

東アジア産オモト(ユリ科スズラン連)の花器維管束の解剖学的研究

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Frederick H. UTECH* : Floral Vascular Anatomy of the East Asian *Rohdea japonica* (THUNB.) A. W. ROTH (Liliaceae-Convallarieae)**

F. H.ユーテック* : 東アジア産オモト (ユリ科スズラン連) の花器維管束の解剖学研究**

Introduction

The east Asian genus *Rohdea* A. W. ROTH (1821) named in honor of Michael ROHDE, a physician and botanist from Bremen who did early descriptive work on *Cinchona* (ROHDE, 1804), has two species. *Rohdea japonica* (THUNBERG) A. W. ROTH occurs in the warm temperate regions of Japan and China (OHWI, 1965; *Flora Reipublicae Shinicae*, 1978; *Iconographica Cormophytorum Sinicorum*, 1976), whereas *R. watanabei* HAYATA (= *Campylandra watanabei* (HAYATA) DANDY, 1933) is described as endemic to Taiwan (HAYATA, 1915, 1916; LI *et al.*, 1978). In the older taxonomic literature, *Rhodea* is an often seen, orthographic variant and synonym of *Rohdea*.

In the Englerian system (ENGLER, 1888; KRAUSE, 1930), *Rohdea* is placed in the tribe Convallarieae and the subtribe Aspidistrinae with *Gonioscypha* BAKER, *Campylandra* BAKER, *Tupistra* KER.-GAWL., and *Aspidistra* KER.-GAWL. Except for the additional genus, *Evvardiella* GAGNEPAIN, HUTCHINSON (1934, 1959) has grouped *Rohdea* with the same Englerian genera, but has raised the group to tribal rank, the Aspidistreae. HUTCHINSON, furthermore, indicates that it is from this group that there is further development to the Araceae, tribe Orontieae. Interestingly enough, *Rohdea japonica* is based on THUNBERG'S (1784) *Orontium japonicum*.

Two extremely interesting, but dated, reports of snail pollination in *Rohdea japonica* have been summarized by KUNTH (1909). However, critical in the field observations and confirmation are needed for these reports. Numerous illustrations of *R. japonica* have been published (AGARDH, 1858; BLUME, 1834; SCHNIZLEIN, 1846; KITAMURA *et al.*, 1975; *Flora Reipublicae Popularis Sinicae*, 1978; *Iconographica Cormophytorum Sinicorum*, 1976). Cytologically, this often cultivated species is known to be $2n=38$ (MATSUURA & SUTO, 1935; SATO, 1942; NAGAMATSU & NODA, 1970).

This report on the floral vascular anatomy of *R. japonica* presents the vascular network underlying the berry fruit, and provides additional information for a

future evaluation of its tribal grouping and the broader question of the evolution of the berry fruit within the Liliaceae and the Convallarieae.

Materials and Methods

Floral material of *Rohdea japonica* used in this study consisted of two inflorescences with approximately 30 flowers each. Each inflorescence had floral material which ranged in age from closed buds to flowers in late anthesis. This floral material had been fixed in FAA from cultivated material in the gardens of Kyoto University (KYO), Japan, and was given as a research gift by Gen MURATA of Kyoto University for which the author is indebted.

A sample of twenty five flowers of varying age from both inflorescences were embedded in wax following the traditional TBA series. Standardized paraffin sectioning (12-16 μ m) and staining (safranin-methylene blue) techniques (JOHANSEN, 1940; SASS, 1958) were employed on a total of 20 complete, serial cross-sectionally prepared flowers as well as five longitudinally prepared flowers. Checks on these preparations were made by observing whole flowers which had been cleared in 10% NaOH and stained in 1% fuchsin (FUCHS, 1963; UTECH and KAWANO, 1976). Permanent slides from this study have been deposited in the slide collection to Carnegie Museum of Natural History (CM) as a voucher.

Photomicrographic composites (Figs. 1-3) show selected aspects of the floral morphology and the associated vascular floral anatomy of *R. japonica*. Summary diagrams (Figs. 4-5) which emphasize the continuity of the vasculature from the pedicel to stigma are also presented. The methodology of vasculature diagramming and presentation parallels that used in our previous liliaceous studies (UTECH, 1978 a-e, 1979 a-b; UTECH and KAWANO, 1975, 1976a, 1976b, 1980, 1981).

Observations

Rohdea japonica is a glabrous, evergreen perennial

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from a stout, ascending to creeping rhizome with thick adventitious roots and has two-ranked, coriaceous,

oblanceolate to lanceolate, basal leaves. Overshadowed by the slightly lustrous, surrounding basal leaves is a

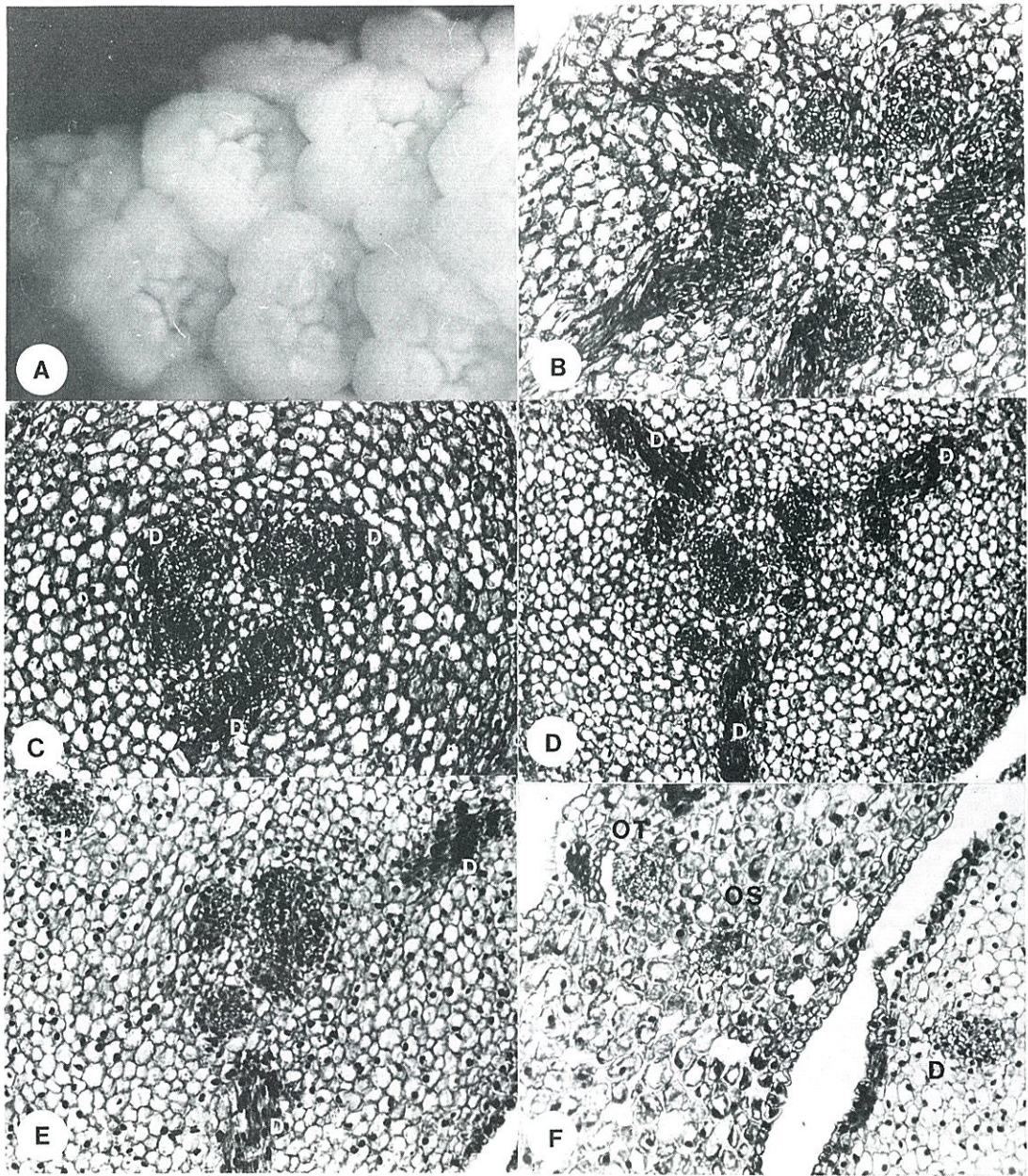


Fig.1. Floral close up of a part of an inflorescence of *Rohdea japonica* showing the fleshy campanulate corolla and the broadly tri-lobed stigma ($\times 2$). B. Lower receptacle base showing the three parted subdivision of the three pedicel zone bundles, see Figs. 4B-C, 5B-C ($\times 35$). C. Lower gynoecial cross-section showing the formation of the three fusion dorsals (D), see Figs. 4D, 5D ($\times 35$). D. Lower gynoecial cross-section showing the early departure of the three fusion dorsals (D), see Fig. 4D-E, 5D-E ($\times 35$). E. Gynoecial cross-section showing the terminating departure of the three dorsals (D) and the inward formation of the ventral supply which consists of three pairs of continuing bundles ($\times 35$). F. Cross-section through the floral tube and the outer carpellary wall showing an outer tepal trace (OT), an outer stamen trace (OS) and a dorsal bundle (D) ($\times 45$)

central, densely flowered, simple spike. The essentially sessile, pale yellow flowers of the spike have a highly connate and broadly campanulate corolla (Fig. 1 A).

The short, free tepal tips are incurved. Subtending each flower is a small, broadly deltoid bract. The showy berry fruits are normally red and congested along the



Fig.2. Serial cross-sections through the gynoecium of *R. japonica*. A. Opening of one of the three locules following the passage of a dorsal bundle under the unopened locule region ($\times 45$). B. Three opened locules; centrally are the three paired ventrals with a fusion septal axial being formed between each pair ($\times 40$). C. Attachment of the lower ovule rank; stigmatic tissue present around the funicular region; paired ventrals and septal axials present ($\times 40$). D. Section showing the maximum of two ovules per locule; central gynoecial zone not subdivided ($\times 40$). E. Subdivision of the central gynoecial zone evident with the distal septal wing tips freed; paired ventrals (V) and septal axial (SA) present in each septal wing ($\times 40$). F. Upper gynoecium showing an ovule pair; the funicular bundle of each ovule is derived directly from a ventral; stigmatic tissue is present on the septal wing tips ($\times 40$).

inflorescence axis.

Pedicle and Receptacle Vascularization: Since the pedicels are normally only several mm long, the flowers are essentially sessile. However, within this short distance of the floral axis, there is a distinct three

bundle vascular configuration in cross-section (Figs. 4A; 5A). Below the base of the receptacle each of the three bundles simultaneously undergoes a three-parted division which yields a nine bundled, ring configuration in cross-section (Figs. 1B; 4A; 5A). The three bundles

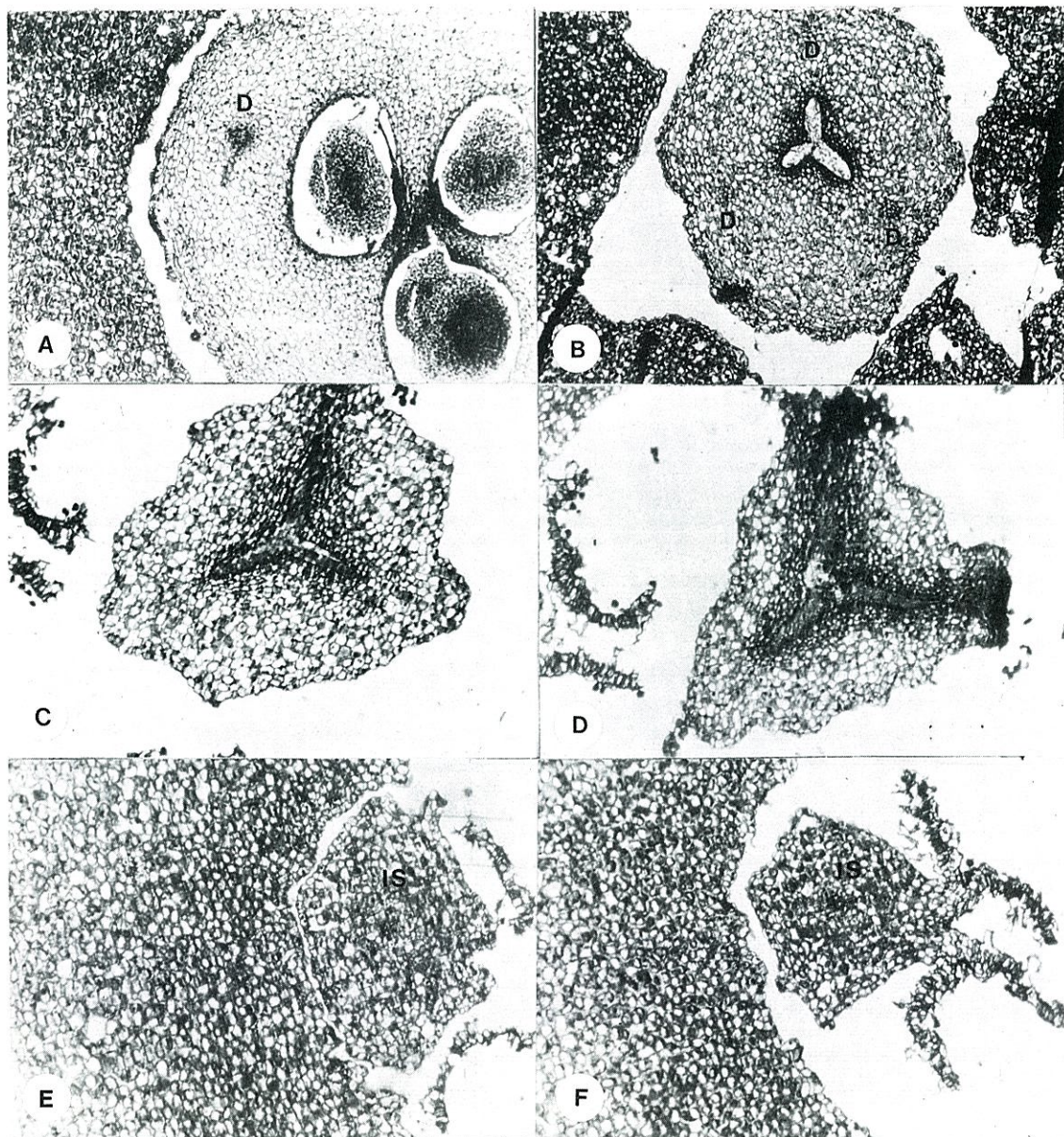


Fig. 3. Serial cross-sections through the floral tube, upper gynoecium and stylar region of *R. japonica*. A. Upper gynoecium and part of the surrounding floral tube; a dorsal (D) and the upper ovule of each locule are shown ($\times 35$). B. Upper gynoecium and lower stylar region; three dorsals (D) are present; lateral closing of the three locules occurs along the dorsal radii ($\times 40$). C. Style (circular in cross-section); the three dorsals are absent; stigmatic tissue completely lines the stylar canal ($\times 50$). D. Upper style (triangular in cross-section); opening of the stigmatic surfaces occurs along the dorsal radii ($\times 50$). E. Floral tube and freed filament of an inner stamen; inner stamen trace (IS) indicated ($\times 50$). F. Section above E showing the adaxial attachment of the opened anther sacs; inner stamen trace indicated (IS) ($\times 50$).

which are in the central position of each triplet product are in themselves compound bundles and further up the floral axis supply via additional divisions the vasculature of the three outer tepals and the three outer stamens. In the lower receptacle area, these same three central bundles of each triplet are denoted as the common outer tepal and outer stamen bundles (common OTS). The two lateral bundles of each triplet, on the other hand, undergo addition fusions and divisions and subsequently supply the inner tepals, the inner stamens and all of the carpellary vasculature comprising the dorsal and ventral supplies.

Due to the three triplet divisions which resulted in the nine bundled, ring configuration, there are two lateral bundles adjacent to and on each side of the three common OT-OS bundles. Each adjoining pair of lateral bundles, and there are three such pairs, is composed of a right and a left bundle which were derived from different pedicel bundles. In cross-section, the three common OTS bundles are 120° apart. The radii passing through these three bundles will eventually pass through the three dorsals (D) (Figs. 4B; 5B). Midway between the three common OTS bundles is a gap. There is 120° between each of the gaps. Eventually the gaps are closed by fusion products which are formed by adjoining lateral bundle pairs (Figs. 4B-C; 5B-C). In cross-section, a given lateral bundle is 30° from a common OTS bundle and 30° from a gap.

Repeated divisions and fusions are characteristic of the lateral bundles. Each lateral bundle undergoes three progressive radial divisions along the floral axis. Each division occurs within a distinctly different plant along the floral axis. Furthermore, each division is associated with the formation of a fusion product.

The first radial division among the lateral pairs results in three fusion products which are formed and close the aforementioned gaps. One trace from each of the two adjoining the lateral bundle divisions is involved in the formation of the fusion product, whereas the other parental bundle remains in the same position. In cross-section, there is a 12-bundled ring configuration—the three common OTS bundles, the three newly formed, gap closing bundles, and the six (3 pairs) of continuing lateral bundles (Figs. 4C; 4D). It is from the gap closing, fusion products that the inner tepal and inner stamen vasculature will be derived (Figs. 4C-E; 5C-E). These fusion products are denoted as the common inner tepal-inner stamen bundles (common ITS).

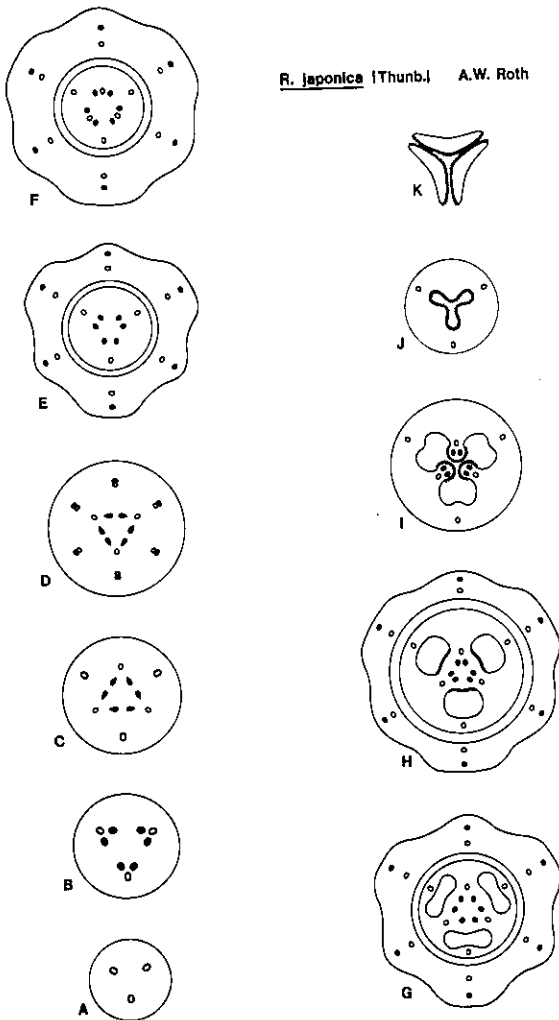
The second radial division among the continuing lateral bundles again results in fusion products. Where one trace from each of the two adjoining lateral bundle divisions is involved in the formation of a fusion product, the other division branch remains in the same parental position. The fusion products formed in this second tier of radial divisions are the three dorsals (D) (Figs. 1C-D; 4C-D; 5C-D) and they lie along the common OT-OS radii.

The third radial division among the continuing lateral bundles again results in fusion products. The fusion products formed in this third radial division are the three septal axials (SA) (Figs. 2E; 4E-F; 5E-F) and they lie along the common ITS radii. The six remaining bundles in the lateral position function directly as the ventrals (V).

The three sets of progressive radial division all occur within the lower receptacle area. It should be noted that there is an alternation in direction which is associated with the formation of the fusion products (cf. arrows, Fig. 5). The first set of fusion products formed, that is the three common ITS bundles, close the gaps along the IT-IS-SA radii. The second set of fusion products formed, that is the three dorsals (D), is along the OT-OS-D radii. The third set of fusion products formed, that is the three septal axials (SA), is again along the IT-IS-SA radii.

Gynoecial Vascularization: In cross-section, the upper receptacle prior to the formation of the floral tube has 15 bundles arranged in several concentric whorls (Figs. 4D; 5D). From the outermost whorl inwards, the bundles in each whorl are as follows: the three common OTS bundles, the three common ITS bundles, the three dorsals (D), and the six lateral bundles which are grouped in three pairs. In cross-section, the cumulative angular distances between the radii of these bundles are as follows: common OTS and D—0°, lateral—30°, common ITS and SA —60°, lateral—90°, and the next common OTS and D—120°. The vascularization of the floral tube by the respective tepal and stamen traces occurs as the floral tube is freed from the superior gynoecium. At this level there are nine gynoecial bundles in the circular cross-section—the three dorsals (D), and the six (3 pairs) laterals (Fig. 1E-F). The septal axials (SA) are formed further up the floral axis.

With the formation and isolation of the floral tube from the gynoecium, the three dorsals (D) depart outward under the unopened locules along the OT-OS



R. japonica (Thunb.) A.W. Roth

Fig. 4. Serial cross-sections of *R. japonica* from the pedicel zone to the stigmatic zone. A. Circular pedicel zone section showing the three-bundled configuration; each bundle is compound. B. Circular receptacle base zone section showing the three parted subdivision of the pedicel zone bundles; each resulting triplet has two laterals (black) and one, common outer tepal-stamen bundle (White). C. Circular lower receptacle zone section showing the formation of three fusion products (white) from the laterals (black); these fusion products are the common inner tepal-stamen bundles. D. Formation of the fusion dorsals (white) from the laterals (black); both the common outer and inner tepal-stamen supplies are in a peripheral position. E. Formation of the surrounding floral tube; subdivision of the common outer and common inner tepal-stamen supplies into tepal bundles (black) and stamen bundles (white); the dorsals (white) are in an outer carpellary position and the paired laterals (black) are in a ventral position. F. Formation of the fusion septal axials (white) between the ventral pairs (black); dorsals have passed under the unopened locules. G. Opening of the three locules with a large central placental area present; lobing evident in the floral tube. H. Enlargement of the locules, zone of ovule attachment; nurse cells present along inner locule surface. I. Subdivision of the central placental zone; paired ventrals and septal axials (white) positioned; each ventral bundle supplies a single ovule; floral tube not shown. J. Upper gynoecium zone section showing the closing of the locules; nurse cells lining the inner surface; dorsal bundles present, ventrals and septal axials have terminated; floral tube not shown. K. Upper stigmatic zone section showing the tri-lobed stigmatic surfaces; dorsals absent; floral tube not shown, but it is this upper area that there is further subdivision of the outer and inner tepal bundles into lateral bundle pairs.

-D radii. There is no further division among the dorsals which remain unbranched in their peripheral position into the region of the style-stigmas. However, as the dorsals reach their peripheral position, the lateral bundle pairs between each dorsal undergo their final division and fusion to form the three septal axials (SA). The formation of the septal axials (SA) occurs in three independent ventral plexuses as the lateral bundle pairs move inward. The formation of the plexuses are coplanar, but exist only for a short vertical distance along the floral axis. It is from these plexuses that the fusion septal axials (SA) arise as well as the continuing laterals which function directly as the ventrals (V). All of the gynoecial vasculature has normally disposed

xylem and phloem.

The gynoecium is essentially circular in cross-section from its freed base to the area of stigma divergence (Figs. 3A-D; 4; 5). The three locules open along a perpendicular to the OT-OS-D radii (Figs. 2A; 4G; 5G). At mid-gynoecial height, the central area composed of fused inner septal wing tips is sub-divided (Figs. 2B-D; 4H-I; 5H-I). The septal arms are relatively thick, and when the septal axials (SA) are formed, they occur within the wing tip areas (Fig. 2E). There is no inter-connection between any of the elements in the dorsal supply and those in the ventral supply. Both supply systems are simple and direct. Whereas the dorsals are fusion products, the ventrals are not. In the

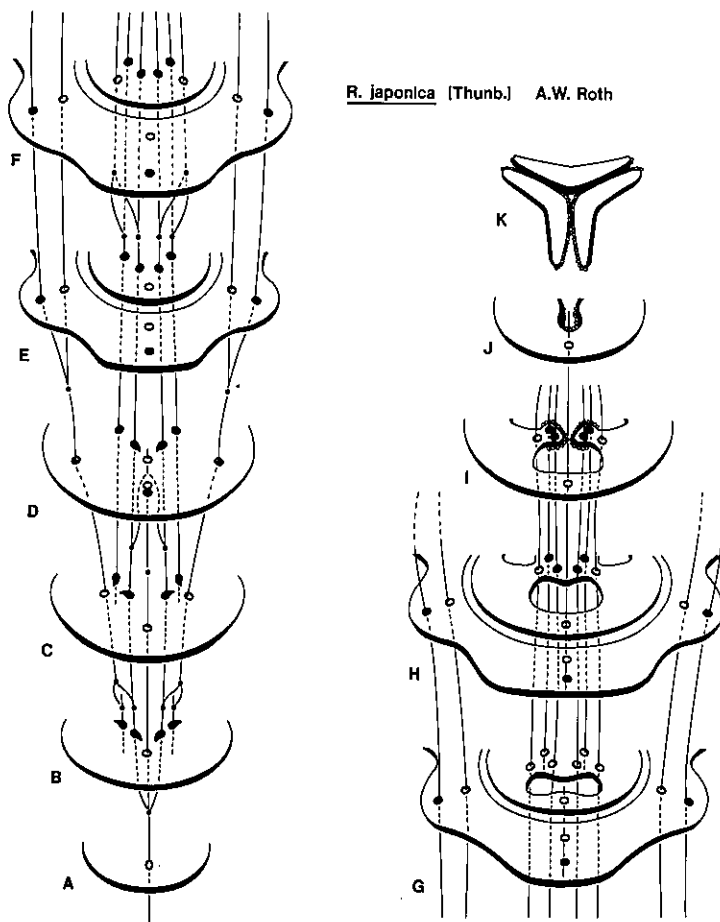


Fig. 5. *Rohdea japonica*, the same cross-sections as presented in Fig. 4, following transformational projections of each section and selected vascular bundles connected. The letters of each section correspond to those presented in Fig. 4.

upper gynoecium, the only remaining vasculature is the three dorsals (D) (Fig. 3A-D). A short vertical common style occurs, but it soon is sub-divided into the three broadly lobed and recurved styles which characterize this species. Papillae (nurse cells) line the upper surface of stigma as well as the common style. A different type of nurse cell, one which lacks the extended papillae, replace the former and is continuous downward into the septal wing tip area of the gynoecium.

Tepal and Stamen Vascularization: The campanulate floral tube has six bundles basally when it is freed—the common OTS and the three common ITS bundles. Divisions occur within both sets of common bundles and the result is a set of stamen traces and a set of bundles which will supply the floral tube (Figs. 4D-E; 5D-E). The three outer stamen (OS) bundles, as well as the three inner stamen (IS), are each formed in a distinct

plane. The outer stamen bundles (OS) are formed at a lower level than the inner stamen (IS) bundles. At or above the midgynoecial height filaments for the three outer stamens are cut off (Fig. 3E-F) and at a slightly higher level up the floral axis, the three inner filaments are freed. The filaments are short and the anthers are attached to their midpoint to the adaxial surface of the respective filaments. The introrse anthers dehisce laterally.

The floral tube is relatively thick from its base to the upper open area where slightly recurved tepal tips are present. Rhaphides are found scattered throughout the floral tube as well as the outer gynoecial wall.

Basal vascularization of the floral tube occurs as follows. Each of the common tepal-stamen bundles divides into a common tepal bundle and a respective stamen bundle. There are three outer stamen bundles (OS) and three inner stamen bundles (IS). The outer and inner common tepal bundles are along the respective medians. The six common tepal bundles, there are three in the outer tepal median position and three in the inner tepal median position, may undergo an additional tripartite division in the upper floral tube.

This division is a similar to that observed among the three bundles in the lower pedicel which underwent a tripartite division. The central bundle of the tepal triplet is the median, that is the outer tepal median (OTM) and the inner tepal median (ITM) respectively. The two lateral bundles of the tepal triplet are the laterals, that is the outer tepal laterals (OTL) and the inner tepal laterals (ITL) respectively. The total tepal vasculature therefore consists of 3 OTM, 6 OTL, 4 ITM and 6 ITL. There is no inter-connection between any of the medians or laterals of either cycle in their vertical ascend.

Concluding Remarks

The floral vascular anatomy of *Rohdea japonica* is characterized by compound bundles which divide and undergo repeated fusion. From the three compound

pedicel bundles each of which undergoes a three parted division the total floral vasculature is established. The central bundle of each triplet directly establishes the outer tepal bundle (median) and two laterals as well as the outer stamen bundle. The two lateral bundles resulting from each pedicel bundle's triplet division in association with adjoining triplet laterals undergo three distinctive sets of divisions and fusions to establish first the inner tepal and inner stamen vasculature, then the dorsals and finally the ventral supply. The resulting inner tepal bundles are compound and within the fused, campanulate floral tube undergo another three parted division which results in a median and two laterals. The three dorsals and the three septal axials are all fusion products. The two simple ventrals per carpel of the fused tri-carpellate gynoecium supply a single ovule each. Essentially all of the floral vasculature is established below the superior ovary. Only the three parted divisions within the floral tube which established the outer and inner tepal laterals occurs above the receptacle area. Furthermore, there is no terminal fusion within the floral tube or within the gynoecium between any of the various supply elements, that is between the tepal laterals and medians or between the dorsal or ventral supplies.

The three carpels are completely fused. There is no indication of terminal septal glands, basal nectaries within the floral tube or dorsal grooves or notches. Rhaphides are commonly present in both the floral tube and the outer carpellary wall. Two ovules are present in each of the three carpels, but commonly only one seed matures within the gynoecium.

This report on the floral vascular anatomy of *Rohdea* is the first for the genus as well as for any member of the Englerian subtribe Aspidistrinae, tribe Convallarieae. It is certainly to soon to make any intra-generic or tribal comparison or comment on the relationships of *Rohdea* to associated genera. Reports on members of the Englerian sister subtribe Conval-larine, *Theropogon* (UTECH, 1979 a) and *Convallaria* (UTECH and KAWANO, 1976 b), are so dissimilar (UTECH, 1979 a) that a comparison here to *Rohdea* is certainly premature. Additional work detailing the floral vascular anatomy of members of both subtribes is certainly in order and needed.

Summary

1. The floral vascular anatomy of *Rohdea japonica* is established basally from a series of divisions and

fusions among bundles derived from three compound pedicel zone bundles. Each of these pedicel bundles undergoes a division into three bundles. The central bundle of each resulting triplet directly establishes the outer tepal and outer stamen vasculature, whereas the lateral bundles of each triplet in association with adjoining triplet laterals undergo three distinctive sets of divisions and fusions to establish first the inner tepal and inner stamen vasculature, then the dorsals and finally the ventral supply which has fusion septal axials and paired ventrals. Formation of the various cycles to bundles occurs below the superior ovary. No terminal fusion occurs within the upper gynoecium between any of the elements of the dorsal or ventral supplies nor between any of the elements in the floral tube.

2. The relatively fleshy, campanulate, floral tube is subtended basally by a deltoid bract. The three carpels are completely fused, and there is no indication of terminal septal glands or nectaries basally within the floral tube. Rhaphides are present in both the floral tube and the outer carpellary wall. Two ovules are present in each of the three flowering carpels. A short common style terminates into three broadly recurved stigma lobes.

Acknowledgments

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要 約

1. オモトの花部維管束の解剖学的研究を行なった。研究の対照となったのは、花梗基部より花器へと走行する3つの複合維管束から導かれる、一連の分裂や融合の系列である。
2. 花梗部維管束のそれぞれは1回の分裂で3つの維管束群となる。この3つの群のそれぞれのうち、まん中の維管束は直接に外花被片と外側雄ずいの維管束をつくる。一方、側方の維管束は、隣接する3組の側方の維管束と共に、内花被と内側雄ずいの維管束を形成する過程で、まず3回の明瞭な分裂と融合を繰り返す。さらに、背面を走行する維管束群と、外花被の中軸維管束と対をなす腹側維管束とが融合してできた腹部維管束とを形成する。
3. 維管束群のさまざまな輪状構造の形成は、上位子房の下部で起る。雌ずいの上部では、背部、腹部を走行する維管束群のいずれとも融合が起らないばかりでなく、花筒部のどの維管束群とも融合が起らない。
4. 比較的肉質で、つり鐘状の花筒部は、三角状の1枚の苞によってその基部が抱かれている。3枚の心皮は完全に融合し、花筒基部にはその底部に腺や蜜腺は認められない。細胞内結晶体 (rhopalids) は花筒部にも心皮外壁にも存在する。3枚の心皮のそれぞれには2個の胚珠がある。花柱は短かく、そり返った3片の部分よりなる柱頭に終る。

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○ 沖縄自然研究会編：沖縄県自然環境保全地域指定候補地学術調査報告書—知花グスク・斎場御嶽とその周辺地域 沖縄県，1982. 3 発行。B5 版130頁。非売品。

沖縄県内のグスク跡や御嶽などは、その地域の自然が残されていて、史蹟や文化財に指定し保護されている所が多い。本調査報告は表題の2ヶ所を自然環境保全地域に指定するための資料として取りまとめられた。本会員天野鉄夫氏は世話人であり、且、植物の調査を担当された。

○ 池原貞雄編：琉球列島における島嶼生態系とその人為的変革 (II) 琉球大学島嶼生態系研究会，1982. 3 発行。B5 版 288頁。非売品。

文部省「環境科学」特別研究による調査報告集である。島嶼では環境としての容量が限定され、大陸とくらべると多くの点で島嶼特有の生態的な特色がみられるが、島嶼に関する研究は、従来、多数あっても、島の生物・地形・地質・経済・文化などのいずれかに関する断片的なもので、特に人間の生活に密接に関与する環境科学の立場からの研究は皆無であるから、この総合調査では、久米島を対象に行なったものである。非売品であるが、実費 (2,000円+送料300円) で入手出来るとのことであるから、入手御希望の方は儀間小夜子氏 (〒901-24 沖縄県中城村南上原琉球大学理学部生物学教室) に連絡されるとよい。

○ 宮脇 昭編：日本植生誌，四国，至文堂(〒162 東京都新宿区西早稲田2-11-13)，1982. 2. 28発行。19.5×26.5cm，540 頁+別冊 (付表と植生図)。定価49,000円。

屋久島 (1980)，九州 (1981) に引続き、全10巻を予定する大著述の中の第3巻である。内容は申すまでもなく、四国の植生を群落組成表、現存・潜在自然植生図、植生断面模式図とともに総合的にまとめたものである。(里見信生)