Annals of Botany **80**: 767–786, 1997

Comparative Stem Anatomy and Systematics of *Eriosyce sensu lato* (Cactaceae)

RETO NYFFELER*† and URS EGGLI‡

* *Institut für Systematische Botanik, Universität Zürich, Zollikerstrasse 107, CH-8008 Zürich, Switzerland and* ‡ *Städtische Sukkulenten-Sammlung, Mythenquai 88, CH-8002 Zürich, Switzerland*

Received: 12 May 1997 Accepted: 20 August 1997

The genus *Eriosyce* as circumscribed by Kattermann (*Succulent Plant Research* **1**: 1–176, 1994) comprises six subsections with 33 species and 38 heterotypic infraspecific taxa and is restricted in distribution to Chile and NW Argentina. A total of 19 anatomical and gross morphological characters were studied from stem material of 27 taxa of *Eriosyce* and six outgroup taxa from the genera *Austrocactus*, *Copiapoa*, *Corryocactus*, *Eulychnia* and *Neowerdermannia* (all from the tribe Notocacteae of subfamily Cactoideae). Comparisons between field-collected and glasshouse-cultivated plant material, as well as comparisons between samples from different positions on the stem, allowed an assessment of the variability of various characters.

A detailed cladistic investigation with different character composition and character coding was conducted to check for combinations of characters that support a number of different clades. *Eriosyce* subsect. *Chileosyce* (including *E. napina* and *E. odieri*, but excluding *E. laui*) and *E.* subsect. *Neoporteria* are very well characterized by a number of the attributes investigated, such as a papillate or completely flat epidermal relief, a very soft and strongly mucilaginous cortex, or a tuberculate stem with the podaria arranged in helical lines. The usefulness of the anatomical and morphological data was examined further by a cladistic analysis of a subgroup of 21 taxa supplemented with data on flowers, fruits and seeds (data from published sources). The present circumscription of *Eriosyce* (including *Horridocactus*, *Neoporteria*, and *Thelocephala*) is not seriously questioned by these cladistic analyses, with the possible exception of *Islaya*. The position of *E. laui* remains unresolved.

Key words: Cactaceae, cacti, *Eriosyce*, Argentina, Chile, anatomy, epidermis, hypodermis, cortex, mucilage, cladistics, classification.

INTRODUCTION

The classification of the family Cactaceae (98 genera, and about 1500 species according to Barthlott and Hunt, 1993) has traditionally been based on external characters of stems, flowers and fruits. The disposition, shape and outline of tubercles and their arrangements into vertical or helical lines, the number and position of spines within the areoles, and characters of the indumentum of flowers and fruits have been especially used in various combinations to delimit taxa at various ranks. Since parallel reduction, and even complete loss, of characters in different lineages are prominent trends in cactus evolution, misinterpretations are common and the lack of agreement on supraspecific relationships in the family is notorious.

Anatomical characters have very rarely been taken into consideration in systematic studies of cacti (for exceptions see Gibson and Horak, 1978; Lüthy, 1995). This is the more surprising since many stem features, such as presence or absence of mucilage, size proportions and macroscopical architecture of vascular bundles, colouring of cortex tissues, firmness of the dermal system and special structures of the epidermal relief, are readily observable without using sophisticated methods. Most anatomical investigations have focused an anatomy *per se*, concentrating on the study of selected structural features (e.g. Schleiden, 1845; Boke, 1980). Rather few studies have been conducted in a more comparative manner which may permit conclusions concerning questions of systematic interest. The early studies by Lauterbach (1889) on mucilage cavities and by Nommensen (1910) on the dermal system suffered from an inadequate classification system. Other studies had an excessively broad approach with inadequate numbers of samples, and did not allow systematic conclusions to be drawn (e.g. Schill *et al.*, 1973 on stem surface relief characters; Condé, 1975 on various features of the dermal system, cortex and vascular system). However, all these studies showed, to a greater or lesser degree, the great wealth of anatomical features present in cacti which can now be exploited concentrating on a more systematic background (e.g. Mauseth, 1996).

The present comparative investigation of *Eriosyce* (*sensu lato*, s.l.) concentrated on characters of the dermal system which were found to show considerable variation. The dermal system of cacti generally consists of a uniseriate epidermis covered with a cutin layer, and a well-developed, multiseriate hypodermis of collenchyma cells (Schleiden, 1845; Gibson and Nobel, 1986). The outer periclinal walls of the epidermal cells are commonly flat or slightly convex, but bumpy or papillate stem surfaces are known in a number of different genera. The cell walls of the hypodermis layers are often considerably thickened with accumulations of pectic substances and hence contribute to a large extent to the firmness and xeromorphy of the dermal system.

† Current address: Department of Organismic and Evolutionary Biology, Harvard University Herbaria, 22 Divinity Avenue, Cambridge, MA 02138, U.S.A.

0305-7364/97/060767+20 $25.00/0 bo970518

Mucilage cells are widely reported in cacti (Lauterbach, 1889; Gibson and Nobel, 1986) and their presence can be confirmed macroscopically because of the slimy nature of the tissue. They commonly occur as solitary and often enlarged idioblasts dispersed in the parenchymatic tissue of the cortex. The functional significance of mucilage is not yet fully understood, but is commonly related to its water-retaining capacity (Gregory and Baas, 1989).

The genus *Eriosyce* Philippi, in its present circumscription by Kattermann (1994), comprises six subsections (in two sections) with 33 species and 38 heterotypic infraspecific taxa (subspecies and varieties). According to this broad concept, *Eriosyce* includes the following formerly separate genera (species number as given in Kattermann, 1994): (1) *Pyrrhocactus* (A. Berger) A. W. Hill (in the sense of Backeberg, 1959; five spp.; W. Argentina); (2) *Islaya* Backeberg (one sp.; N. Chile, S. Peru); (3) *Horridocactus* Backeberg (incl. *Neochilenia* Dölz pro parte and *Thelocephala* Y. Ito pro parte; 15 spp.; C. Chile); (4) *Thelocephala* Y. Ito pro parte, excluding the type (as *Eriosyce* subsect. *Chileosyce* Kattermann; five spp.; C. Chile); (5) *Neoporteria* Britton & Rose (five spp.; C. Chile).

This group of genera has had a chequered history as testified by the number of generic synonyms (Kattermann, 1994; compiled by Hunt, Taylor and Zappi). Long recognized as a closely related group of taxa, different classifications have been proposed by various authors. Narrow generic concepts were favoured by Backeberg (1959) and Ritter (1980), while Buxbaum (1975) and especially Donald and Rowley (1966) were more conservative; the latter authors united all but *Eriosyce* into *Neoporteria*. The broad concept of *Eriosyce* in the sense of Kattermann (1994), originated in earlier discussions for the IOS Consensus Classification initiative (Hunt and Taylor, 1990).

The infrageneric and specific classification of *Eriosyce* is partly unresolved. The present study was conducted to investigate the potential of various anatomical characters to elucidate interrelationships and possible lines of evolution in *Eriosyce*. For the sake of simplicity, the most recent synoptic classification by Kattermann (1994) is used here as the working basis for identification and discussion.

The relationships of *Eriosyce sensu lato* within the Cactaceae are little-explored. Kattermann (1994) touched on the subject very briefly and mentioned *Austrocactus* Britton & Rose, *Copiapoa* Britton & Rose, *Eulychnia* Philippi, and *Neowerdermannia* Fric as possible allies. The cladistic analysis by Wallace (in Kattermann, 1994) used *Corryocactus brevistylus* (Vaupel) Britton & Rose as outgroup.

TABLE 1. *Taxa investigated with the infrageneric classification of* Eriosyce *by Kattermann* (1994) *and acronyms used in the character study and cladistic analyses. All taxa were included in the cladistic analyses of* Search I. *Those incorporated in* Search II *are marked with an asterisk*

Eriosyce	
Eriosyce subsect. *Chileosyce* Kattermann	
E. aerocarpa (F. Ritter) Kattermann*	Chi.aer
E. krausii (F. Ritter) Kattermann*	Chi.kra
E. laui J. Lüthy*	Chi.lau
Eriosyce subsect. *Eriosyce*	
E. aurata (Pfeiffer) Backeberg*	Eri.aur
Eriosyce subsect. *Horridocactus* (Backeberg) Kattermann	
E. aspillagae (Söhrens) Kattermann*	Hor.asp
E. curvispina (Colla) Kattermann*	Hor.cur
E. curvispina var. *tuberisulcata* (Jacobi) Kattermann	Hor.cur.tu
E. heinrichiana (Backeberg) Kattermann [ssp. *heinrichiana*]*	Hor.hei.1
	Hor.hei.2
E. heinrichiana ssp. *simulans* (F. Ritter) Kattermann	Hor.hei.si
E. kunzei (C. F. Förster) Kattermann*	Hor.kun
E. marksiana (F. Ritter) Kattermann*	Hor.mar
E. napina (Philippi) Kattermann*	Hor.nap
E. odieri (Salm-Dyck) Kattermann [ssp. *odieri*]*	Hor.odi
E. odieri ssp. *glabrescens* (F. Ritter) Kattermann	Hor.odi.gl
E. taltalensis (Hutchison) Kattermann [ssp. and var. *taltalensis*]*	Hor.tal
E. taltalensis ssp. *paucicostata* (F. Ritter) Kattermann	Hor.tal.pa
E. taltalensis var. *pygmaea* (F. Ritter) Kattermann	Hor.tal.py
Eriosyce subsect. *Islaya* (Backeberg) Kattermann	
E. islayensis (C. F. Förster) Kattermann*	Isl.isl
Eriosyce subsect. *Neoporteria* (Britton & Rose) Kattermann	
E. chilensis (K. Schumann) Kattermann*	Neo.chi
E. senilis (Backeberg) Kattermann [ssp. *senilis*]*	Neo.sen
E. senilis ssp. *coimasensis* (F. Ritter) Kattermann	Neo.sen.co
E. subgibbosa (Haworth) Kattermann [ssp. *subgibbosa*]*	Neo.sub
E. subgibbosa ssp. *clavata* (K. Schumann) Kattermann	Neo.sub.cl
E. villosa (Monville) Kattermann*	Neo.vil
Eriosyce subsect. *Pyrrhocactus* (A. Berger) Kattermann	
E. andreaeana Kattermann*	Pyr.and
E. bulbocalyx (Werdermann) Kattermann*	Pyr.bul
E. strausiana (K. Schumann) Kattermann*	Pyr.str
Austrocactus patagonicus (Weber) Backeberg	Aus.pat
Copiapoa cinerea (Philippi) Britton & Rose	Cop.cin
Copiapoa krainziana F. Ritter	Cop.kra
Corryocactus brevistylus (K. Schumann ex Vaupel) Britton & Rose*	Cor.bre
Eulychnia castanea Philippi	Eul.cas
Neowerdermannia chilensis Backeberg	New.chi

MATERIALS AND METHODS

Plant material

For this investigation, stem material from 33 different taxa (27 taxa representing 20 species of *Eriosyce* and six outgroup taxa) was available (Table 1; supplemented with the supraspecific classification and the acronyms used for Tables and the cladistic analyses). In total, 52 collections were investigated (Appendix 1), of which 24 samples were collected in the field and 28 samples were prepared from plants cultivated in the glasshouses at the Botanischer Garten der Universität Zürich, the Botanischer Garten Berlin-Dahlem and the Städtische Sukkulenten-Sammlung Zürich. In most cases, only one or two samples were available for each taxon. In the case of *Eriosyce heinrichiana* ssp. *heinrichiana*, the three samples of this taxon turned out to be anatomically very heterogeneous and fell into two

TABLE 2. *List of characters and character states*

Epidermis
1. Epidermal relief: flat [0]; bumpy [1]; short-papillate [2]; long-papillate [3].
2. Thickness of the epidermis layer (excluding bulging outer periclinal walls (maxima): 20–30 μm [0]; 31–40 μm [1]; 41–70 μm [2].
3. Secondary cell divisions of epidermis cells: only periclinal [0]; periclinal or oblique [1]; not applicable (no secondary cell divisions) [—].
4. Number of periclinal and oblique secondary cell divisions in non-papillate cells: none [0]; few (< 0·33 of all non-papillate cells) [1]; some (0·33–0·66) [2]; many (> 0·66) [3].
5. Number of periclinal and oblique secondary cell divisions in papillate cells: none [0]; few (< 0·33 of all papillate cells) [1]; some (0·33–0·66) [2]; many (> 0·66) [3]; not applicable (no papillae) [—].

Hypodermis
6. Number of cell layers in the hypodermis (maxima): 1–2 [0]; 3 [1]; 4–7 [2]; not applicable (no hypodermis) [—].
7. Thickness of the hypodermis layer (maxima): 30–50 μm [0]; 60–110 μm [1]; 140–350 μm [2]; not applicable (no hypodermis) [—].

Cortex and pith
8. Firmness of the cortex tissue: soft or very soft [0]; intermediate [1]; tough [2].
9. Presence of mucilage in stem sections: not mucilaginous [0]; slightly or locally mucilaginous [1]; distinctly mucilaginous [2]; intensively mucilaginous [3].
10. Colour of the central and inner cortex (yellowish colours are not coded): pale greenish or whitish [0]; intermediate [1]; green [2].
11. Ratio of pith to plant diameter (in transverse sections at the widest diameter): 0·15–0·20 [0]; 0·22–0·28 [1]; 0·30–0·45 [2].

Stems
12. Stem shape (ratio of height to diameter): subglobular (ratio < 0·75) [0]; globular (0·75–2·0) [1]; subcolumnar (2·1–6·0) [2]; columnar (> 6·0) [3].
13. Disposition of podaria: in orthostichies (in straight lines) [0]; in parastichies (in helical lines) [1].
14. Formation of podaria: in ribs [0]; in tuberculate ribs [1]; as distinct tubercules [2].
15. Shape of main spines: straight [0]; intermediate [1]; curved [2].
16. Orientation of main spines: downwards or porrect [0]; upwards or sideways [1]; radiating [2]; appressed [3].

Roots
17. Root system: fibrous [0]; intermediate [1]; turbinate (with taproot) [2].
18. Shape of taproot: broad and massive [0]; narrow and rather small [1]; not applicable (no taproot) [—].
19. Necklike constriction between stem and taproot: absent [0]; present [1]; not applicable (no taproot) [—].

Codings for the cladistic analyses are given in square brackets.

groups. They were, therefore, treated as separate units for the character study and the cladistic analyses (acronyms Hor.hei.1 and Hor.hei.2). Voucher specimens of the field-collected material are deposited in one or more of the following herbaria: Berlin (B), Córdoba (CORD), Mendoza (MERL), Santiago de Chile (SGO) and Städtische Sukkulenten-Sammlung Zürich (ZSS). Vouchers prepared from glasshouse-cultivated plants are housed at ZSS.

Character study

The macromorphological stem and root characters were recorded from live plants for herbarium specimens. Stem measurements represent mean maxima typical for each taxon. Plant and pith diameter were measured at the broadest part of the stems.

Samples for anatomical investigations were taken from mature stem regions that were at least two growing seasons old. After fixation in FAA (1 part formaldehyde 37%, 1 part acetic acid and 18 parts ethanol 70%) for at least 20 d, stem material was washed and transferred to 70% ethanol for storage.

Characters were studied from three to five hand sections for both the dermal system and the inner cortex region stained with ruthenium red (0·01% in 70% ethanol). Relief features were studied from epidermal strips peeled off with the help of a lancet-needle. This screening allowed the definition of 19 characters and the corresponding states (Table 2) for further investigations. Some characters that were given attention at first were later omitted from consideration because they proved to be too variable or because sufficient appropriate material was not available for comparative study. Variation in all characters examined is quantitative. Accordingly, the circumscription of the different character states was not straight-forward (Stevens, 1991); however, in view of the limited number of samples, no special efforts were given to this problem.

Four individual plants (*Eriosyce aspillagae* ex cult. Z, *E. islayensis* ex cult. Z, *E. napina* Ritter 249, *E. subgibbosa* ssp. *subgibbosa* Jucker 142) from cultivation were examined in more detail, with samples from different positions along the stems to ascertain the variability of the characters within individuals. Furthermore, differences in characters comparing glasshouse-cultivated and field-collected material were investigated for 12 taxa for which material from both sources were available.

For microtome sectioning, small stem samples were removed from upper rib flanks or tubercles, dehydrated in an ethanol series, embedded in hydroxyethyl-methacrylate resin and cut at 4–6 μm with a Leitz rotation microtome (Igersheim, 1993; Igersheim and Cichocki, 1996). Sections were stained with toluidine blue O (0·02%).

For SEM study, epidermal strips were taken from rib flanks near the areoles, cleaned in an ultrasonic bath for approx. 1 min. and critical point dried. Samples were then mounted on metal stubs, sputter-coated with gold, and examined with a Cambridge Stereoscan S4 SEM.

Data analysis

The usefulness of the anatomical and morphological stem characters to elucidate interrelationships was investigated with the help of a number of cladistic analyses. The unchanged adoption of the character conceptualization designed for the comparative investigation necessitated the coding of inapplicable character states (Platnick, Griswold and Coddington, 1991). Characters with a variable expression were scored as missing values. Multistate characters were coded either as unordered to minimize hypotheses concerning character evolution, or as ordered (except for characters 13, 16, 18 and 19, for which no transformation series could be proposed) to represent morphoclines or evolutionary trends (Hauser and Presch, 1991; Wilkinson, 1992).

Cladograms were constructed using the software Hennig86 (Farris, 1988) with the heuristic search options (mh* followed by bb*). Problems were encountered with multiple islands in the most parsimonious cladograms (Maddison, 1991). In order to reduce this effect, all analyses were run five times each with a different order of the terminals in the data matrix.

Strict consensus cladograms were calculated to check for those clades that are present in all original cladograms.

Search I comprised a detailed cladistic study of 34 terminals—27 ingroup taxa (*E. heinrichiana* ssp. *heinrichiana* coded as two distinct terminals) and six outgroup taxa—and the 19 anatomical and morphological characters examined for this investigation. Initial analyses showed that the data contained a considerable amount of homoplasy. While a number of clades were found to be well supported, their interrelationships proved to be very unstable, which is probably also due to the discrepancy between the number of characters and terminals. Tests with character-weighting strategies (Farris, 1969; successive weighting) did not remove this problem but created further uncertainties (Swofford *et al*., 1996). Finally, a method of sequential removing of individual characters and groups of characters from the original data matrix was used to compile 56 different variants of data matrices for the cladistic investigation (Appendix 2). This approach, somewhat resembling a jackknife resampling technique (a similar approach was proposed by Davis, 1993), was used to check for the presence of a number of different monophyletic groups and the positions of the outgroup taxa. Furthermore, it allowed the identification of those characters which are crucial in the support of particular clades. This approach was favoured here as the most 'objective' way to deal with the present data.

The inclusion of infraspecific taxa was justified here with reference to the problem of polymorphic character states (Nixon and Davis, 1991; subtaxon coding). Furthermore, the present study revealed that some of the taxa classified at infraspecific level by Kattermann (1994) may represent distinct species. The cladograms were rooted with *Corryocactus brevistylus*.

Search II was an analysis of 21 selected terminals of *Eriosyce* (marked with an asterisk in Table 1; *E. heinrichiana* coded as two distinct terminals) and *Corryocactus brevistylus* as the outgroup taxon. The 19 anatomical and morphological characters of this study were supplemented by a further 39 characters from flowers, fruits and seeds which were extracted from the cladistic analysis by Wallace (in Kattermann, 1994; Appendix 3). Effectively this amounts to a replacement of the original data on vegetative characters with that from this investigation. For comparison, a strict consensus cladogram of the same subgroup of taxa but with the original data was calculated.

RESULTS

Variability of stem characters within individuals

A more detailed anatomical examination of four selected individual plants revealed a certain degree of variability in various characters of the dermal system, depending on the position on the stem from which the sample was taken (e.g. from the top of a tubercle or from its base). Features of epidermal relief appear to be most affected by this intra-individual variability. Two strikingly different relief patterns were found in *Eriosyce islayensis*, where the typical bumpy relief with somewhat sunken stomata (Fig. 1) is replaced by an unstructured smooth surface in samples from the rib base (Fig. 3). However, a study of transverse sections of both samples showed that the basic architecture (in the case of *E. islayensis* a multilayered epidermis from numerous periclinal and oblique cell divisions) is not affected (Figs 2 and 4). Similar differences in surface architecture, though not as fundamental as in *E. islayensis*, were also observed in other taxa, and made it clear that samples must be taken from similar positions for comparison. The age of the tissue does not seem to have much effect on the architecture of the dermal system.

A certain amount of size variation in the cells of the parenchymatic cortex was found, depending on position and age. The cells are generally largest some distance from the central cylinder. Colouring of the cortex was always studied from transversal sections of the stems at the vertical position where the colour was best developed. In general (except for taxa of *E.* subsect. *Neoporteria*), there is a gradual transition from a greenish layer formed by the chlorophyll-containing and palisade-like outer cortex to the pale inner cortex obviously devoid of chlorophyll. Deviations from this pattern are found in very young as well as in older parts of the stems.

Differences between field-collected and glasshouse-cultivated stem samples

The dermal system of plants collected in the field is markedly more xeromorphic compared with that from individuals of the same taxon grown in the glasshouse (Figs 5 and 6). Specimens from natural habitats generally have a thicker cuticle and thicker outer periclinal walls in the outermost epidermal layer. Furthermore, the hypodermis often consists of a larger number of cell layers (at least when more than two or three layers are typical for the taxon) and the hypodermal cell walls are more strongly thickened.

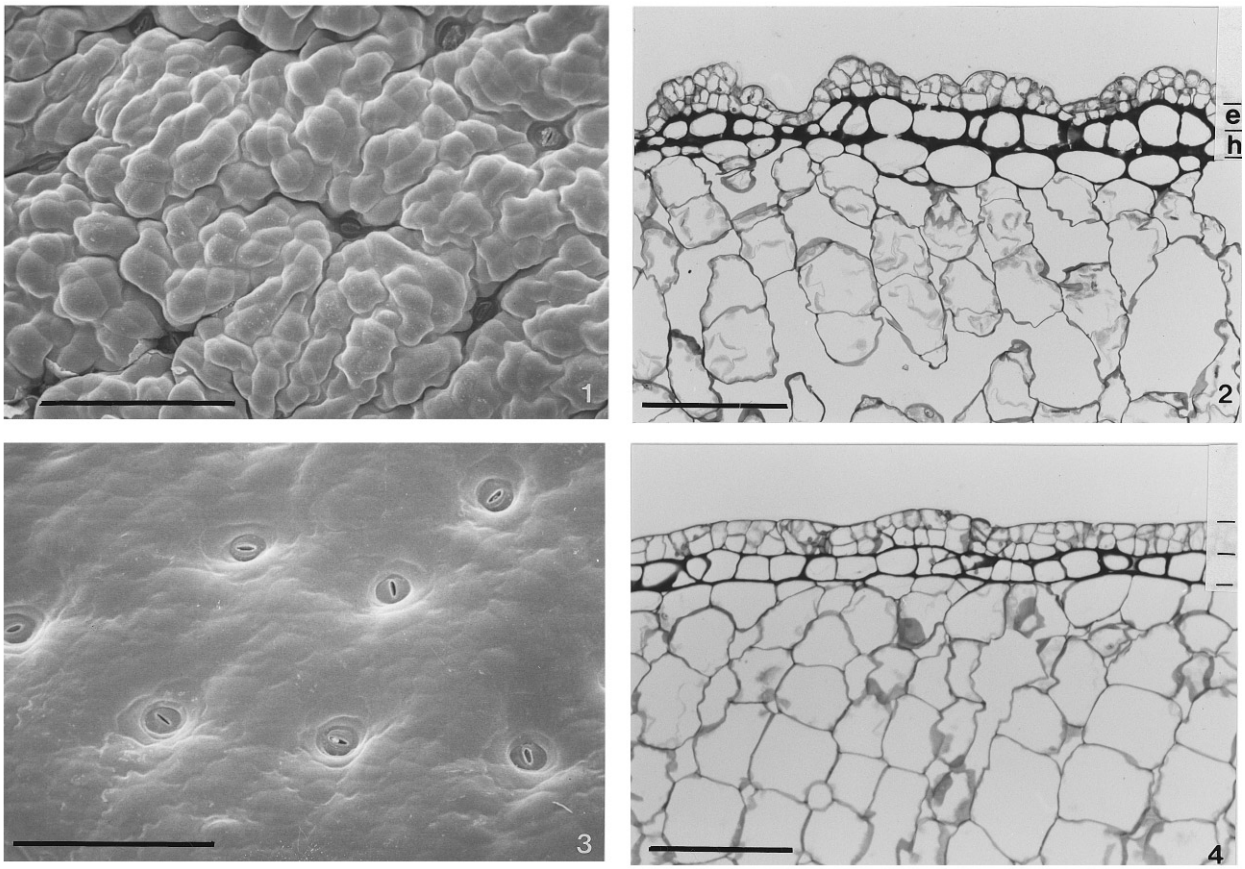
Characters of the cortex, such as firmness of the cortical tissue or presence of mucilage idioblasts, show minor quantitative differences when field-collected and glasshouse-cultivated material is compared. In contrast to the differences found in the dermal system, those of the cortex are more difficult to understand, and it is uncertain whether they were induced by different environmental conditions or whether they represent inter-individual variability.

Discussion of the characters

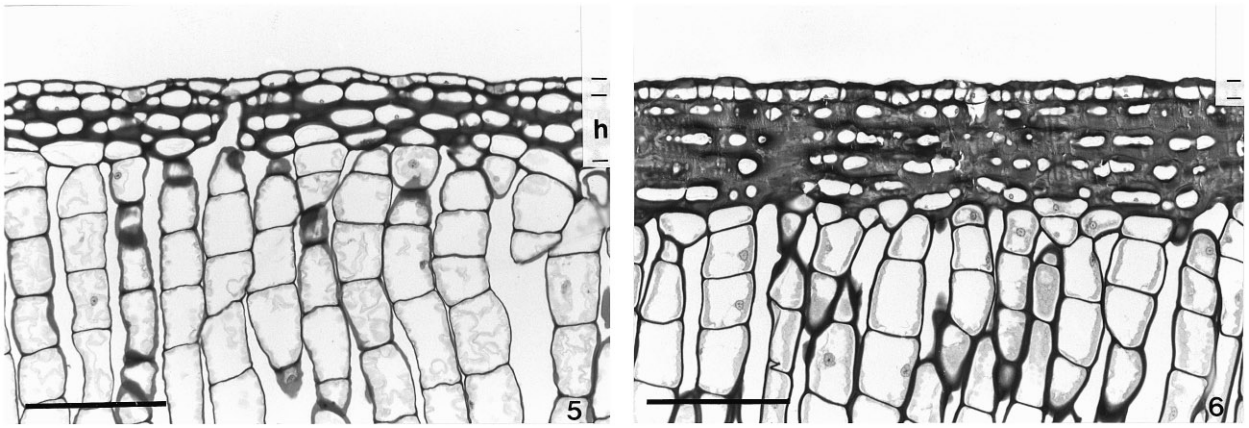
For each taxon, details on the 19 characters investigated are listed in Tables 3, 4 and 5 (data II in the sense of Stevens, 1996).

Epidermis

Relief (*Character 1, Table 3*). A great diversity of relief structures was found amongst the taxa of *Eriosyce*. Except



FIGS 1–4. Variation in the epidermal relief within a single individual of *Eriosyce islayensis* [hort. Z]. Fig. 1. SEM photograph of the epidermal relief from the top of the rib. Fig. 2. Transverse section of a similar area as shown in Fig. 1. Fig. 3. SEM photograph of the epidermal relief from the base of the rib flank. FIG. 4. Transverse section of a similar area as shown in Fig. 3. Bars = 250 μm. Note the characteristic irregularly multiseriate epidermis present in both samples (Figs 2 and 4). Bars at the right margin of Figs 2 and 4 mark the dermal system with epidermis (above; e) and hypodermis (below; h).



FIGS 5–6. Differences in the dermal system between glasshouse-grown and field-collected specimens of *Eriosyce strausiana*. Fig. 5. Specimen from cultivation [Kattermann 572]. Fig. 6. Specimen collected in the field [Nyffeler, Eggli & Lüthy 383]. Conspicuous differences between the two samples are the thickness of the outer tangential walls of the epidermis, the number of hypodermal layers and the accumulation of pectic substances in the hypodermis. Bars = 250 μm. Bars at the right margin mark the dermal system with epidermis (above) and hypodermis (below; h).

TABLE 3. *Comparative data of epidermis and hypodermis characters*

Taxon	Character 1 Epidermal relief	(Character 1) Height of papillae (maxima; in μm)	Character 2 Thickness of epidermal layer (excluding papillae; in μm)	Character 3 Secondary cell divisions of epidermal cells	Character 4 Number of periclinal or oblique secondary cell divisions in non-papillate cells	Character 5 Number of periclinal or oblique secondary cells in papillate cells	Character 6 Number of cell layers in the hypodermis	Character 7 Thickness of the hypodermal layer (maxima; in μm)
Chi.aer	Short-papillate	20	20–30	Periclinal/oblique	Few	Some	1–2	40–60
Chi.kra	Short-papillate	30	25–30	Periclinal/oblique	None	Few	1–2	40–60
Chi.lau	Short-papillate	30	40–70	—	None	None	—	—
Eri.aur	Short-papillate	30	25–35	Only periclinal	Few	Few	4–7	200–350
Hor.asp	Bumpy	—	30–35	—	None	—	2–3	60–80
Hor.cur	Bumpy	—	30–40	—	None	—	2–3	80–100
Hor.cur.tu	Bumpy	—	30–40	—	None	—	2–3	80–90
Hor.hei.1	Bumpy	—	30–40	Periclinal/oblique	Some	—	2–3	80–100
Hor.hei.2	Bumpy	—	25–35	—	None	—	2–3	100–110
Hor.hei.si	Short-papillate	20	20–25	Periclinal/oblique	None	Some	2–3	80–100
Hor.kun	Bumpy	—	30–40	Only periclinal	Few	—	2–3	80–100
Hor.mar	Bumpy	—	30–40	—	None	—	2–3	70–100
Hor.nap	Long-papillate	80	25–30	Periclinal/oblique	Some	Many	2–3	60–80
Hor.odi	Long-papillate	50	20–30	Periclinal/oblique	Some	Many	1	50–60
Hor.odi.gl	Short-papillate	20	20–25	Periclinal/oblique	None	Some	1–2	40–60
Hor.tal	Flat	—	20–25	—	Few	—	1–2	40–70
Hor.tal.pa	Long-papillate	70	20–25	Periclinal/oblique	Some	Many	1–2	50–80
Hor.tal.py	Bumpy	—	30–35	—	None	—	1–2	30–50
Isl.isl	Bumpy	—	50–90	Periclinal/oblique	Many	—	1–2	50–200
Neo.chi	Flat	—	30–35	—	None	—	1	30–40
Neo.sen	Bumpy	—	15–25	—	None	—	1–2	20–40
Neo.sen.co	Bumpy	—	30–40	—	None	—	2–3	50–60
Neo.sub	Flat	—	25–30	—	None	—	1–2	40–60
Neo.sub.cl	Short-papillate	20	15–20	Periclinal/oblique	Few	Many	1–2	20–40
Neo.vil	Flat	—	20–25	—	None	—	1	30–40
Pyr.and	Bumpy	—	30–40	—	None	—	1–2	40–60
Pyr.bul	Bumpy	—	20–25	—	None	—	4–6	130–180
Pyr.str	Bumpy	—	20–30	—	None	—	4–6	120–250
Aus.pat	Bumpy	—	30–40	—	None	—	2–3	50–80
Cop.cin	Long-papillate	60	30–40	Only periclinal	Many	Many	3–4	80–100
Cop.kra	Long-papillate	50	40–60	Only periclinal	Many	Many	3–4	100–140
Cor.bre	Bumpy	—	40–50	Only periclinal	Many	—	2–4	150–200
Eul.cas	Bumpy	—	30–40	Only periclinal	Many	—	2–3	60–80
New.chi	Flat	—	30–40	—	None	—	1–2	30–70

TABLE 4. *Comparative data on cortex characters*

Taxon	Character 8 Firmness of the cortex tissue	(Character 8) Diameter of cortex cells (mean maxima in μm)	Character 9 Presence of mucilage in stem sections	Character 10 Colour of the central and inner cortex	Character 11 Ratio of pith to stem diameter
Chi.aer	Soft	250–300	?	Pale greenish	0·40
Chi.kra	Soft	150–200	?	Pale greenish	0·35
Chi.lau	Very soft	160–200	Not mucil.	Whitish	0·25
Eri.aur	Tough	160–200	Not mucil.	Whitish	0·25
Hor.asp	Intermediate	250–350	Not mucil.	Pale greenish	0·33
Hor.cur	Tough	120–140	Not mucil.	Whitish	0·25
Hor.cur.tu	Tough	120–140	Not mucil.	Whitish	0·30
Hor.hei.1	Intermediate	200–250	Slightly mucil.	Dark yellow	0·35
Hor.hei.2	Intermediate	250–300	Slightly mucil.	Yellow	0·32
Hor.hei.si	Intermediate	280–300	Distinctly mucil.	Pale greenish	0·23
Hor.kun	Tough	200–250	Slightly mucil.	Whitish	0·38
Hor.mar	Tough	120–150	Not mucil.	Pale greenish	0·22
Hor.nap	Soft	250–300	Slightly mucil.	Intermediate	0·25
Hor.odi	Soft/intermediate	200–280	Not mucil.	Intermediate	0·45
Hor.odi.gl	Intermediate	200–250	Not mucil.	Intermediate	0·35
Hor.tal	Intermediate	250–300	Slightly mucil.	Pale greenish	0·28
Hor.tal.pa	Intermediate	250–350	Not mucil.	Pale greenish	0·26
Hor.tal.py	Intermediate	300–320	Not mucil.	Pale greenish	0·36
Isl.isl	Tough	200–250	Not mucil.	Pale greenish	0·25
Neo.chi	Soft	250–300	Intensively mucil.	Green	0·32
Neo.sen	Soft	250–300	Intensively mucil.	Intermediate	0·28
Neo.sen.co	Intermediate	?	Intensively mucil.	Intermediate	0·24
Neo.sub	Soft	250–300	Intensively mucil.	Green	?
Neo.sub.cl	Intermediate	250–300	Intensively mucil.	Green	0·24
Neo.vil	Soft	250–350	Intensively mucil.	Green	0·25
Pyr.and	Tough	160–200	Not mucil.	Pale greenish	0·25
Pyr.bul	Tough	150–180	Not mucil.	Pale greenish	0·26
Pyr.str	Tough	120–150	Not mucil.	Pale greenish	0·28
Aus.pat	Soft	?	Intensively mucil.	Intermediate	0·15
Cop.cin	Intermediate	250–300	Not mucil.	Yellowish	0·26
Cop.kra	Intermediate	200–250	Not mucil.	Yellowish	0·20
Cor.bre	Intermediate	250–280	Slightly mucil.	Pale greenish	0·18
Eul.cas	Intermediate	250–300	Not mucil.	Whitish	0·22
New.chi	Soft/intermediate	250–300	Not mucil.	Whitish	0·26

for *E. islayensis*, where the hypodermal cells contribute to the bumpy surface (Figs 1 and 2), these features are the product of the epidermal layer. Four basic types are differentiated for this study—long-papillate (Figs 7 and 8), short-papillate, bumpy (Figs 9 and 10) and flat (Figs 11 and 12)—all of which are interconnected and not always clearly distinguishable. The circumscription of these different states relies to some extent on the height of the papillae formed by the outer periclinal wall. Depending on the position on the stems from which the sample was taken, taxa which typically have a papillate epidermis occasionally show outer periclinal walls which form only small bumps or are completely flat (see above). The relief structures form a 'reduction series' from a long-papillate and short-papillate state to a bumpy and finally to a flat state. Correspondingly, the most derived (in complexity) state was coded for the different samples.

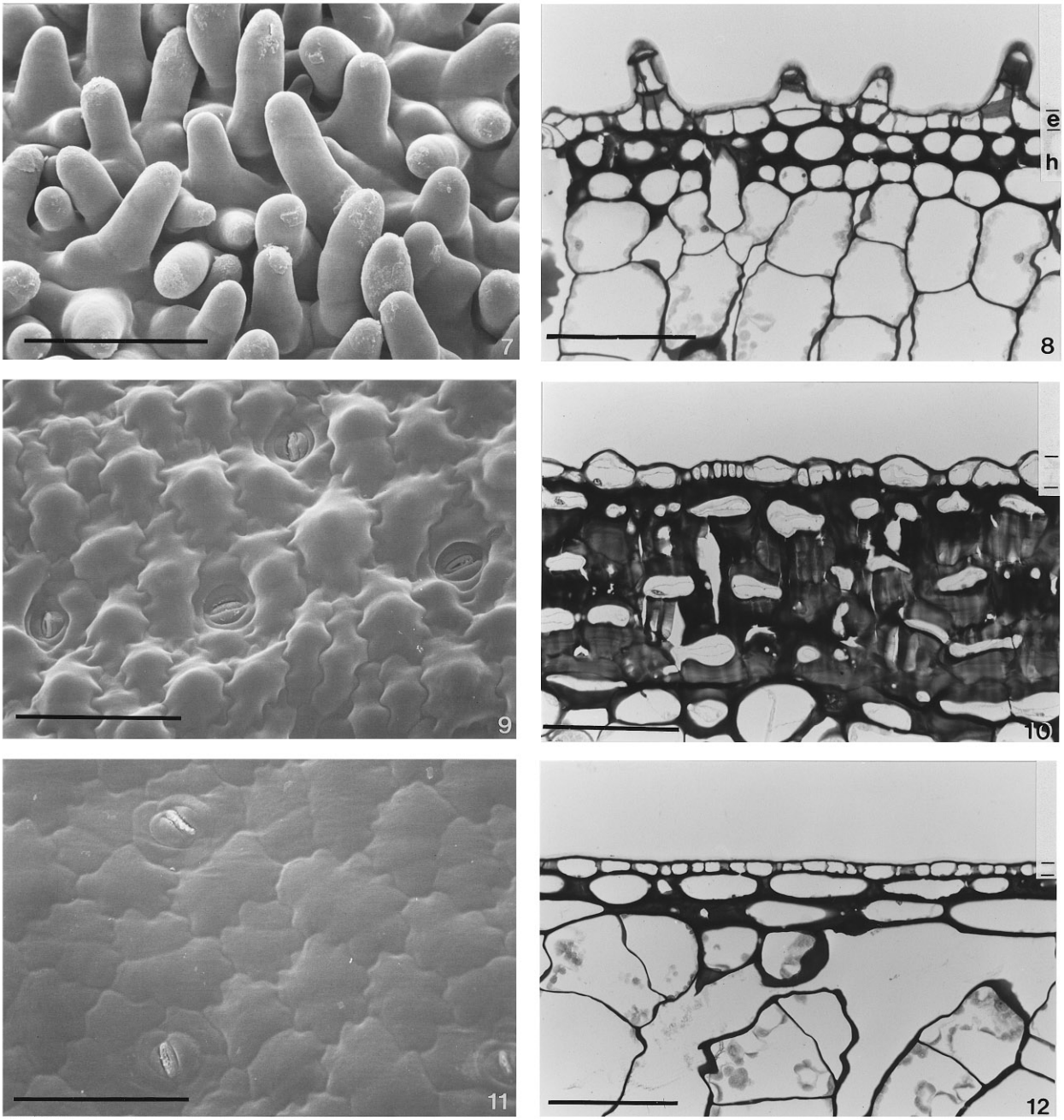
Papillae 50 to 80 μm long are typical for *E. napina* (Figs 7 and 8), *E. odieri* ssp. *odieri* and *E. taltalensis* ssp. *paucicostata*. Long papillae, but more acute at the tips, were also found for the outgroup taxa of *Copiapoa* (Fig. 21). Distinctly papillate epidermal cells occur in the taxa of *E.* subsect. *Chileosyce* (Fig. 17), *E. aurata* (Figs 9 and 10), *E. heinrichiana* ssp. *simulans* (Fig. 14; very inconspicuous) and *E. subgibbosa* ssp. *clavata* (Fig. 15). In these taxa papillae are up to 30 μm long. The epidermal bulges of *E. laui* are formed by large undivided cells—much larger compared to those of all other taxa of *Eriosyce*. A bumpy epidermal relief with slightly convex periclinal walls is found in a number of taxa of *Eriosyce* (Figs 5 and 13) but also in the outgroups of *Austrocactus* (Fig. 22), *Corryocactus* (Fig. 19) and *Eulychnia* (Fig. 20). The epidermal relief of *E. islayensis* is noteworthy for the secondary structure, which is introduced by groups of vertically elongated hypodermal cells and somewhat sunken stomata (Fig. 2). Finally, a more or less flat epidermis is found in *E.* subsect. *Neoporteria* (Fig. 16), *E. taltalensis* var. *taltalensis* (Figs 11 and 12) and the outgroup of *Neowerdermannia*.

Thickness (*Character 2, Table 3*). The thickness of the epidermal layer ranges between 15 and 40 μm in taxa with a predominantly uniseriate layer (e.g. *E. taltalensis* var. *taltalensis*; Fig. 12), whereas multiseriate layers are up to 90 μm thick (*E. islayensis*, Figs 2 and 4).

Anticlinal secondary cell divisions. The anticlinal walls of the epidermal cells are often undulate (Fig. 9). At maturity,

TABLE 5. *Comparative data on gross-morphological characters*

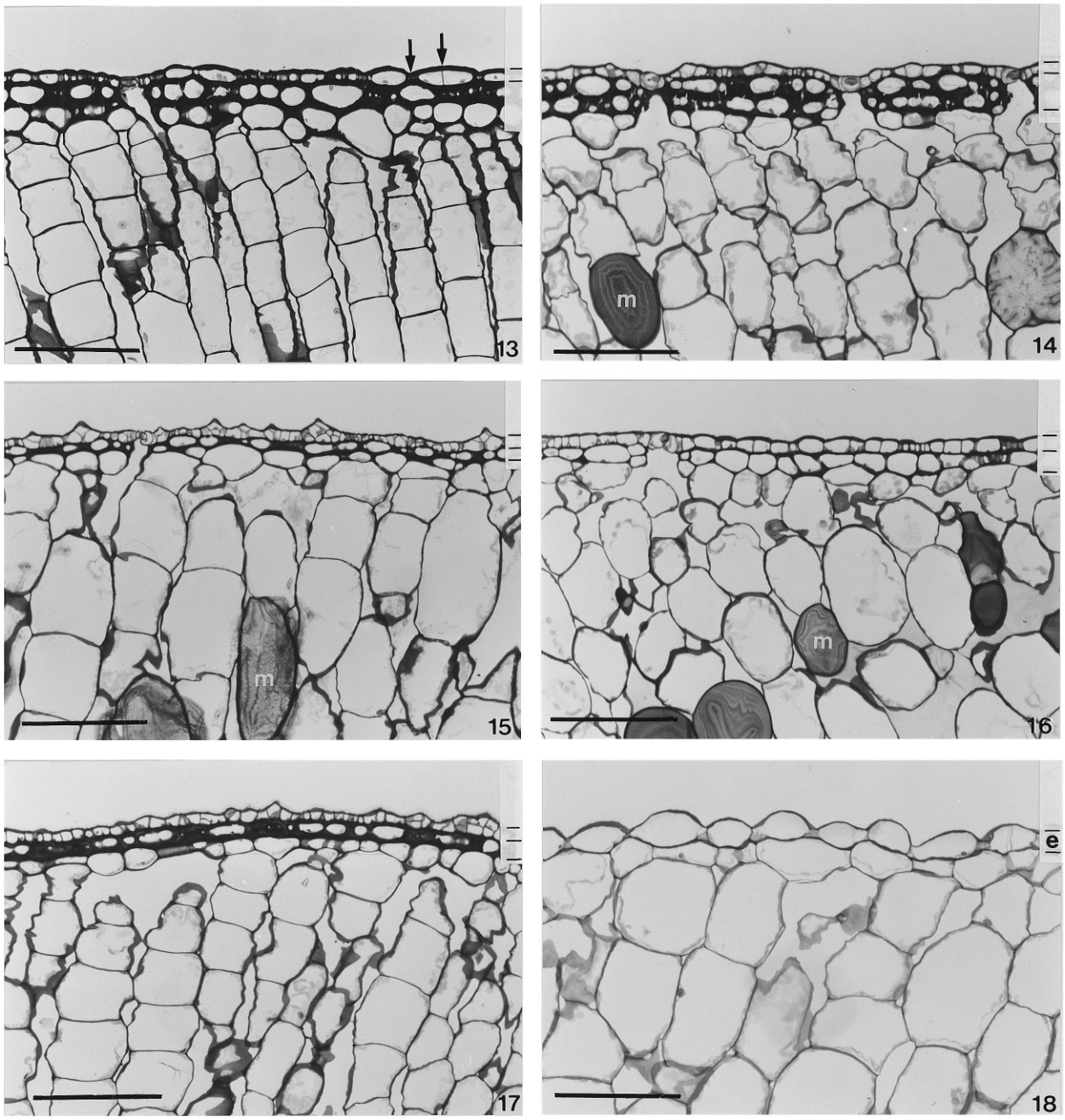
Taxon	Character 12 Stem shape	(Character 12) Stem height × diameter (mean maxima in cm)	Character 13 Disposition of podaria	Character 14 Formation of podaria	Character 15 Shape of main spines	Character 16 Orientation of main spines	Character 17 Root system	Character 18 Shape of taproot/s	Character 19 Neck-like constriction between stem and taproot
Chi.aer	Globular	3 × 3	Parastichies	Distinct tubercles	Curved	Appressed	Turbinate	Broad	Present
Chi.kra	Subglobular	3 × 5	Parastichies	Distinct tubercles	Curved	Appressed	Turbinate	Broad	Absent
Chi.lau	Globular	2 × 2	?	Tuberculate ribs	Straight	Radiating	Turbinate	Broad	Absent
Eri.aur	Globular	90 × 60	Orthostichies	Ribs	Curved	Upwards/sideways	Fibrous	—	—
Hor.asp	Globular	5 × 6	Orthostichies	Tuberculate ribs	Curved	Upwards/sideways	Fibrous	—	—
Hor.cur	Globular	15 × 20	Orthostichies	Ribs	Curved	Upwards/sideways	Fibrous	—	—
Hor.cur.tu	Globular	8 × 15	Orthostichies	Tuberculate ribs	Intermediate	Upwards/sideways	Fibrous	—	—
Hor.hei.1	Globular	6 × 7	Orthostichies	Tuberculate ribs	Intermediate	Upwards/sideways	Turbinate	Broad	Present
Hor.hei.2	Globular	5 × 6	Orthostichies	Tuberculate ribs	Intermediate	Upwards/sideways	Turbinate	Narrow	Absent
Hor.hei.si	Globular	6 × 6	Orthostichies	Ribs	Straight	?	Turbinate	?	?
Hor.kun	Globular	5 × 5	Orthostichies	Tuberculate ribs	Curved	Upwards/sideways	Fibrous	—	—
Hor.mar	Subglobular	11 × 18	Orthostichies	Ribs	Curved	Upwards/sideways	Fibrous	—	—
Hor.nap	Subglobular	2 × 3	Parastichies	Tuberculate ribs	Curved	Appressed	Turbinate	Broad	Present
Hor.odi	Subglobular	2 × 4	Parastichies	Distinct tubercles	Curved	Appressed	Turbinate	Broad	Absent
Hor.odi.gl	Subglobular	2 × 3	Parastichies	Distinct tubercles	Intermediate	Appressed	Turbinate	Broad	Present
Hor.tal	Globular	12 × 7	Orthostichies	Ribs	Intermediate	?	Fibrous	Narrow	Absent
Hor.tal.pa	Globular	10 × 7	Orthostichies	Tuberculate ribs	Intermediate	Upwards/sideways	Intermediate	Narrow	Absent
Hor.tal.py	Globular	5 × 5	Orthostichies	Tuberculate ribs	Curved	Upwards/sideways	Intermediate	Narrow	Absent
Isl.isl	Subcolumnar	15 × 7	Orthostichies	Ribs	Straight	Downwards/porrect	Fibrous	—	—
Neo.chi	Subcolumnar	25 × 6	Orthostichies	Tuberculate ribs	Straight	Upwards/sideways	Fibrous	—	—
Neo.sen	Subcolumnar	12 × 6	Orthostichies	Ribs	Straight	Upwards/sideways	Fibrous	—	—
Neo.sen.co	Globular	6 × 8	Orthostichies	Ribs	Curved	Upwards/sideways	Fibrous	—	—
Neo.sub	Columnar	80 × 10	Orthostichies	Ribs	Intermediate	Upwards/sideways	Fibrous	—	—
Neo.sub.cl	Subcolumnar	60 × 12	Orthostichies	Ribs	Intermediate	Upwards/sideways	Fibrous	—	—
Neo.vil	Subcolumnar	35 × 6	Orthostichies	Tuberculate ribs	Intermediate	Upwards/sideways	Fibrous	—	—
Pyr.and	Subcolumnar	15 × 5	Orthostichies	Ribs	Straight	Upwards/sideways	Fibrous	—	—
Pyr.bul	Subcolumnar	40 × 10	Orthostichies	Ribs	Curved	Upwards/sideways	Fibrous	—	—
Pyr.str	Subcolumnar	35 × 12	Orthostichies	Ribs	Curved	Upwards/sideways	Fibrous	—	—
Aus.pat	Columnar	40 × 5	Orthostichies	Ribs	Straight	Downwards/porrect	Fibrous	—	—
Cop.cin	Subcolumnar	70 × 12	Orthostichies	Ribs	Straight	Radiating	Fibrous	—	—
Cop.kra	Subcolumnar	90 × 15	Orthostichies	Ribs	Straight	Radiating	Fibrous	—	—
Cor.bre	Columnar	250 × 8	Orthostichies	Ribs	Straight	Radiating	Fibrous	—	—
Eul.cas	Columnar	80 × 5	Orthostichies	Ribs	Straight	Downwards/porrect	Fibrous	—	—
New.chi	Globular	7 × 6	Orthostichies	Tuberculate ribs	Straight	Downwards/porrect	Turbinate	Broad	Absent



FIGS 7–12. Different relief structures found in the dermal system of *Eriosyce* with SEM photographs (left) and transverse sections (right). Figs 7 and 8. Long papillae in *E. napina* [Ritter 249, ex cult.]. Note secondary cell walls subdividing the papillae. Figs 9 and 10. Short papillae and bumps in *E. aurata* [hort. Z]. Figs 11 and 12. Flat epidermal relief in *E. taltalensis* var. *taltalensis* [Jucker 65, ex cult.]. Bars = 150 μm. Bars at the right margin in Figs 8, 10 and 12 mark the dermal system with epidermis (above; e) and hypodermis (below; h).

most epidermal cells of *Eriosyce* show predominantly straight or slightly curved secondary anticlinal cell walls. Occasionally, repeated secondary divisions subdivide the primary cells to such a degree that the original cell pattern is no longer traceable. In transverse sections of the dermal system, anticlinal secondary cell divisions are recognized based on their thinner walls. Most of the variation between undulate and straighter anticlinal walls seems to be age-related, with young tissue showing undulate walls more often than older material. The only taxa for which no indication of secondary anticlinal divisions were found is *E. laui*.

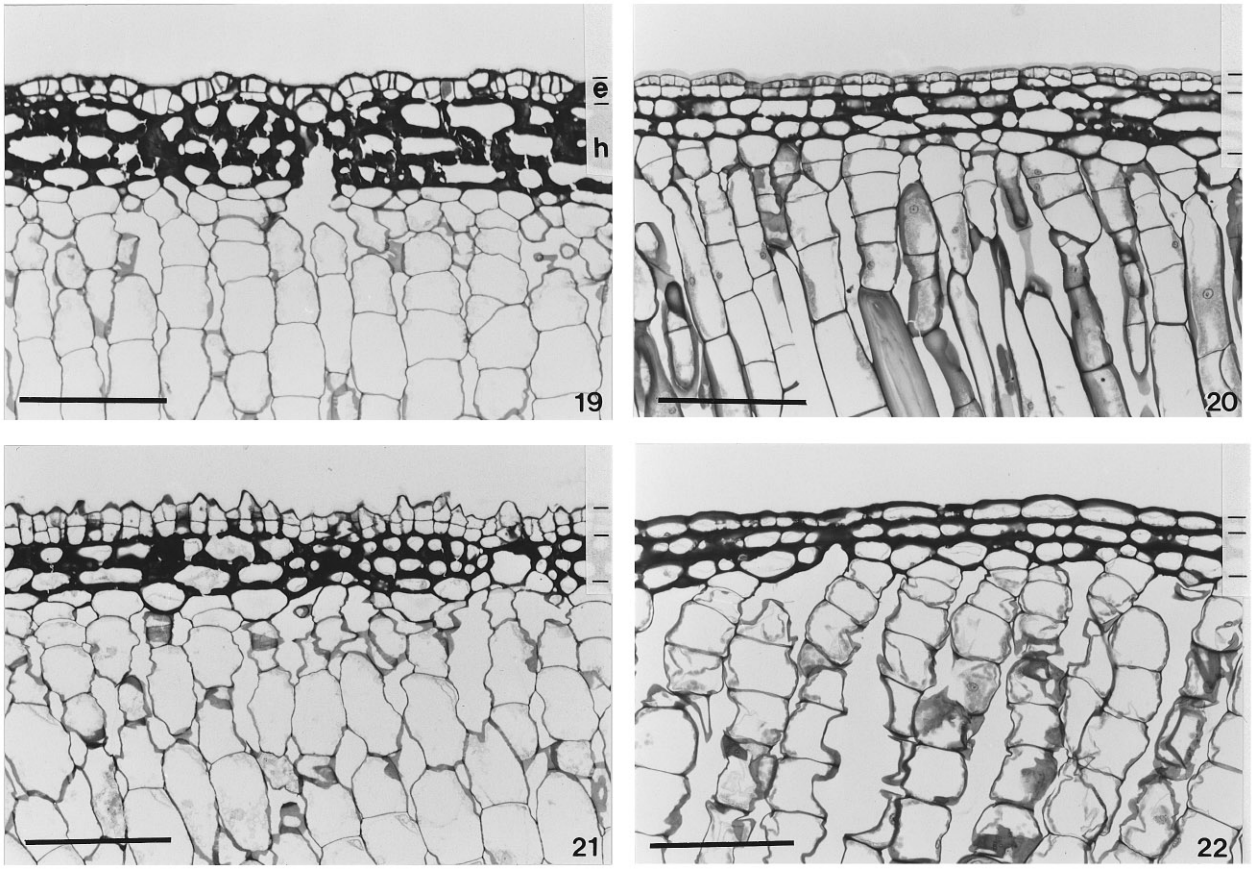
Periclinal and oblique secondary cell divisions (*Characters 3, 4 and 5, Table 3*). Whereas secondary cell divisions parallel to the anticlinal walls are probably ubiquitous in *Eriosyce*, secondary cell divisions more or less parallel to the periclinal walls are restricted to a number of taxa of *Eriosyce* and some outgroups. They are formed strictly



FIGS 13–18. Diversity in the dermal systems of taxa of *Eriosyce*. Fig. 13. *E. curvispina* [Jucker 146, ex cult.] with a slightly bumpy epidermis. Note the difference between primary and secondary anticlinal cell walls (at arrow). Fig. 14. *E. heinrichiana* ssp. *simulans* [Jucker 128, ex cult.] with a bumpy or slightly papillate epidermis. Mucilage idioblasts (m) are present in the cortex (also in Figs 15 and 16). Fig. 15. *E. subgibbosa* ssp. *clavata* [Jucker 132, ex cult.] with a distinctly papillate epidermis with a large number of periclinal and oblique secondary cell divisions, and a weakly developed hypodermis. Fig. 16. *E. chilensis* [hort. Z] with a flat strictly uniseriate epidermis, and a scarcely developed hypodermis. Fig. 17. *E. aerocarpa* [Jucker 110, ex cult.] with a papillate epidermis with some periclinal or oblique secondary cell divisions. Fig. 18. *E. laui* [Lau 1541, ex cult. ZSS] with a broadly papillate epidermis. The hypodermis layer is completely absent. Bars = 250 μm. Bars at the right margin mark the dermal system with epidermis (above) and hypodermis (below; h).

parallel to the periclinal walls in *E. aurata* and *E. kunzei*, as well as in the outgroups of *Copiapoa* (Fig. 21), *Corryocactus* (Fig. 19) and *Eulychnia* (Fig. 20). Depending on the number of epidermal cells that are affected by these divisions, a distinctly multilayered epidermis may result (Figs 20 and 21). In other taxa, these secondary cell divisions lack a definite orientation parallel to the periclinal walls and occur at various angles (Figs 4, 8 and 15).

The frequency of such periclinal and oblique secondary cell divisions varies greatly, and was therefore coded



FIGS 19–22. Diversity in dermal system of outgroup taxa. Fig. 19. *Corryocactus brevistylus* [hort. B] with a bumpy, partly biseriate epidermis. Fig. 20. *Eulychnia castanea* [Nyffeler, Eggli & Lüthy 391] with a slightly bumpy completely biseriate epidermis. Anticlinal secondary cell divisions are mainly found in the outer cell layer (similar to Fig. 19). Fig. 21. *Copiapoa krainziana* [Eggli & Leuenberger 2660] with a biseriate epidermis. The cells of the outer layer are distinctly papillate. Fig. 22. *Austrocactus patagonicus* [Nyffeler, Eggli & Lüthy 370] with a slightly bumpy, uniseriate epidermis. Bars = 250 μm. Bars at the right margin mark the dermal system with epidermis (above; e) and hypodermis (below; h).

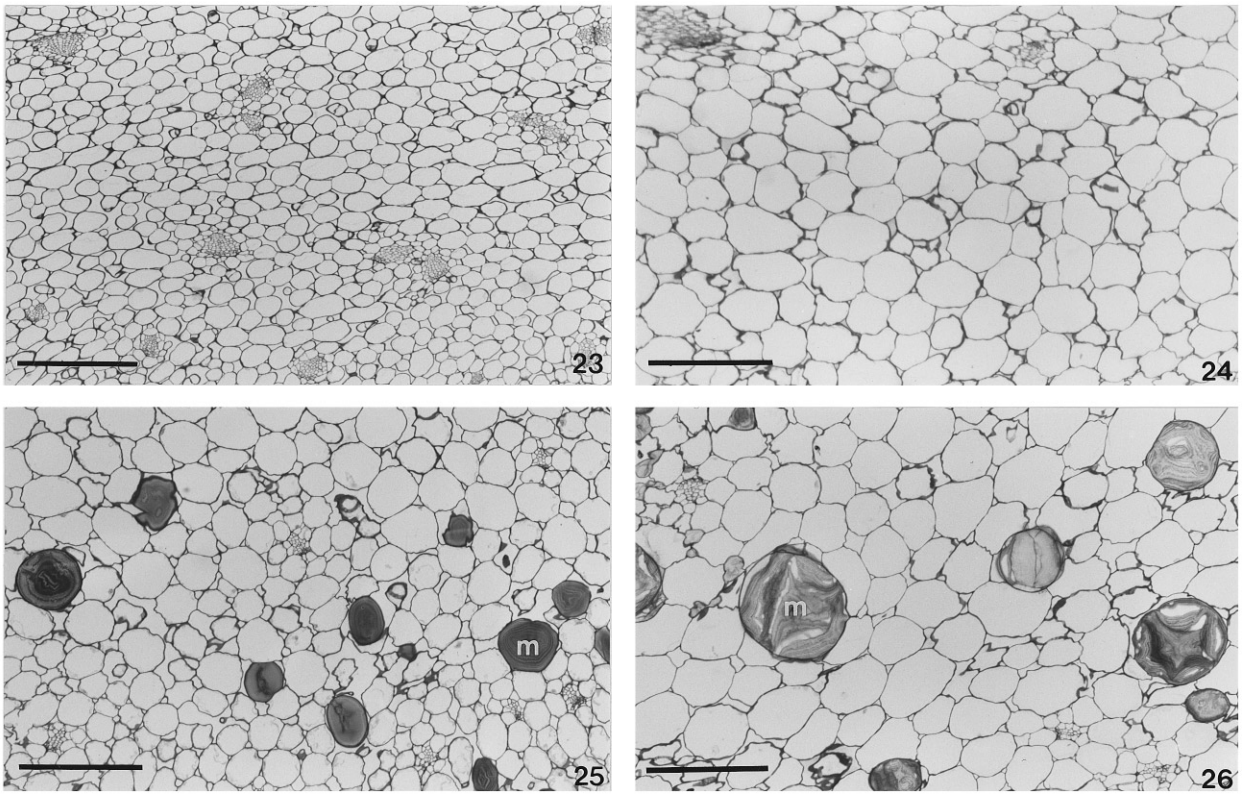
separately for non-papillate and papillate cells. Most commonly, these divisions are found in papillate cells of the taxa with long papillae (Fig. 8) and in the taxa with a coherent multi-layered epidermis (Figs 2, 4, 20 and 21). A possible age- or environment-dependence of these divisions remains to be checked.

Hypodermis

Number of cell layers and thickness (*Characters 6 and 7, Table 3*). With the exception of *E. laui* (Fig. 18), all taxa show a distinct hypodermis consisting of one or several layers of tabular collenchyma cells. In taxa of *E.* subsect. *Chileosyce* (Fig. 17) and *E.* subsect. *Neoporteria* (Figs 15 and 16) the hypodermis comprises one or two cell layers and measures between 20 and 60 μm. A very similar architecture is also found for *E. andreaeana* and *E. taltalensis* var. *taltalensis* (Fig. 12). The hypodermis of *E. islayensis* (Figs 2 and 4) also has only one or two cell layers; however, they are very uneven in thickness, ranging from 50 to 200 μm. Most other taxa of *Eriosyce* (Figs 13 and 14), as well as the outgroups from *Austrocactus* (Fig. 22), *Copiapoa* (Fig. 21), *Corryocactus* (Fig. 19) and *Eulychnia* (Fig. 20), have up to three or four layers and a thickness of 60 to 200 μm. Even more layers were typically found for *E. bulbocalyx*, *E. strausiana* (Figs 5 and 6), and especially for *E. aurata* (Fig. 10) with up to seven layers and 350 μm in thickness. The formation of the hypodermis is affected to a certain extent by environmental factors (see above). Correspondingly, growing conditions must be taken into consideration in comparisons of hypodermal characters.

Cortex and pith

Firmness (*Character 8, Table 4*). Great differences were observed in the firmness of the cortex tissue while preparing samples for the present study. Species such as *E. aurata*, *E. curvispina*, *E. islayensis* and *E. strausiana* were found to have very tough cortex tissue, whereas taxa of *E.* subsect. *Chileosyce*, and especially those of *E.* subsect. *Neoporteria*, have soft cortex tissue. *E. laui* is also noteworthy for its very soft cortex tissue. However, many other taxa are indifferent, and therefore difficult to characterize (coded as inter-



FIGS 23–26. Transverse sections of the central cortex. Note the different size of the parenchyma cells and the presence of mucilage idioblasts (m) in Figs 25 and 26. Fig. 23. *Eriosyce strausiana* [Leuenberger & Eggli 4466]. Fig. 24. *E. taltalensis* var. *taltalensis* [Jucker 65, ex cult.]. Fig. 25. *E. heinrichiana* ssp. *simulans* [Jucker 128, ex cult.]. The lower part shows the transition zone to the outer cortex with distinctly smaller parenchyma cells. Fig. 26. *E. subgibbosa* ssp. *clavata* [Jucker 132, ex cult.]. Bars = 500 μm.

mediate). The rather subjective impression of tissue firmness can be assessed more objectively by measuring the mean upper diameter of parenchyma cells from the central cortex. A somewhat tough tissue has small cortical cells with a diameter often considerably below 200 μm (Fig. 23), whereas the mean upper diameter in a soft tissue may reach up to 350 μm (Fig. 26). Accordingly, taxa coded for an intermediate state of tissue firmness showed cell diameters often in between the two extremes (Figs 24 and 25). The large number of cortical bundles often found in taxa with a rather tough tissue certainly contribute to the distinct firmness (Fig. 23).

Mucilage (*Character 9, Table 4*). The presence of mucilage is easily determined from fresh stem sections with the help of a wetted finger on the basis of their slimy nature. Taxa of *E.* subsect. *Neoporteria* and the outgroup of *Austrocactus* are intensively mucilaginous, whereas *E. aurata*, *E. islayensis* and many taxa of *E.* subsect. *Horridocactus* and *E.* subsect. *Pyrrhocactus* are characterized by a complete lack of mucilage idioblasts. Some taxa were found to be either slightly or distinctly mucilaginous (representing states between the two extremes). As in many other characters, the circumscription of the different states is difficult and inexact. Problems are also encountered in cases where the mucilage idioblasts are not regularly distributed in the stem tissue but are locally concentrated. This character can be quantified from microtome sections of the cortex tissue with measurements of the proportion of mucilage idioblasts per area (Figs 25 and 26).

Colour of the central and inner cortex (*Character 10, Table 4*). Chlorenchyma cells are, in general, restricted to the outermost part of the cortex. This layer of photosynthetic cells is either strictly delimited from the pale inner water-storage cortex or it changes rather gradually. The taxa of *E.* subsect. *Neoporteria* are very distinctive, having a completely green cortex and pith. This phenomenon is not restricted to small seedlings, but is also observed in larger plants with a stem diameter of up to 10 cm or more, whereas plants of comparable size of *E.* subsect. *Horridocactus* have a whitish or pale greenish cortex (Fig. 27). *E. crispa* (not included in this study due to lack of adequate material) and *E. heinrichiana* ssp. *heinrichiana* are characterized by a very distinctive yellowish cortex and pith. As this colour has a different genetic background, it was not treated as a separate state for this character.

Ratio of pith and stem diameter (*Character 11, Table 4*). The ratio between pith diameter and stem diameter is an interesting attribute of stem-succulents, and shows great variation. In *Eriosyce*, broad piths (ratios $\geqslant 0{\cdot}30$) are generally found in taxa of *E.* sect. *Chileosyce* and *E.* subsect. *Horridocactus*, whereas narrow piths (ratios $\leqslant 0{\cdot}22$) are found in the outgroup taxa of *Austrocactus*, *Copiapoa* (except *C. cinerea*), *Corryocactus* and *Eulychnia*. While it is not always very easy to measure this character very exactly,

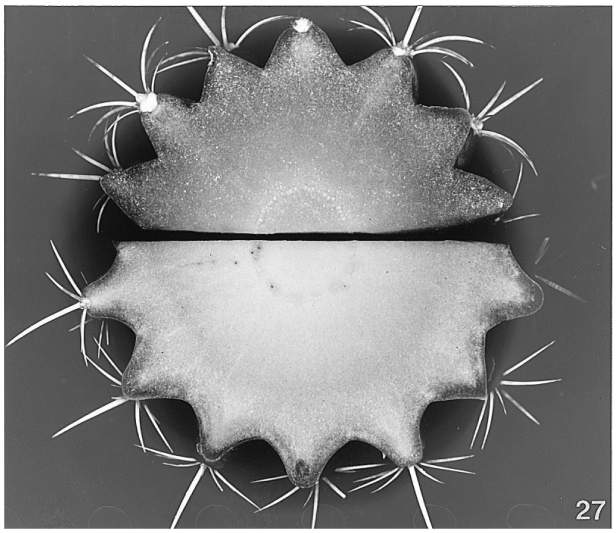


FIG. 27. Stem segments from transverse sections of *Eriosyce subgibbosa* ssp. *clavata* [Jucker 132, ex cult. Z] (above) and *E. curvispina* [Jucker 146, ex cult. Z] (below). Note the differences in the colouring of the inner cortex and pith, which is distinctly green (showing as grey here) for taxa of *E.* subsect. *Neoporteria* (above) but whitish or pale greenish for the other members of *Eriosyce* (below). Stem diameters ± 60 mm.

the general tendencies are clearly visible. It remains to be checked how far this character is correlated with the stem shape.

Macromorphological characters

Stem shape (*Character 12, Table 5*). Four different states for the stem shape are differentiated here on the basis of the ratio between stem height and stem diameter. Most taxa of *Eriosyce* have globular or subglobular stems, except for *E. islayensis* and a number of taxa of *E.* subsect. *Neoporteria* and *E.* subsect. *Pyrrhocactus* whose stems are mostly subcolumnar or even columnar.

Disposition and formation of podaria (*Characters 13 and 14, Table 5*). Podaria (leaf-bases) are produced in straight lines (in orthostichies) in most taxa of *Eriosyce* and are generally coalesced into vertical ribs. Helical lines (parastichies) of distinct tubercles are typical for *E.* subsect. *Chileosyce* (except for *E. laui* where both types of phyllotaxy were found) as well as for *E. napina* and *E. odieri* of *E.* subsect. *Horridocactus*. Quite often the coalescent podaria remain distinct to some extent and form tuberculate ribs.

Shape and orientation of main spines (*Characters 15 and 16, Table 5*). A great diversity in size and appearance of the spines is found in these cacti. However, many taxa of *Eriosyce* show a very distinct pattern in shape and orientation of the main spines. They are regularly curved like a sabre and point upwards or sideways; in contrast, *E. islayensis* and the outgroup taxa have more or less straight spines pointing downwards, or are radiate or porrect. The taxa of *E.* subsect. *Chileosyce* (excluding *E. laui*), as well as *E. napina* and *E. odieri*, have short spines appressed to the stems.

Root system (*Characters 17, 18 and 19, Table 5*). Most taxa of *Eriosyce* and the outgroups from *Austrocactus*, *Copiapoa*, *Corryocactus* and *Eulychnia* have fibrous root systems. Turbinate roots occur in *E.* subsect. *Chileosyce* and *E.* subsect. *Horridocactus*. They are either broad and massive, occasionally with a neck-like constriction above, or rather narrow and then often in small clusters.

Cladistics

The most important findings from the comparison of the 56 different cladistic analyses of *Search I* are summarized in Tables 6 and 7. The 24 analyses which produced a memory overflow (at approx. 2730 most parsimonious cladograms) were excluded from further considerations and are not listed. The remaining 32 analyses had consistency indices (CI) from 0·31 to 0·37 and retention indices (RI) from 0·64 to 0·73.

In 15 of the 32 considered analyses, terminal reordering revealed different topologies for the strict consensus cladograms (SCCs). The number of most parsimonious cladograms found by the five different analyses from terminal reordering for each varaint of character composition varied up to ten times or more. However, most often the differences in the topology of the SCCs were rather minor. While looking for a number of terminals being members either of the outgroup grade or of four ingroup clades, all topological variants were considered, and only those groups found in all five SCCs are listed in Tables 6 and 7.

In general, the analyses with multistate characters coded as ordered were better resolved than those with unordered character coding. Both types of analyses identified more or less the same groups of taxa, however, with some minor differences. Almost all cladistic analyses with different character compositions showed the outgroup taxa *Copiapoa cinerea*, *C. krainziana*, *Corryocactus brevistylus* and *Eulychnia castanea* in a basal position as a grade. In most cases, *Eriosyce islayensis* occurred as the terminal part of this grade and hence represents the most basal ingroup taxon. Very well supported ingroup clades proved to be *E.* subsect. *Chileosyce* (including *E. napina* and *E. odieri*, but excluding *E. laui*) and *E.* subsect. *Neoporteria* (with the occasional exception of *E. senilis* ssp. *coimasensis*). *Austrocactus patagonicus* was part of this latter clade in all analyses with an ordered character coding. Furthermore, *E. aurata*, *E. bulbocalyx* and *E. strausiana* were regularly placed in a distinct clade occasionally together with *E. aspillagae*, *E. curvispina*, *E. kunzei* and *E. marksiana*. In a number of analyses (conspicuously concentrated in those with an unordered character coding), the two distinct forms of *E. heinrichiana* ssp. *heinrichiana* (Hor.hei.1 and Hor.hei.2) were placed together as a distinct group. Other ingroup taxa, such as *E. andreaeana*, *E. heinrichiana* ssp. *simulans*, *E. laui* (quite often associated with *Neowerdermannia chilensis*), *E. taltalensis* ssp. *paucicostata* and *E. taltalensis* var. *pygmaea*, were very unstable concerning their positions in the cladograms.

Spine characters proved to be decisive for a separation of the ingroup from a number of outgroup taxa (Table 6, data matrix variant 8) and hence represent potential synapomorphies for the genus *Eriosyce*. Similarly, the omission of

TABLE 6. *Clades and basal grades found in all strict consensus cladograms from the different cladistic analyses of* Search I (*characters ordered except for characters 13, 16, 18 and 19*)

Data matrix variant	1	2	4	5	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	27	28
Length	126	77	80	110	119	109	114	112	117	124	114	120	117	120	118	113	122	119	116	125	120	115	120	123	122
CI	31	32	35	32	31	32	31	33	32	31	32	30	32	31	32	32	31	31	31	31	31	33	30	31	32
RI	67	68	73	68	66	68	67	69	68	67	68	67	67	67	67	68	66	67	67	67	66	68	67	67	68
Min. num. cladog.	8	307	483	565	44	270	1264	1239	1440	138	12	13	90	104	283	4	310	829	32	8	44	192	8	4	8
Max. num. cladog.	8	360	503	705	688	1042	1352	1444	1548	305	56	212	259	104	283	4	312	1232	90	8	665	204	8	4	8
Diff. consens. topol.	1	1	1	3	2	4	1	1	2	3	3	3	3	1	1	1	1	2	1	1	3	1	1	1	1
Cor.bre	+	+	+	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Cop.cin	+	+	+	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Cop.kra	+	+	+	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Eul.cas	+	+		+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Isl.isl	+	+		+	+		+	+	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+
Chi.aer	*		*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Chi.kra	*		*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Hor.nap	*		*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Hor.odi	*		*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Hor.odi.gl	*		*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Aus.pat	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*		*	*	*	*	*	*	*	*
Neo.chi	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*		*	*	*	*	*	*	*	*
Neo.sen	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*		*	*	*	*	*	*	*	*
Neo.sen.co	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*			*	*	*	*	*	*	*	*
Neo.sub	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*		*	*	*	*	*	*	*	*
Neo.sub.cl	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*		*	*	*	*	*	*	*	*
Neo.vil	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*		*	*	*	*	*	*	*	*
Hor.tal																									
Eri.aur	*	*	*		*		*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Pyr.bul	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Pyr.str	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Hor.cur	*						*	*	*		*			*	*				*	*			*	*	*
Hor.cur.tu	*							*	*		*			*					*	*			*	*	*
Hor.kun	*							*	*		*			*	*				*	*			*	*	*
Hor.mar	*						*	*	*		*			*					*	*			*	*	*
Hor.asp	*							*	*		*			*					*	*			*	*	*
Hor.hei.1							*																	*	*
Hor.hei.2							*																	*	*

Numbers refer to data matrix variants given in Appendix 2. Data on cladogram length, consistency index (CI) and retention index (RI) are for the most parsimonious cladograms. Minimum and maximum numbers of cladograms found in dependence of terminal order in the matrix, as well as number of different strict consensus topologies are also listed. For five different groups of terminals are those marked that are members of the clade (*) or the basal grade (+).

TABLE 7. *Clades and basal grades found in all strict consensus cladograms from the different cladistic analyses of* Search I (*all characters coded unordered*)

Data matrix variant	2	4	5	6	11	18	21
Length	66	74	110	86	104	103	101
CI	37	37	32	38	36	35	36
RI	66	69	68	67	64	65	65
Min. num. cladog.	148	90	565	1462	1260	1023	50
Max. num. cladog.	1629	105	705	1746	1350	1137	108
Diff. consens. topol.	2	1	3	2	2	2	1
Cor.bre	+	+	+	+		+	+
Cop.cin		+	+				+
Cop.kra	+	+	+	+		+	+
Eul.cas			+				+
Isl.isl			+				+
Chi.aer	*	*	*	*	*	*	*
Chi.kra	*	*	*	*	*	*	*
Hor.nap		*	*	*	*	*	*
Hor.odi		*	*	*	*	*	*
Hor.odi.gl		*	*	*	*	*	*
Aus.pat			*				
Neo.chi	*	*	*		*	*	
Neo.sen	*	*	*		*		
Neo.sen.co			*				
Neo.sub	*	*	*			*	
Neo.sub.cl	*	*	*		*	*	
Neo.vil	*	*	*		*	*	
Hor.tal					*		
Eri.aur							*
Pyr.bul	*		*				*
Pyr.str	*		*				*
Hor.cur							
Hor.cur.tu							
Hor.kun							
Hor.mar							
Hor.asp							
Hor.hei.1		*		*	*	*	*
Hor.hei.2		*		*	*	*	*

Numbers refer to data matrix variants given in Appendix 2. Data on cladogram length, consistency index (CI) and retention index (RI) are for the most parsimonious cladograms. Minimum and maximum numbers of cladograms found in dependence of terminal order in the matrix, as well as number of different strict consensus topologies are also listed. For five different groups of terminals are those marked that are members of the clade (*) or the basal grade (+).

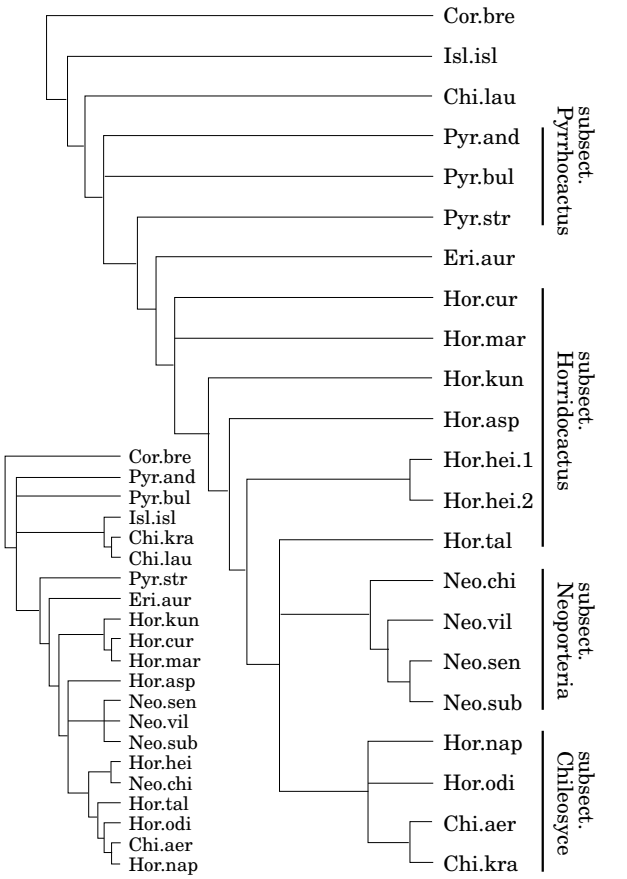


FIG. 28. Strict consensus of 16 most parsimonious cladograms of length 228 (CI = 0·44 and RI = 0·59), rooted with the outgroup *Corryocactus brevistylus* (Cor.bre). Multistate characters were coded as unordered. Inset, Strict consensus cladogram from the cladistic analysis based on the same terminals but with the original data from Wallace in Kattermann (1994).

various morphological characters (podaria as distinct tubercles and arranged in helical lines; spines appressed to the stems) and of cortex characters (especially cortex colour) from the cladistic analyses distorted the distinct caldes of *E.* subsect. *Chileosyce* and *E.* subsect. *Neoporteria*, respectively (Table 6, variants 2 and 19; Table 7, variant 6).

The cladistic analysis of *Search II* with a subgroup of the taxa investigated and supplemented with data on flowers, fruits and seeds produced 16 most parsimonious cladograms of length 228 (CI = 0·44, RI = 0·59). The strict consensus cladogram (Fig. 28) supports two distinct clades in a terminal position, on one hand *E.* subsect. *Chileosyce* (including *E. napina* and *E. odieri*, but excluding *E. laui*), and on the other hand *E.* subsect. *Neoporteria*. *E. taltalensis* (var. *taltalensis*) is found in close association to these two groups. The basal part of the cladogram is formed by a grade consisting of *E. islayensis* (the most basal taxon of the ingroup) followed by *E. laui*, the taxa of *E.* subsect. *Pyrrhocactus*, *E. aurata* and, finally, those of *E.* subsect. *Horridocactus*. The analysis with the original data on vegetative characters and reproductive structures yielded four most parsimonious cladograms of length 193 (CI = 0·45, RI = 0·56). The strict consensus cladogram (Fig. 28, inset) is less resolved with members of the subsections *Chileosyce*, *Horridocactus* and *Neoporteria* partly intermingled.

DISCUSSION

The various cladistic analyses coherently confirmed the distinct status of two groups of taxa. The first group comprises *E. aerocarpa*, *E. krausii*, *E. napina* and *E. odieri* (including *E. odieri* ssp. *glabrescens*), characterized by: (1) the papillate epidermal relief; (2) the tuberculate stems (tubercles arranged in helical lines); (3) appressed spines; and (4) the tuberous root system. While Ritter (1980) placed all taxa of this group in his genus *Thelocephala*, Kattermann (1994) segregated the first two species (*E. aerocarpa*, *E.*

krausii) in *E.* subsect. *Chileosyce* and placed the remaining two species (*E. napina*, *E. odieri*) in *E.* subsect. *Horridocactus*. However, the present cladistic analyses clearly support the coherence of this group, and while not specifying a resurrection at the rank of genus, a modification of Kattermann's (1994) classification is suggested.

The second distinct group found in most variants of the cladistic investigation is formed by *E.* subsect. *Neoporteria*. This group of plants has been recognized as a distinct taxon for a long time, and has often been given separate generic status (e.g. Backeberg, 1959). *Eriosyce chilensis*, which lacks the typical hummingbird flowers regarded as the key character for this group, was traditionally not included in *Neoporteria* (*sensu stricto*). However, *E. chilensis* clearly shows the characteristic anatomical features of this group, which include: (1) the often flat outer periclinal walls of the epidermis; (2) the weakly developed hypodermal layer; (3) the soft cortex tissue; (4) the abundant mucilage idioblasts in the cortex; and (5) the green inner cortex and pith.

The other taxa of *Eriosyce* (*E. aurata*, *E. islayensis*, taxa of *E.* subsect. *Horridocactus* and of *E.* subsect. *Pyrrhocactus*) commonly form a grade basal to the two distinct clades of *E.* subsect. *Chileosyce* and *E.* subsect. *Neoporteria*. *E. islayensis* is distinct in its multilayered epidermis derived from repeated periclinal or oblique secondary cell divisions. Most of the different cladistic analyses placed this species at the base of *Eriosyce* in close association to the outgroup taxa of the genus *Copiapoa*. A cladistic investigation including both *Copiapoa* and *Eriosyce* must clarify the final position of *E. islayensis* (representing the formerly distinct genus *Islaya*). *E. aurata*, *E. bulbocalyx* and *E. strausiana* are characterized by: (1) the thick hypodermis, consisting of several cell layers; (2) the tough cortex tissue; (3) the absence of mucilage cells in the cortex; and hence, are often found in close association. Similar characters are found also in *E. curvispina*, *E. marksiana*, and *E. kunzei* representing *E.* subsect. *Horridocactus*. *E. taltalensis* var. *taltalensis* is found in a number of analyses close to *E.* subsect. *Neoporteria*, which is supported by a very similar and not especially xeromorphic dermal system, and a somewhat similar flower architecture.

Based on anatomical characters, *E. heinrichiana* in the sense of Kattermann (1994) represents a very heterogeneous taxon; *E. heinrichiana* ssp. *simulans* is very different due to: (1) the presence of mucilage cells in the cortex; and (2) a spination pattern very uncommon for *Eriosyce*.

The present investigation clearly stresses the distinct status of *E. laui*. This taxon is characterized by a number of unique features, namely: (1) the huge (compared with other taxa of this study) and broadly papillate epidermal cells lacking any secondary cell divisions; (2) the complete absence of a hypodermal layer; and (3) the very soft cortex tissue. The position of *E. laui* in the different cladograms varied considerably, but none of the various cladistic analyses associated this species with the taxa of *E.* subsect. *Chileosyce*, where it was placed by Kattermann (1994). Instead, *E. laui* appears to represent a distinct lineage branching off much closer to the base. Its relationships are still far from clear.

Austrocactus patagonicus shares several anatomical features with *E.* subsect. *Neoporteria*, such as: (1) the soft cortex tissue; and (2) the huge number of mucilage cells in the cortex, and is therefore found in close association to this clade in most analyses of *Search I*. This similarity is without doubt the product of parallel evolution as seen from the many different features in flowers and fruits that separate *Austrocactus* and *Eriosyce*.

The present study uncovered various anatomical features which are useful either for diagnostic or for synthetic purposes. Many taxa of *Eriosyce* can be placed in their proper subsection based simply on a combination of characters from the dermal system and from the cortex, such as epidermal relief structures, number of cell layers in the hypodermis, presence of mucilage cells, or size of the parenchymatic cortex cells. Anatomical characters contribute to the circumscription of the infrageneric taxa in *Eriosyce*, partly supporting the present grouping by Kattermann (1994) and partly suggesting minor rearrangements. The findings of this investigation, despite its limitation from the restricted sampling and the problems with the circumscription of the different character states, may be used as a basis for further comparative anatomical studies of cacti with a definite systematic background.

ACKNOWLEDGEMENTS

The authors are grateful to A. Igersheim for his untiring support in technical matters and to U. Jauch, Institut für Pflanzenbiologie, Universität Zürich, for help with the SEM photographs. Stimulating discussions with B. E. Leuenberger have greatly contributed to this study. Furthermore, various comments and suggestions by C. D. K. Cook and the two reviewers J. D. Mauseth and N. P. Taylor helped to improve earlier versions of this manuscript. Plant material was kindly provided by the Botanischer Garten der Universität Zürich, the Botanischer Garten Berlin-Dahlem and the Städtische Sukkulenten-Sammlung Zürich as well as by F. Kattermann (USA), and W. Mächler (Switzerland). Grants of the Swiss Academy of Natural Sciences and the Cactus and Succulent Society of America to RN and of the Swiss National Science Foundation (no. 31.39176.93) to UE to study cacti for the Flora of Chile project are kindly acknowledged.

This paper is dedicated to the late Professor Dr K. U. Kramer, who introduced the authors to the interesting world of systematic botany.

LITERATURE CITED

Backeberg C. 1959. *Die Cactaceae*. Vol. 3. Jena: VEB Gustav Fischer Verlag.

Barthlott W, Hunt DR. 1993. Cactaceae. In: Kubitzki K, ed. *The families and genera of vascular plants*. Vol. 2. Berlin: Springer Verlag, 161–197.

Boke NH. 1980. Developmental morphology and anatomy in Cactaceae. *BioScience* **30**: 605–610.

Buxbaum F. 1975. Provisorische Neugliederung der Tribus Notocacteae. In: Krainz H, ed., *Die Kakteen*, Liefg. 60, CVI.

Condé LF. 1975. Anatomical comparisons of five species of *Opuntia* (Cactaceae). *Annals of the Missouri Botanical Garden* **62**: 425–473.

Davis JI. 1993. Character removal as a means for assessing stability of clades. *Cladistics* **9**: 201–210.
Donald JD, Rowley GD. 1966. Reunion of the genus *Neoporteria*. *Cactus and Succulent Journal of Great Britain* **28**: 54–58, 74–77.
Farris JS, 1969. A successive approximations approach to character weighting. *Systematic Zoology* **18**: 374–385.
Farris JS. 1988. *Hennig 86*. Software and handbook. Distributed by the author.
Gibson AC, Horak KE. 1978. Systematic anatomy and phylogeny of Mexican columnar cacti. *Annals of the Missouri Botanical Garden* **65**: 999–1057.
Gibson AC, Nobel PS. 1986. *The cactus primer*. Cambridge, Mass.: Harvard University Press.
Gregory M, Baas P. 1989. A survey of mucilage cells in vegetative organs of Dicotyledons. *Israel Journal of Botany* **38**: 125–174.
Hauser DL, Presch, W. 1991. The effect of ordered characters on phylogenetic reconstruction. *Cladistics* **7**: 243–265.
Hunt DR, Taylor NP, eds. 1990. The genera of Cactaceae: progress towards consensus. *Bradleya* **8**: 85–107.
Igersheim A. 1993. The character states of the Caribbean monotypic endemic *Strumpfia* (Rubiaceae). *Nordic Journal of Botany* **13**: 545–559.
Igersheim A, Cichocki O. 1996. A simple method for microtome sectioning of prehistoric charcoal specimens, embedded in 2-hydroxyethyl methacrylate (HEMA). *Review of Palaeobotany and Palynology* **92**: 389–393.
Kattermann F. 1994. *Eriosyce* (Cactaceae). The genus revised and amplified. *Succulent Plant Research* **1**: 1–176.
Lauterbach C. 1889. Untersuchungen über Bau und Entwicklung der Sekretbehälter bei den Cacteen. *Botanisches Centralblatt* **37**: 257–264, 289–297, 329–336, 369–375, 409–413.
Lüthy JM. 1995. *Taxonomische Untersuchung der Gattung Mammillaria Haw*. (*Cactaceae*). Frankenthal: Arbeitskreis für Mammillarien-freunde.
Maddison DR. 1991. The discovery and importance of multiple islands of most-parsimonious trees. *Systematic Zoology* **40**: 315–328.
Mauseth JD. 1996. Comparative anatomy of tribes Cereeae and Browningieae (Cactaceae). *Bradleya* **14**: 66–81.
Nommensen R. 1910. *Beiträge zur Kenntnis der Anatomie der Kakteen, insbesondere ihres Hautgewebes*. PhD Thesis, Kiel.
Nixon KC, Davis JI. 1991. Polymorphic taxa, missing value and cladistic analysis. *Cladistics* **7**: 233–241.
Platnick NI, Griswold CE, Coddington JA. 1991. On missing entries in cladistic analysis. *Cladistics* **7**: 337–343.
Ritter F. 1980. *Kakteen in Südamerika*. Vol. 3: Chile. Spangenberg (D): published by the author.
Schill R, Barthlott W, Ehler N, Rauh W. 1973. Raster-Elektronen-Mikroskopische Untersuchungen and Cactaceen-Epidermen. *Tropische und Subtropische Pflanzenwelt* **4**: 1–14.
Schleiden MJ. 1845. Beiträge zur Anatomie der Cacteen. *Mémoires de l'Académie Impéeriale des Sciences de St.-Péterbourg* **4**: 335–380, 10 pl.
Stevens PF. 1991. Character states, morphological variation, and phylogenetic analysis: a review. *Systematic Botany* **16**: 553–583.
Stevens PF. 1996. On phylogenies and data bases—where are the data, or are there any? *Taxon* **45**: 95–98.
Swofford DL, Olsen GJ, Waddell PJ, Hillis DM. 1996. Phylogenetic inference. In: Hillis DM, Moritz C, Mable BK, eds. *Molecular systematics*. 2nd edn. Sunderland: Sinauer Associates, 407–514.
Wilkinson, M. 1992. Ordered versus unordered characters. *Cladistics* **8**: 375–385.

APPENDIX

Appendix 1.

Collections examined, with provenance, collection number and herbarium where permanent vouchers are deposited. EL for Eggli & Leuenberger; LE for Leuenberger & Eggli; NEL for Nyffeler, Eggli & Lüthy. Field collected material is marked with an asterisk. The geographical origin of each collection is given in square brackets (provinces for Argentina, 'Región' for Chile). Permanent vouchers of the specimens examined are deposited in herbaria as indicated (acronyms according to Index Herbariorum, ed. 8, Regnum Vegetabile 120, 1990).

Austrocactus patagonicus [Argentina, Rio Negro]: NEL 370* (B, MERL, ZSS); hort. (ZSS).
Copiapoa cinerea [N Chile, Antofagasta]: EL 2641* (B, CONC, SGO, ZSS).
Copiapoa krainziana [N Chile, Antofagasta]: EL 2660* (B, CONC, SGO, ZSS).
Corryocactus brevistylus [N Chile, S Peru]: hort. B (B).
Eriosyce aerocarpa [N Chile, Atacama]: Jucker 110 (ZSS); hort. Z (ZSS).
Eriosyce andreaeana [Argentina, La Rioja]: LE 4412 (B, CORD, SGO, ZSS); hort. ZSS.
Eriosyce aspillagae [C Chile, Talca]: hort. Z (ZSS).
Eriosyce aurata [C Chile, Coquimbo]: EL 2558* (B, CONC, SGO, ZSS), hort. Z (ZSS).
Eriosyce bulbocalyx [Argentina, San Juan]: LE 4471* (B, CORD, ZSS); hort. Z (ZSS).
Eriosyce chilensis [C Chile]: hort. Z (ZSS).
Eriosyce curvispina [C Chile, Coquimbo and Valparaíso]: EL 2554* (CONC, SGO, ZSS); Jucker 146 (ZSS).
Eriosyce curvispina var. *tuberisulcata* [C Chile, Valparaíso]: NEL 392* (B, SGO, ZSS).
Eriosyce heinrichiana [ssp. *heinrichiana*] [C Chile, Coquimbo]: (1) EL 2578* (B, SGO, ZSS); EL 2674* (CONC, SGO, ZSS); (2) Jucker 125 (ZSS).
Eriosyce heinrichiana ssp. *simulans* [C Chile, Coquimbo]: Jucker 128 (ZSS).
Eriosyce islayensis [S Peru]: hort. Z (ZSS); hort. ZSS (ZSS).
Eriosyce krausii [N Chile, Atacama]: EL 2624* (B, CONC, SGO, ZSS); EL 2628* (B, CONC, SGO, ZSS).
Eriosyce kunzei [N Chile, Atacama]: Jucker 123 (ZSS).
Eriosyce laui [N Chile, Antofagasta]: Lau 1541 (ZSS).
Eriosyce marksiana [C Chile, Maule]: NEL 397* (B, SGO, ZSS).
Eriosyce napina [N Chile, Atacama]: Ritter 249 (ZSS); hort. Z (ZSS).
Eriosyce odieri [ssp. *odieri*] [N Chile, Atacama]: EL 1794* (SGO, ZSS).
Eiosyce odieri ssp. *glabrescens* [N Chile, Atacama]: EL 2604* (ZSS); Flaskamp s.n. (ZSS).
Eriosyce senilis [ssp. *senilis*] [C Chile, Coquimbo]: EL 2553* (B, SGO, ZSS); Jucker 136 (ZSS).
Eriosyce senilis ssp. *coimasensis* [C Chile, Valparaiso]: NEL 389* (B, SGO, ZSS).
Eriosyce strausiana [Argentina, Mendoza and Rio Negro]: Kattermann 572 (ZSS); LE 4466* (B, CORD, ZSS); NEL 383* (B, MERL, ZSS).
Eriosyce subgibbosa [ssp. *subgibbosa*] [C Chile, Coquimbo]: Jucker 142 (ZSS).
Eriosyce subgibbosa ssp. *clavata* [C Chile]: EL 2676* (B, CONC, SGO, ZSS); Jucker 132 (ZSS).
Eriosyce taltalensis [ssp. and var. *taltalensis*] [N Chile,

Antofagasta]: EL 2654* (B, CONC, SGO, ZSS); Jucker 65 (ZSS).

Eriosyce taltalensis ssp. *paucicostata* [N Chile, Antofagasta]: EL 2665* (B, CONC, SGO, ZSS); hort. Z (ZSS).

Eriosyce taltalensis var. *pygmaea* [N Chile, Atacama]: EL 2671* (B, ZSS).

Eriosyce villosa [C Chile, Coquimbo]: EL 2675* (B, CONC, SGO, ZSS); Jucker 113A (ZSS).

Eulychnia castanea [C Chile, Aconcagua and Coquimbo]: EL 1656* (B, SGO, ZSS); NEL 391* (ZSS).

Neowerdermannia chilensis [N Chile, Tarapacá]: Kattermann 350 (ZSS).

Appendix 2.

Different variants of character composition used for the cladistic analyses of *Search I*.

Data matrix variant	Characters included in the matrix
1. All characters included	1–19
2. Excl. morphological characters	1–11
3. Excl. anatomical characters	12–19
4. Excl. epidermis characters	5–19
5. Excl. hypodermis characters	1–5, 8–19
6. Excl. cortex characters	1–7, 11–19
7. Excl. podaria characters	1–12, 15–19
8. Excl. spine characters	1–14, 17–19
9. Excl. root characters	1–16
10. Excl. character on relief features	2–19
11. Excl. character on epidermis thickness	1, 3–19
12. Excl. character on orientation of secondary cell divisions	1–2, 4–19
13. Excl. character on number secondary cell divisions in non-papillate cells	1–3, 5–19
14. Excl. character on number secondary cell divisions in papillate cells	1–4, 6–19
15. Excl. character on number of hypodermis cell layers	1–5, 7–19
16. Excl. character on hypodermis thickness	1–6, 8–19
17. Excl. character on cortex firmness	1–7, 9–19
18. Excl. character on presence of mucilage	1–8, 10–19
19. Excl. character on cortex colour	1–9, 11–19
20. Excl. character on ratio of pith to plant diameter	1–10, 12–19
21. Excl. character on stem shape	1–11, 13–19
22. Excl. character on disposition of podaria	1–12, 14–19
23. Excl. character on formation of podaria	1–13, 15–19
24. Excl. character on shape of main spines	1–14, 16–19
25. Excl. character on orientation of main spines	1–15, 17–19
26. Excl. character on root system	1–16, 18–19
27. Excl. character on shape of taproot	1–17, 19
28. Excl. character on presence of a necklike constriction between stem and taproot	1–18

Appendix 3.

Characters and character states of flowers, fruits and seeds [data taken from the cladistic analysis by Wallace in Kattermann (1994)] used as supplementary data for the cladistic analysis of *Search II*.

20. Flower produced from areoles: on side of stem [0]; old areoles in a circle around apex [1]; young areoles in a circle at apex [2].
21. Number of flowers per areole: one [0]; several [1].
22. Wool length: short [0]; long [1].
23. Pericarpel bristle present: yes [0]; no [1].
24. Pericarpel bristle number: clusters of 3 or more [0]; clusters of 1–2 [1]; clusters of 0–1 [2]; always 0 [3].
25. Pericarpel bristle length: short (5–10 mm) [0]; long (> 10 mm) [1].
26. Pericarpel bristle shape: straight [0]; curved or tortuous [1].
27. Pericarpel bristle orientation: not porrect [0]; porrect [1].
28. Ovary locule apex: drawn up to flat [0]; drawn down [1].
29. Tube bristle number: clusters of 3 or more [0]; clusters of 1–2 [1]; bristles solitary [2].
30. Tube bristle length: short (5–10 mm) [0]; long (> 10 mm) [1]; absent [2].
31. Tube bristle shape: straight [0]; curved or tortuous [1].
32. Tube bristle thickness: thin, flexible [0]; thick, stiff, spine-like [1].
33. Tube bristle orientation: not porrect [0]; porrect [1].
34. Disposition of perianth segments: erect to curved outward [0]; curved inward [1].
35. Nectary shape: simple [0]; modified, type I [1]; modified, type II [2].
36. Disposition of stigma-lobes: spreading to recurved [0]; upright to spreading [1]; clasped together [2].
37. Stigma-base: not stepped [0]; stepped [1].
38. Fruit dehiscence: indehiscent [0]; dehiscent by partial circumscissile basal splitting [1]; dehiscent by complete circumscissile basal splitting [2].
39. Fruit abscission: absent [0]; incomplete [1]; complete [2].
40. Fruit wall thickness (at time of maturity): > 2 mm [0]; 1–2 mm [1]; < 1 mm [2].
41. Fruit wall (2 weeks after reaching maturity): fleshy or juicy [0]; dry [1].
42. Fruit elongation: not elongating (no more than 1·5 times the diameter) [0]; elongating (1·5–3 times the diameter) [1]; strongly elongating (> 3 times the diameter) [2].
43. Seed retention (withing fruit): in fruit pulp [0]; loose/restricted [1]; loose [2].
44. Wrinkles/ ridges on testa: not wrinkled [0]; wrinkled [1].

45. Rib types: none [0]; single rows of testa cells [1]; multiple rows of testa cells [2].
46. Keel (on dorsal side of seed): absent [0]; present [1].
47. Testa-cell size (measured in mm²): large (0·0049–0·01) [0]; medium (0·003–0048) [1]; small (0·015–0·028) [2].
48. Anticlinal boundary of testa-cells: exposed [0]; covered by striation or other structures [1].
49. Testa-cell interstices (cell corner intersections): not sunken or pitted [0]; sunken or pitted [1].
50. Periclinal testa-cell wall-shape: moderately convex (0·5–1 × diameter); low convex (< 0·5 × diameter); flat [2].
51. Secondary sculpture of testa-cell periclinal wall: absent, smooth [0]; present [1].
52. Distribution of secondary periclinal sculpturing: total surface [0]; centre only (33–67 %) [1]; centre only (< 33 %) [2].
53. Tertiary sculpture of testa-cell periclinal wall: absent [0]; present [1].
54. Distribution of tertiary periclinal sculpturing: edge only (33 % or less) [0]; edge only (33–67 %) [1]; total surface [2].
55. Position of the hilum tissue: superficial [0]; impressed [1].
56. Position of micropyle relative to hilum rim: flat [0]; raised [1]; beneath [2].
57. Shape of hilum: oval/ovate [0]; narrow oval [1]; wide keyhole [2]; narrow keyhole [3].
58. Hilum rim modification at micropyle: not modified [0]; slightly modified [1]; strongly modified [2].

Appendix 4.

Data matrix used for *Search I*.

	0 1	1
	1234567890	123456789
Chi.aer	20112010?0	211223201
Chi.kra	2010101 0?0	201223200
Chi.lau	22-00--000	11?10220?
Eri.aur	2101122200	1100210--
Hor.asp	11-0-11100	2101210--
Hor.cur	11-0-11200	1100210--
Hor.cur.tu	11-0-11200	2101110--
Hor.hei.1	1112-1111?	210111201
Hor.hei.2	11-0-1111?	210111210
Hor.hei.si	2010211120	11000?2?0
Hor.kun	1101-11210	2101210--
Hor.mar	11-0-11200	1000210--
Hor.nap	3011311011	101123201
Hor.odi	3011301?01	201223200
Hor.odi.gl	2010201101	201213201
Hor.tal	00-1-01110	11001?010
Hor.tal.pa	3012301100	110111110
Hor.tal.py	11-0-00100	210121110
Isl.isl	1213-02200	1200000--
Neo.chi	01-0-00032	2201010--
Neo.sen	10-0-00031	1200010--
Neo.sen.co	11-0-11131	1100210--
Neo.sub	00-0-01032	?300110--
Neo.sub.cl	2011300132	1200110--
Neo.vil	00-0-00032	1201110--
Pyr.and	11-0-01200	1200010--
Pyr.bul	10-0-22200	1200210--
Pyr.str	10-0-22200	1200210--
Aus.pat	11-0-11031	0300000--
Cop.cin	3103321 10?	1200020--
Cop.kra	3203322 10?	0200020--
Cor.bre	1203-22110	0300020--
Eul.cas	1103-11100	1300000--
New.chi	01-0-01?00	110100200

For Appendix 5 see next page.

Appendix 5.

Data matrix used for *Search II.*

	0 1	2	3	4	5	5
	1234567890	1234567890	1234567890	1234567890	1234567890	12345678
Cor.bre	1203-22110	0300020--0	0000000000	0000000000	000?00?000	?00??000
Chi.aer	2011201 0?0	2112232012	0100101001	1010010222	1110002100	11100132
Chi.kra	201010 10?0	2012232002	0100100001	1010100222	1120002001	110?1021
Chi.lau	22-00--000	11?10220??	0?13??????	???0000212	122000?001	100?0010
Eri.aur	2101122200	1100210--1	0113??0021	11?0010 2?0	0020001111	100?1000
Hor.asp	11-0-11100	2101210--2	0111110001	0000000111	0120000102	12100132
Hor.cur	11-0-11200	1100210--2	0013???111	1000021211	0020000100	00110131
Hor.hei.1	1112-1111?	2101112012	0101110101	0000020211	0121212100	11100132
Hor.hei.2	11-0-1111?	2101112102	0101110101	0000020211	0121212100	11100132
Hor.kun	1101-11210	2101210--2	0113???111	1000020211	0120000100	11100132
Hor.mar	11-0-11200	1000210--2	0013???110	1000020211	0020002101	10110232
Hor.nap	3011311011	1011232012	0100100001	0000010211	0111201100	02100132
Hor.odi	3011301?01	2012232002	0101010001	0000010211	0111201100	11100232
Hor.tal	00-1-01110	11001?0102	0101110?01	000011?211	0121201100	11100132
Isl.isl	1213-02200	1200000--2	0102?00001	1000?00212	1220012010	000?1020
Neo.chi	01-0-00032	2201010--2	0101110101	0000000211	0121211100	11120032
Neo.sen	10-0-00031	1200010--2	?012?00011	0001200211	0121212100	12120032
Neo.sub	00-0-01032	?300110--?	1013???011	0001200211	0121202100	12100132
Neo.vil	00-0-00032	1201110--?	1100110001	0001200211	0120012100	12100032
Pyr.and	11-0-01200	1200010--2	0100110000	0000020212	1020000001	00121000
Pyr.bul	10-0-22200	1200210--1	0000010000	0000020002	1010000001	001200?0
Pyr.str	10-0-22200	1200210--2	0100100001	1000010212	1020001101	00121000