

ECHINOPSIS REVISITED, April 28, 2004.

By Bob Schick

I. INTRODUCTION

For the past two years, I've been carrying out a study on the genus *Echinopsis*, s.l. (sensu latu, in a broad sense) with the aim of defining its component groups as full genera or subgenera. I had intended to maintain a Web site to show my progress but, for various reasons, I have not done that. Thus, this post to the Cactus etc. Web site to briefly describe the current state of my study (and just in case something happens to me). The study is based solely on the collection of *Echinopsis*, s.l., at the Huntington Botanical Gardens in San Marino, California. Though the collection is extensive, there are many forms not represented. Because of the only partial representation and because my understanding of some floral structures is still in the learning process, this report should be regarded as a work in progress.

Several major groups of species are represented in *Echinopsis*, s.l. My original intent was to treat these groups as separate genera, because *Echinopsis*, s.l., in my view, was a too massive and overly diverse genus. Moreover, I was able to define the major groups by using the floral and seed characters not usually utilized for the genus. Then I realized that dividing *Echinopsis*, s.l., into the several genera would mask their presumed common evolutionary origin, so I decided instead to treat all the major groups (except for a new genus containing *leucantha*) as subgenera of *Echinopsis*, s.l. A further advantage of recognizing only a single genus was that it gave me more freedom to subdivide *Echinopsis*, s.l., into major subgeneric categories. But now, in a compromise, I've decided to recognize three genera in *Echinopsis*, s.l., instead: *Echinopsis*, *Trichocereus* and the new genus represented by *leucantha*. This divides *Echinopsis*, s.l., into its two major groups--*Echinopsis* and *Trichocereus*--while still emphasizing the distinctness of *leucantha* and continuing to show, at least to a considerable extent, the evolutionary cohesiveness of *Echinopsis*, s.l., and permitting me to recognize additional subgenera with a clear conscience.

The several groups, with some of their component species as examples, are listed below:

ECHINOPSIS, S.L.

A. genus *Echinopsis*

1. subg. *Echinopsis* (e.g., *eyriesii*, *oxygona*; Mamillosa group)
2. subg. *Pseudolobivia* (e.g., *Obrepanda* group, *ancistrophora*)
3. subg. (new) for *subdenudata*
4. subg. *Lobivia* (e.g., *arachnacantha*, *aurea*, *cinnabarina*, *haematantha*)
5. subg. (new) for *Pseudolobivia* x *Lobivia* hybrids (e.g., *calorubra*, *rojasii*)
6. subg. (new) for *Maximiliana* group
7. subg. *Chamaecereus* (*chamaecereus*, *saltensis*)

B. genus *Trichocereus*

8. subg. *Helianthocereus* (e.g., *bruchii*, *formosa*, *huascha*)
9. subg. *Trichocereus* (e.g., *candicans*, *spachianus*, *thelegonus*)
10. subg. (new) for *Trichocereus* x *Helianthocereus* hybrids (*pseudocandicans*?)

C. new genus (e.g., *leucantha*, *rhodotricha*)

To simplify presentation of data, I will indicate generic or subgeneric status only for *Echinopsis* and *Trichocereus*, e.g., genus *Echinopsis* and subg. *Echinopsis*. *Lobivia* is cited as an ancestral group to

the other subgenera because of its great diversity and the apparent primitiveness of some of its features. Regarding terminology, I will use the terminology in Edward Anderson's, "The Cactus Family", whenever practical, and if there is a choice between technical and less technical variants of terms in the book, I will choose the less technical. In some cases, though, I will have to employ new terms.

I will now very briefly discuss some characters I've used to define the genera and subgenera which might not be familiar to readers of *Cacti* etc. Unfortunately, photos or illustrations are necessary to adequately visualize them, but this is not possible on a mailing list. Instead, as a poor substitute, I will refer to the photographs in five popular books to illustrate at least some of the characters. The books are, (a) "The Cactus Family," by Anderson, (b) "Cacti," by Innes and Glass, (c) "Cacti, the Illustrated Dictionary," by the Preston-Mafhams, (d) "The Encyclopedia of Cacti", by Cullmann, Götz & Gröner, and (e) "Kakteen," by Götz and Gröner.

II. STAMENS

1. Rim and throat stamens.

One of the hallmarks of *Echinopsis*, s.l., is the presence of two sets of stamens, one an upper series and the other a lower series. There has been no consistent terminology for either set of stamens and terms that are used may not be entirely clear without knowledge of their definitions. To make the terms more accessible and also proper, I will call the upper series, *rim stamens*, since they originate on the rim of the throat, and the lower series, *throat stamens*--perhaps not an original term--since they originate within the throat itself. The rim stamens are arranged in a circle around the throat, their orientation varying from an erect position to forming a rather flat horizontal spray against the petals, while the throat stamens take on different configurations in the different groups.

2. Radial symmetry of flowers.

The stamen arrangement of *lobivias* is probably the most primitive of *Echinopsis*, s.l. In this type of symmetry, the rim stamens are all similarly curved so that when arranged as a horizontal spray the petals, form a more or less perfect circle, while the throat stamens form a broad swathe completely circling the throat. For photos showing the rim and throat stamens, see Anderson, *Echinopsis coronata*, p. 264 and *Echinopsis pentlandii*, p. 276; Innes and Glass, *Lobivia jajoiana*, p. 146; Preston-Mafhams, *L. cinnabarina*, p. 76 and *L. jajoiana*, p 79; Cullmann et al., *Lobivia* spp., p.197-200; and Götz & Gröner, *Lobivia* spp., p. 189, 192, 194-196.

Notice that the rim and throat stamens are arranged so that they extend out from or around the flowers' central axis in a radial pattern. This is obvious for the rim stamens when they form a more or less flat spray over the petals and not so obvious for the throat stamens since they are arranged cylindrically up and down the throat. Nevertheless, the symmetry for both is *radial*, i.e., any plane, whether vertical, horizontal or slanted, that passes through a flower's central axis will divide the flowers into more less symmetrical halves. Unfortunately, many of the above photographs do not clearly show the radial symmetry, especially for the throat stamens, because the photos were shot to one side of the flowers and not directly above.

3. Bilateral symmetry of flowers.

The throat stamens undergo a remarkable transformation in subg. *Echinopsis*, *Pseudolobivia* and subg. *Trichocereus*, the rim stamens also becoming altered, though not as markedly as the throat stamens. Regarding the throat stamens of these subgenera, those in the ventral half (see below for explanation) of the throat have grown in length to form a prominent exserted (projecting) cluster,

the *throat stamen cluster*, while the throat stamens in the dorsal half (see below) of the throat tend to decrease in numbers, usually greatly so (*Pseudobolivia*), or disappear entirely (subg. *Echinopsis* and subg. *Trichocereus*). The stamen symmetry in these groups is *bilateral*, i.e., a flower divided down its vertical midline results in a right and left half, which are more or less mirror images of each other. Some structures of a flower whose stamens are bilaterally symmetrical can be described as having a top-side and a bottom side or, to be more concise, a *dorsal* side and a *ventral* side.

I must note I'm using dorsal and ventral here more like a zoologist, whose interest is in fish or four-legged animals, than a botanist, although Barthlott and Hunt, in their book on cactus seeds, do refer to a dorsal and ventral side of seeds. As a zoological example, the fin of a fish located on the top side of its body is the dorsal fin and the fin located on the fish's bottom side is the ventral fin. The dorsal fin was made famous in the movie, "Jaws", as it projected menacingly above the surface of the water.

In the *Trichocereus* photographs of the following references, notice that the throat stamen cluster is quite prominent and restricted to the ventral (bottom) half of the throat and there are no stamens in the dorsal (top) half: Anderson, "*Echinopsis*" *macrogonia*, p. 273 and "*E.*" *spachiana*, p. 280; Innes & Glass, *Trichocereus* spp., p. 297; Cullmann et al., *Trichocereus 'theleflora'*, p. 305, *Trichocereus* hybrid, p. 306 and *T. candicans*, p. 307; and Götz & Gröner, *Trichocereus* spp., p. 301, and *Trichocereus-Hybriden*, p.302. The Preston-Mafhams' photos do not show the throat stamen cluster clearly. But what about the photo of "*Echinopsis*" *arboricola* on page 257 of the Anderson book? The throat stamen cluster appear to be located in the dorsal half of the flowers! However, Myron Kimmach informed me that the photo is actually upside down.

An interesting modification of the filaments of the throat stamen cluster occurs in subg. *Echinopsis* and *Pseudobolivia*. An extensive basal portion of the filaments in these subgenera have an adhesive surface that serves to hold the stamens together as a compact group in the throat. Many throat stamens in subg. *Trichocereus* are also held together by the stickiness of their filaments to form a similar adherent cluster, but other stamens run courses through the throat independent of the adherent cluster so that, unlike subg. *Echinopsis* and *Pseudobolivia*, the cluster is not compact in the throat, but appears as a broad, loose assemblage of stamens.

The rim stamens in the three subgenera also show bilateral symmetry: Looking at a flower from a top view, the rim stamens on the ventral half of the flower tend to be hook-shaped while those on the dorsal half are merely weakly curved. As a result, when the rim stamens are arranged in a horizontal spray over the petals, they do not form a perfect circle, as in radially symmetrical flowers, but a circle that is somewhat flattened on its ventral side. The flower tube of bilaterally symmetrical flowers is sometimes also modified: Its ventral side is slightly longer than the dorsal side, so that the surface of the flower is slightly inclined.

Bilateral symmetry is obviously a very important feature in *Echinopsis*, s.l. But why develop such a radical modification of the stamens in the first place? An obvious answer seems to be that bilateral symmetry functions as part of the pollination syndrome (strategies for attracting particular kinds of pollinators) and serves to attract a different class of pollinators than those of radially symmetrical flowers.

III. THE THROAT OF ECHINOPSIS, S.L., FLOWERS

To see the throat divisions clearly, a flower must be cut longitudinally in two. The throat in all *Echinopsis*, s.l., is transversely partitioned into two or three horizontal sections. In those with three sections, the divisions, from the base upward, are: the nectar chamber, the zone of throat stamens and the distal throat division. (a) The *nectar chamber* is typically a distinctly defined, hollow compartment at the base of the throat. It is a very long, narrow cavity in all subg. *Echinopsis* and *Pseudolobivia*; very short to only moderately long or completely absent in *lobivias*; very short and broadening toward its tip in *Chamaecereus*; very short to absent in *Helianthocereus*; and in subg. *Trichocereus*, very short to moderately long, usually the former. The absence of a nectar chamber doesn't necessarily mean that nectar is not secreted by a flower, for at least in some cases, nectar is still produced, though perhaps not in the volume of those flowers in which the chamber is developed. (b) The *zone of throat stamens*, between the nectar chamber and distal throat division, is the region where the throat stamens originate as free structures. The division is present in all *Echinopsis*, s.l., of course, since all have throat stamens. (c) The *distal throat division*, the upper section of the throat, is a hollow chamber whose dividing line with the zone of throat stamens is not always distinct. It is greatly reduced or essentially absent in some species of *Lobivia* and in *Helianthocereus* and *Chamaecereus*.

In many *Echinopsis*, s.l., a terminal portion of the distal throat division appears to be modified to serve as a nectar guide. There are many different types of guides, but I'll mention only one of the common types. It is the *throat-circle*, a term coined by Buxbaum, found in *lobivias* and *helianthocereus*. The throat-circle appears as a narrow colored ring that circles the inner wall of the distal throat division along the division's top edge. Its color differs from and contrasts to the portion of the distal throat division below it and to the color of the flower petals situated adjacent to the circle. The throat-circle apparently serves as an attractant for day-flying pollinators to an opened flower and/or to orient a pollinator, already on a blossom, to the throat itself. The throat-circle is often set upon a slight bulge of the throat wall that circles the tip of the distal throat division. I term this bulge, the *annulus*. The annulus is variably developed in *Echinopsis*, s.l., but is most prominent in *lobivias*. It apparently functions to make the throat-circle more evident to a pollinator. In some cases, though, an annulus is not necessary at all, for a throat-circle may be present when an annulus is greatly reduced or apparently absent. The flared throats of some members of some *lobivias*, such as *kuehnrichii*, which have a throat-circle, would appear to have no need for one since much of the white of the throat is exposed due to the flaring. (The flaring could act as a nectar guide in itself, but possibly just functions as a platform for insects, such as butterflies, to rest upon while feeding on nectar.)

Examples of a throat-circle are shown in the following references: Anderson, *Echinopsis backebergii*, p. 258 (the partial yellow circle); Innes & Glass, *Lobivia jajoiana* and *L. marsoneri*, p. 146 (the partial or nearly complete yellow or bright purple circles); Preston-Mafhams, *L. acanthoplegma* and *L. acanthoplegma* v. *patula*, p. 74 (the white circles); *L. amblayensis*, p. 78 (the partial yellow circle), and *L. jajoiana*, p. 79 (the purple circles); Cullmann et al., *L. pentlandii*, p. 191 (the partial white circles), *L. jajoiana*, p. 197 (the partial purplish circles, some appearing white due to glare) and *L. kuehnrichii* group, p. 198 (the partial yellow circles); Götz and Gröner, *L. pentlandii*, p. 189 (the partial white circles), *L. jajoiana* (the partial purplish circles, some appearing white due to glare) and *L. kuehnrichii* (*Formenkreis*), p. 195 (the yellow circles).

If you look closely at the throat-circles in the above photographs, you will see they actually consist of a circular line of tightly packed, small squares or rectangles, these giving the throat-circles their

color. I call the squares and rectangles *trace terminals*. They are the expanded tips of rim stamen traces that are covered by a thin, transparent layer of throat tissue. *Stamen traces* are vascular bundles located within the tissue of the floral tube itself. The stamen traces extend as narrow filaments from the base of the throat upward to various places in the tube, where they exit as free stamens. The traces of throat stamens exit in the zone of throat stamens and the traces of the rim stamens exit from the end of the throat or from the throat-circle, when present.

The throat-circle is of special interest in the Marsoneri group of *Lobivia*, which includes *jajoiana*. In many forms in the group, the throat, including the throat-circle, is covered by a thin, stiff, transparent layer which is highly reflective. An insect looking down at a flower would see a series of gorgeous, iridescent purple trace terminals that flashed on and off as the flower fluttered in the breezes. This apparently is a great signal to attract six-legged pollinators. Buxbaum used the term, *hymen*, to describe the reflective throat-circle of *jajoiana*. Actually, the hymen is not membranous at all, despite the name. Moreover, it is just a special case of the throat-circle that is developed only in some forms of the Marsoneri group. Various authors (including myself) have applied this term to the throat-circle of other *Echinopsis*, s.l., but strictly speaking, hymen should be applied only to the condition in the Marsoneri group.

I'd like to inject a personal anecdote about traces here. Many years ago, when I drove through the southeastern United States, I came across national monument signs indicating historic traces. I was intrigued by the term "traces"--romantic and all that. These traces, I later learned, were narrow trails made by the passage of people or animals through the early 19th century wilderness of the old southeastern United States (considered the southwest, then). They were main routes before roads and rail lines were built. The one I still remember seeing is the Natchez Trace which, according to the Britannica, was an Indian trail that extended from Alabama to Tennessee and was the most important highway in the Old Southwest. Well, a couple of years back, when I started dissecting *echinopsis* flowers, I noticed the internal vascular trails of stamens in floral tubes. I'm not a botanist, my background being in Entomology and Arachnology, so in my ignorance, I thought I needed a term for these vascular trails. The Natchez Trace immediately came to mind and, in reports on my research, trace was the word I used. No one objected to the term. Then I found out why when I read "The Cactus Primer" by Gibson and Nobel. Trace was actually the accepted botanical term for those vascular bundles! I still smile when I think of the coincidence. Apparently, botanists were also fascinated by the Natchez trace.

IV. THE FRUITS OF ECHINOPSIS, S.L.

Cactus fruit seeds are connected to the inner walls of the ovary by cord-like bundles called *funiculi*. In *Echinopsis*, s.l., at least, the funiculi comprise closely pressed mucous-filled globules with a single vascular trace running through each funiculus. Two major types of fruits may be recognized in *Echinopsis*, s.l., based upon the fragility of the membrane enclosing the globules.

1. Fragile funicular membranes and wet fruits.

A fragile-type of membrane is found in genus *Trichocereus*. At a fruit's dehiscence (splitting open) in this genus, the membranes of the globules break down within only a day or so after exposure to air, releasing their mucousy contents into the interior of the fruit. The membranes also show their fragility when subjected to a mechanical stimulus. I can manually rupture the membranes of a newly dehisced fruit by an even very gentle prod with a sharpened probe. (The membranes of the outermost funiculi, on the other hand, persist to form a thin but rather tough outer layer that

prevents the mucousy contents of the fruit from escaping.) This type of mucous-filled fruit is described as *wet*.

2. Resistant funicular membranes and dry and semi-dry fruits.

In the genus *Echinopsis*, the membranes of the funiculi are tough and relatively resistant to exposure to air and even to my pricking with a fine needle. Two types of funiculi are found in this genus: (a) In subg. *Echinopsis*, *Pseudolobivia* and most *lobivias*, the funicular membranes do not break down after a fruit's dehiscence. Rather, they dry out within a few days, the funiculi shriveling to form irregular dry cords. The mucousy contents of the funicular globules apparently have simply evaporated. This type of fruit is described as *dry*. (b) In some *lobivias*, the mucousy contents of the funicular globules are apparently of a different type and the globules remain turgid with mucous for a long period after dehiscence. This type of fruit is apparently referred to as *semi-dry* by Anderson. I still have to make observations on semi-dry fruits to compare them with the dry type.

V. THE SEEDS OF ECHINOPSIS, S.L.

I used the book, "Seed-diversity in the Cactaceae, subfam. Cactoideae," by Barthlott and Hunt as a reference to the structure of seeds. It is a must for anyone interested in the use of seeds in taxonomy. I do deviate, though, from some of the terminology in the book by changing the name of the "border" (Saum in German) to *collar* and by considering a seed to be divided into a usually narrow collar and broader *body*. The collar is the usually narrow portion of a seed bordering the hilum-micropylar region (HMR), this region a part of a seed upon which the funiculus is adpressed, though the seed's actual connection to a funiculus is through the hilum (a simple cavity in the HMR). To study the seeds, I used my old stereoscopic microscope with magnifications of up to 150 diameters. Some characters I found useful for taxonomy were not covered in the Barthlott and Hunt book. They are explained as follows.

1. Cuticular striations (microrelief) of the body cells

Three types of cuticular striations were apparent as seen under high power with my dissecting microscope. (a) In one type, found in subg. *Echinopsis*, the body cells are flattish and, owing to reflections from my microscope lamp, dotted with sparse white, and often blue or green pinpoints of light amidst barely perceptible cuticular folds. I found myself staring at these cells in fascination and could not help but to imagine another world down there, a quaint city at nighttime with homes lit by dim lights. How to name this fantasy land? *"Micro-city"*, I decided. At low power, the luster of the cells showing "Micro-city" cuticular striations is semi-matte or matte. (b) In *Pseudolobivia* and *Pseudolobivia* x *Lobivia* hybrids, the body cells are low-domed and awash in barely discernable reflected faint specks of white light like distant stars on a clear night and, as if in the background, the surface of the cells are dotted with nano-sized punctations. I called this type of striation, *"Starry Night"*. Groups of "Starry Night" cells, under low power, appear mirror-like as they brightly reflect light of the microscope lamp. (c) In the *Subdenudata* subgenus, the testa (hardened seed coat) is uniquely glass-like in appearance and lacks striations. The luster of these cells under low power is glossy. I must mention that the appearance of an unprepared seed under a dissecting microscope, especially the cuticular striations and color of the HMR and other structures, is quite different from that of a seed seen with a scanning electron microscope and might be useful as an adjunct to an SEM.

2. "Magmatized" multicellular sculptures.

Multicellular sculptures are depressions of the testa involving several or many adjacent body cells. Two types of sculptures may be recognized in *Echinopsis*, s.l.: rounded craters and elongate rills

(like the rills of the moon). In some subg. *Echinopsis* with multicellular sculpturing and in *subdenudata*, the interior of the seeds seems to be a source of an orangish, magma-colored light. In subg. *Echinopsis*, the floor of the craters and rills are handsomely lit with this magma color. The cause of the color, unfortunately is not very romantic. It is apparently a case of neoteny, i.e., the seeds retaining their immature color. Regretfully, the magma color eventually fades. A bright magma-colored light also appears to emanate from inside of the translucent seeds of *subdenudata*. Gorgeously jewel-like, this light seems to illuminate the entire glass-like seed's surface from below, the spaces between the conical portions of the cells lit more brightly. This magma color, much to my regret, also fades after a few months.

3. "Golden halo".

The HMR in *Echinopsis*, s.l., is a flat, mostly soft-tissued structure, usually whitish in color and either recessed below the rim of the surrounding testa or situated about level with the testa's rim. In some subg. *Echinopsis* (*Sucrensis* group), the HMR is produced to form a broad, yellowish donut-shaped structure that just barely projects beyond the testa of the collar. I can find no reference to this structure in the few sources I've read, so I angelically refer to it as the "golden halo". A somewhat similar, but more striking modification of the HMR occurs in the *Mamillosa* group of subg. *Echinopsis*. The HMR here is also yellowish, but nearly the entire HMR, not just the periphery, is puffed out to extend well beyond the collar. Although not particularly halo-like, I'll also refer this structure as a "golden halo" so as to not coin still another word. The lateral (side) edge of the halo of *mamillosa* is shown in the Barthlott & Hunt book, p. 91, fig. 36.5, as a broad pale band.

VI. TAXONOMY SECTION

The classification of *Echinopsis*, s.l., is discussed in the following sections.

A. GENUS ECHINOPSIS

The only reliable character distinguishing this genus from genus *Trichocereus* is the type of fruit. It is dry or semi-dry in *Echinopsis* vs. wet in *Trichocereus*. That said, I certainly do not like to rely on a single character to distinguish genera, or any taxon. In this case, though, the type of fruit seems to represent a fundamental difference between subg. *Echinopsis* and subg. *Trichocereus* and supporting data relating to their pollination syndromes (strategies for attracting particular kinds of pollinators) appear to support this interpretation, as further suggested in the following discussion.

Subg. *Echinopsis* and subg. *Trichocereus* appear to be adaptive twins as far as their pollination syndromes are concerned: flowers open at night, stamens bilaterally symmetrical, petals white and floral tubes and throats long. *Lobivia* and *Helianthocereus* also are adaptive twins: flowers of most or all open diurnally, stamens radially symmetrical, petals generally are colored, and floral tubes and throats short. All these are adaptive features that relate to their pollination syndromes. If *lobivias* represent an ancestral stock of *Echinopsis*, s.l., and subg. *Echinopsis* and subg. *Trichocereus* are derived from *lobivias*, the similar pollination syndromes of the two subgenera can be explained as a result of convergence. This would explain why the two have been difficult to distinguish as separate taxa. The similarity of the pollination syndromes of *Helianthocereus* to *Lobivia* can be accounted for by *Helianthocereus* simply representing a line derived from *lobivias*. But this is all speculation. The more important question, I think, involves subg. *Echinopsis* and subg. *Trichocereus*: Is there more substantial evidence for evolutionary convergence of these two subgenera? I'll address that question, as follows, by pointing out the differences between them that suggest separate evolutionary origins.

Though the flowers of both subg. *Echinopsis* and subg. *Trichocereus* are bilaterally symmetrical, their throat stamen clusters differ in a basic way. Those of all subg. *Echinopsis* I've examined are compact within the throat, this the result of an adhesive coating of the filaments, while the throat stamen cluster of all the subg. *Trichocereus* I've seen, form a more diffuse assemblage in the throat, due to a different arrangement of the stamens within the throat, though a perhaps weaker adhesiveness is still a factor in holding many of the stamens together. On one hand, the two forms of the throat stamen cluster appear to represent a fundamental difference between the two subgenera, which can be interpreted as resulting from convergence. On the other hand, the presence of adhesive filaments seems like such a unique character that it might indicate a closer relationship between the genera. But before I discuss this possibility, I should point out that there seems to be a general tendency in cacti to form bilaterally symmetrical flowers, specifically by the development of throat stamen clusters. This is shown in many diverse genera: *epicacti* and, based upon photographs, also in *Aporocactus*, *Brasilicereus*, *Epiphyllum*, *Harrisia*, *Heliocereus* and *Selenicereus*, as examples, each presumably developing its own version of the bilateral condition but none, as far as I can tell, with the aid of adhesive stamen filaments. A possible explanation for this is that the *Echinopsis*, s.l. condition uniquely leads to the adhesive filament condition. Perhaps a way to investigate this is to determine if the filaments of some *lobivias* whose throat stamens in the ventral half of the throat appeared to have lengthened--and could represent a first step toward the definitive bilateral condition--are indeed adhesive. If I have time, I will investigate this. But there are other differences between subg. *Echinopsis* and subg. *Trichocereus* that suggest they represent separate phyletic (evolutionary) lines.

One of the differences involves the scales of the floral tubes. In subg. *Echinopsis*, the scales tend to be more elongate (8 to 29 times longer than broad, though only 5 times longer than broad in the *Mamillosa* group), and in subg. *Trichocereus* only 3 to 10 times longer than broad. This suggests a different evolutionary process for the lengthening of the floral tubes in the two subgenera. Perhaps associated with this evolutionary process, the nectar chambers tend to be much longer in subg. *Echinopsis* than in subg. *Trichocereus*: 12 to 40 mm vs. 3 to 13 mm. Of interest, the rim stamens are differently colored in the two subgenera, always white in subg. *Echinopsis* and the inner side of the rim stamens being green in subg. *Trichocereus*. This difference is possibly a factor in attracting different pollinators or just a different way of attracting the same pollinators. There is another perhaps very importance difference between the two subgenera involving the traces of rim stamens in the throat, but I still have to study this.

1. SUBGENUS ECHINOPSIS.

Diagnosis: Stem with relatively few ribs, 8-12, except in *Mamillosa* group, 22-26, central spines straight. Flowers typically white, fragrant and "early nocturnal-type" (fully opened in the evening before 9PM, standard time), symmetry bilateral, throat stamen cluster forming compact bundle in the throat owing to adhesiveness of filaments, throat stamens absent in dorsal half of throat. Rim stamens white. Floral tube with scales 8-29 times longer than broad, except in *Mamillosa* group, only 5 times longer than broad. Throat long, length 103-188 mm; nectar chamber long, length 12-40 mm. Fruit dry-type. Seeds with body cells semi-matte to matte black, cuticular striations of body cells "Micro-city".

Subgenus *Echinopsis* comprises several species groups. Briefly, the major groups are, (a) the *Eyriesii* group, defined by features of the stem and seeds, and comprising, e.g., *eyriesii*, *oxygona*, *?tubiflora* and *?tapecuana* (labeled *obrepanda* subsp. *tapecuana* in Anderson, p.275), (b) the *Sucrensis* group, defined by floral tube and fruit scale characters, type of fruit dehiscence and HMR of seeds with

"golden halo", (c) a group comprising two unidentified minutely spined species, and (d) the Mamillosa group, characterized by large globular stem with many ribs that are divided into low rounded tubercles, and relatively short floral tube scales and unusual seeds whose HMR is produced into a puffy, strongly exerted "golden halo". Also, very unusual for subg. Echinopsis, the petals of two members of the Mamillosa group are colored, kermesina in red (from lit.) and a plant from the Huntington collection, dark pink tones. The latter might have resulted from hybridization.

There are interesting similarities between the Mamillosa and Sucrensis groups, conceivably indicating a common phyletic line: The floral tube of the Sucrensis group and at least some of the Mamillosa group have deeply incised fleshy scales, distal scales with prominently hooked bracteoles and an HMR that is produced into a "golden halo", though the halo is much more prominent in the Mamillosa group. Because of this possible relationship I've taken a conservative approach to the Mamillosa group and am treating it as a member of subg. Echinopsis. Besides, I've seen only three members of the group and can't generalize on their condition.

Also at the Huntington is *E. cochabambensis* whose narrow, curved, columnar stem is peculiar for subg. Echinopsis, and *E. huotii*. *Huotii* shows some similarity to the Sucrensis group in its hooked bracteoles and presence of a "golden halo".

The Echinopsis subgenus is contrasted to other subgenera as follows:

Subg. Echinopsis vs. Pseudolobivia.

(a) Throat stamens: absent in much of the dorsal half of the throat in subg. Echinopsis vs. typically present in the dorsal half of Pseudolobivia, (b) central spines: straight in subg. Echinopsis vs. gently curved to hook-like in Pseudolobivia, (c) body cells of seeds: matte to semi-matte in subg. Echinopsis vs. glossy in Pseudolobivia and (d) cuticular striations of body cells: "Micro-city" in subg. Echinopsis vs. "Starry Skies" in Pseudolobivia. Less reliable because of overlapping, (e) flowers open nocturnally in subg. Echinopsis vs. at least sometimes diurnally in Pseudolobivia, and (f) number of ribs: tending to be fewer in subg. Echinopsis, 8-14 (but up to 26 in Mamillosa group) vs. 12-28 in Pseudolobivia.

Subg. Echinopsis vs. Lobivia and Helianthocereus.

(a) Stamen symmetry: bilateral in subg. Echinopsis vs. radial in Lobivia and Helianthocereus and (b) throat length, as measure of floral tube length: longer in subg. Echinopsis, 103-188 mm vs. 15-59 mm in Lobivia and Helianthocereus. Less certain due data lacking in some species, (c) flowers opening nocturnally in subg. Echinopsis vs. opening diurnally in Lobivia and Helianthocereus. And less reliable because of overlapping, (d) flower color: white in great majority of subg. Echinopsis vs. usually colored in Lobivia and Helianthocereus, (e) relative length of floral tube scales: 8-29 times longer than broad in subg. Echinopsis (only 5 times longer than broad in Mamillosa group) vs. 1-15 times longer than broad in Lobivia and Helianthocereus, and (f) length of nectar chamber: longer in subg. Echinopsis, 12-33 mm vs. 0-13 mm in Lobivia and Helianthocereus.

Subg. Echinopsis vs. subg. Trichocereus.

(a) Fruit: dry-type in subg. Echinopsis vs. wet-type in subg. Trichocereus, (b) throat stamen cluster: a compact bundle in throat of subg. Echinopsis vs. a diffuse bundle in throat of subg. Trichocereus, (c) rim stamen filaments: white in subg. Echinopsis vs. inner surface green in subg. Trichocereus, and (d) floral tube base: narrower in subg. Echinopsis, diameter near base, 8-11 mm (13 mm in Mamillosa group) vs. 15-23 mm in subg. Trichocereus. Less reliable because of overlapping, (e)

floral tube scales: tending to be more elongate in subg. *Echinopsis*, 8-29 times longer than broad (but only 5 times longer than broad in *Mamillosa* group) vs. 1-10 times longer than broad in subg. *Trichocereus*, and (f) nectar chamber: tending to be longer in subg. *Echinopsis*, 12-33 mm vs. 0-13 mm in subg. *Trichocereus*.

2. SUBGENUS PSEUDOLOBIVIA

Diagnosis: Stem with relatively moderate number of ribs to many, 12-26, spines at least moderately long, central spines curved or hooked. Flowers white, variable in opening times, from "late nocturnal-type" (opening fully after 9 PM, standard time) to diurnal, symmetry bilateral, throat stamen cluster forming compact bundle in throat, throat stamens typically present in dorsal half of throat (absent in "*coronata*"), rim stamens filaments white or green on inner surface. Floral tube with scales 8-15 times longer than broad. Throat long, length 64-168 mm; nectar chamber long, length 18-48 mm. Fruit dry-type. Seeds with body cells glossy brown or black, low-domed in most species, conical in *subdenudata*, cuticular striations "*Starry Skies*".

Pseudolobivia is defined here in a much narrower sense than its author, Curt Backeberg, who interpreted *Pseudolobivia* as standing "halfway between *Echinopsis* and *Lobivia*". In my treatment, I've included only those species which have bilaterally symmetrical white flowers, throat stamens in the dorsal half of the throat and a long floral tube. Species represented are *ancistrophora*, *obrepanda* and similar forms, and *polyancistra*.

I've seen only a few species of *Pseudolobivia*, but an *Obrepanda* group appears to be recognizable. Their rib tubercles and areoles are more or less offset to one side and the radial spines tend to be characteristically long, stout, recumbent and pectinate.

Three specimens from the same collection, labeled *coronata*, pose a problem. The description and photo of *coronata* in Anderson does not match this specimen, so I've indicated the three plants as "*coronata*", indicating their questionable identity. More disturbing from a taxonomic view, the plants lack throat stamens in the dorsal half of the throat. This is unusual for *Pseudolobivia*, but the plants do show the other *pseudolobivia* characters in the curved central spine and seeds whose body cells are mirror-like glossy with "*Starry Night*" cuticular striations.

Subg. *Pseudolobivia* is contrasted to other subgenera as follows:

Pseudolobivia vs. *Lobivia* and *Helianthocereus*.

(a) Stamen symmetry: bilateral in *Pseudolobivia* vs. radial in *Lobivia* and *Helianthocereus*, (b) throat length, as measure of floral tube length: longer in *Pseudolobivia*, 64-168 mm vs. 15-59 mm in *Lobivia* and *Helianthocereus*, and (c) nectar chamber: longer in *Pseudolobivia*, 18-48 mm vs. 0-13 mm in *Lobivia* and *Helianthocereus*. Less reliable due to overlap are (d) flower color: white in *Pseudolobivia* vs. usually colored in *Lobivia* and *Helianthocereus*, and (e) floral tube scales: 8-15 times longer than broad in *Pseudolobivia* vs. 1-15 times longer than broad in *Lobivia* and *Helianthocereus*.

Subg. *Pseudolobivia* vs. subg. *Trichocereus*.

(a) Fruit: dry-type in subg. *Pseudolobivia* vs. wet-type in subg. *Trichocereus*, (b) throat stamens: forming compact bundle in throat of *Pseudolobivia* vs. diffuse bundle in throat in subg. *Trichocereus*, and (c) floral tube base: narrower in *Pseudolobivia*, diameter near base 6-9 mm vs. 15-23 mm in subg. *Trichocereus*. Less reliable because of overlapping, (d) relative length of floral tube

scales: tending to be more elongate in *Pseudolobivia*, 8-15 times longer than broad vs. 1-10 times longer than broad in subg. *Trichocereus*, and (e) length of nectar chamber: tending to be longer in *Pseudolobivia*, 18-48 mm vs. 0-13 mm in subg. *Trichocereus*.

Differentiation from *Lobivia*, *Helianthocereus* and subg. *Trichocereus* is covered above under subg. *Echinopsis*.

The throat stamens in the dorsal half of the throat of *Pseudolobivia* show a great deal of variation in number even from flower to flower of a given plant, ranging from none or a few to many. (I will refer to these dorsal stamens as *radial throat stamens* for conciseness.) The mere presence and, importantly, the variation of the throat stamens in the dorsal half of the throat raises an interesting question. Is their presence merely a retention from some ancestral line or is it the result of hybridization? This really involves the origin of *Pseudolobivia*. But why consider hybridization at all? The reason is that radial throat stamens also occur in my subg. *Echinopsis* x *Lobivia* hybrids where they show the same variation as in *Pseudolobivia*, and a similar situation occurs also in *Pseudolobivia* x *Lobivia* hybrids, discussed below. It appears, then, that the variation is the result of hybridization, which implies that *Pseudolobivia* is a hybrid genus, presumably derived from a subg. *Echinopsis* x *Lobivia* cross or crosses. Is there any hint of what the lobivian parent could be? Subg. *Echinopsis* and *Pseudolobivia* both have seeds of similar form, a type almost round in cross-section, but the luster of their body cells are different (matte or semi-matte in subg. *Echinopsis* vs. glossy in *Pseudolobivia*). The only present-day lobivias with a rounded type of seed, as far as I know, are *arachnacantha* and *mizquensis*, so if seeds are an indicator of parentage, an ancestor from the *arachnacantha* or *mizquensis* lines might be the lobivia parent. Just for the fun of speculating which of these two lines would more probably represent the lobivian parent, *Mizquensis* would be the answer, for the ribs of this species are divided into well-developed acute tubercles, as in the *Obrepanda* group.

This isn't the end of the subject of possible hybridization concerning *Pseudolobivia*, though. There are several collections from Entre Rios in Bolivia (Lau 400 collection) of ancistrophora-like plants at the Huntington. All these plants differ from typical ancistrophora, as described in Backeberg's Lexicon, in the fewer number of ribs, 12-13 rather than 15-16. Each of the plants shows an extreme range of variation from flower to flower in the number of the radial throat stamens, varying from none to many. There is also an oddity about the ovaries. They generally lack ovules or have only a few! Obviously enough are present, though, for the Entre Rios population to persevere. There is one other oddity about the Lau 400 plants. They appear form fruits without a pollinate partner. A very interesting population!

3. NEW SUBGENUS FOR SUBDENUDATA CARDENAS

Diagnosis: Stem with 13 acute ribs, divided into low tubercles, spines minute. Flowers white, "early nocturnal-type" (fully opened in the evening before 9PM, standard time, as in subg. *Echinopsis*), symmetry bilateral, throat stamen cluster forming compact bundle in throat, throat stamens absent in dorsal half of throat, or several present more usually, rim stamens filaments white. Floral tube with scales 13 times longer than broad. Throat long, length 131 mm; nectar chamber long, length 33 mm. Fruit dry-type. Seeds with translucent, glass-like testa and seeming internal source of magma light when seeds fresh, body cells low-conical, "lit" by magma glow, cuticular striations lacking at 150 power under dissecting microscope.

Subdenudata can be distinguished from all other *Echinopsis*, s.l., by its seeds, as described above, and also from *Pseudolobivia* by its minute spines. Though the presence of throat stamens in the dorsal half of the throat suggests a relationship with *Pseudolobivia*, the minute stem spines is a character shared with some species of subg. *Echinopsis* as is the early nocturnal-type flowers, which are typical of subg. *Echinopsis*.

4. SUBGENUS LOBIVIA

Diagnosis: Stem with ribs undivided or divided into tubercles, tubercles when present, either in straight or oblique rows. Pollination syndrome very variable, involving petals, stamens, or throat structures. Floral symmetry typically radial with suggestion of incipient development of bilateral symmetry in some *cinnabarina*. Rim stamens usually colored, at least distally, but not green. Floral tube with scales usually short, 2-15 times longer than broad. Throat short, length 15-58 mm; nectar chamber often absent, when developed, tending to be short, length 0-13 mm. Fruit dry- or "semi-dry" types. Seeds extremely variable.

Lobivia is a large and remarkably diverse subgenus, so diverse that it would appear to be polymorphic (represented by more than one evolutionary line). This diversity points to *Lobivia* as the oldest major group of *Echinopsis*, s.l. Many species groups are represented and it would be a major project to characterize them all, which I shall not attempt. Instead I will only discuss two species groups which differ so significantly from the "usual" type of *lobivia* that, in my estimation, both deserve the rank of subgenus separate from *lobivias*. And they are so treated here, a new subgenus for the *Maximiliana* group and the subg. *Chamaecereus* for *E. chamaecereus*, as follows:

5. MAXIMILIANA NEW SUBGENUS

There are many different forms, listed as varieties of species *maximiliana*, that were ascribed to this group by Walter Rausch in his "*Lobivia* '85", the last complete revision of genus *Lobivia*. Obviously, *maximiliana* is quite variable then. The variation I have personally seen involves a great difference in the length of the floral tube (the throat, as a measure of the length, substantially varying from 8 to 32 mm long), the relative length of the scales, the breadth of the nectar chamber and the thickness of the superior (upper) ovary wall. But what is really peculiar about this subgenus is a major modification of the floral tube and of the rim stamens found in no other *Echinopsis*, s.l. The distal end of the tube is uniquely produced to form a very thin, broadly truncated-conical tube-like structure, obliterating the distal throat division in the process, and the rim stamens originate at the tip of the tube-like structure as an adpressed conical cluster that completely encloses the stigma when the flower first opens. The group of rim stamens opens later the same day or the next day (I'm not certain which) to form a tiny aperture over the stigma, thus permitting pollination. Also very unusual, for at least some members of the subgenus, the throat stamens in the base of the zone of throat stamens tend to be rather widely spaced, adding extra room to the nectar chamber for nectar production and/or storage.

6. SUBGENUS CHAMAECEREUS

Diagnosis: Throat essentially a reddish urn-like chamber with a very short, broadening pale nectar chamber and without a distinct distal throat division, the throat thus almost entirely comprising only a zone of throat stamens; cells of tissue lining zone of throat stamens elongate-low-tuberculate, glistening in the cut-opened throat. Throat stamens red, short, hook-shaped and sparsely distributed over the entire zone of throat stamens.

The throat and throat stamens of *Chamaecereus*, as described above, distinguishes this subgenus from all other *Echinopsis*, s.l. Because of the almost identical throat and throat stamens of *E. saltensis* and *E. chamaecereus*, which seem very unlikely to have resulted from convergence, I'm placing both in the same subgenus to emphasize their relationship, despite the differences in their stems.

E. saltensis differs from *E. chamaecereus* not only in its short-cylindrical stem, as opposed to the uniquely thin-cylindrical and soft trailing stem of *chamaecereus*, but also in the orientation of the rim stamens which, in *saltensis*, converge toward the center of the throat when the flower first opens, leaving a somewhat narrow aperture over the stigma (until it opens more fully later on, probably on the second day of flowering, as in the *Aurea* group of *Lobivia*), while in *E. chamaecereus*, the rim stamens open fully right from the start, though the circle formed by the rim stamens is not obvious from a top view of the flower.

7. PSEUDOLOBIVIA x LOBIVIA HYBRIDS.

In the Preston-Mafhams' book, published in 1991, there is the following passage in Appendix 1 concerning *Echinopsis obrepanda*: "Its wide distribution through the highlands of central and south Bolivia has caused this species to show a perplexingly broad range of variation. As a result, many individual populations showing their own distinctive characteristics of body morphology, spination and flower colour have been named as discrete species or varieties. A number of these names were based mainly on flower colour, but as populations are now known where a full range of colours--from white through pink and magenta to red and scarlet--can be found on adjacent plants, this form of splitting now seem untenable... In some of these populations only a single flower colour is found, e.g. white or magenta, while in others the full range described above occurs."

Is *obrepanda* just a very variable species, or is there another explanation to explain the broad range of variation in its flowers and stems? *E. obrepanda* is interpreted here in a very restricted sense, as a group of perhaps varieties of the *Obrepanda* group (subg. *Pseudolobivia*) whose flowers are white and whose radial spines are more or less characteristically long, recumbent and pectinate. But what about those plants mentioned by the Preston-Mafhams with colored flowers? There are many of these in the Huntington collection. They have been interpreted as varieties of *E. obrepanda* or full species (as mentioned by the Preston-Mafhams). I have studied them carefully, and though there is still further work to be done, one thing seems evident. These plants are hybrids derived from crosses between a member or members of the *Obrepanda* group and one or more unknown *lobivias*. Which *lobivias* they could be, I don't know, but two in the Huntington collection, *Echinopsis* (subg. *Lobivia*) *mizquensis* and *E. (subg. Lobivia) pojoensis* Rausch, or species like these, are possible candidates. Both are red-flowered forms regarded as varieties of *Lobivia calorubra* by Rausch in his "Lobivia '85" book, but listed as subspecies of *Echinopsis obrepanda* by Anderson.

To investigate the possibility that the variant plants can really be interpreted as *Obrepanda* group x *Lobivia* hybrids, I made a table of five characters which show quite a range of variation in the putative hybrids. The five are, (a) throat length (as a measure of floral tube length): short in the *lobivias* and long in the *Obrepanda* group, (b) flower color: red in the *lobivias*, white in the *Obrepanda* group, (c) throat color: red in the *lobivias*, light greenish in the *Obrepanda* group, (d) rim stamen color: red in the *lobivias* and white in the *Obrepanda* group, and (e) throat stamen color: red in the *lobivias*, distally white and light green basally in the *Obrepanda* group. I refer to these characters in the table as *lobivia*-type, *obrepanda*-type and intermediate-type (intermediate between

the two, possibly resulting from hybridization). I hope to add more characters this coming flowering season.

I then listed the three groups of plants--suspected ancestral lobivia types, putative hybrids and obrepanda--in a table arranging them in order of their throat lengths, from shortest to longest. The suspected lobivia parental types (*pojoensis* Rausch and *mizquensis*) came first since their throats were the shortest, while the representative of the Obrepanda group, an obrepanda specimen from Cordoba in Argentina, was last since its throat was the longest. The hybrids fell in between, from those with the shortest throat (*megalocephala* Rausch, a taxon missed by Anderson) to those with the longest throat (the "Calorubra assemblage").

The throat lengths in the table revealed four groupings, the first two overlapping some: (a) throat lengths 33 to 43 mm (the suspected ancestral-type lobivian forms), (b) lengths 36 to 60 mm (five collections of hybrids I refer to as *megalocephala*), (c) lengths 77 to 129 mm (15 miscellaneous collections of hybrids, the "Calorubra assemblage") and (d) lengths 150 to 166 mm (obrepanda).

How did the five characters mentioned above sort out in these four groupings?

- (a) In the suspected ancestral lobivian forms (33 to 43 mm throats), all five characters were all lobivia-type, of course,
- (b) in the hybrids I refer to as *megalocephala* (36-60 mm throats), the five characters in some plants were all lobivia-type, but in others was a mixture of lobivia- and intermediate-types,
- (c) in the hybrids of the "Calorubra assemblage", (77-129 mm throats), most plants showed a mixture of intermediate and obrepanda-type characters and others showed a mixture of lobivia, intermediate and obrepanda-type characters in different combinations,
- (d) in obrepanda (150-168 mm throats, a range in this plant), all characters were obrepanda-type, of course.

From the above data, the putative lobivia and obrepanda parental forms showed no variation in the five characters; *megalocephala* showed relatively little, only lobivia- and intermediate-type being present; while in the "Calorubra assemblage" there was marked variation, every individual showing combinations of either two or three of the lobivia-, intermediate- and obrepanda-type characters. The occurrence of intermediate-type characters and mixtures of the three different types in virtually all of the presumed hybrids, I think is a good indication that, indeed, they do have a hybrid origin.

I should note that I had not considered *E. (subg. Lobivia) cinnabarina* as a possible parental type at first. I've changed my mind since then. This species, which is a complex of different forms, shows the same lobivia-type characters as *pojoensis* Rausch and *mizquensis*. But it doesn't really matter if *cinnabarina* was excluded from the table. The results would have remained the same. However, it seems more likely that one or more *cinnabarina* forms would represent a lobivian parent or parents since *cinnabarina* is more widely distributed than the other two species.

There are distinct geographically isolated populations of the obrepanda hybrids, centered from the mid Cochabamba department to the northern Chuquisaca department in Bolivia. The differences in the data of *megalocephala* vs. the "Calorubra assemblage" in the table does indicate such a population diversity. The localities are known for many of the hybrid specimens listed in the table. There are five collections at the Huntington from Pojo in which four hybrids have red flowers (a lobivia-type character) and the fifth, an orange flower, which I interpret as an intermediate-type. Regarding the four other characters, more than half are lobivia-type and the rest, intermediate-type.

The question now arises, should the hybrid Pojo population be considered as a distinct taxon and, if so, what should it be called? I'm inclined to recognize this population as distinct, indeed a species, mainly because the short floral tube sets it apart from the other populations and there is a preponderance of lobivia-type characters in the four other categories, as shown in the table. Since Pojo happens to be the type locality of megalocephala, calling this form *E. megalocephala* seems justified.

But what about the other populations in the table? There is collecting data only for two others, one from Aiquile and the second from Sucre. The specimens from both places showed a mixture of lobivia-, intermediate and obrepanda-type characters (one of the situations mentioned by the Preston-Mafhams). Should these two populations each be regarded as distinct taxa? Probably not. They apparently have no feature or features to distinguish them from each other and probably not from other populations, unless adaptation to a specific habitat be considered. But they cannot be considered as varieties of a single species, either, since the origins of the different populations have occurred in different places and probably involved different parental varieties or species, for this would make the single broadly distributed species polyphyletic (comprising forms of different evolutionary lines). (This is why I favor calling megalocephala a full species.) Some of the above putative hybrids in the Huntington collection have been identified as calorubra or as varieties of calorubra by Friedrich Ritter, so I'm just informally calling the entire group, the "Calorubra assemblage" and let someone else worry about it.

Now that that problem's solved, I'll briefly mention that the seeds of the hybrids I've examined are more or less similar enough to consider all the hybrids as belonging to the same group. Most of the seeds are beautiful, glossy gems (not as great as subdenudata, though), but I've not been able to connect the seeds to any extant lobivian species for possible parentage. Species or variety names that are probably Obrepanda group (or perhaps other Pseudolobivia) x Lobivia hybrids are: calliantholilacina, calorubra, frankii, megalocephala, purpurea and rojasii. There are undoubtedly others.

The Preston-Mafhams mentioned there are localities where only a single flower color is found. The white-flowered populations would probably be a form of the Obrepanda group, as defined here.

Pseudolobivia x Lobivia hybrids (those known to me at least) can be distinguished from both subg. Echinopsis and Pseudolobivia by their colored flowers and often from subg. Echinopsis by their rib tubercles, most of which are hatchet-shaped at least in the apical portions of the stems.

B. GENUS TRICHOCEREUS

As previously mentioned, the only significant character distinguishing Trichocereus as a genus from Echinopsis is the fruit: wet type in Trichocereus vs. the dry or semi-dry type in Echinopsis. There may also be significant genetic barriers to successful hybridization between the two genera, especially when columnar Trichocereus are involved, based upon some crosses I carried out, but I don't have enough data to substantiate this.

Two subgenera may be recognized in Trichocereus, Helianthocereus and subg. Trichocereus. These can be distinguished by (a) stamen symmetry: radial in Helianthocereus vs. bilateral in subg. Trichocereus and, with possible exceptions, (b) flower pigmentation: colored in Helianthocereus vs. white in Trichocereus, and (c) opening of flowers: diurnal and remaining open more than a single

day in *Helianthocereus* vs. "early nocturnal-type" (fully opening before 9PM, standard time) and remaining open only one day (or less) in subg. *Trichocereus*.

Most or perhaps all of the above *Helianthocereus* characters, except fruit type, are shown by *Lobivia*, the presumably ancestral group and *Helianthocereus* may be assumed to be derived from that subgenus. *Helianthocereus* and subg. *Trichocereus* are possibly monophyletic (representing a single evolutionary line). If this is the case, subg. *Trichocereus* may have branched off from a *Helianthocereus* ancestor as it underwent convergence with subg. *Echinopsis* in its pollination syndrome (white, scented, bilaterally symmetrical nocturnal flowers).

8. SUBGENUS HELIANTHOCEREUS

The species I've seen belonging to this subgenus are *bruchii*, *crassicaulis* (and an allied species), *grandis* (a large globose form sometimes incorrectly referred to as *formosa*, which is a tall cylindrical species), *huascha* and *rubriflorus*. Except for *crassicaulis* and its allied species, the stems and floral tubes of the other species are more massive than those of *Lobivia*. Also, the nectar chamber of *Helianthocereus* is less well developed than in *Lobivia*, from being absent to very short, 0-2 mm in length vs. 0-13 mm in *Lobivia*.

Trichocereus pasacana, currently synonymized with *atacamensis*, might belong to this subgenus, but I have not seen its flower clearly enough to determine that. *Pasacana* conceivably could be a *Helianthocereus* x subg. *Trichocereus* hybrid.

9. SUBGENUS TRICHOCEREUS

This is a very large group and I've seen only a few of its species. Its pollination syndrome, similar to that of subg. *Echinopsis*, subg. *Trichocereus* is distinguished from the other by its diffuse cluster of throat stamens in the throat, rim stamens which are green along their inner surface, a stouter floral tube and less elongate scales. These differences were detailed under subg. *Echinopsis*.

I've had experience with but a few species: *candicans*, '*imperialis*', *spachianus*, *thelegonus* and *werdermannianus* (= *terscheckii*). These represent different growth forms: shrubby, trailing and treelike. Nevertheless, I can offer little insight into this subgenus except for contrasting it to *Echinopsis*.

10. HELIANTHOCEREUS x SUBGENUS TRICHOCEREUS HYBRIDS.

Helianthocereus x subg. *Trichocereus* hybrids evidently occur in nature. The hybrids can be recognized by the presence of a throat stamen cluster and throat stamens in the dorsal half of the throat (radial throat stamens). The clearest indication of hybridization in the wild, to my knowledge, was shown by Andreas Wessner in the *Hybriden-Journal* (v. 2001, no. 2 and 3), a publication published by the German "Arbeitsgruppe *Echinopsis*-Hybriden". Wessner, traveling in northwestern Argentina, observed presumed hybrids wherever *T.* (subg. *Helianthocereus*) *huascha* and *T.* (subg. *Trichocereus*) occurred together (syntopy), but not where only one was present. The flowers in these populations were variously colored and some individuals in Wessner's photographs evidenced the hybrid type of throat stamen development. Wessner suggests that *pseudocandicans*, a rejected name according to David Hunt's "CITES Cactaceae checklist", may also be a hybrid derived from these inter-subgeneric crosses. There are also specimens at the Huntington that appear to be *Helianthocereus* x *Trichocereus* hybrids. One of them, a shrubby plant in the Desert Garden, becomes rather spectacular when covered by its dark red flowers.

C. NEW GENUS FOR LEUCANTHA AND RELATIVES

I originally had considered the *Leucantha* genus as outside the realm of *Echinopsis*, s.l., but am taking a more conservative approach now. Fundamental differences between the two are, an absence of a distinct circle of rim stamens, the development of radial symmetrical, extraordinarily numerous throat stamens and a type of seed I haven't seen in *Echinopsis*, s.l. There is little to connect the genus with s.l., only its elongate floral tube with some minute tufts of hairs in the areoles and, of uncertain significance, a wet-type fruit, similar (this is only from memory) to that of genus *Trichocereus*. If this new genus is indeed a member of s.l., its closest ally, would seem to be subg. *Trichocereus*. Characters indicating a relationship--a very distant one to be sure--are white, nocturnal flowers and wet-type of fruit. On the other hand, the narrow stalk of its floral tube is like that of subg. *Echinopsis*. However, the radial symmetry of the *Leucantha* flower sets it far apart from both genera.

I have seen two species which belong to this genus, the globose to short cylindrical *leucantha* and the taller cylindrical *rhodotricha*. Stephen Jankalski considers *adolphofriedrichii* as a third member of the group.

VII. POLLINATION SYNDROMES AND EVOLUTION

The flowers of many or perhaps most *Pseudolobivia* and, more certainly of most or all *Lobivia*, open during the daylight hours. But, regarding *Pseudolobivia*, why should a plant with white flowers, an adaptation for nocturnal pollinators, be diurnal rather than nocturnal? Four suppositions are necessary explain this. The first is that *Pseudolobivia* originated from one or several subg. *Echinopsis* x *Lobivia* crosses, as discussed under Subgenus *Pseudolobivia*. The second supposition is that *Lobivia* flowers are adorned with UV patterns on their petals (bees can see UV), the presence of UV on petals known for other day-flowering plants. Third, as a result of such subg. *Echinopsis* x *Lobivia* crosses, the *lobivia* UV patterns was passed on to the hybrids (*Pseudolobivia*). But what advantage would *Pseudolobivia* gain from its hybrid origin? That leads to the fourth supposition, that there was a climate change which resulted in the reduction in numbers or disappearance of night flying insect pollinators of subg. *Echinopsis*, these insects attracted to the flowers of this subgenus by their perfume and/or white color. Plants of subg. *Echinopsis* would thus be put at a disadvantage and hybridization with a *lobivian* parent would have been selected for.

Another question is, what advantage would *Helianthocereus* have gained in differentiating from its *lobivian* ancestors, since both subgenera typically have colored flowers? The main advantage actually might not relate to flower color, but to fruit type, more specifically to method of seed distribution. *Helianthocereus* has a wet-type of fruit, presumably derived from the dry or semi-dry type of one of more ancestral *lobivias*. Perhaps a change of climate took place here, too, resulting in a selective advantage for *Helianthocereus* to evolve a different type of fruit for attracting different insects or birds to distribute their seeds.

Any advantage to the hybridization between *Trichocereus huascha* and *T. candicans*, as mentioned under *Helianthocereus* x *Trichocereus* hybrids is less clear since they both have a wet-type of fruit. I can speculate on that, but without knowing if the petals of *Helianthocereus* has UV markings, it would just be guessing.

VIII. A LAST NOTE

Although my suppositions on the phyletic relationships within *Echinopsis*, s.l., may be in question, or indeed wrong, I am sure the stamens provide very important, even crucial, information in the

study of the taxonomy of *Echinopsis*, s.l., and recommend strongly that anyone working on the group include an analysis of these structures in their work.

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