

**MOLECULAR PHYLOGENETICS OF *ECHINOPSIS* (CACTACEAE):
POLYPHYLY AT ALL LEVELS AND CONVERGENT EVOLUTION
OF POLLINATION MODES AND GROWTH FORMS¹**

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- *Premise of the study:* In its current circumscription, *Echinopsis* with 100–150 species is one of the largest and morphologically most diverse genera of Cactaceae. This diversity and an absence of correlated characters have resulted in numerous attempts to subdivide *Echinopsis* into more homogeneous subgroups. To infer natural species groups in this alliance, we here provide a plastid phylogeny and use it to infer changes in growth form, pollination mode, and ploidy level.
- *Methods:* We sequenced 3800 nucleotides of chloroplast DNA from 162 plants representing 144 species and subspecies. The sample includes the type species of all genera close to, or included in, *Echinopsis* as well as a dense sample of other genera of the Trichocereae and further outgroups. New and published chromosome counts were compiled and traced on the phylogeny, as were pollination modes and growth habits.
- *Key results:* A maximum likelihood phylogeny confirms that *Echinopsis* s.l. is not monophyletic nor are any of the previously recognized genera that have more than one species. Pollination mode and, to a lesser extent, growth habit are evolutionarily labile, and diploidy is the rule in *Echinopsis* s.l., with the few polyploids clustered in just a few clades.
- *Conclusions:* The use of evolutionary labile floral traits and growth habit has led to nonnatural classifications. Taxonomic realignments are required, but further study of less evolutionary labile traits suitable for circumscribing genera are needed. Surprisingly, polyploidy seems infrequent in the *Echinopsis* alliance and hybridization may thus be of minor relevance in the evolution of this clade.

Key words: Cactaceae; chromosome counts; *Echinopsis*; growth form evolution; phylogenetics; pollination modes; polyploidy; Trichocereae.

Cactaceae comprise some 1870 species in 130 genera (Nyffeler and Eggli, 2010) and are estimated to have diversified since the mid-Tertiary, about 30 million years ago (Ma) (Hershkovitz and Zimmer, 1997). They are an important component of seasonally dry tropical and subtropical ecosystems, where their adaptations for water conservation and water storage permit them to survive even pronounced droughts. Different growth habits, such as columnar, globular, or barrel growth, may characterize larger species groups, but molecular-phylogenetic studies in Cactaceae have rarely addressed the evolution of growth forms (but see Hernández-Hernández et al., 2011). Similarly, floral characters and pollinator affiliation in cacti have rarely been studied in an evolutionary context, mostly for lack of large phylogenies and fieldwork on pollination biology. That polyploidy relates to diversification has been suggested for several clades of cacti (Remski, 1954; Pinkava et al., 1985;

Cota and Philbrick, 1994; Cota and Wallace, 1995; Pinkava, 2002; Negrón-Ortiz, 2007), but again the evidence is limited due to a paucity of chromosome counts for species (or clades) of known relationships. Nevertheless, it is thought that polyploidy may be an important speciation mechanism in some Cactaceae (Negrón-Ortiz, 2007; Arakaki et al., 2007, and citations therein).

One of the least understood groups of cacti is the *Echinopsis* alliance, which includes 100–150 species that exhibit a great diversity in architecture and that variously are pollinated by bees, hummingbirds, or sphingids (Schlumberger and Badano, 2005; Schlumberger and Raguso, 2008; Schlumberger et al., 2009; Walter, 2010; Ortega-Baes et al., 2011). The *Echinopsis* alliance belongs in the Trichocereae (Anderson, 2001, 2005; Hunt, 2006) or Trichocereinae of a more broadly circumscribed Cereae (Nyffeler and Eggli, 2010). The species occur from southeastern Brazil to the coast of Chile and north to northern Ecuador, with a center of species diversity in the eastern Andes of northern Argentina and Bolivia. With more than 500 species names, *Echinopsis* is taxonomically problematic and much in need of study of natural intraspecific variation as well as molecular phylogenetic work (Anderson, 2001; Hunt, 2006; Nyffeler and Eggli, 2010). In the broad circumscription of Hunt (2006), *Echinopsis* includes 18 genera, including the well-known and species-rich *Lobivia* Britton & Rose and *Trichocereus* Riccob. Because of the problematic generic boundaries, recent studies continue to lump these difficult genera “to be conservative” (Arakaki et al., 2011: p. 8383). The 18 genera included in *Echinopsis* by Hunt initially were created based on traits, such as diurnal vs. nocturnal flowering, flower color, and growth form, i.e., globular vs. columnar: Thus, the name *Lobivia*

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applied to mostly globular cacti from the medium to high Andes with short, diurnal flowers of various colors; *Trichocereus* was used for mostly columnar, sometimes tree-like cacti with flowers that are usually large, white, and nocturnal; and *Echinopsis* in the original sense applied to globular plants with white, funnel-shaped flowers of predominantly nocturnal anthesis. Species combining these characters were placed in separate genera, such as *Helianthocereus*, created for species of columnar habit, but with diurnal flowers (see Table 1 for a short history of *Echinopsis* taxonomy).

Here we present a densely sampled molecular phylogeny for *Echinopsis* that includes 144 species and subspecies, including the type species of all relevant generic names, as well as representatives of all genera in recent years assigned to the tribe Trichocereae, again including relevant generic type species. To assess the role of chromosome number changes, we generated new counts for 37 selected taxa and added these to previous counts for a phylogenetically distributed sampling. We use these data to address the following questions: (1) Is *Echinopsis* in the broad sense monophyletic? (2) What is the level of variation of growth habit and pollination mode, characters that have been used to define clades in *Echinopsis* sensu lato? And (3) How common are ploidy changes in the *Echinopsis* alliance, and are they clustered in certain subclades, perhaps indicating a role for hybridization in the evolution of certain species groups.

MATERIALS AND METHODS

Taxon sampling—Molecular phylogenies to date have included three to nine species of *Echinopsis* plus few of the potentially embedded related genera of Trichocereae (Nyffeler, 2002; Ritz et al., 2007; Hernández-Hernández et al., 2011). We obtained tissue samples from 162 plants representing 31 genera, 129 species, 8 subspecies, and 2 varieties; 74 species belong to *Echinopsis* s.l., the remaining ones are species not previously assigned to *Echinopsis* (see Table 2 for taxonomic names and their authors, as well as information about generic type species). Our sample includes representatives of all nine infrageneric groups of *Echinopsis* defined by Friedrich and Glätzle (1983) and representatives of the 13 sections of *Lobivia* defined by Rausch (1985). We further included 54 species representing the 24 genera of the tribe Trichocereae (Anderson, 2005), and part of the Browningieae-Cereae-Trichocereae (BCT) clade of Nyffeler (2002). For rooting, we chose *Neowerdermannia vorwerkii* from core Notocactae, based on Nyffeler (2002).

Material was field-collected by the first author or obtained from documented material from public and private collections. All species identifications were made or confirmed by the first author. Vouchers are listed in Table 2.

TABLE 1. Major steps in the history of *Echinopsis* taxonomy.

Study	
Hunt, 2006	<i>Echinopsis</i> Zucc. (<i>Echinopsis</i> s.str., <i>Lobivia</i> and <i>Trichocereus</i> as artificial infrageneric groups)
Anderson, 2001, 2005	<i>Acanthocalycium</i> Backeb., <i>Echinopsis</i> Zucc. (2005: <i>Echinopsis</i> s.str., <i>Lobivia</i> and <i>Trichocereus</i> as artificial infrageneric groups)
Backeberg, 1958–1962	<i>Acanthocalycium</i> Backeb., <i>Acantholobivia</i> Backeb., <i>Chamaecereus</i> Britton & Rose, <i>Echinopsis</i> Zucc., <i>Helianthocereus</i> Backeb., <i>Leucostele</i> Backeb., <i>Lobivia</i> Britton & Rose, <i>Pseudolobivia</i> Backeb., <i>Soehrensia</i> Backeb., <i>Trichocereus</i> Riccob.
Britton and Rose, 1919–1923	<i>Chamaecereus</i> Britton & Rose, <i>Echinopsis</i> Zucc., <i>Lobivia</i> Britton & Rose, <i>Trichocereus</i> Riccob.
Schumann, 1899	<i>Cereus</i> Mill. (in part), <i>Echinopsis</i> Zucc.

DNA extraction, amplification, sequencing, and alignments—Samples were collected from floral or vegetative tissue and silica-dried. Total genomic DNA was extracted using the NucleoSpin extraction kit (Macherey-Nagel, Düren, Germany), following the manufacturer's protocol, but with an elongated lysis step over night at 4°C.

We amplified three noncoding chloroplast DNA regions using published standard primers: the *trnS-G* intergenic spacer (Hamilton, 1999), the *trnL* region (Taberlet et al., 1991), and the *rpl16* intron (Asmussen, 1999). PCR reactions were performed in 25 µL reactions (1.25 µL DNA, 0.1 µL *Taq* polymerase, 0.8 µL primer (10 µM), 0.5 µL 1.5 mmol/L MgCl₂, 4 µL 5× buffer, 4 µL 1.25 mmol/L dNTP, 0.25 µL BSA) as follows: initial denaturation was at 95°C for 5 min; followed by 35 cycles of 95°C for 30 s (denaturation), 48–55°C for 1 min (annealing) and 72°C for 2 min (elongation); and 72°C for 40 s (final extension). PCR reaction products were purified using the Wizard SV PCR clean-up kit (Promega GmbH, Mannheim, Germany). Sequencing reactions were performed with the Big Dye Terminator kit (Applied Biosystems, Warrington, UK), and cleaned with the Sephadex G-50 gel filtration system (Amersham, Uppsala, Sweden) using MultiScreen TM-HV membrane plates (Millipore, Bedford, Massachusetts, USA) according to the manufacturer's protocol. Reactions were run on an ABI 3100 Avant capillary sequencer. Sequences were edited and assembled using the program Sequencher 4.5 (Gene Codes, Ann Arbor, Michigan, USA). Sequences were aligned using Prank (Löytynoja and Goldman, 2005) and corrected by eye in the program MacClade 4.08 (Maddison and Maddison, 2003).

Phylogenetic analyses—Chloroplast partitions were first analyzed separately to check for possible contamination or mislabeling that might have led to incongruent topologies, and in the absence of statistically supported topological contradictions (defined as >70% maximum likelihood bootstrap support), all sequences were combined. Phylogenetic inference relied on maximum likelihood (ML) under the GTR + G model as implemented in the program RAxML BlackBox (Stamatakis et al., 2008, <http://phylobench.vital-it.ch/raxml-bb/>).

Chromosome counts—Root tips were collected from plants cultivated at the Munich Botanical Garden and immediately transferred to 2 mmol/L 8-hydroxyquinoline to arrest metaphases, then fixed in 3c:1 ethanol–acetic acid, and stored until use at –20°C. Chromosome spreads were obtained after hydrolysis in 0.5 N hydrochloric acid at 60°C for 10 min and staining with a saturated orcein-glacial acetic acid solution. Our sampling includes species from all groups (genera) embedded in *Echinopsis* or newly revealed as closely related by our molecular data.

Pollination modes and growth forms—All species sequenced were assigned to one or several pollinator groups (bee, hummingbird, bat, or sphingid) on the basis of either our own field observations or inferred from combinations of floral traits, such as anthesis time, floral bauplan (i.e., mostly shape and length of the hypanthium), and nectar production. For growth form, we assigned species to one of two types, globular growth or columnar growth.

RESULTS

Relative frequencies of changes in pollination mode, growth architecture, and chromosome number—We generated 457 new chloroplast sequences (Table 2). The concatenated aligned matrix comprised 3866 nucleotides. Maximum likelihood analysis of these data yielded the tree shown in Fig. 1A and B, which also shows growth form (categorized as globular or columnar), pollination mode, and chromosome number. Inspection of the tree reveals many more changes in pollination modes than in growth form, and even though chromosome counts are not available for all species, polyploidy (tetraploidy) appears common in the *Oreocereus* clade and in *Weberbauerocereus*, and rare elsewhere (Fig. 1, Table 3; more about chromosome numbers in the next section). Major clades were named using oldest available genus names.

A monophyletic *Echinopsis* would need to include *Acanthocalycium* Backeb., *Arthrocareus* A.Berger, *Cephalocleistoctactus* F.Ritter, *Cleistocactus* Lem. (including *Borzicactus*

TABLE 2. Species and loci sequenced newly for this study, their sources and provenance, voucher informations, herbarium code, and GenBank accession numbers. Generic types are indicated (GT) and synonymous names are given where they are still widely used.

Species	DNA source	Geographic origin of sample or distribution	<i>trnS-trnG</i> intergenic spacer	<i>trnL-trnF</i> intergenic spacer	<i>rpl16</i> intron
<i>Acanthocalycium ferrarii</i> Rausch	B.O.Schlumpberger 482 (CORD)	Tucuman, Argentina*	JQ779438	JQ779600	JQ779744
<i>Acanthocalycium glaucum</i> F.Ritter	B.O.Schlumpberger x08 (M) J. & B.Piltz 394	Catamarca, Argentina**	JQ779439	JQ779601	JQ779745
<i>Acanthocalycium spiniflorum</i> (Schumann) Backeb., GT	B.O.Schlumpberger x07 (M) J. & B.Piltz 204	Córdoba, Argentina**	JQ779441	JQ779603	JQ779747
<i>Acanthocalycium spiniflorum</i> (Schumann) Backeb., GT	B.O.Schlumpberger 323 (CORD)	Córdoba, Argentina*	JQ779440	JQ779602	JQ779746
<i>Acanthocalycium thionanthum</i> (Spegazzini) Backeb.	B.O.Schlumpberger 523 (CORD)	Salta, Argentina*	JQ779437	JQ779599	JQ779743
<i>Arthroceres rondonianus</i> Backeb. & Vell	B.O.Schlumpberger x102 (M) L.Horst 145	Minas Gerais, Brazil**	JQ779506	JQ779668	JQ779804
<i>Arthroceres spinosissimus</i> (Buining & Brederoo) F.Ritter	B.O.Schlumpberger x103 (M) L.Horst 328	Mato Grosso, Brazil**	JQ779505	JQ779667	JQ779803
<i>Browningia hertlingiana</i> (Backeb.) Buxb.	B.O.Schlumpberger x101 (M)	Southern Peru	JQ779526	JQ779688	JQ779822
<i>Cephalocleistocactus chrysocephalus</i> F.Ritter, GT	B.O.Schlumpberger x111 (M)	La Paz, Bolivia	JQ779507	JQ779669	JQ779805
<i>Cereus aethiops</i> Haw.	B.O.Schlumpberger 330 (CORD)	San Luis, Argentina*	JQ779503	JQ779665	JQ779801
<i>Cleistocactus baumannii</i> Lem., GT	B.O.Schlumpberger 597 (M)	Córdoba, Argentina*	JQ779500	JQ779662	
<i>Cleistocactus sepium</i> (Kunth) F.A.C.Weber ex Rol.-Goss. (= <i>Borzicactus sepium</i> (Kunth) Britton & Rose)	B.O.Schlumpberger x117 (M)	North & central Ecuador	JQ779463	JQ779625	JQ779768
<i>Cleistocactus sextonianus</i> (Backeb.) D.R.Hunt (= <i>Borzicactus sextonianus</i> (Backeb.) Kimnach)	B.O.Schlumpberger x61 (M)	South & central Peru	JQ779462	JQ779624	JQ779767
<i>Cleistocactus smaragdiflorus</i> (F.A.C.Weber) Britton & Rose	B.O.Schlumpberger 424 (M)	Catamarca, Argentina*	JQ779499	JQ779661	JQ779798
<i>Denmoza rhodacantha</i> (Salm-Dyck) Britton & Rose, GT	B.O.Schlumpberger 366 (CORD)	La Rioja, Argentina*	JQ779446	JQ779608	JQ779752
<i>Discocactus zehntneri</i> subsp. <i>buenerkeri</i> (W.R. Abraham) P.J.Braun & Esteves (incl. <i>D. zehntneri</i> subsp. <i>boomianus</i> Buining & Brederoo) N.P.Taylor & Zappi)	cult 08/2533 B.O.Schlumpberger x113 BGM	Bahia, Brazil	JQ779511	JQ779673	JQ779809
<i>Echinopsis ancistrophora</i> Speg.	B.O.Schlumpberger 152 (CORD)	Salta, Argentina*	JQ779367	JQ779529	JQ779691
<i>Echinopsis ancistrophora</i> Speg.	B.O.Schlumpberger 96 (CORD, M)	Jujuy, Argentina*	JQ779368	JQ779530	JQ779692
<i>Echinopsis</i> cf. <i>ancistrophora</i> Speg.	B.O.Schlumpberger x133 (M)	unknown	JQ779369	JQ779531	JQ779693
<i>Echinopsis angelesiae</i> (R.Kiesling) G.D.Rowley	B.O.Schlumpberger 383 (CORD)	Salta, Argentina*	JQ779413	JQ779575	JQ779725
<i>Echinopsis arachnacantha</i> (Buining & F.Ritter) H.Friedrich	B.O.Schlumpberger 656 (LPB)	Santa Cruz, Bolivia*	JQ779400	JQ779562	JQ779714
<i>Echinopsis atacamensis</i> subsp. <i>pasacana</i> (F.A.C.Weber) G.Navarro	B.O.Schlumpberger 518 (CORD)	Catamarca, Argentina*	JQ779486	JQ779648	
<i>Echinopsis atacamensis</i> subsp. <i>pasacana</i> (F.A.C.Weber) G.Navarro	B.O.Schlumpberger 593 (CORD)	Tucuman, Argentina*	JQ779487	JQ779649	JQ779787
<i>Echinopsis aurea</i> Britton & Rose	B.O.Schlumpberger 309 (CORD)	Córdoba, Argentina*	JQ779472	JQ779634	JQ779776
<i>Echinopsis aurea</i> Britton & Rose	B.O.Schlumpberger 313 (CORD)	Córdoba, Argentina*	JQ779471	JQ779633	JQ779775
<i>Echinopsis aurea</i> Britton & Rose	B.O.Schlumpberger x29 (M) W.Rausch 116 (<i>E. leucomalla</i> (Wessner) H.Friedrich)	San Luis, Argentina**	JQ779475	JQ779637	
<i>Echinopsis aurea</i> subsp. <i>fallax</i> (Oehme) M.Lowry	B.O.Schlumpberger x05 (M) J. & B.Piltz 137	La Rioja, Argentina**	JQ779474	JQ779636	
<i>Echinopsis aurea</i> subsp. <i>shaferi</i> (Britton & Rose) M.Lowry	B.O.Schlumpberger x100 (M) C.Hunkeler 300	Catamarca, Argentina**	JQ779473	JQ779635	JQ779777
<i>E. aurea</i> var. <i>callochrysea</i> (F.Ritter) J.Ullmann	B.O.Schlumpberger 384 (CORD)	Salta, Argentina*	JQ779476	JQ779638	JQ779778
<i>Echinopsis backebergii</i> Werderm.	B.O.Schlumpberger x33 (M) F.Ritter 1312 (<i>Lobivia winteriana</i> F.Ritter)	Huancavelica, Peru**	JQ779386	JQ779548	JQ779703
<i>Echinopsis backebergii</i> Werderm.	B.O.Schlumpberger x65 (M) W.Rausch 407 (<i>Lobivia zecheri</i> Rausch)	Ayacucho, Peru**	JQ779387	JQ779549	
<i>Echinopsis bonnieae</i> (Halda, Hogan & Janeba) Halda & Malina	B.O.Schlumpberger x127 (M)	Catamarca, Argentina	JQ779502	JQ779664	JQ779800
<i>Echinopsis boyuibensis</i> F.Ritter	B.O.Schlumpberger 301 (M)	Santa Cruz, Bolivia*	JQ779371	JQ779533	
<i>Echinopsis breviflora</i> (Backeb.) M.Lowry (= <i>Lobivia sanguiniflora</i> var. <i>breviflora</i> (Backeb.) Rausch)	B.O.Schlumpberger x80 (M)	Salta, Argentina	JQ779469	JQ779631	JQ779773

TABLE 2. Continued.

Species	DNA source	Geographic origin of sample or distribution	<i>trnS-trnG</i> intergenic spacer	<i>trnL-trnF</i> intergenic spacer	<i>rpl16</i> intron
<i>Echinopsis bridgesii</i> subsp. <i>vallegrandensis</i> (Cárdenas) M.Lowry	B.O.Schlumpberger 657 (LPB)	Cochabamba, Bolivia	JQ779403	JQ779565	JQ779717
<i>Echinopsis bridgesii</i> subsp. <i>vallegrandensis</i> (Cárdenas) M.Lowry	B.O.Schlumpberger 691 (LPB)	Santa Cruz, Bolivia*	JQ779404	JQ779566	JQ779718
<i>Echinopsis bruchii</i> (Britton & Rose) A.Cast. & H.V.Lelong	B.O.Schlumpberger x106 (M)	Northwestern Argentina	JQ779422	JQ779584	JQ779731
<i>Echinopsis caineana</i> (Cárdenas) D.R.Hunt	B.O.Schlumpberger x125 (M) W.Rausch 197	Cochabamba, Bolivia**	JQ779402	JQ779564	JQ779716
<i>Echinopsis calliantholilacina</i> Cárdenas	B.O.Schlumpberger x13 (M) W.Rausch 63	Chuquisaca, Bolivia**	JQ779381	JQ779543	
<i>Echinopsis callichroma</i> Cárdenas	B.O. Schlumpberger x24 (M) W.Rausch 461	Cochabamba, Bolivia**	JQ779380	JQ779542	
<i>Echinopsis calochlora</i> K.Schum.	B.O.Schlumpberger x10 (M)	Southwestern Brazil, east Bolivia	JQ779485	JQ779647	JQ779786
<i>Echinopsis calorubra</i> Cárdenas	B.O.Schlumpberger x90 (M)	South-central Bolivia	JQ779382	JQ779544	JQ779699
<i>Echinopsis calorubra</i> Cárdenas	B.O.Schlumpberger x128 (M) W.Rausch 463 (<i>Lobivia mizquensis</i> Rausch)	Cochabamba, Bolivia**	JQ779383	JQ779545	JQ779700
<i>Echinopsis candicans</i> (Gillies ex Salm-Dyck) D.R.Hunt	B.O.Schlumpberger 348C (CORD)	Córdoba, Argentina*	JQ779411	JQ779573	JQ779723
<i>Echinopsis candicans</i> (Gillies ex Salm-Dyck) D.R.Hunt	B.O.Schlumpberger 332 (CORD)	San Luis, Argentina*	JQ779412	JQ779574	JQ779724
<i>Echinopsis cardenasiana</i> (Rausch) H.Friedrich	B.O.Schlumpberger x116 (M) W.Rausch 498	Tarija, Bolivia**	JQ779370	JQ779532	
<i>Echinopsis chamaecereus</i> H.Friedrich & Glaetzle (= <i>Chamaecereus silvestrii</i> (Speg.) Britton & Rose)	B.O.Schlumpberger x37 (M)	Supposedly Salta/ Tucuman, Argentina	JQ779434	JQ779596	
<i>Echinopsis chiloensis</i> (Colla) H.Friedrich & G.D.Rowley	B.O.Schlumpberger x77 (M)	Chile*	JQ779489	JQ779651	JQ779789
<i>Echinopsis chrysantha</i> Werderm.	B.O.Schlumpberger x83 (M) W.Rausch 5	Salta, Argentina**	JQ779470	JQ779632	JQ779774
<i>Echinopsis chrysochete</i> Werderm.	B.O.Schlumpberger 576A (CORD)		JQ779394	JQ779556	
<i>Echinopsis chrysochete</i> Werderm.	B.O.Schlumpberger 577 (CORD) (<i>Lobivia chrysochete</i> var. <i>minutiflora</i> (Rausch))	Salta, Argentina*	JQ779395	JQ779557	JQ779709
<i>Echinopsis cinnabarina</i> (Hook.) Labor.	B.O.Schlumpberger 706 (LPB)	Santa Cruz, Bolivia*	JQ779390	JQ779552	JQ779706
<i>Echinopsis coronata</i> Cárdenas	V.Beyer & B.O.Schlumpberger x30 (M) W.Rausch 613	Santa Cruz, Bolivia**	JQ779372	JQ779534	
<i>Echinopsis crassicaulis</i> (Backeb. ex R.Kiesling) H.Friedrich & Glaetzle	B.O.Schlumpberger x23 (M)	Catamarca, Argentina	JQ779418	JQ779580	
<i>Echinopsis densispina</i> Werderm.	cult N/2956 B.O.Schlumpberger x107 BGM	Salta, Argentina**	JQ779482	JQ779644	JQ779784
<i>Echinopsis famatimensis</i> (Speg.) Werderm.	B.O.Schlumpberger x48 (M)	La Rioja, San Juan, Argentina	JQ779501	JQ779663	JQ779799
<i>Echinopsis ferox</i> (Britton & Rose) Backeb.	B.O.Schlumpberger 563 (CORD)	Jujuy, Argentina*	JQ779384	JQ779546	JQ779701
<i>Echinopsis formosa</i> (Pfeiff.) Jacobi ex Salm-Dyck subsp. <i>korethroides</i> (Werderm.) M.Lowry	B.O.Schlumpberger 390 (CORD)	Salta, Argentina*	JQ779420	JQ779582	
<i>Echinopsis formosa</i> (Pfeiff.) Jacobi ex Salm-Dyck	B.O.Schlumpberger 460 (CORD)	La Rioja, Argentina*	JQ779420	JQ779583	JQ779730
<i>Echinopsis haematantha</i> (Speg.) D.R.Hunt	B.O.Schlumpberger 175 (CORD)	Salta, Argentina*	JQ779480	JQ779642	JQ779782
<i>Echinopsis haematantha</i> (Speg.) D.R.Hunt	B.O.Schlumpberger 493 (CORD)	Salta, Argentina*	JQ779481	JQ779643	JQ779783
<i>Echinopsis hahniana</i> (Backeb.) R.S.Wallace	B.O.Schlumpberger x85 (M)	Northeast Paraguay	JQ779426	JQ779588	JQ779734
<i>Echinopsis hertrichiana</i> (Backeb.) D.R.Hunt	B.O.Schlumpberger x34 (M) W.Rausch 414	Cuzco, Peru**	JQ779396	JQ779558	JQ779710
<i>Echinopsis huascha</i> (F.A.C.Weber) H.Friedrich & G.D.Rowley	B.O.Schlumpberger 374 (CORD)	La Rioja, Argentina*	JQ779409	JQ779571	JQ779721
<i>Echinopsis huascha</i> (F.A.C.Weber) H.Friedrich & G.D.Rowley	B.O.Schlumpberger 351 (CORD)	La Rioja, Argentina*	JQ779408	JQ779570	
<i>Echinopsis huascha</i> subsp. <i>robusta</i> (Rausch) M.Lowry	B.O.Schlumpberger 519 (CORD)	Catamarca, Argentina*	JQ779410	JQ779572	JQ779722
<i>Echinopsis jajoiana</i> (Backeb.) Blossf.	B.O.Schlumpberger x88 (M) W.Rausch 213	Jujuy, Argentina**	JQ779467	JQ779629	JQ779771
<i>Echinopsis jajoiana</i> (Backeb.) Blossf.	B.O.Schlumpberger x79 (M) W.Rausch 815 (<i>Lobivia jajoiana</i> var. <i>fleischeriana</i> Backeb.)	Jujuy, Argentina**	JQ779468	JQ779630	JQ779772
<i>Echinopsis lageniformis</i> (C.F.Först.) H.Friedrich & G.D.Rowley	B.O.Schlumpberger x39 (M)	Bolivia	JQ779449	JQ779611	JQ779755

TABLE 2. Continued.

Species	DNA source	Geographic origin of sample or distribution	<i>trnS-trnG</i> intergenic spacer	<i>trnL-trnF</i> intergenic spacer	<i>rpl16</i> intron
<i>Echinopsis lamprochlora</i> (Lem.) F.A.C.Weber ex H.Friedrich & Glaetzle	B.O.Schlumpberger 318 (CORD)	Córdoba, Argentina*	JQ779416	JQ779578	JQ779728
<i>Echinopsis lateritia</i> Gürke	B.O.Schlumpberger x126 (M) W.Rausch 490	Chuquisaca, Bolivia**	JQ779398	JQ779560	JQ779712
<i>Echinopsis leucantha</i> (Gillies ex Salm-Dyck) Walp.	B.O.Schlumpberger 324 (CORD)	Córdoba, Argentina*	JQ779443	JQ779605	JQ779749
<i>Echinopsis leucantha</i> (Gillies ex Salm-Dyck) Walp.	B.O.Schlumpberger 329 (CORD)	San Luis, Argentina*	JQ779444	JQ779606	JQ779750
<i>Echinopsis leucantha</i> (Gillies ex Salm-Dyck) Walp.	B.O.Schlumpberger 382C (CORD)	Catamarca, Argentina*	JQ779442	JQ779604	JQ779748
<i>Echinopsis lobivoides</i> Backeb.	B.O.Schlumpberger 422 (CORD)	Catamarca, Argentina*	JQ779419	JQ779581	JQ779729
<i>Echinopsis mamillosa</i> Gürke	B.O.Schlumpberger x38 (M)	South Bolivia	JQ779401	JQ779563	JQ779715
<i>Echinopsis marsoneri</i> Werderm.	B.O.Schlumpberger x94 (M) D.Hardy 373	Jujuy, Argentina**	JQ779466	JQ779628	JQ779770
<i>Echinopsis maximiliana</i> Heyder ex A.Dietr.	B.O.Schlumpberger 621A (LPB)	La Paz, Bolivia*	JQ779391	JQ779553	JQ779707
<i>Echinopsis mirabilis</i> Speg.	V.Beyer & B.O.Schlumpberger x35 (M)	Dry Chaco, Argentina	JQ779445	JQ779607	JQ779751
<i>Echinopsis obrepanda</i> (Salm-Dyck) K.Schum.	B.O.Schlumpberger x132 (M)	Bolivia	JQ779376	JQ779538	JQ779695
<i>Echinopsis obrepanda</i> (Salm-Dyck) K.Schum.	B.O.Schlumpberger 629A (LPB)	Cochabamba, Bolivia*	JQ779377	JQ779539	JQ779696
<i>Echinopsis obrepanda</i> K.Schum.	B.O.Schlumpberger 686A (LPB)	Santa Cruz, Bolivia*	JQ779375	JQ779537	JQ779694
<i>Echinopsis obrepanda</i> K.Schum.	B.O.Schlumpberger 713A (LPB)	Santa Cruz, Bolivia*	JQ779379	JQ779541	JQ779698
<i>Echinopsis oligotricha</i> (Cárdenas) M.Lowry	B.O.Schlumpberger 638 (LPB)	Cochabamba, Bolivia*	JQ779397	JQ779559	JQ779711
<i>Echinopsis oxygona</i> (Link) Zucc.	B.O.Schlumpberger x01 (M) N.Gerloff 114	Rio Grande do Sul, Brazil**	JQ779483	JQ779645	
<i>Echinopsis oxygona</i> (Link) Zucc.	B.O.Schlumpberger x06 (M) L.Bercht 892	Rio Grande do Sul, Brazil**	JQ779484	JQ779646	JQ779785
<i>Echinopsis</i> cf. <i>pachanoi</i> (Britton & Rose) H.Friedrich & G.D.Rowley	B.O.Schlumpberger 721 (LPB)	Santa Cruz, Bolivia*	JQ779451	JQ779613	JQ779757
<i>Echinopsis pachanoi</i> (Britton & Rose) H.Friedrich & G.D.Rowley	B.O.Schlumpberger x78 (M)	Ecuador, Peru	JQ779450	JQ779612	JQ779756
<i>Echinopsis pentlandii</i> Salm-Dyck	B.O.Schlumpberger 622 (LPB)	La Paz, Bolivia*	JQ779388	JQ779550	JQ779704
<i>Echinopsis pereziensis</i> Cárdenas	B.O.Schlumpberger x95 (M) K.Knize 933	Santa Cruz, Bolivia	JQ779406	JQ779568	JQ779719
<i>Echinopsis pojoensis</i> Cárdenas	B.O.Schlumpberger x32 (M)	Cochabamba, Bolivia	JQ779374	JQ779536	
<i>Echinopsis pugionacantha</i> Rose & Boed.	B.O.Schlumpberger 566 (CORD)	Jujuy, Argentina*	JQ779385	JQ779547	JQ779702
<i>Echinopsis rojasii</i> Cárdenas	B.O.Schlumpberger 647 (LPB)	Santa Cruz, Bolivia*	JQ779378	JQ779540	JQ779697
<i>Echinopsis rowleyi</i> H.Friedrich (= <i>Lobivia grandiflora</i> Britton & Rose)	B.O.Schlumpberger 391 (CORD)	Catamarca, Argentina*	JQ779417	JQ779579	
<i>Echinopsis saltensis</i> Speg.	B.O.Schlumpberger x50 (M)	Salta & Tucuman, Argentina	JQ779435	JQ779597	JQ779741
<i>Echinopsis saltensis</i> Speg.	B.O.Schlumpberger 163B (CORD)	Salta, Argentina*	JQ779436	JQ779598	JQ779742
<i>Echinopsis schickendantzii</i> F.A.C.Weber	B.O.Schlumpberger 538 (CORD)	Jujuy, Argentina*	JQ779423	JQ779585	
<i>Echinopsis schieliana</i> F.A.C.Weber	B.O.Schlumpberger x124 (M) W.Rausch 205 (<i>Lobivia schieliana</i> var. <i>quiabayensis</i> (Rausch) Rausch)	La Paz, Bolivia**	JQ779392	JQ779554	JQ779708
<i>Echinopsis schreiteri</i> (A.Cast.) Werderm.	B.O.Schlumpberger 227 (CORD)	Tucuman, Argentina*	JQ779433	JQ779595	JQ779740
<i>Echinopsis smrziiana</i> Backeb.	B.O.Schlumpberger x02 (M) J. & B.Piltz 177A	Salta, Argentina**	JQ779432	JQ779594	JQ779739
<i>Echinopsis</i> sp.	B.O.Schlumpberger 652 (LPB)	Santa Cruz, Bolivia*	JQ779754	JQ779448	JQ779610
<i>Echinopsis</i> sp.	B.O.Schlumpberger 717 (LPB)	Cochabamba, Bolivia*	JQ779753	JQ779447	JQ779609
<i>Echinopsis strigosa</i> (Salm-Dyck) H.Friedrich & G.D.Rowley	B.O.Schlumpberger 343 (CORD)	La Rioja, Argentina*	JQ779414	JQ779576	JQ779726
<i>Echinopsis subdenudata</i> Cárdenas	B.O.Schlumpberger x25 (M)	Tarija, Bolivia	JQ779373	JQ779535	
<i>Echinopsis sucrensis</i> Cárdenas	B.O.Schlumpberger x41 (M) W.Rausch 483	Potosí, Bolivia**	JQ779405	JQ779567	
<i>Echinopsis tacaquirensis</i> (Vaupel) H.Friedrich & G.D.Rowley	B.O.Schlumpberger 118 (CORD, M)	Potosí, Bolivia*	JQ779407	JQ779569	JQ779720
<i>Echinopsis tarijensis</i> (Vaupel) H.Friedrich & G.D.Rowley	B.O.Schlumpberger 562 (CORD)	Jujuy, Argentina*	JQ779430	JQ779592	JQ779738
<i>Echinopsis tarijensis</i> subsp. <i>bertramiana</i> (Backeb.) M.Lowry	B.O.Schlumpberger 631 (LPB)	Cochabamba, Bolivia*	JQ779428	JQ779590	JQ779736
<i>Echinopsis tegeleriana</i> (Backeb.) D.R.Hunt	B.O.Schlumpberger x66 (M) W.Rausch 443	Ayacucho, Peru**	JQ779393	JQ779555	
<i>Echinopsis terscheckii</i> (Parmentier ex Pfeiff.) H.Friedrich & G.D.Rowley	B.O.Schlumpberger 354 (CORD)	La Rioja, Argentina*	JQ779488	JQ779650	JQ779788

TABLE 2. Continued.

Species	DNA source	Geographic origin of sample or distribution	<i>trnS-trnG</i> intergenic spacer	<i>trnL-trnF</i> intergenic spacer	<i>rpl16</i> intron
<i>Echinopsis thelegona</i> (F.A.C.Weber) H.Friedrich & G.D.Rowley	B.O.Schlumpberger 208 (CORD, M)	Salta, Argentina*	JQ779415	JQ779577	JQ779727
<i>Echinopsis thelegonoides</i> (Speg.) H.Friedrich & G.D.Rowley	B.O.Schlumpberger 543 (CORD)	Jujuy, Argentina*	JQ779427	JQ779589	JQ779735
<i>Echinopsis tiegeliana</i> (Wessner) D.R.Hunt	V.Beyer & B.O.Schlumpberger x82 (M) W.Rausch 323	Tarija, Bolivia**	JQ779389	JQ779551	JQ779705
<i>Echinopsis tubiflora</i> (Pfeiff.) Zucc. ex K.Schum.	B.O.Schlumpberger 106 (CORD)	Tucuman, Argentina*	JQ779479	JQ779641	JQ779781
<i>Echinopsis tubiflora</i> (Pfeiff.) Zucc. ex K.Schum.	B.O.Schlumpberger 386 (CORD)	Salta, Argentina*	JQ779477	JQ779639	JQ779779
<i>Echinopsis tubiflora</i> (Pfeiff.) Zucc. ex K.Schum.	B.O.Schlumpberger 387 (CORD)	Salta, Argentina*	JQ779478	JQ779640	JQ779780
<i>Echinopsis vasquezii</i> (Rausch) G.D.Rowley	B.O.Schlumpberger 722 (LPB)	Santa Cruz, Bolivia*	JQ779425	JQ779587	JQ779733
<i>Echinopsis vasquezii</i> (Rausch) G.D.Rowley	B.O.Schlumpberger x86 (M)	Cochabamba/ Santa Cruz, Bolivia	JQ779424	JQ779586	JQ779732
<i>Echinopsis volliana</i> (Backeb.) H.Friedrich & G.D.Rowley	B.O.Schlumpberger 635 (LPB)	Cochabamba, Bolivia*	JQ779429	JQ779591	JQ779737
<i>Echinopsis walteri</i> R.Kiesling (H.Friedrich & Glaetzle)	B.O.Schlumpberger x11 (M) J. & B.Piltz 177	Salta, Argentina**	JQ779431	JQ779593	
<i>Echinopsis yuquina</i> D.R.Hunt (incl. <i>Lobivia rauschii</i> Zecher)	B.O.Schlumpberger x81 (M) F.Ritter 807	Chuquisaca, Bolivia**	JQ779399	JQ779561	JQ779713
<i>Espostoa guentheri</i> (Kupper) Buxb. ex Eggl (= <i>Vatricania guentheri</i> (Kupper) Backeb., GT)	B.O.Schlumpberger x70 (M)	Central Bolivia	JQ779495	JQ779657	JQ779795
<i>Espostoa lanata</i> (Kunth) Britton & Rose, GT	B.O.Schlumpberger x54 (M)	North Peru, south Ecuador	JQ779454	JQ779616	JQ779760
<i>Espostoa dybowski</i> (Rol.-Goss.) Buxb., GT	B.O.Schlumpberger x112 (M)	Bahia, Brazil	JQ779509	JQ779671	JQ779807
<i>Facheroa ulei</i> (Gürke) Werderm., GT	B.O.Schlumpberger x109 (M)	Bahia, Brazil	JQ779527	JQ779689	
<i>Gymnocalycium andreae</i> (Boed.) Backeb.	B.O.Schlumpberger x84 (M)	Córdoba & San Luis, Argentina	JQ779512	JQ779674	JQ779810
<i>Gymnocalycium mostii</i> (Gürke) Britton & Rose	B.O.Schlumpberger 305 (CORD)	Córdoba, Argentina*	JQ779513	JQ779675	JQ779811
<i>Haageocereus pseudomelanostele</i> (Werderm. & Backeb.) Backeb., GT	B.O.Schlumpberger x56 (M)	Central Peru	JQ779456	JQ779618	JQ779762
<i>Harrisia gracilis</i> (Miller) Britton, GT	B.O.Schlumpberger x120 (M)	Jamaica	JQ779492	JQ779654	JQ779792
<i>Harrisia martinii</i> (Labor.) Britton & Rose	B.O.Schlumpberger x58 (M)	Argentina, Paraguay	JQ779493	JQ779655	JQ779793
<i>Harrisia pomanensis</i> (F.A.C.Weber) Britton & Rose	B.O.Schlumpberger 119 (CORD)	Salta, Argentina*	JQ779491	JQ779653	JQ779791
<i>Harrisia tetraacantha</i> (Labor.) D.R.Hunt	B.O.Schlumpberger 643 (LPB)	Cochabamba, Bolivia*	JQ779490	JQ779652	JQ779790
<i>Harrisia tortuosa</i> (J.Forbes ex Otto & A.Dietr.) Britton & Rose	B.O.Schlumpberger x53 (M)	Argentina, Uruguay, Paraguay; Bolivia?	JQ779494	JQ779656	JQ779794
<i>Lasiocereus fulvus</i> F.Ritter	B.O.Schlumpberger x59 (M)	Amazonas, Peru	JQ779525	JQ779687	JQ779821
<i>Leocereus bahiensis</i> Britton & Rose, GT	Eggl 1283 (ZSS)	Bahia, Brazil*	JQ779510	JQ779672	JQ779808
<i>Matucana haynei</i> (Otto ex Salm-Dyck) Britton & Rose, GT	B.O.Schlumpberger x118 (M)	Peru	JQ779460	JQ779622	JQ779765
<i>Matucana haynei</i> subsp. <i>hystrix</i> (Rauh & Backeb.) Mottram (incl. <i>Matucana</i> <i>multicolor</i> Rauh & Backeb.)	B.O.Schlumpberger x119 (M)	Peru	JQ779459	JQ779621	
<i>Matucana intertexta</i> F.Ritter	B.O.Schlumpberger x60 (M)	Peru	JQ779458	JQ779620	JQ779764
<i>Micranthocereus densiflorus</i> Buining & Brederoo	B.O.Schlumpberger x69 (M)	Bahia, Brazil	JQ779524	JQ779686	JQ779820
<i>Mila caespitosa</i> Britton & Rose, GT	B.O.Schlumpberger x47 (M)	Central Peru	JQ779457	JQ779619	JQ779763
<i>Neowerdermannia vorwerkii</i> Frič, GT	B.O.Schlumpberger x74 (M)	Northern Argentina & Bolivia	JQ779528	JQ779690	JQ779823
<i>Oreocereus celsianus</i> (Lem. ex Salm-Dyck) Riccob., GT	B.O.Schlumpberger 569 (CORD)	Jujuy, Argentina*	JQ779464	JQ779626	JQ779769
<i>Oreocereus trollii</i> (Kupper) Backeb.	B.O.Schlumpberger 559 (CORD)	Jujuy, Argentina*	JQ779465	JQ779627	
<i>Oroya peruviana</i> (K.Schum.) Britton & Rose, GT	B.O.Schlumpberger x99 (M)	Central Peru	JQ779461	JQ779623	JQ779766
<i>Praeocereus euchlorus</i> F.A.C.Weber (N.P.Taylor)	B.O.Schlumpberger 700 (LPB)	Santa Cruz, Bolivia*	JQ779504	JQ779666	JQ779802
<i>Pygmaeocereus bieblii</i> var. <i>kuehhasii</i> Diers	B.O.Schlumpberger x46 (M)	Central Peru	JQ779452	JQ779614	JQ779758
<i>Pygmaeocereus bylesianus</i> Andreae & Backeb., GT	B.O.Schlumpberger x115 (M)	Southern Peru	JQ779453	JQ779615	JQ779759
<i>Rauhocereus riosaniensis</i> Backeb., GT	B.O.Schlumpberger x110 (M)	Northern Peru	JQ779455	JQ779617	JQ779761

TABLE 2. Continued.

Species	DNA source	Geographic origin of sample or distribution	<i>trnS-trnG</i> intergenic spacer	<i>trnL-trnF</i> intergenic spacer	<i>rpl16</i> intron
<i>Rebutia arenacea</i> Cárdenas (= <i>Sulcorebutia arenacea</i> (Cárdenas) F.Ritter)	B.O.Schlumpberger x76 (M)	Cochabamba, Bolivia	JQ779522	JQ779684	
<i>Rebutia atrovirens</i> (Backeb.) Pilbeam (= <i>Mediolobivia atrovirens</i> (Backeb.) Britton & Rose)	B.O.Schlumpberger x71 (M) H.Joschko 75	Jujuy, Argentina**	JQ779517	JQ779679	JQ779815
<i>Rebutia fabrisii</i> Rausch	B.O.Schlumpberger x104 (M) W.Rausch 688	Salta, Argentina**	JQ779516	JQ779678	JQ779814
<i>Rebutia haagei</i> Fric & Schelle (incl. <i>Mediolobivia pygmaea</i> (R.E.Fr.) Krainz, <i>Rebutia pygmaea</i> (R.E.Fr.) Britton & Rose)	B.O.Schlumpberger x75 (M) W.Rausch 333	Jujuy, Argentina**	JQ779519	JQ779681	JQ779817
<i>Rebutia heliosa</i> Rausch	B.O.Schlumpberger x97 (M) A.B.Lau 405	Tarija, Bolivia**	JQ779520	JQ779682	JQ779818
<i>Rebutia margarethae</i> Rausch (<i>R. padcayensis</i> Rausch)	B.O.Schlumpberger x73 (M) A.B.Lau 550	Jujuy/Salta, Argentina**	JQ779514	JQ779676	JQ779812
<i>Rebutia minuscula</i> K.Schum., GT	B.O.Schlumpberger x108 (M)	Northern Argentina	JQ779515	JQ779677	JQ779813
<i>Rebutia muscula</i> F.Ritter & Thiele ex F.Ritter (= <i>Aylostera muscula</i> (F.Ritter & Thiele ex F.Ritter) Backeb.; incl. <i>Rebutia fiebrigii</i> (Gürke) Britton & Rose)	B.O.Schlumpberger x98 (M) F.Ritter 753	Tarija, Bolivia**	JQ779521	JQ779683	JQ779819
<i>Rebutia neocumingii</i> (Backeb.) D.R.Hunt (<i>Weingartia neocumingii</i> Backeb.)	B.O.Schlumpberger x72 (M)	Bolivia, south-central Andes	JQ779523	JQ779685	
<i>Rebutia pygmaea</i> (R.E.Fr.) Britton & Rose (= <i>Mediolobivia pygmaea</i> (R.E.Fr.) Krainz)	B.O.Schlumpberger & G.Brokamp 670 (M)	Oruro, Bolivia*	JQ779518	JQ779680	JQ779816
<i>Samaipaticereus corroanus</i> Cárdenas, GT	B.O.Schlumpberger 720 (LPB)	Santa Cruz, Bolivia*	JQ779498	JQ779660	
<i>Stetsonia coryne</i> (Salm-Dyck) Britton & Rose, GT	B.O.Schlumpberger x57 (M)	Chaco of Argentina, Bolivia and Paraguay	JQ779508	JQ779670	JQ779806
<i>Weberbauerocereus weberbaueri</i> (K.Schum. ex Vaupel) Backeb., GT	B.O.Schlumpberger x55 (M)	Southwestern Peru	JQ779496	JQ779658	JQ779796
<i>Yungasocereus inquisivensis</i> (Cárdenas) F.Ritter ex Eggl, GT	B.O.Schlumpberger x121 (M)	Bolivia	JQ779497	JQ779659	JQ779797

Notes: * wild-collected, ** samples from cultivated plants of documented origin

Riccob.), *Denmoza* Britton & Rose, *Espostoa* Britton & Rose (including *Vatricania* Backeb.), *Haageocereus* Backeb., *Harrisia* Britton, *Matucana* Britton & Rose, *Mila* Britton & Rose, *Oreocereus* (A.Berger) Riccob., *Oroya* Britton & Rose, *Pygmaeocereus* H.Johnson & Backeb., *Rauhocereus* Backeb., *Samaipaticereus* Cárdenas, *Weberbauerocereus* Backeb., and *Yungasocereus* F.Ritter, all of which are part of a well-supported clade (100% bootstrap support) interspersed with species of *Echinopsis* (Fig. 1A, B). Species previously assigned to *Lobivia*, i.e., species with diurnal flowers, *Trichocereus*, i.e., columnar species, or *Echinopsis* s.str., i.e., globular species with funnel-shaped flowers of nocturnal anthesis, do not form clades. The genera *Espostoa*, *Cleistocactus* s.l. (i.e., sensu Hunt, 1999, 2006) and *Matucana* are polyphyletic (Fig. 1), and *Acanthocalycium* is paraphyletic since *Echinopsis leucantha* is embedded among its species. Our sampling also reveals a few taxonomic problems at the species level: thus, *E. aurea* is polyphyletic, with the isolated northernmost form (*E. aurea* var. *callochrysea*) close to *E. tubiflora*.

Chromosome numbers—Table 3 lists new chromosome counts for numerous *Echinopsis* (sub) species or varieties included in the phylogeny as well as for 11 outgroup species from eight genera. The basic chromosome number is $2x = 22$. We discovered six cases of tetraploidy of which two involve intraspecific variation between diploidy and tetraploidy. In

the *Helianthocereus* clade, tetraploids occurred in *E. thelegonoides* and *E. candicans* (Fig. 1B). In the *Lobivia* clade, we found diploids and tetraploids in *E. tiegeliana*, and in the *Oreocereus* clade we found tetraploids in *Espostoa* and *Oreocereus* itself (Fig. 1, Table 3). In *Rebutia* K.Schum., we found tetraploidy in a species previously assigned to *Mediolobivia* Backeb.

DISCUSSION

We now address the main questions posed in this study, namely (1) Is *Echinopsis* in the broad sense monophyletic? (2) What is the level of plasticity of growth habit and pollination mode, characters that have been used to define clades in *Echinopsis* sensu lato? And (3) How common are ploidy changes in the *Echinopsis* alliance and are they clustered in certain subclades?

Monophyly of *Echinopsis* sensu lato—*Echinopsis* as circumscribed by Anderson (2001) or Hunt (2006) would become monophyletic with the inclusion of *Acanthocalycium* (part of *Echinopsis* in Hunt, 2006, but not in Anderson, 2001 and 2005), *Arthrocereus*, *Cephalocleistocactus*, *Cleistocactus* (including *Borzicactus*), *Denmoza*, *Espostoa* (including *Vatricania*), *Haageocereus*, *Harrisia*, *Matucana*, *Mila*, *Oreocereus*,

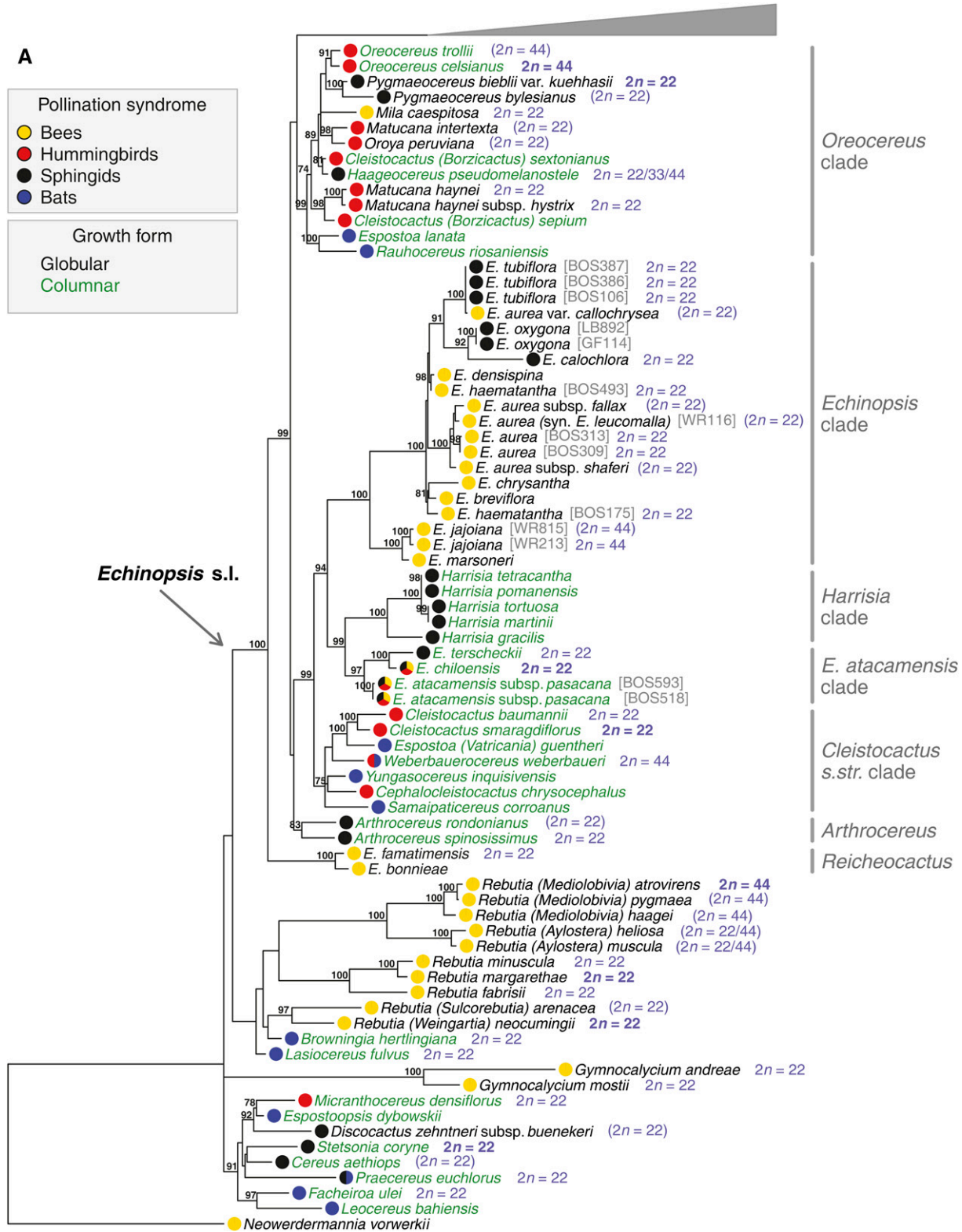


Fig. 1. (A, B). Maximum likelihood (ML) phylogram for 144 taxa of *Echinopsis* and relatives obtained from 3866 aligned nucleotides of chloroplast DNA. Numbers at nodes indicate ML bootstrap support >70% from 100 replicates. Known or putative pollinators are indicated by pie diagrams, with the color codes explained in the inset; sphingid-adapted taxa with bees as backup pollinators are treated as sphingid-pollinated. Growth form is indicated by different taxon name colors as explained in the inset. New or previously published chromosome counts are shown as follows: Bold numbers indicate counts that were made from the same plant as was sequenced; numbers in parentheses refer to counts made from a closely related taxon; the remaining numbers refer to counts from the same taxon but not the sequenced individual (see Table 2 for sources). Collection numbers behind plant names refer to vouchers cited in Table 1; they are given only for species represented by multiple accessions.

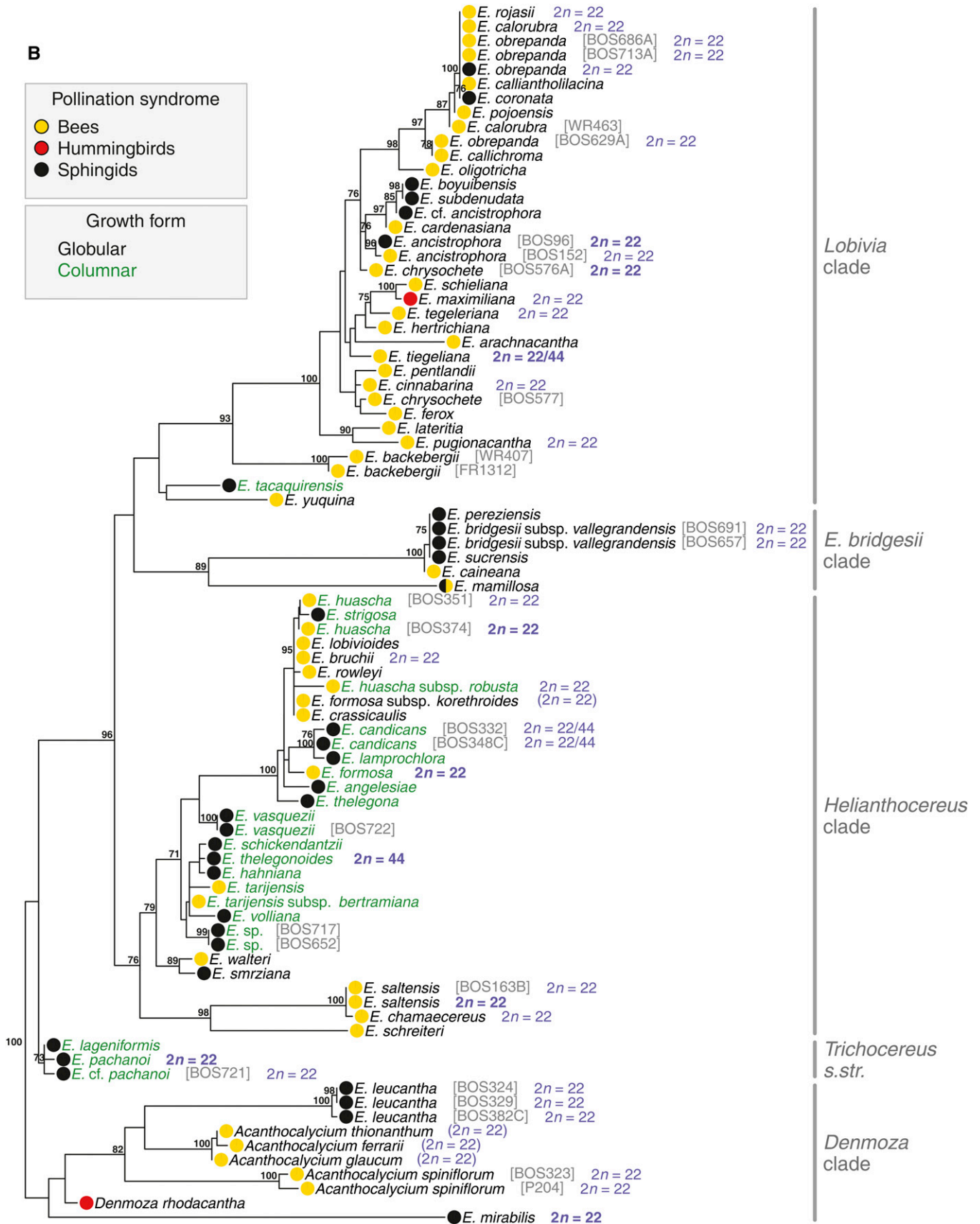


Fig. 1. Continued.

TABLE 3. Chromosome numbers in *Echinopsis* and related Trichocereae. Authors for taxon names can be found in Table 1, except for taxa not sequenced for which they are listed here. Abbreviations: BGM—Botanical Garden Munich. Collectors' acronyms are BOS: B. O. Schlumpberger, DH: D. Herzog, ES: E. Scholz, FR: F. Ritter, GF: N. Gerloff, HJW: H. J. Wittau, HUN: C. Hunkeler, KK: K. Kniže, LB: L. Bercht, LK: L. Kunte, MN: M. Winberg, P: J. & B. Piltz, UE: U. Eggli, WR: W. Rausch, and many individual collections are also cited in Table 1. Details for those not cited there are available online under <http://ralph.cs.cf.ac.uk/cacti/fieldno.html>.

Species	Infraspecific taxa and synonyms	2n	No. of counts	Origin of material studied or reference
<i>Echinopsis ancistrophora</i>		22	8	BGM: BOS96, P231, MN125, ES80
<i>E. aurea</i>		22	3	BGM: BOS313
<i>E. aurea</i>	<i>E. aurea</i> Britton & Rose var. <i>albiflora</i> (Rausch) J.Ullmann	22	5	BGM: BOS596
<i>E. aurea</i>	<i>Lobivia cylindracea</i> Backeb.	22	?	Diers, 2008a
<i>E. backebergii</i> Werderm. subsp. <i>wrightiana</i> (Backeb.) M.Lowry		44	?	Diers, 2008a
<i>E. bridgesii</i> subsp. <i>vallegrandensis</i>	<i>E. cotacajesii</i> Cárdenas	22	5	BGM: WR604
<i>E. bridgesii</i> subsp. <i>vallegrandensis</i>	<i>E. cochabambensis</i> Backeb.	22?	?	Diers, 2008a
<i>E. bruchii</i>		22	?	Diers, 2008a
<i>E. calliantholilacina</i>		22	3	BGM: WR63
<i>E. callichroma</i>		22	3	BGM: WR461
<i>E. calochlora</i>		22	?	Diers, 2008a
<i>E. calorubra</i>	<i>E. rauschii</i> Friedrich var. <i>megalcephala</i> Rausch	22	5	BGM: WR272
<i>E. candicans</i>		22	5	BGM: BOS404
<i>E. candicans</i>		22/44	17	BGM: BOS380
<i>E. candicans</i>		44	27	BGM: BOS328
<i>E. candicans</i>		44	?	Las Peñas et al., 2009
<i>E. chamaecereus</i>	<i>Chamaecereus silvestrii</i>	22	?	Ross, 1981
<i>E. chiloensis</i>		22	3	BGM: BOSx77
<i>E. chiloensis</i>		22	?	Katagiri, 1952
<i>E. chrysochete</i>		22	5	BGM: BOS576
<i>E. chrysochete</i>	<i>Lobivia minutiflora</i>	22	4	BGM: BOS577
<i>E. cinnabarina</i>	<i>Lobivia pseudocinnabarina</i> Backeb.	22	?	Diers, 2008a
<i>E. coronata</i>		22	?	Diers, 2008a
<i>E. crassicaulis</i>		22	9	BGM: BOSx23
<i>E. densispina</i>		22	3	BGM: ES31, ES37
<i>E. deserticola</i>	<i>Trichocereus fulvilanus</i> F.Ritter	22	?	Diers, 2008a
<i>E. famatimensis</i>	<i>Lobivia pectinifera</i> Wessner	22	?	Diers, 2008a
<i>E. formosa</i>	<i>E. formosa</i> subsp. <i>formosa</i>	22	2	BGM: BOS460
<i>E. formosa</i>	<i>E. formosa</i> (Pfeiff.) Jacobi ex Salm-Dyck subsp. <i>rosarioana</i> (Rausch) M.Lowry	22	3	BGM: WR528
<i>E. haematantha</i>		22	5	BGM: ES66
<i>E. haematantha</i>	<i>Lobivia amblayensis</i> Rausch	22	?	Diers, 2008a
<i>E. haematantha</i>	<i>Lobivia amblayensis</i> Rausch var. <i>albispina</i> Rausch	22	?	Diers, 2008a
<i>E. huascha</i>		22	10	BGM: BOS368, BOS374
<i>E. huascha</i>		22	?	Diers, 2008a
<i>E. huascha</i> subsp. <i>robusta</i>		22	16	BGM: BOS380
<i>E. jajoiana</i>		44	?	Diers, 2008a
<i>E. leucantha</i>		22	5	BGM: BOS329
<i>E. maximiliana</i>		22	3	BGM: HJW189
<i>E. maximiliana</i>		22	?	Diers, 2008a
<i>E. maximiliana</i>	<i>Lobivia corbula</i> Britton & Rose	22	9	BGM: ES133
<i>E. maximiliana</i>	<i>Lobivia intermedia</i> Rausch	22	1	BGM: LK37
<i>E. maximiliana</i>	<i>Lobivia miniatiflora</i> F.Ritter	22	8	BGM: BOS676 (LPB)
<i>E. mirabilis</i>		22	3	BGM: BOSx35
<i>E. mirabilis</i>		22	?	Diers, 2008a
<i>E. obrepanda</i>		22	?	Diers, 2008a
<i>E. oxygona</i>	<i>E. eyriesii</i> Pfeiff. & Otto	22	?	Sato, 1958; Katagiri, 1952; Diers, 2008a
<i>E. oxygona</i>	<i>eyriesii</i>	22	2–10	Arakaki et al., 2007
<i>E. oxygona</i>	<i>E. multiplex</i> (Pfeiff.) Zucc. ex Pfeiff. & Otto	22	?	Sato, 1958
<i>E. oxygona</i>		22	?	Katagiri, 1952
<i>E. oxygona</i>	<i>E. turbinata</i> Pfeiff. & Otto	22	?	Diers, 2008a
<i>E. pachanoi</i>		22	3	BGM: BOSx78
<i>E. pereziiensis</i>		22?	?	Diers, 2008a
<i>E. pugionacantha</i>		22	5	BGM: BOS566
<i>E. rhodotricha</i> K. Schum.	<i>E. klingleriana</i> Cárdenas	22	?	Diers, 2008a
<i>E. rojasii</i>		22	?	Diers, 2008a
<i>E. rowleyi</i>	<i>Lobivia grandiflora</i> Britton & Rose	22	?	Diers, 2008a
<i>E. saltensis</i>		22	5	BGM: BOSx50
<i>E. saltensis</i>	<i>Lobivia nealeana</i> Backeb.	22	?	Diers, 2008a
<i>E. spachiana</i> (Lem.) H. Friedrich & G. D. Rowley		22?	?	Diers, 2008a

TABLE 3. Continued.

Species	Intraspecific taxa and synonyms	2n	No. of counts	Origin of material studied or reference
<i>E. spachiana</i>		44	?	Katagiri, 1952
<i>E. tegeleriana</i>		22	?	Diers, 2008a
<i>E. terscheckii</i>		22	?	Diers, 2008a
<i>E. thelegona</i>		22	1	BGM: BOS208
<i>E. thelegonoides</i>		44	4	BGM: BOS543
<i>E. tiegeliana</i>		22/44	?	BGM: R323
<i>E. tiegeliana</i>		22	5	BGM: BOSx82
<i>E. tiegeliana</i>		22	14	BGM: WR84a
<i>E. tubiflora</i>		22	?	Katagiri, 1952; Sato, 1958; Diers, 2008a; Las Peñas et al., 2009
Other genera				
<i>Acanthocalycium spiniflorum</i>	<i>Acanthocalycium violaceum</i> (Werderm.) Backeb.	22	?	Diers, 2008a
<i>Acanthocalycium spiniflorum</i>		22	3	BGM: BOS401
<i>Acanthocalycium thionanthum</i>		22	6	BGM: ES9
<i>Arthrocereus</i> A. Berger, 2 taxa		22	?	Diers, 2008a
<i>Browningia candelaris</i> (Meyen) Britton & Rose		22	?	Diers, 2008a
<i>Cereus</i> Mill., 3 taxa		22	?	Sato, 1958
<i>Cereus</i> 5 taxa		22	?	Diers, 2008a
<i>Cereus</i> 4 taxa		22	?	Katagiri, 1952
<i>Cleistocactus baumannii</i>	<i>Cleistocactus</i> s.str.	22	?	Ross, 1981
<i>Cleistocactus icosagonus</i> F.A.C.Weber	<i>Borzicactus aurivillus</i> Britton & Rose	22	?	Katagiri, 1952; Sato, 1958
<i>Cleistocactus samaipatanus</i> (Cárdenas) D.R.Hunt	<i>Bolivocereus samaipatanus</i> Cárdenas	22	?	Diers, 2008a
<i>Cleistocactus smaragdiflorus</i>	<i>Cleistocactus</i> s.str.	22	5	BGM: BOS424
<i>Cleistocactus</i> Lem., 5 taxa	<i>Borzicactus</i> , <i>Loxanthocereus</i>	22/44	2–10	Arakaki et al., 2007
<i>Cleistocactus</i> 3 taxa	<i>Borzicactus</i>	22	?	Baker, 2002
<i>Cleistocactus</i> 3 taxa	<i>Cleistocactus</i> s.str.	22/44	?	Diers, 2008a
<i>Discocactus</i> Pfeiff., 2 taxa		22	?	Diers, 2008a
<i>Espostoa blossfeldiorum</i> (Werderm.) Buxb.		22	2–10	Arakaki et al., 2007
<i>Espostoa lanata</i>		22/44/66	2–10	Arakaki et al., 2007
<i>Espostoa</i> Britton & Rose, 2 taxa		22/44?	?	Diers, 2008a
<i>Espostoa melanosteale</i> (Vaupel) Borg subsp. <i>nana</i> (F.Ritter) G.J.Charles		22	4	Cultivated at BGM, no voucher
<i>Espostoa senilis</i> (F.Ritter) N.P.Taylor		22	2–10	Arakaki et al., 2007
<i>Espostoa</i> sp.		44	4	Cultivated at BGM, no voucher
<i>Facheiroa ulei</i>		22	?	Diers, 2008a
<i>Gymnocalycium</i> Pfeiff., 9 taxa		22	?	Diers, 2008a
<i>Gymnocalycium</i> 4 taxa		22	?	Katagiri, 1952
<i>Gymnocalycium</i> 30 taxa		22/44/66	?	Lambrou and Till, 1993
<i>Gymnocalycium</i> 2 taxa		22/44	?	Ross, 1981
<i>Haageocereus</i> Backeb., 11 taxa	17 taxa fide Arakaki et al., 2007	22/33/44	2–10	Arakaki et al., 2007
<i>Lasiocereus fulvus</i>		22	2–10	Arakaki et al., 2007
<i>Lasiocereus rupicola</i> F.Ritter		22	2–10	Arakaki et al., 2007
<i>Matucana haynei</i>		22	2–10	Arakaki et al., 2007
<i>Matucana</i> Britton & Rose, 4 taxa		22	?	Diers, 2008a
<i>Micranthocereus densiflorus</i>		22	2	BGM: BOSx69
<i>Micranthocereus</i> Backeb., 3 taxa		22	?	Diers, 2008b
<i>Mila caespitosa</i>		22	2–10	Arakaki et al., 2007
<i>Oreocereus celsianus</i>		44	12	BGM: BOS569
<i>Oreocereus pseudofossulatus</i> D.R.Hunt	<i>Oreocereus. fossulatus</i> var. <i>gracilior</i> (K.Schum.) Backeb.	44	?	Diers, 2008b
<i>Oroya borchersii</i> (Boed.) Backeb.		22	?	Diers, 2008b
<i>Praecereus euchlorus</i>		22	?	Diers, 2008c
<i>Pygmaocereus bieblii</i> var. <i>kuehhasii</i>		22	6	BGM: BOSx46
<i>Rebutia</i> K. Schum., 3 taxa	<i>Aylostera</i>	22/44	?	Diers, 2008c
<i>Rebutia atrovirens</i>		44	6	BGM: J75
<i>Rebutia glomeriseta</i> Cárdenas	<i>Sulcorebutia mensesii</i> (Cárdenas) Backeb.	22	?	Diers, 2008c
<i>Rebutia minuscula</i>	<i>Rebutia marsoneri</i> Werderm. & <i>R. senilis</i> Backeb.	22?	?	Diers, 2008c
<i>Rebutia padcayensis</i> Rausch	<i>R. margarethae</i> Rausch	22	4	BGM: L550
<i>Rebutia neocumingii</i>	<i>Weingartia</i>	22	1	BGM: BOSx72
<i>Rebutia</i> 4 taxa	<i>Rebutia</i> , <i>Sulcorebutia</i>	22	?	Ross, 1981
<i>Stetsonia coryne</i>		22	5	BGM: BOSx57
<i>Weberbauerocereus</i> Backeb. 3 taxa		44/ca. 88	?	Diers, 2008c
<i>Weberbauerocereus weberbaueri</i>		44	2–10	Arakaki et al., 2007
<i>Weberbauerocereus</i> 2 taxa		44/88	2–10	Arakaki et al., 2007



Fig. 2. Examples for convergent evolution in *Echinopsis*. Floral adaptation to hawkmoth pollination in *E. ancistrophora* (A, *Lobivia* clade) and *E. tubiflora* (B, *Echinopsis* s.str. clade) and columnar growth in *E. tarijensis* (C, *Helianthocereus* clade) and *E. atacamensis* subsp. *pasacana* (D, *E. atacamensis* clade).

Oroya, *Pygmaeocereus*, *Rauhocereus*, *Samaipaticereus*, *Weberbauerocereus*, and *Yungasocereus*. Alternatively, *Echinopsis* will need to be divided into smaller, more homogeneous units, requiring the resurrection of generic names and transfers of species epithets. We now briefly discuss the main clades found in this study.

Echinopsis s.s. is well supported (100% bootstrap support; the type species is *E. oxygona*) and homogeneous in growth

form. Its sister group consists of the likewise well-supported *E. atacamensis* clade and the genus *Harrisia* (100% and 97% bootstrap, respectively, Fig. 1A), refuting suggestions that *Harrisia* might be part of the Hylocereae (A. Areces-Mallea, personal communication, cited in Anderson, 2001) or the Echinocereae (Barthlott and Hunt, 1993). Of the ca. 20 species of *Harrisia*, we sampled *H. gracilis* from the Caribbean and four species from central South America.

The *Cleistocactus* s.str. clade (Fig. 1A, 100% bootstrap) comprises the columnar cacti *Espostoa guentheri* (syn. *Vatricania*), *Samaipaticereus*, *Weberbauerocereus*, *Yungasocereus*, *Cephalocleistocactus*, and *Cleistocactus*. Species formerly placed in *Borzicactus* but transferred to *Cleistocactus* (Hunt, 2006) turn out not to belong there but instead to the *Oreocereus* clade (Fig. 1A), and future studies will have to investigate if other species transferred to *Cleistocactus* from *Winterocereus* (syn. *Winteria* and *Hildewintera*) and *Bolivocereus* also instead belong to *Borzicactus*. Most species in the *Cleistocactus* clade are adapted to pollination by bats (*Espostoa*, *Samaipaticereus*, and *Yungasocereus*) or hummingbirds (*Cephalocleistocactus* and *Cleistocactus*), and *Weberbauerocereus* species are visited, and apparently pollinated, by both bats and hummingbirds (Sahley, 1996). That *Espostoa* (*Vatricania*) *guentheri* is not grouping with *E. lanata*, the type species of *Espostoa*, fits with an anatomical study that found it to have “the greatest number of unusual features” among six species of *Espostoa* studied (Mauseth, 1999: p. 36). One of these unusual features, a two-layered hypodermis with clusters of columnar cells, resembles the hypodermis of *Cleistocactus strausii* and *Weberbauerocereus albus*, which are related to species that group with *Espostoa* (*Vatricania*) *guentheri* in our study.

Next closest is the *Reicheocactus* clade (Fig. 1A). The relatively early-diverging species *E. famatimensis* and *E. bonnieae* have long troubled Cactaceae taxonomists. First described as *Echinocactus famatimensis* (Spegazzini, 1921), the former was subsequently transferred to *Rebutia* (Spegazzini, 1923) and *Lobivia* (Britton and Rose, 1919–1923), and in 1942 to the new genus *Reicheocactus* Backeb. (as *Reicheocactus pseudoreicheanus*). In recent years, it was usually included in *Echinopsis* (Anderson, 2001; Hunt 2006; but see Kiesling et al., 2001, who returned it to *Lobivia*). *Echinopsis bonnieae* likewise has been moved between *Lobivia* (as *Lobivia bonnieae* Halda & Horáček, 1999) and *Echinopsis*.

Another well-supported group is the *Oreocereus* clade (Fig. 1A, 99% bootstrap), which includes the type species of *Oreocereus* plus the eight genera *Borzicactus* (here referred to *Cleistocactus*, according to Anderson, 2001 and Hunt, 2006), *Espostoa*, *Haageocereus*, *Matucana*, *Mila*, *Oroya*, *Pygmaeocereus*, and *Rauhocereus*, with a total of about 60 species (Hunt, 2006).

Next in the tree comes the *Denmoza* clade (Fig. 1B), which contains the monotypic *Denmoza rhodacantha*, *E. mirabilis* (syn. *Setiechinopsis*, monotypic as well), *E. leucantha*, and *Acanthocalycium*. *Acanthocalycium* was synonymized under *Echinopsis* s.l. by Hunt (2006), but was kept separate by Anderson (2001, 2005). All these taxa are endemic to northwestern Argentina, and their flowers are adapted to pollination by hummingbirds (*Denmoza*), bees (*Acanthocalycium*), or moths (*E. leucantha* and *E. mirabilis*, the latter unique in its short life-cycle, flowers closing before dawn, and autogamy; Kiesling and Ferrari, 2005).

The *Trichocereus* s.str. clade (Fig. 1B) is here represented by *Echinopsis pachanoi* and *E. lageniformis*, both columnar species characterized by few, blunt ribs, poor spination, and a moderate stem diameter (usually <20 cm). The type species of *Trichocereus*, *E. macrogona* [*Cereus macrogonus* Salm-Dyck; *Trichocereus macrogonus* (Salm-Dyck) Riccob.], is based on a cultivated specimen of unknown origin and appears related to *E. pachanoi* (Anderson, 2005; R. Kiesling, CONICET, Mendoza, Argentina, personal communication). The taxonomy is further complicated by *E. pachanoi*, a species long cultivated and hence widely distributed (“San Pedro cactus”).

The *Helianthocereus* clade (Fig. 1B) consists of species of mostly columnar to rarely globular growth with flowers adapted to pollination by bees or hawkmoths. Friedrich (1974) and Friedrich and Glätzle (1983), in a study of seed morphology for which they sampled ca. 20 of the species from this clade, found that all had seeds with an obliquely placed oval hilum surrounded by flat testa cells. Next in the tree comes the *E. bridgesii* clade (89% bootstrap support), which consists of five species from central Bolivia and northern Argentina with globular to short-columnar growth and flowers suggesting either bee or moth pollination. The recently described *Lobivia krahn-juckeri* (Diers, 2009) may also belong here. A final group worth discussing is the *Lobivia* clade (Fig. 1B), with a well-supported core clade (93% bootstrap support) and an unresolved group of early-branching species. Typical “lobivoid” species are small, mostly globular plants with short diurnal flowers. However, the *Lobivia* clade also includes species with long (>20 cm) white flowers adapted to pollination by sphingids (Schlumpberger and Raguso, 2008; Schlumpberger et al., 2009; Fig. 2A). Examples for those are *E. ancistrophora*, *E. obrepanda*, and *E. rojasii*.

In sum, the molecular data presented here conflict in large parts with previous taxonomic classifications of *Echinopsis* and its relatives (Anderson, 2001, 2005; Hunt, 2006). Morphological characters other than those traditionally used will have to be found to circumscribe natural taxonomic groups in the Trichocereae, but large morphological differences may be difficult to find since the entire Trichocereinae/Cereinae clade is only 7.5–6.5 Myr old (Arakaki et al., 2011).

Relative phylogenetic plasticity of growth habit and pollination syndromes—In most of the clades revealed by our molecular data, growth form (globular vs. columnar) is phylogenetically conserved. The *Helianthocereus* clade (Fig. 1B), however, comprises globular species (*E. crassicaulis*, *E. lobivoides*), barrel cacti (*E. formosa* subsp. *korethroides*), species with thin, creeping or upright columns (*E. huascha*, *E. candicans*, *E. thelegona*), and large, robust columnar cacti (*E. tarijensis*, *E. formosa* subsp. *formosa* BOS460; Fig. 1B, 2C, 2D).

Pollination modes are evolutionary less conserved. Switches from bee to hawkmoth pollination or vice versa appear to be especially common. Examples are found in the *Lobivia*, *Helianthocereus* and *Echinopsis* s.s. clades (Fig. 1A, B). The finding of closely related species having different pollinators fits with population-level variation between bee and sphingid pollination, and nocturnal or diurnal flower opening (Schlumpberger and Raguso, 2008; Schlumpberger et al., 2009). A review of inferred evolutionary shifts between pollinators in genera of Cactaceae more generally is provided in Schlumpberger (2012).

The role of polyploidy in the evolution of the *Echinopsis* clade—The 37 new chromosome counts reported here support the basic chromosome number of $2x = 22$ inferred for Cactaceae (Remski, 1954; Pinkava et al., 1985). Tetraploidy is present in the *Lobivia* and *Helianthocereus* clades (Fig. 1A, B) and has also been reported from a few species not included in our tree, such as *E. spachiana* (likely part of our *Helianthocereus* clade) and *E. backebergii* subsp. *wrightiana* (*Lobivia* clade; Diers, 2008a; Table 3). Overall, the distribution of diploid and tetraploid (or higher) numbers on the phylogeny does not point to particularly frequent polyploidy events, compared for example with similarly sized clades in *Aristolochia*, *Passiflora*, *Carex*, and *Helianthus* (Ohi-toma et al., 2006; Hansen et al.,

2006; Hipp et al., 2007; Timme et al., 2007). It has been suggested that hybridization plays a major role in the evolution of Cactaceae (Rowley, 1994; Machado, 2008) and has also been hypothesized for *Echinopsis* (Friedrich, 1974; Font and Picca, 2001; Anderson, 2005) and related genera (Rowley, 1994). Observations in the field also suggest occasional hybridization, for example, between *E. atacamensis* subsp. *pasacana* × *E. huascha* subsp. *robusta*, *E. terscheckii* × *E. candicans*, *E. terscheckii* × *E. huascha*, and *E. ancistrophora* × *E. saltensis* (B. Schlumberger, unpublished data). However, at least the first cross in this list involves homoploidy (BS, unpublished data), and the relative scarcity of tetraploidy in the phylogeny (Fig. 1) thus does not necessarily reflect a rarity of hybridization.

Conclusions—The chloroplast DNA phylogeny presented here for 144 species and subspecies representing all major groups of *Echinopsis* sensu lato as well as all genera of Trichocereaceae demonstrates the polyphyly of this genus as currently circumscribed. The phylogeny further reveals much convergent evolution in flower traits that relate to pollination modes (see Fig. 2A, B) and less convergent evolution in growth forms (but see Fig. 2C, D). There is no conspicuous role of genome doubling in the evolution of *Echinopsis* sensu lato. A new generic classification of the Trichocereaceae 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.

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