Espostoa (*Vatricania*) *guentheri* have unusual cephalia or pseudocephalia

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Abstract: Espostoa (Vatricania) guentheri is a peculiar putative Espostoa, having some traits in common with Espostoa sensu stricto (cephalia in which many or most epidermal cells produces a spine, bristle, or trichome), some traits in common with Thrixanthocereus (cephalia with bristles instead of hairs; patches of epidermal cells in the cephalium that lack spines, bristles, hairs or trichomes), and some unique traits (gradual transition to cephalium formation; disjunct habitat). Gradual cephalium formation in *E. guentheri* is common, but not universal, which might be either because Vatricania is not closely related to Espostoa or that Vatricania is of hybrid origin. *E. guentheri* may have a pseudocephalium, rather than a true cephalium, with the reproductive part of shoots in subgenus Vatricania being morphologically intermediate between those of subgenus Espostoa and subgenus Thrixanthocereus.

Keywords: cephalium, Espostoa, disjunct species, hybrid origin, pseudocephalium, Thrixanthocereus, Vatricania

INTRODUCTION

Previously (Gorelick, 2016: 118), I defined 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. Bristles and 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. Lateral cephalia appear to lean to the side, at least at the shoot apical meristem, but the entire shoot eventually seems to straighten via the addition of new ribs. All of these criteria must be met for something to be a cephalium.

In hindsight, I should relax this definition, allowing for occasional stomata in cephalia and to not require that periderms be particularly thick. Phyllotaxy also need not be modified in cephalia, but could remain the same as in vegetative growth, but the cephalium ribs could be cryptic because of their low stature and because many (or most?) epidermal cells in the cephalium, including those between ribs, produce spines, bristles, or trichomes. It is not even obvious whether all cephalia have a common evolutionary origin - with presence of cephalia possibly confined to the Browningieae-Cereeae-Trichocereeae clade of the Core Cactoideae II versus having independently evolved in the Pachycereinae of the Core Cactoideae I sensu Hernández-Hernández et al. (2011).

With this revised definition of a cephalium, at first blush, *Espostoa guentheri* (Kupper) Buxbaum



Figure 1. Like all cephalia, those of *Espostoa guentheri* arise from the shoot apical meristem.

[synonym Vatricania guentheri (Kupper) Backeberg] seems to be cephalium-bearing. Cephalia of E. guentheri arise at or just below the shoot apical meristem (Fig. 1). Their flowers only arise from cephalia, which have an incredible density of confluent or nearly confluent spines and long thin flexible spines (also known as bristles) that obscure the underlying epidermis thereby precluding photosynthesis. Cross-sections of their shoots show sunken cephalia, i.e. the normally thick cortex of the photosynthetic part of the shoot is much thinner in their cephalia, whereas epidermal cells in the cephalium produce a periderm hence the cephalium lacks chlorenchyma (Fig. 2). Phyllotaxy is obscured by cephalia, with much higher density of possibly contiguous areoles and ribs in cephalia than in photosynthetic nonflowering parts of a shoot. If there are ribs in their cephalia, they are so low as to hardly be able to dis-



Figure 2. Cross-section of *Espostoa guentheri* shoot with cephalium. Note that the cephalium has low ribs, no underlying chlorenchyma, and a narrower cortex than photosynthetic parts of the shoot, resulting in a so-called 'sunken' cephalium. Photo James Mauseth.

tinguish ribs from troughs between ribs (Mauseth, 1999). As with other species of *Espostoa* Britton & Rose, cephalia appear to be epi-phyllotactic — growing on top of, rather than from, underlying ribs – in *E. guentheri*, often covering an increasing proportion of the circumference as the cephalium-bearing shoot grows taller (Figs. 3, 4), sometimes with a cephalium eventually enveloping the entire shoot apex. All these are traits of *bona fide* cephalia, although there are some ambiguities that I will describe in the next three paragraphs, hinting that *E. guentheri* may instead have pseudocephalia.

Whereas most of the epidermis of flowering regions in *Espostoa guentheri* looks like a true cephalium in that many or most epidermal cells produce a spine or bristle (a modified spine), there are oc-



Figure 5. Espostoa (Thrixanthocereus) senilis, cross-section through pseudocephalium. Flowers arise from shoots that are only modified by producing more and longer bristles in areoles, with chlorenchyma still underlying each such areole, making this a pseudocephalium, rather than a true cephalium. There is no reduction in width of the cortex nor change in phyllotaxy in the pseudocephalium of *E. senilis*. Photo Paul Hoxey.

casional small patches of epidermis without spines, bristles, hairs or trichomes that only occur at the peak of the seemingly flattened rib of the putative cephalium (Mauseth 1999). Ribs in *E. guentheri* continue into the putative cephalium — i.e. rib number is conserved – but ribs are much flatter (lower height) than in photosynthetic regions of the shoot. Very few new ribs are added when a shoot first becomes reproductive. The vegetative ribs at the same height on the shoot as the putative cephalium remain vertical — that is, cephalium-bearing shoots have orderly vertical vegetative ribs – unlike some, but not all, other species of *Espostoa sensu stricto*.



Figures 3 & 4. Espostoa guentheri cephalium starts out only covering a small portion of shoot, but can continue getting wider, eventually covering the entire circumference of a shoot.



Figure 6. Gradual development of *Espostoa guentheri* cephalium. Photo Jürgen Menzel.

Like *E. guentheri, E. blossfeldiorum* (Werdermann) Buxbaum [synonym *Thrixanthocereus blossfeldiorum* (Werdermann) Backeberg] and *E. senilis* (F. Ritter) N.P. Taylor [synonym *Thrixanthocereus senilis* F. Ritter] seem to show no changes in phyllotaxy nor additions of extra ribs when a cephalium or pseudocephalium is first formed on a shoot (Anderson, 2001). Note that members of subgenus *Thrixanthocereus* unambiguously have pseudocephalia, i.e. distinct areoles separated by normal depth photosynthetic ribs and areoles that are separated by normal internodes, i.e. internode length is the same in vegetative tissue and pseudocephalium tissue in subgenus *Thrixanthocereus* (Fig. 5) (Charles 2015, Gorelick 2016).

The underlying pattern and number of ribs at first does not appear to change in the transition to cephalium formation in *Espostoa guentheri*. There is no noticeable lean downwards of the shoot apical meristem during initial cephalium development. But as the cephalium continues to develop a denser set of bristles covering a greater diameter of the shoot, the shoot apical meristem does start to lean downwards slightly towards the side with the putative cephalium (Fig. 1). At least in a large subset of individuals, the transition to cephalium formation seems to be more gradual in E. guentheri than in any other cephaliumbearing cactus (Figs. 6, 7). Furthermore, in E. guentheri, growth will occasionally revert back from putative cephalium formation to no cephalium, in which the ribs seem to remain continuous throughout the transitional zone (Fig 8). For these reasons, E. guentheri seems to be intermediate in character between



Figure 7. Gradual development of *Espostoa guentheri* cephalium. Production of typical long flexible spines (bristles) in *E. guentheri* before formation of a true cephalium. In this transitional zone with long bristles on the lower portions of this photo, the underlying tissue contains distinct areoles, contains chlorenchyma, and lacks periderm.



Figure 8. Reversion to photosynthetic growth from an *Espostoa guentheri* cephalium. Note flower bud in cephalium and maintenance of rib phyllotaxy both above and below cephalium. Photo Jan Nequin and Jean Noël.

having a cephalium and a pseudocephalium, being morphologically intermediate between subgenus *Espostoa* and subgenus *Thrixanthocereus*. The only other cactus in which there routinely is a gradual transition to cephalium growth is the unrelated *Pachycereus militaris* (Audot) D.R. Hunt [synonym *Backebergia militaris* (Audot) Bravo ex Sánchez-Mejorada], which also has reproductive structures intermediate between that of a cephalium and pseudocephalium (Gorelick 2016, Vázquez-Sánchez *et al.* 2016). *Pachy-*



Figure 9. Gradual transition in development of a cephalium or pseudocephalium in *Pachycereus (Backebergia) militaris.* This species always seems to produce a few centimeters of growth during cephalium formation in which an intermediate number of ribs are produced and the short stout spines of vegetative growth are gradually replaced with cephalium-like long flexible bristly spines. Photo James Mauseth.

cereus militaris does a gradual transition to cephalium formation in two separate ways, by (1) adding several centimeters of shoot height with many extra otherwise normal ribs before a cephalium first forms (Fig. 9) and (2) having a chlorenchymatous cephalium for the most recent year or two of growth, after which time the chlorenchyma is replaced (overgrown) by a periderm derived from the epidermis (Vázquez-Sánchez *et al.* 2016).

In cacti, dimorphism between cephalia and the photosynthetic shoots on which they grow is striking because the transition from juvenile photosynthetic growth to non-photosynthetic adult growth of a cephalium is incredibly abrupt. In Melocactus very rarely a few extra ribs are added before a cephalium appears, but each new rib has only one or two areoles before a bona fide cephalium is formed. Gradual transitions to cephalium or pseudocephalium formation are extremely rare in cacti. See Fig. 7 in Gorelick (2016) for a few examples. But otherwise there is usually no indication given by a juvenile shoot that cephalium formation is imminent. The only species in which a gradual transition to putative cephalium or pseudocephalium formation are fairly common is Espostoa guentheri and Pachycereus (Backebergia) militaris. I have never seen this gradual transition in any other species of lateral cephalium-bearing cacti, although I have seen it with a few species of lateral pseudocephalium-bearing cacti, such as Micranthocereus Backeberg and Facheiroa Brit-



Figure 10. 1.5 m tall *Espostoa guentheri* in a 15 cm diameter clay pot.

ton & Rose (Gorelick 2016). Figures 3, 7, 10, and 11 show this gradual transition in which areoles on one side of a shoot of *E. guentheri* become larger and start growing bristly spines typical of a cephalium before areoles become confluent and before chlorenchyma disappears under a fully formed cephalium with periderm. Flowers in *E. guentheri* only seem to arise from completely formed cephalia, i.e. with confluent areoles and no obvious underlying photosynthetic tissue (Figs. 11, 12). Flowers do not seem to arise from transitional



Figure 11. Same individual of *Espostoa guentheri* as in Figs. 1, 3, 7, and 10, here with its very first flower, which arose from the cephalium, not from the transitional zone.

zones in *E. guentheri*. These transitional zones in cephalium formation in *E. guentheri* can be up to 35 cm long.

In cultivation, *Espostoa guentheri* can grow 20-30 cm taller in a single growing season (Mauseth et al, 2002, Anon. 2005). The 1.5 m tall plant in Figs. 10, 11 has grown 40 cm in the 1.5 years since the transitional zone started and 25 cm in the year since the cephalium started, despite being in the same 15 cm diameter pot that I acquired it in as a 25 cm plant eight years ago. Even after only a year of cephalium growth, the cephalium already covers half the diameter of the shoot, i.e. half of the ribs. I have not added new soil nor fertilizer in those eight years, but may finally remedy that next summer. This specimen has been in a greenhouse in Ottawa, Ontario, Canada, in which many cactus species typically grow slowly, even when well cared for. The specimen of Espostoa lanata (Kunth) Britton & Rose in the same greenhouse grows at one-tenth the growth rate of E. guentheri, despite me repotting E. lanata and sometimes putting it outdoors for summers. Thus, it is plausible that the transition zone in cephalium formation in E. guentheri grows in a single season, which was the case for the plant in Figs. 1, 3, 7, 10, and 11. But that is still a very long transition zone for cephalium formation. It also seems that shoots of E. guentheri grow more rapidly once a cephalium/pseudocephalium forms, as is also seen in Pachycereus schottii (Engelmann) D.R. Hunt [synonym Lophocereus schottii (Engelmann) Britton & Rose] (Parker 1988).

The miniscule pot (1.5 m tall plant in a 0.15 m diameter clay pot; Fig. 10) in which this cultivated



Figure 12. Flowers only seem to arise in *Espostoa guentheri* once a true cephalium is formed, without underlying chlorenchyma, No flowers appear in the transition zone with lots of long bristles. Photo André Labat.



Figure 13. *Espostoa cremnophila*, which has about as extreme a lean of the cephalium-bearing shoot as is ever seen in cacti. Graham Charles and Paul Hoxey do not know if these leaning shoots eventually grow straighter as they grow taller (personal communication), as seems to happen in many other cephalium-bearing species. Photo Graham Charles.

Espostoa guentheri, with a cephalium that now covers half the width of that single shoot, is indicative of something else important. The plant and pot are standing alone on the greenhouse bench, without support and without falling over. This indicates the extremely vertical growth of the shoot, without any marked tilting of the shoot apical meristem once the cephalium started growing. Tilting of cephalium-



Figure 14. *Espostoa mirabilis* with radical change in rib phyllotaxy and addition of new ribs once cephalium starts growing. Photo Graham Charles.

bearing shoots can be prominent, the most extreme case of which is in E. cremnophila Hoxey (Fig 13). While there seems to be a slight tilt to the shoot apex that could be compensated for by the shoot growing many new ribs on the opposite side from the cephalium, as happens with many plants with lateral cephalia, e.g. E. mirabilis F. Ritter and Coleocephalocereus goebelianus (Vaupel) Buining; (Figs. 14-16), for the E. guentheri in Figs. 1, 3, 7, 10, and 11 only one new rib was added and the existing ribs have maintained their phyllotaxy. Maintenance of vertical phyllotaxy upon reaching the flowering stage is typical for many pseudocephalium-bearing species, such as Espostoa senilis. However, even those species in which we typically see radical changes in rib number and lack of vertical orientation of ribs upon development of a cephalium, such as E. mirabilis and C. goebelianus, do not always show such a change in all plants (Figs. 17, 18).

Maybe not too coincidentally, the cephalium of *Espostoa guentheri* is composed of long flexible spines, sometimes called bristles, much like those found in subgenus *Thrixanthocereus*, i.e. *E. senilis* and *E. bloss-feldiorum*. *E. guentheri* does not have hair-like spines in its cephalium — which may simply be spines lacking much lignin — as do all other members of the genus *Espostoa* (nobody has studied the development and anatomy of such hairs, let alone their relative lignin content compared with stout spines and flexible bristly spines). Morphologically, *E. guentheri*



Figure 15. *Espostoa mirabilis* var. *primigena* F. Ritter with change in rib phyllotaxy once cephalium starts growing. However, note that eventually nice orderly phyllotaxy with vertical ribs starts again once the cephalium is sufficiently tall. Photo Graham Charles.



Figure 16. Coleocephalocereus goebelianus with change in rib phyllotaxy once cephalium starts growing. However, note that eventually nice orderly phyllotaxy with vertical ribs starts again once the cephalium is sufficiently tall.

is similar to *E. senilis* in terms of bristles in its cephalium or pseudocephalium (Figs. 1, 7, 11), patches of somewhat normal epidermis in its cephalium or pseudocephalium; little or no change in phyllotaxy once a cephalium or pseudocephalium forms; and virtually no lean at the top of flowering shoots (Lodé 2015).

In some specimens of Espostoa guentheri, the transition to cephalium development is incredibly abrupt, much like in virtually all cephalium-bearing cacti (Fig. 19). In some specimens of E. guentheri, cephalium development is gradual, first only covering a small proportion of the circumference of a shoot, gradually covering more and more of the shoot as the shoot grows taller (Fig. 4). In some specimens of E. guentheri, cephalium development is extremely gradual, growing longer bristles and bigger areoles in a very gradual process, sometimes over one-third of a meter vertical span (Figs. 1, 7, 10, 12). All three cases — abrupt cephalium development, gradual cephalium development, and extremely gradual cephalium development — all seem fairly common in cultivated specimens of E. guentheri. Unfortunately, I have not visited this plant in habitat in Bolivia to ascertain the frequency with which cephalium production is gradual. Furthermore, sometimes in a single plant, some shoots show much more gradual transition to cephalium development than others (Figs. 20, 21).



Figure 17. *Espostoa mirabilis* with no change in rib phyllotaxy and no new ribs once the cephalium started growing. Photo Graham Charles.



Figure 18. *Coleocephalocereus goebelianus* with no change in rib phyllotaxy and only one new rib once the cephalium started growing.



Figure 19. *Espostoa guentheri* with abrupt formation of cephalium, i.e. no gradual transition to cephalium formation.

Why does *Espostoa guentheri* seem more likely to gradually transition to cephalium formation, more so than other species of *Espostoa* and more so than other cephalium-bearing cacti? In all *Espostoa* species except for *E. guentheri*, the vascular cambium produces less wood under the cephalium than under vegetative parts of the shoot (Mauseth 1999). In *E. guentheri*, lignin production around a shoot is symmetrical, with no difference between cephalium and photosynthetic parts of the same shoot (Mauseth 1999). Another not mutually exclusive possible reason for the unique gradual transition to cephalium development in *E. guentheri* is that maybe this taxon is not a true *Espostoa*.

What do experts on cactus classification say about the relationship of *Espostoa guentheri* with other cacti, especially possible congeners? Schlumpberger & Renner (2012) place *Espostoa (Vatricania) guentheri* in the *Cleistocactus* Lemaire *sensu stricto* clade, whereas they place *Espostoa lanata* in the *Oreocereus* (A. Berger) Riccobono clade. Even more radically, Ancheschi & Magli (2013) have transferred *Espostoa guentheri* to *Echinopsis* Zuccarini, as *Echinopsis guentheri* (Kupper) Anceschi & Magli, hint-

ing that they might also subsume all *Espostoa* species in Echinopsis, part of what they deem "Schlumpberger's nightmare". E. guentheri looks like a typical Espostoa, in terms of its flowers, and fruits (Figs. 11-12). E. guentheri is geographically disjunct from the rest of the genus, being the only species found in Bolivia (Yetman, 2007). All other species of Espostoa are from Peru and Ecuador. E. guentheri is from the Río Grande valley in the south-central Bolivian Departments of Santa Cruz and Chuquisaca, near the northwestern border of these two Departments, at roughly 1,000 m elevation. Schlumpberger & Renner's (2012) phylogeny was strictly based on chloroplast DNA and assumed maternal inheritance of organelles. However, depending on the species, organelles in cacti can be maternally inherited, paternally inherited, biparentally inherited, or can vary between individuals and across generations (Corriveau & Coleman 1988). It is therefore not obvious whether Schlumpberger & Renner's (2012) phylogenetic placement of *E. guentheri* within *Cleistocactus* is correct (Gorelick 2014).

One other problem with basing phylogenies on chloroplast inheritance, even if their inheritance ends up being strictly maternal for Espostoa, Echinopsis, Oreocereus, and Cleistocactus, is that such phylogenies cannot take into account hybridization, introgression, and reticulation. There is certainly a possibility that Espostoa guentheri arose as a hybrid between a male Espostoa and a female Cleistocactus Lemaire, such as *Cleistocactus ritteri* Backeberg [synonym Cephalocleistocactus ritteri (Backeberg) Backeberg]. Such hybridization could possibly cause a more gradual transition to cephalium or pseudocephalium formation. I say that the putative female parent was Cleistocactus by assuming, possibly erroneously, that chloroplasts are maternally inherited. But we could never infer such an interesting hybridization event by only using maternally inherited molecular markers. A putative hybrid between Pachycereus (Backebergia) miltaris and P. pecten-aboriginum Britton & Rose shows an intermediate level of cephalium/pseudocephalium formation, no loss of chlorenchyma, but enlarged areoles containing long flexible spines, aka bristles, in the apical flowering region, and addition of a few additional ribs that are still vertical (Mauseth et al. 2005), and Rowley (1994, 2004) suggested that a few putative Espostoa species, but not necessarily E. guentheri, are natural hybrids between Cleistocactus and Espostoa, namely ×Espostocactus baumannii (Kníže) G.D. Rowley (synonym Espostoa baumannii Kniže) and Espostocactus × mirabilis (Rauh & Backeberg) G.D. Rowley [synonym Espostoa mirabilis Rauh & Backeberg]. Ritter (1979) suggested that the enigmatic Cephalocleistocactus chrysocephalus F. Ritter, with the extreme vertical lean of their lateral pseudocephalium, may be a natural hybrid between Cleistocactus and Vatricania (i.e. Espostoa guentheri).

In the end, I do not know why gradual transitions to cephalium/pseudocephalium formation are more common, albeit not ubiquitous, in *Espostoa guentheri* than in all other cactus species, except for



Figures 20 & 21. A single plant of *Espostoa guentheri* with four equal length branches from the base (plus a pair of shorter, more recent, branches from the base). The middle two of four shoots have a gradual transition to cephalium formation, while the other two shoots have an abrupt transition. The four cephalia all start growing at roughly the same height and have the oddity that the cephalia never seem to cover much of the circumference of each shoot.

Pachycereus (Backebergia) militaris. I do not even know whether to call the reproductive structures of *E. guentheri* cephalia versus pseudocephalia. None-theless, *Espostoa (Vatricania) guentheri* is an unusual species, worthy of further study, including anatomy of its cephalium or pseudocephalium, its nuclear DNA, and possible hybrid origin.

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All photos by the author unless otherwise noted. All specimens of *Espostoa guentheri* (but not of other species) are of cultivated specimens.



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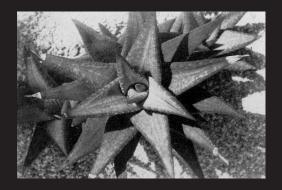
















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