AXILLARY BRANCHING OF LATERAL CEPHALIA OF *COLEOCEPHALOCEREUS* (CACTACEAE)

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Abstract: The arborescent *Coleocephalocerus goebelianus* occasionally has axillary branches arising from lateral cephalia, which is unexpected due to stem asymmetries in cephalia and the resulting mechanical stress. Axillary branching from cephalia is much more common in *C. decumbens*, *C. fluminensis*, and *C. buxbaumianus,* but these branches are largely (but not exclusively) on decumbent stems, therefore the cephalia act as less of a mechanical constraint. The clade containing *Coleocephalocereus*, *Siccobaccatus*, *Melocactus*, and *Discocactus* is sister to the clade containing *Arrojadoa* and *Stephanocereus*, the latter two genera usually branch from cephalia, indicating that axillary branching may be plesiomorphic in *Coleocephalocereus*.

A trio of papers on *Cephalocereus columna-trajani* (Karw.) K. Schum. proffered a pair of related hypotheses about lateral cephalia (Zavala-Hurtado, Vite & Ezcurra, 1998; Valverde, Vite, Perez-Hernandez & Zavala-Hurtado, 2007; Vázquez-Sánchez, Terrazas & Arias, 2007). First, *C. columna-trajani* tilts away from the sun by producing asymmetrical stems. In cross (transverse) section, the wedge of tissue extending from the center of the pith to epidermis of the lateral cephalium is quantitatively different from the remainder of the cross section of stem (see below for details). Second, they hypothesized that no axillary branching can occur from a cephalium because the tilted stem would physically break or fall over. Curiously Vázquez-Sánchez et al. (2007) noted that the apex of *C. senilis* Pfeiff. does not tilt, but nonetheless remains unbranched. The purpose of this short note is to indicate that their hypotheses can be applied across all cacti with true lateral cephalia and, primarily, to highlight some exceptions to their second hypothesis of no axillary branching of cephalia, branching that occurs in species from *Coleocephalocereus* subgenus *Coleocephalocereus*, and also in a few individuals of *Coleocephalocereus goebelianus* (Vaupel) Buining (*Coleocephalocereus* subgenus *Simplex* N.P. Taylor).

A lateral cephalium consists of ribs that are devoid of chlorenchyma because all or a vast majority of epidermal cells form trichomes (Buxbaum, 1964; Gibson & Nobel, 1986; Vázquez-Sánchez et al., 2007). A true lateral cephalium continues growing from the apical meristem once the cephalium starts forming, usually without any reversions back to vegetative growth. In cephalia, this intensive trichome production occurs along a continuous segment of a branch, not just at discrete nodes (areoles), originating from the apical meristem once the individual branch has reached a certain size or age. In a cephalium, distance between areoles drops to zero (areoles become contiguous), while the size of trichome-rich areoles increases.

Stems with lateral cephalia are asymmetrical for several reasons. Cephalia often produce cork (outer bark, aka periderm), from epidermis, hypodermis or cortex, which can inhibit water loss. Photosynthetic portions of the stem lack cork because they need the light, whereas blocking of light by cork is not a constraint in the tissues of a cephalium (lateral or terminal) because they already lack photosynthetic cells. In species with lateral cephalia that never completely encircle a branch, the vascular cambium produces less wood on the side of the stem with the cephalium than the photosynthetic side (Mauseth, 1999). With secondary xylem, fibers form, but differentiate relatively late, making secondary xylem on the cephalium-bearing side of the stem more parenchymatous than on the vegetative side (Mauseth, 1989; Vázquez-Sánchez et al., 2007). Vessels are typically narrower on the cephalium-bearing side of the stem (Mauseth, 1999). In many species, lateral cephalium-bearing ribs are thinner and have less cortex and pith underlying them (Vázquez-Sánchez, Terrazas & Arias, 2005; Mauseth, 2006). These factor contribute to the noticeable tilt and sunken appearance in most lateral cephalia – at least in those species in which cephalia never completely encircle the branch (e.g. *Espostoa guentheri* (Kupper) Buxb. ex Eggli and *Cephalocereus senilis* have cepahalia that completely encircle the stem).

Figure 1. Axillary branching from ring cephalia. (a) *Stephanocereus leucostele*. (b). *Arrojadoa rhodantha var. aureispina*.

Figure 2. Dichotomous branching of cephalium-bearing stems (a) Terminal cephalia: *Melocactus ernestii* f. *multiceps* (b) Lateral cephalia: *Siccobaccatus* (*Micranthocereus*) *dolichospermaticus.*

It seems that virtually every cactus with a lateral or terminal cephalium lacks axillary branching from the cephalium, except for species with ring-like terminal cephalia in which vegetative growth alternates with cephalia. See Fig.. 1 of *Stephanocereus leucostele* A. Berger and *Arrojadoa rhodantha* Britton & Rose var. *aureispina* (Buining & Brederoo) P.J. Braun & Esteves, in which axillary branches appear to arise from cephalia. What makes *Stephanocereus leucostele* and all plants in the genus *Arrojadoa* Mattf. all the more peculiar and worthy of study is that they usually branch at ring-like terminal cephalia. Only occasionally do they branch from the vegetative zones between cephalia (Nigel P. Taylor, pers. comm.). In stark contrast, in almost all other cacti, axillary branching invariably appears to occur

Figure 3. Branching cephalia on *Coleocephalocereus goebelianus.* (a) Frontal view of cephalia; plant 4.5 m tall. (b) Close-up of cephalia; note vegetative branches arising from older cephalia. (c) Side view, showing tilting of stems and addition of ribs as cephalia grow.

from stems or portions of stems without cephalia. If branching occurs in cacti without ring cephalia, it is typically from portions of the stem that are below a cephalium. This indicates that taxa whose lateral cephalium-bearing stems do not tilt probably are also asymmetrical in cross section.

Axillary branching does not generally occur in cacti with lateral or terminal cephalia, but dichotomous branching can occur because it should not place as much stress on stems as does axillary branching. Isotomous branching (equal sized, symmetrical branches) appears in several *Melocactus* species, e.g. *M. intortus* (Mill.) Urb. and *M. ernestii* Vauple (Fig.. 2a), but is much rarer with lateral cephalia, possibly because of the extra load (moment arm) on the stems. Figure 2b depicts isotomous branching of a cephalium-bearing specimen of the usually unbranched *Siccobaccatus dolichospermaticus* (Buining & Brederoo) P.J. Braun & Esteves, but this is very unusual (Gorelick, 2009).

Coleocephalocereus goebelianus is a conspicuous plant, albeit often hidden amongst trees, throughout south central Bahia, extending just into northern Minas Gerais. It is readily distinguishable from all other cacti in this region. It is fairly common; Taylor & Zappi (2004) list its conservation status as of 'least concern'.

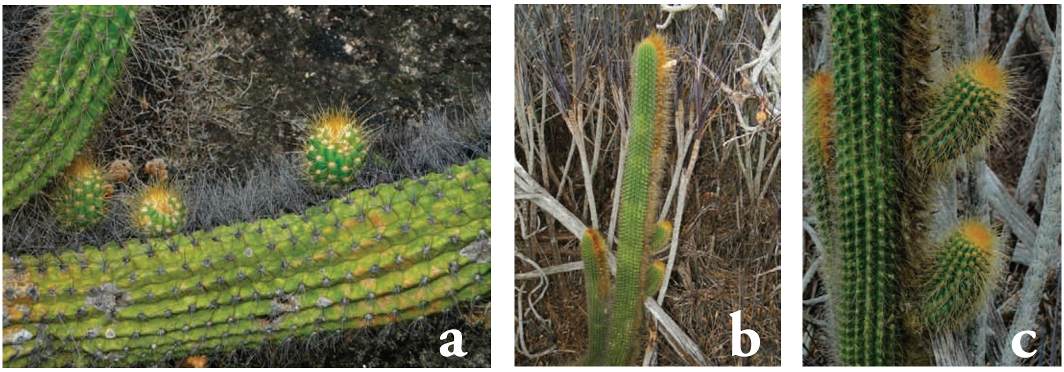
Several populations of *Coleocephalocereus goebelianus* contain individuals with sporadically branching lateral cephalia (Fig.. 3). The branches appear to be

Figure 4. Typical *Coleocephalocereus goebelianus*, without branches. Note how vertical the chlorenchymous ribs are until the cephalium.

axillary, with young vegetative branches arising from relatively far down on older well-established cephalia. While the stem tips of these specimens do indeed tilt in one direction, over time, secondary growth seems to compensate for the tilt, allowing these plants to grow to massive proportions, up to 4.5 meters tall (to 6 meters according to Taylor & Zappi (2004)), with cephalia on the top 2.5 meters of such branches. And these are massive cephalia, often enveloping one-third of the circumference of the branch. Yet, none of these plants seemed to have broken branches nor seemed in jeopardy of falling over due to too great of a lean. More typically *C. goebelianus* individuals are single stemmed (unbranched; Fig.. 4). Note that in both the unbranched and branched specimens, ribs appear utterly vertical until cephalium formation, at which point they appear to bend towards the lateral cephalium (Figs. 3-4).

Taylor & Zappi (2004: 363) describe *Coleocephalocereus goebelianus* as, "Stem solitary, normally

Figure 5. *Coleocephalocereus buxbaumianus.* (a) Decumbent cephalium. (b) Upright cephalium. (c) Close-up of upright cephalium.



branching only if damaged, but occasionally forming short branches at the point where the stem develops the cephalium". Yet, the plants in Fig. 3 have branches arising from up to 35 cm above where the cephalium initially formed and some of these newly arisen branches were about one meter long. Theses branches appear to have arisen from well within the cephalium and not along its lateral margins.

Taylor (1991) notes that *Coleocephalocereus goebelianus* is much like *Melocactus* Link & Otto, but unlike all other species of *Coleocephalocereus* and most other species in the tribe Cereeae F. Ritter, in having determinate growth of areoles. Determinate growth of areoles on photosynthetic stems would render axillary branching impossible. The only option for axillary branching in *C. goebelianus* is via the confluent areoles in its cephalium, which presumably have indeterminate growth or at least retain active growth for a longer period of their lives.

Coleocephalocereus goebelianus is morphologically very similar to *Cephalocereus columna-trajani* and *C. senilis*. All three species are erect, tall, and usually unbranched trees, with massive lateral cephalia and, for two of these species, tilting of the stem apices only once lateral cephalia have formed (*C. senilis* stem apices do not tilt). Yet some *Coleocephalocereus goebelianus* somehow manages to have unbroken branching lateral cephalia.

Figure 6. *Coleocephalocereus decumbens*

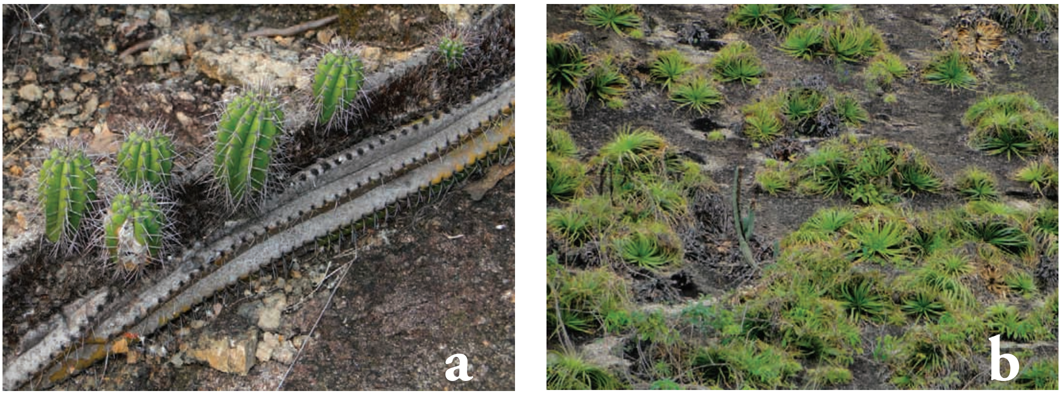


Figure 7. *Coleocephalocereus fluminensis.* (a) Decumbent cephalium. (b) Upright cephalium.

Coleocephalocereus buxbaumianus Buining, *C. decumbens* F. Ritter [synonym *C. fluminensis* (F. Ritter) subsp. *decumbens* N.P. Taylor & Zappi], and *C. fluminensis* (Miq.) Backeb. – all of which are in the subgenus *Coleocephalocereus* – also have cephalia with axillary branching (Figs. 5-7). Cephalia from which branches arise are usually decumbent, obviating constraints on stem architecture due to mechanical stress being placed on the asymmetrical stem, as hypothesized for *Cephalocereus columna-trajani* and *C. senilis*. However, sometimes axillary branching occurs in upright cephalia of *Coleocephalocereus buxbaumianus* and *C. fluminensis* (Figs. 5c, 5d, 7c), indicating that *C. goebelianus* (subgenus *Simplex*) is not unique in this peculiar branching habit.

The three subgenera of *Coleocephalocereus* have different branching patterns when uninjured. Subgenus *Simplex* axillary branches only arise from cephalia. Subgenus *Coleocephalocereus* axillary branches arise from both vegetative (photosynthetic) portions of the stem and from cephalia. These plants are unconstrained in two ways: their areoles presumably all have indeterminate growth and their branches are largely decumbent. Subgenus *Buiningia* (Buxb.) P.J. Braun axillary branches only arise from vegetative portions of the stem, usually near the base of the plant (Fig. 8). While presumably all their areoles have indeterminate growth, stem architecture in the subgenus *Buiningia* may be mechanically constrained by upright growth, as hypothesized in *Cephalocereus columna-trajani*, or by apical dominance and therefore only branching from their base.

How do the anatomical features of both branched and unbranched cephalia of *Coleocephalocereus goebelianus, C. buxbaumianus, and C. fluminensis* compare with those of *Cephalocereus* Pfeiff. and *Espostoa* Britton & Rose? Judging from the changing orientation of the ribs and tilting of the apex of the stem once cephalia form, we strongly suspect that *Coleocephalocereus goebelianus, C. buxbaumianus,* and *C. fluminensis* have asymmetrical stem sections at each lateral cephalium. How or whether those cephalium-bearing stems compensate for the tilting and stem asymmetries with differential secondary growth, possibly with extra fibers, is an interesting question. Our hope is that one of the great new generation of Brazilian plant anatomists takes climbing equipment or ladders along with a saw and section a few of the branching cephalia of *C. goebelianus*, as well as sectioning *C. buxbaumianus* and *C. fluminensis*. This will help tell us how much of a functional constraint lateral cephalia truly are. It would also be useful to have a better understanding for how long growth continues in areoles in the cephalia of these species.

The genus *Coleocephalocereus* apparently contains the only cacti that regularly have axillary branching from any cephalium, except for those genera with ring-like terminal cephalia. The clade containing *Coleocephalocereus, Siccobaccatus, Melocactus,* and *Discocactus* is sister to the clade containing *Arrojadoa* and *Stephanocereus* (Marlon Machado, Reto Nyffeler, Urs Eggli, and Anita Lendel, unpublished). In this as yet unpublished work, Machado et al. used cladistic and Bayesian methods to construct phylogenetic trees using four chloroplast markers (intergenic spacers trnS-trnG and trnS-trnfM, introns rpl16 and rps16), using 97 species that included (1) at least two species from each genus currently circumscribed in the Cereeae, including type species from all subgenera, (2) at least one species from each genus previously included in the Cereeae, (3) one species from each genus whose placement in Cereeae is uncertain (*Facheiroa, Gymnocalycium, Uebemlannia*), and (4) species from nine genera of Browningieae, Trichocereeae, and Notocacteae, as outgroups. Curiously, species of *Arrojadoa* and *Stephanocereus* usually only branch from ring-like terminal cephalia. Thus, axillary branching from cephalia in *Coleocephalocereus* may represent the retention of an ancestral condition, i.e. may be a plesiomorphic character. The apparent distinctiveness of *Coleocephalocereus* possessing axillary branching from lateral cephalia could consequently be explained as the result of genealogy, rather than being a characteristic unique to this genus.

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Figure 8. *Coleocephalocereus aureus*

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