The floral vascular anatomy and carpel morphology of the coastal Californian endemic *Scoliopus bigelovii* Torrey are presented and this is followed by a comparison to its assumed Paridean relative of eastern North America *Medeola virginiana* L. The floral vasculature of *S. bigelovii* is established from a 15-bundled, axial pedicel configuration, which consists of an outer zone of 12 bundles and an inner zone of three large bundles. Six of the outer zone bundles depart directly as the three outer and the three inner tepal medians. Each of the six remaining outer zone bundles undergo two successive radial divisions whereupon 12 tepal laterals and six ventrals are formed. Basally each of the six tepals receives three bundles, that is, a median and two laterals. Whereas several radial divisions occur laminally within the outer tepal laterals to create a maximum of 13 bundles, that is, 12 laterals and a median, no such radial division occurs within the inner tepal laterals. Between each of the three pairs of ventrals a fusion septal axial of short vertical duration is formed. Two-ranked, horizontal funicular traces depart directly from each of the paired ventrals. Whereas the ventral vasculature has an outer zone origin, the three dorsals and the three outer stamens (there are no inner stamens) are division products of the three large inner zone bundles. The dorsals are unbranched and terminate in the tips of the three recurved stylar arms. There is no interconnection between the dorsal and ventral supplies.

Several aspects of the floral morphology are derived or advanced and relate to the pollination and seed dispersal (myrmecochory) of this species. Basally the broad, recurved outer tepals are imbricated into grooves on the abaxial surface of the narrow erect inner tepals. The adaxial surfaces of the outer tepals are lined with nectiferous

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tissue which in conjunction with the basal tepal imbrication forms a floral tube. Opposite and above these tepal nectaries are the extrorse anthers, which are also versatile. The tricarpellate, syncarpous gynoecium is unilocular from the level of opening into the common style. The triquetrous ovary is flattened along the dorsal area and ridged along the ventral area. The bitegmic ovules are attached in two-ranked rows in the ventral corners. Stigmatoidal tissue is continuous from the three recurved stigma tips down through the common style and along the funicular-ventral margins. Whereas rhaphides are not present, subepidermal cells with colored material are.

Floral vascular evidence has been added to the continuing discussion on the relationships of the four genera of the Englerian Parideae (or the Hutchinsonian Trilliaceae). The vascularization of *S. bigelovii* differs markedly from that of *Medeola virginiana*. Besides these differences, previously reported differences in vegetative and floral morphology, embryology, and cytology are summarized as a step towards an overall tribal evaluation.

**Introduction**

Though distinctive and showy, the genus *Scoliopus* Torrey is small with only two species—*S. bigelovii* Torrey and *S. hallii* Watson. These two species are respectively confined to the Coastal and the Cascade Mountain Ranges of California and Oregon. In California, the coastal distribution of *S. bigelovii* (Fig. 1) approximates the generalized, paleoenemic range of the "coastal redwood," *Sequoia sempervirens* (D. Don) Endl. Such similarities in present-day, relictual ranges are usually indicative of an isolated Arcto-Tertiary element (Munz and Keck, 1959; Stebbins and Major, 1965; Axelrod, 1976; Raven and Axelrod, 1978). The Oregonian endemic, *S. hallii*, on the other hand, is only known from the western slopes of the Cascades and the coastal mountains from Tillamook County south to the Californian line (Hitchcock and Cronquist, 1973). Therefore, within the mountains of the far west *Scoliopus hallii* is replaced southward by *S. bigelovii*.

Since 1857 when Torrey first described and illustrated *S. bigelovii* (t. 22) as a new species, it has repeatedly been illustrated (Regel, 1875, t. 834; Hooker, 1897, t. 7566; Parsons, 1907:263; Thomas, 1961: Fig. 49). A photograph of the type specimen, which is presented (Fig. 2), shows enough similarities to the illustration presented by Torrey (1857: t. 22) to know with some certainty that this material was used for the artwork. From this material (Fig. 2) a lectotype is designated.

Four common names have been used for *S. bigelovii*—"slink pod," "slink lily," "fetid adder’s tongue," and "brownies." Each name and its usage denote some particular aspect of this species' biology. Both "slink pod" and "slink lily" are in reference to the looped twisting or coiling of the elongated fruiting pedicels, which locates each terminal "pod" on the ground near or under the parental leaves whereupon the released seeds are dispersed by ants (myrmecochory) (Berg, 1959). *Scoliopus*, Torrey (1857), means crooked foot and is also an allusion to the tortuous course of the fruiting pedicels (Fig. 2). "Fetid adder’s
"Brownies" also refers to the genus Scoliopus bigelovii Torrey based on specimens in the University of California-Berkeley (UCB) herbarium. Tongue, on the other hand, combines a reference to the reddish-brown mottling on the two, expanded, basal leaves and an unpleasant floral odor, which is not unlike that of beached star-fishes (Parsons, 1907) or decaying seaweed (Hooker, 1897). "Brownies" also refers to the gen-
Fig. 2—The above sheet (NY) represents a mixed collection from two distinct gatherings. Both fortunately were the only two gatherings cited by Torrey (1857:145) in the type description. One gathering is limited to flowering material, whereas the other is chiefly of fruiting material. Both materials were used for the composite type description and the accompanying illustration (t. 22) judging from the materials and the sketches on
eralized reddish-brown mottling on the leaves as well as the floral parts. Jepson (1922) pointed out that this common name was confined to Humboldt County, California. The coastal populations of *S. bigelovii* in this county are clearly disjunct from those further south along the coast (Fig. 1). Flowering occurs between January and February within the total range and seed dispersal between May and June.

Taxonomically *Scoliopus* has been associated with *Trillium, Medeola* and *Paris*. This association began with Watson’s (1879) Liliaceae monograph and has continued in the present Englerian (Engler, 1888; Krause, 1930) tribe Parideae and the Hutchinsonian (Hutchinson, 1934, 1959) family Trilliaceae. Berg (1959, 1962a, 1962b) strongly questioned this association for both *Scoliopus* and *Medeola*. For the former, Berg (1959) presented a thorough investigation of the gross vegetative and floral morphology of *S. bigelovii*, which also including brief observations on the floral vascular anatomy. Additional and critical observations on the embryogenesis, pollination ecology, and seed dispersal provided abundant data (Berg, 1959) to seriously question this association for *Scoliopus* (Berg, 1962b).

The present research report on the floral vascular anatomy of *S. bigelovii* as a representative of the genus *Scoliopus*, which only has two species, is part of a long range study on the evolution of the liliaceous berry (Utech and Kawano, 1975, 1976a, 1976b, 1976c; Utech 1978a, 1978b, 1978c, 1978d, 1978e). Whereas the floral vascular anatomy of the monotypic *Medeola virginiana* has previously been presented (Utech, 1978a) and is here compared to that of *S. bigelovii*, a final appraisal of the tribal relationships of *Scoliopus* must await the

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the upper portion of the sheet. Consequently, the specimens from both gatherings are potential types. In the lower left one-quarter, there are two flowering elements each with elongated pedicels. These are the second of the gatherings cited by Torrey, that is “specimens in full flower, collected by Mr. Samuels, but in what part of California we have not been informed.” A note on the sheet under these two elements further indicates “rec’d from Dr. Gray, Dec. 1856.” The other gathering is of a complete, mature specimen with numerous, looped pedicels and is centered directly on the sheet. Most of the flowers are past anthesis which corresponds to Torrey’s note, “past flowering early in April.” This element is clearly the Bigelow collection made during the 1853–1854 Whipple Railway Route Expedition (Torrey, 1857), and was cited first by Torrey and should be designated the lectotype for *Scoliopus bigelovii*. The Samuels’ collection therefore becomes a paralectotype. In the lower left corner is a standard Whipple Expedition label with Dr. J. M. Bigelow printed as the collector, California as the locality, and *Scoliopus* hand written, presumably by Torrey, on it. The lower right corner has this hand written information—“Tamul Pass, California, Whipple’s Exped., Dr. Bigelow.” Torrey’s Tamul Pass is presently Mt. Tamalpais, California, which is just north of San Francisco. (Photograph courtesy of the New York Botanical Garden.)
Fig. 3.—Pedicel and receptacle vascularization in *Scolioptus bigelovii*. A) Upper pedicel cross-section showing a large and small lobe and the two zones of vascular bundles, which are in the 15-bundled configuration (25×). B) Enlargement of A with emphasis on the 15-bundled configuration, that is, the three large, inner zone bundles and the 12, outer zone bundles which can be further subdivided into the three OTM establishing bundles (arrows), the three ITM establishing bundles located 60° from each of the former, and six additional bundles each located between an OTM and an ITM establishing bundle (40×). C) Upper pedical showing two of the three large inner bundles, a marked ITM, but no ITL at this level and the radial origin of the OTL bundles (white dotted lines); the two OTM (top and bottom) are further from the center than the marked ITM (40×). D) Lower receptacle showing the origin of both the ITL and the OS bundles; the two ITL which accompany each ITM are radially derived; each inner zone bundle which
completion of our work on *Trillium* and *Paris* (manuscripts in preparation).

**MATERIALS AND METHODS**

Floral material of *Scoliopus bigelovii* used in this study consisted of buds through fully opened flowers, as well as isolated gynoecia of varying ages. These flowers had been fixed, processed through a TBA series and embedded in wax by Marion S. Cave (Botanical Garden, University of California–Berkeley), and given as gift research material for which the author is indebted. The isolated gynoecia had been fixed in Craf fixative, whereas the other materials had been fixed in FAA. Both fixatives were noted on tags within the wax. The collection locality was tag noted as "Muir Woods" (Marin Co., California). Though no collection dates were given for these wax materials, a reference to slide material made in 1948 by Cave (1966) indicated Muir Woods. Presumably the materials used for these slides and that in the wax were from the same gathering or at least from the same general area and collected at a different time.

Standardized paraffin sectioning (12–16 μ) and staining (safranin-methylene blue) techniques (Johansen, 1940; Sass, 1958) were used on the above materials. A total sample of 35 complete, serial cross-sectional series were prepared on flowers of varying ages, as well as several serial longitudinal sections. Fig. 1 presents a distribution map for *S. bigelovii* based on specimens in the herbarium at the University of California–Berkeley (UCB). Fig. 2 is a photograph of the lectotype of *S. bigelovii*, which was collected north of San Francisco (Mt. Tamalpais). Figs. 3–5 are photomicrograph composites, which show selected aspects of the floral morphology and the associated vascular anatomy. Figs. 6–8 are summary diagrams for the pedicel to stigma vascularization. The methodology of vasculature diagramming and presentation, as well as the letter coding of bundles, parallels that in our previous liliaceous studies (Utech, 1978a, 1978b, 1978c, 1978d, 1978e). Although the letters for the various vascular bundles used here are similar to those of our previous papers, a correspondence should be given between them and those used by Berg (1959) for *S. bigelovii*: D (dorsal) = m.s. (median carpellar strand); V (ventral) = p.s. (placental strand). Table 1 compares the vasculature of *S. bigelovii* as presented in this paper with that of *Medeola virginiana* (Utech, 1978a).

**OBSERVATIONS**

**Pedicel Vascularization**

The sympodial umbel of *Scoliopus bigelovii* commonly contains three to eight, rarely up to 12, flowers. Each flower is attached to a slender, bractless, erect pedicel, which is shorter than or equal to the leaves at anthesis. The flowering pedicels are green and often spotted with reddish-brown dots, which according to Berg (1959) are "most numerous on pedicels or pedicel parts exposed to the sun." The length divides forms an outer stamen (OS) trace abaxially and a dorsal (D) adaxially (35×). E) Upper receptacle showing the departure of the inner tepal vasculature (an ITM and two ITL) and the OS traces; the dorsal and ventral establishing bundles are located centrally (30×). F) Lower gynoecium showing the formation of the septal axials (SA) between each ventral (V) pair; subepidermal cell with stained (colored, cf. text) material indicated (lower arrow); no rhaphides are present (35×).
of the flowering pedicel usually averages 15.0 cm, although the fruiting pedicel is longer and recurved to the ground. In cross-section the pedicel is triangular for most of its length. However, near the base of each flower, the number of pedicel angles is six, that is, the three continuing ones, each 120° apart and three smaller, alternating ones. The three larger pedicel angles are continuous with the lower midribs of the three outer tepals (Figs. 3A, 6A–D, 7A–D).

Throughout the triangular portion of the flowering pedicel, a 15-bundled configuration occurs in cross-section (Figs. 3A–B, 6A, 7A). All of these bundles have a normal phloem (abaxial) and xylem (adaxial) arrangement. The 15-bundles can be grouped into two broad, concentric zones. The inner-most zone contains three large bundles each of which lies along a radius that passes through one of the pedicel’s triangular edges (Fig. 3B, arrow). The outer zone contains 12 bundles. Six of these are closer to the pedicel’s periphery than the remaining six. The outer six are spaced 60° apart and establish at a higher level the tepal median supply of both the outer and inner tepal whorls, that is, the three outer tepal medians (OTM) and the three inner tepal medians (ITM) (Fig. 8). The three bundles, which establish the three outer tepal medians (OTM), like the three larger inner bundles, are also on the radii of the pedicel’s triangular edges. Besides the six tepal median establishing bundles in the outer zone, there are six additional bundles that alternate with them. This overall vascular pattern characterizes the elongated pedicel for most of its length. Furthermore, Berg (1959) presented a cross-sectional figure (Fig. 24), which clearly shows this pedicel vascular configuration and organization in the short stem below the level of leaf attachment.

Approximately 5 mm below the base of the flower or receptacle, changes occur in both the pedicel’s cross-sectional shape and its vascular configuration. The pedicel changes from three-angled to six-angled. The three new lobes are smaller and alternate with the three larger lobes. Radii which bisect the smaller lobes also pass through the inner tepal medians (ITM). With an increase in the pedicel’s cross-sectional area, the six tepal medians depart outward radially along the radii of the six lobes (Figs. 3C–D, 6A–C, 7A–C). Also at this level there is a radial division within each of the six, outer, nontepal median establishing bundles (Fig. 8). Consequently, the upper pedicel has 21 bundles, that is, the six tepal medians, the 12 outer zone bundles (six pairs via the radial divisions), which alternate with the medians, and the three larger inner bundles.

The erect flowering pedicel lacks a perivascular sclerenchymous sheath. However, such a fibrous sheath is present in the twisted, looped fruiting pedicel. The postanthesis pedicel recurvation is not a geotropic response, but rather is due to a differential rate of elongation
within the pedicel and the delayed appearance of the sclerenchymous sheath. Before the fruit dehisces on the ground, the looped pedicel is extremely turgid. A double pedicel loop with the fruit directed upwards is not uncommon. The pedicel then, however, loses its turgidity and collapses downward along with its terminal fruit. Subsequently the dehiscing fruit with its oil-appendaged seeds is grounded closer to the parental plant than would have occurred had the pedicel remained erect and had fallen laterally.

_Tepal Morphology and Vascularization_

The flowers of _Scoliopus bigelovii_ are of the general liliaceous type, viz. bisexual, actinomorphic, hypogynous, cyclic, and trimerous. They deviate from the typical liliaceous flowers in only having three, outer stamens and no inner stamens opposite the inner tepals. The flowers are consequently tetracyclic.

Although the segments of the two tepal cycles are different, both the outer and inner tepals are distinct and free. The broadly lanceolate to ovate outer tepals are spreading and recurved at their midlengths, and average 16.2 mm (range: 14.5–17.8 mm) in length and 6.9 mm (range: 5.8–7.4 mm) in width. The outer tepals are showy. Their basic color is greenish-yellow with prominent reddish-brown longitudinal stripes. Berg (1959) notes that these stripes are due to \"densely placed individual color dots, which results from individual cells containing coloring matter.\"

The three, linear to subulate, inner tepals, on the other hand, are erect with their upper tips curved inwards over the top of the gynoecium. The lengths of the ascending inner tepals equals that of the recurved outer tepals. However, a significant size difference occurs in their width. The inner tepals only average 1.3 mm (range: 0.8–1.7 mm) at their widest point. The inner tepals also show a color difference from the outer tepals. Both the upper adaxial and abaxial surfaces of the inner tepals are a deep maroon purple, whereas the basal portions of the inner tepals are a palish yellow adaxially and reddish-brown striped abaxially. This reddish-brown basal striping is \"again caused by colored, papillate epidermal cells, arranged more or less distinctly in three longitudinal stripes, one median and two marginal\" (Berg, 1959). These colored stripes correspond to the locations of the inner tepal's vasculature. Whereas the stripes on the inner tepals are restricted to the lower abaxial surface, the numerous, colored stripes on the outer tepals are found on the adaxial surface.

During anthesis, the open flower has a cup-like appearance, which is due to the lower imbrication of the two tepal cycles (Figs. 4A–B, 6C–E, 7C–E). The outer tepal margins fit laterally into longitudinal grooves on the abaxial surface of the inner tepals. This imbrication
Fig. 4.—Tepal and stamen vascularization in *S. bigelovii*. A) Basal tepal cross-section showing the lateral edges of two outer tepals (OT) imbricated into abaxial grooves on an erect inner tepal; the ITM and the two ITL are indicated; each inner tepal has a maximum number of only three veins (40×). B) Basal outer tepal (OT) and outer stamen (OS) cross-section showing basally divergent anther sacs, the free filament (Fil) and the large, multibundled outer tepal with nectiferous tissue adaxially; each outer tepal has a maximum number of 13 veins, that is, six OTL plus an OTM plus six OTL (25×). C) Lower level stamen cross-section showing the free filament (Fil) with normally arranged phloem and xylem in the OS bundle and the free anther in which the phloem and xylem of the OS are reversed due to its downward course; another sac dehiscence is via vertical, abaxial slits (extrorse); the outer tepal nectiferous tissue is still present (25×). D) Midlevel stamen cross-section showing the fusion of the free filament and the free anther as well as stigmatic tip of the recurved stylar (St) arm (cf. Figs. 6I–J; 7I–J) (25×). *Scoliopus bigelovii* only has three outer stamens.

(Fig. 4A–B) persists up to the level where the outer tepals recurve. The lower inner surfaces of the outer tepals have a broad, centrally located band of nectiferous cells (Fig. 4B), which extends from the level where the outer tepals are freed up into the recurved region. The tepals are cut-off from the lobed or angled regions of the upper pedicel. The three outer tepals are freed first with the three outer stamens (filaments) adnated to them for a short vertical distance. The imbri-
cated tepal arrangement and basal outer tepal nectaries are directly related to the outbreeding pollination mechanism of this species.

As the morphology of the two tepal whorls differs significantly, so too does the vascularization of these two whorls. Within the expanded, six-lobed upper pedicel, the three outer tepal medians (OTM) and the three inner tepal medians (ITM) depart outward along the six lobe radii. There is no division within or fusion among the medians of either whorl from their axial course in the pedicel to their termination in the upper tepal tips. With the departure of the six medians, the outer zone of the upper pedicel has 12 remaining bundles, that is, the six pairs noted earlier. The two bundles, which are adjacent to the departing outer tepal median (OTM), are pair halves of two different radial divisions and they depart outward with the centered outer tepal median (Figs. 6A–D, 7A–D). Three such two-bundle sets, that is, a total of six of the 12 outer ring bundles, exhibit this departure pattern, and directly establish the outer tepal lateral (OTL) vascular network.

Although each outer tepal receives three bundles basally, that is, the outer tepal median (OTM) and two outer tepal laterals (OTL) (Figs. 6A–D, 7A–D, 8), the expanded recurved outer tepals usually have 13 vein bundles, that is, the outer tepal median (OTM) and 12 laterals. Six tepal laterals (OTL) are on each side of the OTM. To form this large number of laterals, the two basally derived laterals (OTL) each undergo a series of successive radial divisions (Figs. 6D–H, 7D–H, 8). There is no cross-connection between the laterals within the laminal tepal surface and each laterals ends marginally within the upper tepal surface.

Another radial division occurs among the six remaining outer zone bundles. The level of this second radial division is within the receptacle. The division product halves which are adjacent to the departing inner tepal medians (ITM) depart with the centered median (Figs. 4A, 6C–H, 7C–H, 8). These bundles are the inner tepal laterals (ITL). Basally, therefore, each inner tepal receives a median (ITM) and two laterals (ITL) (Fig. 8). But unlike the outer tepals, there is no further radial subdivision among the laterals within the narrow, inner tepals. The six remaining bundles after the departure of the inner tepal laterals (ITL) directly establish the gynoecium’s ventral supply (Fig. 8). The bundles in the outer pedicel ring, therefore, establish the six, independent tepal medians and via successive radial divisions the outer and inner tepal laterals as well as the ventral supply.

**Stamen Morphology and Vascularization**

There are only three stamens in *Scoliopus bigelovii* and these three are consistently in the outer staminal position. No vestigial traces of the inner stamens or of staminodes were observed in our material, nor
Fig. 5.—Gynoecial vascularization in *S. bigelovii*. A) Midlevel cross-section showing the tricarpellate, unilocular gynoecium; the dorsal (D) bundles are along the flattened sides, whereas the ventral network is in the ridged corners (20×). B) Enlargement of A showing the paired ventrals in the corner; dorsals (D) indicated (40×). C) Upper gynoecium cross-section with nine bundles, that is, the three dorsals (S) and the three pairs of ventrals; stigmatoidal tissue covers the funicular attachment area and is continuous from the basal locular region up into the common style (25×). D) Cross-section showing the transition from the upper ovary to the common style; the unilocular cavity closes as it opened, that is, along the dorsal (D) radii; ventral bundle pairs still present; colored cells present in the subepidermis (25×). E) Cross-section showing the erect common style;
have any ever been reported. The three stamens are basally adnated to the outer tepals for a short distance, ca. 0.5 mm (Figs. 6E–H, 7E–H). The free filaments are short (ca. 5 mm), slightly dilated in cross-section and curved outwards at the level of anther attachment. The greenish-yellow, oblong anthers are adaxially attached slightly below their midlengths (Fig. 4B–D). Between the anther sacs, the connective tissue is flat. The anther sacs are, however, free and divergent basally (Fig. 4B). Due to the location and level of filament attachment, the anthers are versatile. Dehiscence is extrorse, that is, via two vertical abaxial slits (Fig. 4C–D). The endothecial cells, which line the anther sacs, have banded thickenings.

Whereas the origins of both the tepal and ventral vasculatures can be traced to the outer ring of pedicel bundles (Fig. 8), the origin of the three outer stamens (OS) traces is from the three, large, inner pedicel bundles (Figs. 3D–E, 6A–D, 7A–D). The three inner ring bundles share common radii with the outer tepal medians (OTM). Each inner bundle undergoes a division that leaves two bundles along each centered OTM radius. This division is unlike the radial divisions associated with the formation of the tepal laterals and the ventrals. It is an internal division or splitting, whereby the derived outer stamen bundles appear to be derived from within the large parental bundles. The outer most bundle of each division is the outer stamen (OS) trace, whereas the inner most becomes the dorsal (D) bundle (Figs. 3D–E, 6C–F, 7C–F, 8). The OS traces may in all likelihood be fusion products due to the rapid opening-closing division of the large (compound) inner bundles. The OS traces depart directly and horizontally following their formation.

The OS traces exhibit a peculiar downturned course as they enter the connective regions of the anthers. A cross-section through the lower anthers shows a given OS trace in two places, that is, in the filament where a normal arrangement of phloem and xylem occurs and in the lower connective tissue where the arrangement of the conducting cells is reversed (Fig. 4D). One could infer that the anther had been inverted such that the existing extrorse condition had been derived (evolutionarily) from a pre-existing introrse condition. The abaxial zone of pollen dispersal is a definite adaptation for outbreeding, and conforms to the tepal geometry with its nectary.
Gynoecium Morphology and Vascularization

Unlike most tricarpellate, syncarpous, liliaceous gynoecia in which the dorsal regions correspond to the corner or ribbed portions of the pistil, the dorsal regions in Scoliopus bigelovii are laterally flattened or compressed and the ventral regions occupy the corner or ribbed portions of the pistil (Figs. 5A–B, 6G–I, 7G–I). The compound gynoecium is formed by limited fusion along the outer septal margins which subsequently forms the three ribs. The gynoecium is triangular in cross-section with the ventral regions occupying the points.

Furthermore, most liliaceous gynoecia have septal wings, which are laterally fused and protrude into the common locular spaces. Septal glands may often occur in areas where the lateral septal fusion is incomplete. This septal inrolling and fusion usually results in the mar-

Fig. 6.—Serial cross-section of S. bigelovii. A) Three-lobed mid-pedicel with 15-bundled configuration, which consists of three bundles in an inner zone and 12 bundles in an outer zone. B) Six-lobed upper pedicel with 21-bundled configuration, which occurs following the origin of the six outer tepal laterals (OTL); the six tepal medians (3 OTM plus 3 ITM) are peripheral in the six lobes; and three inner zone bundles remain centrally located. C) Upper pedicel transition to the receptacle with 21 bundles; the outer and inner tepals defined. D) Receptacle base showing the origin of the inner tepal laterals (ITL) via radial division of outer zone bundles, and the three outer stamens (OS) and the three dorsals (D) via divisions along the OTM radii; radial division has occurred in the outer tepals to increase the number of laterals present; the three inner zone bundles divided to form the dorsals adaxially and the outer stamen bundles abaxially. E) Additional radial division within the outer tepals to increase the number of laterals; the inner tepal laterals (ITL) depart with their centered median (ITM); a nine-bundled configuration remains centrally, that is, the three dorsals (D) and the three pairs of ventrals (V). F) Gynoecium freed from the tepals and stamens; the three outer stamens, there are no inner stamens, are adnated to the outer tepals for a short vertical duration; the inner tepals only have three bundles (an ITM and two laterals), whereas continued radial division occurs within the outer tepal lateral supply; the three outer stamens remain along the OTM-OS radii, whereas the paired ventrals (V) close the gaps along the three ITM radii. G) The three outer stamens (OS) are freed from the outer tepals; additional radial division has occurred within the laterals of the outer tepals; the locale centrally and along the dorsal radii; three septal axials (SA) are formed, one for each ventral pair; the outer tepal lateral margins are imbricated into grooves on the abaxial surface of the small, erect, inner tepals. H) Triquetrous gynoecium with flattened dorsal (D) sides and ridged ventral (V) corners; the three septal axials have ended; ovule supply is via ranked, horizontal funicular (F) traces from the corner ventral pair; stigmataloid tissue present in the ventral corners; each outer tepal has 13 bundles, that is, six OTL plus an OTM plus six OTL. I) Upper gynoecium located centrally with three, recurved stylar arms located peripherally; the phloem and xylem of the dorsals (D) in the stylar arms are reversed in relation to the arrangement in the carpellary walls; the stylar arms of the tripartite style pass over the top of the three extrorse anthers. J) Upper gynoecium with only the three dorsal (D) bundles remaining in the common stylar portion and in the three recurved arms.
ginal placentae being centrally located with an associated reversal of the phloem and xylem elements of the ventral bundles. Neither protruding septal wings nor central placentae with reversed conducting elements occurs in the gynoecium of *S. bigelovii*, and in comparison to other liliaceous gynoecia, the gynoecium of the former must be considered as secondarily primitive or highly reduced.

The gynoecium of *S. bigelovii* is also unusual in that it is unilocular from its basal level up through the common hollow style. The locule opens from the center outwards along the dorsal radii. Since the various gynoecial bundles remain in a peripheral position as the locule opens to its maximum size, there is no inward movement of the ventrals (V) (Figs. 3F, 5A–B, 6F–I, 7F–I). The placentation is parietal, due to the peripheral and corner position of the ventrals (Fig. 5A–B). At anthesis the greenish color of the gynoecium is marked with reddish-brown dots that are located in the subepidermal cells of the pericarp. However, no rhaphides were observed in the gynoecium or in the other floral elements of the various flowers of the different ages examined.

The upper gynoecium is also strongly three-angled (Fig. 5C) and unilocular. As the common gynoecial cavity (locule) closes along the three dorsal radii in a pattern similar to its opening, a hollow stylar canal is formed. This canal is lined with papillate, stigmatoidal cells (Fig. 5D–E), which are continuous from this stylar region down along the three placental edges of the inner gynoecium (Fig. 5A–B) to the basal level of the gynoecium. The common ascending style is short and is subdivided into three, free, recurved, stylar branches (Fig. 5F). This stylar recurving is along the dorsal radii. A cross-section in the stylar region shows a given dorsal in two places, that is, in the style with a reversed orientation of its xylem and phloem and in the carpellary wall or upper common style where the arrangement of the conducting elements is normal. The recurved stylar branches pass over the tops of the anthers (Fig. 4D). Each stylar branch has an upwardly and outwardly open groove, which is directed away from the same flower’s anther and pollen. The stigmas, which terminate each of the well-developed stylar arms, are minute. The tripartite style with localized stigmas is a further adaptation for outbreeding.

The ovule position in *S. bigelovii* is peripheral, because the ventrals (V) are along the angled periphery of the gynoecium and the placentae

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Fig. 7.—*S. bigelovii*, cross-sections of Fig. 6 after transformational projections with selected vascular bundles connected. Lettered cross-sections correspond to those in Fig. 6.
do not protrude into the common locule. The anatropous, bitegmic ovules are arranged in loose, two-rowed ascending ranks. Each angled periphery has two rows of ovules (Fig. 5A). The epidermis of the distinct funiculus is stigmatoidal like the placentae. The funicular trace (F) is a simple division product of the ventrals (Fig. 8). An average ovule number of 30 is not uncommon for the gynoecium of S. bigelovii.

The oblong to lanceolate, mature fruit is strongly three-angled and is terminated by the persistent, tripartite style. The pericarp is thin and membranous with no fleshy or pulpy tissue evident. The reddish-brown dots of the flowering gynoecium persist into the fruiting stage. The dehiscence is irregular and causes by parenchymatic cell degeneration of pericarp tissue between the dorsals and ventrals. Each fruit has six such zones. This splitting does not follow the normal zone of weakness, that is, the dorsals (loculicidal dehiscence) or the ventrals (septicidal dehiscence). The fruit is a capsule for the following reasons: it dehisces; it remains attached to the pedicel and the plant; it possesses no pulpy tissue. Berg (1959) used the term “untypically loculicidal” for this type of capsule dehiscence and added further, that “in comparison with other liliaceous capsules, the ScoUopus capsule must be considered highly reduced, because of its lack of sclerenchyma and normal dehiscence.”

The gynoecial vascularization is relatively simple. As the tepals of both cycles and the three outer stamens are freed, the gynoecial base has nine distinct bundles (Figs. 3F, 6E–G, 7E–G). This vascularization is all peripheral for three reasons. The gynoecium is widely unilocular throughout, the placental margins are unprotruding and the septal wing fusion is minimal. Three of the nine bundles are the dorsals (D). They do not branch to form dorsal laterals or fuse throughout their vertical gynoecial course (Fig. 8). However, the styles and their associated dorsals are recurved. The dorsals (D) and the outer stamens (OS) share a common axial vascular origin (Fig. 8).

The six remaining gynoecial bundles of the basal nine establish a simple ventral supply. These six bundles, a pair between each dorsal, are continuous below with those outer ring bundles of the pedicel that underwent repeated radial divisions to form the lateral tepal network (Fig. 8). A fusion product with a short vertical duration is formed between each ventral pair located in the gynoecial angles. These three fusion products are the septal axials (SA) (Figs. 3A, 6F–G, 7F–G, 8). The paired ventrals have a normal phloem-xylem arrangement due to their peripheral position and the lack of inrolling of the lateral septal wings (Figs. 5A–B). A pair of ventrals (V) supplies via ranked, horizontal, funicular (F) traces two ascending rows of ovules (Figs. 5B, 8). Following ovule vascularization, the ventrals continue upwards into the common stylar region (Fig. 5C–D), but terminate as the tripartite,
Fig. 8—Summary longitudinal diagram for the floral vascular anatomy of Scoliopeus bigelovii. The various bundles are labeled with text-introduced letter codes: OTM = outer tepal median, OTL = outer tepal lateral, ITM = inner tepal median, ITL = inner tepal lateral, OS = outer stamen, D = dorsal, V = ventral, SA = septal axial, and F = funicular. The terminal portions of three dorsals (D) are recurved outwardly. The basal portion of the bundle from which a dorsal and an outer stamen are derived is not connected with an outer tepal median. These bundles merely share a common radius.
recurved style is formed (Fig. 5E). There is no terminal interconnection between the ventrals or with the dorsal network (Fig. 8).

**SUMMARY OF THE FLORAL VASCULAR ANATOMY OF *SCOLIOPUS BIGELOVII***

The floral vascularization of *Scoliopus bigelovii* is determined by a multiaxial configuration of bundles, which are established in the stem below the level where the pedicels are freed (Figs. 6–8; Table 1). The pedicel configuration is constant throughout its complete length. All of the pedicel bundles have a normal phloem (abaxial) and xylem (adaxial) arrangement. In cross-section, there are two concentric rings or zones of pedicel bundles. Within the inner ring or zone, there are three large bundles, which establish via internal divisions the three outer stamen (OS) traces and the three dorsals (D). The outer pedicel ring or zone has 12 bundles, which can be subdivided into two groups of six. One group of six directly establishes the tepal median supply, that is, the three outer tepal medians (OTM) and the three inner tepal medians (ITM), whereas the six remaining bundles undergo several radial divisions each and thereby establish both the tepal lateral supply (OTL and ITL) and the ventral network. Therefore, although the dorsals (D) have their origins from within the inner pedicel area, the ventral supply is derived from the peripheral area.

All of the tepal medians and laterals of both whorls are derived from bundles in the peripheral pedicel area, that is, from among the 12 bundles in the outer zone. The six median establishing bundles are 60° apart, for example a given OTM is 60° from ITM on both sides and 120° from OTM on both sides. Between these six median bundles, there are six additional bundles, which divide radially to form an outer tepal lateral (OTL). A pair of OTL depart with each OTM. The continuing, axial portion undergoes another radial division to form an inner tepal lateral (ITL). Similarly, a pair of ITL depart with each ITM. Basally each outer and inner tepal receives three bundles, that is, a median and two laterals. However, in the outer whorl each basal tepal lateral undergoes several successive radial divisions to form a maximum number of six laterals. This division does not occur within the inner tepals. Consequently, there is a significant difference in the maximum number of tepal bundles within the two whorls. Each outer tepal has six OTL plus an OTM plus six OTL for a total of 13 veins, whereas each inner tepal has only three veins, that is, an ITL plus an ITM plus an ITL.

The gynoecial base has a nine-bundled configuration, which is composed of the three dorsals (D) derived from the inner pedicel (receptacle) zone and the six ventrals (V) derived from the peripheral zone. The dorsals (D) continue directly into the recurved tripartite stylar
| Character                  | Medeola virginiana L.                                                                 | Scoliopus bigelovii Torr.                                           |
|---------------------------|--------------------------------------------------------------------------------------|---------------------------------------------------------------------|
| Underground parts         | Stem tuber; symподial growth; duration 1 year; dispersal by stolon; vegetative reproduction immediate and considerable; short-lived, fragile roots, many roots per year | Rhizome; long-lived; contractile roots                                |
|                           | (Bell, 1974; Berg, 1959, 1962a, 1962b)                                                |                                                                     |
| Stem                      | Terminates underground stem; unbranched; erect; leafy, not scapose; dies down each season; sclerenchyma present; hairy  | Subterraneous; unbranched; erect; leafy, not scapose; dies down each season; sclerenchyma cylinder absent |
|                           | (Bell, 1974; Berg, 1959, 1962a, 1962b)                                                |                                                                     |
| Leaves                    | Several; clustered on stem, in two groups; verticillate; convergent-reticulate venation | Two; near stem apex; alternate; parallel-veined                      |
|                           | (Bell, 1974; Berg, 1959, 1962a, 1962b)                                                |                                                                     |
| Inflorescence             | Subterminal, symподial umbel; fruiting pedicel with sclerenchyma; short pedicel recurved upwards in fruit | Terminal, bractless; sympodial umbel; fruiting pedicel with sclerenchyma; long pedicel recurved downwards in fruit |
|                           | (Berg, 1959, 1962a, 1962b; Utech, 1978a)                                              |                                                                     |
| Flowers                   | Perianth segments distinct and inconspicuous; tepal whorls alike; perianth deciduous; six stamens in two whorls; filaments free, hypogynous; anthers dorsifixed; extorse dehiscence via vertical (abaxial) slits; single pollination unit; no nectaries present; hercogamous | Perianth segments distinct and showy; outer tepals petaloid, inner linear; perianth deciduous; three outer stamens; filaments free, hypogynous; anthers versatile; extorse dehiscence via vertical (abaxial) slits; three pollination units; tepal nectaries present; not hercogamous |
|                           | (Bell, 1974; Berg, 1959, 1962a, 1962b; Utech, 1978a)                                  |                                                                     |
| Gynoecium (Pistil)        | Tricarpellous, syncarpous; ovary globose; parietal placenta; protruding placentae; placentae between angles; placental epidermis stigmatoidal; seeds central and ± horizontal; style nearly absent; stigmata large; apical part of carpels deciduous | Tricarpellous, syncarpous; ovary triquetrous; parietal placenta; unprotruding placentae; placentae in angles of locules; placental epidermis stigmatoidal; seeds peripheral and ascending; style well-developed, tripartite; stigma minute; apical part of carpels persistent |
|                           | (Berg, 1959, 1962a, 1962b; Utech, 1978a)                                              |                                                                     |
| Character                  | *Medeola virginiana* L.                                                                 | *Scolius bigelovii* Torr.                                                                 |
|---------------------------|----------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------|
| Fruit                     | Berry; pulp from pericarp and placenta                                                 | Capsule (cf. text); fruit not berry descendant; dehiscence irregularly loculicidal       |
| (Berg, 1959, 1962a,       |                                                                                        |                                                                                        |
| 1962b; Utech, 1978a)      |                                                                                        |                                                                                        |
| Seed                      | More or less rounded; brownish, smooth and unstriated; no appendage; embryo small and   | More or less rounded; brownish, coloring uneven; minutely pubescent, striated; appendage   |
| (Berg, 1959, 1962a,       | straight                                                                                | small via cell enlargement only; oil in appendage; embryo small and straight               |
| 1962b; Utech, 1978a)      |                                                                                        |                                                                                        |
| Dispersal                 | Endozoochorous                                                                         | Myrmecochorous                                                                           |
| (Berg, 1959, 1962a,       |                                                                                        |                                                                                        |
| 1962b)                    |                                                                                        |                                                                                        |
| Ovule                     | Anatropus shape; central pleurotropous orientation; indistinct funiculus; stigmatoidal  | Anatropus shape; hypotropous orientation; distinct funiculus; stigmatoidal tissue present; |
| (Berg, 1959, 1962a,       | present; raphides absent                                                               | raphides absent, but colored cells present                                               |
| 1962b)                    |                                                                                        |                                                                                        |
| Nucellus                  | Medium size; periclinal walls in epidermis absent; basal part short                    | Large size; periclinal walls in epidermis present; basal part medium                      |
| (Berg, 1959, 1962a,       |                                                                                        |                                                                                        |
| 1962b)                    |                                                                                        |                                                                                        |
| Embryo sac                | *Fritillaria*-type length/width ratio 2.5; haustorium absent; synergid filiform         | Normal-type (monosporic); length/width ratio 2.5; haustorium absent; synergid filiform   |
| (Berg, 1959, 1962a,       | apparatus absent; polar nuclei do not fuse before fertilization; 3–2 antipodals; nuclear| apparatus present; polar nuclei fuse before fertilization; 3 antipodals; nuclear           |
| 1962b)                    | type of endosperm                                                                       | type of endosperm                                                                         |
| Pedicel vascularization   | 12-bundled configuration; broad zone with six outer bundles alternating with six inner  | 15-bundled configuration; peripheral zone with six outer bundles alternating with six inner |
| (Anderson, 1940;          | bundles; all bundles with normally arranged phloem and xylem                           | bundles plus three large inner zone bundles; all bundles with normally arranged phloem   |
| Berg, 1959, 1962a;        |                                                                                        | and xylem                                                                                |
| Utech, 1978a)             |                                                                                        |                                                                                        |
| Tepal vascularization     | Outer tepal:                                                                            | Outer tepal:                                                                             |
| OTM = outer median        | OTL + OTM + OTL                                                                         | 6 OTL + OTM + OTL                                                                        |
| ITM = inner median        | Inner tepal:                                                                            | Inner tepal:                                                                             |
| OTL = outer lateral       | ITL + ITM + ITL                                                                         | ITL + ITM + ITL                                                                          |
Table 1.—Continued

| Character | Medeola virginiana L. | Scolopus bigelovii Torr. |
|-----------|-----------------------|-------------------------|
| ITL = inner lateral | OTM and ITM directly derived from axial pedicel supply; OTL and ITL derived via radial divisions | OTM and ITM directly derived from axial pedicel supply; OTL and ITL derived via radial divisions; multiple laterals in outer tepal |
| Stamen vascularization | Three outer and three inner stamens; OS and IS are radially derived branches; OS and IS traces extending upwards in the connective tissue | Three outer stamens only; each derived via a planar division within the three large inner zone bundles; shared origins with the dorsals; OS recurved downwards in connective tissue |
| OS = outer stamen | Base of gynoecium: $3 \, D + 6 \, V + 3 \, SA$ | Base of gynoecium: $3 \, D + 6 \, V$ |
| IS = inner stamen | followed by: $3 \, D + 6 \, D_i + 6 \, V + 6 \, V_{\perp} + 3 \, SA$ | followed by: $3 \, D + 6 \, V + 3 \, SA$ |
| Gynoecial vascularization | The D, $V_{\perp}$ and SA bundles are fusion products, the $D_i$ and V bundles are not; vertical duration of SA is complete; neither lateral nor terminal inter- or intraconnection between the dorsal and ventral supplies; funicular (F) supply horizontal and direct from the ventrals (V); average ovule number—18 | The SA bundles are fusion products of short vertical duration, whereas the dorsals (D) may be compound, there is no fusion involved in their origin; neither lateral nor terminal inter- or intraconnection between the dorsal and ventral supplies; funicular (F) supply horizontal and direct from the ventrals (V); average ovule number—30 |
| D = dorsal | | Upper gynoecium: only the D bundles are in the upper common style and continue into the freed triradiate stylar arms |
| V = ventral | | |
| $D_i$ = dorsal lateral | | |
| $V_{\perp}$ = ventral lateral | | |
| SA = septal axial | | |
| F = funicular | | |
| vl = ventral lateral branch | | |
| (Berg, 1959, 1962a; Utech, 1978a) | | |
| Chromosome number | Basic chromosome number $x = 7$ | Basic chromosome number $x = 7, 8$ |
| (Cave, 1966, 1970; Johansen, 1932; Stewart and Bamford, 1942; Woodward, 1948) | | |
arms unbranched and without any fusion. A pair of ventrals (V) occurs between each of the three dorsals (D) from the base to the upper gynoecium (Figs. 6–8). A fusion septal axial (SA) of short vertical duration is formed between each ventral pair. Ovule supply is via direct, horizontal funicular (F) branches from the ascending ventrals (V). Within each ventral pair the funicular branching is ranked. Each of the three locular angles has an average of 10 ovules, that is, an average of 30 ovules per gynoecium. There is no vascular inter- or intraconnection between any bundles of the dorsal and ventral supplies.

Though there are some shared similarities in the floral vascular anatomy of S. bigelowii and Medeola virginiana (Utech, 1978a), the differences are significant (Table 1). The pedicels of both have multibundled axial configurations—S. bigelowii has 15 bundles, whereas M. virginiana has 12 bundles. Basally both the outer and inner tepals in both species receive three bundles, that is, a median and two laterals, which is not unusual in the Liliaceae (Anderson, 1940). The six tepal medians in both species are established directly and simply from axial pedicel bundles, whereas the 12 tepal laterals in both species are the result of radial divisions. In M. virginiana, both freed tepal whorls have a maximum number of three bundles, which contrasts markedly with the 13 maximum bundles in the outer whorl and three in the inner whorl of S. bigelowii. The six stamen bundles and the three dorsals in M. virginiana are fusion products from radial divisions within the receptacle’s periphery, whereas the three stamens and the three dorsals in S. bigelowii are not fusion products and their origins are from more central receptacle areas. The branched dorsal laterals (D₁) that occur in M. virginiana are not present in S. bigelowii. Though three fusion septal axials (SA) occur in the ventral networks of both species, the overall ventral network in M. virginiana is more complex than that in S. bigelowii. In the former, in addition to the ascending ventrals and the septal axials, there are three additional fusion bundles in the ventral network. These fusion bundles, the ventral laterals (V₁), divide in the upper gynoecium with the resulting ventral lateral branches (vlb) continuing along with the dorsals (D) into the terminal areas of the style. There is no interconnection between the dorsal and ventral supplies in either species above their level of origin within the receptacle.

**Discussion and Concluding Remarks**

The history and debate concerning the correct tribal position of Scoliopus is as remarkable as the plant. Torrey (1857:145) placed his new genus Scoliopus at the end of the Melanthaceae “chiefly on account of it extrorse anthers, notwithstanding its one-celled fruit and parietal placentation. The somewhat dichlamydeous flowers are suggestive of
Trilliaceae, but the extrorse anthers, as well as other characters, would seem to forbid its being placed in that group." The Melanthaceae used by Torrey (1857) was based on an older, stricter concept of the Liliaceae Alliance (Gray, 1856), and essentially corresponds to the current Englerian subfamily Melanthioideae (Engler, 1888; Krause, 1930).

Baker (1879:405), when revising the Liliaceae Alliance, placed Scoliopus in his Colchiaceae, a group that somewhat corresponded to the older Melanthaceae in part. Yet within this rank, Baker (1879) did not assign Scoliopus to a definite tribe. Rather he placed it in an appendaged group, "genera anomala Colchicacearum." Earlier doubts of Baker (1875:509) on the tribal status of Scoliopus resulted in his reference of this genus to a group containing aberrant liliaceous tribes. One of these was the monotypic Scoliopeae.

In Watson's (1879:222, 227) revision of the North American Liliaceae, Scoliopus is transferred from the older Melanthaceae to the Trilliaceae, which then included Trillium and Medeola. (Paris is an Old World genus.) The association of Scoliopus with Trillium and Medeola dates from Watson's monograph (1879). Watson's tribe, Trilliaceae, was redefined and enlarged with Scoliopus placed in its own subtribe, Scoliopeae, to show that Scoliopus was only remotely related to the other genera.

Watson's inclusion of Scoliopus in the Trilliaceae was accepted by Bentham and Hooker (1883:762; cf. Medeoleae), by Engler (1888:83; cf. Asparagoideae-Parideae) and others, and soon became the established view on the genus' classification. Doubts were expressed by Hooker (1897), who noted in Curtis' Botanical Magazine that Scoliopus "clearly belonged to the tribe Medeoleae of Liliaceae, as determined by Bentham (Bentham and Hooker, 1883), but is not very closely allied to any congener in that group." However, modern taxonomic treatments, for example those of Krause (1930:373; cf. Asparagoideae-Parideae which follows Engler, 1888) and Hutchinson (1934: 8, 104; cf. Trilliaceae, which follows and elevates the association of Bentham and Hooker, 1883), give the impression of a close natural, and unquestionable relationship between Scoliopus and the other members of the association (Berg, 1959).

Berg's initial studies on the vegetative and floral morphology and anatomy of both Scoliopus (Berg, 1959) and Medeola (Berg, 1962a) were followed (Berg, 1962b) by detailed embryological observations for these two genera, as well as for Trillium and Paris, and concluded with a comprehensive comparison and summary of the four genera in the Englerian Parideae. Neither Scoliopus nor Medeola are at all similar to each other (Table 1), and both are vastly different from Trillium and Paris, which, on the other hand, do show a very high degree of similarity. Furthermore, Berg (1962b) concluded that only Trillium and
Paris should be kept together within the liliaceous tribe Parideae, that Medeola should be transferred as a monotypic tribe (Medeoleae) to the Englerian subfamily Lilioideae, and that Scoliopus should be returned as a monotypic tribe to the subfamily Melanthioideae. However, considerable work still needs to be done within these two subfamilies to demonstrate the affinities and relationships, if any, of Medeola and Scoliopus to these proposed recipient subfamilies.

On all levels of biological organization differences occur between Scoliopus bigelovii and Medeola virginiana. These differences have been summarized in Table 1. Because both genera are small, Scoliopus has two species and Medeola is monotypic, the summarized differences provide an excellent generic circumscription of each. Berg's reported (1959, 1962a, 1962b) morphological and embryological differences are included in Table 1, as well as our reported (Utech, 1978a) differences on their floral vascular anatomy.

The most remarkable features of S. bigelovii, in addition to its flowers, are its reduced, subterranean stem with two alternate (not opposite) distichous leaves, which are mottled reddish-brown, its contracted sympodial umbel with elongate fruiting pedicels that are twisted and recurved, and its "irregular loculicidal" capsules with seeds that are ant dispersed due to oil-containing appendages (raphe derived), or elaiosomes. The adaptive significance of the appendaged seeds, the twisted to the ground pedicels, and the short stems are inter-related into an advanced pattern of dispersal.

The structural adaptive significance of the showy flowers correlates with its mode of pollination. Berg (1959) demonstrated that a single Scoliopus flower actually functions as three "secondary flowers" or independent pollination subunits, a feature usually associated with Iris. Each of the three petaloid outer tepals is lined adaxially with nectariferous tissue and is laterally imbricated to form a broad cup or shallow floral tube via the interdigitating of the lateral edges of the outer tepals into grooves on the narrow, abaxial surface of the inner tepals. Because the triquetrous gynoecium is ridged along the ventral position, which is opposite the narrow, appressed inner tepals and is flattened along the dorsal surface, which is opposite the outwardly expanded outer tepals and extrorse anthers, a configuration of three independent pollination subunits is established. The three versatile stamens, and there are consistently three, are in the outer position. Each extrorse anther dehisces along two vertical abaxial slits such that the pollen dispersal zone is within the space between the flatten dorsal region of the gynoecium and the outwardly expanded outer tepal. The style is tripartite terminally with each free stylar arm recurved over the top of the anther. The minute stigmas are located terminally and along the abaxial surface, which is removed from the pollen dispersal zone. The
recurved style, the extrorse anthers, the unusual triquetrous gynoeicum and the large, nectiferous outer tepals are all inter-related for outbreeding.

The embryology of *S. bigelovii* also differs from *Medeola virginiana* (Table 1), as well as from *Trillium* and *Paris* (Berg, 1962). *Scoliopus* has a Normal-type (monosporic) of embryo sac, whereas *Medeola* has a *Fritillaria*-type (tetrasporic). Furthermore, *Scoliopus* possesses a distinct funiculus with stigmatoidal tissue, a series of subepidermal coloring cells and a fusion of its polar nuclei prior to fertilization.

Chromosome counts for both species of *Scoliopus* are known. Cave (1966) reported from a single Oregonian population of *S. hallii* a count of $2n = 14$. However, Johansen's report (1932) of $2n = 14$ for *S. bigelovii* was not confirmed by Cave (1966, 1970) who observed counts of $2n = 16$ from several different populations. One population from Humboldt County, California, for example, had a somatic (root tip) number of $2n = 16$ but also had several extra small meiotic chromosomes, which indicates a certain degree of structural hybridity within the northern part of the range. Consequently the chromosomal base number of *Scoliopus* should be associated with both $x = 7$ and $x = 8$ until further research is done. Although *Medeola virginiana* also has a base number of $x = 7$, there are significant morphological differences between its karyotype and that of *Scoliopus* (Cave, 1970; Stewart and Bamford, 1942; Woodward, 1948). Both *Paris* and *Trillium* are based on a chromosome number of $x = 5$.

*Scoliopus bigelovii* Torrey, Pac. Rail. Report 4:145, pl. 22. 1857.

* Lectotype.—Tamul Pass (Mt. Tamalpais), California, Whipple’s Railway Expedition, April 1854, J. M. Bigelow s.n. (NY!)—center element; *Paralectotype.—California, Samuels s.n., s.d. (NY!)—lower left element, same sheet as above, Torrey's note: “rec'd from Dr. Gray, Dec. 1856,” cf. Fig. 2.

*Specimens examined.—California: Humboldt Co.: Hubbard's Station, 10 June 1899, J. B. Davy & W. C. Blasdale 5399 (UCB); Near Glendale on Mad River, elev. 0–500 ft, 2 April 1905, J. P. Tracy 2156 (UCB); Near Hydesville, elev. 200 ft, 9 March 1913, J. P. Tracy 4017 (UCB); Dinsmore’s Ranch, Van Duzen River, opposite Buck Mt., elev. 2500 ft, 20 June 1913, J. P. Tracy 4223 (UCB); Lawrence Creek, near Kneeland Prairie, elev. 2000 ft, 9 March 1924, J. P. Tracy 6615 (UCB); Big Lagoon, elev. 300 ft, 26 March 1933, J. P. Tracy 10,941 (UCB), Kneeland Prairie, elev. 2500 ft, 26 April 1936, J. P. Tracy 14,808 (UCB). Marin Co.: West end of Alpine Lake, 13 February 1955, R. Y. Berg s.n. (UCB); Lagunitas Creek, 21 March 1891, Chesnut & Drew s.n. (UCB); Mill Valley, 26 January 1913, A. Eastwood 2450 (UCB); Mt. Tamalpais, 22 February and 30 March 1889, E. L. Greene s.n. (UCB); Mt. Tamalpais, Lagunitas Road, 1 February 1925, H. L. Mason 1231 (UCB); Sequoia Canyon, 31 January 1892, Michener & Bioletti 2111 a (UCB); West side of Bolinas Ridge, east of Bolinas Lagoon, elev. ca. 750 ft, 23 February 1963, H. K. Sharsmith 5174 (UCB); Pipeline trail up Mt. Tamalpais, 30 March 1932, B. O. Schreiber 112 (UCB). San Mateo Co.: King's Mt., 18 March
1902, C. F. Baker 322 (UCB); Lake Pelareitos, 28 February 1902, A. Eastwood s.n. (UCB); San Andreas, s.d., A. E. Ehlers 278 (UCB); Above Portola on La Honda Road, 3 March 1939, R. F. Hoover 3897 (UCB); Pilarcitos Lake, 13 April 1946, F. A. Pitelka s.n. (UCB); San Mateo Creek at SE end of Buriburi bridge, 12 March 1955, G. B. Rossbach 214 (UCB). Santa Cruz Co.: Big Tree Grove, April 1887, C. F. Sonne s.n. (UCB); San Lorenzo River, ca. 3.5 miles from mouth of river near Southern Pacific Railroad trestle, elev. ca. 300 ft, 24 March 1954, J. H. Thomas 2897 (UCB). Sonoma Co.: Near Guerneville, 3 April 1898, M. S. Baker s.n. (UCB); Redwood Canyon ca. 2.5 mi S of Ft. Ross, elev. 100 ft, 25 February 1939, F. W. Gould 562 (UCB); Occidental, 18 March 1906, E. Lobenstein s.n. (UCB).

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