A molecular phylogenetic assessment of the advanced Asiatic and Malesian didymocarpoid Gesneriaceae with focus on non-monophyletic and monotypic genera.

ORIGINAL ARTICLE

A molecular phylogenetic assessment of the advanced Asiatic and Malesian didymocarpoid Gesneriaceae with focus on non-monophyletic and monotypic genera

Michael Möller · Alan Forrest · Yi-Gang Wei · Anton Weber

Abstract Based on a considerably enlarged sampling, a phylogenetic analysis of the largest group of didymocarpoid Gesneriaceae, the "advanced Asiatic and Malesian genera", was performed, covering all but 3 of the 60 genera presently recognised in this group (20 of these, mostly from China, are monotypic). The results suggest that no fewer than 17 out of the 57 genera examined are poly- (or rarely para-)phyletic. Highly polyphyletic are *Briggsia*, *Chirita*, *Henckelia* and *Raphiocarpus*. Only a dozen of the non-monotypic genera (including the three species-richest genera, *Cyrtandra*, *Aeschynanthus* and *Agalmyla*) are confirmed as monophyletic entities, though some exhibit considerable genetic variation. For eight genera, no statement can be made, as only one (of two or several) species was included in the analysis. For a dozen of the (particularly Chinese) monotypic genera a close relationship (or possible congenerity) with other genera was found. In China, only *Allostigma*, *Cathayanthe*, *Conandron* and *Metapetrocosmea* seem to have no strong affinities to other genera, indicating that they represent phylogenetically isolated lineages or represent remnants of previously larger and earlier diversified groups. The present study forms the foundation for targeted molecular, morphological and phytogeographic studies of the polyphyletic and monotypic genera and particular of clades of genera with interrelations uncovered here for the first time.

Keywords Bayesian inference analysis · ITS · Maximum parsimony · Molecular phylogeny · Monotypic genera · Old World didymocarpoid Gesneriaceae · Taxonomy · *trn*L-F intron-spacer

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Introduction

Recently, a preliminary molecular-phylogenetic analysis of the largest group of Old World Gesneriaceae, the "didymocarpoid Gesneriaceae" (sensu Weber 2004), was presented (Möller et al. 2009). The analysis revealed that traditional tribal classifications of the group (Bentham 1876; Fritsch 1893–94; Burtt 1962; Burtt and Wiehler 1995) do not work and have to be abandoned. In contrast, the study revealed a strong geographic pattern, with the European and African and Madagascan genera forming monophyletic groups. Both are embedded in the Asiatic Gesneriaceae, with a rather small number of genera forming a basal grade ("basal Asiatic genera", mainly confined to the Asiatic mainland) and a large number representing the "advanced Asiatic and Malesian genera". In the latter group all genera with twisted fruits (plus a few containing also straight fruits) fell in a single well-supported clade. Otherwise, little support was obtained for internal tree structures retrieved for the remaining large number of straight-fruited genera. One reason may be that only 46 out of the 78 genera listed by Weber (2004) for the didymocarpoid Gesneriaceae were included in the analysis.

Moreover, the list of genera has changed to some extent: *Jerdonia*, categorised as 'genus with uncertain familial affiliation' in Weber (2004) was found to belong to the didymocarpoids, forming the most basal lineage among this group. Some genera have been newly described [*Paralagarosolen* (Wei 2004), *Wentsaiboea* (Fang and Qin 2004), *Litostigma* (Wei et al. 2010)], while others were sunk into synonymy [*Linnaeopsis* into *Streptocarpus* (Darbyshire 2006), *Micraeschynanthus* into *Aeschynanthus* (Middleton 2007)]. This brings the current genus count in the didymocarpoids to 80, of which 60 can be referred to the "advanced Asiatic and Malesian genera". The late B.L. Burtt thought that there are too many genera described, particularly from China. Indeed, the Chinese Gesneriaceae include as many as 14 out of 20 monotypic genera, and another 10 out of 12 with two to four described species. One of the aims of the present study, which is based on all but three genera of the advanced Asiatic and Malesian genera, is to investigate the relationships of these genera with one or very few species and to search for possibilities of synonymization.

Another important outcome of Möller et al. (2009) was that several medium to large genera, such as *Briggsia*, *Chirita* and *Henckelia*, proved to be polyphyletic, with *Chirita* appearing in at least five clades. This suggests strong deficiencies in the taxonomic delineation at the generic level.

To assess the level of para- and polyphyly and the validity of the many monotypic genera among the advanced Asiatic and Malesian genera, we collected samples of 26 additional genera of this group. Because of the large number of species and complex taxonomic interaction between species of *Chirita* (80–140 species) and *Henckelia* (180 species), these genera will be dealt with in more detail in separate papers. Here we keep samples of these genera to a minimum without compromising the outcome of our analyses. We will show that about one third of the genera are not monophyletic and that a high number of monotypic genera can be related to larger genera (and possibly synonymised). Our results will show that changes in the generic delineations are urgently required.

Materials and methods

Plant material

Plant material for DNA extraction of newly acquired sequences came predominantly from recent field collections (Table 1). Samples included in the study here covered 67 out of the 80 genera presently classified in the Old World didymocarpoid Gesneriaceae (Weber and Skog 2007 onwards; Wei et al. 2010). The large genus *Streptocarpus* was included to represent the eight didymocarpoid African and Madagascan genera here, as the present paper focuses on the advanced Asiatic and Malesian genera. It was shown in earlier work that the African and Madagascan genera form a single natural lineage (Möller and Cronk 2001a, b; Möller et al. 2009).

Of the nine basal Asiatic genera (Weber 2004; Weber and Skog 2007 onwards; Wei et al. 2010), only six were included: *Corallodiscus* and *Jerdonia* were excluded, as their ITS sequences were deemed too difficult to be aligned satisfactorily with the rest of the samples. For *Beccarinda* no reliable *trn*L-F data could be acquired (preliminary data suggest that *Beccarinda* belongs to the basal Asiatic genera, M. Möller, unpublished). The monotypic *Sepikea cylindrocarpa* is likely an abnormally tetrandrous *Cyrtandra* (Burtt 1998) and placed 'tentatively' into the synonymy of *Cyrtandra* (Burtt 2001a). Samples for analysis were unavailable for analysis, however, as were samples for the monotypic *Championia* and *Deinostigma*.

Outgroup choice

Based on recent molecular work, the outgroup taxa were chosen from the basal Asiatic genera (Fig. 3 in Möller et al. 2009) included here; *Boeica* (with *B. multinervia*, *B. ferruginea*), *Leptoboea*, *Platystemma*, *Rhynchotechum* (with *R. discolor*, *R. parviflorum*) and *Tetraphyllum*, the newly described *Litostigma* (with *L. coriaceifolium*, *L. crystallinum*) and the European genera; *Haberlea*, *Jancaea*, *Ramonda* (with *R. myconi*, *R. nathaliae*). Additionally, nine species of the African genus *Streptocarpus* were included to represent the African and Madagascan lineage that resides between the basal and derived Asiatic and Malesian genera (Möller et al. 2009). The trees were rooted on *Tetraphyllum*, the genus on a most basal lineage of didymocarpoid Gesneriaceae that could still be aligned well in the ITS matrix (Möller et al. 2009).

Ingroup taxa

The 169 ingroup samples came from the advanced Asiatic and Malesian group and covered 164 species, 2 varieties and 3 unidentified samples representing 57 genera (Tables 1, 2). Eight genera were included to represent the *Boea* group, an assemblage of genera with predominantly twisted fruits; *Boea* (with *B. hygrometrica*, *B. magellanica*, *B. philippensis*), *Emarhendia*, *Kaisupeea*, *Ornithoboea* (with *O. arachnoidea*, *O. wildeana*), *Paraboea* (with *P. acutifolia*, *P. capitata*, *P. crassifolia*, *P. umbellata*), *Rhabdothamnopsis*, *Spelaeanthus* and *Trisepalum*.

Among the ingroup taxa were 20 monotypic genera, samples of 13 smaller genera (with ≤4 spp.) and of 18 medium sized genera (>4–30 species). Of species-rich

Table 1 Alphabetical list of 191 didymocarpoid Gesneriaceae samples included in the molecular phylogenetic analysis, with voucher number, deposition of vouchers, origin information and GenBank accession numbers

Taxon	Voucher number	Deposited in	Origin	trnL–F	ITS or ITS1/ITS2
Aeschynanthus bracteatus Wall. ex DC.	Y.Z.Wang 991113	PE	China, Yunnan, Xichou county	FJ501501	–
Aeschynanthus bracteatus Wall. ex DC.	R.Cherry 123 [cult. RBGE 19970165]	E	Vietnam; Lao Cai	–	AF349203/AF349284
Aeschynanthus lancilimbus W.T.Wang	Y.Z.Wang S-10868	PE	China, unknown locality	FJ501499	HQ632992
Aeschynanthus longicalyx Ridl.	P.Woods 600 [cult. RBGE 19680624]	E	Peninsula Malaysia, Genting Highlands	HQ632895	FJ501333
Aeschynanthus micranthus C.B.Clarke	M.Moeller MMO 01-79	E, WU	China, Yunnan, Hekou county	FJ501500	–
Aeschynanthus micranthus C.B.Clarke	A.Reid & J. Fernie 004 [cult. RBGE 19951561]	E	China; Yunnan, Xishuangbanna Dai Aut. Pref.	–	AF349218/AF349299
Aeschynanthus roseoflorus Mendum	G.Argent 87/14	E	Indonesia, Seram	HQ632896	HQ632993
Agalmyla biflora (Elmer) Hilliard & B.L.Burtt	RBGE-PNH1998 25435 [cult. RBGE 19980287],	E	Philippines, Palawan, Near summit of Cleopatra Needle	FJ501541	–
Agalmyla biflora (Elmer) Hilliard & B.L.Burtt	RBGE-PNH1998-25517 [cult. RBGE 19980292]	E	Philippines, Palawan, near Thumb Peak	–	FJ501361
Agalmyla bilirana Hilliard & B.L.Burtt	RBGE-PNHE 1999 12	E	Philippines, Leyte Island	HQ632891	HQ632988
Agalmyla clarkei (Elmer) B.L.Burtt	RBGE-PNH1999(P99) 13 [cult. RBGE 19991911]	E	Philippines, Leyte, Leyte Island, Mt. Lobi	FJ501540	–
Agalmyla clarkei (Elmer) B.L.Burtt	RBGE-PNH1997 IS26 [cult. RBGE 19972530A]	E	Philippines, Luzon, Barangay Penicuason	–	FJ501360
Agalmyla glabra (Merr.) Hilliard & B.L.Burtt	RBGE-PNHE 1999 28	E	Philippines, Camiguin Island	HQ632892	HQ632989
Agalmyla paucipilosa Hilliard & B.L.Burtt	Smith & Galloway 261	E	Indonesia, Sulawesi	HQ632893	HQ632990
Agalmyla sojoliana Hilliard & B.L.Burtt	Smith & Galloway 321	E	Indonesia, Sulawesi	HQ632894	HQ632991
Allocheilos guangxiensis H.Q.Wen, Y.G.Wen, Y.G.Wei & S.H.Zhong	Y.G.Wei 06-02	IBK	China, Guangxi, Yongfu county	HQ632897	HQ632994
Allostigma guangxiense W.T.Wang	M.Möller MMO 05-755	E	China, Guangxi, Longzhou county	HQ632880	HQ632977
Ancylostemon aureus (Franch.) B.L.Burtt (= *A. concavus* **Craib**)	M.Möller MMO 01-153	E, WU	China, Yunnan, Binchuan county	FJ501505	FJ501336
Ancylostemon convexus Craib	M.Möller MMO 01-176	E, WU	China, Yunnan, Dali county	FJ501506	FJ501337
Ancylostemon ronganensis K.Y.Pan	M.Möller MMO 06-776	E	China, Guangxi, Rongan county	HQ632927	HQ633023
Anna mollifolia (W.T.Wang) W.T.Wang & K.Y.Pan	M.Möller MMO 01-146	E, WU	China, Guangxi, Napo county	FJ501543	AF055050/AF055051
Anna ophiorrhizoides (Hemsl.) B.L.Burtt & R.Davidson	M.Möller MMO 08-1280	E	China, Sichuan, Emei Shan	HQ632937	HQ633034
Anna submontana Pellegr.	M.Möller MMO 01-85	E, WU	China, Yunnan, Maguan county	FJ501542	FJ501362
Boea hygrometrica (Bunge) R.Br.	Z.J.Gu 01-6184	KUN	China, unknown locality	FJ501476	FJ501319
Boea magellanica Lam.	Lambinon 87/830	L	Papua New Guinea, Morobe Province	FJ501478	FJ501321
Boea philippensis C.B.Clarke	S.Scott 02-142	E	Indonesia, Sulawesi	HQ632862	HQ632953
Boeica multinervia K.Y.Pan	Y.Z.Wang 015	PE	China, Yunnan, Yingjiang	HQ632861	HQ632951
Boeica ferruginea Drake	M.Möller MMO 01-182B ex Zhang Chang Qin 200012	E, WU	China, SE Yunnan	FJ501440	Wei et al. (2010)

Table 1 continued

Taxon	Voucher number	Deposited in	Origin	trnL_F	ITS or ITS1/ITS2
Bournea sinensis Oliv.	M.Möller MMO 08-1329	E	China, Guangdong, Boluo county	HQ632912	HQ633008
Briggsia dongxingensis Chun ex K.Y.Pan	M.Möller MMO 06-875	E	China, Guangxi, Guiping county	HQ632878	HQ632975
Briggsia kurzii (C.B.Clarke) W.E.Evans	M.Möller MMO 08-1249	E	China, Sichuan, Emei Shan	HQ632874	HQ632970
Briggsia longifolia Craib	M.Möller MMO 08-1239	E	China, Yunnan, Jing Dong county	HQ632934	HQ633030
Briggsia longipes (Hemsl. ex Oliv.) Craib	M.Möller MMO 01-122	E, WU	China, Yunnan, Xichou county	FJ501545	AF055052/AF055053
Briggsia mihieri (Franch.) Craib	Y.Z.Wang 11315B	PE	China, Chongqing, Nanchuan county	FJ501544	FJ501363
Briggsia muscicola (Diels) Craib	Kew (1995-2229)	K	Unknown origin	FJ501548	FJ501366
Briggsia rosthornii (Diels) B.L.Burtt	Sino-American Bryological Expedition, no. 398 (US 229325)	US	China, Guizhou, Jiangkou Xian	FJ501547	FJ501365
Briggsia stewardii Chun	M.Möller MMO 06-917	E	China, Guangxi, Sanjiang county	HQ632926	HQ633022
Briggsiopsis delavayi (Franch.) K.Y.Pan	W.Fang 1	IBK	China, Chongqing, Nanchuan county	HQ632879	HQ632976
Calcareoboea coccinea C.Y.Wu ex H.W.Li	M.Möller MMO 01-141	E, WU	China, Guangxi, Napo county	FJ501516	FJ501365
Cathayanthe biflora Chun	M.Möller MMO 01-1327	E	China, Hainan, Tongshi county	HQ632899	HQ632996
Chirita anachoreta Hance	D.J.Middleton et al. 4480	E	Thailand, Chiang Mai, Doi Suthep	HQ632870	HQ632966
Chirita asperifolia (Blume) B.L.Burtt	P.Woods 1071 (C6570)	E	Indonesia, Java, forest above Tjibodas Garden	FJ501538	JF501359
Chirita caliginosa C.B.Clarke	ex HB München-Nymphenburg: M.Kiehn & M.Pfosser 2000-1 [cult. HBV GS-96-02]	WU	Peninsula Malaysia	FJ501488	FJ501325
Chirita dielsii (Borza) B.L.Burtt	M.Möller MMO 08-1211	E	China, Yunnan, Jingdong county	HQ632871	HQ632967
Chirita gemella D.Wood	L.Averyanov 1987 [cult. RBGE 19941913]	E	Vietnam, Hong Quang Special Region, Cat Hai	FJ501523	FJ501345
Chirita hamosa R.Br.	J.M.Li; LJM1181	PE	China	DQ872822	DQ872822
Chirita lavandulacea Stapf	Cult. RBGE 20000897	E	China	FJ501487	FJ501324
Chirita longgangensis W.T.Wang	A.Takhtajan & N.Aruzytov 1975 [cult. RBGE 19941915]	E	Vietnam	AJ492290	FJ501347
Chirita pinnata W.T.Wang	Expedition Beijing 896526 (US 294374)	US	China, Guangxi, Rongshui county	FJ501526	FJ501349
Chirita pinnatifida (Hand.-Mazz.) B.L.Burtt	Q.J.Xie J-037 (US 422838)	US	China, Guangdong, Lianxian county	FJ501527	FJ501350
Chirita pumila D.Don	Gaoligong Shan Expedition 1996 7938 [cult. RBGE 19962271]	E	China, Yunnan, Nujiang Lisu Aut. Pref., Fugong county	FJ501491	FJ501327
Chirita sinensis Lindl.	T.C.Godfrey 369 [cult. RBGE 19791050]	E	China, Hong Kong	FJ501524	FJ501348
Chirita spadiciformis W.T.Wang	ex Smithsonian Institute 94-087 [cult. RBGE 19951205]	E	China, unknown locality	AJ492291	FJ501346
Chirita urticifolia Buch.-Ham. ex D.Don	EMAK 109 H (Edinburgh-Makalu Expedition 1991)	E	Nepal, Sankhuwasabha distr., Arun valley	FJ501492	FJ501328
Chirita walkerae Gardner	L.Skog 7736 (US 590934) [cult. Smithsonian 94-250]	US	Sri Lanka; leg. in US 11.03.1996	FJ501490	FJ501326
Chiritopsis glandulosa D.Fang, L.Zeng & D.H.Qin var. yangshuoensis Fang Wen, Q.X.Zhang & Yue Wang	M.Möller MMO 06-912	E	China, Guangxi, Yangshuo county	HQ632948	HQ633045
Chiritopsis repanda W.T.Wang var. *guilinensis* W.T.Wang	ex Smithsonian Institute 94-083 [cult. RBGE 19951206]	E	China, Guangxi, Guilin city	AJ492292	FJ501351

Table 1 continued

Taxon	Voucher number	Deposited in	Origin	trnL-F	ITS or ITS1/ITS2
Conandron ramondioides Sieb. & Zucc.	Takeda Herbal Garden Kyoto [cult. RBGE 19691267]	E	Japan	FJ501515	FJ501340
Cyrtandra cumingii C.B.Clarke	G.Kokubugata 11134	TNS	Japan, Ruykyus, Iriomote Island	HQ632905	HQ633002
Cyrtandra cupulata Ridl.	A.Weber 840806-2/4	WU	Peninsula Malaysia, Perak, Maxwell's Hill	FJ501532	AY818826/AY818861
Cyrtandra glabra Banks ex C.F.Gaertn.	Q.C.B.Cronk & D.Percy T91	E	French Polynesia: Society Is.: Tahiti: Mt. Tearoa Col	AY423136	FJ501353
Cyrtandra kasaimontana Hosok.	NTBG 960873	PTBG	Federated States of Micronesia, Caroline Islands	HQ632907	–
Cyrtandra kasaimontana Hosok.	Flynn 5995	PTBG	Federated States of Micronesia, Caroline Islands	–	EU919945
Cyrtandra longifolia (Wawra) Hillebr. ex C.B.Clarke	M.Kiehn 920825-2/1 [cult. HBV]	WU	USA, Hawaii, Kauai	FJ501531	EU919939
Cyrtandra pendula Blume	A.Weber & Anthonysamy 860730-1/2 [cult. HBV]	WU	Peninsula Malaysia	FJ501530	FJ501354
Cyrtandra pulchella W.P.Rich ex A.Gray	Lorence 8525	PTBG	Samoa Islands	HQ632906	EU919941
Dayaoshania cotinifolia W.T.Wang	Q.M.Chuan 01	IBK	China, Guangxi, Dayaoshan, Jinxiu conuty	HQ632914	HQ633010
Deinocheilos jiangxiensis W.T.Wang	M.Möller MMO 09-1451	E	China, Fujian, Jiangle county	HQ632933	HQ633029
Didissandra frutescens (Jack) C.B.Clarke	A.Weber 840805-1/2	WU	Peninsula Malaysia, Perak, Maxwell's Hill	FJ501522	–
Didissandra frutescens (Jack) C.B.Clarke	A.R.Rafidah, FRI 64355	FRIM	Peninsula Malaysia, Perak, Kuala Kangsar	–	HQ632952
Didymocarpus antirrhinoides A.Weber	K.Jong 9009 [cult. RBGE 19650167]	E	Peninsula Malaysia, Perak, Bujong Melakah, Ipoh.	FJ501513	DQ912671
Didymocarpus citrinus Ridl.	P.Davis 69437 [cult. RBGE 19830510]	E	Peninsula Malaysia, Perlis, Kedat Peak	AJ492293	DQ912669
Didymocarpus cordatus Wall. ex A.DC.	A.Weber 860816-2/1	WU	Peninsula Malaysia, Perak, Maxwell's Hill	AJ492294	DQ912673
Didymocarpus cortusifolius (Hance) W.T.Wang	M.Möller MMO 09-1434	E	China, Zhejiang, Jinhua city	HQ632898	HQ632995
Didymocarpus hancei Hemsl.	M.Möller MMO 08-1342	E	China, Guangxi, Hezhou city	HQ632944	HQ633041
Didymocarpus podocarpus C.B.Clarke	H.Noltie, Pradhan, Sherub & Wangdi 193	E	Bhutan, Deothang District	FJ501514	DQ912688
Didymocarpus purpureobracteatus W.W.Sm.	Y.Z.Wang 991106	PE	China, Yunnan, Pingbian county	FJ501510	–
Didymocarpus purpureobracteatus W.W.Sm.	M.Möller MMO 01-70	E, WU	China: Yunnan, Pingbian county	–	DQ912676
Didymocarpus stenanthos C.B.Clarke	M.Möller MMO 01-156	E, WU	China, Yunnan, Binchuan county	FJ501512	DQ912687
Didymocarpus villosus D.Don	B.Adhikari SB 9	E	Nepal, Sundarijal	HQ632904	HQ633001
Didymostigma obtusum (C.B.Clarke) W.T.Wang	M.Möller MMO 08-1310	E	China, Guangdong, Fengkai county	HQ632875	HQ632971
Didymostigma trichanthera C.X.Ye & X.G.Shi	M.Möller MMO 08-1335	E	China, Guangdong, Longmen county	HQ632876	HQ632972
Dolicholoma jasminiflorum D.Fang & W.T.Wang	M.Möller MMO 06-851	E	China, Guangxi, Napo county	Wei et al. 2010	Wei et al. (2010)
Emarhendia bettiana (M.R.Hend.) Kiew, A.Weber & B.L.Burtt	R.Kiew, FRI 55716	FRIM	Peninsula Malaysia	HQ632864	HQ632955
Gyrocheilos chorisepalus W.T.Wang var. synsepalus W.T.Wang	Y.G.Wei 07-708	IBK	China, Guangdong, Xinyi county	HQ632900	HQ632997
Gyrocheilos lasiocalyx W.T.Wang	M.Möller MMO 06-881	E	China, Guangxi, Guiping county	HQ632901	HQ632998
Gyrocheilos retrotrichus W.T.Wang var. oligolobus W.T.Wang	Y.G.Wei 06-208	E	China, Guangxi, Rongshui county, Sirong town	HQ632903	HQ633000

Table 1 continued

Taxon	Voucher number	Deposited in	Origin	trnL–F	ITS or ITS1/ITS2
Gyrocheilos retrotrichus W.T.Wang	M.Möller MMO 07-1136	E	China, Guangxi, Wuming county	HQ632902	HQ632999
Haberlea rhodopensis Friv.	[cult. RBGE 19754106]	E	(Greece)	AJ492296	Möller and Cronk (2001a)
Hemiboea bicornuta (Hayata) Ohwi	Smithsonian Institute [cult. RBGE 19951207]	E	Unknown origin	FJ501534	FJ501356
Hemiboea cavaleriei H.Lév.	Z.J.Gu G3	KUN	China, unknown locality	FJ501533	FJ501355
Hemiboea fangii Chun ex Z.Yu Li	M.Möller MMO 08-1284	E	China, Sichuan, Emei Shan	HQ632882	HQ632979
Hemiboea follicularis C.B.Clarke	Y.G.Wei G03	IBK	China, Guangxi, Huanjiang county	HQ632885	HQ632982
Hemiboea gracilis Franch.	Y.Z.Wang 11317	PE	China, Chongqing, Nanchuan county	FJ501536	Wei et al. (2010)
Hemiboea longgangensis Z.Yu Li	Y.G.Wei 07-550	IBK	China, Guangxi	HQ632889	HQ632986
Hemiboea longzhouensis W.T.Wang	M.Möller MMO 07-1127	E	China, Guangxi, Longan county	HQ632888	HQ632985
Hemiboea magnibracteata Y.G.Wei & H.Q.Wen	M.Möller MMO 08-1347	E	China, Guangxi, Guilin city	HQ632887	HQ632984
Hemiboea omeiense W.T.Wang	M.Möller MMO 08-1271	E	China, Sichuan, Emei Shan	HQ632886	HQ632983
Hemiboea rubribracteata Z.Yu Li & Yan Liu	M.Möller MMO 07-1093	E	China, Guangxi, Jingxi county	HQ632890	HQ632987
Hemiboea subcapitata C.B.Clarke	Y.Z.Wang 11306	PE	China, Chongqing, Chengkou county	FJ501535	FJ501357
Hemiboeopsis longisepala (H.W.Li) W.T.Wang	Y.M.Shui 73170	KUN	China, Yunnan, Jinping county	HQ632868	HQ632963
Henckelia albomarginata (Hemsl.) A.Weber	A.Weber 840805-1/12	WU	Peninsula Malaysia, Perak, Maxwell's Hill; base	AJ492297	HQ632961
Henckelia corrugata Mendum	RBGE-PNHE 1998 na	E	Philippines, Palawan	FJ501484	HQ632962
Henckelia ericii A.Weber	A.Weber 840723-1/2	WU	Malaysia, Malaya	FJ501479	HQ632956
Henckelia floccosa (Thwaites) A.Weber & B.L.Burtt	C.G.Jang [G 157]	WU	Sri Lanka	FJ501486	HQ632964
Henckelia incana (Vahl) Spreng.	S.Vogel SVG	E	India, Nilghiri mts	HQ632869	HQ632965
Hexatheca fulva C.B.Clarke	J.Sang & C.Geri S99358	E	Malaysia, Sarawak, Bau, fairy cave	HQ632873	HQ632969
Isometrum lanciifolium (Franch.) K.Y.Pan	M.Möller MMO 09-1624	E	China, Sichuan, Mianning county	HQ632924	HQ633020
Isometrum lungshengense (W.T.Wang) W.T.Wang & K.Y.Pan	M.Möller MMO 06-916	E	China, Guangxi, Longsheng county	HQ632917	HQ633013
Isometrum primuliflorum (Batalin) B.L.Burtt	M.Möller MMO 09-1605	E	China, Sichuan, Danba county	HQ632923	HQ633019
Jancaea heldreichii Boiss.	E.G.Cairns [cult. RBGE 19771605	photo E	Greece, Mt Olympus	FJ501439	Möller et al. (1999)
Kaisupeea herbacea (C.B.Clarke) B.L.Burtt	K.Larsen 44272 [cult. RBGE 19972918]	E	Thailand, Prov. Chachoengsao, Khao Tak Groep	FJ501459	FJ501309
Lagarosolen ainstiifolius W.H.Chen & Y.M.Shui	Y.M.Shui et al. 44071	KUN	China, Yunnan, Maguan county	HQ632941	HQ633038
Lagarosolen coriaceifolius Y.G.Wei	M.Möller MMO 06-913	E	China, Guangxi, Yangshuo county	HQ632943	HQ633040
Lagarosolen hechiensis Y.G.Wei, Yan Liu & F.Wen	M.Möller MMO 07-1077	E	China, Guangxi, Hechi city	HQ632942	HQ633039
Lagarosolen hispidus W.T.Wang	Y.M.Shui et al. 82661	E	China, Yunnan, Maguan county	HQ632939	HQ633036
Lagarosolen integrifolius D.Fang & L.Zeng	M.Möller MMO 06-865	E	China, Guangxi, Longzhou county	HQ632940	HQ633037
Lagarosolen lui Yan Liu & W.B.Xu	Y.G.Wei 8012	IBK	China, Guangxi, Jingxi county	HQ632938	HQ633035
Leptoboea multiflora (C.B.Clarke) Gamble subsp. *grandifolia* B.L.Burtt	Larsen et al. 32065	E	Thailand, SE, Khaso Phra Bat, N of Chanthaburi	FJ501442	Wei et al. (2010)
Litostigma coriaceifolium Y.G.Wei, F.Wen & M.Möller	M.Möller MMO 07-1162	E, IBK	China, Guizhou, Xingyi county	Wei et al. (2010)	Wei et al. (2010)

Table 1 continued

Taxon	Voucher number	Deposited in	Origin	trnL-F	ITS or ITS1/ITS2
Litostigma crystallinum Y.M.Shui & W.H.Chen	Y.M.Shui 43865	KUN	China, Yunnan, Malipo county	Wei et al. (2010)	Wei et al. (2010)
Loxostigma fimbrisepalum K.Y.Pan	Y.Z.Wang 991005	PE	China, Yunnan, Jinping county	FJ501507	Wei et al. (2010)
Loxostigma glabrifolium D.Fang & K.Y.Pan	Y.G.Wei 709	IBK	China, Guangxi, Napo county	HQ632910	HQ633006
Loxostigma griffithii (Wight) C.B.Clarke	Kew/Edinburgh Kanchenjunga Expedition (1989) 940 [cult. RBGE 19892473A]	E	Nepal, Yamphudin	FJ501508	FJ501338
Loxostigma sp.	Gaoligong Shan Expedition 1996 7668	E	China, Yunnan	AY423137	HQ633005
Lysionotus chingii Chun ex W.T.Wang	Y.Z.Wang S-10669	PE	China, unknown locality	FJ501498	FJ501332
Lysionotus forrestii W.W.Sm.	Gaoligong Shan Expedition 1996 7925 [cult. RBGE 1996269A]	E	China, Yunnan, Nujiang Lisu Aut. Pref., RBGE 1996269A]	FJ501495	AF349152/ AF349233
Lysionotus pauciflorus Maxim.	M.Möller MMO 01-101	E, WU	China, Yunnan, Xichou county	FJ501497	FJ501331
Lysionotus petelotii Pellegr.	M.Möller MMO 01-100/4	E	China, Yunnan, road to Xichou	FJ501496	HQ632974
Metabriggsia ovalifolia W.T.Wang	N.B.Ming 06-1	IBK	China, Guangxi, Napo county	HQ632883	HQ632980
Metabriggsia purpureotincta W.T.Wang	M.Möller MMO 06-813	E	China, Guangxi, Tianlin county	HQ632884	HQ632981
Metapetrocosmea peltata (Merr. & Chun) W.T.Wang	Y.G.Wei 07-702	IBK	China, Hainan, De Long	HQ632872	HQ632968
Opithandra acaulis (Merr.) B.L.Burtt	M.Möller MMO 08-1328	E	China, Guangdong, Zhaoqing county	HQ632916	HQ633012
Opithandra primuloides (Miq.) B.L.Burtt	T.Tsuzuki [cult. RBGE 19842178A]	E	Japan, unknown locality	FJ501546	FJ501364
Opithandra sinohenryi (Chun) B.L.Burtt	M.Möller MMO 07-1150	E	China, Guangxi, Fangcheng county	HQ632913	HQ633009
Orchadocarpa lilacina Ridl.	R.Kiew, RK 5410	FRIM	Peninsula Malaysia, Pahang, Fraser's Hill	HQ632863	HQ632954
Oreocharis argyreia Chun ex K.Y.Pan	M.Möller MMO 07-1131	E	China, Guangxi, Wuming county	HQ632919	HQ633015
Oreocharis aurea Dunn	M.Möller MMO 06-980	E	China, Yunnan, Jinping county	HQ632920	HQ633016
Oreocharis auricula (S.Moore) C.B.Clarke	M.Möller MMO 03-304	E	China; Guizhou, Jiangkou county	FJ5011481	FJ501323
Oreocharis magnidens Chun ex K.Y.Pan	M.Möller MMO 06-896	E	China, Guangxi, Jinxiu county	HQ632930	HQ633026
Oreocharis dasyantha Chun var. *ferruginosa* K.Y.Pan	Y.G.Wei 07-700	E	China, Hainan, Ledong	HQ632918	HQ633014
Oreocharis xiangguiensis 1 W.T.Wang & K.Y.Pan	M.Möller MMO 05-741	E	China, Guangxi, Lingui county	HQ632932	HQ633028
Oreocharis xiangguiensis 2 W.T.Wang & K.Y.Pan	M.Möller MMO 06-915	E	China, Guangxi, Longsheng county	HQ632931	HQ633027
Ornithoboea arachnoidea (Diels) Craib	ex HBV [cult RBGE 19972903]	E	Thailand, Chiang Mai, Doi Chiang Dao	FJ501461	FJ501312
Ornithoboea wildeana Craib	Y.Z.Wang 00401	PE	China, Yunnan, Xichou county	FJ501462	FJ501313
Paraboea acutifolia (Ridl.) B.L.Burtt	A.Weber 86805-2/1	WU	Peninsula Malaysia, Kedah, Pulau Langkawi, Bukit Terbak	FJ501464	FJ501314
Paraboea capitata Ridl.	A.Weber 870522-5/2 [cult. HBV]	WU	Peninsula Malaysia, Perak, Kinta district	AJ492298	FJ501315
Paraboea crassifolia (Hemsl.) B.L.Burtt	M.Möller MMO 01-83	E, WU	China, Yunnan, Maguan county	FJ501472	FJ501318
Paraboea umbellata (Drake) B.L.Burtt	M.Möller MMO 01-147	E, WU	China, Guangxi, Napo county	FJ501470	FJ501317
Paraisometrum mileense W.T.Wang	Y.M.Shui 65214	KUN	China, Yunnan, Shilin county	HQ632928	HQ633024
Paralagarosolen fangianus Y.G.Wei	M.Möller MMO 07-1168	E	China, Guangxi, Napo county	Wei et al. (2010)	Wei et al. (2010)
Petrocodon dealbatus Hance	Q.J.Xie J-042 (US 422841)	US	China, Guangdong, Lianxian county	FJ501537	FJ501358
Petrocodon ferrugineus Y.G.Wei	M.Möller MMO 06-784	E	China, Guangxi, Xincheng county	HQ632946	HQ633043

Table 1 continued

Taxon	Voucher number	Deposited in	Origin	trnL-F	ITS or ITS1/ITS2
Petrocosmea kerrii Craib	cult. RBGE 19715592	E	Unknown origin	FJ501502	FJ501334
Petrocosmea minor Hemsl.	Sino-Amer. Bot. Expedition, no. 1574 (US 56119)	US	China, Yunnan, Lunan Xian	FJ501504	Wei et al. (2010)
Petrocosmea nervosa Craib	Smithsonian Institute 78-057 [cult. RBGE 19933232]	E, US	China, N Yunnan	AJ492299	FJ501335
Petrocosmea sericea C.Y.Wu ex H.W.Li	Z.J.Gu 99-1104	KUN	China, unknown locality	FJ501503	Wei et al. (2010)
Phylloboea glandulosa **B.L.Burtt**	D.J.Middleton & P.Triboun 5202	BK, E	Thailand, Kanchanaburi, Thong Pha Phum, Ti Pugae	HQ632867	HQ632959
Platystemma violoides **Wall.**	Projektteam 197-241	WU	Nepal, SE Kathmandu, Pulchoki	FJ501443	Wei et al. (2010)
Primulina tabacum **Hance**	Q.J.Xie & C.X. Ye [cult. RBGE 19951540]	E	China, Guangdong, Lian River	AJ492300	FJ501352
Pseudochirita guangxiensis (S.Z.Huang) W.T.Wang var. glauca Y.G.Wei & Yan Liu	M.Möller MMO 05-751	E	China, Guangxi, Jingxi county	HQ632909	HQ633004
Pseudochirita guangxiensis (**S.Z.Huang) W.T.Wang**	M.Möller MMO 06-798	E	China, Guangxi, Mashan county	HQ632908	HQ633003
Ramonda myconi (L.) Rchb.	Lausanne Botanic Garden [cult. RBGE 19711477]	E	Spain, Pyrenees	AJ492301	Möller et al. (1999)
Ramonda nathaliae Pančić & Petrov.	[cult. RBGE 19784020]	E	Macedonia, unknown	AJ501438	Möller et al. (1999)
Raphiocarpus begoniifolius (H.Lév.) B.L.Burtt	Y.Z.Wang 991108	PE	China, Yunnan, Yuanyang county	FJ501517	FJ501342
Raphiocarpus macrosiphon (Hance) B.L.Burtt	M.Möller MMO 08-1321	E	China, Guangdong, Zhaoqing county	HQ632881	HQ632978
Raphiocarpus petelotii (Pellegr.) B.L.Burtt	S.Goodwin & R.Cherry 92/208 [cult. RBGE 19982405]	E	Vietnam, Lao Cai Province	FJ501518	FJ501343
Raphiocarpus sesquifolius (C.B.Clarke) B.L.Burtt	M.Möller MMO 08-1275	E	China, Sichuan, Emei Shan	HQ632911	HQ633007
Raphiocarpus sinicus **Chun**	M.Möller MMO 07-1141	E	China, Guangxi, Shangsi county	HQ632877	HQ632973
Raphiocarpus sp.	M.Möller MMO 01-69	E,WU	China, Yunnan, Pingbian county	FJ501494	FJ501330
Rhabdothamnopsis sinensis **Hemsl.**	[ex cult Kew 1988 4866]	K	China, unknown locality	AJ492302	–
Rhabdothamnopsis sinensis **Hemsl.**	M.Möller MMO 08-1059	E	China, Sichuan, Mianning county	–	HQ632960
Rhynchotechum discolor (Maxim.) B.L.Burtt	RBGE-PNH Expedition 1997/SM8 [cult. RBGE 19972562]	E	Philippines, Luzon, Isabela	FJ501436	Wei et al. (2010)
Rhynchotechum parviflorum **Blume**	M.Mendum, G.Argent & Hendrian 00148	E	Central Sulawesi, Mt. Sojol	FJ501437	Wei et al. (2010)
Ridleyandra petiolata (Ridl.) A.Weber	M.A.Mohd.Hairuf, FRI 60092	FRIM	Peninsula Malaysia, G. Inas	HQ632935	HQ633032
Ridleyandra porphyrantha (A.Weber & R.Kiew) A.Weber	A.Weber 870420-2/4	WU	Malaysia, Pahang, side ridge of Gunung Bunga Buah	FJ501520	HQ633031
Ridleyandra quercifolia (Ridl.) A.Weber	Y.T.Leong, FRI 65405	FRIM	Peninsula Malaysia, Perak, Maxwell Hill,	HQ632936	HQ633033
Senyumia minutiflora (**Ridl.) Kiew, A.Weber & B.L.Burtt**	A.R.Rafidah, R.Kiew & M.A.Mohd.Hairul, FRI 55722	FRIM	Peninsula Malaysia, Pahang, Gunung Senyum	HQ632865	HQ632957
Spelaeanthus chinii **Kiew, A.Weber & B.L.Burtt**	A.Weber 860709-2/2	WU	Peninsula Malaysia, Pahang, Jerantut distr., Taman Negara	FJ501457	FJ501307
Streptocarpus andohahelensis Humbert	M.Möller MM 9717	E	Madagascar, Tuléar, Ranomafana	FJ501449	AF316903
Streptocarpus beampingaratrensis Humbert	M.Möller MM 9715	E	Madagascar, Tuléar, Ranomafana	FJ501448	AF316905
Streptocarpus dunnii Hook.f.	I.LaCroix [cult. RBGE 19941745]	E	Swaziland, Mbabane	FJ501456	AF316951

Table 1 continued

Taxon	Voucher number	Deposited in	Origin	trnL–F	ITS or ITS1/ITS2
Streptocarpus hilsenbergii R.Br.	B.L.Burtt [cult. RBGE 19631505]	E	Madagascar, Mandrake valley	FJ501450	AF316907
Streptocarpus holstii Engl.	Cornell University (Bail. Hort) [cult. RBGE 19592272]	E	Tanzania, unknown locality	AJ492304	AF316917
Streptocarpus ibityensis Humbert	E.Fischer 250/93 [cult. RBGE 19932867]	E	Madagascar, Antananarivo	FJ501455	AF316926
Streptocarpus papangae Humbert	M.Möller MM 9718	E	Madagascar, Tuléar, Ranomafana	FJ501444	AF316929
Streptocarpus rexii (Hook.) Lindl.	K.Jong [cult. RBGE 19870333]	E	South Africa, NE Cape, Grahamstown	AJ492305	AF316979
Streptocarpus saxorum Engl.	A.Chautems & M.Perret 01-023	G	cult. CJBG	FJ501447	–
Streptocarpus saxorum Engl.	I.C.Mather 4 [cult. RBGE 19721499]	E	Tanzania, Tanga region	–	AF316914
Tetraphyllum roseum Stapf	H.K.Kurzweil 798	WU	Thailand, Krabi Province	FJ501434	HQ632950
Tengia scopulorum Chun	W.Fang 2010-02	IBK	China, Guizhou, Xiuwen county	HQ632947	HQ633044
Thamnocharis esquirolii (H.Lév.) W.T.Wang	D.W.Zhang 723	IBK	China, Guizhou, Anlong county	HQ632915	HQ633011
Tremacron aurantiacum K.Y.Pan	[cult. RBGE 20060865]	E	China, unknown locality	HQ632925	HQ633021
Tremacron begoniifolium H.W.Li	M.Möller MMO 08-1221	E	China, Yunnan, Jing Dong county	HQ632929	HQ633025
Tremacron forrestii Craib	M.Möller MMO 07-1072	E	China, Sichuan, Pan Zhi Hua county	HQ632921	HQ633017
Tremacron urceolatum K.Y.Pan	M.Möller MMO 09-1633	E	China, Sichuan, Liangshan Yizu county	HQ632922	HQ633018
Trisepalum birmanicum (Craib) B.L.Burtt	M.Möller MMO 06-862	E	China, Guangxi, Jingxi county	HQ632866	HQ632958
Wentsaiboea luochengensis Yan Liu & W.B.Xu	M.Möller MMO 07-1163	E	China, Guangxi, Luocheng county	HQ632949	HQ633046
Wentsaiboea renifolia D.Fang & D.H.Qin	M.Möller MMO 06-791	E	China, Guangxi, Duan county	Wei et al. (2010)	Wei et al. (2010)
Wentsaiboea tiandengensis Yan Liu & B.Pan	M.Möller MMO 07-1164	E	China, Guangxi, Tiandeng county	HQ632945	HQ633042

Entries in bold indicate generic type species

Table 2 List of monotypic and non-monotypic genera of the advanced Asiatic and Malesian Gesneriaceae, the latter grouped into monophyletic, non-monophyletic genera according to molecular phylogenetic analyses. Eight smaller genera (except *Trisepalum*) were represented by only one sample, and three genera were not included

Genus	Species described/ included	Genus	Species described/ included
Monophyletic (12)		**Non-monophyletic (17)**	
Aeschynanthus Jack	160/5	*Ancylostemon* Craib	12/3
Agalmyla Blume	97/6	*Boea* Lam.	14/3
Anna Pellegr.	3/3	*Briggsia* Craib	22/8
Cyrtandra J.R. & G.Forst.	>600/7	*Chirita* D.Don	80–140/15
Didymostigma W.T.Wang	3/2	*Chiritopsis* W.T.Wang	9/2
Gyrocheilos W.T.Wang	4/3	*Didymocarpus* Wall.	70/9
Loxostigma C.B.Clarke	7/3	*Hemiboea* C.B.Clarke	23/11
Lysionotus D.Don	30/4	*Henckelia* Spreng.	180/5
Ornithoboea C.B.Clarke	11/2	*Isometrum* Craib	14/3
Paraboea (C.B.Clarke) Ridl.	100/4	*Lagarosolen* W.T.Wang	6/7
Petrocosmea Oliv.	27/4	*Metabriggsia* W.T.Wang	2/2
Ridleyandra A.Weber & B.L.Burtt	20/3	*Opithandra* B.L.Burtt	10/3
		Oreocharis Benth.	28/6
		Petrocodon Hance	4/2
Monotypic (20)		*Raphiocarpus* Chun	11/5
Allostigma W.T.Wang	1/1	*Tremacron* Craib	7/4
Briggsiopsis K.Y.Pan	1/1	*Wentsaiboea* D.Fang & D.H.Qin	3/3
Cathayanthe Chun	1/1		
Conandron Sieb. & Zucc.	1/1		
Dayaoshania W.T.Wang	1/1	**Only 1 species included (8)**	
Dolicholoma D.Fang & W.T.Wang	1/1	*Allocheilos* W.T.Wang	2/1
Emarhendia Kiew, A.Weber & B.L.Burtt	1/1	*Bournea* Oliv.	2/1
Hemiboeopsis W.T.Wang	1/1	*Calcareoboea* [C.Y.Wu ex]H.W.Li	2/1
Metapetrocosmea W.T.Wang	1/1	*Deinocheilos* W.T.Wang	2/1
Orchadocarpa Ridl.	1/1	*Didissandra* C.B.Clarke	8/1
Paraisometrum W.T.Wang	1/1	*Hexatheca* C.B.Clarke	4/1
Paralagarosolen Y.G.Wei	1/1	*Kaisupeea* B.L.Burtt	3/1
Phylloboea Benth.	1/1	*Trisepalum* C.B.Clarke	13/1
Primulina Hance	1/1		
Pseudochirita W.T.Wang	1/1		
Rhabdothamnopsis Hemsl.	1/1	**Not included (3)**	
Senyumia Kiew, A.Weber & B.L.Burtt	1/1	*Beccarinda* Kuntze	8/–
Spelaeanthus Kiew, A.Weber & B.L.Burtt	1/1	*Deinostigma* W.T.Wang & Z.Y.Li	1/–
Tengia Chun	1/1	*Sepikea* Schltr.	1/–
Thamnocharis W.T.Wang	1/1		

genera (>70 species), several species were included: e.g. *Aeschynanthus*: five species out of ca. 185, *Agalmyla*: six out of 97, *Cyrtandra*: seven out of (perhaps) 450–600, *Didymocarpus* s.str.: ten out of ca. 70 and *Hemiboea*: 11 out of 23. For genera that were found non-monophyletic in our previous analysis (Möller et al. 2009), samples of as many species as possible were included: for *Briggsia*: nine

out of 22, for *Oreocharis*: six out of 28 and for *Raphiopcarpus* Chun: five out of 11.

The number of species included for the large and highly polyphyletic genera *Chirita* (15 out of 80–140) and *Henckelia* (four out of ca. 180) was not increased from our previous analysis, as these genera will be dealt with in separate, more focused and detailed papers. The same

approach was taken for the large genus *Paraboea* whose close links to *Trisepalum* (Möller et al. 2009) and *Phylloboea* (Burtt 1960) will be addressed in separate works.

DNA extraction, PCR and direct sequencing

Molecular methods and protocols followed Möller et al. (2009). For the current analyses, sequences of the *trn*L-F intron-spacer (*trn*L-F) and the ITS regions were acquired. The newly acquired sequences here have been deposited in GenBank.

Phylogenetic analysis

For this study 89 *trn*L-F and 97 ITS sequences were newly acquired, 5 *trn*L-F and 18 ITS sequences came from previous publications (Möller et al. 1999; Möller and Cronk 2001a, b; Wei et al. 2010), and the remaining sequences were retrieved from GenBank (Table 1). Both sequence regions were acquired for all samples.

The matrices were subjected to maximum parsimony (MP), on unordered and equally weighted characters, implemented in PAUP* v4.0b10 (Swofford 2002), and Bayesian MCMC inference (BI; Yang and Rannala 1997) in MrBayes v3.1.2 (Huelsenbeck and Ronquist 2001, 2007). The *trn*L-F and ITS sequences were analysed combined (analysing the datasets individually resulted in strict consensus trees with low resolution for both the MP and BI analyses). The combinability of the two datasets was determined by the incongruence length difference (ILD) test of Farris et al. (1995a, b), implemented in PAUP* (as partition-homogeneity test), on 100 replicates of repartitioning with TBR and MulTrees on (saving no more than 10 trees per replicate).

Parsimony ratchet (Nixon 1999), implemented with 1,000 replicates in PAUPRat (Sikes and Lewis 2001) and PAUP*, was used to find starting trees in order to find all islands of most parsimonious trees that may exist. The saved trees were further optimised in PAUP*, with both TBR and Multrees on. Tree statistics [consistency index (CI: Kluge and Farris 1969), and retention index (RI: Farris 1989)] were obtained in PAUP*. Statistical branch support analyses were performed as 10,000 heuristic bootstrap replicates (BS; Felsenstein 1985) with TBR swapping on and MulTrees off (Möller et al. 2009) in PAUP*.

For the BI analysis models and parameter priors were obtained independently for the *trn*L-F and ITS matrices using MrModeltest v2.3 (Nylander 2004). The model suggested for *trn*L-F was GTR+G and for ITS SYM+I+G, as suggested by the Akaike Information Criterion (AIC; Akaike 1974). Five million generations were run in two independent analyses each with four Markov Chain Monte Carlo (MCMC) chains, with one tree sampled every 500 generations (=10,000 trees). The first 1,000,000 generations, or the first 2,000 trees, were discarded (burn-in). The remaining trees from both parallel runs were used to reconstruct majority rule consensus trees in PAUP*, and posterior probabilities (PP) were obtained. They are not strictly comparable to bootstrap values (Möller et al. 2009), but are indicators of clade robustness (Lewis 2001; Alfaro et al. 2003; but see Cummings et al. 2003; Erixon et al. 2003). A high correlation of the PP support values was found between the two parallel runs of the Bayesian analysis (Online Resource 1, 2, 3).

Results

Matrix characteristics

The combined matrix had a length of 1,980 characters for analysis (*trn*L-F: 1,094 characters, ITS: 886). Of these, 943 were constant, 323 variable but parsimony uninformative, and 714 (36%) parsimony informative.

Phylogenetic analyses

The ILD test indicated a high level of congruence between the two datasets ($P = 0.25$), and the data was deemed combinable. The MP analysis on the combined datasets yielded 97,723 most parsimonious trees of 6,003 steps length, a CI of 0.3075 and a RI of 0.6454. The majority rule consensus tree was highly resolved and showed seven near-terminal polytomies (Fig. 1). The BI tree recovered was basically congruent to the MP tree in areas where the branches were well supported (Fig. 2). Thus, phylogenetic relationships are described on the MP tree with reference to the BI tree where necessary.

The MP tree was rooted on the basal Asiatic genus *Tetraphyllum*. The European genera fell near the remaining basal Asiatic genera with *Haberlea* as sister to the latter. This relationship did not receive any branch support and is likely an artefact of sampling in this region of the tree (omission of *Jerdonia* and *Corallodiscus*). This was supported by the BI tree where *Ramonda*/*Jancaea* and *Haberlea* fell together on a polytomy.

The next grade was formed by the recently described genus *Litostigma*, followed by the African and Madagascan *Streptocarpus* clade (BS = 87%). A clade (BS = 99; PP = 1.0) consisting of predominantly twisted fruited genera formed the next grade, informally named 'Boea group' (Weber 2004), with the straight fruited *Didissandra* as sister (BS = 51%; PP = 0.84). Within the *Boea* group, few internal branches were highly supported; the *Boea*
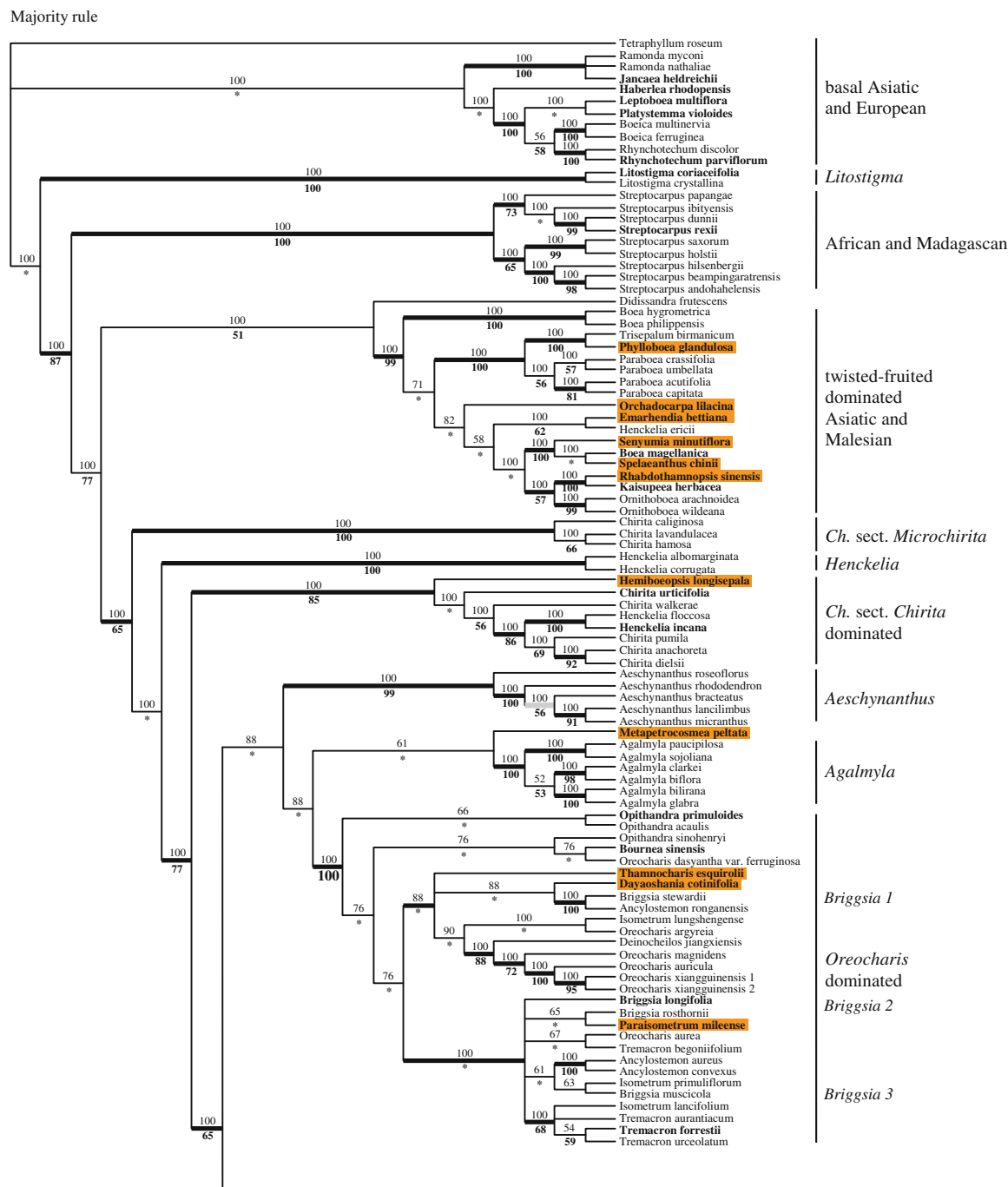
Majority rule

Fig. 1 Majority rule consensus tree of 97,723 most parsimonious trees of 6,003 steps based on combined *trn*L-F and ITS sequences of 191 didymocarpoid species (CI = 0.3075, RI = 0.6454). Majority rule frequencies are given above the branches. Bootstrap values (*bold*) are given below branches. *Asterisks* indicate branches with <50%

support values. *Branches* in *bold* are present in the Bayesian inference analysis with 0.99 (*grey*) or 1.0 (*black*) PP values. *Names* in *bold* indicate generic types. *Names* highlighted *red* indicate monotypic genera

samples included fell in two places; the two species from China and the Philippines (*B. hygrometrica* and *B. phil-ippensis,* respectively) formed a sister pair (BS = 100%; PP = 1.0) on the most basal branch. *Boea magellanica* from Papua New Guinea was sister to *Spelaeanthus chinii*

(PP = 0.84), which in turn was sister to *Senyumia minu-tiflora* (BS = 100%; PP = 1.0). *Trisepalum* and *Phyllo-boea* were sister taxa (BS = 100%; PP = 1.0) and formed a clade with the *Paraboea* samples (BS = 100%; PP = 1.0). *Emarhendia* was sister to *Henckelia ericii*
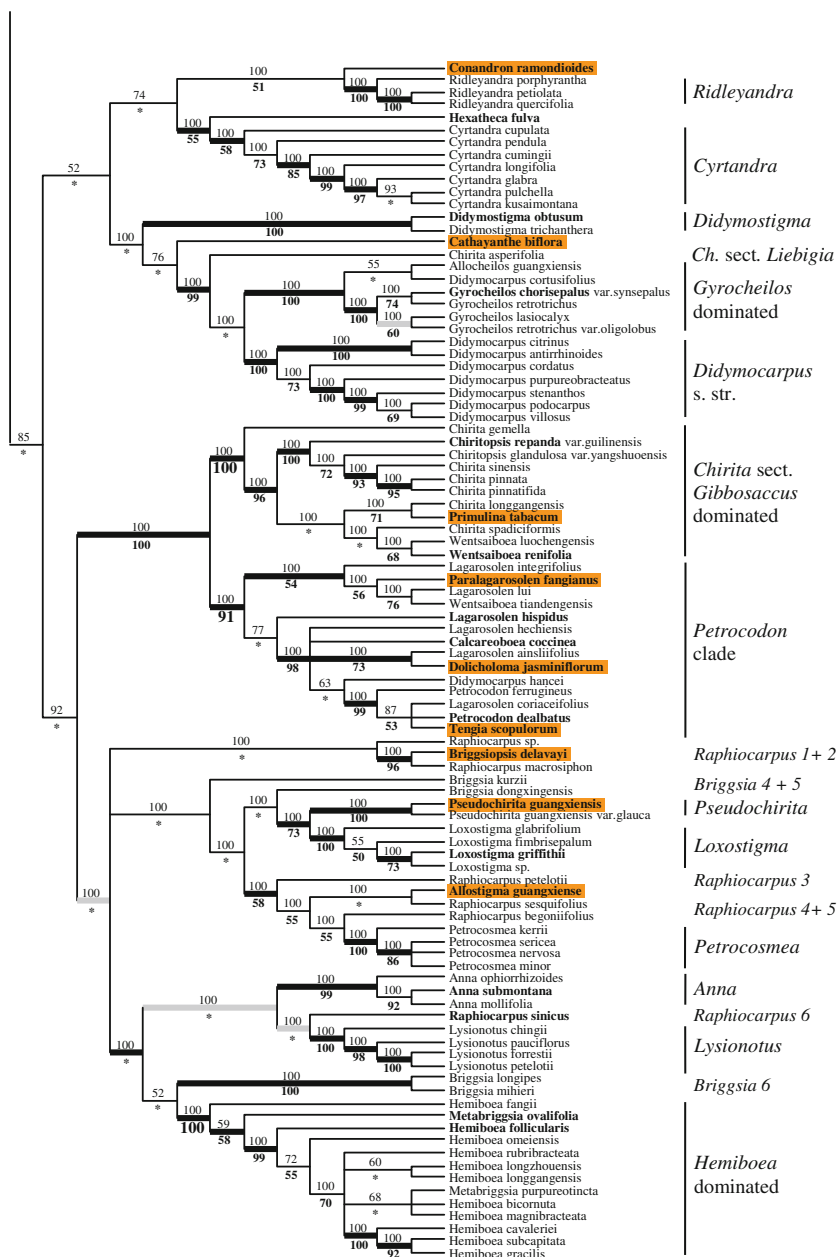
Fig. 1 continued

[= *Loxocarpus holttumii*] (BS = 62%; PP = 0.82). The sister pair *Rhabdothamnopsis sinensis* and *Kaisupeea herbacea* (BS = 100%; PP = 1.0) together with the two *Ornithoboea* species (BS = 99%; PP = 1.0) formed a clade (BS = 57%; PP = 1.0).

The next two grades included a clade of three *Chirita* species of section *Microchirita* (BS = 100%; PP = 1.0), and a clade including two *Henckelia* species from the Malay Peninsula and the Philippines (*Henckelia albomarginata* and *Henckelia corrugata,* respectively) (BS = 100%; PP = 1.0), though in the BI analysis the two

clades formed sister clades. Neither constellation received significant support in the two phylogenetic analyses.

The five samples of *Chirita* section *Chirita* included here were placed in a clade, together with a sister pair of the South Indian-Sri Lankan *Henckelia*, *H. floccosa* and *H. incana* (BS = 100%; PP = 1.0), nesting here as sister (BS = 86%; PP = 1.0) to a clade of *C. anachoreta, C. dielsii* and *C. pumila* (BS = 69%; PP = 0.79). Sister to this *Chirita/Henckelia* clade was the monotypic *Hemiboeopsis longisepala* (BS = 85%; PP = 1.0). Together they formed the next grade (BS = 77%; PP = 1.0).
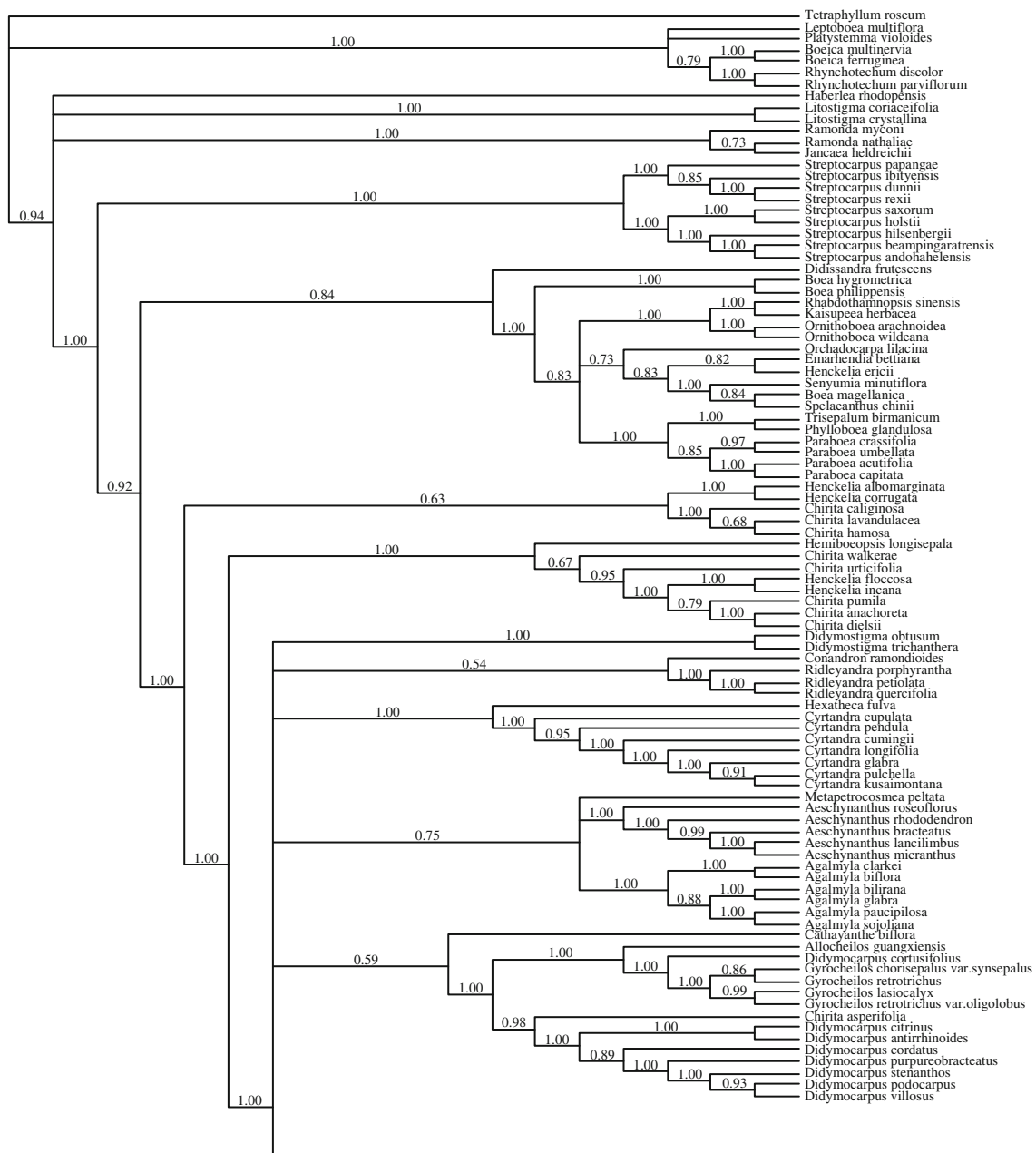
Fig. 2 Majority rule consensus tree based on Bayesian inference analysis with posterior probabilities based on combined *trn*L-F and ITS sequences of 191 didymocarpoid Gesneriaceae samples

The remainder of the advanced straight-fruited Asiatic and Malesian didymocarpoids fell in five larger clades in the MP analysis, but with low support as reflected in the backbone polytomy in the BI analysis (Fig. 2).

The first clade included three well-supported subclades, one comprising all *Aeschynanthus* samples with high support (BS = 99%; PP = 1.0), another all *Agalmyla* samples (BS = 100%; PP = 1.0), plus the monotypic *Metapetrocosmea peltata* as sister, but with no branch support. This is reflected in the BI analysis, where this monotypic genus fell on a polytomy with the two monophyletic clades of

Aeschynanthus and *Agalmyla* samples. The third subclade, with *Oreocharis* as the largest genus, received high clade support (BS = 100%; PP = 1.0). Few internal branches herein were highly supported, but the topology was very similar between the MP and BI analyses. The clade contained samples of no less than 11 genera, including three monotypic genera, *Dayaoshania cotinifolia*, *Paraisometrum mileense* and *Thamnocharis esquirolii*, and samples of the small genera *Bournea* (one of two species included) and *Deinocheilos* (1/2). None of the multiple samples of the medium-sized genera *Ancylostemon* (3/12), *Isometrum*

Fig. 2 continued
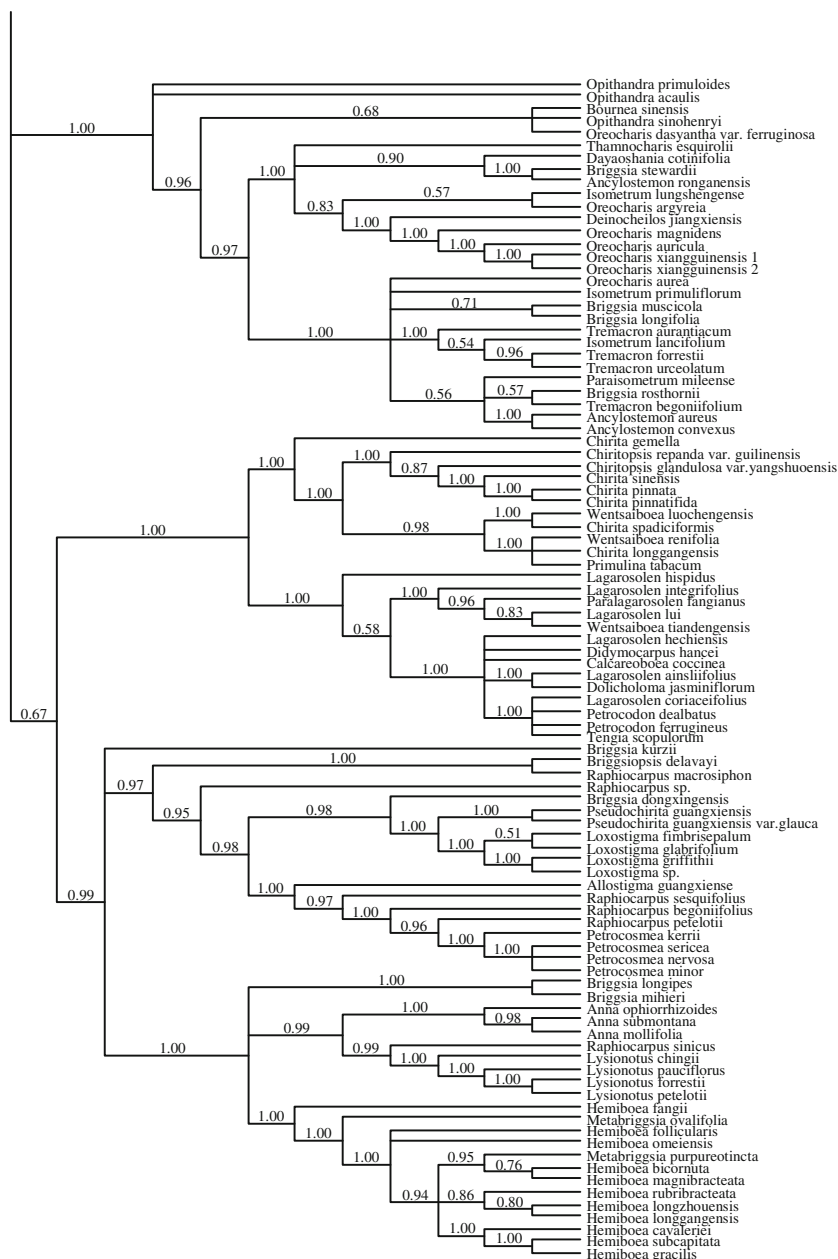
(3/14), *Opithandra* (3/10), *Oreocharis* (6/28 polyphyletic) and *Tremacron* (3/7) formed a monophyletic clade. This subclade also included four (*Briggsia* 1–3) of the eight samples of *Briggsia* (8/22) included here, *B. longifolia*, *B. muscicola*, *B. rosthornii* and *B. stewardii*. No pattern appeared to emerge from the relationships of the genera; samples of *Oreocharis* clustered with *Bournea*, with *Deinocheilos* (BS = 88%; PP = 1.0), with *Isometrum* and *Tremacron*; *Isometrum* clustered with *Tremacron* (BS = 68%; PP = 1.0), and *Briggsia* with *Paraisometrum* and *Ancylostemon* (BS = 100%; PP = 1.0). Most of these relationships received low branch support. The likely reasons are the short backbone branches of this clade (Fig. 3).

The phylogram also shows the reason for the high branch support for the pair, *Briggsia stewardii* and *Ancylostemon ronganensis*, a high similarity between the sequences (identical for *trn*L-F).

The second clade split into two subclades, one containing a monophyletic *Cyrtandra* (BS = 58%; PP = 1.0) with *Hexatheca fulva* as sister (BS = 55%; PP = 1.0). This subclade was sister to a monophyletic *Ridleyandra* (BS = 100%; PP = 1.0) with *Conandron* as sister to the latter, though the position of *Conandron* here was not supported by high bootstrap or PP values (BS = 51%; PP = 0.54). The other subclade included the *Didymocarpus* samples (BS = 100%; PP = 1.0), except *D.*

Fig. 3 Phylogram of a single most parsimonious tree based on combined *trn*L-F and ITS sequences of 191 didymocarpoid species (CI = 0.3075, RI = 0.6454), illustrating the distribution of base substitutions across the tree and the isolation of individual clades. *Shading* indicates well-supported clades
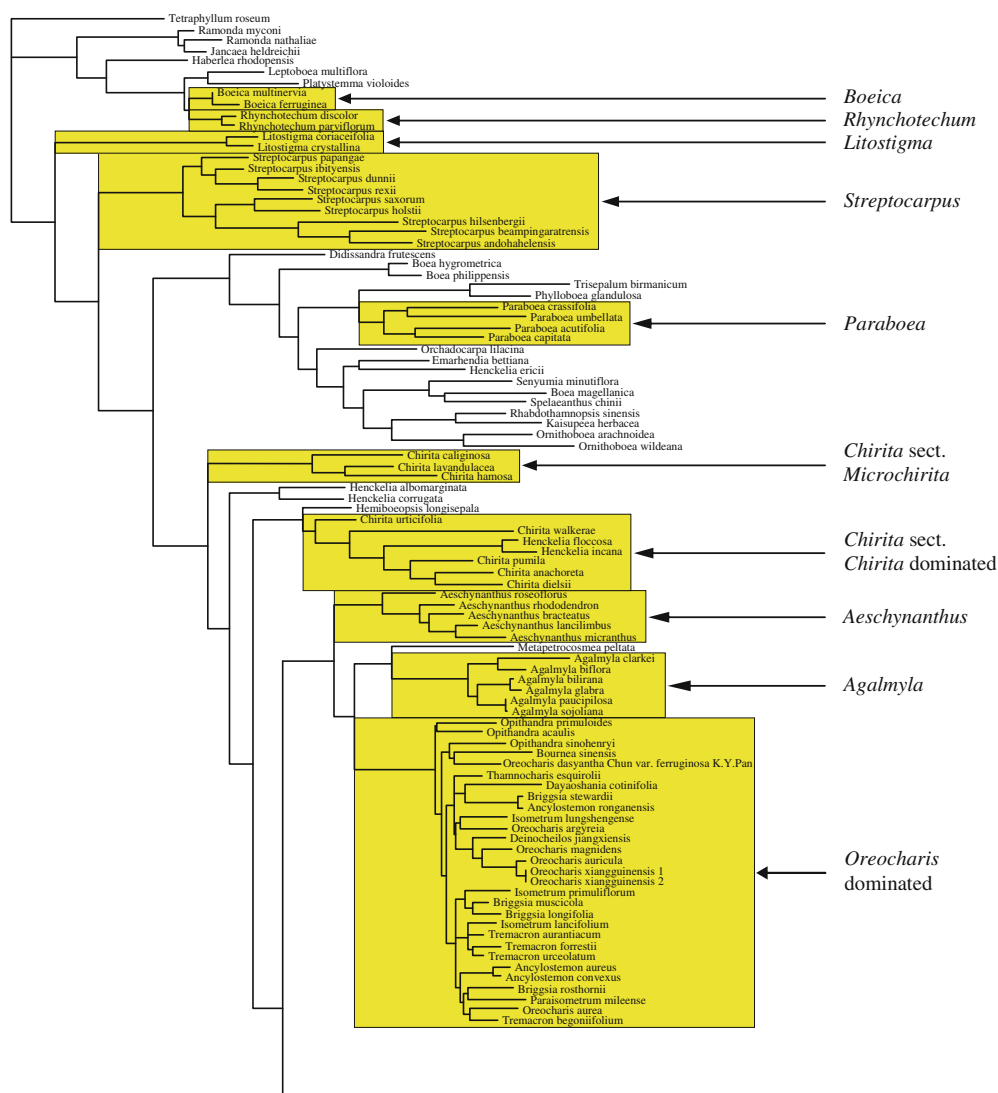

cortusifolius and *D. hancei*. The former species was sister to *Allocheilos guangxiensis* in the MP analysis (though with no branch support) and these together sister (BS = 100%; PP = 1.0) to the monophyletic *Gyrocheilos* samples (BS = 100%; PP = 1.0). In the BI analysis *Allocheilos guangxiensis* and *Didymocarpus cortusifolius* formed grades to *Gyrocheilos* (PP = 1.0). This clade was in turn sister to the *Didymocarpus* clade, though only with PP support (PP = 1.0). These differences between MP and BI analyses were likely due to the position of *Chirita asperifolia*, which fell as sister to the *Allocheilos/Gyrocheilos/Didymocarpus* samples in the MP analysis, but as sister to the *Didymocarpus* clade in the BI analysis. *Chirita asperifolia* together with the *Allocheilos/Gyrocheilos/Didymocarpus* samples formed a well-supported monophyletic clade (BS = 99%; PP = 1.0), with the monotypic *Cathayanthe biflora* as sister, though with low support (PP = 0.59). Sister to these samples were the two

Didymostigma samples, though this was not supported in the BI analysis. The two *Didymostigma* samples themselves formed a strongly supported relationship (BS = 100%; PP = 1.0).

The third clade split into two subclades, which were highly supported (BS = 100%; PP = 1.0 and: BS = 91%; PP = 1.0, respectively). The first included samples of four genera, specifically all *Chirita* samples of section *Gibbosaccus*, the two samples of *Chiritopsis* included here, two of the three species of *Wentsaiboea*, *W. renifolia* and *W. luochengensis*, and the monotypic *Primulina tabacum*. The second, *Petrocodon* subclade, included samples from seven genera, including the two monotypic genera *Dolicholoma* and *Paralagarosolen*, all described species of *Lagarosolen*, two out of four described species of *Petrocodon* (*P. dealbatus* and *P. ferrugineus*), *Calcareoboea coccinea*, *Wentsaiboea tiandengensis* and *Didymocarpus hancei*. *Lagarosolen* was highly polyphyletic, with the

Fig. 3 continued
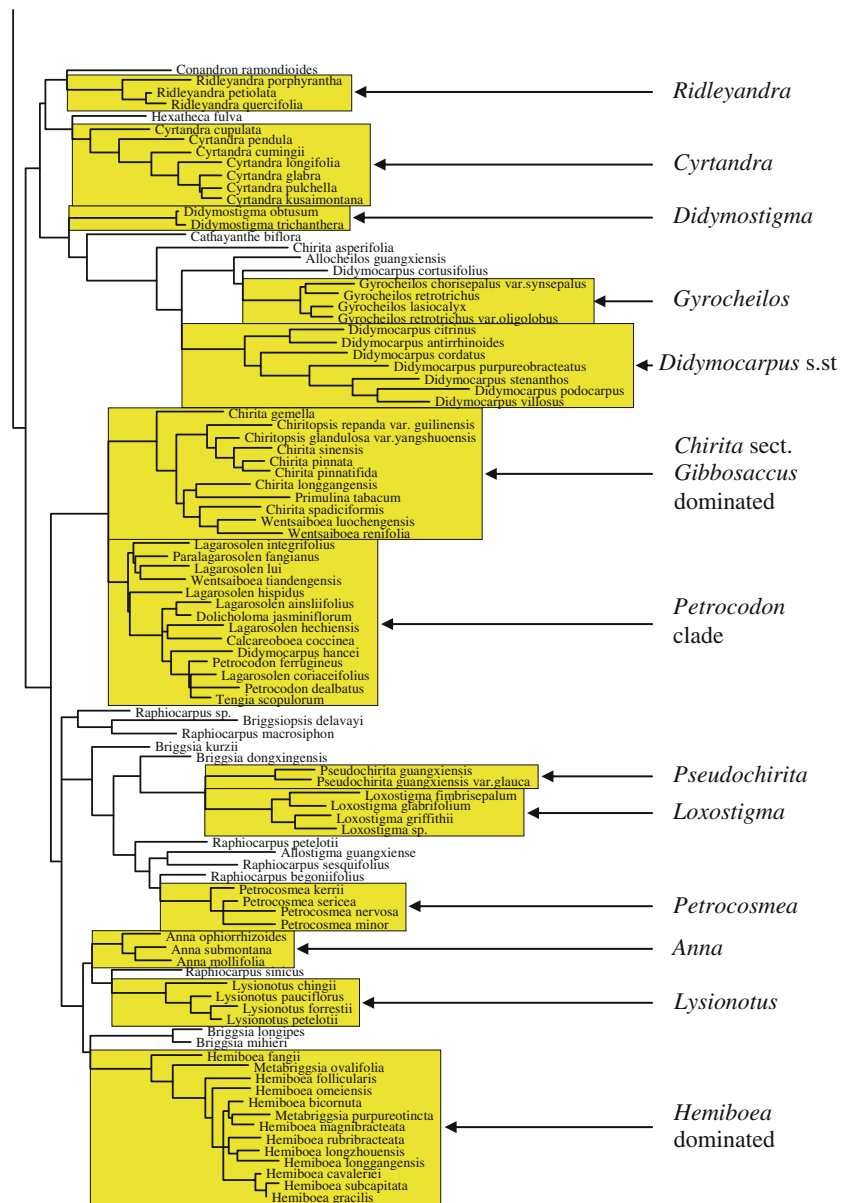
other genera scattering among its species. *Lagarosolen ainsliifolius* and *Dolicholoma jasminiflorum* were sister (BS = 73%; PP = 1.0), as were *Lagarosolen lui* and *Wentsaiboea tiandengensis* (BS = 76%; PP = 0.83). *Petrocodon* was paraphyletic, with *Lagarosolen coriaceifolius* and *Tengia scopulorum* nesting inside this genus (BS = 99%; PP = 1.0).

The fourth and fifth clades were characterised by the scattered positions of samples of *Briggsia* (*Briggsia* 4–6) and *Raphiocarpus* (*Raphiocarpus* 1–6). The two clades were on a polytomy with two *Raphiocarpus* samples (*Raphiocarpus* 1 and 2) plus the monotypic *Briggsiopsis delavayi*, which formed a strong sister relationship with *R. macrosiphon* (BS = 96%; PP = 1.0). This pair was sister

to the core of the fourth clade in the BI analysis and *Briggsia kurzii* on the polytomy. In the MP analysis *Briggsia kurzii* was sister to the fourth clade. In neither analysis were the different positions of *Briggsia dongxingensis* and *Briggsia kurzii* supported. The fourth clade included a strongly supported monophyletic *Loxostigma* (BS = 100%; PP = 1.0), as sister to a well-supported monophyletic *Pseudochirita* (BS = 100%; PP = 1.0). The clade consisting of these two genera received some support (BS = 73%; PP = 1.0). *Briggsia dongxingensis* was sister to this clade, but with no branch support. The *Petrocosmea* samples formed a highly supported monophyletic clade (BS = 100%; PP = 1.0), linked to three *Raphiocarpus* samples arranged in grades, with the monotypic *Allostigma*

in a sister relationship with *R. sesquifolius*, albeit with no support. In the BI analysis *Allostigma* fell as a separate grade, forming the basal lineage.

The fifth clade was split into two subclades. One included a highly supported monophyletic *Lysionotus* (BS = 100%; PP = 1.0) and *Anna* (BS = 99%; PP = 1.0). *Raphiocarpus sinicus* was sister to the *Lysionotus* samples, though only with BI support (PP = 1.0). The *Hemiboea* and *Metabriggsia* samples formed the other subclade. Both *Metabriggsia* samples fell among the *Hemiboea* samples, *M. purpureotincta* nested deep in the genus in a clade with *H. bicornuta*, *H. magnibracteata* and *M. ovalifolia* closer to the base (BS = 58%; PP = 1.0) but inside a strongly supported *Hemiboea* clade (BS = 100%; PP = 1.0).

Discussion

Phylogenetic analysis

Our analysis is to date the most comprehensive for the "didymocarpoid Gesneriaceae", with all but 3 genera out of 60 belonging to the "advanced Asiatic and Malesian genera" included. Only *Beccarinda*, *Deinostigma* and *Sepikea* could not be included. While the maximum parsimony analysis resulted in a relatively fully resolved tree, the backbone of this tree was not highly supported. This was reflected in the Bayesian inference analysis that showed lower resolution. However, where the topology was well supported, the two analyses were congruent (Figs. 1, 2).

While intergeneric and clade relationships were sometimes not well supported, branch support for a number of monotypic genera was high and suggests that these genera form good natural entities (see below). This pattern was also found in our previous analyses including samples across the whole family (Möller et al. 2009), but including 28 fewer didymocarpoid genera. Apparently, adding more genera did not help stabilise the analysis. Even though the two studies are not directly comparable due to the different taxonomic sampling ranges (i.e., Möller et al. 2009, sampled across the whole family; here we sampled the didymocarpoid genera only) and sampling densities (i.e. Möller et al. 2009, included 141 samples across the didymocarpoids, here we included 191 samples), some topologies were consistently recovered, e.g. the relationship among *Hemiboea*, *Lysionotus* and *Anna* representing the fourth and fifth clades; the relationship between *Petrocodon* and *Calcareoboea*, and *Chirita*, *Chiritopsis* and *Primulina* representing the third clade. The link among the latter three genera and *Wentsaiboea* was already hinted at in an earlier publication (Wei et al. 2010).

Species content and representation of the didymocarpoid genera analysed here

Of the 57 genera of the "advanced Asiatic and Malesian genera" included here, 20 were monotypic, 12 small (≤4 species), 18 medium sized (>4 to <30 species) and seven large (>70 species) (Table 2). Of the non-monotypic genera, for 7 (mostly small) genera only one sample was included: *Trisepalum* (13 species), *Kaisupeea* (3), *Hexatheca* (4), *Deinocheilos* (2), *Didissandra* (8), *Bournea* (2) and *Calcareoboea* (1-3).[1]

Monophyly of genera

From the 29 "advanced Asiatic and Malesian genera" with multiple samples included, 12 were found to be monophyletic: *Aeschynanthus*, *Agalmyla*, *Anna*, *Cyrtandra*, *Didymostigma*, *Gyrocheilos*, *Loxostigma*, *Lysionotus*, *Ornithoboea*, *Paraboea*, *Petrocosmea* and *Ridleyandra*. Their monophyletic positions in the phylogenetic trees received very high statistical support in most cases in both MP and BI analysis and based on individual or combined data (Table 3). Their relative isolated position from other genera can also be demonstrated through a phylogram, depicting the length of branches in relation to the amount of genetic differences to other clades (Fig. 3). Here, all (except *Cyrtandra*) show long branches leading to the first diversification points for the genera, suggesting that these represent well-defined genetic entities. In the following, the particular genera are commented on.

Aeschynanthus

This is a genus of some 160 species, ranging from South China, North and South India through Malesia to New Guinea and the Solomon Islands. Our sampling (species from China, the Malay peninsula and Vietnam) included only five species roughly representing its range, but there is a large sampling in previous molecular studies (Denduangboripant and Cronk 2000, 2001; Denduangboripant et al. 2001). So far, no indication has been found that *Aeschynanthus* is not monophyletic, and this matches well with the relative uniformity of the genus in vegetative, floral and fruit characters compared to other genera.

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[1] Originally, the genus was established as monotypic with *C. coccinea* (Li 1982) and characterised by the presence of red, long-tubed flowers with a four-lobed upper lip and single-lobed lower lip. Burtt (2001b) transferred the generically misplaced *Didymocarpus bonii* to *Calcareoboea*, though it did not match any of the floral characters mentioned. In the same paper he also announced the transfer of *Didymocarpus hancei* to *Calcareoboea*, but this action was never taken.

Table 3 Branch support for genera and selected clades in maximum parsimony (MP) and Bayesian inference (BI) analyses of separate *trn*L-F, ITS and combined data of the 191 advanced didymocarpoid Gesneriaceae samples analysed

	MP (%)			BI (PP)		
	*trn*LF	ITS	Combined	*trn*LF	ITS	Combined
Aeschynanthus (5/160)[a]	[99%[b]][c]	[88%]	[99%]	[1.0]	[1.0]	[1.0]
Agalmyla (6/97)	[98%]	[100%]	[100%]	[1.0]	[1.0]	[1.0]
Anna (3/3)	[95%)	[84%]	[99%]	[1.0]	[1.0]	[1.0]
Cyrtandra (7/>600)	[61%]	[<50%]	[58%]	[0.98]	[0.88]	[1.0]
Didymocarpus s.s. (7[d]/70)	[90%]	[100%]	[100%]	[1.0]	[1.0]	[1.0]
Didymostigma (3/2)	[100%]	[100%]	[100%]	[1.0]	[1.0]	[1.0]
Gyrocheilos (3/4)	[95%]	[100%]	[100%]	[1.0]	[1.0]	[1.0]
Loxostigma (3/7)	[94%]	[98%]	[100%]	[1.0]	[1.0]	[1.0]
Lysionotus (4/30)	[51%]	[100%]	[100%]	[0.96]	[1.0]	[1.0]
Petrocosmea (4/27)	[95%]	[96%]	[100%]	[1.0]	[1.0]	[1.0]
Pseudochirita (1, 2var/1, 2var)	[100%]	[100%]	[100%]	[1.0]	[1.0]	[1.0]
Ridleyandra (3/20)	[90%]	[99%]	[100%]	[1.0]	[1.0]	[1.0]
Cyrtandra & *Hexatheca* (1/4)	–	[–]	[55%]	–	[1.0]	[1.0]
Loxostigma & *Pseudochirita* (1/1)	[73%]	[<50%]	[73%]	[1.0]	[0.62]	[1.0]
Gyrocheilos, *Allocheilos* (1/2) and *Didymocarpus cortusifolius*	[58%]	[100%]	[100%]	[0.97]	[1.0]	[1.0]
Hemiboea (11/23) & *Metabriggsia* (2/2)	[<50%]	[100%]	[100%]	[0.55]	[1.0]	[1.0]
Oreocharis clade [incl. *Oreocharis* (6/28), *Ancylostemon* (3/12), *Briggsia stewardii*, *B. longifolia*, *B. muscicola*, *B. rosthornii*, *Bournea* (1/2), *Dayaoshania* (1/1), *Deinocheilos* (1/2), *Isometrum* (3/14), *Opithandra* (3/10), *Paraisometrum* (1/1), *Thamnocharis* (1/1), *Tremacron* (4/7)]	[<50%]	[100%]	[100%]	[1.0]	[1.0]	[1.0]
Petrocodon clade [incl. *Petrocodon* (2/4), *Calcareoboea* (1/2), *Didymocarpus hancei*, *Dolicholoma* (1/1), *Lagarosolen* (6/7), *Paralagarosolen* (1/1), *Tengia* (1/1), *Wentsaiboea tiandengensis*]	[53%]	[84%]	[91%]	[0.97]	[1.0]	[1.0]
Primulina clade [incl *Primulina* (1/1), *Chirita* sect *Gibbosaccus*, *Chiritopsis* (2/9), *Wentsaiboea renifolia*, *Wentsaiboea luochengensis*]	[54%]	[100%]	[100%]	[0.91]	[1.0]	[1.0]
Petrocodon clade & *Primulina* clade	[76%]	[100%]	[100%]	[1.0]	[1.0]	[1.0]

[a] Species included/species described

[b] Clade support

[c] [ ] denotes presence of monophyletic clade

[d] Excluding *D. cortusifolius* and *D. hancei*

Agalmyla

This genus took its present form only in the recent past by the inclusion of *Dichrotrichum* and *Tetradema* (Burtt 1968) and thus including erect and climbing species, sessile or long-stalked inflorescences, and flowers with two and four stamens. In the revision of Hilliard and Burtt (2002), which by the description of over 60 new species (applying a rather narrow species concept) grew to a genus of 97 species and with a distribution from Sumatra to New Guinea, three sections were distinguished: sects. *Agalmyla*, *Exannularia* and *Dichrotrichum*. Our sampling covers species from all these sections. The close relationship of the morphologically very similar *A. paucipilosa* and *A. sojoliana* (sect. *Exannularia*) as well as *A. bilirana* and *A. glabra* (sect. *Dichrotrichum*) is well reflected in the tree (sister

positions), but must not be read as an indication of monophyly of the respective sections, as in an extended molecular phylogenetic study using ITS sequences that included 17 *Agalmyla* samples of 16 species, none of the sections were found to be monophyletic (Chapman 2003).

Anna

All three species recognised so far have been included in the analysis. They form a well-supported clade and thus prove the monophyly of the genus. The clade is sister to the likewise monophyletic *Lysionotus* plus *Raphiocarpus sinicus*, the little known type species of a clearly polyphyletic genus. The relationship of *Anna* and *Lysionotus* is plausible from the similar habit and the fact that both have appendaged seeds (subulate in *Anna*, hair-like in

Lysionotus). Wang and Pan (1982) and Wang et al. (1990, 1998), therefore, placed *Anna* and *Lysionotus* in tribe Trichosporeae (which as an entity, however, proved polyphyletic; Möller et al. 2009).

Cyrtandra

This is by far the largest genus in Gesneriaceae with more than 600 species. Here we included seven species right across the distribution range of the genus, from Peninsula Malaysia to Hawaii. There is no suggestion for the genus not to represent a single natural lineage, though no analysis exists to specifically test this (previous phylogenetic analyses included as outgroup only one or two species of *Aeschynanthus* (Atkins et al. 2001; Bramley et al. 2004; Cronk et al. 2005; Clark et al. 2008, respectively). Perhaps adding more *Cyrtandra* species might stabilise the analysis with respect to the monophyly of the genus.

Remarkable is the sister position of *Cyrtandra* (+ *Hexatheca*) to *Ridleyandra* (+*Conandron*). Though support is only weak, this is in good agreement with chromosomal data (both have $n = x = 34$ chromosomes; Kiehn and Weber 1998) and similarities in the fruit: *Ridleyandra* has thick-walled, somewhat fleshy, dehiscent fruits, while they are thick-walled (sclerocarpous or fleshy) and indehiscent in *Cyrtandra* (see discussion in Weber and Burtt 1998b).

Didymostigma

Two of the three species, including the type species, have been included in the analysis. They form a well-supported clade in a larger (rather ill-supported) clade comprising *Didymocarpus*, *Gyrocheilos* and others.

Gyrocheilos

Three of the four species (including the type species, but not the type variety) have been included in the analysis. They form a well-supported clade in a grade comprising *Chirita asperifolia* (for the accommodation of which recently *Chirita* sect. *Liebigia* was re-established; Hilliard 2004), *Allocheilos guangxiensis* and *Didymocarpus cortusifolius*. In fact, the close relationship of *Gyrocheilos* with *Didymocarpus* is well known, *Gyrocheilos* mainly differing in the undivided upper lip of the corolla.

Loxostigma

Four of the ca. seven species, including the type species, have been included in the analysis. They form a well-supported clade sister to the monotypic genus *Pseudochirita*. Nonetheless, the genus, as currently circumscribed, remains problematic in some respects (inclusion of species

with appendaged and unappendaged seeds, of terrestrial and epiphytic species, etc.). However, it is important to have evidence that at least some species around the type species can be considered as a good taxonomic entity.

Lysionotus

This is a genus of some 30 species, of which 4 have been included in the analysis. They form a well-supported clade with high support at all nodes. *Lysionotus* has never been considered a problematic genus and is morphologically well defined (epiphytic subshrubs, flowers diandrous, seeds with a hair-like appendage at the apical end and a capillary funicle at the hilar end). For its likely close relationship with *Anna*, see above.

Ornithoboea

Though only 2 species of this genus of 11 species have been included in the analysis, we are confident that *Ornithoboea* will stand as a good genus. The species have a most characteristic corolla (with upper lip of two short blunt lobes, lower lip much larger, three-lobed; palate with a beard of large unicellular club-shaped hairs; a line of hairs forming a circlet around the corolla), two fertile stamens and twisted fruits. The latter character is reflected in the position of the clade within the "advanced Asiatic genera with twisted fruits". Also the sister clade (*Rhabdothamnopsis* + *Kaisupeea*) consists of taxa with twisted fruits.

Paraboea

From this large genus of more than 100 species, 4 species have been included in the present analysis. They form a clade, but support is not very high. However, together with the sister clade (*Trisepalum* + *Phylloboea*) a clade of high support results. In other trees (Möller et al. 2009) *Trisepalum* appeared nested within *Paraboea*. Further studies are underway to settle the status of *Paraboea*.

Petrocosmea

From this genus of some 27 species, 4 species (representing all three sections distinguished by Wang 1985) have been included in the analysis. They form a well-supported clade in an otherwise ill-defined complex of taxa. So there is good evidence that *Petrocosmea* is monophyletic.

Ridleyandra

From this genus of over 20 species, established recently by Weber and Burtt (1998b) with two sections, 3 species have

been included in the analysis. They form a well-supported clade that is (along with the monotypic *Conandron*) sister to *Hexatheca* and *Cyrtandra.* The three species all belong to the type section (sect. *Ridleyandra,* corolla usually long-tubed, Malay peninsula). Whether the species of sect. *Stilpnothrix* (corolla campanulate or flat-faced, Borneo) join remains to be seen.

Poly- and paraphyly of genera

The most surprising result of the present study was that in the "advanced Asiatic and Malesian genera" more than a third, specifically 17, were found not to be monophyletic (Figs. 1, 2; Table 2). The likely polyphyly of genera such as *Briggsia*, *Chirita* and *Henckelia* was already indicated in earlier papers (Möller et al. 2009; Wei et al. 2010) and is here, based on a much larger sampling, further corroborated. In a number of cases the indicated polyphyly is above all doubt (and also can be retraced morphologically); in other cases support is still weak, and further studies are required before any taxonomic conclusions can be drawn.

Ancylostemon

This is a genus of a dozen Chinese species belonging to the *Oreocharis* alliance (Wang et al. 1998), which position is clearly reflected in the present phylograms. Three species have been included in our analysis. They fell in two subclades of the "*Oreocharis*-dominated clade": one (*A. ronganensis*) into the first subclade, forming a well-supported sister pair with *Briggsia stewardii* (a strikingly similar species with regard to habit, flower form and pink flower coloration), while two (*A. aureus* and *A. convexus*) formed a well-supported clade in the second subclade. The latter two belong to the core group with yellow-orange flowers and their close relationship is evident. In conclusion, *Ancylostemon* seems to be (at least) diphyletic.

Boea

The genus *Boea* was redefined in the recent past by Burtt (1984), representing a small group of ca. 14 species characterised by simple straight hairs and consistently twisted fruits versus the much larger *Paraboea* (ca. 100 species) with an indumentum of interwoven arachnoid hairs and variable (twisted or straight) fruits. Even in this restricted sense, *Boea* does not seem to represent a natural genus. Two species (*B. hygrometrica,* China, and *B. philippensis,* the Philippines) fell as sister to the rest of the clade of the advanced Asiatics with twisted fruits, while *B. magellanica* (the type species of *Boea,* Papua

New Guinea and surrounding Islands) grouped—surprisingly and inexplicably—with the monotypic genera *Senyumia* and *Spelaeanthus* from the Malay peninsula. For this enigma and the fact that only three species (out of 14) have been included here, we abstain from a detailed discussion and leave this genus to be dealt with in a more focused, separate paper where more species samples of the complex with twisted fruits are included.

Briggsia

At present, over 20 species are recognised in *Briggsia.* Our samples (eight species) fell in six positions: in three different places in the *Oreocharis*-dominated clade, in two places (weakly supported) near the clade comprising mainly *Pseudochirita/Loxostigma* and *Petrocosmea*, and as a (weakly supported) sister clade to the *Hemiboea/Metabriggsia* clade.

It is well known that the genus is not well defined (p 272, Wang et al. 1998), and particularly three species treated in the "Flora of China", *B. kurzii*, *B. longicaulis* and *B. dongxingensis,* had been earmarked to belong probably to *Loxostigma.* They are clearly caulescent (with 10–60 cm tall stems) and have herbaceous, not leathery, leaves similar to *Loxostigma*; only the absence of seed appendages suggested their placement in *Briggsia* (see Wang et al. 1998; reversely, Burtt 1975 had transferred *Briggsia kurzii*, the only species of the alliance then known, to *Loxostigma*). Two of the three species in question, namely *B. kurzii* and *B. dongxingensis*, have been included in our analysis. Though they did not cluster directly with *Loxostigma*, they fell as sister to the clade comprising *Loxostigma* and *Pseudochirita.* It is likely that the third species, *B. longicaulis*, will fall here as well.

The morphologically similar *Briggsia longipes* and *B. mihieri* (differing from each other only in degrees of leaf shape, leaf margin and peduncle pubescence) formed a strong sister relationship in our analysis. Their clade is near *Hemiboea*, but in an unsupported position and thus difficult to comment on at this point.

Briggsia longifolia (the type species), *B. muscicola* and *B. stewardii,* all with rosette habit, fell in three positions in the clade dominated by *Oreocharis.* At present it is difficult to speculate on the reasons for the scattered appearance of the *Briggsia* samples in this clade, as most positions were not well supported. However, *B. stewardii* and *Ancylostemon ronganensis* formed a strongly supported sister relationship. Indeed, they were found to be very similar in their sequences (identical in *trn*L-F), and a comparison of their morphology indicated very few differences, and there is little doubt that these two species, though traditionally referred to distinct genera, are closely related or may even be conspecific.

Calcareoboea

The genus was originally established with *C. coccinea* as a monotpyic genus (Li 1982). This is a rosette plant with scapose inflorescences of spectacular red flowers (with upper lip of four short teeth and a tongue-like lower lip), apparently addressed to bird pollinators. For reasons morphologically difficult to understand at first sight, Burtt (2001b) added a second species in that he transferred *Didymocarpus bonii* to *Calcareoboea*. In the same paper he also announced the transfer of *Didymocarpus hancei* to that genus (which, however, was never made). Both species of "*Didymocarpus*" exhibit little similarity to *Calcareoboea*. Two species of this trio (*Calcareoboea coccinea* and *Didymocarpus hancei*) were included in our analysis and indeed fell into the same clade, viz. the *Petrocodon* clade. Though they did not form a sister pair (proving definitely the congenerity), the predicted relationship is remarkable.

Chirita

The polyphyly of *Chirita* was indicated in previous papers (Möller et al. 2009; Wei et al. 2010). Detailed studies relating specifically to *Chirita* and *Henckelia* are underway, based on the inclusion of more species in all lineages. Therefore, no comments are given here.

Chiritopsis

The two *Chiritopsis* species analysed (out of the nine species of the genus) fell in grades in the *Primulina* clade among the species of *Chirita* sect. *Gibbosaccus*. The non-monophyly of *Chiritopsis* was shown earlier (Li and Wang 2007), based on a larger sampling (six species covering the two sections *Chiritopsis* and *Schistophyllos*), and will be treated in more detail in the announced study of *Chirita* and *Henckelia*.

Didymocarpus

This genus, in its restricted sense (Weber and Burtt 1998c), proved monophyletic in the present analysis, with the exception of two species: *D. cortusifolius*, which fell in a clade with *Allocheilos guangxiensis* and the species of *Gyrocheilos*, and *D. hancei* (for that species see under "*Calcareoboea*"). At the moment, the topology is difficult to interpret in terms of poly- or paraphyly.

Hemiboea

Hemiboea proved to be a well-supported group (sister to the clade of *Briggsia longipes* and *B. mihieri*), but with the

two species of *Metabriggsia* nesting in different positions in the genus. For further comments, see "Metabriggsia".

Henckelia

The polyphyly of *Henckelia* (sensu Weber and Burtt 1998c) was indicated already in Möller et al. (2009). Detailed studies are in progress (see comments under "Chirita").

Isometrum

It is well known that *Isometrum* belongs into the *Oreocharis* alliance (p 251, Wang et al. 1998), and this is reflected in the present analysis. However, the three species (out of 14) included, each falls into a different part of the *Oreocharis*-dominated clade.

Lagarosolen

Six species of *Lagarosolen* have been included in the analysis and turned up in scattered positions in a clade comprising also *Paralagarosolen* (monotypic), *Dolicholoma* (monotypic), *Tengia* (monotypic), *Calcareoboea*, *Petrocodon* (two species each) and *Didymocarpus hancei*. This *Petrocodon* clade proved, along with the *Oreocharis*-dominated clade, to be the best-supported clade of the advanced Asiatics with straight fruits.

Metabriggsia

Though the name suggests a close affinity to *Briggsia* (differing in the presence of only two fertile stamens and only one carpel being fertile from *Briggsia*, Wang 1983), the two species of *Metabriggsia* definitely belong in the alliance of *Hemiboea* and appear nested within that genus (in different places) in the present analysis.

Opithandra

This genus is close to *Oreocharis* and distinguished by the presence of only two (vs. four) fertile stamens (Burtt 1956, 1958). But it is not, as usual, the posterior stamen pair that is reduced, but the anterior one. In other words, it is the adaxial pair that persists in a functional state. This condition is very rare in Gesneriaceae (otherwise only known from *Sarmienta*, *Epithema* and the problematic *Sepikea*) and thus might be considered as a good synapomorphy of *Opithandra*. However, in view of the considerable variation of the (then six) species known to Burtt (1958), he sent out a signal of warning: "…it cannot be gainsaid that *Opithandra* is a somewhat artificial genus…" and that it would be possible "…that these species have all been

derived independently from different tetrandrous ancestors…". The position of the three species included in the analysis, on two lineages at the base of the phylogenetic tree, hints that the adaxial stamens are an ancestral condition for the *Oreocharis*-dominated clade from which tetrandry evolved, though such a scenario is not well supported given the absence of branch support in this area of the tree.

Oreocharis

Oreocharis is a fairly large genus, comprising nearly 30 species, 6 of which have been included in our analysis. They fell in four different positions within the *Oreocharis*-dominated clade, which proved—along with the *Petrocodon* clade—one of the best-supported larger clades of the advanced Asiatic genera with straight fruits. The phylogram (Fig. 3) shows a very long branch leading to the first node, a considerable depth of this clade, but rather short backbone branches, suggesting a phase of rapid radiation at the beginning of the diversification of the group.

This is likely the reason that most relationships in this clade were not well supported, except a clade comprising four *Oreocharis* species: *O. argyreia* grouped with *Isometrum lungshengense* (but with weak support) and *O. aurea* (in the second subclade) with *Tremacron begoniifolium* (with likewise weak support). The interpretation of the scattered appearance of the *Oreocharis* species in the clade is difficult. Either the genus is polyphyletic by convergence, or the species represent relicts of a once larger and widespread genus, within which the many other groups and monotypic genera evolved (paraphyly). Obviously, more species are in need of being included in future analyses.

Satellite genera of *Oreocharis* are the very small or monotypic genera *Thamnocharis*, *Paraisometrum*, *Deinocheilos* and *Dayaoshania*. The two latter have flowers with only two fertile stamens (or sometimes only one in *Dayaoshania*), but—in contrast to *Opithandra*—it is the adaxial stamen pair that is reduced. The *Oreocharis*-dominated clade is thus an exemplary alliance demonstrating the independent reduction of stamens, both with regard to the adaxial and abaxial ones.

Petrocodon

The two species of *Petrocodon* did not form a sister relationship, but formed a well-supported clade also comprising *Lagarosolen coriaceifolius* and the monotypic *Tengia* (characterised by urceolate, actinomorphic flowers with five stamens). The close relationship of *Tengia* and *Petrocodon* (with zygomorphic, diandrous flowers) was predicted already by Burtt (1970). He was the first to suggest that in the Gesneriaceae actinomorphic flowers have

evolved from zygomorphic flowers and used *Tengia* and *Petrocodon* as a striking example. In both species the corolla is or tends to be urceolate, and is thus very different from *Lagarosolen* (long- and narrow-tubed funnel-shaped corolla) and other members of the clade, in which *Petrocodon* is situated.

Raphiocarpus

The six samples of *Raphiocarpus* each fell in separate positions. *Raphiocarpus sinicus,* the type species, fell sister to *Lysionotus,* and the clade *Lysionotus/Raphiocarpus sinicus* sister to *Anna* (with some PP support). As will be shown elsewhere, the seeds of *Anna* and *Raphiocarpus sinicus* indeed share a very similar testa pattern, and a closer relationship is probable.

Three other species, *R. begoniifolius*, *R. petelotii* and *R. sesquifolius,* fell in grades with *Allostigma guangxiensis* as sister to the last species. Superficially, the latter closely resembles *Pseudochirita* of the sister clade, though *Allostigma* has a bilocular ovary, while *Pseudochirita* has, like *Raphiocarpus*, a unilocular ovary. The phylogenetic relationships are not well supported here, and more data are needed to fully understand the relationships between *Allostigma* and *Raphiocarpus*. At any rate, the polyphyly of *Raphiocarpus* is not a great surprise. Its probable artificial nature was already mentioned when it was re-established for accommodation of the Chinese species described under *Didissandra*, but not being related with the Malesian species of true *Didissanda* (Weber and Burtt 1998a).

Tremacron

This is another genus of the *Oreocharis* alliance (Wang et al. 1998), and that placement is confirmed here. The genus has seven species, four of which (including the type species, *T. forrestii*) have been included in the analysis. All fall in one of the two subclades of the *Oreocharis*-dominated clade: two (plus *Isometrum lancifolium*) groups with the type species, the third groups with *Oreocharis aurea* (but with weak support). To fully resolve the species relationships here, more data are needed.

Wentsaiboea

This was recently described as a monotypic genus (Fang and Qin 2004), but two further species have now been described, named *W. luochengensis* and *W. tiandengensis* (Liu et al. 2010). In our analysis, *W. renifolia* (the type species) and *W. luochengensis* formed a sister pair in the clade with the species of *Chirita* sect. *Gibbosaccus*, while *W. tiandengensis* fell in a different clade, closest to *Lagarosolen lui*.

Monotypic and small genera

Our study suggests that B.L. Burtt (personal communication) was right in his assumption that too many genera, and particularly too many monotypic genera, have been established, particularly among the Chinese Gesneriaceae. We have found close relationships for a good number of monotypic and small (essentially Chinese) genera: *Allocheilos* (close to *Gyrocheilos* and *Didymocarpus cortusifolius*), *Bournea* (*Oreocharis*-dominated clade), *Briggsiopsis* (close to *Raphiocarpus macrosiphon*), *Calcareoboea* (*Petrocodon* clade), *Dayaoshania* (*Oreocharis*-dominated clade), *Deinocheilos* (*Oreocharis*-dominated clade), *Dolicholoma* (*Petrocodon* clade), *Hemiboeopsis* (close to *Chirita* sect. *Chirita*), *Paraisometrum* (*Oreocharis*-dominated clade), *Paralagarosolen* (*Petrocodon* clade), *Primulina* (*Chirita* sect. *Gibbosaccus*-dominated), *Pseudochirita* (sister to *Loxostigma*), *Tengia* (*Petrocodon* clade) and *Thamnocharis* (*Oreocharis*-dominated clade). These genera and alliances will be treated in detail in forthcoming papers. There is promise that at least some can be sunk into synonymy.

Four Chinese genera remain phylogenetically problematic: *Allostigma*, *Cathayanthe*, *Conandron* and *Metapetrocosmea*. These occupied unsupported positions in the phylogenetic trees. This suggests that they are genetically quite distinct from other genera, and as such seem to represent good genera, possibly remnants of larger groups that have become largely extinct, or have not yet been discovered, as the recent example of *Litostigma* indicates. Interestingly, *Cathayanthe* possesses fleshy plagiocarpic fruits, a combination that is unique in Gesneriaceae. Its phylogenetic position is in the vicinity of but not with *Cyrtandra*, another genus with fleshy fruits. Given the absence of branch support in this area of the tree, it would be interesting to see where the genus settles once more data become available, whether the fleshiness of its fruits is linked to *Cyrtandra* or represents a parallel event, such as in *Rhynchotechum*.

The monotypic genera *Emarhendia*, *Orchadocarpa*, *Phylloboea*, *Rhabdothamnopsis*, *Senyumia* and *Spelaeanthus* fell in the predominantly twisted-fruited *Boea* group and will be studied in more detail in due course. More species need to be added before the full picture can emerge.

Genera not included in the analysis

With regard to the "advanced Asiatic and Malesian genera" (as defined in the introduction), numbering 60 genera, only three remain unstudied, *Beccarinda*, *Deinostigma* and *Sepikea*. The authors aim to include these in future studies. The placement of *Beccarinda* with the basal Asiatic genera was already hinted at (see above).

Conclusions

We think that with the present data another important step towards a better understanding of the Old World Gesneriaceae and its phylogenetic differentiation has been made. Previously we have shown that the available tribal arrangements of this group were highly artificial and must be redefined (Weber 2004; Möller et al. 2009). In the present paper, we demonstrate that current generic delineations are far from perfect, with many genera not forming monophyletic lineages. In many cases, the reasons lie in the insufficient or incomplete taxonomic knowledge of the genera. Particularly for the many Chinese genera, key characteristics are often not known or not recorded (e.g. fruit structure and dehiscence mode; completely unknown in the genus *Paraisometrum*, *Metabriggsia purpureotincta* and in many species of *Ancylostemon*, *Briggsia*, *Isometrum*, *Opithandra* and *Tremacron*; seed types unknown, e.g. in *Calcareoboea*, *Dayaoshania*, *Lagarosolen*, *Paraisometrum* and *Thamnocharis*). Generally, flower morphology is better known, but characters such as anther fusion, anther dehiscence, corolla form, etc., are often difficult to establish from (sometimes very scanty or bad) herbarium material.

Single character taxonomy is another problem. It becomes increasingly clear that Gesneriaceae are prone to parallelisms and reversals (e.g. parallel and independent origin of actinomorphic flowers in *Bournea*, *Conandron*, *Ramonda*, *Tengia* and *Thamnocharis* (Möller et al. 1999, 2009; Wang et al. 2010), parallel changes in flower zygomorphy, with the upper lip becoming undivided in *Gyrocheilos*, *Deinocheilos* and species of *Ancylostemon*; or four-lobed in *Allocheilos*, *Paraisometrum*, *Calcareoboea coccinea* and *Ancylostemon saxatile*, manifold parallel reduction of anterior or posterior stamen pair, parallel loss of fertility of one carpel in *Hemiboea*, *Briggsiopsis*, *Hemiboeopsis*—apparently closer to *Chirita* sect. *Chirita* rather than to *Hemiboea*, and species of *Chirita* sect. *Gibbosaccus*). The need for a combination of characters for defining genera is obvious. Nonetheless, also combinations of characters may be subject of parallelisms, especially when functionally tied together. Therefore, in modern systematics the combination of molecular and morphological data is inevitable. "With molecular systematics and morphology (in its widest sense) we are able to combine two independent and equally potent disciplines into a system of mutual elucidations. Morphology must serve as a tool for recognition of weaknesses in molecular classifications and vice versa. The resulting spiral of increasing knowledge and accuracy should replace the unidirectional approach of morphological and molecular systematics" (Weber 2003, p 3). With respect to the didymocarpoid Gesneriaceae, our study highlights many taxonomic

problems, and these need to be clarified by proper investigations of proper specimens in a concerted effort. It provides the framework for many future studies that can be targeted at specific problems. This top-down approach is urgently needed to create stable generic boundaries.

Further work also needs to focus at solving inter-clade relationships, and the appropriate way forward will be the addition of more molecular markers and preferentially conserved chloroplast sequences in order to obtain support for the backbone topology of the phylogenetic trees.

We have come a long way, but we have to finish again with the last sentence of our previous paper (Möller et al. 2009): 'much work is waiting'.

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