A phylogenetic study of *Echidnopsis* Hook. f. (Apocynaceae-Asclepiadoideae) - taxonomic implications and the colonization of the Socotran archipelago

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Abstract. We investigated the phylogeny, taxonomy and biogeography of the Eritreo-Arabian genus *Echidnopsis* Hook. f. (Apocynaceae-Asclepiadoideae). Phylogenetic reconstructions based on nrITS sequence data were obtained using maximum likelihood and parsimony analyses. The results reveal two weakly supported clades, each with a mix of African and Arabian taxa, including the genus *Rhytidocaulon*, and with four Socotran species forming a subclade of their own. Rather than a vicariance origin of these island elements, our data suggest a single dispersal event from eastern Africa. *Echidnopsis* thus parallels biogeographic patterns found for other Socotran endemic plants. Our revised taxonomy recognizes 28 species and 4 subspecies in the genus. Two new combinations, *E. planiflora* subsp. *chrysantha* and *E. sharpei* subsp. *bavazzani* are proposed.

Key words: Biogeography, *Echidnopsis*, morphology, nrITS, phylogeny, Socotra, taxonomy.

Introduction

Echidnopsis Hook. f. belongs to the Old World tribe Ceropegieae Decne. ex Orb. (Apocynaceae-Asclepiadoideae), which is characterized by clear latex, a lack of apical anther appendages and erect pollinia with pellucid margins (cf. Meve and Liede 2004). Within this tribe, the genus *Echidnopsis* is part of subtribe Stapeliinae G. Don, to which *Brachystelma* Sims and *Ceropegia* L. also belong. The stapeliads, or "carrion flowers", are the most speciose group in the tribe, accounting for ca. 400 species in 38 genera of predominantly African, Arabian and Indian distribution (Albers and Meve 2002). In a stapeliad phylogeny based on nuclear and plastid DNA data, *Echidnopsis* has been shown to be closely related to *Rhytidocaulon* P.R.O. Bally and *Caralluma* R. Br. (Meve and Liede 2002). Plants of *Echidnopsis* bear small flowers on creeping succulent stems which are many-angled, ca. 1–2 cm in diameter and form dense clusters or mats. They grow on sand or loam, often covered by bushes, in sand pouches on rocks, or creeping along rock fissures, sheltered by rocks or uncovered. *Echidnopsis* thus exhibits a typical behaviour of stapeliads, especially for such small-stemmed species with procumbent-ascending growth (cf. Albers et al. 1989). *Echidnopsis* is a medium-sized genus comprising 45 decribed species of which 28

plus four subspecies are accepted here (Table 1). The first complete and comprehensive revisions of *Echidnopsis* were published by Bruyns (1988) and Plowes (1993). These revisions represent rather extreme taxonomic concepts, but while Bruyns favoured a rather generous lumping and the establishment of infraspecific categories, Plowes splitted every morphologically discernable element into a full species. Müller and Albers (2002) offered a compromise between these revisions, adopting some necessary corrections of Bruyns' revision pointed out by Plowes (1993), but without accepting his many seemingly superfluous new taxa.

The present distribution of *Echidnopsis* from Tanzania to Oman adheres closely to Takhtajan's (1986) Eritreo-Arabian Subregion and the Somali-Masai regional centre of endemism of White (1983). Takhtajan's subregion covers large parts of north-eastern Africa, southern Arabia and the Socotran archipelago. These three areas equate to the three Provinces of this subregion recognised by Takhtajan, the Somalo-Ethiopian, South Arabian and Socotran Provinces. The vast majority of species can be exclusively attributed to one of its three floristic provinces (Table 2). The entire region is generally very rich in asclepiadaceous taxa, but with eastern and southern Africa as the uncontested centre of diversity. Whereas some taxa occur in both Africa and Arabia (e.g. *Kanahia* R. Br., *Huernia* R. Br., *Glossonema* Decne., *Duvalia sulcata* N.E. Br., *Ceropegia variegata* Decne., *Edithcolea grandis* N.E. Br., *Monolluma socotrana* (Balf. F.) Meve & Liede, *Pentatropis nivalis* (J.F. Gmel.) D.V. Field J.R.I. Wood), a considerable number occurs only in the Arabian Peninsula (cf. Miller and Morris 1988, Miller and Cope 1996, Wood 1997, Collenette 2000). In contrast, the island of Socotra is home to fewer Asclepiadoideae than the African and Arabian mainland (cf. Mies 1998, 2001). Among the Socotran endemics are the genus *Duvaliandra* M.G. Gilbert (with two species if *Socotrella* Bruyns is included), a single species each in the genera

Marsdenia R. Br., *Sarcostemma* R. Br., and *Vincetoxicum* Wolf. With five endemic species *Echidnopsis* Hook. f., however, represents the largest Asclepiadoideae taxon on Socotra (Bruyns 2004).

In the present paper we focus on three main goals: 1) To reconstruct the phylogeny of *Echidnopsis* using sequence data of the nuclear internal transcribed spacer (nrITS; Baldwin et al. 1995, Alvarez and Wendel 2003) 2) We address the taxonomy of the genus *Echidnopsis*, by evaluating whether existing infrageneric classifications are supported by molecular phylogenetic data and by defining this concept again. Therefore, we focus on species complexes particularly exposed to different taxonomic views in the past, such as *E. sharpei/ E. repens*, *E. scutellata/E. planiflora*, and *E. watsonii/E. radians*, as well as on the question whether *E. malum* deserves to be recognized as a genus separate from *Pseudopectinaria* Lavranos, one of the most disputed problems in *Echidnopsis* taxonomy (Bruyns 1988, Plowes 1993, Lavranos 2006) 3) We investigate the biogeography of *Echidnopsis* in the Eritreo-Arabian Subregion, focussing on the question of the geographic origins of the Socotran endemics and whether the archipelago was colonized through a single invasion event and subsequent radiation or if multiple stochastic colonization events occurred.

Materials and methods

Taxa. The material used in this study, including voucher specimen, author name, donor or collector of material, area of distribution and EMBL number is summarized in Table 2. The ingroup comprises 32 accessions of *Echidnopsis* in 26 different taxa according to the verified taxonomy of *Echidnopsis* as proposed in this paper (Tables 1, 2). Due to the lack of living material available to us, the Socotran *E. milleri* and *E. virchowii* were not investigated. Material of *E. seibanica* was available, however, sequencing of nrITS failed. *Caralluma subulata*, *C. priogonium*, *Monolluma socotrana*, *Rhytidocaulon macrolobum* and *R. fulleri* were used as outgroups (Table 2).

Table 1. Taxonomic concepts in *Echidnopsis* (taxa here accepted are printed in bold), and chromosome numbers (new counts marked by *, otherwise taken from Albers and Meve 2001)

Taxon	Bruyns 1988	Plowes 1993	Thiv and Meve, this paper	Chromosome number (2n)
E. angustiloba E.A. Bruce & P.R.O Bally	*E. angustiloba*	*E. angustiloba*	**E. angustiloba**	22
E. archeri P.R.O. Bally	*E. archeri*	*E. archeri*	**E. archeri**	22
E. ballyi (Marn.-Lapost.) P.R.O. Bally	*E. ballyi*	*E. ballyi*	**E. ballyi**	22
E. bavazzani Lavranos	= *E. sharpei*	*E. bavazzani*	**E. sharpei** subsp. **bavazzani**	22* (voucher:Lavranos 24979)
E. bentii N.E. Br. ex Hook. f.	- insuff. known species - (Bruyns 2004: *E. bentii*)	*E. bentii*	**E. bentii**	22* (voucher: Wolf s.n., UBT)
E. bihendulensis P.R.O. Bally	*E. bihendulensis*	*E. bihendulensis*	**E. bihendulensis**	22* (voucher: Specks s.n.)
E. cereiformis Hook. f.	*E. cereiformis*	*E. cereiformis*	**E. cereiformis**	22
E. chrysantha Lavranos	= *E. scutellata* subsp. *planiflora*	*E. chrysantha*	**E. planiflora** subsp. **chrysantha**	44
E. chrysantha var. *filipes* Lavranos	*E. scutellata* subsp. *planiflora*	*E. chrysantha* subsp. *filipes* (*Lavranos*) *Plowes*	= **E. planiflora** subsp. **chrysantha**	22
E. ciliata P.R.O. Bally	*E. sharpei* subsp. *ciliata* (P.R.O. Bally) Bruyns	*E. ciliata*	**E. ciliata**	22
E. dammanniana Spreng.	*E. dammanniana*	*E. dammanniana*	**E. dammanniana**	22
E. ericiflora Lavranos	*E. ericiflora*	*E. ericiflora*	**E. ericiflora**	22
E. fartaqensis McCoy & Orlando	— (descr. 2003)	— (descr. 2003)	= **E. globosa**	22* (voucher: Lavranos & Mies 31326, UBT)
E. flavicorona Plowes	Type specimen incl. in *E. scutellata* subsp. *planiflora*	*E. flavicorona*	= **E. planiflora** subsp. **planiflora**	–
E. globosa Thulin & Hjertson	– (descr. 1995)	— (descr. 1995)	**E. globosa**	22
E. hirsuta Plowes	Type specimen incl. in *E. scutellata* subsp. *planiflora*	*E. hirsuta*	= **E. planiflora** subsp. **planiflora**	–
E. inconspicua Bruyns	— (descr. in 2005)	— (descr. in 2005)	**E. inconspicua**	–
E. insularis Lavranos	*E. insularis*	*E. insularis*	**E. insularis**	–

Table 1. (Continued)

Taxon	Bruyns 1988	Plowes 1993	Thiv and Meve, this paper	Chromosome number (2n)
E. jacksonii P.R.O. Bally ex Plowes	= *E. urceolata*	*E. jacksonii*	- insuff. known taxon -	–
E. lavraniana Plowes	Type specimen incl. in *E. sharpei*	*E. lavraniana*	= *E. sharpei* subsp. *bavazzani*	22
E. leachii Lavranos	*E. leachii*	*E. leachii*	*E. leachii*	22
E. malum (Lavranos) Bruyns ≡ Pseudopectinaria malum	*E. malum*	*Pseudopectinaria malum*	*E. malum*	22
E. mariae Lavranos	= *E. scutellata* subsp. *australis* Bruyns	*E. mariae*	= *E. scutellata* subsp. *australis*	22
E. mijerteina Lavranos	*E. mijertina*	*E. mijertina* var. *mijertina*	*E. mijertina*	22
E. mijerteina var. *marchandi* Lavranos	= *E. mijertina*	*E. mijertina* var. *marchandii*	= *E. mijertina*	22
E. milleri Lavranos	– (descr. in 1993)	– (descr. in 1993)	*E. milleri*	–
E. modesta P.R.O. Bally ex Plowes	= *E. watsonii*	*E. modesta*	= *E. radians*	–
E. montana (R.A. Dyer & E.A. Bruce) P.R.O. Bally	*E. montana*	*E. montana*	*E. montana*	22
E. nubica N.E. Br.	= *E. cereiformis*	*E. nubica*	= *E. cereiformis*	22 (22*, voucher: Specks 1264, UBT)
E. oviflora McCoy	– (descr. in 2003)	– (descr. in 2003)	= *E. leachii*	22 / 44
E. planiflora P.R.O. Bally	*E. scutellata* subsp. *planiflora* (P.R.O. Bally) Bruyns	*E. planiflora*	*E. planiflora* subsp. *planiflora*	–
E. plowesiana Orlando	– (descr. in 2004)	– (descr. in 2004)	= *E. planiflora* subsp. *planiflora*	
E. radians Bleck	= *E. watsonii*	*E. radians*	*E. radians*	22* (voucher: Powys s.n., MSUN)
E. repens R.A. Dyer & I. Verdoorn	*E. sharpei* subsp. *repens* (R.A. Dyer & I. Verdoorn) Bruyns	*E. repens*	*E. repens*	22* (voucher : Specks 635, UBT)
E. rubrolutea Plowes	– (descr. in 1993)	*E. rubrolutea*	= *E. planiflora* subsp. *planiflora*	44

E. scutellata (Deflers) A. Berger	*E. scutellata* subsp. *scutellata*	**E. scutellata** subsp. **scutellata**	22
E. scutellata subsp. *dhofarensis* Bruyns	*E. scutellata* subsp. *dhofarensis*	**E. scutellata** subsp. **dhofarensis**	22 22* (voucher: Butler & Lauchs s.n., UBT)
E. seibanica Lavranos	*E. seibanica*	**E. seibanica**	44
E. sharpei A.C. White & B. Sloane	*E. sharpei* subsp. *sharpei*	**E. sharpei** subsp. **sharpei**	22
E. similis Plowes	Type specimen incl. in *E. archeri E. similis*	= **E. archeri**	–
E. socotrana Lavranos	– (descr. in 1993)	**E. socotrana**	22* (voucher: Thiv 3203, UBT)
E. specksii McCoy	– (descr. in 2003)	= **E. urceolata**	(22*, voucher: Specks 787, UBT)
E. squamulata (Decne.) P.R.O. Bally	*E. squamulata*	**E. squamulata**	44
E. urceolata P.R.O. Bally	*E. urceolata*	**E. urceolata**	22
E. virchowii K. Schum.	*E. virchowii* var. *virchowii*	**E. virchowii**	22
E. virchowii var. *stellata* (Lavranos) Plowes	= *E. virchowii*	= **E. virchowii**	–
E. watsonii P.R.O. Bally	*E. watsonii*	**E. watsonii**	44
E. yemenensis Plowes	Type specimen incl. in *E. scutellata*	**E. scutellata** subsp. **scutellata**	22

Table 2. Voucher material, species distribution and EMBL Nos

Taxon	Species distribution	No.	Herbarium	Location	Collector	nrITS EMBL No.
Caralluma priogonium K. Schum.	Eastern Africa	49388	MSUN	Somalia	Koenen & Krapp	AJ488780
Caralluma subulata Decne.	Arabia, Eastern Africa	28	UBT	Yemen	Mangelsdorff	DQ469521
Echidnopsis angustiloba E. A. Bruce & P.R.O. Bally	Kenya	959	UBT	Kenya	Meve et al.	DQ469522
E. archeri P. R. O. Bally	Kenya, Somalia	s.n.	UBT	Kenya	McCoy	DQ469523
E. ballyi (Marn.-Lapost.) P. R. O. Bally	Somalia	167	no voucher	Somalia	Bailes	DQ469524
E. bentii N.E. Br. ex Hook.f.	Socotra	s.n.	UBT	Socotra	Wolf & Wolf	DQ469526
E. bihendulensis P. R. O. Bally	Somalia	s.n.	UBT (photo)	Somalia	Specks	DQ469527
E. cereiformis Hook. f.	Arabia, Eastern Africa	s.n.	UBT	Ethiopia	ex hort. Bochum	DQ469529
E. cereiformis Hook. f.	Arabia, Eastern Africa	11795	UBT	Yemen	Botanical Research Inst.	DQ469528
E. ciliata P. R.O. Bally	Eastern Africa	134	K, BOL	Somalia	Bailes	DQ469530
E. dammanniana Spreng.	Eastern Africa	24754	ZSS 12441	Somalia	Lavranos et al.	DQ469531
E. ericiflora Lavranos	Kenya	9305	PRE, ZSS, UBT	Kenya	Lavranos	DQ469532
E. globosa M.Thulin & M.Hjertson ("*E. fartaqensis*")	Yemen	31326	UBT	Yemen	Lavranos & Mies	DQ469533
E. globosa M. Thulin & M. Hjertson	Yemen	9635	UPS	Yemen	Thulin & al.	DQ469534
E. inconspicua Bruyns	Socotra	19103	E	Socotra	Miller	DQ469535
E. insularis Lavranos	Socotra	20010	E	Socotra	Miller	DQ469536
E. leachii Lavranos	Tanzania	1075	UBT	Tanzania	Specks & Specks	DQ469537
E. leachii Lavranos ("*E. oviflora*")	Tanzania	1264	UBT	Tanzania	Specks & Specks	DQ469538
E. malum (Lavranos) Bruyns	Eastern Africa	s.n.	no voucher	Ethiopia	McCoy	DQ469539
E. mijerteina Lavranos	Somalia	23385	no voucher	Somalia	Carter	DQ469540
E. montana (R. A.Dyer & E. A.Bruce) P. R. O. Bally	Ethiopia, Somalia	7946	UBT	Ethiopia	Plowes	DQ469541
E. planiflora P. R. O. Bally subsp. *planiflora*	Eastern Africa	8491	BOL	Ethiopia	Bruyns	DQ469542
E. radians Bleck	Kenya	18591	MSUN (photo)	Kenya	Lavranos & Jenkins	DQ469543
E. repens R. A. Dyer & Verdoorn	Kenya, Tanzania	942	UBT	Kenya	Meve	DQ469545
E. repens R. A. Dyer & Verdoorn	Kenya, Tanzania	635	UBT	Tanzania	Specks	DQ469544
E. scutellata A. Berger subsp. *dhofarensis* Bruyns	Arabia, Eastern Africa	s.n.	UBT	Oman	Butler & Lauchs	DQ469546

Taxon	Region	Collector	Voucher	Origin	GenBank
E. sharpei A. C. White & B. Sloane ssp. *sharpei*	Eastern Africa	Bischofsberger	299 in hort. ZSS	Ethiopia	DQ469547
E. sharpei subsp. *bavazzani* (Lavranos) Meve & Thiv	Eastern Africa	Bruyns	8486 BOL	Ethiopia	DQ469525
E. socotrana Lavranos	Socotra	Miller	14088 E	Socotra	DQ469548
E. socotrana Lavranos	Socotra	Thiv	3203 UBT	Socotra	DQ469549
E. squamulata (Decne.) P. R. O. Bally	Yemen	Mangelsdorff	Y27 UBT	Yemen	DQ469550
E. urceolata P. R. O. Bally ("*E. specksii*")	Eastern Africa	Specks & Specks	787 UBT	Ethiopia	DQ469551
E. urceolata P. R. O. Bally	Eastern Africa	Vlk	s.n. UBT	Ethiopia	DQ469552
E. watsonii P. R. O. Bally	Eastern Africa	Cole	3176 no voucher	Kenya	DQ469553
Monolluma socotrana (Balf. f.) Meve & Liede	Socotra, Eastern Africa	ex hort. W. Bosma	s.n. in hort. UBT	Kenya	AJ488806
Rhytidocaulon fulleri Lavranos & Mort	Arabia	Collenette	8439 UBT	Oman	AJ488823
Rhytidocaulon macrolobum Lavranos subsp. *minimum* Meve & Collenette	Arabia	Collenette	8792 K, UBT	Saudi Arabia	DQ469554

Laboratory work. Two different chloroplast DNA regions and one nuclear genetic marker were used; the rps16 intron (Oxelman et al. 1997) was sequenced for *E. bentii*, *E. squamulata*, *E. dammaniana* and *E. ericiflora* and 624 bp of *mat*K (Johnson and Soltis 1994, 1995; Sang et al. 1997) were sequenced for all *Echidnopsis* species of the present study. The resulting sequence variation of the two chloroplast DNA regions, however, was not useful for phylogenetic reconstructions. No genetic variation was found in the *rps*16 intron over a length of 830 bp. Only very low genetic variation was detected in the *mat*K region yielding 11 variable and 5 phylogenetic informative characters for all *Echidnopsis* species. As a consequence, the most parsimonious *mat*K tree is only scarcely resolved. Therefore, we decided to exclude these data. Accordingly, we selected a marker which has been demonstrated to be more variable and useful at the specific level in other plant taxa, the ITS region of the nrDNA. To overcome the problem of polymorphisms of this repetitive multi-copy marker (Baldwin et al. 1995, Alvarez and Wendel 2003), we repeated direct sequencing of nrITS of multiple amplification products of 10 taxa and we sequenced multiple, available accessions of five species (*E. leachii*, *E. cereiformis*, *E. urceolata*, *E. repens* and *E. socotrana*).

DNA was extracted from living plants, herbarium material or silica dried samples using DNeasy plant extraction kit (Qiagen, Hilden Germany) according to the manufacturer's protocol. PCR amplifications were performed using 1.5 mM Buffer, 0.625 mM $MgCl_2$, 0.2 mM dNTPs, 0.05 U/µl Taq DNA polymerase (Amersham Biosciences), 0.325µM primer and 5 ng/µl DNA template. PCR profiles included 33 cycles of 94°C for 1 min, 55°C for 1 min, and 72°C for 2–3 min. For amplifications and sequencing the following primers were used. nrITS: ITS-A 5′-GGAAGGAGAAGTCGTAAC-AAGG-3′, ITS-B 5′-CTTTTCCTCCGCTTATTG-ATATG-3′ (Blattner 1999). PCR products were cleaned using the PCR purification kit (Qiagen). Using the described primers, cycle sequencing was conducted using ABI PRISM BigDye 2.1 such that at least two strands were available for each sequence (also using primers ITS-D 5′-CTCTCGGCAACG-GATATCTCG-3′ (Blattner 1999) and ITS2 5′-GCTGCGTTCTTCATCGATGC-3′ (White et al. 1990). Resulting products were separated using automated sequencing systems ABI PRISM 3100 (PE Biosystems, Foster City U.S.A.).

Chromosome numbers. The chromosome numbers (Table 1) were obtained from adventitious root tip squash preparations. For details and a review of karyology of Asclepiadoideae see Albers and Meve (2001).

Data analysis. Sequences of ITS1 and ITS2 including the 5.8S rDNA were aligned using the default alignment parameters in Clustal X (Thompson et al. 1997), and then manually adjusted. The alignment is available under Treebase SN2854. Phylogenetic analyses were performed using PAUP* 4.0 (Swofford 1998). After MODELTEST3.0 analysis (Posada and Crandall 1998), maximum likelihood (ML) analyses were made. Using the SYM + I + G model, heuristic searches were conducted using the stepwise additional all, ''as is'' and tree bisection-reconnection (TBR) options. Using the same options a ML Bootstrap with 1,000 replicates was performed. Maximum Parsimony (MP) analyses were carried out using 100 random addition sequence, and TBR. Simple indel coding according to Simmons and Ochoterena (2000) was applied. Using the described options and maxtrees set to 5,000, MP Bootstrap analyses with 1,000 replicates were calculated.

Results

No indications of polymorphisms of nrITS were detected by repeating direct sequencings or by sequencing multiple accessions of several species or that the paralogues sequences, if present, are identical. Out of the 636 characters of nrITS 107 were variable and 56 potentially parsimony informative. The selected optimal model of sequence evolution for the nrITS dataset was the SYM + I + G model (Zharkikh 1994): equal base frequencies, a rate matrix with rAC = 0.9042, rAG = 2.3612, rAT = 1.0916, rCG = 0.3085, rCT = 4.9914, a proportion of invariable sites of 0.4307 and a gamma shape of 0.6563. The analysis using these parameters yielded an optimal ML tree with a log-likelihood score of –lnL = 1819.15. This tree including ML/MP bootstrap supports above 50% is shown in figure 1. The MP analysis yielded 84 most parsimonious trees with a length of 154 steps, a CI of 0.792 and a RI of 0.841. The strict consensus tree (not shown) is highly congruent with the ML tree,

showing no conflict, but a slightly lesser resolved tree. These unresolved nodes are indicated in Fig. 1. In addition, a sister group relationship between both accessions of *E. repens* was only indicated in the MP tree.

According to the nrITS topology, *Echidnopsis* is not monophyletic with *Rhytidocaulon* being nested in a weakly supported clade A (53/58% bootstrap support) together with *E. montana*, *E. malum*, *E. leachii*, and *E. dammaniana*/*E. cereiformis*. The other poorly resolved main clade (B) comprises *Echidnopsis ericiflora*, *E. bihendulensis*/*E. planiflora* subsp. *planiflora*, *E. mijerteina*/*E. scutellata* subsp. *dhofarensis*, *E. archeri* (Fig. 2a), *E. repens*, *E. sharpei* subsp. *sharpei*, *E. urceolata*, *E. angustiloba*, *E. watsonii*, *E. sharpei* subsp. *bavazzanii*, *E. radians*, *E. ballyi*, *E. squamulata*, *E. fartaqensis*/*E. globosa*, *E. ciliata*, and the Socotran *E. bentii*, *E. socotrana* (Fig. 2b), *E. inconspicua* and *E. insularis*.

Discussion

Phylogeny and taxonomy. The nrITS data set revealed two weakly supported major lineages. Clade A includes *Echidnopsis montana*, *E. malum*, *E. leachii*, *E. dammaniana*, *E. cereiformis* and *Rhytidocaulon*. The remainder of *Echidnopsis* is found in a poorly resolved clade B. Using *Caralluma* and *Monolluma* species as outgroups, the inclusion of *Rhytidocaulon* in clade A of *Echidnopsis* is corroborated by nrITS, however without appreciable bootstrap support. This contrasts the results of Meve and Liede (2002), who showed *Echidnopsis* to be monophyletic and sister to *Rhytidocaulon* based on nrITS data, but without considering species of Clade A. In the previous analysis based on *trn*L data both genera were unresolved (Meve and Liede 2002). The relationships among species of clade B are poorly resolved in the nrITS topology and branches are weakly supported. The Socotran species *E. bentii*, *E. socotrana*, *E. inconspicua* and *E. insularis* group together and are sister to *E. ciliata*. Despite a bootstrap support below 50% of the Socotran lineage in the molecular
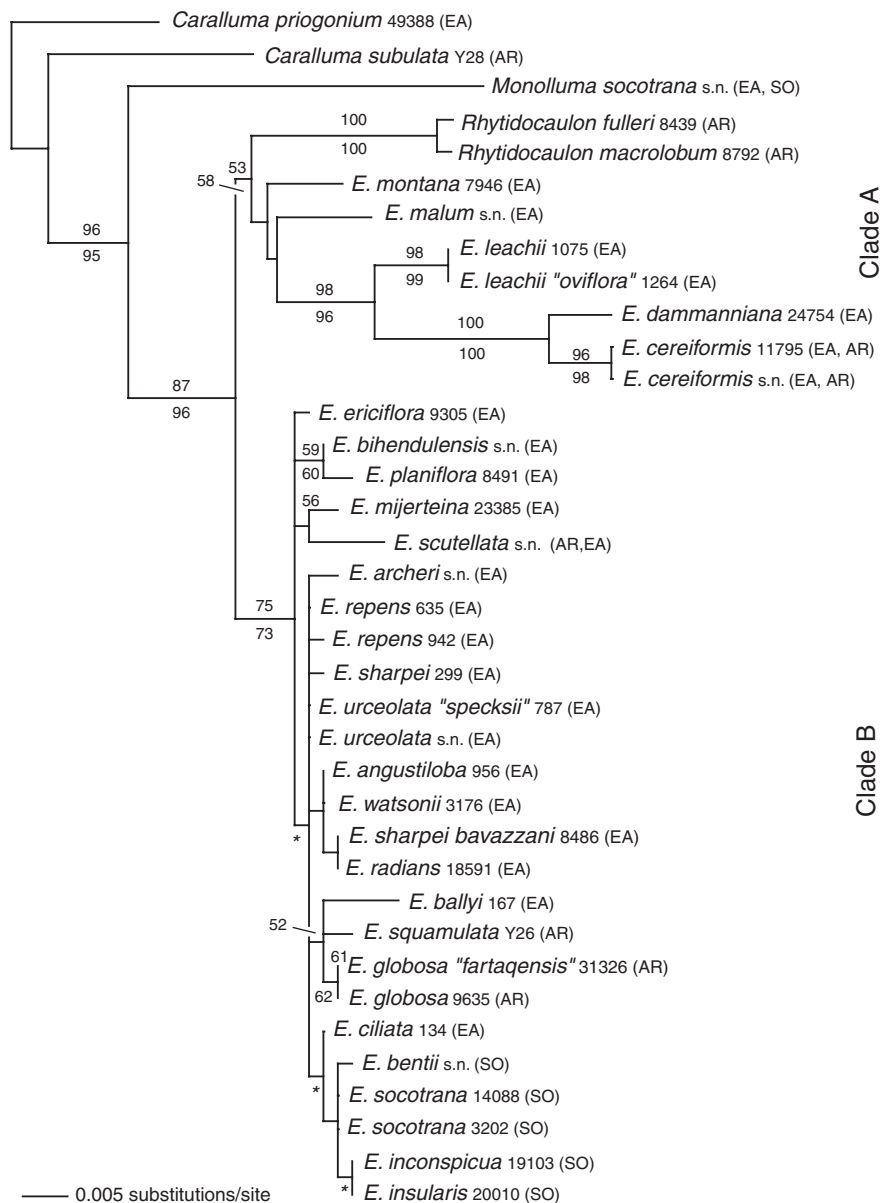
Fig. 1. ML tree of *Echidnopsis* based on nrITS sequences. ML- and MP-Bootstrap values (> 50%) are above and below branches, respectively. Areas of distribution are given in parentheses. *EA* = eastern Africa (Somalo-Ethiopian Province of Takhtajan 1986), *AR* = Arabia (South Arabian Province), *SO* = Socotra (Socotran Province). For species distribution area see table 2. Asterisks mark nodes collapsed in the MP strict consensus tree. *E.* = *Echidnopsis*. Numbers following species names refer to the collection numbers given in Table 2

analysis, this clade is supported by morphology. All species share 6–8 stem ribs, while *E. ciliata* has 8–10 ribs. We thus propose that the Socotran species form a monophyletic clade which might have been descended from an element related to the East African *E. ciliata*. Whether the fifth Socotran element, *E. milleri*, still not investigated in molecular phylogenetic studies, belongs to this group as well is still to be answered (cf. also Bruyns 2004).

Considering the weakly resolved and supported topologies, we argue that the phylogenetic relationships still need further investigation. Future analyses should aim at
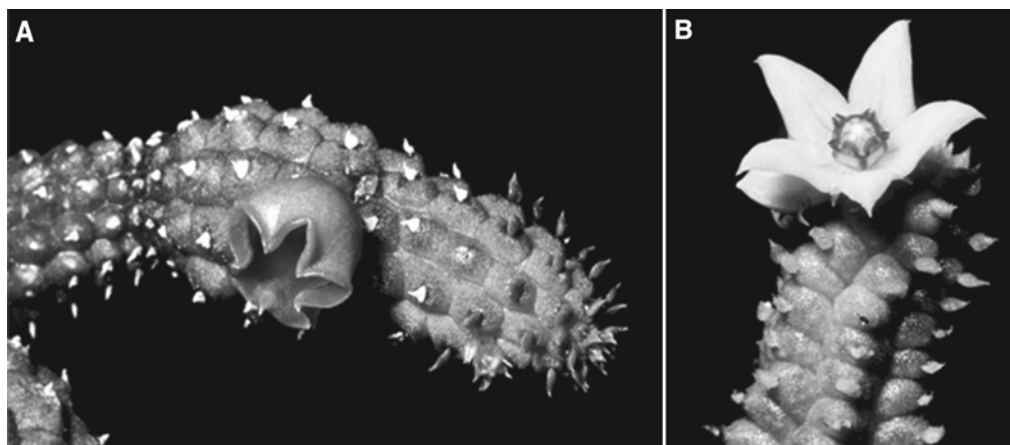
Fig. 2. Flowering stems of *Echidnopsis*. **A** *Echidnopsis archeri* (Kenya, McCoy s.n.); **B** *Echidnopsis socotrana* (Socotra, Thiv 3202). Photo: U. Meve

the addition of more informative phylogenetic markers in order to increase the resolution, and the support for the nodes in question.

The taxonomy of *Echidnopsis* has been the subject of much debate during recent decades (Bruyns 1988, Plowes 1993, Müller and Albers 2002). Supported or not contradicted by our molecular data, but mainly considering morphology, we here slightly refine the taxonomical concept of the genus. All taxa that have been accepted in *Echidnopsis* by previous as well as the present authors are shown in Table 1 (with the names accepted here printed in bold). The sectional concept of Bruyns (1988), who recognized four sections, is blurred by our molecular data. Instead, *Echidnopsis* falls into two clades. This is not corroborated by morphological details. *E. dammanniana* and *E. cereiformis* are closely related as proposed by Bruyns (1988), but not a single of Bruyns' (1988) four sections is pictured in our cladogram. Because we believe all *Echidnopsis* species to be closely related, and none of the major clades could be keyed out morphologically, recognition of sections is not appropriate. Some specific and infraspecific treatments nevertheless need to be discussed in more detail and several taxonomic changes are implemented here.

Bruyns (1988) included the monotypic genus *Pseudopectinaria* (*P. malum*) in *Echidnopsis*, but the genus was resurrected again by Plowes in 1993 (Table 1). Lavranos (2006) upholds the idea of a genus *Pseudopectinaria*, emphasizing the amazing "lobster pot corolla" and stem characteristics. However, *P. malum* is nested in *Echidnopsis* in the molecular tree. Therefore, it cannot be regarded as a genus of its own without making *Echidnopsis* paraphyletic a second time.

Bruyns (1988) has demonstrated the broad in flower morphology amplitude found in *E. urceolata*. The recently described *E. specksii* clearly falls within this range, and since stem and corona morphology are also indistinguishable from those of *E. urceolata*, and no molecular difference could be found either (Fig. 1), *E. specksii* is put into synonymy.

Echidnopsis planiflora and *E. scutellata* are found in different subclades within clade B (Fig. 1). This contradicts their conspecifity (*E. scutellata* with several subspp.) as proposed by Bruyns (1988). The necessary separation into two different species is also indicated by the somewhat different shape of the stems and leaf rudiments (cf. illustrations in Bruyns 1988; Plowes 1993): *E. planiflora* has 11–15-angled stems and long, acute leaf rudiments, whereas *E. scutellata* usually has 8-angled stems and shorter, less acute leaf rudiments. Most similar to *Echidnopsis planiflora* is *E. chrysantha*, accepted as species by Plowes but subsumed

under *E. scutellata* subsp. *planiflora* by Bruyns (1988). *Echidnopsis chrysantha* can be well distinguished from *E. planiflora* by its flower morphology, but not by vegetative characters. We therefore propose to treat 1) *E. planiflora* as a species of its own, and 2) *E. chrysantha* as subspecies of *E. planiflora*.

Molecularly, the complex of *Echidnopsis bavazzani/E. ciliata/E. repens/E. sharpei* is shown to be very closely related, but this is also true for a handful of additional species (Fig. 1). Among the species of clade B, *E. ciliata* is found in a different subclade and is more closely related to the Socotran taxa (Fig. 1). Examining flower and stem morphology in more detail, *Echidnopsis bavazzani/E. ciliata/E. repens/E. sharpei* clearly fall into two groups. Subcampanulate corollas with corona/gynostegium enclosed by the corolla tube and repent, firm stems with elongated, flattened tubercles bearing lanceolate leaf rudiments with stipules are characteristic of *E. repens* and *E. ciliata*. Whereas rotate corollas with corona/gynostegium exserted, and repent-ascending, soft stems with subcircular, prominent tubercles bearing heart-shaped leaf rudiments without stipules are characteristic of *E. sharpei* and *E. bavazzani*. We propose taxonomic changes at infraspecific (*E. sharpei* and *E. sharpei* ssp. *bavazzani*) and specific level (*E. repens, E. ciliata*) according to this grouping. Morphologically, *E. ciliata* could be properly treated as a subspecies of *E. repens*. However, we here propose re-establishment of species rank for *E. ciliata* due to the indications provided by the molecular analysis (Fig. 1).

Bruyns (1988) subsumed *Echidnopsis radians* under *E. watsonii*. Plowes (1993) reinstated *E. radians* – a view which was followed by Müller and Albers (2002) and by ourselves. Both taxa share the same subclade in our nrITS phylogeny but at the same time they do not seem to be sister taxa (Fig. 1). *Echidnopsis radians* is also karyologically and geographically differentiated from *E. watsonii*, since it is diploid (cf. Table 1) and distributed in Kenya,

whereas *E. watsonii* is tetraploid and restricted to Somalia.

Typical *E. leachii* has shortly campanulate flowers, whereas the recently described *E. oviflora* McCoy, which is based on a single specimen only, differs only in the shape and size of the corolla, which is ovoid-suburceolate and fairly large. Since no other substantial differences, and no molecular evidence (Fig. 1) could be found, and with both of these strictly Tanzanian elements being so markedly characterized by their slightly bullate stem surfaces similar to those of *Rhytidocaulon*, *E. oviflora* cannot maintained as a distinct species. At the most, one might regard it as a variety of *E. leachii*, but more collections, also from the type locality of *E. oviflora*, would be needed in order to determine whether or not an independent status should be supported.

Finally, *E. fartaqensis*, molecularly not deviating from *E. globosa* (Fig. 1), is only differing in flower size. Therefore, it should be recognized as synonym of *E. globosa*, as recently proposed by Bruyns (2004).

Formal taxonomic changes have become necessary in the following cases as discussed above:

1. Echidnopsis malum (Lavranos) Bruyns, Bradleya 6: 43 (1988).
≡ *Pseudopectinaria malum* Lavranos, Cact. Succ. J. (Los Angeles) 43(1): 10 (1971).
Type: Somalia, 22 km N Erigavo, *Lavranos* 6721 (FT, holo; in spiritu, now dried out).
Distribution: Somalia.

2. Echidnopsis planiflora P.R.O. Bally, Cact. Succ. J. Gr. Brit. 18: 109 (1956).
≡ *Echidnopsis scutellata* subsp. *planiflora* (P.R.O. Bally) Bruyns, Bradleya 6: 19 (1988).
Type: Ethiopia, 2 miles NW Dire Dawa, *Mitford-Barberton* s.n. in *Bally* S105 (ZSS, holo).
= *Echidnopsis flavicorona* Plowes, Haseltonia 1: 73 (1993).
= *Echidnopsis hirsuta* Plowes, Haseltonia 1: 74 (1993).

= *Echidnopsis plowesiana* Orlando, Kakt. and. Sukk. 55: 158 (2004), *syn. nov.*

Key to the subspecies of *E. planiflora*:
a. Flowers rotate, corolla (mostly) ciliate, corona subsessile or stalked, flattish to slightly cup-shaped .... *E. planiflora* subsp. *planiflora*
b. Flowers subcampanulate, glabrous, corona sessile, cup-shaped .... *E. planiflora* subsp. *chrysantha*

2a. subsp. ***planiflora***
Distribution: Djibouti, Ethiopia, Somalia.

2b. *E. planiflora* subsp. ***chrysantha*** (Lavranos) Meve & Thiv, *comb. nov.*

≡ *E. chrysantha* Lavranos, Cact. Succ. J. (Los Angeles) 43(2): 65 (1971). Type: Somalia, 4 km NW Erigavo, *Lavranos* 7325 [FT, holo (in spiritu, now dried out); K, ZSS].
= *E. chrysantha* subsp. *filipes* (Lavranos) Plowes, Haseltonia, 1: 75 (1993) ≡ *Echidnopsis chrysantha* var. *filipes* Lavranos, Cact. Succ. J. (Los Angeles) 46: 184 (1974).
Distribution: Somalia.

With the separation of *E. planiflora*/ *E. chrysantha* from *E. scutellata* s.l., three subspecies remain in *E. scutellata* (subsp. *scutellata*, subsp. *australis* = *E. mariae* sensu Plowes (1993), and subsp. *dhofarensis*).

3. *Echidnopsis repens* R.A. Dyer & I. Verdoorn, Cact. Succ. J. (Los Angeles) 11: 68 (1939).

≡ *Echidnopsis sharpei* subsp. *repens* (R.A. Dyer & Verdoorn) Bruyns, Bradleya 6: 37 (1988).
Type: Tanzania, Aldenyo, near Mt. Meru, *Pole-Evans & Erens* 1020 (PRE, holo).
Distribution: Tanzania, Kenya.

Echidnopsis repens can be keyed out against *E. ciliata* as follows:
Flowers 7–9 mm diam, glabrous or adaxially with scattered hairs, abaxially greenish: .... *E. repens*
Flowers 10–15 mm diam., adaxially densely hairy, abaxially spotted purple on grey-green *E. ciliata*

4. *Echidnopsis ciliata* P.R.O. Bally, Cact. Succ. J. Gr. Brit. 19: 58 (1957).

≡ *E. sharpei* A.C. White & B. Sloane subsp. *ciliata* (P.R.O. Bally) Bruyns, Bradleya 6: 38 (1988). Type [lecto]: Somalia, upper Sheikh Pass, 1440 m, 1 May 1949, *Bally* 7167 [icono: Cact. Succ. J. Gr. Brit. 19: 59, top fig., 1957); lectotype selected by Bruyns (1988: 38)].
Distribution: Somalia.

5. *Echidnopsis sharpei* A.C. White & B. Sloane, Cact. Succ. J. (Los Angeles) 11: 67 (1939).

Type: Kenya, 30 miles S Lake Turkana, *Sharpe & Jex-Blake* s.n. [K, lecto (selected by Bruyns 1988: 33); ZSS, isolecto].

Key to the subspecies of *E. sharpei*:
a. Stems 6-angled, gynostegium with corona sessile .... *E. sharpei* subsp. *sharpei*
b. Stems 8-angled, gynostegium with corona subsessile to stalked................................... *E. sharpei* subsp. *bavazzani*

a. subsp. ***sharpei***
Distribution: Kenya.

b. *E. sharpei* subsp. ***bavazzani*** (Lavranos) Meve & Thiv, *comb.* et *stat. nov.*

≡ *Echidnopsis bavazzani* Lavranos, Cact. Succ. J. (Los Angeles) 46: 181 (1974).
Type: Somalia, 7 km S Las Anod, *Lavranos & Bavazzani* 8428 [FT, holo (not found); SRGH].
= *Echidnopsis lavraniana* Plowes, Haseltonia 1: 79 (1993), *syn. nov.*
Distribution: Ethiopia, Somalia.

6. *Echidnospsis globosa* M. Thulin & M. Hjertson, Nordic J. Bot. 15(3): 261 (1995).

Type: Yemen, Hadramaut, 14 km from the turning of the Masila field on the road from Al Mukalla to Sayun, *Thulin, Eriksson, Gifri & Langström* (UPS, holo; K).
= *Echidnopsis fartaqensis* McCoy & Orlando, Cact. Succ. J. (Los Angeles) 75(3): 116 (2003), *syn. nov.*
Distribution: Yemen.

7. *Echidnopsis leachii* Lavranos, Natl. Cact. Succ. J. 27: 69 (1972).

Type: Tanzania, Ruaha River Gorge (*Leach & Brunton* 10143 (EA, holo; K; ZSS).
    = *Echidnopsis oviflora* T.A. McCoy, Kakt. and. Sukk. 54(8): 214 (2003), *syn. nov.*
    Distribution: Tanzania.

8. *Echidnopsis urceolata* P.R.O. Bally, Candollea 18: 342 (1963).

Type: Kenya, Northern Frontier Prov., Malka Murri, *Williams* s.n. in *Bally* B8008 (K, holo; ZSS).
    = *Echidnopsis urceolaris* P.R.O. Bally, Cact. Succ. J. Gr. Brit. 18: 108 (1956), *nom. inval.* (Art. 36.1).
    = *Echidnopsis specksii* T.A. McCoy, Kakt. and. Sukk. 54(8): 215 (2003), *syn. nov.*
    Type: Ethiopia: Sidamo Prov., *Specks* 787 (MO, holo; UBT, UPS).
    Distribution: Ethiopia, NE Kenya.

Biogeography. The Socotran archipelago constitutes a former fragment of continental Arabia (Richardson et al. 1995, Fleitmann et al. 2004). Though dating of its separation is still debated, with estimates ranging from 10 mya (Miller and Morris 2004) to 65–70 mya (Kopp 1999, Mies 2001), recent geological studies narrow this age to 35–15 mya (Fleitmann et al. 2004, Van Damme, pers. comm.) before the opening of the Gulf of Aden, e.g., when Arabia and Africa were still connected (Laughton et al. 1970, Richardson et al. 1995, Fleitmann et al. 2004). Socotra harbours five species of *Echidnopsis*. These taxa are here regarded as a natural group, though, statistical support is lacking in the molecular analysis (Fig. 1). We largely follow Bruyns (2004) who grouped *E. bentii*, *E. inconspicua*, *E. insularis*, and *E. milleri* together based on corona morphology and placed *E. socotrana* with *E. sharpei* and related species. Emphasizing characters of the interstaminal corona, stem and leaves, however, we suggest a close relationship of *E. socotrana* to *E. inconspicua*. The putative sister group of the Socotran lineage, *E. ciliata*,

is native to eastern Africa. Because this insular group appears to be nested within the mostly east African clade B (Fig. 1), we conclude this area to be the source area for the Socotran lineage. This parallels biogeographic patterns found in other taxa. The majority of Socotran endemics has been shown to be of eastern African origin, e.g., *Duvaliandra dioscorides* (Lavranos) M.G. Gilbert (Apocynaceae-Asclepiadoideae: Meve 1997; Meve and Liede 2002), *Chapmannia* Torr. & Gray (Fabaceae: Lavin et al. 2000), *Aerva* Forssk. (Amaranthaceae: Thiv et al. 2006), and *Thamnosma socotrana* Balf. f. (Rutaceae: Thiv et al., unpubl. data.).

A vicariance origin of the Socotran *Echidnopsis* clade, e.g. a rafting from the mainland with continental drift, would predict a sister-group relationship to an Arabian taxon and a separation age of the Socotran lineage which corresponds to that of the archipelago (35–15 mya). There are two arguments against such a hypothesis. As pointed out, an eastern African origin is more likely as other species of the clade have African distributions. Moreover, the low genetic variation found in plastid and nuclear markers indicates a rather recent age for the corresponding nodes (Gaut 1998, Olmstead et al. 1998) contradicting a vicariance origin. Unfortunately, no calibration points were found to date the phylogeny. We argue for long distance dispersal as the colonization mechanism. This would be easily promoted by the very small (ca. 3×1.5 mm), comose seeds of *Echidnopsis*, which are among the smallest and lightest of all Asclepiadoideae (Meve, unpubl.).

Although the support obtained in the molecular analyses is low, morphological evidence (discussed above) suggests a close relationship between the four Socotran taxa here examined. Such minor radiation is in sharp contrast to the patterns observed on other oceanic island groups, e.g. the Canary Islands or Madagascar, where many taxa underwent a broad radiation (Grant 1998). Examples include *Echium* L. (Böhle et al. 1996), Macaronesian Sempervivoideae (Mes 1995, Mort et al. 2002), *Argyranthemum* Webb ex Sch. Bip. (Francisco-Ortega et al. 1997) and

Kalanchoe Adans. (Allorge-Boiteau 1996). One can only speculate as to why this lineage has not radiated more on Socotra. A possible correlation can be sought between this phenomenon and the accessibility of ecological niches (Schluter 2000). In contrast to the volcanic origins of the Canarian and Hawaiian archipelagos, Socotra is of continental origin (Mies 2001, Miller and Morris 2004). This might have led to a continuous vegetation on the island rather than an abrupt and simultaneous availability of an array of new niches. A second possible reason for the moderate degree of radiation is the island's small size. Compared with Madagascar, for example, Socotra is much smaller and thus, offers less space for establishment of essential minimum population sizes (MacArthur and Wilson 1967). Other explanations could be that the group is too young for much speciation or extinction events to have taken place.

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