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# SYSTEMATIC POSITION OF *XYRIS*: FLOWER AND SEED ANATOMY

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Flower anatomy, embryology, and seed anatomy are described for some Brazilian species of *Xyris* section *Nematopus* and reviewed with respect to the systematic position of *Xyris* and allied taxa in Commelinanae. Apart from tenuinucellate ovules (shared with Poales, *Mayaca*, and Eriocaulaceae), *Xyris* lacks some of the synapomorphies of other genera that are sometimes included in Xyridaceae (*Aratitiyopea*, *Achlyphila*, *Abolboda*, and *Orectanthe*), such as inaperturate spinulate pollen; *Xyris* has monosulcate reticulate pollen. There is an unusual degree of variation among different genera of Xyridaceae for characters such as tapetum type, indicating that the monophyly of the family requires testing. However, while several characters indicate two generic groups, there is much missing critical information for embryological and seed coat characters in other Xyridaceae.

*Keywords:* systematics, *Xyris*, monocotyledons, systematics, pollen, flower, seed.

## Introduction

*Xyris* L. is the largest of five genera of Xyridaceae. It includes ca. 300 species of perennial herbs with ensiform leaves, mainly from Central and South America but with representatives also in Australia, Africa, and India (Kral 1988). The other four genera of Xyridaceae (*Aratitiyopea* Steyerm. & Berry, *Achlyphila* Maguire & Wurdack, *Abolboda* Kunth, and *Orectanthe* Maguire) have fewer species (up to ca. 20 species in *Abolboda*) and more restricted distribution in tropical South America. The monophyly of Xyridaceae is not yet established, and some authors have recognized Abolbodaceae as a distinct family, including *Abolboda* and at least *Aratitiyopea* and *Orectanthe*, which share characters such as inflorescence structure, stamen number, and stylar appendages (e.g., Steyermark 1984). Carlquist (1960) noted a close relationship between *Abolboda* and *Orectanthe* with respect to morphological characters such as leaf anatomy and pollen morphology (table 1) and observed that *Achlyphila* shares some characters with both this group and *Xyris*. *Aratitiyopea* was described relatively recently (Steyermark 1984) and is poorly known for most characters. This intermediacy of *Achlyphila* between *Xyris* and *Aboldoda* has led most authors to regard all five genera as a single family, Xyridaceae (Kral 1988).

However, there is an unusual degree of variation in several critical micromorphological characters within Xyridaceae *sensu lato* (table 1), some of which has been noted in previous morphological analyses of commelinoid systematics (e.g., Linder and Kellogg 1995). In particular, tapetum type is often significant in commelinoids and, except in this instance, does not otherwise vary within monocot families (Furness and Rudall 1998). Tiemann (1985) reported a plasmodial tapetum in *Abolboda* in contrast to the secretory tapetum of *Xyris* (e.g., Weinzieher 1914), and the consistency of this record for *Xyris* therefore requires checking.

Xyridaceae clearly belong in the commelinoid clade (Commelinanae: Chase et al. 1995), based on several morphological characters, especially the presence of ferulic acid in cell walls (Harris and Hartley 1980; Rudall and Caddick 1994), together with molecular data. However, within Commelinanae, Xyridaceae have been associated with several different families, including Eriocaulaceae, Rapateaceae, Commelinaceae, and Mayacaceae, with which they share a perianth differentiated into petals and sepals (e.g., Dahlgren et al. 1985), especially Eriocaulaceae (e.g., Linder and Kellogg 1995; Stevenson and Loconte 1995). Based largely on analysis of molecular sequence data, the Angiosperm Phylogeny Group (1998) recognized four commelinoid orders: Arecales (Arecaceae), Commelinales (four families), Poales (16 families, including Xyridaceae and Eriocaulaceae), and Zingiberales (eight families), with six other commelinoid families still unplaced. Although molecular data for Xyridaceae are sparse so far, both *Xyris* and *Orectanthe* have now been sequenced for *rbc*L. Givnish et al. (in press), in an analysis of molecular sequence data from *rbc*L for commelinoids, found only 45% (or 51%) jackknife support for a monophyletic Xyridaceae, indicating that this requires further testing. Xyridaceae and Eriocaulaceae were weakly supported (31%) as a sister pair and were weakly embedded in Poales. In contrast, in a three-gene analysis with fewer taxa and excluding *Orectanthe* and Eriocaulaceae (which have only been sequenced for *rbc*L), Chase et al. (in press) found strong bootstrap support for the inclusion of *Xyris* within Poales.

The aims of this article are to present new observations on flower and seed structure in three Brazilian species of *Xyris* (section *Nematopus*; Smith and Downs 1968), together with a review of characters that have proved significant in determining family relationships within Commelinanae, highlighting the gaps in the morphological data set for these characters.

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## Table 1

**Floral and Embryological Characters in Genera of Xyridaceae**

| | *Xyris* | *Abolboda* | *Achlyphylla* | *Orectanthe* | *Arratityopea* |
|---|---|---|---|---|---|
| Stylar appendages | Absent | Present | Absent | Present | Present |
| Tapetum | Secretory | Plasmodial | ? | ? | ? |
| Microsporogenesis | Successive | Successive | ? | ? | ? |
| Pollen apertures | Monosulcate | Inaperturate | Inaperturate | Inaperturate | Inaperturate |
| Pollen surface | Reticulate | Spinulate | Reticulate | Spinulate | Spinulate |
| Anther wall formation | Reduced type | Monocot type | ? | ? | ? |
| Endothecial thickenings | Spiral, inconspicuous | Inconspicuous, U shaped | Spiral | Spiral | ? |
| Ovule shape | Orthotropous | Anatropous | Anatropous | Campylotropous | ? |
| Ovule (nucellus) development | Tenuinucellate | Crassinucellate | Crassinucellate | ? | ? |
| Embryo sac development | *Polygonum/Allium* type | Polygonum type | ? | ? | ? |
| Endosperm | Nuclear | Helobial | ? | ? | ? |
| Number of cell layers in outer integument | Two | Two | Two | Three + | ? |
| Tanniniferous layer | Absent | Inner layer of inner integument | ? | Both layers of inner integument | ? |
| Number of integuments forming micropyle | Two | Two | ? | ? | ? |
| Seed operculum | Micropylar | Chalazal | Chalazal | Chalazal | ? |
| Cuticle layers in seed coat | Cuticle present between nucellus and inner integument | ? | ? | ? | ? |
| Seed coat mechanical layer origin | Both layers of inner integument | Both layers of inner integument | ? | Outer layer of outer integument | ? |

Note. Data for *Abolboda* from Carlquist (1960) and Tiemann (1985), for *Achlyphylla and Orectanthe* from Carlquist (1960). Nowicke (in Steyermark 1984) reported inaperturate spinulate pollen in *Aratitiyopea*. Characters that are unknown in particular genera are indicated with a question mark.

It is intended that, after further work on other genera of Xyridaceae (L. Campbell and D. W. Stevenson, unpublished data), this will contribute to a further joint morphological analysis of commelinoid relationships, following those of Stevenson and Loconte (1995), Linder and Kellogg (1995), and Rudall et al. (1999). Previous anatomical studies on *Xyris* flowers are scanty. Embryology has been described in three species of *Xyris* section *Xyris*: *Xyris indica* (Weinzieher 1914), *Xyris pauciflora* (Govindapa 1956), and *Xyris schoenoides* (Ramaswamy and Raju 1982). Floral vasculature has been described in seven Brazilian species (Sajo et al. 1997) and also in *X. indica* (Tukshetty et al. 1968).

Although largely beyond the scope of this article, the subgeneric taxonomy of *Xyris* also needs further attention: currently there are three sections, based entirely on ovary placentation (Kral 1988; Doust and Conn 1994). In section *Xyris*, which is widespread, there is a unilocular ovary with parietal placentation; in section *Pomatoxyris*, which is exclusively Australian, there is a trilocular ovary (sometimes incompletely trilocular; Conn and Doust 1997) with axile placentation; and in section *Nematopus*, which is exclusively Central and South American, the ovary is unilocular with mainly free-central placentation.

## Material and Methods

Material of three species of *Xyris* was collected from their natural habits at Serra do Cipó (Minais Gerais), Brazil, and fixed in FAA. Vouchers are deposited at Herbario, Rio Claro, Brazil (Rio Claro, São Paulo, Brazil) as (*a*) *Xyris longiscapa* Alb. Nilsson: M. G. Sajo and J. Semir on August 20, 1997, and M. G. Sajo on December 16, 1997; (*b*) *Xyris obtusiuscula* Alb. Nilsson: M. G. Sajo, December 16, 1997; and (*c*) *Xyris trachyphylla* Mart.: M. G. Sajo and J. Semir, August 20, 1997, and M. G. Sajo, December 16, 1997.

For SEM observation, fixed buds were carefully dissected and transferred to 70% alcohol, dehydrated through an alcohol series to absolute ethanol, then critical-point dried using a Balzers CPD 020. Flowers and dried seeds were mounted on stubs and coated with gold, using an Emscope SC 500 sputter-coater, and examined in a Cambridge 240 SEM.

For light microscope observation, fixed material was dehydrated through an alcohol series to absolute ethanol, then placed in histoclear, embedded in Paraplast, and serially sectioned using a rotary microtome. Sections were stained in safranin and Alcian blue and mounted in Euparal. Photomicrographs were taken using a Leitz Diaplan photomicroscope.

A cladistic analysis was undertaken using the branch and bound parsimony algorithm of the software package PAUP for Macintosh (Phylogenetic Analysis Using Parsimony; Swofford 1993), together with MacClade 3.04 (Maddison and Maddison 1992) for data entry. Characters were unordered and equally weighted. Bromeliaceae were designated as the outgroup taxon. This analysis is intended to illustrate systematic problems in Xyridaceae and must be regarded as preliminary, because it is not comprehensive for taxa of Commelinanae. Planned future analyses will be scored at the genus level. This analysis includes some characters that were not scored in either Stevenson and Loconte's (1995) morphological monocot analysis or the subsequent broad commelinoid analysis that assessed the relationships of *Hanguana* (Rudall et al. 1999) because there are still missing data for other commelinoid taxa. Several other characters were not used in this analysis, mainly because much information is missing for most taxa of Xyridaceae (e.g., anther wall formation and endosperm development; table 1).

## Observations

*Xyris* flowers are trimerous and hypogynous with distinct sepals and petals and only three stamens. Since there are relatively few differences in floral morphology and anatomy between the three closely related Brazilian species examined, they are described here collectively as *Xyris*, except where there is some variation between species. The three coriaceous calyx members are free from each other and are unequal, the median one being larger than the others, hoodlike, and caducous at anthesis. Three free yellow petals alternate with three plumose staminodes, which have long uniseriate hairs composed of bulbous cells with a thick cuticle (fig. 1*A*, *C*). Petals and staminodes are fused together at the base. The staminodes may facilitate pollination by collecting pollen from adjacent anthers and presenting it to the visiting insects. There are three functional adnate stamens with basifixed, tetrasporangiate anthers that dehisce by longitudinal extrorse slits (fig. 1*C*). The ovary lacks appendages in the species examined here, although Sajo et al. (1997) recorded rudimentary stylar appendages in some *Xyris* species. The fruit is a capsule that opens by three longitudinal fissures. The ovary is unilocular in *Xyris* flowers examined here. The style is apically tribranchiate, and the stigmatic surface is covered by multicellular hairs (fig. 1*A*, *D*).

### *Stamens*

A transverse section of a young anther shows meristematic tissue surrounded by a well-defined epidermis. The anther later becomes four lobed, and a hypodermal tissue of archesporial cells differentiates in each lobe (fig. 2*A–D*). Each archesporial cell undergoes a periclinal division, giving rise to parietal and primary sporogenous tissues. The former divides periclinally and produces the endothecium and tapetum (fig. 2), characterizing the "reduced type" of anther wall formation, where there are no middle wall layers (Davis 1966).

As the anthers develop, the epidermal cells (exothecium) enlarge to become more conspicuous and protuberant (papillate), with a thick striate cuticle (fig. 4*C–E*). The cells of the hypodermal layer (endothecium) are tangentially elongated and show inconspicuous spiral thickenings (fig. 4*E*). The tapetum is secretory and consists of uninucleate cells with a dense cytoplasm (fig. 3*A*, *B*). As the tapetal mother cells enter mitosis, these cells increase in size, their cytoplasm becomes vacuolated, and occasionally the tapetum becomes two layered and, later, somewhat disorganized. At the time of dehiscence, the epidermis and endothecium are still intact and the anther connective is wide but thin.

### *Microsporogenesis and Pollen*

The cells of the sporogenous tissue produce microsporocytes (microspore mother cells), distinguishable by their large size, dense cytoplasm, and conspicuous nucleus. Before commenc-

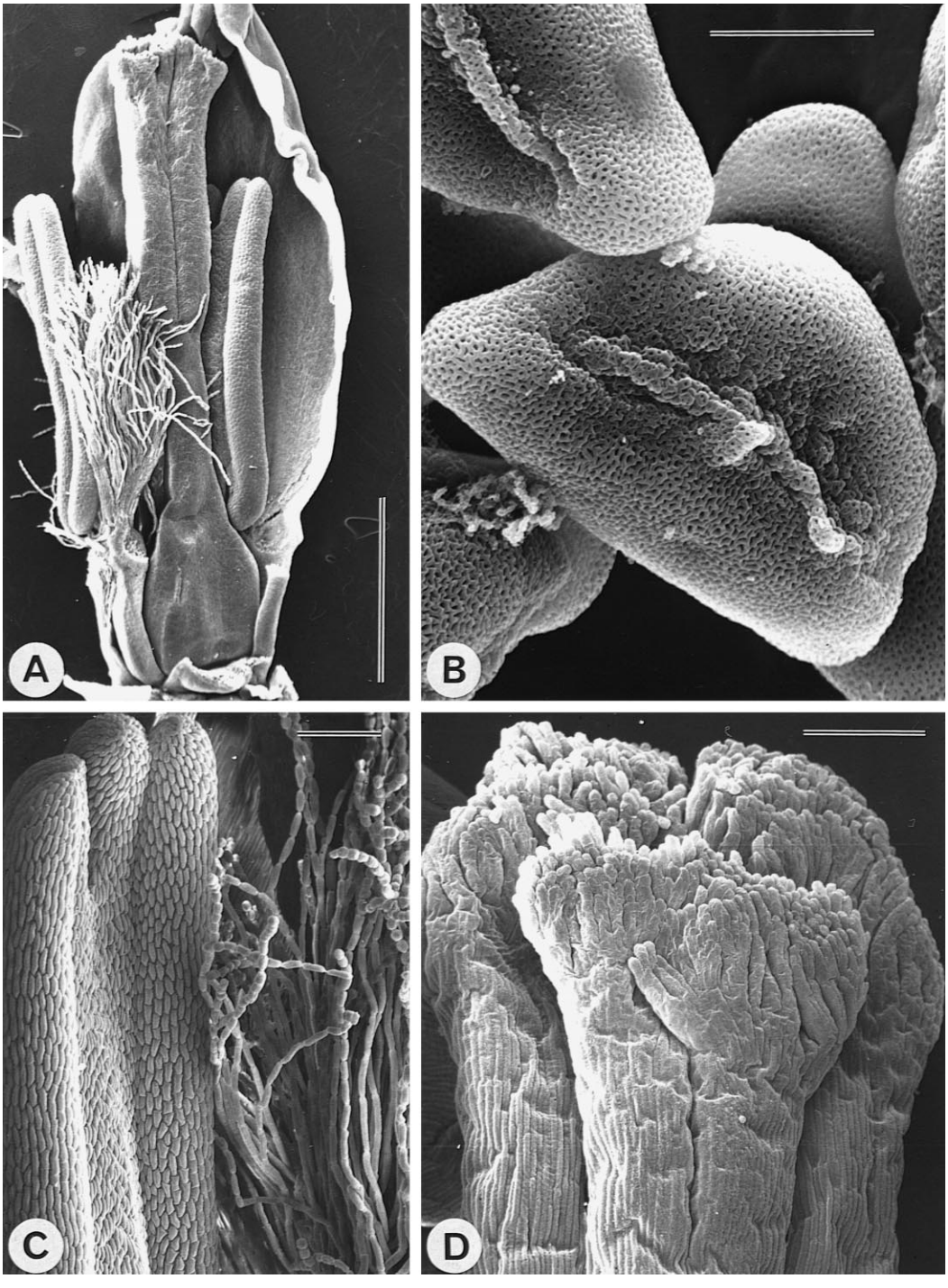


**Fig. 1** Scanning electron micrographs, *Xyris obtusiuscula*. *A*, Open flower with sepals, two petals, and one stamen removed, showing gynoecium with superior ovary and apically tribranchiate style, two stamens, and plumose staminode; bar = 1 mm. *B*, Pollen grains, monosulcate with apertural operculum; bar = 10 $\mu$m. *C*, Extrorse stamen and plumose staminode; bar = 200 $\mu$m. *D*, Stigma; bar = 200 $\mu$m.

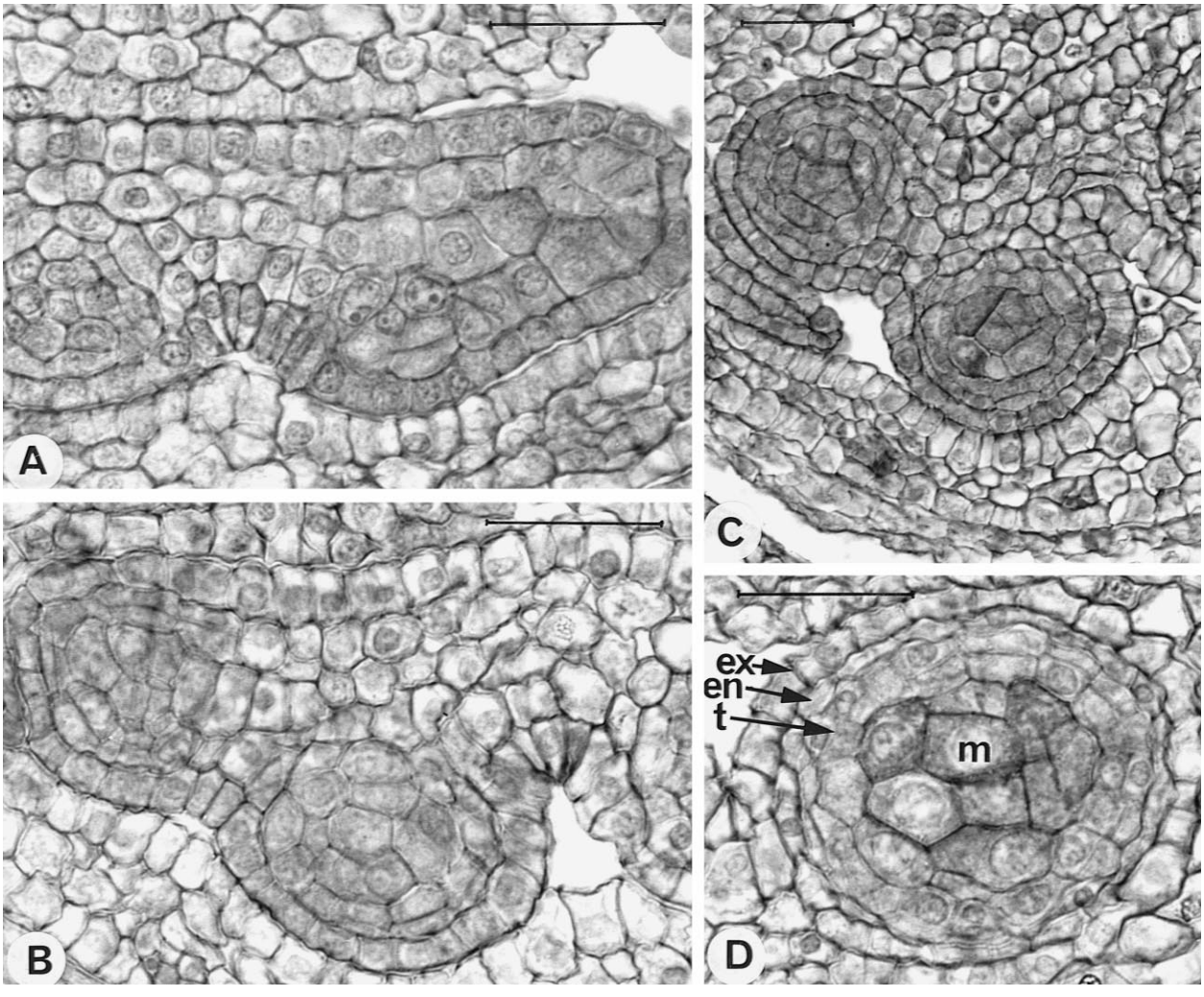


**Fig. 2** *Xyris trachyphylla*, photomicrographs of cross sections of developing anthers. *A–D*, Successive stages of development showing reduced type of microsporangium wall origin and microsporocyte (pollen mother cell) differentiation. *en*, endothecial layer; *ex*, exothecium (anther epidermis); *m*, microsporocytes; *t*, tapetum. Bars = 50 μm.

ing reductional divisions, the microsporocytes become globose and a callose wall is formed (fig. 3*C*, *D*). Cytokinesis is successive and results in tetragonal (isobilateral) tetrads with a thick layer of callose at their adjoining walls (fig. 4*A*, *B*). Pollen grains are elongate, flattened in lateral view, and monosulcate with a reticulate exine structure and an apertural operculum (fig. 1*B*).

### *Ovary and Ovules*

The style has three vascular bundles and a single, central, tripartite stylar canal. The numerous ovules are orthotropous and inserted in axillary placentation (fig. 5*A*).

The ovule primordium is massive, and the apical part of it develops into the nucellus. The inner and outer integuments are initiated almost simultaneously and are dermal in origin (fig. 5*B*). The hypodermal archesporial cell gives rise directly to the megasporocyte (fig. 5*B*), without first forming parietal tissue, which is the tenuinucellate condition

The megasporocyte (megaspore mother cell) is distinguishable by its size, dense cytoplasm, and large nucleus. After meiosis, the resulting tetrad is linear and the three micropylar megaspores degenerate, the chalazal megaspore being functional (fig. 5*C*, *D*). The large functional megaspore has dense cytoplasm and a large nucleus near the center and divides three times. The micropylar quartet becomes organized into a three-celled egg apparatus and one polar nucleus, while the chalazal quartet gives rise to the antipodal cells and the other polar nucleus. The female gametophyte is thus of the *Polygonum* type. The upper and lower polar nuclei migrate to the center of the embryo sac (fig. 5*G*) and later fuse to form a fusion nucleus. At anthesis, the nucellus is one layered around the sides and three to four layered toward the chalaza. The mi-

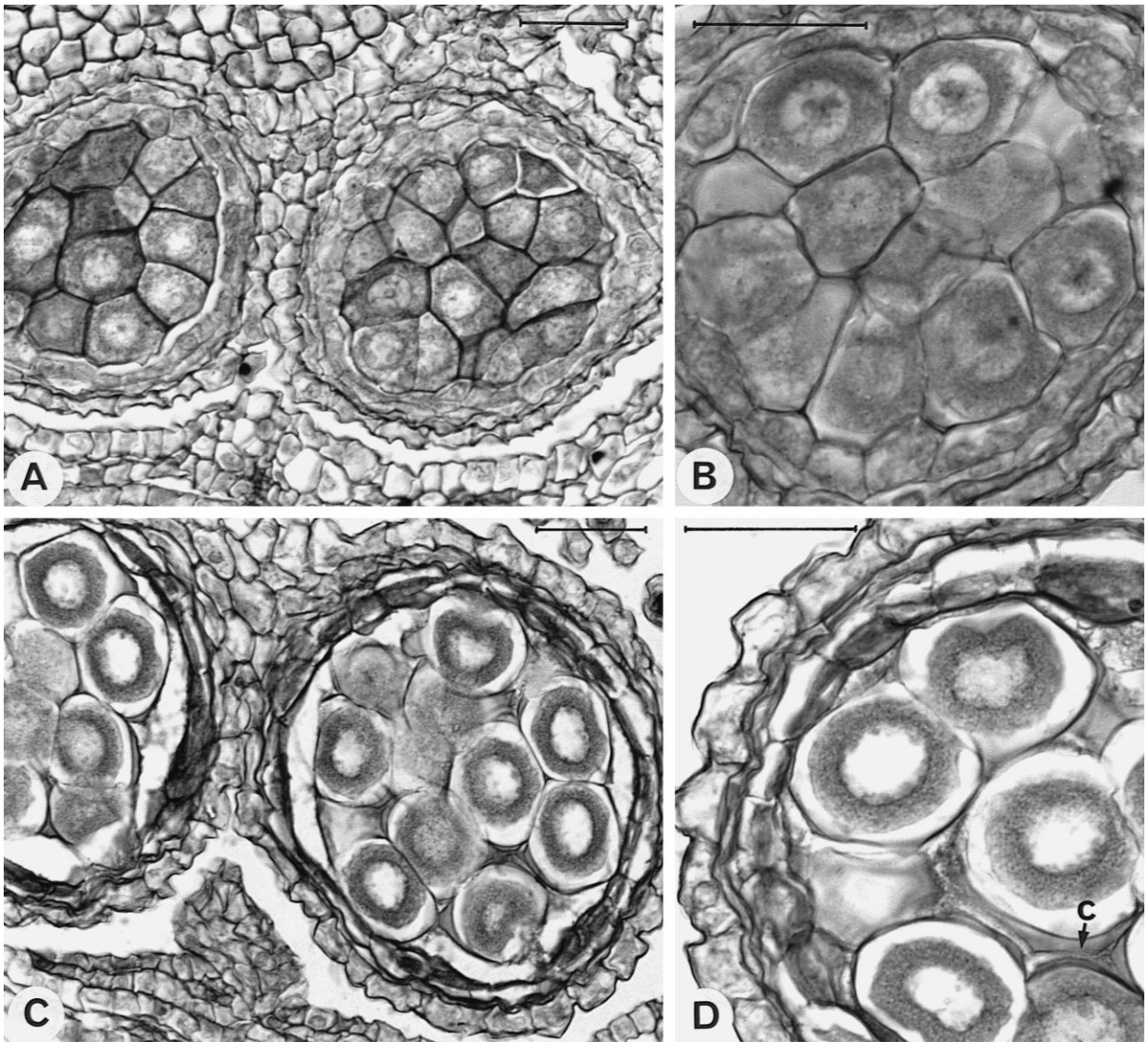


**Fig. 3** *Xyris trachyphylla*, photomicrographs of cross sections of developing anthers. *A*, *B*, Developing microsporocytes. *C*, *D*, Older stage; microsporocytes with thick layers of callose. *m*, microsporocytes; *t*, tapetum. Bars = 50 $\mu$m.

cropyle is formed by both outer and inner integuments (fig. 5*D*).

### *Seed Development*

After fertilization, the cells of the outer integument remain parenchymatous, and those of the inner integument become large and thick walled. The outer integument is two layered in *Xyris*, as in *Abolboda* and *Achlyphila*, although it has three or more layers in *Orectanthe* (Carlquist 1960). As the cells of the inner integument grow, they stretch the outer integument (fig. 6*A*) and eventually remove it, so *Xyris* seed coats are tegmic in origin. The outer layer of the inner integument differentiates into an exotegma, and its cells show a jigsaw pattern in paradermal view and a characteristic surface pattern (fig. 7). The inner layer of the inner integument differentiates into an endotegma, and its cells are narrow and longitudinally elongated. There is apparently no tanniniferous layer. The cells of the inner integument become lignified. A thick cuticle is formed between the nucellus and inner integument for their whole length and also between inner and outer integuments in the micropylar region (fig. 6).

The zygote is pear shaped with a conspicuous nucleus, and the small globular proembryo is situated near the micropyle (fig. 6*C*). There is no obvious suspensor. The primary endosperm nucleus divides after fertilization, but subsequent early stages of endosperm development were not observed here. After fertilization, the lateral cells of the nucellus became elongated, and those at the chalazal end of the embryo sac are short, compact, and thick walled. In the micropylar region, the inner layer of the inner integument divides to form another

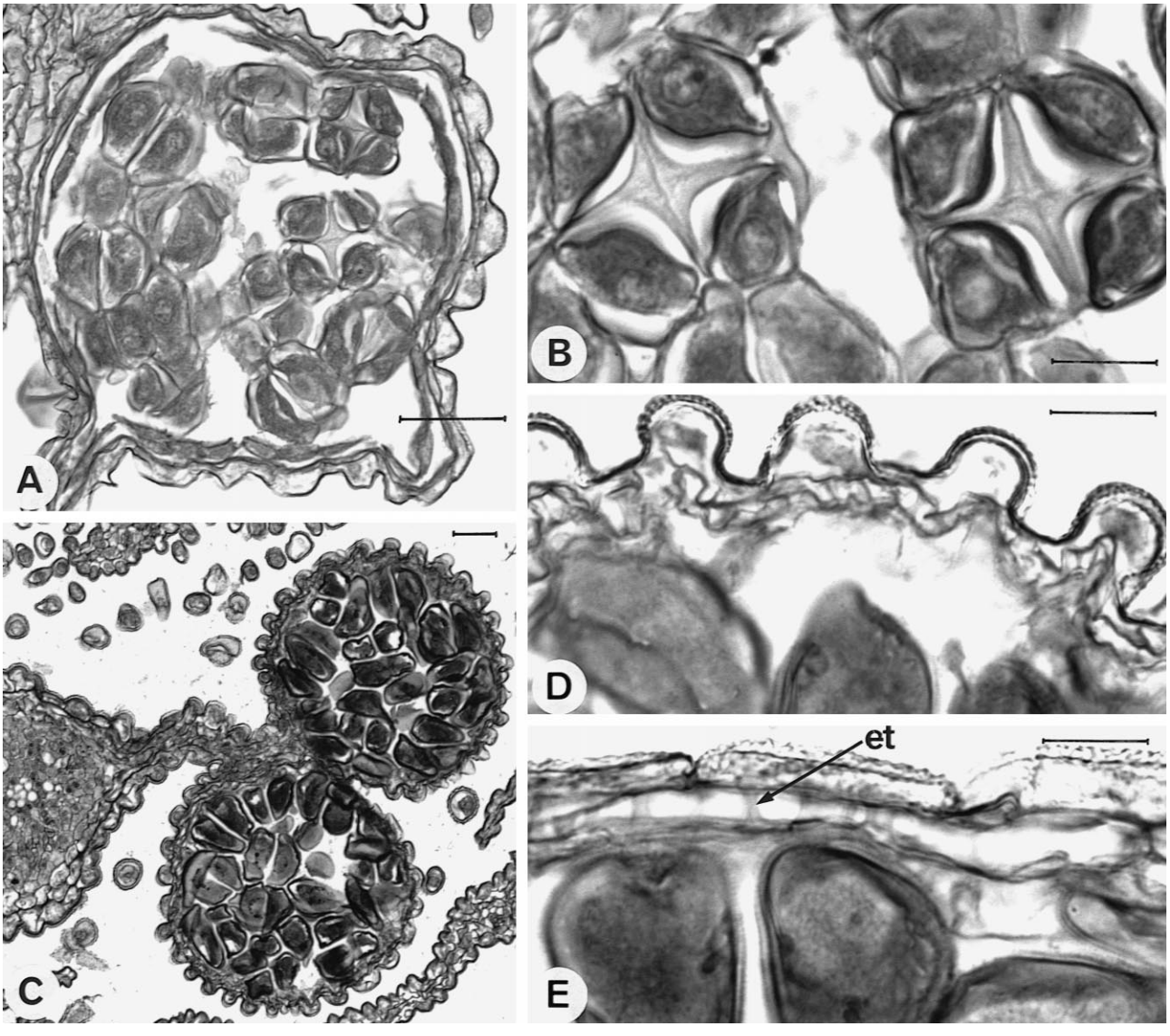


**Fig. 4** *Xyris trachyphylla*, photomicrographs of cross sections of anthers. *A*, *B*, Tetragonal (isobilateral) microspore tetrads. *C*, Anther in open flower, with free microspores. *D*, *E*, Cross and longitudinal sections of anther wall with inconspicuous endothecial thickenings (*et*). Bars: *A*, *C* = 50 μm; *B*, *D*, *E* = 20 μm.

layer; this forms a seed operculum, which apparently becomes detached at germination.

## Discussion

### *Floral Characters*

Floral characters that are potentially significant in commelinoid systematics are summarized in table 1 in order to illustrate characters that vary between genera and to demonstrate the gaps in the dataset for these characters in genera allied to *Xyris*.

*Stylar appendages*. The most compelling evidence for a link between *Abolboda*, *Orectanthe*, and some Eriocaulaceae is the presence of stylar appendages, which T. Stützel (1990, personal communication) regarded as homologous structures derived from wet stigmas rather than from septal nectaries. *Xyris* species lack these unique stylar nectaries; Sajo et al. (1997) recorded rudimentary stylar appendages in one *Xyris* species, but none were seen here, and this aspect needs further investigation.

*Tapetum*. Our results confirm Weinzieher's (1914) record of a secretory tapetum in *Xyris* species, in contrast to the plasmodial tapetum of *Abolboda* (Tiemann 1985). Other commelinoid taxa with a plasmodial tapetum include Bromeliaceae, Commelinaceae, Haemodoraceae, Typhaceae, *Hanguana*, and all families of Zingiberales, whereas Eriocaulaceae and most Poales have a secretory tapetum (see Furness and Rudall 1998).

Dahlgren and Clifford (1982; probably reporting from Wunderlich 1954) recorded a binucleate tapetum for *Xyris*, and

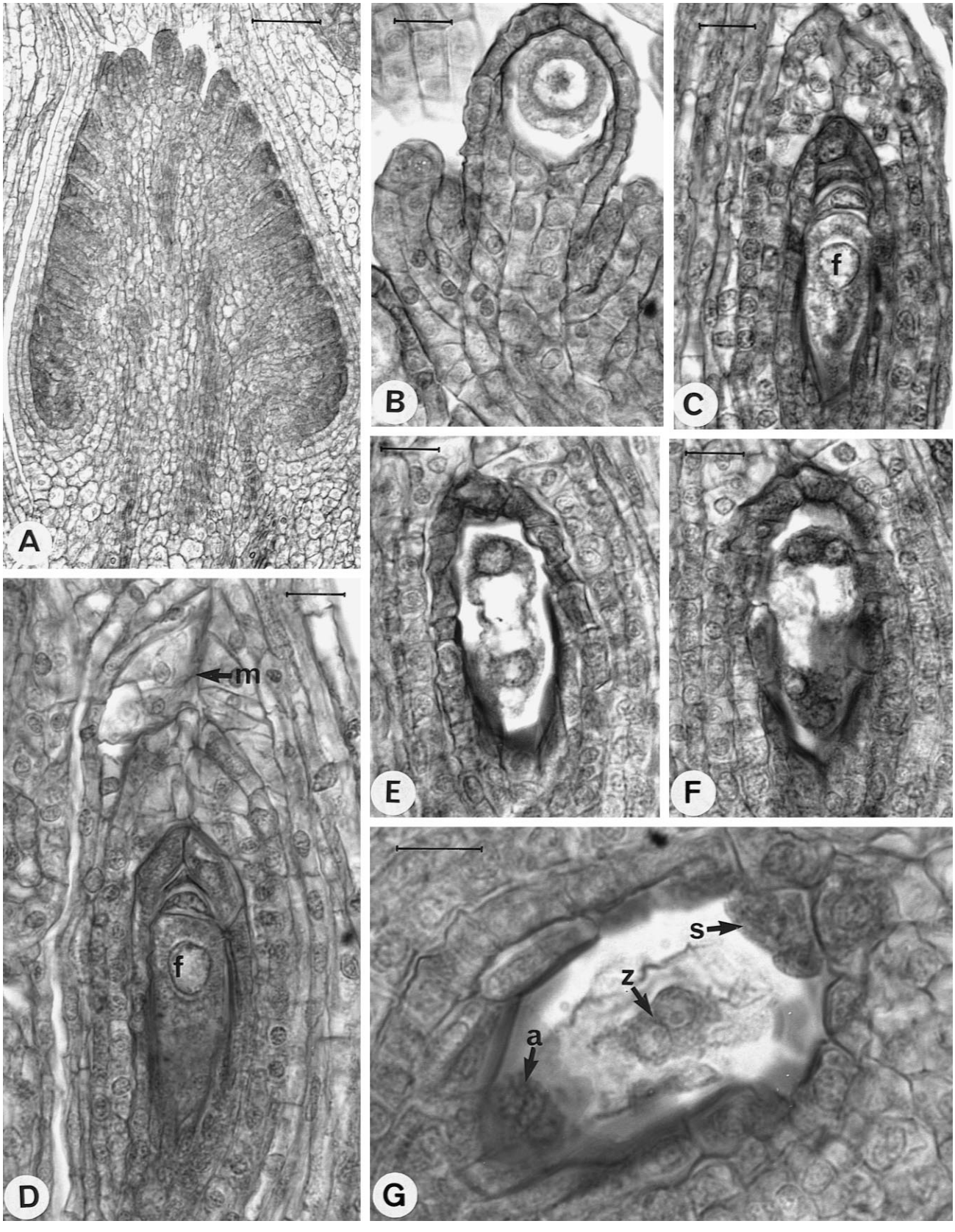


**Fig. 5** *Xyris trachyphylla*, Longitudinal section ovary and ovules. *A*, Ovary with orthotropous ovule primordia in axillary placentae. *B*, Tenuinucellate ovule primordium showing integument initiation and conspicuous megasporocyte (megaspore mother cell). *C*, *D*, Stages with linear tetrads. *E*, Two-nucleate stage. *F*, Four-nucleate stage. *G*, Eight-nucleate stage. *a*, antipodals; *f*, functional megaspore; *m*, micropyle; *s*, egg apparatus (synergids + egg cell); *z*, polar nuclei. Bars: *A* = 100 $\mu$m; *B*–*G* = 20 $\mu$m.

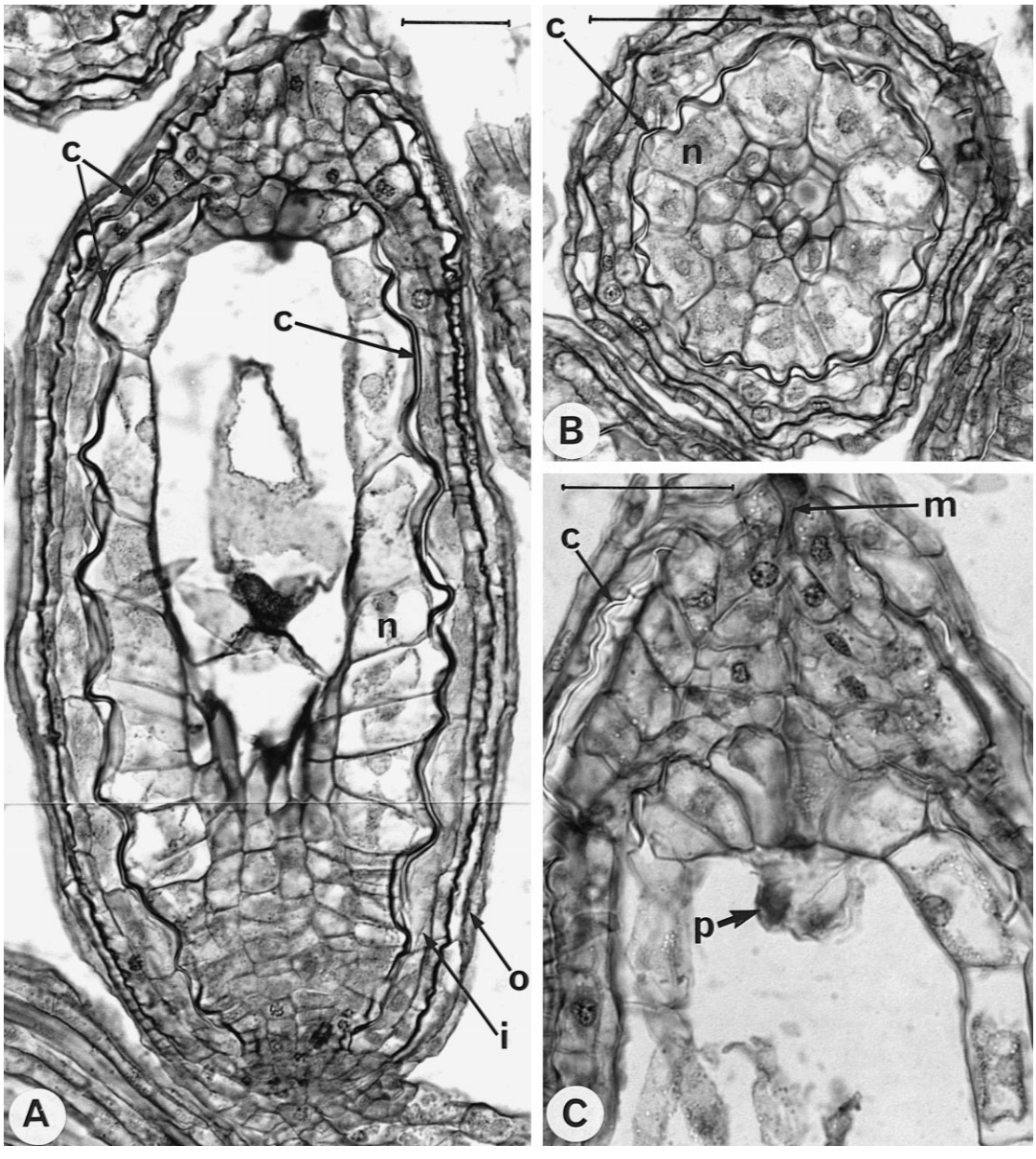


**Fig. 6** *Xyris longiscapa*, developing seed. *A*, Longitudinal section showing seed coat origin from inner integument. *B*, Transverse section podium at chalazal region. *C*, Longitudinal section at micropylar region with small pear-shaped proembryo and free endosperm nuclei. *c*, cuticle; *i*, inner integument; *m*, micropyle; *n*, nucellus; *o*, outer integument; *p*, proembryo. Bars = 50 μm.

Tiemann (1985) a uninucleate or binucleate tapetum. We observed only uninucleate tapetal cells but often a two-layered tapetum (fig. 2*D*). Although the number of nuclei in tapetal cells is sometimes considered taxonomically significant (Dahlgren and Clifford 1982), it may vary depending on differences in stages studied, even in the same tapetum (Rudall and Furness 1997), and its systematic significance at this level is therefore doubtful.

*Microsporogenesis.* Microsporogenesis is predominantly successive in monocotyledons, but with at least four simultaneous lineages (Furness and Rudall, in press). Within Commelinanae, simultaneous microsporogenesis occurs in (*a*) some palms and (*b*) a group of three families within Poales: Cyperaceae, Juncaceae, and Thurniaceae. Other commelinoids, including Eriocaulaceae, Mayacaceae, and Xyridaceae, have mainly successive microsporogenesis, although in Eriocaulaceae and Flagellariaceae there are occasional records of simultaneous or irregular microsporogenesis.

*Pollen.* *Xyris* has monosulcate or disulcate pollen (e.g., Straka and Friedrich 1984), but pollen is inaperturate in *Abolboda*, *Orectanthe*, *Aratitiyopea*, and *Achlyphila* (table 1). As in most monocotyledons, monosulcate pollen is predominant in Commelinanae, but there are some exceptions. Most Zingiberales have inaperturate pollen, although a few are spira-

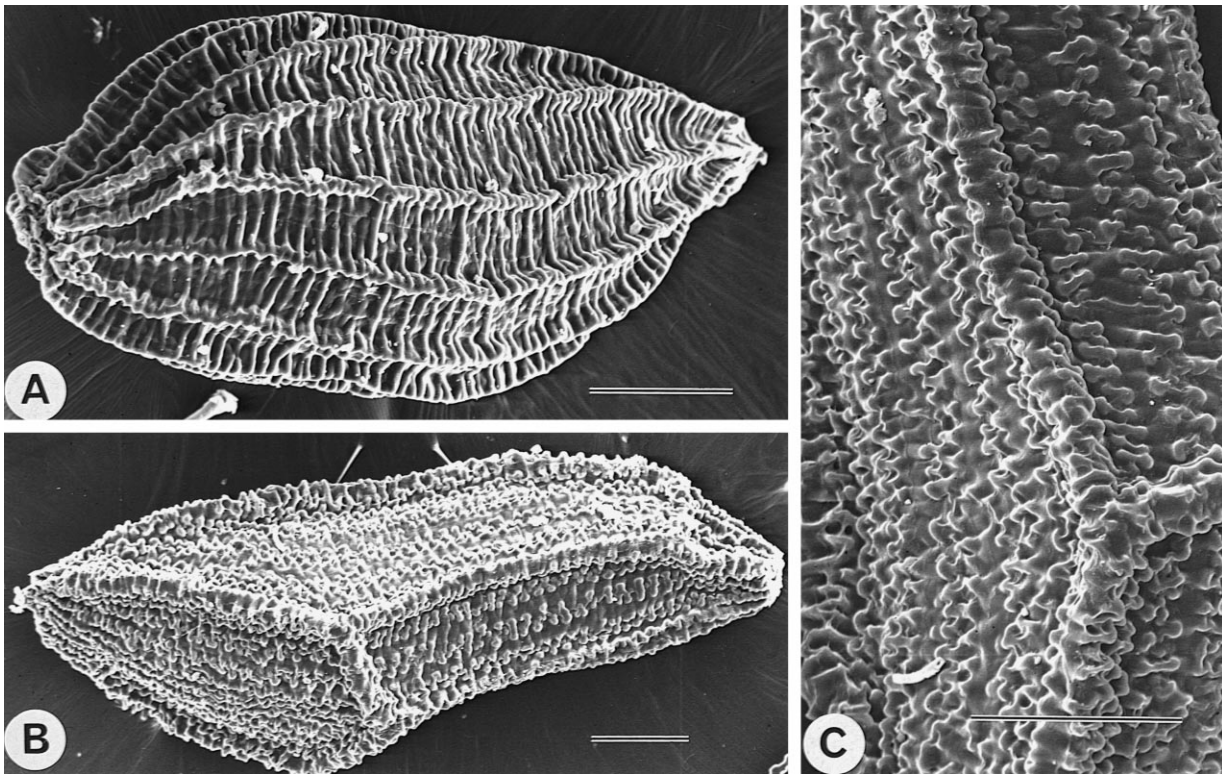


**Fig. 7** Scanning electron micrographs of seeds. *A*, *Xyris longiscapa*. *B*, *C*, *Xyris trachyphylla*. Bars = 100 μm.

perturate or porate. Pollen is also inaperturate in *Hanguana* and a few genera of Bromeliaceae and spiraperturate in Eriocaulaceae. Since spiraperturate and inaperturate pollen often occur in closely related taxa, this supports a close relationship between *Abolboda* and its allies and Eriocaulaceae, also indicated by shared stylar appendages. The presence of an apertural operculum in *Xyris* pollen examined here (fig. 1*B*) is consistent with some other commelinoid taxa (Simpson 1987; Linder and Kellogg 1995), and this character merits further attention.

*Anther wall.* Our record of the reduced type of anther wall formation in *Xyris* differs from that of Weinzieher (1914), reported by Dahlgren and Clifford (1982), who described *Xyris* as having the "monocot type" of anther wall formation and related the reduced type (with no middle wall layers) only to aquatic monocot families. In the monocot type, the outer secondary parietal layer develops directly into the endothecium, and the inner one divides periclinally to form the tapetum and a single middle layer, with the reverse orientation in the "dicot type" (Davis 1966). In the "basic type," both secondary parietal layers divide periclinally. Most monocotyledons have either the monocot type or the reduced type. However, the basic type is recorded in Commelinaceae (Grootjen and Bouman 1981), Rapateaceae (Venturelli and Bouman 1988), Mayacaceae (Venturelli and Bouman 1986), and some Zingiberales, and the reduced type is recorded here in *Xyris*. Other Xyridaceae (*Achlyphila*, *Aratitiyopea*, and *Orectanthe*) are unknown for this character (table 1). M. Buzgo (personal communication) recorded both types in *Acorus*, and it seems possible that this character is systematically uniformative in monocotyledons, although it requires further review.

Govindapa (1956) reported endothecial thickenings absent in *Xyris pauciflora*, but they are present in species examined here, together with other Xyridaceae (Carlquist 1960) and many other Commelinanae (Dahlgren and Clifford 1982).

*Ovule shape.* Orthotropous ovules occur in several groups of Commelinanae, including *Eriocaulon* (Govindapa and Ramaswamy 1980), Commelinaceae (Grootjen and Bouman 1981), Mayacaceae (Venturelli and Bouman 1986), and *Hanguana* (Rudall et al. 1999), although in *Achlyphila*, *Abolboda*, and *Orectanthe* ovules are anatropous (Carlquist 1960). Endress (1990, 1995) suggested a correlation between orthotropous ovules and mucilage-mediated pollen tube transmission, as there is less constraint on ovules of these species to be curved and to direct the micropyle toward the placenta. Mucilage-filled ovaries occur in several groups of monocotyledons (Rudall et al. 1998), the mucilage usually being secreted by intraovarian trichomes. Mucilage-filled ovaries occur mainly in aquatic plants or plants of moist habitats (e.g., *Acorus*, Araceae, many Zingiberales, and *Hanguana*; Rudall et al. 1999), indicating that a constant water supply is necessary. However, although *Xyris* grows in wet habitats and has orthotropous ovules, the ovary locules are not densely mucilage filled.

*Nucellus.* The tenuinucellate condition occurs in *Xyris*, where the nucellus lacks parietal tissue derived from the archespore. This condition was also reported in *Xyris indica* (Weinzieher 1914), *X. pauciflora* (Govindapa 1956), and *Xyris*

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Xyris* | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 01 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 |
| *Abolboda* | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | ? |
| *Achlyphylla* | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | ? | ? | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | ? | ? | ? |
| *Orectanthe* | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | ? | ? | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | ? | ? | 1 | ? |
| Eriocaulaceae | 0 | 0 | 1 | 1 | 1 | 1 | 01 | 01 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | ? |
| Commelinaceae | 0 | 01 | 01 | 0 | 1 | 1 | 01 | 01 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | ? |
| Rapateaceae | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| *Mayaca* | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 |
| Restionaceae | 01 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 01 | 1 | 0 | 1 | 1 |
| *Anarthria* | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | ? | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| *Prionium* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | ? | 1 | ? |
| Zingiberales | 0 | 01 | 0 | 0 | 0 | 1 | 01 | 01 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 01 | 0 | 1 | 1 | 1 |
| *Hanguana* | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | ? | 1 | 1 | 0 |
| Haemodoraceae | 01 | 0 | 0 | 0 | 0 | 1 | 01 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 01 | 1 | 0 | 1 | 0 | 0 | 1 | 0 |
| Bromeliaceae | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 01 | 0 | 0 | 01 | 1 | 0 | 0 | 0 | ? | ? | ? |

**Fig. 8** Preliminary data matrix for four genera of Xyridaceae and a selection of commelinoid taxa. Data taken from Carlquist (1960); Tomlinson (1969); Monteiro-Scanavacca and Mazzoni (1978); Ramaswamy and Arekal (1981); Rudall and Linder (1988); Linder and Rudall (1993); Kellogg and Linder (1995); Munro and Linder (1997); Rudall et al. (1999); P. J. Rudall, personal observations; and other sources cited in the text. *Column 1*, Leaves bifacial = 0; unifacial, ensiform = 1. *Column 2*, Multiseriate adaxial leaf hypodermis absent = 0; present = 1. *Column 3*, Silica bodies present = 0; absent = 1. *Column 4*, Raphide crystals present = 0; absent = 1. *Column 5*, Axillary glandular or "slime-secreting" hairs absent = 0; present = 1. *Column 6*, Perianth with inner tepals bracteal (0) petaloid (1). *Column 7*, Number of functional stamens: 6 = 0, 3 = 1. *Column 8*, Staminodes absent = 0; present = 1. *Column 9*, Tapetum secretory = 0; plasmodial = 1. *Column 10*, Microsporogenesis successive = 0; simultaneous = 1. *Column 11*, Pollen exine not spinulate = 0; spinulate = 1. *Column 12*, Pollen grains monosulcate = 0; inaperturate, spiraperturate = 1. *Column 13*, Gynoecial appendages absent = 0; present = 1. *Column 14*, Ovary trilocular with axile placentation = 0; unilocular with parietal or central placentation = 1. *Column 15*, Ovary superior = 0; inferior = 1. *Column 16*, Septal nectaries absent = 0; present = 1. *Column 17*, Ovary locule not mucilage filled = 0; mucilage filled = 1. *Column 18*, Ovules anatropous = 0; orthotropous = 1. *Column 19*, Ovules crassinucellate = 0; tenuinucellate = 1. *Column 20*, Micropyle formed by both integuments = 0; inner integument = 1. *Column 21*, Tanniniferous layer absent from seed coat = 0; present = 1. *Column 22*, Seed coat cuticle absent = 0; present between nucellus and inner integument = 1.

*schoenoides* (Ramaswamy and Raju 1982). In contrast, in *Abolboda*, ovules are crassinucellate (Tiemann 1985). The crassinucellate condition (the plesiomorphic state) predominates in monocotyledons, including most commelinoids: Arecaceae, Bromeliaceae, Dasypogonaceae, Haemodoraceae, Philydraceae, Pontederiaceae, Rapateaceae, all Zingiberales, and some Poales (Cyperaceae, Flagellariaceae, Juncaceae and Typhaceae). The tenuinucellate condition is sparsely but widely distributed and occurs in Eriocaulaceae, Mayacaceae, and some Poales (Centrolepidaceae, Ecdeiocoleaceae, most Restionaceae, and some Poaceae, especially festucoid grasses; Rudall 1997), and is therefore one of the main morphological characters linking Eriocaulaceae and *Xyris* (but not *Abolboda*) with Poales.

*Embryo sac development.* Both *Polygonum* and *Allium* types of embryo sac development are recorded in *Xyris*: the *Polygonum* type in *Xyris* spp. (this article) and *X. indica* (Weinzieher 1914), the *Allium* type in *X. pauciflora* (Govindapa 1956) and *X. schoenoides* (Ramaswamy and Raju 1982). The *Allium* type has also been reported in Commelinaceae and *Flagellaria* (Subramanyam and Narayana 1972); otherwise, most commelinoid taxa have the *Polygonum* type, including *Abolboda* (Tiemann 1985), *Eriocaulon* (Govindapa and Ramaswamy 1980), Rapateaceae (Tiemann 1985; Venturelli and Bouman 1988), Commelinaceae (Grootjen and Bouman 1981) and *Mayaca* (Venturelli and Bouman 1986). Other Xyridaceae (*Achlyphila*, *Orectanthe*, and *Aratitiyopea*) are unknown in this respect (table 1).

*Endosperm.* Endosperm development has been recorded as nuclear in *X. pauciflora* (Govindapa 1956) and helobial in *Abolboda* (Tiemann 1985). Nuclear endosperm development is the most common type in Commelinanae, including *Eriocaulon* (Govindapa and Ramaswamy 1980), Rapateaceae (Tiemann 1985; Venturelli and Bouman 1988), Commelinaceae (Grootjen and Bouman 1981), and *Mayaca* (Venturelli and Bouman 1986), although Steinecke and Hamann (1989) recorded the helobial type in Haemodoraceae. *Achlyphila*, *Orectanthe*, and *Aratitiyopea* are unknown in this respect (table 1).

*Seed coat.* Several seed coat characters may well be taxonomically significant but require further data. The presence of a tanniniferous layer in the seed coat (usually the inner layer of the inner integument) is apparently almost ubiquitous in Commelinanae, including *Abolboda* and *Orectanthe* (Carlquist 1960), but absent from *Xyris* species examined here. A conspicuous cuticle is present between the nucellus and inner integument in the seed coat in *Xyris* (fig. 6), Rapateaceae (Venturelli and Bouman 1988), and *Mayaca* (Venturelli and Bouman 1986), but this aspect is poorly known for other Xyridaceae/Abolbodaceae (fig. 8). A micropylar seed operculum is

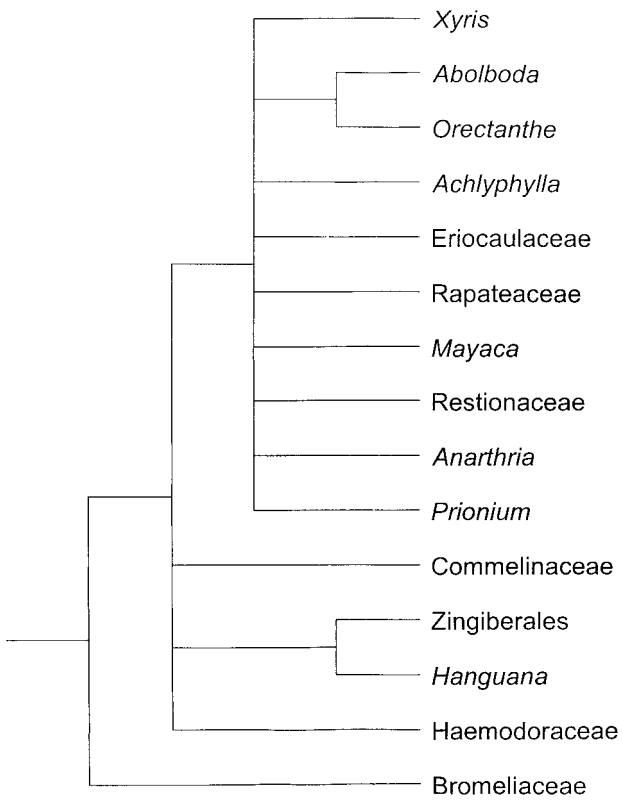


**Fig. 9** Strict consensus tree illustrating lack of resolution in relationships among selected commelinoid taxa (see "Discussion").

recorded here in Xyris, but this conflicts with Carlquist's (1960) interpretation of the seed operculum in *Achlyphila*, *Abolboda*, and *Orectanthe* as chalazal, since a micropylar and chalazal seed operculum are doubtfully homologous. A micropylar seed operculum is recorded in several Commelinanae (Werker 1997), such as *Eriocaulon* (Govindapa and Ramaswamy 1980), Commelinaceae (Grootjen and Bouman 1981), Rapateaceae (Tiemann 1985; Venturelli and Bouman 1988), *Typha* (Werker 1997), and some Zingiberales (Grootjen 1983; Grootjen and Bouman 1988; Graven et al. 1996).

### *Systematic Discussion*

Results of a branch and bound analysis based on the data in figure 8 found 15 trees of 60 steps, with a consistency index of 0.66 and a retention index of 0.63. The strict consensus tree (fig. 9) shows a monophyletic group including *Xyris*, *Achlyphila*, *Abolboda* + *Orectanthe*, Eriocaulaceae, Rapateaceae, Mayacaceae, and other Poales.

The relationships between *Xyris*, *Achlyphila*, *Abolboda* and its allies (*Orectanthe* and probably *Aratitiyopea*), Eriocaulaceae, Rapateaceae, Mayacaceae, and Poales are still unresolved, pending more comprehensive morphological and molecular analyses of the commelinoid clade. Although *Abolboda* and *Orectanthe* are a sister pair, the results of this preliminary morphological analysis (fig. 9) are inconclusive with respect to the monophyly of Xyridaceae or their relationships with other Poales. As this investigation has demonstrated, there is an unusual degree of variation within Xyridaceae for such characters as tapetum type and nucellus type (table 1), indicating that two separate families may yet be justified: Xyridaceae (*Xyris*) and Abolbodaceae (*Abolboda*, *Orectanthe*, and *Aratitiyopea*), although this requires further testing. The relationships of *Achlyphila* are currently uncertain.

Based on both morphological (Linder and Kellogg 1995) and molecular (Chase et al., in press; Givnish et al., in press) evidence, a close relationship seems likely at least between *Xyris*, Eriocaulaceae, *Mayaca*, and Poales, which all share tenuinucellate ovules. However, *Abolboda* and its allies may be more distantly related; a relationship between them and Rapateaceae requires further study. All Xyridaceae share several characters with Eriocaulaceae, Rapateaceae, and Mayacaceae: absence of silica bodies (also absent in some Commelinaceae and some Poales, e.g., *Anarthria*), absence of raphide crystals (also absent in many Poales), a perianth differentiated into petals and sepals (also in Commelinaceae and other commelinoids such as Bromeliaceae, Haemodoraceae, Zingiberales, but not Poales), only three functional stamens (also in some Commelinaceae, Haemodoraceae and Zingiberales, but not Poales), and absence of septal nectaries (also absent in Commelinaceae and Poales). Absence of cell inclusions may be regarded as a poor basis for indicating relationship; presumably the "real" character states are the underlying cell chemistry. However, the presence of silica bodies is a significant synapomorphy for the commelinoid clade (e.g., see Rudall et al. 1999), and the presence of raphide crystals is a monocot character, although they are absent from certain groups, notably some Liliales, some Poales, and all Alismatidae (Prychid and Rudall, in press). Nectaries are entirely lacking in the wind-pollinated Poales and also in Eriocaulaceae, Rapateaceae, Mayacaceae, and Xyridaceae, although the gynoecial appendages of *Abolboda* and its allies (Xyridaceae) and Eriocaulaceae (Stützel 1990) may represent nectaries derived from wet stigmas (T. Stützel, personal communication), which would represent another nectary type in monocotyledons.

*Abolboda* shares characters with Commelinaceae (plasmodial tapetum, also present in Zingiberales, *Hanguana,* Typhaceae, and Philydrales; Furness and Rudall 1998) and with Zingiberales (inaperturate pollen; present in *Abolboda*, *Orectanthe*, *Aratitiyopea*, and *Achlyphila*, and also in *Hanguana*; Furness and Rudall 1999). However, since inaperturate and spiraperturate pollen types often occur in closely related taxa (Furness and Rudall 1999), this may indicate a relationship with Eriocaulaceae, which have spiraperturate pollen.

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