

A cladistic analysis of morphological features in *Bidens* L. and *Coreopsis* L. (Asteraceae-Heliantheae) with notes on generic delimitation and systematics

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A cladistic analysis of morphological characters obtained from representative species of *Bidens* from North, Central & South America and Africa, and *Coreopsis* from North and South America indicate that: (a) *Bidens* and *Coreopsis* are not monophyletic; (b) *Bidens* is a paraphyletic genus and is closer to *Cosmos*, *Thelesperma*, *Heterosperma*, *Isostigma*, etc., than it is to *Coreopsis*; (c) the African species that were formerly kept in *Coreopsis* form a paraphyletic grade within *Bidens* that are sister to western hemisphere groups; (d) *Coreopsis* is paraphyletic with two major clades and is restricted to the New World; and (e) the phylogeny based on morphology shows certain similarities to one generated from DNA sequences, but the relationships portrayed differ in several basic respects.

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Introduction

Bidens L. and *Coreopsis* L. belong to the tribe Heliantheae, subtribe Coreopsidinae of Asteraceae. In a systematic review of the tribe, the Coreopsidinae was subdivided into seven informal groups (Stuessy 1977). *Bidens* L. and *Coreopsis* L., along with other genera, were put in group 1. A number of authors also place *Bidens* near *Coreopsis*, *Cosmos* Cav. and *Coreocarpus*

Benth. (Smith 1975, 1989; Melchert & Turner 1990; Karis & Ryding 1994). Recently the systematic position of *Bidens* within the Coreopsidinae has been the focus of studies by Ryding & Bremer (1992) and by Karis & Ryding (1994). The latter stated that *Bidens* and *Coreopsis* offer one of "the most striking examples of difficulties with generic delimitation" in the Asteraceae.

In a cladistic analysis of the Coreopsidinae (given as tribe Coreopsideae), Ryding & Bremer (1992: 653) recognized three large generic groups, although their strict consensus tree does not resolve relationships among the groups. An analysis of 18 of the same genera (four genera have been relegated to synonymy, cf. Bremer 1994; Veldkamp & Kreffer 1991), with fuller data sets than hitherto, also produced an unresolved strict consensus tree. Shannon & Wagner (1997) pointed out that the conclusions of Ryding & Bremer (1992) "... concerning relationships within the Coreopsideae should be viewed with some caution ..." Much data are missing from their matrix (*e.g.* 23 of 37 characters are unknown for *Cyathomone* S.F. Blake, and approximately a third of the characters for *Bidens* and *Coreopsis* are recorded as variable).

One reason given for the unresolved position of *Bidens* in the cladograms generated by Ryding & Bremer (1992) was lack of diagnostic characters between it and *Coreopsis*. The traditional delimitation of these genera, which, as shown elsewhere as inadequate (*e.g.* Wild 1967; Agnew 1974; Mesfin Tadesse 1984, 1986), are adopted in their work. A number of studies, particularly on *Cosmos* (Melchert 1967, 1968, 1990a), *Dahlia* Cav. (Sorensen 1969; Giannasi 1972, 1975a, 1975b), *Coreopsis* (many articles by Crawford & Smith), *Bidens* (Hart 1979; Ballard 1986; Ganders & Nagata 1983, 1984; Mesfin Tadesse 1984, 1986, 1993; Helenurm & Ganders 1985; Mesfin Tadesse *et al.* 1995a, 1995b, 1996; Roseman 1986), *Coreocarpus* (Smith 1989; Melchert & Turner 1990), and *Thelesperma* Less. (Melchert 1963), have indicated that prior circumscriptions of genera are in need of modification in light of newly emerging data. Melchert (1975) reiterated that the main reason that *Bidens* and *Cosmos* "appear to intergrade is due to the *a priori* inclusion of all annuals with beaked or rostrate achenes within *Cosmos*. Similarly, the inclusion of all taxa with

winged achenes in *Coreopsis* (Sherff 1936), without considering other features, has blurred the boundary between this genus and *Bidens*. Smith & Parker (1971) showed that the presence or absence of wings on achenes of *Coreopsis tinctoria* L. is under simple genetic control. Similar problems exist with delimiting *Coreocarpus* from *Bidens* and *Coreopsis* (Smith 1983b, 1984b, 1989; Melchert & Turner 1990).

Most North American (excluding Mexico) species of *Bidens* are annual plants and are distinct from *Coreopsis* both in capitular and gross morphology. The Mexican species, however, intergrade particularly with *Cosmos* and *Coreocarpus* (Melchert 1990b). The only true species of *Coreopsis* in the eastern hemisphere are the few cultivated and/or ornamental species: *C. grandiflora* Hogg, *C. verticillata* L. and *C. lanceolata* L.

The paucity of features distinguishing *Bidens* from *Coreopsis*, the instability of the characters traditionally used for segregating the two genera, and the large amount of phenotypic plasticity of particularly *Bidens* as exemplified by studies on amphibious taxa (Wheedon 1974) and those of oceanic islands, have obscured the boundary between *Coreopsis* and *Bidens*.

There are morphological similarities between some species of *Bidens* and *Coreopsis*. However, there are also capitular and foliar resemblances between some species of *Bidens* and other related genera, *i.e.* *Cosmos*, *Coreocarpus*, *Isostigma* Less., etc. In order to determine the relationships between particularly *Bidens* and *Coreopsis*, a cladistic analysis of genera of the Coreopsidinae incorporating data from previous (Ryding & Bremer 1992; Mesfin Tadesse *et al.* 1995a, 1995b) and current studies is attempted here.

The objectives of the present work are a) to determine the phylogenetic positions of *Bidens* and *Coreopsis* within the Coreopsidinae, b) to test the monophyly of *Bidens* and *Coreopsis*, and also evaluate the characters that have been

used traditionally for generic segregation, c) to provide a cladistic analysis of the relationships between *Bidens* and *Coreopsis*, (including those African species which have previously been kept in *Coreopsis*), and d) to provide an assessment of the utility of certain characters used for sectional classification in *Bidens*.

Materials and methods

Taxa

For the initial cladistic analysis of subtribe Coreopsidinae, sensu Ryding & Bremer (1992), a total of 15 genera and 28 characters were included (Appendix 1 and Table 1). From the twenty-five genera included in the subtribe by Ryding & Bremer (1992), four (*i.e.* *Eryngio-phyllum* Greenm. (= *Chrysanthellum* Rich.), *Glossogyne* Cass., *Guerreroia* Merr., and *Neuractis* Cass. (= *Glossocardia* Cass.; cfr. Veldkamp & Kreffer 1991; Bremer 1994) have since then been relegated to synonymy. Of the remaining 21 genera, *Cyathomone* S.F. Blake, *Dicranocarpus* A. Gray, *Goldmanella* Greenm., *Ericentrodea* S.F. Blake & Sherff and *Petrobium* R.Br. are excluded from the analysis due to lack of complete data or specimens. *Megalodonta* Greene (Roberts 1985; Bremer 1994), which was considered by Sherff (1937) as a monotypic section of *Bidens* and was embedded in *Bidens* in the ITS phylogeny by Kim *et al.* (1999)), was included in the present analysis. *Trioncinia* (F. Muell.) Veldkamp (a monotypic North Australian genus 'distinguished from *Bidens* only by its alternate leaves') was likewise included in the present analysis.

Genera rather than species were used as terminal units for this analysis. It is possible that some of the genera may not be monophyletic. However, since we are not interested in investigating the phylogenetic status of genera other than *Bidens* and *Coreopsis*, it is unnecessary to replace the genera with species. Furthermore, it seems inevitable to allow some terminal units

to be paraphyletic (Rieseberg & Brouillet 1994).

The first run on the entire data matrix (18 genera, 28 characters) produced an unresolved consensus tree (tree not shown). Subsequently, a few of the heterogeneous genera (*Chrysanthellum*, *Coreocarpus*, and *Fitchia* Hook.f.) and those, which assumed many different positions (*Chrysanthellum*, *Coreocarpus*, *Moonia* Arn. and *Henricksonia* B.L. Turner) on the cladograms, were excluded from the analysis, except for *Coreocarpus*. This did not adversely affect the topology. The result is presented in Fig. 1.

As shown in Fig. 1, *Bidens* is closely related to several other genera, *i.e.* *Thelesperma* Less., *Cosmos*, *Megalodonta*, *Heterosperma* Cav., *Narvalina* Cass., *Trioncinia*, and *Coreocarpus*. *Coreopsis* is sister to the clade containing the above mentioned taxa, as well as *Dahlia* Cav. and *Isostigma*. Therefore, in the subsequent cladistic analysis of *Bidens* and *Coreopsis*, a representative from each of the *Dahlia-Isostigma* clade, *Cosmos-Megalodonta-Thelesperma* clade, and *Heterosperma-Narvalina-Trioncinia-Coreocarpus* clade was also included. A total of 32 species and 45 characters (Appendix 2 and Table 2) were used. Several representatives of *Coreopsis* from North America (6 spp.) and Mexico & South America (3 spp.), were included. In the case of *Bidens*, several members from Africa (10 spp.), North America excluding Mexico (5 spp.), and South America & Mexico (5 spp.), were also included in the analysis.

Characters

The characters used in the analysis were obtained from herbarium specimens, plants cultivated in the greenhouse at Ohio State University and from the literature. Specimens were obtained on loan from the following herbaria (abbreviations according to Holmgren *et al.* 1990): BM, F, K, MO, OS and WAG. Details concerning character measurement

and assessment are provided in Mesfin Tadesse *et al.* (1995a). Characters that require additional explanations are provided in Appendix 2.

Character states were polarised based on out-group comparison. The characters were coded as '0' (plesiomorphic character state) and '1' or upwards (apomorphic character state).

Some genera are variable in certain features. Characters shared by all taxa in the 'in-group' and autapomorphies were excluded from the analyses.

Data analyses

MacClade 3.0 (Maddison & Maddison 1992) was used to edit the data set (Tables 1 and 2) for input into PAUP 4.0b4a (Swofford 2000). Phylogenetic analysis was performed with the aid of PAUP using Power Macintosh G3. For initial cladistic analysis of Coreopsidinae, a branch and bound search strategy was employed using maximum parsimony with characters unordered and equally weighted. In a subsequent analysis of *Bidens*, *Coreopsis*, and several other closely related genera, heuristic search option with TBR branch swapping and MULPARS on was used. A search for multiple islands of trees (Maddison 1991) was carried out with 100 replications of "random" taxa addition. Relative support for individual clades was estimated with 100 bootstraps (Felsenstein 1985) using simple addition sequence and TBR branch swapping for each bootstrap (max tree = 20000). Decay analysis (Bremer 1988; Donoghue *et al.* 1992) was also employed to provide an assessment of support for clades with trees that are three or fewer steps longer than the minimal length tree.

Choice of outgroups

Guizotia (currently in subtribe Melampodiinae, one of the subtribes allied to the Coreopsidinae according to Karis 1993) was chosen as an

outgroup for the genera of the Coreopsidinae. Formerly *Guizotia* was placed within the Coreopsidinae (Stuessy 1977). *Fitchia speciosa* was chosen as the outgroup for the subsequent analysis of *Bidens* and *Coreopsis* because in the cladistic analysis of morphological features of the Heliantheae by Karis (1993), *Fitchia* is the sister group to *Coreopsis* and the group of genera allied to it. Chloroplast DNA restriction site data by Jansen & Kim (1996) also produced a similar relationship.

Results and discussion

Genera of Coreopsidinae

The analysis of fifteen genera of Coreopsidinae (Table 1, Fig. 1), for which nearly complete morphological data were assembled, resulted in six equally most parsimonious trees with a tree length of 51, consistency index (CI) of 0.58 and retention index (RI) of 0.60. *Coreopsis* is sister to a lineage that includes *Bidens*, *Thelesperma*, *Cosmos*, *Heterosperma*, *Coreocarpus*, and other mainly American genera. Thus, *Coreopsis* appears as a basal element within New World elements of Coreopsidinae.

Bidens and Coreopsis

The subsequent analysis of *Bidens* and *Coreopsis*, including several other closely related genera, produced 3098 most parsimonious trees with a length of 139, consistency index (CI) of 0.43, and retention index (RI) of 0.79 (Table 2; Fig. 2). As can be seen from Fig. 2, the strict consensus tree is not fully resolved. *Cosmos*, *Heterosperma*, *Isostigma* and *Coreocarpus*, representing the various clades in Fig. 1, are clustered with the North and South American/Mexican *Bidens*, indicating their derived position within the Coreopsidinae. There is moderate support for certain clades such as Mexican and South American *Coreopsis*, *Bidens barteri*-*B. prestinaria* and North American *Bidens* (Fig. 2). One of the 3098 equally parsimonious trees was ran-

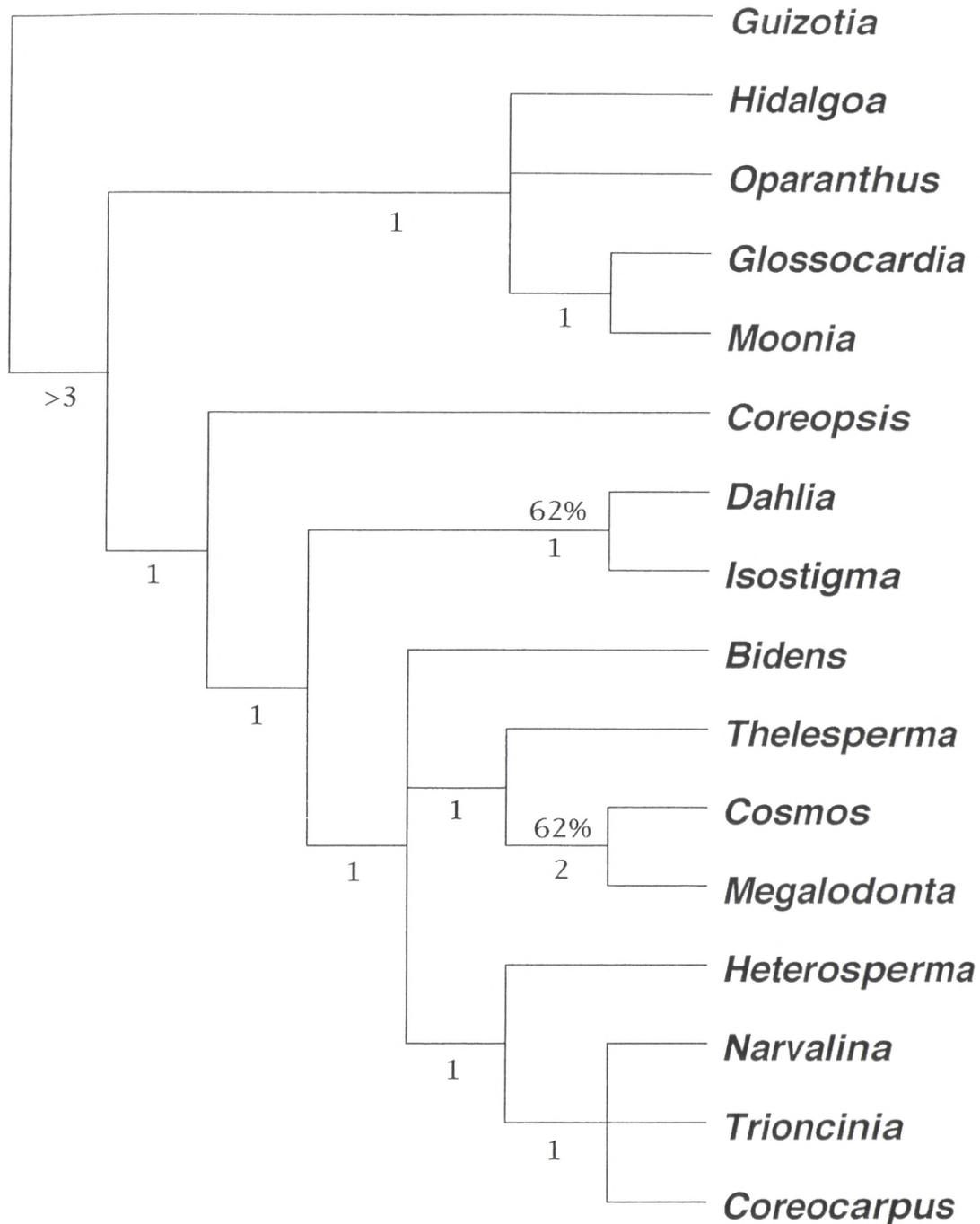


Fig. 1. Strict consensus of 6 equally parsimonious trees of genera of Coreopsidinae depicting the position of *Bidens* in relation to *Coreopsis* obtained using *Guizotia* as an outgroup. Bootstrap (%) and decay values (below horizontal lines) are given. The characters are given in Appendix 1 and the data in Table 1.

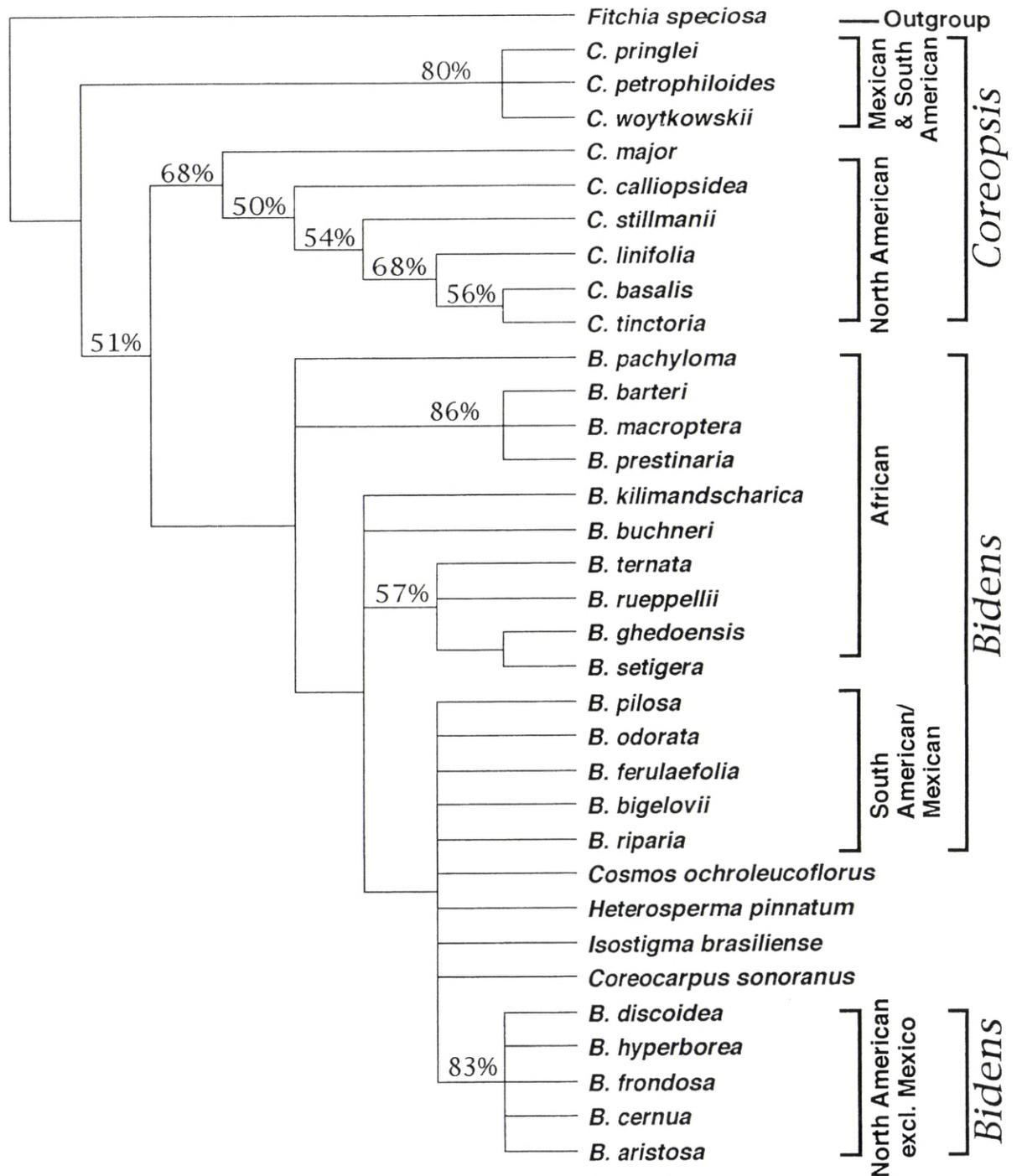


Fig. 2. Strict consensus of 3098 equally parsimonious trees of *Bidens*, *Coreopsis* and allied genera. The characters are given in Appendix 2 and the data in Table 2. Bootstrap (%) values are indicated.

domly chosen to map some of the characters on the cladogram (Fig. 3). Many of the mapped characters have not been previously employed for generic delimitation. Some of the achenial features, however, have been used in both generic delimitation and infra-generic classifications. The consistency index shows that there is considerable homoplasy but this is not unexpected in any analysis of morphological features (cf. Jansen *et al.* 1987; Ryding & Bremer 1992; Karis 1993). However, the clades are constant and they are supported by a number of non-homoplastic characters.

The shrubby or perennial Mexican and South American *Coreopsis* sect. *Pseudoagarista* (Figs. 2 and 3) forms the basal group and it is sister to the rest of *Coreopsis* and *Bidens*. This lineage is characterized by a single non-homoplastic feature (pubescence of paleae, character 16) and two homoplastic characters, one of which is seen only in one other section of *Coreopsis*, *i.e.* *C.* sect. *Pugiopappus* (A. Gray) Blake (*C. calliopsidea* (DC.) A. Gray), wherein the paleae are attached to the achene at the base and are deciduous with it (character 17). *Coreopsis* sect. *Pseudoagarista* is also distinguished from the rest of the species in *Coreopsis* and *Bidens* by an autapomorphic feature, *i.e.* regularly or irregularly 3-cleft paleae. This section of *Coreopsis* is unique in consisting of taxa with invariable achene morphology but diverse foliar features. The group occurs in Mexico, Colombia, Peru, Ecuador, and Chile. Other species within *Coreopsis* and *Bidens* have developed other means of fruit dispersal, such as winged or flat fruits, retrorsely barbed pappi, etc.

The North American species of *Coreopsis* excluding *C.* sect. *Pseudoagarista* form a monophyletic group with weak to moderate support (Fig. 2). It is supported by one non-homoplastic (character 38) and several homoplastic features (Fig. 3). These sections of *Coreopsis* have been the subject of numerous taxonomic,

chemosystematic, biosystematic, and molecular systematic studies and the relationships between the sections and the species have been well documented (cf., as examples, Crawford 1969, 1970, 1971, 1976; Crawford & Bayer 1981; Crawford & Smith 1983a, 1983b, 1984, 1985; Crawford & Stuessy 1981; Crawford *et al.* 1980, 1984, 1990a & b, 1991, 1992; Smith 1972, 1973, 1975, 1976, 1982, 1983a, 1983b, 1983c, 1984a, 1984b; Smith & Crawford, 1981; Smith & Parker 1971, etc.).

Bidens and *Coreopsis* share a number of synapomorphies but these are beset with reversals (Fig. 3). Compared to *Coreopsis*, *Bidens* has more non-homoplastic synapomorphies. These include a phytomelanin layer characterized by black, commonly irregular peg-like deposits (character 34/4), and basic chromosome numbers of 12, 16, 17, 18, and 21 (character 44/2). The large germinal pores of the pollen (character 45), although homoplastic, are found only in *Bidens*. The penicellate and attenuate style arm apices with decurrent sweeping hairs (character 21), shown to be homoplastic (reversed in *Cosmos*, Fig. 3), are not found in *Coreopsis*. As shown in an earlier paper (Mesfin Tadesse *et al.* 1995b), the pollen grains of *Bidens* and *Coreopsis* are very similar and only few quantitative and qualitative differences were obtained. Of these, the difference in the size of the germinal pore (os) was quite significant with all the examined species of *Bidens* having much wider and longer ora. There was no overlap in this feature in pollen of the two genera. Although many species of *Bidens* have chromosome numbers based on $x = 12$, this number is also found in a few sections of *Coreopsis*.

As shown in Fig. 3, those African species with winged achenes, which were formerly placed in *Coreopsis* (Sherff 1936; Ryding & Bremer 1992), form a paraphyletic grade (with *B. pachyloma* being basal) and cluster with the rest of *Bidens*. The strongly supported (86%) *B.*

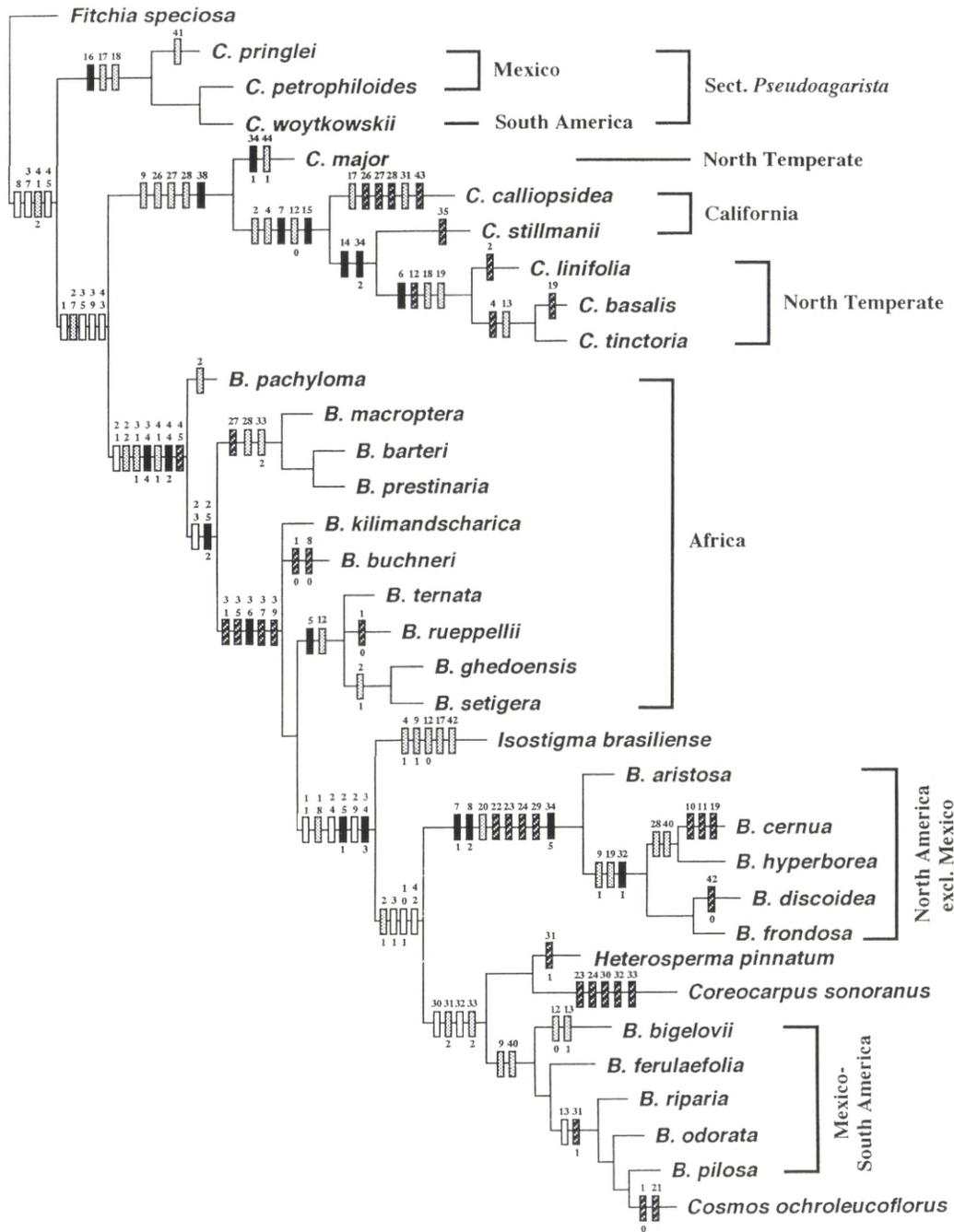


Fig. 3. One of the 3098 equally parsimonious trees of *Bidens*, *Coreopsis* and allied genera illustrating character distributions. *Fitchia speciosa* is the outgroup. Solid bars indicate non-homoplastic synapomorphies; open bars indicate homoplastic synapomorphies with reversal; stippled bars indicate parallelisms; striped bars indicate reversal. Characters and data set are as for Appendix 2 and Table 2.

macroptera-*B. prestinaria* clade is sister to the rest of *Bidens* and the other genera in the subtribe. The remaining African *Bidens*, *i.e.* *B. kilimandscharica* to *B. setigera*, form a paraphyletic grade with the *B. ternata*-*B. setigera* clade sister to all remaining *Bidens* and four other genera. Both the North and South American species of *Bidens* have accumulated a higher number of autapomorphies than the African *Bidens* (characters 7, 8/2, 25/1, 32, 34/3, 34/5). The New World taxa could thus be hypothesized as having a relatively recent origin.

A general comparison of the phylogeny generated from the present study may be made with the phylogeny for *Bidens* and *Coreopsis* produced by Kim *et al.* (1999) from nucleotide sequences of the internal transcribed spacer region of nuclear ribosomal DNA (ITS). More detailed analyses of the morphological and molecular data sets are in progress and will be reported later; here, we consider only basic similarities and differences, and do not attempt to evaluate the causes of nonconcordance. Only North Temperate *Bidens* form the same monophyletic groups in the two phylogenies (cf. Figs. 3, 4). Relationships in *Coreopsis* are quite different in the two phylogenies. In the present study, *C. sect. Pseudoagarista* is basal, and a monophyletic assemblage (Fig. 3). By contrast, the ITS phylogeny has Mexican and South American members of the section in different clades with neither being basal (Fig. 4). The phylogeny produced from morphology does not place the California and North Temperate *Coreopsis* in separate clades (68% bootstrap value), as is done in the ITS phylogeny (Figs. 3 & 4). African *Bidens* form a paraphyletic grade in the present study (Fig. 3) whereas they are a strongly supported monophyletic group in the ITS phylogeny (Fig. 4). The Mexican and South American *Bidens* group together in the phylogeny generated from morphological characters, but with several other genera embedded in the clade (Fig.

3). The ITS phylogeny also contains a strongly supported clade of Mexican and South American *Bidens* (Fig. 4), but since other genera such as *Cosmos*, *Heterosperma* and *Coreocarpus*, were not included in the Kim *et al.* (1999) study it is not known whether they would appear in the clade if their sequences were included. However, preliminary results from ITS studies suggest that none of the genera embedded in the North Temperate *Bidens* clade (Fig. 3) occur with *Bidens* in an ITS tree (Crawford *et al.*, unpublished data).

Sectional and geographical distribution of characters.

In *Bidens* the characters display more aggregation within geographically segregated taxa than within previously delimited sections. For instance, the species from Mexico and South America form a group distinct from those from the United States and Canada (Fig. 2). Within the latter group are members of sections *Meduseae* (Nutt.) Sherff and *Platycarpaea* DC. and within the former fall members of the large and heterogeneous section *Psilocarpaea* DC. The African species are dispersed in three major groups; those with winged achenes form the basal group (*B. pachylooma*-*B. prestinaria*), and those without winged achenes are sisters to the species in the New World. Square stems, characteristic of many annual species of *Bidens* sect. *Psilocarpaea*, also occur in a few of the African species. Two other characters utilized to delimit sections of Old World *Bidens* by Sherff (1937), *i.e.* adnate inner phyllaries and medially thickened corolla, are homoplastic. However, character 5, *i.e.* setigerous foliar teeth, which was utilized by Sherff (1937) in defining a section of African *Bidens*, *i.e.* *B. sect. Steppia* (Sch. Bip. ex Walp.) Sherff, is found to be non-homoplastic.

Sherff (1937) kept the African species of *Bidens* in sections *Psilocarpaea* DC., *Steppia* (Sch. Bip. ex Walp) Sherff, *Lesperthema* Sherff and



Fig. 4. Strict consensus tree for *Bidens* and *Coreopsis* based on ITS sequence. Condensed and modified from Kim *et al.* (1999). All branches shown have bootstrap support above 80% except for North Temperate *Bidens* with 77%.

Ebussa Sherff and noted that sect. *Psilocarphaea*, which also includes all the Mexican and South American taxa, may need to be split into smaller groups. Currently a more thorough re-examination of species in the sections mentioned above is being carried out.

The delimitation of *Coreopsis* into sections, by contrast, is relatively clear-cut with the exception of section *Pseudoagarista*. Although supported by morphological data (Jansen *et al.* 1987, this study), the molecular data (Kim *et al.* 1999) does not support the monophyly of this section.

Conclusion

Using morphological features, *Bidens* and *Coreopsis*, the two largest and most complex genera of the *Coreopsidinae*, are shown not to be monophyletic. *Bidens* is a paraphyletic genus that is more closely related to six other mainly North

American genera than to *Coreopsis*. Morphologically, it can be distinguished from *Coreopsis* by the striate and grooved achenes. These are thin-walled parenchymatous and often translucent areas on the achene wall, which break up easily during seed germination. The seedlings of *B. bipinnata* were observed to emerge by breaking open this thin-walled area of the achene surface (Mesfin Tadesse *et al.*, in prep.). Retrorsely barbed aristae are also features found in many species of *Bidens* and have not been observed in any species of *Coreopsis*. The North American (excl. Mexico) and the South American & Mexican *Bidens* form distinct clades within the genus. The infra-generic relationships, particularly sectional relationships within this large genus, need to be investigated further.

Coreopsis is paraphyletic with two major lineages. *Coreopsis* sect. *Pseudoagarista*, constituting one of these lineages, is basal within the genus.

In spite of some shared features with some of the North American species, this section consists of species with a number of unique features. Taxa from the African continent formerly kept in *Coreopsis* (*B. pachyloma*, *B. macroptera*, *B. barteri* and *B. prestinaria*) are shown to belong to *Bidens*.

The African and North American *Bidens* with flattened (and sometimes also winged) achenes are different from the largely Mexican and South American species with usually tetragonal and unwinged achenes. The latter have also developed traits such as white or purplish ray florets, which set them apart from the species in Africa (except for two species in south-central Africa) and North America. These major trends in the diversification of *Bidens*, observed during this study, deserve further studies.

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Appendix 1. Characters used in the analysis of the genera of Coreopsidinae.

1. (0) Herbs or small shrubs; (1) trees or large shrubs.
2. Duration: (0) perennial; (1) annual.
3. Stem or branches: (0) erect; (1) decumbent or prostrate; (2) climbing.
4. Roots: (0) non-tuberiferous; (1) tuberiferous.
5. Petiole: (0) stiff, not tendril-like; (1) tendril-like.
6. Leaves: (0) herbaceous/foliaceous; (1) coriaceous.
7. Leaves: (0) opposite; (1) alternate.
8. Capitula: (0) heterogamous or homogamous, radiate or discoid; (1) ligulate.
9. Capitula: (0) heterogamous; (1) homogamous.
10. Involucre: (0) campanulate-hemispheric; (1) cylindrical-campanulate.
11. Inner phyllaries: (0) free except at base; (1) united at least up to 1/3rd of length.
12. Ray floret apex: (0) 3-5-fid; (1) entire, emarginate or deeply bifid.
13. Ray florets: (0) pistillate, fertile or sterile; (1) neuter.
14. Ray florets: (0) yellow or orange-yellow; (1) white, purple or pink.
15. Paleae and phyllaries: (0) homomorphic; (1) heteromorphic.
16. Disc florets: (0) hermaphrodite and fertile; (1) abortive or functionally male.
17. Disc corolla: (0) 5; (1) 3-4.
18. Disc floret style: (0) bifid; (1) entire or only notched at apex.
19. Filament: (0) glabrous; (1) hairy.
20. Apex of disc floret style branches: (0) short; (1) long and appendaged.
21. Ray and disc achenes: (0) dissimilar; (1) monomorphic or graded monomorphic.
22. Disc achenes: (0) not striated; (1) striated.
23. Disc achenes: (0) smooth; (1) grooved or sulcate.
24. Disc achenes: (0) not winged; (1) winged.
25. Apex of disc achenes: (0) not beaked; (1) beaked.
26. Pappus of disc achenes: (0) scales; (1) 2-4 aristae; (2) 5-16 aristae.
27. Pappus: (0) smooth or coroniform; (1) antrorsely barbed; (2) retrorsely barbed.
28. Length of pappus: (0) less than 1/2 of achene; (1) greater than half to exceeding achene.

Appendix 2. Characters used in the analysis of *Bidens* and *Coreopsis*.

Habit and stem The stems and/or branches display a few important features, *e.g.* stature, persistent petiole bases, shape, pubescence, etc. While a large number of the species of *Bidens* have erect stems, a few of the African, Central American and Mexican taxa have prostrate, decumbent, scandent or climbing (vine-like) stems. In

Table 1. Data for the Coreopsidinae Less., using *Guizotia* (Melampodiinae Less.) as outgroup. The characters are provided in Appendix 1. Variable (V), unknown (?) and inapplicable (-) characters are indicated.

Character number 12345	1 67890	11111 12345	11112 67890	22222 12345	222 678
<i>Guizotia</i>	00000	00000	00000	00000	00000	---
<i>Bidens</i>	0VV00	00000	00001	0V000	111VV	VV0
<i>Coreocarpus</i>	0V000	00001	010V0	00000	10010	120
<i>Coreopsis</i>	0V000	00000	00001	0V000	100V0	VV0
<i>Cosmos</i>	0V010	00000	00111	00010	11101	220
<i>Dahlia</i>	00V10	00000	00011	00001	11100	---
<i>Glossocardia</i>	0V000	01011	00011	11V00	10100	100
<i>Heterosperma</i>	01000	00001	00001	00000	01110	120
<i>Hidalgoa</i>	00201	00000	01001	10100	00000	100
<i>Isostigma</i>	00000	01000	00011	00001	11100	1V0
<i>Megalodonta</i>	00100	00000	00100	00000	1? ?01	221
<i>Moonia</i>	00000	00110	00001	11100	0- - - -	---
<i>Narvalina</i>	10000	1000?	01000	00000	11100	110
<i>Opavanthus</i>	10000	10000	01001	11100	00010	100
<i>Thelesperma</i>	00000	00000	10101	00000	1? ?00	120
<i>Trioncinia</i>	00000	01001	11000	01000	11100	120

many of the African species of *Bidens* and the Mexican and South American *Coreopsis* the main stem is terete and the branches are diffusely multi-ribbed to quadrangular. Tetragonal stems are characteristic of specially the annual Mexican and some central African species of *Bidens*.

1. Habit: (0) tree, shrub or subshrub with several stems from a rhizomatous, thickened or tuberous rootstock; (1) herb with solitary, herbaceous or woody stem.
2. Duration: (0) perennial; (1) annual.
3. Main stem: (0) terete or multi-ribbed; (1) tetragonal.

Leaves. Leaves in *Bidens* and *Coreopsis* are quite variable in a number of features including the degree of dissection of the lamina. There is sometimes considerable variation even within one individual plant. Interpretation of leaf margins in compound leaves can be misleading. Various dissected leaflets could be described as having serrate or lobulate margins. It is only in simple leaves that interpretation of margins becomes consistent. Consequently, only the following among leaf characters were chosen.

4. Leaf arrangement: (0) opposite; (1) alternate.
5. Leaf teeth: (0) short, acute; (1) setigerous.

Receptacle. The receptacle, in longitudinal section, may be flat, convex, conical or globular. Often those species with flat or convex receptacles have erect, basally thickened or indurate inner phyllaries which are never reflexed in fruit thus keeping the achenes firmly enclosed within. Species with globular receptacles have thin to thickish phyllaries that are either totally reflexed at maturity exposing the fruits or bent inwards. The Mexican and South American species of *Bidens* allied to *B. pilosa*, *B. bipinnata*, *B. riparia*, etc., have globular receptacles with totally reflexed phyllaries and radiating fruits at post anthesis. The North American *Coreopsis* sect. *Coreopsis* have globular or conical receptacles but the phyllaries are not reflexed.

6. Receptacle: (0) flat or convex; (1) conic or globular.

Phyllaries. The phyllaries display a number of characters and states such as shape, pubescence, length, etc., which are useful for species recognition. The ratio of the outer phyllary to the inner was found most useful in distinguishing most members of *Bidens* from *Coreopsis*. The colour and number of striae of the inner phyllaries also display these differences.

7. Ratio of length of outer to inner: (0) 0.7-1.5; (1) 1.5-5; (2) 0.1-0.7.
8. Texture: (0) woody to coriaceous; (1) subcoriaceous, bracteaceous; (2) leaf-like.

9. Pubescence of inner phyllaries: (0) one or both surfaces hairy; (1) glabrescent to glabrous.
10. Colour of inner phyllaries: (0) orange yellow or brown; (1) greenish-yellow, yellowish brown, or brownish-green.

Ray Florets. The ray floret number appears to follow the fibonacci series, *i.e.*, 0, 3, 5, 8, 13, and 21. The modal number in *Bidens* appears to be 5 (in Mexican, Central and South American species) and 8 (mostly African species), while in *Coreopsis* it is 8. There is far greater variation in number of florets in individual plants in *Bidens* than in *Coreopsis*. Some species in *Bidens* have fewer florets or these may even totally be absent.

11. Number based on: (0) 8; (1) 3 or 5.
12. Sexual condition: (0) pistillate; (1) neuter.
13. Colour: (0) yellow; (1) yellow with reddish/purple blotch; white; (2) pink, purple.
14. Apex: (0) entire to minutely 1-3-fid or dentate; (1) deeply 3-4-lobed with the central lobe longer than the laterals. Note: Interpretation of this state is problematical. The fused and apically 3-lobed or 3-fid ray floret of the Heliantheae is often considered more primitive than other types involving 3 corolla lobes (Smith 1975; Jeffrey 1977).
15. Shape: (0) oblong, oblong-elliptic; (1) linear, linear-lanceolate, attenuate.

Paleae. The paleae display a number of unique features that are shared by only a few of the species in both genera. In *Bidens* they are generally glabrous with individuals of a few species possessing a few moniliform hairs towards the apex, commonly oblong or oblong-elliptic and free from the achenes. In *Coreopsis* sect. *Pseudoagarista* and *Pugiopappus*, the paleae possess long, flexuose, twin hairs similar to those found on the achenes. They are attached to the achene at the base and are dislodged and dispersed from the receptacle together at maturity. The paleae in *Coreopsis* are more varied in shape.

16. Pubescence: (0) hairy; (1) glabrous or glabrescent.
17. Attachment to achene: (0) attached; (1) free or clasping.
18. Shape: (0) oblong to oblong-elliptic; (1) linear, linear-lanceolate or attenuate.

Disc florets. The corolla lobes are commonly 5 in both *Bidens* and *Coreopsis* but 4 corolla lobes are known in 2 sections of North American *Coreopsis* and 3 corolla lobes in some species of *Bidens* from South America and Mexico (*e.g.* *B. leoniti*). Of the other characters of the corolla displaying

differences between taxa, the ratio of the tube to the limb is found to be useful. The corolla in many species of both *Bidens* and *Coreopsis* is ampliate, *i.e.* the limb is abruptly widened at the apex of the tube. Usually there is little difference in size between the limb and the tube. In some species of *Bidens* of South America, the corolla is nearly tubular with a very small portion of it being constituted by the tube. The ampliate corolla is considered less derived in other Asteraceae (Jeffrey 1977; Zhang & Bremer 1993).

19. Corolla lobes: (0) 5; (1) 3 or 4.
20. Corolla shape: (0) tubular or funnellform, tube and throat not sharply differentiated; (1) tubular, tube and throat sharply differentiated.
21. Style arm apex: (0) conic, cuspidate to truncate with limited sweeping hairs; (1) penicellate or attenuate with decurrent sweeping hairs.

Achenes. In both *Bidens* and *Coreopsis* the achene surface is carbonized (Robinson 1981). In many species of *Bidens* this carbonized layer is interrupted by longitudinal bands of parenchyma which are referred to as striations. They are also sunken areas or grooves along the achene surface. These areas were recently (Mesfin Tadesse & Crawford, in prep.) found to be weak spots along the achene surface through which the cotyledons and the hypocotyl emerge during germination of the seed. In achenes where these parenchymatous areas are absent, the germinating seedlings emerge by breaking through the margins at the lower half of the achene. The presence of thin-walled parenchyma along the achene wall appears to be an adaptation for successful germination and hence it is considered to be a derived feature.

22. Surface: (0) not striated; (1) striated.
23. Texture: (0) smooth; (1) grooved.
24. Compression: (0) 2-sided; (1) 4-sided. Note: Many species of *Bidens* and *Coreopsis* have dorsiventrally flattened achenes. The majority of the Mexican, Central and South American species of *Bidens* have quadrangular achenes. Many species of North American *Bidens* have cuneate achenes with the upper part being conspicuously 3-4-ridged or angled.
25. Number of grooves on each face: (0) no grooves; (1) 2; (2) 4-8(-16). Note: In bifacial or dorsiventrally flattened achenes with grooves the number of grooves on each surface ranges between 6 and 16 while in quadrangular achenes they are predominantly 2, except in *B. lemmonii* and *B. gardneri*, where there are 4 grooves on one or more surfaces.
26. Surface hairs: (0) twin hairs; (1) absent or wart-like processes.

27. Twin hairs: (0) long and flexuous; (1) short and stiff; (2) absent. Note: Twin hairs are characteristic features of the achenes of many Asteraceae (Robinson 1981) occurring in the Astereae, Eupatorieae, Vernoniaeae, Heliantheae (Small 1919: 72) and Mutisieae. There are both long and flexuous and short and rigid twin hairs associated with the achenes of *Bidens*. The short ridged twin hairs are more or less similar in all species of *Bidens*. These are absent in *Coreopsis* but the long and flexuous types are found in *C. sect. Pugiopappus* and *Pseudoagrists*.
28. Hairs on margins: (0) appressed, antrorse; (1) spreading; (2) retrorse; (3) not present.
29. Ratio of length to width: (0) 1-5; (1) 7-20. Note: Differences between taxa in qualitative features such as shape could be expressed quantitatively to portray relationships better. The achenes of many South American and Mexican species of *Bidens* have been described as clavate, linear, linear-tetragonal and club-shaped and those of African species as ovate, oblong, oblong-lanceolate, obovate, oblanceolate, etc. The length/width ratio provides a better grouping of the species within *Bidens* and *Coreopsis* than the descriptive qualitative features. It was also noted that species with narrow but long achenes were, in many instances, associated with the annual habit.
30. Apex: (0) not differentiated; (1) elongated, narrowed above.
31. Size: (0) more or less uniform; (1) graded monomorphic; (2) dimorphic. Note: In most of the species of *Bidens* and *Coreopsis*, the achenes are monomorphic but there are progressive differences in size and sometimes also in shape centrifugally. Dimorphous achenes are more prevalent in Mexican and South American species of *Bidens* than in the African and North American species of the genus and also in *Coreopsis*. In the later group there are differences in size and shape between the disc and ray floret achenes, but often these differences are not strikingly evident. In the former group, several of the achenes towards the periphery of the capitula are club-shaped (clavate), and yellowish or rubrocastaneous while those near and in the centre of the capitula are linear-tetragonal and black. Dimorphism is thus associated more with the disc floret achenes of Mexican and South American *Bidens*.
32. Exsertion: (0) included or barely exceeding the involucre; (1) achenes exserted above the involucre. Note: In many species of *Bidens* the phyllaries are often thickened at base. In a number of species these thickenings often extend medially to the apex. Yet in some species the thickening also extends into the receptacle making the whole lower portion of the

Table 2. Data for the analysis of *Bidens* and *Coreopsis* with *Fitchia speciosa* as the outgroup. The characters are listed in Appendix 2. Unknown (?) and inapplicable (-) characters are indicated.

Character number	1	1111	111112	22222	22223	33333	33334	44444
	12345	67890	12345	67890	12345	67890	12345	67890	12345
<i>Fitchia speciosa</i>	00000	00000	-----	10000	00000	00000	00000	00000	000?0
<i>Bidens aristosa</i>	11100	01211	01000	10101	10000	01000	00050	10000	11110
<i>B. barteri</i>	11000	00110	01000	10000	11102	00100	10241	01010	101?0
<i>B. bigelovii</i>	11100	00111	10100	10100	11111	01011	21230	10000	11110
<i>B. buchneri</i>	00000	00000	01000	10000	11102	01000	00040	10000	101?0
<i>B. cernua</i>	11100	01200	01000	10101	11000	01200	00150	10001	11110
<i>B. discoidea</i>	11100	01211	-----	10111	10000	01000	00150	10000	10110
<i>B. ferulaefolia</i>	11100	00111	11000	10100	11111	01011	21230	10000	11110
<i>B. frondosa</i>	11100	01211	11000	10111	10000	01000	00150	10000	11110
<i>B. ghedoensis</i>	11001	00110	00000	10000	11102	01000	00040	10000	10120
<i>B. hyperborea</i>	11100	01211	11000	10111	11000	01200	00150	10001	11110
<i>B. kilimandscharica</i>	10000	00100	01000	10000	11102	01000	00040	10000	101?0
<i>B. macroptera</i>	10000	00100	01000	10000	11102	00100	10241	01010	10120
<i>B. odorata</i>	11100	00111	11200	10100	11111	01011	11230	10000	11110
<i>B. pachyloma</i>	11000	00110	01000	10000	11000	01000	10041	01010	101?0
<i>B. pilosa</i>	11100	00111	11200	10100	11111	01011	11230	10001	11110
<i>B. prestinaria</i>	11000	00110	01000	10000	11102	00100	10241	01010	10120
<i>B. riparia</i>	11100	00111	11000	10100	11111	01011	21230	10001	11110
<i>B. rueppellii</i>	00001	00110	00000	10000	11102	01000	00040	10000	10120
<i>B. setigera</i>	11001	00110	00000	10000	11102	01000	00040	10000	10120
<i>B. ternata</i>	10001	00100	00000	10000	11102	01000	00040	10000	10120
<i>Coreocarpus sonoranus</i>	00000	00111	00000	11100	0?000	12300	100?1	10000	2111?
<i>Coreopsis basalis</i>	11000	12100	01111	10100	00000	12300	00021	01110	20101
<i>C. calliopsidea</i>	11010	02100	00001	11000	00000	00100	20001	01110	20001
<i>C. linifolia</i>	10010	12100	01011	10110	00000	12300	00021	01110	20101
<i>C. major</i>	10000	00110	01000	10000	00000	12300	00011	01110	20111
<i>C. petrophiloides</i>	00000	00110	01000	01000	00000	00100	00000	01000	20001
<i>C. pringlei</i>	00000	00110	01000	01000	00000	00100	00000	01000	10001
<i>C. stillmanii</i>	11010	02110	00011	10000	00000	12300	00020	-----	2--01
<i>C. tinctoria</i>	11000	12100	01111	10110	00000	12300	00021	01110	20101
<i>C. woytkowskii</i>	00000	00110	01000	01000	00000	00100	00000	01000	20001
<i>Cosmos ochroleucoflorus</i>	00000	00111	11200	11101	01111	01011	112?1	10000	2111?
<i>Heterosperma pinnatum</i>	11100	00111	00000	11100	01111	12301	212?1	10000	2111?
<i>Isostigma brasiliense</i>	00010	00110	10000	11100	11111	01010	000?0	10000	201??

involucre appear swollen. The thickened portion is due to the deposition of layers of sclerotic parenchyma and collenchyma. As a result of this deposition a number of species have phyllaries that are never reflexed at maturity but remain erect keeping the fruits firmly enclosed within. In such cases the dispersal of fruits is apparently ballistic. In a number of particularly annual species, the phyllaries are not thickened at the base. They are thin and flexible and at maturity both the phyllaries and the paleae are reflexed exposing the achenes. The thin phyllaries are probably adaptations to zoochory and anemochory.

33. Shape: (0) linear-oblong, oblong-elliptic, obovate to oblanceolate; (1) cuneate, tapering to the base; (2) linear-fusiform or linear-attenuate, tapering to the apex and/or base.
34. Type of phytomelanin deposition pattern: (0) A; (1) B; (2) C; (3) D; (4) E; (5) F. Note: The outer surface of the pericarp is carbonized in many species of *Bidens* and *Coreopsis*. This carbonized layer, also referred to as phytomelanin, is either black or light to yellowish-brown. The light to yellowish-brown phytomelanin gets deposited along cell walls and cell surfaces leav-

ing small to large circular to slit-like openings. In cross-section, the pericarp appears smooth. In those species with black pericarp, in addition to the deposition along cell walls and cell surfaces, the phytomelanin on adjacent cell surfaces fuse forming circular to elliptical "pegs" with elaborate deposition pattern. The six different types of phytomelanin deposition patterns (A-F) are: A = along the radial and tangential walls in an irregular manner; B = along several cell surfaces octagonally; C = either uniformly covered or slit-like openings in the middle; D = black, irregular, globular or rectangular deposits across several cell walls; E = black, narrow bands along the radial axis of hypodermal cells; F = regular deposition along cell walls, not across cell surfaces.

35. Margins: (0) not winged to narrowly hyaline or tuberculate; (1) winged with flat, spongy or corky wings. Note: In both *Bidens* and *Coreopsis* a number of species have flat or corky achene margins. In some species of *Bidens*, the margins are covered with narrow hyaline tissue or the fused bases of the twin hairs may again be joined to each other creating a wing-like structure on the margin. The marginal thickenings and wings are made up of sclerified parenchyma that vary in size from short concentric to long columnar types. Often the sclerified parenchyma forms an easily detachable cover on the pericarp and it may also form globular or peg-like (verrucose) projections from the achene surface.

Pappus. In describing the structure of the Composite achene pappus, Small (1919: 77-80) recognized setose, paleaceous and aristate types. Although a seta is not defined, it appears that he used this term to refer to the individual cells making up the pappus. But he also used it in a different sense. He defined a scabrid seta as 'composed of uniseriate rows of cells fused together'. Small defined an arista as 'a thick, more or less ridged structure'. Both *Bidens* and *Coreopsis* are described by Small (1919: 80) as having 'barbato-aristate' pappus with the 'bristles projecting downwards in *Bidens*, or upwards as in *Coreopsis*'. The acute end of the seta is referred to as a bristle. From these statements and definitions, it appears that the difference between setose and aristate pappi lies in the way the cells fuse to each other, *i.e.* in the aristate pappus, the cells 'fuse in a clump' rather than laterally forming a file of cells.

The structure of the pappus in *Bidens* and *Coreopsis* was discussed in a previous article (Mesfin Tadesse *et al.* 1995a) and it was related therein that the paleaceous type is found in *Coreopsis*. Also the type described by Small (1919: 79) as aristate is found in *Coreopsis* sect. *Eublepharis* (cf. Mesfin Tadesse *et al.* 1995a). These terms (*i.e.*, seta, arista, awn, bristle) have been loosely utilized in the literature in reference to the achene pappus in *Bidens* and *Coreopsis*. As discussed in Mesfin Tadesse *et al.* (1995a), the cells making up the pappi are sclerotic parenchyma with different degrees of cell wall thickness and fusion. Those at the centre of the pappus (the shaft) are cylindrical and those toward the periphery more elliptic, oblong or oblong-lanceolate. Those that project from the sides are linear with sharp pointed apices. The shaft may be composed of few to many rows of cylindrical cells. One difference between *Bidens* and *Coreopsis* appears to lie in the composition of the pappus rather than in its gross morphology. In *Bidens* and *Coreopsis* sect. *Pseudoagarista*, the shaft is composed of many rows of cells and in cross-section it is circular or triquetrous. In *Coreopsis* sect. *Coreopsis*, *Pugiopappus*, etc., the shaft is absent or composed of few rows of cells with flat or star-shaped uniseriate wings.

36. Nature: (0) scale-like or paleaceous; (1) setaceous.
 37. Outline in cross-section: (0) cylindrical; (1) triquetrous, flat or star-shaped.
 38. Morphology: (0) multi-layered and fibrous; (1) unilayered and parenchymatous.
 39. Plane: (0) 3-angled at least at base; (1) flat.
 40. Number: (0) 2, rarely 3; (1) 3-5, rarely 2 or 5. Note: In *Bidens*, the number of pappi is related to the shape of the achene. Dorsiventrally flattened achenes commonly have 2 pappus aristae while the quadrangular achenes have 4-5 retrorsely directed pappus aristae. Species with the later type of pappus are predominantly annual herbs.
 41. Relative size: (0) one-half to exceeding achenes; (1) up to one-half; (2) absent to up to 1/3.
 42. Barb direction on pappus: (0) antrorse or nude; (1) retrorse.
 43. Barb size: (0) long & flexuous; (1) short & rigid or absent.
 44. Chromosome number based on: (0) 13; (1) 10, 11 or 12; (2) 16, 17, 18 or 21.
 45. Width of os of pollen: (0) 8.3-11.8; (1) 1.1-5.8.