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ORIGINAL ARTICLE

Comparative morphology and anatomy of *Backebergia militaris* (Echinocereeae–Cactaceae) cephalium

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Abstract The morphology and anatomy of the *Backebergia militaris* cephalium is characterized in comparison with its vegetative branch and with apical and lateral cephalia of other species. Our working hypothesis was that the *B. militaris* cephalium is more similar to the apical or lateral cephalia of other taxa than to its own vegetative branch. Our results revealed that the differences between the vegetative branch and the cephalium are primarily morphological: there is a change in the phyllotaxy, there are no interareolar spaces, making the ribs indistinguishable and abundant trichomes and bristles are produced in the areoles. In addition, a comparison between the vegetative branch and the cephalium shows differences in the epidermal cell size, thickness of the hypodermis and abundance of cortical bundles and mucilage cells. Unlike *Melocactus intortus* apical cephalia, *B. militaris* retains stomata in the epidermis and chlorenchyma, allowing the cephalium near the apical meristem to perform photosynthesis. The development of periderm in each areole after flowering and fruiting is a distinctive and defining feature of lateral and apical cephalia. In addition to early periderm development, the necrosis of cortical and pith parenchyma and fibers in secondary xylem and phloem in *B. militaris* distinguishes it from other cephalia described to date.

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Introduction

Flowering regions are a distinctive characteristic of cacti with arborescent (monopodial or sympodial), shrubby and globose forms. Their development is characterized by the growth of hairy regions with bristles and spines, termed pseudocephalia and cephalia (Buxbaum 1964; Terrazas and Mauseth 2002; Mauseth 2006). Buxbaum (1964) defined pseudocephalia as flowering areas that are present in the ribs or tubercles that lose their hairy parts after flowering but maintain their vegetative function, whereas cephalia are hairy flowering areas whose areoles are modified and lack vegetative function. Cephalia and pseudocephalia are found in species of the Cereeae, Echinocereeae and Trichocereeae tribes of the Cactoideae subfamily (Mauseth 1989; Barthlott and Hunt 1993; Mauseth 1999; Vázquez-Sánchez et al. 2005, 2007; Arias and Terrazas 2006; Gorelick 2009, 2013, 2014a; Machado 2009). In the particular case of the Echinocereeae tribe, *Lophocereus* Britton & Rose species and some *Cephalocereus* Pfeiff and *Pachycereus* (A.Berger) Britton & Rose species have pseudocephalia (Arias and Terrazas 2006), and two *Cephalocereus* species have lateral cephalia (Vázquez-Sánchez et al. 2005, 2007). Although in *Backebergia militaris*, a member of Echinocereeae, apical cephalia has been described (Barthlott and Hunt 1993; Bravo-Hollis and

Sánchez-Mejorada 1978), there is a lack of morphological and anatomical information about the structure of *Backebergia* cephalia.

Studies describing cephalium anatomy are scarce (Mauseth 1989; Vázquez-Sánchez et al. 2005, 2007). Anatomical differences and similarities between lateral cephalia and their vegetative stems have been shown for *Cephalocereus* (Echinocereeae; Vázquez-Sánchez et al. 2005, 2007), *Espostoa* Britton & Rose, *Pseudoespostoa melanostele*, *Thrixanthocereus senilis* and *Vatricania guentheri* (Trichocereeae; Mauseth 1999); such differences include displacement of the apical meristem, delayed differentiation of the secondary xylem fibers, and early development of the periderm. *Melocactus intortus* (Cereeae) is the only species with apical cephalium that has been described (Mauseth 1989). However, based on macroscopic observations, it has also been reported that *Discocactus* Pfeiff. has an apical cephalium with successive cambia (Gorelick 2014a). Mauseth (1989) notes that the apical cephalium of *M. intortus* has lost its stomata, chlorenchyma and sclerenchyma tissues. This interruption of vegetative development at the level of the apical meristem suggests that the apical cephalium does not allow the plant to continue its vegetative growth. These anatomical modifications contrast with those of the lateral cephalia, which have stomata, chlorenchyma and sclerenchyma (Mauseth 1999; Vázquez-Sánchez et al. 2005, 2007).

There are few detailed morpho-anatomical studies on the cephalium to be able to assess character homology, which is essential for future studies of character evolution in Cactaceae. Based on the characteristics of apical and lateral cephalia known up to date, we hypothesized that the cephalium in *Backeberia militaris* will share more morpho-anatomical modifications with the apical cephalia of *M. intortus* than with the lateral cephalia of other taxa and those morpho-anatomical traits will be more similar among *B. militaris* cephalia than with its vegetative branch. This study was designed to investigate the morphological and anatomical differences between the vegetative branch and cephalium of *B. militaris*, as well as to compare the cephalium of *B. militaris* with the cephalia of other previously studied taxa of the Cereeae, Echinocereeae and Trichocereeae.

Materials and methods

We collected six branches containing cephalia at different developmental stages from four *Backebergia militaris* individuals (*S. Arias 1338, 1339, 1404, 1405*; MEXU) growing in the state of Michoacán, Mexico. The samples represented developmental phases spanning the initiation of the cephalium, with its first light yellow bristles, to a cephalium of over 50 cm in length, with black, reddish and light yellow coloration (Fig. 1). Additionally, two vegetative branches were collected for the purpose of morphological comparison without dissection. To analyze and describe the morphology of the cephalia, they were dissected by removing the bristles and trichomes and cutting a furrow of approximately 10 cm in width from the basal end to the apex.

The cephalia were cut into 3–5 cylinders that were 10 cm tall, and each was subdivided into smaller portions that included tissue from the epidermis to the pith. The vegetative branches were divided into three regions: apical, middle and basal (Fig. 2a, b). Tissue from both the vegetative branches and the cephalia was fixed in formalin–acetic acid–alcohol, dehydrated with tert-butyl alcohol in a Leica automatic TP1020 changer, embedded in paraffin (Histoparaffin Leica) 56–58 °C fusion point (Ruzin 1999), sectioned (transverse and longitudinal) 14–20 μm thick with a rotary microtome and disposable blades. Thirty measurements of the height and width of the epidermal cells, width of hypodermis and cortex, as well as vessel diameters of secondary xylem were obtained. The number of cortical bundles and mucilage cells, as well as the secondary xylem vessel number, was obtained by counting 30 fields of 1^2 mm each. All measurements were taken in the apical and basal regions of the vegetative branches and the cephalia using an image analyzer IMAGE-Pro Plus version 3.1 (Media Cybernetics 1997) that was adapted to an Olympus BX–50 microscope. The data were analyzed via variance analysis followed by pairwise means comparison (SAS Institute 2008) to evaluate significant differences between the characters of the apical and basal regions of the vegetative branches and the cephalia.

Results

Morphology

Backebergia militaris is a 5–6-m-tall tree with a well-defined trunk and sympodial lateral or mesotonic branches that correspond to the Leeuwenberg architectural model sensu Hallé et al. (1978). Upon reaching maturity, a cephalium differentiates at the apex of each branch (Fig. 1a–c). The green vegetative branches have a diameter of 12 cm and possess 8–10 ribs that are 2.2–3.5 cm deep × 2.5–4 cm wide at the base. The areoles are circular or slightly elliptical (4–6 mm long × 4.5–5 mm wide) and can be naked or have gray trichomes. They contain 12 radial, gray acicular spines that are 8–10 mm long and 1–3 central gray acicular spines that are 6–10 mm long. The interareolar distance is 10–33 mm.

The cephalium can reach 70 cm or more in length and is 20–22 cm in diameter at its base. The areoles have

Fig. 1 The morphology of *Backebergia militaris* **a** Adult plants in the field. **b** Vegetative (*arrows*) and reproductive branches (*arrow heads*). **c** Individual with cephalia in different stages of growth (*arrow heads*); young cephalia having only yellow bristles and older cephalia with yellow bristles in the apical region and dark brown color in the distal region. **d** The initial formation of a cephalium with yellow bristles. **e** Detail of a cephalium with bristles ranging from yellow to dark brown and a flower at anthesis

abundant trichomes, bristles and pale yellow spines at their apices; these spines gradually turn golden yellow, then reddish-yellow and finally black. The surface is not visible because of this dense mass of trichomes and spines (Figs. 1, 3). Beneath this mass, the areoles are embedded in a light brown surface (Fig. 3a, c). Their number increases toward the apex, leading to the loss of the interareolar space, and their arrangement gradually becomes helical, but the apical meristem maintains it position (Fig. 3a). The apex of the cephalium is a dense region of helically organized tubercles that are embedded in a green surface (Fig. 3b); the removal of trichomes and bristles releases alkaloids that cause the surface to rapidly darken (Fig. 3a). The areoles in the apical region are associated with a conical leaf shape (Fig. 3b), and their phyllotaxy varies from 8/21 to 13/21 depending on the development of the cephalium. The basal area is dark brown in color, and cross sections reveal necrotic tissue inhabited by many insects.

Fig. 2 Diagram showing
sections for anatomical study.
a Cephalium. *Numbers* the
sequence from the proximal to
the distal regions. **b** Vegetative
branch. The *letters* indicate
a apical, *m* medium and *b* basal
region. Both transverse sections
indicate with the *dark line* the
position of tissue sampled from
the epidermis towards the pith
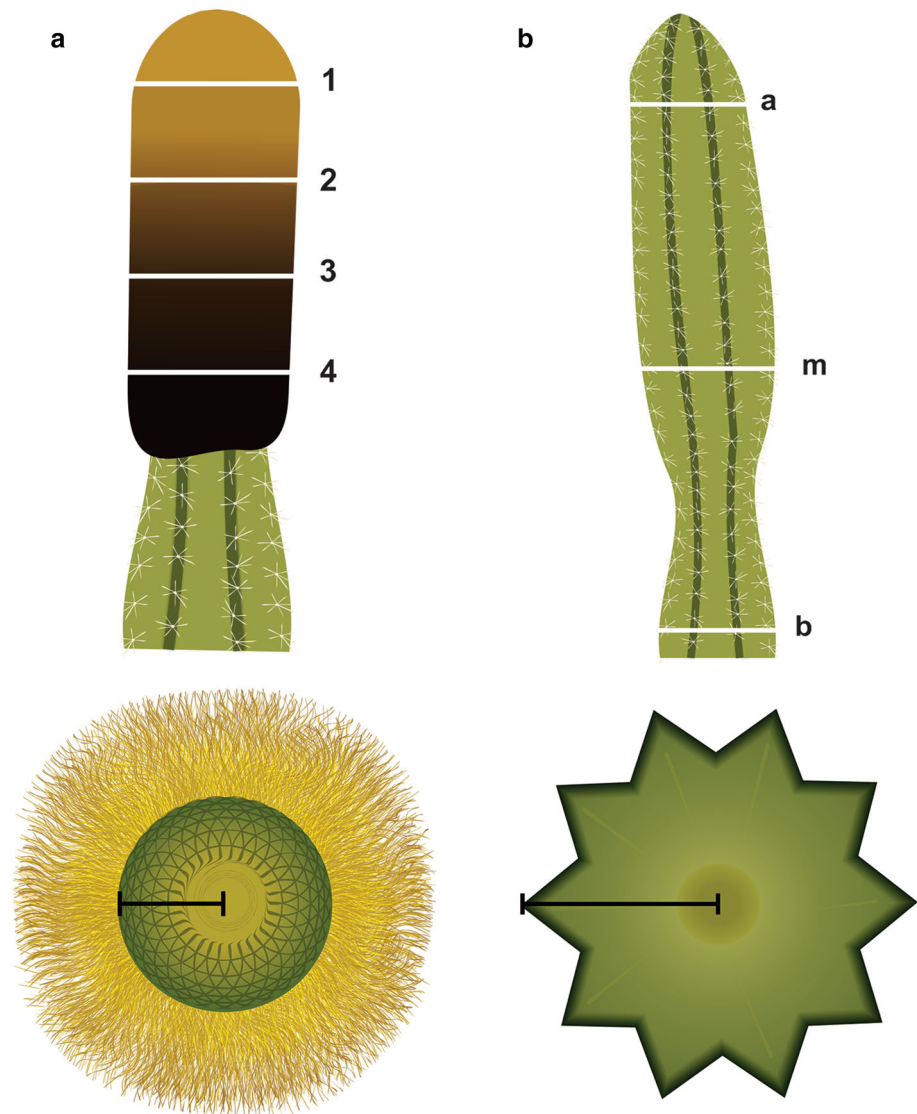
Anatomy

Cuticle and epidermis

The cuticle is smooth and is thicker in the vegetative branch (>1 μm) than in the cephalium (<1 μm). The epidermis is simple, and it is composed of larger cells in the vegetative branch than in the cephalium (Table 1). The epidermis (Fig. 4a) is present exclusively in the inter-areolar regions in the cephalium. The length of epidermal cells at the apex varies between the vegetative branch and the cephalium ($F = 9.94$, gl $= 1$, $P < 0.004$, Table 1), but not the width ($P = 0.86$) as seen in transverse sections. Paracytic stomata are more abundant in the valley ribs and tubercles. At the base of the tubercles, the epidermis generates trichomes that are lost in the vegetative branch but have greater longevity in the cephalium (Fig. 4b, c). The

trichomes have nucleated cells that undergo continuous division and differentiation; they elongate, lose their nuclei and sclerify. At early stages of differentiation, the bristles contain square-shaped cells with prominent nuclei. The bristles then elongate (Fig. 4d) and vascular tissue differentiates at their base.

Hypodermis

The hypodermis is multilayered, collenchymatous and continuous, except in the substomatal chambers. The vegetative branch has 4–6 layers of thick-walled cells (Fig. 4e), whereas in the cephalium, there are four layers (Fig. 4f). The thickness of the apical hypodermis ($F = 465.05$, gl $= 1$, $P < 0.0001$) varied between vegetative branch and the cephalium, being wider in the vegetative branch (Table 1).
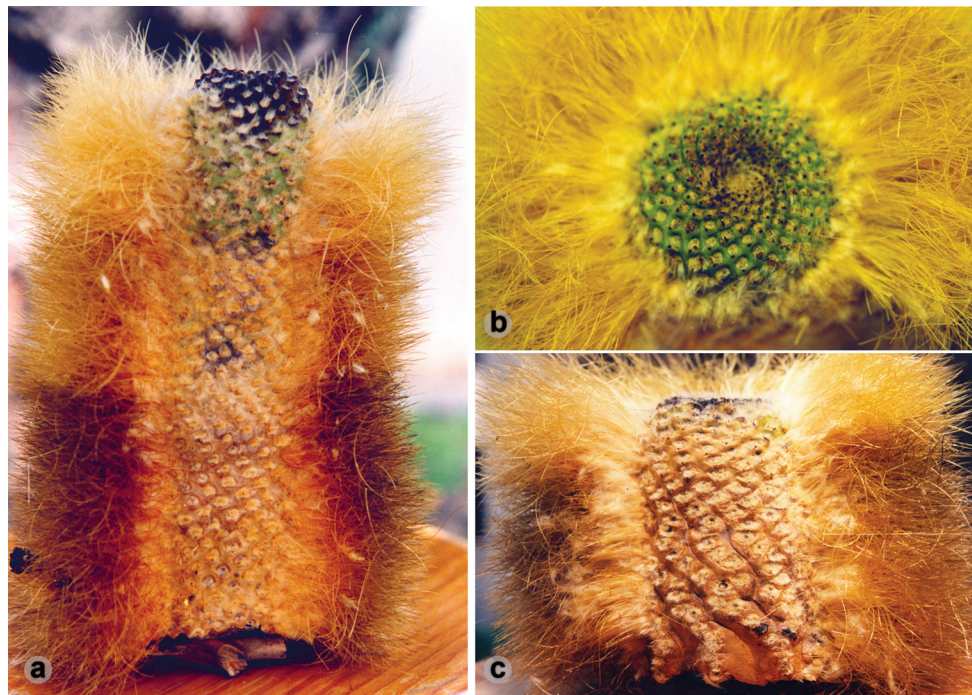
Fig. 3 The morphology of the *Backebergia militaris* cephalium after removing the bristles and trichomes. **a** The proximal region near the apical meristem (green tissue) and the distal region (brown color), corresponding to the periderm. **b** Top view of the apical meristem showing the helical arrangement of the areoles. The dark spots associated with the areoles correspond to bracts. **c** Detail showing how the periderm seals the surface including the areole and the absence of interareolar spaces

Table 1 Mean and standard deviation for quantitative characters of the dermal, fundamental and secondary xylem tissues of the vegetative branch and the cephalium of *Backebergia militaris*

Character	Vegetative branch	Cephalium
Epidermal cell (length × width) apex, μm	$36.8 \pm 4.4^a \times 20.9 \pm 3.1^A$	$33.7 \pm 3.3^b \times 21.1 \pm 2.3^A$
Epidermal cell (length × width) base, μm	$37.1 \pm 4.8 \times 20.5 \pm 2.7$	None
Hypodermis thickness apex, μm	144 ± 11.29^a	64 ± 8.58^b
Hypodermis thickness base, μm	146 ± 8.36	None
Cortical bundles/mm² apex	5 ± 2^a	10 ± 3^b
Cortical bundles/mm² base	2 ± 2^a	2 ± 2^a
Mucilage cells/mm² apex in cortex	18 ± 6^a	26 ± 7^b
Mucilage cells/mm² base in cortex	8 ± 2^a	9 ± 4^a
Pith bundles/mm² apex	2 ± 1^a	3 ± 2^a
Pith bundles/mm² base	2 ± 2^a	1 ± 1^a
Mucilage cells/mm² apex in pith	7 ± 3^a	9 ± 3^a
Mucilage cells/mm² base in pith	4 ± 2^a	6 ± 3^a
Vessels/mm² apex	22 ± 6^a	25 ± 7^a
Vessel diameter apex, μm	13.4 ± 2.9^a	12.1 ± 2.9^a
Vessels/mm² base	12 ± 8^a	42 ± 11^b
Vessel diameter base, μm	70.1 ± 9.2^a	48.2 ± 6.0^b

Different letter between columns indicates statistical differences ($P < 0.05$)

Cortex

Chlorenchyma and storage regions are found in both vegetative branch and cephalium. The chlorenchyma has typical radially elongated cells with abundant chloroplasts forming a palisade parenchyma (Fig. 4e, f), and no cortical bundles or mucilage cells; some cells in the middle and basal areas are sclerified (Fig. 4g). The storage regions contain parenchyma cells, cortical bundles, mucilage cells, spherocrystals, and abundant starch grains. The number of
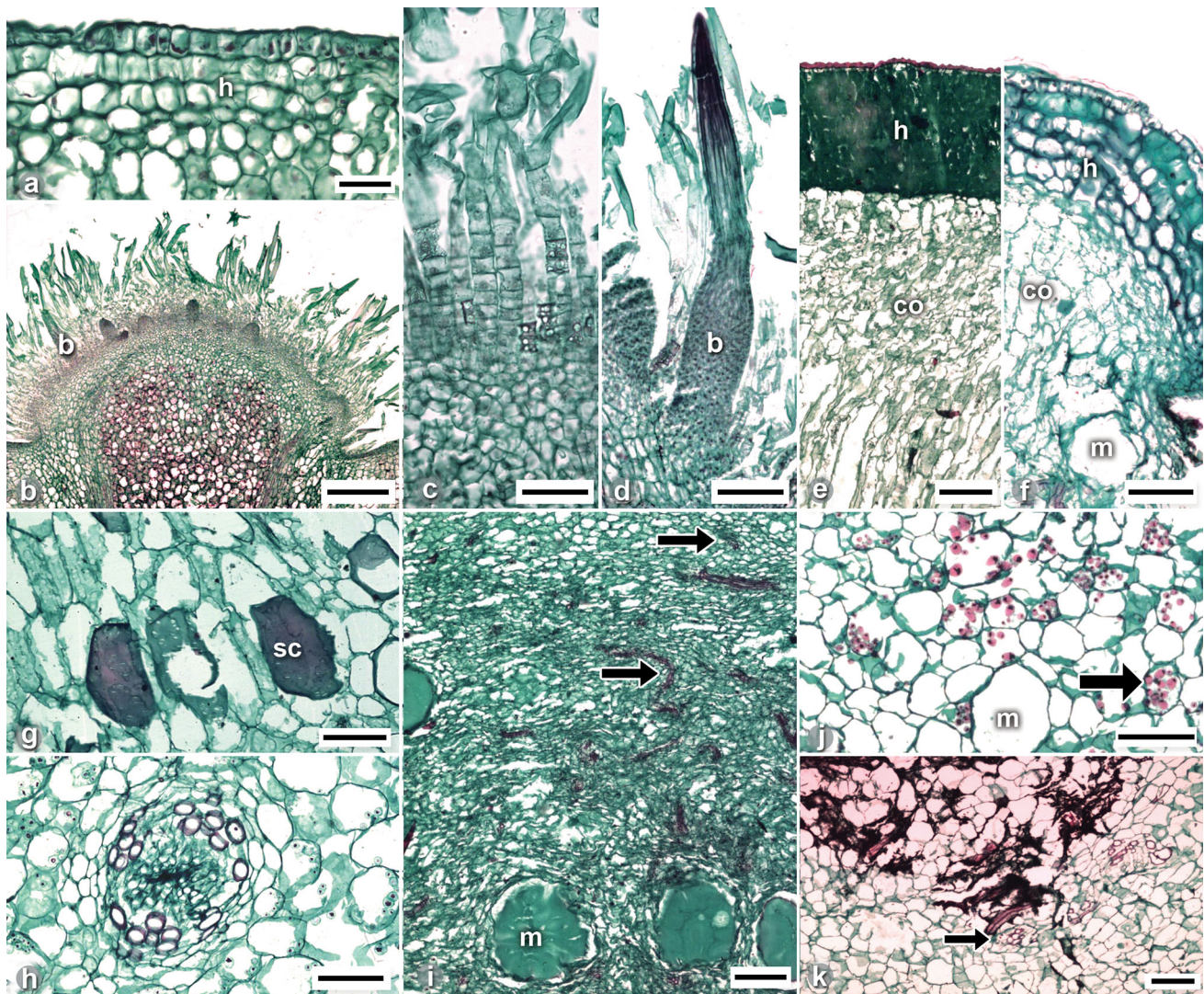
Fig. 4 Cross sections showing the primary tissue of a cephalium and a vegetative branch of *Backebergia militaris*. **a–d** Cephalium. **a** Epidermis in the apical region. **b** Overview of an areole with abundant trichomes and bristles. **c** Detail of the trichomes. **d** Detail of a bristle. **e** Hypodermis of the vegetative branch. **f** Hypodermis of the cephalium. **g** Detail of sclereids in the palisade parenchyma in the cortical region of the cephalium. **h** Amphivasal bundle. **i** Collapsed cortex in the middle of the cephalium. *Arrows* cortical bundles. **j** Pith with abundant starch grains (*arrow*) in the middle region of the cephalium. **k** Pith with necrotic cells in the basal region of the cephalium. *Bar* 50 μm in **a**, **c**; 300 μm in **b**; 100 μm in **d**, **f**, **h**; 200 μm in **e**, **g**, **i–k**. *b* Bristle, *co* cortex, *h* hypodermis, *m* mucilage cell, *sc* sclereid

cortical bundles at the apices of the vegetative branch and the cephalium varies ($F = 20.45$, gl $= 1$, $P < 0.0001$) and bundles are more numerous in the apex of the cephalium (Table 1), no differences were found at the bases ($P = 0.39$). Cortical and amphivasal bundles are common (Fig. 4h). Mucilage cells (Fig. 4f, i) differ ($F = 8.6$, gl $= 1$, $P < 0.007$) and are more abundant at the cephalium apex (Table 1), no differences were detected at the bases ($P = 0.16$) of vegetative branch and cephalium. A change in the parenchyma that is associated with the discoloration of the cephalium's bristles and trichomes (dark brown or black) indicates that the tissue is beginning to

collapse (Fig. 4i), with subsequent necrosis of the cortical cells. However, the parenchyma cells around the cortical bundles and the vascular cylinder remain alive.

Pith

The pith is parenchymatous (Fig. 4j), with collateral and amphivasal pith bundles showing secondary growth. There is no difference in the number of pith bundles in the apical ($P = 0.2$) and basal ($P = 0.5$) regions of the vegetative branch and cephalium (Table 1). Mucilage cells are rare ($2–11$ cells/mm^2), and there is no difference in their

abundance between the apical ($P = 0.07$) and the basal ($P = 0.09$) regions of vegetative branch and cephalium. Starch grains are abundant in the apex of the vegetative branch and throughout the cephalium, except at the base where necrotic cells are also present (Fig. 4k).

Vascular cylinder

There are a few differences in the secondary xylem and phloem of the vegetative branch and cephalium. The secondary xylem is fibrous with diffuse porosity; the vessels are solitary or in groups of two and are circular in cross section; the parenchyma is scanty paratracheal, the fibers are libriform and moderately thick-walled and rays are multiseriate with lignified cells (Fig. 5a, b). Vessel frequency is different ($F = 66.9$, gl $= 1$, $P < 0.0001$) and higher at the base of the cephalium (Table 1) than at the base of the vegetative branch. At the apices of the vegetative branch and cephalium, vessel diameter is similar ($P = 0.05$), but vessel diameter is wider at the base of the vegetative branch than at the base of the cephalium ($F = 48.3$, gl $= 1$, $P < 0.008$, Table 1).

Secondary phloem has two distinct zones: a conductive region and a nonconductive region (Fig. 5c). The conductive region is characterized by the presence of small sieve tubes with simple, horizontal sieve plates, companion cells and axial parenchyma. In the nonconductive region, the phloem parenchyma cells divide and expand between the collapsed conductive elements, and they sclerify. Additionally, in this region, there is a cap of 2–6 fibers differentiated during primary growth (Fig. 5c).

Periderm

The periderm develops primarily in the stem base and within the constraints of the vegetative branches, marking vegetative growth (Fig. 5d). Periderm has phellem and phelloderm in stem base, constraints of the vegetative branches and cephalium (Fig. 5e–g). The phellem has thin- and thick-walled cells, which alternate. By contrast, the phelloderm has thin-walled cells with chloroplasts and occasionally contains abundant mucilage and sclereids (Fig. 5e, g). In the early stages of cephalium development (Fig. 5f) and after reproductive events, the epidermis is replaced by the periderm. The phellogen of this early periderm originates from periclinal divisions of the epidermal cells of the interareolar region as occurs in the stem base. At the base of the areole, the periderm develops similarly, but there are no hypodermal remnants (Fig. 5f, h). The periderm completely covers the reproductive cephalium region and corresponds to the region with darker colored bristles (Fig. 3a, c).

Discussion

The vegetative branch vs. the cephalium

The morphology and anatomy of *Backebergia militaris* cephalium are distinct from those of vegetative branches. The phyllotaxis modification in the cephalium compared to the vegetative branch is a consequence of the lack of interareolar spaces and ribs, thus tubercles are helically arranged. It will be interesting to investigate which hormones or genes drive to these changes. Moreover, the abundant bristles and trichomes in the cephalium, compared to the vegetative branch that lack them, do not allow to see the surface. In addition, the color change of these trichomes as they move away from the apical region is probably associated with the surface changing from green to dark brown due to peridermal development as the cephalium grows (Fig. 3a), as well as to necrosis of the cortical and pith tissue at the base of the cephalium. These morphological differences in *B. militaris* cephalium make its reproductive region distinctive from the vegetative one. Mauseth (2006) mentions that when the cephalium is terminal (apical) the stem continues growing, elongating annually and producing flowers and fruits while the vegetative portion ages. Our observations of *B. militaris* indicate that both the vegetative region and the cephalium grow; the number of ribs increases in the vegetative region, and ribs become whiter in the distal region of the cephalium due to the discoloration associated with aging.

The anatomy of the vegetative branch and the cephalium are similar, although in the cephalium the cells tend to be smaller. For example, epidermal cells and stomata are only present in reduced intercostal regions and only up to a few millimeters from the apical meristem in the cephalium, but they are preserved for years in the ribs of the vegetative branch. In the cephalium, the epidermal cells divide periclinally to generate periderm close to the apical meristem. The periderm covers the entire cephalium, which is a feature that differentiates the cephalium from the vegetative branch in which periderm is only present in the constraints of growth. Moreover, as in other cacti, periderm is also present near the base of the trunk. The periderm of the cephalium has extensive chlorenchymatous phelloderm, which may favor the mobilization of photosynthates, as has been suggested for other dicotyledonous plants with chloroplasts in the phelloderm (Nilsen 1995). Like other members of the Echinocereeae (Gibson and Horak 1978; Terrazas and Loza-Cornejo 2002; Loza-Cornejo and Terrazas 2003), the hypodermis is multilayered and collenchymatous in both the vegetative branch and the cephalium. However, in the cephalium, the hypodermis is thinner and restricted to the tubercles. The chlorenchyma in
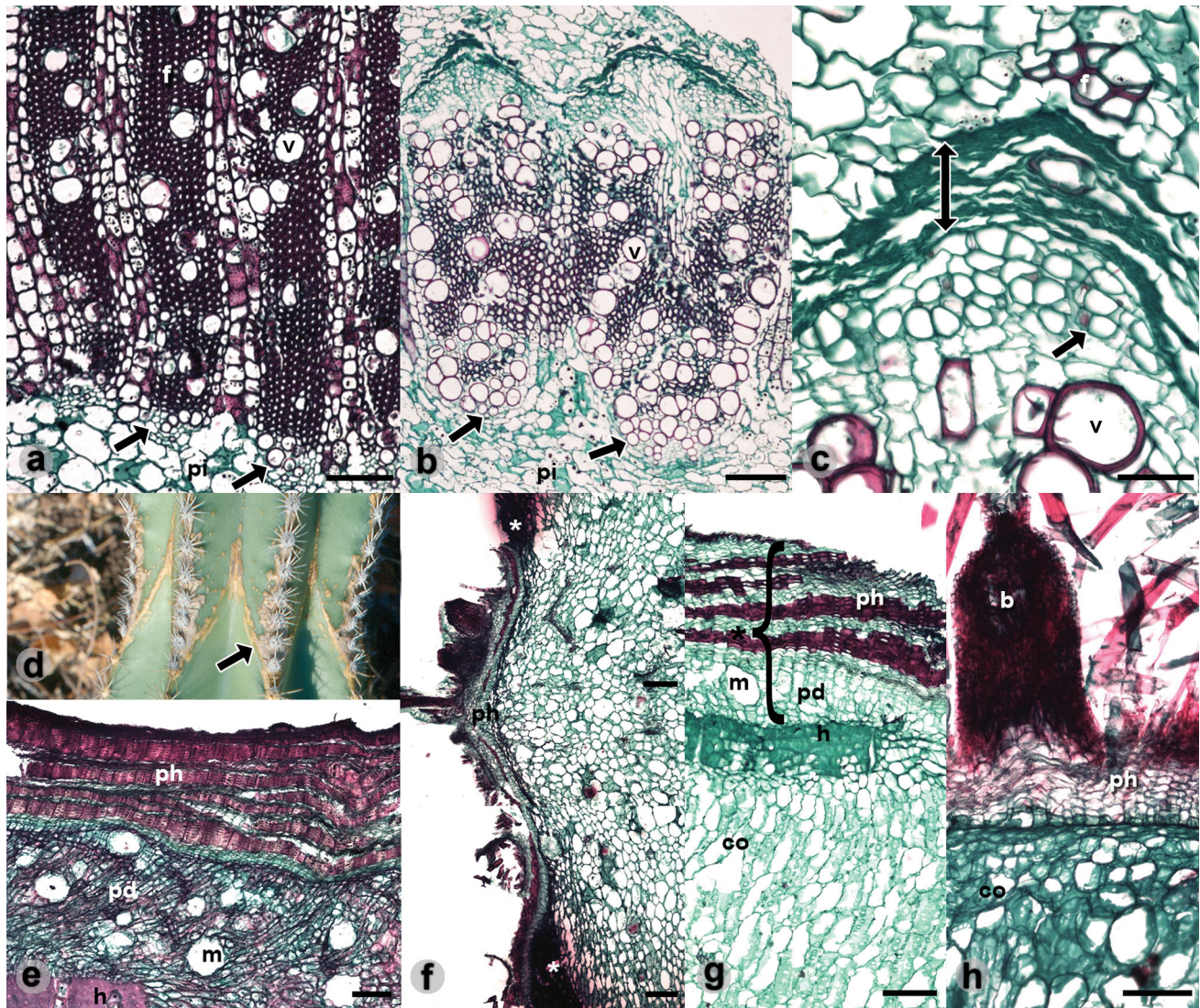
Fig. 5 Cross sections of the secondary tissue of a cephalium and a vegetative branch of *Backebergia militaris*. **a**, **b** Secondary xylem (*arrows*, absence of fibers). **a** Vegetative branch. **b** Cephalium. **c** Detail of a phloem conductive region (*arrow*, sieve tube and companion cell) and nonconductive region (*double arrow*). **d** Detail of the annual branch growth mark (*arrow*, periderm). **e** The periderm of the vegetative branch at the base of the stem. **f** Cephalium periderm showing both ends (*asterisk*) of the interareolar region and an areole in the center. **g** Detail of the periderm (*asterisk*) in the interareolar region with phellem and phelloderm. **h** Detail of the periderm in the areole. *Bar* 200 μm in **a**, **b**, **e**–**g**; 50 μm in **c**; 100 μm in **h**. *b* Bristle, *co* cortex, *f* fiber, *h* hypodermis, *m* mucilage cell, *pd* phelloderm, *ph* phellem, *pi* pith, *v* vessel

the apex of the cephalium contains abundant chloroplasts, which is similar to the chlorenchyma in the vegetative branch and in other Cactoideae species (Sajeva and Mauseth 1991; Terrazas et al. 2005; Soffiatti and Angyalossy 2007). In *B. militaris*, the cortical bundles are amphivasal in the vegetative branch and the cephalium, a feature that distinguishes *Backebergia* from other members of the Pachycereinae subtribe, which have collateral cortical bundles (Terrazas and Loza-Cornejo 2002). The greater number of cortical bundles in *B. militaris* is probably a consequence of the reduction of the interareole spaces, which allows for the efficient mobilization of

photosynthates to developing fruits. In *B. militaris* cephalium, the cortical bundles closest to the apical meristem show primary and secondary growth. The secondary xylem and phloem of the cephalium and the vegetative branch in *B. militaris* are similar. In both, similar to other species of the Echinocereeae tribe (Gibson 1973; Terrazas and Loza-Cornejo 2002; Terrazas et al. 2005), the secondary xylem is fibrous, and the presence of a few sclereids in the nonconductive secondary phloem is a characteristic shared with other Echinocereeae species (Terrazas and Loza-Cornejo 2002). Differences in vessel diameter size and number between the apex and the base of

the vegetative branch and the cephalium are interpreted as part of the variation along the axis of the branch, as has been recorded for other members of Echinocereeae (Bernal-Salazar and Terrazas 2005), but the other differences between vegetative branch and cephalium as for epidermal cell size, hypodermis thickness and abundance of cortical bundles and mucilage cells are related to the specialization of the cephalium as the structure bearing reproductive organs.

The cephalium of *Backebergia militaris* vs. the cephalia of other species

Comparatively, the unique combination of morphological and anatomical characters in the apical cephalium of *Backebergia militaris* makes it distinctive from other cephalia described to date (Table 2). For example, the altered phyllotaxis and the helical arrangement of the tubercles do not occur in species with lateral cephalia such as *Cephalocereus*, whose cephalia preserve the orderly arrangement of the ribs and whose phyllotaxis remains unchanged (Vázquez-Sánchez et al. 2005, 2007). Unfortunately, no information about these features in the other species with lateral cephalia (*Coleocephalocereus* Backeb., *Espostoa* Britton & Rose, *Pseudoespostoa* Backeb., *Thrixanthocereus* Backeb.) is available. It is unknown if there is a change in the phyllotaxis of the apical cephalia of *Discocactus* and *Melocactus* Link & Otto. Detailed morphological studies that follow a similar methodology as described here will show if the morphological characteristics of the apical cephalium are unique to *B. militaris* or shared with *Discocactus* and *Melocactus* species.

One of the characters shared between apical and lateral cephalia of different genera is the occurrence of abundant spines or bristles and trichomes on the areole that completely cover the cephalium (Mauseth 1989, 1999; Vázquez-Sánchez et al. 2005, 2007; Machado 2009; Gorelick 2009, 2013, 2014a). These features protect the floral meristems, which are located exclusively in this apical region.

According to Niklas and Mauseth (1980) and Terrazas and Mauseth (2002), the apical cephalium is produced by the same apical meristem that produces the vegetative stem. In the particular case of *B. militaris*, the apical meristem retains its position in the center of the apex, a position that contrasts with the displacement of the apical meristem toward the lateral cephalium region in *Cephalocereus columna-trajani* and *Cephalocereus senilis* (Vázquez-Sánchez et al. 2005, 2007). The relative volume of the tissue in the apical region does not significantly change between the vegetative growth phase and the reproductive phase (cephalium), except perhaps during the initial change in phyllotaxis and reduction of the

interareolar spaces in *B. militaris*. Moreover, the modifications associated with growth and aging also differ among species; in *B. militaris*, as already mentioned, there is a change in the phyllotaxis and in the coloring of the bristles and trichomes covering the cephalium (Fig. 1e), whereas in the lateral cephalia of *C. columna-trajani* and *C. senilis*, there is an increase in the number of ribs and bristles, and the deciduous trichomes drop from the areoles, exposing the periderm (Vázquez-Sánchez et al. 2005, 2007). In *Coleocephalocereus aureus*, there is also a color change in the trichomes as seen in the photos shown by Gorelick and Machado (2012), and we do not know if this color change is related to the anatomical characters mentioned here for *B. militaris*.

The meristem located on the areoles of the cephalium has a short life. That is, once it produces a flower and the fruit has matured, the periderm differentiates from epidermal cells and seals the entire areole (Figs. 4b–d, h, 5f). In monopodial species, this differentiation may come at a great cost: the areoles will never be active again, and it is not uncommon for cephalia to produce branches. However, there are exceptional events, as in *Coleocephalocereus* (Gorelick and Machado 2012) and *Espostoa* (Gorelick 2014b) in which old areoles within the cephalium may produce a flower or an axillary vegetative branch. The sympodial growth of *B. militaris* means that new branches—and, therefore, new cephalia—are formed. Thus, we suggest that the plant maintains a balance between vegetative branches and cephalium and when a damage occurred it has the ability to produce new branches. In the case of species such as *M. intortus* (Mauseth 1989), which does not have the ability to produce new branches when the apical cephalium is damaged, the possibility of developing a new cephalium is minimal.

Early in the development of the cephalium, the epidermal cells divide periclinally and differentiate in a periderm, attribute that is characteristic of species with cephalia (Mauseth 1989, 1999, 2006; Vázquez-Sánchez et al. 2005, 2007). The periderm of the *B. militaris* cephalium grows bidirectionally, whereas it grows unidirectionally in *M. intortus* (Mauseth 1989, 1999, 2006) and in species with lateral cephalia (Mauseth 1999; Vázquez-Sánchez et al. 2005, 2007), meaning that they do not have phelloderm. The presence of stomata, a reduced hypodermis and numerous chlorenchyma cells in the apical region of the cephalium in *B. militaris* markedly differs from *M. intortus*, which lacks stomata, hypodermis and chloroplasts (Mauseth 1989). Other species with lateral cephalia also have a few stomata, may have or not hypodermis and lack chloroplasts (Mauseth 1999; Vázquez-Sánchez et al. 2005, 2007), however, information is lacking for most species with cephalia (Table 2). This observation suggests a trade off towards the loss of stomata and chlorenchyma and the

Table 2 A comparison of the morphological and anatomical characteristics of species with cephalia

Species	Tribe	Position	Ribs	Phyllotaxis	Color	Meristem	Periderm	Phelloderm	Necrotic	Hypodermis	Chlorenchyma	Stomata	Fibers
Backebergia militaris (Audot) Bravo ex Sanchez-Mej.	Echi.	a	-	+	+	-	+	+	+	+	+	+	+
Cephalocereus columna-trajani (Karw. ex Pfeiff.) P.V. Heath (1)	Echi.	1	+	-	-	+	+	-	-	+	-	+	-
Cephalocereus senilis Pfeiff. (2)	Echi.	1	+	-	-	+	+	-	-	+	-	+	-
Coleocephalocereus aureus F.Ritter (3)	Cere.	1	?	?	+	?	?	?	?	?	?	?	?
Coleocephalocereus buxbaumianus Buining (3)	Cere.	1	?	?	-	?	?	?	?	?	?	?	?
Coleocephalocereus fluminensis (Miq.) Backeb. (3)	Cere.	1	?	?	-	?	?	?	?	?	?	?	?
Coleocephalocereus goebelianus (Vaupel) Buining (3)	Cere.	1	?	?	-	?	?	?	?	?	?	?	?
Coleocephalocereus purpureus (Buining & Brederoo) F.Ritter (4)	Cere.	1	?	?	-	?	+	-	?	?	-	?	?
Discocactus Pfeiff (5)	Trich.	a	?	?	-	?	+	-	?	?	?	?	?
Espostoa lanata (Kunth) Britton & Rose (6)	Trich.	1	+	?	-	?	+	-	-	+	-	-	-
Espostoa mirabilis F.Ritter (6)	Trich.	1	+	?	-	?	+	-	-	-	-	-	-
Espostoa ritteri Buining (6)	Trich.	1	+	?	-	?	+	-	-	-	-	-	-
Melocactus intortus (Mill.) Urb. (7)	Cere.	a	-	?	-	?	+	-	-	-	-	-	-
Pseudoespostoa melanostele (Vaupel) Backeb. (6)	Trich.	1	+	?	-	?	+	-	-	-	-	-	-
Trichocereus senilis F.Ritter (6)	Trich.	1	+	?	-	?	+	-	-	-	-	+	-
Vatricania guentheri (Kupper) Backeb. (6)	Trich.	1	+	?	-	?	+	-	-	+	-	+	-

Tribe: Echinocereeae, Echi.; Cereeae, Cere; Trichocereeae, Trich. Position (*a* apical, *l* lateral), ribs distinctive in the cephalium, change in phyllotaxis, color change in trichomes and bristles, apical meristem displacement, periderm, necrotic tissue, hypodermis, chlorenchyma, stomata, fibers in secondary xylem. –, Absent; +, present; ?, unknown; ±, rare. (1, Vázquez-Sánchez et al. 2007; 2, Vázquez-Sánchez et al. 2005; 3, Gorelick and Machado 2012; 4, Gorelick 2013; 5, Gorelick 2014a; 6, Mauseth 1999; 7, Mauseth 1989)

increase of cortical bundles, which is possibly related to more efficient translocation of photosynthates from the vegetative region to the cephalium, regardless of the type of cephalium (lateral or apical). In the cephalium of *B. militaris*, like the lateral cephalium of *Cephalocereus* (Vázquez-Sánchez et al. 2005, 2007), the cortical bundles closest to the apical meristem show primary and secondary growth probably favoring higher translocation of photosynthates (Mauseth and Sajeva 1992), which is in contrast to the primary growth observed in other cephalia of Cereeae and Trichocereeae tribes (Mauseth 1989, 1999).

The presence of fibers in the secondary xylem of the *B. militaris* cephalium is a feature that distinguishes it from other species with apical (*M. intortus*) or lateral cephalia (*C. columna-trajani*, *C. senilis*, *Espostoa lanata*, *E. mirabilis*, *E. ritteri*, *P. melanostele*, *Trichocereus senilis*, *V. guentheri*), which lose fibers in this region but have fibrous wood in the vegetative branch (Mauseth 1989, 1999; Vázquez-Sánchez et al. 2005, 2007). The secondary xylem of the *M. intortus* cephalium is made of abundant parenchyma and few vessels and lacks fibers and wide band tracheids. According to Mauseth (1989), the covering of spines and trichomes provides support and fibers do not differentiate. This is not the case for the apical cephalium of *B. militaris*; despite having numerous bristles and trichomes, it retains fibers in the xylem and phloem.

Conclusions

A combination of morphological and anatomical characters in the cephalium of *B. militaris* makes it different from the apical and lateral cephalia that have been reported for other cacti species in anatomical studies to date. Moreover, differences found between the vegetative branch and the cephalium of *B. militaris* appear to be unique, since they have not been previously described for other studied species. A homologous trait that *B. militaris* cephalia share with other cephalia is the early development of the periderm that originates in the epidermal cells. However, additional morpho-anatomical studies in Cereeae and Trichocereeae are needed to understand the evolution of this complex structure in Cactoideae. Studies on the physiology of the cephalium of *B. militaris* will help clarify whether its anatomical changes are related to its morphological changes, especially those related to the color of its bristles and spines, and whether they represent an adaptation to its native climate.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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