ANATOMY OF GUAYANA XYRIDACEAE: ABOLBODA, ORECTANTHE, AND ACHLYPHILA

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The discovery of exceptionally interesting new entities referable to Xyridaceae in the Guayana Highland by Maguire and his colleagues (Maguire, Wurdack et al. 1958, 1960) has led to a reappraisal of the limits of the family and its relationships within the monocotyledons. On another level, there are problems of generic and specific differences and relationships and their evolutionary implications. Anatomical studies are important aids in solving these problems. Dr. Maguire, who has organized studies on these taxa, has recognized the helpfulness of anatomical data and has provided me with an excellent collection of suitable material. I should like to express sincerest appreciation to him for his gratifying interest in the studies recounted below, his generous sharing of material with me, and his invitation of this contribution. Of particular significance is the fact that the writer reached the conclusions set forward at the end of this paper on the basis of anatomical material alone. Dr. Maguire and I exchanged manuscripts when our studies were completed so that we could take advantage of each other's findings in a final presentation, but the great similarity in our conclusions, based on different methods of study, derives from the fact that anatomical features show the same patterns of likeness and diversification with reference to the taxonomic system as do features of gross morphology. I acknowledge with pleasure Dr. Maguire's interest in my independent development of such facts, and his use of these when they became available to him. If there had been any major divergences of opinion, we should have exposed these and attempted to resolve them, but in fact, no such disagreements in interpretation of materials did occur.

MATERIALS AND METHODS

Both liquid-preserved and herbarium materials were given to the writer. Herbarium material was treated with warm 2.5 per cent aqueous NaOH to expand it to its natural proportions, washed, and stored in 50 per cent ethyl alcohol. Both liquid-preserved and treated herbarium material were embedded, sectioned, and stained according to the techniques described earlier by the writer (1958). Pollen preparation techniques are described below in connection with that topic.

The specimens studied are listed below. All specimens are represented by a mounted collection in the New York Botanical Garden Herbarium. Taxa recognized correspond with those of Maguire, Wurdack, et al. (1958, 1960).

Liquid-preserved, assorted parts: Abolboda acaulis Maguire, Maguire & Politi 27700, Maguire 32820, Maguire 33730, Maguire et al. 40669; A. acicularis Idrobo & Smith var. acicularis, Maguire et al. 41439; A. americana (Aublet) Lanjouw, Maguire et al. 41537; A. ciliata Maguire & Wurdack, Maguire et al. 42420; A. linearifolia Maguire, Maguire et al. 41680; A. macrostachya Spruce ex Malme var. angustior Maguire, Maguire et al. 41541; A. macrostachya Spruce ex Malme var. macrostachya, Maguire et al. 41446; A. macrostachya Spruce ex
Malme var. robustior Steyermark, Maguire et al. 28176; A. sprucei Malme, Maguire et al. 41721; Achlyphila disticha Maguire & Wurdack, Maguire et al. 42402; Orectanthe sceptrum (Oliver) Maguire subsp. occidentalis Maguire, Maguire et al. 40567.

Liquid-preserved, pollen only: Abolboda bella Maguire, Maguire et al. 34514; A. ebracteata Maguire, Maguire et al. 30467; A. grandis Grisebach var. quyanensis Maguire, Maguire et al. 27561; A. macrostachya Spruce ex Malme var. angustior Maguire, Maguire et al. 36342; A. macrostachya Spruce ex Malme var. robustior Steyermark, Maguire et al. 28176; Orectanthe pteritepuiana (Steyermark) Maguire, Maguire et al. 32823, Steyermark & Wurdack 523, Steyermark & Wurdack 1221; O. sceptrum (Oliver) Maguire, Maguire et al. 40567, Maguire et al. 33180.

Dried materials, assorted portions: Abolboda macrostachya Spruce ex Malme var. macrostachya, Maguire et al. 39957; A. macrostachya Spruce ex Malme var. robustior Steyermark, Maguire et al. 28176; Orectanthe pteritepuiana (Steyermark) Maguire, Maguire et al. 32766, Maguire 32823, Steyermark & Wurdack 908; O. sceptrum (Oliver) Maguire, Maguire et al. 33342, Maguire et al. 40567; O. sceptrum (Oliver) Maguire subsp. occidentalis Maguire, Maguire & Politi 28451.

ANATOMICAL DESCRIPTIONS

ROOT

Solereder and Meyer (1929) summarize the work of Nilsson, Poulsen, and Malme, as well as their own, on root anatomy of Xyridaceae. Although their data apply chiefly to Xyris, with only a few references to Abolboda, they provide a framework for the expression of data. Almost every character they cite is represented by a number of Xyris species, and detailed mention of these, other than acknowledgment of occurrence of those characters in Xyris, is unnecessary here.

Certain characteristics, on the basis of the present study, appear to be of greater value than others for systematic purposes. Characters which appear relatively reliable in this respect include:

1. Presence of a continuous pericycle, as opposed to its interruption by vessels.

2. Shape and thickening of endodermis cells.

3. Number of vessels present in the vascular core (only insofar as the number is relatively large or small; a certain variation in the number of xylem poles is always present.

Other characteristics, such as the relative extent of the cortex, may have some significance. Solereder and Meyer (1929) follow Nilsson in discriminating between ordinary roots and mechanical roots. This contrast is probably more one of degree than of kind. In the present study, the roots of Achlyphila disticha (fig. 7) might be said to be mechanical roots on account of their sclerenchymatous vascular core in which phloem is minimal. The presence of sclerenchyma in the core, with small scattered patches of phloem cells, suggests such a designation for the roots of A. lineartifolia (fig. 2) described below, but their difference from other roots is relatively minor. Likewise, the roots of A. sprucei and A. macrostachya might bear such a designation, and Solereder and Meyer place roots of the latter species in that category, along with A. longifolia.
Figs. 1–4. Portions of transections of roots of *Abolboda*, each with the vascular core below and the cortex and exodermis above. Fig. 1. *A. sprucei*. × 166. Fig. 2. *A. linearifolia*. × 155. Fig. 3. *A. acaulis*. × 245. Fig. 4. *A. macrostachya* var. *macrostachya*. × 143.
The figure by Malme (1925) of *A. vaginata* shows much greater sclerification of the vascular core than any of the species in the present study, so that this species should probably be mentioned in this regard. In only a few instances (*Abolboda acaulis, A. americana*) were relatively large phloem groups, distinctly alternate with xylem poles, observed. The roots studied here differ little in structure of the cortex, which consists of large cells associated with relatively small intercellular spaces. This condition is reported for *Abolboda vaginata* and the species of *Xyris* section *Xyris* by Solereder and Meyer. There are, in roots of *Abolboda sprucei* and *A. americana*, occasional groups of stellate parenchyma cells in the cortex. This condition is mentioned by Solereder and Meyer for *Abolboda vaginata* and a number of species of *Xyris*. The walls, especially the inner, of the hypodermis and sometimes the adjacent walls of the subhypodermal layer are thickened in all the species studied here (figs. 1,2,7). Very light thickenings were noted in the hypodermal layer of *A. americana* and *A. macrostachya* var. *macrostachya* (fig. 4, upper right). Hypodermal thickenings, making possible the designation of an "exodermis," were noted by Solereder and Meyer in *Xyris indica* and *X. lanata*.

**Abolboda.**

1. *A. acaulis*. Endodermal cells in this species (fig. 3) are very thick-walled, with a small lumen which is nearer the outer than the inner surface of the endodermis. The stele is tetrarch or pentarch; no central vessel is present. The pericycle is unbroken.

2. *A. acicularis* (fig. 6). The endodermis is composed of cells only moderately thickened on all surfaces. The inner wall is very slightly thicker than the radial or inner wall. Monarch, tetrarch, and 8-arch conditions were observed; in the last-named, a central vessel was present. Interruption of the pericycle by vessels is various, and both a single and all but a single vessel in contact with the endodermis were observed in different roots.

3. *A. americana* (fig. 5). In all the numerous roots examined, comprising several collections, the endodermis was composed of cells the inner walls of which were markedly thickened. This thickening tapers on the radial walls to rather thin at their juncture with the outer walls, on which no thickening is present. The following stelar conditions were observed: 2-, 3-, 4-, 5-, and 6-arch. All vessels are in contact with the endodermis, with the occasional exception of one or two.

4. *A. linearifolia* (fig. 2). The walls of the endodermal cells are thickened in a U-shaped manner, but thickenings on the radial walls are tapered abruptly to their point of contact with the exterior walls. A ring of parenchyma cells with noticeable thickenings ensheaths the endodermis. The stele is 7- or 8-arch, with one or two central vessels. Phloem groups are small and scattered; cells of the stele other than vascular elements are thick-walled. The pericycle is not interrupted by vessels.

5. *A. macrostachya* var. *macrostachya* (fig. 4). The root observed possessed endodermal cells much more radially elongate than those of the preceding ones. The walls are markedly thickened, with the lumen quite eccentrically placed toward the exterior side of the cells. The stele is very large, and the root observed was 15-arch, with 15 central vessels. Phloem groups are small and scattered throughout the stele. The pericycle is not interrupted by vessels.
Fig. 5. _Abolboda americana_, transection of vascular core of root. × 286.  Fig. 6. _Abolboda acicularis_ var. _acicularis_, transection of root, showing cortex and exodermis at right. × 127.  Fig. 7. _Achlyphila disticha_, transection of root showing cortex and exodermis at right. × 157.  Fig. 8. _Achlyphila disticha_, transection of rizome, exterior above. × 70.
6. *A. macrostachya* var. *robustior*. The roots observed in this variety are similar to those of the above variety, but differ in the following respects. Two, rather than one, exodermis layers are present. The parenchyma sheath around the endodermis is two cells wide at points. The two roots observed were 13-arch with 18 central vessels and 15-arch with 16 central vessels respectively. The central vessels cannot be differentiated from the peripheral ones at all points.

7. *A. sprucei* (fig. 1). The cortex of roots of this species is quite distinctive in consisting of only two cell layers internal to the exodermis. The outer of these layers is composed of quite large cells, the inner of smaller cells which ensheath the endodermis. Plates of small arm-parenchyma cells interrupt this condition in places. The endodermis consists of cells thickened in a peculiar fashion, so that the lumen is turbinate as seen in transversal outline. Rarely, the endodermis is two-layered (two such instances are seen in figure 1) to the extent of one or two pairs of cells per stele. The root examined was 7-arch with a central vessel. The pericycle is not interrupted by peripheral vessels.

*Achlyphila*.

In respect of exodermis and cortex structure, the root of *Achlyphila disticha* (fig. 7) conforms to the pattern outlined above. The endodermis, which stains bright orange-red (rather than pink, as in *Abolboda*) with safranin, possesses U-shaped thickenings not exactly like any mentioned above. The endodermis may be two cells wide in places, although this condition is rare and localized. Two roots examined proved to be 11-arch and 13-arch respectively. No central vessels are present. This is surprising in view of the large diameter of the vascular core. Instead, one to several cells that have the wall-thickening and staining characteristics of endodermis cells (figure 7, dark area in center of vascular core) are present in this position. On account of their characteristics, they probably should be regarded as endodermal cells, despite their location. Phloem groups are extremely small and are scattered among the sclerified cells of the vascular core. The pericycle is not interrupted. Significantly, there are two or three layers of cells (as compared to fewer in *Abolboda*) between the pericycle and the outermost vessels. Occlusion by tannin-like materials is characteristic of many vessels.

*Orectanthe*.

No roots of *Orectanthe* were available for study.

**Vessels.**

For each of the above species, serial longitudinal sections were prepared to show the presence of vessels. All the species described above proved to have true vessel elements with simple perforation plates. Vessels have been reported by Solereder and Meyer (1929) in roots of *Xyris lacera*, *X. lanata*, and *X. indica*. Likewise, Cheadle (1942) indicates vessels with simple perforation plates for roots of *Xyris flexuosa* and *X. smalliana*.

**Discussion.**

The species of *Abolboda* described here offer no features not previously mentioned by Solereder and Meyer for *Abolboda* or *Xyris*. The possibility that
endodermis-cell characteristics could be used as specific characteristics, suggested by Malme in 1925, appears to be valid. Malme shows very thick-walled endodermal cells with centrally placed lumina for *A. pulchella* and *A. vaginata*. He reports prominent thickenings on the inner wall, tapering sharply on the radial walls, and absent on the outer walls, for endodermal cells in roots of *A. poepiggii*, *A. grandis*, and *A. macrostachya*. Malme’s figure for *A. macrostachya* is markedly different from the condition illustrated here for that species. The endodermal cell thickenings Malme reports for *A. poarchon* and *A. abbreviata* are like those illustrated in the present study for *A. acicularis*.

Interestingly, Malme’s figures all show an uninterrupted pericycle (*A. vaginata*, *A. macrostachya*, *A. poarchon*). The species of *Abolboda* in the present study in which uninterrupted pericycle was observed all belong to the group termed “larger-stemmed abolbodas” in sections below. Malme’s figures also suggest a larger number (six or more) of xylem poles, a feature also characteristic of the group just named. Thus as Malme (1925) claims, different types of root anatomy in *Abolboda* appear to be characteristic of species or species-groups; from the example of *A. sprucei* described above, one may surmise that such characters are not always limited to the stele, but may be found in the cortical zone as well.

The several layers of cells between endodermis and outermost vessels, the absence of central vessels, the presence of endodermis-like cells in their place, and the distinctively staining endodermis thickenings are characteristics which, taken together, would seem to give the roots of *Achlyphila* a generic differentiation from the other three genera. In fact, some of these characteristics seem new to *Xyridaceae*, although the sum of characteristics in this genus would not exclude it from the family.

On the basis of the present study, one may conclude that the roots of *Abolboda* offer no anatomical features (other than greater size, and therefore more numerous vessels) which cannot also be found in *Xyris* roots, as the account of Solereder and Meyer (1929) illustrates.

**STEM**

As the summary of Solereder and Meyer shows, remarkably little is known about stem anatomy in *Xyridaceae*. The only facts that have been established are that bundles are amphivasal, individual bundles may be sheathed with sclerenchyma (incompletely in *X. lanata*), and that (in *X. lanata*) the bundles may form concentric bands. As an additional generalization, the writer would like to add the fact that in all taxa he examined, vascular bundles tend to be more or less amphivasal except where they are demarcated as leaf traces, in which case the structure of the bundles tends to be more nearly collateral.

The data given below are derived from study of mature portions of rosette stems, except for *Achlyphila*, which has a rhizomatous habit. At and near the base of a stem, especially in the smaller-stemmed species of *Abolboda*, departing roots may be numerous in the cortex, and the vascular bundles may form a very small group in the center of the stem. In *A. americana*, no part of the stem (except the very youngest) was free from departing roots. The types of stem anatomy observed in the *Xyridaceae* under study here fall into four main groups.
Smaller-stemmed Abolbodas.

The four species, *A. acaulis* (fig. 9), *A. acicularis* (fig. 10), *A. americana*, and *A. ciliata* (fig. 11), that are considered under this category show four features: (a) the bundles other than those that are leaf traces are most often enclosed in a slerenchyma cylinder; (b) slerenchyma ensheaths departing leaf traces individually; (c) the ground tissue of the stem (other than slerenchyma) consists of more or less spongy tissue lacking in starch; and (d) the bundles (except leaf traces) are present in a cylinder and no bundles are present in the central portion of the stem. The variations on this pattern are as follows.

1. *A. acaulis* (fig. 9). In this species, departing leaf traces are most often incompletely sheathed with slerenchyma; such sleroids are few or absent at the outer (phloem) pole. Centrally placed in the core of parenchyma is a nest of sleroids. This nest of sleroids occurs along the length of the stem, and is present even in the most basal region, where other slerenchyma is wholly lacking.

2. *A. acicularis* (fig. 10). The central portion of the stem, including bundles other than leaf traces, is slerified. Slerenchyma forms a conspicuous sheath around leaf traces; it is more abundant at the xylem pole of each bundle. The bundles other than leaf traces form a single ring. Slerenchyma may form a cylinder, as illustrated, may occupy the entire central portion of the stem, or may, as illustrated for *A. acaulis*, form a nest within the ring of bundles. The latter condition occurs in the base of the stem, and the cylinder is characteristic of the upper portion of a stem.

3. *A. americana*. Slerenchyma (other than that which forms a cylinder in the center of the stem) is present only at the xylem pole of departing leaf traces.

4. *A. ciliata* (fig. 11). This species shows essentially the same features as *A. americana*, although the stem is somewhat larger.

Larger-stemmed Abolbodas.

This group includes *A. linearifolia* (fig. 12), *A. macrostachya* and its varieties (fig. 13, var. angustior), and *A. sprucei* (fig. 14). These species agree in possessing (a) much wider stems than species of the above group; (b) no slerenchyma other than individual sheaths on bundles; (c) compact, never spongy ground tissue, often differentiated into a starch-poor zone outside and an inner core (figs. 12, 13, inside dotted lines) which contains numerous elongate starch grains; and (d) bundles throughout the central portion of the stem, more numerous in a cylinder just inside the outer limit of starch-rich tissue. In all preparations, the ground tissue consists of more or less isodiametric cells associated with relatively small intercellular spaces. Starch may be expected to vary in amount depending on the state of development of the plant. Variations with respect to species are as follows.

1. *A. linearifolia* (fig. 12). Many of the bundles lack slerenchyma. Where present, it takes the form of a semicircle at the interior pole of the bundle. Slerenchyma is associated with the larger bundles, and may be an indication of major bundles which enter leaves a short distance above the level of sectioning.

2. *A. macrostachya*. In *A. macrostachya* var. *macrostachya* and var. *robustior*, the same condition described for *A. linearifolia* was observed. In *A. macrostachya* var. *angustior* (fig. 13), however, all bundles were found to be associated with sleroids, which may be quite abundant near some bundles. Some leaf traces are completely ensheathed by such slerenchyma.
Figs. 9–14. Portions of transections of rosette stems of *Abolboda*, exterior above, patterned to show distribution of various tissues. Fig. 9. *A. acaulis*. Fig. 10. *A. acicularis* var. *acicularis*; leaf base in paradermal section, above; endogenous root at right. Fig. 11. *A. ciliata*. Fig. 12. *A. linearifolia*. Fig. 13. *A. macrostachya* var. *angustior*. Fig. 14. *A. sprucei*. Broken line in figures 12, 13 delimits the outer starch-poor region from the inner starch-rich zone. Patterns as follows: stippled = sclerenchyma; white inside bundles = phloem; black = xylem; parenchymatous ground tissue left bank. Scale = 2 mm. in 1 mm. divisions.
3. *A. sprucei* (fig. 14). All bundles are associated with abundant selerenchyma sheaths, with few exceptions. Such selerenchyma may in fact incorporate several bundles. Bundles that lack sheaths are frequently transversely oriented and tend to delimit a cortical zone, in which leaf traces are present, from the central zone.

**Orectanthe.**

As might be expected, the large stems of *Orectanthe* have an anatomy quite distinct from that of the above species. There is a difference between the pattern found in *O. ptaritepuiana* (fig. 15) and that which was observed in *O. sceptrum* (fig. 16). In *O. ptaritepuiana*, a cortical zone is clearly delimited by a selerenchymatous cylinder which consists of lignified parenchyma cells. The inner margins of this cylinder are irregular, for some bundles and their selerenchymatous sheaths are joined to it and others are independent in the thin-walled central ground tissue. Outside of the selerenchyma cylinder, the parenchyma is also thin-walled. Bundles in this region are smaller than those within the cylinder, and are either lacking in selerenchyma sheaths or very sparingly provided with such tissue. In *O. sceptrum* (fig. 16) the entire central portion of the stem consists of lignified ground tissue. Wall thickenings are much greater toward the exterior of the selerenchymatous core. In addition, wall thickenings are greater on the 2-3 layers of cells that sheath bundles in the selerenchymatous zone. The cortical region consists of non-lignified parenchyma which contains vascular bundles smaller than those encased in the selerenchyma core. These leaf traces are ordinarily provided with fibrous sheaths which completely encase them.

**Achlyphila.**

In the single species, prostrate rhizomatous stems are present. Upright stems are formed in connection with production of inflorescences, and these are considered under "Inflorescence Axis" below. The stem described here, therefore, is the rhizome, which differs from rosette stems of *Xyris*, *Abolboda*, and *Orectanthe* in its long internodes. This rhizome (fig. 8) possesses a marked cylinder of thick-walled sclereids which delimits the cortical region of thin-walled parenchyma cells. The outermost layer of this cylinder consists of cells that are, in their thickening patterns and staining properties, very similar to root endodermis cells. The occurrence of endodermis in rhizomes of monocotyledons is not uncommon, and these cells should be so interpreted here. The inner margins of the selerenchyma cylinder are irregular in outline. In the central portion of

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**Figs. 15, 16. Portions of transections of rosette stems, of Orectanthe, exterior at right. Fig. 15. O. ptaritepuiana. Fig. 16. O. sceptrum.** Scale for figures 15 and 16 = 2 mm in 1 mm divisions. Figs. 17-20. Portions of transections of inflorescence-axis bracts, exterior at right. Fig. 17. Abolboda ciliata, section midway along length of bract. Fig. 18. A. macrostachya var. macrostachya, section from tip of bract. Fig. 19. Same, section midway along length of bract. Fig. 20. A. macrostachya var. robustior, section midway along length of bract. Fig. 21. Orectanthe sceptrum, transection of a flattened sepal. Figs. 22-24. Transections of bracts of inflorescence proper, taken midway along length of bract, exterior face above. Fig. 22. Abolboda macrostachya var. robustior. Fig. 23. A. linearifolia. Fig. 24. A. americana. Scale for figures 17-24 = 2 mm in 1 mm divisions. Patterns as follows: fine stippling = thick-walled selerenchyma. coarser stippling = thin-walled selerenchyma. cross-hatched = chlorenchyma; white in bundles = phloem; black = xylem; parenchymatous ground tissue left blank.
Figs. 25-30. Transections of leaves, taken approximately midway along length of leaf, adaxial face above. Fig. 25. Abolboda americana. Fig. 26. A. acicularis var. acicularis.
the stem, bundles are embedded in thin-walled parenchyma. Each bundle in this region is completely ensheathed by lignified cells like those of the sclerenchyma cylinder. Leaf traces are uncommon in the cortical region (on account of the long internodes), but where these are present, each bears a sclerenchyma cap on the xylem face of the bundle. There are occasionally a few thick-walled lignified parenchyma cells in the cortical region.

**Discussion.**

Despite the fact that the meager literature on stem anatomy does not suggest the usefulness of this organ for systematic purposes, excellent generic and specific characteristics are seemingly present, as outlined above. The smaller-stemmed species of *Abolboda* are distinctive in their lack of central bundles, their sclerenchyma cylinder, and their spongy, starch-free parenchyma, as compared to the larger-stemmed species. The two species of *Orectanthe* are like the larger-stemmed species of *Abolboda* in bundle distribution, but show a prominent lignification of parenchyma; this lignified core is clearly delimited from a thin-walled cortical region. The rhizomatous stem of *Achlyphila* is distinctive in *Xyridaceae*, but is not extremely unlike stems of *Abolboda* in its construction. Features of generic value include its prominent sclerification, distribution of bundles, and development of an endodermis.

**Vessels.**

Longitudinal sections of stems in all the taxa named above were prepared, and these were used to demonstrate that in all taxa named, vessel elements with simple perforation plates occur. Cheadle (1942) has indicated such vessel elements for two species of *Xyris*.

**LEAF**

The same groupings used for descriptions of stem anatomy may be used here. The species and species-groups prove highly diversified, so that few generalizations can be offered.

**Smaller-stemmed Abolbodas.**

Species in this group are distinctive in their smaller leaf size, the relative lack, or restriction of, photosynthetic tissue, and the presence of longitudinally-oriented pockets of parenchyma which collapses at maturity and appears to have been composed, in some instances at least, of chlorenchyma cells. Hypodermis is absent, or present only in the more apical portions of the leaf. Stomata are restricted to the lower surface.

1. *A. acaulis* (figs. 31, 35). The basal portion of a leaf (fig. 31) consists of parenchyma, isodiametric as seen in transectional outline, in which 4–5 veins are embedded. Between the veins, zones of collapsed parenchyma are present. Sclerenchyma completely ensheaths the veins; such sheaths are usually two cells in thickness. At a higher level (fig. 36) a hypodermis begins to be differentiated; it is prominent (by virtue of contrast with chlorenchyma) only in the most apical portions of the leaf, where it consists of gelatinous-walled sclereids.
at least in places. In the section shown (fig. 36) three main veins, with fibrous sheaths, are present, and chloroplasts are present in the mesophyll parenchyma, although they are rather sparse.

2. *A. acicularis* (fig. 26). Leaves of this species are similar to those of *A. acaulis*. A section approximately halfway along the length of the leaf (fig. 26) reveals three veins, each surrounded by sclerenchyma and embedded in chloroplast-free parenchyma cells isodiametric in transsection. Cells rich in chloroplasts form a layer immediately beneath the epidermis on both surfaces. Between the veins, pockets of collapsed parenchyma cells occur. A thick-walled hypodermis occurs in the most apical portion of the leaf, where the mesophyll is composed of spherical chlorenchyma.

3. *A. americana* (fig. 25). This leaf shows little differentiation from base to apex, except for reduction in number of veins. Especially prominent are the longitudinal zones of collapsed parenchyma. Some of the smaller bundles lie in these zones. All of the bundles are completely ensheathed by sclerenchyma. The parenchyma is composed of cells, isodiametric in transsection, with relatively few chloroplasts. These cells may be weakly differentiated as a hypodermis in the adaxial portion of the leaf. The leaves of *A. americana* are certainly within the range of variation of *Abolboda*, but an additional similarity may be noted to leaves figured by Arber (1925) for *Eriocaulon septangularis*.

4. *A. ciliata* (figs. 27, 35). An extensive series of transsections of a leaf of this species showed the nature of differences, characteristic of *A. ciliata*, between base and apex. The most basal portion (leaf sheath) consists only of thin-walled parenchyma in which approximately seven bundles, without fibrous sheaths, are embedded. In the upper portion of the leaf sheath, sclerenchymatous sheaths are present and collapsed parenchyma cells occur between veins, resembling the condition shown for *A. acaulis* in figure 31. The margins of the leaf at this level are biseriate. Segments of this wing split off, forming the "'clia'" implied in the species name. Above the level of the sheath, (fig. 27), the leaf is markedly thicker, lacks tapered margins, and has a hypodermis, one or two cells thick, on the adaxial face of the leaf. The mesophyll (other than the pockets of collapsed cells) consists of spherical cells with numerous chloroplasts. Seven bundles, each surrounded by a sclerified sheath, are present at this level. At higher levels, such as that shown in figure 35, the outermost bundles are not present. At the margins of the leaves, a portion of the hypodermis, which extends around the edges of the leaf toward the abaxial surface, consists of sclerified cells. At this uppermost level, the chlorenchyma cells are differentiated (mostly by relative size of intercellular spaces) into palisade and spongy tissue. The level shown in fig. 35 is notable for the greater thickness of the leaf, a thickness due not only to the greater number of hypodermis layers, but to the greater number of chlorenchyma layers as well.

**Larger-stemmed Abolbodas.**

Despite certain distinctive features in the leaf of *A. linearifolia*, there is agreement among *A. linearifolia*, *A. macrostachya*, and *A. sprucei* in the following respects: leaves thicker and larger than those of the above group; hypodermis present, consisting of 3–5 layers of cells; parenchyma like that of the hypodermis (polygonal in transsection, markedly elongate in longitudinal section) also present and bundle sheaths (surrounding fibrous bundle-sheath layers)
Figs. 31–33. Transections of leaves of *Abolboda*, adaxial face above. Fig. 31. *A. acaulis*, section taken toward base of leaf. $\times$ 80. Fig. 32. *A. linearifolia*, section taken toward base of leaf. $\times$ 65. Fig. 33. The same, section taken midway along length of leaf; margin at right. $\times$ 65.
and bundle-sheath extensions; the remainder of the parenchyma being either of globular chlorenchyma cells or collapsed parenchyma cells.

1. *A. linearifolia* (figs. 32, 33). In the basal portion of the leaf (fig. 32) there is a large number of vascular bundles. These alternate with pockets of collapsed tissue. Most significant is the fact that veins occur as bundle-groups. Most of the veins are thus compound, and consist of 2–3 bundles. This condition is unique in *Abolboda*, and proves an exception to the statement of Solereder and Meyer (1929)—that the bundle-group type of construction in *Xyridaceae* is restricted to *Xyris*. Each bundle in the bundle-groups is surrounded by a fibrous sheath which is fused with the sheaths of neighboring bundles in the group. At a higher level (fig. 33) the same type of bundle is evident. There are, as described for *A. ciliata*, marginal hypodermal fibers, and the hypodermis other than this consists of about five cell layers. Bundle-sheath extensions are present, but relatively infrequent—only 1–3 may be present in a section at this level. The remaining mesophyll consists of spherical chlorenchyma cells which occur beside the hypodermis, lower epidermis, and around the bundle sheaths. Mesophyll not adjacent to these areas consists of collapsed parenchyma cells. The structure of leaf-tips is considered below in a separate section.

2. *A. macrostachyia*. The sheathing portion of the leaf of *A. macrostachyia* var. *macrostachyia* (fig. 34) is like that described for *A. linearifolia* in the nature of chlorophyll-free and collapsed parenchyma distribution. It is thinner, however, and the bundles, which are not grouped, possess massive sclerenchyma bundle sheaths. At upper levels in the leaf of *A. macrostachyia* var. *robustior* (fig. 28) a hypodermis of 3–4 layers occurs. Bundle sheath extensions consist of cells similar to the hypodermis and are present on all but the smallest veins. The remaining mesophyll consists of chlorenchyma, more densely arranged toward the adaxial surface. Only the larger veins have lignified elements in the bundle sheath; these are more abundant on the abaxial faces of the bundles. In comparable portions of the lamina of *A. macrostachyia* var. *macrostachyia* and var. *angustior*, which are much alike in leaf anatomy, only 1–3 bundle sheath extensions are present. Fibrous bundle sheaths generally are complete in var. *angustior*, whereas they often are present only along the abaxial surface of veins in var. *macrostachyia*. In other respects the three varieties are alike. Structure of the leaf tips is described below.

3. *A. sprucei* (fig. 37). The sheath portion of the leaf in this species is like that shown for *A. macrostachyia* (fig. 34) and requires no further comment. The upper portion of the lamina in *A. sprucei* (fig. 37) also shows similarity to that of *A. macrostachyia*. A hypodermis 2–5 cell layers wide is present, and no marginal sclerenchyma occurs. The remaining mesophyll consists of globular chlorenchyma cells which are more densely arranged beneath the hypodermis. The bundle sheath of all veins, in addition to the outer layer of chlorophyll-free parenchyma, consists of a massive fibrous sheath.

4. Leaf-tip. The three species above are alike in having a thorn-like terminus which occupies the 1–2 mm at the leaf apex. This type of apex in itself is not exceptional, nor is the fact that xylem alone without phloem composes the terminal portion of the vein, for this condition has been reported in other monocots (Arber, 1925). The tracheids in these species (fig. 41) tend to be separated from each other by parenchyma cells. The genuinely remarkable feature concerning these tracheids is the presence of very wide bands which
Fig. 34. Abolboda macrostachya var. macrostachya, transection of leaf base, adaxial face at right. × 74. Fig. 35. A. ciliata, transection of upper portion of leaf, adaxial face at right; margin below. × 90. Fig. 36. A. aquata, transection of upper portion of leaf; margin at left, adaxial face above. × 123. Fig. 37. A. sprucei, portion of transection taken midway along length of leaf; margin at right, adaxial face above. × 108. Fig. 38. A. sprucei, transection of ovary crest. × 108.
form the helical wall thickenings (fig. 41, enlarged in fig. 40). These bands, which are homologous with the typical helical or annular bands on protoxylem tracheids, are up to half the lumen in width. In helical tracheids more than one helix (usually two) may be present per tracheid. The bands are thicker toward the center of the cell, reflecting a "bordered" condition, as seen in figure 40, left. As seen in a transection of the leaf tip (fig. 42), the tracheids appear like fibers, because the wide bands resemble the thick walls of fibers. There seems little doubt that these represent specializations of ordinary annular and helical protoxylem tracheids. The transition to them from normal tracheids is abrupt, but elements with transitional width of thickening bands may in fact be found. The elements with the widest bands occur at the most apical portion of the leaf tip. The function of these peculiar tracheids is difficult to imagine. There is no hydathode formation in the terminal portion of the leaf (which is covered with one to several layers of hypodermal sclereids), nor any stomata in the terminus, so that this function may be ruled out. Although these tracheids are probably rare in angiosperms at large, they have been described in Cactaceae, as the account of that family in Metcalfe and Chalk's *Anatomy of the dicotyledons* shows (Cf. also A. Brongniart, Arch. Mus. Hist. Nat. Paris 1: 405–461. 1839).

**Orectanthe.**

Leaves of *Orectanthe* are basically not unlike those of the species of *Abolboda* just described, but differ from them in having a broad, flat shape, and an abaxial hypodermis (in some places, at least) as well as an adaxial one. The chlorenchyma cells are elongate in longitudinal section, and have symmetrically placed short arms (fig. 43). They correspond to the cells shown for *Xyris lanata* by Solereder and Meyer (1929, fig. 11b).

1. *O. ptaritepuiana* (fig. 29). In this species, 3–4 cell layers of hypodermis are present on the adaxial surface. The same type of parenchyma cells which comprise the hypodermis are present as a sheath extension on the larger veins, and as a single layer of hypodermis on the abaxial surface between the bundle-sheath extensions (at least in some places). The remaining portions of the mesophyll are pockets, oriented longitudinally in the leaf, which contain a uniform tissue composed of the peculiar chlorenchyma cells described above. The smaller bundles which do not have sheath extensions are embedded in this tissue. The bundles are elongate in transactional outline, and are completely ensheathed by a sclerified bundle sheath. These bundles are strictly collateral in structure.

2. *O. sceptrum*. Both typical *O. sceptrum* and subsp. *occidentalis* (fig. 30) are alike in having leaves thinner than those of *O. ptaritepuiana*. They are like leaves of *O. ptaritepuiana* in all details of anatomy except that (1) they often have an abaxial hypodermis nearly as wide as the adaxial one, (2) they have a prominently sclerified epidermis, and (3) the bundles are round, not elongate, in outline. The thickenings on the walls of the epidermis are narrowest on the outer wall. In upper levels of the leaf of *O. sceptrum* subsp. *occidentalis*, the parenchyma of the hypodermis and bundle-sheath extension was found to be more thick-walled and lignified. A section of the sheath portion of the leaf in this subspecies reveals that the structure of this portion of the leaf is identical with that of the leaves of the larger-stemmed abolbodas.
Fig. 39. *Achlyphila disticha*, portion of sagittal section of upper leaf, showing sclereids which comprise the epidermis. × 200. Fig. 40. *Abolboda sprucei*, enlarged portion of a section also shown in figure 41; at left, a tracheid with very wide annular thickenings; in center, a parenchyma cell; at right, out of focus, wide band from a helically thickened tracheid. × 915. Fig. 41. The same, showing a larger area of a sagittal section of the thorn-like tip of a leaf. Portions of tracheids (with very thin intervening walls) are shown, right, and left, and in the center (dark) parenchyma cells. The tracheids, left, have annular bands; those at right shown annular bands above and helical bands below. × 533. Fig. 42. *A. macrostachya var. macrostachya*, transection of thorn-like leaf tip, showing wide-helix and wide-annular band tracheids interspersed among parenchyma cells. × 288. Fig. 43. *Orectanthe ptaritepuiana*, portion of parasagittal leaf section, showing abaxial epidermis (above) and about three layers of arm-palisade cells. × 238.
Figs. 44-47. Amblyphylla disticha. Fig. 44. Half of transection of upright stem (inflorescence axis). × 31. Fig. 45. Portion of transection of sheathing base, adaxial surface at right. × 100. Fig. 46. Transection of leaf base, at higher level than figure 45, showing
Achlyphila.

Corresponding with the equitant habit of leaves, *Achlyphila disticha* shows anatomical features unusual or unique in *Xyridaceae*. Among these features are the sclerified epidermis, the bands of sclerenchyma in the leaf sheath, and the central zone of thick-walled parenchyma in the upper portions of the leaf. A transection of the sheathing portion of the leaf (fig. 45) shows three distinct zones of mesophyll: the outermost consists of spherical chlorenchyma cells; interior to this is a band of sclerenchyma in which the bundles lie. This sclerenchyma zone represents the widening, and fusion, of the individual sclerenchymatous bundle sheaths, which are separate at higher levels (figs. 46, 47) in the leaf. The innermost layers, present only on the adaxial surface of the central leaf sheath (fig. 46), consist of thick-walled parenchyma cells, isodiametric and polygonal in transection. Because of the equitant habit, sections at higher levels show the fusion of the two halves (fig. 46) into a conformation elliptical in transection (fig. 46). Here the bundles and their sheaths are separate, with no intervening sclerenchyma. The chlorenchyma can be differentiated into palisade and spongy at this level. The cells at the dorsal and ventral edges of the leaf (sclerified epidermis) are prominently elongate as seen in transection, forming irregular shapes. As seen in longitudinal section (fig. 39), the adjacent edges of epidermal cells are often raised into emergences, whereas the central surface of such cells is depressed. This configuration of epidermal cells is reported by Solereder and Meyer (1929) for several *Xyris* species and figured for *X. montivaga*. The elongate sclerified epidermal cells, as seen in transection, closely match those which Arber (1925) figures for *X. anceps*, although this species, unlike *X. montivaga*, does not have the undulate contours of epidermal cells as seen in longitudinal section. Sections of the leaf of *Achlyphila* at the level shown in figure 47 show that the central parenchyma of the leaf is thick-walled, probably lignified, and has an elliptical shape. At higher levels, there is a diminution both in the area of the central parenchyma and the number of bundles which surround it.

Discussion.

Malme's claim in 1925 that leaf anatomy is rather stereotyped in *Abolboda* as compared to *Xyris*, except for the number of veins, does not appear to be justified on the basis of the present study. A number of seemingly excellent specific and species-group characteristics have been described above. Leaf anatomy of *Orectanthe* reveals the similarity of that genus to *Abolboda* as well as the generic distinctions of the two species.

The leaf of *Achlyphila* is not unlike those of other *Xyridaceae* in its general structure. For example, *Xyris asperata* has a similar equitant habit (although the anatomy is quite different), as illustrated by Arber (1925). The presence of a ring of bundles around a zone of thick-walled parenchyma seems unique in the family, however. The epidermal characteristics although quite unlike those of *Abolboda* and *Orectanthe*, find parallels in *Xyris*. 

portions of the two wings. X 70. Fig. 47. Transection of upper (equitant) portion of leaf, showing slightly more than half; orientation as in figure 46—morphologically adaxial portion of leaf above. X 80.
Vessels.

Although Solereder and Meyer (1929) do not mention the occurrence of vessel elements in leaves of Xyridaceae, longitudinal sections of leaves revealed vessel elements with simple perforation plates in the following species: Abolboda linearifolia, A. macrostachya var. angustior, A. macrostachya var. macrostachya, and A. macrostachya var. robustior. Vessels, therefore, definitely do occur in leaves of at least the larger-leaved species of Abolboda. Vessels with simple perforation plates are indicated by Cheadle (1942) for leaves of Xyris flexuosa and X. smalliana.

INFLORESCENCE AXIS

Solereder and Meyer (1929) have concluded that Xyris differs from Abolboda in the general structure of the inflorescence axis. Xyris, according to these authors, possesses bundles embedded in (rarely outside of) the sclerenchyma ring, whereas Abolboda has bundles scattered through the central ground tissue ("pith") as well. This contrast appears to be justified on the basis of the present study. Solereder and Meyer also claim that bundles of the graminean type are absent in the inflorescence axes of Abolboda although they are present in Xyris. I have found that the more basal portions of inflorescence stems in Abolboda tend to have "ordinary" collateral bundles, or ones which are somewhat amphivasal. At higher levels, the graminean-type bundles were seen in "pith" of all the taxa considered here except Abolboda acicularis, A. americana, and Acklyphila disticha.

Abolboda.

Variables within a single inflorescence axis of Abolboda include the relative presence of photosynthetic tissue and the thickness of the sclerenchyma ring. Chlorenchyma appears to be absent from those portions of the axis most distal and most proximal to the base of the plant. Chlorenchyma, where present, consists of nearly spherical cells; some may be somewhat elongate radially, and form a palisade. If chlorenchyma is not present, parenchyma cells polygonal in outline in transsection (elongate in longitudinal section) extend from the epidermis to the sclerenchyma ring. If chlorenchyma is present, a single layer of non-photosynthetic parenchyma is often present outside the sclerenchyma ring. If chlorenchyma is present, a single layer of non-photosynthetic parenchyma is often present outside the sclerenchyma ring, particularly at those points where bundles are adjacent to the outer face of that ring. The sclerenchyma ring consists of several layers of thick-walled lignified cells. The outermost may have much thicker walls than layers internal to it.

1. A. acaulis. Because of the nearly sessile habit of the inflorescence in this species, no structure comparable to the inflorescence axis in the other species can be studied.

2. A. acicularis. This species (fig. 49) shows a number of features typical for the genus. Within the epidermis, both palisade and spongy palisade chlorenchyma occur. The single layer of non-photosynthetic parenchyma outside the sclerenchyma ring is ordinarily present. The outer face of each of the bundles (about 7) which occur outside the ring is sheathed by a single layer of sclerenchyma. No bundles occur within the sclerenchyma ring itself,
which is about three layers thick. A number of scattered bundles are present in the "pith" region.

3. *A. americana* (fig. 48). The cortical region of the inflorescence stem is notable for the occurrence of pockets (which run longitudinally in the exis) of collapsed parenchyma cells—like those which occur in a similar manner in the leaves of this species. The collapsed parenchyma pockets occur alternately with bundles of the outer circle. The remainder of the cortical region consists of globular parenchyma cells. The bundles adjacent to the outer margin of

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**Figs. 48-52.** Portions of transections of inflorescence axes of *Abolboda*, exterior above. Fig. 48. *A. americana*. Fig. 49. *A. acicularis var. acicularis*. Fig. 50. *A. ciliata*. Fig. 51. *A. linearisfolia*. Fig. 52. *A. sprucei*. Scale = 0.5 mm in 0.1 mm subdivisions.
the sclerenchyma ring are not completely ensheathed by sclerenchyma, but have a few such cells at their phloem poles. A single layer of thick-walled sclereids forms the outer layer of the ring. Internal to this layer are several layers of lignified parenchyma cells. Just interior to these cells, in the periphery of the central zone of the central zone of thin-walled parenchyma, is a single ring of about 5 bundles.

4. *A. ciliata* (fig. 50). At the level shown, the inflorescence axis is surrounded by a bract. This may account for the occurrence of lignified papillate epidermal cells. The cortical zone consists of spherical chloroencehyema cells. A number of bundles, each surrounded by an arc of sclereids, is present outside the sclerenchyma ring. The inner portion of the ring intergrades with the thin-walled parenchyma in the "pith" region. Within this latter zone, several (about 6) bundles occur. These bundles are notable for the occurrence of a prominent protoxylem lacuna which is separated from the remainder of each bundle. An additional set of bundles is interposed between those just mentioned and the inner margin of the sclerenchyma ring at lower levels in the inflorescence axis, and presumably these bundles supply a bract, and are thus absent at the level shown.

5. *A. linearifolia* (fig. 51). Although inflorescence stems in this species are larger in diameter than the above, they are not markedly different in most respects. One notable feature is the occurrence of a single hypodermis layer. At levels lower than that shown, two layers were apparent. A feature not previously indicated is the presence of bundles (in addition to those at the outer margins of the sclerenchyma ring) within the ring itself. Additional bundles are present in the "pith" region. At lower levels, all bundles (except those at the outer margin of the ring) are located in the thin-walled portion of the central ground tissue.

6. *A. macrostachyana var. angustior*. Upper levels in the inflorescence axis of this variety show a structure like that mentioned for such levels in *A. linearifolia*, except that the cortical region consists wholly of parenchyma cells like those of the hypodermis. At lower levels, however, 2–3 hypodermis layers are present; interior to these is chlorenchyma. Outside of the sclerenchyma ring, numerous bundles occur; these are embedded in the non-photosynthetic parenchyma. A single layer of strongly thickened sclereids forms the outermost layer of the sclerenchyma ring, and several layers of lignified parenchyma occur within that layer, as described for *A. americana*. Numerous bundles are present in the central thin-walled ground tissue. The tendency toward amphivasal construction of bundles is prominent at lower levels.

7. *A. macrostachyana var. macrostachya* (fig. 53). In the section shown, the cortical tissue consists of non-photosynthetic parenchyma. At higher levels, chlorenchyma is present interior to one or two layers of hypodermis. In addition to the bundles at the outer margin of the sclerenchyma ring, there are a few embedded in its inner margin (fig. 53). Many bundles occur in the thin-walled central ground tissue. Each of these bundles possesses a few lignified elements near the phloem pole. Such elements are absent at lower levels.

8. *A. macrostachyana var. robustior* (fig. 54). This inflorescence axis is quite similar to that of the above variety, but several features are worthy of note. The bundles at the exterior of the sclerenchyma ring are much smaller than
those in the interior of the stem. The outermost layer of sclerenchyma is much more thick-walled than interior layers, which grade into the thin-walled condition of the central ground tissue. Exceptionally large protoxylem lacunae, and intergradation to a graminean type of bundle construction may be seen.

Figs. 53–55. Transsections of inflorescence axes, exterior at right. Fig. 53. Abolboda macrostachya var. macrostachya. Fig. 54. A. macrostachya var. robustior. Fig. 55. Orectanthoe scepturn. Scale = 0.5 mm in 0.1 mm subdivisions.
9. *A. sprucei* (fig. 52). The inflorescence stem of this species shows no features not indicated above, but illustrates the generic characters rather clearly. The cortical zone of this axis is composed of spherical chlorenchyma cells. Exterior to the sclerenchyma ring is a circle of bundles; this circle is enveloped by a layer of non-photosynthetic parenchyma. The outermost layer of the sclerenchyma ring is very thick walled, and several less prominently sclerified cell layers occur internal to it. All the central bundles occur in the thin-walled ground tissue, although some are adjacent to the sclerenchyma ring. Bundles are of the graminean type or transitional to that type from the ordinary collateral.

**Orectanthe.**

An inflorescence axis of only one species, *O. sceptrum* (fig. 55), was sectioned. This stem showed a number of noteworthy features. A sclerified epidermis is present. Beneath this are about two cell-layers differentiated as a hypodermis. The remainder of the cortical zone consists of spongy chlorenchyma. Within the chlorenchyma are a number of bundles, most of which have a sclerenchymatous sheath. The sclerenchyma ring contains a number of bundles, not disposed in concentric circles. The thin-walled ground tissue intergrades into the sclerenchyma ring. Bundles of the sclerenchyma ring and central ground tissue are intermediate between amphivasal and collateral patterns.

**Achlyphila.**

The markedly flattened inflorescence axis of this genus (fig. 44) suggested that more or less prominent differences from *Abolboda* would be present. In fact, despite the obvious differences in shape, the similarities are perceptible. To be sure, the epidermis (which is two-layered in places at the edges of the axis) is heavily sclerified. Then, too, bundles (each with a fibrous sheath) occur in the cortical region on each edge of the axis. Aside from these differences, one can cite similarities in the chlorenchyma: two layers of palisade and several spongy layers are present. Adjacent to the outer margin of the sclerenchyma ring—or “ellipse”—bundles are present, each sheathed by a single layer of fibers along the outer surface, as in *Abolboda*. Bundles are present in the sclerenchyma, toward the inner margins of its extent. The central ground tissue consists of thin-walled parenchyma and (unlike *Abolboda*, but like *Xyris*) contains no bundles. The last-cited feature suggests that the resemblances of *Achlyphila* may lie closer to *Xyris* than to *Abolboda*.

Because *Achlyphila* is unique among *Xyridaceae* in not having a congested inflorescence, elongate pedicels are present. As is shown in figure 82, the pedicel is triangular in outline. Like the inflorescence axis, the pedicel has a sclerified epidermis. Two circles of bundles, one adjacent to the inner margin of the sclerenchyma ring (or, at lower levels, just within the ring) may be found. A central zone of thin-walled parenchyma is present.

**Discussion.**

The above descriptions must not be construed as exhibiting the full range of variation either in a species or in an individual axis, although an attempt is made to suggest the nature of such variation. Because of this variability,
species characters are difficult to offer. The inflorescence stems of *Abolboda macrostachya* are distinctive on account of their greater size (with more numerous bundles). Special features in the axes of *A. americana* (a single circle of "pith" bundles; collapsed parenchyma pockets) and *A. ciliata* (1–2 circles of "pith" bundles; prominent protoxylem lacunae in these) may be noted. The extent of sclerenchyma seems roughly correlated, in *Abolboda*, with size of the axis, and the sclerenchyma ring in *A. macrostachya* is much wider than in *A. americana*. Likewise, the very wide sclerenchyma cylinder in *Orectanthe* may be correlated with the large diameter of that axis. The sclerified epidermis, the lack of concentric arrangement of bundles, the presence of scattered bundles in the cortical region, and the presence on these of fibrous sheaths are all characters which differ to a certain extent from comparable conditions in *Abolboda*, and enforce the generic status of *Orectanthe*. The descriptions of *Achlyophila* above have shown that inflorescence-axis anatomy serves both to distinguish this genus generically, and to relate the genus to other *Xyridaceae*, probably to *Xyris* most closely.

**Vessels.**

Solereder and Meyer (1929) cite a report of vessels with simple perforation plates in inflorescence axes of *Xyris caroliniana*, *X. indica*, and *X. lacera*. In the present study, such vessel elements were observed in longitudinal sections of inflorescence axes of the following taxa: *Abolboda acicularis*, *A. americana*, *A. macrostachya* var. *macrostachya*, *A. macrostachya* var. *robusitior*, and *Orectanthe sceptrum*. Cheadle (1942) indicates vessels with simple perforation plates in *Xyris flexuosa* and *X. smalliana*.

**INFLORESCENCE BRACTS**

One or more bracts tend to occur along the inflorescence axis, and several are associated with the congested inflorescence itself. The former are here termed inflorescence-axis bracts and the latter inflorescence bracts. These bracts show patterns of structure different from those of sepals or leaves, and are worthy of description. In some instances (*Abolboda acicularis*, *A. ciliata*) the difference between structure of inflorescence-axis bracts and sepals is not very great. Because inflorescence-axis bracts and inflorescence bracts vary in structure from base to apex, and even within a plant, depending on their position, their structure is difficult to categorize accurately in all instances. Sections studied are discussed by species.

**Abolboda.**

1. *A. acaulis*. Because of the subsessile nature of the inflorescence in this species, bracts might best be regarded as inflorescence bracts. Such bracts have three veins in a non-photosynthetic parenchyma. Sclerenchyma is absent.

2. *A. americana* (fig. 24). An inflorescence bract is illustrated for this species. Three veins are present. The middle one of these is embedded in a sclerenchyma band which extends between the two surfaces.

3. *A. ciliata* (fig. 17). The illustration represents the basal portion of an inflorescence-axis bract. Numerous veins are present. These are encased in sclerenchyma sheaths, some of which are continuous with the sclerified adaxial surface. Chlorenchyma is present on the abaxial surface.
4. *A. linearifolia.* An inflorescence bract is illustrated in figure 23. The abaxial epidermis is sclerified; the mesophyll is divisible into three zones, from outside to inside: chlorenchyma, non-photosynthetic parenchyma, and sclerenchyma.

5. *A. macrostachya* var. *angustior.* The outer portion of an inflorescence-axis bract consists of spongy chlorenchyma. The adaxial portion of the mesophyll, in which veins are located, consists of non-photosynthetic parenchyma. A few fibers are present on the phloem poles of larger bundles.

5. *A. macrostachya* var. *macrostachya.* The two sections shown (figs. 18, 19) illustrate a great deal of difference between the median region and the most apical portion of an inflorescence-axis bract. At the lower level (fig. 19), the mesophyll contains sclerenchyma on the adaxial face, and a few bands of such tissue on the abaxial face. Chlorenchyma and non-photosynthetic parenchyma form bands within the bract. At the highest level (fig. 18), the entire mesophyll consists of thin-walled sclerenchyma.

6. *A. macrostachya* var. *robustior* (figs. 20, 22). The inflorescence-axis bract is distinctive in that the ground tissue consists of sclerenchyma, more nearly thin-walled halfway between the surfaces of the bract, which contains pockets of parenchyma, possibly chlorenchyma. In addition to the main series of veins, a few smaller veins are adjacent and exterior to the parenchyma pockets. They have the same collateral orientation as the main veins. The inflorescence bract (fig. 22) is not dissimilar in structure, although it has more thick-walled sclerenchyma, definite chlorenchyma, and bundles adaxial to the chlorenchyma.

**Orectanthe.**

An inflorescence-axis bract of *Orectanthe sceptrum* subsp. *occidentalis* shows a notable lack of mesophyll differentiation. The entire mesophyll consists of thin-walled parenchyma. Small fibrous bundle caps are present on the phloem poles of the veins. Inflorescence-axis bracts of *O. pteritepuiana* showed an identical structure.

**Achlyphila.**

The bracts in this plant (fig. 66) are thin, papery inflorescence bracts, not entirely comparable with any of the above because of the distinctive inflorescences of this plant. The three bundles are each ensheathed with a fibrous bundle sheath.

**Discussion.**

Obvious distinctive modes of bract structure occur in the taxa mentioned above. The lack of mesophyll differentiation in *Orectanthe* and *Achlyphila* bracts is interesting, for considerable differentiation occurs in comparable bracts of *Abolboda*. In *Abolboda*, particular types of bract structure (depending at least in part on the location of the bract on the plant and the level of section within a bract) suggests caution in the formulation of differences among the species of *Abolboda* in bract anatomy.

**SEPALS**

With the exception of *Achlyphila*, all the taxa studied here have keeled sepals. Some *Xyridaceae*, such as *Orectanthe*, have both keeled and non-keeled
sepals. The non-keeled sepals were found to have approximately the same structure as the winged portion of a keeled sepal (compare, for example, figures 21 and 64), so that separate descriptions are not necessary. The chief variation of significance is the relative distribution and presence of selerenchyma and (if present) chlorenchyma. To a large extent, the distribution of these tissues in comparison with non-photosynthetic parenchyma cells provides distinctions of taxonomic importance. The patterns are best summarized in terms of species.

**Abolboda.**

1. *A. acaulis* (fig. 56). The majority of the sepal is composed of lignified parenchyma, in which the three bundles are embedded. Chlorenchyma occurs in the keel of the sepal.

2. *A. acicularis* (fig. 57). The adaxial face of the sepal is composed of thick-walled selerenchyma; the pattern of distribution parallels the outline of the bract; the portion adaxial to the keel contains the single vascular bundle. The outer face of the bract contains spherical chlorenchyma cells; a small zone of non-photosynthetic parenchyma is present in the keel.

3. *A. americana* (fig. 58). The structure of this sepal is virtually the same as that shown for *A. acaulis*.

4. *A. citiata* (fig. 59). The sepal of this species contains selerenchyma, which is present on the adaxial face and extends toward the keel, where it encloses the midvein. An additional strand of selerenchyma is present in the most abaxial portion of the keel. Chlorenchyma occurs on the abaxial face of the bract.

5. *A. linearifolia* (fig. 60). This sepal is distinctive in the limited amount of sclerenchyma present on the adaxial face. The remainder of the bract consists of parenchyma cells which are polygonal as seen in transection. The central portion of this parenchyma contains numerous chloroplasts. Five veins are present in the mesophyll.

6. *A. macrostachya* var. *angustior* (fig. 61). This sepal has sclerenchyma distribution similar to that of *A. linearifolia*, but the adaxial band is wider and is connected with at least a partial abaxial band in the wings (at levels higher than that shown). Selerenchyma is very thick-walled. Five bundles are present in the non-photosynthetic parenchyma which composes the remainder of the sepal.

7. *A. macrostachya* var. *macrostachya*. The sepal in this variety in intermediate between those of var. *angustior* and var. *robustior* in that the abaxial selerenchyma band is better developed than in var. *angustior*. Some of the lateral bundles are embedded in the selerenchyma of the wings.

8. *A. macrostachya* var. *robustior* (fig. 62). The sclerenchyma on the adaxial surface is paralleled (and in places, fused with) a band which parallels the abaxial surface along the wings. The abaxial sclerenchyma extends farther into the keel than in the other varieties. The five bundles are present in the non-photosynthetic parenchyma which comprises the remainder of the sepal.

9. *A. sprucei* (fig. 63). This sepal shows two distinct zones of sclerenchyma: an adaxial one which parallels the inner face of the sepal, and an abaxial zone in the keel. Approximately nine bundles are present. A narrow band of chlorenchyma is present on the abaxial face of the bract.
Orectanthe.

1. *O. ptaritepniana*. The sepal of this species consists wholly of lignified parenchyma, except in the central portion of the keel, where thin-walled parenchyma occurs. This thin-walled parenchyma presumably contains a moderate number of chloroplasts, as it does in *O. sceptrum*.

2. *O. sceptrum*. As shown in figure 64, sepals of *O. sceptrum* subsp. *occidentalis* are like those of *O. ptaritepniana* except that pockets of thin-walled parenchyma, like that in the keel region, occur in the wing regions between veins. Liquid-preserved material was used to demonstrate the presence of chloroplasts in this soft-walled parenchyma. The central portion of a flattened sepal of this species, shown in figure 21, illustrates these same structural features.

Achlyphila.

The three sepals of *Achlyphila disticha* (fig. 65) are rounded rather than keeled. They contain about five bundles, which are embedded in the thin-walled parenchyma, composed of cells polygonal in outline, in the central portion of the sepal. This parenchyma contains chloroplasts in moderate numbers. The inner and outer faces of the sepal are sclerenchyma. At lower levels, this sclerenchyma takes the form of lignified parenchyma which intergrades with the thin-walled parenchyma in the center of the bract, but at higher levels, such as that shown, the sclerenchyma is thick-walled and clearly definable from the chlorophylla.

Discussion.

The sepals of *Orectanthe* are different from those of *Abolboda* in that (1) they are much larger; (2) they consist wholly of lignified parenchyma cells except for pockets of chlorenchyma in the keel and between some of the veins; and (3) they contain a much greater number of veins, and veins have a scattered distribution in the keel region. Sclerenchyma is present around veins in *Orectanthe* sepals regardless of location of veins. Sepals of *Achlyphila* are very simple in structure, corresponding with other seemingly unspecialized features of this genus. The presence of both an adaxial and an abaxial band of sclerenchyma together with the lack of a keel, is notable. The species of *Abolboda* seem to agree in their tendency toward production of an adaxial sclerenchyma band, and in the relative paucity of sclerenchyma in the abaxial portion of the sepal. Only a single series of bundles is present (unlike the condition in *Orectanthe*). The patterns of distribution of sclerenchyma, thin-walled parenchyma, and chlorenchyma undoubtedly lend themselves to use as specific criteria, and are self-evident, in the varied patterns illustrated, in

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Fig. 56–65, sepals, transections taken about midway along length of sepal; half of a keeled sepal is shown for each species. Fig. 56. *Abolboda acutula*. Fig. 57. *A. acicularis* var. *acicularis*. Fig. 58. *A. americana*. Fig. 59. *A. ciliata*. Fig. 60. *A. linearifolia*. Fig. 61. *A. macrostachya* var. *angustior*. Fig. 62. *A. macrostachya* var. *robustior*. Fig. 63. *A. spreuei*. Fig. 64. *Orectanthe sceptrum*. Fig. 65. *Achlyphila disticha*. Fig. 66. *Achlyphila disticha*, transection of bract of inflorescence proper. Patterns as follows: finest stippling = thick-walled sclerenchyma; coarser stippling = thin-walled sclerenchyma; cross-hatched = chlorenchyma; white in bundles = phloem; black = xylem; parenchymatous ground tissue left blank. Scale = 2 mm in 1 mm divisions; applies to all figures.
sepals of *Abolboda*. Because of variation in such patterns between the base and apex of a sepal, however, such patterns should be applied with caution. Unfortunately, no liquid-preserved sepals of *Xyris* were available for study. The writer suspects that these would show much resemblance to sepals of *Abolboda*, and would be worth investigating in any case.

**FLORAL VENATION**

The flowers of *Abolboda* and *Orectanthes* are alike in a number of features. The flowers of *Orectanthe* differ in having non-keeled sepals, in lacking staminodia, and in having larger parts which are more richly vascularized at least in some instances (corolla lobes, sepals) than the corresponding portions of *Abolboda* flowers. The general venation pattern in the two genera is sufficiently similar so that variations are considered below after a description of a typical venation pattern in *Abolboda*.

*Abolboda.*

The flower of *A. linearifolia* (figs. 67–81) proved convenient material for a study of venation, and does not appear to differ appreciably from other species in these respects. The levels shown offer a series of selected sections from the base of the flower to the top. Because of venation complexities, a series of sections appeared preferable. The broken line in figures 67–69 is merely used to indicate incomplete separation of a sepal from tissue of the inflorescence receptacle at those levels.

At the lower level indicated (fig. 67) a vascular cylinder can be seen. The bundles of the cylinder have branched, at a level lower than that shown, to supply the approximately five traces present in each sepal. At the next level (fig. 68) sepal traces are in their characteristic positions, and divergence of median corolla bundles is indicated. Only ovary bundles are present on the central area a short distance above this level. Five traces depart to each third of the corolla tube; these thirds correspond to the three corolla lobes at a higher level. This is more evident in figure 69, which shows two of the three staminodia that will be alternate with these thirds of the corolla tube. There is a clearly definable midvein in each third of the corolla tube (see particularly figure 72). At the level shown in figure 69, as well as in figure 70, the nature of ovary venation is evident. There are three dorsal carpellary traces and three ventral ones, although the latter are fused together at these levels. At the next higher level (fig. 71) separation of the axial portion of the ovary into three placentas, each with a vein (or in some preparations, a pair of veins) is shown.

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**Figs. 67–81. Abolboda linearifolia, successive transections of a flower.** Sepals are omitted in figures 72–75, and style only is shown in figures 76–81. **Fig. 67.** Departure of traces to sepals. **Fig. 68.** Departure of traces to corolla. **Fig. 69.** Base of ovary. **Fig. 70.** Level at which placentas are united; note three staminodes, each opposite a locule of ovary. **Fig. 71.** Level at which placentas are separate. **Fig. 72.** Upper end of ovary locules. **Fig. 73.** Level of ovary crests; note the triangular style base in center, the three staminodes just inside the corolla, and the two style appendages. **Fig. 74.** Departure of stamen traces; base of anthers; note several traces in each style appendage. **Fig. 75.** Level of stamen connectives; note cylindrical conformation of bundles in style of appendages. **Fig. 76.** Departure of style appendages from style. **Figs. 77–80.** Branching of bundles in upper portions of style. **Fig. 81.** Stigma. Vascular bundles in all figures represented by circles (or modified shapes). Scale = 2 mm in 1 mm divisions.
Figure 72 shows the termination of the ventral carpellary traces (below the level shown). The dorsal traces turn inward as the ovary narrows into the style, and only the three dorsal traces are present in the style base (fig. 73). In figure 73, the ovary appears fragmented into three portions (other than the style and style-appendages), and the larger triangular shapes represent the ovary crests. At the next level (fig. 74) departure of stamen traces, by branching from the median corolla traces, can be seen. The uppermost of the staminodia shown terminates at this level. In figure 75, the three corolla lobes become free from each other. Concomitantly with their greater widening into an imbricate conformation, there is considerable ramification of veins. The upper tips of two of the ovary crests may be seen at this level. The following figures show the changes in vascularization of the style. In figure 76, departure of ovary appendages may be seen. These appendages are recurved, so that description of changes in their anatomy from departure to tip proceeds in the reverse order, in terms of figure numbers. The bundles that depart into the ovary appendages are branches of the three style traces, not the traces themselves. One of the appendages is very short; the other two (fig. 75) show an alteration in vascularization. A cylindrical organization of the bundles is attained. At a lower level (fig. 74), these cylinders subdivide into several bundles, and at the tip of the appendages (fig. 73) only a single bundle is present. This bundle, in each, does not extend all the way to the appendage apex. Returning to the style proper (fig. 77), one may see that the three veins branch. This branching continues (figs. 78–81) so that numerous vein-endings enter the ultimate fringes of the stigma. Development of a central cavity in the style is illustrated in figure 80.

Variation in venation among the species of *Abolboda* seems to occur only in the number of bundles per sepal (see above) and the relatively abundant or few veins in the corolla, depending largely on corolla size.

The question naturally arises, what interpretation of the ovary appendages seems most appropriate in terms of their venation, position, and histology. They cannot be regarded as equivalent to two of the three stigmas (if two are present), on account of their venation. They represent, rather, branches of the style bundles. The vein in each appendage does not terminate as a hydathode, nor do the contents of cells in the appendage suggest a nectary function, although this possibility should not be ruled out. The function of these structures—if they do have any prominent function—may well be related to a pollination mechanism in some way, but without further knowledge, speculations concerning function would be pointless. A feature of some interest is the nature of bundles in the very large ovary appendages of *Orectanthe*. In *O. sceptorum*, the bundle was observed to be large and rather diffuse, with isolated patches of xylem and phloem cells.

In respects other than numbers of veins and absence of staminodia, the resemblance between *Abolboda* and *Orectanthe* flowers are close, and ovary and style of *Orectanthe* flowers have a venation identical to that in *Abolboda*.

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Figs. 82–87. *Achlyphila diaticha*, successive transsections from flower. Sepals omitted in figure 86, and only style base shown in figure 87. Fig. 82. Pedicel. Stippling represents thick-walled sclerenchyma. Fig. 83. Departure of sepal traces. Fig. 84. Base of petals. Fig. 85. Departure of stamen traces. Fig. 86. Ovary at level of ovules. Fig. 87. Style base. Vascular bundles in all figures represented by circles (or modified shapes). Scale = 2 mm in 1 mm divisions.
Achlyphila.

The venation of the flower of Achlyphila is relatively simple in comparison with that of Abolboda. Fewer levels therefore suffice to show the principal features, and are shown in figures 82–87. The pedicel, illustrated in figure 82, contains two circles of bundles. The outermost of these circles departs into the bases of the three sepals (fig. 83), in such a way that five traces are present in each sepal (fig. 84). Successive levels (figs. 84, 85) illustrate that above the level of sepal departure, the three whorls—petals, stamens, and gynoecium—become separate at approximately the same point. As in Abolboda, the stamen traces branch from the vein which can be demarcated as the midvein of each petal. No traces indicate any vestige of three other stamens, or of staminodia, which might be assumed to have been present primitively. About five traces are present in each petal, although these probably originate from about three traces in each petal base. The venation of the ovary is identical to that of Abolboda, as a higher level (fig. 86) indicates. As in Abolboda, widening of the petals is concomitant with branching of veins. Ridges, which fit into interstices between the sepals, were observed on the abaxial surface of the petals, and presence of these ridges alters the appearance of petal vascularization somewhat, for these ridges are vascularized. The venation of the style is as in Abolboda, except that no branching of the three veins takes place, as no appendages are present.

The similarities between Abolboda (e.g., A. linearifolia) and Achlyphila in respect to floral venation are quite striking. The only major differences are in the relative levels at which veins depart. Staminodia and ovary appendages are absent in Achlyphila, and three, rather than two, sepals are present (although some species of Abolboda also have three sepals).

**FLORAL HISTOLOGY**

Certain details of floral anatomy other than venation are worthy of description here because of their importance in suggesting specific and generic relationships. Some of these have been mentioned in connection with sepal structure.

**Corolla Lobe.**

Corolla lobes, as might be expected, are thicker in their central portion than at their margins. The maximum width of corolla lobes was found to offer a convenient point of comparison. The corolla lobe of Abolboda linearifolia (fig. 92), like those of the other species of Abolboda, has a maximum width of approximately four mesophyll cells. The maximum mesophyll width in corolla lobes of Orectanthe scopdtrum subsp. occidentalis (fig. 91) proved to be about 10 cell layers; these cells are much larger than those of Abolboda. In Achlyphila disticha, the maximum width (excluding ridges) appeared to be about 8 layers, as shown in figure 93, with a lignified sheath around veins.

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*Figs. 88–90. Portions of transections of anthers. Fig. 88. Abolboda linearifolia. Fig. 89. Orectanthe scopdtrum. Fig. 90. Achlyphila disticha. Figs. 91–93. Portions of transections of corolla lobes or petals. Fig. 91. Orectanthe scopdtrum. Fig. 92. Abolboda linearifolia. Fig. 93. Achlyphila disticha. Scale for figures 91–93 is shown beside figure 92. All scales are in 1 mm divisions.*
Epidermal Relief.

In *Abolboda*, both corolla (fig. 92) and ovary exhibit epidermal relief. Such relief occurs on both surfaces of the corolla lobes. The formation is not merely a cuticular relief. The epidermal wall is raised into delicate, ridged eminences which run, predominantly, in a longitudinal direction on the organ concerned. These eminences are particularly prominent above radial walls of epidermal cells. The cuticle follows outlines of the epidermal cell-wall relief. Outlines of the cuticle, therefore, are parallel to those of the wall relief, but less detailed.

In *Orectanthe sœptrum* subsp. *occidentalis* (fig. 91), similar ridges were observed on the epidermis of corolla lobes, but they are much coarser and less detailed than those of *Abolboda linearifolia*. On the ovary, virtually no relief occurs.

On petals of *Achlyphila disticha* (fig. 93), no appreciable relief could be detected on epidermal cells. On the ovary, however, there are forms of epidermal cell relief which correspond closely with those of *Abolboda linearifolia*. Cuticular relief thus suggests similarity between the two genera.

Anthers.

The anthers in the three genera offer distinctive points of comparison. In *Abolboda* (e.g., *A. linearifolia*, fig. 88), the connective is wide but thin. Between the veins and the anther sacs, the mesophyll of the connective is spongy. The endothecium is a single layer of cells wide. In *Orectanthe sœptrum* subsp. *occidentalis* (fig. 89) the connective is rounded. The endothecium is a single layer of cells wide except at the portions of the anther sacs nearest the connective. The endothelial cells are large, and the thickening bands are narrow. The anthers of *Achlyphila* (fig. 90) have a connective narrowed at their contact with the anther sacs. The connective itself is relatively narrow. The endothecium is a single of cells wide except where it is adjacent to the connective. Thickening on endothelial cells are relatively wide compared with those of *Orectanthe* and even *Abolboda*. Mention should be made of the conspicuous epidermal relief that occurs on the surfaces of the anther sacs. This feature offers a further point of comparison between *Achlyphila* and other *Xyridaceae*.

Ovary Crests.

The ovary crests of *Abolboda*, a characteristic of that genus, consist of large lignified cells. This is shown for *A. sprucei* in fig. 38.

Capsule Wall.

Mature capsule valves were available only in *Abolboda* and *Orectanthe*. As shown for *A. macrostachya* var. *angustior* (fig. 104) capsule valves in *Abolboda* consist of thick-walled sclerenchyma. Cells at the points where loculicidal dehiscence occurs are small and non-lignified. Likewise, the septa are not lignified, at least in their inner portions, and lignification is likewise absent where the valves are joined to the ovary base. The epidermal cells may be somewhat radially elongate, especially opposite the septa. In the fruits of *Orectanthe* (fig. 105) on the contrary, lignification even in mature fruits is mostly limited to the epidermal layer. Cells in this layer are mostly markedly elongate radially and sclerified.
SEED AND EMBRYO

Ovule.

Ovules of all species of Abolboda for which appropriate stages were available showed the same features. The ovule is anatropous, with two integuments which are distinct from each other and the nucellus well back into the chalazal region. The integuments are each two cells wide. The megaspore mother cell is separated from the surface of the nucellus by a single layer of cells. The ovules of A. macrostachya var. robustior showed some degree of wing formation, reminiscent of the condition in Orectanthe. Ovules of Orectanthe were insufficiently well preserved to gain an accurate idea of their structure. They appear to be decidedly laterally flattened, however, so that a wing, composed on one side of the funiculus and on the other side, of the outer integument, is present. This wing is more than two cell layers in width, and this greater width extends to parts of the ovule other than the wing, as the several layers between epidermis and tanniferous layers in the seed shown in figure 103 indicate. An idea of the extent of the wing can be gained from the figure of the seed of O. sceptrum given by Maguire, Wurdack et al. (1958, fig. 1m). The inner integument is not involved in wing formation.

The ovules of Achlyphila disticha are identical in structure with those of Abolboda acicularis and other species which lack wings; in turn, these conform to the pattern described by Weinzicher (1913) for Xyris indica.

Seed.

The seed of Abolboda is seemingly quite complex because of the four distinctive layer of cells. These four layers are shown in the longitudinal section (fig. 99) as well as the transection (fig. 100) and in the successive "paradermal" (tangential) sections shown in figures 94—97. The chalazal-micropylar axis is considered here as the longitudinal axis, and a sagittal section is considered a longitudinal section that passes through the funiculus and bisects the ovule.

The outermost layer of the seed is collapsed, or nearly so, at maturity. The cells are longitudinally elongate (fig. 94). These cells represent the relatively unmodified epidermis of the ovule. The cells of the hypodermal layer (fig. 95, excepting ridges) are large and highly vacuolate. They are enlarged in such a way as to occupy the valleculae of the wave-crest conformations of the layer beneath (see on fig. 100). The cells of the hypodermis are fewer than those of the epidermis, and are elongate laterally (fig. 95). They lack living contents at maturity. The two cell layers beneath the epidermis and hypodermis are distinctive in that (1) their walls are fairly thick and composed of a substance very refractory to staining, and (2) during their maturation stages, they first accumulate droplets of, then are entirely filled with a resin-like or tannin-like substance which stains bright red with safranin. The outer of these two layers (fig. 96) consists of cells that are tangentially elongate. In places, longitudinal ridges develop because of radial elongation of cells in this layer (fig. 100; tips of these ridges are seen in figure 95). These account for the longitudinal ridges seen in gross aspect on seeds of Abolboda, as illustrated by Maguire, Wurdack et al. (1958). The outer cell wall of each cell of this layer shows a relief, which consists of relatively large ridges. There is an adjustment, during maturation, so that cells of the hypodermis occupy spaces between the ridges, but are exceptionally thin atop the ridges.
Figs. 94–97. Parasagittal sections of seed of *Abolboda americana*. Fig. 98. Sagittal section of chalazal end of ovule, showing ovule trace. Fig. 99. Sagittal section of seed coat,
The innermost layer (fig. 97) consists of more or less isodiametric cells, with contents as noted above. Cell layers internal to this layer (i.e., nucellar layers) are completely collapsed at maturity, and only a thin membrane of collapsed cell walls separates the endosperm from the innermost layer just mentioned. At the chalazal end of the ovule (fig. 98), the structure is altered. Instead of the four distinctive layers, numerous layers are present. These consist of cells like those of the innermost seed coat layer, with the same dense contents. They form a sort of operculum in the seed. In immature seeds, a number of nucellar layers which might be mistaken for a haustorium are present; during maturation stages, these collapse. The way in which the two layers with contents are altered at the micropyle is indicated in figure 101. The lumen of these cells is quite small in comparison with the thickness of the wall, and a two-layered wall condition is visible in the outer row of cells. Mention should be made of the fact that during maturation of the seed, walls of the cells with contents are obliterated, so that limits between these cells may be difficult to ascertain.

Orectanthe.

The single section shown (fig. 103) will serve to indicate the nature of the seed coat in this genus. The number of layers outside of the inner two may be greater or fewer than that shown, but is never fewer than three cell layers and usually more, depending on ring formation. The outermost layer of cells consists of thin-walled sclereids. A number of thin-walled but persistent cells are present between the epidermis and the inner pair of cell layers. The persistent tissue is distinctive only in the presence of intercellular deposits, which occur in irregular patches and are of the same material which fills lumina of the innermost pair of cell layers of the seed coat. The inner two cell layers are distinctive, as in Abolboda, in their occlusion with the resin-like or tannin-like contents. In origin and nature, these cell layers are precisely homologous with those two layers in Abolboda. The outer of these layers does not exhibit the remarkable alteration into ridges which occurs in Abolboda, however.

Comparison of Seed Coats in Xyridaceae.

Unfortunately, no seeds of Achlyphila disticha were available. There are descriptions of seeds of Xyris in the literature, although only for one species, X. indica (Weinzieher 1913; Netolitzky 1926). These descriptions show a layer of cells with dark contents, formed into longitudinal ridges on the seeds, which has sculpturing on the outer wall surface and appears to correspond with the similar layers with contents in Abolboda and Orectanthe. Weinzieher, however, suggests that the origin of this layer is from the inner layer of the outer integument, rather than the outer layer of the inner integument, as is the case in Abolboda. Careful comparative studies of ovules in Abolboda and Orectanthe.
Fig. 101. *Abolboda americana*, embryo from sagittal sections of embryo sac. Note basal and hypobasal cell and haustorial "flaps." Endosperm shows many nuclei (stippled) per cell, starch grains (with shrunken hilum indicated), and protein storage globules (black). Micro-structure below. Fig. 102. *Orectanthe sceptrum*. Embryo, same view as that shown in figure 101. Fig. 103. *O. sceptrum*, section of seed coat from longitudinal section of seed. Section represents a portion between the prominent wings on the seed, which are therefore not involved in this section. Fig. 104. *Abolboda macrostachya* var. *angustior*, transection of capsule valve.
showed that the outer thin-walled layers, without contents, are derived from the outer integument, whereas the inner pair of cells with occluded lumina are derived from the inner integument. From very casual observations on seeds of *Xyris*, the writer is of the opinion that the respective layers in *Xyris* actually have a similar origin, and that the interpretation of Weinzieher is open to question.

The differences in seed structure between *Abolboda* and *Orectanthë* appear to be very distinctive expressions of the same basic pattern, and may be used both to separate the genera and to emphasize an underlying similarity. The writer believes that seeds of *Xyris*, upon further study, will probably also reveal similar conspicuous variations on a pattern common to the whole family. Study on seeds of *Achlyphila* is needed for the same reasons.

**Endosperm.**

Weinzieher (1913) and Netolitzky (1926) indicate rounded compound starch grains and protein spheroids in endosperm of *Xyris*. Presumably both of these accounts are based on Weinzieher’s study of *X. indica*. All the species for which material was available of *Abolboda* (fig. 101) and *Orectanthë* showed these features. Immature stages in the endosperm of *A. sprucei* showed the multinucleate condition of endosperm cells very clearly.

**Embryo.**

Weinzieher (1913) has illustrated stages in the development of the embryo of *Xyris indica*. The embryo consists of relatively few cells. A broad, flat cotyledon is evident, but Weinzieher figures no differentiation of a suspensor or any meristematic region. Features like these occur in *Abolboda*, as illustrated for *A. americana* in figure 101. A basal and a hypobasal cell are evident, however. The cotyledon consists of large cells, with dark-staining contents that suggest the haustorial function of this structure which is closely appressed to the endosperm. At the edges of the cotyledon, flap-like extensions are evident. The embryo of *Abolboda americana* shows no differentiation of an apical area, and is larger and composed of more numerous cells than that of *X. indica*. Significantly, the embryo of *Orectanthë sceptrum* (fig. 102) shows precisely the same features as the embryo of *Abolboda americana*, but is larger, corresponding to the larger size of all organs in this species. A basal and a hypobasal cell appear to be present. If a meristematic area is present, it is not appreciably differentiated from other areas of the embryo. Unfortunately, no embryos of *Achlyphila* were available. Likewise, no stages in gametogenesis or early embryo development were visible on account of the nature of preservation.

**Methods**

Pollen grains of *Xyridaceae* are subject to decomposition by various reagents. As Erdtman (1952) notes, his acetolysis method degrades the exine. Sodium
Hydroxide, a reagent commonly used in pollen-preparation techniques, partly or wholly dissolves the exine. Except for two specimens (figs. 112, 120) in which NaOH treatment was very gentle and merely revealed some textural differentiation in the exine—probably because of preferential solubility of certain parts—this substance proved useless. Even the pollen of fixed material which formed the main basis for this study was, in some cases, altered. Because of this extreme sensitivity to a wide variety of reagents, the simplest methods for preparation of pollen grains for observation appeared to be (1) sectioning and staining of flowers (with their included pollen) according to the techniques described at the beginning of this paper; and (2) transferring fixed anthers through an alcohol series to absolute ethyl alcohol, staining in safranin dissolved in absolute ethyl alcohol, and following this by transferring anthers to xylene and making whole mounts of grains in Canada balsam. Undoubtedly both of these techniques resulted in dehydration and perhaps other changes which could alter size and possibly induce artifacts. However, a number of grains in each of the collections studied appeared to be reasonably unaffected, and were considered suitable for study. Note should be made of the fact that the spines (or other excrescences of the exine) that stain bright red are seemingly unchanged by any of the reagents mentioned, and data concerning these are without doubt quite reliable. The exine wall, which stains green with a safranin–fast green combination, is the structure that is sensitive to reagents.

Because the grains are large, and few in number per anther, because good material (grains from anthers just before or at anthesis) were necessarily limited, and because many grains were collapsed, or degenerate, the number of grains that could provide reliable measurements was extremely small. The data on pollen grain diameter below represent, therefore, averages of measurements of only those grains that the writer judged to be turgid and otherwise unaltered in form. On account of the exceptional susceptibility of pollen grains in this family to various changes, truly exact data can probably be obtained only from fresh material. Such material is virtually impossible to view because of the remote locations in which these species grow. Terminology for pollen morphology used below follows the usage of Erdtman (1952).

**Pollen Grain Size.**

Pollen grains of *Abolboda*, *Orectanthe*, and *Achlyphila* are sphaeroidal, a fact which may be related to their nonaperturate condition. Because of this shape, only one dimension is necessary. Dimensions do not include the spines or other excrescences.

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Within the genus *Abolboda*, some taxa seem obviously to have larger pollen grains than others; species with exceptionally large grains include *A. linearifolia*, *A. macrostachya* (at least in part), *A. grandis*, and *A. sprucei*. The pollen grains of *Orectanthe* are markedly larger, in general, than those of *Abolboda*. The markedly smaller diameter of *Achlyphila* pollen grains is interesting; this size is comparable to the sizes reported by Erdtman (1952) for species of *Xyris*. Pollen grains of *Xyris*, as described below, do differ in morphology from those of *Achlyphila*.

Previous reports on pollen-grain diameter include those of Malme (1933) on "*Abolboda*" (now *Orectanthe*) *sceptrum* ("about 105 μ") and Erdtman (1952) for *Abolboda poarchon* ("105 μ"), *A. pulchella* ("105 μ"), and *A. vaginata* ("at least 75 μ"). Maguire, Wurdack et al. (1958) give the following measurements: *Abolboda bella*, 120–140 μ; *A. paniculata*, 140–150 μ; and *Orectanthe* (as a genus), 160–250 μ.

**Pollen Grain Wall ("sporoderm").**

Sectioned material showed two distinct parts of the pollen grain wall in all taxa: the inner portion, which stains brightly with fast green, and the spines, or other ornamentation (including the minute pila on the surface of the interspinal areas), which stain bright red with safranin. These two portions appear to correspond with Erdtman's definitions of nexine and sexine respectively, except that a thin layer, which stained pale green, on the inner surface of the pollen grain wall in *Abolboda* could be interpreted as the intine. This interpretation was suggested by observation of germinating pollen grains on a style of *A. grandis*. In these, this layer covered the emerging pollen tube. Such a layer could not be distinguished in pollen grains of *Orectanthe*, possibly because of difficulties in preservation, but a comparable layer did appear present in grains of *Achlyphila* (fig. 128).

The nexine in sectioned material and in whole mounts appears to stain homogenously in most preparations. In two preparations in which sodium hydroxide had been employed (fig. 112, 120), radial fibrillae or striae appeared to be present in the outer two-thirds of the nexine. This appearance may have been caused by differential solution of materials in the nexine, or by expansion of the wall by means of the treatment. Among the various taxa, the nexine thickness appears to be a distinctive character. In most of the *Abolboda* species studied, it appears to range between 5 and 7 μ. It is much thicker than that in *A. grandis* var. *guayanensis*, *A. macrostachya* var. *macrostachya*, *A. macrostachya* var. *robustior*, and *A. sprucei*. Certainly the great thickness of the nexine of *A. grandis* var. *guayanensis* and *A. sprucei* represents a distinctive characteristic. In *Orectanthe*, the nexine does not appear to exceed 5 μ in thickness. In *Achlyphila*, the width of this layer is about 3 μ.
Figs. 106-117. View of pollen grains in species of *Abolboda*. All figures except figures 113, 115-117 represent a portion of a median microtome section of a pollen grain, and have been drawn to show one of the large ornaments; intine is indicated below by sparser stippling. Fig. 106. *A. acaulis*. Fig. 107. *A. acicularis* var. *acicularis*. Fig. 108. *A. bella*. Fig. 109.
The outermost layer of the pollen grain wall, or sexine, is basically a thin membranous layer which may be partly detached in damaged grains. Minute pila (seen in surface view, figs. 113, 129) are embedded in this membrane. A feature that seems quite important to the writer does not seem to have been mentioned in the literature on Xyridaceae pollen grains, namely, that these minute pila are, in fact, homologous with the large spines or knob-like ornaments in Abolboda and Orectanthé. These larger excrescences are deposited on the membranous layer just as the pila are, and appear to be composed of the same material, despite the vast difference in size between the two types of ornamentation on the same grain. Rarely, as in Orectanthé scep-trum (fig. 125), knobs transitional in size between these two categories may be observed. The pila in Orectanthé are noticeably larger than those in Abolboda. Pollen grains of Achlyphila (figs. 128, 129) show the largest pila of any of the grains studied here. In Achlyphila, the pila tend to be aggregated in flake-like patches. In places between these patches, the pilate layer is absent. In Abolboda, a thin hyaline layer was observed immediately beneath the pilate layer. Such a layer may also occur in pollen grains of Orectanthé and Achlyphila.

The spines on pollen grains of Abolboda are so characteristic of that genus, and are so subject to distinctive variations in the species, that they have been figured for all the species studied (figs. 106-120). Basically, as in A. acaulis or A. linearifolia, they have an inverted funnelform shape. Sodium hydroxide treatment (figs. 112, 120) reveals that lacunae, not visible in other preparations, are probably present in the spine base. Some species show markedly narrow spines: A. bella (fig. 108), A. acicularis (fig. 107), and A. ciliata (fig. 109). Very short, wide spines occur in A. ebracteata (fig. 110) and A. macrostachya var. robustior (fig. 120). The three varieties of A. macrostachya appear different on the basis of spine size and shape. Within a single flower of A. sprucei, various alterations in spine shape were noted. The basic condition seems to be that shown in figure 114, but multiple spines on a single base (fig. 115), very much reduced lobes (fig. 116), and merely the vestige of the spine-base (fig. 117) were also observed.

Erdtman (1952) has illustrated the spines of pollen grains of three species and given dimensions: A. poarchon (spines 8.3 μ long; basal diameter 5.5 μ), A. pulchella (spines 9.3 μ long; basal diameter 8.3 μ), and A. vaginata (spines 8.3 μ long; basal diameter 8 μ). Erdtman figures spines in the latter species which appear about like the spines in A. macrostachya var. angustior.

The comparable ornamentation on pollen grains of Orectanthé is generically different from that of Abolboda. In Orectanthé, the emergences take the form of a large knob, or other shape much wider and more blunt than the spines of Abolboda, with the possible exception of the much smaller structures in A. sprucei. In O. pitaritepuiana (figs. 121-124) a variety of shapes was noted, varying with the collection from which the grain was taken: short, with a rounded apex (fig. 121), elongate (fig. 122), with a curved apex (fig. 123), or with folds or bulges on the sides (fig. 124). Evidently considerable variation is

A. ciliata. Fig. 110. A. ebracteata. Fig. 111. A. grandis var. guayanensis. Fig. 112. A. linearifolia (from NaOH-treated specimen). Fig. 113. Same, surface view of interspinal sexine ornamentation. Fig. 114. A. sprucei. Fig. 115-117. Same, variations (within a single flower) or ornament shape. Scale = 5 μ.
Figs. 118-129. Views of pollen grains. Conventions as in figures 106-117. Fig. 118. Abolboda macrostachya var. angustior. Fig. 119. A macrostachya var. macrostachya. Fig. 120. A. macrostachya var. robustior (from NaOH-treated specimen). Fig. 121. Orectanthe ptaritepuiana. Figs. 122-124. The same, variations in ornament shape. Fig. 125. O. seepe-
present in these characters. In preparation of pollen grains in this species, the
knobs appeared to be sunken in slight depressions; this may well be an artifact
of fixation or preparation. The knobs of Orectanthe sceptrum pollen grains are
different from those of O. pitardepiiana in that the apical portion is widened,
so that a capstan-like shape is achieved. The only variation in structure of these
knobs is found in the formation of additional small knobs on the base (fig. 127)
as compared to the normal condition (fig. 125), or the formation of a roughened
base (fig. 126).

Discussion.

In summary, the pollen grains of the three genera show excellent generic
characters. The presence of large excrescences in Orectanthe relates this genus
closely to Abolboda, but the differing shape is a good generic character. Like-
wise, the larger pila in the surface between emergences differentiates Orectanthe
from Abolboda. The absence of such large emergences in Achlyphila, and the
grouping of pila into flake-like aggregations on the exine surface, marks this
genus off from other genera of Xyridaceae. Within Abolboda, differing exine
widths and distinctive spine shapes and sizes serve to differentiate the species,
so that of the species studied, most could be identified by means of the pollen
grains alone. Similar considerations apply to distinctions between the two
species of Orectanthe.

Erdtman (1952) has emphasized the great distinction between Abolboda and
Xyris in pollen-grain structure. Much of this distinction may be attributed
to the large spines on the surface of Abolboda pollen grains. The lack of such
larger ornaments on grains of Achlyphila, which are (like those of Abolboda,
but unlike those of Xyris) nonaperturate, may vitiate this contrast, and pro-
vide an intermediate form. The pilate layer in pollen grains of Abolboda, Orec-
tanthe, and Achlyphila probably has a counterpart in Xyris. The presence of
the pilate layer, although different in each genus, tends to provide a common
characteristic, as does the rather thick nexine, lacking in lipophilic compounds.
The writer suspects from Erdtman’s reports of both “OL” and “LO” sexine
patterns that a layer of united pila may compose the sexine in at least some
Xyris pollen grains. The exine of Achlyphila seems midway between that of
Abolboda and Orectanthe on one hand, and Xyris on the other. The relatively
thick, baculate sexine and the thin nexine of Xyris pollen grains do not seem
at odds with the condition in Achlyphila. Probably the three major patterns
represent striking variations on the same basic pattern. Careful work is needed
both to provide additional data on Xyris and to demonstrate whether the affinity
Erdtman (1952) suggests between the grains of the Abolboda-type and those of
Liliaceae and Zingiberaceae is close or not.

SUMMARY

The writer has found that an attempt to summarize anatomical character-
istics of genera of Xyridaceae in chart form is virtually impossible because (1)
there are exceptional species within a genus; (2) reference to particular conditions in lengthy anatomical terms, or with the aid of illustrations is necessary; and (3) some relatively subtle characteristics cannot be summarized in this manner. The most important anatomical lines of evidence are cited below, and the reader is referred to the foregoing descriptions, particularly to the "discussion" section terminating each of the major portions above.

**Specific Characteristics.**

1. **Abolboda.** Characteristics of leaf anatomy and stem anatomy suggested recognition of two species-groups, termed here "smaller-stemmed" abolbodas and "larger-stemmed" abolbodas. Recognition of these as subgenera would probably be premature. Within each of these groupings, leaf and stem anatomy suggest specific characteristics also. Characteristics other than these do not emphasize the two species-groups as much as they suggest characteristics of individual species. The large stelar of roots defines *A. macrostachya*, but genuinely remarkable specific characteristics are offered by the peculiar patterns of endodermis-cell thickening. In the inflorescence axis, thickness of selerenchyma ring, presence of fibrous sheaths on pith bundles, and sclerification of epidermal cells offer a number of characteristics. Distinctive patterns in number of bundles, size, selerenchyma and chlorenchyma presence and distribution offer further characteristics in sepals, and, to a lesser extent, in bracts. Perhaps the best specific characteristics are evident in pollen in such respects as shape and size of spines, nexine thickness, and diameter.

2. **Orectanthe.** Anatomical features by which *O. pitaritepuiana* may be differentiated from *O. sceptrum* include relative lignification of the central portion of the stem; thickness, epidermal sclerification and shape of bundles in leaves; distribution of parenchyma in the sepals; size and sexine ornamentation of pollen grains.

**Generic Differences.**

The closest relationships among genera of *Xyridaceae* is that between *Abolboda* and *Orectanthe*. Segregation of the latter genus is well deserved, however. *Orectanthe* has larger stems with a distribution of selerenchyma different from that in *Abolboda*. *Orectanthe* has more bundles in its leaves, more bundle-sheath extensions, a tendency towards abaxial hypodermis production, and no thorn-like leaf-tip with peculiar tracheids. It has spongy chlorenchyma and lignified bundle sheaths in the cortex of the inflorescence axis. It has distinctive sepal size and anatomy, and the inflorescence-axis bract is notably lacking in selerenchyma or other differentiation. *Orectanthe* lacks staminodia, has more elaborate corolla venation, and a massive anther connective. Capsule-valve anatomy and especially seed anatomy provide excellent characteristics to distinguish the two genera. Pollen morphology provides an exemplary instance of a generic degree of distinction between *Abolboda* and *Orectanthe*.

*Achlyphila* could probably be defined, on the basis of present knowledge, on a number of anatomical features. The root offers peculiar endodermis characters and vessels well toward the interior of the core, which, however, lacks central vessels. The stem shows modifications corresponding with its rhizomatous habit, such as a stem endodermis. The leaves have a peculiar equitant habit, and the
central core of lignified parenchyma in upper portions is peculiar. The flattened inflorescence axis, lacking veins in the "pith" region, is distinctive. Sepal anatomy could be used to separate Achlyphia from the other genera, and floral venation reveals both a lack of staminodia and a choripetalous condition. Pollen is peculiar because it combines a peculiar patch-like presence of long pila with a lack of major ornaments and a nonaperturate condition.

Detailed comments cannot be made on Xyris, because it has been excluded from this study. Such characteristics as lack of "pith" bundles in the inflorescence axis, distinctive seed anatomy, and the peculiar nature of the monosulcate pollen provide features which, as extended descriptions would show, amply enforce the generic distinction of Xyris within the family.

Composition of Xyridaceae: Relationships of the Four Genera.

In respect to either gross morphology or anatomy, three relatively isolated groups are apparent: (1) Abolboda and Orectanthe; (2) Achlyphia; and (3) Xyris. Before showing the anatomical common denominators among these groups, similarities among pairs of genera may be mentioned.

Abolboda and Orectanthe, as mentioned above, are amply distinct, but the resemblances are close. For example, the presence of style appendages and their venation pattern is a striking similarity. Winged seeds occur both in Orectanthe and, to some degree, in Abolboda macrostachya. Seed-coat anatomy of the two genera reveals two variations on the same basic pattern, as do the embryos. The inflorescence axis in both genera contains bundles in the "pith" region. Most significantly, perhaps, both genera possess pollen grains in which an outer layer contains both minute pila and large spine- or knob-like ornaments.

Abolboda resembles Xyris in exhibiting a similar range of anatomical characteristics in roots. Equitant leaves and compound bundles in leaves occur in both genera. The embryo of Abolboda, although larger than that of Xyris, is very similar. Better knowledge of seed anatomy in Xyris might reveal similarities in this respect.

Abolboda is like Achlyphia in relatively few aspects, because the relationship of Achlyphia to Xyris appears closer. In addition to features common to all genera mentioned below, one may mention resemblances in epidermal relief in flowers, identical ovules, similarities in floral venation, and certain features of root anatomy and inflorescence-axis structure.

Relationships between Achlyphia and Xyris include those of equitant leaves and their anatomical consequences, the presence of sclerified epidermis and undulate epidermal contours on leaves, the lack of bundles in the "pith" region of the inflorescence axis, and resemblances in pollen. The pollen of both genera lacks the differentiation of sexine into major and minor ornaments, and is relatively small in diameter.

Review of anatomical characteristics reveals a number in which the genera are alike, or in which the genera appear as variations on a common basis. One significant feature is the presence of vessel elements with simple perforation plates in all parts of the plant. As the work of Cheadle (1942) shows, this high degree of specialization occurs in only a few families of monocots. The amount of similarity among the three genera in this study in respect to floral venation is remarkable, and study of Xyris might enable inclusion of that genus in this respect. The choripetalous condition in Achlyphia is really not...
appreciably different from the tubular condition of the corolla in *Abolboda* and *Orectanthe*, and the venation reveals no appreciable alterations in this respect. To be sure, *Achlyphila* is less specialized in its choripetalous condition, but one might assume that presence of staminodia was a primitive character in *Abolboda*. Certainly the development of style ("ovary") appendages in *Abolboda* and *Orectanthe* are advanced characteristics, whatever their significance may be. Unfortunately comparable data is not available on seed anatomy for the four genera, but I suspect that this will reveal a common basis upon which variations have been evolved. Similar considerations also apply to morphology of the embryo; the three genera for which this is now known all have the same peculiar type, with variations chiefly in size. The most significant anatomical character in *Xyridaceae* with respect to difficulties in interpretation might seem to be pollen morphology. Much has been made of the difference between *Abolboda* (with *Orectanthe*) and *Xyris* in these respects. Because monosulcate pollen is so basic in the monocots, the nonaperturate condition in *Abolboda, Orectanthe, and Achlyphila* would seem to be derived. If this were true, one might also expect a more primitive exine condition in *Xyris* also. The lack of differentiation of the sexine elements, and their even distribution, appear to be unspecialized. Exine in *Achlyphila* consists of only one type of sexine element, small pila arranged in flake-like patterns. This ornamentation is close to that of *Xyris*, in the writer's opinion, although *Achlyphila* is like the other two genera in the nonaperturate condition. The most logical explanation of the exine in *Abolboda* and *Orectanthe* seems to be that differentiation into two types of elements—minute pila and large spines or knowbs—has taken place; this differentiation most likely would have started from a condition like that found in *Achlyphila*. The relatively thick nexine, lacking in lipophilic compounds, offers a common basis among the genera. More study of *Xyris* pollen is required before a definite phylesis can be suggested, but the above interpretations appear most likely at the present moment.

The reader will note that the taxonomic conclusions expressed above bear a very close resemblance to those of Maguire, Wurdack, et al. (1958, 1960). The writer agrees with these authors in their conclusion that the four genera of *Xyridaceae* are highly distinctive, but show more common resemblance than any resemblance of any one to a genus of another family. The writer was pleased to find, in addition, that his anatomical material lends such clear-cut support to specific and even subspecific (*Abolboda macrostachya*) designations of these authors.

**Literature Cited**


