



A new delineation for *Oreocharis* incorporating an additional ten genera of Chinese Gesneriaceae

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Abstract

Based on molecular data and a morphological evaluation, evidence is provided that the species of eleven, mostly small-sized and monotypic genera of Chinese Gesneriaceae (*Ancylostemon*, *Bournea*, *Briggsia* s.str., *Dayaoshania*, *Deinocheilos*, *Isometrum*, *Opithandra*, *Oreocharis*, *Paraisometrum*, *Thamnocharis*, *Tremacron*) form a highly-supported group in which the species interrelationships run across traditional generic boundaries. The data confirm previous doubts on the naturalness of some of these genera and, after a detailed discussion of the particular genera, the conclusion is reached that the whole group is best regarded as a single genus, *Oreocharis*, which is thus expanded to comprise over 80 species. A list of the species is given and the necessary transfers are made. The new delimitation provides a framework for studying the species relationships and working out an infrageneric classification. *Oreocharis* provides an excellent example of a major monophyletic group that has experienced a rapid radiation early in its evolution and shows manifold convergences in floral characters (corolla form and coloration, fertility of stamens, anther shape and dehiscence mode), apparently reflecting different pollination strategies, but has little variation in vegetative habit and fruit structure.

Key words: *Ancylostemon*, *Bournea*, *Briggsia*, *Dayaoshania*, *Deinocheilos*, *Isometrum*, Lamiales, molecular systematics, *Opithandra*, *Paraisometrum*, pollination syndromes, *Thamnocharis*, *Tremacron*

Introduction

Recent molecular phylogenetic work on the Old World Gesneriaceae has revealed a high level of polyphyly on the one side, and species relationships running across traditional generic boundaries on the other (Möller *et al.* 2009, 2011). Examples include the several different lineages of *Chirita* Buch.-Ham. ex Don (1825: 89)—the one including the type now being included in *Henckelia* Sprengel (1817: 402)—and the expanded definitions of *Hemiboea* Clarke (1888: t. 1798) and *Petrocodon* Hance (1883: 167; Wang *et al.* 2011, Weber *et al.* 2011a, b, c).

In the present paper we focus on a case where molecular data suggest an extreme restructuring of existing genera and their union into one: *Oreocharis*. In this paper, we will define this genus anew to include species from 11 previously accepted genera (or 14 if the previously synonymised genera *Dasydesmus*, *Perantha* and *Schistolobos* are taken into account). A strongly supported clade comprising samples of *Oreocharis* mixed with species from several other genera was already found by Möller *et al.* (2011). In that work the clade included 29 samples of 28 species. Here, we increase the sampling in this *Oreocharis*-dominated clade to 43 samples, representing 39 species. The clade, and the new generic definition based upon it, is characterised by

rather uniform vegetative habit and fruit characters, but high diversity in floral traits, particularly in corolla shape and colour, and in stamen fertility.

We use molecular data of two gene regions, the chloroplast *trnL-F* intron-spacer and the nuclear ribosomal ITS regions, for the reconstruction of phylogenetic relationships. These have proven useful in many previous analyses of Gesneriaceae at genus and species level (Möller *et al.* 1999, 2009, 2011, Zimmer *et al.* 2002, Smith *et al.* 2004, Roalson *et al.* 2005, Li & Wang 2007, Wei *et al.* 2010a, Weber *et al.* 2011a, b, c).

Prior to the analysis presented here, we included the newly added samples in the large matrices of Weber *et al.* (2011a) to confirm that these fall in the *Oreocharis*-dominated clade. This top-down approach is critical, particularly for an analysis of Old World didymocarpoid Gesneriaceae, where it is sometimes difficult to predict which species or even genera to include in a particular analysis, since generic delineation, particularly for those found in China, is poorly supported by morphology. Such a case was previously found in the clade dominated by *Lagarosolen* Wang (1984: 11), which included species from seven genera and gave rise to a new definition of *Petrocodon* (Weber *et al.* 2011b).

Material and Methods

Plant material

Silica gel dried leaf material for newly acquired sequences was obtained during recent field collections (Table 1). The bulk of the data came from previous work (Möller *et al.* 2009, 2011, Weber *et al.* 2011a). Data for eight samples were newly acquired and seven downloaded from GenBank (Table 1). In total, 55 samples were included in the analyses, representing 51 species (including one new species), one variety and three duplicate species samples (*Dayaoshania serrulata* sp. *ined.*, *Oreocharis auricula*, *Paraisometrum mileense*).

TABLE 1: List of the 55 didymocarpoid Gesneriaceae samples included in the phylogenetic analysis, including voucher number and deposition, origin information and respective GenBank accession numbers. Names in bold denote generic type species.

Taxon	Voucher number	Deposited in	Origin	trnL-F	ITS or ITS1 / ITS2
<i>Aeschynanthus lancilimbus</i> W.T.Wang (1975: 64)	<i>Y.Z.Wang S-10868</i>	PE	China, unknown locality	FJ501499	HQ632992
<i>Aeschynanthus rhododendron</i> Ridley (1896: 500)	<i>P.Woods 600 [Cult. RBGE 19680624]</i>	E	Peninsular Malaysia, Genting Highlands	HQ632895	FJ501333
<i>Aeschynanthus micranthus</i> C.B.Clarke (1883: v. 27)	<i>M.Möller MMO 01-79</i>	E, WU	China, Yunnan, Hekou county	FJ501500	-
<i>Aeschynanthus micranthus</i> C.B.Clarke (1883: v. 27)	<i>A.Reid & J. Fernie 004 [Cult. RBGE 19951561]</i>	E	China, Yunnan, Xishuangbanna Dai Aut. Pref.	-	AF349218 / AF349299
<i>Agalmyla clarkei</i> (Elmer) B.L.Burtt (1968: 224)	<i>RBGE-PNH1999(P99) 13 [Cult. RBGE 19991911]</i>	E	Philippines, Leyte Island, Mt. Lobi	FJ501540	-
<i>Agalmyla clarkei</i> (Elmer) B.L.Burtt (1968: 224)	<i>RBGE-PNH1997 IS26 [Cult. RBGE 19972530A]</i>	E	Philippines, Luzon, Barangay Penicuason	-	FJ501360
<i>Agalmyla paucipilosa</i> Hilliard & B.L.Burtt (2002: 80)	<i>Smith & Galloway 261</i>	E	Indonesia, Sulawesi, Mt Rantemario	HQ632893	HQ632990
<i>Agalmyla sojoliana</i> Hilliard & B.L.Burtt (2002: 78)	<i>Smith & Galloway 321</i>	E	Indonesia, Sulawesi, Mt Sojol	HQ632894	HQ632991

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TABLE 1 (continued)

Taxon	Voucher number	Deposited in	Origin	trnL-F	ITS or ITS1 / ITS2
<i>Ancylostemon aureus</i> (Franch.) B.L.Burtt (1958b: 305).	<i>M.Möller MMO 01-153</i>	E, WU	China, Yunnan, Binchuan county	FJ501505	FJ501336
<i>Ancylostemon convexus</i> Craib (1920a: 235)	<i>M.Möller MMO 01-176</i>	E, WU	China, Yunnan, Dali county	FJ501506	FJ501337
<i>Ancylostemon humilis</i> W.T.Wang (1975: 100)	<i>Liang R.H.SC-YB</i>	PE	China, Sichuan	GU350665	GU350633
<i>Ancylostemon mairei</i> (H.Lév.) Craib (1920b: 267)	<i>Liang R.H.YN-Qj</i>	PE	China, Yunnan	GU350689	GU350658
<i>Ancylostemon rhombifolius</i> K.Y.Pan (1988a: 435)	<i>Liang, R.H. LRH-07-01</i>	PE	China, Sichuan	GU350664	GU350632
<i>Ancylostemon ronganensis</i> K.Y.Pan (1988a: 436)	<i>M.Möller MMO 06-776</i>	E	China, Guangxi, Rongan county	HQ632927	HQ633023
<i>Bournea leiophylla</i> (W.T.Wang) W.T.Wang & K.Y.Pan in Wang <i>et al.</i> (1990: 135)	<i>Zhou X.R. ZXR-05-01</i>	PE	China, Fujian	GU350676	GU350644
<i>Bournea sinensis</i> Oliver in Hooker (1893: t. 2254)	<i>M.Möller MMO 08-1329</i>	E	China, Guangdong, Bolou county	HQ632912	HQ633008
<i>Briggsia longifolia</i> Craib (1920a: 238)	<i>M.Möller MMO 08-1239</i>	E	China, Yunnan, Jingdong county	HQ632934	HQ633030
<i>Briggsia muscicola</i> Craib (1920b: 264).	Kew (1995-2229)	K	unknown origin	FJ501548	FJ501366
<i>Briggsia rosthornii</i> (Diels) B.L.Burtt (1958b: 306)	<i>Sino-American Bryological Expedition, no. 398 (US 229325)</i>	US	China, Guizhou, Jiangkou county	FJ501547	FJ501365
<i>Briggsia stewardii</i> Chun (1946: 303)	<i>M.Möller MMO 06-917</i>	E	China, Guangxi, Shanjiang county	HQ632926	HQ633022
<i>Cyrtandra cumingii</i> C.B.Clarke (1883: v. 263)	<i>G.Kokubugata 11134</i>	TNS	Japan, Ruykyus, Iriomote Island	HQ632905	HQ633002
<i>Cyrtandra pendula</i> Blume (1826: 768)	<i>A.Weber & Anthony 860730-1/2 [Cult. HBV]</i>	WU	Peninsular Malaysia, Negeri Sembilan, Kuala Pilah distr., Jeram Toi	FJ501530	FJ501354
<i>Cyrtandra pulchella</i> W.P.Rich ex A.Gray (1862: 38)	<i>Lorence 8525</i>	PTBG	Samoa Islands	HQ632906	EU919941
<i>Dayaoshania cotinifolia</i> W.T.Wang (1983a: 320)	<i>Q.M.Chuan 01</i>	IBK	China, Guangxi, Jinxiu conuty	HQ632914	HQ633010
<i>Dayaoshania serrulata</i> Yan Liu & W.B.Xu sp.ined. 1	<i>F.Wen 0901</i>	IBK	China, Guangxi, Wuzhou City	JF687580	JF697568
<i>Dayaoshania serrulata</i> Yan Liu & W.B.Xu sp.ined. 2	<i>F.Wen 2010-04</i>	IBK	China, Guangxi, Wuzhou City	JF697581	JF697569
<i>Deinocheilos jiangxiense</i> W.T.Wang (1986: 4)	<i>M.Möller MMO 09-1451</i>	E	China, Fujian, Jiangle county	HQ632933	HQ633029
<i>Didymocarpus citrinus</i> Ridley (1896: 508)	<i>P.Davis 69437 [Cult. RBGE 19830510]</i>	E	Peninsular Malaysia, Perlis, Kedah Peak	AJ492293	DQ912669
<i>Didymocarpus purpureobracteatus</i> W.W.Smith (1912: 153)	<i>Y.Z.Wang 991106</i>	PE	China, Yunnan, Pingbian county	FJ501510	-

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TABLE 1 (continued)

TAXON	VOUCHER NUMBER	DEPOSITED IN	ORIGIN	trnL-F	ITS OR ITS1 / ITS2
<i>Didymocarpus purpureobracteatus</i> W.W. Smith (1912: 153)	<i>M.Möller MMO 01-70</i>	E, WU	China: Yunnan, Pingbian county	-	DQ912676
<i>Didymocarpus stenanthos</i> C.B.Clarke (1888: t. 1799)	<i>M.Möller MMO 01-156</i>	E, WU	China, Yunnan, Binchuan county	FJ501512	DQ912687
<i>Isometrum farreri</i> Craib (1920a: 250).	<i>Zhou Ping ZP 2010-020</i>	E	China, Shaanxi, Mian county	JF697585	JF697573
<i>Isometrum lancifolium</i> (Franch.) K.Y.Pan (1986: 30)	<i>M.Möller MMO 09-1624</i>	E	China, Sichuan, Mianning county	HQ632924	HQ633020
<i>Isometrum lungshengense</i> (W.T.Wang) W.T.Wang & K.Y.Pan in Wang <i>et al.</i> (1990: 187)	<i>M.Möller MMO 06-916</i>	E	China, Guangxi, Longsheng county	HQ632917	HQ633013
<i>Isometrum primuliflorum</i> (Batalin) B.L.Burtt (1960: 93)	<i>M.Möller MMO 09-1605</i>	E	China, Sichuan, Danba county	HQ632923	HQ633019
<i>Opithandra acaulis</i> (Merr.) B.L.Burtt (1958a: 303)	<i>M.Möller MMO 08-1328</i>	E	China, Guangdong, Zhaoqing county	HQ632916	HQ633012
<i>Opithandra burtii</i> W.T.Wang in Weitzman <i>et al.</i> (1998: 430)	<i>F.Wen 2010-05</i>	IBK	China, Guangdong, Wengyuan county	JF697582	JF697570
<i>Opithandra dalzielii</i> (W.W.Sm.) B.L.Burtt (1958a: 303)	<i>F.Wen 2010-06</i>	IBK	China, introduced from Guangdong, Shantou county	JF697583	JF697571
<i>Opithandra dinghushanensis</i> W.T.Wang (1987: 10)	<i>Lin Q.B. LQB06-01</i>	PE	China, Guangdong, Zhaoqing	GU350675	GU350643
<i>Opithandra primuloides</i> (Miq.) B.L.Burtt (1956: 162)	<i>T.Tsuzuki [Cult. RBGE 19842178A]</i>	E	Japan, unknown locality	FJ501546	FJ501364
<i>Opithandra sinohenryi</i> (Chun) B.L.Burtt (1958a: 303)	<i>M.Möller MMO 07-1150</i>	E	China, Guangxi, Fangcheng county	HQ632913	HQ633009
<i>Oreocharis argyreia</i> Chun ex K.Y.Pan (1987: 283)	<i>M.Möller MMO 07-1131</i>	E	China, Guangxi, Wuming county	HQ632919	HQ633015
<i>Oreocharis argyreia</i> var. <i>angustifolia</i> K.Y.Pan (1987: 285)	<i>Liang R.H. GX-SS-01</i>	PE	China, Guangxi	GU350671	GU350639
<i>Oreocharis aurea</i> Dunn (1908b: 19)	<i>M.Möller MMO 06-980</i>	E	China, Yunnan, Jinping county	HQ632920	HQ633016
<i>Oreocharis auricula</i> 1 (S.Moore) C.B.Clarke (1883: 64)	<i>M.Möller MMO 03-304</i>	E	China; Guizhou, Jiangkou county	FJ5011481	FJ501323
<i>Oreocharis auricula</i> 2 (S.Moore) C.B.Clarke (1883: 64)	<i>Liang R.H. GX-LG-02</i>	PE	China; Guangxi	GU350672	GU350640
<i>Oreocharis benthamii</i> C.B.Clarke (1883: 63)	<i>M.Möller MMO 08-1317</i>	E	China, Guangdong, Zhao Qin	JF697584	JF697572
<i>Oreocharis dasyantha</i> var. <i>ferruginosa</i> K.Y.Pan (1987: 283)	<i>Y.G.Wei 07-700</i>	E	China, Hainan, Delong	HQ632918	HQ633014
<i>Oreocharis henryana</i> Oliver in Hooker (1890: t. 1944)	<i>M.Möller MMO 10-1691</i>	E	China, Sichuan, Lushan county	JF697586	JF697574
<i>Oreocharis magnidens</i> Chun ex K.Y.Pan (1987: 276)	<i>M.Möller MMO 06-896</i>	E	China, Guangxi, Jinxiu county	HQ632930	HQ633026

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TABLE 1 (continued)

TAXON	VOUCHER NUMBER	DEPOSITED IN	ORIGIN	trnL-F	ITS OR ITS1 / ITS2
<i>Oreocharis xiangguinensis</i> W.T.Wang & K.Y.Pan in Pan (1987: 285)	<i>M.Möller MMO 05-741</i>	E	China, Guangxi, Lingui county	HQ632932	HQ633028
<i>Paraisometrum mileense</i> 1 W.T.Wang in Weitzman <i>et al.</i> (1998: 434)	<i>Y.M.Shui 65214</i>	KUN	China, Yunnan, Shilin county	HQ632928	HQ633024
<i>Paraisometrum mileense</i> 2 W.T.Wang in Weitzman <i>et al.</i> (1998: 434)	<i>Y.G.Wei 0901</i>	IBK	China, Guangxi, Longlin	JF697587	JF697575
<i>Thamnocharis esquirolii</i> (H.Lév.) W.T.Wang (1981: 485)	<i>D.W.Zhang 723</i>	IBK	China, Guizhou, Anlong county	HQ632915	HQ633011
<i>Tremacron aurantiacum</i> K.Y.Pan (1988a: 431)	Voucher from Cult. RBGE 20060865	E	China, unknown locality	HQ632925	HQ633021
<i>Tremacron begoniifolium</i> H.W.Li (1983: 12)	<i>M.Möller MMO 08-1221</i>	E	China, Yunnan, Jingdong county	HQ632929	HQ633025
<i>Tremacron forrestii</i> Craib (1918: 217)	<i>M.Möller MMO 07-1072</i>	E	China, Sichuan, Pan Zhi Hua city	HQ632921	HQ633017
<i>Tremacron urceolatum</i> K.Y.Pan (1988a: 429)	<i>M.Möller MMO 09-1633</i>	E	China, Sichuan, Liangshan Yizu county	HQ632922	HQ633018

In previous analyses the *Oreocharis*-dominated clade was shown to be highly supported and had the longest branch length leading to the clade (Möller *et al.* 2011, Weber *et al.* 2011a). To ensure the newly acquired sequences fell in the *Oreocharis*-dominated clade, we used a top-down approach and added these to the comprehensive didymocarpoid Gesneriaceae matrix of Weber *et al.* (2011a; in total then comprising 259 samples), and found that all 15 newly added samples fell inside the *Oreocharis*-dominated clade (data not shown). This gave us confidence in the validity of our analysis here, which is focussed on the *Oreocharis*-dominated clade. Based on the results from the extended analysis and previously published data (Möller *et al.* 2009, 2011, Weber *et al.* 2011a), we selected three species each of the genera *Agalmyla* Blume (1826: 766), *Aeschynanthus* Jack (1823: 42), *Cyrtandra* Forster & Forster (1776: t. 3) and *Didymocarpus* Wallich (1819: 378) as outgroup samples, and the trees were rooted on *Didymocarpus*.

The ingroup comprised 43 samples. These belonged to 11 genera. For 10 genera all samples included fell within the ingroup; *Ancylostemon* (6 included/12 described), *Bournea* (2/2), *Dayaoshania* (2/2), *Deinocheilos* (1/2), *Isometrum* (4/14), *Opithandra* (6/10), *Oreocharis* (8/28), *Paraisometrum* (1/1), *Thamnocharis* (1/1), and *Tremacron* (4/7). Only four of the eight included species of *Briggsia* in previous work (out of 22 described) fell in the *Oreocharis*-dominated clade (*B. longifolia*, *B. muscicola*, *B. rosthornii*, *B. stewardii*) (Möller *et al.* 2011).

DNA extraction, PCR, and sequencing

The molecular methods followed previously published protocols (Möller *et al.* 2009, 2011, Weber *et al.* 2011a). For all samples sequences of both the *trnL-F* intron-spacer (*trnL-F*) and the ITS region were available for analysis. Newly acquired sequences were deposited in GenBank.

Phylogenetic analysis

Our top-down-approach taken here has several advantages: (a) the inclusion of all species and genera that belong to the *Oreocharis*-clade. In Möller *et al.* (2009) samples of *Ancylostemon*, *Briggsia*, *Opithandra* and *Oreocharis* were first implicated in this clade. In Wang *et al.* (2010) only species of *Bournea*, *Isometrum* and *Thamnocharis* were additionally included without explicit justification. Only comprehensive analyses (e.g.

Möller *et al.* 2011, Weber *et al.* 2011a, data not shown) including all but one genus [i.e. *Deinostigma* Wang & Li (1992: 356)] of the advanced didymocarpoid Gesneriaceae, showed the full extent of the genera belonging to the *Oreocharis* clade in that species of an additional four genera (i.e. *Dayaoshania*, *Deinocheilos*, *Paraisometrum* and *Tremacron*) also need to be considered; (b) the inclusion of only the species relevant for the *Oreocharis* clade (i.e. only a few but not all samples of *Briggsia*); (c) the inclusion of all molecular characters (i.e. hypervariable regions that had to be excluded in the larger analyses due to alignment ambiguities, particularly in the ITS spacer region); and (d) due to the above more accurate phylogenetic reconstruction results. The narrower taxonomic range of the reduced *Oreocharis*-focussed analyses here allowed a re-alignment of the matrices and a more accurate determination of primary sequence homologies, reducing the homoplasy resulting in fewer parsimony trees retrieved.

Maximum parsimony (MP) and Bayesian inference (BI) analyses were performed as described previously (Möller *et al.* 2009, 2011, Weber *et al.* 2011a), using PAUP* v4.0b10 (Swofford 2002), and MrBayes v3.1.2 (Huelsenbeck & Ronquist 2001, 2007). Only combined *trnL-F* and ITS sequences were analysed. Their combinability was tested using the incongruence length difference (ILD; $P=0.52$) test implemented as the partition homogeneity test (PHT) in PAUP*. Alignment gaps with consistent boundaries were coded as additional characters according to the simple method of Simmons & Ochoterena (2000), 9 in *trnL-F*, 12 in ITS. MP branch support came from bootstrap analyses as described previously (Möller *et al.* 2009, 2011) with 10000 replicates, TBR on and MulTrees off.

Best-fitting models for MrBayes were obtained separately for *trnL-F*, the ITS spacers and the 5.8S gene through AIC in MrModeltest 2.3 (Nylander 2004), and were GTR+G, GTR+G and SYM+I, respectively. The gaps were treated as standard characters. The analysis was run for 2.5 million generations for the 55 sample matrix, with a burn-in of 4% determined by plotting likelihoods against generations (Appendix 1). Posterior probabilities (PP) were taken from MrBayes 50% majority rule consensus trees using the ‘sumt’ command. The PP branch support values showed a high correlation between the two parallel Bayesian runs (Appendix 1).

Results

Matrix characteristics

The 55 sample matrix was 1632 characters long (*trnL-F*: 870 characters, ITS: 762) which included 364 (22.3%) parsimony informative characters.

Phylogenetic analyses

The MP analysis on combined data resulted in 70 most parsimonious trees of 1245 steps (CI=0.6321, RI=0.7243). The resulting majority rule consensus tree was highly resolved (Fig. 1). The phylogram illustrates the distribution of genetic diversity and the primarily short backbone branches in the *Oreocharis* clade (Fig. 2). The BI tree was less resolved but fully congruent (virtually identical) where the MP branches received bootstrap support (Fig. 3). MP branches with bootstrap support <50% collapsed in the BI tree.

The monophyly of each of the outgroup genera was highly supported (BS=98–100%; PP=1.00), although the intergeneric relationships between *Aeschynanthus*, *Agalmyla* and *Cyrtandra* received no or low support values and the relationships differed between the MP and BI analysis. The *Oreocharis* clade received maximum branch support (BS=100%; PP=1.00). Within the clade the backbone structure received no MP branch support or collapsed to a polytomy in the BI analysis.

Opithandra acaulis and *O. dinghushanensis* were sister (BS=100%; PP=1.00), and were resolved as sister to the rest of the samples only in the MP analysis, but with no BS support. In the BI analysis this clade fell on a backbone polytomy with several other lineages or individual samples, including the type species *Oreocharis benthamii*. In the MP analysis the *Oreocharis* type formed a grade between the *Opithandra* clade and two larger clades, Clade I and II. However, these received no support.

Majority rule

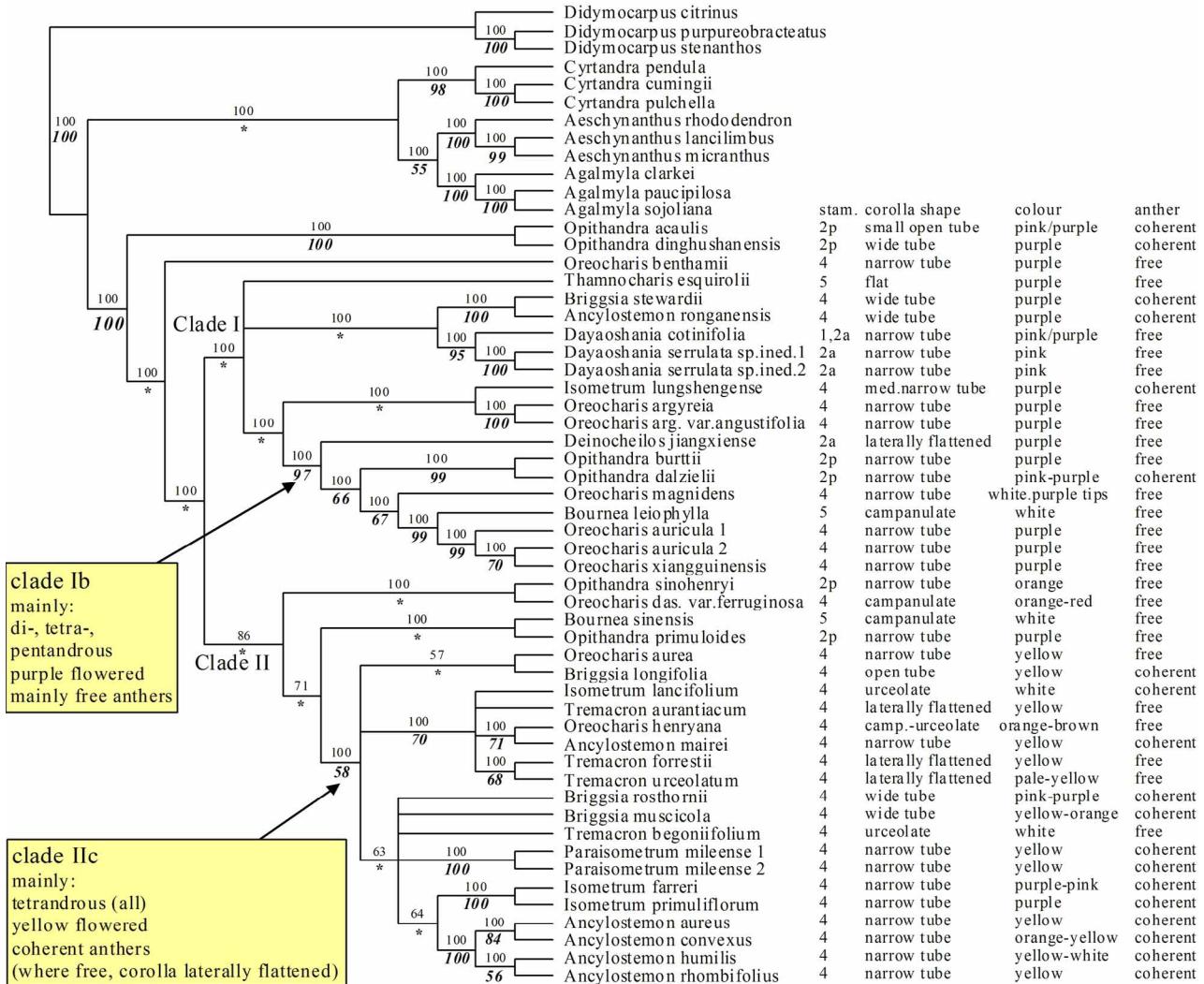


FIGURE 1: Majority rule consensus tree of 70 most parsimonious trees, based on combined *trnL-F* and ITS data plus gap characters (tree length 1245 steps, CI = 0.6321, RI = 0.7243). Numbers along branches, above are majority rule frequencies, below (bold, italics) bootstrap values, * indicates branches with <50% bootstrap values. Number of fertile stamens (stam.: a, anterior pair; p, posterior pair), corolla shape, colour and anther coherence (anther) indicated in box.

In the MP Clade I, *Briggsia stewardii* and *Ancylostemon ronganensis* were strongly supported as a sister pair (BS=100%; PP=1.00), as were the three samples of *Dayaoshania* (BS=95%; PP=1.00). The two *Dayaoshania serrulata* sp. ined. samples were closest (BS=100%; PP=1.00) in this genus. The two varieties of *Oreocharis argyreia* included were sister (BS=100%; PP=1.00). A group of samples forming a highly supported clade Ib (BS=97%; PP=1.00), included *Bournea sinensis*, *Deinocheilos jiangxiense*, two *Opithandra* and three *Oreocharis* species. Within this clade the two *Opithandra*, *O. burttii* and *O. dalzielii*, formed a sister pair with high branch support (BS=99%; PP=1.00). The two *Oreocharis auricula* samples plus *O. xiangguinensis* formed a highly supported clade (BS=99%; PP=1.00), with *Bournea sinensis* as sister (BS=99; PP=1.00).

Within the MP Clade II, few relationships received branch support. Clade IIc, with 19 samples from 6 genera (*Ancylostemon*, *Briggsia*, *Isometrum*, *Oreocharis*, *Paraisometrum*, *Tremacron*) received some branch support, high in the BI analysis (BS=58%; PP=1.00). Within this clade, the BI tree showed higher resolution with medium branch support. *Oreocharis aurea* and *Briggsia longifolia* fell on a polytomy sister to the 17 remaining samples (PP=0.79). On the next grade with medium support (PP=0.80) fell a well supported clade (BS=70%; PP=1.00) with six samples. Within this BI clade, *Oreocharis henryana* and *Ancylostemon mairei*

were sister (BS=71%; PP=0.95), as were two *Tremacron* species, *T. forrestii* and *T. urceolatum* (BS=68%; PP=0.92). The remaining 11 samples formed a clade, only weakly supported in the BI analysis (PP=0.80). Among these samples, only few relationships received high support; the two *Paraisometrum mileense* samples (BS=100%; PP=1.00), *Isometrum farreri* and *I. primuliflorum* (BS=100%; PP=1.00) and four of the six *Ancylostemon* species here included (BS=100%; PP=1.00). Within this *Ancylostemon* clade, *A. aureus* and *A. convexus* were sister (BS=84%; PP=1.00), as were *A. humilis* and *A. rhombifolius* (BS=56%; PP=0.69). The Bayesian posterior probabilities were often higher than the bootstrap support values (see also Möller *et al.* 2009).

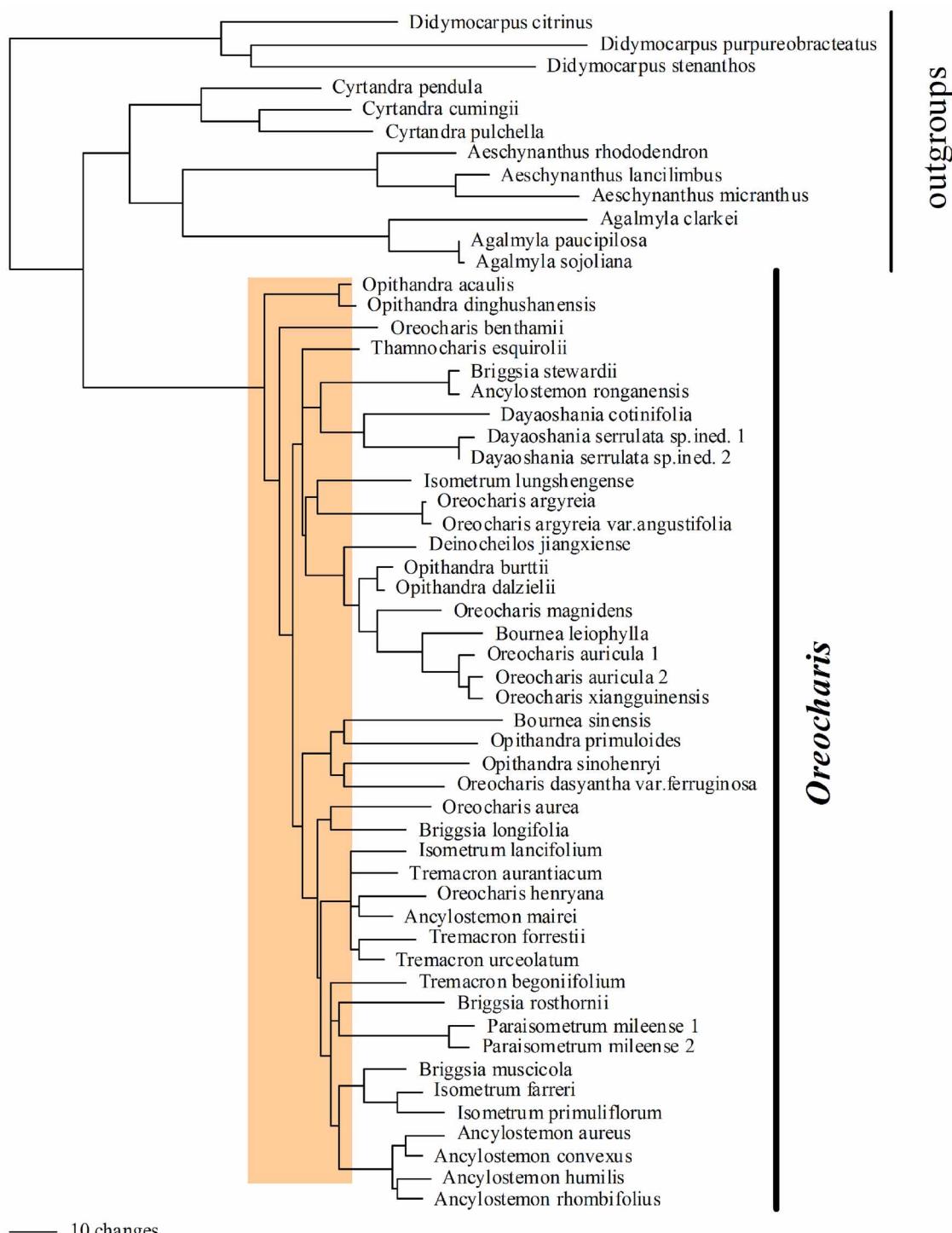


FIGURE 2: One of 70 most parsimonious trees depicted as a phylogram to illustrate the length of the backbone branches. Shaded area indicates period of rapid radiation.

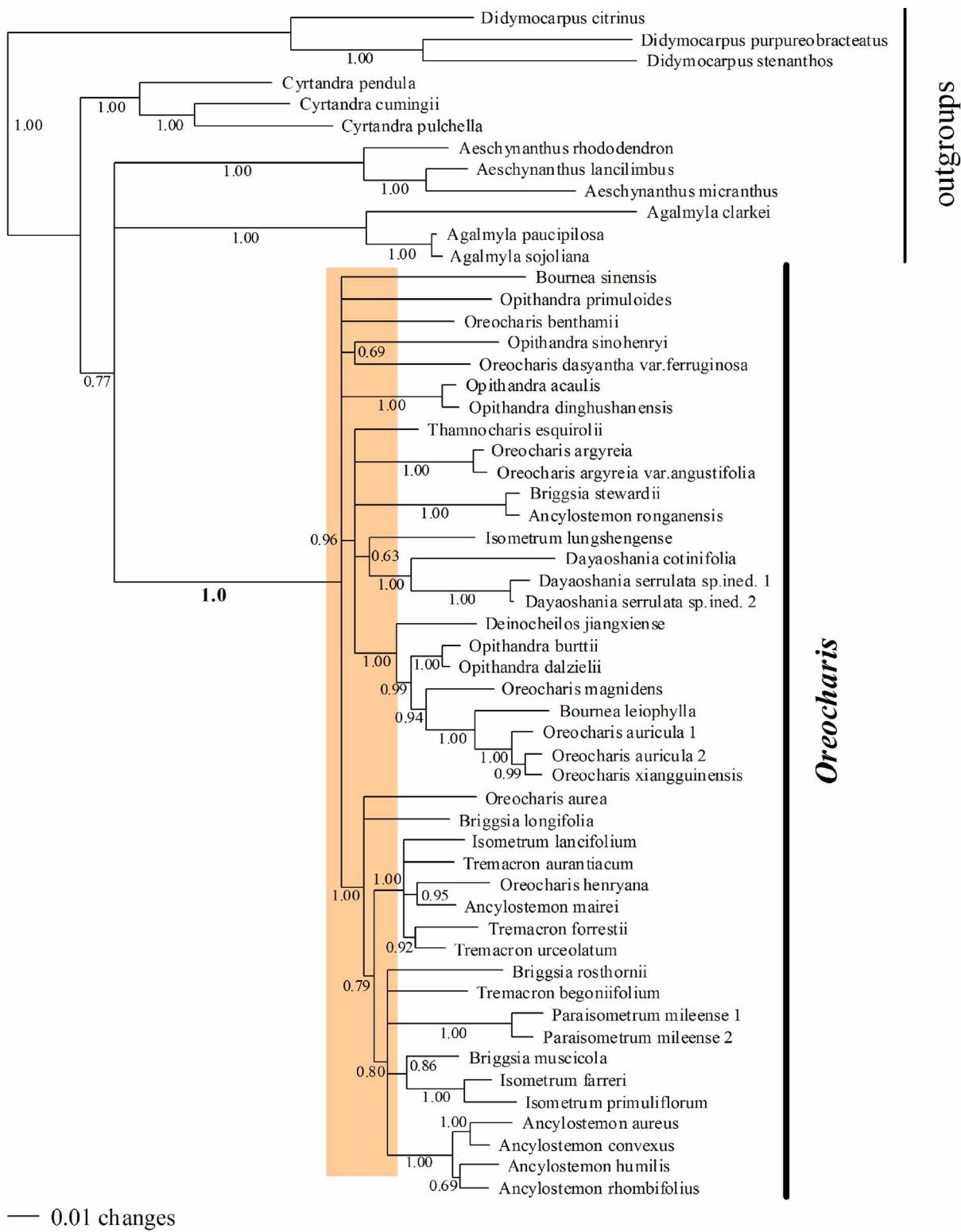


FIGURE 3: Bayesian inference tree with average branch lengths, based on combined *trnL-F* and ITS data plus gap characters. Numbers above branches indicate posterior probabilities. Shaded area indicates period of rapid radiation.

Discussion

In the present molecular phylogenetic study species of no fewer than 11 extant Chinese gesneriad genera (even 14, if genera in synonymy, *Dasydesmus*, *Perantha* and *Schistolobos*, are taken into account, see formal

treatment) form a monophyletic clade, the *Oreocaris* clade. This clade has maximum statistical branch support. Within the clade, the well-supported species relationships do not conform to traditional generic delimitations. The only exception is *Dayaoshania*, whose two species appear in a sister relationship. However, the results of the phylogenetic study do not necessarily mean that the whole alliance should be combined into a single genus. At first sight it may appear undesirable to do so, since it would result in a large and, with respect to flower morphology, very variable genus of over 80 species. Therefore, our molecular results require a detailed justification for such a measure. We justify our conclusions through: (1) molecular analyses, (2) examination of weaknesses in the traditional generic delimitations, (3) an evaluation of morphological characters hitherto used for generic definitions, and (4) a discussion of relationships between particular species. We conclude that the overall results clearly indicate that the reduction of all these genera under *Oreocaris*, the oldest generic name in the alliance, is indeed the most sensible solution.

(1) Molecular phylogenetic analyses

The present molecular analysis demonstrates that all species (investigated) of the genera *Oreocaris* (28 species / 8 included in the analysis), *Ancylostemon* (12/6), *Opithandra* (10/6), *Isometrum* (14/4), *Tremacron* (7/4), *Dayaoshania* (2/2), *Deinocheilos* (2/1), *Bournea* (2/2), *Thamnocharis* (1/1) and *Paraisometrum* (1/1) fall into the *Oreocaris* clade. In addition, four species of *Briggsia*, all with yellow flowers, were retrieved in this clade, but other species of that genus (usually with different flower colours) were found in five other places in the analyses of Möller *et al.* (2009, 2011). This suggests that the present delineation of *Briggsia* (c. 22 spp.) is highly artificial and needs to be resolved.

The present analysis includes sequence data for nearly half the species described in these genera (39 of 80). Given that we included most of the morphological diversity of these genera, the addition of further taxa, though desirable, is not likely to alter our conclusions.

All non-monotypic genera with multiple samples here included were found to be non-monophyletic (except the two *Dayaoshania* species), with mixed-generic clades often receiving high branch support (Figs. 1, 3). This is a further strong indication that the addition of more samples will not likely increase the level of monophyly among the 11 genera in the *Oreocaris* clade. We are thus confident that our systematic conclusions and taxonomical consequences are justified.

(2) Weaknesses of traditional delimitations

The weaknesses of delimiting the core genera of the present alliance (*Oreocaris*, *Opithandra*, *Briggsia*, *Ancylostemon*, *Isometrum*, *Tremacron*) are well known. Before addressing these in some detail, it may be useful to briefly survey their taxonomic history. This started with the original wide definition of *Didymocarpus*, which included species with di- and tetrandrous flowers, coherent or free anthers and a huge geographical range in Asia (later extended to Africa, Madagascar and Australia) (see Weber & Burtt 1998b). Bentham (1876) suggested that *Didymocarpus oreocaris* and two other species be moved to his new genus *Oreocaris*. The formal transfer was not made by Bentham himself, but by Clarke (1883) who accepted *Oreocaris* as a genus with four fertile and non-coherent anthers and established the new name *Oreocaris benthamii* for *Didymocarpus oreocaris*. Clarke (1883) also separated another alliance from *Didymocarpus*, also with four stamens, but these cohering in pairs, or all together. This was named *Didissandra* Clarke (1883: 65). The seven species included were very heterogeneous and Clarke (1883) established no fewer than four sections for their accommodation. Ridley (1905), working with the Malesian species of *Didissandra*, was the first to suggest the likely artificial nature of the genus, but he did not take any action to rectify it. Craib (1918, 1920a, b), working with the species in the northern part of the distribution range (N Thailand, China), split *Didissandra* up into smaller entities, including *Briggsia*, *Ancylostemon*, *Isometrum* and *Tremacron*. Genera established later (*Opithandra* by Burtt 1956, *Thamnocharis* by Wang 1981) have their roots either in *Oreocaris* (*Bournea* was described by Oliver in Hooker 1893 as an independent genus, but also placed in the vicinity of *Oreocaris*), or in *Didissandra* (*Paraisometrum* by Wang in Weitzmann *et al.* 1998). The essential difference of the two lineages is the non-coherence vs. coherence of the anthers. The only genus described

independently from these two lines was *Dayaoshania*, which was thought to be allied to *Petrocosmea* Oliver in Hooker (1887: t. 1716) (Wang 1983a). However, the molecular data unequivocally places the genus in the *Oreocharis* clade.

The difficulties in separating the genera of the alliance under consideration were clearly seen by Wang *et al.* (1998). Statements such as “Using only vegetative or fruit characters, it [*Oreocharis rhytidophylla*] cannot be placed definitely in *Oreocharis*, since other genera (e.g. *Tremacron*, *Isometrum* and *Ancylostemon*) are virtually indistinguishable in these characters” or “*Oreocharis* is related to *Ancylostemon*, *Tremacron* and *Isometrum*. As noted above it can be difficult to distinguish these genera, and some species, notably *O. delavayi* [Franch.], are intermediate between them. *Oreocharis delavayi* has exserted stamens and adaxial corolla lobes much smaller than abaxial ones, characters which relate it to *Tremacron*” (Wang *et al.* 1998: 252) give testimony to the difficulties of placing particular species correctly.

The difficulty of separating *Briggsia* from *Oreocharis* was addressed by Burtt (1954a: 188) as follows: “There are some fourteen species in this genus [*Briggsia*], but they are of varied habit and appearance, and are associated entirely on their floral characters: large, ventricose corollas, arched filaments and anthers cohering in pairs tip to tip. Even this last feature is not quite constant, for we now have species in cultivation which have all the characteristics of *Briggsia* except that on dehiscence the anthers separate and the filaments straighten. There is, then, at full flowering, very little to separate these from *Oreocharis*”.

In several genera sections have been established (*Opithandra*: 5 sections for some 10 species, *Oreocharis*: 4, *Isometrum*: 3), sometimes based on characters (such as anther coherence, see below) otherwise used for generic delimitation. Some sections are monotypic [*Opithandra* sect. *Microstigma* Wang (1987: 9), *Opithandra* sect. *Stenosiphon* Wang (1987: 9), *Opithandra* sect. *Schistolobos* Wang (1992: 291), *Isometrum* sect. *Chorianthera* W.T.Wang & K.Y.Pan in Pan (1988a: 432)], and *Opithandra* sect. *Schistolobos* was previously described as a genus. Thus, the question arises, what is the difference between the monotypic sections and the monotypic genera? The answer is simple: there are a number of rather isolated species that cannot be placed satisfactorily and only make sense in a widely defined genus.

(3) Character evaluation

As stated above, the genera of the *Oreocharis* clade scarcely differ in vegetative habit and in fruit characteristics (loculicidal, bivalved capsules, usually long and cylindrical, occasionally ovoidal). All are rosette plants (with spirally arranged leaves, Fig. 4) with scapose, axillary inflorescences. The distinctive features are in the flower, particularly in corolla shape and colour, and in stamen morphology (number and placement of fertile stamens, anther coherence, anther shape and dehiscence). Traditional taxonomy is heavily based on floral characters and this has remained so in Old World Gesneriaceae until now. Through the work of Wiehler (1983), and manifold molecular studies, the situation is otherwise in Neotropical Gesneriaceae (e.g., Kvist & Skog 1996, Skog & Kvist 2000, Perret *et al.* 2001, 2003, Roalson *et al.* 2002, 2003). In the New World floral similarity lost its paramount importance for defining genera as it became increasingly clear that floral characters are evolutionarily plastic (and, therefore, taxonomically unreliable) due to their link to the functional constraints of pollination. The floral characters of the *Oreocharis* alliance should be reconsidered in the same light.

Clade IIc includes all taxa with yellow flowers. This suggests that this trait has evolved once with perhaps a few reversals to purple. However, the flower and anther morphologies are highly diverse (see below). Preliminary investigations on seed testa cell ornamentations revealed that the clade includes seeds with striate, reticulate and verruculose patterns, while all taxa in clade I which have been investigated have verruculose testa cells (data not shown).

The reason for this lack of character correlation possibly lies in the early evolution of the *Oreocharis* clade. The short backbone branches (Figs. 2, 3) support a hypothesis of rapid radiation early on in the diversification of the lineage. This is not conducive for a detectable phylogenetic hierarchy to become established. Rather, this clade has been shaped by a mixture of independently evolving characteristics due to selection pressures from different pollinators, often several times independently.

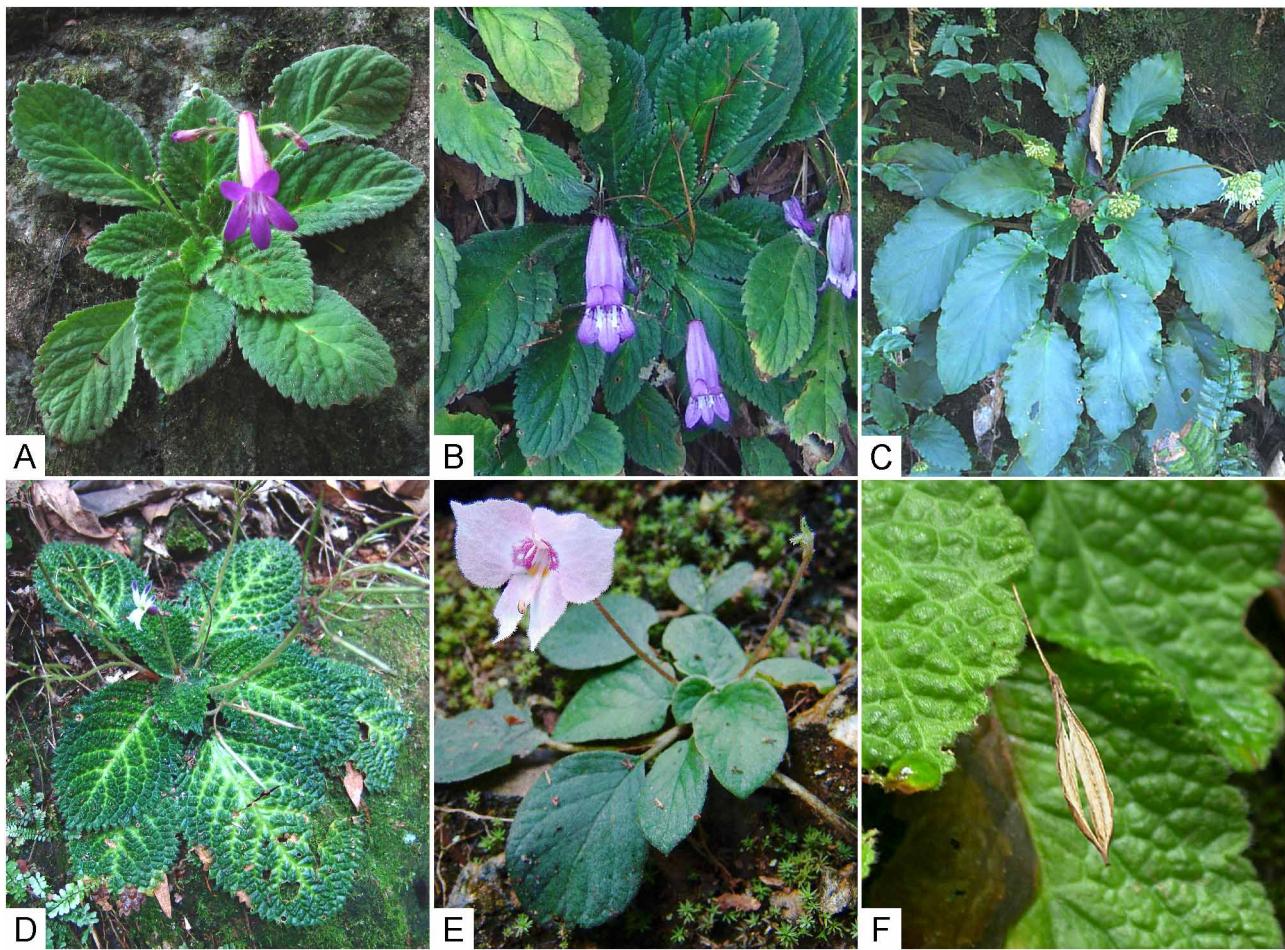


FIGURE 4: Examples of habit of various taxa belonging to the *Oreocallis* clade: A) *Ancylostemon ronganensis*; B) *Briggsia stewardii*; C) *Bournea leiophylla*; D) *Oreocallis magnidens*; E) *Dayaoshania cotinifolia*; F) dehisced fruit of *Deinocheilos jiangxiensis*.

Flower symmetry and corolla features

Corolla symmetry, shape and coloration are the most important elements to define pollination syndromes. Among the samples included in the *Oreocallis* clade there are narrow- and wide-tubed, laterally flattened, urceolate and radially symmetrical corolla forms, predominantly purple or yellow (Figs. 5, 6). These features suggest different pollination syndromes. It is difficult to discuss the evolution of these syndromes across the phylogenetic tree, as the internal branches are short and receive only low branch support. There is some probability that the yellow flower colour has evolved from a purple colour, since a subclade (clade IIc) in derived position includes all yellow-flowered taxa (plus a few purple ones), from five genera (*Ancylostemon*, *Briggsia*, *Oreocallis*, *Paraisometrum*, *Tremacron*). However, these include a considerable variety of flower shapes (narrow and wide tube, urceolate, laterally flattened), suggesting that the adaptation to different pollinators has played a strong role in the diversification of the taxa.

A very similar situation is encountered in the African genus *Streptocarpus* Lindley (1828: pl. 1173) The *Streptocarpus* phylogeny shows similar short internal and backbone branches (Möller & Cronk 2001) and the floral diversity suggests six different pollination syndromes, having sometimes clearly evolved in parallel (Harrison *et al.* 1999, Hughes *et al.* 2006). Nobody has suggested splitting *Streptocarpus* into several genera. In order to provide a consistent classification for Gesneriad genera, we suggest accepting a wider range of floral morphological variation within genera and defining *Oreocallis* to include the florally divergent lineages.



FIGURE 5: Examples of floral diversity arranged by phylogenetic relationships of various taxa belonging to the *Oreocaris* Clade I: A) *Ophithandra dinghushanensis*; B) *Oreocaris benthamii*; C) *Thamnocharis esquirolii*; D) *Aencylostemon ronganensis*; E) *Briggsia stewardii*; F) *Dayaoshania cotinifolia*; G) *Isometrum lungshengense*; H) *Oreocaris argyreia*; J&K) *Deinocheilos jiangxiensis*; L) *Ophithandra burttii*; M) *Oreocaris magnidens*; N) *Oreocaris auricula*.

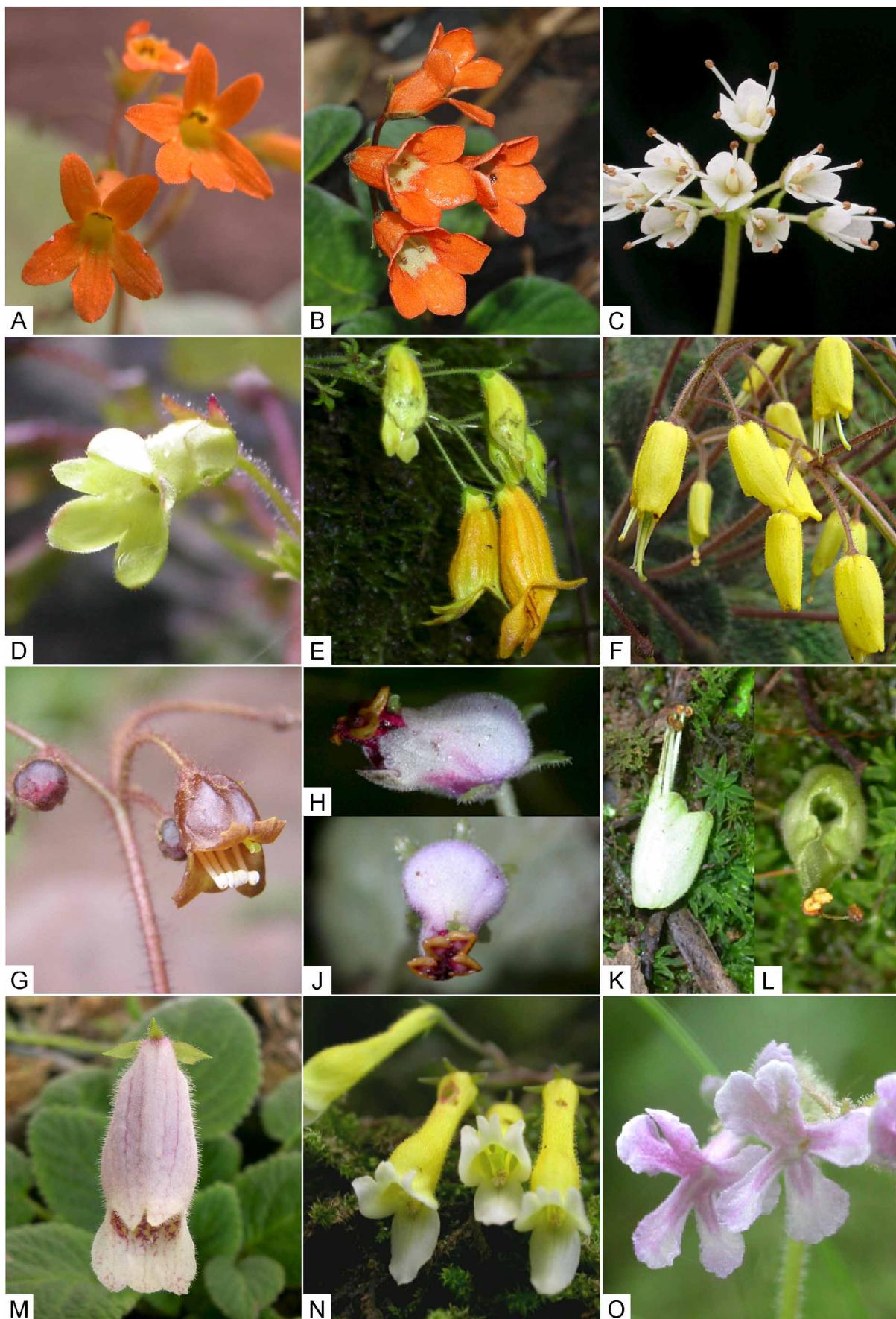


FIGURE 6: Examples of floral diversity arranged by phylogenetic relationships of various taxa belonging to the *Oreocaris* Clade II: A) *Opithandra sinohenryi*; B) *Oreocaris dasyantha* var. *ferruginosa*; C) *Bournea sinensis*; D) *Oreocaris aurea*; E) *Briggsia longifolia*; F) *Tremacron aurantiacum*; G) *Oreocaris henryana*; H&J) *Tremacron begoniifolium*; K&L) *Tremacron urceolatum*; M) *Briggsia rosthornii*; N) *Paraisometrum mileense*; O) *Isometrum primuliflorum*.

Number of fertile stamens

The taxa of the *Oreocharis* clade include species with two (*Dayaoshania*, *Deinocheilos*, *Opithandra*), five (*Bournea*, *Thamnocharis*) and four fertile stamens (rest). The diandrous taxa differ in the position of the fertile stamen pair in the flower. In *Dayaoshania* and *Deinocheilos* they are in the anterior position, while those in *Opithandra* are in the posterior position. Posterior stamen fertility is a character that has evolved also outside the *Oreocharis* clade in the South American *Sarmienta* Ruiz & Pavon (1794: 4) and the Asian/African *Epithema* Blume (1826: 737).

Even taking into account that some relationships in the *Oreocharis* clade are not well supported, there is evidence that the stamen position is a variable character, since a highly supported clade (clade Ib, Fig. 1) includes taxa with four different androecial conditions, with five (*Bournea*), four (*Oreocharis*), two anterior (*Deinocheilos*) respectively two posterior (*Opithandra*) stamens. This indicates that differences in the androecium are not good characters at the generic level. Precedents for currently recognized monophyletic genera showing variation in stamen characteristics are available and include *Rhynchoglossum* Blume (1826: 741) and *Agalmyla* (Burtt 1962, Hilliard & Burtt 2002). In the African *Acanthonema strigosum* Hooker (1862: t. 5339) this characteristic is variable even within the species; different flowers on individual plants can have two or four fertile stamens.

The possibly parallel stamen reduction in (and thus possible polyphyly of *Opithandra* has been explicitly addressed by Burtt (1958a: 301), when adding some more species to his originally monotypic *Opithandra*): “In leaf characters and in the form of the stigma, however, there is variation and it cannot be gainsaid that *Opithandra* is a somewhat artificial genus with the single character of fertile posticus stamens the one feature of paramount importance” and “It may well be suggested that these species have all been derived independently from different tetrandrous ancestors, and consequently that the genus *Opithandra* as here constituted is quite artificial”. The molecular data prove conclusively that *Opithandra* is indeed polyphyletic, the species being scattered over clade I.

Free or fused anthers

The coherence of anthers is an important aspect of the functioning of the flower. They facilitate a targeted deposition of pollen on the pollinator (e.g. head of birds in *Aeschynanthus*), or guide the amount of pollen deposited (e.g. virtually all pollen is deposited on a single visit by long-tongued flies in *Streptocarpus*, MM pers. observ.). Free anthers are often observed for flowers with constricted corollas (*Deinocheilos*, *Tremacron*) or radially or almost radially symmetrical flowers (*Bournea*, *Thamnocharis*, some *Oreocharis* and *Isometrum*). These characteristics have been used as generic (*Bournea*, *Thamnocharis*, *Tremacron*) or sectional descriptors (*Isometrum*, *Oreocharis*, *Opithandra*), but as our phylogeny indicates, appear to be highly plastic, and unsuited as characters for generic delimitation in the *Oreocharis* clade.

(4) Relationships between selected species within the *Oreocharis* clade

The artificial nature of the current generic system can be illustrated by statistically well supported examples of intergeneric sister relationships. For example, *Ancylostemon ronganensis* and *Briggsia stewardii* have identical *trnL-F* sequences and differ only by 4 nucleotide changes in ITS but share 2 ITS insertions unique in the *Oreocharis* clade. They are genetically certainly closely related and morphologically difficult to distinguish (Fig. 5D, E) especially in vegetative habit (Fig. 4A, B). Their fruits, unknown when they were first described, are now known and do not differ significantly. The differences that are recorded are that *B. stewardii* has 2 bracts (in *A. ronganensis* “apparently absent”), corolla blue to pale purple (v. pink), and filaments sparsely glandular pubescent (v. glabrous), which can hardly be considered generic characters. It is difficult to see why they were described in different genera, perhaps incomplete descriptions or specimens masked the similarities.

Among the taxa in the yellow flowered clade is the monotypic *Paraisometrum* with an interesting history. It was rediscovered after 100 years of absence from herbarium records (Shui & Jie 2007). W.T. Wang noticed that a herbarium specimen collected in 1898 from the southeast of Yunnan was distinctive with regard to the

corolla lobes and stamen arrangements from other genera and with colleagues established a new genus (Weitzman *et al.* 1998). The corolla has four upper lobes and one lower lobe and the anthers are “coherent in pairs by adaxial surfaces, thecae parallel” (Wang *et al.* 1998). However, photographs of corollas of *Ancylostemon saxatilis* in Li & Wang (2004) clearly show 4 upper lobes and one lower lobe [as do the flowers of *Calcareoboea* C.Y.Wu in Li (1982: 241), a member of the *Petrocodon* clade, Weber *et al.* 2011b, fig. 3B]. In *Ancylostemon*, the anthers are described as “coherent in pairs, thecae divergent”. In our opinion, this does not constitute a generic difference and we interpret this as support for our combination of these genera.

Taxonomic consequences

The molecular data, the well-known weaknesses in generic delimitations, and the unreliability of floral characters for defining genera, have lead us to the conclusion that it is best to include the whole *Oreocaris* clade into *Oreocaris*, which is the oldest name in the alliance. This circumscription of *Oreocaris* includes all species of *Ancylostemon*, *Bournea*, *Dayaoshania*, *Deinocheilos*, *Isometrum*, *Opithandra*, *Oreocaris*, *Paraisometrum*, *Thamnocharis* and *Tremacron*, but only four of *Briggsia* (including the type species). The other *Briggsia* species cannot be placed generically at present and must await further studies. In the “formal treatment” a list is given which includes the species of *Oreocaris* currently recognised and those here transferred from the other genera to be included in *Oreocaris*. All are given in alphabetical order.

Outlook

It would be desirable to fully resolve, with statistical support, the relationships among the taxa of the *Oreocaris* clade. However, simply adding more genes may not be the answer, as an example in the Saxifragales suggests, unless a huge number of characters are added, in this case an increase from 9000 to 50000bp (Jian *et al.* 2008). How deep the problem might be lies in the density, or shortness of the branches involved (or the period of time) of radiation. The shorter the branches the less likely it is that signals of a possible phylogenetic hierarchy can be retrieved. In a very short burst of radiation no hierarchy may have existed in the first place and any retrieved may be an artefact of factors such as long branch attraction (Siddall & Whiting 1999). The backbone branches in the *Oreocaris* clade are very short (Figs. 2, 3), and it is not certain whether a stable, robust phylogenetic hierarchy can ever be established.

Whether one can get to the stage of defining sections remains to be seen. Judging from a superimposition of the sectional system of the largest genus, *Oreocaris*, the prospects are not promising, as only the members of the type section *Oreocaris* and section *Orthoanthera* Pan (1987: 281) included in our analysis fall into a “section”-clade. Members of *Oreocaris* section *Stomactin* (C.B.Clarke) Fritsch (1893–1894: 145) are scattered in both main clades. Since the sections are based on corolla form (Pan 1987), and corolla form is here found to be most unsuited for classification purposes, this is not a surprising result. A classification based on phylogenetic hypotheses and character mapping (e.g. Palee *et al.* 2006) would be the most promising approach.

Formal treatment

Oreocaris Bentham (1876: 995, 1021).

Lectotype: *O. benthamii* C.B.Clarke (selected by Burtt 1954b).

Heterotypic synonyms:

Bournea Oliver in Hooker (1893: tab. 2254). Type: *B. sinensis* Oliv.

Perantha Craib (1918: 212). Lectotype: *P. forrestii* Craib (selected by Burtt 1954b).

Tremacron Craib (1918: 217). Type: *T. forrestii* Craib

Ancylostemon Craib (1920a: 233). Lectotype: *A. concavus* Craib [= *A. aureus* (Franch.) B.L.Burtt] (selected by Burtt 1954b).

Briggsia Craib (1920a: 236), pro parte incl. type. Lectotype: *B. longifolia* Craib (selected by Burtt 1954b).
Isometrum Craib (1920a: 250). Lectotype: *I. farreri* Craib (selected by Burtt 1954b).
Dasydesmus Craib (1920a: 253). Type: *D. bodinieri* Craib
Opithandra Burtt (1956: 162). Type: *O. primuloides* (Miq.) B.L.Burtt
Thamnocharis Wang (1981: 485). Type: *T. esquirolii* (H.Lév.) W.T.Wang
Dayaoshania Wang (1983a: 319). Type: *D. cotinifolia* W.T.Wang
Schistolobos Wang (1983b: 16). Type: *S. pumilus* W.T.Wang
Deinocheilos Wang (1986: 1). Type: *D. sichuanense* W.T.Wang
Paraisometrum W.T.Wang in Weitzman *et al.* (1998: 431). Type: *P. mileense* W.T.Wang

The following list includes all species and infraspecific taxa hitherto described in *Oreocharis* and those transferred to that genus on the basis of the present analysis. Arrangement is in alphabetical order. Notes are given where appropriate.

***Oreocharis acaulis* (Merr.) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Chirita acaulis* Merrill (1934: 47).

Homotypic synonym:—*Opithandra acaulis* (Merr.) B.L.Burtt (1958a: 303).

Distribution:—China (Guangdong).

Notes:—Type and only species of *Opithandra* sect. *Microstigma*.

***Oreocharis amabilis* Dunn (1908a: 362).**

Distribution:—China (Yunnan).

Notes:—Referred to *Oreocharis* sect. *Stomactin* by Pan (1987), Wang *et al.* (1990) and Li & Wang (2004).

***Oreocharis argyrea* Chun ex Pan (1987: 283).**

Distribution:—China (Guangxi, Guangdong).

Notes:—Referred to *Oreocharis* sect. *Oreocharis* by Pan (1987), Wang *et al.* (1990) and Li & Wang (2004).

***Oreocharis argyrea* var. *angustifolia* Pan (1987: 285).**

Distribution:—China (Guangxi).

***Oreocharis aurantiaca* Franchet (1888: 716).**

Basionym:—*Perantha aurantiaca* (Franch.) Pellegrin (1926: 873).

Heterotypic synonym:—*Perantha forrestii* Craib (1918: 213).

Distribution:—China (Yunnan).

Notes:—Referred to *Oreocharis* sect. *Stomactin* by Pan (1987), Wang *et al.* (1990) and Li & Wang (2004).

***Oreocharis aurea* Dunn (1908b: 19).**

Distribution:—China (Yunnan), Vietnam.

Notes:—Referred to *Oreocharis* sect. *Stomactin* by Pan (1987), Wang *et al.* (1990), Li & Wang (2004) and Wei *et al.* (2010b).

***Oreocharis aurea* var. *cordato-ovata* (C.Y.Wu ex H.W.Li) K.Y.Pan *et al.* in Weitzman *et al.* (1998: 430).**

Basionym:—*Oreocharis cordato-ovata* C.Y.Wu ex Li (1983: 7).

Distribution:—China (Yunnan).

***Oreocharis auricula* (S.Moore) C.B.Clarke (1883: 64).**

Basionym:—*Didymocarpus auriculus* Moore (1875: 229).

Homotypic synonym:—*Perantha auricula* (S.Moore) Pellegrin (1926: 873).

Heterotypic synonyms:—*Chirita sericea* H.Lév. & Vaniot in Léveillé (1906: 428), non Ridley, *Didymocarpus sericeus* Léveillé (1906: 427), non Ridley, *Oreocharis sericea* Léveillé (1911a: 329).

Heterotypic synonyms:—*Oreocharis esquirolii* Léveillé (1911b: 447), non Léveillé (1911a: 329), *Oreocharis leveilleana* Fedde (1911: 64).

Distribution:—China (Anhui, Fujian, Guangdong, Guangxi, Guizhou, Hubei, Hunan, Jiangxi, Sichuan).

Notes:—Referred to *Oreocharis* sect. *Stomactin* by Pan (1987), Wang *et al.* (1990) and Li & Wang (2004). Léveillé (1911b) erroneously gave two different species the same name, *Oreocharis esquirolii*. The mistake was realised and corrected soon afterwards (Fedde 1911).

***Oreocharis auricula* var. *denticulata* Pan (1987: 276).**

Distribution:—China (Fujian).

***Oreocharis begoniifolia* (H.W.Li) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Tremacron begoniifolium* Li (1983: 12).

Distribution:—China (Yunnan).

***Oreocharis benthamii* C.B.Clarke (1883: 63, as: “*benthami*”).**

Basionym:—*Didymocarpus oreocharis* Hance (1866: 230).

Distribution:—China (Guangdong, Guangxi, Hong Kong, Hunan, Jiangxi).

Notes:—Type species of *Oreocharis*. Referred to *Oreocharis* sect. *Oreocharis* by Pan (1987), Wang *et al.* (1990) and Li & Wang (2004).

***Oreocharis benthamii* var. *reticulata* Dunn (1908a: 362).**

Distribution:—China (Guangdong, Guangxi).

***Oreocharis bodinieri* Léveillé (1915b: 40).**

Basionym:—*Dasydesmus bodinieri* (H.Lév.) Craib (1920a: 254).

Distribution:—China (Sichuan, Yunnan).

Notes:—Referred to *Oreocharis* sect. *Oreocharis* by Pan (1987), Wang *et al.* (1990) and Li & Wang (2004).

Type species of *Dasydesmus*.

***Oreocharis bullata* (W.T.Wang & K.Y.Pan) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Ancylostemon bullatus* W.T.Wang & K.Y.Pan in Wang (1992: 289).

Distribution:—China (Yunnan).

***Oreocharis burttii* (W.T.Wang) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Opithandra burttii* W.T.Wang in Weitzman *et al.* (1998: 430).

Distribution:—China (Jiangxi).

Notes:—Referred to *Opithandra* sect. *Opithandra* by Wang (1987; as “*Opithandra* sp. Burtt”) and Li & Wang (2004).

***Oreocharis cavalieri* Léveillé (1909: 258).**

Distribution:—China (Guizhou).

Notes:—Referred to *Oreocharis* sect. *Orthoanthera* by Pan (1987), Wang *et al.* (1990) and Li & Wang (2004).

***Oreocharis chienii* (Chun) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Briggsia chienii* Chun (1946: 300).

Distribution:—China (Anhui, Jiangxi, Zhejiang).

***Oreocharis cinerea* (W.T.Wang) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Opithandra cinerea* W.T.Wang (1982: 39).

Distribution:—China (Guizhou).

Notes:—Referred to *Opithandra* sect. *Briggsioides* by Wang (1987), Wang *et al.* (1990) and Li & Wang (2004).

***Oreocharis cinnamomea* Anthony (1934: 200).**

Distribution:—China (Yunnan).

Notes:—Referred to *Oreocharis* sect. *Stomactin* by Pan (1987), Wang *et al.* (1990) and Li & Wang (2004).

***Oreocharis concava* (Craib) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Ancylostemon concavus* Craib (1920a: 234, as: “*concavum*”).

Heterotypic synonyms:—*Roettlera aurea* Franchet (1899b: 250), *Didymocarpus aureus* (Franch.) Diels (1912b: 355), *Ancylostemon aureus* (Franch.) Burtt (1958b: 305).

Distribution:—China (Yunnan).

Notes:—Type species of *Ancylostemon*.

***Oreocharis concava* var. *angustifolia* (K.Y.Pan) Mich.Möller & A.Weber., comb. nov.**

Basionym:—*Ancylostemon aureus* (Franch.) B.L.Burtt var. *angustifolius* Pan (1988a: 434).

Distribution:—China (Yunnan).

***Oreocharis convexa* (Craib) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Ancylostemon convexus* Craib (1920a: 235).

Distribution:—China (Yunnan).

Oreocharis cordato-ovata C.Y.Wu ex Li (1983: 7) ≡ *Oreocharis aurea* var. *cordato-ovata*, see there.

***Oreocharis cordatula* (Craib) Pellegrin (1926: 873).**

Basionym:—*Perantha cordatula* Craib (1918: 214).

Distribution:—China (Yunnan, Sichuan).

Notes:—Referred to *Oreocharis* sect. *Stomactin* by Pan (1987), Wang *et al.* (1990) and Li & Wang (2004).

***Oreocharis cotinifolia* (W.T.Wang) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Dayaoshania cotinifolia* Wang (1983a: 320).

Distribution:—China (Guangxi).

Notes:—Type and hitherto only species of *Dayaoshania*. There is an additional species tentatively referred to *Dayaoshania*, but not yet formally described: *D. serrulata*, sp. ined. (mentioned in Wei *et al.* 2010b: 152, 153). Two samples of this species have been included in the present analysis and they appear associated with *D. cotinifolia*. It is suggested here that it should be formally published under *Oreocharis*.

***Oreocharis craibii* Mich.Möller & A.Weber, nom. nov.**

Basionym:—*Tremacron forrestii* Craib (1918: 217).

Distribution:—China (Sichuan, Yunnan).

Notes:—Type species of *Tremacron*.

***Oreocharis crenata* (K.Y.Pan) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Isometrum crenatum* Pan (1986: 27).

Distribution:—China (Hubei).

Notes:—Referred to *Isometrum* sect. *Isometrum* by Pan (1986), Wang *et al.* (1990) and Li & Wang (2004).

***Oreocharis dalzielii* (W.W.Sm.) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Chirita dalzielii* Smith (1918: 171).

Homotypic synonym:—*Opithandra dalzielii* (W.W.Smith) B.L.Burtt (1958a: 303).

Distribution:—China (Fujian, Guangdong).

Notes:—Referred to *Opithandra* sect. *Briggsioides* by Wang (1987), Wang *et al.* (1990) and Li & Wang (2004).

***Oreocharis dasyantha* Chun (1946: 287).**

Distribution:—China (Hainan).

Notes:—Referred to *Oreocharis* sect. *Orthoanthera* by Pan (1987), Wang *et al.* (1990) and Li & Wang (2004).

***Oreocharis dasyantha* var. *ferruginosa* Pan (1987: 283).**

Distribution:—As for species.

***Oreocharis delavayi* Franchet (1888: 715).**

Heterotypic synonym:—*Oreocharis elliptica* Anthony (1934: 200).

Heterotypic synonym:—*Oreocharis elliptica* var. *parvifolia* W.T.Wang & K.Y.Pan ex Pan (1987: 282).

Distribution:—China (Sichuan, Xizang, Yunnan).

Notes:—Wang *et al.* (1998) state that *O. delavayi* is intermediate between *Oreocharis*, *Ancylostemon*, *Tremacron* and *Isometrum*, approaching the latter particularly in the exserted stamens and adaxial corolla lobes which are much smaller than the abaxial ones.

***Oreocharis dentata* A.L.Weitzman & L.E.Skog in Weitzman *et al.* (1998: 431).**

Distribution:—China (Sichuan).

Notes:—The species is not explicitly referred to a section by the authors (Weitzman *et al.* 1998), but is said to be most similar to *O. aurantiaca* and *O. minor*. Both belong to *Oreocharis* sect. *Stomactin*. Wang *et al.* (1990) and Li & Wang (2004), therefore, placed it in that section.

***Oreocharis dinghushanensis* (W.T.Wang) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Opithandra dinghushanensis* Wang (1987: 10).

Distribution:—China (Guangdong).

Notes:—Referred to *Opithandra* sect. *Briggsioides* by Wang (1987), Wang *et al.* (1990) and Li & Wang (2004).

***Oreocharis esquirolii* Léveillé (1911a: 329).**

Homotypic synonym:—*Thamnocharis esquirolii* (H.Lév.) Wang (1981: 485).

Distribution:—China (Guizhou).

Notes:—Flowers actinomorphic, 4- or 5 merous.

***Oreocharis eximia* (Chun ex K.Y.Pan) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Isometrum eximum* Chun ex K.Y.Pan (1988a: 432).

Distribution:—China (Sichuan).

Notes:—Type and only species of sect. *Isometrum* sect. *Chorianthera* (Pan 1988a, Wang *et al.* 1990, Li & Wang 2004).

***Oreocharis fargesii* (Franch.) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Didissandra fargesii* Franchet (1899a: 123).

Homotypic synonym:—*Isometrum fargesii* (Franch.) Burtt (1960: 92).

Distribution:—China (Sichuan).

Notes:—Referred to *Isometrum* sect. *Pachysiphon* Pan (1986: 26) by Pan (1986), Wang *et al.* (1990) and Li & Wang (2004).

***Oreocharis farreri* (Craib) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Isometrum farreri* Craib (1920a: 250).

Distribution:—China (Gansu, Shaanxi, Sichuan).

Notes:—Type species of *Isometrum*.

Oreocharis filipes Hance (1883: 166) ≡ ***Paraboea filipes*** (Hance) B.L.Burtt, see Burtt (1984).

***Oreocharis flabellata* (C.Y.Wu ex H.W.Li) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Ancylostemon flabellatus* C.Y.Wu ex Li (1983: 16).

Distribution:—China (Yunnan).

***Oreocharis flavida* Merrill (1922: 354).**

Distribution:—China (Hainan).

Notes:—Referred to *Oreocharis* sect. *Platyanthera* (Pan 1987: 289) by Pan (1987), Wang *et al.* (1990), Li & Wang (2004) and Wei *et al.* (2010b).

Oreocharis fokienensis Franchet (1899c: 212) = ***Oreocharis maximowiczii*** C.B.Clarke, see there.

***Oreocharis forrestii* (Diels) Skan (1917: t. 8719).**

Basionym:—*Roettlera forrestii* Diels (1912a: 224).

Distribution:—China (Sichuan, Yunnan).

Notes:—Referred to *Oreocharis* sect. *Orthoanthera* by Pan (1987), Wang *et al.* (1990) and Li & Wang (2004).

***Oreocharis gamosepala* (K.Y.Pan) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Ancylostemon gamosepalus* Pan (1988a: 434).

Distribution:—China (Sichuan).

***Oreocharis georgei* Anthony (1934: 202).**

Distribution:—China (Yunnan, Sichuan).

Notes:—Referred to *Oreocharis* sect. *Stomactin* by Pan (1987), Wang *et al.* (1990) and Li & Wang (2004).

***Oreocharis giraldii* (Diels) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Didissandra giraldii* Diels (1905: 98).

Homotypic synonym:—*Isometrum giraldii* (Diels) Burtt (1960: 92).

Distribution:—China (Shaanxi).

Notes:—Referred to *Isometrum* sect. *Isometrum* by Pan (1986), Wang *et al.* (1990) and Li & Wang (2004).

***Oreocharis glandulosa* (Batalin) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Didissandra glandulosa* Batalin (1892: 175).

Homotypic synonym:—*Isometrum glandulosum* (Batalin) Craib (1920b: 267).

Distribution:—China (Gansu, Sichuan).

Notes:—Referred to *Isometrum* sect. *Pachysiphon* by Pan (1986), Wang *et al.* (1990) and Li & Wang (2004).

***Oreocharis hekouensis* (Y.M.Shui & W.H.Chen) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Ancylostemon hekouensis* Y.M.Shui & W.H.Chen in Chen & Shui (2006: 448).

Distribution:—China (Yunnan).

Oreocharis henryana Oliver in Hooker (1890: tab. 1944).

Heterotypic synonym:—*Oreocharis squamigera* Léveillé (1915a: 24).

Distribution:—China (Gansu, Sichuan, Yunnan).

Notes:—Referred to *Oreocharis* sect. *Orthoanthera* by Pan (1987), Wang *et al.* (1990) and Li & Wang (2004).

Oreocharis heterandra D.Fang & D.H.Qin in Fang *et al.* (1994: 563).

Distribution:—China (Guangxi).

Notes:—The species was not explicitly referred to a section by the authors, but was said to be allied to *O. aurea*, which belongs to sect. *Stomactin*. Wang *et al.* (1990) and Li & Wang (2004) and Wei *et al.* (2010b), therefore, placed it in that section.

Oreocharis hirsuta Barnett (1961: 9).

Distribution:—Thailand.

Notes:—Referred to *Oreocharis* sect. *Oreocharis* by Pan (1987), Wang *et al.* (1990) and Li & Wang (2004).

Oreocharis humilis (W.T.Wang) Mich.Möller & A.Weber, *comb. nov.*

Basionym:—*Ancylostemon humilis* Wang (1975: 100).

Heterotypic synonyms:—*Didissandra saxatilis* var. *microcalyx* Hemsley (1890: 227), *Ancylostemon saxatilis* (Hemsl.) Craib var. *microcalyx* (Hemsl.) Craib (1920b: 266).

Distribution:—China (Hubei, Sichuan).

Oreocharis jiangxiensis (W.T.Wang) Mich.Möller & A.Weber, *comb. nov.*

Basionym:—*Deinocheilos jiangxiense* Wang (1986: 4).

Oreocharis lancifolia (Franch.) Mich.Möller & A.Weber, *comb. nov.*

Basionym:—*Didissandra lancifolia* Franchet (1887–1888: 63).

Homotypic synonyms:—*Isometrum lancifolium* (Franch.) Pan (1986: 30). *Ancylostemon lancifolius* (Franch.) Burtt (1958b: 305).

Heterotypic synonym:—*Ancylostemon purpureus* Burtt & Davidson (1954: 216).

Distribution:—China (Sichuan).

Notes:—Referred to *Isometrum* sect. *Isometrum* by Pan (1986), Wang *et al.* (1990) and Li & Wang (2004).

Oreocharis lancifolia var. *mucronata* (K.Y.Pan) Mich.Möller & A.Weber, *comb. nov.*

Basionym:—*Isometrum lancifolium* (Franch.) K.Y.Pan var. *mucronatum* Pan (1986: 30).

Distribution:—China (Sichuan).

Oreocharis leiophylla Wang (1975: 99).

Homotypic synonym:—*Bournea leiophylla* (W.T.Wang) W.T.Wang & K.Y.Pan in Wang *et al.* (1990: 135).

Distribution:—China (Fujian).

Notes:—Flowers actinomorphic, 5-merous.

Oreocharis leveilleana Fedde (1911: 64) = *Oreocharis auricula* (S.Moore) C.B.Clarke, see there.

Oreocharis leucantha (Diels) Mich.Möller & A.Weber, *comb. nov.*

Basionym:—*Didissandra leucantha* Diels in Pax (1922: 487).

Homotypic synonym:—*Isometrum leucanthum* (Diels) Burtt (1960: 92).

Distribution:—China (Sichuan).

Notes:—Referred to *Isometrum* sect. *Isometrum* by Pan (1986), Wang *et al.* (1990) and Li & Wang (2004).

***Oreocharis longifolia* (Craib) Mich.Möller & A.Weber, comb. nov.**

Briggsia longifolia Craib (1920a: 238).

Distribution:—China (Gansu, Sichuan, Yunnan), Myanmar.

Notes:—Type species of *Briggsia*. The type variety is found only in Yunnan and Myanmar.

***Oreocharis longifolia* var. *multiflora* (S.Y.Chen ex K.Y.Pan) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Briggsia longifolia* var. *multiflora* S.Y.Chen ex Pan (1988b: 453).

Distribution:—China (Gansu, Sichuan).

***Oreocharis lungshengensis* (W.T.Wang) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Opithandra lungshengensis* Wang (1975: 102).

Homotypic synonym:—*Isometrum lungshengense* (W.T.Wang) W.T.Wang & K.Y.Pan in Wang *et al.* (1990: 187).

Distribution:—China (Guangxi).

Notes:—Referred to *Isometrum* sect. *Isometrum* by Pan (1986), Wang *et al.* (1990) and Li & Wang (2004).

***Oreocharis magnidens* Chun ex Pan (1987: 276).**

Distribution:—China (Guangxi).

Notes:—Referred to *Oreocharis* sect. *Stomactin* by Pan (1987), Wang *et al.* (1990) and Li & Wang (2004).

***Oreocharis mairei* Léveillé (1912: 301).**

Basionym:—*Tremacron mairei* (H.Lév.) Craib (1918: 218).

Distribution:—China (Yunnan).

Notes:—This is not identical with *Ancylostemon mairei*, which is based on *Didymocarpus mairei*, described in the same publication as *Oreocharis mairei*. *Didymocarpus/Ancylostemon mairei* is given the new name *Oreocharis wangwentsaai* (see there).

***Oreocharis maximowiczii* C.B.Clarke (1883: 63).**

Heterotypic synonym:—*Oreocharis fokienensis* Franchet (1899c: 212).

Distribution:—China (Fujian, Jiangxi).

Notes:—Referred to *Oreocharis* sect. *Oreocharis* by Pan (1987), Wang *et al.* (1990) and Li & Wang (2004).

Oreocharis micrantha Léveillé (1915a: 24) = ***Didymocarpus stenanthos*** C.B.Clarke var. *stenanthos*, see Wang *et al.* (1990, 1998).

***Oreocharis mileensis* (W.T.Wang) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Paraisometrum mileense* W.T.Wang in Weitzman *et al.* (1998: 434).

***Oreocharis minor* (Craib) Pellegrin (1926: 873).**

Basionym:—*Perantha minor* Craib (1918: 213).

Distribution:—China (Sichuan, Yunnan).

Notes:—Referred to *Oreocharis* sect. *Stomactin* by Pan (1987), Wang *et al.* (1990) and Li & Wang (2004).

***Oreocharis muscicola* (Craib) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Briggsia muscicola* Craib (1920b: 264).

Distribution:—China (Xizang, Yunnan), Bhutan, northeast India, Myanmar

***Oreocharis nanchuanica* (K.Y.Pan & Z.Y.Liu) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Isometrum nanchuanicum* K.Y.Pan & Liu (1995: 100).

Distribution:—China (Sichuan).

Notes:—Referred to *Isometrum* sect. *Pachysiphon* by Pan (1986), Wang *et al.* (1990) and Li & Wang (2004).

***Oreocharis nemoralis* Chun** (1946: 288).

Distribution:—China (Hunan, Guangdong).

Notes:—Referred to *Oreocharis* sect. *Stomactin* by Pan (1987), Wang *et al.* (1990) and Li & Wang (2004). The type variety is found only in Hunan.

***Oreocharis nemoralis* var. *lanata* Zheng & Xia** (2002: 34).

Distribution:—China (Guangdong).

Oreocharis notha Clarke (1883: 64). = ***Napeanthus primulifolius* (Raddi)** Sandw., see Leeuwenberg (1958).

***Oreocharis notochlaena* (H.Lév. & Vaniot)** Léveillé (1911a: 330).

Basionym:—*Didissandra notochlaena* H.Lév. & Vaniot in Léveillé (1906: 425).

Homotypic synonyms:—*Didymocarpus notochlaenus* Léveillé (1906: 428; “*notochlaena*”), nom. inval., see Vitek *et al.* (1998, 2000), *Ancylostemon notochlaenus* (H.Lév. & Vaniot) Craib (1920b: 266).

Distribution:—China (Guizhou).

***Oreocharis obliqua* C.Y.Wu ex Li** (1983: 6).

Distribution:—China (Yunnan).

Notes:—Referred to *Oreocharis* sect. *Stomactin* by Pan (1987), Wang *et al.* (1990) and Li & Wang (2004).

***Oreocharis obliquifolia* (K.Y.Pan) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Tremacron obliquifolium* Pan (1988a: 429).

Distribution:—China (Sichuan).

Oreocharis obovata Barnett (1961: 10). = ***Ridleyandra flammea* (Ridl.)** A.Weber, see Weber & Burtt (1998a).

***Oreocharis obtusidentata* (W.T.Wang) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Opithandra obtusidentata* Wang (1982: 38).

Distribution:—China (Hunan).

Notes:—Referred to *Opithandra* sect. *Briggsioides* by Wang (1987), Wang *et al.* (1990) and Li & Wang (2004).

***Oreocharis pankaiyuae* Mich.Möller & A.Weber, nom. nov.**

Basionym:—*Tremacron aurantiacum* Pan (1988a: 431).

Distribution:—China (Sichuan, Guizhou).

Notes:—The new name honours the Chinese botanist Pan Kai-Yu. Her many papers on Chinese Gesneriaceae included revisions of *Oreocharis* (Pan 1987), *Isometrum* (Pan 1986) and *Tremacron* (Pan 1988a). The type variety is found only in Sichuan.

***Oreocharis pankaiyuae* var. *weiningense* (S.Z.He & Q.W.Sun) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Tremacron aurantiacum* var. *weiningense* S.Z.He & Q.W.Sun in He *et al.* (2010: 199).

Distribution:—China (Guizhou).

***Oreocharis primuloides* (Miq.) Benth. & Hook.f. ex Clarke (1883: 63).**

Basionym:—*Boea primuloides* Miquel (1867: 190).

Homotypic synonyms:—*Didymocarpus primuloides* (Miq.) Maximowicz (1874: 536), *Chirita primuloides* (Miq.) Ohwi (1936: 662), *Opithandra primuloides* (Miq.) B.L.Burtt (1956: 162).

Heterotypic synonym:—*Opithandra primuloides* f. *albiflora* (Makino) Yamazaki (1993: 379).

Distribution:—Japan (Honshu, Shikoku, Kyushu).

Notes:—Type species of *Opithandra* and sect. *Opithandra*.

***Oreocharis pumila* (W.T.Wang) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Schistolobos pumilus* Wang (1983b: 16).

Homotypic synonym:—*Opithandra pumila* (W.T.Wang) Wang (1992: 293).

Distribution:—China (Guangxi).

Notes:—Type and only species of *Opithandra* sect. *Schistolobos* (Wang 1992).

***Oreocharis pinnatilobata* (K.Y.Pan) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Isometrum pinnatilobatum* Pan (1986: 34).

Distribution:—China (Hubei, Sichuan).

Notes:—Referred to *Isometrum* sect. *Isometrum* by Pan (1986), Wang *et al.* (1990) and Li & Wang (2004).

***Oreocharis primuliflora* (Batalin) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Didissandra primuliflora* Batalin (1895: 176).

Homotypic synonym:—*Isometrum primuliflorum* (Batalin) Burtt (1960: 93).

Distribution:—China (Sichuan).

Notes:—Referred to *Isometrum* sect. *Isometrum* by Pan (1986), Wang *et al.* (1990) and Li & Wang (2004).

***Oreocharis rhombifolia* (K.Y.Pan) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Ancylostemon rhombifolius* Pan (1988a: 435).

Distribution:—China (Sichuan).

***Oreocharis rhytidophylla* C.Y.Wu ex Li (1983: 9).**

Distribution:—China (Yunnan).

Notes:—The status and sectional placement of this species is uncertain. It is known only from fruiting specimens and, therefore, was omitted from the treatment in the Flora of China (Wang *et al.* 1998: 251). Wang *et al.* (1998: 260) state that it is similar to *Oreocharis benthamii* var. *reticulata*.

***Oreocharis ronganensis* (K.Y.Pan) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Ancylostemon ronganensis* Pan (1988a: 436).

Distribution:—China (Guangxi).

***Oreocharis rosthornii* (Diels) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Didissandra rosthornii* Diels (1900: 574).

Homotypic synonym:—*Briggsia rosthornii* (Diels) Burtt (1958b: 306).

Heterotypic synonym:—*Briggsia hians* Chun (1946: 302).

Distribution:—China (Guizhou, Hubei, Sichuan, Yunnan).

Notes:—The type variety is found in Guizhou, Hubei, Sichuan.

***Oreocharis rosthornii* var. *crenulata* (Hand.-Mazz.) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Briggsia crenulata* Handel-Mazzetti (1934: 20).

Homotypic synonym:—*Briggsia rosthornii* var. *crenulata* (Hand.-Mazz.) K.Y.Pan in Wang *et al.* (1990: 223).

Distribution:—China (Guizhou).

***Oreocharis rosthornii* var. *wenshanensis* (K.Y.Pan) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Briggsia rosthornii* var. *wenshanensis* Pan (1988b: 456).

Distribution:—China (Yunnan).

***Oreocharis rosthornii* var. *xingrenensis* (K.Y.Pan) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Briggsia rosthornii* var. *xingrenensis* Pan (1988b: 456).

Distribution:—China (Guizhou).

***Oreocharis rotundifolia* Pan (1987: 280).**

Distribution:—China (Yunnan).

Notes:—Referred to *Oreocharis* sect. *Stomactin* by Pan (1987), Wang *et al.* (1990) and Li & Wang (2004).

***Oreocharis rubra* (Hand.-Mazz.) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Tremacron rubrum* Handel-Mazzetti (1936: 877).

Distribution: China (Yunnan).

***Oreocharis saxatilis* (Hemsl.) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Didissandra saxatilis* Hemsley (1890: 227).

Homotypic synonyms:—*Didymocarpus saxatilis* (Hemsl.) Léveillé (1906: 427), *Ancylostemon saxatilis* (Hemsl.) Craib (1920b: 266).

Distribution:—China (Gansu, Hubei, Sichuan).

Oreocharis seguinii Léveillé (1906: 427, as: “*seguini*”), nom. nud. = ***Paraboea rufescens*** (Franch.) B.L.Burtt, see Xu *et al.* (2008).

Oreocharis sericea Léveillé. (1911a: 329) = ***Oreocharis auricula*** (S.Moore) C.B.Clarke, see there.

***Oreocharis sichuanensis* (W.T.Wang) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Deinocheilos sichuanense* Wang (1986: 2).

Distribution:—China (Sichuan, Jiangxi).

***Oreocharis sichuanica* (K.Y.Pan) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Isometrum sichuanicum* Pan (1986: 33).

Distribution:—China (Sichuan).

Notes:—Referred to *Isometrum* sect. *Isometrum* by Pan (1986), Wang *et al.* (1990) and Li & Wang (2004).

***Oreocharis sinensis* (Oliv.) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Bournea sinensis* Oliver in Hooker (1893: tab. 2254).

Distribution:—China (Guangdong).

Notes:—Type species of *Bournea*; distinctive in the actinomorphic, 4-merous flowers.

***Oreocharis sinotheoryi* (Chun) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Didymocarpus sinotheoryi* Chun (1946: 290).

Homotypic synonym:—*Opithandra sinotheoryi* (Chun) Burtt (1958a: 303).

Distribution:—China (Guangxi).

Notes:—Referred to *Opithandra* sect. *Opithandra* by Wang (1987), Wang *et al.* (1990) and Li & Wang (2004).

Oreocharis squamigera Léveillé (1915a: 24) = ***Oreocharis henryana*** Oliv., see there.

***Oreocharis stenosiphon* Mich.Möller & A.Weber, nom. nov.**

Basionym:—*Rottlera fargesii* Franchet (1899b: 251).

Homotypic synonym:—*Opithandra fargesii* (Franch.) Burtt (1958a: 303).

Distribution:—China (Sichuan).

Notes:—Type and only species of *Opithandra* sect. *Stenosiphon* (Wang 1987, Wang *et al.* 1990, Li & Wang 2004).

***Oreocharis stewardii* (Chun) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Briggsia stewardii* Chun (1946: 303).

Distribution:—China (Guangxi).

Oreocharis tonkinensis Kraenzlin (1928: 216) ≡ *Didymocarpus tonkinensis* (Kraenzl.) Handel-Mazzetti (1936: 883) ≡ *Boeica tonkinensis* (Kraenzl.) Burtt (1977: 373) = *Boeica porosa* Clarke (1883: 136), see Wang *et al.* (1990, 1998).

***Oreocharis trichantha* (B.L.Burtt & R.Davidson) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Ancylostemon trichanthus* Burtt & Davidson (1954: 218).

Distribution:—China (Yunnan).

***Oreocharis tubicella* Franchet (1899b: 249).**

Distribution:—China (Sichuan, Yunnan).

Notes:—Referred to *Oreocharis* sect. *Oreocharis* by Pan (1987), Wang *et al.* (1990) and Li & Wang (2004).

***Oreocharis tubiflora* Pan (1987: 287).**

Distribution:—China (Fujian).

Notes:—Referred to *Oreocharis* sect. *Oreocharis* by Pan (1987), Wang *et al.* (1990) and Li & Wang (2004).

***Oreocharis urceolata* (K.Y.Pan) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Tremacron urceolatum* Pan (1988a: 429).

Distribution:—China (Sichuan).

***Oreocharis villosa* (K.Y.Pan) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Isometrum villosum* K.Y.Pan (1986: 31).

Distribution:—China (Sichuan).

Notes:—Referred to *Isometrum* sect. *Isometrum* by Pan (1986), Wang *et al.* (1990) and Li & Wang (2004).

***Oreocharis vulpina* (B.L.Burtt & R.Davidson) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Ancylostemon vulpinus* Burtt & Davidson (1954: 217).

Distribution:—China (Yunnan).

***Oreocharis wangwentsaaii* Mich.Möller & A.Weber, nom. nov.**

Basionym:—*Didymocarpus mairei* Léveillé (1912: 301).

Homotypic synonym:—*Ancylostemon mairei* (H.Lév.) Craib (1920b: 267).

Distribution:—China (Yunnan, Sichuan).

Notes:—The new name is chosen in honour of the eminent Chinese gesneriologist Prof. Wang Wen-Tsai, Beijing. See also notes under *Oreocharis mairei*. The type variety is found only in Yunnan.

***Oreocharis wangwentsaaii* var. *emeiensis* (K.Y.Pan) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Ancylostemon mairei* (H.Lév.) Craib var. *emeiensis* Pan (1988a: 434).

Distribution:—China (Sichuan).

***Oreocharis wanshanensis* (S.Z.He) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Isometrum wanshanense* He (2006: 454).

Distribution:—China (Guizhou).

Notes:—The species is said to be closely related to *Isometrum villosum* by He (2006) and thus can be referred to *Isometrum* sect. *Isometrum*.

***Oreocharis wentsaaii* (Z.Yu Li) Mich.Möller & A.Weber, comb. nov.**

Basionym:—*Opithandra wentsaaii* Li (2003: 73).

Distribution:—China (Guizhou).

Notes:—Referred to *Opithandra* sect. *Briggsioides* by Li (2003), who says that “it is most closely related to *O. cinerea* W.T.Wang”.

***Oreocharis xiangguiensis* W.T.Wang & K.Y.Pan in Pan (1987: 285).**

Distribution:—China (Hunan, Guangxi).

Notes:—Referred to *Oreocharis* sect. *Oreocharis* by Pan (1987), Wang *et al.* (1990) and Li & Wang (2004).

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Appendix 1: Diagnostics of the Bayesian inference analysis of the *Oreocharis* dataset of combined *trnL-F* and ITS sequence data plus alignment gap matrix.

Number of taxa = 55
Number of characters = 1632
Number of generations = 2500000

Average standard deviation of split frequencies: 0.010898

Analysis completed in 44263 seconds
Analysis used 44262.85 seconds of CPU time
Likelihood of best state for "cold" chain of run 1 was -9387.23
Likelihood of best state for "cold" chain of run 2 was -9396.93
Acceptance rates for the moves in the "cold" chain of run 1:
With prob. Chain accepted changes to
54.02 % param. 1 (revmat) with Dirichlet proposal
20.50 % param. 2 (revmat) with Dirichlet proposal
57.63 % param. 3 (revmat) with Dirichlet proposal
19.96 % param. 4 (state frequencies) with Dirichlet proposal
15.31 % param. 6 (state frequencies) with Dirichlet proposal
19.86 % param. 9 (gamma shape) with multiplier
45.24 % param. 10 (gamma shape) with multiplier
69.87 % param. 11 (prop. invar. sites) with sliding window
14.45 % param. 12 (topology and branch lengths) with extending TBR
23.78 % param. 12 (topology and branch lengths) with LOCAL
Acceptance rates for the moves in the "cold" chain of run 2:
With prob. Chain accepted changes to
50.90 % param. 1 (revmat) with Dirichlet proposal
20.95 % param. 2 (revmat) with Dirichlet proposal
58.89 % param. 3 (revmat) with Dirichlet proposal
19.81 % param. 4 (state frequencies) with Dirichlet proposal
15.09 % param. 6 (state frequencies) with Dirichlet proposal
20.48 % param. 9 (gamma shape) with multiplier
45.24 % param. 10 (gamma shape) with multiplier
69.81 % param. 11 (prop. invar. sites) with sliding window
14.29 % param. 12 (topology and branch lengths) with extending TBR
23.78 % param. 12 (topology and branch lengths) with LOCAL

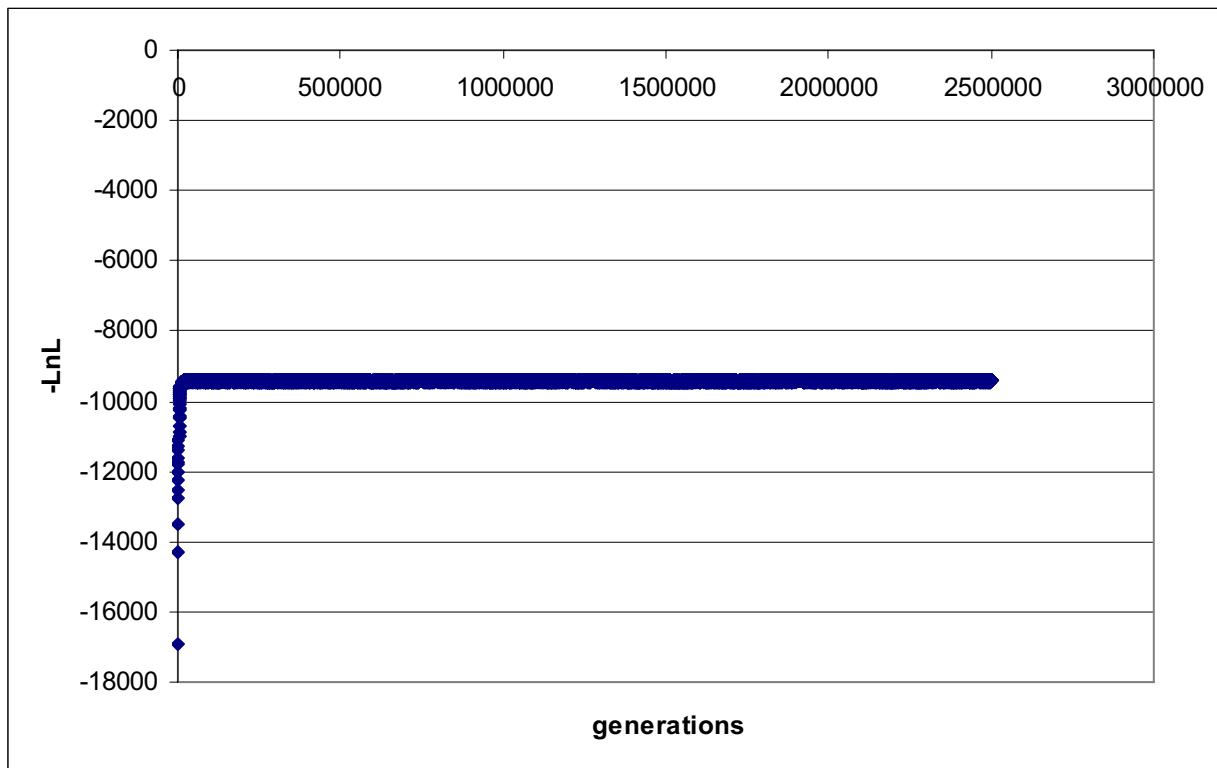
Chain swap information for run 1:

	1	2	3	4
1	0.19	0.01	0.00	
2	415635		0.23	0.02
3	416899	417311		0.30
4	416255	416695	417205	

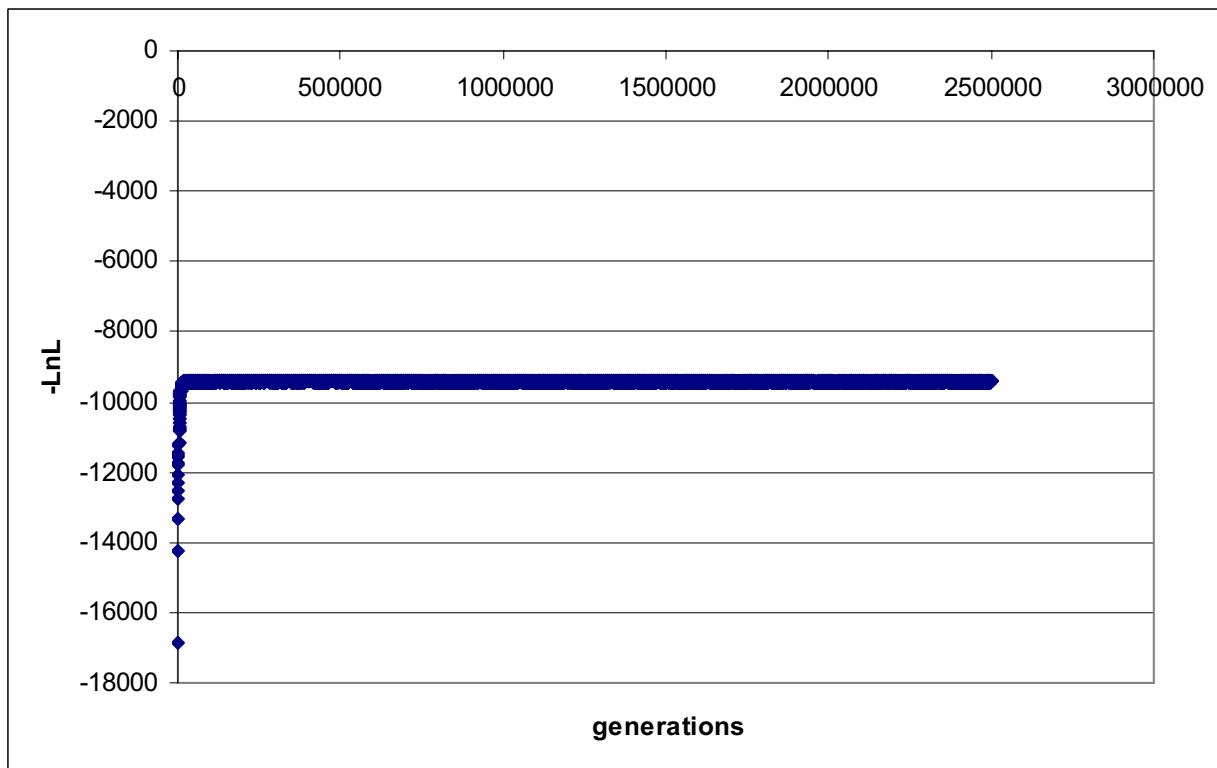
Chain swap information for run 2:

	1	2	3	4
1	0.16	0.01	0.00	
2	416978		0.24	0.03
3	417053	415321		0.31
4	417026	416960	416662	

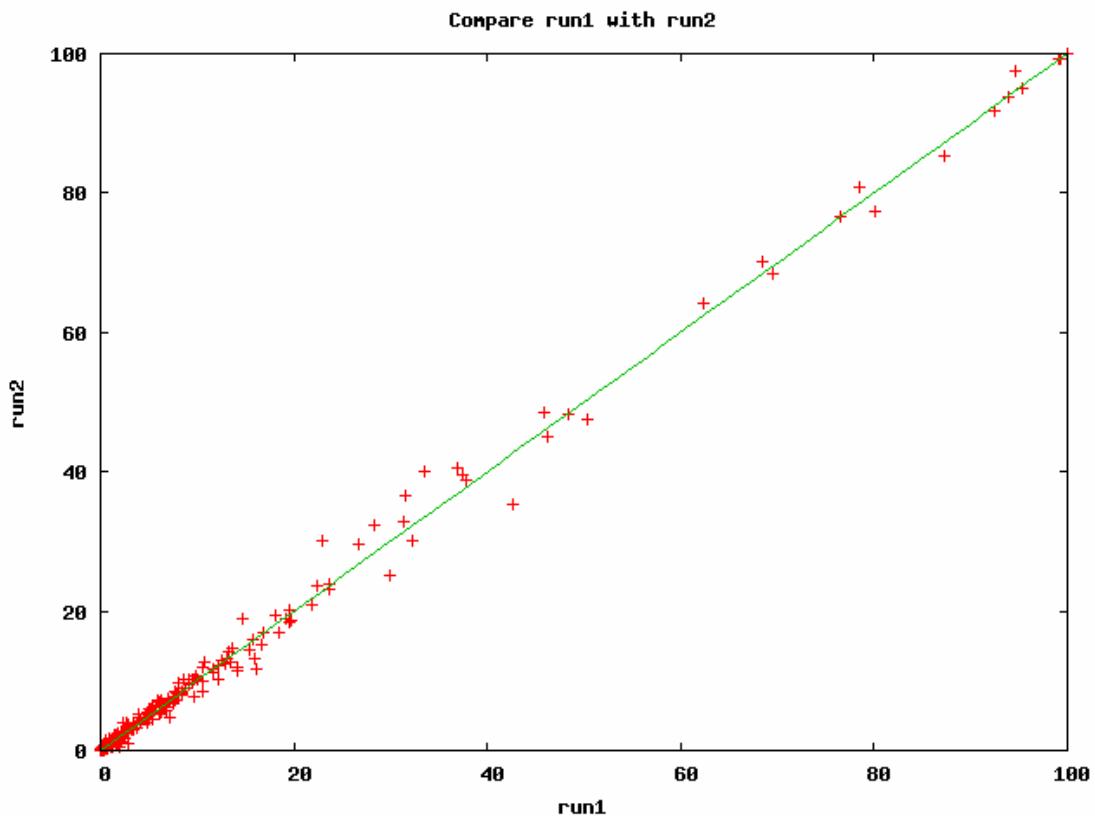
Upper diagonal: Proportion of successful state exchanges between chains
Lower diagonal: Number of attempted state exchanges between chains



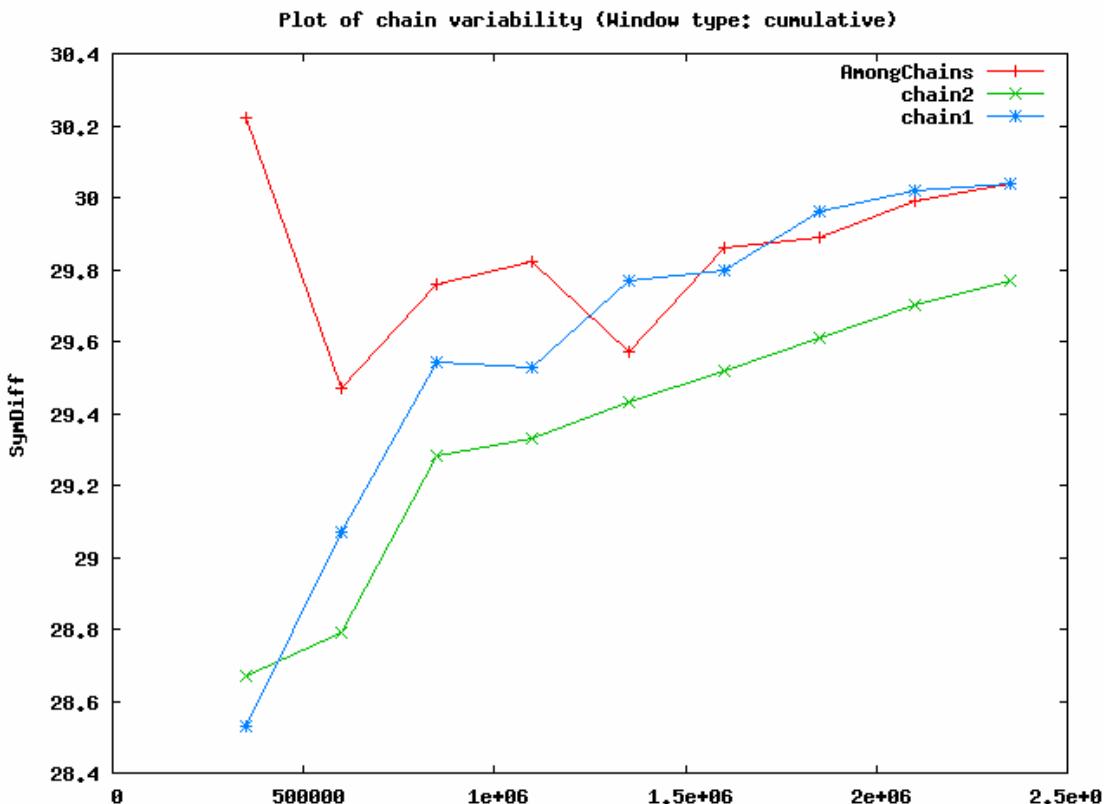
generations vs $-lnL$ values, run 1
burn-in 4%



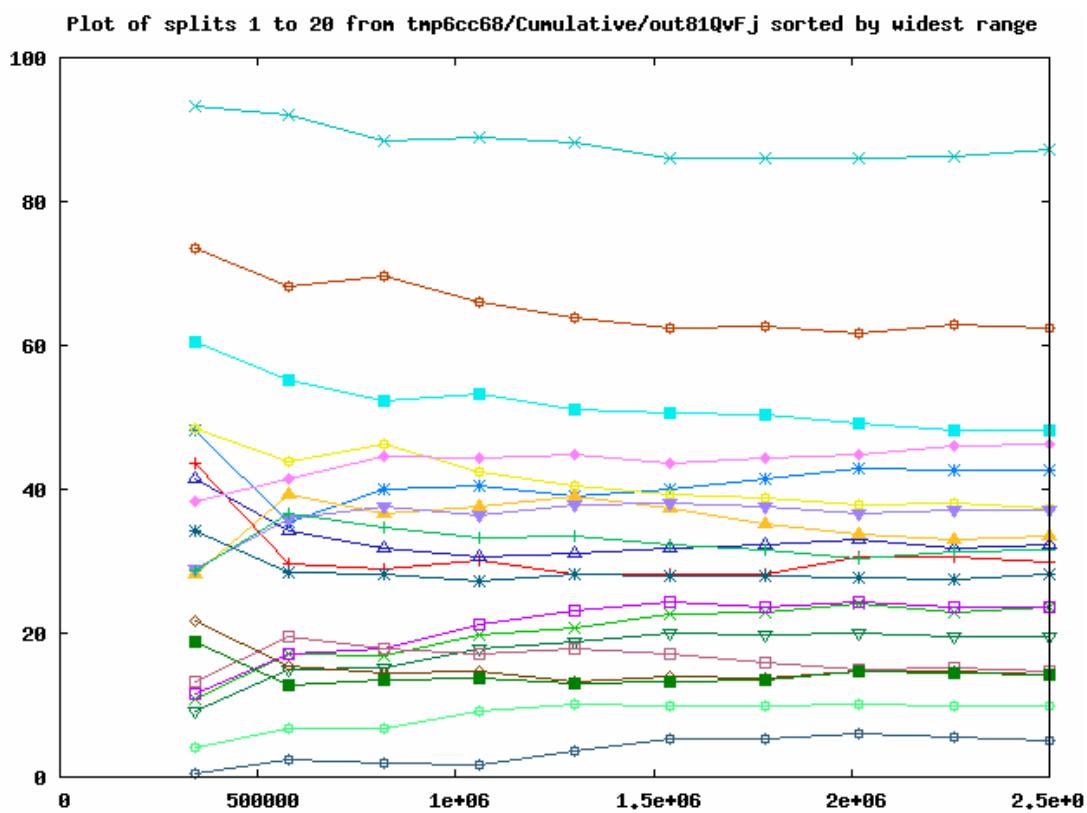
generations vs $-lnL$ values, run 2
burn-in 4%



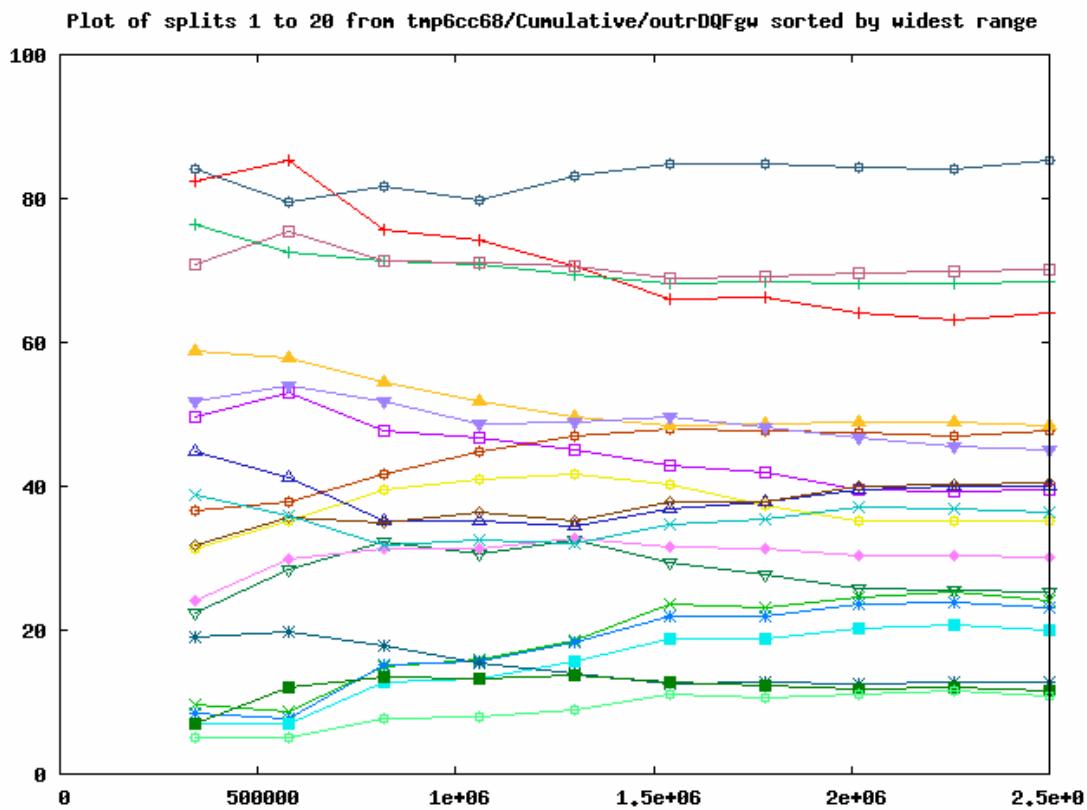
Oreocharis combined data. Posterior probabilities run 1 versus run 2.



Oreocharis combined data: Symmetric tree differences within and between run 1 vs run 2.



Run 1



Run 2