

The basal grade of Compositae: Mutisieae (sensu Cabrera) and Carduoideae

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INTRODUCTION

There is no doubt that understanding Mutisieae (sensu Cabrera 1977) is key to understanding the systematics, early evolution, and biogeography of Compositae, because in all molecular and recent morphological studies its members occupy the first branches of the family phylogeny (Fig. 12.1 on p. 200). In the last few years there have been various definitions of the tribe and all parts of it have been placed in informal groups, subtribes, or subfamilies by a variety of authors (Bremer 1994; Katinas 1994; Panero and Funk 2002, 2007, 2008; Hind 2007; Katinas et al. 2008). In this discussion, the taxon Mutisieae (sensu Cabrera) is meant to represent the historic circumscription of the tribe as defined by Cabrera in 1977. This is in no way meant as a negative reflection on the many contributions of Cabrera (see Chapter 1), in fact, his 1977 paper is a classic—one that is always cited as the first comprehensive treatment of the tribe. Within this paper he had many insights and some of his groups have a direct correlation to the results of the molecular analyses. In science, and especially in taxonomy, we all “stand on the shoulders of giants” and Cabrera’s contributions are certainly the foundation for all modern work in the tribe. The results of the most recent and comprehensive molecular work (Panero and Funk 2002, 2007, 2008) established many new super-generic taxa and the relationships between the morphological and molecular

treatments are not always clear. In this discussion, taxa will be referred to as various clades, groups, or their proper scientific names depending on the context. A detailed comparison with all the current and past super-generic names can be found in Tables 12.1 and 12.2.

The need for a re-evaluation of Mutisieae (sensu Cabrera) has been clear since the work of Jansen and his collaborators. Many have tackled this difficult group and much has been accomplished using characters from morphology, palynology, and DNA sequencing. The major goals of these studies were to: (1) find morphological synapomorphies that support the monophyly of proposed groups, (2) establish the position of some problematic genera within the phylogeny, (3) circumscribe the various taxonomic groups (be they subtribes, tribes, or subfamilies), (4) investigate the differences between the morphological and molecular results, and hopefully (5) agree on a placement of all species once housed under the umbrella of Mutisieae (sensu Cabrera).

The synantherology community has been partially successful in accomplishing these goals and this discussion attempts to summarize those results and identify those goals that are yet to be achieved. This chapter has four parts:

1. An explanation of Mutisieae (sensu Cabrera) based on morphology and molecular data.
2. A discussion of groups of proposed clades from

former Mutisieae (sensu Cabrera) that are not found in other chapters or that require some additional information (orphan clades).

3. A treatment of *Catamixis* incertae sedis.
4. An introduction to the subfamily Carduoideae, which is nested within Mutisieae (sensu Cabrera).

Finally, this treatment also serves as a guide to the chapters that follow, which treat clades that were once considered part of Mutisieae (sensu Cabrera).

MUTISIEAE (SENSU CABRERA 1977)

Morphological data

Beginning with Lagasca (1811), who recognized a group of genera with bilabiate florets under the name Chaenanthophorae, through Cassini (1819) who described the group as Mutisieae, to Cabrera (1977) who provided the first full modern treatment of the group, taxonomists have used the broadest concept of the tribe. There were comments as to the lack of overall agreement on morphology and statements about which subtribes or groups of genera were distinct, but there was little fluctuation in the number of genera and species according to the different authors. The main taxonomic categories and generic groups recognized by modern authors are shown in Table 12.2. The first modern circumscription was that of Cabrera (1977) who defined the tribe by its bilabiate corollas, caudate anthers, and characteristic style shape. However, he indicated that many genera housed in the tribe did not fit morphological descriptions, and he stated that it was difficult to accurately circumscribe the tribe. Cabrera recognized four subtribes: Barnadesiinae, Gochnatiinae, Mutisiinae, and Nassauviinae. Of these subtribes, he felt that Nassauviinae were the most distinct and natural. The other three were, according to Cabrera (1977), more heterogeneous and would require much investigation before the natural position of their genera would be known with any degree of certainty. Furthermore, Cabrera established some possible generic relationships showing some evolutionary lines from primitive to evolved genera for some, but not all, of the genera.

Before Cabrera, the morphological heterogeneity of Mutisieae was emphasized by authors such as Jeffrey (1967; Table 12.2), who broke the tribe up into twelve groups or series. Jeffrey (1967) did not recognize subtribal categories, and his informal series were mostly based on style features.

The first morphological phylogenetic analysis of the tribe by Hansen (1991) accepted a monophyletic Mutisieae alleging the type of ray epidermal cells as a synapomorphy of the tribe. Hansen accepted the exclusion of Barnadesiinae from Mutisieae on the basis of Bremer's (1987) cladogram of Compositae. He also excluded several

genera to achieve a better circumscription of the tribe; these exclusions are, with the exception of *Adenocaulon*, currently supported by the molecular data. Many of Hansen's generic groups have provided the morphological basis for many tribes or subfamilies recognized by further molecular phylogenies.

Another morphology-based analysis of Compositae, with emphasis on the basal groups, was by Karis et al. (1992). These authors made it clear that the tribe was most likely paraphyletic. This analysis showed that the separation between subtribes Mutisiinae and Gochnatiinae was not justified. Based on this morphological work and the molecular studies of Jansen and Palmer (1987), Bremer (1994) accepted only two subtribes (Mutisiinae and Nassauviinae) and discussed several generic groups within them. Bremer stated that although Mutisieae seemed clearly paraphyletic, there was no basis at that time for splitting the tribe into smaller monophyletic tribes. He also noted that understanding the relationships among the branches of Mutisieae would provide an understanding of the basal branches of the entire family.

Hind (2007), in the *Asterales* volume of *The Families and Genera of Vascular Plants* (series ed.: K. Kubitzki), split Mutisieae (sensu Cabrera) into twelve units, some of them recognized formally as subtribes, and others only informally as generic groups. In the same treatment, Jeffrey (2007) produced a general classification of Compositae where Mutisieae (sensu Cabrera) are recognized at the level of subfamily, a category suggested by others (e.g., Bremer 1996; Panero and Funk 2002). However, some examination of the history of the Mutisieae treatment is required in order to understand the different concepts in this present book. This is particularly so because some contemporaneous and more recent accounts are critical of the infratribal taxa proposed, the genera included within them, and even the tribe Mutisieae. Although largely based on morphological data, Hind's account (Hind 2007) was in part based on an unpublished draft of the 'supertree'. Unfortunately, when the 'supertree' was finally published (Funk et al. 2005) a disagreement had led to the removal of approximately 20 taxa. This removal of taxa resulted in the collapse and realignment of some clades/grades. Consequently, Jeffrey (2007) suggested there were a number of 'misplaced' genera, simply because the location of these genera differed between the draft and the published 'supertree'. As a result, Jeffrey (2007) should not be considered as a different treatment of taxa. Editorial demands, and limitations of space, precluded any explanation of the background to the concepts employed in the Kubitzki series volume accounts. Similarly, much of the text discussing genera, and informal groups, was considerably shortened or removed. To this end, any explanation as to the inclusion of the Carduoid groups, such as the *Dicoma* group, and the *Pertya* group, etc., was not provided. Importantly,

at that time the authors of Cardueae were understandably somewhat reluctant to add them to their account, hence the inclusion of genera 82 (*Oldenburgia* Less.) to 91 (*Myriopsis* Bunge) within the broad concept of Mutisieae. Because the guidelines of the Kubitzki series precluded the formalizing of any new taxa within the volume, a number of taxa were left as informal groups. More importantly, perhaps, is that the subsequent analyses, including many additional genera, has further realigned some groups (Panero and Funk 2008). Also, recognition of the clades Gochnatieae, Hecastocleideae, and Pertyeae, as well as the alignment of Tarchonantheae, Oldenburgieae, and Dicomeae within Carduoideae, has been subsequently supported by on-going molecular analysis.

Katinas et al. (2008) produced a monograph including all genera considered by previous modern authors to be part of Mutisieae (excluding Barnadesieae), describing and evaluating morphological and palynological characters of taxonomic value. They used subfamilial status, and Mutisioideae were divided into the three tribes Mutisieae, Nassauvieae, and Stifftieae on the basis of style features. Katinas et al. (2008) recognized some generic groups within the tribe Mutisieae without giving them formal status. Style morphology was found to be helpful in circumscription of the subfamily, approaching that of Cabrera's (1977) concept, although excluding some genera.

Molecular data

The advance of molecular techniques deeply changed the systematic organization of the entire family (Fig. 12.1). First, the concept of evolution in the family was turned upside down by the work of Jansen and Palmer (1987): gone was the 'Heliocentric' (as mentioned by Robinson 1981: 4) view of the family. Mutisieae (sensu Cabrera) were now at the base and Heliantheae s.l. and Eupatorieae were highly nested. The subtribe Barnadesiinae was removed from Mutisieae (sensu Cabrera) by Bremer and Jansen (1992) and raised to subfamilial status, taking into account its unique morphology and the absence of a large chloroplast DNA inversion present in remaining Compositae (Jansen and Palmer 1987).

The results of the phylogenetic analyses by Kim et al. (2002) and Panero and Funk (2002), based on the sequencing of different markers of cpDNA, clearly showed the non-monophyletic character of Mutisieae. Principally the cladograms of Panero and Funk (2002), followed by Funk et al. (2005) and Panero and Funk (2008) (Fig. 12.1), displayed Mutisieae (sensu Cabrera) made up of several clades, which were then described as different subfamilies and tribes. Many of these new taxa represent groups that had already been mentioned by some workers as being different or separate from core Mutisieae, e.g., clades identified by Hansen (1991) and others: *Ainsliaea*

group, *Dicoma* group, Tarchonantheae, etc., as well as confirmation of the unusual nature of some genera such as *Hecastocleis* A. Gray.

Table 12.1 gives the molecular assignment of all genera of Mutisieae (sensu Cabrera), lists where they fall in the molecular study (Panero and Funk 2008), and indicates how the placement differs from the treatments of Cabrera (1977). Detailed discussions of most of the taxa included in former Mutisieae (sensu Cabrera) are included elsewhere in this volume (Chapters 13–19, 21). There are, however, a few taxa (e.g., Stifftieae) that are left out of these chapters because they fall into clades in the molecular studies that have not been previously proposed as separate groups, some of which are difficult to support morphologically. There is also one unplaced genus, *Catamixis*.

ORPHAN CLADES

Most clades from former Mutisieae (sensu Cabrera) are covered in other chapters: Barnadesioideae, Barnadesieae (Chapter 13); Mutisioideae, Mutisieae s.str., Onoserideae, Nassauvieae (Chapter 14); Wunderlichioideae p.p, Hyalideae (Chapter 15); Gochnatioideae, Gochnatieae (Chapter 15); Hecastocleidoideae, Hecastocleideae (Chapter 16); Carduoideae, Dicomeae (Chapter 17), Tarchonantheae (Chapter 18), Oldenburgieae (Chapter 19), Cardueae (Chapter 20), and Pertyoideae, Pertyeae (Chapter 21). However, there are three clades that are part of the basal grade of Compositae that are not treated in other chapters of this book and they will be discussed here (Fig. 12.1): (1) the molecularly circumscribed tribe Stifftieae (subfamily Stifftioideae; not in agreement with any morphological treatment), (2) the tribe Wunderlichieae (agreeing with the *Wunderlichia* clade in the morphological analysis of Katinas et al. 2008), and (3) the subfamily Wunderlichioideae (Wunderlichieae + Hyalideae clade; not found in any morphological treatment). These clades contain members of Compositae that are found on the Guiana Shield as well as in South America and Asia (see Chapter 44 for a detailed phylogeny).

Two of the clades mentioned above have members from the Guiana Shield of northeastern South America. The high elevation areas (up to ~3000 m) of the Shield (also referred to as the Guayana or Guiana Highlands) have generated considerable interest among plant biologists because of their unique flora, high levels of endemism, and biogeographic isolation. This area is home to more than 50 tabletop mountains, each known as a *tepui* (Huber 1995). Some genera of Mutisieae (sensu Cabrera) that are found on this Shield are among the most fascinating members of the family. The tepui-centered genera, that were known to science at the time, were treated in

Table 12.1. Current taxonomy of Mutisieae (sensu Cabrera 1977) based on results of the molecular analyses (numbers in parentheses refer to literature references at the end of the table).

Molecular placement	Placement by Cabrera	Molecular placement	Placement by Cabrera
I. Barnadesioideae (Chapter 13)		Nassauviinae or Nassauvia clade	
Barnadesieae		<i>Acourtia</i> D. Don (1,3)	Nassauviinae
<i>Arnaldoa</i> Cabrera (2,6)	Barnadesiinae	<i>Ameghinoa</i> Speg. (5)	Nassauviinae
<i>Barnadesia</i> Mutis (2,3,6)	Barnadesiinae	<i>Berylsimpsonia</i> B.L. Turner	New
<i>Chuquiraga</i> Juss. (2,3,5,6)	Barnadesiinae	<i>Burkartia</i> Crisci	New
<i>Dasyphyllum</i> Kunth (2,3,6)	Barnadesiinae	<i>Calopappus</i> Meyen	Nassauviinae
<i>Doniophyton</i> Wedd. (2,3,5,6)	Barnadesiinae	<i>Cephalopappus</i> Nees & Mart.	Nassauviinae
<i>Dusenilla</i> K. Schum. (5,6)	Gochnatiinae	<i>Criscia</i> Katinas	New
<i>Fulcaldea</i> Poir. ex Lam. (2,6)	Barnadesiinae	<i>Dolichlasium</i> Lag. (3)	Nassauviinae
<i>Huarpea</i> Cabrera (2,6)	Barnadesiinae	<i>Holocheilus</i> Cass. (5)	Nassauviinae
<i>Schlechtendalia</i> Less. (2,6)	Barnadesiinae	<i>Jungia</i> L.f. (1,3,5)	Nassauviinae
		<i>Leucheria</i> Lag. (1,3,5)	Nassauviinae
		<i>Leunisia</i> Phil.	Nassauviinae
		<i>Lophopappus</i> Rusby (3)	Nassauviinae
		<i>Macrachaenium</i> Hook. f.	Nassauviinae
		<i>Marticoenia</i> Crisci	Nassauviinae
		<i>Moscharia</i> Hook. f. (5)	Nassauviinae
		<i>Nassauvia</i> Comm. ex Juss. (1,3,5)	Nassauviinae
		<i>Oxyphyllum</i> Phil.	Nassauviinae
		<i>Pamphalea</i> Lag. (5)	Nassauviinae
		<i>Perezia</i> Lag. (1,3,5)	Nassauviinae
		<i>Pleocarphus</i> D. Don	Nassauviinae
		<i>Polyachyrus</i> Lag. (5)	Nassauviinae
		<i>Proustia</i> Lag. (1,3,5)	Nassauviinae
		<i>Triptilion</i> Ruiz & Pav. (1,5)	Nassauviinae
		<i>Trixis</i> P. Browne (1,3)	Nassauviinae
		*III. Stifftioideae (Chapter 12) Stifftieae	
		<i>Stifftia</i> genus	
		<i>Stifftia</i> J.C. Mikan (1,3)	Gochnatiinae
		<i>Gongylolepis</i> clade	
		<i>Achnopogon</i> Maguire	Mutisiinae
		<i>Duida</i> S.F. Blake (1,3)	Mutisiinae
		<i>Eurydochus</i> Maguire & Wurdack	Mutisiinae
		<i>Glossarion</i> Maguire & Wurdack	Mutisiinae
		<i>Gongylolepis</i> R.H. Schomb. (3)	Mutisiinae
II. Mutisioideae (Chapter 14)			
Mutisieae s.str. or Mutisieae clade			
<i>Adenocaulon</i> Hook. (1,3)	Not listed		
<i>Amblyperma</i> Benth.	New		
<i>Brachyclados</i> D. Don (3,5)	Mutisiinae		
<i>Chaetanthera</i> Ruiz & Pav. (1,3,5)	Mutisiinae		
<i>Chaptalia</i> Vent. (1,3)	Mutisiinae		
<i>Chucoa</i> Cabrera	Gochnatiinae		
<i>Eriachaenium</i> Sch.Bip.	Not listed		
<i>Gerbera</i> L. (1,3)	Mutisiinae		
<i>Leibnitzia</i> Cass. (1)	Mutisiinae		
<i>Lulia</i> Zardini	New		
<i>Mutisia</i> L.f. (1,3,5)	Mutisiinae		
<i>Pachylaena</i> D. Don ex Hook. & Arn. (1,3,5)	Mutisiinae		
<i>Perdicium</i> L.	Mutisiinae		
<i>Trichocline</i> Cass. (3)	Mutisiinae		
<i>Uechtrizia</i> Freyn	Mutisiinae		
Onoserideae or Onoseris clade			
<i>Aphyllocladus</i> Wedd. (1,3)	Gochnatiinae		
<i>Gypothamnium</i> Phil.	Gochnatiinae		
<i>Lycoseris</i> Cass. (3)	Gochnatiinae		
<i>Plazia</i> Ruiz & Pav. (1,3)	Gochnatiinae		
<i>Onoseris</i> Wedd. (1,3)	Gochnatiinae		
<i>Urmenetia</i> Phil. (5)	Gochnatiinae		

Table 12.1. Continued.

Molecular placement	Placement by Cabrera	Molecular placement	Placement by Cabrera
Neblinaea Maguire & Wurdack	Mutisiinae	<i>Dicoma</i> Cass. (1,3)	Gochnatiinae
Quelchia N.E. Br.	Mutisiinae	<i>Erythrocephalum</i> Benth. (4)	Gochnatiinae
Salcedoa F. Jiménez Rodr. & Katinas	New	Gladiopappus Humbert	Gochnatiinae
<i>Hyaloseris</i> clade		<i>Macedium</i> Cass. (3,4)	Gochnatiinae
<i>Dinoseris</i> Griseb. (3)	Mutisiinae	<i>Pasaccardoa</i> Kuntze (1,3,4)	Gochnatiinae
<i>Hyaloseris</i> Griseb. (3)	Mutisiinae	<i>Pleiotaxis</i> Steetz (4)	Gochnatiinae
*IV. Wunderlichioideae		Oldenburgieae (Chapter 19)	
Wunderlichieae or <i>Wunderlichia</i> clade (Chapter 12)		<i>Oldenburgia</i> Less. (2,3,4)	Gochnatiinae
<i>Chimantaea</i> Maguire (3)	Gochnatiinae	Tarchonantheae (Chapter 18)	
<i>Stenopadus</i> S.F. Blake (3)	Gochnatiinae	<i>Tarchonanthus</i> L. (1,3,4)	Not listed
<i>Stomatochaeta</i> (S.F. Blake) Maguire & Wurdack (3)	Gochnatiinae	<i>Brachylaena</i> R. Br. (3,4)	Not listed
<i>Wunderlichia</i> Riedel ex Benth. (3)	Gochnatiinae		
*Hyalideae (Chapter 15)		Cardueae (Chapter 20) – Thistles – not Mutisieae s.l.	
<i>Hyalis</i> clade		VIII. Pertyoideae (Chapter 21)	
<i>Ianthopappus</i> Roque & D.J.N. Hind (3)	Gochnatiinae	Pertyeae	
<i>Hyalis</i> D. Don ex Hook. & Arn. (3)	Gochnatiinae	<i>Ainsliaea</i> DC. (1,3)	Gochnatiinae
<i>Leucomeris</i> clade		Diaspananthus Maxim.	Gochnatiinae
<i>Leucomeris</i> D. Don (3)	Gochnatiinae	Macroclinidium Maxim.	Gochnatiinae
<i>Nouelia</i> Franch. (3)	Gochnatiinae	<i>Myriopsis</i> Bunge (1)	Mutisiinae
V. Gochnatioideae (Chapter 15)		<i>Pertya</i> Sch.Bip. (1,3)	Gochnatiinae
Gochnatieae		Catamixis Thompson, incertae sedis	Mutisiinae
<i>Cnicothamnus</i> Griseb. (1,3)	Gochnatiinae		
<i>Cyclolepis</i> D. Don (3)	Gochnatiinae		
<i>Gochnatia</i> Kunth (1,3)	Gochnatiinae		
Pentaphorus D. Don	Gochnatiinae		
<i>Richterago</i> Kuntze (3)	Gochnatiinae		
VI. Hecastocleidoideae (Chapter 16)			
Hecastocleideae			
<i>Hecastocleis</i> A. Gray (1,3)	Gochnatiinae		
VII. Carduoideae p.p.			
Dicomeae (Chapter 17)			
<i>Cloiselia</i> S. Moore (1)	Gochnatiinae		

The left column has the taxa arranged according to Panero and Funk (2002, 2007, 2008) and the supertree of Funk et al. (2005). The right column is the placement in Cabrera (1977). Some genera were listed by Cabrera but are now placed in other sections of the family phylogeny: *Hesperomannia* Gray (Vernonieae), *Moquinia* DC. (Moquinieae), and *Warionia* Benth. & Coss. (Cichorieae).

"New" indicates taxa described or resurrected since 1977 and "Not listed" indicates taxa that Cabrera did not include in his tribe Mutisieae; * = under discussion. Names in bold indicate genera for which there are no known sequence data.

1 = Kim et al. 2002 [*ndhF*]; 2 = Gustafsson et al. 2001 [ITS & *trnL*]; 3 = Panero & Funk 2008 [ten chloroplast gene regions]; 4 = Ortiz et al., unpub. [ITS & *ndhF*]; 5 = Katinas et al. 2008 [ITS]; 6 = Gruenstaeudl et al. 2009 [ITS & nine chloroplast gene regions].

the tribe Mutisieae by Bentham (1873) and subsequent authors. Don (1830) described the tribe Stifftieae to include the Brazilian-centered *Stiffitia* and some species of *Gochnatia*. Later on, similarities between *Stiffitia* and some tepui-centered genera were noted by several authors (e.g., Baker 1884; Maguire 1956; Maguire et al. 1957). Indeed, Maguire (1956; Maguire et al. 1957), who extensively studied these genera, included *Chimantaea*, *Quelchia*, *Stiffitia*, *Stenopadus*, and *Stomatochaeta* in Gochnatiinae, and *Achnopogon*, *Duidaea*, *Neblinaea*, *Glossarion*, and *Gongylolepis* in Mutisiinae, both subtribes of Mutisieae. This alignment was followed by Cabrera (1977), who placed

the tepui-centered genera with actinomorphic tubular corollas in the subtribe Gochnatiinae and those with bilabiate corollas in the subtribe Mutisiinae.

Previous to Cabrera's treatment of Mutisieae, Jeffrey (1967) divided Mutisieae into twelve series. All of the tepui-centered genera were placed in the *Stiffitia* series, which also contained the mainly Brazilian genera *Stiffitia* and *Wunderlichia*, the Bolivian-Argentine *Cnicothamnus*, the more widespread *Gochnatia*, the Asian *Nouelia*, and the African *Oldenburgia*. Pruski (1991) thought that the tepui-centered genera belonging to subtribe Gochnatiinae as well as those once placed in subtribe Mutisiinae shared a

Table 12.2. Main morphological taxa delimited within Mutisieae (sensu Cabrera) by modern authors. Only those genera considered to be part of groups are cited (in some cases with numbers in parentheses); genera currently placed in Barnadesioideae are not cited.

Author	Main taxonomic category	Generic groups and species
Jeffrey (1967)	Tribe Mutisieae	<i>Chionopappus</i> series: <i>Chionopappus</i> <i>Anisochaeta</i> series: <i>Anisochaeta</i> <i>Pleiotaxis</i> series: <i>Achyrothalamus</i> , <i>Erythrocephalum</i> , <i>Pasaccardoa</i> , <i>Pleiotaxis</i> <i>Pertya</i> series: <i>Hesperomannia</i> , <i>Macroclidium</i> , <i>Moquinia</i> , <i>Myriopsis</i> , <i>Pertya</i> <i>Dicoma</i> series: <i>Ainsliaea</i> , <i>Catamixis</i> , <i>Dicoma</i> , <i>Hochstetteria</i> , <i>Leucomeris</i> <i>Mutisia</i> series, <i>Gerbera</i> subseries: <i>Brachyclados</i> , <i>Chaetanthera</i> , <i>Chaptalia</i> , <i>Chucoa</i> , <i>Gerbera</i> , <i>Leibnitzia</i> , <i>Lycoseris</i> , <i>Macrachaenium</i> , <i>Perdicium</i> , <i>Piloselloides</i> , <i>Trichocline</i> , <i>Uechtrizia</i> , <i>Urmenetea</i> ; <i>Onoseris</i> subseries: <i>Gypothamnium</i> , <i>Onoseris</i> , <i>Plazia</i> ; <i>Mutisia</i> subseries: <i>Mutisia</i> ; <i>Pachylaena</i> subseries: <i>Pachylaena</i> , <i>Proustia</i> <i>Trixis</i> series: <i>Cyclolepis</i> , <i>Jungia</i> , <i>Lophopappus</i> , <i>Trixis</i> <i>Nassauvia</i> series: <i>Ameghinoa</i> , <i>Leucheria</i> , <i>Moscharia</i> , <i>Nassauvia</i> , <i>Oxyphyllum</i> , <i>Panphalea</i> , <i>Perezia</i> , <i>Polyachyrus</i> , <i>Triptilion</i> <i>Seris</i> series: <i>Gladiopappus</i> , <i>Hecastocleis</i> , <i>Hyalis</i> , <i>Richterago</i> <i>Hyaloseris</i> series: <i>Dinoseris</i> , <i>Hyaloseris</i> <i>Stiffitia</i> series, <i>Gochnatia</i> subseries: <i>Achnopogon</i> , <i>Cnicothamnus</i> , <i>Gochnatia</i> , <i>Nouelia</i> , <i>Oldenburgia</i> ; <i>Wunderlichia</i> subseries: <i>Wunderlichia</i> ; <i>Stiffitia</i> subseries: <i>Stiffitia</i> , <i>Stomatochaeta</i> ; <i>Quelchia</i> subseries: <i>Duidaea</i> , <i>Glossarion</i> , <i>Gongylolepis</i> , <i>Quelchia</i> <i>Barnadesia</i> series
Cabrera (1977)	Tribe Mutisieae Subtribe Barnadesiinae Subtribe Gochnatiinae Subtribe Mutisiinae Subtribe Nassauviinae	 (1) <i>Actinoseris</i> , <i>Chucoa</i> , <i>Cyclolepis</i> , <i>Gochnatia</i> , <i>Pleiotaxis</i> (2) <i>Chimantaea</i> , <i>Quelchia</i> , <i>Stenopadus</i> , <i>Stomatochaeta</i> , <i>Wunderlichia</i> (1) <i>Chaptalia</i> , <i>Gerbera</i> , <i>Leibnitzia</i> , <i>Perdicium</i> , <i>Piloselloides</i> , <i>Trichocline</i> , <i>Uechtrizia</i> (2) <i>Achnopogon</i> , <i>Duidaea</i> , <i>Eurydochus</i> , <i>Glossarion</i> (syn. <i>Guaicaia</i>), <i>Gongylolepis</i> (syn. <i>Cardonaea</i>), <i>Neblinaea</i>
Hansen (1991)	Tribe Mutisieae Subtribe Barnadesiinae Subtribe Gochnatiinae Subtribe Mutisiinae Subtribe Nassauviinae Excluded	 <i>Gochnatia</i> group: <i>Actinoseris</i> , <i>Cyclolepis</i> , <i>Gochnatia</i> (incl. <i>Leucomeris</i>), <i>Hyalis</i> , <i>Nouelia</i> <i>Ainsliaea</i> group: <i>Ainsliaea</i> , <i>Myriopsis</i> , <i>Pertya</i> <i>Plazia</i> group: <i>Aphyllocladus</i> , <i>Gypothamnium</i> , <i>Plazia</i> <i>Guayana</i> group: <i>Chimantaea</i> , <i>Quelchia</i> , <i>Stenopadus</i> , <i>Stomatochaeta</i> <i>Guayana</i> group: <i>Achnopogon</i> , <i>Duidaea</i> , <i>Eurydochus</i> , <i>Glossarion</i> , <i>Gongylolepis</i> , <i>Neblinaea</i> African genera: <i>Achyrothalamus</i> , <i>Erythrocephalum</i> , <i>Pasaccardoa</i> , <i>Pleiotaxis</i> , <i>Adenocaulon</i> , <i>Anisochaeta</i> , <i>Berardia</i> , <i>Brachylaena</i> , <i>Chionopappus</i> , <i>Dicoma</i> , <i>Gladiopappus</i> , <i>Hochstetteria</i> , <i>Tarchonanthus</i> , <i>Warionia</i>

Table 12.2. Continued.

Author	Main taxonomic category	Generic groups and species
Bremer (1994)	Tribe Mutisieae	
	Subtribe Mutisiinae	<i>Stenopadus</i> group: <i>Achnopogon</i> , <i>Chimantaea</i> , <i>Duida</i> , <i>Glossarion</i> , <i>Gongylolepis</i> , <i>Neblinaea</i> , <i>Quelchia</i> , <i>Stenopadus</i> , <i>Stomatochaeta</i> <i>Gochnatia</i> and relatives: <i>Actinoseris</i> , <i>Chucoa</i> , <i>Cyclolepis</i> , <i>Hyalis</i> , <i>Gochnatia</i> , <i>Nouelia</i> <i>Ainsliaea</i> group: <i>Ainsliaea</i> , <i>Macroclinidium</i> , <i>Myriopsis</i> , <i>Pertya</i> <i>Brachylaena</i> and <i>Tarchonanthus</i> <i>Plazia</i> group: <i>Aphyllocladus</i> , <i>Gypothamnium</i> , <i>Plazia</i> <i>Dicoma</i> group: <i>Achyrothalamus</i> , <i>Dicoma</i> , <i>Erythrocephalum</i> , <i>Gladiopappus</i> , <i>Pasaccardoa</i> , <i>Pleiotaxis</i> <i>Onoseris</i> and <i>Urmenetea</i> <i>Mutisia</i> and <i>Hyaloseris</i> <i>Chaetanthera</i> group: <i>Brachyclados</i> , <i>Chaetanthera</i> , <i>Pachylaena</i> <i>Gerbera</i> group: <i>Chaptalia</i> , <i>Gerbera</i> , <i>Leibnitzia</i> , <i>Perdicium</i> , <i>Trichocline</i> , <i>Uechtritzia</i>
	Subtribe Nassauviinae	<i>Proustia</i> group: <i>Acourtia</i> , <i>Burkartia</i> , <i>Lophopappus</i> , <i>Proustia</i> <i>Leucheria</i> group: <i>Holocheilus</i> , <i>Leucheria</i> , <i>Macrachaenium</i> , <i>Moschardia</i> , <i>Nassauvia</i> (incl. <i>Calopappus</i>), <i>Oxyphyllum</i> , <i>Panphalea</i> , <i>Perezia</i> , <i>Polyachyrus</i> , <i>Triptilion</i> <i>Adenocaulon</i> and <i>Eriachaenium</i>
	Excluded	<i>Warionia</i>
Hind (2007)	Tribe Mutisieae	
	Stiffitia group	<i>Hyaloseris</i> , <i>Stiffitia</i> , <i>Wunderlichia</i>
	<i>Stenopadus</i> group	<i>Achnopogon</i> , <i>Chimantaea</i> , <i>Eurydochus</i> , <i>Glossarion</i> , <i>Gongylolepis</i> , <i>Neblinaea</i> , <i>Quelchia</i> , <i>Salcedoa</i> , <i>Stenopadus</i> , <i>Stomatochaeta</i>
	Subtribe Nassauviinae	<i>Acourtia</i> , <i>Adenocaulon</i> , <i>Ameghinoa</i> , <i>Berylsimpsonia</i> , <i>Burkartia</i> , <i>Cephalopappus</i> , <i>Criscia</i> , <i>Dolichlasium</i> , <i>Eriachaenium</i> , <i>Holocheilus</i> , <i>Jungia</i> , <i>Leucheria</i> , <i>Leunisia</i> , <i>Lophopappus</i> , <i>Macrachaenium</i> , <i>Marticoenia</i> , <i>Moschardia</i> , <i>Nassauvia</i> , <i>Oxyphyllum</i> , <i>Panphalea</i> , <i>Perezia</i> , <i>Pleocarphus</i> , <i>Polyachyrus</i> , <i>Proustia</i> , <i>Triptilion</i> , <i>Trixis</i>
	Subtribe Mutisiinae	<i>Aphyllocladus</i> , <i>Brachyclados</i> , <i>Chaetanthera</i> , <i>Chucoa</i> , <i>Cnicothamnus</i> , <i>Cyclolepis</i> , <i>Gypothamnium</i> , <i>Hyalis</i> , <i>Ianthopappus</i> , <i>Lulia</i> , <i>Lycoseris</i> , <i>Mutisia</i> , <i>Onoseris</i> , <i>Pachylaena</i> , <i>Plazia</i> , <i>Urmenetea</i>
	Subtribe Gerberinae	<i>Amblyperma</i> , <i>Chaptalia</i> , <i>Gerbera</i> , <i>Leibnitzia</i> , <i>Perdicium</i> , <i>Trichocline</i> , <i>Uechtritzia</i>
	Subtribe Gochnatiinae	<i>Gochnatia</i> , <i>Pentaphragus</i> , <i>Richterago</i>
	<i>Hecastocleis</i> group	<i>Hecastocleis</i>
	<i>Nouelia</i> group	<i>Leucomeris</i> , <i>Nouelia</i>
	<i>Catamixis</i> group	<i>Catamixis</i>
	Subtribe Tarchonanthinae	<i>Brachylaena</i> , <i>Tarchonanthus</i>
	<i>Dicoma</i> group	<i>Dicoma</i> , <i>Erythrocephalum</i> , <i>Gladiopappus</i> , <i>Oldenburgia</i> , <i>Pasaccardoa</i> , <i>Pleiotaxis</i>
	<i>Pertya</i> group	<i>Ainsliaea</i> , <i>Macroclinidium</i> , <i>Myriopsis</i> , <i>Pertya</i>
Katinas et al. 2008	Subfamily Mutisioideae	
	Tribe Mutisieae	(1) <i>Ainsliaea</i> , <i>Macroclinidium</i> , <i>Myriopsis</i> , <i>Pertya</i> (2) <i>Adenocaulon</i> and <i>Eriachaenium</i> (3) <i>Hecastocleis</i> (4) <i>Achnopogon</i> , <i>Duida</i> , <i>Eurydochus</i> , <i>Glossarion</i> , <i>Gongylolepis</i> , <i>Neblinaea</i> , <i>Salcedoa</i> (5) <i>Actinoseris</i> , <i>Cnicothamnus</i> , <i>Cyclolepis</i> , <i>Gochnatia</i> , <i>Hyalis</i> , <i>Ianthopappus</i> , <i>Nouelia</i>
	Tribe Stiffitieae	<i>Chimantaea</i> , <i>Quelchia</i> , <i>Stiffitia</i> , <i>Stomatochaeta</i> , <i>Stenopadus</i> , <i>Wunderlichia</i>
	Tribe Nassauvieae	
	Excluded	<i>Brachylaena</i> , <i>Cloiselia</i> , <i>Dicoma</i> , <i>Dicomopsis</i> , <i>Erythrocephalum</i> , <i>Gladiopappus</i> , <i>Hesperomannia</i> , <i>Macledium</i> , <i>Moquinia</i> , <i>Pasaccardoa</i> , <i>Pleiotaxis</i> , <i>Tarchonanthus</i> , <i>Warionia</i>

common ancestry and formed a monophyletic group. In addition, close relationships among tepui-centered genera and *Wunderlichia* and *Stiffia* were also indicated by Robinson (1991) and Pruski (1991).

Katinas et al. (2008), based on morphological studies with an emphasis on the corolla, style and pollen features, redefined Don's (1830) tribe Stiffieae to include *Chimantaea*, *Quelchia*, *Stenopadus*, *Stiffia*, *Stomatochaeta*, and *Wunderlichia* with mostly actinomorphic deeply 5-lobed corollas and rugulose styles. The remaining tepui-centered genera with bilabiate or ligulate corollas and glabrous styles were kept in their redefined tribe Mutisi-

ae. For the sake of clarification, the actinomorphic corolla tepui genera are referred to as the *Stenopadus* clade (after Bremer 1994) and the non-actinomorphic group is referred to as the *Gongylolepis* clade. This clarification is necessary because the molecular data produced different results.

Molecular studies using ten regions of chloroplast DNA (Panero and Funk 2008) indicated two monophyletic groups that contain tepui-centered clades (Fig. 12.1). The first is tribe Stiffieae (subfamily Stiffioideae), which can be divided into three clades, the basal branch which has only the Brazilian-centered genus *Stiffia* (actinomorphic

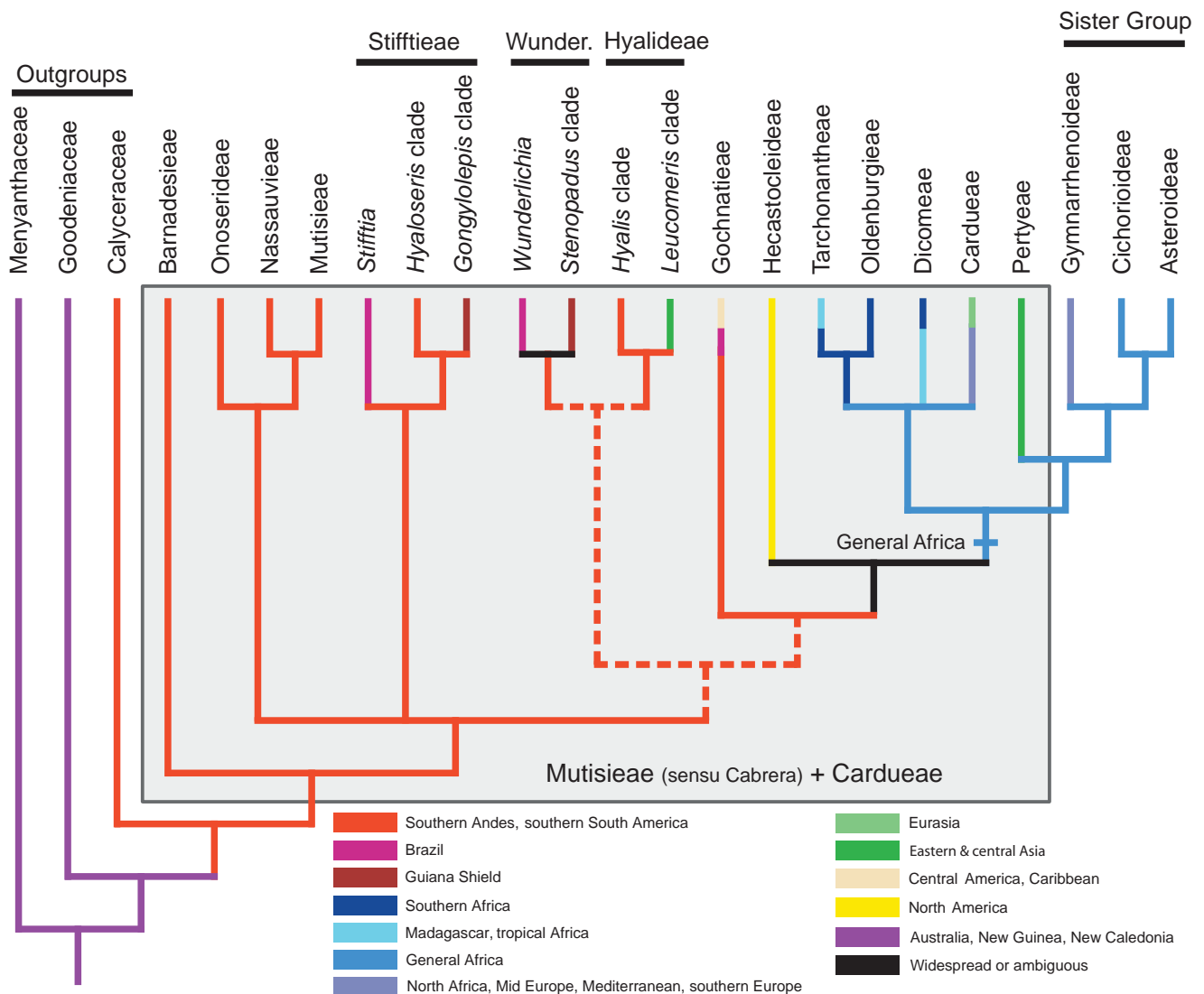


Fig. 12.1. A section of the Compositae phylogeny that highlights the basal grade of the family. A generic-level phylogeny can be found in Chapter 44. Wunder. = Wunderlichieae; the gray box denotes Mutisieae (sensu Cabrera). Cabrera never put Cardueae or Tarchonantheae into Mutisieae. Dashed lines indicate branches that are not as well supported as the remainder of the tree (Panero and Funk 2008): Wunderlichioideae have 52% bootstrap support in the parsimony tree and 91 posterior probability in the Bayesian tree; the branch connecting Wunderlichioideae to the rest of the family collapses in the parsimony tree and has a 97 posterior probability; the Gochnatieae branch has 65% bootstrap support and 100 posterior probability.

corollas; Fig. 12.2C–E), and two sister clades, the tepui-centered *Gongylolepis* clade (bilabiate corollas, rarely somewhat ligulate; Fig 12.2.A, B, F and Fig. 12.3B–E), and the Bolivian–Argentine *Hyaloseris* clade (ligulate or nearly ligulate, sub–bilabiate, or rarely bilabiate corollas; Fig. 12.3A) containing *Dinoseris* and *Hyaloseris*. Each of these three clades has a distinct morphology and there are no known apomorphic morphological characters that group the three together. The second group is tribe Wunderlichieae, including the tepui-centered *Stenopadus* clade (Fig. 12.4D, E and Fig. 12.5A–D) and the Brazilian genus *Wunderlichia* (Fig. 12.4A–C). This clade is well-supported by the morphology (Katinas et al. 2008). However, the subfamily Wunderlichioideae has both Wunderlichieae and its sister group the tribe Hyalideae, a clade containing the southern South American genera *Ianthopappus* (Fig. 12.6B, C) and *Hyalis* (Fig. 12.6A), and an Asian clade with *Leucomeris* and *Nouelia* (Fig. 12.7; see also Chapter 21; Table 12.1).

Currently there are no known morphological or palynological synapomorphies that support grouping the three molecular clades of Stifftioideae, the two tribes of Wunderlichioideae, or the two clades of the tribe Hyalideae (Table 12.1). For example, genera with actinomorphic and zygomorphic corollas, as well as glabrous and rugulose or papillose styles, are found in more than one clade.

Descriptions

Wunderlichieae (*Wunderlichia* clade). — Actinomorphic, tubular florets, receptacles commonly paleate, and styles bullate or rugulose beyond the bifurcation point of branches: *Chimantaea* (9 species), *Stenopadus* (15 species), *Stomatochaeta* (6 species), and *Wunderlichia* (6 species). These genera, the *Stenopadus* clade, plus *Stiffitia* (the genus that molecular data placed with the *Gongylolepis* and *Hyaloseris* clades) have been traditionally related based on morphology (e.g., Maguire 1956; Maguire et al. 1957). On the other hand, recent studies show that the molecularly defined clade Wunderlichieae is the only basal clade with style branches that are papillose below the bifurcation and paleaceous receptacles, and that *Stiffitia* does not have either of these (Roque, pers. comm.). Other characters such as the presence of more than 100 bristles in the pappus (Wunderlichioideae and Stifftioideae) and acute appendages on the anther connective (Wunderlichieae and Stifftioideae) show some signs of being useful, and all of these need to be further investigated (Roque, pers. comm.).

Floral venation in genera of the *Wunderlichia* clade was analyzed by Carlquist (1957) and summarized by Bremer (1994); it showed that the venation in the corollas of the species of *Stenopadus* was considered by Carlquist (1957) to be one of the most complex found in Compositae. There

are various degrees of union among the lateral veins (they extend from the lobe margins into the corolla tube), the median veins (they do or do not extend into the tube from the middle of each lobe), and the subsidiary veins (may be present or not; they branch from the lateral veins at various points). The fusion between veins led to complex patterns resulting in 2–5–veined corolla lobes and in 10–15–veined corolla tubes in the different species of *Stenopadus*.

Many features of members of this clade, such as the tubular corollas with 3–veined lobes and paleaceous receptacles of *Stenopadus* and *Wunderlichia*, have been regarded as primitive (Cronquist 1955; Carlquist 1957, 1976; Wagenitz 1976), in fact, Bremer (1994) hypothesized a “*Stenopadus* like” ancestral morphology for Compositae. However, this is ambiguous in the current molecular analysis and therefore difficult to speculate at this time.

Pollen of the *Wunderlichia* clade is heterogeneous, with three different exine types being found in this clade: *Mutisia*, *Stenopadus*, and *Wunderlichia* types (Katinas et al. 2008; Tellería 2008). Only the *Stenopadus* type, with two layers of single columellae in concordant pattern, appears as exclusive of some species of this genus; the remaining exine types are shared with genera of other taxonomic groups.

Hyalideae. — This tribe includes two clades, the South American genera *Hyalis* (2 species) and *Ianthopappus* (1 species), which are labeled on Fig. 12.1 as the *Hyalis* clade, and the Asian genera *Leucomeris* (2 species) and *Nouelia* (1 species) referred to on Fig. 12.1 as the *Leucomeris* clade. These genera have been considered part of the *Gochnatia* group together with *Actinoseris*, *Cnicothamnus*, *Cyclolepis*, and *Gochnatia* (Freire et al. 2002; Roque and Hind 2001) on the basis of apiculate anther appendages and smooth style branches. However, the large number of pappus bristles in the Hyalideae genera is similar to Wunderlichieae and not Gochnatieae (Roque, pers. comm.). This tribe is discussed in Chapter 15.

Stiffitia. — This genus is the sister group of the *Gongylolepis* and *Hyaloseris* clades (Fig. 12.1; Fig. 12.2C–E; Table 12.1). It is a genus of seven species occurring in Brazil and French Guiana; its members have actinomorphic corollas and glabrous (rarely sub–rugulose) styles. As mentioned above, *Stiffitia* is generally believed to be related to the tepui-centered genera with tubular corollas. The somewhat rugulose styles observed in some species (e.g., *Stiffitia chrysantha* Mikan; Katinas et al. 2008) would also support this relationship. However glabrous styles were also found in some of its species as well as other representatives of the *Gongylolepis* clade. However, such characters as pollen features, a large number of pappus bristles, glabrous achenes (except *Chimantaea*), and acute connectival appendages of anthers do link *Stiffitia* with members of the *Gongylolepis* clade and with the *Wunderlichia* clade (Katinas et al. 2008; Tellería 2008; Roque, pers. comm.).

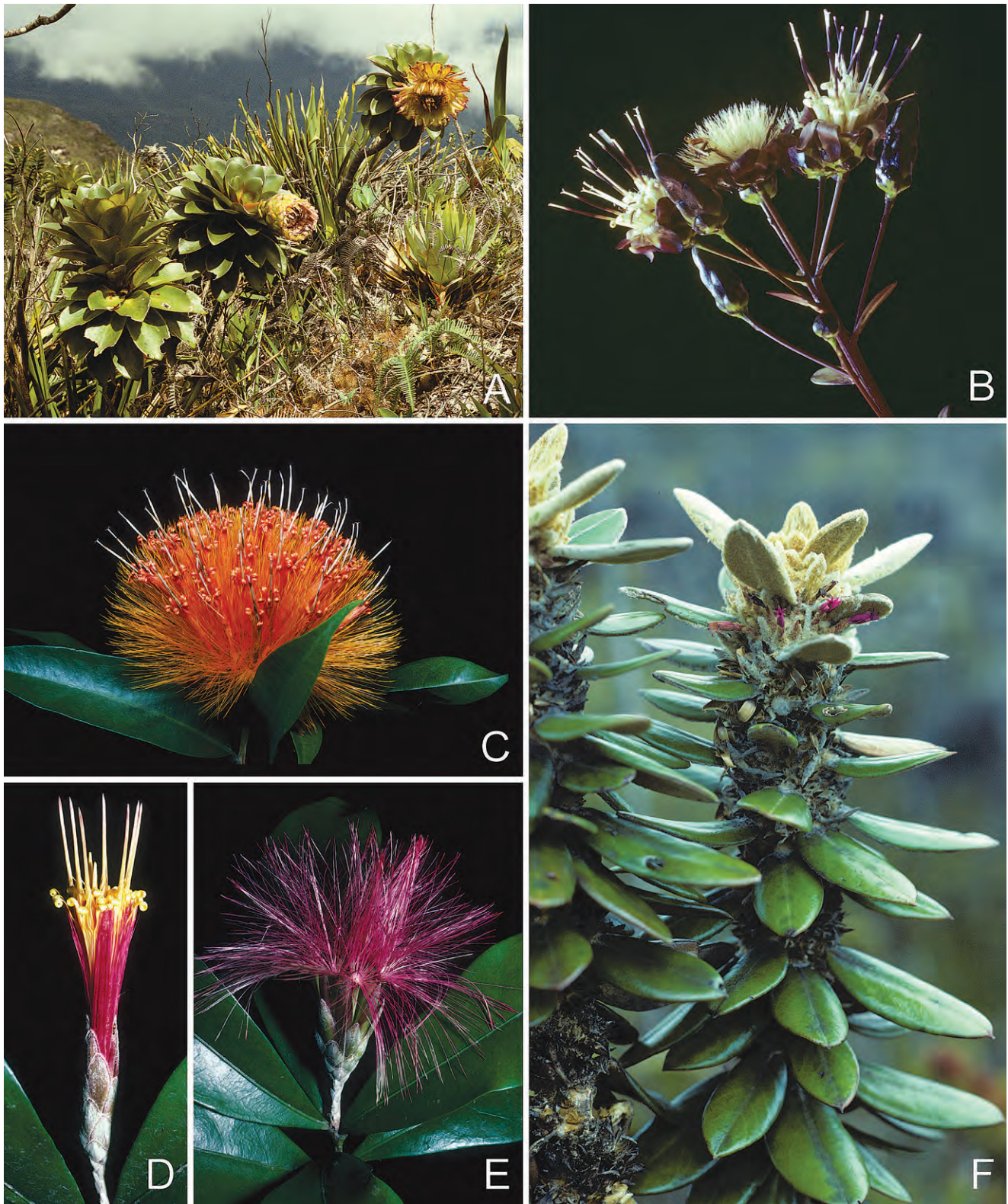


Fig. 12.2. **A** *Gongylolepis jauaensis* (Aristeg., Maguire & Steyerl.) V.M. Badillo (Venezuela: Cerro Coro Coro); **B** *Gongylolepis huachamacari* Maguire (Venezuela: Neblina; Funk 6725); **C** *Stiffitia chrysantha* Mikán var. *flavicans* Toledo ex Dedecca (Brazil); **D, E** *Stiffitia fruticosa* (Vell.) D.J.N. Hind & Semir (Brazil); **F** *Quelchia eriocalis* Maguire, Steyerl. & Wurdack (Venezuela: Chimantá massif). [Photographs: A, F, O. Huber; B, V.A. Funk; C–E, G. Lewis.]



Fig. 12.3. **A** *Hyaloseris cinerea* (Grieseb.) Grieseb. (Argentina, La Rioja, near Chilecito); **B** *Duidaea rubriceps* S.F. Blake (Venezuela: Duida; Fernández et al. 8010); **C** *Neblinaea promontorium* Maguire & Wurdack (Venezuela: Neblina); **D** *Duidaea marahuacensis* Steyerm. (Venezuela: Duida; Fernández et al. 8194); **E** *Achnopogon virgatus* Maguire, Steyerm. & Wurdack (Venezuela, Chimantá massif). [Photographs: A, J.M. Bonifacino; B–D, V.A. Funk; E, O. Huber.]

Gongylolepis clade. — This clade includes genera with all bilabiate florets, epaleate (but pilose) receptacles, and smooth style branches (Fig. 12.2A, B, F; Fig. 12.3B–E): *Achnopogon* (2 species), *Duidaea* (4 species), *Eurydochus* (1 species), *Glossarion* (2 species), *Gongylolepis* (14 species), *Neblinaea* (1 species), *Quelchia* (4 species plus one hybrid), and the more recently added (Jiménez Rodríguez et al. 2004) *Salcedoa* (1 species). Species of *Quelchia* have 1-flowered capitula, and the corollas range from tubular, slightly zygomorphic to bilabiate. The particular venation of the bilabiate genera, such as *Gongylolepis* with additional veins in the 3-lobed limb that branch off at the sinuses, led Carlquist (1957) to interpret this condition as a reflection of the vascular system of the actinomorphic corolla, which is generally assumed to be ancestral to the zygomorphic condition. The stem anatomical studies of Carlquist (1958) showed the presence of laticiferous cells in species of *Gongylolepis*, *Neblinaea*, and *Quelchia*. The presence and distribution of sclerenchyma in stems and involucre bracts as well as the presence or absence of laticiferous cells in the genera analyzed were viewed by Carlquist (1958) as significant in differentiating the genera with tubular corollas from the genera with bilabiate corollas.

Pollen of the genera of this clade was recently analyzed in detail (Zao et al. 2006; Katinas et al. 2008; Tellería 2008). Within this group, the exine *Gongylolepis* type relates the genera *Duidaea*, *Glossarion*, *Quelchia*, and *Gongylolepis*. The exine *Wunderlichia* type characterizes *Eurydochus* and *Salcedoa*, whereas the *Mutisia* exine type characterizes *Neblinaea* (Tellería 2008). Pollen features partially support the *Stiffia*-*Gongylolepis* clade since *Stiffia* has *Mutisia* exine type with microechinate or slightly echinate sculpture (such as the pollen of *Neblinaea*) whereas *Gongylolepis* presents a *Gongylolepis* exine type, which is mainly characterized by strong spines and a very perforate exine surface as occurs in many Cardueae (Tellería 2008).

Hyaloseris clade. — It is not surprising that the two southern South American (Bolivia–Argentina) genera *Dinoseris* (1 species) and *Hyaloseris* (7 species; Fig. 12.3A) appear as sister taxa, since *Dinoseris salicifolia* Griseb. was originally a species of *Hyaloseris* (Ariza Espinar 1973). Both genera share opposite leaves (sometimes alternate in *Hyaloseris*), homogamous capitula, epaleate receptacles, all isomorphic bisexual florets, and usually ligulate corollas with shallowly 5-dentate limbs (occasionally the corollas in species of *Hyaloseris* have their segments partially connate producing sub-bilabiate or bilabiate corollas); both genera have pollen with an exine of a *Mutisia* type: microechinate (Tellería and Katinas 2004; Katinas et al. 2008). Roque reports that the styles are bifid and the style branches are long and papillose below the bifurcation (Roque, pers. comm.).

Similarities and differences between the molecular and morphological studies can be summarized using Tables

12.1 and 12.2. All the clades recovered in the molecular data are reasonable, although perhaps more finely divided than the morphology would suggest (with the exception of those mentioned above). As pointed out above, with the exception of few authors (e.g., Jeffrey 1967; Pruski 1991), the tepui-centered genera have been regarded as belonging to two different groups based on their morphology (Maguire 1956; Maguire et al. 1957; Cabrera 1977; Hansen 1991). Building on those data, Katinas et al. (2008) redefined the two groups pointing out that the main characters to distinguish them are style and secondly corolla shape. Those genera with rugulose styles beyond the bifurcation point of branches and deeply cleft actinomorphic corollas have been included in one of the groups: the *Stenopadus* clade. These genera are, in part, represented in the tribe Wunderlichieae obtained by molecular data (Panero and Funk 2008). The second group, the *Gongylolepis* clade has glabrous styles and bilabiate corollas and this clade is found in one group within the molecularly defined Stifftieae. The sister group (in the molecular data) to the *Gongylolepis* clade, the *Hyaloseris* clade, has mostly ligulate corollas and styles dorsally papillose only at the branches. This type of corolla and style is different from the other members of the molecularly defined Stifftieae, which have actinomorphic or bilabiate corollas and styles glabrous or subrugulose beyond the bifurcation point of branches. Usually *Hyaloseris* and *Dinoseris* have been regarded as related to *Mutisia* (Cabrera 1965; Bremer 1994) in which papillose style branches and often ligulate corollas occur.

Finally, the placement of the *Wunderlichia* clade as the sister group to the *Hyalis* clade is unusual since the characteristics of styles and corollas are very different in both groups of genera (see Chapter 15). The *Hyalis* clade is usually thought to be related to the Gochnatieae (Hansen 1991; Bremer 1994; Freire et al. 2002; Katinas et al. 2008), by the presence of glabrous styles, apiculate apical appendages of the anthers, and epaleate receptacles, among other characteristics. However, *Hyalis* and *Ianthopappus* have pappus and achene characters that are different from Gochnatieae (Roque, pers. comm.). The *Hyalis* clade (Table 12.1; Fig. 12.6A) and *Wunderlichia* clade (Figs. 12.4 and 12.5) differ also in pollen features. In Hyalideae, pollen characters are more or less homogeneous given that most genera share the *Mutisia* exine type (Katinas et al. 2008) whereas in Wunderlichieae three types of exine can be found (Katinas et al. 2008; Tellería 2008).

In summary we can point out that Cabrera (1977) recognized four subtribes: Barnadesiinae, Gochnatiinae, Mutisiinae, and Nassauviinae. The first and the last have remained largely intact, with the former now a subfamily and the latter a tribe. Mutisiinae are somewhat redefined but largely intact as a subfamily with three tribes (Mutisieae, Onoserideae, Nassauvieae; Panero and Funk



Fig. 12.4. **A, B** *Wunderlichia mirabilis* Riedel (Brazil: Minas Gerais, Serra do Cipó; Roque 1622); **C** *Wunderlichia senaei* Blaz. (Brazil: Minas Gerais, Diamantina; Roque 1649); **D** *Stomatochaeta acuminata* Pruski, habit only (Venezuela: Chimantá massif); **E** *Stomatochaeta cymbifolia* (S.F. Blake) Maguire & Wurdack (Venezuela: Chimantá massif). [Photographs: A–C, N. Roque; D, E, O. Huber]



Fig. 12.5. **A** *Chimantaea eriocephala* Maguire, Steyer. & Wurdack; **B** *Chimantaea humilis* Maguire, Steyer. & Wurdack; **C** *Chimantaea mirabilis* Maguire, Steyer. & Wurdack; **D** *Stenopadus chimantensis* Maguire, Steyer. & Wurdack. All from Venezuela, Chimantá massif. [Photographs: A, B, C. Brewer; C, D, O. Huber.]



Fig. 12.6. **A** *Hyalis argentea* D. Don ex Hook. & Arn. (Argentina: Mendoza, near Tunuyán); **B, C** *Ianthopappus corymbosus* (Less.) N. Roque & D.J.N. Hind (Brazil: Rio Grande do Sul, Reserva Biológica de Ibirapuitã; Deble and Oliveira-Deble 7993). [Photographs: A, J.M. Bonifacino; B, C, L.P. Deble & A.S. Oliveira.]

2008). Gochnatiinae, which contained most of the taxa with actinomorphic corollas, have fragmented into many smaller groups that in the molecular data are now recognized as different tribes and subfamilies (Table 12.1). Most of the clades have morphological characters that define them but some do not.

CATAMIXIS INCERTAE SEDIS

The genus *Catamixis* (Fig. 12.8) is monotypic and found only in the northern part of India and adjacent Nepal. Its

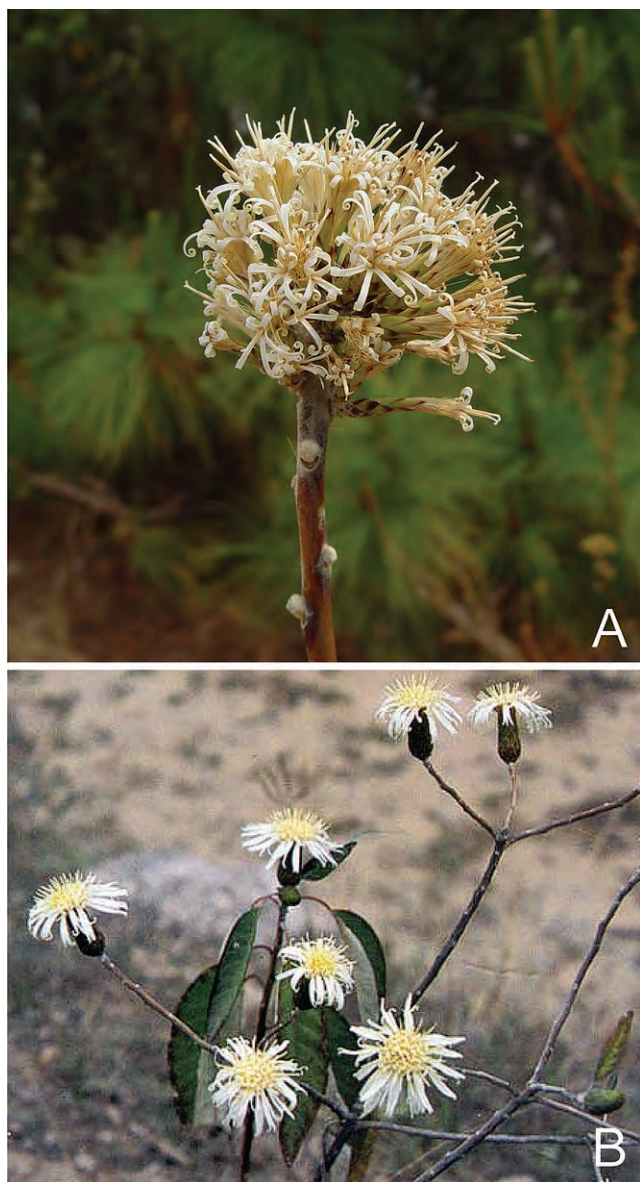


Fig. 12.7. **A** *Leucomeris* sp. (China: Yunnan); **B** *Nouelia insignis* Franch. (China: Yunnan). [Photographs: A, Wang Hong; B, Tao Guoda.]

DNA has not been sequenced, and it was not discussed by Panero and Funk (2002, 2008). Recent morphological treatments have not made a definite recommendation on where it should be placed. Bremer (1994) put this genus in his large, paraphyletic Mutisiinae (including Gochnatiinae). Katinas et al. (2008) placed it in a more restricted Mutisieae but did not feel strongly that it belonged there, and Freire (Chapter 21) did not include it in the *Pertya* clade (Pertyeae). Jeffrey (2007), however, did place *Catamixis* into the tribe Pertyeae. The major features that are used to place taxa in Mutisieae (sensu Cabrera) using morphology are the corolla shape, style pubescence, and style apex. The corolla of *Catamixis* is ligulate with five shallowly divided lobes, but the lobes are irregular in shape and size (Fig. 12.8F, O, P). Since this is probably an independently derived character, an autapomorphy, it is not useful for grouping. The shaft of the style of *Catamixis* is, for the most part, glabrous except for a few scattered hairs near the base (Fig. 12.8I). The style branches are relatively short and slightly rounded at the apex (not acute or attenuate) and are short-papillose (Fig. 12.8J).

The pollen grains of *Catamixis* (Fig. 12.9) have 3-colporate apertures and 2-layered exine with a surface that is spinulose with widely dispersed spinules (<1 μm in height). The surface of the grain (Fig. 12.9B) is microperforate and spinose, and part of a fractured section (Fig. 12.9C) shows a 2-layered exine exposing a broad and thickened lower (proximal) layer of columellae and an upper (distal) layer of considerably denser and shorter columellae. The grains are rather small, 30–35 μm . The pollen characteristics tell us that *Catamixis* is definitely a member of one of the clades of former Mutisieae (sensu Cabrera), but many of the clades have similar pollen so it does not offer any immediate help with determining its position on the phylogeny. A more detailed study may provide additional data.

Catamixis, therefore, shares with Pertyeae the dorsally short papillose nature of the style branches and the ligulate corollas of some of Pertyeae, although the corolla limbs of Pertyeae are deeply 5-lobed (vs. shallowly 5-lobed in *Catamixis*); the distribution of *Catamixis* might also suggest a Pertyeae affinity. However, there are no data that clearly place *Catamixis* in any of the existing groups and at this time it seems best to list it as ‘unplaced’ until fresh material has been obtained so that its DNA can be sequenced.

Catamixis T. Thomson in J. Linn. Soc. Bot. 9: 342. 1865

– Type: *C. baccharoides* T. Thomson.

Small erect, poorly branched shrub. Stems densely tomentose at first, later glabrescent. Leaves alternate, petiolate, petiole winged, lamina simple, obovate, base long-cuneate, midrib prominent beneath, margins coarsely

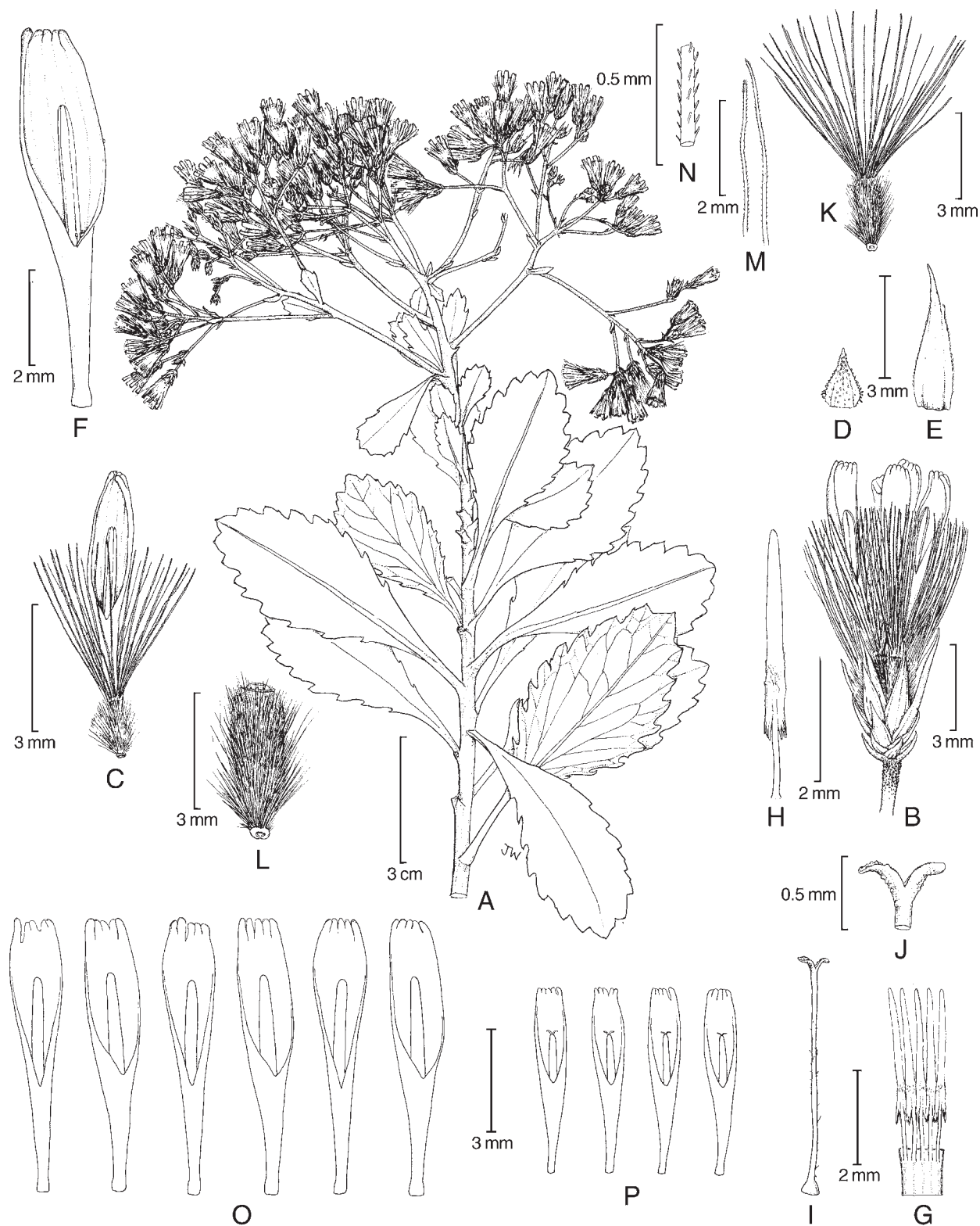


Fig. 12.8. *Catamixis baccharoides* T. Thomson. **A** habit; **B** head; **C** floret with pappus; **D** outer involucre bract; **E** inner involucre bract; **F** floret; **G** anthers opened; **H** close up of anther; **I** style; **J** style branches and stigmatic surface; **K** achene with pappus; **L** mature achene; **M**, **N** pappus bristles; **O**, **P** corolla variation in size and depth of lobes. **A–F**, **K–N** & **P** from *Upendranath Kanjilal 1020*; **G–J** & **O** from *Stewart 209/BS* syntype. [Drawing by J. Beentje.]

serrate, apices obtuse to sub-acute. Inflorescences terminal, eventually overtopped by vegetative branches, corymbose, well-branched, capitula pedunculate, pedicels subtended by short linear bracteole at base, pubescent with numerous short hairs; capitula homogamous, ligulate, numerous; involucre 4–5-seriate, scarcely imbricate, turbinate; phyllaries, gradate, margins ciliate and lacinate, apices long-acute, often purplish; receptacle convex, glabrous, epaleate, \pm alveolate. Florets few (6), hermaphrodite, corollas whitish to pale yellow, glabrous, ligule teeth equal or unequal; apical anther appendages narrow-triangular, about three times longer than wide, apices sub-acute, somewhat rounded, anther collar indistinguishable from filament; basal anther appendages tailed, lacinate; style shaft commonly glabrous, style base with basal node; style arms relatively short, dorsally short papillose, apices slightly rounded. Achenes densely long-setuliferous/sericeous, apices acute; carpodium distinct, annular, pappus setae uniseriate, long-barbelate, white. (Description provided by Hind, pers. comm.; Figs. 12.8 and 12.9.)

Catamixis is endemic to the Eastern Himalaya region (see discussion at <http://www.biodiversityscience.org/publications/hotspots/Himalaya.html>) and is listed as “vulnerable” on the list of ‘Threatened Plants of Uttaranchal’ (http://www.wii.gov.in/nwdc/threatened_plants_uttaranchal.pdf). It has no known chromosome counts and it has no known common names or uses.

SUBFAMILY CARDUOIDEAE CASS. EX SWEET (1826)

Perennial, biennial or less often annual herbs, shrubs or rarely trees, rarely scandent. Leaves alternate, usually simple, entire, serrate, denticulate or lobulate, especially in herbaceous members often spiny. Capitula homogamous or heterogamous, discoid or discoid with marginal florets sterile and radiant, rarely bilabiate-radiate, radiate or ligulate. Involucre narrowly cylindrical to urceolate-subglobose, phyllaries 3- to many-seriate, imbricate, often spiniferous. Receptacle epaleaceous and very often setulose, rarely paleaceous. Florets 1- to many, 5-merous, all or inner regular or subregular, outer sometimes radiant, rarely bilabiate-radiate or radiate, very rarely all ligulate; corolla lobes long, those of inner lip of bilabiate florets straight or with incurved apex, very rarely coiled. Anthers calcarate and caudate, very rarely ecalcarate, tails usually long, sometimes pilose or fringed. Pollen usually ecaevate, spiny or microechinate. Style arms short to long, obtuse to rarely acute, glabrous or with dorsal hairs, sometimes not divergent for most of their length, with stigmatic papillae covering all inner surface; style shaft often with an articulation at or below the branching point, marked by a ring of hairs and/or an increase in diameter, glabrous below the articulation, usually hairy above it. Achenes with twin hairs, simple hairs, or glabrous. Pappus usually present, of bristles or scales, isomorphic or heteromorphic. (Description adapted from Jeffrey, 2007.)

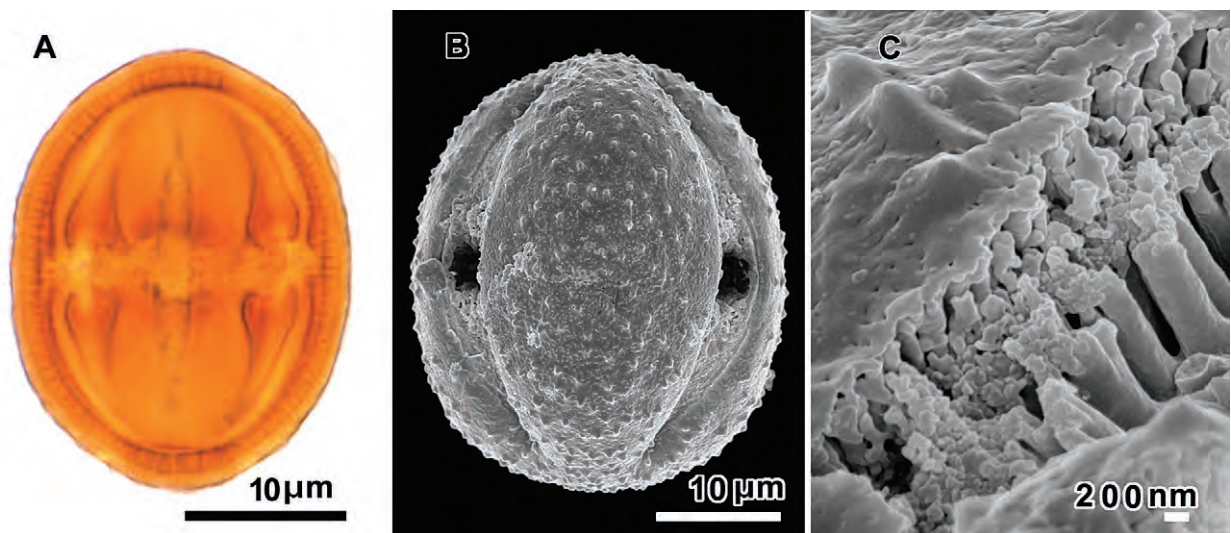


Fig. 12.9. *Catamixis baccharoides* T. Thomson. **A** Light micrograph (LM). Lateral (equatorial) view showing 3-colporate apertures and 2-layered exine. **B** Scanning electron micrograph (SEM) of pollen surface (orientation similar to LM in Fig. 12.9A) showing relatively few and widely dispersed spinules ($< 1 \mu\text{m}$ in height) and colporate apertures. **C** SEM of broken grain showing microperforate and spinose surface and part of a fractured section through 2-layered exine (as described in Fig. 12.9A) exposing a broad and thickened lower (proximal) layer of columellae and an upper (distal) layer of considerably denser and shorter columellae. [Photographs, A. Wortley.]

Carduoideae comprise at least 93 genera and 2600 species, mostly in the Old World. The subfamily as here circumscribed includes all mutisioid genera that in molecular studies come out in a clade with Cardueae s.l. (Fig. 12.10). The constancy of the *Gochnatia* type of testa epidermal cell wall thickening (Grau 1980) or its derivatives define the subfamily. Although this type of cell wall thickening also occurs in some Mutisieae, possibly as a parallelism, it is there associated with different style and/or pollen types.

All the available phylogenetic information indicates that the origin of the great tribe Cardueae, centered in the Old World, can be tracked to African representatives of old Mutisieae s.l. (presently tribes Dicomeae, Tarchonantheae and Oldenburgieae), following progressive drying up of the African climate at the end of the Tertiary. These changes led to a rapid deforestation of the

continent. Perhaps the best candidate with the most plesiomorphic characters in Carduoideae is tribe Dicomeae, which has some characters that are generalized among Cardueae, but are usually missing in Mutisieae s.str.

The most important characters of Cardueae are: (1) leaves with spiny apices (*Dicoma paivae* S. Ortiz & Rodr. Oubiña, *Dicoma tomentosa* Cass., *Macladium canum* (Balf.f.) S. Ortiz, *Macladium spinosum* (L.) S. Ortiz, etc.); (2) coriaceous phyllaries with spiny tips (*Dicoma*, *Macladium*, *Pasaccardoa*), and (3) achenes obconical (*Cloiselia*, *Dicoma*, *Gladiopappus*, *Macladium*) or broadly cylindrical (*Erythrocephalum*, *Pasaccardoa*), often with pericarp reinforced with strips of sclerenchyma and apical groove below insertion of the pappus. One of the taxa with the largest number of plesiomorphic characters, *Pleiotaxis*, shows oblong, scarcely sclerified achenes without an apical groove, similar to the achenes of most primitive Cardueae. *Pleiotaxis*

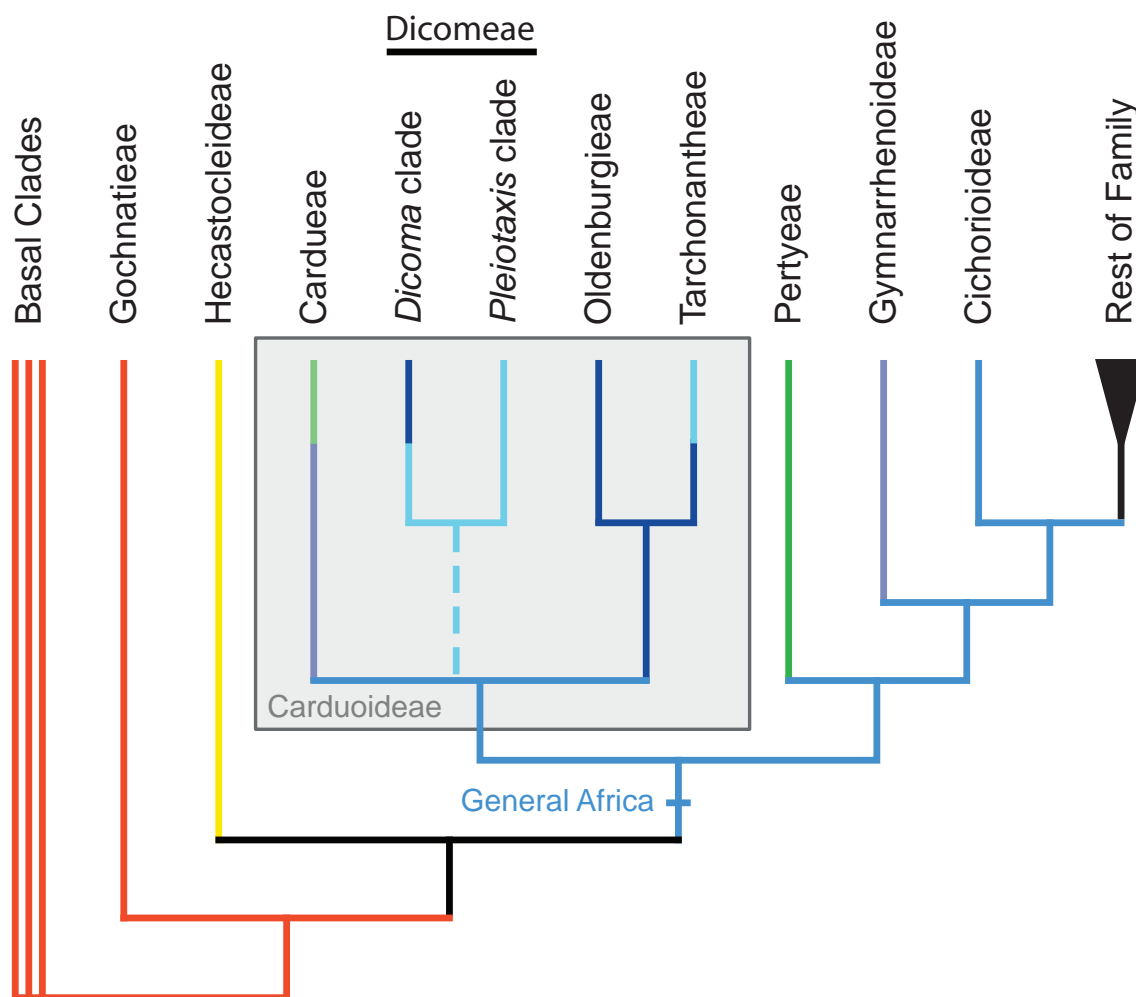


Fig. 12.10. A section of the Compositae phylogeny emphasizing relationships within the subfamily Carduoideae. The gray box denotes Carduoideae. For color chart see Fig. 12.1.

or other related genera could be the intermediates between Dicomeae and Cardueae. Achenes of Cardueae and Dicomeae would have evolved in parallel ways leading to the presently widespread sclerified type.

CONCLUSION

If we return to the overall goals of this ongoing research effort, we find that some have been met while others require further attention. In particular, some molecular clades have strong morphological support but some have no support or they conflict with the morphology; many genera have been satisfactorily placed on the phylogeny but some have not; and some super-generic taxa (be they subtribes, tribes, or subfamilies) are easy to recognize and have been accepted by most synantherologists (e.g., Nassauvieae, Wunderlichieae, Pertyeae) and some have not (e.g., Stifftieae). There are many possible reasons for these discrepancies and a better understanding of what characters are plesiomorphic would help us to understand the placement of some genera. We must also keep in mind that: some difficult taxa have only one set of sequences available, and the possibility of error exists; taxa are missing from the analyses and their addition might change the

topology; and some of the branches are not as strongly supported as one would like. Each new study brings additional data and insights on relationships.

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Note added in proof

A recent paper has shown that two separate base pair deletions link *Catamixis* with Pertyoideae. Panero, J. 2008. Shared molecular signatures support the inclusion of *Catamixis* in subfamily Pertyoideae. *Phytologia* 90: 418–424.