



Leaf and inflorescence axis anatomy of Brazilian species of Rapateoideae (Rapateaceae, Poales)

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ABSTRACT

The anatomy of leaves and inflorescence axes of *Spathanthus* (2 spp.), *Rapatea* (2 spp.), *Cephalostemon* (1 sp.), and *Duckea* (1 sp.) (Rapateoideae, Rapateaceae) was studied to identify useful characters for taxonomy. The cross-section shape of inflorescence axis differentiates the genera, while the cross-section shape and structure of leaf midrib has a specific value. The following characteristics are exclusive of *Spathanthus*: silica cells randomly distributed in the leaf epidermis; plicate chlorenchyma in the leaf blade; presence of fiber bundles in the mesophyll and in the inflorescence axis parenchyma. *Spathanthus* is also distinguished by the number, type and distribution of vascular bundles in the inflorescence axis. The genus *Rapatea* is characterized by the presence of stomata and silica cells only on the abaxial epidermis of the leaves and chlorenchyma composed of arm cells in the leaf blade. Characteristics with diagnostic value for *Cephalostemon riedelianus* are: leaf epidermal cells with straight to slightly sinuous walls in frontal view, inflorescence axes presenting a defined cortex, fiber bundles facing the larger vascular bundles and a fistulous pith. The anatomical characteristics of the leaves and inflorescence axes thus proved to be of taxonomic value in generic and specific levels. They are also useful to differentiate Rapateoideae from other subfamilies of Rapateaceae.

Key words: anatomy, *Cephalostemon*, *Duckea*, Poales, *Rapatea*, Rapateaceae, *Spathanthus*.

INTRODUCTION

Rapateaceae comprise approximately 100 species in 16-17 genera (Stevenson et al. 1998, Givnish et al. 2004) and are a basal family in Poales along with Bromeliaceae and Typhaceae (Linder and Rudall 2005, Givnish et al. 2010). The family has a restricted distribution in South America, mostly in the Guayana Shield, with the exception of *Mascalocephalus dinklagei* that occurs in western

Africa (Maguire 1958, Stevenson et al. 1998). In Brazil, approximately 39 species and nine genera are found, growing primarily in the Amazon region (Monteiro 2014). They are perennial herbs with a short stem from which distichous or spirodistichous leaves and inflorescence axes (scapes) originate (Maguire 1958, Stevenson et al. 1998).

Rapateaceae are divided into three subfamilies: Rapateoideae, Monotremoideae, and Saxo-fridericioideae (Givnish et al. 2004). Rapateoideae are the earliest divergent ones and comprise the

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genera *Spathanthus*, *Rapatea*, *Cephalostemon*, and *Duckea* (Givnish et al. 2004). *Spathanthus* is the sister group of *Rapatea* and *Cephalostemon* (Givnish et al. 2004). These three genera were the first to diverge and are remarkable for presenting dispersion ranges that extend out of the Guayana Shield to the Amazon Basin (Givnish et al. 2000).

The genus *Duckea* (made up of four species) was described by Maguire (1958) and later synonymized as *Cephalostemon* by Steyermark (1988) due to their morphological similarities. However, Berry (2004), in his survey on Rapateaceae of the Venezuelan Guayana Flora, once again separates the genera based on the morphology of seeds, leaves and inflorescence axes. In the most recent phylogenetic study of the family (Givnish et al. 2004), which presents suprageneric taxonomic changes, *Duckea* is also treated as a separate genus. *Duckea squarrosa*, that was studied here, is one of three species of the genus that occurs in Brazil and it is endemic (Monteiro 2014).

Cephalostemon is made up of eight species, five of which are found in Brazil, and *Cephalostemon riedelianus*, that was studied here, is also endemic (Maguire 1958, Monteiro 2014). *Spathanthus* comprises two species, both occurring in Brazil (Maguire 1958, Monteiro 2014) and studied in this work. *Rapatea* comprises about 20 species (Stevenson et al. 1998), among which 14 occur in Brazil (Monteiro 2014), and two of them were also studied.

In the literature, studies on Rapateaceae are scarce and include taxonomy (Maguire 1958, 1965, Stevenson et al. 1998, Berry 2004), pollen morphology (Carlquist 1961), anatomy of roots, leaves, stems and inflorescence axes (Carlquist 1966, 1969, Ferrari et al. 2014), embryology (Venturelli and Bouman 1988), floral anatomy (Oriani and Scatena 2012), and phylogeny (Givnish et al. 2000, 2004).

According to Carlquist (1969) who analyzed the anatomy of vegetative organs and inflorescence axis of 15 of the 17 genera of the family, the leaves

in Rapateaceae are anatomically characterized by: paracytic stomata only on the abaxial surface; presence of silica cells in the epidermis; mesophyll differentiated into palisade and spongy tissue, the last composed of arm parenchyma; and slime-producing trichomes in the leaf axils.

The inflorescence axes in Rapateaceae are characterized by: hypodermal fibers as a continuous sheath or as strands; a ground parenchyma composed of sphaeroidal or arm cells; presence of phenolic idioblasts; and vascular bundles nearer to the centre enclosed by a common fibrous sheath (Carlquist 1969).

Given the importance of identifying anatomical characteristics with taxonomic value, this paper aimed to describe the anatomy of leaves and inflorescence axes of *Spathanthus bicolor*, *S. unilateralis*, *Rapatea paludosa*, *R. ulei*, *Cephalostemon riedelianus*, and *Duckea squarrosa* (Rapateoideae) to characterize the subfamily and the genera, contributing to the understanding of infrafamilial relationships.

MATERIALS AND METHODS

The anatomy of leaves and inflorescence axes was analyzed in six Brazilian species of Rapateoideae. The species studied, collecting areas and voucher numbers are presented in Table I. The vouchers were deposited in the Herbarium Rioclarense (HRCB) at Universidade Estadual Paulista – UNESP. The collected material was fixed in 50% FAA (37% formaldehyde, glacial acetic acid, 50% ethanol, 1:1:18 v/v) and subsequently stored in 70% ethanol (Johansen 1940) for the anatomical studies. Only for *Duckea squarrosa* the anatomical study was performed on herborized material, which was previously boiled in water and glycerin for tissue rehydration. We analyzed at least three individuals of each species, collected from different populations.

Cross, longitudinal, and paradermal sections in the median region of the leaves (blade and sheath) and inflorescence axes (scapes) were made by hand, using disposable razor blades. The

TABLE I
Species studied, collecting areas and voucher numbers.

Species	Localization	Voucher number
<i>Cephalostemon riedelianus</i> Körn.	Parque Nacional da Serra do Cipó, Santana do Riacho, Minas Gerais	Scatena et al. 298
<i>Duckea squarrosa</i> (Willd. ex Link) Maguire	Parque Nacional do Viruá, Caracarái, Roraima	Lombardi et al. 7579
<i>Rapatea paludosa</i> Aubl.	Jalapão, Tocantins	Scatena et al. 442
<i>Rapatea ulei</i> Pilg.	Reserva Florestal Adolpho Ducke, Manaus, Amazonas	Lombardi et al. 7611
<i>Spathanthus bicolor</i> Ducke	Parque Nacional do Viruá, Caracarái, Roraima	Lombardi et al. 7580
<i>Spathanthus unilateralis</i> Desv.	Reserva Florestal Adolpho Ducke, Manaus, Amazonas	Lombardi et al. 7618

sections were double stained with basic fuchsin and astra blue (Roeser 1972) and mounted on semi-permanent slides with glycerin gelatin. The presence of phenolic compounds was tested with aqueous FeCl_3 (Johansen 1940). Cross and longitudinal sections were also obtained by using a microtome (Leica, RM 2245). For this purpose, leaf and inflorescence axis samples were dehydrated in an *n*-butyl alcohol series and embedded according to Feder and O'Brien (1968) in (2-hydroxyethyl)-methacrylate (Leica Historesin Embedding Kit). These sections were stained with periodic acid, Schiff's reagent (PAS), and toluidine blue (O'Brien et al. 1964, Feder and O'Brien 1968) and mounted on permanent slides using Entellan (Merck).

The results were documented with a camera (Leica, DFC 450) coupled to a microscope (Leica, DM 4000B), using the LAS software (Leica Application Suite V.4.0.0).

RESULTS

LEAF

The variable characteristics of the studied species are presented in Table II. In frontal view, the epidermal cells have sinuous (Figs. 1-3) or straight to slightly sinuous walls (Fig. 4). The stomata are tetracytic (Figs. 3-4) and may occur on both sides or only on the abaxial leaf surface. When present on both sides, the stomata are more abundant on the abaxial surface.

All species have epidermal cells containing silica bodies that may be present on one or both leaf surfaces. In frontal view, these silica cells have a random distribution (Figs. 1 and 2 - arrows) or are distributed in longitudinal rows (Figs. 3 and 4 - arrows).

In cross-section, the epidermis is single-layered with rounded or tabular cells (Figs. 5-9) of similar size on both leaf sides (Figs. 17-28). The epidermal cells have slightly thickened outer periclinal walls (Figs. 6-9). Subepidermal fiber strands (Fs) are present on both leaf sides (Figs. 6, 7, 9, 11, 13-15). Species of *Spathanthus* also have fiber bundles (Fb) scattered in the mesophyll (Figs. 5, 11, 12, 29 and 30). In this genus, the mesophyll presents a plicate chlorenchyma (Figs. 5, 9, 18 and 20), while in *Rapatea* the chlorenchyma is composed of arm cells (Figs. 7, 22 and 24). *Cephalostemon riedelianus* (Fig. 26) and *Duckea squarrosa* (Figs. 8 and 28) are distinguished by having a regular chlorenchyma. At the midrib region of the blade, all species have chlorenchyma with arm cells (Figs. 29-34). With the exception of *Rapatea paludosa* and *D. squarrosa*, all species have idioblasts containing phenolic compounds dispersed in the mesophyll (Figs. 11 and 23 - arrows).

The vascular bundles are collateral and surrounded by a double sheath (Figs. 18, 20, 23-34). The outer sheath consists of thin-walled cells, while the inner sheath consists of thin or thick-

TABLE II
Anatomical characteristics of the leaves of Rapateoideae
(Rapateaceae) with taxonomic value. 1: *Spathanthus unilateralis*,
2: *S. bicolor*, 3: *Rapatea paludosa*, 4: *R. ulei*, 5: *Cephalostemon*
***riedelianus*, 6: *Duckea squarrosa* (+ = present, - = absent).**

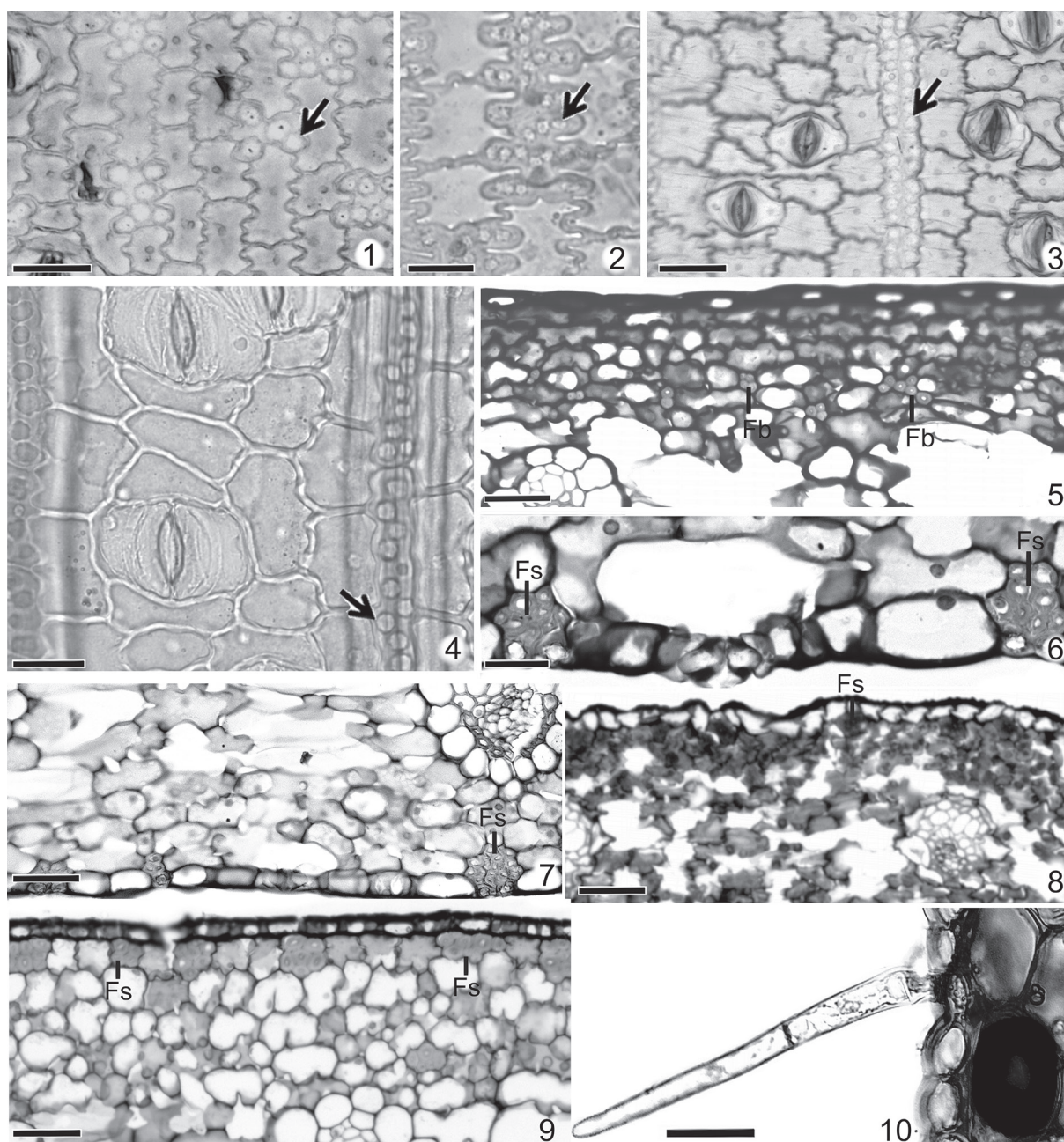
Characteristics	1	2	3	4	5	6
Epidermal cells with sinuous walls	+	+	+	+	-	+
Epidermal cells with straight to slightly sinuous walls	-	-	-	-	+	-
Stomata on both surfaces	+	+	-	-	+	+
Stomata only on the abaxial surface	-	-	+	+	-	-
Epidermal cells with silica bodies on both surfaces	+	+	-	-	+	+
Epidermal cells with silica bodies only on the abaxial surface	-	-	+	+	-	-
Silica cells randomly distributed in the epidermis	+	+	-	-	-	-
Silica cells distributed in longitudinal rows in the epidermis	-	-	+	+	+	+
Fiber bundles scattered in the mesophyll	+	+	-	-	-	-
Plicate chlorenchyma	+	+	-	-	-	-
Chlorenchyma with arm cells	-	-	+	+	-	-
Regular chlorenchyma	-	-	-	-	+	+
Vascular bundles sheath extensions facing both leaf surfaces	-	-	+	-	-	-
Midrib plane-convex with numerous vascular bundles randomly arranged	+	-	-	-	-	-
Midrib curvilinear with numerous vascular bundles randomly arranged	-	+	-	-	-	-
Midrib curvilinear with a central vascular bundle and two smaller ones	-	-	+	-	-	-
Midrib biconvex with numerous vascular bundles randomly arranged	-	-	-	+	-	-
Midrib concave-convex with a central vascular bundle	-	-	-	-	+	-
Midrib biconvex with a central vascular bundle and several smaller bundles around	-	-	-	-	-	+

walled cells (Figs. 18, 20, 23-27, 31-33). Only *Rapatea paludosa* presents sheath extensions in the larger vascular bundles facing both leaf surfaces (Fig. 22).

The cross-section shape and structure of the midrib varies among the species. It is plane-convex in *Spathanthus unilateralis* (Fig. 29) and curvilinear in *S. bicolor* (Fig. 30), both with numerous vascular bundles randomly arranged. In *Rapatea paludosa* the midrib is curvilinear with one large vascular bundle and two smaller ones (Fig. 33), and in *R. ulei* it is biconvex with numerous vascular bundles randomly arranged

(Fig. 34). *Cephalostemon riedelianus* has a concave-convex midrib with only one central vascular bundle (Fig. 31), while the midrib in *Duckea squarrosa* is biconvex with one central vascular bundle surrounded by several smaller ones (Fig. 32). The vascular bundles of the midrib region present a conspicuous fiber sheath on the phloem in all studied species (Figs. 29-34).

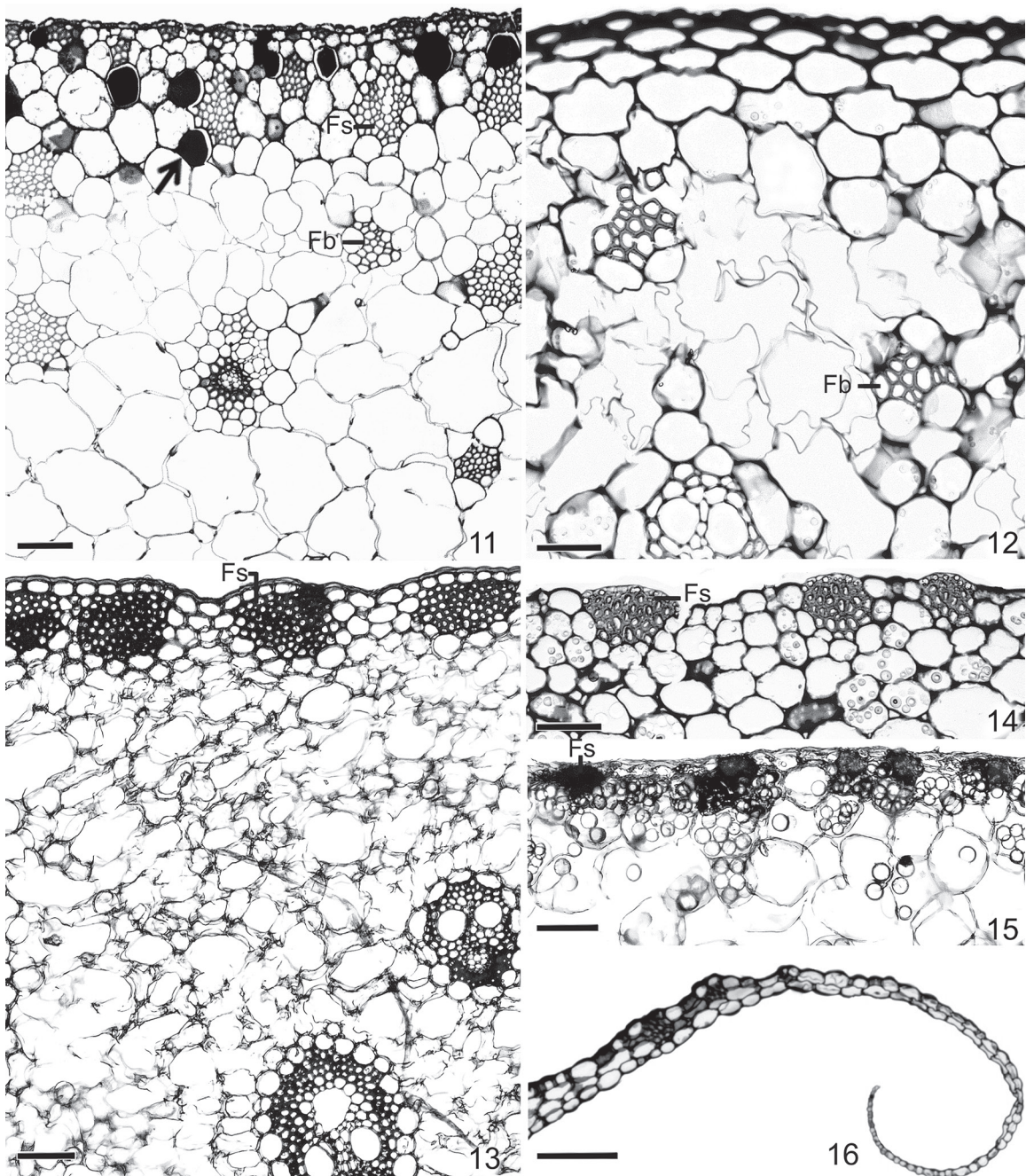
The leaf margin is acute in most of the species (Figs. 19, 21, 23 and 25), with the exception of *Spathanthus bicolor* (Fig. 17) and *Duckea squarrosa* (Fig. 27), which show obtuse



Figures 1-10 - Anatomical characteristics of the leaves of Rapateoideae species. (1-4) Frontal view of the leaf blade epidermis. (1) *Spathanthus bicolor*, adaxial surface. (2) *S. unilateralis*, adaxial surface. (3) *Rapatea paludosa*, abaxial surface. (4) *Cephalostemon riedelianus*, abaxial surface. (5-7) Cross sections of the leaf blade. (5-6) *S. unilateralis*. (7) *R. paludosa*. (8) *Ducea squarrosa*. (9) *S. bicolor*. (10) Detail of the trichomes present on the adaxial surface of the leaf sheath of *S. bicolor*. The arrows indicate the cells with silica bodies. (Fb = fiber bundle; Fs = fiber strand). Scale bar = 50 μ m (1, 3, 5, 7-9); 25 μ m (2, 4, 6, 10).

margin. Sclerenchyma may occur just below epidermis as in *S. bicolor* (Fig. 17), *Cephalostemon riedelianus* (Fig. 25) and *D. squarrosa* (Fig. 27), or

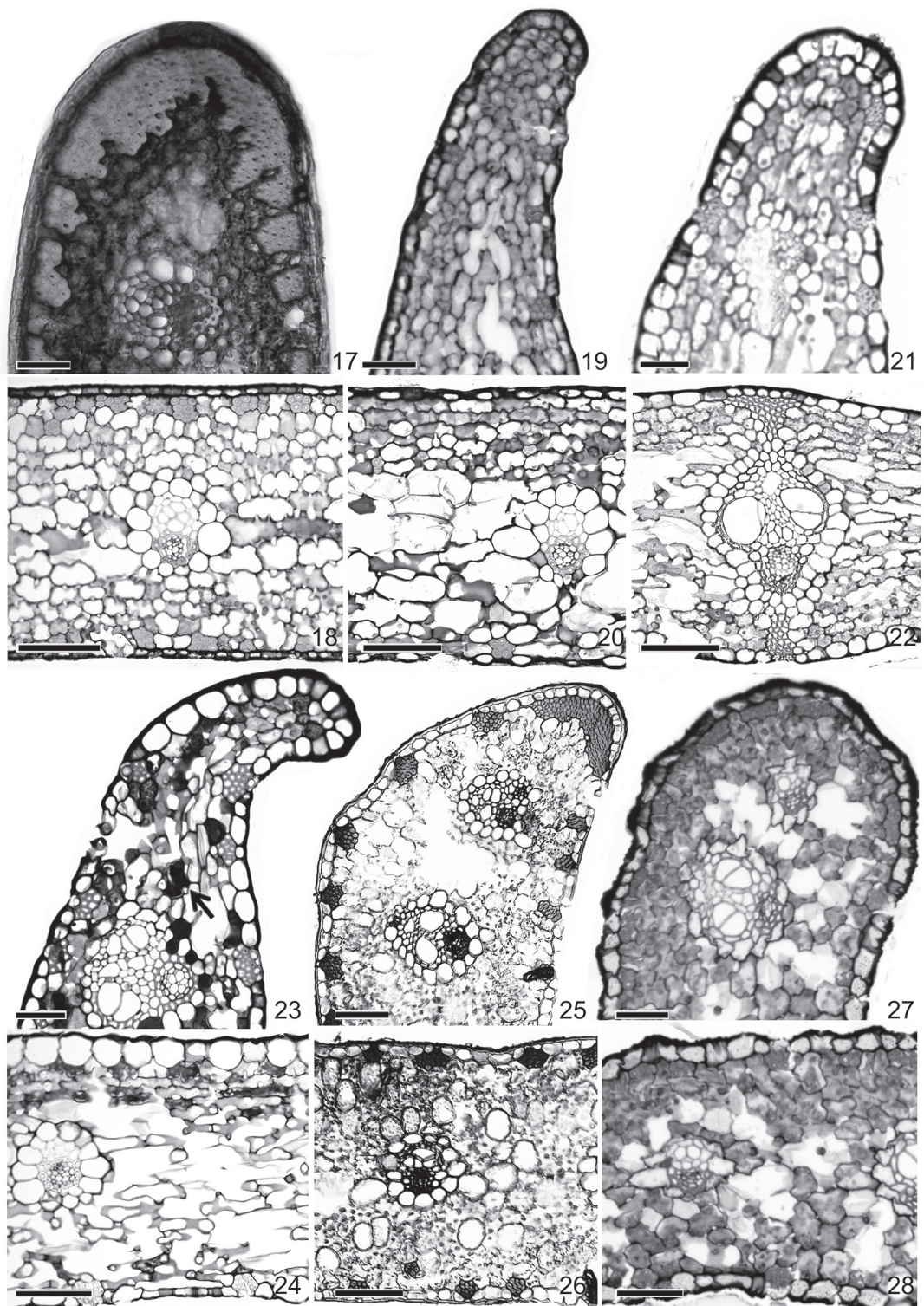
chlorenchyma may be found, such as in *Spathanthus unilateralis* (Fig. 19), *Rapatea paludosa* (Fig. 21) and *R. ulei* (Fig. 23).



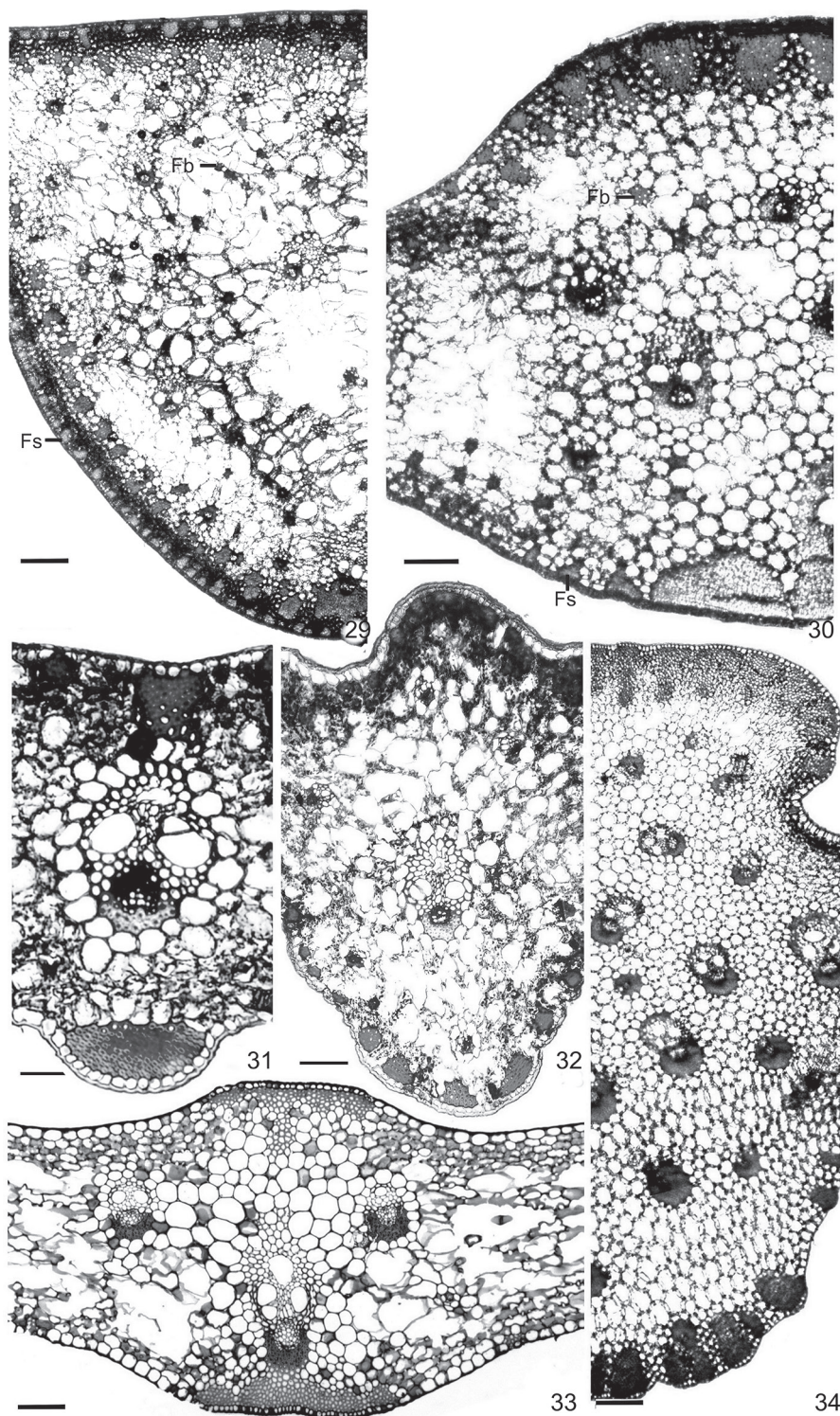
Figures 11-16 - Cross sections of the leaf sheath of Rapateoideae species. (11) *Spathanthus bicolor*. (12) *S. unilateralis*. (13) *Rapatea ulei*. (14) *R. paludosa*. (15 - 16) *Cephalostemon riedelianus*. The arrow indicates a phenolic idioblast. (Fb = fiber bundle; Fs = fiber strand). Scale bar = 100µm (11, 13-16); 50µm (12).

The anatomy of the leaf sheath is similar to the blade, except for the type of chlorenchyma, which is composed of arm cells in the leaf sheath (Figs. 11-15). In all studied species, the sheath has

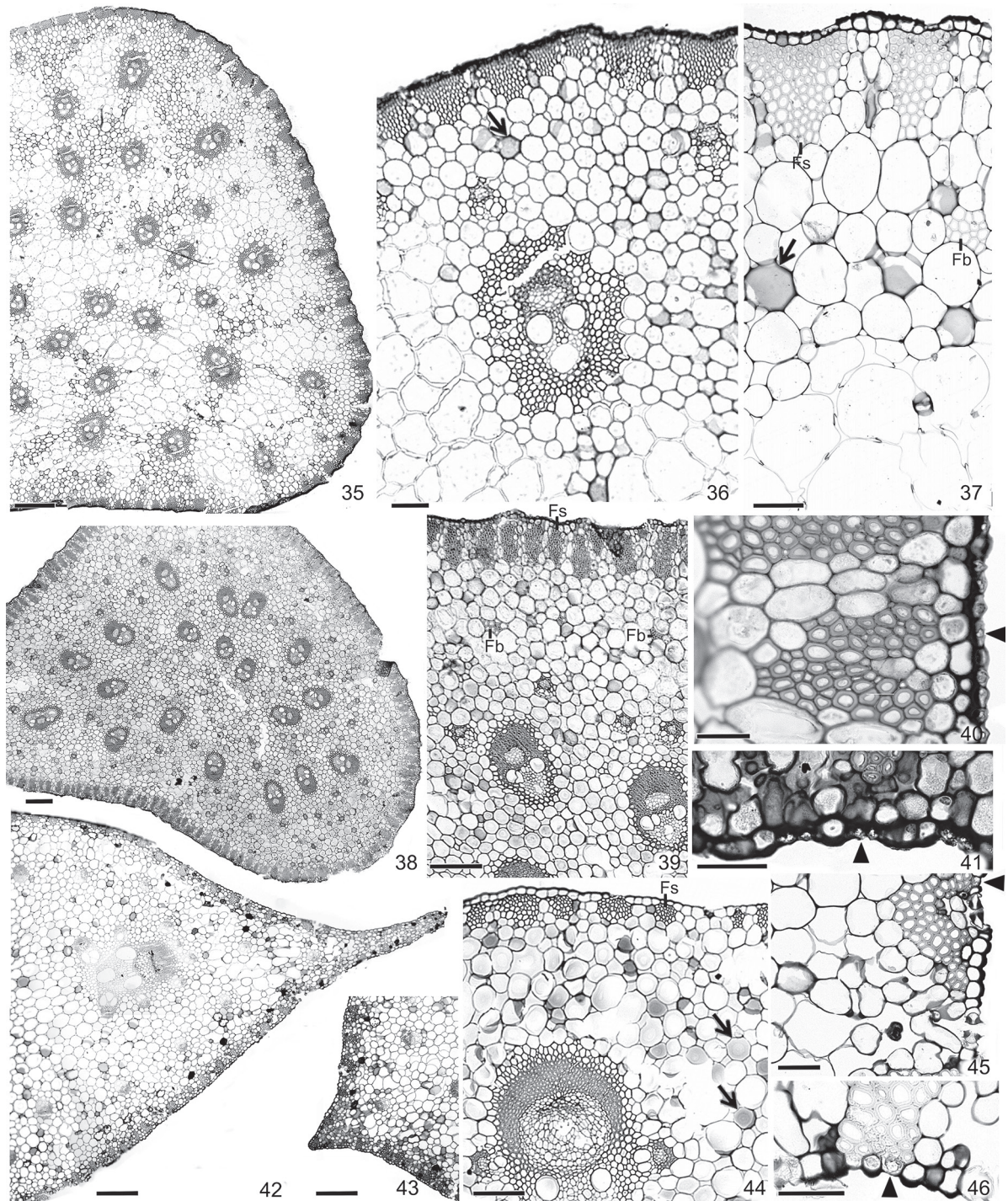
multicellular, uniseriate trichomes on the adaxial surface (Fig. 10) that produce mucilage. The margin of the sheath is formed by the extension of the epidermis (Fig. 16).



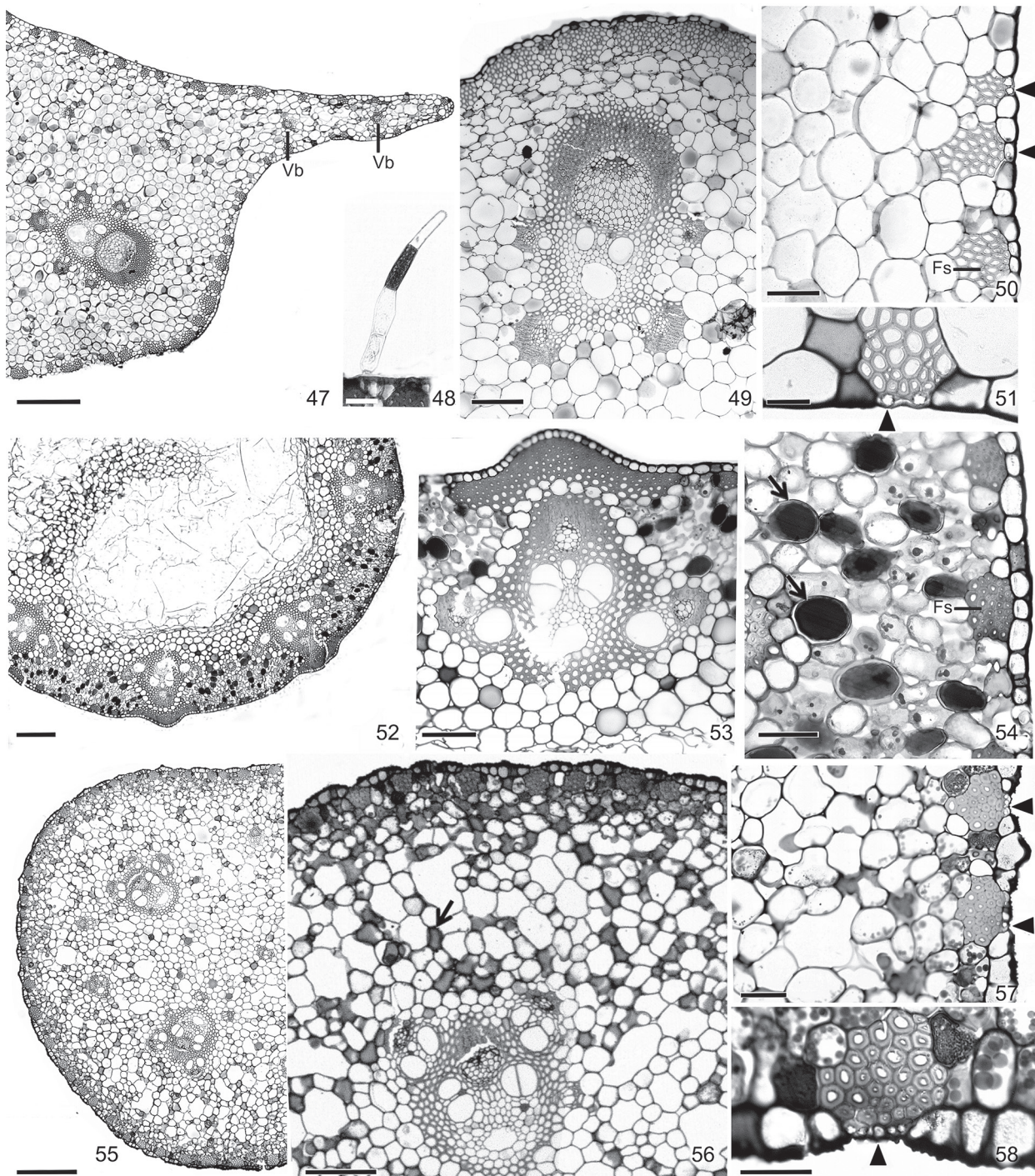
Figures 17-28 - Cross sections of the leaf blade of Rapateoideae species, showing details of the margin and mesophyll. (17-18) *Spathanthus bicolor*. (19-20) *S. unilateralis*. (21-22) *Rapatea paludosa*. (23-24) *R. ulei*. (25-26) *Cephalostemon riedelianus*. (27-28) *Duckea squarrosa*. The arrow indicates a phenolic idioblast. Scale bar = 50 μ m (17, 19, 21, 23, 25, 27); 70 μ m (18, 20, 22, 24, 26, 28).



Figures 29-34 - Cross sections of the leaf midrib of Rapateoideae species. (29) *Spathanthus unilateralis*. (30) *S. bicolor*. (31) *Cephalostemon riedelianus*. (32) *Duckea squarrosa*. (33) *Rapatea paludosa*. (34) *R. ullei*. (Fb = fiber bundle; Fs = fiber strand). Scale bar = 200 μ m (29-30, 34); 50 μ m (31-32); 100 μ m (33).



Figures 35-46 - Cross sections of the inflorescence axes of Rapateoideae species. (35) General view, (36) detail of the vascular bundle, and (37) detail of the epidermis of *Spathanthus bicolor*. (38) General view, (39) detail of the vascular bundle, and (40-41) details of the epidermis of *S. unilateralis*. (42) General view, (43) detail of the opposite wing, (44) detail of the vascular bundle, and (45-46) details of the epidermis of *Rapatea paludosa*. The arrows indicate the phenolic idioblasts and the arrowheads indicate the epidermal cells with silica bodies. (Fb = fiber bundle; Fs = fiber strand). Scale bar = 500 μ m (35, 38); 100 μ m (36, 39, 44); 50 μ m (37, 40, 45); 25 μ m (41, 46); 200 μ m (42-43).



Figures 47-58 - Cross sections of the inflorescence axes of Rapateoideae species. (47) General view, (48) detail of the trichome, (49) detail of the vascular bundle, and (50-51) details of the epidermis of *Rapatea ulei*. (52) General view, (53) detail of the vascular bundle, and (54) detail of the epidermis of *Cephalostemon riedelianus*. (55) General view, (56) detail of the vascular bundle, and (57-58) details of the epidermis of *Duckea squarrosa*. The arrows indicate the phenolic idioblasts and the arrowheads indicate the epidermal cells with silica bodies. (Fs = fiber strand; Vb = vascular bundle). Scale bar = 500µm (47); 50µm (48, 50, 54, 57); 100 µm (49, 53, 56); 25µm (51, 58); 200 µm (52, 55).

INFLORESCENCE AXIS

The anatomical characteristics that differentiate genera or species are presented in Table III. The cross-section shape of the inflorescence axis varies among the genera. It is triangular in *Spathanthus* (Figs. 35 and 38), elliptical in *Rapatea* (Figs. 42 and 47), and circular in *Cephalostemon riedelianus* (Fig. 52) and *Duckea squarrosa* (Fig. 55). In *Rapatea*, the inflorescence axis has two wings, one opposite to the other, which are of different sizes in *R. paludosa* (Figs. 42 and 43) and of the same size with vascular bundles in *R. ulei* (Fig. 47). In *C. riedelianus*, the inflorescence axis presents ribs at the region of the larger vascular bundles (Figs. 52 and 53).

The epidermis is single-layered in all studied species and has cells with slightly thickened outer periclinal walls (Figs. 37, 40, 41, 45, 46, 50, 51, 54, 57 and 58) and tetracytic stomata. The epidermal cells may contain silica bodies (Figs. 40, 41, 45, 46, 50, 51, 57 and 58 - arrowheads) or phenolic compounds (Figs. 36, 45 and 54). They are papillose in *Spathanthus unilateralis* (Fig. 40) and *Duckea squarrosa* (Fig. 57), and rounded in the remaining species (Figs. 37, 45, 50 and 54). Multicellular, uniseriate trichomes are present in *S. unilateralis*, *Rapatea ulei*, and *Cephalostemon riedelianus*. In *R. ulei*, these trichomes contain phenolic compounds (Fig. 48).

In most of the studied species the cortex is not defined (Figs. 35, 38, 42, 47 and 55) and the vascular bundles are randomly distributed in a parenchyma, which is constituted by isodiametric and arm cells that delimit air canals (Figs. 35-39, 44, 49, 50, 55-57). Subepidermal fiber strands (Fs) and phenolic idioblasts (arrows) are also present (Figs. 37, 39, 40, 44, 45, 49, 50, 56 and 57). In addition to the subepidermal fiber strands, there are also fiber bundles (Fb) randomly scattered in the parenchyma of inflorescence axis of *Spathanthus* species (Figs. 37 and 39). *Cephalostemon riedelianus* is the only species that presents a defined cortex, with vascular bundles forming a ring (Fig. 52). In this species the cortex is composed of spongy chlorenchyma and

presents phenolic idioblasts (arrows), subepidermal fiber strands (Fs) (Fig. 54) and fiber bundles facing the larger vascular bundles, forming the ribs (Fig. 53).

All species present collateral vascular bundles surrounded by a double sheath: the outer sheath is composed of thin-walled cells, and the inner sheath is composed of thick-walled cells (Figs. 36, 39, 44, 49, 53 and 56). In *Spathanthus*, the vascular bundles are simple (Figs. 36 and 39), while in the remaining species there are simple or compound vascular bundles (Figs. 42, 49, 53 and 56).

Larger vascular bundles, in number of 5 to 10, have a circular distribution in *Rapatea* (Figs. 42 and 47) and in *Duckea squarrosa* (Fig. 55), while smaller vascular bundles are randomly distributed in the parenchyma. In *Spathanthus* (Figs. 35 and 38), the larger vascular bundles are more numerous (>10) and both, smaller and larger ones, are randomly distributed. In *Cephalostemon riedelianus*, the larger vascular bundles, in number of 5 to 10, alternate with the smaller ones, forming the ring that delimits a parenchymatous, fistulous pith (Fig. 52).

DISCUSSION

According to the results, the leaves of the studied species can be characterized by the presence of a single-layered epidermis with silica cells; tetracytic stomata; a regular, plicate, or arm chlorenchyma in the mesophyll; and collateral, double-sheathed vascular bundles. The leaf sheath has mucilage-secreting trichomes on the adaxial surface; a chlorenchyma composed of arm cells; and margin formed by the extension of the epidermis.

The inflorescence axes are characterized by having a single-layered epidermis with silica cells; tetracytic stomata; a parenchyma composed of isodiametric or arm cells delimiting air canals; phenolic idioblasts; and collateral vascular bundles. These features were also observed in the leaves and inflorescence axes of other representatives of Rapateaceae (Carlquist 1966, 1969, Ferrari et al. 2014) and may be used to describe the family.

TABLE III
Anatomical characteristics of the inflorescence axes
of Rapateoideae (Rapateaceae) with taxonomic value.
1: *Spathanthus unilateralis*, 2: *S. bicolor*, 3: *Rapatea*
***paludosa*, 4: *R. ulei*, 5: *Cephalostemon riedelianus*, 6:**
***Duckea squarrosa* (+ = present, - = absent).**

Characteristics	1	2	3	4	5	6
Triangular shape in cross-section	+	+	-	-	-	-
Elliptical shape in cross-section	-	-	+	+	-	-
Circular shape in cross-section	-	-	-	-	+	+
Unequal wings, without vascular bundles	-	-	+	-	-	-
Wings of the same size, with vascular bundles	-	-	-	+	-	-
Ribs in the region of the larger vascular bundles	-	-	-	-	+	-
Trichomes with phenolic compounds	-	-	-	+	-	-
Fiber bundles scattered in the parenchyma	+	+	-	-	-	-
Defined cortex	-	-	-	-	+	-
Fiber bundles facing the larger vascular bundles	-	-	-	-	+	-
Simple vascular bundles	+	+	-	-	-	-
Simple and compound vascular bundles	-	-	+	+	+	+
Number of the larger vascular bundles ranging from 5-10	-	-	+	+	+	+
Number of the larger vascular bundles above 10	+	+	-	-	-	-
Vascular bundles with a cylindrical distribution, forming a ring	-	-	-	-	+	-
Fistulous pith	-	-	-	-	+	-

According to Carlquist (1969), the presence of paracytic stomata only on the abaxial surface of the leaves is a distinctive feature of Rapateaceae. The results obtained here, however, showed that this characteristic varies among the genera, which may include species with stomata on both leaf surfaces. Our results also showed that the stomata are tetracytic, in agreement with the results obtained by Ferrari et al. (2014) for species of *Monotrema*, *Stegolepis* and *Saxofridericia*, therefore, this is probably a characteristic of the family.

Carlquist (1969) also reported the presence of central vascular bundles enclosed by a common fibrous sheath in the inflorescence axes as a characteristic of the family. Nevertheless, in

most of the species studied here the cortex of the inflorescence axis is not defined and the vascular bundles are randomly distributed in the parenchyma.

The presence of silica bodies, a common characteristic of leaves and inflorescence axes of all studied species, was also observed in other organs of Rapateaceae, such as stems, bracts and flowers (Carlquist 1966, 1969, Stevenson et al. 1998, Oriani and Scatena 2012). Carlquist (1966) used the presence of silica cells associated with subepidermal fiber strands in the stem to characterize the subfamily Rapateoideae. For the leaves and inflorescence axes, however, epidermal cells with silica bodies also occur in species that belong to different subfamilies (Carlquist

1969, Ferrari et al. 2014). The likely function of silica bodies is to reduce the transpiration and to improve photosynthesis, through efficient light distribution in the parenchyma (Prychid et al. 2004). They may also help maintain the rigidity of stems and inflorescence axes and reduce herbivory on leaves (Prychid et al. 2004). Silica bodies are present in representatives of other families of Poales as Poaceae, Cyperaceae, Thurniaceae, Bromeliaceae, Centrolepidaceae, Ecdiocolaceae, and Joinvilleaceae (Tomlinson 1969, Dahlgren et al. 1985, Silva and Alquini 2003, Prychid et al. 2004, Arruda and Neves 2005, Proença and Sajo 2007). They also occur in other commelinid families (included in Arecales, Zingiberales and Commelinales) and may represent a synapomorphy of the clade with several secondary reversals (Prychid et al. 2004).

The mucilage-secreting trichomes in the leaf sheath were reported for different genera of Rapateaceae (Carlquist 1969, Ferrari et al. 2014) and may represent an apomorphy of the family. The function of the mucilage may be to protect the leaves from solar irradiation and this feature may be related to the environment where the family arose, which was at the lowlands of the Guayana Shield (Givnish et al. 2000, 2004). The mucilage production in leaves may even be related to different functions depending on the type of substance produced. It may protect the leaves not only from intense light, but also from herbivores and pathogens, extreme temperatures, and excessive water loss (Werker 2000).

Our results show that the following characteristics are exclusive of Rapateoideae: leaves and inflorescence axes with epidermal cells with slightly thickened outer periclinal walls and subepidermal fiber strands; vascular bundles of the leaf midrib region with a conspicuous fiber sheath on the phloem; and inflorescence axes with phenolic idioblasts in the epidermis and parenchyma. These features are not present in species of *Monotrema* (Ferrari et al. 2014), a genus

previously included in the Rapateoideae (Maguire 1958), corroborating the actual circumscription of the subfamily (Givnish et al. 2004).

The data obtained in this study also show the occurrence of characteristics that delimit the genera. *Spathanthus* species have leaves with randomly distributed silica cells in the epidermis, fiber bundles scattered in the mesophyll, and a plicated chlorenchyma. In these species, the inflorescence axes are triangular in cross-section and present fibers bundles randomly distributed in the parenchyma and above ten simple vascular bundles as diagnostic characteristics. *Rapatea* species have leaves with stomata and silica bodies only on the abaxial epidermis and with a chlorenchyma composed of arm cells, besides elliptical and winged inflorescence axes. *Cephalostemon* is distinguished by presenting leaves with epidermal cells with straight to slightly sinuous walls in frontal view and ribbed inflorescence axes with a defined cortex, fiber bundles facing the larger vascular bundles, and a fistulous pith.

When we compare the studied genera, it may be noticed that *Cephalostemon* and *Duckea* share the greatest number of features, followed by *Rapatea* and *Duckea*. The anatomical similarities between *Cephalostemon* and *Duckea* reflect their morphological similarities, already reported by other authors who even synonymized *Duckea* as *Cephalostemon* (Steyermark 1988). The high similarity between *Cephalostemon*, *Duckea*, and *Rapatea* also corroborates the phylogenetic analysis of the family in which *Cephalostemon* and *Rapatea* appear as sister groups (Givnish et al. 2000, 2004).

Besides delimiting the genera, some characteristics proved to be diagnostic for species such as the cross-section shape and structure of the leaf midrib. The size and composition of the wings present in the inflorescence axis of *Rapatea* differentiate the species from each other. *Rapatea paludosa* is also distinguished by presenting vascular bundle sheath extensions facing both leaf surfaces.

It may be emphasized that the anatomical characteristics identified in the leaves and inflorescence axes of Rapateoideae not only have taxonomic value but may also have an adaptive value. The presence of silica bodies in both organs and mucilage-producing trichomes in the leaf sheath are examples, whose probable function has been discussed previously. The presence of air canals in the leaves and inflorescence axes may also be related to environment. Since the species grow predominantly in wet or flooded areas (Berry 2004, Givnish et al. 2000), the presence of air canals may increase the aeration of these organs, thus facilitating gas exchange (Kawase and Whitmoyer 1980).

Arm cells delimiting air canals and fiber bundles scattered in the mesophyll are also present in the leaves of some species of Bromeliaceae (Proença and Sajo 2007, Tomlinson 1969), corroborating the phylogenetic proximity between these two families, which have a basal position in Poales (Linder and Rudall 2005, Givnish et al. 2010).

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RESUMO

Estudou-se a anatomia de folha e eixo da inflorescência de *Spathanthus* (2 spp.), *Rapatea* (2 spp.), *Cephalostemon* (1 sp.) e *Duckea* (1 sp.) (Rapateoideae, Rapateaceae), buscando levantar caracteres úteis para a taxonomia. A forma do eixo da inflorescência em secção transversal diferencia os gêneros, enquanto a forma e estrutura da nervura central do limbo foliar tem valor específico. São caracteres exclusivos de *Spathanthus*: células epidérmicas

com corpos silicosos com distribuição aleatória e parênquima clorofiliano plicado no limbo foliar; e presença de feixes de fibras no mesofilo e no parênquima do eixo da inflorescência. *Spathanthus* distingue-se também pelo número, tipo e distribuição dos feixes vasculares no eixo da inflorescência. O gênero *Rapatea* caracteriza-se pela presença de estômatos e células epidérmicas com corpos silicosos apenas na face abaxial da folha e pela presença de parênquima clorofiliano bráquiforme no limbo foliar. São caracteres com valor diagnóstico para *Cephalostemon riedelianus*: folha com células epidérmicas com paredes retas a levemente sinuosas em vista frontal e eixo da inflorescência com córtex definido, com cordões esclerenquimáticos subepidérmicos voltados aos feixes vasculares maiores e com medula fistulosa. Dessa forma, a partir de características anatômicas de folha e eixo da inflorescência é possível distinguir gêneros e espécies de Rapateaceae. As características levantadas também permitem diferenciar Rapateoideae das demais subfamílias de Rapateaceae.

Palavras-chave: anatomia, *Cephalostemon*, *Duckea*, Poales, *Rapatea*, Rapateaceae, *Spathanthus*.

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