaves. Those from the Kinki District, central Honshū (Figs. 27C, D, 28D), named *H. breviscapa* var. *flavida* (Hara 1947), have white, slightly longer, narrowly oblong-oblanceolate tepals with a slightly gibbous base. When some typical representatives of these varieties are compared, they may look somewhat distinct from one another. However, they are rather indistinct in delimitation due to a gradational variation between them when many samples from different localities are compared (Tanaka 1998a). For instance, plants from eastern Shikoku (Tokushima Pref.; Figs. 27B, 28C) have tepals scarcely inflated at the base and often tinged with purple toward the base like those from Kyūshū. Some plants from the Kinki District of Honshū also have tepals tinged purplish proximally and scarcely gibbous at the base (Figs. 27D, 28D). Fuse *et al.* (2004) stated that the leaves of *H. breviscapa* var. *flavida* are somewhat thin and spotted with reddish brown in winter, while those of *H. breviscapa* var. *breviscapa* are slightly thicker and spotted with brown to blackish purple in winter. In my observation, however, this distinction is not necessarily constant between them. For instance, under a cultivated condition in Tokyo, the leaves of plants from Kyūshū (*H. breviscapa* var. *breviscapa*) often turn reddish brown in winter. Those from different localities (Kyūshū, Shikoku, and the Kinki District of Honshū) often turn similarly brownish, irrespective of the original localities (Fig. 27A–D). Such coloration of the leaves appears to reflect coldness in winter, and may change to some extent in response to the fluctuation of temperature and habitat conditions. It seems more reasonable to regard these varieties (*breviscapa*, *yakusimensis*, *flavida*) as local forms (races) not distinctly delimited from one another. I have noticed that the flowers of some plants from Kyūshū (Fukuoka and Miyazaki Pref.) and Shikoku (Tokushima Pref.) are fragrant, while those from the Kinki District (Nara, Mie, and Wakayama Pref.) are odorless. This intraspecific variation in floral fragrance needs a further survey. Despite these variations, *Helonias breviscapa* as a whole appears to retain a fairly high unity, possessing a unique combination of features as noted earlier. It is noteworthy that *Helonias breviscapa* (Fig. 27G) and *H. koreana* (Fig. 23H) share somewhat thin, dull or subdull leaf blades usually with minutely undulate margins. They usually occur in regions which are drier and less snowy in winter than the habitats of *H. orientalis*. *Helonias breviscapa* occurs in warmer regions than *H. koreana*. The relationship between the species of *H. ser. Heloniopsis* and the geographic and climatological features of their ranges are discussed in Part III-5. Tanaka (1998a) once assigned *Scilla japonica* to *Helonias breviscapa* on the basis of the description by Thunberg (1784) (especially of floral color: *corolla albo purpurea*) and the scapes figured in Thunberg (1802). Very recently (July 2018) I had an opportunity to examine the image of the scapes of the type material (*Thunberg s.n.*, UPS-THUNB 8323\*). Unexpectedly, the scapes looked fairly similar to those of *H. orientalis*. Further studies are necessary to precisely identify them. *Scilla japonica* is tentatively placed in the above synonymy. Nakai (1933) described the perianth of *Heloniopsis japonica* var. *flavida* as greenish yellow at anthesis, but did not cite any specimen. White tepals of *Helonias breviscapa* turn yellow or yellowish green soon after the peak anthesis, and moreover, the floral parts are persistent even at the fruiting stage. So the flowers after anthesis are often taken as those at anthesis with yellow or yellowish green tepals. At present there is no means to examine Nakai's taxon as to the flowering stage and floral color on a specimen basis. A few herbarium specimens of *Helonias breviscapa* record the flowers as yellow, e.g., Kanagawa Pref., Hakone, May 1910, fl. yellow, *G. Koizumi s.n.* (paratype of *Heloniopsis japonica* var. *albiflora*, TI!); Mie Pref., Suzuka Mts, Gozaisho-dake, 20 Apr. 1941, fl. yellow, *Morimoto no. 5* (TI!). The flowers appear to be past the flowering stage, implying the possibility that they were white at anthesis. Doi (1983: 135) recorded a yellow-flowered form of *Helonias breviscapa* as “*Heloniopsis orientalis* C. Tanaka subsp. *breviscapa* Kitam. f. *satsumensis* Doi” based on a specimen from southern Kyūshū, Japan (Kagoshima Pref., Ijūin-chō, April 1938, *Toshio Shin*, currently preserved at HIRO, the image seen). However, the

name did not accompany a description nor a diagnosis in Latin, hence it was invalidly published. He noted that the flowers are yellow from the beginning of flowering. Such a yellow-flowered form has not been reported from anywhere since then. Studies based on fresh living plants seem necessary for a more precise understanding of this form.



**FIGURE 29.** Distribution of six species belonging to two series of subsect. *Heloniopsis* in EAsia. B: *Helonias breviscapa*. Ka: *H. kawanoi*. Ko: *H. koreana*. L: *H. leucantha*. O: *H. orientalis*. U: *H. umbellata*. Ser. *Umbellatae* comprises Ka, Land U. Ser. *Heloniopsis* consists of B, Ko and O.

### Part III. Evolution and phyogeography

Evolutionary aspects of various characters (Part I) and taxa (Part II), and the historical background of the current distribution of *Helonias* (Part II) are discussed.

## 1. Pseudoduality in generation of flowering stems in vernal species, and variation in dormancy of leaf and flower buds

**Pseudodual generation of flowering stems in vernal species, and its origin:**—In mature plants of vernal species, such as *Helonias bullata*, *H. thibetica* and *H. orientalis*, two kinds of buds are produced in a basal rosette (Fig. 1A, B; Part I-2). One is a flower bud (inflorescence bud) that develops into a flowering stem (sexual reproductive organ; *F* in Fig. 1); the other is a leaf bud that develops a basal rosette of leaves (vegetative organs; *L* in Fig. 1). Both types of buds may be regarded as of the same generation, since they develop in the same growing season (Fig. 1C, D). Contemporaneous development of two kinds of buds in *Helonias* is unusual. Many related perennials, such as *Veratrum* L. and *Anticlea* Kunth (Melanthiaceae - Melanthieae; Dahlgren 1985), produce only one kind of bud that develops into vegetative and sexual reproductive organs consecutively. In these plants, development of vegetative organs precedes development of sexual organs. They complete their yearly growth cycle within a single growing season (from spring through autumn). *Helonias* differs from *Veratrum* and allied genera in having leaves that persist after a single season, but their mode of development appears basically similar. As in *Veratrum*, the two organs of *Helonias* develop successively. That is, in temperate vernal species of *Helonias*, a leaf bud sprouts in the growing season (spring to summer), and around the time when the development of most fresh leaves is nearly completed, the flower bud starts to form (usually from July to September). Unlike in *Veratrum* and its allies, the flower bud of *Helonias* is formed, but does not sprout. Instead, it remains dormant until the coming spring (*F* in Figs. 1A, B, 4). The vegetative and the sexual organ of *Helonias* thus develop successively as in *Veratrum*, but their growth periods are largely separated by a cold season inserted in the middle of the yearly growth cycle. A flower bud initially forms in one year and the fresh flowering stem develops in the next (*F* in Fig. 1C, D). Rosulate leaves sprouted in the preceding year (*R* in Fig. 1) are regarded as of the same generation, since they originate within a single growth cycle, then develop sequentially. Two kinds of buds sprouting nearly concurrently in the spring from a rosette (*F* and *L* in Fig. 1C, D), mentioned above, are regarded as two generations, or two consecutive generations. That is, the flower bud (*F* in Fig. 1A, B) is of the same generation as the rosulate leaves sprouted in the preceding year (*R* in Fig. 1C, D); the leaf bud (*L* in Fig. 1A, B) to sprout in the current growing season is of the next generation. Thus the flower buds (flowering stems) superficially look dual in generation. Supposedly, ancestral *Helonias* grew in warmer regions with no severe cold season, and the two kinds of organs developed nearly consecutively as in *Veratrum*. Then the climate became cooler and was accompanied by a cold season or, alternatively, the plants extended their range to cooler regions with severe winters. Through the course of evolution, the ancestors eventually acquired a gapped, prolonged yearly growth cycle in which the development of the sexual organs became separated seasonally from development of vegetative organs due to the insertion of a cold season. This yearly growth cycle naturally requires a longer span than a non-gapped growth cycle as seen in *Veratrum*. It takes a span over two years (or two growing seasons with a cold season in between) when estimated from the time of sprouting of a leaf bud (in spring) to the death of a flowering stem in the following year (usually in late spring to early summer). If estimated from the time of initial formation of a leaf bud, usually from summer to early autumn in the year preceding sprouting, then an entire growth cycle spans over three years (or three growing seasons with two cold seasons in between) (Fig. 2). *Chamaelirium* (including *Chionographis*), which is closely allied to *Helonias* (Tanaka 1997e, 2017a, b), also has such a gapped, prolonged yearly growth cycle and a flowering stem pseudodual in generation, suggesting that *Chamaelirium* and *Helonias* are sister groups sharing a common ancestor.

**Reduced dormancy in leaf and flower buds of Asian subtropical species:**—In *Helonias kawanoi* and *H. jinpingensis* in the subtropics, anthesis is usually in late summer to autumn. In *H. kawanoi*, the flower bud sprouts shortly after most fresh leaves nearly complete their development (Figs. 2, 16A, D, E). That is, the two organs develop nearly consecutively. This mode of development differs from other temperate vernal species in which the sprouting of a flower bud is suppressed until the spring (*F* in Figs. 1A, B, 4). The yearly growth cycle of *H. kawanoi* and *H. jinpingensis* was probably secondarily acquired as a result of adaptation to a warm subtropical climate. Under such a climate with no severe cold season, dormancy of the flower bud may have been reduced or lost. In temperate vernal species of *Helonias*, the leaf bud is similar to the flower bud, initially formed from summer to early autumn in the central portion of a rosette, then remaining dormant until spring (*L* in Figs. 1A, B, 4). In *H. kawanoi*, *H. leucantha* and *H. umbellata*, however, the leaf bud often begins to sprout in autumn and winter (Figs. 16A, D, E for *H. kawanoi*, 18F for *H. leucantha*), although growth appears more or less suppressed under the cooler conditions (Fig. 2). In these species the dormancy of the leaf bud appears to have been reduced. The basic mode of development of ancestral *Helonias* (or of the *Helonias* and *Chamaelirium* lineage) might have been similar to that of the subtropical species. The phenological process of a yearly entire growth cycle in seven species of *Helonias* is schematized in Fig. 2. Ancestral *Helonias* is presumed to have existed somewhere in the northern circumpolar region in the Paleogene when temperatures became

predominantly lower toward the end of the period (for a geological and climatological aspect, see: Chaney 1947, Tanai 1967, 1972, 1988, 1992, Uemura 1995, Ogasawara & Uemura 2006). The historical background of the migration or extension of the ancestral populations of *Helonias* is discussed below (section 5).

## 2. Trends in the evolution of characters and structures

**Evaluation of character states from an evolutionary perspective:**—In the course of evolution, simple structures of plants often become more complex by fusion of similar or dissimilar parts or by developing additional structures. In general, with an increase of such complexity, the level of structural organization or specialization becomes higher. It is often difficult to determine evolutionary directions in phenotypic characters, but in characters showing stepwise structural changes, it seems possible to draw fairly reasonable inferences on directions. In *Helonias*, for instance, the tepals and the filaments of several species (e.g., *H.* sect. *Helonias*, *H.* subsect. *Ypsilandra*) are free and the nectaries are more or less shallow, while those of some other species (*H.* ser. *Heloniopsis*) are adnate to form saccate or tubular nectaries (Part I-8). These are judged to be derived, more advanced structures (i.e. apomorphies). As for the pistil, the degree of connation among three carpels to form a single columnar style varies among taxa (Part I-8). It is evident that the carpels least connate among them are most primitive in state, and those entirely connate along their length are most advanced (Part III-2-3). Evolution in the reverse direction (or retrogressive evolution), from a higher level of organization or specialization to a lower level, is highly improbable in these structures of *Helonias*. Inferences from these structures therefore appear to be applicable to the determination of evolutionary directions of characters (Part III-2) and to the elucidation of the process of phyletic diversification in this genus (Part III-3, -4). In inferring evolutionary trends of characters, the corresponding character states in other related genera, such as *Chamaelirium*, *Xerophyllum* and *Veratrum*, were also taken into account (e.g. floral color, nectar-secretion in tepals, morphology of ovaries, capsules and seeds). Table 10 shows evolutionary trends of several characters thus inferred.

**TABLE 10.** Presumed direction of evolutionary changes of phenotypical characters in *Helonias*.

Character	Primitive (plesiomorphic) state	Derived (apomorphic) state	Representative taxa with derived character state
Dormancy of flower and leaf buds	present	reduced or lost	<i>H. jinpingensis</i> , <i>H.</i> ser. <i>Umbellatae</i>
Inflorescence	racemose	(sub)umbellate	Part of <i>H.</i> ser. <i>Umbellatae</i> , <i>H.</i> ser. <i>Heloniopsis</i>
Floral bract	absent	present	<i>H. jinpingensis</i> , <i>H. kawanoi</i>
Flower number / inflorescence	comparatively many	few	<i>H. kawanoi</i> ; <i>H.</i> ser. <i>Heloniopsis</i>
Tepal			
Proximal, submarginal wings	absent	present	<i>H.</i> ser. <i>Heloniopsis</i>
Connation between adjoining tepals	absent	present	<i>H.</i> ser. <i>Heloniopsis</i> (occasionally also in <i>H. umbellata</i> )
Adnation to opposing filament (forming sheathing nectary)	absent	present	<i>H.</i> ser. <i>Heloniopsis</i>
Depth of nectary	shallow	deep	<i>H.</i> ser. <i>Heloniopsis</i>
Stamen			
Filament			
Base (position)	adnate or close to ovary base	adnate or close to tepal base	<i>H.</i> subsect. <i>Heloniopsis</i>
Fusion to opposing tepal (forming sheathing nectary)	absent	present	<i>H.</i> ser. <i>Heloniopsis</i>
Anther			
Number of locule	1	(virtually) 2	<i>H.</i> subsect. <i>Heloniopsis</i>
Apical confluence between thecae	present	rudimentary	<i>H.</i> subsect. <i>Heloniopsis</i>
Site of anther connective affixed to filament	base	slightly above base	<i>H.</i> ser. <i>Heloniopsis</i>

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**TABLE 10.** (Continued)

Character	Primitive (plesiomorphic) state	Derived (apomorphic) state	Representative taxa with derived character state
Pistil			
Height vs anthers and tepals	lower	higher (exserted)	<i>H. thibetica</i> , <i>H. subsect. Heloniopsis</i>
Connation among carpels to form columnar style	slight	complete or nearly so	<i>H. thibetica</i> , <i>H. subsect. Heloniopsis</i>
Lobing of stigma	deeply seected	unlobed (entire)	<i>H. thibetica</i> , <i>H. subsect. Heloniopsis</i>
Ovule number / locule or ovary	comparatively few	many	e.g., <i>H. ser. Heloniopsis</i> . See Table 1.
Seed			
Shape	subfusiform (flat)	linear	<i>H. sect. Heloniopsis</i>
Wings on sides	comparatively wide	narrow	<i>H. sect. Heloniopsis</i>
Maturation of stigma and anthers	adichogamous	protogynous	<i>H. thibetica</i> , <i>H. subsect. Heloniopsis</i>

**Inflorescence:**—*Helonias* has different types of inflorescence (Part I-7). *Helonias* sect. *Helonias* and *H. subsect. Ypsilandra* (*H. sect. Heloniopsis*) have a raceme, while *H. subsect. Heloniopsis* has a raceme, subumbel or an umbel. From a structural point of view, umbels appear more advanced or specialized than racemes. Flowers considered to be primitive, such as those of *H. sect. Helonias*, are borne in racemes, while flowers regarded as advanced, such as those of *H. ser. Heloniopsis*, form umbels. In related genera such as *Chamaelirium*, *Xerophyllum* and *Veratrum*, racemes or panicles are common (Britton & Brown 1896, Tamura 1998, Utech 2002). Considering these facts, it is highly probable that the inflorescence of *Helonias* was originally a raceme, but evolved to become a subumbel or an umbel through abbreviation of the rachis. With this change, the arrangement of flowers on the rachis also changed from spiral (in a raceme; e.g. Fig. 13C) to subverticillate (in an umbel; e.g. Fig. 23E). In *H. sect. Helonias* and *H. subsect. Ypsilandra*, the nectary at the base of the tepal is shallow and the nectar is exposed (Part I-8), so even insects with short mouthparts (trophi) could suck the nectar. In *H. ser. Heloniopsis* (*H. subsect. Heloniopsis*), the nectary is saccate or tubular (Part I-8), suggesting that the flowers of *H. ser. Heloniopsis* are adapted to pollinators that can extract nectar from such deeper nectaries. The evolutionary shift from raceme to umbel may also be related to the kinds and habits of pollinators. This shift is supposed to have improved the efficiency in pollination. Whether the inflorescence is a raceme or an umbel, flowers in aggregation (e.g. Figs. 4A–E, 13C, 25A–D) must have been more effective in attracting insects. This state is likely to have increased the opportunity for pollination. The ebracteate inflorescence of *Helonias* (e.g. Figs. 13C, 18D, 23G) is also shared by the closely allied *Chamaelirium* (Tanaka 2017b), so it must have been the original state. The bracteate inflorescences of *H. jinpingensis* and *H. kawanoi* (Fig. 16C) appear to be secondarily derived (Table 10).

**Pistil:**—In *Helonias*, the three carpels are connate to form a columnar style the relative length of which differs among the species (Part I-8; Tanaka 1997c, e). The style is shortest in *H. bullata* (Fig. 5D, Table 6; Tanaka 1997a). In *H. thibetica* (*H. subsect. Ypsilandra*) and *H. subsect. Heloniopsis* the style is well developed and the pistil often exceeds the stamens (Part I-8; e.g. Figs. 13B, C, 16B, 27A–D, 28A, Table 6 for *H. thibetica*). In *Helonias*, pistils with a relatively short style (columnar part) and long stigmatic segments, such as those of *H. bullata* (Fig. 5D) and *H. yunnanensis* var. *yunnanensis* (Fig. 7B), are regarded as more primitive. This state apparently shifted evolutionarily toward a relatively long style and short stigmatic segments. A pistil with a long style and discoid or (sub)capitate stigma occurs in *H. thibetica* (e.g. Figs. 3A–C, 14A) and subsect. *Heloniopsis* (e.g. Figs. 3D, E, 20D, 22A, 24F, 28A; Tanaka 1997c, e), and is regarded as the most advanced state. The evolution of the pistil in *Helonias* thus appears to be directional and anagenetic.

**Anthers:**—The anthers of *Helonias* vary in structure, shape, size, and in position relative to the stigmas (Part I-8). The anthers of *H. bullata* (*H. sect. Helonias*) and *H. subsect. Ypsilandra* are unilocular and basifixated (e.g. Figs. 5B, 14E). They expose their pollen not only laterally but also apically (Fig. 2 in Tanaka 1997a), hence they may readily smear pollen on insects foraging for pollen and/or nectar. In *H. subsect. Heloniopsis* the filament tends to be located closer to the opposing tepal (Figs. 19B–E, 22A–E, 28B, C, E; Tanaka 1997b, c, e). The anthers are virtually bilocular, extrorse, and often comparatively long (Figs. 22F, 24F, 28F; Tanaka 1997c), accordingly their pollen is likely to be smeared on insects trying to extract nectar from the base of the tepals. They appear to be more adapted to insects seeking nectar (Tanaka 1997e), although insects seeking only pollen, such as flies, also visit and pollinate the flowers, as reported by Takahashi (1988). During the course of evolution the anthers of *Helonias* appear to have changed from unilocular to bilocular (Tanaka 1997c). Almost perfectly bilocular anthers are produced in *H. breviscapa* (Fig. 28F;

Tanaka 1997c) and may represent the ultimate evolutionary outcome. It is also noteworthy that the anthers of *H. ser. Heloniopsis*, especially of *Helonias koreana* (Fig. 24F) and *H. orientalis*, are (sub)dorsi-basifixed, i.e. the anther is affixed to the filament adaxially slightly above the connective base (Part I-8). This state is obviously apomorphic.

**Floral structure:**—Flowers of *Helonias* are highly diversified especially in structure (Part I-8). For instance, the tepals are almost flat or only slightly canaliculate in *H. sect. Helonias* and *H. subsect. Ypsilandra*, while they are more prominently grooved especially in *H. ser. Heloniopsis*. Nectaries are nearly flat or only slightly concave in *H. sect. Helonias* and *H. subsect. Ypsilandra*, they are markedly saccate in *H. ser. Heloniopsis* (Part I-8). In *H. sect. Helonias*, *H. subsect. Ypsilandra* and *H. ser. Umbellatae*, the filaments and tepals are distinct or almost so. They are basally fused in *H. ser. Heloniopsis* (Part I-8). From a structural point of view, the floral evolution of *Helonias* appears to have advanced stepwise from the state in *H. sect. Helonias* (Figs. 4, 5) and *H. subsect. Ypsilandra* (e.g. Fig. 7), through *H. ser. Umbellatae* (e.g. Figs. 17, 19, 20, 22), and lastly to *H. ser. Heloniopsis* (e.g. Figs. 24, 26, 28; Tanaka 1997e). The flower of *H. ser. Heloniopsis*, which is made up of a single pistil and six surrounding subunits each consisting of a stamen and the opposing tepal that jointly form a saccate or tubular nectary, is viewed as an integrated apparatus for achieving efficient pollination through the behavior of certain insects (Tanaka 1997e).

**Ties with insects:**—The flowers of many species of *Helonias* are fragrant and the tepals are nectariferous and often pink, bluish, violet or white (Part I-8). It is obvious that these features effectively attract insects foraging for nectar and/or pollen (Part I-11, Takahashi 1988). The flowers of *Helonias* are basically similar to one another, so they must have been coevolving with the insects since their origin. In this connection, it is notable that the flowers of *H. leucantha* (*H. ser. Umbellatae*), *H. breviscapa*, *H. koreana*, and *H. orientalis* (*H. ser. Heloniopsis*) are often odorless or nearly so, perhaps indicating that fragrance is not always necessary for attracting some kinds of pollinators, which may discern the flowers by other sensory means, such as vision. In the most closely allied *Chamaelirium* the flowers have no nectaries (Tanaka 2017b). It is therefore obvious that close ties with insects foraging for nectar have been a principal factor for the evolution of *Helonias* (Fig. 30, List 2).

**Traits securing seed production under poor availability of pollen vectors:**—*Helonias orientalis* blooms in early to mid spring. Although infrequently visited by insects (Takahashi 1988, as *Heloniopsis*), the flowers produce numerous seeds in the field (Kawano & Masuda 1980). The following three traits of this species appear to cooperate effectively to secure seed production under poor availability of pollen vectors: high self-compatibility (known also in *H. bullata* and *H. thibetica*; Part I-12), long flowering duration (known also in many species such as *H. bullata*, *H. thibetica* and *H. subsect. Heloniopsis*; Part I-8), and widely open, funnel-shaped flowers that are structurally highly accessible for a wide variety of insects (known also in *H. bullata*; Part I-11). Judging from the high similarity in sexual reproductive characters (e.g. self-compatibility, floral morphology, flowering phenology, pollination ecology) among the species, these three traits appear to have been cooperating as essential, effective sexual means to survive over the course of evolution in *Helonias*.

**Evolution of structurally advanced flowers of *Helonias* ser. *Heloniopsis* coupled with a reduction in flower number and an increase in ovule number:**—Flowers of *Helonias* ser. *Heloniopsis* appear to be the most advanced in *Helonias*. For instance, the tepals are proximally adnate to the opposing filament to form a saccate or tubular nectary (Utech & Kawano 1981 for *Heloniopsis orientalis*; Tanaka 1997b, e) and also connate to adjoining ones (Figs. 24C–E, 26A, C, 28E). The inflorescence comprises a comparatively small number of flowers (up to 14; Figs. 23, 25, 27) each bearing numerous ovules (e.g. to 189 per locule in *H. orientalis* (Table 1); Utech 1978 for *H. orientalis*; Tanaka 1997c, d). Such advanced floral structures appear to have evolved as a result of adaptation to insects foraging mainly for nectar. Presumably, the flowers improved pollination efficiency through restructuring and thereby enabled a reduction in flower number and an increase in ovule number in individual flowers. Utech (1978) reported that the total number of ovules per inflorescence is, on average, similar between *Helonias bullata* and *Heloniopsis orientalis*, although the number of flowers per inflorescence and the number of ovules per locule differ significantly. From my observations, I believe that *H. bullata* is the more primitive species and *H. orientalis* is one of the most advanced in the genus. The two species nearly represent the two extremes of phyletic evolution (Fig. 30, List 2). Similar data come from studies on plastid DNA sequences (Kim *et al.* 2016). The evolutionary trend toward *H. orientalis*, which produces comparatively fewer flowers and more numerous ovules, appears to be well reflected in this data. Floral evolution in *Helonias* thus appears to have been directional and anagenetic. In both *Helonias bullata* and *H. orientalis*, seedling establishment in habitats is equally very low (Part I-15; Kawano & Masuda 1980, Sutter 1984), and asexual reproduction by rhizomic division is fairly limited. Accordingly, to survive, they need to produce numerous seeds enough to cover the low rates of seedling and rhizomic recruitment. This necessity of producing numerous seeds needed for survival may account for the similarity in the total number of ovules per inflorescence between the two species (Utech 1978) mentioned above. Presumably, in *H. bullata* bearing comparatively few ovules (per locule or ovary; Table 1), production of a necessary

number of ovules for survival was achieved by producing many flowers (per scape), while in *H. orientalis* having comparatively few flowers (per scape), it was attained by producing numerous ovules in individual flowers. Since the ovules similar in total number are produced by fewer flowers, the pollination efficiency in individual flowers of *H. orientalis* is regarded as higher than that of *H. bullata*. An increase in ovule number per locule may have resulted in producing narrower seeds, because a locular space available for fertilized ovules to develop is likely to be more or less limited. Divergence in seed width (Part I-10) must have occurred at an early stage of evolution in *Helonias*, as it is seen between the two sections *H. sect. Helonias* (*H. bullata*) and *H. sect. Heloniopsis* (including *H. orientalis*).

### 3. Phylogenetic divergence and relationships

Evolutionary facets of the respective taxa (Part II) are outlined mainly on the basis of comparative studies of character states (Parts I, III-2).

***Helonias*:**—*Helonias* is most closely allied to *Chamaelirium* in North America and eastern Asia (Tanaka 1997e, 2017b). They share many similar features; for instance, the persistent oblanceolate or spatulate leaves in a basal rosette, a flowering stem with the growth period usually markedly separated from development of the rosette in the preceding year (Part III-1; *F* and *R* in Fig. 1C, D; Fig. 2), peduncles with scale-like leaves (e.g. Figs. 1C, 21A, B), ebracteate pedicels (e.g. Figs. 12A, 13C), and carpels connate dorsally to adjoining ones along their ventral sutures (e.g. 26C–E). *Helonias* as a genus is monophyletic (Fig. 30, List 2), consisting of two sections *Helonias* and *Heloniopsis* (Part II).

**Sect. *Helonias*:**—*Helonias bullata* has three styles distinct nearly to the base (Fig. 5D; Tanaka 1997a), suggesting that it is the most primitive member of the genus, at least in style characteristics. *Helonias bullata* also has fewer ovules (per locule or ovary) and slightly larger (broader) seeds than its congeners (Fig. 5F, Table 1; Tanaka 1997c). The surface of the nectary is nearly flat. These character states may also be primitive in *Helonias*. *Helonias* sect. *Helonias* is regarded as paraphyletic (Tanaka 1997e).

**Sect. *Heloniopsis*:**—In *Helonias* sect. *Heloniopsis* the three styles (carpels) are consistently connate to one another partially or entirely along their length to form a single column (e.g. Figs. 9A–C, 12, 14A, 22A). This character state is regarded as more advanced than in *H. sect. Helonias*. *Helonias* sect. *Heloniopsis* is monophyletic (Fig. 30, List 2), and all members are in eastern Asia (Figs. 15, 29, 31, 32). This section is composed of two subsections: *H. subsect. Ypsilandra* and *H. subsect. Heloniopsis* (Part II). The former subsection is considered to be more primitive (Part II; Tanaka 1997e) and occurs west of the range of the latter (Fig. 32). The species of *H. subsect. Heloniopsis* are either insular or coastal (Figs. 29, 31-3, -4, 32-3, -4).

**Subsect. *Ypsilandra*:**—*Helonias* subsection *Ypsilandra* appears more advanced in several characters than *H. sect. Helonias*. For instance, the styles (columnar part) are longer (Figs. 9A–C, 10E, 12, 14A, Table 6), the stigmatic segments are relatively shorter (Figs. 7B, 9A–C, 10E, Table 6), and the stigmatic portion is sometimes simple and unlobed (Figs. 3A–C, 13A–C), the anthers are unilocular and not septate between the thecae (Fig. 14E), and the seeds are significantly more numerous and narrower (Figs. 7G, 9D, Table 1). In *H. subsect. Ypsilandra*, *Helonias yunnanensis* var. *yunnanensis* is regarded as the most primitive taxon, since it has the shortest style and a deeply trifurcate stigma (Fig. 7B, Table 6). All other members of the section are regarded as descendants from the ancestral lineage of this variety (Fig. 30, List 2). *Helonias jinpingensis* with a short style and a somewhat deeply trifurcate stigma also appears to be primitive. *Helonias alpina*, with longer styles and slightly shorter stigmatic segments (Fig. 10E) than *H. jinpingensis*, may be slightly more advanced. *Helonias parviflora* (Figs. 11, 12), with a very slightly trilobed (or nearly trigonous) stigma, is regarded as more advanced, at least in pistil characters. *Helonias thibetica* (Figs. 13, 14) with a relatively long slender style and a small capitate or discoid stigma (Figs. 3A–C, 14A, Table 6) is the most advanced in pistil characteristics in this subsection. In *H. subsect. Ypsilandra*, the flowers have shifted from nearly adichogamous (in species other than *H. thibetica*) to protogynous (in *H. thibetica*) (Part I-13). This subsection is regarded as paraphyletic (Tanaka 1997e), and presumed evolutionary relationships between the members are shown in Fig. 30 (List 2). From plastid DNA sequence analyses, Fuse & Tamura (2016) suggested that *Helonias* s.str. (*H. sect. Helonias* in the present paper), *Ypsilandra* (*H. subsect. Ypsilandra*) and *Heloniopsis* (*H. subsect. Heloniopsis*) are all monophyletic. *Heloniopsis* is monophyletic as shown in Fig. 30 and in Tanaka (1997e), but the monophyly of *Helonias* and *Ypsilandra* is not supported by the present study, because many characteristics of *Heloniopsis*, such as long united styles, discoid or subdiscoid stigmas, and filaments liberated from the ovary base (List 2-14), cannot have been derived if they did not pass through the precursory stages as possessed by *Helonias* and *Ypsilandra*. It is highly improbable that similar characteristics have developed independently in *Ypsilandra* and *Heloniopsis* as an outcome of parallel evolution, and the ancestral lineage of *Heloniopsis*, which linked *Helonias* and *Heloniopsis* directly and had intermediate character states between them, was entirely extinct, whereas species of *Ypsilandra* are extant. This

discordance in results between morphology and DNA sequence analyses probably stems from the difference in research objects (whole characters of organisms manifested as the total sum of all genic activities involved vs. selected fractions of DNA molecules) and methods employed (clustering objects by synapomorphies vs. degree of similarity among DNA sequences).

**Subsect. *Heloniopsis*:**—Several character states of *Helonias* subsect. *Heloniopsis* are regarded as more advanced than those of *H.* subsect. *Ypsilandra*. For instance, the tepals are usually more markedly canaliculate toward the base (Figs. 19D, E, 20A, B, 22D, E, 24D, E, 26A, 28E), the nectaries are usually more prominently saccate (Figs. 22D, E, 24A–E, 26A–C), the stamens tend to be located closer to the tepals (Figs. 19B–E, 22B–E, 24B–E, 26A–C, 28B, C, E; Tanaka 1997e–Fig. 2), and the anthers are virtually bilocular, extrorse, and often longer (Figs. 20C, 24F, 28F). These character states are considered to be apomorphies, and this subsection is regarded as monophyletic in sharing them (Fig. 30, List 2). *Helonias thibetica* (*H.* subsect. *Ypsilandra*) has protogynous flowers, tepals slightly canaliculate toward the base, a pistil exserted beyond the tepals, and a capitate or discoid stigma. These features approach those of *H.* subsect. *Heloniopsis* (Part II), suggesting that *H.* subsect. *Heloniopsis* originated from the ancestry of *H. thibetica* (Fig. 30, List 2; Tanaka 1997c, d, e). *Helonias* subsect. *Heloniopsis* consists of two series: *H.* ser. *Umbellatae* and *H.* ser. *Heloniopsis* (Part II).

**Ser. *Umbellatae*:**—Several character states of *Helonias* subsect. *Heloniopsis* are regarded as more advanced than those of *H.* subsect. *Ypsilandra*, as stated in the preceding section. In addition, the umbels, sub-umbels or somewhat compact racemes in species of *H.* ser. *Umbellatae* (Part I-7, II-2) also appear to be more advanced character states. The apex of the leaves of *H.* ser. *Umbellatae* tends to be slightly more prominently apiculate than in its congeners (apiculus of *H.* ser. *Umbellatae* to ca. 2 mm long vs. to ca. 1.3 mm long in other species), probably suggesting that species in this series originated from the same ancestry (List 2-14). Of the three species of *H.* ser. *Umbellatae*, *H. kawanoi* appears to be the most primitive in some floral characters. For instance, the inner filaments of *H. kawanoi* are close to the base of the ovary (Fig. 17E), thereby approaching *H.* subsect. *Ypsilandra*, where the inner filaments are adnate to the base of the ovary (Fig. 14C; Tanaka 1997a). Further, the tepals of *H. kawanoi* are shallowly canaliculate proximally and the nectary is least concave. The autumnal flowering is also indicative of an old origin of this species. These facts suggest that *H. kawanoi* diverged earlier than *H. umbellata* and *H. leucantha* from the ancestral lineage of *H.* ser. *Umbellatae* (Fig. 30, List 2). *Helonias kawanoi* (Figs. 16, 17) is a dwarf plant with small comparatively thin leaves, short slender flowering stems, bracteate pedicels, and solitary or a few small autumnal flowers. All these character states are considered to be apomorphies (Fig. 30, List 2). Supposedly, *H. kawanoi* has acquired many of its unique features as a consequence of adaptation to an ecologically unusual location. Being small, the plants can not only utilize microhabitats for their life space, but also colonize on such unusual locations as steep cliffs and banks along streams that may overflow after heavy rainfall. Often growing among mosses, *H. kawanoi* may be viewed as an element of the moss layer community in the vertical stratification of vegetation. *Helonias leucantha* (Figs. 18–20) is normally larger than *H. umbellata* (Figs. 21, 22), and usually has larger leaves and slightly larger, pendulous, campanulate flowers that bloom from (late December) January through mid March. All of these character states are viewed as apomorphies. *Helonias leucantha* grows on shady moist rocky slopes near streams. It appears to share an immediate ancestry with *H. umbellata* (Fig. 30, List 2). *Helonias umbellata* usually grows on moist rocky slopes in shade or semi-shade at low to high elevations of Taiwan. It usually flowers from (late January) February through March, except on high peaks. *Helonias umbellata*, endemic to Taiwan, is geographically isolated from two Ryukyuan species *H. leucantha* and *H. kawanoi* (Fig. 29; Tanaka 1997e, 1998a). The Ryukyuan species overlap in distribution on four small islands; Tokunoshima, Okinawa, Ishigaki and Iriomote (Tanaka 1998a), but there are no reports of their co-occurrence in the same habitats on these islands, thereby implying that their habitat preferences subtly differ. Moreover, their flowering periods scarcely overlap (Tanaka 1997d). The three species of *H.* ser. *Umbellatae* therefore appear to be isolated from one another, at least by one or more of the following; geography, ecology, sexual reproduction. Flowers of both *Helonias umbellata* (e.g. Figs. 21A–C, 22A) and *H. kawanoi* (e.g. Figs. 16A, B, 17C) are similar in shape (both obconic), but differ in size. Flowers of *H. umbellata* and *H. leucantha* (e.g. Figs. 18B, D, 19A) differ in shape, degree of fragrance, and usually in size (Table 8). Their pollinators are also likely to differ to some extent in kind and/or visiting frequency.

**Ser. *Heloniopsis*:**—*Helonias* ser. *Heloniopsis* comprises *Helonias koreana*, *H. orientalis*, and *H. breviscapa* (see Part II). They share subumbels or umbels of comparatively few flowers (Figs. 23A–G, 25A–E, 27A–D), tepals with submarginal wings (lamellae) by which they are connate basally to adjoining tepals and adnate to opposing filaments (e.g. Figs. 24C–E, 26A, 28E), and sheath-like (tubular) nectaries formed by the adnation (e.g. Figs. 24A–E, 26A–C, 28E). All of these structures are obviously apomorphies. *Helonias* ser. *Heloniopsis* is therefore a monophyletic group (Fig. 30; Tanaka 1997e). In *H.* ser. *Umbellatae*, the proximal submarginal portions of the tepal are raised or ridged,

but not winged (Figs. 17D, 19D, E, 20A, B, 22D, E). Further, unlike *H. ser. Heloniopsis*, they are not connate between adjoining tepals in *H. kawanoi* (e.g. Fig. 17D) and *H. leucantha* (e.g. Fig. 19E). In *H. umbellata*, however, they are occasionally minutely connate basally between adjoining tepals (Fig. 22D). In all three species of *H. ser. Umbellatae*, there is no adnation between the tepals and their opposing filaments (Figs. 17D, E, 19D, E, 22B, D, E; Tanaka 1997b, e, 1998a). There is no doubt that the proximal submarginal wings of the tepals of *H. ser. Heloniopsis* are derived from the ridged or raised submarginal portion of the tepal of *H. ser. Umbellatae*. As aforementioned, like *H. ser. Heloniopsis*, *H. umbellata* occasionally has proximal ridges minutely connate basally to those of adjoining tepals (Fig. 22D). The floral structure of *H. ser. Heloniopsis* therefore appears to have originated from the one as seen in *H. umbellata* (Tanaka 1997b, e). Evolution in the reverse direction, i.e. from *H. ser. Heloniopsis* to *H. ser. Umbellatae*, is unlikely. It is also improbable that the floral structure exactly the same as that of *H. ser. Heloniopsis* developed independently in a different lineage as a consequence of parallel evolution. Taking all these improbabilities into account, the cladogram based on some fractions of plastid DNA sequences presented by Fuse & Tamura (2003, as *Heloniopsis*) does not appear to reflect the actual phylogeny (cladogenesis). In their analyses, two species of *H. ser. Heloniopsis* (*Helonias orientalis* and *H. breviscapa* here circumscribed) cluster with three species of *H. ser. Umbellatae* (here circumscribed), but not with the Korean species (*Heloniopsis koreana* and *H. tubiflora* in their paper) of the same *H. series Heloniopsis*. Their observations on the floral structure also do not necessarily coincide with mine (see also related remarks under *H. koreana* in Part II of present paper). Results of my observations on phenotypic characters thus markedly contradict those of their analyses on DNA sequences and floral morphology. As stated above, in my data, *Helonias koreana* is phylogenetically close to the rest of species of *H. ser. Heloniopsis* (Fig. 30), and in data published by Fuse & Tamura (2004), Korean species deviate significantly from the remaining (Japanese and Taiwanese) species of *H. subsect. Heloniopsis*. This incongruence might suggest that the degree of divergence in DNA sequence is not necessarily correlated with phylogenetic distance. Obviously, this issue needs further studies. In *Helonias koreana* (including *Heloniopsis tubiflora*), the adnate portion between a tepal and the opposite filament is nearly as high (long) as or slightly higher (longer) than the connate portion between adjoining tepals (Figs. 24C, D), while in *H. orientalis* and *H. breviscapa* the adnate portion is consistently higher (longer) than the connate portion (Figs. 26A, 28E). In this respect, I regard the character state of *H. orientalis* and *H. breviscapa* to be more advanced than in *H. koreana*. This view is reflected in constructing the phylogram in Fig. 30 (List 2) in which *H. orientalis* and *H. breviscapa* are clustered as sister species. *Helonias ser. Heloniopsis* appears most closely allied to *Helonias umbellata* of *H. ser. Umbellatae* (Tanaka 1997e), since the tepals of the latter are sometimes basally connate (Fig. 22D) like those of *H. ser. Heloniopsis*. *Helonias ser. Heloniopsis* and *H. umbellata* are hence likely to be monophyletic, sharing a common ancestry (Fig. 30, List 2). Two species of *H. ser. Umbellatae*, *H. kawanoi* and *H. leucantha*, are somewhat specialized and do not appear to be directly related to *H. ser. Heloniopsis*. *Helonias umbellata*, on the contrary, appears less specialized except for some characters (e.g. umbellate inflorescence) and even occurs at high elevations on Taiwan, implying that it can survive a cooler climate. The ancestor of *H. umbellata* may have evolved the lineage of *ser. Heloniopsis* while staying somewhere in or around the current range (such as Japan and Korea) of *ser. Heloniopsis* as a consequence of northward migration. The three species of *H. ser. Heloniopsis* appear to have individual preferences for climatic conditions. They appear to have phyletically diverged as a result of adaptation to different climatic types covering maritime regions of the Far East. For related remarks see section 5.

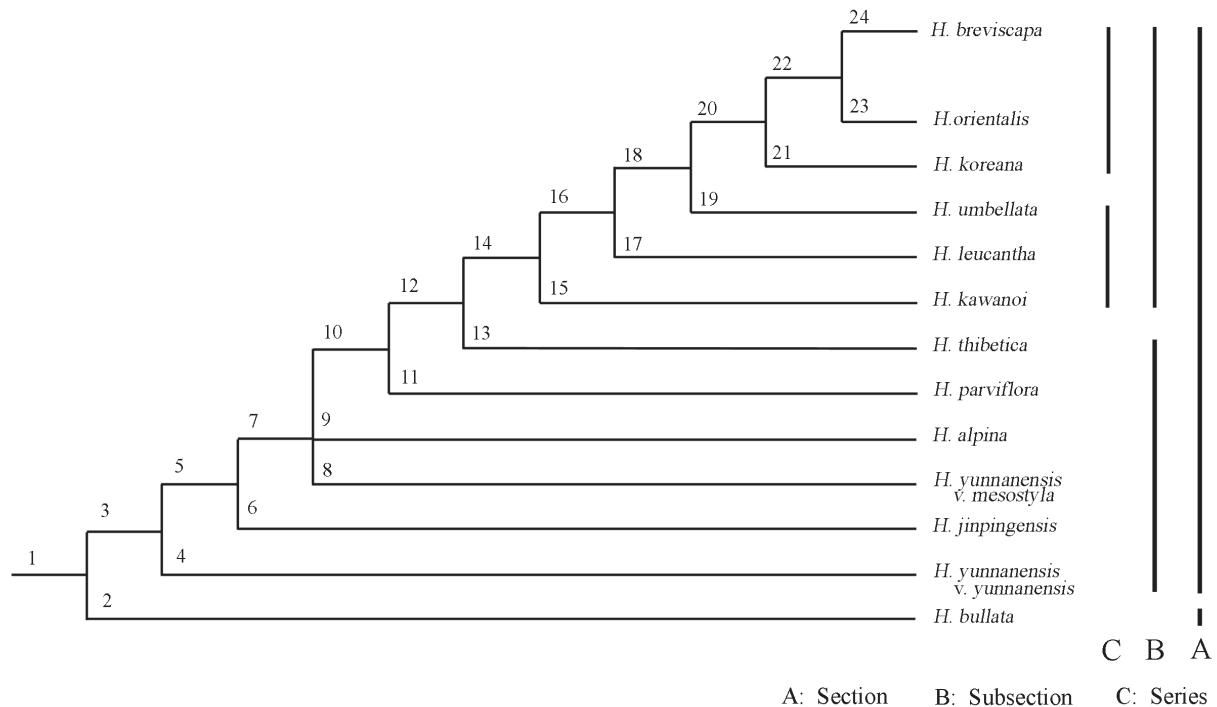
#### 4. Process of phyletic diversification

A phylogenetic tree or phylogram (phenogram) based on cladistic analyses of phenotypic characters is shown in Fig. 30. It is revised from Tanaka (1997e) and was constructed from hypotheses based on observations in the present study.

Attempts to construct phylogenograms (cladograms) from analyses of DNA sequences are valuable, but we need to be cautious especially in applying the results to classifications of organisms. DNA fractions used for phylogenetic analysis are generally limited in portion and sampling and hence the results may fluctuate to some degree. For instance, if samplings from highly variable species are strongly biased, the resultant phylogram inferred may more or less deviate in topology from the true one. Further, as stated earlier (Part III-3), analyses based only on the degree of similarity between DNA sequences often override paraphyletic lineages recognizable by phenotypical cladism, and hence it seems difficult for them to faithfully trace the true process of phylogenetic diversification. To obtain a phylogram closer to the actual phylogenesis, data from other aspects (particularly phenotypic characters) need to be taken into account.

In this study, in constructing the phylogenetic tree, the taxa are clustered by synapomorphies inferred from

comparative surveys of character states (Part I, III-2). The character states regarded as apomorphies are enumerated in List 2 under the respective lineages or clades that correspond to those in Fig. 30. Synapomorphies for lineage 1 rest on the presumption that *Chamaelirium* (including *Chionographis*) is the sister lineage of *Helonias*, which is also supported by plastid DNA sequence data (Fuse & Tamura 2000, Givnish *et al.* 2016, Kim *et al.* 2016).



**FIGURE 30.** Phylogram of 12 species of *Helonias* constructed from analyses of phenotypical characters. Each lineage is numbered 1 to 24. Infrageneric categories, A to C, are shown as vertical lines on right corner. Character states regarded as apomorphies acquired by respective lineages are enumerated in List 2.

**LIST 2.** Character states regarded as apomorphies, which are presumed to have been acquired by each lineage in Fig. 30, are enumerated below under the respective lineage numbers corresponding to those in Fig. 30.

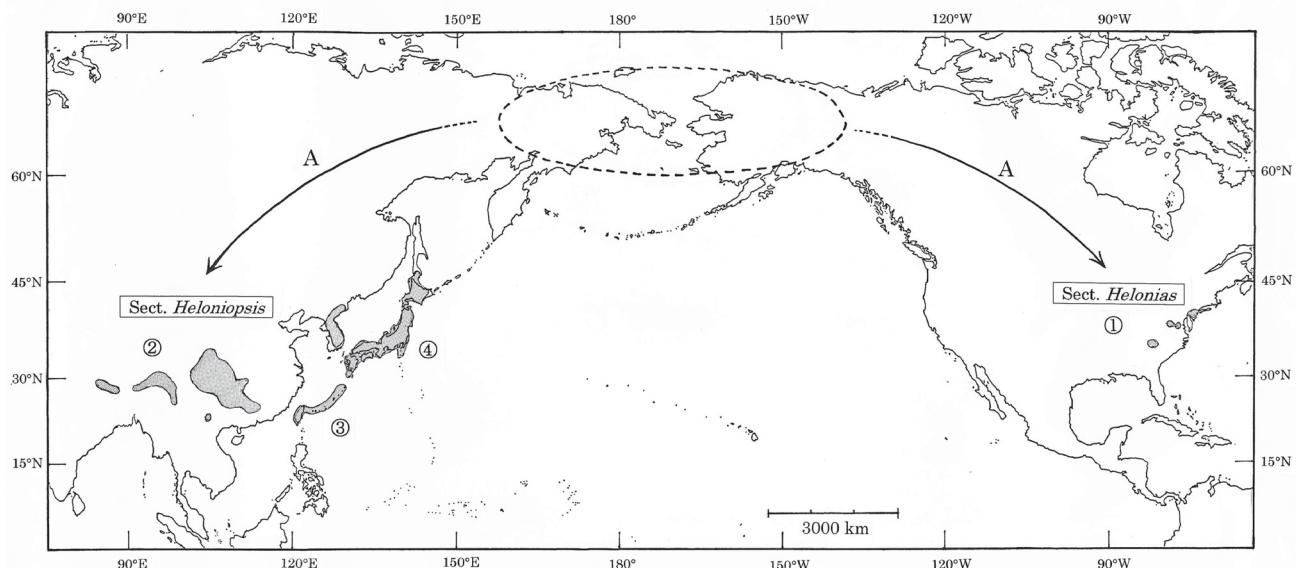
- 1) Immediate (closest) ancestral lineage common to lineages 2 and 3 (vs. lineage of *Chamaelirium*).
  1. Anthers become distinctly unilocular, losing adaxial septum (furrow) between thecae.
  2. Apex of ovary becomes emarginate-depressed.
  3. Carpels of ripe fruit become abaxially protruding subdistally.
  4. Three styles become connate basally to form very short column.
- 2) Lineage of *Helonias bullata*.
  1. Tepals become pink.
- 3) Immediate ancestral lineage common to lineages 4 and 5.
  1. Plants become somewhat smaller, as reflected in leaf size and scape height.
  2. Pedicels become slightly shorter.
  3. Stamens become slightly shorter.
  4. Anthers become latrorse (except apical part which is antrotorse dehiscent).
  5. Abaxial septum (furrow) between thecae as in *H. bullata* becomes lost (i.e. anthers become perfectly unilocular with no septum between thecae).
  6. Style (columnar part) becomes slightly longer.
  7. Ovules per locule become more numerous.
  8. Seeds (with testa) become more slender (linear-fusiform).
- 4) Lineage of *Helonias yunnanensis* var. *yunnanensis*.
  1. Whole body (habit) often becomes reduced in size, as reflected in leaf size, scape height, and flower size.
  2. Stamens usually become further shortened.
- 5) Immediate ancestral lineage common to lineages 6 and 7.
  1. Style (columnar part) becomes slightly longer.
- 6) Lineage of *Helonias jinpingensis*.

1. Pedicels become relatively slightly longer.
  2. Pedicels become bracteate at base.
  3. Flowering in late summer to early autumn.
- 7) Immediate ancestral lineage common to lineages 8, 9 and 10.**
1. Style becomes relatively slightly longer.
  2. Stigmatic lobing becomes relatively slightly reduced.
- 8) Lineage of *Helonias yunnanensis* var. *mesostyla*.**
1. Apomorphy not yet specified.
- 9) Lineage of *Helonias alpina*.**
1. Tepals become slightly longer.
  2. Tepals become narrowly oblong(-ob lanceolate).
  3. Style becomes slightly longer.
  4. Stigmatic lobing slightly reduced.
  5. Filaments become longer.
- 10) Immediate ancestral lineage common to lineages 11 and 12.**
1. Stigma becomes only slightly trilobed.
- 11) Lineage of *Helonias parviflora*.**
1. Flowers become slightly smaller, as reflected in tepals.
- 12) Immediate ancestral lineage common to lineages 13 and 14.**
1. Pedicels become longer.
  2. Flowers become protogynous.
  3. Flowers tend to become slightly larger.
  4. Stigma and stamens usually become exserted beyond tepals.
  5. Stigma becomes discoid.
- 13) Lineage of *Helonias thibetica*.**
1. Stigma becomes slightly smaller.
  2. Stigma usually becomes (sub)capitate.
- 14) Immediate ancestral lineage common to lineages 15 and 16.**
1. Apiculus at leaf apex becomes (relatively) slightly more prominent.
  2. Racemes tend to become slightly more compact at anthesis.
  3. Inner filaments become liberated from base of ovary.
  4. Anthers become adaxially affixed to filament (i.e. adaxially basifix ed).
  5. Anthers become extrorse.
  6. Anthers become virtually bilocular with traces of apical confluence between thecae.
- 15) Lineage of *Helonias kawanoi*.**
1. Whole body (habit) becomes significantly smaller, as reflected in rhizome, leaves, height of scape, caudine scaly leaves, flowers.
  2. Leaves become somewhat thinner (in texture).
  3. Main parallel veins of leaves become slightly raised adaxially.
  4. Flowering in late summer to autumn (or dormancy in development of flowering stem becomes almost lost).
  5. Pedicels become bracteate.
  6. Flowers (per scape) become fewer.
  7. Inflorescence becomes usually (sub)umbellate.
  8. Ovary becomes sessile.
  9. Seeds (incl. testa) become smaller (shorter).
- 16) Immediate ancestral lineage common to lineages 17 and 18.**
1. Tepals become more distinctly canaliculate toward base.
  2. Proximal submarginal portions of tepal become more prominently raised.
  3. Nectary at base of tepal becomes more prominently concave.
  4. Filaments tend to become slightly closer basally to opposing tepal (rather than to base of ovary).
- 17) Lineage of *Helonias leucantha*.**
1. Entire body (habit) becomes slightly larger, as reflected in leaves.
  2. Flowering in (late December) January through early March.
  3. Flowers become campanulate with tepals recurved distally.
  4. Flowers become less fragrant (nearly odorless).
  5. Tepals usually become narrowly oblong-elliptic.
  6. Ovary sometimes becomes (nearly) sessile (due to abbreviation of short gynophore or gynophore-like floral axis).
- 18) Immediate ancestral lineage common to lineages 20 and 21.**
1. Racemes become slightly more compact.
  2. Proximal submarginal ridges of tepal become more closely juxtaposed basally with those of adjoining tepals.
- 19) Lineage of *Helonias umbellata*.**

1. Inflorescence usually becomes (sub)umbellate.
  2. Proximal submarginal ridges of tepal sometimes become minutely connate basally to those of adjoining tepals.
  3. Ovary sometimes becomes (almost) sessile (due to abbreviation of short gynophore or gynophore-like floral axis).
- 20)** Immediate ancestral lineage common to lineages 22 and 23.
1. ?Apiculus at leaf apex becomes moderate.
  2. Flowers (per scape) tend to become fewer.
  3. Flowers tend to become less fragrant or odorless.
  4. Proximal submarginal ridges of tepal become lamellate (winged) and directed inward.
  5. Proximal submarginal wings (lamellae) of tepal become connate basally to those of adjoining tepals.
  6. Proximal submarginal wings of tepal become adnate proximally to opposing filament, forming sheathing nectary.
  7. Anthers often become affixed (to filament) slightly above base of connective (i.e. (sub)dorsi-basifixed).
  8. Anthers tend to become slightly longer.
  9. Traces of apical confluence between thecae tend to become slightly less distinct.
  10. Ovary becomes perfectly sessile.
- 21)** Lineage of *Helonias koreana*.
1. Leaf blades become slightly thinner (in texture).
  2. Leaf blades become nearly dull.
  3. Filaments become slightly dilated toward base.
  4. Filaments become more complanate and often subancipital (two-edged or narrowly winged) toward base.
- 22)** Immediate ancestral lineage common to lineages 23 and 24
1. Basal adnation between proximal submarginal wings of tepal and opposing filament becomes more advanced (viz. adnate portion becomes longer).
- 23)** Lineage of *Helonias orientalis*.
1. Leaves become somewhat firmer (thicker) in texture.
  2. Proximal submarginal wings of tepal become relatively longer.
  3. Basal adnation between proximal submarginal wings of tepal and opposing filament becomes slightly more advanced (viz. adnate portion becomes longer).
- 24)** Lineage of *Helonias breviscapa*.
1. Basal abaxial gibbosity of tepal often becomes less conspicuous.
  2. Nectary at adaxial base of tepal becomes relatively higher in position (surface of nectary becomes nearly as high as base of ovary or top of receptacle).
  3. Traces of apical confluence between thecae often become indistinct.
- 

## 5. Historical background of the current geographic ranges

The distributions of the sections of *Helonias* are remarkably disjunct. *Helonias bullata* is restricted to eastern North America (Figs. 6, 31), while *H. sect. Heloniopsis* is restricted to eastern Asia (Figs. 31, 32). The main factor behind this large scale disjunction may have been drastic climatic change. According to paleobotanical surveys, the so-called Arcto-Tertiary Geoflora, which comprises many species of deciduous broad-leaved trees, once extensively covered northern circumpolar regions (Chaney 1947, Tanai 1967, 1972, 1988, 1992, Uemura 1995, Ogasawara & Uemura 2006). The flora began to migrate southwards in response to lowering temperatures toward the end of the Eocene and early Oligocene. Ancestral plants of *Helonias*, which are presumed to have been members of the Geoflora, may also have migrated southward and in the process may have separated into two groups, one reaching Asia and the other North America (Fig. 31) (Tanaka 1997e). *Helonias bullata* (Figs. 4, 5) of North America appears to be the most primitive, since its three styles tend to be largely free (Fig. 5D, Part III-3). This remarkable disjunction in the range of *Helonias* appears to have originated at an early stage of diversification (Fig. 30; Tanaka 1997e) before the existence of many of the current species of *Helonias* (most species of *H. sect. Heloniopsis* such as *H. parviflora*, *H. thibetica*, *H. umbellata*, and *H. orientalis*).

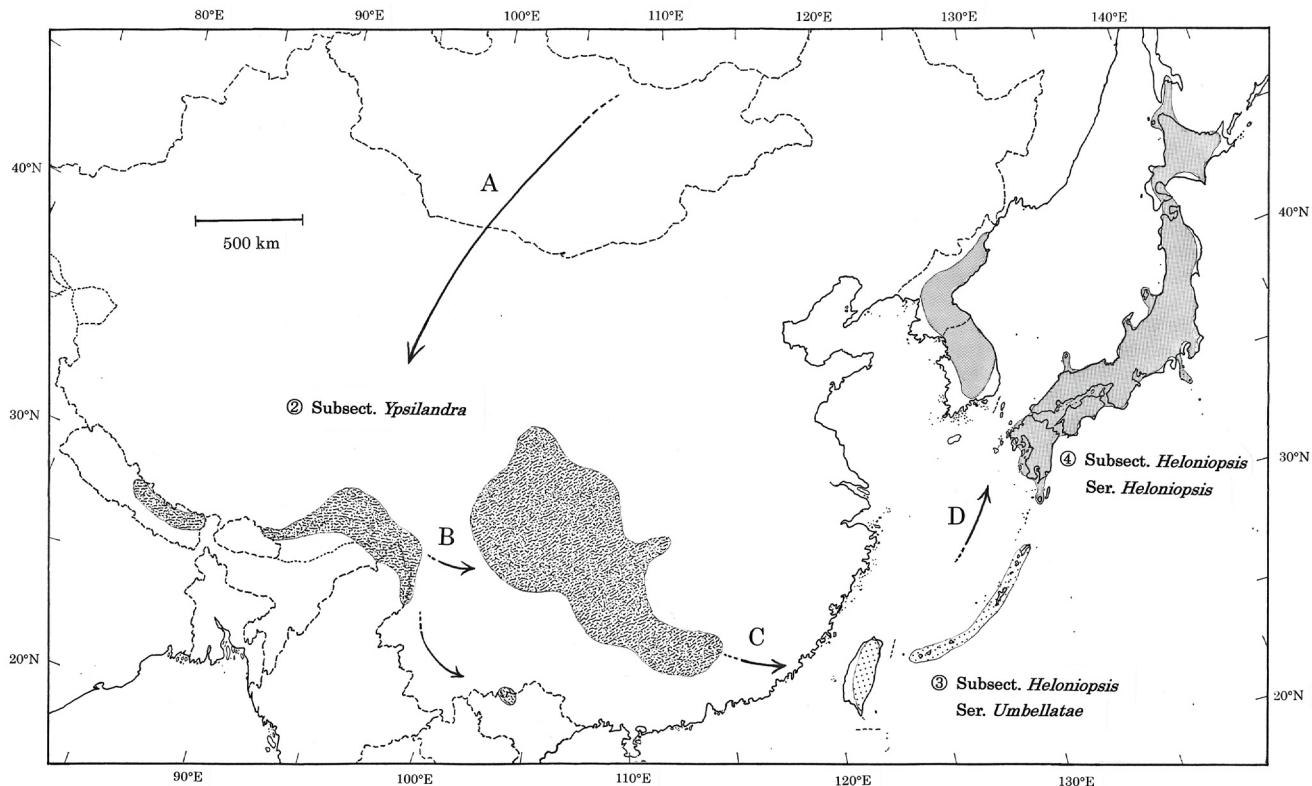


**FIGURE 31.** Geographic ranges of two sections *Helonias* and *Heloniopsis*. Ancestral plants of *Helonias* are presumed to have been in northern high latitudes approximate area of which is encircled with broken line. They are supposed to have been separated into two groups, and eventually one group reached eastern N. America and the other eastern Asia as consequence of their southward migrations (A). ① Sect. *Helonias*. ②–④ Sect. *Heloniopsis*. ② Subsect. *Ypsilandra*. ③ Subsect. *Heloniopsis* ser. *Umbellatae*. ④ Subsect. *Heloniopsis* ser. *Heloniopsis*. For historical aspect of range extension, see also Figs. 32, 33 and text (Part III).

Of the Asian members of *Helonias* (*H. sect. Heloniopsis*), *H. yunnanensis* var. *yunnanensis* (Figs. 7, 15-Yy) appears to be the most primitive (Fig. 30), since it has the shortest style (Fig. 7B, Part III-3; Tanaka 1997c, e). Presumably, the ancestral plants of this *Helonias yunnanensis* migrated from area at high latitudes (encircled by broken line in Fig. 31) to somewhere in or around the Tibetan Plateau and the Himalaya of today (Figs. 31, 32). After having settled there, they probably underwent gradual uplift caused by the subduction of the so-called Indian Plate (Indo-Australian Plate) under the Eurasian Plate. The ancestors of *H. yunnanensis* var. *yunnanensis* must have gradually adapted to alpine or subalpine environments created by the orogenesis of that region. This variety is now confined to the highlands between ca. 2700 and 4300 m (Fig. 15-Yy). Plants in such harsh alpine situations have inevitably become smaller and mostly correspond to *Ypsilandra yunnanensis* var. *micrantha* (or var. *himalaica*). *Helonias alpina* (Figs. 10, 15-A; elev. 3962–4267 m) may also have differentiated in the highlands. Some ancestors of *H. yunnanensis* var. *yunnanensis* in the eastern part of the plateau may have evolved species such as *H. jinpingensis* now on the border between southern Yunnan and northern Vietnam (Fig. 15-J) and *H. parviflora* in Guizhou (China) (Fig. 15-P). The ancestor of *H. parviflora* is likely to have branched off the lineage of *H. thibetica* which is now widespread over the eastern stretch or periphery of the Himalaya and Tibetan Plateau (Figs. 15-T, 30, 32). Ancestral plants of *H. ser. Umbellatae* (subsect. *Heloniopsis*), whose descendants are now in Taiwan and the Nansei Islands (including the Ryukyus) in Japan (Figs. 29-Ka, -L, -U, 31, 32), may have originated from the ancestor of *H. thibetica* (Figs. 15-T, 30) which was once in the Far East maritime regions (including today's southern China, Taiwan, the Nansei Islands, and lands subsided under the Taiwan Strait and East China Sea).

Thus, the geographic range of ancestral Asian *Helonias* after settlement in or around the present Tibetan Plateau and the Himalayan regions is presumed to have extended eastward over time and through evolutionary progression (Figs. 30, 32-B, -C; Tanaka 1997e). Li (1944) recognized 14 phytogeographic regions in China. If his regional divisions are adopted, a presumable approximate course of range extension of ancestral Asian *Helonias* (*H. subsect. Ypsilandra* and probably *H. ser. Umbellatae* in part) would be:—Tibetan Highland Region (14) → Sino-Himalayan Region (4) → Southwestern China Plateau Region (3) → Southern China Maritime Region (1) (number in parentheses assigned by Li, 1944).

During warmer geological periods the ancestors of *Helonias* ser. *Umbellatae* (or of *H. umbellata*; Figs. 29, 31-3, 32-3) are supposed to have extended their range to somewhere in or around today's Japan and Korea (Fig. 32-D). After the climate cooled again, some may have migrated south, while others may have remained to form the ancestral lineage of *H. ser. Heloniopsis* (Figs. 29, 30, 31-4, 32-4).

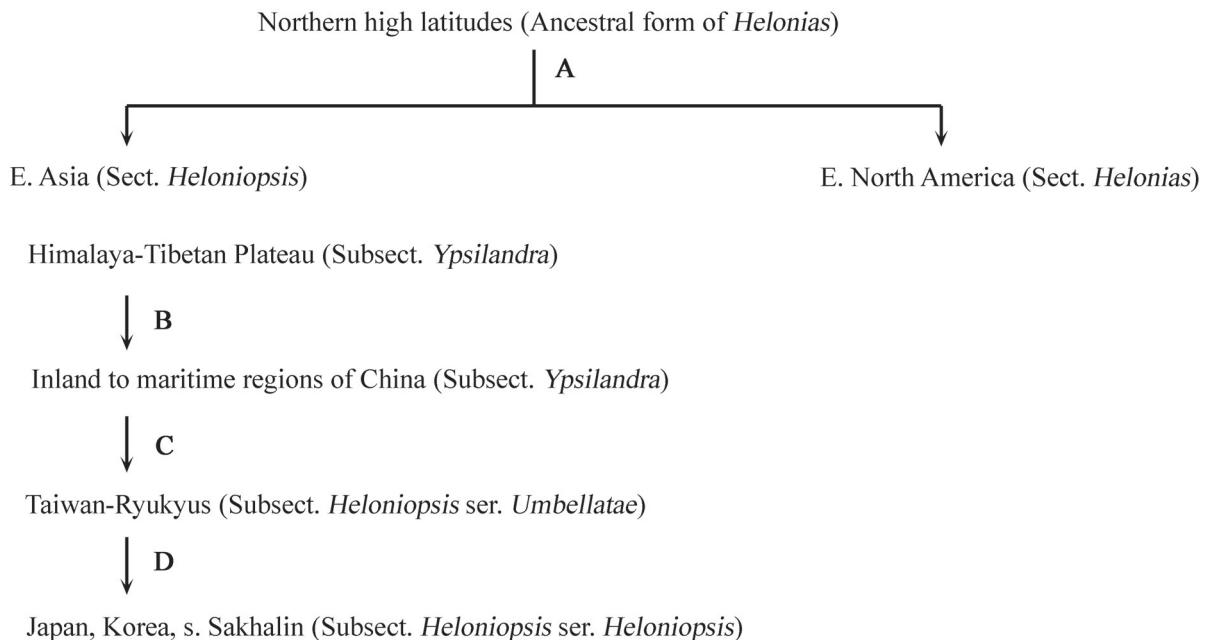


**FIGURE 32.** Geographic ranges of Sect. *Heloniopsis* in Asia with presumable approximate course of range extension in past. A–D: Presumable approximate course of migration or extension of range of ancestral plants of *Helonias*. Ancestral plants are supposed to have arrived in or around present Tibetan Plateau from northern high latitudes (A; see also Fig. 31) and have further extended their range eastward (B, C) and northeastward (D).

The approximate course of migration or extension of geographic range of *Helonias* traced from this study is outlined in Fig. 33. Infrageneric taxa, such as *H.* subsect. *Ypsilandra* and *H.* ser. *Umbellatae*, have their own geographical ranges disjunct from one another (Figs. 29, 31, 32), and the largest scale disjunction between the two sections (*Helonias* and *Heloniopsis*) appears to reflect not only the most drastic climatic change in the evolutionary history of *Helonias* but also the deepest diversification in the genus.

Fuse & Tamura (2004) suggested that *Heloniopsis* as a remnant of the Arcto-Tertiary flora has migrated from the north to the present range (via Sakhalin in case of species distributed in Japan and Taiwan). However, no remarks were made on the migration route of *Ypsilandra* (*Helonias* subsect. *Ypsilandra*) and the geological age and palaeogeological states of eastern Asia when the migration had occurred. It is hard to accept their view, considering the process of phylogenetic progression in *Helonias* s.lat. as traced from the present study (Figs. 30–33, List 2).

The three species of *Helonias* ser. *Heloniopsis*, *H. koreana*, *H. orientalis* and *H. breviscapa*, appear to be adapted to different climates. *Helonias orientalis* (Fig. 29-O) in Japan and southern Sakhalin, Russia, tends to be more abundant in snowy regions, such as along the coast of Honshû facing the Sea of Japan (see Japan Meteorological Agency 1971, 1972, for climatological data). *Helonias breviscapa* (Fig. 29-B), which is confined to southwestern Japan mainly facing the Pacific, appears to prefer a somewhat warmer climate with less snowfall in winter (Tanaka 1998a). *Helonias koreana* (Fig. 29-Ko), endemic to the Korean Peninsula, appears to be adapted to a bitter cold, drier, and less snowy winter (see Central Meteorological Observatory, Tokyo 1929).



**FIGURE 33.** Flowchart illustrating probable approximate course of migration of ancestral population of *Helonias* (cf. Figs. 31 & 32). A. Southward migration from northern high latitudes, which resulted in large-scale disjunction in distribution. B, C. Eastward extension of range. D. Northeastward extension of range.

Plants, such as *Helonias orientalis* and *H. koreana*, that occur in very cold regions may be protected from coldness and dryness by being covered by snow. The three different types of climate appear to be closely related to the geographic features of the respective regions. It is generally accepted that the following three factors are prerequisite for creating such different climatic types: a) high atmospheric pressure develops over the Siberian region in winter, resulting in strong seasonal wind toward Japan; b) the Sea of Japan between the eastern Asian mainland and the Japanese archipelago provides moisture to the dry air mass blowing from the Siberian region; c) the high mountains in Honshû, Japan obstruct the northwesterly wind, creating two markedly contrasting climatic types in winter (Uemura 2011).

The three species of *Helonias* ser. *Heloniopsis* may be closely related to such geographic and climatic features. These features appear to have become remarkable especially from the mid-Pleistocene onward (e.g. maps 30-27-30 in Minato *et al.* 1965 for the process of palaeogeographical changes in eastern Asia). If the timing of establishment of these features (or the above three factors) becomes more precise, the approximate time of origin of the three species may also become clearer.

Because of fluctuating temperatures in the Neogene period of the Tertiary and in the Quaternary (Minato *et al.* 1965, Tanai 1972, 1992, Uemura 1995, Ogasawara & Uemura 2006), some north-southward migration of vegetation, including *Helonias*, must have occurred. The occurrence of *H. orientalis* in southern Sakhalin, Russia (Miyabe & Kudo 1932, Sugawara 1937, 1939), which is at the northernmost limit of its range (Fig. 29), may have resulted from such migrations during the Quaternary. Despite such migrations, the relative geographic ranges of the species of *Helonias* may not have changed extensively.

*Helonias* are small hemicryptophytes with basal rosulate leaves spreading on the ground. They prefer moist or wet situations, such as swamps, meadows or steep rocky slopes along streams in forests, that are not necessarily so heavily covered by larger plants. In general, these habitats are more exposed than closed, dense forest floors, and are hence more likely to soon dry if water becomes scarce. Ample precipitation may therefore be required to maintain stable populations.

**TABLE 11.** Worldwide occurrence of *Helonias* (taxa at rank of form were omitted).

Geographic (GR) or administrative region (AR)	Number of species in each GR or AR (endemic taxa)	Species in each GR or AR
N. America	1(1)	<i>H. bullata</i> *
Nepal	1(0)	<i>H. yunnanensis</i> (var. <i>yunnanensis</i> )
Bhutan	1(0)	<i>H. yunnanensis</i> (var. <i>yunnanensis</i> )
India	1(0)	<i>H. yunnanensis</i> (var. <i>yunnanensis</i> )
Myanmar	2(1)	<i>H. alpina</i> *, <i>H. yunnanensis</i> (var. <i>mesostyla</i> , var. <i>yunnanensis</i> )
China (incl. Tibet)	4(2) <sup>1)</sup>	<i>H. yunnanensis</i> (var. <i>mesostyla</i> , var. <i>yunnanensis</i> ), <i>H. jinpingensis</i> , <i>H. parviflora</i> *, <i>H. thibetica</i> *
Vietnam	1(0)	<i>H. jinpingensis</i>
Taiwan	1(1)	<i>H. umbellata</i> *
Japan	4(3)	<i>H. leucantha</i> *, <i>H. kawanoi</i> *, <i>H. breviscapa</i> *, <i>H. orientalis</i>
Korea	1(1)	<i>H. koreana</i> *
Russia	1(0)	<i>H. orientalis</i>

<sup>1)</sup> *Helonias alpina* (*Ypsilandra alpina*) recorded from China is excluded, see the text.

\* Taxa endemic to respective GR or AR.

The main factors for the eastward migration in Asia of *Helonias* sect. *Heloniopsis* (Fig. 32-B–D) may have been ample precipitation and moderate temperatures. Asian *Helonias* appears to be more abundant and diversified in regions blessed with such climatic factors, e.g., maritime regions of the Far East including Japan and Taiwan, and the Himalaya and Tibetan Plateau (Fig. 32, Table 10; Yan 2002 for climatological data for China). Eastern North America, where *H. bullata* occurs (e.g. Figs. 6, 31), resembles eastern Asia in climate, especially in precipitation and temperature (e.g. plates 20, 24, 26 in Good 1974).

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## References

- Adanson, M. (1763) *Familles des Plantes*. Vincent, Paris, 640 pp.
- Amakawa, T. (Ed.) (1975) *The Flora and Vegetation of Fukuoka Prefecture*. Hakuyôsha, Fukuoka, 339 pp.
- Baillon, H. (1894) *Histoire des Plantes* 12. Librairie Hachette & Cie, Paris, 611 pp.
- Baker, J.D. (1874) On a new species of *Heloniopsis* from Formosa. *Journal of Botany, British and Foreign* 12: 278.
- Baker, J.D. (1879) A synopsis of Colchicaceae and the aberrant tribes of Liliaceae. *Journal of the Linnean Society, Botany* 17: 405–510.
- Bentham, G. (1883) Liliaceae. In: Bentham, G. & Hooker, J.D. (Eds.) *Genera Plantarum* 3 (2). L. Reeve & Co., Williams & Norgate, London, pp. 748–836.
- Britton, N.L. & Brown, H.A. (1896) *An Illustrated Flora of the Northern United States, Canada and the British Possessions* 1. New York, Charles Scribner's Sons, 612 pp.
- Britton, N.L. & Brown, H.A. (1913) *An Illustrated Flora of the Northern United States, Canada and the British Possessions*. Second ed.,

1. New York, Charles Scribner's Sons, 680 pp.
- Central Meteorological Observatory (Tokyo) (1929) *Climatic Atlas of Japan and her Neighbouring Countries*. Tokyo, 27 pp., 95 plates.
- Chafin, L.G. (2007) Swamp Pink (*Helonias bullata*), updated on February 2010 by K. Owers by adding pictures. In: Georgia Department of Natural Resources, Wildlife Resources Division, Species Fact Sheets. Available from: [http://georgiawildlife.com/sites/default/files/wrd/pdf/fact-sheets/swamp\\_pink\\_2010.pdf](http://georgiawildlife.com/sites/default/files/wrd/pdf/fact-sheets/swamp_pink_2010.pdf) (accessed 7 August 2018).
- Chaney, R.W. (1947) Tertiary centers and migration routes. *Ecological Monographs* 17: 141–148.
- Chen, S.-C. (1980) *Ypsilandra*. In: Wang, F.T. & Tang, T. (Eds.) *Flora Reipublicae Popularis Sinicae* 14: 15–18. [in Chinese]
- Chen, W.H., Shui, Y.M. & Yu, Z.Y. (2003) A new species of *Ypsilandra* (Liliaceae) and its geographic implication of SE Yunnan province. *Bulletin of Botanical Research, Harbin* 23 (3): 267–268.
- Chen, X.-Q. & Tamura, M.N. (2000) *Ypsilandra*. In: Wu, Z.-Y. & Raven, P.H. (Eds.) *Flora of China* 24. Science Press, Beijing, & Missouri Bot. Garden, St. Louis, pp. 86–87.
- Chong, T.H. (1956) *Korean Flora 2 (Herbaceous plants)*. Synji Sa, Seoul, 1025 + 129 pp. [in Korean]
- Dahlgren, R.M.T., Clifford, H.T. & Yeo, F. (1985) *The Families of the Monocotyledons*. Springer-Verlag, Berlin, 520 pp.
- Doi, Y. (1983) *Hiroshima-ken Shokubutsu Mokuroku (Enumeratio Plantarum in Pref. Hiroshima (Provincia Aki et Bingo) Sponte Nascentium)*. Hakushinkan Press, Hiroshima, 148 pp. [in Japanese]
- Endlicher, S.L. (1836–1841) *Genera Plantarum Secundum Ordines Naturales Disposita*. Fr. Beck Univ. Bibl., Vindobonae (Wien), 1483 pp.
- Engler, A. (1887) Liliaceae. In: Engler, A. & Prantl, K. (Eds.) *Die Natürlichen Pflanzensammlungen 2 (5)*. Verlag von W. Engelmann, Leipzig, pp. 10–91.
- Environment Agency of Japan (Ed.) (2000) *Threatened Wildlife of Japan. Red Data Book 2nd ed. 8. Vascular Plants*. Japan Wildlife Research Center, Tokyo, 660 pp. [in Japanese]
- Fernald, M.L. (1950) *Gray's Manual of Botany, eighth edition*. American Book Company, New York, 1632 pp.
- Franchet, A. (1887–1888) Plantae Davidianae ex Sinarum imperio 2. Plantes du Thibet oriental. *Nouvelles Archives du Muséum d'Histoire Naturelle*. Paris Sér. 2, 10: 33–198, pls. 10–17.
- Franchet, A. (1888) *Plantae Davidianae ex Sinarum Imperio 2. Plantes du Thibet Oriental*. [Reprint of Franchet 1887–1888]. G. Masson, Paris, 234 pp., pl. 2–17.
- Franchet, A. & Savatier, L. (1877–1878) *Enumeratio Plantarum in Japonia Sponte Crescentium*. Vol. 2. F. Savy, Paris, pp. 1–256 [Part 1 '1877']; pp. 257–624 [Part 2 '1878'].
- Fuse, S. & Tamura, M.N. (2000) A phylogenetic analysis of the plastid *matK* gene with emphasis on Melanthiaceae *sensu lato*. *Plant Biology* 2: 415–427.
- Fuse, S. & Tamura, M.N. (2003) Investigation of maintaining mechanisms of species in case of the genus *Heloniopsis* (Melanthiaceae, Liliaceae *sensu lato*). *Bunrui* 3: 33–38. [in Japanese]
- Fuse, S. & Tamura, M.N. (2016) Biosystematic studies on the genus *Heloniopsis* (Melanthiaceae) I. Phylogeny inferred from plastid DNA sequences and taxonomic implications. *Nordic Journal of Botany* 34: 584–595.  
<https://doi.org/10.1111/njb.01055>
- Fuse, S., Lee, N.S. & Tamura, M.N. (2004) Biosystematic studies on the genus *Heloniopsis* (Melanthiaceae) II. Two new species from Korea based on morphological and molecular evidence. *Taxon* 53: 949–958.
- Gates, R.R. (1918) A systematic study of the North American Melanthiaceae from the genetic standpoint. *Journal of the Linnean Society, Botany* 44: 131–172.
- Givnish, T.J., Zuluaga, A., Marques, I., Lam, V.K.Y., Gomez, M.S., Iles, W.J.D., Ames, M., Spalink, D., Moeller, J.K., Briggs, B.G., Lyon, S.P., Stevenson, D.W., Zomlefer, W. & Graham, S.W. (2016) Phylogenomics and historical biogeography of the monocot order Liliales: out of Australia and through Antarctica. *Cladistics* 32: 581–605.  
<https://doi.org/10.1111/cla.12153>
- Gleason, H.A. (1952) *The New Britton and Brown Illustrated Flora of the Northeastern United States and Adjacent Canada, vol. 1*. New York Bot. Gard., Hafner Press, New York, 482 pp.
- Godt, M.J.W., Hamrick, J.L. & Bratton, S. (1995) Genetic diversity in a threatened wetland species, *Helonias bullata* (Liliaceae). *Conservation Biology* 9: 596–604.
- Good, R. (1974) *The Geography of the Flowering Plants*. Fourth ed., Longman, London, 557 pp.
- Gray, A. (1837) Melanthacearum Americae septentrionalis revisio. *Annals of the Lyceum of Natural History of New York* 4: 105–140.
- Gray, A. (1848) *A Manual of the Botany of the Northern United States*. James Munroe & Co., Boston & Cambridge, 710 pp.
- Gray, A. (1859) Diagnostic characters of new species of phaenogamous plants, collected in Japan by Charles Wright, botanist of the U. S. North Pacific Exploring Expedition. *Memoirs of the American Academy of Arts and Sciences* New series, 6: 377–454.
- Gray, A. (1868) *Manual of the Botany of the Northern United States*. 5th ed. (8th issue). Ivison, Blakeman, Taylor & Co., New York & Chicago, 703 pp. + 20 pls.

- Handel-Mazzetti, H.R.E. (1923) Plantae novae Sinenses, diagnosibus brevibus descriptae a Dre Heinr. Handel-Mazzetti. *Anzeiger der Akademie der Wissenschaften in Wien. Mathematische-naturwissenschaftliche Klasse* 60: 152–155.
- Hara, H. (1947) Annotationes miscellaneae ad plantas Asiae-Orientalis (III). *Journal of Japanese Botany* 21: 143–150. [in Japanese]
- Hara, H., Stearn, W.T. & Williams, L.H.J. (1978) *An Enumeration of the Flowering Plants of Nepal 1*. British Museum (Natural History), London, 154 pp.
- Harris, J.G. & Harris, M.W. (1994) *Plant Identification Terminology: An Illustrated Glossary*. Spring Lake Publishing, Spring Lake, 197 pp.
- Hatusima, S. (1971) *Flora of the Ryukyus*. Okinawa Seibutsu Kyōikukai, Naha, 940 pp. [in Japanese]
- Hatusima, S. (1975) *Flora of the Ryukyus*. Added and corrected. Okinawa Seibutsu Kyōikukai, Naha, 1002 pp. [in Japanese]
- Hatusima, S. (1986) *Kaitei Kagoshima-ken Shokubutsu Mokuroku* [Revised List of Plants of Kagoshima Prefecture]. Kagoshima-ken Shokubutsu Dōkōkai, Asahi Insatsu, Kagoshima, 290 pp. [in Japanese]
- Hatusima, S. & Amano, T. (1977) *Flora of the Ryukyus, South of Amami Island*. Deigo Shuppansha, Naha, 282 pp. [in Japanese]
- Hayata, B. (1917) *General Index to the Flora of Formosa. Supplement to Icones Plantarum Formosanarum 6*. Bureau of Productive Industries, Government of Formosa, Taihoku, 155 pp.
- Hayata, B. (1920) *Icones Plantarum Formosanarum 9*. Bureau of Forestry Industries, Government of Formosa, Taihoku, 155 pp., 7 pls.
- Hennig, W. (1966) *Phylogenetic systematics (translated by D. Dwight Davis & Rainer Zangerl)*. University of Illinois Press, Urbana, 263 pp.
- Hickey, M. & King, C. (2000) *The Cambridge Illustrated Glossary of Botanical Terms*. Cambridge University Press, Cambridge, 208 pp.
- Hiyama, K. (1939) Shirobana-syōjyōbakama. *Yaso* 5: 77–80. [in Japanese]
- Honda, M. (1938) Species of *Heloniopsis*. *Shokubutsu oyobi Dōbutsu (Botany and Zoology)* 6: 1675–1680. [in Japanese]
- Hsu, T.-W., Kono, Y., Chiang, T.-Y. & Peng, C.-I. (2011) *Ypsilandra* (Melanthiaceae; Liliaceae sensu lato), a new generic record for Taiwan. *Botanical Studies* 52: 99–104.
- Hutchinson, J. (1934) *The Families of Flowering Plants 2. Monocotyledons*. Macmillan & Co., London, 243 pp.
- Iinuma, Y. (1861) *Sōmoku-dzusetsu* [Illustrated flora of Japan], *zenpen* [part 1] 6, Ôgaki [in Gifu], 53 pp. [in Japanese]
- Iinuma, Y. (rev. ed. by Tanaka, Y. & Ono, M.) (1875) *Shintei sōmoku-dzusetsu*, *zenpen* [part 1] 6: Heirinsô, Gifu, 53 pp. [in Japanese]
- Itô, K. (1829) *Taisei Honzô-meiso, Ge-kan* [second part], Kajô-sho'oku, Nagoya, 29 pp. [in Japanese]
- IUCN [International Union for Conservation of Nature and Natural Resources] (1994) *1994 IUCN Red List Categories and Criteria version 2.3*. Available from: <http://www.iucnredlist.org/technical-documents/categories-and-criteria/1994-categories-criteria#introduction> (accessed 24 January 2019)
- IUCN [International Union for Conservation of Nature] (2001) *IUCN Red List Categories and Criteria: Version 3.1. First ed.* IUCN, Gland, Switzerland and Cambridge, UK.
- Iwasaki, T. (1824) *Bukô-sanbutsu-shi. Bukô-ryakuzu*. Edo (Tokyo), 18 pp., 1 map. [in Japanese]
- Japan Meteorological Agency (1971) *Climatic Atlas of Japan 1*. Chijin-shokan, Tokyo, 59 plates.
- Japan Meteorological Agency (1972) *Climatic Atlas of Japan 2*. Chijin-shokan, Tokyo, 90 plates.
- Jarvis C.E., Barrie, F.R., Allan, D.M. & Reveal, J.L. (1993) *A List of Linnean Generic Names and their Types*. [Regnum Vegetabile 127] Koeltz Scientific Books, Königstein, 100 pp.
- Kawakami, T. (1910) *A List of Plants of Formosa*. Bureau of Productive Industry, Government of Formosa. Taihoku (Taipei), 165 + 119 pp.
- Kawano, S. (1975) The productive and reproductive biology of flowering plants II. The concept of life history in plants. *Journal of the College of Liberal Arts, Toyama University* 8: 51–86.
- Kawano, S. (1976) Japanese flora, its natural history background (9): temperate forest elements (part 4). *Shokubutsu to shizen (Nature and Plants)* 10: 6–11. [in Japanese]
- Kawano, S. & Masuda, J. (1980) The productive and reproductive biology of flowering plants VII. Resource allocation and reproductive capacity in wild populations of *Heloniopsis orientalis* (Thunb.) C. Tanaka (Liliaceae). *Oecologia* 45: 307–317.
- Kawano, S. & Masuda, J. (2004) Life history characteristics of *Helonias orientalis* (Thunb.) N.Tanaka (Liliaceae). In: Kawano, S. (Ed.) *Life-History Monographs of Japanese Plants 1, Spring Plants Volume 1*. Hokkaido Univ. Press, Sapporo, pp. 73–80. [in Japanese with English summary]
- Kawano, S., Masuda, J. & Utech, F.H. (2007) Life-history monographs of Japanese plants 9: *Helonias orientalis* (Thunb.) N.Tanaka (Liliaceae). *Plant Species Biology* 22: 231–237.
- Kim, S.C., Kim, J.S., Chase, M.W., Fay M.F. & Kim, J.H. (2016) Molecular phylogenetic relationships of Melanthiaceae (Liliales) based on plastid DNA sequences. *Botanical Journal of the Linnean Society* 181: 567–584.  
<https://doi.org/10.1111/boj.12405>
- Kitamura, S. (1964) Liliaceae. In: Kitamura, S., Murata, G. & Koyama, T. (Eds.) *Coloured Illustrations of Herbaceous Plants of Japan (Monocotyledoneae) 3*. Hoikusha, Osaka, pp. 90–157. [in Japanese]

- Kitamura, S. & Murata, G. (1966) New names and new conceptions adopted in Kitamura, Murata, and Koyama, Coloured Illustrations of Herbaceous Plants of Japan III (Monocotyledoneae). *Acta Phytotaxonomica & Geobotanica* 22: 65–74.
- Koidzumi, G. (1925, December) Contributiones ad cognitionem florae Asiae orientalis. *Botanical Magazine (Tokyo)* 39: 299–318.
- Koidzumi, G. (1930). *Florae Symbolae Orientali-Asiaticae*. Publisher not indicated, Kyoto, 115 pp.
- Koidzumi, G. (1934) Shôjôbakama zoku ni tsuite [On the genus *Heloniopsis*]. *Acta Phytotaxonomica & Geobotanica* 3: 42–43. [in Japanese]
- Koidzumi, G. (1937) Ryûkyû san shôjôbakama shinpin [New species of *Sugeriokia*]. *Acta Phytotaxonomica & Geobotanica* 6: 46–47.
- Koidzumi, G. (1939) Contributiones ad cognitionem florae Asiae orientalis. *Acta Phytotaxonomica & Geobotanica* 8: 50–61.
- Koidzumi, H. (1921) Shinshû shokubutsu no kenkyû [Studies on the flora of Shinshû (Nagano prefecture)] 1. *Shinano Kyôiku* 421: 10–24. [in Japanese]
- Krause, K. (1930) Liliaceae. In: Engler, A. (Ed.) *Die Natürlichen Pflanzenfamilien* 15a. W. Engelmann, Leipzig, pp. 227–386.
- Lee, N.S. (2007) *Heloniopsis*. In: Park, C.-W. (Ed.) *The Genera of Vascular Plants of Korea*. Academy Publ. Co., Seoul, pp. 1308–1309.
- Lee, Y.N. (2002) *Flora of Korea*, ed. revised & enlarged. Kyohak Publ. Co. Ltd., Seoul, 1269 pp. [in Korean]
- Lee, Y.N. (2006) *New Flora of Korea* 2. Kyohak Publ. Co. Ltd., Seoul, 885 pp. [in Korean]
- Léveillé, H. (1905) Liliacées, Amaryllidacées, Iridacées et Hémodoracées de Chine. *Memorie della Pontificia Accademia Romana dei nuovi Lincei* 23: 333–379.
- Li, H.L. (1944) The phytogeographic divisions of China, with special reference to the Araliaceae. *Proceedings of the Academy of Natural Sciences of Philadelphia* 96: 249–277.
- Lin, Y., Yang, Z., Zhang, X., Sun, Z., Du, Q., Wu, Z., Mi, S. & Li, H. (2014) Lectotypifications of eighteen names in monocotyledons. *Acta Botanica Boreal.-Occidentalis Sinica* 34: 411–415.
- Linnaeus, C. (1753) *Species Plantarum* 1. Impensis Laurentii Salvii, Holmiae, 560 pp.
- Linnaeus, C. (1754) *Genera Plantarum*, ed. 5. Impensis Laurentii Salvii, Holmiae, 500 + 22 pp.
- Makino, T. (1891) Nihon shokubutsu hôchi [Notes on Japanese plants] XII. *Botanical Magazine (Tokyo)* 5 (50): 124–126. [in Japanese]
- Masamune, G. (1934) Floristic and geobotanical studies on the island of Yakushima, province Ôsumi. *Memoirs of the Faculty of Science and Agriculture, Taihoku Imperial University* 11, Botany 4: 1–608.
- Masamune, G. (1957) Enumeratio tracheophytarum Ryukyu insularum IX. *Science Reports of the Kanazawa University* 5 (2): 85–121.
- Masamune, G. (1969) *Color illustrated flora of Nippon* 8. Koyo Shoin, Tokyo, 295 pp. [in Japanese]
- Matsumura, J. (1905) *Index Plantarum Japonicarum* 2 (1). Maruzen, Tokyo, 315 pp.
- Maximowicz, C.J. (1867) Diagnoses breves plantarum novarum Japoniae et Mandshuriae 3. *Bulletin de l'Académie Impériale des Sciences de Saint-Pétersbourg*. St. Petersburg 11: 433–439.
- Michaux, A. (1803) *Flora Boreali-Americana* 1. Apud fratres Levrault, Parisiis & Argentorati, 330 pp.
- Miller, P. (1760) *Figures of the Most Beautiful, Useful, and Uncommon Plants Described in the Gardeners Dictionary [etc.]* 2. Printed for the author, sold by John Rivington [etc.], pp. 101–200, pls. 151–300, index.
- Minato, M., Gorai, M. & Hunahashi, M. (Chief Eds.) (1965) *The Geologic Development of the Japanese Islands*. Tokyo, Tsukiji Shokan, 442 pp.
- Miquel, F.A.W. (1866) Over de verwantschap der flora van Japan met Aziën Noord-Amerika [reprint of Miquel 1867a], 25 pp.
- Miquel, F.A.W. (1866–1867) *Prolusio Flora Iaponicae* [mainly a reprint of Miquel 1867b]. Apud C.G. van der Post, Amstelodami, et apud C. van der Post Jm, Traiecti ad Rhenum, 392 pp.
- Miquel, F.A.W. (1867a) Over de verwantschap der flora van Japan met Aziën Noord-Amerika. *Verslagen en Mededeelingen van de Afdeeling Natuurkunde; Koninklijke Akademie van Wetenschappen* Ser. 2, 2 (1): 65–89.
- Miquel, F.A.W. (1867b) *Prolusio flora iaponicae* (pars 5 & 6). In: Miquel, F.A.W. (Ed.) *Annales Musei Botanic-Lugduno-Batavi* 3: 91–209.
- Miquel, F.A.W. (1870) Contributions à la flore du Japon. *Archives Neerlandaises des Sciences Exactes et Naturelles* 5: 89–96.
- Miyabe, K. & Y. Kudo (1932) Flora of Hokkaido and Saghalien III. Monocotyledoneae, Araceae to Orchidaceae. *Journal of the Faculty of Agriculture, Hokkaido Imperial University* 26: 279–387, pl. 5.
- Mochizuki, R. (1978a) A supplement to list of plants in Akita Prefecture (2). *Journal of Geobotany* 26: 12–16.
- Mochizuki, R. (1978b) Shin-hinshu, Kibana-syôjôbakama [A new form *Heloniopsis orientalis* (Thunb.) C. Tanaka form. *lutea* R. Mochizuki]. *Akita Shizenshi Kenkyû* 10: 11. [in Japanese]
- Morison, R. (1699) *Plantarum Historiae Universalis Oxoniensis* 3. E Theatro Sheldoniano, Oxonii, 657 pp., plus plates and index pages.
- Murray, J.A. (1784) *Systema Vegetabilium [etc.]*, ed. 14, Jo. Christ. Dieterich, Gottingae, 987 pp. + pp. 988–1004 (index).
- Nakai, T. (1933) Notulae ad plantas Japonicae & Koreae 43. *Botanical Magazine (Tokyo)* 47: 235–267.
- Nakai, T. (1952) A synoptical sketch of Korean flora. *Bulletin of the Natural Science Museum* 31: 1–152.
- Nemoto, K. (1936) *Nippon Shokubutsu Soran Hoi (Flora of Japan, Supplement)*. Shunyôdô, Tokyo, 1436 pp. [in Japanese]
- Ogasawara K. & Uemura, K. (2006) Nihon rettô no oitachi to dô-shokubutsu-sô no yurai [Historical background of the Japanese

- Archipelago and the derivation of the Japanese fauna and flora]. In: National Science Museum (Ed.) *Natural History of the Japanese Islands*. Tokai University Press, Hadano, 339 pp. [in Japanese]
- Ohba, H., Akiyama, S. & Thijssse, G. (2005) Miquel's new taxa of the vascular plants described from Japan in *Prolusio Florae Japonicae* and some other works. In: Ohba, H. & Boufford, D.E. (Eds.) The Botanical Collections: Proceeding of the Symposium 'Siebold in the 21st Century' held at the University Museum, the University of Tokyo, in 2003. *University Museum, University of Tokyo, Bulletin* 41: 31–140.
- Ohwi, J. (1930) Symbolae ad floram Asiae orientalis. *Botanical Magazine (Tokyo)* 44: 565–573.
- Ohwi, J. (1953a) *Flora of Japan*. Shibundo, Tokyo, 1383 pp. [in Japanese; March 1953]
- Ohwi, J. (1953b) New names and new combinations adopted in my "Flora of Japan." *Bulletin of the Natural Science Museum* 33: 66–90. [July 1953]
- Ohwi, J. (1965) *Flora of Japan (in English)*. Smithsonian Institution, Washington, D.C., 1067 pp.
- Plukenet, L. (1692) *Leonardi Plukenetii Phytographia* 3. Sumptibus autoris, Londini, tab. 121–250.
- Plukenet, L. (1696) *Almagestum Botanicum*. Sumptibus Autoris, Londini, 402 pp.
- Rafinesque, C.S. (1837, as '1836') *Flora Telluriana* 2. H. Probasco, Philadelphia, 112 pp.
- Reichenbach, H.G.L. (1828) *Conspectus Regni Vegetabilis per Gradus Naturales Evoluti. Pars I.* Apud Carolum Cnobloch, Leipzig, 294 pp.
- Sakaguchi, S. (1924) *General Index to the Flora of Okinawa*. Ishizuka Shoten, Syuri, 152 pp.
- SCPCA (2017) *Helonias bullata*. South Carolina Plant Conservation Alliance. Available from: <https://scplantconservation.org/priority-species/helonias-bullata/> (accessed 6 August 2018)
- Shaw, J.M.H. (2008) Three new Crūg Farm introductions. *Plantsman* New series, 7: 39–43.
- Shui, Y.-M. & Chen, W.-H. (2006) *Seed Plants of the Karst Region in China 1 (Southeast Yunnan)*. Science Press, Beijing, 260 pp.
- Smith, W.W. & Jeffrey, J.F. (1916) *Ypsilandra yunnanensis* W.W.Sm. & Jeffrey. *Notes from the Royal Botanic Garden, Edinburgh* 9: 143–144.
- Stafleu, F.A. (1966) F. A. W. Miquel, Netherlands Botanist. *Wentia* 16: 1–95.
- Stafleu, F.A. & Cowan, R.S. (1981) *Taxonomic literature 3: Lh–O. Second ed.* Bohn, Scheltema & Holkema, Utrecht; dr. W. Junk b.v., The Hague, 980 pp.
- Sugawara, S. (1937) *Plants of Saghalien*. Toyohara, Saghalien, 490 pp. [in Japanese]
- Sugawara, S. (1939) *Illustrated Flora of Saghalien II. Araceae–Magnoliaceae*. Gansyōdo, Tokyo, 969 pp. [in Japanese]
- Sutter, R.D. (1984) The status of *Helonias bullata* L. (Liliaceae) in the southern Appalachians. *Castanea* 49: 1–16.
- Takahashi, H. (1988) The pollination biology of *Heloniopsis orientalis* (Thunb.) C. Tanaka (Liliaceae). *Plant Species Biology* 3: 117–123.
- Takahashi, H. (1989) Kakujitsuni shushi wo tsukuru shikumi [Mechanisms for securing seed production] In: Kawano, S. (Ed.) *Newton special issue, Shokubutsu no Sekai [The world of plants]* 4. Kyoikusha, Tokyo, pp. 104–107. [in Japanese]
- Takahashi, M. & Kawano, S. (1989) Pollen morphology of the Melanthiaceae and its systematic implications. *Annals of the Missouri Botanical Garden* 76: 863–876.
- Takhtajan, A. (1987) *Systema Magnoliophytorum*. Nauka, Leninopoli, 439 pp. [in Russian]
- Takhtajan, A. (1997) *Diversity and Classification of Flowering Plants*. Columbia University Press, New York, 643 pp.
- Takhtajan, A. (2009) *Flowering Plants. Second ed.* Springer Science & Business Media B.V., 871 pp.
- Tamura, M.N. (1998) Melanthiaceae. In: Kubitzki, K. (Ed.) *The Families and Genera of Vascular Plants 3*. Springer-Verlag, Berlin, pp. 369–380.
- Tanai, T. (1967) Tertiary floral changes of Japan. In: *Jubilee Publication of Commemoration Professor Sasa's 60th Birthday*. Sapporo, pp. 317–333.
- Tanai, T. (1972) Tertiary history of vegetation in Japan. In: Graham, A. (Ed.) *Floristics and Paleofloristics of Asia and Eastern North America*. Elsevier, Amsterdam, pp. 235–255.
- Tanai, T. (1988) Kaede-zoku no shinka [Evolution of the genus *Acer*]. In: Kawano, S. (Ed.) *Newton Special Issue, Shokubutsu no Sekai [the world of plants]* 3. Kyoikusha, Tokyo, pp. 106–111. [in Japanese]
- Tanai, T. (1992) Tertiary vegetational history of East Asia. *Bulletin of the Mizunami Fossil Museum* 19: 125–163. [in Japanese with English abstract]
- Tanaka, N. (1996) What is a species? *Acta Phytotaxonomica & Geobotanica* 47: 239–252. [in Japanese with English summary]
- Tanaka, N. (1997a) Taxonomic significance of some floral characters in *Helonias* and *Ypsilandra* (Liliaceae). *Journal of Japanese Botany* 72: 110–116.
- Tanaka, N. (1997b) Evolutionary significance of the variation of the floral structure of *Heloniopsis*. *Journal of Japanese Botany* 72: 131–138.
- Tanaka, N. (1997c) Phylogenetic and taxonomic studies on *Helonias*, *Ypsilandra* and *Heloniopsis* I. Comparison of character states (1).

- Journal of Japanese Botany* 72: 221–228.
- Tanaka, N. (1997d) Phylogenetic and taxonomic studies on *Helonias*, *Ypsilandra* and *Heloniopsis* I. Comparison of character states (2). *Journal of Japanese Botany* 72: 286–292.
- Tanaka, N. (1997e) Phylogenetic and taxonomic studies on *Helonias*, *Ypsilandra* and *Heloniopsis* II. Evolution and geographical distribution. *Journal of Japanese Botany* 72: 329–336.
- Tanaka, N. (1997f) The logic and methodology of taxonomy. *Proceedings of the Japan Society of Plant Taxonomists* 13: 39–44. [in Japanese with English summary]
- Tanaka, N. (1998a) Phylogenetic and taxonomic studies on *Helonias*, *Ypsilandra* and *Heloniopsis* III. Taxonomic revision. *Journal of Japanese Botany* 73: 102–115.
- Tanaka, N. (1998b) What is a species? (II). *Journal of Japanese Botany* 73: 236–240. [in Japanese with English summary]
- Tanaka, N. (2009) Taxonomic treatments for two taxa of *Ypsilandra* (Melanthiaceae) from the Sino-Vietnamese border. *Journal of Japanese Botany* 84: 188–191.
- Tanaka, N. (2017a) Diversity in fruit and seed characters of *Chamaelirium* and *Chionographis* (Melanthiaceae). *Taiwania* 62: 67–74.  
<http://doi.org/10.6165/tai.2017.62.67>
- Tanaka, N. (2017b) A synopsis of the genus *Chamaelirium* (Melanthiaceae) with a new infrageneric classification including *Chionographis*. *Taiwania* 62: 157–167.  
<http://doi.org/10.6165/tai.2017.62.157>
- Tanaka, T. (1925) On certain Thunbergian plants from Japan. *Bulleten Scienca de la Fakultato Terkultura, Kjusu Imperia Universitato, Fukuoka* 1: 191–209.
- Thunberg, C.P. (1784, August) *Flora Japonica*. In Bibliopolio J.G. Mülleriano, Lipsiae., 418 pp.
- Thunberg, C.P. (1794) Botanical observations on the Flora japonica. *Transactions of the Linnean society. London* 2: 326–342.
- Thunberg, C.P. (1802) *Icones Plantarum Japonicarum* 4. Litteris Johann. Fred. Edman, Reg. Acad. Typogr., Upsaliae, 10 plates.
- Trew, C.J. (1771) *Plantae Selectae* 8: 36–43, tab. 71–80.
- Uemura, K. (1995) Nihon no furora-shi [History of the Japanese flora]. In: *Syūkan Asahi Hyakka* [Weekly Asahi Encyclopedia], *Shokubutsu no Sekai* [The World of Plants] 87. Asahi Shimbunsha Co., Tokyo, pp. 94–95. [in Japanese]
- Uemura, K. (2011) Koyū shokubutsu no rekishi [History of endemic species]. In: Kato, M. & Ebihara, A. (Eds.) *Endemic Plants of Japan*. Tokai University Press, Hadano (Kanagawa), pp. 24–28 (Japanese).
- USFWS (1988) *Endangered and threatened wildlife and plants; Determination of *Helonias bullata* (Swamp Pink) to be a threatened species*. [U.S. Fish & Wildlife Service, Interior. Federal Register 53, no. 175.] Newton Corner, Massachusetts, 5 pp. Available from: [https://ecos.fws.gov/docs/federal\\_register/fr1468.pdf](https://ecos.fws.gov/docs/federal_register/fr1468.pdf) (accessed 7 August 2018)
- USFWS (1991) *Swamp Pink (*Helonias bullata*) Recovery Plan*. Region Five, U.S. Fish & Wildlife Service, Newton Corner, Massachusetts, 56 pp. Available from: [https://ecos.fws.gov/docs/recovery\\_plan/910930c.pdf](https://ecos.fws.gov/docs/recovery_plan/910930c.pdf) (accessed 7 August 2018)
- Utech, F.H. (1978) Vascular floral anatomy of *Helonias bullata* (Liliaceae-Helonieae), with a comparison to the Asian *Heloniopsis orientalis*. *Annals of Carnegie Museum* 47: 169–191.
- Utech, F.H. (1980) Somatic karyotype analysis of *Helonias bullata* L. (Liliaceae), with a comparison to the Asian *Heloniopsis orientalis* (Thunb.) C. Tanaka. *Annals of Carnegie Museum* 49: 153–160.
- Utech, F.H. (2002) *Helonias*. In: Flora of North America Editorial Committee (Ed.) *Flora of North America North of Mexico* 26. Oxford Univ. Press, New York, pp. 69–70.
- Utech, F.H. & Kawano, S. (1981) Vascular floral anatomy of the East Asian *Heloniopsis orientalis* (Thunb.) C. Tanaka (Liliaceae-Helonieae). *Botanical Magazine (Tokyo)* 94: 295–311.
- Wang, F.T. & Tang, T. (1936) Notes on Chinese Liliaceae 3. *Bulletin of the Fan Memorial Institute of Biology, Botany* 7: 81–90.
- Wang F.T. & Tang, T. (1943) Notes on Chinese Liliaceae 6. *Bulletin of the Fan Memorial Institute of Biology* New series 1: 106–111.
- Wang F.T. & Tang, T. (1949) Notes on Chinese Liliaceae 8. *Contributions from the Institute of Botany, National Academy of Peiping* 6: 105–114.
- Watson, S. (1879) Revision of the North American Liliaceae. *Proceedings of the American Academy of Arts and Sciences* 14: 213–303.
- Wiley, E.O. (1981) *Phylogenetics. The Theory and Practice of Phylogenetic Systematics*. Wiley-Liss, New York, 439 pp.
- Yamaguchi, T., Kato, N., Fujii, S., Tamura, M.N., Nagamasu, H. & Wada, H. (2003) The specimens of Japanese plants collected by Ph. F. von Siebold, H. Bürger and von Siebold's collaborators, and now housed in the National Herbarium of the Netherlands and the Botanische Staatssammlung München. *Angiospermae. Calanus (Bulletin of the Aitsu Marine Station, Kumamoto University, Japan)* Special Number 5: 259–576.
- Yan, H. (Ed.) (2002) *Climatological Atlas of the People's Republic of China*. China Meteorological Press, Beijing, 250 pp.
- Ying, S.S. (1980) *Coloured illustrations of herbaceous plants of Taiwan* 1. Published by the author, Taipei, 256 pp.
- Zhao, R.-N. & Peng, Z.-X. (1987) A new species of *Ypsilandra* from Gansu province, China. *Acta Botanica Boreali-Occidentalis, Sinica* 7: 57–59.