AXILLARY BRANCHING OF LATERAL CEPHALIA IN CACTACEAE IS NOT CONSTRAINED BY TILTING OF SHOOT APICES

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Abstract: Cephalia occasionally have axillary branching in all three tribes of South American cephalium-bearing cacti. I document axillary branching of the cephalium of *Espostoa ritteri* (synonym: *E. lanata*), as well as provide three arguments for why axillary branching of cephalia should not be constrained by the physics of having a massive leaning lateral shoot.

Keywords: Plant physics, lateral cephalium, *Coleocephalocereus*, *Cephalocereus*

INTRODUCTION

Cephalia (singular: cephalium) are peculiar reproductive structures in the family Cactaceae. Most species of cacti do not have cephalia, but in those that do, flowers can only arise from a cephalium, which grows directly from a shoot apical meristem (Buxbaum 1964). The cephalium is generally a non-photosynthetic part of the shoot (Mauseth 2006). The cephalium is perennial (not an inflorescence) and contains a dense mass of spines and bristles (both modified leaves) and trichomes. Cephalia can either cover the entire apex of the plant, known as a terminal cephalium (even if the growth is apical, not terminal), or just a vertical strip of the shoot, known as a lateral cephalium. The shoot apices of lateral cephalium-bearing cacti usually lean in the direction of the cephalium because the shoot is "sunken" at the cephalium due to lots of cork production and a diminished cortex underneath the cephalium (Mauseth 2006, Gorelick 2013). The cortex is usually believed to be diminished because the cephalium is not photosynthetic (or not very photosynthetic) and does not have many or any stomata (Mauseth 2006).

Gorelick and Machado (2012) showed that some lateral cephalia can have axillary branching. Some species of *Coleocephalocereus* Backeberg only have axillary branches from photosynthetic (vegetative) parts of the shoot; some only have axillary branching from the reproductive part of the shoot, i.e. the cephalium; while others have axillary branches arising from both (see below for additional details). This partly debunked the notion that, in general, lateral cephalia cannot branch axially because the cephalium-bearing part of the stem leans downwards and production of a branch from therein would put inordinate stress on the shoot, causing the shoot to break.

The original work suggesting constraints on axillary branching in lateral cephalium-bearing shoots was with *Cephalocereus columna-trajani* (Karwinsky) K. Schumann (Zavala-Hurtado et al. 1998, Vázquez-Sánchez et al. 2007). Here I do not provide evidence either for or against lateral cephalia being a constraint in this species. However, I argue herein that (1) *C. columna-trajani* is a difficult plant to generalize from, (2) while the apex of lateral cephalium-bearing shoots tilt, the shoot usually ultimately remains vertical, (3) lateral cephalia on decumbent species of *Coleocephalocereus* indicate lack of a constraint because their cephalia tilt upward, and (4) I provide evidence for axillary branching in *Espostoa ritteri* Buining, which—while also in the Browningieae-Cereeae-Trichocereeae (BCT) clade—is not that closely related to *Coleocephalocereus*.

NEW EVIDENCE REGARDING AXILLARY BRANCHING AND STEM TILTING OF LATERAL CEPHALIA

I concur with Zavala-Hurtado et al. (1998) and Vázquez-Sánchez et al. (2007) that lateral cephalia of *Cephalocereus columna-trajani* never branch. Nor do I dispute their assertion that, in shoots with long cephalia, there is sometimes breakage (vertical splitting) of the photosynthetic parts of the shoot on the side of the shoot diametrically opposite the cephalium (Vázquez-Sánchez et al. 2007). But this species never has any axillary branching, from either the reproductive nor vegetative parts! Lack of branching in *C. columna-trajani* is probably as much a function of determinant growth of all areoles (aka axillary buds)—both vegetative and flowering—as it is a function of mechanical stress imposed by massive leaning cephalium-bearing shoots.

While the apex of lateral cephalium-bearing shoots often tilt in most species, ultimately the shoot manages to grow vertically. The world is not filled with lateral cephalium-bearing shoots that form

Figure 1. *Espostoa mirabilis* in habitat, showing production of new ribs to compensate for tilting of the shoot. [photo: Graham Charles]

spirals (although that would be quite beautiful) nor with lots of broken shoots with lateral cephalia littering the ground. In fact, the only taxon in which abscised cephalia litter the ground around their parent is *Pachycereus militaris* (Audot) D.R. Hunt (synonym *Backebergia militaris* (Audot) Bravo ex Sánchez-Mej.), which has terminal cephalia, and hence no imbalance. Somehow, lateral cephalium-bearing shoots manage to straighten themselves out by various means that probably include production of tension wood and addition of extra vegetative ribs. Even lateral cephalia that are over two meters long usually appear on vertical shoots, with only the apex tilted away from vertical. Before they grow a lateral cephalium, phyllotaxy is invariably quite elegant in these plants, with a constant number of evenly spaced ribs as the juvenile shoot grows taller. However, in many species, especially in the Core Cactoideae II (sensu Hernández-Hernández et al. 2011), as soon as the lateral cephalium starts forming, phyllotaxy gets ugly, with extra ribs being added and almost no ribs remaining vertical, even though the entire shoot is vertical (Figure 1).

A few lateral cephalium-bearing cacti are decumbent, rather than upright, such as *Coleocephalocereus fluminensis* (Miquel) Backeberg and the aptly named *C. decumbens* F. Ritter (synonym *C. fluminensis* subsp. *decumbens* (F. Ritter) N.P. Taylor & Zappi). For these plants, the cephalium grows on the adaxial (dorsal) surface of the shoot and the apex of the shoot tilts towards the side bearing the cephalium, as in all other cephalium-bearing cacti. With vertically oriented species, the tilt is towards the direction of gravity, while with decumbent species the tilt is opposite the direction of gravity. But eventually the shoots in the decumbent species grow horizontally once a half-meter or so past the apex. And, as with the vertically growing species, the decumbent species do not form spiraled lateral cephalium-bearing shoots. These decumbent species show that formation of cork under a cephalium and the consequent apical tilting are not much of a developmental constraint. This is especially evident in that close relatives in the genus *Coleocephalocereus* are vertically columnar, sometimes massively so, with shoots sometimes over 5 meters tall with 3 meters of lateral cephalium in *C. goebelianus* (Vaupel) Buining. Furthermore, while most plants of *C. buxbaumianus* Buining and *C. fluminensis* are decumbent, occasional individuals are vertically columnar and otherwise look like perfectly normal and healthy members of the genus (Gorelick and Machado 2012).

Figures 2–4 are of a cultivated specimen of *Espostoa ritteri* Buining, a synonym of *Espostoa lanata* (Kunth) Britton & Rose (according to Hunt et al. 2006), that has produced an axillary branch from a cephalium. As in the case with axillary branches of cephalia in *Coleocephalocereus*, the branch in this *Espostoa* Britton & Rose arises from the center of the cephalium, not from its edges nor from the start (bottom) of the cephalium. In this plant, axillary branching occurs from both vegetative and reproductive parts of the shoot.

Graham Charles does not recall ever seeing axillary branching of cephalia in the field, so the axillary branching depicted in Figures 2–4 may be an aberration due to cultivation. However, I suspect that

Figures 2 and 3. *Espostoa ritteri* with axillary branching of lateral cephalium. [Figures 2-4 were taken of the same plant (owned and photographed) by Jürgen Menzel]

axillary branching of cephalia is simply rare (i.e. not due to peculiar conditions in cultivation) because I have not seen other cultivated specimens of *Espostoa* with axillary branching of cephalia. Furthermore, in the field, axillary branching of cephalia is rare in *Coleocephalocereus goeblianus* (Taylor and Zappi 2004, Gorelick and Machado 2012).

CONCLUDING REMARKS

Gorelick and Machado (2012) documented axillary branching of cephalia in the tribe Browningieae (*Arrojadoa* Britton & Rose spp. and *Stephanocereus leucostele* A. Berger) and the tribe Cereeae (various species of *Coleocephalocereus*). The only other remaining tribe of cephalium-bearing cacti in the Core Cactoideae II is the Trichocereeae, which includes the genus *Espostoa*. Thus, while axillary branching of cephalia is relatively uncommon, there is evidence for it in all three tribes of the Browningieae-Cereeae-Trichocereeae (BCT) clade. To reiterate, this provides no evidence—pro nor con—regarding possible axillary branching of cephalia in the Core Cactoideae I, which are all restricted to the tribe Pachycereeae. Instead, the pictured *Espostoa ritteri*, in conjunction with our earlier work on *Coleocephalocereus*, implies that axillary branching of cephalia is likely not constrained by mechanical stress in the Core Cactoideae II.

Despite some potentially elegant botanical applications of the theory of physics of solids (e.g. Niklas and Spatz 2012) and some fine modeling of interception of light by tilted shoot apices of *Cephalocereus*

Figure 4. *Espostoa ritteri* with axillary branching of its lateral cephalium and vegetative parts. [photo: Jürgen Menzel]

columna-trajani (Zavala-Hurtado et al. 1998), what appear to be constraints on morphology and development of plant shoots, often are not. Cephalia can branch without the shoot toppling or breaking. Only by pursuing natural history with an eye for outliers across diverse taxa (Taleb 2010, Anderson 2011) can we better understand what drives evolution of plant architecture.

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