

Population Variability in the Genus *Trichocereus* (*Cactaceae*) in Central Chile

By

Philip W. Rundel, Irvine (California)

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Abstract: *Trichocereus* has 4 species in central Chile. Population analyses indicate that introgressive hybridization has occurred between *T. chilensis* and *T. litoralis* in the Valparaíso and Santiago coast ranges. A taxonomic key is presented.

The genus *Trichocereus* includes nearly fifty species of arborescent or semi-arborescent cacti, occurring from Equador south to central Chile and east to Bolivia and central Argentina (BACKEBERG 1966). Throughout its geographic range significant taxonomic problems have occurred due to a poor understanding of the morphological variability associated with individual species. This situation has been particularly true with respect to the four species of *Trichocereus* endemic to central Chile: *T. chilensis* (COLLA) B. et R., *T. litoralis* (JOHON) LOOSER, *T. skottsbergii* BACKEBG., *T. coquimbanus* (MOL.) B. et R. This paper describes the population variability of these species, with special emphasis on *T. chilensis* and *T. litoralis*, and discusses the relative taxonomic significance of individual morphological features in the genus.

Considerable confusion has existed in the past over the taxonomy of *Trichocereus* in central Chile. While populations of tall arborescent taxa in the Coast Ranges and Andean Cordillera of Valparaíso and Santiago Provinces have generally been considered to be *T. chilensis*, the lower, semi-arborescent coastal populations of *Trichocereus* in Valparaíso, Aconcagua and Coquimbo Provinces have been poorly understood. Much of this confusion has resulted from a lack of appreciation of the range of population variability which is present in many of the standard morphological features used in taxonomic descriptions. Species of *Trichocereus* have been described from single specimens, some of these

apparently atypical of the taxa they represent. Phenotypic variability within and between populations has only rarely been considered. For these reasons, most of the existing descriptions of *Trichocereus* taxa from central Chile (BRITTON & ROSE 1920, JOHOW 1921, LOOSER 1929, and BACKEBERG 1966) are inadequate to distinguish species. The taxonomic characteristics of *T. chilensis* and *T. litoralis* have recently been clarified, however (RUNDEL 1974).

A careful field examination of populations of *Trichocereus* in central Chile shows a clear geographic separation of the four existing species (Fig. 1). *Trichocereus chilensis* is widespread in the foothills and lower slope of the Andean cordillera, where it is the dominant species on xeric north-facing slopes up to 1,800 m elevation. Common associates are *Puya chilensis* MOL. and *Colliguaya odorifera* MOL. The other three species are restricted to coastal habitats. From Valparaíso Province to Pichidangui in southern Coquimbo Province, *T. litoralis* occurs commonly on coastal bluffs and slopes with *Eulychnia castanea* PHIL., *Puya venusta* PHIL. plus a diverse assemblage of deciduous and evergreen shrubs. From Pichidangui north to Talinay, *T. litoralis* is replaced by *T. skottsbergii*. This latter species is common on coastal bluffs and near-coastal slopes. Typical associates include *Heliotropium stenophyllum* H. et A. and *Oxalis gigantea* BARN. North of Talinay, *T. coquimbanus* attains dominance on coastal bluffs, remaining important northward to the Atacama coastal fog zone communities of Antogagasta Province. Common associates in northern Coquimbo Province are *Eulychnia spinibarbis*, *Heliotropium stenophyllum* and *Oxalis gigantea*.

In the coast ranges of Santiago and Valparaíso Provinces, populations normally considered to be *T. chilensis* show considerable gene flow from *T. litoralis* along the adjacent coast. These populations, to be discussed later in this paper, appear to represent introgressive hybridization between these two species.

Material and Methods

Field work for this study was carried out in Chile from July to December 1972, and in September, 1974. Twelve populations of *Trichocereus* in Valparaíso, Santiago, Aconcagua, and southern Coquimbo Provinces were selected for intensive study. In each of these populations, ten typical individuals were sampled carefully for morphological characteristics. Critical examination of populations throughout central Chile before intensive sampling indicated that the following morphological characteristics were most diagnostic: number of ribs, length of primary central spine, stem diameter, and maximum height. Characteristics of secondary importance measured were primary spine diameter, spine formation on areoles, and flower shape. Where possible, mean numbers of stigma lobes were also measured.

Spine measurements were made on a sample of five spines equally spaced around the stem at the point of the first fully mature areole which corresponded to the point of initial full stem width. Stem diameter was also measured at this point.

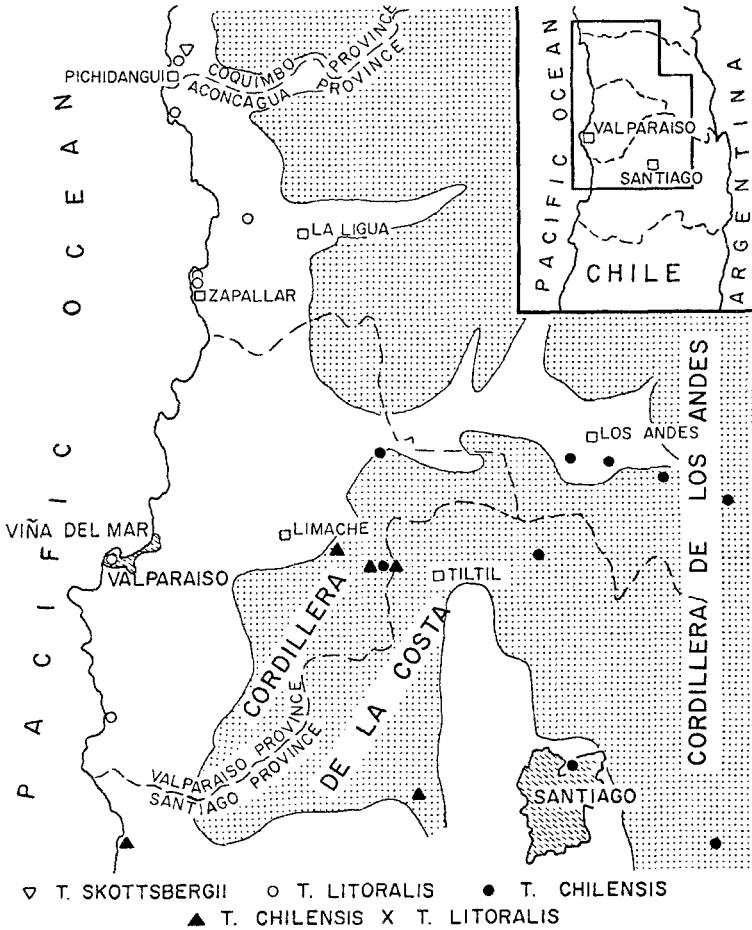


Fig. 1. Populations of *Trichocereus* studied in central Chile

Variability of Taxonomic Characteristics

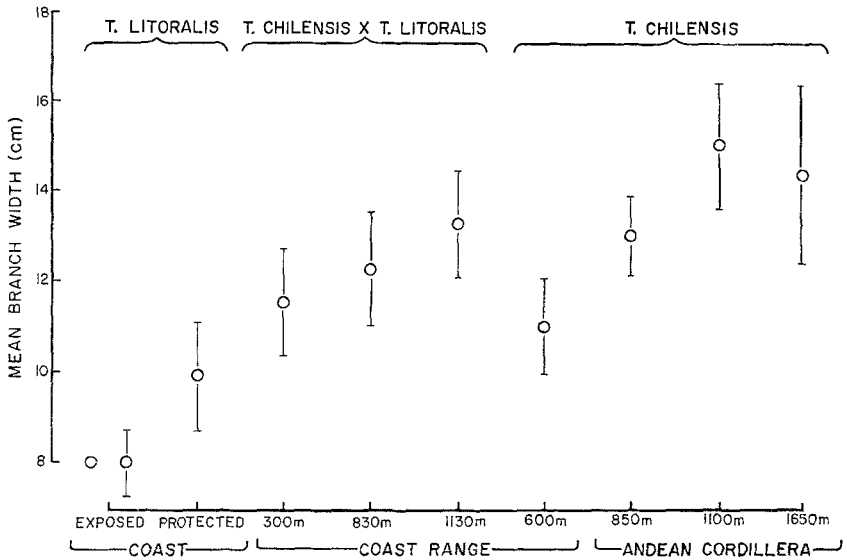
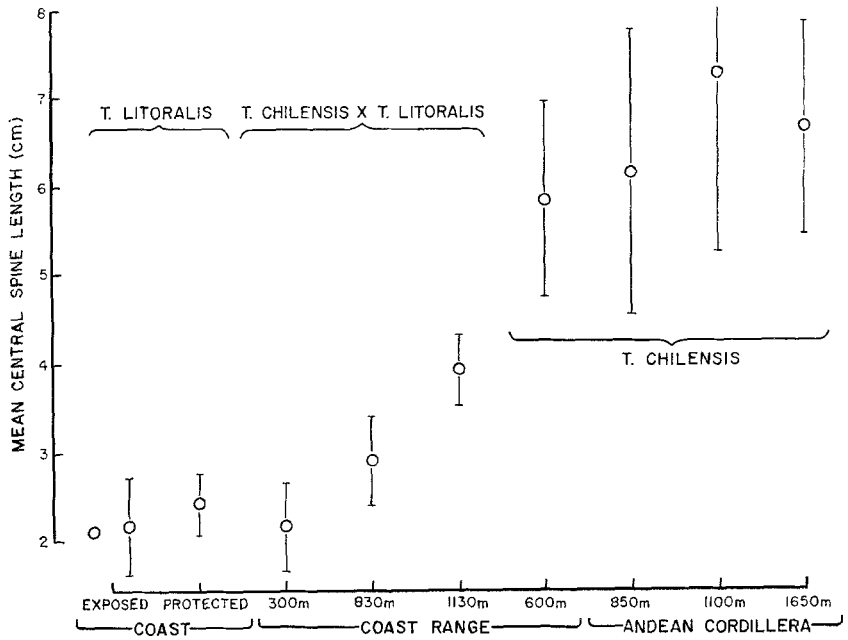
Mean number of ribs. While the mean number of ribs for a population serves as an extremely useful taxonomic characteristic, considerable variation of ribs number on individual plants may occur. *Trichocereus litoralis* and *T. skottsbergii*, both with a mean of 18 ribs, are particularly variable. From 15 to 22 ribs may be present on adjacent individuals in

a population. Very young branches occasionally have even fewer ribs. Rib variability is lower in *T. chilensis*, while *T. coquimbanus* in northern Coquimbo Province is extremely consistent. In most species, a variation of one or two ribs between branches on the same plant is frequently encountered. No obvious ecological correlates of rib number within or between populations could be identified.

Mean length of primary spine. Individual lengths of primary spines vary greatly on individual plants. In the longer-spined species, individual spines on a stem may vary $\pm 50\%$ of the mean spine length. Spine length is clearly subject to considerable environmental control. Along the length of individual stems, consistent patterns of long and short spines can be seen, apparently relating to growing season conditions in the past. Secondary branches of *T. skottsbergii* frequently have shorter and thicker spines than primary stems, although mean spine length increases slightly on secondary branches as they become taller. Near Quilimari (Coquimbo Province) at a site 7 km inland, shorter, and heavier-spined individuals of *T. skottsbergii* increase in frequency on upper slopes, in relation to more typical long, thin-spined individuals low on the slopes. In individuals of *T. litoralis* at Pichidanguí (Coquimbo Province), mean spine length increases greatly on a single stem as the stem emerges from a sheltered position to an exposed position. The relationship of wind exposure to spine length is not at all clear, however, as no regular pattern of spine variation with respect to wind is present in many populations (Fig. 2). Because of the importance of environment, spine measurements of cultivated *Trichocereus* taxa may be expected to differ significantly from mean field values.

Mean stem diameter. Although mean stem diameters shows significant variability between populations, intrapopulational variability is relatively low. In *T. chilensis*, mean stem diameter increases with elevation (Fig. 3), a fact perhaps relating to the adaptive value of decreased surface to volume ratio in cold tolerance. In the coastal species, the relative exposure of populations to onshore winds is inversely related to stem diameter. Exposed populations of *T. litoralis* (Fig. 3) and *T. skottsbergii* are approximately 2 cm narrower in diameter than moderately sheltered populations. Very exposed coastal populations of *T. coquimbanus* in northern Coquimbo Province have extremely small diameters.

Mean maximum height. While mean maximum height is potentially a useful characteristic in separating species of *Trichocereus*, the extreme disturbance to natural vegetation existing throughout central Chile reduces its value. Recolonization of disturbed and eroded hillsides by



Figs. 2 (above) and 3 (below). Mean central spine length and mean branch width (with one standard deviation bracketed) of representative populations of *Trichocereus litoralis* and *T. chilensis* along a west to east geographical gradient

T. chilensis and *T. skottsbergii* often results in populations of low individuals, atypical of their taxa. Populations of *T. litoralis* vary considerably in height, depending on their relative exposure (RUNDEL 1974).

Primary spine diameter. Diameters of central spines are proportional to spine length in all species except *T. skottsbergii*. This species is characterized by extremely thin, long, and flexible gray spines, although shorter more typical spines may also be present as described previously.

Spine formation on areoles. Considerable variability of arrangement of central and radial spines is present in all species. In *T. chilensis*, a single long central is present with 8–12 coarse radials. The other three species, however, are characterized by up to six centrals with anywhere from 15–29 short radials. Very often the separation of centrals and radials is blurred, although some of the radials may be only coarse bristles.

Hybridization

Although populations of *Trichocereus* in the Coast ranges of Valparaíso and Santiago Provinces superficially appear to be *T. chilensis*, they show many characteristics intermediate between this species and *T. litoralis*. Such intermediate populations are best represented on the western slopes of the Cuesta de la Dormida, northwest of Santiago. Similar intermediate populations were also observed farther south on the coast ranges and along the coast of Santo Domingo beyond the southern limit of *T. litoralis* (Fig. 1). These intermediate populations evidently represent hybridization between the two taxa. On the east slope of the Cuesta de la Dormida and rarely at higher elevations on the west slope, pure populations of *T. chilensis* do exist.

The hybrid populations of *T. chilensis* × *T. litoralis* have rib numbers and spine formations characteristic of *T. chilensis*, but they are intermediate between the parental types in the mean length of the central spine and in mean branch diameter (Table 1). Evidence for introgressive hybridization can be seen in these latter two characteristics. Spine length (Fig. 2) and branch diameter both show a blended variation correlating with both geographic and elevational gradients. As previously discussed, this gradient of variation in stem diameter may relate to the adaptive value of broader stems with increasing cold at higher temperatures, and thus provide equivocal evidence for introgression. The situation with spine length is very clear, however. Pure populations of both parents show little variability in mean spine length, while hybrid populations show a gradient of intermediate lengths. The intermediate characteristic of these hybrid populations is shown graphically in Fig. 4.

Although the situation has not been studied in detail, my field studies indicate that hybrid populations of *T. skottsbergii* × *T. coquimbanus* may be present near Bahia El Teniente in Coquimbo Province. More detailed investigations are needed to resolve this situation.

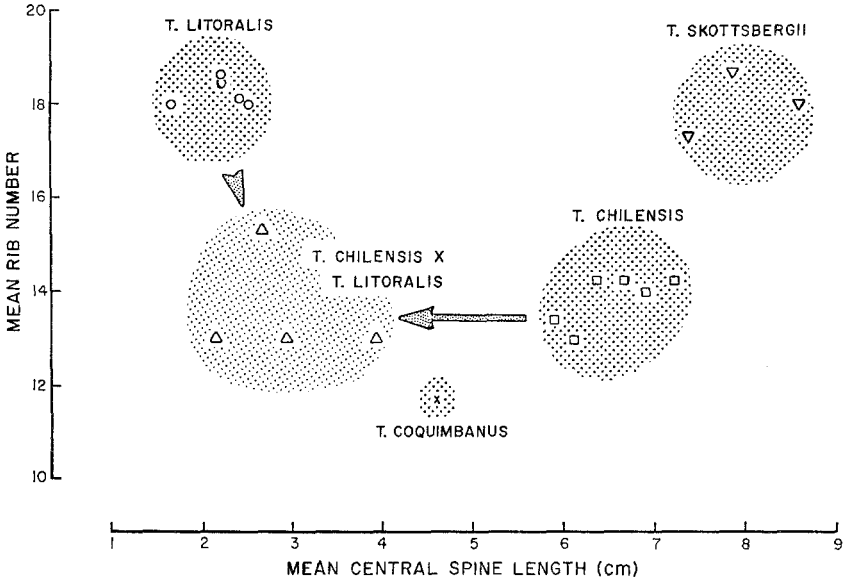


Fig. 4. Scatter diagram of populations of *Trichocereus* in central Chile

Speciation in Chilean *Trichocereus*

All four species of *Trichocereus* discussed in this paper appear to be closely related, although *T. coquimbanus* has some distinct differences from the other three species. The pattern of speciation observed hypothetically relates to the geographic isolation of populations of an ancestral taxon following Pleistocene and Altithermal climatic shifts. Along the coast, the pattern of the geographic replacement of species with decreasing latitude is consistent with this hypothesis. A very close parallel can be seen in the speciation of *Eulychnia*, an endemic Chilean genus of arborescent (rarely semi-arborescent) cacti. Companion species of *Eulychnia* with strikingly similar geographic ranges occur with each of the three coastal species of *Trichocereus*: *E. castanea* PHILIPPI—*T. litoralis*, *E. acida* PHILIPPI—*T. skottsbergii*, and *E. spinibarbis* (OTTO) B. & R.—*T. coquimbanus*. Similar patterns of species replacement occur in other genera of Chilean cacti including *Copiapoa* and *Neochilenia*. This pattern of speciation is analogous in many respects to the classic

example of *Cupressus* and closed-cone pines along the coast of California and Baja California.

The observed hybridization of *T. chilensis* and *T. litoralis* in the coast ranges may relate to a past influx of *T. litoralis* genes during a period corresponding with the altithermal in the Northern Hemisphere when conditions were warm enough to allow migration of *T. litoralis* away from the coast. More detailed studies of speciation in other plant groups in central Chile may help to resolve this question.

Taxonomic Treatment and Key

Much of the confusion in delineating species of *Trichocereus* in central Chile has resulted from a poor understanding of the species and a lack of recognition of hybridization between *T. chilensis* and *T. litoralis*. The following key serves to identify *Trichocereus* species in Coquimbo, Aconcagua, Santiago, and Valparaíso Provinces:

1. Mean rib number of mature plant 18; growing at or near coast
 2. Mean length of primary spine 1.6–2.4 cm; primary spine 0.8–1.3 mm in diameter, stem diameter (at 1 m ht) 8–10 cm; coast from San Antonio (Santiago Prov.) north to Pichidangui (Coquimbo Province) *Trichocereus litoralis*
 2. Mean length of primary spine 8 cm (5.1–9.6 cm); primary spine thin, typically 0.5–0.8 mm in diameter; coast from Quilimari to Talinay (Coquimbo Province) *T. skottsbergii*
1. Mean rib number of mature plant 11 to 14; growing inland, or at coast north of Talinay or South of Algarrobo
 3. Mean length of primary spine 4–5 cm; plants to 1 m; flowers open and campanulate; coast north of Talinay (Coquimbo Province) *T. coquimbanus*
 3. Mean length of primary spine 2–8 cm; mature plants > 1 m; flowers with extended tube; inland or coast south of Algarrobo (Valparaíso Province)
 4. Mean length of primary spine 2–4 cm; coast ranges or coast south of Algarrobo (Valparaíso Province) *T. chilensis* × *T. litoralis*
 4. Mean length of primary spine 6–8 cm; Andean Cordillera and Coast Range (primarily east slope) *T. chilensis*

Summary

Considerable confusion of the systematics of *Trichocereus* (*Cactaceae*) in central Chile has resulted from a poor understanding of the range of population variability present in natural populations. Four species of

Trichocereus occur in central Chile south of La Serena. *T. chilensis* dominates in the Andean Cordillera, while *T. litoralis*, *T. skottsbergii*, and *T. coquimbanus* are present along a latitudinal gradient in coastal sites. In the coast ranges of Valparaiso and Santiago Provinces, variable populations traditionally considered to represent *T. chilensis* appear to represent introgressive hybridization between this species and *T. litoralis*. The most important diagnostic morphological characteristics separating these species are rib number, primary spine length, and stem diameter, while areole structure, spine diameter, maximum height and flower shape were of secondary importance. Most morphological characteristics are subject to environmental variability, particularly spine length, stem diameter, and maximum height. Patterns of speciation of *Trichocereus* suggests isolation of ancestral populations following Pleistocene and altithermal climatic shifts. Patterns of replacement in the coastal species of *Trichocereus* are closely parallel to those of coastal species of another genus of arborescent cacti, *Eulychnia*, and similar patterns occur in other genera of Chilean cacti including *Copiapoa* and *Neochilenia*.

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Address of the author: PHILIP W. RUNDEL, Department of Ecology and Evolutionary Biology, University of California, Irvine, CA 92664, U.S.A.