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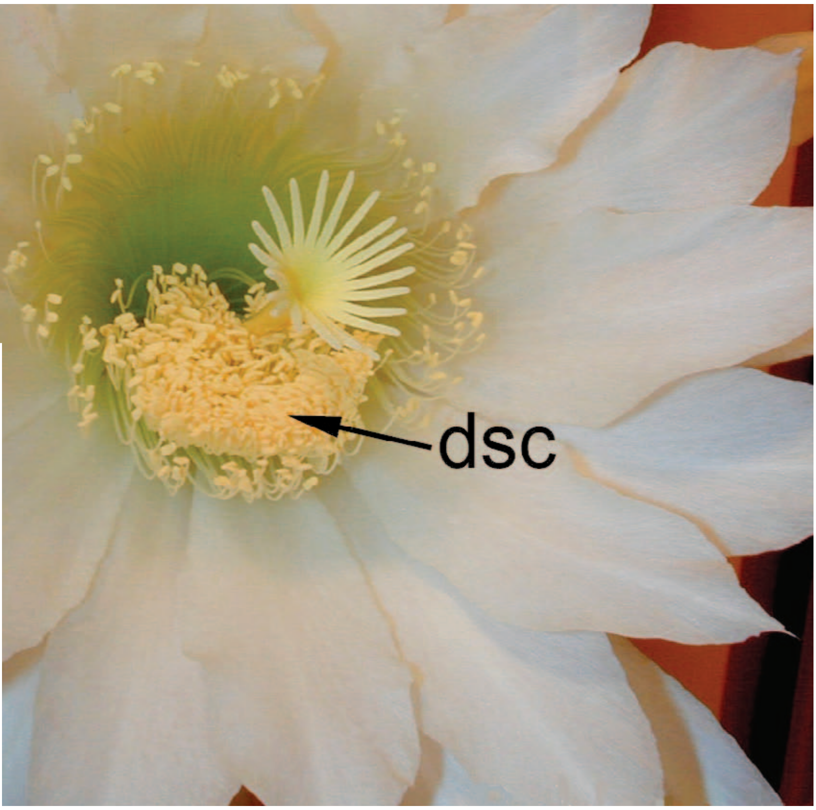
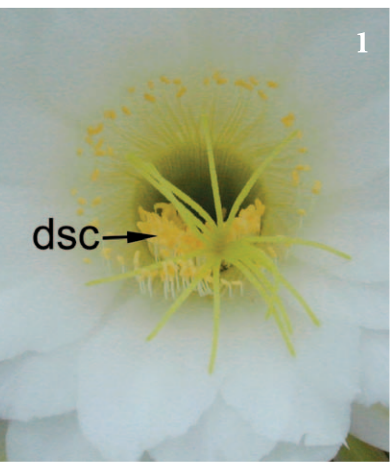
Echinopsis *sensu stricto* and *Trichocereus*: Differentiating the Genera

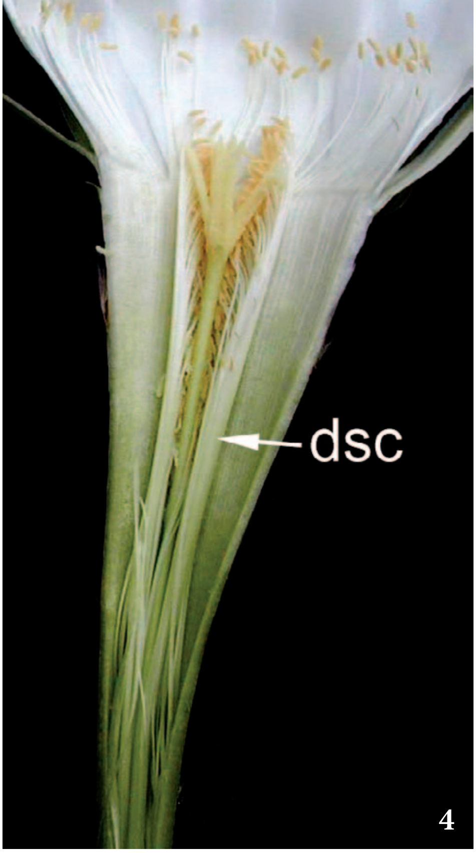
E*chinopsis* s.l. is currently treated as a large, highly variable genus that comprises a number of subsumed genera. As a student of *Echinopsis* s.l., I prefer a different approach to its classification and as a step in that direction, this article shows a way to distinguish between two of the major subsumed genera, *Echinopsis* s.s. and *Trichocereus*. These were among the first to be subsumed, starting the trend that culminated in all *Echinopsis* s.l. being assembled into one great supergenus. For the sake of briefness, *Echinopsis* s.s. will be simply referred to as *Echinopsis* hereinafter.

This article is based on the two major species of *Echinopsis* s.s. recognized by Hunt et al. (2006):





1 *Echinopsis bridgesii* ssp. *yungasensis* flower, showing a dorsal stamen cluster in a dorsal (bottom) portion of the throat while stamens are absent in the ventral (top) portion, this arrangement typical of nocturnal flowering *Echinopsis* s.l. Stigma prominent, with long lobes. 2 *Trichocereus thelegonus* flower, another nocturnal flowering cactus, its stamen arrangement the same as in *Echinopsis bridgesii* ssp. *yungasensis*. However, the internal structure of the dorsal clusters is far different.



3 *Echinopsis* sp. 2, a midsagittal section, showing a lateral view of the dorsal stamen cluster. The labeled arrow indicates the brush-like section of the dorsal stamen cluster, and the unlabeled arrow, a sheet of parallel sticky filaments oriented longitudinally. Notice the position of the stigma: it has sunk down into the throat and against the brush-like part of the cluster. 4 *Echinopsis oxygona,* frontal section, which divides the flower and its dorsal stamen cluster into a top half and a bottom half, the bottom half viewed from above, the brush portion cut off. Note the style has retracted far into the throat.

Echinopsis bridgesii and *E. oxygona* and several of their synonymized forms, and on the following species of *Trichocereus*: *T. candicans*, *T. thelegonus*, *T. spachianus*, and *T. imperialis,* a supposed *Echinopsis* × *Trichocereus* hybrid[1]. These few species of *Trichocereus* would seem to represent an inadequate sample for a proper comparison of the two genera, but all four show four fundamental features that separate *Trichocereus* from *Echinopsis* and which are expected to be applicable throughout the two genera.

The four distinguishing fundamental features are as follows:

1. Structure of the dorsal stamen clusters. The dorsal stamen cluster is a group of densely spaced stamens which project out of the dorsal (lower) region of the throat, as in *Echinopsis* (Fig. 1) and *Trichocereus* (Fig. 2). The face views of these two flowers are otherwise similar in general appearance, the dorsal stamen cluster being the most prominent feature, the ventral (upper) region of the throat, only an open space devoid of stamens. In spite of an overall similarity of the face views, midsagittal sections of the flowers reveal a great difference between the dorsal stamen clusters of the two genera.

In *Echinopsis* the dorsal stamen cluster is a highly specialized structure here termed the *Echinopsis* type. As seen in a lateral view, all of the cluster's filaments are positioned side by side, adhering against one another owing to their sticky surfaces. They form what appears to be a continuous sheet, which in cross section curves upward like the rockers of a rocking chair (Fig. 3, *white arrow*). The filaments appear to peel off from the sheet's top edges and, no longer adhesive, angle upward to form a brush-like structure that ends in the anthers. This is the dorsal stamen cluster as shown in Fig. 1.

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[1] *Trichocereus imperialis* was described as an *Echinopis* × *Trichocereus* hybrid, but a plant from the Huntington Botanical Gardens identified by that name shows no indication at all of such a hybrid background.

5 *Trichocereus candicans,* a midsagittal section, the white arrow indicating a point about halfway up the nectar chamber. The stamens of the throat are grouped into a broad but loose dorsal stamen cluster which runs a simple course through the throat, the stamens more or less straight for most of their lengths then all distally curving too one side. 6 *Trichocereus thelegonus.* The dorsal stamen cluster is somewhat similar to that of *T. candicans.* 7 *Trichocereus imperialis* The dorsal stamen cluster is somewhat similar to that of *T. candicans.*

The sheet of filaments of the above flower does not appear to curve upward very far, but the situation is different in one of the forms of *Echinopsis oxygona* (Fig. 4). The image is a top view of the sheet that was created by a frontal plane cut in which I unintentionally (but fortunately) cleaved off the tips of the stamens of the dorsal stamen cluster's brush-like part, this making the top view possible. Visible is the elongate body of the dorsal stamen cluster as well as a gap between the two edges of the rounded sheet through which the style and stigma can be seen. Both the body and gap are narrow at the body's basal end, but gradually increase in size distally, the gap disproportionately so. The style is lying on top of the decapitated stamens and squashing them, while the stigma seems to have protected the stamens beneath it from that fate.

The *Trichocereus* type of dorsal stamen cluster is usually much simpler. It differs from that of *Echinopsis* in two major ways:

(1) The filaments are also arranged in parallel, but form a single broad bundle that in its basal portion follows a more or less straight course though the throat then distally curves off to one side (Figs. 5, 6, 7, 8). This appears to be the typical condition in *Trichocereus.*

Rather strange is the dorsal stamen cluster of *T. spachianus* (Fig. 9). The stamens of the throat are totally unlike those of the other trichocerei and are so complexly organized that a simple midsagittal section cannot reveal all of the intricacies. Most


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8 *Helianthocereus rowleyi* cpx. The dorsal stamen cluster is somewhat similar to that of *T. candicans,* but a discrete nectar chamber is not developed, a not unusual circumstance in *Helianthocereus.* 9 *Trichocereus spachianus.* The stamens of the throat complexly developed and totally unlike those of the other trichocerei. The black arrow indicates a massive asymmetric funnel-like structure mentioned in the text.

prominent is a massive asymmetric funnel-like structure comprising groups of very unusual fascicles, several free stamens issuing from each one, the funnel ending in an impressive sweeping crescent-shaped crown composed of the free stamens.

A further observation on the dorsal stamen cluster of *Trichocereus* is shown by an apparent *Lobivia* × *Trichocereus* hybrid, *Lobivia rowleyi,* which is a member of a complex of different forms that I have placed in the hybrid genus *Helianthocereus.* The hybrid condition of *L. rowleyi* is indicated by its short columnar stems, a *Trichocereus* type of floral tube, the lobivian dark red flowers and presence of small rounded reflective structures on the "hymen." Despite those features, *L. rowleyi* shows the typical *Trichocereus* dorsal stamen cluster (Fig. 8), this indicating the importance and stability of the *Trichocereus* type.

(2) The *Trichocereus* filaments of the dorsal stamen cluster adhere to one another as in *Echinopsis*, but more weakly so. This can be demonstrated as follows:

Using a blade, cut off an *Echinopsis* or *Trichocereus* flower from the stem somewhere near its base, then slowly turn the flower upside down. The *Echinopsis* type of stamen cluster will drop all the way down to the opposite side of the throat as a single intact unit (though sometimes the style will cut the cluster in two), while the *Trichocereus* type cluster might or might not drop all the way down, but in any case will break up into small groups and/or single stamens. Why the difference from

Echinopsis? The adhesiveness of the trichocerean filaments is not nearly as strong (including those of *T. spachianus*).

2. Retraction of the style. *Echinopsis* is a nocturnal genus whose period of anthesis (flower opening) extends into the morning hours of the next day (as in *Trichocereus*). However, something interesting happens to the *Echinopsis* flower thereafter, starting at about daybreak. Its stigma begins gradually retracting from a protruded position beyond the throat to one within the throat, finally to become buried in a cushion of anthers of the dorsal stamen cluster (Figs. 3, 4, 10). The cause of the movement is a mystery, but the occurrence of retraction is so pervasive in the genus, that it must serve a definite function. One is suggested by the timing of pollination in *Trichocereus.*

Pollination has been found to be *bimodal* in that genus. It first occurs from about dusk to midnight carried out by hawkmoths, then resumes during the following morning by insects, mainly bees. This has been shown by Schlumpberger & Badano (2005) in *Trichocereus atacamensis* ssp. *pasacana*; Walter (2009) in *Trichocereus chiloensis* ssp. *chiloensis* (2009); and Ortega-Baes et al. (2010) in *Trichocereus terscheckii.*

What about *Echinopsis?* I have seen no reference at all in the literature concerning a pattern of pollination in the genus[2], but there *is* a suggestion of a bimodal pattern, for the flower, like that in *Trichocereus,* remains open into the following morning hours when stigma retraction takes place.

Thus, it seems logical to assume that *Echinopsis* also shows a bimodal *pollination syndrome*, though whether it involves hawkmoths as nocturnal pollinators remains to be seen. If such a pollination syndrome is indeed the case, the difference between *Echinopsis* and *Trichocereus* becomes clearer. Both show a bimodal pollination pattern but retraction of the stigma occurs only in *Echinopsis.*

But what possible function could be served by the stigma being ensconced in the cluster? An interesting question!

3. Nectar storage. A third basic difference between *Echinopsis* and *Trichocereus* lies in where the nectar is stored. In both genera, it is secreted at the base of the narrow, tubular nectar chamber. Enclosed by the walls of the hypanthium, the chamber in *Echinopsis* s.l. typically extends distally to where the stamens of the throat begin to emerge from the hypanthial walls as free structures. But there is something special about the nectar chamber in *Echinopsis* (Fig. 11, *nc*). It continues unchanged past those free stamens as a *distal extension* for a variable distance (*de*), its length perhaps depending upon the species. The extension then gradually widens, the stamens within it becoming more numerous, then finally widens so greatly, it is no longer recognizable as part of the nectar chamber-extension. The central cavity then abruptly broadens even further to become the widest part of the throat.

In a midsagittal dissection of the *Echinopsis* throat (Fig. 11), the style is visible lying on the walls of the nectar chamber proper and much of the distal extension. If the style with its stigma are lifted off, some large globules of nectar are revealed on the underlying wall. The nectar had been squeezed in the very narrow space between the style and its walls. How far distally the nectar reaches in the distal extension I have not determined, but if it extends into the widened portion, which seems likely, the volume held in that part of the system would be considerably increased.

By what means does nectar rise in the nectar chamber-extension, simply by the force of the secretion? Probably only in part. I think it principally rises owing to the capillary action afforded by the tight space between the walls of the nectar guide-extension and style, then farther along in the distal extension, possibly via the small spaces between the stamens or between the stamens and the walls.

Note that the narrowed portions of the combined chambers correspond externally with narrowed floral tubes (Fig. 10). Thus, it can be assumed that a flower with such a narrowed tube also has a nectar chamber-extension system and the *Echinopsis* type of pollination syndrome.

The nectar chamber in *Trichocereus* (Figs. 5, 6, 7, 9, *unlabeled arrows*) is typically much shorter than in *Echinopsis* and evidently cannot store much nectar, almost certainly not enough for their nocturnal pollinators: hawkmoths. Can this meager supply be supplemented, in some way, to feed the considerable appetite of the moths? Of course it can. Here too, capillary action comes into play. The nectar is drawn up into the throat

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[2] *Echinopsis ancistrophora* was mentioned in an article about pollination syndromes. In my work, I consider this complex of forms as belonging to *Pseudolobivia,* a hybrid genus, and not as *Echinopsis* s.s.

10 *Echinopsis bridgesii* ssp. *vallegrandensis* flower showing stigma nestled into brush of dorsal stamen cluster. **11** *Echinopsis oxygona,* in midsagittal section. The long nectar chamber is divided into two parts, basally the nectar chamber (*nc*) proper without internal stamens and distally a distal extension (*de*) with internal stamens. The white tic mark shows the point of division.

right above the nectar chamber due to the narrow spaces between the throat stamen filaments themselves and is stored in the lower portion of the throat among the filaments. Note the filaments are strongly arched in a basal portion of the throat of *Trichocereus imperialis* (Fig. 7) and *T. spachianus* (Fig. 9)—better seen on their left sides). They are similarly arched in *T. candicans* (Fig. 5) and *T. thelegonus* (Fig. 6) when seen in a different view of the throat. This arching creates relatively large spaces between the filaments and throat wall, the combined spaces creating a fairly extensive space for nectar storage. *Echinopsis* filaments are not arched. Their nectar is stored entirely in the nectar chamber-extension system.

The diameter of the basal portion of the *Trichocereus* floral tube is relatively wide compared to that of *Echinopsis* (cf., e.g., Fig. 5 & Fig. 11), this probably indicating a larger volume occupied by nectar. If indeed there *is* a difference in the actual volume of stored nectar, the nocturnal pollinators may also differ in the two genera, this further suggested by their structurally different nectar chambers. But what nocturnal pollinators could there be other than hawkmoths? I don't know.

4. Funiculi of ovules. Three types of funiculi are found in *Echinopsis* s.l. They differ in the length of time their membrane coverings remain intact after dehiscence of the fruit and how permeable the membranes are to the mucus-like contents of the funiculi. In *Echinopsis* the funiculi are plump and filled with clear mucus upon dehiscence, but quite permeable to the mucus, so they rapidly dry out and in about two days all that is left of the funiculi are dry, shriveled cord-like remnants. This type of resistant funicular membrane is found in all echinopsoid genera and in many or most lobivioids.

In *Trichocereus*, the funicular membranes are fragile. They begin to disintegrate soon after the fruit splits open and in a matter of hours, all will have vanished leaving in place a seed mass enmeshed in the funicular mucus which will eventually harden. This type of fruit is also found in *Helianthocereus*, *Soehrensia* and an unnamed genus containing *Echinopsis leucantha* and a related form.

(In some lobivioids, one finds a third type of funiculus, which besides being resistant to breaking down, is relatively impermeable to its mucus. Consequently, the funiculi remain swollen with their mucus contents for a long period, over a week-and-a-half before drying out.)

A comment. A reasonable objection to the proposed re-separation of *Echinopsis* and *Trichocereus* is its being based on only four species of the latter genus, though as already pointed out, the four characters utilized in distinguishing the genera are fundamental. If they were not, they would not be common in other *Trichocereus* species — a total of 26 (based on Hunt et al., 2006) — and chances are the four *Trichocereus* forms examined here would not *all* show evidence of the four differentiating characters. Returning to funiculi for a moment, the type found in *Trichocereus* is one of the basic characters uniting the trichocereoid genera which are *Helianthocereus*, *Soehrensia* and *Trichocereus*. So, if that type is fundamental to the trichocereoids, it must ipso facto be fundamental to *Trichocereus*.

The Reunion and beyond. It is instructive to go back to the historic publication in 1974 that began the subsuming of former *Echinopsis* s.l. genera into a large and heterogeneous supergenus. That publication, by G.D. Rowley, is titled, *Reunion of the Genus Echinopsis,* and as stated by the author, is based on research by H. Friedrich (1974). I will quote the first paragraph of the *Reunion s*ince it shows the rationale behind Rowley's synonymies:

"In uniting *Trichocereus* with *Echinopsis*, Dr. Friedrich is putting into effect what many of us have felt for many years should be done. Indeed, it can be regarded only as an accident of history that *Trichocereus* has been unquestioningly accepted by so many botanists in the 65 years since its elevation to generic status, and the only reason that reunion has been delayed has been a sentimental attachment for a name that becomes further and further embedded in popular literature. However, sentiment must not blind us to facts, and the undeniable truth is that the only way you can decide whether a plant belongs to *Trichocereus* or *Echinopsis* today is by applying a tape measure [to] its stem and hoping a short stem is not merely a measurement of juvenility. The flowers and fruit show no constant and recognizable differentia. Further, we know species that bridge the gap so there is no sharp discontinuity between tall (cereoid) and dwarf (cactoid) growth forms."

I must admit I was impressed at how fair and reasonable Rowley sounded and was almost starting to be convinced of his viewpoint. But no, the statement that the flowers and fruit of *Echinopsis* and *Trichocereus* showed no constant and recognizable differences is obviously not the case and negates any valid rationale for the reunion of the two genera. Nonetheless, Rowley's viewpoint has persisted until the present day, for instance in *The New Cactus Lexicon* of Hunt et al. (2006). There, the authors used an admittedly defective key to "putative" *Echinopsis* genera that separates *Trichocereus* from *Echinopsis* (and other genera), but only by stem form, as follows: "body cylindric, elongate, sometimes massively columnar" in *Trichocereus* vs. "body depressed-globose or shortly columnar, not massive …" in *Echinopsis.*

Rowley had also suggested that some of the old generic names could still be retained as subgenera or at other levels. This indicates he was considering his generic synonymies as permanent changes. Hunt et al. (2006) differ from that approach by subsuming all the *Echinopsis* s.l. genera under *Echinopsis,* but they do so on a provisional basis, stating, "Current botanical opinion favours uniting several popularly recognized but closely interrelated genera under *Echinopsis*, *pending a better understanding of the group as a whole…*" (italics mine).

I find Hunt et al's basis for subsuming the genera in most cases to be quite justified. They state that the "lines" between the major groups of *Echinopsis* s.l. (e.g., *Echinopsis* and *Trichocereus*) were "broken by smaller groups and individual species *with a foot in more that one camp*. (italics mine)." Later, the authors add: "Many artificial hybrids have been raised, both within and between these quasi-generic groups."

Those statements taken together could imply that Hunt et al. were suggesting hybridization was the cause of the interrelationships. Indeed, based upon my study of the floral and fruit morphology of *Echinopsis* s.l., intergeneric hybrids probably *do* exist and may even be surprisingly common. This of course would preclude any attempt at classification as Hunt et al. infer.

So what is to be done? It seems generally assumed we should wait for molecular analysis to solve the classification problem with *Echinopsis* s.l. in the meanwhile languishing just as a list of species names arranged alphabetically with little other use. But what if the molecular approach also shows that intergeneric hybridization is responsible for the interconnectivity of the subsumed genera? Then we'd be right back to where we started from with no classification system, just the alphabetical arrangement of the species. There is an alternative, however.

I am presently working on a study to resurrect many of the subsumed genera and this is how I deal with the problem caused by the apparent hybridizations. Very briefly, I recognize two types of species in resurrected problem genera: "normal" species and *restricted* species. I treat normal species with customary descriptions, but those of restricted species have an added explanation of how they differ from the genus in which placed and, if applicable, how they show significant similarities to other genera. However, restricted species are only "attached" to a genus and are neither included in formal generic descriptions, nor in a generic key, though their names are mentioned at the end of generic descriptions.

Thus, we have a full generic system for *Echinopsis* s.l. back in place, with all its forms out in the open, available for examination and interpretation by other workers. It is not an easy task, though. A taxonomist must know most of *Echinopsis* s.l. thoroughly including the details of flower morphology (some of which I hope to supply before too long), and most genera will have to be conceptually redesigned, as well as not being too broadly or narrowly defined.

What a challenge! ◆

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