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Similarity is only skin-deep: The use of comparative plant anatomy as illustrated by a study of columnar cacti from Chile (*Eulychnia* and *Echinopsis*, Cactaceae)

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Abstract

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Eulychnia iquiquensis and *Echinopsis deserticola* occur sympatrically in coastal regions of the Chilean Atacama desert. They often grow in mixed stands and their superficial appearance and general morphology is so strikingly similar that the two species are easily confused when not in flower or fruit. However, the stem anatomy of the two rather distantly related taxa is fundamentally different. *Eulychnia* has a flat stem surface with stomata at the surface and two different forms of idioblastic sclereids in the cortex, while the studied species of *Echinopsis* have a bumpy surface with the stomata deeply sunken between bulges, and mucilage idioblasts in the cortex and pith. Many of these features are easily recognized from stem cross-sections with the help of a hand-lens. Due to their diagnostic value, they allow rapid identification of even small sterile stem fragments and are therefore of potential value for resolving typification problems.

Key words: Cactaceae, *Echinopsis deserticola*, *Eulychnia iquiquensis*, Chile – comparative stem anatomy, plant identification.

Introduction

Comparative data in systematics are used in two different ways, either for diagnostic purposes (characterization and identification of organisms) or for synthetic purposes (classification and inference of phylogenetic relationships). Morphological characters are the classical data source for systematic investigations of both type, and they are still the primary base for daily taxonomical work. Such data is easily accessible and readily observable by the naked eye, which explains the predominant reliance on this kind of structural data in this context. As a consequence, taxa of vascular plants are in general differentiated on the basis of external

gross-morphological characters, especially from flowers and fruits. Comparative data from anatomy, palynology, cytology or other biological disciplines are rarely used for specimen identification but rather evaluated for phylogenetic investigations. Especially in recent years, characters that are not usually considered to be of potential value for phylogenetic studies are not given further attention.

Comparative anatomical data are often more difficult to observe than gross morphology, but, nevertheless, may prove to be immensely useful for the identification of fragmentary specimens, including plant fragments in industrial goods and other products, such as contaminants, spices, and medicinal herbs (Metcalf 1968, 1979). A striking example of the significance of comparative anatomy for diagnostic purposes arose during our on-going studies of cacti from South America.

Cactus anatomy

The comparative study of cacti and their classification until recently relied almost completely on flowers, fruits, and seeds, as well as on external gross-morphology, e.g. the disposition of ribs, tubercles and areoles, and the number and arrangement of spines. Most anatomical investigations have focused on anatomy *per se* (see Boke 1980 for a summary). Some recent comparative anatomical studies, however, revealed that valuable information can be gleaned from stem anatomy (e.g. Gibson and Horak 1978, Mauseth 1996, Nyffeler and Eggli 1997). Variation is found in the structure of the stem surface, in the dermal system (i.e. epidermis and hypodermis complex), and in the presence (or absence) of various idioblasts (e.g. sclereids and cells containing crystal druses or mucilage) in the parenchymatous water-storage tissue of the cortex and pith. These characters, when investigated in a comparative way, can be used for diagnostic purposes in cases where more readily observable characters are absent due to fragmentary or incomplete specimens.

Columnar cacti in Chile

The cactus flora of Chile, despite being relatively well known from semi-popular and popular publications such as those of Ritter (1980) and Hoffmann (1989), still presents numerous major problems concerning the generic classification and the circumscription of species. Columnar cacti are characteristic and sometimes dominant elements in some areas of the Atacama desert, including a narrow strip along the coast in the northern half of the country comprising the coastal cordillera as well as some of the major inland valleys. This region is dominated by species of the genera *Eulychnia* Philippi and *Echinopsis* Zuccarini. Taxa of both genera occur sympatric over a considerable part of their range in Chile, and are often found growing together in mixed stands.

Eulychnia (5 accepted species; Hunt 1999) is endemic to Chile with the exception of *E. ritteri* Cullmann from South Peru. All species are cereoid, and growth form varies from shrubby to arborescent. The genus is well characterized by flowers and fruits, and by its internal anatomy with conspicuous idioblastic sclereids (Nyffeler et al. 1997). Our investigation presented here centers on *E. iquiquensis* (K. Schumann) Britton & Rose. Sometimes, these plants are also identified as *E. saint-pieana* F. Ritter.

Echinopsis (61 accepted species; Hunt 1999) has a vast geographical range in southern South America. Since the predominantly cereoid genus *Trichocereus* (A. Berger) Riccobono is now treated as a generic synonym of *Echinopsis*, growth forms found in this genus vary from small globular plants with white nocturnal or coloured diurnal flowers to shrubby or arborescent, branched or unbranched plants with predominantly white or whitish nocturnal flowers. For Chile, Hunt (1992) lists 3 accepted and 6 provisionally accepted species. Seven

out of these nine names, including *Echinopsis deserticola* (Werdermann) H. Friedrich & G. D. Rowley, belong to the taxonomically difficult species complex of *Echinopsis chiloensis* (Colla) H. Friedrich & G. D. Rowley sensu lato. Pending further taxonomic research, we use here the name *E. deserticola* for the slender-stemmed low-growing taxon with predominantly basal branching that occurs North of La Serena (see Leuenberger and Eggli 1996 for the typification of this name).

Material and methods

Stem material from five samples of *Eulychnia iquiquensis* and three samples of *Echinopsis deserticola* were collected by the second author in the field during three trips to Central and Northern Chile to study the cactus flora for the Proyecto Flora de Chile (Table 1). Illustrations for the present publication have been prepared from plants growing in a mixed stand N of Taltal, Chile (Eggli, 1915, Eggli 1915a).

Stem samples were collected about 4–5 cm below the stem tips. The material was immediately fixed in an ethanol-glycerine-formaline-water-mixture (50:5:5:40 by volume) at ambient temperature for 5 weeks and then transferred to 70% ethanol. After a preliminary screening from hand sections, small blocks of ca. 8 × 5 × 3 mm were dehydrated in an ethanol series, imbedded in HEMA (2-hydroxyethyl methacrylate resin) and sectioned at 4 or 5 µm on

Tab. 1. Material investigated

Eulychnia iquiquensis

Eggli & Leuenberger 1755: Chile, Región II, Prov. Antofagasta, 17 km N of Taltal towards Paposo. 25.11.1991. Vouchers B, SGO, ZSS.

Eggli & Leuenberger 2639a: Chile, Región II, Prov. Antofagasta, Quebrada Taltal, 13 km NW of Panamericana towards Taltal, 25° 29.15' S / 70° 25.71' W, 600–800 m. 13.12.1994. Vouchers B, ZSS.

Eggli & Leuenberger 2661: Chile, Región II, Prov. Antofagasta, Quebrada San Ramón just N of Taltal, 25° 22.94' S / 70° 23.25' W, 500 m. 16.12.1994. Vouchers B, CONC, SGO, ZSS.

Eggli 2906: Chile, Región III, Prov. Chañaral, W of Cerro Paso Malo, c. 5 km S of Chañaral, 26° 22.60' S / 70° 38.90' W, 350–450 m. 7.10.1997. Vouchers B, CONC, SGO, ZSS.

Eggli 2915a: Chile, Región II, Prov. Antofagasta, coastal cordillera of the Cerro Perales, immediately N of Taltal, 25° 25.50' S / 70° 25.24' W, 600–800 m. 10.10.1997. Photographic vouchers B, ZSS.

Echinopsis chiloensis complex

Nyffeler & Eggli 390: Chile, Región IV, Prov. Petorca, c. 40 km N from crossing of Panamericana with access road to Papudo towards La Serena, 32° 11.41' S / 71° 31.22' W, 80 m., 7. 1. 1996. Vouchers B, SGO, ZSS.

Echinopsis deserticola

Eggli & Leuenberger 2653: Región II, Prov. Antofagasta, 6 km E of Paposo, 25° 0.97' S / 70° 26.21' W, 550–600 m. 15.12.1994. Vouchers B, CONC, SGO, ZSS.

Eggli 2888: Chile, Región III, Prov. Chañaral, Falda Verde, slopes of Cerro W of Cerro Chañaral 4–5 km N of Chañaral, 26° 17.41' S / 70° 38.27' W, 400–500 m. 5.10.1997. Vouchers B, CONC, SGO, ZSS.

Eggli 2915: Chile, Región II, Prov. Antofagasta, coastal cordillera of the Cerro Perales, immediately N of Taltal, 25° 25.50' S / 70° 25.24' W, 600–800 m. 10.10.1997. Vouchers B, CONC, SGO, ZSS.

a rotation microtome (Igersheim and Cichocki 1996). Sections were stained with toluidine blue O (0.02 %), which stains lignified sclerenchyma cells greenish blue and mucilage idoblasts densely dark blue (O'Brien et al. 1965). Surface characters were studied from epidermis strips taken from rib flanks close to the areoles. These were cleaned in an ultrasonic bath for ca. 1 min. and critical point dried, mounted on metal stubs, sputter-coated with gold, and examined with a Cambridge Stereoscan S4 SEM.

Results

Distribution and habitat

The distribution area of *Eulychnia iquiquensis* ranges from halfway between Caldera and Chañaral in the South up to Iquique (if *Eulychnia ritteri* is included in this species the distribution extends into southern Peru). Populations of *Echinopsis deserticola* are found from La Serena northwards to the vicinity of Paposo. Both species grow sympatrically at a number of localities, sometimes in tightly mixed groups. They seem to prefer, especially in the northern part of their range, W oriented slopes influenced by fog. However, the ecology of both taxa is poorly known and it remains unclear why at some localities they occur together while at others only one of them is present.

Gross morphology

In general, *Eulychnia iquiquensis* produces predominantly basal branches and ultimately becomes shrubby in habit. Some ascending branches may reach heights of up to 3 m or more and the overall aspect of old mature plants is more or less candelabriform. *Echinopsis deserticola* produces lots of basal branches and forms thickets of several meters in diameter. Branches generally do not exceed 1.5 m. In cases where *Echinopsis deserticola* is growing next to a shrubby specimen of *Eulychnia iquiquensis*, distinguishing the two species is often very difficult (Fig. 1).

A number of morphological stem characters of the two taxa are summarized in Table 2. Most of the variation in these characters distinctly overlap and an identification of sterile

Tab. 2. Stem morphology of *Eulychnia iquiquensis* and *Echinopsis deserticola*

	<i>Eulychnia iquiquensis</i>	<i>Echinopsis deserticola</i>
maximum plant height	3–5 m	0.6–1.5 m
stem diameter	45–90 mm	40–50 mm
rib height	11–17 mm	12–15 mm
number of ribs	10–15	8–11
number of central spines	1–3	2–3
length of central spines	35–140 mm	60–95 mm
number of radial spines	5–15	9–12
presence of hair-like radial spines	present ¹	absent
diameter of areoles	7–9 mm	9–11 mm ²
colour of young areolar wool	dark brown	yellow–ochre
colour of old areolar wool	grey	grey

¹ not present on all individuals nor on all areoles along a stem segment

² areoles elongated; measurement given for the longer axis

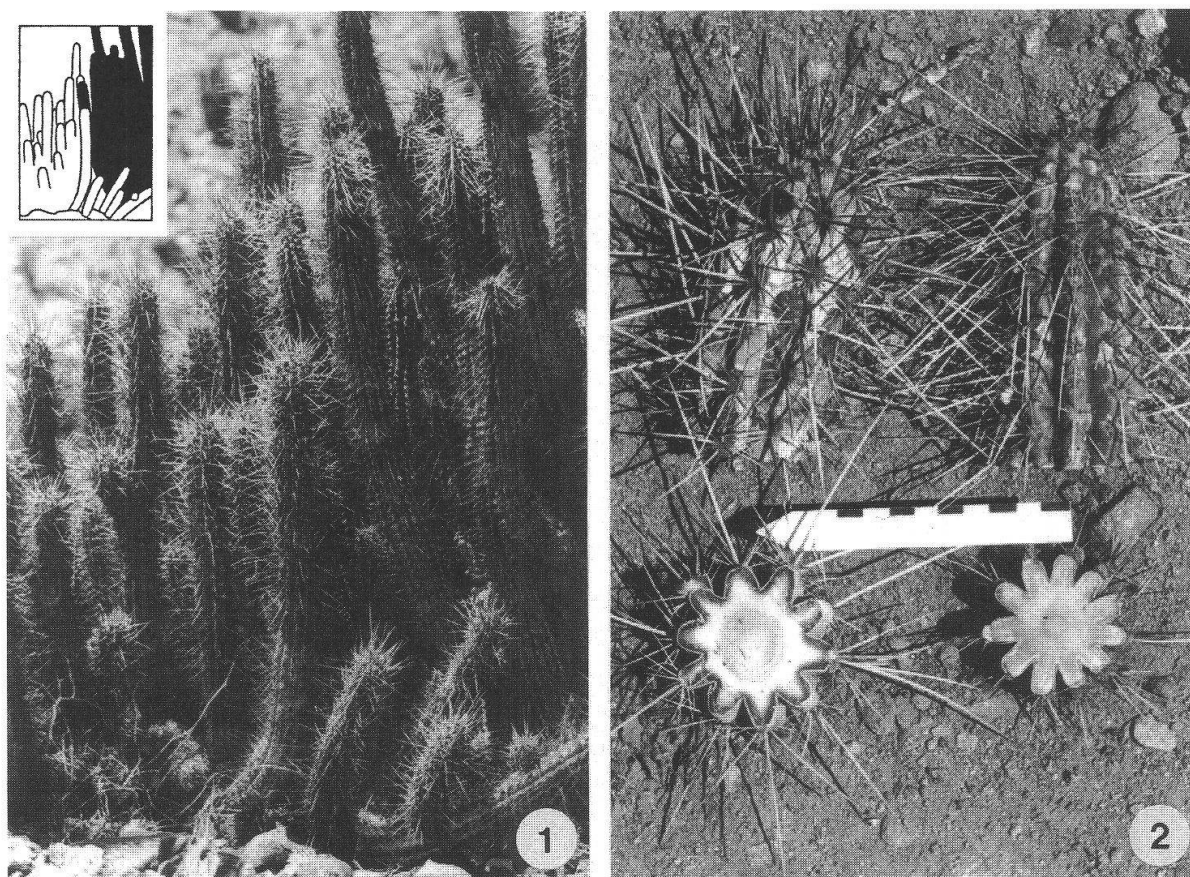


Fig. 1. At the habitat of *Eulychnia iquiquensis* (Eggli 2915a) and *Echinopsis deserticola* (Eggli 2915) in the Sierra Potrero near Taltal, Chile, at 640 m. Inset gives demarcation between these two very similar looking and tightly intermingled growing plants of *Eulychnia iquiquensis* (right) and *Echinopsis deserticola* (left).

Fig. 2. Stem material of *Eulychnia iquiquensis* (Eggli 2915a; right) and *Echinopsis deserticola* (Eggli 2915; left) collected for this comparative anatomical study. Note the greyish colouring of the cortex tissue in *Eulychnia iquiquensis* and the distinct chlorenchyma layer close to the dermal system in *Echinopsis deserticola*.

material is often very difficult. In general, specimens of *Eulychnia iquiquensis* reach stem diameters up to 90 mm, while *Echinopsis deserticola* often measures around 40 to 50 mm. Characters such as rib number, rib height, and number and length of spines do not reveal distinct and consistent differences. The only character that is in part a reliable marker to distinguish between the two species is the shape of the areoles and the presence of hair-like radial spines in *Eulychnia iquiquensis* (not always present on all individuals nor on all areoles along a stem segment) which are absent in all species of *Echinopsis* from coastal Chile.

Stem anatomy

Many of the anatomical differences in the stems of the two species investigated for this study are immediately and easily discernible macroscopically from stem cross-sections (Fig. 2). *Eulychnia iquiquensis* is immediately recognized by the granular "sandy" aspect of its cortex tissue which, furthermore, has an orange, when freshly cut, and later brownish colour. *Echinopsis deserticola*, in contrast, has a rather soft and mucilaginous, pale water-

Tab. 3. Stem anatomy of *Eulychnia iquiquensis* and *Echinopsis deserticola*

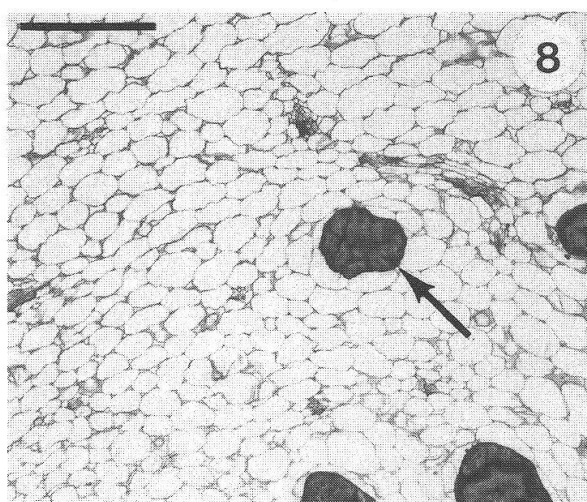
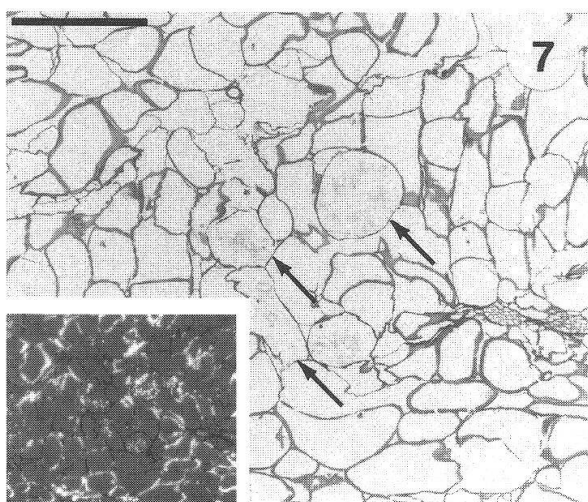
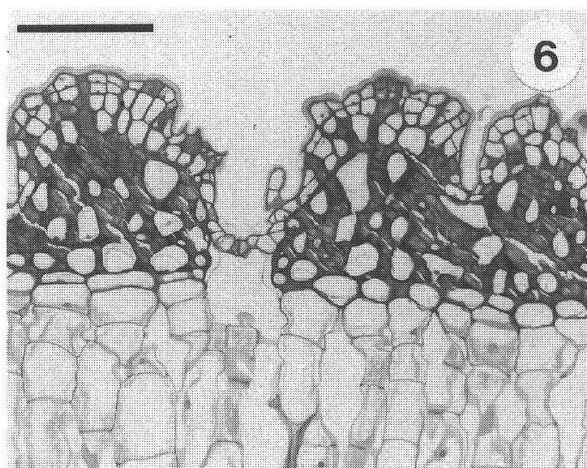
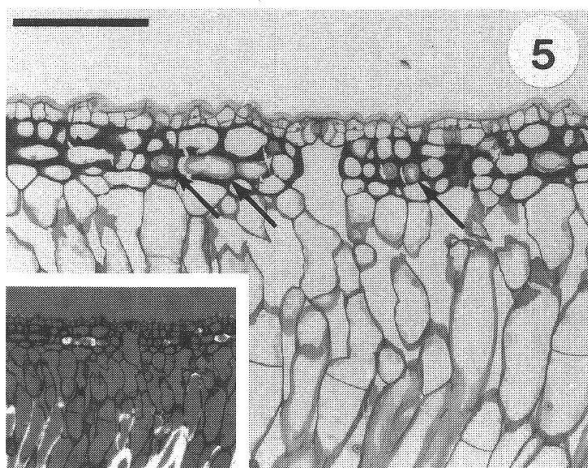
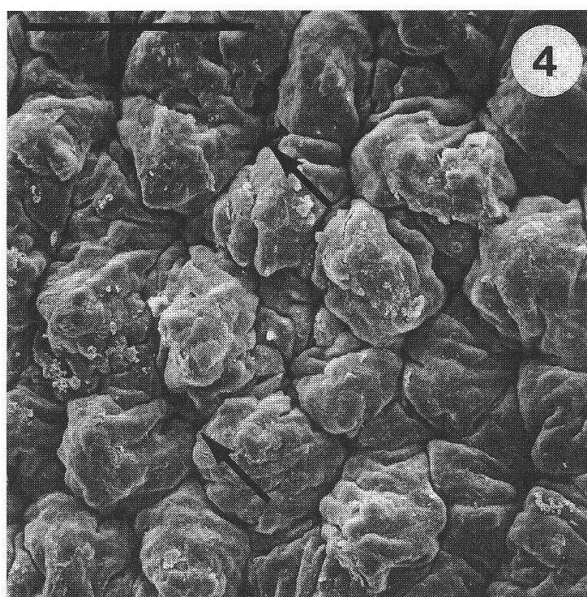
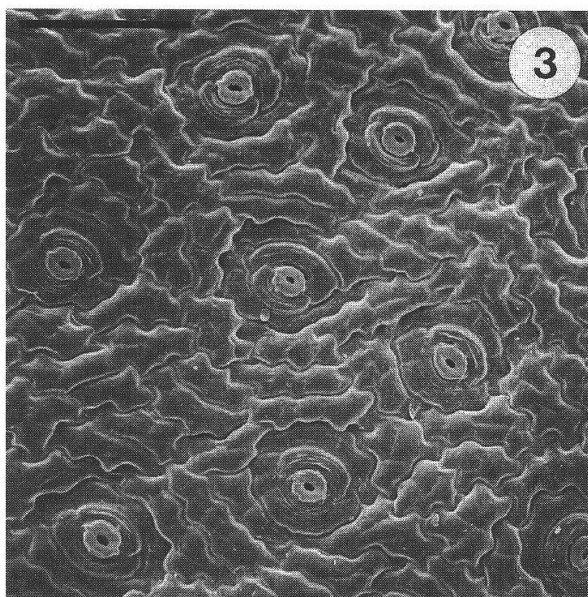
	<i>Eulychnia iquiquensis</i>	<i>Echinopsis deserticola</i>
stem surface	flat, with individual convex cell walls	strongly bumpy
position of stomata	level with the stem surface	at the bottom of cavities between the bumps
epidermis cell layer	irregularly multiseriate	uniseriate or regularly biseriate
thickness of the hypodermis layer	50–200 μm	40–60 μm
elongated sclereids in outer cortex	present	absent
globular to subglobular sclereids in the inner cortex	present	absent
mucilage idioblasts	absent	present

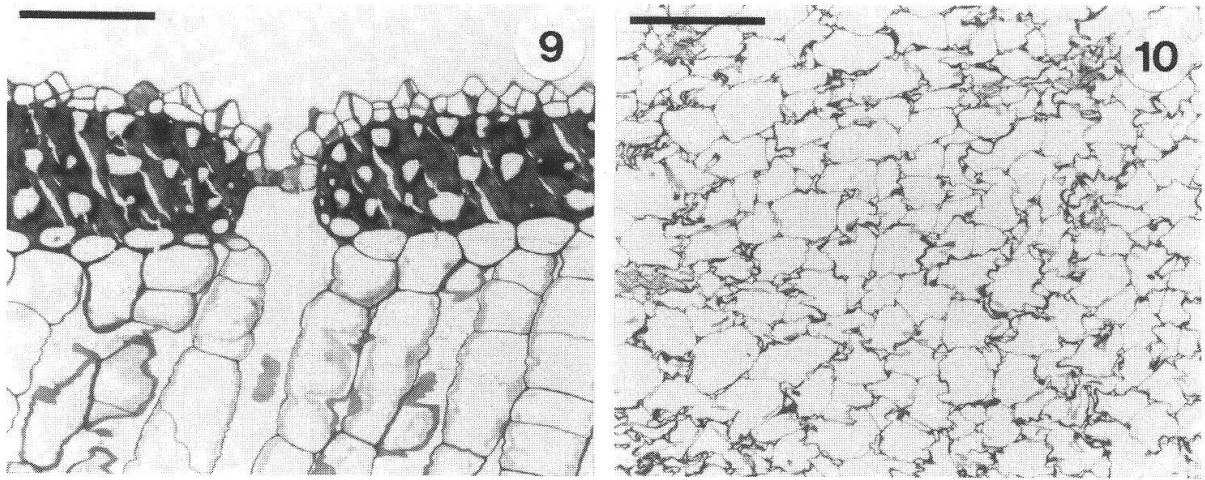
storage tissue which is easily distinguished based on the slimy or sticky nature of fresh sections. The cortex tissue of dried herbarium specimens of this latter species is distinctly shrunk-en and collapsed.

Comparative anatomical investigations disclosed further details of the differences between the two species (Table 3, Figs. 3–8). Distinct and consistent differences are found in the form of the stem surface, in the dermal system and in the cortex tissue. In general, the dermal system of *Eulychnia iquiquensis* is not particularly xeromorphic, consisting of a more or less flat or slightly wavy surface with some individual outer epidermis cell walls being slightly convex, and a basically uniseriate or sometimes regularly biseriate epidermis (Fig. 3). The stomata are level with the stem surface. The hypodermis generally consists of two or three layers of tabular collenchyma cells and sometimes with secondary cell wall thickening (Fig. 5, arrows). The cortex is characterized by distinct idioblastic sclereids which, as far as known, are unique to *Eulychnia* within the Cactaceae (Nyffeler et al. 1997). These sclereids are elongated and often distinctly needle-shaped in the outer chlorenchymatic layer of the cortex close to the dermal system (Fig. 5). The inner cortex, consisting of large parenchymatic cells used for water-storage, contains globular or subglobular idioblasts up to 200 μm wide (Fig. 7).

The dermal system of *Echinopsis deserticola* is very distinctive due to the formation of massive bumps up to 300 μm in diameter and about 200 μm in height (Fig. 4). The stomata are located at the bottom of cavities between these dermal structures (Fig. 4, arrows). The bumpy

Figs. 3–8. Dermal system and cortex of *Eulychnia iquiquensis* (Eggli 2915a) and *Echinopsis deserticola* (Eggli 2915). Fig. 3. Stem surface of *E. iquiquensis*. The slightly wavy surface results from individual convex cell walls, and the stomata are at the surface. Fig. 4. Stem surface of *E. deserticola* with its characteristic bumps of up to 300 μm diameter. The stomata are deeply sunken in cavities (arrows). Fig. 5. Cross-section of the dermal system of *E. iquiquensis*. Note the tips of elongated sclereids at the bottom of the illustration (compare with inset photographed with polarized light). Secondary wall thickenings are also found in some cells of the hypodermis (arrows). Fig. 6. Cross-section of the dermal system of *E. deserticola*. The stoma in the center is located at the bottom of the cavity. The bumpy surface is predominantly the product of bulges of the hypodermis layer. Fig. 7. Section of the cortex tissue of *E. iquiquensis*. Globular and subglobular idioblastic sclereids are scattered among the parenchymatic cells (compare inset photographed with polarized light). Idioblasts containing crystal druses are also present (arrows). Fig. 8. Section of the cortex tissue of *E. deserticola*. Mucilage idioblasts are deeply stained and distinctly larger than the surrounding parenchymatic cells (arrow). Bars = 400 μm in Figs. 3–4; bars = 200 μm in Figs. 5–6; bars = 500 μm in Figs. 7–8.





Figs. 9–10. Dermal system and cortex of *Echinopsis chiloensis* s. lat. (Nyffeler & Eggli 390) from near Papudo, Chile. Fig. 9. Cross-section of the dermal system. In this taxon of *Echinopsis* the surface is papillate but not strongly bumpy as typical for *Echinopsis deserticola*. Even though, the stomata are distinctly sunken and not at the stem surface as found in *Eulychnia iquiquensis*. Fig. 10. Section of the cortex tissue. Note the absence of any mucilage idioblasts. Bar = 200 μm in Fig. 9; bar = 500 μm in Fig. 10.

surface appears to be the product of bulges in the hypodermis (Fig. 6). The epidermis is often irregularly multiseriate. Finally, the cortex contains distinct mucilage idioblasts (Fig. 8, arrow) but lacks sclereids and, to a large part, idioblasts containing crystal druses.

A comparative study of additional material, including other species shows that the genus is rather uniform in its characteristic anatomical features. Some variation is commonly found in the size and shape of the idioblasts in the cortex and in some quantitative characters of the dermal system. For *Echinopsis*, a preliminary screening of material belonging to the complex of *Echinopsis chiloensis* sensu lato shows considerably more variation in anatomical characters. Specifically for this species complex, a stem sample from a plant somewhat intermediate between typical arborescent *Echinopsis chiloensis* and the low-growing *Echinopsis littoralis* (Johnson) H. Friedrich & G. D. Rowley, collected near Papudo, revealed a quite different dermal system which consists of a papillate epidermis derived from mostly irregular cell divisions and a flat layer of hypodermis cells (Fig. 9). Similar to *Echinopsis deserticola* the stomata are at least somewhat sunken into the hypodermis layer. The cortex of this distinct form differs from other Chilean species of *Echinopsis* by the absence of mucilage cells (Fig. 10). No instance was found, however, where the stem anatomy of *Echinopsis* even distantly approached that of *Eulychnia*.

Discussion

The exceedingly similar vegetative morphology of the taxa examined is puzzling and deceptive. In fact, the type material of *Cereus deserticola* Werdermann, which consists of a number of isotypes housed at various herbaria (the holotype at Berlin (B) was destroyed during World War II), represents a mixture of material from *Echinopsis* (flowers) and *Eulychnia* (vegetative material) (Leuenberger and Eggli 1996). Since a photograph of the destroyed holotype (Werdermann 1937) clearly shows the same composition of flowers from *Echinopsis* and stem segments from *Eulychnia*, and since an unpublished list of collections by Werder-

mann still housed at Berlin does not contain any entries for *Eulychnia*, it must be concluded that the mixture occurred when the material was collected in the field (Leuenberger pers. comm.).

The material used to illustrate this study (Figs. 1–8) was collected very close to the type locality of *Cereus deserticola* in the immediate vicinity of Taltal (Eggli 2915, Eggli 2915a). However, the fundamental and consistent differences in the stem anatomy of both taxa are readily observable by the naked eye, easily allowing the secure identification of the material in question to the genus.

Many more instances of easily discernible and diagnostic anatomical characters have been found during our work on South American cacti. Species of the genus *Neoporteria* Britton & Rose s. str. are easily differentiated from those of *Horridocactus* Backeberg based on the former's weakly developed dermal system and soft, greenish coloured, strongly mucilaginous cortex tissue (Nyffeler and Eggli 1997). Furthermore, *Pyrhocactus* (A. Berger) Backeberg & Knuth s. str. is distinguished from *Austrocactus* Britton & Rose by the presence of a very thick dermal system and a rather tough, non-mucilaginous cortex tissue. These anatomical characters can prove very useful for the identification of plants to genus in the field and for herbarium work with fragmented and incomplete specimens. For example, consideration of anatomical variation may be of value for resolving the still numerous typification problems that hamper systematic studies of the Cactaceae.

Detailed, interspecific studies of anatomical characters are not only useful for diagnostic or synthetic purposes. Comparative data are also the primary data source for many evolutionary studies (e.g. Harvey and Pagel 1991). A comparison of the correlation between different characters, or the correlation of characters with certain environmental factors in different species may give deeper insight into the evolutionary significance of these characters. Comparative molecular studies based on the chloroplast DNA marker *matK* revealed that *Eulychnia* is rather closely related to the genus *Corryocactus* Britton & Rose, while *Echinopsis* is tightly nested within an expanded Trichocereae clade (Nyffeler in prep.). Therefore, the strikingly similar external morphology of *Eulychnia* and *Echinopsis* represents a convergent adaptation to life in the arid habitats in Chile. The fundamental differences in the stem anatomy of the two species obviously stand for different "solutions" to the life under the harsh environmental conditions they experience. However, the precise role which these various anatomical features play within a physiological and ecological context is unknown. A most plausible hypothesis for the usefulness of the idioblastic sclereids is that they give mechanical support and reinforcement in order to prevent the parenchymatic tissue from collapsing during dry periods. Adaptation against herbivory might be an alternative explanation for these sclereids. Mucilage idioblasts are often found in plants from xeric habitats and are generally found to be related to their water-retaining capacity (Gregory and Baas 1989). Hence, the present comparative anatomical investigation might also be useful as a starting point for a more detailed evolutionary study of the biology of these strikingly similar looking columnar cacti from Chile.

Material for this study has been collected in connection with a study of the Cactaceae for the Proyecto Flora de Chile. UE is grateful to the Swiss National Science Foundation for financing this project (no. 31-39176.93), and both authors acknowledge support for field work from the Schweizerische Akademie der Naturwissenschaften and (to RN) the Cactus and Succulent Society of America. Further thanks go to Beat Leuenberger (Berlin) for his involvement with the project, to Anton Igersheim and Urs Jauch (both University of Zürich) for help with the anatomical work and the SEM, and to David Baum (Harvard University) and an anonymous reviewer for critical comments.

Zusammenfassung

Eulychnia iquiquensis and *Echinopsis deserticola* kommen sympatrisch in den küstennahen Gebieten der chilenischen Atacamawüste vor. Sie wachsen oft in gemischten Gruppen, und das oberflächliche Erscheinungsbild und die allgemeine Morphologie sind so ähnlich, daß die beiden Arten ohne Blüten und Früchte leicht verwechselt werden können. Im Gegensatz dazu ist die Sproßanatomie der beiden nicht näher verwandten Taxa stark verschieden. *Eulychnia* hat eine flache Sproßoberfläche mit an der Oberfläche liegenden Stomata und weist in der Rinde zwei verschiedene Formen von idioblastischen Sklereiden auf, während die untersuchten Arten von *Echinopsis* eine stark gewellte Sproßoberfläche mit tief zwischen den Aufwölbungen eingesenkten Spaltöffnungen zeigen und sowohl in der Rinde wie im Mark Schleimidioblasten aufweisen. Viele dieser Merkmale können bereits mit einer Handlupe an Sproßquerschnitten erkannt werden. Wegen ihres diagnostischen Wertes sind sie bei der raschen Identifikation selbst von kleinen sterilen Sproßfragmenten nützlich und können zur Lösung von Typifizierungsproblemen beigezogen werden.

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