

Comparative Anatomy of *Lachnanthes* and *Lophiola* (*Haemodoraceae*)¹

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Summary

Aspects of vegetative and floral anatomy of the monotypic genera *Lachnanthes* and *Lophiola* are described and compared. *Lophiola* and *Lachnanthes* are anatomically very distinct from one another and the taxonomic placement of both genera within the same tribe is not supported. The relationships of the genera to other taxa remain unclear.

Introduction

The *Haemodoraceae* is a relatively small family of monocotyledons. The most recent treatment by GEERINCK (1969) circumscribed the family as composed of rhizomatous, often stoloniferous, scapose to subscapose herbs with basal, equitant, "Iris-like" leaves which are basally sheathing and distally unifacial by longitudinal folding and fusion. The inflorescence is terminal and usually branched and is composed of bisexual, often externally tomentose flowers with 6 tepals, 3–6 stamens, and a superior to inferior ovary; fruits are usually loculicidal capsules with endospermous seeds.

The family (sensu GEERINCK 1968, 1969) contains 13 genera and 76 species, with distributions in South Africa, Australia, South America, Central America, Mexico, and eastern North America. However, a precise delimitation and satisfactory intra-familial classification of the *Haemodoraceae* remain unavailable. Several authors have proposed different combinations of tribes and genera (see GEERINCK 1968; ROBERTSON 1976). Among recent family treatments, MELCHIOR (1964), in the "Syllabus der Pflanzenfamilien", recognized three tribes: *Haemodoreae*, *Conostylideae*, and *Conanthereae*. HUTCHINSON (1934, 1959, 1973) grouped the *Haemodoraceae* with five other families in the order *Haemodurales* and divided the family into two tribes: *Haemodoreae* with 11 genera and *Conostylideae* with 6 genera; the *Conanthereae* being included with the family *Tecophilaeaceae* of the *Liliales*. GEERINCK (1969) also recognized the *Haemodoreae* and *Conostylideae* although differed from HUTCHINSON by removing *Lanaria* from the family, transferring *Lophiola* to the *Haemodoreae*, and merging genera previously recognized as distinct. Among contemporary system makers, CRONQUIST (1968) classified the *Haemodoraceae* within the *Liliales* of the *Liliidae*. TAKHTAJAN'S (1969) treatment essentially agreed with that of CRONQUIST, and regarded the *Hypoxidaceae* and *Velloziaceae* as closely related families. THORNE

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(1976) lowered the family to subfamilial status within the *Liliaceae* and DAHLGREN (1975, 1977) placed the *Haemodoraceae*, along with the *Pontederiaceae* and *Philydreae*, in the *Haemoderales* of the superorder *Lilianaes*.

The eastern North American representation of the family consists of two superficially similar and apparently monotypic genera, *Lachnanthes caroliniana* (LAM.) DANDY and *Lophiola aurea* KER-GAWLER. Although some recent publications still refer to the species of *Lophiola* as *L. americana* (PURSH) WOOD, ROBERTSON (1976) presented a convincing case that the name *L. aurea* KER-GAWLER has priority. *Lachnanthes caroliniana* is locally common and ranges, with several disjunctions, from southern Nova Scotia to Cuba, including the Atlantic and Gulf coastal plain of the southeastern United States. *Lophiola aurea* is somewhat rarer, occurring as a disjunct along the coastal plain in western Nova Scotia, the pine barrens of New Jersey, and in scattered localities from southeastern North Carolina to the Florida panhandle and southern Mississippi. Both species typically grow in bogs and low, wet areas in savannahs and pinelands, although *Lachnanthes caroliniana* is also common in swamps and roadside ditches.

The taxonomic position of *Lachnanthes* within the *Haemodoraceae* is apparently reasonably well established. ROBERTSON (1976), who provided a thorough morphological characterization of the two genera, noted that, in his opinion, *Lachnanthes* clearly belongs to the tribe *Haemodoreae*, being most closely related to *Haemodorum* of Oceania and *Dilatris* of South Africa. The evolutionary relationships of *Lophiola*, however, are quite unclear, having been placed variously in the *Amaryllidaceae*, *Hypoxidaceae*, and *Haemodoraceae* (GEERINCK 1969).

No detailed anatomical, embryological, or palynological studies have been undertaken on either *Lachnanthes* or *Lophiola*. Accordingly, this initial anatomical investigation was undertaken to provide information which may eventually provide a more definitive family circumscription and intrafamilial classification.

Materials and Methods

Material was collected in the field and voucher specimens deposited in the herbarium of The University of North Carolina at Chapel Hill (NCU). Vegetative organs, floral buds, and mature flowers were fixed in formalin-acetic acid-alcohol (FAA). Both fresh sections and prepared slides were employed for study. Permanent slides were prepared using standard anatomical techniques of dehydration, paraffin infiltration, and microtome sectioning (JOHANSEN 1940). Sections were stained with safranin-fast green or safranin-haematoxylin. Both transverse and longitudinal sections of roots, rhizomes, scapes, and leaves were made. Tepal vestiture was examined from temporary wet mount slides. Floral vasculature was studied utilizing a combination of serial sections of mature floral buds and cleared flowers. Mature whole flowers were cleared in 5.25% sodium hypochlorite and stained with pararosaniline hydrochloride (BOKE 1970). Stomatal ontogeny was observed from temporary whole mounts of immature leaf bases, fixed in 3:1 absolute ethanol and glacial acetic acid (CARNOY'S Fluid) and stained with acetocarmine (TOMLINSON 1974). Vessels were studied from both longitudinal sections and macerations; thin slivers of fresh roots, rhizomes, and leaves were macerated in 10% aqueous chromic acid: 10% aqueous nitric acid (JEFFREY'S solution) for 2-3 days, teased gently with needles, and mounted unstained in HOYER'S solution. Prepared slides are deposited in the anatomical slide collection of The University of North Carolina at Chapel Hill.

Observations

Vegetative Anatomy

Lachnanthes caroliniana

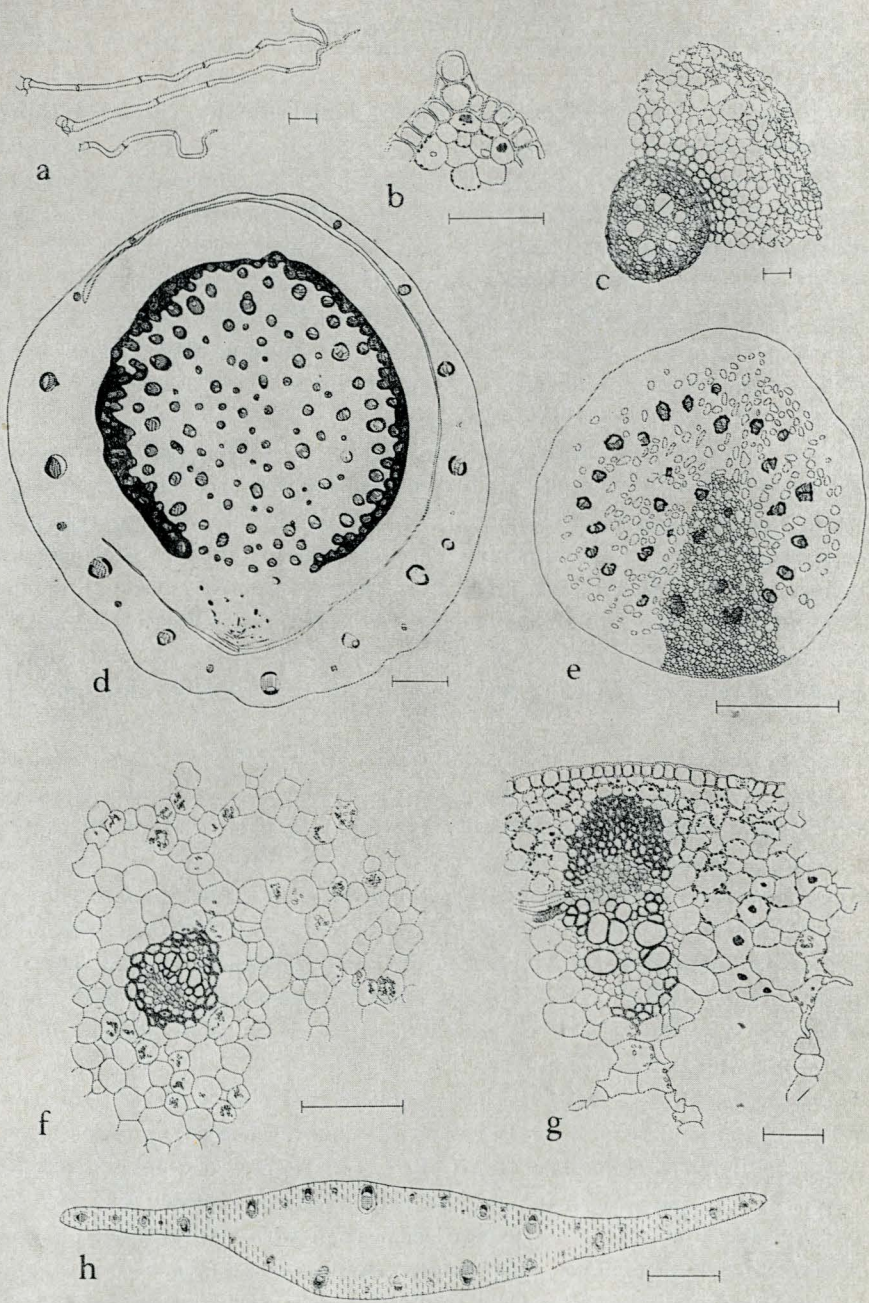
Root (Fig. 1c). *Epidermis* uniseriate, with longitudinally extended thin-walled cells. *Cortex* with a peripheral, uniseriate exodermal layer of crushed cuboidal cells, an extensive aerenchymatous middle zone, and a 2–3 layered inner zone of thick-walled, sclerified cells; internal cortical cells radially aligned with endodermal cells. *Endodermis* uniseriate, with thick-walled cells which are uniformly lignified on inner and outer tangential walls. *Pericycle* uniseriate, slightly lignified. *Xylem* polyarch, with 10–11 protoxylem poles and a central core of sclerified parenchyma; vessels with simple perforation plates (Fig. 6a, b), ca. 0.8–1.4 mm long. *Phloem* in clusters of 1–2 sieve tube elements flanked by smaller elements and companion cells, alternating with protoxylem poles. *Crystals* absent.

Rhizome (Fig. 1e, f). *Epidermis* uniseriate; cells thin-walled, longitudinally extended; outer wall thickly cutinized with tuberculate outer surface. *Ground tissue* differentiated into narrow outer region of thin-walled, spheroidal parenchyma and extensive inner region of schizogenous aerenchyma, forming an alveolar network. *Endodermis* absent. *Vasculature* atactostelic; bundles radially extended, enclosed by 1–2 layers of sclerenchyma. *Xylem* endarch; vessels to ca. 1.9 mm long, with multi-barred perforation plates (Fig. 6c). *Phloem* oriented in a wide tangential band. *Starch grains* numerous in aerenchyma. *Raphides* present, scattered throughout ground tissue.

Rhizome at aerial shoot base considerably expanded (Fig. 1d). *Intercellular spaces* small. *Stelar region* enclosed by a multilayered sclerenchyma sheath in endodermal region; no distinct endodermis present. *Vascular bundles* collateral to amphivasal. *Xylem* typically C-shaped, enclosing phloem.

Scape. *Epidermis* uniseriate; cells rectangular to cuboidal in transection, with thick, warty outer cuticles. *Cortex* of an outer chlorenchymatous zone and inner aerenchymatous zone separated by a ring of fibers; dark-staining, rod-shaped bodies present in chlorophyllous cells. *Vascular bundles* collateral, scattered throughout central region; bundles wholly or partially enclosed by sclerenchymatous sheath. *Starch grains* and *crystals* absent.

Leaf (Fig. 1g, h). Leaves "Iris-like", bifacial and sheathing at base, unifacial above by longitudinal fusion. Leaves narrowly spindle shaped in transection, with two marginal flanges. *Epidermis* thin-walled; cells cubic to oblong in transection, outer walls with a thick, often papillate or ridged cuticle. *Stomata* with two laterally flanking subsidiary cells (Fig. 5e); guard cells each with two cutinized ridges, projecting into stomatal openings; substomatal cavities small (Fig. 1g). *Stomatal development* initiated by an unequal cellular division of a protodermal cell at its distal end (toward leaf apex, Fig. 5a), the resultant guard cell mother cells surrounded by four "neighboring cells" (sensu TOMLINSON 1974) (Fig. 5b); the two lateral neighboring cells divide unequally and non-obliquely to form two lateral "contact cells"



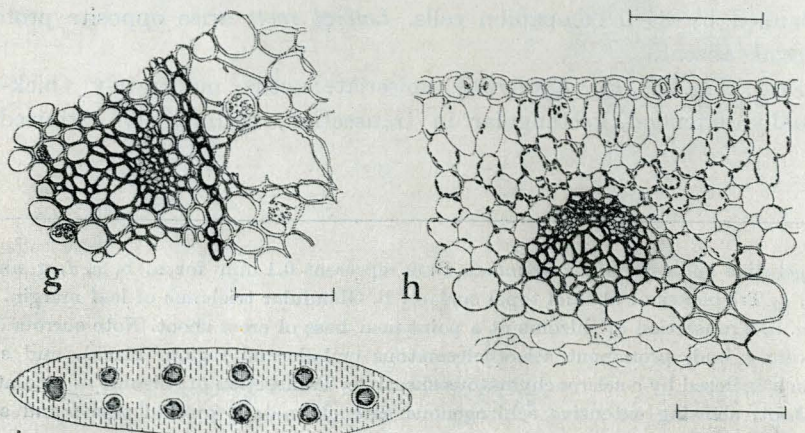
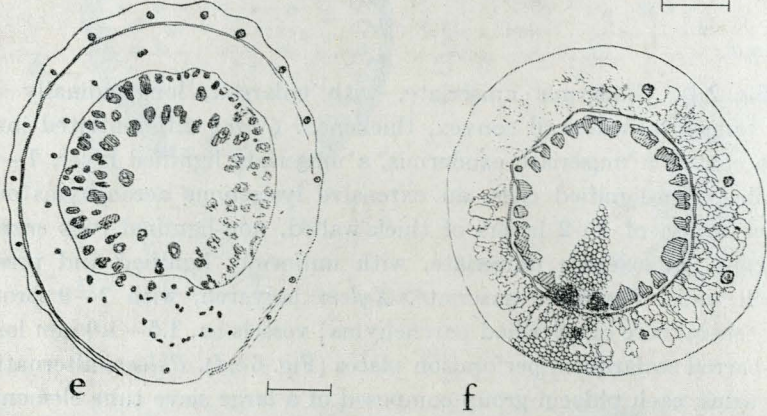
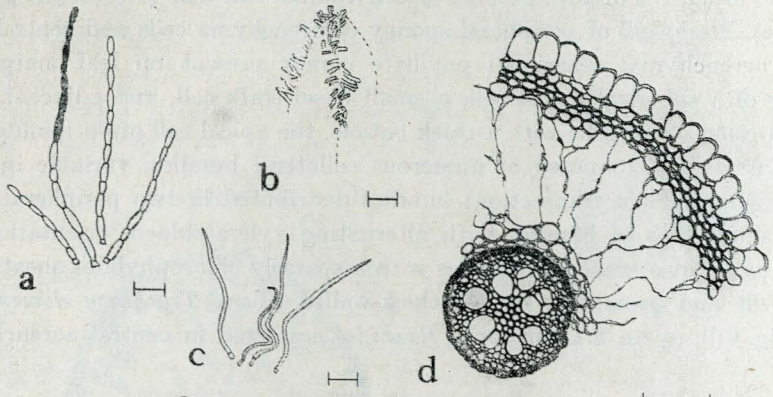
(sensu TOMLINSON, loc. cit.), which expand to function as subsidiary cells (Fig. 5c); guard cell mother cell divides parallel to longitudinal leaf axis to form the guard cells (Fig. 5d, e). *Mesophyll* of peripheral spongy chlorenchyma cells and central achlorophyllous aerenchyma, occasional papillate *glands* present on leaf margins, each consisting of a spherical apical cell, a small basal stalk cell, and adjacent, flanking epidermal cells; gland cells with a thick cuticle, the apical cell often minutely tuberculate. *Vasculature* composed of numerous collateral bundles, variable in size and generally ellipsoidal in transection; bundles distributed in two peripheral rows except for single files of bundles with alternating xylem/phloem orientation in leaf marginal extensions; vascular bundles with a sparsely chlorophyllous sheath of thin-walled cells and prominent cap of thick-walled fibers. *Tracheary elements* imperforate (Fig. 6d), up to 2.1 mm long. *Raphides* scattered in central aerenchymatous tissue.

Lophiola aurea

Root (Fig. 2d). Epidermis uniseriate, with enlarged, longitudinally elongate cells; outer tangential cell wall convex, thickened. *Cortex* differentiated into (from periphery to center) a uniseriate exodermis, a uniseriate lignified layer, 1–2 layers of thick-walled, non-lignified cells, an extensive lysigenous aerenchymatous zone, and an inner region of 1–2 layers of thick-walled, non-lignified cells surrounding the endodermis. *Endodermis* uniseriate, with uniformly lignified and presumably suberized cell walls. *Pericycle* uniseriate. *Xylem* polyarch, with 7–9 protoxylem poles and a central core of sclerified parenchyma; vessels ca. 1.5–1.9 mm long, with long, multi-barred scalariform perforation plates (Fig. 6e, f). *Phloem* alternating with protoxylem arms, each phloem group composed of a large sieve tube element centrally flanked by 3–5 companion cells. *Lateral roots* arise opposite protoxylem poles. *Crystals* absent.

Rhizome (Fig. 2f, g). *Epidermis* uniseriate; cells moderately thick-walled, longitudinally extended, rectangular in transection, with thinly cutinized outer

Fig. 1. Vegetative anatomy of *Lachnanthes*. Bars represent 0.1 mm for a, b, c, f, g and 1 mm for d, e, h. a, Trichomes of abaxial tepal surface. b, Glandular trichome of leaf margin. c, Root transection. d, Transection of rhizome at a point near base of erect shoot. Note surrounding leaf sheath, axillary bud, prominent sclerenchymatous endodermal region (black), and scattered bundles, each enclosed by a sclerenchymatous sheath. e, Transection of rhizome at a point distant to erect shoot, showing extensive schizogenous aerenchymatous ground tissue and scattered vascular bundles. f, Transection of rhizome vascular bundle in a region distant to erect shoot. Note sclerenchymatous bundle sheath and surrounding aerenchyma. g, Leaf transection, illustrating stoma, and vascular bundle with prominent fibrous bundle cap. h, Mid-leaf transection, illustrating region of chlorenchyma (vertical bars) and numerous veins with sclerenchymatous caps (black) and surrounding chlorophyllous sheaths (white). Key to tissues: lines, xylem; stipple, phloem; solid black, sclerenchyma; verticle bars, chlorenchyma.



walls. *Cortex* differentiated into a 2—4 layered, sclerified, subepidermal region with sparse intercellular spaces and an inner unligified lysigenous aerenchymatous zone. *Endodermis* uniseriate, highly lignified. *Pericyclic region* multi-layered, partially sclerified. *Vascular bundles* collateral, in a single ring. *Xylem* endarch; tracheary elements presumably imperforate (Fig. 6g), up to 1.4 mm long. *Pith* composed of thick-walled, unligified cells with prominent intercellular spaces. *Starch grains* numerous in ground tissue. *Raphides* scattered in internal cortical zone.

Rhizome at base of aerial shoot (Fig. 2e) enlarged and anatomically altered. *Cortex* devoid of aerenchyma, with few starch grains. *Vasculature* atactostelic, with numerous outer, collateral bundles and fewer inner, amphivasal bundles; sheath cells of bundles occasionally smaller, with numerous starch grains. *Ground tissue* centrally partially sclerified, with sparse intercellular spaces and numerous starch grains.

Scape. *Epidermal cells* longitudinally elongate, with thick inner and outer tangential walls, thinly cutinized. *Stomata* numerous, resembling those of the leaf. *Ground tissue* differentiated into a narrow outer chlorenchymatous zone of spherical, thin-walled cells with prominent intercellular spaces and an extensive inner parenchymatous zone of outer thick-walled and central thin-walled cells. *Vascular bundles* collateral, scattered in periphery of inner parenchymatous zone; inner bundles with a C-shaped region of tracheary elements partially to wholly encircling the phloem and an outer fibrous bundle cap usually dividing the phloem into two or more discrete units; bundles near periphery with xylem and phloem positioned along a tangential plane; outermost bundles (leaf or tract traces) with a prominent sclerenchymatous outer cap and radially extending fibers which separate the phloem into two groups. *Starch grains* essentially absent. *Raphides* scattered in inner region of ground tissue.

Leaf (Fig. 2h, i). Leaves basally bifacial and sheathing, distally unifacial by longitudinal fusion, oriented perpendicular to the scape. Leaves narrowly-elliptic to narrowly oblong in transection. *Epidermis* uniseriate, cells longitudinally elongate, cubic to radially oblong in transection; inner and outer tangential walls thick; cu-

Fig. 2. Vegetative anatomy of *Lophiola*. Bars represent 0.1 mm for a, b, c, d, g, h and 1 mm for e, f, i. a, Trichomes of adaxial tepal surface. b, Trichomes of apical, adaxial tepal surface. c, Trichomes of abaxial tepal surface. d, Transection of root, showing large epidermal cells and lysigenous aerenchymatous cortex. e, Transection of rhizome at a point near base of erect shoot, showing surrounding leaf sheath, endodermis, and peripherally scattered, concentric, vascular bundles. f, Transection of rhizome at a point distant to erect shoot, illustrating lysigenous aerenchymatous inner cortex, endodermis, and ring of collateral vascular bundles. g, Transection of rhizome vascular bundle at a point distant to erect shoot. h, Leaf transection, illustrating stomata, mesophyll layers, and vascular bundles. i, Leaf transection, showing chlorenchymatous region (vertical bars) and veins. Each vein is surrounded by an inner sclerenchymatous sheath (black) and an outer chlorophyllous sheath (white). Key to tissues: lines, xylem; stipple, phloem; solid black, sclerenchyma; vertical bars, chlorenchyma.

ticle moderately thick. *Stomata* of two longitudinally oriented guard cells surrounded by four cruciately arranged "neighboring cells", none of which are specialized as subsidiaries (Fig. 5i): guard cells with two cutinized ridges of wall material which project into stomatal cavity (Fig. 2h); stomatal cavities small. *Stomate development* initiated by an unequal distal division of a protodermal cell, the smaller, distal product functioning as the guard cell mother cell (Fig. 5f, g); cells undergo some expansion before the guard cell mother cell divides longitudinally into two guard cells (Fig. 5h). *Mesophyll* composed of an outer region of two or three layers of loosely arranged, columnar palisade cells and a central region of spheroidal spongy chlorenchyma cells, which are usually crushed and achlorophyllous. *Vasculature* consisting of an ellipse of vein bundles positioned just inside the palisade cells; a single vein, or two partially fused veins, occur at each leaf margin; bundles uniform, collateral, orbicular in transection, surrounded by an outer sheath of thin-walled, sparsely chlorophyllous cells and an inner sheath of thick-walled, sclerenchyma cells. *Xylem* endarch, with occasional protoxylem lacunae; tracheary elements presumably imperforate, ranging to 2.3 mm in length (Fig. 6h). *Phloem* characteristically separated into two groups by fibers extending radially from the inner bundle sheath to the outer metaxylem. *Raphides* scattered throughout achlorophyllous central region.

Floral Anatomy

Lachnanthes caroliniana

General morphology and anatomy. Flowers are bisexual, actinomorphic, bracteate, and pedicellate with a perianth of six epigynously positioned tepals in two whorls: an outer whorl of three linear-triangular tepals and an inner whorl of three larger oblanceolate tepals. The androecium consists of a single whorl of three stamens positioned opposite the inner, larger, somewhat involute tepals. The stamens are exserted, and bear basifixed, bilocular anthers with longitudinal introrse dehiscence. The gynoecium consists of a syncarpous, tricarpellate, pistil with an inferior, three-lobed ovary. Each of the three locules contains a transversely oriented, protruding, peltate, axile placenta bearing 9–12 bitegmic, anatropous ovules. The ovules are positioned along the entire margin of the peltate placenta with their micropyles oriented toward the juncture of the placental stalk and central ovary axis and are, thus, pleurotopous, in position with the raphe facing the center of each peltate placenta. The single, terete style has a slightly expanded, unlobed stigma.

A whitish tomentum covers the inflorescence branches, pedicles, outer ovary wall, and abaxial tepal and bract surfaces. Trichomes are simple (unbranched), uniseriate, and composed of a short basal cell and 2–8 (usually four) elongate and filiform cells, including a tapering apical cell (Fig. 1a). The adaxial tepal surfaces are glabrous.

Raphides are scattered in all parts of the flower, occurring most profusely in the placentae.

Vascular anatomy. The pedicel contains an irregular complex of vascular tissue, consisting of approximately 9–12 concentrically arranged peripheral bundles and

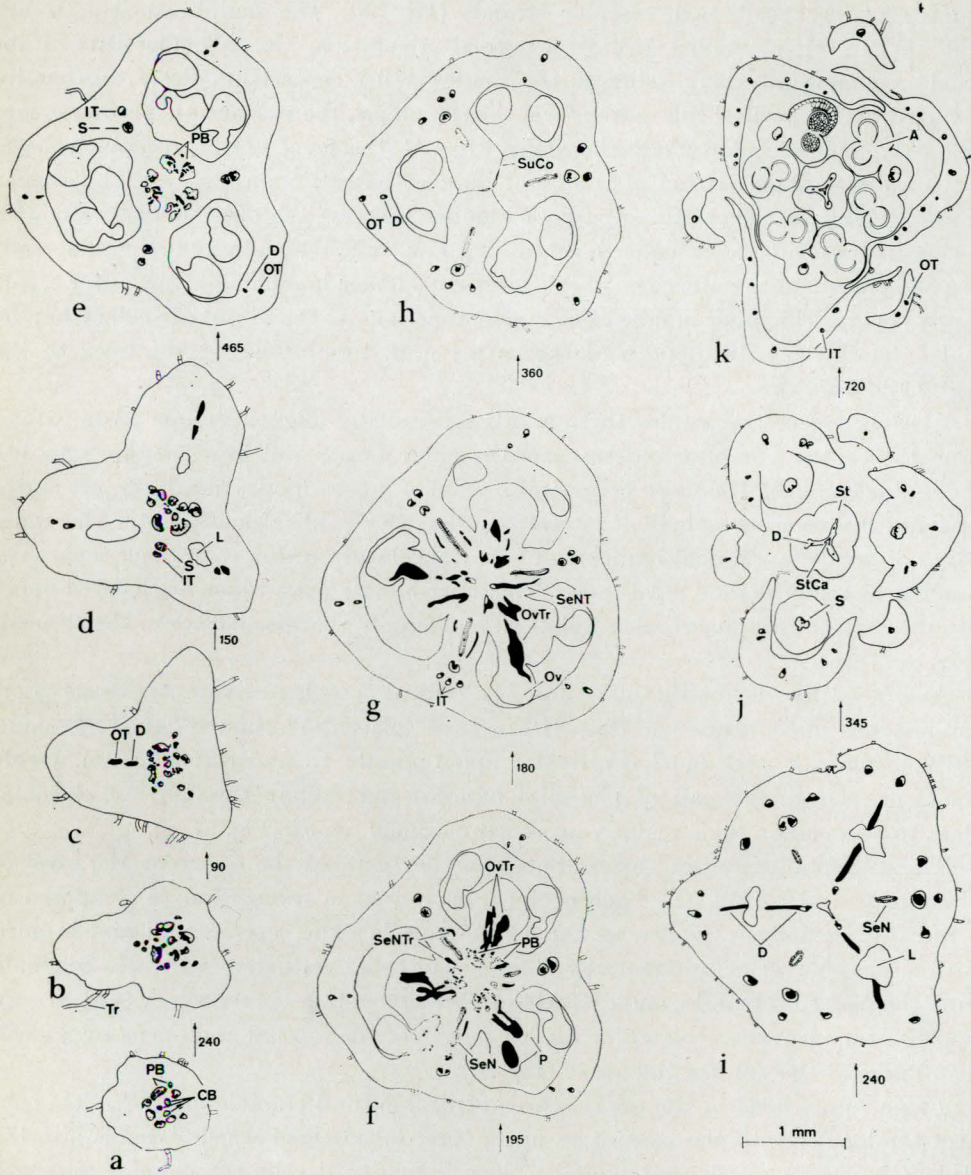


Fig. 3. *Lachnanthes*. Camera lucida drawings of serial transections of mature bud from pedicel (a) to apex (k). Distance between successive sections indicated in microns. Key to tissues: solid black, xylem or lateral trace; stipple, phloem. Abbreviations: A, Anther; CB, Central Bundles; D, Dorsal carpellary bundle; IT, Inner Tepallary bundle; L, Locule; OT, Outer Tepallary bundle; Ov, Ovule; OvTr, Ovule Trace; P, Placenta; PB, Placental Bundle; S, Stamen bundle; SeN, Septal Nectary; SeNTr, Septal Nectary Trace; St, Style; StCa, Styler Canal; SuCo, Sutural Commissure; Tr, Trichome.

three centrally positioned vascular strands (Fig. 3a). The peripheral strands are collateral in organization and have a normal orientation, i.e., xylem positioned abaxially, phloem adaxially, whereas the three smaller central bundles are generally inverted. As the pedicel enlarges to form the receptacle, the vasculature becomes more profusely and irregularly branched (Fig. 3b). At the level of the receptacle base, three radially aligned pairs of collateral bundles extend from the central vascular complex (Fig. 3c). These three pairs of bundles traverse the outer ovary wall, with each pair branching at a higher level into two or three tangentially oriented strands prior to entering the outermost whorl of tepals; further branching in the outer tepals rarely occurs. The inner bundle of each pair functions as the dorsal carpellary bundle and extends the entire length of the carpel wall, terminating at the apex of the style (Fig. 3d-k).

At the base of the locules three additional radially aligned bundle pairs extend from the central complex and traverse the outer ovary wall in a position opposite the septa (Fig. 3d). The more peripheral bundle of a pair divides at a level just above placenta insertion into three collateral bundles which subsequently enter the inner whorl of tepals; additional branching of the vasculature within each inner tepal may result in as many as nine tepal traces. The inner bundle pairs which are located opposite the septa are amphicribal or collateral and supply the vasculature to the stamens (Fig. 3e-k).

At a level just below the placentae, the central complex of vascular tissue is organized into three diffuse and dissected pairs of "placental" bundles (sensu STERLING 1972), each pair positioned centripetal and opposite to a carpel (Fig. 3e). Ovule traces arise from the pair of placental bundles and radiate through the placental stalk to vascularize the circularly arranged marginal ovules (Fig. 3f, g).

Three "septal nectaries" are initiated in the septa of the ovary at the level of placenta insertion (Fig. 3f). Each nectary, as viewed in transection, is composed of a radially elongate schizogenous canal that parallels the septum wall and is lined with a single layer of differentially staining epithelial cells. Lateral traces originate from the placental bundles and extend to either side of the septal nectary (Fig. 3f-g). Each nectary traverses the entire verticle length of the septum and opens by a small distal pore at the apex of the ovary (Fig. 3i).

At an upper level in the ovary, three ventral sutural commissures (Fig. 3h) connect the locules with the base of an open, three-lobed canal which extends into the style. The stylar canal is composed of loosely arranged cells throughout its length and a small central lacuna. No ventral sutures are evident in the style (Fig. 3i-k).

Lophiola aurea

General morphology and anatomy. The flowers of *Lophiola* are bisexual and actinomorphic, with bracteate pedicels. The perianth is composed of six similar lanceolate to narrowly triangular tepals positioned in two whorls. The tepals are epihypogynous in position, arising from the ovary at about two-thirds the ovary height. The androecium is composed of two whorls of three stamens each, the outer whorl

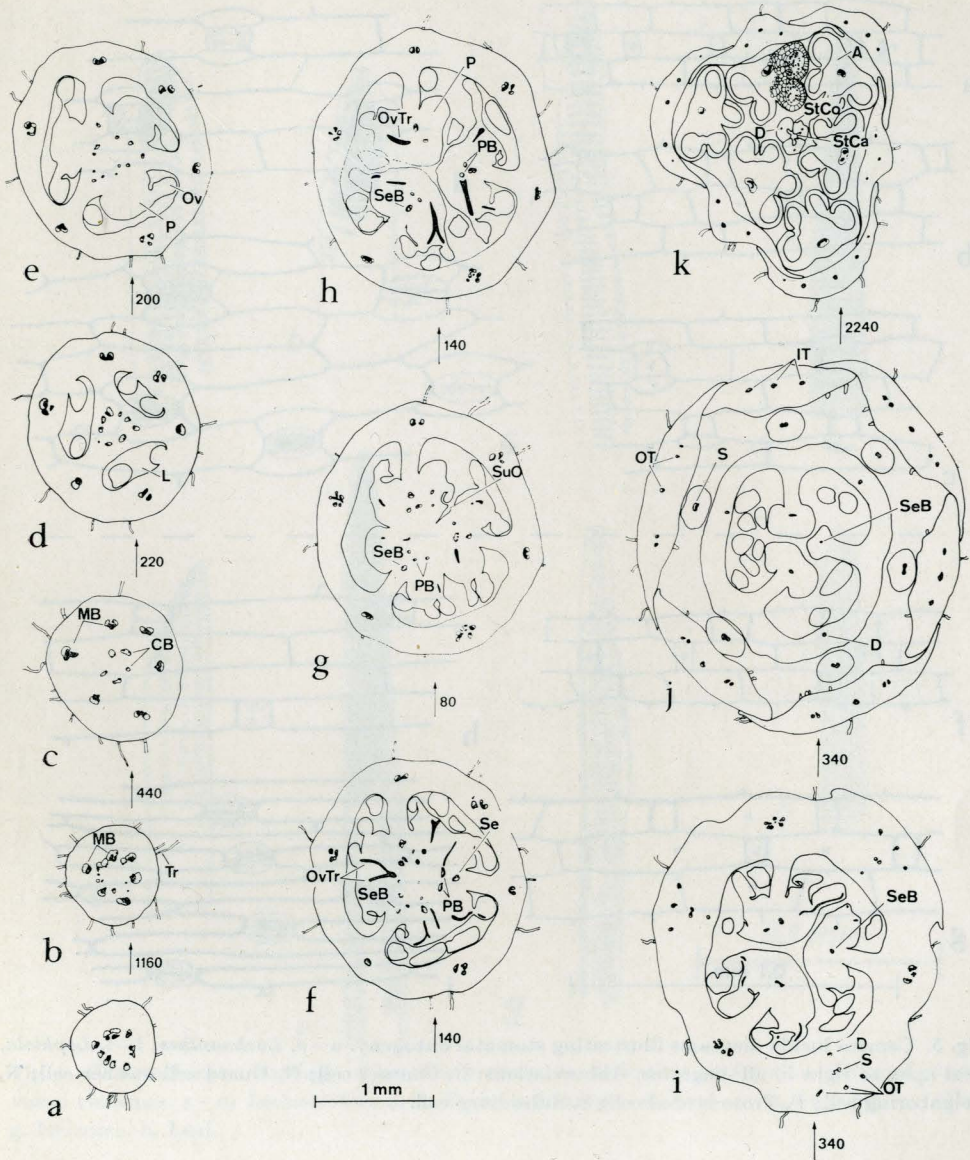


Fig. 4. *Lophiola*. Camera lucida drawings of serial transections of mature bud from pedicel (a) to apex (k). Distance between successive sections indicated in microns. Key to tissues: solid black, xylem or lateral trace; stipple, phloem. Abbreviations: A, Anther; CB, Central Bundle; D, Dorsal carpellary bundle; IT, Inner Tepallary bundle; L, Locule; MB, Major Bundle; OT, Outer Tepallary bundle; Ov, Ovule; OvTr, Ovule Trace; P, Placenta; PB, Placental Bundle; S, Stamen bundle; SeB, Septal Bundle; StCa, Styler Canal; StCo, Styler Commissure; SuO, Sutural Opening, Tr, Trichome.

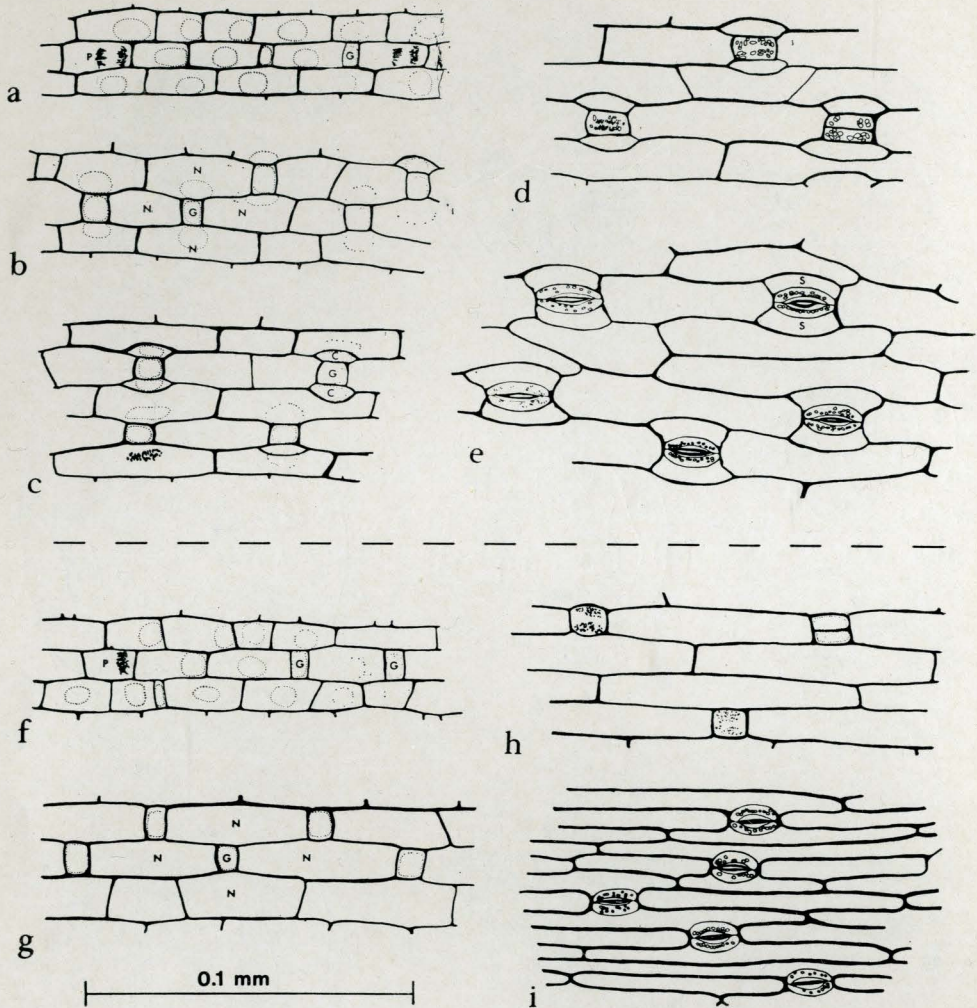


Fig. 5. Camera lucida diagrams illustrating stomatal ontogeny. a–e, *Lachnanthes*; f–i, *Lophiola*. Leaf apex to right in all diagrams. Abbreviations: C, Contact cell; G, Guard cell mother cell; N, Neighboring cell; P, Protodermal cell; S, Subsidiary cell.

situated opposite the outermost whorl of tepals. Anthers are basifixed and bilocular at maturity with longitudinal, introrse dehiscence. The gynoecium is syncarpous and tricarpellate. The half-inferior ovary is 3-locular with axile placentation below and unilocular with three parietal placentae above. The placentae are slightly protruding, each bearing numerous (ca. 30) ovules. Ovules are anatropous, bitegmic, and heterotropous, i.e., have a variable micropyle orientation with respect to the ovary. The single style is terete and the stigma unlobed.

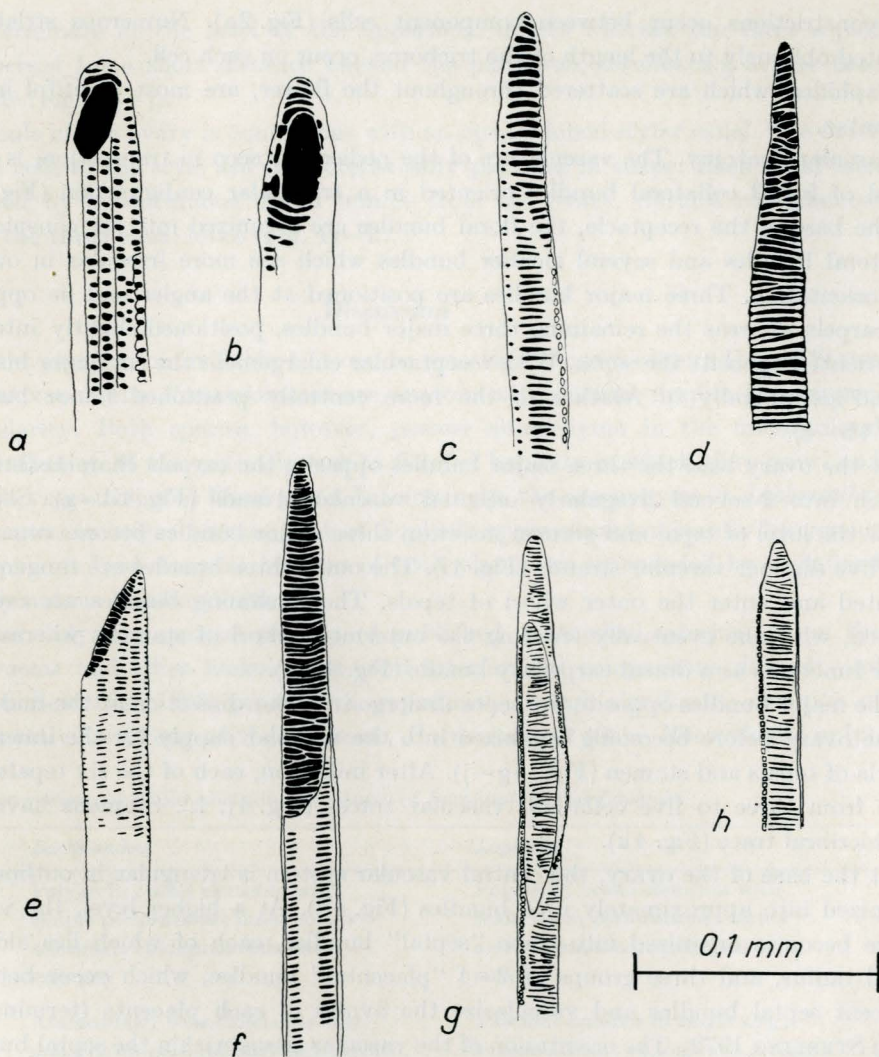


Fig. 6. Camera lucida drawings of tracheary elements, including perforation plates of obvious vessel elements. a—d, *Lachnanthes*. a, b, Root. c, Rhizome. d, Leaf. e—h, *Lophiola*. e, f, Root. g, Rhizome. h, Leaf.

Inflorescence branches, pedicels, hypanthium, and abaxial surfaces of the bracts and tepals are covered with a dense whitish tomentum. The whitish colored trichomes are simple (unbranched), uniseriate, and bicellular. The basal cell of each trichome is somewhat isodiametric, whereas the apical cell is long and filiform (Fig. 2c). Numerous short, terete, unicellular trichomes with rounded ends are found at the apex of each tepal, occurring along the extreme apical margins and midvein on the adaxial surface (Fig. 2b). A dense tuft of bright orange trichomes occurs at the base of the adaxial surface of each tepal; these hairs are simple, uniseriate, multicellular, and moniliform,

i.e., constrictions occur between component cells (Fig. 2a). Numerous striations, oriented obliquely to the length of the trichome, occur on each cell.

Raphides, which are scattered throughout the flower, are most plentiful in the placentae.

Vascular anatomy. The vasculature of the pedicel, as seen in transection, is composed of 9–12 collateral bundles oriented in a triangular configuration (Fig. 4a). At the base of the receptacle, the floral bundles are organized into six conspicuous collateral bundles and several smaller bundles which are more irregular in outline and orientation. Three major bundles are positioned at the angles and lie opposite the carpels whereas the remaining three major bundles, positioned slightly internal, are oriented opposite the septa. With receptacular enlargement the six major bundles extend peripherally in relation to the more centrally positioned minor bundles (Fig. 4b–c).

At the ovary base the three major bundles opposite the carpels characteristically branch into 2–several irregularly oriented vascular strands (Fig. 4d–g). Slightly below the level of tepal and stamen insertion these major bundles become organized into five distinct vascular strands (Fig. 4i). The outer three bundles are tangentially oriented and enter the outer whorl of tepals. The remaining bundles are radially aligned, with one eventually entering the outermost whorl of stamens whereas the other functions as a dorsal carpellary bundle (Fig. 4j, k).

The major bundles opposite the septa undergo irregular dissection at the mid-level of the ovary before becoming organized into the vascular supply for the innermost whorls of tepals and stamen (Fig. 4g–j). After initiation, each of the six tepals may have from three to five collateral vascular traces (Fig. 4j, k). Stamens have one amphicribal trace (Fig. 4k).

At the base of the ovary, the central vascular system is triangular in outline and organized into approximately nine bundles (Fig. 4d). At a higher level, the vasculature becomes organized into three “septal” bundles, each of which lies along a septal radius, and three groups of 2–4 “placental” bundles, which occur between adjacent septal bundles and vascularize the ovules of each placenta (terminology sensu STERLING 1972). The orientation of the vascular tissue within the septal bundles is variable, being collateral, bicollateral, or collateral with phloem and xylem oriented tangentially. The placental bundles are almost always inverted with phloem centripetal to the xylem. Slightly above the ovary base, each placental bundle branches with the resulting veins terminating within two (rarely three) ovules. Septal bundles remain unbranched as they traverse the central ovary, only rarely contributing a vascular trace to the placenta (Fig. 4f–i).

At about the level of tepal and stamen attachment, sutural openings radially divide each placenta, resulting in a apically unilocular ovary. Two placental bundles (each derived from the originally axile placentae of two adjacent carpels) and a single septal bundle vertically traverse the now parietal placentae. Each placental bundle develops lateral branches which subsequently bifurcate, regularly vascularizing two of the four ranks of ovules occurring on the parietal placentae. The placenta

bundles terminate at the level of the uppermost ovules whereas the three septal bundles persist for a short distance beyond the placentae, terminating at the base of the style (Fig. 4g—j).

The locule of the ovary is continuous with an open 3-lobed styler canal. The outer epidermal cells of the style are characteristically papillose in shape. Each canal lobe is traversed by a continuous dorsal bundle from the ovary. Sutural commissures delineate the three canal lobes (Fig. 4j—k).

Discussion

From the comparison in Table 1, it can be seen that the two eastern United States representatives of the *Haemodoraceae* are anatomically distinct despite their superficial similarity. Both species, however, possess aerenchyma in the underground stems, a reflection of the generally wet to flooded habitats in which they grow, and raphides in vegetative and floral parts. Interestingly, the aerenchyma in *Lachnanthes* is schizogenous in origin whereas that of *Lophiola* appears predominantly lysigenous in development. Leaf vascular bundles of both plants are surrounded by ill-defined chlorenchymatous bundle sheaths.

Unfortunately, the general paucity of published anatomical information on the *Haemodoraceae* and allies makes intra- and interfamilial comparisons difficult and premature. SCHULZE (1893) provided a superficial, though significant, synopsis of the comparative anatomy of the *Liliaceae*, *Haemodoraceae* (tribe *Haemodoreae* only),

Table 1. Comparison of major anatomical features of *Lachnanthes* and *Lophiola*

	<i>Lachnanthes</i>	<i>Lophiola</i>
Root	Polyarch; vessel elements with simple perforations; inner cortex sclerified; epidermal cells not enlarged	Polyarch; vessel elements with scalariform perforations; cortex aerenchymatous; epidermal cells enlarged
Rhizome	Atactostelic; vessel elements with scalariform perforations; endodermis absent; ground tissue aerenchymatous	Vascular bundles in single ring; vessels absent; endodermis present; cortex aerenchymatous
Leaf	Vascular bundles numerous, variable in size and ellipsoidal in transection, with sclerenchymatous caps; vessels absent; palisade cells absent; subsidiary cells present; raphides present	Vascular bundles 8—12, of uniform size and circular in transection, with sclerenchymatous sheaths; vessels absent; palisade layers present, subsidiary cells absent; raphides present
Flower	Placental bundles 2 per carpel; septal bundles absent; septal nectaries present; septal commissures present; styler commissures absent; ovules anatropous, bitegmic, pleurotropic; raphides present	Placental bundles 2—4 per carpel; septal bundles present; septal nectaries absent; septal opening present; styler commissure present; ovules anatropous, bitegmic, heterotropic; raphides present

Hypoxidoideae of the *Amaryllidaceae* (including the tribe *Conostylideae*), and *Velloziaceae*. Both *Lachnanthes* and *Lophiola* are included in this study. SCHULZE concluded that the *Haemodoreae* and *Conostylideae* are closely related on the basis of shared anatomical characteristics, predominantly the possession of stomatal subsidiary cells and a "mechanischer Ring" (sclerenchymatous sheath) in the underground stem. *Lachnanthes* differs from the remaining 6 genera of the *Haemodoreae* investigated in lacking axially extended epidermal cells which basally encircle the trichomes. *Lophiola* differs from the remaining 4 genera of the *Conostylideae* studied in lacking characteristic highly branched trichomes. More importantly, however, *Lophiola* stands apart from all other genera of the *Haemodoreae* and *Conostylideae* in lacking both stomatal subsidiary cells and the ring of sclerenchyma in the rhizome.

With the exception of *Lachnanthes*, all *Haemodoraceae* thus far examined have vessels confined to the roots, most of these with simple perforation plates (CHEADLE 1968). CHEADLE has noted, however, that three species of *Tribonanthes*, belonging to the tribe *Conostylideae*, and a single species of both *Dilatris* and *Lanaria*, belonging to the tribe *Haemodoreae*, possess root vessel elements with scalariform perforations. A similar condition is present in *Lophiola*. Although inconclusive in regards to the tribal relationships of *Lophiola*, these data tend to support the conjecture of MELCHIOR (1964) and CHEADLE (1969) that a natural alliance may exist between the *Haemodoraceae* and *Tecophilaeaceae*, which has vessel elements similar to *Tribonanthes*, *Dilatris*, *Lanaria*, and *Lophiola*. *Lachnanthes*, on the other hand, contains vessel elements with simple perforation plates in the root and ones with scalariform plates in the stem.

Within the *Haemodorales* (sensu HUTCHINSON 1934, 1959, 1973) CHEADLE (1968) reported the *Velloziaceae* to have advanced vessel members in the roots and elements with scalariform perforations in stems and leaves. The *Apostasiaceae* is variable in vessel type and position, ranging from primitive elements that are restricted to roots to advanced vessel members in both root and stems. The *Hypoxidoaceae*, *Philydraceae*, and *Taccaceae* all possess relatively primitive vessel elements in roots only.

STEBBINS & KHUSH (1961) found all ten genera of *Haemodoraceae* examined by them to have stomata with two lateral subsidiary cells, generally confirming the results of SCHULZE (1893). TOMLINSON (1974), furthermore, described the stomatal ontogeny of a single species of the haemodoraceous genus *Xiphidium* and showed that the subsidiary cells were derived from non-oblique divisions in a manner identical to that reported here for *Lachnanthes*. These two genera have consistently been placed in the same tribe (GEERINCK 1969). The few specimens of *Hypoxidoaceae*, *Velloziaceae*, and *Philydraceae* that have been studied also possess a pair of lateral subsidiary cells (STEBBINS & KHUSH 1961). As far as is known, the *Taccaceae* lack subsidiary cells. The lack of subsidiary cells in *Lophiola*, accordingly, may prove taxonomically significant as additional members of the family are examined. Foliage of the putatively closely related family *Velloziaceae* differs noticeably from *Lachnanthes* and *Lophiola* in possessing prominent sclerenchymatous girders and strands and in lacking raphides (AYENSU 1969, 1974).

Despite the differences between *Lophiola* and *Lachnanthes*, the floral vasculature of both genera is basically similar to the general pattern described for the *Liliaceae* by STERLING (1972, 1977, and papers cited therein). In the lilies the floral venation is characterized by tepals being three trace structures, stamens receiving a single trace, and carpels being supplied by a dorsal bundle, 1–2 “septal” bundles, and 2 (4) placental bundles. STERLING (1972, 1973) tentatively described the following floral morphological features to be primitive in *Liliaceae*: incomplete fusion between carpel “wings”, lack of fusion between pistil and floral cup, the presence of gynoeceial sutural openings (most primitive) or sutural commissures, the presence of two septal bundles per carpel (as opposed to one or none), and the presence of bitegmic ovules.

Both *Lachnanthes* and *Lophiola* have laterally fused carpels with the ovary of *Lophiola* being half-inferior in position and that of *Lachnanthes* in a more advanced inferior position. Ovary position is correlated with the presence of carpellary sutural openings and styler commissures in *Lophiola* and their absence in *Lachnanthes*. Both genera possess a single dorsal bundle per carpel and styler canals. Advancement in the carpels of *Lophiola* is indicated by the presence of a solitary septal bundle whereas septal bundles are entirely absent in *Lachnanthes*. The occurrence of septal nectaries in *Lachnanthes*, a common feature in the *Liliales* (BROWN 1938), undoubtedly represents an additional specialization. The presence of 2 to 4 placental bundles in both genera is similar to the pattern of ovular vascularization in the *Liliaceae*. In contrast to several species of the primitive liliaceous subfamily *Wurmbaeoideae* (STERLING 1972), both *Lachnanthes* and *Lophiola* lack gynoeceial vascular bundles that arise laterally from the dorsal carpellary bundle.

Although it is abundantly clear that considerably more detailed and extensive information is required in order to satisfactorily assess the evolutionary relationships of the *Haemodoraceae* and related families, available anatomical and morphological data tends to refute the placement of *Lophiola* in the tribe *Haemodoreae* as done by GEERINCK (1969). The same conclusion was reached by ROBERTSON (1976). *Lophiola* demonstrates several anatomical dissimilarities, both from *Lachnanthes*, as seen in the present study, and, as recorded by SCHULZE (1893), from other members of both the *Haemodoreae* and *Conostylideae*. ERDTMAN (1966) observed that *Lophiola* differs palynologically from all other investigated taxa of the *Conostylideae* (and *Haemodoreae*) and is perhaps more closely related to the *Conanthereae* (= *Tecophilaceae*, sensu HUTCHINSON 1934, 1959, 1973). This conjecture is in general agreement with that of CHEADLE (1969), based on vessel element morphology. However, ORNDUFF (1979), based on chromosome counts of several genera of the *Haemodoraceae*, including *Lachnanthes* and *Lophiola*, concluded that *Lophiola* “seems more at home in the *Haemodoreae* than in the *Conostylideae*”. Additional study of the family appears necessary before the taxonomic placement of *Lophiola* can be firmly established.

A continuing investigation of the *Haemodoreae* is underway by the senior author.

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