

FURTHER INSIGHTS AND NEW COMBINATIONS IN AYLOSTERA (CACTACEAE) BASED ON MOLECULAR AND MORPHOLOGICAL DATA

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Abstract

The Genus *Rebutia* K. Schum. is a taxonomically complex genus of Cactaceae subfamily Cactoideae. This genus was subjected to splitting and lumping treatments through the years. Molecular data revealed that *Rebutia* sensu lato must be divided in a clade corresponding to former *Rebutia* section *Rebutia* (*Rebutia* sensu stricto), related to the clade formed by *Weingartia/Cintia/Sulcorebutia*. Only this clade corresponds to genus *Rebutia* in our results. The other sections of *Rebutia* s. l. (*Aylostera*, *Digitorebutia*, *Cylindrorebutia*) cluster together to form another clade not directly related to *Rebutia* s. str. For priority reason this clade is recombined as genus *Aylostera* Speg. An analytical key is provided, to identify genera *Rebutia* K. Schum., *Aylostera* Speg., and *Weingartia* Werderm. (including *Sulcorebutia* Backeb. and *Cintia* Knize & Riha) and in *Aylostera*, at infrageneric level, the subgenera *Aylostera* and *Mediolobivia*. Further investigations are needed to assume taxonomic decisions about the clade *Weingartia/Sulcorebutia/Cintia* that, as a whole, should be assigned to genus *Weingartia* Werderm. A list of taxa belonging to genera *Rebutia* K. Schum. and *Aylostera* Speg., is provided. In this treatment the necessary combinations following the separation of *Aylostera* as a genus autonomous from *Rebutia* are proposed. The ATPB-rbcL IGS fragment revealed to be enough variable to be used for Barcoding of species among Cactaceae. All species here considered are in CITES appendix II, with frequent determination difficulties.

Introduction

The genus *Rebutia* K. Schum., was described in 1895. Since the beginning the genus was subjected to various rearrangements. This tendency lead to decisions sometimes extreme, both on a “splitter” and on a “lumper” point of view.

An example of a “lumper” treatment was the rearrangements that lead, quite recently, to the fusion of *Rebutia* with the genera *Sulcorebutia* Backeb. and *Weingartia* Werderm (Hunt & Taylor, 1990; Hunt, 1999; 2006). On the contrary an example of a “splitter” point of view was in the previous treatments as that by Backeberg (1966), who subdivided *Rebutia* in three genera: *Rebutia* K. Schum. sensu stricto, *Aylostera* Speg., and *Mediolobivia* Backeb., with the allied genera *Sulcorebutia* and *Weingartia*.

An intermediate treatment was carried out by Donald (Donald, 1975a; Donald & Brederoo, 1975), who finally decided to divide the genus *Rebutia* K. Schum. (excluding *Sulcorebutia* and *Weingartia*) into five sections without subgenera: *Rebutia* K. Schum. (including subsections

Rebutia Buining & Donald and *Mediorebutia* Buining & Donald), *Aylostera* Speg., *Digitorebutia* (Frič & Kreunz. ex Buining) Buining & Donald, *Cylindrorebutia* Buining & Donald and *Setirebutia* Buining & Donald. This point of view was accepted also by Mosti (1999).

Moreover, Donald (1975b) and Donald & Brederoo (1976a; 1976b; 1976c; 1976d; 1977a; 1977b; 1978a; 1978b) revised four of the five sections. The fifth section, *Digitorebutia*, was revised by Mosti (1999; 2000a; 2000b).

Rausch, the most important discoverer of *Rebutia* sensu lato, since 1986 treated *Digitorebutia* and the few species belonging to *Cylindrorebutia* and *Setirebutia* under the genus *Lobivia* Britton & Rose (Rausch, 1986). Moreover, this last genus was recently included in *Echinopsis* Zucc., by Hunt & Taylor (1990). Rausch’s opinion about the inclusion of part of *Rebutia* in *Lobivia* and, transitively, in *Echinopsis*, is not currently accepted (Sida, 1997; Hunt, 1999; Mosti, 1999; Anderson, 2001). A summary about the history of the main taxonomic treatments about *Rebutia* and allied genera is given in Table 1.

Table 1. History of the taxonomic treatment of genera: *Rebutia*, *Aylostera*, *Weingartia*, *Sulcorebutia* and *Cintia*.

Backeberg (1966)	Donald (1975)	Rowley (2009)	Mosti & Papini (2011)
Genus <i>Rebutia</i> K. Schum.	Genus <i>Rebutia</i> K. Schum sect. <i>Rebutia</i>	Genus <i>Rebutia</i> K. Schum subgen. <i>Rebutia</i>	Genus <i>Rebutia</i> K. Schum.
Genus <i>Aylostera</i> Speg.	Genus <i>Rebutia</i> sect. <i>Aylostera</i>	Genus <i>Aylostera</i> Speg. subgen. <i>Aylostera</i>	Genus <i>Aylostera</i> Speg. subgen. <i>Aylostera</i>
Genus <i>Mediolobivia</i> Backeb.	Genus <i>Rebutia</i> sections <i>Digitorebutia</i> , <i>Cylindrorebutia</i> and <i>Setirebutia</i>	Genus <i>Aylostera</i> Speg. subgen. <i>Mediolobivia</i> (Backeb.) Rowley	Genus <i>Aylostera</i> Speg. subgen. <i>Mediolobivia</i> (Backeb.) Rowley
Genus <i>Weingartia</i> Werderm.	Genus <i>Weingartia</i> Werderm.	Genus <i>Rebutia</i> subg. <i>Weingartia</i> (Werderm.) Rowley	Genus <i>Weingartia</i> Werderm. including genera <i>Sulcorebutia</i> Backeb. and <i>Cintia</i> Knize & Riha
Genus <i>Sulcorebutia</i> Backeb.	Genus <i>Sulcorebutia</i> Backeb.	Genus <i>Rebutia</i> subg. <i>Sulcorebutia</i> (Backeb.) Brandt	

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Digitorebutia, *Cylindrorebutia* and *Setirebutia*, or as a whole the subgenus “*Mediolobivia*” sensu Pilbeam (1997), as the other rebutias, should be considered separated from the *Lobivia/Echinopsis* group because of essential morphological differences, including indehiscent fruits and stamens disposed in only one series which are present only in *Rebutia* s.l.

Ritz *et al.*, (2007) proposed, on the basis of molecular data, to separate *Rebutia* group I, that is, the few analysed by them corresponding to genera *Aylostera* Speg. (*R. deminuta*, *R. fiebrigii* and *R. pseudodeminuta*) and *Mediolobivia* Backeb. (*R. einsteinii*, *R. pygmaea* and *R. steinmannii*) after Backeberg (1966), from *Rebutia* group II (*R. minuscula*, and *R. padcayensis*) corresponding to genus *Rebutia* K. Schum s. str. in Backeberg’s (1966) system.

The species belonging to group II resulted closely related to *Sulcorebutia/Weingartia* (clade E) in Ritz *et al.*, (2007). The proposal to consider *Rebutia* s. str. separated from *Aylostera* and *Mediolobivia* was based both on biomolecular data and enforced by morphological characters: *Rebutia* sensu Backeberg (1966) (corresponding to *Rebutia* s. str.) own in fact hairless pericarps, while on the contrary, *Aylostera* and *Mediolobivia* have hairy and bristly pericarps. This proposal, partially corresponding with Backeberg’s (1966) idea to consider *Rebutia* s. l. (excluding *Sulcorebutia* and *Weingartia*) as splitted in more than one genera, was not followed by a formal taxonomical recombination by Ritz *et al.*, (2007).

On the basis of Ritz *et al.*, (2007) findings, Rowley (2009) proposed a classification of *Rebutia* s.l. separating *Rebutia* s.str., including *Weingartia* and *Sulcorebutia* as subgenera and the genus *Aylostera* was divided in the two subgenera *Aylostera* and *Mediolobivia*. *Aylostera* Speg., has in fact priority with respect to *Mediolobivia* Backeb., to *Digitorebutia* Frič & Kreuz. ex Buining and to *Setirebutia* Frič and *Cylindrorebutia* Frič & Kreuz.. These last three names were never described as genera with a Latin diagnosis.

The aim of our investigation was to verify and enforce the data obtained by Ritz *et al.*, (2007), that included a too limited number of species of *Rebutia*, by adding new molecular data on taxa belonging to genus *Rebutia* s.l., that is sensu Buining & Donald (1963; 1965) (hence excluding gen. *Sulcorebutia* and *Weingartia*), and correlating them with morphological characters, in order to clear the complex taxonomical classification of this group.

A secondary aim was to test a single molecular marker, the ATPb-rbcL spacer as potential Bar-coding marker for Cactaceae. All species here considered are in CITES appendix II, with frequent determination difficulties: the possibility of using a molecular marker to identify them with certainty might be of interest for conservation purpose.

Materials and Methods

Plant material: The plants used in the analysis are cultivated by the Botanical Garden of Florence “Giardino dei Semplici” and collection S. Mosti and were obtained via vegetative propagation from the samples collected by older researchers in the wild before the insertion of Cactaceae in Appendix 1 and 2 of CITES rules. The original samples were those used for species description. The indicated field numbers are those used by the

collectors in the wild. Our samples are deposited in the Tropical Herbarium of Florence (FT). The taxa used for the molecular analysis are known often for a single or few populations in *Aylostera*, *Mediolobivia* and *Rebutia*. The same can be said in other genera such as *Echinopsis*.

We added the following taxa to Ritz *et al.*, (2007) data set (DNA Genbank accession at the end of each sample): *Rebutia wessneriana* Bewer. subsp. *berilloides* (Buining & Donald) Donald, f. n. (field number) Rausch 819, cult. S. Mosti 2011 (FT!), GU084402; *R. kariusiana* Wessner, s.n., cult. S. Mosti 2011 (FT!), GU084394; *R. fabrisii* Rausch var. *aureiflora* Rausch, f. n. Rausch 687, cult. S. Mosti 2011 (FT!) belonging to sect. *Rebutia* even if Pilbeam (1997) links *R. fabrisii* to *Aylostera* (for this species we chose this yellow flowered variety with a single population, but even a red flowered population is known.); GU084401; *Rebutia donaldiana* A.B. Lau & G.D. Rowley, f. n. Lau 348, cult. S. Mosti 2011 (FT!), GU084399; *R. muscula* F. Ritter & Thiele, f. n. Ritter 753, cult. S. Mosti 2011 (FT!) belonging to subgen. *Aylostera*, GU084400; *Rebutia haagei* Frič & Schelle, f. n. Rausch 35, cult. S. Mosti 2011 (FT!) (*R. haagei* is a species characterized by a slight variability in some populations. The variability regards the shape of the petals with a more or less evident mucrone and some slight variation in the color of the flowers), GU084396; *R. christinae* Rausch, f. n. Rausch 492a, cult. S. Mosti 2011 (FT!), GU084398; *R. friedrichiana* Rausch, f. n. Rausch 646, cult. S. Mosti 2011 (FT!) belonging to subgen. *Mediolobivia* (Backeb.) Rowley, GU084397.

Moreover we included in the analysis some samples of taxa that, they do not even belong to genus *Rebutia* s.l., but are noteworthy for an analysis about south american mountain cacti. All these taxa belong to genus *Echinopsis* s. l.: *Lobivia haematantha* (Speg.) Britton & Rose var. *haematantha* (= *Echinopsis haematantha* (Speg.) D.R. Hunt), s.n., cult. S. Mosti 2011 (FT!), GU084392.; *Lobivia (Chamaecereus) silvestrii* (Speg.) G.D. Rowley (= *Echinopsis chamaecereus* H. Friedrich & Glaetzel), s.n., cult. A. Papini 2011 (FT!), GU084395; *Acanthocalycium glaucum* F. Ritter (= *Echinopsis glaucina* H. Friedrich & G.D. Rowley), s.n., cult. S. Mosti 2011 (FT!), GU084391 and *Echinopsis melanopotaamica* Speg. (recently included in *Echinopsis leucantha* (Gillies ex Sal-Dyck) Walp.), s.n., cult. S. Mosti 2011 (FT!), GU084393.

E. melanopotaamica and *L. haematantha* are, respectively, an *Echinopsis* s.str. and a *Lobivia* s.str. *L. silvestrii* is a species of interest because of its morphology, resembling to that of *Rebutia* for its thin and lengthened stem, for its short and fragile spines and the cespitous habit. *Acanthocalycium glaucum*, finally, is a representative of the only genus of *Echinopsis* s.l. not included in Ritz *et al.*, (2007) analysis.

All new samples introduced in the analysis are endemic of North Argentina/South Bolivia living at high altitude (more than 3000 m above sea level).

For the phylogenetic analysis we used the same outgroups used by most recent molecular studies (Nyffeler, 2002; Ritz *et al.*, 2007. The ingroup taxa represent South American cacti of the “BCT clade” as defined by Nyffeler (2002) with an emphasis on the genera *Gymnocalycium*, *Rebutia*, *Sulcorebutia*, and *Weingartia*.

Molecular data: We amplified the DNA fragment ATPB-rbcL spacer, with the same primers used by Ritz *et*

al., (2007). This fragment showed the highest variability among the three used by Ritz *et al.*, (2007), that is more than half of the informative substitutions and half of the informative indels within the ingroup.

Genomic DNAs were isolated from flowers in buds (3-4 days before anthesis) of individual plants using a modified CTAB extraction protocol (Doyle & Doyle, 1990; tissue ground in sea-sand, 70% [v/v], isopropanol substituted for the RNAase step). DNA concentrations were estimated by gel electrophoresis on 1% agarose. We used one sample for each accession.

ATPB-rbcL fragment sequencing and phylogenetic analyses: Primer sequences for the 50 region of the atpB-rbcL IGS were taken from Savolainen *et al.*, (1994): "2" 5'-GAAGTAGTAGGATTGATTCTC-3' and "10" 5'-CATCATTATTGTATACTCTTTC-3', as suggested by Ritz *et al.*, (2007). The amplification was performed for 180 s at 95°C; followed by 28 cycles of 30 s at 95°C, 60 s at 42°C, and 120 s at 72°C; and a final extension for 180 s at 72°C. Single-banded fragments were purified and directly sequenced in both directions by using the amplification primers. Cycle Sequencing and the BigDye Terminator Ready Reaction Kit (Applied Biosystems) were used. Data were collected on ABI Prism 373A automated gel reader in the laboratory CIBIABI of the University of Florence. Resulting sequences were further checked by eye with the software CHROMAS 2.3 (www.technelysium.com.au). A BLAST (Altschul *et al.*, 1997) search was performed to exclude the sequencing of any contaminant organism. The boundaries of the fragments were determined by comparison with previously published sequences. We added our new data on ATP-rbcL IGS to the previous alignment by Ritz *et al.*, (2007), including there data on trnL-trnF and trnK-rps16 IGS sequences. The matrixes were combined with the Python (Python version 2.6.4; Biopython 1.57) program combinex1_0.py, written by one of the authors, A. Papini, released under GPL licence and available at www.unifi.it/caryologia/PapiniPrograms.html.

Optimal multiple alignment was obtained with CLUSTALW 1.81 (Thompson *et al.*, 1994) and checked by eye. Parsimony analysis was performed with PAUP* 4.0b1 (Swofford, 1998). We used a successive weighting approach (Farris, 1969) because of the high number of trees obtained by a simple hsearch command. We used the first 20000 trees to reweight characters (command REWEIGHT) for a second hsearch analysis and so on until, since the third run, the characters weight did not change anymore.

At this point a heuristic search analysis was run with TBR branch-swapping, multrees option on, addseq = simple, ten randomised replicates., a hsearch analysis was performed with a maximum number of saved trees of 65197 to reduce computational effort (50000 were retained by Ritz *et al.*, 2007). All characters were weighted equally, and character state transitions were treated as unordered. Gaps were treated as "simple indel coding" after Simmons & Ochoterena (2000), coding them with the software Gapcoder (Young & Healy, 2003). This process codes indels as separate characters in a data matrix, which is then considered along with the DNA base characters in phylogenetic analysis.

A maximum likelihood (Felsenstein, 1981) search was done as follows: we used Modeltest 3.06 (Posada &

Crandall, 1998) to evaluate the likelihood of 56 different models of sequence evolution on the basis of our data. The likelihood ratio test option was used to compare likelihood scores in a nested design. We used the most likely model of evolution from Modeltest 3.06 as settings in a maximum likelihood (ML) phylogenetic analysis in PAUP. We used the obtained model to calculate the likelihood value of the maximum parsimony trees.

Because of computational time problem with PAUP, we performed a maximum likelihood analysis with the GARLI package (Zwickl, 2006) that uses a stochastic genetic algorithm-like approach to simultaneously find the topology, branch lengths and substitution model parameters that maximize the log-likelihood (lnL). The package was used on a server provided by the Cipres portal (Miller *et al.*, 2009 for the site address). The indels-derived characters were excluded for the maximum likelihood analysis.

Bootstrap (Felsenstein, 1985) resampling was performed using setting search = faststep (with no TBR branch-swapping because of computational time limits) with ten random taxon entries per replicate and multrees option in effect (with 10000 replicates) under parsimony criterion.

MrMODELTEST 2.0 (Nylander, 2004) was used to test the best model of sequence evolution (based on the Akaike Information criterion, Akaike, 1974) to be used with the program for Bayesian Inference MrBayes 3.4b4 (Huelsenbeck, 2001). For the indels-coded characters we used the same evolutionary model used for restriction sites that are coded as binary character states (as implemented in MrBayes).

The Bayesian phylogenetic analysis was used for assessing the robustness of tree topology and the support for clades. The posterior probability of the phylogenetic model was estimated using Markov chain Monte Carlo (MCMC) sampling with the Metropolis-Hastings-Green algorithm. Four chains were run, three heated and one cold, for 10^6 generations and sampled every 100 generations. Following the analysis, the posterior probabilities were checked in the output of MrBayes to estimate the number of trees that should be discarded as "burn-in". Stationarity was reached at approximately generation 30,000, so the first 300 trees or "burn-in" period of the chain were discarded. Phylogenetic inferences are therefore based on those trees sampled after generation 30,000. After the "burn-in" trees were removed from the data set, the remaining trees were used to produce a 50% majority-rule consensus tree (with PAUP) in which the percentage support indicated a measure of the Bayesian posterior probabilities.

To test the significance of the difference of less parsimonious trees with respect to the most parsimonious solution, the Templeton (Wilcoxon signed-ranks) test (Templeton, 1983) was used as implemented in PAUP. This test was used to evaluate the significance of an alternative position of taxa of *Rebutia* s. l.

A matrix of the genetic distances among the different species of *Rebutia* was calculated with PAUP and presented in Table 2. The distances were obtained by calculating the total difference (number of total substitutions in the matrix of DNA sequences).

The trees were edited for better readability with Dendroscope (Huson *et al.*, 2007).

Table 2. Matrix of distances obtained by total difference (number of total substitutions in the matrix of DNA sequences). First row: abbreviations of species reported in the first column.

	sulc	pse	fie	de	pyg	ste	ein	pad	min	fab	kar	wes	haa	fri	chr	don	mus
<i>Sulcorebutia steinbachii</i>	0	4	30	31	39	20	34	39	24	15	18	18	26	26	27	30	28
<i>Rebutia pseudodeminuta</i>		0	0	0	12	11	12	10	12	0	0	0	0	0	0	0	0
<i>Rebutia fiebrigii</i>			0	13	32	31	28	26	33	17	19	19	21	21	22	16	15
<i>Rebutia deminuta</i>				0	25	19	31	30	31	16	17	17	12	12	13	6	4
<i>Rebutia pygmaea</i> CA08					0	4	28	37	38	27	28	28	14	14	15	27	26
<i>Rebutia steinmannii</i>						0	16	16	21	9	11	11	1	1	1	10	9
<i>Rebutia einsteinii</i>							0	30	32	16	18	18	19	19	20	19	19
<i>Rebutia padcayensis</i>								0	32	23	24	24	34	34	35	36	35
<i>Rebutia minuscule</i>									0	7	4	4	19	19	20	24	24
<i>Rebutia fabrisii</i>										0	4	4	15	15	14	17	17
<i>Rebutia kariusiana</i>											0	0	17	17	18	21	21
<i>Rebutia wessneriana</i> ssp. <i>beryllioides</i>											0	17	17	18	21	21	
<i>Rebutia haagei</i>												0	0	1	14	14	
<i>Rebutia friedrichiana</i>													0	1	14	14	
<i>Rebutia christinae</i>													0	13	13		
<i>Rebutia donaldiana</i>														0	3		
<i>Rebutia muscula</i>															0		

Results

The total alignment consisted of 2866 characters, of which 2335 resulting from nucleotides sequence alignment of ATPb-rbcL, trnL-trnF and trnK-rps16 IGS sequences, while other 531 characters were added as a result of indels coding. *Echinopsis atacamensis* subsp. *pasacana* and *Lobivia haematantha* showed a big insertion in 384-492 position of the ATPb-rbcL alignment.

The successive weighting and maximum parsimony analysis yielded 65197 trees (restriction of retained trees with MAXTREE=65197) with L=1089.233 (some weights are between 0 and than 1); CI=0.872; RI=0.880. The strict consensus tree (Fig. 1, Bootstrap support above branches) had L = 1094.249; CI = 0.868; RI = 0.875. The maximum likelihood analysis obtained with GARLIC is shown in Fig. 2 (Bayesian support above branches). GARLIC identified the following nucleotide substitution rates: AC = 0.779, AG = 0.637, AT = 0.269, CG = 0.782, CT = 0.327, GT = 1.000. This rates were quite different from those obtained with MODELTEST particularly for the A-C and A-T substitution rates.

Our analysis largely agreed with Ritz *et al.*, (2007) and for this reason same clade labels were used.

The clade E (*Weingartia*, *Sulcorebutia*, *Cintia*, *Rebutia* II, *Browningia*) was confirmed in our analysis both with the strict consensus tree (parsimony) and the maximum likelihood tree but with Bayesian and Bootstrap support lower than 50%. We added to *Rebutia* II *R. kariusiana*, *R. wessneriana* and *R. fabrisii*. All these *Rebutia* clustered together with 99% Bayesian Support (BS), Decay Index (DI) = 4 and 90% Bootstrap support (BO). This clade corresponds to *Rebutia* sect. *Rebutia* sensu Donald (1975a). Within Clade E the two species of

Browningia resulted as Outgroup to the rest of the clade. The two *Browningia* did not cluster together.

Keeping the two representatives of *Browningia* together resulted in trees L=1113.60343 (1094.24857 the strict consensus of the maximum parsimony trees) with CI=0.853 and RI=0.858. The difference resulted statistically significant after the Templeton test (p=0.0068). Keeping together the whole clade E but *Browningia* collapsing the node dividing *Rebutia* sect. *Rebutia* from *Weingartia*, *Cintia* and *Sulcorebutia*, resulted in trees L=1096.75376, CI = 0.866 and RI=0.873 and the difference resulted statistically significant after the Wilcoxon test (but with p=0.0273, while statistical significance is considered to be for p<0.05 in PAUP).

The clade D, corresponding to *Rebutia* I (*Aylostera*, *Mediolobivia*) by Ritz *et al.*, (2007), was monophyletic with 94% Bayesian support BS and DI = 1 (Bootstrap support lower than 50%). Representatives of subgen. *Mediolobivia* (labelled with A on Figs. 1 and 2) formed a clade with 94% BS and DI=3 excluding *R. einsteinii* that clustered as outgroup to the rest of *Mediolobivia* in the maximum parsimony analysis (Fig. 1) and as outgroup to both *Mediolobivia* and *Aylostera* in the maximum likelihood analysis (Fig. 2).

Moving *Aylostera* clade to the *Rebutia* s. str. clade (that is keeping together the whole genus *Rebutia* s.l., both those from clade E and those from clade D) resulted in trees L=1097.95757, CI=0.865, RI=0.872 and the difference resulted statistically significant after the Wilcoxon test (p=0.0225). Moving *Rebutia* s. str. to the *Aylostera* clade resulted in trees of L=1096.79986, CI=0.866, RI=0.873 with significant difference after the Templeton test (p=0.0146). Noteworthy P values resulting by keeping *Rebutia* s. str. together with *Aylostera* were not far from the 0.05 of significance value.

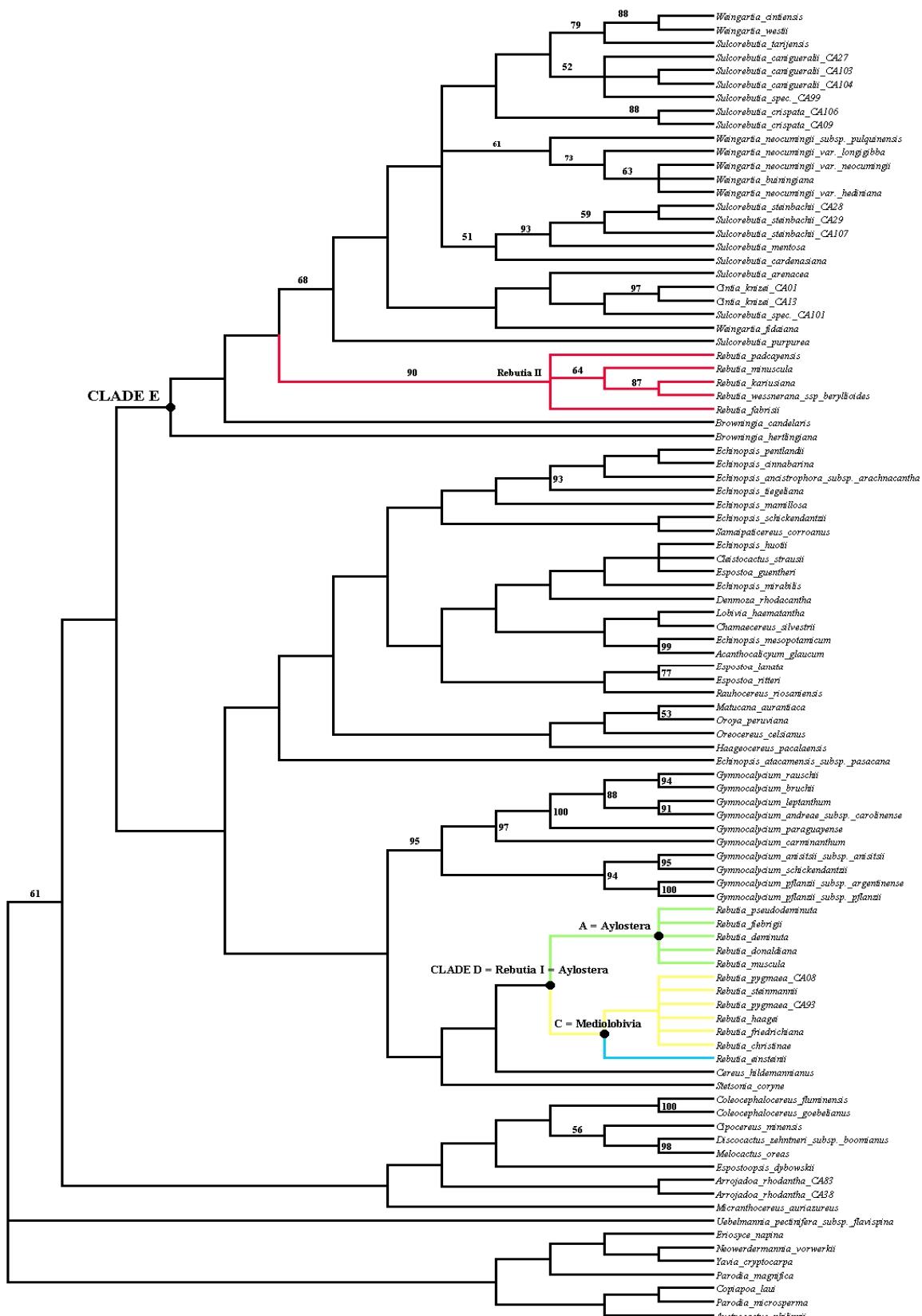


Fig. 1. Strict consensus tree of 65197 maximum parsimony trees (both ATPb-rbcL IGS sequence and derived indels data). Bootstrap support (1000 replicates no TBR branch swapping on) above branches. Clade E = *Weingartia*, *Sulcorebutia*, *Cintia*, *Rebutia II*, *Browningia* as in Ritz *et al.*, (2007). A = *Aylostera* subgen. *Aylostera*; C = *Aylostera* subgen. *Mediolobivia*. The whole genus *Aylostera* corresponds to letter D and *Rebutia I* after Ritz *et al.*, (2007).

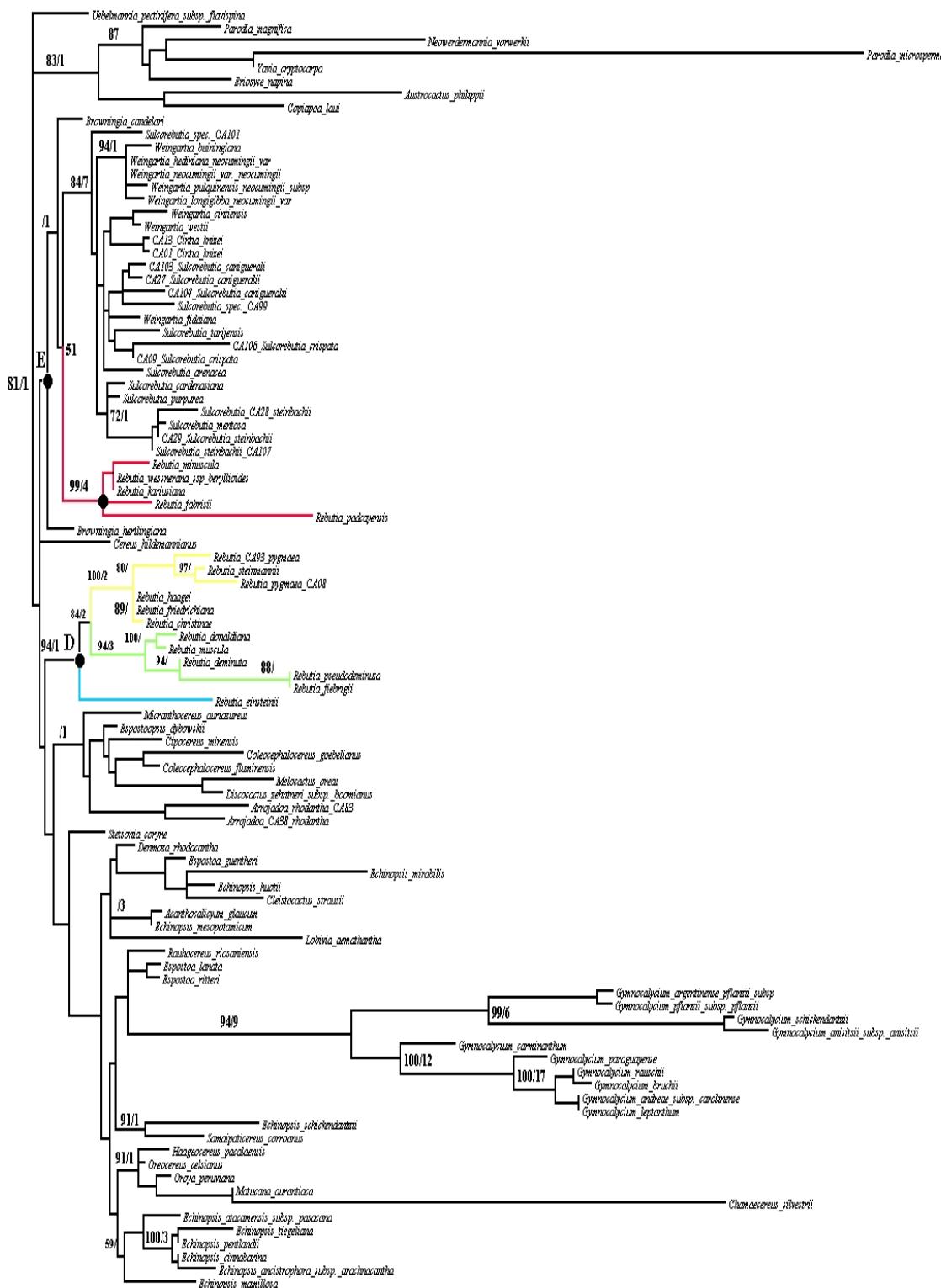


Fig. 2. Maximum likelihood tree obtained with GARLIC package. Bayesian support (indels treated with restriction site model) and Decay indexes above branches. Labels as in Fig. 1.

The matrix of the genetic distances (total number of substitution) among the different species of *Rebutia* calculated with PAUP (Table 2) showed that the sequences used in this analysis were useful to verify the relationships among different species.

Discussion

In clade E *Rebutia* K. Schum. sect. *Rebutia* (Buining & Donald, 1963, 1965; Donald & Brederoo, 1975) clustered together with one representative of *Browningia*, while the other *Browningia* resulted either as outgroup to

the rest of clade E or in uncertain position. In Ritz *et al.*, (2007) *Browningia candelaris* resulted outgroup to *Rebutia* s.str., with *B. hertlingiana* in uncertain position.

The position of *Browningia* prevented us to consider *Rebutia* sect. *Rebutia* and the clade composed by *Weingartia*+*Sulcorebutia*+*Cintia* as belonging to the same genus as proposed by Rowley (2009), who did not consider the position of *Browningia*. The consequence is that the species belonging to *Rebutia* sect. *Rebutia* remain the only representatives of genus *Rebutia* K. Schum.

This genus corresponds to *Rebutia* s.str., which is those species inserted in *Rebutia* K. Schum. by Backeberg (1966) or to sect. *Rebutia* of genus *Rebutia* K. Schum.-in the sense of Buining & Donald (1963, 1965), but without *Sulcorebutia*/*Weingartia*/*Cintia*. These three genera are probably to be considered as congeneric, *Weingartia* (for priority reasons) as was indicated also by Hentzschel & Augustin (2008), but to be considered separated by *Rebutia* (*Rebutia* group II after Ritz *et al.*, 2007), also because of fundamental morphological characters (Augustin *et al.*, 2000 and our further studies): the areoles are in eccentrical position and sunken on the higher (adaxial) part of the tubercle in *Weingartia*/*Sulcorebutia*, while they are more superficial and on the central (distal) part of the tubercle in *Rebutia*. The scales of the flower tube are broad and imbricated in *Weingartia*/*Sulcorebutia*; they are more narrow and not imbricated in *Rebutia*. Finally the spines are quite fragile and subtle in *Rebutia*, and more robust and thick in *Weingartia*/*Sulcorebutia*.

Clade D resulted separated from clade E *Rebutias*. This result confirmed Ritz *et al.*, (2007) results also with our larger species sampling. The Wilcoxon test confirmed that our data prevent keeping all *Rebutia* together. The consequence is that clade D should be considered a separate genus by using the priority name *Aylostera* Speg. This genus corresponds to subgen. *Aylostera* and the subgen. *Mediolobivia* (Backeb.) Rowley (corresponding to the sections *Digitorebutia* (Frič & Kreuz. ex Buining) Buining & Donald, *Cylindrorebutia* Buining & Donald and *Setirebutia* Buining & Donald of *Rebutia* K. Schum.). *R. einsteinii* resulted included in subgen. *Mediolobivia* in the maximum parsimony analysis, while it was outgroup to all the other accessions of the new genus *Aylostera* in the maximum likelihood analysis. *R. einsteinii* is the only representative of sect. *Cylindrorebutia* inserted in the analysis, and its position in the maximum likelihood analysis would be compatible with a treatment of the genus as subdivided in sections. The sect. *Setirebutia* (not inserted in the analysis since it is synonymized in our treatment with *Mediolobivia*) is considered belonging to genus *Aylostera* because of its hairy pericarpels.

Only a few chromosome counts are available for *Rebutia* s.l. in our knowledge. Anyway Ross (1981) observed that *R. minuscula* and *R. violaciflora*, both belonging to *Rebutia* s. str., have n=11 chromosomes as *Sulcorebutia steinbachii* (*Rebutia steinbachii* in Ross, 1981). These three species all belong to clade E. On the contrary *R. kupperiana* and *R. spegazziniana*, both to be assigned to clade D (*Aylostera*) had n=22. Hence these few chromosome counts would confirm our molecular results.

Taxonomic treatment

The taxonomical consequences of our analysis lead to a modified classification with respect to the recent reappraisal by Rowley (2009) as reported underneath. The new classification is preceded by an analytical key that permits to identify genera *Rebutia* K. Schum., *Aylostera* Speg., and *Weingartia* Werderm. (including *Sulcorebutia* Backeb. and *Cintia* Knize & Riha) and in *Aylostera*, at infrageneric level, the subgenera *Aylostera* and *Mediolobivia*.

About the clade *Weingartia*/*Sulcorebutia*/*Cintia* we did not take either taxonomic decisions or new recombinations since the knowledge about this group require further investigation, also about taxa delimitation. The monotypic genus *Cintia* Knize & Riha, despite its phylogenetic position closely related to *Weingartia* and *Sulcorebutia*, as observed in the molecular analysis (Ritz *et al.*, 2007 and our data), shows peculiar morphological characters (autoapomorphies) such as lack of spines and very short (or even absent) floral tube. The flower appears sunken in the areole.

We report also a description of genera *Rebutia* and *Aylostera* and of the subgenera within this last genus: *Aylostera* and *Mediolobivia*. Finally we report the list of taxa in our opinion belonging to genera *Rebutia* K. Schum., and *Aylostera* Speg. About *Rebutia* K. Schum., we did not cite the infraspecific taxa since further systematic investigations are still necessary. We only cited *R. wessneriana* subsp. *berilloides* since our sample was identified as such and we preferred to maintain this name for the molecular analysis. The same can be said about *R. einsteinii* (*Aylostera* subgen. *Mediolobivia* in our treatment). In any case we preferred not to accept the combination *Rebutia einsteinii* Frič subsp. *aureiflora* (Boed.) Hjertson (Hunt 2006), since it was not supported by any morphological or biomolecular data. For this reason the two taxa (*R. einsteinii* e *R. aureiflora*) should be kept separated at the species level (until further data is available).

In this treatment we propose necessary combinations following the separation of *Aylostera* as a genus independent from *Rebutia*. It is to remark that those species belonging to subgen. *Mediolobivia* described as representatives of genus *Lobivia* Britton & Rose by Rausch (1986), were recombined as *Rebutia* by Sida (1997) and Mosti (1999; 2000a; 200b).

With respect to the revision of *Rebutia* sect. *Digitorebutia* (Mosti 1999; 2000a; 2000b), here inserted in subgen. *Mediolobivia*, we added seven taxa: *Rebutia froehlichiana* Rausch, *R. iridescens* F. Ritter, *R. tropaeolipicta* F. Ritter, and the recently described *R. mariae* La. Fisch & Halda, *R. odehnali* Halda, Seda & Sorma, *R. raffaelii* Mosti & Papini, *R. rovidana* Mosti & Papini. In the same subgenus we added also the *Cylindrorebutia* and *Setirebutia*: *R. einsteinii* Frič ex Kreuz. & Buining, *R. gonjianii* Kiesling, *R. aureiflora* Backeb., *R. brighignae* Mosti & Papini and *R. fischeriana* Slaba. All these names are treated exhaustively underneath and, where necessary, recombined.

In Hunt's (2006) checklist, only three species (*R. fabrisii*, *R. minuscula* and *R. padcayensis*) of *Rebutia* K. Schum. and only a few taxa (10) of *Aylostera* Speg., were considered valid at the species level (all under *Rebutia*).

Among the ten species of *Aylostera*, six (with five subspecies) were assigned to subgen. *Aylostera*, four (with three subspecies) to subgen. *Mediolobivia*. A high number of other taxa were synonymized with these taxa. Moreover our studies in the field showed that considering the species of the group *Aylostera/Rebutia* (particularly those belonging to subgen. *Mediolobivia*) as few species with wide geographical distribution range would be distant from the real situation. We observed in the field that these taxa are often composed by micropopulations often living in rock fissures and separated from other populations by long distances and geographical barriers.

However, the list of taxa belonging to genus *Aylostera* reported as follows should not be considered always as an assertion of the systematic validity of the taxa, but in some cases only from a nomenclature point of view. As a matter of fact, the number of “good species” of subgen. *Aylostera* is probably lower than the total number of names here reported, as stated, for instance in Hunt's (2006) checklist. We assume that some of these taxa should be probably synonymized in a revision of

Aylostera subgen. *Aylostera*. We recombined all the available taxa under *Aylostera*, since an updated revision of this subgenus is still lacking and attempts to synonymize taxa without more exhaustive data may be misleading.

For instance, our analysis of genetic distances (total number of substitutions, see table 2) indicated that some of the taxa considered synonyms by Hunt (2006) showed a genetic distance comparable to that between taxa considered different species by the same author. For instance *R. donaldiana* is considered synonym of *R. fiebrigii* by Hunt (2006), while the genetic distance between these two species is 16, the same as the distance between *R. steinmannii* and *R. einsteinii*, that are considered “good” species in Hunt (2006) treatment.

For the above mentioned reason, in our opinion the definitive number of species belonging to Genus *Aylostera* cannot be yet established, even because of different opinions about this aspect (Mosti, 1999; 2000a; 2000b and Hunt, 2006) and without a complete systematic investigations.

Analytical key

- 1a. Axils of the floral scales with hairs, hairs and bristles or woolly 2 ***Aylostera***
- 1b. Axils of the floral scales naked (occasionally with slight tomentum) 3
- 2a. Style and filaments coalescent with the internal side of the receptacular wall for its whole length; axils of the floral scales with both hairs and bristles ***Aylostera* subgen. *Aylostera***
- 2b. Style and filaments free from the receptacular wall or coalescent with the internal side of receptacular wall only for its lower part; axils of the floral scales with hairs or woolly but never bristly ***Aylostera* subgen. *Mediolobivia***
- 3a. Areoles inserted, more superficially, on the central (distal) part of the tubercle; scales of the floral tube narrow and not imbricated. Spines quite fragile and subtle ***Rebutia***
- 3b. Areoles on the tubercle in eccentric position, sunken in its higher (adaxial) part; floral tube scales broad and imbricated. Spines more robust and thick. (Spines and floral tube lacked in *Cintia*) ***Weingartia* (with *Sulcorebutia* and *Cintia*)**

Rebutia K. Schum., Monatsschr. Kakteenk. 5: 102. 1985.

Small cactus (2-5 cm tall and 2-8 cm wide), flattened-globular to globular or exceptionally sub-cylindrical. Fusiform or rapiform root system. Spiralled or vertically directed ribs scarcely developed, and resolved in low isodiametrical, hexagonal tubercles spiralled or vertical. Areoles small, round or oval or narrow elongated in the centre of the tubercles, felted and initially without spines. Spines often subtle and fragile, short to relatively short (0.1-3 cm), bristly to acicular, adpressed or porrect, never hooked, laterals and centrals often indistinguishable (15 to 35 in number), weak. Flowers (1-6.5 cm long and 1-5.5 cm wide), funneliform, arising only from a base or sides of plant, never from the young areoles in the crown; anthesis-time usually 2 days; stile and filaments not coalescent to partially coalescent with the receptacle wall; receptacular scales usually narrow, exceptionally broad; scale axils of receptacle naked (occasionally with slight tomentum). Fruit a small berry with persistent floral remains, globose, naked, becoming papery at maturity. Seeds black, conical cap shaped, with cuticula separated from the testa and with verrucose testa and prominent white hilum. Plants mostly self-fertile, but also sometimes self-sterile (*Rebutia calliantha* Bewer., *R. kariusiana*

Wessner). Habitat: environments mostly shady.

Type: *Rebutia minuscula* K. Schum.

Checklist of species and infraspecific taxa

1. ***Rebutia calliantha*** Bewer., Sukkulantenkunde 2: 25. 1948. [= *Rebutia minuscula* subsp. *wessneriana* in Muruaga et al., (2008)]
2. ***Rebutia fabrisii*** Rausch, Kakt., and. Sukk. 28(3): 52. 1977.
- Rebutia kariusiana*** Wessner, Kakt. And. Sukk. XIV. 149. 1963.
4. ***Rebutia krainziana*** Kesselr., Succulentenkunde 2: 23. 1948.
5. ***Rebutia margarethae*** Rausch, Kakt. And. Sukk. 23(1): 4. 1972.
6. ***Rebutia marsoneri*** Werderm., Kakteenkunde 1937: 2. 1937.
7. ***Rebutia minuscula*** K. Schum., Monatsschr. Kakteenk.

5: 102. 1895. [*Rebutia minuscula* subsp. *minuscula* in Muruaga *et al.*, (2008)].

8. *Rebutia padcayensis* Rausch, Kakt. & Sukkulent. XXI. 65. 1970.

9. *Rebutia senilis* Backeb., Kakteenfreund 1: 124. 1932. [= *R. minuscula* subsp. *minuscula* in Muruaga *et al.*, (2008)].

10. *Rebutia violaciflora* Backeb., Blatt. Kakteenf. 1935, Pt 8. 1935. [*Rebutia minuscula* subsp. *minuscula* in Muruaga *et al.*, (2008)].

11. *Rebutia wessneriana* Bewer., Sukkulantenkunde 2: 24. 1948. [= *Rebutia minuscula* subsp. *wessneriana* in Muruaga *et al.*, (2008)].

11a. *Rebutia wessneriana* Bewer. subsp. *berylloides* (Buining & Donald) Donald, Ashingtonia 2 (4): 71. 1976. [= *Rebutia minuscula* in Hunt (2006)].

12. *Rebutia xanthocarpa* Backeb., Kakteenfreund 1: 131. 1932. [= *R. minuscula* subsp. *minuscula* in Muruaga *et al.*, (2008)]

Aylostera Speg., Anal. Soc. Cient. Argent. 96: 75. 1923.

Small cactus (2-8 tall and 1-5 cm wide) flattened-globular to cylindrical with rapiform or fusiform root-system. Ribs poorly to well developed forming spiralled or vertical rows of more or less small, isodiametrical, circular or hexagonal tubercles, sometime prominent. Areoles small, round or oval or narrow elongated in centre of the tubercles, felted and initially without spines. Spines relatively short: (0.1-) 0.2-2 (-4) cm long, relatively weak to always straight, bristly to acicular, pectinate or porrect, never hooked, laterals and centrals often distinguishable for a total amount of (4-) 7 to 40 (-50) ca. in number. Flowers (0.8-5.5 cm long and 1.2-6 cm wide) funnelform to campanulate with an almost cylindrical to cylindrical receptacle, arising only from basal or lateral areoles, never from the young areoles in the crown; anthesis-time usually 2 days; tube scales usually narrow, exceptionally broad; scale axils of receptacle with hairs, hairs and bristles or woolly; style and filaments free from the internal side of the receptacle wall or coalescent with the receptacle wall for its whole length or only with the lower part. Fruit a small berry with persistent floral remains, flattened to roundish, naked, hairy or bristly, becoming papery at maturity. Seeds brown to black, sometimes with separated cuticula and with verrucose testa. Plants either self-sterile or self-fertile.

Habitat: environments mostly exposed to open sun.

Type: *Echinopsis pseudominuscula* Speg.

Aylostera Speg. subgen. **Aylostera**

Plants flattened-globular, globular, sub-cylindrical, or cylindrical; sometime with bronzed epidermis. Ribs poorly developed from circular or hexagonal tubercles. Spines up to 4.0 cm long and about 50 in number. Flowers funnelform with, usually, a narrow cylindrical tube; style

and filaments usually coalescent with the internal side of the receptacular wall for the whole length of receptacle; scale axils with both hairs and bristles. Fruits bristly. Plants mostly self-fertile.

Type: *Echinopsis pseudominuscula* Speg.

Checklist of species and infraspecific taxa, including taxonomic novelties

1. *Aylostera albiareolata* (F. Ritter) Mosti & Papini, comb. nov.

Basionym: *Rebutia albiareolata* F. Ritter, Kakt. And. Sukk. 28(4): 78. 1977.

Type: Bolivia. Tarija, Arce, "Padcaya", -/1/1963, Ritter 761 (holotype, U; isotype, ZSS-SR14416 (Eggli *et al.*, 1995)).

2. *Aylostera albiflora* (F. Ritter & Buining) Backeb., Descr. Cact. Nov. 3: 5. 1963.

3. *Aylostera albipilosa* (F. Ritter) Backeb., Descr. Cact. Nov. 3: 5. 1963.

4. *Aylostera albopectinata* (Raush) Mosti & Papini, comb. nov.

Basionym: *Rebutia albopectinata* Rausch, Kakt. And. Sukk. 23 (9): 236. 1972.

Type: Bolivia. Sud Cinti, near Culpina, 3400 m, s.d., Rausch 312 (holotype, ZSS).

5. *Aylostera azurduyensis* J. de Vries, Succulenta 85(2): 54, 56, 59. 2006.

6. *Aylostera brunescens* (Rausch) Mosti & Papini, comb. nov.

Basionym: *Rebutia brunescens* Rausch, Kakt. And. Sukk. 23(9): 235. 1972.

Type: Bolivia. Chuquisaca, near Tarabuco, 3550 m, s.d., Rausch 480a (holotype, W; isotype ZSS).

7. *Aylostera buiningiana* (Rausch) Mosti & Papini, comb. nov.

Basionym: *Rebutia buiningiana* Rausch, Kakt. And. Sukk. 23(4): 98. 1972.

Type: Argentina. Jujuy, near Iruya, 2700 m, s.d., Rausch 511 (holotype, W; isotype ZSS).

8. *Aylostera cajasensis* (F. Ritter) Mosti & Papini, comb. nov.

Basionym: *Rebutia cajasensis* F. Ritter, Succulenta 56(3): 64. 1977.

Type: Bolivia. Tarija, Mendez, near Cajas, 1963, Ritter 1141 (holotype, U; isotype, SGO-124626).

9. *Aylostera cintiensis* (F. Ritter) Mosti & Papini, comb. nov.

Basionym: *Rebutia cintiensis* F. Ritter, Ashingtonia 2(10): 206. 1977.

Type: Bolivia. Chuquisaca, Nor Cinti to the north of Camargo, s.d., Ritter 938 (holotype, U; isotype, SGO-124605).

10. *Aylostera deminuta* Britton & Rose, Cactaceae (Britton & Rose) 4: 285. 1923.

11. *Aylostera donaldiana* (A.B.Lau & G.D.Rowley) Mosti & Papini, comb. nov.
Basionym: *Rebutia donaldiana* A.B. Lau & G.D. Rowley, Ashingtonia 1(7): 76. 1974.

Type: Bolivia. Santa Cruz, Valle Grande, Pucara, 2400 m, "growing in crevices in steep granite rocks facing north", s.d., Lau 348 (holotype, HEID).

12. *Aylostera fiebrigii* (Gurke) Backeb., Kaktus-ABC: 274. 1936.

13. *Aylostera flavistyla* (F. Ritter) Mosti & Papini, comb. nov.
Basionym: *Rebutia flavistyla* F. Ritter, Ashingtonia 3(1) 12. 1978.

Type: Bolivia. Tarija, Méndez, below Cajas, 1958, Ritter 756 (holotype, U; isotypes, SGO-124584, ZSSR14408).

14. *Aylostera fulviseta* (Rausch) Mosti & Papini, comb. nov.
Basionym: *Rebutia fulviseta* Rausch, Kakt. & Sukkul. XXI. 29. 1970.

Type: Bolivia. Arque, near Padcaya, 2200 m, s.d., Rausch 319 (holotype, W; isotype ZSS).

15. *Aylostera fusca* (F. Ritter) Mosti & Papini, comb. nov.
Basionym: *Rebutia fusca* F. Ritter, Kakt. And. Sukk. 28(4): 78 1977.

Type: Bolivia. Tarija, "westlich Tarija", 1959, Ritter 940 (holotype, U).

16. *Aylostera heliosa* (Rausch) Mosti & Papini, comb. nov.
Basionym: *Rebutia heliosa* Rausch, Kakt. And. Sukk. XXI. 30. 1970.

Type: Bolivia. Tarija, near Tarija on the road to Narvaez, 2400-2500 m, s.d., Rausch 314 (holotype, W; isotype, ZSS).

16a. *Aylostera heliosa* (Rausch) Mosti & Papini **subsp. *cajasensis*** (Donald) Mosti & Papini, comb. nov. & stat. nov.

Basionym: *Rebutia heliosa* Rausch var. *cajasensis* Donald, Aschingtonia 3(5-6): 144-145. 1979.

Type: Bolivia. Tarija: Abra Cajas, 2400 m, s. d., Lau 405 (holotype, K).

16b. *Aylostera heliosa* (Rausch) Mosti & Papini **subsp. *condorensis*** (Donald) Mosti & Papini, comb. nov. & stat. nov.

Basionym: *Rebutia heliosa* Rausch var. *condorensis* Donald, Aschingtonia 3(5-6): 143-144. 1979.

Type: Bolivia. Tarija: Abra Condor, 2500 m, s. d., Lau 401 (holotype, K).

17. *Aylostera hoffmannii* (Diers & Rausch) Mosti & Papini, comb. nov.
Basionym: *Rebutia hoffmannii* Diers & Rausch, Kakt. And. Sukk. 28(5): 105. 1977.

Type: Argentina. Salta, near Santa Victoria, s.d., Rausch 521a (holotype, ZSS).

18. *Aylostera jujuyana* (Rausch) Mosti & Papini, comb. nov.
Basionym: *Rebutia jujuyana* Rausch, Kakt. And. Sukk. 24(7): 147-148. 1973.

Type: Argentina. Jujuy, Quebrada de Humahuaca, s.d., Rausch 220 (holotype, ZSS).

19. *Aylostera kieslingii* (Rausch) Mosti & Papini, comb. nov.
Basionym: *Rebutia kieslingii* Rausch, Kakt. And. Sukk. 28(8): 177-178. 1977.

Type: Argentina. Salta, near Caspala, 3200 m, s.d., Rausch 694 (holotype, ZSS).

20. *Aylostera kupperiana* (Boed.) Backeb. in Backeb. & F.M. Knuth, Kaktus-ABC 275. 1936.

21. *Aylostera mamillosa* (Rausch) Mosti & Papini, comb. nov.
Basionym: *Rebutia mamillosa* Rausch, Succulenta 51(4): 69. 1972.

Type: Bolivia. Chuquisaca, Sud Cinti, west of Camargo, 3300 m, s. d., Rausch 302 (holotype, ZSS).

22. *Aylostera mandingaensis* R. Wahl & Jucker, Kakteen Sukk. 59(4): 101-105. 2008.

23. *Aylostera muscula* (F. Ritter & Thiele) Backeb., Descr. Cact. Nov.: 3. 5. 1963.

24. *Aylostera narvacense* Cárdenas, Cact. Succ. J. 43(6): 245. 1971.

25. *Aylostera nitida* (F. Ritter) Mosti & Papini, comb. nov.
Basionym: *Rebutia nitida* F. Ritter, Ashingtonia 3(1): 14. 1978.

Type: Bolivia. Tarija, Mendez, Cajas, 2000 m, 1958, Ritter 769 (holotype, U [not found]; isotypes, ZSS-S10437 [seeds only], SGO-124596).

26. *Aylostera nogalensis* (F. Ritter) Mosti & Papini, comb. nov.
Basionym: *Rebutia nogalensis* F. Ritter, Kakt. And. Sukk. 28(4): 78. 1977.

Type: Bolivia. Chuquisaca, Azurduy, "Tarvita, rocky slopes", 1958, *Ritter* 768 (holotype, U; isotype, SGO-124595).

27. *Aylostera patericalyx* (F. Ritter) Mosti & Papini, comb. nov.

Basionym: *Rebutia patericalyx* F. Ritter, Kakt. And. Sukk. 28(4): 78. 1977.

Type: Bolivia. Chuquisaca, Sud Cinti, "La Cueva", 1963, *Ritter* 757 (holotype, U; isotypes, SGO-124585, ZSS-SR14409).

28. *Aylostera perplexa* (Donald) Mosti & Papini, comb. nov.

Basionym: *Rebutia perplexa* Donald, Ashingtonia 3(5-6): 150. 1980.

Type: Bolivia. Tarija/Chuquisaca, prope Rio Pilaya, s.d., *Lau* 329a (holotype, K; isotype, ZSS).

29. *Aylostera pseudodeminuta* (Backeb.) Backeb., Backeb. & F.M. Knuth, Kaktus-ABC: 275. 1936.

30. *Aylostera pseudominuscula* (Speg.) Speg., Anal. Soc. Ci. Argent. 96: 75. 1923.

31. *Aylostera pulchella* (Rausch) Mosti & Papini, comb. nov.

Basionym: *Rebutia pulchella* Rausch, Kakt. And. Sukk. 23(12): 340. 1972.

Type: Bolivia. Chuquisaca, to the north of Padilla, 2200 m, s.d., *Rausch* 320 (holotype, W; isotype, ZSS).

32. *Aylostera pulvinosa* (F. Ritter & Buining) Backeb., Descr. Cact. Nov. 3: 5. 1963.

33. *Aylostera robustispina* (F. Ritter) Mosti & Papini, comb. nov.

Basionym: *Rebutia robustispina* F. Ritter, Succulenta 56(3): 64. 1977.

Type: Bolivia. Tarija, mountains N of Tarija, 1966, *Ritter* 763 (holotype, U; isotypes, ZSS-SR14421, ZSS-SR14422).

34. *Aylostera rubiginosa* (F. Ritter) Backeb., Descr. Cact. Nov. 3: 5. 1963.

35. *Aylostera schatzliana* (Rausch) Mosti & Papini, comb. nov.

Basionym: *Rebutia schatzliana* Rausch, Kakt. And. Sukk. 26(11): 224-225. 1975.

Type: Bolivia. Chuquisaca, Nor Cinti, near Pucara, 3200 m, s.d., *Rausch* 640 (holotype, ZSS).

36. *Aylostera simoniana* (Rausch) Mosti & Papini, comb. nov.

Basionym: *Rebutia simoniana* Rausch, Kakt. And. Sukk. 35(9): 205. 1984.

Type: Bolivia. Chuquisaca, Sud Cinti, south of and above La Cueva, 3500 m, s.d., *Rausch* 739 (holotype, ZSS).

37. *Aylostera spegazziniana* (Backeb.) Backeb., Backeb. & F.M. Knuth, Kaktus-ABC 276. 1936.

38. *Aylostera spinosissima* (Backeb.) Backeb., Backeb. & F.M. Knuth, Kaktus-ABC 275. 1936.

39. *Aylostera sumayana* (Rausch) Mosti & Papini, comb. nov.

Basionym: *Rebutia sumayana* Rausch, Succulenta 65(4): 74. 1986.

Type: Bolivia. Chuquisaca, Sud Cinti, near Sumaya, 3200 m, s.d., *Rausch* 738 (holotype, ZSS).

40. *Aylostera supthutiana* (Rausch) Mosti & Papini, comb. nov.

Basionym: *Rebutia supthutiana* Rausch, Kakt. And. Sukk. 27(6): 121-122. 1976.

Type: Bolivia. Tarija, O'Connor, at Tambo, s.d., *Rausch* 629 (holotype, ZSS).

41. *Aylostera tamboensis* (F. Ritter) Mosti & Papini, comb. nov.

Basionym: *Rebutia tamboensis* F. Ritter, Ashingtonia 2(10): 207. 1977.

Type: Bolivia. Tarija, O'Connor, east of Tarija, "at the upper end of the Tambo gorge", 2500 m, 1962, *Ritter* 1142 (holotype, U; isotype, SGO-124627). i

42. *Aylostera tarijensis* (Rausch) Mosti & Papini, comb. nov.

Basionym: *Rebutia tarijensis* Rausch, Kakt. and. Sukk. 26(9): 195-196. 1975.

Type: Bolivia. Tarija, east of Tarija, 2600 m, s.d., *Rausch* 87 (holotype, ZSS).

43. *Aylostera tarvitaensis* (F. Ritter) Mosti & Papini, comb. nov.

Basionym: *Rebutia tarvitaensis* F. Ritter, Kakt. and. Sukk. 28(4): 78. 1977.

Type: Bolivia. Chuquisaca, Azurduy, at Tarvita, 1958, *Ritter* 773 (holotype, U; isotypes, SGO-124599, ZSS-SR14432).

44. *Aylostera tuberosa* (F. Ritter) Backeb., Descr. Cact. Nov. 3, 5. 1963.

45. *Aylostera vallegrandensis* (Cárdenas) Mosti & Papini, comb. nov.

Basionym: *Rebutia vallegrandensis* Cárdenas, Cact. Succ. J. (Los Angeles) 42: 35. 1970.

Type: Bolivia. Santa Cruz, Valle Grande, near Candelaria on the way to Rio Piraymiri, 2000 m, s.d., Card. 6307 (holotype, LIL (Cárdenas Herbarium)).

46. *Aylostera vulpina* (F. Ritter) Mosti & Papini, comb. nov.

Basionym: *Rebutia vulpina* F. Ritter, Succulenta 56(3): 66. 1977.

Type: Bolivia. Tarija, Méndez, west of Tarija, 1959, Ritter 939 (holotype, U; isotype, SGO-124606)..

47. *Aylostera wahliana* (Rausch) Mosti & Papini, comb. nov.

Basionym: *Rebutia wahaliana* Rausch, Succulenta 64(12): 257. 1985.

Type: Bolivia. Tarija, at Cuesta de Sama, s.d., *Rausch* 645 (holotype, ZSS).

48. *Aylostera walteri* (Diers) Mosti & Papini, comb. nov.
Basionym: *Rebutia walteri* Diers, Kakt. And. Sukk. 40(8): 189-190. 1989.

Type: Argentina, Salta, Santa Victoria, 2500-2700 m, s.d., *Hoffmann* 1960a (holotype, KOELN).

49. *Aylostera waltheriana* (Backeb.) Y. Ito, Explan. Diagr. Austroechinocactinae: 129. 1957.

Aylostera Speg. subgen. **Mediolobivia** (Backeb.) Rowley, Cactus World 27(2): 88-90. 2009

Plants flattened-globular, globular, sub-cylindrical or cylindrical; often with bronzed epidermis. Ribs well or sometimes poorly developed forming spiralled or vertical rows of rounded tubercles. Spines often with thick bulbous bases up to 1-20 (-60 mm in *Aylostera aureiflora*) mm long and 4-20 in number. Flowers funnelform or campanulate; style and filaments usually coalescent with the internal side of the receptacular wall for the lower part of the receptacle, or free from the receptacular wall; scale axils pilose (to very woolly) but never bristly. Fruits usually naked or only weakly pilose. Plants either self-sterile or self-fertile.

Type: *Rebutia haagei* Frič & Shelle.

Checklist of species and infraspecific taxa, including taxonomic novelties

50. *Aylostera amblypetala* (F. Ritter) Mosti & Papini, comb. nov.

Basionym: *Rebutia rosalbiflora* F. Ritter var. *amblypetala* F. Ritter, Kakt. And. Sukk. 28(4): 76. 1977.

Type: Bolivia. Potosí, Sud Chichas, Impora above Tarata, s.d., *Ritter* 1119 (holotype, U [not found]). i

51. *Aylostera applanata* (Rausch) Mosti & Papini, comb. nov.

Basionym: *Lobivia steinmannii* (Solms-Laub.) Backebg. var. *applanata* Rausch, Lobivia 85: 145, 129. 1986.

Type: Bolivia. Chuquisaca, north of Camargo, Rio Hondo, 3600 m, s.d., *Rausch* 486 (holotype, ZSS).

52. *Aylostera atrovirens* (Backeb.) Mosti & Papini, comb. nov.

Basionym: *Lobivia atrovirens* Backeb. in Backeb. & F.M. Knuth, Kaktus-ABC, 242, 414. 1936. Locality at the protologue: Argentina. Salta to Jujuy, from high mountains (to be typified).

53. *Aylostera aureiflora* (Backeb.) Mosti & Papini, comb. nov.

Basionym: *Rebutia aureiflora* Backeb., Kakteenfreund 1: 124. 1932.

Type: Argentina. Salta: Quebrada del Toro, s. d., s. coll. (lectotype (Hjertson, 2003), photograph in Kakteen-Freund 1: 24. 1932).

54. *Aylostera brachyantha* (Wessner) Mosti & Papini, comb. nov.

Basionym: *Lobivia brachyantha* Wessner, Kakt. And. Sukk. 1937 (9): 129, 207. 1937.

Type: Bolivia. Potosí, near Potosí, s.d., s.n. (lectotype (Hunt & Taylor, 2006), illustration in Kakt. And. Sukk. 1937 (9): 131-132.).

55. *Aylostera brunneoradicata* (F. Ritter) Mosti & Papini, comb. nov.

Basionym: *Rebutia brunneoradicata* F. Ritter, Kakt. And. Sukk. 28(4): 77-78. 1977.

Type: Bolivia. Tarija, Mendez, "San Antonio", 1962, *Ritter* 1109 (holotype, U).

56. *Aylostera brighignae* (Mosti & Papini) Mosti & Papini, comb. nov.

Basionym: *Rebutia brighignae* Mosti & Papini, Cactus & Co. 9(1): 60-61. 2005.

Type: Argentina. Jujuy, Abra de Pives, s.d., *Rausch* 751, cult. S. Mosti (holotype, FT!).

57. *Aylostera camargoensis* (Rausch) Mosti & Papini, comb. nov.

Basionym: *Rebutia camargoensis* Rausch, Succulenta 55(3): 42. 1976.

Type: Bolivia. Chuquisaca, Nor Cinti, west of Camargo, 3200 m, s.d., *Rausch* 311 (holotype, ZSS)..

58. *Aylostera canacruzensis* (Rausch) Mosti & Papini, comb. nov.

Basionym: *Rebutia canacruzensis* Rausch, Kakt. And. Sukk. 27(3): 49-50. 1976.

Type: Bolivia. Chuquisaca, Nor Cinti, near Cana Cruz (Caña Cruz?), 3700 m, s.d., *Rausch* 642 (holotype, ZSS).

59. *Aylostera carmeniana* (Rausch) Mosti & Papini, comb. nov.

Basionym: *Rebutia carmeniana* Rausch, Kakt. And. Sukk. 29(5): 105. 1978.

Type: Argentina. Salta, "in ravines near Caspala", 3100 m, s.d., *Rausch* 690 (holotype, ZSS).

60. *Aylostera christinae* (Rausch) Mosti & Papini, comb. nov.

Basionym: *Rebutia christinae* Rausch, Kakt. And. Sukk. 26(7): 145. 1975.

Type: Argentina. Salta, between Nazareno and Rodeo, 3500 m, s.d., *Rausch* 492a (holotype, W).

61. *Aylostera cincinnata* (Rausch) Mosti & Papini, comb. nov.
Basionym: *Rebutia cincinnata* Rausch, Kakt. And. Sukk. 27(1): 4. 1976.

Type: Bolivia. Potosí, near Cuchu Ingenio, 3600 m, s.d., *Rausch* 300 (holotype, ZSS).

62. *Aylostera colorea* (F. Ritter) Mosti & Papini, comb. nov.
Basionym: *Rebutia colorea* F. Ritter, Kakt. And. Sukk. 28(4): 78. 1977.

Type: Bolivia. Tarija, Mendez, "San Antonio", 1962, *Ritter* 1106 (holotype, U).

63. *Aylostera crassa* (Rausch) Mosti & Papini, comb. nov.
Basionym: *Lobivia haagei* (Fric & Shelle) Wessner var. *crassa* Rausch, Lobivia 85: 140, 56. 1986.

Type: Bolivia. Tarija, "in regionibus altis apud Sama", at Iscayachi, s.d., *Rausch* 501 (holotype, ZSS).

64. *Aylostera diersiana* (Rausch) Mosti & Papini, comb. nov.
Basionym: *Rebutia diersiana* Rausch, Kakt. And. Sukk. 26(2): 25-26. 1975.

Type: Bolivia. Chuquisaca, Sud Cinti, Yuquina near Culpina, 3200 m, s.d., *Rausch* 631 (holotype, ZSS).

64a. *Aylostera diersiana* (Rausch) Mosti & Papini subsp. *atrovirens* (Rausch) Mosti & Papini, comb. nov. & stat. nov.
Basionym: *Rebutia diersiana* Rausch var. *atrovirens* Rausch, Kakt. And. Sukk. 26(2): 26.

Type: Bolivia. Chuquisaca: Sud Cinti, above Salitre near Culpina, 3200 m, s. d., *Rausch* 633 (holotype, ZSS).

65. *Aylostera einsteinii* (Frič ex Kreuz. & Buining) Mosti & Papini, comb. nov.
Basionym: *Rebutia einsteinii* Frič ex Kreuz. & Buining, Succulenta 1949: 65. 1949.

Type: Argentina. Jujuy, Quebrada del Toro, s.d., *Lau* 477? (lectotype (Hjertson, 2003), photogr. in Kaktusar 3: 16. 1932)

66. *Aylostera eos* (Rausch) Mosti & Papini, comb. nov.
Basionym: *Rebutia eos* Rausch, Succulenta 51(1): 2. 1972.

Type: Argentina. Jujuy, near Tafna, 3600 m, s.d., *Rausch* 333 (holotype, W).

67. *Aylostera fischeriana* (Slaba) Mosti & Papini, comb. nov.
Basionym: *Rebutia fischeriana* Slaba in Kaktusy (Brno) 38(3): 69. 2002.

Type: Argentina. Jujuy, s.d., *L. Fischer* 54 (holotype, PR).

68. *Aylostera friedrichiana* (Rausch) Mosti & Papini, comb. nov.
Basionym: *Rebutia friedrichiana* Rausch, Succulenta 55(6): 103. 1976.

Type: Bolivia. Chuquisaca, Sud Cinti, near La Cueva, 3500 m, s.d., *Rausch* 646 (holotype, ZSS).

69. *Aylostera froehlichiana* (Rausch) Mosti & Papini, comb. nov.
Basionym: *Rebutia froehlichiana* Rausch, Succulenta 54(12): 226. 1975.

Type: Bolivia. Chuquisaca, Sud Cinti, near Yuquina, 3200 m, s.d., *Rausch* 649 (holotype, ZSS).

70. *Aylostera gavazzii* (Mosti) Mosti & Papini, comb. nov.
Basionym: *Rebutia gavazzii* Mosti, Cactus & Co. 3(4): 207-209. 1999.

Type: Bolivia, Tarija, s.d., *Rausch* 493, cult. S. Mosti (holotype, FI!).

71. *Aylostera gonjianii* (Kiesling) Mosti & Papini, comb. nov.
Basionym: *Rebutia gonjianii* Kiesling, Bol. Soc. Arg. Bot. 15: 132. 1973.

Type: Argentina. Jijuy, Tilcara, "a cuatro horas a mulas oeste de Huacalera", Jan. 1973, *B. Gonjian* 2 (holotype, LP).

72. *Aylostera haagei* (Frič & Shelle) Mosti & Papini, comb. nov.
Basionym: *Rebutia haagei* Frič & Shelle, Kaktusar 1: 88. 1930.

Type: Argentina, Jujuy, s.d., s.n. (lectotype (Hjertson, 1994), photograph in Frič & Schelle. 1930).

72a. *Aylostera haagei* (Frič & Shelle) Mosti & Papini subsp. *elegantula* (Rausch) Mosti & Papini, comb. nov.
Basionym: *Lobivia haagei* Frič & Shelle var. *elegantula* Rausch, Lobivia 85: 140, 57. 1986.

Type: Argentina. Jujuy, Río San Juan de Oro, s.d., *Rausch* 502 (holotype, ZSS).

72b. *Aylostera haagei* (Frič & Schelle) Mosti & Papini subsp. *mudanensis* (Rausch) Mosti & Papini, comb. nov. & stat. nov.
Basionym: *Rebutia mudanensis* Rausch, Kakt. And. Sukk. 27(8): 169. 1976.

Type: Argentina. Salta: east of Mudana near Santa Ana, 3500-4300 m, s. d., *Rausch* 689 (holotype, ZSS).

73. *Aylostera haefneriana* (Cullmann) Mosti & Papini, comb. nov.
Basionym: *Mediolobivia haefneriana* Cullmann, Kakt. And. Sukk. 6(2): 119. 1955. Locality at the protologue: Bolivia. Potosí, s.d., s.n. (to be typified).

74. *Aylostera huasiensis* (Rausch) Mosti & Papini, comb. nov.

Basionym: *Rebutia huasiensis* Rausch, Kakt. And. Sukk. 28(2): 25. 1977.

Type: Bolivia. Chuquisaca, Inca Huasi, near Culpina, 3300 m, s.d., *Rausch 313* (holotype, ZSS).

75. *Aylostera iridescens* (F. Ritter) Mosti & Papini, comb. nov.

Basionym: *Rebutia iridescens* F. Ritter, Kakt. And. Sukk. 28(4): 76. 1977.

Type: Bolivia. Potosí: Sud Chicas, W of Mal Paso, /-/1962, *Ritter 1434* (holotype, U).

76. *Aylostera iscayachensis* (Rausch) Mosti & Papini, comb. nov.

Basionym: *Rebutia ischayachensis* Rausch, Succulenta 56(1): 3. 1977.

Type: Bolivia. Tarija, Mendez, above Cana Cruz, near Iscayachi, 3500 m, s.d., *Rausch 335b* (holotype, ZSS).

77. *Aylostera knizei* (Rausch) Mosti & Papini, comb. nov.

Basionym: *Lobivia pygmaea* (R. E. Fr.) Backeb. var. *knizei* Rausch, Lobivia 85: 144, 116. 1986.

Type: Bolivia. Oruro, prope Challapata, 3800 m, s.d., *Rausch 676a* (holotype, ZSS).

78. *Aylostera leucacantha* (Rausch) Mosti & Papini, comb. nov.

Basionym: *Lobivia steinmannii* (Solms-Laub.) Backebg. var. *leucacantha* Rausch, Lobivia 85: 145, 129. 1986.

Type: Bolivia. Chuquisaca, Cinti australis, supra La Cueva, 3700 m, s.d., *Rausch 644* (holotype, ZSS).

79. *Aylostera leucanthesma* (Rausch) Mosti & Papini, comb. nov.

Basionym: *Rebutia leucanthesma* Rausch, Kakt. And. Sukk. 26(6): 125. 1977.

Type: Bolivia. Chuquisaca, Nor Cinti, Cana Cruz, 3600 m, s.d., *Rausch 305* (holotype, ZSS).

80. *Aylostera major* (Rausch) Mosti & Papini, comb. nov.

Basionym: *Lobivia steinmannii* (Solms-Laub.) Backebg. var. *major* Rausch, Lobivia 85: 146, 129. 1986.

Type: Argentina. Jujuy, apud Tafna, 3600 m, s.d., *Rausch 334* (holotype, ZSS).

81. *Aylostera marieae* (Lad.Fisch. & Halda) Mosti & Papini, comb. nov.

Basionym: *Rebutia marieae* Lad.Fisch. & Halda, Acta Mus. Richnov., Sect. Nat. 9(1): 71-72. 2002.

Type: Argentina. Jujuy, 2001-1-15, L. Fischer s.n. (holotype, PR).

82. *Aylostera melanocentra* (Rausch) Mosti & Papini, comb. nov.

Basionym: *Lobivia steinmannii* (Solms-Laub.) Backebg. var. *melanocentra* Rausch, Lobivia 85: 146, 129. 1986.

Type: Bolivia. Tarija, ab Iscayachi, "ab occidentem versus", 3600 m, s.d., *Rausch 744* (holotype, ZSS).

83. *Aylostera minor* (Rausch) Mosti & Papini, comb. nov.

Basionym: *Rebutia diersiana* Rausch var. *minor* Rausch, Succulenta 58(11): 258. 1979.

Type: Bolivia. Sud Cinti at Yuquina, near Culpina, 3600 m, s.d., *Rausch 630* (holotype, ZSS).

84. *Aylostera mixticolor* (F. Ritter) Mosti & Papini, comb. nov.

Basionym: *Rebutia mixticolor* F. Ritter, Kakt. And. Sukk. 28(4): 77. 1977.

Type: Bolivia. Tarija, Méndez, "San Antonio", 1966, *Ritter 1108* (holotype, U).

85. *Aylostera nazarenoensis* (Rausch) Mosti & Papini, comb. nov.

Basionym: *Digitorebutia nazarenoensis* Rausch, Succulenta: 58(8): 186. 1979.

Type: Argentina. Salta, near Nazareno, 3350 m, s.d., *Rausch 484* (holotype, ZSS).

86. *Aylostera nigricans* (Wessner) Mosti & Papini, comb. nov.

Basionym: *Lobivia nigricans* Wessner, Beitr. Sukkulanten. Sukkulantenpflege 3: 51. 1940.

Type: Argentina. Salta, s.d., s.n. (lectotype (Hjertson, 2005), photograph of flowering plant showing flower from the side in Beitr. Sukkulanten. Sukkulantenpflege 3: 51. 1940).

86a. *Aylostera nigricans* (Wessner) Mosti & Papini subsp. *albispina* (Rausch) Mosti & Papini, comb. nov.

Basionym: *Lobivia nigricans* Wessner var. *albispina* Rausch, Lobivia 85: 142, 98, 100. 1986.

Type: Argentina. Salta, Escoipe (Cuesta de Obispo), 2700 m, s.d. *Rausch 771* (holotype, ZSS).

87. *Aylostera oculata* (Werderm.) Mosti & Papini, comb. nov.

Basionym: *Rebutia oculata* Werderm., Kakt., and. Sukk. 25, tab 99. 1935.

Type: Argentina, Jujuy, s.d., s.n. (lectotype, icon in Kakt. And. Sukk. 25: t. 99. 1935).

Syn.: *Lobivia euanthema* Backeb., Backeb. & F. M. Knuth, Kaktus-ABC, 240, 414. 1936.

87a. *Aylostera oculata* (Werderm.) Mosti & Papini subsp. *tilcarensis* (Rausch) Mosti & Papini, comb. nov. & stat. nov.

Basionym: *Lobivia euanthema* Backeb. var. *tilcarensis* Rausch, Lobivia 85: 138, 36. 1986.

Type: Argentina. Jujuy: "in summis montibus apud Tilcara", s. d., *Rausch 700* (holotype, ZSS).

88. *Aylostera odehynalii* (Halda, Seda & Sorma) Mosti & Papini, comb. nov.

Basionym: *Rebutia odehynalii* Halda, Seda & Sorma, Acta Mus. Richnov., Sect. Nat. 9(1): 72-73. 2002.

Type: Bolivia. s.d., *J.J. Halda, J. Odehynal & V. Seda, s.n.* (holotype, PR).

89. *Aylostera orurensis* (Backeb.) Mosti & Papini, comb. nov.

Basionym: *Lobivia orurensis* Backeb., Backeb. & F.M. Knuth, Kaktus-ABC: 243, 415. 1936. Locality at the protologue: Bolivia. Oruro, Poopo, near Oruro, 3800 m. (to be typified).

90. *Aylostera pallida* (Rausch) Mosti & Papini, comb. nov.

Basionym: *Rebutia pallida* Rausch, Succulenta 56(10): 234. 1977.

Type: Bolivia. Chuquisaca, Sud Cinti, around La Cueva, 3500 m, s.d., *Rausch 645* (holotype, ZSS).

91. *Aylostera parvula* (Rausch) Mosti & Papini, comb. nov.

Basionym: *Lobivia steinmannii* (Solms-Laub.) Backebg. var. *parvula* Rausch, Lobivia 85: 146, 129. 1986.

Type: Bolivia. Potosi, Cucho Ingenio, 3800 m, s.d., *Rausch 296* (holotype, ZSS).

92. *Aylostera pauciareolata* (F. Ritter) Mosti & Papini, comb. nov.

Basionym: *Rebutia pauciareolata* F. Ritter, Kakt. And. Sukk. 28(4): 77. 1977.

Type: Bolivia. Tarija, Mendez, "San Antonio", 1962, *Ritter 1121* (holotype, U; isotype, SGO-124623).

93. *Aylostera pelziana* (Rausch) Mosti & Papini, comb. nov.

Basionym: *Lobivia haagei* (Frič & Schelle) Wessner var. *pelziana* Rausch, Lobivia 85: 140, 57. 1986.

Type: Argentina. Jujuy, apud Tafna, 3600 m, s.d., *Rausch 333a* (holotype, ZSS).

94. *Aylostera polypetala* (Rausch) Mosti & Papini, comb. nov.

Basionym: *Lobivia pygmaea* (R.E. Fr.) Backeb. var. *polypetala* Rausch, Lobivia 85: 144, 116. 1986.

Type: Bolivia. Potosi, Cucho Ingenio, 3700 m, s.d., *Rausch 301* (holotype, ZSS).

95. *Aylostera pseudoritteri* (Rausch) Mosti & Papini, comb. nov.

Basionym: *Lobivia atrovirens* Backeb. var. *pseudoritteri* Rausch, Lobivia 85: 137, 13. 1986.

Type: Bolivia. Tarija, Abra de Sama, s.d., *Rausch 506* (holotype, ZSS).

96. *Aylostera pygmaea* (R.E. Fr.) Mosti & Papini, comb. nov.

Basionym: *Echinopsis pygmaea* R.E. Fr., Nova Acta Regiae Soc. Upsal. ser. 4, 1(1): 120. 1905.

Type: Argentina. Prov. Jujuy, Yavi, c. 3400 m, s.d., *R.E. Fries 999* (lectotype (Hjertson, 1994), S).

97. *Aylostera raffaellii* (Mosti & Papini) Mosti & Papini, comb. nov.

Basionym: *Rebutia raffaellii* Mosti & Papini, Cactus & Co. 9(1): 56-57. 2005.

Type: Argentina. Jujuy, presso Tafna, s.d., *Rausch 333c*, cult. S. Mosti (holotype, FT!).

98. *Aylostera raulii* (Rausch) Mosti & Papini, comb. nov.

Basionym: *Rebutia raulii* Rausch, Kakt. And. Sukk. 31(6): 171. 1980.

Type: Bolivia. Chuquisaca, north of Camargo, at the Rio Honda, s.d., *Rausch 485* (holotype, ZSS).

99. *Aylostera ritteri* (Wessner) Mosti & Papini, comb. nov.

Basionym: *Lobivia ritteri* Wessner, Beitr. Sukkulantenk. Sukkulantenpflege 1: 3. 1938.

Type: Bolivia. Tarija: Iscayachi *Ritter 03/-1931* s. n. (lectotype (Hjertson, 2005), illus. in Beitr. z. Sukk. u.-pfl. 1:3. 1938).

100. *Aylostera rovidana* (Mosti & Papini) Mosti & Papini, comb. nov.

Basionym: *Rebutia rovidana* Mosti & Papini, Cactus & Co. 9(1): 58-59. 2005.

Type: Argentina. Jujuy, presso Tafna, s.d., *Rausch 333b*, cult. S. Mosti (holotype, FT!).

101. *Aylostera steinmannii* (Solms) Backeb., Cactaceae (Backeberg) 3: 1528. 1959.

Basionym: *Echinocactus steinmannii* Solms, Bot. Zeit. 65(1): 133. 1907.

Type: Bolivia. s. d., s. coll. (lectotype (Hjertson, 2005), fig. 4 in Bot. Zeit. 65(1): plate 2. 1907).

102. *Aylostera tafnaensis* (Rausch) Mosti & Papini, comb. nov.

Basionym: *Lobivia pygmaea* (R. E. Fr.) Backeb. var. *tafnaensis* Rausch, Lobivia 85: 144, 116. 1986.

Type: Argentina. Jujuy, apud Tafna, 4000 m, s.d., *Rausch 508a* (holotype, ZSS).

103. *Aylostera torquata* (F. Ritter & Buining) Mosti & Papini, comb. nov.

Basionym: *Rebutia torquata* F. Ritter & Buining, Succulenta 56(3): 63. 1977.

Type: Bolivia, Potosi, Sud Chichas, "Mal Paso", -/11/1962, *Ritter 1117* (holotype, U).

104. *Aylostera tropaeolipicta* (F. Ritter) Mosti & Papini, comb. nov.

Basionym: *Rebutia tropaeolipicta* F. Ritter, Kakt. And. Sukk. 28(4): 78. 1977.

Type: Bolivia. Potosí, Sud Chichas, "Mal Paso", 1962, Ritter 1114 (holotype, U; isotype, ZSS).

105. *Aylostera tuberculata* (Rausch) Mosti & Papini, comb. nov.

Basionym: *Lobivia steinmannii* (Solms-Laub.) Backebg. var. *tuberculata* Rausch, Lobivia 85: 145, 129. 1986.

Type: Bolivia, Cinti meridionalis, in pago La Cueva, s.d., Rausch 743 (holotype, ZSS).

106. *Aylostera violaceostaminata* (Rausch) Mosti & Papini, comb. nov.

Basionym: *Lobivia pygmaea* R.E. Fr. var. *violaceostaminata* Rausch, Lobivia 85: 144, 116. 1986.

Type: Bolivia. Chuquisaca, Cinti australis, apud La Cueva, 3300 m, s.d., Rausch 742 (holotype, ZSS).

107. *Aylostera violascens* (F. Ritter) Mosti & Papini, comb. nov.

Basionym: *Rebutia violascens* F. Ritter, Kakt. And. Sukk. 28(4): 76. 1977.

Type: Bolivia. Chuquisaca, Nor Cinti, north of Camargo, 1958, Ritter 352 (holotype, U).

108. *Aylostera yuncharasensis* (Rausch) Mosti & Papini, comb. nov.

Basionym: *Lobivia atrovirens* Backeb. var. *yuncharasensis* Rausch, Lobivia 85: 137, 13. 1986.

Type: Bolivia. Tarija, Yunchara, s.d., Rausch 91 (holotype, ZSS).

109. *Aylostera yuquinensis* (Rausch) Mosti & Papini, comb. nov.

Basionym: *Rebutia yuquinensis* Rausch, Kakt. And. Sukk. 31(10): 307. 1980.

Type: Bolivia. Chuquisaca, Sud Cinti, Yuquina, 3200 m (9800 ft), s.d., Rausch 632 (holotype, ZSS).

110. *Aylostera zecheri* (Rausch) Mosti & Papini, comb. nov.

Basionym: *Rebutia zecheri* Rausch, Succulenta 56(2): 30. 1977.

Type: Bolivia. Tarija, Iscayachi, near Pueblo Viejo, 3000 m (9850 ft), s.d., Rausch 650 (holotype, ZSS).

References

- Akaike, H. 1974. A new look at the statistical model identification. *IEEE Transactions Automatic Controls*, 19: 716-723.
- Altschul, S.F., T.L. Madden, A.A. Schäffer, J. Zhang, Z. Zhang, W. Miller and D.J. Lipman. 1997. Gapped BLAST and PSI-BLAST: a new generation of protein database search programs. *Nucl. Acids Res.*, 25: 3389-3402.
- Anderson, E.F. 2001. The Cactus Family. Timber Press Portland, Oregon.
- Augustin, K., W. Gertel and G. Hentschel. 2000. *Sulcorebutia*, kakteenzwerge der bolivianischen Anden. Eugen Ulmer Verlag, Germany.
- Backeberg, C. 1966. Das Kakteenlexicon, 1th ed. Gustav Fischer Verlag, Jena, Germany.
- Buining, A.F.H. and J.D. Donald. 1963. Die Gattung *Rebutia* K. Schumann. *Sukkulenkunde*, 7/8: 96-107.
- Buining, A.F.H. and J.D. Donald. 1965. The revision of the genus *Rebutia* K. Schum. *Cactus and Succulent Journal of Great Britain*, 27: 36-41.
- Donald, J.D. 1975a. The Classification of the Rebutias. *Ashingtonia*, 2(1): 6-7, 10-11.
- Donald, J.D. 1975b. The Rebutias Part 3: Systematics of Rebutia K. Sch. Section *Rebutia* Buin. & Don. *Ashingtonia*, 2(3): 42-43, 50-54, 57, 59-60.
- Donald, J.D. and A.J. Brederoo. 1975. The Rebutias Part 2 Systematics. *Ashingtonia*, 2(2): 30-31, 34-35.
- Donald, J.D. and A.J. Brederoo. 1976a. The Rebutias Part 4: Systematics *Rebutia* K. Sch. Section *Rebutia* Buin. & Don. *Ashingtonia*, 2(4): 66-72, 74, 77-79.
- Donald, J.D. and A.J. Brederoo. 1976b. The Rebutias Part 5: Systematics *Rebutia* K. Sch. Section *Setirebutia* Buin. & Don. *Ashingtonia*, 2(5): 82-91.
- Donald, J.D. and A.J. Brederoo. 1976c. Rebutia Part 6: Systematics - Section *Cylindrorebutia* Buin. & Don. *Ashingtonia*, 2(6): 107-112.
- Donald, J.D. and A.J. Brederoo. 1976d. The Rebutias Part 7: Systematics: *Rebutia* K. Sch. Section *Aylostera* Speg. & *Digitorebutia* (Buin.) Buin. & Don. *Ashingtonia*, 2(7): 138-147.
- Donald, J.D. and A.J. Brederoo. 1977a. Systematics of Rebutia Part 7 continued Section *Aylostera* continued 'The Fiebrigii group'. *Ashingtonia*, 2(9): 181-190.
- Donald, J.D. and A.J. Brederoo. 1977b. Systematics of Rebutia Part 7 continued Section *Aylostera* continued 'The Spegazziniana group'. *Ashingtonia*, 2(10): 203-206.
- Donald, J.D. and A.J. Brederoo. 1978a. The Systematics of Rebutia Part 7 continued Section *Aylostera* - The Spegazziniana Group continued. *Ashingtonia*, 3(2): 26-31.
- Donald, J.D. and A.J. Brederoo. 1978b. Systematics of Rebutia K. Sch. Part 7 continued Section *Aylostera* - The Spegazziniana Group continued. *Ashingtonia*, 3(3/4): 78-83.
- Eggli, U., M.M. Schick and B.E. Leuenberger. 1995. Cactaceae of South America: The Ritter Collections. Englera, 16.
- Farris, J.S. 1969. A successive approximations approach to character weighting. *Systematic Zoology*, 18: 374-385.
- Felsenstein, J. 1981. Evolutionary trees from DNA sequences: A maximum likelihood approach. *J. Mol. Evol.*, 17: 368-376.
- Felsenstein, J. 1985. Confidence limits on phylogenies: An approach using the bootstrap. *Evolution*, 39: 783-791.
- Hentschel, G. and K. Augustin. 2008. Die Gattung *Weingartia* Werdermann. *Gymnocalycium*, 21(2): 767-782.
- Hjertson, M. 1994. The Identity of *Echinopsis pygmaea* R.E. Fr. (Cactaceae). *Taxon*, 43: 455-457.
- Hjertson, M. 2003. Notulae Systematicae Lexicon Cactearium Spectantes III: *Rebutia*. *Cactaceae Consensus Initiatives*, 14: 9-10.
- Hjertson, M. 2005. Furter notes on Rebutia. *Cactaceae Syst. Initiatives*, 19: 18-23.
- Huelsenbeck, J.P. and F. Ronquist. 2001. MrBayes: Bayesian inference of phylogenetic trees. *Bioinformatics*, 17: 754-755.
- Hunt, D.R. 1999. *Cites Cactaceae checklist*. Royal Botanic Garden Kew, Richmond, UK.
- Hunt, D.R. and N. Taylor. 1990. The genera of Cactaceae: progress towards consus. *Bradleya*, 8: 85-107.
- Hunt, D.R. and N. Taylor. 2006. *Cactaceae Syst. Initiatives*, 21: 10.

- Kishino, H., T. Miyata and M. Hasegawa. 1990. Maximum likelihood inference of protein phylogeny and the origin of chloroplasts. *J. Mol. Evol.*, 30: 151-160.
- Miller, M.A., M.T. Holder, R. Vos, P.E. Midford, T. Liebowitz, L. Chan, P. Hoover and T. Warnow. 2009. The CIPRES Portals. CIPRES. 2009-08-04. URL: http://www.phylo.org/sub_sections/portal
- Mosti, S. 1999. *Digitorebutia* Buining & Donald an interesting section of the vast genus *Rebutia*. *Cactus & Co.*, 3(4): 187-209.
- Mosti, S. 2000a. *Digitorebutia* Buining & Donald an interesting section of the vast genus *Rebutia*. *Cactus & Co.*, 4(1): 36-50.
- Mosti, S. 2000b. *Digitorebutia* Buining & Donald an interesting section of the vast genus *Rebutia*. *Cactus & Co.*, 4(2): 87-102.
- Muruaga, N.B., M.F. Figueiroa Romero and R. Kiesling. 2008. Circumscription de *Rebutia minuscula* (Cactaceae, Cactoideae). *Darwiniana*, 46(2): 318-327.
- Nyffeler, R. 2002. Phylogenetic relationships in the cactus family (Cactaceae) based on evidence from trnK/matK and trnL-trnF sequences. *Amer. J. Bot.*, 89: 312-326.
- Nylander J.A.A., F. Ronquist, J.P. Huelsenbeck and J.L. Nieves-Aldre. 2004. Bayesian Phylogenetic Analysis of Combined Data. *Syst. Biology*, 53(1): 47-67.
- Nylander, J.A.A. 2004a. Mr Modeltest, version 1.0b. Department of Systematic Zoology, EBC, Uppsala University, Uppsala, Sweden.
- Pilbeam, J. 1997. *Rebutia*. The Cactus File Handbook 2. Cirio Publishing Services Ltd, UK.
- Posada, D. and A. Crandall. 1988. Modeltest: testing the model of DNA substitution. *Bioinformatics*, 14: 817-818.
- Rausch, W. 1986. *Lobivia* 85. Rudolf Herzig Verlag. Wien.
- Ritz, C.M., L. Martins, R. Mecklenburg, V. Goremykin and F.H. Hellwig. 2007. The Molecular Phylogeny of *Rebutia* (Cactaceae) and its allies demonstrates the influence of paleogeography on the evolution of South American mountain cacti. *Amer. J. Bot.*, 94(8): 1321-1332.
- Ross, R. 1981. Chromosome counts, cytology and reproduction in Cactaceae. *Amer. J. Bot.*, 68(4): 463-470.
- Rowley, G. 2009. *Rebutia* reappraised. *Cactus World*, 27(2): 88-90.
- Savolainen, V., J.F. Manen, E. Douzery and R. Spichiger. 1994. Molecular phylogeny of families related to Celastrales based on rbcL 5' flanking sequences. *Molecular Phylogenetics and Evolution*, 3: 27-37.
- Shimodaira, H. and M. Hasegawa. 1999. Multiple Comparisons of Log-Likelihoods with Applications to Phylogenetic Inference. *Molecular Biology and Evolution*, 16: 1114-1116.
- Sida, O. 1997. Rod Rebutia. Brno.
- Simmons, M. P. and H. Ochoterena. 2000. Gaps as characters in sequence-based phylogenetic analyses. *Syst. Biol.*, 49: 369-381.
- Swofford, D.L. 1998. PAUP* 4.1. Phylogenetic Analysis Using Parsimony. Test version. Sinauer Associates. Sunderland, MA.
- Templeton, A.R. 1983. Phylogenetic inference from restriction endonuclease cleavage site maps with particular reference to the evolution of humans and the apes. *Evolution*, 37: 221-244.
- Thompson, J.D., D.G. Higgins and T.J. Gibson. 1994. ClustalW: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position specific gap penalties and weight matrix choice. *Nucl. Acids Res.*, 22: 4673-4680.
- Young, N.D. and J. Healy. 2003. GapCoder automates the use of indel characters in phylogenetic analysis. *BMC Bioinformatics*, 4: 6.
- Zwickl, D.J. 2006. *Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion*. Ph.D. dissertation, The University of Texas at Austin.

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