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FLORAL VASCULAR ANATOMY OF THE HIMALAYAN *THEROPOGON PALLIDUS* MAXIM (LILIACEAE—CONVALLARIEAE)

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ABSTRACT

The floral vascular anatomy and carpel morphology of the berry-fruited, monotypic, Himalayan endemic *Theropogon pallidus* are presented and compared to that of its tribal cohort *Convallaria*. The down turned flowering pedicels of *Theropogon* have three large compound bundles from which the total floral vasculature is derived. Through a series of radial divisions these three pedicel bundles establish branch bundles, which fuse between the gaps of the divisions and also fuse between the original three bundles. The three outer tepals, the three outer stamen bundles, and the three dorsals are fusion products along gap radii which bisect the large pedicel bundles. Similarly the three inner tepal medians, the three inner stamen bundles, and the three septal axials are fusion products along radii mid-way between the three pedicel bundles. The fleshy imbricated tepals have only a single bundle, that is a median—there are no tepal laterals in either whorl. There is no terminal interconnection between the dorsal and ventral supplies. The six simple ascending ventrals have direct horizontal funicular branches. Due to the large number of fusion bundles and radial divisions which can be traced to the three compound pedicel bundles, the overall floral vasculature must be viewed as reduced and advanced. The vascularization of the berry fruit in *Theropogon* is different from that in *Convallaria*.

The trilobed gynoecium in *Theropogon* is tricarpeolate, syncarpous, non-stipitate, and unilocular terminally. Septal grooves, which persist, are present, but there are no septal glands. Rhaphides were not observed. The average ovule number is 24. The gynoecium morphology of *Theropogon* is different from that in *Convallaria*.

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INTRODUCTION

Theropogon pallidus Maximowicz is an endemic species of the Himalayan region (Baker, 1875; Hooker, 1894; Engler, 1888; Krause, 1930). This perennial species has a stocky rhizome with numerous, thick fibrous roots (Fig. 1A, C). The radial, distichous leaves are annual, glaucous above and below, and have prominent median costa (Fig. 1B). The scape is acutely angled to narrowly winged longitudinally and is shorter than the ascending leaves. Each terminal raceme has between five to eighteen flowers. Each flower is subtended by both a linear-subulate bract (B), and a linear but shorter bracteole (Brt) (Fig. 1D). Both the bract and the bracteole are shorter than the associated down-curved pedicel (Fig. 1D). The pale, rose-red perianth of the campanulate-shaped flowers are inverted during anthesis.

Though this species has been known since the latter part of the last century (Maximowicz, 1871) and figured in *Curtis' Botanical Magazine* (Hooker, 1875; t. 6154), floral anatomical information is scarce. Nair and Sharma (1965) using light microscope observations briefly described the pollen grains of this species, and Stenar (1953) reported a "very probably" *Polygonum*-type of embryogenesis.

Engler (1888) and Krause (1930) placed *Theropogon* Maxim. in the tribe Convallarieae subtribe Convallarine with *Convallaria* L. (Europe, eastern North America, and eastern Asia), *Speiranthe* (= *Speirantha*) Baker (eastern Asia), and *Reineckea* Kunth (Japan), whereas Hutchinson (1934, 1959) circumscribed the same genera in his tribe Convallarieae without the use of a subtribe. The berry fruit of *Theropogon* is the chief character used for this tribal association. Because the vascular floral anatomy of the berry-fruited genus *Convallaria* has been previously presented (Utech and Kawano, 1976), this presentation of the vascular floral anatomy of *Theropogon* and subsequent comparison to *Convallaria* are desirable for classical tribal evaluation.

MATERIALS AND METHODS

For observation a series of buds through mature flowers of *Theropogon pallidus* were selected from excess material on unmounted herbarium sheets (Nepal: Thare-Dunche, 200 m, 25 June 1960, Kanai and Shakya 672,012, TI). The flowers were rehydrated in 4% KOH, dehydrated in an ethanol series to 70% ethanol, and passed through the usual TBA-wax series (Johansen, 1940; Sass, 1958). Fifteen flowers of varying age (buds to fruits) were sectioned between 12 to 16 μ and stained in safranin and methylene blue. Several of the rehydrated flowers that were cleared in the basic solution were stained in 1% fuchsin (Fuchs, 1963) to show the total vasculature.

This report presents the pattern of floral vascularization from the pedicel to the tips of the stamens and stigma, and does not imply either ontogenetic nor teleological development in the manner of presentation. Cross-sectional, projected cross-sectional, and roll out longitudinal diagrams are presented for this species (Figs. 2-4). This illustrative style of vascular presentation parallels that of our previous floral vascular studies (Utech, 1978a, 1978b, 1978c, 1978d, 1978e). Table 1 compares the vasculature *Theropogon* and *Convallaria*.

OBSERVATIONS

Pedicle Vascularization

The inflorescence of *Theropogon pallidus* is a simple, erect raceme that usually attains a height of 2.0 to 4.0 dm (average 3.1 dm). The flowering raceme portion usually spans the upper one-third of the inflorescence. Each of the five to eighteen flowers is subtended by a linear to subulate bract, which averages 1.7 cm in length (range 1.0–2.4 cm), and by a smaller linear bracteole, which average 0.6 cm (range 0.4–0.9 cm) in length. Both the bract and the bracteole are persistent (Fig. 1D). Each bract has a single, unbranched midvein and two lateral veins, whereas the bracteole has a single midvein.

There is a single flower per node (Fig. 1D). The departing pedicels clearly exhibit a spiral (1/3) phyllotaxy around the raceme axis. At each point of pedicel attachment, the pedicels are triangular in cross-section, and recurved downwards. In cross-section the flowering pedicel lacks a sclerenchymatous sheath around the pedicel vasculature, however, a sclerenchymatous sheath is associated with the pedicel vasculature in the fruiting pedicel. The pedicel is gibbose below the receptacle.

For most of the flowering pedicel's length, there are three large vascular bundles. Near the base of the flower, that is, the inverted receptacle, the pedicel is circular in cross-section (Figs. 2A, 3A), which represents a shape change from the lower triangular cross-section. Near the receptacle base each of the three pedicel bundles undergoes a radial division that results in three pairs of pedicel bundles (Figs. 2B, 3B).

Tepal and Stamen Vascularization

The six reddish-rose tepals of the inverted campanulate flower are free to their bases. There is no connate floral tube as in *Convallaria* (Utech and Kawano, 1976). In *Theropogon* a slight basal size difference occurs between the three outer tepals and three inner tepals. The outer tepals are thicker basally (Figs. 2C–D, 3C–D). The ovate to subacute tepals are basally fleshy and enlarged throughout their midrib regions. From the middle of the tepals to their bases, the outer and inner tepals are broadly imbricated. During anthesis the tepal tips which have adaxial papillae are outwardly recurved. Both tepal cycles have a single midrib vein, that is, an outer tepal bundle (OT) in each of the three outer tepals and an inner tepal bundle (IT) in each of three inner tepals. Weakly differentiated nectiferous cells occur on the lower inner bases of all six tepals.

Morphological elaboration occurs in the inverted receptacle as the tepals and stamens are freed. The transition from the circular pedicel to a broadly six-lobed receptacle is sudden (Figs. 2B–D, 3B–D). The

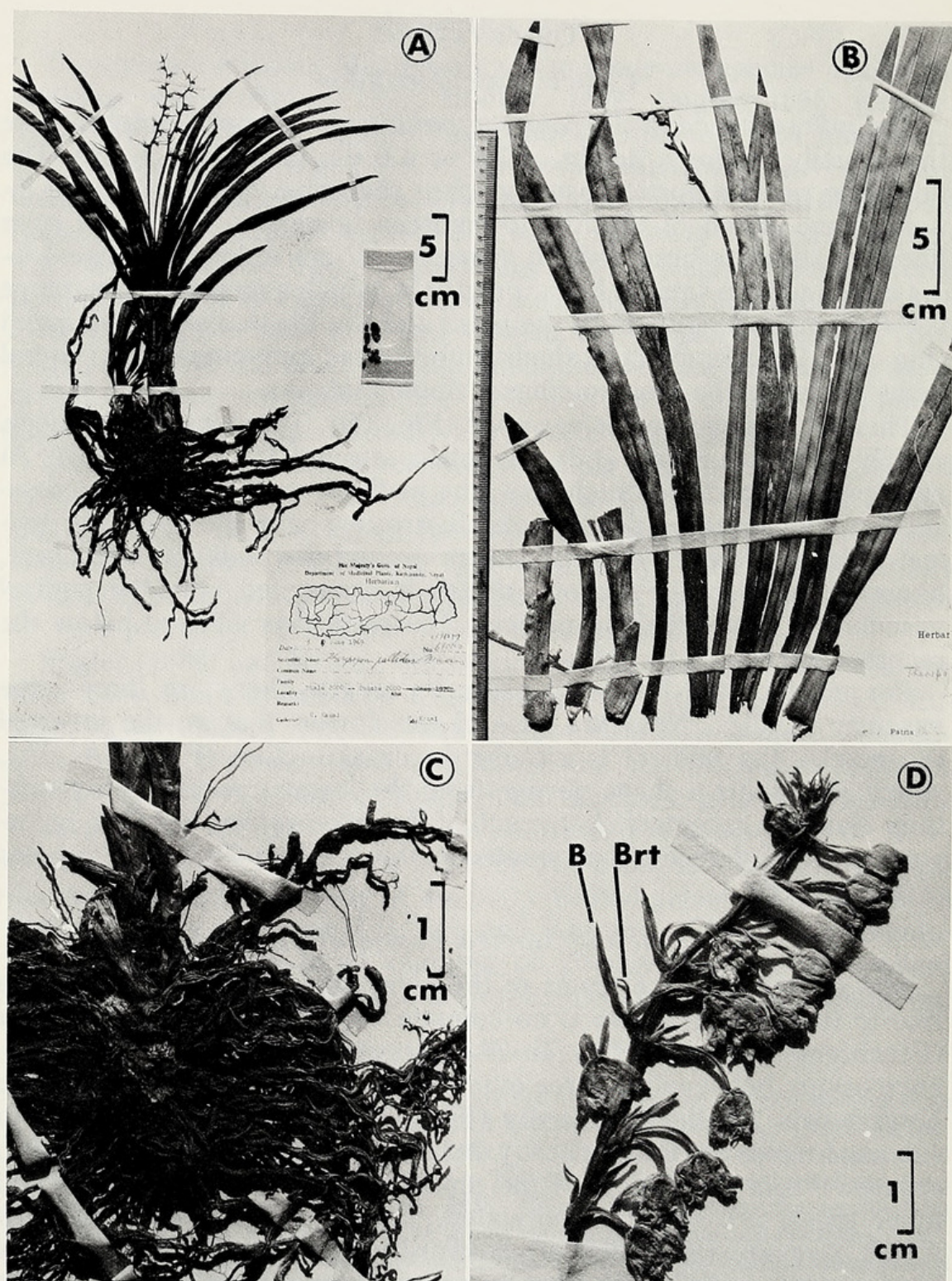


Fig. 1.—Herbarium specimens of *Theropogon pallidus* Maxim. showing gross vegetative and floral morphology. A) Specimen from Nepal showing the root and shoot systems (Kanai 610,100 TI). B) Size gradient in basal leaves, prominent median costa evident, leaves longer than inflorescence. C) Thick fibrous root from stout rhizome. D) Upper flowering raceme showing noding, campanulate flowers each subtended by both a bract (B) and a bracteole (Brt). (Scale indicated) (Photographs courtesy of the University Museum, University of Tokyo, Japan, TI).

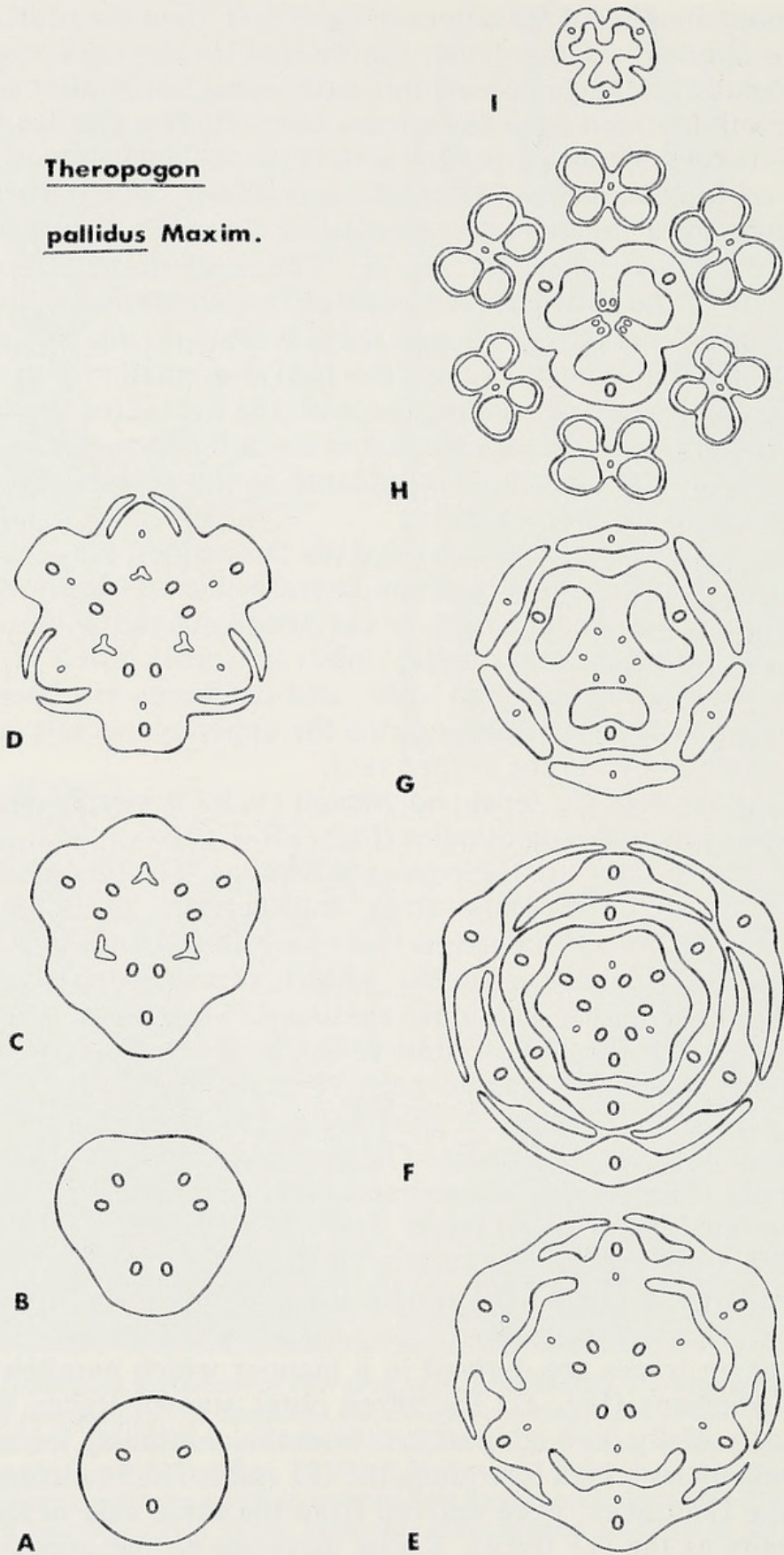
lateral, inner margins of the outer are freed first, then the adaxial zones along the midribs. At this level, the midribs of the outer tepals are fleshy (Figs. 2D, 3D). Following this outer tepal initiation, the gynoecium is partially freed from the adnate outer stamen and outer tepals along the outer (dorsal) carpellary wall (Figs. 2E, 3E). Shortly thereafter all six tepals are freed from the gynoecium. A shallow filament tube results from the lateral connation of the filament bases which surround the gynoecium (Figs. 2F, 3F). The depth of the filament tube corresponds to the distributional zone of the nectiferous cells on the lower, adaxial tepal bases. Though there is limited epitepaly between the tepal and the stamen cycles, the lateral connation between the dilated filament bases in conjunction with the nectiferous tepal bases probably has a functional significance in the pollination of this species. In *Convallaria*, the filaments are adnate to the connate floral tube, and there are no nectiferous cells.

The six stamens, the three outer and the three inner, are equal, much shorter than the tepals, incurved and laterally dilated (fleshy) throughout. The filaments are attached to the lower abaxial anther surface between the divergent outer anther lobes (introrse). Each of the yellowish brown anthers has four cells, and dehisces via lateral slits. The anthers are tilted inwards and ring the upper gynoecium. Connective tips extend beyond the anther sacs.

Vascularization of the tepal and stamen cycles is simple and direct, and involves sets of fusion bundles (Figs. 2B–E, 3B–E, 4). At the base of the receptacle there are three pairs of bundles. The three outer tepal medians (OT) are formed first along radii between the three bundle pairs via fusing branches derived from each pair member. The inner tepal medians (IT) have a similar pattern of origin from the lower receptacle bundle pairs. The inner median (IT) formation involves radially derived branches followed by fusion between different members of the lower receptacle bundle pairs (Fig. 4). Both the OT and IT medians are fusion products. A given OT is 120° from another OT, and 60° from an adjacent IT bundle. The formation and departure of the tepal supply is extremely horizontal within the expanded receptacle. Each free tepal has a single trace. There is no further radial division basally or within the laminal surface to form tepal laterals. The tepal traces are large in cross-section with the xylem portion broadly two-armed.

The stamen traces are derived in a manner which parallels that of the tepal medians (Fig. 4). The three outer stamen traces (OS) are formed via radially derived branches from the continuing lower receptacle bundle pairs which fuse along the OT radii. The branches, which formed the OS traces, were derived from the same side of the lower bundle pairs as the OT traces. Radial divisions on the opposite sides

Theropogon
pallidus Maxim.



of these pair bundles and fusions along the IT radii result in the formation of the three inner stamen traces (IS) (Fig. 4). All six stamen traces depart horizontally through the receptacle soon after their formation. Both the tepal and stamen vascularization originates within a limited vertical distance. The various sets of tepal and stamen bundles are derived from the three, lower, axial, receptacle pairs. These same axial bundle pairs continue and establish the total gynoeceal vascular supply.

Gynoeceal Morphology and Vascularization

The ovoid to subglobose gynoeceium in *Theropogon pallidus* is non-stipitate, tricarpellate, and unilocular terminally (Figs. 2D–G, 3D–G). In the various floral stages examined, raphides were not observed, though they were common in *Convallaria* (Utech and Kawano, 1976). Though dorsal grooves are lacking, there are longitudinal septal grooves in the upper gynoeceium which continue up the complete length of the narrow elongated style (Figs. 2H–I, 3H–I). However, these upper septal grooves showed no evidence of forming septal nectaries. Though the fruit is a black, fleshy berry, there are persistent gynoeceal indications of weakened zones along the septa. The anther tips attain approximately the same height as the upper ovary. The style length including the minute stigma is approximately twice that of the flowering ovary.

As the outer tepals are cut off (Figs. 2D–E, 3D–E), three fusion dorsals (D) are formed like the OT and OS traces via radial branches

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Fig. 2.—Serial cross-sections of *Theropogon pallidus*. A) Circular midpedicel section with the three-bundled configuration. B) Trilobed upper pedicel with the six-bundled configuration which is due to radial divisions. C) Six-lobed lower receptacle showing the formation of the fusion outer (OT) and inner (IT) tepal median bundles from the six, continuous, axial bundles; the OT bundles are formed at a lower level than the IT bundles. D) Upper receptacle showing the formation of the fusion outer (OS) and inner (IS) stamen traces from the six continuing axial bundles, both the OT and OS bundles and the IT and IS bundles share a common radii. E) Receptacle above D showing the tepal and stamen formation, fusion dorsals (D) are present along the OT-OS radii. F) Lower gynoeceium surrounded by a laterally connate staminal tube, both tepal cycles freed; each fleshy tepal has a single unbranched fusion bundle; dorsals in peripheral position; fusion septal axials (SA) formed between the inner paired sets of ventrals (V) along the IT-IS radii. G) Midgynoeceal section showing the fused central placentae; the locules have opened transverse to the OT-OS-D radii; the septal axials (SA) have terminated; the free filaments are laterally dilated; the tepal cycles have been omitted. H) Upper gynoeceal section showing the centrally free placentae; ventrals (V) present on the inner septal wing margins; six large anthers surround the upper gynoeceium; the tepal cycles have been omitted. I) Mid-stylar section showing the tripartite, unilocular cavity; septal margins grooved; the dorsals (D) evident and unbranched; both the tepal stamen cycles have been omitted.

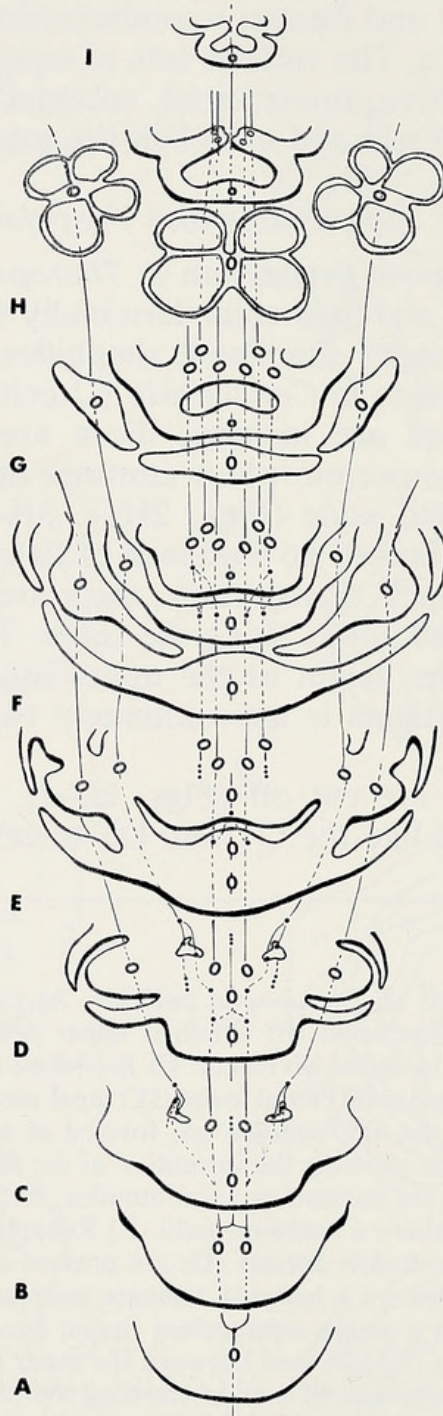
Theropogon pallidus Maxim.

Fig. 3.—*Theropogon pallidus*, cross-sections of Fig. 2 after transformational projections with selected vascular bundles connected. The letter sections correspond to those in Fig. 2.

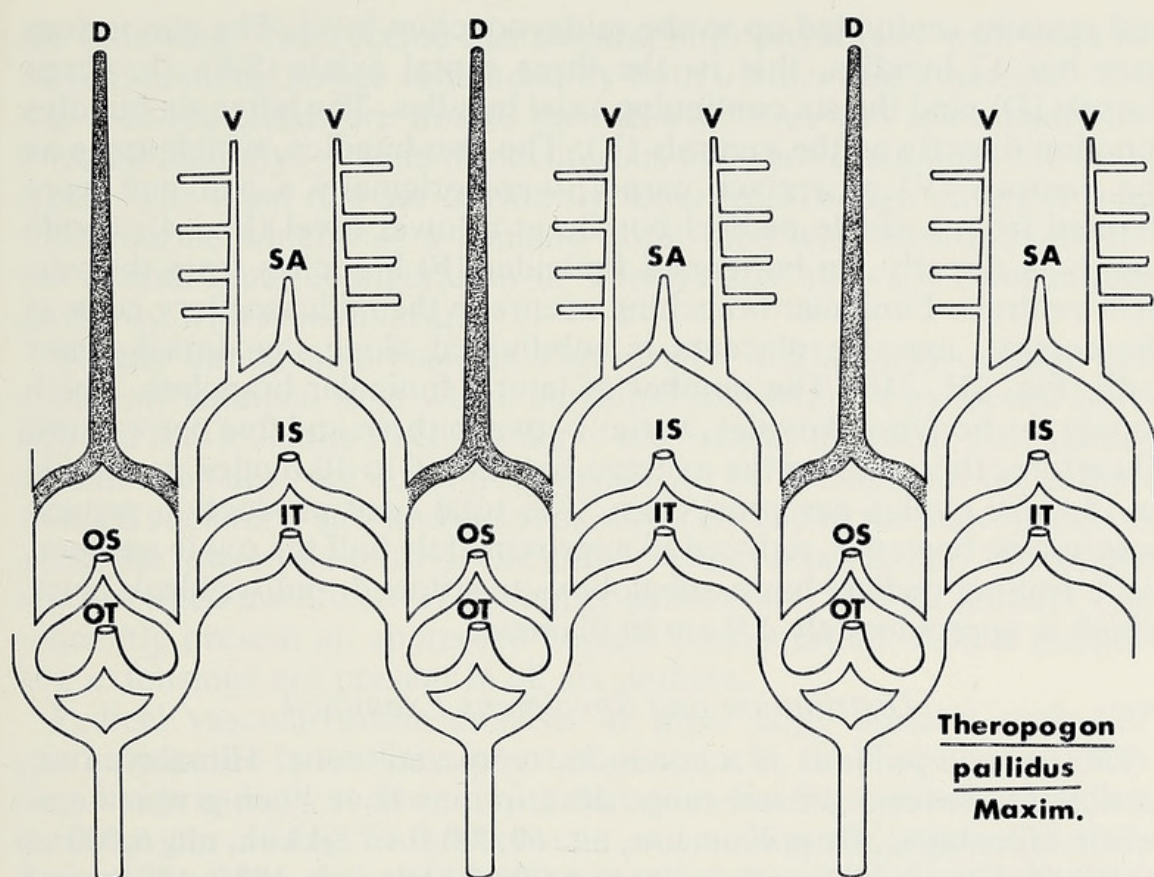


Fig. 4.—Roll-out longitudinal summary diagram for the floral vasculature of *Theropogon pallidus*. The various text discussed bundles have been coded: OT = outer tepal, IT = inner tepal, OS = outer stamen, IS = inner stamen, D = dorsal, SA = septal axial, and V = ventral.

from the inner axial bundle pairs, which fuse (Figs. 2D–E, 3D–E, 4). There is a direct, horizontal movement to the carpellary periphery of the newly formed dorsals under the unopened locules. The three dorsals (D) remain in this peripheral position to the tip of the style without branching or fusion.

Following the formation of the three dorsals (D), the freed gynoecium in cross-section is smoothly six-lobed. Along the IT-IS radii another set of three fusion bundles is formed. These three fusion bundles are the septal axials (SA). Their location is slightly more peripheral than that of the six remaining central axial bundles. Though the unbranched vertical course of the three septal axials (SA) is limited, the septal axial formation is similar to that of the dorsal (D) (Fig. 4). A given dorsal (D) is 60° from an adjacent septal axial (SA) (Figs. 2, 3F).

The simultaneous opening of the three locules is transverse to the dorsal-center radii (Figs. 2G, 3G). The central placental region is large

and remains undivided up to the midgynoecium level. The gynoecium base has 12 bundles, that is, the three septal axials (SA), the three dorsals (D), and the six continuing axial bundles. The latter six bundles function directly as the ventrals (V). The two bundles, which serve as the ventrals (V) of a given carpel, were originally a pair and were derived from a single pedicel bundle at a lower level (Fig. 4). Ovule supply is directly via horizontal funicular (F) branches from the vertical ventrals. Funicular branching occurs in the midcarpellary zone as the central, massive placenta is subdivided along the dorsal-center radii (Fig. 2H, 3H). The number of lateral funicular branches, which supply the horizontal ovules, varies between three and five per ventral. Therefore, there are on the average between 6 to 10 ovules per locule or 18 to 30 ovules per gynoecium. The total seed production per gynoecium is, however, reduced to approximately half the ovule number. Each fruiting pedicel has a subglobose to trilobed, pulpy, black berry which is approximately 1.0 cm in diameter.

Distribution and Specimens Examined

Theropogon pallidus is a common, temperate zone, Himalayan region plant. Several general range descriptions have been given—temperate Himalayas, from Kumaon, alt. 60,000 ft to Sikkim, alt. 6,000 to 10,000 ft, Khasia Hills, alt. 5,000 to 6,000 ft (Hooker, 1875, 1894), and Himalaya: Kumaon, Nepal, Sikkim, Khasia Hills, Tibet (Kihara, 1953). Nair and Sharma (1965) observed pollen from plants collected in Cherrapunji (Assam).

The following cited specimens were observed at the University of Tokyo (TI) in 1975. Besides detailed itineraries and maps, floristic compilations of the University of Tokyo's botanical expeditions to the eastern Himalayas are available (Hara, 1966, 1971; Ohashi, 1975).

Theropogon pallidus (Wall. ex Kunth) Maxim., in Bull. Acad. Sci. St. Petersb., 15:89. 1871.

Ohiopogon pallidus Wallich (Cat. no. 2138 (1829)) ex Kunth, Enum. 5:300. 1850.

Specimens examined—BHUTAN: Dugye Dzong to Gunitsaura, elev. 2900 m, 21 June 1966, Nishioka s.n. (TI). Gunitsura to Cheka, elev. 2900 m, 24 June 1966, Nishioka s.n. (TI). NEPAL: Tare to Dunche, elev. 200 m, 25 June 1970, Kanai and Shaky 672,012 (TI). Gosinkund to Dhunche, 2100 m, 3 June 1969, Hara, Kanai, Kurosawa and Ohashi 69,614 (TI). Gosinkund, Ramche (1800 m) to Thare (2200 m), 2 June 1969, Hara, Kanai and Kurosawa 69,615 (TI). Thare, elev. 6000 ft, on shady place on mossy rock, flowers pink, 10 June 1969, Samen and Bista 13,032 (TI). Thare (2000 m) to Dunche (200 m), 3 June 1969, Kanai 670,100 (TI). Kalingchok, Thala (2050 m) to Tale Bisauna (2750 m), 10 September 1970, Kanai, Chuma and Nagano 674,258 (TI).

SUMMARY AND CONCLUDING REMARKS

The floral vascular anatomy of *Theropogon pallidus* has been presented, and the most salient features of this monotypic species include

the following. The raceme has a spiral (1/3) phyllotaxy with each inverted, nodding flower subtended by both a bract and bracteole. This six, rose-red tepals are free to their fleshy bases and are broadly imbricated laterally. A zone of nectiferous cells adaxially lines the outer tepals. The tepal tips are outwardly recurved. Though different from *Convallaria*, which has a connate floral tube with adnate filaments, the overall tepal configuration in *Theropogon* shows a campanulate similarity with *Convallaria*.

Basally the filament bases in *Theropogon* are laterally connate into a shallow staminal tube which surround the inverted gynoecial base. Beyond this level the freed filaments are broadly dilated. This stamen modification does not occur in *Convallaria*. In *Theropogon* the anthers dehisce via lateral slits and are abaxially attached to the short filaments along the lower one-third of the anther length (dorsifixed). The anther tips are tilted inwards over the upper gynoecium. The six anthers consequently present an appressed conical configuration. Apical connective extensions are present in all six anthers.

Pedicle vascularization consists of three large bundles each 120° apart. Near the base of the inverted receptacle, the three pedicle bundles divide radially to form a ring that contains three pairs of bundles. It is via gap-closing fusion between and among the pairs of radially derived branches that the tepal, stamen, and gynoecial vasculature is established. The three outer tepal bundles (OT), the three outer stamen traces (OS) and the three dorsal bundles (D) are gap-closing fusion products formed along the radii, which bisect the three lower pedicle bundles. The three inner tepal bundles (IT) and the three inner stamen (IS) bundles similarly are gap-closing fusion products, but their radii of formation are 60° from those of the outer whorl bundles. The six ventrals (V), that is, the three continuing, unfused bundle pairs, supply the ovules via simple, horizontal funicular (F) branches.

Table 1 presents a morphological and anatomical comparison of *Theropogon* and *Convallaria*. Though comparative emphasis is on the floral vascular anatomy of both genera, other vegetative characters are compared. Additional data on *Convallaria* for Table 1 have been taken from Utech and Kawano (1976), Streveler (1966), Stenar (1941, 1953), and Björnstad (1970). The gross morphological differences between *Theropogon* and *Convallaria* include the following. Mature flowering specimens of *Theropogon* have numerous elongate grass-like leaves with prominent costa, massive fibrous roots from a stocky rhizome, and flowers, which are subtended by both a bract and a bracteole. The three similar, but disjunct species of *Convallaria* (*C. majalis* L., *C. keiskei* Miq., and *C. montana* Green), on the other hand, have flowering individuals with long petiolate, paired leaves, an elongate rhizome with scattered roots, and a single, simple bract, which subtends each inverted flower.

Table 1.—*Floral comparison between Theropogon and Convallaria.*

Character	<i>Theropogon pallidus</i>	<i>Convallaria</i> spp. (Utech and Kawano, 1976; and as indicated)
Number of species and range	Monotypic, endemic to the Himalayan region of Nepal and India	Three temperate species; Europe, eastern U.S. and eastern Asia (Strevelar, 1966)
Root system	Stout rhizome with numerous, thick, and clustered roots	Elongate rhizome with numerous, thin and scattered roots
Sheath leaves	Basal, two-six, membranaceous	Basal, two-six, membranaceous
Main leaves	Annual; 12–16, distichous, grass-like, narrowly elongate leaves with prominent median costa; parallel-veined (Fig. 1) Larger leaves Length: 15.0–45.0 cm; Mean: 36.0 cm Width: 0.6–2.0 cm; Mean: 1.4 cm L/W Ratio: 25.70	Spring ephemeral; typically leaves paired; petiolate; strongly net-veined (Streveler, 1966—composite) Larger leaves Length: 25.0–45.0 cm; Mean: 34.0 cm Width: 6.0–11.5 cm; Mean: 7.5 cm L/W Ratio: 4.05
Inflorescence	Terminal raceme with 5–18–(20) inverted flowers; raceme central and axial to imbricated leaves; raceme shorter than leaves	Terminal raceme with (3)–5–12–(20) inverted flowers; raceme outside and lateral to paired leaves; raceme longer than leaves
Flowers	Trimerous, hypogynous, bisexual, actinomorphic	Trimerous, hypogynous, bisexual, actinomorphic
Bract	Present; linear-subulate, 3-nerved, persistent, one per node (Fig. 1) Length: 1.0–2.4 cm; Mean: 1.7 cm	Present; lanceolate, 1-nerved, persistent, one per node (Streveler, 1966—composite) Length: 0.6–1.5 cm; Mean: 0.9 cm
Bracteole	Present; linear, 1-nerved, persistent, one per node Length: 0.4–0.9 cm; Mean: 0.6 cm	Absent
Pediceal	Down turned during anthesis; triangular in cross-section at node, circular at receptacular base; sclerenchyma sheath present in fruit	Down turned during anthesis; triangular in cross-section at node, circular at receptacular base; sclerenchyma sheath present in fruit

Table 1.—(Continued)

Character	<i>Theropogon pallidus</i>	<i>Convallaria</i> spp. (Utech and Kawano, 1976; and as indicated)
	Vascularization: three large compound bundles each with broadly V-shaped xylem; 120° apart	Vascularization: six compound bundles (3 large + 3 small) each 60° apart
Perianth (OT = outer tepal) (IT = inner tepal)	Pale pink to reddish rose; non-persistent; fragrant (?); campanuloid, tepals free to base and broadly imbricated; tepal tips with adaxial papillae and re- curved outwards; lower adaxial base of outer tepals with a zone of nectiferous (secretory) cells OT: 1-nerved (fusion) IT: 1-nerved (fusion) No tepal laterals OT and IT are fusion bundles of receptacular origin formed among and between the three pedicel bundles (Figs. 2-4) Tepal and stamen traces free from each other	Creamy to yellowish white with light green on the tepal tips; non-persistent; sweet scented; campanu- late, tepals fused into floral tube; tepal tips free and recurved outwards; necti- ferous cells absent from the inner surface of the floral tube OT: 1-nerved (fusion) IT: 1-nerved (fusion) No tepal laterals OT and IT are fusion bundles of receptacular origin formed from the six compound, axial pedicel bundles Tepal and stamen traces free from each other
Stamens (OS = outer stamen) (IS = inner stamen)	Six filaments free from the tepals and gynoecium to their bases; free filaments broadly dilated; filament bases laterally connate into a shallow staminal tube; filament cycles equal Anthers six, yellowish brown; abaxially attached to filaments within lower ½ length (dorsifixed); anthers tilted forward to surround the upper gynoecium; lateral de- hiscence (introrse); 2-sacs, 4-celled, fibrillar thicken- ings on endothelial cells; connectives apically extended	Six filaments adnate to a floral tube for ca. ½ the tube length; filaments ovoid to circular in cross- section; short, but equal cycle lengths Anthers six, yellow; abaxially attached to filaments within lower ½ length (dorsifixed); anthers tilted forward to surround the upper gynoecium; lateral de- hiscence (introrse); 2-sacs, 4-celled, fibrillar thicken- ings on endothelial cells; no apical connective extensions

Table 1.—(Continued)

Character	<i>Theropogon pallidus</i>	<i>Convallaria</i> spp. (Utech and Kawano, 1976; and as indicated)
Gynoecium (D = dorsal) (V = ventral) (P = placental) (SA = septal axial) (F = funicular)	Both OS and IS bundles are fusion products formed within the receptacle among and between the three pedicel bundles which divide	Both OS and IS bundles are fusion products formed within the receptacle from the six axial pedicel bundles
	Tricarpellate, syncarpous, non-stipitate (sessile), unilocular terminally subglobose; septal groove (indentation) present, but no septal gland, no dorsal groove	Tricarpellate, syncarpous, non-stipitate (sessile), unilocular terminally, globose; no dorsal or septal grooves or glands present
	Rhapides not observed	Rhapides present
	Locules open perpendicular to the dorsal-center radii; basal septa fused centrally and freed in lower levels prior to ovule attachment	Locules open perpendicular to the dorsal-center radii; basal septa fused centrally and freed in mid-ovary above lower ovule tier attachment
	Gynoecium trilobed in cross- section (Figs. 2–3)	Gynoecium circular in cross- section
	Placental epidermis weakly stigmatoidal, but con- tinuous into style	Placental epidermis strongly stigmatoidal and con- tinuous into style
	Style columnar; stigma minute; trilobed in cross-section	Style columnar; stigma capitate; circular in cross-section
	Embryogenesis: <i>Polygonum</i> -type (Stenar, 1953)	Embryogenesis: <i>Allium</i> -type (Stenar, 1941; Björnstad, 1970)
	Ovule number—average of eight per locule	Ovule number—average of four per locule
	Fruit: berry; black, subglobose to shallowly trilobed due to persistent septal grooves; inde- hiscent, pulpy; style per- sistent	Fruit: berry; red, globose, indehiscent; no dorsal or septal fruit markings, pulpy, style deciduous with scar evident
	Dorsals (D) fusion products, unbranched, no terminal fusion, ends in upper style	Dorsals (D) fusion products, unbranched, no terminal fusion, ends in upper style

Table 1.—(Continued)

Character	<i>Theropogon pallidus</i>	<i>Convallaria</i> spp. (Utech and Kawano, 1976; and as indicated)
	Ventral plexus: simple ascending ventral (V) supply with direct, horizontal funicular (F) supply; two ventrals (V) per septum	Ventral plexus: simple ascending ventral (V) supply with parallel, ascending placental bundles, funicular (F) traces associated (1:1) with placental (P) bundles; two ventrals (V) per septum, four or more placentals per septum
	Septal axial (SA): one per septum; present in lower levels only, absent as locules open; no inter-connection to ventral supply	Septal axial (SA): two simple bundles which may fuse per septum; terminates in upper gynoecium without vascular inter-connection to ventral supply
Chromosome number	Unknown	$2n = 38$ (Strevelar, 1966; Fedorov, 1969; Moore, 1973).

In both *Theropogon* and *Convallaria*, the flowers are nodding, but there are significant tepal and stamen differences between the two genera. In *Theropogon* the broadly imbricated tepals are free to their bases and have a basal adaxial nectiferous zone, whereas in *Convallaria*, a fused floral tube is present and there is no nectiferous tissue associated with the perianth. The tepal tips in both genera are outwardly recurved. The filaments in *Theropogon* are free to their bases and there are laterally connate for a short vertical distance into a shallow filament tube. In *Convallaria*, on the other hand, the filaments are adnate to the surrounding floral tube for most of their filament length. In neither genus is there any evidence of tepal or staminal adnation to the outer gynoecial wall. Whereas the "lily-of-the-valley" scent of *Convallaria* is well known, it was impossible in this study, because of the material used, to determine whether or not *Theropogon* had a scent. None has been reported.

Significant differences also occur between the gynoecia of *Theropogon* and *Convallaria*. In the former, septal grooves, which persist into the fruit, are present, whereas these carpellary indentations are lacking in *Convallaria*. The species of *Convallaria* have abundant raphides distributed throughout the mature pericarps, septal wings, and funicular stalks. No raphides were observed in *Theropogon*. Though

both genera have simple fusion dorsals, there are differences in their ventral supplies. A fusion septal axial occurs only basally in each septum of *Theropogon*, whereas two simple ascending septal axials, which may or may not fuse, occur in each septum of *Convallaria*. Funicular branches depart directly and horizontally in *Theropogon* from the simple ascending ventral traces. In *Convallaria*, on the other hand, the ventral supply is more complicated. Besides the simple ascending ventral bundles, two per septum, placental bundles branch from these ventral bundles and ascend parallel to them. It is from these parallel ascending placental bundles that the funicular traces are derived in *Convallaria*. The average ovule in *Convallaria* is 12, whereas the average number in *Theropogon* is 24. Embryogenesis also differs between the two genera—*Theropogon* has a reported *Polygonum*-type (Stenar, 1953), whereas *Convallaria* has a reported *Allium*-type (Stenar, 1941; Björnstad, 1970). Though the chromosome number of *Theropogon* is still unknown, comparison to the repeatedly verified count of $2n = 38$ for *Convallaria* (Strevelar, 1966; Fedorov, 1969; Moore, 1973) should prove interesting.

Though there are superficial similarities in the inflorescence and floral vasculature, the overall dissimilarities far outweigh the similarities (Table 1). Furthermore, whereas many of the similarities (Table 1) are basic and widespread throughout the Liliaceae Alliance (Anderson, 1940), other similarities, such as the floral shape and berry fruit, which has a different morphology and pattern of vascularization in *Theropogon* and *Convallaria*, are undoubtedly the result of convergent evolution. Parallel observations on the floral vascularization and carpel morphology in *Speiranthe* and *Reineckea*, which are Englerian tribal cohorts, are needed to fully assess the berry as an evolutionary unit and as a taxonomic unit in the Convallarieae.

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