

What is a cephalium?

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Summary: There are problems with previous attempts to define ‘cephalium’, such as via production of more hairs and spines, confluence of areoles, or periderm development at or underneath each areole after flowering. I propose using the term ‘cephalium’ only for a combination of these criteria, i.e. flowering parts of cacti that have confluent hairy or spiny areoles exterior to a thick periderm, where these hairs, spines, and periderms arise almost immediately below the shoot apical meristem, and with more hairs and spines on reproductive parts than on photosynthetic parts of the shoot. Periderm development and confluent areoles preclude photosynthesis of cephalia, which therefore lack or mostly lack stomata. There is almost always a discrete transition from photosynthetic vegetative tissues to a non-photosynthetic flower-bearing cephalium, both of which arise from the same shoot apical meristem. Cephalia have different phyllotaxy than vegetative parts of the shoot and appear to be on top of existing vegetative phyllotaxy. If flowering parts only have a subset of the above characteristics of cephalia, then I propose calling these structures ‘pseudocephalia’.

Zusammenfassung: Es gibt Probleme mit bisherigen Versuchen, den Begriff „Cephalium“ zu definieren, etwa über die Bildung von mehr Haaren und Dornen, die Verschmelzung von Areolen oder die Periderm-Entwicklung auf oder unterhalb jeder Areole nach der Blüte. Ich schlage vor, den Begriff „Cephalium“ nur für eine Kombination dieser Kriterien zu verwenden, also für blühende Abschnitte von Kakteen, die zusammenfließende behaarte oder bedornete Areolen außen an einem dicken Periderm besitzen, deren Haare, Dornen und Peridermen fast unmittelbar unter dem Triebspitzenmeristem entspringen und die mehr Haare und Dornen auf den reproduktiven Abschnitten als auf den photosynthetisch aktiven Sprossteilen haben. Periderm-Entwicklung und zusammenfließende Areolen schließen eine Photosynthese der Cephalien aus, die daher keine oder fast keine Spaltöffnungen besitzen. Es

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gibt meist einen abgrenzbaren Übergang vom photosynthetisch aktiven Gewebe zum nicht photosynthetisch aktiven und blümentragenden Cephalium, die beide vom gleichen Triebspitzenmeristem abstammen. Cephalien haben eine andere Phyllotaxis als die vegetativen Sprossabschnitte und sitzen der vorhandenen vegetativen Phyllotaxis auf. Wenn blühende Abschnitte nur einen Teil der oben genannten Merkmale aufweisen, schlage ich vor, diese Strukturen als „Pseudocephalien“ zu bezeichnen.

Introduction

Most cacti (Cactaceae) are peculiar plants, even for angiosperms, with highly succulent stems, numerous highly lignified leaves aka spines, lack of functional photosynthetic leaves, CAM photosynthesis, huge sunken shoot apical meristems, and fantastic stem architectures (Buxbaum, 1950; Gibson & Nobel, 1986; Mauseth, 2006). The few cactus species that lack most of these traits – such as many species of *Pereskia* Mill., with broad photosynthetic leaves, non-succulent woody stems, and C3 photosynthesis – are thus antithetically considered anomalous, even though they superficially resemble typical angiosperms (Leuenberger, 2008; Griffith, 2008; Butterworth & Edwards, 2008). Here, I focus on more stereotypical succulent cacti in the subfamily Cactoideae, which includes all cacti other than *Pereskia* (sensu lato, including *Leuenbergeria* Lodé), *Maihuenia* Phil., and the subfamily Opuntioideae (prickly pears and chollas). In particular, I focus on cacti that only flower from specialized reproductive structures, called cephalia (singular: cephalium) or pseudocephalia (singular: pseudocephalium), both of which only occur in some species of the Cactoideae.

Cephalium-bearing cacti are the platypus of the plant kingdom insofar as they look like a hoax: two very different looking organisms seemingly grafted onto one another to resemble a chimera between a photosynthetic non-flowering part and a non-photosynthetic flowering part. Or, as Charles Darwin more eloquently said in his letter



Figures 1a, & b. *Pilosocereus densiareolatus*
 This is a pseudocephalium because the flowering regions are discontinuous, photosynthetic, and possibly not produced directly at the shoot apical meristem.

to Joseph Dalton Hooker about *Welwitschia mirabilis* Hook.f., dated 18 December 1861, “a vegetable *Ornithorhyncus*”. Like the platypus, cephalium-bearing cacti are real. However, most of us do not consider cephalium-bearing cacti to be quite as striking as the platypus because western science has been familiar with the genus *Melocactus* Link & Otto since Christopher Columbus returned from his first trip to Hispaniola in 1492, while the platypus was introduced to western science three centuries later, in 1799.

Mauseth (2006) defined a cephalium as the reproductive parts of those cactus plants in which there is a distinct juvenile-to-adult transition in morphology. This is a great starting point for defining a cephalium, but is too circular because the only way to genuinely distinguish juvenile from adult morphology is by whether or not axillary buds (aka areoles in cacti) are capable of flowering. This is why paedomorphism is so hard to define in plants (Olson, 2007). Clearly Mauseth (2006), Buxbaum (1964), and other botanists realized the circularity of this definition of a cephal-





Figure 2. *Pilosocereus gounellei* subsp. *zehntneri*. This is a pseudocephalium because the flowering regions are discontinuous and photosynthetic.

ium and therefore proposed a suite of other criteria for what constitutes a cephalium or pseudocephalium. In this paper, I synthesize their attempts and, in so doing, highlight the continuum in degrees of cephalium development, especially where gradual transitions shed light on the otherwise abrupt transition to cephalium development, as well as the exceptions that seemingly prove the rule.

History of the term cephalium

For a history of the term ‘cephalium’, see the first few pages of Buxbaum (1952) and Gorelick (2013), which I summarize here.

In 1831, William Jackson Hooker first used the term ‘cephalia’ in Latin diagnoses in Curtis’s *Botanical Magazine*, albeit without definition or elaboration, in reference to *Melocactus intortus* (Mill.) Urb. However, between 1831 and 1845, he also used the term to refer to hairy flower buds in other genera that we do not currently consider to be cephalium-bearing, such as *Echinocereus rigidissimus* Rose, *Echinopsis eyriesii* Pfeiff. & Otto, *Ferocactus glaucescens* Britton & Rose, and *Parodia ottonis* (Lehm.) N.P. Taylor.

According to Buxbaum (1952), Schumann (1897–1899) used the term cephalium for *Cephalocereus* Pfeiff. and *Melocactus* and no other genera. Schumann (1897–1899) used the term cephalium for reproductive structures completely enveloped in hairs, in which the flowering tissues widened in both vertical and circumferential directions – thereby excluding most lateral cephalia – and the hair-bearing areoles are helically or spirally arranged. He then, quizzically, applied the term ‘cephalium’ to both *Melocactus* and *Cephalocereus*, even though flower-bearing areoles in *Cephalocereus* are not helically arranged, but maintain the vertical phyllotaxy of juvenile ribs.

Berger (1907: 61) provided the first explicit definition of a cephalium as “the floriferous region of the plant is differentiated from the rest”. However, this was for *Cephalocereus*, which many researchers today consider to have a pseudocephalium (e.g. Valverde *et al.*, 2007). Gürke (1908) also used the term ‘cephalium’ for *Cephalocereus*, although his notion of the genus included what we now call *Micranthocereus* Backeb. and *Facheiroa* Britton & Rose.

In their four-volume monograph, Britton & Rose (1919–1923) confined use of the term ‘cephalium’ to *Melocactus* Link & Otto and *Discocactus* Pfeiff., with all other cacti having a pseudocephalium or having neither a cephalium nor pseudocephalium.

Berger (1926, 1929) concurred with Britton and Rose and only used the term cephalium to refer to the terminal (aka apical) cephalium, such as in *Melocactus* and *Discocactus*. Berger (1926, 1929) used the term pseudocephalium for *Espositoa*, *Cephalocereus*, and *Arrojadoa* Mattf.. Berger (1926, 1929) declined to apply the term ‘pseudocephalium’ even to the hairier species of *Pilosocereus* Lem. (now known as *Pilosocereus* Byles & G.D. Rowley), but referred to the long-lived areoles of *Neoraimondia* Britton & Rose and *Neoabbottia* Britton & Rose (subsequently subsumed in *Leptocereus* Britton & Rose) as being real cephalia, albeit he distinguished long-shoot from short-shoot cephalia.

Werdermann (1933) and Buxbaum (1952, 1964) defined hairy floriferous regions of the shoot to be cephalia if they originated from the shoot apical meristem and to be pseudocephalia if their hairy areoles that bore flowers grew hairs later in development, i.e. hairs developed on areoles from far below the shoot apical meristem. Buxbaum (1975) realized that there is a continuum between cephalia and pseudocephalia – How soon after mitotic divisions of the shoot apical meristem do the hairs need to grow? – but never proposed an alternative.

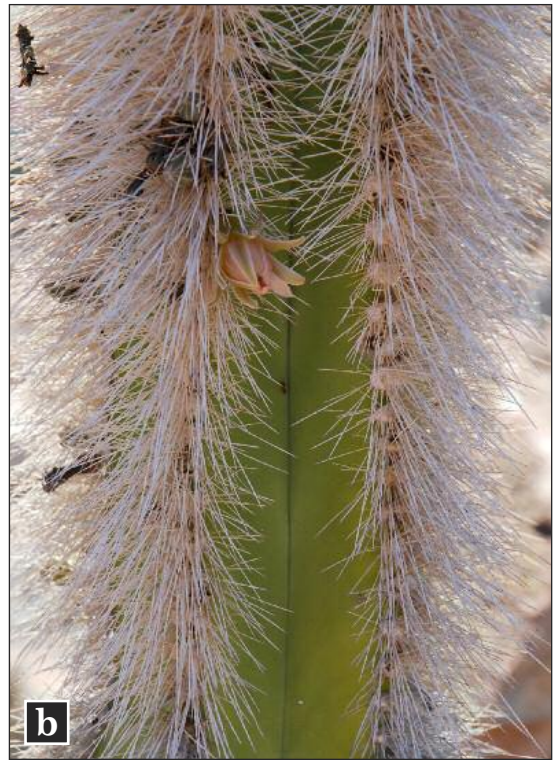


Figure 3. *Pachycereus (Lophocereus) schottii*. This is a pseudocephalium because the flowering regions are discontinuous and photosynthetic (3a,b). Furthermore, flowers are sometimes produced from morphologically juvenile areoles with short stout spines (3c) or from areoles that are intermediate between juvenile and adult morphologies (3d).



Figure 4. *Arrojadoa eriocaulis*. Each cephalium here is smaller than a single areole in *Neoraimondia arequipensis*.

In a paper titled “What is a cephalium?” Croizat (1942: 169) noted that, “neither Britton & Rose nor Werdermann seem to define the cephalium”. But then Croizat declined to define a cephalium, instead asserting that there is no way to do so.

Buxbaum (1952) noted that *Espostoa* Britton & Rose lateral cephalia had lower ribs, lower than vegetative ribs, and the vascular cylinder was depressed underneath the cephalium, making the cephalium appear sunken. But Buxbaum did not consider the sunken nature of flowering areoles to be a defining characteristic of lateral cephalia, thereby subsuming *Pseudoespostoa* Backebg. within *Espostoa*.

Rauh (1957) largely reiterated the work of others, extolling Buxbaum (1952). Rauh’s main contributions were introducing the nomenclature ‘terminal cephalium’ and ‘lateral cephalium’, the latter of which he subcategorized as either long-shoot lateral cephalia (“Langtriebcepha lien”) or short-shoot lateral cephalia (“Kurztriebcepha lien”). Long-shoot lateral cephalia are found in *Espostoa*, *Coleocephalocereus*, etc. Short-shoot



Figure 5. *Pachycereus marginatus*. Flowers arise from confluent areoles. But does this make it a pseudocephalium?

lateral cephalia are, according to Rauh (1957), only found in *Neoraimondia* and a few species of *Neoabbottia*, now known as *Leptocereus*, although Rauh also toyed with – but ultimately dismissed – the notion that short-shoot cephalia may also exist in *Lophocereus schottii* (Englem.) Britton & Rose. Rauh’s (1957) other contribution was his Figure 10, appended at the end of his paper without any discussion. This is a schematic of radial sections of shoots showing reduced thickness of cortex/periderms underlying both apical and lateral cephalia, but no change in cortex/periderm thickness underlying both apical and lateral pseudocephalia.

Finally, Mauseth (1989: 1–2; citations omitted) provided the following extensive characterization of cephalia:

“Cephalium-bearing cacti ... are species which are strongly dimorphic: during their juvenile phase, they resemble most other cacti in having monopodial globular or columnar bodies covered by spine clusters (short shoots called areoles). In this stage they are incapable of flowering. When plants reach reproductive



a



b



c



d



e

Figure 6. Many relatively long stout spines on juvenile growth and shorter, sparser spines more flexible on later growth from which flowers arise.
a. *Carnegiea gigantea* juvenile growth
b. *Carnegiea gigantea* adult growth
c. & d. *Browningia candelaris* Photographs: James D. Mauseth **e.** *Stetsonia coryne*.

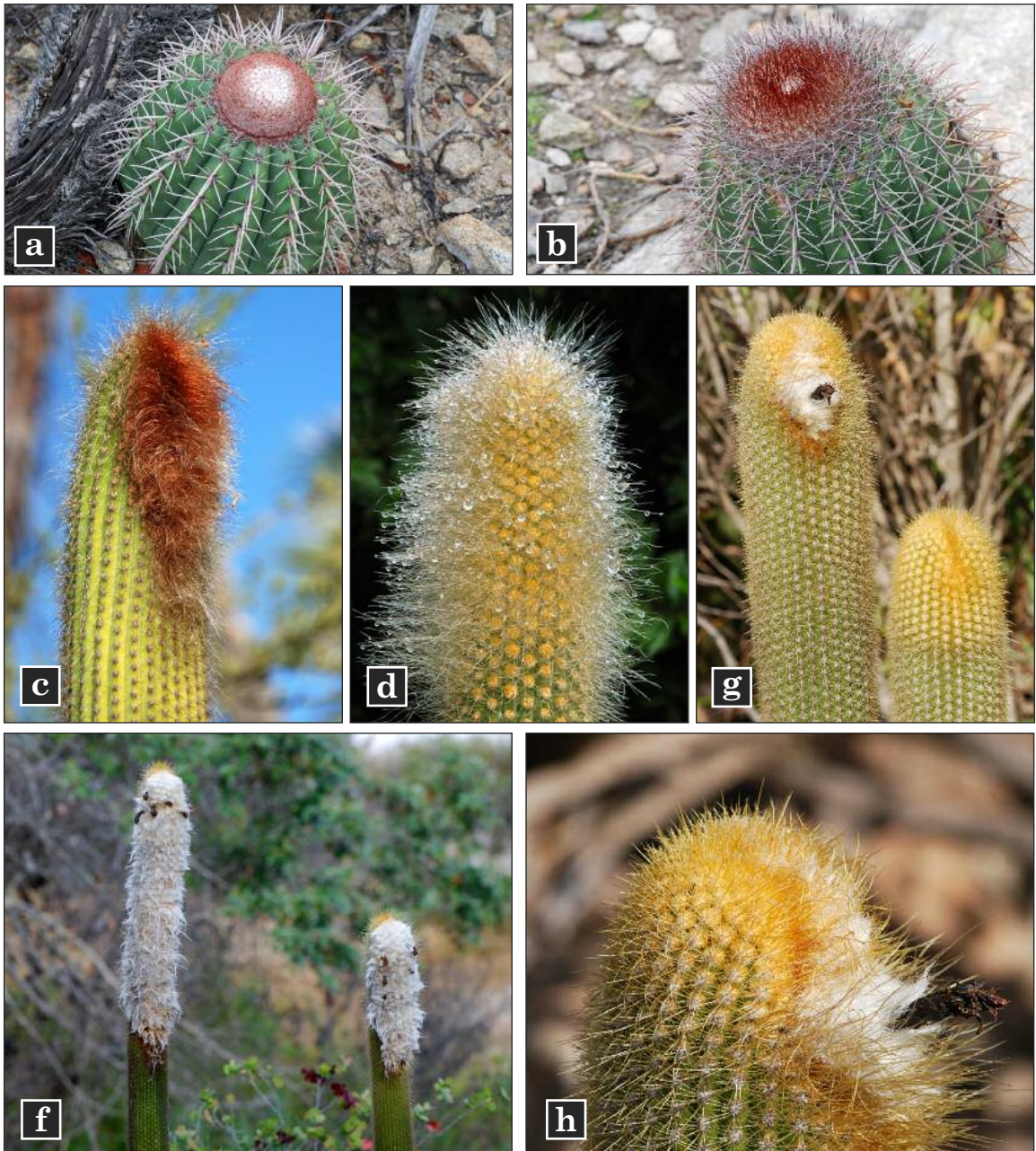


Figure 7. Gradual transition from juvenile to adult morphology — gradual transitions are only found in aberrant individuals. **a.** *Melocactus oreas* normal discrete transition from vegetative to reproductive tissue of cephalium. **b.** *Melocactus oreas* highly unusual gradual transition from vegetative to reproductive tissue of cephalium. **c.** *Espostoa (Vatricania) guentheri* normal discrete transition from vegetative to reproductive tissue of cephalium. **d.** *Espostoa (Vatricania) guentheri* highly unusual gradual transition from vegetative to reproductive tissue of cephalium. Photograph: Jürgen Menzel. **e. (opposite page)** *Micranthocereus (Coleocephalocereus) albicephalus* normal discrete transition from vegetative to reproductive tissue of pseudocephalium. **f.** *Micranthocereus (Coleocephalocereus) albicephalus* normal discrete transition from vegetative to reproductive tissue of pseudocephalium. **g. & h.** *Micranthocereus (Coleocephalocereus) albicephalus* highly unusual gradual transition from vegetative to reproductive tissue of pseudocephalium.



maturity, new shoot growth is strikingly different: it is narrower than the juvenile portion, its phyllotaxy is altered, and areoles are so closely packed that the cephalium epidermis is completely hidden by spine and trichomes. Due to the dense, opaque covering, the cephalium is incapable of photosynthesis, and is nourished by translocation up from the persistently photosynthetic juvenile portion of the shoot. Structural dimorphism is correlated with functional dimorphism: the juvenile portion is autotrophic and nonreproductive but the adult portion is autotrophic and reproductive. It is important to emphasize that these plants are monopodial and the cephalium is the direct continuation of the juvenile shoot; once the transition occurs, there is no reversion.”

Four possible definitions of cephalium

I present four criteria for defining cactus cephalia, highlighting the advantages and disadvantages of each: (1) an area of denser spination and hairs from which flowers arise, (2) an area of confluent areoles, (3) an epi-phyllotactic reproductive part of the shoot, and (4) a flowering region with extensive periderm development that lacks stomata and chlorenchyma. While individually each of these four criteria have problems, together they provide a decent definition of

cephalia. I briefly also describe two other traits that cephalia may have, namely that cephalia are not an inflorescence and that cephalia have spines that are shorter and more flexible than spines on photosynthetic parts of the shoot.

Definition 1: Area of dense spines and hairs from which flowers arise

A cephalium could be defined as a region of extraordinarily dense development of modified leaves (spines) and unbranched uniseriate trichomes (hairs) from which flowers originate. A cephalium is produced by the same shoot apical meristem as vegetative (photosynthetic) tissue, either simultaneously with a lateral cephalium or sequentially with an apical (aka terminal) cephalium.

Note that in cacti, spines are modified leaves or possibly highly modified bud scales, which are themselves highly modified leaves. A few species, such as *Cephalocereus senilis* Pfeiff. and *Espositoa guentheri* (Kupper) Buxb. (synonym *Vatricania guentheri* (Kupper) Backeb.), begin their reproductive shoots with a lateral cephalium that eventually encircles the entire shoot, thereby eventually becoming an apical cephalium.

The above definition captures our usual naïve gestalt of cephalia as woolly and spiny specialised flowering structures. This definition seems to



Figure 8. Various levels of pseudocephalium formation in *Micranthocereus*.

a. *Micranthocereus purpureus*

b. *Micranthocereus purpureus*

c. *Micranthocereus polyanthus*

d. *Micranthocereus violaciflorus*

e. *Micranthocereus auri-azureus*

f. (opposite page) *Micranthocereus auri-azureus*



nicely encompass cap-like apical cephalia, ring-like apical cephalia in which reproductive and vegetative growth alternate from the shoot apical meristem (and in which cephalia are definitely not terminal), and lateral cephalia. Furthermore, at first blush, this definition appears to apply across all clades in which cephalia supposedly occur, namely the Browningieae-Cereeae-Trichocereae (BCT) clade in the Core Cactoideae II and the Pachycereae plus *Leptocereus* and *Neoraimondia* in the Core Cactoideae I (sensu Hernández-Hernández *et al.*, 2011).

This definition implies that cephalia are part of primary growth, arising directly from the shoot apical meristem (Buxbaum, 1952, 1964). This would also apply to some species of *Pilosocereus*, which are usually acknowledged to have either a pseudocephalium or neither a cephalium nor pseudocephalium. A pseudocephalium is generally considered to be composed of dense tufts of hairs (uniseriate trichomes) that grow from flowering areoles, but often long after areoles were formed from the shoot apical meristem. Areoles in cacti are short shoots, like spurs on an apple or ginkgo tree, hence can have secondary growth, often called 'indeterminate growth' of areoles (Gibson & Nobel, 1986; Taylor, 1991; Gorelick & Machado, 2012). For example, *Pilosocereus densiareolatus* F. Ritter forms dense tufts of hairs

well below the stem apex (Figure 1), with these long dense tufts of hairs being discontinuous, i.e. in not contiguous thatches vertically arranged on a shoot (Taylor & Zappi, 2004). By contrast, *Pilosocereus gounellei* (F.A.C. Weber ex K. Schum.) Byles & G.D. Rowley subsp. *zehntneri* (Britton & Rose) Byles & G.D. Rowley (synonym: *P. braunii* Esteves) grows long hairs from the shoot apical meristem (Figure 2), implying that, with this definition, *Pilosocereus gounellei* subsp. *zehntneri* has no less of a cephalium than found in *Cephalocereus senilis* and *C. columna-trajani* (Karw. Ex Pfeiff.) P.V. Heath (see below regarding the next criterion/definition of a cephalium for discussion of these two *Cephalocereus* species, which, in fact, have pseudocephalia). It seems plausible that the genus *Pilosocereus* has some taxa with true cephalia or pseudocephalia because the closest relatives of *Pilosocereus* are probably *Arrojadoa*, *Melocactus*, and *Discocactus* (Hernández-Hernández *et al.*, 2011).

Members of both the Core Cactoideae I and II present potential problems for this definition of a cephalium. In the Core Cactoideae I, *Pachycereus schottii* (Englem.) D.R. Hunt (synonym *Lophocereus schottii*) would seem to form a cephalium by this and several other definitions. Its flowers are usually only produced from larger areoles with longer denser spination per areole than on the

vegetative parts of the shoot with their short stout spines (Figures 3a,b). However, in this species, flowers are occasionally produced on areoles with juvenile morphology, i.e. on those areoles with just a few spines that are short and stout (Figures 3c,d). Furthermore, juvenile portions of shoots of *Pachycereus (Lophocereus) schottii* grow very slowly, whereas a huge increase in shoot growth rate occurs once cephalium/pseudocephalium development and flowering begin (Parker, 1988; Martorell *et al.*, 2006; Gorelick, 2016). A different problem for this definition may occur in Core Cactoideae II with some species of *Discocactus*. While the vegetative portions of all *Discocactus* species are produced by the same shoot apical meristem as the cephalium, the possibility exists that a new meristem seems to grow at the base of the cephalium that produces new photosynthetic non-reproductive tissue and typical juvenile spines and areoles, even though these tissue may end up being produced after the cephalium (Gorelick, 2014c). Thus, in *Discocactus heptacanthus* Britton & Rose subsp. *catinica* (Buining & Brederoo) N.P. Taylor & Zappi, *D. placentiformis* K. Schum., and *D. bahiensis* Britton & Rose subsp. *gracilis* P.J. Braun & Esteves, the cephalium and parts of the vegetative body on which it sits may be produced by different meristems. However, we may be able to dismiss these concerns with *Discocactus* if vegetative shoot development is extremely slow, at least for photosynthetic parts that develop immediately before cephalium development (see Gorelick, 2014c for what Jim Mauseth termed the 'Mount St Helens effect'). In many ways this is very similar to *Pachycereus (Lophocereus) schottii* with very slow shoot apical meristem growth before cephalium/pseudocephalium development and with a discrete transition to rapid growth once the cephalium/pseudocephalium has formed.

Pachycereus (Lophocereus) schottii also highlights the delicate matter of how dense and continuous the development of spines and hairs must be. Each areole is a dense mass of trichomes and modified leaves. Like cephalia, at least per the next definition, areoles are shoots in which every epidermal cell produces a leaf or trichome, without stomata and without chlorenchyma. Building on earlier observations by Rauh (1957), Mauseth & Kiesling (1997) hinted that individual areoles can be cephalia in *Neoraimondia roseiflora* Backebg. (synonym: *Neoraimondia arequipensis* (Meyen) Backeb.) and *Neocardenesia herzogiana* Backebg. (synonym: *Neoraimondia herzogiana* (Backebg.) Buxb. & Krainz) because their flowering areoles have huge amounts of cork, no stomata, indeterminate growth for several decades, and many flowers. And maybe not too surpris-

ingly, Rauh (1957) speculated that *Pachycereus (Lophocereus) schottii* flowering areoles were each individual cephalia. But to be somewhat of a devil's advocate, this would make every areole on every cactus a cephalium, which therefore becomes a vacuous definition. In some ways, this was Croizat's (1942) point. So, instead, the area over which dense development of spines and trichomes develop, with lots of underlying cork and no stomata, would have to be larger than a single areole to constitute a cephalium, which bring us to a second definition of a cephalium.

Definition 2: Contiguous/confluent axillary buds/areoles

A cephalium could be defined as a large flowering area comprised of contiguous or confluent axillary buds/areoles. This area could be large in a vertical direction (lateral cephalia), horizontal direction (ring-like apical cephalia), or both directions (cap-like apical cephalia).

This second definition of cephalia means that individual flowering areoles would not be considered small cephalia. The problem is that several plants that we typically think of as possessing cephalia, would no longer be considered cephalium-bearing. In the Pachycereae, the so-called cephalia of *Cephalocereus senilis*, *C. columna-trajani*, and *Pachycereus militaris* (Audot) D.R. Hunt (synonym *Backebergia militaris* (Audot) Sánchez-Mej.) are formed of discrete (non-contiguous) areoles (Vázquez-Sánchez *et al.*, 2005, 2007, 2016). Their flowering areoles are close together, but still with some space between them. These flowering areoles each reside on their own tubercle, with stomata between areoles. I do not know whether the flowering areoles of the ring-like cephalium of *Cephalocereus apicicephalium* E.Y. Dawson are contiguous/confluent, but suspect that they are not, but instead are on discrete areoles on discrete tubercles with stomata between them like their congeners.

How large of a spatial area does something need to be to be considered a cephalium? The ring-like cephalia of some species of *Arrojadoa*, such as *A. eriocaulis* Buining & Brederoo (Figure 4), are of much smaller area than the area of a single *Neoraimondia arequipensis* flowering areole/cephalium. But for this definition of cephalium to be effective, we need some measure of spatial extent. And we cannot simply count number of flowering areoles if areoles are confluent.

Another problem with this second definition is that many members of the Pachycereae that we usually do not think of as cephalium-bearing would qualify as cephalium-bearing. *Pachycereus marginatus* (DC.) Britton & Rose has confluent

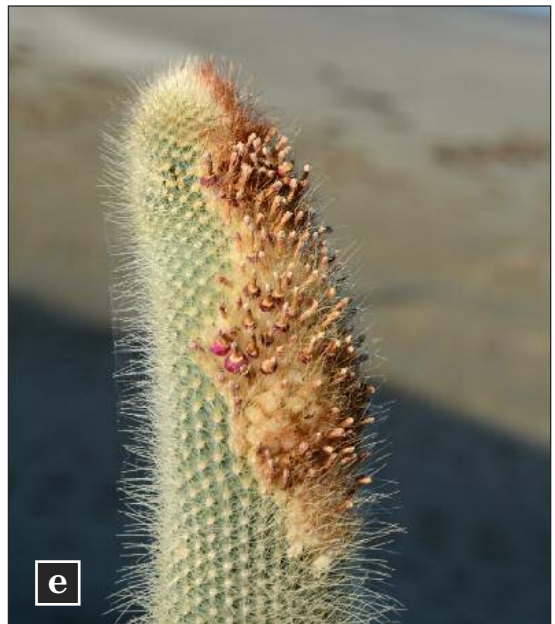


Figure 9. Epi-phyllotaxy — Cephalium appears to drift across the underlying parallel structure of photosynthetic ribs in 9a–9c. Rib development is invisible in cross-section 9d.

a. *Espostoa melanostele*

b. *Espostoopsis dybowskii* — see the rightmost shoot

c. *Coleocephalocereus purpureus*

d. *Coleocephalocereus purpureus* cross-section

e. *Micranthocereus streckeri* — unlike the other species in this figure, this species has a pseudo-cephalium

flowering areoles, implying that we should consider each rib of mature shoots to be a lateral cephalium (Figure 5). *Pachycereus (Lophocereus) schottii* is really little different from *Cephalocereus senilis*, with longer denser modified leaves on larger areoles in flowering portions of a shoot. Actually all species of *Pachycereus* Britton & Rose sensu lato, including *Carnegiea gigantea* Britton & Rose, show such vestiges of cephalium production. Flowering portions of *C. gigantea* shoots markedly differ from non-flowering portions in having fewer spines, almost confluent areoles, and larger areoles (Figures 6a,b).

The differentiation between relatively spineless flowering portions of the shoot and relatively spiny portions of the non-flowering portions of the shoot in the Pachycereeae (Core Cactoideae I) is also seen in *Browningia candelaris* (Meyen) Britton & Rose and *Stetsonia coryne* (Salm-Dyck) Britton & Rose (Core Cactoideae II) (Figures 6c-e). Are we ready to say that *Pachycereus* spp., *Carnegiea gigantea* (which is very closely related to *Pachycereus*), *Browningia candelaris*, and *Stetsonia coryne* all have cephalia?

A few species of Core Cactoideae II shed some light on whether confluent/contiguous flowering areoles make for a good criterion of whether a true cephalium exists. However, while almost all cephalium formation seems virtually instantaneous, a few specimens of a few species show a more gradual transition from vegetative to reproductive structures. This is more than a few extra ribs being added to the vegetative growth immediately before cephalium production, but up to 15cm of transitional growth, where areoles are much bigger but not quite confluent nor producing spines typical of cephalia. Figures 7a–h show this transitional behavior in cephalium development in *Melocactus oreas* Miq. and *Espostoa (Vatricania) guentheri*, and, to a lesser extent, in pseudocephalia of *Micranthocereus albicephalus* (Buining & Brederoo) F. Ritter (synonym: *Coleocephalocereus albicephalus* (Buining & Brederoo) F.H. Brandt). In the Core Cactoideae I, *Pachycereus (Backebergia) militaris* also shows this transition between vegetative and reproductive growth, although the transitional area is usually no longer than 8cm in vertical extent (Mauseth *et al.*, 2005; Vázquez-Sánchez *et al.*, 2016).

Not only is cephalium/pseudocephalium development in *Micranthocereus (Coleocephalocereus) albicephalus* sometimes seemingly gradual, but there is a large variation in whether cephalia or pseudocephalia are formed in the rest of the genus *Micranthocereus* Backeb. Some species, such as *M. purpureus* (Gürke) F. Ritter and *M. streckeri* Van Heek & Van Criel. form

what appear to be pseudocephalia with virtually contiguous areoles (Gorelick, 2013), albeit on separate tubercles, much as in *Cephalocereus columna-trajani* and *C. senilis*, while other species never form pseudocephalia (e.g. *M. auri-azureus* Buining & Brederoo), while with other species it is uncertain whether the flowering-bearing areoles are contiguous (e.g. *M. violaciflorus* Buining, *M. polyanthus* (Werderm.) Backeb.) (Figures 8a–d).

Definition 3: Epi-phyllotactic reproductive structure

Lateral cephalia seem to be developmentally ‘painted’ over existing phyllotaxy. In some specimens of *Espostoa melanostele* (Vaupel) Borg vegetative ribs remain vertical while the lateral cephalium seems to helically drift across those ribs (Figure 9a). We see the same pattern in some specimens of *Espostoopsis dybowskii* (Rol.-Goss.) Buxb., in which the cephalium seems to wander across and grow on top of ribs, something that could be termed ‘epi-phyllotactic’ (Figure 9b). The epi-phyllotactic nature of lateral cephalia is particularly evident in the globose species of *Coleocephalocereus* Backeb. (i.e. subgenus *Buiningia* (Buxb.) P.J. Braun), such as *C. aureus* F. Ritter and *C. purpureus* (Buining & Brederoo) F. Ritter, where the vegetative rib architecture disappears underneath the contiguous white cephalium hair and spines (Figures 9c). The ring-like terminal cephalia of *Arrojadoa* spp. and *Stephanocereus leucostele* are certainly not associated with the vertical vegetative ribs. By contrast, *Cephalocereus senilis* and *C. columna-trajani* reproductive structures are on specific ribs and flowering areoles are not contiguous. Having flowering areoles/tubercles ascribed to specific ribs makes these two species of *Cephalocereus* not epi-phyllotactic, hence they possess pseudocephalia.

Epi-phyllotactic cephalia, i.e. cephalia existing as being on top of vegetative phyllotaxy, is also evident in other taxa. In those *Discocactus* species that grow new photosynthetic tissues after cephalium formation – which may be all species in the genus given the wide flattened eponymous disc-like nature of their vegetative shoot – no new ribs grow from this novel meristem, but instead the original vegetative ribs continue to lengthen, i.e. phyllotaxy is maintained after the cephalium grows (admitting that photosynthetic portions of shoots in some *Discocactus* species have helical phyllotaxy in lieu of ribs). In *Micranthocereus streckeri*, the width of the cephalium/pseudocephalium both increases and decreases as a shoot grows, encompassing more or fewer ribs (Figure 9e). Note that only with this and the first definition of cephalia (epi-phyllotactic and dense spina-



a



b



c



d

Figure 10. Ring-like cephalia (or possibly pseudocephalia).

a. *Arrojadoa rhodantha* Britton & Rose

b. *Arrojadoa rhodantha* subsp. *aureispina* (Buining & Brederoo) P.J. Braun & Esteves

c. *Arrojadoa marylandiae* Soares Filho & M. Machado

d. *Stephanocereus leucostele*

tion and uniseriate hairs in flowering regions) is *M. streckeri* considered to have a cephalium, whereas with the other two definitions (confluent areoles and increased cork/decreased chlorenchyma) this species would have a pseudo-cephalium.

Figure 9a is a cultivated rooted top cutting of *Espostoa melanostele*, in which the long lower portion of the cephalium grew before the cutting was taken. The cutting was planted with a different compass orientation and subsequently underwent about a year of growth without a cephalium, albeit with a depression in the shoot. Eventually a new lateral cephalium formed. Despite this being an artificial situation, notice how growth of the lateral cephalium stopped and then restarted, which is really no different from what happens in *Arrojadoa* and *Stephanocereus leucostele* (Figures 10a,b) with their ring-like apical cephalia.

Definition 4: Flowering region with increased cork/periderm and decreased stomata and chlorenchyma

A cephalium could be defined as a flowering region with reduced number of stomata, reduced chlorenchyma, and increased periderm (cork) formation that is produced from proximal epidermal layers. “The development of periderm in each areole after flowering and fruiting is a distinctive and defining feature of lateral and apical cephalia” (Vázquez-Sánchez *et al.*, 2016: 245). Periderm production from epidermis, hypodermis, or cortex invariably results in the cephalium having a much narrower or non-existent cortex than does the vegetative portion of the shoot (Rauh, 1957). For lateral cephalia, the narrower cortex results in titling of the shoot towards the cephalium and the shoot supposedly can no longer safely have axillary branching above the point on the shoot where the lateral cephalium started growing (Valverde *et al.*, 2007), although there are exceptions with relatively common axillary branching of cephalia in *Coleocephalocereus* Backeb. subgenus *Coleocephalocereus* and *Coleocephalocereus* subgenus *Simplex* N.P. Taylor (Gorelick & Machado, 2012), as well axillary branching of a cephalium in at least one cultivated specimen of *Espostoa lanata* Britton & Rose (Gorelick, 2014a).

This definition of a cephalium suffers in a way we have seen above: How reduced do the number of stomata and amount of chlorenchyma need to be and how increased does the underlying layer of periderm need to be? When does this definition become sufficiently attenuated that most or all *Pachycereus* species are considered cephalium-bearing? For instance, does *Pachycereus marginatus* have fewer stomata underlying its

confluent flowering areoles than on juvenile portions of its shoot with discrete areoles or between ribs on reproductive parts of the shoot and thereby qualify as a cephalium? By this definition, areoles of both *Neoraimondia* species and some *Leptocereus* species each constitute a cephalium (Rauh, 1957; Mauseth & Ross, 1988; Mauseth & Kiesling, 1997). It remains to be seen whether deeming *Pachycereus marginatus*, some *Leptocereus* species, and *Neoraimondia* cephalium-bearing is a problem.

Mauseth (1999) looked at *Espostoa lanata*, *E. mirabilis*, *E. ritteri*, *Pseudoespostoa (Espostoa) melanostele*, *Thrixanthocereus (Espostoa) senilis*, and *Vatricania (Espostoa) guentheri*. “Only samples of *E. mirabilis*, *T. senilis*, and *V. guentheri* had patches of bark in the cephalium” (Mauseth, 1999: 36). This contradicts what I found in *Espostoa (Pseudoespostoa) melanostele* — where not only did I see bark underlying the cephalium, but felt the resistance of the scalpel as I was cutting through that cork — and seems to contradict what Paul Hoxey depicted for *Espostoa (Thrixanthocereus) senilis* that does not show any obvious bark formation (Charles, 2015). It might be worth taking another look at *Espostoa sensu lato* for bark underneath cephalia.

Defining cephalia by periderm development after flowering and fruiting seems too restrictive. While this developmental chronology applies to *Pachycereus (Backebergia) militaris*, in most cephalium-bearing members of the Core Cactoideae II, such as *Melocactus*, *Discocactus*, *Espostoa*, and *Coleocephalocereus*, periderms seem to form before flowering. Plus most arborescent cacti eventually form periderms on older portions of shoots, sometimes long after flower and fruit production, but clearly without a cephalium, e.g. *Brasiliopuntia brasiliensis* (Willd.) A. Berger.

Because cephalia are generally not photosynthetic, it is often believed that cephalia could do without stomata, replacing cephalium epidermal tissue with periderm. This pattern is seen in cephalia of the Core Cactoideae II and some species of *Leptocereus* and both species of *Neoraimondia* in the Core Cactoideae I. But, given that areoles in cephalia/pseudocephalia of the *Pachycereae* in the Core Cactoideae I are not usually contiguous or confluent, it seems that stomata and chlorenchyma are found between tubercles in their cephalia/pseudocephalia. But even in the *Pachycereae*, photosynthesis is highly reduced in cephalia/pseudocephalia, sometimes with additional cork formed under the cephalia/pseudocephalia, at least relative to nearby non-reproductive epidermal tissue.

Figure 11.(below & top right) Narrower cortex with more periderm in apical and lateral cephalia. Cross-sections.

a. *Discocactus zehntneri* var. *araneispinus* (Buining & Brederoo ex J. Theun.) P.J. Braun

b. *Espostoa melanostele*

c. *Coleocephalocereus purpureus*



Figure 12.(right) Two diametrically opposite cephalia/pseudocephalia per shoot.

a. *Espostoa melanostele*

b. *Micranthocereus streckeri*



Figure 13. *Coleocephalocereus goebelianus* (Vaupe) Buining. Phyllotaxy changes once the cephalium is formed. Below the cephalium, vegetative ribs are parallel and virtually unbranched. Once the cephalium is formed, vegetative ribs branch and are no longer parallel.

Narrower cortex is evident in both apical and lateral cephalia (Figures 12a–c). With cap-like apical cephalia in *Melocactus* and *Discocactus*, cephalia are noticeably narrower than the photosynthetic parts of the shoot below. *Melocactus* vegetative parts do not grow again once a cephalium starts nor do their cephalia get any wider due to secondary growth. *Discocactus* shoot radial sections also show this narrower cortex in cephalia (Buining, 1980; Gorelick, 2014c). However, the vegetative parts of some (all?) *Discocactus* grow wider after cephalium production, so the cephalium looks disproportionately narrow compared with *Melocactus* (Gorelick, 2014). *Pachycereus* (*Backebergia*) *militaris* cephalia/pseudocephalia

are also slightly narrower than the juvenile vegetative parts of their shoots, with slightly narrower cortex, although this is not obvious without sectioning because the long spines of the cephalium/pseudocephalium hide the slightly narrower underlying reproductive portion of the shoot (Mauseth *et al.*, 2005).

I have not sectioned the ring-like apical cephalia of *Arrojadoa* spp. or *Stephanocereus leucostele* (Gürke) A. Berger to look for increased periderm production and thinner cortex underlying their flowering areoles. However, Rauh (1957) shows no such changes in shoot architecture in his Figure 10.II. Nonetheless, it would be worth sectioning *Arrojadoa* spp. and *Stephanocereus leucostele* because I do not agree with Rauh's labelling of Figure 10.IV, in which he shows narrower cortex/periderm underlying cephalia of *Espostoa*, *Facheiroa* Britton & Rose, *Cephalocereus*, and *Thrixanthocereus* Backeb., which is definitely not the case for *Cephalocereus senilis* and *Thrixanthocereus senilis* F. Ritter, also known as *Espostoa senilis* (F. Ritter) N.P. Taylor (see discussion below). This is an odd error for Rauh (1957) to have made given that he recognized that *Thrixanthocereus* did not have sunken cephalia/pseudocephalia.

Cork layers underlie lateral cephalia. Lateral cephalia, at least in the Core Cactoideae II, appear sunken because the cortex underlying the cephalium is narrower than under photosynthetic non-reproductive portions of the shoot. This causes the shoot apical meristem to tilt in the direction of the lateral cephalium. Thus, juvenile shoots of many species of lateral cephalium-bearing cacti are erect and extremely vertical, but once they start growing a cephalium, the apex of the shoot tilts towards the cephalium growing side of the shoot. Photos of cultivated specimens of *Cephalocleistocactus chrysocephalus* F. Ritter (synonym *Cleistocactus chrysocephalus* (F. Ritter) Mottram) show this exact behaviour: vertical juvenile shoots that start growing with a significant tilt as soon as the lateral cephalium or pseudocephalium develops, with its long flexible spines, and the plant starts to flower (Hunt *et al.*, 2006; Lodé, 2015).

A few species of lateral cephalium-bearing and pseudocephalium-bearing plants do not have tilted shoot apices. Two ways have evolved to avoid apical tilting of lateral cephalia: (1) having the cephalium widen around the circumference of the shoot so that it eventually becomes a cap-like apical cephalium (e.g. *Cephalocereus senilis*, *C. columna-trajani*, and some shoots of *Espostoa* (*Vatricania*) *guentheri*) and (2) growing a second lateral cephalium on the diametrically opposite



Figure 14. Cephalia with longer spines than on juvenile photosynthetic portions of shoot.
a. *Arrojadoa penicillata* Britton & Rose
b. & c. *Siccobaccatus dolichospermaticus* (Buining & Brederoo) P.J. Braun & Esteves [synonym *Micranthocereus dolichospermaticus* (Buining & Brederoo) F. Ritter]
d. *Discocactus horstii* Buining & Brederoo
e. *Discocactus zehntneri* subsp. *boomianus*



Figure 15. *Stephanocereus luetzelbergii* reproductive portions of shoots are narrower and have more hair per areole.

side of the shoot, e.g. some shoots in *Espostoa* spp. and *Micranthocereus streckeri* (Figures 12a,b) (Gorelick, 2013).

While the apex of lateral cephalium-bearing shoots often tilt, ultimately all shoots manage to grow vertically, except possibly in *Espostoa cremnophila* Hoxey which we still know too little about (Hoxey, 2014). The world is not filled with lateral cephalium-bearing shoots that form spirals nor is the ground littered with cephalia that have broken off because of the stress on tilted cephalium-bearing shoot. Instead, shoots bearing lateral cephalia manage to straighten themselves as they

grow (Gorelick, 2014a). The one glaring difference in architecture once a lateral cephalium starts growing is in the arrangement of ribs. Prior to formation of a lateral cephalium, ribs are vertical and evenly spaced and of constant number. As soon as the lateral cephalium starts growing, however, the shoot adds photosynthetic ribs and these morphologically juvenile ribs – although they are chronologically and developmentally of the same age as the cephalium – are almost never vertical (Figure 13). This cobbled together architecture probably keeps the shoot growing vertically, probably also with some help from extra tension wood.

[I have, thus far, alluded to all genera of cephalium- and pseudocephalium-bearing cacti, except for the enigmatic Venezuelan endemic *Cereus mortensenii*, (Croizat) D.R. Hunt & N.P. Taylor, which has sometimes been considered *Pilosocereus mortensenii* (Croizat) Backeb. Mauseth (1999) illustrates a cross section through a pseudocephalium-bearing shoot of *C. mortensenii*, showing discrete hair-bearing ribs that are lower than the non-hairy ribs and showing chlorenchyma underlying the pseudocephalium. But I know too little about this taxon to say any more.]

Traits often associated with cephalia

Cephalia are usually thought of as possessing two other characteristics – not being inflorescences and having shorter spines than on juvenile photosynthetic parts – neither of which should be thought of as definitions of cephalia.

Cephalia are specialized perennial reproductive structures that live for as long as the shoot on which they grow. Cephalia are thus not inflorescences because inflorescences are ephemeral. This characterization of cephalia seems to apply to all taxa, except *Pachycereus (Backebergia) militaris*, in which cap-like apical cephalia/pseudocephalia and a small portion of the vegetative tissue just below cephalia/pseudocephalia abscise after several years of reproductive growth (Mauseth *et al.*, 2005). The area around a mature plant is often filled with decomposing abscised cephalia/pseudocephalia, which die and never seem to form adventitious roots. These cephalia/pseudocephalia can grow to about a meter tall, but all eventually are abscised. After abscission, one or more new shoots grow from the remaining vegetative part of the plant, often just below the abscission layer. Thus, while *Pachycereus (Backebergia) militaris* cephalia/pseudocephalia are perennial structures, they are also ephemeral compared with all other cephalia considered herein. Therefore *Pachycereus (Backebergia) militaris* reproductive parts could be considered long-lived inflorescences, not true cephalia. *Neoraimondia* cephalia can also be considered inflorescences if they later de-differentiate back in to vegetative long-shoots, which they sometimes do in *N. arequipensis*.

The second trait often associated with cephalia is that their spines are more slender and flexible than spines in vegetative parts of the shoot. This seems to be true in all cephalium-bearing taxa. However, Mauseth (2006) says that spines on cephalia are shorter than spines on vegetative portions of the shoot, but this seems to not be universal. A diverse assemblage of counter-examples, some of which contain cephalia and some pseudo-

cephalia, includes *Pachycereus (Backebergia) militaris*, all *Arrojadoa* species, most *Micranthocereus* species (at least those with pseudocephalia, including those segregated into *Siccobaccatus*), many *Espostoa* species, *Espostopsis dybowskii*, *Facheiroa ulei* (Gürke) Werderm., *Discocactus horstii* Buining & Brederoo, and *D. zehntneri* Britton & Rose subsp. *boomianus* (Buining & Brederoo) P.J. Braun, all of which have longer and more robust spines in their cephalia or pseudocephalia (Figures 14a–d).

Integrated approach to defining cephalium and pseudocephalium

I propose defining a cephalium as part of a cactus shoot arising directly from the shoot apical meristem, with the cephalium composed of confluent areoles from which flowers originate, bearing copious spines and trichomes, and underlain by a thick periderm in lieu of an even thicker cortex. Hairs on flowering parts are longer than those on non-flowering parts. Cephalia lack chlorenchyma and stomata. Cephalia are epiphyllotactic with very different phyllotaxy from photosynthetic portions of the shoot. All of these criteria must be met for something to be a cephalium.

I propose defining a pseudocephalium as a discrete portion of a cactus shoot from which flowers originate, but a portion of the shoot that is missing one or more – but not all – of the above criteria for being a cephalium.

As an aside, I do not like the prefix ‘pseudo-’ in pseudocephalium because of its pejorative connotations, but am reluctant to create new jargon. There is absolutely no evidence that plants with pseudocephalia are any less fit than closely related taxa with cephalia. I wonder whether this is why Berger (1926) replaced the term ‘pseudocephalium’ with the more descriptive ‘wollzonen’, i.e. ‘wool-zone’.

A few species and a few individuals of other species show a gradual transition from juvenile photosynthetic parenchymous portions of shoots with stomata to flowering non-photosynthetic periderm-laden portions of shoots without functional stomata, such as *Pachycereus (Backebergia) militaris* and some specimens of *Espostoa (Vatricania) guentheri*. As with many aspects of biology, reproductive parts of these plants do not fall neatly into the cephalium category, but only because their developmental transition from juvenile to adult stages is not instantaneous. However, analogously, day and night are still well-defined concepts despite the existence of dusk and dawn.

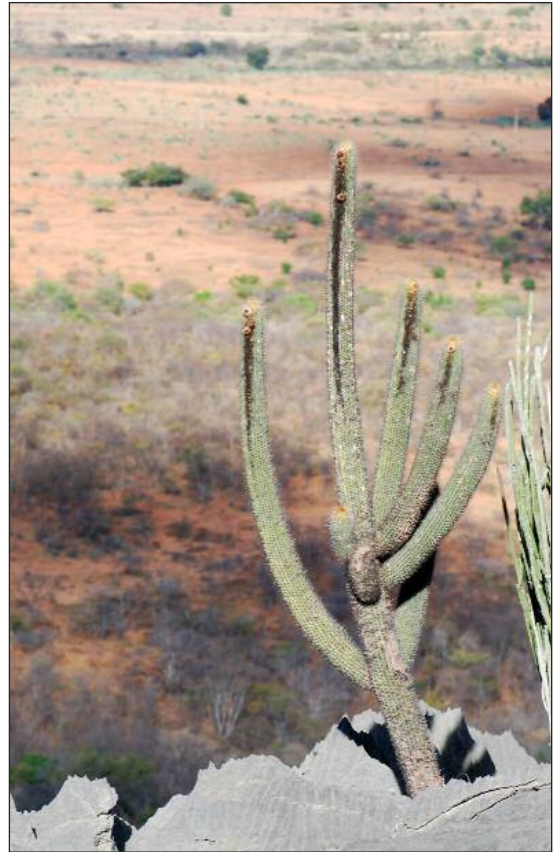
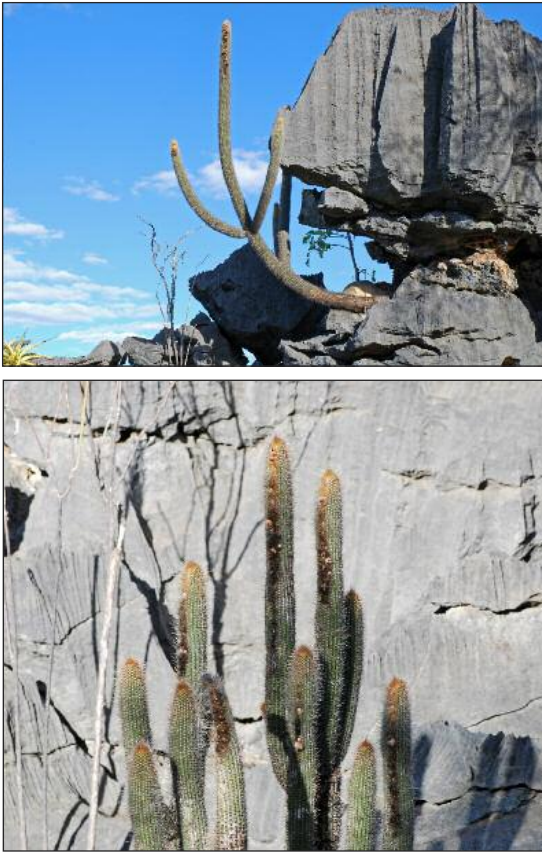


Figure 16. *Facheiroa cephaliomelana* var. *estevesii*

Definitions are peculiar things in science. Hypotheses can be false or not. Theories can be right or wrong. Theories can even be falsifiable or not, although we usually strive for the former in order to consider something scientific. Data may be typical or anomalous. Facts may or not be context sensitive. But definitions are rather arbitrary, with no decent gauge except for their utility and consistency (Wagner, 2010; Gorelick, 2011a,b).

There is even more than utility to make something a decent definition. Definitions should reflect commonsense, which will reflect current paradigms. And, to quote the famous title of Theodosius Dobzhansky's (1973) popular article, "Nothing in biology makes sense except in the light of evolution." To this end, it would be nice if a definition of cephalium reflected phylogeny, although this could be a pipe dream given the flux in accepted (i.e. inferred) evolutionary relationships (Gorelick, 2014b). It would be nice to know whether a trait such as presence of a cephalium is a homology versus an analogy, but this may be too much to ask at this time.

Several cactus genera have a range of devel-

opment of cephalia or pseudocephalia between species. *Stephanocereus* A. Berger contains one species, *S. leucostele*, with ring-like cephalia or pseudocephalium from which flowers originate, similar to that found in *Arrojadoa*, and another species, *S. luetzelbergii* (Vaupel) N.P. Taylor & Eggli, that has only a few extra spines or trichomes in flowering areoles, but has modified shoot shape in flowering regions, much like *Melocactus* (Figure 15). Given that the flowering portions of *S. luetzelbergii* shoots are photosynthetic all the way around the circumference, it is doubtful that there are periderms formed underneath their flowering areoles. *Micranthocereus* contains species with and without modified flowering areoles, i.e. with and without pseudocephalia. *Facheiroa* contains species without any specially differentiated flowering areoles or periderms underlying those areoles, such as *F. squamosa* (Gürke) P.J. Braun & Esteves, to species that have copious long spines and hairs on flowering parts, such as *F. ulei* (Gürke) Werderm. and *F. cephaliomelana* Buining & Brederoo var. *estevesii* (P.J. Braun) N.P. Taylor & Zappi (Figure 16). I

suspect that these latter two taxa have pseudocephalia because their areoles do not seem to be confluent and seem to be phyllotactic, not epiphyllotactic.

The most poignant and, in some ways, the most contentious genus regarding cephalium and pseudocephalium development is *Espostoa* sensu lato, including *Vatricania* Backeb. and *Thrixanthocereus* Backeb. *Espostoa* sensu stricto contain what seem to have bona fide lateral cephalia with contiguous areoles and massive amounts of underlying periderm formation. The monotypic genus or subgenus (or nothogenus?) *Vatricania* also has contiguous flowering areoles, massive amounts of underlying periderm, but what starts as a lateral cephalium eventually encircles the entire shoot. Furthermore the transition from juvenile to reproductive morphology can be more gradual in *Vatricania* than in *Espostoa* sensu stricto. While there may be problems with cactus phylogenies based solely on chloroplast DNA – because chloroplast genomes in cacti are not strictly maternally inherited (Corriveau & Coleman, 1988; Gorelick, 2014b) – one such phylogeny (Schlumpberger & Renner, 2012) places *Vatricania* in the *Cleistocactus* sensu stricto clade and *Espostoa* sensu stricto in the not very closely related *Oreocereus* clade. Should chloroplast DNA be sufficient to segregate *Vatricania* from the rest of *Espostoa*, especially in light of (1) *Vatricania* and *Espostoa* sensu stricto having morphologically similar cephalia and (2) it being unknown whether chloroplasts are maternally inherited in these taxa? *Thrixanthocereus*, which contains between two and four species, seems to not have true cephalia, but instead pseudocephalia. *Espostoa senilis* (F. Ritter) N.P. Taylor (synonym: *Thrixanthocereus senilis* F. Ritter) has long hairs in its flowering areoles, but flowering areoles are not confluent and do not have any substantial underlying cork, and have a photosynthetic epidermis (Figure 17a) (Charles, 2015). Reproductive structures of *T. senilis* look almost identical to pseudocephalia in *Micranthocereus streckeri* (compare Figures 17a & b) (Gorelick, 2013). Should lack of a true cephalium be sufficient to segregate *T. senilis* into a separate genus from the rest of *Espostoa* (cf. Buxbaum, 1959)?

Leptocereus provides a challenging case. Only three of the roughly fifteen species contain cephalia (*L. grantianus* Britton, *L. paniculatus* (Lam.) D.R. Hunt, *L. quadricostatus* Britton & Rose). Mauseth & Ross (1988) showed that *L. quadricostatus* only flowers from true apical cephalia that are small, old and slow growing, with no chlorenchyma, probably with every epidermal cell producing trichomes or spines and no



Figure 17. Pseudocephalia have non-confluent areoles and are photosynthetic.

a. *Espostoa* (*Thrixanthocereus*) *senilis*

Photograph: Paul Hoxey

b. *Micranthocereus streckeri*

stomata, a thin cortex, many highly lignified (and suberized?) cells underlying the epidermis that were probably mostly from epidermally-derived periderms. While standard reference works (e.g. Anderson, 2001; Hunt *et al.*, 2006) mention these cephalia, they do not illustrate them. Clearly *Leptocereus* cephalia are apical, on the ends of long shoots, growing from the same shoot apical meristem as the photosynthetic juvenile portion of the shoot. Yet for some inexplicable reason, Rauh (1957) unambiguously referred to these as short-shoot cephalia (“Kurztriebcephalien”). *Leptocereus* and *Neoraimodia*, the two taxa Rauh (1957) described as having short-shoot lateral cephalia, are relatively ancestral members of the Core Cactoideae I (Hernández-Hernández *et al.*, 2011) and possibly the only two genera of the Core Cactoideae I with true cephalia; *Cephalocereus* and *Backebergia* have pseudocephalia. *Leptocereus* pretty much eliminates the possibility that the term ‘cephalium’ will have any phylogenetic basis.

My integrated definition of ‘cephalium’ is in some ways in accord with and in some ways diverges with the definition given by Mauseth (1989). The similarities are that we both agree



Figure 18. *Melocactus conoideus* Buining & Brederoo showing reversion from a cephalium to vegetative growth. Note the gradual transition during this reversion, as the plant still has floral remains while the cephalium-bearing part of the shoot grew wider. However, flowering stopped once phyllotaxy straightened and chlorenchyma returned. This plant is in cultivation at the Huntington Botanical Garden.

Photograph: Matt Ritter.

that cephalia arise from strongly dimorphic monopodial growth in which photosynthetic portions of the shoot are not reproductive, while reproductive parts of the shoot are not photosynthetic. Mauseth (1989) claimed that cephalia show a change in phyllotaxy, whereas I claim something slightly different, namely that cephalium phyllotaxy is on top of original phyllotaxy of the juvenile shoot. I place much greater emphasis on periderms underlying cephalia being a defining trait of cephalia than Mauseth (1989), with such periderm formation resulting in the sunken look of cephalia and their lack of chlorenchyma. I have shown that transition from vegetative and reproductive growth is not always abrupt, although usually is. But the most important difference between our definitions is that I allow for reversions between reproductive and non-reproductive growth. Such reversions are obvious with ring-like cephalia and pseudocephalia

in *Arrojadoa*, *Stephanocereus leucostele*, and *Cephalocereus apicicephalum* (Figure 10). Reversions from reproductive to non-reproductive growth occur frequently in *Neoraimondia roseiflora* (synonym: *N. arequipensis*), where long-lived flowering short-shoot cephalia often eventually elongate to form photosynthetic long shoots (Mauseth & Kiesling, 1997). While much less frequent, in cultivation, specimens of *Espostoa* and *Melocactus* are known to revert from cephalium to photosynthetic non-reproductive tissues and sometimes back again to cephalium (Figures 9a & 18).

How do these new integrated definitions of cephalium and pseudocephalium bode for some of the other more enigmatic taxa? While *Stephanocereus luetzelbergii* has a silhouette resembling that of a large *Melocactus*, such as *M. levitesta* Buining & Brederoo, *Stephanocereus luetzelbergii* has a pseudocephalium by virtue of the more copious hairs on flowering areoles (Figure 15). These flowering areoles arise just below the shoot apical meristem, are not confluent, and are on photosynthetic ribs, further indicating that these are pseudocephalia. Those taxa that have fewer spines and trichomes on flowering areoles than on juvenile areoles, such as with *Browningia candelaris*, *Stetsonia coryne*, and *Carnegiea gigantea*, have neither pseudocephalia nor cephalia by the definitions herein. The famed San Pedro cactus, *Trichocereus pachanoi* Britton & Rose (synonym: *Echinopsis pachanoi* (Britton & Rose) H. Friedrich & G.D. Rowley), is very similar, having fairly long spines as a seedling, but becoming increasingly spineless as it matures. More problematic are the reproductive portions of shoots of some Pachycereeae, such as *Pachycereus marginatus*, *Pachycereus (Lophocereus) schottii*, and *Pachycereus (Backebergia) militaris*. *Pachycereus marginatus* has confluent flowering areoles, despite no hairs and no thick periderms, hence by the definition herein, this species has a pseudocephalium. *Pachycereus (Lophocereus) schottii* seems to have a pseudocephalium, unless looking at specimens that flower from juvenile areoles with only a few short stout spines per areole (Figure 3c), so I am not sure how to classify their reproductive parts. *Pachycereus (Backebergia) militaris* has periderm formation that occurs probably a year after new growth from the shoot apical meristem, flowering areoles that are never quite confluent, and reproductive structures that are an inflorescence. This species therefore has pseudocephalia.

Ultimately, I hope the modified definitions of cephalium and pseudocephalium herein will provide a convenient way to answer questions in evo-

lution and ecology. For instance, to ask whether cephalia are adaptive or not presupposes that we can identify what constitutes a cephalium. But that is work for another day.

Acknowledgments

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