Arctotideae

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HISTORICAL OVERVIEW

The tribe Arctotideae, described by Cassini (1819), was merged with the thistles by Lessing (1831, 1832), who gathered an unnatural assemblage of taxa into a large tribe Cynareae (now Cardueae). Bentham (1873a) re-established the tribe Arctotideae and recognized three subtribes later known as Arctotidinae (Figs. 25.1–25.4), Gorteriinae (Figs. 25.5–25.10), and Gundeliinae (Chapter 24). Hoffmann (1890–1894) approved Bentham's classification, although with some differences in generic circumscriptions. Beauverd (1915) surveyed the subtribe Arctotidinae while Lewin (1922) made a more comprehensive revision of this subtribe. Gorteriinae were monographed by Roessler (1959, 1973). Norlindh (1977) retained the three Benthamian subtribes, but he also included the monotypic subtribe Eremothamninae, as first proposed by Leins (1970) based on palynological data. Since Norlindh's (1977) review, studies of achene anatomy (Reese 1989), ray limb epidermis (Baagøe 1978), embryology (Ahlstrand 1992), external achene morphology (McKenzie et al. 2005), and a cladistic analysis of Gorteriinae morphology (Karis 2006) have been published. Molecular studies have been published on Arctotideae (Funk et al. 2004) and the two well-supported subtribes, Arctotidinae (McKenzie et al. 2006c; Funk et al. 2007; McKenzie and Barker 2008) and Gorteriinae (Funk and Chan 2008).

Bremer (1987) undertook a cladistic analysis of Asteraceae based on morphology using tribes or subtribes as terminals. Arctotideae were united with Cardueae due to the alleged synapomorphies of dissected, spiny leaves, and styles with a ring of sweeping hairs below the bifurcation.

However, all molecular analyses, starting with the study by Kim and Jansen (1995), have yielded a monophyletic subfamily Cichorioideae s.str. wherein Arctotideae are nested, and so this chapter deals only with that placement. Early molecular studies containing Arctotideae representatives (Jansen et al. 1990; Bergqvist et al. 1995; Kim and Jansen 1995) included only 2–4 terminals from the tribe and so could not effectively deal with the question of monophyly. This was not the case in the morphological analysis by Karis et al. (1992). Here, *Eremothamnus* and *Arctotis* were united and placed in a large clade comprising Cichorieae, Liabeae, and Asteroideae, whereas *Berkheya* was placed as the sister taxon to this clade. One very uncommon family character indicated to be a synapomorphy for the clade *Eremothamnus* + *Arctotis* was soft anther appendages. However, the placement of genera was rather unstable in the analysis by Karis et al. (1992), and *Berkheya* was furthermore erroneously coded as not having arctotoid disc floret styles, i.e., with longer hairs in a ring well below the bifurcation. Admittedly, this feature is not so conspicuous in all species of *Berkheya*. Bremer conducted a morphological analysis (1994) of Arctotidinae and Gorteriinae as well as *Gundelia*, *Heterolepis*, and *Platycarpha*, and he used genera as terminals. Consequently, the monophyly of the genera could not be tested. Regardless of the choice of outgroup, the subtribes were monophyletic with *Platycarpha* sister to Arctotidinae, while Gorteriinae also included *Gundelia*. Karis et al. (2001) included one species each of *Arctotis*, *Haplocarpha* (both are Arctotidinae), *Berkheya*, *Didelta*, *Gazania* (all three are Gorteriinae), *Eremothamnus* and *Hoplophyllum*, in a study based solely on DNA sequence data from the chloroplast region *ndhF*.

All these terminals were united into a clade with 69% parsimony jack-knife support. Furthermore, the subtribes Arctotidinae and Gorteriinae, and the *Eremothamnus* + *Hoplophyllum* clade received 100%, 69%, and 100% parsimony jackknife support, respectively, but the three clades were united into a trichotomy.

PHYLOGENY

Funk et al. (2004) surveyed phylogenetic relationships in Arctotideae utilizing two chloroplast DNA regions (*ndhF*, *trnL-F*) and one nuclear DNA region (ITS). The dataset was considerably expanded in comparison with previous molecular investigations and included six terminals from Arctotidinae, eighteen from Gorteriinae, as well as all "problem genera" (see below; Table 25.1). It was indeed not straightforward to analyze the full dataset using many other Cichorioideae s.str. as the closest outgroup in different combinations (Funk et al. 2004). Yet, the subtribes received strong bootstrap support, whereas the support for Arctotideae including *Heterolepis*, and *Eremothamnus* + *Hoplophyllum* (the latter two genera are herein classified in Eremothamneae; see Chapter 26) was below 50%. The strong morphological (Bremer 1994; Funk et al. 2004; Karis 2006, 2007) and molecular support (Funk et al. 2004) for both subtribes as well-supported clades, in combination with an increased number of researchers studying these taxa, subsequently led to separate phylogenetic analyses of the subtribes (see Biogeography section below). *Heterolepis* (Chapter 31), *Eremothamnus* and *Hoplophyllum* (Eremothamneae; Chapter 26), *Platycarpha* (Plathycarpheae; Chapter 29), and *Gundelia* (Cichorieae; Chapter 24) were all at one time placed within Arctotideae. However, they are herein treated as separate clades (see Chapter 23 for an overview) and will not be considered further in this chapter.

Arctotidinae

Species relationships within Arctotidinae have been the focus of several recent molecular phylogenetic studies based on non-coding and coding cpDNA and ITS sequence data (Funk et al. 2004; McKenzie et al. 2006c; Funk et al. 2007; McKenzie and Barker 2008). A simplified phylogeny summarizing the major lineages in the subtribe is shown in Fig. 25.4. These studies demonstrated that *Arctotis* and *Haplocarpha* are polyphyletic as presently circumscribed. A combined analysis of the published sequences resolved nine major clades or monotypic lineages, each with strong bootstrap and Bayesian posterior probability support. Species that are currently placed in *Haplocarpha* were distributed among five lineages and two sections within *Arctotis* (sects. *Anomalae* and *Austro-orientales*) and need to be removed in order to render the

genus monophyletic. The *Landtia* clade comprises three *Haplocarpha* species, two of which (*H. nervosa* (Thunb.) Beauverd and *H. rueppellii* (Sch.Bip.) Beauverd) were previously placed in the segregate genus *Landtia* (e.g., Lessing 1831, 1832; Bentham 1873b), and is sister to the rest of the subtribe. *Haplocarpha oocephala* (DC.) Beyers, *H. scaposa* Harv. and *Dymondia margaretae* Compton comprise monotypic lineages diverging towards the base of the phylogeny. Most of the extant diversity in Arctotidinae is found in three major lineages that are indicated to have diverged rapidly; the nodes linking these lineages are weakly supported. The *Cymbonotus* clade contains the three Australian-endemic species as well as the southern African *Arctotis arctotoides* (L.f.) O. Hoffm. species complex and the East African *Haplocarpha schimperi* (Sch.Bip.) Beauverd. The clades *Arctotheca*, *Haplocarpha* s.str. and *Arctotis* sect. *Anomalae* form a well-supported lineage (McKenzie et al. 2006c; McKenzie and Barker 2008). *Arctotis* is the largest clade in Arctotidinae, comprising "perennial" and "annual" clades well supported by ITS data, and with the annual *A. breviscapa* Thunb. sister to both of these clades (Fig. 25.4). At present, few morphological synapomorphies supporting the major clades have been identified; instead, the clades are supported by combinations of morphological characters (R.J. McKenzie, unpub.).

Gorteriinae

Funk and coworkers (Funk et al. 2004; Funk and Chan 2008; Fig. 25.10) used nuclear and chloroplast DNA sequence data and obtained the same pattern within Gorteriinae throughout all analyses, viz. two groups, one containing *Gazania*, *Gorteria*, and *Hirpicium* (the *Gorteria* clade), a second comprising *Berkheya*, *Cullumia*, *Cuspidia*, *Didelta* and *Heterorhachis* (the *Berkheya* clade).

Funk and Chan (2008) furthermore obtained two well-supported sister groups within the *Berkheya* clade, viz. one containing the two species of *Didelta* plus *Berkheya spinosissima* Willd., and the other including the rest of the sampled taxa. Funk and Chan (2008) sampled 46 species with more than one terminal from all non-monotypic genera, and most monotypic genera were represented by more than one accession, which allowed monophyly of the genera to be examined. *Berkheya* and *Hirpicium* proved to be paraphyletic. This study also indicated that *Cullumia* might be paraphyletic since *Berkheya cruciata* Willd. was placed as sister to two *Cullumia* species, with three others in turn as their sister group. *Hirpicium* may have experienced past hybridization because *H. echinus* Less. has different sister groups in the nuclear and chloroplast data (Fig. 25.10). However, several strongly supported clades were found in *Berkheya* and the monotypic genera did not fall within any of them. Furthermore the study showed that some of the series recognized by Roessler (1959) corresponded to well-supported clades.

Table 25.1. Different classifications of Arctotideae. Estimated current number of species in each genus shown within parentheses. Modified after Funk et al. (2004).

Bentham 1873b (modified)	Heywood et al. 1977	Bremer 1994	Karis 2007	Barcelona 2008
Subtribe Arctotidinae Less.				
Arctotheca Vaill. (5)	Arctotinae	Arctotinae	Arctotidinae	Arctotidinae
Arctotis L., paraphyletic (60–70)	Arctotinae	Arctotinae	Arctotidinae	Arctotidinae
Cymbonotus Cass. (3)	Arctotinae	Arctotinae	Arctotidinae	Arctotidinae
Dymondia Compton (1)	Arctotinae	Arctotinae	Arctotidinae	Arctotidinae
Haplocarpha Less., paraphyletic (9)	Arctotinae	Arctotinae	Arctotidinae	Arctotidinae
Subtribe Gorteriinae Benth.				
Berkheya Ehrh., paraphyletic (79+)	Gorteriinae	Gorteriinae	Gorteriinae	Gorteriinae
Cullumia R. Br., paraphyletic? (15)	Gorteriinae	Gorteriinae	Gorteriinae	Gorteriinae
Cuspidia Gaertn. (1)	Gorteriinae	Gorteriinae	Gorteriinae	Gorteriinae
Didelta L'Hér. (2)	Gorteriinae	Gorteriinae	Gorteriinae	Gorteriinae
Gazania Gaertn. (17)	Gorteriinae	Gorteriinae	Gorteriinae	Gorteriinae
Gorteria L. (3)	Gorteriinae	Gorteriinae	Gorteriinae	Gorteriinae
Heterorhachis Sch.Bip. ex Walp. (1)	Gorteriinae	Gorteriinae	Gorteriinae	Gorteriinae
Hirpicium Cass., paraphyletic (13)	Gorteriinae	Gorteriinae	Gorteriinae	Gorteriinae
Heterolepis Cass. (3)	Gorteriinae (Norlindh) Mutisieae (Merxmüller)	Unassigned to subtribe	Unassigned to subtribe	Gorteriinae(?) or unassigned to subtribe
Subtribe Gundeliinae Benth.				
Gundelia L. (1)	Gundeliinae	Gorteriinae	Gundelieae DC. ex Lecoq & Juillet (Jeffrey)	Gundelieae
Eremothamnus O. Hoffm. (1)	Eremothamninae Leins	Unassigned to tribe	Unassigned to subtribe	Eremothamneae
Hoplophyllum DC. (2)	Vernonieae	Unassigned to tribe	Unassigned to subtribe	Eremothamneae
Platycarpha Less. (3)	Cynareae (Norlindh, rejected by Dittrich)	Unassigned to subtribe	Unassigned to subtribe	Platycarpheae

Morphological data from 43 ingroup terminals (Karis 2006) obtained the same sister group relationship between the *Gorteria* clade and *Berkheya* clade, but relationships within the latter remained uncertain. Again, *Berkheya* and *Hirpicium* were indicated to be paraphyletic. Karis (2006) found that several floral micromorphological characters were phylogenetically informative, and both sister groups were therefore defined by sets of diagnosing synapomorphies derived from anthers and styles, as well as from external morphology. As expected, the morphologically well-diagnosed small genera *Cullumia*, *Cuspidia*, *Didelta*, and *Heterorhachis* were all entrenched in the vast, paraphyletic *Berkheya* (Funk et al. 2004; Karis 2006; Funk and Chan 2008). Likewise, the morphologically diverse genus *Hirpicium* is split between two lineages in the *Gorteria* clade. In a separate study Howis (2007) reconstructed a phylogeny of *Gazania* based on sequences from nuclear ribosomal DNA (ETS, ITS) and four non-coding cpDNA regions. Of the fifteen species sampled, only seven were supported as being monophyletic; the remaining species formed a large, poorly resolved clade. This study only partially supported Roessler's (1959) morphology-based species circumscriptions in *Gazania*.

Phylogenetic investigations focused on the *Gorteria/Hirpicium* clade (F. Stångberg and P.O. Karis, unpub.), *Berkheya* clade (N. Netnou et al., unpub.), and *Cullumia* and *Didelta* (V.A. Funk and M. Koekemoer, unpub.) are in progress.

SUBTRIBAL TREATMENTS

Much of the taxonomy was covered in Karis (2007). Table 25.1 summarizes the current classification and number of species per genus. Since the two subtribes differ substantially in morphology, we have chosen to treat them separately throughout. As a result, there are two subtribal descriptions, rather than one disparate tribal description.

ARCTOTIDINAE

Taxonomy
Subtribe Arctotidinae (Cass.) Dumort., Anal. Fam. Pl.: 32. 1829 – Type: *Arctotis* L. (Figs. 25.1–25.4)

Leaves entire or lobed to pinnatisect, usually with woolly hairs. Heads pedunculate or scapose, but sessile in *Dymondia*, radiate. Scapes woolly, often with uniseriate septate hairs. Involucral bracts free, outer with foliaceous tips, inner obtuse with scarious tips. Ray florets usually 3-lobed, disc florets usually shallowly lobed, styles with a markedly thickened, basally truncate or tapering, apical part with broadly subulate sweeping hairs. Anthers

distinctly ecaudate, apical appendages usually obtuse or rounded, soft, ± wrinkled, endothecium radial, collar usually inconspicuous, cells not reinforced. Achenes dorsiventrally asymmetric, usually with conspicuous abaxial ribs or wings, pericarp with subepidermal sclerifications of 1–2 oblong (cross-section) cell layers, testa epidermis with reinforcements, with twin hairs, short uniseriate or unicellular hairs. Pappus scales of very elongate, narrowly oblong cells, in 1–2 series, rarely coroniform or absent.

Arctotidinae can generally be distinguished in the field by their radiate capitulum, the free, scarious-margined inner involucral bracts, the rather shallowly lobed disc floret corolla, the dorsiventrally asymmetric, and often ribbed or winged, achenes, and the scaly pappus (which is absent in a few species). Another set of morphological and anatomical features can be considered to be synapomorphies and many of them are found in the anthers (McKenzie et al. 2006c; Karis 2007), viz. no tails, the short, blunt, soft and wrinkled apical appendage, inconspicuous filament collar (with *Cymbonotus* an exception), and radial endothecial tissue. Another probable synapomorphy is the small, subulate-ensiform sweeping hairs of the style (Karis 2006).

Norlindh (1977) accepted five genera in the subtribe Arctotidinae (Table 25.1): *Arctotheca*, *Arctotis*, *Cymbonotus*, *Dymondia*, and *Haplocarpha*. This taxonomy was retained by Karis (2007). However, recent molecular studies (Funk et al. 2004, 2007; McKenzie et al. 2006c; McKenzie and Barker 2008) have resulted in Fig. 4, which demonstrates that this classification does not reflect the evolutionary history of the group and significant taxonomic changes are needed. In addition, the alpha taxonomy of southern African Arctotidinae, particularly that of *Arctotis*, is confused and blighted by nomenclatural problems, which are in the process of being resolved (McKenzie et al. 2006a, b, 2008a, b; McKenzie and Barker 2007).

Morphology
Habit and life history. — Perennial shrublets and shrubs are common in Arctotidinae (Figs. 25.1–25.3). The orientation of the vegetative shoots in these species ranges from obligately prostrate through to erect in different species. Many of the prostrate species form adventitious roots to varying degrees (Fig. 25.3A). A truly rhizomatous habit is rare in Arctotidinae, and a significant number of the herbs are scapose (species of *Arctotheca*, *Arctotis*, *Cymbonotus*, and *Haplocarpha*) (Figs. 25.1–25.3). Fire is an important factor in the ecology of fynbos in South Africa (Cowling 1992). Many of the fynbos-endemic Arctotidinae respond to fire cycles by resprouting from either rhizomes or woody subterranean rootstocks (e.g., *Arctotis acaulis* L., *A. semipapposa* (DC.) Beauverd), or reseeding through seed germination. Species with an annual life history comprise a minority in the subtribe but notably comprise an important clade

Fig. 25.1. Arctotidinae: *Arctotis*. **A** *Arctotis arctotoides* (L.f.) O. Hoffm. (South Africa, Western Cape coast); this species is a member of a vegetatively polymorphic species complex centered in southeastern South Africa and Lesotho. **B** *A. acaulis* L. (South Africa, Northern Cape: *Funk and Koekemoer 12548*). **C** *A. acaulis* (South Africa, Northern Cape: *Koekemoer and Funk 1948*); the free involucral bracts of this species are characteristic of the subtribe. [Photographs: A, R.J. McKenzie; B, C, V.A. Funk.]

Fig. 25.2. Arctotidinae: *Arctotis* (continued). **A** *Arctotis fastuosa* Jacq. (South Africa, Northern Cape: *Funk and Koekemoer 12646*); *Arctotis* is one of the major components of the spectacular spring flower displays in the winter-rainfall region of southern Africa. **B** *Arctotis* sp. (Namibia). **C** *A. leiocarpa* Harv. (Namibia). [Photographs: A, V.A. Funk; B, C, C.A. Mannheimer.]

Fig. 25.3. Arctotidinae: *Arctotheca*, *Cymbonotus*, *Dymondia*, and *Haplocarpha*. **A** *Arctotheca populifolia* (P.J. Bergius) Norl. (South Africa, Eastern Cape); this semi-succulent species is a primary colonizer of coastal dunes. **B** *Arctotheca calendula* (L.) Levyns (South Africa, Eastern Cape); commonly known as "capeweed", this weedy annual has naturalized in numerous countries in

both hemispheres. **C** *Cymbonotus maidenii* (Beauverd) A.E. Holland & V.A. Funk (Australia, Queensland). **D** *Dymondia margaretae* Compton (South Africa, Western Cape). **E** *Haplocarpha lyrata* Harv. (South Africa, Eastern Cape). **F** *Haplocarpha scaposa* Harv. (South Africa, Free State: *Funk and Koekemoer 12406*); this species, like the others in this subtribe, has free involucral bracts. [Photographs: A, B, E, R.J. McKenzie; C, T. Bean; D, P. Sollinger; F, V.A. Funk.]

in *Arctotis* centered in the semi-arid parts of the winter-rainfall region of southern Africa.

Leaves. — All Arctotidinae have alternate leaves, but the scapose taxa have a more or less pronounced leaf rosette. Leaf shape varies considerably between and even within some species (e.g., *Arctotis arctotoides*) from simple and entire to pinnately compound in varying degrees. Certain *Arctotis* species (*Arctotis argentea* Ait., *A. linearis* Thunb.) inhabiting the Cape Floristic Region (Linder 2003) have xeromorphic linear leaves. Unlike Gorteriinae, no Arctotidinae species has spiny leaves. Owing to the tri- or multi-lacunar nodes it is common that three (often more) separate veins are distinguished already when entering the leaf in most Arctotidinae, regardless of whether the leaves are entire or dissected. Some *Arctotis* species have decurrent or auriculate leaf bases.

Trichomes. — As in all other tribes, various kinds of trichomes are common. Woolly hairs (Drury and Watson 1966) are commonly found on the stems, leaves, and involucres in all genera, if not in all species. These woolly hairs are frequently longitudinally oriented along the stem and form a felt-like indumentum. Uniseriate, often reddish-purple, septate hairs of differing length are abundant on the stems, peduncles, outer involucral bracts and sometimes along the leaf veins in some Arctotidinae. Both uniseriate glands of various length and biseriate, often short glands are common on various organs in the subtribe. There is a striking diversity of trichomes on the achenes of Arctotidinae (McKenzie et al. 2005), which is unparalleled in the rest of the tribe, or in fact, in most other clades of the family (see Achenes).

Capitula, involucres and receptacles. — All Arctotidinae have radiate capitula. In general, the heads are solitary in both herbs and woody members of the subtribe (Figs. 25.1–25.3). The general pattern is of female ray florets and hemraphroditic disc florets, but *Arctotheca* and *Arctotis* sect. *Anomalae* have sterile ray florets and in *Arctotis* s.str. the central disc florets are male or sterile while the outermost one or two series are hemraphroditic (McKenzie et al. 2005, 2006c). The involucres commonly comprise graded involucral bracts in numerous series (Fig. 25.1C). The involucral bracts are free and the outer bracts have foliaceous tips, whereas the inner bracts have a conspicuous, obtuse or rounded, scarious lamina (Fig. 25.1C). Arctotidinae have a smooth or shallowly honeycombed receptacle, and in some *Arctotis* species long, bristle-like scales are borne on the shallow alveoles.

Corollas. — Arctotidinae have "true" ray florets with a 3-lobed and 4-veined limb (Figs. 25.1–25.3) (Bremer 1988). Baagøe's (1978) survey of the ray floret corolla epidermis revealed that the epidermal cells in general are larger in Arctotidinae than in Gorteriinae, and that Arctotidinae have longitudinally striate cuticle ornamentation. Many Arctotidinae have yellow ray florets,

but considerable diversification in ray floret color has occurred in *Arctotis* s.str. often within the same species. A contrasting darker or yellow spot at the base of the ray floret limb is especially common in *Arctotis* s.str. Typically, the disc corolla is yellow, but in many *Arctotis* s.str. and a few other species, the unopened disc corolla lobes are blackish, in contrast with the ray color. The disc corollas are shallowly lobed. In *Arctotis* s.str. species the abaxial surface of each disc floret corolla lobe bears a ± applanate, thickened elaboration so that the unopened florets form a flat, interlocking central disc; in other Arctotidinae the elaboration is ± tuberculate.

Stamens. — As in most clades outside the subfamily Asteroideae, the anthers of Arctotidinae are calcarate and without exception ecaudate (also noted by Lewin 1922). The short, soft and wrinkled apical anther appendages have long been noticed (Bremer 1994). An unusual attribute of Arctotidinae is their inconspicuous filament collar where the cells are devoid of wall reinforcements (although rather conspicuous in *Cymbonotus*), while all other taxa of the tribe investigated have elaborate collars with conspicuous wall reinforcements (Karis 2006, 2007; McKenzie et al. 2006c). A few species, notably the *Arctotheca* + *Haplocarpha* s.str. + *Arctotis* sect. *Anomalae* clade, have papillose filaments (Bremer 1994; McKenzie et al. 2006c). Ornamented or even hairy filaments otherwise occur in disparate taxa of Asteraceae (e.g., Cardueae, mutisioid clades, Coreopsideae). Another unusual characteristic of all Arctotidinae investigated so far is the radial endothecial tissue, i.e., the cells have reinforcements on the anticlinal walls all around the cells, which differ with the interpretation for at least Senecioneae, where radial reinforcements are confined to the inner anticlinal walls (Vincent and Getliffe 1988).

Styles (disc floret). — Even though the arctotoid style has been mentioned as a plausible synapomorphy for the tribe, there are subtle or even obvious differences both between and within the subtribes (Bremer 1994; Karis 2006, 2007). The only feature all arctotoid styles have in common is the ring of longer sweeping hairs well below the bifurcation, but the sweeping hairs themselves differ in size and shape, and they are ca. 20 μm long, patent and broadly subulate in Arctotidinae. Arctotidinae have disc floret styles with a thickened apical portion, and this is emphasized by a truncate base in *Arctotheca* and *Arctotis* sect. *Anomalae*, while it is less pronounced in the rest of the subtribe with their rounded to tapering bases. Many Arctotidinae style branches are uneven, or even markedly 3-lobed (*Dymondia*). Robinson (1984) examined style rotation of Asteraceae, i.e., the orientation of the style branches in relation to the orientation of the flowers in the head. The only representative of Arctotideae studied was *Haplocarpha scaposa*, which has radial disc styles but tangential ray styles, a combination

otherwise found only in the subfamily Asteroideae (Robinson 1984). All styles throughout the tribe have an entire stigmatic surface that is safe to say must be plesiomorphic.

Achenes. — Almost all taxa of the tribe conform to the most common pattern of the family, where the pericarp is well developed, often lignified, and makes up the main protective envelope for the embryo. Reese (1989) studied achene anatomy of representative species from most genera of the tribe. The pericarp of Arctotideae is developed centripetally and is only a few cell layers thick, although it may be considerably thicker in ribs or ridges.

The pericarp of all investigated Arctotidinae have oblong (in cross-section) sclerified cells in one or two subepidermal layers. Reese (1989) observed that all Arctotidinae have a prominent, persistent testa epidermis with different reinforcement patterns. Crystals occur in the mesocarp in at least some Arctotidinae. The diversity of achene forms and trichomes in Arctotidinae is especially extraordinary considering the size of the clade. McKenzie et al. (2005) surveyed external achene and pappus morphology in Arctotidinae by means of SEM and concluded that it was possible to align the 40 investigated species into 13 more or less distinguished groups. The specific achene morphology is diagnostic for many species. The achenes of most Arctotidinae have a marked dorsiventral symmetry, and most of the species have two adaxial ribs and three abaxial, more or less pronounced ribs or wings of different size and shape. In the *Arctotis* s.str., *A.* sect. *Anomalae* and *Cymbonotus* clades the achenes have two or three well-developed wings that form either one or two furrows or "cavities" (Beauverd 1915; Lewin 1922; McKenzie et al. 2005). Four *Haplocarpha* species have rather smooth achenes with more weakly developed ribs, of which two species have a variable number of ribs in each achene (Reese 1989). The achenes of only a few species are entirely glabrous (McKenzie et al. 2005). Trichome diversity is wide in Arctotidinae (Lewin 1922; Herman 2001; McKenzie et al. 2005). Twin hairs are often present as a basal ring (or "coma", a term more often applied for hair tufts on seeds) associated with the carpopodium (Lewin 1922; McKenzie et al. 2005). Twin hairs also cover the achene surface in *Haplocarpha* s.str. (*H. lanata* Less. and *H. lyrata* Harv.), whereas most other Arctotidinae bear either uniseriate clothing trichomes with a long whip-like terminal cell, which often form a dense, woolly indumentum on at least part of the achene surface, or short uniseriate or unicellular trichomes of several forms (McKenzie et al. 2005).

The almost ubiquitous pappus in the form of scales of different sizes and shapes has been noted since Cassini (1819). However, some clades or species are devoid of a pappus, as in most of the *Cymbonotus* clade, a few *Arctotis* and two *Arctotheca* species (McKenzie et al. 2005). The

scales are arranged in one or two, usually unequal series, and in three species the scales are at least partially fused forming a coroniform pappus (McKenzie et al. 2005; Karis 2006). So far as is known, all scales in Arctotidinae are composed of very elongate, narrowly oblong cells with thinner adaxial walls (Lewin 1922), thus enabling hygrochastic movement of the scales. At least in some *Haplocarpha* species, the scales have a thicker central part that continues into a narrow, almost bristle-like apical point. Most other Arctotidinae generally have obovate scales with an obtuse or rounded apex.

Pollen

Palynological data are not easily interpreted in terms of homologies, and Arctotideae do not depart from this general statement. Arctotideae pollen has cavities in the foot layer, but these are not confined to the areas between the apertures, as is the case in most caveate Asteroideae (Skvarla et al. 1977; Bremer 1987). However, it has also been suggested that a range of Arctotideae in fact share an ecaveate pattern (Bolick 1978, 1991; Bolick and Keeley 1994), but that this pattern should have evolved from an ancestral caveate type common to the entire vernonioid clade (Skvarla et al. 2005). Skvarla et al. (1977) recognized an "arctotoid" pollen type that was confined to the investigated samples of Arctotidinae. Subsequently, Vezey et al. (1994) characterized at least *Arctotis* pollen to be of the "lactucoid" exine stratification type, i.e., with an internal tectum of more than one layer (also found in Cardueae).

A recent paper described the pollen of all the major lineages of Arctotideae and discussed the pollen characteristics in detail (Wortley et al. 2008). From that work we find that the pollen of tribe Arctotideae is oblate-spheroidal and tricolporate, with a perforated tectum (Fig. 25.11). The pollen of the two subtribes differs in several ways.

The pollen of subtribe Arctotidineae is in general 16–27 μm in diameter, with narrow colpi (Fig. 25.11). The infratectum is 0.8–1.3 μm thick and comprises two columellate layers. The columellae are usually aggregated beneath the spines (except in *Dymondia*) and the grains are at least partially caveate. Arctotidineae pollen is echinate, with between 40 and 80 spines each 2–4 μm high and 3–4 μm in basal diameter, perforated throughout. The pollen of this subtribe may be distinguished by its smooth tectum and outer infratectum thinner than the inner infratectum.

Chromosome numbers

Arctotheca and *Arctotis* have a chromosome number of $2n = 18$, which is common in Asteraceae (Karis 2007). The heterogeneous *Haplocarpha* has $2n = 10$, 12, and 18 (Karis 2007) but has also been reported to display $2n = 30$ (*H. rueppellii*) and $2n = 36$ (*H. schimperi*) (Hedberg and

Hedberg 1977). This is consistent with the polyphyly of the genus (McKenzie et al. 2006c; McKenzie and Barker 2008).

Chemistry

Very little is known about the chemistry of Arctotidinae except that there are sesquiterpene lactones in *Arctotis arctotoides* (Sultana and Afolayan 2003).

Ecology

Dymondia margaretae may be a clonal species as it rarely, if at all, sets seeds in the field. *Dymondia* inhabits vlei edges and pans and withstands seasonal inundation and extreme drought conditions (Rourke 1974). The capitula of *Haplocarpha nervosa* and *H. schimperi* are "actively geocarpic", i.e., they bury their mature heads into the ground after anthesis and thus mature achenes may have little or no opportunity for dispersal (Barker 2005). The coastal primary-dune colonizer *Arctotheca populifolia* is "passively geocarpic", i.e., following anthesis the peduncle coils and often the heads are buried by subsequent accumulation of sand, creating a suitable habitat for germination without

dispersal of the achenes (Barker 2005). McKenzie and Barker (2008) suggested running water may be an effective achene-dispersal vector in *H. nervosa* and *H. rueppellii*, which often grow in mesic habitats such as bogs or beside streams. The effectiveness of the pappus scales for dispersal of *Arctotis* achenes over long distances has been questioned (Lewin 1922). In some Arctotidinae, notably the *Cymbonotus* and "annual *Arctotis*" clades, the achenes are small and the pappus is lost or highly reduced. Despite their seemingly poor dispersability, both clades (especially the former) have achieved wide geographic distributions.

Biogeography

The phylogeny for Arctotidinae (Fig. 25.4) is color-coded for distribution, and it is clear that the extant major clades originated in southern Africa. Biogeographic relationships within Arctotidinae were explored by McKenzie and Barker (2008). In this subtribe the basalmost extant lineages are often found in mesic habitats and the accrual of xerophytic adaptations and invasion of semi-arid regions are indicated to be nested more highly in the phylogeny. The basal lineages have an afromontane-afroalpine distribution and tend to occur in mesic climates or perennially wet habitats, such as bogs, stream banks and seepages. The next extant lineage to diverge, *Dymondia margaretae*, inhabits seasonally flooded and summer-arid vleis on the Agulhas Plain, South Africa. One interpretation is that a preference for mesic habitats might be plesiomorphic in Arctotidinae (McKenzie and Barker 2008). The divergence of these lineages might have coincided with the establishment of a more humid regime during the early mid-Miocene (Dingle and Hendey 1984), which persisted in southern Africa until the late Miocene (Partridge 1997).

Most of the extant diversity in Arctotidinae is resolved into three well-supported lineages that are indicated to have diverged during a rapid radiation in southern Africa possibly during the late Miocene (McKenzie and Barker 2008). These lineages are centered in the Fynbos and Succulent Karoo biomes, which together correspond with what some authors define as the Greater Cape Floristic Region (GCFR; e.g., Born et al. 2007). McKenzie and Barker (2008) hypothesized that this radiation coincided with the trend towards increasingly seasonal rainfall and aridification in southern Africa following increased glaciation in Antarctica 14 Ma (Zachos et al. 2001) and strengthening of the South Atlantic high-pressure cell (Linder 2005), resulting in the dramatic speciation of the *Arctotis* s.str. clade in the currently winter-rainfall and presently more arid regions. Divergence of a clade within *Arctotis*, centered in semi-arid Namaqualand and with an exclusively annual life history was likely to have been an adaptation to the greater aridity and seasonal rainfall in that region.
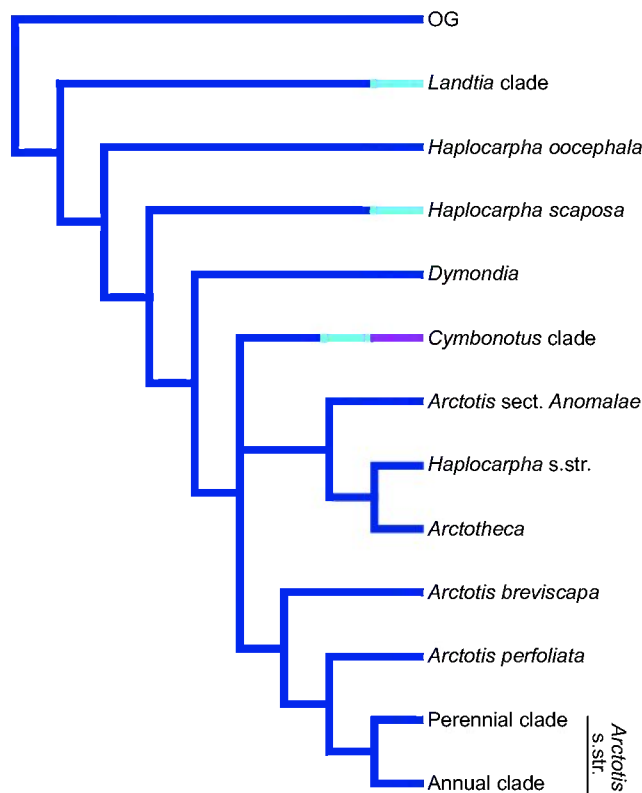

Fig. 25.4. Simplified phylogeny of Arctotidinae. The tree is adapted from McKenzie and Barker (2008) and Funk et al. (2007). Dark blue = southern Africa; light blue = tropical Africa and Madagascar; purple = Australia. See Chapter 44 for metatree of the family.

A remarkable and well-corroborated example of long-distance dispersal from southern Africa to Australia is that of the *Cymbonotus* clade (Holland and Funk 2006; McKenzie et al. 2006c; Funk et al. 2007; McKenzie and Barker 2008). It is worth pointing out the huge distance involved, viz. well over 7000 km in a direct line for the two closest points (Funk et al. 2007). Within the same clade, migration from southern Africa to East Africa has given rise to *Haplocarpha schimperi* (McKenzie et al. 2006c; McKenzie and Barker 2008). One wonders what it is about the morphology of *Cymbonotus* clade that allows it to travel so far while others in the clade do not.

Economic uses

A few species are used in traditional medicine. In the Eastern Cape, extracts from *Arctotis arctotoides* are used by small-scale farmers to treat heart water in goats (Dold and Cocks 2001) and by Xhosa people to treat a variety of human ailments (Watt and Breyer-Brandwijk 1962). Compounds produced by *A. arctotoides* and *A. auriculata* Jacq. have microbial-inhibitory activity (Salie et al. 1996; Afolayan et al. 2002, 2007; Afolayan 2003; Sultana and Afolayan 2003).

Arctotis species have been hybridized to create a range of half-hardy perennial hybrids, which are popular ornamentals worldwide. The annual species *A. fastuosa* and *A. venusta* Norl. are also of horticultural importance.

Invasives

A number of Arctotidinae species have naturalized abroad principally in regions experiencing a Mediterranean-type climate. It is significant to note that each of these species exhibit weedy tendencies in their native ranges. Only one species, *Arctotheca calendula*, which is commonly known as "capeweed", is classified as invasive, viz. in Australia (Groves et al. 2003) and California (Brossard et al. 2000). In Australia, *A. calendula* is a widespread weed on pastoral and agricultural land, and there has been much research into its ecology (e.g., Arnold et al. 1985; Thomson et al. 1998; Dunbabin and Cocks 1999). A bipyridyl herbicide-resistant biotype is known in Victoria, Australia (e.g., Powles et al. 1989). *Arctotheca prostrata* Britten is naturalized, but not declared to be invasive, in many of the same countries where *A. calendula* is found. In California it is reported to be "usually sterile" (Mahoney and McKenzie 2008) and therefore largely dependent on clonal spread. *Arctotis stoechadifolia* P.J. Bergius has naturalized on parts of the Australian coastline due to its popularity as a garden ornamental plant and its use as a dune stabilizer (Mahoney and McKenzie, 2008). In Australia the species is classified as a minor problem weed in natural ecosystems (Groves et al. 2003), where it may outcompete smaller indigenous plants and alter dune topography.

GORTERIINAE

Taxonomy

Subtribe Gorteriinae Benth., Gen. Pl. 2: 167, 211. 1873 – Type: *Gorteria* L. (Figs. 25.5–25.10)

Herbs or shrubs (rarely small trees in *Didelta spinosa* Ait.) with latex. Leaves entire or lobed to pinnatisect, spiny sometimes unarmed but then often tomentose-hispid with longitudinally striate hairs, usually also with woolly hairs. Capitula pedunculate, scapose or sessile, radiate, rarely discoid, receptacle deeply alveolate. Peduncles woolly, sometimes also with short or long glands. Involucral bracts connate to different degrees (free in *Didelta*), usually graded, spiny, spinulose, and glabrous or variously hairy. Ray florets usually 4-lobed, sterile disc florets deeply lobed, usually with sclerifications along the lobe margins. Anthers inconspicuously or conspicuously caudate, or ecaudate, apical appendage short to long, firm, endothecium usually without lateral wall thickenings or with some polarized, collar conspicuous. Achenes somewhat dorsiventrally asymmetric, usually ribbed, enclosed to different degrees in the receptacle alveoles, pericarp with subepidermal sclerifications of 1–2 roundish (in cross-section) cell layers, testa weakly developed only in *Gorteria*, usually with twin hairs, sometimes glandular. Pappus of small to large scales in 1–2 series, rarely absent.

In the field, Gorteriinae are recognized as latex-containing herbs or shrubs with leaves that either are spiny or tomentose to hispid, having more or less connate involucral bracts, sterile ray florets with often 4-lobed limbs, deeply alveolate receptacles, and a pappus of scales.

Norlindh (1977; Table 25.1) accepted nine genera in Gorteriinae. Karis (2007) maintained this taxonomy, but *Heterolepis* was unassigned to a subtribe. It is clear from recent studies (Funk et al. 2004; Karis 2006; Funk and Chan 2008) that *Berkheya* and *Hirpicium*, and maybe also *Cullumia*, are not monophyletic. Especially problematic is the circumscription of the largest genus *Berkheya*. Revisions of all genera are currently in progress.

Within Gorteriinae, *Gazania*, *Gorteria*, and *Hirpicium* made up a well-diagnosed clade in Bremer's (1994) cladistic analysis of Arctotideae, and this was in line with earlier suggestions by Roessler (1959) and Leins (1970). Due to the approach of using genera as terminals, Bremer (1994) could only suggest that the large and heterogeneous genus *Berkheya* probably is paraphyletic. *Berkheya cruciata* was united with *Cullumia* in Funk and Chan's (2008) extended analysis of Gorteriinae, which agrees with the placement of *B. cruciata* in Roessler's (1959) treatment and in Karis's (2006) tree, although the composition of the clades in question differs between the two cladistic studies. Two noteworthy features, viz. "endothecial wall thickening plate displaced towards the connective-facing

Fig. 25.5. Gorteriinae: *Berkheya.* **A, B** *Berkheya canescens* DC. (Namibia); the ray flowers of this subtribe often have four teeth, a character that is unique to Gorteriinae; the tomentose leaves are common in this tribe when taxa are found in very dry environments; as with many members of this tribe in Namibia, it grows in dry and/or rocky areas. **C, D** *Berkheya spinosissima* Willd. (Namibia: C, *V.A. Funk and M. Koekemoer 12694*; D, *V.A. Funk and M. Koekemoer 12692*); two individuals of this species were

side, ± sickle-shaped" and glabrous achenes, supported this small clade comprising *Cullumia* and *B. cruciata* (Karis 2006).

Morphology

Habit and life history. — Perennial shrublets and shrubs are common in the Gorteriinae, but *Cuspidia*, *Gorteria*, and some *Hirpicium* species are annuals. A truly rhizomatous habit is most common in *Berkheya* and *Gazania* and a few species of *Hirpicium* are scapose. As in the Arctotidinae, different adaptations to fire have arisen among fynbos endemics. For instance, *Berkheya barbata* (L. f.) Hutch. is a common re-sprouter on the Western Cape mountains, where young, often multi-stemmed exemplars are found in burnt areas, whereas *Berkheya cruciata* and *Heterorhachis* are examples of re-seeders.

Leaves. — Most Gorteriinae have alternate leaves, and the scapose taxa have a more or less pronounced leaf rosette, but a few species in the *Berkheya* clade have opposite leaves. Leaf shape varies considerably between and even within some species (e.g., *Gazania krebsiana* Less.) from simple and entire to pinnately compound to varying degrees. It is common that three (often more) separate veins are distinguished already when entering the leaf in some Gorteriinae, regardless of whether the leaves are entire or dissected. Some shrublet species inhabiting the Succulent Karoo and Fynbos biomes have xeromorphic, rather narrow leaves (e.g., *Hirpicium alienatum* Druce, *H. integrifolium* Less., *Berkheya angusta* Schltr., *B. angustifolia* (Houtt.) Merr., *Cullumia patula* Less., and *C. squarrosa* R. Br.), a situation paralleled in many plant groups inhabiting regions with a Mediterranean-type or semi-arid climate. *Didelta* usually has more or less succulent leaves. Field collection of specimens of many Gorteriinae generally renders bloodshed owing to their spinescent, often thistle-like character. Spiny leaves diagnose the *Berkheya* clade (although spines are found on the involucral bracts in *Didelta carnosa* Ait.) and the majority of the armed species have spines along the leaf margins and midribs, but a few species are also spiny on the upper leaf surface and stems. Some species of *Cullumia* have peculiar leaves with a sclerified margin in the form of a "frame" provided with a double or single row of spines. A few species of *Berkheya* have decurrent or auriculate petiole bases and some have strongly convex leaves and/or leaf lobes.

Trichomes. — As in Arctotidinae, various kinds of trichomes occur in Gorteriinae. Woolly hairs are commonly found on stems, peduncles, leaves, and involucres in all genera, if not in all species. These woolly hairs are frequently longitudinally oriented along the stem, but in some genera they are felted (e.g., *Gorteria*) or even floccose (some *Gazania*). Longitudinally striate hairs are one of the distinguishing features of the *Gorteria* clade (also containing *Gazania* and *Hirpicium*; Karis 2006, 2007). These hairs are sometimes very similar to the leaf hairs of Heliantheae, viz. rigid and provided with a flat or more raised multicellular base, but the 'Heliantheae' hairs are always uniseriate (Karis 2006, 2007). The corollas in *Gorteria* and some *Hirpicium* species have short, longitudinally striate hairs. Both uniseriate glands of various length and biseriate, often short glands, are common on various organs.

Capitula, involucres and receptacles. — Only ca. 15 species of the *Berkheya* clade are discoid while all remaining Gorteriinae are radiate. The heads are, in general, solitary and the size span is very large between the smallest species of *Gazania* and the large-headed *Berkheya* species. All Gorteriinae have sterile ray florets and the disc florets are hermaphroditic. The involucres commonly comprise graded involucral bracts in many series, but they are dimorphic in *Didelta* and even trimorphic in *Heterorhachis*. The involucral bracts are more or less connate (free in *Didelta*), usually acute, and they are all armed in the *Berkheya* clade but furnished with longitudinally striate hairs in the *Gorteria* clade. When the achenes are ripe the combination of fused involucral bracts and a lignified receptacle results in a hard, seed-bearing structure in all Gorteriinae but it is much less evident in *Berkheya*. More or less deeply alveolate receptacles distinguish all Gorteriinae, where the alveolar margins often are provided with projections in the form of teeth or smooth spines (Fig. 25.7B).

Corollas. — All Gorteriinae usually have 4-lobed, 5-veined ray florets (Figs. 25.5–25.9). However, the numbers of lobes is not consistent in a capitulum or on a plant and 2- or 3-lobed ray florets also occur. Most species of the *Berkheya* clade and several species of the *Gorteria* clade have yellow ray florets (Figs. 25.5–25.9). In *Gazania* and *Gorteria*, the ray floret color may vary profoundly within the same species and it is common for the ray floret limbs to have a contrasting, mostly darker, often ocellated spot at the base (Figs. 25.6E, F, 25.8). This reaches its most intriguing level of development in *Gorteria diffusa*, where in many populations one, two, three, or four of the rays bear

found in a dry river bed along the dirt road from Aus to Helmeringhausen; they were the only plants in bloom; note spiny involucral bracts and unique ray florets. **E** *Berkheya cirsiifolia* (DC.) Roessler (South Africa, Free State: *Funk and Koekemoer 12409*). A bushy herb of 5 meters with large heads, this species can have either yellow or white corollas. **F** *Berkheya purpurea* (DC.) Mast. (South Africa); the purple color of the florets is unusual in this genus; other *Berkheya* species are yellow or occasionally white. [Photographs: A, B, C.A. Mannheimer; C–F, V.A. Funk; E, M. Koekemoer.]

Fig. 25.6. Gorteriinae: *Berkheya*, *Cuspidia*, and *Gorteria*. **A, B** *Berkheya chamaepeuce* (S. Moore) Roessler (Namibia); this species is one of the very spiny, large-headed species. **C** *Cuspidia cernua* (L. f.) B.L. Burtt (South Africa, Eastern Cape: *McKenzie 1426*); this monotypic genus is the only annual in the *Berkheya* clade. **D** *Cullumia bisulca* Less. (South Africa: *Funk and Koekemoer 12271*); the leaves of this genus have spiny apices. **E** *Gorteria diffusa* Thunb. (South Africa: *Koekemoer and Funk 1945*); the dark spots on florets are believed by some to attract pollinators. **F** *Gorteria corymbosa* DC. (Namibia). [Photographs: A, B, F, C.A. Mannheimer; C, R.J. McKenzie; D, E, V.A. Funk.]

Fig. 25.7. Gorteriinae: *Didelta spinosa* Ait. **A** (South Africa, Northern Cape: *Funk and Koekemoer 12641*); this species is often a large shrub that is locally common. **B** Same as A; this species has an alveolate receptacle, which is common in this subtribe. **C** (South Africa, Western Cape: *Koekemoer and Funk 1936*); the corollas are entirely yellow. [Photographs, V.A. Funk.]

Fig. 25.8. Gorteriinae: *Didelta, Gazania.* **A** *Didelta carnosa* Ait. var. *tomentosa* (Less.) Roessler (Namibia: *Funk and Koekemoer 12685*); this collection was found growing on large sand dunes west of Lüderitz, Namibia; the leaves were covered with tomentum; this species has dark tips on the disc corollas, the head fragments into 3–5 parts, and each part has dark, stiff hairs; the heads of this plant had five parts. **B** *Didelta carnosa* Ait. var. *carnosa* (South Africa, Northern Cape: *Funk and Koekemoer 12648*);

a bulging, blackish spot that mimics a Bombyliid bee-fly species (Figs. 25.6E, F) (Johnson and Midgley 1997; Yamamura 2006). Almost all Gorteriinae have sclerified disc corolla lobe margins, and in general they are broad in the *Berkheya* clade but notably narrower in the *Gorteria* clade (Karis 2006).

Stamens. — The Gorteriinae anthers are calcarate, and are caudate with somewhat branched tails in the *Berkheya* clade (except in *Didelta*), while the *Gorteria* clade with few exceptions have ecaudate anthers. The appendages are also in general rather short compared with other non-Asteroideae clades and those in the *Gorteria* clade have seemingly fringed margins (Karis 2006). In contrast with the endothecium of Arctotidinae, the endothecium is highly variable in Gorteriinae (Karis 2006). Those in the *Gorteria* clade mostly display cells without plates, i.e., inner periclinal walls without reinforcements, while most members of the *Berkheya* clade have plates that in turn may be furnished with pores or slits. It should be pointed out that it is the outer pollen sacs that show different endothecial patterns, while the inner ones always are polarized.

Styles. — The sweeping hairs are ca. 50 µm long and erecto-patent, clavate to more acute but always mammillate in the *Berkheya* clade, and ca. 30 µm long, subulate-ensiform in the *Gorteria* clade (Karis 2006). In the *Gorteria* clade the sweeping hairs are arranged more or less in longitudinal rows. All style branches in Gorteriinae are tapering towards the apex.

Achenes. — Only a few Gorteriinae have oblong (in cross-section) sclerified cells in one or two subepidermal layers in the pericarp (Reese 1989), while the rest of the investigated species have cells about as long as wide (Reese 1989; Karis 2006). *Gorteria* has a weakly developed, disintegrating testa epidermis, which is coupled to the fact that the receptacle itself is the main protective cover for the embryo. Many Gorteriinae have subepidermal crystals in the testa (Reese 1989; Karis 2006). *Cullumia* is devoid of a carpopodium, and is further diagnosed by possessing elaiosomes, although they are rather inconspicuous. Gorteriinae achenes have a rather inconspicuous dorsiventral symmetry, often bear less conspicuous ribs, and are enclosed within the receptacular alveolae to differing degrees between the genera (Karis 2006). This is least apparent in *Gazania* (Karis 2006), while *Gorteria* has a

strongly lignified receptacle enclosing the achenes, which have a much reduced pericarp. Only a few species are reported to be entirely glabrous (Karis 2006), and the hairy achenes all bear twin hairs of different form, length and color (Karis 2006, 2007). Only *Cuspidia* differs with twin hair-like uniseriate trichomes, and similar hairs are found in Arctotidinae (see above; McKenzie et al. 2005). Many of the Gorteriinae twin hairs are conspicuously forked or have very unequally long cells, and in *Cullumia* they are rarely deeply cleft. *Gorteria* has long, twisted, curly twin hairs, while *Gazania* have very long, straight hairs. Most achenes in *Gazania* and *Hirpicium* have large, globose glands in distinct rows, but smaller glands are also present in *Gorteria* (Karis 2006, 2007).

Some clades or species are devoid of a pappus, such as some *Berkheya* and most *Cullumia* species (Karis 2006, 2007). The scales are arranged in one or two series, sometimes more in some species, that may be alike or dimorphic, and in some cases they are pigmented. The pappus scales in Gorteriinae consist of short cells that do not show a trace of the anatomy found within Arctotidinae, but the diversity is nevertheless large. It is not surprising that the pappus is reduced or absent in the more or less enclosed achenes of some Gorteriinae (*Gorteria*, *Cullumia*).

Karis (2006) reported latex (the actual milky juice) or laticifers (the cells producing or containing the latex) from 26 investigated species of Gorteriinae. It may be safe to conclude that laticifers are present in all Gorteriinae, but so far as is known latex is absent in all other Arctotideae taxa. The presence of latex is not so evident in the field in, e.g., ericoid species such as *Hirpicium alienatum*, *H. integrifolium*, *Cullumia* and *Cuspidia*, whereas some *Gazania* and many *Berkheya* species really "bleed" if a leaf or a branchlet is broken.

Pollen

Echinate pollen is common in the subtribe, but many species and genera have lophate pollen. The latter kind of grain, which is found only outside the subfamily Asteroideae, was surveyed throughout the family by Blackmore (1986). Lophate pollen in many Gorteriinae is distinguished from similar pollen in other clades in that it has tectal microperforations of two considerably different sizes, instead of just one. Leins and Thyret (1971)

this collection was found in Namaqua National Park; its leaves are glabrous and the head fragments into three parts. **C** *Gazania krebsiana* Less. (South Africa, Northern Cape: *Koekemoer and Funk 1947*); this species is extremely variable in the color of the ray limb. **D** *Gazania* sp. (South Africa, Northern Cape, Nieuwoudtville: US); the spectacular displays of the winter rainfall area of southern Africa consist of many different members of Compositae; in this photo there are at least five tribes represented: *Gazania* and *Gorteria* (Arctotideae), *Cotula* (Anthemideae), *Monoculus* (Calenduleae), *Senecio* (Senecioneae), and *Felicia* (Astereae). **E** *Gazania leiopoda* (DC.) Roessler (South Africa, Northern Cape). **F** *Gazania* ×*rigens* Gaertn. "Sunshine Mix" or "Treasure Flowers" (native to South Africa, cultivated: OKL Greenhouse); *Gazania* is widely cultivated and hybrids can have brightly colored corollas. [Photographs: A–E, V.A. Funk; F, C. Lemke.]

Fig. 25.9. Gorteriinae: *Gazania*, *Hirpicium*, *Heterorhachis*. **A, B** *Gazania jurineaefolia* DC. subsp. *scabra* (DC.) Roessler (Namibia: *Funk 12687*); this small annual was growing along a very dry roadside between Aus and Lüderitz; **B** the involucral bracts are fused and there are stripes on the undersurface of the ray corollas. **C, D** *Hirpicium alienatum* Druce (South Africa, Northern Cape: *Koekemoer and Funk 1956*). **E, F** *Heterorhachis aculeata* (Burm. f.) Roessler (South Africa, Northern Cape: *Funk 12550*); the flowers are greenish in color and the plants have a spiny habit; collected on old farm land near Nieuwoudtville. [Photographs, V.A. Funk.]

identified a "*Gazania* pollen type" that was characteristic for the *Gorteria* clade, but Blackmore (1986) found the same exosculpturing (psilolophate grains) in *Berkheya acanthopoda* (DC.) Roessler. Pollen anatomy shows significant diversity in the large, paraphyletic genus *Berkheya*, where echinate, echinolophate, and psilolophate pollen is found.

The pollen of subtribe Gorteriinae is more variable than that of Arctotidinae (Wortley et al. 2008), although it is usually lophate or sublophate (with the exception of *Berkheya cuneata*) (Fig. 25.11). It is generally larger than that of Arctotidinae, 20–60 μm in diameter. The infratectum

is 0.5–2.5 μm thick and comprises one or more columellate layers. The grains are at least partially caveate and may be psilo- or echino-lophate. In the latter case there are 50–80 spines, 1–6 μm in height and 1.5–7.0 μm in diameter, perforated throughout except in *Heterorhachis* where they have a solid apex. For lophate grains there are always six equatorial and six polar lacunae; the numbers of other lacunae are variable.

Chromosome numbers

Gazania has a variety of chromosome numbers, viz., $2n$ = 10, 12, 14, and 16, but here the variation rather owes
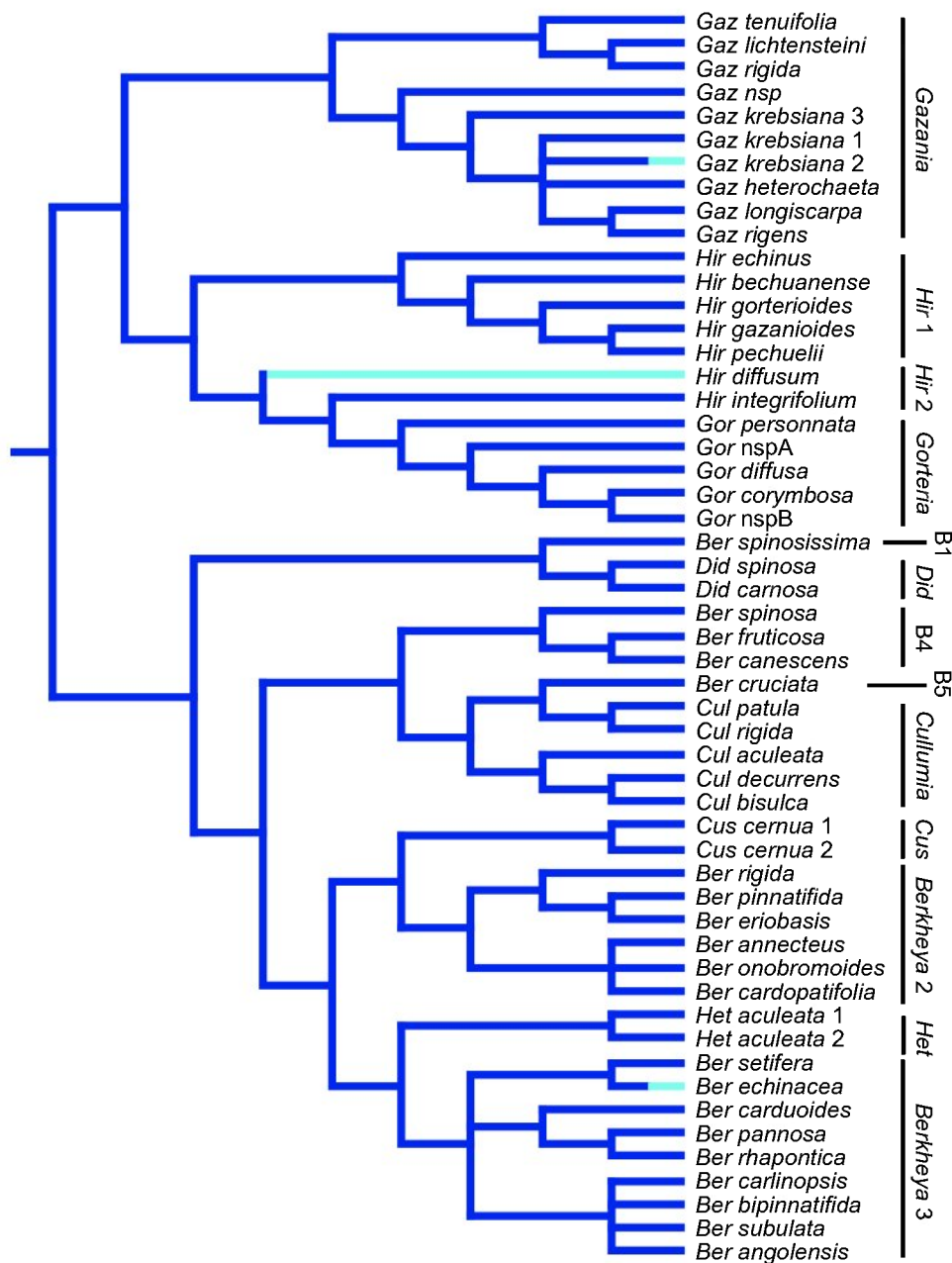

Fig. 25.10. Phylogeny of Gorteriinae with branches color-coded for distribution and clades indicated (phylogeny from Funk and Chan 2008) [Ber = *Berkheya*; Cul = *Cullumia*; Cus = *Cuspidia*; Did = *Didelta*; Gaz = *Gazania*; Gor = *Gorteria*; Hir = *Hirpicium*]. Dark blue = southern Africa; light blue = tropical Africa and Madagascar.
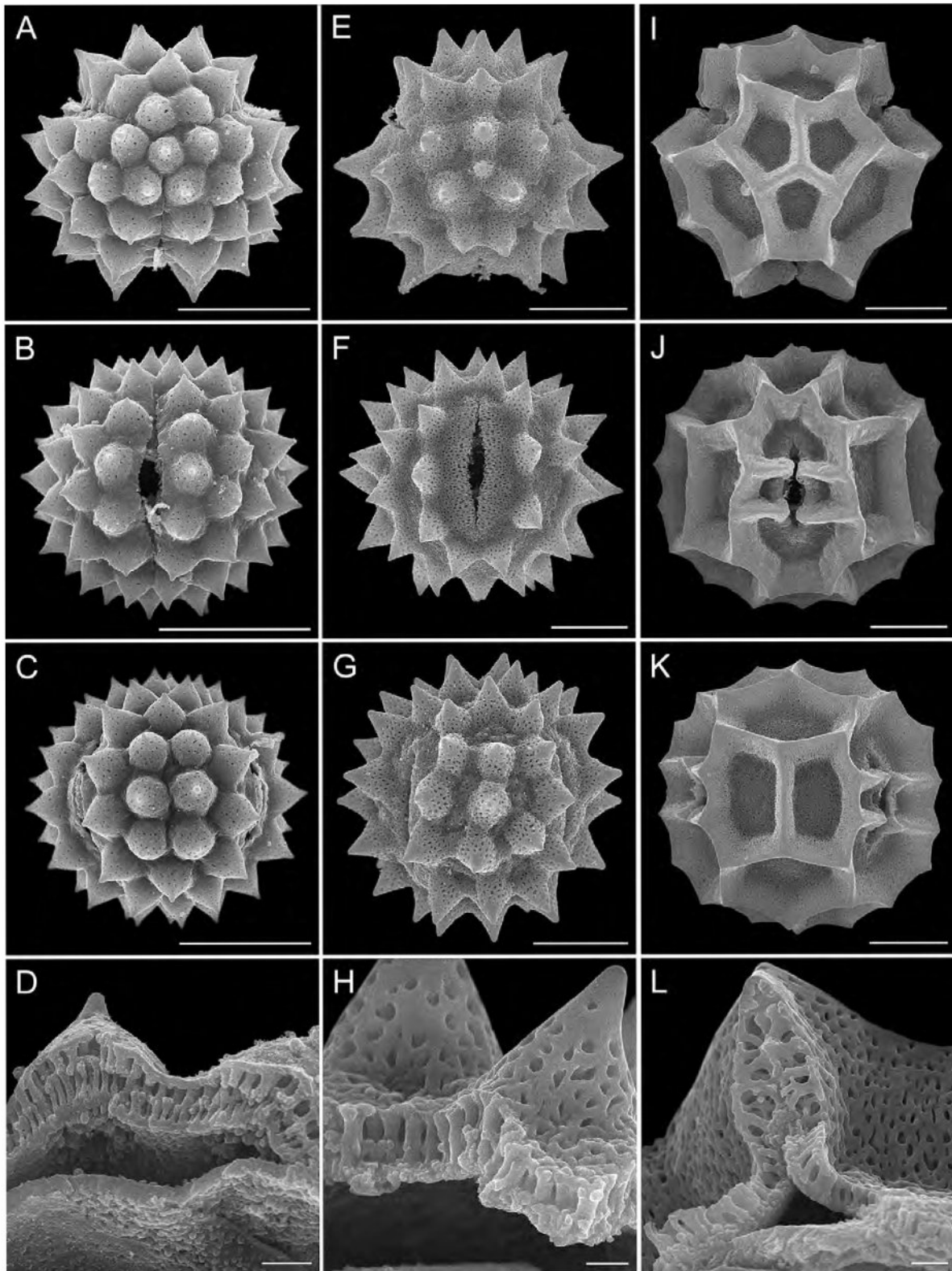
Fig. 25.11. Pollen of Arctotideae. **A** *Arctotis decurrens* Jacq., polar view; **B** *A. glandulosa* Thunb., apertural view; **C** *A. decurrens*, equatorial view; **D** *A. decurrens*, fractured grain; **E** *Didelta spinosa* Harv., polar view; **F** *D. carnosa* Ait., apertural view; **G** *D. spinosa*, equatorial view; **H** *D. carnosa*, fractured grain; **I** *Berkheya rigida* (Thunb.) Bolus & Wolley-Dod ex Levyns, polar view; **J** *B. rigida*, apertural view; **K** *B. rigida*, equatorial view; **L** *B. rigida*, fractured grain. [From Wortley et al., 2008, by permission of the authors.]

to complicated patterns of relationships including possible hybridization events. *Berkheya* has 2*n* = 14 and 16, and *Hirpicium* 2*n* = 10 (Karis 2007).

Chemistry

There is no information on the chemistry of Gorteriinae.

Ecology

In most Asteraceae the achenes act as diaspores, but in *Gorteria* the entire, lignified heads fall off and constitute diaspores. In *Didelta carnosa*, the lignified receptacles with adnate withered involucral bracts break apart into three to five separate diaspores. In both these cases, the ca. 1–5

seedlings germinate directly out of the old heads/parts of heads. This mode of dispersal is apparently not the case in *Cuspidia* and *Heterorhachis*, two other Gorteriinae taxa with more or less lignified receptacles.

Pollination has been investigated primarily in *Gorteria* (Johnson and Midgley 1997; Yamamura 2006). The capitula of *G. diffusa* (Fig. 25.6E) contain a variable number of raised dark spots at the base of the ray floret limbs. Johnson and Midgley (1997) hypothesized that the spots mimic resting individuals of the bee-fly pollinator, *Megapalpus nitidus* (Bombyliidae). Evidence for this hypothesis was supported by the mere removal of spotted rays, which resulted in a major decrease in pollination (Johnson and
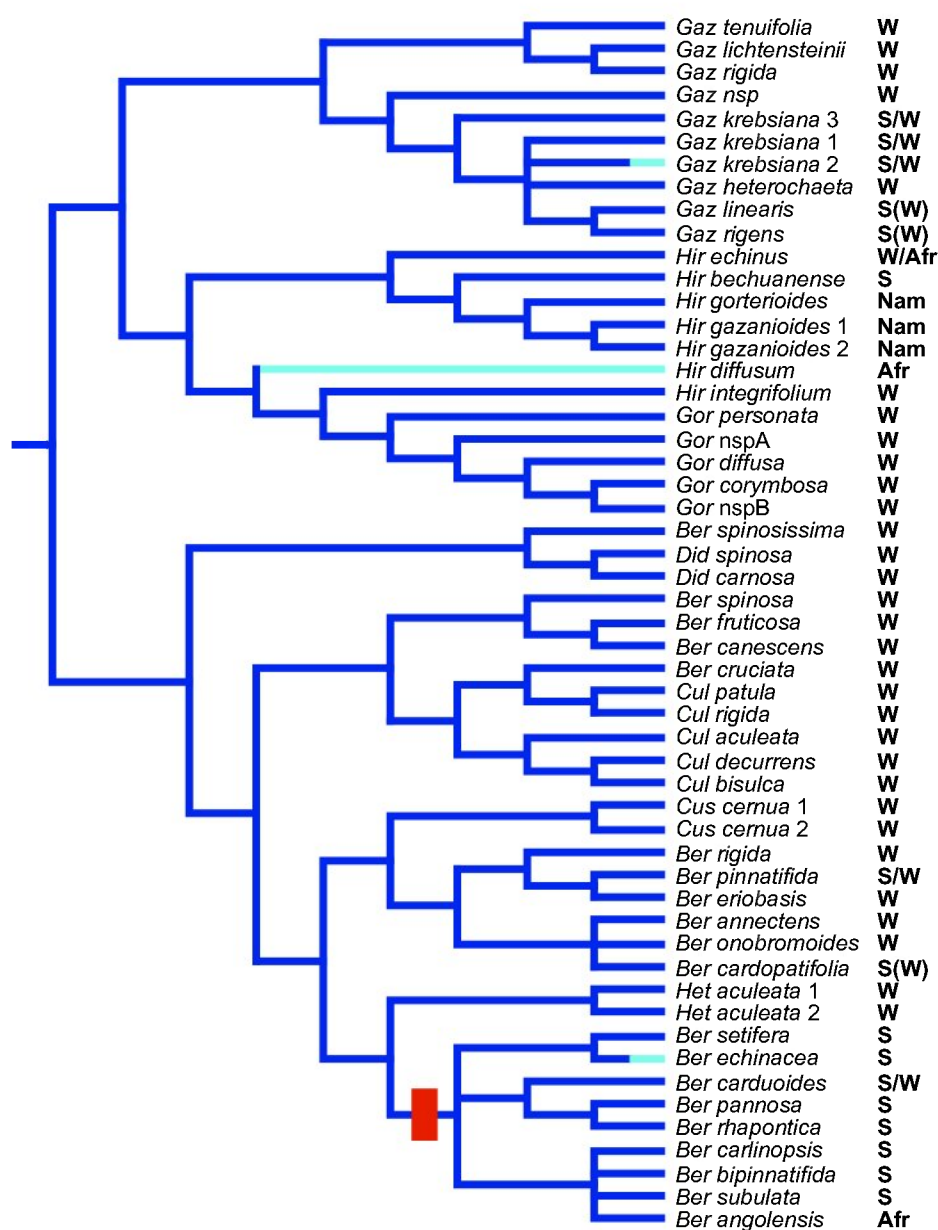

Fig. 25.12. Phylogeny of Gorteriinae showing rainfall area for each terminal taxon (phylogeny from Funk and Chan 2008). Ber = *Berkheya*; Cul = *Cullumia*; Cus = *Cuspidia*; Did = *Didelta*; Gaz = *Gazania*; Gor = *Gorteria*; Hir = *Hirpicium*; Afr = Africa outside South Africa/Namibia; Nam = Namibia (outside the winter-rainfall area); S = summer rainfall; W = winter rainfall (includes southern Namibia). The red box indicates a probable radiation of species in the summer-rainfall region. Dark blue = southern Africa; light blue = tropical Africa and Madagascar.

Midgley 1997). However, *G. diffusa* is visited by a number of other insects as well, not only this particular bee-fly (F. Stångberg and P.O. Karis, pers. obs.).

Biogeography

To date, no study with the aim of untangling the phytogeography of Gorteriinae has been attempted, other than a recent investigation focused on the genus *Gazania* (Howis 2007). Much of the following discussion is based

Table 25.2. List of characters discussed in the text and "optimized" on the tree in Fig. 25.13.

1. Latex/laticifers
2. Leaf spines
3. Ray florets neuter/female sterile
4. Anthers ecaudate
5. Apical anther appendages soft
6. Arctotoid styles, sweeping hairs in a ring below the bifurcation
7. Pappus scales
8. Longitudinally striate hairs
9. Longitudinally grooved leaves
10. Involucral bracts connate
11. Inner involucral bracts apically with a scarious lamina
12. Receptacle deeply alveolate
13. Ray florets 4-lobed
14. Ray florets with an adaxial, narrow lobe
15. Disc corolla lobes short(?)
16. Disc corolla lobes with sclerified margins
17. Anther filament collar inconspicuous
18. Apical anther appendages with fringed margins
19. Anther endothecium radial
20. Anther endothecium without a plate
21. Inner periclinal wall of anther endothecium cells with band-like thickenings in lower half of cells
22. Pollen of the *Gazania* type
23. Sweeping hairs small, patent
24. Sweeping hairs oblong, erecto-patent, mammillate
25. Sweeping hairs subulate-ensiform
26. Sweeping hairs two or three together
27. Pericarp with tannic substances
28. Testa with subepidermal crystals
29. Pappus scale cells very long, abaxial wall reinforced

on the geographical distribution of the terminals in the phylogenies at hand. Although the sampling is not fully congruent, both molecular (Funk and Chan 2008) and morphological (Karis 2006) data support a 'derived' radiation of many summer-rainfall species and the few tropical species of the *Berkheya* clade (Fig. 25.12). Thus both possible summer-rainfall radiation events are well embedded within apparent GCFR clades (Greater Cape Floristic Region). *Berkheya* has a significant representation in the GCFR (24 spp.), but the centre of diversity is in the summer-rainfall region (at least 46 spp.). The picture in the *Gorteria* clade is less clear due to more limited sampling in both these studies (Karis 2006; Funk and Chan 2008), but only five of the species are restricted to summer-rainfall or tropical Africa. Howis (2007) reconstructed a phylogeny of *Gazania* based on sequences from nuclear ribosomal DNA (ETS, ITS) and four non-coding cpDNA markers and hypothesized an origin for *Gazania* in the arid and/or semi-arid winter-rainfall regions of southern Africa with migration southwards and eastwards during periods of aridification. Two summer-rainfall/tropical *Gazania* species are subsumed well within the clade (Fig. 25.12). Both in the *Gorteria* clade and the subtribe as a whole, the presence of two large sister groups obscures possibilities to evaluate geographical 'origin', owing to the lack of obvious basalmost lineages containing one or few species only. However, at this point it is safe to hypothesise a GCFR (including adjacent arid areas) origin of Gorteriinae and most likely in the winter-rainfall area, but evaluation of finer phytogeographical details must await additional studies based on larger sampling.

Economic uses

Berkheya speciosa O. Hoffm. and *B. spekeana* Oliver are used traditionally to treat numerous human ailments in several African countries (Chifundera 1998; Sparg et al. 2000; Cos et al. 2002; Fennell et al. 2004). *Berkheya spekeana* possesses antiviral activity (Cos et al. 2002).

Only a few Gorteriinae species are of horticultural significance. The most commonly cultivated are *Gazania krebsiana*, *G. linearis* Druce, *G. rigens* and their hybrids, which are widely grown as ornamentals (Fig. 25.8F). *Berkheya coddii* Roessler has potential use for phytoremediation of sites contaminated with toxic metals, as it is a nickel hyperaccumulator and has been used to treat soil contaminated with nickel (Robinson et al. 2003). In addition, certain *Berkheya* species (e.g., *B. purpurea* and *B. multijuga*) and both *Didelta* species are available from horticultural suppliers.

Invasives

Berkheya rigida is a declared weed of coastal scrubland in parts of Australia (Parsons and Cuthbertson 2001). *Gazania* species, principally *G. linearis* and *G. rigens*, have

CHARACTER EVOLUTION

During recent decades, some characters of Arctotideae have been discussed as alleged synapomorphies (Table 25.2) for the tribe, and possible character evolution of some features is illuminated in Fig. 25.13. The tree is based on the results of Funk and Chan (2008) and on unpublished data.

The evolution of characters included here may indeed show complicated patterns within taxa from outside Arctotideae and which are displayed here as single terminals. The sister group of Cichorioideae, viz., subfamily Asteroideae, is included in the tree.

Latex/laticifers probably evolved in parallel in Cichorieae and in Gorteriinae; this appears to be the case regardless if latex is considered to be ancestral for Liabeae or not. At this point, the absence of latex can be considered plesiomorphic; on the other hand, latex/laticifers diagnose Gorteriinae, as has previously been suggested (Bremer 1994; Karis 2006).

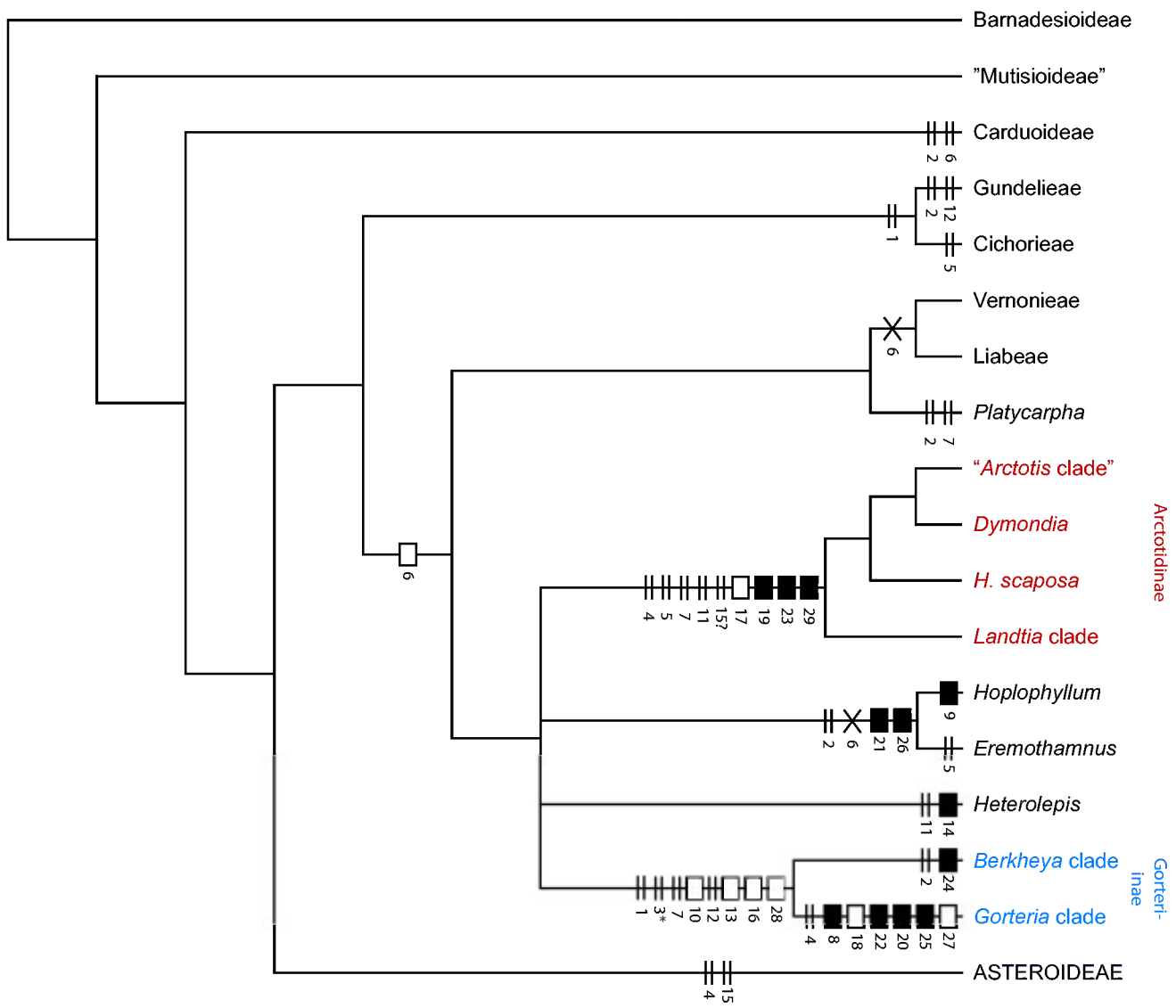Spiny leaves appear no less than five times on the cladogram.

Fig. 25.13. Selected characters mapped onto a cladogram of Compositae with emphasis on Cichorioideae. Characters are listed in Table 25.2. Black boxes are synapomorphies, white boxes are homoplasious characters, parallel bars are parallelisms.

Inner involucral bracts with an apical, scarious lamina diagnose Arctotidinae, but are also typical of *Heterolepis*.

Sterile ray florets apparently evolved independently in the common ancestor to Gorteriinae and within Arctotidinae, viz., in the ancestor of the *Arctotheca + Haplocarpha* s.str. + *Arctotis* sect. *Anomalae* lineage (with a reversal in *Haplocarpha* s.str.) and within the *Landtia* clade (*H. parvifolia* (Schltr.) Beauverd p.p.).

Ecaudate anthers have three independent origins: in Arctotidinae, in the *Gorteria* clade, and it is also most likely ancestral for the subfamily Asteroideae. It should be noted that ecaudate anthers and "shortly lobed disc floret corollas" are the only features that also involve discussion on the corresponding character states in Asteroideae.

Soft apical anther appendages arose independently in Arctotidinae and in *Eremothamnus*.

The ring of sweeping hairs below the style bifurcation is interpreted to be a parallelism found in the thistles (Cardueae) and in Cichorioideae (Karis et al. 1992; Bremer 1994). The possible placement of *Platycarpha* on the Liabeae-Vernonieae branch would force reconsideration of the evolution of the arctotoid style in Cichorioideae.

The scaly pappus is a feature that has evolved at least three times in parallel. The most parsimonious interpretation of pappus scales in Arctotidinae is that they evolved in the common ancestor to the group. The Arctotidinae pappus scales are distinctive, with very long cells furnished with an abaxially thickened cell wall, and the scales are anatomically different from those in the other clades. The combination of these two facts makes more sense if a parallel gain of pappus scales is hypothesized.

The often enumerated synapomorphies for the subtribes and clades therein (see above; Bremer 1994; Funk et al. 2004; McKenzie et al. 2006c; Karis 2006, 2007) are also displayed on the tree (Fig. 25.13), but it should be emphasized that some characters are not investigated for all, or even many, species in all clades. Even though a phylogeny and precise patterns of relationships are not yet established in Arctotideae, it is clear that some morphological/anatomical features need to be re-evaluated in terms of homologies. One obvious example is the pappus scales, which are so fundamentally different in Arctotidinae and in the rest of the clades.

CONCLUSION

There are striking differences in morphology in virtually every part and organ between the two subtribes, but this fact alone is not evidence enough to argue that these taxa might not be one another's closest relatives. Current molecular data do not refute either hypothesis, they merely provide alternative solutions. The large morphological and anatomical diversity displayed in both subtribes might indeed be the result of repeated adaptations to similar environmental conditions, pollinators, etc., but which has been expressed in different ways in the two lineages. Hopefully, ongoing work will clarify the taxonomy and our understanding of the evolution and biogeography of Arctotideae.

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