Stem and root anatomy of two species of *Echinopsis* (Trichocereeae: Cactaceae)

Anatomía de la raíz y del tallo de dos especies de *Echinopsis* (Trichocereeae: Cactaceae)

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Abstract. This study characterizes and compares the stem and root anatomy of *Echinopsis calochlora* and *E. rhodotricha* (Cactaceae) occurring in the Central-Western Region of Brazil, in Mato Grosso do Sul State. Three individuals of each species were collected, fixed, stored and prepared following usual anatomy techniques, for subsequent observation in light and scanning electronic microscopy. *Echinopsis calochlora* revealed uniseriated epidermis, while *E. rhodotricha* had patches of bisseriated epidermis; all species showed thick cuticle, parallelocytic stomata at the epidermis level, and a well-developed hypodermis. Cortical and medullary bundles are present in the studied species, as well as mucilage cells in the cortex region. The secondary phloem is composed by sieve tube elements, companion cells, axial and radial parenchyma. Sclereids were found at the outer regions of phloem in the roots. The secondary xylem is non fibrous in the stems of *E. calochlora*, and fibrous in the stems of *E. rhodotricha* and in the roots of both species. Many of these characteristics are commonly found in Cactaceae, and represent important adaptations for survival in xeric environments.

Key words: cortical bundles, epidermis, non fibrous wood, wood anatomy.

Resumen. Este estudio está enfocado a caracterizar y comparar la anatomía de tallos y raíces de *Echinopsis calochlora* y *E. rhodotricha* (Cactaceae) que habitan en la región centro-oeste de Brasil, en el Estado de Mato Grosso do Sul. Se recolectaron 3 individuos de cada especie, los cuales fueron fijados, almacenados y preparados siguiendo las técnicas comunes de anatomía, para observarlos en microscopía de luz y electrónica de barrido. *Echinopsis calochlora* mostró epidermis uniseriada, mientras que la de *E. rhodotricha* fue biseriada; todas las especies presentaron cutícula gruesa, estomas paralelocíticos a nivel de la epidermis y una hipodermis bien desarrollada. Se presentaron haces vasculares corticales y medulares en las especies estudiadas, así como células mucilaginosas en la región cortical. El floema secundario está compuesto de elementos de tubo criboso, células acompañantes y parénquima axial y radial. Se encontraron esclereidas en las regiones externas del floema en las raíces. El xilema secundario es no-fibroso en los tallos de *E. calochlora* y fibroso en los de *E. rhodotricha* y en las raíces de ambas especies. Muchas de estas características están presentes comúnmente en especies de Cactaceae, lo que representa adaptaciones importantes para la supervivencia en ambientes xéricos.

Palabras clave: haces corticales, epidermis, madera no-fibrosa, anatomía de la madera.

Introduction

The subfamily Cactoideae (Cactaceae) comprises the largest number of species, is the most diversified in terms of life-forms and habit (Taylor, 2000; Terrazas and Arias, 2003), and it is divided in 9 tribes, in which Cereeae, Rhipsalideae, Trichocereeae, Echinocereeae, and Hylocereeae occur in Brazil (Taylor and Zappi, 2004).

The importance of anatomical studies in Cactaceae are undeniable (Gibson and Horak, 1978; Gasson, 1981;

Gibson and Nobel, 1986; Soffiatti and Angyalossy, 2003, 2005, 2007; Terrazas and Arias, 2003; Arruda et al., 2005), considering the representativeness of the family, and the problems in circumscribing groups, especially within tribes, as well as enabling a better understanding of the group evolution (Terrazas and Arias, 2003) and their adaptations for survival in arid environments (Mauseth, 2006).

Eggli (2002) mentioned the lack of information on Cactaceae in Brazil in the Brazilian southwestern region, elaborating a checklist of 33 native species for the states of Mato Grosso and Mato Grosso do Sul. From those, 27

species belong to Cactoideae, and 6 genera were recorded for tribe Trichocereeae: *Arthrocereus* (A. Berger) Backeb. et F.M. Knuth, *Cleistocactus* Lem., *Discocactus* Pfeiff., *Echinopsis* Zucc., *Gymnocalycium* Pfeiffer in Pfeiffer et Otto, and *Harrisia* Britton, all being very poorly studied, especially in the state of Mato Grosso do Sul.

Echinopsis is one of the largest genus of Trichocereeae, composed by 128 species distributed in several regions of South America, and due to the large number of species, it shows a very controversial circumscription (Anderson, 2001). *Echinopsis calochlora* K. Schum. is endemic to the high altitudes of the Maciço do Urucum (Eggli, 2002), in western Mato Grosso do Sul, and was recently included in the Brazilian list of threatened species (IBAMA, 2008), because its habitat has been intensively exploited, for iron and manganese mining (Silva et al., 2000). *Echinopsis rhodotricha* K. Schum. has a broader distribution, occurring Brazil, Paraguay and Argentina (Anderson, 2001). This work describes comparatively the anatomy of stem and root of *E. calochlora* and *E. rhodotricha*.

Materials and methods

Individuals were collected in rocky outcrops and sandy-clay formations from natural populations as follows: *E. calochlora* at Corumbá County, in Pantanal (voucher number CGMS 17536; *J. S. Garcia 54*), and *E. rhodotricha*, at Porto Murtinho, in Chaco (voucher number CGMS 17590; *J. S. Garcia 61*). Vouchers were deposited at the Herbarium - CGMS/UFMS, Federal University of Mato Grosso do Sul.

For the qualitative anatomical study of the stem, 3 individuals of each species were sectioned at the basal, medium, and apical regions. For the root, only the very base was used. Samples were fixed with FAA 70 for 72 hours, rinsed in water and stored in ethanol 70% (Jensen, 1962). Paradermal sections were taken at the median region of the stem. Transverse and longitudinal sections of stems and roots were made by hand. Samples were also embedded in polyethylene glycol (PEG) 1500 (Richter, 1985) and transverse and longitudinal sections were made in rotative microtome. Root samples of *E. rhodotricha* were sectioned in a sliding microtome. Sections were stained with astrablue and safranin and mounted in glycerine 50%. Macerations were prepared using a modified Franklin method (Franklin, 1945), stained with safranin and mounted in glycerin.

The following hystochemical tests were carried out: floroglucyn (Johansen, 1940) to detect lignified secondary walls; lugol (Johansen, 1940) to detect starch; for mucilage we followed Richter (1977). The analysis was carried out in a Leica DMLB light microscope, connected to an image capture system, and a digital camera DC 300F.

Paradermal and transversal sections of the dermal system of the stem median region were prepared for scanning electron microscopy (SEM) analysis. Samples were dehydrated, critical-point dried, mounted on aluminum stubs, and coated with gold-palladium in a sputter system. SEM analysis and electron micrographs were made with a JEOL JSM 5800 scanning electron microscope.

Results

Stem. Uniseriate epidermis (Fig. 1) occurred in photosynthesizing regions of the stem, as well as in apical and median regions. It was composed by square to rectangular cells in cross sections, with thick cuticle. *Echinopsis rhodotricha* showed patches of bisseriate epidermis in the median region (Fig. 2), formed by periclinal divisions of epidermal cells, rarely observed in *E. calochlora*.

Parallelocytic stomata were found in both species at the same level of epidermal cells in *E. calochlora* (Fig. 1) while *E. rhodotricha* had sunken stomata (Fig. 2). Substomatal chambers crossed the hypodermis (Figs. 1, 2).

The phellogen was originated in the epidermis. Peridermis covered the non photosynthesizing portions of the stem (Figs. 3, 4); composed of pheloderm formed by rectangular cells in cross section, with primary walls. Cork had layers of cells with suberized walls that alternate with layers of cells with lignified walls, which are very numerous in *E. rhodotricha* (Fig. 4).

We observed a collenchymatic hypodermis in the stem (Figs. 1, 2, 5), composed of cells with irregularly thickened primary walls, connecting through ramified channels.

Cortex was divided in an outer region forming a palisade (Fig. 5), and an inner region composed of large parenchyma cells and vascular bundles (Fig. 5), constituted by phloem and xylem, arranged collaterally. Druses were rare in the cortex. Large mucilage cells occurred throughout the whole cortex (Fig. 6) and pith. Vascular bundles occurred also in the pith (Fig. 7).

At the base of stem, primary phloem was collapsed and in *E. rhodotricha* caps of sclereids were seen outside secondary phloem (Fig. 8). Secondary phloem was composed of narrow sieve tube elements and companion cells, with simple sieve plate, transverse to slight oblique, axial and radial parenchyma.

Both species had non fibrous wood, mainly composed of wide band tracheids and a few vessel elements, surrounded by axial and radial unlignified parenchyma cells (Figs. 9-11). Wide band tracheids presented ring, helical or mixed wall thickenings (Fig. 11). Vessel elements had simple perforation plates. Both species had a storied structure in the non fibrous wood (Fig. 11), being
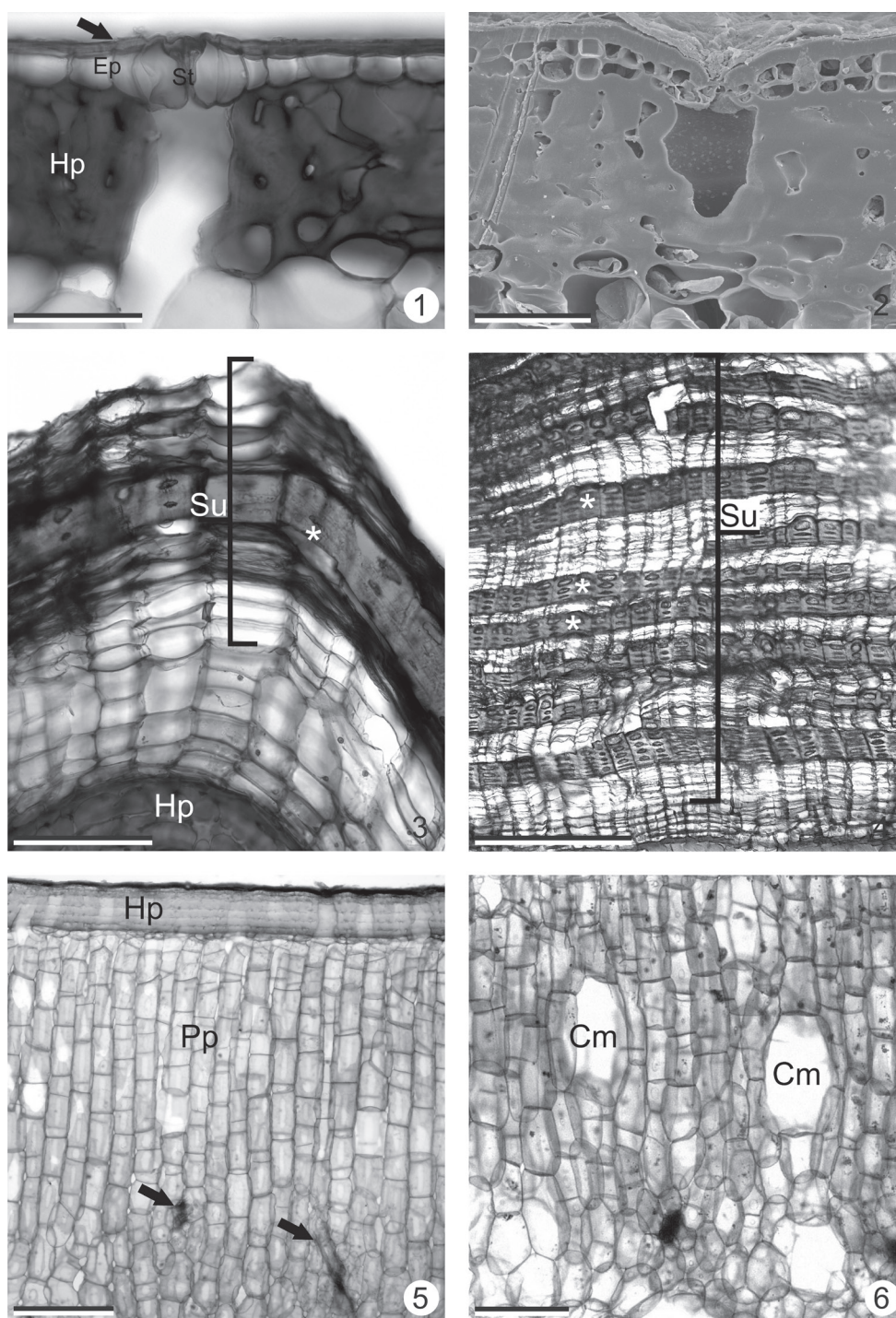
Figures 1-6. Stem cross sections. 1-2, epidermis covered by a thick cuticle (arrow). Stomata chamber crossed hypodermis. 1, *Echinopsis calochlora*. Uniseriate epidermis. Stomata at the same level as ordinary epidermal cells. 2, *E. rhodotricha*. Scanning electron micrograph (SEM). Bisseriate epidermis and sunken stomata. 3-4, peridermis with pheloderm composed of layers of parenchyma cells; cork composed of layers of cells with suberized walls alternating with layers of cells with lignified walls (*). 3, *E. calochlora*. 4-6, *E. rhodotricha*. 5, organization of cortex: hypodermis followed by layers of palisade parenchyma and inner isodiametric parenchyma cells. Cortical bundles (arrows). 6, cortex. Numerous scattered mucilage cells. Scale bars: 1= 100 μm; 2= 5 μm; 3-4= 200 μm; 5= 500 μm; 6= 250 μm. Cm- mucilage cell; Ep- epidermis; Hp- hypodermis; Pp- palisade parenchyma; St- stomata; Su- suber.
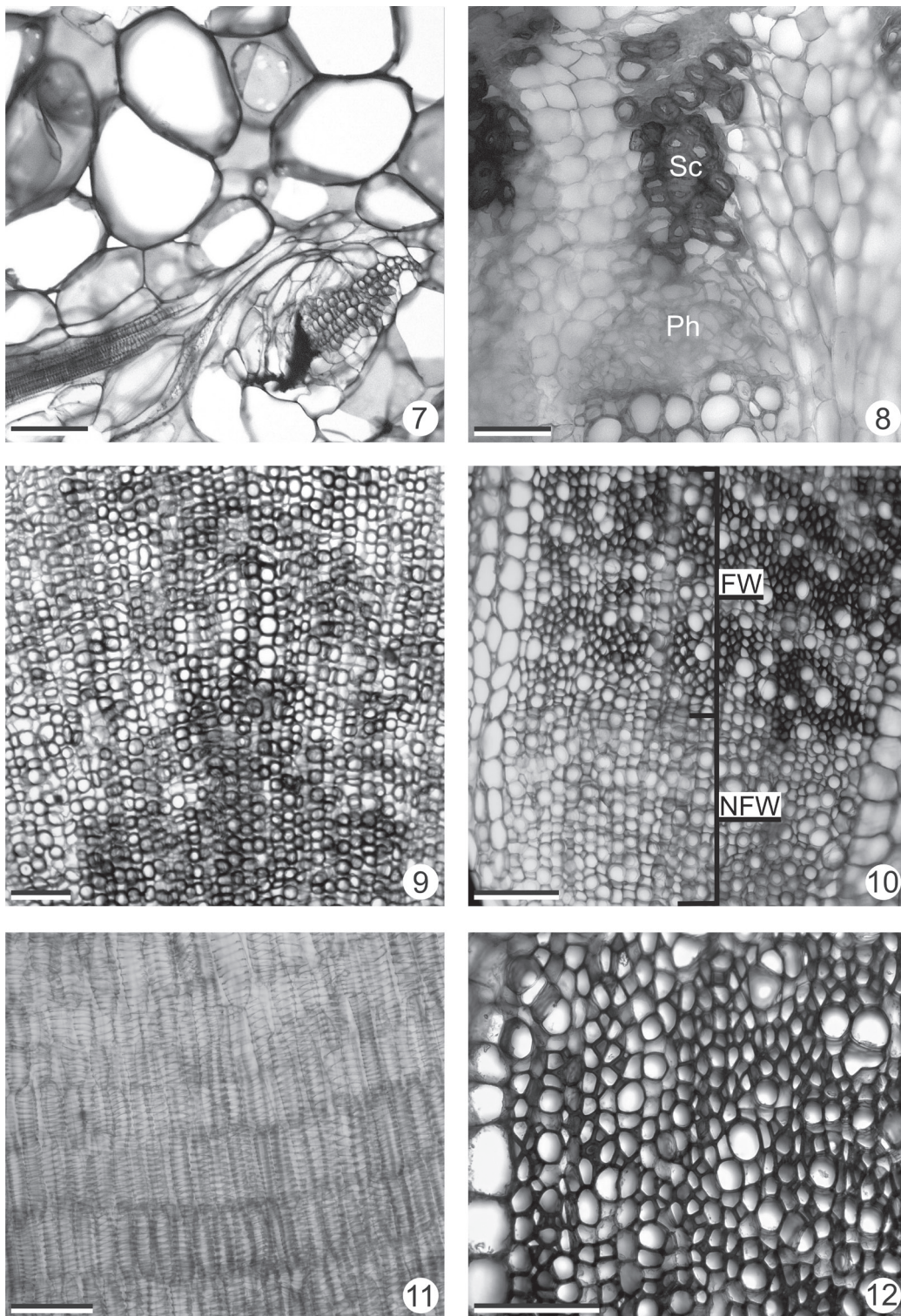
Figures 7-12. 7-10, 12, cross sections. 11, tangential section. 7, *Echinopsis calochlora*. Pith with medullary bundle. 8, *E. rhodotricha.* Vascular system. Phloem. Caps of sclereids in the periphery of secondary phloem. 9, *E. calochlora*. Non fibrous wood mainly composed of wide band tracheids. 10, *E. rhodotricha*. Fibrous and non fibrous wood. 11, *E. calochlora.* Non fibrous wood composed of wide band tracheids with helical thickenings. 12, *E. rhodotricha.* Fibrous wood composed of vessel elements, fibres and scanty paratracheal parenchyma (part of a ray is seen on the left). Scale bars: 7, 9-12= 200 µm; 8= 400 µm. FW- fibrous wood; NFW- non fibrous wood.

most pronounced in *E. calochlora*. Fibrous wood occurred only in *E. rhodotricha*, outside non fibrous wood (Figs.10, 12-15), diffuse porous, with wide band tracheids absent, composed of vessels predominantly solitary and multiples of 2 to 3, and less frequent, of 4 to 5; vessel elements walls had helical to pitted secondary walls; intervessel pits were bordered; vessel-parenchyma pits simple to half-bordered, scalariform, opposite to alternate; perforation plates were simple (Fig. 14), transverse to oblique; some vessels had 3 perforation plates; intermediate forms between scalariform with one incomplete bar to irregular and reticulate were observed (Fig. 15). Parenchyma was scanty paratracheal (Fig. 12). Multiseriate wide and high heterogeneous rays (Fig. 13) were composed of procumbent, upright or/and square cells, with lignified and unlignified portions; starch grains occurred in ray cells (Figs. 10, 12). Libriform fibres were present, rare septate. Bands of unlignified parenchyma including axial and radial parenchyma were present in fibrous wood (Fig. 10).

Root. Adult roots were covered by a peridermis, similar to the stem (Fig. 16); composed of pheloderm formed by 5 to 6 layers of rectangular cells in cross section, with primary walls; cork was formed by several layers of cells with suberized walls, which alternate with layers of cells with lignified walls.

Cortex was composed of parenchyma cells with primary walls. Druses were less frequent in *E. calochlora*, and absent in *E. rhodotricha* .

The primary phloem was collapsed (Figs. 16, 17), with caps of sclereids outside secondary phloem (Fig. 17). Secondary phloem (Fig. 17) comprised narrow and short sieve tube elements, with simple sieve plate, transversal to slightly oblique; companion cells; axial and radial parenchyma. Secondary xylem was fibrous in both species (Figs. 16-20), diffuse porous, composed of vessels predominantly solitary and multiples of 2 to 3, and less frequent, of 4 to 5 vessel elements with simple perforation plate, transverse to oblique; in *E. rhodotricha*, intermediate forms between scalariform with one incomplete bar to irregular and reticulate were observed, similar to the stem fibrous wood; intervessel pits were bordered; vessel-parenchyma pits were simple to half-bordered, scalariform, opposite to alternate. Wide band tracheids were absent. Scanty paratracheal parenchyma present (Fig. 17). Unlignified, multiseriate wide and high heterogeneous rays (Figs. 16-19) were composed of procumbent, upright or/and square cells. Druses and starch grains (Fig. 19) occurred in ray cells. Libriform fibres were present, septate (rare) only in *E. rhodotricha* (Fig. 20). Unlignified parenchyma was present including also axial parenchyma, forming bands, more evident in *E. rhodotricha* .

Discussion

The anatomical characteristics observed in the studied species are commonly observed in other Cactaceae species, as extensively described in the literature (Terrazas-Salgado and Mauseth, 2002; Soffiatti and Angyalossy, 2003, 2007, 2009; Terrazas and Arias, 2003; Arruda et al., 2005; Mauseth, 2006).

The 2 *Echinopsis* species have a thick cuticle, an important adaptation for xeric habitats, protecting the plant body from water loss and pathogens. Unusual in Cactaceae (Gibson and Nobel, 1986; Loza-Cornejo and Terrazas, 2003), they showed a secondarily biseriated epidermis, which has also been reported for a few other genera in Trichocereeae, such as *Harrisia* (Mauseth et al., 1998); a multiseriate epidermis was mentioned for *Espostoa* Britton and Rose (Mauseth, 1999). Reports of multiseriated epidermis exist for other tribes such as Pachycereeae (Gibson and Horak, 1978; Barthlott and Hunt, 1993; Terrazas-Salgado and Mauseth, 2002), Cacteae (Terrazas-Salgado and Mauseth, 2002), Notocacteae (Nyffeler and Eggli, 1997; Terrazas-Salgado and Mauseth, 2002), Cereeae (Darling, 1989; Mauseth, 1996), and Browningieae (Mauseth, 1996). As stated by Loza-Cornejo and Terrazas (2003), multiple epidermis in cacti occur in unrelated genera and seem to have appeared several times in Cactaceae.

Parallelocytic stomata and a long substomatal chamber were observed in the investigated species, a common feature for the members of the family (Gasson, 1981; Eggli, 1984). In contrast with most xerophytes, several species of Cactaceae show superficial stomata (Eggli, 1984; Gibson and Horak, 1978; Fahn and Cutler, 1992; Loza-Conejo and Terrazas, 2003; Soffiatti and Angyalossy, 2007), where guard cells are on the same level as the other epidermal cells. The long substomatal chamber, due to the thick hypodermis, reduces water loss when the stomata are open (Fahn and Cutler, 1992). According to Darling (1989), the reduced transpiration rates are combined with low CO_2 and O_2 exchange rates, prioritizing water conservation. Sunken stomata were observed in *E. rhodotricha*, a situation reported for some other genera (Metcalfe and Chalk, 1950; Gasson, 1981; Eggli, 1984; Loza-Cornejo and Terrazas, 2003), maximizing water loss prevention. Nevertheless, this is a variable feature in the genus, once superficial stomata were observed in other species, such as in *Echinopsis aurea* Britton et Rose (Eggli, 1984), and in *E. calochlora*, while in *E. eyriesii* (Turpin) Zucc. these are sunken, as in *E. rhodotricha*.

The organization of cortical tissues in both studied *Echinopsis* species is typical of cacti (Gibson and Nobel, 1986; Loza-Cornejo and Terrazas, 2003; Mauseth,
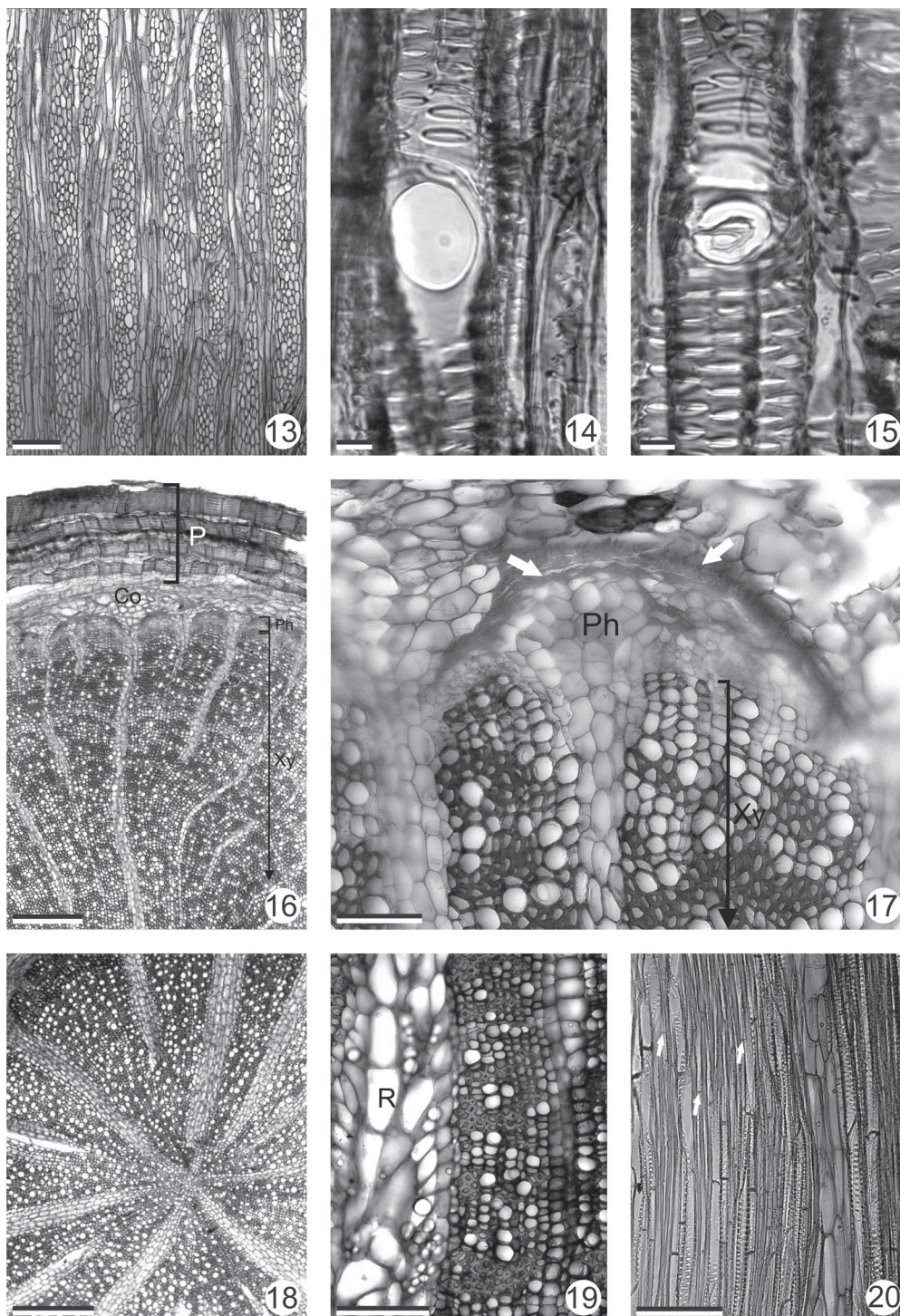
Figures 13-20. 13-15, stem secondary xylem; tangential sections. *Echinopsis rhodotricha*. 13, large rays. 14, simple perforation plate of a vessel element. 15, incomplete perforation plate of a vessel element. 16-20, root and cross sections (16-19). 20, tangential section. 16-17, *E. calochlora*. 16, general view; note peridermis composed of several layers of cells with lignified walls alternate with cells with suberized walls; fibrous wood with large unlignified rays. 17, phloem and xylem. Collapsed phloem (arrows) outside functional secondary phloem. 18-19, *E. rhodotricha*. 18, fibrous wood with large unlignified rays. 19, detail of unlignified rays containing starch grains. 20, *E. calochlora* tangential sections; septate fibres (arrows). Scale bars: 13= 400 µm; 14-15= 10 µm; 16, 18= 500 µm; 17= 100 µm; 19-20= 200 µm. Co-cortex; P- peridermis; Ph- phloem; R- rays; Xy- xylem

2006; Soffiatti and Angyalossy, 2007): there is a thick hypodermis composed of several layers of colenchymatic cells, followed by a photosynthetic palisade parenchyma and the inner cortex, composed of isodiametric parenchymatic cells. The hypodermis, being a flexible tissue, has important functions in giving support to the stem and accommodating the stem changes in volume due to shrinkage and swelling, also protecting the inner tissues against pathogens (Gibson and Nobel, 1986). As the stems in most cacti are the main photosynthesizing organ, the organization of the chlorenchyma or palisade parenchyma is very similar to a leaf (Sajeva and Mauseth, 1991). The internal cortex cells store water (Mauseth, 1993b), and the large cells are able to expand and contract depending on hydration state or water availability (Mauseth, 2006).

Both species presented cortical and medullary bundles with secondary growth, spread out in all directions very similar to leaf veins. Like leaf veins, they are collateral and form a network that extends to the base of the palisade parenchyma. Cortical bundles are considered a synapomorphy for Cactoideae, present in nearly all species (Mauseth, 2006). They perform important functions in sugar and water transport to and from cortex cells and to the vascular system (Mauseth and Sajeva, 1992; Terrazas-Salgado and Mauseth, 2002; Mauseth, 2006). Mauseth (2004) considers that the presence of cortical bundles explains the large volume of cortex, as succulent euphorbias, for instance, do not possess cortical bundles and their stems never reach such a large size as cacti. Medullary bundles have the same function as cortical bundles, transporting water and nutrients (Mauseth, 1993a, 2006; Terrazas-Salgado and Mauseth, 2002), occurring only in Cactoideae (Mauseth, 1993a, 2006). According to Gibson and Nobel (1986) pith diameter increased during Cactaceae evolution and this event probably led to the emergence of medullary bundles.

In the basal and older regions of the stem, as well as in the root of these 2 *Echinopsis* species, the epidermis is substituted by a peridermis, as noted for many species in the family. The origin of phellogen from periclinal divisions of epidermal cells is very common in cacti (Gibson and Nobel, 1986; Terrazas-Salgado and Mauseth, 2002; Soffiatti and Angyalossy, 2003; Mauseth, 2006). Although the origin of phellogen in a plant organ can be variable, from different cell types, such as epidermal, colenchymatic, parenchymatic or even phloematic cells, the most common origin is from subepidermal layers of cells, according to Evert (2006). It was seen in *E. calochlora* and *E. rhodotricha* that phellem in both root and stem is composed by layers of suberized cells which alternate with layers of lignified cells, also a common feature for species of the family (Mauseth, 2006).

The phloem was composed of sieve tube elements and companion cells, axial and radial parenchyma and sometimes, non functional phloem might become lignified, similar to what was described for several Cactaceae stems (Mauseth, 1999; Terrazas-Salgado and Mauseth, 2002; Soffiatti and Angyalossy, 2003, Arruda et al., 2005; Mauseth, 2006), and roots (Mauseth and Ross, 1988; Mauseth, 1989). *Echinopsis rhodotricha* has fibre caps outside phloem; in *E. calochlora* they are absent, typical of species which have non fibrous wood (Mauseth et al., 1998).

Echinopsis calochlora and *E. rhodotricha* present fibrous wood in the roots while in the stems they both have non fibrous wood, corroborating the fact established by Mauseth and Stone-Palmquist (2001). These authors stated that the structure of wood in the stem and root of the same plant can be very different. *Echinopsis rhodotricha* has also fibrous wood in the stem, characterizing what is termed dimorphic wood: when young the plant produces one type of wood and later on, the cambium produces another type (Mauseth and Plemons, 1995; Mauseth and Plemons-Rodríguez, 1998). In the present work, it was observed a typical situation in *E. rhodotricha*: which first forms non fibrous wood, when the body is young and small and does not need special investment in support, and when mature, the cambium starts forming fibrous wood since support is then needed due to the larger size (Terrazas-Salgado and Mauseth, 2002). The fibrous and non fibrous wood types observed in the present study have the same structure as described in literature, with fibrous wood composed of vessel elements in a matrix of libriform fibres, and non fibrous wood composed of vessel elements in a matrix of wide band tracheids (Gibson, 1973; Gibson and Nobel, 1986; Terrazas-Salgado and Mauseth, 2002; Mauseth, 2006; Soffiatti and Angyalossy, 2009). The only difference between the fibrous wood of the stem and root of *E. rhodotricha* is the presence of the storied structure in the stem, absent in the root. A noticeable feature observed in the secondary xylem of the stem in both species is the occurrence of a storied structure in the secondary xylem. This feature has been described in the literature for several species of Cactoideae, including *E. calochlora*, by Gibson (1973). This author observed that the rays are rarely storied, and mentions that the storied structure is more evident in specialized growth forms, such as globose and epiphytic species. Gibson (1973) also stated that in non fibrous wood it is a difficult feature to distinguish due to differences in the length of vessel elements and wide band tracheids, but this was not the case in the present study. Storied wood is a feature that occurs in several phylogenetically unrelated groups and it is found in groups where fusiform cambial initials are shorter (Carlquist, 2001). In the present study,

the non fibrous wood showed a storied structure, especially regarding wide band tracheids, more pronounced in *E. calochlora* than *E. rhodotricha*.

Many of the characteristics presented in this work corroborate the descriptions that had already been reported for other species of Cactoideae. Some anatomical features can be used as diagnostic, allowing for the segregation of the 2 species of *Echinopsis* studied, such as: presence of biseriated epidermis, sunken stomata, and fibrous and non fibrous wood in the stem of *E. rhodotricha*. As *Echinopsis* comprises a large number of species (ca. 128 species, Anderson, 2001), some intrageneric variability is expected for this genus, and more species should be investigated, in order to establish the diagnostic value of those traits mentioned.

Acknowledgements

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