ツクバネソウ(ユリ科)花器の解剖学的特徴

Frederick H. UTECH* and Shoichi KAWANO** : Vascular Floral Anatomy of the Japanese *Paris tetraphylla* A. GRAY(Liliaceae-Parideae)

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Introduction

Paris tetraphylla A. GRAY, a Japanese endemic of section *Paris* HARA (=*Euparis* FRANCH.), is characterized by leaves usually in whorls of 4 (rarely 5), connectives which do not extend beyond the anthers, the absence of an inner whorl of tepals (petals) and an indehiscent baccate fruit (OHWI 1965; HARA 1969). In Japan this species exhibits a North to South pattern of clinal variation in both floral and vegetative characters with the differential variation between populations most pronounced between the Japan Sea side and the Pacific side of the Japanese Islands (HARA and KANAI 1958, map 95; HARA 1969; HOTTA 1974, p. 284; KAWANO *et al.*, 1980). As a diploid species with $2n=10$, its karyotype is well known (HAGA 1961; KAYANO 1961; NODA 1963; HARA 1969), and quite distinct from the other diploids, triploids and tetraploids of section *Paris* (*sensu* HARA 1969) which includes *P. verticillata* BIEBERSTEIN (Japan, Korea, China and Siberia: OHWI 1965; KOMAROV 1935), *P. incompleta* BIEBERSTEIN (Caucasus: KOMAROV 1935), and *P. quadrifolia* L. (Europe, Caucasus and Siberia; generic type: HEGI 1939; KOMAROV 1935).

Though the vascular floral anatomy of *P. tetraphylla* is unknown, its flowers are most interesting in the genus in that they represent a reduction in both the number of outer sepals (4) and the total absence of petals (inner tepals). Consequently, its floral anatomy is presented as both an evolutionary and taxonomic benchmark for further studies within the section and genus, as well as the family (or tribe) that includes *Trillium*. Special attention has been given to the peduncle, sepal and stamen vascularization relative to the absence of the inner petal whorl, and though the floral vascular anatomy has been presented in a simulated ascent from the peduncle through the ovary, no ontogenetic or teleological implications are intended.

Materials and Methods

Both buds and flowers were collected from near Bijyodaira, Tateyama Mountain Range, elev. 1100 m, Toyama Prefecture and fixed in acetic ethanol (1:3) for 6 hours with subsequent storage in 70% ethanol. Ten flowers of varying age were serially sectioned (10-12μm) by the standard paraffin technique (SASS 1958) with staining in safranin and methylene blue. Several whole flowers were also simultaneously cleared and stained in a 1% fuchsin-10% NaOH mixture as a check on the serially prepared material (FUCHS 1963; UTECH and KAWANO 1975).

Observations

Peduncle to Receptacle Vascularization: The peduncle to receptacle vasculature is based on two different bundle systems, i.e. as inner and outer supply which determines the sepal-stamen and the gynoecial traces respectively. In cross-section, the lower peduncle is evenly fluted with 8 lobes (Fig. 1 A). Each lobe has one of the 8 outer bundles. The inner supply consists of two large bundles, and with repeated radial divisions forms four, then eight bundles (Fig. 1 A-C). Though radial division, divergence and fusion occur simultaneously within both the outer whorl of 8 and within the inner bundles, both bundle systems are independent and will be presented separately.

1. *Sepal vascularization:* Changes in peduncle

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cross-section correlate with trace development. The outer peduncle bundles begin to change position as the 8-lobed peduncle becomes broadly 4-sided with 4 small pointed lobes at the corners (Fig. 1 D). The four bundles opposite the small points form, via radial division, a pair of lateral branches which diverge into the broader peripheral areas on each side (Fig. 1 D-E). The parent bundles however remain peripherally for some time, then move inward along their preestablished radii. With the lateral branching of these 4 bundles, the 4 remaining and alternating bundles move inward without branching. With this central movement, a broad trace departs horizontally from each along the same radius as its previous inward movement (Fig. 1 D). Via radial division each of these 4 traces has two lateral branches near the periphery (Fig. 1 F). The central continuing strand becomes the sepal (outer tepal) median (SM), while its two diverging laterals fuse in the corners with other lateral branches from adjoining peduncle bundles to form the two sepal laterals (SL) of each sepal.

The 4 freed sepals receive 3 traces each (Figs. 1 G, I; 3), a median directly and two laterals, each of which is a fusion product of lateral branches of adjoining peduncle bundles. The cross innervation of the recurved sepals can be related to the characteristic radial division of the supplying bundles and to the compound nature of the laterals it receives.

2. *Stamen Vascularization:* Following the formation of the sepal vasculature, there are 8 bundles which remain in a broad ring of two whorls (Figs. 1 G; 2 A). These are the stamen traces. Four of them are directly from the sepal lateral supplying peduncle bundles which did not divide radially to form a petal median. The other four are continuations of those peduncle bundles which supplied the sepal medians (SM) and with which they share a common radius. There is no indication of fusion in their formation, though they are in all likelihood compound. The outer whorl of stamen traces has been denoted as the outer stamen traces (OS), while those of the inner and alternating whorl have been called the inner stamen traces (IS). There was no indication in our material of any radial division of the inner stamen traces to form a single petal median.

Gynoecial Vascularization: At the lower peduncle levels, the inner vascular core consists of two large, opposite and broadly bifid bundles. Each divides radially at the receptacle base giving 4 bundles which are also bifid (Fig. 1 A-B). These four bundles are along the same radii as the 4 peduncle bundles which at the periphery points branched in the formation of the sepal laterals. The 4 inner bundles undergo a final radial division and form an inner ring of 4 pairs (Fig. 1 C). The gaps left between these inner pairs lie along the same radii as those peduncle bundles which become the inner stamen (IS) traces. Within each of the 4 inner pairs, fusion occurs first via laterally departing branches from adjacent members of adjoining pairs. This results in the formation of 4 fused carpel dorsals (D) which lie on the same radii as the outer stamen (OS) and sepal median (SM) traces. The remaining halves of the 4 pairs then fuse in the opposite direction, thus closing the gap formed in the pair formation and forming the 4 compound ventral bundles (V) (Fig. 2 A).

The 4-carpellate, non-stipitate ovary is freed early from the sepals and stamens which remain fused basally in a shallow floral cup. There is no nectiferous tissue on the ovary either basally or terminally. Septal glands are absent, as are both dorsal and septal grooves which would represent zones of pericarp weakness and/or dehiscence. (The fruit is baccate and indehiscent.) In both buds and mature flowers, raphides are common throughout the peduncle and ovary wall.

With locule opening, the dorsal's position remains unchanged from its region of formation. The ventral bundles, on the other hand, move inward along their radius of formation. Their double nature becomes evident with the formation of the various sets of funicular (F) bundles. Each locule usually contains 4 ovules, rarely 2, in a two tiered ovule arrangement with one pair inserted lower than the other. The 4 ovules of a given carpel are supplied by traces from inner bundle pairs which were formed opposite the dorsal that supplies their carpel (Figs. 2 D-F; 3). The 4 ascending ventrals con-

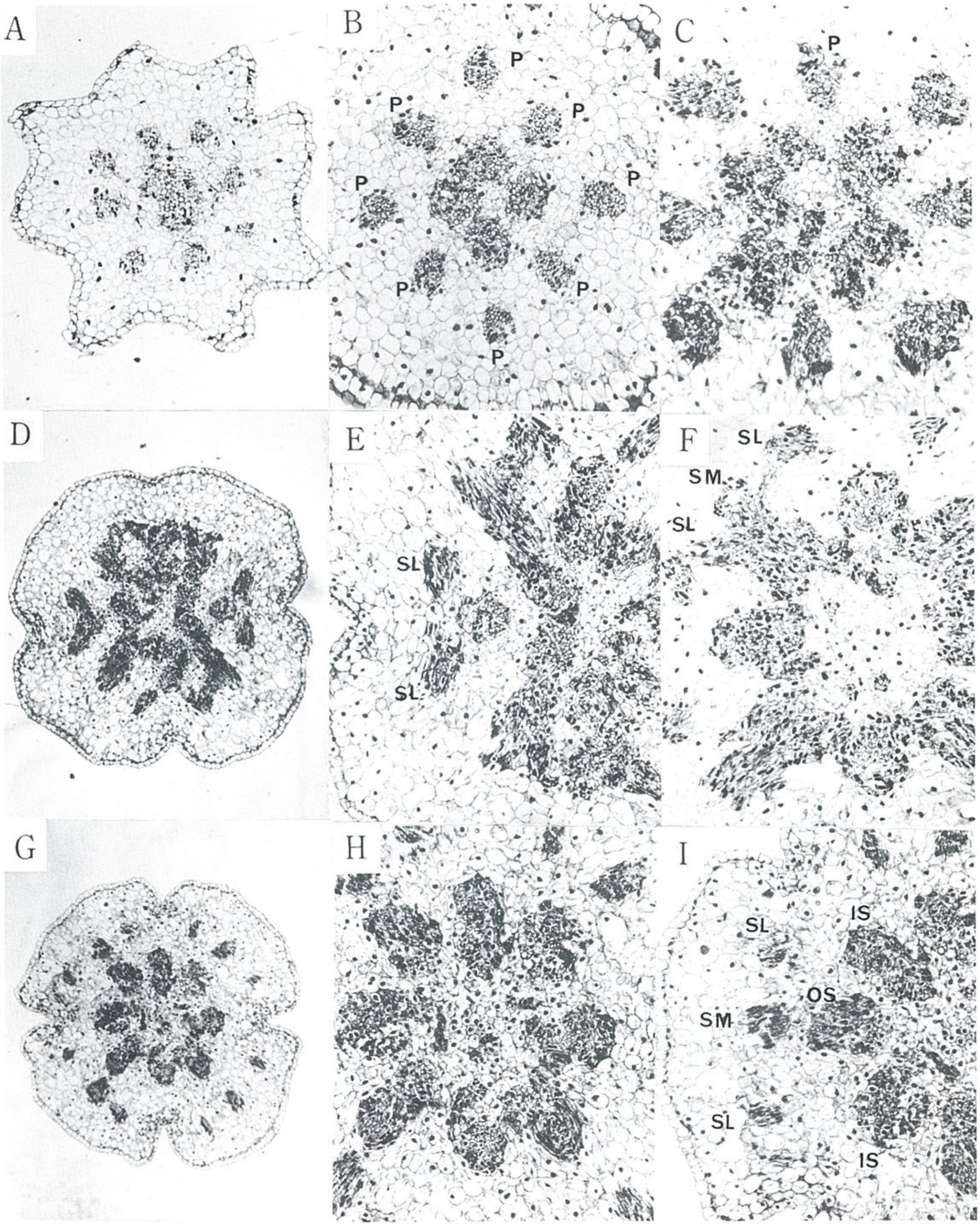

Fig. 1. Cross-sections showing peduncle to receptacle vascularization in *Paris tetraphylla*.
A. Eight-lobed peduncle with 8 outer bundles and 2 inner, (20×). B. Peduncle with 8 peripheral (p) bundles and 4 inner, (35×). C. Peduncle with 8 peripheral and 8 inner bundles (4 pairs), (40×). D. Origin of sepal and stamen vasculature in the 4-sided peduncle, (20×). E. Two lateral branches (SL) departing from an outer peripheral bundle; each lateral will fuse with a lateral from an opposite peduncle bundle to form the compound sepal lateral, (40×). F. Departing sepal median (SM) with its pair of diverging lateral branches (SL), (40×). G. Four-sided peduncle near receptacle base showing the establishment of the sepal traces and the orientation of the stamen and gynoecial supply, (17.5×). H. Double ring of 8 outer stamen traces and 8 inner gynoecial traces, (40×). I. Sepal base showing median (SM) and two fused laterals (SL), an outer stamen trace (OS) is opposite the median, (40×).

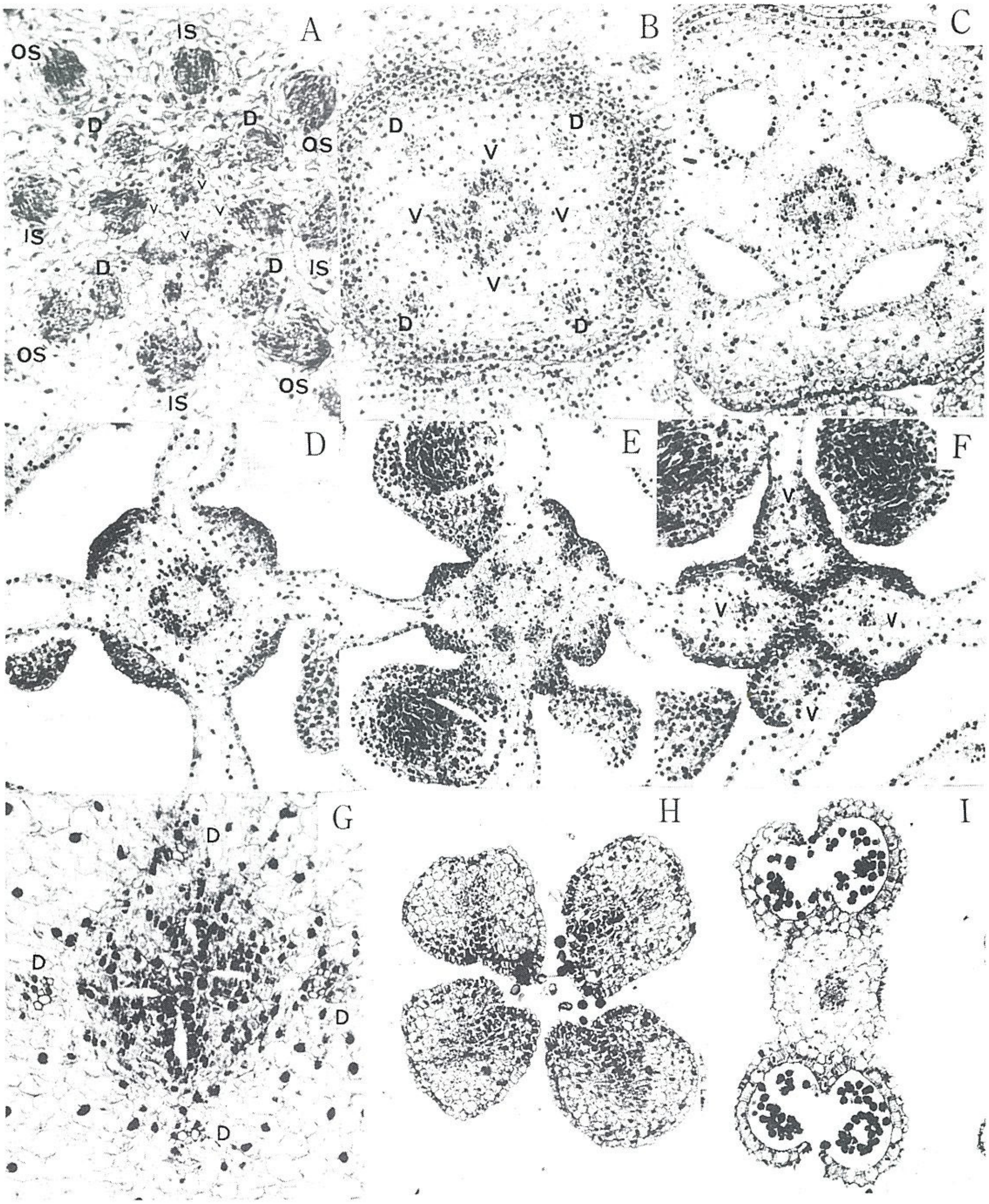

Fig. 2. Cross-section showing receptacle and gynoecial vascularization in *Paris tetraphylla*.
A. Double whorl of 8 stamen traces (OS and IS) and inner gynoecial traces (4 fused dorsals and the 4 double ventral supplying bundles), (45×). B. Freed ovary base with dorsals (D) in same position as in A, but the ventral supply positioned centrally, neither branched basally, (45×). C. Locule opening, (50×). D. Basally fused septa with ventral supply, stigmatoidal tissue evident, (45×). E. Funicular supply to lower ovule tier, stigmatoidal tissue associated with micropylar zone, (45×). F. Unilocular upper ovary showing terminating ventral supply (V) in the centrally freed septa, (45×). G. Four-radiate common stylar canal with continuing dorsals (D), (90 ×). H. Freed styles, (45×). I. Laterally dehiscent, linear anther, (40×).

tinue in their respective septa following upper ovule supply, but end there without any terminal cross-connection (Fig. 2 G). The 4 dorsals, on the other hand, continue unbranched from the ovary base to the tips of the 4 long and free styles (Fig. 2 H).

It should be stressed that the gynoecial supply is relatively simple, notwithstanding the fact that the bundles are characteristically compound. Neither septal nor peripheral (lateral) axials derived via lateral branching basally or terminally from the dorsal and ventral supplies were observed.

The 4 septa are fused basally to approximately the middle to upper carpellary level, whereupon they are freed centrally. The upper ovary region is consequently unilocular. With locule closure and contact reduction of the inner septal margins, a 4-radiate hollow stylar canal is formed (Fig. 2 G) which extends for a short distance (0.75-1.85mm) above the ovary within a common style. The 4 free and greatly elongated

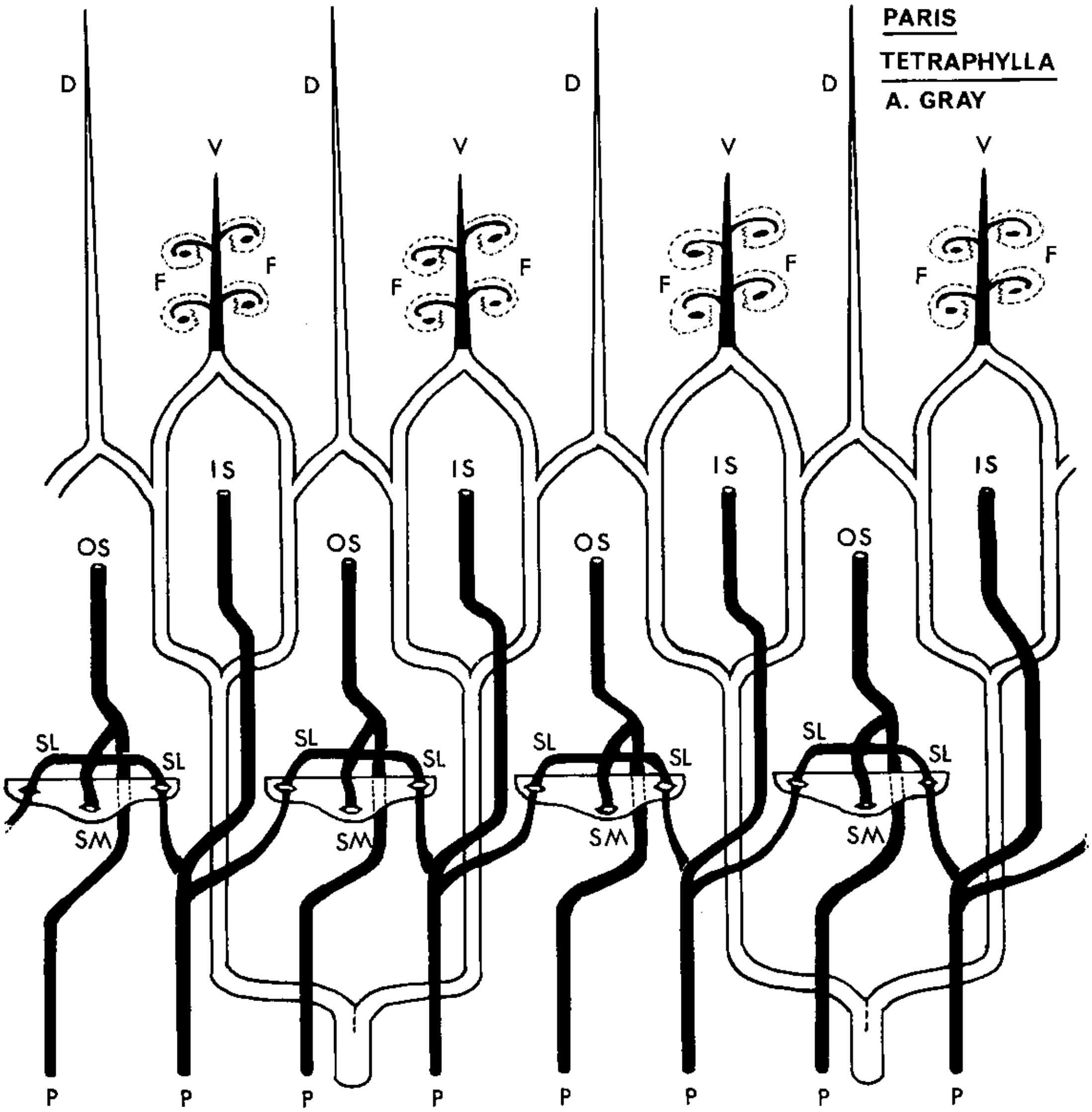

Fig. 3. Vascular summary diagram for *Paris tetraphylla*.
Vascular abbreviations as introduced in text: SM= sepal median, SL= sepal lateral, OS= outer stamen, IS= inner stamen, D= fused carpel dorsal, V= ventrals, and F= funicular.

(15.0-22.0mm) styles are derived from the common style.

The 4 free styles are characteristically convex with a non-papillate stigmatoidal tissue lining their incurved ventral margins (Fig. 2 H). These lining cells have large nuclei and thin walls. Similar non-papillate cells are furthermore observed in the 4-radiate common stylar canal, on the inner marginal faces of the adjoining, anchor-shaped septal wings and along a vertical zone to the base of each locule which passes the micropylar openings of the inserted ovules (Fig. 2 D-H). These cells represent a continuous stigmatoidal tissue system related directly to the course of pollen tube growth.

Summary and Concluding Remark

The vascular floral anatomy of *Paris tetraphylla* beginning in the peduncle consists of outer and inner supply systems. From the 8 peripheral bundles, the 4 sepal medians, 8 sepal laterals and the 8 stamen traces (2 whorls) are derived. Each sepal receives a median directly and two fusion laterals. The 4 outer stamen traces are derived from the same peripheral bundles which branched in forming the sepal medians. No similar perianth branching was observed among those bundles which became the inner stamen traces. Were such a branch to commonly occur as a petal median and develop with linear, laminal tissue, it would correspond to the petal observed in the rare form *corollata* MIZUSHIMA (MIZUSHIMA 1952, fig. 1; HARA 1969, fig. 11 K). Such linear petals are characteristic of other members of section *Paris*. The gynoecial supply arises from the inner peduncle vascular core via repeated radial division and results in four fused dorsals and four (double) ventral supplying bundles. Septal glands are absent, but raphides are common.

Though carpel number and fruit type are variable in the genus *Paris* (BERG 1962; HARA 1969), they form a variation series. Section *Paris* has 4-5 carpellate species with roundish ovaries, few ovules / carpel and baccate, indehiscent fruits. Section *Kinugasa* (TATEWAKI & SUTO) HARA, which is limited to *P. japonica* (FRANCH. & SAV.) FRANCHET, another Japanese endemic, has 6-10 carpellate, roundish ovaries with terminal disks, many ovules / carpel and also baccate, indehiscent fruits. Section *Euthyra* (SALISB.) FRANCHET which includes the highly variable Asian *P. polyphylla* complex (HARA 1969) has angular ovaries (3-6 carpellate) with elevated longitudinal ridges and terminal disks, numerous ovules / carpel and capsular, dehiscent fruits.

In *Trillium*, a similar fruit variation series was related to dispersal by BERG (1958) for those species with pulpy, indehiscent fruits and those with dehiscent capsules. Apparently an homologous series of parallel variation occurs in both genera. With fruit type a key taxonomic character in these genera, as well as within the whole Liliaceae Alliance, an investigation of the underlying vascular floral anatomy is most crucial in discriminating those evolutionary relationships which are strictly phyllogenetic, from those which represent similarities due to parallel and convergent evolution, and freqently share a common functional aspect, i. e. dispersal.

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摘　　要

ツクバネソウ（ユリ科）の花の維管束の走行と解剖学的特徴が観察され，他の系統群との関係が論じられた。花梗の周縁部を走る８本の維管束から，萼へ入る12本（中脈４＋側脈８）と雄芯に入る８本の維管束が由来する。雄芯外列へ入る４本の維管束は，萼の中脈に入る維管束から枝分れしたものである。雌芯への推管束は，花梗の中心部の維管束に由来し，数回分裂した後，再び癒合して４本の背面を走る維管束と４本の腹面を走る維管束へとなる。萼に腺は欠けるが，束晶(raphid)は存在する。

エンレイソウ属との関係についても２，３の論議を試みた。

○　大滝末男・石戸　忠共著　**日本水生植物図鑑**　北隆館発行（昭和55年９月５日），Ｂ５版，318頁，8,000円。

本書で述べる水生植物は一般的に水草と呼ばれているもので，水生であり，維管束をもつ高等植物をさす場合が多い。わが国では昔から水草が豊富に生育し，その種類は少なくなかった。しかし，近年，各地で水質汚濁が進み，貴重な水草が失なわれて行く現状である。著者の一人，大滝末男氏はそれを憂ひ，本書の必要性を痛感するまゝ，愛車を自ら運転して全国を廻り，集めた材料を石戸　忠氏が忠実に画いた。この共同作業が今回見事にみのり，本書の誕生となった。

○　山本　正・高畑　滋・森田弘彦共著　**北海道山菜誌**　北海道大学図書刊行会（〒060 札幌市北区北８条西８丁目，北大生協会館内）発行（昭和55年５月25日），Ｂ６版，256頁＋索引８頁，1,200円。

最近の山菜に関する本と異なり，若者等は山菜を通じて本当の食物とは何かを論じ，正しい食文化の発展を考えること、山菜や野草の分類，分布，生態を，植物学から説明し，身近かに科学に触れてもらうことと，山菜と人間とのかゝわり合いの歴史を明らかにすることによって，山菜文化の現代的意義を出張し，同時にわれわれの祖先が歩んだきびしい生活のあとを明らかにすることなどを意図して著述したと言う。それには料理自慢の高畑，植物にくわしい森田，古いことなら山本と，生れも育ちも異なり，山菜の見方も少しづつ違う３人がお互いに影響しあって書き上げたものであるから，一読に価するものと推奨する。

○　斉藤信夫著　**三厩での私**　たねの会（〒036 弘前市豊原１丁目２の１，東北女子大学生物学教室内）発行（昭和55年２月10日），Ｂ６版，172頁，1,300円（含送料）

著者は弘前大学を卒業して津軽半島の北端に近い三厩中学校に赴任された。昭和50年の事である。それ以来，５年間，春にはじまり秋に終る山歩きを，毎年繰り返す間に出会った植物の中から，著者の印象深い50種ばかりについて，あたかも対話するような態度で書いているのが，読む人に感銘を与える。そして，いつか一度訪ねて見たい気持になるのは私だけであるまい。しかし，一方では三厩もいづれ海底トンネルで北海道につながったら，否応なく，にぎやかさを増すことであろう。その時，この本に書かれた植物たちにとって安住の土地であるだろうか。　（里見信生）