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A molecular phylogeny and generic rearrangement of the stapelioid Ceropegieae (Apocynaceae-Asclepiadoideae)

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Abstract. Representatives of nearly all genera of the taxon-rich stem-succulent stapeliads and most of the few related, leafy genera were analyzed. Sequence data from two non-coding molecular markers (ITS region of nrDNA and *trn*T-L and *trn*L-F spacers as well as the *trn*L intron of cpDNA) support the traditional tribal affiliation of the genera, which form a monophyletic group. This monophylum breaks into a basal *Neoschumannia*/*Anisotoma*/*Riocreuxia*/*Sisyranthus* clade, from which the core Ceropegieae are derived. The four *Ceropegia* species included are not monophyletic, and their relationship to *Brachystelma* changes depending on the marker studied. The stem succulent taxa fall in a number of well supported, but unresolved clades, the most prominent being the predominantly southern African clade comprising *Orbea*, *Stapelia* and some other genera. The most derived taxa of NE Africa, *Duvaliandra* and *Whitesloanea*, are basal to this southern African clade. The other clades comprise the more basal genera of stem-succulent stapeliads, including the members of the *Caralluma* complex. Of the 17 genera accepted by Plowes for the *Caralluma* complex, seven are recognized: *Caralluma*, *Apteranthes*, *Australluma*, *Boucerosia*, *Caudanthera*, *Desmidorchis* and *Monolluma*. New combinations are proposed in 15 cases; *Caralluma adscendens* var. *geniculata* is raised to specific rank. *Anomalluma* is reinstated, and *Pseudolithos mccoyi* is transfered to it. A broadened concept for *Orbea* (incl. *Angolluma* and *Orbeopsis*) is recognized, but *Orbeanthus* is kept separate. The monotypic *Ballyanthus*, recently separated from *Orbea*, is nested within *Duvalia*. *Piaranthus* (incl. *Huerniopsis*) is monophyletic. The bitypic *Notechidnopsis* is reduced to the type species, *N. tessellata*, while *N. columnaris* is transferred to a new genus, *Richtersveldia*.

Key words: Apocynaceae-Asclepiadoideae, *Caralluma*, Ceropegieae, cpDNA, ITS region, molecular systematics, nrDNA, *Richtersveldia*, stapeliads, taxonomy, *trn*T-L spacer, *trn*L intron, *trn*L-F spacer.

Only sixty years after Linné (1753: 217) described the first stapeliad species, *Stapelia* (*Orbea*) *variegata* (L.) L. C. Leach and *Stapelia hirsuta* L., the taxonomic treatment of the stem-succulent (stapelioid) members of the tribe Ceropegieae Orb. started to become subject to frequent changes, a trend continuing to this date. In the early days, when most of the new plants originated from South Africa, stapeliads were described in only one genus, *Stapelia* [(e.g. Masson 1796 in "Stapelieae Novae"; Jacquin 1806–1819)]. But with an increasing number of new species, R. Brown (1810) and Haworth (1812) realized that there are groups of species united by significant characters deserving formal taxonomic recognition. Brown (1810) and Haworth (1812) introduced genera such as *Caralluma*, *Duvalia*, *Huernia*, and *Pectinaria*, *Piaranthus*, *Tridentea* and *Tromotriche*, all of which are still widely accepted. In the late nineteenth and twentieth century not only the number of species described exploded, but also the number of stapeliad genera increased to over 30 (cf. Bruyns and Forster 1991). This taxonomic trend culminated in the split of the genus *Caralluma* into 17 genera by Plowes (1995). During the completion of the present study, we saw a reversal of this trend with the inclusion of *Huerniopsis* in *Piaranthus* (Bruyns 1999a), and of *Angolluma*, *Pachycymbium*, *Orbeanthus* and *Orbeopsis* in *Orbea* (Bruyns 2001). However, new monotypic genera such as *Baynesia* and *Ballyanthus* were also created (Bruyns 2000c, 2001). In addition to these two, an additional 25 stapeliad genera are accepted by Endress and Bruyns (2000) in the tribe Ceropegieae Orb., which encompasses also 15 less fleshy, herbacous to woody genera.

The stem-succulent stapeliads were always regarded as a group of closely related species of common ancestry, a monophylum (cf. Schumann 1898, Good 1947). Bentham and Hooker (1876) raised this succulent group to tribal level, the Stapelieae, while keeping the (mostly) non-succulent rest of the tribe separate as Ceropegieae. Today, succulent and non-succulent taxa possessing clear latex, erect pollinia with germination crest along the inner margin, or on the apex, are considered as a single tribe, Ceropegieae Orb. (Bruyns and Forster 1991, as Stapelieae Decne.). For many years, the origin of stem-succulent stapeliads was supposed to be in India (Good 1947) because the only stapeliad possessing an unreduced true foliage, *Boucerosia frerei* (= *Frerea indica*), is endemic to this subcontinent. But Albers (1983) expressed first doubts about this hypothesis with regard to the derived genome size of the polyploid *B. frerei* ($2n = 44$) in contrast to the otherwise diploid Indian *Boucerosia* (*Caralluma*) taxa (cf. Albers and Meve 2001). Recently, Meve (1997) demonstrated that the centre of stapeliad origin is identical to the centre of highest diversity in the basal *Caralluma* s.l. group, which is in East Africa. Bruyns (2000b) adopted Meve's (1997) concept for which he (Bruyns 2000b) found support in a cladistic biogeographical analysis. The large number of species (ca. 350) in stem-succulent Ceropegieae, distributed in S Europe, Africa, Arabia and parts of Asia, and their often disputed generic affiliations, have impeded phylogenetic analysis. Bruyns (2000a) offered a cladistic analysis using 55 morphological characters. However, in the light of the still unknown, but presumably considerable extent of parallelisms and homoplasies in stem and flower morphology as response to specific habitat conditions and pollinator pressure (e.g. Meve and Liede 1999, Liede and Meve 2000), Bruyns' (2000a) resulting phylograms must be examined with caution. A phylogeny based on data independent from morphological similarities is therefore necessary. The *trn*T-L and *trn*L-F spacers as well as the *trn*L intron of cpDNA has been used successfully in Asclepiadoideae for the delimitation of tribes, subtribes and groups of genera (Liede 2001, Liede and Täuber 2000, and in press). As most of the genera analyzed here were suspected to be closely related, the more variable ITS region of ribosomal nuclear DNA was analyzed as well. Two previous studies in the Ceropegieae s.l. using the same markers led to the inclusion of *Macropetalum* and *Tenaris* in *Brachystelma* (Meve and Liede 2001a), and the resurrection of *Larryleachia* against *Lavrania* (Meve and Liede 2001b). The latter investigation pointed to the occurrence of hybrid origin and lineage sorting in stapeliads, so that the use of two markers of independent inheritance on a larger scale will provide more insight in these patterns.

Material and methods

Taxa. The material used in this study, including voucher specimens, authors of species and donors of material, are summarized in Table 1. Throughout this study, especially in the phylograms, the names accepted, based on the results of our investigations, are used (for the often better known synonyms, see Table 1).

Table 1. Voucher and locality information, and EMBL accession numbers for plant material used in the molecular studies

Species	Origin	Voucher	EMBL acc. no. *trn*T-L spacer *trn*L intron *trn*L-F spacer	EMBL acc. no. ITS
Outgroup				
Secamone alpinii Schult. (Secamoneae)	South Africa: Eastern Cape	*Liede 2931* (UBT)	AJ4218828 AJ428829 AJ428830	–
Gymnema sylvestre (Retz.) Schult. (Marsdenieae)	Cameroon: E of Mokolo	*Meve 919* (B, UBT)	AJ402118 AJ402137 AJ402142	–
Anisotoma cordifolia Fenzl	South Africa: Eastern Cape	*Nicholas 2811* (UDW)	AJ410016 AJ410017 AJ410018	AJ310780
Neoschumannia cardinea (S. Moore) Meve	Tanzania: Amani Forest Reserve	*Liede & Meve 3359* (B, UBT)	AJ410049 AJ410050 AJ410051	AJ310790
Neoschumannnia kamerunensis Schltr.	Cameroon: Mt. Cameroon	*Meve & Etuge 910* (B, K, UBT)	AJ410052 AJ410053 AJ410054	AJ310791
Riocreuxia burchellii Decne.	South Africa: KwaZulu-Natal	*ex hort. Shirley* (MSUN)	AJ488306 AJ488307 AJ488308	AJ488771
Sisyranthus compactus N.E. Br.	South Africa: Kei Mouth	*Nicholas 2825* (UDW)	AJ410067 AJ410068 AJ410069	AJ310795
Ingroup				
Anomalluma mccoyi (Lavranos & Mies) Meve & Liede = *Pseudolithos mccyoi* Lavranos & Mies	Oman: Mirbat	*Butler & Lauchs s.n.* (UBT)	AJ488309 AJ488310 AJ488311	AJ488772
Apteranthes europaea (Gussone) Plowes var. *europaea* = *Caralluma europaea* (Gussone) N.E. Br.	Spain: Capo da Gata	*Albers 87-23-004-20* (MSUN)	AJ488312 AJ488313 AJ488314	AJ488773

Table 1 (continued)

Species	Origin	Voucher	EMBL acc. no. *trn*T-L spacer *trn*L intron *trn*L-F spacer	EMBL acc. no. ITS
Apteranthes munbyana (Decne. ex Munby) Meve & Liede = *Caralluma munbyana* (Decne. ex Munby) N.E. Br. = *Borealluma munbyana* (Decne. ex Munby) Plowes	Spain: Murcia	*Berthet s.n.* (UBT)	AJ488315 AJ488316 AJ488317	AJ488774
Apteranthes tuberculata (N.E. Br.) Meve & Liede = *Caralluma tuberculata* N.E. Br. = *Borealluma tuberculata* (N.E. Br.) Plowes	s. loc.	*sub Specks 731* (MSUN)	AJ488318 AJ488319 AJ488320	AJ488775
Australluma peschii (Nel) Plowes = *Caralluma peschii* Nel	Namibia: s. loc.	*ex hort. Bosma* (MSUN, UBT)	AJ488321 AJ488322 AJ488323	AJ488776
Boucerosia frerei (Rowley) Meve & Liede = *Caralluma frerei* Rowley = *Frerea indica* Dalz.	India: SE of Poona	*Sakaria sub K 781* (MSUN)	AJ488324 AJ488325 AJ488326	AJ488777
Boucerosia umbellata (Haw.) Wight & Arn. = *Caralluma umbellata* (Haw.) N.E. Br.	India: Tumkur	*Sarkaria 81-75* (in hort. UBT)	AJ488327 AJ488328 AJ488329	AJ488778
Brachystelma burchellii (Decne.) Peckover = *Macropetalum burchellii* Decne.	South Africa: Bloemfontein	*Peckover* sub *Specks 3156* (UBT)	AJ410046 AJ410047 AJ410048	AJ310789
Brachystelma pygmaeum (Schltr.) N.E. Br. ssp. *flavidum* R.A. Dyer	South Africa: KwaZulu-Natal	*Ward s.n.* (UDW)	AJ410031 AJ410032 AJ410033	AJ310784
Caralluma adscendens (Roxb.) N.E. Br. var. *attenuata* Wight	India: Madurai	*Sarkaria J 24-90* (UBT)	AJ488330 AJ488331 AJ488332	AJ488779

Table 1 (continued)

Caralluma arachnoidea (P.R.O. Bally) M.G. Gilbert	Kenya: Rukanga	*Meve 934* (UBT)	AJ410037 AJ410038 AJ410039	AJ310785
Caralluma priogonium K. Schum.	Somalia: N Mogadiscio	*Koenen & Krapp* 49388 (MSUN)	AJ488333 AJ488334 AJ488335	AJ488780
Caralluma subulata (Forssk.) Decne.	Sudan: Darfur	*Plowes 7481* (UBT)	AJ488336 AJ488337 AJ488338	AJ488781
Caudanthera edulis (Edg.) Meve & Liede = *Caralluma edulis* (Edg.) Benth. = *Cryptolluma edulis* (Edg.) Plowes	Oman: W of Salalah	*Butler C312* (UBT)	AJ402116 AJ402139 AJ402140	AJ402162
Caudanthera sinaica (Decne.) Plowes = *Caralluma sinaica* (Decne.) A. Berger	Israel: Miszpe Shalem	*Bruyns 2484* (K, UBT)	AJ488339 AJ488340 AJ488341	AJ488782
Ceropegia bulbosa Roxb.	India: s. loc.	*Rowland sub Butler* C 726 (UBT)	AJ488342 AJ488343 AJ488344	AJ488783
Ceropegia distincta N.E. Br. ("*C. brevirostris*")	Tanzania: Amani	*Liede & Meve 3376* (EA, UBT)	AJ488345 AJ488346 AJ488347	AJ488784
Ceropegia juncea Roxb.	India: Tamil Nadu	*Řičánek & Hanáček 92* (UBT)	AJ428798 AJ428799 AJ428800	AJ488785
Ceropegia striata Meve & Masinde	Madagascar: Antsirabe	*Rauh 75007* (HEID, MSUN)	AJ410043 AJ410044 AJ410045	AJ310788
Desmidorchis acutangulus Decne. = *Caralluma acutangula* (Decne.) N.E. Br.	Somalia: s. loc.	*Koenen & Krapp 22647* (in hort. UBT)	AJ488348 AJ488349 AJ488350	AJ488786

Table 1 (continued)

Species	Origin	Voucher	EMBL acc. no. *trn*T-L spacer *trn*L intron *trn*L-F spacer	EMBL acc. no. ITS
Desmidorchis adenensis (Deflers) Meve & Liede = *Caralluma adenensis* (Deflers) A. Berger = *Crenulluma adenensis* (Deflers) Plowes	Oman: Wadi Afal	*Collenette 8389* (MSUN)	AJ488351 AJ488352 AJ488353	AJ488787
Desmidorchis arabicus (N.E. Br.) Meve & Liede = *Caralluma arabica* N.E. Br. = *Crenulluma arabica* (N.E. Br.) Plowes	Oman: Ra's al-Hamra	*Jonkers HAJ 16* (MSUN)	AJ488354 AJ488355 AJ488356	AJ488788
Desmidorchis flavus (N.E. Br.) Meve & Liede = *Caralluma flava* N.E. Br. = *Crenulluma flava* (N.E. Br.) Plowes	Oman: Mugsail	*Collenette s.n.* (MSUN)	AJ488357 AJ488358 AJ488359	AJ488789
Desmidorchis lavrani (Rauh & Wertel) Meve & Liede = *Caralluma lavranii* Rauh & Wertel = *Crenulluma lavranii* (Rauh & Wertel) Plowes	Yemen: s. loc.	*Frank 119* (MSUN, UBT)	AJ488360 AJ488361 AJ488362	AJ488790
Desmidorchis penicillatus (Deflers) Plowes = *Caralluma penicillata* (Deflers) N.E. Br.	Yemen: N of Taizz	*Řičánek & Hanáček 249* (UBT)	AJ488363 AJ488364 AJ488365	AJ488791
Duvalia angustiloba N.E. Br.	South Africa: E of Beaufort West	*Meve 321* (MSUN)	AJ488366 AJ488367 AJ488368	AJ488792
Duvalia eilensis Lavranos	Somalia: Eil	*Lavranos et al. 24952* (MSUN)	AJ488369 AJ488370 AJ488371	AJ488793

Table 1 (continued)

Duvalia polita N.E. Br.	South Africa: Hammannskraal	*Meve 469* (MSUN)	AJ488372 AJ488373 AJ488374	AJ488794
Duvaliandra dioscorides (Lavranos) M.G. Gilbert = *Caralluma dioscorides* Lavranos	Yemen (Socotra): Adho Dhemalu	*Lavranos 1821* (UBT)	AJ488375 AJ488376 AJ488377	AJ488795
Echidnopsis angustiloba E.A. Bruce & P.R.O. Bally	Kenya: N of Longobito	*Meve 959* (MSUN)	AJ488378 AJ488379 AJ488380	AJ488796
Echidnopsis repens R.A. Dyer & Verdoorn	Kenya: Mt. Maktau	*Meve 942* (MSUN, UBT)	AJ488381 AJ488382 AJ488383	AJ488797
Echidnopsis squamulata (Decne.) P.R.O. Bally	Yemen: E of Al Thaluth	*Mangelsdorff Y27* (UBT)	AJ488384 AJ488385 AJ488386	AJ488798
Edithcolea grandis N.E. Br.	Tanzania: Mkomasi	*Liede & Meve 3385* (in hort. UBT)	AJ488387 AJ488388 AJ488389	AJ488799
Hoodia gordonii (Masson) Sweet	South Africa: Pofadder	*Jürgens 22837* (MSUN, UBT)	AJ488390 AJ488391 AJ488392	AJ488800
Hoodia officinalis (N.E. Br.) Plowes	Namibia: E of Aus	*Meve 176* (MSUN, UBT)	AJ488393 AJ488394 AJ488395	AJ488801
Huernia keniensis R.E. Fries	Kenya: N of Maralal	*Meve 963* (MSUN)	AJ488396 AJ488397 AJ488398	AJ488802
Huernia kennedyana Lavranos	South Africa: W of Cradock	*Meve 458* (K, MSUN, NBG)	AJ488399 AJ488400 AJ488401	AJ488803
Larryleachia cactiformis (Hook.) Plowes	South Africa: Numees	*Teissier 097* (UBT)	AJ402120 AJ402135 AJ402144	AJ402159
Larryleachia perlata (Dinter) Plowes	South Africa: Richtersveld	*Jürgens* s.n. (UBT)	AJ402121 AJ402134 AJ402145	AJ402158

Table 1 (continued)

Species	Origin	Voucher	EMBL acc. no. *trn*T-L spacer *trn*L intron *trn*L-F spacer	EMBL acc. no. ITS
Lavrania haagnerae Plowes	Namibia: Khowarib Gorge	*Haagner* sub *Plowes* 5046 (PRE, MSUN)	AJ402119 AJ402136 AJ402143	AJ402160
Monolluma hexagona (Lavranos) Meve & Liede	Yemen: s. loc.	*s. coll.* (*sub Plowes* 5095) (UBT)	AJ488402 AJ488403 AJ488404	AJ488804
Monolluma quadrangula (Forssk.) Plowes = *Caralluma quadrangula* Forssk.)	Yemen: NW of Sanáa	*Ričánek* & *Hanáček 201* (UBT)	AJ488405 AJ488406 AJ488407	AJ488805
Monolluma socotrana (Balf. f.) Meve & Liede = *Caralluma socotrana* Balf. f. = *Sanguilluma socotrana* (Balf. f .) Plowes	Kenya: Baringo	*ex hort. W. Bosma* (in hort. UBT)	AJ488408 AJ488409 AJ488410	AJ488806
Notechidnopsis tessellata (Pillans) Lavranos & Bleck	South Africa: Nieuwouldtville	*Meve 256* (MSUN)	AJ402123 AJ402132 AJ402147	AJ402156
Ophionella arcuata (N.E. Br.) Bruyns ssp. *arcuata*	South Africa: Eastern Cape	*Bruyns 4966* (UBT)	AJ488411 AJ488412 AJ488413	AJ488807
Orbea gerstneri (Letty) Bruyns ssp. *gerstneri* = *Orbeopsis gerstneri* (Letty) L.C. Leach	South Africa: Empangeni	*Bayer & de Kock s.n.* (MSUN)	AJ488414 AJ488415 AJ488416	AJ488808
Orbea keithii (R.A. Dyer) Meve & Liede = *Pachycymbium keithii* (R.A. Dyer) L.C. Leach	South Africa: Ingwavama	*Strey 7332* (MSUN, UBT)	AJ488417 AJ488412 AJ488419	AJ488809
Orbea lutea (N.E. Br.) Bruyns ssp. *lutea* = *Orbeopsis lutea* (N.E. Br.) L.C. Leach	South Africa: W of Potchefstrom	*Albers 3525* (in hort. UBT)	AJ488420 AJ488421 AJ488422	AJ488810

Table 1 (continued)

Orbea prognatha (P.R.O. Bally) L.C. Leach = *Ballyanthus prognathus* (P.R.O. Bally) Bruyns	Somalia: s. loc.	*de Kock 883* (UBT)	AJ488423 AJ488424 AJ488425	AJ488811
Orbea semitubiflora (L.E. Newton) Bruyns = *Angolluma semitubiflora* (L.E. Newton) Plowes	Tanzania: Arusha	*Meve & Liede 3372* (UBT)	AJ488426 AJ488427 AJ488428	AJ488812
Orbea semota (N.E. Br.) L.C. Leach	Tanzania: Arusha	*Specks 921* (UBT)	AJ488429 AJ488430 AJ488431	AJ488813
Orbea valida (N.E. Br.) Bruyns ssp. *valida* = *Orbeopsis valida* (N.E. Br.) L.C. Leach	Namibia: N of Grootfontein	*Rawe s.n.* (in. hort. UBT)	AJ488432 AJ488433 AJ488434	AJ488814
Orbea variegata (L.) L.C. Leach	South Africa: St. Helena Bay	*Bruyns 4571* (MSUN)	AJ488435 AJ488436 AJ488437	AJ488815
Orbea wissmannii (O. Schwartz) Bruyns var. *wissmannii* = *Angolluma wissmannii* (O. Schwartz) Plowes	Yemen: N	*Noltee 483* (MSUN)	AJ488438 AJ488439 AJ488440	AJ488816
Orbeanthus hardyi (R.A. Dyer) L.C. Leach	South Africa: Strijdom Tunnel	*Bruyns 2030* (BOL, MSUN)	AJ488441 AJ488442 AJ488443	AJ488817
Pectinaria articulata (Ait.) Haw. ssp. *borealis* Bruyns	South Africa: Hellskloof	*Albers* & *Meve* 32 (MSUN)	AJ402124 AJ402131 AJ402148	AJ402155
Piaranthus comptus N.E. Br.	South Africa: Klaarstroom	*Albers K 1123* (MSUN)	AJ402126 AJ402129 AJ402160	AJ402153
Piaranthus decipiens (N.E. Br.) Bruyns = *Huerniopsis decipiens* N.E. Br.	South Africa: E of Kuruman	*Meve 580* (MSUN)	AJ488444 AJ488445 AJ488446	AJ488818
Piaranthus framesii Pillans	South Africa: S of Calvinia	*Meve 265* (MSUN)	AJ488447 AJ488448 AJ488449	AJ488819

Table 1 (continued)

Species	Origin	Voucher	EMBL acc. no. *trn*T-L spacer *trn*L intron *trn*L-F spacer	EMBL acc. no. ITS
Pseudolithos migiurtinus (Chiov.) P.R.O. Bally	Somalia: s. loc.	*ex hort. W. Bosma* (UBT)	AJ488450 AJ488451 AJ488452	AJ488820
Quaqua incarnata (L.f.) Bruyns ssp. *incarnata*	South Africa: S of Klawer	*Albers & Meve 06* (MSUN)	AJ488453 AJ488454 AJ488455	AJ488821
Quaqua ramosa (Masson) Bruyns	South Africa: SW of Laingsburg	*Albers 2481* (MSUN)	AJ488456 AJ488451 AJ488458	AJ488822
Rhytidocaulon fulleri Lavranos & Mort.	Oman: E of Salalah	*Collenette 8439* (UBT)	AJ488459 AJ488460 AJ488461	AJ488823
Rhytidocaulon macrolobum Lavranos ssp. *macrolobum*	Yemen: Damt	*Noltee 1667* (MSUN, UBT)	AJ488462 AJ488463 AJ488464	AJ488824
Richtersveldia columnaris (Nel) Meve & Liede = *Notechidnopsis columnaris* Nel	South Africa: Hellskloof	*Albers & Meve 30* (MSUN)	AJ402122 AJ402133 AJ402146	AJ402157
Stapelia glanduliflora Masson	South Africa: S of Klawer	*Albers & Meve 04* (MSUN)	AJ402127 AJ402128 AJ402151	AJ402152
Stapelia rufa Masson	South Africa: S of Laingsburg	*Albers 2483* (MSUN)	AJ488465 AJ488466 AJ488467	AJ488825
Stapelianthus decaryi Choux	Madagascar: Ihosy	*Barad et al. s.n.* (UBT)	AJ488468 AJ488469 AJ488470	AJ488826
Stapeliopsis neronis Pillans	South Africa: Northern Cape	*Kennedy sub Albers 2525* (MSUN)	AJ488471 AJ488472 AJ488473	AJ488827
Stapeliopsis saxatilis (N.E. Br.) Bruyns ssp. *saxatilis*	South Africa: SE of Oudtshoorn	*Meve 410* (MSUN)	AJ488474 AJ488475 AJ488476	AJ488828

Table 1 (continued)

Tavaresia barklyi (R.A. Dyer) N.E. Br.	Namibia: Gobabis	*Albers & Grabow K1582* (MSUN)	AJ488477 AJ488478 AJ488479	AJ488829
Tridentea virescens (N.E. Br.) L.C. Leach	South Africa: N of Brandvlei	*Lamberti s.n.* (in hort. UBT)	AJ488480 AJ488481 AJ488482	AJ488830
Tromotriche longipes (Lückh.) Bruyns	Namibia: N of Rosh Pinah	*Albers & Meve 75* (MSUN)	AJ488483 AJ488484 AJ488485	AJ488831
Tromotriche ruschiana (Dinter) Bruyns	Namibia: s. loc.	*ex hort Thompson* (MSUN, UBT)	AJ488486 AJ488487 AJ488488	AJ488832
White-sloanea crassa (N.E. Br.) Chiov.	Somalia: Dan Gorayo	*ex seed Lavranos et al.* (HBG)	AJ488489 AJ488490 AJ488491	AJ488833

Nearly all genera of Ceropegieae were investigated except for a few taxa unavailable for different reasons: Due to the complete lack of living material or to herbarium specimens too old for successful DNA extraction, the genera *Baynesia* Bruyns (1 species, decribed in 2000), *Conomitra* Fenzl (1 ephemeral annual species, not recollected within the last decades), *Emplectanthus* N. E. Br. (2 rare species), *Pentasachme* Wight (5 species in Asia) and *Vietnamia* P. T. Li (monotypic endemic of Vietnam) have not been analyzed. Of *Heterostemma* Wight and Arn., two species were sequenced, but with incomplete results due to sequencing problems.

As most distant outgroups, *Secamone alpinii* (Secamonoideae) and *Gymnema sylvestre* (Marsdenieae) were selected (for the cpDNA dataset, only). Furthermore, a number of presumably basal Ceropegieae (*Anisotoma*, *Sisyranthus*, *Riocreuxia*, *Neoschumannia*, *Brachystelma*, *Ceropegia*) were chosen as more closely related outgroups. In the ingroup, 69 representatives of all available stapeliad genera and species groups were chosen (Table 1).

DNA extraction and PCR. DNA was isolated from fresh stem tip tissue according to Doyle and Doyle (1987). PCR primers and protocol for the plastid *trn*T-L and *trn*L-F spacers and the *trn*L intron correspond to Taberlet et al. (1991). The entire Internal Transcribed Spacer region (ITS) of nuclear ribosomal DNA was amplified using the flanking primers ITS4 and ITS5 following a slightly modified protocol from Baldwin (1992) as detailed by Meve and Liede (2001a, b). Sequences were obtained on an ABI Prism Model 310 Version 3.0 sequencer. All sequences have been deposited at EMBL Nucleotide Sequence Database (Accession Numbers see Table 1).

Data analysis. Sequences were pre-aligned with Perkin Elmer Sequence Navigator Version 1.0.1; the alignment was cleaned manually. Indels were coded as "missing" throughout. For the cpDNA dataset, parsimony-informative indels were coded separately following the "simple gap coding" method of Simmons and Ochoterena (2000). Indels resulting from varying lengths of repeats of the same base 6 bp and longer were not coded, because the length of these repeats has been found to vary even within the same species (Liede, unpubl. data). For the ITS dataset, *Secamone* and *Gymnema* cannot be used as outgroups, because they are too distantly related to allow alignment of their ITS sequences with those of Ceropegieae. Instead, the basal Ceropegieae *Anisotoma*, *Riocreuxia* and *Sisyranthus* serve as outgroup. Separate indel coding was not performed for the ITS dataset.

Phylogenetic analysis and tests for clade support were performed using PAUP version 4.0b8a (PPC) (Swofford 1998). Phylogenies were generated using Fitch parsimony as implemented in PAUP* employing heuristic searches, with 1000 replicates, random stepwise addition, MULPARS off, and tree-bisection-reconnection (TBR) branch swapping. The resulting trees were then used as starting trees for a second round of search with MULPARS on. Our search strategy aimed at finding as many different islands of trees as possible. Sets of equally parsimonious trees recovered from each analysis were summarized by strict consensus. Decay indices (Bremer 1988, Donoghue et al. 1992) and bootstrap values (Felsenstein 1985) derived from 1000 replicates (saving a maximum of 100 trees per replicate) were calculated as measures of support for individual clades. Decay analyses were performed with AutoDecay 4.0 (Eriksson 1998) in combination with the reverse constraint option of PAUP*. Sequence data (excluding indel characters) were also analyzed with a Neighbor-Joining (NJ) approach employing Jukes-Cantor (1969) and Kimura 2-parameter (Kimura 1980) distance models.

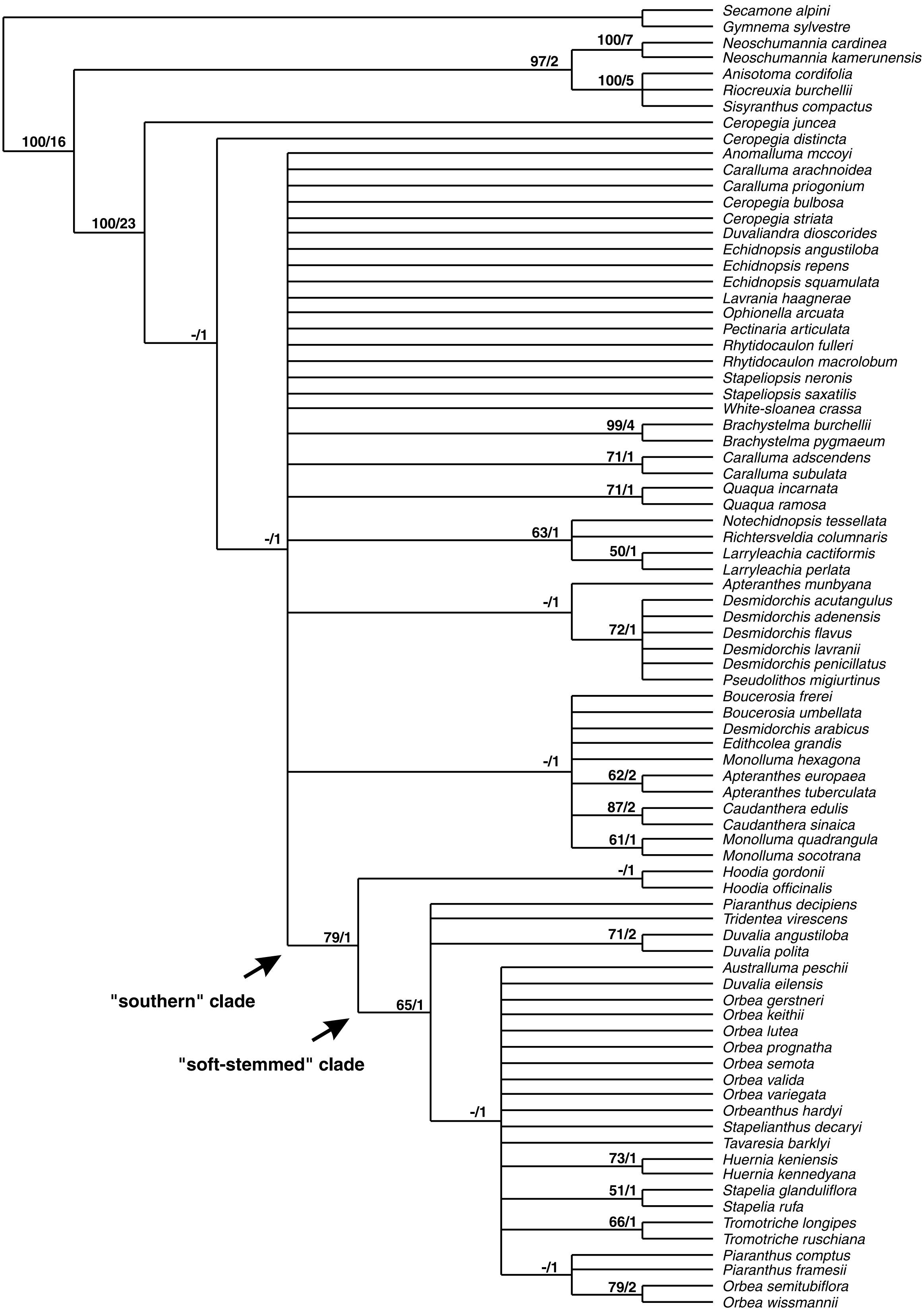
A partition homogeneity test (Bull et al. 1993; as included in PAUP version 4.0b8a) showed that the cpDNA dataset and ITS as a whole are significantly discordant ($P = 0.01$), so that they should not be combined. However, closer analysis revealed that the discordance only applies to ITS and the *trn*L intron ($P = 0.01$), while the two spacer areas and ITS are not significantly discordant ($P = 0.56$ and $P = 0.98$, respectively). Thus, a combined analysis of ITS, the *trn*T-L and *trn*L-F spacer was also conducted without and with the indels coded separately for these two regions.

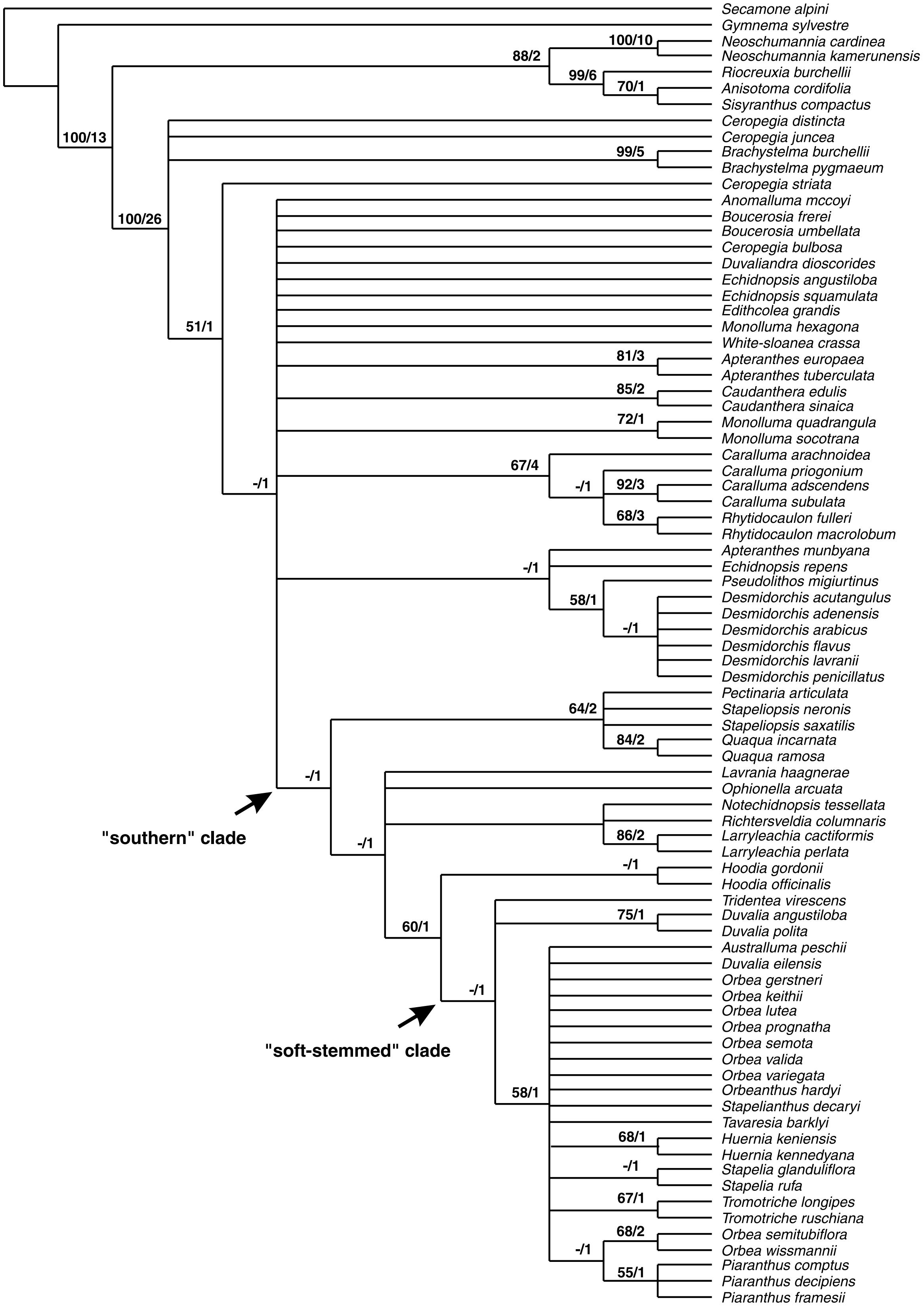
Results

The cpDNA alignment comprises 82 taxa and a total of 1858 characters [964 sequence characters and 14 indels in the *trn*T-L spacer (primers a-b), 542 sequence characters and 3 indels in the *trn*L-intron (primers c-d), and 458 sequence characters and 4 indels in the *trn*L-F spacer (primers e-f)]; 19 data cells are unknown, concerning the end of the *trn*T-L spacer of *Desmidorchis adenensis*. The ITS alignment comprises 80 taxa, 718 sequence characters, 137 data cells are unknown, concerning the beginning and end of *Monolluma hexagona* and the end of *Desmidorchis adenensis*. Both alignments are either available from the authors or can be viewed on the World Wide Web (http://www.uni-bayreuth.de/departments/planta2/) or in Tree-BASE (study accession number = S761, Sanderson 1994).

Parsimony analysis of the cpDNA sequence characters alone (117 parsimony informative characters) resulted in 12800 trees of 332 steps (Fig. 1). The consistency index is 0.667 (exluding uninformative characters) and the retention index is 0.907. Addition of the 21 indels coded as binary characters (138 parsimony informative characters) resulted in 13440 trees of 363 steps. The consistency index is 0.662 (exluding uninformative characters) and the retention indes is 0.90 (Fig. 2). Parsimony analysis of ITS data alone (228 parsimony informative characters) resulted in more than 69000 trees of 690 steps (Fig. 3). The consistency index is 0.565 (exluding uninformative characters) and the retention index is 0.813. Parsimony analysis of ITS combined with the *trn*T-L and the *trn*L-F spacer regions (296 parsimony informative characters) resulted in more than 69000 trees of 886 steps (Fig. 4). The consistency index is 0.583 (exluding uninformative characters) and the retention index is 0.824. Addition of the 17 indels coded as binary characters (311 parsimony informative characters, because two of the indels were uninformative as consequence of the deletion of *Secamone* and *Gymnema* from the matrix) resulted in more than 69000

Fig. 1. Strict consensus tree of 12,800 most parsimonious trees derived from cladistic analysis of cpDNA sequence data [$l = 332$ steps, $CI = 0.667$ (excluding uninformative characters), $RI = 0.907$]


Secamone alpini
Gymnema sylvestre
100/7
Neoschumannia cardinea
97/2
Neoschumannia kamerunensis
Anisotoma cordifolia
100/5
Riocreuxia burchellii
Sisyranthus compactus
Ceropegia juncea
100/16
Ceropegia distincta
Anomalluma mccoyi
Caralluma arachnoidea
Caralluma priogonium
Ceropegia bulbosa
100/23
Ceropegia striata
Duvaliandra dioscorides
Echidnopsis angustiloba
Echidnopsis repens
Echidnopsis squamulata
Lavrania haagnerae
Ophionella arcuata
-/1
Pectinaria articulata
Rhytidocaulon fulleri
Rhytidocaulon macrolobum
Stapeliopsis neronis
Stapeliopsis saxatilis
White-sloanea crassa
99/4
Brachystelma burchellii
Brachystelma pygmaeum
71/1
Caralluma adscendens
Caralluma subulata
71/1
Quaqua incarnata
Quaqua ramosa
Notechidnopsis tessellata
63/1
-/1
Richtersveldia columnaris
50/1
Larryleachia cactiformis
Larryleachia perlata
Apteranthes munbyana
-/1
Desmidorchis acutangulus
Desmidorchis adenensis
72/1
Desmidorchis flavus
Desmidorchis lavranii
Desmidorchis penicillatus
Pseudolithos migiurtinus
Boucerosia frerei
Boucerosia umbellata
Desmidorchis arabicus
Edithcolea grandis
-/1
Monolluma hexagona
62/2
Apteranthes europaea
Apteranthes tuberculata
87/2
Caudanthera edulis
Caudanthera sinaica
61/1
Monolluma quadrangula
Monolluma socotrana
-/1
Hoodia gordonii
Hoodia officinalis
Piaranthus decipiens
Tridentea virescens
79/1
71/2
Duvalia angustiloba
Duvalia polita
Australluma peschii
"southern" clade
Duvalia eilensis
65/1
Orbea gerstneri
Orbea keithii
Orbea lutea
"soft-stemmed" clade
Orbea prognatha
Orbea semota
Orbea valida
Orbea variegata
-/1
Orbeanthus hardyi
Stapelianthus decaryi
Tavaresia barklyi
73/1
Huernia keniensis
Huernia kennedyana
51/1
Stapelia glanduliflora
Stapelia rufa
66/1
Tromotriche longipes
Tromotriche ruschiana
Piaranthus comptus
-/1
Piaranthus framesii
79/2
Orbea semitubiflora
Orbea wissmannii


Secamone alpini
Gymnema sylvestre
100/10
Neoschumannia cardinea
Neoschumannia kamerunensis
88/2
Riocreuxia burchellii
99/6
70/1
Anisotoma cordifolia
Sisyranthus compactus
Ceropegia distincta
100/13
Ceropegia juncea
99/5
Brachystelma burchellii
Brachystelma pygmaeum
Ceropegia striata
Anomalluma mccoyi
Boucerosia frerei
100/26
Boucerosia umbellata
Ceropegia bulbosa
Duvaliandra dioscorides
Echidnopsis angustiloba
Echidnopsis squamulata
Edithcolea grandis
51/1
Monolluma hexagona
White-sloanea crassa
81/3
Apteranthes europaea
Apteranthes tuberculata
85/2
Caudanthera edulis
Caudanthera sinaica
72/1
Monolluma quadrangula
Monolluma socotrana
Caralluma arachnoidea
67/4
Caralluma priogonium
-/1
-/1
92/3
Caralluma adscendens
Caralluma subulata
68/3
Rhytidocaulon fulleri
Rhytidocaulon macrolobum
Apteranthes munbyana
-/1
Echidnopsis repens
Pseudolithos migiurtinus
58/1
Desmidorchis acutangulus
Desmidorchis adenensis
-/1
Desmidorchis arabicus
Desmidorchis flavus
Desmidorchis lavranii
Desmidorchis penicillatus
Pectinaria articulata
64/2
Stapeliopsis neronis
Stapeliopsis saxatilis
84/2
Quaqua incarnata
Quaqua ramosa
Lavrania haagnerae
-/1
Ophionella arcuata
Notechidnopsis tessellata
Richtersveldia columnaris
"southern" clade
86/2
-/1
Larryleachia cactiformis
Larryleachia perlata
-/1
Hoodia gordonii
Hoodia officinalis
Tridentea virescens
75/1
Duvalia angustiloba
60/1
Duvalia polita
Australluma peschii
Duvalia eilensis
-/1
Orbea gerstneri
Orbea keithii
Orbea lutea
"soft-stemmed" clade
Orbea prognatha
Orbea semota
Orbea valida
Orbea variegata
58/1
Orbeanthus hardyi
Stapelianthus decaryi
Tavaresia barklyi
68/1
Huernia keniensis
Huernia kennedyana
-/1
Stapelia glanduliflora
Stapelia rufa
67/1
Tromotriche longipes
Tromotriche ruschiana
68/2
Orbea semitubiflora
-/1
Orbea wissmannii
Piaranthus comptus
55/1
Piaranthus decipiens
Piaranthus framesii

trees of 909 steps (Fig. 4). The consistency index is 0.586 (exluding uninformative characters) and the retention index is 0.824.

In all analyses, the Ceropegieae form a very well supported clade. In the cpDNA analysis, *Neoschumannia*, *Riocreuxia*, *Anisotoma* and *Sisyranthus* form a basal clade with high support; the two *Neoschumannia* species on the one hand and *Anisotoma*/*Riocreuxia*/*Sisyranthus* on the other form even better supported subclades (Figs. 1, 2). The species-rich core Ceropegieae, including *Brachystelma* and *Ceropegia*, form the most stable clade of the analysis with decay values of 23 and 26 in the cpDNA analysis without and with indels, respectively, and 43 in the ITS analysis. Resolution in the cpDNA dataset is too low for a well resolved phylogram; however, some clades are retrieved, and a few are even well supported (Fig. 1). Addition of the indels improves resolution, but changes clades support only insignificantly (Fig. 2).

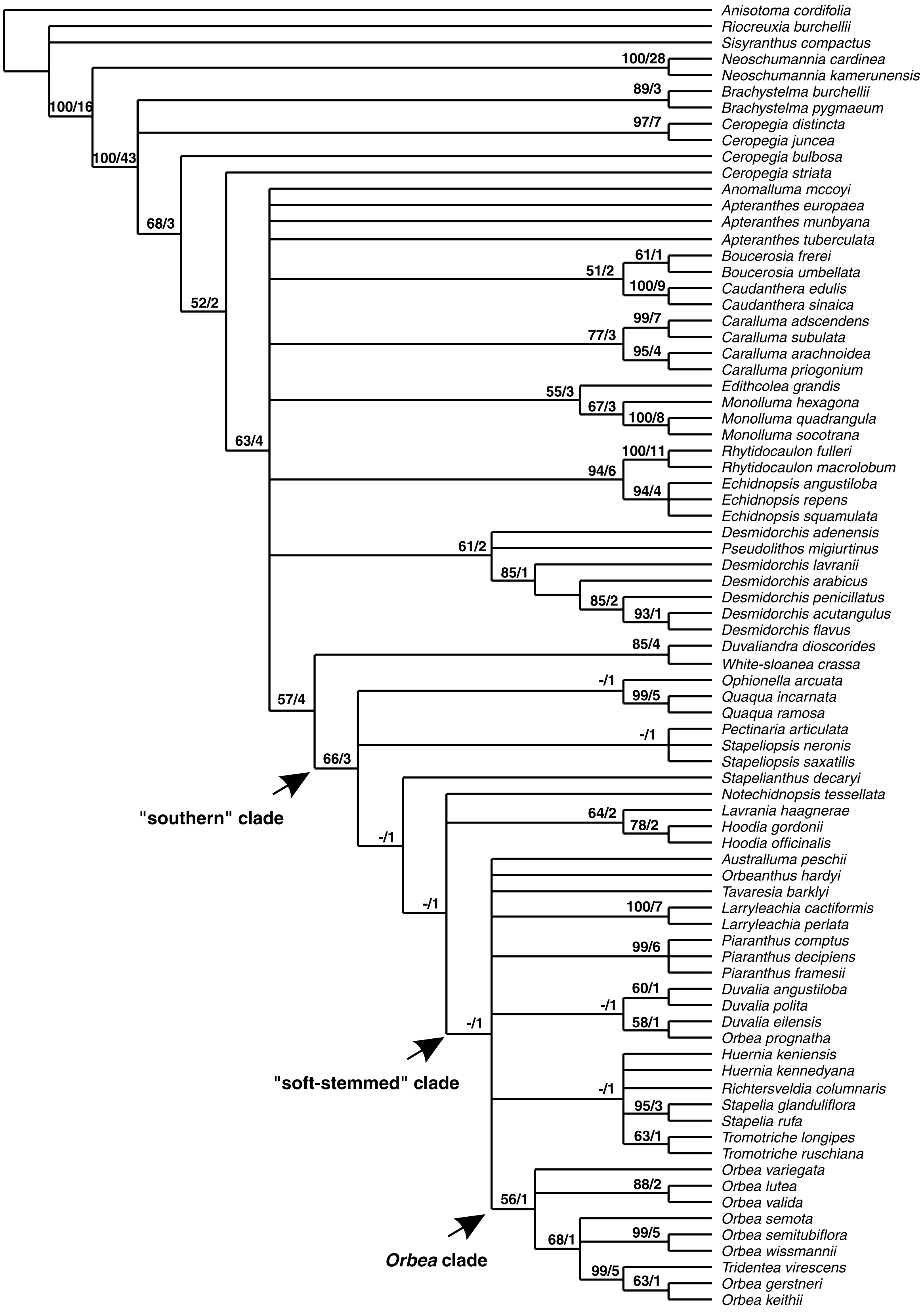
Analysis of the ITS dataset results in a better resolved tree (Fig 3), in which several of the taxa unresolved in the cpDNA dataset are added to the clades described there. Of all datasets analyzed, the combined datasets show the best resolution (Fig. 4). Nevertheless, some basic structure is common to all "gene" trees. *Ceropegia* and *Brachystelma* belong to the core Ceropegieae, and while *Brachystelma* itself is monophyletic [on the basis of the taxa studied in the present paper and the additional eight taxa studied by Meve and Liede (2001a)], *Ceropegia* is not.

Caralluma s.l. (sensu Gilbert 1990) is differentiated in several mostly well-supported clades with representatives of the small northern genera of *Edithcolea* and *Pseudolithos* interspersed. *Echidnopsis* and *Rhytidocaulon* are unresolved in the cpDNA dataset, but form a well-supported clade in the ITS and the combined dataset (Fig. 4). *Pseudolithos*, as presently circumscribed, is polyphyletic.

A large clade of predominantly southern African taxa is retrieved in all analyses, although several members of this clade remain unresolved in the cpDNA dataset (Figs. 1–4). This clade, which comprises the typical stapeliads of the wider Cape as such as *Quaqua*, *Stapelia*, *Stapeliopis*, *Piaranthus*, *Hoodia*, *Duvalia*, *Orbea*, *Huernia*, and *Tromotriche* will be called "southern" clade to simplify the discussion. This "southern" clade is weakly supported in all single analyses, but well supported by the combined datasets. In the ITS and the combined datasets, the northern taxa *Duvaliandra* and *White-sloanea* are sister to each other, and together they are basal to the "southern" clade. Within the "southern" clade, the larger *Orbea*/*Stapelia* relationship, morphologically united by soft stems, and well-developed, usually soft, fleshy and early deciduous leaf rudiments, forms a subclade which will be called "soft-stemmed" (sub)clade throughout the discussion. Again, the clade is retrieved in the cpDNA dataset, but comprises fewer taxa there; this clade is unsupported statistically throughout, but congruent with morphological data. Most conspicuous, "*Caralluma peschii*", an isolated Namibian species, is an undisputed member of the "soft-stemmed" clade, supporting the proposal of Plowes (1995) to treat it as an independent genus, *Australluma*. The Madagascan endemic *Stapelianthus* is nested within the "soft-stemmed" clade as well (Figs. 1–4). *Piaranthus* including *Huerniopsis* is monophyletic. The three species investigated form an unresolved clade of low support by cpDNA (including the indels, Fig. 2), but high support by ITS (Figs. 3, 4). The bitypic *Notechidnopsis* is not monophyletic on the base of both cpDNA and ITS (compare Figs. 1, 2 and Figs. 3, 4). *Orbea prognatha*, representing the monotypic *Bally*-

◄

Fig. 2. Strict consensus tree of 13,400 most parsimonious trees derived from cladistic analysis of cpDNA sequence data and 21 indels coded as binary characters [l = 363 steps CI = 0.665 (excluding uninformative characters), RI = 0.899]


Anisotoma cordifolia
Riocreuxia burchellii
Sisyranthus compactus
100/28
Neoschumannia cardinea
Neoschumannia kamerunensis
89/3
Brachystelma burchellii
100/16
Brachystelma pygmaeum
97/7
Ceropegia distincta
Ceropegia juncea
100/43
Ceropegia bulbosa
Ceropegia striata
Anomalluma mccoyi
Apteranthes europaea
68/3
Apteranthes munbyana
Apteranthes tuberculata
61/1
Boucerosia frerei
51/2
Boucerosia umbellata
100/9
Caudanthera edulis
52/2
Caudanthera sinaica
99/7
Caralluma adscendens
77/3
Caralluma subulata
95/4
Caralluma arachnoidea
Caralluma priogonium
Edithcolea grandis
55/3
Monolluma hexagona
67/3
100/8
Monolluma quadrangula
Monolluma socotrana
63/4
100/11
Rhytidocaulon fulleri
Rhytidocaulon macrolobum
94/6
Echidnopsis angustiloba
94/4
Echidnopsis repens
Echidnopsis squamulata
Desmidorchis adenensis
61/2
Pseudolithos migiurtinus
85/1
Desmidorchis lavranii
Desmidorchis arabicus
85/2
Desmidorchis penicillatus
93/1
Desmidorchis acutangulus
Desmidorchis flavus
85/4
Duvaliandra dioscorides
White-sloanea crassa
-/1
Ophionella arcuata
57/4
99/5
Quaqua incarnata
Quaqua ramosa
-/1
Pectinaria articulata
66/3
Stapeliopsis neronis
Stapeliopsis saxatilis
Stapelianthus decaryi
"southern" clade
Notechidnopsis tessellata
64/2
Lavrania haagnerae
78/2
Hoodia gordonii
-/1
Hoodia officinalis
Australluma peschii
Orbeanthus hardyi
Tavaresia barklyi
-/1
100/7
Larryleachia cactiformis
Larryleachia perlata
99/6
Piaranthus comptus
Piaranthus decipiens
Piaranthus framesii
60/1
Duvalia angustiloba
-/1
Duvalia polita
58/1
Duvalia eilensis
-/1
Orbea prognatha
Huernia keniensis
"soft-stemmed" clade
Huernia kennedyana
-/1
Richtersveldia columnaris
95/3
Stapelia glanduliflora
Stapelia rufa
63/1
Tromotriche longipes
Tromotriche ruschiana
Orbea variegata
88/2
Orbea lutea
56/1
Orbea valida
Orbea semota
68/1
99/5
Orbea semitubiflora
Orbea wissmannii
Orbea clade
99/5
Tridentea virescens
63/1
Orbea gerstneri
Orbea keithii

anthus Bruyns sensu Bruyns (2001), is nested within *Duvalia*, although with weak support. *Tridentea virescens* is part of the *Orbea*-clade (Figs. 3, 4), which includes representatives of the former genera *Angolluma*, *Orbeopsis* and *Pachycymbium* as suggested by Bruyns (2001). *Orbeanthus*, however, takes an unresolved position in the "soft-stemmed" clade.

The results of the two separate Neighbor-Joining analyses based on Jukes-Cantor and Kimura 2-parameter distance models produced trees identical in topology (Fig. 5, for ITS). These trees are highly congruent with the parsimony-based strict consensus phylogenies (Figs. 1–4), but more resolved. The separation between the basal Ceropegieae *Anisotoma*, *Neoschumannia*, *Riocreuxia*, and *Sisyranthus* is illustrated well by the genetic distances between these genera and the other Ceropegieae (Fig. 5). *Ceropegia* and *Brachystelma* are nearest neighbors for both datasets (Fig. 5), but *Ceropegia* is not monophyletic in either (Figs. 1–4).

Discussion

Probably the most important result of our molecular studies is the monophyly of the derived stapeliads to which the Socotran *Duvaliandra* and the Somalian *White-sloanea* take a basal position with low bootstrap value, but a decay index of four (Fig. 3). This position, as well as the monophyly of these two genera is only retrieved in the ITS dataset, in the cpDNA dataset, both taxa are unresolved (Figs. 1, 2). The remainder of this largest clade encompasses the classical carrion flowers, such as *Duvalia*, *Huernia*, *Ophionella*, *Quaqua*, *Stapelia*, *Orbea*, *Piaranthus*, *Larryleachia*, *Lavrania* and *Hoodia*. These genera are distributed mainly in the karroid vegetation of Nambia and South Africa, but a few species belonging to the genera *Duvalia* and *Huernia* are found north of the equator. Only *Orbea* comprises two similarly species-rich groups in southern Africa as well as in northeast Africa/Arabia, with some species extending into northwest Africa. Inclusion of *Angolluma*, *Orbeopsis* and *Pachycymbium* is clearly supported. The interpretation of stem and flower morphology as advanced (cf. also Bruyns 2000a) together with these distributional data hint at the conclusion that *Orbea* might represent the most recent branch of the stapeliads. The "southern" clade also includes the Namibian *Australluma* (*Caralluma) peschii* in an unresolved position, but as member of the "soft-stemmed" clade of *Duvalia*, *Orbea*, *Orbeanthus*, *Tavaresia*, *Larryleachia*, *Richtersveldia*, *Huernia*, *Tromotriche*, *Stapelia* and *Tridentea*. Bruyns (1982) saw a relationship between *A. peschii* and the equally slender-stemmed *Caudanthera* (*Caralluma*) *edulis*, but Gilbert (1990) suggested a relationship outside *Caralluma*. Plowes (1995) created a separate genus, *Australluma*, to accomodate this species, because it possesses stipular glands otherwise absent in *Caralluma* s.l., and widely diverging follicles. Our results from both datasets support the different origin of *Australluma* and the other segregates of *Caralluma* (Figs. 1–3).

The Madagascan endemic *Stapelianthus* is nested right within the "southern" clade, but a sistergroup relationship between *Stapelianthus* and *Tavaresia*, as postulated by Bruyns (2000a) in his cladistic analysis of morphological markers, is not supported. The idea formulated by Leach (1978: 72) that *Stapelianthus* and *Orbeanthus* are closely related because of the morphological similarity (stems, leaves, corolla, corona), in particular of *O. conjunctus* (A. White and B. Sloane) L.C. Leach and *Stapelianthus insignis* Descoings, seems likewise not supported. However, considering morphological data, both *Tavaresia* and *Orbeanthus* still can be considered the closest living relatives of *Stapelianthus*. *Orbeanthus*,

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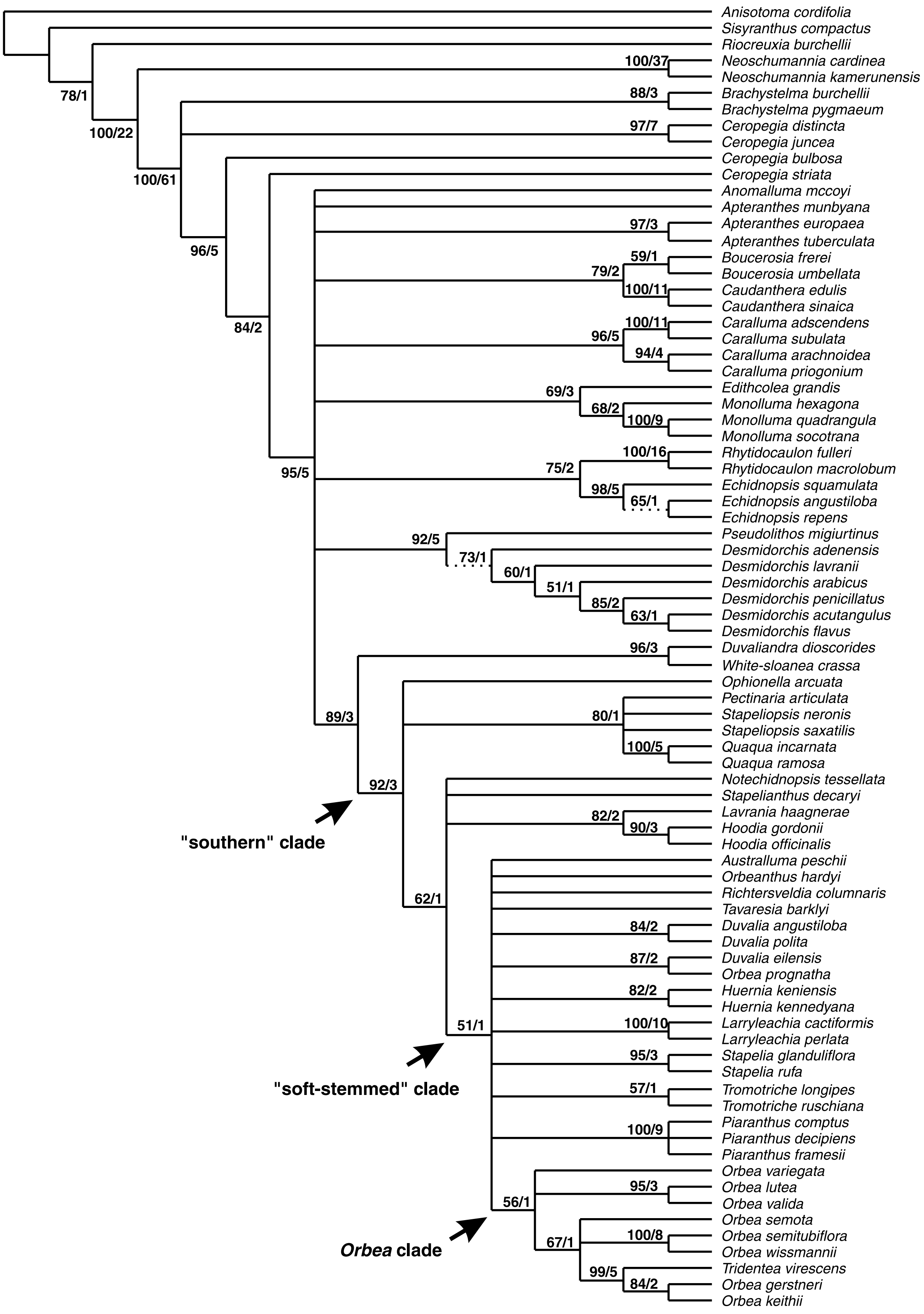
Fig. 3. Strict consensus tree of 69,000 most parsimonious trees derived from cladistic analysis of ITS sequence data [l = 690 steps, CI = 0.565 (excluding uninformative characters), RI = 0.813]


Anisotoma cordifolia
Sisyranthus compactus
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100/37
Neoschumannia cardinea
Neoschumannia kamerunensis
78/1
88/3
Brachystelma burchellii
Brachystelma pygmaeum
100/22
97/7
Ceropegia distincta
Ceropegia juncea
Ceropegia bulbosa
100/61
Ceropegia striata
Anomalluma mccoyi
Apteranthes munbyana
97/3
Apteranthes europaea
96/5
Apteranthes tuberculata
59/1
Boucerosia frerei
79/2
Boucerosia umbellata
100/11
Caudanthera edulis
Caudanthera sinaica
84/2
100/11
Caralluma adscendens
96/5
Caralluma subulata
94/4
Caralluma arachnoidea
Caralluma priogonium
69/3
Edithcolea grandis
68/2
Monolluma hexagona
100/9
Monolluma quadrangula
Monolluma socotrana
100/16
Rhytidocaulon fulleri
75/2
Rhytidocaulon macrolobum
95/5
98/5
Echidnopsis squamulata
65/1
Echidnopsis angustiloba
Echidnopsis repens
92/5
Pseudolithos migiurtinus
73/1
Desmidorchis adenensis
60/1
Desmidorchis lavranii
51/1
Desmidorchis arabicus
85/2
Desmidorchis penicillatus
63/1
Desmidorchis acutangulus
Desmidorchis flavus
96/3
Duvaliandra dioscorides
White-sloanea crassa
Ophionella arcuata
Pectinaria articulata
89/3
80/1
Stapeliopsis neronis
Stapeliopsis saxatilis
100/5
Quaqua incarnata
92/3
Quaqua ramosa
Notechidnopsis tessellata
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Hoodia gordonii
Hoodia officinalis
Australluma peschii
Orbeanthus hardyi
Richtersveldia columnaris
62/1
Tavaresia barklyi
84/2
Duvalia angustiloba
Duvalia polita
87/2
Duvalia eilensis
Orbea prognatha
82/2
Huernia keniensis
Huernia kennedyana
51/1
100/10
Larryleachia cactiformis
Larryleachia perlata
95/3
Stapelia glanduliflora
Stapelia rufa
"soft-stemmed" clade
57/1
Tromotriche longipes
Tromotriche ruschiana
100/9
Piaranthus comptus
Piaranthus decipiens
Piaranthus framesii
Orbea variegata
95/3
Orbea lutea
56/1
Orbea valida
Orbea semota
100/8
Orbea semitubiflora
67/1
Orbea wissmannii
Orbea clade
99/5
Tridentea virescens
84/2
Orbea gerstneri
Orbea keithii

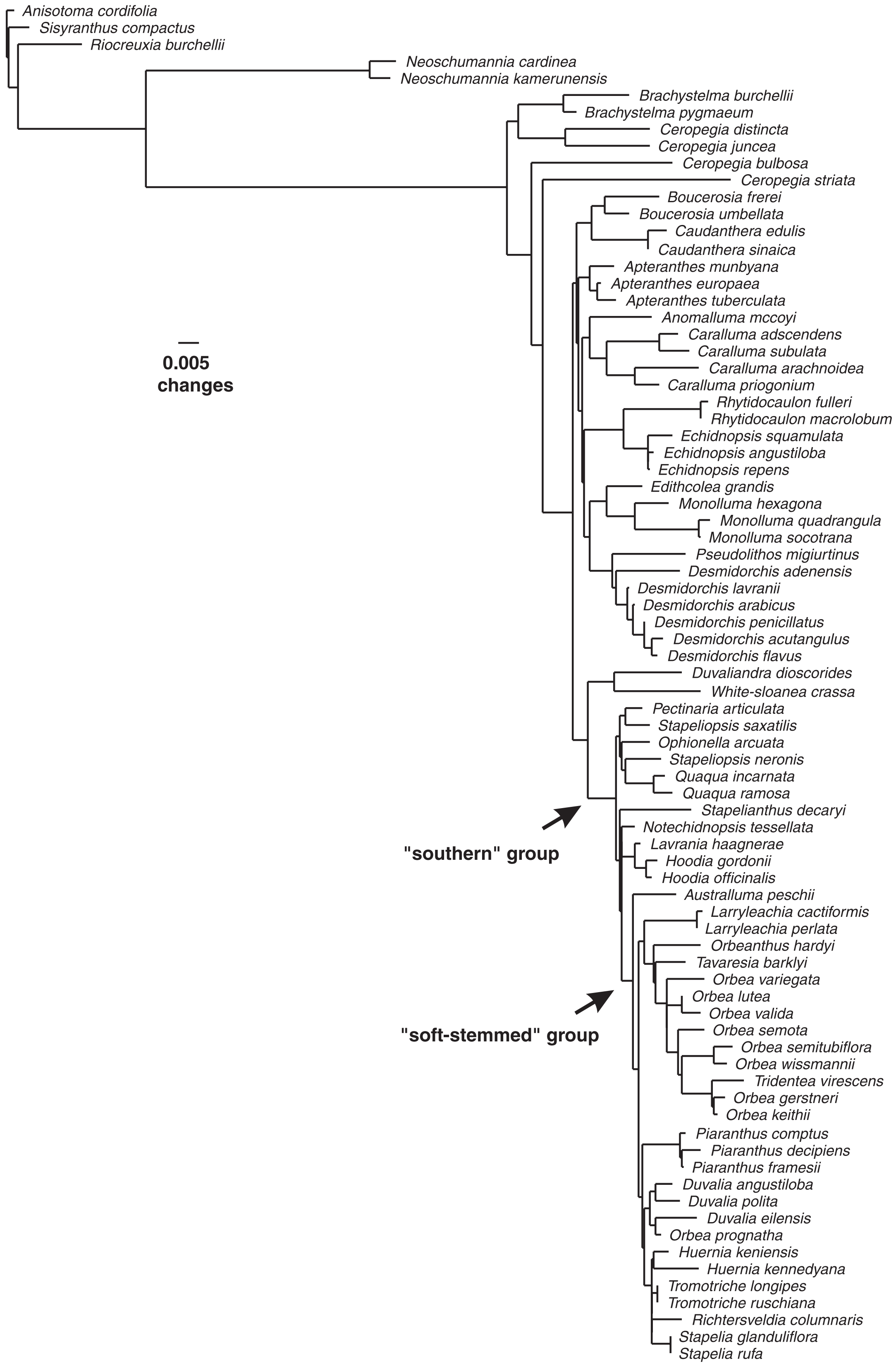
itself, might be classified as *Orbea* applying a generous morphological genus concept. The cpDNA analysis leaves *Orbeanthus*, most *Orbea* species, and several other taxa unresolved (Figs. 1, 2). ITS data support an *Orbea* clade, but without including *Orbeanthus* (Fig. 3). *Orbeanthus*, which has been sunk into synonymy of *Orbea* (Bruyns 2000c), is therefore reinstated here. The inclusion of *Tavaresia* with its unique long tubular flowers and its many-angled stems with unique stipular thorns in *Orbea* would not only create a morphologically undesirable situation, but is also not supported by the ITS data (Fig. 3). The cpDNA leaves *Tavaresia* unresolved in the larger *Orbea* clade (Figs. 1, 2). *Orbea*, as accepted here, includes "only" the former genera *Angolluma*, *Orbeopsis* and *Pachycymbium*, as transposed into synonymy by Bruyns (2001). While *Tridentea virescens* is placed in the *Orbea* clade by the ITS data (Fig. 3), this relationship is only partly supported morphologically, but too little understood to place *Tridentea* in synonymy of *Orbea*. The *Tridentea* revision of Bruyns (1995) gave no further answers as to the assumed generic relationship of the genus except for the citation of Leach (1978, 1980 in Bruyns 1995), that this author first saw closest affinities between *Tridentea* and *Orbea*, but later between *Tridentea* and *Stapelia*. A study using a finer resolving marker and more species is necessary to clarify the boundaries of *Orbea*.

Duvalia has been regarded as sister-genus of *Huernia* (Meve 1997). In the "southern" clade, only *D. angustiloba* and *D. polita* form a subclade in the analysis of cpDNA data (Figs. 1, 2). In the ITS dataset, *D. eilensis* and *Orbea prognatha* form a sister subclade to the former, but support for both sublades and for the *Duvalia* clade as a whole is low (Fig. 3). Thus, *Orbea prognatha*, recently transferred to a genus of its own, *Ballyanthus* (Bruyns 2001), is nested within *Duvalia*. With its club-shaped stems, distinct stipular glands at the base of conical-lanceolate leaf rudiments it is nearly indistinguishable from other representatives of *Duvalia* (cf. Meve 1997). However, the inclusion of *Orbea prognatha* in *Duvalia* would cause considerable taxonomic disorder because of its floral structure. Corolla structure is the same as in *D. velutina*, and the shape of the pollinaria and the germination mouth conforms to all other *Duvalia* (and *Huernia*) species, even its stipitate gynostegium is typical for all *Duvalia* species. However, the corona is not annular as it is diagnostic for *Duvalia* in its classical circumscription, although there is a zone of fusion in interstaminal position. Most "disturbing" for an inclusion of *O. prognatha* in *Duvalia*, however, is one substancial difference in gynostegium structure. In all *Duvalia* species, the guide rails are embedded in gynostegium tissue, and are strongly centrifugal toward the base. In *O. prognatha*, in contrast, guide-rails are free, vertical and parallel over their whole length as it is typical for *Orbea*. A hybrid origin for *O. prognatha* therefore is possible. Because a monotypic genus *Ballyanthus* cannot be accepted, and since no different treatment of *Orbea prognatha* is clearly enforced by our results, we propose to retain the traditional taxonomy of this species.

Meve (1994) regarded *Huerniopsis* and *Piaranthus* as sister taxa while Bruyns (1999a) placed the bitypic *Huerniopsis* within *Piaranthus* (Bruyns 1999a). The monophyly of *Huerniopsis* and *Piaranthus* is well supported by the ITS dataset (Fig. 3), but less clearly by the cpDNA data, where the two *Piaranthus* s.str. species and *P.* (*H.*) *decipiens* only form a weakly supported subclade if the

◀

Fig. 4. Strict consensus tree of 69,000 most parsimonious trees derived from cladistic analysis of combined ITS and *trn*T-L and *trn*L-F spacers, and the respective indels coded as binary characters. l = 886 steps, CI = 0.583 (excluding uninformative characters) RI = 0.824 for the analysis without indels, l = 909 steps, CI = 0.586 (excluding uninformative characters), RI = 0.824 for the analysis with indels. Clades not retrieved in the analysis without indels are indicated by dashed lines


Anisotoma cordifolia
Sisyranthus compactus
Riocreuxia burchellii
Neoschumannia cardinea
Neoschumannia kamerunensis
Brachystelma burchellii
Brachystelma pygmaeum
Ceropegia distincta
Ceropegia juncea
Ceropegia bulbosa
Ceropegia striata
Boucerosia frerei
Boucerosia umbellata
Caudanthera edulis
Caudanthera sinaica
Apteranthes munbyana
Apteranthes europaea
Apteranthes tuberculata
Anomalluma mccoyi
Caralluma adscendens
Caralluma subulata
Caralluma arachnoidea
Caralluma priogonium
Rhytidocaulon fulleri
Rhytidocaulon macrolobum
Echidnopsis squamulata
Echidnopsis angustiloba
Echidnopsis repens
Edithcolea grandis
Monolluma hexagona
Monolluma quadrangula
Monolluma socotrana
Pseudolithos migiurtinus
Desmidorchis adenensis
Desmidorchis lavranii
Desmidorchis arabicus
Desmidorchis penicillatus
Desmidorchis acutangulus
Desmidorchis flavus
Duvaliandra dioscorides
White-sloanea crassa
Pectinaria articulata
Stapeliopsis saxatilis
Ophionella arcuata
Stapeliopsis neronis
Quaqua incarnata
Quaqua ramosa
Stapelianthus decaryi
Notechidnopsis tessellata
Lavrania haagnerae
Hoodia gordonii
Hoodia officinalis
Australluma peschii
Larryleachia cactiformis
Larryleachia perlata
Orbeanthus hardyi
Tavaresia barklyi
Orbea variegata
Orbea lutea
Orbea valida
Orbea semota
Orbea semitubiflora
Orbea wissmannii
Tridentea virescens
Orbea gerstneri
Orbea keithii
Piaranthus comptus
Piaranthus decipiens
Piaranthus framesii
Duvalia angustiloba
Duvalia polita
Duvalia eilensis
Orbea prognatha
Huernia keniensis
Huernia kennedyana
Tromotriche longipes
Tromotriche ruschiana
Richtersveldia columnaris
Stapelia glanduliflora
Stapelia rufa
0.005
changes
"southern" group
"soft-stemmed" group

indel pattern is considered (Fig. 2). However, incompatibility in artificial crossings between plants of *Huerniopsis* and *Piaranthus* and different flower flavonoid patterns as reported by Meve (1994), supplemented by restricted distribution areas in either summer rainfall or winter rainfall area, respectively, point to a phylogentic differentiation between *Huerniopsis* and *Piaranthus* (Meve 1994) by far larger than usually found between species of other stapeliad genera.

The spiny, shrubby and orthotropic *Hoodia* and the non-spiny plagiotropic *Lavrania* share a subclade in the ITS gene tree (Fig. 3), which gains support in the combined ITS/*trn*T-L, *trn*L-F tree (Fig. 4). Despite some similarities in flower and stem morphology (in particular between *L. haagnerae* and *H. ruschii*), differences in tubercle and leaf morphology and anatomy (epidermis), corolla and pollinaria morphology (cf. Bruyns 1993) between *Hoodia* and *Lavrania* outweigh similarities by far. An inclusion of *Lavrania* in *Hoodia*, as possible from the molecular results, is therefore rejected. The *Hoodia* (or *Hoodia*/*Lavrania*) clade is sister to the "soft-stemmed" clade. *Larryleachia* has been shown not to be closely related to *Lavrania* (Meve and Liede 2001) as proposed repeatedly by Bruyns (1993, 1999b). The two species of *Quaqua* form a monophyletic clade in the cpDNA gene tree. Adding the indels, the two *Stapeliopsis* species, which do not form a monophyletic clade and *Pectinaria articulata* join the *Quaqua* clade, but with very weak support (Figs. 1, 2). In the ITS tree, the bitypic *Ophionella* joins the *Quaqua* clade, but without support (Fig. 3). A relationship between *Quaqua*, *Stapeliopsis* and *Ophionella* can be assumed for stem-morphological reasons (4-angled stems), whereas *Pectinaria* (6-angled stems) and *Ophionella* are most similar concerning flower morphology (e.g. the common possession of horizontally spreading projections of interstaminal and staminal corona lobes, and pollinia broader than long). The two *Stapeliopsis* species and *Pectinaria* form an unsupported trichotomy (Fig. 3). In the combined tree, the *Stapeliopsis*/*Pectinaria*/*Quaqua* clade has reasonable support (Fig. 4), but *Ophionella* remains unresolved, and *Stapeliopsis* and *Pectinaria* are unresolved. Distance analysis (Fig. 5) demonstrates that the six species studied of these four genera form a group of small genetic distances. The molecular results for this group are almost impossible to translate into a classification, and no taxonomic changes are proposed here. Again, the true affinities within this complex might be concealed by various hybridogeneous events (*Ophionella*?) in the recent evolutionary history of this group. Based on morphological data, Bruyns (1999c) found *Orbea* and *Stapelia* in sistergroup relationship to *Stapeliopsis*, and these three genera in sistergroup position to *Ophionella*, while this group again is sister to *Pectinaria*. However, the unequivocal membership of both *Orbea* and *Stapelia* in the "soft-stemmed" clade by both molecular datasets raises doubts as to the placement of the other three genera by Bruyns (1999c), which is largely a consequence of the coding of inflorescence and seed data for *Orbea* and *Stapelia*.

Bruyns (1999d) concluded that the bitypic *Notechidnopsis* represents a monophyletic group, which is sister to *Pectinaria* (Bruyns 1999d, 2000a). However, both gene trees contradict these views (Figs. 1–3). While cpDNA data point at least to close relationship, albeit not a monophyletic one, of the two *Notechidnopsis* species, ITS data suggest complete different affinities for the two species (cf. also Meve and Liede 2001b). Although morphological support is rather weak, mainly based on differences in stem and leaf rudiments (Meve and Liede 2001b), bract texture and details of the corona (Bruyns 1999d), a congeneric treatment of the two species is rejected because it does not reflect phylogeny. We therefore propose the

Fig. 5. Neighbor-Joining tree based on Jukes-Cantor/Kimura 2-parameter distance models and derived from ITS sequence data

transfer of *N. columnaris* to the newly established genus *Richtersveldia* (see "Taxonomy").

The poorly understood monotypic genera *Duvaliandra* (Socotran endemic; cf. Gilbert 1990) and *White-sloanea* (endemic to the Horn of Africa; Rauh 1997, Bruyns 1998) were placed close to *Caralluma* by Gilbert (1990), but next to *Huernia* and *Duvalia* by Bruyns (2000a). While both are unresolved in the tree resulting from the cpDNA dataset, they form a well supported clade in the ITS dataset, and this clade is basal to the "southern" clade, although without statistical support (Fig. 4). Support for this position, however, increases dramatically if the two datasets are combined (except for the *trn*L intron, as detailed above). From the morphological point of view, a sister-group relationship between *White-sloanea* and *Duvaliandra* has never been suggested; however, they share compact and truly leafless stems and "*Duvalia*-like" pollinaria. Both, their isolated geographic position and the lack of close relatives characterizes these genera as relicts. *White-sloanea*, collected most recently 15 years ago, is most likely extinct in the wild. Their basal position in the "southern" clade suggests that the progenitors of the species-rich "southern" clade originated in NE Africa, eventually Arabia, but radiated extensively in the south of the continent.

The other "northern" taxa fall into a variety of clades dominated by the representatives of *Caralluma* s.l., a "genus" recently split by Plowes (1995) into 17 small genera. This treatment has not been widely accepted since its publication. The present analysis shows that some of these segregates are supported not only by the morphological characters given by Plowes (1995), but also by molecular markers. In some cases, however, Plowes' (1995) segregates need redefinition.

There is good support for the reinstatement of well-circumscribed old genera such as *Apteranthes*, *Boucerosia* and *Desmidorchis*, which have been included in *Caralluma* for over 100 years (Brown 1892). *Apteranthes europaea* and *A. tuberculata* are sister taxa supported by cpDNA data, with support increasing by addition of the indels (Fig. 2), but unresolved by ITS. However, neighbor-joining analysis of ITS shows similarity between all three *Apteranthes* species included in our study. Morphologically, no doubt remains that *A. tuberculata* is sister species of *A. europaea*, replacing the latter in Arabia and Asia. The position of *A. munbyana* is more problematical according to our molecular results. But morphological characters, in particular inflorescence morphology, clearly support its inclusion in *Apteranthes* rather than in a separate genus *Borealluma* together with *A. tuberculata* and *A. staintonii*, as suggested by Plowes (1995). *Apteranthes* is characterized by inflorescences pushed aside by the continuously growing stems into a lateral position, a character to which Wertel (1976) attributed particular importance. The small stems with smooth texture as well as the ovate-lanceolate shape of the conspicuous, well-defined, spreading leaf rudiments are shared by *A. munbyana* as well as by *A. staintonii*, *A. burchardii* and *A. joannis* (not included in the molecular analysis). They are therefore all accepted as or transferred to *Apteranthes*. *Apteranthes* is predominantly found in North Africa, but reached Asia with *A. staintonii*, and *A. tuberculata* occurs intermittently from Arabia to NE India.

Asclepiad phylogenies are often superimposed by geography [e.g. *Funastrum* and *Sarcostemma*, Liede and Täuber (2000) or *Cynanchum*, Liede and Täuber (in press)]. In the Ceropegieae, this pattern is not only relevant to the "southern" clade, but also for the fragments of *Caralluma* s.l., in particular, *Desmidorchis* and *Boucerosia*. Despite sharing a very similar habit, terminal, pseudo-umbellate inflorescences and highly similar flower structures, the analyzed representatives of Indian *Boucerosia* are not closely related to *Desmidorchis*, as might be expected from morphology. *Desmidorchis* forms a moderately supported clade in trees resulting from both datasets, only *D. arabicus* shows a different affiliation in the cpDNA dataset without indels (Fig. 1). The association of *Desmidorchis* with *Pseudolithos migiurtinus*, however, is supported only by the combined dataset. *Desmidorchis adenensis*, *D. arabicus*, *D. flavus* and *D. lavrani* as well as *D. awdelianus* (not included in the molecular analysis), were considered an independent genus, *Crenulluma*, by Plowes (1995). However, apart from molecular evidence, they share the massive, shrub-like (orthotropous) habit, the distinctly crenate stem-angles, the minute heart-shaped to lanceolate leaf rudiments, the umbellate (often compound-umbellate) terminal inflorescences and the rugose and/or papillate corolla surface of *Desmidorchis* and are transferred there. The expanded *Desmidorchis* now represents a genus typically confined to arid/semi-arid habitats predominantly bordering the Red Sea with subcentres in Kenya/Somalia and Yemen/Oman.

The representatives of *Boucerosia* are unresolved members of an *Apteranthes*/*Caudanthera*/*Monolluma* clade without statistical support in the cpDNA gene tree (Fig. 1), and – also without bootstrap support – sister to *Caudanthera* in the ITS gene tree (Fig. 3). In the combined analysis (Fig. 4), statistical support for this sister-group relationship is much improved. *Boucerosia* has been regarded as a homogeneous group of closely related species. This group has been considered independent since Wight and Arnold founded the genus for Indian *Caralluma*-like species. Schumann (1895), however, reduced *Boucerosia* to a section of *Caralluma*, while Gilbert (1990) upgraded it to a subgenus of *Caralluma*, and only Plowes (1995) reinstated the genus *Boucerosia* for these taxa from southern India, Sri Lanka and Myanamar. The present molecular results support generic status for *Boucerosia*. The position of *Boucerosia frerei*, the only stapeliad with well-developed leaves and lateral few-flowered inflorescences, has often been discussed in the past (e.g. Gilbert 1990, Plowes 1993) and it has been considered either a member of *Caralluma* or sole member of *Frerea* Dalz. (*F. indica*). The molecular results presented here show that these plants from India (Poona) belong to the *Boucerosia* affinity, despite rather low bootstrap support. The strict consensus tree published by Potgieter and Albert (2001; based on *trn*L intron and *trn*L-F spacer data of 21 Ceropegieae species and superimposed by fruit and seed data) placed *Boucerosia frerei* (= *Frerea indica*) and *Boucerosia* (*Caralluma*) *crenulata* on different clades. *Boucerosia crenulata* is member of an unresolved "soft-stemmed" clade (sensu this paper), *Boucerosia frerei* takes a basal position corresponding to our results. However, the origin of "*Caralluma*" *crenulata* is given as African by Potgieter and Albert (2001), *Frerea* correctly as Indian, so that most likely the accession was wrongly identified. Taking the African origin of the accession as correct, its position in a clade similar to our "soft-stemmed" clade agrees with our results. The surprising position of the second *Caralluma* in the analysis of Potgieter and Albert (2001) is more easily explained, as *Caralluma gerstneri* is an old synonym for *Orbea (Orbeopsis) gerstneri*, and this taxon appears in a similar place as in our analysis.

Pseudolithos migiurtinus, type species of *Pseudolithos*, is weakly associated with *Desmidorchis*, but never with *Anomalluma* with which it was considered congeneric (Bruyns and Meve 1995: for *A. dodsoniana* (Lavranos) Plowes)). *Anomalluma mccoyi* takes an isolated position in cladistic analysis of both datasets. Distance analysis of both datasets shows (Fig. 5 for ITS) that it has the smallest genetic distance to *Caralluma* s. str., and not to *Pseudolithos*. As *A. mccoyi* is considered very closely related, if not conspecific, with *A. dodsoniana* (Bruyns and Meve 1995), type species of *Anomalluma*, a separate genus for these two species as suggested by Plowes (1993) seems the most appropriate reflection of current phylogenetic knowledge.

Monolluma quadrangula and *M. socotrana* form a monophyletic clade based on both datasets (Figs. 1–3), therefore the monotypic *Sanguilluma* Plowes with its type *S. socotrana* is placed in synonymy under *Monolluma* (see "Taxonomy"). *Monolluma quadrangula* and *M. socotrana* share with *M. cicatricosa* (not included in the molecular study) the single- to few-flowered, (sub)axilliary inflorescences and the characteristic pungent smell of the stem surfaces. *M. hexagona* (and *M. solenophora*, not included in the molecular study), considered as two monotypic genera by Plowes (1995), *Sulcolluma* and *Cylindrilluma*, do not agree in these two characters, but in overall stem and leaf morphology. In the analysis based on the ITS dataset, *M. hexagona* joins the *M. quadrangula*/*M. socotrana* clade basally, although with weak support that is not increased in the combined analysis. Even though, *Monolluma* seems the best place to accomodate *M. hexagona* and *M. solenophora*, despite the aberrant gynostegium structure of the latter. *Edithcolea* is basal to the *Monolluma* clade following the ITS dataset and the combined dataset. However, support is low for this clade and *Edithcolea* and *Monolluma* represent morphologically very dissimilar taxa. Obviously, this "dissimilarity" is rather superficial and due to the extremely large, but short-lobed flowers of *Edithcolea*, and decumbent stems bearing leaves reduced to short, hard and sharp thorns. The position of *Edithcolea*, therefore, was an enigma of stapeliad phylogeny (cf. Field 1970). *Edithcolea* shares the brilliant stem surfaces and the bicolored stems (dark green to purplish markings outlining the axillary buds and leaf rudiments) with *M. cicatricosa*, *M. quadrangularis* and *M. socotrana*. All these species, except for *M. solenophora*, branch in a subcutaneous manner (sensu Plowes 1995). The unsual flowers of *Edithcolea* (concentrically corrugate central corolla tube, echinate staminal corona) are unique within stapeliads, however, of all *Caralluma* s.l. species, *Monolluma socotrana* is most similar in general structure. Finally, the very unusual lateral wings of the mericarps found in *M. cicatricosa* and *M. quadrangularis*, appear again, though to a lesser extent, in *Edithcolea*.

Caudanthera, bitypic in the sense of Plowes (1995), with the type species *C. sinaica*, forms a well supported clade with *C. edulis* (Fig. 4), which Plowes (1995) placed into a separate genus, *Cryptolluma*. In the cpDNA dataset, *Caudanthera* forms an unsupported clade with several *Caralluma* segregates (Fig. 1), in the ITS dataset (Fig. 3), it forms an unsupported clade with *Boucerosia*, which gains support in the combined dataset (Fig. 4). The close relationship of the two very distinct *Caudanthera* species has been presumed by Bruyns (1989). Both species share the slender stems with four rounded angles, large leaf rudiments (the largest in all stapeliads except for the truly leafy *Boucerosia frerei*) accompanied by stipular glands and long-lived elongated-conical terminal portions of the stems which bear one- to two-flowered inflorescences. In addition, both species are characterized karyologically by exceptionally large chromosomes (Albers and Meve 2001). The main difference are the enormous sterile anther appendages of *C. sinaica*. Anther appendages in Ceropegieae must be interpreted as a plesiomorphy, because this character is shared with the Marsdenieae, the sister tribe of Ceropegieae. However, Meve and Liede (2001a) have shown that anther appendages are an insufficient character to separate *Macropetalum* from *Brachystelma*. Plowes (1995) excluded *Caralluma longidens* (together with the very similar *C. mouretii*) from *C. edulis* and even created another new genus for it, *Spiralluma* Plowes, on the basis of spiralled staminal corona lobes and short sterile anther appendages. Bruyns (1989) and Gilbert (1990), after study of type material, treated both species as synonyms of *C. edulis*, a view that is followed here. However, the length of anther appendages in *C. edulis* might follow a clinal distribution pattern, with rudimentary anther appendages extant in the south-saharan representatives ("*C. longidens*", "*C. mouretii*"), while they have completely disappeared in Arabian and Asian representatives. Anther appendages might therefore be symplesiomorphic for the genus *Caudanthera*.

The present analysis follows a pattern frequently encountered in Asclepiadoideae, and similarly in Orchidaceae, as has been demonstrated recently for the speciose Pleurothallidinae (Pridgeon et al. 2001): morphological similarities, in particular those of floral structures, are often a bad guide to phylogenetic relationships, because of a high degree of paralllism and homoplasy. Vegetative characters as a rule are more reliable. In Asclepiadoideae, for example, stipule-like short shoots characterize *Cynanchum* much better than elaborate corona structure, and all stem-succulent Malagasy species are monophyletic, even though they have been placed in different genera according to floral morphology (Liede and Täuber, in press). Very similar floral types have evolved in different geographical areas (*Oxystelma* and *Philibertia*, *Funastrum* and *Sarcostemma*, Liede and Täuber 2000), most likely as response to similar environmental, especially pollinator pressures. In several groups, a pattern similar to the one encountered here was found with well supported species groups, but little resolution between these groups. Liede et al. (in press) have suggested that geographical isolation of species groups and rapid evolution, albeit at different speeds in different areas, causes this pattern. In Ceropegieae, the unresolved *Caralluma* segregates might reflect remnants of a rather old radiation, with some segregates undergoing radiation and others stagnating; while the "southern" clade has most likely undergone more recent radiation after it arrived in its present area from an Arabian/Somalian origin. Following this hypothesis, the youngest members of stapeliads would be those species of *Duvalia*, *Huernia* and *Orbea* that have remigrated north from the south, and constitute the "soft-stemmed" clade.

Taxonomy

New circumscription of the *Caralluma* complex. Following our analysis, the 57 species accepted in *Caralluma* sensu Gilbert (1990) fall in seven distinct genera. Except for *Australluma peschii* (*Caralluma peschii*), which has been shown to be a member of the southern African stapeliad relationship, all these taxa are fairly closely related and representing the core North African/Arabian/Indian group of taxa. Additionally, one taxon treated as variety under *C. adscendens* is raised to species level (*Caralluma geniculata*).

Key to the genera of the *Caralluma* complex:

1 Stems with true leaves .... *Boucerosia frerei*
– Stems with leaf rudiments or more or less leafless 2
2 Stems erect, slender, subcylindrical to sharply 4-angled, stem tips tapering, inflorescences 1–4-flowered, forming false racemes along elongated apical stem portions 3
– Stems creeping, ascending to erect, 4-angled, stem tips blunt or slightly, but abruptly tapering, inflorescences in terminal or extra-axillary pseudo-umbels, or single-flowered and subaxillary 4
3 Leaf rudiments 4–12 mm long, basally accompanied by stipular glands .... *Caudanthera*
– Leaf rudiments 1–5 mm long, basally accompanied by tufts of (stipular) hairs .... *Caralluma*
4 Inflorescences in terminal pseudo-umbels . 5
– Inflorescences not in terminal pseudo-umbels 6
5 Leaf rudiments (broadly) lanceolate, without stipular formings .... *Boucerosia*
– Leaf rudiments absent or minute, suborbiculate, cordate to lanceolate but rarely acute and persistently thorny (*D. foetidus*, *D. speciosus*), with scattered (stipular) glandular hairs .... *Desmidorchis*
6 Stems pungent, leaf rudiments sessile, with tufts of (stipular) glandular hairs or stems not pungent, podaria (teeth of stems) grooved on upper side and without stipular formings .... *Monolluma*
– Stems not pungent, podaria not grooved, leaf rudiments subsessile to petiolate and sometimes swollen (*A. tuberculata*), with stipular glands or stipular formings absent ....*Apteranthes*

Caralluma R. Br., Asclepiadeae: 14 (1810). – Type species: *Caralluma adscendens* (Roxb.) Haw. (*Stapelia adscendens* Roxb.).
= *Saurolluma* Plowes, Haseltonia 3: 54 (1995). – Type species: *Saurolluma furta* (P. R. O. Bally) Plowes (*Caralluma furta* P. R. O. Bally).

= *Somalluma* Plowes, Haseltonia 3: 57 (1995). – Type species: *Somalluma baradii* (Lavranos) Plowes (*Caralluma baradii* Lavranos).

= *Spathulopetalum* Chiov., Ann. Bot. (Rome) 10: 392 (1912). – Type species: *Spathulopetalum dicapuae* Chiov.

Taxa accepted: 21 species (incl. 1 subspecies, 5 varieties). Distribution: Africa, Arabia, India.

Caralluma adscendens (Roxb.) N. E. Br., Mem. Wernerian Soc. 1: 14 (1810). Basionym: *Stapelia adscendens* Roxb., Pl. Corom. 1: 28 (1820). – Lecto(icono)type (designated by Gilbert 1990): Roxburgh 1820: t. 30, but *Wight 1517* in G! and P! possibly represents type material.

Caralluma adscendens var. ***attenuata*** (Wight) Grav. & Mayur., Bull. Madras Govern. Mus., ser. nov., 4(1): 13 (1931). Basionym: *Caralluma attenuata* Wight, Icon. Pl. India Orient. 4: 15 (1848). – Lecto(icono)type (designated by Gilbert 1990): Wight 1848: t. 1268.

Caralluma adscendens var. ***carinata*** Grav. & Mayur., Bull. Madras Govern. Mus., ser. nov., 4(1): 16 (1931). – Lecto(icono)type (designated by Gilbert 1990): Gravely and Mayuraranthan 1931: t. 2: 6.

Caralluma adscendens var. ***fimbriata*** (Wallich) Grav. & Mayur., Bull. Madras Govern. Mus., ser. nov., 4(1): 13 (1931). Basionym: *Caralluma fimbriata* Wall., Pl. As. Rar. 1: 7, t. 8 (1830–32). – Lecto(icono)type (designated by Gilbert 1990): Wallich 1830–32, Pl. As. Rar.: t. 8.

Caralluma adscendens var. ***gracilis*** Grav. & Mayur., Bull. Madras Govern. Mus., ser. nov., 4(1): 14 (1931). – Lecto(icono)type (designated by Gilbert 1990): Gravely & Mayuranathan 1931: t. 2: 5.

Caralluma arachnoidea (P. R. O. Bally) M. G. Gilbert, Natl. Cact. & Succ. J. 32(2): 26 (1977). Basionym: *Caralluma gracilipes* subsp. *arachnoidea* P. R. O. Bally (1969) ≡ *Spathulopetalum arachnoideum* (P. R. O. Bally) Plowes, Haseltonia 3: 56 (1995). – Holotype: Uganda, Karamoja, *Eggeling* 5692 in *Bally* 6294 [G].

Caralluma arachnoidea var. ***breviloba*** (P. R. O. Bally) M. G. Gilbert, Natl. Cact. & Succ. J. 32(2): 26 (1977). Basionym: *Caralluma gracilipes* var. *breviloba* P. R. O. Bally, Candollea 24: 15 (1969). – Type: Kenya, Olorgosailie, June 1960, *Bally* 12267 (S163) [K, holo; ZSS, iso].

Caralluma baradii Lavranos, Cact. & Succ. J. (Los Angeles) 65(5): 246 (1993) ≡ *Somalluma baradii* (Lavranos) Plowes, Haseltonia 3: 57 (1995).– Holotype: Somalia, 40 km W Hobiyo (= Obbia), near Gowein, *Lavranos*, *Carter* et al. 23338 [UPS].

Caralluma bhupinderana Sarkaria, Natl. Cact. Succ. J. 35(3): 68 (1980). – Holotype: Indien, Vallanaduberg, *Sarkaria* J93-78 [Herb. Univ. Punjab, Chandrigar].

Caralluma congestiflora P. R. O. Bally, Candollea 20: 13 (1965) ≡ *Spathulopetalum congestiflorum* (Sarkaria) Plowes, Haseltonia 3: 56 (1995). – Type: Somalia, N Province, near Hargeisa (*Bally* 11996 [K, holo; G, iso].

Caralluma dicapuae (Chiov.) Chiov., in A. C. White & B. Sloane, Stap, ed. 2,1, Addend. A: 187, 1937). Basionym: *Spathulopetalum dicapuae* Chiov., Ann. Bot. 10: 392 (1912). – Holotype: Ethiopia, betw. Chelamet and Oazata, *Terracciano* & *Pappi* 498 (955) [FT].

= *Caralluma dicapuae* subsp. *seticorona* P. R. O Bally, Candollea 24: 17 (1969).

Caralluma edwardsiae (M. G. Gilbert) M. G. Gilbert, Bradleya 8: 13 (1990). Basionym: *Caralluma gracilipes* subsp. *edwardsiae* (as *edwardsii*) M. G. Gilbert, Nat. Cact. Succ. J. 32(2): 30 (1977) ≡ *Spathulopetalum edwardsiae* (M. G. Gilbert) Plowes, Haseltonia 3: 56 (1995). – Type: Ethiopia, Gemu Gofa region, W Hamer Koke, M. & S. *Gilbert* 1730 [K, holo; ETH, iso].

Caralluma flavovirens L. E. Newton, Asklepios 74: 23–25 (1998). – Type: Kenya, Kizima Hill, *Newton* 4604 [K, holo; EA, iso].

Caralluma furta P. R. O. Bally, Candollea 18: 345 (1962) ≡ *Saurolluma furta* (P. R. O. Bally) Plowes, Haseltonia 3: 53 (1995). – Holotype: Somalia, N Sheik Paá, Bihendula, *Bally* 7129 [K].

Caralluma geniculata (Grav. & Mayur.) Meve & Liede, ***stat. nov.*** Basionym: *Caralluma adscendens* var. *geniculata* Grav. & Mayur., Bull. Madras Govern. Mus., ser. nov. 4(1): 16 (1931). – Lecto(icono)type (designated by Gilbert 1990): Graveley and Mayuranathan 1931: t. 2: 7.

This taxon is more closely related to *Caralluma bhupinderana* than to *Caralluma adscendens*. With its rather thin stems and tiny and stiff flowers on bent pedicels (cf. Fig. 6 in Plowes 1990) it nevertheless deserves species rank.

Caralluma gracilipes K. Schum., in Engler, Pfl. Ost. Afr. C: 328 (1895) ≡ *Spathulopetalum gracilipes* (K. Schum.) Plowes, Haseltonia 3: 56 (1995). – Holotype: N Kenya, Kitui-District, *Hildebrandt* 2700 [B].

Caralluma longiflora M. G. Gilbert, Bradleya 8: 13 (1990) ≡ *Spathulopetalum longiflorum* (M. G. Gilbert) Plowes, Haseltonia 3: 56 (1995). – Holotype: Somalia, 53 km on the road betw. Maas and Bulo Burti, *Thulin* & *Warfa* 4604 [K].

Caralluma moniliformis P. R. O. Bally, Candollea 20: 17 (1965) ≡ *Spathulopetalum moniliforme* (P. R. O. Bally) Plowes, Haseltonia 3: 56 (1995). – Holotype: Somalia, E Al Madu Range, Agasur (Sufli), *Bally* 11018 [G].

Caralluma peckii P. R. O. Bally, Candollea 18: 14 (1962) ≡ *Spathulopetalum peckii* (P. R. O. Bally) Plowes, Haseltonia 3: 56 (1995). – Holotype: Kenya, Archers Post near Isiolo, *Peck in Bally* S(61) [K].

Caralluma priogonium K. Schum., Bot. Jahrb. Syst. 34: 327 (1905) ≡ *Spathulopetalum priogonium* (K. Schum.) Plowes, Haseltonia 3: 56 (1995). – Holotype: Tanzania, between Gonja and Kihurio, *Engler* 1521/a [B, destroyed].

= *Caralluma mogadoxensis* Chiov., Fl. Somala 2: 299 (1932) ≡ *Spathulopetalum mogadoxense* (Chiov.) Plowes, Haseltonia 3: 56 (1995).

= *Caralluma elata* Chiov., Miss. Biol. Bolana, Racc. Bot.: 169 (1939).

Caralluma sarkariae Lavranos & Frandsen, Cact. Succ. J. (Los Angeles) 50(5): 211 (1978). – Holotype: India, at base of Nagamalai Mts, 8 km W Madurai, *Sarkaria* J64-77 [E].

Caralluma stalagmifera C. E. C. Fischer, Bull. Misc. Inf. (Kew) 1925: 430 (1925). – Holotype: India, Madras Vandalur, *Mayuranathan* s. n. [K].

Caralluma subulata Forssk. ex Decne., Ann. Sc. Nat. 9: 267 (1838). Basionym: *Stapelia subulata* Forssk., Fl. Aegypt.-Arab.: CVIII (1775). – Lecto(icono)type (designated by Gilbert 1990): Forsskål 1776, Icon. Rer. Nat.: t. 7.

= *Caralluma dalzielii* N. E. Br., Bull. Misc. Inform. (Kew) 1912: 280 (1912).

Caralluma turneri E. A. Bruce, Hook. Ic. Pl. 34: t. 3339 (1938). Basionym: *Caralluma dicapuae* subsp. *turneri* (E. A. Bruce) P. R. O. Bally (1969) ≡ *Spathulopetalum turneri* (E. A. Bruce) Plowes, Haseltonia 3: 56 (1995). – Holotype: Kenya, S Kavirondo, Kanam, Homaberg, *Turner* s.n. sub CM 3692 [K].

Caralluma turneri subsp. ***ukambensis*** (P. R. O. Bally) L. E. Newton, Asklepios 72: 9 (1997). Basionym: *Caralluma dicapuae* (Chiov.) Chiov. subsp. *ukambensis* P. R. O. Bally, Candollea 24: 19 (1969). – Holotype: Kenya, Kitui-District, Ukamba, Ithumbi-Berg, *MacArthur* sub *Bally* S135 [ZSS].

Caralluma vaduliae Lavranos, Cact. & Succ. J. (US) 63(4): 170 (1991) ≡ *Spathulopetalum vaduliae* (Lavranos) Plowes, Haseltonia 3: 56 (1995). – Holotype: Somalia, Galguduud area, 179 km NE Mogadiscio, Harardere direction, *Lavranos* & al. 23275 [UPS].

Apteranthes Mikan, Nova Acta Acad. Caes. Leop.-Carol. Nat. 17(2): 594, t. 41 (1835). – Type species: *Apteranthes europaea* (Guss.) Plowes (*Stapelia europaea* Guss.)

= *Borealluma* Plowes, Haseltonia 3: 63 (1995). – Type species: *Borealluma munbyana* (Decne.) Plowes (*Boucerosia munbyana* Decne.).

Taxa accepted: 6 species (incl. 1 subspecies, 1 variety). Distribution: Canary Islands, SW Europe, northern Africa, Arabia, Asia (Iran to Nepal).

Apteranthes burchardii (N. E. Br.) Plowes, Haseltonia 3: 61 (1995). Basionym: *Caralluma burchardii* N. E. Br., Bull. Misc. Inf. (Kew) 1913: 121 (1913). – Holotype: Canary Islands, Fuerteventura, *Burchard* s.n. [K].

subsp. ***burchardii***

= *Caralluma burchardii* var. *purpurascens* Gattefossé & Maire, Bull. Soc. Hist. Nat. Afr. Nord 36: 100 (1945).

= *Caralluma burchardii* var. *sventenii* E. & B. M. Lamb, Natl. Cact. Succ. J. 11: 77 (1956).

Apteranthes burchardii (N. E. Br.) Plowes subsp. ***maura*** (Maire) Meve & F. Albers, ***comb. nov.*** Basionym: *Caralluma burchardii* var. *maura* Maire, Bull. Soc. Hist. Nat. Afr. Nord 14: 156 (1923) ≡ *Caralluma burchardii* subsp. *maura* (Maire) Meve & F. Albers, Nordic J. Bot. 15: 465 (1995). – Holotype: Morocco, near Agadir-n-Ighir, *Maire* [MPU].

= *Caralluma burchardii* var. *maura* f. *grandiflora* Maire, Bull. Soc. Hist. Nat. Afr. Nord. 33: 89 (1942).

= *Caralluma burchardii* var. *maura* f. *sordida* Maire, Bull. Soc. Hist. Nat. Afr. Nord. 33: 89 (1942).

= *Caralluma burchardii* var. *maura f. viridis* Gattefosse & Maire, Bull. Soc. Hist. Nat. Afr. Nord 36: 99 (1945).

Apteranthes europaea (Guss.) Plowes, Haseltonia 3: 59 (1995). Basionym: *Stapelia europaea* Guss., Flor. Sic. Prod. 1: 65 (1832) ≡ *Boucerosia europaea* (Guss.) Caruel, Parl., Fl. Ital. 6: 725 (1886) ≡ *Desmidorchis europaea* Kuntze, Rev. Gen.: 418 (1891) ≡ *Caralluma europaea* (Guss.) N. E. Br., Gard. Chron. 12: 369 (1892). – Holotype: Italy, Lampedusa, on calcarous rocks close to sea, *Gussone* s.n. [NAP].

var. ***europaea***

= *Apteranthes gussoneana* J. C. Mikan, Nov. Act. Nat. Cur. 17: 594 (1835) ≡ *Stapelia gussoneana* (J. C. Mikan) Jacq. ex Lindl., Bot. Reg., t. 1731 (1835) ≡ *Boucerosia gussoneana* (J. C. Mikan) Hook. f., Bot. Mag. 100. t. 6137 (1874) ≡ *Caralluma europaea* subsp. *gussoneana* (J. C. Mikan) Maire, in Jahandiez & Maire, Cat. Pl. Maroc 3: 582 (1924) ≡ *Apteranthes europaea* subsp. *gussoneana* (J. C. Mikan) Plowes, Haseltonia 3: 59 (1995).

= *Boucerosia maroccana* Hook. f., Bot. Mag. 100, t. 6137 (1874) ≡ *Caralluma maroccana* (Hook. f.) N. E. Br., Gard. Chron. 12: 370 (1892) ≡ *Caralluma europaea* var. *maroccana* (Hook. f.) Berger, Stap. Klein.: 96 (1910) ≡ *Caralluma europaea* subsp. *maroccana* (Hook. f.) Maire, in Jahandiez & Maire, Cat. Pl. Maroc 3: 582 (1924) ≡ *Apteranthes europaea* subsp. *maroccana* (Hook. f.) Plowes, Haseltonia 3: 60 (1995).

= *Caralluma affinis* de Wild., Icon. Select. Hort. Then. 5: 29 (1904) ≡ *Caralluma europaea* var. *affinis* (de Wild.) Berger, Stap. Klein: 97 (1910) ≡ *Apteranthes europaea* var. *affinis* (de Wild.) Plowes, Haseltonia 3: 59 (1995).

= *Caralluma simonis* hort. ex Berger, Monatsschr. Kakt. 14: 6 (1904) ≡ *Caralluma europaea* var. *simonis* (hort. ex Berger) Berger, Stap. Klein.: 95 (1910) ≡ *Boucerosia simonis* (hort. ex Berger) A. C. White & B. Sloane, Stap. 191 (1933) ≡ *Apteranthes europaea* var. *simonis* (hort. ex Berger) Plowes, Haseltonia 3: 61 (1995).

= *Caralluma europaea* var. *marmaricensis* Berger, Stap. Klein.: 95 (1910) ≡ *Apteranthes europaea* var. *marmaricensis* (Berger) Plowes, Haseltonia 3: 61 (1995).

= *Caralluma confusa* Font Quer, Bull. Inst. Cat. Hist. Nat. 1922: 31 (1922) ≡ *Caralluma europaea* var. *confusa* (Font Quer) Font Quer, Mem. Mus. Cienc. Nat. Barcel. 2: 10 (1924) ≡ *Apteranthes europaea* var. *confusa* (Font Quer) Plowes, Haseltonia 3: 61 (1995).

= *Caralluma europaea* subsp. *maroccana* var. *barrueliana* Maire, Bull. Soc. Hist. Nat. Afr. Nord. 26: 218 (1935) ≡ *Apteranthes europaea* subsp. *maroccana* var. *barrueliana* (Maire) Plowes, Haseltonia 3: 60 (1995).

= *Caralluma europaea* subsp. *maroccana* var. *albotigrina* Maire, Bull. Soc. Hist. Nat. Afr. Nord. 27: 79 (1936) ≡ *Apteranthes europaea* subsp. *maroccana* var. *albotigrina* (Maire) Plowes, Haseltonia 3: 61 (1995).

= *Caralluma europaea* subsp. *maroccana* var. *gattefossei* Maire, Bull. Soc. Hist. Nat. Afr. Nord. 27: 79 (1936) ≡ *Apteranthes europaea* subsp. *maroccana* var. *gattefossei* (Maire) Plowes, Haseltonia 3: 61 (1995).

= *Caralluma europaea* subsp. *maroccana* var. *decipiens* Maire, Bull. Soc. Hist. Nat. Afr. Nord. 29: 436 (1938) ≡ *Caralluma europaea* subsp. *gussoneana* var. *decipiens* (Maire) Maire, Bull. Soc. Hist. Nat. Afr. Nord. 32: 214 (1943) ≡ *Apteranthes europaea* subsp. *maroccana* var. *decipiens* (Maire) Plowes, Haseltonia 3: 61 (1995).

= *Caralluma europaea* var. *affinis* f. *parviflora* Maire, Bull. Soc. Hist. Nat. Afr. Nord. 30: 357 (1941).

= *Caralluma europaea* subsp. *gussoneana* var. *tristis* (Maire), Bull. Soc. Hist. Nat. Afr. Nord. 32: 213 (1941) ≡ *Apteranthes europaea* subsp. *gussoneana* var. *tristis* (Maire) Plowes, Haseltonia 3: 59–60 (1995).

= *Caralluma europaea* subsp. *maroccana* var. *micrantha* Maire, Bull. Soc. Hist. Nat. Afr. Nord. 32: 213 (1941) ≡ *Apteranthes europaea* subsp. *maroccana* var. *micrantha* (Maire) Plowes, Haseltonia 3: 61 (1995).

= *Caralluma europaea* var. *schmuckiana* Gattefossé & Maire Bull. Soc. Hist. Nat. Afr. Nord. 34: 183 (1943) ≡ *Apteranthes europaea* var. *schmuckiana* (Gattefossé & Maire) Plowes, Haseltonia 3: 59 (1995).

Apteranthes europaea var. ***judaica*** (Zohary) Plowes, Haseltonia 3: 61 (1995). Basionym: *Caralluma europaea* var. *judaica* Zohary, (Pal. J. Bot. ser. 2: 173, 1941). – Holotype: Israel, Jerusalem, between Beth Hakerem and Bayith Vegan, *D. Zohary* 2189 [HUJ].

= *Boucerosia aaronis* Hart, Trans. Roy. Irish Acad. 28: 436, t. 17 (1885).

= *Caralluma negevensis* Zohary, in Feinbrun-Dothan, Fl. Palest. 3, Appendix, t. 44 (1978) ≡ *Apteranthes negevensis* (Zohary) Plowes, Haseltonia 3: 61 (1995).

= *Caralluma israelitica* M. Zohary & Chaouat, *nomen nudum*, New Analyt. Fl. Israel: 289 (1979).

Apteranthes joannis (Maire) Plowes, Haseltonia 3: 61 (1995). Basionym: *Caralluma joannis* Maire, Bull. Soc. Hist. Nat. Afr. Nord. 31: 27, 1940). – Holotype: Morocco, Aoulouz (*Pitault* s.n., cult. hort. *Gattefossé* (MPU)).

Apteranthes munbyana (Decne.) Meve & Liede, ***comb. nov.*** Basionym: *Boucerosia munbyana* Decne., in Munby, Fl. Alger.: 25 (1847) ≡ *Caralluma munbyana* (Decne.) N. E. Br., Gard. Chron. ser. 3, 12: 278 (1892) ≡ *Borealluma munbyana* (Decne.) Plowes, Haseltonia 3: 63 (1995). – Lectotype (designated by Gilbert 1990): Algeria, Santa Cruz, *Munby* s.n. [G].

= *Boucerosia munbyana* var. *hispanica* Coincy, Journ. de Bot. 250 (1898) ≡ *Boucerosia hispanica* (Coincy) Coincy, Journ.de Bot.: 336 (1998) ≡ *Boucerosia munbyana* subsp. *hispanica* (Coincy) M. B. Crespo & Mateo, Acta Bot. Malacitana 20: 285 (1995).

Apteranthes staintonii (Hara) Meve & Liede, ***comb. nov.*** Basionym: *Caralluma staintonii* Hara, J. Jap. Bot. 52(12): 357 (1977) ≡ *Borealluma staintonii* (Hara) Plowes, Haseltonia 3: 63: (1995). – Holotype: Nepal, Bheri-Valley, Donaihi, *Stainton* 5410 [BM].

Apteranthes tuberculata (N. E. Br.) Meve & Liede, ***comb. nov.*** Basionym: *Caralluma tuberculata* N. E. Br., Gard. Chron. 12: 370 (1892) ≡ *Borealluma tuberculata* (N. E. Br.) Plowes, Haseltonia 3: 63 (1995). – Holotype: Pakistan (Belutschistan), Nullee Salt Range, *Stock* 596 [K].

= *Caralluma plicatiloba* Lavranos, J. South Afr. Bot. 28: 211 (1962).

Australluma Plowes, Haseltonia 3: 54 (1995).

– Type species: *Australluma peschii* (Nel) Plowes (*Caralluma peschii* Nel)

Taxa accepted: 1 species. Distribution: Namibia.

Australluma peschii (Nel) Plowes, Haseltonia 3: 54 (1995). Basionym: *Caralluma peschii* Nel, Kakt.-Jahrb. 1935: 41 (1935). – Holotype: Namibia, Hereroland, Omaruru, *Pesch* s.n., cultivated in Stellenbosch under STE 7082 (BOL).

Boucerosia Wight & Arn., in Wight, Contr. Bot. India: 34 (1834). Basionym: *Caralluma* sect. *Boucerosia* (Wight & Arn.) K. Schum, in Engler & Prantl, Nat. Pfl.fam. 4(2): 278 (1895) ≡ *Caralluma* subgen. *Boucerosia* (Wight & Arn.) M. G. Gilbert, Bradleya 8: 15 (1990). – Type species: *Boucerosia umbellata* (Haw.) Wight & Arn. (*Caralluma umbellata* Haw.).

= *Hutchinia* Wight & Arn., in Wight, Contr. Bot. India: 34 (1834). – Type species: *Hutchinia indica* Wight & Arn.

= *Frerea* Dalz., J. Linn. Soc., Bot. 8: 10, t. 3 (1864). – Type species: *Frerea indica* Dalz.

Taxa accepted: 7 species. Distribution: Asia (India, Sri Lanka, Myanmar).

Boucerosia crenulata (Wall.) Wight & Arn., Contr. Bot. Ind.: 34 (1834). Basionym: *Caralluma crenulata* Wallich, Pl. As. Rar. 1: 6, t. 7 (1830) ≡ *Desmidorchis crenulata* (Wall.) Decne. (1838). – Lecto(icono)type (designated by Gilbert 1990): Wallich 1830: Pl. As. Rar. 1: 6, t. 7.

= *Boucerosia truncato-coronata* Sedgwick, J. Ind. Bot. 2: 125 (1921) ≡ *Caralluma truncato-coronata* (Sedgwick) Grav. & Mayur., Bull. Madras Govern. Mus., ser. nov., 4(1): 21 (1931).

= *Boucerosia nilageriana* (Kumari & Rao) Plowes, Haseltonia 3: 59 (1995) ≡ *Caralluma nilagiriana* Kumari & Rao, J. Bombay Nat. Hist. Soc. 73: 199 (1976).

Boucerosia diffusa Wight, Icon. 6: t. 1287 (1850). Basionym: *Caralluma diffusa* (Wight) N. E. Br., Gard. Chron. ser. 3, 12: 369 (1892). – Lecto(icono)type (designated by Gilbert 1990): Wight 1850: Ic. Pl. Ind. Orient. 4(4): 14, t. 1599.

Boucerosia frerei (Rowley) Meve & Liede, ***comb. nov.*** Basionym: *Caralluma frerei* Rowley, Natl. Cact. Succ. J. 13: 78 (1958), *nom. nov. pro Frerea indica* Dalz., J. Linn. Soc. 8: 10 (1865). – Holotype: India, Bombay Presidency, N Pune ("Poona"), *Dalzell* s.n. [K].

Boucerosia indica (Wight & Arn.) Plowes, Haseltonia 3: 59 (1995). Basionym: *Hutchinia indica* Wight & Arn., Contr. Bot. India: 34 (1834) ≡ *Caralluma indica* (Wight & Arn.) N. E. Br., Gard. Chron. ser. 3, 12: 369 (1892). – Lectotype (designated by Gilbert 1990): India, without precise locality, *Wight* s. n. [K].

= *Boucerosia hutchinia* Decne., in DC, Prodr. 8: 649 (1844) (*nom. illegit. superfl.*).

Boucerosia pauciflora Wight, Madras J. Sc. 6: 473 (1837). Basionym: *Caralluma pauciflora* (Wight) N. E. Br., Gard. Chron. ser. 3, 12: 369 (1892) ≡ *Desmidorchis pauciflora* (Wight) Decne., Ann. Sc. Nat. Ser. 2(9): 266 (1838). – Lectotype (designated by Gilbert 1990): India, Madras, Palamcottai, *Wight* 2429 [K].

Boucerosia procumbens (Grav. & Mayur.) Plowes, Haseltonia 3: 59 (1995). Basionym: *Caralluma procumbens* Grav. & Mayuran., Bull. Madras Govern. Mus., ser.nov., 4(1): 26 (1931). – Lecto(icono)type (designated by Gilbert 1990): Graveley and Mayuranathan 1931: t. 4: 13–17.

Boucerosia umbellata (Haw.) Wight & Arn., Contr. Bot. Ind.: 34 (1834). Basionym: *Caralluma umbellata* Haw., Syn. Pl. Succ.: 47 (1812) ≡ *Stapelia umbellata* (Haw.) Roxburgh (1819) ≡ *Desmidorchis umbellata* (Haw.) Decne. (1838). – Type: E India, cultivated in India 1804 [no type material preserved].

= *Boucerosia campanulata* Wight, Icon. Pl. Ind. Orient. 4(2): 1 t. 1287 (1848) ≡ *Caralluma campanulata* (Wight) N. E. Br., Gard. Chron. 12: 369 (1892).

= *Boucerosia lasiantha* Wight, Icon. Pl. Ind. Orient. 4(2): 1, t. 1286 (1848) ≡ *Caralluma lasiantha* (Wight) N. E. Br., Gard. Chron. 12: 369 (1892).

Caudanthera Plowes, Haseltonia 3: 58 (1995). – Type species: *Caudanthera sinaica* (Decne.) Plowes ≡ *Boucerosia sinaica* Decne. ≡ *Caralluma sinaica* (Decne.) Berger.

= *Cryptolluma* Plowes, Haseltonia 3: 57 (1995). – Type species: *Cryptolluma edulis* (Edgew.) Plowes (*Caralluma edulis* Edgew.).

= *Spiralluma* Plowes, Haseltonia 3: 53 (1995). – Type species: *Spiralluma longidens* (N. E. Br.) Plowes (*Caralluma longidens* N. E. Br.).

Taxa accepted: 3 species. Distribution: Africa, Arabia, Asia (Iran to India).

Caudanthera sinaica (Decne.) Plowes, Haseltonia 3: 58 (1995). Basionym: *Boucerosia sinaica* Decne., in DC, Prodr. 8: 649 (1844) ≡ *Caralluma sinaica* (Decne.) Berger, Stap. Klein.: 55 (1910). – Holotype: Egypt, Sinai, *Aucher-Eloy* 3850 or 2850? [P].

= *Caralluma sinaica* var. *baradii* Lavranos & Newton, Cact. Succ. J. (Los Angeles) 51: 236 (1979)

= *Caralluma maris-mortui* Zohary, Palest. J. Bot., ser. 2: 175 (1941).

Caudanthera mireillae (Lavranos) Plowes, Haseltonia 3: 58 (1995). Basionym: *Caralluma mireillae* Lavranos, Natl. Cact. & Succ. J. 24(4): 78 (1969). – Holotype: Djibouti, SE edge of Barra Yer, 11°21′N, 40°21′E, alt. 525 m, 10th Oct. 1968, *Lavranos* 6842 [PRE].

Caudanthera edulis (Edgew.) Meve & Liede, ***comb. nov.*** Basionym: *Boucerosia edulis* Edgew., J. Linn. Soc. 6: 205 (1862) ≡ *Caralluma edulis* (Edgew.) Benth. & Hook. f., Gen. Pl. 2: 782 (1876) ≡ *Cryptolluma edulis* (Edgew.) Plowes, Haseltonia 3: 57 (1995). – Holotype: India, Multan, *Edgeworth* 6035 [K].

= *Boucerosia stocksiana* Boiss., Fl. Orient. 4: 63 (1879) ≡ *Desmidorchis stocksiana* (Boiss.) Kuntze, Rev. Gen.: 418 (1891)

= *Caralluma longidens* N. E. Br., Gard. Chron. 2: 369 (1892) ≡ *Spiralluma longidens* (N. E. Br.) Plowes, Haseltonia 3: 53 (1995).

= *Caralluma vittata* N. E. Br., Th.-Dyer, Fl. Trop. Afr. 4(1): 483 (1904).

= *Caralluma mouretii* A. Chev., Rev. Bot. Appl. 14: 272 (1934) ≡ *Spiralluma mouretii* Plowes, Haseltonia 3: 54 (195).

Desmidorchis Ehrenb., Abh. Königl. Akad. Wiss. Berlin 1829: 31, 39 (1832). – Type species: *Desmidorchis retrospiciens* Ehrenb. (syn.: *Desmidorchis acutangulus* Decne).

= *Sarcocodon* N. E. Br., J. Linn. Soc. 17: 169 (1878). – Type species: *Sarcocodon speciosus* N. E. Br.

= *Crenulluma* Plowes in Haseltonia 3: 66. 1995. – Type species: *Crenulluma awdeliana* (Deflers) Plowes (*Boucerosia awdeliana* Deflers).

Taxa accepted: 11 species. Distribution: Northern Africa, Arabia.

Desmidorchis acutangulus Decne., Ann Sc. Nat. ser. 2(9): 265 (1838). Basionym: *Caralluma acutangula* (Decne.) N. E. Br., Gard. Chron. ser. 3, 12: 369 (1892) ≡ *Boucerosia acutangula* (Decne.) Decne., Ann. Sc. Nat. 9 (1844) ≡ *Caralluma retrospiciens* subsp. *tombuctuensis* (A. Chev.) A. Chev. var. *acutangula* (Decne.) A. Chev., Rev. Bot. Appl.: 266 (1934) ≡ *Caralluma retrospiciens* var. *acutangula* (Decne.) A. C. White & B. Sloane, Stap., 2nd ed., 1: 242 (1937). – Neotype (designated by Gilbert and Raynal 1980): Mali, *de Wailly* 4872 [P].

= *Caralluma retrospiciens* Ehrenb., Abh. Acad. Berlin: 33 (1831) (*nom. nud.*, *nom. illegit.*) = *Caralluma retrospiciens* Ehrenb. ex N. E. Br., in Th. Dyer, Fl. Trop. Afr. 4(1): 480 (1904).

= *Boucerosia tombuctuensis* A. Chev., Cong. Int. Bot. Paris: 271 (1900) ≡ *Caralluma tombuctuensis* (A. Chev.) N. E. Br., Gard. Chron. 12 : 369 (1892) ≡ *Caralluma retrospiciens* subsp. *tombuctuensis* (A. Chev.) A. Chev., Rev. Bot. Appl.: 266 (1934) ≡ *Caralluma retrospiciens* var. *tombuctuensis* (A. Chev.) A. C. White & B. Sloane, Stap., 2nd ed., 1: 242 (1937).

= *Boucerosia russeliana* Brongn., Bull. Soc. Bot. Fr. 7: 900 (1860) ≡ *Caralluma russeliana* ("*russelliana*") (Brongn.) Cufod., Enum. Pl. Aeth. 30 (1969).

= *Caralluma hirtiflora* N. E. Br., Bull. Misc. Inf. (Kew) 1895: 264 (1895) ≡ *Caralluma* *retrospiciens* var. *hirtiflora* (N. E. Br.) Berger, Stap. Klein. 71 (1910).

= *Caralluma retrospiciens* var. *glabra* N. E. Br., Th. Dyer, Fl. Trop. Afr. 4(1): 481 (1904).

= *Caralluma retrospiciens* var. *laxiflora* Maire, Bull. Soc. Nat. Hist. Afr. Nord 30: 357 (1939).

Desmidorchis adenensis (Deflers) Meve & Liede, ***comb. nov***. Basionym: *Boucerosia adenensis* Deflers, Bull. Soc. Bot. Fr. 43: 115 (1896) ≡ *Caralluma adenensis* (Deflers) Berger, Stap. Klein.: 79 (1910) ≡ *Crenulluma adenensis* (Deflers) Plowes, Haseltonia 3: 66 (1995). – Syntypes: Yemen (S), Aden Peninsula, Scham-Scham Mt., *Deflers* 65 et 518; Wadi Eybad, near Schoukra, *Deflers* 506, 863, 917 et 1019; Mt. Heys, *Deflers* 1163 [all in P].

= *Caralluma kalmbacheriana* Lavranos, Cact. Succ. J. (Los Angeles) 37: 110 (1965) ≡ *Crenulluma kalbacheriana* (Lavranos) Plowes, Haseltonia 3: 67 (1995).

= *Caralluma rauhii* Lavranos, Cact. Succ. J (U.S.) 37: 106 (1965) ≡ *Crenulluma rauhii* (Lavranos) Plowes, Haseltonia 3: 67 (1995).

Desmidorchis arabicus (N. E. Br.) Meve & Liede, ***comb. nov***. Basionym: *Caralluma arabica* N. E. Br., Bull. Misc. Inf. (Kew) 1895: 318 (1895) ≡ *Crenulluma arabica* (N. E. Br.) Plowes, Haseltonia 3: 66 (1995). – Holotype: Yemen (S), Wadi Raida, near Saihut, *Hirsch* 28 [K].

Desmidorchis awdelianus (Deflers) Meve & Liede, ***comb. nov***. Basionym: *Boucerosia awdeliana* Deflers, Bull. Soc. Bot. Fr. 43: 116 (1896) ≡ *Caralluma awdeliana* (Deflers) Berger, Stap. Klein.: 81 (1910) ≡ *Crenulluma awdeliana* (Deflers) Plowes, Haseltonia 3: 66 (1995). – Holotype: Yemen (S), Nakha Mt., close to Bilad Awdeli, *Deflers* 485 [P].

= *Caralluma petraea* Lavranos, Cact. Succ. J. (Los Angeles) 55(1): 23 (1983) ≡ *Crenulluma petraea* (Lavranos) Plowes, Haseltonia 3: 67 (1995).

Desmidorchis edithae (N. E. Br.) Plowes, Haseltonia 3: 58 (1995). Basionym: *Caralluma edithae* N. E. Br., Bull. Misc. Inf. (Kew) 1895: 219 (1895). – Holotype: Somalia, *E. Cole* s.n. [K]).

Desmidorchis flavus (N. E. Br.) Meve & Liede, ***comb. nov***. Basionym: *Caralluma flava* N. E. Br., Bull. Misc. Inf. (Kew) 1894: 335 (1894) ≡ *Crenulluma flava* (N. E. Br.) Plowes, Haseltonia 3: 67 (1995). – Holotype: Yemen (S), Hadrhamaut, Wadi Hadiea, *Lunt* 184 [K].

Desmidorchis foetidus (E.A Bruce) Plowes, Haseltonia 3: 58 (1995). Basionym: *Caralluma foetida* E. A. Bruce, Hook. Icon. Pl. 34: t. 3371 + text (1938). – Holotype: Uganda, Karamoja, Morotofluá, *Eggeling* 2955 [K].

Desmidorchis lavrani (Rauh & Wertel) Meve & Liede, ***comb. nov.*** Basionym: *Caralluma lavranii* Rauh & Wertel, Kakteen Sukk. 16(4): 62 (1965) ≡ *Crenulluma lavranii* (Rauh & Wertel) Plowes, Haseltonia 4: 67 (1995). – Holotype: Yemen (S), above Mukallam, Molam Matr direction, *Rauh* 13300 [HEID].

Desmidorchis penicillatus (Deflers) Plowes, Haseltonia 3: 58–59 (1995). Basionym: *Boucerosia penicillata* Deflers, Voy. Yemen: 169 (1889) ≡ *Caralluma penicillata* (Deflers) N. E. Br., Gard. Chron. ser. 3, 12: 370 (1892). – Holotype: Yemen (S), Mefhak, *Deflers* 97 [P].

= *Caralluma robusta* N. E. Br., in Th. Dyer, Fl. Trop. Afr. 4(1): 482 (1903) ≡ *Caralluma penicillata* var. *robusta* (N. E. Br.) A. C. White & B. Sloane, Stap., 2nd ed., 1: 211 (1937).

= *Echidnopsis golathi* Schweinf. ex Deflers (1896) (*nom. illegit*., *nom. superfl*.).

Desmidorchis somalicus (N. E. Br.) Plowes, Haseltonia 3: 59 (1995). Basionym: *Caralluma somalica* N. E. Br., Bull. Misc. Inf. (Kew) 1895: 264, 1895). – Holotype: Somalia, near Mogadiscio, *Kirk* s.n. [K].

Desmidorchis speciosus (N. E. Br.) Plowes, Haseltonia 3: 59 (1995). Basionym: *Sarcocodon speciosa* N. E. Br., J. Linn. Soc. 17: 170 (1878) ≡ *Caralluma speciosa* (N. E. Br.) N. E. Br., Gard. Chron. ser. 3, 12: 370 (1892) ≡ S*arcocodon speciosa* N. E. Br.,

J. Linn. Soc. 17: 169 (1878). – Holotype: Somalia, Brava, near Mogadiscio, *Kirk* s.n. [K].

= *Caralluma codonoides* K. Schum., in Engler, Pfl.welt Ost-Afr. C: 328 (1895).

= *Caralluma oxydonta* Chiov., Fl. Somala 2: 298 (1932).

Monolluma Plowes, Haseltonia 3: 64 (1995). – Type species: *Monolluma quadrangula* (Forssk.) Plowes (*Stapelia quadrangula* Forssk.).

= *Cylindrilluma* Plowes, Haseltonia 3: 62 (1995). – Type species: *Cylindrilluma solenophora* (Lavr.) Plowes (*Caralluma solenophora* Lavr.).

= *Sanguilluma* Plowes, Haseltonia 3: 65 (1995). – Type species: *Sanguilluma socotrana* (Balf. f.) Plowes (*Boucerosia socotrana* Balf. f.).

= *Sulcolluma* Plowes, Haseltonia 3: 61 (1995). – Type species: *Sulcolluma hexagona* (Lavranos) Plowes (*Caralluma hexagona* Lavranos).

Taxa accepted: 5 species. Distribution: Northeast Africa, Arabia (incl. Socotra).

Monolluma cicatricosa (Deflers) Plowes, Haseltonia 3: 65 (1995). Basionym: *Boucerosia cicatricosa* Deflers, Voyage Yemen: 170 (1889) ≡ *Caralluma cicatricosa* (Deflers) N. E. Br., Gard. Chron. ser. 3, 12: 369, 1892).– Holotype: Yemen (S), Wadi Schidja, *Deflers* 435 [P].

= *Caralluma forskaolii* (Decne.) Plowes, Asklepios 50: 16 (1990) ≡ *Desmidorchis forskalii* Decne., Ann. Sc. Nat. Ser. 2(9): 285 (1838), p.p., excl. *Stapelia quadrangula* ≡ *Boucerosia forskalii* (Decne.) Decne., Ann. Sc. Nat. 9 (1844) (*nom. illegit.*, *nom. superfl.*).

Monolluma hexagona (Lavranos) Meve & Liede, ***comb. nov.*** Basionym: *Caralluma hexagona* Lavranos, J. S. Afr. Bot. 29: 105 (1963) ≡ *Sulcolluma hexagona* (Lavranos) Plowes, Haseltonia 3: 62 (1995). – Type: Yemen (S), Audhali-Plateau, 3 miles S Al Madhan, *Lavranos* 1829 [K, holo; PRE, iso].

= *Caralluma foulcheri-delboscii* Lavranos, J. S. Afr. Bot. 30: 21 (1964) ≡ *Sulcolluma foulcheri-delboscii* (Lavranos) Plowes, Haseltonia 3: 62 (1995).

= *Caralluma foulcheri-delboscii* var. *greenbergiana* Lavranos, (1967) ≡ *Sulcolluma foulcheri-delboscii* var. *greenbergiana* (Lavranos) Plowes, Haseltonia 3: 62 (1995).

= *Caralluma shadbhana* Lavranos, Flow. Pl. Afr. 44(3–4): t. 1743 (1977) ≡ *Sulcolluma shadbhana* (Lavranos) Plowes, Haseltonia 3: 62 (1995).

= *Caralluma hexagona* var. *septentrionalis* Lavranos & L. E. Newton, Cact. Succ. J. (Los Angeles) 51(5): 234 (1979) ≡ *Sulcolluma hexagona* var. *septentrionalis* (Lavranos) Plowes, Haseltonia 3: 62 (1995).

= *Caralluma shadbhana* var. *barhana* Lavranos & L. E. Newton, Cact. Succ. J. (Los Angeles) 51(5): 235 (1979) ≡ *Sulcolluma shabhana* var. *barhana* (Lavranos & Newton) Plowes, Haseltonia 3: 62 (1995).

Monolluma quadrangula (Forssk.) Plowes, Haseltonia 3: 65 (1995). Basionym: *Stapelia quadrangula* Forssk., Fl. Aeg.-Arab.: 52 (1775) ≡ *Boucerosia quadrangula* (Forssk.) Decne., Prodr. 8: 664 (1844) ≡ *Echidnopsis quadrangula* (Forssk.) Deflers, Bull. Soc. Bot. Fr., 113 (1896) ≡ *Desmidorchis quadrangula* (Forssk.) Gilbert & Raynal, Adansonia 19(3): 322 (1980) ≡ *Caralluma quadrangula* (Forssk.) N. E. Br., Gard. Chron. ser. 3, 12: 370 (1892). – Lecto(icono)type (designated by Gilbert 1990): Forsskål 1776: Icon. Rer. Nat., t. 6.

Monolluma socotrana (Balf. f.) Meve & Liede, ***comb. nov.*** Basionym: *Boucerosia socotrana* Balf. f., Proc. Roy. Soc. Edinburgh 12: 79 (1884) ≡ *Caralluma socotrana* (Balf. f.) N. E. Br., Gard. Chron. ser. 3, 12: 370 (1892) ≡ *Sanguilluma socotrana* (Balf. f.) Plowes, Haseltonia 3: 66 (1995). – Lectotype (designated by Bruce, Hook. Ic. 34: 3372 (1938): Yemen (Socotra), *Balfour* s.n. [K].

= *Caralluma rosengrenii* Vierhapper, Österr. Bot. Ztschr. 1905: 91(1905).

= *Caralluma corrugata* N. E. Br., Kew Bull 1912: 280 (1912).

= *Caralluma rivae* Chiov., Fl. Somala 2: 222 (1929).

Monolluma solenophora (Lavranos) Meve & Liede, ***comb. nov***. Basionym: *Caralluma solenophora* Lavranos, J. S. Afr. Bot. 29: 107 (1963) ≡ *Cylindrilluma solenophora* (Lavranos) Plowes, Haseltonia 3: 63 (1995). – Type: Yemen (S), Audhali Plateau, S Mukeirasn, *Lavranos* 1860 [K, holo; PRE, iso].

This rather poorly known species, although not studied by molecular markers, is placed here with regard to the far reaching stem morphological and distributional similarities with *M. hexagona*.

Species inadequadetely known for affiliation to the genera accepted in this paper

Caralluma aucheriana Decne., in DC., Prodr. 8: 649 (1844) ≡ *Crenulluma aucheriana* (Decne.) Plowes, Haseltonia 3: 66 (1995).

Caralluma dolichocarpa O. Schwartz, Fl. Trop. Arab.: 194 (1939) ≡ *Crenulluma dolichocarpa* (O. Schwartz) Plowes, Haseltonia 3: 67 (1995). – Holotype: Yemen (S), Hadramaut, behind Makalla, Wadi Himern, *Wissmann* 1225 [HBG].

Anomalluma reinstated

Anomalluma Plowes, Cact. Succ. J. (Los Angeles) Cact. Succ. J. (Los Angeles) 65(4): 167 (1993). – Type species: *Angolluma dodsoniana* (Lavranos) Plowes (*Caralluma dodsoniana* Lavranos).

Taxa accepted: 2 species. Distribution: Somalia, Oman, S Yemen.

Anomalluma dodsoniana (Lavranos) Plowes, Cact. Succ. J. (Los Angeles) 65(4): 167 (1993). Basionym: *Caralluma dodsoniana* Lavranos Cact. Succ. J. (Los Angeles) 43(2): 69 (1971) ≡ *Pseudolithos dodsonianus* (Lavranos) Bruyns & Meve, Edinburgh J. Bot. 52: 202 (1995). – Holotype: Somalia, 4 km NNW Erigavo, *Lavranos* 7326 (FT, in alcohol, dried out).

Anomalluma mccoyi (Lavranos & Mies) Meve & Liede, **comb. nov.** Basionym: *Pseudolithos mccoyi* Lavranos & Mies, Asklepios 82: 29 (2001). – Holotype: Oman (Dhofar), near Mirbat, *McCoy* 2305 (MO).

The new genus *Richtersveldia*

The view of Bruyns (1999d) that the bitypic *Notechidnopsis* in the original sense of Lavranos and Bleck (1985) is monophyletic, was not supported by the results of the molecular analysis (Figs. 3–5). Meve and Liede (2001) discussed the possibility of a hybrid origin of the genus, however, with regard to the restricted number of taxa analysed, they refrained from splitting the genus *Notechidnopsis*. We decide here to separate *N. columnaris* from the type of *Notechidnopsis*, *N. tessellata* to create a new monotypic genus, *Richtersveldia*.

Richtersveldia Meve & Liede, **gen. nov**.
– Type species: *Richtersveldia columnaris* (Nel) Meve & Liede (*Trichocaulon columnaris* Nel).
Diagnosis: *A genera* Notechidnopsis *et* Lavrania *caulis 8-angulatis cyaneo-viridis, tuberculum prominentibus cum dentibus acuminatus recurvus vel erectus, bracteae carnosae subulatae differt*.

Stems decumbent to erect, scattered and connected by subterranean stolons (plants rarely clump-forming), branching sparsely, 10–20 cm high, 2.0–2.8 cm wide, bluish green, tessellate by tubercles (podaria) which are joined into 8 angles, tubercles ca. 4 × 8 mm diam., conical, centrally tapering into a tooth (remnant of leaf rudiment), teeth ca. 2 mm long, hard, acuminate, spreading horizontally or being recurved. Inflorescences extra-axilliary, close to stem apex, 1–10(15)-flowered, arising on persistent peduncular patches accompanied by a succulent, subulate-acute, ascending upper bract each, ca. 0.7 mm long. Pedicels short, flowers nectariferous; Corolla rotate, 5–11 mm in diam., upper face densely hairy; corolla tube 4–5 mm in diam., corolla lobes deltate to ovate, 2–3 mm long, 2–2.5 mm wide, spreading. Corona 2-seriate, fused to a flat bowl, 3–4 mm in diam., free parts of interstaminal corona deltate, ca. 1 mm long, 0.7 mm wide at base,

spreading, slightly ascending; lobes of staminal corona linear, ca. 1 mm long, obtuse, sometimes emarginate, decumbent on back of anthers. Pollinaria: pollinium D-shaped, ca. 0.35 mm long, 0.25 mm wide. Fruits ca. 40 × 7 mm, erect to suberect, smooth.
Taxa accepted: 1 species. Distribution: RSA, Northern Cape (Richtersveld, only).

Richtersveldia columnaris (Nel) Meve & Liede, **comb. nov**. Basionym: *Trichocaulon columnare* Nel, Kakteenkunde: 133 (1993) ≡ *Echidnopsis columnaris* (Nel) R. A. Dyer & D. S. Hardy, Cact. Succ. J. (Los Angeles) 40: 207 (1968) ≡ *Notechidnopsis columnaris* (Nel) Lavranos & Bleck, Cact. Succ. J. (Los Angeles) 57: 256 (1985). – Holotype: South Africa (Northern Cape Prov.), Hellskloof, Sept 1929, *Herre* sub SUG 6023 [BOL].

Description as for the genus. Illustrations: Bruyns (1999d).

Ceropegieae Orb., Dict. Univ. Hist. Nat. 3: 339 (1843)
= Stapelieae Decne., in Candolle, Prodr. 8: 606 (1844)
= Ceropegieae Horan., Char. Ess. Fam.: 114 (1847)
Angolluma Munster = ***Orbea*** Haw.
Anisotoma Fenzl, Linnaea 17: 330 (1844). – Type species: *Anisotoma cordifolia* Fenzl, *nom. illeg.* (*Anisotoma mollis* (E. Mey.) Schltr. = *Cynoctonum molle* E. Mey.).
Anisotomaria C. Presl, nom. illeg. = ***Anisotoma*** Fenzl.
Anomalluma Plowes, Cact. Succ. J. (Los Angeles) 65(4): 167 (1993). – Type: *A. dodsoniana* (Lavranos) Plowes (*Caralluma dodsoniana* Plowes)
Apegia Necker = ***Ceropegia*** L.
Apteranthes J. C. Mikan, Nova Acta Acad. Caes. Leop.-Carol. Nat. 17(2): 594. t. 41 (1835). – Type species: *Apteranthes europaea* (Guss.) Plowes (*Stapelia europaea* Guss.)
Aulostephanus Schltr. = ***Brachystelma*** Sims
Australluma Plowes, Haseltonia 3: 54 (1995). – Type species: *Australluma peschii* (Nel) Plowes (*Caralluma peschii* Nel)
Ballyanthus Bruyns = ***Orbea*** Haw.
Barrowia Decne. = ***Orthanthera*** Wight
Baynesia Bruyns, Novon 10: 354 (2000). – Type species: *Baynesia lophophora* Bruyns.
Blepharanthera Schltr. = ***Brachstelma*** Sims
Borealluma Plowes = ***Apteranthes*** J. C. Mikan.
Boucerosia Wight & Arn., in Wight, Contr. Bot. India: 34 (1834). – Type species: *Boucerosia umbellata* (Haw.) Wight & Arn. (*Caralluma umbellata* Haw.)
Brachystelma Sims, Bot. Mag. 49: ad t. 2343 (1822). – Type species: *Brachystelmya tuberosum* (Meerburg) R. Br. ex Sims (*Stapelia tuberosa* Meerb.).
Brachystelmaria Schltr. = ***Brachystelma*** Sims
Caralluma R. Br., Asclepiadeae: 14 (1810). – Type species: *Caralluma adscendens* (Roxb.) Haw. (*Stapelia adscendens* Roxb.)
Caruncularia Haw. = ***Tromotriche*** Haw.
Caudanthera Plowes, Haseltonia 3: 58 (1995). – Type species: *Caudanthera sinaica* (Decne.) Plowes (*Boucerosia sinaica* Decne.)
Ceropegia L., Sp. Pl.: 211 (1753). – Type species: *Ceropegia candelabrum* L.
Cinclia Hoffmanns = ***Ceropegia*** L.
Conomitra Fenzl, in Endlicher & Fenzl, Nov. Stirp. Dec.: 65 (1839). – Type species: *Conomitra linearis* Fenzl.
Craterostemma K. Schum. = ***Brachystelma*** Sims
Crenulluma Plowes = ***Desmidorchis*** Ehrenb.
Cryptolluma Plowes = ***Caudanthera*** Plowes
Cylindriluma Plowes = ***Monolluma*** Plowes
Decabelone Decne. = ***Tavaresia*** Welw.
Decaceras Harv. = ***Brachystelma*** Sims
Decodontia Haw. = ***Huernia*** R. Br.
Desmidorchis Ehrenb., Abh. Königl. Akad. Wiss. Berlin 1829: 31, 39 (1832). – Type species: *Desmidorchis retrospiciens* Ehrenb.
Dichaelia Harv. = ***Brachystelma*** Sims
Diplocyatha N. E. Br. = ***Orbea*** Haw.
Dittoceras Hook. f. = ***Heterostemma*** Wight & Arn.
Drakebrockmannia A. C. White & B. Sloane = ***White-sloanea*** Chiov.
Duvalia Haw., Syn. Pl. Succ.: 44 (1812). – Type species: *Duvalia elegans* (Masson) Haw. (*Stapelia elegans* Haw.)

Duvaliandra M. G. Gilbert, Cact. Succ. J. Gr. Brit. 42: 101 (1980). – Type species: *Duvaliandra dioscoridis* (Lavranos) M. G. Gilbert (*Caralluma dioscoridis* Lavranos)

Echidnopsis Hook. f., Bot. Mag.: ad t. 5930 (1871). – Type species: *Echidnopsis cereiformis* Hook. f.

Edithcolea N. E. Br., Bull. Misc. Inform. 1895: 220 (1895). – Type species: *Edithcolea grandis* N. E. Br.

Emplectanthus N. E. Br., in Th.-Dyer, Fl. Cap. 4(1): 771 (1908). – Type species: *Emplectanthus cordatus* N. E. Br.

Eriopetalum Wight = ***Brachystelma*** Sims

Frerea Dalz. = ***Boucerosia*** Wight & Arn.

Gonostemon Haw. = ***Stapelia*** L.

Heterostemma Wight & Arn. in Wight, Contr. Bot. India: 42 (1834). – Type species: *Heterostemma tanjorense* Wight & Arn.

Hoodia Sweet ex Decne., in DC, Prodr.: 8: 664 (1844). – Type species: *Hoodia gordonii* (Masson) Sweet ex Decne. (*Stapelia gordonii* Masson)

Hoodiopsis C. A. Lückh. = ***Hoodia*** Sweet ex Decne.

Huernia R. Br., Asclepiadeae: 11 (1810). – Lectotype species: *Huernia campanulata* (Masson) Haw. (*Stapelia campanulata* Masson).

Huerniopsis N. E. Br. = ***Piaranthus*** R. Br.

Hutchinia Wight & Arn. = ***Boucerosia*** Wight & Arn.

Kinepetalum Schltr. = ***Brachystelma*** Sims

Larryleachia Plowes, Excelsa 17: 5 (1996). – Type species: *Larryleachia cactiforme* (Hook.) Plowes (*Trichocaulon cactiforme*) Hook.

Lasiostelma Benth. = ***Brachystelma*** Sims

Lavrania Plowes, Cact. Succ. J. (Los Angeles) 58: 122 (1986). – Type species: *Lavrania haagnerae* Plowes

Leptadenia R. Br., Asclepiadeae: 23 (1810). – Type species: not designated

Lithocaulon P. R. O. Bally = ***Pseudolithos*** P. R. O. Bally

Lophostephus Harv., nom. illeg. = ***Anisotoma*** Fenzl.

Macropetalum Burch. ex Decne. = ***Brachystelma*** Sims

Micraster Harv. = ***Brachystelma*** Sims

Microstemma R. Br., nom. rej. vs. *Brachystelma* Sims = ***Brachystelma*** Sims

Monolluma Plowes, Haseltonia 3: 64 (1995). – Type species: *Monolluma quadrangula* (Forssk.) Plowes (*Stapelia quadrangula* Forssk.)

Monothylaceum (G. Don) = ***Hoodia*** Sweet ex Decne.

Neoschumannia Schltr., Bot. Jahrb. Syst. 38: 38 (1905). – Type species: *Neoschumannia kamerunensis* Schltr.

Niota Adans. = ***Ceropegia*** L.

Notechidnopsis Lavranos & Bleck, Cact. Succ. J. (Los Angeles) 57: 255 (1985). – Type species: *Notechidnopsis tessellata* (Pillans) Lavranos & Bleck (*Caralluma tessellata* Pillans).

Obesia Haw. = ***Piaranthus*** R. Br.

Oianthus Benth. = ***Heterostemma*** Wight & Arn.

Ophionella Bruyns, Cact. Succ. J. Gr. Brit. 43: 70 (1981). – Type species: *Ophionella arcuata* (N. E. Br.) Bruyns (*Pectinaria arcuata* N. E. Br.)

Orbea Haw., Syn. Pl. Succ.: 37 (1812). – Lectotype species: *Orbea variegata* (L.) L. C. Leach (*Stapelia variegata* L.)

Orbeanthus L. C. Leach, Excelsa Tax. Ser. 1: 71 (1978). – Type: *Orbeanthus conjunctus* (A. C. White & B. Sloane) L. C. Leach (*Stultitia conjuncta* A. C. White & B. Sloane)

Orbeopsis L. C. Leach = ***Orbea*** Haw.

Orthanthera Wight, Contr. Bot. India: 48 (1834). – Type species: *Orthanthera viminea* Wight.

Pachycymbium L. C. Leach = ***Orbea*** Haw.

Pectinaria Haw., Suppl. Pl. Succ.: 14 (1819), *nom. cons.* (non *Pectinaria* Bernh., Syst. Verz. 1: 113, 221. 1800. [Apiaceae], *nom. rej.*) – Type species: *Pectinaria articulata* (Aiton) Haw. (*Stapelia articulata* Aiton)

Pentasachme Wall. ex Wight, Contr. Bot. India: 60 (1834). – Type species: *Pentasachme caudatum* Wall. ex Wight.

Piaranthus R. Br., Asclepiadeae: 12 (1810). – Lectotype species: *Piaranthus punctatus* (Masson) Schult. (*Stapelia punctata* Masson)

Podanthes Haw. = ***Orbea*** Haw.

Pseudolithos P. R. O. Bally, Candollea 20: 41 (1965). – Type species: *Pseudolithos sphaericus* (P. R. O. Bally) P. R. O. Bally (*Lithocaulon sphaericum* P. R. O. Bally)

Pseudopectinaria Lavranos = ***Echidnopsis*** J. D. Hook.

Quaqua N. E. Br., Gard. Chron., ser. 2. 12: 8 (1879). – Type species: *Quaqua hottentotorum* N. E. Br.

Richtersveldia Meve & Liede, this paper. – Type species: *Richtersveldia columnaris* (Nel) Meve & Liede) (*Trichocaulon columnare* Nel)

Riocreuxia Decne., in DC, Prodr. 8: 640 (1844). – Type species: *Riocreuxia torulosa* (E. Mey.) Decne.

Rhytidocaulon P. R. O. Bally. Candollea 18: 335 (1962). – Type species: *R. subscandens* P. R. O. Bally

Sanguilluma Plowes = ***Monolluma*** Plowes

Sarcocodon N. E. Br. = ***Desmidorchis*** Ehrenb.

Sarcophagophilus Dinter = ***Quaqua*** N. E. Br.

Saurolluma Plowes = ***Caralluma*** R. Br.

Scytanthus Hook. = ***Hoodia*** Sweet ex Decne.

Siphonostelma Schltr. = ***Brachystelma*** Sims

Sisyranthus E. Mey., Comm. Pl. Afr. Austr.: 197 (1838). – Type species: *S. virgatus* E. Mey.

Somalluma Plowes = ***Caralluma*** R. Br.

Spathulopetalum Chiov. = ***Caralluma*** R. Br.

Spiladocorys Ridl. = ***Pentasachme*** Wall. ex Wight

Stapelia L., Sp. Pl.: 217 (1753). – Lectotype species: *Stapelia hirsuta* L.

Stapelianthus Choux ex A. C. White & B. Sloane, Stapelieae: 71 (1933). – Type species: *Stapelianthus madagascariensis* (Choux) Choux ex A. C. White & B. Sloane (*Stapeliopsis madagascariensis* Choux)

Stapeliopsis Phillips *nom. illeg.* = ***Stapelianthus*** Choux

Stapeliopsis Pillans, S. Afr. Gard. 18: 32 (1928). – Type species: *Stapeliopsis neronis* Pillans

Stissera Heist. ex Fabr. *nom. illeg.* = ***Stapelia*** L.

Stultitia Phillips = ***Orbea*** Haw.

Sulcolluma Plowes = ***Monolluma*** Plowes

Swynnertonia S. Moore = ***Neoschumannia*** Schltr.

Symphysocarpus Hassk. = ***Heterostemma*** Wight & Arn.

Systrepha Burch. = ***Ceropegia*** L.

Tapeinostelma Schltr. = ***Brachystelma*** Sims

Tavaresia Welw., Ann. Cons. Ultramarino, ser. 1: 79 (1854). – Type species: *Tavaresia angolensis* Welw.

Tenaris E. Mey. = ***Brachystelma*** Sims

Trichocaulon N. E. Br. = ***Hoodia*** Sweet ex Decne.

Tridentea Haw., Syn. Pl. Succ.: 34 (1812). –Type species: *Tridentea gemmiflora* (Masson) Haw. (*Stapelia gemmiflora* Masson)

Tromotriche Haw., Syn. Pl. Succ.: 36 (1812). – Type species: *Tromotriche revoluta* (Masson) Haw. (*Stapelia revoluta* Masson)

Vietnamia P. T. Li, J. South China Agr. Univ. 15: 72 (1994). – Type species: *Vietnamia inflexa* P. T. Li

Virchowia Vatke ex K. Schum. = ***Echidnopsis*** J. D. Hook.

White-sloanea Chiov., Malpighia 34: 541 (1937). – Type species: *White-sloanea crassa* (N. E. Br.) Chiov. (*Caralluma crassa* N. E. Br.)

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