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Molecular phylogeny of the tribe *Astereae* (*Asteraceae*) in SW Asia based on nrDNA ITS and cpDNA *psbA-trnH* sequences

Abstract

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In the present study, nucleotide sequences of the nrDNA ITS and the plastid DNA *psbA-trnH* region were used to reconstruct the phylogeny of the tribe *Astereae* in SW Asia using parsimony, Bayesian and likelihood methods. The ITS analysis showed that the SW Asian representatives of the tribe divide into two groups. One group arises just above the African lineage, while the second is part of the large Australasian polytomy at the crown of the tribe. SW Asian *Aster*, *Crinitina*, *Galatella*, *Lachnophyllum* and *Psychrogeton* appear to be non-monophyletic, whereas *Chamaegeron*, Eurasian *Erigeron* and *Myriactis* are monophyletic. *Dichrocephala integrifolia* is allied with S African members of subtribe *Grangeinae*. *Chamaegeron* and *Lachnophyllum gossypinum* are sister taxa and both are allied with the *Bellis* and *Galatella* group. *Aster bachtiaricus* is the earliest diverging branch of a large polytomy at the crown of the tribe. *Psychrogeton* species form three distinct clades. *Heteropappus altaicus* is nested in the *Aster* clade. *Conyzanthus squamatus* is nested within *Symphotrichum* species.

Additional key words: *Compositae*, *Aster*, *Chamaegeron*, *Galatella*, *Lachnophyllum*, *Psychrogeton*

Introduction

The *Astereae* is the second largest tribe of the *Asteraceae*, with 222 genera and c. 3100 species (Brouillet & al. 2009a). The tribe is characterized by deltate to triangular or lanceolate style appendages (Nesom & Robinson 2007). It is part of the subfamily *Asteroideae* and forms a clade with the *Calenduleae*, *Gnaphalieae* and *Anthemi-deae*, the last of which is often considered its sister tribe (Brouillet & al. 2009a; Funk & al. 2009).

Based on the recent classification of Nesom & Robinson (2007), members of the tribe present in SW Asia can be classified into eight subtribes: *Asterinae* (including *Aster* L., *Crinitina* Soják, *Galatella* Cass., *Heteropappus*

Less., *Psychrogeton* Boiss. and *Tripolium* Nees); *Bellidinae* (*Bellis* L.); *Conyzinae* (*Conyza* Less. and *Erigeron* L.); *Grangeinae* (*Dichrocephala* L'Her. ex DC.); *Homochrominae* (*Chamaegeron* Schrenk and *Lachnophyllum* Bunge); *Lagenophorinae* (*Myriactis* Less.); *Solidagininae* (*Solidago* L.); and *Symphotrichinae* (*Conyzanthus* Tamamsch.). However, *Neobrachyactis* Brouillet, a new genus of three species (type: *Neobrachyactis roylei* (DC.) Brouillet), was not attributed to a subtribe (Chen & al. 2011). In Flora of China, Chen & al. (2011) recognized *Neobrachyactis* as distinct from *Brachyactis* s.str. (the type of which, *B. ciliata* (Ledeb.) Ledeb., belongs to the North American genus *Symphotrichum* Nees) in being glandular and having compressed, 2-ribbed achenes.

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The first global phylogenetic analysis of the tribe based on nrDNA ITS sequence data was done by Brouillet & al. (2009a). The presence of two S African genera, *Denekia* Thunb. and *Printzia* Cass., at the base of the tree suggested that the tribe originated in Africa. The Chinese genus *Nannoglottis* Maxim. is the second lineage in the tribe. It is followed by dispersals to S Africa, South America, New Zealand and Australia. Next, an African lineage gave rise to Asian and Mediterranean members. Finally, the crown lineage of the *Astereae* includes *Callistephus chinensis* (L.) Nees, Australasian lineages, South American lineages and the North American clade.

Hitherto, many Asian members of the tribe (*Chamaegeron*, *Lachnophyllum*, *Neobrachyactis* and *Psychrogeton*) as well as the cosmopolitan *Conyzaanthus* have not been phylogenetically studied using DNA sequences. Only few Eurasian representatives of some genera, especially *Aster* s.str. and segregate genera, were investigated in previous phylogenetic studies (Noyes & Rieseberg 1999; Brouillet & al. 2009a; Li & al. 2012).

The nuclear ribosomal internal transcribed spacer (ITS) and external transcribed spacer (ETS) and plastid sequence data have been used to infer phylogenetic relationships in *Astereae* (Morgan 1997; Noyes & Rieseberg 1999; Noyes 2000; Brouillet & al. 2001; Lowrey & al. 2001; Markos & Baldwin 2001; Cross & al. 2002; Fiz & al. 2002; Liu & al. 2002; Semple & al. 2002; Wagstaff & Breitwieser 2002; Lowell & al. 2003; Morgan 2003; Roberts & Urbatsch 2003, 2004; Urbatsch & al. 2003; Beck & al. 2004; Brouillet & al. 2004; Eastwood & al. 2004; Field & al. 2006; Watanabe & al. 2006; Selliah & Brouillet 2008; Andrus & al. 2009; Brouillet & al. 2009a, 2009b; Karaman-Castro & Urbatsch 2009; Vaezi & Brouillet 2009; Wagstaff & al. 2011; Li & al. 2012; Nakamura & al. 2012; Strijk & al. 2012).

The main goals of this study are (1) to investigate the phylogenetic relationships among SW Asian members of the tribe *Astereae*, and (2) to evaluate the monophyly and relationships of several species-rich genera of the tribe occurring in SW Asia (*Aster*, *Chamaegeron*, *Erigeron* and *Psychrogeton*) mainly based on nrDNA ITS sequence data.

Material and methods

Taxon sampling

The ITS sequences included 142 accessions representing 52 genera and 117 species, with 51 accessions newly sequenced (all from Iran except two from Turkey and one from Kazakhstan) and 91 obtained from GenBank. *Achillea millefolium* L. and *Ursinia nana* DC. (*Anthemideae*), *Anaphalis margaritacea* (L.) Benth. & Hook. f. (*Gnaphalieae*), *Blumea brevipes* (Oliv. & Hiern.) Wild (*Inuleae*) and *Calendula officinalis* L. (*Calenduleae*) were used as outgroups (Noyes & Rieseberg 1999; Funk & al. 2009).

The *psbA-trnH* sequences included 18 accessions representing six genera and 15 species, with 15 accessions newly sequenced (all from Iran) and three obtained from GenBank. *Galatella litvinovii* Novopokr. (*Bellidinae*) was used as an outgroup.

Leaf samples were obtained from specimens in the following herbaria in Iran (herbarium codes according to Thiers 2015+): Ferdowsi University, Mashhad (FUMH), Research Institute of Forests and Rangelands, Tehran (TARI), Tehran University (TUH) and Shahid Bahonar University, Kerman. Respective voucher information and GenBank accession numbers are listed in the Appendix.

DNA extraction, amplification and sequencing

Genomic DNA was extracted using the modified CTAB protocol of Doyle & Doyle (1987). Sodium metabisulfite (1% w/v) was added to the DNA isolation buffer. The entire nrDNA ITS (ITS1–5.8S–ITS2) region was amplified by polymerase chain reaction (PCR) using either the universal primers AB101 and AB102 (Douzery & al. 1999) or ITS5m (Sang & al. 1995) and ITS4 (White & al. 1990). The *psbA-trnH* region was amplified using the *psbA* (Sang & al. 1997) and *trnH* (Tate & Simpson 2003) primers.

The PCR was performed in a 25 µL volume, containing 10 µL deionized water, 10× PCR Buffer with 1.5 mmol/L MgCl₂ (Roche Diagnostics, Canada), 10 µmol/L of each dNTP, 0.5 µL of each primer (10 pmol/µL), 2.5%–5% DMSO, one unit of *Taq* DNA polymerase and 1 µL template DNA (20–70 ng).

PCR procedures for the nrDNA ITS region were 2:30 min at 94 °C for predenaturation, followed by 35–37 cycles of 94 °C for 1 min, 51–58 °C for 1 min, and 72 °C for 1 min plus a final extension of 72 °C for 7 min. For the *psbA-trnH* region, the PCR conditions were 2:30 min at 94 °C for predenaturation, followed by 35–37 cycles of 94 °C for 45s, 58 °C for 40s, and 72 °C for 1–1:10 min plus a final extension of 72 °C for 7 min. The quality of PCR products was checked by electrophoresis on a 1% (w/v) agarose gel (using 1X TBE as the gel buffer) stained with ethidium bromide and then visualized under UV light. Amplified products were cleaned. Cleaned products were sequenced using the Bigdye terminator cycle sequencing ready reaction kit (Applied Biosystems, U.S.A.) with the appropriate primers in an ABI Prism 3730xl DNA sequencer (Applied Biosystems, U.S.A.).

Sequence alignment

Sequences were edited using BioEdit v. 7.0.5.3 (Hall 1999). Matrices were aligned initially using MUSCLE (Edgar 2004) and subsequently edited manually. Insertions and deletions (indels) were observed in all alignments and treated as missing data.

Table 1. Dataset and tree statistics from analyses of nuclear and chloroplast regions.

| | nrDNA ITS | cpDNA <i>psbA-trnH</i> |
|----------------|--------------|---------------------------|
| Sequences(n) | 142 | 18 |
| CI of MPTs | 0.333 | 0.938 |
| RI of MPTs | 0.669 | 0.960 |
| Number of MPTs | 2181 | 66 |
| Length of MPTs | 2371 | 16 |

Phylogenetic analyses

Maximum parsimony — Maximum parsimony analyses were conducted using PAUP* version 4.0b10 (Swofford 2002). The heuristic search option was employed with the following options: MulTrees, tree bisection reconnection (TBR) branch swapping with 100 random addition sequence replicates, and a maximum of 10 000 trees retained.

To evaluate clade support, a bootstrap analysis was performed using a full heuristic search with 1000 replicates (Felsenstein 1985), each with simple addition sequence and TBR branch swapping, and a maximum of 100 trees retained per replicate.

Bayesian method — The most appropriate model and parameter estimates for Bayesian analyses were selected using the program MrModeltest version 2.0 (Nylander 2004) based on the Akaike information criterion (AIC) (Posada & Buckley 2004). On the basis of the Modeltest results, datasets were analysed using the GTR+I+G model for nrDNA ITS and F81+G model for *psbA-trnH* sequences.

Bayesian analysis was performed using MrBayes 3.1.2 (Ronquist & Huelsenbeck 2003). The analysis was carried out with 10 million generations for ITS and 4 million generations for *psbA-trnH*, using the Markov chain Monte Carlo search. MrBayes performed two simultaneous analyses starting from different random trees (Nruns=2) each with four Markov chains and trees sampled at every 100 generations. The first 25 % of trees were discarded as the burn-in. The remaining trees were then used to build a 50 % majority rule consensus tree accompanied with posterior probability values. Tree visualization was carried out using Tree ViewX version 0.5.0 (Page 2005).

Maximum likelihood method — Maximum likelihood analyses were performed for the datasets in raxmlGUI v. 1.3. (Silvestro & Michalak 2012). The model employed for each dataset is the same as that for Bayesian analyses. Parametric bootstrap values for maximum likelihood were calculated in raxmlGUI base on 1000 replicates with one search replicate per bootstrap replicate.

Results

Characterization of nucleotide data

The aligned ITS matrix comprises 142 sequences and 678 characters, including 350 (350/678=52 %) potentially parsimony-informative sites and 328 parsimony-uninformative ones.

For the *psbA-trnH* region, the matrix of 18 sequences contains 356 characters, of which 11 are potentially parsimony-informative sites and 345 are parsimony-uninformative. More information about the datasets and tree statistics from analyses of the nuclear and chloroplast regions is summarized in Table 1.

Phylogenetic analyses

ITS phylogeny (Fig. 1A & B)

Maximum parsimony, maximum likelihood and Bayesian methods gave very similar results. We here show only Bayesian trees along with posterior probability (PP) and bootstrap values from both maximum likelihood (LBS) and maximum parsimony (PBS) analyses. The *Astereae* form a monophyletic group (PP=1.00, LBS=93, PBS=93). The S African genus *Printzia* is sister to all other *Astereae*, followed by the Chinese genus *Nannoglottis*, which is sister to the remaining *Astereae* (PP=1.00, LBS=98, PBS=79). The following clades are successively recovered along the spine of the Bayesian tree: (1) the S African *Mairia* Nees and the New Zealand-paleo-South American clade (PP=0.79); (2) the African clade, the subtribe *Homochrominae* including *Commidendrum robustum* (Roxb.) DC., which is sister to *Amellus strigosus* (Thunb.) Less. and *Felicia aethiopica* (Burm. f.) Grau (PP=1.00, LBS=78, PBS=85); and (3) and a clade (PP=1.00, LBS=89, PBS=79) comprising the remaining *Astereae*. Within (3), the African *Conyza gouanii* (L.) Willd. and *Lachnophyllum noeanum* Boiss. are successive sisters to an unresolved polytomy of the African-S Asian subtribe *Grangeinae*, the Mediterranean-Eurasian *Bellidinae* (sensu Brouillet & al.), C Asian taxa including *Chamaegeron* and *Lachnophyllum gossypinum* Bunge, and a large polytomic clade comprising *Aster bachtiaricus* Mozaff. and the Australasian, South American and North American clades.

Dichrocephala integrifolia (L. f.) Kuntze is sister to *Grangea maderaspatana* (L.) Poir., *Nidorella polyccephala* DC. and *N. resedifolia* DC. (PP=1.00, LBS=93, PBS=79). *Crintina*, *Galatella* and *Tripolium* constitute a well-supported clade (PP=1.00, LBS=100, PBS=97), which is sister to *Bellis annua* L. and *B. perennis* L., this relationship being moderately supported (PP=1.00, LBS=54). *Chamaegeron* and *Lachnophyllum gossypinum* form a moderately supported clade (PP=0.95, PBS=66), which is sister to a clade comprising *Bellis* and the *Galatella* group (PP=0.51). *Aster bachtiaricus* is allied with the large polytomy at the crown of the *Astereae*

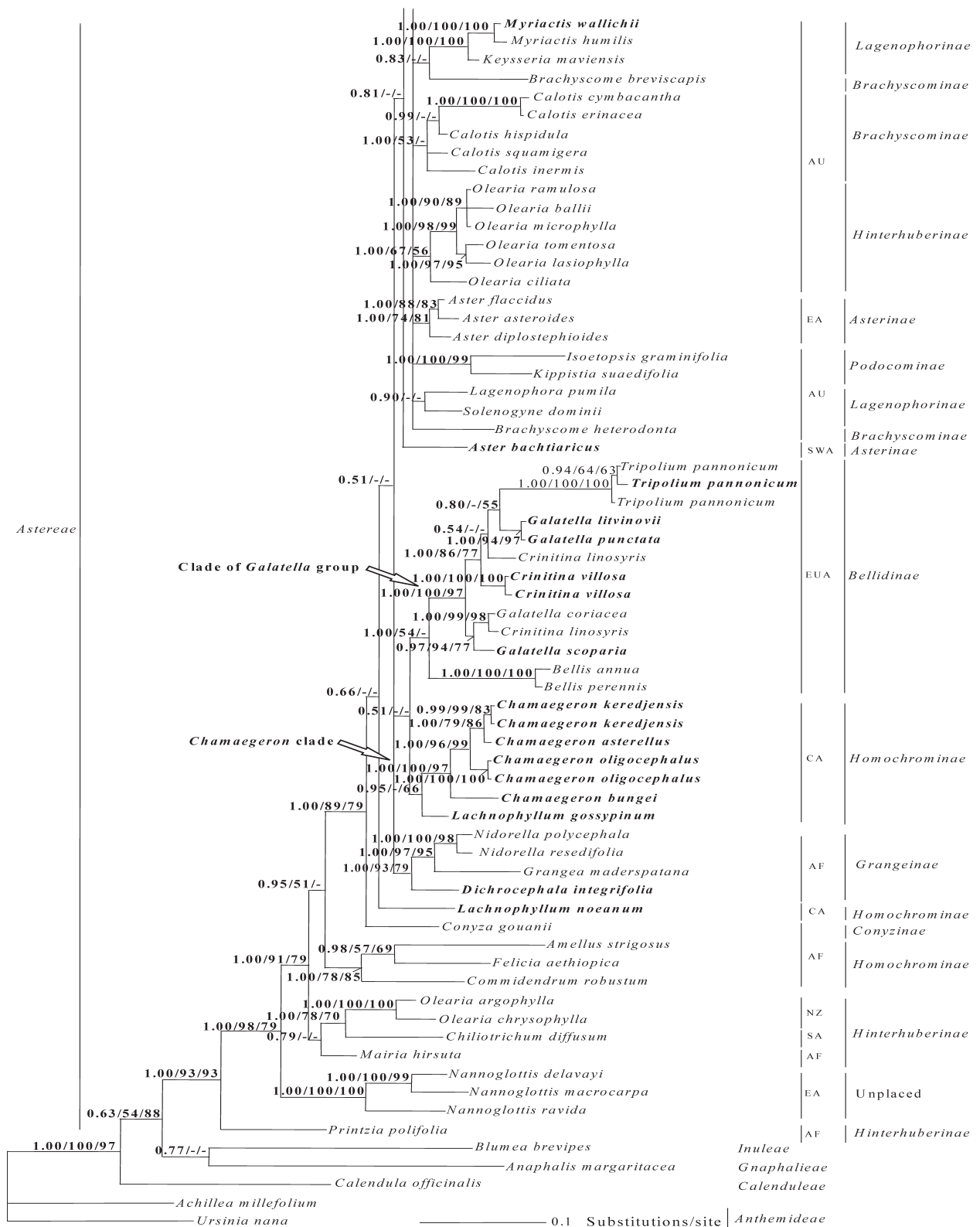


Fig. 1A. Fifty percent majority rule consensus tree resulting from Bayesian analysis of nrDNA ITS dataset. Lower half of tree. Numbers above branches are posterior probability (PP) and bootstrap values from maximum likelihood (LBS) and maximum parsimony (PBS) analyses, respectively. Values <50% are not shown. Region of origin: AF = Africa; AU = Australia; CA = Central Asia; EA = East Asia; EUA = Eurasia; NA = North America; NAF = North Africa; NZ = New Zealand; SA = South America; SWA = Southwest Asia.

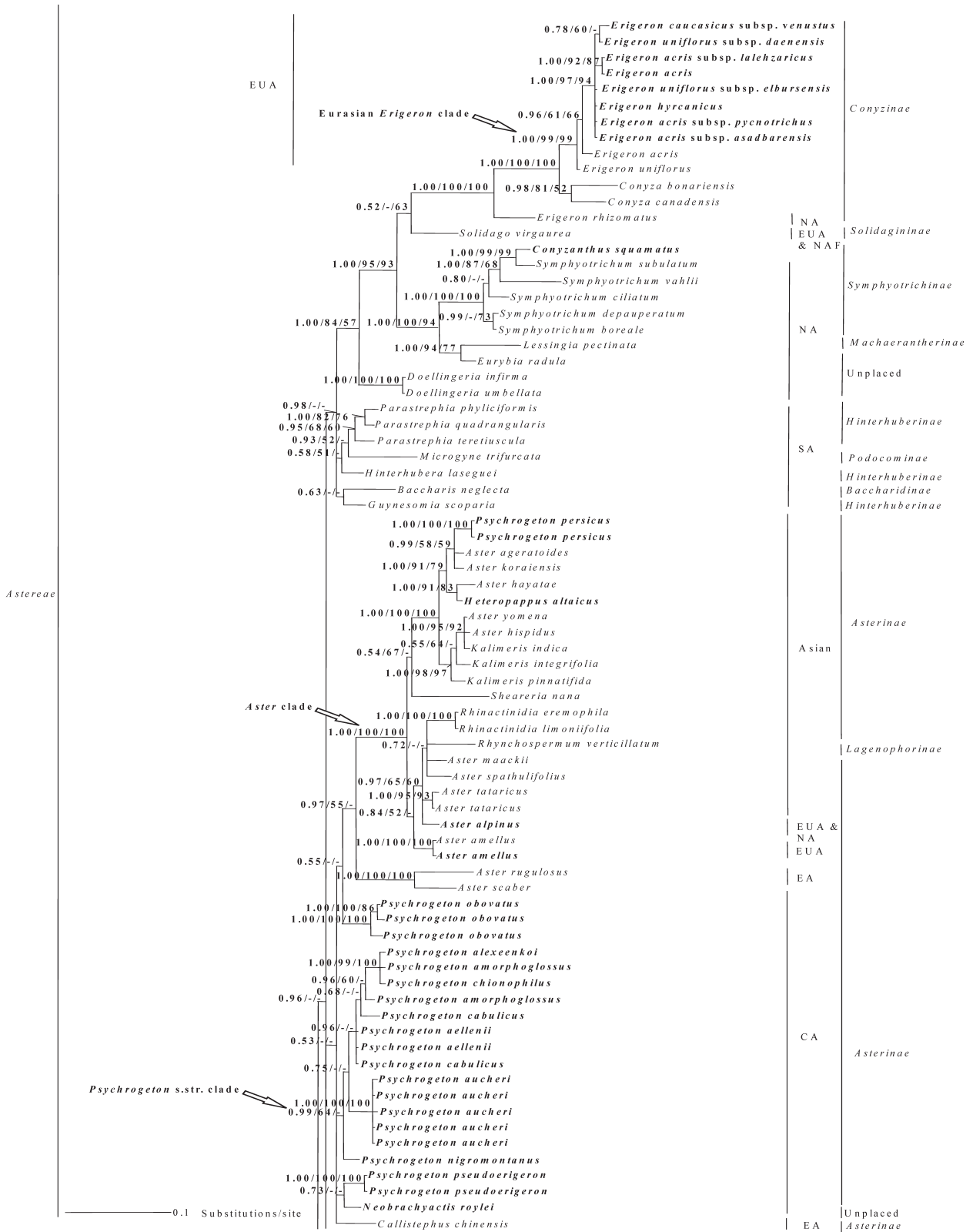


Fig. 1B. Fifty percent majority rule consensus tree resulting from Bayesian analysis of nrDNA ITS dataset. Upper half of tree. For explanation see Fig. 1A.

(PP=0.96). *Myriactis wallichii* Less. is sister to *M. humilis* Merr. (PP=1.00, LBS=100, PBS=100); they form a strongly supported clade with *Keysseria maviensis* (H. Mann.) Cabrera (PP=1.00, LBS=100, PBS=100). The C Asian clade includes *Psychrogeton* species (excluding *P. obovatus* (Benth.) Grierson, *P. persicus* (Boiss.) Grierson and *P. pseudoerigeron* (Bunge) Novopokr. ex Nevski) and is moderately supported (PP=0.99, LBS=64) by the ITS analyses. The three accessions of *P. obovatus* form a well-supported clade (PP=1.00, LBS=100, PBS=100), which is sister to the *Aster* clade (PP=0.55). The two accessions of *P. pseudoerigeron* are closely related to *Neobrachyactis roylei* (PP=0.73). *Aster ageratoides* Turcz., *A. koraiensis* Nakai and *P. persicus* form an unresolved subclade (PP= 0.99, LBS=58, PBS=59), which is sister to the subclade of *A. hayatae* H. Lév. & Vaniot and *Heteropappus altaicus* (Willd.) Novopokr. *Conyzanthus squamatus* is nested within *Symphotrichum*. *Erigeron acris* L. and subspecies, *E. caucasicus* subsp. *venustus* (Botsch.) Grierson, *E. hyrcanicus* Bornm. & Vierh. and *E. uniflorus* L. and subspecies form a strongly supported clade (PP=1.00, LBS=99, PBS=99).

psbA-trnH phylogeny (Fig. 2)

Neither the subtribe *Asterinae* sensu Nesom & Robinson (2007) nor sensu Brouillet & al. (2009a) seems to be monophyletic. *Aster*, *Galatella*, *Psychrogeton*, *Solidago* and *Tripolium* form an unresolved clade (PP=0.96, LBS=74, PBS=72). The phylogram includes: (1) *Aster bachtiaricus*; (2) *Psychrogeton nigromontanus* (Boiss. & Buhse) Grierson; (3) the *Erigeron* clade (PP=0.96, LBS=66, PBS=73), comprising *E. annuus* (L.) Pers. and *E. strigosus* Muhl. ex Willd.; (4) the clade comprising *Solidago gigantea* Aiton as sister to *Aster alpinus* L. and *Psychrogeton persicus* (PP=0.71, LBS=66, PBS=61); (5) the *Psychrogeton* clade (PP=0.99, LBS=83, PBS=83), in which the species occupy unresolved positions; and (6) the *Tripolium*–*Psychrogeton obovatus* clade (PP=0.69, PBS=66).

Discussion

The nrDNA ITS tree for the *Astereae* in the present study (Fig. 1A & B) is topologically similar to that of Brouillet & al. (2009a). We sequenced and analysed several Asiatic taxa that were not included in that study. In contrast to that study, the Eurasian subtribe *Bellidinae* is sister to the *Chamaeeron*–*Lachnophyllum gossypinum* clade rather than to the *Grangeinae*. Also, an assemblage of Asian species of *Aster* and allies, the so-called *Aster* clade (Li & al. 2012), is in the large polytomy at the crown of the *Astereae*, but it does not group with any of the Australian or Asian species of the Australasian lineages. This is in agreement with the nrDNA ITS study of Li & al. (2012).

In the current analysis, the SW Asian representatives of the *Astereae* are generally divided into two groups:

(1) representatives that are outside the crown lineages and are the first lineage to diverge after the *Grangeinae*, including *Chamaeeron*, *Dichrocephala integrifolia*, the *Galatella* group (or *Bellidinae* of Brouillet & al. 2009a, b), *Lachnophyllum gossypinum* and *L. noeanum*; and (2) representatives that are part of the large polytomy at the crown of the tribe, e.g. *Aster*, *Heteropappus*, *Myriactis*, *Neobrachyactis* and *Psychrogeton* occurring in the Australasian polytomy, and the other representatives, e.g. *Conyzanthus* and *Erigeron* (including two species of *Conyza*) nested in the North American clade. Below we examine the status of these genera within the *Astereae* in further detail.

The first genera derived after the African lineage

Lachnophyllum — This is a small C and SW Asian genus of two species (Nesom & Robinson 2007). The genus is characterized by recurved ray flowers and often lanate, long hairs and stipitate glands. The nrDNA ITS data did not support a close relationship between them. *Lachnophyllum gossypinum* is closely allied with *Chamaeeron* (see below), whereas *L. noeanum* appears in an isolated position above *Conyza gouanii*, as sister to an unresolved polytomy of the African subtribe *Grangeinae*, Mediterranean–Eurasian *Bellidinae* (sensu Brouillet & al. 2009a, 2009b), C Asian taxa including *Chamaeeron* and *Lachnophyllum gossypinum* and the large polytomic clade comprising *Aster bachtiaricus* and the Australasian–Asian, South American and North American clades (PP=0.66).

Chamaeeron — This includes four species distributed in C Asia, Iran, Afghanistan and Pakistan. With the exception of *Chamaeeron oligocephalus* Schrenk, the species are endemic to Iran, i.e. *C. asterellus* (Bornm.) Botsch., *C. bungei* (Boiss.) Botsch. and *C. keredjensis* (Bornm. & Gauba) Grierson. *Chamaeeron* has distinctive characters, is glabrous or pubescent with branching habit and basally connate pappus bristles falling as a unit. The *Chamaeeron* clade is strongly supported in the ITS tree (PP=1.00, LBS=100, PBS=97). *Chamaeeron bungei* is the basal species and is characterized by one series of ray florets and obovate leaves that are covered by hirsute and glandular hairs. It is followed by the clade consisting of *C. asterellus*, *C. keredjensis* and *C. oligocephalus* (PP=1.00, LBS=96, PBS=99). This clade is, in turn, divided into two subclades: (1) a subclade of two accessions of *C. oligocephalus* (PP=1.00, LBS=100, PBS=100); and (2) a subclade including *C. asterellus* as sister to two accessions of *C. keredjensis* (PP=1.00, LBS=79, PBS=86). *Chamaeeron asterellus* and *C. keredjensis* are covered by glandular, villous and hirsute hairs, whereas *C. oligocephalus* is glabrous.

***Galatella* group** — According to Nesom (1994), the *Galatella* group includes *Crintina*, *Galatella* and *Tripolium*. They constitute a well-supported clade in the ITS

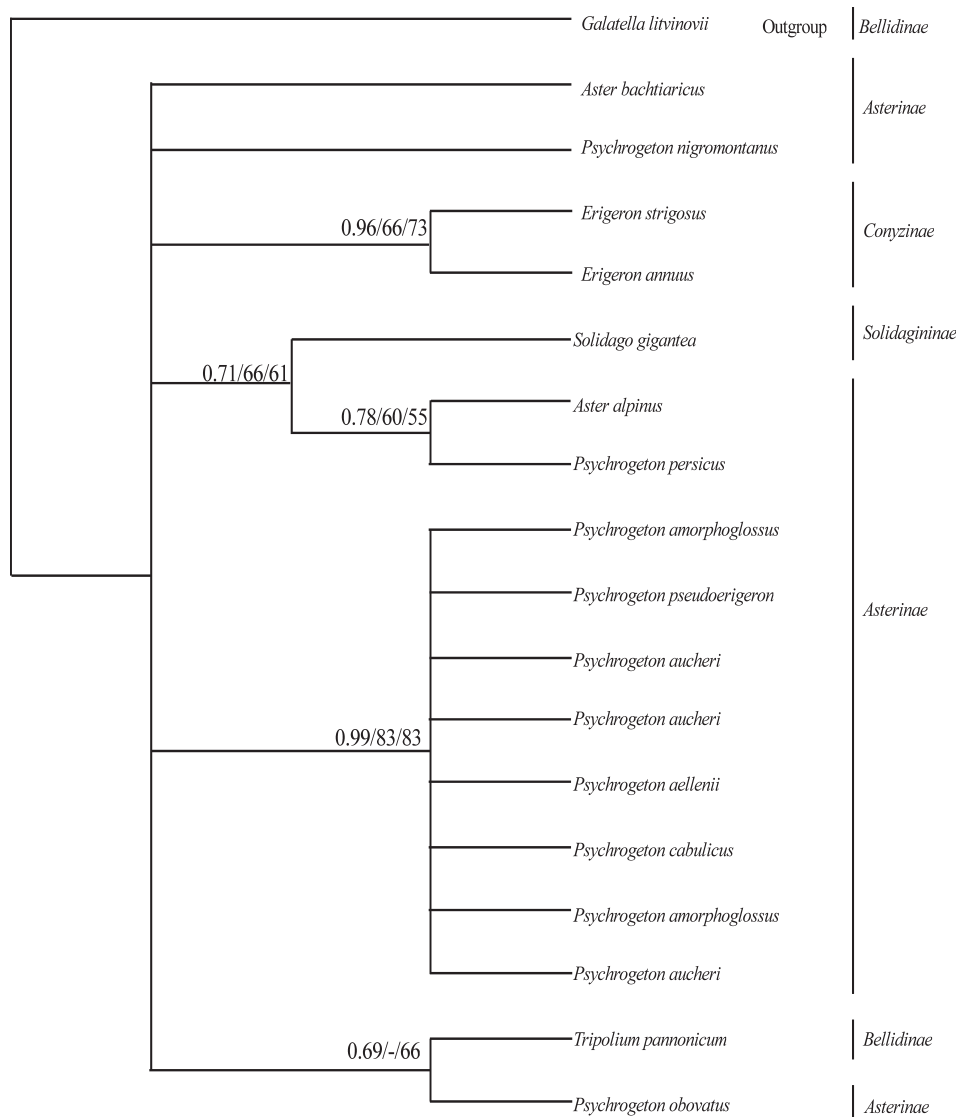


Fig. 2. Fifty percent majority rule consensus tree resulting from Bayesian analysis of plastid *psbA-trnH* dataset. Numbers above branches are posterior probability (PP) and bootstrap values from maximum likelihood (LBS) and maximum parsimony (PBS) analyses, respectively. Values <50% are not shown.

tree (PP=1.00, LBS=100, PBS=97). The present analysis is in agreement with the previous studies (Fiz & al. 2002; Brouillet & al. 2009a, 2009b; Li & al. 2012) regarding the sister-group relationship of the *Galatella* group with the Euro-Mediterranean genus *Bellis* (*B. annua* and *B. perennis*). Brouillet & al. (2009a) pointed out that *Crinitina*, *Galatella* and *Tripolium* should be included in *Bellidinae* rather than in *Asterinae*, which is also consistent with our analyses. The *Galatella* group comprises two well-supported subclades: (1) a subclade including *G. scoparia* (Kar. & Kir.) Novopokr. from Kazakhstan and two sister taxa, *C. linosyris* (L.) Soják and *G. coriacea* Novopokr.; and (2) a subclade comprising *C. linosyris*, *C. villosa* (L.) Soják, *Galatella litvinovii*, *G. punctata* (Waldst. & Kit.) Nees and *T. pannonicum* (Jacq.) Dobrocz.

Galatella is composed of 30 species (Nesom & Robinson 2007) and, as currently understood, the genus is not

monophyletic. *Crinitina* is a small genus of 13 species (Nesom & Robinson 2007). The nrDNA ITS data show that *Crinitina* is also not monophyletic. Two accessions of *C. linosyris* were placed in two different subclades within the group, and were not allied with the congeneric *C. villosa*. It is worth noting that two ITS accessions of *C. linosyris* obtained from GenBank (DQ478987 and AF046949), determined by Karaman-Castro & Urbatsch (2009) and Noyes & Rieseberg (1999), respectively, are completely different from each other and placed in different subclades. Therefore, it appears that one of these accessions may be misidentified. *Crinitina villosa* is similar to *Galatella scoparia* in having yellow discoid capitula. The two accessions of *C. villosa* were not united, however, with *G. scoparia*.

Tripolium is a unispecific genus growing in salt-marshes, salt-marsh meadows and moist meadows across Europe and N Asia to America

(Tamamschjan 1959; Nesom 1994). Nesom (1994) and Brouillet & al. (2009a, 2009b) noted the morphological similarities of *Tripolium* (including its distinctly corymboid capitulescence, herbaceous, broadly rounded, multinervate phyllaries, and tendency for raylessness) to *Crinitina* and *Galatella* and suggested that these taxa may be closely related. Our results support their hypothesis.

Dichrocephala — This contains ten species occurring in Africa and tropical countries according to Nesom & Robinson (2007), who defined it as a member of the *Grangeinae*. *Dichrocephala integrifolia* is characterized by lyrate-pinnatifid leaves and achenes without a pappus. It is allied with *Grangea maderaspatana* and the two species of *Nidorella* in the *Grangeinae*. In the present study, the inclusion of *Chamaegeron* and *Lachnophyllum* showed

that the *Bellidinae* (including the Euro-Mediterranean genus *Bellis* and the Eurasian *Galatella* group) are not sister to the African *Grangeinae*, which disagrees with a previous study (Brouillet & al. 2009b).

Genera belonging to the large crown polytomy of the tribe

Psychrogeton — This includes 20 species from Asia (Grierson 1967; Grierson & Rechinger 1982; Nesom & Robinson 2007). Grierson (1967) recognized *Psychrogeton* as an isolated genus due to the sterile (functionally male) disc achenes. However, two species (*P. chionophilus* (Boiss.) Krasch. and *P. obovatus*) represent exceptions in that the disc florets appear to be fertile. Grierson indicated Pamir-Hindu Kush as the likely biodiversity centre of *Psychrogeton*, with dispersal occurring from there to C Asia, Afghanistan, Iran, NE Iraq, E Turkey and NE Syria. Both the ITS and *psbA-trnH* analyses do not support the monophyly of *Psychrogeton*. In the ITS tree, all species except *P. obovatus*, *P. persicus* and *P. pseudoerigeron* formed a clade (*Psychrogeton* s.str.). *Psychrogeton obovatus* is sister to the *Aster* clade. This species is one of the most isolated species of the genus (Grierson & Rechinger 1982). It is characterized by leaf-like outer involucre bracts, obovate disc achenes (fertile) and coarsely toothed leaves, which are similar to those of *Aster* species. *Psychrogeton persicus*, represented by two accessions, along with *Aster ageratoides* and *A. koraiensis*, is deeply nested within the *Aster* clade. *Psychrogeton pseudoerigeron* is closely related to *Neobrachyactis roylei*. These species have similar geographical distributions and habitats. However, *Neobrachyactis* differs from *P. pseudoerigeron* in being an annual and having fertile disc florets. In addition, the numerous highly reduced ray florets of *Neobrachyactis* contrast with those of *P. pseudoerigeron*, which are much longer than the pappus. *Psychrogeton* s.str. is composed of three lineages. First, *P. nigromontanus* is sister to the remaining species (PP=0.99, LBS=64). It differs from the other taller species (e.g. *P. aucheri* (DC.) Grierson and *P. pseudoerigeron*) in its numerous obliquely cut tubular female ray florets with the corolla $\frac{1}{2}$ – $\frac{2}{3}$ as long as the style. The second lineage is *P. aucheri*, represented here by five accessions. It is characterized by a 2-seriate pappus and ray-floret corollas as long as the style. The third lineage comprises five species: *P. aellenii* (Rech. f.) Grierson, *P. alexeenkoi* Krasch., *P. amorphoglossus* (Boiss.) Novopokr., *P. cabulicus* Boiss. and *P. chionophilus*. Different accessions of *P. aellenii*, *P. amorphoglossus* and *P. cabulicus* did not cluster together. There were some single-nucleotide polymorphisms between the accessions of these species, maybe caused by hybridization. We analysed two accessions of *P. amorphoglossus* and *P. cabulicus* that had morphological differences (e.g. shape of leaves and density of hairs). The separation of *P. amorphoglossus* accessions in different clades can be evidence of hybridization. Considering the

great diversity in chromosome numbers and ploidy levels in the *Astereae* (Ito & al. 1994; Brouillet & al. 2009a), it is possible that there are both diploid and polyploid populations for *P. amorphoglossus* and *P. cabulicus*. One accession of *P. cabulicus* is sister to *P. amorphoglossus* and an unresolved subclade of *P. alexeenkoi*, *P. amorphoglossus* and *P. chionophilus*. The latter three species are caespitose and monocephalous and restricted to C to S Iran.

The *psbA-trnH* analysis (Fig. 2) showed that *P. aellenii*, *P. amorphoglossus*, *P. aucheri*, *P. cabulicus* and *P. pseudoerigeron* form a well-supported clade (PP=0.99, LBS=83, PBS=83). However, *P. nigromontanus* occupies an unresolved position, and *P. obovatus*, as in the ITS tree, is distinct from other *Psychrogeton* species. Chloroplast data show a relationship between *P. persicus* and *Aster alpinus* (PP=0.78, LBS=60, PBS=55).

Asian *Aster* and allies — The ITS tree showed that the *Aster* clade did not group with any of the Australian (e.g. *Brachyscome* Cass., *Calotis* R. Br., *Isoetopsis* Turcz., *Keysseria* Lauterb., *Kippistia* F. Muell. and *Olearia* Moench) or Asian (*Myriactis*) species of the Australasian lineages, in agreement with the study of Li & al. (2012). Of 16 sampled species of *Aster* s.str., *A. asteroides* (DC.) Kuntze, *A. bachtiaricus*, *A. diplostephioides* (DC.) Benth. ex C. B. Clarke and *A. flaccidus* Bunge place in the lower half of the ITS tree (Fig. 1A) while the others place in the upper half of that tree (Fig. 1B). Considering the position of *Kalimeris* (Cass.) Cass., *Heteropappus altaicus* and *Psychrogeton persicus*, which are nested within the Eurasian *Aster* clade, our results confirm the hypothesis of Li & al. (2012) that Eurasian *Aster* is paraphyletic and polyphyletic.

Aster bachtiaricus, a woody perennial plant, is distinct from other *Aster* s.str. in the ITS tree and is isolated within the large polytomy at the crown of the *Astereae* (PP=0.96). It appears to be sister to the vast radiations that occurred in Australasia-Asia and in South and North America. On the *psbA-trnH* tree, *A. bachtiaricus* also has a distinct position and does not ally with *A. alpinus*.

Heteropappus — Molecular data support a close relationship between *Aster* s.str., *Heteropappus*, *Kalimeris*, *Rhinactinidia* Novopokr., *Rhynchospermum* Reinw. and *Sheareria* S. Moore, as has been found in previous studies (Ito & al. 1995, 1998; Noyes & Rieseberg 1999; Fiz & al. 2002; Brouillet & al. 2009a; Gao & al. 2009; Li & al. 2012). Previous studies (Ito & al. 1998; Li & al. 2012; Chen & al. 2011) showed that *Heteropappus* is embedded within *Aster*. Our ITS tree also supports the placement of *Heteropappus* in *Aster*. *Heteropappus altaicus* and *A. hayatae* form a subclade (PP=1.00, LBS=91, PBS=83) that is sister to the unresolved subclade including *A. ageratoides*, *A. koraiensis* and *Psychrogeton persicus* (PP=1.00, LBS=91, PBS=79).

Eurasian *Erigeron* — Grierson & Rechinger (1982) divided *Erigeron* into *E. subg. Erigeron* and *E. subg. Trimorpha* (Cass.) Popov. *Erigeron subg. Trimorpha* (including *E. acris*) with an intermediate series of eligulate female florets differs from *E. subg. Erigeron* (including *E. caucasicus* Steven, *E. hyrcanicus* and *E. uniflorus*) without this kind of intermediate florets. In the ITS tree, *Erigeron* forms a strongly supported clade. *Erigeron acris* subsp. *lalehzaricus* Rech. f. is sister to *E. acris*. *Erigeron caucasicus* subsp. *venustus* and *E. uniflorus* subsp. *daenensis* (Vierh.) Rech. f. form a moderately supported clade, but *E. acris* subsp. *asadbarensis* (Vierh.) Rech. f., *E. acris* subsp. *pyncnotrichus* (Vierh.) Grierson, *E. hyrcanicus* and *E. uniflorus* subsp. *elbursensis* (Boiss.) Rech. f. occupy unresolved positions. *Erigeron uniflorus* (AF046988) and *E. acris* (AF118496), obtained from GenBank are successive sisters to the Eurasian *Erigeron* clade. It is noteworthy that some differences exist between the *E. acris* and *E. uniflorus* accessions obtained from GenBank and those from Iran newly sequenced here. Despite the existence of morphological differences, there are no marked differences between the sequences of species that belong to *E. subg. Erigeron* and *E. subg. Trimorpha*. It has been suggested that a northern migration of *Erigeron* species from North America to Eurasia occurred during the Pleistocene when land bridges may have facilitated intercontinental migration (Huber & Leuchtmann 1992; Noyes 2000). The present study appears to support this hypothesis.

Conyzanthus — Nesom (1994) treated *Conyzanthus squamatus* as *Symphyotrichum squamatum* (Spreng.) G. L. Nesom. Nesom & Robinson (2007) included *Conyzanthus* within *Symphyotrichum subg. Symphyotrichum*. Our results confirm Nesom's view. In the ITS tree, *C. squamatus* is well nested with *Symphyotrichum* species. *Symphyotrichum squamatum* is sister to the other species introduced in Asia: *S. subulatum* (Michx.) G. L. Nesom. Considering the position of *S. ciliatum* and that the clade includes *S. squamatum* and *S. subulatum*, it seems that the species of *Symphyotrichum* migrated to Asia at least two distinct times.

Myriactis — The ITS tree shows a strong relationship between the currently analysed *Myriactis wallichii* and the Australian representative, *M. humilis* (PP=1.00, LBS=100, PBS=100). Morphological characters, including campanulate heads and absent pappus, seem to confirm the relationships.

Conclusions

It appears that, due to the level of homoplasy and many parallel mutations in the ITS dataset, we observe polytomies and low resolution in the respective tree.

The SW Asian representatives of the *Astereae* used in this study form two main groups in the ITS tree. One is composed of *Lachnophyllum*, *Chamaegeron* and the *Galatella* group near the base of the tree; the second comprises *Myriactis*, *Neobrachyactis*, *Psychrogeton*, *Aster*, *Heteropappus* and *Erigeron* as representatives of the large polytomy at the crown of the tree. The current study does not support the monophyly of *Aster*, *Galatella*, *Lachnophyllum* and *Psychrogeton* in their current status. *Aster bachtiaricus* seems to be excluded from *Aster*. More taxon sampling and DNA sequence data, especially of rapidly evolving genes, are definitely needed to get a clear-cut picture of phylogenetic relationships among some members of the tribe, in particular *Psychrogeton*.

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Appendix

The taxa included in the nrDNA ITS and *psbA-trnH* analyses are listed in this Appendix. For each sequence, a voucher or the source together with its GenBank accession number are cited. Herbarium codes are according to Thiers (2015+). A dash “–” indicates that a sequence was not available in GenBank.

| Taxon | Voucher (new sequence in this study) | Source (sequence obtained from GenBank) | GenBank accession no. nrDNA ITS | GenBank accession no. cpDNA <i>psbA-trnH</i> |
|---|--|---|---------------------------------------|---|
| <i>Achillea millefolium</i> L. | | Noyes & Rieseberg (1999) | AF046939 | – |
| <i>Amellus strigosus</i> (Thunb.) Less. | | Noyes & Rieseberg (1999) | AF046942 | – |
| <i>Anaphalis margaritacea</i> (L.) Benth. & Hook. f. | | Noyes & Rieseberg (1999) | AF046937 | – |
| <i>Aster ageratoides</i> Turcz. | | Hong & al. (2012) | HQ154047 | – |
| <i>Aster alpinus</i> L. | Iran: <i>Wendelbo & Assadi</i> 27775 (TARI) | | LC027372 | LC027423 |
| <i>Aster amellus</i> L. | Turkey: <i>Davis 47617</i> (TARI) | | LC027373 | – |
| <i>Aster amellus</i> | | Noyes & Rieseberg (1999) | AF046961 | – |
| <i>Aster asteroides</i> (DC.) Kuntze | | Li & al. (2012) | JN543841 | – |
| <i>Aster bachtiaricus</i> Mozaff. | Iran: <i>Mozaffarian 57812</i> (TARI) | | LC027374 | LC027424 |
| <i>Aster diplostephioides</i> (DC.) Benth. ex C. B. Clarke | | Li & al. (2012) | JN543847 | – |
| <i>Aster flaccidus</i> Bunge | | Li & al. (2012) | JN543844 | – |
| <i>Aster hayatae</i> H. Lévl. & Vaniot | | Hong & al. (2012) | HQ154041 | – |
| <i>Aster hispidus</i> Thunb. | | Hong & al. (2012) | HQ154044 | – |
| <i>Aster koraiensis</i> Nakai | | Hong & al. (2012) | HQ154046 | – |
| <i>Aster maackii</i> Regel | | Hong & al. (2012) | HQ154042 | – |
| <i>Aster rugulosus</i> Maxim. | | Saito & al. (2007) | AB259330 | – |
| <i>Aster scaber</i> Thunb. | | Hong & al. (2012) | HQ154049 | – |
| <i>Aster spathulifolius</i> Maxim. | | Hong & al. (2012) | HQ154050 | – |
| <i>Aster tataricus</i> L. f. | | Chen & Han (unpublished) | FJ980359 | – |
| <i>Aster tataricus</i> | | Hong & al. (2012) | HQ154046 | – |
| <i>Aster yomena</i> (Kitam.) Honda | | Hong & al. (2012) | HQ154048 | – |
| <i>Baccharis neglecta</i> Britton | | Morgan (1997) | U97604 | – |
| <i>Bellis annua</i> L. | | Fiz & al. (2002) | AF490579 | – |
| <i>Bellis perennis</i> L. | | Noyes & Rieseberg (1999) | AF046950 | – |
| <i>Blumea brevipes</i> (Oliv. & Hiern.) Wild | | Noyes & Rieseberg (1999) | AF046936 | – |
| <i>Brachyscome breviscapis</i> C. R. Carter | | Shimamura & Watanabe (unpublished) | AB435100 | – |
| <i>Brachyscome heterodonta</i> DC. | | Noyes & Rieseberg (1999) | AF046955 | – |
| <i>Calendula officinalis</i> L. | | Noyes & Rieseberg (1999) | AF046938 | – |
| <i>Callistephus chinensis</i> (L.) Nees | | Brouillet & al. (2009b) | FJ457947 | – |
| <i>Calotis cymbacantha</i> F. Muell. | | Watanabe & al. (2006) | AB196610 | – |
| <i>Calotis erinacea</i> Steetz | | Watanabe & al. (2006) | AB196609 | – |
| <i>Calotis hispidula</i> (F. Muell.) F. Muell. | | Watanabe & al. (2006) | AB196597 | – |
| <i>Calotis inermis</i> Maiden & Betche | | Watanabe & al. (2006) | AB196599 | – |
| <i>Calotis squamigera</i> C. T. White | | Watanabe & al. (2006) | AB196598 | – |
| <i>Chamaegeron asterellus</i> (Bornm.) Botsch. | Iran: <i>Mirtadzadini 1234</i> (Shahid Bahonar Univer- sity of Kerman) | | LC027375 | – |
| <i>Chamaegeron bungei</i> (Boiss.) Botsch. | Iran: <i>Faghihinia & Hojjat</i> 27968 (FUMH) | | LC027376 | – |
| <i>Chamaegeron keredjensis</i> (Bornm. & Gaub) Grierson | Iran: <i>Assadi & Akhani</i> 61185 (TARI) | | LC027378 | – |
| <i>Chamaegeron keredjensis</i> | Iran: <i>Bothmer & Buttler</i> 1927 (TARI) | | LC027377 | – |
| <i>Chamaegeron oligocephalus</i> Schrenk | Iran: <i>Ayatollahi & Zan- goei 14922</i> (FUMH) | | LC027380 | – |

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|---|--|---|---------------------------------------|---|
| <i>Chamaegeron oligocephalus</i> | Iran: <i>Emadzadeh & al.</i> 37036 (FUMH) | | LC027379 | – |
| <i>Chilotrimum diffusum</i> (G. Forst.) Kuntze | | Noyes & Rieseberg (1999) | AF046945 | – |
| <i>Commidendrum robustum</i> (Roxb.) DC. | | Noyes & Rieseberg (1999) | AF046943 | – |
| <i>Conyza bonariensis</i> (L.) Cronquist | | Noyes (2000) | AF118513 | – |
| <i>Conyza canadensis</i> (L.) Cronquist | | Noyes & Rieseberg (1999) | AF046987 | – |
| <i>Conyza gouanii</i> (L.) Willd. | | Noyes & Rieseberg (1999) | AF046948 | – |
| <i>Conyzanthus squamatus</i> (Spreng.) Tamamsch. (<i>Symphotrichum squa-</i> <i>matum</i> (Spreng.) G. L. Nesom) | Iran: <i>Akramian 38407</i> (FUMH) | | LC027381 | – |
| <i>Crinitina linosyris</i> (L.) Soják | | Noyes & Rieseberg (1999) | AF046949 | – |
| <i>Crinitina linosyris</i> | | Karaman-Castro & Urbatsch (2009) | DQ478987 | – |
| <i>Crinitina villosa</i> (L.) Soják | Turkey: <i>Davis & Hedge</i> 32617 (TARI) | | LC027382 | – |
| <i>Crinitina villosa</i> | Iran: <i>Zehzad & Farbodnia</i> 4018 (TARI) | | LC027383 | – |
| <i>Dichrocephala integrifolia</i> (L. f.) Kuntze | Iran: <i>Bazghandi 34389</i> (FUMH) | | LC027384 | – |
| <i>Doellingeria infirma</i> (Michx.) Greene | | Selliah & Brouillet (2008) | EU200188 | – |
| <i>Doellingeria umbellata</i> (Mill.) Nees | | Noyes & Rieseberg (1999) | AF046966 | – |
| <i>Erigeron acris</i> L. | Iran: <i>Joharchi & Beh-</i> <i>roozian 44170</i> (FUMH) | | LC027385 | – |
| <i>Erigeron acris</i> | | Noyes (2000) | AF118496 | – |
| <i>Erigeron acris</i> subsp. <i>asadbarensis</i> (Vierh.) Rech. f. | Iran: <i>Assadi & Mozaffar-</i> <i>ian 33231</i> (TARI) | | LC027386 | – |
| <i>Erigeron acris</i> subsp. <i>lalehzaricus</i> Rech. f. | Iran: <i>Assadi 83177</i> (TARI) | | LC027387 | – |
| <i>Erigeron acris</i> subsp. <i>pycnotrichus</i> (Vierh.) Grierson | Iran: <i>Wendelbo & Assadi</i> 13317 (TARI) | | LC027388 | – |
| <i>Erigeron annuus</i> (L.) Pers. | | Schlaepfer & al. (2008) | – | EU337691 |
| <i>Erigeron caucasicus</i> subsp. <i>venustus</i> (Botsch.) Grierson | Iran: <i>Mozaffarian 87576</i> (TARI) | | LC027389 | – |
| <i>Erigeron hircanicus</i> Bornm. & Vierh. | Iran: <i>Assadi & Maassoumi</i> 51232 (TARI) | | LC027390 | – |
| <i>Erigeron rhizomatus</i> Cronquist | | Noyes & Rieseberg (1999) | AF046992 | – |
| <i>Erigeron strigosus</i> Muhl. ex Willd. | | Burgess & al. (2011) | – | HQ596691 |
| <i>Erigeron uniflorus</i> L. | | Noyes & Rieseberg (1999) | AF046988 | – |
| <i>Erigeron uniflorus</i> subsp. <i>daenensis</i> (Vierh.) Rech. f. | Iran: <i>Mozaffarian 58164</i> (TARI) | | LC027391 | – |
| <i>Erigeron uniflorus</i> subsp. <i>elbursensis</i> (Boiss.) Rech. f. | Iran: <i>Mozaffarian 66259</i> (TARI) | | LC027392 | – |
| <i>Eurybia radula</i> (Aiton) G. L. Nesom | | Selliah & Brouillet (2008) | EU200207 | – |
| <i>Felicia aethiopica</i> (Burm. f.) Grau | | Noyes & Rieseberg (1999) | AF046941 | – |
| <i>Galatella coriacea</i> Novopokr. | | Fiz & al. (2002) | AF494003 | – |
| <i>Galatella litvinovii</i> Novopokr. | Iran: <i>Zangoeei & Arj-</i> <i>mandi 39249</i> (FUMH) | | LC027393 | LC027425 |
| <i>Galatella punctata</i> (Waldst. & Kit.) Nees | Iran: <i>Ghahreman & Mo-</i> <i>zaffarian 17600</i> (TUH) | | LC027394 | – |
| <i>Galatella scoparia</i> (Kar. & Kir.) Novopokr. | Kazakhstan: <i>Krashninko</i> <i>& al. 3257</i> (TARI) | | LC027395 | – |
| <i>Grangea maderaspatana</i> (L.) Poir. | | Noyes & Rieseberg (1999) | AF046951 | – |
| <i>Guynesomia scoparia</i> (Phil.) Bonif. & G. Sancho | | Karaman-Castro & Urbatsch (2009) | DQ479035 | – |
| <i>Heteropappus altaicus</i> (Willd.) Novopokr. | Iran: <i>Joharchi 15545</i> (FUMH) | | LC027396 | – |
| <i>Hinterhubera laseguei</i> Wedd. | | Karaman-Castro & Urbatsch (2009) | DQ479015 | – |
| <i>Isoetopsis graminifolia</i> Turcz. | | Brouillet & al. (2009b) | GU226433 | – |
| <i>Kalimeris indica</i> (L.) Sch. Bip. | | Gao & al. (2010) | GU724288 | – |

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|--|--|---|---------------------------------------|---|
| <i>Kalimeris integrifolia</i> Turcz. ex DC. | | Noyes & Rieseberg (1999) | AF046960 | – |
| <i>Kalimeris pinnatifida</i> (Maxim.) Kitam. | | Karaman-Castro & Urbatsch (2009) | DQ478988 | – |
| <i>Keysseria maviensis</i> (H. Mann.) | | Karaman-Castro & Urbatsch (2009) | DQ479036 | – |
| <i>Kippistia suaedifolia</i> F. Muell. | | Cross & al. (2002) | AF497660 | – |
| <i>Lachnophyllum gossypinum</i> Bunge | Iran: <i>Faghihinia</i> 27848 (FUMH) | | LC027397 | – |
| <i>Lachnophyllum noeanum</i> Boiss. | Iran: <i>Fattahi & Mirabdali</i> 2783 (TARI) | | LC027398 | – |
| <i>Lagenophora pumila</i> (G. Forst.) Cheeseman | | Karaman-Castro & Urbatsch (2009) | DQ479037 | – |
| <i>Lessingia pectinata</i> Greene | | Markos & Baldwin (2001) | AF251598 | – |
| <i>Mairia hirsuta</i> DC. | | Brouillet & al. (2009b) | FJ457929 | – |
| <i>Microgyne trifurcata</i> Less. | | Sancho & Karaman-Castro (2008) | EF151482 | – |
| <i>Myriactis humilis</i> Merr. | | Noyes & Rieseberg (1999) | AF046959 | – |
| <i>Myriactis wallichii</i> Less. | Iran: <i>Zangoeei & Alvani</i> 15885 (FUMH) | | LC027399 | – |
| <i>Nannoglottis delavayi</i> (Franch.) Y. Ling & Y. L. Chen | | Liu & al. (2002) | AY017167 | – |
| <i>Nannoglottis macrocarpa</i> Y. Ling & Y. L. Chen | | Liu & al. (2002) | AY017166 | – |
| <i>Nannoglottis ravida</i> (C. Winkl.) Y. L. Chen | | Liu & al. (2002) | AY017160 | – |
| <i>Neobrachyactis roylei</i> (DC.) Brouillet | Iran: <i>Mirtadzadini</i> 1238 (Shahid Bahonar University of Kerman) | | LC027400 | – |
| <i>Nidorella polycephala</i> DC. | | Karaman-Castro & Urbatsch (2009) | DQ478999 | – |
| <i>Nidorella resedifolia</i> DC. | | Noyes & Rieseberg (1999) | AF046952 | – |
| <i>Olearia argophylla</i> (Labill.) F. Muell. ex Benth. | | Noyes & Rieseberg (1999) | AF046944 | – |
| <i>Olearia ballii</i> (F. Muell.) Hemsl. | | Cross & al. (2002) | AF497662 | – |
| <i>Olearia chrysophylla</i> Benth. | | Cross & al. (2002) | AF497710 | – |
| <i>Olearia ciliata</i> (Benth.) Benth. | | Cross & al. (2002) | AF497667 | – |
| <i>Olearia lasiophylla</i> Lander | | Cross & al. (2002) | AF497652 | – |
| <i>Olearia microphylla</i> (Vent.) Maiden & Betche | | Cross & al. (2002) | AF497671 | – |
| <i>Olearia ramulosa</i> (Labill.) Benth. | | Cross & al. (2002) | AF497681 | – |
| <i>Olearia tomentosa</i> (J. C. Wendl.) DC. | | Cross & al. (2002) | AF497650 | – |
| <i>Parastrephia phylliciformis</i> (Meyen) Cabrerá | | Karaman-Castro & Urbatsch (2009) | DQ479023 | – |
| <i>Parastrephia quadrangularis</i> (Meyen) Cabrerá | | Karaman-Castro & Urbatsch (2009) | DQ479024 | – |
| <i>Parastrephia teretiuscula</i> (Kuntze) Cabrerá | | Karaman-Castro & Urbatsch (2009) | DQ479026 | – |
| <i>Printzia polifolia</i> (L.) Hutch | | Brouillet & al. (2009b) | FJ457927 | – |
| <i>Psychrogeton aellenii</i> (Rech. f.) Grierson | Iran: <i>Hojjat & Zangoeei</i> 29239 (FUMH) | | LC027401 | LC027426 |
| <i>Psychrogeton aellenii</i> | Iran: <i>Rafeie & Zangoeei</i> 27396 (FUMH) | | LC027402 | – |
| <i>Psychrogeton alexeenkoi</i> Krasch. | Iran: <i>Assadi</i> 83200 (TARI) | | LC027403 | – |
| <i>Psychrogeton amorphoglossus</i> (Boiss.) Novopokr. | Iran: <i>Mozaffarian</i> 66260 (TARI) | | LC027404 | LC027427 |
| <i>Psychrogeton amorphoglossus</i> | Iran: <i>Mozaffarian & Assadi</i> 40873 (TARI) | | LC027405 | LC027428 |
| <i>Psychrogeton aucheri</i> (DC.) Grierson | Iran: <i>Assadi</i> 75131 (TARI) | | LC027409 | LC027429 |
| <i>Psychrogeton aucheri</i> | Iran: <i>Joharchi & Zangoeei</i> 15737 (FUMH) | | LC027406 | – |
| <i>Psychrogeton aucheri</i> | Iran: <i>Mozaffarian</i> 48524 (TARI) | | LC027410 | LC027431 |

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|---|---|--|--|--|
| <i>Psychrogeton aucheri</i> | Iran: Mozaffarian 58130 (TARI) | | LC027408 | LC027430 |
| <i>Psychrogeton aucheri</i> | Iran: Mozaffarian 64992 (TARI) | | LC027407 | – |
| <i>Psychrogeton cabulicus</i> Boiss. | Iran: Assadi & Mozaffarian 35757 (TARI) | | LC027412 | – |
| <i>Psychrogeton cabulicus</i> | Iran: Zangoeei & Hosseinzadeh 24477 (FUMH) | | LC027411 | LC027432 |
| <i>Psychrogeton chionophilus</i> (Boiss.) Krasch. | Iran: Safaian 245 (TARI) | | LC027413 | – |
| <i>Psychrogeton nigromontanus</i> (Boiss. & Buhse) Grierson | Iran: Bothmer & Buttler 1905 (TARI) | | LC027414 | LC027433 |
| <i>Psychrogeton obovatus</i> (Benth.) Grierson | Iran: Mirtadzadini 1200 (Shahid Bahonar University of Kerman) | | LC027417 | – |
| <i>Psychrogeton obovatus</i> | Iran: Mozaffarian 42160 (TARI) | | LC027415 | LC027434 |
| <i>Psychrogeton obovatus</i> | Iran: Mozaffarian 63877 (TARI) | | LC027416 | – |
| <i>Psychrogeton persicus</i> (Boiss.) Grierson | Iran: Joharchi 33846 (FUMH) | | LC027419 | – |
| <i>Psychrogeton persicus</i> | Iran: Mozaffarian 48643 (TARI) | | LC027418 | LC027435 |
| <i>Psychrogeton pseudoerigeron</i> (Bunge) Novopokr. ex Nevski | Iran: Edmonson 1288 (TARI) | | LC027420 | – |
| <i>Psychrogeton pseudoerigeron</i> | Iran: Rafei & al. 2608 (FUMH) | | LC027421 | LC027436 |
| <i>Rhinactinidia eremophila</i> (Bunge) Novopokr. ex Botsch | | Li & al. (2012) | JN543727 | – |
| <i>Rhinactinidia limoniifolia</i> (Less.) Novopokr. ex Botsch | | Li & al. (2012) | JN543724 | – |
| <i>Rhynchospermum verticillatum</i> Reinw. | | Fiz & al. (2002) | AF494001 | – |
| <i>Sheareria nana</i> S. Moore | | Gao & al. (2009) | AY572953 | – |
| <i>Solenogyne dominii</i> L. G. Adams | | Nakamura & al. (2012) | AB604758 | – |
| <i>Solidago gigantea</i> Aiton | | Schlaepfer & al. (2008) | – | EU337305 |
| <i>Solidago virgaurea</i> L. | | Schilling & al. (2008) | EU125378 | – |
| <i>Symphyotrichum boreale</i> (Torr. & A. Gray) Á. Löve & D. Löve | | Vaezi & Brouillet (2009) | EU781390 | – |
| <i>Symphyotrichum ciliatum</i> (Ledeb.) G. L. Nesom | | Vaezi & Brouillet (2009) | EU781410 | – |
| <i>Symphyotrichum depauperatum</i> (Fernald) G. L. Nesom | | Selliah & Brouillet (2008) | EU200226 | – |
| <i>Symphyotrichum subulatum</i> (Michx.) G. L. Nesom | | Vaezi & Brouillet (2009) | EU781409 | – |
| <i>Symphyotrichum vahlii</i> (Gaudich.) G. L. Nesom | | Eastwood & al. (2004) | AY193804 | – |
| <i>Tripolium pannonicum</i> (Jacq.) Dobroc. | Iran: Assadi & Akhani 61625 (TARI) | | LC027422 | LC027437 |
| <i>Tripolium pannonicum</i> | | Brouillet & al. (2009b) | FJ457946 | – |
| <i>Tripolium pannonicum</i> | | Hong & al. (2012) | HQ154043 | – |
| <i>Ursinia nana</i> DC. | | Noyes & Rieseberg (1999) | AF046940 | – |