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FLORAL VASCULAR ANATOMY OF THE MONOTYPIC JAPANESE *METANARTHECIUM LUTEOVIRIDE* MAXIM. (LILIACEAE-MELANTHIOIDEAE)

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ABSTRACT

The Japanese endemic *Metanarthecium luteoviride* Maxim. is a perennial herb with a simple, rarely branched, elongate raceme, and has different tribal positions in the Englerian and Hutchinsonian subdivisions of the primitive liliaceous subfamily Melanthioideae. This study reports on the floral vascular anatomy of this Asian species and is directed at a re-examination of its tribal position. The single flower at each node is subtended by both a bract and a bracteole. The six-merous flower is perfect, though basally both perigyny and a floral tube occur. Incomplete fusion along the basal septa results in the formation of septal (nectiferous) glands. The versatile anthers are abaxially attached and dehisce via longitudinal, lateral slits. Rhaphides are common within the gynoecium at all stages of development. The fruit is a loculicidal capsule, though in flower there are both septicidal and loculicidal subdivisions of the central placenta. The seeds are not appendaged.

Floral vascularization is derived from a six-bundled, axial vascular configuration within the pedicel. Because of perigyny, common fusion bundles are formed between the six axial bundles. The lowest and first formed of these common bundles are the three common outer tepal-outer stamen-dorsal bundles, whereas the upper three are the common inner tepal-inner stamen bundles. Above the perigynous zone, these six common bundles divide into their various components. The common tepal bundles of both cycles subdivide into a median and two laterals. The stamen bundles of both cycles are fusion products, though throughout much of the perigynous zone, the two elements of the fusion product are separated. The dorsals are also fusion products, though their origin occurred below the perigynous zone. The six axial bundles which formed the common

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bundles continue vertically and establish the ventral supply and three fusion septal axials. The vertical course of the latter is limited. There is no dorsal branching or interconnection between the dorsal and ventral supplies. The three dorsals terminate in the elongated style.

INTRODUCTION

The Japanese *Metanarthecium luteoviride* of Maximowicz (1867) is a primitive, perennial, scapose lily. "Nogi-ran," the most frequently used Japanese common name for this species, refers to a beard, that is an elongated Asian chin-beard. Another common name noted by Makino (1974, nr. 3318), but less frequently used, is "kitsuneo-o," which means the tail of a fox. Both common names are allusions to this species' elongated raceme of many, small, pale yellowish green flowers. The Latin specific name is also in reference to the yellowish green flowers. Furthermore, the leaves also have a yellowish green cast.

Metanarthecium luteoviride is endemic to the Japanese Islands (Ohwi, 1965a, 1965b; Kitamura et al., 1965; Makino, 1974; Numata, 1974), and occurs in open sunny sites southward from the northernmost island of Hokkaido, through the major islands of Honshu, Shikoku, and Kyushu. On Yakushima, a small volcanic island south of Kyushu, according to Kitamura et al. (1965:151-152) and Ohwi (1965a, 1965b), a dwarf variety with longer pedicels occurs, that is, var. *nutans* Masamune.

Additional variation southward has been reported from Taiwan (Formosa) (Hayata, 1911), and has been recognized as a second species, *Metanarthecium foliatum* Hayata. Whether the Japanese *M. luteoviride* and the Formosan *M. foliatum* are distinctive or conspecific is debatable, and certainly in need of further systematic research. Nevertheless, this genus with either one or two species is limited to the temperate islands on the western edge of the Pacific Ocean.

Metanarthecium luteoviride has been illustrated twice (Makino, 1974, nr. 3318; Kitamura et al., 1965:151-152, pl. 42). In both floras, the accompanying descriptions are in Japanese. The recent English version of Ohwi's *Flora of Japan* (1965a) does give a good morphological description of *Metanarthecium*, which significantly upgrades the previous western accounts of this species (Maximowicz, 1867; Baker, 1876; Bentham and Hooker, 1883; Engler, 1888; Krause, 1930).

Among the primitive groups of lilies, frequently treated as the subfamily Melanthioideae or as the segregated family Melanthaceae, the tribal position of *Metanarthecium* differs greatly between the Englerian (Engler, 1888; Krause, 1930), and the Hutchinsonian (Hutchinson, 1934, 1959) systems. The genera of the Englerian Helonieae include *Xerophyllum* Michx., *Chamaelirium* Willd., *Helonias* L., *Chionographis* Maxim., *Heloniopsis* A. Gray, *Ypsilandra* Franch., and

Metanarthecium Maxim. The only difference between Engler's (1888) and Krause's (1930) circumscription of the Helonieae is the latter's addition of the Himalayan genus *Ypsilandra*, which has affinities to *Helonias* and *Heloniopsis* (S. Kawano, personal communication). The genera grouped into Hutchinson's Narthecieae (1934, 1959), on the other hand, include *Pleea* Michx., *Tofieldia* Huds. (including *Triantha* Baker and *Japanolirion* Nakai), *Hewardia* Hook., *Xerophyllum* Michx., *Heloniopsis* A. Gray, *Clara* Kunth, *Narthecium* Huds., *Aletris* L. (including *Meta-aletris* Masamune), *Nietneria* Klotzsch, and *Metanarthecium* Maxim.

In Gates' review (1918) of the (Melanthioideae) Melanthaceae, a close relationship between *Metanarthecium* and *Narthecium* was stressed. However, the tribal position of *Metanarthecium* as well as its relationship to *Narthecium* (sensu Gates, 1918) remains unsettled.

A single, known chromosome count of $2N = 52$ by Satō (1952) has repeatedly been cited in the chromosome atlases (Darlington and Wylie, 1955; Fedorov, 1969; also Kitamura et al., 1965) for *Metanarthecium luteoviride*. With only a somatic number and incomplete karyotypic morphology, it is difficult to infer a genome relationship between *Metanarthecium* and the other primitive lilies. However, the $2N = 52$ number is high in comparison to those known for the other tribal members, either in the Helonieae (Engler, 1888; Krause, 1930) or the Narthecieae (Hutchinson, 1934, 1959), and it is extremely probable that a polyploid genome origin can be assigned to *Metanarthecium*.

This report is a serial continuation of the floral vascular anatomical studies on primitive members of the Liliaceae-Melanthioideae (Utech, 1978a—*Xerophyllum*; Utech, 1978b—*Helonias*; Utech, 1978c—*Pleea* (= *Tofieldia*); Utech and Kawano, 1978—*Heloniopsis*). The following observations on the floral vascular anatomy and floral morphology of *Metanarthecium luteoviride* will be presented and organized so as to be comparative to our previous reports.

MATERIALS AND METHODS

Flowering and fruiting inflorescences of *Metanarthecium luteoviride* were personally collected in Japan—Honshu: Toyama Prefecture, Tateyama Mountain Range, open meadow above Bijyodaira in the North Japanese Alps, elev. 2400 m, 24 July 1975. These floral materials were fixed in Farmer's solution (3 absolute ethanol:1 glacial acetic acid) for 12 h, and transferred into 70% ethanol for long-term storage. Standardized paraffin embedding and sectioning (14–16 μ) was followed by staining in safranin and methylene blue (Johansen, 1940; Sass, 1958). A total series of 12 flowers and fruits were serially prepared. As an additional check on these preparations, whole flowers and fruits were cleared and stained in a NaOH-1% fuchsin mixture (Fuchs, 1963; Utech and Kawano, 1975, 1976). The remaining fixed material and the prepared microslides are serving as the vouchers (CM). Herbarium specimens from the following institutions (Holmgren and Keuken, 1974) have been examined: MO, WIS, TNS, KYO, MAK, TI, and TUS.

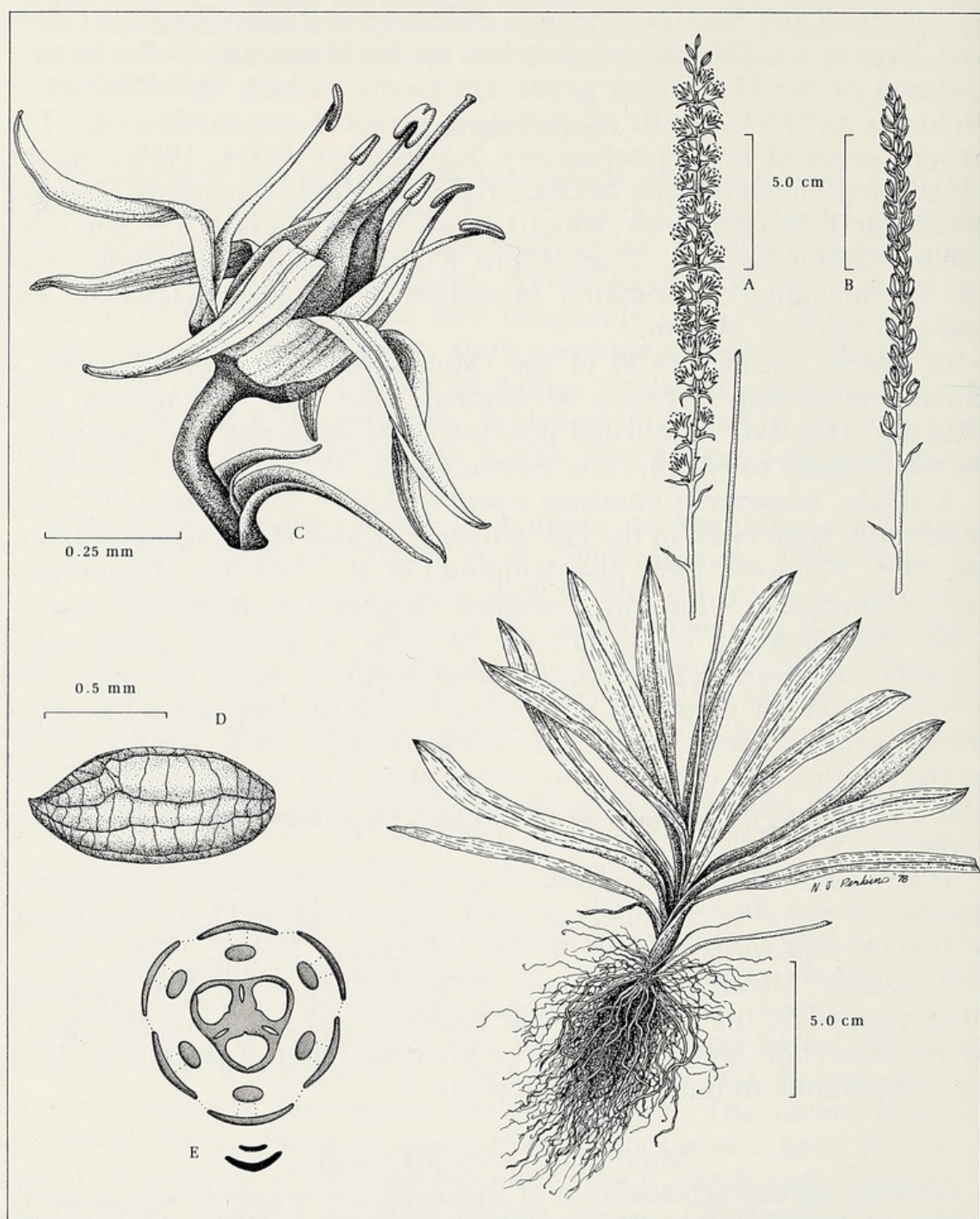


Fig. 1.—Illustration of *Metanarthecium luteoviride* Maxim., scale indicated. A) Flowering raceme with the upper and lower scape detached to show overall habit. B) Fruiting raceme, same scale as A. C) Enlarged flower showing the tepal-stamen arrangement, the abaxially attached, versatile anthers, the basal perigynous zone, and the short pedicel which is basally subtended by both a bract and a bracteole. D) A non-appendaged seed with several longitudinal striations and numerous cross striations shown. E) Floral diagram, bract and bracteole included. (drawing by Ms. Nancy J. Perkins)

OBSERVATIONS

Inflorescence, Bracts, and Bracteoles

Basally the scapes of *Metanarthecium luteoviride* are surrounded by a rosette of spreading radical leaves, which are yellowish green, glabrous, oblanceolate, gradually narrowed to their bases, and abruptly acuminate terminally (Fig. 1). The scapes are usually between 15 and 55 cm tall. The taller individuals of a population may be once or more rarely, twice branched from the lower floral nodes of the spike. The lower scape is weakly glandular-pilose, and interrupted by several, progressively smaller leaflike bracts.

The erect flowering spikes are usually between (5)–10–20 cm long, and this length is directly proportional to the number of flowers present (Fig. 1). At each node of the spike, the solitary flower is subtended both by a linear bract, which is longer than the pedicel, and by a shorter, linear bracteole. Both the bract and the bracteole, which basally subtend a given pedicel, depart in the same direction and from the same side of the spike axis (Fig. 1). Both bract and bracteole are green and vascularized.

Pedicel Morphology and Vascularization

The pedicels in *Metanarthecium luteoviride* are relatively short (2.0–4.0 mm) in comparison to the overall flower size. In cross-section, the pedicel is circular, and lacks the glandular-pilose epidermal modifications, which characterized the lower scape. Within the pedicel there are two vertically separated levels where bundle divisions and fusions occur. Basally in cross-section the lower pedicel has a ring of six central axial bundles (Figs. 5A, 6A). These bundles are large and distinct with normally arranged xylem and phloem. No sclerenchymatous sheath surrounds these bundles. Within the lower one-third of the pedicel, three fusion bundles are formed, each 120° apart, via side branches from each of the six ring bundles (Figs. 2, 5B, 6B). At progressively higher levels, these three fusion bundles will establish the outer tepal, outer stamen, and dorsal supplies (Figs. 5–8). Because these component traces depart at different horizontal levels, it is important to stress that these three bundles had a fusion origin at a lower pedicel level. Also, because of this lower fusion origin, reference to these main bundles up to their level of trace subdivision will be either as the common outer tepal-outer stamen-dorsal (OT-OS-D) bundles or the outer tepal-outer stamen (OT-OS) bundle (Figs. 5–8).

Within the upper one-third of the pedicel, there is a second series of radial divisions again involving the six axial bundles. However, this radial division with departing side branches occurs on the opposite side of the axial bundles as the lower and earlier divisions. Following

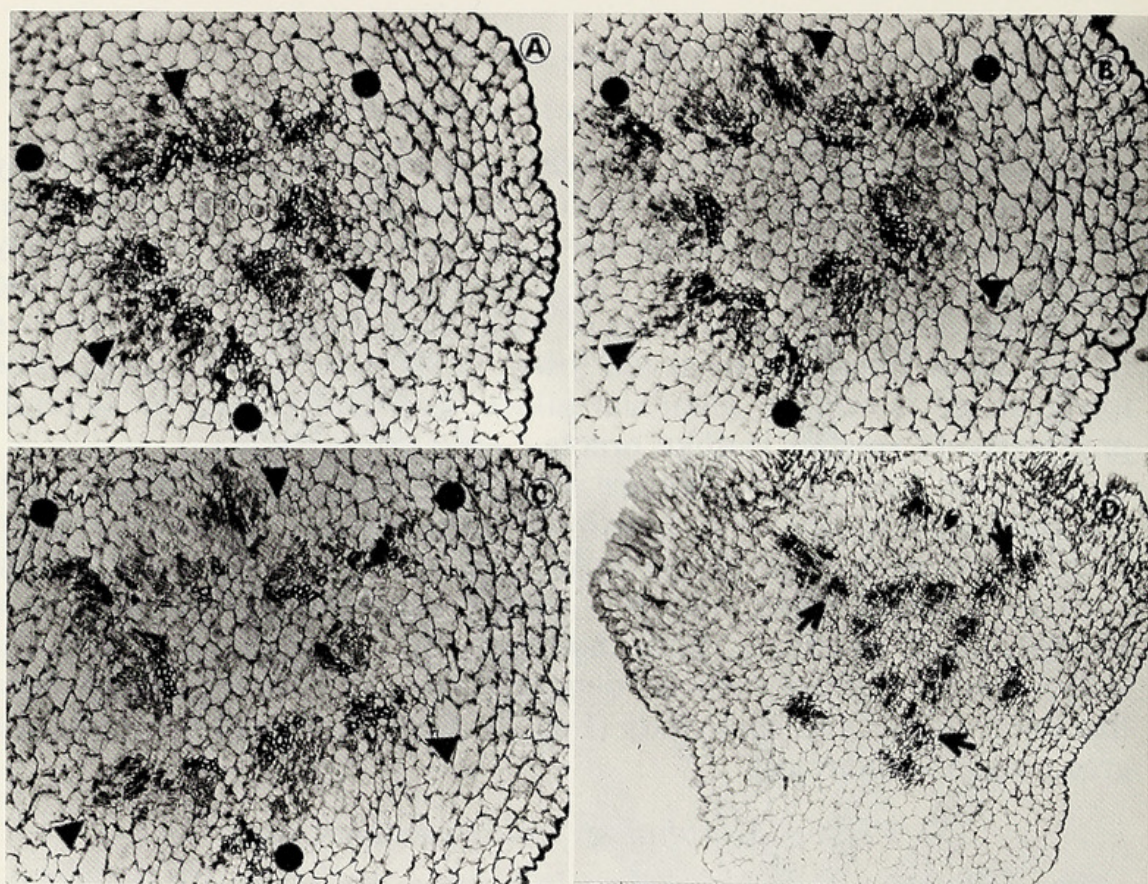


Fig. 2.—Serial cross-sections from the middle to upper pedicel in *Metanarthecium luteoviride*. A–C) Mid-pedicel, vascular transition from the nine- to the 12-bundled configuration. The three common OT-OS-D bundles formed at a lower pedicel level are marked by solid dots, whereas the three alternate radii along which the three common IT-IS bundles are formed and depart are marked by solid triangles. A ring of six axial bundles remains centrally in C (40 $\times$). D) Upper pedicel vascularization showing the formation of the three dorsals (arrows) from the common outer bundles, the departure of the three inner common bundles, the six axial central bundles, and the change from a circular to a six-lobed cross-section (30 $\times$).

fusion three new bundles are formed. Each is 120° apart and 60° from a common OT-OS-D bundle. The three new fusion bundles will establish at higher levels the inner tepal and the inner stamen vascular supplies (Figs. 5–8). The lower fusion bundles will be referred to as the common inner tepal-inner stamen (IT-IS) bundles up to their level of subdivision, which occurs above the level where the common OT-OS divides. The outer and inner common supply bundles have a similar pattern of origin. The common bundles are also an indication of the degree of perigyny present in *Metanarthecium luteoviride*.

Within the pedicel, the following changes in bundle configurations are observed (Figs. 5–8). Basally, there are six central axial bundles. In the lower one-third, there are nine bundles, that is, the six axial

bundles and the three new OT-OS-D common bundles. In the upper one-third region, there are 12 bundles, that is, the nine, which were continuous from below, and the three newly formed fusion bundles, that is, the IT-IS common bundles. The upper pedicel has 12 bundles, which are all on different radii. The three common OT-OS-D bundles are the closest to the periphery, whereas the IT-IS bundles are not as close to the periphery. The six axial bundles, on the other hand, remain in their same relative central position as in the pedicel base.

Receptacle Base, Perigynous Zone, and Floral Tube

The transition from the upper pedicel to the lower receptacle base is associated with a gradual increase in cross-sectional area (Figs. 5 B–D; 6 B–D). The dorsals (D) are formed in this expanding zone. From each of the common OT-OS-D bundles which are broadly trilobed at this level, a dorsal (D) is cut off adaxially from each of these compound bundles (Figs. 5 D–F; 6 D–F). Because these compound common bundles are in a peripheral position, the dorsals are freed peripherally. There is no indication of locule opening at this level, subsequently there is no net outward movement of the freed dorsals (D). Furthermore, because the dorsals (D) were derived from the common OT-OS-D bundles, which in turn were lower pedicel fusion products, the dorsals are indirect fusion products.

Broadening of the cross-sectional area of the receptacle base increases significantly following the formation of the dorsals. Whereas the pedicel was circular in cross-section, the receptacle base is broadly six lobed. Three of these lobes are larger than the other three. The outermost edges of the larger lobes are aligned along the radii of the triwedged OT-OS bundles. The three IT-IS bundles, on the other hand, are associated with radii that bisect the three smaller lobes (Figs. 5 D–F; 6 D–F).

The low level of locular opening in *Metanarthecium luteoviride* indicates perigyny. The three locules open before any tepal or stamen traces of either whorls are established, and below the levels where the tepals and stamens are cut off (Figs. 5 E–G; 6 E–G). There is total circular adnation in both flowering and fruiting material of the floral envelope to the gynoecium. Another indication of perigyny is that the gynoecial vasculature is established before either the tepals and stamens are cut off or their vasculature established.

The perigynous zone extends vertically for some distance before the perianth and the adnate stamens are freed (Fig. 7). The first indications in cross-section of this separation are six crescent-shaped gaps (Figs. 5 F–G; 6 F–G). The ends of each gap are between the common outer and the common inner tepal-stamen supplies. The gynoecium is therefore not freed along either the dorsal or septal regions, but in between.

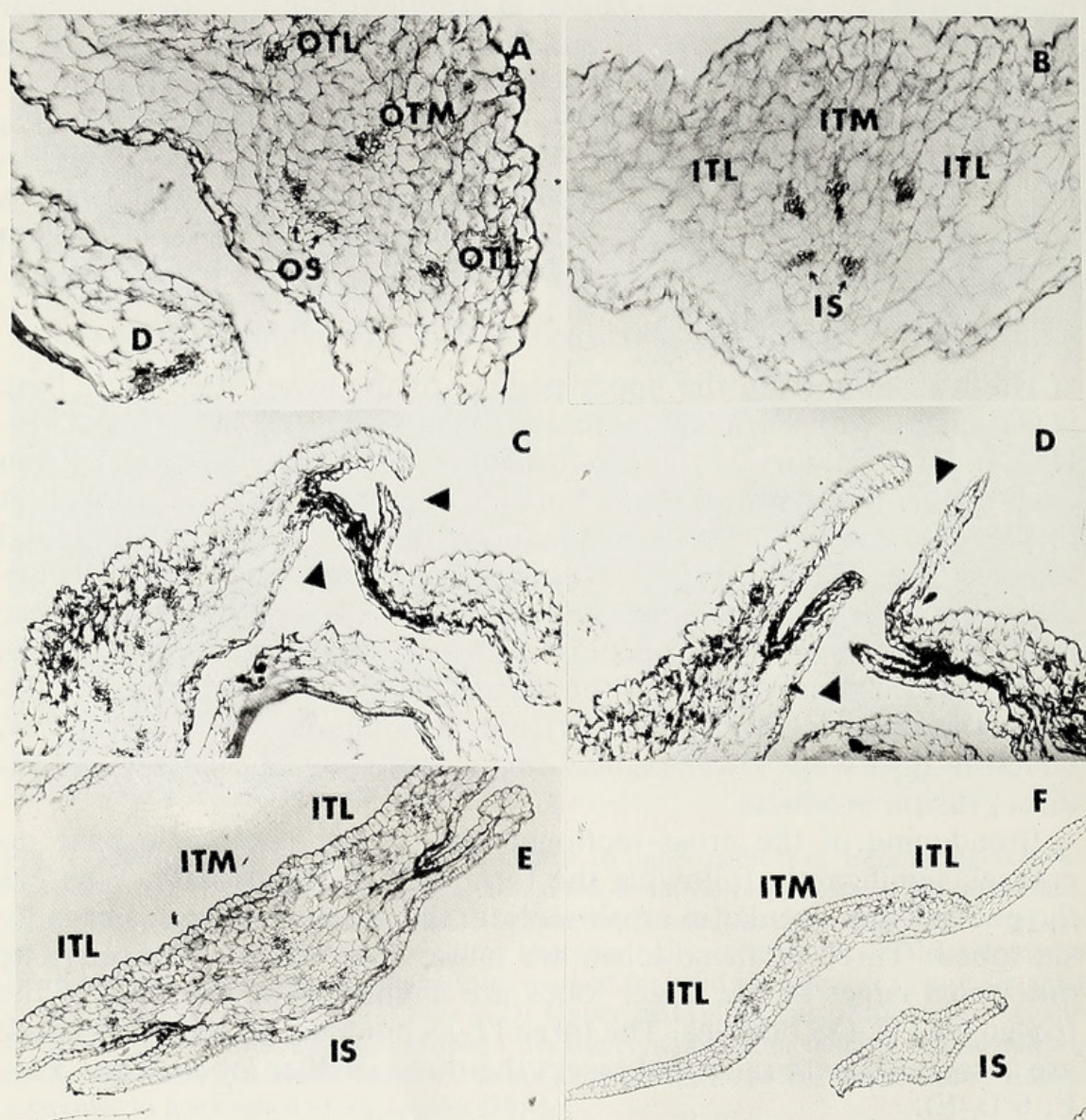


Fig. 3.—Serial cross-section showing tepal and stamen vascularization and adnation in *Metanarthecium luteoviride*. A) A carpellary dorsal (D), and an outer, five-bundled set within the floral tube are shown; the latter set is represented by two outer tepal laterals (OTL), an outer tepal median (OTM), and two inner bundles, which fuse to form the outer stamen (OS) bundle (60 $\times$). B) Floral tube, same height as A, but showing an inner, five-bundled set, that is, two inner tepal laterals (ITL), an inner tepal median (ITM), and two inner bundles which fuse to form the inner stamen (IS) bundle (60 $\times$). C) Fused margin of the floral tube between an outer and inner tepal (triangles) (60 $\times$). D) Section above C showing the marginal separation of the floral tube between an outer and inner tepal (triangles) (60 $\times$). E) Section above D showing inner stamen epitepaly; tepal and stamen bundles indicated (50 $\times$). F) Lower, non-recurved, inner tepal subtending basally a dilated inner filament (25 $\times$).

As these gaps enlarge and meet, a floral tube is formed, which surrounds the gynoecium (Figs. 5 F–G; 6 F–G). Stamen adnation (epitepaly) also characterizes this floral tube, because neither the outer nor the inner stamens or their traces are established when the floral tube is cut off. Neither the outer carpellary wall nor the inner wall of the floral tube, that is, the dilated adaxial filament surface, are characterized by any special type of epidermis, which could function as a basal nectary within the floral tube.

Within the floral tube, the subdivision of the common OT-OS bundle into three outer tepal traces and a double (bifid) outer stamen trace occurs before the subdivision of the common IT-IS bundle into the three inner tepal traces and a double (bifid) inner stamen trace. That all this trace formation from a compound bundle formed in the lower pedicel occurs within the floral tube and the perigynous zone attests to the degree of adnation and cohesion previously unreported for the genus *Metanarthecium*.

Tepal and Stamen Morphology and Vascularization

The freed portions of the six tepals are sublinear to lanceolate, 6.0–8.5 (–11.0) mm long and equal (Fig. 1). The successive separation of these six tepals and the six associated stamens from the floral tube is shown in Figs. 3, 5 F–J, and 6 F–J. During anthesis, the freed tepals of both cycles are recurved or spread (Fig. 1). Tepal color is localized, and similar within both cycles. On the outer surface of the six tepals, there is a central zone on both sides of the midrib, which is light green, whereas the outer marginal surfaces are a yellowish white. The tepals persist into the fruiting stages.

The stamens are shorter than the tepals (Fig. 1). The filaments are basally dilated, filiform terminally, and glabrous (Figs. 3; 5 H–J; 6 H–J; 7). The filaments of *Narthecium*, in comparison, are densely pubescent. In *Metanarthecium*, the filament and anther lengths of both cycles are equal. The observed outward divergence of the filaments during anthesis is associated with the simultaneous recurving of the tepals, which is directly due to the staminal epitepaly above the perigynous zone (Fig. 7).

The oblong anthers are attached to the attenuated filament tips slightly below the anther's mid-length point on their outer, abaxial surface. The anthers are subsequently versatile, and in conjunction with the divergent filaments a wide pollen dispersal zone is created at the same level as the capitate stigma. Anther dehiscence is via longitudinal, lateral slits. The endothelial cell walls of the anthers are marked by banded thickenings.

Because of the basal perigyny, the floral tube, and the stamineal epitepaly in *Metanarthecium* and the subsequent compound, common

bundles, tepal and stamen vascularization will be presented simultaneously. Within the upper pedicel, six compound fusion bundles are formed (Figs. 5 A-E; 6 A-E). Three of these are the OT-OS-D common bundles, and the other three are the IT-IS common bundles (Fig. 8). The three dorsals (D) are cut off from the outer common bundles at a low perigynous level. The remaining portions of these common bundles, that is, the OT-OS common bundles, become broadly trilobed following dorsal (D) departure. Subsequently, each trilobed bundle is radially subdivided into three free bundles (Figs. 5 D-G; 6 D-G; 8). The central bundle of each triplet becomes the outer tepal median (OTM), whereas the two lateral bundles each undergo an additional division. Following this division, there are three peripheral sets of five bundles. Each set is 120° apart.

These three sets of bundles, the most peripheral within the perigynous and floral tube zones, establish the complete outer tepal and stamen vasculature (Fig. 8). The outermost bundle of each set is the OTM with a radially derived pair on each side. This outermost bundle pair establishes the outer tepal laterals (OTL) (Figs. 3; 5 G-J; 6 G-J; 8). The inner bundles of the above pairs will at a higher level fuse and establish the outer stamen (OS) traces. The two inner bundles, which contribute to the OS trace, run parallel in a vertical direction prior to their fusion (Figs. 3; 5 F-K; 6 F-K; 8). This fusion occurs as the outer stamens are freed from the adnate tepals within the epitepaly zone. The filament of each outer stamen, therefore, has a single fusion trace (OS). Each outer freed tepal, on the other hand, has two laterals and a median, that is, an OTL plus an OTM plus an OTL (Figs. 3; 5 G-J; 6 G-J; 8). Past descriptions (Baker, 1876; Engler, 1888; Bentham and Hooker, 1883; Krause, 1930; Ohwi, 1965) have incorrectly noted that the tepals are one-nerved.

The origin of the inner tepal and inner stamen vasculature is similar to that of the outer tepals and outer stamens (Fig. 8). Moreover, the subdivision of the IT-IS common bundle parallels that of the OT-OS common bundle. However, the formation of the inner three five-bundled sets along the septal radii occurs at a higher level than subdivision of the three outer common OT-OS bundles. Each freed inner tepal, like an outer tepal, has three bundles, that is, an ITL plus an ITM plus an ITL. The origin of the IS bundle, which involves unfused parallel traces, is identical to that of the OS bundle. There is consequently a fusion inner stamen (IS) trace in each inner filament.

Gynoecial Morphology and Vascularization

The narrowly ovoid to conical gynoecium of *Metanarthecium luteo-viride* has several noteworthy modifications. Raphides are common throughout the gynoecium at all stages of development. They are es-

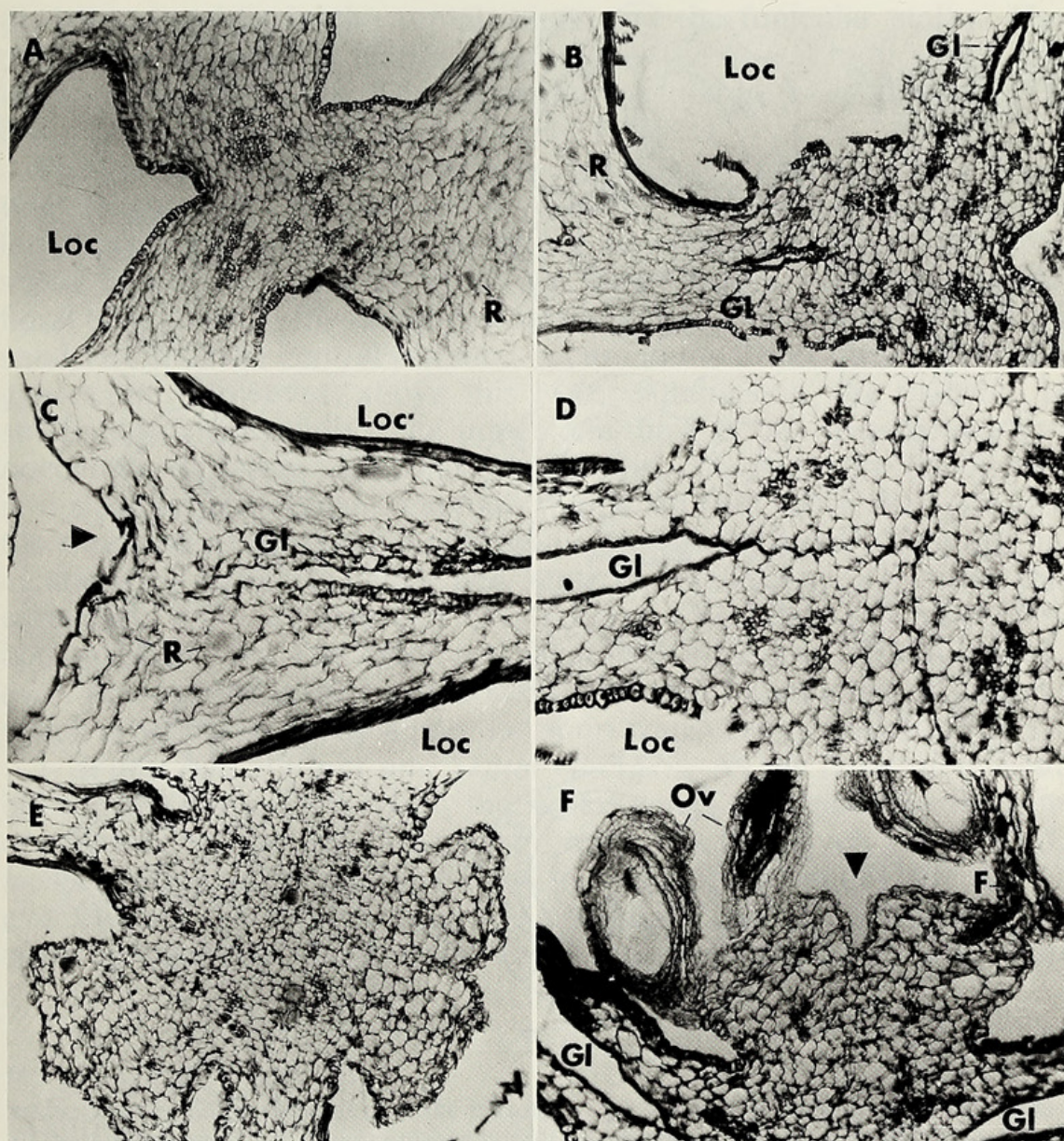


Fig. 4.—Serial cross-section of the gynoecium in *Metanarthecium luteoviride*. A) Gynoecial portion within the perigynous zone showing the wide septal wings and the central placenta, the subdivision of the axial bundles into the ventrals and the fusion formation of the septal axials (SA) (40 $\times$). B) Level of freed floral tube and gynoecium; section shows the inner formation of septal glands (Gl), the absence of septal axials (SA), and the subdivided ventrals; raphides (R) are common (40 $\times$). C) Enlarged section above B, showing the outer, radial extent of a septal gland (Gl), and its external opening (triangle); cells lining the gland (Gl) differ from those lining the locules (Loc) (60 $\times$). D) Section at the same level as C, but showing the inner, radial extent of a septal gland (Gl), and the septicidal subdivision of the central placenta; cells lining the gland (Gl) differ from those along the placental subdivision; ventrals present, but no funicular branching or ovular attachment occurs at this level (60 $\times$). E) Midgynoecial section showing loculicidal subdivision of the placenta (dotted lines); paired obturators extend into each locule; ventrals present (50 $\times$). F) Horizontal attachment of bitegmic ovules (Ov) to obturators; funicular (F) traces derived horizontally from vertical ventrals; placenta loculicidally subdivided (triangle); septal glands (Gl) still present (50 $\times$).

***Metanarthecium*
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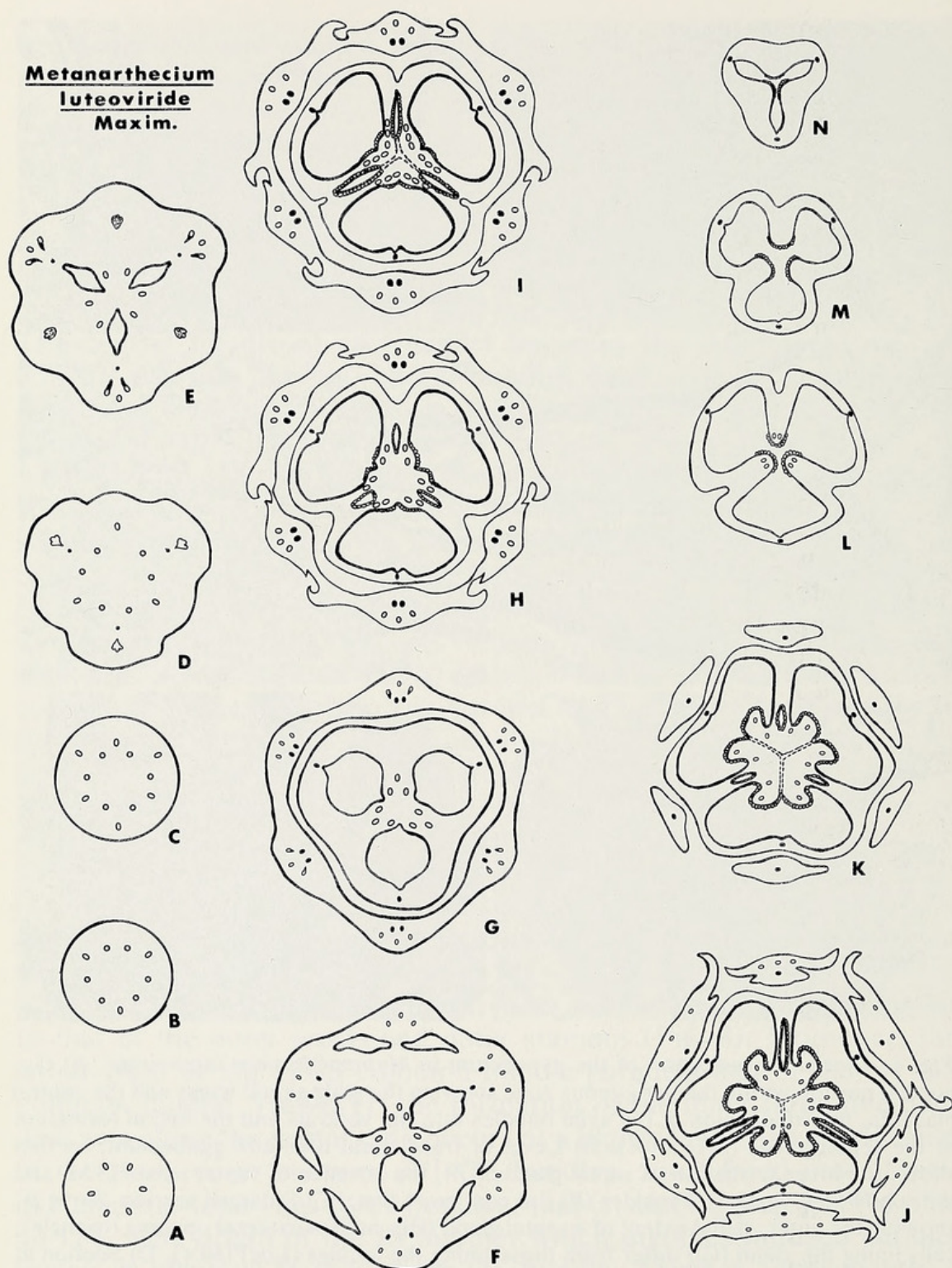


Fig. 5.—Serial cross-sections of *Metanarthecium luteoviride*. A) Lower pedicel with six-bundled configuration. B) Midpedicel with a nine-bundled configuration, the three additional bundles are the common outer tepal-outer stamen-dorsal bundles. C) Upper pedicel with a 12-bundled configuration, the three additional bundles are the common inner tepal-inner stamen bundles. D) Upper pedicel to receptacle transition, the three dorsals segregated from the outer common bundles. E) Perigyny at receptacle base, locules opening, outer common bundles subdividing into a median (OTM) and two lat-

pecially abundant in the septal wings and the funicular stalks. The three locules open via elongate slits along the dorsal radii within the lower perigynous zone. The gynoecial vasculature is established at a lower level than that of the tepals and stamens.

The gynoecium above the perigynous zone is surrounded by a floral tube (Figs. 5–7). Internal dorsal grooves run the whole gynoecial length, external septal indentations are also present basally. The three septal (nectiferous) glands within the three septal wings open in the floral tube zone via the septal indentations (Fig. 7). Complete septicial subdivision of the central placenta occurs in the lower one-third of the gynoecium. However, above this lower subdivision, the placenta is subdivided loculicidally. The upper one-third of this tricarpellate gynoecium is therefore unilocular. The hollow, columnar style terminates in a shallowly trilobulate, capitate stigma. In fruit, both the style and the three carpels dehisce loculicidally, though in flower there are indications of both loculicidal and septicial dehiscence. In fruit, the carpellary walls are thin and chartaceous. The total seed number is approximately 24. The seeds are small (0.6–0.8 mm), reddish brown, oval, non-appendaged, and marked by several longitudinal striations, which are interrupted by numerous short transverse striations (Fig. 1).

1. *Septal Indentations and Septal Glands*.—As the floral tube is cut off and the gynoecium freed, the septal wings are relatively thick in comparison to the outer carpellary walls. At this level, the central, massive placenta, is not subdivided loculicidally or septicially. However, within the locules there are carpellary grooves or notches (in cross-section) over the dorsals. These inner dorsal grooves extend up

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erals, inner common bundles near the periphery, six axials in three pairs near the center. F) Perigynous zone, the outer common bundles each represented by a set of five bundles, that is, the median (OTM), two tepal laterals (OTL) and two elements which will fuse to form the stamen bundle (OS), the inner common bundles subdividing into a median (ITM) and two laterals, septal axials (SA) formed between the paired axial bundles, gaps show zone of floral tube formation. G) Gynoecium base freed from floral tube, both the outer and inner common bundles represented by five-bundled sets. H) Origin of the three septal glands, septal indentations also present, septal axials (SA) have terminated, the paired axials (ventrals) divided into several bundles, internal dorsal notch present, floral tube present. I) Septicial subdivision of the central placenta, septal glands with external connections into the floral tube, further subdivision among the vertical ventrals. J) Loculicidal subdivision of the central placenta, obturators present, septal glands present, marginal separation of the floral tube with tepals and stamens remaining adnate, the two elements of each stamen bundle fuse. K) Filaments freed from the tepals (not shown), septal glands and the loculicidal placenta division shown, obturators with stigmatoid papillae. L) Lower unilocular style, ventrals remaining, dorsal grooves shown. M) Mid-style, ventrals absent. N) Upper style transition to trilobulate, capitate stigma, dorsals present.

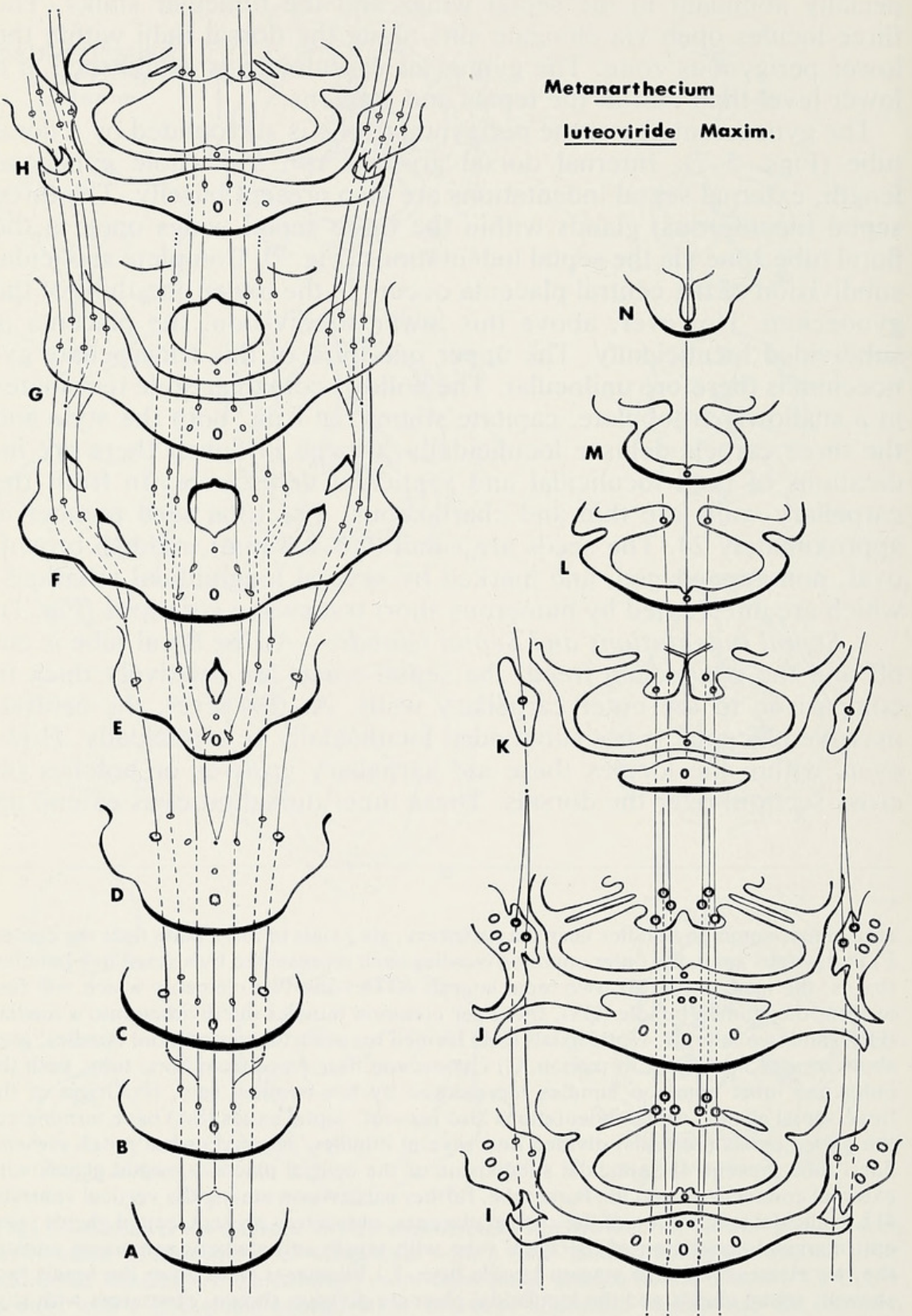


Fig. 6.—*Metanarthecium luteoviride*, cross-sections of Fig. 5 after transformational projections to give a semilongitudinal view, selected vascular bundles are connected, and the lettered cross-sections correspond to those in Fig. 5.

the whole inner gynoecial surface, as well as up the common style (Figs. 5 E-N; 6 E-N; 7). Usually such dorsal grooves are indicative of loculicidal dehiscence. However, there are also in the basal region external septal indentations (Figs. 5 H-I; 6 H-I; 7), which were formed as the inner stamen portions of the floral tubes were cut off. Normally such septal indentations are indicative of septicidal dehiscence. At a higher level within the floral tube, these outer septal indentations become openings for the septal (nectiferous) glands (Fig. 3 B-D). The epidermal linings of both the septal indentations and the outer carpelary walls are identical. The indentation cells do not stain differentially, and are not secretory. The three septal indentations are not observable in the mid- to upper gynoecium (Figs. 5 J-K; 6 J-K; 7).

The three septal (nectiferous) glands are formed in the lower perigynous zone, but extend vertically for some distance within the septa (Figs. 4; 5 H-J; 6 H-J; 7). In cross-section, the three septal glands first appear as slits within the laterally fused septal wings. Confined to the three septal wings, the glands lack basally both external openings and central interconnections. Cells, which stain differently from those of the septal indentations, line the septal glands (Fig. 3 B-F). In all likelihood, these internal gland cells are secretory, and the three septal glands functioning as a basal, gynoecial nectary.

Two types of interconnections are observed within the septal glands. In cross-section, the radial length of the septal glands increases outward, and eventually opens into the three septal indentations along the periphery of the gynoecium (Figs. 4 C; 5 H-J; 6 H-J; 7). Although this gland opening level is basal, it is within the floral tube zone. Furthermore, with this opening the three carpels are only fused centrally within the central placenta. There are no indications of the three peripheral septal indentations above the gland opening level, because the outer margins of the septal wings are fused.

Following the opening of the septal glands and the closure of the outer septal wings, a second type of intragland connection occurs. It is internal, and completely subdivides the central placenta (Figs. 4 E; 5 I-J; 6 I-J; 7). The cells lining this intragland subdivision are similar to those of the surrounding placenta, that is, nonsecretory. The duration of this intragland connection and placental subdivision is vertically limited (Fig. 7). The septal glands, on the other hand, with their secretory cells extend vertically into the upper septal region of the gynoecium (Figs. 4 D-E; 5 H-J; 7).

The septal indentations, the septal glands, and the lower septicidal subdivision of the central placenta are strong indications of how incompletely the three carpels are fused. These septal modifications in conjunction with the floral tube function as a pollination-related nectary. The geometric configuration of the elongated style with its cap-

itate stigma and the versatile anthers is also related to this pollination system.

In the upper one-third of the gynoecium, there is complete loculicidal subdivision of the central placenta (Figs. 4 F; 5 J-K; 7). The upper gynoecium is therefore unilocular, and the columnar style is hollow. It is most interesting that while there are carpellary indications of both loculicidal and septicidal dehiscence, the fruit is a loculicidal capsule. This duality in gynoecial subdivision coupled to the septal (nectiferous) gland has not previously been reported for *Metanarthecium*.

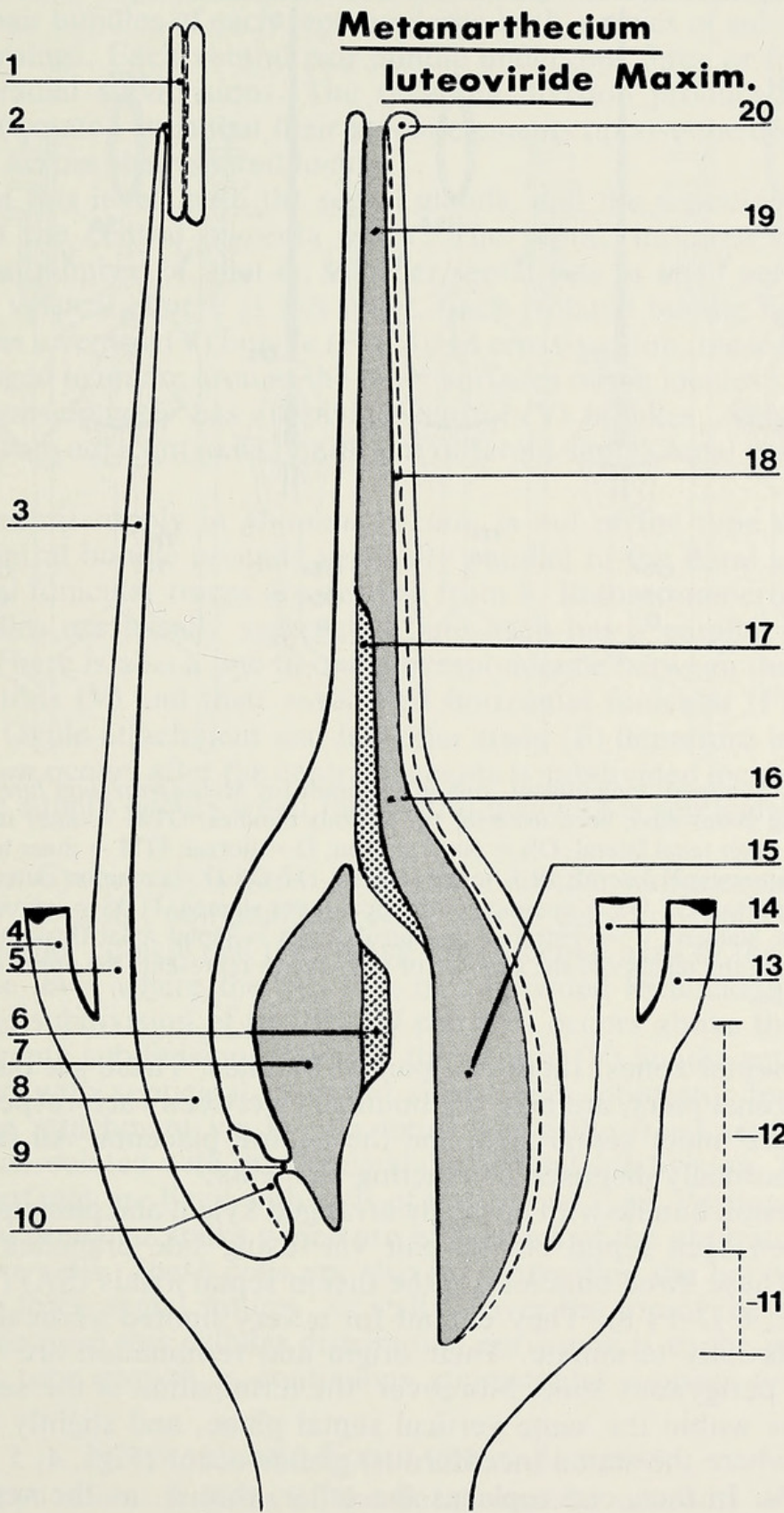
2. *Gynoecial Vascularization*.—The gynoecial vascular supply, like the locular opening, is established in the lower perigynous zone (Figs. 4 A; 5 E-F; 6 E-F; 7). The three dorsals (D), which represent indirect fusion products, are established within the perigynous zone from the three outer OT-OS-D bundles (Figs. 5 D-F; 6 D-F; 8). The complete ventral supply, on the other hand, is more complex than the dorsal supply. As the locules open, the ventral supply is established basally, in part, from the central six ring bundles. These bundles are coaxial with the six pedicel ring bundles (Fig. 8). The three dorsals (D), and the six bundles, which establish the ventral supply, have normally arranged xylem and phloem at this basal level.

The three dorsals (D) neither branch nor fuse with any of the ventral supply elements. Furthermore, the dorsals have an uninterrupted course from their perigynous level of formation to the capitate stigma tip (Fig. 8). A normal relationship between the xylem and phloem is maintained throughout the dorsal course. Because each carpel has an inner dorsal groove, which is the zone of loculicidal dehiscence, the dorsal bundles themselves are split as the capsule opens.

Ventral vascularization occurs at a low level due to the depression of the locules. As the three locules open, three septal zones and a large central placenta are established. The term septal zone is used, because perigyny occurs at this level (Figs. 5 E-F; 6 E-F; 7; 8). In each of the

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Fig. 7.—Median longitudinal diagram of a *Metanarthecium luteoviride* flower. Section passes through both a locule and a septum along the OTM-OS-D-IS-ITM diameter. Reconstructed in part from Figs. 5–6. Number code: 1) Versatile anther with a lateral, longitudinal dehiscence slit. 2) Abaxial anther attachment. 3) Glabrous inner filament. 4) Freed inner tepal (in part). 5) Freed inner filament. 6) Septicidal subdivision of central placenta. 7) Septal (nectiferous) gland. 8) Nectar space between the floral tube and the septal wall of the gynoecium. 9) External septal gland opening. 10) Septal indentation. 11) Height of perigynous zone. 12) Height of the floral tube and epitepaly zone. 13) Freed outer tepal (in part). 14) Freed outer stamen (in part). 15) Locule. 16) Unilocular upper gynoecium. 17) Loculicidal subdivision of the central placenta. 18) Inner dorsal groove. 19) Hollow styler canal. 20) Trilobulate, capitate stigma. Scale indicated.



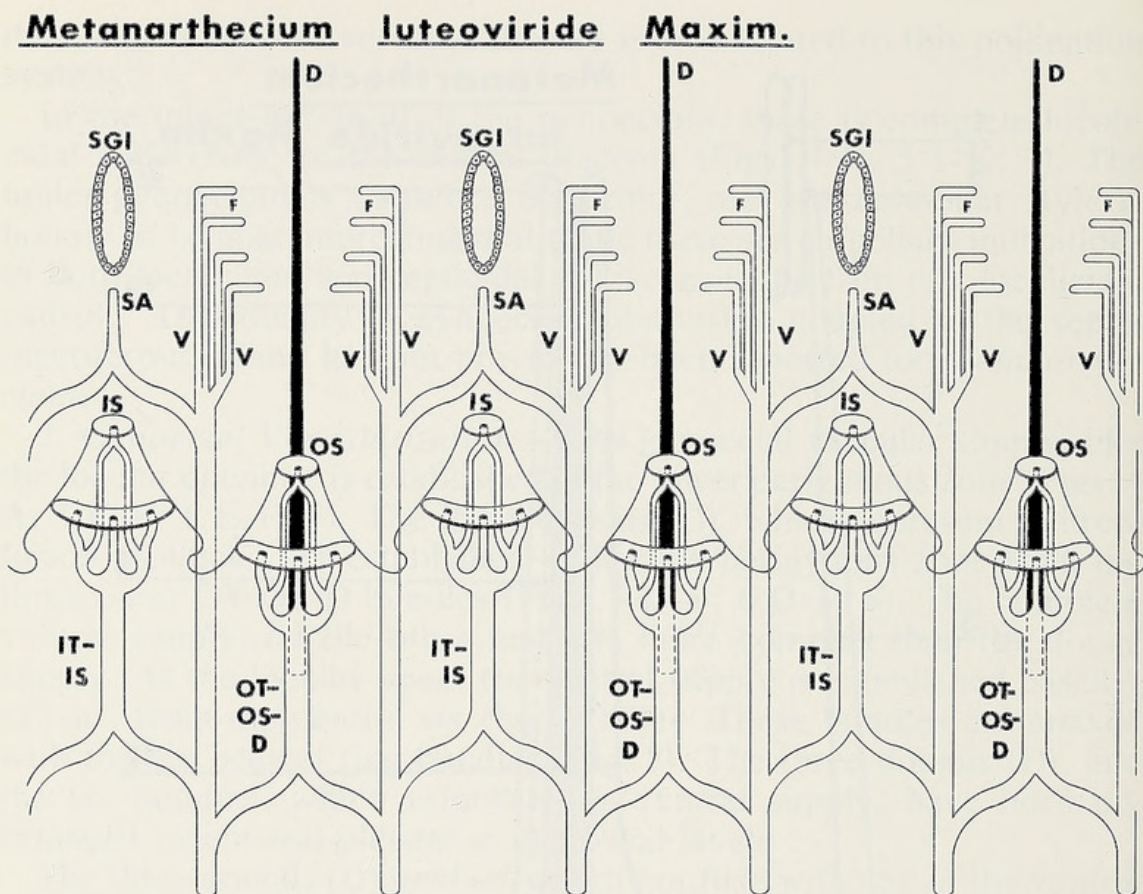


Fig. 8.—Summary longitudinal, roll-out diagram for *Metanarthecium luteoviride*. The following codes have been used for the various bundles: OTM = outer tepal median; OTL = outer tepal lateral; OS = outer stamen; D = dorsal; ITM = inner tepal median; ITL = inner tepal lateral; IS = inner stamen; OT-OS-D = common outer tepal-outer stamen-dorsal; OT-OS = common outer tepal-outer stamen; IT-IS = common inner tepal-inner stamen; V = ventral; F = funicular; SA = sepal axial (fusion). Wavy line connecting the tepals and the stamens of both cycles represents the upper extent of the floral tube.

three sepal zones, there is a pair of bundles. These six bundles, the three zonal pairs, are near the boundary between each respective bundle pairs' inner sepal zone and the central placenta. All six bundles have normally disposed conducting elements.

A fusion bundle with normally arranged xylem and phloem is formed between each sepal bundle pair via fusing side branches from this pair. These three bundles are the fusion sepal axials (SA) (Figs. 4 A; 5 D-E; 6 D-F; 8). They extend for a very limited vertical distance, and abruptly terminate. Their origin and termination are within the sepal perigynous zone. Moreover, the termination of the sepal axials (SA) is within the same vertical sepal plane, and slightly below the level where the sepal (nectiferous) glands occur (Figs. 4; 5 D-I; 6 D-J; 7; 8). In fact, one replaces the other, that is, as the sepal axials terminate within the vertical sepal planes, the sepal glands appear.

As the three septal axials end within the septa, the laterally located ventral pair bundles of each septa undergo both a series of subdivisions and inturnings. Each ventral pair bundle undergoes three or four successive radial subdivisions. The resulting division products are inturned or rotated such that their xylem elements oppose the dorsal (D) which is across their shared locule.

Also at this level, both the septal glands, and the septicidal subdivision of the central placenta occur. The septal, inturned bundles, which can number 24, that is, four per septal side or eight per locule, follow a vertical course at this level. Each isolated bundle functions directly as a ventral (V) bundle (Fig. 8). In cross-section, these bundles are arranged in an arc around the inner surfaces of the locules. A given locule, consequently has supplying ventral (V) bundles, which were derived from adjacent axial bundles of different septal zonal pairs (Fig. 8).

The ventral supply in *Metanarthecium* is not of the type where a single ventral bundle ascends vertically parallel to the floral axis and horizontal funicular traces are derived from it. Rather, numerous ventral bundles are basally segregated, and each has a parallel vertical course. There is also a one to one correspondence between these vertical ventrals (V) and their associated horizontal funicular (F) traces (Fig. 8). Ovule attachment and funicular trace (F) departure in *Metanarthecium* occurs after the central placenta is subdivided loculicidally. No ovule supply occurs when the central placenta is septicidally subdivided.

3. *Inner Gynoecial Surface*.—The inner locular surfaces are lined by rather elongate, non-papilloid cells. These cells are replaced by a second, rather cubical cell type along the placental axes of the locules below the level where the placenta is subdivided loculicidally. This loculicidal subdivision of the central placenta occurs above the septicidal placenta subdivision. Whereas the ventral (V) bundle rotation is associated with septicidal placental subdivision, obturator formation and ovule attachment via locular inturning of the freed septal wing tips, are associated with the loculicidal placental subdivision. The obturator surfaces are lined with cells of the second type. Portions of the horizontal funicular stalks which are extensions of the obturators also have these cells. These cells are also present within the hollow style along the three septal sutures, as well as over the top of the capitate stigma. Because this cellular distribution corresponds to the pathway of pollen tube growth, a continuous stigmatoid support system is present.

SUMMARY AND CONCLUDING REMARKS

The most salient features of the floral vascular anatomy of *Metanarthecium luteoviride* include the following. The paired bract and

bracteole, which subtend each solitary flower, are vascularized. A six-bundled, axial configuration characterizes the lower pedicel's vasculature. No sclerenchymatous sheath occurs between the undifferentiated pith and cortex of the pedicel. The basal perigyny, which extends into a shallow floral tube, obscures the true locular depth and receptacle base.

Because of this perigyny, common fusion bundles are prevalent. Six such bundles are formed in the upper pedicel; one common bundle between each of the six axial bundles. The lowest formed common bundles are the three outer tepal-outer stamen-dorsal bundles. Slightly higher, the other three, the three common inner tepal-inner stamen bundles are formed. Within and above the perigynous zone, these six common bundles divide into their various component bundles.

The common tepal bundles, that is, the common OT and the common IT, subdivide into a median and two laterals. Each outer tepal has an OTL plus an OTM plus an OTL, and each inner tepal has an ITL plus an ITM plus an ITL. The three traces of each tepal are established within the upper perigynous zone. The stamen bundles of both cycles, that is, the OS and IS bundles, are fusion products. The two components of each fusion stamen bundles are derived from the same bundles which established the tepal laterals. Throughout much of the perigynous zone, the two stamen trace components are separated and only fuse as the stamens are cut off from the tepals. The dorsals are also fusion products. Though their origin occurs below the perigynous zone, the dorsals are from the same common bundles which supplied the outer stamens and outer tepals. There is no branching of the dorsals, and each terminated in the upper style.

The six axial bundles, which formed the common bundles, continue vertically up into the base of the perigynous zone, and establish the ventral supply and the three fusion septal axials (SA). The vertical course of the septal axials is limited, and they terminate below the septal (nectiferous) glands. The ventral supply consists of several, basally subdivided bundles per septum. Each bundle has a vertical course and a one to one correspondence with a funicular trace. There is no interconnection above the pedicel-receptacle transition zone between the dorsal and ventral supplies.

The gynoecium has several noteworthy features. There is incomplete fusion along the outer, basal septal margins, which results in the formation of three septal (nectiferous) glands. These septal glands each have an external opening into the floral tube. Raphides are common within the gynoecium at all stages of development. The fruit is a loculicidal capsule, though in flower there are both septicidal and loculicidal subdivisions of the central placenta. Furthermore, there are no interconnections between the septal glands and the zones freed by the

septicidal and loculicidal subdivisions. Though the seeds are not appendaged, they have several longitudinal striations, which are interrupted by numerous cross striations.

Under the Englerian system (Engler, 1888; Krause, 1930), *Metanarthecium* is placed in the tribe Helonieae, whereas Hutchinson (1934, 1959) places *Metanarthecium* in a larger and somewhat differently circumscribed tribe, the Narthecieae. Two genera, *Xerophyllum* and *Heloniopsis* (but not *Helonias*), are common to both tribes. There are some generic groupings within both tribes that are justified and others that are not. *Tofieldia* and *Pleea* are congeneric (Utech, 1978c). *Pleea tenuifolia* was transferred to *Tofieldia* on the basis of the floral vascular anatomy and morphology of the two (Utech, 1978c). The Japanese endemic *Japanolirion osense* Nakai has affinities to *Tofieldia*, and the floral vascular anatomy of the former should be examined. Hutchinson's separation of *Helonias* and *Heloniopsis* does not appear justified, because both share a large number of floral vascular and floral morphological characters (Utech, 1978b; Utech and Kawano, 1978). *Ypsilandra*, an Himalayan genus, has affinities to both *Helonias* and *Heloniopsis*, and also needs to be examined.

Metanarthecium does exhibit several characters in common with *Narthecium* (Utech, 1978c), *Xerophyllum* (Utech, 1978a), *Helonias* (Utech, 1978b), and *Heloniopsis* (Utech and Kawano, 1978), but there are some significant differences. These genera share a loculicidal dehiscence, an axial pedicel vascular configuration from which fusion bundles are derived, and a massive basal placenta, but differ in that *Metanarthecium* exhibits perigyny and septal glands and has non-appendaged seeds. *Tofieldia*, including *Pleea*, is completely different from the above group (Utech, 1978c). This report on the floral vascular anatomy and morphology of *Metanarthecium* must remain incomplete as far as an exact tribal evaluation is concerned, until additional genera from both tribes are examined.

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