Tephrocactus[1]

One of the abundant groups of cacti in the Andes, in terms of genera, species, and sheer number of plants, is the opuntioids. Amongst these are members of *Tephrocactus*, a genus created in 1868 by Charles Lemaire. Lemaire included eight species within the genus:

T. andicolus [unresolved name, but probably now referred to *Maihueniopsis glomerata*]
T. aoracanthus
T. calvus [= *T. articulatus*]
T. diadematus [the type, which is an unresolved name, but probably *T. articulatus*]
T. platyacanthus [= *Maihueniopsis darwinii*]
T. pusillus [unresolved name]
T. retrospinus [unresolved name]
T. turpinii [= *T. articulatus*]

Note that probably a half or more of Lemaire's *Tephrocactus* species were what we would now call *T. articulatus*, which is a widespread and phenotypically variable species.

Herein, we follow the taxonomy of Hunt (2011) and Ritz *et al*. (2012), who list the following nine species of *Tephrocactus*:

T. alexanderi (Britton & Rose) Backeberg
T. aoracanthus (Lemaire) Lemaire
T. articulatus (Pfeiffer) Backeberg
T. bonnieae (D.J. Ferguson & R. Kiesling) Stuppy
[= *Puna bonnieae* D.J. Ferguson & R. Kiesling]
[= *Maihueniopsis bonnieae* (D.J. Ferguson & R. Kiesling) E.F. Anderson]
T. molinensis (Spegazzini) Backeberg
[= *Maihueniopsis molinensis* (Spegazzini) F. Ritter]
T. nigrispinus (K. Schumann) Backeberg
[= *Maihueniopsis nigrispinus* (K. Schumann) R. Kiesling]
T. recurvatus (Gilmer & H.-P. Thomas) D.R. Hunt & Ritz
[= *Maihueniopsis recurvata* (Gilmer & H.-P. Thomas) R. Kiesling]
[= *Cumulopuntia recurvata* Gilmer & H.-P. Thomas]
T. verschaffeltii (F.A.C. Weber) D.R. Hunt & Ritz
[= *Austrocylindropuntia verschaffeltii* (Cels ex. F.A.C. Weber) Backeberg]
T. weberi (Spegazzini) Backeberg

However, we choose to deviate from the above authors in one respect by following Kiesling (1984, 1999) in considering *T. geometricus* (A. Castellanos) Backeberg to be a valid species, i.e. not a synonym of *T. alexanderi*. See our discussion of *T. geometricus*, below, for justification of this segregation. Also note that *T. geometricus* has never been formally named as a subspecies or variety of *T. alexanderi*. We saw seven of these ten species of *Tephrocactus* in northwestern Argentina, just in the provinces of Catamarca, Jujuy, La Rioja, Salta, and Tucumán. For distribution maps of *T. alexanderi*, *T. aoracanthus*, *T. articulatus*, *T. molinensis*, and *T. weberi* see Gilmer & Thomas (1998).

Tephrocactus formerly contained species in what we would now call *Austrocylindropuntia, Cumulopuntia, Maihueniopsis, Punotia,* and *Tunilla*, such as:

Austrocylindropuntia floccosa (Salm-Dyck) F. Ritter
Cumulopuntia boliviana (Salm-Dyck) F. Ritter
Maihueniopsis minuta (Backeberg) R. Kiesling
Punotia lagopus (K. Schumann) D.R. Hunt
Tunilla corrugata (Salm-Dyck) D.R. Hunt & J. Iliff

And, of course, virtually all species that have ever been placed in *Tephrocactus* have also been placed in the huge genus *Opuntia sensu lato*.

The genus *Tephrocactus* is mostly from northwestern Argentina. Except for the two most aberrant species—*T. nigrispinus* (which is often ascribed to *Maihueniopsis*) and *T. verschaffeltii* (which is often ascribed to *Austrocylindropuntia*)—*Tephrocactus* is endemic to the following ten provinces of northwestern Argentina (in alphabetic order): Catamarca, Córdoba, Jujuy, La Rioja, Mendoza, Salta, San Juan, San Luis, Santiago del Estero, and Tucumán. *Tephrocactus nigrispinus* is found in the provinces/regions/departments of Jujuy (Argentina), Tarapacá and probably Arica y Parinacota (Regions I and XV of Chile), and Chuquisaca (Bolivia). We found no records of *T. nigrispinus* in the Bolivian Departments of Potosí or Tarija, although it certainly might exist there. *Tephrocactus verschaffeltii* is found in the northwestern Argentine provinces of Catamarca, Jujuy, Salta, and Tucumán, as well as near the western Bolivian city of La Paz. We found no records of *T. verschaffeltii* in the Bolivian Departments of Oruro or Potosí, although it certainly might

[1]This article was to be part of the special issue on northern Argentina (2013, 85-5), but was delayed due to space considerations. Gorelick and Mahr contributed equally to this paper.

1. One of the spineless forms of *Tephrocactus articulatus*, readily showing acrotonic branching and moniliform stem segments.

2. Large, pale colored seeds of *Tephrocactus alexanderi*. In several species the dried skin of the fruit quickly deteriorates, allowing the seeds to drop to the base of the plant. Such seeds are thought to be dispersed by wind or water rather than moved by birds or rodents.

exist there given its relatively wide distribution.

The genus can be characterized as forming small clumps or mounds, usually no more than about 30–40 cm high, often much less. The stem segments are oval to elongate and often easily detached. They are also characterized by acrotonic or moniliform[2] branching (end-to-end branching at the tip of each segment, with constrictions between, resulting in the appearance of a string of beads or, in this case a stack of carefully glued golf balls) (Fig. 1). The areoles are sunken. Flowers are produced apically and usually white to light pink (but there are exceptions). The fruit is dry and without pulp, and the fruit walls when dry are parchment-like and break down readily, releasing the seeds. In many species the seeds are very large and yellowish to tan in color, somewhat resembling small dried corn seeds, and often easily found at the base of plants (Fig. 2). Molecular studies of Ritz and colleagues (2012) have somewhat redefined this group as outlined above and the interested reader is referred there for details.

Etymology—"*tephros*" from the Greek meaning ash-gray, referring to the color of the stem epidermis of some forms.

[2]Technically, acrotonic branching indicates that the most vigorous branches are at the apex of the previous branch; in the case of *Tephrocactus*, generally all of the branches are at the apex and there are no "less vigorous" stem segments lower on the same branch. Acrotonic does not refer to shape of the branch as moniliform does. *Rhipsalis* species, with long slender apical branches, also exemplify acrotonic branching.

Tephrocactus geometricus

Tephrocactus geometricus is one of the most beautiful and diminutive opuntioids in northwestern Argentina or anywhere else. It is small, spineless or weakly-spined, with pink to rose coloured stems, and plants can either be upright or ground-hugging geophytes (Figs. 3–7). It largely grows on rocky hillsides (many of which may be volcanic in origin?), in landscapes where the tallest vegetation stands no more than 10 cm. These landscapes look like they could be from the high arctic, although, in fact, these are medium-altitude (circa 2,000–2,750 m) landscapes on the eastern flank of the Andes, not far south of the Tropic of Capricorn.

Tephrocactus geometricus (which some have argued is simply a form of *T. alexanderi*) is endemic to the province of Catamarca. Purportedly, *T. geometricus* is only known from areas surrounding Angostura de Guanchín and Tinogasta, in the Department of Tinogasta (Anderson 2001; Akulova-Barlow 2007), which is consistent with the locales in which we saw this taxon, near Chaschuil and Pastos Largos, at elevations of 1,980–2,900 m.

Tephrocactus geometricus and *T. alexanderi* can be found sympatrically and both are quite variable. For example, both species have relatively short and tall forms, and both species have forms with either dark or pale spine colors. We have only seen *T. alexanderi* in flower, not *T. geometricus*. Based on vegetative characteristics, at times it is difficult to distinguish the species in the field, but this may result from our collective naivete. *T. geometricus* looks like a small and

3 & 4. Two spineless examples of *Tephrocactus geometricus* growing very closely pressed and flat to the ground at 2,750 m near Pastos Largos.

5. However, even at the 2,750 m elevation locale, some plants of *T. geometricus* grew substantially more spherical stem segments that contained modest spines.

relatively weakly spined (or spineless) form of *T. alexanderi*. Neither species has ever been formerly named as a subspecies or variety of the other. *T. geometricus* seems like a high altitude variant of *T. alexanderi*, with intergradation or difficulty in distinguishing the two species at intermediate elevations. There may also be natural hybrids where these two species are found in sympatry, but genetic testing of this has not been done. It would be fascinating to compare epidermal anatomy of *T. geometricus, T. alexanderi*, intermediate specimens, and putative hybrids. *T. geometricus* has multiple epidermal layers and hence sunken stomata (Mauseth 2006).

Both the *New Cactus Lexicon* (Hunt et al. 2006) and James Iliff (2002) consider *T. geometricus* to be a synonym of *T. alexanderi*. By contrast, Roberto Kiesling, who has for decades been the leading expert on Argentine cacti, believes them to be distinct species. *T. geometricus* typically lacks spines or only has spines on areoles in upper portions of each stem segment (Figs. 3–7). *T. alexanderi* typically has spines on areoles throughout the stem segment except for the very base (Kiesling 1984). *T. geometricus* spines are conical, unlike the much more needle-like or cylindrical spines of *T. alexanderi*. *T. geometricus* has tubercles that are clearly delimited by a geometric furrow (hence the etymology), whereas *T. alexanderi* tubercles are not so clearly delimited by a furrow. *T. geometricus* is peculiar for a *Tephrocactus*—very much differing from *T. alexanderi*—by its profusion of flowers and apparently disproportionately greater sexual reproduction, both in the field and in cultivation (Kiesling pers. comm. and our own observations). *T. geometricus* has the more flattened seeds of the two species and seed surface patterning more closely resembles that of *T. articulatus* than *T. alexanderi* (Kiesling 1999; Iliff 2002). Likewise, Jacques Lambert (1997) and Guillermo Rivera (pers. comm.) consider these to be two separate species. Curiously, British authors consider these to be a single species, while authors from Argentina and those who have focused on Argentine cacti consider these to be separate species. *Ceteris paribus*, we tend to side with local expertise, hence consider *T. geometricus* to be a valid species. But, the beauty of plant taxonomy is that both perspectives can be considered valid, especially because of the impossibility of a rigourous plant species concept.

Variation in appearance of *Tephrocactus geometricus*, or of any species, can be due to several factors: stage of development (is the plant mature or a seedling?), genetic effects, environmental effects (including soil, water, temperature, competitors), and interactions between these. For example, phenotypic plasticity measures how much appearance depends on the interaction between genetics and the environment. Given that there is diversity of appearance of *T. geometricus*, even in a tiny geographic patch, this species probably has lots of genetic variation and plasticity (compare Fig. 4 with Fig. 5 or compare Fig. 6 with Fig. 7). For another example, even if two stem segments are genetically perfectly identical, they can look different. Even a little more water or a little more shade can make a big difference in appearance

6 & 7. At an elevation of 2,000 m, on the road from Fiambala to the Chilean border and Copiapó, we only saw the more spherical form of *T. geometricus,* some specimens with spines and some completely spineless. Nonetheless, the plants here and elsewhere are always geophytes, with branching occurring below ground level.

of plants, something that we become acutely aware of when trying to cultivate these plants. Spineless clones of *T. geometricus* often grow apical spines in cultivation (Kiesling pers. comm.). Notice that some of the figures show incredible variation within an apparent clone, from large spherical spined stem segments to short flattened spineless ones.

Like many opuntioids, *Tephrocactus* species can reproduce both sexually (via pollination, fertilization, seeds) and asexually (via stem segments detaching and subsequently taking root). For the flattened geophytic specimens of *T. geometricus*, there is also the possibility that large clumps are connected underground, possibly later disconnected as a colony grows, although this probably has never been verified. Both sexual and asexual reproduction, however, can result in copious variation (Gorelick and Heng 2011; Gorelick 2012). Similar magnitudes in genetic diversity due to sexual and asexual reproduction have been documented in several plant families, the most poignant of which may be another important plant in northwestern Argentina: the wine grape (Myles et al. 2011). Sexual reproduction usually results in variation at very small genetic scales, while asexual reproduction results in variation at a larger genetic scale, such as chromosomal rearrangements and duplications, both of which can cause morphological change (Heng 2009; Gorelick and Heng 2011; Gorelick and Olson 2013), such as height of a plant or number and size of spines.

The specimens of *T. geometricus* pictured here (Figs. 3-7) were all from alongside Route 60, the highway that runs from Tinogasta to Copiapó, Chile, although these plants were all living between Angostura de Guanchín (2,100 m) and Pastos Largos (2,800 m). At these locations we saw it growing with *Cumulopuntia boliviana, Denmoza rhodacantha, Echinopsis leucantha, Maihueniopsis minuta, Pterocactus megliolii, Reicheocactus bonnieae, and Tephrocactus bonnieae.*

Etymology—"*geometricus*" refers to the shape of the tubercles, which are in the form of polygons.

8 & 9. Two examples of growth forms of *Tephrocactus alexanderi*. Plants rarely get more than 4-5 stem segments high.

Tephrocactus alexanderi

Britton and Rose (1923) named and described *T. alexanderi* (as *Opuntia alexanderi*) in the appendix to volume 4 of *The Cactaceae*. A specimen was sent to them by W. B. Alexander who collected it in La Rioja province, where we saw it as well. In total we saw it at five locations in northern La Rioja and southern Catamarca provinces, ranging from about 650 to 1,700 m elevation. It is also recorded from San Juan and San Luis provinces (Hunt et al 2006) and Salta province (Anderson 2001).

At all of our locations *T. alexanderi* presented itself as an easily recognizable species. It is a clumping (Fig. 8) or mound-forming (Fig. 9) species, with very oval stem segments usually about 4–8 cm in diameter, stacked usually no more than 3–5 high. Most clumps that we saw were well under 40 cm tall and the largest were not much broader than this. In all of our locations it was a richly-spined species with upwards of 15 spines per areole, up to 2–4 cm long. There are roughly 30–40 large prominent tubercles per stem segment, and the areoles are widely spaced, but many of the spines abruptly bend outward just above the areole,

10 & 11. Spine color of *Tephrocactus alexanderi* is variable. These photos are representative of two populations only 6 km apart and at the same elevation. One population has most plants with pale colored spines while with the other population dark-spined plants predominate. On the road to Termas de Fiambala, southern Catamarca.

12 & 13. Flower color of *Tephrocactus alexanderi* varies from pink to nearly pure white.

14. We often found *Tephrocactus alexanderi* growing in very dry areas where it was a dominant component of the vegetation.

and the spines of each cluster radiate outwards, overlapping with those of adjacent tubercles. Spine color is quite variable from pale straw-colored to charcoal gray (nearly black). Along the road to Termas de Fiambala there are populations of very dark-spined (Fig. 10) and very light-spined (Fig. 11) individuals only about 6 km apart; in both populations one spine color predominates but with a few scattered individuals of the other form, indicating variation in spine color both within and between populations. Flower color is also variable, from pink to white (Figs. 12 & 13).

Note that we consider *T. geometricus* to be a separate taxon (see above). If included within *T. alexanderi* it substantially increases the variability in spination from primarily heavily-spined (as described here) to a range all the way to totally lacking spines.

Some of the locations where we encountered *T. alexanderi* were very dry and sparsely vegetated; other places had a bit more shrubbery. In some locations it was a dominant plant species and populations were relatively dense (Fig. 14). At our various stops we found it growing with several other species of cacti including *Tephrocactus articulatus*, *Opuntia sulphurea*, *Gymnocalycium hossei*, *G. glaucum* (various forms), *Eriosyce bulbocalyx* and *Echinopsis* spp. (in the broad sense) such as *E. huascha*, *E. leucantha*, *E. strigosa*, and *E. terscheckii*, and terrestrial *Deuterocohnia* bromeliads.

Hunt et al (2006) list a few synonyms of *T. alexanderi* in addition to *T. geometricus*; these include *Opuntia bruchii*, *O. halophila*, *Tephrocactus flexuosus* and *T. microsphaericus*.

Etymology—"*alexanderi*" was named for W. B. Alexander who originally collected this species.

15. A nearly spineless form of *Tephrocactus articulatus* with easily detached stem segments, resulting in rather haphazard piles of happily growing plants, probably most of which being all of the same clone. South of Villas Bustos, La Rioja province, 950 m.

Tephrocactus articulatus

With its diversity of interesting and artistic forms, *T. articulatus* is a favorite with growers. If not the most charismatic of all the tephro species, it wins the prize as most whimsical, and it is probably the most variable, at least from the perspective of gross morphology. The great variability has resulted in a surplus of scientific names, at both the species and infraspecies levels. For example Backeberg (1977) accepted eight varieties in addition to the nominal form; many of these (and more!) were originally published as species. Modern workers, at least as reflected by the *New Cactus Lexicon* (Hunt et al. 2006), have done away with all the varietal names, an approach that we found quite understandable based on our observations. We documented this species at 10 different sites with a great range in elevation from 180 to 1,580 m, and, based on the plant communities present at these sites, from quite dry with little vegetation cover to somewhat moister with a diversity of shrubby vegetation. Not surprisingly, the plants of each of the populations we encountered were a little different from the others

16. Another nearly spineless form of *Tephrocactus articulatus*, this with more solidly joined stem segments. We referred to this as the hoodoo form, certainly a show prize winner. North of Carrizal, La Rioja province, 850 m.

17. A population of heavily spined *Tephrocactus articulatus*, probably attributable to the form referred to as '*papyracanthus*'. Such spination was quite variable from location to location; in some cases the papery spines were only in the apical half or third of the stem segment. This population was at Villa Mazan, La Rioja province, at 670 m.

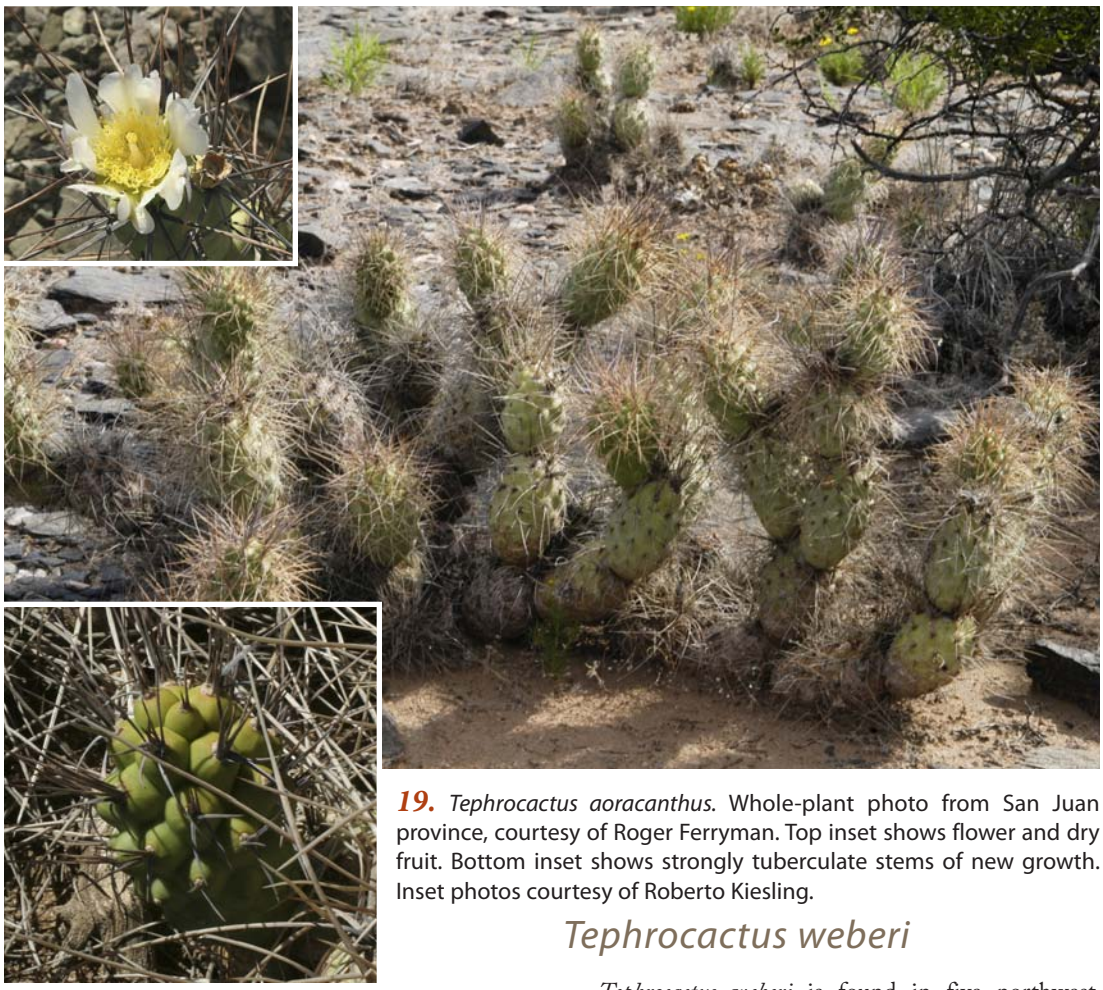
18. The flowers of *Tephrocactus articulatus* that we saw varied from white to pale pink.

when separated by at least a few kilometers. It is also the most widespread species of the genus, extending from Mendoza province in west-central Argentina through all of the northwestern provinces as far north as Salta.

The stem segments are ovoid, usually 3–5 cm long and of similar diameter, but somewhat variable as to size and shape from population to population. The individual segments can sometimes be tenuously attached and easily dislodged, another variable characteristic. For example, south of the village of Villa Bustos in La Rioja province, the stems were apparently self-pruning, with each fallen stem segment rooting and developing a new plant, resulting in low piles of stems which prompted our group to refer to it as the camel-dropping form (Fig. 15). On the other hand, northeast of Anillaco, also in La Rioja, the plants consisted of columns of precariously stacked marshmallows, a dozen or more high, suggesting a fairly firm attachment between stem segments (Fig. 16). Spination is also quite variable, ranging from totally spineless (such as Backeberg's *T. articulatus* var. *inermis* (Spegazzini) or the cultivar commonly seen in cultivation as *T. strobiliformis* (Berger) Backeberg), to a few weak, papery apical spines, to a more complete spination over each segment, and with long, flexible, twisting papery spines (the form often called var. *papyracanthus*) (Fig. 17). Even the papery spines can be variable. Most often we saw them contorted and of a tan color, but at one location they were grey and much narrower and mostly straight, and borne on stem segments that were 1.5–2.0 times longer than broad. Flower color ranges from white to light pink. Ritz et al (2012) consider *T. articulatus* most closely related to *T. aoracanthus* and *T. alexanderi* (and therefore also *T. geometricus*).

Based on its geographical, altitudinal, and climatological ranges we would expect *T. articulatus* to be growing with a diversity of other cacti, which was what we found. Associated species included *Cereus aethiops*, *Cleistocactus baumannii* ssp. *baumannii*, *Echinopsis aurea* ssp. *fallax*, *E. candicans*, *E. glauca*, *E. huascha*, *E. leucantha*, *E. strigosa, E. terscheckii*, *Eriosyce bulbocalyx*, *Gymnocalycium albiareolatum*, *G. bodenbenderianum, G. glaucum*, *G. glaucum* ssp. *ferrari*, *G. hossei*, *G. saglionis, G. schickendantzii, Opuntia quimilo*, *O. sulphurea*, *Stetsonia coryne*, *Tephrocactus alexanderi* and *T. weberi.*

Etymology—"*articulatus*" is from the Latin, meaning jointed, referring to the appearance of the attachment points of the stem segments.



19. *Tephrocactus aoracanthus.* Whole-plant photo from San Juan province, courtesy of Roger Ferryman. Top inset shows flower and dry fruit. Bottom inset shows strongly tuberculate stems of new growth. Inset photos courtesy of Roberto Kiesling.

Tephrocactus aoracanthus

T. aoracanthus is one of the three *Tephrocactus* species that we did not encounter on this trip, even though it is fairly widespread, occurring in the provinces of Córdoba, La Rioja, Mendoza, and San Juan (Fig. 19). It has ovoid stem segments up to 10 cm long with prominent tubercles that are adequately armored with spines to 12 cm or more in length. The flowers are white. Plants can stand as high as 0.5 m. Ritz et al (2012) consider it to be most closely related to *T. articulatus* and *T. alexanderi*. Gilmer & Thomas (1998) also consider it to be most closely related to *T. articulatus* and *T. alexanderi*, but morphologically indistinguishable from *T. articulatus* except for its spines. *T. aoracanthus* never has flattened spines. Instead, the surface of its spines are rounded, although usually triangular in cross section (not acicular). By contrast, *T. articulatus* always has flattened spines.

Etymology—derived from the Greek words *aor*, meaning sword, and *acanthi*, referring to spine.

Tephrocactus weberi

Tephrocactus weberi is found in five northwestern provinces from San Juan north to Salta. We saw it at four locations in Catamarca and Salta provinces, ranging in elevation from 1,100 to 1,800 m. Most of these sites were rather dry appearing and sparsely vegetated. In three of these locations *T. weberi* had a rather scruffy and bedraggled appearance (Fig. 20)—individual plants were small, usually less than 0.3 m across and usually no more than 15–20 cm high. Stem segments were elongate, about 2–3 cm in diameter and 5–10 cm long. They are well armored with 5–10 spines up to 5 cm long per areole. Stem color was yellowish to brownish and spines were usually yellowish to tannish to reddish. The stems readily break off, and we had to watch our foot placement to be certain that detached segments didn't become shoe ornamentation. The nicest population we encountered was in eastern Catamarca just north of the province of La Rioja. Here the hillsides were carpeted with great mounds of this species, often as much as 1 m in diameter, and, though somewhat variable, the spination was quite white (Figs. 21 & 22). From a distance the overall

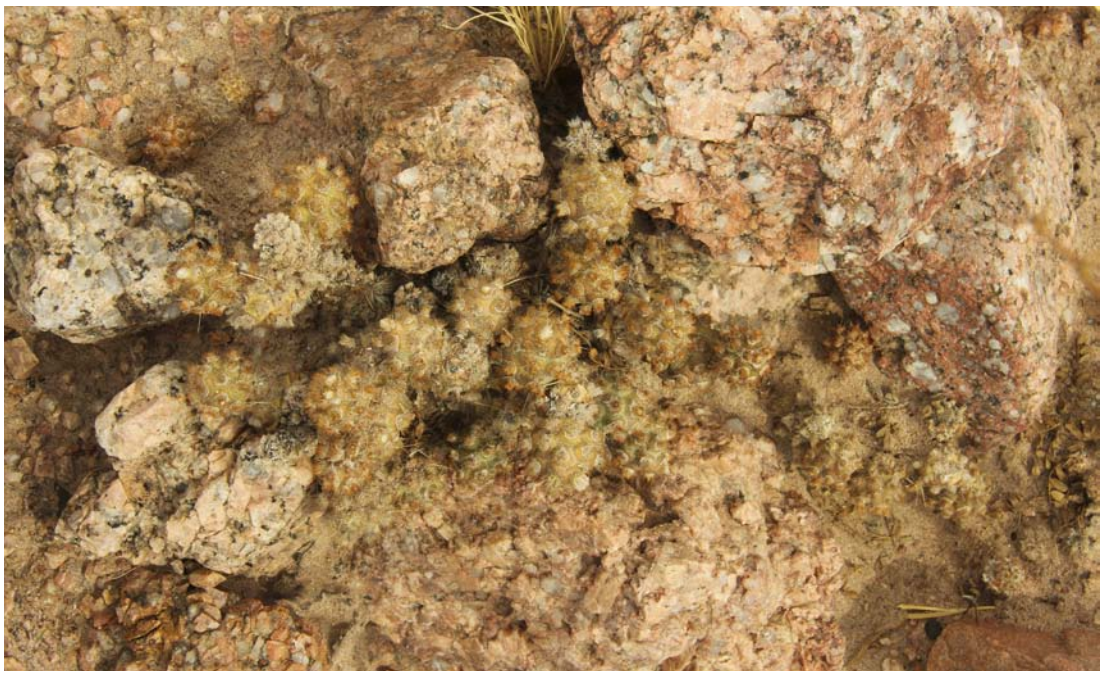
20. At some locations the plants of *Tephrocactus weberi* were small and rather scruffy looking. Southwest Salta province, near the impressive red rock formation known as Los Castillos, at 1530 m.

appearance was a hillside covered with piles of wool. Here it was found in association with *Tephrocactus articulatus, Opuntia sulphurea, Gymnocalycium glaucum,* and *Echinopsis strigosa*. This form is in cultivation and is attractive as a container plant.

Although phenotypically variable, *T. weberi* is fairly distinct and only one synonym is mentioned in the *New Cactus Lexicon* (*Opuntia aulacothele*; however, according to Crook & Mottram (1995), *Opuntia aulacothele* Weber may instead be a synonym of *Tunilla corrugata* (Salm-Dyck) D.R. Hunt & Iliff). Backeberg recognized two named varieties based on differences in spination, *dispar* and *setiger*, but these names are not generally accepted today. In their recent molecular studies, Ritz et al (2012) consider *T. weberi* to be somewhat distinct from other *Tephrocactus* species and mention that some populations have yellow flowers, whereas most members of the genus have white to pink flowers (the only other exceptions being *T. verschaffeltii* with orangish-red and *T. nigrispinus* with red flowers). None of the plants we encountered were in bloom.

Etymology—for Dr. Frédéric Weber (1830–1903), a French military surgeon and amateur botanist.

21 & 22. At this location in eastern Catamarca province *Tephrocactus weberi* occurred in large healthy masses and had a very white spination.



23. *Tephrocactus molinensis* is one of the smallest of the genus and often cryptically blends in with its surroundings. This one was in southwest Salta province, near Los Castillos, at 1530 m.

Tephrocactus molinensis

Tephrocactus molinensis is one of the smaller species in the genus, with globose to ovoid individual stem segments only about 2 cm in diameter and just a bit longer. The plant bodies are usually only a few segments high (maybe up to 7–10 cm), and really healthy plants can be up to 25 cm across, though most of what we saw were much less. In the field the plants are not highly attractive, looking a bit scruffy (Fig. 23), but if you take the time to get up close, especially the new growth can be interesting, with tufts of reddish glochids contrasting with the grayish-green stems (Fig. 24). There are no prominent spines.

The distribution of *T. molinensis* is limited to the Calchaquí valley of Salta. We saw it during three stops, but all within less than 2 km of each other, at about 1,500–1,800 m elevation, in an area of moderately sparse vegetation. Other cacti in the area included *Cumulopuntia boliviana*, *Echinopsis thionantha, Gymnocalycium spegazzinii, Opuntia sulphurea, Parodia microsperma* ssp. *horrida*, and *Tephrocactus weberi.*

Based on their molecular studies, Ritz et al (2012) group *T. molinensis* with the two other species with small stem segments, *T. bonnieae* and *T. recurvatus*. To our knowledge no synonyms or varietal names have been published for *T. molinensis*.

Etymology—"*molinensis*" refers to its occurrence near the village of Molinos, Salta.

24. With tiny stem segments on a tiny plant, *Tephrocactus molinensis* has no prominent spines but is well endowed with glochids.

25. *Tephrocactus bonnieae* in cultivation. Photo courtesy of Graham Charles.

Tephrocactus bonnieae

Tephrocactus bonnieae (Fig. 25) is a charming dwarf geophytic species. During the dry season its large tuberous root contracts and pulls the plant underground, often obscuring the entire plant. Its distribution is very restricted in the Tinogasta district of Catamarca. It was originally discovered in 1990 and ultimately published in this *Journal* in 1997 as *Puna bonnieae* (Ferguson and Kiesling 1997). The difficulty in finding this cryptic species in the field is recounted in that article. Fortunately the trip during which it was discovered occurred after a rainy period when it was in flower, making the tiny plants easier to see. In contrast, no rains had yet come to the area during our trip and only one small plant, degraded by foot traffic, was found, at an elevation of about 2,000 m.

At the time of its description *T. bonnieae* was included in the genus *Puna* with only two other species, *P. clavarioides* and *P. subterranea*. All three species were transferred to *Maihueniopsis* by the IOS Cactaceae Working Party (Anderson 1999). Subsequent studies on seed morphology (Stuppy 2001) showed that the species belonged in *Tephrocactus*, a conclusion later supported by molecular studies (Ritz et al. 2012). Although Kiesling and Ferrari (2005) still upheld the genus *Puna* based on areole, glochid and spine characteristics, the molecular studies of Ritz et al (2012) suggest that the three *Puna* species segregate into different clades, with *P. subterranea* in the *Cumulopuntia* clade, *P. clavarioides* arising from a very basal branch of the *Maihueniopsis* clade, and *P. bonnieae* grouped with *T. recurvatus* and *T. molinensis* in the *Tephrocactus* clade.

The stem segments of *T. bonnieae* are globose to ovoid and under 2 cm in diameter, and, in habitat, rarely stacked more than two high (and not much more than this in cultivation). The overall plant body is tight and usually only 5–8 cm in diameter. There can be 10–20 spines per areole but they are very short (1–4 mm) and closely adpressed to the tubercle.

26. *Tephrocactus nigrispinus* in habitat in Jujuy province. Photo courtesy of Graham Charles.

Because of its perceived limited distribution and its appeal to collectors, *Tephrocactus bonnieae* is listed in the IUCN Red List of Threatened Species as 'endangered' (http://www.iucnredlist.org/details/40822/0).

Etymology—"*bonnieae*" was named after Bonnie Brunkow who discovered the species.

Tephrocactus nigrispinus

We originally thought that we had seen the lovely diminutive red-flowered *Tephrocactus nigrispinus* in Jujuy, north of Humahuaca, which is near the type locality (Hunt et al. 2006), growing with two other red-flowered cacti, *Oreocereus trollii* and *Austrocylindropuntia schaferi*. But Graham Charles identified the diminutive opuntioid that we photographed as his recently described *Cumulopuntia iturbicola* (Hunt et al. 2011). This highlights our confusion over what constitutes *Cumulopuntia* versus *Tephrocactus* versus *Maihueniopsis*, for which we have more to say under *T. recurvatus*.

The "true" *T. nigrispinus*, if such a beast exists, forms a very small mound (less than 10 cm in diameter; not the 1–2 meters reported in Anderson (2001)) of cylindrical shoots, with only a few dark coloured spines per areole, and flowers that have red tepals, styles, and fruits, and a purple stigma (Fig. 26). We can do little better than quote from the *New Cactus*

27. *Tephrocactus recurvatus* in cultivation at Jardin botanique "Les Cèdres" in southern France. Photo courtesy of Graham Charles.

Lexicon (Hunt et al. 2006: 271) about this species:

> A decidedly enigmatic plant. As commented by Iliff (2002/SPR 6: 213–24) 'The seeds alone would preclude Kiesling's reference of the plant to *Maihueniopsis*' but they do not support its inclusion in *Tephrocactus sensu stricto*, and the plant's general appearance and fruit…argue against close kinship with *Tunilla*. Currently it seems the least worst option to leave it in *Tephrocactus sensu lato*.

T. nigrispinus is supposedly not common but widespread, growing on puna from 2,700–3,500 m elevation in Salta, Jujuy, and adjacent southern Bolivia (Kiesling 1984).

Etymology—"*nigrispinus*" derives from the Latin *nigra*, meaning black, and *spinus* meaning spined.

Tephrocactus recurvatus

This species was first described in 2001 as *Cumulopuntia recurvata*. The *New Cactus Lexicon* (Hunt et al. 2006) considers *T. recurvatus* to be a synonym of the widespread *Cumulopuntia boliviana* subsp. *boliviana*. Two years after description, Kiesling & Meglioli (2003) transferred this plant to *Maihueniopsis*, although they also suggested that it might be a hybrid between *Maihueniopsis* and *Tephrocactus*. Hunt & Ritz (2011) transferred this plant to *Tephrocactus*. After seeing many of these plants in northwestern Argentina, we are no longer sure of consistent morphological differences between *Tephrocactus* and *Maihueniopsis*. According to Stuppy (2002), the funicular girdle (part of the seed) is unique in *Tephrocactus* in possessing lots of aerenchyma. But this aerenchyma in the seed does not occur in *T. recurvatus* and *T. nigrispinus* (Ritz et al. 2012). Based on nuclear and chloroplast DNA, Ritz et al. (2012) found that *Maihueniopsis* and *Tephrocactus* are readily distinguishable sister genera.

Tephrocactus recurvatus (assuming it is not simply a variant of *Cumulopuntia boliviana*) is endemic to the province of San Juan, which we did not visit.

Illustrations of *T. recurvatus* show that it closely resembles *C. boliviana*, the latter of which Kiesling & Meglioli (2003) call *Maihueniopsis boliviana*. Both form tight mounds with thick but slightly elongated shoots. A supposed difference between the two species is that only *T. recurvatus* has twisted spines that are half the length of the straight flexible spines of *C. boliviana* (2–5 cm in *T. recurvatus*; 5–10 cm in *C. boliviana*) (Kiesling and Meglioli 2003). *T. recurvatus* is also unusual for *Cumulopuntia* in not having yellow flowers, but instead having white tepals. But flower colour is so variable in flowering plants, with pigments often controlled by only one or a few alleles, that we do not consider this difference alone sufficient to segregate species.

Etymology—"*recurvatus*" is from Latin, meaning curved backwards, referring to the twisted spines.

28

29

30

28–29. *Tephrocactus verschaffeltii* had been considered a member of the genus *Austrocylindropuntia*, which it superficially resembles. The spines are uncharacteristically long in the few plants at this locale, which was a damp foggy cattle pasture not too far from La Infiernillo, Tucumán. ***30.*** It is striking how similar the stems and flowers of *Tephrocactus verschaffeltii* (left) and *Echinopsis formosus* subsp. *bruchii (right)* appear to be at this locale, especially since these plants are not at all closely related (subfamilies Opuntiodieae versus Cactoideae, respectively), but both plants here are somewhat atypical for their taxa.

Tephrocactus verschaffeltii

T. verschaffeltii was long thought to belong in the genus *Austrocylindropuntia*, which it highly resembles. It has large fleshy subulate photosynthetic leaves that can persist for several months; slender cylindrical lime green shoots; and bright orange flowers with a reddish hue (Figs. 28–30), all of which are much more characteristic of *Austrocylindropuntia* than *Tephrocactus*. Yet recent molecular analysis places *T. verschaffeltii* squarely within the genus *Tephrocactus*, sister to *T. nigrispinus* (Ritz et al. 2012). Even the locale in which we saw *T. verschaffeltii* was uncharacteristic of the other species of *Tephrocactus*. *T. verschaffeltii* was growing in a damp high altitude (~2,800 m) cattle pasture alongside a very sparsely- and very short-spined form of *Echinopsis* (=*Soehrensia*) *formosa* subsp. *bruchii* in northwestern Tucumán, just east of Amaicha del Valle, as we started descending into the thick clouds on the east side of the ridge. If anything, this site most closely resembled the habitat in which we saw *Austrocylindropuntia vestita* a few km south of Volcán, Jujuy. Also curiously, from a distance, *Echinopsis* (=*Soehrensia*) *formosa* subsp. *bruchii* and *Tephrocactus verschaffeltii* resembled one another here, both with lime green shoots, a not so dense covering of straw-coloured spines, and reddish orange flowers (okay, you have to be fairly myopic).

The individuals we saw had longer spines than is typical for the species, at 8–11 cm long, versus less than 6 cm long reported in the *New Cactus Lexicon* (Hunt et al. 2006). Otherwise the spines were typical for the species, being 1–7 spines per areole, with each spine being acicular and gently curved. We are not sure how easy this species is to cultivate in the northern hemisphere, but, if possible, this would be a lovely clone to try growing.

Etymology—named for Ambroise Verschaffelt (1825–1886), a Belgian horticulturist.

Acknowledgements

Roberto Kiesling provided many insights and copies of many of his papers, as well as photographs. Most etymologies were derived from Eggli and Newton (2004). We thank the CSSA Field Trips Program and Guillermo Rivera for organizing and conducting the trip that formed the basis of our observations, Graham Charles for proof-reading, identifying some of our images, and with Roger Ferryman, for photographs of species we did not see. All other photos are by the authors.

Literature Cited

Akulova-Barlow, Z. 2007. Argentina's paper spine cacti and notes on *Tephrocactus* cultivation. *Cactus and Succulent Journal* 79: 228–233.

Anderson, E.F. 1999. Some nomenclatural changes in the Cactaceae, subfamily Opuntioideae. *Cactus and Succulent Journal* 71: 324–325.

Anderson, E.F. 2001. The cactus family. Timber Press, Portland.

Backeberg, C. 1977. Cactus lexicon [English translation of German 3rd edition]. Blandford Press, Poole, Dorset.

Britton, N.L. and Rose, J.N. 1923. The Cactaceae. Vol. 4. Carnegie Inst., Washington. [In the 1963 Dover reprint, this description occurs on page 226c, in the appendix to Vol. 1.]

Crook, R. and Mottram, R. 1995. Opuntia index, part 1: Introduction and A-B. *Bradleya* 13: 88–118.

Eggli, U. and Newton, L.E. 2004. Etymological dictionary of succulent plant names. Springer, Berlin.

Ferguson, D.J. and Kiesling, R. 1997. *Puna bonnieae* (Cactaceae), a new species from Argentina. *Cactus and Succulent Journal* 69: 287–293.

Gilmer, K. and Thomas, H.-P. 1998. Die gattung *Tephrocactus* Lemaire s. str. – taxonomie, ökologie und kultur [The genus *Tephrocactus* Lemaire s. str. – taxonomy, ecology and culture] *Schumannia* 2: 85–141.

Gorelick, R. 2012. Mitosis circumscribes individuals; sex creates new individuals. *Biology & Philosophy* 27: 871–890.

Gorelick, R. and Heng, H.H.Q. 2011. Sex reduces genetic variation: a multidisciplinary review. *Evolution* 65: 1088–1098.

Gorelick, R. and Olson, K. 2013. Polyploidy is genetic hence may cause non-adaptive radiations, whereas pseudopolyploidy is genomic hence may cause adaptive non-radiations. *Journal of Experimental Zoology (Part B. Molecular and Developmental Evolution)* 320B: 286–294.

Heng, H.H.Q. 2009. The genome-centric concept: resynthesis of evolutionary theory. *BioEssays* 31: 512–525.

Hunt, D.R. 2011. Classification of the 'cylindroid' opuntias of South America. *Cactaceae Systematics Initiatives* 25: 5–29.

Hunt, D.R. and Ritz, C.M. 2011. *Tephrocactus*. *Cactaceae Systematics Initiatives* 25: 27.

Hunt, D., Taylor, N., and Charles, G. 2006. The new cactus Lexicon. DH Books, Milborne Port.

Iliff, J. 2002. The Andean opuntias: an annotated checklist of the indigenous non-playopuntioid opuntias (Cactaceae-Opuntioideae) of South America. Pages 133–244 *in* D. Hunt and N. Taylor, editors. Studies in the Opuntioidea (Cactaceae), David Hunt, Sherborne.

Kiesling, R. 1984. Estudios en Cactaceae de Argentina: *Maihueniopsis*, *Tephrocactus* y géneros afines (Opuntioideae). *Darwiniana* 25: 171–215.

Kiesling, R. 1999. Cactaceae. Pages 423–489 *in* F.O. Zuloaga and O. Morrone, editors. Catálogo de las plantas vasculares de la Republica Argentina, II (Monographs in Systematic Botany, volume 74), Missouri Botanic Garden Press, St. Louis.

Kiesling, R. and Meglioli, S. 2003. Cactcaceae, Cactáceaes. Pages 161–193, 246–256 *in* R. Kiesling, editors. Flora de San Juan, República Argentina, Volume II, Buenos Aires.

Kiesling, R. and Ferrari, O.E. 2005. 100 cactus Argentinos. Editorial Albatros, Buenos Aires.

Lambert, J.G. 1997. Cacti of Argentina (2nd edition). Concordia-Roeselare, Belgium.

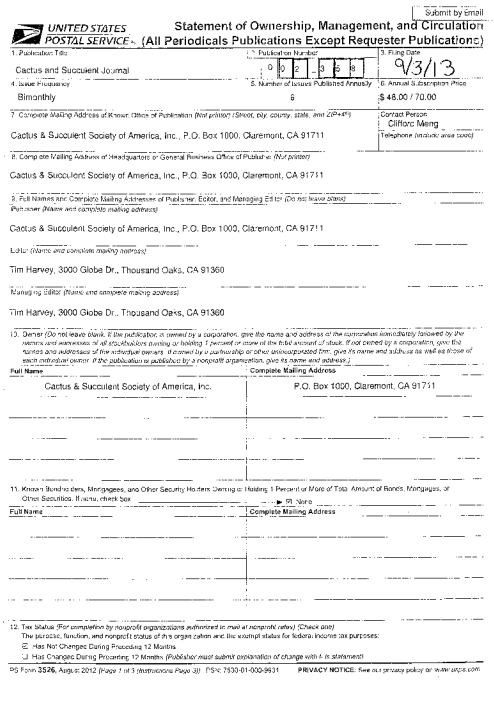
Mauseth, J.D. 2006. Structure-function relationships in highly modified shoots of Cactaceae. *Annals of Botany* 98: 901–926.

Myles, S., Boyko, A.R., Owens, C.L., Brown, P.J., Grassi, F., Aradhya, M.K., et al. 2011. Genetic structure and domestication history of the grape. *Proceedings of the National Academy of Sciences of the United States of America* 108: 3530–3535.

Ritz, C.M., Reiker, J., Charles, G., Hoxey, P., Hunt, D., Lowry, M., et al. 2012. Molecular phylogeny and character evolution in terete-stemmed Andean opuntias (Cactaceae–Opuntioideae). *Molecular Phylogenetics and Evolution* 65: 668–681.

Stuppy, W. 2001. A new combination in *Tephrocactus* Lem. (Cactaceae). *Kew Bulletin* 56: 1003–1005.

Stuppy, W. 2002. Seed characters in the generic classification of the Opuntiodeae (Cactaceae). Pages 25–58 *in* D.R. Hunt and N.P. Taylor, editors. Studies in the Opuntioideae (Cactaceae), David Hunt, Sherborne.



Submit by email

UNITED STATES POSTAL SERVICE — Statement of Ownership, Management, and Circulation (All Periodicals Publications Except Requester Publications)

1. Publication Title: Cactus and Succulent Journal
2. Publication Number: 0 0 2 - 5 6 0
3. Filing Date: 9/3/13
4. Issue Frequency: Bimonthly
5. Number of Issues Published Annually: 6
6. Annual Subscription Price: $ 48.00 / 70.00

7. Complete Mailing Address of Known Office of Publication (Not printer) (Street, city, county, state, and ZIP+4®): Cactus & Succulent Society of America, Inc., P.O. Box 1000, Claremont, CA 91711
Contact Person: Clifford Mesrig
Telephone (Include area code)

8. Complete Mailing Address of Headquarters or General Business Office of Publisher (Not printer): Cactus & Succulent Society of America, Inc., P.O. Box 1000, Claremont, CA 91711

9. Full Names and Complete Mailing Addresses of Publisher, Editor, and Managing Editor (Do not leave blank)
Publisher (Name and complete mailing address): Cactus & Succulent Society of America, Inc., P.O. Box 1000, Claremont, CA 91711
Editor (Name and complete mailing address): Tim Harvey, 3000 Globe Dr., Thousand Oaks, CA 91360
Managing Editor (Name and complete mailing address): Tim Harvey, 3000 Globe Dr., Thousand Oaks, CA 91360

10. Owner (Do not leave blank. If the publication is owned by a corporation, give the name and address of the corporation immediately followed by the names and addresses of the individual owners. If owned by a partnership or other unincorporated firm, give its name and address as well as those of each individual owner. If the publication is published by a nonprofit organization, give its name and address.)

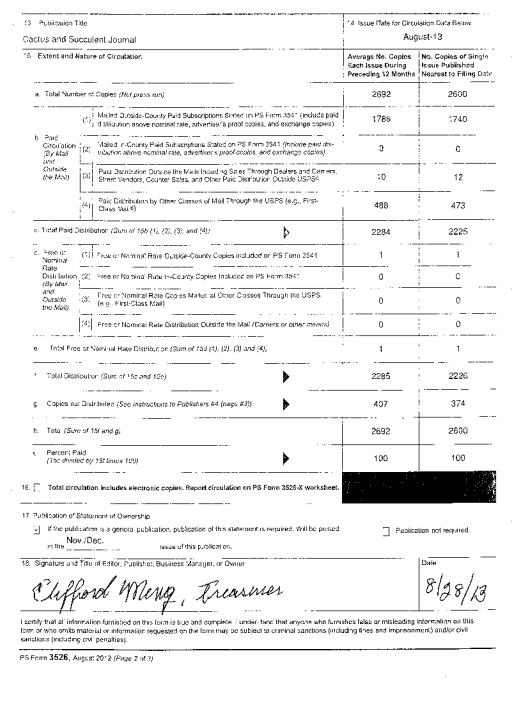
Full Name	Complete Mailing Address
Cactus & Succulent Society of America, Inc.	P.O. Box 1000, Claremont, CA 91711

11. Known Bondholders, Mortgagees, and Other Security Holders Owning or Holding 1 Percent or More of Total Amount of Bonds, Mortgages, or Other Securities. If none, check box → ☑ None

Full Name	Complete Mailing Address

12. Tax Status (For completion by nonprofit organizations authorized to mail at nonprofit rates) (Check one)
The purpose, function, and nonprofit status of this organization and the exempt status for federal income tax purposes:
☑ Has Not Changed During Preceding 12 Months
☐ Has Changed During Preceding 12 Months (Publisher must submit explanation of change with this statement)

PS Form 3526, August 2012 (Page 1 of 3 (Instructions Page 3)) PSN: 7530-01-000-9931 PRIVACY NOTICE: See our privacy policy on www.usps.com



13. Publication Title: Cactus and Succulent Journal
14. Issue Date for Circulation Data Below: August-13

15. Extent and Nature of Circulation		Average No. Copies Each Issue During Preceding 12 Months	No. Copies of Single Issue Published Nearest to Filing Date
a. Total Number of Copies (Net press run)		2692	2600
b. Paid Circulation (By Mail and Outside the Mail)	(1) Mailed Outside-County Paid Subscriptions Stated on PS Form 3541. (Include paid distribution above nominal rate, advertiser's proof copies, and exchange copies)	1786	1740
	(2) Mailed In-County Paid Subscriptions Stated on PS Form 3541 (Include paid distribution above nominal rate, advertiser's proof copies, and exchange copies)	0	0
	(3) Paid Distribution Outside the Mails Including Sales Through Dealers and Carriers, Street Vendors, Counter Sales, and Other Paid Distribution Outside USPS®	10	12
	(4) Paid Distribution by Other Classes of Mail Through the USPS (e.g., First-Class Mail®)	488	473
c. Total Paid Distribution (Sum of 15b (1), (2), (3), and (4))		2284	2225
d. Free or Nominal Rate Distribution (By Mail and Outside the Mail)	(1) Free or Nominal Rate Outside-County Copies included on PS Form 3541	1	1
	(2) Free or Nominal Rate In-County Copies included on PS Form 3541	0	0
	(3) Free or Nominal Rate Copies Mailed at Other Classes Through the USPS (e.g., First-Class Mail)	0	0
	(4) Free or Nominal Rate Distribution Outside the Mail (Carriers or other means)	0	0
e. Total Free or Nominal Rate Distribution (Sum of 15d (1), (2), (3) and (4))		1	1
f. Total Distribution (Sum of 15c and 15e)		2285	2226
g. Copies not Distributed (See Instructions to Publishers #4 (page #3))		407	374
h. Total (Sum of 15f and g)		2692	2600
i. Percent Paid (15c divided by 15f times 100)		100	100

16. ☐ Total circulation includes electronic copies. Report circulation on PS Form 3526-X worksheet.

17. Publication of Statement of Ownership
☐ If the publication is a general publication, publication of this statement is required. Will be printed in the Nov./Dec. issue of this publication.
☐ Publication not required.

18. Signature and Title of Editor, Publisher, Business Manager, or Owner: Clifford Mesrig, Treasurer — Date: 8/28/13

I certify that all information furnished on this form is true and complete. I understand that anyone who furnishes false or misleading information on this form or who omits material or information requested on the form may be subject to criminal sanctions (including fines and imprisonment) and/or civil sanctions (including civil penalties).

PS Form 3526, August 2012 (Page 2 of 3)