



Inclusion of *Metabriggsia* into *Hemiboea* (Gesneriaceae)

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Abstract

Based on molecular data and morphology, *Metabriggsia* is reduced to synonymy with *Hemiboea* and its two species transferred to that genus.

Key words: fruit morphology, Lamiales, molecular systematics, ovary morphology

Introduction

In the Old World Gesneriaceae, particularly among the Chinese representatives, a high number of small or monotypic genera have been described, some representing presumed relatives of well-established genera (often earmarked by the prefixes *Meta-*, *Para-*, or *Pseudo-*), some being rather isolated phylogenetically (Möller *et al.* 2011a). One of these small genera is *Metabriggsia*. It was described by Wang (1983a), based on two new species (*M. ovalifolia*, *M. purpureotincta*) from the northwestern part of Guangxi province in South China. Wang (1983a: 1) related the new genus to two genera, *Briggsia* Craib (1920: 236) and *Didymocarpus* Wallich (1819: 378): “Corollae forma *Briggsiae* Craib similis, a qua staminibus duobus anticis solum fertilibus, placenta parietali unica recedit. A *Didymocarpo* Wall. antheris basifixis apice cohaerentibus, loculis parallelis apice haud confluentibus, placenta parietali unica facile differt”. The name *Metabriggsia* readily suggests a close affinity with *Briggsia*, but *Metabriggsia* differs from *Briggsia* by the presence of two fertile stamens (vs. four in *Briggsia*) and by only one carpel being fertile. As *Didymocarpus* has principally diandrous flowers, the difference with that genus is mainly in the carpel fertility.

What is difficult to understand is why Wang (1983a) did not discuss an affinity with *Hemiboea*, which agrees in both characters with *Metabriggsia*. Since then, Wang may have changed his view as *Metabriggsia* does not appear in close association with *Briggsia* or *Didymocarpus*, but immediately precedes *Hemiboea* in the “*Flora Reipublicae Popularis Sinicae*” (Wang *et al.* 1990, in Chinese) and “*Flora of China*” (Wang *et al.* 1998, in English). The molecular study of Möller *et al.* (2011a) provides evidence that the two species of *Metabriggsia* are not only closely related to each other, but are nested (in different places) in *Hemiboea*. The characters used for generic separation, therefore, have to be critically examined and discussed. As will be shown here, the carpel characters were evidently based on misinterpretations. In our opinion, the two *Metabriggsia* species fit perfectly into *Hemiboea* and should be transferred to that genus.

Material and Methods

Plant material for morphological studies was either fixed (3 : 1 of ethanol : acetic acid) in the field (*Metabriggsia purpureotincta*, MMO 06-813), or from plants cultivated at RBGE [*Corallodiscus lanuginosus* (Wall. ex DC.) Burt (1947: 212), cult. RBGE 20010593; China; *Hemiboea cavaleriei* H.Lév. var. *paucinervis* W.T.Wang & Z.Y.Li in Li (1983: 194), cult RBGE 20020464, MM01-143; China, Guangxi, Napo].

Molecular data came from previous studies (Möller *et al.* 2009, 2011a), the taxa and collection details are given in Table 1. Only sequences for *Hemiboea flaccida* were newly added, following the protocols of Möller *et al.* (2009, 2011a). The newly acquired sequences were deposited in GenBank.

TABLE 1: List of the 24 didymocarpoid Gesneriaceae samples included in the phylogenetic analysis, including voucher number and deposition, origin information and respective GenBank accession numbers. Those in bold denote generic type species.

Taxon	Voucher number	Deposited in	Origin	<i>trnL-F</i>	ITS or ITS1 / ITS2
<i>Anna mollifolia</i> (W.T.Wang) W.T.Wang & K.Y.Pan in Wang <i>et al.</i> (1990: 487)	<i>M.Möller MMO 01-146</i>	E, WU	China, Guangxi, Napo county	FJ501543	AF055050 / AF055051
<i>Anna ophiorrhizoides</i> (Hemsl.) B.L.Burt & R.Davidson (1955: 233)	<i>M.Möller MMO 08-1280</i>	E	China, Sichuan, Emei Shan	HQ632937	HQ633034
<i>Anna submontana</i> Pellegrin (1930a: 46)	<i>M.Möller MMO 01-85</i>	E, WU	China, Yunnan, Maguan county	FJ501542	FJ501362
<i>Briggsia longipes</i> (Hemsl. ex Oliv.) Craib (1919: 262)	<i>M.Möller MMO 01-122</i>	E, WU	China, Yunnan, Xichou county	FJ501545	AF055052 / AF055053
<i>Briggsia mihieri</i> (Franch.) Craib (1919: 262)	<i>Y.Z.Wang 11315B</i>	PE	China, Chongqing, Nanchuan county	FJ501544	FJ501363
<i>Hemiboea bicornuta</i> (Hayata) Ohwi (1936: 662)	Voucher from Cult. RBGE 19951207]	E	unknown origin	FJ501534	FJ501356
<i>Hemiboea cavaleriei</i> H.Léveillé (1911: 328)	<i>Z.J.Gu G3</i>	KUN	China, unknown locality	FJ501533	FJ501355
<i>Hemiboea fangii</i> Chun ex Z.Y.Li in Li (1983: 197)	<i>M.Möller MMO 08-1284</i>	E	China, Sichuan, Emei Shan	HQ632882	HQ632979
<i>Hemiboea flaccida</i> Chun ex Z.Y.Li in Li (1983: 201)	<i>Y.G.Wei 09-76</i>	IBK	China, Guangxi, Longlin county	JF697579	JF697567
<i>Hemiboea follicularis</i> C.B.Clarke in Hooker (1888: t. 1798)	<i>Y.G.Wei G03</i>	IBK	China, Guangxi, Huanjiang county	HQ632885	HQ632982
<i>Hemiboea gracilis</i> Franchet (1899: i. 124)	<i>Y.Z.Wang 11317</i>	PE	China, Chongqing, Nanchuan county	FJ501536	Wei <i>et al.</i> , 2010a
<i>Hemiboea longgangensis</i> Z.Y.Li (1983: 202)	<i>Y.G.Wei 07-550</i>	IBK	China, Guangxi Longzhou county	HQ632889	HQ632986
<i>Hemiboea longzhouensis</i> W.T.Wang in Li (1983: 198)	<i>M.Möller MMO 07-1127</i>	E	China, Guangxi, Longan county	HQ632888	HQ632985
<i>Hemiboea magnibracteata</i> Y.G.Wei & H.Q.Wen (1995: 216)	<i>M.Möller MMO 08-1347</i>	E	China, Guangxi, Huanjiang county	HQ632887	HQ632984
<i>Hemiboea omeiense</i> W.T.Wang in Wang & Pan (1982: 127)	<i>M.Möller MMO 08-1271</i>	E	China, Sichuan, Emei Shan	HQ632886	HQ632983
<i>Hemiboea rubribracteata</i> Z.Y.Li & Yan Liu (2004: 537)	<i>M.Möller MMO 07-1093</i>	E	China, Guangxi, Jingxi county	HQ632890	HQ632987

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TABLE 1 (continued)

Taxon	Voucher number	Deposited in	Origin	<i>trnL-F</i>	ITS or ITS1 / ITS2
<i>Hemiboea subcapitata</i> C.B.Clarke in Hooker (1888: t. 1798)	<i>Y.Z.Wang 11306</i>	PE	China, Chongqing, Chengkou county	FJ501535	FJ501357
<i>Loxostigma fimbriosepalum</i> K.Y.Pan in Wang & Pan (1982: 143)	<i>Y.Z.Wang 991005</i>	PE	China, Yunnan, Jinping county	FJ501507	Wei <i>et al.</i> , 2010a
<i>Loxostigma griffithii</i> (Wight) C.B.Clarke (1883: 60)	<i>Kew/Edinburgh Kanchenjunga Expedition (1989) 940 [Cult. RBGE 19892473A]</i>	E	Nepal, Yamphudin	FJ501508	FJ501338
<i>Lysionotus chingii</i> Chun ex W.T.Wang (1983b: 279)	<i>Y.Z.Wang S-10669</i>	PE	China, unknown locality	FJ501498	FJ501332
<i>Lysionotus pauciflorus</i> Maximowicz (1874: 534)	<i>M.Möller MMO 01-101</i>	E, WU	China, Yunnan, Xichou county	FJ501497	FJ501331
<i>Lysionotus petelotii</i> Pellegrin (1930b: 503)	<i>M.Möller MMO 01-100/4</i>	E	China, Yunnan, road to Xichou	FJ501496	HQ632974
<i>Metabriggsia ovalifolia</i> W.T.Wang (1983a: 2)	<i>B.M.Nong 06-1</i>	IBK	China, Guangxi, Napo county	HQ632883	HQ632980
<i>Metabriggsia purpureotincta</i> W.T.Wang (1983a: 2)	<i>M.Möller MMO 06-813</i>	E	China, Guangxi, Tianlin county	HQ632884	HQ632981

Möller *et al.* (2011a) showed that *Hemiboea* formed a well supported monophyletic clade with the two *Metabriggsia* samples nested deeply in the latter genus. With the addition of *H. flaccida*, the present analysis included 14 ingroup samples (12 *Hemiboea* out of 23 described, 2 *Metabriggsia* out of 2), with three samples each of *Anna* Pellegrin (1930a: 46) and *Lysionotus* Don (1822: 85), and two samples of *Briggsia* and *Loxostigma* Clarke (1883: 59) as outgroups. Based on Möller *et al.* (2011a), the trees were rooted with two *Loxostigma* species (*L. fimbriosepalum*, *L. griffithii*). Maximum parsimony (MP) and Bayesian Inference (BI) analyses followed Möller *et al.* (2009, 2011a, b). MP branch support was obtained by a bootstrap analysis as in Möller *et al.* (2009, 2011a). Best-fitting models for the BI analysis were GTR+G for *trnL-F* and the ITS spacers and SYM+I for the 5.8S gene. The gaps were treated as standard characters. One million generations were run with a burn-in of 4%, determined by plotting likelihoods against generations (Appendix 1). Posterior probabilities (PP) came from MrBayes consensus trees using the ‘sumt’ command. The PP branch support values showed a high correlation between the two parallel Bayesian runs (Appendix 1).

Results and Discussion

Molecular phylogenies

The molecular matrix consisted of 24 samples and had a length of 1581 characters (*trnL-F*: 858 characters, ITS: 723). These included 207 (13.1%) parsimony informative sites. The maximum parsimony analysis resulted in three most parsimonious trees. In the majority rule consensus tree (Fig. 1) and the Bayesian tree (Fig. 2), the samples of the four outgroup genera each formed highly supported clades (BS=99-100%; PP=1.00), with the *Briggsia* clade either between *Loxostigma* and a polytomy of *Anna* and *Lysionotus* (MP, BS=99%), or between *Loxostigma* and *Anna* and *Lysionotus* as sister clades (BI, PP=0.99). *Hemiboea* formed a highly supported clade (BS=100%; PP=1.00), with the two *Metabriggsia* nested within this clade. *Metabriggsia ovalifolia* was sister to *Hemiboea flaccida* (BS=100%; PP=1.00), and *Metabriggsia purpureotincta* was in an unsupported position (MP) or on a polytomy (BI) with several *Hemiboea* samples in

a more derived position. At the base of the *Hemiboea* clade was *Hemiboea fangii* (BS =61%; PP=0.83) in a reasonably supported position, clearly integrating the two *Metabriggsia* samples into *Hemiboea*.

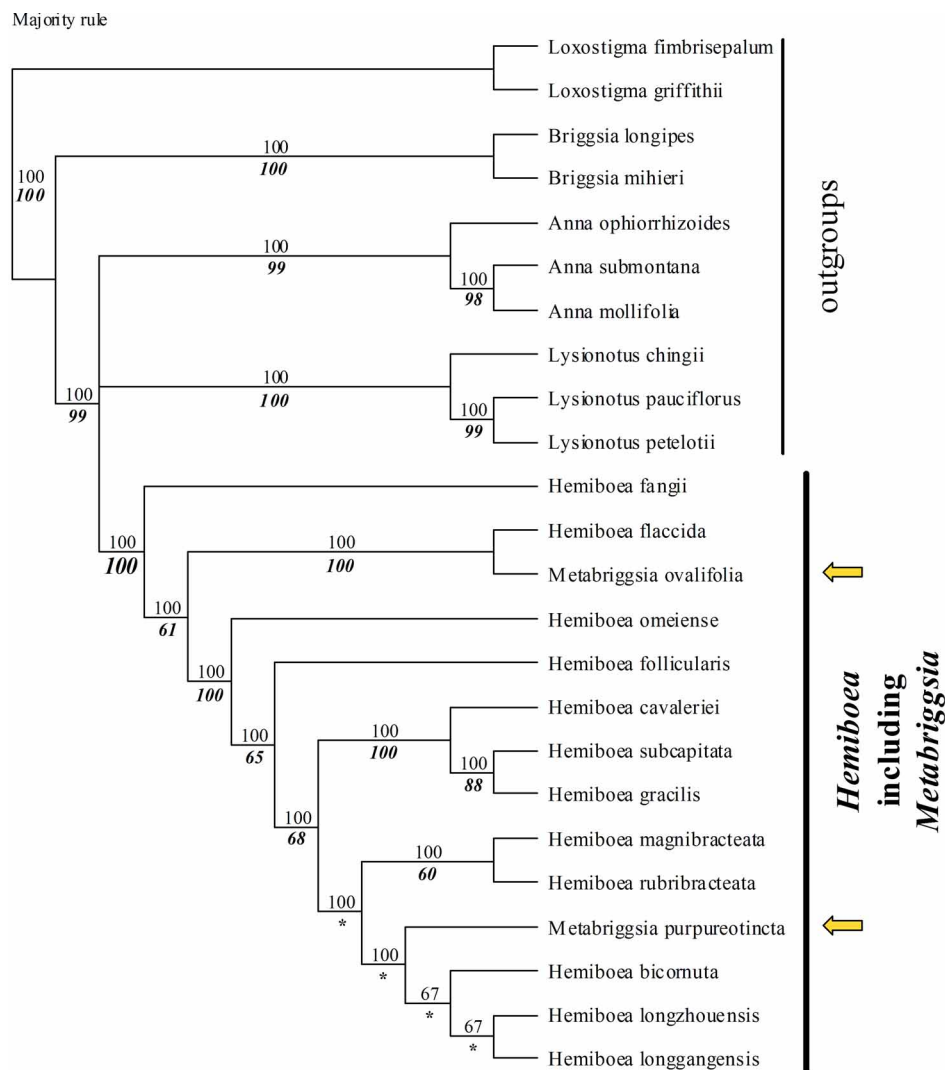


FIGURE 1: Majority rule consensus tree of 3 most parsimonious trees based on combined (PHT: $P=0.07$) *trnL-F*, ITS and gap characters of 577 steps length (CI= 0.7157; RI=0.8078). Numbers along branches, above are majority rule frequencies, below (bold, italics) bootstrap values based on 10000 random additions with TBR on and MulTrees off. Arrows indicate the position of *Metabriggsia* samples.

Morphological considerations

As the molecular analysis does not indicate an affinity of the ingroup samples to *Didymocarpus* or any group of the polyphyletic *Briggsia*, we can concentrate our discussion on *Hemiboea*. Both *Metabriggsia* and *Hemiboea* are caulescent perennials with fairly similar diandrous flowers, and large bracts forming an involucre and, judging from the descriptions presented in the “Flora of China” (Wang *et al.* 1998), the only difference of generic importance lies in the internal structure of the ovary/fruit. The ovary of *Metabriggsia* is said to be “1-loculed, placenta 1, parietal, projecting into locule, undivided” (Wang *et al.* 1998: 294), while that of *Hemiboea* is characterised as “2-loculed, only adaxial locule fertile; placenta 1, axile” (Wang *et al.* 1998: 294). In the original description (Wang 1983a) a figure is presented showing a cross section through the ovary of *Metabriggsia ovalifolia*. The ovary appears strongly compressed with distinct ridges (ribs) on both sides, and with a lens-shaped placenta (ovules or seeds not clearly discernible) protruding from the right side into the single locule. This condition, however, cannot be interpreted as a bicarpellate gynoecium, of which one carpel is fertile and the other sterile. If the orientation of the cross section is correct (with the upper and

lower carpels in the median plane) it would mean that each carpel would be sterile on the left margin, and fertile on the right margin, with the two half-placentae being fused. To the best of our knowledge, such a condition has never been found in Gesneriaceae or any other group of angiosperms.

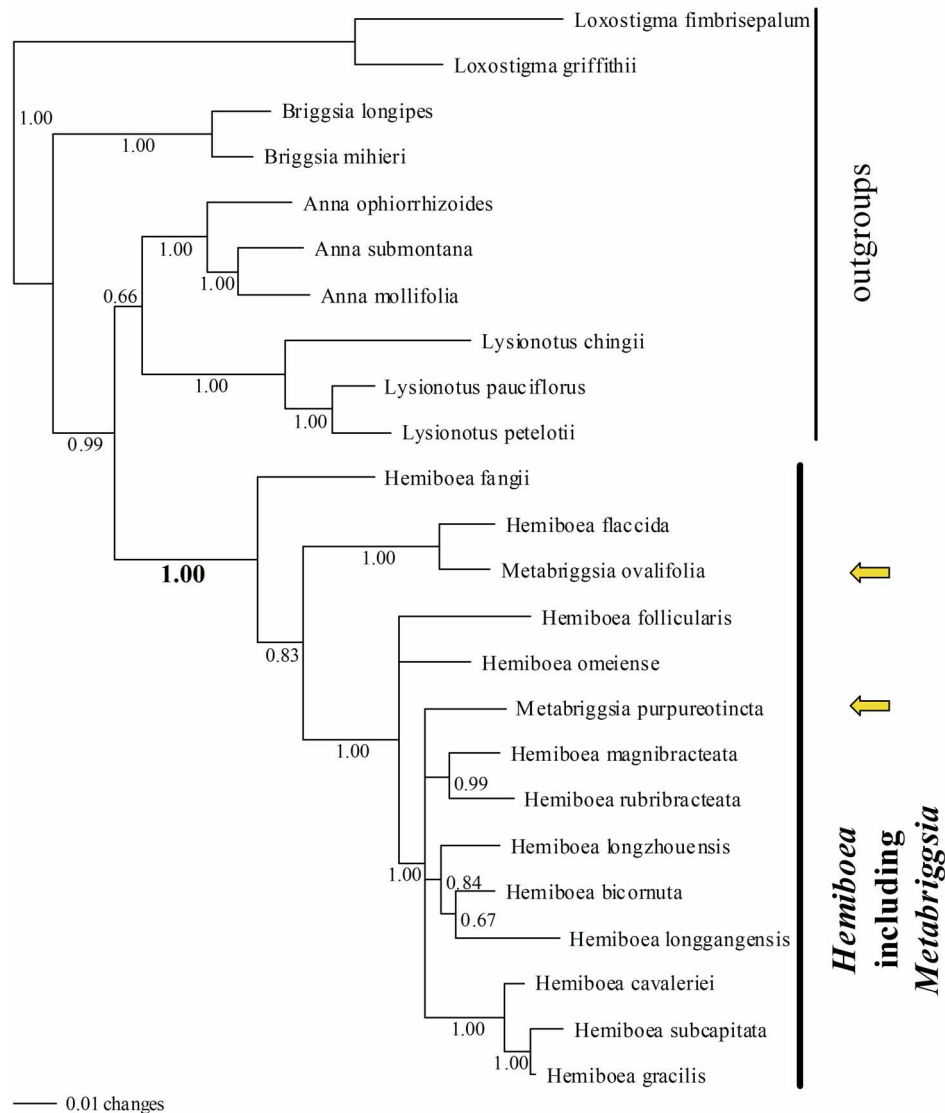


FIGURE 2: Bayesian inference tree with average branch lengths based on combined *trnL-F* and ITS data. Best-fit models were GTR+G for *trnL-F* and the ITS spacers, K80+I for the 5.8S region (AIC in MrModeltest, Nylander 2004), and the gap characters were treated as standard characters in MrBayes 3.1.2 (Huelsenbeck & Ronquist 2007). One million generations were run, with one tree sampled every 250th generation and 4% burn-in. Arrows indicate the position of *Metabriggsia* samples.

The solution to this enigmatic condition is simple: the figure in Wang (1983a) shows the cross section in the wrong orientation. The figure of *Metabriggsia* has to be rotated clock-wise by 90°, the placenta then pointing upwards (Fig. 3B). To understand this condition and that found in *Hemiboea*, it is necessary to compare them to the normal condition [where both carpels are fertile; e.g., *Corallodiscus* Batalin (1892: 176), Fig. 3A]. Moreover, it is necessary to consider the internal structure of the ovary throughout its length. Almost all ovaries of Gesneriaceae (though traditionally marked as “unilocular”) have a bilocular lower part (“synascidiate” zone: see Weber 1971). This zone is usually short and sterile, but also may be prominent and fertile. In the latter case a complete septum is present (the carpels being completely fused along both margins, so that the ovary locules are completely separate), bearing four or (by fusion of the adjacent half-placentae) two “axile” placentae [cf. *Whytockia* Smith (1919: 338), *Monophyllaea* Brown (1838: 121), *Sarmienta* Ruiz & Pavón (1794: 4), see Weber 1971, 1976a, b, Wilson 1974, Burt 1978]. In *Hemiboea* it is this bilocular zone

which is elongated throughout the ovary (Fig. 3C, D; Weber 1971: fig. 9). Here, only the adaxial carpel bears an “axile” placenta while the abaxial carpel is sterile (meaning that in the cavity of the abaxial carpel no placenta is present or only in the form of a ridge lacking ovules, as shown with arrows in Fig. 3C). Thus the ovary appears “unilocular” in cross section. The present explanation shows that the terms uni- and bilocular have different meanings and that “parietal” and “axile” placentae may occur in the same ovary, depending on the part of the ovary where the cross section is made.



FIGURE 3: Ovary and fruit characters. A, Transverse sections through an ovary with both carpels fertile (*Corallodiscus lanuginosus*, RBGE 20010593); B–D, with only adaxial carpel fertile (B, *Metabriggsia purpureotincta*, MMO 06-813; C–D, *Hemiboea cavaleriei*, MM01-143); note abaxial sterile carpel with empty locule in B and C. D, sectioned ovary indicating positions of cuts; E–F, dehiscent fruits of *Metabriggsia purpureotincta* (taken in the field: China, Guangxi, Napo) (E, old capsules with placentae split into halves; F, fruits on plant showing the plagiocarpic fruit attachment) and G, *Hemiboea cavaleriei* (RBGE living collection: RBGE 20020464), note angle between pedicel and capsule in F and G. Bars: A, 100µm; B, 200µm; C, 1mm; E–G, 1cm.

Wang’s (1983a) drawing of *Metabriggsia ovalifolia* shows a single placenta, which (in cross section) is just a lens-shaped lamella, with ovules or seeds not clearly discernible. Probably the cross section is from the basal part of the ovary (hence no ovules). The lens-shaped form of the placenta can be explained as follows. In the lower part of the ovary, the axile placenta of *Hemiboea* develops a conspicuous sterile protrusion in the middle, from which on each side the recurved half-placentae (bearing the ovules) emerge (Weber 1971: Fig. 9V). These fertile portions decrease in size toward the ovary base and there do not produce ovules. In consequence, a sterile, undivided structure protruding into the carpel locule remains, and this is apparently what Wang’s (1983a) illustration shows.

There may be two reasons for the lack of a second (abaxial) locule: (i) either in the herbarium material that was investigated, the sterile locule was squeezed and not discernible, or (ii) the cross section was made (as the lack of ovules/seeds suggest) in the lower part of the ovary, where a sterile locule was no longer

present. In *Metabriggsia purpureotincta*, however, a second (sterile) locule is clearly present (Fig. 3B) and the congruence with *Hemiboea* is immediately apparent.

In conclusion, Wang's statement that only one carpel is fertile is principally correct, but the description and the interpretation of the cross section needs re-assessment. As we have shown, there is no difference in the ovary structure of *Metabriggsia* and *Hemiboea* and, in particular, no difference that would warrant generic separation.

Finally, the fruits also need to be discussed. The fruit of *Metabriggsia ovalifolia* was not described in detail in the original diagnosis, but was referred to in the "Flora of China" (Wang *et al.* 1998: 294) as a "capsule straight in relation to the pedicel, linear, much longer than the calyx, dehiscent loculicidally to base, valves two, not twisted". This is in contrast to *Hemiboea*, where the fruit was described as "capsule straight or oblique in relation to pedicel, usually narrowly lanceolate, somewhat curved, much longer than calyx, dehiscent loculicidally to base only adaxially; valves 2, straight, not twisted" in Wang *et al.* (1998: 294). From this description it may be inferred that there is a major difference between *Metabriggsia* and *Hemiboea* in the fruit orientation. However, in our opinion, this is not the case.

The illustration of *M. ovalifolia* in Li & Wang (2004: 141) shows flowers/young fruits after shedding the corolla, and there is clearly an angle (c. 135°) between the flower and the pedicel. More conclusive are the photos of *M. purpureotincta* in Wei *et al.* (2010b: 179; reproduced in Fig. 3E, F). They show old, boat-shaped fruits, opening only along the upper side and making an angle (sometimes almost 90°) with the pedicel. Wei's description indeed reads "capsule falcate, an angle to pedicel". We conclude that there are therefore no differences in the fruit structure and orientation between *Metabriggsia* and *Hemiboea* (Fig. 3G).

If all this evidence is taken into account, we conclude that *Metabriggsia* does not differ in any character warranting generic separation from *Hemiboea*, and this is in agreement with the molecular data. Thus *Metabriggsia* is here synonymised with *Hemiboea* and its two species are formally included in that genus.

Formal treatment

Hemiboea C.B. Clarke in Hooker (1888: tab. 1798). Type: *H. follicularis* C.B. Clarke.

Heterotypic synonym:—*Metabriggsia* W.T. Wang (1983a: 1), **syn. nov.** Type: *M. ovalifolia* W.T. Wang.

Hemiboea ovalifolia (W.T. Wang) A. Weber & Mich. Möller, **comb. nov.**

Basionym:—*Metabriggsia ovalifolia* W.T. Wang (1983a: 2).

Hemiboea purpureotincta (W.T. Wang) A. Weber & Mich. Möller, **comb. nov.**

Basionym:—*Metabriggsia purpureotincta* W.T. Wang (1983a: 2).

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

Number of taxa = 24
 Number of characters = 1581
 Number of generations = 1000000

Average standard deviation of split frequencies: 0.013005

Analysis completed in 7061 seconds
 Analysis used 7061.30 seconds of CPU time
 Likelihood of best state for "cold" chain of run 1 was -5457.15
 Likelihood of best state for "cold" chain of run 2 was -5459.83
 Acceptance rates for the moves in the "cold" chain of run 1:
 With prob. Chain accepted changes to
 69.11 % param. 1 (tratio) with Dirichlet proposal
 49.17 % param. 2 (revmat) with Dirichlet proposal
 35.59 % param. 3 (revmat) with Dirichlet proposal
 21.36 % param. 4 (state frequencies) with Dirichlet proposal
 22.15 % param. 6 (state frequencies) with Dirichlet proposal
 42.72 % param. 9 (gamma shape) with multiplier
 56.25 % param. 10 (gamma shape) with multiplier
 53.06 % param. 11 (prop. invar. sites) with sliding window
 13.34 % param. 12 (topology and branch lengths) with extending TBR
 22.24 % 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
 69.23 % param. 1 (tratio) with Dirichlet proposal
 49.16 % param. 2 (revmat) with Dirichlet proposal
 35.37 % param. 3 (revmat) with Dirichlet proposal
 21.28 % param. 4 (state frequencies) with Dirichlet proposal
 22.65 % param. 6 (state frequencies) with Dirichlet proposal
 42.34 % param. 9 (gamma shape) with multiplier
 55.95 % param. 10 (gamma shape) with multiplier
 53.21 % param. 11 (prop. invar. sites) with sliding window
 13.25 % param. 12 (topology and branch lengths) with extending TBR
 22.32 % param. 12 (topology and branch lengths) with LOCAL

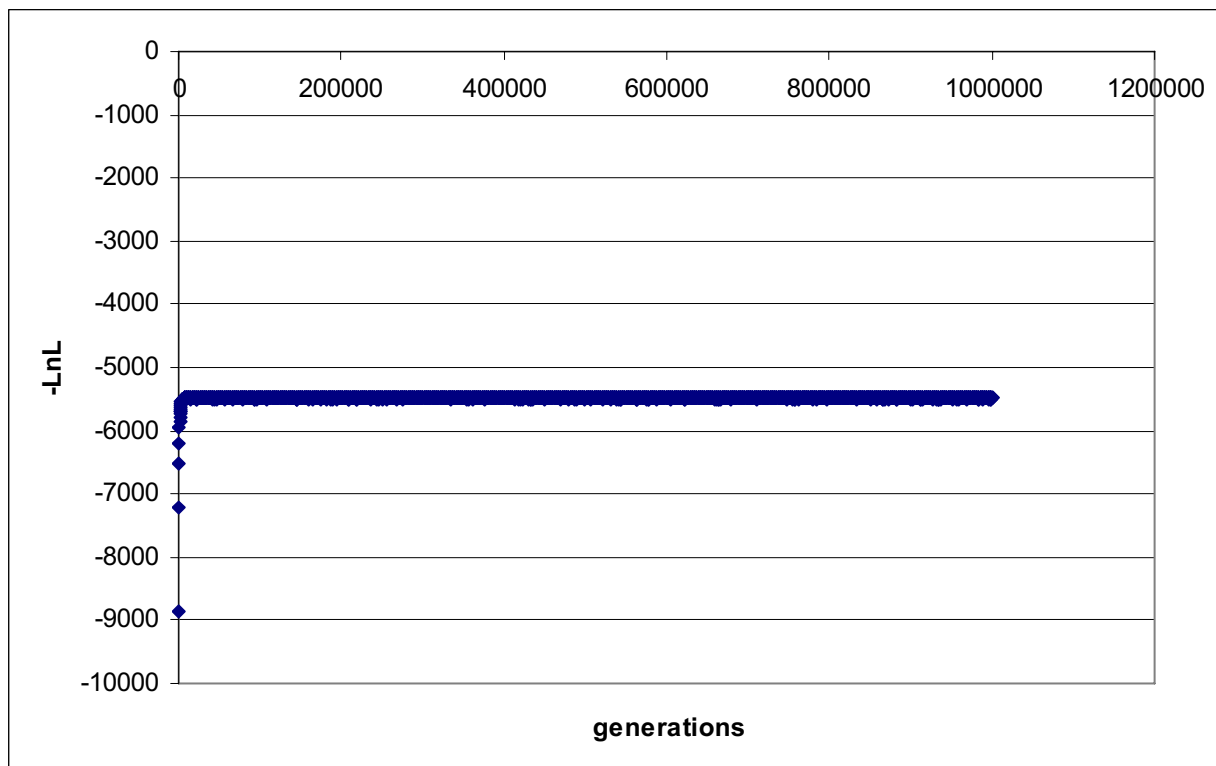
Chain swap information for run 1:

	1	2	3	4
1		0.40	0.11	0.03
2	166880		0.45	0.16
3	166579	166948		0.51
4	166670	166384	166539	

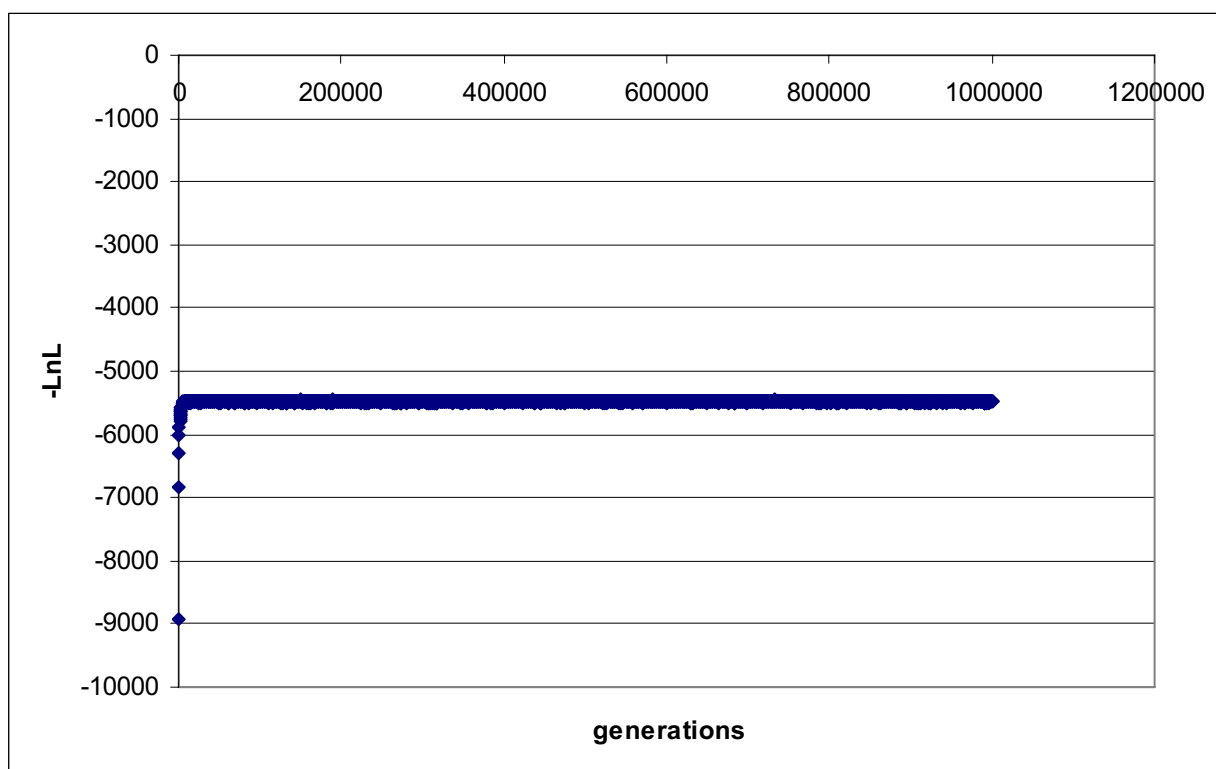
Chain swap information for run 2:

	1	2	3	4
1		0.38	0.10	0.02
2	166303		0.44	0.15
3	166748	166594		0.50
4	166718	166917	166720	

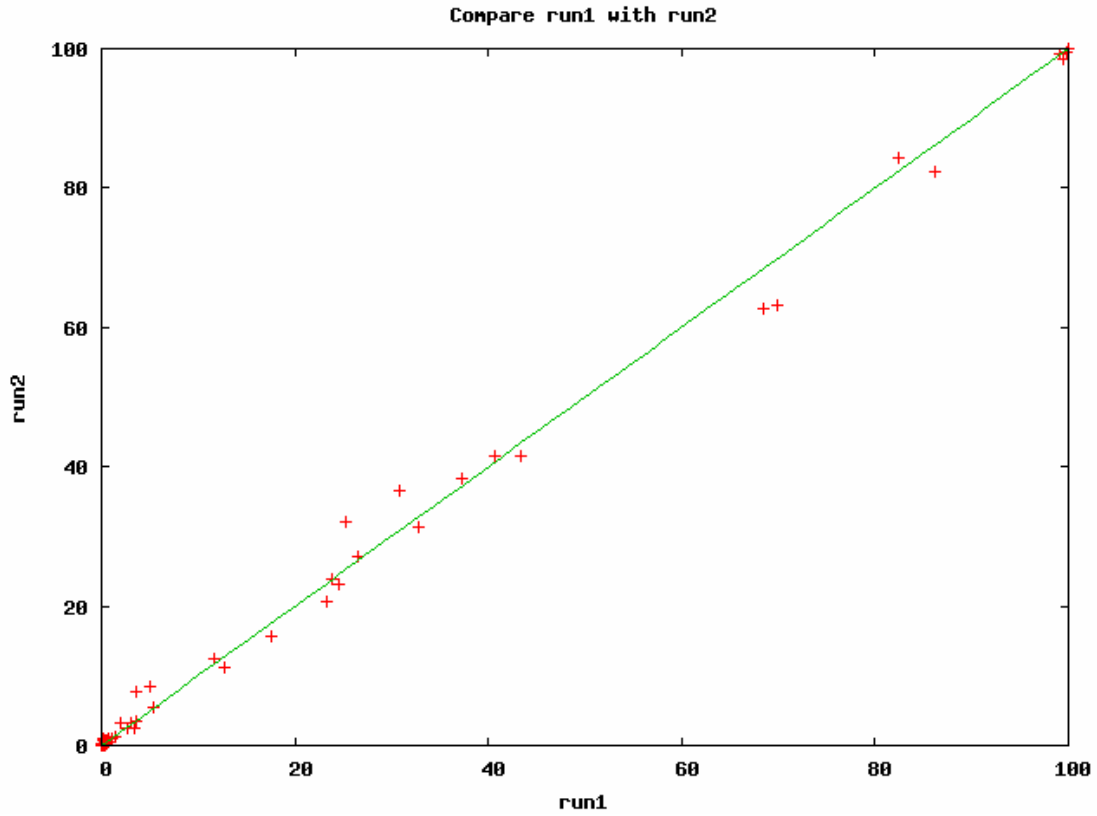
Upper diagonal: Proportion of successful state exchanges between chains
 Lower diagonal: Number of attempted state exchanges between chains



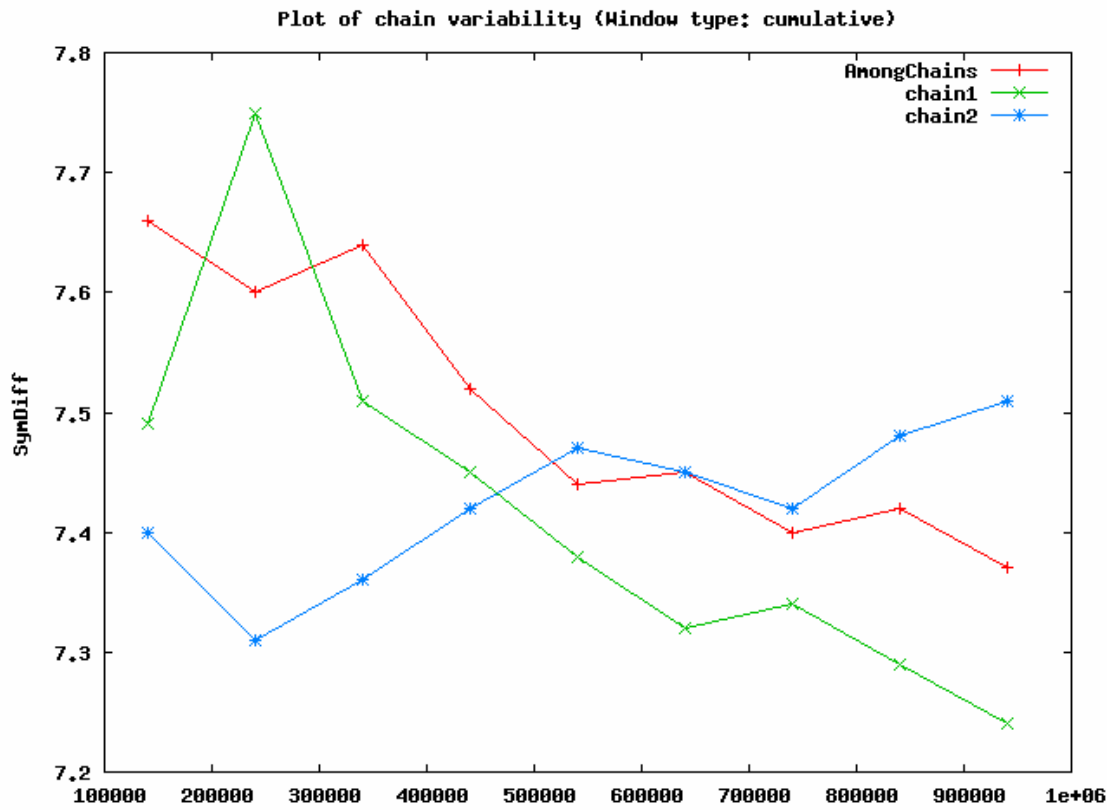
generations vs -lnL values, run 1
burn-in 4%



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



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



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

