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The new monophyletic macrogenus *Echinopsis*
No risk of paraphyly, and the most convincing hypothesis in phylogenetic terms

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Among the materials for the 2013 update of cactusinhabitat.org and the related booklet (Anceschi & Magli 2013b), we consulted the latest issues of CSI (Hunt et al. 2011, 2012) and the work of Schlumpberger & Renner in *Echinopsis* Zuccarini and related genera (2012: 1335-1349). We found the possible opening that emerged from the molecular results conducted by the two authors particularly interesting, it addresses a more natural comprehension of the examined taxa; however, the phylogenetic option adopted by Schlumpberger, and the ensuing taxonomic consequences, published in CSI 28: 29-31, took another direction. Having dealt extensively with the subject, in the part devoted to the taxonomy in our last work (Anceschi & Magli 2013b, 22-29), we would like to summarize, for the CSI readers, the reasons why we think that the option chosen by Schlumpberger is the least convincing in phylogenetic terms.

In order to interpret the examined taxa as natural clades (or monophyletic in Hennig's sense), the possible options as underlined by the molecular results are twofold. The first consists in assimilating in *Echinopsis sens. lat.* as currently conceived (Anderson 2001, 2005, 2011; Hunt et al., 2006; Nyffeler & Eggli 2010), with 15 other genera that never been included until now (Schlumpberger & Renner 2012: 1336, 1341, 1346). The second is to divide *Echinopsis* into smaller units (ibid., 1346–1347), i.e. the division of the examined taxa into a dozen clades, with the resurrection of old generic names and transfers of species epithets. As we know, Schlumpberger (2012: 29-31) opted for the second solution, considering it "a more practical approach"- a new division of *Echinopsis* in small separate genera.

David Hunt (CSI 26: 4), writes that in the recent molecular analysis, the alternative of combining genera into larger units is rarely considered "because cladists argue that it will make them paraphyletic". We do not know these cladists, who claim that the assimilation of all the taxa constituting a probable monophyletic line, into a single clade, might make

it paraphyletic (independent of the number of the taxa it takes to assimilate)*. In the case of Schlumpberger & Renner's work (2012) the assimilation in *Echinopsis sens. lat.* of all the 15 genera indicated by the analysis could just make the genus monophyletic, not paraphyletic, unless we make an *a priori* decision to separate one (Nelson 1971) or two (Wiley & Liebermann 2011, 82) of the 15 genera in question from *Echinopsis*. Indeed, according to Hennig (1966: 146-147) paraphyletic groups are those which "have no ancestor in common only to them, and thus also no point of origin in time in common only to them in the true historical course of phylogeny". The same idea of paraphyletic group is maintained in Wiley & Liebermann (2011: 81). As it has been clarified that it is not the risk of paraphyly preventing us from choosing the first option, we would like to substantiate some objections to the type of interpretation proposed by Schlumpberger.

Objection N°1: Practicality. Schlumpberger (2012, 29) states that, instead of considering the idea of a monophyletic genus *Echinopsis*, which would require the inclusion of 15 genera hitherto never incorporated before, a more practical approach is the splitting of it into separate smaller genera again. Disagreeing with this statement, we recall that one of the synonyms of *Denmoza rhodacantha* (Salm-Dyck) Britton & Rose is *Echinopsis rhodacantha* (Salm-Dyck) Förster, and that the basionym of *Oreocereus hempelianus* (Gürke) D. Hunt is *Echinopsis hempeliana* Gürke. Also, if it is true that a monophyletic *Echinopsis* requires the inclusion of 15 genera, it is also true that the division proposed by Schlumpberger requires the resurrection of at least 7 old genera (*Acanthocalycium, Chamaecereus, Leucostele, Lobivia, Reicheocactus, Soehrensia* and *Setiechinopsis*), but most importantly, it does not solve the internal relationships of the clades *Cleistocactus sens. str.* and *Oreocereus* (Schlumpberger & Renner 2012: 1342). In fact, for consistency with the other solutions adopted, the *Oreocereus (Borzicactus)* clade (99% bootstrap), given the results of the analysis, should include: *Borzicactus, Espostoa, Haageocereus, Matucana, Mila, Oreocereus, Oroya, Pygmaeocereus* and *Rauhocereus*. The clade *Cleistocactus sens. str.* should include at least *Vatricania*

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* Nor do I know of any cladists making such nonsensical claims! I had in mind, for intance, the specific example of *Schlumbergera* sensu Hunt 2012/CSI 26:18, wich cladists will argue is paraphyletic, and the paraphyletic suprageneric taxa pragmatically accepted by Eggli & Leuenberger (see l.c. 31). - Ed.

guentheri (100% bootstrap), if not also *Cephalocleistocactus, Samaipaticereus, Weberbauerocereus* and *Yungasocereus* (100% bootstrap). Therefore, we see that under a practical perspective, Schlumpberger's proposal does not solve the relationships within the group in question in a natural way.

Objection N° 2: Communication, clearness, order. According to Hunt (1999: 8), we think that names, even before classification, serve to communicate. But to communicate, they should have an intrinsic coherence that links them to the reality they attempt to identify. In this context, Schlumpberger's newly modified genera do not even express clearness, let alone order. In contrast to the original genera of Britton & Rose and Backeberg, which although not natural (in Hennig's sense), did show an internal coherence based on the recognizability of one or more characters that unite the members of the generic group. For example: more or less globular/diurnal anthesis = *Lobivia*; globular/white, funnel-shaped flowers/nocturnal anthesis = *Echinopsis sens str*.; columnar/large white flowers/nocturnal anthesis = *Trichocereus*; etc. But if we attempt to define, in the same way, to communicate the distinctions between the genera proposed by Schlumpberger, it generates chaos. In fact, the reinstated genus *Chamaecereus* Britton & Rose includes ex-members (and characters) of *Lobivia*, such as *Lobivia saltensis* Spegazzini, and *Lobivia stilowiana* Backeberg. *Lobivia* Britton & Rose now includes ex-members (and characters) of *Echinopsis*, such as *Echinopsis calochlora* K. Schumann, and *Echinopsis mamillosa* Gürke. *Soehrensia* Backeberg includes ex-members (and characters) of *Lobivia*, such as *Lobivia crassicaulis* R. Kiesling, or of *Trichocereus*, such as *Trichocereus angelesiae* R. Kiesling, etc. We think that Schlumpberger & Renner's conclusion is at least questionable, the conclusion with which the authors wonder about the possibility of finding, "A new generic classification of the Trichocereeae now requires finding morphological characters sufficiently conservative for distinguishing larger groups of species. Seed morphology and growth form, perhaps in combination, seem promising starting points" (2012: 1348). This does not seem to us a serious way of proceeding - to change the names of 48 taxa, and only then to wonder which could be the characters that will identify them. Are the molecular characters not characters in all respects? So, why do they not suffice in defining the groups in question? The answer is: they are *not* sufficient because the chosen phylogenetic hypothesis does not reflect something that exists in nature. Instead, choosing the option of unifying the 15 genera

in *Echinopsis* would make the key to their identification simple: *Echinopsis* groups with floral characters and/or pollination syndromes modified.

Objection N° 3: Something approximating to the truth in nature. Among the results of molecular analysis, the phylogenetic hypothesis should be chosen that provides a valid estimate of something that exists in nature. In other words, the success of the evolutionary model chosen in predicting new data, requires that the fit of data to the model may lead to *something approximating to the truth in nature* (see also Sober 2008). What are *Cleistocactus*, *Denmoza*, *Haageocereus*, *Oreocereus*, *Weberbauerocereus*, etc., if they are not *Echinopsis* taxa with floral characters and/or pollination syndromes modified? The hypothesis is confirmed both at the molecular level, then at the morphological one (or holomorphological, in Hennig's sense). For years, molecular analysis revealed the close relationship between *Echinopsis sens. lat.* and the other genera within the tribe Trichocereeae, or subtribe Trichocereinae (Nyffeler 2002, 317, 319; Lendel et al. 2006, unpubl. data in Nyffeler & Eggli 2010) until Schlumpberger & Renner's latest analysis reaffirmed, even more clearly, that a large part of the genera constituting the tribe Trichocereeae form with *Echinopsis sens. lat.* a single well supported monophyletic clade. In nature the most striking example is the monotypic *Denmoza rhodacantha*, a taxon otherwise attributed by various authors to *Cleistocactus*, *Echinopsis* and *Oreocereus*, which, for us, is the perfect link between the current concept of *Echinopsis sens. lat.* (which is polyphyletic), and a new monophyletic macrogenus *Echinopsis*, which also includes species of *Echinopsis* with floral characters and/or pollination syndromes modified.

Objection N° 4: Coherence. Since molecular biology results are expressed through theories, methods and techniques based on rules and not laws (as for example the process by which are interpreted synapomorphies, or the phylogenetic inferences assigned to ML techniques, etc), coherence by the researcher in the interpretation of the results is essential. We recall that in a similar case, i.e. the genus *Parodia,* the possible options/ interpretations gave rise to opposite choices to those proposed for *Echinopsis*. Nyffeler (1999) gave the IOS Cactaceae Working Party results of molecular analysis conducted using ITS (nuclear ribosomal DNA) and trnL-trnF (cp DNA) as molecular markers, to investigate the relationships between the members of the subtribe Notocactinae, and

especially among those internal to *Parodia sens. lat*. (i.e. *Brasilicactus*, *Brasiliparodia*, *Eriocactus*, *Notocactus*, *Parodia* and *Wigginsia*) (1999, 7: 6-8). After detecting the basal position of *Brasilicactus*/*Brasiliparodia* and *Eriocactus* in the group, which in the words of Nyffeler, "are not true parodias", three options were proposed:

1) Include everything in *Parodia s.l.*, including *Brasilicactus*/*Brasiliparodia, Eriocactus, 'Notocactus' s.s.*, and *Wigginsia*.
2) Recognize *Brasilicactus*/*Brasiliparodia, Eriocactus* and *Parodia s.l. (including 'Notocactus' s.s.,* and *Wigginsia*).
3) Recognize *Brasilicactus*/*Brasiliparodia, Eriocactus,* and probably up to 5 different genera for the rest of the members from '*Notocactus' s.s., Parodia s.s.,* and *Wigginsia*.

At that time Hunt (1999) preferred the first option, arguing "since, in biological nomenclature, the genus is part of the name, stability is best served by reserving that category for the largest readily recognizable 'natural' (i.e. evolutionary or phylogenetic) units, ... This would be my main reason for preferring the more inclusive options Reto identifies". Philosophically we agree with Hunt, and despite the diversity of *Eriocactus* compared with the other members of the group, for coherence we agree also with the phylogenetic option adopted (Anceschi & Magli 2013a). Schlumpberger discussed his conclusions with the NCL "team" (CSI 25: 30; 26: 7; 28: 3-4), and the result is the 48 new proposed combinations in CSI 28: 29-31). We do not see any coherence of approach in this procedure. Perhaps *Cleistocactus* and *Oreocereus* (or *Borzicactus*) should be more "protected" than *Notocactus* and *Eriocactus*? As far as we are concerned we think that time cannot be reversed, and that the indications of the real relationships between the taxa involved in the Schlumpberger & Renner's study are rather clear. As highlighted, we prefer to opt for the solution of a monophyletic macrogenus *Echinopsis*, with the consequent inclusion of the genera indicated in the study of Schlumpberger & Renner, currently involved in cactusinhabitat.org (i.e. *Cleistocactus, Denmoza, Haageocereus, Harrisia, Oreocereus, Vatricania* and *Weberbauerocereus*). For the new names and combinations required in *Echinopsis* see Anceschi & Magli (2013b: 37–40).

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