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Source: *International Journal of Plant Sciences*, Vol. 173, No. 7 (September 2012), pp. 767-779

Published by: [The University of Chicago Press](#)

Stable URL: <http://www.jstor.org/stable/10.1086/666664>

Accessed: 17/09/2013 10:39

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FLORAL ANATOMY OF XYRIDS (POALES): CONTRIBUTIONS TO THEIR REPRODUCTIVE BIOLOGY, TAXONOMY, AND PHYLOGENY

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Xyridaceae, Eriocaulaceae, and Mayacaceae form the xyrid clade, which is weakly supported in Poales. The floral anatomy of xyrid species was studied, to contribute to the understanding of the relationships within the group. Both Eriocaulaceae and Xyridaceae have petals with elongated epidermal cells with straight walls, epipetalous stamens, staminodes, anthers with longitudinal dehiscence, an endothecium with band-like thickenings, and a style vascularized by the dorsal carpellary bundles; these characteristics thus corroborate the close relationship of these groups indicated by phylogenetic analyses. Mayacaceae is distinguished by the presence of papillose epidermal cells in the petals, a reduced inner whorl of stamens, pericidal anthers, an endothecium lacking thickenings, a style and stigma vascularized by the dorsal and ventral carpellary bundles, and the presence of an obturator in the ovary wall. A reduction in the inner whorl of fertile stamens also occurs in Juncaceae and Cyperaceae, linking Mayacaceae to the cyperids. The stylar appendages of *Orectanthe* (Xyridaceae) have been shown to be nectariferous and anatomically similar to those of *Abolboda*, differentiating these two genera from *Xyris* (Xyridoideae) and confirming their placement in Abolbodoideae. Stylar appendages also occur in Eriocaulaceae, with the same function, position, and vascularization, and are therefore homologous structures, reinforcing the phylogenetic proximity between Eriocaulaceae and Xyridaceae.

Keywords: Eriocaulaceae, flower, Mayacaceae, Poales, Xyridaceae, xyrids.

Introduction

The xyrids are a clade of Poales that comprises Xyridaceae, Eriocaulaceae, and Mayacaceae (Linder and Rudall 2005; Givnish et al. 2010). However, the most recent phylogenetic analysis of the Poales (Givnish et al. 2010), which was performed on the basis of both morphological and molecular data, has demonstrated that this is the most weakly supported clade within the order. These three families, together with Rapateaceae and Commelinaceae, had been grouped into the Commelinales (Dahlgren and Clifford 1982; Dahlgren et al. 1985) because of shared features such as a nuclear endosperm and showy flowers with a differentiated perianth, which are characteristics that are considered plesiomorphic for the commelinids.

Xyridaceae and Eriocaulaceae are identified as sister groups in most of the phylogenetic analyses of Poales (Givnish et al. 1999, 2005, 2006; Chase et al. 2000, 2006; Bremer 2002; Christin et al. 2008). Mayacaceae is clustered as a sister group to Eriocaulaceae (Givnish et al. 2010); the cyperid clade, which includes Cyperaceae, Juncaceae, and Thurniaceae (Chase et al. 2000; Christin et al. 2008); or the clade formed by the cyperids plus Eriocaulaceae-Xyridaceae (Givnish et al. 2005, 2006; Chase et al. 2006). According to Givnish et al. (2010), there are a few morphological characteristics that link

Mayacaceae to Eriocaulaceae and Xyridaceae, and there is relatively little evidence that these three families will continue to form a clade when new data are added to future phylogenetic analyses.

Xyridaceae includes five genera and ~300 herbaceous species (Kral 1998). *Xyris* is the largest genus of this family and comprises ~270 species found across a pantropical distribution, mainly in Central and South America (Kral 1998). *Abolboda* includes ~20 species, whereas *Aratitiopea*, *Achlyphila*, and *Orectanthe* are represented by only one or two species, with distribution restricted to the tropical regions of South America (Kral 1998). Studies on the floral anatomy of Xyridaceae have been performed with a taxonomic focus only for *Xyris* (Sajo et al. 1997; Rudall and Sajo 1999). The reproductive biology of *Abolboda* species has been studied by Oriani and Scatena (2011), who first demonstrated the production of nectar by stylar appendages in Xyridaceae and anatomically characterized these nectariferous structures. Within the Xyridaceae, stylar appendages also occur in *Aratitiopea* and *Orectanthe* (Kral 1992, 1998) and constitute one of the characteristics that support the circumscription of the subfamily Abolbodoideae (Stevens 2011).

Eriocaulaceae comprises 10 genera and ~1400 herbaceous species with a pantropical distribution (Stützel 1998; Giulietti et al. 2012). Species of this family are found in the tropical and subtropical regions around the world, with diversity concentrated in South America, especially Brazil (Giulietti and Hensold 1990; Stützel 1998). Floral anatomy studies with a taxonomic and evolutionary focus have been conducted on different species of Eriocaulaceae (Rosa and Scatena 2003, 2007).

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Manuscript received December 2011; revised manuscript received April 2012.

According to Rosa and Scatena (2007), most representatives of the family have declinuous and isostemonous flowers that are probably derived from a hermaphroditic ancestor with diplostemonous flowers. Rosa and Scatena (2003, 2007) also reported the occurrence of nectariferous structures in the gynoeceum of species of Eriocaulaceae, an important feature for the phylogeny of Poales, since it may reinforce the phylogenetic proximity between this family and Xyridaceae.

Mayacaceae comprises only four to 10 species in the single genus *Mayaca*, and all are herbaceous, aquatic, or amphibious plants (Stevenson 1998). With the exception of the African species *Mayaca baumii*, *Mayaca* is limited to Neotropical regions, with a higher concentration of species found in South America (Stevenson 1998). A study conducted on the floral anatomy of Neotropical species of Mayacaceae identified characteristics that distinguish the species as well as characteristics that support the positioning of this family within Poales (Carvalho et al. 2009). According to Carvalho et al. (2009), the number of stamens and microsporangia and the type of ovule and placentation link Mayacaceae to other families of the order.

Given the numerous uncertainties regarding the interfamily relationships within the Poales—particularly the relationships among the Xyridaceae, Eriocaulaceae, and Mayacaceae—this study aims to investigate the floral anatomy of xyrid species in order to identify characteristics on which to base the relative positioning of these three families within the order. For this purpose, we used data already published about representatives of Xyridaceae, Eriocaulaceae, and Mayacaceae (Sajo et al. 1997; Rudall and Sajo 1999; Rosa and Scatena 2003, 2007; Carvalho et al. 2009; Oriani and Scatena 2011), as well as original data obtained in this study.

Material and Methods

The following Brazilian species were studied: *Abolboda macrostachya* Spruce ex Malme (Lombardi et al. 7538, 7539), *Abolboda poarchon* Seub. (Coan & Oriani 61, 72), *Abolboda pulchella* Humb. & Bonpl. (Coan & Oriani 60, 71), *Mayaca fluviatilis* Aublet (Scatena et al. 312, 316; Coan & Oriani 51, 56), *Mayaca sellowiana* Kunth (Scatena et al. 307; Coan & Oriani 53), *Orectanthe sceptrum* (F. Oliver) Maguire (Lombardi et al. 7658), *Xyris pilosa* Kunth (Scatena et al. 308, 310), and *Xyris savanensis* Miq. (Coan & Oriani 84). Most of the specimens were collected from the Serra do Cipó National Park (Minas Gerais State) and Itirapina (São Paulo State), which are both areas of cerrado with grassland vegetation. *Abolboda macrostachya* was collected from the Amazonian campinaranas of the Viruá National Park (Roraima State), and *Orectanthe sceptrum* was collected from the tepuis of the Monte Roraima National Park (Roraima State). Part of the material collected was herborized, identified, and deposited in the Herbarium Rioclaurensis at Universidade Estadual Paulista, and part was fixed in FAA 50 (37% formaldehyde, glacial acetic acid, 50% ethanol, at 1:1:18 v/v; Johansen 1940) for morphological and anatomical studies. The identification of the species was accomplished by using the keys of Smith and Downs (1968), Kral (1992), and Wanderley and Giulietti (2002).

A minimum of three individuals of each species was examined. Isolated flowers were subjected to the *n*-butyl alcohol dehydration series, infiltration, and inclusion in (2-hydroxyethyl)-methacrylate (Leica Histo-resin embedding kit; Feder and O'Brien 1968). The embedded material was sectioned using a Leica Reichert-Jung 2040 rotatory microtome (6–8- μ m thick sections), stained with periodic acid-Schiff's reagent (PAS) and toluidine blue (Feder and O'Brien 1968), and mounted on permanent slides with Entellan (Merck). Photomicrographs were obtained with an IM50 (Leica Image Manager V.5.0) digital imaging system, using an image-capturing device (Leica, DFC 290) coupled to a microscope (Leica, DM LB). Isolated flowers were also immersed in a 1:10,000 solution of neutral red (Kearns and Inouye 1993), to stain secretory structures.

For analysis using SEM (Zeiss, DSM 950), flowers fixed in FAA 50 and dehydrated in 70% ethanol were immersed in FDA (formaldehyde-dimethylacetate; Gerstberger and Leins 1978), subjected to critical-point drying (Balzers, CPD 030), and metallized with gold (Bal-Tec, SCD 050). The results were recorded using a DIPS (Digital Image Processing Software 2.2; Leipzig) digital imaging system.

Results

Mayaca

Mayaca fluviatilis and *Mayaca sellowiana* have monoclinous, dichlamydeous, heterochlamydeous, and actinomorphic flowers (fig. 1A). The flowers are trimerous, dialysepalous, dialypetalous, and haplostemonous (fig. 1A). The stamens have free filaments with basifixed, poricidal anthers (fig. 1A). The ovary is superior and the style is terminal, elongated, and simple (fig. 1A).

The sepals and petals have a single-layered epidermis with thin-walled cells, a parenchymatous mesophyll, and collateral vascular bundles (fig. 2C). The sepals are amphistomatic, with paracytic stomata (fig. 2B). The epidermal cells in the apical region of the petals contain phenolic compounds and are papillose from the frontal view on both petal surfaces (fig. 2A), while the epidermal cells of the sepals are elongated and have straight walls (fig. 2B).

The stamens alternate with petals (fig. 1A) and are opposite to the dorsal carpellary bundles (fig. 2C, 2E, 2F), corresponding to the outer whorl. The walls of the mature anthers are composed of an epidermis with U-shaped thickened cells and an endothecium lacking thickenings (fig. 3D). In a longitudinal section, the thickening of the epidermal cells is discontinuous, thus forming semirings. The anther in *M. fluviatilis* is bithecate bisporangiate (fig. 3B), with an inconspicuous pore opening that points to the stigma (fig. 3E). Pollen grains germinate inside the anthers, and their pollen tubes (arrows) extend to the stigma (fig. 3F). The anthers in *M. sellowiana* are tetrasporangiate (fig. 3C), with a well-developed pore that is formed by the extension of the epidermis and is located below the stigma. The filaments are composed of an epidermis, a subepidermal parenchyma, and a vascular bundle (fig. 2C, 2E, 2F).

The style is hollow (fig. 3A; arrow in fig. 3E) and internally lined with pollen tube transmitting tissue, which protrudes into the locule at the apex of the ovary, characterizing the obturator (fig. 2E; arrowheads in fig. 3G–3I). This tissue strongly

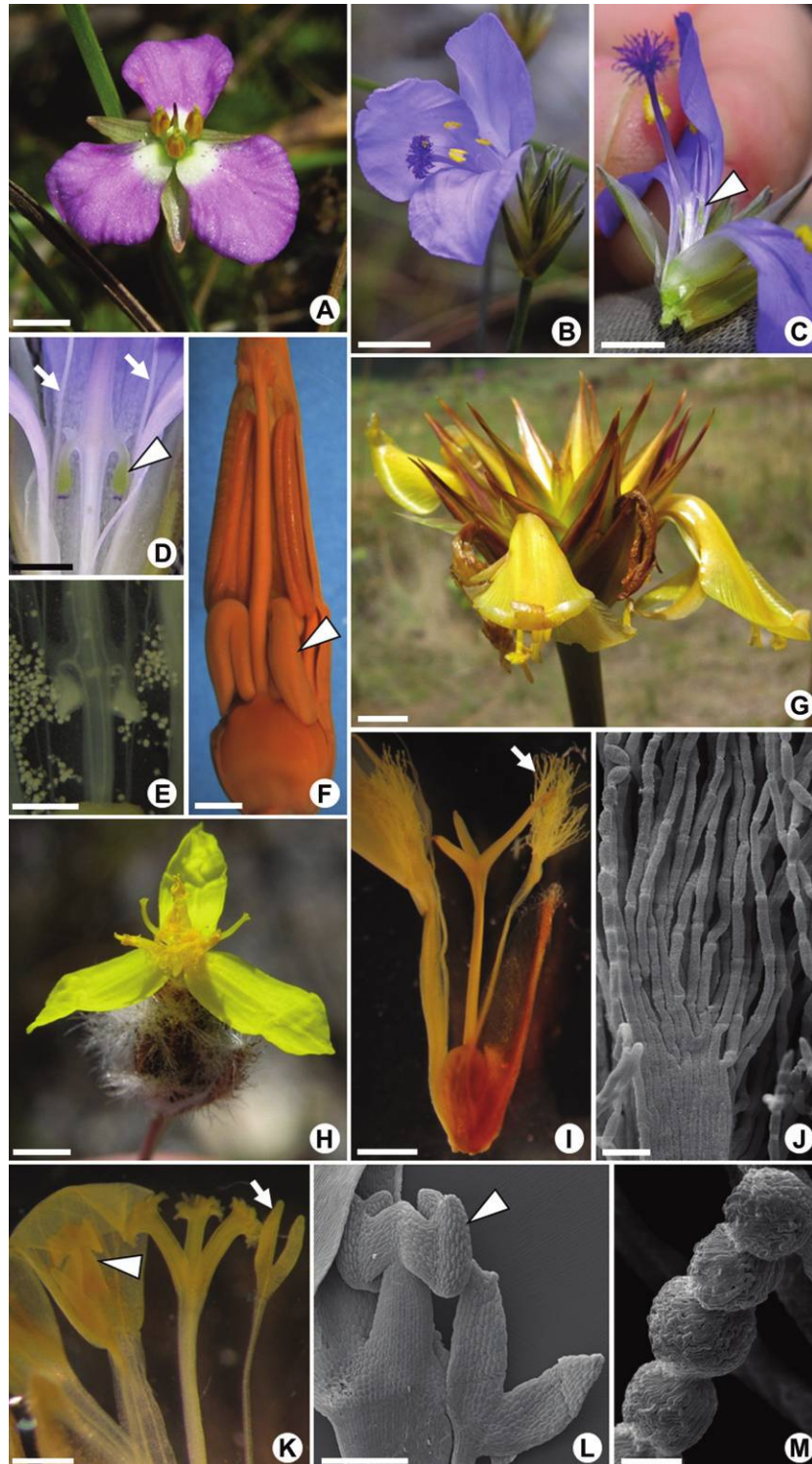


Fig. 1 Morphological characteristics of the flowers of xyrids. *A*, *Mayaca sellowiana*. *B–D*, *Abolboda poarchon*. *B*, Inflorescence. *C*, Detail of the dissected flower; the arrowhead indicates the stylar appendages. *D*, Detail of the stylar appendages (arrowhead) and staminodes (arrows). *E*, *Abolboda pulchella*, detail of the stylar appendages. *F*, *Orectanthe sceptrum*. *F*, Detail of the dissected flower; the arrowhead indicates the stylar appendages. *G*, Inflorescence. *H–J*, *Xyris pilosa*. *H*, Inflorescence. *I*, Detail of the flower; the arrow indicates the staminode. *J*, SEM micrograph of the apical region of the staminode. *K*, *L*, *Xyris savanensis*. *K*, Detail of the flower showing the epipetalous stamen (arrowhead), tripartite stigma, and staminode (arrow); *L*, SEM micrograph showing the epipetalous stamen (arrowhead) and the staminode. *M*, *Xyris pilosa*, SEM micrograph showing a detail of the apical cells of the staminode's trichome. Scale bars: *A*, *F*, 2.5 mm; *B*, 8 mm; *C*, 4 mm; *D*, *E*, 1.5 mm; *G*, 1 cm; *H*, 1.7 mm; *I*, 1 mm; *J*, 25 μ m; *K*, 520 μ m; *L*, 300 μ m; *M*, 5 μ m.

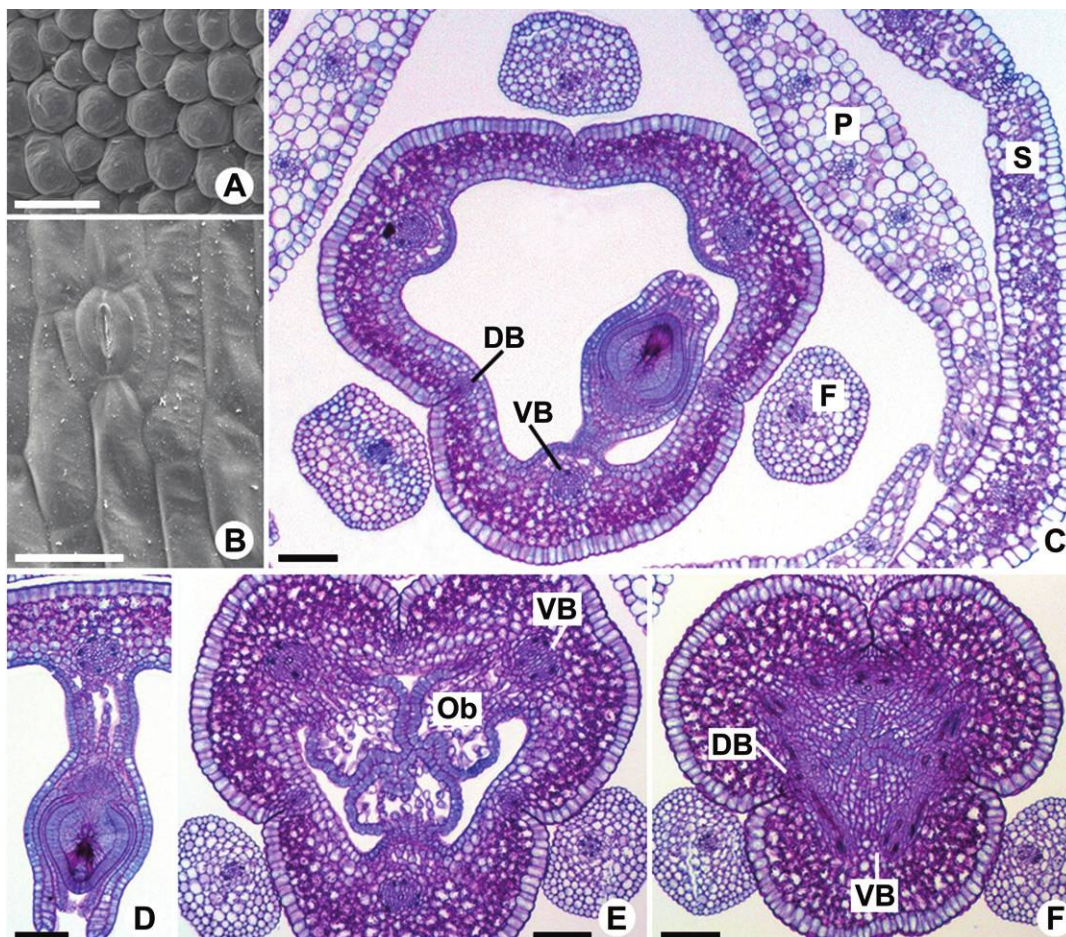


Fig. 2 Anatomical characteristics of the flowers of *Mayaca*. *A, B*, *Mayaca sellowiana*. *A*, SEM micrograph of the adaxial epidermis of the petal. *B*, SEM micrograph of the abaxial epidermis of the sepal, showing paracytic stomata. *C*, *Mayaca fluviatilis*, cross section of the median region of the ovary. *D*, *Mayaca sellowiana*, detail of the orthotropous, bitegmic ovule directly attached to the ovary wall. *E, F*, *Mayaca fluviatilis*. *E*, Cross section of the apical region of the ovary, showing the obturator. *F*, Cross section of the transitional region between the ovary and the style. Scale bars: *A, B*, 40 μm ; *C–F*, 50 μm . DB = dorsal carpillary bundle, F = filament, Ob = obturator, P = petal, S = sepal, VB = ventral carpillary bundle.

stained with neutral red, indicating its secretory activity (fig. 3G). Figure 3H shows details of the obturator in a longitudinal section, and figure 3I shows a scan of the inner ventral wall of the ovary in the apical region, with pollen tubes (arrow) passing through the obturator (arrowheads).

The ovary is tricarpeal and unilocular, with parietal placentation (fig. 2C). It features a single-layered epidermis and a parenchymatous mesophyll and is vascularized by the three dorsal carpillary bundles and three ventral carpillary bundles (fig. 2C). The dorsal bundles extend through the style to the stigma (figs. 2F, 3A). Branches that derive from the ventral bundles vascularize the ovules (fig. 2C) and the obturator (fig. 2E) and also ascend to the style (figs. 2F, 3A). The ovules are orthotropous and bitegmic (fig. 2D).

Abolboda and Orectanthe

Representatives of *Abolboda* and *Orectanthe* have monochlamydeous, dichlamydeous, heterochlamydeous, and zygomorphic flowers (fig. 1B, 1C, 1G). The flowers are dialysepalous

and gamopetalous (fig. 1B, 1C, 1G). The sepal whorl is trimerous in *Orectanthe* and dimerous in *Abolboda* because of the lack of the anterior (inner) sepal. The petal and stamen whorls are trimerous. The fertile stamens have basifixed anthers of longitudinal dehiscence (fig. 1B, 1F). *Abolboda poarchon* and *Abolboda macrostachya* have three staminodes that alternate with petals and are conspicuous and filiform (arrows in fig. 1C, 1D). In both genera, the ovary is superior and the style is terminal, elongated, and simple (fig. 1C, 1F). The style presents three appendages that are inserted in its median region in *Abolboda* (fig. 1C, arrowhead; fig. 1E) and in its basal region in *Orectanthe* (fig. 1E, arrowhead), facing the dorsal region of the carpels. In *Abolboda*, only two appendages are developed, and the third is reduced (fig. 1C–1E). The stigma is tripartite and fimbriate in *Abolboda* (fig. 1B, 1C) and trilobed in *Orectanthe* (fig. 1F, 1G).

The sepals have a single-layered epidermis and are amphistomatic (arrows in figs. 4A, 5A), with paracytic stomata. Tetracytic stomata also occur in *Orectanthe* (fig. 5C). The mesophyll is composed of supporting tissue on the adaxial

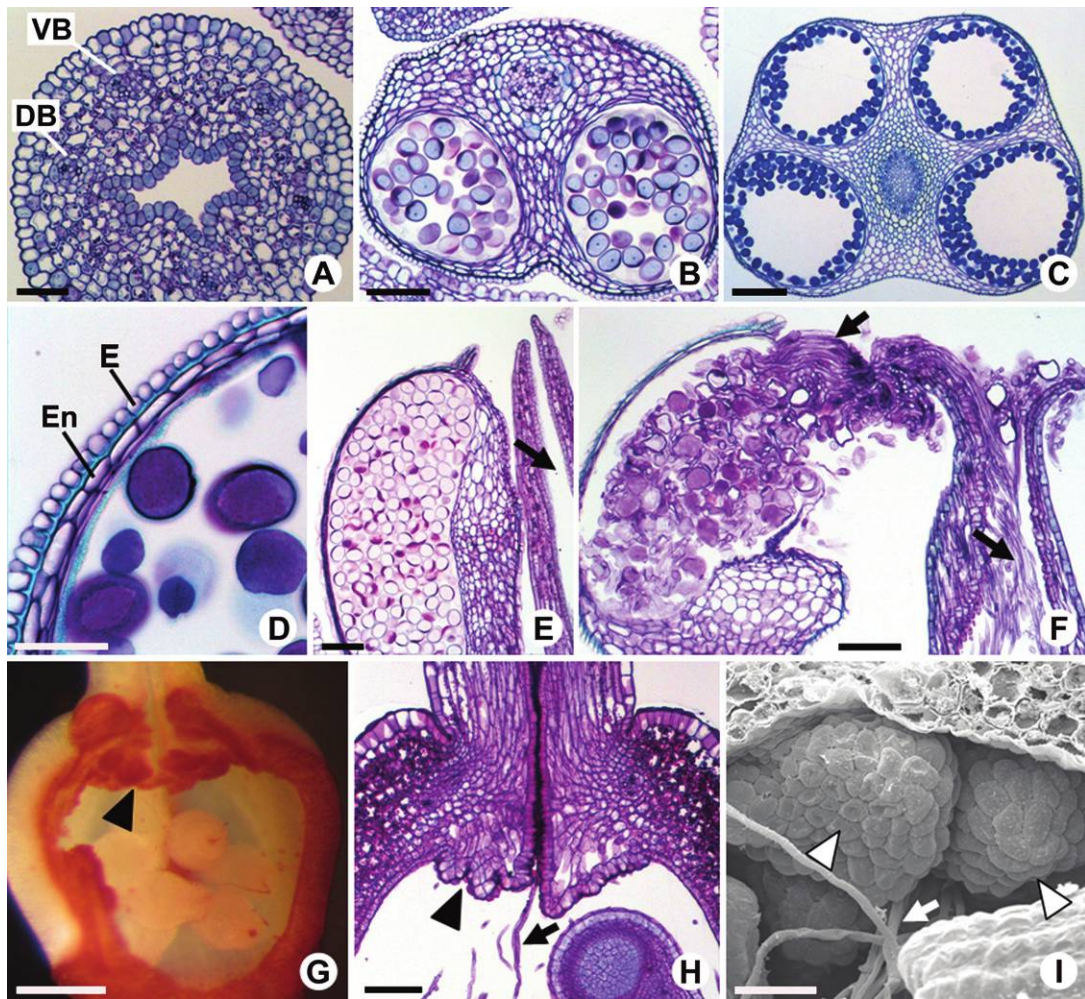


Fig. 3 Anatomical characteristics of the flowers of *Mayaca*. *A, B, Mayaca fluviatilis*. *A*, Cross section of the apical region of the style. *B*, Cross section showing a bisporangiate anther. *C, Mayaca sellowiana*, cross section showing a tetrasporangiate anther. *D–H, Mayaca fluviatilis*. *D*, Detail of the anther wall in cross section. *E*, Longitudinal section of the anther; the arrow indicates the hollow style. *F*, Longitudinal section of the anther and stigma, showing germinating pollen grains; the arrows indicate pollen tubes. *G*, Ovary stained with neutral red, in lateral view; the arrowhead indicates the obturator. *H*, Detail of the apex of the ovary in longitudinal section. *I, Mayaca sellowiana*, SEM micrograph of the apex of the ovary; the arrow indicates pollen tubes and the arrowheads indicate the obturator. Scale bars: *A–C, E, F, H*, 50 μm ; *D*, 20 μm ; *G*, 340 μm ; *I*, 40 μm . DB = dorsal carpellary bundle, E = epidermis, En = endothecium, VB = ventral carpellary bundle.

surface and parenchyma on the abaxial surface in *Abolboda* (fig. 4A); in *Orectanthe*, it is composed of parenchyma on the adaxial surface and spongy chlorenchyma on the abaxial surface (fig. 5A). The lateral sepals are keeled, and the keels are filled with parenchyma in *Abolboda* (fig. 4A) and chlorenchyma and vascular bundles in *Orectanthe* (fig. 5A). The petals have a single-layered epidermis with thin-walled cells and a parenchymatous mesophyll with collateral vascular bundles (figs. 4D, 5D). From the frontal view, the epidermal cells of the sepals and petals are elongated, with straight, tangential walls (figs. 4E, 5B), and they are covered by a cuticle with striated ornamentation (figs. 4F, 5B).

The stamens are epipetalous (figs. 1C, 4D), with tetrasporangiate anthers (fig. 5E). The wall of the mature anther is composed of an epidermis with thin-walled cells, an endothecium with band-like thickenings, and tapetum remnants (figs. 4C, 5F). The filaments consist of epidermis, subepidermal paren-

chyma, and a vascular bundle (fig. 4B, 4D). The staminodes of *A. poarchon* and *A. macrostachya* are vascularized (fig. 4D, arrows) and, on the basis of their position and vascularization, correspond to the outer whorl of stamens.

The style is hollow and vascularized by the dorsal carpellary bundles, which ascend to the stigmas branching out to vascularize the appendages (figs. 1E, 4B, 4D, 4H, 5I, 5L, 5M). The styler appendages have a single-layered epidermis with thin-walled, rounded cells and a subepidermal parenchyma (figs. 4B, 4H, 5H, 5K, 5L); they are vascularized by both xylem and phloem (figs. 4B, 5L), although only the phloem elements can be observed in their distal portion (figs. 4D, 5K). The styler appendages strongly stained with neutral red, indicating their secretory activity. In *Orectanthe*, the style has also secretory ducts that extend to the stigma (detail in fig. 5G).

The ovary is tricarpelar and unilocular, with intrusive parietal placentation; the septa are not fused at the central part of

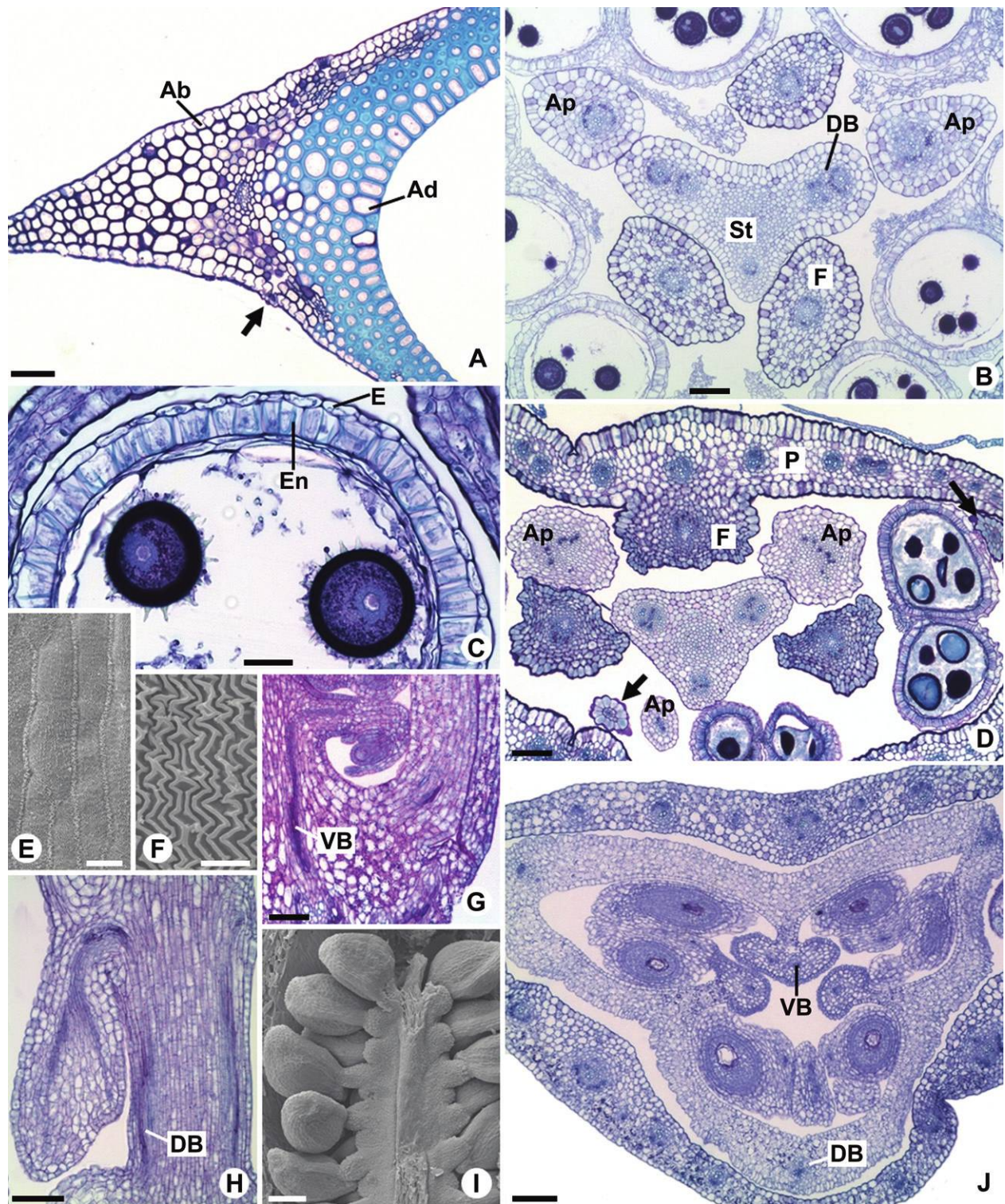


Fig. 4 Anatomical characteristics of the flowers of *Abolboda*. *A*, *Abolboda macrostachya*, cross section of the median region of the sepal; the arrow indicates the stomata. *B*, *Abolboda poarchon*, cross section of the flower showing the style and the proximal portion of the nectariferous appendages. *C*, *Abolboda pulchella*, detail of the anther wall in cross section. *D*, *Abolboda macrostachya*, cross section of the flower showing the style and the distal portion of the nectariferous appendages; the arrows indicate the staminodes. *E*, *F*, *Abolboda poarchon*, SEM micrograph of the adaxial epidermis of the petal and a detail of the ornamented cuticle, respectively. *G*, *H*, *Abolboda pulchella*. *G*, Longitudinal section of the ovary, showing detail of the anatropous ovule. *H*, Longitudinal section of the styler appendages. *I*, *Abolboda poarchon*, SEM micrograph of the interior of the ovary, showing the anatropous ovules with intrusive parietal placentation. *J*, *Abolboda pulchella*, cross section of the median region of the ovary. Scale bars: *A*, 80 μm ; *B*, 10 μm ; *C*, *E*, 30 μm ; *D*, 5 μm ; *F*–*I*, 100 μm ; *J*, 50 μm . Ab = abaxial epidermis, Ad = adaxial epidermis, Ap = nectariferous appendages of the style, DB = dorsal carpillary bundle, E = epidermis, En = endothecium, F = filament, P = petal, St = style, VB = ventral carpillary bundle.

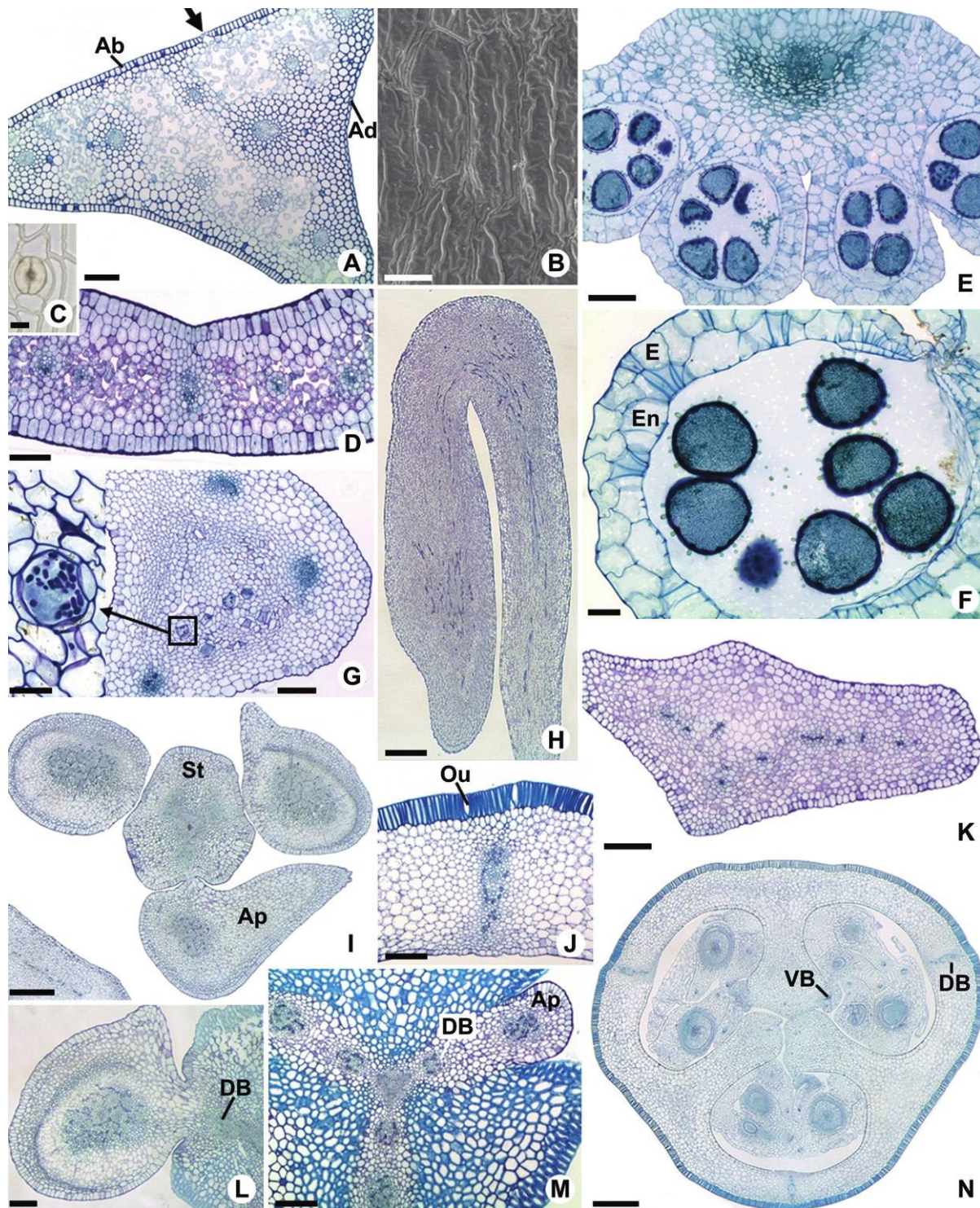


Fig. 5 Anatomical characteristics of the flowers of *Orectanthe sceptrum*. **A**, Cross section of the median region of the sepal; the arrow indicates the stomata. **B**, SEM micrograph of the adaxial epidermis of the petal. **C**, Detail of the abaxial epidermis of the sepal, showing the frontal view of a tetracytic stomata. **D**, Cross section of the median region of the petal. **E**, Cross section of the tetrasporangiate anther. **F**, Detail of the anther wall in cross section. **G**, Cross section of the style, with a detail of the secretory duct. **H**, Longitudinal section of the styler appendage. **I**, Cross section of the style at the proximal portion of the appendages. **J**, Detail of the ovary wall in cross section. **K**, Cross section of the distal portion of the styler appendage. **L**, Detail of the style branching into the appendage. **M**, Cross section of the style, showing the vascularization of the appendages by the dorsal carpellary bundles. **N**, Cross section of the median region of the ovary. Scale bars: **A**, **D**, **E**, **J**, **K**, 150 μm ; **B**, **C**, detail in **G**, 20 μm ; **F**, 50 μm ; **G**, 100 μm ; **H**, **I**, **N**, 500 μm ; **L**, **M**, 200 μm . Ab = abaxial epidermis, Ad = adaxial epidermis, Ap = styler appendages, DB = dorsal carpellary bundle, E = epidermis, En = endothecium, Ou = outer epidermis, St = style, VB = ventral carpellary bundle.

the ovary (figs. 4J, 5N). It has a single-layered outer epidermis, with thin-walled cells in *Abolboda* (fig. 4J) and thick-walled cells in *Orectanthe* (fig. 5J, 5N). The mesophyll is composed of parenchymatous cells and is vascularized by the dorsal and ventral carpellary bundles (figs. 4J, 5J, 5N). The ventral carpellary bundles vascularize the ovules (figs. 4G, 4J, 5N), which are anatropous and bitegmic (figs. 4G, 4I, 4J, 5N).

Xyris

The *Xyris* species have monoclinous, dichlamydeous, heterochlamydeous, and actinomorphic flowers (fig. 1H) that are trimerous, dialysepalous, and dialypetalous (fig. 1H, 1I). The fertile stamens are epipetalous, with basifixed anthers of longitudinal dehiscence (arrowheads in fig. 1K, 1L). Three developed staminodes alternate with the petals (arrows in fig. 1I, 1K). The ovary is superior (fig. 1I) and the style is terminal and tripartite (fig. 1I, 1K).

The anterior (inner) sepal is membranous, abscising as the flower opens, and the other two sepals are subopposite and keeled (fig. 1I). They have a single-layered epidermis with thin- or thick-walled cells (fig. 6A, 6B). Trichomes containing phenolic compounds may be present in the region of the keel (fig. 6B). The mesophyll is composed of parenchyma and a single vascular bundle (fig. 6A, 6B) and is limited to the area of the keel. The petals have a single-layered epidermis and a parenchymatous mesophyll with collateral vascular bundles (fig. 5G). From the frontal view, their epidermal cells, as well as those of the sepals, are elongated, with straight walls, and are covered by a cuticle with striated ornamentation (fig. 6C).

The anthers are tetrasporangiate (fig. 6E) and the mature anther wall is composed of a papillose epidermis and an endothecium with inconspicuous band-like thickenings (fig. 6D). The filaments consist of an epidermis, a subepidermal parenchyma, and a vascular bundle (fig. 6E, 6G). The staminodes are vascularized and composed of parenchymatous cells (fig. 6F). In *Xyris savanensis*, the staminodes are bifid and glabrous (figs. 1K, 1L, 6G), whereas in *Xyris pilosa* they are bifid and have uniseriate, multicellular trichomes in the apical region (figs. 1I, 1J, 6E, 6F). These moniliform trichomes have elongated basal cells (fig. 1J) and rounded apical cells (fig. 1M), both of which are covered by a cuticle with striated ornamentation. An ornamented cuticle also occurs in the epidermal cells of the staminodes of *X. savanensis*.

The ovary is tricarpelar and unilocular, with basal placentation, and has a single-layered epidermis and a parenchymatous mesophyll (fig. 6G, 6H). It is vascularized by the three dorsal carpellary bundles, which extend to the stigmas (fig. 6E). The ventral carpellary bundles branch out at the base of the ovary to vascularize the ovules (fig. 6H). The ovules are orthotropous and bitegmic, with an elongated funicle (fig. 6H).

Discussion

A comparative table (table 1) containing the data obtained in this study and the data obtained from the literature is provided to assist with the discussion. The results of this study provide anatomical evidence that the stylar appendages of *Orectanthe* correspond to nectaries. These appendages are vascularized by xylem and phloem and have an anatomical

structure similar to that of the stylar appendages of *Abolboda*, for which nectar production has been proven (Oriani and Scatena 2011).

The nectaries of angiosperms can be divided into two groups: nonstructural and structural nectaries (Zimmermann 1932). The nonstructural nectaries do not have specially differentiated nectariferous tissue, and the nectar is exuded through stomata. The structural nectaries can mostly be recognized macroscopically and are anatomically differentiated. They generally consist of vascular bundles that supply water and nutrients, a specialized parenchyma that produces and stores the nectar solutes, and an epidermis with or without stomata where the nectar is released to the exterior (Fahn 1979; Nepi 2007), as observed in *Abolboda* and *Orectanthe*. In these two genera the nectar is probably secreted by the thin-walled epidermal cells of the stylar appendages, since these structures do not have stomata.

Stylar appendages with a nectariferous function also occur in representatives of Eriocaulaceae (Rosa and Scatena 2003, 2007). In Paepalanthoideae, which comprises most of the family's genera, the style branches out into three nonvascularized stigmatic portions located in the commissural region of the carpels, which alternate with three nectariferous portions (Rosa and Scatena 2007). These nectariferous portions are opposite to the dorsal region of the carpels and are vascularized by the dorsal carpellary bundles, thus possessing the same function, position, and type of vascularization as the stylar appendages of *Abolboda* and *Orectanthe*. The evidence that the nectariferous stylar appendages of Xyridaceae and Eriocaulaceae are homologous structures is one of the most significant findings of this study, and it supports the close relationship between these two families indicated in most of the phylogenetic analyses of Poales (Givnish et al. 1999, 2005, 2006; Chase et al. 2000, 2006; Bremer 2002; Christin et al. 2008). The homology of these structures is also reinforced by the results of a previous study of the gynoecium ontogeny of species of Eriocaulaceae and Xyridaceae (Stützel 1990), which demonstrated that the stylar appendages have a similar morphogenesis in both families.

While Paepalanthoideae (Eriocaulaceae) and Abolbodoideae (Xyridaceae) have nectariferous appendages on the style, the presence of septal nectaries has been reported for other Poales, for example, Bromeliaceae (Böhme 1988; Bernardello et al. 1991; Sajo et al. 2004) and a few derived Rapateaceae (Givnish et al. 1999, 2000). Nectariferous pistillodes occur in staminate flowers of all species of Eriocaulaceae (Rosa and Scatena 2007) and correspond to an apomorphy of the family.

Nectar production has a significant correlation with animal pollination in Poales (Givnish et al. 2010). According to Givnish et al. (2010), animal pollination is the ancestral condition of the order, with multiple independent origins of wind pollination. Experimental studies conducted on species of Eriocaulaceae (Ramos et al. 2005; Oriani et al. 2009) and Xyridaceae (Oriani and Scatena 2011) have demonstrated pollination by small insects, mainly bees, with nectar as the main floral reward. In the remaining animal-pollinated species of Poales that do not produce nectar, pollen is thought to be the main floral resource used by pollinators.

The flowers of Mayacaceae do not present nectariferous structures; however, characteristics such as their color and size

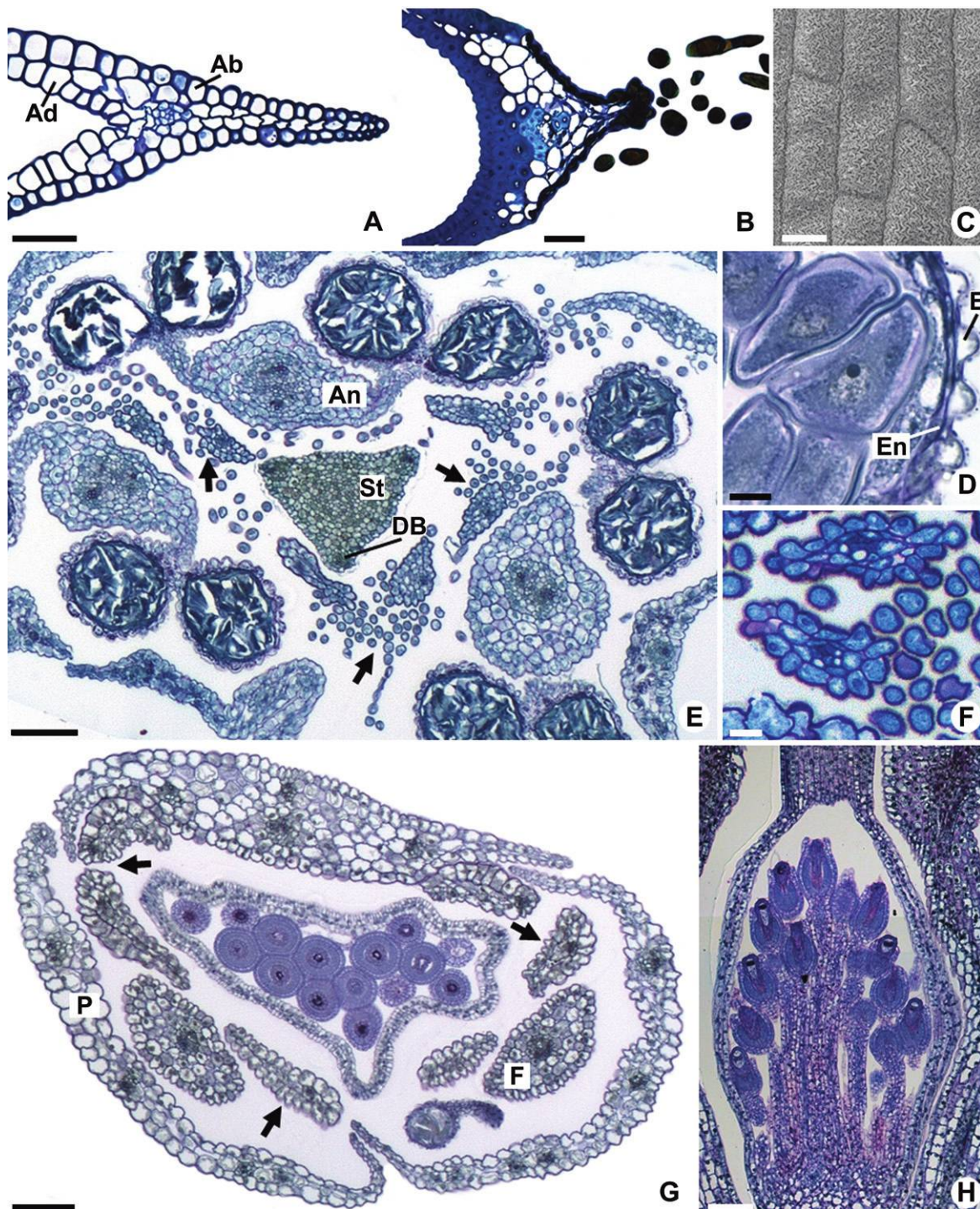


Fig. 6 Anatomical characteristics of the flowers of *Xyris*. *A*, *Xyris savanensis*, cross section of the median region of the sepal. *B*, *Xyris pilosa*, cross section of the median region of the sepal. *C*, *Xyris savanensis*, SEM micrograph of the adaxial epidermis of the petal. *D–F*, *Xyris pilosa*. *D*, Detail of the anther wall in cross section. *E*, Cross section of the flower showing the petals, anthers, staminodes (arrows), and style. *F*, Cross section of the staminode at the region where it branches out. *G, H*, *Xyris savanensis*. *G*, Cross section of the flower showing the petals, filaments, staminodes (arrows), and ovary. *H*, Longitudinal section of the ovary. Scale bars: *A, B, H*, 50 μm ; *C, D, F*, 10 μm ; *E, G*, 100 μm . *Ab* = abaxial epidermis, *Ad* = adaxial epidermis, *An* = anther, *DB* = dorsal carpellary bundle, *E* = epidermis, *En* = endothecium, *F* = filament, *P* = petal, *St* = style.

Table 1

Comparison between the Floral Characters of Mayacaceae, Xyridaceae, and Eriocaulaceae (Xyrids, Poales)

	Xyridaceae				Eriocaulaceae	
	Mayacaceae	Xyris	Abolboda	Orectanthe	Eriocauloideae	Paepalanthoideae
	Classification of the flower with regard to sex	Monoclinous	Monoclinous	Monoclinous	Monoclinous	Diclinous
Symmetry	Actinomorphic	Actinomorphic	Zygomorphic	Zygomorphic	Actinomorphic	Actinomorphic
Calyx	Dialysepalous	Dialysepalous	Dialysepalous	Dialysepalous	Dialysepalous	Gamo/dialysepalous
Keelid sepals	Absent	Present	Present	Present	Absent	Absent
Stomata on the sepals	Present (paracytic)	Absent	Present (paracytic)	Present (paracytic and tetracytic)	Absent	Absent
Corolla	Dialypetalous	Dialypetalous	Gamopetalous	Gamopetalous	Gamo/dialypetalous	Gamo/dialypetalous
Shape of the epidermal cells of the petals	Rounded/papillose	Elongated, straight walls	Elongated, straight walls	Elongated, straight walls	Elongated, straight walls	Elongated, straight walls
Glands in the petals	Absent	Absent	Absent	Absent	Present	Absent
Androecium	Isostemonous free stamens	Isostemonous epipetalous stamens	Isostemonous epipetalous stamens	Isostemonous epipetalous stamens	Diplostemonous, epipetalous stamens	Isostemonous free stamens
Reduced whorl of stamens	Internal	External	External	External	...	External, in staminate flowers
Staminodes	Absent	Present (3) conspicuous, moniliform	Present (3) or absent conspicuous, filiform	Absent	Present (3) in pistillate flowers, inconspicuous	Present (2-3) inconspicuous, scale-like
No. microsporangia	2 or 4	4	4	4	4	2 or 4
Anther dehiscence	Poricidal	Longitudinal	Longitudinal	Longitudinal	Longitudinal	Longitudinal
Thickening of the endothecium	Absent	Band-like	Band-like	Band-like	Band-like	Band-like
Pistillodes	Absent	Absent	Absent	Absent	Present (3) in staminate flowers	Present (2-3) in staminate flowers
Vascularization of the style	Dorsal and ventral carpillary bundles	Dorsal carpillary bundles	Dorsal carpillary bundles	Dorsal carpillary bundles	Dorsal carpillary bundles	Dorsal carpillary bundles
Stylar appendages	Absent	Absent	Present below the stigma	Present below the stigma	Absent	Present at the same height as the stigma
Vascularization of the appendages of the style	Dorsal carpillary bundles	Dorsal carpillary bundles	...	Dorsal carpillary bundles
Obturator	Present	Absent	Absent	Absent	Absent	Absent
No. locules in the ovary	Unilocular	Unilocular	Unilocular	Unilocular	Trilocular	Bi- or trilocular
No. ovules per locule	Multiovulate	Multiovulate	Multiovulate	Multiovulate	Uniovulate	Uniovulate
Type of placentation	Parietal	Basal/central/parietal	Parietal	Parietal	Axile	Axile
Type of ovule	Orthotropous	Orthotropous	Anatropous	Anatropous	Orthotropous	Orthotropous
Phenolic compounds	Present	Present	Absent	Absent	Absent	Absent
Ornamented cuticle	Absent	Present	Present	Present	Absent	Absent

and the presence of poricidal anthers are consistent with pollination by bees. During our field work, bees (Halictidae) were observed visiting flowers of *Mayaca sellowiana* and vibrating their anthers in a typical pollinator behavior. In *Mayaca fluvialis*, the anther pores are inconspicuous and located at the same level as the stigma, favoring self-pollination. The findings presented in this study demonstrate pollen grains germinating within the anthers and pollen tubes growing toward the stigma in closed flowers, indicating cleistogamy. Self-compatibility was also demonstrated in species of Eriocaulaceae (Ramos et al. 2005; Oriani et al. 2009) and Xyridaceae (Oriani and Scatena 2011) and is probably a condition shared by the xyrids.

In addition to the absence of nectaries, species of Mayacaceae differ from other xyrids because of the presence of papillose epidermal cells on their petals, a reduced inner whorl of stamens, poricidal anthers, an endothecium lacking thickenings, a style and stigma that are vascularized by the dorsal and ventral carpellary bundles, and the presence of an obturator in the ovary. The presence of papillose epidermal cells on the petals is probably another floral attribute that serves as an attractant to pollinators. The total reduction of the inner whorl of stamens also occurs in representatives of Juncaceae (Oriani et al. 2012) and Cyperaceae (Goetghebeur 1998; Vrijdaghs et al. 2005), linking Mayacaceae to the cyperids. The phylogenetic proximity between the Mayacaceae, Juncaceae, and Cyperaceae that is suggested in this study corroborates the findings of phylogenetic analyses of Poales in which Mayacaceae appears as a sister group to the cyperid clade (Chase et al. 2000; Christin et al. 2008). In more derived families of Poales such as Poaceae, the inner whorl of stamens is also reduced (Clifford 1986; Soltis et al. 2005).

The presence of an obturator is another characteristic shared by Mayacaceae, Juncaceae, and Cyperaceae, although with distinct shapes and origins. In Juncaceae, the obturator corresponds to trichomes that originate from the placenta (Oriani et al. 2012), while in Cyperaceae the obturator is a papillose outgrowth with funicular origin (Goetghebeur 1998; Coan et al. 2008). The occurrence of an obturator in Mayacaceae is first reported here and corresponds to a modification of the pollen tube transmitting tissue, which protrudes into the locule in the apex of the ovary and exhibits secretory activity. The substances secreted by this tissue probably guide the growth of the pollen tubes to the micropilar region of the ovules through chemotropism, a function of the obturator that was previously demonstrated for other angiosperms (Maheshwari 1950; Tilton and Horner 1980; Herrero 2000).

Eriocaulaceae and Xyridaceae share several other characteristics apart from nectaries, supporting the proximity of the two families as indicated by phylogenetic analyses (Givnish et al. 1999, 2005, 2006; Chase et al. 2000, 2006; Bremer 2002; Christin et al. 2008). These characteristics include petals presenting elongated epidermal cells with straight walls, epipetalous stamens, staminodes, anthers with longitudinal dehiscence, endothecium with band-like thickenings, and a style vascularized solely by the dorsal carpellary bundles.

The staminodes of Eriocaulaceae and Xyridaceae correspond to the reduction of the outer whorl of stamens. They are inconspicuous and microscopic in most species of Eriocaulaceae (Rosa and Scatena 2007), whereas in Xyridaceae they are conspicuous. In *Xyris*, the staminodes are trichoma-

tous, reflecting an apomorphy of the genus. One hypothesis is that because the apical cells of these trichomes are rounded and present an ornamented cuticle, they mimic pollen grains and act as an attractant to pollinators. Another hypothesis is that the pollen grains adhere to the trichomes and consequently, the staminodes are involved in a secondary pollen presentation mechanism. According to Walker-Larsen and Harder (2000), a visual attraction for pollinators and the facilitation of access to pollen are among the roles that the staminodes can assume, thus supporting the above hypotheses. *Xyris savanensis* is one of the few species of *Xyris* that presents glabrous staminodes (Smith and Downs 1968), perhaps corresponding to an intermediate stage in the evolution of stamens to trichomatous staminodes.

Stamens that lose their primary function in pollen production and do not take over a secondary floral function are quickly lost during the evolution of the species (Walker-Larsen and Harder 2000). This process may be occurring in *Abolboda*, a genus in which the presence of staminodes is not constant and, when they are present, they are apparently nonfunctional. According to Sajo et al. (1997), the fact that few species with staminodes occur in *Abolboda* and that staminodes are absent in *Achlyphila* and *Orectanthe* may suggest that there is a tendency for staminodes to revert to the foliar status and incorporate the corolla in Xyridaceae, contributing to the gamopetalous characteristic of these genera.

In addition to the presence of conspicuous staminodes, keeled sepals and the presence of an ornamented cuticle on the floral parts are also diagnostic characteristics of Xyridaceae. Eriocaulaceae is the only family of xyrids that has declinuous flowers and nectariferous pistillodes in staminate flowers, which probably corresponds to the reduction of the gynoecium from an ancestor with hermaphroditic flowers. In these species, the gynoecium has assumed a secondary function of nectar secretion, hence the term “nectariferous pistillodes” (Rosa and Scatena 2007). Moreover, Eriocaulaceae is the only family of xyrids to present a trilocular ovary and ovules with axile placentation. However, this condition may result from a protrusion of the base of the ovary toward the apex that elevates the funicles and results in pendulous ovules (Coan et al. 2010).

The ovaries of species of *Abolboda* and *Orectanthe* (Xyridaceae) have also been described in the literature as trilocular and containing ovules with axile placentation (Smith and Downs 1968; Kral 1992, 1998). However, our results demonstrate that the ovaries in these genera are unilocular, with an intrusive parietal placentation given that the carpels' septa are not fused in the central region of the ovary. This feature is important not only for Xyridaceae, because it links *Abolboda* and *Orectanthe* to *Xyris*, but also for Poales. Ontogenetic studies of species of Eriocaulaceae can confirm the hypothesis that the ovary in this family is actually unilocular and that this condition is common to xyrids.

The anatomical characteristics of the flowers are of taxonomic value not only for delineating the families of xyrids but also at an intrafamily level. In Mayacaceae, the size of the pores and the shape of the stamens, the disposition of the microsporangia, the number of ovules, and the shape of the stylar canal can be used to delimit the species (Carvalho et al. 2009). Although Carvalho et al. (2009) have reported that the

anthers of *Mayaca fluviatilis* are tetrasporangiate, with vertically displaced microsporangia, our results demonstrate that the anthers of *M. fluviatilis* are bisporangiate, thus differentiating this species from the remaining species of *Mayaca* that present tetrasporangiate anthers. This observation is consistent with the taxonomic descriptions of the family that report the occurrence of tetra- and bisporangiate anthers (Stevenson 1998).

In Xyridaceae, the flowers of *Abolboda* and *Orectanthe* have a zygomorphic symmetry, stomata on the abaxial surface of the sepals, a gamopetalous corolla, a simple style with nectariferous appendages, and anatropous ovules. These characteristics distinguish these two genera from *Xyris*, supporting the family's subdivision and the placement of *Xyris* in the Xyridoideae (Stevens 2011). Another anatomical characteristic of the flowers that differentiates *Xyris* from *Abolboda* and *Orectanthe* is the presence of a single vascular bundle restricted to the keeled region of the sepals, which can be explained by the reduced size of the mesophyll. *Xyris* species can be further distinguished from the other genera of Xyridaceae by the anatomical structures of the vegetative organs and the inflorescence axis (Scatena et al. 2011) and by their embryological characteristics (Rudall and Sajo 1999).

The occurrence of tetracytic stomata on the sepals is a diagnostic characteristic of *Orectanthe sceptrum*. The presence of

secretory ducts in the stigma is another diagnostic and novel characteristic of this species and deserves further investigation to elucidate its function.

The results obtained in this study indicate the need for further studies on the floral anatomy of the different genera of Xyridaceae, as well as studies on the reproductive biology of other species of xyrids, for the purpose of understanding the evolution of this group. The floral characteristics identified in this study are expected to be of use in future phylogenetic analysis of Poales to help to clarify, in a more consistent manner, the placement of the families in this order.

Acknowledgments

We thank the Conselho Nacional de Desenvolvimento Científico e Tecnológico (process numbers 141582/2007-3, 471837/2011-3, and 301692/2010-6) and the Pró-Reitoria de Pesquisa da Universidade Estadual Paulista for financial support, and Dr. Thomas Stützel (Lehrstuhl für Evolution und Biodiversität der Pflanzen, Ruhr-Universität Bochum) for the use of the SEM facilities. The anonymous reviewers are also acknowledged for their critical comments that improved the manuscript.

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