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Anatomy of Brazilian Cereeae (subfamily Cactoideae, Cactaceae): *Arrojadoa* Britton & Rose, *Stephanocereus* A. Berger and *Brasilicereus* Backeberg

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RESUMO – (Anatomia de espécies brasileiras pertencentes à tribo Cereeae (subfamília Cactoideae, Cactaceae): *Arrojadoa* Britton & Rose*, Stephanocereus* A. Berger and *Brasilicereus* Backeberg). *Arrojadoa*, *Stephanocereus* e *Brasilicereus* são gêneros endêmicos à Serra do Espinhaço, ocorrendo ao norte de Minas Gerais, e na Chapada Diamantina, ao sul da Bahia, associados aos campos rupestres, cerrados e caatingas. Os gêneros, pertencentes à subfamília Cactoideae, tribo Cereeae, são colunares, eretos ou cespitosos, com exceção da espécie *A. bahiensis*, que é globosa. Este trabalho descreve a anatomia dos tecidos de revestimento, fundamental e vascular das espécies, com o objetivo de buscar caracteres diagnósticos para os gêneros e as espécies. Porções basais dos caules de cada indivíduo foram secionadas transversal e longitudinalmente, e coradas com azul de astra e safranina. Dentre as várias características compartilhadas, citam-se epiderme unisseriada, coberta por espesso estrato cuticular; hipoderme colenquimática bem desenvolvida, contendo cristais prismáticos; córtex diferenciado numa paliçada em sua porção mais externa; periderme com súber constituído por camadas de células lignificadas alternadas com camadas de células suberizadas; feloderme com poucas camadas de células de paredes delgadas; floema secundário composto por elementos de tubo crivado, células companheiras, parênquima axial e radial; xilema secundário com vasos solitários a múltiplos, com placa de perfuração simples, pontoações areoladas a semi-areoladas; parênquima axial vasicêntrico escasso a incompleto; fibras libriformes; raios altos e largos. A ocorrência de parênquima não lignificado no xilema secundário é observada, variando de umas poucas células a faixas contínuas nas espécies. Os caracteres de valor diagnóstico encontrados são: a forma das células lignificadas do súber, cúbicas ou alongadas, que individualizam a espécie *S. leucostele*; hipoderme pouco desenvolvida e a ocorrência de esclereídes no córtex, exclusivos de *B. markgraaffii*.

Palavras-chave: Anatomia do caule, hipoderme colenquimática, Cereeae, Cactaceae

ABSTRACT – (Anatomy of Brazilian Cereeae (subfamily Cactoideae, Cactaceae): *Arrojadoa* Britton & Rose, *Stephanocereus* A. Berger and *Brasilicereus* Backeberg). *Arrojadoa*, *Stephanocereus* and *Brasilicereus* are endemic Brazilian Cereeae, occurring along the Espinhaço Range, in the campos rupestres, cerrados and caatingas, from northern Minas Gerais to southern Bahia. The genera are columnar, erect to semi-erect cacti, except for one species, *A. bahiensis*, which is globose. This study describes the anatomy of dermal, fundamental and vascular systems, aiming to find diagnostic characters for the genera and species. Basal portions of stems were sectioned transversely and longitudinally, and stained with Astrablue and Safranin. The species share a uniseriate epidermis, with thick cuticle; well developed collenchymatic hypodermis, containing prismatic crystals; cortex with numerous mucilage cells, druses and vascular bundles; outside cortex as a palisade parenchyma; periderm composed of lignified cork cells alternating with suberized cells; pheloderm consisting of a few layers of thin-walled cells; phloem composed of solitary or multiple of two to three sieve tube elements, companion cells, axial and radial parenchyma; secondary xylem with solitary to multiple vessels, with simple perforation plates and alternate bordered to semi-bordered pits; axial parenchyma scanty vasicentric to incomplete; libriform septate fibres; large rays. Unlignified parenchyma is seen in the secondary xylem, varying from a few cells to bands among axial and radial elements. The following are considered diagnostic characters: the shape of lignified phellem cells, cubic to radially elongate, which individualizes *S. leucostele*; an underdeveloped hypodermis and the occurrence of sclereids in the cortex are exclusive to *Brasilicereus markgrafii*.

Key words: Stem anatomy, collenchymatic hypodermis, Cereeae, Cactaceae

Introduction

Cereeae Salm. Dyck. is the most representative tribe of cacti in Brazil, with its centre of diversity in Northeastern Brazil, considered the third for Cactaceae (Taylor 1997). The tribe is composed of ten genera; of these *Arrojadoa* Britton & Rose, *Stephanocereus* A. Berger and *Cipocereus* are considered to be a lineage

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of closely related taxa (Taylor & Zappi 2004). The species are all endemic to the *campos rupestres* and *caatingas* of the Espinhaço range in Minas Gerais and Bahia states.

Arrojadoa and *Stephanocereus* consist of four and two species, respectively, as follows: *A. bahiensis* (P.J. Braun & Esteves) N.P. Taylor, *A. dinae* Buining & Brederoo, *A. penicillata* (Gürke) Britton & Rose and *A. rhodantha* (Gürke) Britton & Rose, *S. leucostele* (Gürke) and *S. luetzelburgii* (Vaupel) N.P. Taylor & Eggli. They are a group of columnar, erect or caespitose plants, where only *A. bahiensis* is globose (Taylor & Zappi 2004).

According to Taylor & Zappi (2004), *Stephanocereus* and *Arrojadoa* are closely related genera, based on the occurrence of a ring cephalium, a specialized reproductive structure. The genera differ however regarding the pollination syndrome and the number of ribs (Taylor & Zappi 1989). On the other hand, the closeness of *Stephanocereus* and *Cipocereus* is suggested by the pollination syndrome, chiropterophily, and the bluish color of the fruits (Taylor & Zappi 2004).

Brasilicereus Backeberg is an aberrant genus, to date provisory in the group due to a scaly pericarpel (Taylor & Zappi 2004). It was suggested that it might represent a basal branch in the tribe, though it remains undefined so far (Taylor & Zappi 2004).

In a taxonomic revision of the tribe, based on cladistic analysis using morphological characters, the relationships between the taxa appeared unresolved (Taylor & Zappi 1989). *Cipocereus*, *Brasilicereus* and *Cereus* came up in a basal politomy, while *Arrojada* came up as a paraphyletic genus. This work showed that morphology is insufficient for a deep understanding of the relationships in the tribe. In such a well adapted group, having a highly reduced morphology, convergence will undoubtedly mask characters that might be of use in a phylogenetic analysis (Taylor & Zappi 2004). Based on the results, the authors suggested there is a strong need for other data sources, such as anatomy, phytochemistry and molecular, to better resolve Cereeae phylogeny.

Regarding the anatomy, several studies can be mentioned, especially those correlating taxonomy and systematics (Gibson 1973; 1977; 1978; Mauseth 1989; 1996; 1999; Nyffeler & Eggli 1997; Silva & Alves 1999; Soffiatti & Angyalossy-Alfonso 2003; 2005).

For instance, Gibson & Horak (1978) confirmed the subdivision of Pachycereeae in two tribes, using anatomical characters from dermal and fundamental systems, as well as chemical and morphological ones. Mauseth (1989; 1993; 1996) and Mauseth and collaborators (Mauseth & Plemons 1995; Mauseth & Plemons-Rodriguez 1997; 1998; Mauseth *et al.* 1998) studied extensively the anatomy of members of Cereeae in order to understand the evolution of certain traits in the group and provide additional data for the understanding of relationships in the tribe.

There are a few studies using anatomical characters in a cladistic approach in the family. Nyffeler & Eggli (1997) studied the relationships within the genus *Eriosyce* (tribe Notocacteae) through the anatomy of dermal system and cortex, as well as morphological characters, giving support to the circumscription of the genus. More recently, Terrazas & Arias (2003) made a cladistic analysis for Cactoideae, using anatomical characters surveyed in the literature; they concluded that these might be of use together with other sources.

Regarding Brazilian species, Silva & Alves (1999) studied the anatomy of six species of *Pilosocereus*, and noticed differences allowing the separation of two subgenera. Soffiatti & Angyalossy (2003; 2005) studied the anatomy of *Cipocereus*, searching for diagnostic characters in the dermal, fundamental and vascular systems.

That said, the present work's goal is to characterize the anatomy of the dermal, fundamental and vascular system of the genera *Arrojadoa*, *Stephanocereus* and *Brasilicereus* in order to complement the anatomical studies in the tribe, identify diagnostic characters for the genera and species, and provide additional information in a poorly studied group as regards anatomy in Brazil.

Material and methods

The specimens were collected along the Espinhaço range, in the states of Minas Gerais and Bahia (Tab. 1). Vouchers are deposited in the Bioscience Institute Herbarium of the University of São Paulo (SPF). The identifications were confirmed by Dr. Daniela Cristina Zappi, from the Royal Botanic Gardens, Kew, UK.

Samples of basal portions of the stems were fixed in 70% formalin-acetic-alcohol (Johansen 1940). For the study of dermal and fundamental system, some portions were embedded in Polietilenoglicol 1500 (Richter 1985) before sectioning in rotative microtome. For the study of the xylem, samples were sectioned in a slide microtome (Gerlach 1984). Transverse and longitudinal sections were made, stained with Astrablue

Table 1. Studied species with authority, size, location, habitat and collection number.

Species	Diameter and height	Locality	Habitat	No. Collector
Arrojadoa bahiensis (P.J. Braun & Esteves) N.P. Taylor & Eggli	12 cm/0,3 m 18 cm/0,4 m 14 cm/0,3 m	Piatã – BA	Campo rupestre	Soffiatti 38 Soffiatti 39 Soffiatti40
Arrojadoa dinae Buining & Brederoo	1,5 cm/0,3 m 2 cm/0,6 m 2,3 cm/0,5 m	Palmeiras – BA	Caatinga	Soffiatti 33 Soffiatti 34 Soffiatti 50
Arrojadoa penicillata (Gürke) Britton & Rose	2 cm/2 m 2 cm/2,8 m 2 cm/2,3 m	Lençóis – BA	Caatinga	Soffiatti 31 Soffiatti 32 Soffiatti 51
A. rhodhanta (Gürke) Britton & Rose	5 cm/1,5 m 4 cm/1 m 4 cm/1,3 m	Seabra – BA	Caatinga	Soffiatti 35 Soffiatti36 Soffiatti37
Stephanocereus leucostele A. Berger	8 cm/2,5 m 10 cm/3 m 8 cm/2,7 m	Abaíra – BA	Caatinga	Soffiatti 44 Soffiatti45 Soffiatti46
Stephanocereus luetzelburgii (Vaupel) N.P. Taylor & Eggli	20 cm/1,5 m 25 cm/1,3 m 22 cm/1,6 m	Lençóis – BA	Campo rupestre	Soffiatti 47 Soffiatti48 Soffiatti 49
Brasilicereus markgrafii Backeberg	1,6 cm/1,5 m 2 cm/1,7 m 2 cm/2 m	Grão Mogol – MG	Cerrado	Soffiatti 25 Soffiatti 26 Soffiatti 27

and Safranin. Sections were mounted in synthetic resin. For the study of the phloem, samples were embedded in Historesin®. Transverse and longitudinal sections were made in rotative microtome, varying from 4 to 7 mm thick, and stained with Toluidin blue 0.05% acetate Buffer 4.7 (O'Brien *et al.* 1965). Tests for lignified secondary walls were made using acid floroglucyn (Johansen 1940). Tests to detect crystal composition used glacial acetic acid for calcium carbonate and nitric acid 10% for calcium oxalate (Chamberlain 1932). For SEM analysis, samples were dehydrated, and then critical-point dried, mounted on aluminum stubs, and coated with gold-palladium in a sputter system. Scanning Electron Microscopy (SEM) analysis and electron micrographs were done with a JEOL JSM 5800 scanning electron microscope at the Electron Microscopy Center of the Bioscience Institute, University of São Paulo. Wood anatomy descriptions followed recommendations of the IAWA Committee (1989) and Carlquist (1988).

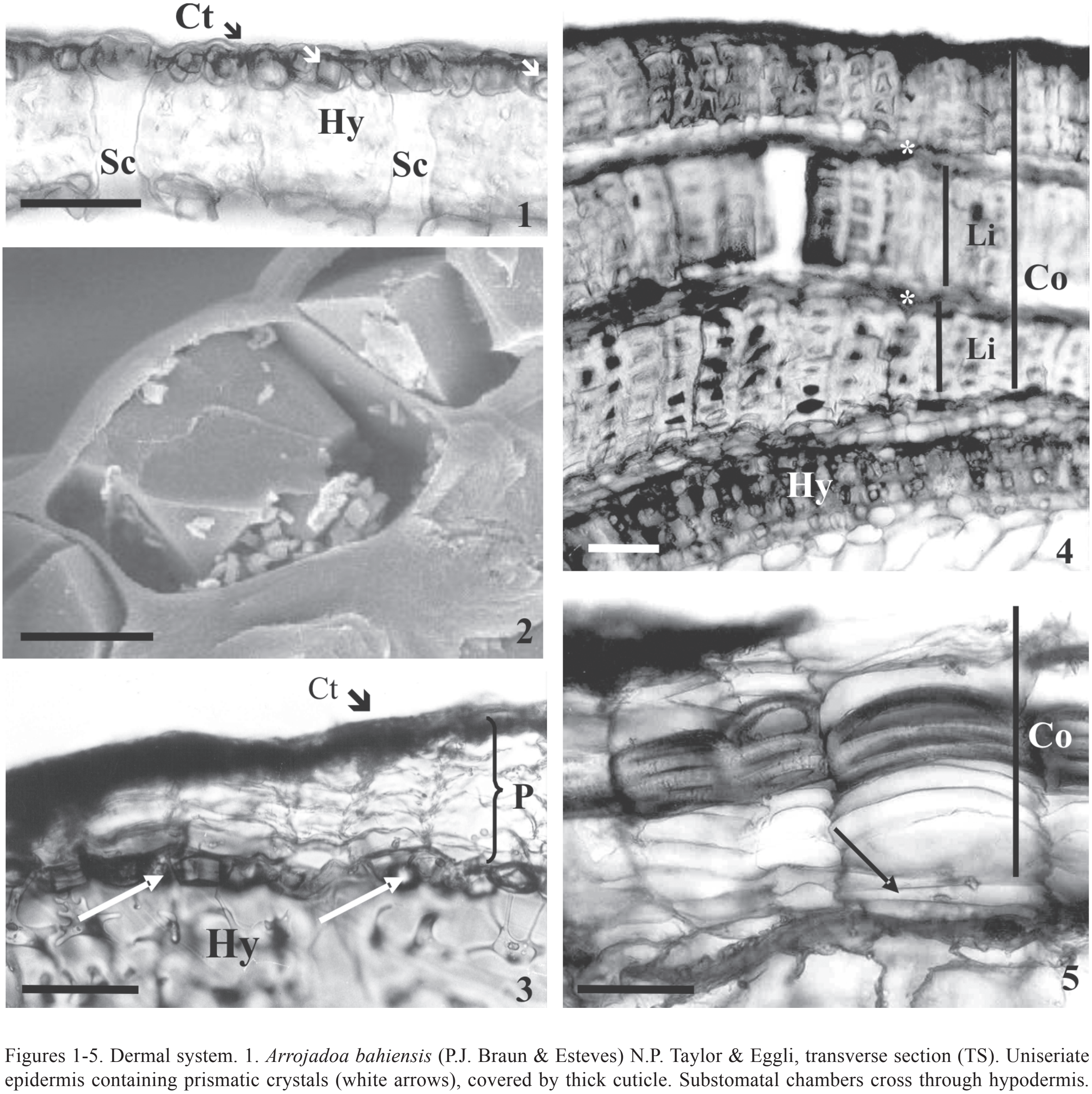
Results

Dermal system – Epidermis is uniseriate, covered by thick cuticle (Fig. 1), containing two sizes of prismatic crystals: large and small (Fig. 2). The stomatal apparatus is of the parallelocytic type, located on the same level as the epidermal cells (Fig. 1). Periderm is located between cuticle and epidermis (Fig. 3). Phellem is composed of tangentially elongated cells in transverse section, with 4 to 10 layers of suberized cells alternating with 3 to 4 layers of lignified cells (Fig. 4-5). Phelloderm is composed of a few thin-walled parenchyma cells (Fig. 4-5). In *Stephanocereus leucostele*, cork cells, in transverse section, are cubic (Fig. 5).

Fundamental system – Hypodermis is collenchymatic, composed of cells with irregularly thickened primary walls, connecting through ramified channels, present in all species, varying from 1 (in *Brasilicereus markgraffii* - Fig. 7) to 6 layers of cells (Fig. 1, 3, 5-6). Hypodermal cells contain prismatic crystals of calcium oxalate (Fig. 6). Substomatal chambers develop through hypodermis (Fig. 1, 6). Cortex (Fig. 8) is divided into a palisade, and an inner region composed of large parenchyma cells and vascular bundles. Cortex parenchyma cells contain druses. Large mucilage cells (Fig. 8) occur throughout the cortex and pith, very abundant in *Arrojadoa bahiensis*. There are vascular bundles in the pith and starch grains are largely present in pith cells.

Vascular system – Secondary phloem (Fig. 9) is composed of solitary and grouped sieve tube elements in numbers of 2 to 3; sieve plate is simple, transverse to inclined (Fig. 10). Sieve tube elements have 1 to 2 companion cells per element (Fig. 9); rays are short. There are caps of sclereids (Fig. 9), originated in the periphery of the conductive secondary phloem.

Secondary xylem is composed of solitary vessel elements (Figs. 11-13) to multiples of 3, rarely 4, small in diameter, with simple perforation plate (Fig. 14). Pits are circular to scalariform (Fig. 14), bordered to half bordered, or simple. Axial parenchyma is scanty paratracheal to scanty vasicentric (especially in *Arrojadoa bahiensis*, *Stephanocereus leucostele* and

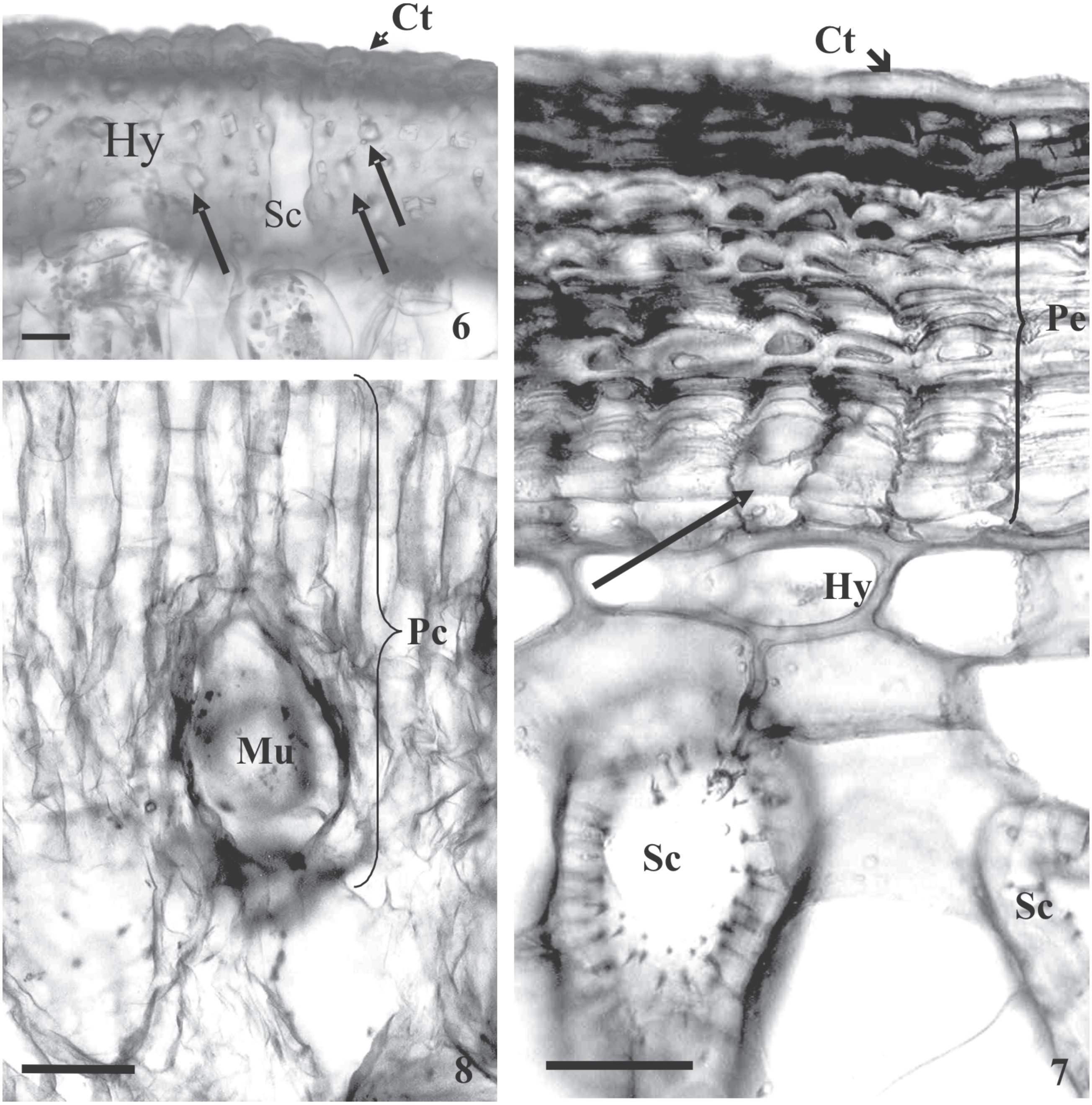


Figures 1-5. Dermal system. 1. *Arrojadoa bahiensis* (P.J. Braun & Esteves) N.P. Taylor & Eggli, transverse section (TS). Uniseriate epidermis containing prismatic crystals (white arrows), covered by thick cuticle. Substomatal chambers cross through hypodermis. 2. *Arrojadoa rhodantha* (Gürke) Britton & Rose (SEM). Prismatic crystals of two sizes in epidermal cells. 3-4. *Arrojadoa penicillata* (Gürke) Britton & Rose (TS). 3. Periderm (P) formed above epidermis (arrow). 4. *Stephanocereus leucostele* A. Berger. Layers of cubic lignified cork cells (Li) alternating with suberized, collapsed cells (*). 5. Cork composed of several layers of cells, tangentially elongated. Note layers of lignified cells alternating with thin walled suberized. Phellogen (arrow). Ct - cuticle, Co - cork, Hy - hypodermis, Sc - substomatal chamber. Scale bar 1 = 25 µm; 2 = 5 µm; 3 = 100 µm; 4 = 10 µm; 5 = 50 µm

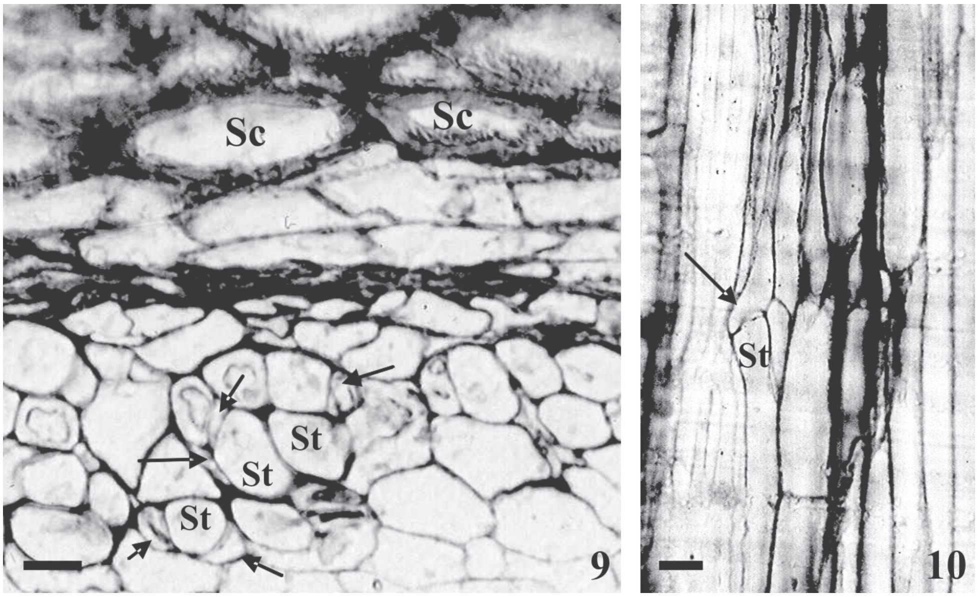
S. luetzelburgii). Fibres are libriform and septate, containing starch grains (Fig. 15-16). Rays are large, wide and tall (Fig. 11-13). Unlignified parenchyma was observed composed of a few cells (*Stephanocereus*), or in continuous bands in *A. dinae*, *A. penicillata* and *A. rhodantha* (Fig. 13), or lines and bands in *A. bahiensis*.

Discussion

In Cactaceae, the epidermis and hypodermis are collectively denominated "skin" (Gibson & Nobel 1986). Besides giving support to the succulent stem, the skin acts to conserve water, protect inner tissues against sunlight and provide defense against organisms



Figures 6-8. Fundamental system. 6. *Stephanocereus leucostele* A. Berger (Transverse section - TS). Hypodermis containing prismatic crystals (arrows) and substomatal chamber (Sc). 7. *Brasilicereus markgraffii* Backeberg, (TS). Phellogen (arrow). Collenchymatic hypodermis composed of only one layer of cells. Note sclereids (Sc) in the cortex. 8. *Arrojadoa bahiensis* (P.J. Braun & Esteves) N.P. Taylor & Eggli (TS). Cortex. Palisade parenchyma containing mucilage cell. Ct - cuticle, Hy - hypodermis, Mu - mucilage cell, Pe - periderm, Pc - palisade cortex. Scale bar 6, 8 = 50 µm; 7= 100 µm.



Figures 9-10. Vascular system: phloem. 9. *Brasilicereus markgraffii* Backeberg (TS). Sieve tube elements and companion cells (arrows). 10. *Arrojadoa dinae* Buining & Brederoo (longitudinal section - LS). Sieve tube element with oblique sieve plate (arrow). St - sieve tube element, Sc - sclereid. Scale bar 23, 25 = 20 µm.

(Gibson & Nobel 1986).

Like the great majority of cacti, *Arrojadoa, Stephanocereus* and *Brasilicereus* have uniseriate epidermis, covered by a thick cuticle (Gibson & Horak 1978; Gasson 1981; Gibson & Nobel 1986; Mauseth 1996, 1999). Stomata are parallelocytic and superficial, commonly observed in Cactoideae members (Eggli 1984). Generally in succulent xerophytes, the epidermis may be composed of several layers of cells, or there is a hypodermis underneath it (Fahn & Cutler 1992). *Arrojadoa* and *Stephanocereus* have a well developed hypodermis, with several layers of collenchyma cells, while in *Brasilicereus* the hypodermis is poorly developed, composed of only one layer of colenchyma cells. These collenchymatic hypodermal cells have well developed primary pit fields, as also observed by Gibson & Horak (1978) in Pachycereeae species. Conde (1975) called them intercell pits in *Opuntia*, while Metcalfe & Chalk (1950) mentioned that they are channels similar to pit channels.

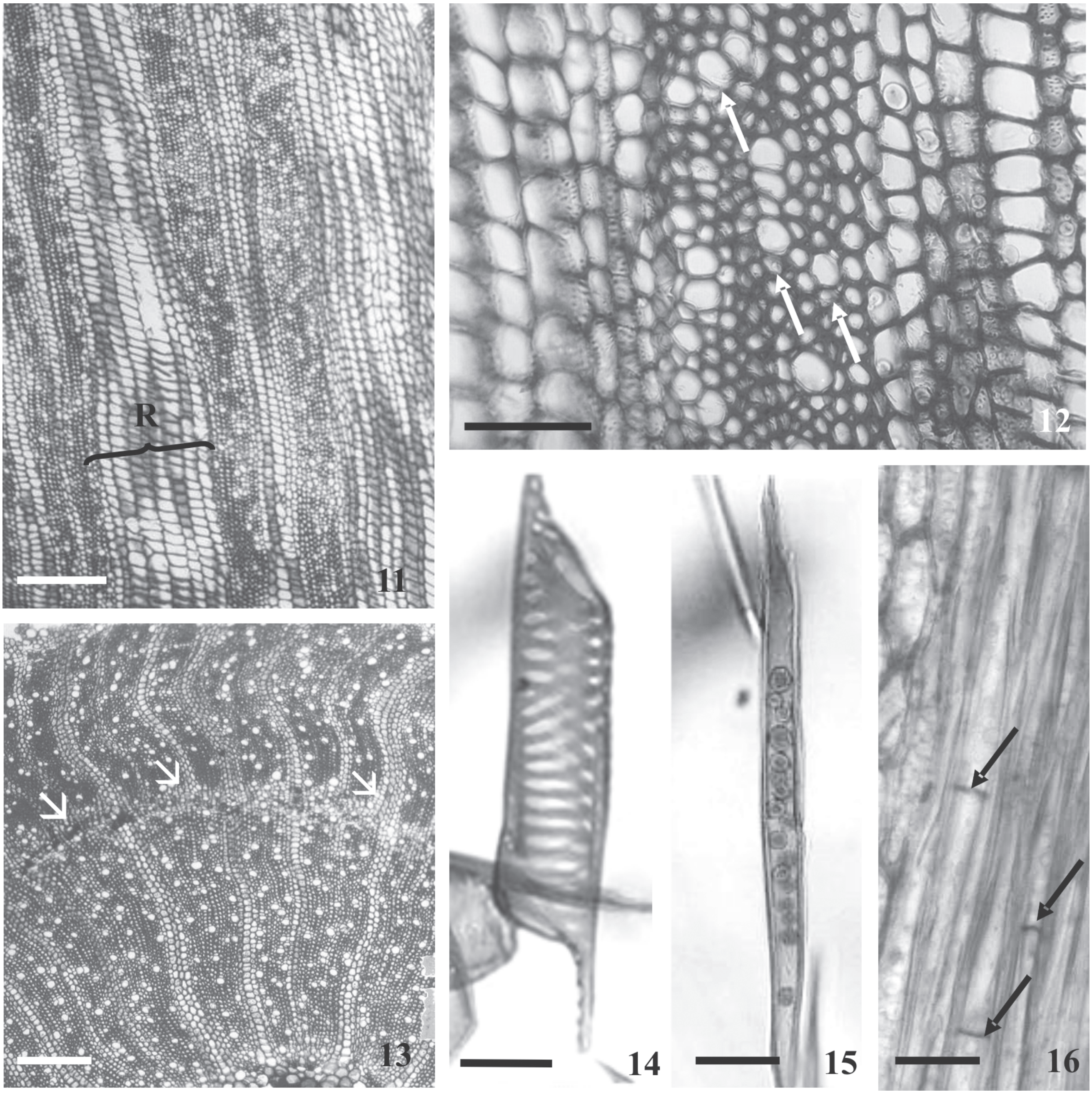
In the family, anatomical characters of the epidermis and hypodermis have taxonomic value, allowing the separation of groups (Gibson & Horak 1978; Gasson 1981; Nyffeler & Eggli 1997). Gibson & Horak (1978) recalled that xeromorphic characters are not always related to ecological conditions. The authors observed in Pachycereeae different species occurring at the same habitat that have distinct characters related to the thickness of the skin.

Distinct from other xerophytes, mostly Cactaceae have stomata situated on the same level as the other epidermal cells (Eggli 1984; Fahn & Cutler 1992). This is due to the photosynthesizing mechanism, CAM, (Gibson & Horak 1978; Fahn & Cutler 1992). The long substomatal chamber which crosses the thick hypodermis permits low transpiration loss, keeping the stomata opened (Fahn & Cutler 1992). Darling (1989) observed that the CO_2 and O_2 rates of exchange are low due to the low transpiration rates.

According to Nakata (2002), crystals play several roles in the plant body, such as controlling ion balance, defense, support, absorption and reflection of light. The occurrence of crystals in the epidermis and hypodermis of cacti, as observed in all studied species, is described by many authors as an adaptation to xeric conditions (Darling 1989; Fahn & Cutler 1992), reflecting the sunlight, and protecting subjacent chlorenchyma.

The occurrence of crystals may be of taxonomic use in the family. Silva & Alves (1999) support the subdivision of splitting *Pilosocereus* into two subgenera based on the presence of crystals. Gibson & Horak (1978) used the occurrence of crystals in the epidermis and hypodermis as a character, among others, to corroborate the division of Pachycereeae in two subtribes, remarking that crystals may play a role in controlling herbivory. However, in *Arrojadoa*, *Stephanocereus* and *Brasilicereus*, the presence and type of crystals do not differ among the species or genera. It is worth noting that in the species there are prismatic crystals of two sizes in the epidermis, not mentioned in the literature so far.

The occurrence of druses seems to be common in cacti. Mauseth & Landrum (1997) mentioned the presence of druses in the old cortex of species of *Pereskia*. In *Leptocereus*, Mauseth (1988a) noticed druses in the cortex and pith, and the ones in the cortex are larger. In the studied species druses are found in cortex and pith, which may play a role in the regulation of total calcium (Volk *et al.* 2002).



Figures 11-16. Vascular system: xylem. 11-12. *Stephanocereus luetzelburgii* (Vaupel) N.P. Taylor & Eggli, (TS). 11. General view of secondary xylem. Note wide rays (R). 12. High magnification. Solitary vessels and scanty axial parenchyma (arrows); note large rays. 13. *Arrojadoa penicillata* (Gürke) Britton & Rose (TS), (TS). Overall view. Note band of unlignified parenchyma (arrows). 14. *Stephanocereus leucostele* A. Berger. Dissociated vessel element with simple perforation plate and bordered pits, scalariform to opposite. 15. *Brasilicereus markgraffii* Backeberg. Dissociated libriform fibre containing starch grains. 16. *Arrojadoa dinae* (Longitudinal Tangential Section - LTS). Libriform septate fibres. Note sept (arrow). R - rays. Scale bar: 11, 13 = 200 µm; 12, 14 = 100 µm, 15-16 = 40 µm.

The epidermal origin of the phellogen has been described for several members of Cactaceae, such as *Uebelmmania* (Nyffeler 1997), *Espostoa* (Mauseth 1999), *Melocactus* (Mauseth 1989; Yoshikawa *et al.* 2005), *Cipocereus* (Soffiatti & Angyalossy 2003) among others (Gibson & Nobel 1986; Mauseth *et al.* 1998).

Several authors (Esau 1967; Mauseth 1988b; Dickison 2000) showed that, when the origin is epidermal, the periderm is formed under the epidermis. However, something quite diverse occurs in *Arrojadoa*, *Stephanocereus* and *Brasilicereus*. Here the periderm is formed above the epidermis, easily recognized by the presence of prismatic crystals. In this case, the periderm is formed through centrifuge differentiation of phellogen, where the dividing epidermal cell forms phellogen to the outside. In the literature, this has only been described by Van Tieghen (1918) for *Salix, Nerium* and *Solanum*, where the author observed the same situation as in *Arrojadoa*, *Stephanocereus* and *Brasilicereus*. This has not been mentioned so far for Cactaceae (Gibson & Nobel 1986; Mauseth 1989; 1999; Nyffeler 1997; Mauseth *et al*. 1998).

The phelloderm in *Arrojadoa*, *Stephanocereus* and *Brasilicereus* has only a few layers of cells, with no special characteristic. Regarding phellem, this is different in *S. leucostele*, where the cells are cube-shaped in transverse section, instead of being tangentially elongated as seen in the other species.

Mucilage cells are commonly found in the cortex and pith of all studied species, more abundantly in *Arrojadoa bahiensis*. According to several authors, (Gibson 1977; Gregory & Baas 1989), mucilage is related to water storage, and is an important adaptation to dry environments.

Gregory & Baas (1989) mentioned that mucilage cells have probably evolved separately in each tribe in Cactaceae, and arose first in the cortex and then in the pith. Mauseth *et al*. (1998) mentioned, however, that the occurrence of mucilage cells in the cortex and pith is not a taxonomic character, due to its variable occurrence, subject to environmental factors. Gibson & Horak (1978) considered that mucilage acquisition in Pachycereeae happened only once in the tribe and once present, was never again lost.

Sclereids were observed in the cortex of *Brasilicereus markgrafii*, as observed in *Cipocereus minensis* (Soffiatti & Angyalossy 2003). This character is only reported for species of *Eulychnia* (Notocacteae, Nyffeler *et al*. 1997). The authors considered that it plays a role in keeping the integrity of the cortex in periods of severe drought. Furthermore, sclereids may also prevent herbivory.

In all studied species, cortex and pith have several vascular bundles. During the evolutionary development of a succulent cortex and pith, it was necessary to improve stem vascularization, through the appearance of vascular bundles in cortex and pith (Mauseth 1988a). According to Fahn & Cutler (1992), cortical bundles are developed independently from the primary vascular system of the stem. Mauseth (1989) compared the cortical bundles to leaf venation, showing that both act in the same way, improving conductivity. In *Leptocereus*, Mauseth (1988a) observed only secondary phloem in cortical bundles. However, Mauseth (1996) noticed cortical bundles with secondary growth in several species belonging to the tribes Cereeae and Browningieae. In *Arrojadoa*, *Stephanocereus* and *Brasilicereus*, there are both phloem and xylem in cortical and pith bundles, although the pith bundles are more developed.

The occurrence of little phloem is widely noted for the family (Gibson & Nobel 1986; Mauseth 1989; 1996; Mauseth *et al.* 1998). Gibson & Nobel (1986) noticed the occurrence of caps of fibres outside conductive phloem, which they considered to have originated from primary collapsed phloem. In *Arrojadoa*, *Stephanocereus* and *Brasilicereus*, the presence of stone cells/sclereids were observed outside conductive phloem. Furthermore, the collapsed primary phloem can still be seen between the secondary phloem and the sclereids. As observed in *Cipocereus* (Soffiatti & Angyalossy 2003), they may have a pericycle origin.

Secondary xylem is similar to what is extensively described for woody representatives of the family (Gibson 1973; 1977; 1978; Gibson & Horak 1978; Mauseth 1989; 1993; 1996; Soffiatti & Angyalossy 2005). Short, narrow vessel elements play a role in preventing cavitation (Mauseth 1993). Septate fibres are common in the studied species and in other members of the family as well, sharing storage functions with axial and radial parenchyma. This set of traits characterizes the secondary xylem of Cactaceae as highly adapted and derived (Gibson & Nobel 1986; Mauseth 1993).

The present work shows a very similar anatomical structure of dermal, fundamental and vascular systems in *Arrojadoa*, *Stephanocereus* and *Brasilicereus* between all species, and to *Cipocereus* (Soffiatti & Angyalossy 2003; 2005). This may reflect the close proximity of woody genera in the tribe, although it does not allow any inference regarding their phylogenetic relationships. Worth mentioning as diagnostic characters are the following: the occurrence of an exclusive phellem in *S. leucostele*, composed of cubic cells in transverse section; the presence of a poorly developed hypodermis in *B. markgraafii*; the occurrence of sclereids in the cortex in *B. markgraafii*. *B. markgraafii* and *C. minensis* (Soffiatti & Angyalossy 2003) share the presence of sclereids in the cortex and a poorly developed hypodermis, which could indicate their closeness. Further molecular studies might clarify these matters.

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References

Carlquist, S. 1988. **Comparative wood anatomy**. Berlin, Springer-Verlag.

Chamberlain, C.J. 1932. **Methods in plant histology**. 5 ed. Chicago, The University of Chicago Press.

Conde, L.F. 1975. Anatomical comparisons of five species of *Opuntia* (Cactaceae). **Annals of the Missouri Botanical Gardens 62**: 425-473.

Darling, M.S. 1989. Epidermis and hypodermis of the *Saguaro cactus* (*Cereus giganteus*): anatomy and spectral properties. **American Journal of Botany 76**: 1698-1706.

Dickson, W.C. 2000. **Integrative Plant Anatomy**. San Diego, Harcourt Academic Press.

Eggli, U. 1984. Stomatal types of Cactaceae. **Plant Systematics and Evolution 146**: 197-214.

Esau, K. 1967. **Plant Anatomy**. New York, John Wiley & Sons, Inc.

Fahn, A. & Cutler, D.F. 1992. **Xerophytes**. Berlin & Sttutgart, Gebruder Borntraeger.

Gasson, P. 1981. Epidermal anatomy of some North American globular cacti. **The Cactus and Succulent Journal of Great Britain 43**: 101-108.

Gerlach, D. 1984. **Botanische Mikrotechnik**. Sttutgart, Sttutgart, Georg Thieme Verlag.

Gibson, A.C. 1973. Comparative anatomy of secondary xylem in Cactoideae (Cactaceae). **Biotropica 5**: 29-65.

Gibson, A.C. 1977. Wood anatomy of *Opuntias* with cylindrical to globular stems. **Botanical Gazette 138**(3): 334-351.

Gibson, A.C. 1978. Wood anatomy of *Platiopuntias*. **Aliso 9**: 279-307.

Gibson, A.C. & Horak, K.E. 1978. Systematic anatomy and phylogeny of Mexican columnar cacti. **Annals of the Missouri Botanical Garden 65**: 999-1057.

Gibson, A.C. & Nobel, P.S. 1986. **The cactus primer**. Cambridge & London, Harvard University Press.

Gregory, M. & Baas, P. 1989. A survey of oil cells in the dicotyledons with comments on their replacement by and joint occurence with mucilage cells. **Israel Journal of Botany 34**: 167-186.

Iawa Committee. 1989. List of microscopic features for hardwood identification. **IAWA Bulletin 10**: 219-332.

Johansen, D.A. 1940. **Plant microtechnique**. New York, McGraw-Hill Book Co. Inc.

Mauseth, J.D. 1988a. Systematic anatomy of the primitive cereoid cactus *Leptocereus quadricostatus*. **Bradleya 6**: 49-64.

Mauseth, J.D. 1988b. **Plant Anatomy**. California, The Benjamin Cummings Publishing Company, Inc. Menlo Park.

Mauseth, J.D. 1989. Comparative structure-function within a strongly dimorphic plant, *Melocactus intortus* (Cactaceae). **Bradleya 7**: 1-12.

Mauseth, J.D. 1993. Medullary bundles and the evolution of cacti. **American Journal of Botany 80**: 928-932.

Mauseth, J.D. 1996. Comparative anatomy of tribes Cereeae e Browningieae (Cactaceae). **Bradleya 14**: 66-81.

Mauseth, J.D. 1999. Comparative anatomy of *Espostoa, Pseudoespostoa* and *Vatricania* (Cactaceae). **Bradleya 17**: 27-37.

Mauseth, J.D. & Landrum, J.V. 1997. Relictual vegetative anatomical characters in Cactaceae: the genus *Pereskia*. **Journal of Plant Research 110**: 55-64.

Mauseth, J.D. & Plemons, B.J. 1995. Developmentally variable, polymorphic woods in cacti. **American Journal of Botany 82**: 1199-1205.

Mauseth, J.D. & Plemons-Rodriguez, B. 1997. Presence of paratracheal water storage tissue does not alter vessel characters in cactus wood. **American Journal of Botany 82**: 1199-1205.

Mauseth, J.D. & Plemons-Rodriguez, B. 1998. Evolution of extreme xeromorphic characters in wood: a study of nine evolutionary lines in Cactaceae. **American Journal of Botany 85**(2): 209-218.

Mauseth, J.D.; Terrazas, T. & Loza-Cornejo, S. 1998. Anatomy of relictual members of subfamily Cactoideae, IOS Group 1a (Cactaceae). **Bradleya 16**: 31-43.

Metcalfe, C.R. & Chalk, L. 1950. **Anatomy of the dicotyledons**. Oxford, Clarendon Press.

Nakata, P.A. 2002. Calcium oxalate crystals morphology. **Trends in Plant Science 7**: 324.

Nyffeler, R. 1997. Stem anatomy of *Uebelmannia* (Cactaceae) - with special reference to *Uebelmannia gumifera*. **Botanica Acta 110**: 489-495.

Nyffeler, R. & Eggli, U. 1997. Comparative stem anatomy and systematics of *Eriosyce sensu lato* (Cactaceae). **Annals of Botany 80**: 767-786.

Nyffeler, R.; Eggli, U. & Leuenberger, B.E. 1997. noteworthy idioblastic sclereids in the stems of *Eulychnia* (Cactaceae). **American Journal of Botany 84**(9): 1192-1197.

O'Brien, T.P.; Feder, N. & McCully, M.E. 1965. Polychromatic staining of plant cell walls by toluidine blue O. **Protoplasma 59**(2): 368-373.

Richter, H.G. 1985. Wood and bark anatomy of Lauraceae II. *Licaria* Aublet. **Iawa Bulletin 6**(3): 187-199.

Silva, D.C. & Alves, J.L.H. 1999. Anatomia dos órgãos vegetativos de seis espécies de *Pilosocereus* Byles & Rowley (Cactaceae). **Boletim de Botânica da Universidade de São Paulo 18**: 53-60.

Soffiatti, P. & Angyalossy-Alfonso, V. 2003. The stem in *Cipocereus* Ritter (Cactaceae). **Bradleya 21**: 39-48.

Soffiatti, P. & Angyalossy-Alfonso, V. 2005. Wood anatomy in *Cipocereus* Ritter (Cactaceae). **IAWA Journal 26**(3): 299-308.

Taylor, N.P. 1997. Cactaceae. In: S. Oldfield (ed.). **Cactus and Succulent Plants - Status Survey and Conservation Action Plan**. IUCN/SSC Cactus and Succulent Specialist Group. IUCN, Gland & Cambridge.

Taylor, N.P. & Zappi, D.C. 1989. An alternative view of generic delimitation and relationship in tribe Cereeae (Cactaceae). **Bradleya 7**: 13-40.

Taylor, N.P. & Zappi, D.C. 2004. **Cacti of Eastern Brazil**. Kew, UK, Royal Botanic Gardens.

Terrazas, T. & Arias, S. 2003. Comparative stem anatomy in the subfamily Cactoideae. **The Botanical Review 68**: 444-473.

Van Tieghen, P.H. 1918. **Éléments de Botanique. I. Botanique Générale**. Paris, Masson et Cie., Éditeurs, Librairies de L'Academie de Médicine.

Volk, G.M.; Lynch-Holm, V.J.; Kostman, T.A.; Goss, L.J. & Francheschi, V.R. 2002. The role of druse and raphide calcium oxalate crystals in tissue calcium regulation in *Pistia stratiotes* leaves. **Plant biology 4**: 34-45.

Yoshikawa, R.C.S.; Soffiatti, P. & Angyalossy, V. 2004. Root and stem anatomy of *Melocactus bahiensis* and *Melocactus concinnus* (Cactaceae, subfamily Cactoideae - tribe Ceereae). **Revista de Biologia Neotropical (1-2)**: 11-22.