



Morphological characters add support for some members of the basal grade of Asteraceae

NÁDIA ROQUE^{1*} and VICKI A. FUNK²

¹*Instituto de Biologia, Universidade Federal da Bahia, Campus Universitário de Ondina, Salvador, Bahia 40170-110, Brazil*

²*US National Herbarium, Department of Botany, National Museum of Natural History, Smithsonian Institution MRC 166, Washington DC, 20013-7012, USA*

Received 17 November 2011; revised 3 April 2012; accepted for publication 1 October 2012

Recent molecular studies in Asteraceae have divided tribe Mutisieae (*sensu* Cabrera) into 13 tribes and eight subfamilies. Each of the major clades is well supported but the relationships among them are not always clear. Some of the new taxa are easily characterized by morphological data but others are not, chief among the latter being three subfamilies (Stiffioideae, Wunderlichioideae and Gochnatioideae) and the tribe Hyalideae. To understand evolution in the family it is critical to investigate potential morphological characters that can help to evaluate the basal lineages of the Asteraceae. The data for this study were taken from 52 species in 24 genera representing the basal groups in the family. Many characters were examined but most of the useful ones were from reproductive structures. Several apomorphies supported a few of the clades. For instance, members of subfamily Wunderlichioideae (Hyalideae and Wunderlichieae) share predominantly ten-ribbed achenes and members of Wunderlichioideae + Stiffioideae share two synapomorphies: 100–150 (200) pappus elements, arranged in (three) four or five series. These apomorphies can be viewed as an indication of a sister-group relationship between the two subfamilies as the placement of Stiffioideae was not well resolved by the molecular data. Members of Wunderlichieae are characterized by having a paleaceous receptacle, style branches that are strongly papillose above and below the bifurcation, and a pappus of scales. *Hyalis* and *Ianthopappus* (Hyalideae) share venation type and an apiculate anther appendage but these are also found in Gochnatioideae. Other clades have fewer supporting characters. These characters are just a beginning. Cladograms with morphology characters plotted, illustrations and a key to the basal grade of Asteraceae are provided. © 2013 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2013, **171**, 568–586.

ADDITIONAL KEYWORDS: character evolution – Compositae – morphology – phylogeny.

INTRODUCTION

For more than 20 years there have been many lively discussions about the circumscription and classification of the higher taxonomic levels in Asteraceae as more data have become available (Jansen & Palmer, 1987; Bremer, 1994, 1996; Kim & Jansen, 1995; Panero & Funk, 2002, 2008; Funk *et al.*, 2005, 2009; Kim, Choi & Jansen, 2005 *etc.*). Although most of the traditional tribes were supported by the new information, two, Mutisieae (*sensu* Cabrera) and Heliantheae *s.l.*, were split up. Some of the suggested

segregations have been accepted but others are still under intense debate (e.g. the breakup of Mutisieae, Ortiz *et al.*, 2009).

It may seem extreme for the family to go from 13 tribes to 42–43, but most of the traditional 13 tribes were found to be monophyletic or could be made monophyletic with a few rearrangements (Funk *et al.*, 2009a; Funk, 2010). Tribes such as Anthemideae, Astereae, Calenduleae, Cardueae, Cichorieae, Senecioideae and Vernonieae all have much the same circumscription as they did from Cassini (1819) to the Asteraceae volumes of Heywood, Harborne & Turner (1977). A few adjustments were necessary; for instance, Inuleae were divided into two tribes that are

*Corresponding author. E-mail: nadiaroque@gmail.com

not sister taxa (Gnaphalieae and Inuleae) and it is still unclear exactly which taxa should be placed in Arctotideae, but these rearrangements were easily accomplished or the subtribes were found to be good, respectively. Even Heliantheae *s.l.*, which were divided into 11 or 12 tribes (depending on acceptance or not of Feddeae), were monophyletic if Eupatorieae were included (Panero & Funk, 2002). However, it should be noted that only two of the newly recognized tribes in the Heliantheae alliance had to be described as new; all of the others had been proposed previously but had not been adopted by the systematic community (Baldwin, Wessa & Panero, 2002). As we continue to examine the family the total number of tribes will probably remain in flux. However, the original 13 tribes described by our predecessors were, for the most part, good, and it is important that we acknowledge them for their insights (Bonifacino *et al.*, 2009; Funk, 2010).

Most of the recent discussion involves the newly described tribes and subfamilies of the traditional Mutisieae (*sensu* Cabrera). Molecular phylogenetic analyses, such as those by Kim, Loockerman & Jansen (2002), Lundberg & Bremer (2003), Olmstead *et al.* (1992) and Panero & Funk (2008), have confirmed that Mutisieae (*sensu* Cabrera) are not monophyletic. The break up began in 1987 when Jansen & Palmer first reported that Barnadesioideae (formerly a subtribe of Mutisieae, now recognized as a tribe and subfamily) were the sister group of the rest of the family. They were described as a separate subfamily by Bremer & Jansen (1992) and all more recent studies cited above have supported this classification.

The only comprehensive overview of Mutisieae was carried out by Cabrera (1977), and this groundbreaking study provided the base for all the changes that synantherologists have been making since the discoveries of Jansen & Palmer (1987). For a detailed discussion of the breakup of Mutisieae (*sensu* Cabrera), see Funk *et al.* (2009a) and Ortiz *et al.* (2009). Here we discuss only the most recent work.

Kadereit & Jeffrey (2007) published the most recent generic level treatment of Asteraceae. The authors recognized two monophyletic groups: the small subfamily Barnadesioideae and the 'non-Barnadesioideae' clade. This latter clade was divided into four subfamilies (Mutisioideae, Carduoideae, Cichorioideae and Asteroideae) and 36 tribes. The basal branches of the 'not-Barnadesioideae' clade have been described as poorly resolved (Panero & Funk, 2008).

Hind (2007), in the same treatment, split Mutisieae (*sensu* Cabrera) into 12 units, some recognized formally as subtribes (Nassauviinae, Mutisiinae, Gerberinae, Gochnatiinae, Tarchonantinae) and others only informally as generic groups (based around *Stiffitia* J.C.Mikan, *Stenopadus* S.F.Blake, *Hecastocleis*

A.Gray, *Nouelia* Franch., *Catamixis* Thomson, *Dicoma* Cass. and *Pertya* Sch.Bip.).

Katinas *et al.* (2008) studied 74 genera which they placed in subfamily Mutisioideae. They recognized three tribes: Mutisieae (43 genera and *c.* 500 species), Nassauvineae (25 genera and *c.* 315 species) and Stifftieae (six genera and 48 species). The genera of tribe Mutisieae were placed in five informal groups: Central Core; *Gochnatia* Kunth complex; Guyana Highland centred bilabiate genera; *Ainsliaea* DC. group; *Adenocaulon* Hook. and *Eriachaenium* Sch.Bip. (generic pair); and *Hecastocleis*, an independent genus.

The most recent family-wide plastid DNA study (Panero & Funk, 2008) supported the basal bifurcation and recognized new subfamilies and tribes in the non-Barnadesioideae clade (Panero & Funk, 2002, 2007). The molecular data showed seven tribes in the basal grade that are involved in a polytomy or have only a weakly supported pattern of relationships (Fig. 1). Mutisioideae included the majority of the South America taxa placed in three lineages: tribes Onoserideae, Mutisieae *s.s.* and Nassauvineae. The remaining genera of Mutisieae (*sensu* Cabrera) were placed in tribes Stifftieae, Wunderlichieae, Hyalidaeae, Gochnatieae and Hecastocleidae or are in tribes that now are in Carduoideae or Pertyoideae (Fig. 1). Some of the new tribes and subfamilies (those in Carduoideae and Pertyoideae) are more or less accepted by the synantherology community but others are not accepted by everyone, principally Stifftieae, Wunderlichioideae and Gochnatieae.

The composition of Stifftieae and Wunderlichioideae (Hyalidaeae and Wunderlichieae) is unusual and contrary to former studies (Bremer, 1994; Kim *et al.*, 2002; Katinas *et al.*, 2008). Although each tribe was supported by the molecular data and has combinations of characters that circumscribe them, there are no known synapomorphies that group the genera in them together. As a result, a conflict was perceived between the results of a morphological study (Katinas *et al.*, 2008) and the molecular work (Ortiz *et al.*, 2009).

According to Funk *et al.* (2005, 2009b), understanding of the phylogenetic relationships in Stifftioideae (Stifftieae), Wunderlichioideae (Wunderlichieae and Hyalidaeae) and Gochnatioideae (Gochnatieae) is crucial to understanding the evolution and biogeography of the family. It was clear that the existing character studies were not sufficient and that morphological characters and additional molecular data were needed. Thus, the main purpose of this work was to investigate or re-evaluate morphological characters that can help us evaluate the basal lineages of Asteraceae (*sensu* Panero & Funk, 2008) and contribute to our understanding of character evolution in the family.

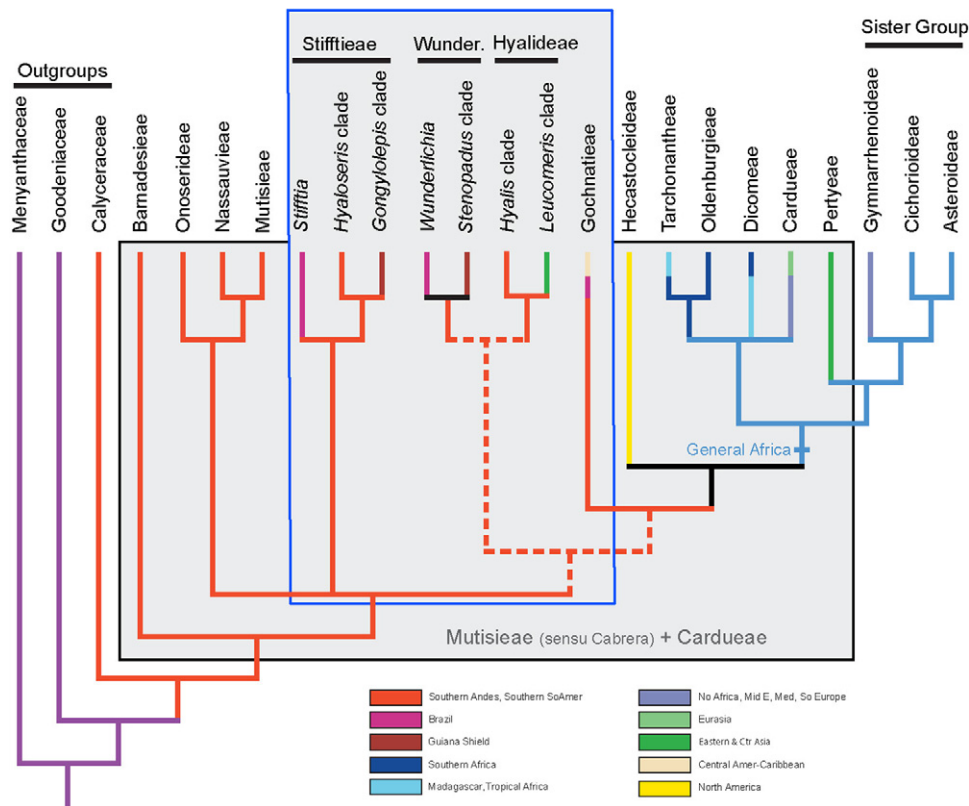


Figure 1. Phylogeny of the basal grade of Asteraceae adapted from Ortiz *et al.* (2009). Branches are coloured to show the distribution of the taxa. Distribution information is a summary from the larger tree presented in Funk *et al.* (2009b).

MATERIAL AND METHODS

The term ‘character’ is frequently used at two levels: (1) as a collection of attributes that are believed to be homologous that are grouped into a character such as ‘style apex’; and (2) for the actual attributes, such as different types of style apices (e.g. style apex acute). Many publications start off by using ‘character’ and ‘character state’, but in the discussion the authors change to using the term character for what had been a character state. Another option is to use the Hennigian concept that each attribute is a character and that we make a hypothesis as to which of these characters are homologous and place those in the same transformation series (Hennig, 1966). The placement of the character in a transformation series may change but the actual character usually does not. The second option is much preferred but is almost never used. We are using the term ‘character’ at both levels and trying to make sure it is obvious which is which.

This study focuses on three subfamilies and four tribes and the genera in each group, along with the number of species, are listed in Table 1. Figure 1 shows a molecular phylogenetic tree adapted from Ortiz *et al.* (2009). The phylogenetic analysis used to

make this summary tree had many more taxa and the resolution of the colour used on each branch was based on this larger sample, as explained in Funk *et al.* (2009b).

Two species of Barnadesioideae, four species of Mutisioideae and the monospecific *Hecastocleis* (*Hecastocleidoideae*) are included for reference. We examined many reproductive structures and selected 21 that showed some indication that they might be useful at the clade level (Table 2). Only two of the vegetative conditions we examined (phyllotaxy and venation) were included in this final table because the remainder were not useful at supergeneric level; the two we did use are only found in two small deeply nested groups: the *Hyalis* and *Hyaloseris* clades.

The data on the morphology were taken from specimens found at US and ALCB herbaria and from freshly collected material (Table 3). Fifty-two species from 24 genera representing the basal grade in the Asteraceae were examined (Table 4). Twenty-three species were illustrated using an Olympus SZH10 stereomicroscope (Table 3, Figs 2–6). The classification used follows Funk *et al.* (2009a).

Venation pattern was analysed using digital X-ray capture (VIVA–Varian Image viewing & Acquisition),

Table 1. Current taxonomy of the study group based on the results of the molecular analyses of Panero & Funk (2002, 2007, 2008) and the metatree of Funk *et al.* (2009); Barnadesioideae, Mutisioideae and Hecastocleidoideae are reference taxa

| | No. of species |
|--|----------------|
| Barnadesioideae | |
| Barnadesieae | 92 |
| Mutisioideae | |
| Onoserideae | 52 |
| Nassauvieae | 313 |
| Mutisieae | 254 |
| Stiftioideae | |
| Stiftieae | |
| <i>Stiftia</i> genus | |
| <i>Stiftia</i> J.C.Mikan | 8 |
| Gongylolepis clade | |
| <i>Achnopogon</i> Maguire, Steyerm. & Wurdack | 2 |
| <i>Duidaea</i> S.F.Blake | 4 |
| <i>Eurydochus</i> Maguire & Wurdack | 1 |
| <i>Glossarion</i> Maguire & Wurdack | 2 |
| <i>Gongylolepis</i> R.H.Schomb. | 14 |
| <i>Neblinaea</i> Maguire & Wurdack | 1 |
| <i>Quelchia</i> N.E.Br. | 4 |
| <i>Salcedoa</i> F.Jimenez Rodr. & Katinas | 1 |
| Hyaloseris clade | |
| <i>Dinoseris</i> Griseb. | 1 |
| <i>Hyaloseris</i> Griseb. | 6 |
| Wunderlichioideae | |
| Wunderlichieae | |
| <i>Wunderlichia</i> genus | |
| <i>Wunderlichia</i> Riedel ex Benth. & Hook.f. | 5 |
| Stenopadus clade | |
| <i>Chimantaea</i> Maguire, Steyerm. & Wurdack | 9 |
| <i>Stenopadus</i> S.F.Blake | 15 |
| <i>Stomatochaeta</i> (S.F.Blake) Maguire & Wurdack | 6 |
| Hyalideae | |
| Hyalis clade | |
| <i>Ianthopappus</i> Roque & D.J.N.Hind | 1 |
| <i>Hyalis</i> D.Don ex Hook. & Arn. | 2 |
| Leucomeris clade | |
| <i>Leucomeris</i> D.Don | 2 |
| <i>Nouelia</i> Franch. | 1 |
| Gochnatioideae | |
| Gochnatieae | |
| <i>Cnicothamnus</i> Griseb. | 2 |
| <i>Cyclolepis</i> D.Don | 1 |
| <i>Gochnatia</i> Kunth | 65 |
| <i>Pentaphorus</i> D.Don | 2 |
| <i>Richterago</i> Kuntze | 17 |
| Hecastocleidoideae | |
| Hecastocleideae | |
| <i>Hecastocleis</i> A.Gray | 1 |

Table 2. Characters evaluated for use in recognizing groups or clades; symplesiomorphies are in bold type; character numbers in relief are mapped on the tree in Figure 7

1. Receptacle: (0) smooth; (1) scrobiculate; (2) pilose; (3) areolate; (4) alveolate; (5) paleaceous.
2. Heads: (0) homogamous; (1) heterogamous.
3. Central floret corollas: **(0) actinomorphic**; (1) subligulate; (2) bilabiate; (3) pseudobilabiate; (4) ligulate.
4. Marginal floret corollas: **(0) actinomorphic**; (1) bilabiate; (2) pseudobilabiate; (3) ligulate.
5. Anther appendage shape: **(0) acute**; **(1) rounded or obtuse**; (2) apiculate; (3) dentate.
6. Anther appendage length (mm): (0) 1; (1) 2–3; (2) 4–6.
7. Anther base caudate: (0) yes; (1) no.
8. Anther base lacinate: no (0); yes (1).
9. Style branch apex: **(0) rounded or obtuse**; (1) acute; (2) truncate.
10. Style branches: **(0) straight**; (1) recurved.
11. Style surface: **(0) glabrous**; (1) papillae above & below the bifurcation; (2) papillae or trichomes only above the bifurcation; (3) minutely papillose (rarely glabrous).
12. Style branch length (mm): **(0) 0.6 or less**; **(1) 0.8–1.4**; (2) 1.5–2.0; (3) 4–5.
13. Pappus type: (0) capillary bristles; (1) villose bristles; (2) plumose; (3) pales; (4) pappus a scale-like corona.
14. Pappus element base: (1) fused; (2) free; (3) entire fused.
15. Pappus persistence: (0) persistent; (1) easily detached; (2) detached as a unit; (3) linked in a fleshy ring.
16. Pappus no. of series: (0) absent; (1) 1; (2) 2; (3) 3; (4) 4; (5) 5.
17. Pappus no. of elements: (0) 15; (1) 20–40; (2) 50–90; (3) 100–120; (4) 130–160; (5) c. 200.
18. Pappus size: (0) equal; (1) unequal.
19. Pappus length: (0) 5 mm or less; (1) 0.6–1.5 cm; (2) 1.6–2.5 cm; (3) 2.6–3.5 cm.
20. Achene ribs: **(0) 5**; (1) 10; (?) could not be determined.
21. Achene: (0) glabrous; (1) sericeous, villose, tomentose or puberulous; (2) papillose
22. Leaf arrangement: **(0) alternate**; (1) opposite.
23. Main leaf vein no.: **1 (0)**; 3 (1); could not be determined (?)

supervised by Sandra J. Raredon, Division of Fishes, NMNH-Smithsonian Institution. Some characters such as style branches, anther appendage, leaf surface (abaxial and adaxial) and pappus morphology were examined using scanning electron microscopy under the supervision of Dr Scott D. Whittaker,

Table 3. Species and specimens analysed and illustrated (asterisk) to the morphological studies

| | |
|--|---|
| Barnadesioideae (D.Don) Bremer & Jansen | |
| <i>Dasyphyllum donianum</i> (Gardner) Cabrera | Brazil. Bahia, 02.vii.2001, <i>Loureiro et al.</i> 296 (ALCB)* |
| <i>Dasyphyllum reticulatum</i> (DC.) Cabrera | Brazil. Minas Gerais, 23.ix.2007, <i>Roque et al.</i> 1639 (ALCB) |
| Mutisioideae (Cass.) Lindl. | |
| <i>Chaptalia nutans</i> (L.) Pol. | Brazil. Bahia, 30.iv.2006, <i>Guedes et al.</i> 12300 (ALCB) |
| <i>Mutisia retrorsa</i> Cav. | Argentina. Neuquen, 07.i.1985, <i>King & Heinz</i> 9369 (US) |
| <i>Onoseris hastata</i> Wedd. | Bolivia. Cochabamba, 23.iii.1994, <i>Ritter</i> 675 (US) |
| <i>Trixis divaricata</i> (Kunth) Spreng. | Brazil. Bahia, 24.v.2008, <i>Roque et al.</i> 1796 (ALCB, US)* |
| Stifftioideae (D.Don) Panero | |
| Stifftieae D.Don | |
| <i>Achnopogon virgatus</i> Maguire, Steyerl. & Wurdack | Venezuela. Bolívar, 11–14.iii.1986, <i>Huber</i> 11508 (US) |
| <i>Dinoseris salicifolia</i> Griseb. | Argentina. Jujuy, 15.ii.1927, <i>Venturi</i> 4913 (US)* |
| <i>Duidaea rubriceps</i> S.F. Blake | Venezuela. Amazonas, 10.x.1992, <i>Huber</i> 13446 (US)* |
| <i>Gongylolepis benthamiana</i> R.H.Schomb. | Venezuela. Bolívar, 02.x.1982, <i>Steyerl. & Leisner</i> 127536 (US) |
| <i>Gongylolepis martiana</i> (Baker) Steyerl. & Cuatrec. | Colombia. Vaupes, 08.xi.1976, <i>Zarucchi</i> 2182 (US) |
| <i>Hyaloseris rubicunda</i> Griseb. | Argentina. Jujuy, 23.i.2001, <i>Simon & Bonifacino</i> 716 (US)* |
| <i>Stifftia chrysantha</i> J.C.Mikan | Brazil. São Paulo, 13.viii.1953, <i>Hoehne s.n.</i> (SPF 15004, US) |
| <i>Stifftia hatschbachii</i> H.Rob. | Brazil. Espírito Santo, 27.ix.1993, <i>Folli</i> 2024 (US); Brazil. Espírito Santo, 09.x.1998, <i>Hatschbach et al.</i> 68368 (ALCB)* |
| <i>Stifftia uniflora</i> Ducke | Brazil. Amapá, 25.viii.1961, <i>Pires et al.</i> 50484 (US) |
| Wunderlichioideae Panero & V.A.Funk | |
| Hyalideae Panero | |
| <i>Hyalis argentea</i> D.Don | Argentina. Buenos Aires, 04.i.1985, <i>King & Heinz</i> 9326 (US)* |
| <i>Hyalis lancifolia</i> Baker | Paraguay. Presidente Ayes, 30.vii.1997, <i>Zardini & Vera</i> 47171 (US) |
| <i>Ianthopappus corymbosus</i> (Less.) Roque & D.J.N.Hind | Brazil. Rio Grande do Sul, 03.v.1986, <i>Wasum s/n</i> UCS 1529 (US); Brazil. Alegrete, 21 Mar 1998, <i>Roque et al.</i> 462 (SPF)* |
| <i>Leucomeris spectabilis</i> D.Don | Nepal. Godavari, 24.iv.1967, <i>Nicolson</i> 3254 (US) |
| <i>Leucomeris decora</i> Kurz | China. Yunnan, iii.1922, <i>Rock</i> 2674 (US) |
| <i>Nouelia insignis</i> Franch. | China. Yunnan, iii.1924, <i>Rock</i> 11714 (US) |
| Wunderlichieae Panero & V.A.Funk | |
| <i>Chimantaea humilis</i> Maguire, Steyerl. & Wurdack | Venezuela. Bolívar, 26.iii.1984, <i>Huber</i> 9240 (US)* |
| <i>Stenopadus campestris</i> Maguire & Wurdack | Colombia. Puerto Inirida, 20.viii.1975, <i>García-Barriga</i> 20878 (US) |
| <i>Stenopadus connellii</i> (N.E.Br.) S.F.Blake | Venezuela. Bolívar, 30.i.1953, <i>Wurdack</i> 34265-A (US)* |
| <i>Stenopadus talaumifolius</i> S.F.Blake | Colombia. Vaupés, 28–31 UG 1953, <i>García-Barriga</i> 14288 (US) |
| <i>Stomatochaeta condensata</i> (Baker) Maguire & Wurdack | Venezuela. Bolívar, 07.v.1964, <i>Steyerl.</i> 93510 (US) |
| <i>Wunderlichia crulsiana</i> Taub. | Brazil. Bahia, 17.ix.1989, <i>Hatschbach et al.</i> 53421 (US); Brazil. Bahia, 04.xii.2003, <i>Roque et al.</i> 878 (ALCB)* |
| <i>Wunderlichia mirabilis</i> Riedel ex Baker | Brazil. Minas Gerais, 28.ix.1998, <i>Roque et al.</i> 466 (SPF, US); Brazil. Minas Gerais, 19.ix.2007, <i>Roque et al.</i> 1622 (ALCB)* |
| <i>Wunderlichia senaei</i> Glaz. ex Maguire & G.M.Barroso | Brazil. Minas Gerais, 25.vii.1998, <i>Hatschbach et al.</i> 68239 (US); Brazil. Minas Gerais, 23.ix.2007, <i>Roque et al.</i> 1649 (ALCB, US) |
| Gochnatioideae (Benth. & Hook.f.) Panero & V.A.Funk | |
| Gochnatieae (Benth. & Hook.f.) Panero & V.A.Funk | |
| <i>Cnicothamnus azafran</i> (Cabrera) Cabrera | Bolivia. Cochabamba, 27.v.1995, <i>Ritter et al.</i> 2111 (US)* |
| <i>Cyclolepis genistoides</i> D.Don | Argentina. Tucumán, 11.ix.1923, <i>Venturi</i> 2581 (US)*; <i>Venturi</i> 451 (US) |
| Gochnatia sect. Gochnatia Less. | |
| <i>Gochnatia arequipensis</i> Sandwith | Peru. Arequipa, 10.viii.1967, <i>Vargas</i> 19920 (US) |
| <i>Gochnatia buchii</i> (Urb.) J.Jiménez Alm. | West Indies. Haiti, 25.xi.1944, <i>Holdridge</i> 2039 (US) |
| <i>Gochnatia ilicifolia</i> Less. | Bahamas Islands. 27.i.1978, <i>Correll & Correll</i> 49433 (US) |
| <i>Gochnatia rotundifolia</i> Less. | Brazil. São Paulo, 12.i.1950, <i>Handro</i> 157 (US) |
| <i>Gochnatia sagrana</i> R.N.Jervis & Alain | Cuba. Havana, 14.iv.1994, <i>Acevedo-Rdz et al.</i> 6523 (US) |
| <i>Gochnatia vernonioides</i> Kunth | Peru. Amazonas, 26.v.1984, <i>Smith & Cabanillas</i> 7117 (US)* |
| Gochnatia sect. Pentaphorus (D.Don) DC. | |
| <i>Gochnatia foliolosa</i> (D.Don) D.Don ex Hook. & Arn. | Chile. 26.ii.1951, <i>Junge</i> 2930 (US) |
| <i>Gochnatia glutinosa</i> (D.Don) D.Don ex Hook. & Arn. | Argentina. Jujuy, 08.i.2001, <i>Simon & Bonifacino</i> 509 (US) |
| Gochnatia sect. Moquiniastrium Cabrera | |
| <i>Gochnatia barrosoae</i> Cabrera | Brazil. Maranhão, 11.viii.1964, <i>Prance & Silva</i> 58663 (US) |
| <i>Gochnatia hatschbachii</i> Cabrera | Brazil. Minas Gerais, 19.viii.2002, <i>Hatschbach et al.</i> 73650 (US) |
| <i>Gochnatia paniculata</i> (Less.) Cabrera | Brazil. Bahia, 22.v.2008, <i>Guedes & Gomes</i> 14364 (ALCB)* |
| <i>Gochnatia polymorpha</i> (Less.) Cabrera | Brazil. Espírito Santo, 14.i.1995, <i>Hatschbach et al.</i> 61410 (US); Brazil. Bahia, 13.xii.1998, <i>Moraes & Stradmann</i> 20 (ALCB)* |
| Gochnatia sect. Hedraiophyllum (Less.) DC. | |
| <i>Gochnatia cordata</i> Less. var. <i>cordata</i> | Brazil. Rio Grande do Sul, 29.iv.1949, <i>Rambo</i> 41315 (US); Brazil. Rio Grande do Sul, 25.ii.2009, <i>Roque et al.</i> 1950 (ALCB)* |
| <i>Gochnatia hypoleuca</i> (DC.) A.Gray | Mexico. Nuevo Leon, 30.i.1998, <i>Panero et al.</i> 7366 (US) |
| <i>Gochnatia palosanto</i> Cabrera | Bolivia. Chuquisaca, 18.x.1997, <i>Wood</i> 12696 (US) |
| <i>Richterago amplexifolia</i> (Gardner) Kuntze | Brazil. Minas Gerais, 13.ii.1972, <i>Anderson et al.</i> 35940 (SPF, US); Brazil. Minas Gerais, 14.xi.2005, <i>Almeida et al.</i> 140 (ALCB)* |
| <i>Richterago angustifolia</i> (Gardner) Roque | Brazil. Minas Gerais, 21.ix.2007, <i>Roque et al.</i> 1643 (ALCB)* |
| <i>Richterago caulescens</i> Roque | Brazil. Minas Gerais, 28.ix.1998, <i>Roque & Hervêncio</i> 470 (SPF, US) |
| <i>Richterago discoidea</i> (Less.) Kuntze | Brazil. Bahia, 14.ix.2008, <i>Roque et al.</i> 1658 (ALCB)* |
| <i>Richterago radiata</i> (Vell.) Roque | Brazil. São Paulo, 27.i.1962, <i>Mimura</i> 210 (SPF, US)*; Brazil. Distrito Federal, 10.i.2007, <i>Pastore</i> 1746 (ALCB)* |
| Hecastocleidoideae Panero & V.A.Funk | |
| Hecastocleideae Panero & V.A.Funk | |
| <i>Hecastocleis shockleyi</i> A.Gray | USA. California, 06.v.1949, <i>Alexander & Kellogg</i> 5676 (US)* |

Table 4. Morphological database

| | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|----|----|---|---|---|---|---|---|---|---|---|---|----|----|----|---|---|---|---|---|---|---|---|---|---|---|
| Barnadesioideae | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 0 | 0 | 3 | 0 | 1 | 2 | 0 | 1 | 1 | 0 | 1 | ? | 1 | 0 | 1 | 0 | 0 | 1 | | |
| <i>Dasyphyllum reticulatum</i> (DC.) Cabrera | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Dasyphyllum donianum</i> (Gardner) Cabrera | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 0 | 0 | 3 | 0 | 1 | 2 | 0 | 1 | 1 | 0 | 1 | ? | 1 | 0 | 1 | 0 | 0 | 1 | 1 | |
| Mutisioideae | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Chaptalia nutans</i> (L.) Pol. | 3 | 1 | 0 | 13 | 0 | 0 | 1 | 0 | 0 | 2 | 1 | 0 | 2 | 2 | 0 | 23 | 3 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Mutisia retrorsa</i> Cav. | 0 | 1 | 2 | 2 | 0 | 2 | 0 | 1 | 0 | 0 | 2 | 0 | 2 | 2 | 2 | 1 | 1 | 0 | 1 | ? | 0 | 0 | 0 | 0 | 0 | ? | ? | |
| <i>Onoseris hastata</i> Wedd. | 2 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 2 | 1 | 0 | 2 | 1 | 23 | 25 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| <i>Trixis divaricata</i> (Kunth) Spreng. | 2 | 0 | 2 | 1 | 1 | 1 | 0 | 1 | 2 | 0 | 2 | 1 | 0 | 2 | 0 | 3 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Stiffioideae | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Stiffieae | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Achnopogon virgatus</i> Maguire, Steyer. & Wurdack | 2 | 0 | 2 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 1 | 5 | 3 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Dinoseris salicifolia</i> Griseb. | ? | 0 | 24 | 13 | 0 | 1 | 0 | 0 | 1 | 1 | 3 | 0 | 2 | 1 | 4 | 4 | 3 | 1 | 2 | ? | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| <i>Duidaera rubriceps</i> S.F.Blake | 2 | 0 | 2 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 2 | 1 | 3 | 3 | 3 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Gongyololepis benthamiana</i> R.H.Schomb. | 2 | 0 | 2 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 2 | 0 | 2 | 1 | 34 | 4 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Gongyololepis martiana</i> (Baker) Steyer. & Cuatrec. | 2 | 0 | 2 | 1 | 0 | ? | 0 | 1 | 0 | 0 | ? | 0 | 2 | 1 | 3 | 3 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Hyaloseris rubicunda</i> Griseb. | ? | 0 | 34 | 13 | 0 | 1 | 0 | 0 | 1 | 1 | 3 | 0 | 2 | 1 | 4 | 5 | 1 | 2 | ? | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Stiffia chrysantha</i> J.C.Mikan | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 1 | 0 | 2 | 1 | 4 | 3 | 1 | 2 | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Stiffia hatschbachii</i> H.Rob. | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 1 | 4 | 4 | 1 | 3 | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Stiffia uniflora</i> Ducke | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 4 | 4 | 1 | 1 | ? | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Wunderlichioideae | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Hyalideae | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Hyalis argentea</i> D. Don | 1 | 0 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 1 | 5 | 5 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 |
| <i>Hyalis lancifolia</i> Baker | ? | 0 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 1 | 5 | 5 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 |
| <i>Ianthopappus corymbosus</i> (Less.) Roque & D.J.N.Hind | 3 | 1 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 4 | 4 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 |
| <i>Leucomeris decora</i> Kurz | 3 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 1 | 0 | 2 | 1 | 2 | 4 | 4 | 1 | 1 | ? | 1 | 0 | ? | 0 | 0 | 0 | 0 | 0 | ? |
| <i>Leucomeris spectabilis</i> D. Don | ? | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 1 | 3 | 2 | 1 | 1 | ? | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Nouelia insignis</i> Franch. | ? | 0 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 1 | 4 | 3 | 1 | 2 | ? | ? | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Wunderlichieae | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Chimantaea humilis</i> Maguire, Steyer. & Wurdack | 5 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 3 | 2 | 1 | 4 | 3 | 1 | 2 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Stenopadus campestris</i> Maguire & Wurdack | 5 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 3 | 2 | 1 | 4 | 3 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Stenopadus connellii</i> (N.E.Br.) S.F.Blake | 5 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 3 | 2 | 1 | 4 | 3 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Stenopadus talaumifolius</i> S.F. Blake | 5 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 3 | 2 | 1 | 4 | 3 | 1 | 3 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Stomatochaeta condensata</i> (Baker) Maguire & Wurdack | 5 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 2 | 1 | 3 | 3 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Wunderlichia crulsiana</i> Taub. | 5 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 3 | 2 | 2 | 5 | 3 | 1 | 3 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Wunderlichia mirabilis</i> Riedel ex Baker | 5 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 3 | 2 | 2 | 5 | 3 | 1 | 3 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Wunderlichia senaei</i> Glaz. ex Maguire & G.M.Barroso | 5 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 3 | 2 | 45 | 3 | 1 | 2 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

Table 4. Continued

| | | | | | | | | | | | | |
|--|---|---|---|----|---|---|---|---|---|---|---|----|
| Barnadesioideae | | | | | | | | | | | | |
| Gochnatoidae | | | | | | | | | | | | |
| Gochnatieae | | | | | | | | | | | | |
| <i>Cnicothamnus azafran</i> (Cabrera) Cabrera | ? | 0 | 0 | 1 | 2 | 0 | 1 | 0 | 0 | 0 | 1 | 3 |
| <i>Cyclolepis genistoides</i> D. Don | ? | 0 | 0 | 0 | 2 | 0 | 2 | 0 | 2 | 1 | 1 | 3 |
| Gochnatieae sect. Gochnatieae Less. | | | | | | | | | | | | |
| <i>Gochnatieae arequipensis</i> Sandwith | ? | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 3 |
| <i>Gochnatieae buchii</i> (Urb.) J. Jiménez Alm. | 3 | 0 | 0 | 0 | 2 | 1 | 0 | 1 | 0 | 0 | 1 | 12 |
| <i>Gochnatieae ilicifolia</i> Less. | 3 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 12 |
| <i>Gochnatieae rotundifolia</i> Less. | 3 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 3 |
| <i>Gochnatieae sagraana</i> R.N. Jervis & Alain | 3 | 0 | 0 | 0 | 2 | 1 | 0 | 1 | 0 | 0 | 1 | 12 |
| <i>Gochnatieae vernonioides</i> Kunth | 3 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 3 |
| Gochnatieae sect. Pentaphorus (D. Don) DC. | | | | | | | | | | | | |
| <i>Gochnatieae foliolosa</i> (D. Don) D. Don ex Hook. & Arn. | ? | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 3 |
| <i>Gochnatieae glutinosa</i> (D. Don) D. Don ex Hook. & Arn. | ? | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 0 | 1 | 3 |
| Gochnatieae sect. Moquintastrum Cabrera | | | | | | | | | | | | |
| <i>Gochnatieae barrosoae</i> Cabrera | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 3 |
| <i>Gochnatieae hatschbachii</i> Cabrera | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 3 |
| <i>Gochnatieae paniculata</i> (Less.) Cabrera | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 3 |
| <i>Gochnatieae polymorpha</i> (Less.) Cabrera | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 3 |
| Gochnatieae sect. Hedraiohyllum (Less.) DC. | | | | | | | | | | | | |
| <i>Gochnatieae cordata</i> Less. | 3 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 3 |
| <i>Gochnatieae hypoleuca</i> (DC.) A. Gray | ? | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 3 |
| <i>Gochnatieae palosanto</i> Cabrera | 3 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 3 |
| <i>Richterago amplexifolia</i> (Gardner) Kuntze | 4 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 3 |
| <i>Richterago angustifolia</i> (Gardner) Roque | 4 | 1 | 0 | 12 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 3 |
| <i>Richterago caulescens</i> Roque | 4 | 1 | 0 | 12 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 3 |
| <i>Richterago discoidea</i> (Less.) Kuntze | 4 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 |
| <i>Richterago radiata</i> (Vell.) Roque | 4 | 1 | 0 | 12 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 3 |
| Hecastocleioideae | | | | | | | | | | | | |
| Hecastocleideae | | | | | | | | | | | | |
| <i>Hecastocleis shockleyi</i> A. Gray | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 4 |

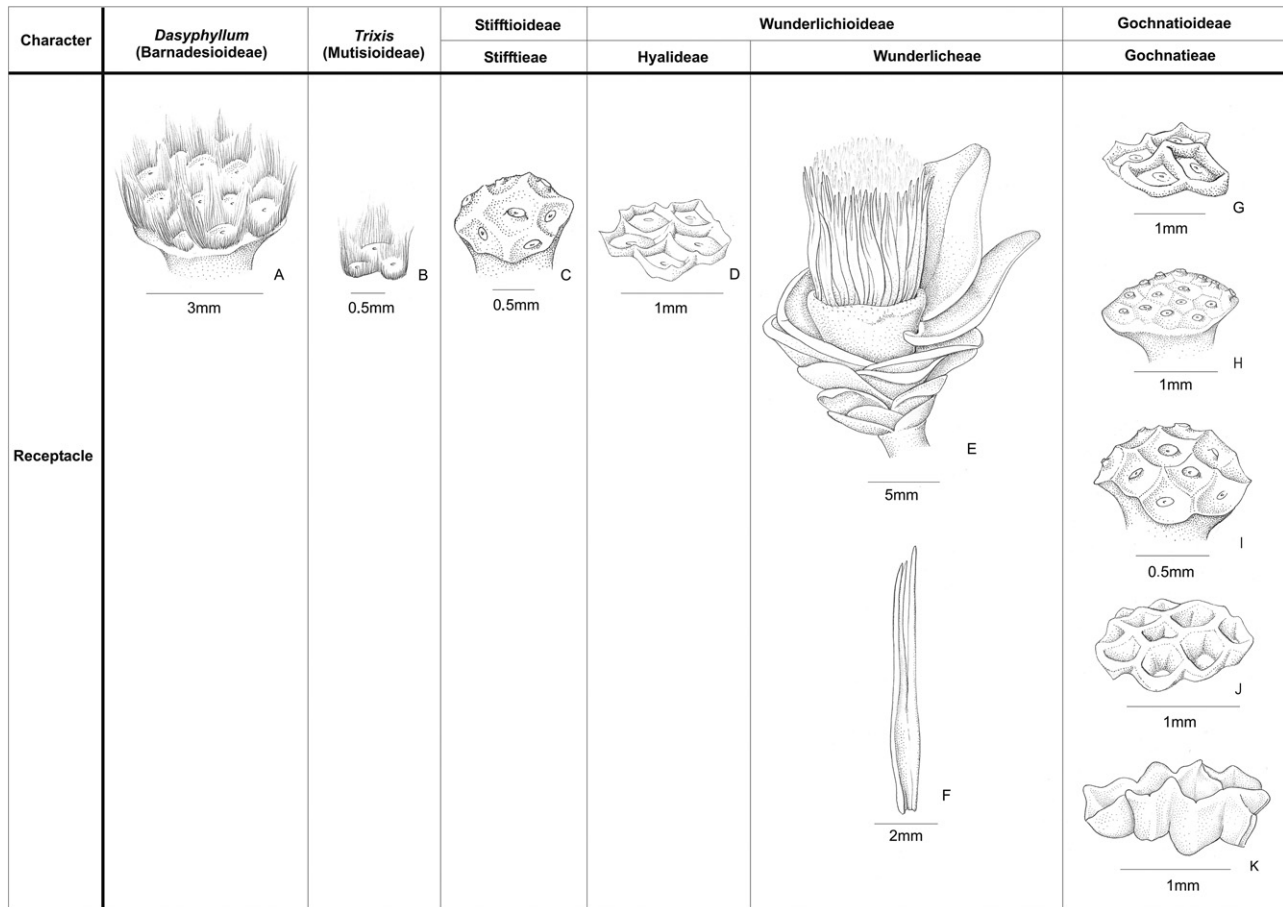


Figure 2. Receptacle types; terms following Small (1919). A, pilose, *Dasyphyllum donianum*; B, pilose, *Trixis divaricata*; C, scrobiculate, *Stifftia hatschbachii*; D, areolate, *Ianthopappus corymbosus*; E, paleaceous, *Wunderlichia crulsiana*; F, one pale, *Wunderlichia mirabilis*; G, areolate, *Gochnatia cordata*; H, scrobiculate, *Gochnatia polymorpha*; I, scrobiculate, *Gochnatia paniculata*; J, alveolate, *Richterago discoidea*; K, alveolate, *Richterago radiata* (Pastore 1746). (The vouchers are listed in Table 3, asterisk.)

NMNH Imaging Lab, Smithsonian Institution. Morphological studies using an Olympus SZH10 stereomicroscope were carried out on dried material in ALCB, Universidade Federal da Bahia, Brazil.

The description of the characters follows Radford *et al.* (1974) and Roque, Keil & Susanna (2009). The receptacles are described using the terminology proposed by Small (1919), which identified six main types of receptacles in Asteraceae: scrobiculate ('when the receptacle is covered with low mounds of tissue with furrows in between'), foveolate ('when it is covered with shallow circular or polygonal depressions'), areolate ('when the depression is polygonal and surrounded by a low, narrow ridge'), fimbriate ('when this ridge is higher with the margin lacerate, denticulate or cut up into a number of short pales'), setiferous ('if the lacinia of the margin are long and narrow like the paleaceous seta of the pappus') and alveolate ('if the ridge is higher still with the margin

entire or variously divided'). In addition to these variations there is a paleaceous receptacle with membranaceous scales, each of which subtends a floret.

Bremer (1994) started the process of updating the characters attributed to a hypothetical ancestor of the family; Lundberg (2009) and Funk *et al.* (2009b) added to the list. Here we have modified the list of Funk *et al.* (2009b) to include only those characters related to the ones we used for this study. The characters listed below are possibly plesiomorphic for the family: receptacle naked; flowers of mostly one type, actinomorphic, some differentiation in floral morphology in peripheral florets possible but without true rays; corolla divided into long lobes; thecae spurred (calcarate) and tailed (caudate); apical anther appendage possibly lacking; styles slender, shortly bifid, without hairs; solid band of stigmatic surface on inside of style branches; pappus of capillary bristles; achene ribbed.

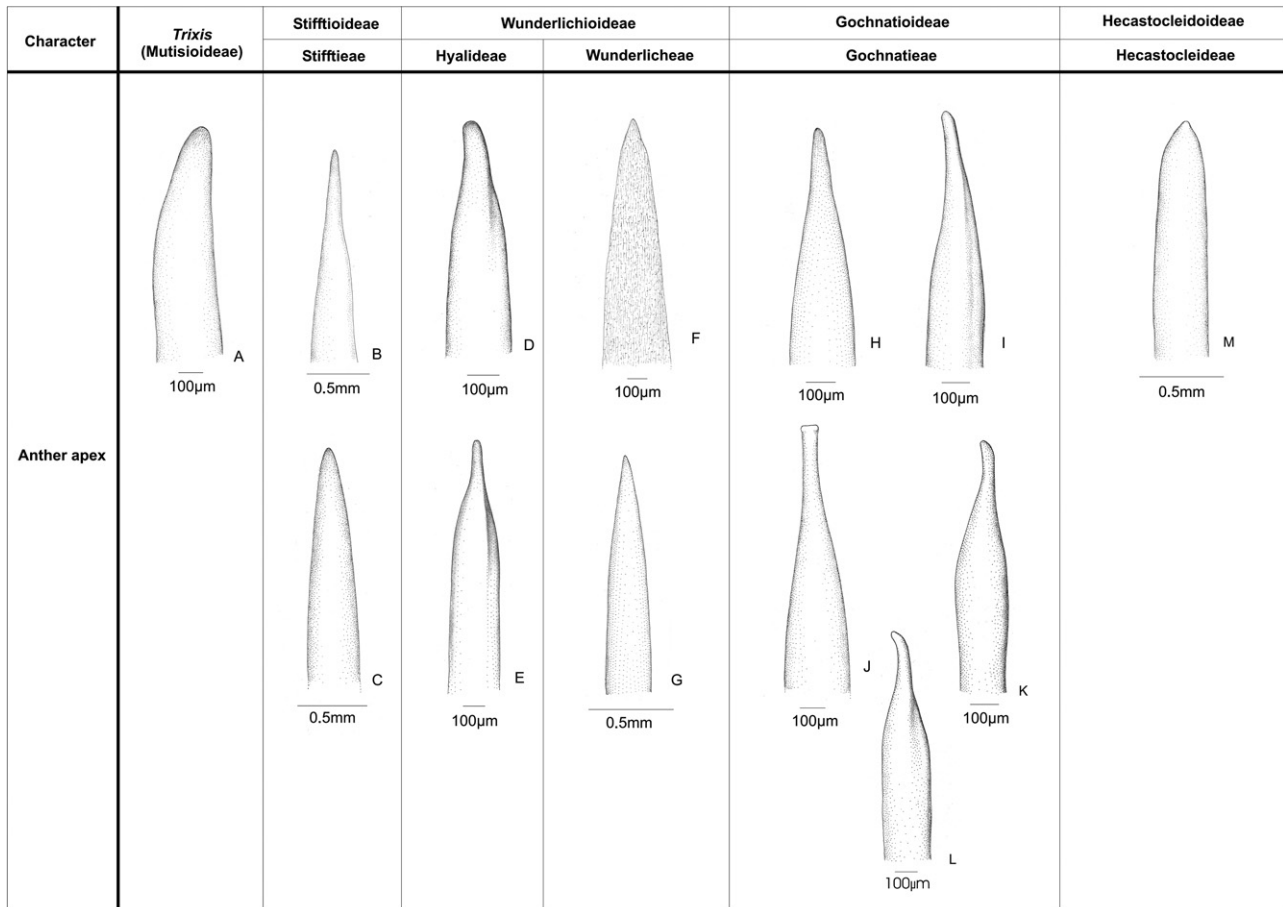


Figure 3. Anther appendage apex. A, obtuse, *Trixis divaricata*; B, acute, *Stiffitia hatschbachii*; C, acute, *Dinoseris salicifolia*; D, apiculate, *Hyalis argentea*; E, apiculate, *Ianthopappus corymbosus*; F, acute, *Chimantaea humilis*; G, acute, *Stenopadus connellii*; H, apiculate, *Cyclolepis genistoides*; I, apiculate, *Gochnatia vernonioides*; J, apiculate, *Cnicothamnus azafran*; K, apiculate, *Richterago amplexifolia*; L, apiculate, *Richterago radiata* (*Mimura* 210); M, obtuse, *Hecastocleis shockleyi*. (The vouchers are listed in Table 3, asterisk.)

Some of the characters in Table 2 could be polarized using the hypothesized plesiomorphic characters, but others could not. Some could be polarized using the outgroups (Mutisioideae, Barnadesioideae, Calyceraceae; Fig. 1) but sometimes that was not possible, either because we lacked adequate information from the outgroups or the characters do not exist in the outgroups or they were variable. Two outgroups, subfamilies Mutisioideae and Barnadesioideae, are variable for most of the characters. At the other extreme, in Hecastocleidoideae with only one species, many characters are either unique or plesiomorphic. Calyceraceae, the sister family of the Asteraceae, were used whenever possible, although some characters used in the study are not present in Calyceraceae. Our attempts to polarize the characters in Table 2 were aided by other literature including Bremer (1994), Katinas *et al.* (2008) and Urtubey & Stuessy (2001).

Figures 7 and 8 show 18 of the 23 characters on a revised version of Figure 1. The remaining characters were omitted from the tree because they were considered uninformative (characters 2, 8, 14) or too variable (7, 18) for this study.

Nested in the genus *Gochnatia* is a clade that has been recognized as a separate genus (*Richterago* Kuntze, see Roque & Pirani, 2001). This genus has a number of apomorphies [1(4), 15(3), 16(1), 17(1)] that differ from the rest of Gochnatieae but as it is highly nested we have not included them on the diagrams.

RESULTS

To facilitate comparisons, members of the studied groups (subfamilies) are discussed together with the reference groups (genera).

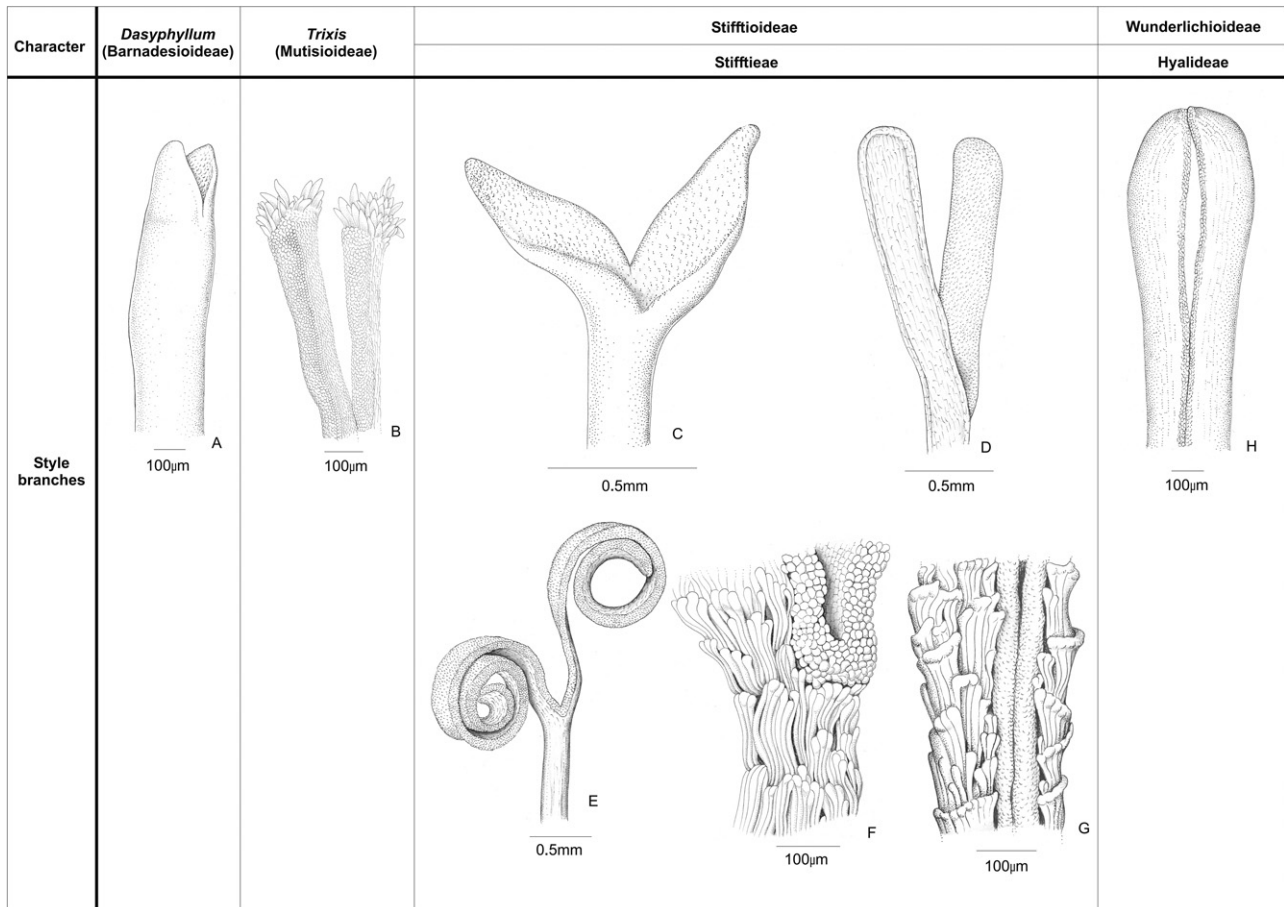


Figure 4. Style branches. F–G, style branches surface. A, obtuse, glabrous, *Dasyphyllum donianum*; B, truncate, penicillate, *Trixis divaricata*; C, obtuse to shortly acute, glabrous, *Stiffitia hatschbachii*; D, rounded, glabrous, *Duidaea rubriceps*; E, F, acute, papillose below, *Dinoseris salicifolia*; G, papillose below, *Hyaloseris rubicunda*; H, rounded, glabrous, *Ianthopappus corymbosus*. (The vouchers are listed in Table 3, asterisk.)

VEGETATIVE CHARACTERS

Two characters can be polarized. All the species analysed have alternate leaves except the sister taxa *Dinoseris* Griseb. and *Hyaloseris* Griseb. (*Hyaloseris* clade), which have opposite leaves (Table 2, character 22). Although opposite leaves also occur in more highly nested taxa in other subfamilies, it seemed logical to use opposite leaves as a synapomorphy for this small clade given that it is not found elsewhere in the basal grade. Likewise, most of the species in the basal grade and outgroups have one main vein (character 23; camptodromous, brochidodromous or craspedodromous) but *Hyalis* D. Don ex Hook. & Arn. and *Ianthopappus* Roque & D.J.N. Hind (*Hyalis* clade) have three main veins which help define the clade. Note that this character is also found in two species of Barnadesioideae [*Dasyphyllum reticulatum* (DC.) Cabrera, *D. donianum* (Gardner) Cabrera and in

Gochnatia rotundifolia Less. (Gochnatioideae). Other vegetative characters examined were not found to be useful at the suprageneric level.

The 'life forms' show some promise for future use. We found that the majority of the species we examined were phanerophytes (shrubs and trees) with the exception of some lianas (two *Stiffitia* spp. and *Mutisia retrorsa* Cav.). A number of taxa are chamaephytes (subshrubs), including *Ianthopappus*, *Richterago amplexifolia* (Gardner) Kuntze, *R. caulescens* Roque and *Dasyphyllum reticulatum*. A few species were hemycryptophytes (herbs), including *Richterago angustifolia* and *R. radiata*, *Chaptalia nutans* (L.) Pol. and *Onoseris hastata* Wedd. However, detailed descriptions of life forms are rarely given in the literature or on herbarium sheets and as a result there was too much missing information to use this character at this time.

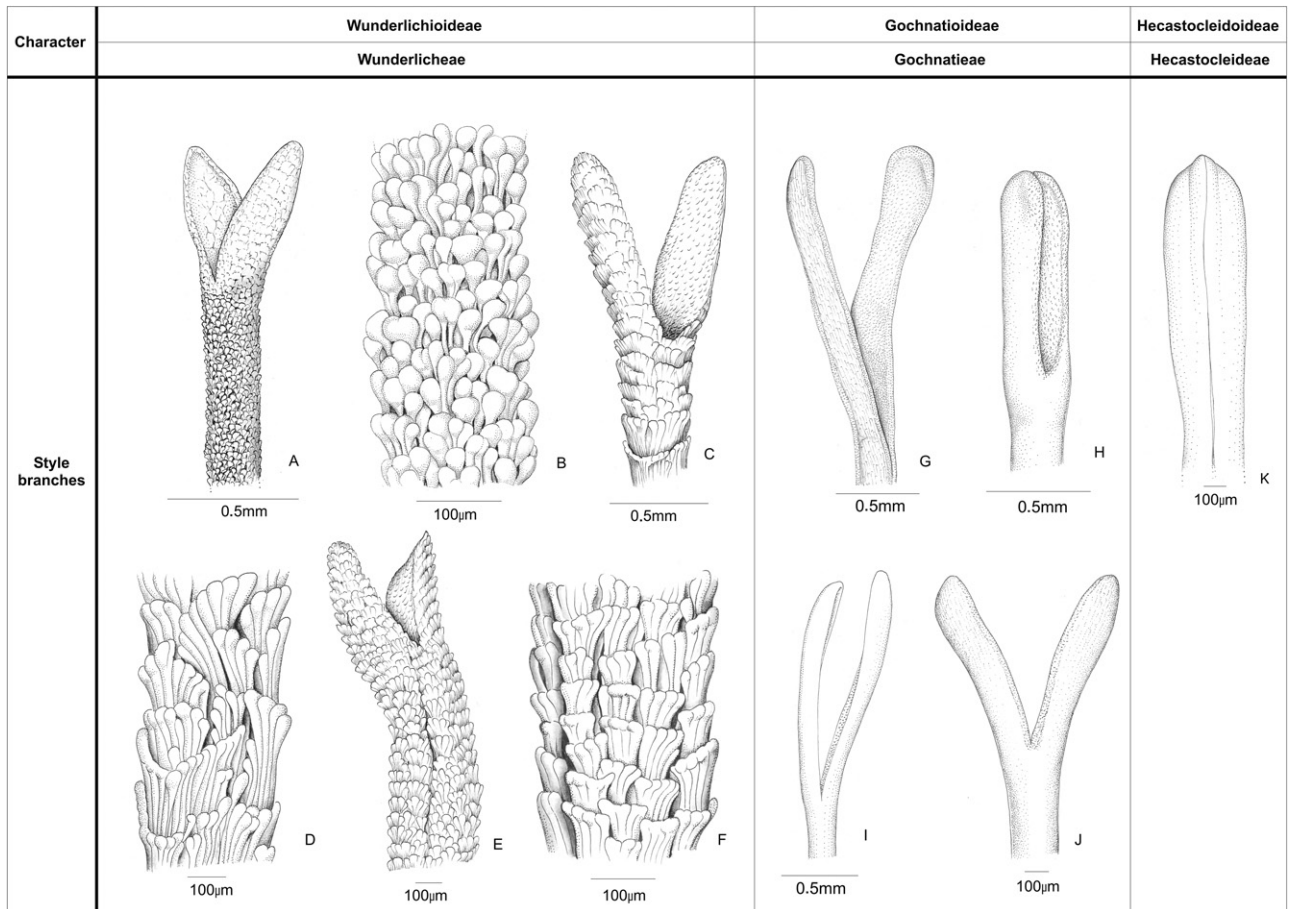


Figure 5. Style branches. B, D, F, style branches surface. A, B, obtuse, papillose below, *Chimantaea humilis*; C, D, obtuse, papillose below, *Stenopadus connellii*; E, F, obtuse, papillose below, *Wunderlichia crulsiana*; G, rounded, glabrous, *Cyclolepis genistoides*; H, rounded, glabrous, *Gochnatia vernonioides*; I, rounded, glabrous, *Cnicothamnus azafran*; J, rounded, glabrous, *Richtergo angustifolia*; K, rounded, glabrous, *Hecastocleis shockleyi*. (The vouchers are listed in Table 3, asterisk.)

REPRODUCTIVE CHARACTERS

The 16 reproductive characters used on Figures 7 and 8 fall into three groups. First, some could be easily polarized using the literature (Lundberg, 2009; Katinas *et al.*, 2009; Stuessy, Urtubey & Gruenstaeudl, 2009; Funk *et al.*, 2009b), the distribution of the character in question in the basal grade, and the attribute found in the outgroups and sister family of the Asteraceae, the Calyceraceae: characters 3, 4, 5, 9, 10, 11 and 12. Second, for some characters all attributes cannot be polarized but some can: characters 13, 16 and 17. Finally, some characters cannot be polarized but we can make a reasonable preliminary assumption about what characters might be synapomorphies: characters 1, 6, 15, 19, 20 and 21. Below we discuss the characters we have chosen to illustrate.

Receptacle (character 1)

In the species studied we found the surface of the receptacle to have useful characters: it can be pilose (*Gongylolepis* R.H.Schomb. clade plus *Dasyphyllum* Kunth, *Onoseris* Willd. and *Trixis* P.Browne) (Fig. 2A, B), paleaceous (only Wunderlichieae) (Fig. 2E, F) or glabrous (*Stiffitia*, Hyalideae, Gochnatioideae, Hecastocleidoideae, *Mutisia* L.f and *Chaptalia* Vent.) (Fig. 2C–D, G–K). However, analysing the glabrous receptacles, we observed different patterns on the surface that were produced by outgrowths of the epidermis which surround the achene (or flowers scars). Following the terminology of Small (1919): the genera *Stiffitia* (Stifftieae) (Fig. 2C) and *Gochnatia* (Gochnatieae) (Fig. 2H, I) have receptacles that are scrobiculate; *Ianthopappus corymbosus* (Less.) Roque & D.J.N.Hind (Hyalideae) (Fig. 2D) and *Gochnatia*

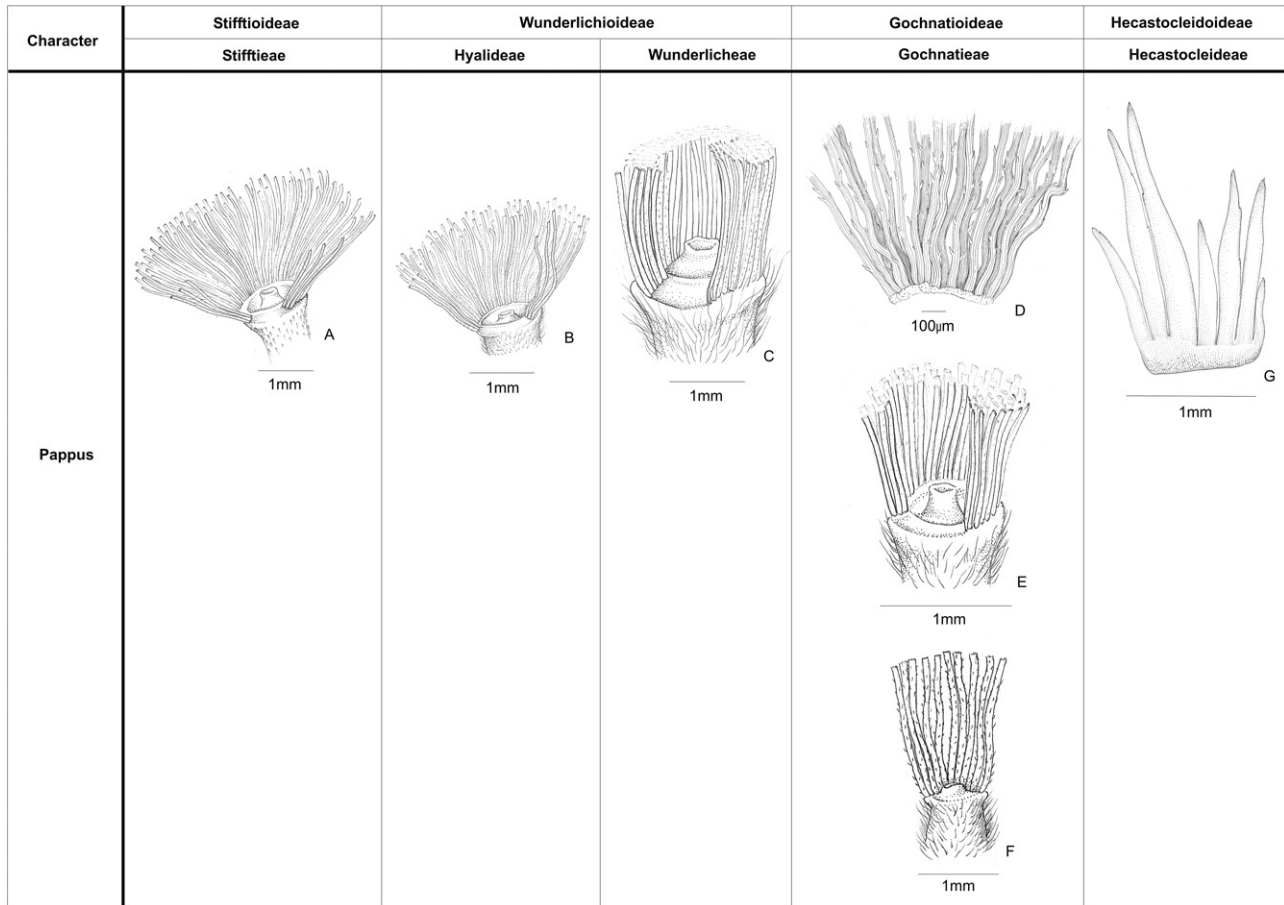


Figure 6. Pappus elements. A, 130–150 bristles, four-seriate, *Stiffia hatschbachii*; B, c. 130 bristles, 4-seriate, *Ianthopappus corymbosus*; C, 100–120 pales, five-seriate, *Wunderlichia mirabilis*; D, c. 60 bristles, three-seriate, *Gochnatia polymorpha*; E, 60–70 bristles, three-seriate, *Gochnatia paniculata*; F, 33–40 bristles, uniseriate, *Richterago amplexifolia*; G, coroniform with dentate pales, fused on the base, *Hecastocleis shockleyi*. (The vouchers are listed in Table 3, asterisk.)

cordata Cabrera (Gochnatieae) (Fig. 2G) have receptacles that are areolate; and *Richterago* (Gochnatieae) is the only genus with a distinctly alveolate receptacle (Fig. 2J, K). *Dinoseris*, *Hyaloseris* (Stifftieae) and *Hyalis*, *Leucomeris* D. Don and *Nouelia* (Hyalidaeae) have receptacles that are glabrous but the heads were too old to determine the details. New studies with fresh material are needed to better describe the receptacles of the genera in these basal groups; however, paleaceous receptacles [Fig. 7; 1(5)] seem to be a synapomorphy for Wunderlicheae because they are only found in this clade.

Anther appendage (Characters 5, 6)

The variability of the anther appendage had some significant results: Stiffioideae (Fig. 3B, C) and Wunderlicheae (3F, G) have an acute apex; Hyalidaeae (Fig. 3D, E) and Gochnatieae (Fig. 3H–L) have an apiculate apex; *Hecastocleis* has an obtuse one (Fig. 3M); and *Trixis* has a rounded apex (Fig. 3A). The

outgroups help to some extent: in Barnadesieae the anther appendage can be slightly apiculate, rounded, acute, absent and rarely dentate or bifid (Stuessy *et al.*, 2009); Mutisieae appendages are usually rounded with a few acute ones (Katinas *et al.*, 2009); Calyceraceae have either no appendage or a small rounded one. Because all clades in the basal grade and Hecastocleis have a rounded anther we selected 'rounded' as the plesiomorphic character. This means that the acute appendage (Fig. 7; 5–0) and the apiculate one (Fig. 7; 5–2) can be used as synapomorphies.

Style branches (Characters 9, 11, 12)

In Stifftieae, there are different types of styles: *Stiffia* has short branches with acute tips (Fig. 4C), *Duida* S.F. Blake has long branches with rounded tips (Fig. 4D), and *Dinoseris* (Fig. 4E and F) and *Hyaloseris* (Fig. 4G) have long branches with acute tips that are papillose below the bifurcation. Hyalidaeae (Fig. 4H), Gochnatieae (Fig. 5G–J) and *Hecastocleis*

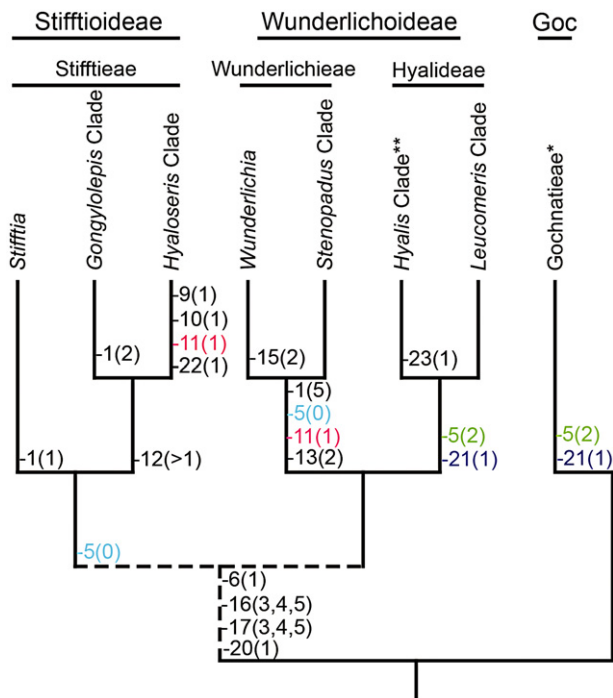


Figure 7. Phylogeny adapted from Ortiz *et al.* (2009) showing the placement of the 15 (out of 18) morphological characters that could be used. Other characters were too variable or not variable enough or otherwise not informative. The dotted line indicates a new relationship proposed based on the characters evaluated in this study. See Fig. 1 for complete phylogeny.

(Fig. 5 K) have medium length branches with an obtuse apex and they are glabrous. Wunderlichieae are different; they have short style branches with an acute apex and are papillose above and below the bifurcation (Fig. 5A–F). The reference taxa (Barnadesioideae, Mutisioideae and *Hecastocleis* in Table 3) show other patterns with *Dasyphyllum* (Fig. 4A) having short, glabrous style branches with a rounded or obtuse apex and *Trixis* (Fig. 4B) having somewhat longer branches that are truncate and crowned by collector hairs at the apex. The style branch apex (character 9) is rounded in Barnadesioideae and Mutisioideae (except for Nassauvieae which have a unique form; Katinas *et al.*, 2009); this makes the acute form a synapomorphy (Fig. 7; 9–1). Character 11, the style surface, has long been used by taxonomists working in this group. Mutisioideae all have pubescence above the bifurcation, except Nassauvieae, members of which have a unique form (Katinas *et al.*, 2009). Barnadesioideae also have a unique form. The styles of Calyceraceae are glabrous as are most of the styles in the clades of the basal grade. Therefore our data support the estimation by Funk *et al.* (2009b) and Lundberg (2009) that the plesiomorphic condition is the presence of a glabrous

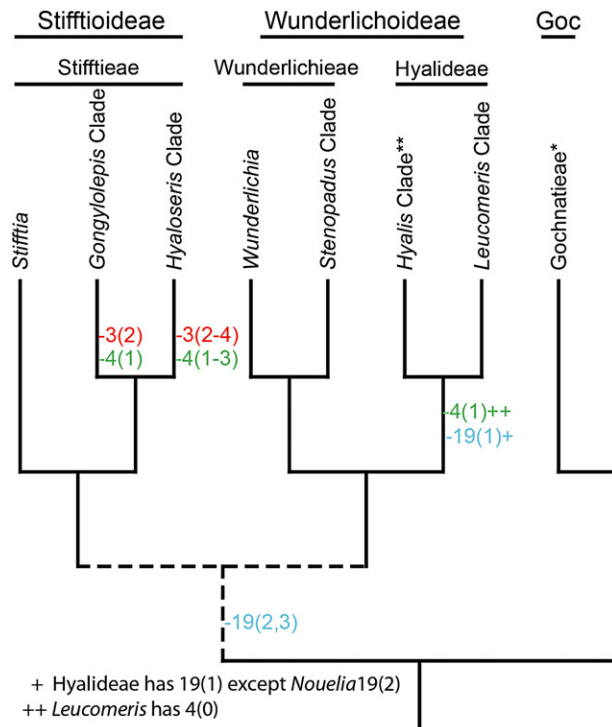


Figure 8. Phylogeny adapted from Ortiz *et al.* (2009) showing the placement of three of the 18 morphological characters that could be used. These characters are more complicated than those in Figure 7. Other characters were too variable or not variable enough or otherwise not informative. The dotted line indicates a new relationship proposed based on the characters evaluated in this study. See Fig. 1 for complete phylogeny.

style. Character 12 is the length of the branches of the style. Estimates by others (Lundberg, 2009; Funk *et al.*, 2009b) have listed ‘short’ style branches as plesiomorphic, but no exact length was specified. Looking across the basal grade (there are no branches on the styles of Calyceraceae) the condition that is present in all clades is 12–0 or 12–1, both of which are ‘short’. That would leave longer style branches as synapomorphic and this character is confined to the *Gongylolepis* + *Hyaloseris* clade and one occurrence in Gochnatieae (Fig. 7).

Pappus (Characters 13, 16, 17)

Most of the studied clades, Stiffieae, Hyalideae and Gochnatieae, have a pappus of barbellate bristles, but pales are found in Wunderlichieae and *Cnicothamnus* Griseb. (Gochnatieae). There is also variation in the number of series and the number of elements; in Stiffieae (Fig. 6A), Hyalideae (Fig. 6B) and Wunderlichieae (Fig. 6C), the pappus has three or four (five) series and 100–200 bristles. However, in Gochnatioideae, the pappus is in one to three series with no more



Figure 9. A, *Stiffia chrysantha* var. *flavicans* (Brazil); B, *Stiffia fruticosa* (Brazil); C, *Gongylolepis jauaensis* (Venezuela); D–E, *Wunderlichia mirabilis* (Brazil); F, *Wunderlichia senaeii* (Brazil); G, *Chimantaea humilis* (Venezuela); H, *Leucomeris decora* (China); I, J, *Gochnatia cordata* var. *cordata* (Brazil); K, *Richterago conduplicata* (Brazil). Photographs: A, B, Gwilym Lewis; C, Otto Huber; D–F, I–K, Nádia Roque; G, Charles Brewer; H, Wang Hong.

than 90 bristles (Fig. 6D, E). *Richterago* is the only genus in Gochnatieae with a uniseriate pappus and it has 25–42 bristles (Fig. 6F). Calyceraceae do not have a pappus and Barnadesioideae have a unique type (villous bristles; Funk & Roque, 2011) as does *Hecastocleis* (pappus a scale-like corona; Fig. 6G). However, it seems obvious that for the non-Barnadesioideae members of the basal grade a pappus of capillary bristles is plesiomorphic. Beyond that we can only identify the increased number of series (character 16–3, 4, 5) and the increased number of bristles (character 17–3, 4, 5) as synapomorphies (Fig. 7).

One character that was used in the past to define Mutisieae was the bilabiate corolla [characters 3(2) and 4(1)]. Bilabiate disc corollas are found only in some groups in the outgroup Mutisioideae and in the *Gongylolepis* and *Hyaloseris* clades but not consistently in the latter (Fig. 8). The bilabiate marginal corolla is more widespread. It is found not only in the *Gongylolepis* and *Hyaloseris* clades but also in Hyalideae (not in *Leucomeris*). It seems certain that the origin of the bilabiate corollas of the *Gongylolepis* and *Hyaloseris* clades are independent of those in Hyalideae. However, it may also be that the bilabiate corolla of the *Hyaloseris* clade is independent of the *Gongylolepis* clade, primarily because, although the *Hyaloseris* clade has only two small genera, it has a variable corolla morphology ranging from ligulate to bilabiate to actinomorphic. It will probably take developmental studies to produce a well-supported hypothesis of corolla evolution in the basal grade of the family. For now we have listed them as separate occurrences (Fig. 8).

Also not illustrated but potentially important is the number of ribs on the achene (character 20). Calyceraceae do not have this character, and Mutisioideae have both five- and ten-ribbed achenes. Stifftioideae and Wunderlichioideae apparently have ten ribs (some are indistinct) and Gochnatioideae and Hecastocleidoideae have five (some are indistinct). The ovary has five veins and the corolla has five lobes, so it seems likely that the character of ten-ribbed achenes is an apomorphy and can therefore be used to help define the proposed Stifftioideae + Wunderlichioideae clade.

DISCUSSION

Based on all available molecular data from Jansen & Palmer (1987) to Panero & Funk (2008), the phylogeny of Asteraceae has a split at the base with the small tribe Barnadesieae (Barnadesioideae) as the sister group of the rest of the family, but other relationships in the basal grade are not as strongly supported. As mentioned above, Panero & Funk (2002, 2008) and Funk *et al.* (2009b) divided Mutisieae (*sensu* Cabrera) into 13 tribes (Fig. 1). A number of them

are distinct morphologically and are accepted as clades at some level (Barnadesieae, Nassauvieae, Onoserideae, Mutisieae, Hecastocleideae, Tarchonantheae, Oldenburgieae, Dicomeae and Pertyeae). Other tribes (Stifftieae, Hyalideae, Wunderlichieae, Gochnatieae) and their subfamilies (Stifftioideae, Wunderlichioideae, Gochnatioideae) are not uniformly accepted (Table 1). Some groupings between pairs of taxa were suggested for the first time in the history of the family and lack supporting morphological characters, a situation that continues to produce doubts (Katinas *et al.*, 2008; Ortiz *et al.*, 2009). In this study we attempted to find or re-evaluate characters that might help in understanding the relationships among these basal groups. As might be expected, we had successes and failures.

According to Cabrera (1977) and Katinas *et al.* (2008), from a morphological point of view, the genera centred in the Guiana Shield can be divided into two groups: (1) those with bilabiate corollas and style branches completely glabrous and (2) those with actinomorphic corollas and style branches papillose below the bifurcation. The molecular data agree with that division of taxa. However, the 'bilabiate corolla' tepui group (*Gongylolepis* clade; Table 1, Fig. 1) is put into a clade with the 'regular corolla' genus *Stifftia* (Brazil and French Guiana) and the ligulate to regular corollas of the *Hyaloseris* clade (Argentina and Chile) which does not fit the concept of Katinas *et al.* (2008). In fact, Katinas *et al.* (2008) placed *Stifftia* with the *Stenopadus* clade (Fig. 1). Another set of nested relationships that is not supported by Katinas *et al.* (2008) is the regular corolla tepui group (*Stenopadus* clade) that is grouped with the Brazilian *Wunderlichia* and then with two clades, one with regular corollas and discoid or radiate heads from Asia (*Leucomeris* and *Nouelia*) and the other with broadly bilabiate marginal florets and radiate heads (*Hyalis* and *Ianthopappus*) from South America (Table 1; Fig. 1).

Now that we have some re-evaluated morphological characters we can examine these relationships again. The characters analysed here may provide fresh insights. Figures 7 and 8 show the characters mapped onto part of Figure 1. Eighteen of the 23 characters in Table 2 were found to be helpful in our quest to find apomorphies to define the groups or perhaps show that the groups are not supported.

The most progress was made in using the anther, pappus and achene features to support a new relationship uniting Wunderlichioideae (Hyalideae and Wunderlichieae) and Stifftioideae (Stifftieae). These two subfamilies are the only members of the basal groups that have an acute anther appendage, 100–150 (200) pappus elements and pappus arranged in (three) four or five series (characters 5, 16, 17; Fig. 7). In the most recent molecular phylogenetic analysis (Panero &

Funk, 2008) the placement of Stifftioideae was unresolved so these characters provide a new hypothesis for the placement as sister to Wunderlichioideae. However, in the molecular study, Wunderlichioideae had some support for a position as the sister taxon of the rest of the family (Fig. 1). We found no characters to support that hypothesis. We can now examine the three major clades: Wunderlichioideae, Stifftioideae and Gochnatioideae (taxa represented in Fig. 9A–K).

WUNDERLICHIOIDEAE

The style has long been important in the classification of the members of what is now referred to as the basal grade of the family, especially the presence of papillae or pubescence above and below the point where the style bifurcates (11). It seems that the plesiomorphic conditions are a glabrous style with short branches. All taxa in our study group are glabrous except Wunderlichieae and the *Hyaloseris* clade which are papillose above and below the branching of the style [11(1)]; *Hyaloseris* is discussed below. In addition to the unusual papillose style, other characters that support Wunderlichieae as a monophyletic group include the pappus type (character 13) and surface of the receptacle (character 1). The plesiomorphic pappus type is the presence of bristles and Wunderlichieae have scales, the only clade in the basal grade that does. Finally, the receptacle of the tribe is paleaceous, also a unique feature among the study groups. This is probably the best supported of the newly proposed tribes. We are confident that this tribe is well supported morphologically.

The morphological support for the sister-group relationship between Wunderlichieae and Hyalideae is limited to the presence of achenes with ten ribs [Fig. 7; character 20(1)].

Support for Hyalideae is found in two characters, the apiculate anther appendage [5(2)] and pubescence on the achenes [21(1)]; these two characters also are present in Gochnatieae, a position suggested by Katinas *et al.* (2008) that is discussed below. The Asian genera *Leucomeris* and *Nouelia* were considered by Hind (2007) to be independent. Both were previously treated by Cabrera (1971) as sections of *Gochnatia*: *Gochnatia* section *Leucomeris* and section *Pentaphorus*, respectively. Hind (2007) grouped *Leucomeris* and *Nouelia* in the 'Nouelia group', and later Panero & Funk (2008) placed them in Hyalideae. Funk *et al.* (2009a) considered them a 'Leucomeris clade' (Fig. 1). The inclusion of *Leucomeris* in Hyalideae has been debated (Ortiz *et al.*, 2009) because it has discoid heads with actinomorphic floret corollas, whereas the other genera (*Ianthopappus*, *Nouelia* and *Hyalis*) have radiate heads with bilabiate marginal floret corollas. Based on the morphological characters

analysed here, it appears that the Hyalideae clade is composed of taxa with radiate heads and bilabiate marginal florets (except for *Leucomeris*). Although the apiculate anther appendage and the areolate and scrobiculate receptacle link the Hyalideae clade with Gochnatioideae, the pappus elements, achene ribs and bilabiate corolla place them elsewhere.

STIFFTIOIDEAE

The *Gongylolepis* and *Hyaloseris* clades (Fig. 7) have already been recognized by the community as monophyletic [characters 3(2, 3, 4), 4(1), 12(> 1)], but their placement as sister taxa and their relationship to *Stifftia* is in question (Ortiz *et al.*, 2009). Our study shows one character that supports Stifftioideae as circumscribed by Panero & Funk (2008), the presence of an acute anther appendage [5(0)]. There is also one character that supports the linking of the *Gongylolepis* and *Hyaloseris* clades: long style branches [12(> 1)].

The position of *Stifftia* as the sister group of the bilabiate tepui genera (especially including the *Hyaloseris* clade) is not supported by previous morphological studies. In fact, Carlquist (1957) mentioned that *Stifftia* pollen grains have many features that resemble those of *Stenopadus* and its allies (Fig. 1, *Stenopadus* clade). However, the morphological characters analysed here do not support a relationship between *Stifftia* and *Stenopadus*, especially as the styles of *Stifftia* are glabrous and the genus lacks the pappus characters of the well-defined Wunderlichieae.

Dinoseris and *Hyaloseris* (*Hyaloseris* clade) are the only genera with opposite leaves and style branches that are 'long and recurved' [character 10(1)] and styles that are papillose above and below the bifurcation (Figs 1, 4E–G). The style branches are very different from those found in Wunderlichioideae (Fig. 5A–F) and Gochnatioideae (Fig. 5G–J). In the remaining Stifftioideae, the *Stifftia* and *Gongylolepis* clades have glabrous style branches (Fig. 4C).

GOCHNATIOIDEAE

The species in this clade are plesiomorphic for most of the characters we studied: a pappus with a lower number of series (one to three series) and elements (25–80 bristles, rarely 90) and a five-ribbed achene [characters 16(1, 2, 3), 17(1, 2), 20(0)]. Other characters, such as the surface of the receptacle, the style branch length and the pappus length, are variable. Two characters define the tribe: the presence of an apiculate anther appendage [character 5(2)] and sericeous, villous, tomentose or puberulous achenes [21(1)]. However, as we mentioned above, these two characters are also found in Hyalideae

(Wunderlichioideae). Based on the strong morphological support for the relationship of Stiffioideae and Wunderlichioideae and the strong molecular support for Gochnatioideae with the rest of the family, we surmise that that these characters (5 and 21) have evolved independently in the two clades.

Although molecular phylogenetic analyses have provoked important and fruitful discussions about the

relationships in Asteraceae, we should not forget that they are not foolproof and that the morphology should make sense in light of the phylogeny. We found receptacle, style, achene and pappus features to be particularly useful and we expect that future studies involving more taxa, characters and collaborators will provide additional characters and shed additional light on the phylogeny.

KEY TO THE TAXA OF THE BASAL GRADE OF ASTERACEAE

(Revised from: Hind, 2007; Kadereit & Jeffrey, 2007; Katinas *et al.*, 2008, 2009; Stuessy *et al.*, 2009)

- 1 Stems commonly with axillary paired spines, trichomes of the barnadesioid types; the involucre consist of phyllaries arranged in many rows, and they terminate in a mucro or spine; corollas usually villous; pappus frequently villous..... Barnadesieae
- 1 Stems unarmed; trichomes various but not 'barnadesioid'; the involucre consist of phyllaries in few to many rows and lack a mucro or spine at apex; corolla glabrous; pappus of capillary bristles, plumose or paleaceous.....2
- 2 Corollas mostly bilabiate; style branches with papillae or trichomes restricted to area above the bifurcation.....3
- 3 Inflorescence mostly laxly to densely corymbose, racemose, paniculate to glomerulose or with pseudocephalia; capitula homogamous, discoid, isomorphic, with all the florets bilabiate; style cleft into two truncate branches, with an apical crown of collector or sweeping hairs (rarely absent).....Nassauvineae
- 3 Inflorescence mostly monocephalous on scapes; capitula usually heterogamous, radiate or disciform, with a great variability in their corollas (bilabiate, sub-bilabiate, tubular, filiform, ligulate); style branches papillose.....4
- 4 Usually shrubs or herbs (*Onoseris*); achene turbinate to cylindrical; pappus two- to four-seriate and heteromorphic..... Onoserideae
- 4 Usually herbs; achene truncate or rostrate at the apex; pappus usually uniseriate, isomorphic.....Mutisieae
- 2 Corollas actinomorphic, bilabiate, or ligulate; style branches glabrous or style surface with papillae above and below the bifurcation.....5
- 5 Leaves with spiny margin; phyllaries spinescent at the apex; capitula discoid single-flowered; pappus a scale-like corona.....Hecastocleideae
- 5 Leaves and phyllaries without spines; capitula discoid or radiate more than one floret; pappus of capillary or paleaceous setae.....6
- 6 Anther appendage length mostly 1 mm; achenes mostly five-ribbed; pappus with one to three series and 20–90 bristles.....Gochnatieae
- 6 Anther appendage length 2–3 mm; achenes mostly ten-ribbed; pappus with three to five series and 100–200 bristles or scales.....7
- 7 Anther appendage apiculate.....Hyalideae
- 7 Anther appendage acute.....8
- 8 Receptacle paleaceous; style surface with papillae above and below the bifurcation; pappus of scales.....Wunderlichieae
- 8 Receptacle pilose or scrobiculate; style surface glabrous (usually) or papillate above and below the bifurcation (only in the *Hyaloseris* clade); pappus of capillary bristles.....9
- 9 Corolla actinomorphic.....*Stiffia*
- 9 Corolla bilabiate, pseudobilabiate or ligulate.....10
- 10 Leaves opposite; style surface with papillae above and below the bifurcation; style branches 4–5 mm long, recurved.....*Hyaloseris* clade
- 10 Leaves alternate; style glabrous; style branches 0.8–2.0 mm long, straight.....*Gongylolepis* clade

ACKNOWLEDGEMENTS

We thank Natanael Nascimento for the lovely and informative line drawings. We are grateful to the reviewers of the manuscript for valuable comments and suggestions. Funding for travel for Nádia

Roque to Washington, DC, was provided by the Smithsonian Institution Cuatrecasas Travel Awards Program. This work was supported by grants from CNPq (PQ 307156/2010-9) and the National Museum of Natural History, Smithsonian Institution.

REFERENCES

- Baldwin BG, Wessa BL, Panero JL. 2002.** Nuclear rDNA evidence for major lineages of helenioid Heliantheae (Compositae). *Systematic Botany* **27**: 161–198.
- Bonifacino JM, Robinson H, Funk VA, Lack HW, Wagenitz G, Feuillet C, Hind DJN. 2009.** Influential synanthrologists. In: Funk VA, Susanna A, Stuessy T, Bayer R, eds. *Systematics, evolution, and biogeography of Compositae*. Vienna: IAPT, 3–38.
- Bremer K. 1994.** *Asteraceae - cladistics & classification*. Portland, OR: Timber Press.
- Bremer K. 1996.** Major clades and grades of the Asteraceae. In: Hind DJN, Beentje HJ, eds. *Proceedings of the International Compositae Conference*. Kew: Royal Botanic Gardens, 1–7.
- Bremer K, Jansen RK. 1992.** A new subfamily of the Asteraceae. *Annals of the Missouri Botanical Garden* **79**: 414–415.
- Cabrera AL. 1971.** Revisión del género *Gochnatia* (Compositae). *Revista del Museo de La Plata, Sección Botánica* **12**: 1–160.
- Cabrera AL. 1977.** Mutisieae - systematic review. In: Heywood VH, Harborne JB, Turner BL, eds. *The biology and chemistry of the Compositae*. London: Academic Press, 1039–1066.
- Carlquist S. 1957.** Anatomy of Guayana Mutisieae. *Memoirs of the New York Botanical Garden* **9**: 441–475.
- Cassini H. 1819.** Suite de Sixieme memoire sur la famille des Synantherees, contenant les caracteres des tribus. *Journal de Physique, de Chimie, d'Histoire Naturelle et des Arts* **88**: 189–204.
- Funk VA. 2010.** Ten things I learned on the way to the Mother Tree (i.e., Mother Ship). *Compositae Newsletter* **48**: 6–21.
- Funk VA, Anderberg AA, Baldwin BG, Bayer RJ, Bonifacino JM, Breitwieser I, Brouillet L, Carbajal R, Chan R, Coutinho AXP, Crawford DJ, Crisci JC, Dillon MK, Freire SE, Galbany-Casals M, Garcia-Jacas N, Gemeinholzer B, Gruenstaeudl M, Hansen HV, Himmelreich S, Kadereit JW, Källersjö M, Karaman-Castro V, Karis PO, Katinas L, Keeley SC, Kilian N, Kimball RT, Lowrey TK, Lundberg J, McKenzie RJ, Tadesse M, Mort ME, Nordenstam B, Oberprieler C, Ortiz S, Pelsner PB, Randle CP, Robinson H, Roque N, Sancho G, Semple JC, Serrano M, Stuessy TF, Susanna A, Unwin M, Urbatsch L, Urtubey E, Vallès J, Vogt R, Wagstaff S, Ward J, Watson LE. 2009b.** Compositae metatrees: the next generation. In: Funk VA, Susanna A, Stuessy T, Bayer R, eds. *Systematics, evolution, and biogeography of Compositae*. Vienna: IAPT, 747–777.
- Funk VA, Susanna A, Stuessy TF, Robinson H. 2009a.** Classification of Compositae. In: Funk VA, Susanna A, Stuessy T, Bayer R, eds. *Systematics, evolution, and biogeography of Compositae*. Vienna: IAPT, 171–192.
- Funk VA, Bayer RJ, Keeley S, Chan R, Watson L, Gemeinholzer B, Schilling E, Panero JL, Baldwin BG, Garcia-Jacas N, Susanna A, Jansen RK. 2005.** Everywhere but Antarctica: using a supertree to understand the diversity and distribution of the Compositae. *Biologiske Skrifter* **55**: 343–374.
- Funk VA, Roque N. 2011.** The monotypic Andean genus *Fulcaldea* (Compositae, Barnadesioideae) gains a new species from northeastern Brazil. *Taxon* **60**: 1095–1103.
- Funk VA, Susanna A, Stuessy TF, Bayer RJ. 2009.** *Systematics, evolution, and biogeography of Compositae*. Vienna: IAPT.
- Hennig W. 1966.** *Phylogenetic systematics*. Urbana, IL: University of Illinois Press.
- Heywood VH, Harborne JB, Turner BL. 1977.** *The biology and chemistry of the Compositae*. London: Academic Press.
- Hind DJN. 2007 [2006].** Tribe Mutisieae. In: Kadereit JW, Jeffrey C, eds. *Families and genera of vascular plants, vol. 8. Flowering plants – eudicots – Asterales*. Berlin: Springer, 90–123.
- Jansen RK, Palmer JD. 1987.** A chloroplast DNA inversion marks and ancient evolutionary split in the sunflower family (Asteraceae). *Evolution* **84**: 5818–5822.
- Kadereit JW, Jeffrey C. 2007 [2006].** Compositae. In: *Flowering plants – eudicots – Asterales. Families and genera of vascular plants, Vol. 8*. Berlin: Springer, 61–588.
- Katinas L, Pruski J, Sancho G, Tellería MC. 2008.** The subfamily Mutisioideae (Asteraceae). *Botanical Review* **74**: 469–716.
- Katinas L, Sancho G, Tellería MG, Crisci JV. 2009.** Mutisieae *sensu stricto* (Mutisioideae *sensu stricto*). In: Funk VA, Susanna A, Stuessy T, Bayer R, eds. *Systematics, evolution, and biogeography of Compositae*. Vienna: IAPT, 229–248.
- Kim H-G, Choi K-S, Jansen RK. 2005.** Two chloroplast DNA inversions originated simultaneously during the early evolution of the sunflower family (Asteraceae). *Molecular Biology and Evolution* **22**: 1–10.
- Kim H-G, Loockerman DJ, Jansen RK. 2002.** Systematic implications of *ndhF* sequence variation in the Mutisieae (Asteraceae). *Systematic Botany* **27**: 598–609.
- Kim K-J, Jansen RK. 1995.** *ndhF* sequence evolution and the major clades in the sunflower family. *Proceedings of the National Academy of Sciences of the United States of America* **92**: 10379–10383.
- Lundberg J. 2009.** Asteraceae and relationships within Asterales. In: Funk VA, Susanna A, Stuessy T, Bayer R, eds. *Systematics, evolution, and biogeography of Compositae*. Vienna: IAPT, 157–169.
- Lundberg J, Bremer J. 2003.** A phylogenetic study of the order Asterales using one morphological and three molecular data sets. *International Journal of Plant Sciences* **164**: 553–578.
- Olmstead RG, Michaels HJ, Scott KM, Palmer JD. 1992.** Monophyly of Asteridae and identification of their major lineages inferred from DNA sequences of *rbcL*. *Annals of the Missouri Botanical Garden* **79**: 249–265.
- Ortiz S, Bonifacino M, Crisci JV, Hansen HV, Hind DJN, Roque N, Sancho G, Tellería MC. 2009.** The basal grade of the Asteraceae: the fate of Mutisieae (*sensu* Cabrera) and

- the Carduoideae. In: Funk VA, Susanna A, Stuessy T, Bayer R, eds. *Systematics, evolution, and biogeography of Compositae*. Vienna: IAPT, 193–213.
- Panero JL, Funk VA. 2002.** Toward a phylogenetic subfamilial classification for the Compositae (Asteraceae). *Proceedings of the Biological Society of Washington* **115**: 909–922.
- Panero JL, Funk VA. 2007.** New infrafamilial new taxa in Asteraceae. *Phytologia* **89**: 356–360.
- Panero JL, Funk VA. 2008.** The value of sampling anomalous taxa in phylogenetic studies: major clades of the Asteraceae revealed. *Molecular Phylogenetics and Evolution* **47**: 757–782.
- Radford AE, Dickison WC, Massey JR, Bell CR. 1974.** *Vascular plant systematics*. New York: Harper & Row.
- Roque N, Keil DJ, Susanna A. 2009.** Illustrated glossary of Compositae. Appendix A. In: Funk VA, Susanna A, Stuessy T, Bayer R, eds. *Systematics, evolution, and biogeography of Compositae*. Vienna: IAPT, 781–806.
- Roque N, Pirani JR. 2001.** Reinstatement of the name *Richterago* and recircumscription of the genus to include species formerly treated as *Actinoseris* (Endl.) Cabrera (Compositae, Mutisieae). *Taxon* **50**: 1155–1160.
- Small J. 1919.** *The origin and development of the Compositae*. New Phytologist Reprint: 11. London: William Wesley & Son.
- Stuessy TF, Urtubey E, Gruenstaeudl M. 2009.** Barnadesieae (Barnadesioideae). In: Funk VA, Susanna A, Stuessy T, Bayer R, eds. *Systematics, evolution, and biogeography of Compositae*. Vienna: IAPT, 215–228.
- Urtubey E, Stuessy TF. 2001.** New hypotheses of phylogenetic relationships in Barnadesioideae (Asteraceae) based on morphology. *Taxon* **50**: 1043–1066.