

BIOSYSTEMATIC STUDIES IN *STENANTHIUM*
(LILIACEAE: VERATREAE) II. FLORAL MORPHOLOGY,
FLORAL VASCULAR ANATOMY, GEOGRAPHY AND
TAXONOMY OF THE MEXICAN *S. FRIGIDUM*
(SCHLECHT. & CHAM.) KUNTH

FREDERICK H. UTECH
Associate Curator, Section of Botany

ABSTRACT

The floral morphology, continuous pedicel to stigma floral vascularization, distribution and taxonomy of *Stenanthium frigidum*, a bulbous lily confined to the Trans-Mexican Volcanic Belt, are presented. The perfect, protandrous flowers with bilobed or v-shaped tepal nectaries are arranged in andromonoecious panicles. Raphide idioblasts were observed in the upper gynoecium and recurved stylar arms. Total floral vascularization is derived from three, compound, lower pedicel bundles. Both outer and inner tepallary and staminal bundles as well as dorsal vasculature are formed above the level at which the ventrals and ovular supplies are established due to an inferior gynoecium with a central capillary hole and epigynous perianth. Within each septal arm, a pair of septal laterals fuse with a pair of ventrals from which they had a common origin. As these septal laterals re-associate with the ventrals, septal indentations occur. The bitegmic, camplyotropous ovules develop into flat, winged seeds.

INTRODUCTION

Four *Stenanthium* species are currently recognized: *S. occidentale* (western North America), *S. gramineum* (eastern North America), *S. sachalinense* (eastern Asia) and *S. frigidum* (central Mexico). Of these, the tall, showy, purplish-black flowered *S. frigidum* (Schlecht. & Cham.) Kunth has the most southern distribution, along with representatives of *Schoenocaulon* (= *Sabadilla*), of the wide-ranging, northern hemispheric Veratreae (Baker, 1879; Engler, 1889; Krause, 1930; Zimmerman, 1958; Melchior, 1964; Hutchinson, 1973) with nearly 80 species world-wide (Dahlgren et al., 1985).

Though poisonous alkaloids are commonly known in the Veratreae (Kupchan et al., 1961; Williaman and Schubert, 1961; Hegnauer, 1963), the only notes concerning such occurrences in *S. frigidum* are "that natives of Mount Orizaba know it to be dangerous to the horses that bite it" (Schiede, 1829), "folia pecoribus lethalia" (Bentham, 1839) and "it may be supposed to furnish a part of the venomous sabadilla seeds of commerce, from which veratria is prepared" (Lindley, 1846). Several common names have been used—"sevoeja" (Schiede, 1829; Lindley, 1849a), "cebadilla de tierra fria" (Lindley, 1849b), "cebolleta" (*Hinton 4612 MO*), "cebolleja" (*Balls 4886 UC*), "flores angostas" (Conzatti, 1947) and "cebadilla" (Sanchez, 1980). During the Mexican botanical exploration of the middle of the last century, the same illustration was used three times by Lindley (1846, 1849a, 1849b) to promote the plant's economic and horticultural value. The species has been figured recently in Sanchez (1980). Chromosome counts are unknown for the species.

This second paper in a series on the genus *Stenanthium* (Utech, 1987) reports

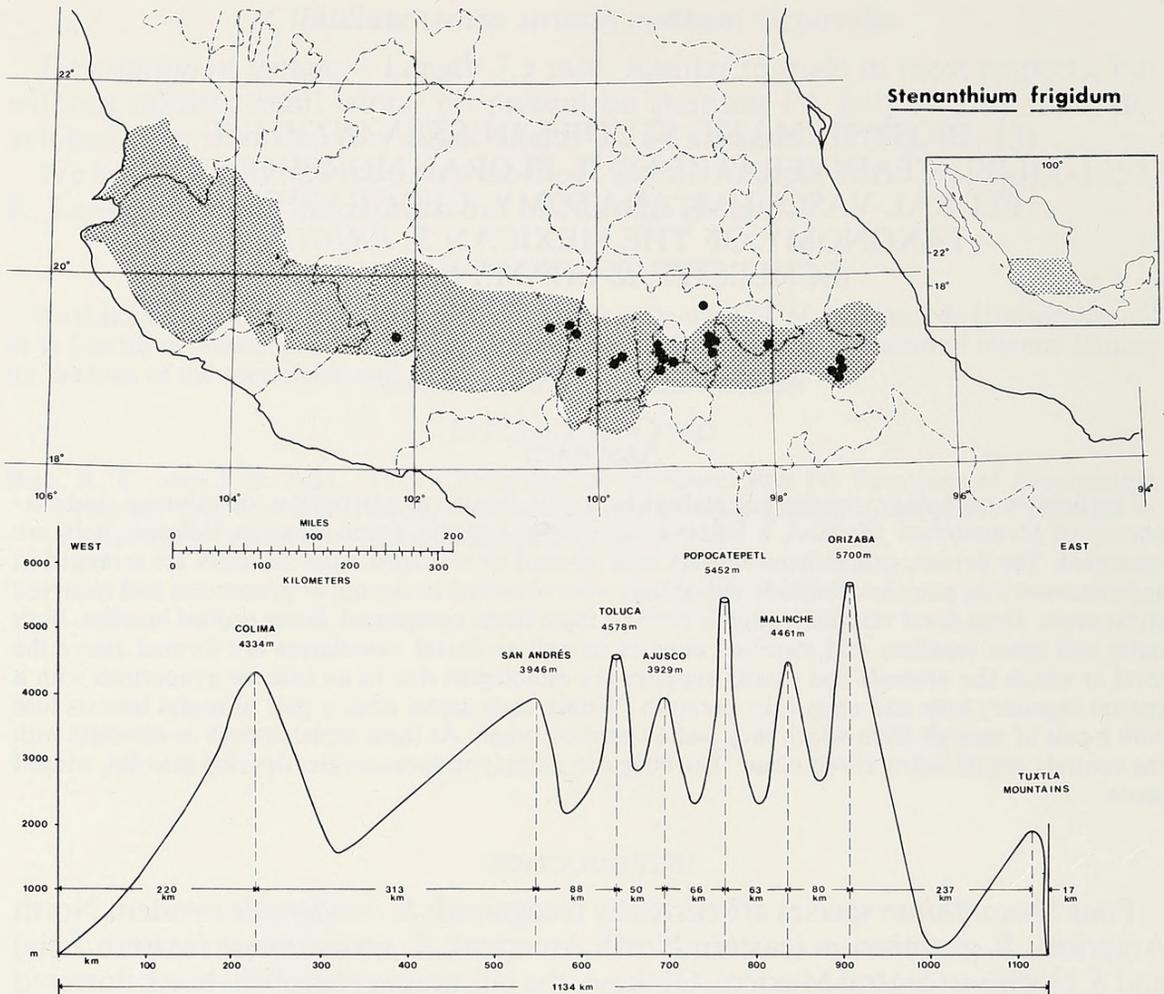


Fig. 1.—Herbarium specimen distribution of *S. frigidum* in the Trans-Mexican Volcanic Belt (Eje Volcanico Transversal) (shaded area). The projection which summarizes the maximum elevation between 18° and 22°N latitude is based in part on Clausen (1959).

on the Mexican species, *S. frigidum*, with emphasis on the inflorescence, flower and the origins of the tepallary, staminal and dorsal bundles for comparisons within the genus and the tribe Veratreae.

MATERIALS AND METHODS

Floral material of *Stenanthium frigidum* fixed in FAA from Monte Rio Frio pass near Llano Grande, Mexico, was made available for this study by Dr. Hugh H. Iltis, University of Wisconsin-Madison (Iltis *et al.* 1085). Samples for standardized transverse (15) and longitudinal (5) paraffin sectioning (14–16 μ) of complete flowers of varying ages were stained in safranin-methylene blue (Johansen, 1940; Sass, 1958). Whole flowers were also cleared and stained in a NaOH-1% fuchsin mixture (Fuchs, 1963) as a check on the prepared sections. Vascular description, presentation and bundle coding follow Utech (1987). Herbarium collections used for distribution (Fig. 1) and floral morphometrics (Fig. 3) are cited in the taxonomic review.

OBSERVATIONS

General morphology. — *Stenanthium frigidum*, a robust, glabrous perennial herb, (4.5) 6.0–11.0 (15.0) dm tall, occurs in scattered clumps from large, 8.5–10.5 cm long by 3.5–5.5 cm wide, bulbs which are covered by a dense, coarse brown tunica.



Fig. 2.—Flowering habit of *S. frigidum*. A. Bracteated panicle with flowers in bud. The progressive reduction in the elongate bracts which subtends the lateral branches is evident. B. Panicle at anthesis showing several nodding terminal segments in which each flower is subtended by a bract as well as the lateral branches. Each flower within a lateral branch is subtended by a bracteole. (Photos A and B from negatives 163 and 159 respectively, courtesy WIS herbarium and vouchered by *Ittis et al.* 902.)

The 35–60 cm long by 1.0–1.5 cm wide, linear, bifacial, basal leaves are sheathing at their bases and gradually narrowed at both ends. The abaxial surfaces have anomocytic stomatal patterns which are generally lacking on the adaxial surfaces. The fusiform epidermal cells are six-sided. The few stem leaves are progressively reduced apically and intergrade into bracts (Fig. 2).

The simple, andromonoecious panicle occupies the upper 35–45% of the plant's height. Within the panicle, the (35) 45–75 (85) bisexual flowers are distributed over (3) 5–14 nodding lateral branches (racemes) and a dominant terminal segment (Fig. 3). Each branch is subtended by a bract. The lower bracts are always longer than the upper. Within each branch, each flower's pedicel is subtended by a scarious, linear bracteole. The lowest bracteole on a branch, like the lower bracts on the main axis, is always larger. Each of the (10) 15–25 flowers on the dominant terminal segment is subtended by a bract. Flowering begins at the base of the inflorescence and proceeds outwards in the lateral branches and upwards in the terminal segment. Maximum anthesis is between July and August.

Floral morphology.—The pendulous, deep fuscous brown to dark blackish maroon flowers on short, glabrous pedicels have long, narrowly acuminate tepals. The bases of the three outer tepals are wider than the inner tepals, though their lengths, 13–16 mm, are similar (Fig. 3). Adaxial, v-shaped tepal nectaries occur basally in both outer and inner tepals (Fig. 8C, D). At anthesis the flowers have

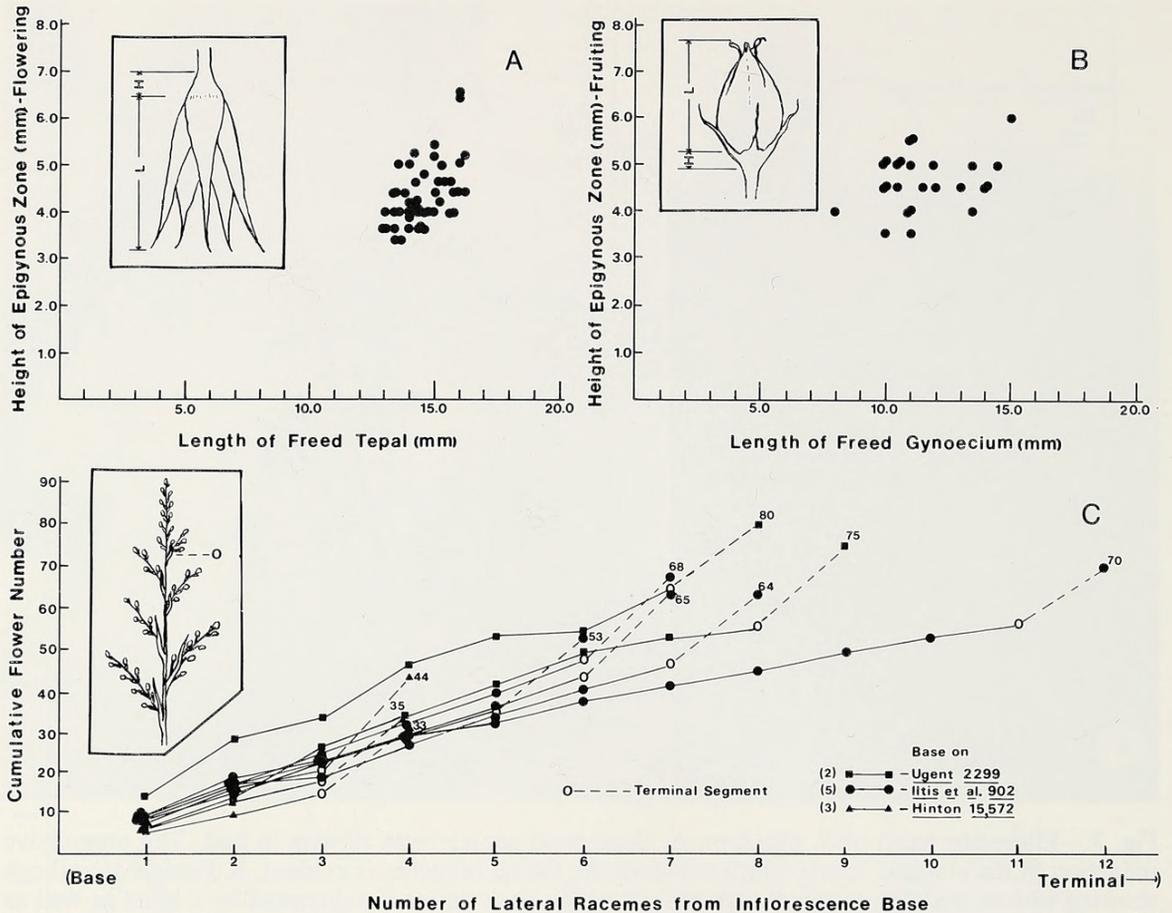


Fig. 3.—Floral and inflorescence patterns in *S. frigidum*. A. Comparison between the length (L) of freed tepals to height (H) of the flowering epigynous zone (mm). B. Comparison between the length (L) of the freed gynoecium (mm) to height (H) of the epigynous zone (mm). C. Inflorescence comparisons showing the total number of flowers and the degree of branching within the panicle. The connecting line indicates the cumulative flower number from one branched increment to the next with the terminal segment marked with an open circle.

a campanulate shape due to tepal spreading from the epigynous zone, but the tips are never reflexed. The six, subulate, glabrous filaments are 3.3–3.6 mm long, with little length differences between the outer and inner sets. The basifixed, extrorse anthers have a valvular dehiscence between the confluent thecae that opens into a reniform, peltate disc. Protandry occurs in *S. frigidum*, since both outer and inner anthers dehisce at the same time, and this is earlier than gynoecial maturity. The free styles and upper areas of the tri-carpellate gynoecium surpass the anther zone at maturity. The pedicels of the fruiting septicidal capsules are erect and elongated compared to anthesis. The ovoid capsules with persistent, withered tepals are 13.5–16.5 cm long and contain numerous winged seeds.

Floral vascular anatomy.—Pedicel vascularization: In transverse section, the flowering pedicels above their subtending bracts (bracteoles) are circular and have three large, centrally arranged bundles. Frequently several phloem caps per bundle are observed, attesting to the compound nature of these bundles. It is from these three bundles that the complete floral vasculature is established. The centers of these bundles are located on radii 120° apart and are designated the outer tepal radii.

Near the pedicel's mid-length, each of the three outer tepal radii bundles under-

goes a tri-partite radial subdivision, which results in three bundles. These divisions are not co-planar, but occur at different levels in a spiral pattern. Gaps along the outer tepal radii are created by the outward departure of the central bundle products from each of the three, tri-partite divisions (Fig. 4A). These departing bundles with normally arranged xylem (adaxial) and phloem (abaxial) remain free of other vasculature and establish the outer tepal medians (OTM). At this level, the pedicels have a triangular shape in transverse section with the corners on the outer tepal radii (Fig. 4B).

Immediately following the OTM bundle formation the two adjacent parental bundles undergo additional radial divisions. The two products closest to the gap depart outward with the OTM. There are three such sets of three bundles which correspond to the dorsal-composite bundle of Sterling (1982), and eventually establish the outer tepallary laterals (OTL), staminal (OS) and dorsal (D) vasculature (Fig. 4B–D).

The two remaining lateral products adjoining a gap following the radial divisions fuse with similar adjacent laterals along the inner tepal radii, which are located halfway between the outer tepal radii (Fig. 4B–D). These fusion bundles are formed at progressively higher levels in a spiral pattern. Each of these three, fusion bundles undergoes a tri-partite subdivision and radial division similar to that observed at a lower level among the three original bundles. The central bundle products of this second series of divisions depart along the inner tepal radii and become the inner tepal medians (ITM). The ITM and the two radial division products which depart with the ITM correspond to the “zwischenbündel” of Sterling (1982) and eventually establish the inner tepallary laterals (ITL) and staminal (IS) vasculature (Fig. 4D, E).

Six sets of three bundles each remain in peripheral positions until the upper epigynous zone. Tepallary, staminal and dorsal vasculature formation will be discussed later in a separate section.

Ventral vascularization: Following the formation and departure of the inner tepal medians (ITM) and associated lateral pairs, three bundle pairs remain along the inner tepal radii in the central area. It is from these bundle pairs that the complete ventral supply is established (Fig. 4C–F, 6A, B, 8A, B).

An inward rotation towards the inner tepal radii among the central bundle pairs occurs as well as a radial subdivision among these remaining bundles. As the locules open, the six inner most division products with reversed conducting elements depart inwards as a pair to establish the ventrals (V) (Fig. 4D, E, 5A, B). In the epigynous zone, two such ventrals (V) are associated with each locule. The remaining parental products may fuse along the inner tepal radii in a septal axial position. These bundles also divide if they fused and their resulting products have conducting elements which are reversed. There are three pairs of such bundles that could be called septal laterals (L) (Fig. 4E, F, 5A–C). They move inward following the same course as the ventrals. A given septal lateral (L) is re-associated with the same ventral (V) of common origin in the inner septal margins. Ovule supply occurs initially from the ventral (V) bundles in the lower epigynous zone, but in the upper freed gynoecium, the ventrals and laterals which fused in the ventral position continue to supply ovules. These continuing ventrals pass into the stylar region without fusion to other ventrals or dorsals. Four rows of 16–24, bitegmic, campylotropous ovules are associated with each carpel. Ovule supply occurs in the lower epigynous zone below the level of dorsal formation. Raphide idioblasts are common in the upper gynoecium and the free spreading stylar arms.

As the locules open perpendicular to the outer tepal radii in a spiral pattern,

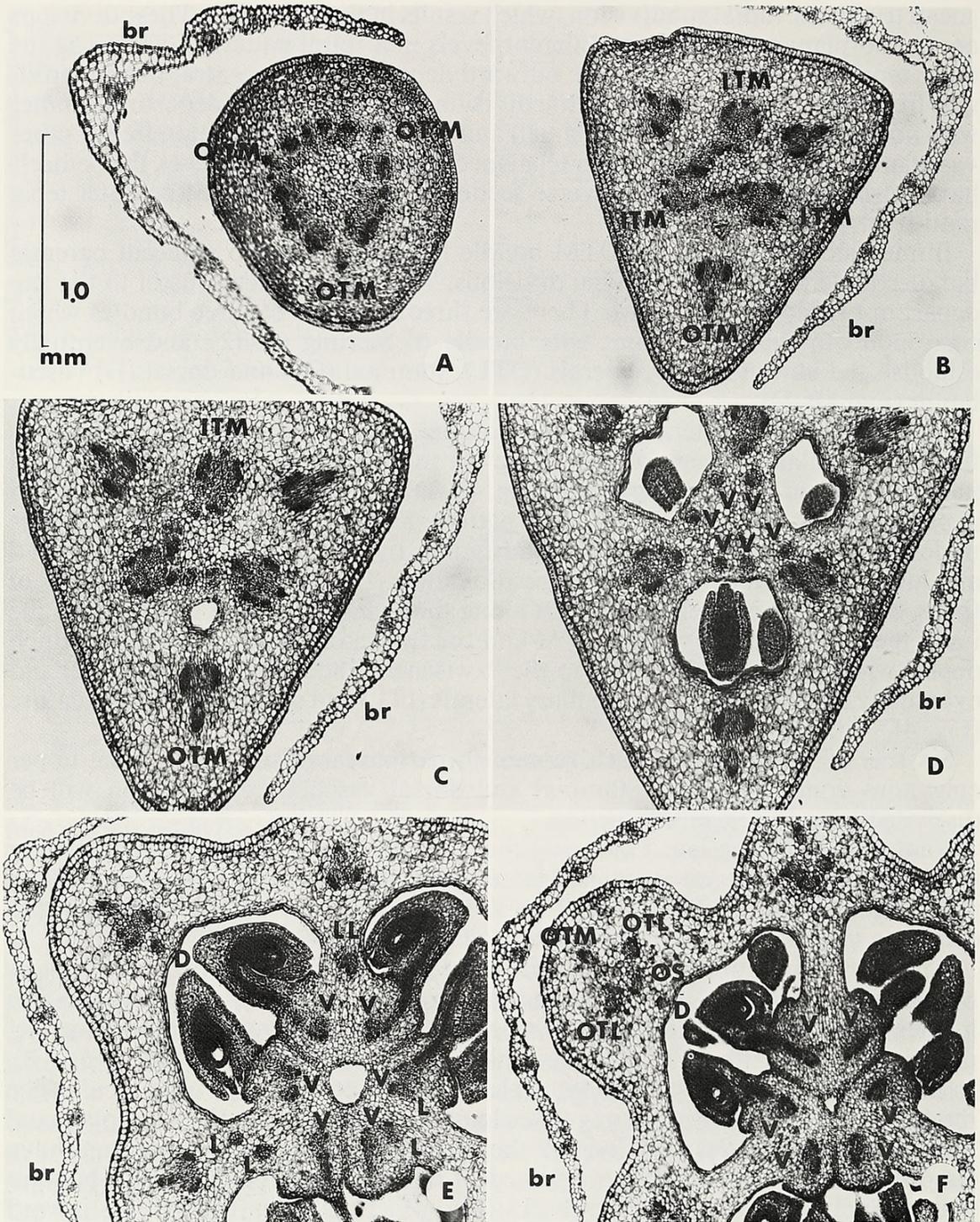


Fig. 4.—Photomicrographs of transverse sections from pedicel to mid-epigynous zone in *S. frigidum*. A. Lower pedicel (circular outline) and subtending bract (br). Three outer tepal medians (OTM) are established at this level. B. Upper pedicel (triangular outline) showing lateral pairs associated with each OTM and the formation of the ITM bundles and their associated lateral pairs. C. Lower epigynous zone showing one open locule and further formation of the ITM bundles, their lateral pairs and ventrals. D. Epigynous gynoecium with three open locules with two ventrals (V) each and the formation of septal laterals. Dorsals are not present at this level. E. Gynoecium with central carpellary hole, inner septal margins subdivided along the inner tepal radii, ovule placentation, septal lateral (L) pairs in the septal arms and dorsal (D) bundles. Outer stamen bundles are not present at this level. F. Re-association of ventrals (V) and laterals (L) in the septal margins. Outer stamen (OS) bundles present.

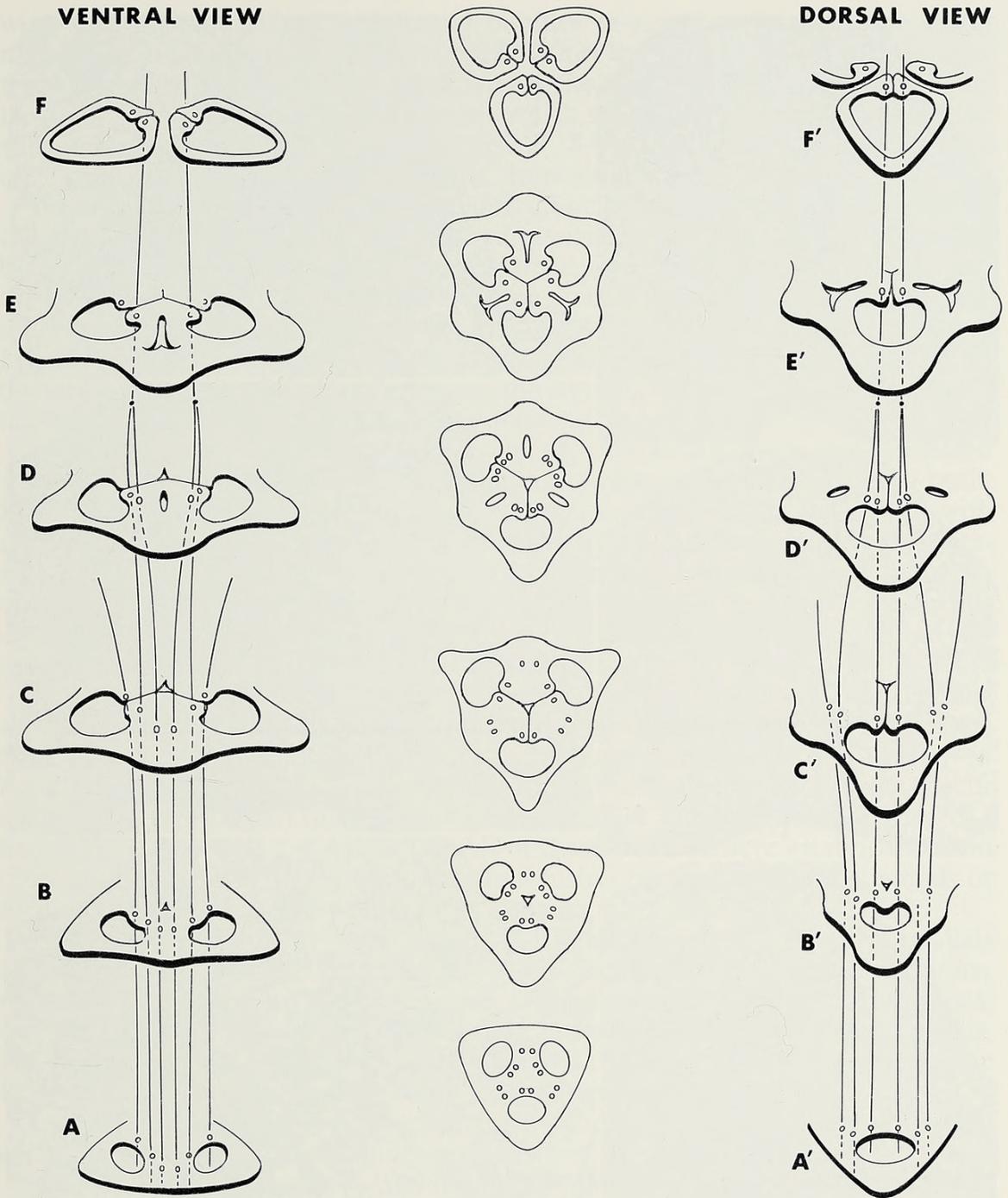


Fig. 5.—Matched ventral (A–F) and dorsal (A'–F') projections of the same section (central column) showing the ventral vascular supply in *S. frigidum*. The ventral projection is along the IS radii, the dorsal along the OS radii. Views A–E are through the epigynous zone, while F is from the freed carpellary zone. View B shows the central carpellary hole, C the subdivided inner septal margins and inter-ocular connections, and D the septal indentations within the septal arms.

three septal arms are established within the lower epigynous zone. A central carpellary hole or opening (Fig. 4D–F, 5B), which is continuous with the open stylar canal, appears in the central area before this region is subdivided along the outer tepal radii. This central subdivision creates three inner septal margins or

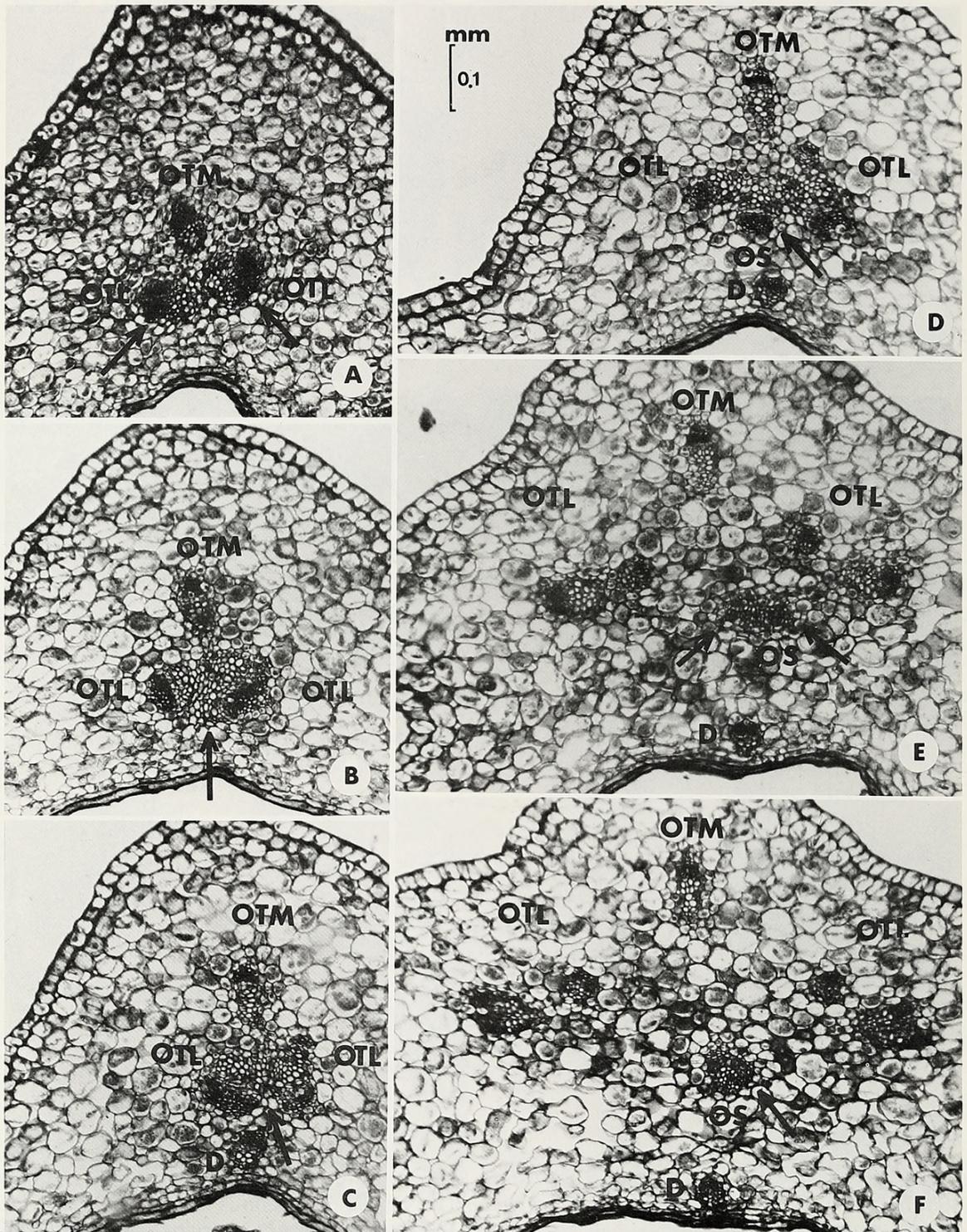


Fig. 6.—Transverse sections through the outer epigynous zone of *S. frigidum* showing the origin of outer tepal, stamen and dorsal vasculature (dorsal-composite bundle). A. Section showing an outer tepal median (OTM) in a distal position and two adjoining, outer tepal laterals (OTL) with laterally orientated phloem caps (arrows). B. Section above A showing xylary fusion and plexus formation between two laterals (OTL). C. Section above B showing a free dorsal with normally arranged conducting elements which was derived from the fusion plexus and the formation of an outer stamen (OS) bundle (arrow). D. Section above C showing an OS bundle with reversed conducting elements. E. Section above D showing the outward departure and division of the outer tepal laterals (OTL) and an OS bundle with two lateral phloem caps (arrows). The OTM and D bundles are correctly

wing tips. As the ventral and lateral bundles re-associate in the inner septal margins, septal indentations or slits open within the septal arms along the inner tepal radii. These indentations occur within the upper epigynous zone, and furthermore, are continuous with the zones which separate the gynoecium from the surrounding stamens and tepals (Fig. 5D–F, 8A–C). The three free carpels are only weakly appressed along the central floral axis.

Tepallary, staminal and dorsal vascularization: Established in the lower pedicel, the three OTM bundles and their pair of associated laterals plus the three ITM bundles and their lateral pairs have remained in a peripheral position through the epigynous zone. The OTM and ITM medians which are along the outer and inner tepal radii, respectively, are not involved in any further division or fusion. Fig. 6 details the origin of the outer tepal laterals (OTL), outer stamen (OS) and dorsal (D) bundles, while Fig. 7 presents the similar, but less complex pattern for the inner tepal laterals (ITL) and inner stamen (IS) bundles.

From the three bundles in an outer group, the two laterals or the pair associated with an OTM undergo an inward rotation and fusion along the outer tepal radii. From this outer vascular plexus and subsequent subdivision, a dorsal (D) with normally arranged conducting elements results. This is followed by an outer stamen (OS) bundle with reversed conducting elements that shifts to a normal arrangement in the upper epigynous zone. It should also be noted that the dorsals are formed before the outer stamen bundles. The dorsals follow an undivided and unfused course into the upper styler arms.

The remaining parental laterals depart as the outer tepal laterals (OTL) flanking the OTM. The laterals undergo additional radial divisions such that when the tepal is freed from the epigynous zone, each outer tepal has as many as seven bundles, that is, three OTL + one OTM + three OTL. Additional divisions occur in the freed outer tepal, such that a maximum of 11 bundles can be observed—five OTL + one OTM + five OTL. All of these bundles were established from three at a lower level. There is no terminal fusion between any of the laterals or medians and all end in the upper tepal margins.

The formation of inner tepal lateral (ITL) and stamen (IS) bundles parallels that for the OTL and OS bundles, except no dorsal is associated with the inner members. At the base of each freed inner tepal, a seven bundled condition exists, that is a median (ITM) and two sets of three laterals (ITL). The freed inner tepals, like the outer tepals, can have a maximum of 11 bundles, that is five ITL + one ITM + five ITL, which were derived from three lower bundles.

Each of the six stamens receives a single bundle or staminal trace. Epitepally occurs in both the outer and inner stamens.

Geography and taxonomy.—*Stenanthium frigidum* occurs in a most specialized ecological zone—the Trans-Mexican Volcanic Belt (Clausen, 1959) or “Eje Volcanico Transversal” (Rzedowski, 1978) (Fig. 1). Scattered clumps are frequently encountered in open, rocky, grassy, alpine meadows associated with *Pinus hartwegii* forests (Beaman, 1962, 1965) between 18° to 22°N latitude at an elevation of 9000–12,000 ft (ca. 2700–3700 m). *Stenanthium frigidum* was first described by Schlechtendal and Chamisso (1831) as *Veratrum frigidum* from a C. J. W.

←

positioned. F. Section above E showing a normal element arrangement for the OS bundle (arrow) and further outward departure of the laterals (OTL).

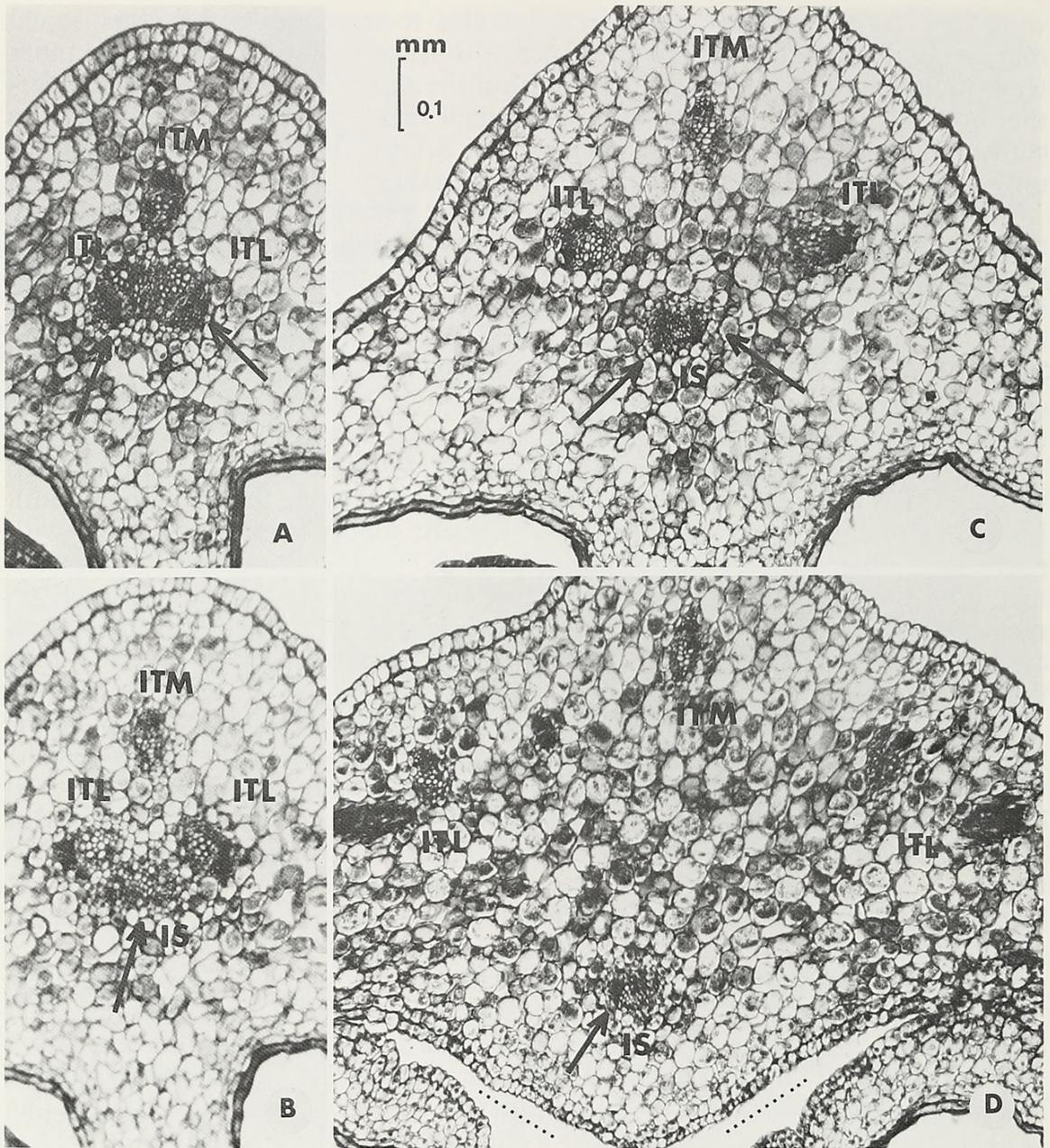


Fig. 7.—Transverse sections through the outer epigynous zone of *S. frigidum* showing the origin of inner tepal and stamen vasculature (zwischenbündel). A. Section showing an inner tepal median (ITM) in a distal position and two inner tepal laterals (ITL) with laterally oriented phloem caps (arrows). Fusion has occurred between the xylar elements. B. Section above A showing laterals (ITL) departing and an inner stamen (IS) bundle with reversed conducting elements (arrow). C. Section above B showing an inner stamen (IS) bundle with two lateral phloem caps (arrows). D. Section above C showing normal element arrangement of the IS bundle and division of both inner tepal laterals (ITL), and the carpellary wall separated from the epitepalous stamen (dotted lines).

Schiede and F. Deppe collection from the alpine regions of Mt. Orizaba (Fig. 9). Schiede and Deppe left Bordeaux in May 1828, arrived at Veracruz in July 1828 and began collecting in the Jalapa and Orizaba areas (Schiede, 1829). Their collections, including type material, are known from the following herbaria (Holmgren et al., 1981): "B (original set destroyed; set *ex herbarium* Baschant extant),

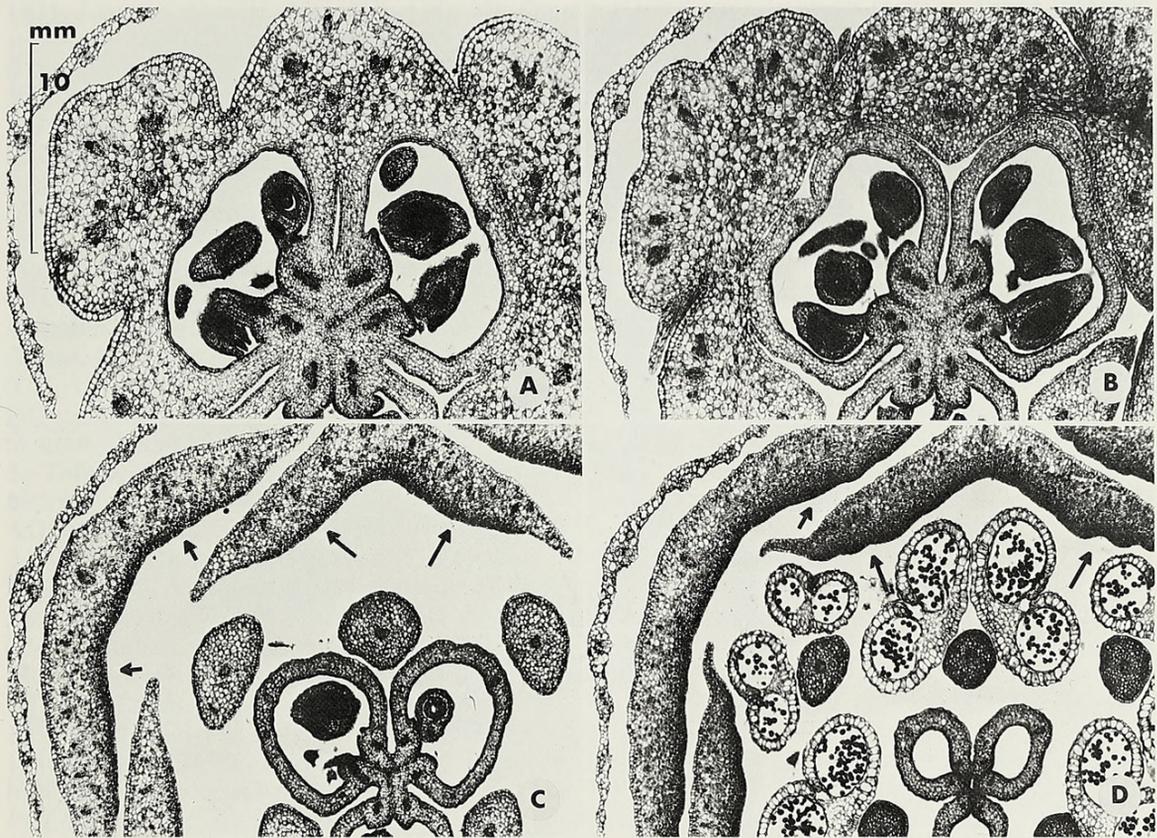


Fig. 8.—Photomicrographs of transverse sections from the upper epigynous zone to the upper floral zone in *S. frigidum*. A. Upper epigynous zone showing the septal indentations along the inner tepal radii within the septal arms. Tepallary and staminal bundles established. B. Separation of gynoecium from surrounding stamens and tepals. Epitelly among both the outer and inner stamens and the formation of additional tepal laterals (OTL and ITL) evident. C. Adaxial surface of freed tepals nectiferous (arrows). Outer (OS) and inner (IS) filaments with a single bundle evident. D. Adaxial tepal nectaries (arrows) at the same level as the reniform, peltate anthers. The adaxial nectiferous surface at higher levels occurs marginally, thus creating a basal V-shaped nectary.

HAL (sent to Schlechtendal); further material BM, BR, C, CGE, F, FI, G, GH, GOET, K, KIEL, LE, LZ (destroyed), M, MO, OXF, P, S, U, US, W, XAL (photos)" (Stafleu and Cowan, 1985). Type material exists for *S. frigidum* (Fig. 9) and it is very probable that additional material is available for lectotypification. Subsequent taxonomic reviews have placed this species in *Zigadenus* (Don, 1832), *Asagraea* (Lyons, 1907) and *Stenanthella* (Gates, 1918). The transfer to *Stenanthium* was made in 1842 by Kunth.

Stenanthium frigidum (Schlechtendal & Chamisso) Kunth

Stenanthium frigidum (Schlechtendal & Chamisso) Kunth, Enum. Plant., 4:190–191. 1842.

Type.—Mexico, Veracruz, Mt. Orizaba, alpine region, 1831, *Schiede & Deppe* 983 (MO!; fragment GH!; Photos CM)—Fig. 9.

Veratrum frigidum Schlecht. & Cham., *Linnaea*, 6:46. 1831.

Zigadenus frigidus (Schlecht. & Cham.) D. Don, *Edinb. New Phil. J.*, 233. 1832.

Asagraea frigida (Schlecht. & Cham.) Lyons, *Pl. Names Scientif. Pop.*, 2nd ed., 508. 1907.

Stenanthella frigida (Schlecht. & Cham.) Gates, *J. Linn. Soc., London, Bot.*, 44:152. 1918.

Representative specimens examined.—MEXICO: DISTRITO FEDERAL: Cima station, hills, 9800 ft, 30 AUG 1905, *Pringle* 13,622 (CAS, GH, LL, TEX, US); Ajusco, Morelos, 3000–3700 m, SEP



Fig. 9.—Type of *S. frigidum* from Mt. Orizaba, Mexico, collected in 1828 by Schiede and Deppe (983). The MO specimen is from the Bernhardt herbarium. (Courtesy of Missouri Botanical Garden.)

1925, *Lyonnet* 22 (GH, MO, NY, US); Mt. Gauzin (Guauhztin), between rocks in alpine meadow, 10,900 ft, 26 AUG 1928, *Antipovitch* 96 (CM); La Portrera, 9000 ft, 22 AUG–19 SEP 1930, *Russell & Souviron* 150 (US); S slope of Serjana de Ajusco, ca ¼ km E of Zampoalo on road to Huitzilac, 3000 m, 15 JUL 1960, *Iltis, Koepfen & Iltis* 253 (WIS); 2 km N of La Cima, SE slope of Cerro Pelado, 1–2 km N and W of La Cima station, 3050–3300 m, 14 AUG 1960, *Iltis, Koepfen, Iltis & Rzedowski* 902 (UC, WIS—8 sheets); Cerro de San Miquel, near summit in grassy area, 31 JUL 1960, *Penalosa* 813 (CAS); Cerro Pelado, Serrania del Ajusca, 3100 m, 14 AUG 1960, *Rzedowski* 12,630 (MSC). **MEXICO:** Zinantecatl Mts., moister places of pine forests of Nevado de Toluca, 12,000 ft, 2 SEP 1892, *Pringle* 4257 (GH, MO, NY, UC, US); Ixtaccihuatl, meadows near timber line, NOV 1905, *Purpus* 1699 (GH, NY, UC, US); Temascaltepec, Cajones, 2480 m, 11 NOV 1932, *Hinton* 2396 (GH), Crucero Aqua Blanca, 3170 m, 29 AUG 1933, *Hinton* 4612 (CAS, MO); Cierrita, 13 AUG 1935, *Hinton* 8353 (GH, NY, UC, US); pine forest, 18 DEC 1935, *Hinton* 8792 (GH, LL, NY, UC, US); Apitza, Mt. Ixtaccihuatl, 12,000 ft, said by natives to be poison to animals, 27 JUL 1938, *Balls* 5136 (UC, US); Valle de Mexico, C. de Llano Grande, 2800 m, 30 JUL 1950, *Matuda* 19,002 (UC); Ixtaccihuatl, 3500 m, 7 JUN 1953, *Matuda* 28,389 (UNC); Telapón, N of Ixtaccihuatl, 3450–3500 m, grassy meadow under *Pinus hartwegii* forest, 4 SEP 1958, *Beaman* 2443 (GH); Ascenso al Nevado de Toluca, en bosque de *P. hartwegii*, 3789 m, 5 SEP 1958, *Hernandez s.n.* (CAS); S of Pan-Am highway at pass of Monte Rio Frio (5 km WNW of Rio Frio) at Llano Grande, 3100–3200 m, 18 AUG 1960, *Iltis, Koepfen & Iltis* 1085 (UC, WIS—4 sheets); 3100–3200 m, 24 SEP 1962, *Ugent* 2299 (WIS—14 sheets); Papayotl (El Papayo), 2 OCT 1966, *Boege* 292 (CAS); Ixtapaluca, Estacion Experimental de Investigacion y Ensenanza de Zoquiapan, 8 km S de Rio Frio, 3190 m, 5 SEP 1975, *Koch & Magana* 75,496 (CAS, F, NY); sotobosque de *Pinus hartwegii*, 3300 m, JUL 1976, *Obieta* 75 (CAS); Ixtapaluca, Llano de San Miquel, 3350 m, 26 AUG 1978, *Garcia s.n.* (TEX). **MICHOACAN:** Mt. Tancitaro, 10,000 ft, rocky ridge in open pine forest, 4th Hoogstraal Biological Expedition, 22 JUL 1941, *Leavenworth & Hoogstraal* 1135 (GH, MO, NY); Zitacuaro-Cerro Pelon, 3600 m, 14 AUG 1938, *Hinton* 13,238 (GH, LL, NY, UC, US); Vicinity of Morelia, Cerros San Miquel, 2200 m, SEP 1910, *Arsene* 5249 (GH, MO, NY, US); Uruapan, Tancitaro, 3450 m, llano in pine forest, flower and root smell like fungus, said to poison cattle, 23 OCT 1940, *Hinton* 15,572 (GH, LL, MO, NY, TEX). **PUEBLA:** Lower slopes of Pico de Orizaba, W of Chalachicomula (Ciudad Serdan), 21 SEP 1957, *Beaman* 1788 (GH). **TLAXLALA:** Mt. Malinche, pine woods, 12,000 ft, 22 JUN 1938, *Balls* 4886 (UC, US); N side Mt. Malinche, in open grassy *Pinus hartwegii* forest, 3770 m, 10 AUG 1958, *Beaman* 2244 (GH). **VERACRUZ:** Mt. Orizaba, 12,000 ft, foliage poisonous to cattle and horses, 6 AUG 1891, *Seaton* 203 (GH, NY); Vaquena del Jacal, 10,000 ft. 1841–43, *Liebmann* 14,681 (US); Mt. Orizaba, 10,000 ft, 1841–43, *Liebmann* 14,682 (GH, UC), 14,683 (GH, MO); 25–26 JUL 1901, *Rose & Hay* 5748 (US); Vertiente del Volcan Pico de Orizaba, 3600 m, 27 JUL 1971, *Nevling & Gomez-Pompa* 2071 (GH, NY).

DISCUSSION

The tall and robust *Stenanthium frigidum* occupies a most unusual geographic and ecological zone, in that it occurs between 9000–12,000 ft in the *Pinus hartwegii* forest of the Trans-Mexican Volcanic Belt and is the southern most and highest occurring member of the tribe Veratreae. The highest elevations attained by *S. occidentale* are near 7500 ft in the Pacific Northwest (Utech, 1987). Numerous other differences also occur between *S. frigidum* and *S. occidentale*.

The branched andromonoecious, bracteated panicle of *S. frigidum* has numerous bisexual, protandrous flowers, in marked contrast to the simple raceme of *S. occidentale* (Utech, 1987) and the highly branched, bracteated panicle of *S. gramineum*. Bracteoles, though small, are present in *S. gramineum*, although Gates (1918) reported their absence. An inflorescence parallel in both *S. gramineum* and *S. frigidum* needs further investigation. Both species have extremes in panicle patterns: one type is lax, open and the other is tight, more compact. The flowers of *S. occidentale* (Utech, 1987) and *S. frigidum* have a characteristic nodding appearance, while in fruit their capsules are erect. A sclerenchymatous sheath surrounds the fruiting pedicel bundles in *S. occidentale* (Utech, 1987), and this also appears true of the erect pedicels in *S. frigidum* based on dried fruiting material.

The dark maroon to purplish-black tepals of *S. frigidum* are not suffused with greenish yellow as in *S. occidentale*, which gives the flowers of the latter a bronze cast. The freed tepals in *S. frigidum* average 14.5 mm in length and appear longer than those of *S. occidentale* (Utech, 1987). This difference is only apparent, since the tepals in *S. frigidum* are not reflexed and those in *S. occidentale* are. Epitepally and similar basal, v-shaped, adaxial, tepal nectaries are found in both species.

Both species have epigynous gynoecium, but their flowering and fruiting proportions differ. In *S. frigidum*, there is little difference in epigynous zone height, which averages 4.3 mm in flower and 4.6 mm in fruit. This zone nearly doubles in *S. occidentale* from a flowering height of 2.3 mm to 4.0 mm in fruit (Utech, 1987). The mature septicial capsules also differ in shape. In *S. occidentale*, they are rather narrowly elongated to a tapering apex of ascending stylar arms, whereas in *S. frigidum* they are more ovoid apically with recurved stylar arms. In fruit, the epigynous zone of *S. frigidum* accounts for 28.5% of the capsule's length, while in *S. occidentale*, the same zone averages 16.5%.

The general floral and carpel morphology as well as the basic floral vascular anatomy of *S. frigidum* are similar to that reported for various species within the tribe Veratreae (Anderson, 1940; El-Hamidi, 1952; Ambrose, 1975, 1980; Sterling, 1982; Utech, 1986, 1987). However, there are some specific differences between *S. frigidum* and *S. occidentale* (Utech, 1987). The septal indentations within the septal arms of the upper epigynous zone of *S. frigidum* were not observed in *S. occidentale*, though both species have a central carpellary hole and spirally inserted floral parts. The equal filaments in *S. frigidum* are considerably shorter than either of the dimorphic ones in *S. occidentale*. Raphide idioblasts were commonly seen in the upper gynoecium of *S. frigidum*, but are lacking in *S. occidentale* (Sterling, 1982; Utech, 1987). Such raphide distribution in *S. frigidum* may be a possible defense against chewing insects. Both species have bitegmic, camplyotropous ovules and flat, oblong, winged seeds.

The major differences in floral vascular patterns of *S. frigidum* and *S. occidentale* involve tepal vascularization that arises from different kinds of compound bundles and the fate of septal-ventral bundles. In the lower areas of the short flowering pedicels of *S. frigidum*, the outer tepal medians (OTM) are established first, followed by a pair of associated laterals from which the outer tepallary, staminal and dorsal bundles are derived. On the other hand, in *S. occidentale*, which has significantly longer flowering pedicels, a compound outer tepal (OT; Utech, 1987) bundle is established first, but in the same position as the OTM bundle in *S. frigidum*. The compound OT bundles in *S. occidentale* divide in the mid-pedicel to form the outer tepallary, staminal and dorsal bundles. A similar pattern is observed in the direct formation of the inner tepal medians (ITM) in *S. frigidum* versus the formation of a compound inner tepal (IT; Utech, 1987) bundle in *S. occidentale* which later divides to form an inner tepal median (ITM), tepallary laterals (ITL) and staminal (IS) bundles.

In the upper epigynous zone of *S. frigidum*, the outer lateral pairs surrounding each outer tepal median (OTM) rotate inwards and fuse along the OT radii. From this fusion plexus, a dorsal is derived first, followed by an outer stamen (OS) bundle which has reversed conducting elements. At their filament bases, the OS bundles have normally arranged conducting bundles. Except for dorsal formation, a similar set of events is associated with the formation of the inner stamen (IS) bundles, including their reversal. This pattern corresponds to that reported for the Veratreae in general (Sterling, 1982), *Amianthium muscaetoxicum* (Utech,

1986) and *Stenanthium occidentale* (Utech, 1987). The OTM and its lateral pair or the compound OT correspond to the dorsal-composite bundle reported within the Veratreae (Sterling, 1982). The ITM and its lateral pair or the compound IT, similarly, correspond to the "zwischenbündel" (Sterling, 1982).

The total outer and inner tepal vascularization in both *S. frigidum* and *S. occidentale* are derived from three bundles, a median and two tepal laterals, which were established in the upper epigynous zone. Medians do not divide or fuse, but follow a direct course to the tepal tips. The laterals, on the other hand, undergo several divisions to innervate the tepal surface. Characteristically, the tepals of *S. frigidum* have a maximum of 11 bundles; those of *S. occidentale* have seven. Though withered, the tepals are persistent in both species.

There is also a significant difference in ventral vascularization between *S. frigidum* and *S. occidentale*. In the latter, following the formation of the ventrals, a fusion septal axial (SA; Utech, 1987) with reversed conducting elements is formed and ends abruptly without fusion or further division in the lower septal arms. In *S. frigidum*, a similar bundle with reversed elements occurs, but it divides radially forming septal laterals which follow a course similar to that of the ventral with which they fuse in the upper freed gynoecium. Below this level of fusion, the ventrals supply the ovules directly, while above, the fusion products in the ventral position do. The formation of septal laterals in *S. frigidum* which later fuse with ventrals of a common origin occurs in the septal arms at the same time as the septal indentations appear.

CONCLUSIONS

The Mexican species *Stenanthium frigidum* has more outer and inner tepal bundles than *S. occidentale*, equal, not dimorphic filaments, septal gynoecial indentations, different patterns of ventral vascularization and raphide idioblasts in the upper carpellary zones. Both *S. frigidum* and *S. occidentale* have v-shaped tepal nectaries, while no nectaries are reported for *S. gramineum*. The chromosome number and karyotype of *S. frigidum* are unknown; neither is the relationship to *S. occidentale* with $2n = 16$ and *S. gramineum* with $2n = 20$.

ACKNOWLEDGMENTS

The author gratefully acknowledges the loan and use of specimens from the following herbaria (CAS, CM, F, GH, LL, MO, MSC, NY, TEX, UC, UNC, US, and WIS) whose acronyms are cited in Holmgren et al., 1981. Without the kind gift of fixed floral material and use of photographic negatives by Dr. Hugh H. Iltis, long a student of the Veratreae and to whom the author is indebted, this study would have been impossible. Mr. William W. Brown deserves special thanks for his artistic aid in figure production.

LITERATURE CITED

- AMBROSE, J. D. 1975. Comparative anatomy and morphology of the Melanthioideae (Liliaceae). Unpublished Ph.D. dissertation, Cornell University, Ithaca, vii + 240 pp.
- . 1980. A re-evaluation of the Melanthioideae (Liliaceae) using numerical analyses. Pp. 65–81, in *Petaloid monocotyledons* (C. D. Brickell, D. F. Cutler, and M. Gregory, eds.), Academic Press, London, ix + 222 pp.
- ANDERSON, C. E. 1940. Some studies on the floral anatomy of the Liliales. Unpublished Ph.D. dissertation, Cornell University, Ithaca, iv + 142 pp.
- BAKER, J. G. 1879. Synopsis of the Colchicaceae and aberrant tribes of the Liliaceae. *Journal of the Linnean Society, Botany*, 17:405–413.
- BEAMAN, J. H. 1962. The timberline of Izatacchuatl and Popocatepetl, Mexico. *Ecology*, 43: 377–385.

- . 1965. A preliminary ecological study of the alpine flora of Popocatepetl and Izatacchuatl. Sociedad Botanica de Mexico, Boletin, 29:63–65.
- BENTHAM, G. 1839. *Plantae Hartwegianae*. 402. *Veratrum frigidum*. Gulielmus Pamplin, London, p. 53.
- CLAUSEN, R. T. 1959. *Sedum* of the Trans-Mexican Volcanic Belt. An exposition of taxonomic methods. Cornell University Press, Ithaca, x + 380 pp.
- CONZATTI, C. 1947. Flora Taxonomica Mexicana (Plantas Vasculares). Sociedad Mexicana de Historia Natural, Mexico, D.F., II:62.
- DAHLGREN, R., H. T. CLIFFORD, AND P. F. YEO. 1985. The families of monocotyledons. Structure, evolution and taxonomy. Springer-Verlag, New York, xii + 520 pp.
- DON, D. 1832. On the characters and affinities of certain genera, chiefly belonging to the Flora Peruviana. Edinburgh New Philosophical Journal, p. 233.
- EL-HAMIDI, A. 1952. Vergleichend-morphologische Untersuchungen am Gynoeceum der Unterfamilien Melanthioideae und Asphodelioideae der Liliaceae. Arbeiten aus dem Institut für allgemeine Botanik, Universität Zürich, ser. A, 4:1–50.
- ENGLER, A. 1889. Liliaceae. Pp. 10–30, in *Die natürlichen Pflanzenfamilien* (A. Engler, and K. Prantl, eds.), Engelmann Verlag, Leipzig, 2:10–91.
- FUCHS, C. 1963. Fuchsin staining with NaOH clearing for lignified elements of whole plants or plant organs. *Stain Technology*, 38:141–144.
- GATES, R. R. 1918. A systematic study of the North American Melanthaceae from a genetic standpoint. *Journal of the Linnean Society, Botany*, 44:131–172.
- HEGNAUER, R. 1963. *Chemotaxonomie der Pflanzen*. Birkhauser Verlag, Basel, 2:269–359.
- HOLMGREN, P. K., W. KEUKEN, AND E. K. SCHOFIELD. 1981. *Index herbariorum*. Part I: The herbaria of the world. Ed. 7. *Regnum Vegetabile*, 106:1–452.
- HUTCHINSON, J. 1973. The families of flowering plants. Vol. II: Monocotyledons. Clarendon Press, Oxford, Ed. 3, 268 pp.
- JOHANSEN, D. A. 1940. *Plant microtechnique*. McGraw-Hill Book Company, New York, xi + 523 pp.
- KRAUSE, K. 1930. Liliaceae. Pp. 227–276, in *Die natürlichen Pflanzenfamilien*. (A. Engler and K. Prantl, eds.), Engelmann Verlag, Leipzig, 2(15a):227–390.
- KUNTH, C. S. 1842. Melanthaceae. *Enumeratio Plantarum*. Hinrichs, Tübingen, 4:189–191.
- KUPCHAN, S. M., J. H. ZIMMERMAN, AND A. ALFONSO. 1961. The alkaloids and taxonomy of *Veratrum* and related genera. *Lloydia*, 24:1–26.
- LINDLEY, J. 1846. 50: *Stenanthium frigidum*. *Journal Horticultural Society, London*. 1:302.
- . 1849a. *Stenanthium*. Medical and oecomenical botany. Bradbury and Evans, London, 55–56 pp., Fig. 91.
- . 1849b. 214: *Stenanthium frigidum* Kunth. *Flore des Serres et des Jardins de l'Europe*, ser. 1, 5:460–468.
- LYONS, A. B. 1907. *Plant names scientific and popular*, 2nd ed., Nelson, Baker and Company, Detroit, p. 508.
- MELCHIOR, H. 1964. *Syllabus der Pflanzenfamilien*. Vol. II: Angiospermen. Gebrüder Borntraeger, Berlin, vi + 666 pp.
- RZEDOWSKI, J. 1978. *Vegetacion de Mexico*. Editorial Limusa, Mexico, D.F., 432 pp.
- SANCHEZ, O. 1980. *La flora del Valle de Mexico*. 6 ed. Editorial Herrero, Mexico, D.F., p. 97, fig. 51.
- SASS, J. E. 1958. *Botanical microtechnique*. Iowa State University Press, Ames, xi + 228 pp.
- SCHIEDE, C. J. W. 1829. *Botanische Berichte aus Mexico*. *Linnaea*, 4(2):205–236.
- SCHLECHTENDAL, D. F. L. VON, AND A. VON CHAMISSO. 1831. 983. *Veratrum frigidum n. sp.* *Linnaea*, 6:46–49.
- STAFLEU, F. A., AND R. S. COWAN. 1985. *Taxonomic literature*. Volume V: Sal-Ste. 2nd Edition. *Regnum Vegetabile*, 112:146–147.
- STERLING, C. 1982. Comparative morphology of the carpel in the Liliaceae: Veratreae. *Journal of the Linnean Society, Botany*, 84:57–77.
- UTECH, F. H. 1986. Floral morphology and vascular anatomy of *Amianthium muscaetoxicum* (Walter) A. Gray (Liliaceae-Veratreae) with notes on distribution and taxonomy. *Annals of Carnegie Museum*, 55:481–504.
- . 1987. Biosystematic studies in *Stenanthium* (Liliaceae-Veratreae) I. Floral morphology, floral vascular anatomy, geography and taxonomy of *S. occidentale* A. Gray. *Annals of Carnegie Museum*, 56:113–135.
- WILLIAMAN, J. J., AND B. G. SCHUBERT. 1961. Alkaloid-bearing plants and their contained alkaloids. United States Department of Agriculture Technical Bulletin, no. 1234.
- ZIMMERMAN, J. H. 1958. A monograph of *Veratrum*. Unpublished Ph.D. dissert., University of Wisconsin, Madison, iii + 321 pp.



BHL

Biodiversity Heritage Library

Utech, Frederick H. 1987. "Biosystematic studies in *Stenanthium* (Liliaceae: Veratreae). II. Floral morphology, floral vascular anatomy, geography and taxonomy of the Mexican *S. frigidum* (Schlecht. & Cham.) Kunth." *Annals of the Carnegie Museum* 56, 197–212. <https://doi.org/10.5962/p.330585>.

View This Item Online: <https://www.biodiversitylibrary.org/item/216939>

DOI: <https://doi.org/10.5962/p.330585>

Permalink: <https://www.biodiversitylibrary.org/partpdf/330585>

Holding Institution

Smithsonian Libraries and Archives

Sponsored by

Biodiversity Heritage Library

Copyright & Reuse

Copyright Status: In Copyright. Digitized with the permission of the rights holder

Rights Holder: Carnegie Museum of Natural History

License: <https://creativecommons.org/licenses/by-nc-sa/4.0/>

Rights: <https://www.biodiversitylibrary.org/permissions/>

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.