

NEW SUBTRIBES FOR NORTH AMERICAN ASTEREAE (ASTERACEAE)

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ABSTRACT

Recent molecular evidence indicates that most genera of North American Astereae comprise a monophyletic assemblage. Within this North American clade are three distinctive generic groups previously hypothesized to be most closely related to subtribes of the Southern Hemisphere—the *Monoptilon* group, the *Pentachaeta* group, and the *Townsendia* group. Additionally, morphological and molecular evidence indicates that the genera *Boltonia*, *Chloracantha*, and *Batopilasia* are closely related among themselves and constitute a coherent group. These four North American groups are recognized here with formal names at subtribal rank: **Chaetopappinae** subtr.nov. (*Chaetopappa*, *Monoptilon*), **Pentachaetinae** subtr.nov. (*Pentachaeta*, *Rigiopappus*, *Tracyina*), **Astrantriinae** subtr.nov. (*Astranthium*, *Dichaetophora*, *Geissolepis*, *Townsendia*), and **Boltoniinae** (*Batopilasia*, *Boltonia*, *Chloracantha*). *Homochrominae* is placed synonymy under subtribe Bellieae.

RESUMEN

Recientes evidencias moleculares muestran que la mayoría de los géneros norteamericanos de Astereae comprenden un conjunto monofilético. Dentro de este clado norteamericano hay tres grupos genéricos sobre los que se hipotetizó previamente que fuesen los más relacionados con las subtribus de hemisferio sur—el grupo *Monoptilon*, el grupo *Pentachaeta*, y el grupo *Townsendia*. Adicionalmente, la evidencia morfológica y molecular indican que los géneros *Boltonia*, *Chloracantha*, y *Batopilasia* están muy relacionados entre ellos y constituyen un grupo coherente. Estos cuatro grupos norteamericano se reconocen aquí con nombres formales en el rango: **Chaetopappinae** subtr.nov. (*Chaetopappa*, *Monoptilon*), **Pentachaetinae** subtr.nov. (*Pentachaeta*, *Rigiopappus*, *Tracyina*), **Astrantriinae** subtr.nov. (*Astranthium*, *Dichaetophora*, *Geissolepis*, *Townsendia*), y **Boltoniinae** (*Batopilasia*, *Boltonia*, *Chloracantha*). Se lectotipifica *Homochrominae*, colocándola en la sinonimia de la subtribu Bellieae.

A primarily morphological overview of the tribe Astereae (Nesom 1994a) recognized 14 subtribes, four of which were hypothesized to be primarily North American (*Machaerantherinae*, *Chrysopsidinae*, *Solidagininae*, and *Symphyotrichinae*). Three distinctive North American generic groups were hypothesized to be most closely related to subtribes of the Southern Hemisphere—the *Monoptilon* group (subtribe *Feliciinae* = Bellieae, primarily Africa and western North America), the *Pentachaeta* group (subtribe Bellieae), and the *Townsendia* group (subtribe *Brachyscominae*, primarily Australia and North America). The genus *Boltonia* was hypothesized to be related to genera of subtribe *Asterinae*, primarily an Eurasian group (Nesom 1994a, 1994b).

Noyes and Rieseberg (1999) used nucleotide sequence data from nuclear ribosomal DNA representing a broad range of Asterean genera to test various hypotheses of

relationship and classification in the tribe. Their results showed that all genera examined of North American Astereae comprise a single, strongly supported clade—thus morphological parallelism rather than homology underlies hypotheses suggesting that dispersal from the Southern Hemisphere and Asia accounts for the origin of the *Monoptilon*, *Pentachaeta*, and *Townsendia* groups and *Boltonia*.

Notwithstanding these unexpected patterns of relationship, the infra-tribal generic groups under consideration have consistently been recognized as coherent (see caveats below regarding *Aphanostephus*, *Geissolepis*, and *Boltonia*). The morphological distinctiveness of these groups is equal to others already recognized at subtribal rank, and with recognition of their origin from within the broad North American clade, they are provided here with formal names at the same rank.

Chaetopappinae Nesom, subtr. nov. TYPE GENUS: *Chaetopappa* DC.

Herbae annuae vel perennes vitae brevis radice palari. Capitula plerumque solitaria; phyllaria marginibus late hyalinis. Corollae radii albae vel caeruleae, valde circinnatae. Pappus setarum, squamarum vel palearum, setarum ac squamarum, vel carens. Numerus basicus chromosomatuum, $x = 8$.

Small, annual or short-lived perennial herbs, taprooted, decumbent (*Monoptilon*, some *Chaetopappa*) to erect. Leaves entire, oblong to oblanceolate-spatulate, alternate. Heads mostly solitary; phyllaries flat to convex, with broad, sharply delimited, hyaline margins. Ray corollas blue to white, strongly coiling. Disc flowers sometimes with sterile ovaries; style branches with obtuse or truncate to triangular collecting appendages. Cypselae eglandular or glandular, terete and multinerved (most *Chaetopappa*) or obovate, flattened, and 2-nerved (*Monoptilon*, some *Chaetopappa*); pappus of persistent bristles, or scales, or pales, or of bristles and scales, commonly in multiples of 5 (in *Chaetopappa*), or absent. Base chromosome number, $x = 8$. Genera included: *Chaetopappa* DC., *Monoptilon* Torr. & A. Gray ex Gray. Distribution primarily in arid habitats in the southwestern and south-central USA and northern Mexico.

This is essentially the "*Monoptilon* group," earlier placed in subtribe Feliciinae = Bellieae (Nesom 1994a) and as "Incertae sedis" (Nesom 2000). The two genera of Chaetopappinae form a monophyletic group sister to *Euthamia* Nutt. ex Cass. in the Noyes and Rieseberg analysis. In the analysis of Lane et al. (1996), the phyletic origin of *Chaetopappa* lies immediately between *Astranthium* and *Townsendia*, although it does not do so in the original analysis from which the DNA data were drawn (Morgan 1990).

The southern European genus *Bellium* L. was earlier included in the *Monoptilon* group (Nesom 1994a), but with the strong indication that *Monoptilon* and *Chaetopappa* are North American in origin, it is probable that the closest relationships of *Bellium* are with the other Old World genera. Similarities between *Bellium* and *Amellus* L. were noted by Nesom (1994a).

Pentachaetinae Nesom, subtr. nov. TYPE GENUS: *Pentachaeta* Nutt.

Herbae annuae radice palari. Folia filiformia vel linearia vel anguste oblanceolata. Capitula solitaria longipedunculata; phyllaria marginibus hyalinis. Corollae radii flavae vel rubescentes, minus

plerumque albae, valde circinnatae. Appendices collectentes linear-i-lanceolatae ramorum stylis floribus disci. Cypselae teretes vel leniter complanatae, anguste oblongae vel oblanceolatae in ambitu; pappus setarum vel squamarum. Numerus basicus chromosomatum, $x = 9$.

Annual herbs, taprooted. Leaves alternate, entire, filiform or linear to narrowly oblanceolate. Heads solitary and long-pedunculate; phyllaries with hyaline margins. Ray corollas yellow to reddish, less commonly white, strongly coiling (lamina absent in some *Pentachaeta*). Disc flowers: style branches with linear-lanceolate collecting appendages. Cypselae terete to slightly compressed, narrowly oblong to oblanceolate in outline, beaked in *Tracyina*, eglandular; pappus 1-seriate (1–2 seriate in *Tracyina*), of persistent bristles frequently in multiples of 5s, sometimes flared at the base and partially connate, or sometimes completely lacking, or of long scales (*Rigiopappus*). Base chromosome number, $x = 9$. Genera included: *Pentachaeta* Nutt., *Rigiopappus* A. Gray, *Tracyina* S.F. Blake. Distribution primarily in grassland habitats of California, USA, with several taxa of *Pentachaeta* reaching Baja California, Mexico; *Rigiopappus* also occurs into Oregon, Washington, Idaho, and Nevada.

This is the “*Pentachaeta* group,” earlier placed in subtribe Feliciinae = Bellieae (Nesom 1994a) and as “*Incertae sedis*” (Nesom 2000). The close resemblance and relationship among these three genera have been noted by Blake (1937), Ornduff and Bohm (1975), and Robinson and Brettell (1973); they were placed as a coherent unit within the “*Chaetopappa* group” by Bremer (1994). The *Pentachaetinae* form a monophyletic group sister to *Ericameria* Nutt. in the Noyes and Rieseberg analysis.

Astranthiinae Nesom, subtr. nov. TYPE GENUS: *Astranthium* Nutt.

Herbae annuae biennes vel perennies plerumque radice palari. Capitula solitaria, plerumque longipedunculata; phyllaria marginibus late hyalinis; receptacula convexa vel conica. Corollae radii plerumque albae vel caeruleae, midfascia abaxiali lavandula, non reflexae aut circinnatae. Corollae discii tubo brevi. Cypselae oblanceolatae vel obovatae, complanatae, 2(–3)-nervatae, laeves vel papillatae, plerumque pubescentes trichomatibus glochidiatis; pappus setarum vel corona demissa setarum et squamarum. Numerus basicus chromosomatum, $x = 9$ et $x = 3, 4, 5$.

Annual, biennial, or perennial herbs, taprooted, often with a branching caudex, rarely fibrous-rooted, mostly strigose with short, white hairs. Leaves alternate, spatulate to linear, entire or few-toothed. Heads solitary, mostly long-pedunculate, rarely sessile; phyllaries with broad, hyaline margins; receptacles convex to conical. Ray corollas white to bluish or pinkish above (rarely yellow in *Townsendia*), usually with a lavender to blue or pink abaxial midstripe, not reflexing or coiling. Disc corollas short-tubed; style branches with triangular-lanceolate collecting appendages. Cypselae oblanceolate to obovate, flattened, 2(–3)-ribbed, the surfaces smooth or papillate, glabrate or usually pubescent with duplex hairs with glochidiate, bifurcate, or entire apices (achenes winged and fringed-ciliate in *Dichaetophora*); pappus 1-seriate, of barbellate bristles or a low crown of setae/bristles and scales (2-awned in *Dichaetophora*). Base chromosome number, $x = 9$ (or $x = 3, 4$, and 5 in *Astranthium*; $x = 3$ in *Dichaetophora*). Genera included: *Astranthium* Nutt., *Dichaetophora* A. Gray, *Geissolepis* B.L. Rob., *Townsendia* Hook. Distribution mostly in western North America north of Mexico (*Townsendia*), Mexico and south-central USA (*Astranthium*), Texas and adjacent Mexico (*Dichaetophora*), and east-central Mexico (*Geissolepis*).

This is the "*Townsendia* group," earlier placed in subtribe Brachyscominae (Nesom 1994a) and as "Incertae sedis" (Nesom 2000). *Aphanostephus* DC. also was earlier included in the *Townsendia* group (by Nesom and various others), but molecular data from several sources (Morgan 1990; Lane et al. 1996; Noyes and Rieseberg 1999; Noyes 2000) consistently indicate that *Aphanostephus* arose from within the Conyzinae. *Astranthium*, *Dichaetophora*, and *Townsendia* comprise a monophyletic group essentially sister to the Conyzinae and Chrysopsidinae in the Noyes and Rieseberg analysis. *Geissolepis* is phylogenetically interposed between the *Townsendia* group and these two related subtribes, but a set of morphological features places it closer to the *Townsendia* group than the Conyzinae or Chrysopsidinae, and the genus can reasonably be included in the Astrantheiinae. Alternately, it presumably would be treated as a monophyletic subtribe.

Geissolepis is similar to the Astrantheiinae "core" genera in its solitary heads, white, straight ray corollas, conical receptacles, and glochidiate cypselar vestiture. It is distinct within the subtribe in its combination of a prostrate habit with creeping, fibrous-rooted, lignescence stolons, succulent leaves, resin canals on the phyllaries, cypselae, and disc corollas, paleate receptacles, ray corollas without an abaxial midstripe, gradually ampliate disc corollas, subterete cypselae with 8 resinous ribs, and pappus of short scales with uncinate-ciliate margins. The chromosome number has been reported as $2n = 16$ (Ralston et al. 1989) and $2n = 18$ (Lane and Li 1993).

Boltoniinae Nesom, subtr. nov. TYPE GENUS: *Boltonia* L'Hérit.

Herbae vel subfrutices perennes rhizomatose caulis ac foliis persistente viridi-glabratis. Folia admodum omnino caulina. Capitula solitaria vel laxe aggregata; phyllaria herbacea, ad apicem rotundata vel obtusa nervis ternis aurantiaci-resinosis. Corollae radii albae vel leniter caerulescentes, circinnatae. Appendices collectentes deltatae ramorum stylis florum disci. Numerus basicus chromosomatum, $x = 9$.

Perennial, herbs or subshrubs (*Chloracantha*), rhizomatous, with persistently green-glabrate stems and leaves, thorny in *Chloracantha*. Leaves essentially all cauline, entire or few-toothed. Heads solitary or very loosely corymboid to paniculate; phyllaries primarily herbaceous, apically rounded to obtuse, with three orange-resinous nerves. Ray corollas white to slightly bluish, coiling. Disc corollas orange-veined; style branches with deltate collecting appendages. Cypselae terete and multinerved or flattened, 2-nerved, and winged (*Boltonia*). Base chromosome number, $x = 9$. Genera included: *Batopilasia* Nesom & Noyes, *Boltonia* L'Hérit., *Chloracantha* Nesom, Suh, Morgan, Sundberg, & Simpson. Distribution in northwestern Mexico (*Batopilasia*), eastern USA (*Boltonia*), and Mexico and the southwestern USA to Louisiana (*Chloracantha*).

Batopilasia, *Boltonia*, and *Chloracantha* apparently are closely related among themselves (summary of ideas and evidence in Nesom & Noyes 2000). *Batopilasia* and *Boltonia* are sister genera in the Noyes and Rieseberg analysis, the pair in a sister relationship to the Symphyotrichinae and Machaerantherinae. *Chloracantha* was not included in this molecular analysis but is morphologically similar to *Batopilasia*, as observed in the original description of the species (Sundberg & Nesom 1990).

Boltonia is set apart from the other two genera by its conical or convex receptacles, short-tubed disc corollas, and flattened, 2-nerved, orange-veined, often winged cypselae with an abbreviated pappus. These specializations prompted the observation that "Boltonia is morphologically isolated in the New World" (Nesom 1994b, p. 163), but molecular evidence has found its close relatives. It is related neither to Old World Asterinae (Nesom 1994b) nor to genera of the *Townsendia* group (Bremer 1994).

With the formal recognition of the four subtribes above, six North American genera of Astereae remain without a clear hypothesis of subtribal affinity. These are among the "primitive' Asters" (Nesom 2000), placed by Nesom (1994a, 1994b) mostly in subtribes Asterinae or Symphyotrichinae: *Doellingeria* Nees, *Eucephalus* Nutt., *Ionactis* Greene, *Oclemena* Greene, *Oreostemma* Greene, and *Tonestus* A. Nelson.

Note on Homochrominae.—My interpretation (Nesom 1994a) of subtribe Homochrominae of Bentham & Hooker as invalid was incorrect. This name was validly published—it was provided with a description and it can be assumed to have been based on a legitimate genus name (*Homochroma* DC.) included by Bentham and Hooker among those genera they placed in the subtribe. Homochrominae presumably formed the nomenclaturally "sister" taxon to the illegitimate Heterochrominae Bentham & Hooker (this name not based on an included genus), but a reasonable lectotypification for Homochrominae already has been effected by Solbrig (1963), who specified the type.

Homochrominae Bentham & Hooker, Gen. Pl. 2:174. 1873. LECTOTYPE: (Solbrig 1963): *Homochroma* DC. (= *Zyrphelis* Cass.).

With this typification, Homochrominae becomes a synonym of Bellieae DC. ex Godr. (in Gren. & Godr., Fl. France 2:83, 104. 1850; type, *Bellium* L.) along with Feliciinae Nesom (Phytologia 76:205. 1994; type, *Felicia* Cass.).

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