

Phylogenetic relationships and generic delimitation of Eurasian *Aster* (Asteraceae: Astereae) inferred from ITS, ETS and *trnL-F* sequence data

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- **Background and Aims** The classification and phylogeny of Eurasian (EA) *Aster* (Asterinae, Astereae, Asteraceae) remain poorly resolved. Some taxonomists adopt a broad definition of EA *Aster*, whereas others favour a narrow generic concept. The present study aims to delimit EA *Aster sensu stricto* (*s.s.*), elucidate the phylogenetic relationships of EA *Aster s.s.* and segregate genera.
- **Methods** The internal and external transcribed spacers of nuclear ribosomal DNA and the plastid DNA *trnL-F* region were used to reconstruct the phylogeny of EA *Aster* through maximum parsimony and Bayesian analyses.
- **Key Results** The analyses strongly support an *Aster* clade including the genera *Sheareria*, *Rhynchospermum*, *Kalimeris* (excluding *Kalimeris longipetiolata*), *Heteropappus*, *Miyamayomena*, *Turczaninowia*, *Rhinactinidia*, eastern Asian *Doellingeria*, *Asterothamnus* and *Arctogeron*. Many well-recognized species of Chinese *Aster s.s.* lie outside of the *Aster* clade.
- **Conclusions** The results reveal that EA *Aster s.s.* is both paraphyletic and polyphyletic. *Sheareria*, *Rhynchospermum*, *Kalimeris* (excluding *K. longipetiolata*), *Heteropappus*, *Miyamayomena*, *Turczaninowia*, *Rhinactinidia*, eastern Asian *Doellingeria*, *Asterothamnus* and *Arctogeron* should be included in *Aster*, whereas many species of Chinese *Aster s.s.* should be excluded. The recircumscribed *Aster* should be divided into two subgenera and nine sections. *Kalimeris longipetiolata*, *Aster batangensis*, *A. ser. Albescentes*, *A. series Hersileoides*, a two-species group composed of *A. senecioides* and *A. fuscescens*, and a six-species group including *A. asteroides*, should be elevated to generic level. With the *Aster* clade, they belong to the Australasian lineages. The generic status of *Callistephus* should be maintained. Whether *Galatella* (including *Crinitina*) and *Tripolium* should remain as genera or be merged into a single genus remains to be determined. In addition, the taxonomic status of *A. auriculatus* and the *A. pycnophyllus*–*A. panduratus* clade remains unresolved, and the systematic position of some segregates of EA *Aster* requires further study.

Key words: Asteraceae, Astereae, ETS, Eurasian *Aster*, generic delimitation, infrageneric classification, ITS, molecular phylogeny, *trnL-F*.

INTRODUCTION

Aster sensu lato (*s.l.*; Asterinae, Astereae, Asteraceae) has been a taxonomic dumping ground for large numbers of morphologically similar but distantly related taxa (Noyes and Rieseberg, 1999; Dorn, 2003). *Aster s.l.* occurs mainly in the Northern Hemisphere in both Eurasia (EA) and North America (NA) and is estimated to comprise 250–1000 species (Ling *et al.*, 1985; Nesom, 1994b; Ito and Soejima, 1995; Noyes and Rieseberg, 1999). Based primarily on achene morphology and cytology, Nesom (1994b) segregated NA *Aster* species from *Aster s.l.* and redistributed them among generic segregates *Symphytichum*, *Doellingeria*, *Eucephalus*, etc. At the same time, he kept the remainder, about 180 species, as *Aster sensu stricto* (*s.s.*), typified by *A. amellus*. Consequently, *Aster*, containing approx. 180 species, is restricted to the Northern Hemisphere of the Old World. Internal transcribed spacer (ITS) sequence phylogenetic data (Noyes and Rieseberg, 1999) support the viewpoint of

Nesom (1994b) that a fundamental difference exists between NA and EA *Aster*. Furthermore, ITS data indicate that EA *Aster* is nested in the Southern Hemisphere grade and does not form a monophyletic group (Noyes and Rieseberg, 1999; Brouillet *et al.*, 2001, 2009b; Fiz *et al.*, 2002), and African *Aster* should be separated from *Aster s.s.* (Brouillet *et al.*, 2009b). The classification and phylogeny of EA *Aster* have remained poorly resolved, however, because of insufficient sampling in these studies.

The circumscription of EA *Aster* has confused botanists for several decades. Many taxonomists have adopted a broad definition of EA *Aster*. In *Flora Europaea*, Merxmüller *et al.* (1976) maintained *Doellingeria*, *Galatella*, *Crinitaria* (the name *Crinitaria* is a synonym of *Galatella*) and species that are considered part of *Crinitaria* should be included in *Crinitina* and *Tripolium* in *Aster*. Similarly, Grieson (1975) accepted *Aster s.l.* in *Flora of Turkey and the East Aegean Islands* because he did not recognize *Kemulariella* and *Tripolium* as segregate genera. In *Flora of Japan*, Ito and

Soejima (1995) merged *Tripolium* as section *Tripolium* into *Aster*, placed *Heteropappus* in section *Pseudocalimeris*, included *Kalimeris* within section *Asteromoea*, and associated *Doellingeria* and *Miyamayomena* into section *Teretiachaenium*.

Other taxonomists have favoured a narrow generic concept of EA *Aster* and have recognized small genera endemic to eastern Asia. Tamamschyan (1959) segregated two new genera (*Kemulariella* and *Conyzanthus*) from *Aster* and recognized many small genera such as *Doellingeria*, *Kalimeris*, *Asterothamnus*, *Krylovia*, *Turczaninowia*, *Galatella*, *Linosyris* (= *Crinitina*) and *Tripolium*. Czerepanov (1995) followed Tamamschyan (1959) except that he placed *Galatella* and *Linosyris* under the genus name *Crinitaria* (= *Crinitina*). Nesom (1994a, b) made *Aster* largely equal to EA *Aster s.s.* and EA *Aster s.l.* almost equal to sub-tribe *Asterinae* Dumort.

Ling et al. (1985) treated Chinese *Asterinae* in the narrow sense of *Aster*, recognizing generic status for *Gymnaster* (= *Miyamayomena*), *Kalimeris*, *Callistephus*, *Heteropappus*, *Doellingeria*, *Turczaninowia*, *Krylovia* (= *Rhinactinidia*), *Asterothamnus*, *Galatella*, *Linosyris* (= *Crinitina*), *Arctogeron* and *Tripolium*. These treatments were followed completely for floras of Chinese provinces (e.g. Zhuang, 2004; Lin, 2007). Despite this, Chinese *Aster s.s.* remains a large genus with approx. 100 species, of which 75 are endemic to China (Fu, 1983; Ling et al., 1985; Chen, 1988, 1990; Zhu and Min, 1990; Li and Liu, 2002; Li and Zhang, 2004). Therefore, China, especially south-western China (the Qinghai–Tibetan and Yunnan–Guizhou Plateaux and Sichuan Province), is the diversity centre of *Aster*, as it is for many genera (Huang, 2011).

Molecular markers, especially ITS and the external transcribed spacer (ETS) of 35S ribosomal DNA, have frequently been used to investigate phylogenetic relationships in *Astereae* (e.g. Noyes and Rieseberg, 1999; Lowrey et al., 2001; Markos and Baldwin, 2001; Cross et al., 2002; Fiz et al., 2002; Roberts, 2002; Lowell et al., 2003; Urbatsch and Roberts, 2003; Urbatsch et al., 2003; Roberts and Urbatsch, 2004; Karaman, 2006; Selliah and Brouillet, 2008; Andrus et al., 2009; Brouillet et al., 2009a,b; Karaman-Castro and Urbatsch, 2009; Vaezi and Brouillet, 2009). Molecular evidence implies that neither EA *Aster s.l.* nor EA *Aster s.s.* is monophyletic (Gu et al., 1994; Ito et al., 1995, 1998; Xiang and Semple, 1996; Noyes and Rieseberg, 1999; Fiz et al., 2002), but only a few species of EA *Aster* have been included in previous analyses. Although molecular data support a close relationship among *Kalimeris*, *Heteropappus*, *Miyamayomena*, *Sheareria*, *Rhynchospermum* and *Aster s.s.* (Ito et al., 1995, 1998; Noyes and Rieseberg, 1999; Fiz et al., 2002; Gao et al., 2009), the phylogenetic relationships among these genera are unresolved owing to limited taxon sampling of EA *Aster s.s.* Recently, 27 species of EA *Aster s.l.* were included in a phylogenetic analysis of *Aster s.l.* (Brouillet et al. 2009b), but no statistical support was presented for the clades of the ITS phylogenetic tree. To date, no molecular data have been provided for *Turczaninowia*, *Krylovia*, *Asterothamnus* and *Arctogeron*, and, in particular, Chinese *Aster s.s.* has not been phylogenetically studied using DNA sequences even though it represents the overwhelming

majority of EA *Aster s.s.* Thus, a reliable phylogenetic analysis based on extensive taxon sampling is essential to determine the inter- and intrageneric relationships of EA *Aster*.

Principally based on nuclear ribosomal DNA (nrDNA) ITS, ETS and plastid *trnL-F* sequence data of *Sheareria nana*, *Rhynchospermum verticillatum* and 62 species of EA *Aster s.l.*, the present study aims to (1) reconstruct the phylogeny of EA *Aster s.l.*; (2) redelimit the genus *Aster* and discuss its infrageneric classification; and (3) discuss the systematic position of EA *Aster* segregates.

MATERIALS AND METHODS

Generic circumscriptions and nomenclature of *Astereae* follow Nesom and Robinson (2007) except for *Turczaninowia*, which follows Ling et al. (1985), and *Crinitina*, which is substituted for *Crinitaria* (a synonym of *Galatella*). The name *Aster setchuenensis* follows the International Plant Names Index. The division of phylogenetic lineages of *Astereae* refers to Brouillet et al. (2009b). Voucher DBY9206 was deposited in the Wenzhou University Herbarium (WZU) and the others in the Hunan Normal University Herbarium (HNNU; see the Appendix).

Taxon sampling

Seventy-six species of *Astereae* and three outgroup species were collected from China and Bulgaria and examined for sequence variations in nrDNA ITS, ETS and plastid DNA *trnL-F* (GenBank accession numbers are given in the Appendix). The vouchers of all accessions were identified using published keys and compared with herbarium specimens in the Institute of Botany, Chinese Academy of Sciences Herbarium (PE), Northwest Agriculture and Forestry University Herbarium (WUK), Sichuan University Herbarium (SZ), Chengdu Institute of Biology Herbarium (CDBI), HNNU, Herbarium of Kunming Institute of Botany, the Chinese Academy of Sciences (KUN), the Herbarium of the South China Botanical Garden, Chinese Academy of Sciences (IBSC), Guangxi Institute of Botany Herbarium (IBK), Institute of Botany, Jiangsu Province and Chinese Academy of Sciences Herbarium (NAS), Guizhou Academy of Sciences Herbarium (HGAS), Central China Normal University Herbarium (CCNU), Wuhan Botanical Garden, Chinese Academy of Sciences Herbarium (HIB), Inner Mongolia University Herbarium (HIMC) and Fudan University Herbarium (FUS). Of the 76 species included in this study (see the Appendix), 41 represent three sections and 20 series of EA *Aster s.s.* (Ling et al., 1985; Chen, 1988; Li and Liu, 2002), 21 represent 12 segregate genera of EA *Aster s.l.*, four generic groups of Nesom's (1994b) *Asterinae*, and two recently recognized close relatives of EA *Aster s.s.* (*S. nana* and *R. verticillatum*; Fiz et al., 2002; Brouillet et al. 2009b; Gao et al., 2009). The data matrix for ITS comprises 110 accessions from 48 genera and 110 species of tribe *Astereae* (see the Appendix). Seventy-six accessions were newly sequenced, and the remaining 34 were obtained from GenBank (Appendix). Of the 110 accessions, 41 species belong to EA *Aster s.s.*, 21 species are 12 separate genera of EA *Aster s.l.*, one is *Astereae incertae sedis*, three are members of

Bellidinae or Grangeinae, and 44 represent the six phylogenetic lineages of Astereae (Brouillet *et al.* 2009b). These phylogenetic lineages of Astereae are the early diverging lineages (e.g. *Madagaster madagascariensis*, *Felicia filifolia* and *Printzia polifolia*), the palaeo-South American clade (e.g. *Chiliotrichum diffusum*), the New Zealand clade (e.g. *Olearia covenyi*), the Australasian lineages, the South American lineages (e.g. *Baccharis neglecta*) and the NA lineage (e.g. *Conyza sumatrensis* and *Symphytotrichum subulatum*). Brouillet *et al.* (2009b) divided the Australasian lineages into seven genus or species groups, whereas ten genus or species groups are, in fact, included in the depiction of the grouping (fig. 37.1 C in Brouillet *et al.* 2009b). In the current analysis, 19 species (Appendix) were sampled to represent these ten groups. Because Brouillet *et al.* (2009b) consider *Olearia s.s.* to be a sister to EA Aster, five species were sampled to represent sub-clades of the *Olearia s.s.* clade.

In the combined matrix of ITS, ETS and *trnL-F*, 78 accessions from 25 genera and 78 species of tribe Astereae were included (Appendix). Seventy-six accessions were newly sequenced, and the remaining two were obtained from GenBank (Appendix). Of the 78 accessions (Appendix), 41 belong to EA Aster *s.s.*, 21 belong to 12 segregate genera of EA Aster *s.l.*, one is Astereae *incertae sedis*, and three are members of Bellidinae or Grangeinae. The remaining 12 accessions represent three phylogenetic lineages of tribe Astereae (Brouillet *et al.* 2009b), the palaeo-South American clade (e.g. *C. diffusum*), the Australasian lineages (e.g. two *Myriactis* spp.) and the NA lineage (seven species such as *C. sumatrensis* and *S. subulatum*). In all analyses, *Chrysanthemum coronarium* and *Dendranthema indicum* of tribe Anthemideae and *Calendula officinalis* of tribe Calenduleae were selected as outgroups for the rooting of the phylogenetic trees (Appendix) because in molecular phylogenetic analyses Anthemideae and Astereae are sisters, and Calenduleae is a sister to tribes Gnaphalieae, Anthemideae and Astereae (Panero and Funk, 2008; Garcia *et al.*, 2010).

DNA extraction, polymerase chain reaction (PCR) and sequencing

Total genomic DNA was isolated from fresh leaf material or silica gel-dried leaves using a modified cetyltrimethylammonium bromide procedure (Doyle and Doyle, 1987). Amplification and sequencing were performed using the primers ITS1 and ITS4 (White *et al.*, 1990) for the ITS region, Ast-8 (Markos and Baldwin, 2001) and 18S-ETS (Baldwin and Markos, 1998) for the ETS region, and c and f (Taberlet *et al.*, 1991) for the plastid DNA *trnL-F* region (*trnL*^{UAA}-*trnL*^{UAA}-*trnL*^{GAA}).

The PCR mixture contained 1 µL (50–100 ng) of sample DNA, 2 × 2 µL of primer (10 pmol), 5 µL of 10 × PCR buffer, 3 µL of Mg²⁺ (25 mM), 0.8 µL of deoxyribonucleotide triphosphate (each 25 mM), 0.5 µL of *Taq* DNA polymerase (5 U µL⁻¹) and sterile water for a final volume of 50 µL. The PCR parameters were as follows: initial denaturation for 4 min at 95 °C followed by 30 cycles of denaturation (95 °C, 1 min), annealing (56 °C, 40 s) and extension (72 °C, 1 min), and a final extension of 10 min at 72 °C.

PCR products were purified using a UNIQ-10 Spin Column PCR Product Purification Kit (Sangon Biotech Co., Ltd, Shanghai, China) following the manufacturer's instructions. Sequencing reactions were performed in both directions by Sangon Biotech Co., Ltd.

Sequence alignment and phylogenetic analysis

Boundaries of the ITS, ETS and *trnL-F* regions were determined through comparison with previously published sequences of tribe Astereae (Noyes and Rieseberg, 1999; Liu *et al.*, 2002; Urbatsch *et al.*, 2003). All DNA sequences were aligned initially using Clustal X1.83 (Jeanmougin *et al.*, 1998) and then adjusted manually in BioEdit (Hall, 1999). The ITS region was analysed separately and in a combined data set with the ETS and *trnL-F* regions. The incongruence length difference test (Farris *et al.* 1994) was carried out to test the homogeneity between data sets using PAUP* version 4.0b10 with 1000 replicates. Maximum parsimony (MP) and Bayesian inference (BI) methods were performed for the data sets using PAUP* version 4.0b10 (Swofford, 2001) and MrBayes version 3.1.2 (Ronquist and Huelsenbeck, 2003), respectively. In the MP analysis, characters were equally weighted and treated as unordered, gaps were treated as missing data, and a heuristic search was implemented with 1000 random additional sequence replicates and sub-tree pruning–grafting branch swapping. Bootstrap analyses based on 1000 replicates with ten random additions per replicate were used to estimate the confidence of the clades. The MaxTrees setting in PAUP* was set to 5000 for the searches and bootstrap tests. For BI analysis of the ITS region and combined data set, the best-fitting model of each sequence partition (ITS1, ITS2, 5-8S, ETS, *trnL-F* intron, exon, the internal guide sequence) was determined using MrModeltest 2.2 (Nylander, 2004). The SYM + G model was chosen for the 5-8S region, and the GTR + I + G model for the ITS1, ITS2 and ETS regions. The GTR + G model was chosen for the intron and the internal guide sequence partitions of the *trnL-F* region and the K80 model for the exon partition. The Markov chain Monte Carlo algorithm was run for 1 000 000 generations, resulting in an overall sampling of 10 000 trees. The first 3000 trees were discarded as a conservation burn-in, and the remaining trees were used to construct the 50 % majority rule consensus tree.

RESULTS

Characterization of nucleotide data

The aligned ITS sequence matrix of 110 taxa contained 689 base pairs, of which 394 were variable and 315 were potentially parsimony informative. Pair-wise distance within ingroup varied from 0 to 18.7 % (average = 6.7 %). The incongruence length difference test indicated that the data sets were not significantly heterogeneous ($P = 0.01$). Therefore, a combined analysis of the three regions was performed using PAUP* and MrBayes. The combined data set of 78 taxa consisted of 2313 positions, with 641 potentially parsimony-informative characters and 283 phylogenetically uninformative variable

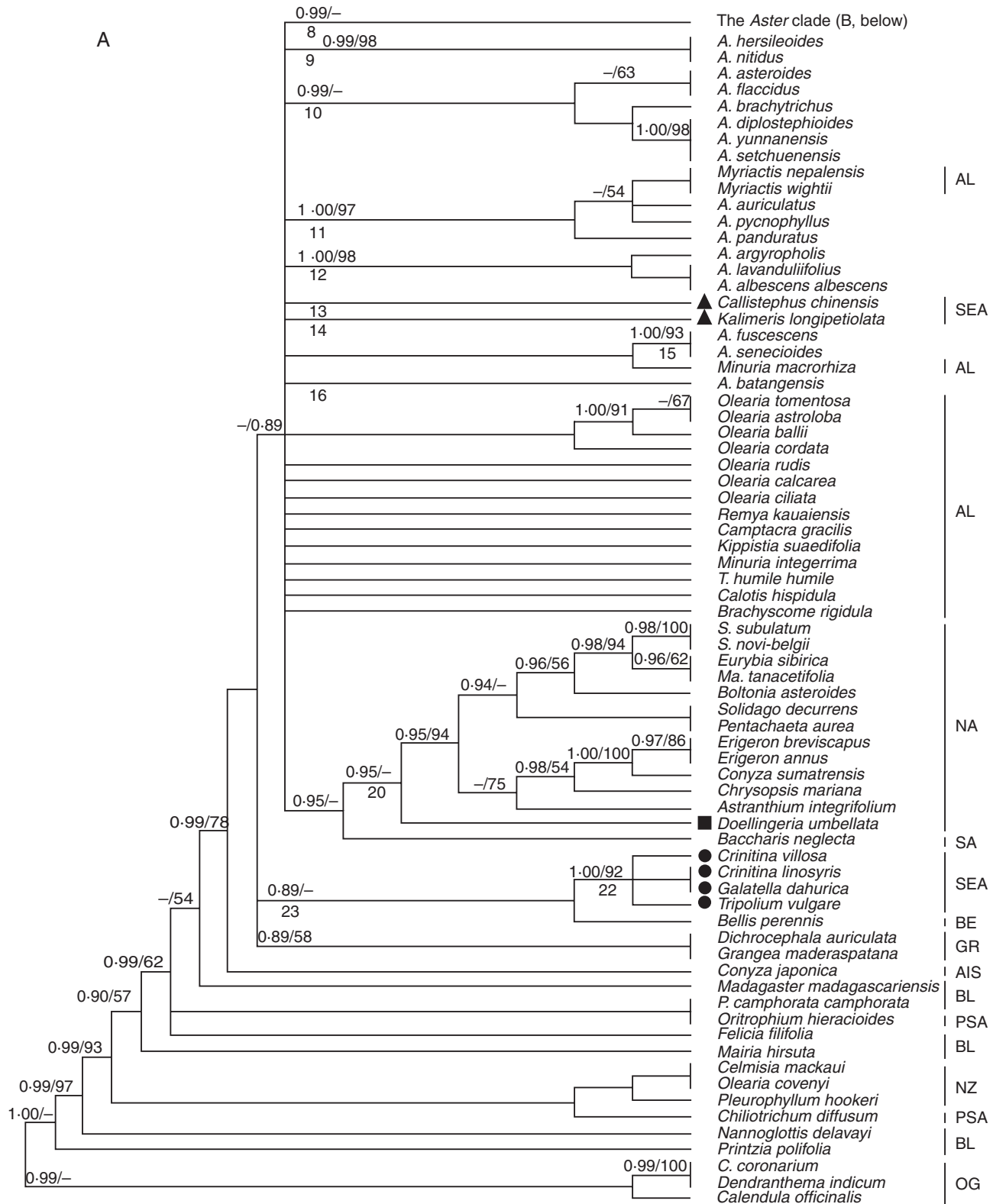


FIG. 1. The 50% majority rule consensus tree from the Bayesian analysis of nuclear ribosomal DNA internal transcribed spacer sequences. (A) Bayesian posterior probabilities (≥ 0.89) and bootstrap values ($\geq 50\%$) are indicated above the branches; '-' indicates that Bayesian posterior probabilities are < 0.89 or bootstrap percentages are $< 50\%$. Some clades are indicated by numbers below the branch. Abbreviations: A., Aster; C., Chrysanthemum; S., Symphyotrichum. Triangles, 'Kalimeris group'; squares, *Doellingeria*; circles, 'Galatella group'. (B) The Aster clade (continued part of A). Bayesian posterior probabilities (≥ 0.89) and bootstrap values ($\geq 50\%$) are indicated above the branches; '-' indicates that Bayesian posterior probabilities are < 0.89 or bootstrap percentages are $< 50\%$. Some clades are indicated by numbers below the branch. Abbreviations: A., Aster; As., *Asterothamnus*; H., *Heteropappus*; M., *Miyamayomena*; R., *Rhynchospermum*. See key for symbols. Some clades are indicated by numbers below the branch. Abbreviations of the lineages are identical to those given in the Appendix and are shown on the right side of the taxa. The labelled species are discussed in groups in the text.

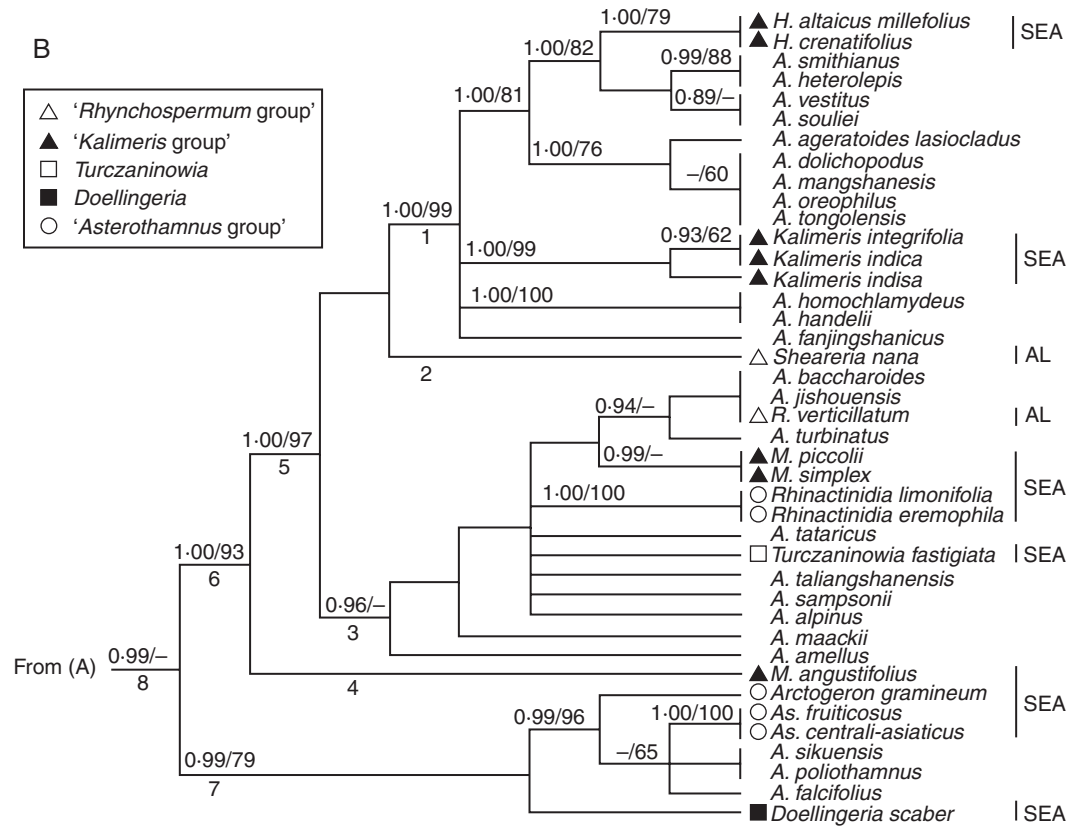


Fig. 1. Continued

characters. Pairwise distance between sequences varied from 0.1 to 11.7 % (average = 4.6 %).

Phylogenetic analyses

For convenience, some clades were numbered (Figs 1A, B and 2). Phylogenetic analyses using ITS and combined data sets yielded generally consistent phylogenetic trees (Bayesian trees; see Figs 1A, B and 2), although the BI and MP analyses based on the combined data generated trees with higher bootstrap support (BS) and Bayesian posterior probability (PP), and some clades (e.g. 17 and 18; Fig. 2) of the combined tree were unresolved in the ITS trees (Fig. 1A). The *Aster* clade (clade 8; Figs 1 and 2) with *A. amellus* (the type species of *Aster*) was strongly supported (PP = 0.99 in Fig. 1; PP = 1.00 and BS = 98 in Fig. 2) by the ITS and combined data set analyses. *Sheareria*, *Rhynchospermum* and some EA *Aster* segregates such as *Heteropappus*, *Kalimeris* (excluding section *Cordifolia*), *Miyamayomena*, *Turczaninowia*, *Rhinactinidia*, *Arctogeron*, *Asterothamnus* and eastern Asian *Doellingeria* were deeply nested within the *Aster* clade (clade 8), whereas other segregates (e.g. *Callistephus*, *Galatella*, *Crinitina*, *Tripolium* and *K. longipetiolata*) and 17 species of *Aster* s.s. (e.g. *A. nitidus*, *A. asteroides* and *A. panduratus*) occurred in other clades and showed close (clade 7; Figs 1A and 2), remote (e.g. clade 18 in Fig. 1A; clade 22 in Fig. 2) or unresolved (e.g. clade 9–16; Fig. 1A) relationships with the *Aster* clade. *Callistephus*, *K. longipetiolata*,

two *Myriactis* spp. and 15 *Aster* spp. formed a moderately supported clade (clade 18; PP = 100; Fig. 2) that was unresolved in the ITS tree (Fig. 1A). *Tripolium*, *Galatella* and *Crinitina* constituted a well-supported clade (clade 22: PP = 1.00, BS = 92 in Fig. 1A; PP = 1.00, BS = 95 in Fig. 2) sister to *Bellis perennis*, but this relationship was weakly supported (clade 23: PP = 0.89 in Fig. 1A; PP = 0.91, BS = 57 in Fig. 2). The monophyly of the NA clade (clade 20) was moderately to strongly supported in both phylogenetic analyses (PP = 0.95 in Fig. 1; PP = 1.00, BS = 100 in Fig. 2).

DISCUSSION

Relationship between EA Aster and NA asters

In this study, the ITS and combined data set analyses (Figs 1 and 2) clearly indicate that the *Aster* clade (clade 8 in Figs 1A and 2) is strongly supported (PP = 0.99 in Fig. 1; PP = 1.00, BS = 98 in Fig. 2) in an unresolved *Astereae* polytomy (Fig. 1A) or is embedded within clade 19 which includes *Myriactis* (sub-tribe *Lagenophorinae*) of the Australian lineages (see Fig. 2), whereas NA *Astereae* forms a moderately to strongly supported clade (clade 20: PP = 0.95 in Fig. 1; PP = 1.00, BS = 100 in Fig. 2). Therefore, EA *Aster* has no close relationship to NA asters. These results support the viewpoint of Nesom (1994b) that a fundamental difference exists between NA and EA *Aster*; they do not support the opinion of Xiang and Semple (1996) that *Aster* s.s. comprises not only EA taxa but also the segregate genus *Eurybia* and that

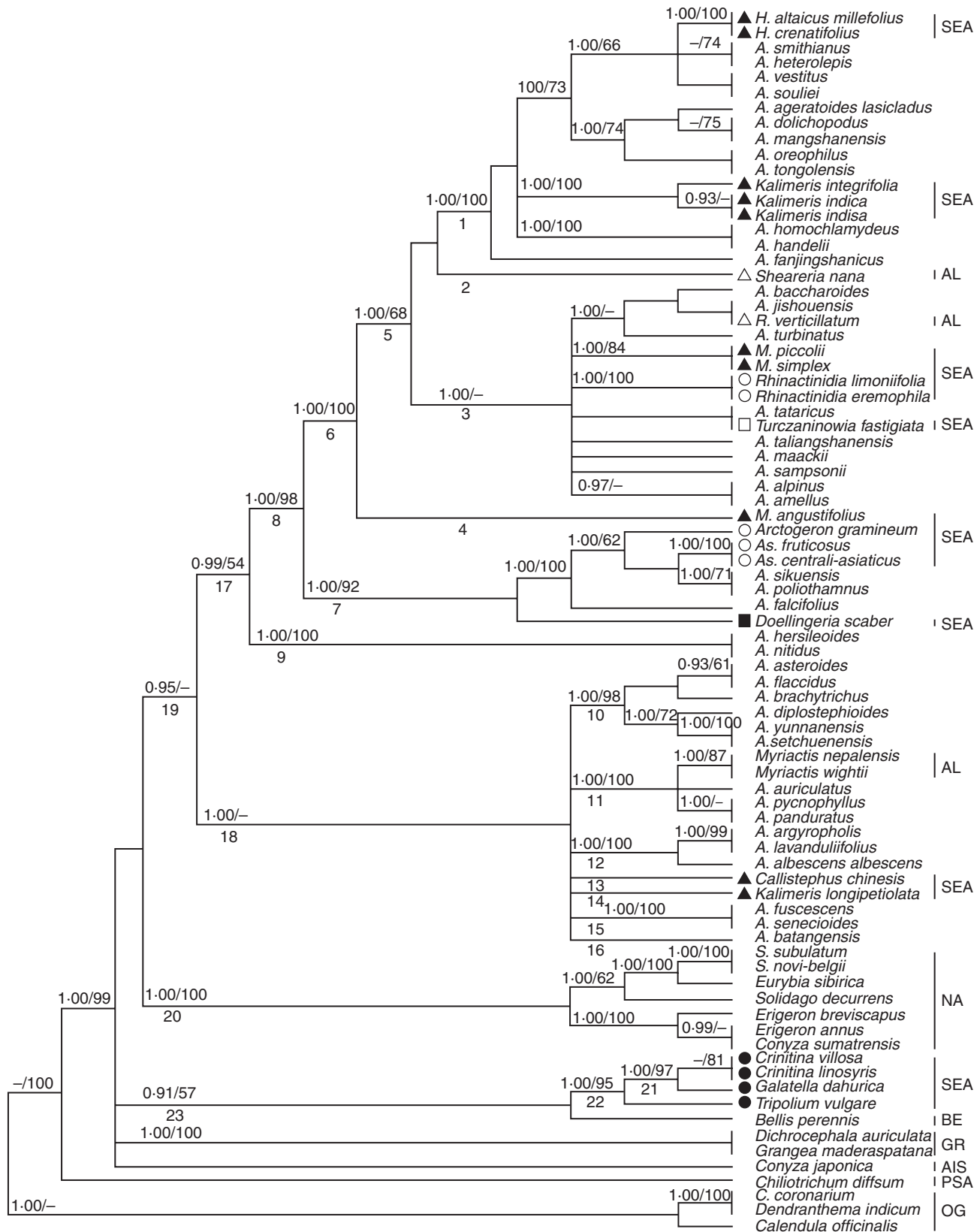


FIG. 2. The 50% majority rule consensus tree from the Bayesian analysis of the combined data set (nuclear ribosomal DNA internal and external transcribed spacer sequences and plastid genome DNA *trnL-F* sequences). Bayesian posterior probabilities (≥ 0.89) and bootstrap values ($\geq 50\%$) are indicated above the branches; ‘-’ indicates that Bayesian posterior probabilities are < 0.89 or bootstrap percentages are $< 50\%$. Some clades are indicated by numbers below the branch. Abbreviations: A., Aster; As., Asterothamnus; C., Chrysanthemum; H., Heteropappus; M., Miyamayomena; R., Rhynchospermum; S., Symphyotrichum. Abbreviations of the lineages are identical to those given in the Appendix and are shown on the right side of the taxa. Some species are labelled with the symbols shown in Fig. 1.

EA *Aster* is derived from NA *Aster*. *Aster alpinus*, distributed in both EA and NA, is deeply nested within the EA *Aster* clade (clade 8; see Figs 1B and 2), which implies that this species originated in EA and dispersed to NA.

Relationship between EA Aster and Australasian lineages

According to Brouillet *et al.* (2009b), Australasian lineages are part of a large polytomy at the crown of Astereae. Although our data sets did not include a large sample of Australasian taxa, the ITS tree (Fig. 1) included 19 sampled species that represented the ten genus or species groups of Australasian lineages of Brouillet *et al.* (2009b). The ITS tree (Fig. 1A) showed that the *Aster* clade (clade 8) is a clade of the large polytomy of the crown of Astereae, but it does not group with any of the Australian (e.g. *Olearia astroloba* and *Remya kauaiensis*), Hawaiian (*Tetramolopium humile*) or Asian (*Myriactis*) species of the Australasian lineages. Brouillet *et al.* (2009b) have proposed that EA *Aster s.s.* was a sister to the Australasian *Olearia s.s.* and had Australasian ancestors. Three species (including the generic type *Olearia tomentosa*) of the Australasian *Olearia s.s.* (Brouillet *et al.* 2009b) constitute a clade (Fig. 1A) but not a sister to the *Aster* clade. The phylogenetic tree from the combined data set, which is more resolved, includes only a few species (*Myriactis* and *Callistephus*) of the Australasian lineages. In the combined tree (Fig. 2), clade 17 (PP = 0.99, BS = 54) with the *Aster* clade (clade 8) is a sister to clade 18 (PP = 1.00) that includes *Myriactis* and *Callistephus* (representatives of the Australasian lineages) and clades 17 and 18 group further into clade 19 (PP = 0.95) which might correspond to the Australasian lineages. Therefore, EA *Aster* (clade 8; Fig. 2) and some of its segregates (clades 9, 10, 12–16, and *Aster* spp. of clade 11; Fig. 2) belong to the Australasian lineages. A more extensive taxon sampling of Australasian Astereae for an analysis of combined DNA sequences is needed to study the origin of both EA *Aster* and its segregates.

Status of the 'Rhynchospermum group'

According to Nesom (1994a) and Nesom and Robinson (2007), two monotypic genera, *Sheareria* and *Rhynchospermum*, belong to the *Rhynchospermum* group of sub-tribe Lagenophorinae. The present study shows that these genera are well nested within the *Aster* clade, however, and not closely related to each other (Figs 1B and 2).

Sheareria. Endemic to China, this was first placed in tribe Astereae and later transferred to tribe Heliantheae (Hoffmann, 1890). Chen (1979) recognized it as belonging to sub-tribe Milleriinae of Heliantheae. Robinson (1981) redefined Heliantheae and considered *Sheareria* to be a member of Astereae. Li *et al.* (2008) provided micromorphological, anatomical and cytological evidence for moving the genus from Heliantheae to Astereae but did not determine its systematic position within tribe Astereae. Nesom (1994a) and Nesom and Robinson (2007) placed *Sheareria* in sub-tribe Lagenophorinae, but Nesom (1994a) doubted a natural alignment with Lagenophorinae. Gao *et al.* (2009) used an ITS data set to show that *Sheareria* formed a strongly supported clade with

Kalimeris integrifolia and *A. amellus* rather than with *Myriactis humilis*, a species of Lagenophorinae, which implies that *Sheareria* should be transferred from Lagenophorinae to Asterinae. Both the ITS (Fig. 1B) and the combined (Fig. 2) trees show that *Sheareria* is well nested within the *Aster* clade. *Sheareria nana* differs noticeably from other species of the *Aster* clade owing to its somewhat reduced leaves (bract-like, linear) and assimilating branches, solitary head with only 5–8 florets, functionally staminate disc flowers and epappose and glabrous achenes. *Sheareria nana* forms a single-species sub-clade (clade 2) of clade 8 in all analyses (Figs 1B and 2), and it could be designated as a section of *Aster*.

Rhynchospermum. The monotypic genus *Rhynchospermum* is distributed in eastern and southeastern Asia (Nesom and Robinson, 2007). Ling *et al.* (1985) included the genus in sub-tribe Bellidinae, and Zhang and Bremer (1993) placed it into their 'Bellis group' with *Bellis* and *Bellium*, whereas Nesom (1994a) and Nesom and Robinson (2007) assigned it to the *Rhynchospermum* group of sub-tribe Lagenophorinae. A previous phylogenetic analysis of ITS (Fiz *et al.*, 2002) suggested that *Rhynchospermum* is related to neither *Bellis* nor *Myriactis* (sub-tribe Lagenophorinae) but to *A. amellus* and *K. integrifolia*. Brouillet *et al.* (2009b) also showed *Rhynchospermum* nested within *Aster s.s.*, which is supported by our ITS and combined data sets (see Figs 1B and 2). In the phylogenetic trees (Figs 1B and 2) *R. verticillatum* is nested within the *Aster* clade (clade 8) and belongs to a clade (PP = 0.94 in Fig. 1B; PP = 1.00 in Fig. 2) with three species of series *Turbinati* of section *Aster* (see the Appendix). Although *Rhynchospermum* has some unique characters, such as a caducous pappus and biseriate pistillate ray florets with a short ligule, our results (Figs 1B and 2) suggest that it should be merged in *Aster s.s.* and placed in series *Turbinati*.

Status of the 'Kalimeris group'

Nesom (1994a, b, 2000) has suggested that the *Kalimeris* group is composed of five small genera: *Boltonia*, *Callistephus*, *Heteropappus*, *Kalimeris* and *Miyamayomena*. This arrangement is unsupported by previous reports and the present study.

Kalimeris. This is native to eastern Asia, and one of its diagnostic characters is short pappi. Its complex taxonomic history has been reviewed in detail by Gu and Hoch (1997). *Kalimeris* shares several floral and achene characters with the small NA genus *Boltonia*, which led Benthams (1861, 1873) to place *Kalimeris* in *Boltonia* as one of three sections. Tamamschyan (1959), Ling *et al.* (1985) and Nesom (1994b, 2000) retained *Kalimeris* as a segregate genus, however. Gu and Hoch (1997) made a detailed comparison of the achenes and pappi of *Boltonia* and *Kalimeris* and concluded that their similarity was rather superficial. Based on ITS data, Fiz *et al.* (2002) and Brouillet *et al.* (2009b) demonstrated that *Kalimeris* and *Boltonia* are in divergent clades. Our phylogenetic analyses show that *Kalimeris* and *Boltonia* belong to different, strongly supported clades (clades 8 and 20, respectively; Fig. 1), supporting the view that no close relationship exists between *Kalimeris* and *Boltonia*.

Kalimeris was sub-divided into two sections by Kitamura (1937): *Kalimeris* and *Cordifolium*. Section *Cordifolium* has cordiform leaves with long petioles, two or three series of sub-equal phyllaries and cylindrical achenes with 4–7 ribs. The section includes two species, *K. miqueliana*, endemic to Japan, and *K. longipetiolata*, endemic to China (Kitamura, 1937; Ling et al., 1985). Gu and Hoch (1997) excluded section *Cordifolium* from *Kalimeris* and left it as part of *Aster*, and Ito and Soejima (1995) merged the section within *Aster* section *Aster*, although restriction fragment length polymorphisms (RFLPs) of plastid DNA supported a close relationship between *K. miqueliana* and *Doellingeria scaber* (Ito et al., 1995, 1998). Nesom (1993) transferred *K. longipetiolata* to *Doellingeria*, as *D. longipetiolata*, but the present results show that it is related to neither NA *Doellingeria* species nor Asian *Doellingeria* species. In the ITS tree, *K. longipetiolata* occupies an unresolved position (clade 14 in Fig. 1B) within the big polytomy, and in the combined tree it belongs to a polytomy (clade 18 in Fig. 2) with two *Myriactis* spp. and many other species of the Australasian lineages. *Kalimeris longipetiolata* should be treated as a new monotypic genus and be placed with the Australasian lineages.

Kalimeris (excluding section *Cordifolium*) has been recognized as having a close relationship with EA *Aster* s.s. and *Heteropappus* according to morphological comparisons (Gu and Hoch, 1997), cytological studies (Huziwaru, 1950; Tara, 1972, 1973), RFLPs of plastid DNA (Ito et al., 1995, 1998) and ITS data (Noyes and Rieseberg, 1999; Fiz et al., 2002; Brouillet et al. 2009b). The taxonomic status of *Kalimeris* remains to be determined, however (Gu and Hoch, 1997). In the two trees in our study, three *Kalimeris* spp. (excluding section *Cordifolium*) are well nested in the *Aster* clade and form a highly supported clade (PP = 1.00 and BS = 99 in Fig. 1B; PP = 1.00 and BS = 100 in Fig. 2). *Kalimeris* (excluding section *Cordifolium*) is characterized by laterally compressed achenes with short pappus bristles no longer than the length of the corolla tube (Gu and Hoch, 1997) and S-type chromosomes (Li, 2006). Thus, *Kalimeris* (excluding section *Cordifolium*) is monophyletic, and treating *Kalimeris* as series *Kalimeris* of *Aster* is reasonable.

In the phylogenetic trees (Figs 1 and 2) *Kalimeris* is nested in clade 1 with *A. ageratoides* and *Heteropappus*, whereas *Miyamayomena* belongs to clade 3 with *A. amellus*. Natural hybridizations between *Kalimeris* and *A. ovatus* (formerly *A. ageratoides* subsp. *ovatus*; Tara, 1972, 1989), between *Kalimeris* and *A. ageratoides* (Li, 2006), and between *Kalimeris* and *Heteropappus* (Tara, 1973) support a close relationship with the *A. ageratoides* complex and *Heteropappus*, as do morphological studies (Gu and Hoch, 1997). Hu (1967) transferred a few species of *Aster*, including *A. smithianus*, to *Kalimeris* based on their short pappi, whereas our analyses showed that *A. smithianus* is not closely related to *Kalimeris* (Figs 1 and 2).

Miyamayomena. This was separated from *Kalimeris* and initially named *Gymnaster* (Kitamura, 1937, 1982; Chen, 1986). It is characterized by a lack of pappi (Kitamura, 1937, 1982; Ling et al., 1985; Chen, 1986). Although there are only five species (Chen, 1986), *Miyamayomena* is as variable morphologically

as the large genus *Aster* and may in fact be an artificial assemblage (Gu and Hoch, 1997). Ito and Soejima (1995) treated *M. savatieri*, the generic type, as a species of *Aster* section *Teretiachaenium* which also includes *A. scaber* (= *D. scaber*). In the phylogenetic trees based on RFLPs of plastid DNA, two species of *Miyamayomena* did not form a clade: *M. koraiensis* was nested in the *Aster* clade, and *M. savatieri* was a sister to the *Aster* clade. Therefore, *Miyamayomena* could be polyphyletic (Ito et al., 1994, 1998). Our analyses (Figs 1B and 2) show that three Chinese *Miyamayomena* spp., *M. piccolii*, *M. simplex* and *M. angustifolius*, are nested within the *Aster* clade (clade 8) and should be merged into *Aster*. These species belong to different clades, implying that a lack of pappi is not a homologous synapomorphy and that *Miyamayomena* is not monophyletic. *Miyamayomena angustifolius* (clade 4) is sister to clade 5 (Figs 1B and 2) and might be designed as a section of *Aster*. *Miyamayomena piccolii* and *M. simplex* form a strongly to weakly supported clade (PP = 0.99 in Fig. 1B; PP = 1.00 and BS = 84 in Fig. 2) embedded within the *A. amellus* clade (clade 3 in Figs 1B and 2) and might be treated as a series of section *Aster*, whereas the taxonomic positions of *Miyamayomena koraiensis* and *M. savatieri*, endemic to Japan and North Korea, respectively, remain to be determined.

Heteropappus. In 1832 the genus *Heteropappus* was established and the type species, *H. hispidus*, was transferred from *Aster* (Lessing, 1832). *Heteropappus* includes approx. 30 species distributed in eastern and central Asia and the Himalayan region (Ling et al., 1985). The genus is characterized by its two series of sub-equal herbaceous phyllaries and dimorphic pappi (shorter on the ray achenes and longer on the disc achenes; Ling et al., 1985; Gu and Hoch, 1997). Some species such as *H. altaicus* have a monomorphic pappus, so Grierson (1964) redefined *Heteropappus* by the unequal corolla lobes of the disc florets. Zygomorphic disc florets are also found in some species of *Aster* and *Kalimeris*, however. RFLPs of plastid DNA show that *H. hispidus* is embedded in *Aster* (Ito et al., 1998), implying that *Heteropappus* should be included in *Aster*. Our analyses (Figs 1 and 2) also strongly support the placement of *Heteropappus* in *Aster*. The two sampled species, representing two sections, form a highly to weakly supported (PP = 1.00 and BS = 79 in Fig. 1B; PP = 1.00 and BS = 100 in Fig. 2) sub-clade of the *A. ageratoides* clade (clade 1), which might indicate that *Heteropappus* should be treated as a series of section *Ageratoides* (corresponding to clade 1).

Callistephus. This is a monotypic genus native to China. Based on its double pappus and unique involucre (outer bracts foliaceous and innermost white scarious), it was distinguished from *Aster* in 1817 by Cassini (Ling et al., 1985; Nesom, 2000). *Heteropappus hispidus* was placed in *Callistephus* by de Candolle as *Callistephus biennis* (Nesom, 2000), implying that *Callistephus* and *Heteropappus* might be related to each other. Zhang and Bremer (1993) suggested that *Callistephus*, *Gymnaster*, *Heteropappus* and *Kalimeris* are closely related to each other and to *Aster*. Nesom (1994b) thought that *Callistephus* is similar to some species of *Myriactis* (sub-tribe Lagenophorinae) in habit and tendency toward pappus

reduction, but he placed *Callistephus* within the *Kalimeris* group given the similar morphology of leaves, receptacles, disc corollas, and papillate collecting appendages of the style branches, the arrangement of the capitulum and the tendency toward pappus reduction (Nesom, 1994a, b, 2000). Our analyses (Figs 1 and 2) reveal that *Callistephus* has no close relationships with the other four genera of the *Kalimeris* group or with *Myriactis*. In the combined tree (Fig. 2), *Callistephus* and *Myriactis* occur in the same polytomy (clade 18) that is part of the Australasian lineages, which is concordant with the result of Brouillet *et al.* (2009b) that placed *Callistephus* in the large Australasian polytomy. We suggest that *Callistephus* maintain its generic status.

Status of *Turczaninowia*

Turczaninowia fastigiata is native to north-eastern Asia (Tamamschyan, 1959; Ling *et al.*, 1985; Ito and Soejima, 1995) and is characterized by its dense vestiture and small heads (with flowers and fruits reduced correspondingly) in a compact capitulescence. *Turczaninowia fastigiata* was originally published as *Aster fastigiatus* in 1812 (Ling *et al.*, 1985) and was segregated as the monotypic genus *Turczaninowia* by de Candolle in 1836 (Nesom, 1994b). Tamamschyan (1959), Ling *et al.* (1985) and Bremer (1994) followed de Candolle's treatment, whereas Nesom (1994b) and Nesom and Robinson (2007) supported the inclusion of the species in *Aster*, and Ito and Soejima (1995) placed this species in *Aster* section *Aster*. The ovarian sterility of some of the inner disc flowers of this species and the triangular collecting appendages of its style branches are considered hallmarks of a possible close relationship with *Galatella* (Ling *et al.*, 1985; Nesom, 1994b). Our phylogenetic trees (Figs 1 and 2) suggest that *T. fastigiata* does not merit generic rank or have a close relationship to *Galatella*; rather it should be transferred to *Aster* section *Aster*.

Status of *Doellingeria*

Nees established *Doellingeria* in 1832, typified by *D. umbellata*. Bentham (1873) advocated a conglomerated *Aster* and included *Doellingeria* within a larger *Aster*. Some botanists continued to recognize *Doellingeria* as a distinct genus, however. Its phylogenetic position is equivocal. Zhang and Bremer (1993) placed *Doellingeria* in the *Aster* group. Nesom classified it first in sub-tribe Solidagininae (Nesom, 1993), then in sub-tribe Symphyotrichinae (Nesom, 1994a) or in sub-tribe Asterinae (Nesom, 1994b), and recently as an unplaced genus of Astereae (Nesom and Robinson, 2007). *Doellingeria* includes 11 species, of which three are NA and eight are eastern Asian species (Nesom, 1993, 1994b). RFLPs of plastid DNA show that eastern Asian *Doellingeria* is embedded in *Aster s.s.* (Ito *et al.*, 1994), and hybridization between eastern Asian *Doellingeria* and *Aster* has been reported (Saito *et al.*, 2007), whereas ITS data support an early-branching position of NA *Doellingeria* (represented by *D. umbellatus*) in the NA Astereae clade (Noyes and Rieseberg, 1999; Brouillet *et al.*, 2001). In our trees (Figs 1 and 2) NA *Doellingeria* belongs to the NA clade (clade 20; Fig. 1A), and eastern Asian *Doellingeria* (represented by

Doellingeria scaber) is embedded in clade 8 (the *Aster* clade; Figs 1B and 2), which implies that *Doellingeria* is biphyletic and that eastern Asian *Doellingeria* should be moved from *Doellingeria* (which is typified by NA *D. umbellatus*) to *Aster*. Ito and Soejima (1995) placed eastern Asian *Doellingeria* and *Miyamayomena* together in *Aster* section *Teretiachaenium*. Our analyses (Figs 1B and 2) show that eastern Asian *Doellingeria* and *Miyamayomena* belong to different sub-clades (clades 6 and 7, respectively) of the *Aster* clade (clade 8), however. In clade 7 (Figs 1B and 2) eastern Asian *Doellingeria* is a sister to a clade with *Arctogeron*, *Asterothamnus* and three species of *Aster s.s.*, showing that it diverged early in *Aster* evolution and suggesting that eastern Asian *Doellingeria* should be treated as an independent section of *Aster*.

Status of *Aster segregates of the 'Asterothamnus group'*

Nesom (1994a, b) set up an *Asterothamnus* group consisting of five small genera, *Asterothamnus*, *Krylovia* (= *Rhinactinidia*), *Arctogeron*, *Kemulariella* and *Psychrogeton*, of which the first four are segregates of *Aster*. The *Asterothamnus* group occurs primarily in central Asia and is characterized by a woody stem base, caespitose habit, sessile–glandular and tomentose stems and leaves, few or solitary heads and strongly coiling rays (Nesom, 1994b). Most of these features may be convergent characters resulting from adaptive modification under harsh environmental conditions (drought or cold), however. Our samples were limited to *Asterothamnus*, *Rhinactinidia* and *Arctogeron* (Appendix) because *Kemulariella* and *Psychrogeton* materials were unavailable.

Asterothamnus. This was segregated from *Aster* in 1950 by Novopokrovskiy, and its generic status has been accepted by several authors (Tamamschyan, 1959; Ling *et al.*, 1985; Zhang and Bremer, 1993; Bremer, 1994; Nesom, 1994b; Czerepanov, 1995; Nesom and Robinson, 2007). The genus comprises seven species endemic to deserts and desert steppes in central Asia (Ling *et al.*, 1985; Zhao, 1996). *Asterothamnus* has distinctive characters: it is a strongly branching sub-shrub with a woody rhizome, linear or narrowly elliptic leaves, densely or thinly tomentose stems and leaves and solitary or few heads in a loose corymb, reflecting adaptation to drought. In our phylogenetic trees (Figs 1B and 2) *Asterothamnus* belongs to the *Aster* clade (clade 8) and should be treated as a member of *Aster*. The two species sampled form a well-supported sub-clade (PP = 1.00 and BS = 100) that is nested in clade 7 with *A. sikuensis*, *A. poliothamnus*, *A. falcifolius*, *Arctogeron* and eastern Asian *Doellingeria* in both phylogenetic analyses (Figs 1B and 2). *Asterothamnus* is obviously different in morphology from the other members of clade 7 and should be regarded as a section of *Aster*.

Arctogeron gramineum. This is the only species of *Arctogeron* and is distributed in north-eastern China, Mongolia and eastern Russia. It occurs on dry mountain slopes or stony slopes and displays characters linked to drought adaptation such as low-growing and mat-forming habit and linear-subulate leaves. The species was originally described in

1753 by Linnaeus as a member of *Erigeron* and then established as a separate genus in 1836 by de Candolle and transferred to *Aster* in 1907 by Komarov (reviewed by Ling *et al.*, 1985). Like *Asterothamnus*, *Arctogeron* belongs to the *Aster* clade (clade 8; Figs 1B and 2) and should be treated as a member of *Aster*. It is well nested in clade 7 (Figs 1B and 2) and should be treated as a monotypic section of *Aster*.

Rhinactinidia. This is a genus of four species native to central Asia and Siberia (Ling *et al.*, 1985; Czerepanov, 1995). It was established as a genus in 1831 by Lessing and was later included in *Aster s.l.* (Ling *et al.*, 1985). Its generic status is currently generally accepted (Tamamschyan, 1959; Ling *et al.*, 1985; Zhang and Bremer, 1993; Bremer, 1994; Nesom, 1994b; Czerepanov, 1995; Nesom and Robinson, 2007). Nesom (1994b) suggested that *Asterothamnus* and *Krylovia* (= *Rhinactinidia*) are closely related in terms of similarities such as keeled phyllaries, a coiling–reflexing disc corolla, and two-veined achenes with glandular surfaces. *Rhinactinidia* is considered different from *Aster* in its diagnostic characters and zygomorphic disc corollas (Ling *et al.*, 1985), but these features can also be found in *Aster s.s.* Our study shows (Figs 1B and 2) that *Rhinactinidia* is well nested within the *Aster* clade, belongs to the *A. amellus* clade (clade 3) and has no close relationship with *Asterothamnus*. Two samples of *Rhinactinidia* form a well-supported clade (PP = 1.00 and BS = 100 in Figs 1B and 2), and *Rhinactinidia* should be treated as a series of section *Aster*.

Status of the ‘Galatella group’

According to Nesom (1994a, b), the *Galatella* group of Asterinae *s.s.* includes three genera, *Galatella* (approx. 30 species), *Crinitina* (13 species) and *Tripolium* (a monotypic genus). These genera have been treated as three sections of *Aster* (*Galatella*, *Linosyris* and *Tripolium*, respectively) by some botanists but as segregate genera in other studies (reviewed by Ling *et al.*, 1985; Nesom, 1994b). Furthermore, Nesom was indecisive about whether *Galatella* and *Crinitina* might belong in Solidagininae (Nesom, 1991) or whether they are more closely related to typical *Aster* (Nesom, 1994b). Based on ITS data, Fiz *et al.* (2002) and Brouillet *et al.* (2009b) found that *Galatella* and *Crinitina* form a well-supported clade, and a few studies have shown that *Galatella* or *Crinitina* are weakly related to Bellidinae rather than to *Aster* (Noyes and Rieseberg, 1999; Fiz *et al.*, 2002; Karaman, 2006). Our phylogenetic analyses (Figs 1 and 2) show that *Galatella*, *Crinitina* and *Tripolium* constitute a well-supported clade (clade 22: PP = 1.00 and BS = 92 in Fig. 1A; PP = 1.00 and BS = 95 in Fig. 2). Furthermore, in the combined analysis (Fig. 2), *Crinitina linosyris*, *Crinitina villosa* and *Galatella dahurica* form a well-supported clade (clade 21: PP = 1.00, BS = 97), which would support the merger of *Crinitina* into *Galatella*. Whether *Tripolium* deserves generic status or whether the three genera should be merged into a single genus remains to be determined. If the latter is reasonable, the oldest name would have to be used for the genus, i.e. *Galatella*. In our analyses the *Galatella*–*Crinitina*–*Tripolium* clade (clade 22; Figs 1A and 2) is closely related to neither the *Aster* clade nor *Solidago*

decurrens (a representative of sub-tribe Solidagininae). Similarities between the *Galatella* group and *Aster* in leaves, disc style branches, achenes and heads (Nesom, 1994b) are superficial and have developed in parallel, and the *Galatella* group should be separated from *Aster*. The trees show a moderate to weak relationship (clade 23: PP = 0.89 in Fig. 1A; PP = 0.91 and BS = 57 in Fig. 2) between the three genera of the *Galatella* group and *Bellis*, which is consistent with the conclusions of Fiz *et al.* (2002). The systematic position of the *Galatella* group remains unresolved.

Redelimitation of Aster

According to our data, all existing generic delimitations of *Aster* are problematic. The EA *Aster* as delimited by some botanists (e.g. Ling *et al.*, 1985; Nesom, 1994b; Nesom and Robinson, 2007) is paraphyletic because it excludes some of the descendants of the most recent common ancestor. Therefore, monophyletic *Aster* should include such genera as *Sheareria*, *Rhynchospermum*, *Kalimeris* (excluding *K. longipetiolata*), *Heteropappus*, *Miyamayomena*, *Rhinactinidia*, *Turczaninowia*, *Asterothamnus*, *Arctogeron* and eastern Asian *Doellingeria*. Conversely, EA *Aster* as delimited by other botanists (e.g. Merxmüller *et al.*, 1976; Ito and Soejima, 1995) is polyphyletic because it includes morphologically similar but distantly related taxa. *Callistephus*, *Galatella*, *Crinitina* and *Tripolium* should be excluded from *Aster*. The *Aster* clade (clade 8) is strongly supported in both the ITS tree (PP = 0.99; Fig. 1B) and the combined tree (PP = 1.00, BS = 98; Fig. 2), so the *Aster* clade is the recircumscribed genus *Aster*. Molecular data (Figs 1 and 2) revealed, however, that many Chinese *Aster* spp. should be excluded from *Aster*, although their status as *Aster* species, except for series *Albescentes*, has not been doubted. Of 41 sampled species of *Aster s.s.* (Ling *et al.*, 1985; Chen, 1988; Ito and Soejima, 1995; Li and Liu, 2002), 17 should be removed from the genus.

Series *Hersileoides* (*Aster* section *Orthomeris*, *sensu* Ling *et al.*, 1985) is endemic to western China and consists of two restricted species, *A. hersileoides* and *A. nitidus* (Ling *et al.*, 1985; Yin *et al.*, 2010). They are characterized by a shrubby habit, solitary capitula at the apex of branches, membranous receptacular bracts and a short outer pappus. A karyotypic study of these species (Yin *et al.*, 2010) showed that they are diploid and have shorter chromosomes and higher asymmetry of karyotype than that with *A. ageratoides*. Our study demonstrates that the series is a well-supported monophyletic group (clade 9: PP = 0.99 and BS = 98 in Fig. 1A; PP = 1.00 and BS = 100 in Fig. 2). Although the systematic position of the series has never been questioned, the ITS phylogenetic tree (Fig. 1A) shows that clade 9, series *Hersileoides*, is not closely related to clade 8, the *Aster* clade, and in the combined tree (Fig. 2) the sister relationship between clades 8 and 9 is only weakly supported (BS = 54), even though the Bayesian PP is high (0.99). Therefore, the series should be removed from *Aster*, and it might be reasonable to elevate the series to a generic level in sub-tribe Asterinae.

Aster albescens var. *albescens*, *A. argyropholis* and *A. lavandulifolius* are representative of series *Albescentes*. Western China is the centre of diversity of this series, with six of the seven species being endemic to the region (the

exception being *A. albescens* which is distributed from western China to the southern Himalayas; Ling *et al.*, 1985; Chen, 1988). Ling *et al.* (1985) established the series and placed it within *Aster* section *Orthomeris*. The series differs from others in the section with its shrubby habit, pinnate primary lateral leaf veins, relatively small heads, small rays and four- to six-veined, sub-cylindric achenes. Our studies (Figs 1A and 2) demonstrate that series *Albescentes* is a well-supported monophyletic taxon (clade 12: PP = 1.00 and BS = 98 in Fig. 1A; PP = 1.00 and BS = 100 in Fig. 2) and should be removed from *Aster*. Nesom (1994b) suggested that series *Albescentes* is closely related to the NA group, in which it would be positioned near NA *Doellingeria*. The present results provide no evidence to support this relationship, however. On the contrary, series *Albescentes* occurs in a polytomy (clade 18: PP = 1.00 in Fig. 2) with *Myriactis* and other segregates of *Aster s.s.*, implying that series *Albescentes* may belong to the Australasian lineages rather than to the NA clade (clade 20; Fig. 2). In the ITS analysis the series occurs at an unresolved position within a polytomy (Fig. 1A) in Astereae. Its systematics requires further investigation; however, series *Albescentes* should undoubtedly be removed from *Aster* and be considered for generic rank.

According to Ling *et al.* (1985), *A. auriculatus* and *A. panduratus* belong to section *Aster* series *Auriculati*, and *Aster pycnophyllus* belongs to section *Orthomeris* series *Sikkimenses*. In the trees (Figs 1A and 2), the three species are well nested in a clade with *Myriactis* (clade 11: PP = 1.00 and BS = 97 in Fig. 1A; PP = 1.00 and BS = 100 Fig. 2) and distantly related to *Aster*, suggesting that they should be removed from *Aster*. Although *Myriactis* is quite different from these three species with its two- to multiple-seriate ray florets, male disc florets and glandular collar, they do not form a sub-clade sister to *Myriactis*. Therefore, the relationships among the three species and *Myriactis* require further study.

Of the 15 sampled species of *Aster* section *Alpigenia* (Appendix), seven fall in the *Aster* clade, and the other eight fall outside it (Figs 1A and 2). Of these eight species, six (*A. asteroides*, *A. brachytrichus*, *A. diplostephioides*, *A. flaccidus*, *A. setchuenensis* and *A. yunnanensis*) form a well-supported clade (clade 10: PP = 0.99 in Fig. 1A; PP = 1.00 and BS = 98 in Fig. 2), implying that these species might become a new genus. The systematic position of this group is unresolved, however. In the ITS tree (Fig. 1A) clade 10 falls within a big polytomy, and in the combined tree (Fig. 2) it belongs to clade 18, a polytomy, with *Myriactis*. *Aster senecioides*, the sole member of a monotypic series of section *Alpigenia*, forms a strongly supported clade (clade 15: PP = 1.00 and BS = 93 in Fig. 1; PP = 1.00 and BS = 100 in Fig. 2) with *A. fuscescens*, also the sole member of a monotypic series of section *Aster* (Ling *et al.*, 1985). These two species are at an unresolved position within the big polytomy in the ITS tree (Fig. 1A) and belong to a polytomy (clade 18; Fig. 2) in the combined tree. Clade 15 might be treated as a separate genus. Similarly, in the ITS tree (Fig. 1A), *A. batangensis* (clade 16) occupies an unresolved position within the big polytomy of EA Astereae, and, in the combined tree (Fig. 2), clade 16 belongs to clade 18. Our phylogenetic trees (Figs. 1A and 2) show that *A. batangensis* seems to deserve the status of a monotypic genus. Thus, *A. series*

Hersileoides, *A. series Albescentes*, a six-species group including *A. asteroides*, a group composed of *A. senecioides* and *A. fuscescens*, and *A. batangensis* should be elevated to generic level, and, together with the *Aster* clade, placed with the Australasian lineages.

Nesom (2000) stated that *Aster*, even in its more restricted morphological definition, still encompasses a great deal of variation, and the description remains correspondingly general. Herein, *Aster* is expanded to include some segregates of *Aster s.l.* and other genera, making *Aster* more complex in some morphological features. For example, treating *Sheareria* as a section of *Aster* adds to *Aster* some new characters such as bract-like leaves, assimilating branches, small heads with only 5–8 florets, and functionally staminate disc flowers. *Arctogeron* brings to *Aster* such new features as caespitose herbs, narrow grass-like leaves with a scabrous ciliate margin and densely silvery pubescent cypselas. The high morphological diversity implies that *Aster* has undergone an evolutionary radiation since it originated. *Aster* displays a broad morphological variability in pappi (e.g. pappi are one- to four-seriate or absent, short or long, persistent or caducous) that, as mentioned above, has been used as a diagnostic character in delimiting some genera. Pappi are absent in clades 2 and 4 and in the *M. piccolii*–*M. simplex* clade of clade 3 (Figs 1B and 2), which implies that the disappearance of a pappus has evolved independently at least three times in *Aster*. *Kalimeris*, *A. smithianus*, *A. dolichopodus* and *A. souliei* share reduced pappi but occur in different sub-clades (Figs 1B and 2), suggesting convergent evolution toward pappus shortening. Dimorphic pappi (different lengths of pappi between ray and disc florets) are a diagnostic feature of *Heteropappus*, but dimorphic pappi are also found in *A. homochlamydeus* (W.-P. Li, unpubl. res.), which is another example of convergent evolution of pappi. Furthermore, no evolutionary relationships occur among dimorphic pappi, short pappi and absent pappi, i.e. no evolutionary series from dimorphic pappi to epappi exists. According to Ling *et al.* (1985), series *Turbinati* is characterized by four- to seven-seriate phyllaries, whereas our phylogenetic trees (Figs 1 and 2) show that three species (*A. turbinatus*, *A. baccharoides* and *A. sampsonii*), *A. jishouensis* (series *Turbinati*), with multi-seriate phyllaries, and *R. verticillatum*, with two- to three-seriate phyllaries, form a clade, and this clade is not closely related to another species with multiseriate phyllaries, *A. sampsonii*. Therefore, the multiseriate phyllaries feature has arisen more than once in *Aster*. Noticeably, six species in one sub-clade of clade 7 (Figs 1B and 2) share a more or less shrubby habit, and clade 9 (sister to clade 8 in Fig. 2) is also characterized by a shrubby habit, which might mean that shrubby habit may represent a symplesiomorphy in clades 8 and 9. Whether EA *Aster*, with predominantly herbaceous perennials, originated from a woody ancestor is worth considering. Nonetheless, in clade 6 (Figs. 1B and 2), the shrubby habit of *A. baccharoides* and *A. smithianus* seems to be a convergence because these species occur within clades 1 and 3, respectively (Figs 1B and 2), and are not closely related to each other, and each of them is the only shrub in its clade. The morphology of *Aster* is so complex that further tracing of important morphological characters in the phylogenetic trees is necessary to reveal their phylogenetic significance.

Infrageneric classification of Aster

After extensive changes in the generic delimitation of *Aster*, its infrageneric systematics should be reconstructed. Three infrageneric taxonomic schemes of EA *Aster s.s.* have been described. First, Ling *et al.* (1985) divided Chinese *Aster s.s.* into three sections [*Aster*, *Orthomeris* (a name based on an NA type in genus *Oclemena*) and *Alpigenia*] and 27 series. Next, Ito and Soejima (1995) recognized five sections of Japanese *Aster*: *Tripodium* (a monotypic section), *Pseudocalimeris* (largely equal to the genus *Heteropappus*), *Teretiachaenium* (including the taxa of *Miyamayomena* and eastern Asian *Doellingeria*), *Asteromoea* (similar to *Kalimeris*) and *Aster* (largely equal to *Aster s.s.*). Finally, Nesom (1994b) divided *Aster* into four sections and taxa *incertae sedis*. The former includes sections *Aster*, *Alpigenia* (including sub-sections *Homochaeta*, *Heterochaeta* and *Senecioides*), *Ageratoides* and *Calimeridei*, and the latter is a six-species group. The current study supports none of these taxonomic systems, however.

We suggest clade 8 (Figs 1B and 2) as the genus *Aster* and clades 6 and 7 (Figs 1 and 2) as two subgenera of *Aster*. In clade 6, each of four sub-clades (clades 1–4; Figs 1B and 2) could be treated as a section. As mentioned above, *M. angustifolius* (clade 4; Figs 1B and 2) and *S. nana* (clade 2; Figs 1B and 2) may be treated as monotypic sections. Clade 1 is well supported in all analyses (PP = 1.00 and BS = 99 in Fig. 1B; PP = 1.00 and PP = 100 in Fig. 2) and could be regarded as section *Ageratoides*, typified by *A. ageratoides* (Nesom, 1994b). Section *Ageratoides* includes all taxa of section *Pseudocalimeris* and section *Asteromoea* and some members of section *Teretiachaenium* and section *Aster* (*sensu* Ito and Soejima, 1995); it corresponds more or less to sections *Ageratoides* of Nesom (1994b) and *Orthomeris* of Ling *et al.* (1985). Clade 3 is well supported only by BI (PP = 0.96 in Fig. 1B; PP = 1.00 in Fig. 2) but not by MP analysis. It might be treated as section *Aster*, typified by *A. amellus*. Although all previous schemes have recognized section *Aster*, their circumscriptions differ from ours. Some members (e.g. *A. dolichopodus*, *A. mangshanensis*, *A. smithianus* and *A. vestitus*) of section *Aster* of Ling *et al.* (1985) are nested in clade 1 (section *Ageratoides*) rather than in clade 3 (section *Aster*), and some members of section *Orthomeris* (e.g. *A. sampsonii*, *A. turbinatus*, *A. baccharoides* and *A. jishouensis*; Ling *et al.*, 1985; Li and Liu, 2002) are nested in clade 3 rather than in clade 1. In fact, Nesom (1994b) agreed with Ling *et al.* (1985) in the circumscription of section *Aster*. As mentioned above, in *Flora of Japan* (Ito and Soejima, 1995) section *Aster* has a much wider definition than ours. Some species of section *Alpigenia* in the classifications of Ling *et al.* (1985) and Nesom (1994b) belong to clade 1 (section *Ageratoides*) or clade 3 (section *Aster*), and the others occur outside of the *Aster* clade, suggesting that section *Alpigenia* should be abandoned.

Clade 7, the other sub-clade of clade 8, is moderately to well supported (PP = 0.99 and BS = 79 in Fig. 1B; PP = 1.00 and BS = 92 in Fig. 2) and could be treated as the other subgenus of *Aster*. The subgenus consists of three segregates (eastern Asian *Doellingeria*, *Asterothamnus* and *Arctogeron*) of *Aster s.l.* and three species (*A. falcifolius*, *A. poliothamnus* and

A. sikuensis) of *Aster s.s.* As discussed above, eastern Asian *Doellingeria*, *Asterothamnus* and *Arctogeron* should be treated as three different sections. According to Ling *et al.* (1985), *A. falcifolius* is the only member of series *Falcifolii* of section *Orthomeris*, and *A. poliothamnus* and *A. sikuensis* belong to series *Vestiti* of section *Aster*. These three species have more or less woody stems that are similar to those of the other taxa of clade 7, *Asterothamnus* and *Arctogeron*. *Aster falcifolius* is characterized by solitary flowers and bracteole leaves that become denser until grading into phyllaries. It should be raised to the sectional level. *Aster poliothamnus* and *A. sikuensis* share some features, such as four- to five-seriate phyllaries and the absence of rhizomes, and form a strongly to weakly supported clade (PP = 1.00, BS = 71; Fig. 2). These two species may deserve the status of a section. As a result, the subgenus (clade 7; Figs 1B and 2) would comprise five sections.

According to Ling *et al.* (1985), the recircumscribed *Aster* has seven series with two or more species included in our analyses. None of these is monophyletic, however. All three species of series *Vestiti* (*A. vestitus*, *A. poliothamnus* and *A. sikuensis*; Ling *et al.*, 1985) were sampled and occur in clades 6 and 7 (see Figs 1B and 2), and they should be placed in different subgenera. *Aster alpinus*, *A. handelii*, *A. heterolepis* and *A. oreophilus* are assigned to series *Alpigenia* (Ling *et al.*, 1985) but occur in four clades of section *Ageratoides* (clade 1; Figs 1B and 2) and section *Aster* (clade 3; Figs 1B and 2). Although *A. fanjingshanicus*, *A. tongolensis* and *A. souliei* of series *Tongolenses* (Ling *et al.*, 1985) belong to clade 1, they are not closely related to one another (Figs 1B and 2). All of the series (*sensu* Ling *et al.*, 1985) of *Aster* must be re-evaluated.

More than half the species of *Aster* (Tamamschyan, 1959; Grieson, 1975; Merxmüller and Schreiber, 1976; Ling *et al.*, 1985; Czerepanov, 1995; Ito and Soejima, 1995) are not included in our study; therefore, a more extensive taxon sampling of molecular sequence data is necessary for a full phylogenetic reconstruction of *Aster*. Because more than half of the sampled species of section *Alpigenia* (*sensu* Ling *et al.*, 1985) should be excluded from *Aster*, it is particularly important to collect molecular data for all the species. Because the combined analysis shows better resolution than that of the ITS phylogeny in *Aster s.l.*, the combined data for the Australasian lineages are needed to resolve the origin and systematic position of *Aster* and its segregates.

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APPENDIX

Taxa sampled, phylogenetic lineages, vouchers and GenBank accessions.

Present taxonomy*	Phylogenetic lineages and infrageneric classification of <i>Aster</i> [†]	Numbers, locations and altitudes of vouchers [‡]	GenBank accession number [§]		
			ITS	ETS	<i>trnL-F</i>
Unplaced taxa					
<i>Doellingeria umbellata</i>	NA	–	AF046966	NA	
<i>Eurybia sibirica</i>	NA	–	AY772421	AY772435	GU480699
<i>Nannoglottis delavayi</i>	BL	–	AY017167	NA	
Sub-tribe					
Homochrominae					
<i>Felicia filifolia</i>	BL	–	FJ457937	NA	
Sub-tribe					
Hinterhuberinae					
<i>Celmisia mackaui</i>	NZ	–	AF422115	NA	
<i>Chiliotrichum diffusum</i>	PSA	–	AF046945	DQ479128	AF452501

Continued

APPENDIX 1. Continued

Present taxonomy*	Phylogenetic lineages and infrageneric classification of <i>Aster</i> [†]	Numbers, locations and altitudes of vouchers [‡]	GenBank accession number [§]		
			ITS	ETS	<i>trnL-F</i>
<i>Madagaster</i>	BL	–	DQ479031	NA	
<i>madagascariensis</i>					
<i>Mairia hirsuta</i>	BL	–	FJ457929	NA	
<i>Olearia astroloba</i>	AL	–	AF497646	NA	
<i>Olearia ballii</i>	AL	–	AF497662	NA	
<i>Olearia calcarea</i>	AL	–	AF497663	NA	
<i>Olearia ciliata</i>	AL	–	AF497667	NA	
<i>Olearia cordata</i>	AL	–	AF497668	NA	
<i>Olearia covenyi</i>	NZ	–	AF497711	NA	
<i>Olearia rudis</i>	AL	–	AF497677	NA	
<i>Olearia tomentosa</i>	AL	–	AF497650	NA	
<i>Oritrophium hieracioides</i>	PSA	–	DQ479116	NA	
<i>Pleurophyllum hookeri</i>	NZ	–	HQ439864	NA	
<i>Printzia polifolia</i>	BL	–	FJ457927	NA	
<i>Pteronia camphorata</i> var. <i>camphorata</i>	BL	–	DQ479118	NA	
<i>Remya kauaiensis</i>	AL		AF497684	NA	
Sub-tribe					
Brachyscominae					
<i>Brachyscome rigidula</i>	AL	–	DQ478994	NA	
<i>Calotis hispidula</i>	AL	–	AB196597	NA	
Sub-tribe Bellidinae					
<i>Bellis perennis</i>	BE	LWP1003008; Changsha, cultivated	JN315918	JN315942	JN315894
Sub-tribe Grangeinae					
<i>Grangea maderaspatana</i>	GR	LWP0802034; Zhaoqing City, 200 m	JN315920	JN315944	JN315896
<i>Dichrocephala auriculata</i>	GR	LWP0708234; Dali City, 2300 m	JN315919	JN315943	JN315895
Sub-tribe					
Lagenophorinae					
<i>Myriactis nepalensis</i>	AL	LWP0509002; Kunming City, 2300 m	JN315921	JN315945	JN315897
<i>Myriactis wightii</i>	AL	LWP0509010; Kunming City, 2200 m	JN315922	JN315946	JN315898
<i>Rhynchospermum verticillatum</i>	AL	LWP0607065; Mt. Emei, 1200 m	JN543706	JN543707	JN543708
<i>Sheareria nana</i>	AL	LWP0701001; Changsha City, 30m	JN543703	JN543704	JN543705
Sub-tribe Baccharidinae					
<i>Baccharis neglecta</i>	SA	–	U97604	NA	
Sub-tribe Podocominae					
<i>Camptacra gracilis</i>	AL	–	AF247069	NA	
<i>Kippistia suaedifolia</i>	AL	–	AF497660	NA	
<i>Minuria integerrima</i>	AL	–	AF046957	NA	
<i>Minuria macrorhiza</i>	AL	–	AF247076	NA	
<i>Tetramolopium humile</i> var. <i>humile</i>	AL	–	DQ479040	NA	
Sub-tribe Asterinae					
<i>Arctogeron gramineum</i>	SEA	LWP0606014; Wulanhaote City, 300 m	JN315928	JN315952	JN315904
<i>Aster</i>	Eurasian <i>Aster</i> s.s.				
<i>Aster amellus</i>	Section <i>Aster</i> series <i>Amelli</i>	LWP0408002; Shumen, Bulgaria, 400 m	JN543742	JN543743	JN543744
<i>Aster maackii</i>	Section <i>Aster</i> series <i>Macrocephali</i>	LWP0609043; Yichun City, 200 m	JN543745	JN543746	JN543747
<i>Aster tataricus</i>	Section <i>Aster</i> series <i>Macrocephali</i>	LWP0108018; Xinglong County, 400 m	JN543748	JN543749	JN543750
<i>Aster fuscescens</i>	Section <i>Aster</i> series <i>Fuscscentes</i>	YGS1007021; Gongshan County, 2500 m	JN543751	JN543752	JN543753
<i>Aster auriculatus</i>	Section <i>Aster</i> series <i>Auriculati</i>	LWP0509059; Yongsheng County, 2200 m	JN543754	JN543755	JN543756
<i>Aster panduratus</i>	Section <i>Aster</i> series <i>Auriculati</i>	LWP1012067; Guiyang City, 1100 m	JN543757	JN543758	JN543759
<i>Aster mangshanensis</i>	Section <i>Aster</i> series <i>Auriculati</i>	LWP0511034; Mt. Mang, 1670 m	JN543760	JN543761	JN543762
<i>Aster poliothammus</i>	Section <i>Aster</i> series <i>Vestiti</i>	LWP0506001; Zhang County, 500 m	JN543763	JN543764	JN543765
<i>Aster sikuensis</i>	Section <i>Aster</i> series <i>Vestiti</i>	LWP0510025; Lueyang County, 300 m	JN543766	JN543767	JN543768

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APPENDIX 1. Continued

Present taxonomy*	Phylogenetic lineages and infrageneric classification of <i>Aster</i> [†]	Numbers, locations and altitudes of vouchers [‡]	GenBank accession number [§]		
			ITS	ETS	<i>trnL-F</i>
<i>Aster vestitus</i>	Section <i>Aster</i> series <i>Vestiti</i>	LWP0509023; Lijiang City, 2610 m	JN543769	JN543770	JN543771
<i>Aster taliangshanensis</i>	Section <i>Aster</i> series <i>Taliangshanensis</i>	LWP0607056; Xichang City, 2800 m	JN543772	JN543773	JN543774
<i>Aster dolichopodus</i>	Section <i>Aster</i> series <i>Smithiani</i>	LWP0409060; Maerkang City, 2500 m	JN543775	JN543776	JN543777
<i>Aster smithianus</i>	Section <i>Aster</i> series <i>Smithiani</i>	LWP0508034; Maerkang City, 2600 m	JN543778	JN543779	JN543780
<i>Aster ageratoides</i> var. <i>lasiocladus</i>	Section <i>Orthomeris</i> series <i>Ageratoides</i>	LWP0112018; Changsha City, 110 m	JN543781	JN543782	JN543783
<i>Aster homochlamydeus</i>	Section <i>Orthomeris</i> series <i>Ageratoides</i>	LWP0508004; Li County, 2600 m	JN543784	JN543785	JN543786
<i>Aster hersileoides</i>	Section <i>Orthomeris</i> series <i>Hersileoides</i>	LWP0807002; Li County, 2100 m	JN543787	JN543788	JN543789
<i>Aster nitidus</i>	Section <i>Orthomeris</i> series <i>Hersileoides</i>	LWP0505007; Nanchuan County, 660 m	JN543790	JN543791	JN543792
<i>Aster albescens</i> var. <i>albescens</i>	Section <i>Orthomeris</i> series <i>Albescentes</i>	LWP0508123; Baoxing County, 2010 m	JN543862	JN543863	JN543864
<i>Aster argyropholis</i>	Section <i>Orthomeris</i> series <i>Albescentes</i>	LWP0409045; Maerkang City, 2500 m	JN543793	JN543794	JN543795
<i>Aster lavandulifolius</i>	Section <i>Orthomeris</i> series <i>Albescentes</i>	LWP0708053; Yajiang county, 2720 m	JN543796	JN543797	JN543798
<i>Aster pycnophyllus</i>	Section <i>Orthomeris</i> series <i>Sikkimenses</i>	LWP0509091; Dali City, 2800 m	JN543799	JN543800	JN543801
<i>Aster falcifolius</i>	Section <i>Orthomeris</i> series <i>Falcifolii</i>	LWP0410050; Mt. Huping, 400 m	JN543802	JN543803	JN543804
<i>Aster baccharoides</i>	Section <i>Orthomeris</i> series <i>Turbinati</i>	LWP0802001; Zhuhai City, 100 m	JN543805	JN543806	JN543807
<i>Aster jishouensis</i>	Section <i>Orthomeris</i> series <i>Turbinati</i>	LWP1012015; Jishou City, 600 m	JN543808	JN543809	JN543810
<i>Aster sampsonii</i>	Section <i>Orthomeris</i> series <i>Turbinati</i>	LWP0511060; Mt. Mang, 1100 m	JN543811	JN543812	JN543813
<i>Aster turbinatus</i>	Section <i>Orthomeris</i> series <i>Turbinati</i>	LWP0110029; Fenghua City, 60 m	JN543814	JN543815	JN543816
<i>Aster alpinus</i>	Section <i>Alpinenia</i> series <i>Alpini</i>	LWP0607020; Wulumuqi City, 2320 m	JN543817	JN543818	JN543819
<i>Aster handelii</i>	Section <i>Alpinenia</i> series <i>Alpini</i>	LWP0708174; Zhongdian County, 3400 m	JN543820	JN543821	JN543822
<i>Aster heterolepis</i>	Section <i>Alpinenia</i> series <i>Alpini</i>	LWP0507004; Jiuzhai County, 2600 m	JN543823	JN543824	JN543825
<i>Aster oreophilus</i>	Section <i>Alpinenia</i> series <i>Alpini</i>	LWP0509016; Lijiang City, 3000 m	JN543826	JN543827	JN543828
<i>Aster fanjingshanicus</i>	Section <i>Alpinenia</i> series <i>Tongolensis</i>	LWP0606082; Mt. Fangjing, 2300 m	JN543829	JN543830	JN543831
<i>Aster tongolensis</i>	Section <i>Alpinenia</i> series <i>Tongolensis</i>	LWP0708147; Xiangcheng County, 3300 m	JN543832	JN543833	JN543834
<i>Aster souliei</i>	Section <i>Alpinenia</i> series <i>Tongolensis</i>	LWP0708084; Litang County, 4000 m	JN543835	JN543836	JN543837
<i>Aster brachytrichus</i>	Section <i>Alpinenia</i> series <i>Latibracteati</i>	LWP0607075; Xichang City, 2800 m	JN543838	JN543839	JN543840
<i>Aster asteroides</i>	Section <i>Alpinenia</i> series <i>Asteroides</i>	LWP0708112; Daocheng County, 2780 m	JN543841	JN543842	JN543843
<i>Aster flaccidus</i>	Section <i>Alpinenia</i> series <i>Asteroides</i>	LWP0607026; Wulumuqi City, 3700 m	JN543844	JN543845	JN543846
<i>Aster diplostephioides</i>	Section <i>Alpinenia</i> series <i>Diplostephioides</i>	LWP0507020; Jiuzhai County, 2600 m	JN543847	JN543848	JN543849
<i>Aster setchuenensis</i>	Section <i>Alpinenia</i> series <i>Diplostephioides</i>	LWP0508007; Maerkang City, 2800 m	JN543850	JN543851	JN543852
<i>Aster yunnanensis</i>	Section <i>Alpinenia</i> series <i>Diplostephioides</i>	LWP0508089; Kangding City, 3500 m	JN543853	JN543854	JN543855
<i>Aster senecioides</i>	Section <i>Alpinenia</i> series <i>Senecioides</i>	LWP0708215; Lijiang City, 2800 m	JN543856	JN543857	JN543858
<i>Aster batangensis</i>	Section <i>Alpinenia</i> series <i>Batangenses</i>	LWP0606039; Lijiang City, 2700 m	JN543859	JN543860	JN543861
<i>Asterothamnus centrali-asiaticus</i>	SEA	LWP0607045; Yinchuan City, 1630 m	JN315930	JN315954	JN315906
<i>Asterothamnus fruticosus</i>	SEA	LWP0607005; Wulumuqi City, 950 m	JN315929	JN315953	JN315905
<i>Callistephus chinensis</i>	SEA	LWP0108021; Anshan City, 340 m	JN315931	JN315955	JN315907
<i>Crinitina linoxyris</i>	SEA	LWP0408001; Shumen, Bulgaria, 400 m	JN315932	JN315956	JN315908
<i>Crinitina villosa</i>	SEA	LWP0408009; Shumen, Bulgaria, 400 m	JN315933	JN315957	JN315909

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APPENDIX 1. *Continued*

Present taxonomy*	Phylogenetic lineages and infrageneric classification of <i>Aster</i> †	Numbers, locations and altitudes of vouchers‡	GenBank accession number§		
			ITS	ETS	<i>trnL-F</i>
<i>Doellingeria scaber</i>	SEA	LWP0108025; Anshan City, 350 m	JN315934	JN315958	JN315910
<i>Galatella dahurica</i>	SEA	LWP0609047; Mt. A'er, Nei Mongol, 400 m	JN315935	JN315959	JN315911
<i>Heteropappus altaicus</i> var. <i>millefolius</i>	SEA	LWP0506010; Zhang County, 600 m	JN543709	JN543710	JN543711
<i>Heteropappus crenatifolius</i>	SEA	LWP0409037; Maerkang City, 3200 m	JN543712	JN543713	JN543714
<i>Kalimeris indica</i>	SEA	LWP0806017; Changsha City, 80 m	JN543715	JN543716	JN543717
<i>Kalimeris incisa</i>	SEA	LWP0609107; Tonghua County, 560 m	JN543721	JN543722	JN543723
<i>Kalimeris integrifolia</i>	SEA	LWP0609077; Mudanjiang City, 360 m	JN543718	JN543719	JN543720
<i>Kalimeris longipetiolata</i>	SEA	LWP0508104; Baoxing County, 2600 m	JN315936	JN315960	JN315912
<i>Miyamayomena angustifolius</i>	SEA	DBY9206; Yongjia County, 200 m	JN543736	JN543737	JN543738
<i>Miyamayomena piccolii</i>	SEA	LWP0510055; Mei County, 300 m	JN543730	JN543731	JN543732
<i>Miyamayomena simplex</i>	SEA	LWP0508083; Kangding City, 2800 m	JN543733	JN543734	JN543735
<i>Rhinactinidia eremophila</i>	SEA	LWP0607036; Wulumuqi City, 2620 m	JN543727	JN543728	JN543729
<i>Rhinactinidia limoniifolia</i>	SEA	LWP0607012; Wulumuqi City, 1800 m	JN543724	JN543725	JN543726
<i>Tripolium vulgare</i>	SEA	LWP0311001; Varna, Bulgaria, 1 m	JN315937	JN315961	JN315913
<i>Turczaninowia fastigiata</i>	SEA	LWP0609030; Daqin City, 150 m	JN543739	JN543740	JN543741
Sub-tribe Solidaginae					
<i>Solidago decurrens</i>	NA	LWP0510116; Lichuan County, 1050 m	JN204176	JN204177	JN204178
Sub-tribe Pentachaetinae					
<i>Pentachaeta aurea</i>	NA	–	AF046972	NA	
Sub-tribe Boltoniinae					
<i>Boltonia asteroides</i>	NA	–	AF477632	NA	
Sub-tribe Machaerantherinae					
<i>Machaeranthera tanacetifolia</i>	NA	–	AF477661	NA	
Sub-tribe Symphyotrichinae					
<i>Symphyotrichum novi-belgii</i>	NA	LWP0606002; Beijing, cultivated.	JN315926	JN315950	JN315902
<i>Symphyotrichum subulatum</i>	NA	LWP1010007; Changsha City, 40 m	JN315927	JN315951	JN315903
Sub-tribe Astranthiinae					
<i>Astranthium integrifolium</i>	NA	–	AF046984	NA	
Sub-tribe Chrysopsidinae					
<i>Chrysopsis mariana</i>	NA	–	GQ892729	NA	
Sub-tribe Conyzinae					
<i>Conyza japonica</i>	AIS	LWP0606032; Lijiang City, 2500 m	JN315938	JN315962	JN315914
<i>Conyza sumatrensis</i>	NA	LWP1009002; Changsha City, 35 m	JN315923	JN315947	JN315899
<i>Erigeron annuus</i>	NA	LWP1010009; Changsha City, 40 m	JN315924	JN315948	JN315900
<i>Erigeron breviscapus</i>	NA	LWP0606055; Lijiang City, 2500 m	JN315925	JN315949	JN315901
Tribe Anthemideae					
<i>Chrysanthemum coronarium</i>	OG	LWP1004010; Changsha, cultivated.	JN315939	JN315963	JN315915
<i>Dendranthema indicum</i>	OG	LWP1012002; Changsha City, 80 m	JN315940	JN315964	JN315916
Tribe Calenduleae					
<i>Calendula officinalis</i>	OG	LWP1004006; Changsha, cultivated.	JN315941	JN315965	JN315917

* Generic circumscriptions and nomenclature of Astereae follow Nesom and Robinson (2007) except *Turczaninowia* which follows Ling et al. (1985) and *Crinitina* Soják is substituted for *Crinitaria* Cass. The name *Aster setchuenensis* follows the International Plant Names Index (IPNI).

† Phylogenetic lineages: follows Brouillet et al. (2009b); infrageneric classification of *Aster* follows Ling et al. (1985). AIS, Astereae *incertae sedis*; AL, Australasian lineages; BE, Bellidinae; BL, early-branching lineages; ETS, external transcribed spacer; GR, Grangeinae; ITS, internal transcribed spacer; NA, North American lineage; NZ, New Zealand clade; OG, outgroup; PSA, palaeo South American clade; SA, South American lineages; SEA, segregates of Eurasian *Aster s.l.*

‡ Information is omitted for the accessions that were obtained from GenBank. Four species were collected from Bulgaria and the others from China.

§ One or two sequence (ETS, *trnL-F*) data unavailable.