SUBDERMAL WOODY THORNS WITH SECONDARY GROWTH MAY SUPPORT SHOOTS OF SENITA, *LOPHOCEREUS SCHOTTII* (CACTACEAE)

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Abstract: *Lophocereus* (*Pachycereus*) *schottii* has lignified thorns with secondary growth connecting areoles to the vascular cylinder, which may help support their massive highly parenchymatous shoots.

INTRODUCTION

Lophocereus schottii (Engelm.) Britton & Rose (synonym *Pachycereus schottii* (Engelm.) D.R. Hunt), senita, is a columnar cactus with a candelabra growth habit. It has fairly massive shoots that are mostly composed of cortex plus wide pith, with a relatively small vascular cylinder, i.e. without much lignification. Almost all new shoots arise as branches from the base of existing shoots and each grows fairly vertically. Therefore much of the weight on shoots is supported by the ground and does not have to be supported by other shoots. Yet still there is need for stiffness of shoots, especially when buffeted by wind.

With regards to *Lophocereus schottii*, Molina-Freanar et al. (1998: 1083) noted that "the stems of columnar cactus species present an interesting biomechanical case study that could shed light on the ability to produce tall and stiff stems capable of growing to substantial heights, yet without benefit of the large amounts of wood found in many other dicot arborescent species." The same authors noted that, "cacti also provide numerous opportunities to identify the extent to which anatomical features correlate with tissue stiffness and strength" (Niklas, Molina-Freaner, and Tinoco-Ojanguren 1999: 774). Here I hypothesize one possible unexplored mechanism by which *L. schottii*, may stiffen its shoots.

Each *Lophocereus schottii* shoot starts off growing slowly. Until one meter tall, on average, shoots grow 6 cm per year, with growth rates decreasing as shoots approach one meter in height (Parker 1988). However, once shoots exceed one meter in height, aver-

Figure 1. An unusual *Lophocereus schottii* with a pseudocephalium on each shoot. *Pachycormus discolor* in left background. Near Cataviña, Baja California.

Figure 2. Decomposing *Lophocereus schottii* skeleton showing disarticulation of woody rods. Note unusual aerial branch at far left. This and remaining figures are of plant #95 at Organ Pipe Cactus National Monument.

Figure 3. *Lophocereus schottii* skeleton with thin thorns and disarticulating woody rods.

age growth rates become 15 times faster than that of juvenile shoots, increasing to a growth rate of 88 cm per year (Parker 1988). This transition to much faster growth occurs at roughly the same time shoots reach sexual maturity, producing an apical pseudocephalium with many long flexible spines per areole (Martorell, Vega, and Ezcurra 2006). Most shoots remain shorter than one meter tall, with individual plants only having one or a few taller shoots with pseudocephalia (Martorell, Vega, and Ezcurra 2006), although in a few specimens most or all shoots appear to produce pseudocephalia (Figure 1).

Skeletons of *Lophocereus schottii* resemble those of closely related cacti with overlapping ranges, such as saguaro (*Carnegiea gigantea* Britton & Rose) and organ pipe (*Stenocereus thurberi* (Engelm.) Buxb.; pitaya dulce) in having a vascular cylinder that decomposes into a ring of vertically oriented parallel discrete lignified rods, with one woody internal rod for each external rib of the shoot (Figure 2). This is a typical architecture for the Pachycereeae, in which the woody rods can be spread farther apart as the shoot develops, allowing the pith to enlarge (Gibson and Nobel, 1986). However, *L. schottii* differs from all other Pachycereeae skeletons that I have seen, including *C. gigantea*, *S. thurberi*, and *Neobuxbaumia mezcalensis* (Bravo) Backeb.; clavija), in that only *L. schottii* have highly lignified protuberances, essentially thorns, extending from the vascular cylinder of the massive shoot out to the areoles (Figures 3–5). Lignified thorns connecting the vascular cylinder to the areoles may provide extra support for the massive highly parenchymous shoots. These completely subdermal thorns are relatively narrow near the apical meristem of the massive shoot and relatively narrow near the areole. Thorns become broader near the base of the massive shoot and become broader centripetally, i.e. become broader closer to the vascular cylinder. It thus appears that *Lophocereus schottii* has secondary growth of the long vascular traces connecting areoles to the deeply embedded vascular cylinder, with a hollow center to each thorn where the vascular traces originally were (Figure 5). There is probably both a fascicular and interfascicular cambium present in the secondary growth of subdermal thorns of *L. schottii* given the solid nature of these woody thorns, vice the reticulate look of wood in shoots of *Cylindropuntia* (Engelm.) F.M. Knuth

Figure 4. Thick thorns on lower part of shoot. Note branch at upper left of this thorny shoot.

Figure 5. Thick thorns with hollow centres on lower part of shoot.

and vascular traces to flowers of *Hylocereus undatus* (Haw.) Britton & Rose (Weidlick 1974; Schwager, Neinhuis, and Mauseth 2015). Vascular traces with lignified secondary growth are known to provide structural support to shoots (Tomlinson et al. 2005). The exceptionally slow growth of the massive shoots of *L. schottii*, at least until one meter tall, may provide time for the shoots to develop large lignified subdermal thorns to support the shoot, especially to support the fast-growing pseudocephalium.

The attached photos of *Lophocereus schottii* skeletons were from a single plant at Organ Pipe Cactus National Monument (Figure 6). This locale is at the extreme northern range for this species, which seems to be cold limited. The photographed plant is tagged as specimen #95, near the north terminus of Senita Basin Road, less than ten kilometers from the Mexico/US border. There are only a few hundred plants of senita native in the U.S. (Parker 1989). Some of these individuals may be clones of one another, with tall shoots eventually bending over after reaching 2.5–4.0 meters tall (Martorell, Vega, and Ezcurra 2006), and then possibly (although this has never been thoroughly documented) striking adventitious roots. This phenomenon of subdermal thorns with secondary growth connecting areoles to a vascular cylinder probably occurs in other individuals of *L. schottii*. While photographs of dead and dying specimens are rare, especially of this relatively photogenic pseudocephalium-bearing species, Arnaud Martin (personal communication) took a photo of a plant from near Cataviña, Baja California with one tall dead shoot that appears to show numerous thin subdermal thorns about 1.0–1.5 meters above ground. Lower portions of the dead shoot are obscured in his photo, which is low-resolution and backlit. Therefore further confirmation of the subdermal thorns in *L. schottii* is needed.

Thick, woody, subdermal thorns make sense for supporting shoots with massive cortex and pith, as found in the Pachycereeae with their fastigiate rods of a vascular cylinder, especially in very slow growing juvenile shoots. What makes less sense is the rapid shoot elongation once shoots reach sexual maturity at approximately one-meter tall to form a pseudocephalium. Adult shoots with pseudocephalia often lean, sometimes precipitously, because they do not have time to grow thick subdermal thorns. But why the rapid shoot elongation? These plants do not need to produce many new areoles because of non-existent

Figure 6. Overview of plant #95, with another senita at upper right, one *Stenocereus thurberi* between the two senitas, and many saguaros in the background on the opposite side of Senita Basin Road.

constraints of determinate growth, as with *Melocactus* Link & Otto. *L. schottii* is able to produce viable flowers and fruits from old areoles of pseudocephalia and are able to simultaneously produce multiple flowers and fruits per areole (Gibson and Nobel 1986)l. Could this rapid elongation of reproductive shoots and subsequent breakage of overly tall shoots be another maladaptive trait, such as with abscission of pseudocephalia on the closely related *Backebergia militaris* (Audot) Bravo ex Sánchez-Mej., tiponchi, synonym *Pachycereus militaris* (Audot) D.R. Hunt (Mauseth et al. 2005)?

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