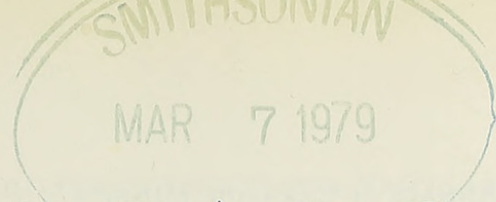


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COMPARISON OF THE VASCULAR FLORAL ANATOMY OF *XEROPHYLLUM ASPHODELOIDES* (L.) NUTT. AND *X. TENAX* (PURSH) NUTT. (LILIACEAE-MELANTHIOIDEAE)

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ABSTRACT

The patterns of floral vascularization in *Xerophyllum tenax* and *X. asphodeloides* (Liliaceae-Melanthioideae) are presented and compared. Both species share a three-bundled (lower), a six-bundled (middle), and a 12-bundled (upper) pedicel vascular configuration. The upper configuration consists of six outer, smaller bundles which alternate with six inner, larger bundles. The six smaller bundles are fusion products formed at lower pedicel levels and directly supply the two whorls of tepals. Each tepal-supplying bundle divides to form a median and two laterals. There is further subdivision of the laterals within the freed tepals.

The six larger remaining bundles undergo repeated radial divisions and fusions to form the two whorls of stamen traces. The outer stamen traces are formed in a similar manner as the inner stamen traces. Both are fusion products and their formation closes the gaps left by the departing tepal supply bundles. Axial continuations of these six larger bundles undergo one final radial division to form the fusion dorsals and the free ventrals. The ventrals have a reversed arrangement of their conducting elements. Septal axials, dorsal laterals, and ventral laterals do not occur in either species. *Xerophyllum asphodeloides* has two basal ovules and two associated funicular traces per locule, whereas *X. tenax* has four ovules and four funicular traces arranged in two tiers per locule. The vascularization of the former represents a simplified version of the latter.

The gynoecium in both species is tricarpellate and unilocular with three free styles. Dorsal notches are present, as well as deep septal indentations. Rhaphides occur in both species, but their abundance increases with maturity. The capsule fruit in both species dehisces loculicidally. *Xerophyllum tenax* has a papilloid carpellary epidermis which *X. asphodeloides* does not. Both species have an internal stigmatoidal support system for pollen tube growth which lines the inner styles and the axial faces of the inner septal wing margins.

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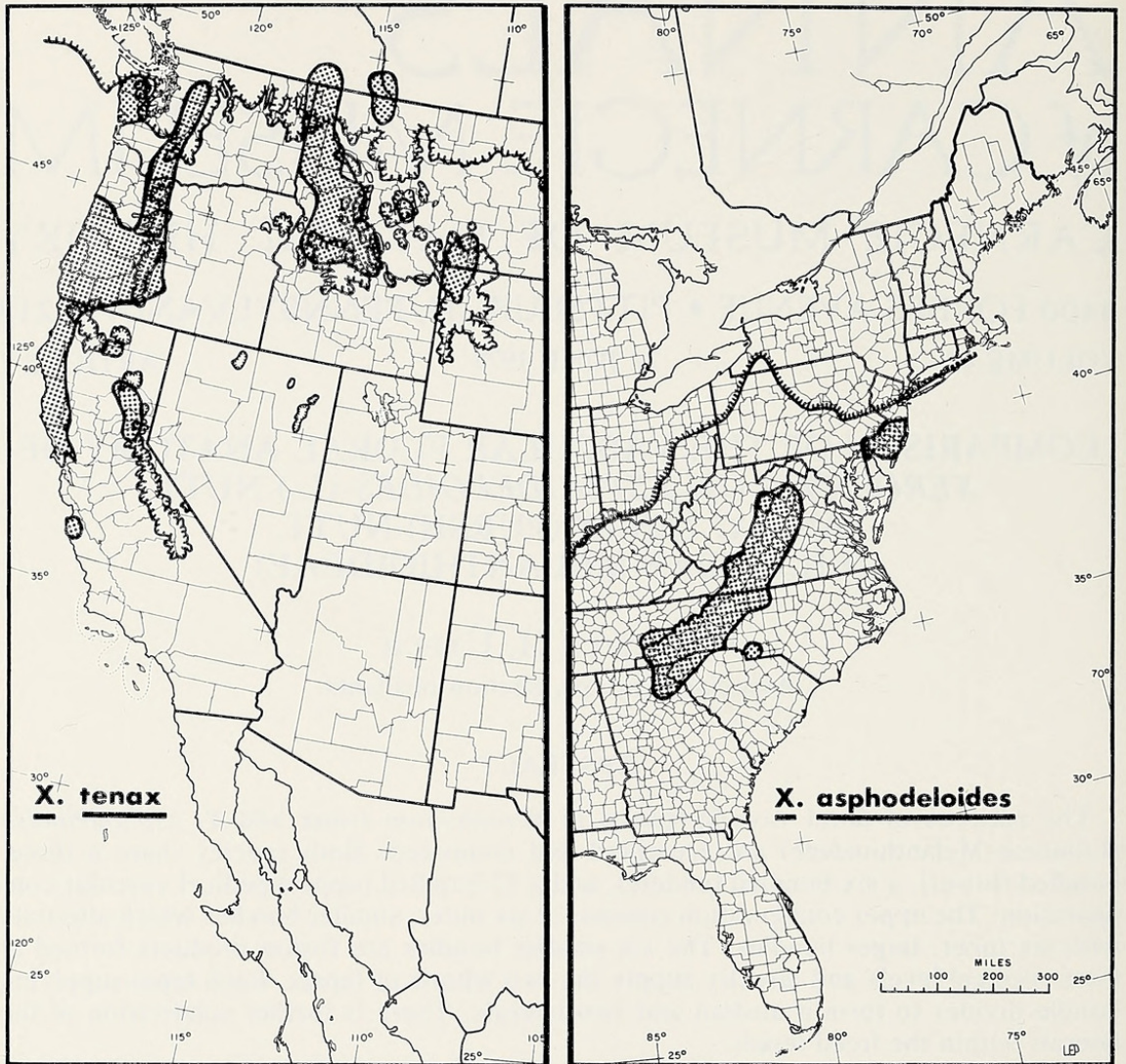


Fig. 1.—Distribution of *Xerophyllum tenax* (“Bear grass;” “Squaw grass”) and *X. asphodeloides* (“Turkey beard”) in western and eastern North America. Ranges based in part on Wood (1972) and Johnson (1969); glacial boundaries from Flint (1971).

INTRODUCTION

The two species of *Xerophyllum* (Rich.) Michx. are endemic to North America. One species, *X. tenax* (Pursh) Nutt. (= *Helonias tenax* Pursh; = *Xerophyllum douglasi* S. Wats.), is confined to the west, whereas the other, *X. asphodeloides* (L.) Nutt. (= *Helonias asphodeloides* L.; = *Xerophyllum setifolium* Michx.), is limited to the east (Fig. 1). Neither species has had extensive range expansion via migration or dispersal across the Pleistocene continental glacial maxima (Fig. 1; Wood, 1972; Flint, 1971; Johnson, 1969; Maule, 1959). Localized elevational shifts have no doubt occurred in both species. *Xerophyllum tenax* has a broader ecological tolerance than *X. asphodeloides*, as well as a morphological variability, which defies geographical delimitation.

tation (Hitchcock et al., 1969). Several chromosome counts are available for *Xerophyllum*—*X. tenax*, $2n = 30$ (Taylor and Brockman, 1966; Cave, 1970), and *X. asphodeloides*, $2n = 30$ (Miller, 1930).

As a primitive lily genus, *Xerophyllum* is distinctive. The tribal association of *Xerophyllum* differs between the Englerian and Hutchinsonian systems. In the former system (Engler, 1888; Krause, 1930), *Xerophyllum* is placed in the tribe Helonieae along with *Helonias*, *Chamaelirium*, *Chionographis*, *Heloniopsis*, and *Metanartheceum*.

Hutchinson (1934), on the other hand, divides these genera and adds others in the formation of two different tribes—Heloniadeae (emend.) with *Helonias*, *Chamaelirium*, *Ypsilandra*, and *Chionographis*, and Nartheciae with *Pleea*, *Tofieldia*, *Hewardia*, *Heloniopsis*, *Clara*, *Nartheceum*, *Metanartheceum*, *Aletris*, and *Nietneria*. *Xerophyllum* is placed in the latter tribe (Hutchinson, 1934).

It is hoped that this detailed comparison of the floral vascular anatomy of both *X. tenax* and *X. asphodeloides* can be used as a floral benchmark in future tribal delineation.

MATERIALS AND METHODS

Materials for this study were collected over a two year period. Both flowering and fruiting materials were collected. Buds through fruits were fixed in 3:1 (absolute ethanol:glacial acetic acid) and stored in 70% ethanol. Living plants are currently in cultivation in Pittsburgh. Voucher specimens have been prepared for both species—*Xerophyllum asphodeloides* (New Jersey: Burlington Co., Mt. Misery, Utech 76-412 CM), and *X. tenax* (Oregon: Clackamas Co., Mt. Hood, Utech 77-401 CM).

Twenty-five flowers (buds to maturing fruits) were sectioned between 12 to 16 μ using standard paraffin techniques and stained in safranin and methylene blue (Sass, 1958; Johansen, 1940). Checks on these serial preparations were made by observing whole flowers that had been both cleared in 10% NaOH and stained in 1% fuchsin (Fuchs, 1963; Utech and Kawano, 1976).

Neither ontogenetic nor teleological implications are intended by the method of vascular description, which traces the hypothetical ascent of the various bundles from the pedicel to the stigmas. In Fig. 3, a series of cross-sections from the lower pedicel (Fig. 3A) to the upper, freed styles (Fig. 3M) is presented for *X. tenax*. These same cross-sections have been projected and redrawn for Fig. 4, such that selected vascular bundles can be followed through the various sections. A scale indicates the approximate level of the various lettered cross-sections. The final summary diagram (Fig. 9) presents the floral vascularization of *X. tenax* as a cylinder which has been opened longitudinally. This type of "roll-out" diagram has been previously used for other liliaceous species (Utech and Kawano, 1975, 1976a, 1976b). Text introduced codes for the various bundles are presented.

OBSERVATIONS

Both species have a many-flowered, simple, terminal raceme. *Xerophyllum tenax* is usually more robust and taller than *X. asphodeloides*, (0.8) –1.2–1.8– (2.0) dm as compared to (4.5) –0.8–1.0– (1.5) dm. *Xerophyllum tenax* also has approximately twice the number of flowers as *X. asphodeloides* (Fig. 2). The lower flowers of both



Fig. 2.—Floral comparison in *Xerophyllum*. A) *X. tenax*, spiral bud arrangement in early anthesis also showing transitional setaceous leaves below flowers ($\frac{1}{4}\times$). B) *X. tenax*, elongated floral raceme at midanthesis, pedicels divergent in the upper half and erect in the lower half ($\frac{1}{5}\times$). C) *X. asphodeloides*, flowering portion of terminal raceme showing divergent pedicels ($2\frac{1}{2}\times$). D) *X. asphodeloides*, loculicidally dehiscent capsules with two erect seeds per locule, fruiting pedicels nearly vertical ($3\frac{1}{2}\times$).

species are bracteate, although the upper ones may have only a reduced bract or one adnate to the pedicel for much of its length. The latter is common in *X. asphodeloides*, especially in the early stages of flowering (Fig. 8A–B). Initially the inflorescence appears corymb-like (Fig. 2A–C), but with maturity the raceme axis is elongated. In *X. asphodeloides*, the flowering portion of the axis is between 1.5 and 3.0 dm long, whereas in *X. tenax*, this same region spans 5.0 to 7.5 dm.

Pedicels and Their Vascularization

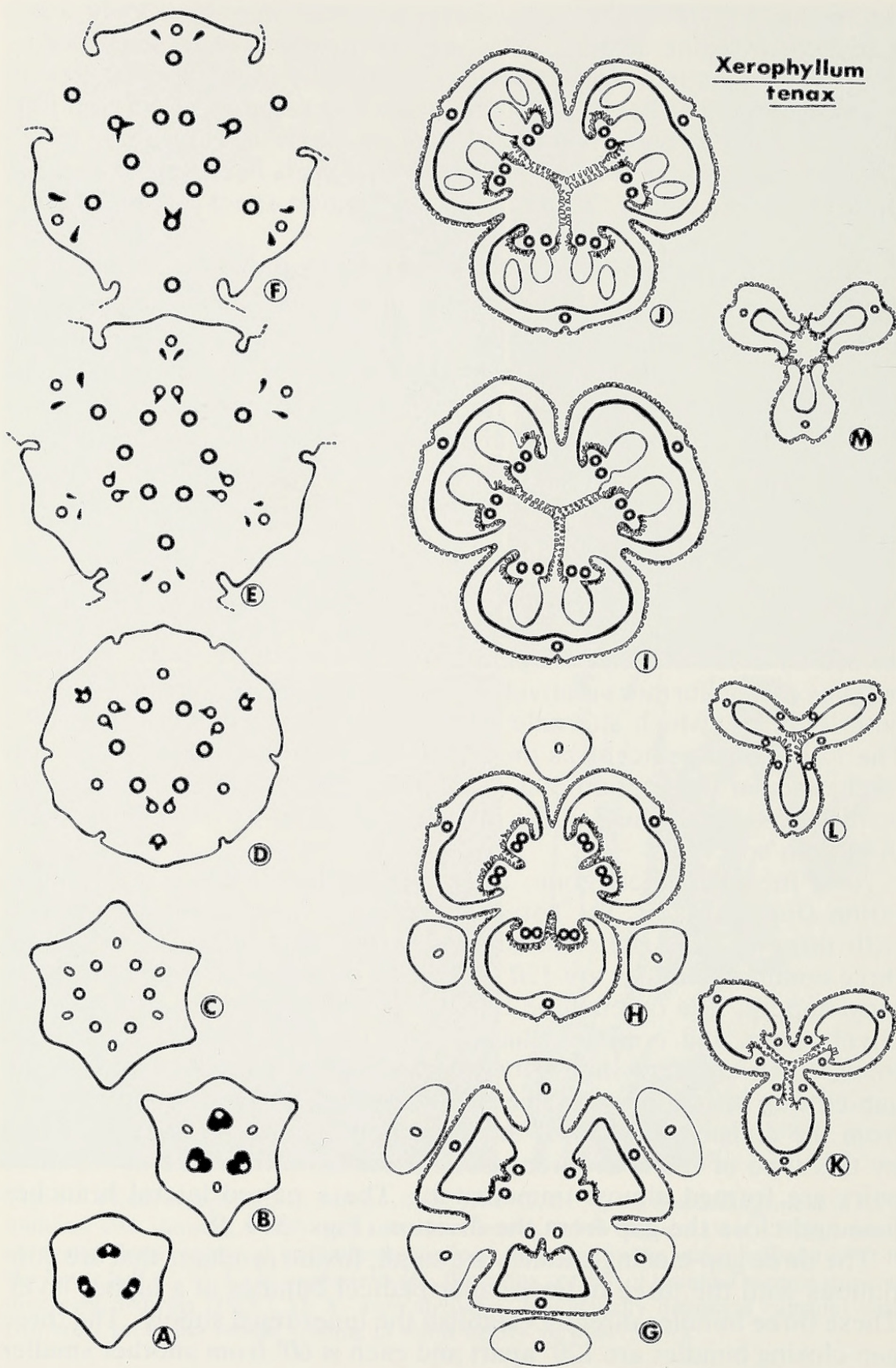
Along the flowering raceme of both species, there is a size gradient in the length of pedicel. However, a consistent pedicel length difference does occur between the two species. From our sampled populations, 50 fruiting pedicels of both species were measured for comparison. In *X. asphodeloides*, the mature pedicel averaged 3.32 cm long (range: 2.11–4.56 cm; SD = 0.14), which is significantly shorter than the average pedicel length of 5.31 cm (ranges: 3.95–6.35 cm; SD = 0.55) for *X. tenax*.

The pedicels in both species of *Xerophyllum* have a similar pattern of vascularization, which can be divided into three distinct parts (Figs. 3A–C, 4A–C, 5A–B, 9). The upper portion of the pedicel is characterized by a 12-bundled configuration (Figs. 3C, 4C, 5A–B). These 12 bundles can be further subdivided into two groups. There are six small outer bundles, which alternate with six large inner bundles (Fig. 5B). The 12-bundled pedicel was the beginning point for Anderson's (1940) brief vascular description of *X. asphodeloides*. Further sectioning towards the base of the pedicel reveals additional patterns (Figs. 3, 4, 9) in both species.

Near the midpedicel zone, there is a six-bundled pedicel configuration (Figs. 3B, 4B, 9). Three of these six bundles are continuous with three of the smaller bundles observed at a higher level. These three common bundles are 120° apart and directly determine the outer tepal supply. The outer three bundles in the midpedicel zone are relatively large and crescent-shaped, and the new bundles arise from them. Each crescent-shaped bundle undergoes a division and partial gap-closing fusion in a short vertical distance. Two new bundles result from the division of each of the large bundles. A gap is also created by this type of radial division. Lateral branches from the new bundle pairs are formed almost immediately. These paired lateral branches fuse and close the gap from the division (Figs. 3–4, 9).

The three gap-closing bundles are small, fusion products that are continuous with the three outer smaller pedicel bundles at a higher level. These three bundles directly establish the inner tepal supply. The three gap-closing bundles are 120° apart and each is 60° from another smaller

Xerophyllum
tenax



outer bundle (Fig. 5A). The change from a six- to a 12-bundled pedicel configuration is due to the radial division products (Figs. 3–4, 9).

Near the junction of the pedicel with the inflorescence axis, there is another type of pedicel-bundle configuration. At this basal level, there are only three large crescent-shaped bundles (Fig. 3A, 4A, 9). These three bundles arise directly from the inflorescence axial supply. The three-bundled condition occurs for only a short vertical distance before it also undergoes a division. Each of the three bundles divides radially with a gap created between the product halves. This gap is quickly closed via fusing lateral branches from the product halves (Figs. 3A, 4A, 9). The three fusion products are continuous with the crescent-shaped bundles (three) that underwent a similar type of division at the midpedicel level. The remaining product halves of the lower division fuse in the opposite direction with bundles of similar origin (Fig. 9). These fusion products are 120° apart and establish the three smaller bundles in outer pedicel, which in turn establishes the outer tepal supply.

Within the pedicels of both species, considerable division and fusion occur in the formation of the 12-bundled pedicel configuration from the three-bundled and the 12-bundled configuration of the lower zones. The 12-bundled configuration is essentially a six smaller plus six larger bundled arrangement. The six smaller, outer bundles are all fusion products that establish in two vertically separated whorls the tepal vascularization. The six larger, inner bundles, which alternate with the

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Fig. 3.—Serial cross-sections of *X. tenax*. A) Lower pedicel with three-bundled configuration. B) Midpedicel with six-bundled configuration. C) Upper pedicel with 12-bundled configuration, that is, six smaller outer and six larger inner. D) Receptacle base, departure of outer tepal supplying bundles, lateral branch pairs forming outer stamen traces. E) Receptacle base, outer and inner tepal supplying bundles dividing to form a median and two laterals, outer stamen traces established, lateral branch pairs about to fuse along septal radii to form the fusion inner stamen traces, six bundles remaining centrally. F) Upper receptacle base, outer and inner stamen traces established, formation of the fusion dorsals, outer tepals cut off, six bundles remaining centrally. G) Gynoecium base with freed outer stamens, dorsals positioned, inner stamen attached along septal radii, paired (three) ventrals centrally, carpellary epidermis with papillae, obturators with papillae. H) Gynoecium with inner stamens freed, dorsal notches present, solid central gynoecium base. I) Mid-gynoecium with central base divided, parietal placentation, unilocular condition, radial division of ventrals (reversed conducting elements), septal indentations evident. J) Mid-gynoecium with second tier of ovules. K) Upper gynoecium and transition to styles, ventral continuations still present. L) Lower common styles with unilocular cavity, septal margin with stigmatoidal papillae on margin tips. (See Fig. 4 for transformational projects and a partial interconnection of the various traces and bundles.)

six smaller outer bundles, establish via continued division and fusion the stamen and synoecial supply (Figs. 3A–C, 4A–C, 5A–B, 9).

Were the complete vasculature of the pedicel not observed, one might conclude that the six outer smaller bundles were established as simple nonfusion bundles within the inflorescence axis and that there was no interconnection between the tepal supplying bundles and those, which supply the stamens and carpels (Fig. 9). On the other hand, the total floral vascularization of the upper pedicel can be traced to three large and, indeed, compound bundles. Furthermore, the tepal supply has its origins within the pedicel and not at some planar level within the receptacle.

Tepals and Their Vascularization

The persistent tepals of both species are dull to creamy-white in flower. The three tepals of both the inner and outer cycle are free and distinct, oblong to ovate in shape and without basal glands (nectaries) or claws. Neither species has a readily detectable odor. The tepals of *X. tenax* tend, on the average, to be longer and wider than those of *X. asphodeloides*. The perianth bud bases of both species have an apparent one-sided asymmetry (semirostate), which is due to the tight spiral packing of the buds (Fig. 1A). This apparent asymmetry is lost at anthesis as the tepals spread. The tepals in *X. tenax* are cut off more directly than in *X. asphodeloides*. The inner and outer tepals of *X. tenax* are equal, whereas in *X. asphodeloides* the inner tepal are slightly narrower and longer than the outer tepals (subequal). Also in the latter, there is a shallow floral tube that is formed by the cohesion of the tepal margins and the adnation of the six stamens (epitepaly) (Fig. 8C). The pedicels are directed outwards during anthesis, whereas in fruit, the pedicels tend to be erect in both species (Fig. 1).

The vascularization of the two tepal whorls is remarkably similar in both species. The outer tepal supply can be traced to the lowest levels of the pedicel where three fusion bundles were formed. Likewise, the inner tepal supply has its origin in the midpedicel zone, again in the formation of three different fusion bundles. An outer tepal supplying bundle is 60° from an inner tepal supplying bundle. The transition from pedicel to receptacle is noted by a sudden increase in cross-sectional area (Figs. 3D–F, 4D–F). As this area increases, three of the smaller outer bundles, which are 120° apart depart outwardly radially. As these three bundles approach the periphery of the receptacle, each undergoes a double radial division. This division results in an outer tepal median (OTM) and two outer tepal laterals (TL) (Figs. 3D–E, 4D–E, 9). The OTM shares the same radius as its parental tepal supplying bundle.

As the three outer tepal supplying bundles divide, the remaining

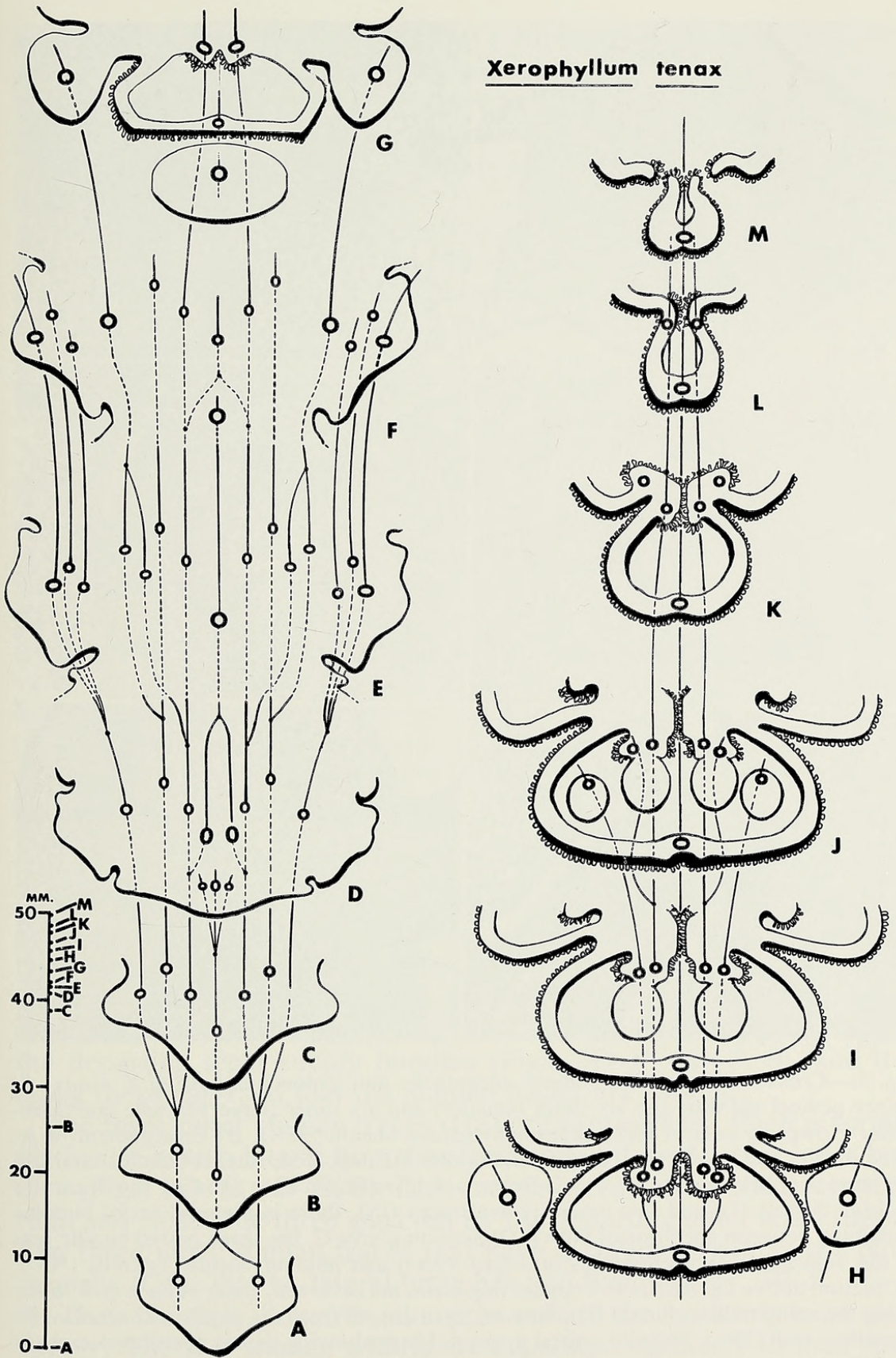


Fig. 4.—*X. tenax*, cross-sections of Fig. 3 after transformational projections with selected vascular bundles connected, lettered cross-sections correspond to those in Fig. 3 and to their relative position on the sectioning scale.

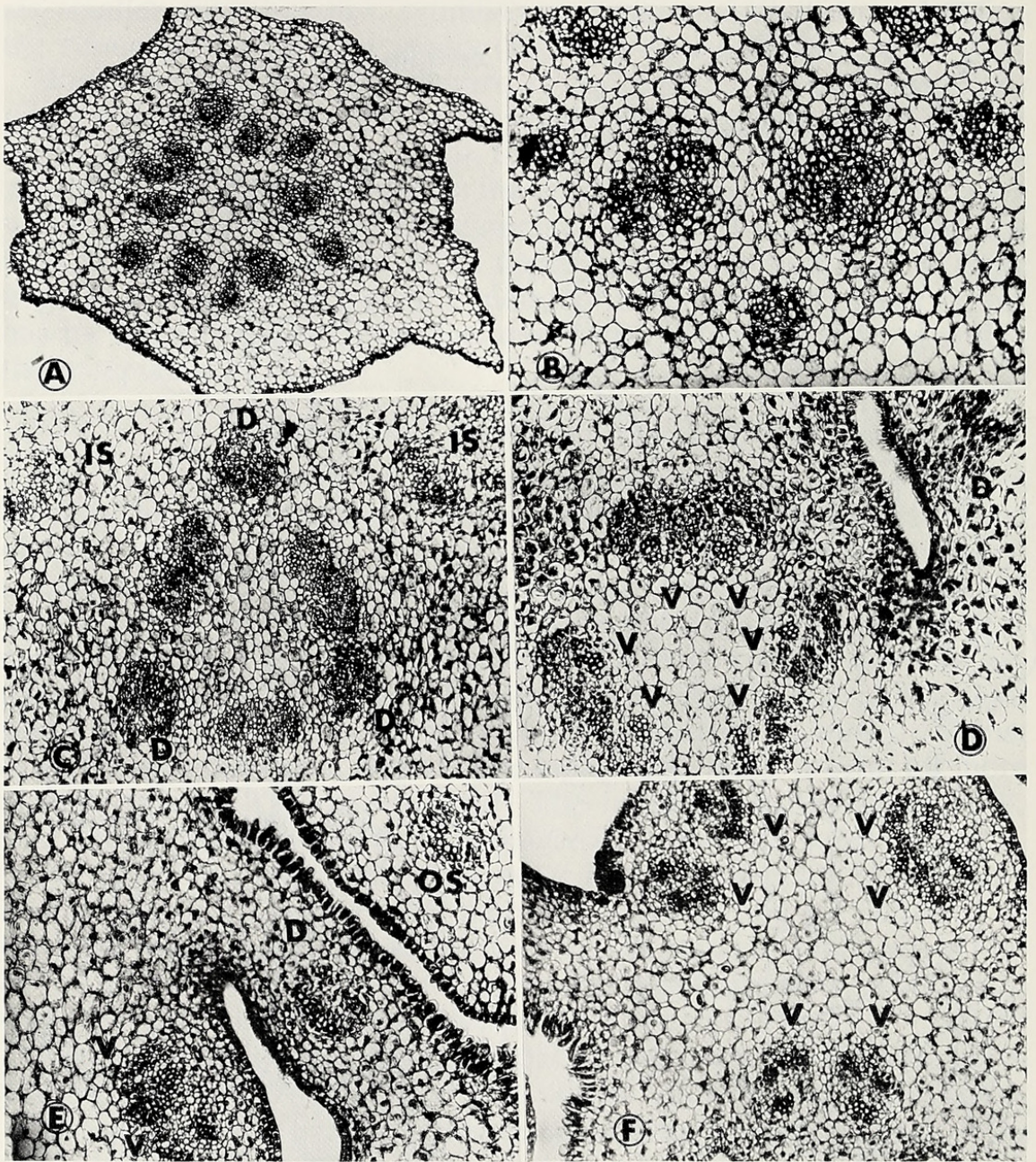


Fig. 5.—Cross-sections of the pedicel, receptacle, and gynoecium base of *X. tenax*. A) Upper pedicel showing the six outer (smaller) and six inner (larger) bundle configurations. Flowering pedicel lacks sclerenchymatous sheath (25 \times). B) Enlargement of A, three smaller and two larger (compound) bundles are indicated, smaller bundles establish the tepal supplies directly (50 \times). C) Receptacle-gynoecium base showing the departure of three dorsals (D) and two inner stamen traces (IS), there is a paired set of bundles remaining between each dorsal (40 \times). D) Section above C, the three paired bundle sets as the ventrals (V) with normally arranged xylem and phloem, locules opening (50 \times). E) Section above D, ventral (V) conducting elements reversed, outer stamen (OS) trace along the same radii as dorsal (D), filament base cut off from the papillae-covered outer carpillary wall (50 \times). F) Solid central gynoecial base showing the six positioned ventrals (V) (50 \times).

three smaller outer bundles also move outward. These three tepal supplying bundles are also compound fusion products and share a common level of pedicel origin. As these three bundles approach the receptacle periphery, they also undergo a similar double radial division, which results in an inner tepal median (ITM) and two inner tepal laterals (TL) (Figs. 3D–E, 4D–E, 9).

Both the outer and inner tepals in *X. tenax* and *X. asphodeloides* are supplied by a three-bundled (trace) pattern of vascularization. Additional radial divisions occur within the laminal surface of the tepals, but these divisions only involve further subdivision of the laterals and not the medians. Once a lateral or its branch is established, there is no terminal cross-innervation of tepal traces.

A differential in the number of lateral divisions exists between the outer and inner whorls. The number of divisions determines the number of veins or traces within a given tepal. In *X. tenax*, the outer tepals usually have five veins, for example, two laterals plus median plus two laterals, due to two radial divisions among the laterals, whereas the inner tepals of this species usually have seven veins, for example, three laterals plus median plus three laterals, due to four radial divisions among the laterals. In *X. asphodeloides* a similar pattern of five veins per outer tepal and seven veins per inner tepal is also observed, but occasionally a five- or six-veined inner tepal is seen. This reduced tepal vein number is directly due to the lack of sequential radial division in a somewhat smaller tepal. The tepal shapes of the two species are similar, only their sizes differ.

Stamens and Their Vascularization

Both species of *Xerophyllum* have similar patterns of stamen vascularization. At the level of stamen trace formation in the receptacle, there are six large inner bundles, which are continuous along their same axes into the pedicel, and six alternating outer bundles, which departed as the tepal supply (Fig. 9). Gaps are left among the radii of the departing tepal supply bundles (Figs. 3D–F, 4D–F, 9), and it is along these gap-radii that the stamen traces are formed.

The three outer stamen traces (OS) are formed first. Each is formed vis fusion of two lateral branches from two different larger inner bundles (Figs. 3D–E, 4D–E, 9). This fusion occurs along the outer tepal radii and closes the three gaps left by the departing outer tepal supply. The three inner stamen traces (IS) have a similar origin as the outer stamens (OS), that is, lateral branches and fusion (Figs. 3E–F, 4E–F, 9). Their fusion is, however, along the radii of the departing inner tepal supply. The two stamen whorls are separated vertically in their level of origin. The three stamens in both cycles are fusion products, and frequently in filament cross-section, their bifid condition can be seen.

The six remaining inner bundles which branched to form the stamen supply continue upward along the same axes, and subsequently establish the total gynoecial supply (Fig. 9).

In both species, the stamens equal or exceed their respective perianths. The filaments of *X. tenax* are longer (7.5–9.5 mm) than those in *X. asphodeloides* (4.5–6.5 mm). The filaments of both are also hypogynous and freed directly. There is a limited amount of epitepaly in *X. asphodeloides* (Fig. 8C). The freeing of the three inner stamens from the receptacle-gynoecial wall opens three triangular wedges in the gynoecial outline (Figs. 3G–I, 4G–I). These spaces become the regions of the unfused septal indentations (Figs. 7C, 8D). At this level, the locules have already opened and the dorsal bundles are positioned.

The anthers are attached at their mid-length point and are not basifixed as is often reported (Fig. 7C–F). There is no confluence of thecae terminally. The connective tissue begins in the mid-length region and is continuous to the anther's tip. The stamen traces (OS and IS) are continuous through the connectives. Dehiscence is via lateral slits (extrorse). Rotation of the anthers is possible due to the mid-level attachment of the filiform filaments. The endothecium cells of the anthers sacs have banded thickenings. The filaments diverge, ca. 30–45°, from the vertical gynoecial axis, and thus create a wide, outer pollen dispersal zone.

Gynoecium and Carpel Vascularization

Both *Xerophyllum tenax* and *X. asphodeloides* have an ovate, tri-carpellate gynoecium with deep septal indentations, dorsal grooves and three free, recurved styles. Raphides are present in the outer carpellary walls (pericarps) of both species. Raphide distribution increases with maturity. In both species, the carpellary epidermis, which includes the outer surface of the septal indentations, has a dense covering of papilloid cells. This epidermal modification is more pronounced in *X. tenax* than in *X. asphodeloides* (Figs. 6C–E, 8D–E).

The septal indentations are formed near the receptacle-gynoecium base, as the inner stamens are cut off (Figs. 3G–H, 4G–H). The three indentations extend to the three free styles which are freed along the septal radii. The two carpellary margins, which subtend a given indentation are fused only at their innermost tips. This is the only anatomical evidence for carpellary fusion within the gynoecium.

A dorsal groove (notch in cross-section) runs the length of the three carpels (Figs. 3, 4). The dorsals are broadly crescent-shaped (bifid) throughout their gynoecial course (Figs. 6F, 8D–E). There is no branching of the dorsals (Fig. 9). The fruit is a loculicidal capsule, because the locules are opened along the dorsal grooves. The dorsal

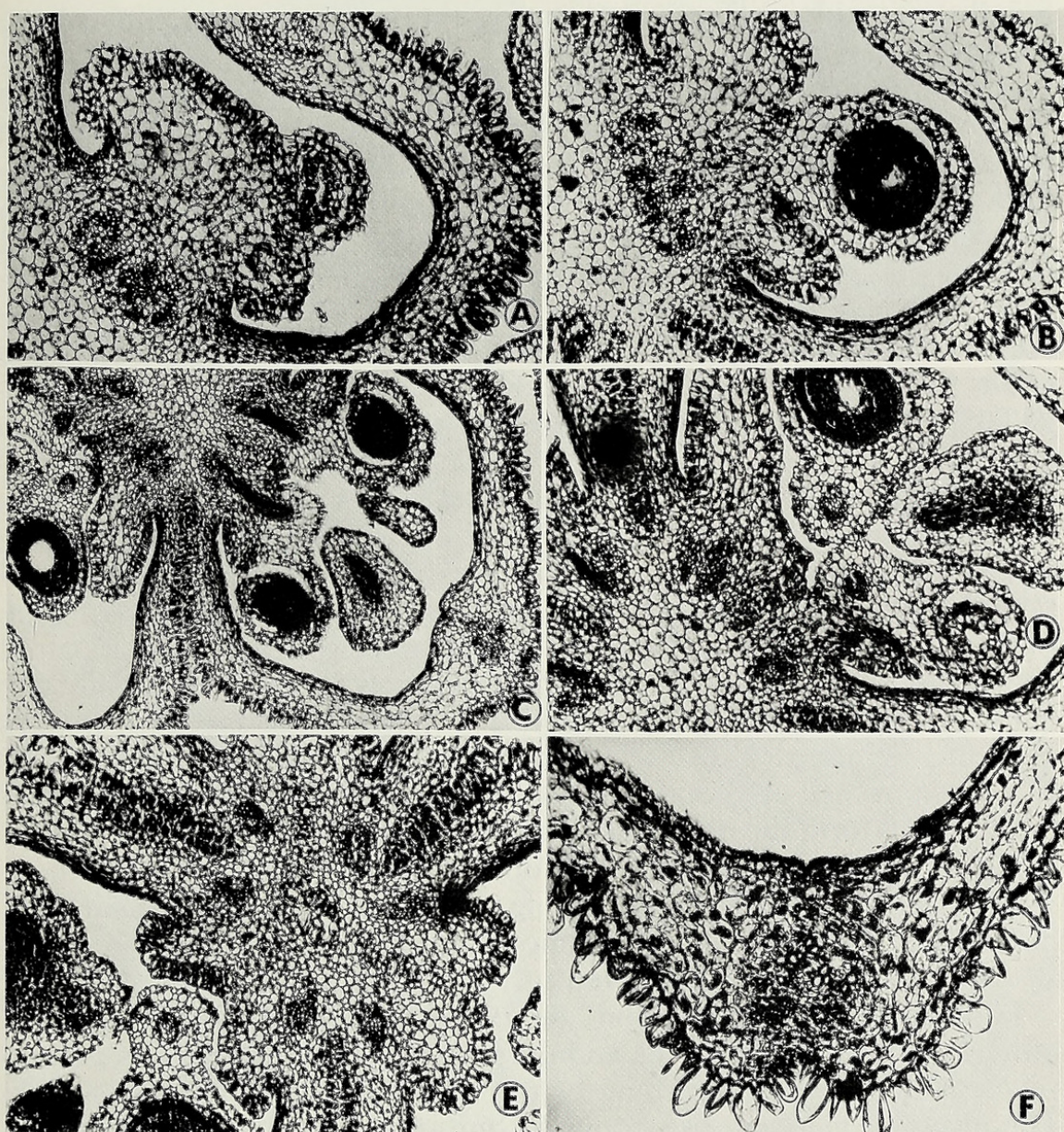


Fig. 6.—Gynoecium cross-section in *X. tenax*. A) Fused septal wing tips protruding into locules, papilloid cells on surface of the wing tips, which differ from those lining the locule and the carpellary epidermis, both ventrals reversed (50 \times). B) Each ventral divides with one half continuing upwards and the other half supplying the ovules of the lower tier, septal wing tip margins modified into obturators (50 \times). C) Second tier ovule supply, funicular traces departing to supply colateral ovules, deep septal indentation evident (37.5 \times). D) Second subdivision of ventrals, one division product supplies the second ovule tier (lacking in *X. asphodeloides*), whereas the other continues upwards into the stylar area (50 \times). E) Six ventrals (V) continuing upwards after second tier ovule supply, obturators still present and the inner central area subdivided along the septal radii creating the unilocular gynoecium (50 \times). F) Enlargement of dorsal notch over the dorsal bundle, also showing the outer epidermal papillae and the small, thin-walled cells lining the locule (60 \times).

bundles are physically divided during the mechanical opening of the locules.

A central ring of six bundles remains in the gynoeceium base following the formation of the inner stamen traces. At this level, all of the stamen traces have departed along the radii between these remaining six bundles. One final planar division that involves all six bundles occurs. This division is radial. There are 12 resulting branch bundles with six of the 12 branches fusing in pairs along the OTM-OS radii. The three resulting fusion products are the dorsals (D) (Figs. 3F, 4F, 5C). The dorsals (D) depart directly and horizontally along the OTM-OS radii under the yet unopened locules. Soon after the dorsals reach the carpellary margins, the outer stamens are cut off. The three dorsals do not branch in their vertical ascent to the three free styles (Fig. 9).

Six bundles remain in the central gynoeceial area after the formation of the dorsals (D) (Figs. 3G, 5C–F). These bundles are the remaining half-strands of the last planar division (Fig. 9). These six bundles directly establish the ventral supply by moving inward radially along the three septa in three paired sets. There is no fusion within each paired set. (Were they to fuse, it would be analogous to the formation of the dorsals.) At this level, the ventrals have normally arranged xylem and phloem, like the dorsals. The two ventrals, which supply the ovules of a given carpel, are continuous at a lower level with the bundles that branched to form the dorsal of that same carpel (Fig. 9). Neither septal axials nor ventral plexuses are involved in the ventral vascularization.

The two paired ventrals (V) along each septal axis disassociate and move apart laterally. With this movement, there is a reversal of the xylem and phloem of all the ventrals (Fig. 5C–E, 6A).

Following this reorientation, there are two ventrals with reversed bundles opposite the locules and dorsals. Concurrent with this ventral reversal, there is an inturning of the septal wing tips to the locules. The inturned margins, for example, obturators, are covered by papiloid cells and are part of the stigmatoid tissue system. The cells, which line the locules, on the other hand, are small, thin-walled, and closely packed (Figs. 3G–J, 4G–J, 6A–F, 8D–E).

The major difference in gynoeceial vascularization between *X. tenax* and *X. asphodeloides* is in the number of ovules and how they are supplied. In *X. tenax*, there are consistently four ovules in each carpel (Figs. 3, 4, 6C–D, 9), whereas *X. asphodeloides* consistently has two ovules per carpel (Fig. 8D). Consequently, *X. tenax* has a significant sexual reproductive advantage over *X. asphodeloides*. There are twice as many flowers per raceme and twice as many ovules (seeds) per carpel in *X. tenax* than in *X. asphodeloides*.

The funicular traces (F) in both species are collateral. The seeds of *X. asphodeloides* (two per carpel) are erect and basally attached (Fig.

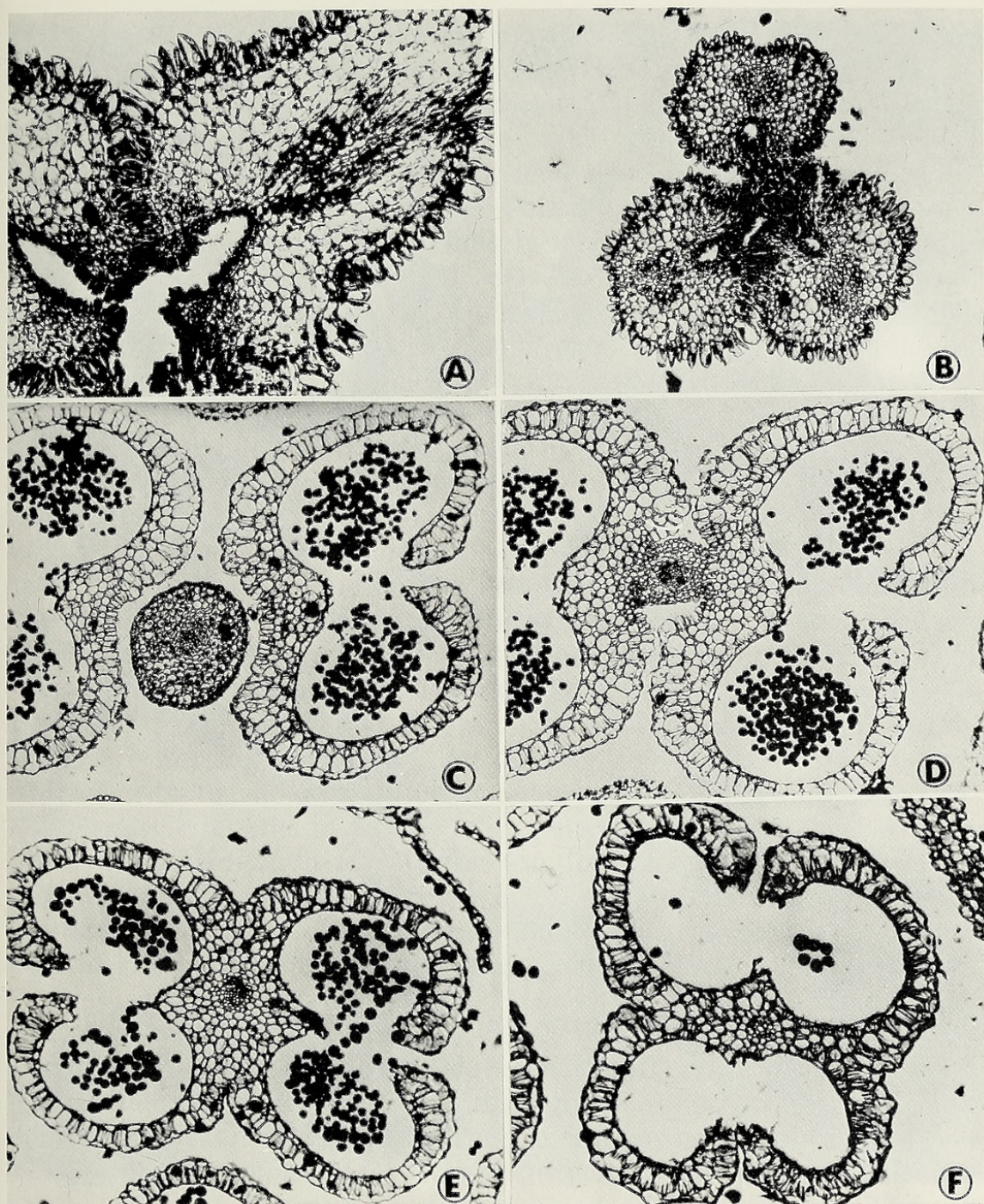


Fig. 7.—Stigma and anther cross-sections in *X. tenax*. A) Upper gynoecium showing common stylar canal, dorsal, and ventrals present (50 \times). B) Three styles freed along the septal radii, outer wall papillae similar and continuous with that of the carpels, septal wing tip papillae different (40 \times). C) Lower anther cross-section showing the free filament surrounded laterally by the two anther sacs, each sac has two chambers and dehisces via a lateral slit, the outer anthers are similar to the inner anthers (20 \times). D) Section above C, filament attached to the two anther sacs at the midanther length (20 \times). E) Section above D, stamen trace centered in connective, lateral slits still in same position (20 \times). F) Section above E, connective and stamen trace still present, no terminal confluence of chambers (20 \times).

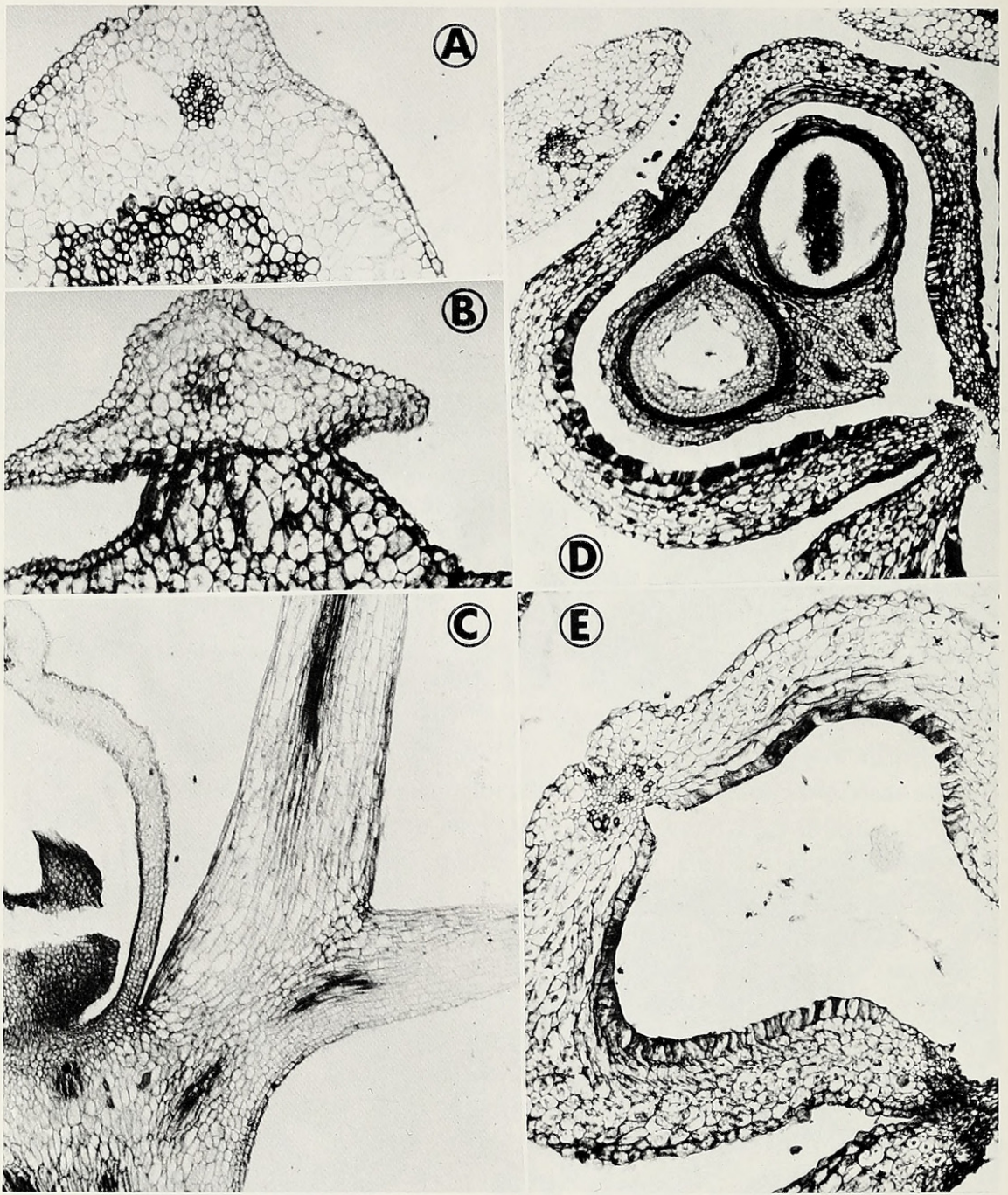


Fig. 8.—Selected floral sections of *X. asphodeloides*. A) Partial pedicel cross-section showing an adnate bract with a single vein, pedicel from the upper portion of the raceme (15 \times). B) Section above A showing the freeing of the bract at midpedicel length (15 \times). C) Longitudinal section showing the degree of epitepaly between an outer stamen and tepal, no similar degree of epitepaly occurs in *X. tenax* (30 \times). D) Mid-gynoecium cross-section showing the two collateral ovules within a locule; a dorsal notch, septal indentation and a central interlocular connection are evident (20 \times). E) Upper gynoecium cross-section showing a bifid dorsal, the dorsal notch and non-papilloid epidermis of the carpellary outer wall; the locule lining cells are similar to those in *X. tenax* (35 \times).

2D), whereas the seeds of the second tier in *X. tenax* (two additional per carpel) are variable in their packing. The seeds of both species are similar in size and shape. They are three-angled and lack terminal wing tips and appendages.

The division of the central gynoecial base continues between the inturred obturators of each locule. This division lags behind the opening of the three locules, but definitely interconnects the three locules along the dorsal radii (Figs. 6E–F, 8D–E). The tricarpellate gynoecium in *Xerophyllum* is, therefore, potentially unilocular (Figs. 3–4). The septal wing margins, however, remain fused along the septal radii, and are anchor shaped in cross-section along the vertical floral axis. The axial faces of the appressed, inner septal margins are covered by interdigitating papillae. These papillae, as those on the obturators, extend from this basal area, past the level of ovule supply, to the inner surface of the three free styler branches. These papilloid cells stain differently from the papilloid cells of the carpellary epidermis. The inner papillae form a continuous, internal stigmatoid support system for the canalized growth of the pollen tubes.

In bud the three free linear styles of both species are initially erect, but at anthesis they are recurved outwards along the dorsal radii. The styler arms are narrow and flexible. The inner exposed bases of these styles are lined with papillae. An opening between the styles is continuous with the upper unilocular cavity of the gynoecium (Fig. 7A–B). The style lengths in *X. tenax* are between 4.5 to 6.0 mm, whereas those in *X. asphodeloides* are not too dissimilar, 4.0 to 5.5 mm. The pollination system in both species is relatively open to both out- and inbreeding, because the versatile stamens are arranged in a circle around and above the divergent and recurved styler arms.

SUMMARY AND CONCLUDING REMARKS

The floral vascularization of both species of *Xerophyllum* is remarkably similar from the pedicel up through the tepals, stamens, and gynoecia. A species specific difference occurs in the gynoecia, however. *Xerophyllum asphodeloides* consistently has two ovules (seeds) per locule, whereas *X. tenax* has four ovules (seeds) per locule. The vascular difference associated with ovule number is merely an additional radial division of the ventral strands in *X. tenax*. The overall flower and fruit size of *X. tenax* is proportionately larger than in *X. asphodeloides*. The floral vascularization of *X. asphodeloides* represents a reduced and simplified version of that in *X. tenax*. Because of a greater ovule and seed number in *X. tenax*, it consequently has a greater sexual reproductive advantage.

The tepal supplying bundles are established in the lower halves of the pedicels. The outer tepal supplying bundles are established via

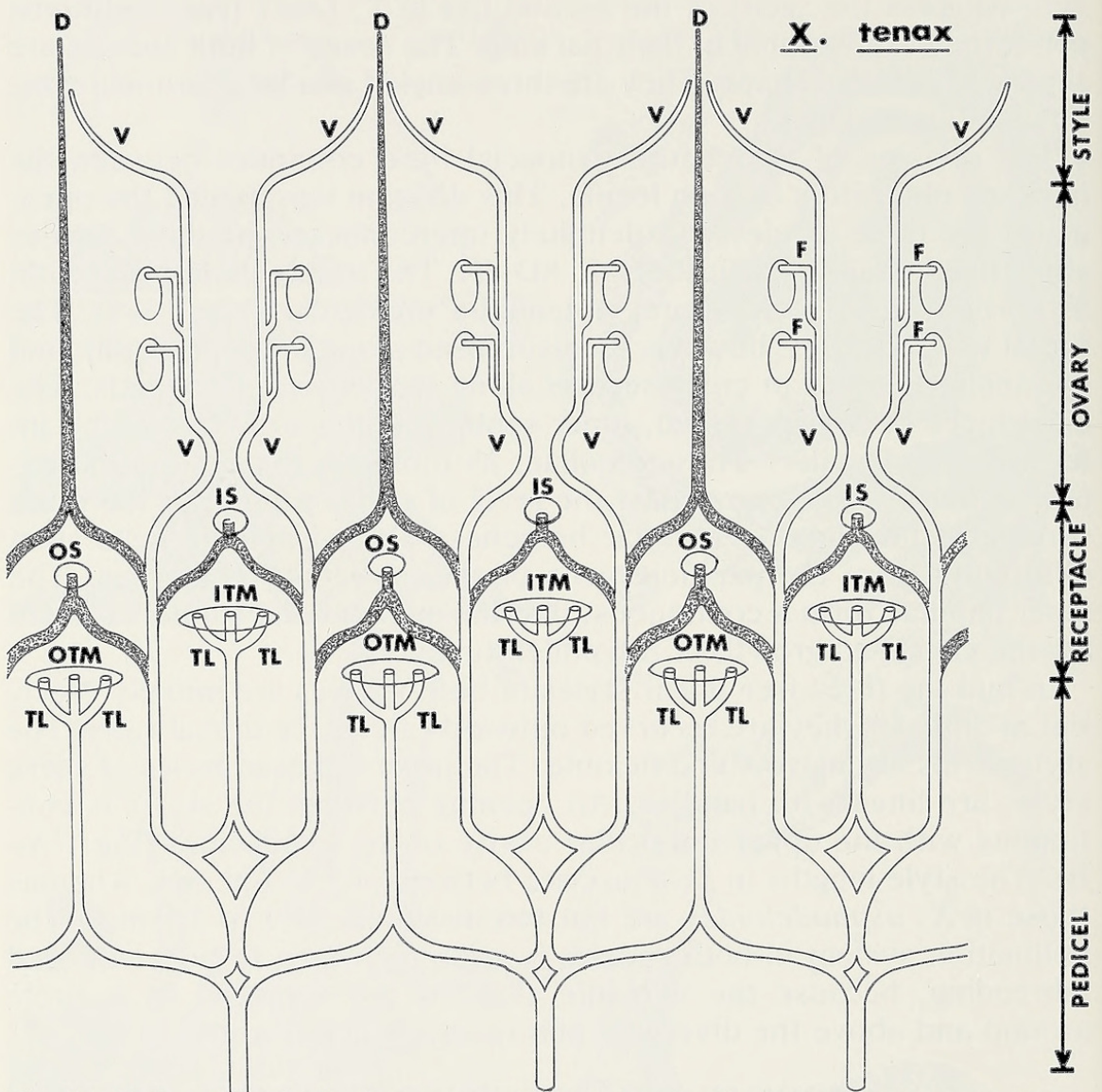


Fig. 9.—Roll-out longitudinal summary diagram for the floral vascular anatomy of *Xerophyllum tenax* [*Xerophyllum asphodeloides* differs in having a single funicular trace (F) from each ventral (V), not two.] The various bundles are labeled with text introduced letter codes: OTM = outer tepal median, ITM = inner tepal median, TL = tepal lateral, OS = outer stamen, IS = inner stamen, D = dorsal, V = ventral, and F = funicular.

fusion near the pedicel attachment to the raceme axis. The inner tepal supplying bundles are established via fusion, but in the midpedicel region. The receptacle base has a double ring of 12 bundles, that is, six outer ring bundles (the tepal supply formed in the pedicel), and six inner core bundles. The bundles of the two rings are on alternate radii.

Each tepal of both whorls receives a similar compound bundle. Each compound bundle divides to form a median and two associated laterals before its tepal is cut off. The pattern of vascularization is the same for both the outer and inner tepals. In mature flowers of both species,

there is a difference in the number of laterals in the outer and inner tepals. This is due to a differential in the number of radial divisions amongst the outermost laterals. *Xerophyllum tenax* has five veins, that is, two laterals plus median plus two laterals in its outer tepals; and seven veins, that is, three laterals plus median plus three laterals in its inner tepals. A similar pattern with a greater vein number in the inner tepals than in the outer tepals also occurs in *X. asphodeloides*.

The stamen traces of both the outer and inner whorls are fusion products. They arrive via radial branches from the inner ring bundles which fuse. The filaments are freed directly from the receptacle; there is a limited amount of epitepaly in *X. asphodeloides*. The filaments within each species are equal in length, dilated basally and filiform terminally. The anthers are versatile, attached at midlength, laterally dehiscent and not confluent terminally.

The basal gynoecium supply in both species of *Xerophyllum* is relatively simple. The gynoecial base has six bundles. The three dorsals are formed as fusion products via side branches from these six bundles. After the establishment and localization of the three dorsals, the six continuing parental bundles associate in three pairs, as ventrals, along the septal radii. The ventrals are characterized by a reversed arrangement of their conducting tissue. The six ventrals directly supply the ovules of the three carpels.

The placentation in *Xerophyllum* has usually been described as axillary and associated with a trilocular gynoecium, but the placentation is actually parietal due to both a pulling apart of the septa along their axial faces and to an inward unrolling of the inner septal (placental) margins as far down as the base of the ovary. The tricarpellate gynoecium is therefore unilocular.

The fruit in *Xerophyllum* is a loculicidal capsule. The flowering gynoecium has dorsal grooves along which the locules are subsequently opened. Septal indentations are also present, but there is no indication of septicidal splitting. The three carpels are fused only along the inner septal margins and the basal wing tips. Rhaphides occur in both species, especially in their gynoecia. In *X. tenax*, the outer carpellary wall has a papilloid epidermis, this is lacking in *X. asphodeloides*. A stigmatoid tissue system composed of a second papilloid cell type was described. These cells are continuous from the three free stylar tips down the common style and into the unilocular ovary along the axial, appressed faces of the inner septal margins.

Anderson (1940) who followed the Englerian system summarized the vascular condition in *Xerophyllum asphodeloides* as follows: "The origin of (all) the traces is most like that of *Veratrum*, and the carpels are as free as in that genus; but there is no perigyny and the receptacle is rather elongated; there are but two ovules. All in all this is the most

primitive member of the group (Melanthioideae), anatomically; and except for the reduction in ovule number there are no advanced characters present." Furthermore, the reduced ovule number in *X. asphodeloides* is part of an evolutionary reductional series from the four ovule per locule condition in *X. tenax*.

Proper and critical assessment of the tribal position of *Xerophyllum* in both the Englerian (Engler, 1888; Krause, 1930) and Hutchinsonian (Hutchinson, 1934) systems must await further anatomical work among the other primitive members of the Melanthioideae. Such work is in progress.

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