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# VEGETATIVE ANATOMY OF *MYOXANTHUS* (ORCHIDACEAE)

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Reestablishment of the genus *Myoxanthus* Poepp. & Endl. is supported by a number of morphological characteristics, including the presence of hispid cauline sheaths, pubescent inflorescences, and elongated petals with expanded apices (Luer, 1982). In some species the glandular apices of the petals are developed as osmophores, resembling those of the petals of *Restrepia* HBK. This combination of characters, which distinguishes *Myoxanthus* from other pleurothallids, is paralleled by a unique assemblage of anatomical features which are detailed here and reenforce the natualness of the genus. The anatomical relationships between *Myoxanthus* and other genera in subtribe Pleurothallidinae are evaluated briefly at the end of this report.

## MATERIALS AND METHODS

Procedures for light microscopy and scanning electron microscopy were identical to those described in Pridgeon & Williams (1979). Voucher specimens of all species examined have been deposited in the herbarium of the Marie Selby Botanical Gardens (SEL). Roots of some species were unavailable for study and these are so indicated in Table 1.

## OBSERVATIONS

### Leaf Anatomy

**Epidermis.** The sunken, glandular trichomes characterizing almost all other pleurothallids are absent or rare in all species of *Myoxanthus* except *M. affinis* and *M. parahybunensis.* Cuticle thickness varies among the species, from thin (less than 3 μm) in *M. affinis*, *M. sarcodactylae*, *M. scandens*, and *M. trachychlamys* to extremely thick (15-20 μm) in *M. chloe*, *M. monophyllus* (Fig. 1), and *M. uxorius.* The cuticle surface is generally smooth (Fig. 1), but minutely papillose in *M. georgei*, *M. hirsuticaulis*, *M. reymondii* and *M. trachychlamys* (Fig. 3.).

In surface views cells are polygonal (mostly hexagonal), elliptical, square, or rectangular (Figs. 2,3). Anticlinal walls are moderately thick (3-5 μm) to thick (5-7 μm) and primary pit-fields are conspicuous (Figs. 2,3). In transection cell shape varies from rectangular, peg-shaped, elliptical, dome-shaped, to isodiametric (Fig. 1). Wall thickenings are uniform in most species, but thicker on the anticlinal walls and inner wall in *M. georgei* and on the inner wall only in *M. reymondii.*

Cells of most species (exceptions: *M. affinis* and *M. monophyllus*) contain corolloid raphide clusters (Figs. 2-4), which appear nowhere else in the Pleurothallidinae in studies to date. These crystals are noticeably appressed to the cell wall (Figs. 2,3) and are visible in both fresh and preserved specimens.

Stomata are restricted to and flush with the abaxial epidermis in all species. Development of subsidiary cells is perigenous with trapezoid cells (Williams, 1979), resulting in 2-4 lateral and 2-4 terminal subsidiary cells (Fig. 3). Mean lengths and widths of guard-cell pairs are listed in Table 1. For the genus as a whole, mean dimensions (taken as the average of the species' dimensions) are 35.06 × 28.39 μm and the mean length/width ratio is 1.24.

**Hypodermis.** All species possess a multiseriate adaxial hypodermis, usually ranging from 2-5 layers (Figs. 1,5). *Myoxanthus chloe* is exceptional in having

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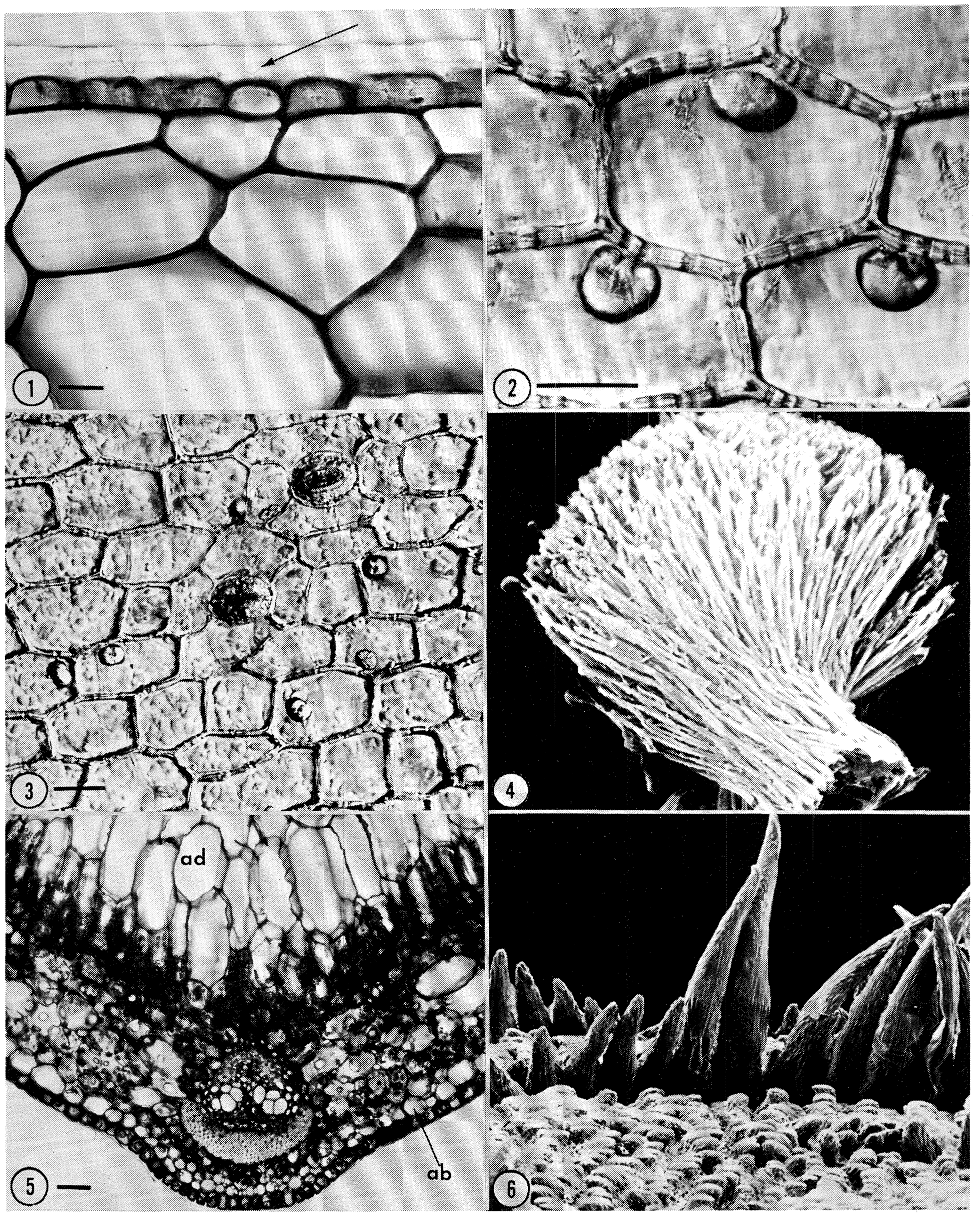



Figures 1-6. 1. *Myoxanthus monophyllus.* Adaxial epidermis and multilayered hypodermis of lamina in transection. Note thick cuticle (arrow). Light microscope (LM) photograph. Scale bar equals 20 μm. 2. *Myoxanthus reymondii.* Adaxial epidermis of lamina. Coralloid raphide clusters are attached to cell walls. Note thick anticlinal walls and conspicuous primary pit-fields. LM photograph. Scale bar equals 20 μm. 3. *Myoxanthus trachychlamys.* Abaxial epidermis of lamina showing 2 stomates, each with 2 lateral and 2 terminal subsidiary cells. LM photograph. Scale bar equals 20 μm. 4. *Myoxanthus trachychlamys.* One coralloid raphide cluster. Scanning electron microscope (SEM) photograph. X 4200. 5. *Myoxanthus ceratothallis.* Transection through lamina at midrib. Shown are adaxial hypodermis (ad), palisade and spongy mesophyll, midvein, and abaxial hypodermis (ab) and epidermis. LM photograph. Scale bar equals 500 μm. 6. *Myoxanthus parahybunensis.* Adaxial surface of cauline sheath covered with long unicellular trichomes and tubercles overlaid with cuticular wax. SEM photograph. X 125.

a hypodermis of eight layers. In transection the cells are polygonal, elliptical, or ovate. Frequently the lowermost cells are anticlinally elongated and elliptical, rectangular, or trapezoidal. A uniseriate abaxial hypodermis of polygonal, rectangular, elliptical, or irregular cells occurs in all species (Fig. 5). Cells of both the adaxial and abaxial hypodermis lack protoplasts at maturity but may contain remnants of chloroplasts, raphides, and/or druses. The spiral thickenings that characterize hypodermal cells in so many pleurothallid genera (Pridgeon, 1981, in press) are completely absent in *Myoxanthus.* Primary pit-fields are apparent in hypodermal cells of many species such as *M. reymondii.*

**Mesophyll.** Chlorenchyma is well-differentiated into 1-3 palisade and 4-10 spongy cell layers (Fig. 5). Palisade cells are rectangular, elliptical, or trapezoidal in transection. Spongy mesophyll consists of a lacunose network of stellately lobed, isodiametric, elliptical, or ovate cells with conspicuous primary pit-fields (Pridgeon & Williams, 1979). Spirally thickened idioblasts of the sort common in most pleurothallid genera (Pridgeon, 1981, in press) are absent in *Myoxanthus*. Druses are abundant in most species.

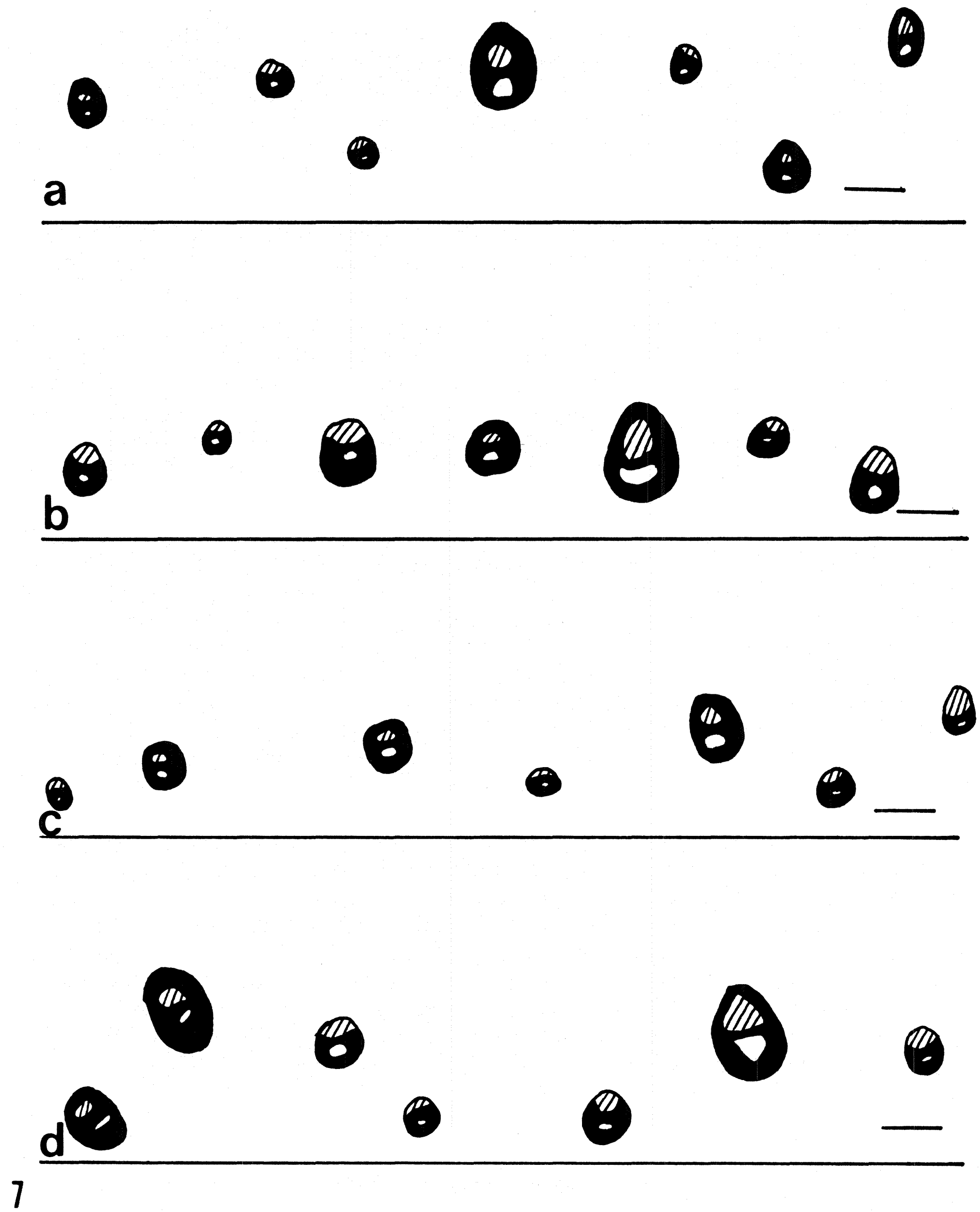
**Vascular bundles.** In many species the collateral vascular bundles are disposed in two irregularly arranged transverse series (Figs. 7a, 7c, 7d, 8a, 8c, 8d) but in only one series in other species (Figs. 7b, 8b). The upper series, if present, occurs immediately beneath palisade mesophyll. The number of bundles present at the middle of the leaf for all species is listed in Table 1. Bundles are of at least three size classes, and as many as five sizes occur in *M. georgei*, *M. hirsuticaulis*, and *M. monophyllus.* Size ratios of vascular bundles are given in Table 1. In all species bundles of the smallest size classes alternate with those of the largest, and a common configuration is 2 or 3 small bundles between large ones (Figs. 7,8). Bundles of the largest size classes typically possess a sclerotic sheath of 2-6 adaxial rows and 3-8 abaxial rows of fibers. The smallest bundles possess only one row of fibers abaxially and none adaxially. Marginal bundles are oriented xylem uppermost except in *M. parvilabius* and *M. georgei* where they are rotated 90° outward (xylem outermost and phloem directed toward the midrib). Transverse commissures with xylem adaxial and phloem abaxial extend between major longitudinal veins in all species, though infrequently. Petasiform (hat-shaped) silica bodies occur in linear files along vascular fibers.

Xylem consists of tracheids with scalariform and circular pits, libriform fibers, and parenchyma. Phloem consists of sieve-tube elements, companion cells, phloem fibers, and parenchyma. A uniseriate row of fibers or a "sclerenchymatous bridge" (Solereder & Meyer, 1930) separates xylem and phloem tissues.

## "Secondary" Stem Anatomy

The cauline sheath of all species examined is invested with unicellular, unbranched trichomes with acute to acuminate apices in single, interrupted transverse rows (Fig. 6). The sheath of *M. parahybunensis* also possesses flat-topped tubercles overlaid with cuticular wax (Fig. 6).

**Epidermis.** Cuticular thickness is variable depending on the species, from thin (less than 5 μm) in *M. scandens* and *M. trachychlamys* to extremely thick (up to 15 μm) in *M. chloe* and *M. monophyllus.* The uniseriate epidermis is sclerotic in all species except *M. parvilabius*, *M. ceratothallis*, *M. chloe*, and *M. scandens.* Cells are isodiametric, elliptical, dome-shaped, or triangular in transection. Chloroplasts and stomates are absent.




Figures 7-8. *Camera lucida* representations of relative size and position of foliar vascular bundles adjacent to midrib. The lower line represents the generalized abaxial epidermis and the scale bar in each case equals 0.1 mm. Hatched regions signify xylem, open regions of the bundles represent phloem, and heavy black regions indicate bundle sheath fibers. 7a. *Myoxanthus affinis.* 7b. *Myoxanthus hirsuticaulis* (similar to *M. ceratothallis, M. parvilabius, M. georgei* and *M. reymondii*). 7c. *Myoxanthus parahybunensis.* 7d. *Myoxanthus monophyllus.* 8a. *Myoxanthus sarcodactylae.* 8b. *Myoxanthus scandens.* 8c. *Myoxanthus trachychlamys* (similar to *M. chloe*). 8d. *Myoxanthus uxorius.*

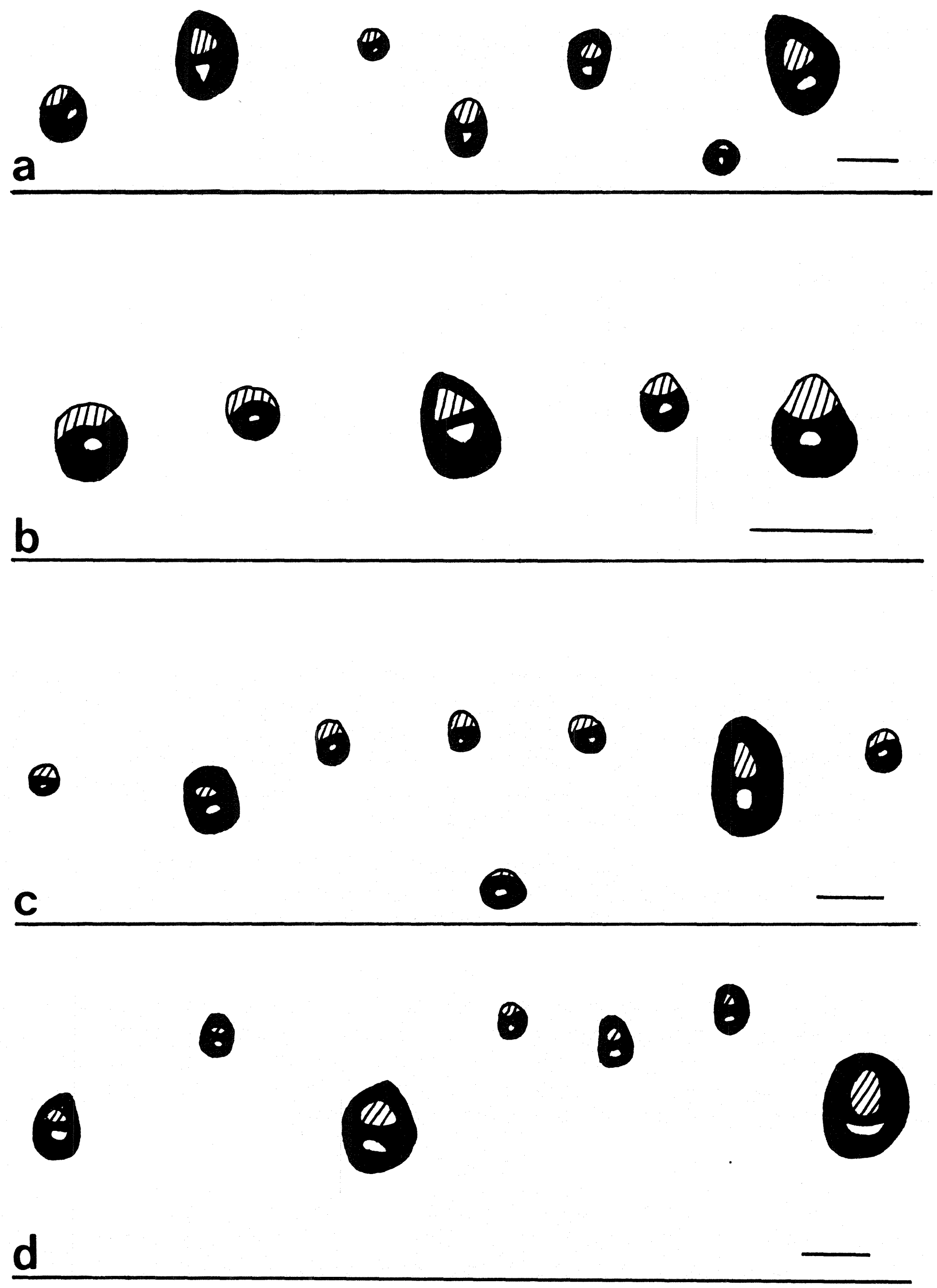



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TABLE 1. Anatomical data for *Myoxanthus*.

| Species | *M. affinis* | *M. parvilabius* | *M. ceratothallis* | *M. chloe* | *M. georg* |
|---|---|---|---|---|---|
| Character | | | | | |
| Mean lengths and widths of guard-cell pairs | 33.20 × 23.80 μm | 33.32 × 28.00 μm | 38.92 × 35.56 μm | 34.72 × 23.80 μm | 27.72 × 25.20 μm |
| Number of vascular bundles at middle of leaf | >100 | 32-37 | 78 | 56 | 45 |
| Vascular bundle size ratio Type I: Type II: Type III: (Type IV): (Type V) | 1:1.5: 2.6 | 1:1.3: 1.7:3.0 | 1:1.6: 2.3:3.1 | 1:1.5: 2.1:3.9 | 1:1.3: 1.8:2.6: 4.5 |
| Number of vascular bundles at middle of "secondary" stem | 43-45 | 17 | 40-42 | 55 | 14 |
| Number of velamen layers | 3 | N/A* | N/A | N/A | N/A |
| Number of root protoxylem strands | 14 | N/A | N/A | N/A | N/A |

*N/A = Not available for study.

**Ground tissue.** The outermost 1-3 layers of the cortex are sclerotic in all species, forming a subepidermal sclerenchymatous ring (Fig. 10). Chlorenchyma is often clearly delimited into cortex and pith by a continuous or intermittent phloic fiber sheath (Figs. 9, 10). Thickness of the sheath ranges from 3-15 interfascicular layers depending on the species. Chlorenchyma cells are typically ovate, elliptical, or isodiametric.

**Vascular cylinder.** "Secondary" stem vasculature comprises 2-5 concentric rings of bundles with the outermost rings embedded in or continuous with the phloic sheath (Fig. 10). The number of vascular bundles at the middle of the secondary stem for all species is presented in Table 1.

Bundles are collateral with xylem internal and phloem external. Xylem consists of tracheids with scalariform and circular pits, libriform fibers, and parenchyma. Phloem consists of sieve-tube elements, companion cells, phloem fibers, and parenchyma. As in the leaf, silica bodies are associated with vascular fibers, and xylem is separated from phloem by a uniseriate or biseriate sclerenchymatous bridge in many instances.

## Root Anatomy

**Epidermis.** The root epidermis of all species examined consists of a velamen with a varying number of cell layers (Table 1). Cells are polygonal, elliptical, or rectangular in transection. Inner and outer tangential walls of velamen cells are thickened, and the thickenings may continue onto radial walls as well.

**Cortex.** The exodermis, or outermost layer of the cortex, is uniseriate in all species. Exodermal cells are polygonal (mostly pentagonal or hexagonal), rectangular, or elliptical in transection and are partially thick and lignified (U-shaped thickenings of Solereder and Meyer, 1930; see Pridgeon and Williams, 1979). Passage cells are regularly present in the exodermis. Cortical

| *irsuti- is* | *M. monophyllous* | *M. parahybunensis* | *M. reymondii* | *M. sarcodactylae* | *M. scandens* | *M. trachychlamys* | *M. uxorius* |
|---|---|---|---|---|---|---|---|
| 30 × 20 μm | 35.60 × 30.20 μm | 41.40 × 30.50 μm | 39.20 × 35.56 μm | 28.80 × 25.20 μm | 39.90 × 29.10 μm | 33.50 × 25.50 μm | 41.20 × 31.40 μm |
| | ~70 | ~80 | 39 | ~65 | 27 | 43 | 30 |
| .4: :2.2: | 1:1.4: 2.5:3.7: 6.8 | 1:1.6: 2.1:3.7 | 1:1.4: 2.1:2.6 | 1:1.6: 2.2:3.7 | 1:1.4: 1.9:2.8 | 1:1.6: 2.1:3.1 | 1:1.3: 2.0:2.8 |
| | >100 | 64 | 16 | 50 | 14 | 21 | 34-36 |
| | 3 | 3 | N/A | 2 | 1 | 2 | 2 |
| | 20 | 18 | N/A | 15 | 9 | 9 | 13 |

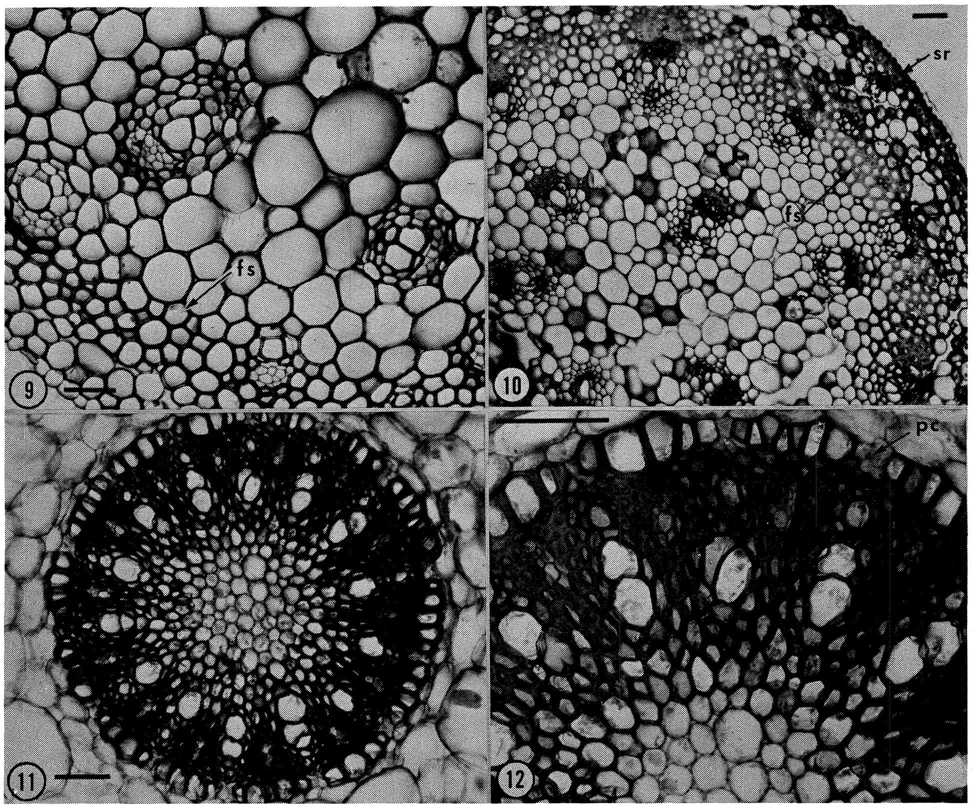
chlorenchyma cells are isodiametric to elliptical and ovate in transection. The endodermis, innermost layer of the cortex, is uniseriate in all species and cells are uniformly thick and lignified (O-shaped thickenings of Solereder and Meyer, 1930; Figs. 11, 12). Passage cells occur opposite protoxylem points. Endodermal cells are rectangular, pentagonal, triangular, or isodiametric in transection (Figs. 11, 12).

**Stele.** As defined here, the stele comprises an outermost, uniseriate pericycle, xylem, phloem, and pith. The pericycle consists of elliptical, rectangular, or isodiametric cells. Its thin-walled parenchyma cells abut on protoxylem elements and its lignified cells on protophloem elements.

The primary xylem of all species studied is polyarch (Figs. 11, 12). The number of protoxylem strands for each species is given in Table 1. Xylem consists of tracheids with helical thickenings and/or scalariform or circular pits, vessel elements with scalariform perforation plates and pitted lateral walls, libriform fibers, and parenchyma. There are 1-3 large metaxylem vessels included in each xylem strand (Figs. 11, 12). Phloem strands alternate with xylem strands and consist of sieve-tube elements, companion cells, phloem fibers, and parenchyma. A parenchymatous pith of 5-16 cells in diameter is present in all species (Figs. 11, 12).

## DISCUSSION

The combination of anatomical characteristics which distinguishes *Myoxanthus* from all other pleurothallid genera includes coralloid raphide clusters in leaf epidermal cells, two series of foliar veins (in many species), hispid cauline sheaths, a high number of xylem strands and a medullated stele in the root. All of these features are extremely rare in the subtribe. Presence of the peculiar crystals, occurring nowhere else in the subtribe, probably reflects a unique biochemical pathway. Two series of veins and a medullated



Figures 9-12. 9. *Myoxanthus scandens.* Transection of secondary stem. A phloic fiber sheath (fs) is interfascicular in the outermost ring of bundles. LM photograph. Scale bar equals 20 µm. 10. *Myoxanthus reymondii.* Transection of secondary stem showing lignified subepidermal layers (sr), phloic fiber sheath (fs), and portions of two concentric rings of bundles. LM photograph. Scale bar equals 500 µm. 11-12. *Myoxanthus affinis.* Transection of root. Note endodermis of uniformly thickened cells, passage cells (pc), and parenchymatous pith. The stele has 14 protoxylem strands. LM photographs. Scale bar equals 50 µm.

stele are found elsewhere only in the *Pleurothallis aspasicensis* complex (which also warrants generic rank for this and other reasons) and in *Octomeria.* Polyarchy in the root also occurs in *Dracula*, the *P. aspasicensis* complex, *Octomeria*, and *Restrepiella* (Pridgeon, 1981, in press). Equally important to anatomical circumscription of *Myoxanthus* is what it lacks: spiral thickenings in hypodermal cells and mesophyll idioblasts, both of which are present in most other pleurothallids. The *P. aspasicensis* complex and *Octomeria*, similarly, lack spiral thickenings in all tissues.

On the basis of these characters and others used in an assortment of multivariate statistical analyses (Pridgeon, 1981), *Myoxanthus* is best positioned between *Octomeria* and the *P. aspasicensis* complex and very distant from other genera with two pollinia, especially *Masdevallia* and *Porroglossum*. This idea is not new, for Garay (1956) placed Lindley's section *Aggregatae* of *Pleurothallis* (which includes some species now in *Myoxanthus*) in the same line as *Octomeria* and *Restrepiella.* However, section *Aggregatae* is extremely artificial; species florally and anatomically unrelated are assigned to it. Furthermore, because *Restrepiella* possesses only one series of foliar veins, spirally thickened idioblasts in the leaf, and glandular trichomes, it is distant from *Myoxanthus* and probably on a different evolutionary line proceeding from *Octomeria* or the putative ancestor of the subtribe.

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LITERATURE CITED

Garay, L. A. 1956. Studies in American orchids. II. The genus *Brachionidium* Lindl. *Canad. J. Bot.* 34: 721-743.

Luer, C. A. 1982. A reevaluation of the genus *Myoxanthus* (Orchidaceae). *Selbyana* 7: 34-54.

Pridgeon, A. M. 1981. Contributions toward the systematics of the Pleurothallidinae (Orchidaceae): anatomical evidence and numerical analyses. Ph.D. dissertation, Florida State University, Tallahassee. 255 pp.

—— In press. Diagnostic anatomical characters in the Pleurothallidinae (Orchidaceae). *Amer. J. Bot.*

Pridgeon, A. M. and Williams, N. H. 1979. Anatomical aspects of *Dresslerella* (Orchidaceae). *Selbyana* 5: 120-134.

Solereder, H. and Meyer, F. J. 1930. Systematische Anatomie der Monokotyledonen. Vol. VI. Microspermae. Gebrüder Borntraeger, Berlin. English translation. 1969. Israel Program for Scientific Translations. 159 pp.

Williams, N. H. 1979. Subsidiary cells in the Orchidaceae: their general distibution with special reference to the Oncidieae. *Bot. J. Linn. Soc.* 78: 41-66.