FLORAL VASCULAR ANATOMY OF JAPONOLIRION OSENSE NAKAI (LILIACEAE) AND ITS TRIBAL RELATIONSHIP

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ABSTRACT

Japonolirion osense, a rare, serpentine endemic of Japan known from only two general areas, has been associated in the limited literature with the tribe Helonieae—Helonias in eastern North America, Heloniopsis in Japan and Korea, and Ypsilandra in western China. This is the first report on the floral vascular anatomy of "the lily of Japan." The pedicel to stigma vasculature of J. osense is a simple axial system with fusion dorsals and unbranched ventrals. The three septicidal carpels are loosely connected with only stigmatic tissue along their central floral axis. Each carpel terminates in a short free style. Three representative genera of the Helonieae have simple dorsals and highly branched ventrals, three fused septa, a massive basal receptacle that is fused along along the floral axis, a fusion style that is depressed into the upper ovary area, winged seeds, and they share loculicidal dehiscence. The tribal association of Japonolirion should be with the Tofieldieae and not the Helonieae.

INTRODUCTION

Japonolirion osense Nakai is among the rarest of flowering plants in the Japanese Islands (Hara and Kanai, 1959; Shimizu and Satomi, 1977). It is limited to serpentine areas in Honshu and Hokkaido. In Honshu the plants are found in the Ose region (Mount Shibutsu) which is the type locality and in the Mount Tanigawa region of Kodzuke Province (Gumma Prefecture). In Hokkaido the plant occurs only in

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the Teshio region (Toikanbetsu). The latter area is characterized by cold, high elevation, serpentine swamps.

Nakai (1930) first described this monotypic genus and its associated species from Ose in Honshu, hence its specific name. The type specimen is in the Herbarium of the University of Tokyo (TI). Makino and Tatewaki, in Tatewaki (1931), described another species from Hokkaido, that is Japonolilion (Japonolirion) saitoi, but this northern population has since been treated as a variety, that is J. osense var. saitoi (Makino & Tatew.) Ohwi. Hara and Kanai (1959) have presented a distribution map of the species, while only the northern var. saitoi was mapped for Hokkaido by Tatewaki (1954). The species has been illustrated in Ohwi's Flora of Japan (1965, fig. 2), Kitamura et al., Illustrated Herbaceous Flora of Japan (1964, vol. III, pl. 43, fig. 271), and Shimizu's New Alpine Flora of Japan (1983, vol. II, pl. 107, fig. 334), and Satake et al., Wild Flowers of Japan (1981, Vol. I, pl. 18, fig. 2).

The systematic relationship of this rare lily was first referred to the Helonieae by Nakai (1930) in his type description. This tribal association was again repeated in Kitamura et al. (1964) and Shimizu (1983). Both authors also repeated the reported $2n = 24$ chromosome count published by Sato (1942). Other than the type description and the limited floristic treatments previously cited, little direct evidence has been provided to substantiate a relationship to the Helonieae. This report presents the floral vascular anatomy of J. osense and is followed by an inference on a new tribal association.

**Materials and Methods**

Collections fixed in FAA of both flowering and fruiting inflorescences of Japonolirion osense var. saitoi sampled near Toikanbetsu, Rumoi, Hokkaido, were presented by Gen Murata of Kyoto University. Standarized, paraffin, serial sections on 30 small flowers were prepared between 12-15 μ and stained in safranin-methylene blue (Johansen, 1940; Sass, 1958). As an additional check on these serial sections, whole flowers were cleared and the vasculature stained in a NaOH-1% fuchsin mixture (Fuchs, 1963).

The method of presenting the continuous floral vascular anatomy follows that used in our previous papers (Utech and Kawano, 1975, 1976, 1980, 1981; Utech, 1978a, 1978b, 1978c, 1978d, 1978e, 1979a, 1979b, 1980, 1982). Figs. 2-4 are composite photomicrographs presenting the vascular floral anatomy, whereas Figs. 5-7 are line-drawn summary diagrams. In Fig. 6, projected views of the vascular continuity are represented from along both the dorsal and ventral radii. No teleological implication is intended by the descriptive manner of vasculature presentation and discussion. The various bundles and traces are letter-coded for ease in comparison and imply no direct homology to previously presented species.

**Observations**

**Pedicel Vascularization**

The inflorescence of Japonolirion osense is a dense, simple, erect raceme with several to relatively many flowers. The inflorescence is
normally 15–40 cm long, glabrous, weakly angled in cross-section or ridged in longitudinal section, and exceeds the leaves in height. There is a single flower per node, and each is subtended by a brownish, scarious bract which is 1.5–3.0 mm long, and one-nerved (Figs. 1, 2A). The bracts subtending each pedicel are similar to those lower on the inflorescence, but only reduced in size. The flowering pedicels are 1.5–3.0 (4.0) mm long and ascending.

For most of the flowering pedicel’s length, there are three, large, equally spaced, vascular bundles in cross-section (Figs. 3A–B, 5A, 6A, A’). Near the base of each flower, the associated pedicel has a triangular shape in cross-section. At this lower receptacle level each of the three
Fig. 2.—Pedicel, tepal and stamen vascularization in *J. osense*. Scale indicated, bar = 1 mm. (A) Pedicel and bract cross-section showing three clusters of bundles in the pedicel at the level of the tri-parted subdivision and a single vein (trace) in the subtending bract (Br). (B) Receptacle cross-section showing the vascularization of the outer tepals (OT), outer stamens (OS) and the common inner tepal-stamen area (ITS). The outer tepal bundles (OT; only 2 shown) shared a common origin with the three outer stamen (OS) bundles at a lower level in the common outer tepal-stamen bundles (OTS; not shown).
pedicel bundles undergoes a tri-parted radial division which results in three sets of three bundles each (Figs. 3C, 5B–C, 6B–C, 6B′–C′, 7).

**Tepal and Stamen Vascularization**

The six, greenish yellow tepals are free to their base and persist after anthesis (Fig. 1). There is a slight size difference between the three outer tepals and the three inner tepals. The tepals of the outer cycle are somewhat shorter in length (1.5–2.0 mm) than those of the inner cycle (2.0–2.5 mm) as well as somewhat narrower. Though small, the tepals of both cycles are broadly lanceolate. There are no glands or basal succate depression associated with the tepals of either cycle. The tepals of both cycles have only a single midrib vein, that is, an outer tepal (OT) bundle and an inner tepal (IT) bundle. There is no formation of tepal laterals in either cycle.

The six stamens, three outer and three inner, are equal in size, similar in shape, and equally spared in their respective cycles. All six stamens are as long as the inner perianth cycle. The white filaments are glabrous and subulate. The ovate anthers are bilocular, basifixed and introrse (Fig. 4F). Connective tips are not present on the anther sacs. There is a single bundle per stamen, that is, an outer stamen (OS) bundle in each of the three outer stamens and an inner stamen (IS) bundle in each of the three inner stamens.

Vascularization of the tepal and stamen cycles is simple and direct, and involves the subdivision of the three existing compound pedical bundles (Fig. 7). In the case of the vascularization of the outer tepals and outer stamens, subdivision of existing compound bundles is involved, whereas the vascularization of the inner tepals and inner stamens occurs via the subdivision of compound fusion bundles formed within the receptacle area (Figs. 2B–E, 3D–E, 5C–H, 6D–H).

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Three pairs of bundles are grouped in the central axial area along the ITS radii. Gaps are present in this central area along the OT-OS radii. (C) Receptacle cross-section above B showing the departure of the three outer stamen (OS) and the three inner stamen (IS). At this level the common ITS bundles have already divided and the blades of the inner tepals have been cut off. In the central axial area, the fusion dorsals are being formed. (D) Receptacle cross-section above C showing the formation of the fusion dorsals (D), the formation of the inner stamens with their bundles (IS) and the final departure of the outer stamens (OS). In the central axial area there are three pairs of bundles. The gaps along the OT-OS radii were closed with the formation of the dorsals, but there are now gaps along the IT-IS radii. (E) Receptacle cross-section above C showing the departure of the inner stamen with their bundles (IS) and the outward movement of the three dorsals (D) under the unopened locules. (F) Lower gynoecial cross-section showing the opened locules with the dorsals (D) in their outer carpellary position and the six ventrals in their central axial position.
Fig. 3.—Vascularization of the pedicel, tepals and lower gynoecium in *J. osense*. Scale indicated, bar = 1 mm. (A) Pedicel cross-section showing the three compound bundles prior to the tri-parted division. (B) Enlargement of A showing the three compound bundles. (C) Pedicel cross-section showing the tri-parted division of the three pedicel bundles. The central product of each division is the common outer tepal-stamen (OTS) bundle. (D) Lower receptacle cross-section showing the departure of the three common OTS bundles and the formation of the common inner tepal-stamen bundles (ITS). (E) Lower gynoecial cross-section showing the three dorsals (D) and the six ventrals (V). (F) Lower gynoecial cross-section showing the departure of the three dorsals (D) and the six remaining ventrals (V).
Fig. 4.—Gynoecial and stamen vascularization and morphology in *J. osense*. Scale indicated, bar = 1 mm. (A) Gynoecial cross-section showing the location of the six ventrals (V) and the weak zone of inter-digitating papillae (arrows) which separate the three carpels. (B) Gynoecial cross-section at the same level as A showing the dorsal (D) bundle surrounded by sheath cells. (C) Overall gynoecial cross-section showing the three carpels with ovules and the ventral and dorsal regions. (D) Upper gynoecial cross-section showing the three freed carpels. Dorsal and ventral bundles are still present at this level. (E) Stylar region cross-section showing the inner facing papillae of the stigmatic zone (arrows). The dorsals are still present at this level. (F) Mid-anthers cross-section showing the bilocular and introrse condition. All anthers are similar in size and shape, basifixed, and contain a single bundle.
Fig. 5.—Selected summary floral cross-section of *J. osense*. (A) Lower pedicel level with three compound bundles each 120° apart. (B) Pedicel level showing the tri-parted subdivision of the three compound bundles. (C) Pedicel level following the tri-parted subdivision. The center bundle of each three which departs establishes the common outer tepal-stamen (OTS) bundle. (D) Lower receptacle level showing the formation of the three common inner tepal-stamen (ITS) bundles via fusion from the inner six remaining bundles. The ITS bundles are midway between the common outer tepal and stamen radii. The outer tepal (OT) and outer stamen (OS) bundles are also formed at this level from the division of their common bundle. (E) Lower receptacle level showing the departure of the three outer tepal traces (OT) and the common inner tepal-stamen traces.
Following the tri-parted radial division of the three large pedicel bundles in the lower receptacle area, the center bundle of each group of three establishes a radius along which the outer tepals and stamens form. These three radii are 120° apart. The three bundles which are along these radii are compound and have been designated as the common outer tepal and outer stamen bundles (OTS). Subsequent subdivision of these bundles results in the formation of the three outer tepal bundles (OT) and the three outer stamen (OS) bundles (Figs. 2B–D, 3D, 5C–H, 7). It should also be noted that the OS-OT-OTS radii are vertically co-planar with the radii of the three pedicel bundles.

Following the formation of the common OTS bundles via the tri-parted divisions, the two lateral bundles which flank each OTS bundle again undergo a radial division. The closest two product halves of these divisions but from different OTS bundles fuse. These three fusion products are 120° apart and mid-way between the OTS bundles. These fusion products have been designated as the common inner tepal-stamen (ITS) bundles (Figs. 2B, 5D, 6D, D', 7). Further subdivision of these bundles results in the formation of the three inner tepal bundles (IT) and the three inner stamen (IS) bundles (Figs. 2C–E, 5F–J, 6F–J, F'–J', 7). The patterns of subdivision of both the common OTS and the common ITS are similar but their origins are different. The OTS was a compound bundle continuous with the pedicel supply following the tri-parted division, whereas the ITS was a compound fusion bundle formed between products of the tri-parted division.

Mid-way between the OTS and ITS radii are the remaining product halves which did not fuse and were derived from the bundles involved

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The three outer stamen (OS) remain in the central area at this level. The cross-sectional shape is decidedly lobed at this level. (F) Lower receptacle level showing the formation of the three dorsals (D) along the common outer tepal and stamen radii from the inner six remaining bundles. There has been no division in the common inner tepal-stamen (ITS) bundles at this level. (G) Departure of the outer tepals with a single bundle (OT) and the division of the three common ITS bundles into inner tepal (IT) and inner stamen (OS) bundles. (H) Departure of the inner tepals with a single bundle (IT) and the outward departure of the OS and D bundles within the receptacle area. (I) Departure of the outer stamens with a single bundle (OS) and the outward departure of the IS bundles within the receptacle area. The three dorsals (D) are each associated with two of the six central bundles and will establish the ventral (V) supply. (J) Departure of the inner stamens (wedge shaped) with a single bundle (IS) and formation of the three weakly connate carpels. The dorsal (D) and ventral (V) supplies are established in each carpel. The three outer filaments have an elliptic cross-section. (K) Lower gynoecial level where the ventrals supply the ovules. The three inner filaments also have an elliptic cross-section. (L) Middle gynoecial level showing the carpellary supply and the relationships of the three carpels. (M) Upper stylar area with only the dorsal supply remaining.
Fig. 6.—Projected cross-sections of *J. osense*. The lettered sections with connected bundles correspond to the same sections in Fig. 5. The series A to M are projected along a dorsal or an outer tepal-stamen radius, while the series A' to F' are projected along a ventral or an inner tepal-stamen radius. Both section A and A' are the same section but viewed from two different radii.

In the formation of the fusion ITS bundles. These centrally located six bundles are arranged in three pairs and they will undergo further subdivision and fusion to establish the dorsal (D) and ventral (V) supplies (Fig. 7).
Fig. 7.—Summary longitudinal diagram for the floral vascular supply of *J. osense*. The various codes for the bundles are explained in the text: OTS = common outer tepal-stamen; ITS = common inner tepal-stamen; OT = outer tepal; OS = outer stamen; IT = inner tepal; IS = inner stamen; D = dorsal; V = ventral.

**Gynoecial Vascularization**

The superior gynoecium in *Japonolirion osense* consists of three weakly connate carpels except apically where the three short (0.5–0.75 mm), recurved styles diverge. The limited lateral carpel fusion is due chiefly to the inter-digitating of papillae along the septal faces. In cross-section, the gynoecium is three lobed (Figs. 2F, 4C–E, 5J, 6J, J’). There are no dorsal grooves to indicate a dehiscent zone. The greenish, glabrous, elliptic, fruiting gynoecium is between 2.5–3.0 mm long and separate septicidally through the weakly connate zone between the carpels. Neither raphides nor other intra-cellular inclusions were observed from the pedicel through the stylar-stigmatic zone.

Vascularization of the carpels is also simple and direct. At the level where the common OTS and ITS bundles are all present, the central gynoecial area has six bundles organized into three pairs. Each of these bundles divides and the two product halves closest to the OTS radii
fuse to form the dorsals (D) (Figs. 2D–E, 3E–F, 5F, 6F, F’, 7). The three dorsals depart outward horizontally under the unopened locules. The locules open via a slit along the OTS radii, not perpendicular to it. When the dorsals are formed, a gap is closed. This gap resulted from the tri-parted division in lower pedicle area (Fig. 7). The dorsals are fusion products which do not undergo any further division. They follow a direct course into the small stylar arms and end (Figs. 4D–E, 5M, 6M).

The other remaining product halves that were not involved in the formation of the fusion dorsals (D), become the six ventrals (V). The two ventrals (V) which supply a given carpel (Figs. 3E–F, 5F–J, 6F–J, F’–J’, 7) are the two remaining and continuing products following the division and and fusion which formed the dorsals. There are neither septal axial bundles of any type nor any inter-connections between the dorsal and ventral supplies following their origins.

Two ovules are supplied from each ventral via simple, direct, horizontal funicular traces. On the average, each carpel has four ovules. One to two wingless seeds are usually observed in each mature carpel. Septicidal dehiscence or parting through the weakly connate septal zones is characteristic of this species.

DISCUSSION AND CONCLUDING REMARKS

The pedicel to style floral vascular anatomy of *Japonolirion osense* can be summarized as follows (see also Fig. 7). There are three, equally spaced, compound bundles in the pedicel. Each of these undergoes a tri-parted division in the lower receptacle area. The central element of each set of three directly establishes the common outer tepal-stamen (OTS) bundle. Following another subdivision of the isolated OTS bundles, the outer tepal (OT) and outer stamen (OS) bundles are formed. The paired lateral elements of the tri-parted division divide and the resulting products closest to each other, but from different sets, fuse to form the common inner tepal-stamen (ITS) bundles. These bundles, like the OTS, divide to form the inner tepal (IT) and inner stamen (IS) bundles. The remaining six elements of the lateral pairs continue and establish the dorsal and ventral supplies. Each of these six bundles divides and the resulting products closest to the OTS radii fuse to form the dorsals (D). Three such fusion dorsals are formed. The other six remaining products, that is those not involved in the formation of the dorsals, become the six simple ventrals (V). No septal axials are formed in this species. There is no interconnection between the dorsal and ventral supplies once the dorsals and ventrals are established. The dorsals follow a direct course into the distal portion of their associated carpels and terminate in the free styles.
The floral morphology of *Japonolirion osense* is characterized by three weakly connate carpels. Each has a free, slightly recurved style. The locules open along the OTS radii, not perpendicular to it. Septicidal dehiscence is the rule for the fruiting gynoecium. Neither septal glands nor nectaries associated with the tepals are present in the species. Raphides were not observed in any floral tissue. Furthermore, no raphides were reported in *Tofieldia* (Sterling, 1979) and *Pleea* (Utech, 1978d).

Three genera, which are commonly grouped in the Helonieae, are *Helonias*, *Heloniopsis*, and *Ypsilandra* (Engler, 1888; Krause, 1930). The monotypic *Helonias bullata* L. occurs locally in eastern North America (Utech, 1978c). Four species of *Heloniopsis* have been described from Korea, Japan, and Taiwan. *Heloniopsis orientalis* (Thunb.) C. Tanaka is the commonest and has the widest range—occurring throughout Japan (Utech and Kawano, 1981). Five species of *Ypsilandra* occurring in the higher Himalayan elevations of Burma, Nepal, Tibet, and western China are known. The Japanese endemic *Japonolirion osense* has been associated with this liliaceous tribe (Nakai, 1930; Kitamura et al., 1964; Shimizu, 1983).

The floral vascular anatomies and morphologies of three representative genera of the Helonieae have been previously investigated: *Helonias bullata* (Utech, 1978c), *Heloniopsis orientalis* (Utech and Kawano, 1981) and *Ypsilandra thibetica* (Utech, manuscript in preparation). Sterling (1980) has also reported a high degree of similarity in the carpel morphology of these three genera. The similarity in floral vascular anatomy and floral morphology between these three species from three different genera is extremely high and almost all of these shared characters are not observed in *Japonolirion*.

The following floral vascular and morphological characters are shared by *Helonias*, *Heloniopsis* and *Ypsilandra*, but do not occur in *Japonolirion*: 6-ridged pedicels, basal tepal nectaries, broad basal receptacle, fused floral axis, locules opening perpendicular to OTS radii, dorsal grooves, fused septa, sunken styles, winged seeds, loculicidal dehiscence, simple (unfused) dorsal bundles, complex (highly branched) ventrals, and septal axials (Utech, 1978c; Utech and Kawano, 1981; Sterling, 1980).

Furthermore, *Helonias bullata* (Utech, 1980) and *Heloniopsis orientalis* (Nakamura, 1967) share a similar $2n = 34$ chromosome number and karyology. Although a count is still lacking for any member of the genus *Ypsilandra*, a count of $2n = 24$ has been reported for *Japonolirion osense* (Sato, 1942).

If the floral and karyological similarity of *Japonolirion* is not with the Helonieae, then what tribal, liliaceous association would be better.
From the limited work on the floral vascular anatomy and floral morphology of the tribe Tofieldieae (Anderson, 1940; Ambrose, 1975; Utech, 1978; Sterling, 1979), there is a high degree of similarity in Tofieldia sensu lato and that reported here for Japonolirion. The tribal association of Japonolirion should be with the Tofieldieae and not with the Helonieae.

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