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Implications of morphological phylogenetics for the placement of the genera *Adenocaulon* and *Eriachaenium* (Asteraceae)

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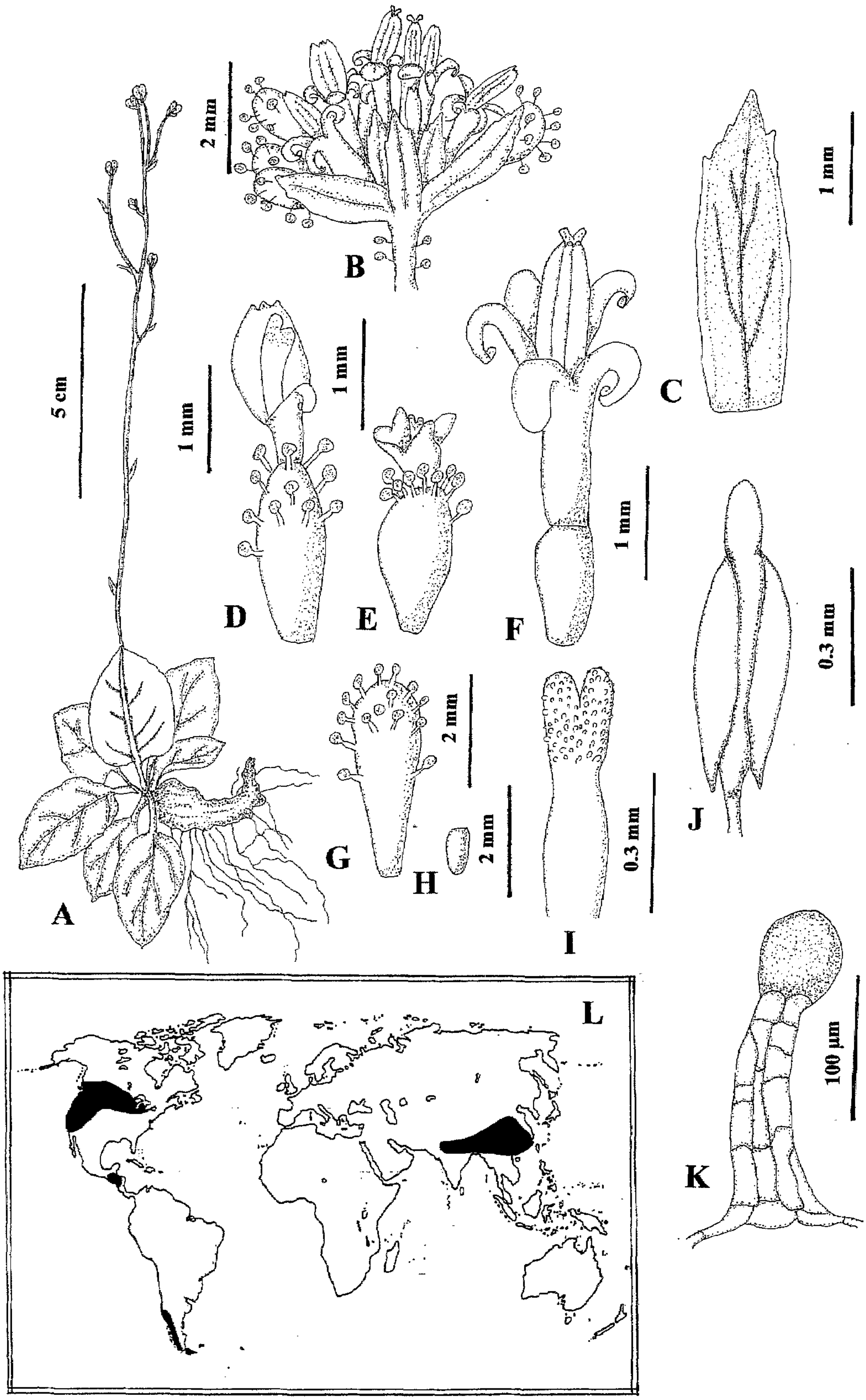
Abstract. *Adenocaulon* and *Eriachaenium* are two problematic genera because their tribal and subfamilial placement in Asteraceae is uncertain. Previous cladistic analyses based on molecular data undertaken to analyze the relationships within Asteraceae, place *Adenocaulon* in the tribe Mutisieae (Cichorioideae). This paper investigates cladistic relationships among *Adenocaulon* and *Eriachaenium* and tribes of subfamilies Cichorioideae and Asteroideae using morphological data. Thirty-eight characters were scored across 52 genera selected as exemplar taxa to represent the current classification system. In the analysis (one tree, length = 86, c.i. = 0.55, r.i. = 0.64) *Adenocaulon* and *Eriachaenium* are sister taxa and appear as an isolated clade nested in Cichorioideae. A new, tentative position among the tribes of the paraphyletic Cichorioideae is proposed for these two isolated genera.

Key words: Asteraceae, Cichorioideae, *Adenocaulon, Eriachaenium*, problematic genera, morphology, phylogenetic analysis.

Adenocaulon (Fig. 1), includes five species (*A. bicolor* Hook., *A. chilense* Less., *A. himalaicum* Edgew., *A. lyratum* S. F. Blake, and *A. nepalense* M. Bittmann), of perennial herbs with a disjunct distribution occurring in the temperate forests of Argentina and Chile in South America, in Guatemala and México, in the northern United States and southeastern Canada, and in northern India, Nepal, China, Japan, Korea and the Amur Region and Primorje Province (southern Russia) (Bittmann 1990a). It grows in moist forests, in the shade of *Nothofagus*, *Pinus* and *Quercus*. *Eriachaenium* (Fig. 2) includes only one species, *E. magellanicum* Sch. Bip., which is a dwarf perennial herb, endemic to Patagonia in Chile and Argentina (Cabrera 1971a, Moore 1983). It grows in mud, sand and pebbles along the coast, estuaries and saline lakes (Moore 1983).

Adenocaulon and *Eriachaenium* are two problematic genera with uncertain tribal and subfamilial placement. Both genera are in many respects so different from any other genus of Asteraceae, that they have been described and tentatively placed in several tribes belonging either to the subfamily Cichorioideae or to subfamily Asteroideae (Table 1).

The reason for this confusion is that *Adenocaulon* and *Eriachaenium* present some characters that link them to Cichorioideae (e.g. disc florets deeply lobed, anthers caudate, pollen wall ecaveate), whereas other characters are typical of Asteroideae (e.g. capitula disciform and heterogamous, anthers much smaller than in Cichorioideae, anther appendage basally constricted). As a consequence, their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generic relationships have been disputed by numerous workers (see Table 1) throughout the taxonomic history of these taxa.

Within Asteroideae it was postulated that the two genera might be grouped together as a distinct subtribe in the Anthemideae (Stix 1960, Leins 1968, Skvarla et al. 1977). Turner in Skvarla et al. (1977) showed that the white coloured rays, floral morphology, and habit indicate that *Adenocaulon* is close to Anthemideae. Furthermore, *Adenocaulon* and/or *Eriachaenium* were placed (see Table 1) in Calenduleae by the short branches of the style; in Heliantheae by the heterogamous capitula with disc florets functionally male (in the current classification these are characters present only in some subtribes of Heliantheae); in Inuleae by the caudate anthers and the style pilose below the branches bifurcation; and in Senecioneae by the heterogamous capitula with 1–2-seriate involucre. The hypothesis that *Adenocaulon* and *Eriachaenium,* as two distinct genera of Asteroideae, are a separate tribe or subtribe was postulated by Rydberg (1917), who created the tribe Adenocauleae with its only genus *Adenocaulon*, and by Cabrera (1961) who classified *Adenocaulon* and *Eriachaenium* in the subtribe Adenocaulinae of Inuleae. All other authors (Bittmann 1990b, Bremer 1994, Jansen and Kim 1996, Maximova 1999) treated these genera as cichorioid, relating them to Cardueae by the anatomy of the cypselas (Maximova 1999; only for *Adenocaulon*), and to tribe Mutisieae.

However, there is not yet total agreement to which subtribe of Mutisieae they belong. Bittmann (1990b) placed *Adenocaulon* close to the subtribe Gochnatiinae, suggesting a resemblance to *Ainsliaea*, *Onoseris*, and *Stenopadus*. Bremer (1994) provisionally classified *Adenocaulon* and *Eriachaenium* in the Mutisieae-Nassauviinae mainly based on their rounded style hairs. Finally, chloroplast DNA phylogenetic analyses (gene sequences of *ndh*F) led to placement of *Adenocaulon* as the sister taxa of *Mutisia*, a genus of the subtribe Mutisiinae (Jansen and Kim 1996) with low bootstrap support, and in the subtribe Nassauviinae (Jansen, pers. com.). Jansen and Kim (1996) pointed out that additional sampling of this tribe is needed to determine accurately the generic affinities of *Adenocaulon* in the Mutisieae.

Adenocaulon and *Eriachaenium*, however, are so different from any genera of Gochnatiinae, Nassauviinae or Mutisiinae, that their morphology seems to dispute a relationship with Mutisieae. The characters used to link *Adenocaulon* and *Eriachaenium* to Mutisieae are: (1) bilabiate corollas (Ornduff et al. 1967, Bittmann 1990b, Bremer 1994); (2) anthers with short tails (Robinson and Brettell 1973a, Bittmann 1990b, Bremer 1994); (3) thickened apical appendage (Bremer 1994); (4) anthemoid (ecaveate) pollen (Ornduff et al. 1967, Robinson and Brettell 1973a, Bittmann 1990b, Bremer 1994); (5) obtuse-rounded style hairs (Bremer 1994); (6) testa epidermis type (Grau 1980); and (7) chromosome number $n = 23$ (Ornduff et al. 1967, Bittmann 1990b). Some of these characters merit brief comment.

Mutisieae are traditionally characterized by their bilabiate corollas, i.e. with an external 3-dentate lip and an internal 2-cleft lip (or corolla 3 + 2). But such corollas are not present in all genera of Mutisieae (e.g. *Dinoseris*, *Gochnatia*, *Stenopadus*), and bilabiate corollas are also present in genera other than Mutisieae, such as *Anacyclus* in Anthemideae, *Heterolepis* in Arctoteae, *Plagiocheilus,* in Astereae, *Mikania* (Cerana and Ariza Espinar 1998) in Eupatorieae. Pseudobilabiate corollas like those of some species of *Adenocaulon*, (3 + 1) are not very common in Mutisieae. *Eriachaenium* lacks bilabiate or pseudobilabi-

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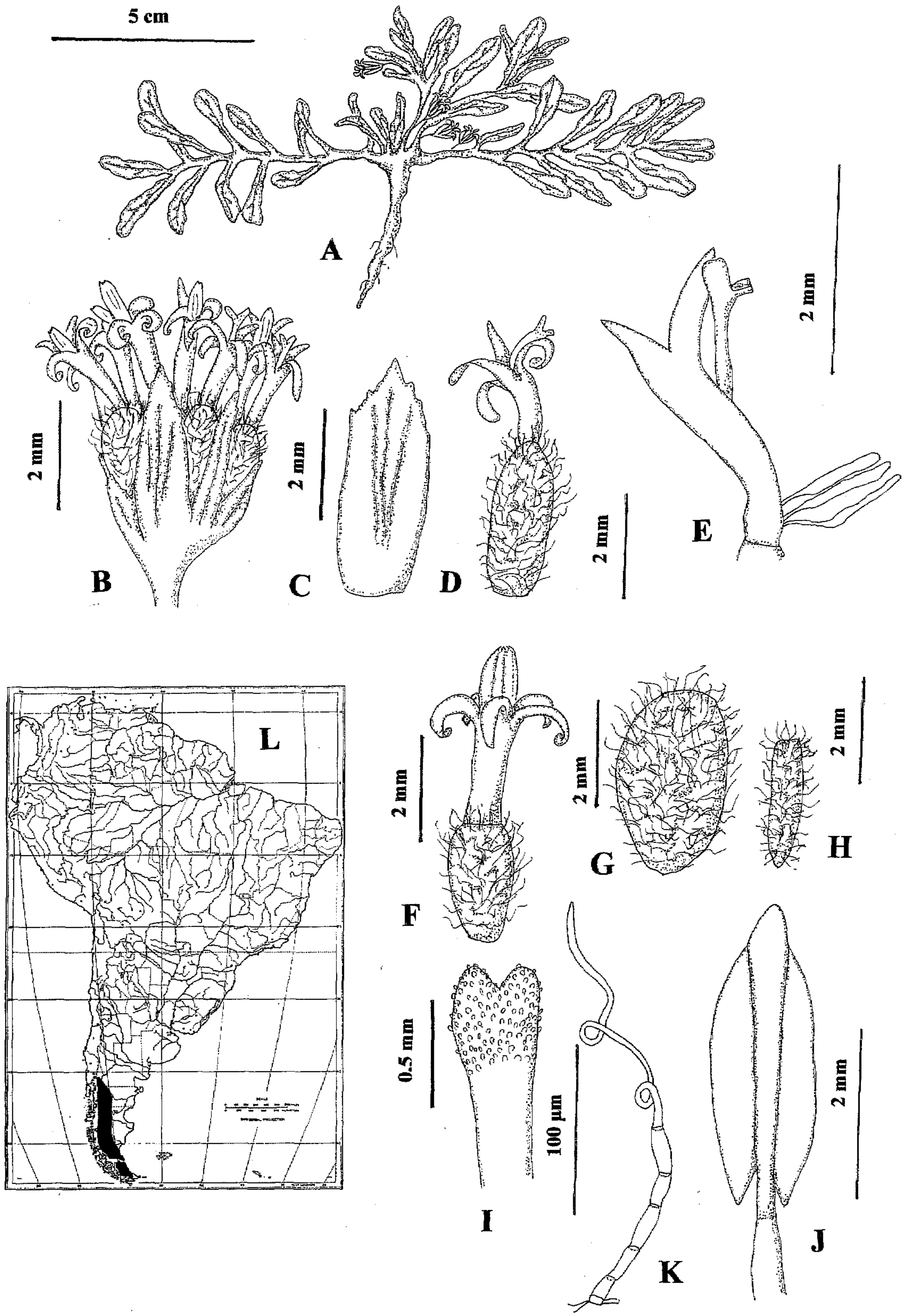
Fig. 1. Diagnostic features of *Adenocaulon*. **A** habit; **B** capitulum; **C** involucral bract; **D–E** ray florets; **F** disc floret; **G** ray cypsela; **H** disc cypsela; **I** upper part of style; **J** stamen; **K** cypsela hair multiseriate capital glandular; **L** distribution. (*A. chilense*: **A** LP *s.n. ex* LPS *16554*; **B–D, F** *Cabrera* et al. *23066* LP; **G–H** *Ricardi* et al. *1983* LP. *A. bicolor*: **E** *Hedgcock s.n.* LP, **I–K** *Morrison 121* LP)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ate corollas. The anthers in Mutisieae have long, conspicuous, sometimes laciniate tails, very different to the short anther tails of *Adenocaulon* and *Eriachaenium*. The only genera with short tails, or entirely absent tails, are currently placed in subfamily Barnadesioideae. Ecaveate pollen is typical of Mutisieae, but it is also present in Anthemideae and most cichorioid tribes (Cardueae, Lactuceae, Liabeae, Vernonieae; Skvarla et al. 1977). Blackmore et al. (1984) showed the distribution of ecaveate pollen in Cichorioideae to be complicated and in need of detailed reinterpretation. Chromosome numbers of $n = 23$ are present in Mutisieae, but also in many genera of other tribes [e.g. *Bidens*, *Melampodium* (Heliantheae), *Senecio* (Senecioneae)].

Another question that has not been clearly addressed since Cabrera (1961) placed both genera in the subtribe Adenocaulinae (tribe Inuleae), is whether *Adenocaulon* and *Eriachaenium* are closely related taxa.

This paper presents a cladistic analysis that includes *Adenocaulon*, *Eriachaenium* and the tribes of Cichorioideae and Asteroideae, based on morphological characters. Although molecular data are an important tool for assessing the phylogeny of taxa, the morphology has a profound contribution to make in the reconstruction of phylogeny. A diversity of approaches, be they molecular and morphological, can contribute to solving the taxonomic position of taxa, such as *Adenocaulon* and *Eriachaenium*.

The objectives here address the following questions:

(1) Are *Adenocaulon* and *Eriachaenium* closely related?

(2) To which tribe or tribes (and thus subfamily) are both genera more closely related? Or, are they two isolated genera within Asteraceae?

Materials and methods

Taxa. Asteraceae currently comprises three subfamilies: Barnadesioideae, Cichorioideae, and Asteroideae (Bremer 1994). Barnadesioideae, with its characteristic axillary spines, barnadesioid hairs in corollas, pappus and cypselas, and the absence of a large chloroplast DNA inversion, constitutes the sister group of Cichorioideae and Asteroideae (see outgroup selection). Therefore, the terminal taxa for the analysis were the genera *Adenocaulon* (Fig. 1), *Eriachaenium* (Fig. 2), the tribes of Cichorioideae, i.e. Arctoteae, Cardueae, Lactuceae, Liabeae, Mutisieae, and Vernonieae, and the tribes of Asteroideae, i.e. Anthemideae, Astereae, Calenduleae, Eupatorieae, Gnaphalieae, Helenieae, Heliantheae, Inuleae, Plucheeae, and Senecioneae (Bremer 1994). The synapomorphies of the group Cichorioideae-Asteroideae are: bristly pappus, twin hairs on cypselas, and chloroplast DNA inversion (Bremer 1987, 1996). *Adenocaulon* is monophyletic defined by the disciform, heterogamous capitula, dimorphic cypselas, and glandular and multiseriate cypsela hairs. Genera belonging to the different tribes were selected to represent the current tribal classification (Bremer 1994) within the family. Fifty-two genera, belonging to the three subfamilies of Asteraceae, represented by 65 species (one to four species per genus), were selected (see Appendix I) using the following criteria: (a) genera well studied morphologically; (b) genera representing the currently recognized tribes (e.g. *Calendula* for Calenduleae, *Senecio* for Senecioneae, *Pluchea* for Plucheeae); (c) genera representing the main morphological variation within a tribe (e.g. genera of Gochnatiinae, Mutisiinae and Nassauviinae for Mutisieae).

Outgroup selection. The cladogram was rooted by determining primitive character states by the outgroup comparison method (Donoghue and Cantino 1984, Maddison et al. 1984). Because the sister group relationship of subfamily Barnadesioideae with the rest of the Asteraceae was well established (Bremer 1987, Jansen and Palmer 1987, Bremer and Jansen 1992, Bremer et al. 1992,

Fig. 2. Diagnostic features of *Eriachaenium magellanicum*. **A** habit; **B** capitulum; **C** involucral bract; **D** ray floret; **E** ray floret opened showing the staminodes; **F** disc floret; **G** ray cypsela; **H** disc cypsela; **I** upper part of style; **J** stamen; **K** cypsela hair flagellate filiform; **L** distribution. (**A** *Birabén and Birabén 242* LP; **B–F I–K** *Sleumer 908* LP; **G–H** LP *s.n. ex* LPS *13745*)

Table 1. Main references of the taxonomic history of *Adenocaulon* and *Eriachaenium* to show the fluctuating placement of these genera within different tribes and even subfamilies of Asteraceae. (1) = authors that included or related *Adenocaulon* and/or *Eriachaenium* to a particular tribe; (2) = authors that excluded *Adenocaulon* and/or *Eriachaenium* from a particular tribe

		Subfamily Cichorioideae		Subfamily Asteroideae					
Tribes		Cardueae	Mutisieae	Adenocauleae	Anthemidae	Calenduleae	Heliantheae	Inuleae	Senecioneae
Adenocaulon	(1)	Maximova 1999	Ornduff et al. 1967, Nordenstam 1977, Bittmann 1990b, Bremer 1994, Jansen and Kim 1996	Rydberg 1917	Stix 1960, Leins 1968, Skvarla et al. 1977	–	Bentham 1873, Gardner 1977	Gray 1873, Hoffmann 1894, Britton and Brown 1943, Cabrera 1961, 1971a, Muñoz Pizarro 1966, Moore 1983	Cronquist 1955, Wagenitz 1964, Morton 1978
	(2)	–	Cabrera 1977, Hansen 1991a	–	–	–	–	Merxmüller et al. 1977, Anderberg 1989, 1991	Nordenstam 1977
Eriachaenium	(1)	–	Robinson and Brettell 1973a, Bremer 1987, 1994, Hansen 1991a	–	Skvarla et al. 1977	S. Bipontinus 1855, Bentham 1873, Hoffmann 1894	–	Cabrera 1961, 1971a, Muñoz Pizarro 1966, Moore 1983	–
	(2)	–	Cabrera 1977	–	–	Norlindh 1977	–	Merxmüller et al. 1977	–

Table 2. Character and character states used for cladistic analysis of *Adenocaulon*, *Eriachaenium* and tribes of Asteraceae

Character	Character states
1. Axillary spines	Present (0) Absent (1)
2. Leaf blade	Entire (0) Dissected (1)
3. Leaf venation	Pinnate (0) Palmate (1) 3-veined (2)
4. Phyllotaxis	Alternate (0) Opposite (1)
5. Leaf margin	Not spiny (0) Spiny or spinulose (1)
6. Capitula	Non radiating (0) Radiating (1)
7. Receptacle	Epaleate (0) Paleate (1)
8. Calyculus	Absent (0) Present (1)
9. Series of involucral bracts	Three to more (0) One or two (1)
10. Involucral bract consistency	Papery to rigid (0) Herbaceous (1) Scarious in the margins (2)
11. Floret dimorphism	Absent (0) Present (1)
12. Marginal floret morphology	Tubular, bilabiate or pseudobilabiate (0) Ligulate (1) Filiform (2)
13. Marginal floret sex	Hermaphroditic (0) Female or neuter (1)
14. Tubular floret shape	Without an expanded limb (0) Differentiated into tube and limb (1)
15. Tubular floret apex	Deeply lobed (0) Shallowly lobed (1)
16. Style branches	Short (=bilobed) (0) Long (1)
17. Distribution of style sweeping hairs	Dorsally along the branches or absent (0) Crowded in a ring (1)
18. Ring of style sweeping hairs on the shaft	Absent (0) Present (1)
19. Style sweeping hairs initial position	Above the branches bifurcation (0) Below the branches bifurcation (1)
20. Style branches apex	Rounded to truncate (0) Acute (1)
21. Stigmatic surface disposition	Continuous (0) In two separate lines (1) In two apically confluent lines (2)
22. Style branches appendage	Absent (0) Present (1)
23. Anther base	Truncate (0) Auriculate (=shortly prolongued) (1) Long prolongued (2)
24. Length/width anther ratio	14–20 (0) 6.5–12 (1) 2.5–4.5 (2)
25. Apical anther appendage shape	Without a constricted base (0) With a constricted base (1)
26. Apical anther appendage glands	Absent (0) Present (1)
27. Tecae blackened	Absent (0) Present (1)
28. Pollen grain exine	Ecaveate (0) Caveate (1)
29. Pollen grain size	More than 25 μm diam (0) 18–25 μm diam (1)
30. Pollen grain surface	Psilate (0) Echinate (1) Lophate (2)
31. Pollen grain spines distribution	No pattern (0) Regular pattern (1)
32. Pollen grain exine internal organization	Unperforated (0) With foramina (1)
33. Cypsela types	Monomorphic (0) Heteromorphic (1)
34. Cypsela epicarp crystals	Absent (0) Present (1)
35. Cypsela walls	Not carbonized (0) Carbonized (1)
36. Cypsela hairs	Barnadesioid (0) Not barnadesioid (1)
37. Pappus	Villous (0) Scaly (1) Absent (2) Aristate or absent (3)
38. Laticiferous tissue	Absent (0) Present (1)

Stuessy et al. 1996), this subfamily was used to root the cladogram.

Characters. Thirty-eight characters (Table 2) from morphology and palynology were selected for the analysis. Multistate characters were treated as unordered. The data were based on examination of herbarium specimens and from floristic and revisionary studies (see Appendix I). Information regarding characters provided in treatments of Asteraceae as a whole were also taken into consideration: Small 1919; Cronquist 1955; Cabrera 1971a, 1974, 1978; Carlquist 1976; Heywood et al. (eds.) 1977; Bremer 1987, 1994; Jansen et al. 1991; Karis et al. 1992; Hind et al. (eds.) 1996.

Floral parts were dissected and studied after boiling in water. Drawings were made by the author.

The characters used in this analysis are as follows:

1. Axillary spines. Most Barnadesioideae have peculiar axillary spines unknown in other Asteraceae.

2. Leaf blade. The degree of the leaf blade partition is highly variable throughout the tribes. There are however, tribes such as Anthemideae and Cardueae with genera showing predominantly dissected leaves.

3. Leaf venation. Many genera of Asteraceae have pinnately veined leaves. Some tribes are characterized by their palmately veined leaves (Liabeae), and 3-veined leaves (Eupatorieae, Helenieae, Heliantheae). Genera within Barnadesioideae have pinnately veined leaves (*Barnadesia*) and 3-veined leaves (*Chuquiraga*).

4. Phyllotaxis. Most Asteraceae have alternate leaves, although Eupatorieae, Helenieae, Heliantheae and Liabeae are characterized by genera with opposite leaves. During early ontogeny of some alternate-leaved groups often there are opposite leaves at the first nodes preceding the alternate leaves, which develop at later stages (Bremer 1987). Where taxa show variation in the leaf position along the stem, i.e. alternate to opposite, they were scored as being opposite. In taxa with rosulate leaves (e.g. *Adenocaulon*; Fig. 1A) the character was coded as question mark.

5. Leaf margin. Spiny leaf margins are present in Cardueae, whereas spinulose leaves are common in Lactuceae. Although many genera of Arctoteae are spiny, *Arctotis* (here analyzed) is unarmed and therefore coded as not spiny.

6. Capitula. Capitula with non-radiating florets include disciform and discoid ones. The disciform capitula have at least two morphologies of florets (e.g. filiform at the margins, and tubular at the center of the capitula) whereas the discoid capitula have all the florets similar (Bremer 1994). Capitula with radiating florets generally have ligulate marginal florets as Arctoteae, Astereae, Calenduleae, and Liabeae. It is common to find tribes with one or the other type: Anthemideae, Helenieae, Heliantheae, Inuleae, Mutisieae, Senecioneae. Barnadesioideae is also variable for this character (radiating in *Barnadesia*, non-radiating in *Chuquiraga*).

7. Receptacle. The genera of Heliantheae studied here have paleate receptacles, while those of Anthemideae have paleate (*Anthemis*) or epaleate (*Soliva*) receptacles.

8. Calyculus. The presence of an outer row of smaller involucral bracts characterizes Senecioneae. The calyculus can also be present in some genera of Helenieae (*Pectis*, *Porophyllum*), and Heliantheae (*Bidens*).

9. Series of involucral bracts. The pluriseriate involucre (three to more rows of bracts) predominates in the genera under study. Involucres 1–2-seriate were found in Calenduleae, Helenieae, Senecioneae, *Adenocaulon* (Fig. 1B), and *Eriachaenium* (Fig. 2B).

10. Involucral bract consistency. Although this character can be variable among genera, some taxa are characterized by their herbaceous involucre (Lactuceae, *Eriachaenium;* Fig. 2C), or bracts with scarious margins (Anthemideae, Calenduleae, *Adenocaulon*; Fig. 1C).

11. Floret dimorphism. Capitula with the same type of corolla in the margin and in the center were found in Cardueae (pseudobilabiate), Eupatorieae (tubular), Lactuceae (ligulate), and Vernonieae (tubular). Floret dimorphism is found in Anthemideae (marginal florets narrowly tubular, ligulate or apetalous, disc florets tubular), Astereae (ligulate and tubular), Arctoteae (ligulate and tubular), Calenduleae (ligulate and tubular), Gnaphalieae (filiform and tubular; ligulate in some genera of Relhaniinae), Heliantheae (marginal florets ligulate or narrowly tubular and 3-lobed, disc florets tubular), Inuleae (ligulate and tubular, except in *Inula conyza* with all florets tubular), Liabeae (ligulate and tubular), and Plucheeae (filiform and tubular). *Adenocaulon* and *Eriachaenium* are also dimorphic. *Adenocaulon* has marginal florets pseudobilabiate (3 + 1; occasionally 3 + 2) or tubular (4–5-lobed) (Fig. 1D–E), and disc florets tubular 5-lobed (Fig. 1F). *Eriachaenium* has florets tubular 4-lobed in the margin (Fig. 2D) and disc florets tubular 5-lobed

(Fig. 2F). Barnadesioideae is polymorphic for this character.

12. Marginal floret morphology. Bilabiate florets (outer lip 3-dentate, inner lip 2-dentate, or 3 + 2) are found in some genera of Mutisieae (e.g. *Mutisia, Nassauvia, Trixis*), whereas other (e.g. *Gochnatia*) have tubular florets. Pseudobilabiate florets (4 + 1; 3 + 1) are frequently found in other tribes (Gardner 1977), and in some species of *Adenocaulon*. Since it was not possible to find any taxa with exclusively bilabiate or pseudobilabiate marginal florets, these two types were coded together with the tubular florets. Ligulate (3- or 5-lobed) and filiform marginal florets, on the other hand, are more reliable at the tribal level as described in character 11, and they were coded separately. Tubular and pseudobilabiate florets are present in Barnadesioideae (*Barnadesia* and *Chuquiraga*, respectively).

13. Marginal floret sex. Throughout the taxa investigated, it was found that those with bilabiate, pseudobilabiate, tubular, and ligulate 5-lobed marginal florets (Lactuceae) are hermaphroditic. The only exceptions were the tubular and/or pseudobilabiate florets of Anthemideae, *Adenocaulon*, and *Eriachaenium* that are female or neuter (with staminodes in *Eriachaenium*; Fig. 2E). The tribes with filiform or ligulate 3-lobed marginal florets are female.

14. Tubular floret shape. Tubular florets (marginal and/or disc florets) can be differentiated into a narrow basal tube and an expanded upper limb in Anthemideae, Cardueae, Helenieae, Heliantheae, and Senecioneae. In the remaining taxa the corolla is gradually widened toward the apex.

15. Tubular floret apex. Presence of deeply lobed tubular florets is one character that distinguishes subfamily Cichorioideae from subfamily Asteroideae. The only exception found here is Eupatorieae, which have both types. *Adenocaulon* and *Eriachaenium* possess tubular corollas that are deeply lobed (Figs. 1F, 2F).

16. Style branches. The style in Asteraceae is generally divided at the top into two lobes or two branches which are stigmatic on the inner face and bears sweeping hairs on the outer face and at the tip. This arrangement is associated with the mode of the pollen presentation in the family. The anthers ripen before the stigmas, and discharge their pollen into the tube formed by the cylinder of fused anthers. At this stage, the style is short and the style branches are pressed together. The style then elongates up the anther tube, from which the pollen is swept by the sweeping hairs of the style branches and presented at the apex of the anther tube to any visiting pollinator. Only later do the style branches separate to expose the stigmatic surfaces. In this study, the style branches were examined only in the central florets of the capitulum to avoid the variation that sometimes exists in the length of the style branches between the ray and disc florets in taxa with floral dimorphism. Bilobed styles were found in Arctoteae, Calenduleae, part of Mutisieae, *Adenocaulon* (Fig. 1I), and *Eriachaenium* (Fig. 2I).

17. Distribution of style sweeping hairs. Sweeping hairs can be sparsely distributed on the style branches, crowded in a ring, they can be absent (e.g. Barnadesioideae), or they are reduced to small punctiform collecting papillae (Arctoteae; Norlindh 1977). *Adenocaulon* and *Eriachaenium* have dorsally distributed sweeping hairs (Figs. 1I, 2I).

18. Ring of style sweeping hairs on the shaft. Arctoteae and Cardueae are recongized by having their styles divided into a glabrous, filiform, lower part, and a shorter and thicker upper part covered by hairs or papillae with a ring of sweeping hairs below the style branches. In spite of this resemblance, recent analysis (Bremer 1994) have shown that these two tribes are not close relatives.

19. Style sweeping hairs initial position. Some taxa have sweeping hairs distributed below the style bifurcation and extending toward the apex (Arctoteae, Cardueae, Lactuceae, Liabeae, Vernonieae, *Adenocaulon* and *Eriachaenium*). Others, have sweeping hairs only above the style bifurcation. Taxa with an apical ring of sweeping hairs were included in the latter category.

20. Style branches apex. Acute branch tips were found in Astereae, Lactuceae, Liabeae, and Vernonieae. The other taxa have style branches with rounded tips.

21. Stigmatic surface disposition. Arctoteae, Cardueae, Lactuceae, Liabeae, Mutisieae, and Vernonieae have styles with the stigmatic area covering the whole surface inside the style branches. Two stigmatic lines are present in Anthemideae, Astereae, Calenduleae, Eupatorieae, Gnaphalieae, Helenieae, Heliantheae, and Senecioneae. In Inuleae and Plucheeae, these lines are fused at the top (Anderberg 1989). The stigmatic papillae cover all the inner style branches in *Adenocaulon* and *Eriachaenium* (Bittmann 1990a).

22. Style branches appendage. Tribes with an apical sterile portion on the tip of the style branches include Astereae, Eupatorieae, Helenieae, and Heliantheae.

23. Anther base. A distinction is usually made to differentiate a fertile prolongation of the

anthers (anthers calcarate) or a sterile prolongation of the anthers (anthers caudate) (Robinson 1983; Bremer 1987, 1994). In this analysis the whole anther unit was considered as prolonged or not. The base of the anthers may be truncate or rounded (Anthemideae, Arctoteae, Astereae, Eupatorieae, Helenieae, Heliantheae, and Senecioneae), auriculate [Calenduleae, Lactuceae, Liabeae, Vernonieae, *Adenocaulon* (Fig. 1J), *Eriachaenium* (Fig. 2J)], or long prolonged (Cardueae, Mutisieae). Other taxa are polymorphic for this character, among them Barnadesioideae (not prolonged in *Barnadesia*, long prolonged in *Chuquiraga*).

24. Length/width anther ratio. A character to distinguish Cichorioideae from Asteroideae is the length of the anthers, i.e. longer in Cichorioideae. It was observed throughout the tribes that taxa with long capitula and florets also have long anthers, so to properly evaluate this character, the length/width ratio of the anther was measured. The length was measured from the anther base to the tip of the apical appendage, and the width was measured in the middle of the anther. Three well – differentiated categories were found: a large ratio of 14–20 (Barnadesioideae, Mutisieae, Cardueae), a small ratio of 2.5–4.5 (Anthemideae, *Adenocaulon*, *Eriachaenium*), and an intermediate ratio of 6.5–12 (the remaining taxa).

25. Apical anther appendage shape. The apical appendage of the anther was traditionally described as a flat continuation of the thecae in Cichorioideae, and basally constricted and demarcated from the thecae in Asteroideae. Exceptions were found in Arctoteae (appendage constricted), and in Gnaphalieae, Inuleae, and Plucheeae (appendage not constricted).

26. Apical anther appendage glands. Glanduliferous anther appendages have been found in Heliantheae and Vernonieae (Bremer 1987, 1994; Robinson 1996a, b).

27. Thecae blackened. Dark anthers were only found in Heliantheae. This pigmentation is apparently located in the epidermis of the thecae (Bremer 1994).

28. Pollen grain exine. Asteroideae is usually considered as having pollen grains caveate, i.e. with the exine columellae physically separated from the foot layer, with only the exception of Anthemideae. Cichorioideae, in contrast, has pollen ecaveate (Skvarla et al. 1977). This distinction has been relevant to the tribal placement of *Adenocaulon* and *Eriachaenium* due to their ecaveate pollen (Robinson and Brettell 1973a, Skvarla et al. 1977, Bittmann 1990a). Skvarla et al. (1977) favored a position in the asteroid Anthemideae for both taxa, whereas Bittmann (1990a; only for *Adenocaulon*), and Bremer (1994) suggested a relation with the cichorioid Mutisieae. Bittmann (1990a) also indicated that the non-caveat exines with an inner row of columellae found in the pollen of *Adenocaulon bicolor* and *A. chilense* is characteristic of Mutisieae. There are, however, other cichorioid tribes (e.g. Cardueae) with this pollen characteristics. Barnadesioideae is polymorphic for this character (*Barnadesia* with pollen caveate, *Chuquiraga* with pollen ecaveate; Skvarla et al. 1977; Hansen 1991a, b).

29. Pollen grain size. Pollen grains smaller (18–25 μm diam) in comparison with the rest of the family were described in Eupatorieae (Robinson and King 1977, Bolick 1991).

30. Pollen grain surface. The three major patterns used in this study follow Skvarla et al. (1977), i.e. smooth, echinate, and lophate. Mutisieae (Wodehouse 1929a, b; Skvarla et al. 1977; Markgraf and D'Antoni 1978; Hansen 1991b) and *Artemisia* (Anthemideae; Markgraf and D'Antoni 1978) have smooth pollen covered by small granules. Lophate pollen is present in Lactuceae and Vernonieae, and echinate pollen in the remaining taxa. Although both *Adenocaulon* and *Eriachaenium* have been related to Mutisieae by their pollen surface, observations of the three taxa led to considering their pollen as different, i.e. smooth in Mutisieae and echinate in *Adenocaulon* and *Eriachaenium*. This character is polymorphic in Barnadesioideae (Urtubey and Tellería 1998).

31. Pollen grain spines distribution. The spines of the echinolophate pollen in Vernonieae are arranged in a regular pattern (Bremer 1994).

32. Pollen grain exine internal organization. The columellae of caveate exines are solid or with perforations (internal foramina). These perforations appear in Astereae, Calenduleae, Eupatorieae, Helenieae, and Heliantheae (Skvarla et al. 1977).

33. Cypsela types. Most taxa investigated have the same cypsela morphology in the center (disc cypselas) and in the margin (ray cypselas) of the capitulum; occasionally there are minimal differences in size. A conspicuous dimorphism, however, has been found in Calenduleae, part of Anthemideae (*Soliva*), and *Adenocaulon*. *Adenocaulon* displays differences, even from the floral stage, between the ray and the disc cypselas, i.e., the ray cypselas are bigger, pubescent, and with blackened walls (Fig. 1G–H). *Eriachaenium* shows differences only in the size of its ray and disc

cypselas (Fig. 2G–H) due to the lack of development of the ovaries in the disc florets. Therefore, it was considered that *Eriachaenium* has homomorphic cypselas.

34. Cypsela epicarp crystals. Crystals of calcium oxalate were described for the cypselas of Liabeae (elongate or subquadrate raphids; Robinson 1983), and Inuleae (one large crystal; Bremer 1994).

35. Cypsela walls. Eupatorieae, Helenieae, and Heliantheae showed blackened or "carbonized" cypselas due to the presence of phytomelanin in their walls (Robinson 1996a). Blackened walls were found in the ray cypselas of *Adenocaulon* (the same coloration is present in the head of its glandular hairs). Pending further investigations to demonstrate if this is caused by phytomelanin, the cypselas in *Adenocaulon* were coded as not carbonized in this study.

36. Cypsela Hairs. One of the morphologically distinctive features of Barnadesioideae is the presence of "barnadesioid hairs" in vegetative and reproductive parts. In these hairs one apical cell is very long, tapering above with thick walls, and one basal cell is broader than long, with thickened walls, articulated to a epidermal cell (Katinas and Stuessy 1997). The rest of Asteraceae completely lack this type of hair, but the cypselas are generally covered by twin hairs (two triangular or rectangular basal cells, one sometimes reduced, and two cylindrical or elliptical hair cells, equal or subequal in length, generally meeting at their tips; Hess 1938, Freire and Katinas 1995). Some taxa develop other types of hairs, e.g. *Adenocaulon* with multiseriate capital glandular hairs (Fig. 1K), and *Eriachaenium* with flagellate filiform hairs (Fig. 2K) (Ramayya 1962). As the pubescence in the cypselas is highly variable within tribes and even genera, twin and non twin hairs (including the glandular hairs) were coded under the same category in this study (as "not barnadesioid"), as a synapomorphy of Cichorioideae and Asteroideae.

37. Pappus. A villous pappus (i.e. constituted by many capillary bristles) is present in most of the investigated taxa. A pappus consisting of scales was found in the species analyzed of Arctoteae and part of Helenieae. Genera of Heliantheae exhibit an aristate pappus or an absence of it. Anthemideae, Calenduleae, *Adenocaulon* (Fig. 1G–H), and *Eriachaenium* (Fig. 2G–H) lack a pappus.

38. Laticiferous Tissue. This tissue type is characteristic of the tribes Lactuceae and Liabeae, and is present in some genera of Arctoteae and Cardueae, but not in the taxa analyzed here.

Characters excluded from the analysis. Some data were missing or uninformative at the tribal level for most taxa selected for investigation, e.g. microcharacters of the ligule (Baagøe 1977), endothecial tissue (Dormer 1962), shape of stylar sweeping hairs (Bremer 1987), anatomy of cypsela testa (Grau 1980), benzopyrans and benzofurans (Proksch and Rodríguez 1983). Although chromosome number is a character used to relate *Adenocaulon* with Mutisieae (Ornduff et al. 1967, Bittmann 1990b), it was excluded from the analysis because of the wide variation in chromosome numbers within the family Asteraceae.

Polymorphic characters. Twenty of the 38 characters were polymorphic in at least one taxon. Empirical studies suggest that polymorphic characters contain significant phylogenetic information but are more homoplastic than fixed characters (Wiens and Servedio 1997). Due to the high number of polymorphic characters used in this study that play an important role in the resulting phylogenies, they were coded as polymorphic, i.e. scoring all the character states present in the taxa under study (Platnick et al. 1991, Wiens 1995) (Table 3).

Phylogenetic analysis. Phylogenetic analysis using maximum parsimony algorithm of PAUP version 4.0 (Swofford 1999) was employed and was run on a Macintosh computer. The branch-and-bound search strategy was used to find the shortest tree(s), with the "mulTrees" option in effect that allow to know the score of the best tree(s). The program MacClade version 3.01 (Maddison and Maddison 1992) was used for examination of character distribution. The bootstrap resampling procedure (Felsenstein 1985) was conducted in PAUP to estimate support for each node; one-hundred replicates were run. In bootstrapping, characters are resampled with replacement, and the frequency by which individual groups occur in the pseudoreplicates are taken as measurement of support.

Results

The analysis from Table 3 resulted in one most parsimonious cladogram with a length of 86 steps, a consistency index of 0.55, and a retention index of 0.64. Figure 3 shows this tree with character distributions. The figure shows that *Adenocaulon* and *Eriachaenium* are

Table 3. Data matrix used in the cladistic analysis. Parentheses denote polymorphic characters. Inapplicable characters have been coded with question marks (?)

Taxon	Character state																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Barnadesioideae	0	0	(02)	0	0	(01)	0	0	0	0	(01)	0	0	0	0	0	0	0
Arctoteae	1	(01)	0	0	(01)	1	0	0	0	0	1	1	1	0	0	0	0	1
Cardueae	1	1	0	0	1	0	0	0	0	0	0	(01)	(01)	1	0	1	0	1
Lactuceae	1	(01)	0	0	1	0	0	0	0	1	0	1	0	?	?	1	0	0
Liabeae	1	0	1	1	0	1	0	0	0	0	1	1	1	(01)	0	1	0	0
Mutisieae	1	(01)	0	0	0	(01)	0	0	0	0	(01)	(01)	(01)	0	0	(01)	(01)	0
Vernonieae	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Anthemideae	1	1	0	0	0	(01)	(01)	0	0	2	1	(01)	1	1	1	1	1	0
Astereae	1	0	0	0	0	1	0	0	0	(01)	1	1	1	0	1	1	0	0
Calenduleae	1	0	0	0	0	1	0	0	1	2	1	1	1	0	1	0	1	0
Eupatorieae	1	0	2	1	0	0	0	0	(01)	0	0	0	0	(01)	0	1	0	0
Gnaphalieae	1	0	0	(01)	0	0	0	0	0	0	1	2	1	0	1	1	1	0
Helenieae	1	(01)	2	1	0	(01)	0	(01)	1	(01)	(01)	(01)	(01)	1	1	1	(01)	0
Heliantheae	1	0	2	1	0	(01)	1	(01)	(01)	(01)	1	1	1	1	1	1	1	0
Inuleae	1	(01)	0	0	0	(01)	0	0	0	0	1	(01)	1	0	1	1	0	0
Plucheeae	1	0	0	0	0	0	0	0	0	0	1	2	1	0	1	1	0	0
Senecioneae	1	(01)	0	0	0	(01)	0	1	1	(01)	(01)	(01)	(01)	1	1	1	1	0
Adenocaulon	1	0	1	?	0	0	0	0	1	2	1	0	1	0	0	0	0	0
Eriachaenium	1	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	0	0

sister taxa supported by three parallelisms [1–2 rows of involucral bracts (character 9); length/width anther ratio = 2.5–4.5 (character 24); and pappus absent (character 37)], and one reversal [style branches bilobed (character 16)]. This clade is strongly supported with a bootstrap value of 80%. Both genera appear nested in a paraphyletic Cichorioideae. The basal node of the cladogram is supported by three synapomorphies [axillary spines absent (character 1); anther base long prolonged (character 23); and cypsela hairs not barnadesioid (character 36)]. The two genera are part of a monophyletic group with Liabeae, Arctoteae, and subfamily Asteroideae, supported by two synapomorphies [floret dimorphism (character 11); and marginal florets female or neuter (character 13)].

Discussion

The cladogram of Fig. 3 shows that in spite of some morphological differences between *Adenocaulon* and *Eriachaenium* (Table 4, Figs. 1, 2), both genera are closely related as suggested by Cabrera (1961) and Skvarla et al. (1977). Other characters that are similar in *Adenocaulon* and *Eriachaenium*, not included in the cladistic analysis, are the presence of 4-lobed corollas in the marginal florets, and the prominent collar of the stamen filament. Both *Adenocaulon* and *Eriachaenium* have tubular 5-lobed disc florets but differ slightly in their marginal florets. *Adenocaulon* has corollas commonly very reduced in size, abortive, tubular 4–5-lobed, pseudobilabiate 3 + 1, and/or bilabiate 3 + 2. *Eriachaenium* has developed tubular 4-lobed marginal florets. The occurrence of tetramerous disc florets within Asteraceae has been reported as relatively widespread in the family, for more than 80 genera in 13 tribes (Gardner 1977). This phenomenon, however, seems to be rare in the marginal florets of the capitulum, and could be considered as indicating strong affinities between these taxa.

Table 3 (continued)

19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
0	0	0	0	(02)	0	0	0	0	(01)	0	(02)	0	0	0	0	0	0	0	0
1	0	0	0	0	1	1	0	0	1	0	1	0	0	0	0	0	1	1	0
1	0	0	0	2	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0
1	1	0	0	1	1	0	0	0	0	0	2	0	0	0	0	0	1	0	1
1	1	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	1	0	1
0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
1	1	0	0	1	1	0	1	0	0	0	2	1	0	0	0	0	1	0	0
0	0	1	0	2	1	0	0	0	0	0	(01)	0	0	(01)	0	0	1	2	0
0	1	1	1	0	1	1	0	0	1	0	1	0	1	0	0	0	1	0	0
0	0	1	0	1	1	1	0	0	1	0	1	0	1	1	0	0	?	2	0
0	0	1	1	0	1	1	0	0	1	1	1	0	1	0	0	1	1	0	0
0	0	1	0	0	1	0	0	0	1	0	1	0	0	0	0	0	1	0	0
0	(01)	1	1	0	1	1	0	0	1	0	1	0	1	0	0	1	1	(01)	0
0	(01)	(01)	1	0	1	1	1	1	1	0	1	0	1	0	0	1	1	3	0
0	0	2	0	(02)	1	0	0	0	1	0	1	0	0	0	1	0	1	0	0
0	0	2	0	(02)	1	0	0	0	1	0	1	0	0	0	0	0	1	0	0
0	0	1	0	0	1	1	0	0	1	0	1	0	0	0	0	0	1	0	0
1	0	0	0	1	2	1	0	0	0	0	1	0	0	1	0	0	1	2	0
1	0	0	0	1	2	0	0	0	0	0	1	0	0	0	0	0	1	2	0

The topology of the cladogram agrees well with other phylogenetic studies of Asteraceae (Bremer 1987, 1994; Bayer and Starr 1998; Jansen et al. 1990; Keeley and Jansen 1991; Karis et al. 1992). Cichorioideae are paraphyletic, and all the tribal relationships in the subfamily remain the same, i.e. the sequence Mutisieae, Cardueae, Lactuceae-Vernonieae, Liabeae, Arctoteae. The subfamily Asteroideae is monophyletic, and includes the monophyletic groups (Gnaphalieae (Inuleae, Plucheeae)), and (Helenieae (Eupatorieae, Heliantheae)). When studies of plant groups that have been examined by both DNA and traditional approaches indicate congruence, this congruence indicates that both approaches are important in inferring the phylogeny (Sytsma 1990). The cladogram shows also, in contrast with the molecular approach that places *Adenocaulon* in Mutisieae (Jansen and Kim 1996), that *Adenocaulon* and *Eriachaenium* are cichorioid genera but not closely related to any other tribe of the subfamily.

These results indicate that, as morphologically problematical genera, *Adenocaulon* and *Eriachaenium* do not fit perfectly in any current tribe. There are many examples of "anomalous" genera that were finally positioned in tribes by morphological and/or molecular data. *Eremothamnus* and *Hoplophyllum* (also related to Mutisieae by some authors) were classified in Arctoteae (Bergqvist et al. 1955, Jansen and Kim 1996), *Ursinia* in Anthemideae (Jansen et al. 1991), and *Corymbium* in Senecioneae (Jansen and Kim 1996) on the basis of molecular data. There are cases where molecular data yielded different placement of anomalous genera, e.g. chloroplast DNA restriction site data placed *Marshallia* in Heliantheae (Watson et al. 1991) and gene sequences of *ndh*F placed this genus in Helenieae (Jansen and Kim 1996). Molecular studies also have revealed that some genera merit transfer to new tribes, e.g. the *Blepharispermum* group (*Athroisma*, *Blepharispermum*, and *Leucoblepharis*; Jansen

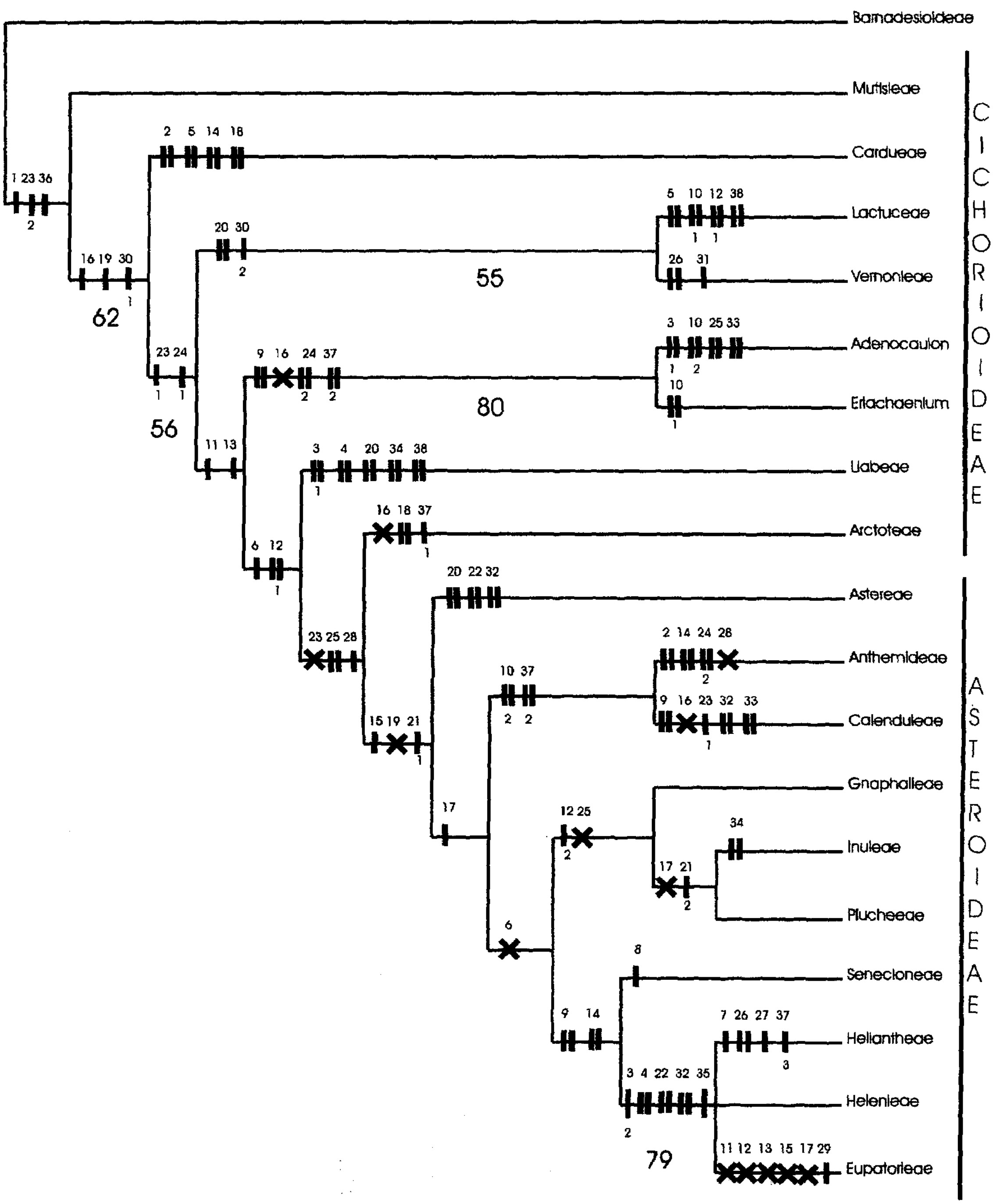

Fig. 3. Cladogram obtained in the cladistic analysis. Character state changes are superimposed on the tree; unique synapomorphies = single lines, parallelisms = double lines, and reversals = X. Numerals below the branches are bootstrap values

and Kim 1996). In other analyses, molecular data have supported morphological data, e.g. *Ursinia* was placed in the Anthemideae (Karis 1993, Jansen and Kim 1996) and *Marshallia* in Helenieae (Karis 1993, 1996). Reviews of the morphology prompted the recognition of some of these genera as forming part of distinct tribes or subtribes: Eremothamneae

Table 4. Main morphological characters that differentiate *Adenocaulon* and *Eriachaenium*

Adenocaulon	*Eriachaenium*
1. Herbs or suffrutices	1. Dwarf herbs
2. Conflorescences cymose	2. Capitula solitary
3. Involucral bracts scarious at the margins	3. Involucral bracts not scarious at the margins
4. Marginal florets tubulose or pseudobilabiate	4. Marginal florets tubulose
5. Marginal florets without staminodes	5. Marginal florets with staminodes
6. Anthers with the apical appendage constricted at the base	6. Anthers with the apical appendage not constricted at the base
7. Cypselas dimorphic	7. Cypselas homomorphic
8. Ray cypselas with multiseriate capital glandular hairs	8. Ray cypselas with flagellate filiform hairs
9. Disc cypselas glabrous or subglabrous	9. Disc cypselas lanose

(Robinson 1973), Marshalliinae (Robinson 1981), and Ursinieae (Robinson and Brettell 1973b).

Brachylaena and *Tarchonanthus*, once considered anomalous genera, represent an interesting case because their taxonomic history resembles that of *Adenocaulon* and *Eriachaenium*. *Brachylaena* and *Tarchonanthus* (Keeley and Jansen 1991) have been placed in Cichorioideae and in Asteroideae, in five different tribes. They are closely related genera that were also included in Mutisieae by pollen morphology and the fruit anatomy. Chloroplast DNA restriction site comparisons indicated that they form a distinct, isolated, monophyletic group near the base of Cichorioideae (Keeley and Jansen 1991), but were subsequently placed again in Mutisieae (Bremer 1994). Later, Jansen and Kim (1996) placed *Brachylaena* and *Tarchonanthus* for the second time in a tribe of their own, Tarchonantheae, based on *ndh*F sequences. A recent treatment based on two non-coding chloroplast sequences (Bayer et al. 2000) shows *Tarchonanthus* coming out a sister of *Gerbera*, a genus of the tribe Mutiseae.

Finally, there are genera traditionally considered asteroid, such as *Cratystylis*, that are currently placed as isolated taxa of Cichorioideae after cladistic analysis based on morphological characters (Anderberg et al. 1992).

All the genera mentioned above have been shown not to fit in any of the established tribes. They were considered as anomalous, representing plesiomorphic or autapomorphic genera within a tribe, or they were considered isolated genera in a tribe of their own.

It was suggested (Bremer 1994, Bergqvist et al. 1995) that when an isolated genus has a sister relationship to a single tribe, classification of the genus in that tribe is possible. If such isolated genera turn out to be sister groups of whole groups of tribes, a new tribe is certainly justified.

Some authors consider that the idea that all the lineages of Asteraceae traditionally worthy of tribal rank are large, consisting of at least 100 species, is no longer tenable. In this way, the process of naming new, small tribal segregates would be justified (Robinson 1994). Bryant (1994), on the other hand, pointed out that apomorphy-based circumscriptions of taxa are problematic and should be avoided. The significance of a single character in delimiting a particular clade is lost with the discovery of homoplasy in that character and can result in major changes to the content of the clade associated with the name. Cantino et al. (1997) postulated that there is no reason why the recognition of subfamilies within a family should require referring every genus to a subfamily. Orphan genera may be left loose in the family if their relationships are uncertain or if they are left over as a single-genus clade when all other genera have been grouped into subfamilies.

In the particular case of *Adenocaulon* and *Eriachaenium*, the results of this study suggest that *Adenocaulon* and *Eriachaenium* belong to Cichorioideae. Both taxa, however, cannot be placed in any of the recognized tribes. The morphological data, in contrast with the molecular data, support the hypothesis that *Adenocaulon* and *Eriachaenium* constitute an isolated phylogenetic lineage positioned within Cichorioideae. It would be premature, however, to establish a new tribe for these genera. Until paraphyletic tribes of Cichorioideae, as Mutisieae and Cardueae are resolved, it is very difficult to place genera like *Adenocaulon* and *Eriachaenium*. They could be aligned with genera split off from these tribes to form a part of a traditional tribe, or segregated to form a new tribe. In addition, further evidence from additional sampling of species within Cichorioideae, especially around the position of *Adenocaulon* and *Eriachaenium* in the cladogram, would help to resolve the placement of these genera. There are some empty spaces within Asteraceae that, like the elements in the periodic table, may be filled someday with many of today's anomalous genera.

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Appendix I. Representative specimens examined in LP and MO (Holmgren et al. 1990) for the cladistic analysis of *Adenocaulon*, *Eriachaenium* and related taxa with vouchers; the relevant literature is in brackets

Subfamily Barnadesioideae

1. *Barnadesia odorata* Griseb.: *Urtubey* et al. *27* (LP); [Urtubey 1999].
2. *Chuquiraga longiflora* (Griseb.) Hieron: *Tortorelli and Abbiatti s.n.* (LP 69064); [Ezcurra 1985].

Subfamily Cichorioideae

Tribe Arctoteae

3. *Arctium stoechadifolia* Berg: *Rodrigo 993* (LP).

Tribe Cardueae

4. *Carduus acanthoides* L.: *Cabrera 6427* (LP).
5. *Carduus thoermeri* Weinm.: *Cabrera 128* (LP).
6. *Cirsium vulgare* (Savi) Tenore: *Cabrera* et al. *22117* (LP).
7. *Cynara cardunculus* L.: *Ringuelet 320* (LP).
8. *Silybum marianum* (L.) Gaertn.: *Cabrera 100* (LP).

Tribe Lactuceae

9. *Lactuca saligna* L.: *Cabrera 201* (LP).
10. *Lactuca serriola* L.: *Cabrera and Kiesling 2006* (LP).
11. *Sonchus asper* (L.) Hill: *Clos 1754* (LP).
12. *Sonchus oleraceus* L.: *s/leg* (LP 11977).
13. *Taraxacum officinale* Weber: *Boffa 6* (LP).

Tribe Liabeae

14. *Liabum solidagineum* (Kunth) Less: *Wurdack 1114* (LP).
15. *Liabum wurdackii* Ferreyra: *Sagástegui and Collantes 4240* (LP); [Ferreyra 1965].
16. *Microliabum polimnioides* (R. E. Fries) H. Robinson: *Fabris 4536* (LP); [Robinson 1990].
17. *Munnozia hastifolia* (Poepp. et Endl.) H. Robinson et Brettell: *Cabrera and Fabris 16119* (LP).

Appendix I (continued)

Tribe Mutisieae
18. *Aphyllocladus spartioides* Wedd.: *Cabrera and Kiesling 20231* (LP).
19. *Brachyclados megalanthus* Speg.: *Cabrera 4789* (LP).
20. *Cnicothamnus lorentzii* Griseb.: *Katinas* et al. *93* (LP).
21. *Dolichlasium lagascae* D. Don: *Cabrera 17942* (LP).
22. *Gochnatia palosanto* Cabrera: *Venturi 1296* (LP); [Cabrera 1971b].
23. *Hyalis lancifolia* Baker: *Schinini 16028* (LP).
24. *Leucheria floribunda* DC.: *Ruiz Leal and Roig 15615* (LP); [Crisci 1976].
25. *Lophopappus cuneatus* R. E. Fries: *Cabrera* et al. *21480* (LP).
26. *Mutisia hamata* Reiche: *Cabrera 8756* (LP); [Cabrera 1965].
27. *Nassauvia axillaris* (Lag.) D. Don: *Cabrera* et al. *15487* (LP); [Cabrera 1982].
28. *Perezia multiflora* (Kunth) Less.: *Ruiz Leal 22330* (LP); [Simpson Vuilleumier 1969].
29. *Trixis praestans* (Vell.) Cabrera: *Roig 4148* (LP); [Katinas 1996].

Tribe Vernonieae
30. *Orthopappus angustifolius* (Sw.) Gleason: *Cabrera* et al. *23704* (LP).
31. *Vernonia incana* Less.: *Ugarte 204* (LP); [Cabrera 1944].
32. *Vernonia mollissima* D. Don ex Hook. et Arn.: *Clos 3952* (LP); [Cabrera 1944].

Subfamily Asteroideae
Tribe Anthemideae
33. *Anthemis cotula* L.: *Cabrera 136* (LP).
34. *Artemisia copa* Phil.: *Cabrera 9045* (LP).
35. *Soliva anthemifolia* (Juss.) Less.: *Schultz 1049* (LP); [Cabrera 1949].
36. *Soliva neglecta* Cabrera: *Cerrate 2515* (LP); [Cabrera 1949].

Tribe Astereae
37. *Aster hirtifolius* S. F. Blake: *Clokey 7738* (LP).
38. *Haplopappus marginalis* Phil.: *Schajovskoy 55* (LP); [Cabrera 1934].
39. *Noticastrum ascendens* DC.: *Zöllner 974* (LP); [Zardini 1985].

Tribe Calenduleae
40. *Calendula officinalis* L.: *Barros 211* (LP), *Mahu 5012* (LP).

Tribe Eupatorieae
41. *Eupatorium arnottianum* Griseb.: *Herzog 1474* (LP).
42. *Stevia balansae* Cabrera: *Schinini 6194* (LP).

Tribe Gnaphalieae
43. *Chevreulia sarmentosa* (Pers.) S. F. Blake: *Buchtien s.n.* (LP 31431).
44. *Gnaphalium tarapacanum* Phil.: *Cabrera* et al. *18329* (LP).

Tribe Helenieae
45. *Pectis odorata* Griseb.: *Pavetti and Rojas 10549* (LP).
46. *Porophyllum lanceolatum* DC.: *Pedersen 4688* (LP); [Johnson 1969].
47. *Tagetes minuta* L.: *Cabrera* et al. *14250* (LP); [Neher 1965].
48. *Tagetes verticillata* Lag. et Rodr.: *s/leg.* (LP 901944); [Neher 1965].

Tribe Heliantheae
49. *Bidens laevis* (L.) Britton, Stern et Poggeng.: *Arbo 612* (LP).
50. *Clibadium heterotrichum* S. F. Blake: *Venturi 1180a* (LP); [Cabrera 1952].
51. *Helianthus annuus* L.: *Cabrera 726* (LP).
52. *Verbesina encelioides* (Cav.) Benth. et Hook. f.: *Cabrera 10737* (LP).
53. *Zinnia peruviana* (L.) L.: *Frenguelli 117* (LP).

Appendix I (continued)

Tribe Inuleae
54. *Inula britannica* L.: *Lejeune and Courtois 482* (LP).
55. *Inula conyza* DC.: *Pedersen 2434* (LP).
56. *Inula dysenterica* L.: *s/leg* (LP).

Tribe Plucheeae
57. *Pluchea microcephala* Godfrey: *Cabrera* et al. *21668* (LP).
58. *Pterocaulon virgatum* (L.) DC.: *Salellas 841* (LP); [Cabrera and Ragonese 1978].

Tribe Senecioneae
59. *Senecio dryophyllus* Meyen et Walp.: *Barros 87* (LP); [Cabrera 1985].
60. *Senecio vernonioides* Sch. Bip. ex Baker: *Reitz and Klein 14181* (LP); [Cabrera 1957].

Adenocaulon [Bittmann 1990a]
61. *Adenocaulon bicolor* Hook: *Allen 12* (MO), *Anderson 3544* (MO), *Barkley 1835* (MO), *Brooks and Freeman* 15571 (MO), *Hedgcock s.n.* (LP 53312), *Hunziker 4943* (LP), *McVaugh 9566* (MO), *Merello* et al. *660* (MO), *Morrison 121* (LP), *Rosendahl 867* (MO), *Solbrig 2808* (LP), *Wilson 504* (MO).
62. *Adenocaulon chilense* Less.: *Alboff s.n.* (LP 4338), *Böcher* et al. *1663* (LP), *Burkart 6405* (LP), *Moore 2827* (MO), *Ricardi* et al. *1923, 1983* (LP), *Werdermann 1237* (MO), *Zöllner 7686, 9601, 13187* (MO), LP *s.n.* (*ex herb. Spegazzini 16554*).
63. *Adenocaulon himalaicum* Edgew.: *Beljaeva s.n.* (MO 3095888), *Boufford* et al. *24592* (MO), *Boufford and Kato 23377* (MO), *Boufford and Wood 19670* (MO), *Henry 417, 9199* (MO), *Ohashi* et al. *28056* (MO), *Tsugaru and Sawada 19259* (MO), *Tsugaru and Takahashi 17138* (MO).
64. *Adenocaulon lyratum* S. F. Blake: *Breedlove 37307, 40678, 41367* (MO).

Eriachaenium [Cabrera 1971a]
65. *Eriachaenium magellanicum* Sch. Bip.: *Birabén and Birabén 242* (LP), *Boelcke* et al. *16325* (LP), *Moore 1525* (LP), *O'Donell 4091*(LP), *Sleumer 908* (LP), LPS *s.n.* (*ex herb. Spegazzini 13745* in LP).

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