

Liabeae

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HISTORICAL OVERVIEW

Liabeae and Barnadesieae (Compositae) are the only major tribes with entirely Neotropical distributions, both having their greatest generic and specific representation in the Andean Cordillera of western South America (Funk et al. 1995). Liabeae are concentrated in the northern and central Andes (Table 27.1) and Barnadesieae are mostly in the southern Andes. Liabeae contain approximately 165 species arranged in 18 genera and represent one of the smaller tribes in the family Compositae. The history of the classification of Liabeae reflects the difficulty in tribal placement encountered by early workers. Cassini (1823, 1825, 1830), Lessing (1832), De Candolle (1836), Weddell (1855–57), and Bentham in Bentham and Hooker (1873) all variously treated groups of taxa that are now placed in this tribe as members of Vernonieae, Heliantheae, Helenieae, Senecioneae and Mutisieae. Rydberg (1927) formally proposed tribal status for the genera of the North American Flora area.

Bentham's classification, which placed the majority of taxa in one genus, *Liabum*, in Senecioneae, was essentially adopted by Hoffmann (1890–1894). Despite work by Rydberg (1927), who established the tribe and recognized genera from Mexico, Central America, and the West Indies, and isolated works by Blake (1935), Cabrera (1954), and Sandwith (1956), which recognized the Liabean affinities of other genera, the tribe Liabeae was not adopted. Instead, Bentham's classification was retained more or less intact and accepted by many modern floristic and taxonomic workers (D'Arcy 1975; Cronquist 1955; Carlquist 1976). Nash and Williams (1976) accepted

Bentham's concept of a single genus but placed the genus in Vernonieae. It was not until Robinson and co-workers published a series of papers bringing the genera together into one tribe (Robinson and Brettell 1973, 1974; see Robinson 1983a for additional references) that the accepted taxonomy began to change. Nordenstam (1977) followed Robinson's tribal circumscription and, although it was included in the same chapter as Senecioneae, he recommended recognition at the tribal level. Robinson (1983a) provided the first modern view of the tribe including a detailed review of previous classification efforts and relevant literature.

Since Robinson's generic review (1983a), there has been some research activity within the tribe, especially discussions of generic boundaries and the description of additional species. For example, the status of Rydberg's (1927) four closely related Mexican and Central American Liabeae genera (*Sinclairia*, *Sinclairiopsis*, *Megaliabum*, *Liabellum*) has been investigated. McVaugh (1984) reverted to earlier work and treated the seven species from southwest Mexico as belonging to a broadly interpreted *Liabum*. Turner (1989) revised the group and recognized three evolutionary lines within the genus *Sinclairia*; one of which equaled the genus *Liabellum*, which was reduced to sectional status. Although the two genera were combined, Turner's treatment essentially agreed with those of Rydberg (1927) and Robinson (1983a) in recognizing the *Sinclairia*–*Liabellum* lineage as distinct from *Liabum*. The question of the hierarchical structure within the *Sinclairia* complex remains controversial (Robinson 1990a). In the most recent treatment Bremer (1994) followed Turner's inclusion of *Liabellum* in *Sinclairia*. Turner (2007) recently

treated the tribe for the flora of Mexico and reported one species of *Liabum* and all others referred to *Sinclairia*.

Robinson has described new species in *Liabum*, *Ferreyranthus*, and *Munnozia* (Robinson 1983b, 1990a, b, 1994). Dillon and Sagástegui (1994a) revised *Ferreyranthus* and described new species in *Chrysactinium* (Sagástegui and Dillon 1994) and *Oligactis* (Dillon and Sagástegui 1994b), both from northern Peru. Zermoglio and Funk (1997) have described a new species of *Chrysactinium* from northern Peru and revised the genus (Funk and Zermoglio 1999). Moran and Funk (2006) revised *Erato* and described a new species from Costa Rica. Funk and Robinson (2001) described a new genus, *Dillandia*, and transferred species from Colombia and Peru that formally were classified as *Munnozia*. *Sampera* (Funk and Robinson, in prep.) has been established for a group of eight species previously classified in *Oligactis* subgenus *Andromachiopsis*.

The tribe was treated in the published results from the International Compositae Conference held at Royal Botanic Gardens, Kew in 1994 (Funk et al. 1996). Most recently, the tribe was treated in Kubitzki and Jeffrey's treatment of the Asterales (Funk et al. 2007).

DISTRIBUTION AND DIVERSITY

Liabeae are distributed throughout much of the Neotropics, but they exhibit their greatest generic and specific concentration in western South America and the most likely place of origin of the modern-day tribe is in the Andean Cordillera. The center of generic diversity is in Peru where 13 of the 18 genera are found, followed by Ecuador (8 genera), Colombia (7 genera), Bolivia (6 genera), Costa Rica (5 genera), Panama (5 genera), Venezuela (4 genera), Mexico (4 genera), Argentina (4 genera), Guatemala (2 genera), El Salvador (2 genera), Honduras (2 genera), Nicaragua, and Caribbean (Cuba, Hispaniola, Jamaica) with one genus each. Recently, *Liabum acuminatum* Rusby was identified (by H. Robinson) from a 1968 collection from Acre, Brazil (*Prance, Ramos and Farias 7310*, US) making it the first confirmed record of the tribe from that country; subsequently *L. amplexicaule* Poepp. & Endl. was recorded from the region (*Daly et al. 9631*, US) (Gutiérrez, pers. comm.). Figure 27.1 illustrates the overall distribution of the tribe within the neotropics and indicates generic diversity for each country where the tribe is represented. The majority of genera possess rather limited distributions (Table 27.1), often confined to small geographic areas and narrow ranges of environmental conditions. Members of the tribe typically occupy sites in forest communities from Mexico to Central America, the West Indies, and throughout western South America from Venezuela to central Argentina (50–4750 m). A few species in several genera are found in open or disturbed habitats associated

with rivers, road cuts, or tree falls. More rarely, a few species occupy seasonally dry scrub or desert habitats in both North and South America. A number of genera are associated with essentially alpine habitats well above forested zones, including *subpáramo*, *páramo*, *jalca*, and *puna* environments (>3000 m) (Dillon 2005).

For purposes of discussion, the genera will be presented as they are arrayed within the strict consensus cladogram (Fig. 27.2) derived from the molecular analysis (Funk and Chan, in prep.). The analysis utilized data from ITS, *trnL-F*, and the 3' end of *ndhF*.

Clade A, contains three *Cacosmia* species, all shrubs and primarily restricted to open habitats in northern Peru and southern Ecuador (1500–3200 m; Funk and Brooks 1991; Fig. 27.3A). The combination of characters, including sheathing leaf bases, opposite, denticulate leaves with adaxial bullate surfaces and densely tomentose abaxial surfaces, loosely aggregated capitula with cylindrical, multiseriate involucre, only five, yellow ray florets, and achenes lacking a pappus, make this a distinctive element of the central Andes (Dillon 2005).

Clade B, containing *Ferreyranthus-Dillandia-Oligactis-Sampera-Liabum*, contains ca. 36.8% of the species diversity and its representatives occur from Mexico to northwestern Argentina (Gutiérrez 2003). *Ferreyranthus* contains eight species which grow from central Peru to central Ecuador in wet to seasonally dry montane habitats. They range in size from small suffrutescent shrubs to small trees seldom over four or five meters (Dillon and Sagástegui



Fig. 27.1. Generic diversity in Liabeae by country.

1994a) (Fig. 27.3B, C). *Dillandia* contains three species of herbs with bullate leaf surfaces, pale yellow anther thecae, solitary to few capitula on long scapes, and is recorded from Colombia, Ecuador and northern Peru (Funk and Robinson 2001) (Fig. 27.3E–G). *Liabum*, *Oligactis*, and *Sampera* are concentrated in South America but range into Central America (Table 27.1). *Liabum* (Fig. 27.3D, H, I) possesses the widest overall distribution of any genus in the tribe stretching from central Mexico and the West Indies to the border between Bolivia and Argentina (Gutiérrez 2003). It is the only genus represented in the West Indies, with five species found in lowland to upland moist forests associated with limestone areas in Cuba, Hispaniola, and Jamaica (150–1400 m) (Gutiérrez and Katinas 2006). A single *Liabum* species (*Liabum bourgeauii* Hieron.) occurs in various types of forest from Mexico to Panama (1000–2000 m); the species diversity of *Liabum* increases in South America where the Andean Cordillera is home to 26 species (200–3000 m). *Oligactis* (s.str.) contains seven species confined to cloud forests from Venezuela, Colombia and Ecuador (1200–3500 m), and two species reaching the oak forests of Panama and Costa Rica (1750–2500 m). *Sampera* was described to accommodate a group of eight species of scandent shrubs and vines from Colombia to

Peru that were previously classified as *Oligactis* subgenus *Andromachiopsis* (Funk and Robinson, in prep.)

Clade C, containing *Sinclairia*-*Sinclairiopsis*-*Liabellum*, contains ca. 15% of the species diversity of the tribe and is essentially a northern hemispheric group with considerable radiation. Its three closely related, and sometimes synonymous genera, *Sinclairia*, *Liabellum*, and *Sinclairiopsis*, are all found in Mexico and Central America with the exception of the widespread species *Sinclairia polyantha* (Klatt) Rydb., which is found in southern Mexico, Central America, and Colombia (Table 27.1). *Sinclairiopsis* is a monotypic Mexican genus and the sister taxon to the remainder of the *Sinclairia* complex. *Sinclairia* (including *Megaliabum*) and *Liabellum* form the *Sinclairia* complex, which contains approximately 20 species, principally confined to moist forests of Mexico and Central America (150–2500 m), with one common species reaching western Colombia (1600–1900 m) (Fig. 27.4). A few of the Mexican species are found in more arid environments associated with tropical scrub and deciduous forests. Turner (1989) treated *Megaliabum andrieuxii* (DC.) H. Rob. & Brettell, *M. pringlei* and *M. moorei* as *Sinclairia*, and these taxa do not all share sister taxa relationships (Fig. 27.2). The status of

Table 27.1. Genera, species diversity, distribution, and latitudinal range of Liabeae.

Genus	Species	Country distribution	Latitudinal range
<i>Bishopanthus</i>	1	Peru	3°S–7°S*
<i>Cacosmia</i> (<i>Cac</i>)	3	Ecuador, Peru	0°–10.5°S
<i>Chionopappus</i> (<i>Chi</i>)	1	Peru	7°S–13°S
<i>Chrysactinium</i> (<i>Chr</i>)	8	Ecuador, Peru	0.5°N–11.0°S
<i>Dillandia</i> (<i>Dil</i>)	3	Colombia, Peru	1.37°N–5.7°S
<i>Erato</i> (<i>Era</i>)	5	Costa Rica, Panama, Venezuela, Colombia, Ecuador, Peru, Bolivia	11°N–18.5°S
<i>Ferreyranthus</i> (<i>Fer</i>)	8	Ecuador, Peru	1°S–15°S
<i>Liabellum</i> (<i>Lib</i>)	5	Mexico	27°N–19.5°N
<i>Liabum</i> (<i>Lia</i>)	27	Mexico, Caribbean, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Venezuela, Colombia, Ecuador, Peru, Bolivia, Brazil, Argentina	21.5°N–23°S
<i>Microliabum</i> (<i>Mic</i>)	5	Bolivia, Argentina	19°S–33°S
<i>Munnozia</i> (<i>Mun</i>)	46	Costa Rica, Panama, Venezuela, Colombia, Ecuador, Peru, Bolivia, Argentina	11°N–23.5°S
<i>Oligactis</i> (<i>Oli</i>)	7	Ecuador, Colombia, Venezuela, Costa Rica, Panama	10°N–4°S
<i>Paranephelius</i> (<i>Par</i>)	7	Peru, Bolivia, Argentina	3°S–22.5°S
<i>Philoglossa</i> (<i>Phi</i>)	5	Colombia, Ecuador, Peru, Bolivia	0.5°N–17°S
<i>Pseudonosseris</i> (<i>Psu</i>)	3	Peru	3°S–17°N
<i>Sampera</i> (<i>Sam</i>)	8	Colombia, Ecuador, Peru	4°N–6°S
<i>Sinclairia</i> (<i>Sin</i>)	20	Mexico, Guatemala, El Salvador, Honduras, Costa Rica, Panama, Colombia	23°N–4°N
<i>Sinclairiopsis</i> (<i>Sio</i>)	1	Mexico	17°N–18°N

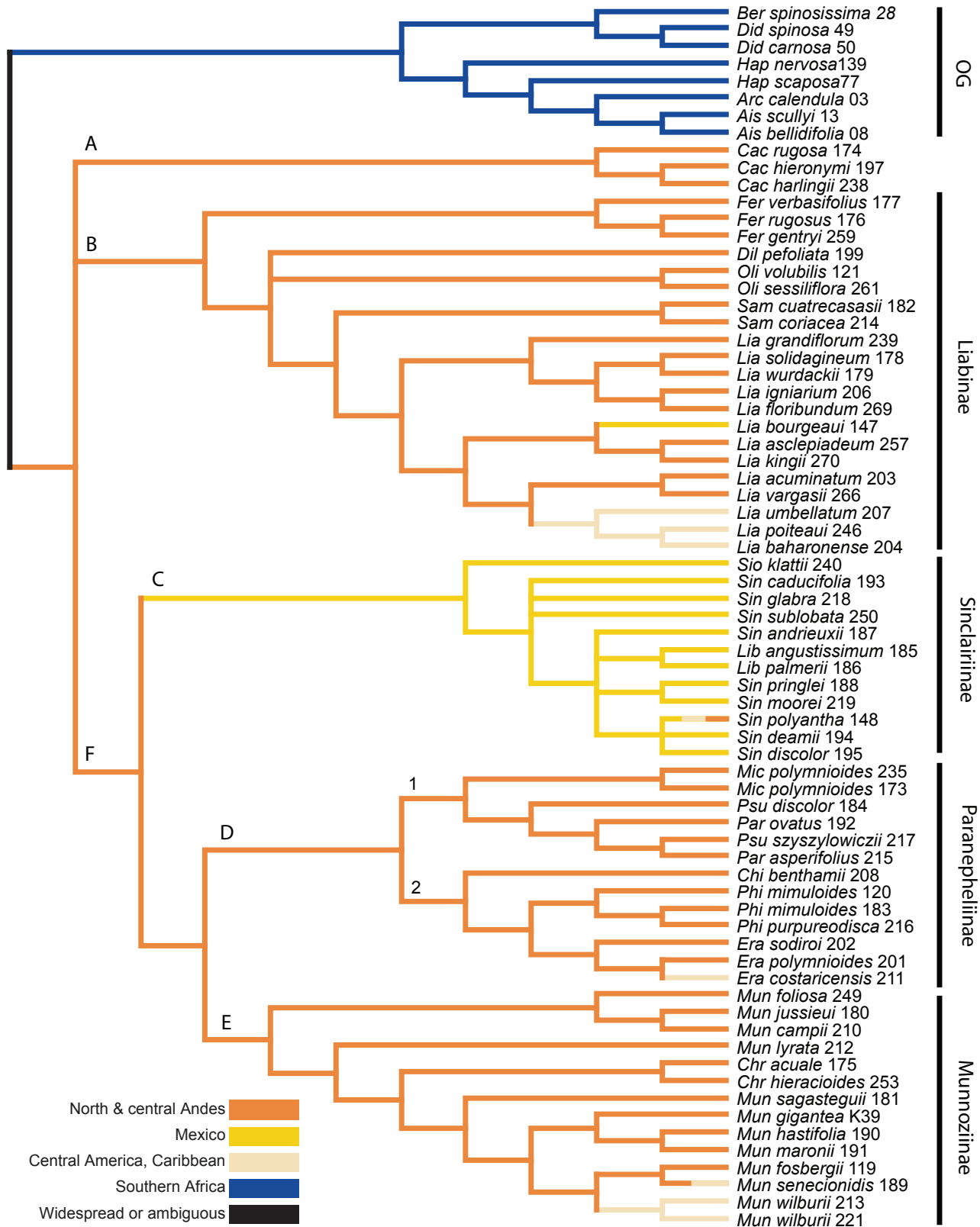


Fig. 27.2. Strict consensus cladogram from molecular studies incorporating sequence data from ITS, *trnL-F*, and the 3' end of *ndhF* markers (Funk and Chan, in prep.). Numbers refer to accessions in the molecular studies. Colors refer to the distribution of the terminal taxa. Generic abbreviations correspond to labels in Table 27.1. See Chapter 44 for complete metatree.

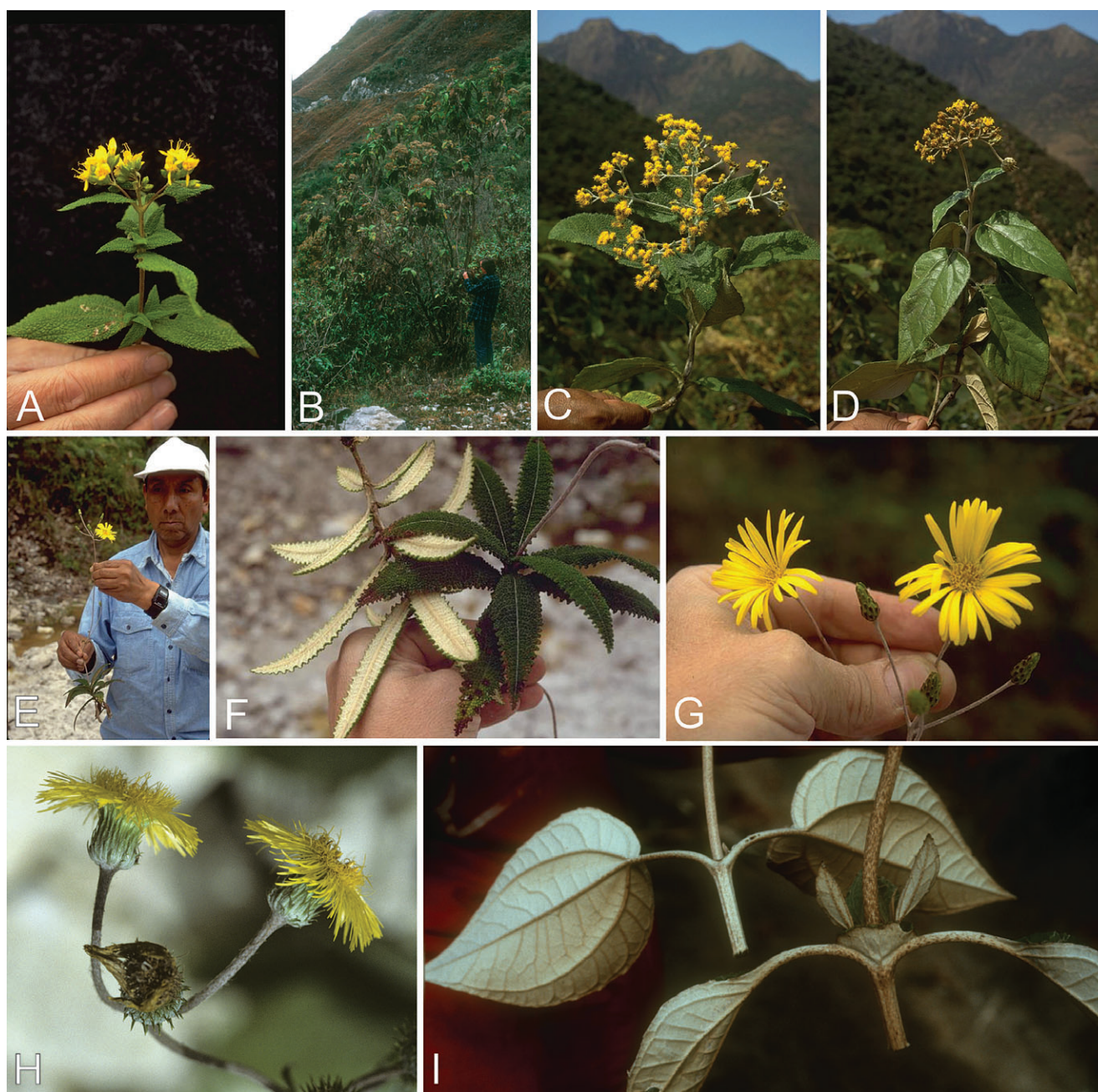


Fig. 27.3. **A** *Cacosmia rugosa* Kunth, a subshrub with bullate leaves and capitula with 5–6 ray florets; **B** *Ferreyranthus excelsus* (Poepp. & Endl.) H. Rob. & Brettell, a weak tree to 6 m tall with radiate capitula; **C** *F. verbascifolia* (Kunth) H. Rob. & Brettell, a large shrub with bullate leaves; **D** *Liabum solidagenium* (Kunth) Less., a large shrub with smooth leaves; **E** *Dillandia subumbellata* (Rusby) V.A. Funk & H. Rob., a weak herb with scandent habit with long peduncles and few capitula; **F** *D. subumbellata*, bullate upper leaf surfaces and densely tomentose lower surface; **G** *D. subumbellata*, capitula with ca. 40 ray florets; **H** *Liabum barahonense* Urban, capitula with nearly 50–75 ray florets with filiform limbs; **I** *L. amplexicaule* showing interpetiolar pseudostipular foliar tissue.

Megaliabum is under evaluation. *Liabellum* is comprised of perhaps five species, mostly restricted to seasonally dry sites in west-central Mexico (1000–2000 m). The group is here formally recognized at the subtribal rank, Sinclairiinae H. Rob. (cf. Appendix 27.1).

Clade D, containing *Microliabum*–*Pseudonosoris*–*Paranephelius*–*Chionopappus*–*Philoglossa*–*Erato*, has ca. 15.5% of the species diversity of the tribe and, with the exception of one species of *Erato* in Costa Rica, is entirely South American in distribution. The most southern genus,

Microliabum, has five species distributed from southern Bolivia to northwestern Argentina (2800–3300 m; Funk and Brooks 1991). *Paranephelius*, with seven species, is found in upper elevation sites (*jalca* and *puna*) from northern Peru to Bolivia and extreme northern Argentina (2200–4600 m) (Fig. 27.5). *Pseudonosseris* contains three species, one, the type, is confined to a narrow distribution in southern Peru (3200–3500 m) and another two restricted to northern Peru (1800–2600 m) (Fig. 27.6A–C). *Philoglossa* with five species is represented by one found in inter-Andean sites from Colombia through the interior of Peru to Bolivia (200–3100 m), and four species restricted to the coastal *lomas* formations or valleys of coastal Peru (100–700 m) (Fig. 27.7E, F). *Erato* has five species, one endemic to Costa Rica, another that ranges from Costa Rica (1200–2500 m) to Venezuela, Colombia, and Ecuador, and another three that are confined to Ecuador, Peru, and Bolivia (900–2900 m) (Fig. 27.7C, D). *Chionopappus* is monotypic and restricted to central Peru (1600–2500 m) and occasionally recorded from coastal *lomas* formations (400–500 m) of northern Peru (Fig. 27.7B). *Bishopanthus*, a monotypic genus tentatively associated with Clade D since it approaches *Chionopappus* in capitular morphology; it has only been recorded once at a site east of the Río Marañón and has not been included in any molecular studies to date (2000 m) (Fig. 27.7A).

Clade E, containing *Munozia-Chrysactinium*, contains ca. 31% of the species diversity in the tribe and with a few exceptions represents an Andean group in a wide variety of habitats. *Munozia* ranges from Costa Rica and Panama, where two species are known, to Andean South America from Venezuela to Bolivia and Argentina where 45 species have been recorded (600–3800 m) (Fig. 27.8C–H). *Chrysactinium*, confined to Ecuador and Peru, has eight species and is predominately found in open, upper elevation sites (*páramo*) and occasionally at the margins of cloud forests (1700–4300 m) (Fig. 27.8A, B).

PHYLOGENY AND SYSTEMATICS

A cladistic analysis was performed, using data from ITS, *trnL-F*, and the 3' end of *ndhF*, and those results are illustrated in Figure 27.2 (cf. Funk and Chan, in prep.). The placement of *Cacosmia* as the sister taxon to the remainder of the tribe was found in ITS trees and in the combined analysis; however, it was never strongly supported. In the chloroplast trees the position of *Cacosmia* varied depending on the outgroup(s) used. Sometimes it was the sister group to Clade B (our preferred placement based on morphology), and other times it was in a polytomy with Clade B and the remainder of the tribe [Clades (C(D, E))]. At this point, it seems best to keep the least resolved

tree, the polytomy, as the working cladogram. Additional markers are being added in an effort to increase resolution of putative relationships.

Subfamily, tribal and subtribal relationships

Until recently Liabeae have resided in the subfamily Cichorioideae s.l., whose members share deeply lobed disk corollas, long-spurred or calcarate anther bases, continuous stigmatic surfaces on the inside of the style branches, long sweeping hairs that cover the outer surface of the style branches and the upper style shaft, and spherical spinose pollen, along with Mutisieae, Cardueae, Lactuceae, Vernonieae, and Arctoteae and miscellaneous small tribes (Robinson and Funk 1987; Bremer 1994; Jansen et al. 1991). However, this definition of the subfamily has been shown to be non-monophyletic, and the most recent circumscription excludes paraphyletic Mutisieae and thistles. As a result, most of the characters that previously united the subfamily are now considered plesiomorphic. Some characters appear to be apomorphic, such as the tendency to produce latex or at least to have the anatomical characters that would allow it to do so. However, this character is missing in most Vernonieae and so is not reliable in determining which taxa 'belong' in this monophyletic group. Another potential apomorphy, the presence of calcarate anthers is either plesiomorphic for the family as a whole or it may be two independent apomorphic characters. Although the characterization of the subfamily is ongoing, it is clear that the four main tribes in the subfamily are Arctotideae, Lactuceae, Liabeae, and Vernonieae. They, along with several small tribes (see Chapter 23), form a strongly supported monophyletic group within the subfamily in every analysis. It also seems clear that the sister group of Liabeae is Vernonieae and/or Arctotideae. The molecular data of Vernonieae (especially the ITS) are so different from Liabeae that they make a poor outgroup, and so Arctotideae were used in the phylogenetic analysis. Lactuceae are always sister to the Liabeae-Vernonieae-Arctotideae clade. The distribution of characters makes it difficult to determine the exact relationships among these three tribes. The presence of latex is shared by Lactuceae and Liabeae and Arctotideae; vernonioid type styles are shared by Vernonieae and Liabeae; and the absence of rays and presence of mostly blue flowers group Vernonieae and Lactuceae. Most present-day taxonomists consider Liabeae to be most closely related to Vernonieae (Chapter 23). However, at present, this grouping is only moderately supported, and the placement of several smaller tribes may alter its position, and as a result, the relationships within this subfamily will require additional study.

Robinson (1983) provided the first efforts to established a subtribal classification, where three subtribes



Fig. 27.4. *Sinclairia* taxa from Mexico. **A** *Sinclairia polyantha* (Klatt) Rydb., leaf underside and capitulescence; **B** *S. polyantha*, lateral view of capitulum illustrating multiseriate involucre; **C** *S. polyantha* capitulum showing loose radiate capitulum; **D** *Sinclairia* (*Megaliabum*) *andrieuxii* (DC.) H. Rob. & Brettell; **E** *S. (Megaliabum) andrieuxii* radiate capitulum showing herbaceous phyllaries; **F** *S. (Megaliabum) andrieuxii* radiate capitulum; **G** *S. (Megaliabum) pringlei* (B.L. Rob. & Greenm.) Rydb. herbaceous, erect perennial; **H** *S. (Megaliabum) pringlei*, discoid capitulum; **I** *S. caducifolia* (B.L. Rob. & Bartlett) Rydb., habit and habitat; **J** *S. caducifolia*, discoid capitula.

were recognized, i.e., Munnoziinae, Liabinae, and Paranepheleinae, largely based upon overall morphology and distribution of endotheical cells. Our knowledge of the internal structure of the tribe is expanding, and the strong support for the monophyletic group represented by *Sinclairia* and its closest putative relatives, i.e., *Sinclairiopsis*, *Megaliabum*, and *Liabellum*, has led to description of Sin-

clairiinae (Fig. 27.1, cf. Appendix 27.1). Further, the current bounds of Paranepheleinae are expanded to include the other members of the strongly supported Clade D containing *Paranepheleus*, *Pseudonosoris*, *Microliabum* and the sister group containing *Chionopappus*, *Philoglossa*, and *Erato*. As with relationships at higher levels, the internal classification of Liabeae is still a work in progress.



Fig. 27.5. **A** *Paranepheleus uniflorus* (Poepp. & Endl.) Sch.Bip. with pinnately divided basal leaves and bullate upper leaf surfaces; **B** *P. uniflorus*, capitula; **C** *P. ovatus* Wedd. with entire leaves and smooth upper leaf surfaces; **D** *P. ovatus*, capitulum.

MORPHOLOGY AND ANATOMY

Liabeae have a series of characters that make it relatively easy to identify; however, as in most tribes, there are taxa with exceptions to some of the tribal characters. The tribe is diagnosed by a combination of morphological characters: the leaves are invariably opposite, but some genera possess leaves in a rosette or congested on short stems so they appear to

be whorled (e.g., *Chrysactinium*, *Paranephelius*, *Pseudonosseris*, and rarely *Liabum*); leaves are often strongly trinervate (pinnatifid in *Ferreyranthus*, *Oligactis*, *Paranephelius*; palmate in *Erato*) and white-tomentose beneath (strigose or pilose in *Erato*; glabrous in *Philoglossa*), yellow ray and disk florets (reddish in *Chionopappus* and one species of *Pseudonosseris*; white in two species of *Munmozia*), disc florets numerous, hermaphroditic with narrowly funnelliform limbs and



Fig. 27.6. **A** *Pseudonosseris discolor* (Muschl.) H. Rob. & Brettell, habit and habitat; **B** *P. discolor*, capitulum (photographs of Quipuscoa 3338, Sandia, Puno, Peru); **C** *Pseudonosseris szyszyłowiczii* (Hieron.) H. Rob. & Brettell capitulum (Dillon et al. 6485); **D** *Microliabum candidum* (Griseb.) H. Rob. capitulum; **E** *M. polymnioides* (R.E. Fries) H. Rob. illustrating interpetiolar pseudo-stipules and white latex from cut stem. [Photographs: D, E, D. Gutiérrez.]

deeply lobed corollas; oblong or columnar achenes usually with a biseriate pappus of outer scales and inner scabrous bristles (absent in *Cacosmia*; bristles only in *Paranephelius*), and the frequent occurrence of white latex (apparently absent in *Ferreyranthus*, *Liabum*, and *Oligactis*).

Other characters are moderately useful such as involucre are cylindrical to hemispherical with 3 to many, sub-imbricate phyllaries, and receptacles are alveolate, naked or more often with projecting squamellae or points (true

paleae are only known in *Chionopappus*); the capitula have pistillate ray florets (absent in *Liabellum* and some *Sinclairia*) with well-developed, 3-lobed lamina.

Some characters are quite variable or otherwise uninformative including the habit which comes in a wide range of forms including cauline, annual to perennial herbs, lianas, shrubs, or small trees, or more rarely acaulescent or short-stemmed herbs; the capitula can be solitary and scapose to sessile, or more often weakly to densely cymose

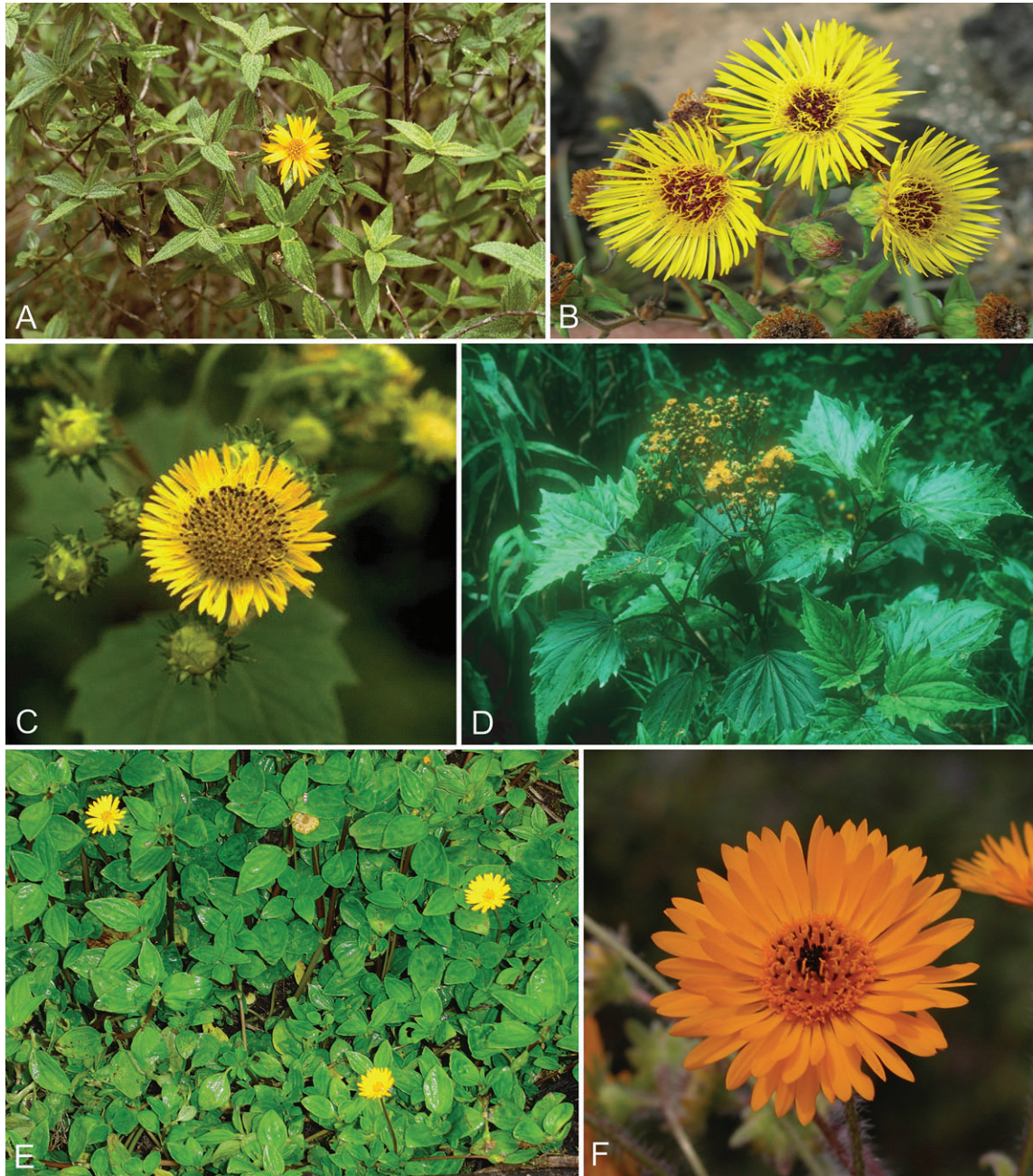


Fig. 27.7. **A** *Bishopanthus soliceps* H. Rob.; **B** *Chionopappus benthamii* S.F. Blake; **C** *Erato stenolepis* (S.F. Blake) H. Rob.; **D** *E. polymnioides* DC.; **E** *Philoglossa mimuloides* (Hieron.) H. Rob. & Cuatrec.; **F** *P. peruviana* DC.

to corymbose-paniculate; anther thecae are usually pale, or occasionally black (e.g., *Chrysactinium*, *Erato*, *Munnozia*, *Philoglossa*), the bases calcarate and tailed or rounded, and the terminal appendages oblong-ovate; style branches in most genera are relatively short and with narrowly obtuse or rounded apices; the inner stigmatic surfaces are undivided and outer branch surfaces and upper shafts are often pubescent with acute trichomes. Achenes (cypselas) are oblong, fusiform, or columnar, with (2-)4-10 ribs, the

surfaces are glabrous or pubescent with glandular and/or elongate trichomes. When present, the biseriate pappus can have an inner pappus of numerous long, scabrid capillary bristles, plumose bristles (*Chionopappus*), or broad squamellae (one species of *Microliabum*). The outer pappus is often a series of shorter bristles or squamellae, but it can also be reduced to awns in *Erato* and some *Philoglossa* species, or totally absent in Paranepheleinae, much of Munnoziinae, *Cacosmia* and *Chionopappus*.



Fig. 27.8. **A** *Chrysactinium hieracioides* (Kunth) H. Rob. & Brettell, habit and habitat; **B** *C. rosulatum* (Hieron.) H. Rob. & Brettell, capitulum; **C** *Munnozia sagasteguii* H. Rob., habit; **D** *M. sagasteguii*, capitulum; **E** *M. sagasteguii*, fleshy roots; **F** *Munnozia senecionidis* Benth., leaves and capitula (Quipuscoa 1099, San Martin, Peru); **G** *M. jussieui* (Cass.) H. Rob. & Brettell, habit; **H**. *M. jussieui*, close-up of capitula.

POLLEN

Liabeae pollen grains are tricolporate with ectoapertures meridionally elongate and endoapertures transversely short and ovoid; spherical to oblate-spheroid in shape; approximately 25–40 μm (occasionally up to

50 μm) in diameter with *Liabum* and *Oligactis* the smallest and *Sinclairia* and *Liabellum* the largest. Stix (1960) and Robinson and Marticorena (1986) should be consulted for detailed measurements of: aperture length and width, exine layer thicknesses, spine dimensions, exine diameters with and without spines, length and diameter

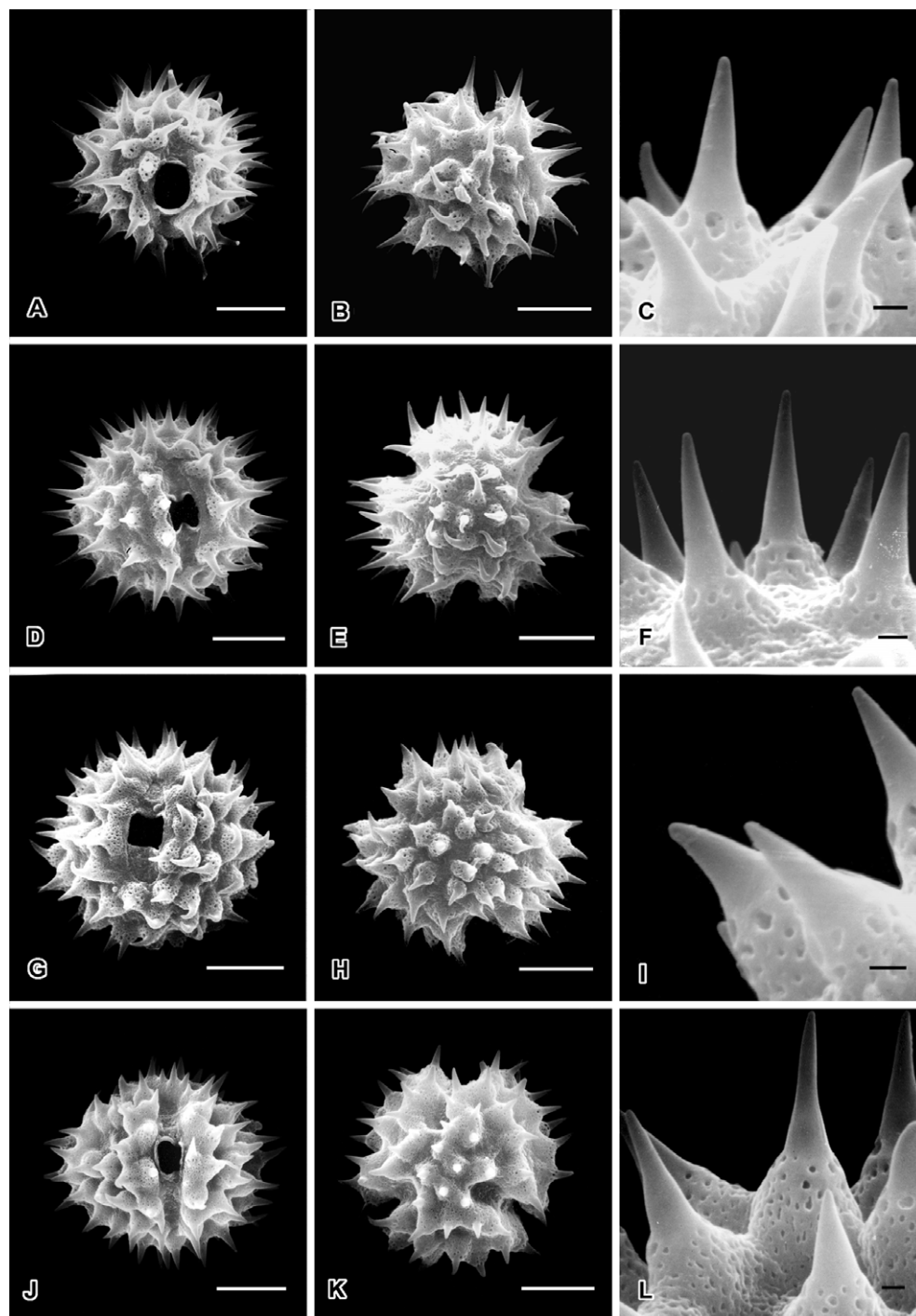


Fig. 27.9. **A–C** *Philoglossa peruviana* DC.; **D–F** *Philoglossa purpureodisca* H. Rob.; **G–I** *Philoglossa mimuloides* (Hieron.) H. Rob. & Cuatrec.; **J–L** *Erato polymnioides* DC. Scale bars for A, B, D, E, G, H, J, K = 10 μm ; for C, F, I, L = 1 μm .

of columellae, etc. The exine surface (tectum) is highly perforate and echinate with both regular and irregularly organized spines and with spine bases either distinct or overlapping (*Philoglossa*, Figs. 27.9A–I; *Erato*, Fig. 27.9J–L; *Munnozia*, Fig. 27.10A–C; *Liabum*, Fig. 27.10D–F; *Sinclairia*, Fig. 27.10G–I; *Chionopappus*, Fig. 27.10J–L). It is noteworthy, as emphasized by Robinson and Marticorena (1986) and Funk et al. (2007), that the irregular organization of the spines and spine bases does not attain the

lophate or psilate condition(s) present in putative tribes Vernoniae, Senecioneae and Lactuceae.

SEM of fractured grains shows prominently thickened basal columellae that are attached proximally to a narrow foot layer (Fig. 27.11C–E, H, J, K) and distally terminate in two levels of lateral and essentially parallel branches. The upper branch is the highly perforate exine surface (tectum, Figs. 27.9A–L, 27.11A–L) and is connected to the lower branch (inner tectum) by

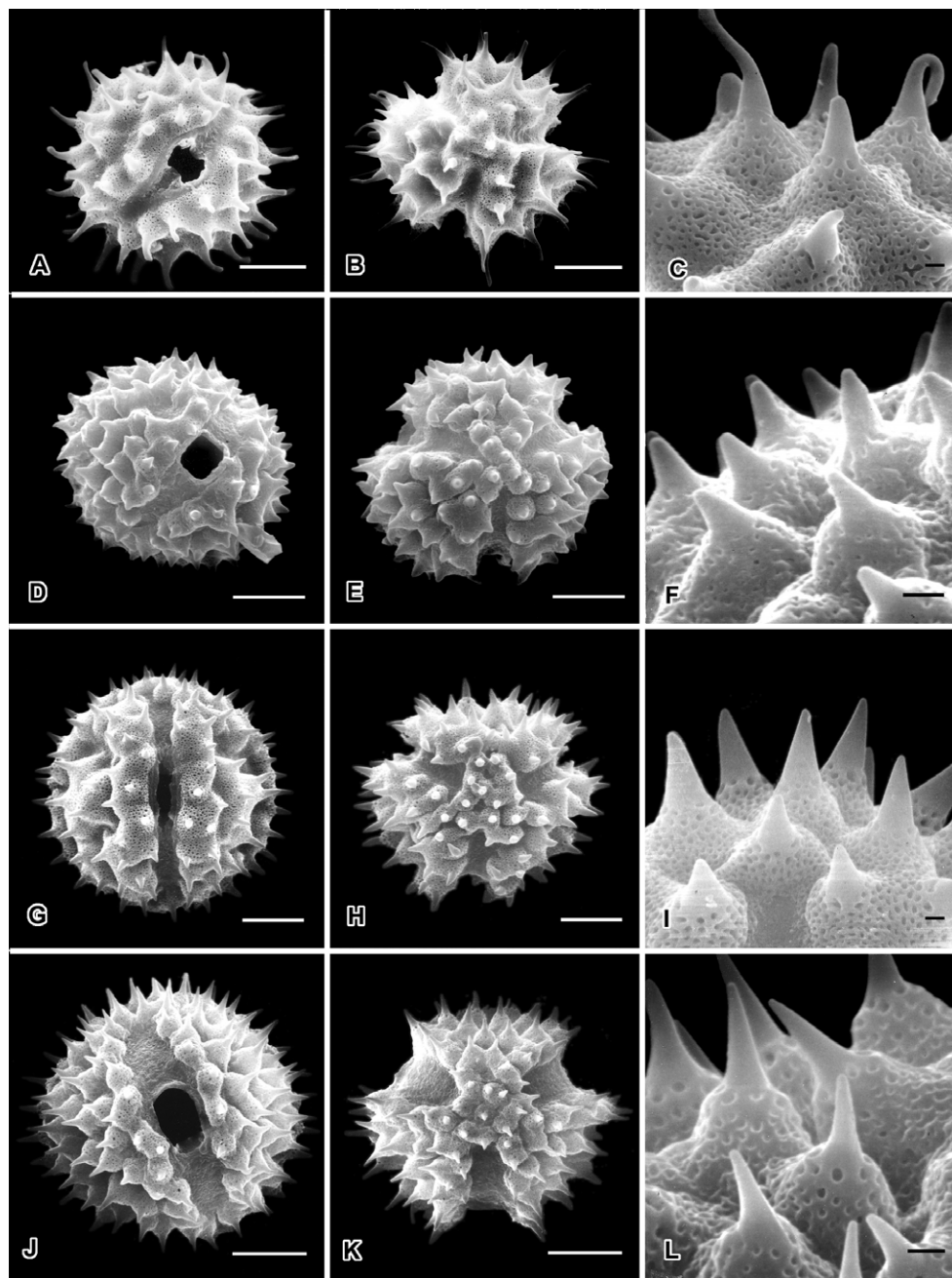


Fig. 27.10. **A–C** *Munnozia lanceolata* Ruiz & Pav.; **D–F** *Liabum ignarium* (Kunth) Less.; **G–I** *Sinclairia caducifolia* Rydb.; **J–L** *Chionopappus benthamii* S.F. Blake. Scale bars for A, B, D, E, G, H, J, K = 10 µm; for C, F, I, L = 1 µm.

short columellae $<1.0\ \mu\text{m}$ in length (Fig. 27.11A–K). Acute spines project from the exine surface in either orderly or unorganized arrangements as well as having bases that are distinct from adjacent spines or confluent with them (Figs. 27.9A–L, 27.11A–L). Basal columellae are either grouped under the spines or are coalesced into hollow cylinders (Fig. 27.11A–K; Robinson and Marticorena 1986) with one cylinder per spine (Funk

et al. 2007: Fig. 27.41D). The particular organization of the spines on the exine surface, spine base independence and confluence, and the relationship of basal columellae with spines are characters found only in Liabeae and are considered by Robinson and Marticorena (1986) as major distinctions from Vernoniaeae pollen where single solid basal columellae span the exine from foot layer to spine tip, a relationship also common in other tribes

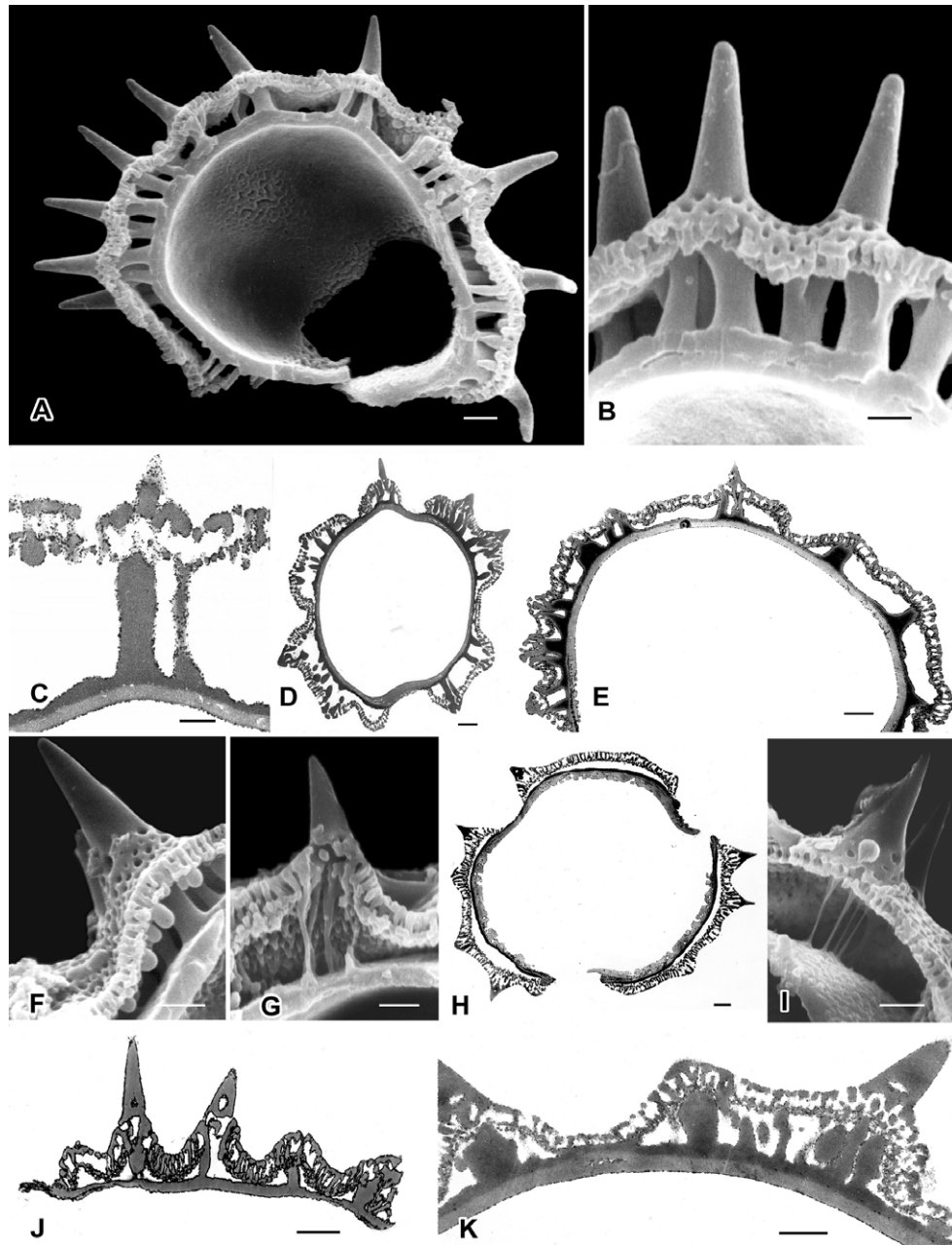


Fig. 27.11. **A, B** *Cacosmia rugosa* Kunth; **C, D** *Ferreyranthus rugosus* (Ferreyra) H. Rob. & Brettell; **E** *Liabum solidagineum* Less.; **F** *Sinclairia polyantha* Rydb.; **G** *Pseudonosoris discolor* (Muschl.) H. Rob. & Brettell; **H** *Paranephelius asperifolius* (Muschl.) H. Rob. & Brettell; **I** *Philoglossa peruviana* DC.; **J** *Chrysactinium acaule* (Kunth) Wedd.; **K** *Munnozia lanceolata* Ruiz & Pav. Scale bars for A, D, E, H–K = $2\ \mu\text{m}$; for B, C, F, G = $1\ \mu\text{m}$.

such as Mutisieae (Zhao et al. 2006), Anthemideae and Cardueae (Skvarla et al. 1977). Extremely thin columellae (ca. $<0.5 \mu\text{m}$ in width) support the internal tectum (Fig. 27.11G–I). While common in Liabeae (Feuer and Dillon 1982; Robinson and Marticorena 1986), slender columellae are also present in Vernonieae (Skvarla et al. 2005) and Lactuceae (Blackmore 1981, 1982). The presence of columellae, both thickened and slender (Figs. 27.11A–K), interrupt what otherwise would be a continuous open space or cavus (Skvarla and Turner 1966) in the exine whereby the outer exine (i.e., lower part of the internal tectum) is separated from the foot layer and with the only union of these layers being at the three aperture margins. The result is what is known as a caveate pollen structure and is characteristic of tribes such as Heliantheae, Senecioneae, Eupatorieae and Helenieae. The caveate feature is problematic only in *Paranephelius* (Fig. 27.11H; Stix 1960; Skvarla et al. 1977) and some species of *Munnozia* (Robinson and Marticorena 1986). In all other Liabeae pollen, the comparable areas are partially occupied by distinctive columellae between the foot layer and the lower part of the internal tectum and we have used the term “pseudocaveate” to describe it.

TEM sections of *Ferreyranthus* (Fig. 27.11C, D), *Liabum* (Fig. 27.11E), *Paranephelius* (Fig. 27.11H), *Chrysactinium* (Fig. 27.11J) and *Munnozia* (Fig. 27.11K), as already indicated, reinforce the data from fractured pollen grains examined in SEM (Fig. 27.11A, B, F, G, I). Especially important are the electron stain differences that indicate a consistently thicker endexine immediately beneath a slightly narrower foot layer (i.e., Fig. 27.11C, K) for all of the Liabeae taxa examined. Globose structures attached to the lower margin of the internal tectum as noted in TEM (Fig. 27.11C) and SEM (Fig. 27.11F) were earlier described for *Liabum barahonense* Urban (Robinson and Marticorena 1986) and *Munnozia tenera* (Sch.Bip.) H. Rob. & Brettell (Funk et al. 2007) and are in need of clarification but appear to be the swollen bases of the short columellae that connect the two tectal layers.

Observations based on SEM and TEM were made on the pollen of 11 genera and 17 species of the tribe (Figs. 27.9–27.11). Liabeae taxa reported earlier include *Dillandia* pollen (Funk and Robinson 2001: Figs. 1–2; Funk et al. 2007: Fig. 41C), *Microlabum* (Funk et al. 2007: Fig. 41A) and *Chrysactinium* (Funk et al. 2007: Fig. 41B). Complimenting these reports is the comprehensive study by Robinson and Marticorena (1986), where they described by SEM whole and fractured pollen grains of *Paranephelius*, *Pseudoseris*, *Bishopanthus*, *Chionopappus*, *Austroliabum*, *Cacosmia*, *Ferreyranthus*, *Sinclairia*, *Liabellum*, *Liabum*, *Oligactis*, *Erato*, *Philoglossa*, *Chrysactinium* and *Munnozia*. *Sampera* is comprised of taxa originally classified as *Oligactis*, and its species have been examined (Robinson and Marticorena 1986).

Structural features described from sectioned pollen from other studies also are in agreement with TEM in Fig. 27.11C–E, H, J, K as indicated by an LM microtome section of *Chionopappus* (Robinson and Marticorena 1986: Fig. 68), the extensive LM/ultraviolet study by Stix (1960) wherein she recognized three structural types based on differences in columellae morphology and TEM of *Cacosmia* and *Liabum* (Skvarla et al. 1977). In the latter study, a distinct morphological difference was noted in exine morphology of *Liabum ovatum* (Wedd.) J. Ball (= *Paranephelius ovatus* Wedd.) as compared to other species of *Liabum*, and Robinson and Marticorena (1986) should be consulted for a detailed explanation of this discordant morphology.

In summary, within Liabeae morphological distinctions have been noted primarily based upon size, spine organization and separation or overlapping of spine bases on the exine surface, tectum layering, and columellae relationships with overlying spines (Robinson and Marticorena 1986). These characters are considered to be unique to Liabeae and distinguishing it from other tribes. Robinson and Marticorena (1986) present in-depth discussions of all of the characters mentioned. The final contribution in this volume (Bibliography of Pollen Literature in Compositae) provides additional references for Liabeae pollen.

CHROMOSOME NUMBERS

Chromosome numbers in the tribe are known from twelve genera, base numbers are $x = 7, 9, 12, 14, 16$, and 18 (Robinson et al. 1985; Carr et al. 1999). A base number of $x = 9$ has been proposed for the tribe (Turner et al. 1967; Robinson et al. 1985). For purposes of discussion, the reported counts are discussed as they are plotted upon a simplified cladogram (Fig. 27.12) derived from the strict consensus cladogram (Funk and Chan, in prep.) (Fig. 27.2). *Cacosmia* has uniformly been reported as $n = 7$ with bivalents of the same size and potentially one small fragment.

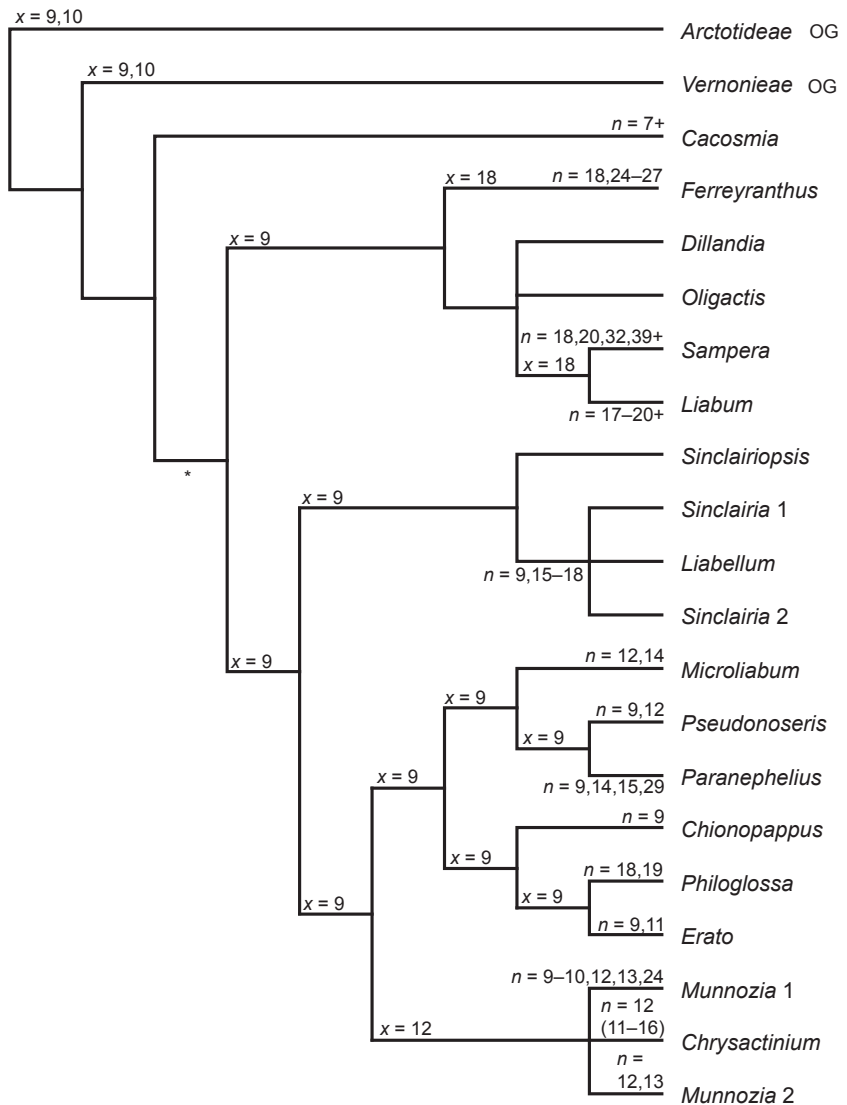
In **Clade B**, *Ferreyranthus* species have been recorded with counts of $n = \text{ca. } 18$, or 19 heteromorphic bivalents (Robinson et al. 1985) and a count of $n = 24\text{--}27$ for *F. excelsus* (Poepp. & Endl.) H. Rob. & Brettell, which must be interpreted as a polyploid derivative (Sundberg and Dillon 1986). Other members of the clade, i.e., *Liabum*, *Oligactis*, and *Sampera* have a hypothetical base number of $x = 9$. *Liabum* with 38 species has counts of $n = 17\text{--}20$ reported (Robinson et al. 1985; Goldblatt and Johnston 1990; Carr et al. 1999) and a hypothetical base number of $x = 9$. Its sister genus, *Sampera*, with eight species, has only one recorded count of $n = \text{ca. } 39$ (*S. pichinchensis* (Hieron.) V.A. Funk & H. Rob.; Jansen and Stuessy 1980) with a base number of $x = 9$. It is distributed farther south than *Liabum*, restricted to Colombia, Ecuador, and Peru. No taxa within *Oligactis* s.str. or *Dillandia* have been counted to date.

In **Clade C**, *Liabellum* (five species) and *Sinclairiopsis* have no recorded counts, and *Sinclairia* (20 species) consistently has reports of 15–18 bivalents. The ancestor of the species of this clade was probably from Mexico or northern Central America and according to Turner (1989) it was most likely a shrub.

In **Clade D-1**, *Microlabium*-*Pseudonosseris*-*Paranephelius*-*Chionopappus*-*Philoglossa*-*Erato*, a wide array of recorded chromosome numbers ranging from $n = 9$ to $n = 29$ have been reported. *Microlabium* has counts of $n = 12, 14$, and 15 ; *M. polymnioides* (R.E. Fries) H. Rob. $n = 12$ (Rozenblum et al. 1985), *M. candidum* (Griseb.) H. Rob. $n = 14$ (Bernardello 1986; Hunziker et al. 1989) and $n = 15$ (Wulff et al. 1996). The sister taxon to *Microlabium* is *Paranephelinae* with *Paranephelius* and *Pseudonosseris*. As discussed in detail below, the interpretation of counts is made more difficult by the putative hybridization

documented in *Paranephelius* with counts of $n = 9, 14$ and 15 (Robinson et al. 1985; Sundberg et al. 1986) and another of $n = \text{ca. } 29$ (Sundberg and Dillon 1986). The report $n = 12$ by Dillon and Turner (1982) for *Pseudonosseris szyszyłowiczii* (Hieron.) H. Rob. & Brettell was termed “anomalous” in Robinson et al. (1985), and the count was questioned first as to the authenticity of the voucher and secondly, that there were no immature heads on the duplicate voucher deposited at US. It was further implied that the count actually was made on material of *Chrysactinium*. Given that it has been unequivocally shown that *P. szyszyłowiczii* is an intergeneric hybrid product involving *Paranephelius* and another element in *Pseudonosseris*, it seems prudent to accept the count of $n = 12$ as within the realm of possibility and given that $n = 12$ has been reported in what can be considered its sister taxon, *Microlabium*.

Fig. 27.12. Reported chromosome numbers plotted upon the strict consensus cladogram (Fig. 27.2) collapsed for simplification.



The genera in **Clade D-2** appear to be centered on $x = 9$. *Erato* has recorded counts of $n = 9$ (Robinson et al. 1985), $n = 11$ (Sundberg and Dillon 1986; Goldblatt and Johnson 1990), and $2n = 9-12$ bivalents (Carr et al. 1999). *Philoglossa* with five species has counts of $n = 18$ (Robinson et al. 1985) and $n = 19$ (Sundberg and Dillon 1986). *Chionopappus* has one count of $2n = 18-20$ which has been interpreted as $x = 9$. Munnoziinae have two genera. *Chrysactinium* with 8 species has recorded counts of $n = 12, 13, 14$ (Sundberg and Dillon 1986) or even 15–16 (Carr et al. 1999) and its paraphyletic sister genus, *Munnozia*, with 46 species has reported counts of $n = 10, 11, 12, \text{ca. } 13, \text{ca. } 24$ (Carr et al. 1999). The one genus that could not be placed in one of the aforementioned groups was *Bishopanthus*. The highly variable nature of counts from throughout Liabeae suggests that polyploidy and chromosomal evolution may have played a role in speciation for the group.

BIOGEOGRAPHY

Since Liabeae find their greatest generic and specific diversity in the Andean Cordillera from 12°N to 24°S latitude, any discussion of biogeography and speciation should include an examination of Andean orogeny. The Andean Cordillera is thought to be of recent origin, formed by the Nazca plate colliding with the South American plate along the Peru–Chile trench (James 1973; Jordan et al. 1983; Orme 2007). We have divided the Cordillera into four areas; the first two are the northern areas, the northeastern zone that begins in western Venezuela and extends to central Ecuador, and the somewhat overlapping zone, the northwestern zone, which extends from northwestern Colombia to northern Peru. The third area is the central zone that stretches from southern Peru to northern Argentina and adjacent Chile. The fourth area, the southern zone, occupies the border between southern Chile and Argentina and does not contain any members of the tribe. The central zone contains almost half the species and most of the genera of the tribe and is the oldest of the three zones containing Liabeae (James 1973; Jordan et al. 1983; Taylor 1991; Windley 1984). The central zone of the Andes is thought to have had its major uplift in the Oligocene (ca. 30 Ma) in northern Chile and southern Peru (James 1973; Jordan et al. 1983). The northern Andes have experienced their primary uplift in the last 5 Myr (Hammen 1974; Gentry 1982) and the *páramo-puna* area (the northeastern zone) is considered the most recent, appearing during the Quaternary (2.0–0.1 Ma; Vuilleumier 1969; Simpson Vuilleumier 1975). The northeastern zone is separated from Peru by the Huancabamba Deflection (also known as the Huancabamba Depression or North Peruvian Low), which has affected distributions of high

elevation plants and animals (Fjeldsa and Krabbe 1990; Haffer 1974, 1981; Pennell 1951; Simpson Vuilleumier 1970; Vuilleumier and Simberloff 1980). However, the Huancabamba Deflection appears to have had an impact only on Liabeae concentrated in the northeastern zone. Those found in the northwestern zone (the majority) are distributed on both sides of the divide, although the more localized genera tend to have most of their species on one side or the other.

Two million years ago the isthmus of Panama was not complete (Gentry 1982) so that the Pacific and West Indies were joined, and in the last million years the sea has repeatedly intruded far into the Orinoco and Amazon basins. As little as 12,000 years ago, the sea level was lowered and as a result the climatic zones in the Andes were lowered (Simpson Vuilleumier 1975). This recent alteration of habitats is believed to have provided ample opportunity for allopatric speciation and may hold the key for current species diversity in Liabeae.

The patterns of generic richness (Fig. 27.1) suggest that the center of the extant diversity of Liabeae is northern Peru and to a lesser extent, Ecuador. This information, in conjunction with an examination of the colored branches of the strict consensus tree (Fig. 27.2), indicates that it is most likely that the extant members of the tribe originated in the central Andes (especially Peru) and repeatedly spread north into the northwestern and northeastern areas and south into Bolivia and Argentina. The non-Andean groups of Liabeae are clearly derived from radiations from Andean ancestors. These include the dispersal of the ancestor of the *Sinclairia* group into Mexico (with one species making it back to South America), which was a single event, and of repeated dispersals of *Erato* (1 sp.), *Oligactis* (1 sp.) and *Munnozia* (2 spp.) into Costa Rica and in the case of *Liabum* into Mexico (1 sp.), and also into the West Indies (one introduction, 6 spp.).

There are two types of migrations northward from Andean South America. The oldest one resulted in the establishment of the *Sinclairia* clade (Clade C), a good example of dispersal (most likely) followed by radiation. A more detailed study of this clade is being planned. A single introduction, possibly into pre-isthmian Central America, followed by radiation in Mexico and Central America is the most likely explanation (Funk et al. 1996). The second pattern has multiple migrations from the Andes to Costa Rica (*Erato*, *Munnozia*, *Oligactis*) all of which are highly nested. There is no evidence that any of these resulted in speciation. Because none of these three genera are sister groups it appears that each of the three genera invaded Central America across the isthmus of Panama separately. The fourth genus, *Liabum*, migrated farther north and is the only genus of the Liabeae to make it to the West Indies having taxa on Jamaica, Cuba, and Hispaniola. *Liabum* also has one species from Costa Rica

up into southern Mexico (*L. bourgeauii*). Since *L. bourgeauii* is not the sister group of the West Indian clade, it is most likely a separate introduction. *Liabum* is the most interesting of the recent migrants and a detailed study of its relationships is planned. Thus, the species of Liabeae that inhabit North America, Central America and the Caribbean are most likely the result of nine independent events of dispersal or vicariance.

The results of this analysis support the idea that all of the clades except one originated in the Central Andes, most likely northern Peru or possibly Ecuador. And the exception, the *Sinclairia* clade, had its origin in the Central Andes as well.

EVOLUTION

Until recently, no documented evidence of interspecific or intergeneric hybridization had been reported for Liabeae, and traditionally it was felt that this was unlikely because the genera were either chromosomally, geographically, and/or elevationally separated. However, there is now evidence of interspecific and intergeneric hybridization in northern Peru between *Paranephelius* taxa and between *Paranephelius* and *Pseudonosseris*.

Soejima et al. (2008) utilized *trnL-F* and ITS markers in an analysis of the subtribe Paranepheleinae. This study found strong support for the monophyly of the subtribe Paranepheleinae, and placed *Pseudonosseris discolor* (Muschl.) H. Rob. & Brettell as the sister taxon to the remainder of *Pseudonosseris* and all *Paranephelius* species. *Pseudonosseris szyszyłowiczii* exhibited intraspecific divergence suggesting intergeneric hybridization between it and *Paranephelius*. *Pseudonosseris szyszyłowiczii* and *P. striata* (Cuatrec.) H. Rob. & Brettell, with similar comparative morphology, are hypothesized to be putative hybrid products between *P. discolor* (Fig. 27.6A) and an unknown element in *Paranephelius*. Further studies are necessary to confirm the origin and timing of this intergeneric hybridization event.

In addition to this instance of intergeneric hybridization, it appears that there has been considerable gene flow in the *Paranephelius* clade as well (Soejima et al., pers. comm.). Hybridization appears to have occurred at several sites in northern Peru and has been responsible for taxonomic confusion and misapplication of names. Currently, two highly variable and polymorphic taxa are recovered with molecular markers within *Paranephelius* roughly corresponding to *P. ovatus* and *P. uniflorus* (Poepp. & Endl.) Sch.Bip. (Fig. 27.5). The taxonomic status of other described entities in *Paranephelius* is under investigation.

The lack of apparent hybridization in most taxa may be a clue to the small size of the tribe. While in many environments, two or more genera exist in full sympatry, for

example, *Erato*, *Munnozia* and *Liabum* are recorded from many sites within the Andes. Genera within the tribe that do have broader distributions (i.e., *Munnozia*, *Liabum*, *Sinclairia*) are the only taxa that appear to have polyploids.

CONCLUSIONS

The development of robust phylogenies with high confidence levels has improved our vision of intertribal relationships in Liabeae. While there may continue to be some disagreement among the various proposed phylogenies, there are a number of groups common to all of them.

The position of *Cacosmia* and its three species as separate from the other main clades was not predicted by cladistic analysis utilizing a morphological dataset (Funk et al. 1996). Examination of the sister group relationships within the clades reveals four major clades: Clade B—*Ferreyranthus-Dillandia-Oligactis-Sampera-Liabum* containing about 64 species; Clade C—*Sinclairia-Sinclairiopsis-Megaliabum-Liabellum* containing about 26 species; Clade D—*Microliabum-Pseudonosseris-Paranephelius-Chionopappus-Philoglossa-Erato* containing about 27 species, and Clade E—*Munnozia-Chrysactinium* containing about 54 species.

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Appendix 27.1. Description of subtribe Sinclairiinae**Sinclairiinae** H. Rob., **subtr. nov.**

Plantae perennes herbaceae vel scandentes ad arborescentes laticiferae; radices tuberosae, caules et folia plerumque abaxialiter albo-tomentosa. Folia opposita vel ternata petiolata, laminiis trinervatis vel lobatis. Capitula interdum eradiata, bracteis involucri imbricatis multiseriatis apice appressis vel patentibus; thecae antherarum base vix crenulatae ecaudatae; basi stylorum non noduliferi; raphidis acheniarum elongatis. Grana pollinis 33–50 μm in diametro, irregulariter spinulosa, columellis subspinosi ca. 4.

Plants are almost exclusively Mexican and Central American. Perennials, with white latex, small herbs to scandent shrubs or trees to 10 meters tall. Roots with distinct tubers at least in early stages. Stems and undersurfaces of leaves usually with white tomentum. Leaves sometimes absent at anthesis, opposite or ternate, with petioles, petioles sometimes winged with wings perfoliate, leaf blades lanceolate to ovate or triangular, venation triplinerved or spreading into narrow lobes, undersurface usually with sparse or dense white tomentum. Inflorescences terminal at stems or branches, more rarely partially axillary, corymbiform or pyramidal, with short or long peduncles. Heads with few to many flowers; involucrel

bracts imbricate in many series, with appressed or spreading tips; receptacles epaleaceous, glabrous; ray florets present or absent, female; disk florets bisexual, lobes elongate; anther thecae pale, spurred, scarcely crenulate at base, without tails; endothelial cells with strap-shaped sclerified shields ending in one or two nodes on transverse walls; apical appendages smooth; nectary sometimes elongate; style base without an enlarged node or only slightly enlarged; style branches shorter than the hispid part of the upper style shaft, stigmatic surface continuous. Achenes prismatic with 8–10 ribs; raphids of achene walls elongate; pappus of 30–50 capillary bristles, not or slightly enlarged distally, with outer series of 15–40 short scales. Pollen grains 33–50 μm in diam. in fluid irregularly spinulose, with cluster of separate columellae under each spine (gazebiform).

Type genus: *Sinclairia* Hook. & Arn.

The subtribe Sinclairiinae has two tendencies not seen elsewhere in Liabeae, i.e., ternate leaves and eradiate heads. However, neither of these character states is widespread in the subtribe. A few consistent characteristics of the subtribe are the tuberous roots and the lack of an enlarged node on the base of the style.