ORGAN PIPE CACTUS, *STENOCEREUS THURBERI*, WITH FLESHY LEAVES ON SPHERICAL SHORT-SHOOTS THAT HAVE INDETERMINATE GROWTH

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Abstract: *Neoraimondia* have short-shoots comprised of a large areole with indeterminate growth ('Kurztriebcephalien'). Flowers of some other cacti are subtended by modestly large photosynthetic leaves. Many specimens of the organ pipe cactus, *Stenocereus thurberi*, seem to have all these traits: large short-shoots with indeterminate growth and fleshy photosynthetic leaves. Short-shoots in organ pipe cactus grow new photosynthetic leaves at their apical meristem and sometimes flower, branch, and form discrete areoles with new spines. However, unlike short-shoots in *Neoraimondia*, spherical short-shoots of *Stenocereus thurberi* seem to retain chlorenchyma and lack extensive cork development.

Keywords: *Stenocereus*, cactus, short-shoot, spur-shoot, leaf

INTRODUCTION

Organ Pipe Cactus National Monument in southern Arizona is a remarkable place to see four species of massive cacti that are far more common on the Sonora side of the border: the eponymous organ pipe cactus (*Stenocereus thurberi*; Fig. 1), senita (*Pachycereus schottii* = *Lophocereus schottii*), saguaro (*Carnegiea gigantea*; Figs. 1, 2), and Colville's barrel cactus (*Ferocactus emoryi*; Fig. 3). But what is most striking is the number of *Stenocereus thurberi* with small spherical protuberances attached to areoles, which make plants superficially look monstrose or diseased, although neither descriptor seems to be accurate. Approximately 1–5% of the organ pipe cacti in that National Park that I saw — which was admittedly an unsystematic and tiny anecdotal survey — have these spherical protuberances, covering many but not all areoles. Plants with this odd phenotype not only were relatively common and otherwise quite healthy looking, but sometimes in easy-to-find locations. One of these was a massive specimen surrounded by a circle of pavement at the Twin Peaks Campground entrance, where a park ranger checks campers in and collects camping fees (Figs. 4–6). Because of this, I am surprised that such spherical protuberances on areoles have never been documented in this species. Some individuals with spherical protuberances were in disturbed conditions, such as in tailings at the Victoria Mine entrance. But other specimens with spherical protuberances, which I show below are short-shoots, seemed to be growing in relatively pristine conditions, such as at the north end of Senita Basin Road and along Alamo Canyon not far uphill from the campground. As the crow flies, Alamo Canyon is approximately 20 km

Figure 1. *Stenocereus thurberi, Carnegiea gigantea, Fouquieria splendens* on margins of Twin Peaks Campground.

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Figure 2. Partially cristate *Carnegiea gigantea* along Victoria Mine Trail.

Figure 3. *Ferocactus emoryi* on margins of Twin Peaks Campground.

from Victoria Mine and Senita Basin, i.e. these odd looking specimens are not confined to a single small geographic locale (Fig. 7).

What are these spherical protuberances on areoles of *Stenocereus thurberi*, what are their functions, if any, and are they related to phenomena in other species? Are the spherical protuberances enlarged areoles, enlarged flower buds, or even short cephalia as in *Neoraimondia*? To answer these questions, we must first define 'areoles'.

WHAT IS AN AREOLE?

It has been well-documented that areoles are themselves highly compressed short-shoots (Buxbaum 1950a, Gibson and Nobel 1986, Mauseth 2017a). Spines are either lignified leaves or lignified bud scales at the base of stems/subapical meristems in the short-shoot. Flowers, stems, and even roots can arise from areoles because of the usually dormant meristem(s) in these areolar short-shoots. Areoles can either have

Figure 4. *Stenocereus thurberi* at campsite fee collection booth to Twin Peaks Campground, with *Larrea tridentata* and *Jatropha cuneata*. Note slight discoloration starting about one-third of the way up long-shoots, where spherical short-shoots begin.

Figure 5. Spherical short-shoots on plant from Fig. 4.

Figure 6. Once spherical short-shoots start growing they continue all the way up the long-shoot. Same plant as Figs. 4 and 5.

determinate or indeterminate growth. This means that they either grow for a finite period of time, often a season or less, (this is determinate growth) or they keep growing forever or for a long time (which is indeterminate growth). *Melocactus* and *Echinocereus* are two examples of the many cacti that usually have determinate growth of their areoles: individual areoles do not change as they age from year to year. By contrast, cacti such as *Opuntia* and *Espostoa* subgenus *Thrixanthocereus* have indeterminate growth of their areoles, hence they often develop a shaggy and disheveled appearance as their spines grow longer and more numerous on old areoles.

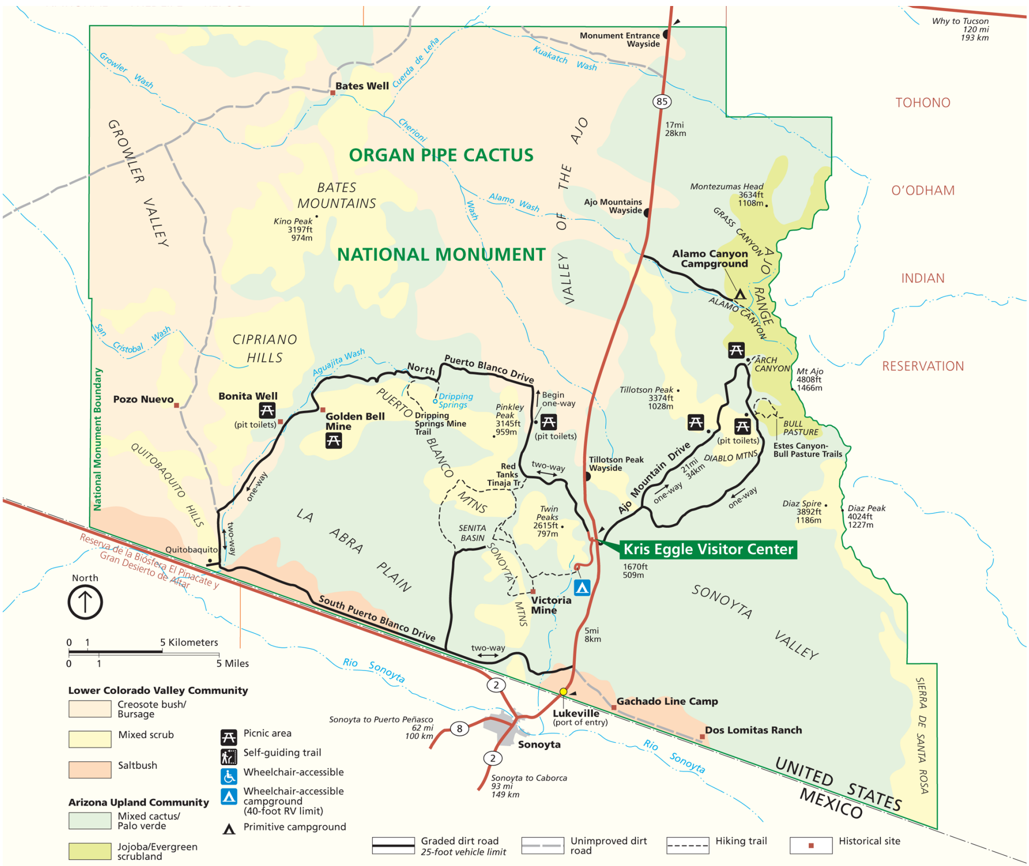

Figure 7. Map of Organ Pipe Cactus National Monument (https://www.nps.gov/orpi/planyourvisit/upload/Park-Map-2015-2.pdf). The light blue tent icon indicates the Twin Peaks Campground.

One distinguishing feature of an areole, as compared with long-shoots, is that an areole usually has a continuous covering of trichomes, therefore the areole looks like a single discrete entity. There are exceptions, such as the bifurcated areoles in *Mammillaria* and *Ariocarpus*, where only the two ends of a long linear areole have trichomes, but these are the exceptions, with intermediate cases such as a thin connecting bridge of trichomes between the two ends of the linear or barbell-shaped areole in *Coryphantha* and *Glandulicactus* (Buxbaum 1950a).

A few cacti have very large elongate areoles with indeterminate growth. These include all species of *Neoraimondia*, including *Neocardenasia*, which is often subsumed in *Neoraimondia*, and several species of *Leptocereus*, at least those formerly included in *Neoabbottia*, such as *L. quadricostatus* (Rauh 1957, Mauseth and Ross 1988, Mauseth and Kiesling 1997). Their areoles tend to grow for the life of the long-shoot on which they reside. Furthermore, flowers only arise from these large elongate areoles. *Leptocereus quadricostatus* also has short spherical areoles that appear to have determinate growth and do not flower. Developmental dimorphism in areoles on a single long-shoot is something that is also known in *Coleocephalocereus*. In *C. goebelianus* only areoles in the cephalium have indeterminate growth, whereas in *C. aureus* all areoles in the cephalium have determinate growth (Gorelick and Machado 2012). The large elongate areoles of *Neoraimondia* have been referred to as 'Kurztriebcephalien', aka short-shoot lateral cephalia, even though these areoles occasionally de-differentiate to form highly photosynthetic long-shoots with long internodes (Rauh 1957).

What are typically referred to as flowers in cacti are also short-shoots. The fleshy leaves, areoles, and spines on the outside of flowers indicates that the true flower is buried inside a short-shoot (Buxbaum 1950b, Mauseth 2017b).

With that background, let's consider the spherical protuberances on areoles of some specimens of *Stenocereus thurberi*, and why they are short-shoots.

GROWTH OF SPHERICAL SHORT-SHOOTS IN *STENOCEREUS THURBERI*

Initial growth of spherical protuberances on *Stenocereus thurberi* areoles superficially resembles a miniature 'football chrysanthemum'. The sphere is formed by inward pointing fleshy leaves that so much resemble flower petals that at first I thought these were flower buds (Figs. 8, 9). These fleshy leaves are golden to light green in colour and probably photosynthetic. Fleshy leaves in the spherical protuberance are visibly shiny. The shininess seems to fade as leaves gradually become less turgid (Fig. 10).

Not all areoles on a long-shoot have spherical protuberances (Figs. 8, 11). Often individual long-shoots of *Stenocereus thurberi* will start growing without any spherical protuberances, but once they start growing spherical protuberances, they continue doing so for the life of the long-shoot (Fig. 4, 12). Thus, the base of a long-shoot will be devoid of these spherical protuberances, but not the apical end, except for the most recent year's growth. Long-shoots are devoid of spherical protuberances near their shoot apical meristems probably because it takes a growing season for these spherical protuberances to fully develop (Fig. 8). But still, once spherical protuberances start growing, they do not appear on every areole or at least are so severely stunted as to be unrecognizable on some areoles (Figs. 5, 8, 9, 11, 14).

Figure 8. Spherical short-shoots only grow after areoles have matured, i.e. there are no spherical short-shoots near the long-shoot apical meristem. Plant growing in tailings at Victoria Mine, but still looks perfectly healthy.

Figure 9. Close-up of Fig. 8, with fleshy leaves on spherical short-shoots.

Spherical protuberances on *Stenocereus thurberi* areoles seem to grow over time. They appear to have

Figure 10. Pair of spherical short-shoots along Alamo Canyon, near trailhead. The top short-shoot is younger and still has fleshy leaves. The bottom short-shoot is slightly older and its leaves have withered.

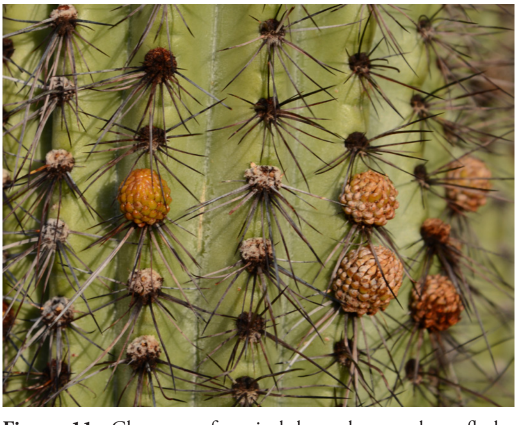

Figure 11. Close-up of typical long-shoot, where fleshy leaves on short-shoots are closer to the top of the long-shoot and not all areoles contain spherical short-shoots. Twin Peaks Campground.

Figure 12. Lower portions of both long-shoots without spherical short-shoots. But once short-shoots start forming, about one-quarter way up both long-shoots, they continue to be produced. Victoria Mine tailings.

Figure 13. Older spherical short-shoot, with withered leaves at its base and new fleshy leaves near its apical meristem, thereby showing indeterminate growth. Twin Peaks Campground.

an apical meristem from which new fleshy golden green leaves arise even after the more basal leaves have turned brown and lost their luster and possibly lost their photosynthetic ability (Fig. 13). Spherical protuberances sometimes branch (Fig. 14). It appears that flowers — or technically short-shoots with flowers embedded in them (Buxbaum 1950b, Mauseth 2017b) — form from spherical protuberances (Figs. 15). Notice how much the leaves on the outside of the floral short-shoot in Fig. 15 resemble leaves on the non-flowering spherical protuberances. This should not be surprising insofar as floral tubes in cacti supposedly arise from the areole's apical meristem, supposedly this being the terminal developmental stage in the life of an areole (Gibson and Nobel 1986). However, Gibson and Nobel (1986) also presumed only one meristem and only one flower per areole, which does not appear to be the case in *Myrtillocactus, Neoraimondia* and *Lepismium*, which often have multiple flowers per areole, sometimes even simultaneously, indicating multiple meristems per areole (Fig. 17).

Spherical protuberances appear to have grown (they are larger) as one proceeds down the rib of a plant, i.e. in chronological order. In Fig. 16, the top areole is the youngest and contains the most chrysanthemum-like spherical protuberance, completely covered in fleshy leaves. The next areole down in Fig. 16 shows further development, with loss of some leaves but with brown trichomes present between leaves. The bottom of the three areoles shows the greatest devel-

Figure 14. Branching of older spherical short-shoots. Zoomed out version of Fig. 13.

Figure 15. Floral remains arising from what appears to be a spherical short-shoot. Twin Peaks Campground along trail to visitor's center.

Figure 16. Sequential development of three spherical short-shoots. The top short-shoot is youngest, with many fleshy leaves and no visible trichomes. The middle short-shoot is of middle age, with an intermediate number of leaves and modest trichome development. The lower short-shoot is oldest, with almost no leaves, lots of trichomes, and a new spine growing from the right side of the short-shoot. Note, though, that these three short-shoots are very close together on a long-shoot with many short-shoots. This seems to be the general order of development along any given rib, but may also have occurred by chance, hence not necessarily reflecting a developmental sequence. Victoria Mine tailings.

opment, with fewer leaves, many brown trichomes, and even the growth of a new spine from the spherical protuberance. Only rarely do spherical protuberances retain most of their fleshy leaves at the time that they grow spines (Fig. 18).

In most plants of *Stenocereus thurberi*, spherical protuberances are non-existent. For those with spherical protuberances, the spherical protuberances usually remain relatively small, not obscuring the epidermis of the long shoot on which they reside. However, a few plants have greatly enlarged spherical protuberances that virtually resemble the huge Kurztriebcephalien areoles of *Neoraimondia* (Figs. 19–21). At the northern terminus of Senita Basin Road, the spherical protuberances on some plants grow to about 1 cm in diameter and contain their own multiple distinct areoles. Figures 22–26 show one of these spherical protuberances that was about 8 mm in diameter. Multiple distinct areoles, many with spines, are visible in Fig. 21. Figure 23 shows the dried-up leaves at the top of the same spherical protuberance, with the leaves surrounding the apical meristem. Fig. 24 shows the proximal side of the same spherical protuberance, with the green object being the substantial vascular connection between long-shoot and short-shoot. Figures 25 and 26 are the radial and transverse sections, respectively, of this spherical protuberance. Note the prominent vascular cylinder, obvious tubercles, heterogeneous chlorenchyma, and one large vascular trace going to the greenest portion of the tissue. The spherical protuberances are therefore unambiguously short-shoots. The spherical short-shoot in Figs. 22–26 yielded very little resistance to my knife during sectioning, indicating minimal cork formation. When cutting through cephalia in *Melocactus, Discocactus, Espostoa*, and *Coleocephalocereus*, it was much harder cutting through the cork layers than through other tissues (Gorelick 2016), so I could deduce absence of cork in *Stenocereus thurberi* short-shoots by the feel of the knife. It appears that flowers do arise from these large spherical short-shoots (Fig. 21), but it is not obvious whether multiple flowers can arise from a single such spherical short-shoot, possibly in different years. But, if multiple flowers could arise from such a spherical short-shoot, these spherical short-shoots would have as much of a right to be called cephalia or Kurztriebcephalien as those in *Neoraimondia*. [I have not discussed the short-shoot cephalia of *Leptocereus quadricostatus* and a few other members of that genus because they are apical short-shoot cephalia, not lat-

Figure 17. *Myrtillocactus geometrizans* with 5–7 flowers per areole.

Figure 18. This is the only spherical short-shoot that I noted that was growing spines while still seemingly retaining its original complement of leaves in a fleshy state. Alamo Canyon near trailhead.

Figure 19. Plant with large spherical short-shoots. Terminus of Senita Basin Road.

Figure 20. Large spherical short-shoots. Portions of this plant are shown in Figs. 21–26. Terminus of Senita Basin Road.

Figure 21. Close-up of Fig. 20 showing floral remains seemingly arising from a spherical short-shoot.

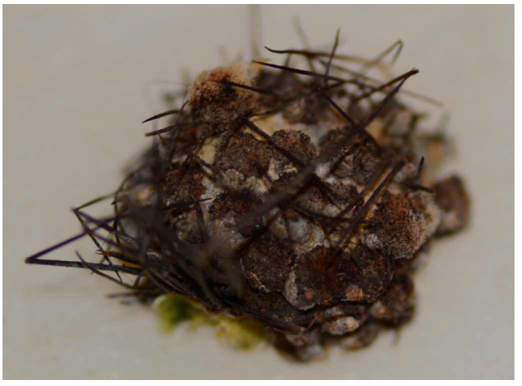

Figure 22. Side view of a large spherical short-shoot from Senita Basin. Point of attachment to long shoot is barely visible as a light green band at the bottom. Apical meristem (not visible) at the top. Note distinct areoles with spines.

Figure 23. Same large spherical short-shoot as Fig. 22, but looking down on its apical meristem at the centre.

Figure 24. Same large spherical short-shoot as Fig. 22, but looking down on the substantial yellowish-green vascular connection to the long-shoot.

eral short-shoot cephalia (Mauseth and Ross 1988).]

Note that both long-shoots and short shoots can arise from different areoles of the same long-shoot. See both on the decapitated long-shoot in Fig. 27.

ADVANTAGES AND DISADVANTAGES OF SPHERICAL SHORT-SHOOTS

An obvious advantage to spherical short-shoots in *Stenocereus thurberi* is additional photosynthetic area, both from their fleshy leaves and from the

Figure 25. Radial section of the same large spherical short-shoot as Fig. 22. Notice prominent vascular cylinder, discrete tubercles, and heterogeneous chlorenchyma.

Figure 26. Cross section of the same large spherical short-shoot as Fig. 22, with discrete tubercles.

chlorenchyma underlying the short-shoot epidermis. Young short-shoots on *Stenocereus thurberi* have so many fleshy leaves that they resemble cactus flower buds, which probably provide substantial extra photosynthesis (Mauseth 2017b). Indeterminate growth of *Stenocereus thurberi* short-shoots means that new fleshy photosynthetic leaves can be produced for several years, much like the ancient slow growth of *Neoraimondia* areoles, but with the added advantage of fixing more CO_2 into sugars. In plants such as larch (*Larix*), Atlanic cedar (*Cedrus atlantica*), and apple (*Malus domestica*), almost all leaves are produced by short-shoots called spur shoots.

When young, these spherical short-shoots are unprotected from medium-sized herbivores, but later grow spines that protect them. So, it is not obvious whether this is advantageous or not.

Lack of cork in the spherical short-shoots and presumptive presence of stomata in their leaf and shoot chlorenchyma would tend to make the plant desiccate more readily, even with CAM photosynthesis.

Some, but not all, long-shoots of *Stenocereus thurberi* underwent a noticeable change in epidermal colour at the point where spherical short-shoots first appeared (Fig. 4). This could possibly be due to the increased desiccation, but will require future investigations to fully quantify and understand this pattern.

Figure 27. Decapitated long-shoot showing both normal long-shoot development from areoles due to lack of apical dominance and spherical short-shoot development, some of which still retain somewhat fleshy leaves.

CLOSING REMARKS

It doesn't much matter whether the spherical short-shoots on *Stenocereus thurberi* are cephalia or not, especially given that all cactus areoles are short-shoots. What matters is that these spherical short-shoots in some specimens of *Stenocereus thurberi* are peculiar structures that may increase photosynthesis, albeit at the expense of water loss. Like cactus 'flowers', these spherical protuberances in *Stenocereus thurberi* are short-shoots. Their resemblance to flower buds might even indicate that these spherical short-shoots are simply highly modified flower buds, with leaves, spines, and trichomes, but seemingly with indeterminate growth.

Given the peculiar nature of these spherical short-shoots, which have otherwise only been noted in the Cactaceae from cephalia, it is surprising that *Stenocereus thurberi* short-shoots have not been previously described. This lack of reporting is striking given that plants with spherical short-shoots are fairly common and in easy-to-reach locations, such as the entrance gate to the 208-spot camp Twin Peak campground, with 174 spots for huge recreational vehicles, along with flush toilets and hot showers. And the plants with the most massive, *Neoraimondia*-like, spherical short-shoots are growing by the one major grove of senita (*Pachycereus schottii*) in the United States (Parker 1989). These are definitely not obscure, rare, diminutive, nor cryptic plants that contain spherical short-shoots. There are still lots of surprises out there if we just stop and patiently look around.

There are many remaining questions. Why do only some specimens of *Stenocereus thurberi* produce spherical short-shoots? How wide-spread is this phenomenon, over geographic scales and within a given locale? *Stenocereus thurberi* is native throughout most of Sonora and Baja California Sur, as well as parts of Baja California, Sinaloa, Chihuahua, and Arizona (Turner et al. 1995). Once a long-shoot starts producing spherical short-shoots does it always continue producing them? What triggers short-shoots to start growing? Are short-shoot leaves and chlorenchyma photosynthetic, with stomata and without cork? Why are the short-shoots that some individual plants produce more massive than others, especially when they seem to start as being large from a year's growth down from the long-shoot apical meristem? Why do spherical short-shoots branch? Do spherical short-shoots ever produce multiple flowers/floral shoots, either in a single year or across multiple years? Why hadn't I noticed any of this nor asked the above questions when I had been living in Arizona?

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