

Coreopsideae

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HISTORICAL OVERVIEW AND PHYLOGENY

Morphological data

A synthesis and analysis of the systematic information on tribe Heliantheae was provided by Stuessy (1977a) with indications of “three main evolutionary lines” within the tribe. He recognized fifteen subtribes and, of these, Coreopsidinae along with Fitchiinae, are considered as constituting the third and smallest natural grouping within the tribe. Coreopsidinae, including 31 genera, were divided into seven informal groups. Turner and Powell (1977), in the same work, proposed the new tribe Coreopsideae Turner & Powell but did not describe it. Their basis for the new tribe appears to be finding a suitable place for subtribe Jaumeinae. They suggested that the previously recognized genera of Jaumeinae (*Jaumea* and *Venegasia*) could be related to Coreopsidinae or to some members of Senecioneae.

In his revision of the tribal and subtribal limits of Heliantheae, based on morphology, anatomy and chromosome studies, Robinson (1981) kept Coreopsideae as a synonym of Coreopsidinae. Bremer (1987), in his studies of tribal interrelationships of Asteraceae, provided Coreopsideae as a subset of Heliantheae. He retained many of the genera assigned to Coreopsidinae by Stuessy (1977a) except for *Guizotia* (placed in Milleriinae), *Guardiola* (in a new tribe Guardioliinae; Robinson 1978), *Jaumea* (placed in Jaumeinae), *Selleophytum* (as a synonym of *Coreopsis*), *Staurochlamys* (placed in Neurolaeninae), and *Venegasia* (in Chaenactidinae).

In a cladistic analysis of morphological features of Heliantheae by Karis (1993), Coreopsidinae were reported to be an ingroup within Heliantheae s.l. The group was represented in the analysis by *Isostigma*, *Chrysanthellum*, *Cosmos*, and *Coreopsis*. In a subsequent paper (Karis and Ryding 1994), the treatment of Coreopsidinae was the same as the one provided above except for the following: *Diodontium*, which was placed in synonymy with *Glossocardia* by Robinson (1981), was reinstated following the work of Veldkamp and Kreffer (1991), who also relegated *Glossogyne* and *Guerreroia* as synonyms of *Glossocardia*, but raised *Glossogyne* sect. *Trioncinia* to generic rank; *Eryngiophyllum* was placed as a synonym of *Chrysanthellum* following the work of Turner (1988); *Fitchia*, which was placed in Fitchiinae by Robinson (1981), was returned to Coreopsidinae; *Guardiola* was left as an unassigned Heliantheae; *Guizotia* and *Staurochlamys* were placed in Melampodiinae; *Jaumea* was put in Flaveriinae; *Microlecan* was kept as a synonym of *Bidens* following the work of Mesfin Tadesse (1984); *Sphagneticola* was assigned to Verbesininae; and *Venegasia* was placed in Chaenactidinae. Stuessy (1988) transferred two species of *Oparanthus* and one species of *Petrobium* to *Bidens*. Shannon and Wagner (1997) reinstated *Oparanthus* and recognized four species in the genus. The genera recognized in this chapter are the same ones recognized by Karis and Ryding (1994) with the exceptions that *Megalodonta* is not segregated from *Bidens* and *Selleophytum* is segregated from *Coreopsis*.

The first cladistic analysis focusing on Coreopsideae was by Ryding and Bremer (1992). Parsimony analysis

recovered three major groups, which were treated as subtribes Coreopsidinae, Petrobiinae, and their new Chrysanthellinae. The monospecific genera *Dicranocarpus* and *Goldmanella* were eventually excluded from their analyses because they occurred in various positions on the cladograms, and inclusion of the genera produced so many shortest trees that computer memory was exhausted. Of special interest, the largest genus *Bidens* occupied various positions in the shortest trees, including occurrence in the two different subtribes Coreopsidinae and Petrobiinae. Karis and Ryding (1994) essentially followed the treatment of Ryding and Bremer (1992) but recognized the entire group as subtribe Coreopsidinae with the three subtribes of Ryding and Bremer (1992) treated as informal groups.

Tribes/subtribes based on molecular data

Jansen et al. (1991) were probably the first to apply comparative cpDNA data to the evaluation of phylogenetic relationships within Asteraceae as a whole. Coreopsidae were represented by *Coreopsis* and *Dahlia*, and cpDNA data supported the segregation of Coreopsidae from the core of Heliantheae. Based on complete sequences of the *rbcL* gene for 25 species of Asteraceae, Kim et al. (1992) did not find strong support for relationships between the tribes but stated that Tageteae, Coreopsidae, Heliantheae and Eupatorieae are close, and maintained Coreopsidae as a tribe. Using chloroplast *ndhF* sequences from *Dahlia*, *Coreopsis* and *Cosmos* of Coreopsidinae, Kim and Jansen (1995) showed that this group is embedded within a clade of Heliantheae s.l., (i.e., including Helenieae, Coreopsidae, Eupatorieae, and Tageteae). Bayer and Starr (1998), using two non-coding chloroplast sequences (*trnL* intron, and *trnL/trnF* intergenic spacer), showed the same relationship between Tageteae, Heliantheae and Eupatorieae as Kim and Jansen (1995). Heliantheae were represented only by *Helianthus* in their analysis. Panero and Funk (2002) used a combined dataset of chloroplast sequences totaling over 13,000 bp to produce a phylogeny-based subfamilial classification for Asteraceae with Coreopsidae treated as a tribe. In the supertree (= metatree) of Funk et al. (2005), Coreopsidae were retained at the tribal level.

Genera based on molecular data

The following observations regarding resolution of relationships within Coreopsidae can be generalized from the morphological studies conducted through the early 1990s. All studies recognized as monophyletic those taxa with C₄ photosynthesis (the *Chrysanthellum* group). *Goldmanella* was placed within Coreopsidae, but was recognized as a somewhat discordant element in the tribe (Stuessy 1977a; Robinson 1981). Without doubt, however, the biggest impediments to understanding relationships within Coreopsidae have been the two largest

genera *Bidens* and *Coreopsis*. Reservations have continually been expressed for decades not only about distinguishing the two genera from each other, but also regarding the monophyly of each genus (Wild 1967; Agnew 1974; Mesfin Tadesse 1984b, 1986, 1993). One of the shortcomings of the phylogenetic analysis of Ryding and Bremer (1992), which they readily acknowledged, is that both *Bidens* and *Coreopsis* were each accepted as “good” genera in their analyses even though neither is likely monophyletic. It was necessary for Ryding and Bremer (1992) to accept both genera because it was beyond the scope of their study to examine these large complex genera in depth. It is evident that until there is better resolution of relationships within and among elements of *Bidens* and *Coreopsis*, as well as clarification of their relationships to other genera, it will not be possible to reach a proper understanding of phylogenetic relationships within Coreopsidae.

Kim et al. (1999) used ITS sequences to provide the first molecular phylogenetic study of *Bidens* and *Coreopsis*. The two shortcomings of the study were limited taxonomic sampling in *Bidens* and inclusion of only representatives of the two genera as the ingroup. Despite the shortcomings, the results of Kim et al. (1999) indicated strongly that neither *Bidens* nor *Coreopsis* was monophyletic. Ganders et al. (2000) used ITS sequences to examine relationships in *Bidens*, with emphasis on ascertaining the continental relatives of Hawaiian and Marquesan members. Their results produced groups of *Bidens* similar to those detected by Kim et al. (1999), but since no other genera were included in the ingroup, the monophyly of *Bidens* was not tested.

Kimball and Crawford (2004) conducted a molecular phylogenetic study of Coreopsidae using ITS sequences from 20 of 24 genera (Table 42.1). Taxon sampling in *Bidens* and *Coreopsis* included representatives of clades recovered by Kim et al. (1999) and Ganders et al. (2000). The tree presented in Fig. 42.1 was constructed with maximum likelihood (ML) analyses of ITS sequences and includes exemplar taxa for clades present in the analysis of Kimball and Crawford (2004). While prior studies used maximum parsimony for tree construction, Mort et al. (2008) and Mort et al. (unpub.) show high congruence between maximum likelihood and maximum parsimony analyses, and only the likelihood tree is shown. All ITS sequences are available in GenBank and have been previously published. Plastid sequences are available for some taxa (Mort et al., 2008) but will be mentioned only when they provide additional insights into relationships or results incongruent with the ITS tree. The only monophyletic group not collapsed in the tree is *Bidens*-2, 3, and the reason for this will be discussed.

The first split in the ingroup is between the small South American genus *Ericentrodea* (Table 42.1; Robinson 1993) and the remainder of the sampled taxa. Two of

Table 42.1. Currently recognized genera of Coreoideae, giving number of species sampled for construction of Fig. 42.1 (followed by approximate total number of species sequenced for ITS in parentheses and total number of species in genus, known chromosome numbers, and assessment of monophyly of each genus with reference to most comprehensive study).

Genus	Taxa	Chromosome number (n)	Monophyletic; reference
1. <i>Bidens</i> L.	11(25)/340	10, 11, 12, 16, 17, 18, 22, 23, 24, 34, 36, 38, 40, 48, 72, ca. 73	N; Kimball and Crawford 2004
2. <i>Chrysanthellum</i> Rich.	1(1)/13	8, 12	?; –
3. <i>Coreocarpus</i> Benth.	4(7)/7	9, 11, 12	N; Kimball et al. 2003
4. <i>Coreopsis</i> L.	16(55)/86	6, 7, 8, 9, 10, 12, 13, 14, 24, 26, 28, 32, 39, 56	N; Kimball and Crawford 2004
5. <i>Cosmos</i> Cav.	3(3)/36	11, 12, 17, 22, 23, 24, 33, 36	Y; Kimball and Crawford 2004
6. <i>Cyathomone</i> S.F. Blake	0/1	–	N/A; –
7. <i>Dahlia</i> Cav.	3(33)/35	16, 17, 18, 32	Y; Saar et al.; 2003; Kimball and Crawford 2004
8. <i>Dicranocarpus</i> A. Gray	1/1	10	N/A; –
9. <i>Diodontium</i> F. Muell.	0/1	–	N/A; –
10. <i>Ericentrodea</i> S.F. Blake	2(2)/6	–	Y; Kimball and Crawford 2004
11. <i>Fitchia</i> Hook. f.	1(3)/6	35–40, 45	Y; W.L. Wagner, pers. comm.
12. <i>Glossocardia</i> Cass.	1(1)/12	12	?; –
13. <i>Goldmanella</i> Greenm.	1/1	–	N/A; –
14. <i>Henricksonia</i> B.L. Turner	1/1	18	N/A; –
15. <i>Heterosperma</i> Cav.	2(2)/5–11?	9, 11, 13, 24, 25	N; Kimball and Crawford 2004
16. <i>Hidalgoa</i> La Llave & Lex.	1(1)/5	15, 16, 17	?; –
17. <i>Isostigma</i> Less.	1(1)/13	9, 12	?; –
18. <i>Moonia</i> Arn.	0/1	–	N/A; –
19. <i>Narvalina</i> Cass.	1/1	60	N/A; –
20. <i>Oparanthus</i> Sherff	1(4)/4	–	Y; W.L. Wagner, pers. comm.
21. <i>Petrobium</i> R. Br.	1/1	–	N/A
22. <i>Selleophytum</i> Urban	1/1	32	N/A
23. <i>Thelesperma</i> Less.	3(5)/15	8, 9, 10, 11, 12, 20, 22, 24, 30	Y; Kimball and Crawford 2004
24. <i>Trioncinia</i> (F. Muell.) Veldkamp	0/1	–	N/A

Y = yes; N = no; N/A = not applicable; ? = not determined; – = not studied.

the six *Ericentrodea* species were included by Kimball and Crawford (2004), and they form a strongly supported monophyletic group (Fig. 42.1). Features of the fruits, in particular, characterize the genus (see generic diagnosis; Robinson 1993; Karis and Ryding 1994). Stuessy (1977a) included this genus in his large group 1 (which includes *Cyathomone* and *Narvalina*), and it was placed near both *Cyathomone* and *Narvalina* in the morphological phylogeny of Ryding and Bremer (1992). As far as we are aware, *Cyathomone* is known only from the meager type specimen, and there is some question as to whether it is distinct from *Ericentrodea* (see below). Available molecular data offer no clues to the closest relatives of *Ericentrodea*, but if

appropriate material were available, it would be instructive to include *Cyathomone* in future analyses.

The small Mexican-Central American genus *Hidalgoa* branches next and is weakly placed (< 50% bootstrap) as sister to the remaining ingroup taxa (Fig. 42.1). Because only one species was sampled, it is not possible to assess the monophyly of *Hidalgoa*. However, the present analysis clearly indicates that the genus is not closely allied with *Petrobium*, as suggested by Ryding and Bremer (1992).

Previous analyses using ITS (Gatt et al. 2000; Kimball and Crawford 2004) and ITS-ETS sequences (Saar et al. 2003) provided strong support for the monophyly of the large genus *Dahlia* (Fig. 42.2G, K). However, somewhat

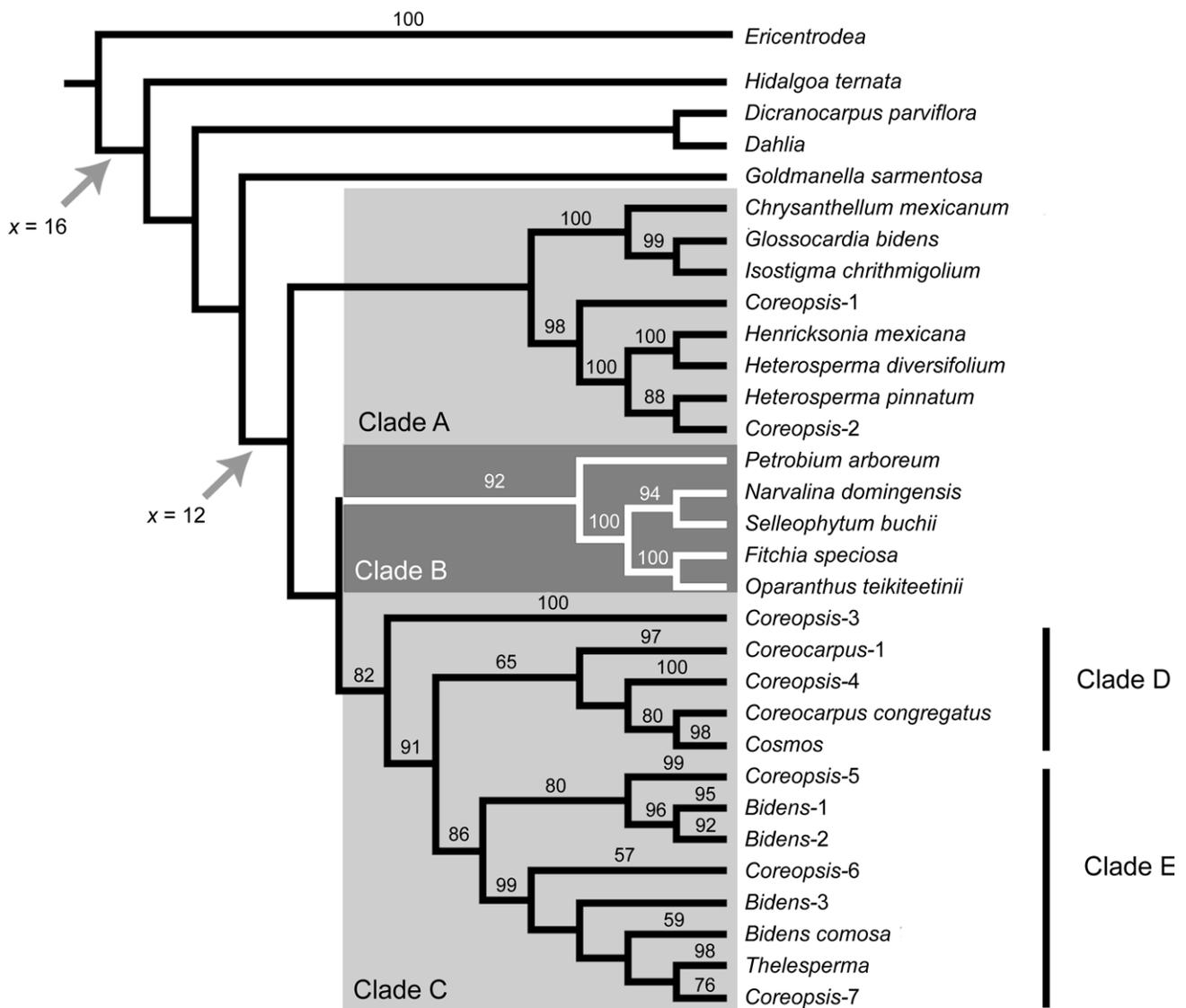


Fig. 42.1. Maximum likelihood (ML) topology inferred from analyses of nrDNA ITS spacers. Well-supported, monophyletic taxa have been collapsed to a single terminal (see Table 42.2 for clade composition). Relative support as assessed via ML bootstrap analyses indicated above branches. MacClade reconstructions of ancestral base chromosome numbers for two clades are indicated by arrows. For a biogeographic analysis see Chapter 44.

unexpected was the recovery of *Dahlia* and the monospecific genus *Dicranocarpus* as sister taxa (Fig. 42.1). We are not aware that a close relationship between these two genera has previously been suggested, ostensibly because they contrast in several morphological features (cf. generic diagnoses below). The results of the molecular study should be viewed with caution, however, because there is not strong support (< 50% bootstrap) for this clade (Fig. 42.1). However, the grouping of *Dahlia* and *Dicranocarpus* is strongly supported (100%) in both maximum likelihood and maximum parsimony analyses of plastid sequences, and in the analyses of the combined ITS/cpDNA dataset (Mort et al., submitted). If indeed the two genera are sister taxa, as the plastid and the combined ITS/cpDNA evidence suggest, then they have diverged significantly from their common ancestor in many features (see generic diagnoses).

The monospecific genus *Goldmanella* was placed in Coreopsideae by both Stuessy (1977a) and Robinson (1981). The former author recognized its distinctive morphology by placing it in its own group, while the latter commented that the genus is best placed in Coreopsideae despite several unusual features (see generic diagnosis). The molecular phylogenetic analysis supports the inclusion of *Goldmanella* in Coreopsideae, but offers no insights into its closest relatives in the tribe (Fig. 42.1).

The vast majority of taxa in Coreopsideae occur in a clade composed of two subclades, one of which (B plus C) is much larger than the other (A) (Fig. 42.1). The smaller subclade (A) in turn contains two highly supported subclades, one consisting of three genera belonging to Stuessy's (1977a) group 3 and the *Chrysanthellum* group of Ryding and Bremer (1992) and Karis and Ryding (1994). Robinson (1981) likewise recognized the *Chrysanthellum* group as natural, with one of the unifying features the Kranz syndrome (C_4 photosynthesis). The molecular phylogenetic analysis confirms prior assessments of the monophyly of the group (Fig. 42.1).

Sister to the *Chrysanthellum* group is a strongly supported clade (98%) comprising two sections of mostly Mexican *Coreopsis* (*Coreopsis*-1, -2; Table 42.2), the monospecific Mexican genus *Henricksonia*, and two representatives of the small southwestern United States, Mexican, and Central American genus *Heterosperma* (Fig. 42.1). The present analysis is concordant with Kimball and Crawford (2004) in showing that neither the two sections of *Coreopsis* nor the two species of *Heterosperma* form monophyletic groups. A cladistic analysis of morphological characters for North American *Coreopsis* (Jansen et al. 1987) did not recover the two Mexican *Coreopsis* sections as sister taxa. To our knowledge, there has been no previous doubt expressed about the monophyly of *Heterosperma*; it has been defined by the dimorphic achenes (see generic diagnosis; Karis and Ryding 1994). A range of chromosome

numbers has, however, been reported for the genus (Table 42.1; Robinson et al. 1981). Further studies are needed, including sequencing of additional species and morphological investigations, to resolve relationships among species assigned to *Heterosperma*. *Henricksonia* was described primarily on the basis of the unusual paleaceous scales comprising the pappus of the disc florets (see generic diagnosis; Turner 1977). Turner (1977) suggested *Coreopsis* sections *Electra* and *Anathysana* (*Coreopsis*-1, -2; Figs. 42.1, 42.2J), among others, as closest relatives of *Henricksonia*. While not suggesting a close affinity, Turner (1977) did indicate that *Henricksonia* would key to *Heterosperma* in the generic key of Sherff and Alexander (1955) for North American Coreopsidinae; available molecular data suggest a close phylogenetic relationship between *Henricksonia* and *Heterosperma* (Fig. 42.1).

The last large clade contains two subclades (B and C; Fig. 42.1) that receive moderate to strong support (92% and 82% bootstrap, respectively). Clade B consists entirely of plants endemic to oceanic archipelagos. Within this clade, the monospecific *Petrobium* from St. Helena in the south Atlantic is sister to a well-supported (100% bootstrap) clade comprising the other four genera (Fig. 42.1); noteworthy, the placement of *Petrobium* is well-resolved in the current analysis whereas it was not in Kimball and Crawford (2004). This difference is the result of modifying the alignment of the ITS sequence data. Various workers have considered *Petrobium* and the two Polynesian genera *Fitchia* (Fig. 42.2A) and *Oparanthus* (Fig. 42.2M) as closely related, and in particular, have viewed the latter two genera as close (Carlquist 1974, 2001; Cronk 1992; Ryding and Bremer 1992; Shannon and Wagner 1997). In the analysis of Ryding and Bremer (1992), *Petrobium*, *Fitchia* and *Oparanthus* are united by several non-homoplastic characters, with the former genus sister to the latter two genera. *Narvalina* was far removed from the other three genera in the trees of Ryding and Bremer (1992), and *Selleophytum* (which was placed in *Coreopsis* by Sherff and Alexander, 1955, but has recently been resurrected by Mesfin Tadesse and Crawford 2006) was not included as a separate element in their study. We are unaware of non-molecular studies suggesting a close relationship between the two monospecific genera *Narvalina* and *Selleophytum*, and the other three insular genera. The common ancestor of this clade may have possessed characters that contributed to their success in dispersal to and establishment in the insular setting. The molecular phylogeny offers no support for the hypothesis that any of the island genera are derivatives of *Bidens* (Carlquist 1974, 2001; Stuessy 1988; Shannon and Wagner 1997) because they are not nested within any of the *Bidens* clades (Fig. 42.1).

The last clade (C, Fig. 42.1) contains about 80% of the species in Coreopsideae, including all representatives of *Bidens* (Fig. 42.2C, D), *Coreocarpus*, *Cosmos* (Fig.

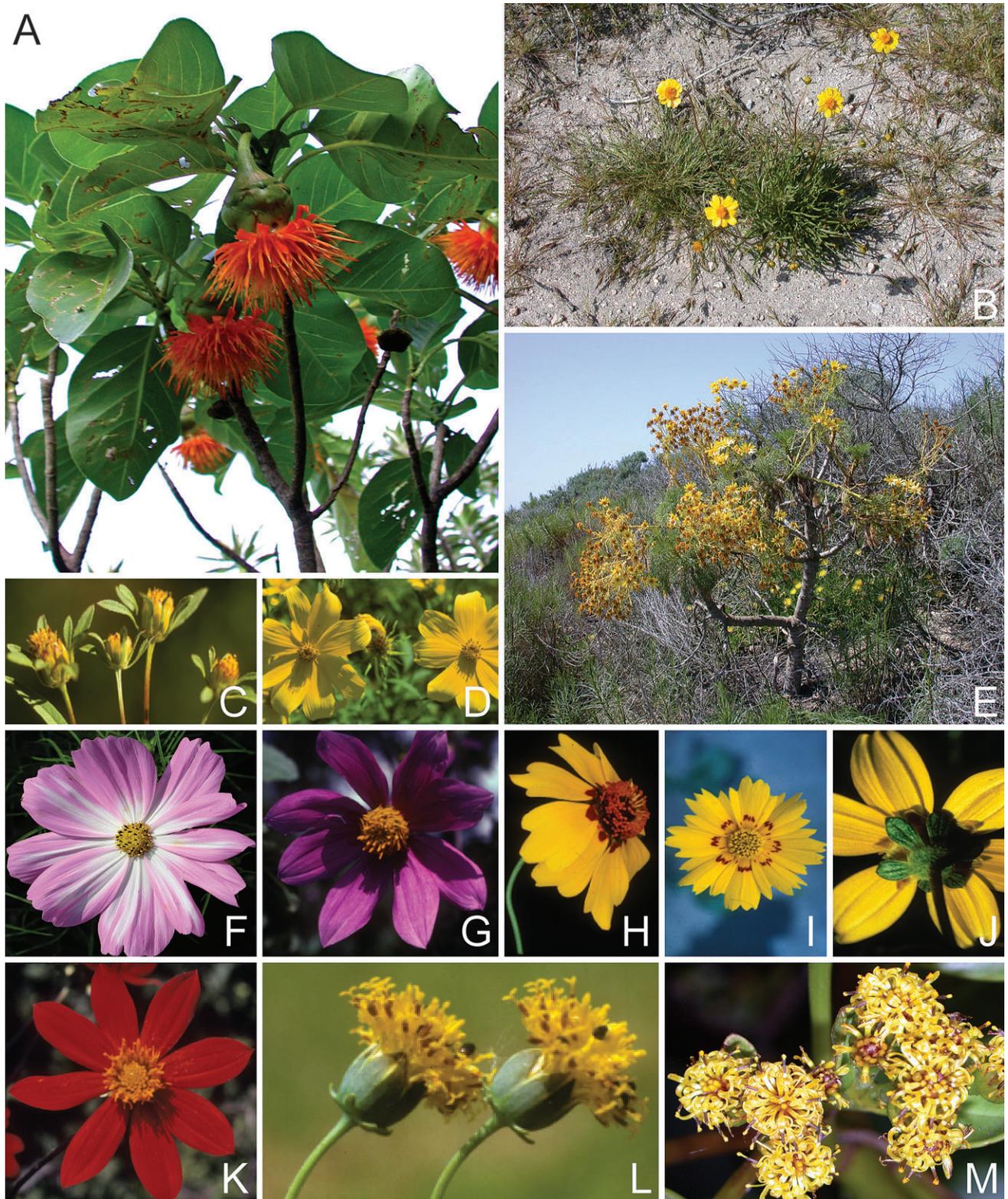


Fig. 42.2. Representatives of Coreopsiadeae. **A** *Fitchia nutans* Hook. f.; **B** *Coreopsis californica* (Nutt.) H. Sharsm.; **C** *Bidens frondosa* L.; **D** *Bidens aristosa* (Michx.) Britton; **E** *Coreopsis gigantea* (Kellogg) H.M. Hall; **F** *Cosmos bipinnatus* Cav.; **G** *Dahlia pinnata* Cav.; **H** *Coreopsis tinctoria* Nutt.; **I** *Coreopsis nuecensis* A. Heller; **J** *Coreopsis mutica* DC., showing outer and inner involucre bracts; **K** *Dahlia coccinea* Cav.; **L** *Thelesperma megapotamicum* (Spreng.) Kuntze, showing fused inner involucre bracts; **M** *Oparanthus coriaceus* (F. Br.) Sherff. [Photographs: A, M, K. Wood; B, E, M. Mort; C, D, G, K, L, C. Freeman; E, H–J, D. Crawford; F, J. Archibald.]

42.2F), and *Thelesperma* (Fig. 42.2L), as well as the majority of *Coreopsis* species (Fig. 42.2H, I). Within clade C, *Coreopsis*-3 (100% bootstrap) is sister to all other taxa and consists of eight species in three sections, all of which are largely restricted to California (Table 42.2; Fig. 42.2B, E). This clade has long been considered a “natural” group (Sharsmith 1938; Smith 1984), and it was the subject of a recent molecular phylogenetic study (Mort et al. 2004) that provided strong support for monophyly. Mort et al. (2004) present the diagnostic characters for this clade and discuss character evolution within it.

Sister to *Coreopsis*-3 in clade C is a very strongly supported clade (91%) that is composed of two major subclades D and E (Fig. 42.1). Subclade D is weakly supported (65% bootstrap) and contains all or some elements of three genera, including *Coreocarpus* (Fig. 42.1). Though a relatively small genus (see generic diagnosis; Table 42.1), delimiting *Coreocarpus* has posed significant problems (Smith 1989; Melchert and Turner 1990; Kimball et al. 2003; Kimball and Crawford 2004). Various combinations of characters including corky achene wings, monomorphic phyllaries, and neutral ray florets have been used with little success to delimit the genus. The molecular phylogenetic study by Kimball et al. (2003) identified a “core” *Coreocarpus* (*Coreocarpus*-1; Fig. 42.1; Table 42.2) that excluded three species. Two of the excluded species were transferred to *Bidens* by Melchert and Turner (1990); this is consistent with the molecular data that grouped the two species with other Mexican *Bidens* (Kimball et al. 2003; Kimball and Crawford 2004). The most enigmatic species in the genus is *Coreocarpus congregatus* (S.F. Blake) E.B. Smith, which was originally described as a *Coreopsis* but was transferred (with some reservations) to *Coreocarpus* by Smith (1983).

Molecular phylogenetic studies using ITS sequences indicate that *C. congregatus* is sister to *Cosmos* (Kimball et al. 2003; Kimball and Crawford 2004; Fig. 42.1). Plastid sequences group *C. congregatus* with *Bidens*-1, 2 (with less than 50% bootstrap support) while the combined nuclear and plastid data partitions show over 80% bootstrap support for it as sister to *Cosmos* (Mort et al., 2008). Although DNA sequence data indicate that *C. congregatus* is sister to *Cosmos*, comparative morphological studies are to be desired to identify diagnostic characters for the clade.

Cosmos is shown as monophyletic by both nuclear and plastid sequences (Kimball and Crawford 2004; Mort et al., 2008); although present taxon sampling is limited (three species), there is strong support for the monophyly of the genus (98% bootstrap; Fig. 42.1). Pubescent filaments serve as a synapomorphy for the genus (see generic diagnosis; Robinson 1981; Ryding and Bremer 1992; Karis 1993). While the three species of *Cosmos* receive strong support as monophyletic, sequences from additional taxa are needed to provide a more thorough assessment of monophyly.

The last element of subclade D to be considered is *Coreopsis*-4, and it will be discussed together with *Coreopsis*-5 of subclade E (Fig. 42.1). *Coreopsis*-4 is well supported (100% bootstrap) and consists of members of *Coreopsis* sect. *Pseudoagarista* from Mexico (Table 42.2). *Coreopsis*-5 includes species of the same section from South America (Table 42.2) and is a well-supported lineage (99% bootstrap). *Coreopsis* sect. *Pseudoagarista* consists of woody perennials, and has been defined by the pubescent achenes with basally attached paleae (Mesfin Tadesse et al. 1995a, 2001). While ITS sequences place Mexican and South American species of the section in different

Table 42.2. Definition of the major clades recovered by ML analyses of the nrDNA internal transcribed spacers shown in Fig. 42.1.

Clade name	Section(s) and their general distribution
<i>Bidens</i> -1	Sects. <i>Campylotheca</i> , <i>Greenmania</i> , and <i>Psilocarphaea</i> ; Caribbean, Hawaii, Mexico, South America, South Pacific
<i>Bidens</i> -2	Sects. <i>Psilocarphaea</i> and unassigned; Africa
<i>Bidens</i> -3	Sects. <i>Bidens</i> and <i>Hydrocarphaea</i> ; north temperate
<i>Coreocarpus</i> -1	All species except <i>C. congregatus</i> (see Fig. 42.1)
<i>Coreopsis</i> -1	Sect. <i>Electra</i> ; Mexico, Central America
<i>Coreopsis</i> -2	Sect. <i>Anathysana</i> ; Mexico
<i>Coreopsis</i> -3	Sects. <i>Leptosyne</i> , <i>Pugiopappus</i> , and <i>Tuckermannia</i> ; mostly California
<i>Coreopsis</i> -4	Sect. <i>Pseudoagarista</i> ; Mexico
<i>Coreopsis</i> -5	Sect. <i>Pseudoagarista</i> ; South America
<i>Coreopsis</i> -6	Sects. <i>Gyrophyllum</i> and <i>Silphidium</i> ; eastern North America
<i>Coreopsis</i> -7	Sects. <i>Calliopsis</i> , <i>Coreopsis</i> and <i>Eublepharis</i> ; eastern North America

Sections of genera that are found in multiple clades (i.e., not monophyletic) are indicated in bold. Excluded from this list are monospecific genera.

clades (Fig. 42.1; Kimball and Crawford 2004), all members of sect. *Pseudoagarista* from the two geographical areas occur together in a moderately robust clade (83% bootstrap) with plastid sequences (Mort et al., 2008). However, combining the two data partitions, as with the ITS data alone, places taxa from the two areas in separate clades (Mort et al., 2008). Additional nuclear sequence data from unlinked loci are required to test rigorously the phylogenetic placement of the Mexican and South American elements of sect. *Pseudoagarista*. Furthermore, comparative morphological studies are needed to ascertain whether diagnostic characters for species in each of the geographical areas can be identified.

In addition to *Coreopsis*-5, the remaining moderately supported subclade E (86%) contains *Bidens* (the largest genus in the tribe), *Thelesperma*, and two other elements of *Coreopsis* (Fig. 42.1). Within subclade E there is moderate support (80% bootstrap) for a lineage comprising the aforementioned *Coreopsis* sect. *Pseudoagarista* from South America (*Coreopsis*-5), southern tropical and subtropical *Bidens* (*Bidens*-1) and *Bidens* from Africa (*Bidens*-2; Table 42.2). Mesfin Tadesse et al. (1995a) mentioned similarities between some species of African *Bidens* and those of Mexico and South America, and it was suggested that these similarities are indicative of a close relationship between the two elements. North temperate *Bidens* (*Bidens*-3; Table 42.2) do not occur with the two other groups of *Bidens*, but rather are in a strongly supported clade (99% bootstrap) with north temperate *Coreopsis* (*Coreopsis*-6, -7; Table 42.2) and *Thelesperma* (Fig. 42.1). Mesfin Tadesse et al. (1995a) commented on the differences in fruits between north temperate and other *Bidens*.

All molecular phylogenetic studies (Kim et al. 1999; Kimball and Crawford 2004; Crawford and Mort 2005) indicate that the three sections comprising *Coreopsis*-7 (Table 42.2) constitute a monophyletic group, as does *Thelesperma* (Kimball and Crawford 2004) (Fig. 42.1). However, neither the two sections comprising *Coreopsis*-6 (Table 42.2) nor the north temperate *Bidens* (*Bidens*-3, *Bidens comosa*; Table 42.2) receive strong support, and relationships among the four groups (*Coreopsis*-6, -7, *Bidens*-3, *B. comosa*, and *Thelesperma*) in this clade likewise do not enjoy strong support (Fig. 42.1). This entire group is in need of additional morphological and molecular studies.

Molecular phylogenetic studies have made valuable contributions toward elucidating phylogenetic relationships in Coreopsideae. Arguably, the most important contribution has been the recovery of strongly supported smaller clades, which in some instances correspond to recognized genera (e.g., *Cosmos*, *Dahlia*, and *Thelesperma*; Fig. 42.1; Table 42.1). On the other hand, molecular data have documented that the two largest genera, *Bidens* and *Coreopsis*, are not monophyletic, a result that is not surprising. However, it is noteworthy that many of the

recovered clades correspond to geographically-confined sections or groups of sections of *Bidens* and *Coreopsis* (Fig. 42.1; Table 42.2). With rare exceptions, for example the *Chrysanthellum* group (Fig. 42.1), the larger clades do not correspond to prior views of taxonomic relationships (Stuessy 1977a) or to clades recovered by cladistic analyses of morphological characters (Ryding and Bremer 1992; Mesfin Tadesse et al. 2001). Mapping of morphological-anatomical characters onto molecular phylogenies indicates that many of the characters that have been used taxonomically are quite labile (Kimball and Crawford 2004; Mort et al. 2004; Crawford and Mort 2005).

Future molecular phylogenetic studies should have two major foci. One focus is additional taxon sampling. Efforts should be made to obtain sequences from monospecific genera such as *Cyathomone*, *Diodontium*, *Moonia*, and *Trioncinia* that have not yet been sampled. Additional representatives of poorly sampled genera such as *Chrysanthellum*, *Cosmos*, *Glossocardia*, *Heterosperma*, and *Isostigma* should be sequenced to test their monophyly. Also, taxon sampling has been quite limited in Mexican and South American *Bidens*, and additional sequences are needed to resolve relationships in many complex groups and to assess the monophyly of *Bidens*-1 (Fig. 42.1; Table 42.2). Support for larger clades (along the spine) is not high (Fig. 42.1), and additional sequences are to be desired to test whether these are “good” clades (i.e., receive stronger support).

While not proposed here, it is apparent that taxonomic changes are needed to reflect relationships recovered by the molecular phylogenetic studies. Recent analyses show that clades present in ITS topologies (Kimball and Crawford 2004) (Fig. 42.1) are also seen in trees generated from plastid sequences, and resolution and support for clades are often enhanced from analyses of combined ITS-cpDNA datasets (Mort et al. 2004; Crawford and Mort 2005; Mort et al., 2008). While we have hesitated to make taxonomic changes based solely on sequences from one region of one genome (ITS), it is now clear that nuclear and plastid sequences, with several exceptions, each produce trees with similar topologies. A major challenge will be to identify diagnostic characters or unique combinations of characters for the clades recovered with strong support in the molecular phylogenetic studies.

TAXONOMY

Characters and character states useful in the diagnosis of the tribe and the genera are in italics.

Tribe Coreopsideae Turner & Powell (1977). Basionym: Coreopsideae Less. in *Linnaea* 5: 153. 1830 – Type: *Coreopsis* L., *Sp. Pl.* 2: 907. 1753

Includes: *Bidens* L. (ca. 340 species), *Chrysanthellum* Rich. (13 species), *Coreocarpus* Benth. (7 species), *Coreopsis* (ca. 86 species), *Cosmos* Cav. (36 species), *Cyathomone* S.F. Blake (1 species), *Dahlia* Cav. (35 species), *Dicranocarpus* A. Gray (1 species), *Diodontium* F. Muell. (1 species), *Ericentrodea* S.F. Blake & Sherff (6 species), *Fitchia* Hook. f. (6 species), *Glossocardia* Cass. (12 species), *Goldmanella* (Greenm.) Greenm. (1 species), *Henricksonia* B.L. Turner (1 species), *Heterosperma* Cav. (ca. 5–11 species), *Hidalgoa* La Llave & Lex (5 species), *Isostigma* Less. (13 species), *Moonia* Arn. (1 species), *Narvalina* Cass. (1 species), *Oparanthus* Sherff (4 species), *Petrobium* R. Br. (1 species), *Selleophyllum* Urban (1 species), *Thelesperma* Less. (15 species), and *Trioncinia* (F. Muell.) Veldk. (1 species).

Herbs, shrubs or rarely small trees or vines, up to 10 m high, glabrous to variously hairy, hairs uniseriate. Leaves opposite or alternate, basal or cauline, simple with entire margins to tripinnatisect, Capitula heterogamous or homogamous, radiate or discoid, solitary to cymose or corymbose, pedunculate. Involucre cylindric to hemispheric, with one-to-many-seriate phyllaries. Outer phyllaries green, linear to ovate, inner phyllaries with few to many brownish-orange striae and scarious margins. Receptacle flat to conical, paleaceous. Paleae linear to lanceolate, with few brownish-orange striae, continuous with inner phyllaries. Ray florets, when present, bright to pale yellow, orange, white, pink, purple, neuter, pistillate and sterile or pistillate and fertile. Disc florets bisexual and fertile or functionally male; corolla yellow, orange or yellow-orange, tubular or “opening by a sinus traversing the ventral side (*Fitchia*), (4–)5-lobed at apex, lobes short triangular, glabrous or with short hairs or papillae, sometimes tinged purple, red or pink; anthers (4–)5, brown or black, rarely yellowish, short tailed at base; style undivided or with short cleft to bifurcate, branches conic with short papillae to penicellate. Achenes dorsally flattened to columnar, black, brown, rarely yellowish-brown or reddish-brown, smooth to striated, with or without wings. Pappus of 2–15 smooth, antrorsely or retrorsely barbed bristles, or of short awns.

Coreopsideae are primarily centered in North and South America. The genera *Diodontium*, *Glossocardia*, and *Trioncinia* are Australian. *Moonia* is known only from India and Sri Lanka, and it is hypothesized to be derived from either *Dahlia* or *Hidalgoa* by long distance dispersal and isolation (Stuessy 1975). *Bidens* and *Chrysanthellum* have cosmopolitan weedy members.

1. *Bidens* L. (1753), rev. Sherff (1937), Mesfin (1984b, 1993)

Herbs or shrubs. Leaves opposite, simple to bipinnatisect. Capitula heterogamous, radiate, rarely homogamous, discoid, small to large. Involucre cylindric to hemispheric; phyllaries 2–3-seriate, outer green, linear to oblanceolate, rarely leafy, inner membranous with scarious margins. Paleae

membranous. Ray florets neuter, rarely pistillate or pistilloid, yellow, white, pink or purple, apex 3-dentate or 3-fid. Disc florets yellow, fertile; corolla 5-lobed, rarely 4-lobed. Achenes linear-oblong, ellipsoid to oblanceolate, flat to 3- or 4-angled, with raised ribs, wings present or absent. Pappus of 2–5 antrorsely or retrorsely barbed aristae, rarely absent.

Distribution: Worldwide, mostly in North and Central America; ca. 340 species.

Habitat: moist forest margins, grassland, wooded grassland, rarely dry bush-land or shrub-land, roadside ditches, margins of cultivations; 1–3600 m (highest record from Ethiopia, lowest from Hawaii).

2. *Chrysanthellum* Rich. (1807), rev. Turner (1988)

Herbs with erect or prostrate stems. Leaves alternate or rosulate, simple to tripinnatisect. Capitula heterogamous, radiate, small. Involucre campanulate; phyllaries 1–3-seriate, rarely absent, linear-lanceolate to ovate with scarious margins. Receptacle flat to convex. Ray florets yellow or orange-yellow, female, fertile, apex entire or bifid. Disc florets dimorphic, pale yellow to orange-yellow, rarely white (outer series), brown or reddish-brown (inner series), fertile or functionally male; corolla 4–5-lobed. Achenes dimorphic: ray achenes thickened, clavate, epappose, not winged, columnar or curved; disc achenes, when present, flat, with thick or corky wings. Pappus absent (of ray florets), or of two minute awns, or a crown (of disc florets).

Distribution: North America: Mexico (9 endemic species), Central America (2 species), West Indies (1 species), Galápagos Islands (1 endemic species); total of 13 species (Veldkamp and Kreffer 1991).

Habitat: limestone hills, short grassland, “thorn forest”, coastal dunes; 0–3500 m.

3. *Coreocarpus* Benth. (1844), rev. Smith (1989)

Herbs or shrubs. Leaves opposite, pinnatifid to bipinnatisect. Capitula heterogamous, radiate, rarely homogamous, discoid, small. Involucre campanulate, 1–2-seriate, monomorphic; outer phyllaries narrowly spatulate or linear, green, inner ovate, or all similar in shape. Receptacle flat. Ray florets yellow (2-toned in some, upper half lemon-yellow, lower half golden yellow) or white, female and fertile or neuter, rarely absent. Disc florets yellow, bisexual, sometimes functionally male. Achenes monomorphic, obovate to oblong or spatulate, winged, wings thin or corky and incurved, entire or narrowly dissected into oblong to obdeltoid teeth. Pappus of 1–2 smooth, antrorsely or retrorsely barbed aristae, or absent.

Distribution: North America (Arizona and Mexico): 7 species (2 species transferred to *Bidens* by Melchert and Turner 1990).

Habitat: rocky slopes in open pine-oak forest, with sparse vegetation, rocky cliffs, shores and canyons, near streams; 5–2200 m.

4. *Coreopsis* L. (1753); rev. Sherff (1937)

Herbs or shrubs. Leaves *opposite* to *alternate*, simple to pinnatisect. Capitula *heterogamous, radiate*. Involucre cylindrical to hemispheric; phyllaries 2-seriate, outer green, herbaceous, equal to or shorter than the inner, inner membranous with scarios margins. Receptacle flat to convex. Ray florets *neuter* or *female and sterile or fertile*, pure *yellow* or with median or basal *orange or reddish blotches*. Disc florets fertile, bisexual; corolla yellow, rarely lobes red-brown to purple, (4–)5-lobed. Achenes *oblong to elliptic*, with or without wings, *wings* thin or corky. Pappus of two *nude or retrorsely* barbed aristae, or absent.

Distribution: North and South America, introduced as ornamental garden plants elsewhere; ca. 86 species.

Habitat: glades in deciduous woodland, pine barrens, peaty bogs, swamps, pond margins, floodplains, prairies, coastal bluffs and dunes, secondarily on roadside ditches, disturbed places; 0–4700 m.

5. *Cosmos* Cav. (1791), rev. Sherff (1932, 1955)

Herbs. Leaves *opposite*, simple to pinnatisect. Capitula *heterogamous, radiate*. Involucre subhemispheric; phyllaries 2-seriate, outer green, herbaceous, spreading, linear-lanceolate, inner membranous, pale at margins. Ray florets *neuter, white, yellow, pink, purple to dark red-purple*. Disc florets *fertile*, bisexual, *yellow*. Anther *filaments hairy*. Achenes *dark brown to black, linear, fusiform-tetragonal*, tapering into a slender *beak, much elongated in the inner ones, erect or slightly curved, 4-lobed in cross-section*. Pappus of 2–4(–6) *retrorsely* barbed aristae.

Distribution: North, Central and South America; ca. 36 species (Melchert 1968; 59 sp. in IPNI, www.ipni.org).

Habitat: dry, rocky mixed pine-oak woodland, wooded grassland; 2–3300 m.

6. *Cyathomone* S.F. Blake (1923)

Shrub or subshrub with *scandent* branches. Leaves *opposite*, ternate to biternate, membranous. Capitula 7–15, cymose, nodding, long-pedunculate. Involucre campanulate, 2-seriate, glabrous. Receptacle convex. Outer phyllaries linear-oblong; inner wider with scarios margins. *Flowers unknown*. Achenes (submature) dorso-ventrally compressed, narrowly obovate, *glabrous, brownish*, widely *winged* with cilia all along the wing margins, contracted at apex. Pappus of two *retrorsely* barbed aristae.

Distribution: Ecuador, 1 species: *C. sodiroi* (Hieron.) S.F. Blake

Habitat: subtropical woods along the Rio Pilaton.

Note: This may not be different from *Ericentrodea* S.F. Blake & Sherff. The constricted achene neck of *E. david-smithii* H. Rob. (Robinson 1993) (Fig. 42.1D) and that of *C. sodiroi* S.F. Blake (Blake 1923) (Fig. 42.1D) are similar except for number of pappus members. The leaf descriptions of the two “species” are also similar.

7. *Dahlia* Cav. (1791), rev. Sørensen (1969); Saar et al. (2003)

Herbs, subshrubs or *epiphytic* lianas. Roots *tuberous*. Leaves with *stipels*, sometimes *petioles hollow*. Leaves *opposite* or *whorled*, simple to tripinnate. Capitula *heterogamous, radiate, large*. Involucre hemispheric, 2-seriate; outer phyllaries *fleshy*, green, linear to ovate or obovate, inner membranous, *red, reddish-brown or brown*, margins scarios, ovate. Receptacle flat. Ray florets *neuter* or *female, sterile, white, pink, purple or yellow*. Disc florets *fertile*, yellow or yellow with pink or purple lobes or limbs; corolla 5-lobed. Achenes *gray or black*, linear to linear-oblongate or spatulate, *flat or 3-angled* (in cross-section), finely striated. Pappus *absent* or of two minute teeth or flexuous *threads*.

Distribution: Mexico, Central America, northeastern South America; 35 species (Saar et al. 2003).

Habitat: cool cloud forests to sclerophyllous forests, oak-pine woodland, roadsides and margins of fields; 350–3100 m.

8. *Dicranocarpus* A. Gray (1854)

Annual herb. Leaves *opposite, once or twice pinnate* with *linear-filiform* segments. Capitula *heterogamous, radiate*, solitary or few and cymose, small. Involucre cylindrical, distinct; outer phyllaries 1 or 2, linear, similar to bracts; inner 3–5, lanceolate with scarios margins. Receptacle convex. Ray florets *female*, ca. 1 mm long, *yellow, fertile*. Disc florets yellow, 3–5, *functionally male*; corolla *5-lobed*. Achenes linear, *yellowish-brown*, ribbed, striated. Pappus of ray achenes 2, large, *widely divergent/spreading to recurved* and *smooth* aristae, almost *perpendicular to body*, those of disc florets often undeveloped.

Distribution: North America (southwestern USA and northern Mexico); 1 species: *D. parviflorus* A. Gray.

Habitat: dry desert, soil alkaline or with gypsum; 900–1700 m.

9. *Diodontium* F. Muell. (1857), rev. Veldkamp and Kreffer (1991); Veldkamp (1992)

Herb with *bushy* habit. Leaves *opposite*, simple, linear or filiform. Capitula *homogamous, discoid*. Involucre (shape not described); phyllaries 2-seriate, outer lanceolate, longer than inner, *inner ca. 2*, ovate, margins not scarios. Ray florets *absent*. Disc florets *bisexual, fertile, yellow*, 3–10; corolla *5-lobed*. Achenes obovoid, *narrowly winged* below, glabrous, *smooth, not ribbed, yellow or yellowish-brown*. Pappus of two *aristae, glabrous* except for barbs at the apex.

Distribution: Australia, Northern Territory; 1 species.

Habitat: granite and sandstone hills; known from the type, which was collected between Sturt Creek and Victoria River.

Diodontium filifolium F. Muell., distinguished from *Glossocardia* by habit, leaf arrangement, and achene characters.

10. *Ericentrodea* S.F. Blake & Sherff (1923), rev. Robinson (1993)

Herbs or shrubs with *scandent branches or vines climbing over shrubs and trees*, clasping by *petioles*. Leaves *opposite*, simple to quadri-ternate, *coriaceous*. Involucre campanulate, *2-seriate*; outer phyllaries herbaceous, linear to oblong, shorter than inner, inner oblong, reddish-yellow. Receptacle flat. Capitula *heterogamous, radiate or homogamous, discoid*. Ray florets, when present, *female and fertile, bright yellow*. Disc florets *bisexual, fertile, pale yellow*; corolla *5-lobed*, up to 18 mm long. Achenes obovoid, margins *winged*, wings densely fringed with bristles. Pappus of 6–15 *retroresely* barbed *aristae*, in two series.

Distribution: South America (Ecuador, Colombia, Peru); 6 species.

Habitat: forests in river valleys; 2000–3300 m.

11. *Fitchia* Hook. f. (1845), rev. Carlquist (1957)

Shrub or tree. Stem with *prop roots*. Leaves *opposite-decussate, simple*, margins entire or serrate (when young), *petioles half to almost the length* of the blade. Capitula *homogamous, discoid*, solitary 2–3 each on *recurved* peduncles. Involucre campanulate, 4–5-seriate; phyllaries *leathery to woody*, large, graded monomorphic, inner with scarios margins. Receptacle flat. Florets *yellow-orange*, all similar; corolla *5-lobed*, sinuses between lobes *a third* (*F. nutans* Hook. f.) to *as deep as the ventral sinus* (*F. tahitensis* Nadeaud). Style *cleft into two tiny branches* at the tip. Achenes flat, winged, 40–45 mm long, light brown, sparsely bristled in middle. Pappus of two *antrorsely* barbed, *vascularized, bristles* continuous with the wings, often *longer than body of achene*.

Distribution: Polynesia: 6 species, Tahiti (2 species), Raiatea Island (1 species), Mangareva (1 species), Rapa Island (1 species), and Rarotonga Island (1 species); *Fitchia speciosa* Cheesman introduced in Hawaii (O'ahu – Honolulu) and has not spread elsewhere (Wagner et al. 1990).

Habitat: “Island slopes” suggested by Ewan (1958) based on the illustrated prop roots of *F. speciosa* Cheesman in Carlquist (1957); *F. nutans* and *F. tahitensis* “swales above 3,000 feet” (Carlquist 1957: 63).

12. *Glossocardia* Cass. (1817), rev. Veldkamp and Kreffer (1991), Veldkamp (1992)

Herbs. Leaves *alternate or basal*, simple to pinnatisect. Capitula *heterogamous, radiate*. Involucre *irregularly* 1–2-seriate (*number of phyllaries variable*); outer phyllaries *few or absent*, linear to ovate; inner phyllaries lanceolate to ovate, 3–7. Receptacle flat. Ray florets 0–12, *female or sterile*, yellow, white, bluish, pink, reddish, violet, or purple. Disc florets *functionally male or bisexual*; corolla 4- or 5-lobed, white, yellow, lilac or pale purple. Achenes oblong to linear-lanceolate, ribbed, black. Pappus of *two short glabrous aristae* or coroniform.

Distribution: Africa (Chad and Niger, 1 species; Tanzania, 1 introduced species; cf. Mesfin Tadesse 1990), Asia (India to Japan and Taiwan), West Pacific Islands south to Australia; 12 species.

Habitat: grassland, coastland, wooded grassland, stream banks, along margins of plantations; 0–1165 m.

13. *Goldmanella* (Greenm.) Greenm. (1908)

Herb with *scandent branches*. Leaves *alternate, simple, oblique or asymmetrical* at base, margins sharply serrate. Capitula *heterogamous, radiate*, axillary and *leaf-opposed*, long-pedunculate. Involucre campanulate, *3–4-seriate*; outer phyllaries yellowish with reddish-brown nerves, ovate, inner oblong, margins scarios. Receptacle *conical*. Ray florets *female*, 5–8, white or yellow. Disc florets yellow; corolla 5-lobed. Achenes *reddish-brown*, glabrous with rough surface, prismatic. Pappus of 2–4 short thick *awns*.

Distribution: Mexico, Belize; 1 species: *G. sarmentosa* (Greenm.) Greenm.

Habitat: wet clearings; moist open areas in tropical evergreen forest.

14. *Henricksonia* B.L. Turner (1977)

Subshrub. Leaves *opposite*, ternately parted, segments lanceolate. Capitula *heterogamous, radiate*, solitary. Involucre hemispheric, 2-seriate; outer phyllaries green, linear; inner linear-lanceolate, brownish, scarios at margins. Receptacle flat. Ray florets *female, fertile*, yellow, 8–12. Disc florets *bisexual, fertile*, yellow; corolla 5-lobed. Achenes *dimorphic*: of ray florets dorso-ventrally flattened, broadly *obovate*, winged, apex with 2(–3) *short awns*; of disc florets *linear-quadrangular*, ribbed, apex with 4 persistent *paleaceous scales*.

Distribution: Mexico; 1 sp.: *H. mexicana* B.L. Turner.

Habitat: vertical cliffs in dry canyons, ca. 1320 m.

15. *Heterosperma* Cav. (1794, cf. *Index Kewensis*)

Annual herbs. Leaves *opposite*, simple to pinnately compound with elongate linear segments. Capitula *radiate*, solitary or few and cymose. Involucre cylindrical, 2-seriate, distinct; outer phyllaries linear to filiform, green, often exceeding involucre, inner membranous and pale yellow or purple, oblong or ovate. Receptacle flat or concave. Ray florets *female, fertile*, pale yellow. Disc florets yellow, *bisexual, fertile*; corolla 5-lobed. Achenes *dimorphic*, of ray florets ellipsoid or obovoid, *winged*, wings corky or pectinate, surfaces tuberculate, glabrous; of disc florets obovoid or tapered and beaked above (innermost the longest, purplish), *not winged*. Pappus *absent* (outermost) or of 2–3 *spreading and retroresely* barbed *aristae* (inner).

Distribution: Southwest US (Arizona, New Mexico, Texas), Mexico, Central and South America, West Indies (introduced); ca. 5–11 species.

Habitat: stream banks in pine-oak wooded grassland, roadside ditches, open mountain slopes; 650–3200 m.

16. *Hidalgoa* La Llave & Lex. (1824), rev. Sherff and Alexander (1955), Sherff (1966)

Woody climbers, the stems climbing using petioles. Leaves opposite, 3-foliolate to palmately 5-parted, leaflets ovate. Capitula radiate, solitary or few, axillary. Involucre campanulate; phyllaries 3–4-seriate, distinct, outer linear-lanceolate to oblanceolate, herbaceous, spreading, inner oblong-ovate, thicker. Receptacle flat. Ray florets female, fertile, yellow, orange, purple or reddish. Disc florets yellow, sterile; corolla 4-lobed. Achenes of ray floret (immature) flat, oblong, dark brown; pappus of two blunt awns; of disc florets not seen.

Distribution: North and South America (Mexico, Guatemala, Costa Rica, Panama, Colombia, Ecuador, and Peru); 5 species.

Habitat: Wet mountain forest, cloud forest; 200–1800 m.

17. *Isostigma* Less. (1831), rev. Sherff (1926, 1931); Peter (2004, 2006)

Herbs or subshrubs, stem often a corm. Leaves rosulate or alternate, rarely opposite, simple to pinnatisect with filiform, linear or lanceolate segments. Capitula radiate or discoid, solitary. Involucre campanulate or subglobose, 2–4-seriate; outer phyllaries linear, green; inner ovate, brown with scarious margins. Receptacle flat to convex. Paleae keeled at base. Ray florets female, yellow, purple or white. Disc florets bisexual, perfect, yellow or purple, corolla 5-lobed. Achenes graded-monomorphic, lengthening inwards, linear, flattened, with 1–3 ribs and striate-sulcate in between ribs, narrowly winged, brown or black with yellow apex, base and wings. Pappus of two erect or slightly divergent, short, smooth or shortly antrorsely barbed aristae, rarely absent.

Distribution: South America (northeastern and central Argentina, southern Brazil, southeastern and central Bolivia, Paraguay and northwestern Uruguay); 13 species.

Habitat: arid and semi-arid to moist grasslands, sub-humid open fields, glades in forests; ca. 400–600 m.

18. *Moonia* Arn. (1836), rev. Stuessy (1975)

Herb (annual, fide Karis and Ryding 1994; shrubby, stems erect, fide Stuessy 1975). Leaves opposite, simple and ovate with broadly dentate margins to pinnately compound with up to five segments. Capitula radiate, small. Involucre campanulate, 2–3-seriate; outer phyllaries green, elliptic to oblanceolate, inner phyllaries narrowly ovate, brownish. Receptacle convex. Ray florets female, fertile, yellow. Disc florets yellow, 10–15, sterile; corolla 4-lobed, anthers 4, style linear, undivided. Achenes (of ray florets) black, obovate, glabrous. Pappus absent.

Distribution: India, Sri Lanka (Ceylon); 1 species: *M. heterophylla* Arn.

Habitat: wet montane forests; 1500–2150 m.

19. *Narvalina* Cass. (1825)

Shrub to 2 m. Leaves opposite, simple, coriaceous, margins sharply dentate. Capitula radiate, small, corymbose. Involucre cylindrical, irregularly 2–3-seriate; outer phyllaries few, green, leaf-like; inner phyllaries coriaceous, light brown with scarious margins, stiff at post-anthesis. Receptacle flat. Paleae coriaceous. Ray florets female, fertile, yellow. Disc florets yellow, fertile, 10–15; corolla 5-lobed. Achenes black, winged, monomorphic, elliptic, dorso-ventrally flattened, wings white, margins antrorsely barbed. Pappus of two retrorsely barbed aristae.

Distribution: Haiti and Dominican Republic; 1 species: *N. domingensis* (Cass.) Less.

Habitat: broad-leaved forest, arid thickets; 350–1300 m.

20. *Oparanthus* Sherff (1937), rev. Stuessy (1977b), Shannon and Wagner (1997)

Shrubs or trees. Leaves opposite, simple, ovate, thin to leathery, margins entire. Capitula radiate, solitary to cymose. Involucre campanulate, 1–2-seriate. Receptacle convex. Phyllaries and paleae coriaceous. Ray florets female, fertile, white, yellow to yellowish-green, 1–2-seriate. Disc florets white or yellow, sterile or fertile, ovary filiform with 1–2 narrow awns; corolla 4-lobed; stigma undivided or only slightly bifid at apex. Achenes (of ray florets) flattened, elliptic to narrowly elliptic, narrowly winged on one or both margins, glabrous; pappus of 2, smooth or ciliate awns, confluent with wings; of disc florets with 1–2 linear awns.

Distribution: Southeast French Polynesia (4 species): Marquesas Islands (2 species) and Rapa in the Austral (Tubuai) Islands (2 species).

Habitat: mesic to wet humid forests with two species approaching the cloud zone; 50–1200 m.

21. *Petrobium* R. Br. (1817), nom. cons. Nicholson (1997), Brummitt (2000)

Tree, dioecious or gynodioecious. Leaves opposite, simple, ovate, membranous, margins dentate. Capitula discoid, corymbose. Involucre (shape not known), 3-seriate; phyllaries and paleae coriaceous. Receptacle (shape not known). Florets yellow, fertile; corolla 4-lobed. Achenes flat to trigonous, narrow, oblong, scabrid-hispid. Pappus of 2–3 stiff aristae.

Distribution: St. Helena (Atlantic Ocean); 1 species: *P. arboreum* (J.R. Forst. & G. Forst.) Spreng.

Habitat: “damp, relict tree-fern thicket or cabbage-tree woodland” (Cronk 2000: 82)

22. *Selleophytum* Urban (1915), rev. Mesfin and Crawford (2006)

Shrub. Leaves simple, opposite, sessile, oblong-lanceolate to narrowly ovate, glabrous, coriaceous, margins entire or inconspicuously undulate. Capitula solitary or up to three terminating main stem or branches, radiate. Involucre campanulate, 2-seriate, coriaceous, glabrous, outer phyllar-

ies green; inner orange-red. Receptacle flat. Ray florets *female*, yellow, *fertile*. Disk florets *fertile*, *yellow or purple*; corolla *5-lobed*. Achenes oblong-linear, gray brown, sub-quadrangular, not winged, densely short-setose at the margin and near the apex, striate-sulcate on both surfaces. Pappus of two *antrorsely* barbed aristae.

Distribution: Haiti and Dominican Republic; 1 species: *Selleophytum buchii* Urban.

Habitat: open pine forest on limestone cliffs; 800–2550 m.

23. *Thelesperma* Less. (1831)

Herbs (*annual* and *perennial*) or subshrub. Leaves *opposite*, mostly basal, once to thrice pinnate with linear or filiform segments. Capitula *radiate* or *discoid*, solitary or in loose corymbs. Involucre hemispheric to urceolate; phyllaries distinct, leathery, 2–3-seriate; outer phyllaries linear, green, short, inner phyllaries oblong-ovate, *connate for up to 3/4 of their lengths*. Receptacle flat or convex. Ray florets, when present, *sterile*, *neuter*, *yellow*, *red-brown* or *bicolored* (yellow and red-brown). Disc florets *fertile*, *yellow or red-brown*; corolla *5-lobed*. Achenes black or gray (dark red-brown), *smooth or verrucose wrinkled*, *margins winged*; outer *incurved*, *dorsally rounded*, *shorter*, inner *linear-oblong*, *columnar*. Pappus of two *divergent*, *white*, *thick*, *retrorsely* barbed aristae.

Distribution: North (southern and western US, Mexico) and South America; 15 species.

Habitat: desert scrub, limestone ridges, alpine meadow; 0–3650 m.

24. *Trioncinia* (F. Muell.) Veldk. (1991), rev. Veldkamp and Kreffer (1991); Veldkamp (1992)

Perennial herb with woody *taproot*. Leaves *basal and closely imbricate*, *alternate*, pinnatifid to bipinnatisect, upper simple. Capitula *radiate*, few. Involucre (shape not recorded). Receptacle (shape not recorded). Phyllaries 1–3-seriate; outer ovate to ovate-oblong with scarios margins. Paleae flat, lanceolate. Ray florets *female*, *sterile*, probably yellow. Disc florets probably yellow; *corolla 4-lobed*. Achenes lanceolate, slightly incurved, glabrous, *ribbed*, *not winged*, *dark brown or black* with many *transverse ridges*. Pappus of *three retrorsely* barbed aristae.

Distribution: Australia; 1 species: *T. retroflexa* (F. Muell.) Veldk.

Habitat: “basaltic plains” (Veldkamp and Kreffer 1991: 481). The taxon is known from the single type specimen and possibly from one additional specimen from “black soil at Blair Athol” (Veldkamp 1992: 743) in Australia.

ANATOMY

The capitulum, with much emphasis given to the structure of the corolla, is the portion of the plant of Coreopsideae

that has been studied in depth anatomically, cf. Koch (1930a, b), Carlquist (1957, 2001), Baagøe (1977), Burt (1977), Jeffrey (1977), Leppik (1977), and Stebbins (1977). There is very little addition to these works. Mesfin Tadesse (1984b) provided foliar and trichome anatomy and micro-characters of ray floret papillae and anthers for *Bidens*. The occurrence of Kranz anatomy has been reported for the three genera *Chrysanthellum*, *Glossocardia*, and *Isostigma* (Smith and Turner 1975; Turner 1988; Veldkamp and Kreffer 1991; Peter and Katinas 2003).

POLLEN

The pollen in Heliantheae s.l. is uniform and hence there are only few additions to the original studies by Skvarla and Turner (1966), Skvarla et al. (1977) and Thanikaimoni (1977). Pollen morphology for *Bidens*, *Glossocardia* and *Coreopsis* is presented by Mesfin Tadesse (1984, 1990) and Mesfin Tadesse et al. (1995b), respectively. Jose (1993) provided pollen morphology for two species each of *Bidens*, *Coreopsis*, *Cosmos*, *Dahlia* and one species of *Glossocardia*.

CHROMOSOME NUMBERS

Chromosome numbers for genera of Coreopsideae are given in Table 42.1. These numbers are taken from Robinson et al. (1981), Goldblatt and Johnson (2006) and other publications in the series, the *Index to Plant Chromosome Numbers Data Base* of the Missouri Botanical Garden (<http://mobot.mobot.org/W3T/Search/ipcn.html>) and from the website *Index to Chromosome Numbers in Asteraceae* maintained by K. Watanabe at Kobe University (<http://www.lib.kobe-u.ac.jp/products/asteraceae/index.html>). As far as we can determine, chromosome counts are lacking for eight of the genera (Table 42.1). All numbers that have been reported are presented unless there is strong reason to believe they are erroneous. As discussed by Semple and Watanabe (Chapter 4), the common ancestor of all Helianthoids was tetraploid, so all Coreopsideae are of polyploid origin. Therefore, in the discussion of numbers, only those taxa with higher numbers that ostensibly result from secondary polyploid events will be designated as polyploids.

Chromosome number evolution within Coreopsideae was inferred using MacClade 4.06 (Maddison and Maddison 2003) and optimizing known numbers on the phylogeny using the default settings (e.g., unordered characters of equal weight) (Fig. 42.1). Certain species within Coreopsideae are known to have multiple base chromosome numbers; these were scored as polymorphic characters and included in the reconstruction. Because terminals were collapsed in the present discussion, we will limit our comments to broad patterns of chromosomal change

across the clade; however, future focused studies of chromosomal evolution within lineages could prove informative. The ancestral base number for the tribe is inferred to be $x = 16$, with the ancestral number for the large clade (consisting of clades A, B, and C) inferred as $x = 12$ (Fig. 42.1). The genera *Dahlia* and *Hidalgoa* (counts available for only one species), which are two of the first taxa to diverge in the ITS phylogeny, have several chromosome numbers in common in the range of $n = 16$ – 18 ; with the more typical low numbers of $n = 12$ and 13 being absent from these basal groups (Fig. 42.1; Table 42.1). Clearly, there has been a dysploid reduction in *Dicranocarpus* (Fig. 42.1; Table 42.1). Polyploidy occurs in *Dahlia*, and both polyploidy and dysploidy have been associated with evolution and diversification in the genus (Gatt et al. 1998, 2000).

Comparison of chromosome numbers in Table 42.1 with the phylogeny in Fig. 42.1 allows several observations to be made with regard to the evolution of chromosome numbers within the large clade consisting of clades A, B, and C. Assuming that $x = 12$ is the ancestral base number for this clade, the first generalization is that the majority of species have retained this number. Over half of the terminals in clades A and C include taxa with $n = 12$, and in most instances this number is the most common one for taxa represented by these terminals. Within clade C, four of the five *Coreopsis* terminals (*Coreopsis*-4 to -7) are composed entirely or nearly so, of $n = 13$ taxa or polyploids based on that number. Thus, two prevalent patterns seen at the “diploid” level are retention of the ancestral number ($x = 12$) and dysploid increase to $x = 13$, and this is especially true in clade C.

Within clade A, there have been several independent dysploid reductions (*Chrysanthellum*, *Isostigma*, and *Heterosperma*) as well as increase to $x = 14$ in *Coreopsis*-1 from the presumed ancestral $n = 12$ (Fig. 42.1; Table 42.1). The three small genera *Chrysanthellum*, *Isostigma*, and *Heterosperma* could prove most interesting subjects for molecular phylogenetic and chromosome studies, given the different chromosome numbers reported for them. For example, the two species of *Heterosperma* included in molecular phylogenetic studies are not sister species (Fig. 42.1; Kimball and Crawford 2004), and they differ in chromosome number with one $n = 9$ and the other $n = 25$. Thus, both dysploidy and polyploidy are known among taxa that have been included in *Heterosperma* (Table 42.1), and only a combination of phylogenetic and cytogenetic studies will elucidate the evolution of chromosome numbers in the genus. With present data, it is impossible to infer whether the number of $n = 18$ for *Henricksonia mexicana* B.L. Turner is the result of secondary polyploidy, or dysploid increase from $n = 12$ or some lower number.

Available chromosome numbers for Clade B, the island endemics, indicate that they are polyploids (Fig. 42.1; Table 42.1). Because chromosome numbers apparently are

not known for the genera *Oparanthus* and *Petrobium*, and only one species of *Fitchia* has been counted (Table 42.1), it is not possible to infer whether all genera evolved from a common polyploid ancestor or polyploidy originated several times. For the two sister genera *Narvalina* and *Selleophytum* in the Caribbean, the former has approximately twice as many chromosomes as the latter (Table 42.1), indicating that an additional polyploid event occurred in *Narvalina* subsequent to divergence from its common ancestor with *Selleophytum*.

As indicated above, most taxa represented by terminals in the large clade C have numbers of $n = 12$ or 13 , or are polyploids based on those numbers. Despite the preponderance of these numbers, it is evident from Table 42.1 that a wide array of “diploid” numbers occurs in several genera, especially in the two largest genera *Bidens* and *Coreopsis*. However, since neither genus is monophyletic, it is instructive to examine whether the diversity is a reflection of different numbers between clades or variation within clades. Within *Bidens*, the vast majority of species are $n = 12$ and polyploids based on that number; reports of $n = 10$ and 11 , and their polyploid derivatives are quite rare. However, species in the African clade (*Bidens*-2; Table 42.2) are noteworthy because they lack the lower numbers (10 , 11 , and 12) found in the other two clades of *Bidens*, and instead exhibit a series of higher numbers with $n = 16$, 17 , 18 , 21 , 23 , 24 , and 36 (Mesfin Tadesse 1984; Mesfin Tadesse and Hedberg 1986). It is not apparent whether the series of numbers (excluding 36 , which is polyploid) was generated by both polyploidy and dysploidy, or only by dysploid increase. In *Coreopsis*, only section *Electra* with $x = 14$ has a number not detected in other clades of the genus. The numbers $n = 6$, 7 , 8 , 9 , and 10 are found in the two closely related species *C. nuecensis* A. Heller and *C. nuecensoides* E.B. Smith of section *Coreopsis* (Smith 1974), and the common numbers $n = 12$ and 13 (Smith 1975) occur in several clades. In the relatively large and apparently monophyletic genera, *Cosmos* and *Thelesperma*, both dysploidy and polyploidy have been associated with evolution and diversification (Table 42.1).

The variety of chromosome numbers that have been reported indicates that much could be learned about chromosomal evolution from a detailed analysis of Coreopsideae. Molecular phylogenetic analyses of many of the clades, combined with the extensive knowledge of chromosome numbers, would provide refined insights into the evolution of chromosome numbers at smaller taxonomic scales. Such studies could be valuable in elucidating common and contrasting patterns of chromosome evolution in different lineages. In addition, there are small genera such as *Isostigma* where the few counts available reveal different numbers (Table 42.1), and suggest that additional counts together with phylogenetic studies could prove interesting with regard to understanding chromosome number

evolution. Also, one third of the genera have no reported chromosome counts, and efforts should be made to obtain the counts. For example, no counts are available for *Ericentrodea*, which is sister to all other ingroup taxa, and knowing the number for this genus would be valuable for reconstructing the evolution of chromosome numbers.

CHEMISTRY

The most characteristic chemical feature of Coreopsideae is the accumulation of flavonoid compounds known as anthochlors, which include both chalcones and aurones. These pigments are important in imparting the yellow color to floral tissues. The most extensive review of anthochlors in Coreopsideae and in Asteraceae as a whole is given by Bohm and Stuessy (2001). While anthochlors are not restricted to Coreopsideae, it is the only group of Asteraceae where they are present in a very high percentage of genera now placed in the tribe (Robinson 1981). Bohm and Stuessy (2001) provide a comprehensive discussion and synthesis of the use of anthochlors and other flavonoid compounds at various taxonomic levels in Coreopsideae.

The use of DNA sequence data for phylogenetic reconstruction has largely replaced earlier attempts to infer phylogeny from the distribution of secondary compounds in plants, including members of Coreopsideae (e.g., Stuessy and Crawford 1983). It would be of interest to map the distribution of structural variation of secondary compounds, flavonoids and otherwise, onto phylogenies generated from DNA sequence data. The major impediment to such a study is finding a group where both a phylogeny and adequate chemical data are available. In Coreopsideae, these two conditions are met for *Dahlia*, where the extensive flavonoid data of Giannasi (1975) could be mapped onto the phylogeny of Saar et al. (2003).

ECONOMIC USES

Bidens

The genus *Bidens* is commonly noted for its weedy habit and for the relative ease in the dispersal of some of the species owing to the nature of the sticky fruits. A few species have also been noted to be of some economic importance: *B. aurea*, both disc and ray florets are bright yellow and keep on producing flowers until late autumn “Bees love them”; Dijk 1997; *B. cernua* (nodding stick-tight, bur-marigold), the fruits (achenes) have been reported as damaging gill arches and bringing about severe fungal infection to young salmon (Allison 1967, cited in Voss 1996: 382); *B. frondosa* (beggar-ticks, stick-tight), used in herbal therapy to prevent the “irritation, inflammation, pain, and bleeding of the urinary tract mucosa”, to treat “benign

prostatic hypertrophy” and to “increase excretion of uric acid, decreasing the risk of gout attacks” (M. Moore 1993, cited in Strother and Weedon 2006: 212); *B. prestinaria* (Adey Abeba), a native of North East Africa, is the symbol of the beginning of the new year in Ethiopia and bouquets of this as well as related species, obtained from their natural growing sites, are presented to families and friends as gifts. The species has also been reported to be used medicinally in abetting blood clotting in southeastern Ethiopia and also as an insecticide; Mesfin Tadesse 1984); *B. pilosa* L. (blackjack, stick-tight) with its large white flowers, is being considered as an important source of nectar for butterflies in Levy County, Florida (Robert Dirig, pers. comm.).

The following species of *Bidens* have been grown in well-drained soils in Mexico and Arizona in the USA from late spring to early fall: *B. aequisquamea* (Fernald) Sherff, disc florets yellow, ray florets red to purple or purplish-pink, the flower heads open up successively; *B. ferulifolia* (Jacq.) DC. (golden goddess), both disc and ray florets are yellow and the flower heads open up successively; *B. triplinervia* H.B.K., both disc and ray florets are bright yellow.

The following species of *Bidens* are noted for their weediness: *B. pilosa* (worldwide, apparently a very recent introduction to North America, north of Mexico, absent from many floras and manuals, e.g., Gleason and Cronquist 1991) and recently recorded from only some states (cf. Strother and Weedon 2006); *B. biternata* (Lour.) Merr. & Sherff (Africa and Asia), and *B. bipinnata* L. (Spanish needles; Asia, southern Africa, Europe and North and South America).

Coreopsis

Members of this genus grow well in any public or residential garden and bloom in summer and fall. The following species are known from cultivation: *C. auriculata* L. (lobed tickseed), disc and ray flowers yellow; *C. basalis* (Dietr.) S.F. Blake, disc flowers yellow, ray flowers yellow with basal red-brown blotch; *C. bigelovii* (A. Gray) H.M. Hall, both disc and ray florets yellow; usually cultivated in southern California (as *C. stillmanii* (A. Gray) S.F. Blake); *C. californica* (Nutt.) H. Sharsm., both disc and ray florets yellow; cultivated in southern Arizona, southern California and northern Baja California (as *C. douglasii* (DC.) H.M. Hall); *C. grandiflora* Hogg in Sweet (big-flowered tickseed), both disc and ray florets yellow, widespread in warm tropics, the name often misapplied for large-headed *C. lanceolata* L.; *C. lanceolata* (long-stalk tickseed), both disc and ray florets yellow, widespread also in Europe and Africa, cultivar “Grandiflora” is applied to large-headed specimens or mistakenly to *C. grandiflora*; *C. tinctoria* Nutt. (golden tickseed, plains tickseed), the most commonly cultivated annual species, disc flowers are

dark red, purple, brown-purple, reddish, ray flowers are yellow with brown-purple base or entirely yellow, brown or purple-red, cultivar “Nana” are low compact annuals; *C. verticillata* L. (thread-leaf tickseed), disc and ray florets yellow; very distinctive in its narrowly cut leaves.

Cosmos

This genus has a few species in cultivation throughout the world: *C. atrosanguineus* (Hook.) A. Voss in Vilmorin (black cosmos, chocolate cosmos), ray florets are dark maroon with chocolate scent, leaves are few-lobed and tinged pale purple; *C. bipinnatus* Cav. (common cosmos, Mexican cosmos), leaves are feathery, ray florets are white, pink or crimson, cultivars with multiple series of ray florets and florets with strips of colors have been produced from this species; *C. sulphureus* Cav. (yellow or orange cosmos), the yellow or orange ray florets and the wider leaves set this apart from the previous species.

Dahlia

This is one of the most important garden ornamental plants that is selected for its large, showy ray florets and green lustrous leaves. Sørensen (1969) and Foulis et al. (2001) state that probably two or three species, including *D. coccinea* Cav. and *D. pinnata* Cav., are the sources of the thousands of the named cultivars and hybrids. Dwarf hybrids of *D. pinnata* are “forced for Easter and Mother’s Day” (Graf 1974). The hybrids are grouped into ten different groups (Foulis et al. 2001) or twelve (Bailey and Bailey 1976) on the basis of the size, number, and shape of the ray florets

making up the flower head. Important species include: *D. coccinea* (common or garden dahlia), described by Sørensen (1969: 405) as the most complex species of the genus, is widely cultivated, disc florets are yellow or scarlet at the apices, ray florets lemon-yellow, orange, scarlet, sometimes variegated yellow and orange; *D. pinnata* (common or garden dahlia), the disc flowers are yellow, sometimes with light purple veins, and the ray florets are pale purple or lavender-purple, often with a basal rosy or yellow spot; *D. imperialis* Roehl (tree or candelabra dahlia), disc flowers are yellow, ray flowers are lavender-pink, large solitary capitula, ray florets in one series and the thick bamboo-like stems are distinctive of this species.

The following species are planted along highway or roadside slopes: *Thelesperma simplicifolium* A. Gray in California (Strother 2006: 201); *Cosmos bipinnatus* (Kiger 2006: 204; MesfinTadesse, pers. obs. in Ohio)

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