

## A phenetic analysis of the genus *Thelocactus*

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**Summary:** A phenetic analysis of the genus *Thelocactus* is presented. The collected data, 65, and the 34 Operational Taxonomic Units used for the study were processed by a principal components analysis method. The ordinations made lead us to conclude that *Hamatocactus setispinus* is not congeneric with *Thelocactus* from which it has to be separated. Some nomenclatural changes are also made in order to adjust the taxonomy of the genus to the results obtained.

**Zusammenfassung:** Es wird eine phänetische Analyse der Gattung *Thelocactus* vorgestellt. Die für die Studie gesammelten Daten (65) und die 34 operationellen taxonomischen Einheiten werden einer Hauptkomponentenanalyse unterzogen. Die Ordinationen führen uns zur Folgerung, dass *Hamatocactus setispinus* nicht in die Gattung *Thelocactus* gehört und separiert werden muss. Einige nomenklatorische Änderungen bringen die Taxonomie der Gattung mit den gefundenen Resultaten in Einklang.

### Introduction

The genus *Thelocactus*, as we know it nowadays, was proposed by Britton and Rose in 1922, including in it twelve species that the original description of the genus unites for being cacti of medium size with few, low or indistinct ribs divided into tubercles, a scaled ovary, the fruits dehiscent by a basal pore and the seeds with a large basal hilum. The name *Thelocactus* appeared for the first time in the literature in the year 1898 in Gesamtbeschreibung der Kakteen, where Schumann used it as a name for a subgenus of *Echinocactus*, arranging in it, besides those taxa that now belong to *Thelocactus*, also many other species that later have been moved to other genera.

After the work of Britton and Rose, many other species have been added to the original group, both as new taxa and as new combinations. Some of the species combined in *Thelocactus* (*T. saueri*, *T. knuthianus*, *T.*

*viereckii*, *T. subterraneus*) have been later segregated by Backeberg (1938, 1951) in an allied genus, *Gymnocactus*, now included in *Turbinicarpus*. In 1978 Anderson, on the basis of the comparison of some characters, proposed to include the species belonging to *Gymnocactus* in *Thelocactus*, but in 1986 he reassessed his previous proposal and put *Gymnocactus* in *Neolloydia*, extending the limits of the latter genus. The Eighties saw the description of some new taxa, both at variety and species rank, and, still by Anderson (1987), a new delimitation of the genus.

In this revision the author included *Hamatocactus setispinus* in *Thelocactus*, grounding his proposal on the similarities observed between *Thelocactus bicolor* and *H. setispinus* for several of the characters he chose to compare these two species. This new delimitation of the genus *Thelocactus* led to a total upset of its limits, as two essential characters on which Britton and Rose based the genus, the presence of tubercles, a character to which the generic name refers, and the basally dehiscent fruits, suddenly failed, *H. setispinus* lacking tubercles and having fleshy indehiscent fruits. From the time of Anderson's revision, other species have been described, *Thelocactus garciae*, *Thelocactus multicephalus*, *Thelocactus panarottoanus* and *Thelocactus flavus*, while others have been segregated from it.

Recently Doweld (1998) has proposed to segregate *Thelocactus conothelos* and its varieties from *Thelocactus* and to include them in a new genus, *Torreycactus*, the whole on the basis of just the difference in the micromorphology of the secondary sculpture of the seed cuticle that in these species is smooth rather than micro-papillate. Anderson regarded the genus *Thelocactus* as consisting of 'several loosely related species and species groups...' The starting point for our work was this statement. We have tried to establish how and how much the different taxa are inter-related, with the aim to verify if the present systematic treatment is congruent with the morpho-



*T. bicolor* ssp. *bicolor*, General Cepeda, Coahuila.  
Photo Jauernig.



*T. bicolor* ssp. *bicolor* (*commodus*), Montemorelos, Nuevo León. Photo Jauernig.



*T. bicolor* ssp. *bicolor* (*schottii*), SB567 Brewster Co., Texas.



*T. bicolor* ssp. *bolaensis*, Cerro Bola, Coahuila.  
Photo Jantschgi.



*T. bicolor* ssp. *bolaensis* ("Pedricena"), San Pedro de las Colonias, Coahuila.



*T. bicolor* ssp. *bolaensis* (*wagnerianus*), Hipolito, Coahuila.



*T. bicolor* ssp. *flavidispinus*, Marathon, Brewster Co., Texas. Photo Bercht.



*T. bicolor* ssp. *flavidispinus*, SB424 Brewster Co., Texas.



*T. bicolor* ssp. *heterochromus*, Rio Nazas, Durango.



*T. bicolor* ssp. *heterochromus* (*pottsii*), Hidalgo del Parral, Chihuahua. Photo Lausser.



*T. bicolor* ssp. *schwarzii*, Calles, Tamaulipas. Photo Jauernig.



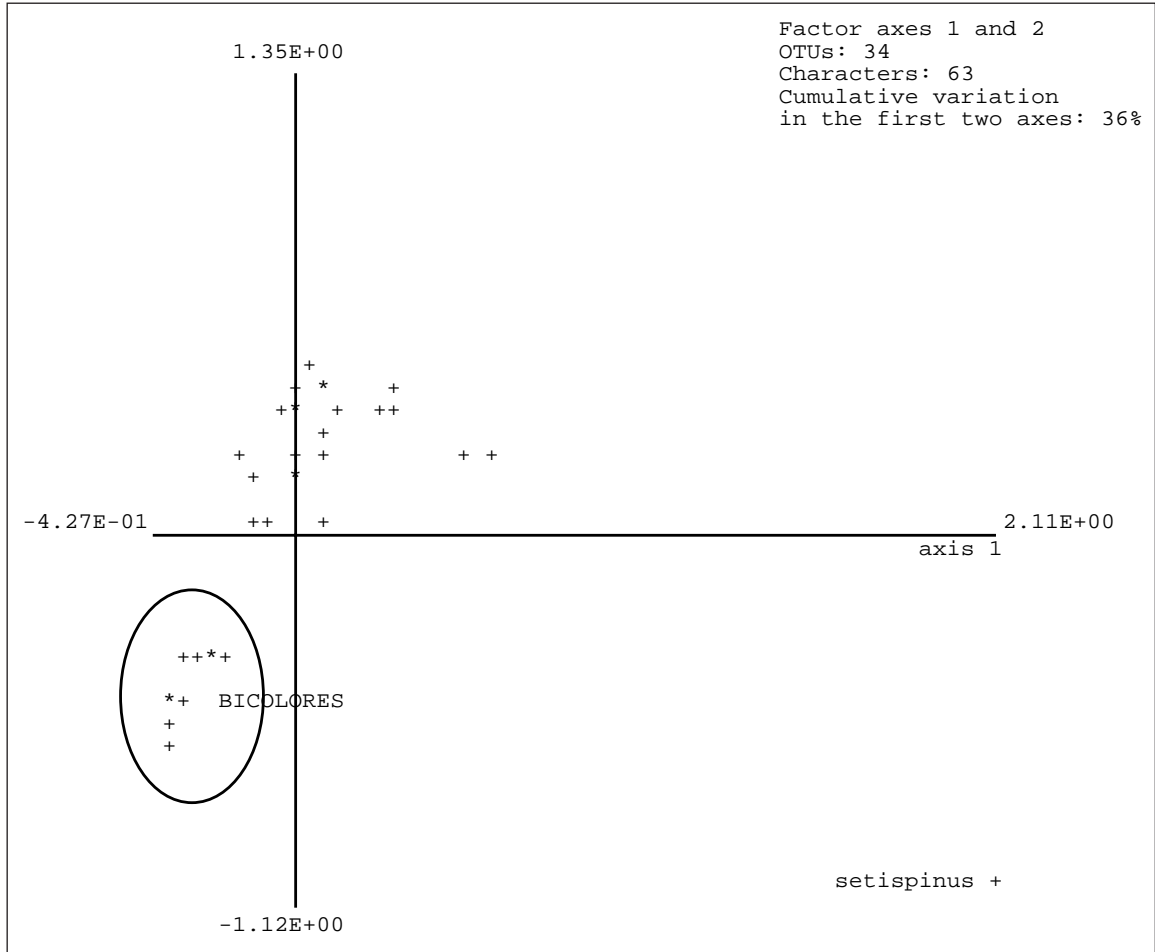
*T. buekii* ssp. *buekii*, La Soledad, Nuevo León.

logical data we have collected. Indeed, there is still not a consensus either on the species to be included in the genus (Doweld, besides excluding *conothelos* and its varieties, retains the monotypic genus *Hamatocactus*) or for the subspecific treatment for the taxa belonging to the *Thelocactus rinconensis* complex (Anderson, 1999; Glass, 1997; Lüthy, 1999, Mosco & Zanovello, 1999). To reach this goal we have chosen a phenetic approach, based on the observation of many morphological characters. The phe-

netic analysis we made has allowed us to reach, we think, a better comprehension of the studied species and to formulate some resultant taxonomic proposals.

### Materials and methods

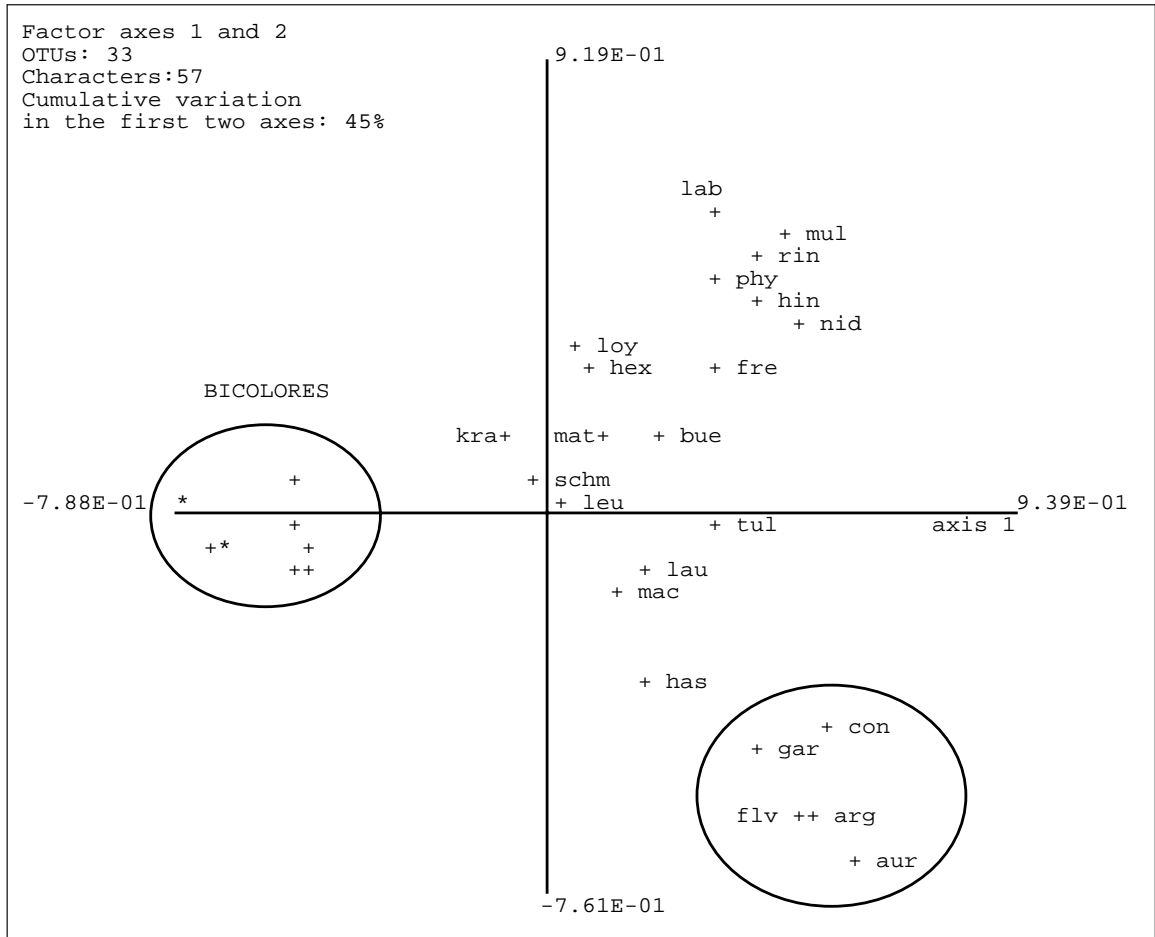
The majority of the data used in our study have been obtained by observations made on the plants in our collections. Most of these plants are provided with field data and have been grown from seed. Some data originate from observations



**Figure 1.** Principal components analysis of *Thelocactus. H. setispinus* included in the ordination. Characters: stem shape I; stem shape II; maximum stem diameter; maximum stem height; head number; epidermis colour I; epidermis colour II; epidermis colour III; number of hypodermal layers; crystals; seedling shape; ribs; orthostichy number; tubercles; tubercle or rib width; tubercle or rib height; areolar glands; minimum total spine number; maximum total spine number; central and radial spines distinguishable; hooked spines; spine colour I; spine colour II; spine colour III; upper spines flattened; shredded spines; minimum flower diameter; maximum flower diameter; minimum petaloid length/width ratio; maximum petaloid length/width ratio; shape of the petaloid apex; margin of the petaloid apex; flower colour I; flower colour II; flower colour III; flower colour IV; style colour I; style colour II; style colour III; stigma colour I; stigma colour II; filament colour I; filament colour II; primary filaments insertion; pollen; scented flowers; early bud development; flowering period; fruit colour; fruit dehiscence; fruit succulence; seed average diameter; seed average length; large HMR; micropyle inside the hilum; micropyle on the edge of the hilum; micropyle outside the hilum; appendages on the hilum edge; funicle rests conspicuous; testa cells shape; sinuate anticlinal cell walls; micro-papillate seedcoat; striate seedcoat.

we made in the field during our travels in Mexico, while still others have been taken from literature. Complete lists of the specimens examined along with the characters used and their scaling are given in an appendix. The material for light microscope anatomical studies was fixed in formalin/acetic acid/ethanol (10:5:85) and then processed for the usual paraffin embedding pro-

cedure. It was sectioned at 30  $\mu\text{m}$  and stained with haematoxylin-eosin. Freshly collected pollen has been embedded in balsam prior to observation. Seeds undergoing Scanning Electron Microscope (SEM) analysis were washed with distilled water, air dried and then gold coated. For SEM analysis we used Philips 500 and Leica Stereoscan microscopes. We used MULVA-4 pro-



**Figure 2.** Principal components analysis of *Thelocactus*. *H. setispinus* excluded from the ordination. OTUs: arg = *argenteus*; aur = *aurantiacus*; bue = *buekii*; con = *conothelos*; flv = *flavus*; fre = *freudenbergeri*; gar = *garciae*; has = *hastifer*; hex = *hexaedrophorus*; hin = *hintonii*; kra = *krainzianus*; lab = "La Bolsa"; lau = *lausseri*; leu = *leucacanthus*; loy = *lloydii*; mac = *macdowellii*; mat = *matudae*; mul = *multicephalus*; nid = *nidulans*; phy = *phymatothelos*; rin = *rinconensis*; schm = *schmollii*; tul = *tulensis*. Characters: stem shape I; stem shape II; maximum stem diameter; maximum stem height; head number; epidermis colour I; epidermis colour II; epidermis colour III; number of hypodermal layers; seedling shape; ribs; orthostichy number; tubercle shape; grooved tubercles; tubercle or rib width; tubercle or rib height; areolar glands; minimum total spine number; maximum total supine number; central and radial spines distinguishable; spine colour I; spine colour II; spine colour III; upper spines flattened; shredded spines; minimum flower diameter; maximum flower diameter; minimum petaloid length/width ratio; maximum petaloid length/width ratio; shape of the petaloid apex; margin of the petaloid apex; flower colour I; flower colour II; flower colour III; flower colour IV; style colour I; style colour II; style colour III; stigma colour I; stigma colour II; filament colour I; filament colour II; primary filaments insertion; pollen; early bud development; flowering period; seed average diameter; seed average length; large HMR; micropyle inside the hilum; micropyle on the edge of the hilum; micropyle outside the hilum; appendages on the hilum edge; funicle rests conspicuous; testa cells shape; sinuate anticlinal cell walls; micro-papillate seedcoat.



*T. buekii* ssp. *matudae*, Galeana, Nuevo León.



*T. conothelos* ssp. *conothelos*, Dr Arroyo, Nuevo León.



*T. conothelos* ssp. *argenteus*, Ascension, Nuevo León.



*T. conothelos* ssp. *aurantiacus*, La Escondida, Nuevo León.



*T. conothelos* ssp. *flavus*, El Huizache, San Luis Potosí.  
Photo Nodari.



*T. conothelos* ssp. *garciae*, Bustamante, Tamaulipas.



*T. hastifer*, east of Cadereyta, Querétaro.



*T. hexaedrophorus*, Sierra El Azul, Nuevo León.



*T. hexaedrophorus (lloydii)*, SB113 Salinas,  
San Luis Potosí.



*T. lausseri*.



*T. leucacanthus* ssp. *leucacanthus*, Mesa del León,  
Querétaro.



*T. leucacanthus* ssp. *schmollii*, Vizarrón, Querétaro.

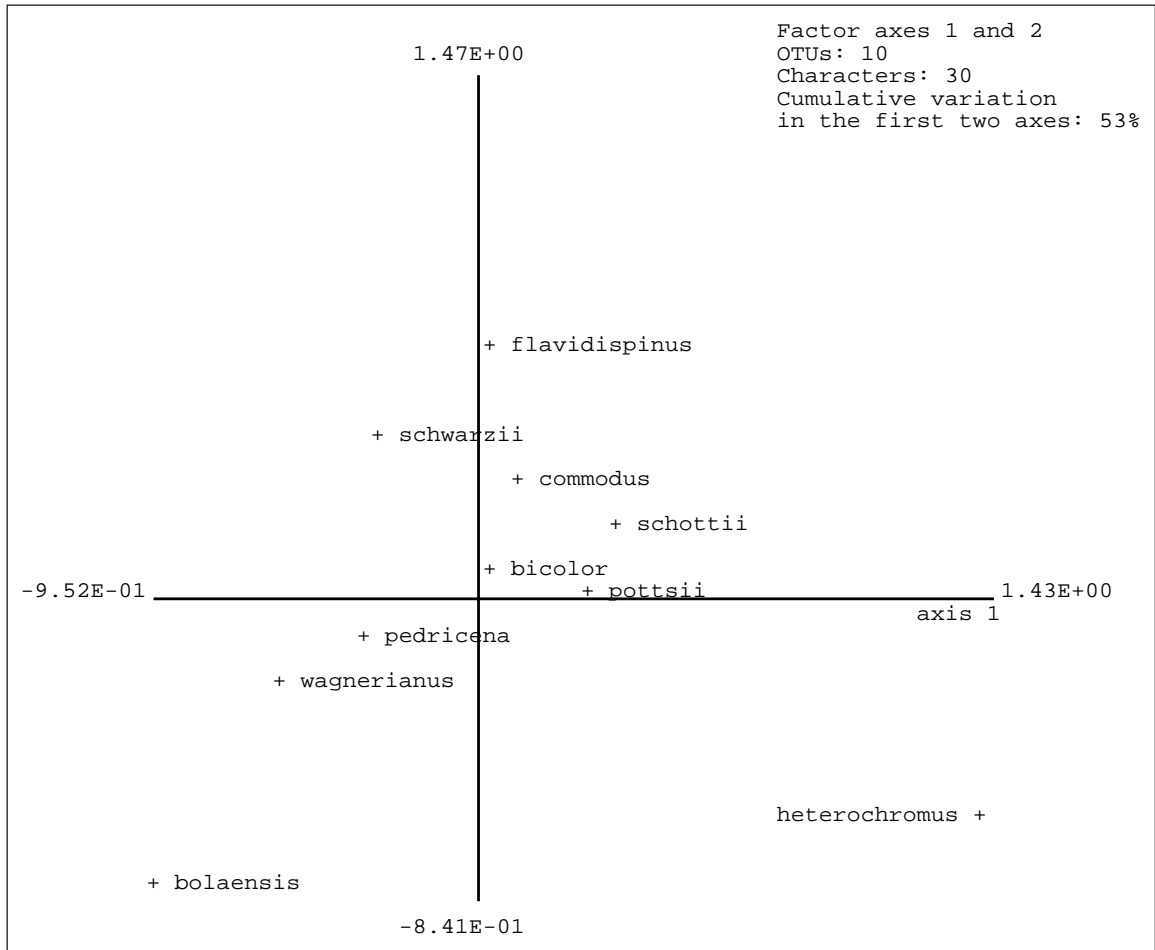
gramme for the multivariate analysis. Character vectors were normalised and the resemblance matrix was obtained by a similarity algorithm. The ordination technique used was a principal components analysis (PCA).

### Results

From the ordination plot (Figure 1) obtained using all the Operational Taxonomic Units (OTU), it becomes immediately evident that *Hamatocactus setispinus* diverges strongly from all other OTUs. It differs from the other taxa in lacking crystals and tubercles, for having hooked central spines, scented flowers, brilliant red, fleshy, indehiscent fruits and smaller seeds with

a striate seedcoat.

In the next ordination made excluding *H. setispinus*, the definition of the phenetic structure of the genus *Thelocactus* is much better (Figure 2). Two OTU groups separate neatly from the other entities of the genus: one is made up of *Thelocactus conothelos* and its subspecies together with *Thelocactus garciae* and *Thelocactus flavus*, the other by *Thelocactus bicolor* and allied taxa. The taxa belonging to the *T. conothelos* group differ from all the other *Thelocactus* in two characters, the peculiar flower tube morphology that in these species bears the insertion of the primary filaments well above the basis of the nectar chamber, and the micromorphology of the



**Figure 3.** Principal components analysis of the *bicolor* complex.

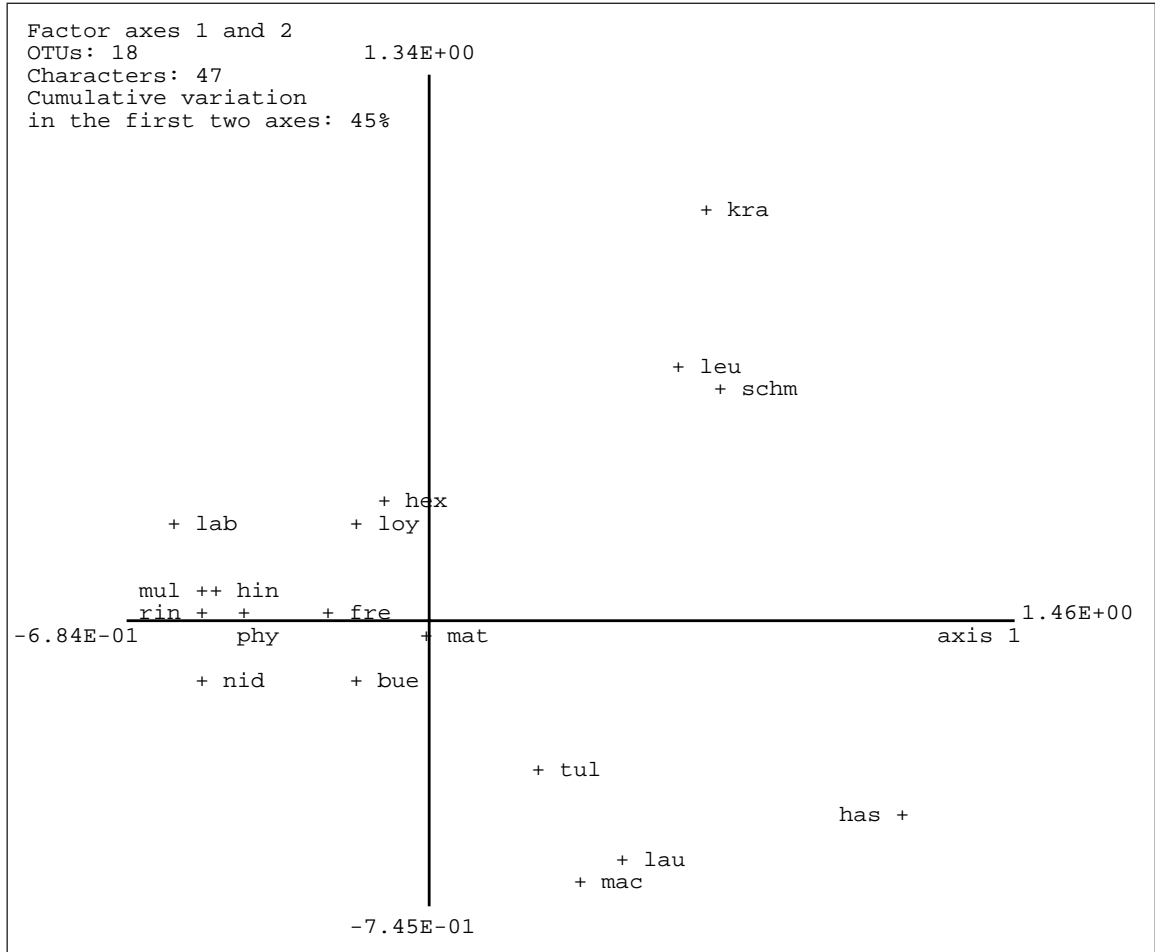
Characters: stem shape I; maximum stem diameter; maximum stem height; head number; epidermis colour I; orthostichy number; tubercle or rib width; tubercle or rib height; areolar glands; minimum total spine number; maximum total spine number; spine colour I; spine colour II; upper spine flattened; minimum flower diameter; maximum flower diameter; minimum petaloid length/width ratio; maximum petaloid length/width ratio; shape of the petaloid apex; margin of the petaloid apex; style colour II; stigma colour I; stigma colour II; filament colour II; flowering period; seed average diameter; seed average length; micropyle inside the hilum; micropyle outside the hilum; appendages on the HMR.



seeds whose testa cells are conical with a smooth surface. *Thelocactus garciae* is very similar, morphologically, to *T. conothelos*, from which it diverges by the different shape of the tubercles, that are rounded, whereas in *conothelos*, at least when young, they are angled; by the epidermis colour, but, mainly, by the micromorphology of the seeds that in this species have not such a large hilum micropilar region as in *conothelos* and

instead have conspicuous funicle rests. In this it is similar to *Thelocactus tulensis*, the only other species, along with *T. flavus*, to have this character. *Thelocactus flavus* is the latest species belonging to this group. It is a close ally of *T. garciae*, from which it differs in the clustering habit, the different spine number and the flower colour.

The *bicolor* group is the richest in entities and to assess the relationships inside it we made a



**Figure 4.** Principal components analysis of *Thelocactus: bicolor* and *conothelos* complexes excluded from the ordination.

OTUs: bue = *buekii*; fre = *freudenbergeri*; has = *hastifer*; hex = *hexaedrophorus*; hin = *hintonii*; kra = *krainzianus*; lab = “La Bolsa”; lau = *lausseri*; leu = *leucacanthus*; loy = *lloydii*; mac = *macdowellii*; mat = *matudae*; mul = *multicephalus*; nid = *nidulans*; phy = *phymatothelos*; rin = *rinconensis*; schm = *schmollii*; tul = *tulensis*.

Characters: stem shape I; stem shape II; maximum stem diameter; maximum stem height; head number; epidermis colour I; epidermis colour II; epidermis colour III; number of hypodermal layers; seedling shape; ribs; orthostichy number; tubercle shape; grooved tubercles; tubercle or rib width; tubercle or rib height; areolar glands; minimum total spine number; maximum total spine number; central and radial spines distinguishable; spine colour I; spine colour II; spine colour III; shredded spines; minimum flower diameter; maximum flower diameter; minimum petaloid length/width ratio; maximum petaloid length/width ratio; margin of the petaloid apex; flower colour I; flower colour II; flower colour III; style colour I; style colour II; filament colour II; pollen; early bud development; flowering period; seed average diameter; seed average length; micropyle inside the hilum; micropyle on the edge of the hilum; micropyle outside the hilum; appendages on the hilum edge; funicle rests conspicuous; testa cells shape; sinuate anticlinal cell walls.

separate ordination (Figure 3). The taxa of this complex differ from the other taxa of the genus in two characters: the flower that has always a more or less deep red throat, and the pollen whose grains are polycolate, a character that we find elsewhere only in *Thelocactus macdowellii*. The PCA results point out the affinity of *T. heterochromus* with *T. bicolor*, so that it stands apart from all the entities of the *bicolor* complex. *Heterochromus* differs from *bicolor* in the stem shape, which is depressed, by having more robust spines and for the absence of areolar glands. Lack of areolar glands is a character common also to other populations, scattered through Durango and Chihuahua, that have been till now considered *bicolor*, which they morphologically resemble, but from which they differ in having rather more robust spines. We have associated, in our analysis, these populations with the plants dis-

tributed by Brack as *Thelocactus bicolor* var. *pottsii*. These originate from an area near Jimenez, in the state of Chihuahua, and have an interesting feature: they have the lower central spine hooked. We followed Brack in the use of the epithet *pottsii* to name this intermediate form, because, with regard to the spine number and stoutness, they fit the description by Salm-Dyck. Inside the *bicolor* group three OTUs all segregate together: *bolaensis*, *wagnerianus* and 'Pedicena'. This last includes some entities distributed by Brack as red-spined *bolaensis* and native of Coahuila, between San Pedro and Boquillas. All these three entities are united, and distinguish from *bicolor*, for having a cylindrical stem, often slightly caespitose, with 8–13 ribs and a greater radial spine number.

Leaving out the ordination the groups of *bicolor* and *conothelos*, we reached an optimum



*T. leucacanthus* ssp. *schmollii* (krainzianus), Peña Miller, Querétaro.



*T. macdowellii*, Higueras, Coahuila.



*T. multicephalus*, Sandia, Nuevo León.



*T. multicephalus* ("La Bolsa"), El Desierto, Nuevo León.



*T. rinconensis* ssp. *rinconensis*, Ramos Arizpe, Coahuila.



*T. rinconensis* ssp. *rinconensis* (*phymatothelos*), Arteaga, Coahuila.



*T. rinconensis* ssp. *freudenbergeri*.



*T. rinconensis* ssp. *hintonii*, Rayones, Nuevo León.  
Photo Jantschgi.



*T. rinconensis* ssp. *nidulans*, Sierra Paila, Coahuila.

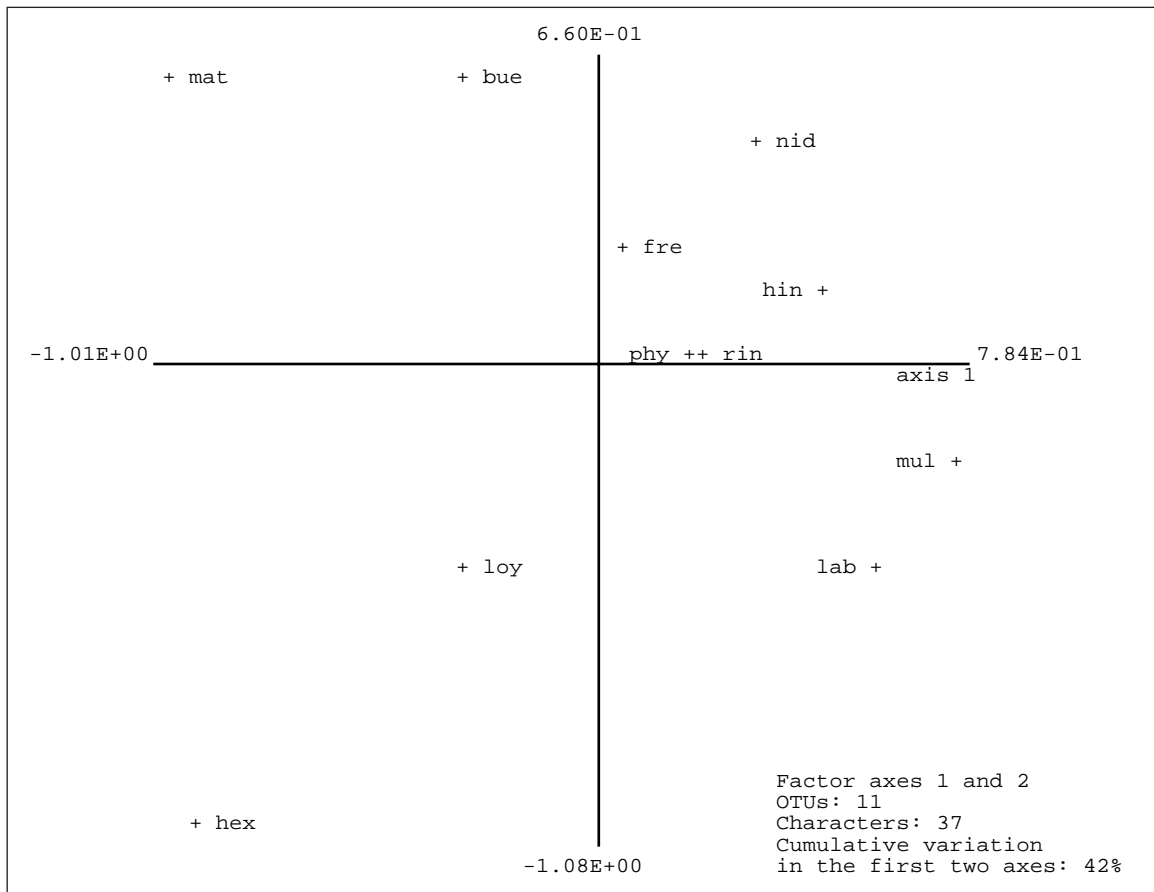


*T. tulensis*, El Huizache, San Luis Potosí.

resolution of the remaining OTUs (Figure 4). Two clusters are recognisable here: the first is formed by *Thelocactus rinconensis* and subspecies, *Thelocactus hexaedrophorus* and subspecies, *Thelocactus multicephalus*, *Thelocactus buekii* and *Thelocactus matudae*; the other by *Thelocactus leucacanthus* and subspecies. The latter group of three related entities is made up by *leucacanthus*, *schmollii* and *krainzianus* sensu Nagl. The OTUs that are not included inside any cluster are formed by four species: *Thelocactus lausseri*, *Thelocactus hastifer*, *Thelocactus macdowellii* and *Thelocactus tulensis*, and are not closely related to any other

species.

The group with the greatest number of OTUs is formed by *rinconensis*, *nidulans*, *freudenbergeri*, *hintonii*, *phymatothelos*, *multicephalus*, 'La Bolsa', *hexaedrophorus*, *lloydii*, *buekii* and *matudae*, and to obtain a good resolution inside it, we made a further ordination with only these OTUs. In the related plot (Figure 5) these OTUs separate into four clusters. The largest is formed by *T. rinconensis* and its subspecies, that share a unique character: they have a multi-layered hypodermis, a feature typical of these entities and present only in this complex in the whole genus. *T. multicephalus*, in its more southern



**Figure 5.** Principal components analysis of *Thelocactus*: the group formed by *buekii*, *hexaedrophorus*, *multicephalus* and *rinconensis* resolved.

OTUs: bue = *buekii*; fre = *freudenbergeri*; hex = *hexaedrophorus*; hin = *hintonii*; lab = "La Bolsa"; loy = *lloydii*; mat = *matudae*; mul = *multicephalus*; nid = *nidulans*; phy = *phymatothelos*; rin = *rinconensis*.

Characters: stem shape I; maximum stem diameter; maximum stem height; head number; epidermis colour I; epidermis colour II; epidermis colour III; number of hypodermal layers; ribs; orthostichy number; tubercle shape; tubercle or rib width; tubercle or rib height; minimum total spine number; maximum total spine number; central and radial spines distinguishable; spine colour II; spine colour III; shredded spines; minimum flower diameter; maximum flower diameter; minimum petaloid length/width ratio; maximum petaloid length/width ratio; margin of the petaloid apex; flower colour I; flower colour II; flower colour III; style colour I; style colour II; flowering period; seed average diameter; seed average length; micropyle inside the hilum; micropyle on the edge of the hilum; micropyle outside the hilum; appendages on the hilum edge; testa cells shape.

forms (OTU La Bolsa) that usually have single depressed stems, resembles a *rinconensis*, but differs from it by two characters: the lack of ribs and the presence of only one hypodermal layer (Figure 6), while *rinconensis* and allied taxa always have the stem divided into ribs and two or three hypodermal layers (Figure 7). *Thelocactus hexaedrophorus* is distributed over a rather large area and has numerous local forms slightly differing from each other and all included in the OTU *hexaedrophorus*. The plants originating from the area near Fresnillo have been identified by Anderson as the *Thelocactus lloydii* of Britton and Rose, so we included them in the OTU *lloydii*. The last two taxa we have taken into consideration for this ordination are *Thelocactus buekii* and *Thelocactus matudae*.

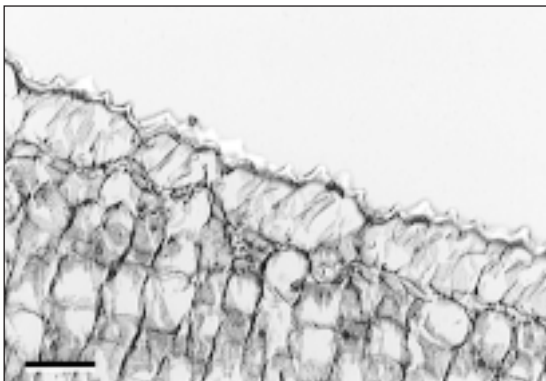
### Discussion

The phenetic structure of the genus *Thelocactus*, as it appears from the PCA, does not match that proposed by Anderson (1986) in his revision of the genus. This is due to the fact that we have used for our study a much greater number of characters, 65 versus 19, to establish the relationships inside the genus. From the comparison made by Anderson among *Hamatocactus setispinus*, *Thelocactus bicolor* and *Thelocactus hexaedrophorus*, it emerged that *setispinus* and *bicolor* share ten of the nineteen characters used, while only four are common to *setispinus* and *hexaedrophorus*. The scantiness of the shared characters between *H. setispinus* and *T. hexaedrophorus* (that is, the type species of the genus) made Anderson uncertain if to include *setispinus* in *Thelocactus* or not. Eventually *H. setispinus* was included in *Thelocactus*, suppressing the monotypic genus *Hamatocactus*, as considered troublesome, but in the meantime making the delimitation of *Thelocactus* awkward.

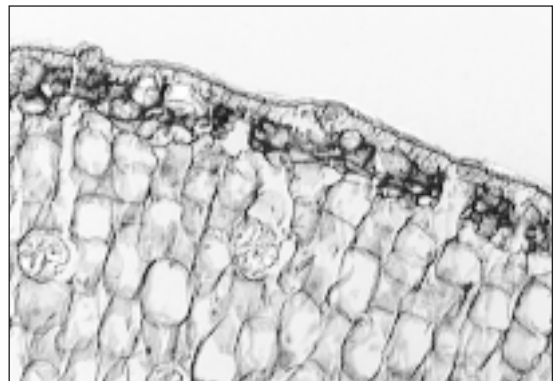
We think that Anderson has underestimated

some characters that are basic to the circumscription of this genus, namely the presence of tubercles and a semi-fleshy fruit dehiscing at maturity. The seed shape, pyriform and with a basal hilum, excludes any relationship of *setispinus* with *Ferocactus*, a relationship once upheld by Benson (1982), but advocates that it belongs to the same phylogenetic line as *Thelocactus*. According to us *H. setispinus*, for the size of the seeds, that are smaller than those of *Thelocactus*, and for the secondary sculpture of the seedcoat, striate rather than micro-papillate, is, closer allied to *Turbinicarpus*, whose seeds have a similar size and, in the majority of the species, a striate seedcoat. An analogous stand has been already taken by Doweld in 1998, with the inclusion of *Hamatocactus* in his new subtribe *Turbinicarpinae* to which *Thelocactus* does not belong. To conclude, in view of the PCA results and of the morphological differences regarding some characters — presence of tubercles, fruit morphology and seed micromorphology, according to us fundamental for the circumscription of the genus *Thelocactus* — we think that *H. setispinus* is not to be included in *Thelocactus* and therefore the monotypic genus *Hamatocactus* is to be retained.

The cuticle micromorphology of *Thelocactus conothelos* and its subspecies led Doweld (1998) to propose a new genus, *Torreyacactus*, for them, placing it in a distinct phylogenetic line, together with *Kadenicarpus* and *Bravocactus*, two other new monotypic genera, including in the first *Turbinicarpus horripilus* and in the second *Turbinicarpus pseudomacrolele*, both having seeds with a smooth cuticle. Our opinion is that segregating *conothelos* from the genus *Thelocactus* only on the basis of this single character is wrong. Moreover, when all the other characters are congruent with those of the other *Thelocactus* species, we do not agree with



**Figure 6.** Outer cell layers of *Thelocactus multicephalus*, HO 809 Sandia, Nuevo León, only one hypodermal layer is present. The bar 100  $\mu$ m long.



**Figure 7.** Outer cell layers of *Thelocactus rinconensis* ssp. *freudenbergeri*, CSD173 Grutas de Garcia, Nuevo León, a several layered hypodermis is present.

Doweld's proposal.

The typical form of *T. conothelos* ssp. *aurantiacus* is morphologically sufficiently distinct from the type species, both for body shape and spination, but there are populations, situated at the beginning of the Aramberri valley and more southerly too, that we have observed near La Escondida and Zaragoza, that are morphologically identical to the ssp. *conothelos*, the sole difference being the flower colour that varies from a deep yellow to orange in the populations near Zaragoza. We think that these entities fall within the normal variability of this subspecies that differs from the type species only for the different flower colour. It is our opinion that this character is sufficient to maintain as distinct these two taxa as the pigments that account for the two colours, betaxanthins for the yellow and betacyanins for the magenta, are the product of two different biosynthetic pathways (Gibson & Nobel, 1986). Of the subspecies *argenteus* are known only some populations native of the Ascension valley. They are all morphologically similar with each other and distinct from the type species for the spination, that is denser, and for the different colour of the central spines, white instead of greyish.

The morphological differences between *T. conothelos* and *T. garciae* are scanty and the differences founded in seed micromorphology seem not sufficient to justify the maintenance of *garciae*, that in the latest CITES Cactaceae Checklist has been listed as provisionally accepted at the species rank, so we think that is more appropriate to treat it as a subspecies of *conothelos*. Also if *flavus* differs from *conothelos* for some more characters, spine number and the clustering habit, than *garciae* does, due to its close relationship with *garciae* based on seed micromorphology, it has to be treated as a subspecies of *conothelos* too. A taxon that can be referred to this group is *Thelocactus panarottoanus* Halda. Halda (1998), in his description full of gaps and not accompanied by any photograph, compared this species with *Thelocactus rinconensis* and *T. conothelos*. The indications of the similarity of the seeds of *T. panarottoanus* with those of *T. conothelos*, along with the flower colour and the generic type locality, make us suppose that it is conspecific with *T. flavus*. The author also states it is related to *T. rinconensis*. Therefore *T. panarottoanus* is comprised in the same OTU of *T. flavus*, and the two epithets are synonymous.

*Thelocactus bicolor* is the species with the greatest distribution area that extends from Texas, north, to San Luis Potosí, south, and from Tamaulipas, east, to Durango, west. It is then natural to find populations that differ from each other more or less neatly and that many of them

have been formally described. Of all the varieties once described, today only two are formally accepted, all the others have increased the synonym list of *T. bicolor*. Moreover the validity of the systematic position of *Thelocactus heterochromus*, at species rank, has been recently questioned, this taxon being listed as provisionally accepted in the new CITES Cactaceae Checklist.

Due to the weak differences, depressed stem, lack of areolar glands and stronger spines, found between *heterochromus* and *bicolor*, we think that it is not justified to use species rank for *heterochromus*, but that it should be considered a subspecies of *bicolor*. We believe that the entities included in the OTU *pottsii*, for the lack of areolar glands, are more closely allied with *heterochromus* than with *bicolor*, so the limits of the former should be extended to include also these forms. This is, at present, the best choice, waiting for more data on the distribution of these entities and of *heterochromus* in this area, data that ascertain or not the opportunity to create a new subspecies to accommodate those entities morphologically intermediate between *bicolor* and *heterochromus*. Anderson (1987) did not consider it appropriate to recognise either *bolaensis* or *wagnerianus* at varietal rank, including both in the synonym list of *T. bicolor*.

We don't agree with this line, but believe that these three entities should be, instead, included in a subspecies of *bicolor*. This would be congruent with the taxonomic treatment reserved for two other entities, *flavidispinus* and *schwarzii*, whose taxonomic rank we feel disposed to accept, but that surely are not phenetically so far from *bicolor* as are *bolaensis* or *wagnerianus*. To conclude the analysis of the *bicolor* complex, we have to comment on two more OTUs: *schottii* and *commodus*. With the name *schottii* are identified some Texas populations whose plants have the characteristic of bearing a flattened, upper radial spine up to 7 cm long, while *commodus* is described as having only one central spine.

At this point it is necessary to open a parenthesis. In *T. bicolor*, as in many other species of the genus, the discrimination between central and radial spines is awkward. Typically *bicolor* has three central spines, of which the lowest is the longest and porrect, while the other two are erect, generally slightly more robust and longer than the radials, with which they can often be mistaken by being appressed against the stem as the radials are. The typical upper spine, flattened and erect, has been considered by us as a radial spine. Based on these premises, *commodus* has three central spines, as does the type species, and the maintenance of this variety or of var. *schottii*, whose only difference with *bicolor* consists in the long upper spine, is not justified.

*T. leucacanthus* and subsp. *schmollii* differ only in the flower colour: yellow in the former and magenta in the latter. As for *T. conothelos* subsp. *aurantiacus*, we think this character is sufficient to maintain these two taxa separate. For many years the identity of *Thelocactus krainzianus* has remained uncertain, and after the description of *Thelocactus matudae* it has been thought possible to identify *krainzianus* with it (Chvastek, 1985; Anderson, 1987). Nagl, in 1991, after he visited some *leucacanthus* populations in the area near Peña Miller, Querétaro, believed that it was possible to identify these plants with the *krainzianus* of Oehme.

The plants of this area fit well the description given by Oehme, have 8 ribs, are clustering and, above all, have the tubercles cross-grooved at the base, characters that do not belong to *matudae*. The presence of a cross-groove on the tubercles is a typical character for this entity, that we found between Peña Blanca and Peña Miller, but can occasionally appear both in *leucacanthus* and *schmollii*. The latter taxon we came across a little north of Vizarron, differing from *krainzianus* also in the size of the tubercles, that are smaller, and in the greater number of radial spines. We believe that these differences are not sufficient to separate *krainzianus* from *schmollii*, as Nagl has just done, proposing the rank of forma for *krainzianus*. Therefore we think it is more appropriate to consider these two taxa synonyms, maintaining the name *schmollii* that is more widespread.

All the taxa belonging to the *rinconensis* group are clearly closely related, but till now a consensus has not been reached on the acceptance of subspecies rank for these entities. Anderson (1999) thinks it is not justified to subdivide *T. rinconensis* into infraspecific taxa because 'there is a continuum from very spiny to spineless forms.' Glass (1997), instead, believed it appropriate to raise *nidulans* and *phymatothelos* to subspecific level. As regards *freudenbergeri* and *nidulans* we feel it is justified to use subspecies rank as they differ significantly from *rinconensis*. *T. nidulans* is well distinguishable for having a greater number of spines, divided into central and radial spines, and *freudenbergeri* both for having a greater spine count, with central and radial spines distinct, and for the different flower colour that in this entity is magenta.

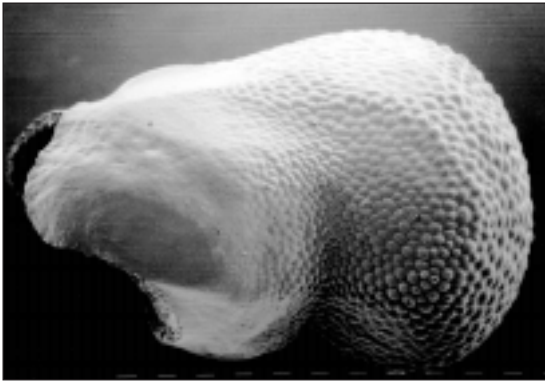
We can say very little about *T. rinconensis* ssp. *hintonii*, as we know this taxon only from the literature and so the data we have are incomplete. Our acceptance of this entity at subspecies rank is based, above all, on the different flower colour, yellow according to the description. If this character proves in the future to be inconsistent (in the photographs published along with the

description the yellow colour of the flower is rather faint), then this entity, whose spine number is variable from 3 to 10, being so intermediate between *rinconensis* and subspecies *freudenbergeri* and *nidulans*, should be treated as a local form of *rinconensis* and the status of the other subspecies, whose acceptance is based mainly on the spine count, should be re-evaluated. Among the various taxa that form this complex we have been in doubt only on the acceptance of *phymatothelos*, which is the entity that separates least from *rinconensis*, distinguished from it for having a more depressed stem and the spines generally shorter and recurved. We have chosen, eventually, to follow Anderson in considering inappropriate the recognition of *phymatothelos* at subspecies rank, as the differences found are too weak.

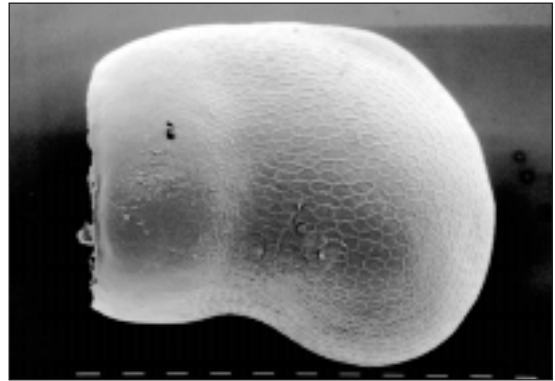
We do not agree with the proposal by Lüthy to include *Thelocactus multicephalus* in *rinconensis*, because, if *multicephalus* morphologically resembles a *rinconensis*, it differs from it by having indistinct ribs and only one hypodermal layer while all the entities belonging to the *rinconensis* group have a multi-layered hypodermis. This latter character is for us sufficient to separate these two taxa. *T. multicephalus* has a distribution area much larger than that reported by Lüthy: it actually extends south as far as Matehuala. The type form can be found near Sandia, Nuevo León, while in the more southerly localities it is replaced by forms with a single depressed stem with shorter spines that we have included in the OTU 'La Bolsa' and that we believe not sufficiently distinct to justify recognition at infraspecific rank.

The original description of *T. hexaedrophorus* reports that this species bears one central spine, whose absence, in the majority of the populations we observed in habitat, is constant. This is not true for the plants coming from Salinas, San Luis Potosí, (SB113) and Fresnillo, Zacatecas (the locality we visited is situated about 10 km north of Fresnillo, on the highway to Saltillo), therefore we are inclined to believe that the original plant could come from this area. We think that Anderson was wrong in identifying them with *T. lloydii*, a species that was described as having eight radial spines, but for which no mention was made on the presence of a central spine.

Recently a photograph was published (Succulenta, 1995) of a *T. hexaedrophorus* coming from La Mancha Durango, near the northern border of Zacatecas and then from an area corresponding to that given in the original description (northern Zacatecas), with heavy spines and without centrals, that fits well the description made by Britton and Rose. Due to species variability we think it is not justified to recognise this



**Figure 8.** Seed of *Thelocactus buekii* ssp. *matudae*, SB973 Galeana, Nuevo León. (x 40).



**Figure 9.** Seed of *Thelocactus tulensis*, s. n. Tula, Tamaulipas. (x 40).

subspecies, or other entities, at a formal rank.

*Thelocactus buekii* and *Thelocactus matudae* are closely related and distinguish from each other by the different shape of the tubercles, that are higher in *matudae*, for the different number of spines, that are more numerous in *matudae*, and for the different flower size, that is larger in *matudae*. We feel that we can accept the subspecies *matudae* provisionally, because the finding of new localities and the presence of intermediate forms, the densely spined forms typical of Rayones intergrading southerly, near Galeana, with less spiny forms bearing only one central spine, could make superfluous the division of these two entities.

Anderson considered both these two taxa as varieties of *T. tulensis*. According to us, however, they have nothing in common with this species, whose seed micromorphology is completely different. The seeds of *buekii* and *matudae* have the testa cells convex, the anticlinal walls straight and the funicle remains not visible (Figure 8), while the seeds of *tulensis* have tabular testa cells, undulate anticlinal walls and the funicle remains conspicuous (Figure 9). We think that these differences are sufficient to consider *T. buekii* unrelated to *T. tulensis* and then to maintain the former taxon at species rank, while *matudae* should be treated as a subspecies of it.

*Thelocactus hastifer*, *Thelocactus lausseri*, *Thelocactus macdowellii* and *Thelocactus tulensis*, are not closely related to any other species. None of the morphological characters is useful to estab-

lish a relationship among these four species and the other thelocacti, but some suggestions can be obtained from seed micromorphology. The flat testa cells of the seeds of *hastifer* and *tulensis* suggest a relationship with *leucacanthus* or *hexaedrophorus*, while *lausseri* and *macdowellii*, having convex testa cells, can be compared to any other species having these characters, except *T. conothelos* whose seeds have conical testa cells with a smooth cuticle.

#### Systematic treatment

***Thelocactus*** Britton & Rose, Bull. Torrey Bot. Club 49: 251 (Aug. 1922). Type: *Echinocactus hexaedrophorus* Lemaire.

*Torreycactus* Doweld, Sukkulenty 1: 19 (1998).

*Stem* single or clustering, depressed, globose, ovoid or cylindrical, 2–20 cm diameter, 3–40 cm high. *Ribs* present or indistinct. *Tubercles* present, rounded to conical. *Areoles* on the apices of the tubercles, sometimes with a short adaxial groove, with or without glands. *Spines* usually straight, variable in diameter, length and colour, central and radial spines generally distinguishable. *Flowers* apical, funnel-shaped, with a scaled tube, white, yellow or magenta. *Fruits* greenish to reddish, semi-fleshy, scaly with the perianth remnants persistent, opening at maturity by a basal pore. *Seeds* pyriform, with a basal hilum, black, testa cells flat, convex or conical, cuticle micropapillate or smooth.

#### Key to the species

- 1a Flowers magenta with a red throat ..... **T. bicolor**
- A Areolar glands absent ..... subsp. **heterochromus**
- AA Areolar glands present
- B Central spines 0(–1) ..... subsp. **schwarzii**
- BB Central spines 3–4
- C Stem slightly clustering, cylindrical, spines 18–29 ..... subsp. **bolaensis**



- CC Stem single, ovoid, spines 11–23
  - D Stem up to 20 cm high, ribs 8, spines 11–22 .....subsp. **bicolor**
  - DD Stem up to 9 cm high, ribs 13, spines 15–23.....subsp. **flavidispinus**
- 1b Flowers white, magenta or yellow without a red throat
  - 2a Primary filaments inserted above the base of the nectar chamber, testa cells conical, cuticle smooth .....**T. conothelos**
    - A Flowers white to magenta
      - B Stem green, tubercles angled, flowers magenta (rarely white), seeds without conspicuous funicle remains
        - C Central spines white and shredding, spines 24–29 .....subsp. **argenteus**
        - CC Central spines greyish, not shredding, spines 11–24.....subsp. **conothelos**
      - BB Stem olive-green or reddish, tubercles rounded, flowers white to pale magenta, seeds with conspicuous funicle remains .....subsp. **garciae**
    - AA Flowers yellow
      - B Stem single, tubercles angled, spines 12–27 .....subsp. **aurantiacus**
      - BB Stem clustering, tubercles rounded, spines 7–9.....subsp. **flavus**
  - 2b Primary filaments inserted near the base of the nectar chamber, testa cells flat or convex, cuticle micro-papillate
    - 3a Central and radial spines white.....**T. macdowellii**
    - 3b Central spines coloured, radial spines white or coloured
      - 4a Flowers small, 25–45 mm diam., whitish with a magenta midstripe .....  
.....**T. lausseri**
      - 4b Flowers 30–100 mm diam., white, magenta or yellow
        - 5a Areolar glands present
          - 6a Stem erect or decumbent, cylindrical, up to 40 cm high, ribs 13–18, spines 24–30  
.....**T. hastifer**
          - 6b Stem erect, globose, up to 15 cm high, ribs 8, spines 9–21.....**T. leucacanthus**
            - A Flowers yellow .....subsp. **leucacanthus**
            - AA Flowers magenta.....subsp. **schmollii**
        - 5b Areolar glands absent
          - 7a Stem depressed to globose, ribs 13–21, tubercles angled, hypodermis with two or three layers .....**T. rinconensis**
            - A Flowers yellow.....subsp. **hintonii**
            - AA Flowers white to magenta
              - B Central and radial spines not distinguishable .....subsp. **rinconensis**
              - BB Central and radial spines distinct
                - C Stem glaucous, spines heavy, shredded, 8–17, flowers white to magenta  
.....subsp. **nidulans**
                - CC Stem green, spines not heavy or shredded, 8–10, flowers magenta.....  
.....subsp. **freudenbergeri**
        - 7b Stem depressed, globose or short cylindrical, ribs 8–21, tubercles angled or rounded, hypodermis with one layer
          - 8a Ribs indistinct, tubercles angled, central and radial spines indistinguishable..  
.....**T. multicephalus**
          - 8b Ribs present or indistinct, tubercles rounded, central and radial spines distinct
            - 9a Stem depressed to globose, glaucous, tubercles rounded, central spines generally missing, flowers white to light magenta.....**T. hexaedrophorus**
            - 9b Stem depressed to short cylindrical, not glaucous, tubercles conical, central spines present, flowers white to magenta
              - 10a Stem globose to short cylindrical, olive-green, ribs present, flowers white to pale pink, seeds with flat testa cells .....**T. tulensis**

- 10b** Stem depressed to globose, olive-green to reddish, ribs generally indistinct, flowers magenta, seeds with convex testa cells.....**T. buekii**  
**A** Tubercles low, pointed, spines 5–12, flowers 35–45 mm diam.....subsp. **buekii**  
**AA** Tubercles high, conical, spines 10–19, flowers 40–80 mm diam. ....subsp. **matudae**

**List of accepted taxa**

***Thelocactus bicolor*** (Galeotti ex Pfeiffer) Britton & Rose, Bull. Torrey Bot. Club 49: 251 (1922). Lectotype: Abbild. Besch. Cact. 2: Pl. 25 (1848).

*Echinocactus bicolor* Galeotti ex Pfeiffer, Abbild. Besch. Cact. 2: pl. 25 (1848). *Ferocactus bicolor* (Galeotti ex Pfeiffer) N. P. Taylor, Cact. Succ. J. Gr. Brit. 41: 30 (1979). *Echinocactus rhodophthalmus* Hooker, Bot. Mag. 76: pl. 4486 (1850). *Echinocactus rhodophthalmus* var. *ellipticus* Hooker, Bot. Mag. 78: pl. 4634 (1852). *Echinocactus ellipticus* Lemaire, Jard. Fleur. 3: pl. 270 (1853). *Echinocactus bicolor* var. *schottii* Engelm., Syn. Cact. U. S. 21 (1856). *Echinocactus schottii* Small, Fl. Southeast U. S. 814 (1903). *Thelocactus bicolor* var. *schottii* Krainz, Die Kakteen, Lfg. 18 (1961). *Echinocactus bicolor* var. *tricolor* Schumann, Gesamtb. Kakt. 303 (1898). *Thelocactus bicolor* var. *commodus* Haas, Kakt. and. Sukk. 39: 86 (1988). *Thelocactus bicolor* ssp. *commodus* (Haas) Doweld, Sukkulenty 1: 30 (1999).

ssp. ***bolaensis*** (Runge) Doweld, Sukkulenty 1: 27–31 (1999). Lectotype: Gartenflora 38: 106, Abb. 21 (1889)

*Echinocactus bolaensis* Runge ('*bolansis*'), Gartenflora 38: 106 (1889). *Echinocactus bicolor* var. *bolansis* Schumann, Gesamtb. Kakt. 303 (1898). *Thelocactus bicolor* var. *bolansis* Berger, Kakteen, 256 (1929). *Ferocactus bicolor* var. *bolaensis* N. P. Taylor, Cact. Succ. J. Gr. Brit. 41: 30 (1979). *Echinocactus wagnerianus* Berger, Kakteen, 256 (1929). *Thelocactus wagnerianus* Berger, Kakteen, 346 (1929). *Thelocactus bicolor* var. *wagnerianus* Krainz, Die Kakteen, Lfg. 18 (1961).

ssp. ***flavidispinus*** (Backeberg) N. P. Taylor, CCI 5: 14 (1998). Lectotype: Beitr. Sukk.-Kunde Pflege 1941: 6 (1941) *Thelocactus bicolor* var. *flavidispinus* Backeb., Beitr. Sukk.-Kunde Pflege 1941: 6 (1941). *Thelocactus flavidispinus* Backeb., Cact. Succ. J. (US) 23: 150 (1951). *Echinocactus flavidispinus* Weniger, Cacti S. W. 87 (1970) nom. nud. *Ferocactus bicolor* var. *flavidispinus* N. P. Taylor, Cact. Succ. J. Gr. Brit. 41: 30 (1979).

***Thelocactus bicolor*** ssp. ***heterochromus*** (Weber) Mosco & Zanovello **comb. et stat. nov.** **Basionym:** *Echinocactus heterochromus*

F. A. C. Weber, Bois Dict. Hort. 466 (1896). Neotype: Durango, 3.5 km al Oeste de la Soledad, R. D. Worthington 10902 (TEX).

*Thelocactus heterochromus* (F. A. C. Weber) van Oosten, Kakteenkunde 58 (1940). *Ferocactus heterochromus* N. P. Taylor, Cact. Succ. J. Gr. Brit. 41: 90 (1979). *Echinocactus bicolor* var. *pottsii* Salm-Dyck, Cact. Hort. Dyck. 173 (1850).

ssp. ***schwarzii*** (Backeberg) N. P. Taylor, CCI 5: 14 (1998). Lectotype: Cact. Succ. J. Gr. Brit. 12: 84 (1950). *Thelocactus schwarzii* Backeb., Cact. Succ. J. Gr. Brit. 12: 81 (1950). *Ferocactus bicolor* var. *schwarzii* N. P. Taylor, Cact. Succ. J. Gr. Brit. 41: 30 (1979). *Thelocactus bicolor* var. *schwarzii* E. F. Anderson, Bradleya 5: 61 (1987).

***Thelocactus buekii*** (Klein) Br. & R., Cact. 4: 8 (1923). Lectotype: Gartenflora 8: 257, Taf. 266 (1859).

*Echinocactus buekii* Klein ('*buckii*'), Gartenflora 8: 257 (1859). *Thelocactus tulensis* var. *buekii* (Klein) E. F. Anderson, Bradleya 5: 65 (1987). *Thelocactus tulensis* ssp. *buekii* (Klein) N. P. Taylor, CCI 5: 14 (1998).

***Thelocactus buekii*** ssp. ***matudae*** (Sanchez-Mej. & Lau) Mosco & Zanovello **comb. nov.** **Basionym:** *Thelocactus matudae* Sanchez-Mej. & Lau, Cact. Suc. Mex. 23: 51–52 (1978). Type: Nuevo León, near Rayones, A. Lau *Rubens* s. n. (MEXU).

*Thelocactus buekii* var. *matudae* (Sanchez-Mej. & Lau) E. F. Anderson, Bradleya 5: 66 (1987). *Thelocactus tulensis* ssp. *matudae* (Sanchez-Mej. & Lau) N. P. Taylor, CCI 5: 14 (1998).

***Thelocactus conothelos*** (Regel & Klein) Backeb. & F. Knuth, Kaktus-ABC, 385 (1935). Neotype: Tamaulipas, 1 mile south-west of La Perdida, 22 Jan. 1961, E. F. Anderson 1725 (POM).

*Echinocactus conothelos* Reg. & Klein, Ind. Sem. Hort. Petrop. 48 (1860). *Gymnocactus conothelos* Backeb., Die Cactaceae V: 2859 (1961). *Torreyocactus conothele* (Regel & Klein) Doweld, Sukkulenty 1: 15–30 (1998). *Echinocactus smithii* Muehlenpf. nom. rej. prop., Allg. Gartenzeitung 14: 370 (1846). *Echinocactus saussieri* Weber, Bois Dict. Hort., 468 (1896). *Thelocactus saussieri* Berger, Kakteen, 257 (1929). *Gymnocactus*

- saussieri* Backeb., Cact. Succ. J. (US) 23: 151 (1951).
- ssp. **argenteus** (Glass & Foster) Glass, Ident. Guide Threatened Cacti of Mexico 1: TH/CON (1997). Type: Nuevo León, about 7 miles west of Ascension, 12 Feb. 1971, *Glass & Foster* 3176 (ZSS).  
*Thelocactus conothelos* var. *argenteus* Glass & Foster, Cact. Succ. J. (US) 44: 48 (1972).  
*Torreycactus conothele* var. *argenteus* (Glass & Foster) Doweld, Sukkulenty 1: 19 (1998).
- ssp. **aurantiacus** (Glass & Foster) Glass, Ident. Guide Threatened Cacti of Mexico 1: TH/CON (1997). Type: Nuevo León, about 9 miles east of La Escondida, 12 Feb. 1971, *Glass & Foster* 3183 (ZSS).  
*Thelocactus conothelos* var. *aurantiacus* Glass & Foster, Cact. Succ. J. (US) 44: 48 (1972).  
*Torreycactus conothele* var. *aurantiacus* (Glass & Foster) Doweld, Sukkulenty 1: 19 (1998).
- Thelocactus conothelos* ssp. flavus** (Mosco & Zanovello) Mosco & Zanovello **comb. et stat. nov.** **Basionym:** *Thelocactus flavus* Mosco & Zanovello Cactus & Co., 3: 20 (1999). Type: San Luis Potosí, Huizache, *Kuenzler* 362, cult. A. Mosco, Nov. 1998 (HG-PAD).  
*Thelocactus panarottoanus* Halda, Acta Mus. Richnov. sect. Nat. 5: 161 (1998).
- Thelocactus conothelos* ssp. garciae** (Glass) Mosco & Zanovello **comb. et stat. nov.** **Basionym:** *Thelocactus garciae* Glass, Ident. Guide Threatened Cacti of Mexico 1: TH/GA (1997). Type: Tamaulipas, Municipio de Bustamante, *J. A. Garcia Luna* 383, (CANTE).
- Thelocactus hastifer*** (Werderm. & Boedeker) F. Knuth, in Backeb. & F. Knuth, Kaktus-ABC, 360 (1935). Type: (B). *Echinocactus hastifer* Werderman. & Boedeker, Notizbl. Bot. Gart. Mus. Berlin-Dahlem 11: 274 (1931).  
*Ferocactus hastifer* N. P. Taylor, Cact. Succ. J. Gr. Brit. 41: 90 (1979).
- Thelocactus hexaedrophorus*** (Lemaire) Britton & Rose, Bull. Torrey Bot. Club 49: 251 (1922). Neotype: Iconographie descriptive des Cactées, Pl. 2 (Dec. 1841).  
*Echinocactus hexaedrophorus* Lemaire, Cact. Gen. Nov. Sp. 27 (1839). *Echinocactus droegeanus* Hildm. ex Schumann, Gesamtb. Kakt. 438 (1898). *Echinocactus hexaedrophorus* var. *droegeanus* R. Meyer, Monatsschr. Kakt.-Kunde 27: 40 (1917). *Echinocactus fossulatus* Scheidw., Allg. Gartenz. 9: 49 (1841).  
*Echinocactus hexaedrophorus* var. *fossulatus* Salm-Dyck ex Labouret, Monogr. Cact. 251 (1853). *Thelocactus fossulatus* Br. & R., Cact. 4: 10 (1923). *Thelocactus hexaedrophorus* var. *fossulatus* Backeb., Die Cactaceae V: 2800 (1961). *Echinocactus hexaedrophorus* var. *labouretianus* Schumann, Gesamtb. Kakt. 438 (1898). *Thelocactus hexaedrophorus* var. *labouretianus* A. Berger, Kakteen 253 (1929).  
*Echinocactus hexaedrophorus* var. *major* Quehl, Monatsschr. Kakt.-Kunde 4: 29 (1894).  
*Thelocactus hexaedrophorus* var. *major* A. Berger, Kakteen 253 (1929). *Echinocactus hexaedrophorus* [var.] *roseus* Lemaire ex Labouret, Monogr. Cact. 251 (1853).  
*Echinocactus hexaedrophorus* [var.] *subcostatus* Salm-Dyck, Cact. Hort. Dyck. 1849, 34 (1850). *Thelocactus hexaedrophorus* var. *decepiens* A. Berger, Kakteen 253 (1929).  
*Thelocactus lloydii* Britton & Rose, Cact. 4: 11 (1923). *Thelocactus hexaedrophorus* var. *lloydii* (Br. & R.) Kladiwa & Fittkau, in Krainz, Die Kakteen Lfg. 61 (1975). *Thelocactus hexaedrophorus* ssp. *lloydii* (Br. & R.) N. P. Taylor, CCI 5: 14 (1998).
- Thelocactus lausseri*** J. Riha & J. Busek, Kakt. and. Sukk. 37: 162–164 (1986). Type: Coahuila, Sierra de las Ovejas, *A. Lausser* s. n. (PR).
- Thelocactus leucacanthus*** (Zucc. ex Pfeiffer) Britton & Rose, Cact. 4: 8 (1923). Lectotype: Abb. Bayer. Akad. Wiss. München 2: Tab. II (1837).  
*Echinocactus leucacanthus* Zucc. ex Pfeiffer, Enum. Cact. 66 (1837). *Ferocactus leucacanthus* N. P. Taylor Cact. Succ. J. Gr. Brit. 41: 90 (1979). *Cereus maelenii* Pfeiffer, Allg. Gartenz. 5: 378 (1837). *Echinocactus maelenii* Salm-Dyck, Cact. Hort. Dyck. 18 (1842).  
*Mammillaria maelenii* Salm-Dyck, Cact. Hort. Dyck. 14 (1845). *Echinocactus maelenii* Hemsley ('*macleanii*'), Biol. Centr. Amer. Bot. 1: 534 (1880). *Cereus tuberosus* Pfeiffer, Enum. Cact. 102 (1837). *Echinocactus tuberosus* Salm-Dyck ex Foerster, Handb. Cact. 287 (1846). *Echinocactus leucacanthus* var. *tuberosus* Foerster, Handb. Cact. 287 (1846).  
*Echinocactus ehrenbergii* Pfeiffer, Allg. Gartenz. 6: 275 (1838). *Thelocactus ehrenbergii* F. Knuth, in Backeb. & F. Knuth, Kaktus-ABC, 359 (1935). *Echinocactus leucacanthus* var. *crassior* Salm-Dyck, Cact. Hort. Dyck. 35 (1850). *Echinocactus porrectus* Lemaire, Cact. Aliq. Nov. 17 (1838).  
*Thelocactus porrectus* F. Knuth, in Backeb. & F. Knuth, Kaktus-ABC, 361 (1935). *Thelocactus leucacanthus* var. *porrectus* Backeb., Die Cactaceae V: 2818 (1961).  
*Echinocactus subporrectus* Lemaire, Cact. Aliq. Nov. 25 (1838). *Echinocactus tuberosus* var. *subporrectus* Foerster, Handb. Cact. 523 (1846). *Echinocactus theloideus* Salm-Dyck, Allg. Gartenz. 18: 396 (1850).
- ssp. ***schmollii*** (Werder.) Mosco & Zanovello, CCI 7: 18 (1999). Lectotype: Kakt. and. Sukk. Pfl.

3: Taf. 160 (1939).

*Thelocactus leucacanthus* var. *schmollii* Werderm., Blüh. Kakt. and. Sukk. Pfl. 3: Taf. 160 (1939). *Thelocactus krainzianus* Oehme, Beitr. Sukk-Kunde Pflege 1; 1 (1940). *Thelocactus leucacanthus* var. *schmollii* fa. *krainzianus* (Oehme) Nagl, Kakt. and. Sukk. 42: 183 (1991). *Thelocactus sanchezmejoradai* Meyrán, Cact. Suc. Mex. 3: 77 (1958). *Thelocactus leucacanthus* var. *sanchezmejoradai* Backeb., Die Cactaceae V: 2817 (1961).

***Thelocactus macdowellii*** (Rebut ex Quehl) Glass, Cact. Suc. Mex. 14: 4 (1969). Neotype: Coahuila, 33 km northeast of Saltillo on hy. 40 to Monterrey, 22 July 1972, *E. F. Anderson* 3182 (US).

*Echinocactus macdowellii* Rebut ex Quehl ('*Mc. Dowellii*'), Monatsschr. Kakt.-Kunde 4: 133–134 (1894). *Echinomastus macdowellii* Br. & R., Cact. 3: 151 (1922). *Neolloydia macdowellii* H. E. Moore, Bailey 19: 166 (1975). *Thelocactus conothelos* var. *macdowellii* Glass & Foster ('*mcDowellii*'), Cact. Succ. J. (US) 49: 220 (1977).

***Thelocactus multicephalus*** Halda & Panarotto, Acta Mus. Richnov. sect. Nat. 5: 40 (1998). Type: Feb. 1985, *J. J. Halda* s. n. (PR). *Thelocactus rinconensis* ssp. *multicephalus* (Halda & Panarotto) Luethy, Kakt. and Sukk. 50: 80 (1999).

***Thelocactus rinconensis*** (Poselger) Britton & Rose, Cact. 4: 7 (1923). Neotype: About 20 km northeast of Saltillo, 22 July 1972, *E. F. Anderson* 3180 (US).

*Echinocactus rinconensis* Poselger, Allg. Gartenz. 23: 18 (1855). *Echinocactus rinconadensis* Schumann, Gesamtb. Kakt. 433 (1898). ?*Echinocactus lophothele* Salm-Dyck, Allg. Gartenz. 18: 395 (1850). *Thelocactus lophothele* Br. & R., Bull. Torrey Bot. Club 49: 251 (1922). *Echinocactus phymatobelos* Poselger ex Ruempler, in Förster, Handb. Cact., ed. 2, 602 (1885). *Thelocactus phymatobelos* Br. & R. ('*phymatobelé*'), Cact. 4: 8 (1923). *Thelocactus rinconensis* var. *phymatobelos* Glass & Foster, Cact. Succ. J. (US) 49: 246 (1977). *Thelocactus rinconensis* ssp. *phymatobelos* (Poselger) Glass, Ident. Guide Threatened Cacti of Mexico 1: TH/RIN (1997). *Thelocactus rinconensis* ssp. *phymatobelos* (Poselger) Doweld nom. superfl., Sukkulenty 1: 30 (1999).

ssp. ***freudenbergeri*** (Haas) Mosco & Zanovello, CCI 7: 18 (1999). Type: *Freudenberger* s. n. in Coll. Haas Nr. 157 (ZSS).

*Thelocactus rinconensis* var. *freudenbergeri* Haas, Kakt. and. Sukk. 43: 96–98 (1992).

ssp. ***hintonii*** Luethy, Kakt. and. Sukk. 48: 39 (1997). Type: Nuevo León, Municipio Galeana,

Weg von Cienega del Toro nach Santa Rosa, 1610 m, 3 Oct. 1995, *Hinton* et al. 25762 (Herbarium G. B. Hinton).

ssp. ***nidulans*** (Quehl) Glass, Ident. Guide Threatened Cacti of Mexico 1: TH/RIN (1997). Type: (B). *Echinocactus nidulans* Quehl, Monatsschr. Kakt.-Kunde 21: 119 (1911). *Thelocactus nidulans* Br. & R., Cact. 4: 9 (1923). *Thelocactus lophothele* var. *nidulans* Kladiwa & Fittkau, in Krainz, Die Kakteen, Lfg. 61 (1975). *Thelocactus rinconensis* var. *nidulans* Glass & Foster, Cact. Succ. J. (US) 49: 245 (1977). *Thelocactus rinconensis* ssp. *nidulans* (Quehl) Doweld nom. superfl., Sukkulenty 1: 30 (1999).

***Thelocactus tulensis*** (Poselger) Britton & Rose, Cact. 4: 11 (1923). Neotype: Tamaulipas, at KM 14 on highway 101 between Tula and the junction at hy. 80, 30 July 1979, *E. F. Anderson* 3202 (US). *Echinocactus tulensis* Poselger, Allg. Gartenz. 21: 125 (1853).

### Specimens examined

If not differently specified, all the data concerning the following OTUs refer to plants grown by A. Mosco.

*bicolor* — specimens observed: Chihuahua: HK74-2170; Coahuila: s.n. Monclova, SB287 Saltillo, SB563 Cuesta la Muralla, Z37 Ojo Caliente; Nuevo León: s.n. Tanquecillos; San Luis Potosí: s.n. Huizache, SB278 Huizache, PAN194 El Coyote; Texas: SB866 Starr Co. Literature: stem diameter and height, Bravo-Hollis & Sanchez-Mejorada (1991).

*bolaensis* — specimens observed: cultivated origin, collection number 54; Coahuila: SB281 Cerro Bola. Literature: stem diameter and height, Runge (1889); head number, Pilbeam (1996).

*commodus* — specimens observed: Nuevo León: s.n. Montemorelos. Literature: stem diameter and height, tubercle height and width, flower maximum diameter, Haas (1988).

*flavidispinus* — specimens observed: Texas: SB424 Brewster Co. Literature: stem diameter, tubercles height and width, radial spines minimum number, Anderson (1987); stem height, Benson (1982); radial spines maximum number, Weniger (1988).

"*Pedricena*" — specimens observed: Coahuila: SB607 San Pedro, SB1715 South Boquillas.

*pottsii* — specimens observed: Chihuahua: SB77 Jimenez; Durango: SB1433 se Cuencamé, s.n. Mapimi. Literature: stem diameter, Pilbeam (1996).

*schottii* — specimens observed: Texas: SB567 Brewster Co. Literature: stem diameter and height, Benson (1982); tubercle height and

- width, Weniger (1988).
- schwarzii* — specimens observed: Tamaulipas: LAU684 Zaragoza, Z107 Calles. Literature: stem diameter and height, head number, Pilbeam (1996); tubercle height, Bravo-Hollis & Sanchez-Mejorada (1991); radial spines maximum number, Anderson (1987).
- wagnerianus* — specimens observed: cultivated origin: collection number 314; Coahuila: Z57 El Dorado. Literature: stem diameter and height, head number, Berger (1929).
- heterochromus* — specimens observed: cultivated origin: collection numbers 63, 266; Chihuahua: SB564 Matamoros, SB608 Hidalgo del Parral, SB1879 south Satevo. Literature: stem diameter and height, flower maximum diameter, Pilbeam (1996); radial spines minimum number, Anderson (1987).
- conothelos* — specimens observed: Nuevo León: s.n. Dr. Arroyo, s.n. east Dr. Arroyo; San Luis Potosí: SB302 Matehuala, CH186 San Antonio, CSD109 Guerrero, CSD115 La soledad; Tamaulipas: s.n. Miquihuana, CH237 Tula. Literature: stem diameter and height, tubercle height and width, Anderson (1987).
- argenteus* — specimens observed: Nuevo León: SB311 Ascension. Literature: stem diameter and height, Anderson (1987); tubercle height and width, Glass (1972).
- aurantiacus* — specimens observed: cultivated origin: collection numbers 75, 136; Nuevo León: s.n. Zaragoza, GL758 Zaragoza, SB329 Aramberri, LAU1009 Aramberri, CH194 Aramberri, CSD149 Marmolejo. Literature: stem diameter and height, Anderson (1987).
- garciae* — specimens observed: Tamaulipas: s.n. Bustamante. Plants observed in habitat: Tamaulipas: s.n. near Bustamante. Literature: orthostichy number, radial spines maximum number, head number, Glass (1997).
- flavus* — specimens observed: San Luis Potosí: HK362 Huizache, s.n. La Hincada. plants observed in habitat: San Luis Potosí: s.n. Huizache.
- buekii* — specimens observed: garden origin: collection number 57; Nuevo León: CH195 Aramberri, CSD133 Escondida, CSD145 Lampacitos, CSD155 Ascension. Literature: all the data regarding morphological characters have been taken from Anderson (1987) and Pilbeam (1996).
- matudae* — specimens observed: garden origin: collection number 71; Nuevo León: LAU744 Rayones, SB973 Galeana, SB1339 Rayones. Literature: stem diameter and height, tubercle height and width, spine count, Anderson (1987); flower maximum diameter, Pilbeam (1996).
- rinconensis* — specimens observed: garden origin: collection number 69; Coahuila: s.n. San Jose de los Nuncios, s.n. Ramos Arispe, HO969 El Chiflon, SB301 Rinconada; Nuevo León: s.n. Santa Catarina, CSD185 Casa Blanca. Literature: stem diameter and height, Pilbeam (1996); tubercle height and width, Bravo-Hollis & Sanchez-Mejorada (1991).
- freudenbergeri* — specimens observed: Nuevo León: s.n. Grutas de Garcia, CSD173 Grutas de Garcia. Literature: stem diameter and height, tubercle height and width, Haas (1992).
- hintonii* — we have been unable to observe any plant of this taxon, therefore all the morphological data have been taken from the literature, Glass (1997) and Lüthy (1997), and the missing data have been considered equal to those of *T. rinconensis*.
- nidulans* — specimens observed: Coahuila: s.n. Sierra de la Paila. Literature: stem diameter and height, Bravo-Hollis & Sanchez-Mejorada (1991); tubercle height and width, Quehl (1911), spine number, Lüthy (1997).
- phymatothelos* — specimens observed: garden origin: collection numbers 41, 64; Coahuila: CH205 Arteaga. Literature: stem diameter, Bravo-Hollis & Sanchez-Mejorada (1991), stem height, Schumann (1898).
- multicephalus* — specimens observed: Nuevo León: HO809 Sandía. Plants observed in habitat: Nuevo León: s.n. Trinidad. Literature: stem diameter and height, tubercle height and width, head number, Halda (1998).
- “La Bolsa” — specimens observed: Nuevo León: s.n. La Bolsa. Plants observed in habitat: Nuevo León: s.n. El Desierto; San Luis Potosí: s.n. south of Matehuala.
- hexaedrophorus* — specimens observed: San Luis Potosí: s.n. Buenavista, s.n. San Luis Potosí, CH230 Charco Blanco, Hayek63 Villar, Hayek71 Moctezuma, PAN137 Rio Verde, SB892 Guaxama, SB1074 Charco Blanco. Nuevo León: BZ44 west of Dr Arroyo, SB291 Dr Arroyo; Tamaulipas: s.n. La Perdida, H2313 Miquihuana. Literature: stem diameter and height, Pilbeam (1996); tubercle height and width, central spines maximum number, Anderson (1987).
- lloydii* — specimens observed: San Luis Potosí: SB113 Salinas. Literature: stem diameter and height, tubercle height and width, spine number, Anderson (1987).
- tulensis* — specimens observed: Tamaulipas: s.n. Tula, BZ28 Tula, CH236 Tula, CSD69 Miguel Hidalgo; San Luis Potosí: s.n. Huizache, s.n. La Libertad, CSD103 Huizache; Nuevo León: CSD127 Dr Arroyo/Mier y Noriega. Literature: stem diameter and height,

Pilbeam (1996); spine number, Anderson (1987).

*macdowellii* — specimens observed: garden origin: collection numbers 121, 143; Coahuila: s.n. Higuera, CSD192 Arteaga. Literature: stem diameter and height, Pilbeam (1996); tubercle height and width, spine number, stylus colour, head number, Anderson (1987).

*lausseri* — specimens observed: garden origin: collection numbers 127, 198. Literature: stem diameter and height Pilbeam (1996); spine number, Anderson (1987).

*leucacanthus* — specimens observed: Hidalgo: s.n. San Francisco, SB514 Ixmiquilpan; Querétaro: s.n. Mesa del León. Literature: stem diameter and height, spine number, flower diameter, Bravo-Hollis & Sanchez-Mejorada (1991); tubercle height and width, Anderson (1987).

*schmollii* — specimens observed: Querétaro: SB579 Vizarrón. Literature: stem diameter and height, spine number, Bravo-Hollis & Sanchez-Mejorada (1991); tubercle height and width, Meyran (1958).

*krainzianus* — specimens observed: garden origin: collection number 108; Querétaro: s.n. west of Peña Miller, Z185 Peña Blanca. Literature: stem diameter and height, Oehme (1940).

*hastifer* — specimens observed: garden origin: collection numbers 115, 255. Literature: stem diameter and height, Guzman (1992); tubercle height and width, spine number, style colour, Anderson (1987); flower diameter, Pilbeam (1996).

*setispinus* — specimens observed: Texas: s.n. Bexar Co., SB851 Jim Hogg Co., SB858 Cameron Co. Literature: stem diameter and height, head number, Weniger (1988); rib height and width, spine number, petaloid length and width, Anderson (1987); flower diameter, Pilbeam (1996).

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### References

ALSEMGEEST, W., BREGMAN R. & VAN VELDHUISEN, R. (1995): Het geslacht *Thelocactus* — 5.

*Succulenta* **74**: 274–279.

ANDERSON, E.F. (1987): A revision of the genus *Thelocactus* B. & R. (Cactaceae). *Bradleya* **5**: 49–76.

ANDERSON, E.F. & RALSTON, M.E. (1978): A study of *Thelocactus* (Cactaceae) I. The status of the proposed genus *Gymnocactus*. *Cact. Succ. J. (US)* **50**: 216–224.

ANDERSON, E.F. (1999): In MOSCO, A. & ZANOVELLO, C.: Nomenclatural adjustments in *Thelocactus* and *Turbinicarpus*. *CCI* **7**: 18–20.

BENSON, L. (1982): *The Cacti of the United States and Canada*. Stanford Univ. Press., Stanford.

BERGER, A. (1929): *Kakteen*. Eugen Ulmer, Stuttgart.

BRAVO-HOLLIS, H. & SÁNCHEZ-MEJORADA (1991): *Las Cactáceas de México*. Vol. 2. Universidad Nacional Autónoma de México, México, D. F.

BRITTON, N.L. & ROSE, J.N. (1923): *The Cactaceae*. Vol. 4. Carnegie Inst. Washington, Washington, D.C.

CHVASTEK, J. (1985): Einige Gedanken zu *Thelocactus krainzianus* Oehme. *Kakt. and Sukk.* **36**: 260–263.

DOWELD, A.B. (1998): An outline of the phylogenetic system of classification of the tribe Cactaeae. I. System of classification of subtribes Sclerocactinae—Bravocactinae—Turbinicarpinae. *Sukkulenty/Succulents (Moscow)* **1**: 15–30.

GIBSON, A.C. & NOBEL, P.S. (1986). *The cactus primer*. Harvard Univ. Press, Cambridge, MA.

GLASS, C. & FOSTER, R. (1972): Two new varieties of *Thelocactus conothele* (Reg. & Klein) Knuth. *Cact. Succ. J. (US)* **44**: 47–50.

GLASS, C. (1997): *Identification guide to threatened cacti of Mexico*. Ediciones CANTE, A. C., Mexico, D. F.

HAAS, R. (1988): *Thelocactus bicolor* (Galeotti) Britton & Rose var. *commodus*. *Kakt. and Sukk.* **39**: 86–87.

HAAS, R. (1992): *Thelocactus rinconensis* (Poselger) Britton & Rose var. *freudenbergeri* R. Haas. *Kakt. and Sukk.* **43**: 96–98.

HALDA, J.J. (1998): New descriptions. *Acta Mus. Richnov., Sect. natur.* **5**: 1–48.

HALDA, J.J., HORACEK L. & PANAROTTO P. (1998): New descriptions. *Acta Mus. Richnov., Sect. natur.* **5**: 161–164.

HUNT, D. (1999): *CITES Cactaceae checklist*. Royal Botanic Gardens Kew & International Organization for Succulent Plant Study, Milborne Port, Sherborne.

LÜTHY, J.M. (1997): *Thelocactus rinconensis* subsp. *hintonii* J. Lüthy — eine neue Unterart aus Nuevo León. *Kakt. and Sukk.* **48**: 37–40.

LÜTHY, J.M. (1999): Ein sprossender *Thelocactus rinconensis* aus dem südlichen Nuevo León. *Kakt. and Sukk.* **50**: 78–82.

- MOSCO, A. & ZANOVELLO, C. (1999): Nomenclatural adjustments in *Thelocactus* and *Turbincarpus*. *CCI* 7: 18–20.
- NAGL, H. (1991): *Thelocactus krainzianus* Oehme. Eine Form von *Thelocactus leucacanthus* var. *schmollii*. *Kakt. and. Sukk.* 42: 182–184.
- OEHME, H. (1940): *Thelocactus krainzianus* Oeh. spec. nov. *Beitr. Sukk.-Kunde Pflege* 1: 1–3.
- PILBEAM, J. (1996): *Thelocactus. The cactus file handbook* 1. Cirio Publishing Services Ltd, Holbury, Southampton.
- QUEHL, L. (1911): *Echinocactus nidulans* Quehl, nov. spec. *Monatsschr. Kakt.-Kunde* 21: 119–120.
- RUNGE, C. (1889): Zwei neue Cacteen. *Gartenflora* 38: 106.
- SCHUMANN, K. (1898): *Gesamtbeschreibung der Kakteen*. J. Neumann, Neudamm.
- THOMAS, R.L. (1975): Orthostichy, parastichy and plastochrone ratio in a central theory of phyllotaxis. *Ann. Bot.* 39: 455–489.
- WENIGER, D. (1988): *Cacti of Texas and neighboring states*. Univ. Texas Press, Austin, TX.

## Appendix

### Characters and their scaling

**Stem shape I:** 0 flattened, 1 flattened to globose, 2 globose to ovoidal, 3 cylindrical. **Stem shape II:** 0 erect, 1 decumbent. **Maximum stem diameter (mm):** 0 ≤ 100, 1 ≤ 150, 2 > 150. **Maximum stem height (mm):** 0 ≤ 50, 1 ≤ 100, 2 ≤ 150, 3 ≤ 200, 4 > 200. **Clustering:** 0 single stems, 1 ≤ 10 heads, 2 ≤ 20 heads, 3 > 20 heads. **Epidermis colour I:** 0 green, 1 olive-green reddish. **Epidermis colour II:** glaucous, 0 no, 1 yes. **Epidermis colour III:** blotched, 0 no, 1 yes. **Number of hypodermal layers:** 0 one layer, 1 two or more layers. **Crystals:** 0 absent, 1 present. **Seedling shape:** 0 globose, 1 cylindrical. **Ribs:** 0 absent, 1 present. **Orthostichy number:** the orthostichy number corresponds to the rib number or, for the plants with indistinct ribs, to the sum of the orthogonal parastichies that, according to the phyllotaxis theory of Thomas (1975), is equal to the number of the present rectiserial orthostichies. 0 8–13, 1 13–21, 2 > 21. **Tubercles:** 0 absent, 1 present. **Tubercle shape:** 0 rounded, 1 angled. **Grooved tubercles:** 0 no, 1 yes. **Tubercle or rib width (mm):** 0 ≤ 5, 1 ≤ 10, 2 ≤ 15, 3 ≤ 20, 4 > 20. **Tubercle or rib height (mm):** 0 ≤ 10, 1 ≤ 15, 2 ≤ 20, 3 > 20. **Areolar glands:** 0 absent, 1 present. **Minimum total spine number:** 0 ≤ 5, 1 ≤ 10, 2 ≤ 15, 3 ≤ 20, 4 > 20. **Maximum total spine number:** 0 ≤ 10, 1 ≤ 15, 2 ≤ 20, 3 ≤ 25, 4 > 25. **Central and radial spines distinguishable:** 0 no, 1 yes. **Central spines**

**hooked:** 0 no, 1 yes. **One or more upper spines flattened:** 0 no, 1 yes. **Shredded spines:** 0 no, 1 yes. **Spine colour I: white:** 0 no, 1 yes. **Spine colour II: ochre to reddish:** 0 no, 1 yes. **Spine colour III: ochre to greyish:** 0 no, 1, yes. **Minimum flower diameter (mm):** 0 ≤ 40, 1 ≤ 50, 2 ≤ 60, 3 > 60. **Maximum flower diameter (mm):** 0 ≤ 50, 1 ≤ 60, 2 ≤ 70, 3 ≤ 80, 4 > 80. **Minimum ratio between length and width of the inner petaloids:** we have chosen to use a ratio instead of length and width absolute values to normalise the variations due to environmental or growth reasons. 0 ≤ 2, 1 ≤ 3, 2 ≤ 4, 3 ≤ 5, 4 > 5. **Maximum ratio between length and width of the inner petaloids:** 0 ≤ 4, 1 ≤ 5, 2 ≤ 6, 3 ≤ 7, 4 ≤ 8, 5 > 8. **Shape of the petaloid apex:** 0 acute, 1 acute or obtuse, 2 obtuse. **Margin of the petaloid apex:** 0 entire, 1 entire or erose, 2 erose. **Flower colour I: white:** 0 no, 1 yes. **Flower colour II: magenta:** 0 no, 1 yes. **Flower colour III: yellow-orange:** 0 no, 1 yes. **Flower colour IV: red throat:** 0 no, 1 yes. **Style colour I: white:** 0 no, 1 yes. **Style colour II: magenta:** 0 no, 1 yes. **Style colour III: yellow:** 0 no, 1 yes. **Stigma colour I: creamy white:** 0 no, 1 yes. **Stigma colour II: orange:** 0 no, 1 yes. If this and the previous character are both zero, then the stigma colour is yellow. **Filament colour I: white:** 0 no, 1 yes. **Filament colour II: magenta:** 0 no, 1 yes. If this and the previous character are both zero, then the filament colour is yellow. **Primary filaments insertion:** 0 low, 1 high. **Pollen:** 0 tricolpate, 1 polycolpate. **Scented flowers:** 0 no, 1 yes. **Early bud development:** 0 no, 1 yes. **Flowering period:** 0 spring (II–IV), 1 spring-summer (IV–X), summer (V–IX). **Fruit colour:** 0 reddish-green, 1 brilliant red. **Fruit succulence:** 0 no, 1 yes. **Fruit dehiscence:** 0 no, 1 yes. **Seed average diameter (mm):** 0 ≤ 1.2, 1 ≤ 1.5, 2 > 1.5. **Seed average length (mm):** 0 ≤ 1.4, 1 ≤ 1.8, 2 > 1.8. **Hilum micropylar region width:** 0 smaller than testa, 1 larger than testa. **Micropyle position I: micropyle inside the hilum:** 0 no, 1 yes. **Micropyle position II: micropyle on the edge of the hilum:** 0 no, 1 yes. **Micropyle position III: micropyle outside the hilum:** 0 no, 1 yes. **Appendages on the hilum edge:** 0 no, 1 yes. **Funicle rests conspicuous:** 0 no, 1 yes. **Testa cell shape:** 0 flat, 1 flat or slightly convex, 2 convex, 3 conical. **Anticlinal cell walls:** 0 straight, 1 sinuate. **Secondary sculpture of the seedcoat I: micro-papillate:** 0 no, 1 yes. **Secondary sculpture of the seedcoat II: striate:** 0 no, 1 yes.

	<b>bic</b>	<b>bol</b>	<b>com</b>	<b>fla</b>	<b>ped</b>	<b>pot</b>	<b>scho</b>	<b>schw</b>	<b>wag</b>	<b>het</b>	<b>con</b>	<b>arg</b>
Stem shape I	ov	cy	ov	ov	cy	gl	ov	ov	cy	gl	ov	ov
Stem shape II	erect	erect	erect	erect	erect	erect	erect	erect	erect	erect	erect	erect
Maximum stem diameter (mm)	125	100	80	70	60	150	120	55	60	150	180	130
Maximum stem height (mm)	200	400	70	90	>150	60	130	90	>200	70	450	180
Head number	1	5	1	1	1	1	1	5	5	1	1	1
Epidermis colour I	gr	gr	gr	gr	gr	gr	gr	gr	gr	gr/red	gr	gr
Epidermis colour II: glaucous	-	-	-	-	-	-	-	-	-	-	-	-
Epidermis colour III: blotched	-	-	-	-	-	-	-	-	-	-	-	-
Number of hypodermal layers	1	1	1	1	1	1	1	1	1	1	1	1
Crystals	+	+	+	+	+	+	+	+	+	+	+	+
Seedling shape	gl	gl	gl	gl	gl	gl	gl	gl	gl	gl	gl	gl
Ribs	+	+	+	+	+	+	+	+	+	+	+	-
Orthostichy number	8	13	8	13	8-13	8	8	13	13	8	21	21
Tubercles	+	+	+	+	+	+	+	+	+	+	+	+
Tubercle shape	rd	rd	rd	rd	rd	rd	rd	rd	rd	rd	rd	ad
Grooved tubercles	-	-	-	-	-	-	-	-	-	-	-	-
Tubercle or rib width (mm)	25	18	18	8	15	25	18	15	14	37	18	15
Tubercle or rib height (mm)	15	9	14	5	6	14	12	13	7	17	16	10
Areolar glands	+	+	+	+	+	-	+	+	+	-	+	+
Minimum total spine number	11	20	14	15	19	12	15	10	18	7	11	24
Maximum total spine number	22	28	16	23	24	16	22	13	29	14	24	29
Central and radial spines distinct	+	+	+	+	+	+	+	+	+	+	+	+
Hooked spines	-	-	-	-	-	-	-	-	-	-	-	-
Upper spine flattened	+	+	+	+	+	+	+	+	+	+	+	-
Shredded spines	-	-	-	-	-	-	-	-	-	-	-	+
Spine colour I: white	-	+	-	-	-	-	-	-	-	-	+	+
Spine colour II: ochre to reddish	+	-	+	+	+	+	+	+	+	+	-	-
Spine colour III: ochre to greyish	-	-	-	-	-	-	-	-	-	-	+	+
Minimum flower diameter (mm)	55	60	50	60	55	60	92	65	60	45	45	50
Maximum flower diameter (mm)	90	80	100	80	70	90	115	80	65	82	60	55
Min petaloid length/width ratio	3	2.9	3	1.9	3.4	3.5	3.6	2.8	3.4	2.8	4.1	3.2
Max petaloid length/width ratio	5	6.6	4.3	3.5	4.4	4.2	5.3	3.9	3.6	4.7	6.6	5.2
Shape of the petaloid apex	a/o	a/o	a/o	a	a	a/o	a/o	a/o	o	a/o	a	a
Margin of the petaloid apex	er	er	er	en/er	er	en/er	er	er	er	er	en	en
Flower colour I: white	-	-	-	-	-	-	-	-	-	-	w	-
Flower colour II: magenta	mg	mg	mg	mg	mg	mg	mg	mg	mg	mg	mg	mg
Flower colour III: yellow-orange	-	-	-	-	-	-	-	-	-	-	-	-
Flower colour IV: red throat	+	+	+	+	+	+	+	+	+	+	-	-
Style colour I: white	w	w	w	w	w	w	w	w	w	w	w	-
Style colour II: magenta	-	-	-	mg	-	-	mg	-	-	mg	mg	mg
Style colour III: yellow	-	-	-	-	-	-	-	-	-	-	-	-
Stigma colour I: creamy white	w	w	-	-	w	w	-	-	w	w	w	w
Stigma colour II: orange	or	-	or	or	-	-	or	or	-	or	-	-
Filament colour I: white	w	w	w	w	w	w	w	w	w	w	w	w
Filament colour II: magenta	mg	-	-	mg	-	-	-	mg	-	-	-	-
Primary filaments insertion	l	l	l	l	l	l	l	l	l	l	h	h
Pollen	poly	poly	poly	poly	poly	poly	poly	poly	poly	poly	tri	tri
Scented flowers	-	-	-	-	-	-	-	-	-	-	-	-
Early bud development	-	-	-	-	-	-	-	-	-	-	-	-
Flowering period	IV-IX	VI-IX	III-VII	V-VII	IV-IX	V-VII	VI	V-VII	IV-X	V-IX	III-VI	III-IV
Fruit colour	gr/red	gr/red	gr/red	gr/red	gr/red	gr/red	gr/red	gr/red	gr/red	gr/red	gr/red	gr/red
Fruit dehiscence	+	+	+	+	+	+	+	+	+	+	+	+
Fruit succulence	-	-	-	-	-	-	-	-	-	-	-	-
Seed average diameter (mm)	1.3	1.31	1.33	1.41	1.3	1.4	1.53	1.33	1.42	1.56	1.57	1.46
Seed average length (mm)	1.68	1.75	2.06	1.74	1.7	1.71	1.84	1.58	1.89	1.75	1.83	1.87
Large hilum micropylar region	-	-	-	-	-	-	-	-	-	-	+	+
Micropyle inside the hilum	-	-	-	-	-	-	-	-	-	-	+	+
Micropyle on the edge of the hilum	+	+	+	+	+	+	+	+	+	+	-	-
Micropyle outside the hilum	+	+	-	-	+	-	-	-	+	+	-	-
Appendages on the hilum edge	+	+	-	-	-	-	-	+	-	-	-	-
Funicle remains conspicuous	-	-	-	-	-	-	-	-	-	-	-	-
Testa cells shape	cvx	cvx	cvx	cvx	cvx	cvx	cvx	cvx	cvx	cvx	con	con
Sinuate anticlinal cell walls	-	-	-	-	-	-	-	-	-	-	-	-
Micro-papillate seedcoat	+	+	+	+	+	+	+	+	+	+	-	-
Striate seedcoat	-	-	-	-	-	-	-	-	-	-	-	-

**Table I.**

Key: a = acute; ad = angled; con = conical; ct = tabular or slightly convex; cvx = convex; cy = cylindrical; de = depressed; en = entire; er = erose; gl = globose; gr = green; h = high; l = low; mg = magenta; o = obtuse; or = orange; ov = ovoid; poly = polycarpate; rd = rounded; tab = tabular; tri = tricolpate; w = white; y = yellow.

**bic** = *bicolor*; **bol** = *bolaensis*; **com** = *commodus*; **fla** = *flavidispinus*; **ped** = "Pedricena"; **pot** = *pottsi*; **scho** = *schottii*; **schw** = *schwarzii*; **wag** = *wagnerianus*; **het** = *heterochromus*; **con** = *conothelos*; **arg** = *argenteus*.



	aur	gar	flv	bue	mat	rin	fre	hin	nid	phy	mul	lab
Stem shape I	ov	ov	ov	gl	gl	gl	gl	gl	gl	de	gl	de
Stem shape II	erect	erect	erect	erect	erect	erect	erect	erect	erect	erect	erect	erect
Maximum stem diameter (mm)	110	140	120	180	150	200	150	200	200	150	200	100
Maximum stem height (mm)	100	100	120	60	140	80	80	80	100	30	150	40
Head number	1	10	11	1	1	1	1	1	5	1	65	1
Epidermis colour I	gr	gr/red	gr/red	gr/red	gr/red	gr	gr	gr	gr	gr	gr	gr
Epidermis colour II: glaucous	-	-	-	-	-	+	-	+	+	+	+	+
Epidermis colour III: blotched	-	-	-	-	-	-	-	-	-	-	+	+
Number of hypodermal layers	1	1	1	1	1	2	2	2	2	2	1	1
Crystals	+	+	+	+	+	+	+	+	+	+	+	+
Seedling shape	gl	gl	gl	gl	gl	gl	gl	gl	gl	gl	gl	gl
Ribs	-	-	-	-	+	+	+	+	+	+	+	-
Orthostichy number	21	21	13	13-21	13-21	25	21	24	25	13	13-21	13-21
Tubercles	+	+	+	+	+	+	+	+	+	+	+	+
Tubercle shape	ad	rd	rd	rd	rd	ad	ad	ad	ad	ad	ad	ad
Grooved tubercles	-	-	-	-	-	-	-	-	-	-	-	-
Tubercle or rib width (mm)	19	15	18	25	20	25	20	20	20	17	20	18
Tubercle or rib height (mm)	14	20	15	24	25	20	20	25	20	13	20	12
Areolar glands	+	+	+	-	-	-	-	-	-	-	-	-
Minimum total spine number	12	12	7	5	10	3	8	3	8	1	3	3
Maximum total spine number	27	18	9	12	19	5	10	10	17	5	5	5
Central and radial spines distinct	+	+	+	+	+	-	+	+	+	-	-	-
Hooked spines	-	-	-	-	-	-	-	-	-	-	-	-
Upper spine flattened	-	-	-	-	-	-	-	-	-	-	-	-
Shredded spines	-	-	-	-	-	-	-	-	+	-	-	-
Spine colour I: white	+	+	-	-	-	-	-	-	-	-	-	-
Spine colour II: ochre to reddish	-	-	-	-	-	-	-	-	-	-	-	-
Spine colour III: ochre to greyish	+	+	+	+	+	+	+	+	+	+	+	+
Minimum flower diameter (mm)	40	26	30	35	40	40	50	45	45	40	30	55
Maximum flower diameter (mm)	60	45	45	45	80	70	60	70	50	65	58	60
Min petaloid length/width ratio	4	2.4	3.3	5	4.4	4	5.3	4	5.5	4.7	3.5	3.6
Max petaloid length/width ratio	4.9	3.5	6	5	6.2	5.3	7	5.3	6.3	6	6.1	6.1
Shape of the petaloid apex	a	a/o	a	a	a	a	a	a	a	a	a	a
Margin of the petaloid apex	en	en	er	en	en/er	en	en	en	en	en	en	en
Flower colour I: white	-	w	-	-	-	w	-	-	w	-	w	w
Flower colour II: magenta	-	mg	-	mg	mg	mg	mg	-	mg	mg	-	-
Flower colour III: yellow-orange	y	-	y	-	-	-	-	y	-	-	-	-
Flower colour IV: red throat	-	-	-	-	-	-	-	-	-	-	-	-
Style colour I: white	-	w	-	w	w	w	-	w	w	w	w	w
Style colour II: magenta	-	mg	mg	mg	mg	-	mg	-	-	-	-	-
Style colour III: yellow	y	-	y	-	-	-	-	-	-	-	-	-
Stigma colour I: creamy white	-	w	w	w	w	w	w	w	w	w	w	w
Stigma colour II: orange	-	-	-	-	-	-	-	-	-	-	-	-
Filament colour I: white	-	w	-	w	w	w	w	w	w	w	w	w
Filament colour II: magenta	-	-	-	-	-	-	-	-	-	-	-	-
Primary filaments insertion	h	h	h	l	l	l	l	l	l	l	l	l
Pollen	tri	tri	tri	tri	tri	tri	tri	tri	tri	tri	tri	tri
Scented flowers	-	-	-	-	-	-	-	-	-	-	-	-
Early bud development	-	-	-	-	-	-	-	-	-	-	-	-
Flowering period	III-IV	II-III	III-IV	III-	II-IX	II-IX	IV	III-	II-V	II-VIII	III-IV	III-IX
Fruit colour	gr/red	gr/red	gr/red	gr/red	gr/red	gr/red	gr/red	gr/red	gr/red	gr/red	gr/red	gr/red
Fruit dehiscence	+	+	+	+	+	+	+	+	+	+	+	+
Fruit succulence	-	-	-	-	-	-	-	-	-	-	-	-
Seed average diameter (mm)	1.58	1.54	1.69	1.45	1.52	1.5	1.56	1.5	1.6	1.57	1.65	1.58
Seed average length (mm)	1.85	2.3	2.21	1.89	2.14	1.9	2.31	1.9	2.07	1.93	2.19	2.04
Large hilum micropylar region	+	-	-	-	-	-	-	-	-	-	-	-
Micropyle inside the hilum	+	+	+	-	-	-	-	-	-	-	-	-
Micropyle on the edge of the hilum	+	-	+	+	+	+	+	+	+	+	+	+
Micropyle outside the hilum	-	-	-	+	+	+	+	+	-	-	+	+
Appendages on the hilum edge	-	-	-	+	+	-	-	-	-	-	+	+
Funicle remains conspicuous	-	+	+	-	-	-	-	-	-	-	-	-
Testa cells shape	con	con	con	cvx	cvx	ct	tab	ct	ct	ct	tab	tab
Sinuate anticlinal cell walls	-	-	-	-	-	-	-	-	-	-	-	-
Micro-papillate seedcoat	-	-	-	+	+	+	+	+	+	+	+	+
Striate seedcoat	-	-	-	-	-	-	-	-	-	-	-	-

Table I. (Continued)

Key: a = acute; ad = angled; con = conical; ct = tabular or slightly convex; cvx = convex; cy = cylindrical; de = depressed; en = entire; er = erose; gl = globose; gr = green; h = high; l = low; mg = magenta; o = obtuse; or = orange; ov = ovoid; poly = polycarpate; rd = rounded; tab = tabular; tri = tricolpate; w = white; y = yellow.

aur = *aurantiacus*; gar = *garciae*; flv = *flavus*; bue = *buekii*; mat = *matudae*; rin = *rinconensis*; fre = *freudenbergeri*; hin = *hintonii*; nid = *nidulans*; phy = *phymatothelos*; mul = *multicephalus*; lab = "La Bolsa".

	hex	loy	tul	mac	lau	leu	schm	kra	has	set
Stem shape I	gl	gl	ov	gl	ov	ov	ov	ov	cy	cy
Stem shape II	erect	erect	erect	erect	erect	erect	erect	erect	dec	erect
Maximum stem diameter (mm)	150	120	80	150	85	70	70	60	55	125
Maximum stem height (mm)	75	60	250	95	100	150	100	80	400	300
Head number	1	1	7	5	1	>50	35	23	28	8
Epidermis colour I	gr	gr	gr/red	gr	gr	gr	gr	gr	gr	gr
Epidermis colour II: glaucous	+	+	-	-	-	-	-	-	-	-
Epidermis colour III: blotched	-	-	-	-	-	-	-	-	-	-
Number of hypodermal layers	1	1	1	1	1	1	1	1	1	1
Crystals	+	+	+	+	+	+	+	+	+	-
Seedling shape	gl	gl	gl	gl	gl	gl	gl	gl	cy	gl
Ribs	+	+	+	-	+	+	+	+	+	+
Orthostichy number	8-13	8	8-13	21	8	8	8	8	18	13
Tubercles	+	+	+	+	+	+	+	+	+	-
Tubercle shape	rd	rd	rd	rd	rd	rd	rd	rd	rd	-
Grooved tubercles	-	-	-	-	-	-	-	+	-	-
Tubercle or rib width (mm)	33	18	20	6	17	14	12	17	5	2
Tubercle or rib height (mm)	11	9	21	4	14	11	10	14	6	18
Areolar glands	-	-	-	-	-	+	+	+	+	+
Minimum total spine number	4	7	6	17	24	9	14	9	24	10
Maximum total spine number	9	11	16	29	31	24	21	16	30	20
Central and radial spines distinct	+	+	+	+	+	+	+	+	+	+
Hooked spines	-	-	-	-	-	-	-	-	-	+
Upper spine flattened	-	-	-	-	-	-	-	-	-	-
Shredded spines	-	-	-	-	-	-	-	-	-	-
Spine colour I: white	-	-	-	+	+	-	-	-	+	-
Spine colour II: ochre to reddish	+	+	-	-	-	-	-	-	-	-
Spine colour III: ochre to greyish	-	-	+	-	+	+	+	+	+	+
Minimum flower diameter (mm)	50	50	30	40	25	35	40	53	35	30
Maximum flower diameter (mm)	100	60	60	65	45	45	65	90	50	42
Min petaloid length/width ratio	3.1	5.5	4.8	4.6	5	3.5	5.4	5.4	4	3.3
Max petaloid length/width ratio	7.2	6.3	6	7	8.4	5.2	6.8	7.1	4.6	3.6
Shape of the petaloid apex	a	a	a	a	a	a	a	a	a	a
Margin of the petaloid apex	en/er	en	en	en	en	en/er	en/er	en/er	en	en
Flower colour I: white	w	w	w	-	-	-	-	-	-	-
Flower colour II: magenta	mg	-	mg	mg	mg	-	mg	mg	mg	-
Flower colour III: yellow-orange	-	-	-	-	-	y	-	-	-	y
Flower colour IV: red throat	-	-	-	-	-	-	-	-	-	+
Style colour I: white	w	w	w	w	w	w	w	w	w	-
Style colour II: magenta	mg	-	mg	mg	mg	mg	mg	mg	mg	-
Style colour III: yellow	-	-	-	-	-	-	-	-	-	y
Stigma colour I: creamy white	w	w	w	w	w	w	w	w	w	-
Stigma colour II: orange	-	-	-	-	-	-	-	-	-	-
Filament colour I: white	w	w	w	w	w	w	w	w	w	w
Filament colour II: magenta	-	-	-	-	-	mg	mg	mg	-	-
Primary filaments insertion	l	l	l	l	l	l	l	l	l	h
Pollen	tri	tri	tri	poly	tri	tri	tri	tri	tri	tri
Scented flowers	-	-	-	-	-	-	-	-	-	+
Early bud development	-	-	-	-	+	-	-	-	+	-
Flowering period	III-VIII	V-VI	III-IX	III-IV	II-VI	VI-IX	V-IX	VI-IX	III-IV	VI-IX
Fruit colour	gr/red	gr/red	gr/red	gr/red	gr/red	gr/red	gr/red	gr/red	gr/red	red
Fruit dehiscence	+	+	+	+	+	+	+	+	+	-
Fruit succulence	-	-	-	-	-	-	-	-	-	+
Seed average diameter (mm)	1.52	1.38	1.38	1.43	1.23	1.38	1.34	1.46	1.53	1.13
Seed average length (mm)	1.72	1.68	1.68	2.04	1.71	1.6	1.55	1.96	1.69	1.39
Large hilum micropylar region	-	-	-	-	-	-	-	-	-	-
Micropyle inside the hilum	+	-	+	+	-	-	-	-	-	-
Micropyle on the edge of the hilum	+	-	+	+	+	+	-	-	-	+
Micropyle outside the hilum	+	+	+	+	-	+	+	+	+	-
Appendages on the hilum edge	-	-	-	-	-	-	-	-	-	+
Funicle remains conspicuous	-	-	+	-	-	-	-	-	-	-
Testa cells shape	tab	ct	tab	cvx	cvx	tab	tab	tab	tab	cvx
Sinuate anticlinal cell walls	-	-	+	-	-	-	-	-	-	-
Micro-papillate seedcoat	+	+	+	+	+	+	+	+	+	-
Striate seedcoat	-	-	-	-	-	-	-	-	-	+

Table I. (Continued)

Key: a = acute; ad = angled; con = conical; ct = tabular or slightly convex; cvx = convex; cy = cylindrical; de = depressed; en = entire; er = erose; gl = globose; gr = green; h = high; l = low; mg = magenta; o = obtuse; or = orange; ov = ovoid; poly = polycarpate; rd = rounded; tab = tabular; tri = tricolpate; w = white; y = yellow.

hex = *hexadrophorus*; loy = *lloydii*; tul = *tulensis*; mac = *macdowellii*; lau = *lausseri*; leu = *leucacanthus*; schm = *schmollii*; kra = *krainzianus*; has = *hastifer*; set = *setispinus*.