

Astereae

Luc Brouillet, Timothy K. Lowrey, Lowell Urbatsch, Vesna Karaman-Castro, Gisela Sancho, Steve Wagstaff and John C. Semple

INTRODUCTION

Tribe Astereae, with an estimated 222 genera and ca. 3100 species (emended from Nesom and Robinson, 2007), is the second largest tribe of family Compositae. Members of the tribe range from the Arctic to the tropics, though they are more numerous in temperate regions. They are mostly found in open habitats, from salt marshes and bogs to deserts, and from sea level to the alpine zone. They are mostly characterized by their ecaudate and ecalcarate anther bases (though a few genera have caudate anther bases), and a disc floret style with two distinct marginal stigmatic lines and deltate to triangular or lanceolate style appendages that are glabrous adaxially and with sweeping hairs abaxially.

The tribe is part of subfamily Asteroideae and belongs to a clade that includes Calenduleae, Gnaphalieae, and Anthemideae, the latter often considered its sister tribe (e.g., Panero and Funk 2002, 2008), though this question is still not fully resolved (e.g., Goertzen et al. 2003). Grau (1977), Bremer (1994), Nesom (1994g), and Nesom and Robinson (2007) summarized the taxonomic history of the tribe. These authors addressed subtribal classification of Astereae, acknowledging the somewhat artificial nature of the traditional divisions. The most significant departure from the classic scheme was that of Nesom (1994g, 2000a), which culminated in the recent classification by Nesom and Robinson (2007). This classification incorporates some, but not all, the molecular phylogenetic information published between 1994 and 2004. Though

an evolutionary tree was presented by Nesom (1994g), it was not based on a phylogenetic analysis of characters. The only cladistic analysis of tribe Astereae (Zhang and Bremer 1993) was subsequently used by Bremer (1994). This analysis, however, was based on a few representatives selected from the existing subtribes, using traditional morphological characters and the sampling did not allow for the assessment of whether or not the subtribes were monophyletic. Nesom (1994g) reviewed this analysis and made extensive comments on the data and conclusions.

Much of the taxonomic literature published since Grau (1977) has been summarized by Bremer (1994), Nesom (1994g, i, 2000a), Müller (2006), Flora of North America Editorial Committee (2006), and in the phylogenetic papers cited herein. This literature will not be repeated here unless necessary.

Molecular phylogenies in the tribe initially were based on cpDNA RFLP analyses, mostly of North American (Suh and Simpson 1990; Zanolovic 1991; Morgan and Simpson 1992; Morgan 1993, 1997; Lane et al. 1996; Xiang and Semple 1996; Zhang 1996; see Semple et al. 1999) or Asian genera (Gu et al. 1994; Ito et al. 1995, 1998). Few papers using cpDNA sequence data were published for Astereae (Denda et al. 1999; Bayer and Cross 2002; Liu et al. 2002; Watanabe et al. 2006; Forest et al. 2007); these data are not cumulative since different markers were used in the studies, which further used a restricted sample of taxa.

Mostly after the publication of the seminal paper by Noyes and Rieseberg (1999), phylogenies of genera or

groups of genera based on the nuclear ribosomal internal transcribed spacer (ITS) were published (Morgan 1997, 2003; Noyes 2000a; Lowrey et al. 2001; Markos and Baldwin 2001; Cross et al. 2002; Fiz et al. 2002; Liu et al. 2002; Wagstaff and Breitwieser 2002; Roberts and Urbatsch 2003, 2004; Urbatsch et al. 2003; Beck et al. 2004; Brouillet et al. 2004; Eastwood et al. 2004; Field et al. 2006; Watanabe et al. 2006; Selliah and Brouillet 2008). Some papers also added the nrDNA 3'ETS region as a phylogenetic tool in Astereae (Markos and Baldwin 2001, 2002; Morgan 2003; Roberts and Urbatsch 2003, 2004; Urbatsch et al. 2003; Brouillet et al. 2004; Selliah and Brouillet 2008).

Given the large number of available ITS sequences in Astereae and the fact that no phylogeny exists for the whole tribe, we firstly present an ITS-based phylogeny of the entire tribe. The resulting lineages are discussed in relation with the pertinent literature. Secondly, we review briefly the various characters (morphological, cytological, chemical) and their distribution in the tribe. Thirdly, economic uses and biological data on Astereae are summarized. Fourthly, we examine the biogeography of the tribe in terms of the ITS phylogeny, contrasting it with hypotheses based on traditional classifications. Finally, we examine the impact of the current molecular phylogeny on generic delimitation and contrast our Astereae ITS phylogeny with the recent classification of Nesom and Robinson (2007).

MATERIALS AND METHODS

The phylogeny was reconstructed using GenBank-available nrDNA ITS sequence data for Astereae, as well as representatives of the sister tribes Calenduleae, Gnaphalieae, and Anthemideae. Details on sequencing methods and phylogenetic analyses, as well as discussions of specific results, are available in the papers where the data were initially published (cited above), as well as in papers being concurrently prepared with the present analysis (Sancho and Karaman-Castro 2008; Karaman-Castro and Urbatsch, pers. comm.; Brouillet et al., pers. comm.). To align the more than 850 available sequences, and more specifically the Astereae sequences with those of the outgroups, we used the 80%-consensus aligned sequences for the tribes of Asteraceae as determined from the ITS secondary structure by Goertzen et al. (2003). Small misalignments in the consensus sequences of Astereae, Gnaphalieae, and Anthemideae were noted in ITS1 (before helix 1A and in helix 1B) and in ITS2 (in helices 2A and 2C). These most likely resulted, for Astereae, from the fact that the sequences used by Goertzen et al. were mostly from derived genera with numerous indels, such as *Erigeron*. The availability of sequences of primitive Astereae, such as *Nannoglottis* and

Printzia Cass., and the large number of available ITS sequences, allowed us to correct these misaligned portions. Duplicate sequences or sequences of dubious origin were removed from the matrix. The resulting matrix included 752 taxa (737 Astereae and 15 outgroup species) by 852 characters, of which 468 were parsimony informative. Gaps were treated as missing characters. Multistate data were treated as uncertainties. Given that sequences came from a number of laboratories, there were missing data, particularly in the outgroups where many lacked the 5.8S portion; otherwise, data were missing mostly from the beginning of ITS1 or the end of ITS2; missing data were usually a few bases only.

Given the size of the matrix, a PAUPRat (Sikes and Lewis 2001) parsimony analysis was carried out using PAUP*10.6b (Swofford 2002) (swap = tbr, nrep = 1, addseq = random, nchuck = 1, chuckscore = 1, wtset = 1). Subsequently, a parsimony analysis starting from the trees obtained in the 15 ratchet runs was done in PAUP* (tbr, maxtree = 20,000) in order to obtain a greater number of trees as a basis for the strict consensus tree. Base chromosome numbers and distribution (as branch color) were manually mapped onto the phylogeny.

RESULTS

Resulting parsimony trees had a length of 7928, a consistency index (non informative characters removed) of 0.15, a homoplasy index of 0.84, and a retention index of 0.79; the rescaled consistency index was 0.12. The strict consensus tree is presented in Fig. 37.1A–E, where subtribes following Nesom and Robinson (2007) are indicated to the right of the cladograms. Given the number of parsimony informative characters, much lower than the number of taxa analyzed, and the relatively recent radiations in many groups of Astereae, homoplasy is high and in part responsible for the low resolution of the trees. More localized analyses (see studies cited above), which exclude taxa from other groups or continents, often produce more resolved trees. Support for clades is usually non-significant, in large part due to the low number of characters defining each branch, particularly along the spine of the tree. The addition of phylogenetically significant indels to the analysis may increase support for individual clades (Brouillet, pers. obs.).

The ITS sequence data, as analyzed here, do not allow us to determine the relationships between Astereae and the three tribes to which it is considered closely related, Calenduleae, Gnaphalieae, and Anthemideae.

Tribe Astereae is monophyletic and resolves into a number of large clades that will each be described below; many have been the object of recent phylogenetic analyses. The phylogeny (Fig. 37.1A–E) includes a basal African

grade, with disjunct Chinese, South American, and New Zealand lineages, and a polytomy of crown groups in Australasia, South America, and North America.

PHYLOGENETIC LINEAGES

Basal lineages: out of Africa, repeatedly

Printzia (Figs. 37.2A, 37.3A) and *Denekia* Thunb. (Fig. 37.3B) have been shown by Bayer and Cross (2002) and Brouillet et al. (pers. comm.) to belong to tribe Astereae and are sister to the remaining members of the tribe (Fig. 37.1AⒶ). Using *rbcL* data, Forest et al. (2007, Supplement 3) also placed *Printzia* within Astereae, but not as sister to the genera studied. Both genera are South African, which supports the hypothesis of an African origin for the tribe (Noyes and Rieseberg 1999). The tailed anthers of *Printzia* and *Denekia* is a symplesiomorphy shared with related tribes and tends to confirm the early diverging position of the taxa in a mostly tail-less tribe. *Printzia* is placed in subtribe Hinterhuberinae by Nesom and Robinson (2007), a position not supported here. *Denekia* has traditionally been placed in tribe Gnaphalieae (e.g., Bayer et al. 2007). Placement within Astereae is novel and post-dates the Nesom and Robinson classification. The capitulum morphology of *Denekia*, with its bilabiate peripheral (rays) and functionally male disc florets, appears odd in Astereae, but some aspects of its morphology certainly agree with a placement near *Printzia*, notably the tomentose abaxial leaf faces. These two genera may deserve a subtribe of their own.

Liu et al. (2002) showed that the Chinese *Nannoglottis* Maxim. is sister to other Astereae, though they postulated an African origin followed by dispersal to Asia. Our data (Fig. 37.1AⒷ) confirm that it is one of the earliest diverging lineages and that it must have dispersed from Africa to China at some early stage of Astereae evolution.

Brouillet et al. (pers. comm.) showed that *Mairia* Nees is an isolated genus among African Astereae, between *Nannoglottis* and the Paleo South American and New Zealand clades (Fig. 37.1AⒸ) (Paleo South American and New Zealand clades: see below). The study also confirmed the separation of *Mairia* into *Mairia* s.str., *Polyarrhena* Cass., and *Zyrphelis* Cass. (Nesom 1994a). The latter are members of subtribe Homochrominae (below). As with *Printzia*, *Mairia* was placed within the Southern Hemisphere subtribe Hinterhuberinae in the Nesom and Robinson classification, a position not supported here.

At the next node in the phylogeny (Fig. 37.1AⒹ), *Pteronia* L. and the Homochrominae form a polytomy with the remaining Astereae. In some trees, *Pteronia* segregates first, while in others, it is sister to Homochrominae. *Pteronia* is a large genus of shrubs with discoid heads. The majority of genera in Homochrominae are radiate, although *Felicia*

Cass. (83 species; Fig. 37.2B), *Amellus* L. (12 spp.), *Engleria* O. Hoffm. (2 spp.), and *Chrysocoma* L. (20 spp.) have taxa with both radiate and discoid heads. Two South African genera, *Heteromma* Benth. and *Engleria*, were not included in the present analysis. *Heteromma* is wholly discoid while *Engleria* has one discoid and one radiate species. All species in both genera are herbaceous perennials with the exception of one annual species of *Engleria*. The affinities of these two taxa are currently unknown. Broader sampling of the southern African taxa is needed to resolve the relationships between *Pteronia*, Homochrominae, and the few genera that remain to be sampled.

Subtribe Homochrominae had been called Feliciinae by Nesom (1994g). He had included the African *Felicia* group, the Asian *Lachnophyllum* Bunge group, and the American-European *Monoptilon* Torr. and A. Gray group in this subtribe. Nesom and Robinson (2007) restricted Homochrominae to the *Felicia* group, thus making it strictly African, as was done by Grau (1973). The current study confirms this circumscription, at least insofar as the genera included are concerned (Fig. 37.1AⒺ). The Nesom (1994g) evolutionary tree showed Homochrominae as nested within a polytomy of subtribes mainly with Australasian and South American elements, but some European and North American as well; such affinities are not supported here. Homochrominae constitute one of the major radiations among the early diverging lineages. A major difference in the composition of Homochrominae between Nesom and Robinson (2007) and the current analysis is the inclusion of the St. Helena endemic trees and shrubs *Commidendron* Lem. and *Melanodendron* DC. In their classification, Nesom and Robinson left these genera unplaced. Nesom (1994g) had placed them within woody Baccharidinae, though noting the lack of comfortable fit in any subtribe. Noyes and Rieseberg (1999) noted the position of *Commidendron* near *Felicia* and *Amellus*, while Eastwood et al. (2004) showed a relationship of both to *Felicia*. Our phylogeny confirms the relationship between the two groups, but places *Commidendron* and *Melanodendron* as a clade sister to the *Felicia* clade. It would appear that these arborescent genera evolved from an ancestor common to the two groups. Within the *Felicia* lineage, *Felicia* does not appear to be monophyletic. *Felicia uliginosa* (J.M. Wood & M.S. Evans) Grau and *F. clavipilosa* Grau group with *Nolletia* Cass., well nested within a lineage that also includes *Amellus*, *Poecilolepis* Grau, and *Chrysocoma*. There are two other unresolved *Felicia* lineages, the *F. namaquana* (Harv.) Merx. and *F. filifolia* Burt Davy lineages. *Polyarrhena* and *Zyrphelis* appear related to the *F. filifolia* lineage, but it is impossible to determine whether the genera are sister to this lineage or whether *Felicia* is paraphyletic to them. *Felicia* is most likely polyphyletic as currently circumscribed and needs more study.

The Madagascan genus *Madagaster* G.L. Nesom was recently segregated from *Aster* by Nesom (1993b), who placed it in his southern Hemisphere subtribe *Hinterhuberinae*; he considered these taxa unrelated to *Aster*, including the African asters. As with *Printzia* and *Mairia*, our study does not support a position in this subtribe (Fig. 37.1A⑥). Instead, it is one of many isolated African lineages along the basal spine of the *Astereae* phylogeny. More genera from Africa need to be included in phylogenetic analyses before the position of *Madagaster* can be settled.

Conyza gouani Willd. is the only African *Conyza* Less. that does not group with *Grangeinae* (see below) (Fig. 37.1A⑦). Further study is required before its position can be ascertained and it can be assigned to a genus of its own. Nesom and Robinson (2007) hinted at the polyphyletic nature of *Conyza*. The morphology of this species appears quite distinct from that of other African conyzas, and its isolated position is therefore not surprising.

Nesom (1994h) and Nesom and Robinson (2007) maintained the African asters within the mainly Asian *Aster* L. s.str. but our results (Fig. 37.1A⑧) do not support such a relationship. As with several other African lineages, these asters appear to be isolated. Additional study is needed to better resolve their affinities.

Brouillet et al. (pers. comm.) have shown that subtribe *Grangeinae* is a monophyletic group of African and south Asian genera, and does not appear to include Australasian or American elements (Fig. 37.1A⑨). A major difference with the generic composition given by these authors is the addition of the African conyzas, *Psiadia* Jacq., and *Welwitschiella* O. Hoffm. to the subtribe. Nesom and Robinson, however, mentioned the potential relatedness of African conyzas to the subtribe. Earlier, Nesom (1994g) had suggested a relationship of the African conyzas to the *Nidorella* Cass. group of *Grangeinae*, as was proposed by Wild (1969a, b). Our data support this relationship, but only generally: *Nidorella* appears more closely related to *Grangea* Adans. than to the conyzas in our analysis. Nesom (1994g) had placed *Psiadia* in *Baccharidinae*, a relation not supported here. It was left unplaced in the Nesom and Robinson classification. Finally, *Welwitschiella*, a genus traditionally placed within *Heliantheae* s.l., also belongs here (Brouillet et al. pers. comm.). This genus has not been treated within *Astereae* before.

Fiz et al. (2002) studied the evolution of subtribe *Bellidinae* s.str. (Fig. 37.2C) and showed it had relationships with *Bellidiastrum* Cass. and the *Galatella* Cass. group (Fig. 37.1A⑩). The current analysis supports this view and suggests that *Bellidinae* should be expanded to include *Bellidiastrum* and the *Galatella* group, placed in *Asterinae* by Nesom and Robinson (2007) and often treated as *Aster* species in the past. Furthermore, an African origin for *Bellidinae* is suggested by their placement on the tree, in a polytomy with mainly African *Grangeinae*.

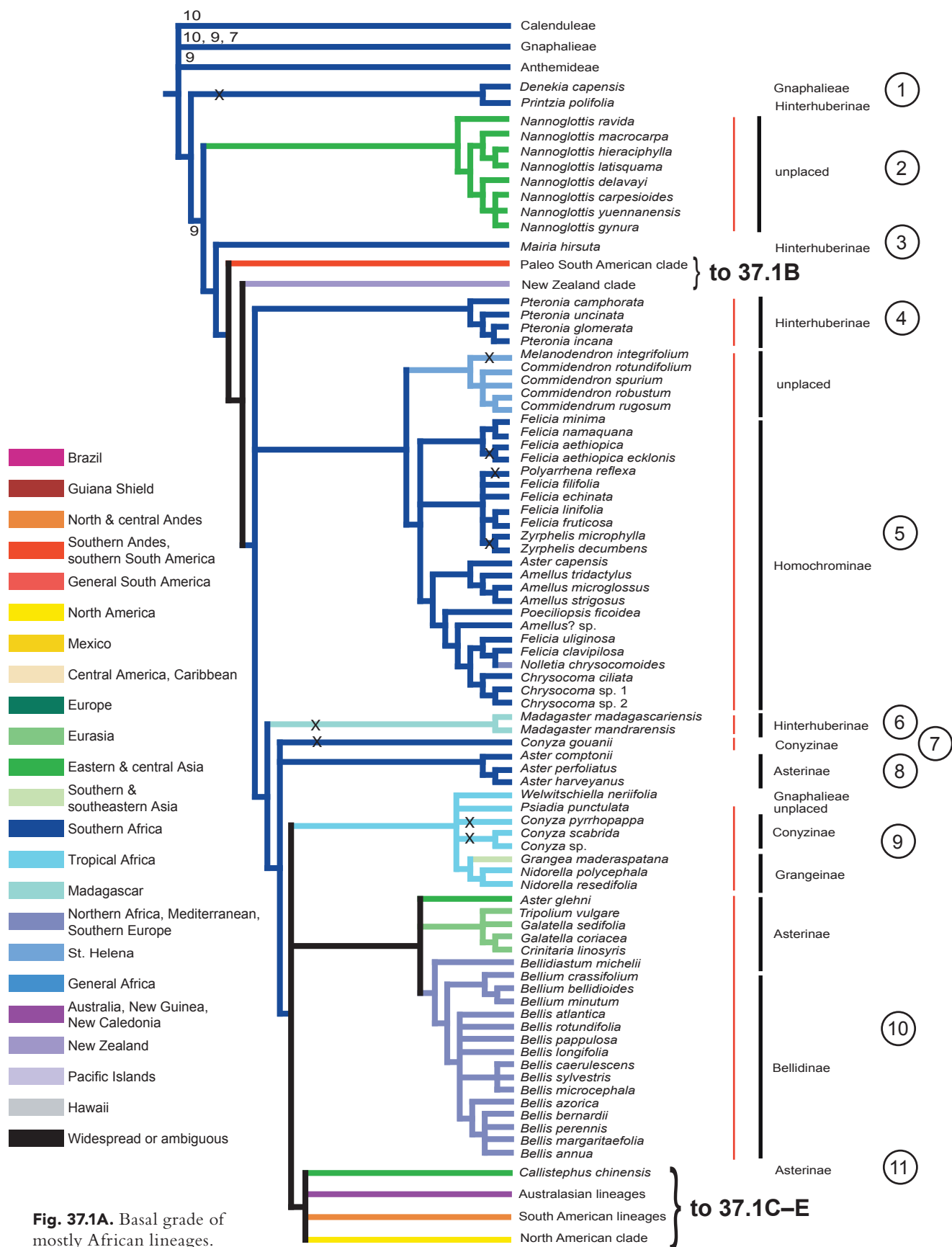
As with *Nannoglottis*, *Callistephus* Cass. (Brouillet et al. 2001; Semple et al. 2002) occupies an isolated position within the *Astereae* phylogeny (Fig. 37.1A⑪–C), usually within the crown group polytomy. It never groups with *Aster* s.str., in contradiction to its classification in subtribe *Asterinae* (Nesom 1994g; Nesom and Robinson 2007). Given that few Asiatic genera have been included in molecular phylogenetic analyses, it is difficult to reach further conclusions concerning this taxon.

Paleo South American clade

The Paleo South American clade (Fig. 37.1B) is placed in the phylogeny between the South African *Mairia* lineage (above) and the New Zealand clade (below). In more restricted phylogenies (Brouillet et al., pers. comm.), it is sometimes sister to the New Zealand clade. The interrelationships of these two clades remain to be ascertained. The clade includes taxa placed within *Hinterhuberinae* by Nesom and Robinson (2007). Our phylogeny shows that subtribe to be polyphyletic. The Paleo South American clade consists of two sister subclades: the *Chiliophyllum* Phil. nom. cons. and the *Oritrophium* (H.B.K.) Cuatrec. clades.

The *Oritrophium* clade (Fig. 37.1B①) includes rosette herbs that are scapose (*Oritrophium*) or acaulescent (*Novenia* S.E. Freire). They are adapted to the climatic and edaphic conditions of the puna and páramo ecosystems, respectively (Freire 1986; Torres et al. 1996). *Oritrophium* is distributed in South America and Mexico. Because of its herbaceous habit, it was considered a highly derived member of subtribe *Hinterhuberinae* (Nesom 1993a). Its rosulate habit, scapose inflorescences, and staminate disk florets define the genus. Recently two new species of *Oritrophium* were described from Mexico (Nesom 1992, 1998b). This is a remarkable

Fig. 37.1. Strict consensus tree of tribe *Astereae* based on a parsimony phylogenetic analysis of ITS sequence data. **A** (opposite page) basal grade of mostly African lineages; **B** (p. 594) Paleo South American and New Zealand clades; **C** (p. 596) Australasian lineages; **D** (p. 597) South American lineages; **E** (pp. 598–599) North American clade. Branches are colored according to geographic distribution, following the color code developed for this volume; Madagascar and St. Helena are color-coded distinctly from tropical Africa (Fig. 37.1A). Numbers along branches are basic chromosome number (x) for all taxa subtended by the branch, unless otherwise indicated; \times on a branch indicates taxa for which chromosome numbers are lacking. Thin red lines to the right of trees indicate groups found in the unpublished ML analysis (Brouillet et al., pers. comm.). Black lines and subtribal names to the right of trees indicate subtribes according to Nesom and Robinson (2007). Circled numbers to the right refer to the groups discussed in text. For a complete biogeography tree of the entire *Compositae* see chapter 44.



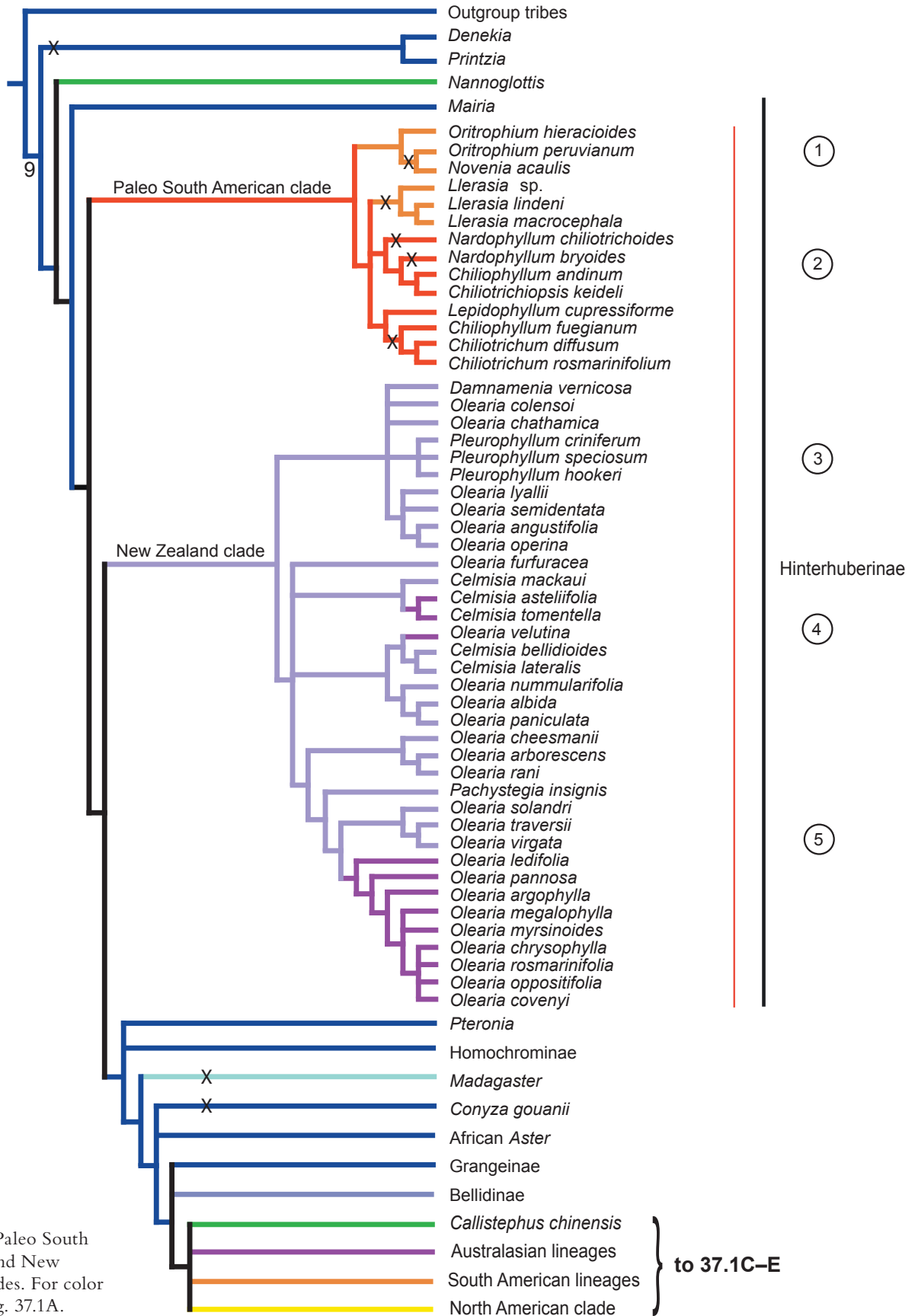


Fig. 37.1B. Paleo South American and New Zealand clades. For color chart see Fig. 37.1A.

finding because the genus has not been found in Central America. Such a disjunct distribution may be attributed to transport by birds, possibly from northern Venezuela (Cuatrecasas 1997). *Novenia*, a monotypic genus, is distributed at high elevations in the Andes from Bolivia to northern Peru and Argentina. *Novenia* is highly reduced, with rigid leaves with axillary clumps of tomentum, numerous sessile, disciform capitula in the center of the rosette, with reduced pistillate corollas and functionally staminate disk florets, and multinerved achenes with a multiseriate pappus of persistent barbellate bristles. These characters and the number of chromosomes typical of Astereae ($n = 9$) justified its transfer from Inuleae (Freire 1986; Anderberg 1991) to Hinterhuberinae (Nesom 1994g). The genus appears to be derived from within *Oritrophium*; more data are needed to evaluate the relationship of these two genera.

The *Chiliophyllum* clade (Fig. 37.1B②) includes resinous shrubby genera with usually white-tomentose leaves, radiate capitula, paleate receptacles, and bisexual disk florets (functionally staminate in *Lepidophyllum* Cass.): *Chiliotrichum* Cass. (Fig. 37.2D), *Chiliotrichiopsis* Cabrera, *Nardophyllum* Hook. & Arn., *Lepidophyllum* (Fig. 37.3C), and *Llerasia* Triana. These are mainly restricted to the arid puna region of southern Chile and Argentina (Patagonia and Tierra del Fuego). *Llerasia* is restricted to the uppermost montane forest of the Andes, below the páramo zone, in Peru, Ecuador, and Colombia. The group is characterized by a pappus of flattened bristles in one to several series. In *Nardophyllum*, pappus bristles vary from flattened to terete and widened apically, whereas pappus bristles in *Llerasia* are terete and scabrous. The presence of receptacular paleae is another defining feature for this group, but receptacles vary from epaleate in *Lepidophyllum* and three species of *Nardophyllum*, to few-paleate in *Chiliotrichum*, and *Llerasia*, to fully paleate in *Chiliotrichiopsis* and *Chiliophyllum* (Bonifacino and Sancho 2001). Variation in the number of receptacular paleae was recorded at the population level in *Nardophyllum* (Bonifacino 2005). *Lepidophyllum* is the only genus in the group with opposite leaves. *Chiliophyllum*, a genus of three species from Argentina and Chile, was traditionally distinguished from *Chiliotrichum* based on the color of ray florets, and from *Chiliotrichiopsis* based on the morphology of pappus bristles. In the present analysis, *Chiliophyllum* appeared polyphyletic. *Chiliophyllum fuegianum* O. Hoffm. in Dusén groups with *Chiliotrichum* and *Lepidophyllum*, and *Chiliophyllum andinum* Cabrera with *Nardophyllum* and *Chiliotrichiopsis*, suggesting that the defining characteristics of the genus are homoplasious (Karaman-Castro and Urbatsch, pers. comm.).

New Zealand clade

In this phylogeny (Fig. 37.1B), the New Zealand clade is located between the Paleo South American clade and a grade of African lineages (see above). A similar clade was

retrieved by Wagstaff and Breitwieser (2002), who noted that Astereae are the most diverse tribe of Asteraceae in New Zealand, and by Cross et al. (2002) as their primary clade II (but including *Chiliotrichum*); it also coincides with the *Olearia/Celmisia* complex of Given and Gray (1986) and the *Celmisia* group of Nesom (1994g). The New Zealand clade is comprised of over 100 endemic species that traditionally have been placed in five genera: *Celmisia* Cass. (Figs. 37.2E, 37.3D, E), *Damnomenia* Given, *Olearia* Moench (Figs. 37.2F, 37.3F), *Pachystegia* Cheeseman (Figs. 37.2G, 37.3G), and *Pleurophyllum* Hook. f. (Fig. 37.3H) (Wagstaff and Breitwieser 2002). All have been classified within Hinterhuberinae by Nesom and Robinson (2007); this taxonomy is not supported here. *Olearia* and *Pachystegia* are woody shrubs, whereas *Celmisia*, *Damnomenia*, and *Pleurophyllum* are subshrubs or herbs that arise from a woody base. These five genera are characterized by tailed anthers, tomentose leaves, and usually large heads, features they share with the South American genus *Chiliotrichum* (Cross et al. 2002). Many of the species are showy ornamental shrubs that are widely cultivated in New Zealand. A chromosome number of $2n = 108$ is the most commonly reported for members of the New Zealand clade, but numbers as high as ca. 432 have been reported for *Olearia albida* Hook. f. (Dawson 2000). The New Zealand clade is not restricted to New Zealand since members of *Celmisia* and *Olearia* s.l. independently dispersed to Australasia. Within the New Zealand clade, two subclades can be recognized: the megaherb clade, including *Damnomenia*, *Pleurophyllum*, and the macrocephalous *Olearia* species (Drury 1968; Given 1973), and the *Celmisia* clade, including *Celmisia*, *Pachystegia*, and the remaining New Zealand *Olearia* species (including the divaricating tree daisies; Heads 1998). *Olearia* is clearly polyphyletic (Cross et al. 2002), hence well-supported clades in New Zealand will likely be recognized as distinct genera.

Members of the megaherb clade (Fig. 37.1B③), *Damnomenia*, *Pleurophyllum* (the megaherbs), and macrocephalous olearias (*Olearia* spp.), were considered related by Drury (1968) and Given (1973). All were included in the current analysis (Fig. 37.1B). In Given's taxonomic scheme, *Damnomenia* and *Pleurophyllum* are closely related to *Olearia colensoi* Hook. f. and *O. lyallii* Hook. f., while the other olearias of the group (*O. oporina* Hook. f., *O. chathamica* Kirk, *O. angustifolia* Hook. f., and *O. semidentata* Decne. ex Hook.) were related only through *Celmisia*; the Australian *Pappochroma palucidola* (S.J. Forbes) G.L. Nesom (as *Erigeron pappochroma* Labill.) (Nesom 1994f, h, 1998a) was also considered tentatively related to *Celmisia* but was not included in molecular analyses and therefore cannot be evaluated (but see *Pappochroma* Raf. in Australasian lineages below). These taxa are concentrated in the subantarctic islands of New Zealand and Australia, and in the highlands of New Zealand (Drury 1968; Given

1973 provides a map of the taxa). Our phylogeny does not support membership of *Celmisia* in this clade but all other taxa identified by Given belong here, as was also noted by Cross et al. (2002). Members of the clade are trees, shrubs or woody-based herbs, with abaxially tomentose leaves, racemose capitulescences or solitary capitula, large capitula with usually purple disc florets (yellow in *O.oporina*) and tailed anthers with prominent apical appendages, and

long-villose achenes. *Dammamenia* is monotypic and based upon the distinctive subantarctic *D.vernica* (Hook.f.) (Given 1973). It was formerly considered as the sole member of *Celmisia* subgenus *Ionopsis*, but was recently recognized as a distinct genus. The distinctness of this taxon from *Celmisia* is confirmed here. *Pleurophyllum* includes three subantarctic island species, *P.speciosum* Hook.f., *P.criniferum* Hook.f., and *P.hookeri* Buchanan, which

to 37.1A, B

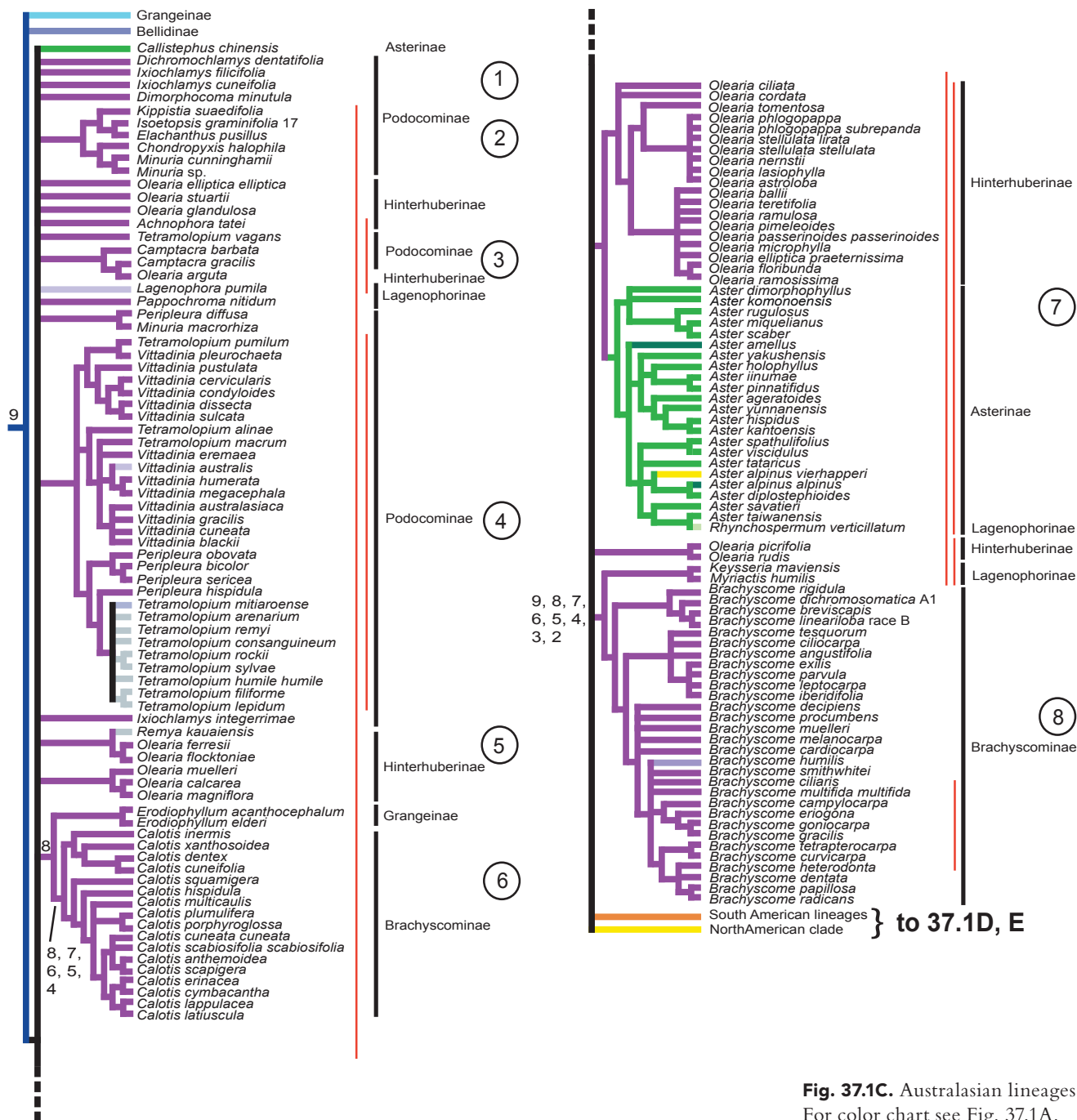
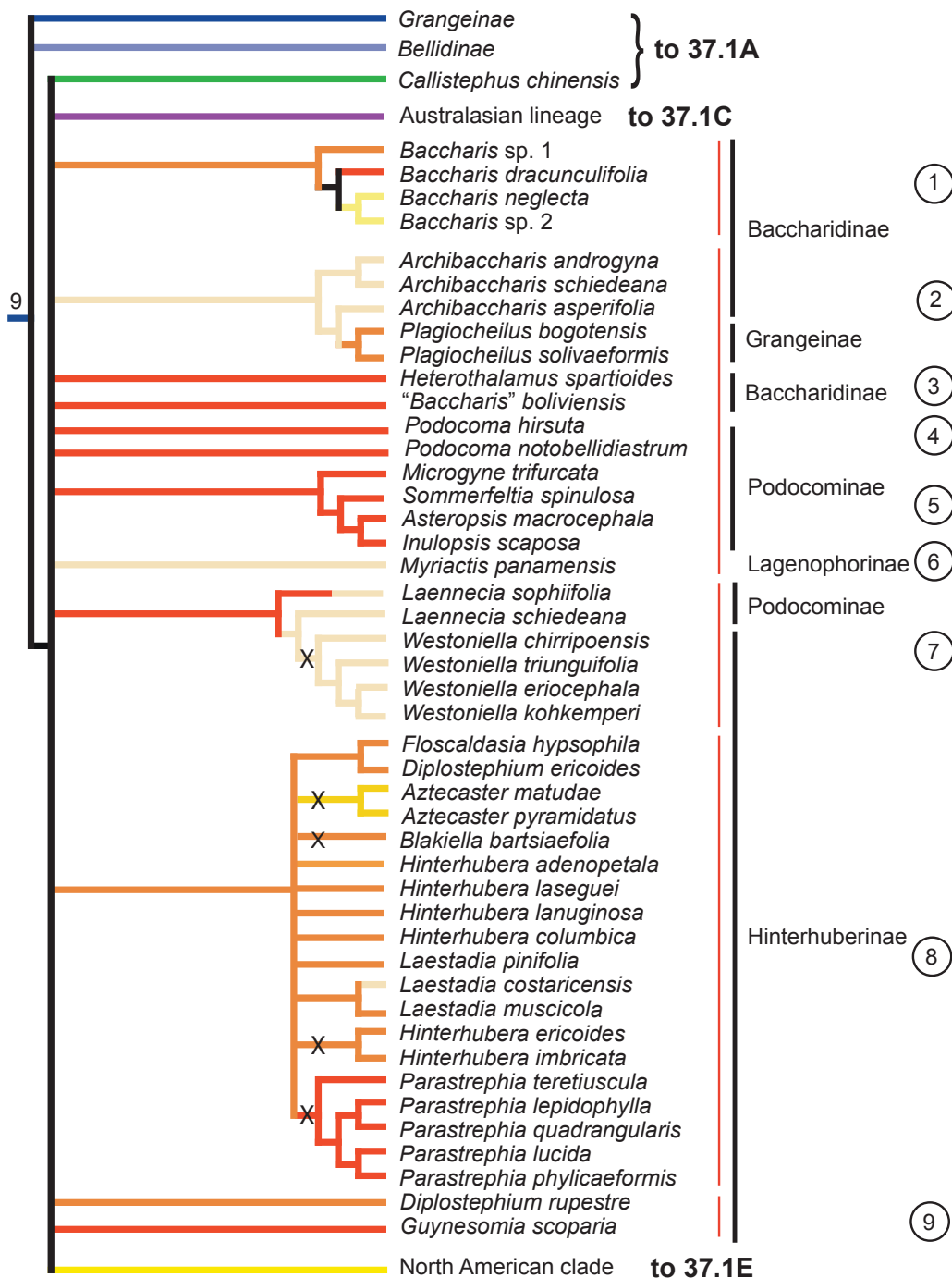


Fig. 37.1C. Australasian lineages. For color chart see Fig. 37.1A.

have purple or whitish-purple rays (Drury 1968). Drury (1968) noted the similarity of the macrocephalous olearias to *Pleurophyllum*, suggesting the inclusion of the former into the latter; Given (1973) proposed to include *O. colensoi* and *O. lyallii* in *Pleurophyllum* and to create a new genus for the others.

The genus *Celmisia* (Fig. 37.1B④) is not fully resolved in our analysis. This may be due to the fact that

only about 20% of the taxa have been included so far (S. Wagstaff, pers. comm.). The clade shows a polytomy comprised of an apparently isolated *O. furfuracea* Hook. f., a large *Pachystegia* clade, and two *Celmisia* lineages, one of which is associated with the *Olearia albida* subclade (clade F of Cross et al. 2002) and the New Guinean *O. velutina* Koster (*O. sp.* WNG in Cross et al., 2002). The *Olearia* groups recognized here coincide with those of the Cross



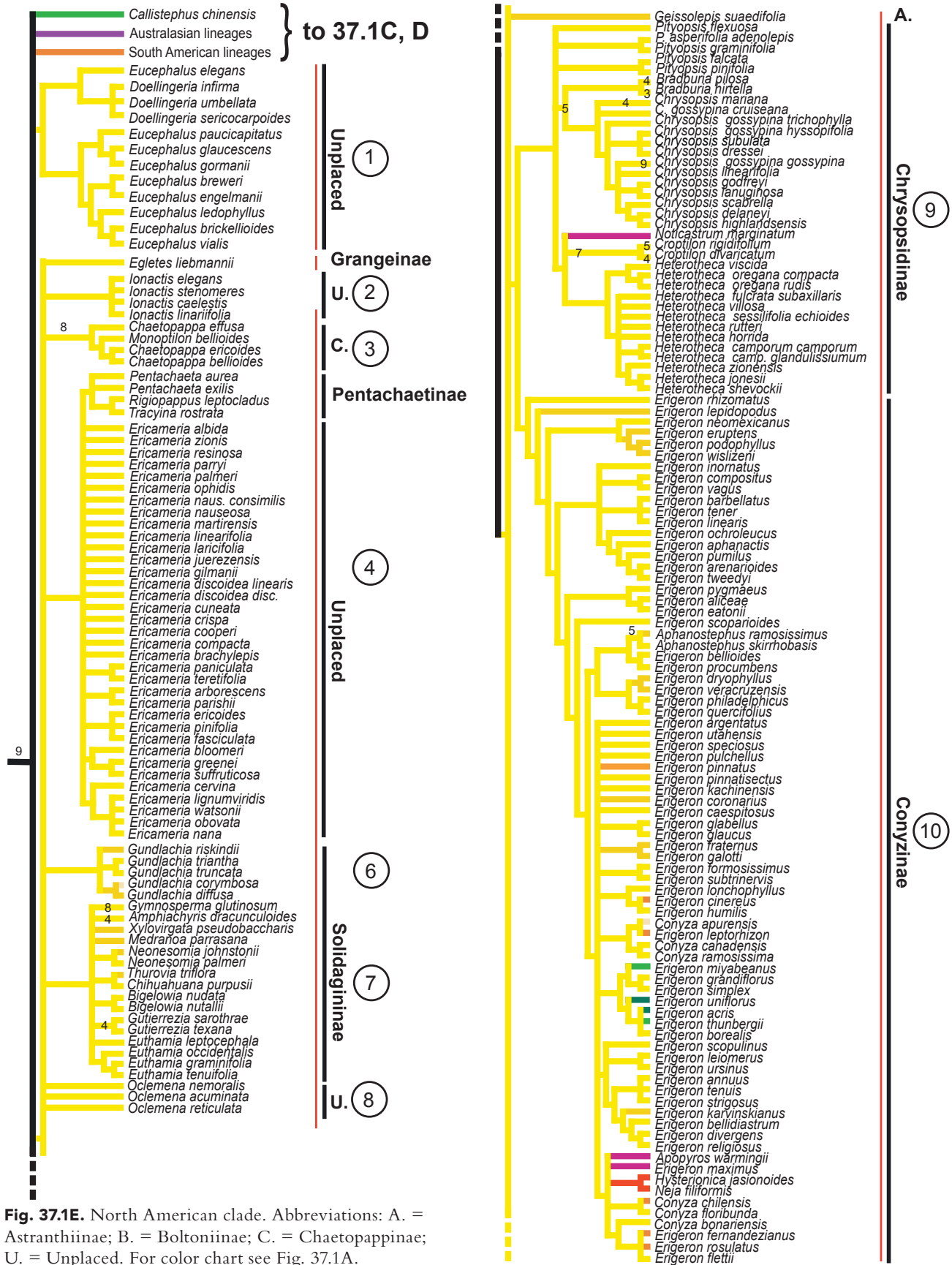


Fig. 37.1E. North American clade. Abbreviations: A. = Astranthiinae; B. = Boltoniinae; C. = Chaetopappinae; U. = Unplaced. For color chart see Fig. 37.1A.

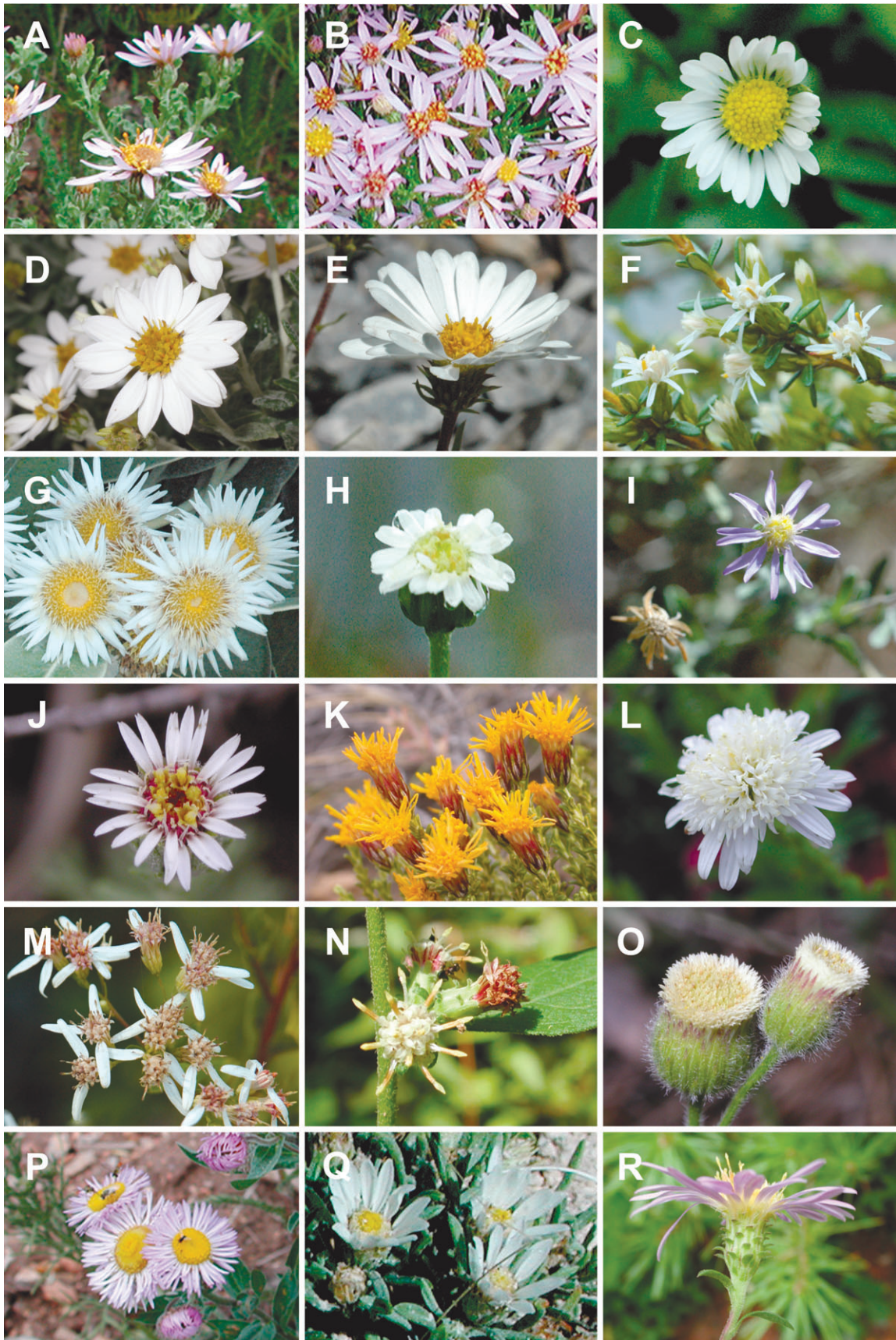


et al. primary clade II, except that the inclusion of more *Celmisia* species modified the relationships of group F and of *O. velutina*. The occurrence of natural intergeneric hybrids between *Celmisia* and *Olearia* species (e.g., Clarkon 1988) would lend support to a close relationship between the two taxa. *Celmisia* includes about sixty endemic New Zealand species and five Australian ones, grouped into six subgenera with eight sections (Given 1969) (the new subgenus *Ionopsis* subsequently described as *Dammamenia* by Given, 1973; see above). In our analysis, *Celmisia* is found in two clades: (1) *C. mackaui* Raoul–*C. asteliifolia* Hook. f.–*C. tomentella* M. Gray & Given, the latter two Australian, and (2) *C. bellidioides* Hook. f.–*C. lateralis* Buchanan. The first clade corresponds to the woody group of Allan (1961, as cited in Given 1969), characterized by biseriate corolla hairs widened at the tip, short pappus hairs, and few achene ribs; their living leaves are equally distributed on the stems. In Given's (1969) classification, *C. lateralis* belongs to subgenus, section, and series *Lignosae*, a group of woody, ericoid, erect subshrubs with globose receptacles, while *C. bellidioides* is a member of subg. *Caespitosae*, a group of softly woody, creeping herbs with short, oblong leaves and obconic receptacles. The relationships of this clade to various *Olearia* s.l. species needs to be explored further. The second clade corresponds to the herbaceous group of Allan, which coincides here with the subg. *Pelliculatae* of Given (1969) insofar as the species sampled are concerned. They are herbs arising from woody rootstocks with the densely compacted, pigmented leaf sheaths forming a pseudostem; the leaves are usually petiolate and firm, and are borne in rosettes at the ends of branches. *Celmisia mackaui* of New Zealand belongs to sect. *Petiolatae*, while the Australian *C. tomentella* and *C. asteliifolia* (the latter Tasmanian) are in sect. *Pelliculatae*, ser. *Linearifoliatae*, characterized by linear, rigid leaves. Gray and Given (1999a, b) report ten species of *Celmisia* in Australia, all derived from New Zealand taxa, including the two sampled species. Given our limited sample of *Celmisia* and *Olearia* species, it would be premature to conclude whether *Celmisia* is poly- or

paraphyletic, however. The presence of large heads (the macrocephalous condition) in the megaherb and *Celmisia* clades suggests either that this trait was acquired in parallel in both lineages or that it is symplesiomorphic to the New Zealand clade. Cross et al. (2002) noted that either their clade F (*O. albida* subclade) or *O. furfuracea* were sister to *Celmisia*. Our analysis confirms a relation between the *O. albida* subclade and *Celmisia*, but is inconclusive concerning *O. furfuracea*. The position of *O. velutina* in our analysis as sister to *Celmisia bellidioides*–*C. lateralis* contrasts with the sister relationship with the *O. cheesemanii* Cockayne & Allan clade (clade G) found by Cross et al. (2002) in a reduced analysis (it was part of the clade II polytomy in their total analysis, however). The *O. albida* subclade is characterized by stellate hairs (Cross et al. 2002), which contrasts with the usually tomentose hairs of *Celmisia*.

The *Pachystegia* clade (Fig. 37.1BⓈ) includes the *Olearia cheesemanii* subclade (clade G of Cross et al. 2002), *Pachystegia*, and the *O. solandri* Hook. f. subclade (divaricating tree daisies; clade H) sister to the Australian *O. ledifolia* (DC.) Benth. subclade (clade E). It is the second most diverse group of New Zealand Astereae. Species of *Olearia* are generally recognized by their shrubby growth habit and usually dense indumentum on the lower leaf surface. However, there is remarkable diversity in phyllotaxis, leaf shape and margin, leaf hairs, position and arrangement of the inflorescences, and pappus bristles. Apart from *Pachystegia*, which has elongate intertwined hairs, all members of this clade appear to have t- or y-type hairs, suggesting the possibility of a single origin for these hair types (Cross et al. 2002). *Pachystegia* is a small genus including three species, only one of which was included here. The species taxonomy is not clearly resolved and further study may show that three variants are also worthy of species rank (Molloy and Simpson 1980). The species of *Pachystegia* are showy, medium-sized shrubs with distinctive thick, leathery leaves. They are confined to one of the driest regions in New Zealand, the northeastern part of South Island. Commonly known as Marlborough

Fig. 37.2. Structure and diversity of the capitulum in tribe Astereae. **A** *Printzia polifolia* (L.) Hutch., Western Cape, South Africa; **B** *Felicia filifolia* Burt Davy, Western Cape, South Africa; **C** *Bellis perennis* L., lawn weed, Canterbury, New Zealand; **D** *Chiliotrichum diffusum* (G. Forst.) Kuntze, Bahía La Pataia, Tierra del Fuego, Argentina; **E** *Celmisia du-rietzii* Cockayne & Allan, Authors Pass National Park, New Zealand; **F** *Olearia solandri* Hook. f., cultivated Landcare Research experimental gardens, New Zealand; **G** *Pachystegia insignis* Cheeseman, cultivated Landcare Research experimental gardens, New Zealand; **H** *Lagenophora strangulata* Colenso, cultivated Landcare Research experimental gardens; **I** *Vittadinia gracilis* (J.D. Hook.) N.T. Burb., naturalized Godley's Head, New Zealand; **J** *Microgyne trifurcata* Less., Las Palmas, Córdoba, Argentina; **K** *Nardophyllum bryoides* (Lam.) Cabrera, Central Chubut, Argentina; **L** *Aster mongolicus* Franch., cultivated Ontario, Canada; **M** *Doellingeria sericocarpoidea* Small, St. Tammany Parish, Louisiana, USA; **N** *Brintonia discoidea* (Elliott) Greene, Alabama, USA; **O** *Conyza monorchis* (Griseb.) Cabrera, Sierra de las Animas, Maldonado, Uruguay; **P** *Erigeron subtrinervis* Rydb., Sandia Mountains, New Mexico, USA; **Q** *Townsendia gypsophila* T.K. Lowrey & P.J. Knight, White Mesa, New Mexico, USA; **R** *Eurybia spectabilis* (Ait.) G.L. Nesom, USA. [Photographs: A, B, P, Q, T.K. Lowrey; C, E–I, S. Wagstaff; D, J, K, O, J.M. Bonifacino; L, N, R, J.C. Semple; M, L. Urbatsch.]



rock daisies, they are widely cultivated. The New Zealand *Olearia solandri* subclade (sect. *Divaricaster*; Heads 1998) is supported by the opposite leaves synapomorphy (Cross et al. 2002). This group is sister to the Australian *O. ledifolia* subclade (clade E, traditionally classified in sect. *Dicerotriche*), as noted by Cross et al. (2002).

Astereae crown lineages. Australasian lineages

In the current analysis, Australasian lineages are part of the large polytomy at the crown of Astereae (Fig. 37.1A–C). The Australasian lineages (Fig. 37.1C) correspond with the primary clade I of Cross et al. (2002). In more restricted analyses (Brouillet et al., pers. comm.), however, the Australasian lineages sometimes form a clade that includes the mainly Asian genus *Aster* s.str. and always excludes members of the New Zealand clade discussed above. All members of *Olearia* that are not part of the latter are found here. No Australasian genus is found associated with South American members of Hinterhuberinae and Podocominae (see below; Fig. 37.1D), where they were placed by Nesom and Robinson (2007). This was also noted in analyses with a more limited taxon sampling (Cross et al. 2002; Brouillet et al., pers. comm.; Karaman-Castro and Urbatsch, pers. comm.). In the current analysis, the Australasian lineages are: (1) *Kippistia* F. Muell., *Isoetopsis* Turcz., *Elachanthus* F. Muell., *Chondropyxis* D.A. Cooke, *Pappochroma*, and *Minuria* DC. species; (2) *Olearia arguta* Benth.–*Camptacra* N.T. Burb.; (3) *Vittadinia* A. Rich.; (4) *Erodiophyllum* F. Muell.–*Calotis* R. Br.; (5) *Olearia* s.str.–*Aster* s.str.; (6) *Keyseria* Lauterbach–*Myriactis humilis* Merr.–*Brachyscome* Cass.; (7) *Remya* Hillebr.–*Olearia* species. There is also a series of ungrouped genera and species, which will be discussed where appropriate.

Two species sometimes classified in *Minuria* do not appear closely related to the genus in our analyses (Fig. 37.1Cⓐ). *Minuria macrorhiza* (DC.) N.S. Lander is sister to *Peripleura diffusa* (N.T. Burb.) G.L. Nesom, a species morphologically and molecularly distinct from other *Peripleura* (Lowrey et al. 2001). The suggestion that *Eurybiopsis* DC. should be reinstated to accommodate *M. macrorhiza* (Watanabe et al. 1996) may have merit; the status of *P. diffusa* should be considered simultaneously. *Minuria integerrima* (DC.) Benth. does not group consistently with other taxa, and particularly not with the

species of *Ixiochlamys* or *Minuria* included in the analyses; the identity of the voucher may need validation. It is a polyploid apomict (Davis 1964), which partly may explain its inconsistent positioning. Brouillet et al. (pers. comm.) showed that *Ixiochlamys filicifolia* Dunlop and *I. cuneifolia* (R. Br.) F. Muell. & Sond. are paraphyletic to *Dichromochlamys*, a result not seen here. This raises the question of the distinction of *Dichromochlamys* from *Ixiochlamys*. No relationships could be identified for this clade within Australasian Astereae. *Pappochroma*, represented by *P. nitidum* (S.J. Forbes) G.L. Nesom (*Erigeron nitidus* S.J. Forbes) (Nesom 1994f–h, 1998a), has an unresolved position in the polytomy, but in more restricted analysis, it groups with the genera discussed here (Brouillet et al. pers. comm.). Nesom and Robinson (2007) classify the genus within subtribe Lagenophorinae. *Lagenophora pumila* Cheeseman also is found in this polytomy, but it groups with *Camptacra* (below) in restricted analyses, not with *Pappochroma*.

Kippistia, *Isoetopsis*, *Elachanthus*, *Chondropyxis*, *Pappochroma*, *Minuria* (Fig. 37.1Cⓑ). Some of these small Australian genera have been excluded at one time from tribe Astereae (e.g., Bremer 1994), but they are currently included by Nesom and Robinson (2007), a position that is confirmed by the analyses of Bayer and Cross (2002) and Brouillet et al. (pers. comm.), and in the current one (Fig. 37.1C). In both the latter, these genera form a small clade, with *Kippistia* sister to *Isoetopsis*–*Elachanthus* and *Minuria* to *Chondropyxis*. These data appear to confirm the segregation of *Kippistia* from *Minuria* (Lander and Barry 1980), though only two of the nine species of *Minuria* s.str. were sampled here. The current study confirms the close relationships of *Isoetopsis* and *Elachanthus* (e.g., Bruhl and Quinn 1990, 1991), though a relationship to *Kippistia* appears novel. These genera never group with South American taxa, as would be expected if they belonged to Podocominae as defined by Nesom and Robinson (2007).

Lowrey et al. (2001) and our analysis (Fig. 37.1Cⓒ) both show that *Camptacra* is paraphyletic to *Olearia arguta*. No relationship of this group suggests itself in the current analysis. Artificial intergeneric hybrids were obtained between *Camptacra* and both *Vittadinia* and Hawaiian *Tetramolopium* Nees (Lowrey et al. 2001), but *Camptacra* and *O. arguta* are isolated from these in the current study.

Fig. 37.3. Growth habit diversity among southern hemisphere members of tribe Astereae. **A** *Printzia polifolia* (L.) Hutch., perennial herb, Western Cape, South Africa; **B** *Denekia capensis* Thunb., perennial herb, Connemara Lake World's View, Nyanda, Zimbabwe; **C** *Lepidophyllum cupressiforme* (Lam.) Cass., Strait of Magellan, close to Primera Angostura, Chile; **D** *Celmisia spectabilis* Hook. f., perennial herb from stout rootstock, near Lake Lyndon, Porter's Pass, New Zealand; **E** *Celmisia sessiliflora* Hook. f., alpine cushion plant, Arthurs Pass National Park, New Zealand; **F** *Olearia paniculata* Druce, small tree, Marlborough, New Zealand; **G** *Pachystegia insignis* Cheeseman, woody subshrub, cultivated Landcare Research experimental gardens, New Zealand; **H** *Pleurophyllum speciosum* Hook. f., megaherb, Campbell Island, New Zealand. [Photographs: A, T.K. Lowrey; B, M. Hyde; C, J.M. Bonifacino; E–H, S. Wagstaff; D, C. Meurk.]



Note that *Achnophora* F. Muell. and *Olearia* are placed in Hinterhuberinae by Nesom and Robinson (2007), and *Camptacra* and *Tetramolopium* in Podocominae. Such positions are not supported here.

The molecular phylogeny of the *Vittadinia* lineage was discussed by Lowrey et al. (2001). In the current analysis (Fig. 37.1C④), this lineage does not appear to be closely related to a specific Australasian group. Despite small differences in the topologies shown here and in the Lowrey et al. study, the relationships among groups within the complex are congruent. Both studies show that *Tetramolopium*, *Vittadinia* (Fig. 37.2H), and *Peripleura* (N.T. Burb.) G.L. Nesom form a clade. The close relationship indicated by the molecular data is supported by morphology (Lowrey et al. 2001). Furthermore, intergeneric hybrids with varying levels of pollen fertility can be produced from among the three genera (Lowrey, Quinn, and Avritt, unpub.). The segregation of *Peripleura* from *Vittadinia* (Nesom 1994e) was rejected by Lowrey et al. (2001) and is not supported here. Highly fertile hybrids have been obtained between the Australian *Peripleura hispidula* (F. Muell. ex A. Gray) G.L. Nesom and several species of Hawaiian *Tetramolopium*. Lowrey et al. (2001) and the current study support the crossing data and indicate that *Peripleura* is sister to the Hawaiian *Tetramolopium*, contradicting the hypothesis that New Guinean *Tetramolopium* are sister to the Hawaiian taxa as suggested by Lowrey (1995) and Lowrey et al. (2005). Finally, morphology, molecular data, and crossing data strongly suggest that the three genera should be merged into a single genus. Nesom and Robinson (2007) placed *Vittadinia*, *Tetramolopium*, and *Peripleura* in subtribe Podocominae. Such a relationship is not supported here, since these genera never group with South American Podocominae.

Remya kauaiensis Hillebr. from Hawaii groups with *Olearia ferresii* (F. Muell.) Benth. and *O. flocktoniae* Maiden & Betche (Fig. 37.1C⑤). Relationships between *Remya* and these *Olearia* species need further study.

In the current analysis, as in Brouillet et al. (pers. comm.), *Erodiohyllum* appears to be sister to *Calotis* (Fig. 37.1C⑥). The molecular phylogeny of *Calotis* by Watanabe et al. (2006), was based on ITS and *matK* sequence data for 17 of the 28 species; *Erodiohyllum* was not included. The *Calotis* clade shown here expresses similar relationships to the ITS and combined trees of those authors, except that

in our analysis, the *Calotis inermis* Maiden clade (their clade A) is sister to the *C. multicaulis* Druce–*C. cuneata* (Benth.) G.L.R. Davis clade (their clade B) plus *C. squamigera* C.T. White and *C. hispidula* F. Muell., both of which are unresolved in their analysis. Clade A, *C. squamigera*, *C. hispidula*, and clade B/E (except *C. anthemoides* F. Muell.) all have a base chromosome number of $x = 8$. This base number has also been reported for *Erodiohyllum* (Watanabe et al. 1996), which would tend to confirm both the sympleiomorphic status of $x = 8$ in *Calotis* and the relationship of the two genera, given that such a number would be synapomorphic in this part of the Astereae tree. Watanabe et al. (2006) noted the similar base number in the two genera and pointed out their uniqueness in Australia, without inferring a relationship between the two. Both genera are herbaceous, with convex (*Calotis*) or conic (*Erodiohyllum*) receptacles. Achenes are somewhat compressed in both and the pappus is absent; more or less developed pericarpic awns (outgrowths of the pericarp), characterize both genera. They inhabit arid areas of Australia. Collectively, these features appear to support a close relationship between the two. Relationships within *Calotis* are discussed in Watanabe et al. (2006). The placement by Nesom and Robinson (2007) of *Calotis* in Brachyscominae and of *Erodiohyllum* in Grangeinae is not supported here. In no analysis (e.g., Cross et al. 2002) does *Calotis* group with *Brachyscome*, which would be the case if both were members of Brachyscominae as hypothesized by Nesom and Robinson. Likewise, *Erodiohyllum* is the sole member of Grangeinae from Australia and seems geographically out of place in this African-south Asian group.

In analyses performed using a large number of species of *Olearia* and *Aster*, *Olearia* s.str. (including the type *O. tomentosa* (Wendl.) DC.) proves to be sister to the primarily Asian (secondarily European) genus *Aster* s.str. (including the type, the European *A. amellus* L.) (Brouillet et al. 2006a) (Fig. 37.1C⑦). Relationships between the mainly Australian *Olearia* s.str. and the Asian *Aster* s.str. (Fig. 37.2L) would indicate that *Aster* originated by dispersal from Australasia into eastern Asia. Fiz et al. (2002) suggested that *Rhynchospermum* was related to *Aster* and not to *Bellis*. Our analysis confirms their finding and places this genus as sister to *A. taiwanensis* Kitam., in a group with *A. savatieri* Makino. Asian segregate genera such as *Kalimeris* (Cass.) Cass. (Gu and Hoch 1997) (e.g.,

Fig. 37.4. Growth habit diversity among northern hemisphere members of tribe Astereae. **A** *Chrysoma pauciflosculosa* Greene, subshrub arising from woody base, Panhandle Florida, USA; **B** *Solidago sempervirens* L., perennial herb from woody rootstock, Santa Rosa Island, Florida, USA; **C** *Ericameria nauseosa* (Pall. ex Pursh) G.L. Nesom & G.I. Baird, woody subshrub, San Gabriel Mountains, California, USA; **D** *Heterotheca jonesii* (S.F. Blake) S.L. Welsh & N.D. Atwood, perennial herb arising from woody taprooted rootstock, Hell's Backbone Ridge, Utah, USA; **E** *Townsendia gypsophila* T.K. Lowrey & P.J. Knight, cushion, White Mesa, New Mexico, USA; **F** *Ampelaster carolinianus* (Walter) G.L. Nesom, vine, central Florida, USA. [Photographs: A, C, D, F, J.C. Semple; B, L. Urbatsch; E, T.K. Lowrey.]



A. holophyllus Hemsl., *A. pinnatifidus* (Hook.) Kuntze, *A. miquelianus* Hara in the current analysis), *Heteropappus* Less. (e.g., *Aster hispidus* Thunb.), and *Miyamayomena* Kitam. (e.g., *A. savatieri*) are also embedded within *Aster*, which suggests that they are not phylogenetically distinct from it. Natural hybrids between *Aster ageratoides* Turcz. and *Kalimeris incisa* (Fisch.) DC. (*Aster incisa* Fisch.) (Tara 1989), for instance, and phylogenetic analyses of cpDNA RFLP data (Ito et al. 1994, 1995, 1998) support this. Indeed, Ito and Soejima (1995) included *Kalimeris* within *Aster*. Members of *Doellingeria* Nees sect. *Cordifolium* (Nesom 1993c) (e.g., *A. dimorphophyllus* Franch. & Savat., *A. komonoensis* Makino, *A. rugulosus* Maxim., *A. scaber* Thunb.), together with *A. miquelianus*, form a clade sister to the rest of *Aster* s.str. (Fig. 37.1C). The name *Doellingeria* (see Saito et al. 2007 for a recent usage) cannot be applied to Asian species since the type of the genus, *D. umbellata* (Mill.) Nees, belongs to the North American clade (Nesom 1993c); such a usage would make *Doellingeria* polyphyletic. These taxa might best be treated within *Aster*.

The *Keysseria-Myriactis humilis-Brachyscome* grouping (Fig. 37.1CⓈ) has been noted first by Brouillet et al. (2006a; ML analysis, unpub.). *Keysseria* and *Myriactis* Less. were not included, however, in the Denda et al. (1999) and Field et al. (2006) phylogenetic studies of *Brachyscome*, respectively based on *matK* and ITS sequence data. All three genera are herbs (perennial, often annual in *Brachyscome*) with campanulate heads, herbaceous phyllaries in 1–2 series (rarely more), rays in one or more series, bisexual disk florets (functionally male in *K. radicans* (F. Muell.) Matf.), achenes without pappus or with a pappus of united bristles, occasionally scale-like, and a base chromosome number of $x = 9$. These features, however, are not significant enough by themselves to confirm a relationship and the hypothesis must be investigated further, since it could be the result of insufficient taxon sampling among Australasian Astereae. *Keysseria* and *Myriactis* were placed in Lagenophorinae by Nesom and Robinson (2007). Only three genera of the subtribe are included here, *Rhynchospermum* Lindl., which is nested within *Aster* s.str. (which see), the Central American *Myriactis panamensis* (S.F. Blake) Cuatr., sometimes included in *Lagenophora* Cass., and *Lagenophora pumila*, a New Zealand species, two taxa that do not group here and in analyses (Cross et al. 2002; Karaman-Castro and Urbatsch, pers. comm.). These data imply that neither *Myriactis* nor *Lagenophora* (Fig. 37.2I) are monophyletic as currently defined. Neither *Lagenophora* species groups with *Keysseria* and *Myriactis* in any analysis, suggesting that their subtribal affinities lie elsewhere. In the absence of further representation of the subtribe it is difficult to assess its status. Relationships and evolution within *Brachyscome* recently were discussed by Denda et al. (1999) and Field et al. (2006). Short (2004) segregated *Allittia* P.S. Short, *Hullisia* P.S. Short, and

Pembertonia P.S. Short from *Brachyscome*. *Allittia cardiocarpa* (F. Muell. ex Benth.) P.S. Short (*Brachyscome cardiocarpa* F. Muell. ex Benth. here) was included in the Field et al. and the current analyses, and is appears nested within *Brachyscome* in both cases. On the basis of the sampling at hand, it would appear that *Allittia* is embedded within *Brachyscome*. Given that *Brachyscome* includes more than 110 species and that our sampling is incomplete, however, it may be premature to assess the taxonomy of the genus. It is noteworthy that long-distance dispersal occurred to New Zealand at least once, as exemplified by *B. humilis* G. Simpson & J.S. Thompson (Fig. 37.1C).

South American lineages

Parsimony (Brouillet et al. 2006a) and ML (unpub.) analyses of the ITS data (using a slightly smaller taxon set) revealed four main South American lineages: (1) *Baccharis* L. s.str. (Baccharidinae); (2) Podocominae plus diverse South American genera classified in Baccharidinae (excluding *Baccharis* s.str.), Lagenophorinae, and Grangeinae; (3) *Laennecia* and *Westoniella* Cuatr.; and (4) Hinterhuberinae genera. In the ML analysis (unpub.), these lineages form a grade to the North American clade (NAC); in the parsimony analysis (Brouillet et al. 2006a), a *Baccharis* lineage diverged prior to a Podocominae–Hinterhuberinae clade, itself sister to the NAC. In the current analysis (Fig. 37.1D), these lineages form a polytomy. In each analysis, the position of *Guynesomia* Bonif. & G. Sancho varied. Below, we discuss these lineages.

The circumscription of Baccharidinae by Nesom and Robinson (2007) includes *Archibaccharis* Heering, *Baccharis*, and *Heterothalamus* Less. In our analysis, all the species of *Baccharis* except for *B. boliviensis* (Wedd.) Cuatr. form a clade (Fig. 37.1DⓈ). In the more restricted analyses mentioned above, these taxa all grouped with subtribe Podocominae (below), not with *Baccharis*. *Baccharis* is a large genus of about 360 species ranging from Argentina to the southern United States. The species are mostly dioecious, although monoecious or polygamo-dioecious species have been reported (Cuatrecasas 1967; Jackson 1975; Giuliano 2000; Müller 2006). The morphological variability in *Baccharis* led Hellwig (1992) to divide the genus into several segregates. In his recent monograph of Bolivian species, however, Müller (2006) maintained the wider delimitation, including *B. boliviensis*. Zanolwiak (1991) conducted a cpDNA RFLP phylogenetic study of Baccharidinae, but sampling outside the subtribe was insufficient to evaluate its monophyly. Our current data, admittedly limited, do not support the monophyly of the subtribe nor of *Baccharis* s.l. They support the segregation of *Aztecaster* G.L. Nesom (Nesom 1993a) and of *Heterothalamus* from *Baccharis*, and do not support the position of Müller (2006) on this topic. A thorough phylogenetic study of *Baccharis* is needed.

As established on the basis of morphology (Nesom and Robinson 2007), Podocominae comprise South American and Australasian (above) genera. In all analyses, Australasian elements never grouped with South American ones. Therefore, Podocominae are restricted here to the South American elements that group with *Podocoma* Cass. The South American genera included by Nesom and Robinson in the subtribe are *Asteropsis* Less., *Inulopsis* O. Hoffm., *Laennecia* Cass., *Microgyne* Less. (Fig. 37.2J), *Podocoma*, and *Sommerfeltia* Less. In more restricted analysis (Brouillet et al. 2006a), the Podocominae clade comprised: *Myriactis* (*Lagenophora*) *panamensis* [Lagenophorinae] (*Podocoma* *hirsuta* Baker (*Baccharis boliviensis*, *Heterothalamus* [Baccharidinae]) [= the *Heterothalamus* subclade]) (*Podocoma* *notobellidiastrum* (Griseb.) G.L. Nesom) ((*Archibaccharis* [Baccharidinae]-*Plagiocheilus* Arn. ex DC. [Grangeinae] [= *Archibaccharis* subclade]) (*Asteropsis* clade)).

Archibaccharis (Fig. 37.1D②) is a mainly Mexican and Central American genus that probably ranges to Bolivia; it includes ca. 32 functionally dioecious species. Its resemblance to *Baccharis* was pointed out by several authors (e.g., Blake 1924; Jackson 1975; McVaugh 1984; Nesom 1994g, 2000a), but it differs by the presence of hermaphrodite florets in the center of the female capitula and by its compressed, 2-nerved achenes (vs. female capitula wholly of pistillate florets and terete, 5–10-nerved achenes in *Baccharis*). Relationships among *Baccharis*, *Archibaccharis*, and *Heterothalamus* have been recognized by authors (e.g., McVaugh 1984; Bremer 1994; Nesom 1994g) mainly based on sexuality and morphology of capitula. *Archibaccharis* and *Heterothalamus* have been seen as phylogenetically “basal” to *Baccharis* (Nesom 2000a) and functionally dioecious species of *Archibaccharis* as evolutionary stages to dioecy in *Baccharis* (Jackson 1975). In Karaman-Castro and Urbatsch (pers. comm.) as well as in our analysis (Fig. 37.1D), *Archibaccharis* is closely related to *Plagiocheilus* Arn. ex DC. (Grangeinae fide Nesom and Robinson 2007). *Plagiocheilus* includes seven species ranging from Colombia to Argentina (Ariza Espinar 1997). Some of the characteristics that have made *Plagiocheilus* difficult to place in the tribe are the deeply pinnatifid leaves, the hemispherical, heterogamous heads, the rays (outer florets) with bilabiate corollas, the functionally male disc florets with tubular corollas, and the epappose achenes. *Plagiocheilus* often has been treated in Anthemideae (e.g., Cabrera 1974; Ariza Espinar 1997), but our molecular analysis confirms its placement in Astereae, as suggested by previous authors (e.g., Robinson and Brettell 1973; Grau 1977; Bremer 1994).

Heterothalamus and *Baccharis boliviensis* form a subclade (Fig. 37.1D③). The Andean *B. boliviensis* departs from other *Baccharis* species by its female capitula with paleate receptacles and corollas with short laminae (vs. female capitula usually epaleate and female corollas apically denticulate

or less commonly minutely limbed in *Baccharis*), although similar characters are sporadically present in some *Baccharis* species (Cabrera 1978; Giuliano 2000). It was originally described as a *Heterothalamus* species (Weddell 1856). Our analysis supports the distinctiveness of this species from *Baccharis*, as previously noted by other authors that treated it under *Heterothalamus* or *Psila* Phil. *Heterothalamus* is a genus of three species (Paz Deble et al. 2005) from Argentina, Brazil, and Uruguay, that are polygamo-dioecious or imperfectly dioecious glandular shrubs. The male capitula have epaleate receptacles and pistillate or neutral rays (pistillate florets), and the female have paleate receptacles and all pistillate, short-limbed rays. In the current analysis, *Heterothalamus* falls in a polytomy, while in some more restricted analyses, it groups with *B. boliviensis* and *Podocoma hirsuta*. In no instance is it related to Baccharidinae s.str.

Podocoma, with eight mainly Argentinian-Brazilian species (Nesom 1994c), has capitula with 2–3-seriate, narrow and short-limbed rays, and typical rostrate achenes. Our analysis (Fig. 37.1D④) shows a non-monophyletic *Podocoma*, in agreement with other molecular and morphological analyses (Sancho and Karaman-Castro 2008). In these, *Podocoma hirsuta* appears to be an early diverging member of the *Heterothalamus* subclade, and *P. notobellidiastrum* to both the *Archibaccharis* subclade and the *Asteropsis* clade. The genus deserves further study.

Only *Asteropsis*, *Inulopsis*, *Microgyne*, and *Sommerfeltia*, four genera with radiate and usually solitary capitula, appear to form a monophyletic group in both the current (Fig. 37.1D⑤) and the more restricted analyses. A close relationship among these genera is in agreement with other studies based on morphological and molecular data (Nesom 1994c, d; Sancho et al. 2006; Sancho and Karaman-Castro 2008).

Myriactis (*Lagenophora*) *panamensis* (Fig. 37.1D⑥) is a Central American member of Lagenophorinae sensu Nesom and Robinson (2007); the other Lagenophorinae in our analysis fall within the Australasian lineages (above). This species is a delicate rosulate herb with basal and cauline leaves, monocephalous, radiate capitula, and epappose, beaked achenes. Along with five other Central American species, it is representative of a genus otherwise known in Asia (Cuatrecasas 1982; Nesom 2000a, 2001; Pruski and Sancho, pers. comm.). Its placement within Podocominae, instead of with Australasian or African lineages, suggests that *Myriactis* as currently conceived is polyphyletic.

In the Brouillet et al. (2006a) parsimony analysis, *Laennecia-Westoniella* (Hinterhuberinae) were sister to Podocominae, a relationship not retrieved here (Fig. 37.1D⑦). *Laennecia* ranges from Argentina to the Dominican Republic and the southern United States (Nesom 1990; Sancho and Pruski 2004). It includes 17 species of commonly woolly or glandular herbs with usually paniculiform or spiciform capitulescences of small, mostly dis-

ciform capitula (Zardini 1981). In our analysis, *Laennecia* forms a monophyletic group with *Westoniella* (Fig. 37.1D), a genus of six species endemic to the páramos of Central America (Cuatrecasas 1977). They are reduced subshrubs, sometimes cushion-like, that inhabit rocky and humid habitats. *Westoniella* was included in the subtribe Hinterhuberinae (Cuatrecasas 1986; Nesom and Robinson 2007) based on morphological features. One of the unique features of the genus are the marginal, bulbous-tubular corollas that somewhat radiate from the capitula (Pruski and Sancho, pers. comm.). Although molecular data relate *Laennecia* and *Westoniella*, these genera differ greatly in habit, capitulescence, capitula, marginal florets, and papus features.

As defined by Nesom and Robinson (2007), subtribe Hinterhuberinae includes 33 genera distributed in Australasia, Africa, Madagascar, and South and Central America, two genera reaching Mexico. Recent molecular analyses do not support the monophyly of the subtribe (Noyes and Rieseberg 1999; Cross et al. 2002; Brouillet et al. 2006a; unpub. ML analysis; Karaman-Castro and Urbatsch, pers. comm.). In the present analysis, South American genera previously classified in Hinterhuberinae belong mainly to two distinct lineages, the Paleo South American clade and a more restricted Hinterhuberinae (Fig. 37.1DⓈ), in a polytomy with Podocomiae, *Diplostephium rupestre* Wedd., and *Guynesomia*. In more restricted analyses, *Diplostephium rupestre* usually is sister to Hinterhuberinae, while the position of *Guynesomia* varies. Two subclades were recognized in restricted analyses (Brouillet et al. 2006a; unpub. ML analysis), (*Floscaldasia* Cuatrec.–*Diplostephium ericoides* (Lam.) Cabrera) (*Blakiella* Cuatrec.–*Aztecaster*), sister to *Parastrephia* Nutt. (*Hinterhubera* Sch.Bip.–*Laestadia* Kunth). In these analyses, Hinterhuberinae are sister either to Podocomiae or to the North American clade. As restricted here, Hinterhuberinae have the following features: disciform or discoid capitula (radiate in *Diplostephium*), epaleate receptacles, zygomorphic to actinomorphic rays (pistillate florets) with more or less reduced laminae (in *Floscaldasia* and *Blakiella*, the laminae are well developed but the florets are minute and the capitula appear disciform), and functionally staminate disc florets (bisexual in *Guynesomia*). *Aztecaster* is the only dioecious genus within Hinterhuberinae. The subtribe includes genera of diverse habits: *Diplostephium* includes small trees and shrubs, *Floscaldasia* is a herbaceous perennial, *Laestadia* includes small subshrubs and herbaceous perennials, *Blakiella* is a subshrub, *Hinterhubera* are mainly low shrubs with more or less densely tomentose, revolute, ericoid leaves, *Parastrephia* and *Aztecaster* are tall shrubs with tomentose ericoid leaves.

Blakiella, a monotypic genus from the páramos of Colombia and Venezuela, has beaked achenes. Its recent transfer from Podocomiae to Hinterhuberinae

(Nesom and Robinson 2007) is supported by this analysis. Achenes in *Blakiella* are cylindrical with 3–5 nerves, unlike the compressed and usually 2-nerved achenes in Podocomiae.

Aztecaster includes two similar but widely allopatric species endemic to Mexico. The dioecy in Baccharidinae and *Aztecaster* probably developed along different pathways (Nesom 1993a), which is also suggested by the current analysis (Fig. 37.1D).

Laestadia is distributed in Costa Rica, Hispaniola, Bolivia, Peru, Ecuador, Colombia, and Venezuela. The genus was considered among the most specialized members of Hinterhuberinae because of its herbaceous habit (Nesom 1994g, 2000a). Unusual features include beaked, epappose achenes, otherwise characteristic of Grangeinae, also found in Lagenophorinae. The multinerved, partially compressed achenes and disk florets with sterile ovaries nest *Laestadia* in Hinterhuberinae, while the similarity of achenes with those in Grangeinae and Lagenophorinae is a result of convergent evolution, as confirmed by the molecular analyses of Karaman-Castro and Urbatsch (pers. comm.) (Fig. 37.1D). In Brouillet et al. (2006a), *Laestadia* was intermixed with *Hinterhubera*, rendering both genera paraphyletic. In the analyses of the combined ITS and ETS datasets (Karaman-Castro and Urbatsch, pers. comm.), the two genera were monophyletic in a weakly supported clade with *Blakiella*. This deserves further investigation.

Diplostephium is a large genus of ca. 90 species, which is distributed in the páramos from Costa Rica to northern Chile. Because of its radiate capitula and partially paleate receptacles, it was thought to be related (Nesom 1994g) to genera here placed in the Paleo South American clade. The most interesting feature in the morphology of *Diplostephium* is the variation of style branch length in disk florets. Blake (1928) suggested that the evolution of the genus was directed towards development of two groups, one with subentire, slightly bifid styles and sterile disk florets, and the other with elongate styles and fertile disk florets. The two species included in the present analysis represent both types, *D. rupestre* has a merely bifid style, and *D. ericoides* has styles with elongate branches. The two taxa formed a weakly supported clade in previous analyses (Karaman-Castro and Urbatsch, pers. comm.), while our phylogeny suggests that the two groups are not immediately related and that the genus is polyphyletic.

Guynesomia (Fig. 37.1DⓈ) is a monotypic genus endemic to Chile that was recently segregated from *Nardophyllum* (Fig. 37.2K), a genus of the Paleo South American clade (Fig. 37.1A), based on its disciform capitula and epaleate receptacles, versus the discoid capitula and paleate receptacles of *Nardophyllum* (Bonifacino and Sancho 2004). Its numerous capitula are arranged in paniculiform or racemiform capitulescences and have bisexual disc florets.

The placement of *Guynesomia* in the South American clade (Fig. 37.1D) strongly supports its distinctness from *Nardophyllum*, although a hypothesized close relationship of *Guynesomia* to the radiate *Diplostephium* (Bonifacino and Sancho 2004) was not confirmed in the present analysis. The relationship of *Guynesomia* to the remaining Hinterhuberinae remains unresolved (Karaman-Castro and Urbatsch, pers. comm.).

North American lineage

Relationships of the North American clade appear to be with South American Hinterhuberinae and Podocominae discussed above (Fig. 37.1D). It is yet unclear whether these clades form a grade to the North American clade or whether they form a monophyletic group sister to it.

Nesom (2000a) provided a generic conspectus and a literature review of tribe Astereae in North America, which integrated parts of the molecular phylogenetic data then published. This paper summarized his views on the subtribal classification of Astereae for the continent, a modification of Nesom (1994g) now superseded by Nesom and Robinson (2007). Most of the molecular phylogenetic analyses then published were based on RFLP of chloroplast DNA (Suh and Simpson 1990; Morgan and Simpson 1992; Morgan 1993, 1997; Lane et al. 1996; Zhang 1996; Semple et al. 1999), though some of these included ITS data as well (e.g., Morgan 1993, 1997). Semple et al. (1999, 2002) published floristic treatments for Ontario goldenrods and asters, respectively, that included phylogenetic discussions. More recently, a complete floristic treatment of North American genera north of the Mexican border was published that incorporated recent phylogenetic findings and pertinent literature (Flora of North America Editorial Committee 2006). Most of the North American genera are endemic to the continent or nearly so, and thus the North American clade has been the object of a thorough treatment at the generic and species level, except for taxa present only in Mexico and adjacent Central America, and those that migrated secondarily to Eurasia and Central and South America (species of *Erigeron* L., *Grindelia* Willd., *Gutierrezia* Lag., *Solidago* L., *Psilactis* A. Gray, and *Symphotrichum* Nees, and South American endemic genera such as *Haplopappus* Cass. and *Noticastrum* DC.).

Noyes and Rieseberg (1999) first revealed the existence of a monophyletic North American clade, a group that had never been recognized before. Phylogenetic analyses of North American groups, based mostly on ITS data but some with cpDNA RFLPs or ETS data as well, have been published subsequently (Noyes 2000a; Markos and Baldwin 2001, 2002; Morgan 2003; Urbatsch et al. 2003; Roberts and Urbatsch 2003, 2004; Beck et al. 2004; Brouillet et al. 2001, 2004; Selliah and Brouillet 2008). These papers provide in-depth analyses and literature

reviews of the studied groups. The following groups can be recognized within the North American clade.

Noyes and Rieseberg (1999) showed *Doellingeria* (Fig. 37.2M) as an early diverging taxon within the North American clade. Subsequent analyses by Brouillet et al. (2001; Semple et al. 2002) showed *Eucephalus* Nutt. and *Doellingeria* together as sister to the North American clade (Fig. 37.1Eⓐ). This complex appears to be of western North American origin, with a more recent invasion of temperate eastern North America by *Doellingeria*. *Doellingeria* as defined here excludes the Asian species (sect. *Cordifolium*) assigned to this genus by Nesom (1993b). The latter, originally treated as *Kalimeris* sect. *Cordifolium*, are part of *Aster* s.str. from Asia (above; Fig. 37.1C). Species of this clade are found in mesic to humid, temperate habitats.

The North American polytomy (Fig. 37.1E) includes clades that have been encountered in all recent phylogenetic studies, though few were strongly supported. In all studies, *Egletes* Cass. occupies an unresolved position in the North American polytomy. The clades are (subtribal names are those of Nesom and Robinson 2007): (1) Chaetopappinae, (2) *Euthamia* (Nutt.) Cass. clade, (3) *Ericameria* Nutt.–Pentachaetinae, (4) Solidagininae, (5) Chrysopsidinae–Conyzinae, (6) Astranthiinae, and (7) Boltoniinae–Symphyotrichinae–Machaerantherinae. The position of the aster genera *Ionactis* Greene (Fig. 37.1Eⓑ) and *Odeomena* Greene (Fig. 37.1Eⓐ) are ambiguous. Ecologically, both are temperate genera of mesic or humid habitats. *Ionactis* is western North American with a single eastern species (*I. linearifolia* (L.) Greene), while *Odeomena* is eastern North American.

Chaetopappinae are of uncertain position in the phylogeny (Fig. 37.1Eⓒ), but may be the earliest diverging group to a large clade including Pentachaetinae–*Ericameria*, Solidagininae, the *Euthamia* clade, and the Chrysopsidinae–Conyzinae (Brouillet et al. pers. comm.). Nesom (2000b) discussed this subtribe.

Pentachaetinae, comprising *Pentachaeta* Nutt., *Tracyina* S.F. Blake, and *Rigiopappus* A. Gray, are sister to *Ericameria* (Fig. 37.1Eⓓ). Pentachaetinae were discussed in Nesom (2000b) and Roberts and Urbatsch (2003). In the analyses of Roberts and Urbatsch (2003, 2004), *Ericameria* (Fig. 37.4C) is monophyletic and does not fall within Solidagininae. *Chrysothamnus* was shown to be polyphyletic in that it contained taxa now representative of basal Solidagininae (*Cuniculotinus* Urbatsch, R.P. Roberts & Neubig species) and more derived entities in this lineage, *Chrysothamnus* Nutt. s.str. and *Lorandersonia* Urbatsch, R.P. Roberts & Neubig, as well as four species now regarded as *Ericameria* (Urbatsch and Roberts 2004). As traditionally conceived, *Ericameria* had been considered a taxon of Mediterranean climate and desert and higher-elevation habitats, mainly of California. With the accretion

of species from *Chrysothamnus* and *Macronema* Nutt., the *Ericameria* radiation now also includes Rocky Mountain habitats and the Great Basin, where certain species are among the dominant taxa of this arid shrubland. Nesom (1994g) regarded *Ericameria* as an ancient disjunct of the primarily South American subtribe Hinterhuberinae, but subsequently he and Robinson (Nesom 2000b; Nesom and Robinson 2007) gave it unplaced status. Its affinity to Solidagininae or the *Euthamia* clade is at most weakly supported. In some analyses, this clade appears sister to Solidagininae, but there is no support yet for such a relationship.

Solidagininae (Fig. 37.1E⑤) exclude the *Euthamia-Gundlachia* A. Gray lineage (below), in contrast to Nesom and Robinson (2007). Thus restricted, Solidagininae (Fig. 37.2N, 37.4A) are one of the largest groups of North American Astereae. The subtribe was investigated by Roberts and Urbatsch (2003) and Beck et al. (2004). *Cuniculotinus* and the white-rayed *Sericocarpus* Nees are basal to an essentially yellow-rayed group of genera found both in mesic and xeric habitats. *Cuniculotinus* is found at high elevations of the Sierra Nevada and adjacent ranges, and *Sericocarpus* in mesic to dry woods of western (two species) and eastern (four species) North America. Most genera of the subtribe appear to inhabit humid or mesic, though sometimes seasonally dry, habitats. *Solidago* (Fig. 37.4B), with some 100 species (77 in North America), radiated mostly in eastern North America, with a secondary radiation in mesic to dry habitats of the prairies and the West. It secondarily spread to Eurasia and South America. *Chrysothamnus* represents a major radiation in xeric habitats in western North America, apparently from mesic ancestors. The polyphyletic nature of *Tonestus* A. Nelson and *Stenotus* Nutt. are evident in the studies cited above and here (Fig. 37.1E).

Gundlachia was sister to the *Euthamia* clade (Fig. 37.1E⑥) in earlier analyses (Urbatsch et al. 2003; Beck et al. 2004) and is discussed here. Urbatsch et al. (2003) commented on the affinities of genera within the *Euthamia* clade. Within this clade, relationships are unresolved. Subsequent to the investigations by Urbatsch et al. (2003), *Xylothamia* was dissolved with the transfer of four of its nine species to *Gundlachia* (Urbatsch and Roberts 2004). The other five species were placed in the new genera *Neonesomia* Urbatsch & R.P. Roberts, *Chihuahuaana* Urbatsch & R.P. Roberts, *Xylovirgata* Urbatsch & R.P. Roberts, and *Medranoa* Urbatsch & R.P. Roberts. These four genera are placed in the *Euthamia* clade rather than close to *Gundlachia*, which support their removal from this genus. In the present analysis the *Euthamia* clade and *Gundlachia* have little affinity to Solidagininae (Fig. 37.1E⑦).

In all analyses so far, *Geisssolepis* Robinson is the earliest branching lineage within the clade or is sister to Conyzinae, but is never found within Astranthiinae where

Nesom & Robinson (2007) placed it. Chrysopsidinae and Conyzinae are sister to each other (Fig. 37.1E). The genera included here within Chrysopsidinae (Fig. 37.1E⑧) are those grouped within the subtribe (Semple 2006): *Pityopsis* Nutt., *Bradburia* Torr. & A. Gray, *Chrysopsis* (Nutt.) Elliott, *Noticastrum* DC., *Croptilon* Raf., and *Heterothea* Cass. (Fig. 37.4D). *Noticastrum* is South American and represents a disjunction between North and South America. Conyzinae (Fig. 37.1E⑩) include the single genus *Erigeron* (Fig. 37.2P), from which authors have segregated *Aphanostephus* DC. (the sole member of the subtribe with a reduced chromosome number of $x = 5$), *Conyza* s.str. (a polyphyletic entity in all analyses, even when excluding African species) (Fig. 37.2O), *Apopyros* G.L. Nesom, *Neja* D. Don, and *Hysterionica* Willd. (see Noyes 2000a). These segregations are not supported by molecular data since they render *Erigeron* paraphyletic (Fig. 37.1E). Early branching lineages within *Erigeron* all are North American, and Eurasian and South American lineages represent secondary dispersals. Dispersal to both continents may have occurred repeatedly in various lineages, but some South American sections of *Erigeron* and the South American segregate genera are closely related (Noyes 2000a).

Astranthiinae include *Townsendia* Hook. (Fig. 37.2Q, 37.4E), sister to *Astranthium* Nutt. and *Dichaetophora* A. Gray, but exclude *Geisssolepis* (Fig. 37.1E⑨).

The Boltoniinae–Symphyotrichinae–Machaerantherinae group (Fig. 37.1E) includes the eurybioid asters (*Oreostemma* Greene, *Herrickia* Wooton & Standl., *Eurybia* (Cass.) Cass., and *Triniteurybia* Brouillet & al.), unplaced in the Nesom and Robinson (2007) classification. Boltoniinae (Fig. 37.1E⑫) are sister to Symphyotrichinae and eurybioids plus Machaerantherinae. This small clade comprises *Chloracantha* G.L. Nesom & al., *Batopilasia* G.L. Nesom & R.D. Noyes, and *Boltonia* L'Hér., which confirms the findings based on cpDNA RFLP (see Nesom et al. 1991) and of Noyes and Rieseberg (1999). Relationships within Boltoniinae were discussed by Nesom and Noyes (2000). These taxa mostly inhabit wetlands, sometimes temporary ones in desert areas, of south-central North America.

Symphyotrichinae comprise, in phylogenetic order (Fig. 37.1E⑬), *Canadanthus* G.L. Nesom, *Ampelaster* G.L. Nesom (Fig. 37.4F), *Almutaster* Á. Löve & D. Löve, *Psilactis*, and *Symphyotrichum*. The first three genera all have a chromosomal base number of $x = 9$, while the latter two are cytologically variable (respectively, $x = 9, 4, 3$, and $x = 8, 7, 5, 4$). This clade had been identified in the cpDNA study of Xhang and Semple (1996). Brouillet et al. (2001) and Semple et al. (2002) have shown that *S. chapmanii* (Torr. & A. Gray) Semple & Brouillet is part of *Symphyotrichum* and not of *Eurybia* (versus Nesom 1994i), in keeping with its unusual base number ($x = 7$) and morphology. *Symphyotrichum* is the largest North American aster genus (some 90 species, 77 of which occur north of

Mexico) and one of the three largest Astereae genera on the continent. Species of *Symphotrichum* have migrated to Eurasia (*S. ciliatum* (Ledeb.) G.L. Nesom) and to southern South America (e.g., *S. vahlii* (Gaudich.) G.L. Nesom), and have become introduced in Eurasia and other continents. Relationships within the genus are unresolved (Brouillet et al. 2001; Semple et al. 2002), in part due to its complex reticulate evolution and to frequent interspecific hybridization.

The eurybioid genera *Oreostemma*, *Herrickia*, *Eurybia* (Fig. 37.2R), and *Triniteurybia* form a grade to subtribe Machaerantherinae (Fig. 37.1E⑭). The rayless, monospecific *Triniteurybia*, until recently placed in *Tonestus*, has been shown to be sister to Machaerantherinae (Brouillet et al. 2004) (Fig. 37.1E⑮). This mesic to semi-xeric, high-elevation, rhizomatous genus with the basal number of $x = 9$, thus appears sister to a major radiation into xeric habitat by the speciose, sometimes taprooted and annual Machaerantherinae with $x = 6, 5, 4$. Relationships among the eurybioid genera are discussed in Selliah and Brouillet (2008). Subtribe Machaerantherinae has been studied recently in a molecular phylogenetic context by Lane et al. (1996), Morgan (1993, 1997, 2003); Morgan and Simpson (1992), and Markos and Baldwin (2001, 2002).

CLASSIFICATION

Generic level

Recent morphological and molecular phylogenetic studies have resolved many issues relating to generic delimitation in Astereae (e.g., *Aster* s.l., Nesom 1994g; *Chrysothamnus*, Roberts and Urbatsch 2004). Nonetheless, it is obvious from the synthesis presented here that many genera are still in need of revision. This is particularly true of *Myriactis* and *Lagenophora* (Fig. 37.2I), which display wide intercontinental disjunctions; taxonomic discussions often raise the difficulty of dealing with such genera with morphology alone, e.g., Nesom's (2000a) discussion of *Myriactis*. Likewise, *Olearia* needs a thorough re-evaluation, since it is clear that the genus artificially groups elements from two widely divergent lineages, the New Zealand clade and the Australasian group, as has been emphasized by Cross et al. (2002), as well as a number of smaller splinter entities. Phylogenetic studies encompassing a wider range of genera are the only solution to this type of problem. A narrow focus on single genera and on few representative species in Astereae can only prove counter-productive. Another example is *Baccharis*, recently revised by Müller (2006) for Bolivia based on morphology; our molecular data show that taxa such as *Heterothalamus* and *Baccharis boliviensis* cannot be included within *Baccharis*. A last example is *Erigeron* and the splinter genera recognized by Nesom and Robinson (2007),

notably *Conyza*, *Neja*, *Hysterionica*, and *Aphanostephus*. All these are deeply embedded within *Erigeron* (Noyes 2000a) and furthermore, *Conyza* is shown to be polyphyletic even as more narrowly circumscribed (i.e., excluding African taxa). Recognition of these genera is mostly based on the perception of greater evolution within these lineages, leading to the acceptance of paraphyletic genera. Other taxonomists may wish to recognize a single monophyletic *Erigeron*. This philosophical difference is but one of the problems that confront systematists in Astereae. Other problems are related to character homology and evolution, and their interpretation by taxonomists. Classically, genera in Astereae were defined on the basis of overall similarity: few if any attempts were made to distinguish homoplasious from homologous characters or symplesiomorphies from synapomorphies. Another difficulty has been the relative paucity of characters that could be used in morphological taxonomic or phylogenetic analyses. Molecular phylogenetic approaches will help resolve such outstanding issues.

Subtribal level

Nesom and Robinson (2007) produced the latest classification of tribe Astereae. We are assessing this classification in terms of the phylogeny presented here (Fig. 37.1), because the subtribes often proved to be polyphyletic and thus the information is scattered in the phylogenetic discussion above. The order of discussion is that of the subtribes in the Nesom and Robinson classification.

Homochrominae. — This southern African subtribe appears monophyletic. It should comprise the unplaced St. Helena woody genera *Commidendron* and *Melanodendron*.

Hinterhuberinae. — This southern hemisphere subtribe is polyphyletic (Fig. 37.1A–D). The elements that belong with the type *Hinterhubera*, are members of one of the derived South American lineages, and they are closely related to or intermixed with some elements of Podocominae and Baccharidinae. As currently defined, the subtribe also includes members of the Paleo South American (*Chiliophyllum* and relatives) and New Zealand (*Celmisia*, parts of *Olearia*, etc.) clades, as well as members of the Australasian lineage (*Olearia* in part). Isolated African elements (*Mairia*, *Madagaster*, etc.) also are included, and notably *Printzia*, which is diverging early in our phylogeny.

Brachyscominae. — Even as narrowly defined as was done by Nesom and Robinson (2007), two of the three genera of this subtribe (*Ceratogyne* Turcz. has yet to be studied) do not form a clade in analyses of Australasian taxa. *Calotis* occurs in a position distinct from *Brachyscome* (Fig. 37.1C). The value of erecting a subtribe for the sole genus *Brachyscome* will depend on its position on the tree, which cannot be ascertained at the present time due to the large polytomy among Australasian lineages.

Bellidinae. — This subtribe is monophyletic but too narrowly defined. Elements classified in Asterinae are closer to *Bellis* (Fig. 37.2C) and *Bellium* than to *Aster* (Fig. 37.2L) (Fig. 37.1A). To be monophyletic, it should be enlarged to include *Bellidiastrum* and the *Galatella* group.

Grangeinae. — This subtribe of mainly African and south Asian elements (Fig. 37.1A) is polyphyletic when American (*Egletes*, *Plagiocheilus*; Fig. 37.1E) and Australasian (*Erodiophyllum*; Fig. 37.1C) taxa are included, as was done by Nesom and Robinson. It may prove monophyletic once these elements are removed, but the position of many south Asian taxa is still unknown. It is noteworthy that *Welwitschiella*, long considered in Heliantheae, is added to this subtribe. Likewise, African members of *Conyza* belong here, except for *C. gouani*. The unplaced *Psiadia*, and possibly unstudied genera related to it, belong here too.

Lagenophorinae. — This subtribe mostly includes parts of the Australasian lineages (Fig. 37.1C). It also comprises genera with trans-Pacific distributions, shown here to be polyphyletic, such as *Myriactis* and *Lagenophora*. *Rhynchospermum* is embedded within *Aster* (Fig. 37.1C). Many elements remain to be investigated.

Baccharidinae. — This subtribe has been characterized by unisexuality. Our phylogeny, however, indicates that this feature has originated more than once among South American lineages, independently in *Baccharis*, *Archibaccharis*, and *Heterothalamus* (Fig. 37.1D). Baccharidinae should be restricted to *Baccharis* sensu stricto.

Podocomininae. — As circumscribed by Nesom and Robinson, this subtribe includes genera from South America and Australasia. In molecular phylogenies, they are mixed with members of other subtribes (Fig. 37.1C, D). Australian elements show no relationship to South American ones. The subtribe as defined is polyphyletic and should be restricted to genera clustering with *Podocoma* in phylogenies (Fig. 37.1D).

Asterinae. — This subtribe is polyphyletic, comprising isolated Asian elements such as *Callistephus* (Fig. 37.1A), the *Galatella* group and *Bellidiastrum* that clearly are related to Bellidinae (Fig. 37.1A), and a series of *Aster* segregates whose status still needs to be assessed, but most of which probably will not prove to be distinct from the primarily Asian *Aster* s.str. African *Aster* species (Fig. 37.1A), left within *Aster* by Nesom (1994i), represent a distinct, isolated lineage among the basal African diversification and should be removed from *Aster*. The relationship of *Aster* to Australasian *Olearia* s.str. (Fig. 37.1C) hints that Asterinae may have to be expanded to include elements that had not previously been considered.

Solidagininae. — With the help of molecular phylogenetic data, this subtribe was recently redefined to include only North American members (Beck et al. 2004). Nonetheless, the inclusion of the *Euthamia* lineage may

make it polyphyletic since it does not form a clade with Solidagininae s.str. (Fig. 37.1E).

Pentachaetinae. — This subtribe of three genera forms a clade with the large *Ericameria*, which is unplaced in the Nesom and Robinson classification (Fig. 37.1E).

Boltoniinae. — This group of three genera is monophyletic and sister to Symphyotrichinae-Machaerantherinae (Fig. 37.1E).

Machaerantherinae. — This is a well-delimited, monophyletic group of North American taxa with $x = 6$. It has a close relationship to the $x = 9$ eurybioid grade (Fig. 37.1E) (*Oreostemma*, *Herrickia*, *Eurybia*, *Triniteurybia*, all unplaced in the classification of Nesom and Robinson); these might best be included there.

Symphyotrichinae. — This is a well-defined clade comprising most of the North American asters. It is sister to eurybioids-Machaerantherinae.

Chaetopappinae. — This group of two genera is monophyletic and early diverging in the North American clade (Fig. 37.1E).

Astranthiinae. — It includes four genera, one of which, *Geissolepis*, does not belong here but with Chrysopsidinae-Conyzinae (Fig. 37.1E). *Geissolepis* either belongs with one of these subtribes or is sister to both. With this genus removed, Astranthiinae are monophyletic.

Chrysopsidinae. — This is a monophyletic group, sister to Conyzinae.

Conyzinae. — This subtribe essentially is equivalent to a monophyletic *Erigeron*. All other genera are derived from within the latter and could be considered synonyms. As stated in Nesom and Robinson (2007), African conyzas belong to Grangeinae.

Doellingeria, Eucephalus, Oclemena, Ionactis. — These unplaced North American taxa all were traditionally classified in *Aster*. Their position is unusual within the North American clade (Fig. 37.1E). *Eucephalus-Doellingeria* represents the most early diverging lineage. *Oclemena* and *Ionactis* are still difficult to assign, but it is likely that they will be early diverging in distinct North American clades, as yet undetermined.

The Nesom and Robinson (2007) classification does not adequately reflect the phylogeny presented here. Firstly, many of the subtribes are polyphyletic. It is worth noting that none of the subtribes with intercontinental disjunctions, except a few between New Zealand and Australia or across the Pacific Islands, have proven to be monophyletic. This would indicate that the criteria used to group genera into subtribes are not diagnostic of relationships or should be reinterpreted (e.g., convergences). Secondly, the basal African grade, with its numerous, sometimes isolated lineages, intermixed with Chinese, South American, and New Zealand lineages, is not represented in it. Thirdly, several major, monophyletic clades are not recognized in the classification, notably the Paleo

South American, New Zealand, and North American clades. Fourthly, the classification fails to recognize the phylogenetic proximity of genera from the same continent, notably the genera belonging to the Australasian and South American lineages. Finally, the classification is over-elaborate in North America, where a large number of subtribes are recognized. These groups are indeed worthy of recognition, but it must be questioned whether this should be done at the subtribal level.

At the present time, we are refraining from proposing a new classification of the tribe because many details of the phylogeny remain to be validated. Nonetheless, we would suggest that the subtribal level should be reserved for the most significant clades of the phylogeny, including the isolated African or Chinese genera or lineages where necessary. The subtribes Homochrominae, Grangeinae, and Bellidinae should be recognized but with a wider membership than defined by Nesom and Robinson (2007). Clades that deserve subtribal recognition but that currently lack a name are the Paleo South American, the New Zealand, and the North American. The name Solidagininae might be applied to the North American clade, though this would extend the concept of this subtribe beyond its traditional content; it would have the virtue of being monophyletic and of providing a name for one of the most important radiations within the tribe. The large polytomies of Australasian and of South American lineages will have to await better resolution before a classification of their elements into subtribes can be entertained. Among the Australasian lineages, the clade that will end up including *Olearia* s.str. and *Aster* s.str. will have to be called subtribe Asterinae, again a departure from past practice but a more natural assemblage. It is unclear whether this group will include all or only part of the Australasian genera. It is likely that subtribe Baccharidinae will be a significant clade, restricted to *Baccharis* s.str. The other South American lineages may either form a grade to the North American clade, or form a sister group to it; the taxonomic disposition of this group must await better supported data. Until better resolution and better support is obtained for the phylogeny of Astereae, it would be premature to propose a new classification.

MORPHOLOGY, ANATOMY, PALYNOLOGY

Since Grau (1977) published his summary, few papers have been devoted solely to the comparative morpho-anatomy or palynology of tribe Astereae, if one excepts cytotoxic or phylogenetic papers including morphological analyses. Wood anatomy was studied for *Melanodendron* and *Commidendron* by Carlquist (2001), *Tetramolopium* by Carlquist and Lowrey (2003), and *Heterothalamus* by De Oliveira et al. (2005). Capitulum and floret developments

were studied in *Erigeron philadelphicus* L. by Harris et al. (1991), and in *Symphotrichum laurentianum* (Fern.) G.L. Nesom by Lacroix et al. (2007). Pullaiah (1978) published on the embryology of *Solidago* and *Erigeron* (*Conyza*), and Noyes and Allison (2005) on that of sexual and apomictic members of *Erigeron strigosus* Muhl. ex Willd. Jordaan and Kruger (1993) studied pollen wall ontogeny in *Felicia muricata* Nees. Jackson et al. (2000) noted a unique pollen wall mutation in $n = 2$ *Xanthisma gracile* (Nutt.) D.R. Morgan & R.L. Hartman (as *Haplopappus gracilis* (Nutt.) A. Gray). Torres (2000) showed a correlation between pollen volume and pistil length in Asteraceae, including several species of Argentinian Astereae.

It was not possible for this paper to re-evaluate and map onto the phylogeny the morphological and anatomical characters that have been used to assess generic relationships and to delimit subtribes. The discrepancy between our molecular phylogeny and the classifications proposed for the tribe, the Nesom and Robinson (2007) classification being the most recent example, indicates that the interpretation of morphological data requires a re-assessment, notably as to whether the characters used represent convergences, or whether they are symplesiomorphic or synapomorphic. Furthermore, the lack of resolution and support of the current phylogeny would prevent us from reaching meaningful conclusions in many cases.

Nonetheless, Cross et al. (2002) suggested that the presence of a tomentum on the abaxial surface of leaves is symplesiomorphic in the tribe. Our data appear to support this hypothesis, since most groups that possess this feature are in the basal grade of Astereae. It is possible that some instances of such a character represent convergences; a detailed examination of the trichomes making up the tomentum would be needed to determine whether this is the case. Also, loss of the tomentum may have occurred independently several times during evolution of Astereae. Grangeinae as well as the crown lineages lack this feature, and the loss may have occurred a single time along the spine below the origin of these taxa. More African genera need to be incorporated in the phylogeny before we can satisfactorily address this issue.

Cross et al. (2002) also proposed that caudate or sagittate anther bases, a feature present in the sister tribes of Astereae, had evolved in parallel several times in Astereae and in those other tribes. We would suggest a different interpretation of this feature: caudate anthers, like abaxially tomentose leaves, may represent a symplesiomorphy in the tribe. Given that all lineages with tailed anthers are among primitive Astereae, being present, for instance, in *Printzia*, *Denekia*, and the Paleo South American and New Zealand clades, it would appear most parsimonious to postulate that anther tails are a primitive feature within Astereae that may have been lost repeatedly in early lineages. It was also possibly lost a single time along the spine

of the phylogeny, resulting in most Astereae genera being tailless. This would explain why tribe Astereae has been traditionally described as having tailless anthers as a defining feature, with apparently random exceptions. Such exceptions are all found among early diverging groups in our phylogeny, though. Tailless anthers, instead of being an absolute defining feature of the tribe, would appear to be one that characterises relatively derived members of the tribe.

CHROMOSOME NUMBERS

There are more than 18,800 chromosome number reports for individuals of tribe Astereae (Chapter 4 and references cited therein). At least one chromosome number report has been published for 140 genera included in the tribe. Twenty genera have only been sampled once. More than 15,000 of the reports are for individuals of just six genera, due primarily to cytogeographic studies on taxa within each genus: *Symphytotrichum* (4578), *Solidago* (3451), *Aster* (2129), *Brachyscome* (1884), *Xanthisma* (ca. 1600), and *Erigeron* including *Conyza* (1370).

The tribe includes the greatest diversity in chromosome numbers and ploidy levels within the family Compositae (Chapter 4). Chromosome numbers in Astereae range from $2n = 4$ (*Xanthisma gracile* (Nutt.) D.R. Morgan & R.L. Hartm. and *Brachyscome dichromosomatica* C.R. Carter) to $2n =$ ca. 432 (*Olearia albida*). Polyploidy occurs in nearly all major clades with a decrease in frequency as ploidy level increases. Tetraploids are known in 48 genera, hexaploids in 23, and octoploids in 11. Higher ploidy levels are rarer. Decaploids are known in *Bellis*, *Boltonia*, *Brachyscome*, *Erigeron*, *Lorandersonia*, *Solidago*, and *Symphytotrichum*. Dodecaploids and higher ploidy levels are known in *Solidago* ($14x$), *Eurybia* ($14x$), and nearly all members of the New Zealand clade ($12x$, $32x$, $36x$, and $48x$). With the exception of the latter, high ploidy levels generally are known in the genera that have been sampled most extensively.

The ancestral number of Astereae is $x = 9$ (Semple 1995). The lack of a DNA-based phylogeny at the time left many of the conclusions speculative. No chromosome numbers have been reported for either *Printzia* and *Denekia*, reported here to form an early diverging lineage in the tribe. Both are native to southern Africa and were included in Gnaphalieae but unassigned to subtribe in Bremer (1994). All major clades within the tribe and the majority of species have a base number of $x = 9$. Machaerantherinae sensu Nesom and Robinson (2007) have a base number of $x = 6$. If they are expanded to include *Oreostemma*, *Herrickia*, *Eurybia*, and *Triniteurybia*, Machaerantherinae s.l. also have a base number of $x = 9$. The small subtribe Chaetopappinae in the North American clade has a base number of $x = 8$.

Dysploid decreases have occurred in several dozen genera and eight subtribes scattered throughout the tribe. Dysploidy is most frequent in the Symphyotrichinae-Machaerantherinae s.l. clade, one of the crown lineages of the North America clade, which includes crown numbers ranging from $x = 9$ to $x = 2$. The longest dysploid series in a single genus occurs within *Brachyscome* s.l. with $x = 9$ to $x = 2$ taxa in the Australasian clade. In the same clade, another long dysploid series is found in *Calotis* ($x = 8, 7, 6, 5, 4$), sister to *Erodiophyllum* ($x = 8$). In the basal grade, dysploidy also is known in *Amellus* ($x = 9, 8, 6$), and *Felicia* ($x = 9, 8, 6, 5$).

Three genera include derived base numbers higher than $x = 9$. *Symphytotrichum* subg. *Ascendentes* has allopolyploid-derived base numbers of $x_2 = 13, 18, 21$ with $x = 8$ and 5 as parental taxa (Brouillet et al., pers. comm.). In *Brachyscome*, counts with $x_2 = 11$ and 13 were reported (Watanabe et al. 1999). The single report for *Isoetopsis* of $2n = 17_{II}$ (as $n = 17$; Turner 1970) occurs in a clade with $x = 9$ as ancestral; if correct, this may be a dysploid derived $x_2 = 17$ from a tetraploid with $2n = 36$.

New approaches have been applied to further our understanding of cytological evolution within genera, notably polymorphic heterochromatic segments (Houben et al. 2000) in *Brachyscome*, fluorescence in situ hybridization (FISH) of nuclear ribosomal DNA probes in *Brachyscome* (Adachi et al. 1997), *Aster* (Saito and Kokubugata 2004), and *Haplopappus* and *Grindelia* (Baeza and Schrader 2005), and genomic in situ hybridization in *Aster* (Matoba et al. 2007).

CHEMISTRY

The chemistry of Astereae first was summarized by Herz (1977b), who underlined the partial nature of our knowledge in terms both of the organs (mostly roots) and of the taxa surveyed. Interpretation of infratribal variation was based on the six traditionally recognized subtribes. Since then, overviews have been provided for the tribe on acetylene (Christensen and Lam 1991) and terpenoid chemistry (Herz 1996). General surveys for Compositae were published by Hegnauer (1977) and Zdero and Bohlmann (1990). The latter provided a framework useful to interpret chemical evolution within Compositae in terms of biosynthetic pathways: chemicals derived from acetyl coenzyme A are polyacetylenes, aromatic compounds, and terpenes and saponins, and those derived from amino acids include flavonoids, phenyl propanes, pyrrolizidin alkaloids, and a few others. Specialist reviews were done on sesquiterpene lactones (Herz 1977a; Seaman 1982), diterpenes (Alvarenga et al. 2005), benzopyranes, and benzofuranes (Proksch 1985), polyacetylenes (Sørensen 1977), leaf wax alkanes (Maffei 1996), steroids (within

a survey of angiosperms; Borin and Gottlieb 1993), flavonoids (Harborne 1977, 1996; Seeligman 1996; Bohm and Stuessy 2001, summarizing data on 48 genera of Astereae), and pharmaceutical uses (Wagner 1977).

Examples (our search was not exhaustive; more is also to be found in the sources above) of new chemical reports within the tribe include (and references therein): surveys of essential oils (Kalemba 1998; Zunino et al. 1997; Barbosa et al. 2005) or volatile compounds (Chung et al. 1997); matricaria esters and lactones (Lu et al. 1998); benzofuranes and terpenoids (Schmidt et al. 2003); flavonoids (Saleh and Mosharrafa 1996; Wollenweber and Valant-Vetschera 1996; Vogel et al. 2005), flavonoids and terpenes (Verdi et al. 2005), or flavonoids and quinic acid derivatives (Kwon et al. 2000; Hur et al. 2001, 2004; Choi et al. 2003; Simoes-Pires et al. 2005); heterocyclic terpenes (Li et al. 2005); cerebrosides and terpene glycosides (Kwon et al. 2003); sesquiterpene hydroperoxide (Choi et al. 2003); monoterpene peroxide glycosides (Jung et al. 2001); diterpenes (Herz et al. 1977; Hoffmann et al. 1982; Waddell et al. 1983; Warning et al. 1988; Zdero et al. 1990, 1991; Zhou et al. 1995; He et al. 1996; Ahmed et al. 2001; Choi et al. 2002; Lee et al. 2005); saponins from *Aster* s.l. (incl. *Galatella*, *Aster*, *Bellidiastrum*) species (Lanzotti 2005); and anti-inflammatory products in *Laennecia* and *Baccharis* (Cifuentes et al. 2001). It is remarkable that much of this research concerns pharmaceutically active compounds and their properties (e.g., *Aster* spp.; Graham et al. 2000; Sok et al. 2003; Oh et al. 2005; Seong Il et al. 2005). Of note were the reports of the sesquiterpene lactone eudesmanolide from *Grangea maderaspatana* (Ruangrunsi et al. 1989) and *Erigeron annuus* Pers. (Li et al. 2005), added to the three known records for the tribe (Seaman 1982).

The studies cited above show that Astereae overall are characterized by a paucity of sesquiterpene lactones, usually of basic skeleton types, an absence of tridecapentayne and derivatives, replaced by C10- and C17-acetylenes (a feature shared with Anthemideae), the presence of aromatic compounds such as prenylated p-hydroxyacetophenones, which accumulate in some Astereae, the presence of phenylpropane derivatives, the common occurrence of coumarins, both simple, prenylated or linked with terpenes or sesquiterpenes, and among diterpenes, the presence of kauranes and derivatives, including the rare abietanes, and of labdanes and clerodanes. Monoterpenoids and sesquiterpenoids are varied and widespread. Flavonoids and other phenolics are present but do not exhibit particular trends.

Taxonomic interpretation of the distribution of compounds within the tribe, however, is currently of limited usefulness because it has been based on traditional genera, many of which have been recently shown to be polyphyletic, and on traditional subtribes, also shown as artificial despite the recent classification of Nesom and Robinson (2007). For chemical data to play a significant

role in our knowledge of the evolution of Astereae, the generic identity of reports will need to be reassessed and the chemical data re-interpreted within the context of both biosynthetic pathways and a well-supported phylogenetic framework. Work on the enzymes regulating biosynthetic pathways in Astereae is promising in this regard (e.g., Prosser et al. 2002, 2004). Chemical data should not be dismissed, however. An example comes from the report by Bohlmann and Zdero (1978) of new diterpenes constituents in *Printzia*, then considered an Inuleae, showing clear relationships to compounds in Astereae, a fact confirmed by the current placement of the genus as an early derived lineage of the tribe.

BIOLOGY AND EVOLUTION

Species of Astereae have been the object of numerous biological or evolutionary studies. Exemplars of recent studies are summarized below in order to show the potential of the tribe for evolutionary and ecological studies, as well as to illustrate the biology of the tribe. An overview of pollination and dispersal morphology and ecology of Indian Compositae (mostly native, some introduced), including several Astereae species (*Aster* s.l., *Centipeda*, *Conyza*, *Dichrocephala*, *Erigeron*, *Grangea*, *Microglossa*, *Myriactis*, *Solidago*), is provided by Mani and Saravanan (1999).

Interspecific hybridization has been documented repeatedly within the tribe. This has been summarized by Nesom (1994j), among others. Some reported intergeneric hybrids, such as those between *Kalimeris* and *Aster*, in fact are between members of genus *Aster* (see Australasian clade). Recently, FISH techniques (Saito and Kokubugata 2004) and molecular phylogenetic evidence (Saito et al. 2007) were used to document the hybrid origin of *Aster* × *sekimotoi* Makino in Japan. Matoba et al. (2007) used GISH techniques to identify the parents and their contribution to genomic organization in the allotetraploid *Aster microcephalus* Franch. & Sav. var. *ovatus* (Franch. & Sav.) A. Soejima & Mot. Ito.

Gottlieb (1981) investigated the number of allozymic gene loci in species of *Almutaster*, *Psilactis*, and *Arida* (as *Machaeranthera* Nees. s.l. and *Aster* s.l.) in North America with chromosome numbers of $n = 4, 5, 9$. He concluded that the absence of multiple isozymes in the species with $n = 9$ suggested it did not arise via polyploidy. In an isozyme study of 6-phosphogluconate dehydrogenase (6PGD) in *Aster* s.str. (as *Kalimeris*), however, Nishino and Morita (1994) found a duplication within the diploids that would not reject the possibility of an allopolyploid event at the base of the $x = 9$ number in the group. If a duplication occurred, it either happened before the origin of Astereae, or it was the result of a single gene or chromosome segment duplication.

As stated above (Cytology section), polyploidy is a frequent phenomenon in tribe Astereae. Allopolyploids are the result of reticulate evolution and thus of interspecific hybridization (see Otto and Whitton, 2000 and Chapman and Burke, 2007 for reviews). Allen (1985, 1986; Allen et al. 1983) showed that *Symphotrichum ascendens* (Lindl.) G.L. Nesom ($n = 13$) and *S. defoliatum* (Parish) G.L. Nesom ($n = 18$) originated through a series of hybridization events between *S. spathulatum* (Lindl.) G.L. Nesom ($n = 8$) and *S. falcatum* (Lindl.) G.L. Nesom ($n = 5$). Chapman and Burke (2007) reported ITS sequence distances among these parental species consistent with a model in which the likelihood of polyploid formation increases with the genetic divergence of the parents (versus in homoploid speciation). Using cpDNA, ITS, and ETS molecular phylogenetic data, Morgan (1997, 2003; Morgan and Simpson 1992) dissected reticulate evolution within the *Machaeranthera* generic complex (see Morgan and Hartman 2003), showing introgression both of chloroplast and ITS in various members.

Apomixis is known in several genera of Astereae and is usually associated with polyploidy. The process of apomixis and the relationships among diploid and polyploid populations within apomictic taxa have been studied in *Erigeron strigosus* (Noyes 2000a, b, 2006, 2007; Noyes and Allison 2005; Noyes and Rieseberg 2000), *Erigeron compositus* Pursh (Noyes et al. 1995), and *Townsendia hookeri* Beaman (Thompson and Ritland 2006; Thompson and Whitton 2006). Apomixis had also been studied from an anatomical standpoint in the Australian *Minuria integerrima* (DC.) Benth. and *Calotis lappulacea* Benth. (Davis 1964, 1968).

Genetic uniformity of *Erigeron* species in the European Alps was shown by Huber and Leuchtmann (1992) using allozymic data, as a result of recent speciation, probably during the glaciations; morphological and ecological differences between them could be the result of changes at few loci. Valdebenito et al. (1992) studied the evolution of six endemic, polyploid *Erigeron* species on the Juan Fernández Islands (Chile) using flavonoid profiles and showed all to derive from a single introduction to Masafuera, followed by colonization of Masatierra. A study of Hawaiian and Cook Islands *Tetramolopium* species based on morphology (Lowrey 1986, 1995), allozymes (Lowrey and Crawford 1985), nuclear DNA RFLP markers (Okada et al. 1997), and ITS-based phylogenetic data (Lowrey et al. 2001) showed low levels of variation within the group, supporting the hypothesis of a recent origin and rapid diversification of the morphologically distinct taxa. Microsatellites were developed to characterize populations of *Solidago sempervirens* L. in North America (Wieczorek and Geber 2002) and *Aster amellus* L. in Europe (Mayor and Naciri 2007), opening new avenues for population genetic studies in Astereae.

The population genetics of rare species of *Aster* was studied using allozymes. The population structure and genetic diversity of the autotetraploid *Aster kantoensis* Kitam. was studied (Maki et al. 1996); Inoue et al. (1998b) showed strong inbreeding depression in selfed individuals; these studies led to the suggestion of conservation measures for the species (Inoue et al. 1998a). The rare, Korean and Japanese, coastal *Aster spathulifolius* Maxim. was shown to have high overall diversity but restricted gene flow (Maki and Morita 1998). The rare, insular endemic *Aster asa-grayi* Makino from the subtropical islands of southern Japan, however, had both low allozyme genetic variability and restricted gene flow (Maki 1999).

Hunziker et al. (2002) reported permanent translocation heterozygosity in the dioecious South American shrub *Baccharis coridifolia* DC., hypothesizing that it was correlated with the maintenance of tightly linked male sex genes on four chromosomes, and that it might explain the excess of male plants in populations in ensuring a sufficient supply of pollen to insect pollinators at flowering time.

Niche ecology of *Ericameria* (as *Haplopappus* and *Chrysothamnus*) species has been studied in the Mojave desert (Cody 1978). Meyer (1997) showed a relation between achene mass variation in *Ericameria* (as *Chrysothamnus*) *nauseosa* and successional status of the community in the habitats of subspecies, accompanied by high between-individual differences. Bernard and Toft (2007) showed that seed size had important consequences on biomass, biomass allocation, and survivorship in seedlings of *E. nauseosa*, and a significant impact on subsequent life stages. Baskin and Baskin (1976) and Flint and Palmbald (1978) have shown germination dimorphism among ray and disc achenes, respectively, in *Heterotheca subaxillaris* (Lam.) Britton & Rusby and *H. grandiflora* Nutt., and Venable and Levin (1985) studied the ecology of achene dimorphism in *H. latifolia* Buckley. Gibson (2000) showed that achene dimorphism in *Grindelia (Prionopsis) ciliata* (Nutt.) Spreng. had little ecological significance but resulted in subtle genetic differences between ray and disc achene groups that could influence metapopulation architecture. Lacroix et al. (2007) studied the floral development, fruit set, and dispersal of a rare endemic saltmarsh species, *Symphotrichum laurentianum*, showing that fruit set is mostly from ray achenes and that dispersal is limited. The growth strategy of *Tripolium vulgare* Nees (*Aster tripolium* L.) in Korea was studied by Lee and Ihm (2004). This species also showed its ability to invade turf-dominated waste landfills (Kim 2002). Gowe and Brewer (2005) demonstrated the evolution of fire-dependency of flowering in sect. *Graminifoliae* of *Pityopsis* using a morphology-based phylogeny.

Butcko and Jensen (2002) studied allelopathic activity of *Euthamia graminifolia* (L.) Nutt. and *Solidago canadensis*,

two species able to form large, monospecific stands. They showed that allelopathic substances may inhibit the establishment, growth, and survival of competing species.

Associations with other organisms have been described for many Astereae genera or species, notably with insects. The papers cited below are but a sample of those available. *Aster scaber* was shown to be tolerant of the nematode *Meloidogyne hapla* (Park et al. 2004). Parker (1984) studied the foraging behavior of a specialist grasshopper (*Hesperotettix viridis*) on *Gutierrezia microcephala* (DC.) A. Gray; food depletion appears to strongly affect the insect and thus direct food selection. Parker (1985) investigated the demographic impact of two specialist insect herbivores on populations of *G. microcephala* in arid grasslands, which showed reduced plant longevity and recruitment under high attacks, and thus vulnerability to local extirpation. Parker and Salzman (1985) showed that protection from herbivory and competition increased growth and survival in *G. microcephala* juveniles. Glendinning et al. (1998) showed the role that taste receptor cells in maxillary palps of caterpillars play in rejecting allelochemical substances from *Grindelia glutinosa* (Cav.) C. Mart. Moran et al. (1999) studied the phylogenetic relationships among aphids of the genus *Uroleucon*, whose primary hosts are Compositae species, including among others *Erigeron*, *Eurybia* (as *Aster*), and *Solidago* (both North American and Eurasian species); the species attacking Astereae genera do not form a monophyletic group, even among North American taxa, and represent repeated colonizations of Astereae hosts by the aphid from other Asteraceae. Olsen (1997) studied pollination effectiveness and pollinator importance in a population of *Heterotheca subaxillaris*; pollination effectiveness was similar for both ray and disc florets, though seed set was higher in the former; the plant species was not under strong selective pressure to co-specialize with specialist visitors, though one bee species was a specialist. Torres and Galetto (2002) studied the relationship between nectar sugar composition, corolla tube length, and diversity of insect visitors on Asteraceae flowers in South America, including *Baccharis*, *Grindelia*, and *Solidago*, and showed a lack of correlation, though more derived lineages of Asteraceae (including Astereae) tended to show evolution toward more generalist pollinators.

Solidago and its insect fauna often were used as models in the evolutionary ecological study of plant-herbivore interactions. Abrahamson and Weis (1997) summarized decades of research on the relationships between the goldenrods, their insect stem gallmakers (*Eurosta solidaginis*, Tephritidae, Diptera), and their natural enemies. Several papers have been published since on the same or related topics: Meyer (1998b), Civenetti et al. (1999), Summerford et al. (2000), Cronin and Abrahamson (1999, 2001a, b), Mapes and Davies (2001a, b), Nason et al. (2002),

Abrahamson et al. (2001, 2003), Eubanks et al. (2003), Stone and Schönrogge (2003), Stireman et al. (2005a, b), Williams and Lee (2005), including educational materials (Yahnke 2006). Other studies involving galling insects and Astereae species include those of Espírito-Santos and Fernandes (2002) and Rudgers and Whitney (2006) in *Baccharis*, and of Floate et al. (1996) on *Ericameria (Chrysothamnus) nauseosa*, in which insect galls were distinctive for each subspecies present in a population. Pak et al. (2004) reported midge-galls (Cecidomyiidae, Diptera) on *Aster scaber* in Korea. Fontes et al. (1994) studied the phytophagous insect guild associated with *Solidago* species in Florida. Shealer et al. (1999) showed the value of goldenrod galls as winter forage for the Eastern gray squirrel in North America.

Morrow et al. (1989) showed the response of the goldenrod leaf beetle (*Trirhabda canadensis*, Chrysomelidae) to volatile odors of the *Solidago altissima* L. host plant in the field, the insect selecting denser colonies or, when winds are strong, the first available plot upwind. Meyer (1998a) studied defoliation recovery mechanisms in the same herbivore-goldenrod system. Dickens and Boldt (1985) showed the greater sensitivity of antennal receptors of *Trirhabda bacharides* (Chrysomelidae) to volatiles emanating from *Baccharis* and other Compositae species. Futuyama and colleagues (Futuyama and McCafferty 1990; Futuyama et al. 1993; Funk et al. 1995a, b; Knowles et al. 1999) studied the evolution of host-insect relationships in the endemic North American leaf beetle genus *Ophraella* (Chrysomelidae); early evolution of the group occurred on Astereae such as *Solidago* (main host), *Symphytotrichum*, and *Eurybia*; there were subsequent shifts in host plant to members of Eupatorieae, Heliantheae, and Anthemideae, shifts that appear to be genetically constrained in descendant groups due to the radical change in plant chemistry from the original Astereae hosts; a later reversal to Astereae hosts (*Heterotheca* and *Solidago multiradiata* Ait.) occurred, which were not involved in the early evolution of the beetles.

Warcup and McGee (1983) reported that the unusual, Australian annual *Isoetopsis graminifolia* Turcz. (classified as Anthemideae) formed both ectomycorrhizae and vascular-arbuscular mycorrhizae, and so does *Chondropyxis halophila* D.A. Cooke (Warcup 1990); the only other Compositae genera doing so were in Gnaphalieae. All other Australian Astereae genera investigated formed only vascular-arbuscular mycorrhizae.

BIOGEOGRAPHY

Grau (1977) and Bremer (1994) noted the distribution of Astereae in lands peripheral to the Pacific and Indian oceans. Based on his subtribal classification, Nesom

(1994g) noted the mostly Southern Hemisphere distribution of subtribes Baccharidinae, Hinterhuberinae, and of his “grangeoid complex” of seven subtribes, which repeatedly show South American–African disjunctions, and the concentration in the Northern Hemisphere of subtribes endemic to North America, to the exception of Asterinae. Southern disjunctions between South America and Australasia were also noted. These patterns were discussed in terms of Tertiary biogeography. Subsequently, the molecular phylogenetic study of Noyes and Rieseberg (1999) showed that Astereae were probably of African origin and that North American Compositae formed a clade. In their meta-analysis of Asteraceae biogeography, Funk et al. (2005) also suggested an African origin for Astereae, with an Australasian central grade and a terminal North American clade. The molecular phylogenetic studies cited in the sections above discussed various aspects of Astereae biogeography pertinent to the group studied, but were limited in geographic and taxonomic scope. It is worth noting that all tribes sister to Astereae in the meta-tree of Funk et al. (2005) are of southern African origin.

The current Astereae phylogenetic tree (Fig. 37.1) provides a more detailed hypothesis of biogeographic relationships within the tribe. The presence at the base of the tree of two South African genera, *Printzia* and *Denekia*, would indicate that the tribe indeed originated on that continent, as hypothesized by Noyes and Rieseberg (1999). The second lineage to diverge is the Chinese genus *Nannoglottis*, which suggests long-distance dispersal or rafting of members of Astereae to eastern Asia early in the evolution of the tribe (Liu et al. 2002). Another isolated, southern African genus, *Mairia*, is next to diverge. Then follow two radiations in southern hemisphere, temperate areas: southern South America (and adjacent Andes) and New Zealand (with subsequent dispersal to Australia). In various analyses, these two clades either form a grade as shown here or are sister to each other. Several scenarios may explain this pattern: (1) independent dispersals directly from Africa to South America and to New Zealand; (2) dispersal to South America followed by dispersal to New Zealand or vice versa (if the two clades are sister, for instance); and (3) given the fact that both southern South America and New Zealand are high-latitude, southern temperate areas, dispersal through Antarctica to southern South America and New Zealand. Members of the New Zealand clade, i.e., species of *Celmisia* and *Olearia* s.l., dispersed to Australia, with little subsequent diversification. All subsequent lineages above this segment are mainly southern African: *Pteronia*, subtribe Homochrominae, *Madagaster*, *Conyza gouani*, the African asters, and subtribe Grangeinae. Homochrominae ancestors gave rise by long-distance dispersal to the St. Helena trees, *Melanodendron* and *Commidendron* (see also Eastwood et al. 2004). Likewise, the Madagascan *Madagaster* originated from Africa via

long-distance dispersal. Grangeinae are wider ranging in Africa and dispersed to southern Asia (Indian subcontinent and adjacent areas), as shown by *Grangea maderaspatana*. The fact that Bellidinae are found on a polytomy with Grangeinae would suggest that this Mediterranean–Eurasian lineage originated in Africa; after diversifying in the Mediterranean basin, it spread through the steppes of central Asia to eastern Asia. In more resolved analyses, the next lineage usually is *Callistephus*, another isolated Chinese genus without clear affinities at the present time. Is it another case of long-distance dispersal from Africa to eastern Asia, as in *Nannoglottis*, but at a later time? Above this level a major polytomy is encountered, indicating a possibly rapid series of independent colonizations and radiations in Australasia and South America. Dispersal could have occurred either directly from Africa to both continents or via Antarctica, as hypothesized above. At the present time, it is unclear whether Australia was colonized once or a few times. What is clear, however, is that Astereae strongly radiated on the continent, giving rise to unique lineages. Some of these lineages in turn migrated north through New Guinea to southeast Asia and the Pacific Islands, including Hawaii. Some species also dispersed to New Zealand, a secondary colonization of this archipelago by Astereae. It is notable that the sister group of the eastern Asian genus *Aster* s.str. (Eurasian by secondary expansion) is the Australasian *Olearia* s.str., and not genera placed by Nesom and Robinson (2007) in subtribe Asterinae: *Aster* s.str. had Australasian ancestors. This represents a fourth independent colonization of temperate eastern Asia by Astereae. Meanwhile, South America was colonized a second time by Astereae in a series of lineages that appear to form a grade in some analyses. In more resolved phylogenies, *Baccharis* appears to be the first lineage of this new colonization, followed by Podocomininae and Hinterhuberinae (though these are not necessarily monophyletic), either in succession or as sister to each other. This radiation was more extensive than that of the Paleo South American lineage. Finally, members of the South American lineages gave rise to the North American clade in apparently a single event of dispersal, followed by a rapid radiation. It is unclear whether this dispersal occurred over long distances or whether the gradual closure of the Isthmus of Panama played a role. The fact that there is no apparent connection between Central American representatives of the South American lineages and the North American clade would seem to eliminate the second option.

Thus, it would appear that the biogeographic history of Astereae is that of a development in Africa both accompanied and followed by repeated dispersals, during the Tertiary, to eastern Asia and to other Southern Hemisphere continents, South America, New Zealand, and Australia, either directly or via Antarctica. Each dispersal led to

more or less intense episodes of diversification in the new environments. Later, the more recent southern lineages (late African, South American, Australasian) gave rise independently to derived clades in the Northern Hemisphere: Bellidinae in the Mediterranean area from Africa, *Aster* in east Asia from Australasia, and the North American clade from South America, the latter to radiate extensively and become a center of diversity of the tribe. Subsequent dispersals occurred from Asia to North America (a single event in *Aster*) or from North America to Eurasia (*Symphotrichum ciliatum* (Ledeb.) G.L. Nesom, *Eurybia sibirica* (L.) G.L. Nesom, *Solidago*, *Erigeron*) and, repeatedly, to South America (*Erigeron*, *Solidago*, *Grindelia*, *Symphotrichum*, the ancestors of *Haplopappus* and *Noticastrum*). Repeated dispersals also occurred throughout the Pacific Islands from Australasia and between New Zealand and Australia, in both directions.

ECONOMIC USES

Although tribe Astereae is the second largest of Compositae, the economic importance of the group is often considered to be rather low and largely limited to garden ornamentals cultivated in temperate gardens (Bremer 1994). There are numerous Astereae that are used medicinally in various parts of the world, however. The list is too long to elaborate on any particular genus or species. Medicinal plant websites and books on economic and medicinal plants are the best sources of information. There are also a number of taxa that have great potential in several categories of economic use including perfume ingredients, commercial resins, and elastic latexes including rubber.

The southern African genus *Pteronia* contains a number of species with highly aromatic foliage. *Pteronia incana* DC. produces a yellowish oil with a strong odor (Mangena and Muyima 1999). The strongly scented oil has chemical properties that make it suitable for use as a fragrance in the perfume industry (Bruns and Meiertoberens 1987). The oil has also been shown to possess antibiotic properties that show promise for use in the cosmetic industry (Mangena and Muyima 1999). Another aromatic species, *P. onobromoides* DC., was used by the Hottentots of southern Africa as a perfume but is yet to be studied commercially (Hutchinson and Phillips 1917).

Species of *Grindelia* from the southwestern United States and South America have generated interest as a source of diterpene resin acids (grindelic acid and others) that have the potential for uses similar to those for pine resins, which are known as “naval stores” (Hoffmann et al. 1984; Hoffmann and McLaughlin 1986). These compounds are used in paper sizing processes, the rubber industry, as ester gums for the food industry, and resins (Thompson 1990). Three species of *Grindelia* have been

studied as potential resin crops including *G. camporum* Greene (native to Central Valley of California), *G. stricta* DC. (coastal estuaries of California), and *G. chilensis* (Cornel.) Cabrera (southern and central Argentina) (Ravetta et al. 1996). A tetraploid accession of *Grindelia chilensis* has been shown to produce the highest yield of diterpene resins (Ravetta et al. 1996). The drop in domestic production of pine resins in the United States and demand for naval stores throughout the world coupled with the high cost of petroleum may well revive interest in the commercial cultivation of *Grindelia*.

Ericameria (endemic to the western United States) includes several species that produce significant amounts of hydrocarbon compounds, of which rubber and resins are economically important (Weber et al. 1986). One of the most widespread species, *Ericameria nauseosa* (Pall. ex Pursh) G.L. Nesom & G.I. Baird, may contain up to 7% rubber as measured in dry weight (Weber et al. 1993) and as much as 35% resin (Bhat et al. 1989). The resin contains a range of terpenoid compounds some of which have potential as insect inhibitors (Weber et al. 1993) and as plastics extenders (Thames 1988).

One of the more promising sources of natural rubber that never went beyond the experimental stage is *Solidago* (goldenrod). The great inventor, Thomas Edison, dedicated the last years of his life to developing a new source of natural rubber as an alternative to the tropical tree, *Hevea brasiliensis* (Willd. ex A. Juss.) Müll. Arg. (Josephson 1959). After several years of testing numerous species from different plant families, he decided that species of *Solidago* from the Southeastern USA showed the most promise. Edison embarked on a series of selection experiments in the late 1920s and eventually developed a strain of *Solidago leavenworthii* Torr. & A. Gray that grew to a height of 14 feet and contained 12% rubber (Josephson 1959; Polhamus 1962). *Solidago* was not developed into a commercial source of rubber since it was too costly at the time, the rubber was inferior to *Hevea* rubber (Swanson et al. 1979), and natural rubber was soon superseded by synthetic rubber obtained from petroleum (Josephson 1959). The notes of Thomas Edison's experiments on rubber-producing plants including *Solidago* are archived at the LuEsther T. Mertz Library at the New York Botanical Garden.

The horticultural importance of Astereae is based on taxa from relatively few genera. In southern hemisphere gardens, *Brachyscome* from Australia and *Felicia* from southern Africa are important ornamental plants in Mediterranean climate gardens (Elliot 2003; Pienaar 2003). The genera that contain most of the species in the commercially important horticultural trade in Europe and North America include *Symphotrichum*, *Solidago*, *Callistephus*, and *Aster* (Halevy 1999). The Asian *Callistephus chinensis* Nees, commonly known as the China aster, is the common aster of florists and flower gardens. Hybrids

between *Symphotrichum novi-belgii* (L.) G.L. Nesom and other eastern North American species have become important greenhouse crops and are currently a major horticultural export from Israel (Halevy 1999). Interspecific hybrids derived from North American species have likewise become important products in the cut-flower trade in Israel, Europe, and North America (Halevy 1999). *Aster amellus* L., native to Europe, is an important garden plant throughout Europe. Numerous other taxa of Astereae are regularly cultivated in their continent of origin but are not of major economic importance in the horticultural trade.

The negative economic impact of Astereae, as weeds, is relatively low. Several late-successional species of *Solidago* and *Symphotrichum* may be considered weedy because they occupy old fields and may prevent succession to forests in North America (e.g., Byrnes et al. 1993; Cain 1997; De Blois et al. 2002). Three species of *Solidago* introduced into European gardens as ornamentals have escaped from cultivation and become weedy in Europe (Weber 1998). *Solidago canadensis* L. has escaped cultivation in China and is rapidly spreading in eastern provinces of the country (Dong et al. 2006). *Erigeron* (*Conyza*) *canadensis* L., one of the most widely distributed Astereae species, has been shown to reduce agricultural productivity (Buhler and Owen 1997). It has become resistant to glyphosate, currently the most commonly used herbicide with genetically modified crops, in several countries, and thus has the potential of becoming noxious (VanGessel 2001). Furthermore, it could potentially transfer its resistance to related *Erigeron* species (for a review, see Zelaya et al., 2007).

CONCLUSION

We have presented the first overall phylogeny of Astereae (Fig. 37.1A–E), based on nuclear ribosomal internal transcribed spacer (ITS) sequence data. Though the tree is not fully resolved, we believe it reflects most of the important features of the evolution of the tribe. Most significantly, we confirmed that Astereae emerged in southern Africa and dispersed early to other continents. Most early lineages diverge in sequence along the spine of the tree and are species poor, but a few provide examples of evolutionary radiations in the southern hemisphere: Homochrominae and Grangeinae (southern Africa), Paleo South American

clade and New Zealand clade. An evolutionary explosion occurred among the crown lineages of Astereae, which conquered in rapid succession Australasia, South America (independently of the paleo invasion), and North America. From each of these new centers of diversification, dispersals occurred widely when opportunity arose, to Asia, the Pacific, Europe, and back to South America. What is most significant here is that radiation in each continent did not involve repeated intercontinental migrations. What is also significant is the dispersal capacity of Astereae, which show few dispersal specializations beyond anemochory.

The taxonomic consequence of this phylogenetic pattern is that, pending the identification of appropriate synapomorphies, continent of origin often reflects intergeneric relationships better than do the subtribal classification of Nesom and Robinson (2007). Despite this, we estimate that this classification, based on morphological and anatomical traits analyzed in a traditional manner, represents a significant advance in our knowledge of the tribe since it was founded on a major re-evaluation of characters and relationships. What is needed now is that character evaluation be done in a more strictly phylogenetic context. The phylogeny needs to be validated using other molecular markers, and the groups confirmed with better support and better resolution. This requires that regions both more conserved and more variable than ITS be explored. Also, the level at which subtribes are recognized will need to be discussed among specialists of the tribe to reach a proper consensus, as was done for Compositae (Panero and Funk 2002).

We have shown that potential economic usages of Astereae are greater than usually recognized, notably in domains such of pharmaceutical applications, rubber production, and horticulture. Likewise, we have shown that Astereae provide great scope for evolutionary and biological studies. Well-resolved phylogenies of the tribe, subtribe, and genera will stimulate such studies, and we hope that this overall phylogeny of Astereae will provide the impetus for further research in this field.

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Note added in proof

Li et al. (2008) provided morpho-anatomical and cytological evidence for moving the Chinese genus *Sheareria* from Heliantheae to Astereae. Li, W.-P., Zhang, P. & Yin, G.-S. 2008. New evidence for the tribal placement of *Sheareria* within Astereae (Compositae). *Journal of Systematics and Evolution* 46: 608–613.