

Cynanchum (Apocynaceae: Asclepiadoideae): A pantropical Asclepiadoid genus revisited

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Abstract *Cynanchum* constitutes one of the very few Asclepiadoid genera that are distributed both in the Old and the New World. The present study of more than 100 species, based on Bayesian and maximum likelihood analysis of five chloroplast and four nuclear markers, resolves nine clades. No unambiguous morphological characters are associated with any particular clade or a combination of several clades, so that a wide concept of *Cynanchum* seems the most appropriate taxonomic solution for the group. For this reason, several hitherto independent genera, *Glossonema*, *Graphistemma*, *Holostemma*, *Metalepis*, *Metaplexis*, *Odontanthera*, *Pentarrhinum*, *Raphistemma* and *Seshagiria* are included in *Cynanchum*. In addition, *Adelostemma* and *Sichuania* are subsumed under *Cynanchum* for morphological reasons. The necessary new combinations are made, resulting in twelve new species combinations, two new subspecies combinations, and two new names.

Keywords cpDNA; Cynanchinae; fruit morphology; *Mahawoa*; nuclear markers; phylogenetic analysis

Supplementary Material Electronic Supplement (Figs. S1–S4; Tables S1 & S2) and DNA sequence alignment are available in the Supplementary Data section of the online version of this article at <http://ingentaconnect.com/content/iapt/tax>

■ INTRODUCTION

In subfamily Asclepiadoideae of Apocynaceae, genera widespread over both the Old and the New World are scarce, namely, *Cynanchum* L. (Liede & Kunze, 2002), *Marsdenia* R.Br. (Rapini & al., 2003), and *Asclepias* L., depending on the circumscription of the genus (see Goyder & al., 2007 versus Goyder, 2009).

The concept of *Cynanchum* has changed considerably throughout its history. In the Old World, the exclusion of *Vincetoxicum* Wolf, based on morphological and chemical reasons (Liede, 1996a), was supported by molecular studies (Liede-Schumann & al., 2012). Also, *Schizostephanus* Hochst. ex Benth. & Hook.f. (Bruyns & Klak, 2009) and *Calciphila* Liede & Meve (Liede-Schumann & Meve, 2006) could be established as small but independent lineages, with *Schizostephanus* considered a member of the Cynanchinae, and *Calciphila* a member of Asclepiadinae (Endress & al., 2014; Surveswaran & al., 2014). On the other hand, a number of stem-succulent genera, most of them endemic to Madagascar, could be shown to be deeply nested in *Cynanchum* and were therefore included in the genus: *Folotsia* Costantin & Bois, *Karimbolea* Desc., *Platykeleba* N.E.Br., and *Sarcostemma* R.Br. (Liede & Täuber, 2002), adding a total of 22 species and 10 subspecies to *Cynanchum* (Liede & Meve, 2001; Liede-Schumann & Meve, 2005; Goyder, 2008; Meve & Liede-Schumann, 2012).

In the New World, the heterogeneous assemblage subsumed under *Cynanchum* by Woodson (1941) could be shown to constitute several independent genera (Liede-Schumann & al., 2005; Liede-Schumann & Meve, 2013), the circumscription and phylogeny of which is constituting an ongoing subject of study: *Metastelma* R.Br. (Liede & Meve, 2004; Liede-Schumann & al., 2014), *Diplolepis* R.Br. (Hechem & al., 2011), *Jobinia* E.Fourn., *Monsanima* Liede & Meve, *Orthosia* Decne., and *Scyphostelma* Baillon (Liede-Schumann & Meve, 2013). Only the species considered as subg. *Mellichampia* (A.Gray) Woodson by Sundell (1981) are recognized as members of *Cynanchum*. The position of *Metalepis* Griseb. (Morillo, 1997), however, is still unclear.

While Liede & Kunze (2002) retrieved representatives of several other genera (*Glossonema* Decne., *Metalepis*, *Metaplexis* R.Br., *Odontanthera* Wight, *Pentarrhinum* E.Mey.) in *Cynanchum*, they did not consider their evidence sufficient to include those genera in *Cynanchum*.

A recent study, focussing on Indian endemic genera (Surveswaran & al., 2014), also retrieved *Graphistemma* (Champ. ex Benth.) Champ. ex Benth., *Holostemma* R.Br., *Raphistemma* Wall., and *Seshagiria* Ansari & Hemadri inside *Cynanchum*. However, these authors retrieved ambiguous support patterns in the Cynanchinae clade, so that a more detailed analysis is necessary to understand the evolution of the different clades inside *Cynanchum*.

In contrast, *Schizostephanus* Hochst. ex Benth. was always retrieved outside *Cynanchum*, and usually in a sister-group position (e.g., Liede & Täuber, 2002), but unresolved with Cynanchinae and Tylophorinae-Asclepiadinae in Surveswaran & al. (2014).

Morphologically, the circumscription of *Cynanchum* has always been rather vague (e.g., Schumann, 1895; Sundell, 1981; Liede & Kunze, 2002; Liede & Täuber, 2002); the most important morphological characters of all Cynanchinae genera are summarized in Table 1. Typical *Cynanchum* species are twiners with basally cordate leaves and prophylls (a pair of smaller and sometimes differently shaped leaves on extremely reduced short shoots; Liede-Schumann & Meve, 2013). Latex is white, cream or yellow, but never transparent. Inflorescences are bostrychoid or sciadioidal, but not branched, bearing flowers

of 5–10 mm diameter. The corolla lobes are nearly free, and are smooth or papillose adaxially; the gynostegial corona is extremely variable and complex, usually with a basal ring-shaped portion of fused staminal and interstaminal parts (C(is) sensu Liede & Kunze, 1993), often with long appendages and inner ligules. Shape of pollinaria and style-head is variable (see, e.g., illustrations in Liede, 1996b). Fruits are usually solitary, slenderly fusiform, containing numerous ovate seeds which are ornamented with papillae or trichomes, winged and have a micropylar coma. However, few of these character states are either unique to *Cynanchum*, or present in all species. For instance, prophylls are unique to *Cynanchum*—but not present in all species, and are always absent in the succulent and geophytic ones. Opaque latex is present in all species for which this character is known, but this is the common condition in

Table 1. Summary of morphological characters in Cynanchinae.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
<i>Schizostephanus</i> (Hochst) ex Benth & Hook.f.) (2)	1	0	1	0	0–1 (rar. basally)	0	1	1	1	0	0	0	1	1	1
<i>Cynanchum</i> L. (ca. 150)	0	0 rar. 1	1 rar. 0	1/0	0	0 rar. 1	0 rar. 1	1 rar. 0	0 rar. 1	0/1	0 rar. 1	0 rar. 1	0/1	1/2	1
<i>Adelostemma</i> Hook.f. (1)	?	0	1	1	0	1	0	0	0	1	1	1	0	?	?
<i>Glossonema</i> Decne. (5)	0	1	0	0	0	0	0	0	0	0	1	2	0	2	1
<i>Graphistemma</i> (Champ. ex Benth.) Champ. ex Benth. (1)	0	0	0	1	0	0	0	1	0	0	1	0	0	2	1
<i>Holostemma</i> R.Br. (2)	0	0	1	0	0	0	0	1	0	0	1	0	0	2	0
<i>Mahawoa</i> Schltr. (1)	?	0	0	?	1	0	0	1	0	0	?	?	?	?	?
<i>Metalepis</i> Griseb. (7)	0	0	1	0	1	0 rar. 1	1	1	1	0	1	0	0	1/2 (apic.)	1
<i>Metaplexis</i> R.Br. (2)	0	0	1	0	0	0	1	1	1	0	1	1	0	2	1
<i>Odontanthera</i> Wight (1)	0	1	1 (vag.)	0	0	1	0	0	0	1	1	1	0	1	1
<i>Pentarrhinum</i> E.Mey. (6)	0	0	1	1	0	0	0	0/1 occ. ciliate	0	0	1	0/1/2	0	1	1
<i>Raphistemma</i> Wall. (2)	0	0	1	0	0	1	0	0	0	0	1	0	0	1	0
<i>Seshagiria</i> Ansari & Hemadri (1)	0	0	1	0	0	0	0	1	0	0	1	1	0	1	?
<i>Sichuania</i> M.G.Gilbert & P.T.Li (1)	?	0	1	0	0	0	0	0	0	0	?	?	?	?	?

Genera according to Endress & al. (2014). Genera in bold are recognized in the present paper. Numbers in brackets indicate numbers of currently recognized species.

Characters and coding are as follows: **1 – Latex:** 0 opaque (white, cream, or yellow), 1 clear; **2 – Habit:** 0 twining, 1 non-twining; **3 – Leaf bases:** 0 not cordate, 1 cordate; **4 – Prophylls:** 0 absent, 1 present; **5 – Inflorescences:** 0 sciadioidal or bostrychoid, but not branched, 1 branched; **6 – Corolla lobes:** 0 basally free to fused for less than ¼ of length, 1 fused for more than ¼ of length; **7 – Corolla lobes, adaxial surface:** 0 without trichomes, 1 with trichomes; **8 – Ring-shaped part of corona:** 0 absent, 1 present; **9 – Gynostegium:** 0 (sub-)sessile, 1 stipitate; **10 – Style-head:** 0 short, rounded or conical, 1 elongated-conical or beaked; **11 – Follicle shape:** 0 slender (more than 5× as long as broad), thin-walled, 1 thick, thick-walled; **12 – Follicle emergences:** 0 absent, 1 present, tubercles, 2 present, soft spines; **13 – Follicle wings:** 0 absent, 1 present; **14 – Seed wings:** 0 absent, 1 present, entire, 2 present, denticulate or lacerate; **15 – Seed ornamentation:** 0 absent, 1 present. — apic., apically; occ., occasionally; rar., rarely; vag., vaguely.

Asclepiadoideae. A gynostegial corona is present in most Asclepiadeae, and a basal, ring-shaped part is known from other Asclepiadeae genera as well (e.g., *Calciphila*, *Orthosia*, *Schizostephanus*), whereas it can be reduced or missing in *Cynanchum* (e.g., *C. laeve* (Michx.) Pers.). Thus, even in the classical circumscription, a unique morphological synapomorphy for *Cynanchum* cannot be given at present.

Glossonema and *Odontanthera* were placed in a separate subtribe, Glossonematinae, by Schumann (1895), because of their seemingly corolline corona. However, the seemingly corolline corona is now considered to be the result of a secondary shift of the originally gynostegial corona (Liede & al., 2002). Mabberley (1980a, b) considered *Glossonema* to be a synonym of *Odontanthera*, and published the necessary new combinations. However, Field (1982) cited the tubular corolla and the long anther appendages of *Odontanthera radians* (Forssk.) Field as main characters to distinguish it from the remaining *Glossonema* species. Following this concept, *Odontanthera* is monophyletic and distinct from *Glossonema*. For *Glossonema*, the treatment by Bullock (1955), who recognized four species, is largely followed here, except that *Glossonema macrosepalum* Chiov., which Bullock (1955) listed as a doubtful species, has been transferred to the synonymy of *G. revoilii* Franch. by Goyder (2006a). *Glossonema pichi-sermollianum* Raimondo & Fici, described in 1993, exhibits a combination of characters that makes it likely that it indeed constitutes a good species. With its sessile leaves it is clearly not a synonym of *G. boveanum* Decne., as The Plant List (2015) suggests. The only other species with sessile leaves is *G. thruppii* Oliv., from which it seems distinct by its small size, its linear, falcate leaves, and the absence of long, soft spine-like processes on the fruit. One name, *G. lineare* (Fenzl) Decne., is a synonym of *Conomitra linearis* Fenzl (Ceropegieae; Field, 1982), but was erroneously placed in *Odontanthera* by Mabberley (1980a, b).

Thick follicles with protuberances (Fig. 1, 8-1) and slipper-shaped corona lobes were listed by Liede & Nicholas (1992) as possible synapomorphies for *Pentarrhinum*. Later, Liede (1997b) transferred three species from *Cynanchum* to *Pentarrhinum*, after morphological analysis had shown that thick fruits were a better indicator of relationship than the degree of fusion of the corona. These results were corroborated by Liede & al. (2002), in which the first molecular analysis including *Glossonema*, *Odontanthera* and *Pentarrhinum*, which was based on the *trnT-trnF* region, confirmed their close relationship. Later, also based on molecular analysis, *Cynanchum ledermannii* Schltr. was transferred to *Pentarrhinum* (Goyder & Liede-Schumann, 2008), even though its fruits are still unknown. Altogether in *Pentarrhinum* ten specific names have been published, one of which includes several subspecific entities. In recent years, several amendments to the genus have been made (Liede & Nicholas, 1992; Goyder, 2000; Goyder & Liede-Schumann, 2008), so that it presently contains six species. *Pentarrhinum fasciculatum* K.Schum. represents a synonym of *Pentatropis nivalis* (J.F.Gmel.) D.V.Field & J.R.I.Wood (Liede & Nicholas, 1992) and *P. iringense* Markgr. constitutes the basionym of *Tylophora iringensis* (Markgr.) Goyder (Goyder, 2006b). Of two species, *P. coriaceum* Schltr. and *P. tylophoroides* K.Schum.,

the type specimens (*Gerrard & McKen s.n.* and *Burchell s.n.*, respectively) are lost. *Pentarrhinum coriaceum* is possibly synonymous to *Tylophora anomala* N.E.Br. (Meve, 1999; but see Goyder's 2012 note in *Flora of tropical East Africa*). The epithet “tylophoroides” and the description of its inflorescences as paniculate (Schumann, 1895: 244) make it likely that the species should also be transferred to *Tylophora*.

The close relationship between *Graphistemma* and *Holostemma* is illustrated by the fact that the only species of *Graphistemma* was originally described in *Holostemma*, from which it was later removed due to its unique corona structure. Three rather thick-fruited East Asian *Cynanchum* species (*C. muricatum* Boerl., *C. ovalifolium* Wight, *C. tuberculatum* Boerl.) were originally described in *Holostemma* as well (Blume, 1826), and Hemsley (1889) attributed *Metaplexis hemsleyana* Oliv. to the genus. In *Flora of China* (Li & al., 1995), *Graphistemma*, *Holostemma* and *Raphistemma* are distinguished from *Cynanchum* mainly by the larger size of their flowers, which measure at least 2 cm in diameter. The unusual campanulate flowers, which are among the largest in Old World Asclepiadeae (3–4 cm diam. and a tube of up to 1.8 cm length; Li & al., 1995), together with a simple, basally unfused corona of staminal parts have made a placement of the two *Raphistemma* species in Asclepiadeae difficult and only the molecular analysis by Surveswaran & al. (2014) could confirm the earlier assumption (Endress & al., 2007, 2014) that it is a member of Cynanchinae. Whereas *Graphistemma* is monospecific, *Holostemma* comprises 14 names but only 2 accepted species. *Raphistemma* comprises 4 names and 2 accepted species. *Raphistemma ciliatum* Hook.f. is a synonym of *Pergularia daemia* (Forssk.) Chiov. (Goyder, 2006c). A detailed account of *Holostemma* and *Raphistemma* can be found in Surveswaran & al. (2014).

The problem of an unusual combination of characters also pertains to *Seshagiria* (Endress & al., 2007), an Indian endemic described as recently as in the seventies of the last century (Ansari & Hemadri, 1971). Its strongly twisted corolla is a feature occasionally associated with *Vincetoxicum* s.l., while its corona of a short outer ring and inner globular staminal parts is vaguely reminiscent of the *Sarcostemma* group of *Cynanchum* s.l. The ovate-lanceolate thick-walled follicles with warty protuberances are reminiscent of *Pergularia* L.

Adelostemma Hook.f. and *Sichuania* M.G.Gilbert & P.T.Li, two Chinese genera, were attributed to Cynanchinae in recent works (Endress & al., 2007, 2014). *Adelostemma* was first described based with a single Himalayan species, *A. gracillimum* (Wall. ex Wight) Hook.f., which was transferred from *Cynanchum* because it lacks a corona (Hooker, 1883). Later, two more species (*A. mairei* Hand.-Mazz., *A. microcentrum* Tsiang) were added, but both have since been synonymized with species of *Biondia* Schltr. (Tylophorinae) in *Flora of China* (Li & al., 1995). *Sichuania* was described by Gilbert & al. (1995) from a specimen originally identified as *Holostemma*, because of its unfused, scale-like corona lobes in interstaminal position.

Metaplexis, also from Asia, is easily recognized by its long, often twisted style-head appendage and long trichomes on the adaxial side of the corolla. It possesses thick-walled,

tuberculate follicles (Fig. 1, 7-1). Of the ten names published, *Metaplexis cavalieriei* H.Lév. is the basionym of *Marsdenia cavalieriei* (H.Lév.) Hand.-Mazz. ex Woodson (Marsdenieae); *M. fimbriata* (Kunth) Spreng. is a synonym of *Matelea fimbriata* (Kunth) Dugand (Gonolobinae) and *M. mucronata* Spreng. is a synonym of *Cynanchum meyeri* (Decne.) Schltr. (fide Liede, 1993: 519). The remaining names are synonyms of the two accepted species, *M. japonica* (Thunb.) Makino and *M. hemsleyana* (Li & al., 1995; Stevens, 2000).

Metalepis, a group of seven species widespread in tropical America (Morillo, 1997), is morphologically distinctive with thyrsoidal, branched and often many-flowered inflorescences, large, thick-walled fruits (to 30 cm long and 6 cm broad), and gynostegium construction with seemingly transversal anther dehiscence reminiscent of Gonolobinae. Based mainly on the gonoloboid-like anther dehiscence, the group has been shuttled between Cynanchinae (Sundell, 1981; Liede & Täuber, 2002) and Gonolobinae (Morillo, 1997; Fontella Pereira & Britto de Goes, 2009) several times. The genus was included in *Cynanchum* by Liede (1997a). Molecular analysis has confirmed this position, even though the type, *M. cubensis* Griseb., could not be sequenced because only very old material was available and the plant was not found again in Cuba despite intense search by the last two coauthors of the present paper. Therefore, a small risk remains that the affinity of the genus lies with Gonolobinae rather than with *Cynanchum*, as suggested again recently by Fontella Pereira & al. (2014). However, the first species of *Metalepis* available for molecular analysis (*M. albiflorum*) was deeply nested in *Cynanchum* (Liede & Kunze, 2002), and the pollinarium morphology of *M. cubensis* corresponds to the other species of the group with pollinia pendent on long, rather straight caudicles. Fontella Pereira & Britto de Goes (2009) even interpret *M. albiflorum* as conspecific with *M. cubensis*, a view not followed here.

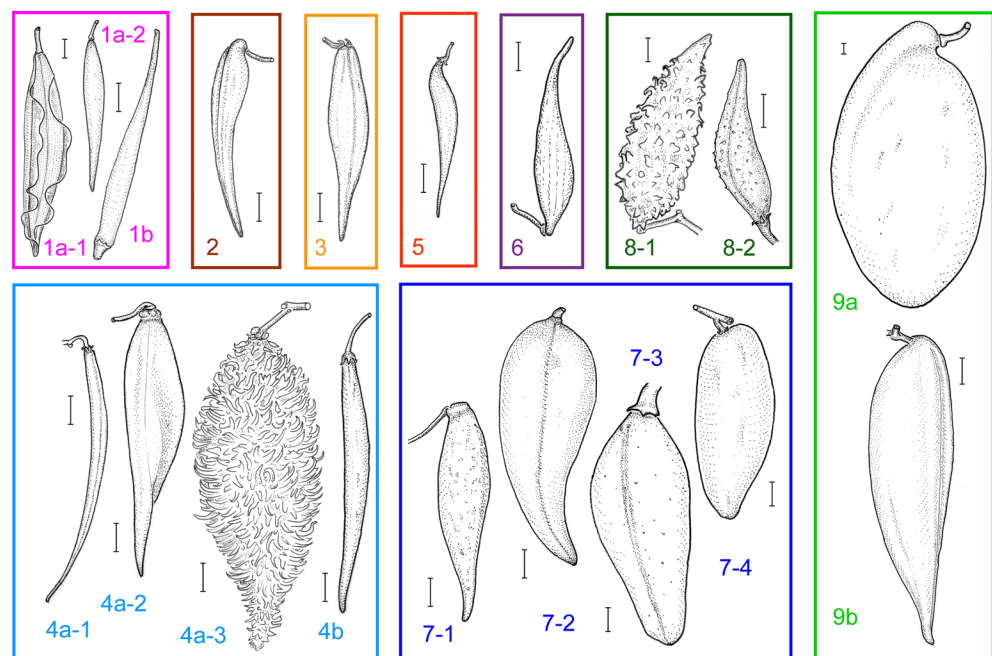
The present molecular study includes all genera of Cynanchinae, except for *Adelostemma* and *Sichuania*, for which no sequenceable material could be obtained, and the obscure *Mahawoa* Schltr. from Sulawesi, the holotype of which was destroyed in B and for which to date no other material or illustration has been found. The present study is designed to clarify the relationships between traditional *Cynanchum* species and the satellite genera included in Cynanchinae. The results of the molecular phylogeny are interpreted in the light of morphological characters commonly used to delimit genera in Asclepiadoideae.

■ MATERIALS AND METHODS

Taxonomic methods. — The assessment of character states of *Cynanchum* and its segregate genera is based on work conducted during the last 18 years at the University of Bayreuth and accessible via http://www.bio.uni-bayreuth.de/planta2/research/databases/delta_as/index.htm. The circumscription of the segregate genera was either adapted from published literature, if available (*Glossonema*: Bullock, 1955; *Holostemma*: Surveswaran & al., 2014; *Metalepis*: Morillo, 1997; *Odontanthera*: Field, 1982; *Pentarrhinum*: Liede & Nicholas, 1992; Liede, 1997b; Goyder & Liede-Schumann, 2008; *Raphistemma*: Surveswaran & al., 2014), or researched here (*Adelostemma*, *Metaplexis*), under consideration of Wu & al. (1995) findings.

Taxon sampling. — The present dataset represents the most comprehensive sampling of Cynanchinae available, including 112 samples of *Cynanchum*, covering 102 species (one with four subspecies) of the ca. 150 species over the whole range of the genus. In addition, six samples representing the six species of *Pentarrhinum* (*P. balense* (Liede) Liede) was

Fig. 1. Fruit types representative for clades 1–9 of *Cynanchum* (see Fig. 2). Clade **1a-1**, *C. danguyanum*; **1a-2**, *C. lineare*; **1b**, *C. marnieranum*; Clade **2**, *C. ellipticum*; Clade **3**, *C. praecox*; Clade **4a-1**, *C. acutum*; **4a-2**, *C. callialatum*; **4a-3**, *C. corymbosum*; **4b**, *C. auriculatum*; Clade **5**, *C. falcatum*; Clade **6**, *C. adalinae*; Clade **7-1**, *Metaplexis japonica*; **7-2**, *C. formosanum*; **7-3**, *Graiphistemma pictum*; **7-4**, *C. physocarpum*; Clade **8-1**, *Pentarrhinum insipidum*; **8-2**, *Odontanthera radians*; Clade **9a**, *Metalepis albiflora*; **9b**, *C. laeve*. — Scale bars = 1 cm. Drawn by U. Meve.



not available), two species each of *Glossonema* and *Metalepis*, two samples representing one species of *Metaplexis*, one species each of *Holostemma*, *Raphistemma*, and *Schizostephanus*, as well as the monospecific *Graphistemma*, *Odontanthera*, and *Seshagiria* cover the whole range of morphological variation in the subtribe (Appendix 1; see there for authors of species and voucher information). There was no sequenceable material available for the monospecific *Cynanchinae* genera *Adelostemma*, *Mahawoa* Schltr., and *Sichuania*.

In most cases, all partial sequences for a species were derived from the same sample; exceptions are *C. crassiantherae* Liede, *C. foetidum* Kunth, *C. praecox* Schltr. ex S.Moore, *C. rubricoroneae* Liede, and *C. rungweense* Bullock (Appendix 1), for which the original material had become unusable. In these cases, species identity was first ascertained morphologically and then additionally checked by comparison of one partial sequence between both samples (ITS for *C. foetidum*, *trnL-trnF* region for the other species). No differences were found in any of these cases, so that, on the taxonomic level studied here, the specific coherence of the two samples was assumed. As outgroups, samples from the sister subtribes Tylophorinae (*Pentatropis nivalis*, *P. madagascariensis*, Decne. and *P. sp.* from Ethiopia) and Asclepiadinae (*Calotropis procera* (Aiton) W.T.Aiton, *Calciphila galgalensis* Liede & Meve, *C. gillettii* Liede & Meve) were used.

DNA extraction, amplification and sequencing. — DNA was extracted from silica-dried leaves (vouchers held at UBT) or from leaf fragments taken from herbarium specimens held at B, CGMS, E, EA, FR, HEID, IBSC, IRAN, L, M, MO, MSUN, NH, OKLA, P, PNMH, PRE, RAW, SUK, ULM, UPS. For *Cynanchum falcatum* Hutchinson & E.A.Bruce (*Friis 3169*), *C. polyanthum* K.Schum., parts of *C. rubricoroneae* and *C. rungweense*, as well as *Pentarrhinum abyssinicum* Decne., extracted DNA from the Kew DNA bank was obtained. For *Cynanchum boudieri* H.Lév. & Vaniot, *C. maximoviczii* Pobed., and *C. wilfordii* Maxim., sequences published in Yamashiro & al. (2004) were used (Appendix 1). A total of 615 partial sequences were obtained newly for this study.

Total DNA was extracted using the DNeasy Plant Mini Kit (Qiagen, Hilden, Germany) following the manufacturer's instructions. PCR primers and protocols for the plastid *trnT-trnL* and *trnL-trnF* spacers and the *trnL* intron correspond to Taberlet & al. (1991). The *trnL* intron and *trnL-trnF* intergenic spacer were amplified either as one fragment using primers c and f or as two separate fragments using primers c and d, and e and f, respectively. For aligning, the two segments were kept separate because most of the older samples used had been amplified separately. The *trnH-psbA* intergenic spacer was amplified with the primers designed by Sang & al. (1997). For several samples, the *rps16* intron was amplified as in Liede-Schumann & al. (2005), using the primer pair *rps16-1F* and *rps16-2R*. The entire internal transcribed spacer region (ITS) of the nuclear-encoded 35S rDNA cistron including 5.8S of ribosomal DNA (rDNA) was amplified using the flanking primers ITS4 and ITS5 following a modified protocol based on Baldwin (1992) described in Meve & Liede (2001). The 5' external transcribed spacer (5'-ETS) of the 35S rDNA was amplified following the

protocol of Yamashiro & al. (2004). Two additional nuclear markers, *At2g06530a* and *At2g34620b* (addressed as NUC1 and NUC2 in the following), were sequenced using the primers and protocol given by Straub & al. (2011). Table S1 in the Electr. Suppl. tabulates the individual data coverage for all accessions (sampled specimens) used in this study.

Phylogenetic analyses. — Sequence data of individual gene regions were aligned with OPAL (Wheeler & Kececioglu, 2007) and checked visually using Mesquite v.3.03 (Maddison & Maddison, 2015).

Single-region (including up to three partitions) ML analyses were used to check for incongruent signals in the underlying data. Maximum likelihood (ML) and Bayesian inference (BI) analyses were performed individually for 5'-ETS and ITS regions (essentially invariable 5.8S rDNA not included) of the nuclear encoded 35S rDNA cistron, the NUC1 (*At2g06530a*) and NUC2 (*At2g34620b*) gene regions, the plastid *trnH-psbA* intergenic spacer, the entire plastid *trnT-trnL-trnF* region (*trnTLF* region), and the plastid *rps16* intron.

The alignments were subjected to tree inference and branch support analyses using RAxML v.8.1.17 (Stamatakis, 2014) for ML and MrBayes v.3.2 (Ronquist & al., 2012) for BI. All RAxML analyses were performed on the LRZ Linux Cluster of the University of Bayreuth using the implemented GTR+ Γ model and fast bootstrapping (-m GTRCAT, invoking the per-site-rate approximation of the Gamma distribution (Stamatakis 2006), number of necessary bootstrap replicates determined by the extended majority-rule criterion (Pattengale & al., 2009; -x autoMRE). MrBayes was run in its stand-alone implementation using two parallel runs for 10 million generations, each using one cold and three heated MCMC chains; every 10,000th topology sampled. Posterior probabilities (PP) were calculated using the sampled topologies of the last 5 million generations of both runs. Following the recommendation by Huelsenbeck & Rannala (2004) the most complex model GTR+ Γ +I was implemented for each partition. ML bootstrap support (BS) and PP (combined and separated analyses) for competing topological alternatives were visualized with SplitsTree v.4.13 (Huson & Bryant, 2006) using “bipartition networks” (Grimm & al., 2006), a special form of consensus networks (Holland & Moulton, 2003) in which the edge lengths are proportional to the frequency of a given bipartition in the bootstrap replicates or BI sampled topologies.

The aligned sequence regions were then concatenated and the concatenated alignment subjected to the partitioned and unpartitioned analyses using the same procedures as for the single datasets. Convergence values of the BI analysis reached stationarity after 4.347 million generations; posterior probabilities (PP) were calculated using the sampled topologies of the last 5 million generations of both runs.

Documentation. — All matrix files used for analysis and result files generated by RAxML and MrBayes as well as used SplitsTree NEXUS files are available as supplementary data (see online version of this article, “Analysis files”). The basic matrix file and preferred ML and BI trees can also be accessed via TreeBase, study number S18621 (<http://purl.org/phylo/treebase/phylo/phylo/study/TB2:S18621>).

■ RESULTS

Phylogenetic signals from individual regions. — Independent of the overall divergence observed in individual gene partitions, all single-region ML and BI analyses (5'-ETS, ITS, NUC1, NUC2, *trnH-psbA*, *trnTLF* region, *rps16* intron) failed to produce a fully resolved, highly supported topology. Nevertheless, a number of corresponding clades received consistently low (BS_{ML} 20 to <60, $PP < 0.6$) to high ($BS_{ML} > 90$, $PP > 0.9$) support from nuclear and plastid regions (Electr. Suppl.: Table S2). The same clades can also be found in the ML- and BI-preferred topologies based on the concatenated data (see below). In addition, we found no moderately (BS_{ML} 60–90, PP 0.6–0.9) to highly supported conflict between nuclear- (5'-ETS, ITS, NUC1, NUC2) or plastid-based (*trnH-psbA*, *trnTLF* region, *rps16* intron) topological alternatives, nor between low- (NUC1, NUC2, *trnTLF* region), medium (5'-ETS, *rps16* intron) and high-divergent partitions (ITS, *trnH-psbA*) (Electr. Suppl.: Table S2). This indicates that even though phylogenetic resolution is limited to certain aspects of Cynanchinae evolution in each individual gene region, the overall signal in nuclear and plastid regions is generally congruent and additive. The partition with the lowest overall support and resolution capacity is the *trnH-psbA* spacer, whereas *trnTLF*, 5'-ETS and ITS provide the strongest, least ambiguous signals.

The highest resolution regarding the most proximal (basal) parts of the Cynanchinae subtree is found in the signal of the *rps16* intron. Resolution towards the tips is limited, which may partly be due to the fact that many accessions are missing to date (Electr. Suppl.: Table S1; Appendix 1).

Phylogeny of Cynanchinae based on the combined data.

— Because supported conflict does not occur in our gene trees, our dataset fulfills the most important predisposition for concatenation (Pirie, 2015). The final, concatenated nuclear and plastid matrix has 6189 characters (nucleotide sites) for 137 terminals (accessions) and allowed inferring an ML topology, where a substantial number of branches received moderate to unambiguous support. We recognize nine major, consistently reconstructed ingroup clades with moderate to high support (Fig. 2; Table 2): Clade 1 comprises all Madagascan species of *Cynanchum* (non-succulent and succulent) and all succulent species from the remainder of the Palaeotropics, with most of the non-succulent Madagascan species (except *C. analamazotrense* Choux, *C. pachycladon* Choux, and *C. chouxii* Liede & Meve) and all succulent species (Madagascan and other) forming two distinct subclades with moderate and high support. Clade 2 comprises five species from southern and two from eastern Africa, while in Clade 3 four northeastern African species are united with the widespread *C. praecox* and the South African *C. orangeanum* (Schltr.) N.E.Br. Clade 4, which falls into two subclades, includes 17 *Cynanchum* species from across Eurasia to Australasia. The first subclade (4a) includes the only western Eurasian species, *C. acutum* L., the type of the genus, and its sister species *C. chinense* R.Br., the Australian *C. floribundum* R.Br. and several species whose distribution includes the Indian subcontinent or is restricted to it. The other subclade (4b) is restricted to Chinese and Japanese species except for

the *C. petrense* Hemsl. & Lace from Pakistan. Clades 5 and 6 accommodate each two (genetically) isolated eastern (Clade 5: *C. falcatum*, *C. schistoglossum* Schltr.) and western African (Clade 6: *C. adalinae* (K.Schum.) K.Schum., *C. longipes* N.E.Br.) *Cynanchum* species. Clade 7 combines five East Asian *Cynanchum* species and five Asian genera: *Graphistemma*, *Holostemma*, *Metaplexis*, *Raphistemma*, *Seshagiria*. Clade 8 groups all *Pentarrhinum* species (essentially eastern Africa) covered in this study with two *Glossonema* species (from North East Africa and Arabia) and *Odontanthera radians* (Forssk.) D.V.Field (also distributed in North East Africa and Arabia). Clade 9 comprises the New World Cynanchinae included in this study: eight *Cynanchum* species from North, Central and South America and two Latin American species of *Metalepis*. Interclade relationships are not unambiguously supported (Fig. 2; Electr. Suppl.: Fig. S2), partly due to several rogue and understudied taxa (missing data, particular *rps16* intron data, see above). The outgroup-inferred Cynanchinae root is placed between *Schizostephanus* and *Cynanchum* s.l.; within *Cynanchum*, Clade 1 is resolved as sister to the remainder, but without support (Fig. 2; Electr. Suppl.: Fig. S2). Ambiguity regarding the phylogenetic affinities of Clades 1 and 2 (box-like central part of graph in Electr. Suppl.: Figs. S2–S4) results mainly from one underrepresented species: *C. chouxii* (no 5'-ETS, ITS, NUC1 and *rps16* intron data). The subtree comprising Clades 3 to 9 is moderately supported (Fig. 2) and the deep relationships within this subtree are fairly resolved despite overall moderate support. Alternatives to most branches seen in the ML tree (Fig. 2) receive no notable support (Electr. Suppl.: Figs. S2–S4). The major sources of ambiguity within this subtree are *C. abyssinicum* Decne. and the two species of Clade 6 (*C. falcatum*, *C. schistoglossum*) which act as rogue taxa inflicting somewhat conflicting signals (expressed both in BS support and PP; Table 3).

■ DISCUSSION

Our results question the current generic delimitation in Cynanchinae, while providing a first robust phylogenetic framework for this group. Although *Glossonema*, *Metalepis* and *Pentarrhinum* form well-supported clades, they are all deeply nested in *Cynanchum*, as are the monospecific genera *Graphistemma*, *Odontanthera* and *Seshagiria*. Although only one of the two accepted species were available for *Holostemma*, *Metaplexis*, and *Raphistemma*, these were also deeply nested in *Cynanchum*. This observation holds, independent of whether the ML/concatenated data (Fig. 2) or BI/*rps16* preferred (Tables 2, 3; Electr. Suppl.: Fig. S2) outgroup-inferred Cynanchinae root is considered.

However, our phylogeny does not suggest a simple solution for the classification of Cynanchinae. With the exception of *Schizostephanus*, which has been retrieved as sister to the remainder of the genera here as in most molecular analyses (e.g., Liede & Kunze, 2002; Bruyns & Klak, 2009), and *Calciphila*, whose position in the Asclepiadinae is confirmed (Fig. 2), all small genera are deeply nested in *Cynanchum*. A separation

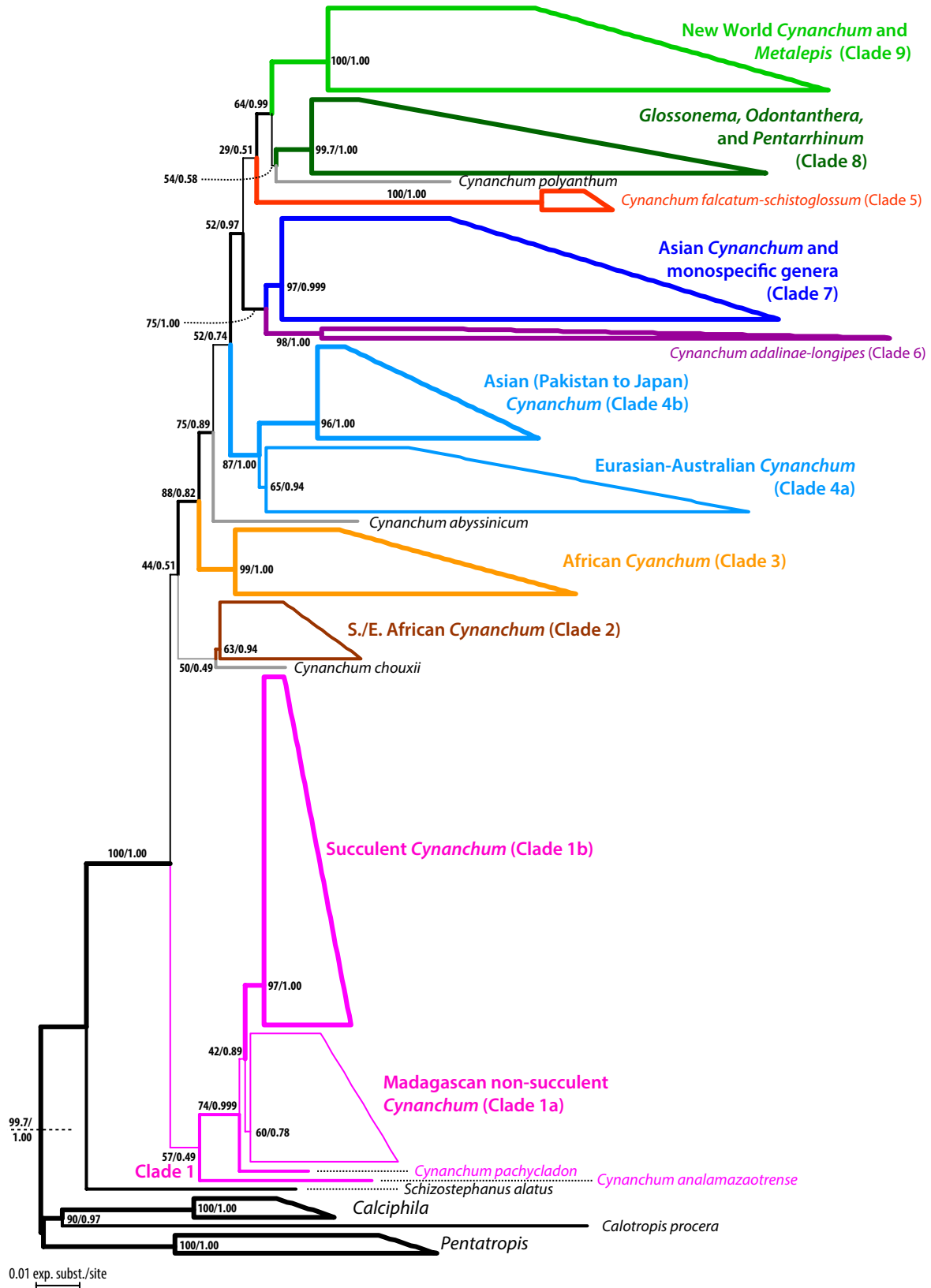


Fig. 2. Maximum likelihood (ML) tree for the Cynanchinae, outgroup-rooted. Major clades are proportionally collapsed to trapezia: horizontal margins of trapezia refer to minimum and maximum root-tip distances, vertical extension of trapezia to number of tips (accessions included in clade). Numbers at branches indicate support as estimated from non-parametric bootstrapping under ML and Bayesian-inferred (BI) posterior probabilities; see Electr. Suppl.: Fig. S1 for a comprehensive tree.

of the Madagascar clade (including all succulent *Cynanchum*, from Madagascar or not) may be tempting in light of the molecular differentiation patterns, but the two new genera would be almost as morphologically heterogeneous as a broad *Cynanchum*, including all genera except for *Schizostephanus* and *Calciphila*, would be. Furthermore, both groups include species showing the most typical morphological character of *Cynanchum*, the stipule-like short shoots at the vegetative nodes (e.g., Liede, 1996b: fig. 14/1, p. 308). While this structure is absent from many species, especially those with linear or strongly reduced leaves, it has never been recorded from any

other genus of Asclepiadoideae. Thus, a generic split separating the Madagascar-succulent lineage would not lead to a better generic concept in Cynanchinae.

Of the characters used for classification in Asclepiadoideae, floral characters have been shown to be highly unreliable (e.g., *Diplolepis*: Hechem & al., 2011; *Philibertia* Kunth: Goyder, 2004; *Hoya* R.Br.: Wanntorp & Forster, 2007). *Cynanchum* is among the groups with the most variable corona composition in the subfamily and considerable variability in the shape of the style-head, while pollinia structure is comparatively uniform. The majority of species possess highly fused coronas,

Table 2. Non-parametric bootstrap support under maximum likelihood from individual partitions for major clades inferred based on the concatenated data, and putative inter-clade relationships including alternatives (ALT) supported by $BS_{ML} > 50$ in at least one of the single- and two-partition analyses (see supplementary “Analysis files” for additional alternative split patterns and posterior probabilities).

	Regions ^a							
	All	<i>trnH-psbA</i>	<i>trnTLF</i>	<i>rps16</i>	5'ETS	ITS	NUC1	NUC2
Number of accessions	137	127	137	92	106	134	104	96
Number of necessary bootstrap replicates ^b	350	450	350	500	650	350	750	950
Phylogenetic split								
Outgroup ingroup (Cynanchinae)	99.7	<20	91	55	N/A	58	<20	<20
ALT: <i>C. falcatum</i> (Clade 5)+ <i>Pentatropis</i>	<1	<20	<10	<15	<20	<20	<20	54
<i>Cynanchum</i> s.l. clade	100	<20	99	22	83	20	80	<20
ALT: <i>Schizostephanus</i> +part of <i>Cynanchum</i>	<20	<20	<20	79	<20	<20	<20	<20
Clade 1 sister to remainder of <i>Cynanchum</i>	44	<20	<20	<15	<20	<20	<20	<20
ALT: <i>C. hastifolium</i> (Clade 3) groups with outgroup	0	<20	<20	88	<20	<20	<20	<20
Clade 1	57	29	31	66	48	93	<20	29
Clade 2	63	<20	55	<20	40	23	<20	<20
Clades 3–9	88	<20	<20	25	<20	<20	<20	<20
Clade 3	99	63	88	<15	88	<20	73	27
Clades 4–9	75	<20	<20	54	<20	<20	<20	<20
Clade 4	87	<20	<20	<20	<20	<20	<20	42
Clades 5–9	52	<20	<20	<20	<20	<20	<20	<20
Clades 5+8+9	29	<20	<20	<20	<20	<20	31	<20
ALT: Clades 6–9	42	<20	<20	<20	<20	<20	<20	<20
Clade 5	100	100	100	100	100	100	– ^c	– ^c
Clades 6+7	75	<20	<20	<20	70	<20	<20	<20
Clades 8+9	64	<20	<20	<20	53	45	58	<20
ALT: Clades 6+9	21	<20	54	<20	<20	<20	<20	<20
Clade 6	98	22	58	<20	– ^c	<20	42	<20
Clade 7	97	<20	65	<20	22	<20	50	<20
Clade 8	99.7	<20	99	<20	78	40	<20	40
Clade 9	100	<20	100	42	74	<20	69	55

Bipartitions represented in the optimised maximum likelihood tree highlighted by grey shading.

^a Including one to three plastid [cp] or nuclear [nc] partitions per gene region: [cp] *trnH-psbA* = *trnH-psbA* spacer; *trnTLF* = *trnTLF* region incl. *trnT-trnL* spacer, *trnL* intron, and *trnL-trnF* spacer (invariable *trnL* exon parts excluded); *rps16* = *rps16* intron; [nc] ETS = 5' external transcribed spacer of the 35S rDNA cistron; ITS = internal transcribed spacers 1 and 2 of the ITS region of the 35S rDNA (nearly invariable 5.8S rDNA excluded); NUC1 = *At2g06530a* gene; NUC2 = *At2g34620b* gene.

^b Number of necessary bootstrap replicates determined using the extended majority-rule criterion (Pattengale & al., 2009).

^c Only a single accession covered by corresponding data.

Table 3. Non-parametric bootstrap support under ML (BS_{ML}) and Bayesian-inferred posterior probabilities (PP) of competing splits linked to putative rogue taxa and clades as inferred from the concatenated matrix, and the placement of the outgroup-defined *Cynanchinae* root.

	Support measure: ^a	BSML	PP
Phylogenetic split			
1 Placement of <i>C. chouxii</i>			
1.1 As sister to Clade 1 (Sister to Clade 1 save <i>C. analamazaotrense</i>)		42 (43)	0.51 (<0.2)
1.2 As sister to Clade 2		50	0.49
2 Placement of <i>C. pachycladon</i> within Clade 1			
2.1 Sister to Clades 1a and 1b		42	0.89
2.2 Sister to Clade 1b		44	<0.10
3 Placement of <i>C. abyssinicum</i> /Clade 5			
3.1 <i>C. abyssinicum</i> sister to Clades 4–9		53	0.81
3.2 Clade 5 sister to <i>C. abyssinicum</i> + Clades 4, 6–9		21	<0.20
4 Placement of Clade 6 in relation to Clades 7–9			
4.1 Clade 6 sister to Clade 7		75	1.00
4.2 Clade 6 sister to Clade 9		21	0.00
4.3 Clade 8 sister to Clade 9 (compatible with split 4.1 but not 4.2)		64	0.99

Bipartitions represented in the optimised maximum likelihood (ML) tree highlighted by grey shading.

^a BS_{ML} based on 350 bootstrap replicates inferred under ML; PP based on 2000 Bayesian-inferred sampled topologies.

and complexity is produced by differently shaped folds and lobes in staminal and interstaminal position. Double coronas (former *Sarcostemma* species) and ligules in staminal position add to this complexity. On the other hand, there are also species with short coronas or reduced ones, or with almost free staminal lobes, and conspicuous structures such as ligules are not restricted to a single clade or groups of clades. Thus, a classification of *Cynanchum* using corona characters would be completely artificial.

On first view, fruit structure seems to separate the genus into a putatively monophyletic thick-fruited (clades 7–9) and a putatively paraphyletic thin-fruited group (clades 1–5) from which the thick-fruited group evolved (Fig. 1). However, there are several problems with splitting *Cynanchum* into a thick-fruited and a thin-fruited genus (aside the issue of the

recognition of new paraphyletic taxa even if systematically useful or inevitable; cf. Hörandl, 2006, 2007). First, the somewhat intermediate Clade 6 could be understood as representing an early thick-fruited lineage, but there is no sharp, obvious morphological boundary between “thin” and “thick” fruits. In addition, while thick fruits are frequently ornamented with tubercles or soft spines, ornamented fruits are also known from thin-fruited clades (e.g., *C. ambovombense* Liede & Meve, *C. corymbosum* Wight). Also, the pericarp is differently structured in thick fruits, either spongy as frequently in Clade 7 (Fig. 3A) or rather solid as usually in Clades 8 and 9 (Fig. 3B). Long sterile beaks, characteristic for most thin fruits, are absent from several fruits of the Madagascan-succulent clade (Clade 1b) (e.g., *Cynanchum viminale* (L.) Bassi). Fruits of non-succulent Madagascan taxa, however, are frequently winged, a

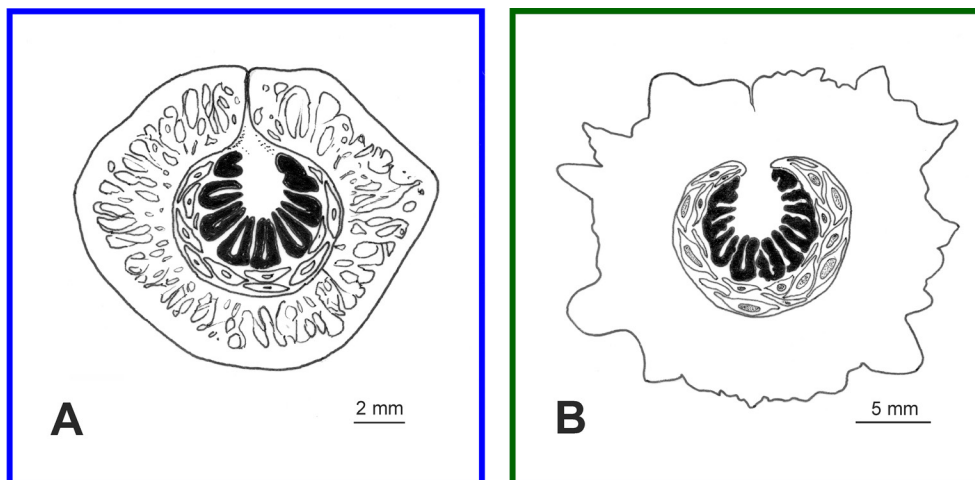


Fig. 3. Pericarp structure of thick fruits. **A**, Spongy mesocarp, often found in Clade 7 (*C. formosannum*); **B**, Solid mesocarp, usually found in Clades 8 and 9 (*Pentarrhinum insipidum*). — Drawn by U. Meve.

character otherwise uncommon in *Cynanchum*. Lastly, the most compelling argument against using fruits as leading character complex for a division of *Cynanchum* at this point is the fact that the fruits of at least 30% of the species are unknown (S. Liede-Schumann, pers. obs.) and that fruiting material of Asclepiadoideae can only be identified with certainty by molecular analysis or if flowers are present in addition.

Because there are no arguments for a split of *Cynanchum* into two or more well-supported and sufficiently distinct (regarding morphological traits) genera, it seems the most stable solution to include the so far separately recognized genera in *Cynanchum*, continuing the process started by including the stem-succulent genera (Liede & Meve, 2001; Liede & Kunze, 2002; Goyder, 2008; Meve & Liede-Schumann, 2012) following the molecular results by Liede & Kunze (2002) and Liede & Täuber (2002). As all hitherto separately recognized genera are small (<10 species), and many species have been described under *Cynanchum* before, it seems the nomenclaturally least upsetting solution to include them into a wide, easily recognizable *Cynanchum*. A similar approach has been suggested for other large genera in Asclepiadoideae (*Vincetoxicum* Wolf: Liede-Schumann & al., 2012, 2016; *Ceropegia* L.: Bruyns & al., 2015; *Hoya*: Wanntorp & al., 2006).

The three Cynanchinae genera for which sequenceable material could not be obtained presently comprise a single species only and are poorly known. In the case of *Adelostemma*, the type specimen from Wallich at K (<http://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.k000872744>) clearly shows the typical stipule-like short shoots of *Cynanchum* (Liede & Täuber, 2002), and they are also depicted in the corresponding illustration (Hooker, 1883: pl. 1427). Because this structure is found only in *Cynanchum*, it seems safe to include the single *Adelostemma* species in *Cynanchum* as well. This conclusion is supported by the deeply cordate leaf bases, which might have inspired Wight (1834) to first describe the plant under *Cynanchum*. The absence of a corona occurs occasionally in many asclepiad genera and cannot be used for generic circumscription (e.g., Liede, 2001).

In the case of *Sichuania*, Gilbert & al. (1995: 12) noted its similarity with *Holostemma* and stated that separate, ovate, scale-like corona lobes alternating with the anthers, the defining character of *Sichuania*, are also found in *Cynanchum contrapetalum* Sundell. Our analysis shows that *C. contrapetalum* (under the current name *C. roulinioides*) is a member of the South American Clade 9a (Electr. Suppl.: Fig. S1) despite its unusual corona. Thus, corona position does not exclude *Sichuania* from *Holostemma*, and, in consequence, from *Cynanchum* as conceived here. This placement is also supported by the deeply cordate leaf bases of the plant. Unfortunately, the type specimen is highly disintegrated, and the paratype cited by Gilbert & al. (1995) is housed in HNWP and could not be consulted.

Mahawoa constitutes the most difficult case, because the type material has been lost in B, and no other material has been recorded. From the protologue, it is apparent that *Mahawoa* represents a member of Asclepiadoideae, because its pollinia are described as pendent. However, the description of the leaves as ovate-elliptic with rounded bases, the inflorescences as

branched cymes, and the corona as fleshy oblong lobes fused over a quarter of their length, highly adnate to the anthers, and connivent at the top raises doubt whether the plant is related to *Graphistemma*, and thus *Cynanchum*, as assumed by Schlechter (1916), or whether it is related to *Vincetoxicum* s.l. (Tylophorinae). Because this problem cannot be solved at present, it seems prudent to list *Mahawoa* as an Asclepiadoideae of uncertain subtribal relationships.

With these changes, *Cynanchum* is another example for the trend described by Humphreys & Linder (2009), that studies involving molecular characters often result in larger genera. *Cynanchum* in the circumscription presented here fulfills the criteria of monophyly and stability (high support for the genus as a whole). In addition, a relatively small number of nomenclatural changes is necessary. However, the question of a single morphological synapomorphy has to remain open, because the single character unique to *Cynanchum*, the possession of prophylls, is not found in all species. All other characters are found in other genera of Asclepiadoideae as well. Nevertheless, in most areas *Cynanchum* is relatively easy to identify, even species without prophylls. In the Americas, large leaves with cordate bases combined with stout fruits distinguish the genus from most members of Metastelmatinae, Orthosiinae and Diplolepinae, that may or may not have a basal ring-shaped corona portion. Some members of *Jobinia* (e.g., *J. formosa* (N.E.Br.) Liede & Meve), however, also possess large cordate leaves, so that the twin fruits typical for Orthosiinae remain the only distinguishing character. Members of Gonolobinae, also with large cordate leaves, usually can be separated by the typical Gonolobinae gynostegium (e.g., Kunze, 1995), but some former *Metalepis* species possess gynostegia strongly reminiscent of Gonolobinae, so that their identity has to be ascertained by molecular methods. In Australasia, the only genus with which *Cynanchum* can be confused is *Vincetoxicum* s.l. (Liede-Schumann & al., 2012). Here, often any combination of clear latex, non-cordate leaf bases, branched inflorescences, presence of a thickened, blunt staminal corona (with or without thinner interstaminal parts), small pollinia and non-structured seed surfaces allow distinction of the latter, but there are exceptions for almost all characters both in *Cynanchum* and *Vincetoxicum*.

In Africa, in addition to *Vincetoxicum* s.l., *Pergularia*, *Calciphila*, and *Schizostephanus* might be confused with *Cynanchum*. *Pergularia* can be easily distinguished by its soft-textured leaves, ciliate corolla lobes, separate staminal corona lobes, and its twin follicles. Chemically, *Pergularia* contains cardenolides, as typical for Asclepiadinae (Liede, 1996c). *Schizostephanus*, sister to *Cynanchum* and only other member of subtribe Cynanchinae according to the concept presented here, can be distinguished by its translucent latex (Bruyns & Klak, 2009). *Calciphila*, a small Somalian endemic genus of two species, differs from *Cynanchum* also in possessing clear latex, small, non-cordate leaves, and wingless seeds (Liede-Schumann & Meve, 2006).

It is apparent from this discussion that the absence of a morphological synapomorphy present in all species weakens the concept of *Cynanchum*. However, inclusion of the segregate

genera does not unduly increase the morphological variability in the genus, because these genera do not introduce character states otherwise never found in *Cynanchum*. Most of these genera are characterized by thick follicles, which are rare, but by no means unknown in *Cynanchum* s.str., (e.g., *C. thesioides* (Freyn) K.Schum., *C. physocarpum* Schltr.). Variation in corona composition and shape cannot be used either to separate segregate genera, because corona shape and construction is an extremely variable character complex in *Cynanchum* s.str. as well (Table 1). Besides, such variation is known also from other asclepiad genera, e.g., *Vincetoxicum* (Liede-Schumann & al., 2012), *Diplolepis* (Hechem & al., 2011), *Philibertia* (Goyder, 2004), or *Hoya* (e.g., Wanntorp & Forster, 2007). As demonstrated above, the combination of characters found in *Cynanchum* justify the present concept allowing both diagnosis and differentiation against related genera (Humphreys & Linder, 2009).

Cynanchum in the circumscription suggested here is found in tropical and subtropical areas of all continents. Its first-branching clades comprise African (incl. Madagascan) species (Fig. 2; Electr. Suppl.: Fig. S1), and its sister genus *Schizostephanus* is likewise distributed in Africa. Species diversity is also highest in continental Africa, with six of the nine clades containing African members, and four clades restricted to mainland Africa. Thus, an African origin of the genus is likely. An early split has separated the speciose Madagascan lineage, out of which some succulent taxa have spread from Madagascar into Africa and Asia (*C. gerrardii* (Harvey) Liede and former “*Sarcostemma*” species, see Meve & Liede, 2002). Two clades (4 and 7) have radiated in Asia. Clade 4b comprises numerous species that have been attributed in the past to sect. *Rhodostegiella* (Pobed.) Tsiang & P.T.Li (Liede, 1996a); however, the type of the section, *C. thesioides*, is retrieved as sister to *Metaplexis japonica* Makino in Clade 7. The New World species of *Cynanchum* are monophyletic, with the Central American and South American species forming two subclades. *Metalepis*, which is widespread throughout tropical America, is a member of the South American subclade. The New World Clade (9) is sister to the *Glossonema*-*Odontanthera*-*Pentarrhinum* Clade (8), which has its centre of distribution in north-eastern Africa and Arabia. Only four lineages in Asclepiadoideae have reached the New World, *Asclepias*, *Cynanchum*, *Marsdenia*, and the MOOG (Metastelmatinae, Orthosiinae, Oxyptalinae, Gonolobinae) clade (Rapini & al., 2003). While no phylogeny is yet available for *Marsdenia*, the MOOG-clade is sister to the Cynanchinae-Asclepiadinae-Tylophorinae clade, and all are sister to two relictual African clades, Eustegieae and Asclepiadeae-Astephaninae (Surveswaran & al., 2014), suggesting an African origin for all Asclepiadeae. A similar picture has been found for *Asclepias* and the Asclepiadinae, for which the large American *Asclepias* s.str. radiation and the equally large African radiation are sister to a few much smaller, mainly African taxa, namely *Calotropis* R.Br., *Kanahia* R.Br., and *Pergularia*, and the North-East African *Trachycalymma pseudofimbriatum* Goyder (Goyder & al., 2007; Fishbein & al., 2011). Thus, the three groups with New World representatives studied so far—MOOG, *Asclepias* and *Cynanchum*—show an “out-of-Africa” distribution pattern.

■ TAXONOMIC TREATMENT

- Cynanchum* L., Sp. Pl.: 212. 1753 – Type: *C. acutum* L.
 = *Holostemma* R.Br. in Mem. Wern. Nat. Hist. Soc. 1: 42. 1810, **syn. nov.** – Type: *H. ada-kodien* Schult.
 = *Metaplexis* R.Br. in Mem. Wern. Nat. Hist. Soc. 1: 48. 1810, **syn. nov.** – Type: *M. stauntonii* R.Br.
 = *Raphistemma* Wall., Pl. Asiat. Rar. 2: 50, pl. 163. 1831, **syn. nov.** – Type: *R. pulchellum* (Roxb.) Wall. (≡ *Asclepias pulchella* Roxb.).
 = *Urostelma* Bunge, Enum. Pl. China Bor.: 44. 1833 – Type: *U. chinense* Bunge.
 = *Odontanthera* Wight in Madras J. Lit. Sci. 7: 143. 1838, **syn. nov.** – Type: *O. reniformis* Wight.
 = *Steinheilila* Decne. in Ann. Sci. Nat., Bot., sér. 2, 9: 339. 1838 – Type: *S. radians* (Forssk.) Decne. (≡ *Asclepias radians* Forssk.).
 = *Pentarrhinum* E.Mey., Comm. Pl. Afr. Austr.: 199–200. 1838, **syn. nov.** – Type: *P. insipidum* E.Mey.
 = *Glossonema* Decne. in Ann. Sci. Nat., Bot., sér. 2, 9: 335, pl. 12D. 1838, **syn. nov.** – Type: *G. boveanum* (Decne.) Decne. (≡ *Cynanchum boveanum* Decne.).
 = *Mastostigma* Stocks in Hooker’s Icon. Pl.: t. 863. 1851 (“1852”) – Type: *M. varians* Stocks.
 = *Holostemma* sect. *Graphistemma* Champ. ex Benth. in Hooker’s J. Bot. Kew Gard. Misc. 5: 53. 1853 ≡ *Graphistemma* (Champ. ex Benth.) Champ. ex Benth. in Benthem & Hooker, Gen. Pl. 2: 760. 1876, **syn. nov.** – Type: *G. pictum* (Champ. ex Benth.) Benth. & Hook.f. ex Maxim.
 = *Metalepis* Griseb., Cat. Pl. Cub.: 179. 1866 ≡ *Cynanchum* subg. *Metalepis* (Griseb.) Woodson in Ann. Missouri Bot. Gard. 28: 213. 1941 ≡ *Cynanchum* sect. *Metalepis* (Griseb.) Sundell in Evol. Monogr. 5: 13. 1981 – Type: *M. cubensis* (A.Rich.) Griseb.
 = *Adelostemma* Hook.f., Fl. Brit. India 4: 20. 1883, **syn. nov.** – Type: *A. gracillimum* (Wall. ex Wight) Hook.f. (≡ *Cynanchum gracillimum* Wall. ex Wight).
 = *Gilgia* Pax in Bot. Jahrb. Syst. 19: 80. 1894 – Type: *G. candida* Pax [originally described as Euphorbiaceae].
 = *Aphanostelma* Schltr. in Léveillé, Fl. Kouy-Tchéou: 39. 1914–1915 – Type: *A. chinensis* Schltr.
 = *Seshagiria* Ansari & Hemadri in Indian Forester 97: 126. 1971, **syn. nov.** – Type: *S. sahyadrica* Ansari & Hemadri.
 = *Sichuania* M.G.Gilbert & P.T.Li in Novon 5(1): 12–13. 1995, **syn. nov.** – Type: *S. alterniloba* M.G.Gilbert & P.T.Li.

Cynanchum alternilobum (M.G.Gilbert & P.T.Li) Liede & Khanum, **comb. nov.** ≡ *Sichuania alterniloba* M.G. Gilbert & P.T.Li in Novon 5: 12–13. 1995 – Holotype: CHINA. Sichuan: S Wushan, *A. Henry 7262* (E barcode E00021288!).

Cynanchum annularium (Roxb.) Liede & Khanum, **comb. nov.** ≡ *Asclepias annularia* Roxb., Hort. Bengal.: 20. 1814 ≡ *Holostemma annularium* (Roxb.) K.Schum. in Engler & Prantl, Nat. Pflanzenfam. 4(2): 250. 1895 (“*annularis*”) ≡ *Holostemma rheedei* Wall., Pl. Asiat. Rar. 2: 51. 1831

(“*rheedii*”), nom. illeg. (superfl.) – Lectotype (designated by Huber in *Abeywickrama*, Rev. Handb. Fl. Ceylon 1(1): 37. 1973): [illustration] “Ada-kodien” in Rheedee, Hort. Malab. 9: t. 7. 1689.

= *Holostemma ada-kodien* Schult. in Roemer & Schultes, Syst. Veg. 6: 95. 1820 – Lectotype (designated by Turner in *Taxon* 62: 154. 2013): East Indies, *Dr Patrick Russell s.n.* (BM barcode BM000948717 [photo!]).

= *Sarcostemma annulare* Roth ex Schult. in Roemer & Schultes, Syst. Veg. 6: 115. 1820 – Lectotype (designated by Turner in *Taxon* 62: 154. 2013): INDIA: *B. Heyne s.n.* [EIC 4469D!] (K-W).

= *Holostemma brunonianum* Royle, Ill. Bot. Himal. Mts.: 276, t. 66. 1835 – **Lectotype (designated here)**: [illustration] “*Holostemma Brunoniana*” in Royle, Ill. Bot. Himal. Mts.: t. 66, fig. 2. 1835.

Note. – The name *Holostemma rheedeanum* Spreng. (Syst. Veg. 1: 851. 1824; published as “*rheedianum*”) probably constitutes a further synonym of *Cynanchum annularium*. However, the description is ambiguous and no type material could be traced.

Cynanchum balense Liede in Ann. Missouri Bot. Gard. 83: 299–301. 1996 ≡ *Pentarrhinum balense* (Liede) Liede in Syst. Bot. 22: 368. 1997 – Holotype: ETHIOPIA. Bale: Rira, 3260 m, 20 Dec 1959, *H.F. Mooney 8359* (K barcode K000305128!; isotypes: ETH barcode ETH000000038!, K barcode K000305129!).

Cynanchum boveanum Decne. in Ann. Sci. Nat., Bot., sér. 2, 4: 82–83. 1835 ≡ *Glossonema boveanum* (Decne.) Decne. in Ann. Sci. Nat., Bot., sér. 2, 9: 335, t. 12D. 1838 ≡ *Odontanthera boveana* (Decne.) Mabb., Bot. Hist. Hort. Malabaricus: 89. 1980 – Neotype (designated by Bruyns & Miller in *Edinburgh J. Bot.* 66: 99. 2009): SAUDI ARABIA. Near Ferihe, 15 Feb 1836, *W.P. Schimper 920* (W; isoneotypes: FI, HBG barcode HBG-502885!, K, P barcodes P00599923–00599926 [4 sheets!]; TUB barcode TUB-003492!).

= *Glossonema affine* N.E.Br. in Bull. Misc. Inform. Kew 1895: 249. 1895 – Holotype: ETHIOPIA. Pedes montium ad fl. Tacase pr. Garrsarfa, alt. 3000–3300 ft., 10 Aug 1854, *G.W. Schimper 2219* (K barcode K000234414!; isotypes: JE barcode JE00019699!, P, S No. S12-8839!, W [2 sheets, sub Nos. W 0006451! & W-Rchb. 1889-0284822!]).

Type specimens could be traced in K, S, W, P (originally from herb. Lenormand, Caen, France) and JE, labelled as *Glossonema echinatum*. Brown, in the protologue, did not cite a herbarium for the type, *Schimper 2219*, however, the specimen in K bears his personal mark “Type! N.E.Brown”, so that no doubt can arise which specimen the author used for preparing the original description (Art. 9.1 of the *Code*, McNeill & al., 2012).

= *Glossonema erlangeri* K.Schum. in Bot. Jahrb. Syst. 33: 322. 1903 – **Lectotype (designated here)**: SOMALIA. Near Hensa (between Zeila and Somadu), 5 Feb 1900, *H. Ellenbeck 195* (K barcode K000234412!).

The holotype at B was destroyed and the lectotype represents a very poor specimen consisting of two leaves and one flower only (probably a “kleptotype”).

Note. – *Glossonema echinatum* Hochstetter ex Di Capua (in *Annuario Reale Ist. Bot. Roma* 8: 214. 1904), is listed in the synonymy of *G. boveanum* by Bullock (1955), but has to be considered as a nomen invalidum subnudum. The specimen ETHIOPIA. Pedes montium ad fl. Tacase pr. Gaurrsafa, alt. 3000–3300 ft., 10 Aug 1854, *G.H.W. Schimper*, ed. *Hohenacker 2219* (JE!) represents material cited in the protologue and supports Bullock’s (1955) conclusion.

Cynanchum boveanum subsp. *nubicum* (Decne.) Khanum & Liede, **comb. nov.** ≡ *Glossonema nubicum* Decne. in Candolle, Prodr. 8: 555. 1844 ≡ *G. boveanum* subsp. *nubicum* (Decne.) Bullock in Kew Bull. 10: 617. 1956 ≡ *Odontanthera boveana* subsp. *nubica* (Decne.) Mabb. in Bot. Hist. Hort. Malabaricus: 89. 1980 – Holotype: SUDAN. Nubicum, ad montem Cordofanum Kohn versus Tekele, Nov 1839, *Kotschy 405* (P [not traced]; isotypes: BR barcode 0000008862204!, HBG barcode HBG-502885!, K barcodes K000234410! & K000234411!, M, MPU barcode MPU000530!, S No. S12-8837!, TUB barcodes TUB-003490! & TUB-003491!).

Type specimens (*Kotschy 405*) are widely distributed, however, the holotype in P could not be traced. Nevertheless, we regard the possibility as high that the P specimen is not lost, and therefore, we resign for now from lectotypification.

= *Glossonema gautieri* Batt. & Trab. in Bull. Soc. Bot. France 53(sess. extraord.): 28. 1907 – **Lectotype (designated here)**: ALGERIA. Ahaggar, Tamanghasset, Aug 1905, *R. Chudeau s.n.* (MPU barcode MPU007544!).

It is not clearly stated in the protologue where type material has been deposited, and since Battandier’s specimens are either located in MPU or AL, lectotypification becomes necessary.

= *Glossonema gautieri* var. *titensis* Batt. & Trab. in Bull. Soc. Bot. France 53(sess. extraord.): 29. 1907 – **Lectotype (designated here)**: ALGERIA. Ahaggar, Tit, alt. 1000 m, 17 Jun 1905, *R. Chudeau s.n.* (MPU barcode MPU007545!). See comment under *Glossonema gautieri* above.

Cynanchum ethiopicum Liede & Khanum, **nom. nov.** ≡ *Pentarrhinum abyssinicum* Decne. in Candolle, Prodr. 8: 553. 1844 – Lectotype (designated by Liede & Nicholas in Kew Bull. 47: 481. 1992): [illustration] “PENTARRHINUM abyssinicum” in De Lessert, Icon. Sel. Pl. 5: t. 70 [erroneously given as t. 80 in Liede & Nicholas, 1992]. 1846. Blocking name: *Cynanchum abyssinicum* Decne. (in Candolle, Prodr. 8: 548. 1844).

Cynanchum ethiopicum subsp. *angolense* (N.E.Br.) Liede & Khanum, **comb. nov.** ≡ *Pentarrhinum abyssinicum* var. *angolense* N.E.Br. in Oliver, Fl. Trop. Afr. 4: 379–380. 1902 ≡ *Pentarrhinum abyssinicum* subsp. *angolense* (N.E.Br.) Liede & Nicholas in Kew Bull. 47: 482. 1992 – Lectotype

(designated by Liede & Nicholas in Kew Bull. 47: 482. 1992): ANGOLA. Icolo e Bengo Distr.: near the Lago de Foro, *F.M.J. Welwitsch 4240* (K barcode K000305119!; isolectotypes: BM, BR barcode BR0000008862037!).

Cynanchum fragrans (Wall.) Liede & Khanum, **comb. nov.** ≡ *Holostemma fragrans* Wall., Pl. Asiat. Rar. 2: 51. 1831 – **Lectotype (designated here):** MYANMAR. Monte Taong Dong, 18 Sep 1826, sub *Wallich Cat. No. 4470* (K barcode K001039067!).

The three specimens in K labelled *Wallich 4470* represent three different collections, either with regard to collecting locality or collecting date. Therefore, only one specimen is chosen as lectotype, K001039067, because it is the only number evidently assembled from a single plant.

Cynanchum gonoloboides Schltr. in Mildbraed, Wiss. Erg. Deut. Zentr.-Afr. Exped., Bot.: 543. 1913. ≡ *Pentarrhinum gonoloboides* (Schltr.) Liede in Syst. Bot. 22: 368. 1997 – Neotype (designated by Liede in Ann. Missouri Bot. Gard. 83: 317. 1996): KENYA. Rift Valley, Nakuru, Doboti, about 9 mi. from Cobb's gate near th Mau Forest Reserve on the track to Nairagi Ngare, 3200 m, *P.E. Glover & al. 1492* (K barcode K000305126!; isoneotypes: EA, FT barcode FT002669!, K barcode K000450251!, S No. S12-10396!).

Cynanchum graphistemmaoides Liede & Khanum, **nom. nov.** ≡ *Holostemma pictum* Champ. ex Benth. in Hooker's J. Bot. Kew Gard. Misc. 5: 53. 1853 ≡ *Graphistemma pictum* (Champ. ex Benth.) Benth. & Hook.f. ex Maxim. in Mélanges Biol. Bull. Phys.-Math. Acad. Imp. Sci. Saint-Petersbourg 9: 776. 1876 – Holotype: CHINA. Guangdong: Hongkong: Mount Victoria *Champion 193* (K barcode K000872740!; isotype: K barcode K000872741!).
Blocking name: *Cynanchum pictum* Vahl, Eclog. Amer. 2: 24–25. 1798.

Note. – Of the three *Champion* specimens available in Kew, K000872740 originates from Herbarium Benthamianum and includes the original drawings, a hand-written description and a label saying “No. 193, *gen. nov.* near *Holostemma*, Hongkong”. A precise locality is not given on this sheet, but a duplicate of *Champion 193*, K000872741, clearly states “not uncommon, Victoria Peak”. Bentham finally decided not to describe a new genus (*Graphistemma*), instead he proposed *Holostemma* sect. *Graphistemma* in the protologue of *H. pictum*. However, he clearly used K000872740 for describing the new species, and therefore this specimen represents the holotype of *H. pictum*. The third specimen of *Champion*, K000872739! from herb. Hookerianum, probably represents another duplicate, but since it lacks precise labelling with regard to collection number and locality, it is excluded from the type material.

Cynanchum hemsleyanum (Oliv.) Liede & Khanum, **comb. nov.** ≡ *Holostemma sinense* Hemsl. in J. Linn. Soc., Bot. 26: 103. 1889 ≡ *Metaplexis hemsleyana* Oliv. in Hooker's Icon. Pl. 20: pl. 1970. 1891 ≡ *Metaplexis sinensis* (Hemsl.)

Hu in J. Arnold Arbor. 6: 143. 1925, nom. illeg. (blocking name: *Metaplexis chinensis* (Bunge) Decne. in Candolle, Prodr. 8: 511. 1844) – **Lectotype (designated here):** CHINA. Hubei: Ichang, Oct 1887, *A. Henry 3992* (K barcode K000872798!).

Oliver cited four syntypes, *A. Henry 2755, 3992, 6625A, and 7262*. Of these, only 2775 and 3992 could be traced in Kew, and the latter is chosen as lectotype here.
= *Metaplexis japonica* var. *platyloba* Hand.-Mazz., Symb. Sin. 7: 994. 1936 – Holotype: CHINA. Hunan: Jiamitou, Xiguang Shan, 840 m, 14 Sep 1918, *Handel-Mazzetti 12640* (WU No. 0060818!).

Cynanchum hooperianum (Blume) Liede & Khanum, **comb. nov.** ≡ *Oxystelma hooperianum* Blume, Bijdr. Fl. Ned. Ind. 16: 1053. 1826–1827 ≡ *Raphistemma hooperianum* (Blume) Decne. in Candolle, Prodr. 8: 516. 1844 – Type: INDONESIA. Java: Mt. Salak, *Blume s.n.* (not traced).
= *Raphistemma brevipedunculatum* Y.Wan in Guihaia 3(3): 197–198, fig. 1. 1983 – Holotype: CHINA. Guangxi: Long'an, open woods, 2 Jul 1981, *D.H. Tan 82329* (GXMS; isotype: CANT).

Cynanchum insipidum (E.Mey.) Liede & Khanum, **comb. nov.** ≡ *Pentarrhinum insipidum* E.Mey., Comm. Pl. Afr. Austr.: 200. 1838 – Lectotype (designated by Liede & Nicholas in Kew Bull. 47: 484. 1992): SOUTH AFRICA. Uitenhage Div., Enon, *C.F. Drège 2220* (K barcode K000305116!; isolectotype: HBG barcode HBG-502807!).

Cynanchum ledermannii Schltr. in Bot. Jahrb. Syst. 51: 140. 1913 ≡ *Pentarrhinum ledermannii* (Schltr.) Goyder & Liede in Kew Bull. 63: 466. 2009 – Neotype (designated by Liede in Ann. Missouri Bot. Gard. 83: 320. 1996): BURUNDI: Bubanza, Mugomero (Rugazi), 2 May 1981, *Reekmans 10069* (K barcode K000305131!; isoneotype: BJA barcode BJA294643914!).
= *Pentarrhinum abyssinicum* subsp. *ijimense* Goyder in Cheek & al., Pl. Mount Oku & Ijim Ridge Cameroon, Conserv. Checklist: 92. 2000 – Holotype: CAMEROON. N.W. Province: Boyo Dcision, Ijim, forest at Ntum, 1810 m, 4 Nov 1999, *M. Cheek & al. 9943* (K No. 77443.000, isotypes: BR, EA, MO, MSTR, PRE, WAG, YA).

Cynanchum pichisermollianum (Raimondo & Fici) Liede & Khanum, **comb. nov.** ≡ *Glossonema pichi-sermollianum* Raimondo & Fici in Webbia 47: 145. 1993 – Holotype: SOMALIA. Dunes near the Lido of Mogadishu, 2 Jun 1976, *Raimondo 91/76* (PAL).

Cynanchum pulchellum (Roxb.) Liede & Khanum, **comb. nov.** ≡ *Asclepias pulchella* Roxb., Fl. Ind. 2: 54, t. 2466. 1824 ≡ *Raphistemma pulchellum* (Roxb.) Wall., Pl. Asiat. Rar. 2: 50–51, pl. 163. 1831 ≡ *Oxystelma pulchellum* (Roxb.) D.Dietr., Syn. Pl. 2: 902. 1840 – **Lectotype (designated here):** INDIA. 1813, *Roxburgh s.n.* (BM barcode BM001014205!).

A single Roxburgh specimen of *Cynanchum pulchellum* could be traced in BM, and this is designated as lectotype here.

Cynanchum radians (Forssk.) Lam., *Encycl.* 2: 236. 1786 ≡ *Asclepias radians* Forssk., *Fl. Aegypt.-Arab.*: 49. 1775 ≡ *Steinheilium radians* (Forssk.) Decne. in *Ann. Sci. Nat., Bot.*, sér. 2, 9: 339–340, t. 12E. 1838 ≡ *Odontanthera radians* (Forssk.) D.V.Field in *Kew Bull.* 37: 343. 1982 – **Lectotype (designated here)**: YEMEN. Beit el Fakih, 1763, *P. Forsskål 276* (C barcode C10001753!).

Hepper & Friis (1994: 82) specify two extant collections, *Forsskål 275* and *Forsskål 276*, but only the latter originates undoubtedly from the type locality and is also better preserved. It is therefore selected as lectotype here.

= *Odontanthera reniformis* Wight in *Madras J. Lit. Sci.* 7: 143. 1838 – **Lectotype (designated here)**: [illustration] “*Odontandra Reniformis*” in *Madras J. Lit. Sci.* 7: [pl. post p. 142]. 1838.

Note. – The description of Wight (1838), which is accompanied by a plate, is based on a specimen by Nimmo, which could nowhere be traced. As the plate is of excellent quality, it is selected as lectotype here.

Cynanchum revoilii (Franch.) Khanum & Liede, **comb. nov.** ≡ *Glossonema revoilii* Franch., *Sert. Somal.*: 40. 1882 – Holotype: SOMALIA. Tigieh (Medjourtines), *M.G. Révoil 69* (P barcode P00152448!).

There is only one specimen of *Révoil* in P, number 69, that bears both the name of the type locality “Tigieh” and the vernacular name “Saska”, both indicated in the protologue. As Franchet worked in P and deposited his types there, this specimen has to be regarded as the holotype.

= *Gilgia candida* Pax in *Bot. Jahrb. Syst.* 30: 81. 1894 – Type: SOMALIA. Ahlgebirge, *J.M. Hildebrandt 889c* (holotype?: B [destroyed]).

= *Glossonema elliotii* Schltr. in *J. Bot.* 33: 304–305. 1895 – Holotype: KENYA. K4, Machakos Dist., Kikumbuliyu, 26 Nov 1893, *G.F. Scott-Elliot 6184* (BM barcode BM000925857!; isotype: K barcode K000234406!).

Schlechter described *Glossonema elliotii* based on a specimen “now in the British Museum” (Schlechter, 1895: 300), and thus also designated the nomenclatural type.

= *Glossonema macrosepalum* Chiov., *Res. Sci. Somal. Ital.* 1: 113. 1916 – Holotype: SOMALIA. El Ure, *G. Paoli 1082* (FT barcode FT002657!).

= *Glossonema rivaei* K.Schum. in *Bot. Jahrb. Syst.* 33: 323. 1903 – **Lectotype (designated here)**: SOMALIA. Dolo near Daa river, *D. Riva 1129* (K barcode K000234409!; isolectotype: FT barcode FT002658!).

The holotype of this species at B was destroyed. Settesoldi & al. (2011) did not list *Riva 1129* as housed at FT. Therefore, although showing the appearance of a “kleptotype” with just a leaf and two separate flowers, the specimen in K is chosen as lectotype here.

Cynanchum rostellatum (Turcz.) Liede & Khanum, **comb. nov.** ≡ *Metaplexis rostellata* Turcz. in *Bull. Soc. Imp. Naturalistes Moscou* 21: 253. 1848, fide Stevens (2000: 256) – **Lectotype (designated here)**: CHINA. E China boreali, *R. Fortune 87A* (KW barcode KW001000455!; isolectotypes BM barcode BM001014188!, MO No. 2760810!, S No. S12-10451!).

Of the two syntypes cited in the protologue, *Kirilow s.n.* and *Fortune 87A*, Kiev houses one specimen each, both indicated as belonging to the original material, and both verified by Turczaninow. The specimen *Fortune 87A*, which is the richest one, is labelled as holotype, however, since it is also marked as “sheet 1 of 2” lectotypification becomes implicitly necessary.

= *Pergularia japonica* Thunb., *Fl. Jap.*: 111. 1784 ≡ *Metaplexis japonica* (Thunb.) Makino in *Bot. Mag. (Tokyo)* 17: 87. 1903 – **Lectotype (designated here)**: JAPAN: Nagasaki, *Thunberg s.n.* (UPS-THUNB No. 6228 barcode UPS: BOT:V-006228!).

Blocking name: *Cynanchum japonicum* C.Morren & Decne. in *Bull. Acad. Roy. Sci. Bruxelles* 3: 172. 1836.

= *Metaplexis stauntonii* R.Br. ex Schult. in *Roemer & Schultes, Syst. Veg.* 6: 111. 1820 ≡ *Urostelma chinense* Bunge, *Enum. Pl. China Bor.*: 44. 1833 (“1831”) ≡ *Metaplexis chinensis* (Bunge) Decne. in *Candolle, Prodr.* 8: 511, 1844, nom. superfl. – Holotype: CHINA. Province of Peckele, *G. Staunton s.n.* (BM barcode BM000797986!).

Note. – The holotype *Staunton s.n.* is combined on one sheet with *Fortune 87A* (barcode BM001014188), isolectotype of *M. rostellata*.

Cynanchum sahyadricum (Ansari & Hemadri) Liede & Khanum, **comb. nov.** ≡ *Seshagiria sahyadrica* Ansari & Hemadri in *Indian Forester* 97(3): 126. 1971 – Holotype: INDIA. Maharashtra: Poona Distr., Sinhadadh, 28 Jun 1963, *M.Y. Ansari 87750* (CAL; isotypes: K barcodes K000881899! & K000881900!).

Cynanchum somaliense (N.E.Br.) N.E.Br. in *Oliver, Fl. Trop. Afr.* 4: 398. 1903 ≡ *Schizostephanus somaliensis* N.E.Br. in *Bull. Misc. Inform. Kew* 106: 250. 1895 ≡ *Pentarrhinum somaliense* (N.E.Br.) Liede in *Syst. Bot.* 22: 368. 1997 ≡ *Cynanchum trifurcatum* Schltr. in *Bull. Herb. Boissier* 4: 448. 1896, nom. superfl. – Holotype: SOMALIA. Boobi, *James & Thrupp s.n.* (K barcode K000305127!).

Notes. – In the protologue, N.E. Brown does not indicate a location for the type, *James & Thrupp s.n.*, however, the specimen in K (the only specimen traced) bears original pencil sketches and his personal note “Type specimen! N.E.Brown”, so that there can be no doubt that this specimen represents the holotype.

Schlechter (1896) overlooked that N.E. Brown (1902) had transferred *Schizostephanus somaliensis* N.E.Br. to *Cynanchum* as *Cynanchum somaliense* (N.E.Br.) N.E.Br. and coined the name *Cynanchum trifurcatum* for the same action, because he was aware that the name *Cynanchum somaliense* existed, but did not realize that it refers to the same species.

Cynanchum subpaniculatum Woodson in Ann. Missouri Bot. Gard. 28: 275–276. 1941 – Holotype: COLOMBIA. Santa Marta, 2000 ft, *H.H. Smith 2410* (MO barcode MO-078193!; isotypes: BR barcode BR0000006963262!, GH barcode 00063631, MO barcode MO-072851, MPU barcode MPU019230!, S No. S03-2274!, US, WIS barcode v0255164 WIS!).

= *Metalepis albiflora* Urb. in Repert. Spec. Nov. Regni Veg. 16: 37. 1919 ≡ *Cynanchum albiflorum* (Urb.) Woodson in Fl. Trinidad 2: 168. 1947, nom. illeg. – Lectotype (designated by Morillo in Pittieria 26: 81. 1997): TOBAGO. Near “The Window”, Mar 1914, *W.E. Broadway 4794* (G barcode G00039951!; isolectotypes: BM barcodes BM000952909! & BM000952908!, GH barcode 00076509!, MO barcode MO-078193!, NY barcode 00111038!, P barcode P00645735!).

Blocking name: *Cynanchum albiflorum* (Franch. & Sav.) Koidz., Fl. Symb. Orient.-Asiat.: 28. 1930.

= *Cynanchum marsdenioides* Woodson in Ann. Missouri Bot. Gard. 31: 235–236. 1944 – Holotype: ECUADOR. Los Rios: Puerto Rico: Mayaguez; Exp. Sta., *R.H. Moore 2163* (US barcode 00112321!).

Note. – For six of the seven species enumerated under *Metalepis* by Morillo (1997), combinations under *Cynanchum* exist. However, Liede (1997a) repeated the error of Woodson (1947) combining the most frequent species as *Cynanchum albiflorum* (Urb.) Woodson, overlooking the earlier *C. albiflorum* (Franch. & Sav.) Koidz. Therefore, a clarification is needed here.

Cynanchum thruppii (Oliv.) Khanum & Liede, **comb. nov.** ≡ *Glossonema thruppii* Oliv. in James, Unkn. Horn Afr.: 320. 1888 ≡ *Odontanthera thruppii* (Oliv.) Mabb. in Bot. Hist. Hort. Malabaricus: 89. 1980 – Holotype: SOMALIA. Ounanuff, Apr 1885, *F.L. James & T.C. Thrupp s.n.* (K barcode K000234408!).

The locality “Ounanuff” makes the only but sufficient indication of (type) material in the protologue seen by the author and this specimen is therefore regarded as the holotype.

= *Glossonema hispidum* Hutch. & E.A. Bruce in Bull. Misc. Inform. Kew 1941: 146. 1942. – Holotype: SOMALIA. Ethiopian border at 8°57'N, 44°10'E, 29 Sep 1932, *Gillett 4081* (K barcode K000234407!).

Cynanchum varians (Stocks) Liede & Khanum, **comb. nov.** ≡ *Mastostigma varians* Stocks in Hooker's Icon. Pl.: t. 863. 1851 ≡ *Glossonema varians* (Stocks) Benth. ex Hook.f., Fl. Brit. India 4: 16. 1883 ≡ *Odontanthera varians* (Stocks) Mabb. in Bot. Hist. Hort. Malabaricus: 89. 1980 – **Lectotype (designated here):** PAKISTAN. Scinde hills, *J.E. Stocks 467* (K barcode K000910076!).

Of the two specimens in K labelled “*Stocks 467*” the specimen K000910076 is richer and also carries the hand-written information “fruit called *Moonga*, much eaten” as cited in the protologue. It is here chosen as lectotype.

= *Glossonema arabicum* Defflers in Bull. Soc. Bot. France 43:

110. 1896 – Holotype: YEMEN. Bilad Fodhli, ad declivia australia montis Nakhaï, 1 Apr 1890, *A. Defflers 516* (not 522 as erroneously given in the protologue) (MPU barcode MPU009682!).

= *Glossonema edule* N.E.Br. in Bull. Misc. Inform. Kew 1895: 183. 1895 – Holotype: OMAN. Foot of Dhofar Mts., 1895, *J.T. Bent 175* (K barcode K000228208!).

= *Glossonema haussknechtii* Bornm. in Beih. Bot. Centralbl., Abt. 2, 61: 80, t. 1. 1941 (nom. inval., Art. 39.1). – Lectotype (designated by Bullock in Kew Bull. 10: 619. 1955): [illustration in] Beih. Bot. Centralbl., Abt. 2, 61: t. 1. 1941.

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■ LITERATURE CITED

- Ansari, M.Y. & Hemadri, K.** 1971. *Seshagiria* Ansari et Hemadri – A new genus of Asclepiadaceae from Sahyadri Ranges, India. *Indian Forester* 97: 126–127.
- Baldwin, B.G.** 1992. Phylogenetic utility of the internal transcribed spacers of nuclear ribosomal DNA in plants: An example from the Compositae. *Molec. Phylog. Evol.* 1: 3–16. [http://dx.doi.org/10.1016/1055-7903\(92\)90030-K](http://dx.doi.org/10.1016/1055-7903(92)90030-K)
- Blume, C.L.** 1826. *Bijdragen tot de flora van Nederlandsch Indië*, 16de Stuk. Batavia: Lands Drukkerij. <http://dx.doi.org/10.5962/bhl.title.115427>
- Brown, N.E.** 1902–1903. Asclepiadaceae. Pp. 231–503 in: Thiselton-Dyer, J. (ed.), *Flora of tropical Africa*, vol. 4(1.2–1.3). London: Reeve. <http://dx.doi.org/10.5962/bhl.title.42>
- Bruyns, P.V. & Klak, C.** 2009. The rediscovery of *Schizostephanus gossweileri* and its phylogenetic position. *S. African J. Bot.* 75: 532–536. <http://dx.doi.org/10.1016/j.sajb.2009.05.003>
- Bruyns, P.V., Klak, C. & Hanáček, P.** 2015. Recent radiation of *Brachystelma* and *Ceropegia* (Apocynaceae) across the Old World against a background of climatic change. *Molec. Phylog. Evol.* 90: 49–66. <http://dx.doi.org/10.1016/j.ympev.2015.04.015>

- Bullock, A.A.** 1955. Notes on African Asclepiadaceae VII. *Kew Bull.* 10: 611–626. <http://dx.doi.org/10.2307/4113775>
- Endress, M.E., Liede-Schumann, S. & Meve, U.** 2007. Advances in Apocynaceae: The enlightenment, an introduction. *Ann. Missouri Bot. Gard.* 94: 259–267. [http://dx.doi.org/10.3417/0026-6493\(2007\)94\[259:AIATEA\]2.0.CO;2](http://dx.doi.org/10.3417/0026-6493(2007)94[259:AIATEA]2.0.CO;2)
- Endress, M.E., Liede-Schumann, S. & Meve, U.** 2014. An updated classification for Apocynaceae. *Phytotaxa* 159: 175–194. <http://dx.doi.org/10.11646/phytotaxa.159.3.2>
- Field, D.V.** 1982. The identity of *Odontanthera* Wight (Asclepiadaceae) with notes on *Glossonema* Decne. and *Conomitra* Fenzl. *Kew Bull.* 37: 341–347. <http://dx.doi.org/10.2307/4109979>
- Fishbein, M., Chuba, D., Ellison, C., Mason-Gamer, R.J. & Lynch, S.P.** 2011. Phylogenetic relationships of *Asclepias* (Apocynaceae) estimated from non-coding cpDNA sequences. *Syst. Bot.* 36: 1008–1023. <http://dx.doi.org/10.1600/036364411X605010>
- Fontella Pereira, J. & Britto de Goes, M.** 2009. Asclepiadoideae (Apocynaceae) do Sudeste do Brasil-II. Novos sinônimos e nova ocorrência para *Metalepis cubensis* no Brasil. *Pesq. Florest. Brasil.* 58: 75–78.
- Fontella Pereira, J., Santos, R.G.P. & Cáceras Moral, S.A.** 2014. Notas taxonômicas em Asclepiadoideae (Apocynaceae). *Bol. Soc. Argent. Bot.* 49: 401–404.
- Gilbert, M.G., Stevens, W.D. & Li, P.T.** 1995. Notes on the Asclepiadaceae of China. *Novon* 5: 1–16. <http://dx.doi.org/10.2307/3391820>
- Goyder, D.J.** 2000. A new *Pentarrhinum* (Asclepiadaceae) from Cameroon. Pp. 92, 115 in: Cheek, M., Onana, J.-M. & Pollard, B.J. (eds.), *The plants of Mount Oku and the Ijim ridge, Cameroon*. Kew: Royal Botanic Gardens.
- Goyder, D.J.** 2004. An amplified concept of *Philibertia* Kunth (Apocynaceae: Asclepiadoideae), with a synopsis of the genus. *Kew Bull.* 59: 415–451. <http://dx.doi.org/10.2307/4110951>
- Goyder, D.J.** 2006a. *Glossonema*. Pp. 161–163 in: Thulin, M. (ed.), *Flora of Somalia*, vol. 3. Kew: Royal Botanic Gardens.
- Goyder, D.J.** 2006b. The identity of *Pentarrhinum iringense* Markgr. (Apocynaceae: Asclepiadoideae). *Kew Bull.* 60: 613.
- Goyder, D.J.** 2006c. A revision of the genus *Pergularia* L. (Apocynaceae - Asclepiadoideae). *Kew Bull.* 61: 245–256.
- Goyder, D.J.** 2008 (publ. 2009). Nomenclatural changes resulting from the transfer of tropical African *Sarcostemma* to *Cynanchum* (Apocynaceae: Asclepiadoideae). *Kew Bull.* 63: 471–472. <http://dx.doi.org/10.1007/s12225-008-9051-9>
- Goyder, D.J.** 2009. A synopsis of *Asclepias* (Apocynaceae: Asclepiadoideae) in tropical Africa. *Kew Bull.* 64: 369–399. <http://dx.doi.org/10.1007/s12225-009-9133-3>
- Goyder, D.J.** 2012. *Tylophora*. Pp. 497–513 in: Beentje, H. (ed.), *Flora of tropical East Africa, Apocynaceae*, part 2. Kew: Royal Botanic Gardens.
- Goyder, D.J. & Liede-Schumann, S.** 2008 (publ. 2009). Notes on *Cynanchum* and *Pentarrhinum* (Apocynaceae: Asclepiadoideae) in tropical Africa. *Kew Bull.* 63: 463–466. <http://dx.doi.org/10.1007/s12225-008-9048-4>
- Goyder, D.J., Nicholas, A. & Liede-Schumann, S.** 2007. Phylogenetic relationships in subtribe Asclepiadinae (Apocynaceae-Asclepiadoideae). *Ann. Missouri Bot. Gard.* 94: 423–434. [http://dx.doi.org/10.3417/0026-6493\(2007\)94\[423:PRISAA\]2.0.CO;2](http://dx.doi.org/10.3417/0026-6493(2007)94[423:PRISAA]2.0.CO;2)
- Grimm, G.W., Renner, S.S., Stamatakis, A. & Hemleben, V.** 2006. A nuclear ribosomal DNA phylogeny of *Acer* inferred with maximum likelihood, splits graphs, and motif analyses of 606 sequences. *Evol. Bioinform. Online* 2: 279–294.
- Hechem, V., Calviño, C.I. & Ezcurrea, C.** 2011. Molecular phylogeny of *Diplolepis* (Apocynaceae-Asclepiadoideae) and allied genera, and taxonomic implications. *Taxon* 60: 638–648.
- Hemsley, W.B.** 1889. 87. Asclepiadaceae. Pp. 100–117 in: Forbes, F.B. & Hemsley, W.B., An enumeration of all the plants known from China proper, Formosa, Hainan, Corea, the Luchu Archipelago, and the Island of Honkong, together with their distribution and synonymy, part VII. *J. Linn. Soc., Bot.* 26: 1–120.
- Hepper, F.N. & Friis, I.** 1994. *The plants of Pehr Forsskål's Flora Aegyptiaco-Arabica*. Kew: Royal Botanical Gardens; Copenhagen: Botanical Museum.
- Holland, B. & Moulton, V.** 2003. Consensus networks: A method for visualising incompatibilities in collections of trees. Pp. 165–176 in: Benson, G. & Page, R. (eds.), *Algorithms in bioinformatics: Third International Workshop, WABI 2003, Budapest, Hungary, September 15–20, 2003; Proceedings*. Berlin, Heidelberg, Stuttgart: Springer. http://dx.doi.org/10.1007/978-3-540-39763-2_13
- Hooker, J.D.** 1883 (“1883–1885”). *Adelostemma gracillimum*, Hook. f. P. 22 & pl. 1427 in: *Hooker's Icones plantarum*, vol. 15 (ser. 3, vol. 5). London: Williams and Norgate. <http://dx.doi.org/10.5962/bhl.title.16059>
- Hörandl, E.** 2006. Paraphyletic versus monophyletic taxa – Evolutionary versus cladistic classifications. *Taxon* 55: 564–570. <http://dx.doi.org/10.2307/25065631>
- Hörandl, E.** 2007. Neglecting evolution is bad taxonomy. *Taxon* 56: 1–5.
- Huelsenbeck, J.P. & Rannala, B.** 2004. Frequentist properties of Bayesian posterior probabilities of phylogenetic trees under simple and complex substitution models. *Syst. Biol.* 53: 904–913. <http://dx.doi.org/10.1080/10635150490522629>
- Humphreys, A.M. & Linder, H.P.** 2009. Concept versus data in delimitation of plant genera. *Taxon* 58: 1054–1074.
- Huson, D.H. & Bryant, D.** 2006. Application of phylogenetic networks in evolutionary studies. *Molec. Biol. Evol.* 23: 254–267. <http://dx.doi.org/10.1093/molbev/msj030>
- Kunze, H.** 1995. Floral morphology of some Gonolobeae (Asclepiadaceae). *Bot. Jahrb. Syst.* 117: 211–238.
- Li, P.T., Gilbert, M.G. & Stevens, W.D.** 1995. Asclepiadaceae. Pp. 189–270 in: Wu, C.Y. & Raven, P.H. (eds.), *Flora of China*, vol. 16. Beijing: Science Press; St. Louis: Missouri Botanical Garden Press.
- Liede, S.** 1993. A taxonomic revision of the genus *Cynanchum* in southern Africa. *Bot. Jahrb. Syst.* 114: 503–550.
- Liede, S.** 1996a. *Cynanchum – Rhodostegiella – Vincetoxicum – Tylophora*: New considerations on an old problem. *Taxon* 45: 193–211. <http://dx.doi.org/10.2307/1224660>
- Liede, S.** 1996b. A revision of *Cynanchum* (Asclepiadaceae) in Africa. *Ann. Missouri Bot. Gard.* 83: 283–345. <http://dx.doi.org/10.2307/2399864>
- Liede, S.** 1996c. On the position of the genus *Pergularia* (Asclepiadaceae). Pp. 481–488 in: Van der Maesen, L.J.G., Van der Burgt, K.M. & Van Medenbach de Roy, J.M. (eds.), *The biodiversity of African plants*. Dordrecht, etc.: Kluwer Academic Press.
- Liede, S.** 1997a. American *Cynanchum* (Asclepiadaceae) – A preliminary infrageneric classification. *Novon* 7: 172–181. <http://dx.doi.org/10.2307/3392191>
- Liede, S.** 1997b. Phylogenetic study of the African members of *Cynanchum* (Apocynaceae – Asclepiadoideae). *Syst. Bot.* 22: 347–372. <http://dx.doi.org/10.2307/2419462>
- Liede, S.** 2001. Molecular considerations on the subtribe Astephaninae Endl. ex Meisn. (Apocynaceae – Asclepiadoideae). *Ann. Missouri Bot. Gard.* 88: 657–668. <http://dx.doi.org/10.2307/3298638>
- Liede, S. & Kunze, H.** 1993. A descriptive system for corona analysis in Asclepiadaceae and Periplocaceae. *Pl. Syst. Evol.* 185: 275–284. <http://dx.doi.org/10.1007/BF00937663>
- Liede, S. & Kunze, H.** 2002. *Cynanchum* and the Cynanchinae (Apocynaceae – Asclepiadoideae) – A molecular, anatomical and latex triterpenoid study. *Organisms Diversity Evol.* 2: 239–269. <http://dx.doi.org/10.1078/1439-6092-00045>
- Liede, S. & Meve, U.** 2001. New combinations and new names in Malagasy Asclepiadoideae (Apocynaceae). *Adansonia*, sér. 3, 23: 347–351.
- Liede, S. & Meve, U.** 2004. Revision of *Metastelma* (Apocynaceae-Asclepiadoideae) in southwestern North America and Central America. *Ann. Missouri Bot. Gard.* 91: 31–86.

- Liede, S. & Nicholas, A. 1992. A revision of the genus *Pentarrhinum* E. Meyer (Asclepiadaceae). *Kew Bull.* 47: 475–490. <http://dx.doi.org/10.2307/4110574>
- Liede, S. & Täuber, A. 2002. Circumscription of the genus *Cynanchum* (Apocynaceae – Asclepiadoideae). *Syst. Bot.* 27: 789–801. <http://dx.doi.org/10.1046/j.1095-8339.2002.00048.x>
- Liede, S., Meve, U. & Täuber, A. 2002. What is the subtribe Glossonematinae (Apocynaceae – Asclepiadoideae)? – A phylogenetic study based on cpDNA spacer. *Bot. J. Linn. Soc.* 139: 145–158. <http://dx.doi.org/10.1046/j.1095-8339.2002.00048.x>
- Liede-Schumann, S. & Meve, U. 2005. Notes on succulent *Cynanchum* species in East Africa. *Novon* 15: 320–323.
- Liede-Schumann, S. & Meve, U. 2006. *Calciophila*, a new genus in African Asclepiadeae (Apocynaceae, Asclepiadoideae), and taxonomic rectifications in *Cynanchum*. *Novon* 16: 368–373. [http://dx.doi.org/10.3417/1055-3177\(2006\)16\[368:CANGIA\]2.0.CO;2](http://dx.doi.org/10.3417/1055-3177(2006)16[368:CANGIA]2.0.CO;2)
- Liede-Schumann, S. & Meve, U. 2013. The Orthosiinae revisited (Apocynaceae, Asclepiadoideae, Asclepiadeae). *Ann. Missouri Bot. Gard.* 99: 44–81. <http://dx.doi.org/10.3417/2010130>
- Liede-Schumann, S., Rapini, A., Goyder, D.J. & Chase, M.W. 2005. Phylogenetics of the New World subtribes of Asclepiadeae (Apocynaceae-Asclepiadoideae): Metastelmatinae, Oxypetalinae, and Gonolobinae. *Syst. Bot.* 30: 184–200. <http://dx.doi.org/10.1600/0363644053661832>
- Liede-Schumann, S., Kong, H.-H., Meve, U. & Thiv, M. 2012. *Vincetoxicum* and *Tylophora* (Apocynaceae: Asclepiadoideae: Asclepiadeae) — two sides of the same medal: Independent shifts from tropical to temperate habitats. *Taxon* 61: 803–825.
- Liede-Schumann, S., Nikolaus, M., Silva, U.C.S.S., Rapini, A., Mangelsdorff, R.D. & Meve, U. 2014. Phylogenetics and biogeography of the genus *Metastelma* (Apocynaceae-Asclepiadoideae-Asclepiadeae: Metastelmatinae). *Syst. Bot.* 39: 594–612. <http://dx.doi.org/10.1600/036364414X680708>
- Liede-Schumann, S., Khanum, R., Mumtaz, A.S., Gherghel, I. & Pahlevani, A. 2016. Going west—A subtropical lineage (*Vincetoxicum*, Apocynaceae: Asclepiadoideae) expanding into Europe. *Molec. Phylog. Evol.* 94: 436–446. <http://dx.doi.org/10.1016/j.ympev.2015.09.021>
- Mabberley, D.J. 1980a. A re-examination of the ‘Indian Catalogues’. Pp. 80–110 in: Manilal, K.S. (ed.), *Botany and history of Hortus Malabaricus*. Rotterdam: Balkema.
- Mabberley, D.J. 1980b. Generic names published in Salisbury’s reviews of Robert Brown’s works. *Taxon* 29: 597–606. <http://dx.doi.org/10.2307/1220331>
- Maddison, W.P. & Maddison, D.R. 2015. Mesquite: A modular system for evolutionary analysis, version 3.03. <http://mesquiteproject.org>
- McNeill, J., Barrie, F.R., Buck, W.R., Demoulin, V., Greuter, W., Hawksworth, D.L., Herendeen, P.S., Knapp, S., Marhold, K., Prado, J., Prud’homme van Reine, W.F., Smith, G.F., Wiersema, J.H. & Turland, N. (eds.) 2012. *International Code of Nomenclature for algae, fungi, and plants (Melbourne Code): Adopted by the Eighteenth International Botanical Congress Melbourne, Australia, July 2011*. Regnum Vegetabile 154. Königstein: Koeltz Scientific Books. <http://www.iapt-taxon.org/nomen/main.php>
- Meve, U. 1999. *Tylophora anomala* (Asclepiadaceae) – A cytologically anomalous species. *Syst. & Geogr. Pl.* 68: 255–263. <http://dx.doi.org/10.2307/3668606>
- Meve, U. & Liede, S. 2001. Reconsideration of the status of *Lavrania*, *Larryleachia* and *Notechidnopsis* (Asclepiadoideae-Ceropegieae). *S. African J. Bot.* 67: 161–168. [http://dx.doi.org/10.1016/S0254-6299\(15\)31115-7](http://dx.doi.org/10.1016/S0254-6299(15)31115-7)
- Meve, U. & Liede, S. 2002. Floristic exchange between mainland Africa and Madagascar: A case study of Apocynaceae-Asclepiadoideae. *J. Biogeogr.* 29: 865–873. <http://dx.doi.org/10.1046/j.1365-2699.2002.00729.x>
- Meve, U. & Liede-Schumann, S. 2012. Taxonomic dissolution of *Sarcostemma* R. Br. (Apocynaceae-Asclepiadoideae). *Kew Bull.* 67: 751–759. <http://dx.doi.org/10.1007/s12225-012-9384-2>
- Morillo, G. 1997. Revisión preliminar de *Metalepis* Grieseb. (Asclepiadaceae). *Pittieria* 26: 65–99.
- Pattengale, N.D., Masoud, A., Bininda-Emonds, O.R.P., Moret, B.M.E. & Stamatakis, A. 2009. How many bootstrap replicates are necessary? Pp. 184–200 in: Batzoglou, S. (ed.), *RECOMB 2009*. Berlin, Heidelberg: Springer. http://dx.doi.org/10.1007/978-3-642-02008-7_13
- Pirie, M.D. 2015. Phylogenies from concatenated data: Is the end nigh? *Taxon* 64: 421–423. <http://dx.doi.org/10.12705/643.1>
- Rapini, A., Chase, M.W., Goyder, D.J. & Griffiths, J. 2003. Asclepiadeae classification: Evaluating the phylogenetic relationships of New World Asclepiadoideae (Apocynaceae). *Taxon* 52: 33–50. <http://dx.doi.org/10.2307/3647300>
- Ronquist, F., Teslenko, M., Van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. 2012. MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Syst. Biol.* 61: 539–542. <http://dx.doi.org/10.1093/sysbio/sys029>
- Sang, T., Crawford, D.J. & Stuessy, T.F. 1997. Chloroplast DNA phylogeny, reticulate evolution, and biogeography of *Paeonia* (Paeoniaceae). *Amer. J. Bot.* 84: 1120–1136. <http://dx.doi.org/10.2307/2446155>
- Schlechter, R. 1895. Asclepiadaceae Elliotianae. *J. Bot.* 38: 300–307.
- Schlechter, R. 1896. Asclepiadaceae. Pp. 445–451 in: Schinz, H. (ed.), *Beiträge zur Kenntnis der afrikanischen Flora (Neue Folge) 4*. *Bull. Herb. Boissier* 4: 409–475.
- Schlechter, R. 1916. Neue Asclepiadaceen von Sumatra und Celebes. *Beih. Bot. Centralbl.* 34: 1–16.
- Schumann, K. 1895. Asclepiadaceae. Pp. 189–305 in: Engler, A. & Prantl, K. (eds.), *Die natürlichen Pflanzenfamilien*, vol. IV(1). Leipzig: Engelmann.
- Settesoldi, L., Tardelli, M. & Raffaelli, M. 2011. *The types of the Tropical Herbarium of Florence*, vol. 3, *Dicotyledons (Buxaceae to Compositae)*. Florence: Centro Studi Erbario Tropicale.
- Stamatakis, A. 2006. Phylogenetic models of rate heterogeneity: A high performance computing perspective. In: *Proceedings 20th International Parallel and Distributed Processing Symposium: April 25–29, 2006, Rhodes Island, Greece; High Performance Computational Biology Workshop*. Piscataway: IEEE. [CD-ROM] <http://dx.doi.org/10.1109/IPDPS.2006.1639535>
- Stamatakis, A. 2014. RAXML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30: 1312–1313. <http://dx.doi.org/10.1093/bioinformatics/btu033>
- Stevens, W.D. 2000. New and interesting milkweeds (Apocynaceae, Asclepiadoideae). *Novon* 10: 243–256. <http://dx.doi.org/10.2307/3393108>
- Straub, S.C.K., Fishbein, M., Livshultz, T., Foster, Z., Parks, M., Weitemier, K., Cronn, R.C. & Liston, A. 2011. Building a model: Developing genomic resources for common milkweed (*Asclepias syriaca*) with low coverage genome sequencing. *B. M. C. Genomics* 12(1): 211. <http://dx.doi.org/10.1186/1471-2164-12-211>
- Sundell, E. 1981. The New World species of *Cynanchum* subgenus *Mellichampia* (Asclepiadaceae). *Evol. Monogr.* 5: 1–62.
- Surveswaran, S., Sun, M., Grimm, G.W. & Liede-Schumann, S. 2014. On the systematic position of some Asian enigmatic genera of Asclepiadoideae (Apocynaceae). *Bot. J. Linn. Soc.* 174: 601–619. <http://dx.doi.org/10.1111/boj.12156>
- Taberlet, P., Gielly, L., Pautou, G. & Bouvet, J. 1991. Universal primers for amplification of three non-coding regions of chloroplast DNA. *Pl. Molec. Biol.* 17: 1105–1109. <http://dx.doi.org/10.1007/BF00037152>
- The Plant List 2015. Version 1.1. Published on the Internet; <http://www.theplantlist.org/> (last accessed 1 Nov 2015).
- Wanntorp, L. & Förster, P.I. 2007. Phylogenetic relationships between

Hoya and the monotypic genera *Madangia*, *Absolmsia*, and *Micholitzia* (Apocynaceae, Marsdeniaceae): Insights from flower morphology. *Ann. Missouri Bot. Gard.* 94: 36–55. [http://dx.doi.org/10.3417/0026-6493\(2007\)94\[36:PRBHT\]2.0.CO;2](http://dx.doi.org/10.3417/0026-6493(2007)94[36:PRBHT]2.0.CO;2)

- Wanntorp, L., Kocyan, A., Van Donkelaar, R. & Renner, S.S.** 2006. Towards a monophyletic *Hoya* (Marsdeniaceae, Apocynaceae): Inferences from the chloroplast *trnL* region and the *rbcL-atpB* spacer. *Syst. Bot.* 31: 586–586. <http://dx.doi.org/10.1600/036364406778388593>
- Wheeler, T.J. & Kececioglu, J.D.** 2007. Multiple alignments by aligning alignments. *Bioinformatics* 23: i559–i568. <http://dx.doi.org/10.1093/bioinformatics/btm226>

- Wight, R.** 1834. *Contributions to the Botany of India*. London: Parbury, Allen.
- Wight, R.** 1838. XII. On a new genus of Asclepiadeae. *Madras J. Lit. Sci.* 7: 142–144.
- Woodson, R.E.** 1941. The North American Asclepiadaceae. *Ann. Missouri Bot. Gard.* 28: 193–244. <http://dx.doi.org/10.2307/2394270>
- Yamashiro, T., Fukuda, T., Yokoyama, J. & Maki, M.** 2004. Molecular phylogeny of *Vincetoxicum* (Apocynaceae – Asclepiadoideae) based on the nucleotide sequences of cpDNA and nrDNA. *Molec. Phylog. Evol.* 31: 689–700. <http://dx.doi.org/10.1016/j.ympev.2003.08.016>

Appendix 1. Taxa, voucher information, and GenBank accession numbers for specimens of *Cynanchinae* and outgroup species used in this study.

Species, origin, voucher, *trnT-L* intergenic spacer, *trnLF* region, *trnH-psbA* intergenic spacer, *rps16* intron, nrITS, 5'-ETS, *At2g06530a*, *At2g34620b*. [] indicate separate sequences for *trnL* intron and *trnL-F* intergenic spacer. An asterisk (*) indicates newly generated sequences.

Calciphila galgalensis Liede & Meve, Somalia: Bari, *Thulin & Warfa 6205* (K, UPS), AJ492337, [AJ492338, AJ492339], HE802681, LN896882*, AJ492756, LN896997*, LN897097*, LN897202*; Somalia: Bari, *Thulin & al. 9433* (UPS), AJ492340, [AJ492341, AJ492342], LN896766*, LN896883*, –, LN896998*, LN897098*, LN897203*; *Calciphila gillettii* Liede & Meve, Somalia: Bari, *Thulin, Dahir & Osman 10122* (UPS), AM229661, [AM229662, AM229663], HE802682, HG530607, AM229664, LN896999*, LN897099*, LN897204*; *Calotropis procera* (Aiton) W.T.Aiton, Gambia, *Huber s.n.* (UBT), AJ428795, [AJ428796, AJ428797], LN896767*, HG530608, AM396900, LN897000*, LN897100*, LN897205*; *Cynanchum abyssinicum* Decne., Tanzania: Arusha, *Liede & Meve 3373* (UBT), AJ428579, [AJ428580, AJ428581], LN896768*, LN896886*, AJ492734, –, LN897103*, LN897208*; *Cynanchum acutum* L., Pakistan: Gilgit-Baltistan, *Khanum & Shabir 36516* (PMNH), LN896697*, LN896736*, LN896770*, –, LN896958*, LN897002*, –, –, Portugal: s.loc., BG Lisboa s.n. (UBT), AJ428582, [AJ428583, AJ428584], LN896769*, AJ699326, AJ492735, LN897001*, LN897104*, LN897209*; *Cynanchum adaliniae* K.Schum. subsp. *adaliniae*, Cameroon: Sud (Mt. Cameroon), *Meve 902* (K, SCA), AJ428585, [AJ428586, AJ428587], LN896771*, LN896887*, AJ492736, LN897003*, LN897105*, LN897210*; *Cynanchum africanum* (L.) Hoffmanns., South Africa: Western Cape, *Liede 2550* (MO), AJ428588, [AJ428589, AJ428590], LN896772*, –, AJ492737, LN897004*, LN897106*, LN897211*; *Cynanchum altiscandens* K.Schum., Kenya: Kiambu, *Liede & Newton 2873* (UBT), AJ428591, [AJ428592, AJ428593], LN896773*, LN896888*, AJ492738, LN897005*, LN897107*, LN897212*; *Cynanchum ampanihense* Jum. & H.Perrier, Madagascar: Toliara, *Liede & al. 2817a* (MSUN), AJ428594, [AJ428595, AJ428596], LN896774*, –, AJ492739, LN897006*, LN897108*, LN897213*; *Cynanchum analamazoitrense* Choux, Madagascar: Antsiranana, *Liede-Schumann 3703b* (UBT), LN896698*, LN896737*, LN896775*, LN896889*, LN896959*, LN897007*, LN897109*, –, *Cynanchum angavokeliense* Choux, Madagascar: s.loc., *Specks s.n.* (UBT), AJ428597, [AJ428598, AJ428599], LN896776*, LN896890*, AJ492733, LN897008*, LN897110*, LN897214*; *Cynanchum antsiranense* (Meve & Liede) Liede & Meve, Madagascar: Antsiranana, *Mangelsdorff RMM 47* (FR), LN896699*, LN896738*, LN896777*, LN896891*, LN896960*, LN897009*, LN897111*, LN897215*; *Cynanchum appendiculatopsis* Liede, Madagascar: s.loc., *Février s.n.* (UBT), AJ492322, [AJ492323, AJ492324], LN896778*, –, AJ492732, LN897010*, LN897112*, LN897216*; *Cynanchum arabicum* (Bruyns & P.I.Forst.) Meve & Liede, Yemen: Sana'a, *Radcliffe-Smith & Henchie 4624* (K, in cult. UBT), LN896700*, LN896739*, LN896779*, LN896892*, LN896961*, LN897011*, LN897113*, LN897217*; *Cynanchum arenarium* Jum. & H.Perrier, Madagascar: Toliara, *Liede & al. 2686* (UBT), AJ428600, [AJ428601, AJ428602], LN896780*, LN896893*, AJ492740, –, –, *Cynanchum auriculatum* Buch.-Ham. ex Wight, Pakistan: Punjab, *Sultan s.n.* (UBT), LN896701*, [LN897297*, LN897300*], LN896781*, LN896894*, LN896962*, LN897012*, LN897114*, LN897218*; *Cynanchum blandum* (Decne.) Sundell, Ecuador: Napo, *Burnham 1668* (MO), AJ428603, [AJ428604, AJ428605], LN896782*, LN896895*, AJ492742, LN897013*, LN897115*, –, *Cynanchum blyttoides* Liede, Somalia: Bari, *Thulin & al. 10681* (UPS), LN896702*, LN896740*, LN896783*, –, LN896963*, LN897014*, –, LN897219*; *Cynanchum boudieri* H.Lév. & Vaniot, Japan: Kagoshima Pref., *Tateishi & Yamashiro 45546* (URO), –, [AB109166, AB109941], AB109134, –, AB109972, AB110035, –, –, *Cynanchum callialatum* Buch.-Ham. ex Wight, Mauritius, *Huber s.n.* (UBT), LN896703*, HG530578, LN896784*, HG530609, LN896964*, LN897015*, LN897116*, LN897220*; *Cynanchum chinense* R.Br., China: Neimenggu, *Wu 98-29* (MO), LN896704*, LN896741*, LN896785*, LN896896*, LN896965*, LN897016*, LN897117*, LN897221*; *Cynanchum chouxii* Liede & Meve, Madagascar: Fianarantsoa, *Kotzafy 442* (MO, UBT), AJ492325, [AJ492326, AJ492327], LN896786*, –, –, –, LN897222*; *Cynanchum comorense* Choux, Comores: Mayotte, *Signal 1104* (P), AJ428612, [AJ428613, AJ428614], LN896787*, –, AJ492744, –, –, *Cynanchum compactum* Choux subsp. *compactum*, Madagascar: s.loc., *Barad s.n.* (UBT), AJ290842, [AJ290843, AJ290844], LN896788*, –, AJ492745, LN897017*, LN897118*, LN897223*; *Cynanchum* aff. *compactum* Choux, Madagascar, *Webb s.n.* (UBT), LN896721*, LN896757*, LN896858*, LN896940*, LN896983*, LN897080*, LN897180*, LN897281*; *Cynanchum corymbosum* Wight, China: Guangdong, *Chen Binghui 6813* (IBSC), LN896705*, LN896742*, LN896789*, LN896897*, LN896966*, LN897018*, –, –, *Cynanchum crassiantherae* Liede, Somalia: Balad, *Hedberg & Warfa 90* (UPS), AJ428615, [AJ428616, AJ428617], –, –, AJ492746, –, –, Somalia: Shabeellaha Dhexe, *Thulin & al. 7231* (UPS), –, LN901559*, LN896790*, –, –, LN897019*, LN897119*, LN897224*; *Cynanchum crassipedicellatum* Meve & Liede, Madagascar: Toliara, *Hardy 2852* (K, MSUN), AJ492328, [AJ492329, AJ492330], LN896791*, LN896898*, AJ492747, LN897020*, LN897120*, LN897225*; *Cynanchum cucullatum* N.E.Br., Madagascar: Antananarivo, *Liede & al. 2868* (MO, MSUN, P), AJ428618, [AJ428619, AJ428620], LN896792*, LN896899*, AJ492748, LN897021*, LN897121*, LN897226*; *Cynanchum dalhousiae* Wight, Pakistan: Punjab, *Khanum 36143* (PMNH), LN896706*, LN896743*, LN896793*, LN896900*, LN896967*, –, LN897122*, LN897227*; *Cynanchum danguyanum* Choux, Madagascar: Antsiranana, *Allorge 2026* (P), AJ428621, [AJ428622, AJ428623], LN896794*, LN896901*, AJ492749, LN897022*, LN897123*, LN897228*; *Cynanchum descoingsii* Rauh, Madagascar: Toliara, *Descoings 28244* (UBT), AJ428624, [AJ428625, AJ428626], LN896795*, LN896902*, AJ492750, LN897023*, LN897124*, LN897229*; *Cynanchum ellipticum* R.Br., South Africa: Eastern Cape, *Liede 2933* (UBT), AJ290847, [AJ290846, AJ290845], HE802679, AJ699327, AJ320444, LN897024*, LN897125*, LN897230*; *Cynanchum erythranthum* Jum. & H.Perrier, Madagascar: Antsiranana, *Rauh 74816* (HEID), AJ428627, [AJ428628, AJ428629], LN896796*, LN896903*, AJ492751, LN897025*, LN897126*, LN897231*; *Cynanchum falcatum* Hutchinson & E.A.Bruce, Ethiopia: Sidamo, *Friis 3169* (K; MWC 8410), AJ428630, [AJ428631, AJ428632], –, –, AJ492752, –, –, Ethiopia: Ogaden, *Kuchar & Abdurizak 21226* (UPS), AJ492334, [AJ492335, AJ492336], AJ492333], LN896797*, LN896904*, AJ492753, LN897026*, –, –, *Cynanchum floribundum* R.Br., Australia: Northern Territory, *Latz 12579* (MO), AJ428633, [AJ428634, AJ428635], LN896798*, LN896905*, AJ492754, –, LN897127*, LN897232*; *Cynanchum foetidum* Kunth, Mexico: Oaxaca, *Campos 3956* (MO), AJ428636, [AJ428637, AJ428638], –, –, AJ492818, –, –, Mexico: Michoacán, *Fishbein 6937* (OKLA), –, –, LN896799*, LN896906*, LN901557*, LN897027*, LN897128*, LN897233*; *Cynanchum folotsioides* Liede & Meve, Madagascar: Toliara, *Rauh 21847* (MSUN), AJ492334, [AJ492335, AJ492336], LN896800*, –, AJ492755, LN897028*, LN897129*, LN897234*; *Cynanchum formosanum* (Maxim.) Hemsl., Taiwan, *Wang & al. 02687* (L), LN896707*, LN896744*, –, –, LN896968*, LN897029*, –, –, *Cynanchum gerrardii* (Harvey) Liede, Kenya: Northern Frontier, *Meve 962* (UBT), AJ428645, [AJ428646, AJ428647], LN896801*, –, AJ492757, LN897030*, –, –, Kenya: Makueni Distr., *Newton 6206* (EA), LN896708*, LN896745*, LN896802*, –, LN896969*, LN897031*, LN897130*, –, Madagascar: Toliara, *Liede & al. 2797* (MSUN), AJ428642, [AJ428643, AJ428644], LN896803*, –, AJ492758, LN897032*,

Appendix 1. Continued

LN897131*, LN897235*; *Cynanchum giraldii* Schltr., China: Shaanxi, *Zhu & al.* 2323 (MO), LN896709*, LN896746*, LN896804*, LN896907*, LN896970*, LN897033*, LN897132*, LN897236*; *Cynanchum grandidieri* Liede & Meve, Madagascar: s.loc., BG Munich s.n. (UBT), AJ290854, [AJ290855, AJ290856], LN896805*, LN896908*, AJ492801*, LN897034*, LN897133*, LN897237*; *Cynanchum hardyi* Liede & Meve, Madagascar: Mahajanga, *Mangelsdorff RMM 43* (UBT), AJ492343, [AJ492344, AJ492345], LN896806*, LN896909*, AJ492759, LN897035*, LN897134*, LN897238*; *Cynanchum hastifolium* K.Schum., Ethiopia: Wardheer, *Kuchar & Abdi 21213* (UPS), LN896710*, LN896747*, LN896808*, LN896911*, LN896971*, –, –, LN897239*; Kenya: Northern Frontier, *Liede & Newton 3226* (UBT), AJ428609, [AJ428610, AJ428611], LN896807*, LN896910*, AJ492743, LN897036*, LN897135*, –, –, *Cynanchum implicatum* Jum. & H.Perrier, Madagascar: Antsiranana, *Mangelsdorff RMM 24* (UBT), AJ428648, [AJ428649, AJ428650], LN896809*, –, –, AJ492760, LN897037*, LN897136*, LN897240*; *Cynanchum insigne* (N.E.Br.) Liede & Meve, Madagascar: Antananarivo, *Rauh 68500* (HEID), AJ290908, [AJ290907, AJ290906], LN896810*, –, –, AJ492815, LN897038*, LN897137*, LN897241*; *Cynanchum itremense* Liede, Madagascar: Fianarantsoa, *Phillipson & al.* 3857 (MO), AJ492346, [AJ492347, AJ492348], LN896811*, LN896912*, AJ492761, LN897039*, LN897138*, LN897242*; *Cynanchum juliani-marnieri* Desc., Madagascar: Toliara, *Teissier s.n.* (UBT), AJ492349, [AJ492350, AJ492351], LN896812*, –, –, AJ492762, LN897040*, LN897139*, LN897243*; *Cynanchum laeve* (Michx.) Pers., U.S.A.: Missouri, *Liede s.n.* (UBT), AJ428651, [AJ428652, AJ428653], LN896813*, HG530610, AJ492763, LN897041*, LN897140*, LN897244*; *Cynanchum leucanthum* subsp. *elongatum* Liede, Madagascar: Antsiranana, *Mangelsdorff RMM 420* (UBT), AJ428654, [AJ428655, AJ428656], LN896815*, LN896913*, AJ492764, LN897043*, LN897142*, LN897246*; *Cynanchum ligulatum* (Benth.) Woodson, Mexico: Sonora, *Fishbein 7461* (OKLA), LN901558*, LN901560*, LN896816*, LN896914*, LN896973*, LN897044*, LN897143*, LN897247*; *Cynanchum lineare* N.E.Br. subsp. *lineare*, Madagascar: Fianarantsoa, *Rössli & Hoffmann 198* (UBT), AJ428660, [AJ428661, AJ428662], LN896817*, –, –, AJ492765, LN897045*, LN897144*, –, –, *Cynanchum longipes* N.E.Br., Ghana: Brong-Ahafo Region, *Jongkind & Schmidt 1739* (MO), AJ428663, [AJ428664, AJ428665], LN896818*, LN896915*, AJ492766, –, –, LN897145*, LN897248*; *Cynanchum lysimachioides* Tsiang & P.T.Li, China: Sichuan, *Boufford & al.* 28499 (MO), LN896711*, LN896748*, LN896819*, LN896916*, LN896974*, LN897046*, –, –, *Cynanchum macranthum* Jum. & H.Perrier, Madagascar: Toliara, *Liede & al.* 2808 (UBT), AJ492372, [AJ492373, AJ492374], LN896820*, LN896917*, AJ492804, LN897047*, LN897146*, LN897249*; *Cynanchum madagascariense* K.Schum., Madagascar: Toliara, *Liede & al.* 2756 (UBT), AJ428666, [AJ428667, AJ428668], LN896821*, LN896918*, AJ492767, LN897048*, LN897147*, LN897250*; *Cynanchum mahafalense* Jum. & H.Perrier, Madagascar: Toliara, *Liede & al.* 2831 (UBT), AJ428669, [AJ428670, AJ428671], LN896822*, –, –, AJ492768, LN897049*, LN897148*, LN897251*; *Cynanchum mariense* (Meve & Liede) Liede & Meve, Madagascar: Toliara, *Liede & al.* 2825 (K, MSUN, UBT), AJ428768, [AJ428769, AJ428770], LN896823*, LN896919*, AJ492805, LN897050*, LN897149*, LN897252*; *Cynanchum marnierianum* Rauh, Madagascar: Toliara, *Rauh s.n.* (MSUN), AJ492352, [AJ492353, AJ492354], LN896824*, –, –, AJ492769, LN897051*, LN897150*, LN897253*; *Cynanchum maximoviczii* Pobed., Japan: Miyagi, *Yamashiro & Yamashiro 7578* (TUS), –, –, [AB109910, AB109942], AB109135, –, –, AB109973, AB110036, –, –, *Cynanchum membranaceum* (Liede & Meve) Liede & Meve, Madagascar: Toliara, *Liede & al.* 2765 (ULM), LN896712*, LN896749*, LN896825*, LN896920*, LN896975*, LN897052*, LN897151*, LN897254*; *Cynanchum messeri* (Buchenau) Jum. & H.Perrier, Madagascar: Toliara, *Liede & al.* 2721 (MO, P, UBT), AJ428672, [AJ428673, AJ428674], LN896826*, –, –, AJ492770, LN897053*, LN897152*, LN897255*; *Cynanchum mevei* Liede, Madagascar: Toliara, *Teissier 215* (UBT), AJ428675, [AJ428676, AJ428677], LN896827*, –, –, AJ492771, LN897054*, LN897153*, LN897256*; *Cynanchum meyeri* Schltr., Namibia, *Van Wyk 9030* (PRE), AJ428678, [AJ428679, AJ428680], –, –, AJ492772, –, –, *Cynanchum montevidense* Spreng., Argentina: Salta, *Liede & Conrad 3100* (ULM), AJ290848, [AJ290849, AJ290850], LN896828*, AJ699328, AJ492773, LN897055*, LN897154*, –, –, *Cynanchum* aff. *montevidense* Spreng., Brazil: Mato Grosso do Sul, *Farinacchio & Felismino 916* (SPF), LN896713*, LN896750*, LN896829*, LN896921*, LN896976*, LN897056*, LN897155*, LN897257*; *Cynanchum moramangense* Choux, Madagascar: Toamasina, *Rakotomalaza & al.* 1202 (MO), AJ492355, [AJ492356, AJ492357], LN896830*, LN896922*, AJ492774, LN897057*, LN897156*, LN897258*; *Cynanchum mulanjense* (Liede & Meve) Liede & Meve, Malawi, *Liede 2902* (UBT), LN896714*, LN896751*, LN896831*, LN896923*, LN896977*, –, –, LN897157*, LN897259*; *Cynanchum natalitium* Schltr., South Africa: s.loc., *Nicholas 2583* (NH), AJ428687, [AJ428688, AJ428689], –, –, AJ492775, –, –, *Cynanchum obovatum* Choux, Madagascar: Antsiranana, *Mangelsdorff M14* (UBT), AJ428801, [AJ428802, AJ428803], LN896832*, HG530611, AJ492776, LN897058*, LN897158*, LN897260*; *Cynanchum obtusifolium* L.f., South Africa: Eastern Cape, *Liede 2925* (UBT), AJ428690, [AJ428691, AJ428692], LN896833*, LN896924*, AJ492777, LN897059*, LN897159*, LN897261*; *Cynanchum officinale* (Hemsl.) Tsiang & H.D.Zhang, China: Anhui, *Liu & al.* 450185 (MO), LN896715*, LN896752*, LN896834*, LN896925*, LN896978*, LN897060*, –, –, *Cynanchum orangeanum* N.E.Br., Botswana: Kgalagadi, *Cole 347* (PRE), AJ492358, [AJ492359, AJ492360], LN896835*, –, –, AJ492778, –, –, South Africa: Northern Cape, *Van Rooyen 4537* (PRE), AJ428693, [AJ428694, AJ428695], LN896836*, LN896926*, AJ492779, –, –, LN897160*, LN897262*; *Cynanchum ovalifolium* Wight, Philippines: Zamboanga, *Liede 3297* (ULM), AJ428696, [AJ428697, AJ428698], HE802680, LN896927*, AJ492780, LN897061*, LN897161*, LN897263*; *Cynanchum pachycladum* Choux, Madagascar: Toliara, *Liede & al.* 2741 (MO, P, UBT), AJ428699, [AJ428700, AJ428701], LN896837*, LN896928*, AJ492781, LN897062*, LN897162*, LN897264*; *Cynanchum papillatum* Choux, Madagascar: Fianarantsoa, *Liede & al.* 2862 (MSUN, UBT), AJ428702, [AJ428703, AJ428704], LN896838*, –, –, AJ492782, LN897063*, LN897163*, LN897265*; *Cynanchum pearsonianum* Meve & Liede, South Africa: Northern Cape, *Liede & Meve 582* (K, MSUN), AJ290909, [AJ290910, AJ290911], LN896839*, LN896929*, AJ492816, –, –, LN897164*, LN897266*; *Cynanchum perrieri* Choux, Madagascar: s.loc., BG Berlin 027-03-74-80 (B), AJ428705, [AJ428706, AJ428707], LN896840*, –, –, AJ492783, LN897064*, LN897165*, LN897267*; *Cynanchum petrense* Hemsl. & Lace, Pakistan: Quetta, *Akhter 97377* (RAW), LN896716*, LN896753*, LN896841*, –, –, LN897065*, –, –, LN897268*; *Cynanchum philipsonianum* Liede & Meve, Madagascar: Antsiranana, *Mangelsdorff M25* (UBT), AJ428708, [AJ428709, AJ428710], LN896842*, LN896930*, AJ492784, LN897066*, LN897166*, LN897269*; *Cynanchum physocarpum* Schltr., Philippines: Mindoro, *Knauer s.n.* (UBT), LN896717*, LN896754*, LN896843*, LN896931*, LN896979*, LN897067*, LN897167*, LN897270*; *Cynanchum polyanthum* K.Schum., Uganda: Buganda, *Synnott 688* (K; MWC 8413), AJ428711, [AJ428712, AJ428713], –, –, AJ492785, –, –, *Cynanchum praecox* Schltr. ex S.Moore, Tanzania: Ufipa, *Goyder & al.* 3828 (PRE), AJ428714, [AJ428715, AJ428716], –, –, AJ492786, –, –, Tanzania: Rukwa, v. *Blittersdorf s.n.* (UTB), –, –, [LN901561*, LN901561*], LN896844*, LN896932*, –, –, LN897168*, LN897271*; *Cynanchum purpureum* (Pall.) K.Schum., China: Neimenggu, *Yian 96015* (MO), LN896718*, LN896755*, LN896845*, LN896933*, LN896980*, LN897068*, –, –, *Cynanchum pycnoneuroides* Choux, Madagascar: Fianarantsoa, Service Forestier 26466 (P), AJ428717, [AJ428718, AJ428719], LN896846*, –, –, AJ492787, LN897069*, LN897169*, –, –, *Cynanchum racemosum* Jacq. cf., Mexico: Tamaulipas, *Liede & Conrad 2609* (ULM), AJ428720, [AJ428721, AJ428722], –, –, AJ492790, –, –, *Cynanchum radiatum* Jum. & H.Perrier, Madagascar: Toliara, *Liede & al.* 2744 (UBT), AJ492362, [AJ492363], LN896847*, –, –, AJ492788, LN897070*, LN897170*, LN897272*; *Cynanchum rauhianum* Desc., Madagascar: Toliara, *Rössli s.n.* sub *Noltee 2662* (UBT), AJ428723, [AJ428724, AJ428725], LN896848*, LN896934*, AJ492789*, –, –, LN897171*, LN897273*; *Cynanchum repandum* Choux, Madagascar: Antananarivo, *Liede & al.* 2867 (MO, P, UBT), AJ428726, [AJ428727, AJ428728], LN896849*, LN896935*, AJ492791, LN897071*, LN897172*, LN897274*; *Cynanchum rossii* Rauh, Madagascar: Toliara, *Singer 072478* (ZSS), AJ428729, [AJ428730, AJ428731], LN896850*, LN896936*, AJ492792, LN897072*, LN897173*, LN897275*; *Cynanchum roulinioides* (E.Fourn.) Rapini, Bolivia: Chuquisaca, *Wood & al.* 13300 (K, UBT), AJ428732, [AJ428733, AJ428734], LN896851*, AJ704461, AJ492793, LN897073*, LN897174*, LN897276*; *Cynanchum rubricoronae* Liede, Somalia: Hiiraan / Bari, *Kuchar 16793* (K, MWC 8414), AJ428735, [AJ428736, AJ428737], –, –, AJ492794, –, –, Somalia: Bari, *Thulin & al.* 10688 (UPS), –, –, LN901562*, LN896852*, –, –, LN897074*, LN897175*, LN897277*; *Cynanchum rungwense* Bullock, Tanzania: Mbeya, *Mwasumbi 16518* (MO, K, MWC 8415), AJ428738, [AJ428739, AJ428740], –, –, AJ492795, –, –, Tanzania: Rukwa, *Biggood & al.* 2525 (K), –, –, [LN901563*], LN896853*, –, –, LN897075*, LN897176*, –, –, *Cynanchum schistoglossum* Schltr., Mozambique: Sofala, *Goyder & Timberlake 4093* (K), LN896719*, LN896756*, LN896854*, LN896937*, LN896981*, LN897076*, LN897177*, –, –, *Cynanchum sessiliflorum* (Decne.) Liede, Madagascar: Antsiranana, *Mangelsdorff M13* (UBT), AJ428741, [AJ428742, AJ428743], LN896855*, LN896938*, AJ492797, LN897077*, –, –, LN897278*; *Cynanchum sigridiae* Meve & Teissier, Madagascar: Toliara, *Teissier 135* (K, MSUN), AJ492366, [AJ492367, AJ492368], LN896856*, –, –, AJ492798, LN897078*, LN897178*, LN897279*; *Cynanchum sinoracemosum* M.G.Gilbert & P.T.Li, China: Yunnan, *Hemp s.n.* (UBT),

Appendix 1. Continued

LN896720*, LN897299*, LN897302*], LN896857*, LN896939*, LN896982*, LN897079*, LN897179*, LN897280*, *Cynanchum taiwanianum* T.Yamaz., Taiwan, Wang & Lin 02452 (L), LN896722*, LN896758*, LN896859*, LN896941*, LN896984*, LN897081*, LN897181*, LN897282*, *Cynanchum thesioides* K.Schum., China: Neimenggu, Qingru 97-81 (MO), AJ492369, [AJ492370, AJ492371], LN896860*, LN896942*, AJ492799, LN897082*, LN897182*, LN897283*, China: Gansu, Wang & al. 93-414 (MO), AJ428747, [AJ428748, AJ428749], LN896861*, LN896943*, AJ492800, LN897083*, LN897183*, LN897284*, *Cynanchum toliari* Liede & Meve, Madagascar: Toliara, McPherson 14770 (MO), AJ428756, [AJ428757, AJ428758], –, –, AJ492802, –, –, –; *Cynanchum tunicatum* (Retz.) Alston, India: Maharashtra, Kamble 1155 (SUK), LN896723*, HG530579, LN896862*, –, LN896985*, –, LN897184*, –, *Cynanchum verrucosum* (Desc.) Liede & Meve, Madagascar: Toliara, Liede & al. 2826 (MSUN, UBT), AJ290878, [AJ290879, AJ290880], LN896863*, LN896944*, AJ492806, –, LN897185*, LN897285*, *Cynanchum viminalis* subsp. *brunonianum* Liede & Meve, Philippines: Mindoro, Liede 3272 (UBT), LN896724*, LN896759*, LN896864*, LN896945*, LN896986*, –, LN897186*, LN897286*, *Cynanchum viminalis* subsp. *suberosum* Liede & Meve, Zimbabwe: Bulawayo, Albers & al. 540 (MSUN, UBT), AJ290914, [AJ290913, AJ290912], LN896865*, LN896946*, AJ492817, –, LN897187*, LN897287*, *Cynanchum viminalis* subsp. nov., Saudi Arabia, Meve 1441 (UBT), LN896725*, LN896760*, LN896866*, LN896947*, LN896987*, LN897084*, LN897188*, LN897288*, *Cynanchum viminalis* (L.) Bassi subsp. *viminalis*, India: Maharashtra, Hanáček & Řičánek 017 (UBT), LN896726*, HG530580, LN896867*, HG530612, LN896988*, LN897085*, LN897189*, LN897289*, *Cynanchum wallichii* Wight, China: Yunnan, Schäfer 2005-48 (M), LN896727*, LN896761*, LN896868*, LN896948*, LN896989*, LN897086*, –, –, *Cynanchum wilfordii* Maxim., Japan: Miyagi Pref., Yamashiro & Yamashiro 7228 (TUS), –, [AB109911, AB109943], AB109136, –, AB109974, AB110037, –, –, *Glossonema revouilii* Franch., Kenya: Northern Frontier, Liede & Newton 3239 (ULM), AJ428804, [AJ428805, AJ428806], LN896869*, LN896949*, AJ492803, –, –, –; *Glossonema varians* Benth. ex Hook.f., Iran: Hormozszgan, Amini Rad & al. 56685 (IRAN), LN896728*, LN896762*, –, LN896950*, LN896990*, –, LN897190*, LN897290*, *Graphistemma pictum* (Champ. ex Benth.) Benth. & Hook.f. ex Maxim., China: Hongkong, Surveswaran s.n. (SUK), LN896729*, HG530581, LN896870*, HG530614, LN896991*, –, LN897191*, –, *Holostemma annularium* (Roxb.) K.Schum., Bhutan, Grierson & Long 2351 (E), LN896730*, LN896763*, LN896871*, LN896951*, LN896992*, LN897087*, –, –, *Metalepis albiflora* Urban, Ecuador: Napo, Burnham 1611 (MO), AJ428774, [AJ428775, AJ428776], –, –, AJ492808, –, –, –; *Metalepis peraffinis* (Woodson) Morillo, Mexico: Chiapas, Alvarez 6895 (MO), LN896731*, LN896764*, LN896872*, LN896952*, LN896993*, LN897088*, LN897192*, LN897291*, *Metaplexis japonica* Makino, China: s.loc., ex hort. Nanking s.n. (UBT), AJ410196, [AJ410197, AJ410198], LN896873*, LN896953*, AJ492741, LN897089*, LN897193*, –, Japan: s.loc., ex BG Tartu (UBT), AJ428810, [AJ428811, AJ428812], LN896874*, HG530616, AJ492807, LN897090*, LN897194*, LN897292*, *Odontanthera radicans* (Forssk.) D.V.Field, North Yemen: Hodeidah, Müller-Hohenstein & Deil 1967 (UBT), AJ428813, [AJ428814, AJ428815], LN896875*, LN896954*, AJ492809, LN897091*, LN897195*, –, *Pentarrhinum abyssinicum* Decne., Tanzania: Ufipa, Bidgood & al. 2440 (K; MWC 8418), AJ428816, [AJ428817, AJ428818], LN896876*, –, AJ492810, LN897092*, LN897196*, –, *Pentarrhinum gonoloboides* (Schltr.) Liede, Kenya: Naivasha, Liede & Newton 3157 (UBT), AJ428819, [AJ428820, AJ428821], –, –, AJ492811, –, –, –; *Pentarrhinum insipidum* E.Mey., South Africa: Orange Free State, Liede 2940 (UBT), AJ410232, [AJ410233, AJ410234], LN896877*, HG530619, AJ492812, LN897093*, LN897197*, LN897293*, *Pentarrhinum ledermannii* (Schltr.) Goyder & Liede cf., Tanzania: Kilimanjaro, Hemp 4138 (UBT), LN896732*, LN897298*, LN897302*], LN896814*, LN896956*, LN896972*, LN897042*, LN897141*, LN897245*, *Pentarrhinum somaliense* (Schltr.) Liede, Kenya: Northern Frontier, Liede & Newton 3225 (UBT), AJ492375, [AJ492376, AJ492377], LN896878*, LN896955*, AJ492814, LN897094*, LN897198*, LN897294*, Ethiopia: Sidamo, Mesfin & Vollesen 4238 (UPS), AJ428822, [AJ428823, AJ428824], LN896879*, –, AJ492813, LN897095*, LN897199*, LN897295*, *Pentatropis madagascariensis* Decne., Madagascar: Toliara, Liede & Conrad 2749 (UBT), AJ410235, [AJ410236, AJ410237], HE793884, LN896884*, AJ320448, HE793968, LN897101*, LN897206*, *Pentatropis nivalis* (J.F.Gmel.) D.V.Field & J.R.I.Wood, Kenya: Kilifi, Meve 949 (UBT), AJ410238, [AJ410239, AJ410240], HE793885, AJ699329, AJ320449, HE793969, –, –, *Pentatropis* sp., Ethiopia: Ogaden, Kuchar & Abdirizak 20905 (UPS V-195021), LN896696*, LN896735*, LN896765*, LN896885*, LN896957*, LN896996*, –, LN897201*, *Raphistemma pulchellum* (Roxb.) Wall., Thailand: Satun, Middleton & al. 5359 (E), LN896733*, HG530583, LN896880*, HG530620, LN896994*, LN897096*, –, LN897296*, *Schizostephanus alatus* Hochst. ex K.Schum., Kenya: s.loc., Noltee s.n. sub IPPS 8111 (UBT), AJ410247, [AJ410248, AJ410249], HE802678, HF547220, AJ320451, –, LN897102*, LN897207*, *Seshagiria sahyadrica* Ansari & Hemadri, India: Maharashtra, Kamble 2122 (SUK), LN896734*, HG530584, LN896881*, HG530621, LN896995*, –, LN897200*, –.