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Browningia candelaris in the Andean pre-puna of northern Chile

ARTHUR C. GIBSON AND PHILIP W. RUNDEL



Figure 1. A 4-meter specimen of *Browningia candelaris* growing on a rocky slope at 2350 m elevation east of Arica, Chile.

In 1833, during his travels in South America, Ferdinand Meyen of the University of Berlin discovered a strange-looking arborescent cactus above Tacna, Peru, on the upper slopes of the Andes. This remarkable cactus is characterized by a dense armature of heavy spines covering its trunk for a height of several meters, but above that, its spreading octopus-like branches appear spineless (Fig. 1). Meyen named this species *Cereus candelaris*. Studies of subsequent collections made by J.N. Rose in 1914 at 2700 m near Arequipa, Peru, convinced Britton and Rose (1920) to create for that species a genus, *Browningia*. The new generic name honored W.E. Browning, an American who served as director of the Instituto Inglés in Santiago, Chile. We know today that *B. candelaris* is restricted naturally to *quebradas* along the arid western slope of the Andes from southern Peru to Mamiña in northern Chile.

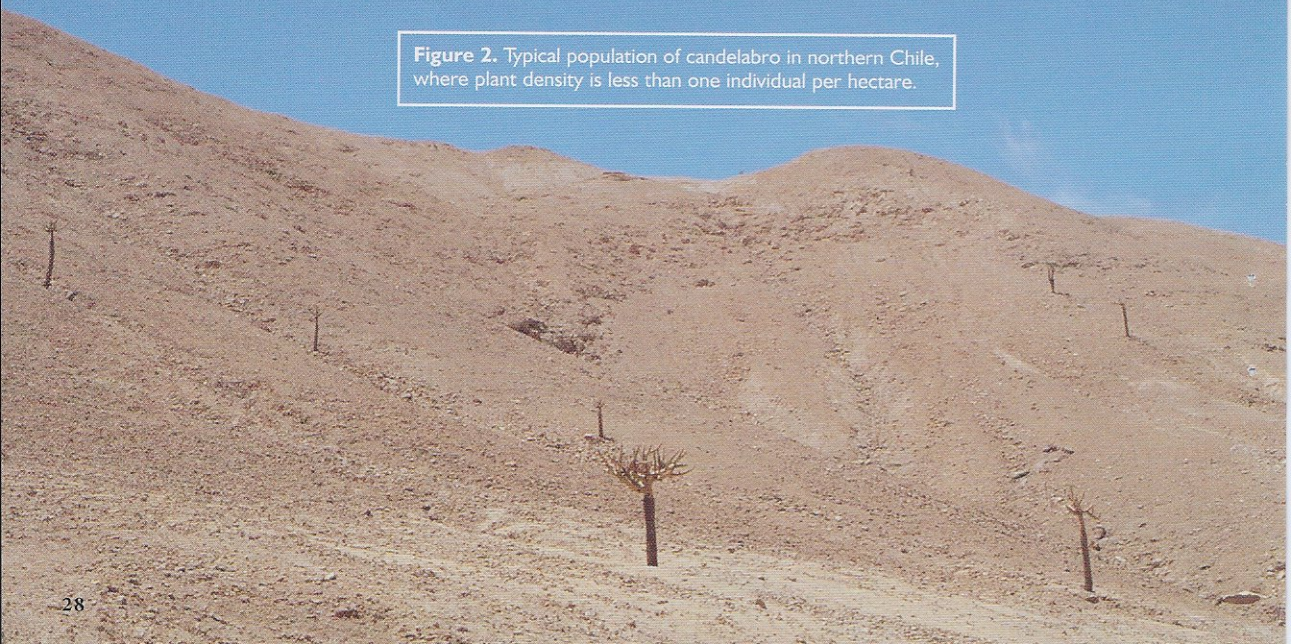
The genus *Browningia* (syn. *Azureocereus* and *Gymnocereus*, and often including *Gymnanthocereus*) is currently treated as a small group of columnar species from Peru and northern Chile in tribe Browningieae of subfamily Cactoideae (Barthlott & Hunt, 1993). Within this tribe, however, *B. candelaris* stands out because of its unusual morphological form (Rauh, 1958; Backeberg, 1958). There are relatively detailed descriptions of its reproductive structures (Buxbaum, 1965) as well as colored photographs of flowers (Innes & Glass, 1991). But despite more than a century and a half that has passed since the discovery of this species, there are gaps in the morphological description in vegetative form and ecology.

We studied *B. candelaris* (Meyen) Britt. & Rose in the Andean Cordillera of far northern Chile. Here this tree grows at 2200 to 2800 m elevation along Highway 11, which connects the Chilean port city of Arica with La Paz, Bolivia. Arica is perhaps the driest major city in the world, with a few millimeters of rain falling only once or twice per decade. With the exception of agricultural areas irrigated with ground water, slopes above Arica are literally devoid of any living plant, from sea level to approximately where *B. candelaris* is first encountered at 67 kilometers due east of the city.

Known locally as *candelabro*, *B. candelaris* grows here on steep canyon slopes with no apparent preference for slope angle or exposure (Fig. 2). Not only is *B. candelaris* the dominant species in its habitat, here it is virtually the only species! Few other plant species can tolerate such harsh conditions, where ten years or more may pass between scant rainfall events. Plants of *candelabro* are widely spaced on the rocky rubble slopes, with typical spacing less than one per hectare, and no more than eight individuals per hectare. Large slope areas are mostly devoid of individuals. No young plants were observed, suggesting that this population is in decline. However, *B. candelaris* clearly is a long-lived species, and thus decades without successful seedling establishment may not lead to irreversible decline.

The habitat of this *browningia* is termed a pre-puna community, with the term puna referring to the arid altiplano at higher elevations. Our careful searching of this pre-puna habitat found only a handful of perennial species. These

Figure 2. Typical population of *candelabro* in northern Chile, where plant density is less than one individual per hectare.



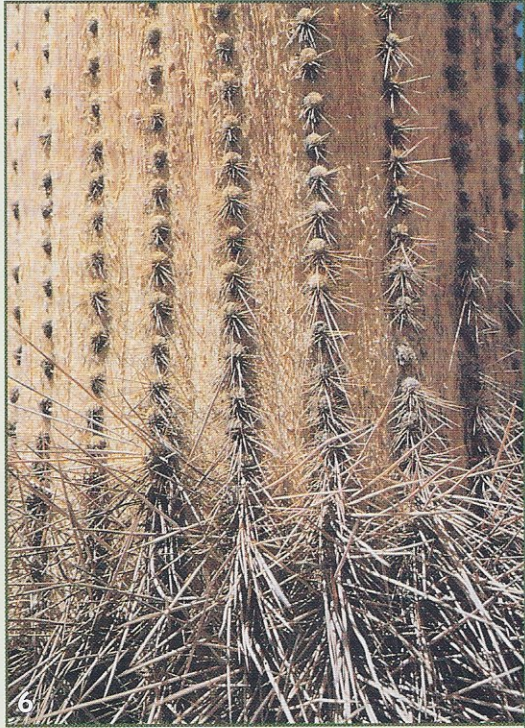
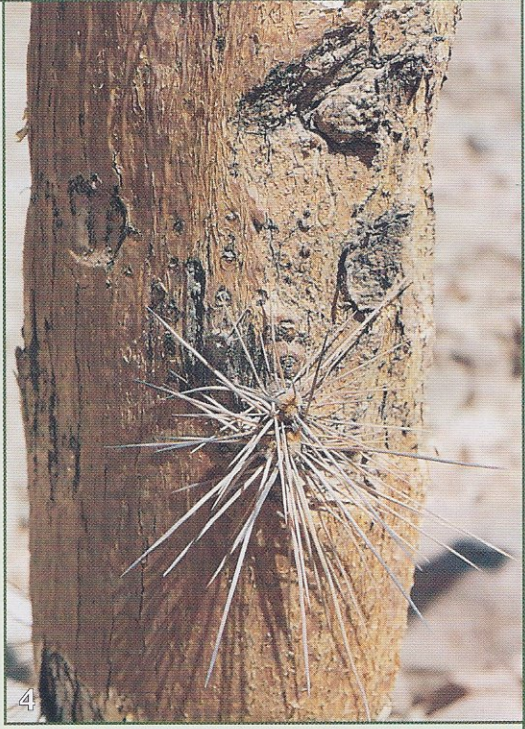
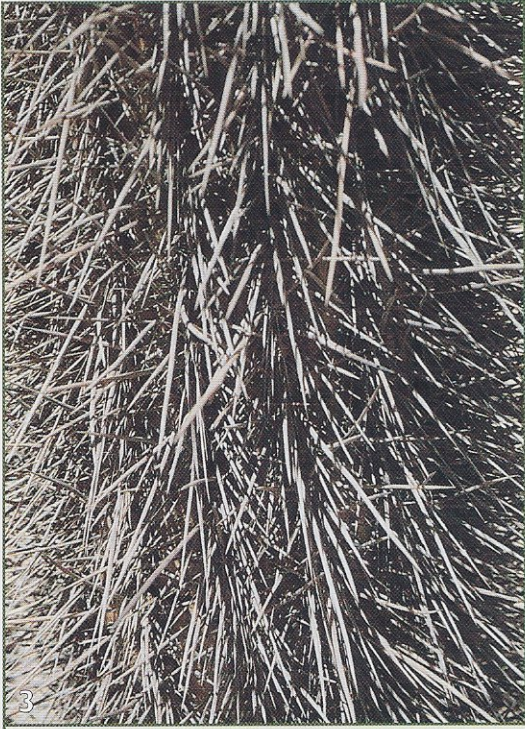


Figure 3. Drab gray spines covering the trunk of *Browningia candelaris*. The longest, generally downward-pointing spine on each areole often exceeds 15 cm in length. On this individual, spination is so dense that the stem surface cannot be seen. **Figure 4.** A relatively young tree on which bark is forming and all but one areole have been shed. **Figure 5.** Mature bark at the trunk base of an old tree, from which all areoles have been shed. **Figure 6.** A transition zone on the trunk at 2.5 m, where very long, stiff spines are being replaced by fewer shorter and thinner spines. This individual, which had 23 ribs, has bark, so that the trunk is no longer photosynthetic.

included two other cacti, *Tephrocactus atacamensis* (Philippi) Back. and *Haageocereus fascicularis* (Meyen) Ritter. Also present were scattered individuals of four semi-woody subshrubs: *Atriplex imbricata* (Moq.) Dietr. (Chenopodiaceae), *Tarasa operculata* (Cav.) Krap. (Malvaceae), *Ambrosia artemisioides* Meyen & Walp. and *Chuquiragua kuschelii* Acev. (Asteraceae). These species were represented more by dead skeletons than living plants, suggesting less tolerance to hyperarid conditions than *B. candelaris*.

Standing 4 to 7 m in height, *Browningia candelaris* is a very tall columnar cactus to be at such a high elevation. In this Chilean population, the straight trunk is 2.5 to 3.5 m in height, and up to 20 spreading branches arise from the top of the main axis; a photograph by Werner Rauh (Backeberg, 1958) showed more branches than that. The trunk has 19 to 29 ribs, most commonly 24, for many years bearing very large areoles, each with dozens of very hard, stiff spines that can fully cover the trunk of a middle-aged tree and thereby hide the epidermis (Fig. 3). The longest spines—up to 22 cm in length (not 20–50 cm, as claimed in Mauseth, 1993a)—often point downward. Trunk spines are yellow-red mostly aging gray or black, but some specimens retain the brighter colors. However, on older plants areoles are gradually shed as bark accumulates (Fig. 4), and wound periderm forms wherever the stem is injured. The initial phellogen forms from epidermal cells via periclinal divisions (parallel to the surface; see Gibson & Nobel, 1986), while the underlying hypodermis remains intact; it appears first along the areole-bearing rib margins and then expands into the stem valleys. Thereafter, the copper-colored periderm develops as plates of scaly, brown-orange bark (not gray, as stated in Mauseth, 1993a), especially thick at the trunk base of old individuals (Fig. 5).

A transition is present at 2.0 and 2.5 m above ground level. Here the long, thick trunk spines are represented instead by thin and yellowish shorter and fewer spines (Fig. 6) and then with fewer short, fine spines on the upper branches (Fig. 7). The lowest branches are formed approximately half a meter above the transition, 2.5 to 3.5 m from the ground. Branches develop irregularly, without an obvious sequence or pattern, except that when a branch breaks, several new branches may arise just below the broken surface from areolar meristems.

Young, fully green stems are 8 to 10 cm in

diameter, and the terminal 0.5 m of each branch remains green. Terminal shoots may have more than 30 low ribs with 10 or 11 areoles along 10 cm of the ridge margin. At first the rib margin is strongly tuberculate (Fig. 7) but expands to produce straight ridges and valleys farther from the shoot tip (Fig. 8). Areoles are small and circular with short (1 cm), fine, yellow-orange spines and tannish to white trichomes. Spines are worn from the upper stem (Fig. 9) but persist longer on the lower surface, and eventually all areoles of the branches become spineless, in contrast to the horrific persistent spines of the trunk. Green tissue persists longer on the lower side and in stem valleys on the upper side (Fig. 8), suggesting that sun-scalding is the initial cause for periderm formation.

Cortex and pith of terminal stems is solid, not at all juicy, and lacks mucilage. Absence of stem mucilage is considered a primitive feature for columnar cacti (Gibson & Horak, 1978; Gibson, 1992), and here correctly fits a member of a relatively ancient lineage of columnar cacti, albeit a highly derived growth form. Moreover, the pith has a very low density of medullary bundles (Mauseth, 1993a), which are absent or poorly developed in all basal (primitive) lineages of Cactoideae.

Browningia candelaris has a cylinder of trunk wood enclosing solid pith that, combined, are strong enough to support the weight of the canopy. We found dried wood skeletons 15 cm thick in radius, and likely older intact specimens have much wider woody cores (Fig. 10). Trunk wood has lens-shaped holes (primary rays; Gibson, 1978) arranged in vertical rows beneath the areoles and solid wood, several centimeters thick, opposite the stem valleys (Fig. 11). The base of the trunk appears to have a massive pith, probably exceeding 15 cm, tapering to a much smaller pith just below branches. The wood skeleton on terminal shoots is very similar in design to that previously reported in trichocereis (Gibson, 1978).

Wood of this species is not very strong, so is easily sectioned with a razor blade. Its softness is due to the presence of large primary rays and very wide multiseriate vascular rays with proportionally narrow fibrous zones (Mauseth, 1993b), very similar to arborescent species of *Echinopsis* (Gibson, 1973). The vascular rays, often 10 cells wide, are comprised of squarish cells with secondary cell walls having simple pits but little or no lignin. In harder, fibrous zones (axial secondary xylem) the libriform wood fibers are living and relatively thin-walled, and

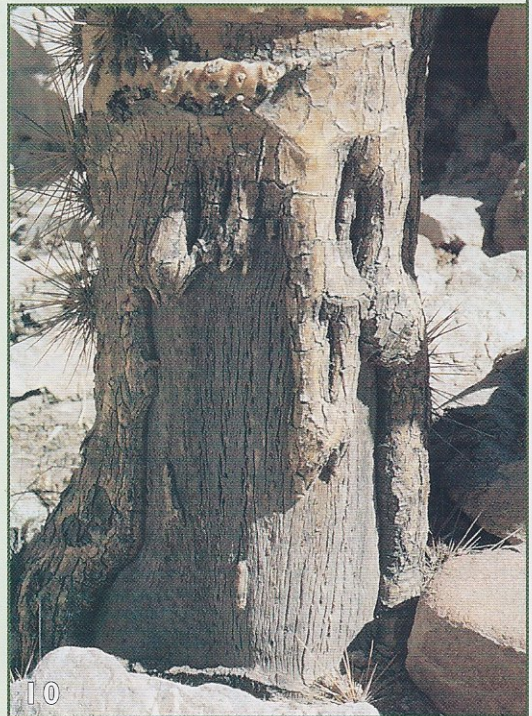
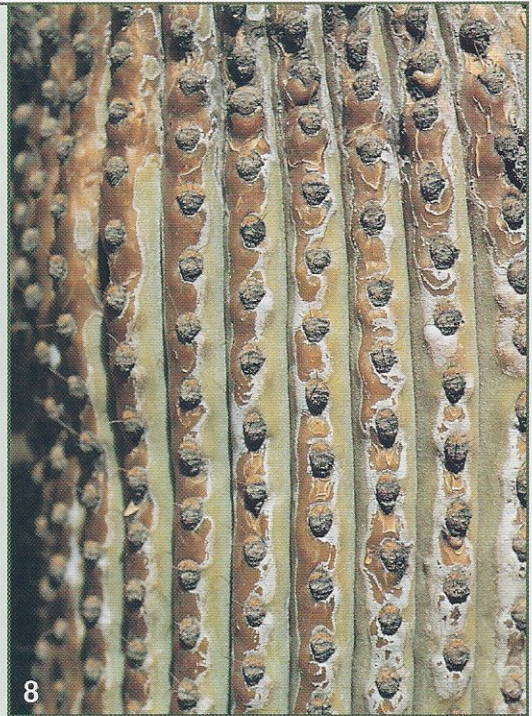


Figure 7. Fully green young canopy shoot of *Browningia candelaris*, showing many low ribs bearing small areoles with white trichomes and short, thin spines. Clearly seen in this photograph is the spiral arrangement of areoles formed at the shoot tip. **Figure 8.** Formation of periderm on a relatively young canopy branch. Periderm occurs initially along the ridges of the ribs, while the stem valleys remain green and photosynthetic. By this point, all spines have been shed and ribs and valleys no longer show the original tuberculate design. **Figure 9.** Periderm on an older stem of a canopy branch. Here periderm has completely replaced the green photosynthetic tissues, and all spines have been shed. **Figure 10.** Damaged bark and exposed, weathered wood of an old tree, having a basal trunk diameter of 40 cm.

mean vessel diameter was 80 μm at the trunk base of a large tree. In branches, the outer wood lacks wood fibers and the parenchyma cells have very thin, often primary cell walls (Mauseth, 1993b). This is definitely not a strong material for construction or burning, but in a place where wood is otherwise absent, obviously *B. candelaris* was used out of necessity.

Some individuals in the Chilean population showed concentric rings of damage on the trunk, indicating cold damage, as seen also in columnar cacti of Arizona. Episodic cold, which can descend from the higher Andes, may also be the cause of branch death, which was common throughout the stand of *B. candelaris*.

The origin of this growth habit, in comparison with more conventional forms of Brownieae (Gibson, 1992), still needs to be explained. Certainly *B. candelaris* produces many more ribs than its relatives by using a higher phyllotactic fraction, probably 8/21 for the main stem (rib number in low 20's) and 13/34 for terminal shoots (rib number near 30). Marked spine dimorphism on the two shoot tips suggests to us that the trunk is a juvenile form and the terminal shoots an adult form, a phenomenon expressed elsewhere in Cactaceae.

How can we explain the unusual morphological combination of heavily-spined trunks and bare branches of *B. candelaris*? In considering the evolutionary selection for the extremely spiny trunks of this species, it is interesting to note also the equally spiny trunks of *Echinopsis atacamensis* (Philippi) Friedr. & Rowley (Tribe Trichocereae). This arborescent species grows at 2600 to 3800 m in the northern Chilean Andes near San Pedro de Atacama, occupying a similar ecological niche as *B. candelaris*. *Echinopsis atacamensis* grows up to 7 m in height with a trunk diameter up to 70 cm, and produces a trunk densely covered with sharp,



Figure 11. Lens-shaped primary rays in weathered trunk wood of *el candelabro*.

downward-pointing spines that, remarkably, reach 30 cm in length (Hoffmann, 1989)!

Such well-defended trunks, as in both *B. candelaris* and *E. atacamensis*, appear to represent an evolutionary convergence as a strategy to protect these long-lived arborescent cacti from herbivores. A diversity of small rodents occurs along the ranges of these species in the Andes of northern Chile and southern Peru, and spination could prevent any of these from reaching flowers and fruits. But the most serious threat of herbivory probably came from the guanaco, *Lama guanicoe*. Guanacos, large cameloids weighing about 120 kg,

are able to survive in the harsh landscapes of the Andean slopes by successfully feeding on a wide variety of plant tissues, from leaves and stems to roots. It is also possible that other large Pleistocene herbivores, now extinct, exerted strong selective pressure on these arborescent cacti. Their unprotected fleshy tissues would certainly represent an important food source for herbivores in such a barren landscape. This skirt of spines around the trunk of *B. candelaris* is high enough to put the unarmed branches out of harms way. The down side to having spines is, as research has shown, that spines block sunlight from reaching the photosynthetic stems and hence would be expected to slow vertical growth (for a review, see Gibson & Nobel, 1986). Such heavy, dense armature would be considered then as an evolutionary trade-off, preventing mammalian herbivory but giving up higher growth rate.

Historically, humans have heavily exploited *B. candelaris*. From pre-Columbian time, during the colonial period, and up through the last century, the wood of this cactus had been used commonly in constructing roof beams, window frames, doors, and siding for outbuildings. Firewood harvested from its trunk, along with the woody cushion plant *Azorella compacta* Philip-

pi (Apiaceae) that grows in the puna at higher elevations, suffered major exploitation during the era of nitrate mining in the late 19th and early 20th century. Whereas *B. candelaris* is not an ideal wood source for either construction or firewood, the highly arid Andean slopes where this species grows offers few other alternatives for woody species. Illegal collecting of small plants for the succulent trade has become an increasing problem in recent years. Today *B. candelaris* is classified for conservation purposes as vulnerable (Hoffmann, 1989).

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All photos are by Arthur C. Gibson.

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Arthur Tischer (1895–2000)

Obituary by Steven Hammer

Dr. Arthur Tischer, the renowned mesemb botanist, died in his sleep on the 7th of September 2000, well into his 106th year. He was born on the 20th of April 1895, in Freiburg, Germany, and died in Heidelberg, where he had spent his second half-century. Tischer attributed his remarkable longevity to patience, composure, and the consumption of a "little glass of schnapps" in the morning, followed by wine at lunch and dinner. Patience and moderation were his trademarks. Never in a hurry, he grew mesembs at a natural, unforced tempo and always waited several years before describing a species he believed to be new. His many letters (to Hall, Bolus, de Boer, Kimmach, Littlewood, and Rawe) are proof of a careful, thoughtful character, as are his many descriptions of species in *Conophytum* and other genera of compact mesembs: *Titanopsis*, *Cheiridopsis*, *Gibbaeum*, *Nelia*, *Faucaria*, and *Lithops*. It was Tischer who gave us the most famous and least unnatural of cultivars, *L. optica* 'Rubra' (as *L. rubra* Tischer).

Along with Schwantes, Tischer was a pioneer in sphaeroid systematics. The *Conophytum* hierarchies he proposed in the 1960s have held up very well, and his excellent precis of mesemb cultivation, published in Labarre's *Mesembryanthema* (1931) fully retains its value via its uncommon common sense. Tischer published articles from 1925 to 1970, from the just-post-heyday of Brown to the death of Bolus. He spent much of that period preparing a monograph on *Conophytum* which was, regrettably, never published, though its insights were utilized by several other authors. Tischer's non-verbal legacy consists of his efforts to propagate the species he described, as well as those given to him by Brown and Bolus. To Tischer we owe the preservation of dozens of precious clonotypes, from *C. auriflorum* to *C. ricardianum* subsp. *rubriflorum*. He was such a steady and important force in the mesemb world that one tends to forget his "other" careers, jurisprudence and oenology. ■