

Anatomy of the floral scape of Bromeliaceae¹

SUZANA LÚCIA PROENÇA^{2,3} and MARIA DAS GRAÇAS SAJO²

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ABSTRACT – (Anatomy of the floral scape of Bromeliaceae). This paper describes the anatomy of the floral scape for 12 species of Bromeliaceae, belonging to the subfamilies Bromelioideae, Tillandsioideae and Pitcairnioideae. Although all the scapes have a similar organization, there are variations in the structure of the epidermis, cortex and vascular cylinder. Such variations are described for the studied scapes and, when considered together they can help to identify the species. These aspects are described for each scape and discussed under a taxonomic point of view.

Key words - anatomy, Bromeliaceae, floral scape

RESUMO – (Anatomia do escapo floral de Bromeliaceae). Este trabalho descreve a anatomia do escapo floral de doze espécies de Bromeliaceae pertencentes às subfamílias Bromelioideae, Tillandsioideae e Pitcairnioideae e tem como objetivo ampliar o conhecimento anatômico da família e desse órgão em particular. Embora todos os escapos apresentem uma organização similar, observam-se variações na estrutura da epiderme, do córtex e do cilindro vascular. Tais variações são descritas para os escapos estudados e, quando são analisadas em conjunto, podem auxiliar na identificação das espécies. Esses aspectos são descritos para cada um dos escapos e discutidos dentro de um contexto taxonômico.

Palavras-chave - anatomia, Bromeliaceae, escapo floral

Introduction

Bromeliaceae comprises about 2,600 Neotropical species, except for *Pitcairnia feliciana* (A. Chev.) Harms & Mildbraed that occurs in West Africa (Smith and Till 1998). It is included in the order Poales (APG II 2003), close to the Typhaceae (*Typha* e *Sparganium*) and Rapateaceae (Bremer 2002, Davis *et al.* 2004, Linder & Rudall 2005), and has traditionally been divided in to three subfamilies: Pitcairnioideae, Tillandsioideae and Bromelioideae, according to the growth habit, the ovary position and fruit and seed morphology (Smith & Downs 1974, 1977, 1979). Recent phylogenetic analyses (Crayn *et al.* 2000, Horres *et al.* 2000, Barfuss *et al.* 2005) confirmed the monophyly of the Bromelioideae and Tillandsioideae, but indicated the Pitcairnioideae as a polyphyletic group (Crayn *et al.* 2000, Horres *et al.* 2000).

Bromeliaceae plants are herbaceous with reduced stems usually covered with spiraled leaves although in some cases distichous or subdistichous phyllotaxy also occurs. The simple or composed inflorescence is borne on a terminal scape or, sometimes, on a lateral scape originating from lateral buds (Smith & Downs 1974, 1977, 1979).

There are few studies on the floral scape anatomy of Bromeliaceae, the more important is Tomlinson's revision (1969) of the results of Mez (1896 *apud* Tomlinson 1969), Solereder and Meyer (1929) and Foster (1945 *apud* Tomlinson 1969). Using these results Tomlinson (1969) comments the distribution of the vascular pattern in the central cylinder of the scape amongst the three subfamilies. Lately, Segecin & Scatena (2004a) described the floral scape anatomy of 11 *Tillandsia* species focusing on to find features of taxonomic importance and of adaptive value to the epiphytic habit.

The present study supplies anatomical data of the floral scape of 12 Bromeliaceae growing in the *cerrado* areas of São Paulo State and discuss these results in a taxonomic context.

Materials and methods

The material was collected in their natural environment on the *cerrado* remnants of São Paulo State. The vouchers, deposited at the Herbário Rioclarense (HRCB), are registered as follow in the table 1.

The scapes of at least two representatives of each species were fixed in FAA in ethanol 50% (Johansen 1940) for 48h and stored in 50% ethanol. Cross sections were made by free hand in the median third of all the scapes collected. The sections were stained with safranin and Astra blue (Bukatsch 1972 modified by Kraus & Arduin 1997) and mounted on slides with glycerinated gelatin (Kaiser 1880).

Sections of fresh material were used to test the presence/absence of phenolic compounds (Johansen 1940), starch (Johansen 1940), lignin (Sass 1951), lipids compounds

1. Part of PhD thesis developed at Universidade Estadual Paulista Rio Claro, SP, Brazil.
2. Universidade Estadual Paulista, Instituto de Biociências, Departamento de Botânica, Caixa Postal 199, 13506-900 Rio Claro, SP, Brazil.
3. Corresponding author: suzanaproenca@hotmail.com

Table 1. Species of Bromeliaceae studied.

Subfamily/Species	Locality	Voucher
BROMELIOIDEAE		
<i>Acanthostachys strobilacea</i> (Schult. f.) Klotzsch	Reserva Biológica de Moji-Guaçu	S.L. Proença 201
<i>Aechmea bromeliifolia</i> (Rudge) Baker	Área de Proteção Ambiental de Corumbataí	S.L. Proença 212
<i>Ananas ananassoides</i> (Baker) L. B. Sm.	Estação Experimental de Itirapina	S.L. Proença 192
	Área de Proteção Ambiental de Corumbataí	S.L. Proença 205
	Universidade de São Paulo, <i>Campus</i> de Pirassununga	S.L. Proença 214
<i>Billbergia distachia</i> (Vell.) Mez	Reserva Biológica de Moji-Guaçu	S.L. Proença 208
<i>Billbergia porteana</i> Brongn. ex Beer	Reserva Biológica de Moji-Guaçu	S.L. Proença 198
PITCAIRNIOIDEAE		
<i>Dyckia tuberosa</i> (Vell.) Beer	Estação Experimental de Itirapina	S.L. Proença 196
	Universidade de São Paulo, <i>Campus</i> de Pirassununga	S.L. Proença 213
TILLANDSIOIDEAE		
<i>Tillandsia loliacea</i> Mart. ex Schult. f.	Área de Proteção Ambiental de Corumbataí	S.L. Proença 202
<i>Tillandsia pohliana</i> Mez	Reserva Biológica de Moji-Guaçu	S.L. Proença 186
	Pratânia/cerrado	S.L. Proença 216
	Reserva Biológica de Moji-Guaçu	S.L. Proença 190
<i>Tillandsia recurvata</i> (L.) L.	Estação Experimental de Itirapina	S.L. Proença 194
	Pratânia	S.L. Proença 215
<i>Tillandsia tenuifolia</i> L.	Reserva Biológica de Moji-Guaçu	S.L. Proença 189
<i>Tillandsia tricholepis</i> Baker	Estação Experimental de Itirapina	S.L. Proença 195
	Área de Proteção Ambiental de Corumbataí	S.L. Proença 204
<i>Vriesea</i> sp.	Estação Experimental de Itirapina	S.L. Proença 217

(Gerlach 1984) and to determine the crystals chemical nature (Chamberlain 1932).

The results were registered on a photomicroscope Olympus BX40.

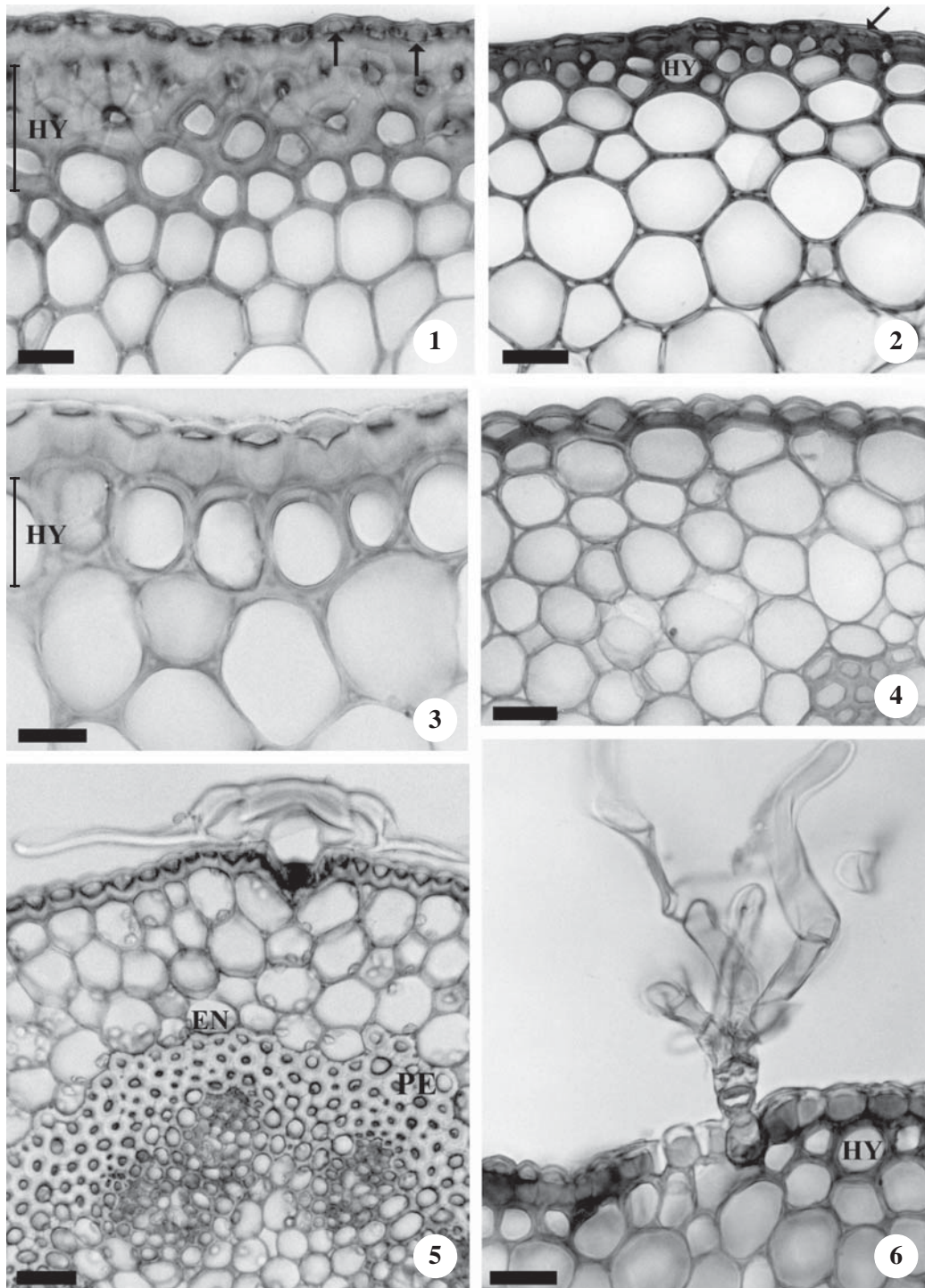
Results

The scapes of Bromelioideae and Tillandsioideae originate from the rhizome apical meristem and those of the Pitcairnioideae *Dyckia tuberosa* (Vell.) Beer have an axillary origin. Most of the studied species have erect scapes but they are pendent in the Bromelioideae *Billbergia porteana* and *Acanthostachys strobilacea*. The scape bears composed inflorescences in *Vriesea* sp. (Tillandsioideae) and *D. tuberosa* (Pitcairnioideae) and simple inflorescences in the other species. Within Tillandsioideae, the *Tillandsia* inflorescence have two to ten flowers that may be up to 2.5 cm long; in *Vriesea* sp., the inflorescence is multi-flowered and each flower is around 5 cm long. In the Bromelioideae and Pitcairnioideae, each scape bears many flowers that can be up to 9 cm long.

In cross-section, the scapes are cylindrical and covered by a cuticle of variable thickness (figures 1, 2,

3, 4). The epidermis is one-layered and its cells are of different size and shape (figures 1-11) and contain spherical silica bodies (figures 1, 2). In most Bromelioideae *Ananas ananassoides* (figure 1), *Aechmea bromeliifolia* (figures 2, 9), *Billbergia porteana* (figure 6) and *Acanthostachys strobilacea* (figure 8), all the epidermal cells have thickened and lignified walls although in *B. distachia* the thickened walls are of cellulosic nature as in the Tillandsioideae *Tillandsia loliacea* (figures 11, 14) and *T. tenuifolia* scapes. In *T. pohliana* (figures 3, 7, 16) all the epidermal cells have thickened and lignified walls but in the others Tillandsioideae *Tillandsia recurvata* (figures 5, 10), *T. tricholepis* (figure 15) and *Vriesea* sp., as well as in the Pitcairnioideae *Dyckia tuberosa* (figure 13), the epidermal cells have thickened walls, although the outer periclinal wall is cellulosic and the others lignified. In all *Tillandsia* species the outer periclinal wall is convex and the inner is concave (figures 4, 5, 10, 11, 15), except for *T. pohliana* (figure 3).

The stomata are sunken in the scape epidermis of *T. pohliana* (figure 7) while in *Acanthostachys strobilacea* (figure 8) the scape surface presents marked depressions



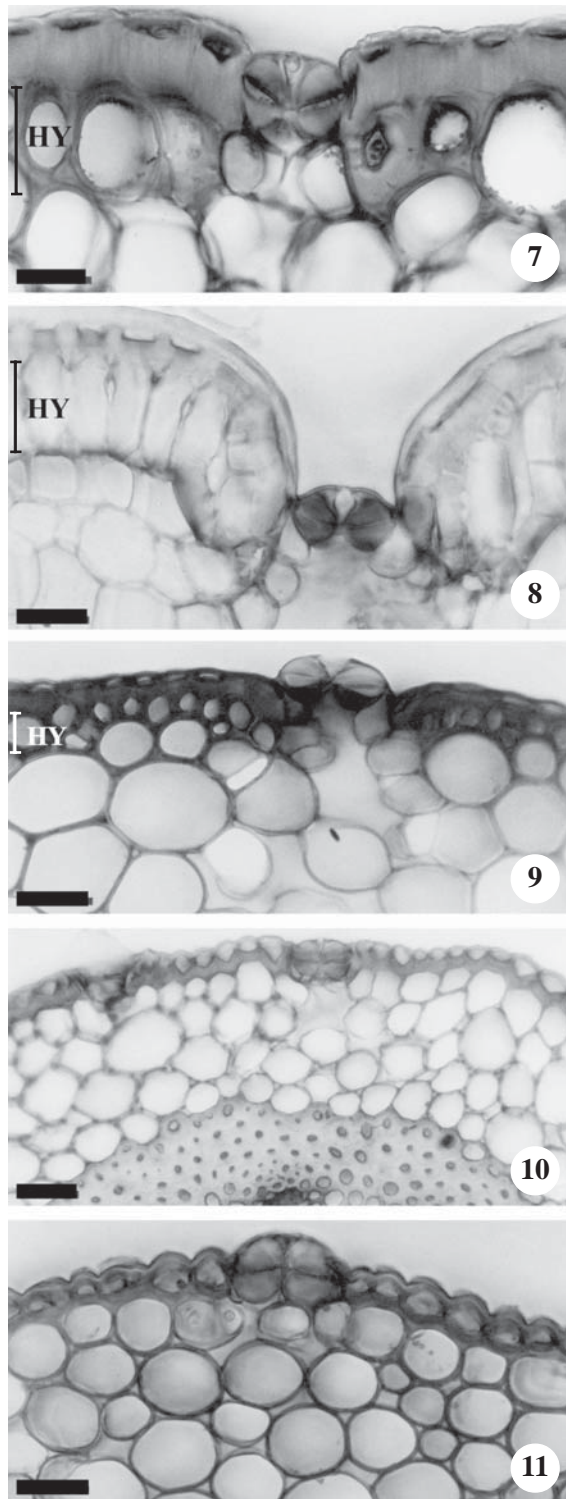
Figures 1-6. Cross section of floral scapes. 1. *Ananas ananassoides*. 2. *Aechmea bromeliifolia*. 3. *Tillandsia pohliana*. 4. *Tillandsia tricholepis*, without mechanical hypodermis. 5. *Tillandsia recurvata*, showing scale and pericycle fibers limiting the central cylinder. 6. *Billbergia porteana*, showing stellate trichome. The arrows indicate spherical silica bodies inside epidermal cells. (HY = mechanical hypodermis; EN = endodermis; PE = pericycle). Bar = 20 μm (2, 3, 4, 6), 30 μm (1, 5).

(figure 19), where the sunken stomata (figure 8) and the scales are located. In *Aechmea bromeliifolia* (figure 9), *Ananas ananassoides*, *Billbergia distachia*, *Billbergia porteana*, *Dyckia tuberosa* and *Tillandsia tenuifolia* the

stomata are project above epidermis level, while in *T. recurvata* (figure 10), *T. loliacea* (figure 11), *T. tricholepis* and *Vriesea* sp., they occupy the same level of the other epidermal cells (table 2).

Table 2. Anatomical and morphological characteristics of the studied scapes. (+ = present; - = absent).

Subfamily/species	Epidermis		Cortex		Vascular system		Scape surface
	Stomatal cell position	Trichomes	Hipodermis		Organization of the central vascular region	Re-entrances	
			Cells shape	N. layers			
BROMELIOIDEAE							
<i>Acantosthachys strobilacea</i>	sunken	scale	anticlinally elongated	1	+	Bundles scattered in the central vascular region	+
<i>Aechmea bromeliifolia</i>	above	stellate	rounded	1	-	Central cylinder surrounded by a continuous ring of pericyclic fibers	-
<i>Ananas ananassooides</i>	above	scale	rounded	3-4	-	Central cylinder limited by the proximity of the peripheral bundles	-
<i>Billbergia distachia</i>	above	-	rounded	1-2	-	Central cylinder surrounded by a continuous ring of pericyclic fibers	-
<i>Billbergia porteana</i>	above	stellate	rounded	1	-	Bundles scattered in the central vascular region	-
PITCAIRNIOIDEAE							
<i>Dyckia tuberosa</i>	above	stellate	rounded	1-2	-	Central cylinder surrounded by a continuous ring of pericyclic fibers	-
TILLANDSIOIDEAE							
<i>Tillandsia loliacea</i>	same level	-	rounded	-	-	Central cylinder surrounded by a continuous ring of pericyclic fibers	-
<i>Tillandsia pohliana</i>	sunken	scale	rounded	1	-	Central cylinder surrounded by a continuous ring of pericyclic fibers	-
<i>Tillandsia recurvata</i>	same level	scale	rounded	-	-	Central cylinder surrounded by a continuous ring of pericyclic fibers	-
<i>Tillandsia tenuifolia</i>	above	-	rounded	-	+	Central cylinder limited by the proximity of the peripheral bundles	-
<i>Tillandsia tricholepis</i>	same level	-	rounded	-	-	Central cylinder surrounded by a continuous ring of pericyclic fibers	-
<i>Vriesea</i> sp.	same level	-	rounded	-	-	Central cylinder surrounded by a continuous ring of pericyclic fibers	-

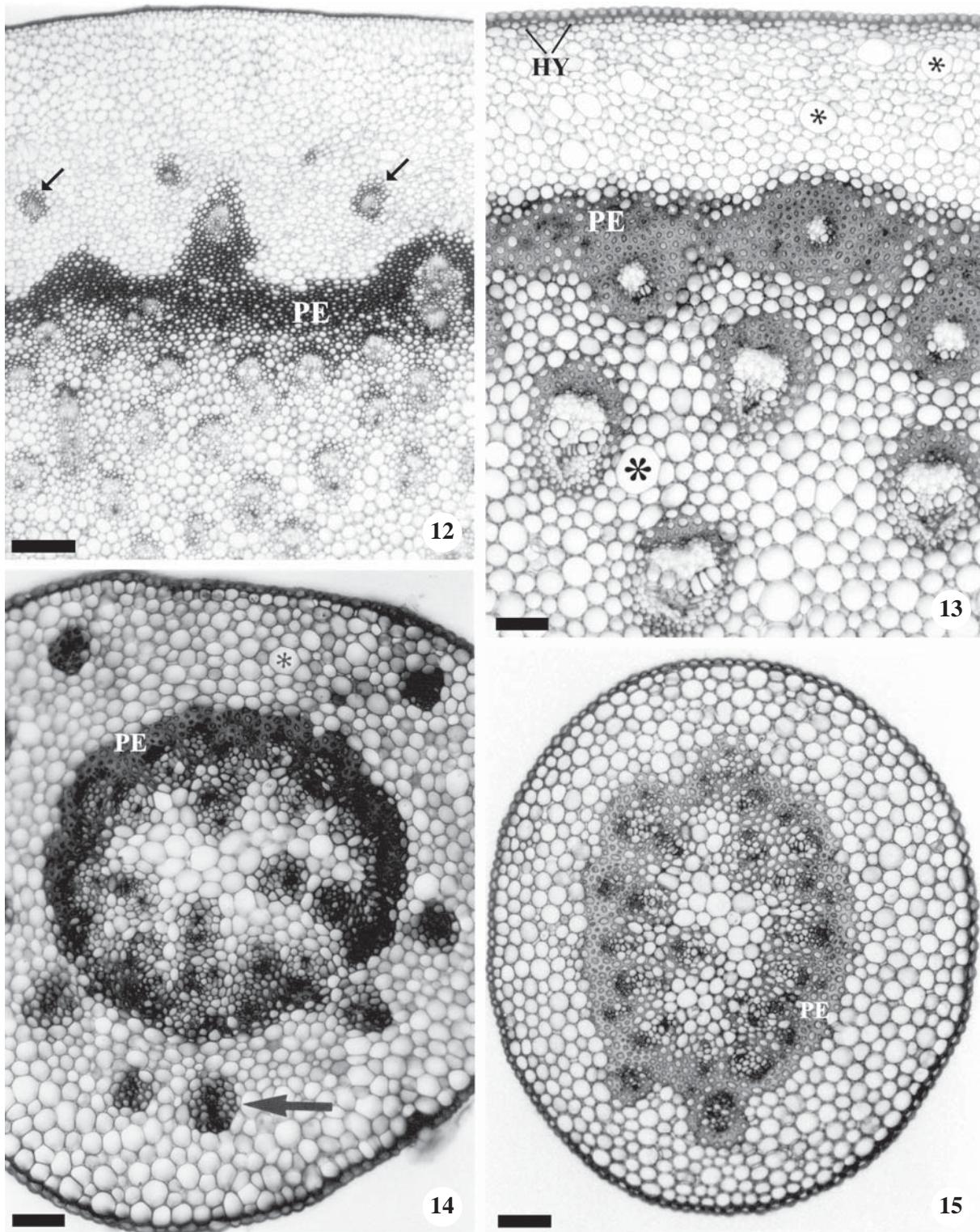


Figures 7-11. Cross section of floral scapes. 7. *Tillandsia pohliana*, with stomata below the epidermis cells level. 8. *Acanthostachys strobilacea*, with stomata deeply below the epidermis cells level. 9. *Aechmea bromeliifolia*, with stomata above epidermis cells level. 10. *Tillandsia recurvata*, with stomata at the same level as the epidermis cells. 11. *Tillandsia loliacea*, with stomata at the same level as the epidermis cells. (HY = hypodermis). Bar = 20 μm (7, 8, 9, 11), 30 μm (10).

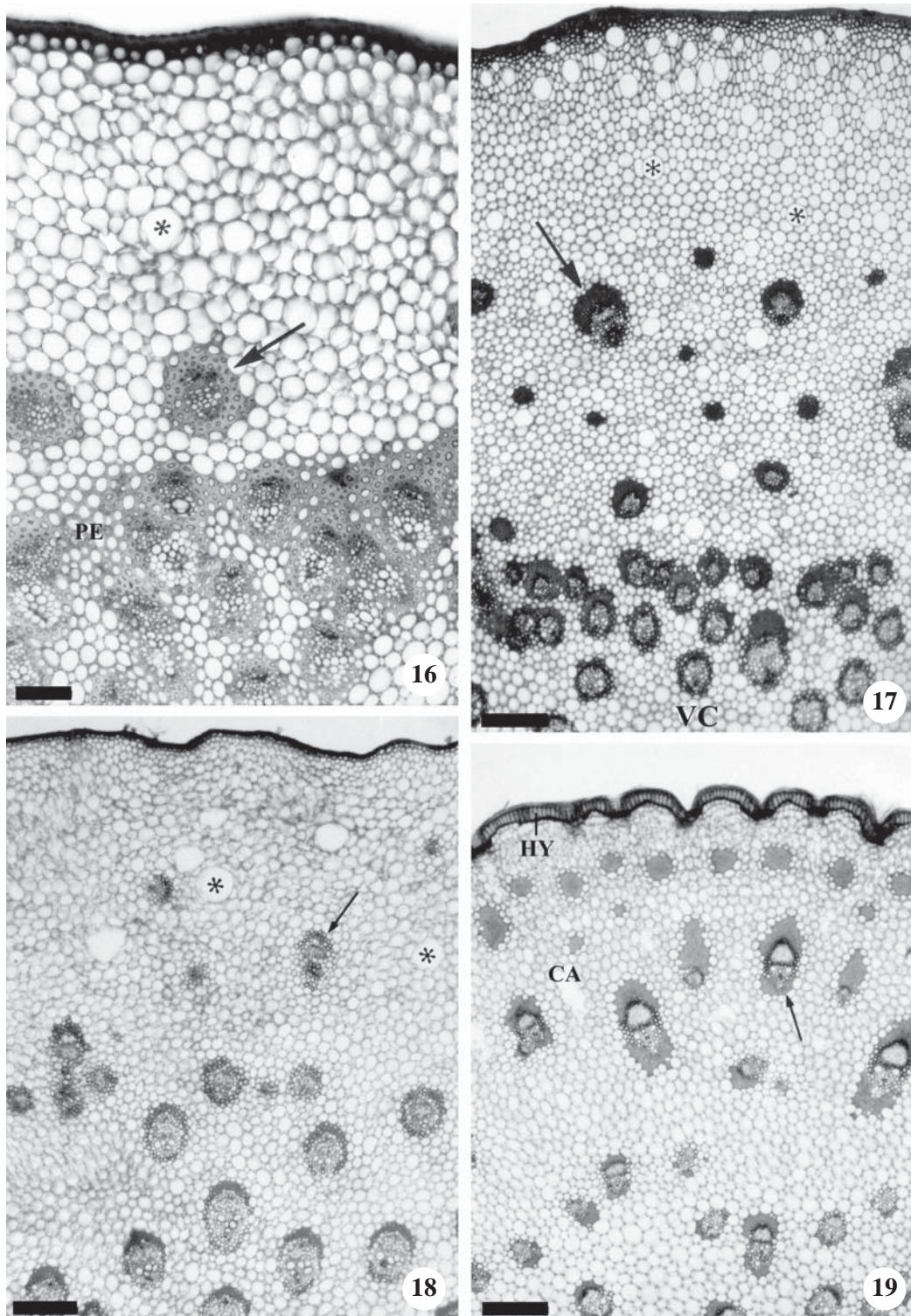
Stellate trichomes occur in the scapes of *B. porteana* (figure 6), *Aechmea bromeliifolia* and *D. tuberosa*, and scales in those of *T. recurvata* (figure 5), *Acanthostachys strobilacea*, *Ananas ananassoides* and *T. pohliana* (table 2). No epidermal appendage was observed for the scapes of *B. distachia*, *T. loliacea*, *T. tricholepis*, *T. tenuifolia* and *Vriesea* sp. (table 2).

The cortex is parenchymatous with small intercellular spaces and its rounded cells are of different size (figures 1-6, 9-19). A hypodermis of sclerified cells forms one layer in the scape of *Aechmea bromeliifolia* (figures 2, 9), *B. porteana* (figure 6), *T. pohliana* (figures 3, 7) and *Acanthostachys strobilacea* (figures 8, 19) and 3-4 layers in the scape of *Ananas ananassoides* (figure 1) (table 2). The hypodermis is also 1-2 layered in *D. tuberosa* (figure 13) and *B. distachia* but its thick walled cells are of cellulosic nature (table 2). In *Acanthostachys strobilacea*, the hypodermis cells are anticlinally elongated (figure 8). A morphologically differentiated hypodermis is absent in the scape of the others *Tillandsia* (figures 4, 5, 10, 11, 14, 15) and of *Vriesea* sp. (figure 12) (table 2). Groups of scattered fibers occur on the peripheral region of the scape cortex in *Acanthostachys strobilacea* (figure 19). In this species, as well as in *T. tenuifolia*, air canals were observed between the bracts traces (figure 19). In all scapes, the endodermis does not present Casparian strips or starch grains being recognized only by its position (figure 5). Idioblasts of calcium oxalate raphides are frequent in all scapes especially in the cortex region (figures 13, 14, 16-18).

Collateral bundles randomly dispersed form the vascular system; these bundles can be partially or completely surrounded by sclerified cells (figures 5, 12-19). In the Bromelioideae *B. porteana* (figure 18) and *Acanthostachys strobilacea* (figure 19) all the vascular bundles are scattered in the scape center and there is no clear distinction between the cortex and the central cylinder (table 2). In the scapes of the Bromelioideae *Ananas ananassoides* (figure 17) and of the Tillandsioideae *T. tenuifolia*, the limit between the central cylinder and the cortex is made only by the proximity of the peripheral bundles (table 2). However, in *Ananas ananassoides* these bundles are smaller and surrounded by more fiber layers than the central ones (figure 17) while in *T. tenuifolia* all the bundles are of a similar size and surrounded by cellulosic thick-walled cells. In the scape of most Tillandsioideae *Tillandsia recurvata* (figure 5), *Vriesea* sp. (figure 12), *T. loliacea* (figure 14), *T. tricholepis* (figure 15) and *T. pohliana* (figure 16), of the Pitcairnioideae *D. tuberosa* (figure 13) and of the Bromelioideae *Aechmea bromeliifolia* and *B. distachia*, the peripheral bundles of the central



Figures 12-15. Cross sections of floral scapes with pericycle fibers limiting the vascular cylinder. 12. *Vriesea* sp. 13. *Dyckia tuberosa*. 14. *Tillandsia loliacea*. 15. *Tillandsia tricholepis*. The arrows indicate bract traces. (HY = hypodermis; PE = pericycle; * = idioblasts of raphides). Bar = 70 μ m (13, 14, 15), 200 μ m (12).



Figures 16-19. Cross section of floral scapes. 16. *Tillandsia pohliana*, showing aggregated vascular bundles surrounded by pericycle fibers on the periphery of the central cylinder. 17. *Ananas ananassoides*, with aggregated vascular bundles on the vascular cylinder periphery. 18. *Billbergia porteana*, showing vascular bundles scattered in the scape central region. 19. *Acanthostachys strobilacea*, with vascular bundles scattered in the scape central region; note the re-entrances on the epidermis and the cortical groups of extravascular fibers. The arrows indicate trace of bracts. (CA = air canal; HY = hypodermis; PE = pericycle; VC = vascular cylinder; * = idioblasts of raphides). Bar = 70 μ m (16), 200 μ m (17, 18, 19).

cylinder are surrounded by a continuous ring of pericyclic cells with thick, lignified walls (table 2). This ring is only discontinuous where the bract traces pass through (figures 12, 14, 16).

Discussion

The scapes vary in size and structure being the inflorescences usually small and few flowered in *Tillandsia* and larger with many flowers in *Vriesea* sp. and in the representatives of Bromelioideae and Pitcairnioideae, as reported by Smith & Downs (1974, 1977, 1979). Most of the species have erect scape, except for *B. porteana* and *Acanthostachys strobilacea* (Bromelioideae) with pendent ones. The scapes of these two species are also similar in the scattered distribution of the bundles and in the absence of a clear limit between the central cylinder and the cortex. Although Tomlinson (1969) describes the occurrence of a ring of developed vascular bundles limiting the central cylinder of the *Acanthostachys strobilacea* scape, no clear limit between the cortex and the cylinder was observed here. However, we observed vascular bundles in more than one series in the cortical region, as described by Tomlinson (1969), besides extravascular fibers, not mentioned by this author.

Considering the other studied species, it is possible to recognize two types of scapes based on the central cylinder bundles arrangement: a) in the first one, the peripheral bundles are close together and delimit the central cylinder from the cortex; b) in the second, the peripheral bundles are surrounded by a ring of pericyclic fibers that demarcates the cylinder from the cortex. Thus, the scapes of the Bromelioideae *Ananas ananassoides* and of the Tillandsioideae *T. tenuifolia* belong to the first type. The scape of the others Bromelioideae (*Aechmea bromeliifolia* and *B. distachia*) and Tillandsioideae (*T. pohliana*, *T. loliacea*, *T. recurvata*, *T. tricholepis* and *Vriesea* sp.) as well as that of *D. tuberosa* (Pitcairnioideae) fit in the second pattern.

Within Bromelioideae, the floral scapes of *Acanthostachys strobilacea* are distinct by the presence of re-entrances on its surface, where the stomata and scales are located, by the occurrence of a one-layered hypodermis of anticlinally elongated cells with thick lignified walls, and by the occurrence of groups of fibers and air canals in the cortex. Both in *Aechmea bromeliifolia* and *B. porteana*, the scapes have a one-layered hypodermis but its cells are not anticlinally developed and, in these cases, the stomata are projected on the epidermis level and there are stellate trichomes on the surface. However, they differ in the central cylinder organization. In *Ananas*

ananassoides, the scape has a (3-4)-layered hypodermis of rounded sclerified cells, stomata projected on the epidermis level and scales on the surface. The scapes of *B. distachia* have no differentiated hypodermis and neither trichomes or scales on the epidermis. Within *Billbergia*, the scapes of *B. porteana* (subgenus *Helicoidea*) and *B. distachia* (subgenus *Billbergia*) differ in the central cylinder organization: in *B. porteana*, the bundles are scattered in the center and there is no clear distinction between the cortex and the central cylinder, while in *B. distachia* the bundles are grouped in the periphery of the cylinder and surrounded by a continuous ring of pericyclic cells of lignified walls. Furthermore, in the scapes of *B. porteana* there are trichomes (absent in *B. distachia*) as well as lignified epidermal and hypodermal cells (cellulosic in *B. distachia*). The anatomical characteristics of the epidermis, cortex and vascular cylinder vary for the studied scapes and, when considered together they can help to identify the species.

Within Tillandsioideae, the scape of *T. pohliana* has a one-layered hypodermis of lignified cells, sunken stomata and epidermal scales. The scapes of the others Tillandsioideae have an undifferentiated hypodermis and stomata leveled with the epidermis or occupying a higher position; only in *T. pohliana* and *T. recurvata* were observed scales. In *Vriesea* sp. the central cylinder is clearly limited by a ring of pericyclic fibers. Central cylinder clearly limited by a ring of pericyclic fibers also occurs in the scapes of *Tillandsia* that belong to the subgenus *Diaphoranthema* (*T. loliacea*, *T. recurvata* and *T. tricholepis*) and in *T. pohliana* (subgenus *Anoplophytum*). For *T. recurvata*, Segecin & Scatena (2004a) reported this same feature for specimens that occupy gallery forests or rocky outcrops. A vascular cylinder demarcated only by the proximity of the peripheral bundles characterizes the scape of *T. tenuifolia*, also included in the subgenus *Anoplophytum*. Such characteristic also was observed for this species by Segecin & Scatena (2004a) as well as air canals in the cortex. Tomlinson (1969) also reported variations in the cylinder structure of these two subgenera (*Diaphoranthema* and *Anoplophytum*) suggesting that this feature is not a good diagnostic for the *Tillandsia* species.

Silica bodies are frequent inside the scape epidermal cells. Since these bodies are indigestible, their presence has been associated with the plant resistance to the insects and fungi attack and since they are highly refractive too their presence has been associated with transpiration reduction (Krauss 1949a, Yoshida *et al.* 1962). Silica bodies also occur in other Poales, such as Poaceae, Cyperaceae, Thurniaceae, Rapateaceae, Centrolepidaceae,

Ecdeiocoleaceae and Joinvilleaceae (Prychid *et al.* 2004), suggesting that this feature is a plesiomorphy for the order. In Bromeliaceae, the silica bodies are always of spherical shape and only occur in the epidermal cells as reported by Krauss (1948, 1949a), Tomlinson (1969), Flores (1975), Souza & Neves (1996), Sajo *et al.* (1998), Aoyama & Sajo (2003), Arruda & Costa (2003), Proença & Sajo (2004), Scatena & Segecin (2005), Sousa *et al.* (2005) and Proença & Sajo (2007) for both vegetative and reproductive organs. This fact corroborates the supposition of Prychid *et al.* (2004) for whom the shape and localization of these bodies, although genetically controlled and little influenced by environmental factors, can present a systematic potential for some groups of monocotyledons.

Calcium oxalate raphides are particularly common in the cortical region of all studied scapes. The occurrence of raphides also has been registered in both vegetative and reproductive organs of Bromeliaceae (see Krauss 1948, 1949a, b; Braga 1977; Brighigna *et al.* 1984; Souza & Neves 1996; Arruda & Costa 2003; Aoyama & Sajo 2003; Segecin & Scatena 2004a, b; Sajo *et al.* 2004, 2005; Scatena & Segecin 2005; Sousa *et al.* 2005; Proença & Sajo 2007). Within Poales (APG II 2003), such crystals occur in Eriocaulaceae, Joinvilleaceae, Sparganiaceae and Typhaceae (Dahlgren *et al.* 1985) and probably represent a plesiomorphy for the order. Although the presence or absence of a determinate crystal has a taxonomic value in some groups (Prychid & Rudall 1999), the presence of calcium oxalate crystals is generalized within Bromeliaceae and thus do not constitute a good feature to group or separate the family taxa.

According to Brighigna *et al.* (1984), calcium oxalate crystals neutralize the oxalic acid produced by the plants and can represent either forms of calcium and oxalic acid storage, reintroduced in the metabolism when necessary (Sunell & Healey 1979), or deposits of metabolic wastes that would otherwise be toxic to the cell or tissue (Prychid & Rudall 1999). For Mauseth (1988), Finley (1999) and Prychid & Rudall (1999), the calcium oxalate raphides also make the plants little palatable to herbivores. According to Fahn & Cutler (1992) these crystals has been considered to be of adaptive value in xerophytic conditions. However, the occurrence of raphides has been registered in many bromeliads that occupy different habitats (see Braga 1977; Arruda & Costa 2003; Segecin & Scatena 2004a, b; Sousa *et al.* 2005; Proença & Sajo 2007), indicating that, in this case, the presence of such crystals is not related to water availability in the environment.

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