

THE GENUS *ASTER* (ASTERACEAE) IN THE STRICTEST SENSE

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ABSTRACT

Aster amellus L. (the type of *Aster* L.), *A. indamellus* Grierson, and *A. aitchisonii* Boiss. appear to comprise a natural group, as suggested by Grierson in 1964 — this is *Aster* in the strictest sense. A taxonomic summary is given for these species and a lectotype is designated for *Aster pseudamellus* Hook. f. Among species sampled for DNA sequence data, the closest relative of *A. amellus* is *A. alpinus*, which shares production of woody rhizomes with the *A. amellus* trio. *Aster maackii* also is indicated by molecular data to be closely related but produces non-woody rhizomes.

The genus *Aster* in Eurasia is morphologically diverse and evolutionarily complex. Recent molecular-phylogenetic analyses have shed light on the evolutionary relationships of these species although many species are yet to be included in the sampling. The most significant analysis (including the greatest number of species) for understanding patterns has been that of Li et al. (2012) — subsequent studies have significantly added to the Li et al. data set (e.g., Jafari et al. 2015; Korolyuk et al. 2015; Zhang et al. 2015; Fu et al. 2019). A distinct pattern emerges and has been discussed in detail by Li et al.

In parallel with restructuring the subtribal taxonomy of Astereae (Nesom 2020a), I have initiated a revision of *Aster* taxonomy, recognizing new genera indicated by molecular data to be distinct, providing morphological characterizations, and using morphology to find related species not included in the molecular sampling. As with the subtribal taxonomy, and as always, these newly recognized genera are hypotheses to be tested by further sampling of species and analysis of morphological and molecular data.

Studies of Astereae and *Aster* have been done over the spring and summer of 2020, using pertinent literature and online images available through JSTOR and various herbaria and consortia that post specimen images and related information. Details of trichomes and florets are difficult to observe but packet dissections sometimes are included in images and, overall, a surprisingly large amount of information is available.

Eurasian asters primarily occur in three main clades, with a few 'grade' species — most have been placed in subtribe Asterinae (Fig.1, duplicated here from Nesom 2020a). Li et al. (2012) considered *Aster* sensu stricto to comprise species of the **Asterothamnus branch** and **Aster branch** and recognized that species of the **Psychrogeton branch** and **Hersileoides branch** should be placed in genera outside of strictly defined *Aster*. The **Asterothamnus branch** is excluded here from *Aster* as it includes clearly defined and generally accepted genera (i.e., *Asterothamnus* and *Arctogeron*; *Kemulariella* has not been included in molecular sampling but appears to belong in this clade; the position of *Rhinactinidia* is ambiguous but morphology and geography favor its placement here [Nesom 2020a]; *Cardiagyris*, *Chaochienchangia*, and *Sinobouffordia* are morphologically and molecularly distinct). Newly proposed genera, including a total of 64 species) in the branches of Figure 1 are validated and detailed in publications contemporary with this one.

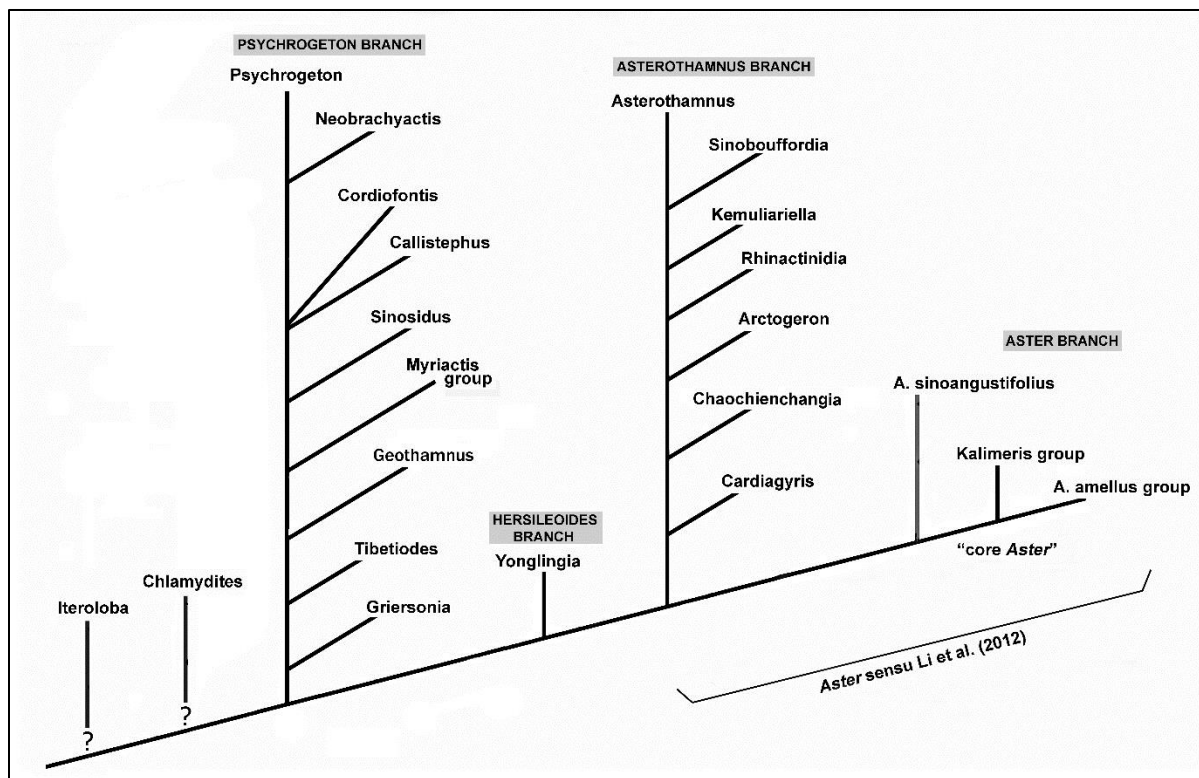


Figure 1. Astereae subtribe Asterinae (from Nesom 2020a). An intuitively constructed consensus tree, summarizing published phylogenetic analyses based on DNA sequence data. The diagram position of some taxa is speculative, chosen from among ambiguous placements in molecular phylogenies or placed by morphology if not included in molecular sampling.

Even in its restricted definition, *Aster* (**core Aster**, sensu Fig. 1) remains morphologically heterogeneous. The phylogenetic structure of **core Aster** may become more complex as more species are sampled, and some of the species groups may ultimately be accepted at generic rank.

The **Kalimeris group** includes *Kalimeris*, *Heteropappus*, *Miyamayomena*, *Sheareria*, and the 'ageratoides' group (*Aster* sect. *Ageratoides* sensu stricto plus other species in the larger *A. ageratoides* clade (Nesom 2020a for details). The **Aster amellus group** includes *A. amellus* (the type of the genus), *A. alpinus*, *Rhynchospermum*, *Turczaninovia*, and a group of other distinctive species in largely unresolved phylogenetic placement.

The Li et al. analysis places *Aster alpinus* (Figs. 15–18) as sister to *A. amellus* but additional species probably will modify this interpretation (especially *A. indamellus* and *A. aitchisonii* and species potentially closely related to *A. alpinus*). Onno's ser. *Macrochaeti* subser. *Alpini* (1932, p. 7) included *A. alpinus* and 11 other monocephalous species of otherwise highly disparate morphology. In *Aster* sect. *Alpinaster* (type, *A. alpinus*), Tamamshyan (1959) included morphologically complex *A. alpinus* and four other species: *A. fallax*, *A. korshinskyi*, *A. serpentimontanus*, and *A. tolmatshchevii*. In *Aster* ser. *Alpini* (type, *A. alpinus*), Ling (1985) included *A. alpinus* (including varieties) and nine other species (of these nine, *A. handelii*, *A. heterolepis*, and *A. oreophilus* cluster with the *A. ageratoides* clade of the **Kalimeris group** (Li et al. 2012); the other six are molecularly unsampled). *Aster* sect. *Alpigeni* of Chen et al. (2011) includes 44 species — including *A. alpinus* with four varieties and *A. oreophilus* and *A. heterolepis*, which, based on their key to species, appear to be most closely similar to *A. alpinus*.

***Aster amellus* and *Aster* in its strictest sense**

In discussion of *Aster indamellus* (a replacement name for *A. pseudamellus* Hook. f.), Grierson (1964, p. 88) provided a hypothesis that serves as a starting point for a strict definition of *Aster*. *Aster indamellus* "is one of a group of related species the common ancestor of which must once have been widespread in the continent of Asia. It appears to have given rise to *A. amellus* in Europe, *A. indamellus* and *A. aitchisonii* in the Western Himalaya, *A. maackii* in Eastern Siberia, and although less closely allied, probably also to *A. vestitus* and *A. poliothamnus* in the East Himalaya regin. Of these *A. indamellus* is most closely related to *A. amellus*."

Plants of *Aster amellus*, *A. indamellus*, and *A. aitchisonii* (Figs. 2–11) are subshrubs — they have persistent, woody stem bases and woody or lignescent caudex branches or rhizomes (rhizomes becoming caudex branch-like?). Phyllaries are strongly graduate in length. *Aster indamellus* and *A. aitchisonii* have not been included in molecular analyses, but the hypothesis here predicts that this is a monophyletic group, *Aster* in the strictest sense. *Aster alpinus* is similar in habit (woody caudex/rhizomes) but is monocephalous and phyllaries are equal to subequal in length. The similarity between *A. amellus* and *A. alpinus* in proximal woodiness appears to be a specialized feature indicating common ancestry — all other species in the **Aster amellus group** also are rhizomatous but the rhizomes are non-woody (personal observation; Chen et al. 2011).

Molecular data place *Aster maackii* (Figs. 12–14) in the **Aster amellus group** (Fig. 1) but the species does not appear to be in the immediate relationship of *A. amellus* and *A. alpinus*. The analysis of Zhang et al. (2015) places *A. maackii* as sister to *A. piccolii*, which is remarkably similar in morphology, except for the reduced pappus of the latter. *Aster maackii* and *A. piccolii* resemble *A. indamellus* and *A. aitchisonii* in inflorescence form, strictly erect stems, toothed leaves, and strongly graduate phyllaries, but the plants are herbaceous perennials arising from short, densely fibrous-rooted, non-woody rhizomes. *Aster vestitus* is in the **Kalimeris group** and relatively distantly related to *A. amellus*. *Aster poliothamnus* (in the **Asterothamnus branch**) is even more distantly related and has been included in the genus *Sinobouffordia* (Nesom 2020b).

Taxonomic summary of typical *Aster* L.

1. ***Aster amellus* L.**, Sp. Pl. 2: 873. 1753. **LECTOTYPE** (Semple 2006): **Europe**. Habitat in Europae australis asperis collibus, Herb. Linn. 997.16 (LINN). Figures 2 and 3.

Montane habitats from central France and northern Italy eastward to Belarus, Ukraine, and southeastern Russia, and into Turkey, Georgia, Armenia, Azerbaijan, and Iran (see map in Münzbergová et al. 2011).

Aster amellus is a polymorphic aggregate including diploids, tetraploids, and hexaploids (summary in Münzbergová et al. 2011). Three species within the aggregate were recognized by Tamamshyan in his *Aster* ser. *Amelliae* (1959, 89–92): *A. amellus*, *A. ibericus* Stev., and *A. amelloides* Bess., supported by morphology, chromosome number, and geography. Tzvelev (2002) treated *A. amellus* with three subspecies, corresponding to the species above: subsp. *amellus*, subsp. *ibericus* (Stev.) Avetisjan, and subsp. *bessarabicus* (Rchb.) Soó. More recent cytological studies, however, as well as isozyme and cpDNA analyses, support the treatment of *A. amellus* as a single polymorphic species instead of multiple independent taxa (summary in Münzbergová et al. 2011). Ling's *Aster* ser. *Amelli* (1985, 134–135) is typified by *A. amellus* but it includes only *A. indamellus* (*A. amellus* and *A. aitchisonii* do not occur in China).

2. ***Aster indamellus* Grierson** [nom. nov.], Notes Roy. Bot. Gard. Edinb. 26: 87. 1964. *Aster pseudamellus* Hook. f., Fl. Brit. India 3: 249. 1881 (not Wenderoth 1831). **LECTOTYPE** (designated here): **INDIA: Uttarakhand**. Kumaon, Pangi, Kanawar, 8-9000 ft, 18 Aug 1847, *T. Thomson s.n.* (K 890408 image). Figures 7 and 8. **Protologue**: "Western Himalaya,

Jacquemont; Kumaon, alt. 8-9000 ft, *Thomson*. Lahul, *Jaeschke*." The collections by Jacquemot and Jaeschke also are at K.

Afghanistan, China (Xizang: Mt. Xixabangma, Yang Si), India (Himachal Pradesh, Punjab, Uttarakhand), Kashmir, Nepal, Pakistan.

Grierson (1964, p. 89) noted that *Aster amellus* and *A. indamellus* "generally resemble one another in habit, but *A. amellus* is less leafy and usually eglandular. Furthermore, its phyllaries are mostly obtuse, imbricate and distinctly ciliate." Leaf margins of *A. indamellus* and *A. aitchisonii* usually are serrate with 1–3(–4) pairs of teeth, while those of *A. amellus* are consistently entire or shallowly and nearly indistinctly toothed.

3. *Aster aitchisonii* Boiss., Fl. Orient. [Boissier] Suppl. 287. 1888. **TYPE: PAKISTAN.** Kurram Valley plants, Shid Doi, shrub on rocks, 7000-8000 ft, 11 Jul 1879, *J.E.T. Aitchison 812* (holotype: G fide Grierson 1964, photo & fragment-E; isotypes: BM image, K image-Figs. 9 and 11, S image). Protologue: "Hab. ex rupibus verticalibus pendulus in valle Kuran Affghaniae 7-8000 ft (Aitch. 812)."

Paratype: **Afghanistan [Pakistan]**. Chapri, Shid Doi Naba, hanging from rocks, 7000 m, 14 Jul 1880, *Aitchison 323* (BM as cited by Grierson, K image-Fig. 10).

Apparently known only from the type locality or immediate area. Dr. (Surgeon Major) Aitchison made the type collection and his "323" near the end of the Second Anglo-Afghan War — the label locality is noted as Afghanistan but the Kurram Valley is in western Pakistan.

Aster aitchisonii is distinguished from *A. amellus* and *A. indamellus* "by the smaller size of its capitula and also by its tougher xerophytic habit. The stems tend to be densely leafy and on the peduncles the uppermost leaves overlap and to some extent become confused with the lowermost phyllaries. In *A. aitchisonii*, however, the leaves are always pale greyish-green and bear a few sharp-pointed teeth on the margins, the phyllaries are coriaceous, completely lacking the foliaceous tips of *A. indamellus*, and their margins are fringed with fine white cilia" (Grierson 1964, p. 89).

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Figure 2. *Aster amellus*. Lectotype, Herb. Linn. 997.16 (LINN).



Figure 3. *Aster amellus*. Details from the lectotype, Herb. Linn. 997.16 (LINN).



Figure 4. *Aster amellus*. Turkey, Winter 218 (US). Woody rhizomes, lignescent stem bases.



Figure 5. *Aster amellus*. Turkey, Balls 1983 (E). Woody rhizomes, lignescent stem bases.



Figure 6. *Aster amellus*. Turkey, Davis 46665 (E). Woody rhizomes, lignescent stem bases.



Figure 7. *Aster indamellus*. Lectotype, Thomson s.n. (K).



Figure 8. *Aster indamellus*. Details from lectotype, Thomson s.n. (K).



Figure 9. *Aster aitchisonii*. Isotype, Aitchison 812 (K).

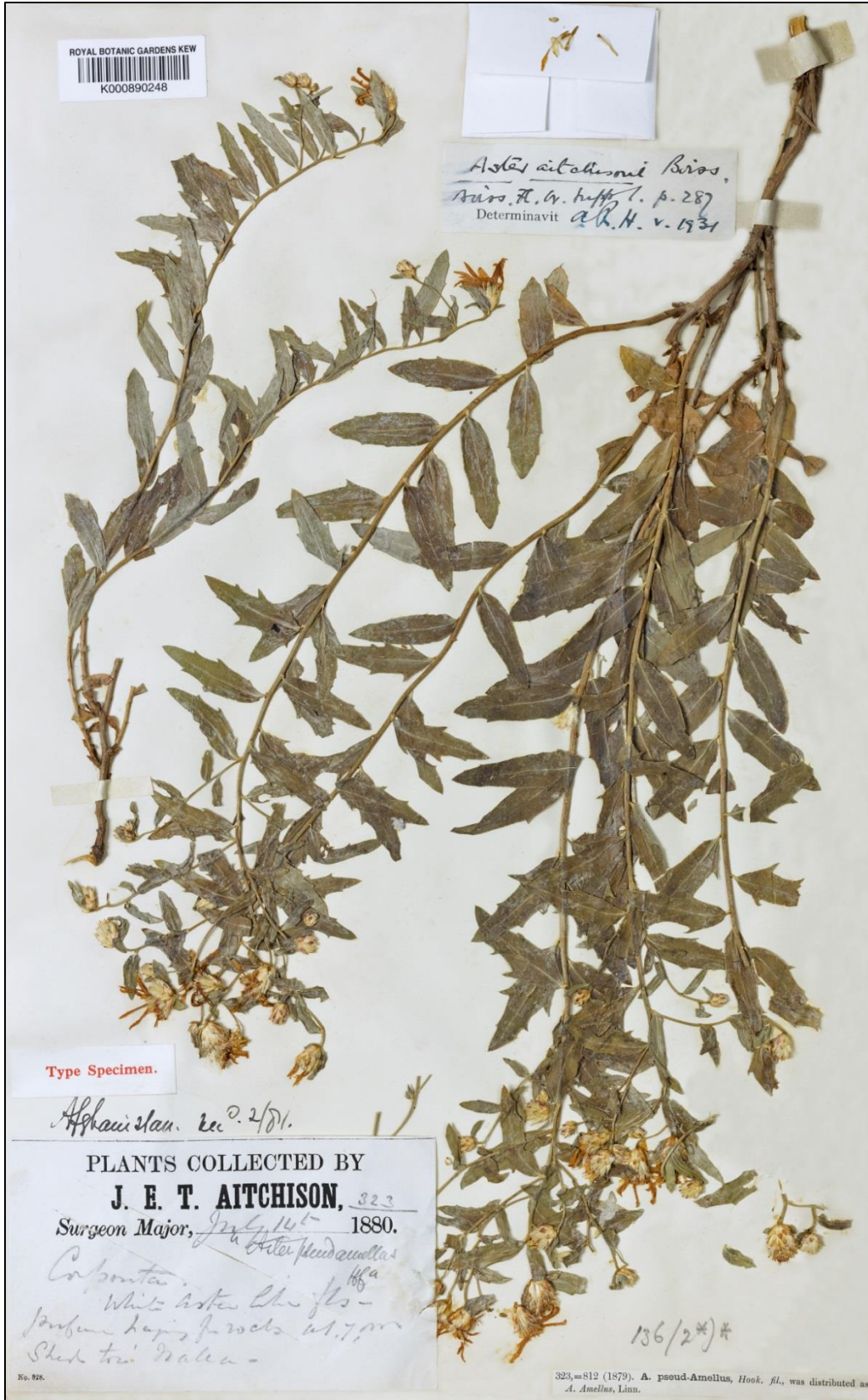


Figure 10. *Aster aitchisonii*. Paratype, Aitchison 323 (K).



Figure 11. *Aster aitchisonii*. Details from K isotype.



Figure 12. *Aster maackii*. Russia. Solomon & Barkalov 19608 (US).



Figure 13. *Aster maackii*. Russia. ЯКУБОВ s.n. (US).



Figure 14. *Aster maackii*. Russia. Solomon & Barkalov 19883 (US).



Figure 15. *Aster alpinus*. Germany. Schuhwerk 92/248 (US).



Figure 16. *Aster alpinus*. Russia. *Elias et al.* 803B (US).



Figure 17. *Aster alpinus*. China. (HMC).



Figure 18. *Aster alpinus*. Russia. Joukov s.n. (KUN).