The *Coryphantha sneedii* complex is indeed complex and continuously intergrades with *Coryphantha vivipara*

Root Gorelick

Department of Biology, School of Mathematics & Statistics, and Institute of Interdisciplinary Studies, Carleton University, 1125 Raven Road, Ottawa, Ontario K1S 5B6 Canada.
email: root.gorelick@carleton.ca

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Abstract: The *Coryphantha sneedii* complex is a confusing assemblage of the following intergrading or ill-defined varieties: *orcuttii, organensis, sandbergii, villardii, albicolumnaria, leei, guadalupensis, sneedii*, and possibly other undescribed taxa. These varieties comprise a continuum of morphological forms, many with overlapping or proximate distributions, and with some morphological variability possibly arising from phenotypic plasticity to the point that the various variety names are not warranted. There is also debate about geographic range of varieties, e.g. is the type variety actually found in Carlsbad Caverns National Park, Big Bend National Park, and Bishop's Cap. Not only is it impossible to consistently distinguish individual plants of the different varieties of *Coryphantha sneedii* (Britton & Rose) A. Berger, but it is also sometimes impossible to distinguish them from the sympatric *Coryphantha vivipara* (Nuttall) Britton & Rose, especially from *C. vivipara* var. *neomexicana* (Engelmann) Backeberg. *Coryphantha vivipara* and *C. sneedii* are distinguishable from all other species of *Coryphantha* by their 0.5–1.0 mm diameter lenticular druses and usually (but not always) having green fruits/pericarpels, but these two species with overlapping distributions are not always clearly distinguishable from one another. I therefore propose subsuming the entire *Coryphantha sneedii* complex as a single variety of *C. vivipara*.

Keywords: Big Bend National Park, Carlsbad Caverns National Park, *Coryphantha sneedii*, *Coryphantha vivipara*

INTRODUCTION

When I lived in Las Cruces, New Mexico in the 1990s, I did not understand the *Coryphantha sneedii* complex. Since moving away from New Mexico in 1998, I have returned several times to study this lovely group of cacti that seem to have radiated from the Organ and Franklin Mountains. I explored from Anthony's Nose, north through Anthony Gap, North Anthony's Nose, Filmore Gap, Bishop's Cap, Peña Blanca, Achenbach Canyon, Soledad Canyon, Dripping Springs, and Baylor Pass, even once the east side of the Organ Mountains with permission to enter the Fort Bliss bombing range and its buffer zone. But I still do not understand the *C. sneedii* complex.

The *Coryphantha sneedii* complex is complex for at least two reasons. First, this complex contains many highly variable taxa, spread over a fairly large geographic range. Second, at least in the heart of this complex, from the southern Organ Mountains to northern Franklin Mountains, other *Coryphantha* species grow sympatrically, some of which are vegetatively indistinguishable from *Coryphantha sneedii* (Britton & Rose) A. Berger [synonym *Escobaria sneedii* Britton & Rose], unless you section a shoot to examine druses. *Coryphantha sneedii* and the closely related *C. vivipara* (Nuttall) Britton & Rose and the unrelated *Echinocereus stramineus* (Engelmann) F. Seitz [synonym *E. enneacanthus* var. *stramineus* (Engelmann) L.D. Benson] — all three of which grow in the Organ and Franklin Mountains — contain 0.5–1.0 mm diameter lenticular (lens-shaped) druses (calcium oxalate crystals) throughout their cortex and pith (Zimmerman, 1985, Zimmerman & Parfitt, 2004). The Mohave Desert endemics *C. alversonii* (Coulter) Orcutt and *C. chlorantha* (Engelmann) Britton & Rose, which should probably both be reduced to synonyms of *C. vivipara* var. *rosea*, also have 0.5–1.0 mm lenticular druses, but are geographically far from any forms of *C. sneedii* (Benson, 1969, 1982; Zimmerman, 1985). In, "plants of *C. vivipara* [and *C. sneedii*], cross-sections of the lower (oldest) parts of the stems appear to be filled with whitish sand owing to the accumulation of these crystal aggregates" of giant lenticular druses (Zimmerman 1985: 297). All other *Coryphantha* species, including *Escobaria*, have spherical (not lenticular) druses that are 0.1–0.4 mm in diameter, except for *C. hesteri* Y. Wright that has intermediate-sized lenticular druses. Note that in *Coryphantha* sensu lato "all druses are more numerous in wild plants than in cultivated ones" (Zimmerman 1985: 140). While large lenticular druses are a great diagnostic character that is always available, even when plants are not in flower or fruit, I am reluctant to slice open the

Figure 1. *Coryphantha sneedii* var. *sneedii*, Anthony's Nose, Franklin Mountains State Park, Texas (11 June 2012). Each shoot 1.5–2.5 cm diameter. Note lack of small shoots, which is unusual for this variety unless it only has one or a few shoots.

Figure 2. *Coryphantha sneedii* var. *sneedii*, Anthony's Nose, Franklin Mountains State Park, Texas (1 May 2005). Note both large shoots (1.5–2.0 cm diameter) and small shoots, with flower buds only on the largest shoot.

Figure 3. *Coryphantha sneedii* var. *sneedii*, Anthony's Nose, Franklin Mountains State Park, Texas, with both large and small shoots (16 August 2017). Largest shoot ca. 2.3 cm diameter.

base of a cactus shoot to identify a plant by size and shape of its druses, especially of an endangered plant like *C. sneedii*.

I will first show the morphological variation in the *Coryphantha sneedii* complex. There is a quite a bit of variation given that these are all small, mostly white-spined, and mostly clumping plants. Next, I will briefly describe sympatric *C. sneedii* look-alikes, both in the heart of the range by the Texas-New Mexico border just east of the Rio Grande, as well as in the Big Bend region, such as *C. vivipara*, *C. dasyacantha* (Engelmann) Orcutt, and *C. tuberculosa* (Engelmann) Britton & Rose. Some of these are what Zimmerman (1985: 346) called "important misidentifications". At least *C. robustispina* (Schott ex Engelmann) Britton & Rose and *C. macromeris* (Engelmann) Britton & Rose, which are sympatric with *C. sneedii* var. *sneedii*, are very easily distinguishable from both *C. sneedii* and *C. vivipara*.

Plants in the *Coryphantha sneedii* complex usually have small flowers that do not open very wide, with bright yellow anthers and white stigma lobes. They typically have greenish fruits/pericarpels. These flower and fruit/pericarpel traits are sometimes, but not always, useful for distinguishing *C. sneedii* sensu lato from congeners.

I must provide a few precautionary caveats. I have not seen *Coryphantha sneedii* var. *guadalupensis* (S. Brack & K.D. Heil) A.D. Zimmerman because of scheduling trips to the Guadalupe Mountains — i.e. to Carlsbad Caverns National Park and Guadalupe National Park — during federal shutdowns. I have not seen *C. sneedii* var. *sandbergii* because of never obtaining permission to enter secured parts of White Sands Missile Range. Therefore, I may be inadvertently misidentifying some of the plants pictured herein, and not just differing with others about naming conventions, e.g. whether *Escobaria guadalupensis* S. Brack & K.D. Heil is synonymous with the type variety/subspecies of *C. sneedii* (Baker & Johnson, 2000). [At species rank, *Escobaria guadalupensis* should probably be called *Coryphantha guadalupensis*, however that binomial has never been published, but at least there exists the properly published variety name *Coryphantha sneedii* var. *guadalupensis* (S. Brack & K.D. Heil) A.D. Zimmerman]. I consider *Escobaria* to be a synonym, vis-à-vis a subgenus, of *Coryphantha* (Gorelick, 2015, 2020), as do many North American botanists (e.g. Benson, 1982; Zimmerman, 1985; Zimmerman & Parfitt, 2004; Powell & Weedin, 2004; Allred, 2010).

CORYPHANTHA SNEEDII — SUBSPECIES AND VARIETIES

Coryphantha sneedii (Britton & Rose) A. Berger **var. *sneedii*** A.D. Zimmermann

The type variety *Coryphantha sneedii* var. *sneedii* (or, alternatively, type subspecies) is possibly endemic to the Franklin Mountains and Bishop's Cap (Zimmerman, 1985), but see the next section for a contrary view (Baker, 2004 [2007]) in which the

Figure 4. *Coryphantha sneedii* var. *sneedii*, Anthony's Nose, Franklin Mountains State Park, Texas (16 August 2017) with matching rose-colored epidermis and limestone. Largest shoot ca. 2.5 cm diameter. It is possible, but untested, that illegal collecting of plants was done more often when plant epidermis did not match the color of native limestone simply because such plants were easier for people to find.

type variety is supposedly common in parts of the Guadalupe Mountains in Eddy County, New Mexico. The Guadalupe Mountains are approximately 180 km east of the Franklin Mountains, with the intervening Tularosa Basin being inhospitable habitat for *C. sneedii*. Plants at Bishop's Cap may be putative hybrids between *C. sneedii* var. *sneedii* and *C. tuberculosa* (Zimmerman, 1985). Bishop's Cap is 8 km from the northern end of the Franklin Mountains and 1.5 km from the southwest end of the Organ Mountains. In many parts of the Franklin Mountains that have not been overrun by humans and on appropriate limestone substrate, the type variety of *C. sneedii* is still relatively common.

Coryphantha sneedii var. *sneedii* is usually highly branched; spines snowy white, with reddish tips that quickly fade to white; shoots spherical to slightly columnar, about 1–2 cm diameter; offsets several, smaller. Spines are sufficiently dense that the shoot epidermis is barely visible (Figs. 1–4). The epidermis is usually dark green when plants are actively growing (Figs. 5–6), but rose colored if the plant is stressed, such as due to lack of rains (Fig. 4). I have only ever seen plants wedged in cracks in limestone that is as white as the plant's spines, albeit limestone with some rose colored hues that can match the epidermal color and spine tip color of *C. sneedii* var. *sneedii*, as well as of the sympatric *Epithelantha micromeris* (Engelmann) F.A.C. Weber ex Britton & Rose. *C. sneedii* var. *sneedii* has also been reported from more mesic environs, such as growing in "a shady area near a mountain spring where the soil is so damp that moss thrives nearby" (Champie, 1974: 43).

Champie (1974: 44) provided the following report of a two-foot (60 cm) diameter clump of *Coryphantha sneedii* var. *sneedii* in the Franklin Mountains:

Figure 5. *Coryphantha sneedii* var. *sneedii* in cultivation in North Kawartha, Ontario (14 June 2020). This is a fairly large diameter shoot (3.0 cm) with very visible green epidermis probably because of mesic conditions.

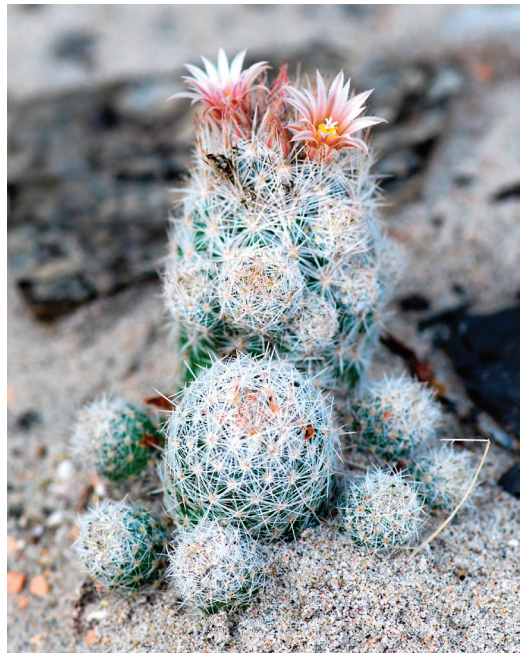

Figure 6. *Coryphantha sneedii* var. *sneedii* (SB 173) in cultivation in Ottawa, Ontario with candy-striped pink flowers and both large and small shoots (25 May 2007). Largest shoot 7 × 3 cm, which is atypically large for plants in habitat.

> A plant of the latter size was found in the Franklins by the author, growing upside down in a wash, with light reflected from the white limestone rock being sufficient to keep it in a normal state of growth. Perhaps even more remarkable was the fact that this giant-sized plant was facing north.

If a 60 cm clump were circular, tightly packed with 2 cm diameter large shoots, with no neotenic small shoots, then the clump would contain 900 shoots. With only tightly packed neotenic small shoots, which are usually about 0.5 cm in diameter, a 60 cm diameter clump of *C. sneedii* var. *sneedii* would contain 14,400 shoots. The assumption of shoots being tightly packed means these are over-

Figure 7. *Coryphantha sneedii* var. *sneedii*, Anthony's Nose, Franklin Mountains State Park, Texas (28 February 2020). The camera lens cap is 7 cm in diameter and the entire plant is 20 cm in diameter with over 100 shoots. Several other equal size clumps of *C. sneedii* var. *sneedii* still exist at this locale as of 28 February 2020.

estimates of the number of shoots by a factor of 2 to 4. The largest clumps I have seen are about one-third the diameter of what Champie (1974) found. Approximately 100 shoots are visible in Figure 7 of a 20 cm diameter clump of *C. sneedii* var. *sneedii* from Anthony Gap (Fig. 7). Scaling up from the plant in Figure 7, a 60 cm diameter clump would have about 900 shoots.

Coryphantha sneedii var. *sneedii* grows from the base to the peak of the Franklin Mountains, an elevation range of 4,000–7,000 ft (1,220–2,134 m), but is only found in some locales therein (Champie, 1974). Zimmerman (1985: 344) asserted that, "At least in Dona Aña County, New Mexico, *C. s. sneedii* is always found on or within a few meters of Silurian-Ordovician-Cambrian limestone (S-O-C) — in contrast to *C. tuberculosa*, which occurs indiscriminately on both S-O-C limestone and the relatively abundant Pennsylvanian, Mississippian, and Devonian limestone that is nearby." It pays looking at a geological map before looking for the type variety of *C. sneedii*.

Flowers of *Coryphantha sneedii* var. *sneedii* only appear on the large shoots and often do not open very far. Flower color is variable between individuals (Figs. 5, 6, 8). The original description by Britton & Rose (1923: 56) mentioned flower color could be either pink or "saffron", i.e. golden orange. Champie (1974: 44) notes that "the flowers are a pale pink or pinkish-brown." Tepals usually have a darker mid-stripe. Pinkish-brown flowers are sometimes also found on *C. sneedii* var. *villardii* (Fig. 20).

Regarding *Coryphantha sneedii* var. *sneedii* in El Paso, Texas, "The fruit, from the first flowering, which matures by August is mostly light green in color but occasionally, a yellowish pink. The author has seen one plant with a deep pink or scarlet fruit" (Champie, 1974: 44). Thus, fruit color in the type variety of the *C. sneedii* complex is variable and not necessarily green, as is often claimed.

Plants of *Coryphantha sneedii* var. *sneedii* pictured here in habitat were all from Franklin Mountain State Park in Texas, less than 0.5 km from the New Mexico state line (Figs. 1–4, 7). While apparently

Figure 8. *Coryphantha sneedii* var. *sneedii* in cultivation in Tempe, Arizona with brick-red flowers and both large and small shoots (27 April 2005). Flowering shoots ca. 2.5 cm diameter.

this was a well-known locale that had been plundered by collectors (Zimmerman, 1985), I found numerous plants there from 2006–2020. The 20 cm diameter clump (Fig. 7) was still there in February 2020, as were several other clumps of equal size. At this locale, *C. dasyacantha* (Engelmann) Orcutt, *Epithelantha micromeris*, and *Glandulicactus uncinatus* (Galeotti) Backeberg var. *uncinatus* (Engelmann) Backeberg, and *C. sneedii* var. *sneedii* grow within a dozen meters of one another (Gorelick, 2006). *C. sneedii* was also fairly common on Bishop's Cap, assuming that these plants were not putative hybrids.

INTRODUCTION TO REST OF THE *CORYPHANTHA SNEEDII* COMPLEX

The best guide to *Coryphantha sneedii* complex is still Allan Zimmerman's 1985 PhD dissertation, with distribution maps on pages 337–338 and 381–382. Others may quibble with some of his notions, such as whether plants in the Guadalupe Mountains that resemble the type variety of *C. sneedii* are actually *C. sneedii* var. *guadalupensis* or whether *C. sneedii* var. *villardii* (Castetter, P. Pierce & K.H Schwerin) A.D. Zimmerman exists in Doña Ana County, NM, as claimed by Ferguson (1998e), or whether *Coryphantha sneedii* var. *organensis* A.D. Zimmerman [synonym *Coryphantha organensis* D.A. Zimmerman] is a synonym of *Coryphantha sneedii* var. *orcuttii*. But Zimmerman (1985) is a fabulous start to understanding the confusing *C. sneedii* complex.

Zimmerman (1985) showed the center of distribution of the *Coryphantha sneedii* complex in the Franklin Mountains and nearby Bishop's Cap, i.e. where the type variety is located. According to Zimmerman (1985), to the north lies *C. sneedii* var. *organensis* in the Organ Mountains, and, farther north, *C. sneedii* var. *sandbergii* in the San Andres Mountains. To the east-northeast lies *C. sneedii* var. *villardii*, in the southwestern Sacramento Mountains. To the east lies *C. sneedii* var. *leei* (Rose ex Bödeker) L.D. Benson and *C. sneedii* var. *guadalupensis* in the Guadalupe Mountains, possibly along with *C. sneedii* var. *sneedii* and intermediates. *C. sneedii* var. *guadalupensis* was the one taxon that was not yet described when Zimmerman submitted his 1985 PhD thesis, but was formally recognized by Heil & Brack (1986) the following year. About 300 km southeast of the Franklin Mountains lies *C. sneedii* var. *albicolumnaria* (Hester) A.D. Zimmerman, in and around Big Bend. To the south of *C. sneedii* var. *sneedii* in the Franklin Mountains lies a pair of unnamed varieties of *C. sneedii*, in the state of Chihuahua, that Zimmerman (1985) simply labeled varieties #1 and #2. Finally, to the west lies *C. sneedii* var. *orcuttii* in the Florida, Hatchet, Peloncillo, and Chiricahua Mountains.

There is another view that *Coryphantha sneedii* var. *sneedii* also exists in the Guadalupe Mountains of Eddy County, New Mexico, near *C. sneedii* var. *leei* and *C. sneedii* var. *guadalupensis*, and exists there in huge numbers (Heil & Brack, 1985, Baker & Johnson, 2000). Heil & Brack (1985) reported over 100,000 specimens of *C. sneedii* var. *sneedii* in Carlsbad Caverns National Park. I will discuss this population after discussing *C. sneedii* varieties *leei* and *guadalupensis*. A far less authoritative source (Anon., 2000) reported *C. sneedii* var. *sneedii* in Culberson and Hudspeth Counties, Texas, as well as in the Lincoln National Forest in New Mexico, but did so without citation, so should be dismissed.

Baker (2004 [2007]) asserted that the evolutionary center of radiation of the *Coryphantha sneedii* complex was in Carlsbad Caverns National Park because this locale had the greatest number of individuals and the greatest amount of morphological diversity. A center of radiation for the *C. sneedii* complex in Carlsbad Caverns National Park is no more nor less defensible than the center being in the Franklin Mountains. For plants, centers of diversity often differ from centers of origin (Cain, 1944). Plus, the Franklin/Organ/San Andres Mountains, which form one continuous chain created by the Rio Grande Rift zone — have incredible morphological diversity for the *C. sneedii* complex. While the Guadalupe Mountains supposedly have *C. sneedii* var. *leei, C. sneedii* var. *sneedii, C. guadalupensis*, and putative hybrids between the latter two species (Baker, 2004 [2007]), the Franklin/Organ/San Andres Mountains have *C. sneedii* var. *sneedii, C. sneedii* var. *organensis* [synonym *C. sneedii* var. *orcuttii*], and *C. sneedii* var. *sandbergii*, and possibly *C. sneedii* var. *villardii*, as well as a putative hybrid between *C. sneedii* var. *sneedii* and *C. tuberculosa* var. *tuberculosa*. Morphological diversity often arises from environmental variation, such as unusual and varied edaphic conditions, which partly explains the diversity of flora on California serpentine soils, odd morphologies of cacti on novaculite limestone in the Marathon Basin of Texas (see below for some examples), and the possible yellow spine color of *C. sneedii* var. *organensis* on igneous rocks in the Organ Mountains. Because of the great morphological diversity of the *C. sneedii* complex in areas surrounding Bishop's Cap and Anthony Gap, my gestalt is to place the centre of diversity and center of radiation of the *C. sneedii* complex in the Franklin/Organ/San Andres Mountains. Herein, I show photos with huge amounts of vegetative morphological diversity amongst *Coryphantha*s in the documented range of the *C. sneedii* complex, possibly including some *C. vivipara* and *C. tuberculosa* look-alikes, demonstrating that classification of this group is complex. Because of this morphological diversity, Baker (2004 [2007]: 16) is probably correct that "identification at the varietal level based on a single individual within *E*[*scobaria*] *sneedii* may not always be possible."

Morphological diversity with lots of endemism is expected in areas such as northern parts of the Chihuahuan Desert Region because this is a relatively young desert with many 'sky islands' (Smith & Farrell, 2005). Late Pleistocene glaciation occurred as far south as Sierra Blanca, New Mexico (Richmond, 1964), which is approximately 30 km north of the current range of *Coryphantha sneedii* var. *villardii*. The area currently circumscribed by the northern Chihuahuan Desert contained mesic woodlands until 11,000–8,000 years ago; grasslands from 8,000–4,500 years ago; and desert for only the past 4,000 years (Van Devender, 1986). But it is also difficult inferring secondary contact between *C. sneedii* and *C. vivipara* insofar as *C. vivipara* migrated relatively quickly during the late Holocene, as far as southern Canada.

I will start by assuming, *in arguendo*, that it is possible to distinguish distinct varieties of *Coryphantha sneedii*. However, I tend to agree with Patrick Alexander (n.d.) that this "species has previously been split up into a several indistinct species, but I won't bother with these as they are obnoxious & not recognized in the *Flora of North America*." Separate varieties may be indistinguishable for the entire *C. sneedii* complex, a point also made by Baker & Johnson (2000) and Baker (2004 [2007]) for the small stemmed taxa of varieties *sneedii*, *leei*, and *guadalupensis*.

Coryphantha sneedii var. *organensis*

(D.A. Zimmerman) A.D. Zimmerman

Coryphantha sneedii var. *organensis* was originally described as a separate species, *C. organensis* D.A. Zimmerman, from high elevation igneous rocks on Fort Bliss Army Base in the central Organ Mountains (Zimmerman, 1972b). When originally described, it was apparently the only member of the *C. sneedii* complex that did not grow on limestone and was unique in having golden or sulphur yellow

Figure 9. *Coryphantha sneedii* var. *organensis* (with white spines) and *Echinocereus coccineus* Engelmann var. *rosei* (Wooton & Standley) W. Blum & Rutow on cliffs overlooking waterfall at western end of Soledad Canyon, along BLM's Soledad Canyon hiking trail (12 March 2020).

Figure 11. *1.Coryphantha sneedii* var. *organensis* (SB 823) in cultivation in North Kawartha, Ontario with bright pink flowers (28 June 2019). 4 cm diameter. Figures 10–12 are of different individuals.

central spines (Zimmerman, 1972b; Zimmerman, 1985). However, *C. sneedii* var. *organensis* was later found on limestone, in which central spines were white (Zimmerman, 1985). Figure 9 is of this taxon on Bureau of Land Management (BLM) public lands by the base of the waterfall at the western end of Soledad Canyon. *C. sneedii* var. *organensis* supposedly differs from *C. sneedii* var. *sneedii* by having larger shoots and fewer offsets, much like varieties *sandbergii*, *villardii*, and *orcuttii*. Plants of *C. sneedii* var. *organensis* start to offset upon reaching flowering size at about 2.5 cm (1 inch) diameter, and then offset almost as much as typical plants of *C. sneedii* var. *sneedii* (Figs. 9–10). Spines are not particularly yellow on cultivated plants with Steve Brack's collection number SB 823 (Figs. 10–12), although the spines are yellow while still growing (Fig. 12). [Steve Brack was a remarkable purveyor of cactus seeds for over 45 years. He and a small trusted network of associates, such as Ralph Peters and Dave Ferguson, collected seeds in habitat, which Steve then cultivated for sale of the next generation of seeds (Mygatt,

Figure 10. *Coryphantha sneedii* var. *organensis* (SB 823) in cultivation in Ottawa, Ontario with dark pink flowers resembling those of *C. vivipara*, as well as with white (not yellow) spines and many small shoots resembling those of *C. sneedii* var. *sneedii* (25 May 2007). Large shoot 5 cm diameter.

Figure 12. *Coryphantha sneedii* var. *organensis* (SB 823) in cultivation in North Kawartha, Ontario (28 May 2017). Note the yellow color of newly grown spines, a color that is not retained in maturity here, possibly because this plant is growing in metamorphic river rock, rather than igneous rocks of the Organ Mountains. 4 cm diameter.

2007).] *Coryphantha sneedii* var. *organensis* may be phenotypically plastic with regards to edaphic conditions. "*C. sneedii* var. *organensis* itself is polymorphic with respect to spine-color; its centrals can be tan, brown, or white, in addition to yellow" (Zimmerman, 1985: 407). "*E*[*scobaria*] *organensis* is distinct as a whole, it may be difficult to assign some plants in the population to a specific taxon without the aid of geographic information. In particular, *Escobaria organensis* intergrades with *E. sneedii* var. *sneedii* in the northern Franklin Mountains. *Escobaria organensis* is also difficult to distinguish from *E. sandbergii* that occurs in the San Andres Mountains to the north" (Ferguson, 1998a). I cannot morphologically distinguish the four varieties *sandbergii*, *villardii*, *orcuttii,* and *organensis* — for a similar view see Butterworth (n.d.) — therefore the oldest name at that rank should have priority, which is *C. sneedii* var. *orcuttii*.

Figure 13. *Coryphantha sneedii* var. *sandbergii,* San Andres Mountains, White Sands Missile Range (3 April 2010). Photo courtesy of Patrick Alexander.

Coryphantha sneedii var. *sandbergii*

(Castetter, P. Pierce & K.H. Schwerin) A.D. Zimmerman

Like *Coryphantha sneedii* var. *organensis*, *C. sneedii* var. *sandbergii* grows only at relatively high elevations, albeit about 10–15 km farther north of *C. sneedii* var. *organensis*, but on limestone rather than mostly on igneous rocks. *Coryphantha sneedii* var. *sandbergii* has large shoots and relatively few of them. *Coryphantha sneedii* var. *sandbergii* grows exclusively on the western side of the San Andres Mountains in the White Sands Missile Range, from the ridge at San Andres Peak at 7,400 ft (2,256 m) down the western slope to at least 6,000 ft (1830 m). I have not seen this taxon because of never obtaining permission to enter White Sands Missile Range, but have included photos courtesy of Patrick Alexander (Figs. 13–14).

From a conservation perspective, the large portions of the southeastern Organ Mountains and virtually contiguous San Andres Mountains that lie within the White Sands Missile Range and Fort Bliss buffer zones are a blessing. While it took me a few months to secure a 48-hour window for exploring the Fort Bliss buffer zone, there were no signs of any bombs or military hardware in the buffer zone, thereby forming a large protected natural area. This was made up for by huge amounts of exploded and unexploded ordinance in the adjacent Tularosa Basin. If the White Sands Missile Range buffer zone is similar, populations of *Coryphantha sneedii* var. *sandbergii* and *C. sneedii* var. *organensis* are in great conservation shape.

Figure 14. *Coryphantha sneedii* var. *sandbergii,* San Andres Mountains, White Sands Missile Range, New Mexico (9 February 2010). The white columns of these five shoots strikingly resemble *C. sneedii* var. *albicolumnaria*. Photo courtesy of Patrick Alexander.

Figure 15. *Coryphantha sneedii* var. *villardii* (labeled *Escobaria villardii*). Photo courtesy of Tyler Johnson, from the New Mexico Rare Plants website (http://nmrareplants.unm.edu/rarelist_single.php?SpeciesID=87), with permission to reproduce granted by Daniela Roth. Compare with Figure 16.

Figure 16. *Coryphantha vivipara*, western flank of Peña Blanca, Organ Mountains, New Mexico (9 March 2016). 5 cm diameter. This specimen looks almost identical to Figure 15 of *C. sneedii* var. *villardii*, the latter of which is known from the southwestern Sacramento Mountains and possibly the northern Franklin Mountains of New Mexico, but not the Organ Mountains. The individual in Figure 16 is not an outlier, but is part of the morphological continuum of *C. vivipara* on the western flank of Peña Blanca. This indicates either a range extension for *C. sneedii* var. *villardii* or that *C. sneedii* var. *villardii* is indistinguishable from *C. vivipara*.

Coryphantha sneedii var. *villardii*

(Castetter, P. Pierce & K.H. Schwerin) A.D. Zimmerman

In terms of vegetative morphology, *Coryphantha sneedii* var. *villardii* seems identical to varieties *sandbergii, orcuttii*, and *organensis*. Zimmerman (1985: 413) wrote:

> At least in their vegetative parts, some short-spined individuals of var. *villardii* are more or less identical to typical plants of var. *sandbergii* and brown- or white-spined individuals of var. *organensis*. However, the majority of the *villardii* plants are identifiable without flowers, at least with practice. The flowers of var. *villardii* average slightly larger and seem to be consistently wider-throated than those of any other variety of *C. sneedii*, but these differences are slight and possibly not always consistent.

The holotypes of both *C. sneedii* var. *villardii* (*Bob Reeves* 3984) and *C. sneedii* var. *sandbergii* (*Prince Pierce* 3409) are of sterile specimens without flowers or fruits. The primary distinguishing feature of *C. sneedii* var. *villardii* is that it is found on western slopes of the southern Sacramento Mountains, separated from varieties *sandbergii* and *organensis* by about 75 km of the Tularosa Basin, which is inhospitable habitat for *C. sneedii*.

The New Mexico Rare Plants website (Ferguson, 1998e) tentatively notes that *Coryphantha sneedii* var. *villardii* can also be found in the northern Franklin Mountains in Doña Ana County, New Mexico, albeit only noting unvouchered specimens. Furthermore,

Figure 17. *Coryphantha sneedii* var. *villardii* (labeled *Escobaria villardii*). Photo courtesy of Tyler Johnson, from the New Mexico Rare Plants website (http://nmrareplants.unm.edu/rarelist_single.php?SpeciesID=87), with permission to reproduce granted by Daniela Roth. Compare with Figure 18.

Figure 18. *Coryphantha vivipara* in cultivation in North Kawartha, Ontario of a collection from Fremont County, Colorado (18 August 2019). 3.3 cm diameter. This specimen looks almost identical to Figure 17 of *C. sneedii* var. *villardii*, indicating that *C. sneedii* var. *villardii* may be indistinguishable from *C. vivipara*.

Figure 19. *Coryphantha sneedii* var. *villardii* in cultivation in North Kawartha, Ontario with lavender flowers (31 July 2019), much like *C. tuberculosa* in Figure 23. 3.3 cm diameter. Note the leaning shoots and narrow base of the cultivated plants in Figures 19–20, also much like that of *C. tuberculosa*.

Figure 20. *Coryphantha sneedii* var. *villardii* in cultivation in North Kawartha, Ontario, 3.3 cm diameter shoot, with pinkish-brown flowers (26 July 2019), a color morph that is akin to what Champie (1974) described for the flower color morphs of *C. sneedii* var. *sneedii* in the Franklin Mountains.

Ferguson (1998e) stated, "Most, if not all populations of *E*[*scobaria*] *sneedii* var. *sneedii* and var. *leei* contain a few individuals that lack small, clustered sterile stems (a characteristic of *E. villardii*). If such an individual with unusually long reddish spines were taken from a population of *E. sneedii* var. *sneedii*, it could be identified as *E. villardii*." One of New Mexico Rare Plants website photos of *C. sneedii* var. *villardii* is reproduced here with permission as Figure 15, which looks identical to plants of *C. vivipara* at the very southwest end of the Organ Mountains (Fig. 16). The plant in Figure 16 is not an outlier, but is part of the morphological vegetative continuum of *C. vivipara* on the western flank of Peña Blanca, thereby indicating that var. *villardii* is more widespread than just the Sacramento Mountains or, alternatively, that it is impossible to consistently distinguish varieties of *C. sneedii* from one another or from *C. vivipara*. My hunch is that the latter is true, that consistent identification is impossible, especially given that another photo of *C. sneedii* var. *villardii* on the New Mexico Rare Plants website (reproduced here with permission as Fig. 17) closely resembles a cultivated specimen of *C. vivipara* [probably *C. vivipara* var. *neomexicana* (Engelmann) Backeberg] from Fremont County, Colorado (Fig. 18).

The above confusion over identification of *Coryphantha sneedii* var. *villardii* is not meant as an indictment of the New Mexico Rare Plants website nor or of the photographer, Tyler Johnson. I believe they correctly identified *C. sneedii* var. *villardii* in Figures 15 and 17, but that these plants, when not in flower, and possibly even when in flower, are indistinguishable from *C. sneedii* var. *orcuttii* and possibly indistinguishable from *C. vivipara* var. *neomexicana*.

In cultivation, *Coryphantha sneedii* var. *villardii* shoots superficially resemble *C. tuberculosa*, being fairly tall with narrow bases, shoots that lean and do not offset much. *Coryphantha sneedii* var. *villardii* also has fairly wide open flowers, compared with *C. sneedii* var. *sneedii*, while *C. sneedii* var. *villardii* flower color varies from plant-to-plant (Figs. 19–20), this is one of the few varieties of *C. sneedii* that sometimes has purplish-lavender flowers (Fig. 19) of a similar hue to that found in most plants of *C. tuberculosa* (Fig. 21). *Coryphantha tuberculosa* is ubiquitous throughout those parts of the range of the *C. sneedii* complex that are east of the Rio Grande, i.e. the range of the entire *C. sneedii* complex except for *C. sneedii* var. *orcuttii* sensu stricto.

Figure 21. *Coryphantha tuberculosa* in cultivation in Tempe, Arizona with typical lavender flowers (12 May 2005) akin to what Champie (1974) described for the flower color morphs of *C. sneedii* var. *sneedii* in the Franklin Mountains. Shoot ca.5 × 3 cm.

Coryphantha sneedii var. *orcuttii* (Bödeker) Gorelick

I will continue reviewing taxa with large shoots, beginning with the only member of the *Coryphantha sneedii* complex in the U.S. found west of the Rio Grande, *C. sneedii* var. *orcuttii*.

As traditionally circumscribed, going east to west, *Coryphantha sneedii* var. *orcuttii* is native to the (1) Florida Mountains, (2) Big and Little Hatchet Mountains, and (3) the Peloncillo and Chiricahua Mountains. In each of these three locales, *C. sneedii* var. *orcuttii* has sometimes been given separate variety names, which seems superfluous, especially because plants in these three locales cannot be morphologically distinguished from *C. sneedii* var. *organensis* and *C. sneedii* var. *sandbergii* in the Organ/San Andres Mountains nor from *C. sneedii* var. *villardii* in the Sacramento Mountains. There are probably five 'waves' of *C. sneedii* var. *orcuttii*, which, from east-to-west, are:

- *villardii* in the southwestern Sacramento Mountains
- *sandbergii* and *organensis* in the San Andres and Organ Mountains, respectively
- *orcuttii* var. *koenigii* in the Florida Mountains
- *orcuttii* var. *macraxina* in the (Big and Little) Hatchet Mountains
- *orcuttii* var. *orcuttii* in the Peloncillo and Chiricahua Mountains

Loflin & Loflin (2009) list *Coryphantha sneedii* var. *albicolumnaria* from the Big Bend of Texas region as a synonym of *C. sneedii* var. *orcuttii*, but seem to be the only authors of this opinion.

Coryphantha sneedii var. *albicolumnaria* (Hester) A.D. Zimmerman

The final member of the *Coryphantha sneedii* complex with large shoots is the disjunct *C. sneedii* var. *albicolumnaria*, endemic to the Big Bend region, far from the rest of the complex, except for maybe Zimmerman's unnamed variety #1 in neighbouring Chihuahua. *Coryphantha sneedii* var. *albicolumnaria* grows about 250 km south of *C. sneedii* var. *guadalupsensis*, which only has small shoots, and over 300 km southeast of the nearest member of the complex with large shoots, namely *C. sneedii* var. *organensis* (or *C. sneedii* var. *villardii* if it appears at Peña Blanca or the north Franklin Mountains). But, as Zimmerman (1985: 415) asserted, "a few plants of varieties *organensis*, *sneedii*, and *albicolumnaria* are (at least to me) indistinguishable from var. *villardii* unless viewed in the context of populational samples."

Compared with the rest of the *Coryphantha sneedii* complex, *C. sneedii* var. *albicolumnaria* has large and usually unbranched shoots and usually has more vibrant colored flowers (Figs. 22–23). *Coryphantha sneedii* var. *albicolumnaria* has flowers that are vibrant rose-pink to bright magenta, especially near the mid-vein of each tepal. While seemingly not common in any locale, *C. sneedii* var. *albicolumnaria* seems widespread throughout Big Bend National Park and is also found in nearby Pecos County, Texas (Powell & Weedin, 2004). The epithet *albicolumnaria* refers to a white column, which is an apt description of typical plants, albeit these are relatively short columns that are 8–25 cm tall. This description of a white column could also apply to *C. sneedii* var. *sandbergii* (see Fig. 13).

Figure 22. *Coryphantha sneedii* var. *albicolumnaria* in cultivation in Tempe, Arizona, with typical bright pink to magenta flowers, with darker pigment along the midline of each tepal (7 April 2005). Ca. 5 cm diameter.

As with *Coryphantha tuberculosa* and *C. dasyacantha*, "the fruits are crimson on some *C. sneedii* var. *albicolumnaria* and on [Allan Zimmerman's] two undescribed Chihuahuan varieties of *C. sneedii*" (Zimmerman, 1985: 330). While the two developing fruits on Figure 23 are still immature, they are clearly more pink or red than green. Thus, Big Bend has a variety of *C. sneedii* with large shoots that do not offset, robust spines, rose-pink to bright magenta flowers, and red fruits, which is probably not how Britton & Rose (1923) envisioned their newly described taxon *Escobaria sneedii*. *Coryphantha sneedii* var. *albicolumnaria* looks like an etiolated version of *C. vivipara* var. *neomexicana* (Fig. 43), with the exception that *C. vivipara* var. *neomexicana* has solid-colored tepals whereas *C. sneedii* var. *albicolumnaria* has tepals that are lighter colored away from the mid-vein.

Like everyone else, I just asserted that *Coryphantha sneedii* var. *albicolumnaria* is geographically disjunct from this rest of the complex. But is this true? There are several plants in Big Bend National Park that look almost exactly like *C. sneedii* var. *sneedii*, at least when not in flower (Fig. 24). Figure 24 and nearby plants vegetatively resemble *C. sneedii* var. *sneedii*, but may be *C. tuberculosa*. The type variety of *C. tuberculosa* tends to offset far more in the southern Big Bend region (anonymous reviewer)

Figure 23. *Coryphantha sneedii* var. *albicolumnaria*, Big Bend National Park, Mules Ears trail, approximately ¼ to ½ km from trailhead (27 May 2011). 9 × 4 cm. Note the large fuzzy white areoles on new growth and developing fruits, which are pink, not green. There had been no measurable precipitation for the preceding ten (10) months that included three record hard freezes, so new growth and incipient fruits were surprising, especially given that this plant did not seem to be growing near water nor in shade.

Figure 24. Either *Coryphantha sneedii* var. *sneedii* or *C. tuberculosa*, with both large and small shoots, Big Bend National Park, Texas, along north side of main park road just west of Boquillas Tunnel (26 April 2011). Largest diameter shoots ca. 3.0–3.5 cm. Specimens of *C. tuberculosa* tend to be highly branched at Big Bend. Extreme drought and recent extreme cold (see Figure caption 23) possibly meant no fruits nor flowers to easily distinguish *C. sneedii* from *C. tuberculosa*.

Figure 25. *Coryphantha tuberculosa*, Big Bend National Park, along north side of main park road just west of Boquillas Tunnel, about 10 m from Figure 24 (26 April 2011). Note what look like both large and small shoots. Largest diameter shoots ca. 3 cm.

Figure 26. *Coryphantha tuberculosa*, near Shafter, Texas (24 April 2011). Largest diameter shoots ca. 2.5 cm. Note rose-colored epidermis so often seen on *C. sneedii* var. *sneedii* at Anthony Gap (compare with Fig. 4). This plant, like those at Big Bend, had been stressed by a long drought and record freezes.

with both large and small shoots (Fig. 25), than it does farther north (Figs. 30–32) and sometimes even gets the rose-colored epidermis so often seen on *C. sneedii* var. *sneedii* at Anthony Gap (compare Figs. 4 and 26). The only hint in the literature of *C. sneedii* var. *sneedii* occurring in Big Bend is the distribution map for that taxon in Loflin & Loflin (2009), who only list two varieties of *C. sneedii* in Texas — varieties *sneedii* and *albicolumnaria* — the latter of which they considered to be a synonym of *C. sneedii* var. *orcuttii*. Their map probably contains a large inadvertent error here because they show an extensive distribution for *C. sneedii* var. *sneedii* in Big Bend without any comment in their text.

Figure 27. *Coryphantha sneedii* subsp. *leei* in cultivation in North Kawartha, Ontario (9 August 2019). Note deflexed spines and no large shoots on this clump. The largest shoot is 0.9 cm in diameter.

Figure 28. *Coryphantha sneedii* subsp. *leei* in cultivation in North Kawartha, Ontario (9 August 2019). Note spreading spines and presence of both large and small shoots. The largest shoot is 1.6 cm in diameter.

Coryphantha sneedii* var. *leei (Rose ex Bödeker) L.D. Benson

The remaining named taxa in the *Coryphantha sneedii* complex are found in the Guadalupe Mountains: *C. sneedii* var. *leei*, *C. sneedii* var. *guadalupensis*, and possibly *C. sneedii* var. *sneedii*.

Coryphantha sneedii var. *leei* is a taxon of rare diminutive plants from a small geographic area at low elevations in the northeastern Guadalupe Mountains, in Eddy County, New Mexico, near Carlsbad Caverns. Heil & Brack (1985) report that only 1,000–2,000 individuals exist in its native range. It is likely a highly localized neotenic form, much as *Pediocactus knowltonii* L.D. Benson is likely a highly localized neotenic form of *P. simpsonii* (Engelmann) Britton & Rose. *P. knowltonii* not only possesses diminutive shoots, but also diminutive slender spines. *C. sneedii* var. *leei* clearly has diminutive shoots, but it is not obvious that its spines are particularly diminutive, even on the smaller shoots, despite the claim that "juvenile spination is retained throughout the life of the plant" (Ferguson, 1998d). *Coryphantha sneedii* var. *leei* resembles *C. sneedii* var. *sneedii* in having some relatively large flowering shoots in addition to smaller non-flowering shoots. However, some plants of *C. sneedii* var. *leei* only have small shoots (Fig. 27). Compared with *C. sneedii* var. *sneedii*, *C. sneedii* var. *leei* has more small (neotenic) shoots, which are smaller than those in *C. sneedii* var. *sneedii*. *C. sneedii* var. *leei* can have up to 250 such tiny shoots, whereas supposedly *C. sneedii* var. *sneedii* usually has fewer than 100 total shoots (Zimmerman, 1985).

Spines on *Coryphantha sneedii* var. *leei* may be either spreading (Fig. 28) or highly appressed (Fig. 27), with this trait being consistent within an individual plant. In the latter instance, "all spines are highly appressed (with the exception of some inner centrals), even reflexed toward the stem, resulting in a knobby appearance of the stem" (Powell & Weedin, 2004: 422). Some authors, however, only consider specimens with highly appressed or deflexed spines (e.g. Fig. 27) to be *C. sneedii* var. *leei*. For example, Baker (2004 [2007]: 17) stated that:

> They [Heil & Brack, 1985] separate the two taxa based on spine orientation, *E. sneedii* var. *leei* having deflexed spines and *E. sneedii* var. *sneedii* having spreading spines. An alternate view suggests (Zimmerman 1993 [which is an unpublished letter to Karen Lightfoot that is on file at the Forestry and Resource Conservation Division of New Mexico]) that differences in morphology among populations of *E. sneedii* within CCNP [Carlsbad Caverns National Park] may due to introgression stemming from hybridization between *E. sneedii* var. *leei* and *Escobaria guadalupensis*, or that these intermediate forms represent ancestral populations from which both *E. sneedii* and *E. guadalupensis* have radiated.

Spine orientation — whether spreading or deflexed — seems to be variable in many cacti [e.g. *Echinocereus reichenbachii* (Terscheck) J.N. Haage], even in seedlings grown from a single fruit, therefore this single character should probably not be diagnostic of a variety. See my concluding remarks for a more general critique of using spination to classify cacti. Baker (2004 [2007]: 21) noted, "The taxonomic recognition of *E. sneedii* var. *leei*, as separate from that of *E. sneedii* var. *sneedii*, was shown to be tenuous." The same could probably be said for all varieties and subspecies in the *Coryphantha sneedii* complex.

In cultivation outdoors in Ontario, some clones of *Coryphantha sneedii* var. *leei* largely die back to below ground level each winter and then regrow new aboveground shoots each spring. The specimen that I have been growing for the longest (Fig. 29) typically has only a few shoots each year, all less than 1.0 cm tall and 0.6 cm in diameter, almost all of them newly grown each spring. The spreading spines and existence of a few longer central spines on this specimen of *C. sneedii* var. *leei* with Steve Brack's collec-

Figure 29. *Coryphantha sneedii* subsp. *leei* (SB 397) in cultivation in North Kawartha, Ontario (27 July 2019). The largest shoot is 0.6 cm in diameter and about 1.0 cm tall. Note the spreading spines and numerous central spines. This plant has survived for five winters in Canada, usually dying back to ground level each winter, then producing a few above ground shoots each summer. This plant resembles a largely unbranched *C. sneedii* var. *sneedii*, but only with small shoots. Note Steve Brack's collection number for this specimen.

tion number SB 397 also make it resemble *C. sneedii* var. *sneedii* and — even more so — *C. sneedii* var. *guadalupensis*.

Coryphantha sneedii* var. *guadalupensis (S. Brack & K.D. Heil) A.D. Zimmerman

Coryphantha sneedii var. *guadalupensis* is the most recently described taxon in the *C. sneedii* complex, initially described as *Escobaria guadalupensis* S. Brack & K.D. Heil. It is a localized endemic to the highest peaks in Culberson County, Texas, in the southwestern portion of the Guadalupe Mountains, in Guadalupe Mountains National Park (Heil & Brack, 1986). It is characterized by having only a few small shoots per plant and living at an elevation of 6,500–8,700 ft (2,000–2,650 m). A typo in the original description has this taxon growing to an elevation of 12,650 m, which is 43% taller than Mt Everest.

Coryphantha sneedii var. *sandbergii* and *C. sneedii* var. *organensis* grow at an elevation similar to that of *C. sneedii* var. *guadalupensis* (Zimmerman, 1972b, Castetter et al., 1975, Zimmerman, 1985, Ferguson, 1998a,b). The only morphological difference between the two taxa from the San Andres/Organ Mountains (varieties *sandbergii* and *organensis*) and *C. sneedii* var. *guadalupensis* from the Guadalupe Mountains is that *C. sneedii* var. *guadalupensis* has smaller shoots and often has shorter length and smaller diameter spines. But those differences are minimal. In general, cactus clones when grown in both warm and cold environments are much smaller in the cold environment (Gorelick & Gorelick, 2021), something that Weniger (1969) documented in *Echinocereus triglochidiatus* var. *gonacanthus* (Engelmann & J.M. Bigelow) Boissevain. Given that *C. sneedii* var. *guadalupensis* looks very much like a high elevation morph of several different varieties of the *C. sneedii* complex, could this taxon from Guadalupe Mountains National Park in Texas simply be an example of phenotypic plasticity in the *C. sneedii* complex, sensu Clausen, Keck, and Hiesey's (1948) study of *Achillea* from sea level at San Francisco Bay to the peaks of the Sierra Nevada in California?

Coryphantha sneedii* var. *sneedii in the Guadalupe Mountains?

Several researchers consider there to be a large population of over 100,000 individuals of *Coryphantha sneedii* var. *sneedii* in Carlsbad Caverns National Park, just west of the single small population of *C. sneedii* var. *leei*, some within 50 m of *C. sneedii* var. *leei* (Heil & Brack, 1985; Baker & Johnson, 2000; Baker, 2004 [2007]), although Baker & Johnson are candid that several of these plants may be hybrids. By contrast, Powell & Weedin (2004) and Powell, et al. (2008) consider *C. sneedii* var. *sneedii* to be endemic to the Franklin Mountains and nearby Bishop's Cap. Others consider this large population of plants in Carlsbad Caverns National Park to be an intermediate form, possibly a hybrid, between *C. sneedii* varieties *leei* and *guadalupensis* (Ferguson, 1998c,d). Ferguson's comments here are particularly insightful and partly rely on the morphometric analysis of Baker & Johnson (2000):

> Although the population of *E*[*scobaria*] *sneedii* var. *sneedii* is distinct as a whole, it may be difficult to assign some plants in the population to a specific taxon without the aid of geographic information and this variation continues to present difficult taxonomic problems. For example, plants from the Guadalupe Mountains that intergrade between *E. sneedii* var. *leei* and *E. guadalupensis* are morphologically indistinguishable from *E. sneedii* var. *sneedii* of the Franklin Mountains (Baker and Johnson 2000).
>
> — Ferguson (1998c)

> Although the population of *E*[*scobaria*] *sneedii* var. *leei* is distinct as a whole, it may be difficult to assign some plants to a specific taxon without detailed analysis because it intergrades with *E. guadalupensis* that is found at higher elevations toward the southern end of the Guadalupe Mountains (Baker and Johnson 2000). Some call these intermediate plants *E. sneedii* var. *sneedii*.
>
> — Ferguson (1998d)

If the only way to distinguish taxa is by their geographic locales, then there is no need to assign separate names at the rank of variety or species. If the only way to distinguish taxa is by examining aggregations of individuals, rather than individuals themselves, then we are taking a non-Darwinian approach to classification. Such an approach is probably not warranted in *Coryphantha sneedii*, in which it is entirely unambiguous what constitutes an individual

Figure 30. *Coryphantha tuberculosa*, Anthony's Nose, Franklin Mountains State Park, Texas, with its typical bright red fruits (16 August 2017). Shoot ca. 3 cm diameter.

Figure 31. *Coryphantha tuberculosa*, Anthony's Nose, Franklin Mountains State Park, Texas (1 May 2005). Note deciduous areoles near base, which happens frequently with this species. Largest shoot ca. 2.5 cm diameter.

because *Coryphantha* species are never clonal (despite Thomas Nuttall's claims about vegetative viviparity in *C. vivipara*), unlike many clonal species of *Opuntia* and *Cylindropuntia*.

Regarding the *Coryphantha sneedii* complex in the Guadalupe Mountains, Zimmerman's (1985: 333) noted that, "the one pair of taxa co-occurring in a single mountain range (*leei* and a form of var. *sneedii*, in the Guadalupe Mountains [subsequently known as var. *guadalupensis*]) form an array of intermediates and polymorphic populations (one of which was once claimed to be a case of sympatry, but I do not share this interpretation; cf. discussion under var. *leei*), with the two 'extreme' phenotypes confined to opposite ends of the mountain chain".

SYMPATRIC PLANTS THAT LOOK LIKE *CORYPHANTHA SNEEDII*

Thus far, we have seen plants from Big Bend and Carlsbad Caverns National Parks that are vegetatively indistinguishable from *Coryphantha sneedii* var. *sneedii* in the Franklin Mountains. We have seen plants that supposedly are *C. sneedii* varieties *organensis, sandbergii, villardii*, and *orcuttii* that are vegetatively indistinguishable from one another and from *C. vivipara*. There are many plants that grow alongside or nearby the varieties of *C. sneedii* that look just like them, unless plants are in fruit or we start measuring druses in sectioned shoots. *Coryphantha sneedii* often, but not always, has greenish fruits and always has many large (0.5–1.0 mm) lenticular druses. In the United States and Chihuahua, in the genus *Coryphantha* sensu lato (i.e. including *Escobaria*), only *C. vivipara* and *C. sneedii* have large lenticular druses and only these two species and some populations of *C. tuberculosa* have green fruits/pericarpels (Zimmerman, 1985; Zimmerman & Parfitt, 2004; Hunt et al., 2006). In this respect, *C. vivipara* and *C. sneedii* are distinguishable from all other species of *Coryphantha*, but are not always distinguishable from one another.

Coryphantha tuberculosa (Engelmann) Britton & Rose

Coryphantha tuberculosa grows sympatrically with *C. sneedii* in most of its range except for southwestern New Mexico, where *C. sneedii* var. *orcuttii* sensu stricto is found. *Coryphantha tuberculosa* can be distinguished by its red (not green) fruits (Fig. 30), lavender flowers (Fig. 21), and smaller more spherical druses. *Coryphantha tuberculosa* shoots are often, but not always, narrowest at their base, something also seen with *C. sneedii* var. *villardii* and *C. sneedii* var. *sandbergii*. *Coryphantha tuberculosa* shoots often, but not always, have deciduous spines/areoles near their base (Fig. 31). *Coryphantha tuberculosa* has fewer spines per areole than *C. sneedii*, so often has a more visible epidermis (Fig. 32). But still, when not in flower, some specimens of *C. tuberculosa* are virtually indistinguishable from *C. sneedii*. Some specimens of what I think are *C. tuberculosa* in the New Mexico portion of the Franklin Mountains (Figs. 33–34) closely resemble *C. sneedii* var. *organensis*, *C. sneedii* var. *villardii*, and even *C. vivipara* and *C. dasyacantha*. Like *C. sneedii* and *C. vivipara*, some populations of *C. tuberculosa* seem to consistently have green fruits (Zimmerman, 1985).

Coryphantha tuberculosa is a wide-ranging species — in the states of Chihuahua, Coahuila, Durango, Nuevo León, Texas, and New Mexico — that sometimes goes by the synonym *C. strobiliformis* (Poselger) Moran. Zimmermann (1985) noted that Poselger's material of *C. strobiliformis* was comprised of at least two distinct taxa: the wide-ranging *C. tuberculosa* and the more narrow-ranging *C. strobiliformis* in Chihuahua and Durango. Hunt, et al. (2006) argued that this confusion and misapplication of the epithet justifies that *C. strobiliformis* be called *C. chihuahuensis* (Britton & Rose) A. Berger, whose range does not overlap with that of *C. sneedii*, except possibly with Allan Zimmerman's unnamed *C. sneedii* var. #2.

Figure 32. *Coryphantha tuberculosa*, Anthony's Nose, Franklin Mountains State Park, Texas (16 August 2017). Presence of both large and small shoots, however, indicates that this might possibly be *C. sneedii* var. *sneedii*, which grows just up the hill on much more exposed limestone outcrops. Larger shoots ca. 3 cm diameter; smaller shoots ca. 1.5 cm diameter.

Figure 33. *Coryphantha tuberculosa*, Anthony's Nose, Franklin Mountains State Park, Texas (1 May 2005). Vegetatively, this specimen very closely resembles *C. dasyacantha*, which also grows here (see Figs. 35–36). Largest shoot ca. 4 cm diameter.

Figure 34. The three shoots on the right are *Coryphantha tuberculosa*, at Anthony's Nose, Franklin Mountains State Park, Texas. The three shoots on the left are either *C. tuberculosa* or *C. sneedii* var. *sneedii*. Largest diameter shoot ca. 2.5 cm.

Figure 35. *Coryphantha dasyacantha*, Anthony's Nose, Franklin Mountains State Park, Texas (1 May 2005). This is at the range limit for this species, just south of the New Mexico border. Largest diameter shoots 3.5–4.0 cm.

Figure 36. *Coryphantha dasyacantha*, Anthony's Nose, Franklin Mountains State Park, Texas (11 June 2012). While superficially resembling some plants of *C. tuberculosa*, the large number of spines per areole and the four inner central spines per areole with bulbous bases indicates that this is probably *C. dasyacantha*. Largest shoot ca. 3.5 cm diameter.

Coryphantha dasyacantha (Engelmann) Orcutt

In northern portions of the Franklin Mountains, when not in flower or fruit, *Coryphantha dasyacantha* (Figs. 35–36) closely resembles some of the larger forms of *C. sneedii*, such as varieties *orcuttii, organensis, sandbergii*, and *villardii* (Gorelick, 2006). Red fruits, green stigmas, and small spherical druses are the only traits that distinguish *C. dasyacantha* from larger forms of *C. sneedii*. Like *C. sneedii*, *C. dasyacantha* has small spherical shoots that readily offset and have dense spination, to the point that Allred (2010) attributed all reports of *C. dasyacantha* in New Mexico to be *C. sneedii*. Note that I previously believed that *C. dasyacantha* was found in New Mexico (Gorelick, 2006), but this population at Anthony Gap is, in fact, in Texas, approximately 100–200 m from the New Mexico border, at the northern edge of Franklin Mountains State Park — I had previously misjudged location of the state border.

Figure 37. *Coryphantha tuberculosa* var. *varicolor*, Big Bend National Park, Texas, main road south of Paint Gap (27 April 2011). Ca. 9 × 4 cm.

Coryphantha tuberculosa* var. *varicolor (Tiegel) A.D. Zimmerman

[synonym: ***Coryphantha dasyacantha* var. *varicolor*** (Tiegel) L.D. Benson]

Coryphantha tuberculosa var. *varicolor* is a largely non-offsetting (i.e. usually single-stemmed) form of *C. tuberculosa*, but this could be a plastic response to edaphic conditions of growing on igneous or metamorphic rocks rather than the more typical sedimentary limestones (Zimmerman & Parfitt, 2004). The still existing controversy about whether this is a valid variety and of which species — *C. tuberculosa* versus *C. dasyacantha* — indicates how confusing *Coryphantha* taxonomy is in the Chihuahuan Desert. Typical forms of *C. tuberculosa* var. *varicolor* (Fig. 37) vegetatively resemble the sympatric *C. sneedii* var. *albicolumnaria* (Fig. 23) in the southern Big Bend region (Powell & Weedin, 2004), with shoots often twice as tall (6–10 cm) as wide (3–5 cm). There are also short flat-topped forms of *C. tuberculosa* var. *varicolor*, where each shoot is approximately 3–4 cm in diameter, but only about 1.5 cm tall. These short flat-topped forms typically grow on novaculite formations near Marathon, just north of Big Bend National Park (Figs 38–39). Novaculite is an igneous substrate in which many cacti take on miniature forms, such as *Coryphantha minima* Baird, *Thelocactus bicolor* (Galeotti) Britton & Rose subsp. *flavidispinus* (Backeberg) N.P. Taylor, and *Echinocereus viridiflorus* Engelmann var. *davisii* (Houghton) W.T. Marshall (Benson, 1982, Weniger, 1984, Powell & Weedin, 2004, Powell, et al., 2008, Konings & Konings, 2009). Figures 38–39 are not *Thelocactus bicolor* var. *flavidispinus*, which also grows at this locale south of Marathon, with much larger and more visible areoles, more colorful and thicker spines, and shoots that never offset (Fig. 40). The short flat-topped form of *C. tuberculosa* var. *varicolor* is also found on sedimentary rocks near Shafter, just east of Big Bend National Park (Fig. 41), indicating that this morphology is not just due to edaphic plasticity. I have not seen *C. tuberculosa* var. *varicolor* in flower or fruit, but vegetatively it looks as though they could be a truly aberrant form of *C. sneedii*.

Figure 38. *Coryphantha tuberculosa* var. *varicolor*, short flat-topped form on novaculite outcrop 4 miles south of Marathon, Texas (28 April 2011). Ca. 1.0 × 3.0 cm.

Figure 39. *Coryphantha tuberculosa* var. *varicolor*, short flat-topped form on novaculite outcrop 4 miles south of Marathon, Texas (28 April 2011). Largest shoot ca. 1.5 × 3.5 cm.

Figure 40. *Thelocactus bicolor* var. *flavidispinus*, on novaculite outcrop 4 miles south of Marathon, Texas, a few meters from Figures 37–38 (28 April 2011). Ca. 1.0 × 2.5 cm.

Figure 41. *Coryphantha tuberculosa* var. *varicolor*, near Shafter, Texas (24 April 2011). Largest shoot ca. 1.5 × 4.0 cm. This short flat-topped form is usually found on novaculite outcrops, a rock type that does exist near Shafter.

Figure 42. *Coryphantha vivipara*, in cultivation in North Kawartha, Ontario, of a collection from central New Mexico (9 August 2019). 5.0 cm diameter.

Figure 43. *Coryphantha vivipara* in cultivation in North Kawartha, Ontario of a collection from 7500 ft (2286 m) elevation in southern Colorado (22 June 2020). 5.0 cm diameter. This is probably *C. vivipara* var. *neomexicana* based on its pale stigma lobes and white spines (Zimmerman 1985).

Coryphantha vivipara (Nuttall) Britton & Rose

Many plants in the Organ Mountains, especially on western alluvial fans, could be identified as either *C. sneedii* var. *organensis* or *C. vivipara* var. *neomexicana* — compare Figures 12 and 16. Both C. *sneedii* and *C. vivipara* have a huge amount of vegetative morphological variation. Both C. *sneedii* and *C. vivipara* have numerous 0.5–1.0 mm diameter lenticular druses and usually have green fruits/pericarpels. This resemblance is striking for forms of *C. vivipara* var. *neomexicana* with many snowy white spines per areole (Figs. 42–44), including specimens from the far western flanks of Peña Blanca in the southwestern Organ Mountains (Fig. 44). There is no geographic separation between these two species — wherever one finds *C. sneedii* sensu lato, one also finds *C. vivipara* (Zimmerman, 1985). Several plants ostensibly of *C. vivipara* at Anthony Gap offset readily with only small shoots (Fig. 45). "A direct phenetic link to *C. sneedii* is provided by some plants of *C. vivipara* var. *neomexicana*, which sometimes are difficult to identify in vegetative condition because their spine-clusters are so similar to those the largest varieties of *C. sneedii*." (Zimmerman 1985: 223–224). While fruits, seeds, flowers, and shoots of *C. sneedii* are generally smaller than those of *C. vivipara* (Zimmerman, 1985), it is not obvious that such a size difference warrants separate species, especially because there is a large overlapping range of sizes of shoots, flowers, and fruits/pericarpels. Given the extraordinary similarities between these two taxa in the southern edge of *C. vivipara*'s vast range from Mexico to Canada, *C. sneedii* sensu lato should probably be reduced to a synonym of *C. vivipara*, albeit as a new variety.

Figure 44. *Coryphantha vivipara*, western flank of Peña Blanca, Organ Mountains, New Mexico (9 March 2016). Largest shoot ca. 8 × 4 cm. This specimen resembles both *C. sneedii* var. *villardii* and *C. sneedii* var. *organensis*.

Figure 45. *Coryphantha vivipara*, north side of State Route 404, Anthony Gap, New Mexico (11 March 2020). Each shoot is about 2.5 cm diameter. All shoots seem to be connected, i.e. these are not separate unbranched seedlings.

Coryphantha vivipara var. ***sneedii*** (Britton & Rose) **Gorelick, comb. et stat. nov.**

Basionym: *Escobaria sneedii* Britton & Rose. Cactaceae IV, 56; Fig. 54. 1923. Type: U.S.A. Texas. El Paso Co., Franklin Mountains: McKelligon Canyon, west side of limestone cliffs; ca. 8 miles north of El Paso [according to a letter from sometime after 27 June 1923 but before publication of Cactaceae IV in late 1923, from Mrs. S. L. Pattison of Canutillo, Texas to Joseph N. Rose, that was in reply to a first letter from Pattison to Rose that included the type specimen in February 1921]. *J.R. Sneed* s.n. (Lectotype designated by Benson, 1982, Cacti of US & Canada: *US* (on 2 numbered sheets).

Coryphantha albicolumnaria (Hester) D.A. Zimmerman, *Cact. Succ. J.* 44: 157. 1972.
Coryphantha orcuttii (Rose ex Orcutt) D.A. Zimmerman, *Cact. Succ. J.* 44: 156. 1972.
Coryphantha organensis D.A. Zimmerman, *Cact. Succ. J.* 44: 114. 1972.
Coryphantha pygmaea Frič, *Ceskoslov, Zahradnickyck Listu [Kakt. Sukk.]* 1924: 121.
Coryphantha sneedii (Britton & Rose) A. Berger var. *leei* (Rose ex Bödeker) L.D. Benson. *Cact. Succ. J.* (U.S.) 41: 189. 1969.
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Coryphantha sneedii (Britton & Rose) A. Berger var. *sandbergii* (Castetter, P. Pierce & K.H. Schwerin) A.D. Zimmerman. Systematics of genus *Coryphantha* 417. 1985.
Coryphantha sneedii (Britton & Rose) A. Berger var. *villardii* (Castetter, P. Pierce & K.H. Schwerin) A.D. Zimmerman. Systematics of genus *Coryphantha* 409. 1985.
Coryphantha strobiliformis (Poselger) Moran var. *orcuttii* (Rose ex Orcutt) L.D. Benson. *Cacti Ariz.* ed. 3, 26. 1969.
Escobaria albicolumnaria Hester. *Desert Pl. Life* 13: 129 (-132). 1941.
Escobaria guadalupensis S. Brack & K.D. Heil. *Cact. Succ. J.* 47: 165 (-167). 1986.
Escobaria leei (Rose ex Orcutt) Bödeker, *Ein Mammillarien Vergleichs-Schluessel* 17. 1933.
Escobaria orcuttii Rose ex Bödeker, *Ein Mammillarien Vergleichs-Schluessel.* 17, 1933.
Escobaria orcuttii (Rose ex Orcutt) Bödeker var. *koenigii* Castetter, P. Pierce & K.H. Schwerin, *Cact. Succ. J.* 47: 68 (-69). 1975.
Escobaria orcuttii (Rose ex Orcutt) Bödeker var. *macraxina* Castetter, P. Pierce & K.H. Schwerin, *Cact. Succ. J.* 47: 66 (-68). 1975.
Escobaria organensis (D.A. Zimmerman) Castetter, P. Pierce & K.H. Schwerin, *Cact. Succ. J.* 47: 60. 1975.
Escobaria sandbergii Castetter, P. Pierce & K.H. Schwerin, *Cact. Succ. J.* 47: 62 (-64). 1975.
Escobaria sneedii Britton & Rose, *Cactaceae* 4: 56, f. 54. 1923.
Escobaria sneedii Britton & Rose subsp. *leei* (Rose ex Bödeker) D.R. Hunt. *Cactaceae Consensus Init.* 4: 5. 1997.
Escobaria sneedii Britton & Rose subsp. *orcuttii* (Bödeker) Lüthy, *Kakt. and. Sukk.* 50: 278. 1999.
Escobaria sneedii Britton & Rose subsp. *organensis* (D.A. Zimmerman) Lüthy, *Kakt. and. Sukk*. 50: 278. 1999.
Escobaria sneedii Britton & Rose var. *leei* (Bödeker) D.R. Hunt, *Cact. Succ. J. Gr. Brit. 40:* 30. 1978.
Escobaria sneedii Britton & Rose var. *orcuttii* (Bödeker) A.D. Zimmerman. Systematics of genus *Coryphantha* 369. 1985.
Escobaria villardii Castetter, P. Pierce & K.H. Schwerin, Cact. Succ. J. 47: 64 (-66). 1975.
Mammillaria sneedii (Britton & Rose) Cory. *Rhodora 38*: 407. 1936.

In this view, *Coryphantha sneedii* is simply a variety of *C. vivipara* that has smaller shoots, smaller flowers that do not open as wide, smaller fruits/pericarpels, sometimes more offsets, and sometimes more spines per areole than other varieties of *C. vivipara*.

Coryphantha vivipara var. *neomexicana* and *C. sneedii* have a large overlapping range, without any obvious edaphic or other ecological niche differences. The range of *C. sneedii* var. *albicolumnaria* also overlaps with that of *C. vivipara* var. *vivipara* in Pecos County, Texas, while the range of *C. sneedii* var. *orcuttii* overlaps with that of *C. vivipara* var. *arizonica* (Engelmann) W.T. Marshall (or an intermediate between varieties *arizonica* and *neomexicana*) in Hidalgo, Luna, and possibly far southern Grant Counties, New Mexico (Zimmermann, 1985; Powell & Weedin, 2004). I consider *Coryphantha sneedii* to be a variety, rather than a subspecies, of *C. vivipara* because of their extensive overlapping geographic ranges (Stuessy, 2009).

CONCLUDING REMARKS

The *Coryphantha sneedii* complex is a taxonomic mess. It is often impossible to decide which infraspecific taxon an individual belongs to, sometimes even if one knows its geographical origin. At this juncture, we cannot even be sure whether the type variety is endemic to the Franklin Mountains. Does the putative population on Bishop's Cap represent a hybrid between *C. sneedii* var. *sneedii* and *C. tuberculosa*? Does the putative population in Carlsbad Caverns National Park represent a hybrid between *C. sneedii* var. *leei* and

C. sneedii var. *guadalupensis*? Amongst other varieties of *C. sneedii*, the exceptions too often prove the rule. Not all specimens have green fruits, especially with *C. sneedii* var. *albicolumnaria*. Several varieties contain a few individuals whose flower color is as vibrant magenta as seen in *C. vivipara*. *Coryphantha sneedii* var. *organensis* (Figs. 9–10) may have almost as many diminutive offsets as does the type variety. This may be due to phenotypic plasticity in *C. sneedii*, as was apparent in *C. sneedii* var. *organensis*, which grows white (rather than yellow) spines when growing on limestone. It is disconcerting that we can only identify varieties of *C. sneedii* for populations, rather than for individuals, when individuals are usually considered the most important unit of selection.

At first blush, maybe we can divvy up the *Coryphantha sneedii* complex by size of shoots, with varieties *leei*, *sneedii*, and *guadalupensis* forming a group with small shoots and the remaining taxa all having large shoots. But that does not account for some of the shoots on *C. sneedii* var. *sneedii* that supposedly perfectly mimic varieties *villardii* and *sandbergii*. Likewise, we cannot parse the *C. sneedii* complex by segregating those taxa having both large and small shoots because some specimens of *C. sneedii* var. *leei* only have neotenic small shoots and some specimens of *C. sneedii* var. *sneedii* only have large shoots (which, admittedly, are still only 2–3 cm in diameter). The *C. sneedii* complex is highly variable, with continuous variation, which does not lend itself to easy classification, although there may be communication value in informally designating infraspecific and infravarietal combinations.

Things are no simpler if we want to know about phylogeny rather than just classification. There may be troubles with inferring evolutionary histories in such a highly variable and complex clade as that containing *Coryphantha sneedii* and *C. vivipara*. The key to constructing phylogenies that accurately reflect evolutionary history is identifying homologous traits (Young & Richardson, 1982). But what exactly constitutes homologies in seed plants, especially in cacti? In apples and gingkoes, does it make sense to identify as a homologous trait the number or size of leaves produced over the life of each spur-like short shoot? Probably not. But that is exactly what we do with cacti when using the number and length of spines per areoles to segregate taxa. Areoles are short shoots containing spines that are highly lignified leaves without an abscission zone (except for glochids in subfamily Opuntioideae, which do abscise; Mauseth, 2017). Does longevity of areolar meristems or shoot apical meristems constitute a homology? Does architecture of cortical bundles in subfamily Cactoideae constitute a homology? Cactus taxonomy may be muddled because we have not properly identified morphological homologies. Cactus taxonomy may also be muddled because their molecular phylogenies are often based on chloroplast genomes with the assumption of maternal inheritance of chloroplasts, even though some members of subfamily Cactoideae have biparental inheritance of chloroplasts (Corriveau & Coleman, 1988; Gorelick, 2002, 2014). Are cacti sufficiently odd that we have largely erred with choices of traits used to identify and classify cacti? Could this, in part, explain the muddled taxonomy of the *Coryphantha sneedii* complex?

The only consistent morphological difference between *Coryphantha sneedii* sensu lato and *C. vivipara* is that *C. sneedii* have smaller shoots, smaller flowers, and smaller fruits, but even then there seems to be a continuum between these two taxa. For that reason, I recommend subsuming all forms of *C. sneedii* sensu lato as a single variety of *C. vivipara*. With that, *C. vivipara* sensu lato are the *Coryphantha*s with large lenticular druses and (mostly) green fruits. Mark Porter is starting to perform a genetic analysis of the *C. sneedii* complex, using ddRADSeq analysis, using *C. vivipara* and *C. tuberculosa* as outgroups. While I am not sure that *C. vivipara* makes a good outgroup here, *C. tuberculosa* probably does. Porter's analysis will provide a way to test the ideas I have proposed here.

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NOTES

I did not collect any plants for this work and did not cut open plants in the field to examine druses. All cultivated plants illustrated herein were purchased from licensed vendors. All cultivated plants have been grown outdoors year-round in the author's garden.

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