

## ***Coleocephalocereus purpureus* has a cephalium; *Micranthocereus streckeri* has a pseudocephalium (Cereeae, Cactoideae, Cactaceae)**

*Root Gorelick*

Department of Biology, School of Mathematics & Statistics, and Institute of Interdisciplinary Studies  
Carleton University, 1125 Colonel By Drive, Ottawa, Ontario K1S 5B6 Canada.  
(email: Root.Gorelick@carleton.ca).

Photographs by the author

*Summary:* The putatively closely related cactus genera of *Coleocephalocereus*, *Micranthocereus*, *Cereus*, *Monvillea*, and *Stetsonia* have a wide range in specialization of reproductive portions of the shoot, from cephalium to pseudocephalium to no specialization. After briefly summarizing the shifting uses of the terms 'cephalium' and 'pseudocephalium', I provide gross morphological evidence that *Coleocephalocereus purpureus* has a true cephalium that is formed of a continuous swath of bristles and hairs, with its underlying thick cortex of parenchyma replaced by a narrow layer of cork. By contrast, *Micranthocereus streckeri* has a pseudocephalium composed of nothing more than larger hairier areoles in which the underlying epidermis is still photosynthetic and the underlying cortex is still a thick layer of parenchyma without any noticeable cork.

*Zusammenfassung:* Die vermuteterweise nahe miteinander verwandten Kakteengattungen *Coleocephalocereus*, *Micranthocereus*, *Cereus*, *Monvillea*, und *Stetsonia* haben ein weites Spektrum an Spezialisierungen der reproduktiven Sprossabschnitte, variierend von Cephalien zu Pseudocephalien, und ohne Spezialisierung. Nach einer kurzen Zusammenfassung der im Laufe der Zeit unterschiedlichen Verwendungen der Begriffe 'Cephalium' und 'Pseudocephalium' stelle ich allgemeine morphologische Evendenzen vor, dass *Coleocephalocereus purpureus* ein echtes Cephalium hat, das aus einem kontinuierlichen Streifen aus Borsten und Haaren besteht, dessen darunterliegender dicker parenchymatischer Cortex durch eine dünne Korkschicht ersetzt wird. Im Gegensatz dazu hat *Micranthocereus streckeri* ein Pseudocephalium, das lediglich aus grösseren und stärker behaarten Areolen besteht, bei dem die darunterliegende Epidermis weiterhin photosynthetisch bleibt, und bei dem der darunterliegende Cortex weiterhin aus einer dicken Parenchym-schicht besteht, ohne auffällige Korkbildung.

### **Introduction**

Cactaceae (cacti) in the tribe Cactoideae have a wide range of reproductive anatomies ranging from cephalia to pseudocephalia to forms where reproductive and vegetative structures are indistinguishable (Buxbaum, 1964, 1975; Mauseth, 2006).

For instance, *Melocactus* Link & Otto, *Disco-cactus* Pfeiffer, and *Espostoa* Britton & Rose have true cephalia in which the flowering parts are not photosynthetic because every epidermal cell contains a modified leaf that is a hair, bristle, or spine, with no stomata amongst the epidermal cells (Mauseth, 2006). Furthermore, there are changes to the internal anatomy of cephalia, where the underlying cortex is not a wide swath of highly succulent parenchyma, but instead a thin layer of cork.

By contrast, pseudocephalia are composed of relatively normal areoles that simply grew more hairs or bristles. The areoles themselves may also be larger and closer to being confluent. The epidermis of a pseudocephalium is still photosynthetic (chlorenchyma) with stomata, and the underlying cortex is unchanged, with a thick layer of succulent parenchyma (Mauseth, 2006). As with true cephalia, pseudocephalia usually grow directly from the shoot apical meristem, as in *Pilosocereus* Byles & G.D. Rowley and *Cephalocleistocactus* F. Ritter (cf. Buxbaum, 1964). Many cacti with pseudocephalia are also like those with cephalia in that flowers are only produced from specialized areoles, i.e. those with long copious hairs and bristles, although a few species such as *Arrojadoa hofackeriana* (P.J. & Esteves) P.J. Braun & Esteves [synonyms: *Micranthocereus hofackeriana* (P.J. Braun & Esteves) Machado and *Arrojadoa multiflora* F. Ritter subsp. *hofackeriana* P.J. Braun & Esteves] can produce flowers from both the pseudocephalium and more juvenile-looking (non-wooly) areoles (Braun & Esteves Periera, 2007).



**Figure 1.** *Pilosocereus gounellei* subsp. *zehntneri*, with pseudocephalia arising from shoot apical meristems.



**Figure 2.** *Espostoa melanostele*, radial section of young cephalium, with flower bud.



**Figure 3.** *Espostoa melanostele*, cross section (of excised section from Figure 2) with cephalium on left.



**Figure 4.** *Coleocephalocereus purpureus*, in habitat.



**Figure 5.** *Coleocephalocereus purpureus*, shoot that was sectioned in Figures 6-8.



**Figure 6.** *Coleocephalocereus purpureus*, cross section.

My modest goal was to determine whether *Coleocephalocereus purpureus* (Buining & Brederoo) F. Ritter and *Micranthocereus streckeri* Van Heek & Van Creik. have a cephalium or instead a pseudocephalium. Both species are in the tribe Cereeae (Hernández-Hernández *et al.*, 2011), which contains plants with cephalia (*Melocactus*, *Discocactus*, *Arrojadoa* Britton & Rose), plants with pseudocephalia (several *Pilosocereus* species), plants with neither a cephalium nor pseudocephalium (*Cereus* Miller; with the possible exception of the enigmatic *C. mortensenii* (Croizat) D.R. Hunt & N.P. Taylor), and a few plants that are ambiguous (e.g. *Stetsonia coryne* (Salm-Dyck) Britton & Rose, which is like *Carnegiea gigantea* Britton & Rose and *Browningia candelaris* (Meyen) Britton & Rose in only flowering from relatively spineless areoles).

Surprisingly, there has been almost no published work on the morphology of cephalia and pseudocephalia. These structures have been sectioned and the results published on only a few cacti, such as *Melocactus* spp., *Espostoa* spp., *Cephalocereus senilis* Pfeiffer, *C. columna-trajani* (Karw.) K. Schum., and *Pachycereus militaris* (Audot) D.R. Hunt [synonym: *Backebergia militaris* (Audot) Sánchez-Mej.] (Mauseth, 1999, 2006; Mauseth *et al.*, 2005; Vázquez-Sánchez *et al.*, 2005, 2007), but apparently not on other taxa, such as the two species investigated herein.

### A short history of the terms cephalium and pseudocephalium

The above distinction between cephalia and pseudocephalia is modern, with older literature and even some current literature giving different definitions of these two terms. I therefore give a brief history of the use of these terms.

Hooker used the term ‘cephalium’ in several of his Latin diagnoses in *Curtis’s Botanical Magazine*, but never defined the term and seemed to use the term somewhat indiscriminately, for example, from a panoply of plants that we now usually call *Melocactus intortus* (Mill.) Urb. (1831, Vol. 58, Tab 3090), *Parodia ottonis* (Lehm.) N.P. Taylor (1831, Vol. 58, Tab 3107), *Echinopsis eyriesii* Turpin (1835, Vol. 62, Tab 3411), *Gymnocalycium gibbosum* (Haw.) Pfeiffer ex. Mittler (1837, Vol. 64, Tab 3561) and *Echinocereus rigidissimus* Rose (1845, Vol. 71, Tab 4190).

The earliest definition I could find of a ‘cephalium’ is “the floriferous region of the plant is differentiated from the rest” in Berger’s (1907: 61) description of the genus *Cephalocereus* Pfeiffer. Nowadays, some would call the reproductive structures of *Cephalocereus* a cephalium (e.g. Vázquez-Sánchez *et al.*, 2005, 2007), while others – including me – would call this a pseudocephal-

ium (e.g. Zavala-Hurtado *et al.*, 1998, Valverde *et al.*, 2007). Similarly, Gürke (1908) used the term ‘cephalium’ for all specialized woolly floriferous portions of cactus shoots, when speaking of *Facheiroa ulei* (Gürke) Werderm. [as *Cephalocereus ulei* Gürke] and *Micranthocereus purpureus* (Gürke) F. Ritter [as *Cephalocereus purpureus* Gürke].

Britton & Rose (1919-1923) confined use of the term ‘cephalium’ to *Melocactus* and *Discocactus*, calling all other specialized reproductive structures ‘pseudocephalia’. A “cephalium [is] composed of a central woody core surrounded by a dense mass of long wool, bristles or both” (Britton & Rose, 1922: 216). “Flowering areoles develop an abundance of wool which confluent forms a dense mass called a pseudocephalium either at the top or on one side near the top” (Britton & Rose, 1920: 25). Britton & Rose (1920) referred to all known species of *Coleocephalocereus* Backeberg and *Micranthocereus* Backeberg as *Cephalocereus*, which they claimed had pseudocephalia. Many subsequent authors followed Britton & Rose’s tradition of reserving the term ‘cephalium’ exclusively for *Melocactus* and *Discocactus*, e.g. Gibson & Nobel (1986). Anderson (2001: 697) even more explicitly concurred with Britton & Rose by defining a pseudocephalium as “a lateral cephalium”.

Backeberg (1934-1938) applied the term ‘cephalium’ to the following taxa (I have listed modern names, not Backeberg’s): *Melocactus*, *Discocactus*, *Arrojadoa*, *Stephanocereus leucostele*, *Facheiroa* Britton & Rose, *Espostoa*, *Espostoopsis* Buxbaum, *Coleocephalocereus*, *Cephalocereus*, and *Neobuxbaumia macrocephala* (F.A.C. Weber ex K. Schum.) E.Y. Dawson. Backeberg only used the term ‘pseudocephalium’ for *Micranthocereus* and *Pilosocereus* Byles & G.D. Rowley. Note, however, that he claimed that *Cephalocereus purpureus* Gürke and *Cephalocereus macrocephalus* F.A.C. Weber ex K. Schum. have cephalia, even though I would label these plants *Micranthocereus purpureus* (Gürke) F. Ritter and *Neobuxbaumia macrocephala*, respectively, and say that they probably have pseudocephalia, as I believe do all *Micranthocereus* and *Cephalocereus* species that have specialized woolly flowering areoles. Backeberg (1934-1938) also noted whether some lateral cephalia were channeled or sunken in a cleft, as in *Coleocephalocereus fluminensis* (Miquel) Backeberg, *Espostoa lanata* (Kunth) Britton & Rose, and *E. melanostele* (Vaupel) Borg.

Buxbaum (1964) said that cephalia and pseudocephalia are densely hairy regions of a shoot – hairier than vegetative parts of the shoot – from which flowers originate. If these hairy regions originated from the shoot apical meristem,



**Figure 7.** *Coleocephalocereus purpureus*, cross section.



**Figure 8.** *Coleocephalocereus purpureus*, radial section, showing apical meristem, flower buds (one or two), and a scintilla of chlorenchyma underneath cephalium (near curve).



**Figure 9.** *Coleocephalocereus purpureus* with a 25 cm cephalium, shoot that was sectioned in Figures 10-11.



**Figure 10.** *Coleocephalocereus purpureus*, radial section, showing replacement of thick parenchymatous cortex with a thinner cork layer as soon as cephalium starts.



**Figure 11.** *Coleocephalocereus purpureus*, radial section, facing section of Figure 9.

Buxbaum called the flowering region a cephalium. If these hairy regions developed later as subsequent growth on existing areoles, Buxbaum called these flowering regions a pseudocephalium. Buxbaum (1975) realized that there is a continuum between these two developmental extremes, but never seems to have proposed an alternative way to define points along this ontogenetic continuum.

There is also the problem that a cactus shoot can do both. That is, an individual shoot can grow woolly areoles directly from the shoot apical meristem and later grow more woolly modified spines as the areoles slowly grows larger over the years (Gorelick, in review, a). By Buxbaum's (1964) definition of a cephalium being woolly areoles produced by the shoot apical meristem, *Micranthocereus* and several taxa of *Pilosocereus*, such as *P. gounellei* (F.A.C. Weber ex. K. Schum.) Byles & G.D. Rowley subsp. *zehntneri* (Britton & Rose) Byles & G.D. Rowley [synonym: *P. braunii* Esteves] (Figure 1), have cephalia, even though these are some of the few taxa that Backeberg (1934-1938) claimed had pseudocephalia.

Buxbaum (1964) understood that lateral cephalia, at least of *Espostoa*, not only originated from the shoot apical meristem, but that the cephalium was also sunken within the surrounding photosynthetic parts of the shoot and that the vascular cylinder was flattened on the side of the shoot underlying the cephalium. He also understood that the areoles were confluent in the cephalium, with less prominent ribs and tubercles near the transition between vegetative and reproductive tissues. This presages Mauseth's (2006) definition of a cephalium, which I have largely borrowed here. But curiously, Buxbaum never relied on these characteristics for differentiating cephalia from pseudocephalia, possibly because he had not sectioned many taxa.

It is beyond the scope of this paper to justify which definitions of cephalia and pseudocephalia are best. This is a difficult task insofar as definitions are neither testable nor falsifiable. "Quality of a definition is gauged by its utility and consistency of meaning and connotation across many contexts" (Gorelick, 2012: 872). This is probably why Buxbaum (1964) asked how did cephalia originate and is there phylogenetic signal in presence/absence of cephalia and pseudocephalia. But answers to these questions will have to await another day. Here, I simply want to describe gross morphological details of cephalia and pseudocephalia in a few taxa.

### ***Espostoa melanostele*: a classic lateral cephalium**

Figure 2 shows a radial (vertical) section of a

cephalium of *Espostoa melanostele*. The bottom quarter of the image grew before the cephalium formed and is radially symmetrical, with equally thick cortex on both sides of the vascular cylinder and lots of chlorenchyma on both sides of the shoot. No photosynthesis occurs underneath (centripetal to) the cephalium. A cross (horizontal) section of the same shoot (Figure 3) also shows radial asymmetry and lack of green photosynthetic tissue underneath the cephalium. Figure 11 in Buxbaum (1964) illustrates the confluent areoles in the cephalium, diminished cortex underneath the cephalium, and diminished pith underneath the cephalium, albeit in *Espostoa lanata* (labelled as *E. sericata* J. West).

The cephalium in *E. melanostele* (and all other species of *Espostoa*; see Buxbaum, 1964; Mauseth, 1999, 2006) grows from the shoot apical meristem and, very soon after initiation of cephalium growth, the shoot narrows on the cephalium-bearing side, with the shoot developing a thin but dense layer of cork underneath the cephalium in lieu of a wide layer of parenchyma. Simultaneous with formation of the cork layer, the highly succulent parenchyma layer of cork underneath the nascent cephalium diminishes. The only green tissue of the cephalium is the small side branch, which is a flower bud. Above that flower bud, the cork has almost entirely replaced the parenchymous cortex. Other than spines, the cork underlying the cephalium is the only difficult part to slice when sectioning the plant. At the very top of the cork layer is the shoot apical meristem, which is displaced from a vertically apical position, tilted towards the cephalium-bearing side of the shoot.

### ***Coleocephalocereus purpureus* and *Micranthocereus streckeri***

*Coleocephalocereus purpureus* and *Micranthocereus streckeri* may seem like odd choices for study, especially since both are highly restricted endemics of eastern Brazil and suspected of being of recent hybrid origin (but of what parents?). *Coleocephalocereus purpureus* (Buining & Brederoo) F. Ritter is sometimes confused with *Micranthocereus purpureus* (Gürke) F. Ritter (e.g. <http://www.arkive.org/cactus/coleocephalocereus-purpureus/image-G72084.html>; accessed 16 June 2013; I have requested that this error be remedied), which is somewhat expected given that some species have been transferred between these two genera, e.g. *M. albicephalus* (Buining & Brederoo) F. Ritter is synonymous with *C. albicephalus* (Buining & Brederoo) F.H. Brandt. Cultivated specimens of both *C. purpureus* and *M. streckeri* were available for dissection and they eventually flowered, allowing unambiguous identification. Curiously, *M. streckeri* is like several



**Figure 12.** *Micranthocereus streckeri*, in habitat.



**Figure 13.** *Micranthocereus streckeri*, double-sided cephalium with flowers and fruits.



**Figure 14.** *Micranthocereus streckeri*, both cephalia arising from one shoot apical meristem.



**Figure 15.** *Micranthocereus streckeri*, shoot that was sectioned in Figures 16-17.



**Figure 16.** *Micranthocereus streckeri*, cross section.



**Figure 17.** *Micranthocereus streckeri*, cross section.

species of *Espostoa* in that a pair of lateral cephalia/pseudocephalia sometimes grows on diametrically opposite sides of a single shoot (Figures 10-11), a phenomenon that is rare. Figures 4 and 9 are habitat photos of *C. purpureus* at its type locality in Minas Gerais and of *M. streckeri* at its type locality in Bahia. Figures 5 and 12 are photos of the cultivated plants of these two species, in flower, prior to sectioning. Figures 6-8 and 16-17 are sections of Figures 5 and 15, respectively.

In sectioning these plants, it was immediately obvious that *Coleocephalocereus purpureus* possessed a true cephalium, while *Micranthocereus streckeri* possessed a pseudocephalium because only the former had a cork layer that made cutting difficult, but only just underneath the surface of the cephalium. The rest of *C. purpureus* (except for the spines) cut like butter, as is typical for young to middle-aged non-cephalium-bearing cactus shoots (old columnar cacti sometimes develop a corky base). There is a very similar localized resistance to cutting the cork layer underlying the cephalia of *Melocactus* and *Discocactus* (Gorelick, in review, b). By contrast, all portions of the shoot of *Micranthocereus streckeri*, including the pseudocephalium, cut like butter.

The cephalium of *Coleocephalocereus purpureus* is not on the ribs, but rather occupies a continuous area that goes on top of and between ribs (Figures 5-7). For the most part – although see below for a small exception – there is no obvious photosynthetic tissue underneath the cephalium, while hairs and bristles in the cephalium seem to arise from every epidermal cell (Figures 6-8). The cork layer underneath the cephalium is obvious in Figure 10, where the cork has a brown colour compared with the white of the succulent parenchyma underneath the surface of photosynthetic tissue. Because the cephalium of *C. purpureus* in Figures 5-8 was young and small, the radial section of the upper half of the cephalium plus adjacent photosynthetic tissue (Figure 8) was not as elegant as that of *Espostoa melanostele*. Nonetheless, a comparison of Figures 2 and 8 shows very similar architecture. The dark green from which the two short bristles at the top of Figure 8 are growing is the shoot apical meristem of *C. purpureus*. This radial section sliced through one fairly large flower bud, which looks like a small side shoot. Not far above that flower bud is probably the start of another flower bud, which also shows the red colour of the perianth parts. The only thing surprising in this radial section is the very small amount of chlorenchyma that appears in the apparent curve in the cephalium. This may be because the cephalium is young. Otherwise, *Coleocephalocereus purpureus* has a typi-

cal true cephalium.

Figures 10-11 are of the pair of facing radially sections of a 25 cm long cephalium of *Coleocephalocereus purpureus*, where the intact plant is shown in Figure 9. At the shoot apical meristem – which is tilted far towards the cephalium-bearing side and is at the top of the cephalium – the cephalium occupies about half the circumference of the shoot. The cork immediately underlying the cephalium was the only portion that was difficult to cut. The cork layer varied in thickness as the cephalium grew, but the number of ribs that the cephalium covered also varied. Unlike with *Espostoa melanostele*, as soon as the cephalium appeared in *C. purpureus*, the succulent parenchyma in the cortex underlying the cephalium immediately disappeared and was replaced by the cork layer. Unlike in the smaller plant of *C. purpureus* in Figure 8, there is absolutely no evidence of chlorenchyma underlying this much larger cephalium (close-ups not shown).

The cross section in Figures 16-17 is through the widest portion of the pseudocephalium of the *Micranthocereus streckeri* shoot, near the pair of mature red fruits in Figure 15. Even before sectioning the shoot, it was somewhat obvious that the pseudocephalium is formed from simply a part of the shoot with larger and hairier areoles, even though these grew right from the shoot apical meristem. Note how the pseudocephalium did not disrupt phyllotaxy. As the cephalium grew wider and then narrower again in Figure 15, the ribs continued on through in a straight line, with underlying architecture of the ribs remaining unchanged. The cross section shows photosynthetic tissue in between areoles, as well as underneath them (Figure 16). The cross section of the shoot is circular, i.e. radially symmetrical, with no obvious cork formation underneath the flowering areoles (Figure 17). *Micranthocereus streckeri* has a typical pseudocephalium, sensu Mauseth (2006).

### Concluding remarks

Based on five characters – (1) cork, (2) radial asymmetry, (3) chlorenchyma, (4) confluent areoles, and (5) phyllotaxy – *Coleocephalocereus purpureus* has cephalia, whereas *Micranthocereus streckeri* has pseudocephalia.

Hernández-Hernández *et al.* (2011) show a virtual polytomy in the tribe Cereeae with the five genera *Coleocephalocereus* Backeberg, *Micranthocereus*, *Cereus*, *Monvillea* Britton & Rose, and *Stetsonia* Britton & Rose. Specialization of reproductive structures can clearly vary greatly across a clade. It is even possible that within a single genus that there may be species with cephalia and pseudocephalia or with pseudocephalia and no specialization into morphologically distinct flow-

ering areoles, such as possibly with *Pilosocereus*, *Stephanocereus* A. Berger, or *Micranthocereus*.

However, it appears that all species of *Coleocephalocereus* have a true cephalium because the hairs and bristles appear to be independent of the phyllotaxy, i.e. independent of the ribs, whereas no species of *Micranthocereus* have a true cephalium because you can distinguish individual areoles in the pseudocephalium and these rows of areoles line up nicely with those of the older green non-reproductive portions of the shoot (Taylor & Zappi, 2004). Pseudocephalia and cephalia may be homologous, with the pseudocephalia merely having chlorenchyma and stomata, while lacking the thin cork layer in the cortex. But the only way to test such a hypothesis is to start by collecting natural history observations of the gross morphology of these flowering regions.

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