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VASCULAR PATTERNS IN STEMS OF ARACEAE: SUBFAMILY POTHOIDEAE¹

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A B S T R A C T

The stem vasculature of representative species of ten of the 11 genera in the Pothoideae was analyzed with the aid of films of series of transverse sections. In all species a leaf trace typically diverges from a continuing axial bundle before departing to a leaf, with the possible exception of *Heteropsis*. However, within this common organizational scheme a considerable range of variation exists, e.g., with respect to degree of branching of axial bundles, and distance from a leaf-trace branch to the point of leaf-trace departure to a leaf. In addition, we have found a wide variety of patterns of bud-trace organization in different genera of the Pothoideae. For example, prominent arcs composed of numerous bud traces occur in the central cylinder of *Pothos*, *Pothoidium*, and *Heteropsis*. Comparative anatomy leads to the conclusion that *Pothos* and *Pothoidium* more closely resemble *Heteropsis* than *Anadendrum*. *Anadendrum* should be dissociated from the tribe Pothoeae. With respect to other genera in the Pothoideae, our preliminary results suggest that each of the genera *Anthurium*, *Culcasia*, *Zamioculcas*, *Acorus*, and *Gymnostachys* are highly distinct from each other.

VAN TIEGHEM (1867) published the only comparative study of the organization and distribution of stem vascular bundles in the Araceae. He observed that aroid stems could contain either "simple" vascular bundles (i.e., with a single strand of xylem and phloem) or "compound" bundles (i.e., with two or more discrete strands of xylem and phloem that remain distinct for considerable distances). The present paper is the second of a series of reports on our survey of the vascular organization of the Araceae, which began with a description of our approach and preliminary observations (French and Tomlinson, 1980). Our principal goals are to determine: 1) the extent to which the course of simple vascular bundles in aroids follows the pattern typical of palms and other monocotyledons; 2) the extent to which the three-dimensional organization of compound vascular bundles in aroids resembles the pattern recently worked out for pan-

dans (Zimmermann, Tomlinson, and LeClaire, 1974); 3) the usefulness of systematic comparisons of vasculature in understanding evolution of the Araceae, and 4) the usefulness of stem vasculature as a primary diagnostic character in the Araceae.

In this paper we are concerned with representation of Engler's subfamily Pothoideae in which are included many distantly related genera that lack both trichosclereids (some exceptional species of *Pothos* have them) and laticifers. The subfamily includes 11 genera currently grouped in six tribes. Most genera have: 1) bisexual flowers, except for *Culcasia*, *Gonatopus* and *Zamioculcas*, which are unisexual, and 2) a perianth, except for *Culcasia* and *Heteropsis* which have naked flowers.

METHODS—Table 1 lists the species examined and location of voucher specimens. Transverse sections (T.S.) were made from either fixed or living stems using a Reichert OME sliding microtome fitted with a special clamp to accommodate long stem pieces (Tomlinson, 1970; Zimmermann, 1976). Depending on internode length, every section or sections at various regular intervals were kept for processing. In nonfleshy stems the average section thickness in different species ranged from 60–130 μm and up to 250 μm in fleshy stems. Sections were cleared in 10% Clorox and concentrated HCl, stained in basic fuchsin, mounted in Karo syrup; and photographed with a Bolex 16-mm movie camera mounted on a stand above a Wild M20 microscope. The sec-

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tions were oriented for photography by means of outline drawings of bundles made with a camera lucida attachment (Zimmermann and Tomlinson, 1966), and two frames were exposed per section. Films were projected for analysis with an L-W 224 A Photo Optical Data Analyzer, permitting variable speed frame-by-frame analysis. Plots of bundle pathways were made from measurements of relative bundle distance from the center of the stem against position along its length. In the subsequent description, the courses of vascular bundles are followed basipetally, i.e., from the appendage (leaf or branch) into the main axis. This is purely a descriptive convention and obviously does not refer to the generally acropetal method of development of the vascular system. The limitations of our present method of presentation should be made clear; the plots refer to a few selected, representative vascular bundles from the total system presented in the analytical movies. For this reason we have also presented gross analytical diagrams which convey some of the overall structural impressions obtained from the analyses. In labeling the plots of bundles (Fig. 33–41) after fusion of a leaf trace (open circle) and axial bundle (closed circle) an intermediate symbol (half open) is used for the next few points. The point at which the half circle is changed back to full is arbitrary and meant only to suggest that anatomical changes, such as the loss of protoxylem, are observed as a leaf trace is integrated into the vascular system of the central cylinder.

RESULTS—Morphology—Species we examined from six of the genera—*Pothos*, *Pothoidium*, *Anadendrum*, *Heteropsis*, *Culcasia*, and *Anthurium*—are vines climbing by means of roots ("root-climbing vines"), and four are rhizomatous—*Gonatopus*, *Zamioculcas*, *Gymnostachys*, and *Acorus*. Phyllotaxis is distichous in *Pothos*, *Pothoidium*, *Anadendrum*, *Heteropsis*, *Culcasia*, *Acorus*, and *Gymnostachys*, but spiral in the species of *Anthurium* we examined. *Zamioculcas* has a pattern of leaf distribution with alternate scale and foliage leaves, in which the leaves are essentially spiridistichous (Engler and Krause, 1905–1920). The morphology of *Gonatopus marattioides* has not been described in detail (see fig. 4 in Bogner, 1978 for an illustration of habit). Inflorescences are lateral in *Pothos*, *Pothoidium* and *Heteropsis*, and terminal in the other genera.

Pothos scandens (Fig. 1, 3, 24–27, 33): This is a root-climbing vine with distichous leaves; the inflorescences are axillary, the shoot system a monopodium.

Internode T.S. (Fig. 1): The cortex is wide and relatively undifferentiated but with a well-developed system of over 100 vascular bundles, each with a well-developed continuous sclerenchymatous sheath. Each larger cortical bundle has a single wide metaxylem element and a narrow phloem strand. There is no endodermis, but the central cylinder is delimited abruptly by a broad sclerotic layer, gradually transitional to the thinner-walled, unligified central ground parenchyma. Most vascular bundles in the crowded peripheral region have a single wide metaxylem element and a conspicuous phloem strand, but they alternate with a few much narrower ones. Evidently, many of the central bundles are recently inserted leaf traces that have a poorly differentiated sclerenchymatous bundle sheath and well-developed narrow protoxylem elements. Closer to the nodes there may be occasional small bundles, usually the distal ends of branch traces.

Node T.S. (Fig. 3): In a single section in the nodal region the most conspicuous feature is the broad arc of branch-trace tissue which penetrates deeply into the central cylinder. Most of the branch-trace elements are undifferentiated vascular bundles, although the proximal extension can be recognized as discrete traces. Laterally, anastomosing between cortical bundles is also evident. At a restricted level immediately below the node there are 6–8 adventitious root traces, each of which is inserted opposite lateral leaf traces (e.g., Fig. 27).

Course of the vascular bundles, (a) node. (Fig. 24–27): Within the stem, the leaf-trace system consists of an arc of about ten wide bundles, each of which continues into the central cylinder. The central bundle is a conspicuous median trace (Fig. 3). A larger number of narrow leaf traces enter and remain confined to the cortex.

The cortical system remains discrete, but there is anastomosing between cortical bundles, beginning first just above the node, i.e., immediately above the axillary bud. This is initially recognizable by displacement of those cortical bundles in the path of the entering leaf trace (Fig. 24). These bundles are displaced in a tangential direction, and anastomose freely with other bundles. Anastomosis continues laterally on each side of the node and is completed below it. Part of this cortical anastomosing also involves root traces, incoming leaf traces, and bud traces, so that vascular continuity at the node is complete. Anastomosing cortical bundles change from collateral to a mass of narrow tracheary elements at the level of anastomosing. A detail of this kind of change is shown in Fig. 6.

TABLE 1. *Species examined, listed according to tribal arrangement of Engler (1905), updated by Bogner (1978)*

	Araceae—Subfamily I. Pothoideae	Collection
Tribus I.	Pothoeae: <i>Pothos scandens</i> L. <i>Pothodium lobbianum</i> Schott <i>Pedicellarum</i> M. Hotta <i>Anadendrum microstachyum</i> (de Vriese et Miq.) Backer et Alderw.	Kew 000-69.51673 Bogner 1272 (M) not examined Bogner 1314 (M)
Tribus II.	Heteropsidaeae: <i>Heteropsis jenmanii</i> Oliv.	1) Prévost 670 Piste de St. Elie, Fr. Guiana 2) P. Blanc, Munich Bot. Garden Access. No. 48/78
Tribus III.	Anthurieae: <i>Anthurium polyschistum</i> R. E. Schultes & Idrobo	French s.n. (FTG)
Tribus IV.	Culcasieae: <i>Culcasia</i> sp.	Bogner 250 (M) Tanzania
Tribus V.	Zamioculcaseae: <i>Zamioculcas zamiifolia</i> (Lodd.) Engl. <i>Gonatopus marattioides</i> (A. Peter) Bogner	French 32 (FTG) Bogner 247 (M) Tanzania
Tribus VI.	Acoreae: <i>Acorus calamus</i> L. <i>Acorus gramineus</i> Soland <i>Gymnostachys anceps</i> R.Br.	French 41 (FTG) French 33 (FTG) Howard s.n. (FTG)

The median leaf trace enters the central cylinder accompanied by the two arcs of branch traces but passes rapidly to the center of the stem. Lateral traces also pass obliquely into the central cylinder but are not associated directly with branch traces, although they are indirectly attached via cortical anastomoses. Instead, each lateral trace at the level of its departure from the central cylinder is associated with a root trace—the leaf trace essentially diverges through the region of root-trace attachment (Fig. 27).

Branch traces become recognizable at the periphery of the branch trace arc as narrow strands which attach over a short distance to axial bundles and leaf traces.

Course of the vascular bundles, (b) several internodes (Fig. 33, 35): Leaf traces can be followed over several internodes below their node of insertion. They pass obliquely into the central cylinder to a subcentral position, but over a distance of several internodes gradually migrate towards the crowded periphery. In doing so, they progressively lose their protoxylem, and eventually the xylem comes to be represented by a single, wide metaxylem element. Ultimately, they may be represented by the narrowest peripheral bundles. The origin of these peripheral bundles, which are probably the basal extremities of leaf vascular bundles, is best appreciated by following analytical movies acropetally. At intervals, small bundles

diverge from either central axial bundles or leaf traces and migrate abruptly, but with a revolving component not present in other bundles, to the periphery of the central cylinder. They are then recognizable as the ultimate proximal extensions of traces that will enter leaves at higher levels. In a single transverse section these traces are structurally very similar to branch traces, but the two can be distinguished readily by their courses and points of attachment. Branch traces are continuous into branches shortly above the level at which they are first recognizable, whereas axial bundles follow the long course already described and over long and variable distances. The two types are contrasted in the middle of Fig. 33.

Conclusions: The distinctive features of the vascular arrangement in *Pothos* are: 1) the horseshoe-shaped insertion of the bud traces and their incorporation into the central cylinder essentially without changing its outline (Fig. 3); 2) the cluster of bud traces associated exclusively with the median leaf trace; 3) the well-developed cortical system and its nodal anastomosing (Fig. 24, 25); 4) the absence of regular, direct continuity between axial bundles and leaf traces at the level of insertion of leaf traces (Fig. 33, 35), and 5) the close association between lateral leaf traces and adventitious roots (Fig. 27). Despite the lack of direct continuity between certain components of the vascular system, vascular continuity is

complete but takes place primarily at the node and involves anastomosing on the one hand between leaf and branch traces, and on the other hand between bud traces, cortical traces, and root traces.

Pothoidium lobbianum (Fig. 2, 5, 6, 12, 13, 34): This is a root-climbing vine with the same morphology and basic anatomy as *Pothos*.

Stem organization and vasculature: This is so similar to *Pothos* that it does not merit detailed description. One notable difference is the presence of trichosclereids in the cortex (Fig. 12, 13). Nodal and internodal anatomy of the two genera are otherwise similar, except for size differences, as can be seen by comparing Fig. 1–3, 5. Plots of representative leaf traces in Fig. 34 show that in this genus, unlike *Pothos*, there is a tendency for leaf traces to fuse with axial bundles a little below their level of entry into the central cylinder (cf., the leaf traces plotted in the upper part of Fig. 34 and those in Fig. 33 and 35).

Anadendrum microstachyum (Fig. 7, 8, 36): This is a root-climbing vine with distichous leaves. The inflorescences are terminal in the adult sympodial phase. We have examined the vegetative, monopodial phase as being morphologically most directly comparable to *Pothos* and *Pothoidium*. As in these genera, the stem vascular bundles are simple.

Internode in T.S. (Fig. 7): This is asymmetrical; the broad cortex is uniformly parenchymatous, with some lignification of superficial layers. On one side there is a series of about five large vascular bundles near the central cylinder as well as about the same number of smaller bundles nearer the periphery. All are leaf traces; there is no vascular system confined exclusively to the cortex. Further asymmetry is achieved by a series of vascular bundles at the periphery of the central cylinder connected by a loosely continuous band of sclerenchyma. This system is always on the side of the opposite the numerous leaf traces. There is no endodermis. The central cylinder includes no sclerenchyma other than the peripheral arc and that forming the vascular bundle sheaths. Most central vascular bundles include one or more wide metaxylem elements and a narrow sclerotic bundle sheath, forming in T.S. an arc around the phloem. Recently entered leaf traces can be recognized by their more abundant sclerenchyma and numerous narrow protoxylem elements.

Node in T.S. (Figs. 8, 28): The axis widens appreciably at the node. A single root is attached on the side with the sclerotic arc, with a broadly anastomosing series of root traces inserted over about one-quarter of the total circumference of the central cylinder. Thus the sclerotic arc is the site of insertion of the root and is presumably that side of the axis directed

→

Fig. 1–6. Transsections. 1. *Pothos scandens* internode showing cortex and central cylinder. $\times 19$. 2. *Pothoidium lobbianum* internode, with cortex, central cylinder, axial bundle, leaf traces. $\times 12$. 3. *Pothos scandens* node, showing cortex, anastomosing cortical bundles (arrows), roots, lateral leaf traces, midvein trace, bud traces. $\times 15$. 4. *Gonatopus marattioides* internode, with ring of vascular bundles. $\times 12$. 5. *Pothoidium lobbianum* node, with bud traces, midvein leaf trace, cortex, anastomosing cortical bundles, leaf trace. $\times 28$. 6. *P. lobbianum* internode with anastomosing cortical bundles, cortex. $\times 200$.

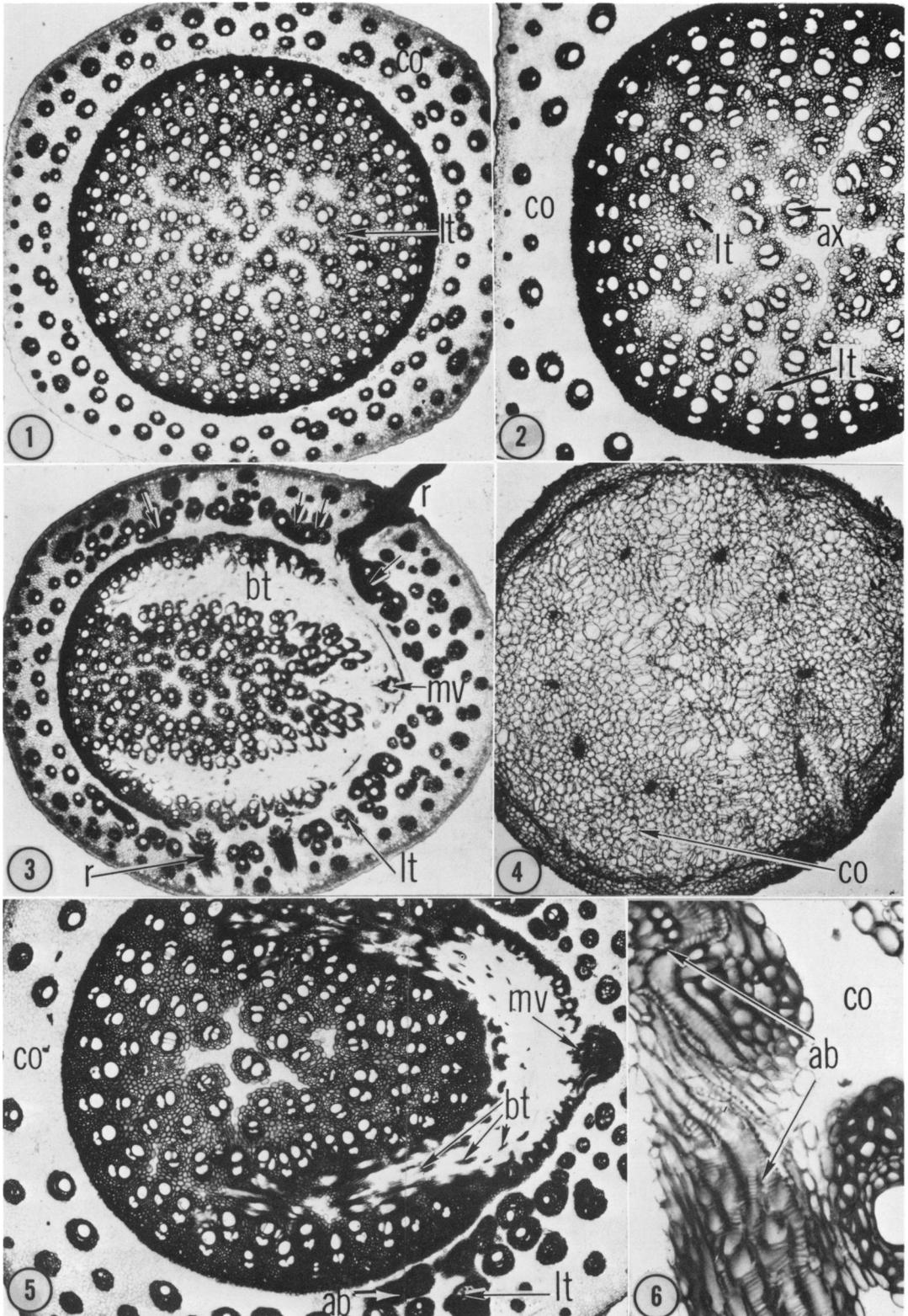
KEY TO LABELING: cortex (co), axial bundle (ax), leaf trace (lt), anastomosing cortical bundles (ab), root (r), midvein leaf trace (mv), bud traces (bt).

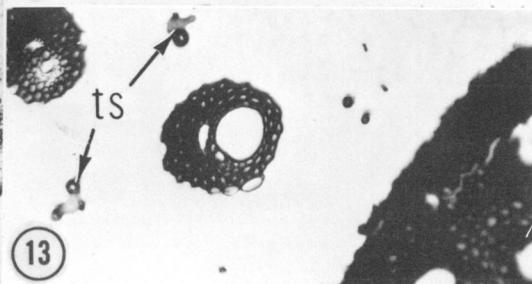
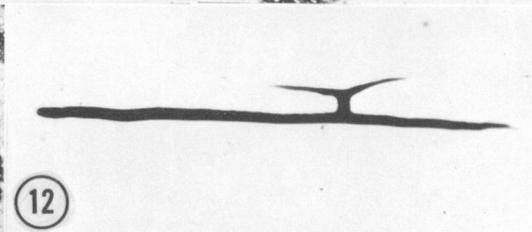
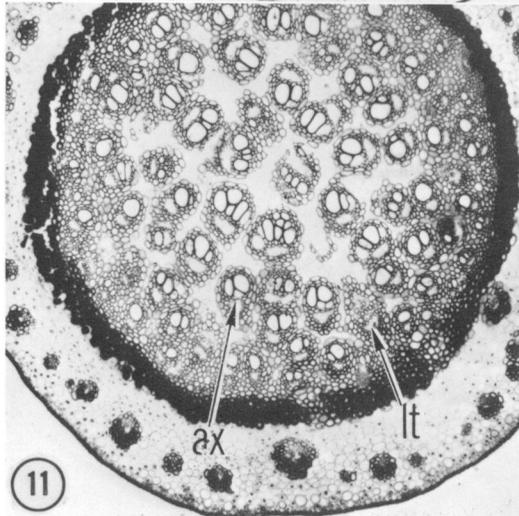
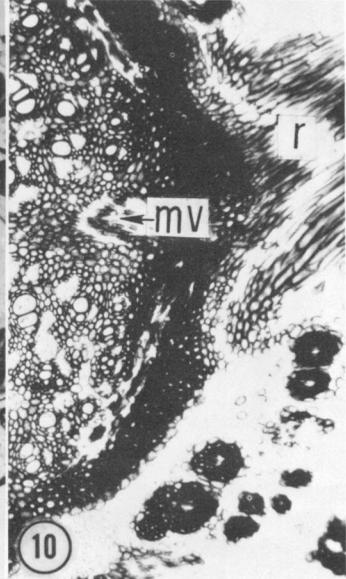
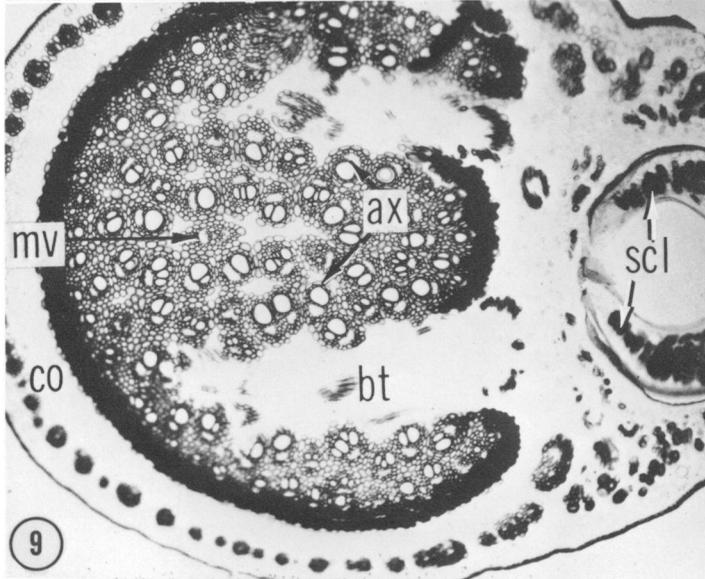
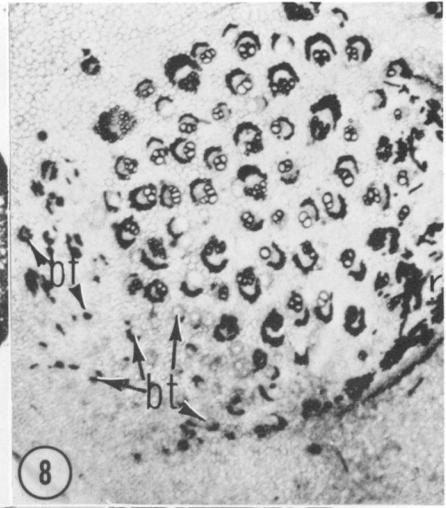
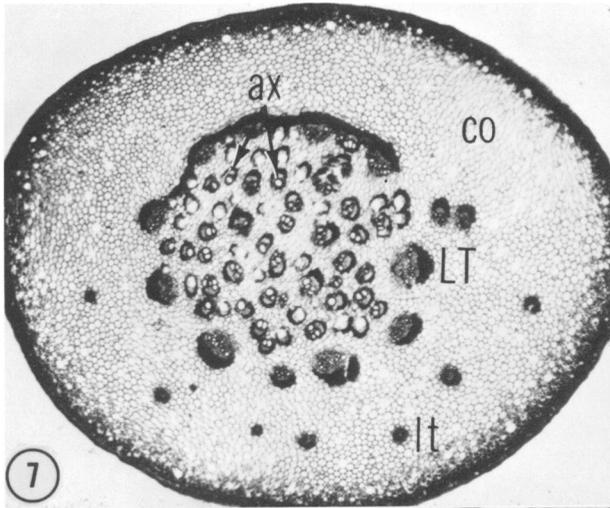
Fig. 7–13. 7. *Anadendrum microstachyum*. Transsection (TS) of internode with major leaf traces (LT) minor leaf traces (lt), cortex, axial bundles, $\times 21$. 8. *A. microstachyum*. TS of node with bud traces, part of the root attachment. $\times 26$. 9. *Heteropsis jenmanii*. TS of node, showing arcs of bud traces, bud scales with sclereids, cortex, midvein trace from next distal leaf. $\times 34$. 10. *H. jenmanii* node with view of midvein trace and root attachment. $\times 46$. 11. *H. jenmanii*. TS of internode, with leaf trace, axial bundle. $\times 32$. 12. *Pothoidium lobbianum* trichosclereid. $\times 106$. 13. *P. lobbianum*. TS of internode showing trichosclereids in cortex. $\times 102$.

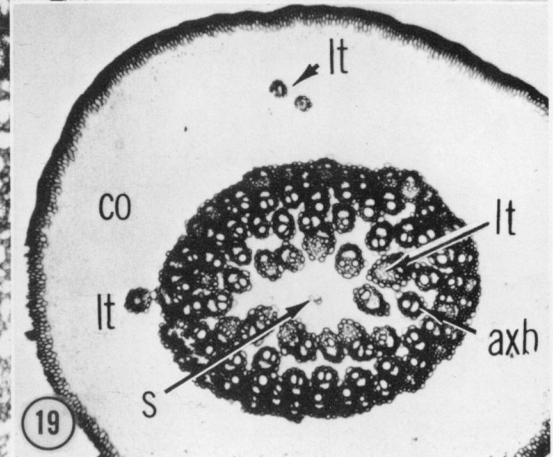
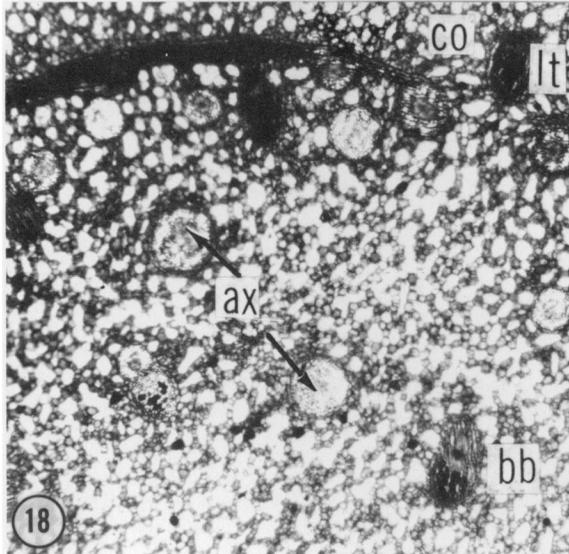
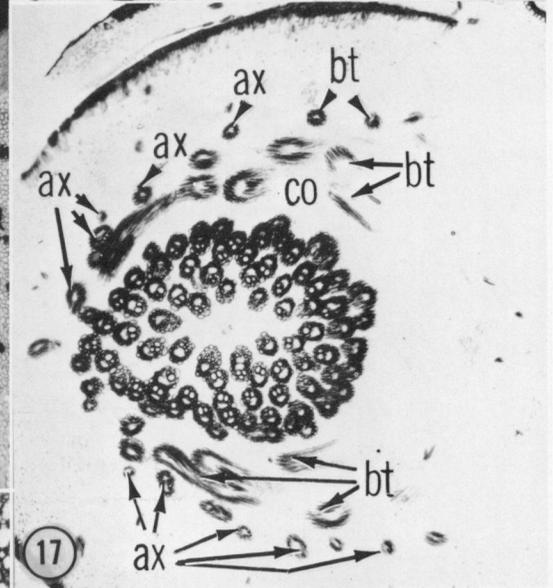
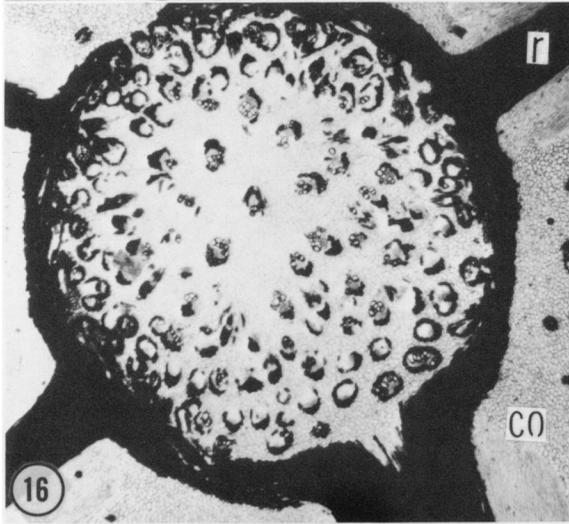
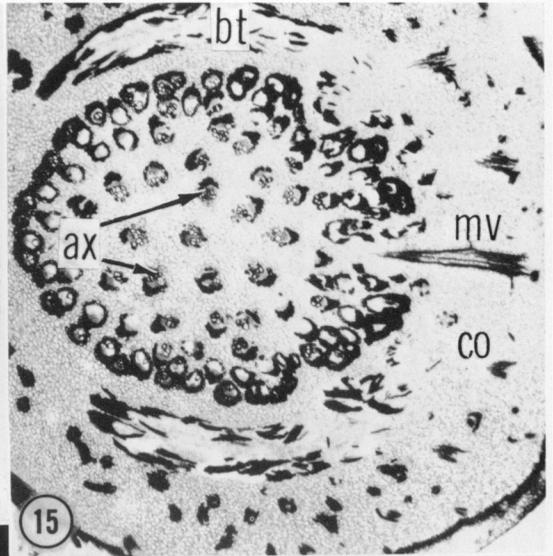
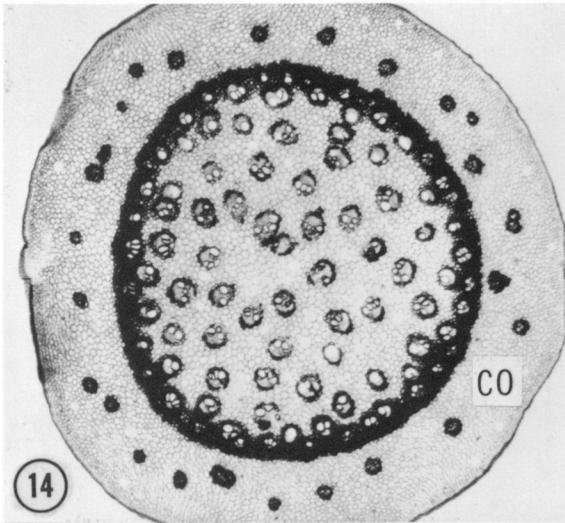
KEY TO LABELING: cortex, (co), axial bundle (ax), bud trace (bt), root (r), sclereids (scl), midvein leaf trace (mv), minor leaf trace (lt), major leaf trace (LT), axial bundle (ax), trichosclereid (ts).

Fig. 14–19. Transsections. 14. *Anthurium polyschistum*. Internode with cortex, central cylinder, $\times 18$. 15. *A. polyschistum*. Node with cortex, bud traces, axial bundle, midvein leaf trace, $\times 11$. 16. *A. polyschistum* with root attachment to a vascular plexus, cortex. $\times 14$. 17. *Culcasia* sp. Node with bud traces, axial bundles, cortex. $\times 29$. 18. *Acorus calamus*. View of stem with leaf trace, axial bundles, cortex, bipolar bundle. $\times 39$. 19. *Culcasia* sp. Internode with cortex, axial bundle, leaf trace, minor leaf traces in cortex. $\times 39$.

KEY TO LABELING: cortex (co), bud traces (bt), axial bundle (ax), midvein leaf trace (mv), root attachment (r), leaf trace (lt), bipolar bundle (bb), secretory canal (s).







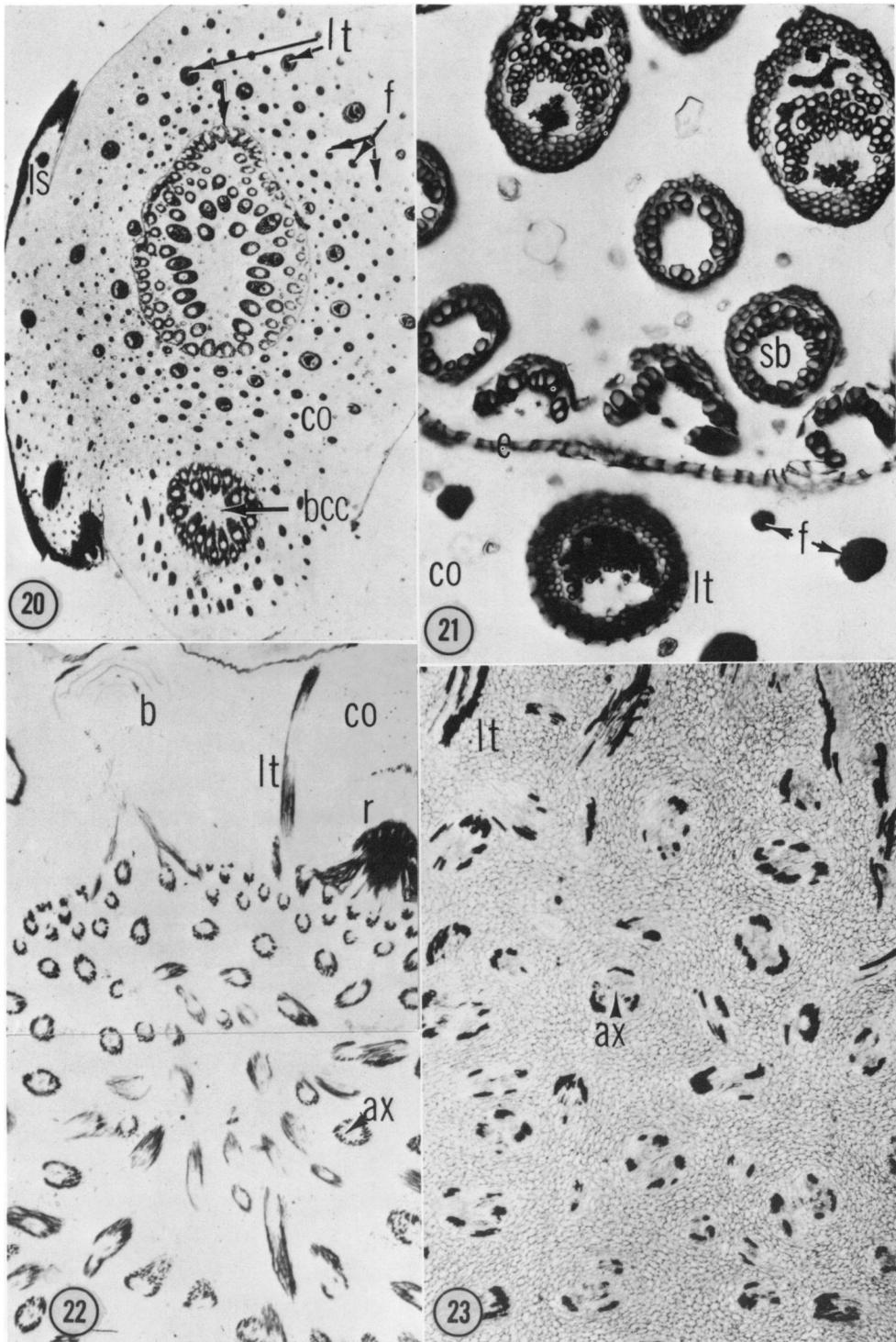


Fig. 20–23. Transections. 20. *Acorus gramineus*. View of node with leaf sheath, cortex, fiber strands, leaf traces, central cylinder of branch (bcc), central cylinder of next distal branch bulges from central cylinder of main axis (arrow). $\times 14$. 21. *A. gramineus*. View of leaf trace in cortex, fiber strands, endodermis, small peripheral amphivasal bundles in central cylinder. $\times 130$. 22. *Gymnostachys anceps*. Nodal view showing bud, root, cortex, leaf trace, axial bundle. $\times 8.5$. 23. *Zamioculcas zamiifolia*. Nodal view showing leaf trace, axial bundle. $\times 90$.

KEY TO LABELING: leaf sheath (ls), cortex (co), fiber strands (f), branch central cylinder (bcc), leaf trace (lt), endodermis (e), small peripheral amphivasal bundles (sb), bud (b), root (r), cortex (co), leaf trace (lt), axial bundle (ax).

towards the substrate. The branch-trace complex is also asymmetric (Fig. 28). It consists of a series of poorly differentiated vascular strands (in nodes with undeveloped buds) connected to two different sectors of the central cylinder. In the root-bearing side, the branch traces anastomose with the bundles that form part of the sclerotic arc. On the opposite side of the stem, the branch traces anastomose with peripheral bundles, including leaf traces that entered at the node above. Successive nodes are more or less mirror images of each other with respect to asymmetry of root insertion, branch-trace insertion, and asymmetry of the leaf-base system.

Course of the vascular bundles, (a) node: This has been accounted for in the above description of the node.

Course of the vascular bundles, (b) several internodes (Fig. 36): Approximately 12-14 leaf traces enter at each node but may anastomose with each other to some extent. Those on the root-bearing side of the axis enter the central cylinder abruptly but remain at or near its periphery as part of the sclerotic arc. The majority of traces on the opposite side remain in the cortex for at least one internode before gradually entering the central cylinder (e.g., traces in upper part of Fig. 36). The outermost four or five narrow bundles of the leaf-trace system remain in the cortex longest but do not persist as a cortical series.

In the central cylinder the majority of leaf traces unite with an axial bundle within one or two internodes of their insertion, the axial bundle always being very narrow. Representative plots of leaf traces in Fig. 36 show this. In certain instances axial bundles followed downward appear to end blindly in the center of the stem. This may be because we have failed to recognize their attachment to leaf traces, or because the differentiation at the interconnection is incomplete. Furthermore, any regularity in the system tends to be obscured by numerous branch traces. The loss of protoxylem from axial bundles and their gradual displacement basipetally towards the periphery of the central cylinder occurs in the usual manner.

Conclusions: Distinctive features of *Anandendrum* vasculature include: 1) asymmetrical construction; 2) absence of any independent cortical vascular system; 3) presence of a persistent sclerotic arc, associated with root traces and a portion of the leaf-trace system; 4) asymmetrical entry of bud traces at the node and different methods of insertion into the central system on opposite sides of the stem; 5) oblique entry of leaf traces over relatively long distances, and 6) fairly regular divergence of a narrow axial bundle from outgoing leaf traces.

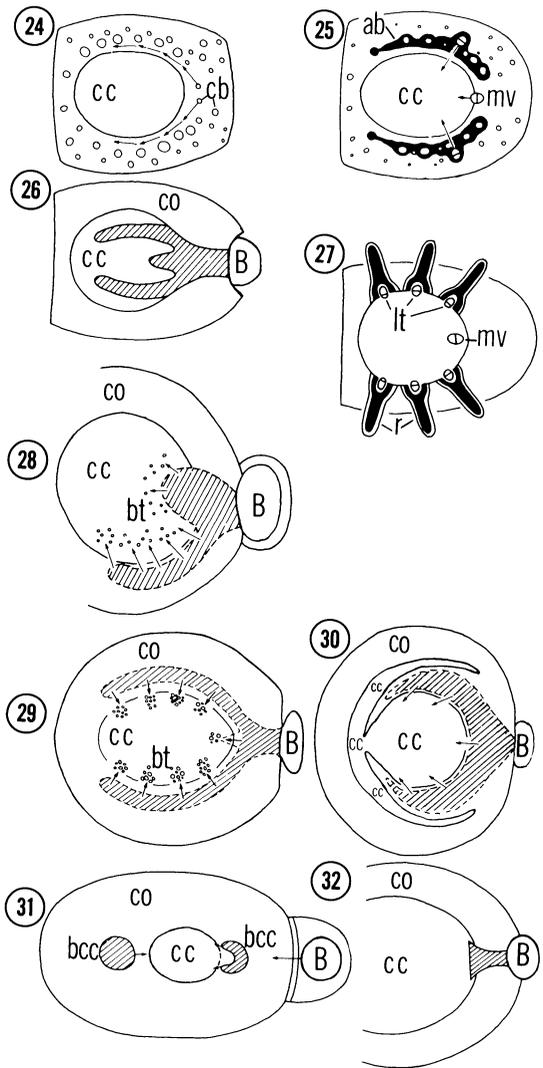


Fig. 24-32. Diagrams of nodal vasculature. Fig. 24-27. *Pothos scandens*. 24. Diagram of stem just above insertion of bud, with cortex containing numerous cortical bundles (circles). A small number of cortical bundles in the pathway of the bud traces (two are shown attached to arrows), migrate along a pathway (arrows) around the central cylinder and form a plexus with cortical bundles and leaf traces. 25. Plexus (black area with included cortical bundles and leaf traces—arrows) formed by anastomosing bundles at the node. The view is a composite of several sections. 27. Relationship between root and leaf trace, midvein trace. 28. *Anadendrum microstachyum*. Asymmetrical pathway of bud traces. 29. *Anthurium polyschistum*. Encircling pathway of bud traces through cortex and into central cylinder. 30. *Culcasia* sp. Bud traces migrate inside the flared arcs of bundles from central cylinder. 31. *Acorus gramineus*. Branch central cylinders shown in relation to main axis central cylinder. 32. *Gymnostachys anceps*. Peripheral attachment of bud traces.

KEY TO LABELING: Central cylinder (cc), cortical bundles (cb), midvein trace (mv), bud (b), leaf trace (lt), bud traces (bt), branch central cylinder (bcc), anastomosing bundles (ab).

The system is still highly integrated, with direct interconnection between root, leaf, and branch traces, but the configuration is very different from that found in *Pothos* and *Pothoidium*.

Heteropsis jenmanii (Fig. 9–11, 37): This is a root-climbing vine with distichous leaves. The inflorescence is axillary, so that shoots are monopodial. Buds are inserted about 1 cm above the node. Vascular bundles in the stem are all simple.

Internode in T.S. (Fig. 11): The cortex is narrow, with only the epidermis sclerotic. There is a single series of irregularly alternate large and small cortical bundles each of which has a more or less continuous sclerenchymatous sheath and only the larger ones have conspicuous conducting tissue. There is no endodermis. The wide central cylinder is abruptly delimited by a narrow band of sclerenchyma. Otherwise, sclerenchyma is associated only with the vascular bundles as moderately thick-walled cells. The central bundles are more or less uniformly distributed, although peripheral bundles tend to be narrow and somewhat congested. Each bundle has a fibrous sheath that is well-developed next to the phloem in some samples, less so in others. Individual bundles usually include several wide metaxylem elements. The leaf traces are distinguished by their numerous narrow protoxylem elements.

Node in T.S.: The node is distinguished by the two symmetrical arcs of relatively undifferentiated tissue that represent the bud-trace complex (Fig. 9), which crosses the central cylinder almost completely at its widest part. Individual bud traces are evident at the periphery of this complex, which is inserted considerably above the level of insertion of leaf traces. The median leaf trace is large and produces a "gap" in the peripheral sclerenchyma. Numerous thick-walled sclereids are present in the cortex near the bud insertion, part of the same system of sclereids in the prophyll and scale leaves which envelop the bud (Fig. 9). A single root trace is inserted at the side of the midvein trace (Fig. 10).

Course of the vascular bundles, (a) node:

The vascular configuration at the node is largely accounted for in the above description. Bud traces fuse with axial bundles for some distance below the node. There is prolific nodal anastomosing between existing and newly inserted cortical traces so that a single dorsal series is reinstated just below the node.

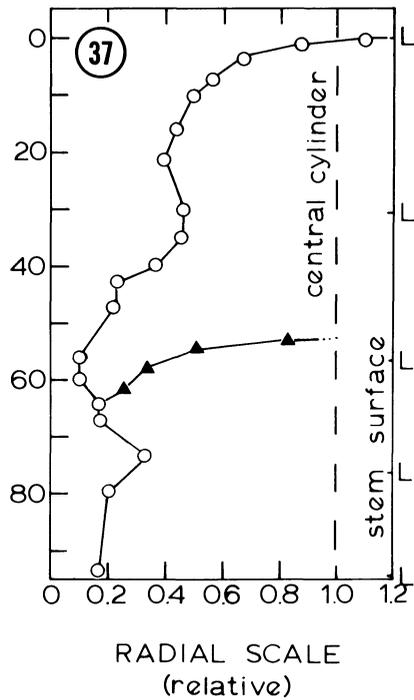
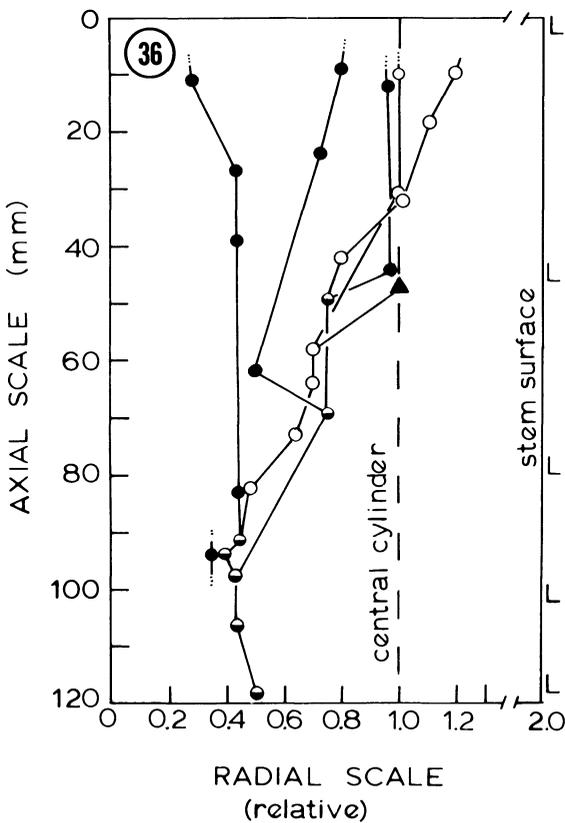
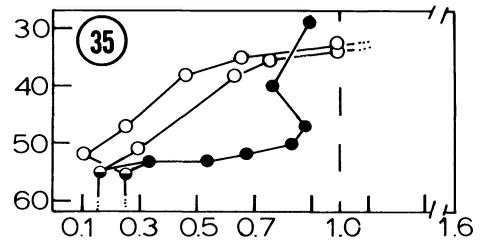
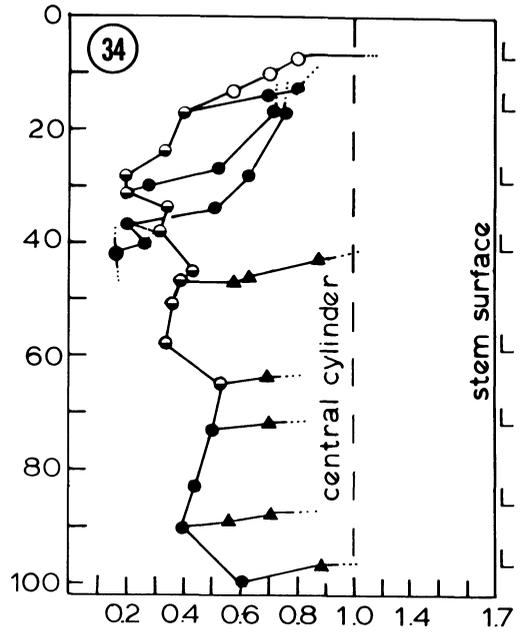
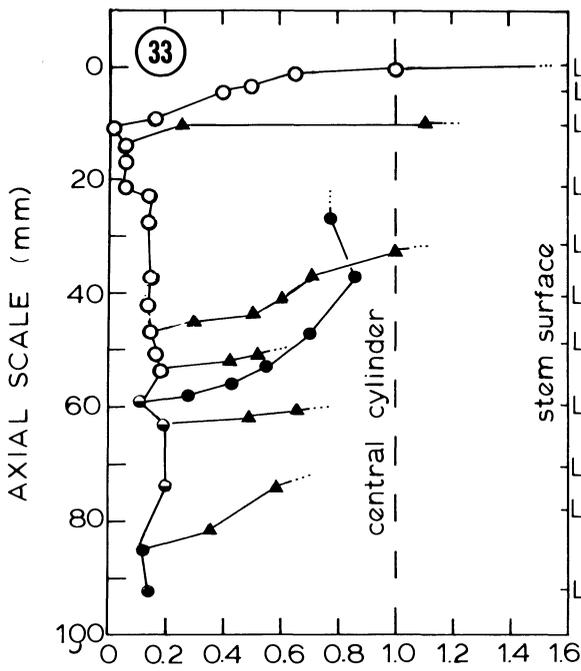
Course of vascular bundles, (b) several internodes (Fig. 37): Leaf traces move abruptly into the central cylinder and maintain their identity for long distances below the level of entry—to at least five internodes for the prominent median veins. No continuity between leaf traces and axial bundles was observed in the short length of stem analyzed (five nodes). Bundles remained relatively fixed in position, orientation, and construction. The major disturbance occasioned by bud trace insertion at each node disrupts this uniformity. The method by which axial continuity is maintained is thus not obvious in our preliminary analysis. However, it is clear that the bud traces have a pronounced integrative effect.

Conclusions: Distinctive features of the vascular system of *Heteropsis* include: 1) the prominent midvein of the leaf trace system at each node; 2) the well-developed bud-trace complex penetrating deeply into and almost across the central cylinder; 3) the well-developed uniseriate cortical vascular system; 4) the absence of obvious axial continuity between outgoing leaf traces and axial bundles, and 5) the close association between the root trace and midvein leaf trace at each node.

Anthurium polyschistum (Fig. 14–16, 29, 38): The representative of this very large genus is a root-climbing vine with spirally arranged leaves. In the adult phase the monophyllous sympodium (Madison, 1978) is developed, but in this aspect of our study we have restricted ourselves to an analysis of the monopodial vegetative phase to obtain a more direct comparison with other members of the Pothoideae. Analyses of the sympodial phase have been made but are not reported on here. A study of the mechanism of internodal elongation in this species by French (1977) shows the presence of an uninterrupted meristem.

Fig. 33–37. Plots of pathways of bundles in stems. 33. *Pothos scandens*. 34. *Pothoidium lobbianum*. 35. *Pothos scandens*. Isolated from Fig. 33 for clarity, showing branched axial bundle. 36. *Anadendrum microstachyum*. 37. *Heteropsis jenmanii*.

KEY TO LABELING: entering leaf trace (open circle); vascular bundle just below point of divergence of leaf trace from axial bundle (half circle); axial bundle (closed circle); bud trace (closed triangle); leaf position on stem (L); series of three dots mark continuing unplotted course of a bundle.



Internodes are exceptionally long in relation to their diameter and the nodes are somewhat swollen. The vascular bundles are simple throughout.

Internode in T.S. (Fig. 14): The cortex is broad and the ground tissue undifferentiated except for peripheral secretory canals. It includes a series of bundles, each with a more or less complete cylinder of sheathing sclerenchyma and reduced vascular tissue. There is no endodermis. The wide central cylinder is abruptly delimited by a narrow peripheral sclerotic region which contains a more or less single series of bundles. The central bundles are rather regularly but diffusely distributed; each has a more or less continuous but narrow bundle sheath. The narrower peripheral bundles usually include a single wide metaxylem element and a narrow phloem strand. Central bundles include varying numbers of narrow protoxylem elements. Obvious leaf traces have only protoxylem elements.

Node in T.S. (Fig. 15, 16): Slightly above the level of leaf insertion structural configuration is determined by two broad bands of bud traces that encircle the central cylinder (Fig. 15, 29). At a slightly lower level, where the sclerenchymatous peripheral layer is interrupted, the major leaf traces are evident. At the lowest level, a series of root traces is inserted from a circle of adventitious roots. The root traces encircle the periphery of the central cylinder and are ultimately continuous with peripheral axial bundles.

Course of vascular bundles (Fig. 38): Virtually all vascular anastomosing takes place at the node, little displacement or fusion of bundles occurring in the internode. Traces entering from a single leaf cross the cortex into the central cylinder over a short vertical distance. A distinct median vein is evident. Most of these traces soon fuse with existing axial bundles. The leaf contact distance can be very short, as shown for the median vein of a leaf in Fig. 38. Other anastomoses in the nodal region include leaf traces with bud traces, bud traces with axial bundles, and adjacent axial bundles directly with each other, or indirectly via a short bridge.

The bud traces themselves divide into two major groups which migrate mostly through the cortex (Fig. 15). Small groups of traces branch from each cluster and enter the central cylinder (indicated by arrows in Fig. 29). The ultimate extensions of the bud traces reach almost to the side opposite their insertion before entering the central cylinder.

Cortical traces anastomose with each other and with newly entering cortical traces from

the leaf. They also may receive branches from the bud-trace complexes but apparently never from the root traces.

Conclusions: *Anthurium polyschistum* is distinctive because of the following features: 1) there is an independent cortical vascular system; 2) bud traces encircle the node largely outside the central cylinder, and 3) axial continuity is maintained in part by upward branching of the leaf trace shortly before it diverges from the central cylinder.

It is difficult to assess the significance of these features in such a large and morphologically diverse genus, but limited observations on a number of other species suggest that these distinctive features are representative of some other members of the genus.

Culcasia sp. (Fig. 17, 19, 30, 39): This is a root-climbing vine with long internodes and distichous leaves. The portion of the shoot system examined was a monopodium without inflorescences. The bundles are always simple. This species is very similar in its vasculature to *C. scandens*, already described in some detail by French and Tomlinson (1980).

Internode in T.S. (Fig. 19): The cortex is wide and undifferentiated except for a peripheral region of sclerenchyma (a hypodermis) and a ring of unligified secretory canals approximately mid-way between the epidermis and the central cylinder. The cortex usually contains a few (1-4) bundles which are leaf traces; there is no discrete cortical vascular system. The central cylinder is abruptly delimited by a sclerenchymatous region that includes congested peripheral vascular bundles. Perimedullary bundles are larger, less congested, and not associated with sclerotic ground tissue. The stem center is free of large bundles, but may have a secretory canal with lignified epithelium (Fig. 19). Individual vascular bundles at the periphery include a single wide metaxylem element and a more or less continuous sclerenchyma sheath usually distinguishable from the sclerotic ground tissue. Central vascular bundles are recognizable as leaf traces by their well-developed protoxylem and a fibrous bundle sheath associated only with the phloem.

Node in T.S. (Fig. 17, 30): Nodal anatomy is dominated by a crescent-shaped arc of bud-trace tissue in which collateral bundles, each with a well-developed fibrous sheath, can be recognized (Fig. 17). Ultimate extensions of this arc, which encircles the central cylinder completely, are inserted nearly 180° from the side of attachment of the bud (Fig. 30). Immediately below the bud on one side of the stem, one or more roots are inserted, the root

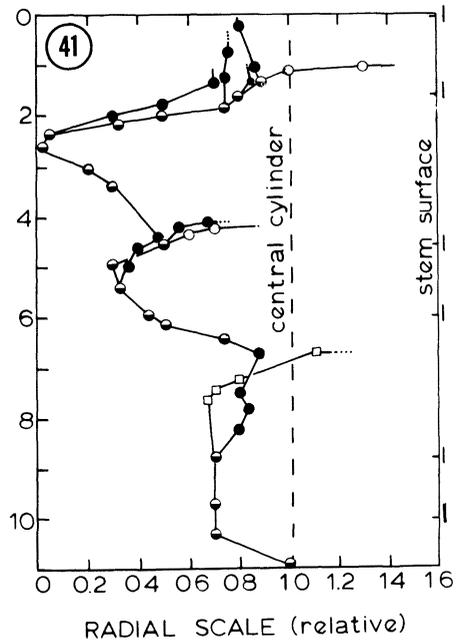
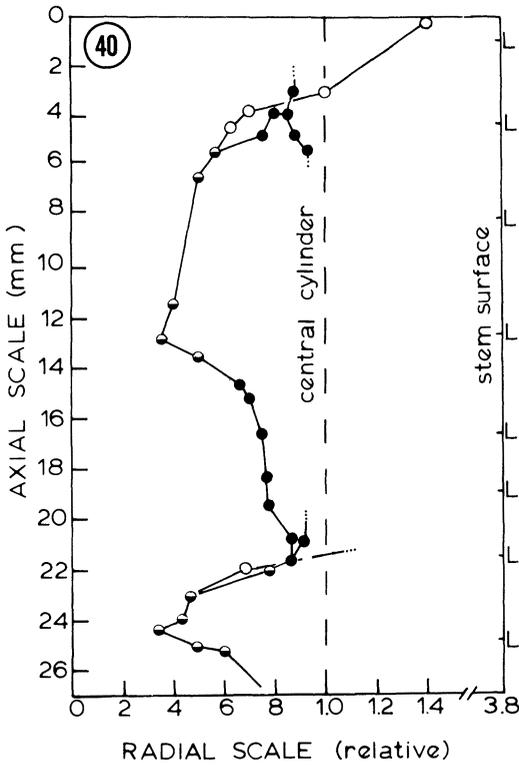
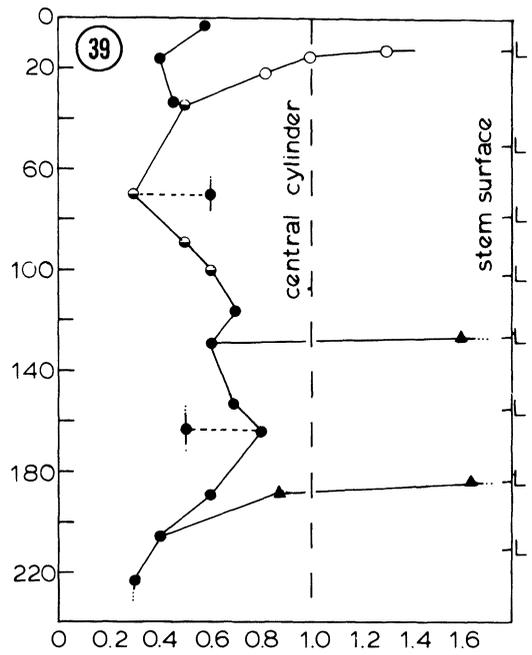
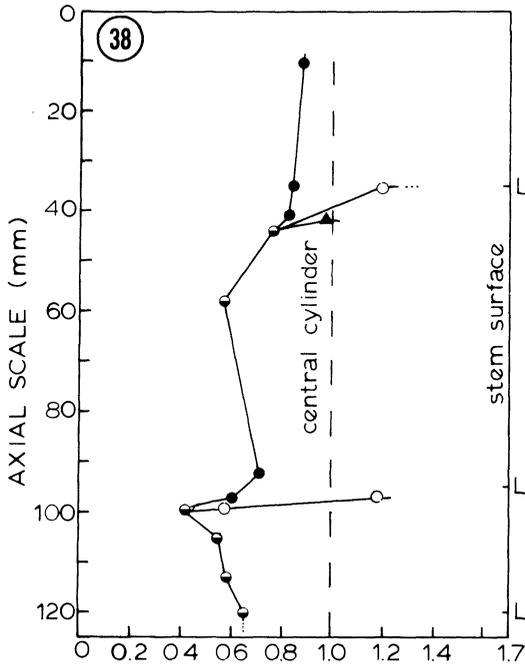


Fig. 38-41. Plots of pathways of bundles in stems. 38. *Anthurium polyschistum*. 39. *Culcasia* sp. 40. *Acorus gramineus*. 41. *Gymnostachys anceps*.

KEY TO LABELING: entering leaf trace (open circle); vascular bundle just below point of divergence of leaf trace from axial bundle (half circle); axial bundle (closed circle); bud trace (closed triangle); leaf position on axis (L).

traces attached directly to the axial bundle of the central cylinder, often at quite deep levels. Leaf traces are largely obscured by the extensive branch and root-trace plexi.

Course of the vascular bundles, (a) node: Bud traces so completely dominate nodal vasculature that it is difficult to account for other systems. They nearly encircle the central cylinder but also penetrate it and displace many of the peripheral axial bundles. The broad and deep root-trace insertion adds further obscurity. It seems likely that incoming and recently entering traces are also involved in anastomosis.

Course of the vascular bundles, (b) over several internodes (Fig. 39): The essential features described for *C. scandens* by French and Tomlinson can be observed in this species. Published plots show that axial continuity is maintained by a proportion of leaf traces that make direct contact with axial bundles shortly below the node of insertion. Others fuse with leaf traces inserted at the next node above and number of leaf traces pass gradually across the cortex over a distance of one internode before entering the central cylinder. Their further continuity is obscured by the bud-trace complex.

A very regular configuration is shown by a solitary vascular bundle on the ventral side of the leaf, which diverges *downwards* from the central cylinder just above the node, splits, and becomes incorporated in the ventral part of the bud complex. This configuration is repeated at every node.

Conclusions: Features distinctive of this genus include: 1) absence of an independent cortical system (except for the single bundle described in the previous paragraph); 2) the broad arc of bud traces which encircle as well as penetrate the central cylinder at the node, and 3) the somewhat imprecise configuration of leaf traces in the central cylinder.

As in previously described genera, the integration of the vascular cylinder occurs at the node and is effected largely by the bud-trace complex.

Zamioculcas zamiifolia. (Fig. 23): This species has a sympodial, fleshy underground rhizome system the morphology of which is obscure, although it probably corresponds to a monophyllous sympodium. The foliage leaf on each segment is pinnately compound. This is the only member of the subfamily without simple vascular bundles, although the compound bundles are indistinct.

Internode in T.S. (Fig. 23): The cortex is narrow and undifferentiated except for some

suberization of surface layers. The wide central cylinder has no limiting endodermis and no sclerotic tissue. Vascular bundles are rather uniformly distributed, but are somewhat irregular in construction. Many have an obliquely irregular course. Bundles are collateral, but they frequently appear aggregated as indistinct compound bundles.

Node in T.S.: This is not distinguishable anatomically from the internode.

Course of the vascular bundles: Followed inwardly, leaf traces become associated with, but do not fuse with, existing axial bundles. However, the course of bundles is too irregular to allow any recognizable pattern to be observed. The trace complex to a displaced terminal inflorescence can be recognized as a series of central bundles diverging toward the peripheral bundles of the central cylinder. No observations on the method of insertion of lateral branch complexes have been possible.

Conclusions: Although our observations are incomplete and our understanding of the three-dimensional vasculature of the axis is unsatisfactory, it seems clear that *Zamioculcas* is distinctive within the Pothoideae in the following features: 1) absence of a cortical vascular system, and 2) aggregation of leaf traces and axial bundles to form indistinct compound bundles.

Further analysis of this species would best be made by studying the vascular system developmentally in serial sections of growing apices.

Gonatopus marattioides (Fig. 4): The axis is a fleshy subterranean horizontal rhizome with alternately arranged scale leaves. Foliage leaves are produced only at intervals. The inflorescence is apparently terminal; the shoot is best described as a sympodium. Adventitious roots occur at intervals along the axis.

Internode in T.S. (Fig. 4): The axis is uniformly parenchymatous and little differentiated. Surface layers are slightly suberized. The vascular system consists of a cylinder of about ten very narrow collateral vascular bundles without sclerotic bundle sheaths. There is no endodermis.

There is no structural discontinuity between nodes and internodes.

Course of the vascular bundles: Incoming leaf traces fuse directly with the axial bundles of the central cylinder, which themselves anastomose somewhat in a tangential direction. We have no information about bud traces.

Conclusions: Our limited information about the vascular system in *Gonatopus* is sufficient

to show that it is related to the specialized morphology of the shoot and is clearly very different from other members of the Pothoideae.

Acorus calamus (Fig. 18): This is a rhizomatous marsh plant, the sympodial rhizome obviously segmented into annual increments, each increment normally terminated by an erect inflorescence. Foliage leaves are unifacial and horizontally distichous. Each annually produced rhizome segment initially begins its development (as a lateral bud) with a series of scale leaves. Only distal foliage leaves on each increment subtend lateral buds, one or more of which may continue the sympodium or produce a branch. Roots are usually restricted to the lower surface of the rhizome.

Internode in T.S. (Fig. 18): The cortex is wide and consists of lacunose parenchyma that appears reticulate in section. The surface four or five layers of cells are compact and somewhat thick-walled, the outermost suberized. The cortex is traversed by numerous collateral leaf traces, each with a continuous but narrow bundle sheath of sclerenchyma. Bundles vary in diameter and the smallest consist only of fibers.

The central cylinder is wide and delimited by a distinct endodermis that is interrupted by the entry of leaf traces. The ground tissue is lacunose, like the cortex; the central vascular cylinder has very diffusely distributed amphivasal bundles. Leaf traces close to their divergence into the leaf can be recognized by the abundant narrow protoxylem elements which contrast with the wide elements of the amphivasal metaxylem. The periphery of the central cylinder is delimited by a narrow plexus of anastomosing vascular bundles. Frequent girdling root traces are evident, especially on the lower surface of the rhizome.

Node in T.S.: Nodal regions are not clearly circumscribed because traces to appendages are inserted obliquely and the roots are not restricted to nodes. For example, two or even three separate branch-trace complexes may be recognized in a single section. A branch-trace complex consists of a cylinder of amphivasal vascular bundles enclosed by a common endodermis and so representing a miniature version of the central cylinder of the parent axis.

Course of vascular bundles, (a) node: A series of about 100 leaf traces enter the node from each leaf base. Larger bundles pass fairly abruptly into the central cylinder, smaller ones more acutely. Many of these smaller bundles end blindly in the outer cortex, but without

anastomosing. There is thus only a very limited independent cortical system. The branch-trace complex fuses gradually with a peripheral sector of the central cylinder of the main axis, each endodermis of the two systems confluent without discontinuity. Most individual branch traces unite with the peripheral anastomosing system of axial bundles. Root traces anastomose entirely with the peripheral anastomosing system; their distal extension can frequently be seen as girdling traces.

Course of the vascular bundles, (b) over several internodes: Below the leaf base, major leaf traces migrate towards the center of the central cylinder, fusing with an axial bundle in the peripheral region of the central cylinder. The fusion of collateral leaf traces with amphivasal axial bundles produces an amphivasal bundle with well-developed protoxylem elements on one side. Further below, the bundle continues towards the center of the axis, then abruptly diverges towards the stem periphery (the "double-curve" of von Mohl, 1849). During this outward curve the protoxylem is progressively reduced and disappears; at its basal extremity the bundle consists solely of amphivasal metaxylem. It either fuses with a leaf trace entering at a lower node or with the peripheral anastomosing cortical system. This leaf-contact distance (Zimmermann and Tomlinson, 1974) is short in *Acorus*; see plots. The system is repeated quite regularly in minor leaf traces (i.e., bundles with a limited radial displacement). Minor bundles may fuse with the peripheral system within one internode of insertion.

The bundle course in *Acorus calamus* thus resembles that described in the palm *Rhapis excelsa*, the "Chamaedorea-type" of Zimmermann and Tomlinson (1974).

Acorus gramineus (Fig. 20, 21, 31, 40). This species is smaller than *A. calamus*; its sympodial rhizome is not clearly segmented. The ground tissue is not lacunose and the central vascular bundles are proportionately wider and more congested. The course of vascular bundles and their anastomoses are essentially as in *A. calamus*. The most conspicuous difference between the two species is the presence of a discrete system of anastomosing fibrous bundles in the cortex of *A. gramineus* (Fig. 21). Figure 40 shows a representative plot with a leaf-contact distance of about six nodes.

Conclusions: The axis of *Acorus* is distinguished by: 1) the well-developed bundle plexus at the periphery of the central cylinder; 2) an endodermis; 3) the discrete cylindrical

branch-trace complex inserted at the periphery of the central cylinder of the parent axis (Fig. 31); 4) amphivasal vascular bundles, and 5) an obvious "palm-type" of vascular construction.

Gymnostachys anceps (Fig. 22, 32, 41): This is a rhizomatous plant with distichous, linear, bifacial leaves. The rhizome is a fairly regular sympodium with long, slender, erect inflorescences terminating each unit. The segments are short, with only two to three foliage leaves on each. The inflorescence is unique among aroids because its axis bears a series of lateral, cincinnus-like aggregates of spadices, each spadix associated with a narrow, scale-like (never spathe-like) bract. Roots are inserted mainly on the lower side of the rhizome.

Internode in T.S. (Fig. 22): The cortex is wide but without an independent series of cortical bundles. The surface layers form a distinct periderm consisting of suberized radially arranged cells that may be derived from a storied phellogen. The central cylinder is wide but without a limiting endodermis or sclerotic tissues; vascular bundles are somewhat narrower and crowded towards the periphery. Individual bundles are amphivasal and lack a sclerotic sheath.

Node in T.S.: There is no discrete structural discontinuity between nodes and internodes. Trace complexes representing the terminal inflorescences are evident as a narrow cylinder of congested vascular bundles. Frequently, two such aggregates are visible in a single section. These complexes should not be confused with the lateral branch-trace complex of *Acorus*. One undeveloped lateral bud had a narrow, superficial insertion on the periphery of the central cylinder (Fig. 32).

Course of the vascular bundles (Fig. 41): In the analytical movies, the structural discontinuity to be expected with an articulated, sympodial system was not evident. The trace complex of the inflorescence can be followed into the center of the central cylinder, where its bundles spread out and become incorporated into the axial system.

Leaf traces entering the central cylinder have a somewhat irregular course, but, over the short length of stem analyzed, the displacement corresponds to von Mohl's double curve (Fig. 41). Leaf traces also fuse with existing vascular bundles, according to the *Rhapis* structural principle, but differ in that they frequently fuse with more than one such bundle. The change in the vascular anatomy of the leaf trace, when it becomes associated with the amphivasal axial bundle, is much as in *Acorus* but without the same regularity.

Root traces are attached to the periphery of the central cylinder, where they form a girdling anastomosing vascular system of the type common in monocotyledonous rhizomes.

Conclusions: *Gymnostachys* is distinctive in the following features: 1) absence of a cortical system; 2) amphivasal vascular bundles and 3) sympodial development of the vascular system, each new unit maintaining axial continuity along the rhizome independently of the regular, displaced complex of bundles entering the terminal inflorescence.

Acorus and *Gymnostachys* share some features of vascular organization related to their sympodial organization, but the axes are basically distinguishable because the segments are long in *Acorus* and short in *Gymnostachys*.

DISCUSSION—It is clear from both morphology and anatomy that *Pothos* and *Pothoidium* are closely related taxa that belong in the tribe Pothoeae. Therefore, it is not surprising that trichosclereids, already known in two species of *Pothos*, occur in *Pothoidium*.

The stem anatomy of *Anadendrum* differs in many respects from *Pothos* and *Pothoidium*, although the three genera are placed in the same tribe. In *Anadendrum*, the absence of a cortical system, gross difference in organization of bud traces, and the pathway of leaf traces and bud traces contrast with the other two genera. In addition, the pollen of *Anadendrum* is exceptional in the tribe being inaperturate with a bacculate exine (Thanikaimoni, 1969). We agree with Bogner (1978), that the genus belongs in a tribe separate from *Pothos* and *Pothoidium*. Actually, the organization of bud traces in *Anadendrum* bears a stronger resemblance to the pattern of bud traces in *Amydrium* and viny monsterooids (e.g., *Epipremnum*, *Monstera*, *Rhaphidophora*) than to that of *Pothos* (French and Tomlinson in prep.).

Heteropsis is a small (12 species) South American genus with a peculiar viny-bushy habit and is rarely seen in cultivation. Flowers of *Heteropsis* lack a perianth and have four stamens, as do those of the Monsteroideae. *Heteropsis* was placed in its own tribe by Engler next to the Pothoeae and after *Anadendrum* (Table 1). Anatomically, *Heteropsis* more closely resembles *Pothos* and *Pothoidium* than *Anadendrum*. Although *Heteropsis* is obviously quite distinct from *Pothos* and *Pothoidium*, we have found some basic anatomic similarities, suggesting that additional features of these three genera deserve closer attention (e.g. leaf and floral structure). Some of the features shared by *Heteropsis*, *Pothos*, and *Pothoidium* are: 1) prominent arcs of bud

traces in the central cylinder, arranged in a pattern not found in the other pothoids we examined; 2) prominent midvein traces; 3) root traces with close spatial relationship to leaf traces, and 4) monopodial growth habit, unusual among aroids.

The large, extremely diverse genus *Anthurium* exhibits several anatomical features that are distinctive and serve to set it apart from other genera in the Pothoideae. Most notable is the peculiar bud-trace organization in *Anthurium*, which has no parallel in the Araceae we have examined to date. Because our preliminary survey of *Anthurium* included only five of the over 700 species, our knowledge of the anatomy of the genus is, of course, extremely limited. In the species we have examined, however, the organization of bud traces is basically like that shown in Fig. 29. The bud traces form prominent arcs in the cortex which nearly encircle the central cylinder. This pattern contrasts markedly with the organization of the bud traces in *Pothos*, *Pothoidium*, and *Heteropsis* (cf., Fig. 26).

The endemic African genus *Culcasia* is unusual among the Pothoideae in having inaperturate pollen (Thanikaimoni, 1969) and unisexual flowers; both are considered advanced features by Bogner (1978), who advocated the removal of *Culcasia* from the Pothoideae. Our anatomical studies show that the genus is isolated within the Pothoideae. The configuration of bud traces at each node is unusual and distinctive. A single-layered arc of bundles from the central cylinder is flared out into the cortex, and the migrating bud traces nearly encircle the central cylinder within the flared bundles (Fig. 30). This pattern is found in the three species of *Culcasia* we have examined to date. A similar pattern of bud-trace organization occurs in the African genus *Cercestis* (Lasioideae, unpubl. observ.). *Cercestis* is a viny genus with an inflorescence having similarities to *Culcasia* (pers. commun., J. Bogner and S. Mayo). *Culcasia* was originally placed in Pothoideae by Engler because it lacked laticifers, which are present in all other subfamilies with unisexual flowers except Pistioideae. It seems to us that too much emphasis on the presence or absence of laticifers may be an unfortunate feature of Engler's system; the subfamily Pothoideae acquired a catch-all function as a result. A more natural classification might be achieved by using a diversity of characters.

The other two endemic African genera with unisexual flowers, *Gonatopus* and *Zamioculcas* (tribe Zamioiculcaseae), exhibit vascular systems typical of fleshy rhizomes and corms

with short internodes. Comparisons with the viny genera of the Pothoideae are not very useful for systematic purposes.

The last two genera that Engler included in the Pothoideae under one tribe, the Acoreae, are *Acorus* (two species), and *Gymnostachys* (monotypic). The differences in reproductive and vegetative anatomy and morphology between *Acorus* and *Gymnostachys* are considerable and will be dealt with by us in a separate paper. On the other hand, similarities in vascular organization are appreciable but, again, should be weighed against the complex of contrasting features.

Although it would be appropriate to make general comparisons of our findings on vascular organization in the Pothoideae with other monocotyledons at this time, we will take up this topic in a later paper dealing with the vasculature of the Monsteroideae.

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