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STEM AND ROOT ANATOMY OF *MELOCACTUS BAHIENSIS* AND *M. CONCINNUS* (CACTACEAE, SUBFAMILY CACTOIDEAE, TRIBE CEREEAE)

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ABSTRACT: In this work are discussed and illustrated the anatomical features of the cephalium, the globose stem and the root in *Melocactus bahiensis* (Britton & Rose) Luetzelb. and *M. concinnus* Buining & Brederoo. As a dermal tissue we found a uniseriate epidermis covered by a thick cuticle in the photosynthesizing stem. The epidermis originates the phellogen, which will form the peridermis, found in the cephalium, base of stem and root. The ground tissue is characterised by a thick hypodermis (poorly developed in the cephalium), and a palisade parenchyma below it (absent in the cephalium). The inner cortex is composed by large parenchyma cells. Mucilage cells are present in the cortex and the pith. In the cephalium and apex of the globose stem, the secondary vascular system is organised in bundles. In the medium portion of the stem, the secondary xylem is mainly composed of vascular tracheids. At the base of stem and root, the secondary xylem is composed of vessel elements with bordered pits, simple perforation plate, axial scanty paratracheal parenchyma, libriform septate fibres and large primary and secondary rays. The phloem is composed of sieve tube elements, with simple sieve plates, companion cells and parenchyma. The anatomy of the specialized non photosynthesizing cephalium is much simpler than of the globose stem. The globose stem is the photosynthesizing organ of the plant, so its anatomy shows several adaptations towards the exchange of gas, storage and transport of water, plus mechanical support.

KEY WORDS: Wood anatomy, Cactaceae, *Melocactus,* vascular tracheids.

RESUMO: Neste trabalho são discutidos e ilustrados vários aspectos anatômicos do cefálio, caule globoso e raiz de *Melocactus bahiensis* (Britton & Rose) Luetzelb. e *M. concinnus* Buining & Brederoo. Como tecido de revestimento, no caule fotossintetizante, ocorre uma epiderme unisseriada, coberta por espessa cutícula. A epiderme origina o felogênio, e este, por sua vez, a periderme, encontrada no cefálio, base do caule e raiz. O tecido fundamental é caracterizado por uma hipoderme espessa (pouco desenvolvida no cefálio), e um parênquima paliçádico abaixo desta. O córtex interno é composto por células parenquimáticas grandes. Células de mucilagem ocorrem no córtex e na medula. No cefálio e ápice do caule, o sistema vascular está organizado em feixes, com crescimento secundário. Na porção mediana do caule, o xilema secundário é composto principalmente por traqueídes vasculares. Na base do caule e na raiz, o xilema secundário é composto por elementos de vaso pontoados, placa de perfuração simples, parênquima axial paratraqueal escasso, fibras libriformes septadas e raios primários e secundários largos. O floema secundário é composto por elementos de tubo crivado com placa crivada simples, células companheiras e parênquima. A anatomia do cefálio mostra-se muito mais simples do que a do caule. O caule globoso, como órgão fotossintetizante, possui várias adaptações anatômicas voltadas para trocas de gases, armazenamento e condução de água, e suporte mecânico.

PALAVRAS-CHAVE: Anatomia do lenho, Cactaceae, *Melocactus,* traqueídes vasculares.

Introduction

The genus *Melocactus* (L.) Link & Otto is composed of 32 species, ranging from Mexico to South-eastern Brazil, with its centre of diversity represented in Eastern Brazil, where 15 species are endemic (Taylor, 2000). About the other 17 species, three are found in the Amazon region, nine in the Caribbean, and five species occurs in the Andes, from western Mexico to southern Peru (Taylor, 2000). The genus belongs to the subfamily Cactoideae Salm-Dyck sensu F. Buxb., to the tribe Cereeae K. Schum., where it is considered one of the most derived taxon due to its dimorphic shoot, with the presence of a cephalium (Taylor & Zappi, 1989). The epigeal portion of *Melocactus* is divided in two different portions: a globose stem and a cephalium, which is a terminal specialized reproductive structure which bears the flowers and fruits.

Melocactus have a monopodial shoot, developing a globose photosynthesizing stem for several years, when the apex shoot meristem changes and starts to form a different structure at the top of the globose stem, the so called "cephalium" or "head" (Mauseth, 1989). The cephalium is a reproductive non photosynthesizing structure, fully covered in spines and trichomes, which bears flowers and fruits (Gibson & Nobel, 1986; Mauseth, 1989). In *Melocactus*, the cephalium is terminal, and once it is formed, the photosynthesizing globose stem ceases to grow, and only the cephalium elongates (Mauseth, 1989).

With respect to the anatomy of the genus, Mauseth and collaborators presented several works treating the anatomy of cephalium and stem of *Melocactus intortus* (Mill.) Urb. Mauseth (1989) compared the globose stem and the cephalium, discussing their different functions and structures. Sajeva & Mauseth (1991) correlated the structure of the photosynthetic stem with the structure of Angiosperms leaves. Yet Mauseth et al. (1995) discussed the occurrence of polymorphic wood in several genera of Cactaceae, including *M. intortus*. In several other papers (Mauseth, 1996; Mauseth & Plemons-Rodriguez, 1997, 1998) the authors discussed the anatomy, taxonomy and evolution of several other cacti species, including the above mentioned species. As stated by Mauseth (1989), species which are dimorphic offer a great opportunity for structure-function investigation, as different parts of the same individual can be analyzed and compared.

In the present work the anatomy of *Melocactus bahiensis* (Britton & Rose) Luetzelb. and *M. concinnus* Buining & Brederoo is studied and illustrated, and correlations between anatomical structure, habit and habitat are discussed.

Material and methods

Material

Two adult specimens of *Melocactus bahiensis* (Soffiatti 30 and 31) were collected in Grão Mogol, Minas Gerais, Brazil, and one of *M. concinnus* (Soffiatti 32) was collected in Palmeiras, Bahia, Brazil. Both species occur in the *campos rupestres* of the Espinhaço Range. The samples were identified by D. Zappi (Royal Botanic Gardens, Kew, UK), and deposited at the Herbarium of the University of São Paulo (SPF).

Methods

Samples from the cephalium - central and peripheral regions - and the globose stem - divided in three portions: base, medium and apex - and the root - taken from the very basal portion - were fixed in 70% formalin-acetic-alcohol (Johansen, 1940). The samples were embedded in polyetihenoglycol (PEG 1500) and prepared according to standard techniques (Gerlach, 1984), double-stained with safranin and astrablue. The sections were mounted in synthetic resin.

Maceration was prepared using Jeffrey's solution (Johansen, 1940), stained with safranin and mounted in a 50/50 solution of glycerine and water.

The epidermis was dissociated according to Ghouse & Yunus (1972), and stained with fucsine and astrablue for the stomata observations. The presence of mucilage was detected with astrablue,

according to Richter (1977). Tests for starch were made according to Jensen (1962).

The wood descriptions are based on the recommendations outlined in the IAWA List of Microscopic Features for Hardwood Identification (IAWA, 1989).

The quantitative data (Tab. I) were based on 20 measurements for vessel diameter and length, tracheids diameter and length, sieve tube elements diameter, fibres length, rays height and width, taken on the basal portions of the stem and the root. The tangential and radial mucilage cells diameters were measured at the apex of stem. The measurements were realised using a Zeiss optical microscope attached to a computer, using the program KS100/3.0. For each feature the mean and the standard deviation were calculated.

Results

Dermal tissue system

Epidermis: uniseriate, covered by a thin cuticle in the central portion of the cephalium (Fig. 1) and by a thick cuticle in the apex and medium regions of the globose stem (Fig. 4); prismatic crystals are present in the epidermis of the stem; stomatal apparati are localized at the same level of epidermal cells (Fig. 3 & 4); stomata are parallelocytic type.

Periderm: occurs in the peripheral region of the cephalium; in the stem it starts as scattered patches in the medium region of the stem; it is well developed at the base of the stem (Fig. 5), as well as in the root (Fig. 6). Phellogen differentiates from the epidermis. The cork is formed by several layers of lignified cells that alternate with suberized cells. In the stem and cephalium, the cork cells are tangentially elongated (Fig. 5), while in the root, radially elongated (Fig. 6). The pheloderm is composed of one or two layers of flat thin walled cells in the cephalium and stem (Fig. 5), and several layers in the root (Fig. 6).

Ground tissue system

Hypodermis: poorly developed in the cephalium (Fig. 1); absent in the root; present in the stem as a whole (Fig. 3 & 4). In the photosynthesizing regions, is very well developed, constituted of five or more layers of collenchymatic cells, irregularly thickened, containing prismatic crystals. Large substomatal chambers develop through hypodermis (Fig. 3 & 4).

Cortex: composed of rounded and irregular parenchymatic cells in the cephalium (Fig. 1). In the photosynthesizing stem, is divided into two regions: the outer cortex, organized in a palisade chlorenchyma, and the inner cortex, consisting of rounded and irregular thin walled parenchimatic cells, and many intercellular spaces (Fig. 7). Mucilage cells occur in the internal cortex of cephalium and stem, and are absent in the root. *Melocactus concinnus* has larger mucilage cells in the apex region of the stem, when compared with *M. bahiensis* (Tab. I). In the base of the stem, mucilage cells have a tangential diameter varying within 250-420-600 mm and radial diameter within 230-320-450 mm. Starch grains are abundant in the stem, in the cortex and pith.

Vascular tissue system

Cortical and medullary vascular bundles (Fig. 7) occur in the cephalium and stem, presenting secondary growth.

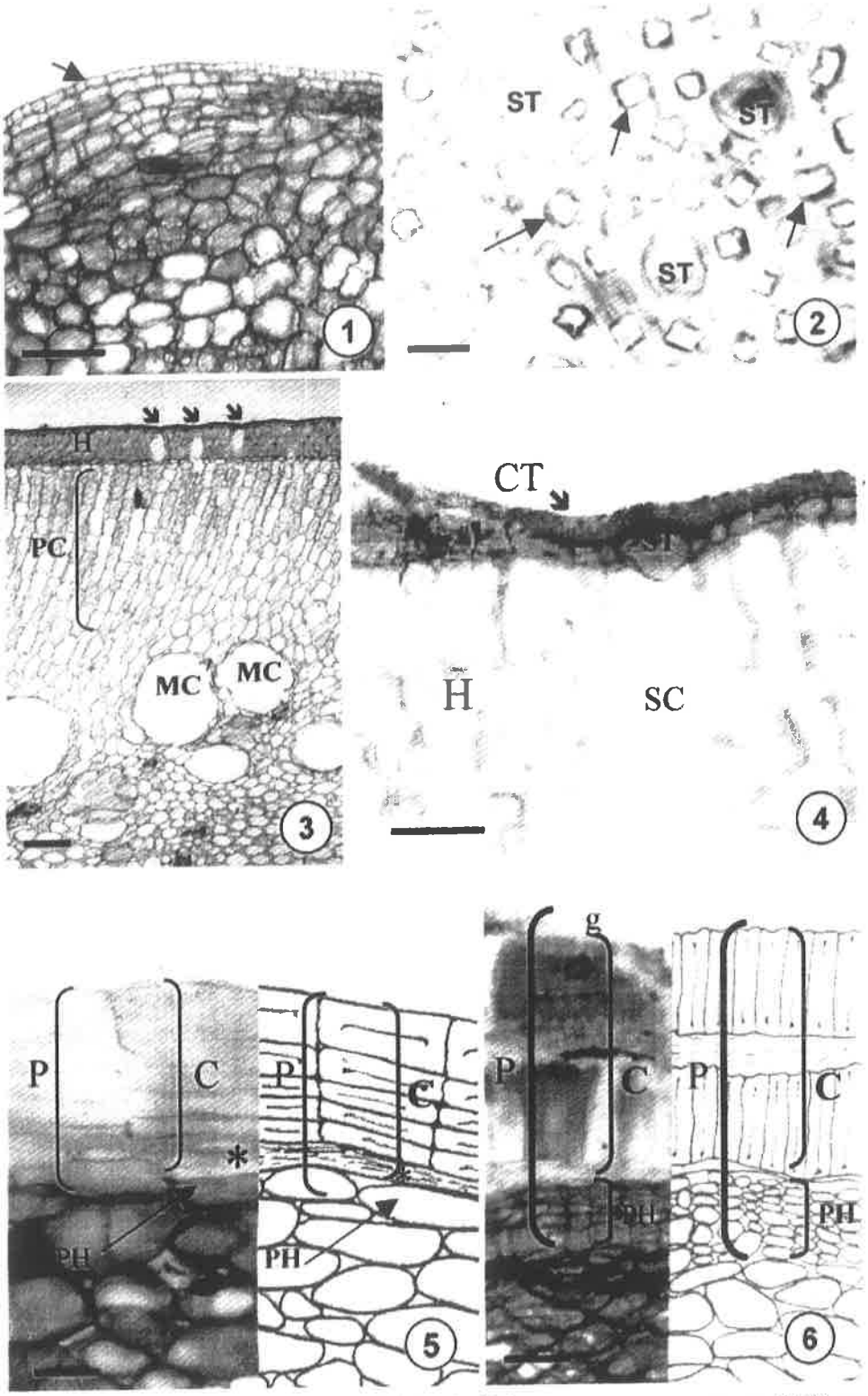
The vascular system at the cephalium and the apex of the stem (Fig. 7) consists of vascular bundles which already present secondary growth; the fascicular cambium forms only axial elements of xylem and phloem in each bundle. At the medium region of the stem, the vascular system is far more developed (Fig. 8), organized in an almost complete cylinder. At this stage the interfascicular cambium is already formed, and originates the primary rays (Fig. 8); the fascicular cambium continues forming the axial elements of xylem and phloem; the secondary xylem is mainly composed by vascular tracheids (Fig. 9 & 10), a few vessels, large rays (Fig. 10) and no fibres. The vascular tracheids are fusiform cells (Fig. 11), shorter and wider than a vessel element, with annular or helical secondary walls (Figs. 10-11), which protrude into the cell lumen. At the base of the stem, the vas-

cular system is organized in a complete cylinder, where one can easily distinguish two regions in the secondary xylem (Figs. 13-14): the one formed mainly by vascular tracheids, and the last formed, composed of vessel elements (Fig. 12) with bordered pits and simple perforation plates, axial parenchyma, septate fibres (Fig. 16) and large rays (Fig. 15). At this stage of development, the fascicular and interfascicular cambia have the same activity. It can also be noticed at this stage the occurrence of rays with non lignified walls (Figs. 14-15). A non lignified axial parenchyma can be observed within the lignified cells of secondary xylem. The secondary phloem is relatively small when compared to the amount of secondary xylem formed (Fig. 17). The primary phloem can be seen as a collapsed region outside the secondary phloem (Fig. 17); the secondary phloem is composed of sieve tube elements, companion cells, axial and radial parenchyma. In earlier stages of development (Fig. 19), sclereids precursors can be seen in the periphery of secondary phloem. These sclereids precursors are parenchyma cells which undergo lignification of their walls, and at the base of the stem, adjacent to the secondary phloem they will occur in patches of sclereids (Fig. 18). In longitudinal section these sclereids are rectangular (Fig. 19).

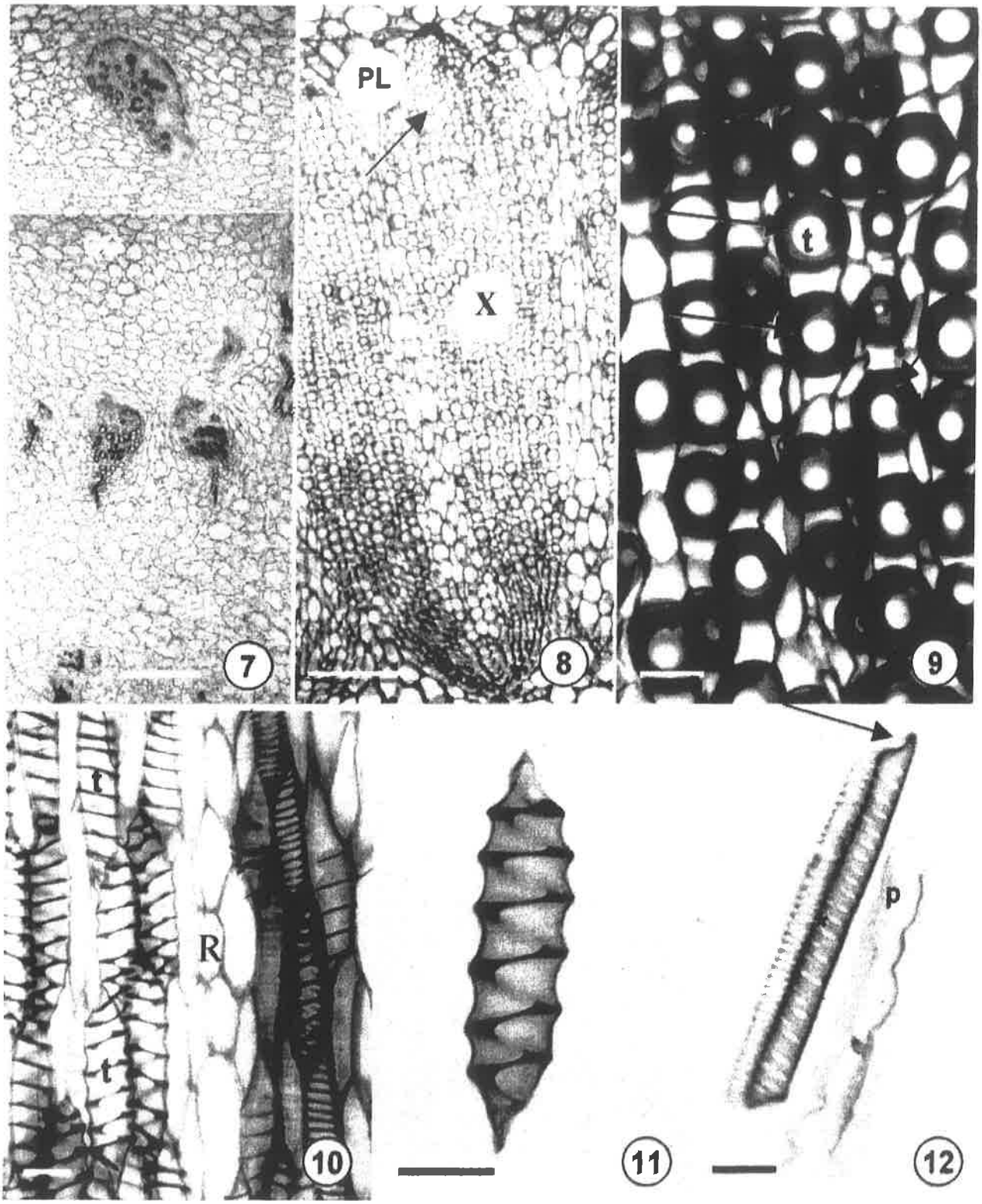
In the root (Fig. 20-23), the secondary xylem is similar to the stem in its composition, composed of vessel elements with bordered pits, simple perforation plate, scanty paratracheal parenchyma, septate libriform fibres, non lignified large primary and secondary rays (Figs. 20-21). A non lignified parenchyma observed in patches within the axial lignified elements of secondary xylem (Figs. 20-21, 23). In this patches there are only vessel elements and parenchyma cells; the fibres are absent (Fig. 23). Vascular tracheids are absent in the root. The secondary phloem is composed of sieve tube elements, companion cells, axial and radial parenchyma, similar to observed in the stem. There are no sclereids in the periphery of secondary phloem, differently from the stem; only the collapsed primary phloem can be seen (Fig. 21). The quantitative data are shown in the Table I.

Table 1 : Quantitative data of *Melocactus bahiensis* and *M. concinnus*. Observations: In *M. bahiensis* the given values are the average for the two specimens studied (*Soffiatti 30* and *31*); the mucilage cells were measured at the apex of stem.

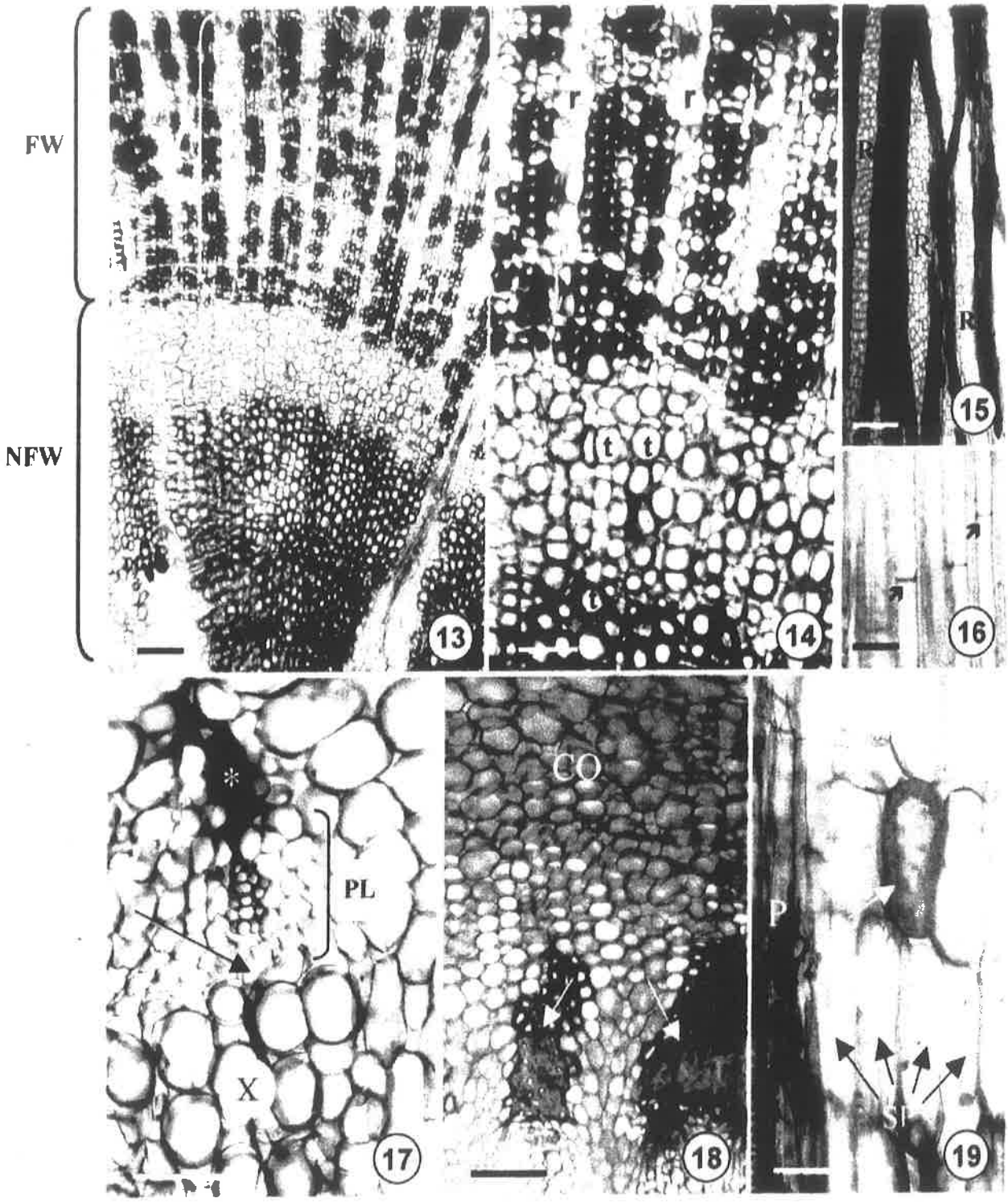
Species			Mucilage cells		Secondary xylem							Secondary phloem
					Vessel elements		Vascular tracheidss		Fibres	Rays		Sieve tube elements
			rd diam. (μm)	tg diam. (μm)	diam. (μm)	lenght (μm)	diam. (μm)	lenght (μm)	lenght (μm)	width (μm)	height (mm)	diam. (μm)
Melocactus bahiensis	Stem	X	321	275	28	236	57	258	506	193	1,8	7
		s	67,82	46,16	6,27	63,86	10,12	56,77	137,48	40	384,42	0,96
		Min/max	155-470	189-381	16-39	111-375	31-82	138-456	240-782	134-286	1,2-2,6	5-9
	Root	X	-	-	29	286	-	-	472	154	2,4	7
		S	-	-	9,78	86,72	-	-	112,37	50,84	149,98	0,67
		Min/max	-	-	14-45	106-456	-	-	228-702	78-273	2,2-2,5	5-8
Melocactus concinnus	Stem	X	494	446	26	271	54	290	532	174	1,8	8
		S	141,66	130,83	6,8	51,4	8,27	72,9	130,36	37,2	31,2	0,96
		Min/max	241-740	244-600	14-43	191-362	35-71	195-427	255-809	132-301	1,1-2,2	6-9
	Root	X	-	-	28	360	-	-	539	115	2,4	16
		s	-	-	5,2	58,7	-	-	115,05	34,4	255,68	3,42
		Min/max	-	-	19-43	244-463	-	-	262-745	68-191	2,1-2,7	11-24



Figures1-6 - Dermal tissue system of *Melocactus bahiensis* (Britton & Rose) Luetzelb. (*Soffiatti 30* and *31*) and *M. concinnus* Buining & Brederoo (*Soffiatti 32*). **1-2**. *Melocactus bahiensis*. **1**. Longitudinal section of cephalium; note uniseriate epidermis (arrow), covered by a thin cuticle, and hypodermis composed of 2 or 3 layers of cells (h) (*Soffiatti 31*). Scale bar = 50 mm. **2**. Paradermic view of epidermis, medium portion of globose stem; note numerous prismatic crystals (arrows) and stomata (st) (*Soffiatti 30*). Scale bar = 50 mm. **3-4**. *M. concinnus*, transverse section. **3**. Apex of globose stem; note general organization of tissues: epidermis covered in thick cuticle, stomatal chamber (sc) crossing hypodermis (h), palisade cortex (pc), inner cortex with mucilage cells (mc). Scale bar = 260 mm. **4**. Medium portion of globose stem; note thick cuticle (arrow), covering uniseriate epidermis; stomatal apparatus (st) at the same level as epidermal cells; hypodermis (h) with many layers of collenchimatic cells; stomatal chamber (sc) crossing hypodermis (h). Scale bar = 65 mm. **5-6**. *M. bahiensis*, transverse sections; periderm (p). **5**. Periphery of cephalium; cork (c) composed of layers of tangentially elongated lignified cells and crushed suberized cells (*); pheloderm (ph) with one layer of thin walled cells (*Soffiatti 31*). Scale bar = 55 mm. **6**. Root; cork (c) composed of layers of radially elongated lignified cells and crushed suberized cells; pheloderm (ph) with several layers of thin walled cells (*Soffiatti 30*). Scale bar = 35 mm.



Figures 7-12 - Vascular system of *Melocactus bahiensis* (Britton & Rose) Luetzelb. (*Soffiatti 30 and 31*) and *M. concinnus* Buining & Brederoo (*Soffiatti 32*); globose stem. **7-10**. *Melocactus concinnus*. **7-9**. Transverse section. **7**. Apex. General view of cortical bundles (arrow on the top) and medullary bundle (arrow on the bottom); co-cortex; pi-pith. Scale bar = 240 mm. **8-9**. Medium region. **8**. Secondary xylem composed mainly by vascular tracheids (t); note primary rays. pl-secondary phloem; x-secondary xylem; fascicular cambium region (arrow). Scale bar = 450 mm. **9**. Vascular tracheids (t); note the thick secondary walls that protrude to the lumen of the cells. Scale bar = 45 mm. **10-12**. Base. **10**. Longitudinal tangencial section, vascular tracheids (t); note the annular or helicoidal secondary walls, parenchyma cells and rays (R). Scale bar = 45 mm. **11-12**. *M. bahiensis* (*Soffiatti 30*). Maceration. **11**. Vascular tracheid . Scale bar = 55 mm. **12**. Vessel element with pits and simple perforation plate (arrow). Scale bar = 50 mm.



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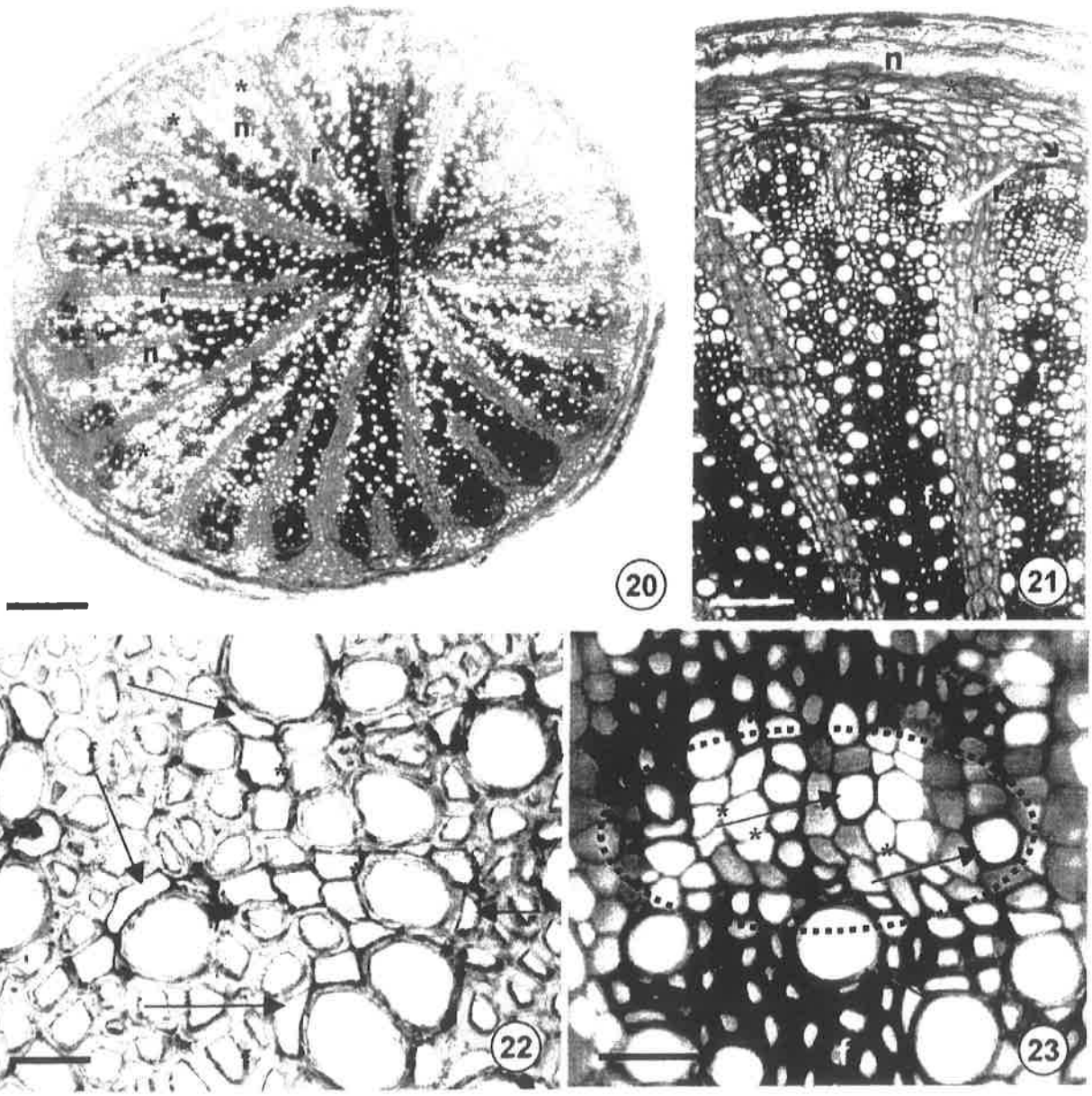
Figures 13-19 - Vascular system of *Melocactus bahiensis* (Britton & Rose) Luetzelb. (*Soffiatti 30* and *31*) and *M. concinnus* Buining & Brederoo (*Soffiatti 32*); globose stem. **13-14**. *Melocactus concinnus*, transverse section of base. **13**. Two distinct regions of the secondary xylem: the inner one corresponding to the non fibrous wood, where the vascular tracheids (t) are abundant (nfw); the outer one is the later formed fibrous wood (fw). Scale bar = 220 mm. **14**. High magnification view of the same region; the fibrous wood is composed of vessel elements, fibres, and axial and radial parenchyma, while the non fibrous wood is formed mainly by vascular tracheids, and the fibres are absent. Scale bar = 60 mm. **15**. M. bahiensis. Base. High and wide rays (r) (*Soffiatti 31*). Scale bar = 150 mm. **16-18**. *M. concinnus*. **16**. Base, septate libriform fibres (arrows). Scale bar = 20 mm. **17**. Medium portion; note secondary phloem (PL) and the crushed primary phloem (*); secondary xylem mostly composed of vascular tracheids (t); vascular cambium region (arrow). Scale bar = 90 mm. **18**. Base, note patches of sclereids (arrows) adjacent to the secondary phloem. Co-cortex. Scale bar = 110 mm. **19**. *M. bahiensis*, longitudinal section of medium portion. Sclereids precursors (sp) and one sclereid in differentiation (sc) adjacent to the phloem region (p); these sclereids precursors are parenchyma cells that will undergo lignification, forming the sclereids patches adjacent to the phloem (*Soffiatti 31*). Scale = 30 mm.



Figures 20-23 - Transverse section of the root of *Melocactus bahiensis* (Britton & Rose) Luetzelb. (*Soffiatti 30* and *31*) and *M. concinnus* Buining & Brederoo (*Soffiatti 32*). **20-21**. *Melocactus bahiensis* (*Soffiatti 31*). General view. Note primary and secondary non lignified rays. Scale bar = 330 mm. **21**. Secondary xylem composed of fibrous wood, with vessel elements, fibres, and axial and radial parenchyma; note the patches of non lignified parenchyma (white arrows). Scale bar = 100 mm. **22**. *M. concinnus*, high magnification; secondary xylem with vessel elements, scanty paratracheal parenchyma (arrow) and fibres. Scale bar = 25 mm. **23**. *M. bahiensis*, high magnification of a region of non lignified parenchyma in the secondary xylem (circle); note non lignified parenchyma cells scattered among vessel elements (arrows), and the lower region with larger vessel elements (*) and fibres (f) (*Soffiatti 30*). Scale bar = 40 mm.

Discussion

The globose stem of *Melocactus bahiensis* and *M. concinnus* is covered by what Gibson & Nobel (1986) called "skin" and is composed by the epidermis covered by a thick cuticle and the underlying hypodermis. This system represents an efficient protection against the solar radiation and the loss of water (Darling, 1989) allowing the exchange of gases and providing support to the plant body (Gibson & Nobel, 1986). The hypodermis also plays a role in water storage. Paviani (1978) mentioned that the high concentration of cellulose in the thick primary walls of the hypodermis cells is probably related to water storage, considering the hygroscopic properties of cellulose. The crystals present in the hypodermis cells reflect the sun rays, and thus protect the photosynthesizing tissues of the cortex (Darling, 1989; Fahn & Cutler, 1992). Being leafless plants, the stem is the photosynthesizing organ, and has all the adaptations for an efficient gas exchange, protection against the sun light and water loss.

The parallelocytic stomata type observed in *Melocactus bahiensis* and *M. concinnus*, on the same level as the epidermal cells, is commonly present in other members of Cactoideae (Eggli, 1984).

In the cephalium of the two species of *Melocactus* studied, the epidermis was uniseriate, lacking stomata, with a poor developed hypodermis and the outer cortex was not differentiated in a palisade parenchyma. One must consider that the cephalium is a reproductive structure, not involved in photosynthesis, and the thick cover of trichomes and spines provides the support and protection for inner tissues. Thus, as also stated by Mauseth (1989) in the study of *Melocactus intortus*, the protection of a thick "skin" is not necessary.

The Periderm was observed in the cephalia, and globose stems, and the roots of *Melocactus bahiensis* and *M. concinnus*. The phellogen originated from the below epidermis, as seen in *M. intortus* (Mauseth, 1989) and *Cipocereus* (Soffiatti & Angyalossy, 2003). The Periderm protects the regions where there is no photosynthesis. Cooke (1948) pointed out that the Periderm probably acts also as a thermo isolator, protecting the basal portions of the stem and the roots from the high temperatures of the ground.

The cork cells of the root were distinct when compared with the cork of the stem and cephalium in the studied species. In the stem and cephalium, it was composed of tangentially elongated lignified cells, while in the root the cells were radially elongated. In *Melocactus intortus*, the only difference found between stem and root was that the *Periderm* was more developed in the former than in the latter. Mauseth (1989) also observed the cork outer layers made of isodiametric sclereids, while the inner layers were "flat radially", although in *M. bahiensis* and *M. concinnus* this situation was not noticed. Actually, what Mauseth (1989) called "sclereids", were the lignified cork cells here observed in *M. bahiensis* and *M. concinnus*.

In *M. bahiensis* and *M. concinnus*, the outer cortex was organized in a palisade chlorenchyma, while the inner was a loose tissue, composed of large irregularly parenchyma cells. Such a strikingly similar to a leaf organization of the cortex in two regions is commonly observed in cacti in general (Gibson & Nobel, 1986; Mauseth, 1989, 1996; Silva & Alves, 1999; Soffiatti & Angyalossy, 2003).

The occurrence of mucilage was noticeable when we handled the specimens. Mucilage cells were found both in the cephalium and the stem, more frequently in the inner cortex, although also present in the photosynthesizing palisade cortex and pith. The mucilage cells, as pointed out by several authors (Gibson, 1977; Gregory & Baas, 1989; Fahn & Cutler, 1992), are highly hygroscopic, favoring the storage of water.

The occurrence of cortical vascular bundles gives also to the stem the appearance of a leaf structure. These bundles, as mentioned by Mauseth (1989) for *M. intortus*, as well as some other authors (Mauseth & Sajeva, 1992; Silva & Alves, 1999; Soffiatti & Angyalossy, 2003) for other species of cacti, vascularize the broad cortex, acting like the secondary veins of a leaf (Mauseth, 1989). The cortical bundles are apparently independent

of the main vascular system of the stem (Mauseth, 1989) and have no connections with the areole traces (Gibson, 1978).

Regarding the vascular system, one can notice a distinct activity of the vascular cambium, roughly divided in this study in three phases: first, the fascicular cambium forming only the axial system; later the interfascicular cambium differentiated and forms only primary rays; and in the adult portions of stem and root the cambia form a continuous cylinder, originating axial and radial systems in the xylem and phloem.

Melocactus bahiensis and *M. concinnus* presented fibrous and non-fibrous wood in the stem. The non-fibrous wood is normally found in small globose cacti, as those belonging to tribes Echinocereeae, Trichocereeae, Notocacteae and Cacteae (Terrazas & Arias, 2003).

The fibrous wood in cacti is present in all tree-like and columnar species (Gibson, 1973; Mauseth & Kiesling, 1997; Mauseth, 1999; Silva & Alves, 1999; Soffiatti & Angyalossy, accepted). Although quite uniform in the family, the cacti fibrous wood shows several adaptations towards a safe and efficient water transport and storage. It is characterized by narrow and short vessel elements, with simple perforate plates, libriform septate fibres and large rays, all considered highly specialized characters for the wood (Bailey, 1962; Carlquist, 1975).

In *Melocactus bahiensis* and *M. concinnus* the fibrous wood was observed at the base of stem and root. In both species the vessel elements showed similar diameter and length comparing stem and root (Tab. I).

However, unlike other cereoid cacti, in *Melocactus* there is also the non-fibrous wood, a peculiar situation related to the activity of the vascular cambium towards the formation of the elements of secondary xylem. The cambium produces different conductive elements at different stages of development. At the cephalium and apex of the stem, the secondary xylem in the vascular bundles had vessel elements as the main conductive cell element. However, at the largest, medium portion of the globose stem, the secondary xylem was formed almost exclusively by vascular tracheids. At base of the stem and root, providing support and conduction, the secondary xylem was composed of vessel elements, fibres, axial and radial parenchyma.

The main characteristic of a non-fibrous wood is the presence of vascular tracheids, a few vessels and the absence of fibres (Gibson & Nobel, 1986). The vascular tracheids are conductive elements exclusively found in Cactaceae, and their origin is suggested to be from modified fibres, because normally fibres are absent when vascular tracheids are present (Gibson & Nobel, 1986). Somehow the vascular fusiform initials from the cambium cease to form fibres, and originate only vascular tracheids and a few vessels. It is important to note that the non-fibrous wood is highly parenchymatous, composed also of axial and radial non lignified parenchyma (Gibson & Nobel, 1986).

The vascular tracheids are generally shorter and wider than vessel elements, and have helical or annular secondary wall, that deeply protrudes towards the cell lumen. Mauseth & Plemons (1995) called them "wide band tracheids" or "WBT", due to this expansion of the secondary walls. In *Melocactus bahiensis* and *M. concinnus*, the tracheids tend to have twice the diameters of vessel elements, although they are similarly long (Tab. 1).

In addition, there is a definitive advantage to have the xylem composed of tracheids instead of vessel elements. When a vessel element cavitates, the entire vessel is lost, while when a tracheid does so, only that single cell is lost (Mauseth, 1993). In *Melocactus*, the largest portion of the stem is mainly adapted for water storage, with more quantity of parenchyma tissues, represented by the large cortex, and the secondary xylem almost exclusively composed of vascular tracheids and parenchyma.

The high adaptation of the secondary xylem of *Melocactus* species for the storage of water is truly remarkable. The vascular tracheids massively present in the globose body can shrink and expand due to their spiraled secondary walls, accommodating their size to the availability of water in the environment. Thus showing how this part of the plant body can efficiently acts as a water reservoir.

The occurrence of non-lignified axial parenchyma cells within the axial and radial elements in the secondary xylem was another character correlated to the storage of water, observed in the stem and root of *Melocactus bahiensis* and *M. concinnus*. Mauseth (1989) mentioned the same situation in *M. intortus* and in *Cereus* (Mauseth, 1996), as well as Soffiatti & Angyalossy (accepted), in *Cipocereus*. Metcalfe & Chalk (1950) described the presence of these non lignified cells in species of Crassulaceae, which they called "unlignified parenchymatous cells". The occurrence of these non lignified cells in the wood of these cacti is another evidence of the high specialization of their wood.

The present study of *Melocactus bahiensis* and *M. concinnus* shows that the species dimorphism is equally reflected in the anatomy, which illustrates the cephalium and stem distinctiveness in form and function.

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