

Cichorieae

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INTRODUCTION

Cichorieae (also known as Lactuceae Cass. (1819) but the name Cichorieae Lam. & DC. (1806) has priority; Reveal 1997) are the first recognized and perhaps taxonomically best studied tribe of Compositae. Their predominantly Holarctic distribution made the members comparatively early known to science, and the uniform character combination of milky latex and homogamous capitula with 5-dentate, ligulate flowers, makes the members easy to identify. Consequently, from the time of initial description (Tournefort 1694) until today, there has been no disagreement about the overall circumscription of the tribe. Nevertheless, the tribe in this traditional circumscription is paraphyletic as most recent molecular phylogenies have revealed. Its circumscription therefore is, for the first time, changed in the present treatment.

The easy recognition of the members of the tribe comes along with a major drawback: the tribe is not only conspicuously poor in morphological features, but extensive parallel evolution of features further renders the recognition of natural groups difficult. This situation has given rise to considerable differences in the generic and suprageneric classification of the members of the tribe by various students of Cichorieae.

Molecular phylogenetic studies have essentially improved our understanding of a few groups of the tribe since the 1990s. But only now the results of the molecular phylogeny of a large dataset (428 taxa of 83 genera; Gemeinholzer et al., in prep.), representing the entire tribe, have become available, and this has enabled us to provide an essentially revised treatment of Cichorieae. While the

general lines seem sufficiently clear so far, our knowledge is still insufficient regarding a good number of questions at generic rank as well as at the evolution of the tribe.

HISTORICAL OVERVIEW

Tournefort (1694) was the first to recognize and describe Cichorieae as a taxonomic entity, forming the thirteenth class of the plant kingdom and, remarkably, did not include a single plant now considered outside the tribe. This reflects the convenient recognition of the tribe on the basis of its homogamous ligulate flowers and latex. He called the flower “flos semiflosculosus”, paid particular attention to the pappus and as a consequence distinguished two groups, the first to comprise plants with a pappus, the second those without.

Tournefort’s pupil, Vaillant, coined for his teacher’s thirteenth class the name “Cichoracées” (Vaillant 1719) and distinguished five “sections” based on features of the habit, pappus, and receptacle, the first including all scapose taxa irrespective of their pappus, the second including those with a pappus of trichomes or scales and a naked receptacle, the third those with a plumose pappus and a naked receptacle, the fourth those lacking a pappus, and the fifth those with receptacular trichomes or paleae (Vaillant 1723; for an evaluation of Vaillant’s work on Compositae see Greuter et al. 2005).

Lamarck and De Candolle (1806) validated Vaillant’s pre-Linnaean name for the tribe and subdivided Cichorieae into four subtribes according to pappus features. The lasting merit of these and the other 19th century authors

dealing with the systematics of the Asteraceae in general and the tribe Cichorieae in particular, namely Cassini (1827, 1830), Don (1828), Lessing (1832), De Candolle (1838), Bentham (1873), and Hoffmann (1890–1894), is their analysis, comparison, description, and classification in species and genera of the enormously increased plant diversity that successively became known to science in the course of this century, rather than their suprageneric systems of subdividing the tribe. All attempts had in common classifications based on one or a few key features, pappus and receptacle characters having been particularly highly appreciated (for further details see Stebbins 1953: 65–67). Extensive convergent evolution, especially in the pappus of the Cichorieae, however, condemned the resulting systems from Tournefort in 1694 up to Hoffmann in 1894 to be largely artificial.

Hoffmann's (1890–1894) subdivision of the tribe, which had been influential until well into the 20th century, illustrates the stagnation in the development of the suprageneric classification from the late 17th to the late 19th century. He coined the name pair “Liguliflorae (Cichorioideae)” and “Tubuliflorae” (Hoffmann 1890–1894: 118) and separated Cichorieae as Liguliflorae on subfamily rank from all other tribes, which he united as Tubuliflorae. Hoffmann divided the tribe into five subtribes, of which his three larger subtribes are entirely based on pappus features: Cichoriinae unite all genera without or with non-setaceous pappi, Leontodontinae include all New and Old World genera with plumose pappus, and Crepidinae include all genera with setaceous, non-plumose pappus. In addition, he placed *Scolymus* in a subtribe of its own and united *Dendroseris* and *Fitchia* (the latter actually an odd liguliflorous Heliantheae; Carlquist 1947) because of their arborescent life form.

In the middle of the 20th century, a fruitful cooperation of two American botanists, Stebbins and Babcock (Babcock and Stebbins 1938), revolutionized our understanding of Cichorieae, as of plant systematics in general. Studying the American species of *Crepis*, they discovered the crucial role of hybridization and formation of polyploid complexes in the evolution of species. In the course of their subsequent cytological and taxonomic work in Crepidinae s.l., they re-established and monographed Cassini's Asian genus *Youngia* (Babcock and Stebbins 1937, 1943). Stebbins studied also the Asian *Crepis* relatives *Ixeris* (Stebbins 1937c), *Dubyaea* and *Sorosseris*, hereby making fundamental contributions to our knowledge of the vascularization of the ovary (Stebbins 1940). The pair also investigated the genera *Lactuca* and *Prenanthes* (e.g., Stebbins 1937a, b) and provided a survey of karyology and phylogeny in Cichorieae (Stebbins et al. 1953). By then Babcock had completed his monumental taxonomic revision of *Crepis*, which takes karyological, morphological, and biogeographical data into account (Babcock 1947).

Stebbins (1950), one of the key figures of the Modern Evolutionary Synthesis, crowned his studies in Cichorieae with a new subtribal classification, based on a phenetic multi-evidence approach by considering morphology (in particular pappus, shape of the stigma branches, pollen, and indumentum), geographical distribution, and chromosomal data (Stebbins 1953). In contrast to previous classifications, Stebbins considered “each genus separately, placing it nearest to those genera which it most nearly resembles in respect to the largest number of characteristics of external morphology, plus the nature of the chromosomes and the geographic distribution” (Stebbins 1953: 69). He arranged the 62 genera recognized by him into eight subtribes, thereby grouping genera with no pappus together with genera possessing a pappus, which, however, resemble one another in other characteristics. Within these groups the genera not always feature common characters but are sometimes united by transitional genera. Stebbins recognized the close affinity of the endemic New World genera and placed them into two new subtribes, Malacothricinae and Stephanomerinae, which are distinguished by geographic distribution and chromosome numbers.

Jeffrey (1966), in another phenetic approach undertaken in the context of his studies of Cichorieae in tropical East Africa, considered additional micro-morphological characters (length of collecting trichomes on the style, trichome shapes on stigmatic surfaces, and pubescence of the corolla tube), which he incorporated in his system to improve Stebbins's classification. He defined groups and subgroups but refrained from providing a formal taxonomic classification due to the “uncertain status of the ligulate Compositae within the family” (Jeffrey 1966: 428). Jeffrey's classification of five groups, eight subgroups and eighteen series resulted in several natural groupings, especially on the lower taxonomic levels. However, sometimes features are placed into a doubtful evolutionary context, e.g., he grouped the *Scorzonera* subgroup within the *Hypochaeris* group due to the paleaceous/plumose pappus and medium to long style-arms, and the *Crepis* subgroups within the *Cichorium* group due to long style-arms and large collecting trichomes, not taking into account the possible different evolutionary pathways by which these homologous characters could have evolved.

Bremer (1994) provided the first cladistic analysis of the tribe, based on morphological characters, by studying a selection of 23 from altogether 98 genera recognized, which either represent presumed monophyletic groups, or distinct or isolated taxa. As result of this, he divided the tribe in eleven subtribes, establishing the new subtribes Catananchinae, Malacothricinae, and Sonchinae, and left two genera, *Cichorium* and *Scolymus*, unassigned to a subtribe. Due to the isolated position of *Scolymus*, he stated the necessity of a separate subtribe; however, in

his treatment, monogeneric subtribes were avoided. For *Cichorium* he proposed a relationship close to Crepidinae, or Stephanomeriinae, or to the basally branching lineages within the tribe.

Bremer's major achievement towards a more natural classification is the subdivision of former Crepidinae s.l. (Stebbins 1953) into the subtribes Crepidinae s.str., Lactucinae, and Sonchinae, although their exact circumscriptions need revision. His treatment of the basically New World genera in the three subtribes Malacothricinae, Microseridinae, and Stephanomeriinae, in contrast, constitutes a moderate improvement only, since none of them has been found to be monophyletic in later molecular analyses (compare Lee et al. 2003: 620, fig. 1). Bremer's recognition of the subtribe Hieraciinae, which corresponds to Jeffrey's *Tolpis* group (except *Koelpinia*, which on palynological evidence is correctly placed in Scorzonerinae), maintains the advantages of Jeffrey's (1966) classification over that of Stebbins (1953). His Catananchinae, comprising *Catananche*, *Hymenonema*, and *Rothmaleria*, are an artificial unit.

Although molecular analyses in Cichorieae date back to the early 1990s (Jansen et al. 1991; Crawford et al. 1992; Kim et al. 1992; Sang et al. 1994), the data were still too meager to play a role in Bremer's classification. Molecular analyses in Cichorieae were initially focused on the phylogeny of selected subtribes, apart from a single early approach by Whitton et al. (1995) using chloroplast DNA restriction site variation upon 60 Cichorieae taxa. Whitton et al. (1995) addressed relationships among major lineages of the tribe, and their results agree very well with the only other, most recent attempt by Gemeinholzer et al. (in prep.), using DNA sequences of the nuclear ITS region and covering 438 taxa. Both analyses revealed similar major lineages and confirm that groups and basal branches are better resolved with increasing number of taxa.

Molecular analyses at subtribal rank have been carried out for the Sonchinae/Dendroseridinae (Crawford et al. 1992; Sang et al. 1994; Kim et al. 1996, 1997, 1999a, b, 2004, 2007; Lee et al. 2005), Lactucinae (Koopman et al. 1998, 2001), Hypochaeridinae (Samuel et al. 2003, 2006; Tremetsberger et al. 2005), Scorzonerinae (Mavrodiev et al. 2004) and the predominantly North American subtribes (Jansen et al. 1991; Lee et al. 2003). They have added a wealth of new data, provided some new insights into the phylogeny, which led to a number of taxonomic changes regarding the circumscription of genera. The more prominent examples are *Sonchus* (paraphyletic and either to include all its previous segregates plus the Pacific islands endemics *Dendroseris* and *Thamnoseris*, or, alternatively, to be split in several monophyletic units to be newly established), *Scorzonera* (polyphyletic and to be divided up by re-establishing several former segregates), *Leontodon* (diphyletic, making re-establishment of *Scorzoneroideae*

necessary), *Lactuca* (paraphyletic or polyphyletic depending on circumscription, but none of the existing morphological genus concepts being monophyletic) and *Malacothrix* (diphyletic). Further details are provided in the sections on phylogeny and taxonomy, below.

The most recent overview of Cichorieae is the treatment by one of us (Lack 2007) for the *Families and Genera of Flowering Plants*, which broadly followed the classification of Bremer (1994), with more substantial modifications restricted to Sonchinae (inclusion of the Dendroseridinae and with a wider circumscription of *Sonchus*, based on the work by Kim et al. 1996, 1997, 1999a, b) and Lactucinae (wider circumscription of *Lactuca* based on Koopman et al. 1998). In the light of the most recent molecular studies, we provide an essentially updated classification here.

Circumscription of Cichorieae

The traditional circumscription of Cichorieae as a conveniently recognized tribe, diagnosed by the unique combination of homogamous capitula with 5-dentate, ligulate flowers and the presence of milky latex, has been altered recently on the basis of molecular data (Gemeinholzer et al., in prep.) to accommodate two genera hitherto variously placed: *Gundelia* and *Warionia*. Both have milky latex but otherwise homogamous capitula with tubular flowers only. By inclusion of these genera the homogamous capitula with 5-dentate, ligulate flowers no longer characterize all the members of the tribe. On the other hand, although milky latex is otherwise present in some genera of Arctotideae, Cardueae, Liabeae, Mutisieae, and Vernonieae (Carlquist 1976), and in a few cases in Asteroideae, the presence of lactiferous canals in both the subterranean and aerial plant parts seem to be an exclusive feature of Cichorieae as circumscribed here (Augier and Méric 1951; Wagenitz 1976; Bremer 1987, 1994). Homogamous capitula with 5-dentate, ligulate flowers are present in a few genera of Mutisieae (*Catamixis*, *Glossarion*, *Hyaloseris*; Bremer 1987, 1994) and, quite evidently by convergent evolution, in Heliantheae-Coreopsidinae (*Fitchia*) of subfamily Asteroideae (Carlquist 1957); 5-dentate, ligulate marginal flowers occur in Vernonieae (*Stokesia*; Bremer 1987, 1994).

Both *Gundelia* and *Warionia* share the presence of both (functional) oil ducts and latex canals in the roots (Augier and Méric 1951), which has been reported otherwise from only two Cichorieae genera, viz. *Scolymus* and *Scorzonera* s.l. (Tieghem 1872; Col 1903–04). The two species of *Gundelia*, with a much-derived synflorescence of one-flowered capitula aggregated to secondary capitula, have spiny leaves and pollen (Blackmore 1981; Robinson 1994) similar to *Scolymus*. *Gundelia* has been shown to form a monophyletic trichotomy with *Scolymus* and the rest of Cichorieae (Karis et al. 2001;

based on *ndhF* data). *Warionia* has been shown to form a sister group relationship to the Cichorieae by Funk et al. (2004; based on *trnL-F*, *ndhF* and ITS data) and the basalmost branch of Cichorieae clade by Goertzen et al. (2003: fig. 3; based on ITS data). A rather conservative taxonomic conclusion from these results was drawn by Jeffrey (2007), who re-established a separate tribe Gundelieae near to Cichorieae to include both genera. Formerly *Gundelia* had been associated with Arctotideae and *Warionia* with Mutisieae.

Our new molecular-based analyses using the nuclear ITS and the plastid *matK* region with a much larger dataset (including 428 taxa belonging to 83 genera), and especially the inclusion of several basally branching taxa in the analyses, revealed that both genera cluster within Cichorieae, which now are monophyletic, statistically supported by 100% bootstrap value and 1.0 posterior probability. *Gundelia* clusters with *Catananche*, *Hymenonema*, and *Scolymus* (Gemeinholzer et al., in prep.) in Scolyminae, however, only supported by posterior probability (1.0). The monospecific *Warionia*, with densely pilose achenes (rare in Cichorieae but also occurring, e.g., in many species of *Scorzoneria*), is branching off basally and is found to be the sister group to all Cichorieae (*Gundelia* included). For *Warionia* a new subtribe of its own is established (see Appendix 24.1). These results do not contradict earlier studies (Karis et al. 2001; Funk et al. 2004) but reveal the closer relationship of both genera to Cichorieae than to any other tribe, which therefore justifies the treatment presented here.

For outgroup selection an alignment comprising the ITS region of 214 Cichorieae taxa and 103 GenBank sequences of potential outgroup taxa was analyzed (Arctotideae 37 sequences, Gnaphalieae 36, Inuleae [incl. Plucheeae] 14, Liabeae 5, Carduoideae 4, Barnadesioideae 2, Mutisieae 2, Vernonieae 2, Anthemideae 1). Statistical support for the monophyly of Cichorieae including *Warionia* and *Gundelia* was strong, supporting the statement of Goertzen et al. (2003) that a key factor for a successful ITS alignment is the large sample of sequences included. The same ingroup branching pattern within Cichorieae was also revealed with a reduced outgroup selection to nine taxa comprising *Brachylaena discolor* DC. AY826236, *Cardopatum corymbosum* Pers. AY826238, *Ericentrodea corazonensis* S.F. Blake & Sherff AY429088, *Ericentrodea decomposita* S.F. Blake & Sherff AY429089, *Heterolepis aliena* Druce AY504700, *Geigeria ornativa* O. Hoffm. U84774, *Oldenburgia intermedia* Bond AY826303, *Pluchea indica* (L.) Less. AF430795, and *Saussurea maximowiczii* Herder AY826324. Further reduction of outgroup taxa or selection of only the nearest neighbors (as shown by Karis et al. 2001 and Panero and Funk 2002 for cpDNA-analyses) resulted in unresolved branching patterns, provided unstable tree topologies, and/or changed the ingroup relationships considerably.

PHYLOGENY

The major clades within Cichorieae and the recognition of subtribes

Recent molecular analyses of a large dataset (428 taxa of 83 genera) of Cichorieae (Gemeinholzer et al., in prep.) revealed the existence of five major clades, with a total of eleven subclades, within the tribe (Fig. 24.1).

The first three main clades branching off basally are in general not very species-rich. Clade 1 is sister group to the remainder and includes solely *Warionia* (Clade 1, recognized as a new subtribe Warioniinae; see Appendix 24.1). Clade 2 represents the subtribe Scorzonerinae, which is statistically well supported and sister to clades 3–5. Clade 3 represents the subtribe Scolyminae, which is sister group to clades 4–5 (Fig. 24.1). The monophyly of Scolyminae is supported by a posterior probability of 1.0 but features no bootstrap support and comprises the former subtribe Catananchinae (Bremer 1994; Lack 2007). The remaining two large clades 4 (Fig. 24.2) and 5 (Fig. 24.3) comprise roughly 80% of the species (microspecies not considered) of the tribe. Clade 4 includes the subtribes Chondrillinae, Crepidinae, Hyoseridinae, Hypochaeridinae, and Lactucinae. Clade 5 includes the subtribes Cichoriinae, Hieraciinae, and Microseridinae s.l.

Clade 1. — The monospecific genus *Warionia* is the only member of Clade 1, Warioniinae (Fig. 24.1). *Warionia* is closer to Cichorieae than to any other tribe of Compositae according to molecular and morphological characters, but it is so distinct from all other genera within the tribe that it requires a separate subtribe Warioniinae. *Warionia* is endemic to SE Morocco and NW Algeria. The genus and subtribe is characterized by a frutescent habit, latex, essential oils, the presence of both oil ducts and latex canals in the roots (Augier and Mérac 1951; Carlquist 1976: 481; Ramaut et al. 1985), homogamous capitula with slightly zygomorphic 5-dentate, tubular, yellow flowers with 10 corolla bundles (see Morphology and anatomy below), densely pilose achenes with a pappus of coarse, scabrid bristles, and a basic chromosome number of $x = 17$ (Reese 1957; Humphries et al. 1978; Oberprieler and Vogt 1993).

Clade 2. — Scorzonerinae (Fig. 24.1) form a well-supported clade in all phylogenetic analyses of the tribe based on morphological (Bremer 1994) and molecular data (Mavrodiev et al. 2004; Gemeinholzer et al., in prep.). The molecular data with high statistical support of monophyly confirm its recognition as subtribe Scorzonerinae in its traditional morphological characterization and circumscription (Stebbins 1953, but lacking *Koelpinia*; Blackmore 1981; Bremer 1994; Lack 2007). Scorzonerinae are characterized by predominantly linear-lanceolate and parallel-veined leaves, an indumentum being soft or absent, uni- to multiseriate involucre bracts,

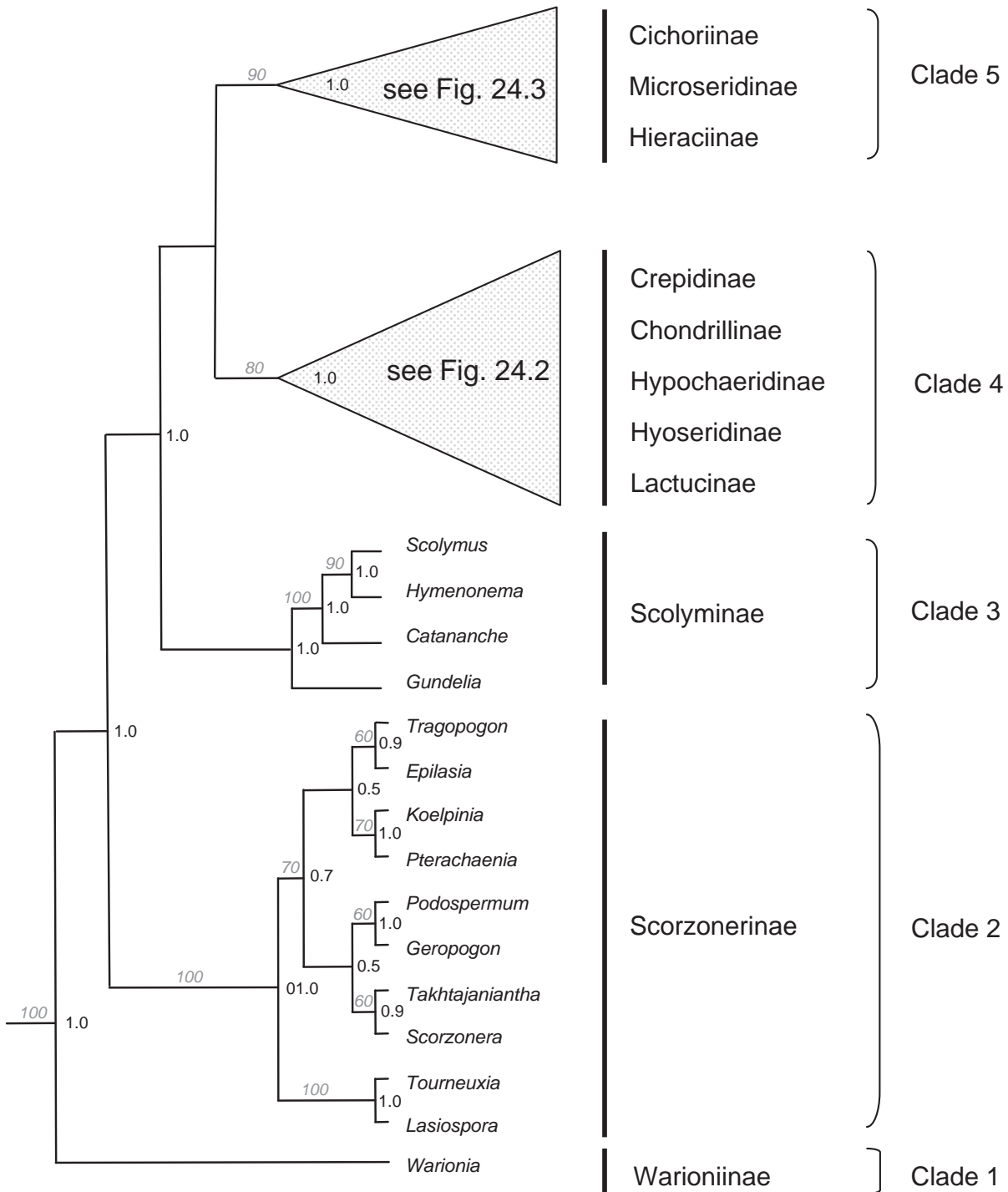


Fig. 24.1. Scheme of the molecular phylogeny of Cichorieae based on the nuclear ITS region (ITS1, 5.8S rDNA, ITS2) presenting the relationships of Cichorieae as well as within clades 1–3. Clades 4 and 5 (triangles within the tree) are only schematic here; relationships within these clades are presented in Figs. 24.2 and 24.3. This scheme, as well as the ones in Figs. 24.2 and 24.3, are inferred from majority consensus phylograms of partitioned Bayesian analyses (Ronquist and Huelsenbeck 2003) calculated on a GRID network (4×4 independent unlinked chains, all model parameters being unlinked, gamma distribution rate variation among sites, 10 million generations of the MCMC chains, trees saved every 100 generations and burn-in of the first 2500 trees). Numbers at branch nodes represent posterior probabilities. The topology is in large part congruent to the calculated MP analysis with 1000 bootstrap replicates (not shown), branches statistically supported $< 50\%$ are depicted in italics along the branches. Only genera for which molecular data are available are presented here.

plumose pappus rays with soft pinnulae, and distinct types of echinolphate pollen (with equatorial ridges replaced by a lacuna, the aperture being divided into two lacunae, and with a characteristic exine stratification). If the pappus is absent as in *Koelpinia*, the characteristic pollen type of this alliance still allows unequivocal placement (Blackmore 1981).

Generic delimitation within the subtribe has been controversial, mainly regarding the circumscription of *Scorzonera* and the recognition of the segregates *Epilasia*, *Podospermum*, *Pterachaenia*, *Takhtajiantha*, and *Tourneuxia*. A recent molecular phylogeny of the subtribe by Mavrodiev et al. (2004) confirmed the polyphyly of *Scorzonera* and provided support for recognition of the aforementioned segregates as well as for the separation of *Geropogon* from *Tragopogon*. Further molecular analyses of the subtribe (Gemeinholzer et al., in prep.), including more sequences from the core of *Scorzonera*, revealed paraphyletic groupings even within *Scorzonera* s.str. (Mavrodiev et al. 2004). However, due to the yet incomplete taxon sampling, the paraphyletic status of *Scorzonera* is presented here (see Appendix 24.1) without a revised taxonomic treatment, as this is still subject to ongoing studies (Gemeinholzer et al., in prep.).

Clade 3. — Within Scolyminae (Fig. 24.1), *Catananche* is sister group to *Hymenonema* and *Scolymus*. *Gundelia* is sister group to this monophyletic group with high posterior probability (1.0), however, with no bootstrap support (for discussion see Circumscription of Cichorieae, above). *Rothmaleria* formerly has also been associated with the first three genera for palynological reasons (Blackmore 1981) and has been placed together with *Catananche* and *Hymenonema* in a separate subtribe (or informal entity, respectively; Jeffrey 1966; Bremer 1994; Lack 2007). According to our molecular data, *Rothmaleria* is not related to *Catananche* and *Hymenonema* but to *Tolpis* as Stebbins (1953) and Jeffrey (1966) already assumed from morphological data.

Morphologically clade 3 is characterized by an annual or perennial life form, entire to pinnatifid-pinnatisect or coarsely lobed-pinnatisect, spiny leaves, receptacular scales or bristles, and the pappus being either absent or of denticulate-fimbriate scabrid bristles or lanceolate scales. Both *Gundelia* and *Scolymus* are laticiferous spiny leafy herbs with sessile capitula or syncalathia, respectively.

Clade 4. — This clade (Fig. 24.2) is by far the largest, with about 900 species or roughly 2/3 of the entire tribe (microspecies not considered). Its monophyly is supported by bootstrap value (80) and posterior probability (1.0). In all of our analyses of this clade, five subclades, although with weak support, can be delimited. However, there is little resolution of relationships among most major lineages within clade 4 for parsimony and Bayesian analyses, although not as result of an overall lack of resolution, but

due to the uncertain placement of only few genera (e.g., *Phitosia*, *Prenanthes*, and *Urospermum*). The analyzed nuclear and plastid markers of these genera reflect different phylogenetic relationships, perhaps pointing to hybridization across lineages, possibly with former chloroplast capture and backcrossing to one parent. This might explain the overall weak support of the lineages within this clade. However, it could also be due to rapid diversification. As nuclear markers in general better resemble morphological characters, and as additional evidences for the placement of the uncertain genera are supported by morphological characteristics, we decided on the group delimitations featured in Fig. 24.2.

Subclade 4-1. The Lactucinae subclade as found in our analyses deviates considerably from the subtribe Lactucinae as previously circumscribed by Bremer (1994) and Lack (2007), which has been revealed to be polyphyletic. In the cladogram presented in Fig. 24.2 the Lactucinae are monophyletic and received bootstrap support of 80% and 1.0 posterior probability.

The delimitation of *Prenanthes* from *Lactuca* has puzzled generations of botanists, but the former is not a member of Lactucinae. In fact *Prenanthes* s.l. has been a dustbin for a number of totally unrelated elements with a combination of plesiomorphic characters. Re-circumscription on the basis of morphological data has been recently attempted by Shih (1987), who not only re-established *Nabalus* Cass. for chiefly the North American members but also removed East Asian species from *Prenanthes* and placed them in the new genus *Notoseris* on the basis of morphological analyses. Sennikov (2000) and Sennikov and Illarionova (2000) morphologically further narrowed down the circumscription of *Prenanthes*. Sennikov and Illarionova (2001), however, returned to the former, very wide circumscription of *Prenanthes*, giving the similar achene anatomy of all *Prenanthes* segregates. Our molecular phylogenies based on both nuclear and plastid markers confirm a very narrow circumscription of *Prenanthes* (perhaps being even monospecific), which, however, is not part of Lactucinae. *Prenanthes* species of the former circumscription now belong in large part to the subtribe Crepidinae (see *Nabalus*), minor parts to genera of Lactucinae (*Cicerbita*, *Lactuca* s.l., *Notoseris*) and Cichoriinae (see *Erythroseris*), which is supported by the nuclear and plastid phylogenies. For *Prenanthes* s.str. the molecular data revealed a surprising affinity to Hypochaeridinae for the nuclear marker, but in the chloroplast analysis (not presented here) it appeared to branch off basally to Lactucinae with very low posterior probability (0.50). The deviating molecular patterns of markers from different origin most likely reflect ancient hybridization with other members of the tribe, but further investigations are needed to find parental relationships.

Syncalathium, included into Lactucinae by Bremer (1994) and Lack (2007), is diphyletic according to the

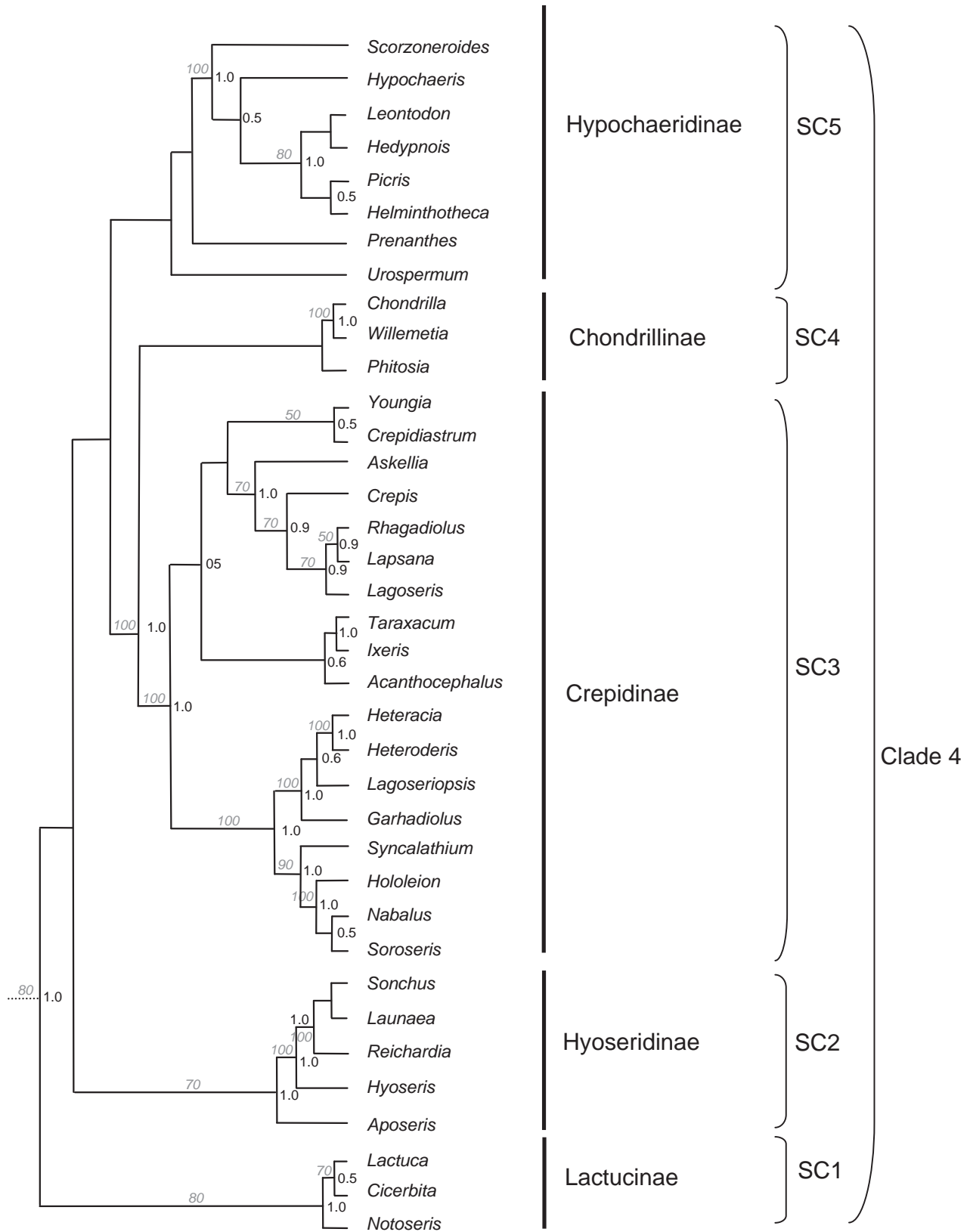


Fig. 24.2. Clade 4 as scheme of the molecular phylogeny of Cichorieae based on the nuclear ITS region (for details see legend in Fig. 24.1). SC = subclade; clades and subclades correspond to descriptions in section Phylogeny.

molecular phylogenies (Gemeinholzer et al., in prep.). The larger group of species has 5-ribbed achenes, includes *S. disciforme* (Mattf.) Y. Ling, *S. porphyreum* (C. Marquand & Airy Shaw) Y. Ling, and *S. kawaguchii* (Kitam.) Y. Ling (= *S. sukaczewii* Lipsch, providing the type of the genus name) and belongs to Crepidinae with a relationship to *Nabulus* and *Soroseris* (Fig. 24.2). The other part of the genus, represented by *S. souliei* (Franch.) Y. Ling, has achenes with one rib on either side, and belongs in Lactucinae close to *Notoseris*. This finding has also been corroborated by a recent karyological study (Zhang et al. 2007), where *S. souliei* was found to have the same chromosome number ($2n = 16$) as *Syncalathium* s.str. (represented by *S. kawaguchii*) and *Soroseris*, but with a karyotype formula quite different from them. Blackmore and Persson (1996), who included *S. porphyreum* in their palynological studies and phylogenetic analysis based on morphological data, also found an affinity with Crepidinae and not with Lactucinae, but revealed a relationship with *Ixeris* and *Youngia* rather than with *Soroseris*.

What remains in the subtribe Lactucinae is a morphologically rather diverse alliance, in which the morphological delimitation of natural entities at generic rank has posed almost insolvable problems. A key issue is the circumscription of *Lactuca*, as has already been discussed by Koopman et al. (1998), who provided an initial molecular study. Combined molecular-morphological analyses by Kilian and Gemeinholzer (in prep.) on the basis of a much enlarged sample will provide a new approach of generic subdivision of the *Lactuca* alliance; however current results provide only a preliminary taxonomy.

Subclade 4-2. This subclade comprises a re-circumscribed subtribe Sonchinae, to be named Hyoseridinae. In the cladogram presented in Fig. 24.2, subclade 2 is sister group to subclades 3–5, with monophyly supported by bootstrap values of 70% only and posterior probability of 1.0. As already stated earlier (Kim et al. 1996, 1997, 1999a, b, 2004, 2007), Bremer's (1994) subtribe Sonchinae needs to include *Dendroseris* to become monophyletic, a solution also favored by Lack (2007). Meanwhile the inclusion of the monospecific, less known genus *Thammoseris*, which has been closely associated to *Dendroseris* (Jeffrey 1966; Bremer 1994; Lack 2007), has been confirmed by molecular analysis (Kim, pers. comm., March 2007).

The core of the subtribe consists of the *Sonchus-Launaea* alliance including *Reichardia*, with a monophyly supported by 100% bootstrap value and 1.0 posterior probability. The recently described Central Asian monospecific genus *Hexinia* has been placed within *Launaea* by Kilian (1997) based on morphological evidences, which are confirmed by molecular data (Kilian, in prep.). The various species-poor genera, established within the *Sonchus* alliance on often vague morphological grounds for species of the Canary Islands (*Chrysoprenanthes*, *Babcockia*, *Lactucosonchus*,

Sventenia, *Taekholmia*, *Wildpretia*) and of Australia/New Zealand (*Actites*, *Embergeria*, *Kirkianella*), were placed within *Sonchus* in all recent molecular studies (Kim et al. 1996, 1997, 1999a, b, 2004, 2007). The same has been confirmed for the monospecific Mediterranean *Aetheorhiza* as well as for *Dendroseris* and *Thammoseris*, which are endemic to the Pacific Juan Fernández and Desventuradas Islands off the coast of Chile (Kim et al. 2007; S.-C. Kim, pers. comm., March 2007). A reconsideration of *Sonchus* s.l., aiming at recognition of monophyletic, morphologically delimited entities at generic or subgeneric rank, is in preparation by Kim and Mejías (pers. comm., March 2007).

Our own recent results (Gemeinholzer et al., in prep. and see Fig. 24.2) revealed also that *Aposeris* and *Hyoseris* have to be included in Sonchinae. Blackmore (1981) stated that the palynological evidence is inconclusive for the placement of *Hyoseris*, reflecting a possible relationship to the *Hypochaeris* alliance as likely as to the *Sonchus-Launaea* alliance. The placement of *Hyoseris* along with *Aposeris* within the *Hypochaeris* alliance was chosen by Jeffrey (1966), Bremer (1994), and Lack (2007). In contrast, molecular data revealed that neither species is related to the *Hypochaeris* alliance (Samuel et al. 2003) but form a sister group relationship to the *Sonchus-Launaea* alliance (Gemeinholzer et al., in prep.; Kim, unpub., pers. comm., March 2007). *Aposeris*, lacking a pappus, is sister to all other genera of this subtribe, which are rather closely related to each other, while *Hyoseris*, with an inner pappus of basally strongly widened bristles, is sister group to the clade including the *Sonchus-Launaea* alliance. Inclusion of *Hyoseris* unfortunately requires a change of name of the subtribe from Sonchinae to Hyoseridinae because of priority.

Subclade 4-3. Here redefined Crepidinae (Fig. 24.2 and Appendix 24.1) are monophyletic with high statistical support (bootstrap value 100%, posterior probability 1.0). They comprise two subclades (Fig. 24.2). The first subclade is predominantly Asian, with *Heteracia* and *Heteroderis* as sister groups (bootstrap value 100% and posterior probability 1.0) sharing a common ancestor with *Lagoseriopsis* (0.6 posterior probability), and all three being sister group to *Garhadiolus* (bootstrap value 100% and posterior probability 1.0). The sister group to these four genera comprises *Nabulus* and *Soroseris* sharing a common ancestor with *Hololeion* (bootstrap value 100% and posterior probability 1.0) and all three being sister to *Syncalathium* (bootstrap value 90% and posterior probability 1.0). The second subclade comprises predominantly Eurasian taxa: here newly included *Lapsana* and *Rhagadiolus* (monophyly with 50% bootstrap value and 0.9 posterior probability) are sister group to *Lagoseri* (70% bootstrap value and 0.9 posterior probability) in a monophyletic group with *Crepis* (70% bootstrap value and 0.9 posterior probability). The genus *Askellia* has been separated from *Crepis* and is

basal to those four genera and forms a sister group relationship to *Crepidiastrum* and *Youngia* with bootstrap value of 70% and 1.0 posterior probability. The other branch of this second subclade comprises *Taraxacum* next to *Ixeris* featuring a common ancestor with *Acanthocephalus* (posterior probability 0.6). The phylogenetic relationships of *Dubyaea*, *Ixeridium*, and *Lapsanastrum* are yet uncertain.

With ca. 360 species (the *Taraxacum* microspecies not counted), comprising 2/5 of the species of clade 3 and more than 1/4 of the tribe, the subtribe Crepidinae is the largest of Cichorieae. We mentioned the removal of the *Chondrilla* alliance as a separate subtribe and the addition of *Nabalus* and *Syncalathium* formerly placed into Lactucinae. Molecular analyses (Whitton et al. 1995; Gemeinholzer et al., in prep.) show that the genera *Rhagadiolus* and *Rhagadiolus* formerly placed in subtribe Hypochaeridinae (Bremer 1994; Lack 2007), and *Hololeion* formerly placed in subtribe Hieraciinae (Bremer 1994; Lack 2007), belong to Crepidinae. The recognition of *Nabalus* as a genus separate from *Prenanthes*, including all North American and several Central and East Asian members of the latter genus, as suggested by our analysis, confirms Stebbins (1940: 63). He concluded from studies of the achene vascularization that the species of *Nabalus* are much closer to *Dubyaea* and *Sorosseris* than to *Prenanthes purpurea*, which provides the type of *Prenanthes*. The previously assumed placement of the little known monospecific genera *Dianthoseris* and *Lagoseriopsis* in Crepidinae (Bremer 1994; Lack 2007) has been confirmed by our molecular analyses (Fig. 24.2; Gemeinholzer et al., in prep.), *Dianthoseris*, however, has been found to be a congener of *Crepis*, see below.

The relationship of *Syncalathium* (s.str., compare subclade 1, above) with *Nabalus* and *Sorosseris* revealed in our analyses has 1.0 posterior probability and 90% bootstrap value.

Our molecular analyses (Fig. 24.2; Gemeinholzer et al., in prep.) revealed *Crepis* sensu Babcock to be polyphyletic. Several *Crepis* species (e.g., *C. bupleurifolia* (Boiss. & Kotschy) Freyn & Sliint., *C. elymaitica* Bornm.) are of uncertain position within Crepidinae and will have to be tested against a greater sampling of species in the subtribe and morphologically investigated to assign their definitive status. *Crepis* species from Babcock's sections *Intybellia*, *Lagoseris*, *Microcephalum*, *Phaeacium*, and *Pterotheca* cluster in the nuclear and plastid analyses in a monophyletic group as sister group to *Lapsana* and *Rhagadiolus* (Enke and Gemeinholzer 2008). To make *Crepis* monophyletic, this would either necessitate recognition of *Lagoseris* as a separate genus in the tradition of Bobrov and Tzvelev (1964), or inclusion of *Lapsana* and *Rhagadiolus* in *Crepis*. *Lagoseris* differs distinctly from the latter two genera in fruit morphology, but the absence of a pappus in *Lapsana* and *Rhagadiolus* is not regarded as decisive, since a loss of pappus occurs also in *Crepis*. The achenes of *Lapsana*

are strongly compressed and the achenes of *Rhagadiolus* are presented in a star-like way; neither of these forms is known from *Crepis* s.l. *Lapsana* is traditionally considered to be closely related to *Crepis*, both belonging to the *Ixeris-Youngia* line (Stebbins 1953), the *Crepis* series (Jeffrey 1966) and Crepidinae (Bremer 1994). After separation of the former East Asian members from *Lapsana* as the new genus *Lapsanastrum* by Pak and Bremer (1995) for chiefly carpological reasons, *Lapsana* is monospecific (only comprising *L. communis* L.), which is supported by our molecular results.

The Central Asian and North American species of *Crepis* sect. *Ixeridopsis* are clearly isolated from *Crepis* s.str. and have been transferred to *Askellia* based on morphological dissimilarities in overall habit, involucre shape and flower number per capitulum as well as on molecular, cytological and biogeographical data (Sennikov and Illarionova 2007; Enke and Gemeinholzer, in press). *Askellia* clusters as sister group to the clade comprising *Crepis* s.str., *Lagoseris*, *Lapsana*, and *Rhagadiolus* on one branch, and *Ixeridium*, *Ixeris*, *Paraixeris*, *Taraxacum*, and *Youngia* on the other branch. Babcock (1947) already recognized the intermediate position of *Askellia* between *Crepis* and *Ixeris*, even though most of the species (e.g., *A. nana*, *A. flexuosa*) used to be treated under *Youngia* to which they were recently reassigned (Adylov and Zuckerwanik 1993). However, *Askellia* features terete achenes and a basic chromosome number of $x = 7$ (otherwise not present in *Crepis*), while the achenes of *Youngia* are compressed and angular and the chromosome number is $x = 8$. Other members of Crepidinae, e.g., *Ixeridium* (Pak and Kawano 1992), even though having a basic chromosome number of $x = 7$ such as *Askellia*, differ by their fusiform and flattened achenes. *Ixeris* is, in achene morphology, similar to *Ixeridium* and differs from *Askellia* in chromosome number and number of flowers per capitulum, which are both higher in *Ixeris*, confirming the close relationship of *Ixeridium*, *Ixeris*, and *Youngia*, a clade to which also *Paraixeris* and *Taraxacum* have to be added, based on molecular evidence, achene morphology, and base chromosome number range of $x = 8, 7, 6, 5$.

The monospecific afroalpine *Dianthoseris*, according to Blackmore and Persson (1996) with distinct pollen characteristics (subechinolphate pollen grains with rudimentary paraporal lacunae, rounded abpolar lacunae) more similar to *Dubyaea* and *Sorosseris* than to *Crepis* (echinolphate pollen grains, tricolporate, ectocolpi divided into three lacunae, somewhat angular, large abpolar lacunae), is nested in our analyses right within *Crepis* s.str. (Enke et al. 2008; Gemeinholzer et al., in prep.).

Subclade 4-4. This subclade is not statistically supported, but is recognized by us as subtribe Chondrillinae comprising the genera *Chondrilla*, *Phitosia*, and *Willemetia*. The former two genera have been hitherto treated as members of subtribe Crepidinae (Bremer 1994; Lack 2007).

Chondrillinae (subclade 4) and Crepidinae (subclade 3) form a monophyletic group of 100% bootstrap value and posterior probability of 1.0 (Fig. 24.2). Since the sister group relationship of Crepidinae and Chondrillinae presented here has been proven less stable when combining different molecular datasets (*matK* and ITS; Gemeinholzer et al., in prep.), we have refrained from treating subclades 3 and 4 as a single subtribe Crepidinae. Next to *Chondrilla* and *Willemetia*, the third genus in subclade Chondrillinae is *Phitosia*, a monospecific genus recently established for a species removed from *Crepis* for cytological and carpological reasons (Kamari and Greuter 2000).

Subclade 4-5. This subclade comprises subtribe Hypochaeridinae in the sense of Bremer (1994) and Lack (2007) but excluded are (1) *Aposeris* and *Hyoseris*, which group with the *Sonchus-Launaea-Reichardia* alliance (subtribe Hyoseridinae), (2) *Garhadiolus* and *Rhagadiolus* (subtribe Crepidinae), and (3) *Arnosseris* (its relationship to the *Tolpis* alliance rather than to the *Hypochaeris* alliance is confirmed; see Cichoriinae).

The core of this subtribe (0.5 posterior probability) is formed by the *Hypochaeris-Leontodon-Picris* alliance (Fig. 24.2). Its relationship has been well resolved in a number of molecular studies (e.g., Samuel et al. 2006). *Hypochaeris*, which has a curious disjunct distribution with ca. twelve species in the Mediterranean and Europe, one species in Asia and forty species in South America (Cerbah et al. 1999), is monophyletic and has colonized South America apparently via long-distance dispersal (Samuel et al. 2003; Weiss-Schneeweiss et al. 2003, 2008; Tremetsberger et al. 2005). *Hedypnois*, the only genus in this alliance with a scabrid instead of plumose pappus, is nested right within the alliance (Samuel et al. 2006), indicating a reverse development of the plumose pappus, which is plesiomorphic in Cichorieae, back to a scabrid pappus. *Picris* and the closely related *Helminthotheca* are both monophyletic, whereas *Leontodon* in its current circumscription is diphyletic (Samuel et al. 2006), which necessitates recognition of *L.* subg. *Oporinia* as separate genus *Scorzoneroides* (Greuter et al. 2006).

Prenanthes purpurea L. (providing the type of the name *Prenanthes*) and *Urospermum* are included in subclade 5, but statistical support is missing most likely as result of ancient hybridization across lineage resulting in intermediate positions: *P. purpurea* is sister group to core Hypochaeridinae and *Urospermum* sister group to the latter two. In case of the bispecific *Urospermum*, this result is not unexpected, since the predominantly Mediterranean *Urospermum* with its plumose *Hypochaeris* type pappus, the hispid indumentum, and a pollen type very similar to *Hypochaeris* and *Picris* (Lack and Leuenberger 1979) has in spite of the uniseriate, basally connate involucre and its unique achenes, unequivocally been placed into Hypochaeridinae since Hoffmann (1890–1894). In contrast, *Prenanthes* has never

been associated with Hypochaeridinae, and morphology does not provide any support for this placement. Reticulate hybridization events with one parent from Hypochaeridinae and the other from Crepidinae or some other members within clade 4 could be possible explanations for the statistically uncertain placement of the genus. At present we provisionally place it within Hypochaeridinae to which it most commonly clusters based upon our molecular results, but further investigations reassessing its phylogeny are needed. The chloroplast marker (*matK*) indicates a basal branching position within Lactucinae.

Clade 5. — The monophyly of this clade is statistically supported by bootstrap value of 90% and posterior probability of 1.0. Within this clade three monophyletic groups can be detected. Hieraciinae are sister to a clade including (1) the principally North American genera plus the South American *Picrosia* (Microseridinae), and (2) Cichoriinae (Fig. 24.3).

Subclade 5-1. Hieraciinae (bootstrap value 100% and posterior probability 1.0) represent the subtribe in the circumscription of Lack (2007) but without *Tolpis*, which clusters with *Cichorium*, and without *Hololeion*, which according to our analysis is a member of Crepidinae. *Hololeion*, with a basic chromosome number of $x = 8$, was odd within the subtribe as otherwise all taxa feature a basic chromosome number of $x = 9$. With its exclusion, the basic number of $x = 9$ is characteristic for the subtribe. Hieraciinae sensu Bremer (1994) also included *Arnosseris*, a genus that Lack (2007) placed into Hypochaeridinae, but which clusters in our analysis (Gemeinholzer et al., in prep.) with *Cichorium*, too. *Hieracium intybaceum* Lam., which is restricted to the siliceous Alps, was separated in the 19th century as the genus *Schlagintweitia*, which is in our analyses (Fehrer et al. 2007; Gemeinholzer et al., in prep.) sister to the rest of the alliance, comprising *Andryala*, *Hieracium*, *Hispidella*, and *Pilosella* (bootstrap value 80% and posterior probability 1.0; see Fig. 24.3). This result necessitates the re-establishment of *Schlagintweitia* as a segregate of *Hieracium*, with which, however, it produces fertile hybrids (C. Zidorn, pers. comm., May 2007). Intergeneric hybridization within Hieraciinae resulting in cytoplasmic inheritance has also been reported in earlier studies, e.g., from *Hieracium* subg. *Chionoracium* to *Pilosella* and from the introgressed *Pilosella* lineage to *Andryala* (Fehrer et al. 2007), and has been revealed by incongruent topologies of nuclear and chloroplast analyses inferred from chloroplast (*trnT-trnL*, *matK*) and nuclear (ITS) sequence data. In general, the ITS data analysis is in accordance with morphological and other evidence and, therefore, is assumed to reflect species relationships. Hereby, a sister group relationship between *Pilosella* and *Hispidella* (bootstrap value 80% and posterior probability 1.0) and a joint clade of these and

Hieracium (*H.* subg. *Hieracium* and *H.* subg. *Chionoracium* [= *Stenotheca*]) (100% bootstrap value and 0.7 posterior probability) is revealed (Fig. 24.3). *Andryala* represents a third major lineage of the clade including *Pilosella*, *Hispidella*, and *Hieracium*, which has 80% bootstrap support and 1.0 posterior probability.

Subclade 5-2. Sister group to Hieraciinae is a clade supported by posterior probability of 0.7 (Fig. 24.3), which includes the North American genera plus the South American *Picosia* in one clade (bootstrap value of 80% and posterior probability of 0.8 support the monophyly) and Old World Cichorieae in a second clade sister

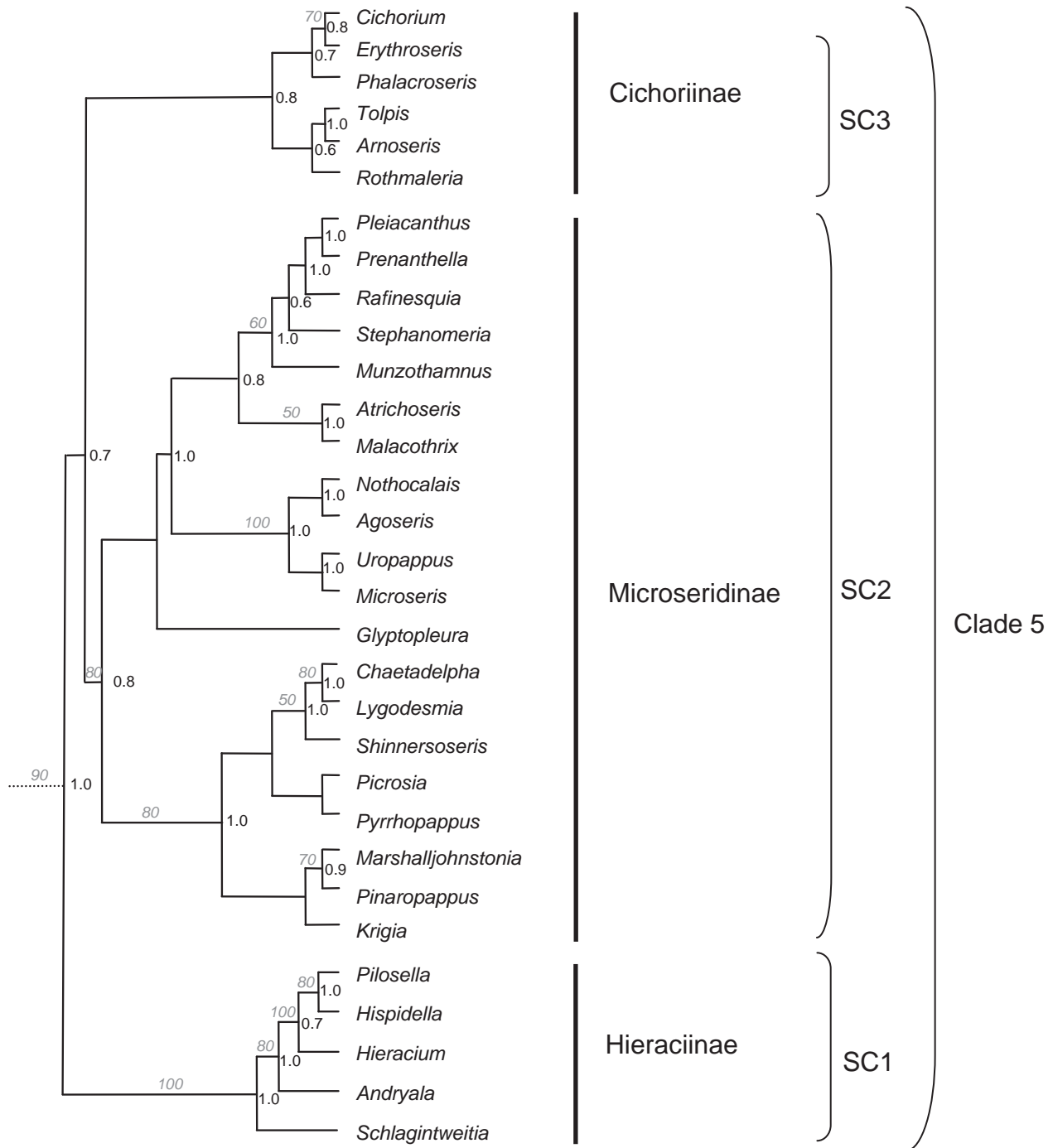


Fig. 24.3. Clade 5 as scheme of the molecular phylogeny of Cichorieae based on the nuclear ITS region (for details see legend in Fig. 24.1). SC = subclade; clades and subclades correspond to descriptions in section Phylogeny.

to the former (0.8 posterior probability). The radiation of the principal American Cichorieae genera from a single common ancestor as found by Lee et al. (2003) has been confirmed by our analyses of a much larger dataset, in which the sequences of the American clade by these authors were included, with the odd exception of *Phalacroseris*. This monospecific localized NW American genus, which is sister to the remainder of the American clade in the analyses by Lee et al. (2003), is nested in our analyses within Cichoriinae (Gemeinholzer et al., in prep.).

The American clade has previously been treated as two (Jeffrey 1966), three (Stebbins 1953; Bremer 1994; Lack 2007) or, based on the recent molecular evidence, as nine (Lee and Baldwin 2004) subtribes or informal entities, respectively. Apart from *Phalacroseris*, the suprageneric classification of the American clade by Lee and Baldwin (2004) best corresponds to the available datasets. It is, however, much more consistent with the phylogeny and the suprageneric classification of the entire tribe to reserve the subtribal rank for the American clade as such and to apply Lee and Baldwin's classification to a subordinate informal rank. We therefore recognize the American clade of our analyses as a single subtribe Microseridinae.

Subclade 5-3. Cichoriinae (Fig. 24.3) comprise six genera, four of which, viz. *Arnosseris*, *Cichorium*, *Rothmaleria*, and *Tolpis*, were united already by Stebbins (1953) in subtribe Cichoriinae with, however, other unrelated genera. Later classifications (Jeffrey 1966; Bremer 1994; Lack 2007) split these four elements apart. The relationship of *Arnosseris* with *Tolpis* (Stebbins 1953; Jeffrey 1966; Bremer 2004) rather than with the *Hypochaeris* alliance (Lack 2007) is morphologically supported by short style branches with short trichomes, corolla tubes covered externally with crisped trichomes, and has otherwise been supported by palynological data (Blackmore 1981) featuring small pollen grains with double rows of spines on the equatorial ridges. To these four genera our analyses added as sister group to *Cichorium* the genus *Erythroseris*, a genus most recently established for two species from the Horn of Africa and Socotra Island formerly placed in *Prenanthes* (Kilian and Gemeinholzer 2007), and the localized North-West American monospecific *Phalacroseris* (posterior probability 0.7), which features oblong-ellipsoid, unbeaked achenes and no pappus.

Monophyletic Cichoriinae (supported by posterior probability of 0.8 but no bootstrap support) are divided into two subclades (Fig. 24.3). In the first subclade (supported by posterior probability of 0.7 but no bootstrap support) *Erythroseris* is sister group to *Cichorium*, forming a monophyletic group (bootstrap value 70%, posterior probability 0.8), while *Phalacroseris* branches off basally to both. In the other subclade (being supported by posterior

probability of 0.6) *Arnosseris* is sister to *Tolpis* (posterior probability of 1.0 but no bootstrap support), while *Rothmaleria* is sister group to *Arnosseris* plus *Tolpis*, which is supported by 0.6 posterior probability only. The chloroplast analyses of Whitton et al. (1995), Park et al. (2001), and Gemeinholzer et al. (in prep.) reveal *Tolpis* (and *Arnosseris*; Gemeinholzer et al., in prep.) not to cluster at all within the *Cichorium-Tolpis* clade but within clade 4. The deviating phylogenies of the nuclear and the chloroplast markers, with different underlying modes of inheritance, can only be explained by reticulate evolution with an unknown parent most likely being a precursor of one of the today's species of clade 4 preceding generic and species divergence of *Tolpis* and *Arnosseris*, resulting in subsequent chloroplast capture. All molecular analyses feature different sampling of ingroup and outgroup taxa and result in slightly different placements of *Tolpis*, which is, however, most often closely related to *Hyoseris* and *Urospermum*; this could be indicative for the former potential hybrid partners. The most comprehensive sample was carried out by Gemeinholzer et al. (in prep.), where, in contrast to Park et al. (2001), *T. staticifolia* (All.) Sch.Bip. as well as *T. capensis* (L.) Sch.Bip. cluster right within the *Tolpis* group in the nuclear as well as the chloroplast analysis, most likely as result of a broader taxa sampling size.

Two possible relationships have been suggested in the past for the monospecific SW Mediterranean genus *Rothmaleria*, namely either *Catananche* and *Hymenonema* (Jeffrey 1966; Bremer 1994; Lack 2007) or *Cichorium* (Stebbins 1953; Lack et al. 1980). The latter relationship is not only favored by our molecular results, it is also morphologically supported by similar achenes, the non-aristate paleaceous pappus, and the long collecting trichomes of the style (Lack et al. 1980).

TAXONOMY

Tribe Cichorieae Lam. & DC. (1806)

= Lactuceae Cass. (1819), Catanancheae D. Don (1829), Crepideae Lindl. (1829), Hieracieae D. Don (1829), Hypochaerideae D. Don (1829), Scorzonereae D. Don (1829), Taraxaceae D. Don (1829), Gundelieae Lecoq & Juillet (1831), Hyoserideae Kostel. (1833), Scolymeae Kostel. (1833), Chondrilleae W.D.J. Koch (1837), Leontodontae (Sch.Bip.) W.D.J. Koch (1834), Picrideae Sch.Bip. (1834), Tragopogoneae Sch.Bip. (1834), Urospermeae Sch.Bip. (1834)

In the present treatment the tribe includes ca. 93 genera. Of these, 90 genera comprise approximately 1400 species, while 3 genera (*Hieracium*, *Pilosella*, and *Taraxacum*) have larger numbers of hybridogenous and/or apomictic species (*Hieracium*: ca. 770 sexually reproducing species + 5200 apomictic microspecies [pers. comm.

G. Gottschlich, April 2007]; *Pilosella*: ca. 110 sexually reproducing species + ca. 700 apomictic microspecies and weakly competitive hybrids [pers. comm. G. Gottschlich, April 2007]; *Taraxacum* ca. 1600 apomictic species [Sterk 1987, IPNI 2007]).

The new, revised classification of the tribe summarized here recognizes eleven subtribes based on the molecular and morphological analyses as discussed in the preceding part. Compared to the most recent treatments of the tribe by Bremer (1994) and Lack (2007), several subtribes are not maintained, two subtribes are newly recognized (Chondrillinae, Warioniinae) and the circumscription of most of the remaining ones as well as of several accepted (or provisionally accepted) genera has changed. It has thus been found appropriate to provide, in Appendix 24.1, a complete taxonomic overview of the tribe, including synonymies and type designations, to serve as a basis for further work. Generic delimitation in several cases is not yet fully settled; the number of genera may therefore still change in the future. Brief notes to the subtribes preceding the list of genera address such remaining problems in generic delimitation or classification.

MORPHOLOGY AND ANATOMY

Habit

The perennial herb, acaulescent (Fig. 24.4D, E, G) or scapose to caulescent (Fig. 24.4F), sometimes stoloniferous, represents the predominant habit of the tribe. Besides many paucennial and annual herbs, more rarely subshrubs, (spiny) shrubs (Fig. 24.4B), rosette shrubs (Fig. 24.4A) to rosette trees (Fig. 24.4C) and, exceptionally, scandent vines occur. The available molecular phylogenies indicate that the perennial herbaceous growth is plesiomorphic in the tribe and that both the annual and frutescent habits are derived. Annual species have evolved in all subtribes (apart from monospecific Warioniinae). In general, habit types are systematically valuable only on the species level.

Frutescent growth occurs in several subtribes (Cichoriinae: *Erythroseris*, *Tolpis*; Crepidinae: *Crepis kilimandscharica*; Hyoseridinae: *Launaea*, *Reichardia*, *Sonchus*; Hypochaeridinae: *Hypochaeris oligocephala* (Svent. & Bramwell) Lack only; Lactucinae: *Lactuca* s.l.; Microseridinae: *Marshalljohnstonia*, *Munzothamnus*, *Pleiacanthus*, *Stephanomeria*; Scorzonarinae: *Scorzonera* s.l.; Warioniinae: *Warionia*). Four reasons indicate the apomorphy of the frutescent growth in the tribe: (1) All forms of frutescent growth in Cichorieae are modifications of the growth and function of the rosette axis (= caudex; see Babcock 1947: 43). The rosette shoot (= caudical axis with extremely reduced internodes) is either increased in its growth, lignification and its branching, leading to the growth form of the rosette shrublets, shrubs and trees (Fig. 24.4A, C). Alternatively

the rosette axis is to some minor or larger extent disintegrated while lignified, leading to subshrubby to shrubby growth forms in which the long-articulate flowering stems are more or less included in the system of lignified caudical axes, present in the spinescent (Fig. 24.4B), scoparious or otherwise non-rosette subshrubs and shrubs of, e.g., *Scorzonera*, *Lactuca*, *Launaea* (Kilian 1997: 28–32). (2) The molecular phylogenies of Hyoseridinae (Kim et al. 1996, 1997, 1999a, b, 2004, 2007), which include the most spectacular and extensive occurrence of frutescent taxa, strongly indicate that the frutescent taxa have evolved independently at different times from herbaceous ancestors. (3) The frutescent growth occurs independently and is correlated with similar environmental conditions in different branches of the tribe. (4) The frutescent growth is restricted to (a) species on oceanic islands (see Carlquist 1974), mainland cliff habitats or, rarely, the tropical alpine zone (the rosette shrublets, rosette shrubs or rosette trees [Fig. 24.4C] of *Launaea*, *Reichardia*, and *Sonchus* s.l. [incl. *Dendroseris* and *Thamnosaris*], in Hyoseridinae, *Crepis kilimandscharica* O. Hoffm. in Crepidinae, *Erythroseris* and *Tolpis* in Cichoriinae) and (b) to semiarid, often montane environments (non-rosette shrubs: *Warionia* in Warioniinae, *Scorzonera* s.l. in Scorzonarinae, *Launaea* in Hyoseridinae, *Lactuca* in Lactucinae, *Erythroseris* in Cichoriinae, *Marshalljohnstonia*, *Munzothamnus*, *Pleiacanthus*, *Stephanomeria* in Microseridinae), which do not, as far as we know, represent the primary or original habitats of the tribe (see below).

A few species of Cichorieae are scandent vines of still unresolved relationships in the *Lactuca* alliance (subtribe Lactucinae), occurring in subtropical to temperate montane rain forests and savannahs of SE Asia (E Himalaya, SE China, Sumatra) and E Africa (Stebbins 1937b, under *Lactuca* and *Prenanthes*; Tjitrosoedirdjo 2002, under *Prenanthes*).

Underground parts

Four different types of underground parts can be distinguished but are systematically valuable only on the species level. Likely plesiomorphic is (1) the taproot with variously developed lateral root system. From this have evolved independently several times (2) the rhizome (e.g., present in Crepidinae: *Crepis* (initially assumed to be the plesiomorphic condition in the genus by Babcock, 1947: 43, later recognized as apomorphic by Babcock, 1949 and also by Enke and Gemeinholzer, 2008), *Nabalus*; Hypochaeridinae: *Leontodon*, *Prenanthes*; Microseridinae: *Chaetadelpa*, *Malacothrix*, *Microseris*, *Stephanomeria*, etc.), (3) the tuberous roots (e.g., Crepidinae: *Nabalus*; Hyoseridinae: *Launaea*, *Sonchus*; Hypochaeridinae: *Leontodon*; Microseridinae: *Krigia*, *Pyrrhopappus*; Scorzonarinae: *Scorzonera* s.l.), and the (4) shoot-bearing roots (e.g., Hyoseridinae: *Launaea*, *Sonchus*; Scorzonarinae: *Tragopogon*).



Fig. 24.4. Habits of Cichorieae species. **A** *Launaea picridioides* (Webb) Engl., cushion-forming rosette shrub, Cape Verde Isl., S. Antão; **B** *L. arborescens* (Batt.) Murb., cushion-forming shrub with spinescent synflorescences, Cape Verde Isl., Boa Vista; **C** *Sonchus arboreus* DC., rosette tree to 2 m tall, Spain, Canary Isl.; **D** *Soroseris gillii* (S. Moore) Stebbins, acaulescent perennial with syncalathium, China, Hengduanshan; **E** *Soroseris umbrella* (Franch) Stebbins, acaulescent perennial with densely tufted capitula, China, Hengduanshan; **F** *Schlagintweitia intybacea* (All.) Griseb., perennial caulescent herb, Austria, Venedigergruppe; **G** *Ascellia nana* (Richardson) W.A. Weber, (sub)acaulescent perennial, Russia, Altai. [Photographs: A, B, N. Kilian; C, K. Rabe; D, E, M. Smalla; F, B. Gemeinholzer; G, N. Enke.]

Excretion organs

All members of the tribe are characterized by the presence of lactiferous canals in both the subterranean and aerial parts, being identical to those occurring in the aerial parts of Arctotideae, whereas other tribes of Cichorioideae merely have lactiferous cells (Augier and Mérat 1951; Wagenitz 1976). In addition to the lactiferous canals, only a few members of the tribe possess a system of endodermal oil ducts in their roots, which are commonly present instead of the lactiferous ducts in other tribes, especially of Asteroideae. The ducts are formed within the endodermis after cell divisions having led to a dedoublement (doubling) of the endodermis. Endodermal oil ducts containing oil have been reported from *Gundelia*, *Scolymus*, *Scorzonera* s.l., and *Warionia* (Tieghem 1872; Col 1903–04; Augier and Mérat 1951). Endodermal ducts without oil have been reported from *Tragopogon* (Tieghem 1885) and *Krigia* (Holm 1926) and dedoublement of the endodermis without formation of ducts from *Cichorium* and *Lapsana* (Tieghem 1885). According to these data, functional oil ducts occur in the three basally branching clades of the tribe, while relics of them (non-functional ducts or endodermis dedoublement) occur rarely here and there among other clades. This may be indicative for a successive reduction of the endodermal oil ducts in the phylogeny of Cichorieae.

Indumentum

Stems, leaves and involucre may be glabrous or variously covered with trichomes or bristles. No systematic survey across the tribe is available, so a few examples illustrating the range of variation may be given. Glandular trichomes, in particular on the peduncles and involucre are present, e.g., in *Crepis* (Crepidinae), *Sonchus* (Hyoseridinae), and *Schlagintweitia* (Fig. 24.4F; Hieraciinae); bristles, in particular on stems, occur, e.g., in *Crepis* (Crepidinae), *Lactuca* (Lactucinae), and *Urospermum* (Hypochoeridinae), stellate trichomes on leaves, stems and involucre occur in species of *Leontodon* and *Scorzoneroides* and rigid anchor-shaped trichomes are diagnostic for *Picris* (Fig. 24.5C, Hypochoeridinae). A tomentose indumentum of simple trichomes occurs, e.g., in species of *Scorzonera* s.l. (Scorzonerinae) and is characteristic for the peduncle and basal involucre of many *Sonchus* species (Hyoseridinae). Woolly leaf axils occur, e.g., in species of *Erythroseris* (Cichoriinae), *Launaea*, and *Sonchus* (Hyoseridinae). In general, indumentum types are systematically valuable at infrageneric or specific level, and more rarely, e.g., in Hypochoeridinae (*Leontodon*, *Scorzoneroides*: see Pittoni 1973; Widder 1975; Greuter et al. 2006; *Picris*: see Lack 1975), at generic level.

Leaves

The leaves are rosulate and/or alternate (as an exception in *Shimmersoseris* the lower leaves are opposite), usually sessile

(petiolate in *Sonchus* p.p. [*Dendroseris*]) and often clasping the stem, sometimes decurrent (extremely so in some species of *Lactuca* and *Scolymus*), entire to dentate or pinnatisect. As exceptions, peltate leaves occur in one of the montane scandent vines of Lactucinae (Stebbins 1937b; Ebel 1998), grasslike and parallel-veined leaves occur in some *Scorzonera* s.l. and *Tragopogon* (Scorzonerinae), and spinose leaves in *Gundelia* and *Scolymus* (Scolyminae). Apart from these exceptions, leaf shape is systematically valuable only at the species level.

Synflorescence

The capitula are variously arranged in monopodial to (partly) sympodial synflorescences containing few to very many capitula. More rarely, the capitula are borne singly on scapes (Cichoriinae: *Phalacroseris*, *Rothmaleria*; Crepidinae: *Dubyaea* p.p., *Taraxacum*; Hieraciinae: *Pilosella* p.p.; Hyoseridinae: *Hyoseris*, *Sonchus* p.p.; Hypochoeridinae: *Hedypnois*, *Hypochoeris* p.p., *Leontodon* p.p., *Scorzoneroides* p.p.; Microseridinae: *Agoseris*, *Anisocoma*, *Nothocalais*; Scorzonerinae: *Pterochaenia*). Morphological transitions to synflorescences with few capitula exist (e.g., Cichoriinae: *Arnoseris*; Hypochoeridinae: *Leontodon* p.p., *Scorzoneroides* p.p.; Microseridinae: *Pinaropappus*, *Pyrrhopappus*). It has been hypothesized by Stebbins (1974: 188) that the scapose synflorescence of *Nothocalais* (sub *Microseris*) and *Agoseris* may have evolved in response to a short growing season from branched synflorescences in the *Microseris* alliance, which is basically in line with the molecular analyses by Lee et al. (2003). The molecular analyses of the latter authors indicate that scapose synflorescences have evolved only once in the *Microseris* alliance, since *Agoseris* and *Nothocalais* form a distinct clade sister to the rest of the alliance. Within the subtribe Microseridinae the scapose synflorescence has evolved independently a second time in the *Malacothrix* alliance with *Anisocoma*. As it is evident from the list of scapose taxa given above, similar trends have occurred in most other subtribes, too.

Aggregation of the capitula by reduction of both synflorescence axes and peduncles to a secondary capitulum (= syncalathium) surrounded by leaves or bracts has, apparently independently, evolved in a few genera in alpine habitats (Crepidinae: *Sorosseris*, *Syncalathium*; Lactucinae: *Lactuca* s.l.; see Fig. 24.4D). Densely tufted capitula, occurring in acaulescent taxa in both alpine and savannah habitats (e.g., Crepidinae: *Dubyaea*, *Sorosseris* [Fig. 24.4E]; Hyoseridinae: *Launaea*, *Sonchus*; Lactucinae: *Lactuca* s.l.) may be seen as morphological transitions to syncalathia. Some correlation of the aggregation of capitula with acaulescent habit and habitats in which the latter preferably have evolved is notable. Although in all those cases the individual capitula are still easily discernable within the syncalathium, another case of syncalathia is unique in the tribe: *Gundelia* (Scolyminae) possesses syncalathia in

which usually six one-flowered capitula (with much reduced involucre) form a secondary capitulum, of which again a few dozen are aggregated in what appears to be the real capitulum (Fig. 24.5B) but actually represents a second order syncalathium (Claßen-Bockhoff et al. 1989).

Induration and lignification of the usually divaricately branched synflorescence axes after the capitula have performed their function and fallen off (and transformation of the peduncles into subulate, more or less spine-like terminal segments), occurs most conspicuously in *Launaea* (see Fig. 24.4B subtribe Hyoseridinae), otherwise, and in a



Fig. 24.5. Capitula of Cichorieae species. **A** *Warionia saharae* Benth. & Coss., Morocco, AntiAtlas; **B** *Gundelia* aff. *tournefortii* L., Armenia, Mt. Aragats; **C** *Picris scabra* subsp. *abyssinica* (Sch.Bip) Smalla, cult. BG Berlin from Yemen; **D** *Tragopogon pratensis* L., Germany, Graswangtal; **E** *Podospermum purpureum* (L.) W.D.J. Koch & Ziz, Germany, at Deetz; **F** *Cichorium intybus* L., Germany, Quedlinburg; **G** *Lactuca triquetra* (Labill.) Boiss., cult. BG Berlin from Cyprus; **H** *Crepis aurea* (L.) Cass., Austria, Venedigergruppe. [Photographs: A, J. Mutke; B, E. Vitek; C, E. Dieckmann; D–F, H, B. Gemeinholzer; G, N. Kilian.]

less pronounced way, in *Cichorium* (subtribe Cichoriinae), *Lactuca* s.l. (subtribe Lactucinae), and *Scorzonera* s.l. (subtribe Scorzonerinae). Independent evolution of spinescence in these cases seems apparent and has been corroborated by the molecular analysis of *Launaea* even within a single genus (Kilian, in prep.). The case of *Cichorium spinosum* L., which strongly differs from the closely related *C. intybus* by its spinescent habit, has been thoroughly studied by Gemeinholzer and Bachmann (2005). The surprising result of their molecular phylogenetic study is that all methods applied (ITS, AFLP, microsatellites) failed to significantly discriminate between the two easily recognized species, indicating that apparently for the spinescent trait only mutations in a few crucial loci are responsible (Gemeinholzer and Bachmann 2005).

In general, the synflorescence type can systematically be valuable at generic, infrageneric and species levels.

Peduncle

The peduncle is the terminal segment of the capituliferous axis. Mostly the peduncle is not further differentiated from the preceding part of the axis. In several cases (e.g., Cichoriinae: *Arnoseris*; Hieraciinae: *Hispidella*; Hypochaeridinae: *Picris humilis* DC.; Microseridinae: *Microseris*; Scorzonerinae: *Tragopogon*) the peduncle is somewhat inflated, which has been interpreted in the context of diaspore dispersal, since the inflated peduncle provides more contact surface area for the wind to shake the achenes off the capitulum (Hoffmann 1890–1894: 114). In other cases (e.g., Hyoseridinae: *Launaea*; Hypochaeridinae: *Leontodon*; Microseridinae: *Microseris*) the peduncle is nodding in bud and/or in fruit, in the latter case evidently serving in diaspore dispersal. A particular specialization of the peduncle is its modification into subulate spine-like segments, treated above under synflorescence types. The peduncle types are systematically valuable only at the species level.

Capitula

The capitula of Cichorieae are homogamous, of perfect flowers only. The number of flowers per capitulum ranges from one in *Gundelia* (primary capitulum) to 3–5(–7) in a number of taxa (e.g., Cichoriinae: *Cichorium*; Crepidinae: *Ixeris*, *Sorosieris* [Fig. 24.4D], *Syncalathium*; Hypochaeridinae: *Picris*; Lactucinae: *Lactuca* s.l. [Fig. 24.5G], *Notoseris* s.l.), and to more than 600 in *Sonchus* s.l. However, the capitula mostly comprise one dozen to several dozens of flowers (see Fig. 24.4–24.5). The molecular phylogenies provide some indication that both the very large and the very small capitula in terms of flower number are derived. The first is clearly demonstrated by the phylogenetic reconstruction of Hyoseridinae and *Sonchus* s.l. (Kim et al. 1996, 1997, 1999a, b, 2004), where *Sonchus* s.l., with generally rather large capitula, is the most terminal

member of the subtribe, and where within *Sonchus* the taxa with the largest capitula also occur predominantly in more terminal clades. The second is less obvious, since species with very few flowers per capitulum occur rather scattered in several genera or alliances. In the case of the *Lactuca* alliance, where very few-flowered species such as *Lactuca muralis* (L.) Gaertn. and *L. viminea* (L.) J. Presl. & C. Presl. hold rather terminal positions in their corresponding clades, it seems very likely that these species are derived (Kilian and Gemeinholzer, in prep.).

Involucre

The involucre, as in all Asteraceae, basically consists of a number of spirally arranged, more or less imbricate bracts. At least at anthesis, the involucre is differentiated in most cases into inner and outer series of bracts, the outer series often grading into the bracts of the peduncle.

Involucre characters are systematically valuable at generic, infrageneric or species level.

In a minority of cases across the tribe (e.g., in species of *Catananche*, *Crepis*, *Dubyaea*, *Rothmaleria*, *Scorzonera*), the inner and outer series are not differentiated in length, so that the involucre is fully imbricate.

Otherwise, those of the (usually single) inner series are of equal length and evoke the impression of standing in one row; those of the outer series increase in length centripetally. The differentiation of the outer series from the inner ones varies considerably: the bracts of the outer series may be strongly imbricate, and the innermost bracts of the outer series may equal the inner series in length, or, to the other extreme, the outer series may not infrequently be reduced to a tiny single row (then termed “calculus” by some authors), often with intermediate forms present in the same genus. More striking is the unique case of *Helminthotheca* (Hypochaeridinae), where the ca. 5 ovate outer bracts in one row are equal in length to the inner row of lanceolate bracts, with a third row of tiny bracts in between (Holzapfel 1999). Conspicuous are the several cases where the involucre has become uniseriate by abortion of the outer series and where the bracts of the remaining inner series may be connate at its base (Cichoriinae: *Arnoseris*, *Phalacroseris*; Crepidinae: *Syncalathium*; Hypochaeridinae: *Urospermum*; Microseridinae: *Picosia*; Scorzonerinae: *Epilasia*, *Geropogon*, *Koelpinia*, *Tragopogon*).

The texture of the involucrel bracts ranges from fully herbaceous to herbaceous with a scarios margin (more distinctly so, e.g., in several *Launaea*, *Reichardia* of subtribe Hyoseridinae, or in *Anisocoma* of subtribe Microseridinae), to, rarely (*Catananche*), scarios except for the (basal) midvein region.

The involucre mostly reaches its final length during anthesis. However, in several cases the involucre (or at least the inner row of involucrel bracts) continues its longitudinal growth after flowering, simultaneously with the ripening

of the fruit (e.g., in species of *Scorzonera*, *Podospermum*, *Tragopogon* [Scorzonerinae], *Launaea* [Hyoseridinae], *Lactuca* s.l. [Lactucinae], *Anisocoma* [Microseridinae]). The longest involucre occurs in *Tragopogon*, measuring up to 80 mm in *T. porrifolius* L. and up to 90 mm in *T. paradoxus* S.A. Nikitin (Borisova in Bobrov and Tzvelev 1964).

After anthesis the innermost involucre bracts in several annual species may become indurate, ranging from having a hardened main rib (e.g., Hyoseridinae: *Hyoseris radiata* L.; Hypochaeridinae: *Picris asplenoides* L.; Lack 1975) to a transformation into an entirely sclerophyllous structure (e.g., Crepidinae: *Heteracia szovitsii* Fisch. & C.A. Mey., *Rhagadiolus stellatus* (L.) Gaertn.; Voytenko 1989). In addition, the innermost involucre bracts may become keeled and enclose partly or completely the outermost achenes, resulting in indehiscent star-like structures of various forms with the broad-based achenes coalesced to the receptacle; the epithet “stellatus” (star-like) alludes to this situation. In these cases the outermost achenes will not easily become detached from the involucre and will not be dispersed by wind like the central achenes. The apothecis of this development is found in involucre bracts that are provided with massive, hard hooks and which at fructification tightly enclose all achenes. The generic name *Acanthocephalus* (“head of spines”; Crepidinae) very appropriately refers to this situation. The solid hooks are reminiscent of those on the achenes in some species of *Koelpinia* (Scorzonerinae): both structures are best interpreted as an adaptation to epizoochorous dispersal, possibly by ungulates. Since these specializations have been observed only in annual species native to Eurasia and N Africa scattered widely over two subtribes, there is reason to assume that they should be interpreted as derived characters.

Receptacle

The receptacle is usually flat, slightly convex or concave and usually rather indistinctly areolate or alveolate (= areoles bordered by a ridge or membranous fringe, e.g., in *Warionia* and some *Crepis*). Receptacular paleae (= scales or bristles) are present in several cases. Receptacular scales occur in Cichoriinae: *Rothmaleria*; Crepidinae: *Crepis* p.p.; Hypochaeridinae: *Hypochaeris*; Microseridinae: *Pinaropappus*, *Agoseris* p.p.; Scolyminae: *Scolymus*, *Hymenonema*; receptacular bristles are restricted to Crepidinae (*Lagoseris*), Microseridinae (*Malacothrix* alliance: *Agoseris* p.p., *Anisocoma*, *Calycoseris*, *Malacothrix* p.p.), and Scolyminae (*Catananche*). Receptacular paleae were regarded as apomorphic in Asteraceae (Bremer 1987) but as plesiomorphic in Cichorieae (Bremer 1994: 165). As it has been shown repeatedly that the genetic basis of the presence or absence of receptacular paleae is rather simple (e.g., in the case of the receptacular scales in *Crepis*; Collins 1924; Babcock and Cave 1938), rather frequent and repeated reversals regarding this character have to

be taken into consideration. Since receptacular paleae occur in only one of the three basally branching clades (Scolyminae) but in both terminal clades (clades 4 and 5, see Phylogeny), Bremer’s assumption appears plausible.

Flower morphology

The corolla is divided into a tube and the 5-dentate ligule in all but two genera, the ratio of tube and ligule being of some variation within the tribe. The ligule may be longer than the tube, equaling it in length, or be shorter than the tube; different ratios may be taxonomically valuable on the specific and perhaps generic level; they seem, however, of no phylogenetic significance.

The flowers of *Gundelia* (Fig. 24.5B, Scolyminae) and *Warionia* (Fig. 24.5A, Warioniinae) markedly deviate from the typical Cichorieae flower by being entirely tubular instead of ligulate. The tubular corolla of *Warionia*, which is divided in its upper wider half into five very long teeth, is not radially symmetrical. Instead, the incisions between the teeth are of different lengths; the two incisions opposite to the longest incision are the shortest and the ones neighboring the longest one are intermediate in length. It is evident from the phylogeny of the family that the typical ligulate Cichorieae flower is derived from a tubular flower (Bremer 1994: 43, 157), and it is safe to assume from the molecular phylogenies that the tubular flowers of *Gundelia* and *Warionia*, the former also with five very long teeth but being radially symmetrical, are plesiomorphic within the tribe. This is further confirmed by the flower anatomy of *Warionia* with a primitive type of venation (see below).

Flower color. — The flower color is predominantly of some shade of yellow (= “xanthic”) between the rather rare extremes cream (whitish yellow; Fig. 24.4E, F) and deep orange-yellow (Fig. 24.5H). The marginal flowers show abaxially often longitudinal stripes of a grayish-bluish-purplish tinge (Fig. 24.5C). Corollae of some shade of blue (incl. purple and whitish so = “cyanic”, Fig. 24.5E–G) occur in the following subtribes and genera (exclusively or together with yellowish-flowered species): Cichorieae: *Cichorium*, *Erythroseris*; Crepidinae: *Crepis*, *Dubyaea*, *Ixeris*, *Nabalus*, *Syncalathium*, *Taraxacum*; Hyoseridinae: *Launaea* (?); Hypochaeridinae: *Prenanthes*; Lactucinae: *Cicerbita*, *Lactuca* s.l., *Notoseris*; Microseridinae: *Atrichoseris*, *Chaetadelphia*, *Glyptopleura*, *Lygodesmia*, *Malacothrix*, *Munzothamnus*, *Picrosia*, *Pinaropappus*, *Prenanthes*, *Rafinesquia*, *Shinnersoseris*, *Stephanomeria*; Scolyminae: *Catananche*, *Gundelia*; Scorzonerinae: *Epilasia*, *Geropogon*, *Scorzonera* s.l., *Tragopogon*. Exclusively yellowish-flowered taxa are thus only Chondrillinae, Hieraciinae, and Warioniinae. Bluish flower colors in two of the three basally branching clades, as well as in most of the other clades, seem to indicate the presence of this feature already in the early phylogeny of the tribe. This appears plausible also consid-

ering the particularly frequent occurrence (compared to the Asteroideae) of bluish corollae in the subfamilies Barnadesioideae and Cichorioideae (Wagenitz 1976; Bremer 1994). Both the abaxial bluish-purplish stripes of the corolla in very many of the yellow-flowered species as well as the common presence of bluish and yellowish corollas in several alliances may be taken as an indication for a rather limited number of mutations responsible for the corolla color in Cichorieae to change, as was already assumed by Cronquist (1955: 488).

Usually the capitula are uniform in their flower color, but in several cases a color differentiation between the center and the remainder of the capitulum occurs. This effect is present in the cases where the corolla is pale yellow or pale bluish, because of the usually concolorous but darker anther tubes (see, e.g., *Hololeion maximoviczii* Kitam., *Ixeris chinensis* (Thunb.) Nakai in Lee 2006: 374, 376). It is more marked in cases where the anther tube color differs from that of the ligules as, e.g., in *Taraxacum coreanum* Nakai with pale bluish ligules and yellow anther tubes (see Lee 2006: 371). Only in a few cases the corolla itself is bicolored: in *Hispidella hispanica* Lam. (Hieraciinae), *Reichardia tingitana* (L.) Roth (Hyoseridinae), and *Tolpis barbata* (L.) Gaertn. (Cichoriinae) the basal part of the ligule and the upper part of the tube are blackish-red or blackish-brown while the remainder of the corolla is yellow, providing the flowering capitulum with a dark center.

Corolla epidermis. — The micromorphology of the corolla epidermis in Cichorieae has been investigated by Baagøe (1980). The ligules in the tribe are characteristically rather thin, stomata-free, without mesophyll, with cell wall thickenings rather rare, and with anticlinal walls usually septate. Papillae, which are usually hooked and point distally, are formed on the distal end of mostly oblong cells, and any differentiation of the adaxial epidermis begins at or above the middle of the ligule. The differentiation in cell shape and cuticle type across the tribe cannot easily be interpreted from a phylogenetic point of view (Bremer 1994).

Anthers. — The anthers of Cichorieae are in general calcarate (i.e., the fertile part of the thecae is prolonged on either side below the point of filament insertion) and caudate (i.e., with tails of sterile tissue at the thecae basis on either side of filaments) and have a soft apical appendage, but no systematic survey of anther morphology and micromorphology across the tribe is available. The anthers vary considerably in length, but this variation probably occurs repeatedly within many genera and is therefore only of taxonomic relevance on the species level.

Style. — The style of Cichorieae is of the so-called vernonioid type (Hoffmann 1890–1894: 106; Bremer 1994: 32), which is generally slender, with long, filiform style branches and collecting trichomes continuing from the style branches further down the style shaft. The new

members of the tribe, *Gundelia* and *Warionia*, also have this type of style. Shorter style branches, however, occur in several cases (e.g., within Microseridinae), and are probably apomorphic.

Floral anatomy. — The vascular anatomy of most of the Cichorieae flowers is of the *Lapsana* type (Koch 1930: 948): the corolla tube is traversed by five veins, one of which divides immediately at the split in the tube so that six veins continue into and traverse the ligule; two run along the margins and four towards the sinuses between the five teeth. The five veins represent each the fused lateral veins of neighboring petals.

Since the pseudomonomeric, unilocular but actually bicarpellate inferior ovary of Compositae is formed by the adnation of the basal parts of the sepals, petals and stamen whorls to the gynoeceum, the vascular bundles of the ovary wall are the product of various fusions (Carlquist 1962: 132–140): one inner series represents the bundles of the two carpels, which continue as two strong separate bundles into the style and its branches; one of two outer series of originally five bundles each represents the “principle bundles” and is homologous with the united median calyx bundles, the fused lateral corolla lobe bundles and the stamen bundles; the other series represents the “supernumerary bundles” and is homologous with the united lateral calyx and median corolla bundles (Stebbins 1940: 55–64). The five principal and five supernumerary bundles continue in the ten corolla veins, which are still present in some members of the family (Koch 1930). With the successive reduction of the median corolla veins in the phylogeny of the family, the supernumerary bundles end at the ovary apex.

In Cichorieae, with only two known exceptions, the median corolla veins are absent. The first, remarkable exception, confirming the aforementioned evolutionary trend postulated by Koch (1930), is the tubular flower of *Warionia* (Warioniinae): besides the lateral bundles fused at the sinuses of the teeth as in all Cichorieae and Compositae, the median bundles of all five corolla lobes are present from the tip of the teeth to the base of the corolla, so that the *Warionia* corolla has the primitive constitution of ten corolla bundles. In the single other tubular flower of the tribe, in *Gundelia* (Scolyminae), in contrast no median corolla bundles are extant. The second exception is among the ligulate flowers, where *Dubyaea atropurpurea* Stebbins (Crepidinae) is reported by Stebbins (1940: 56) to have relics of median bundles in the teeth of the corolla lobes.

Within Cichorieae, the number of supernumerary as well as of the principal bundles in the ovary wall apparently has undergone successive reduction, as was discovered by Stebbins (1940: 55ff). He found a complete series of reduction from ten supernumerary and principal to only five principal bundles in the genus *Dubyaea* (Crepidinae) and a further reduction from only five principal bundles

to two in *Lactuca* (Lactucinae) (Stebbins 1940). The data available from Crepidinae (*Crepis*, *Dubyaea*, *Nabalus*, *Sorosseris*: Babcock and Stebbins 1937; Stebbins 1940; Babcock 1947; Milstead 1964), Hyoseridinae (*Launaea*: Kilian 1997), and Lactucinae (*Lactuca* alliance: Stebbins 1940; Milstead 1964; Kilian 2001; Kilian and Hand 2004) corroborate the trend of a reduction in the number of bundles. These findings seem largely congruent with the molecular phylogenies. In subtribe Crepidinae, the genera with the highest numbers of supernumerary bundles, i.e., *Nabalus* and *Sorosseris*, are more basally branched than *Crepis*, which is usually without supernumerary bundles, and in the *Lactuca* alliance the species with five principal bundles are more basally branched than those with only two to three principal bundles.

Pollen

Wodehouse (1935) was the first to provide detailed descriptions of the basic morphology of Cichorieae pollen by light microscopic studies. He described these pollen grains as “globular, generally tricolpate, occasionally tetracolpate, or being sometimes abnormal, with higher numbers of furrows” comprising an outer exine that is raised in a pattern of echinate ridges (lophae) surrounding depressions (lacunae), which he named “echinolophate”. In contrast, “echinate” pollen types, having less elaborate spine patterns, are regarded as being plesiomorphic in the tribe and according to Blackmore (1981) occur in almost all subtribes, which makes this feature an unreliable indicator of affinities.

The complex apertures of Cichorieae pollen have been interpreted in a variety of ways by different taxonomists (e.g., Erdtman 1952; Faegri and Iversen 1975; El-Ghazaly 1980) and various terminologies have been proposed, which are discussed and reviewed by Blackmore (1982a) who recommended retaining Wodehouse’s (1935) terminology, which therefore is applied here. Blackmore (1982b, 1984) distinguished seven pollen types in the tribe: (1) *Scorzonera humilis* L. type (echinate), (2) *Scorzonera laciniata* L. type (echinolophate, and two equatorial lacunae per mesocolpium), (3) *Tragopogon pratensis* type (echinolophate, and one equatorial lacuna per mesocolpium), (4) *Sonchus oleraceus* L. type (echinolophate, and three lacunae at each pole), (5) *Lactuca sativa* L. type (echinolophate, and polar area a triradiate ridge), (6) *Armoseris minima* (L.) Schweigg. & Körte type (echinolophate, and broad equatorial ridges with two rows of echinae), and (7) *Cichorium intybus* type (echinolophate, and narrow equatorial ridges with one row of echinae). The last type is by far the most common pollen type in the tribe; types 1–3 are restricted to the subtribe Scorzonerinae. A somewhat modified system of nine pollen types is given by Blackmore (1986). Although useful for pollen identification, these pollen types are often not congruent with taxonomic entities recognized by molecular and other morphological

characters. Nevertheless, pollen morphological characters were successfully used for certain taxonomic decisions, e.g., on tribal level as by Stebbins (1940, 1953) and Jeffrey (1966), or for subtribal delimitation, e.g., by Blackmore (1981, 1982b) (see Phylogeny, above).

Achenes

The achenes of Cichorieae are in many cases indispensable for the identification of the genera and species and provide the systematically most valuable features on all taxonomic levels. Its analysis, however, has to consider that heterocarpy occurs in several alliances (Voytenko 1989; Voytenko and Oparina 1990) and may involve size, ribbing pattern, base, apex, shape, surface and anatomy, separately or in combination, resulting in two or more morphs within a single capitulum.

Achene size. — Variation in achene size across the tribe is tremendous, ranging from less than 1 mm length in *Tolpis* to a maximum of 45–55 mm length (without pappus) in *Tragopogon porrifolius* and *T. paradoxus* (Borisova in Bobrov and Tzvelev 1964; Blanca and Díaz de la Guardia 1997); the commonest size class is probably 2.5–5 mm. In contrast to the more common trend towards size reduction, *Tragopogon*, as a derived genus of subtribe Scorzonerinae (Mavrodiev et al. 2004 and see Phylogeny), illustrates an evolutionary trend towards increased size of capitula, flowers and fruits, as has already been stated by Stebbins (1950: 495).

Ribbing patterns. — The principal bundles of the ovary wall (see Flower anatomy, above) usually seem to correspond to the longitudinal main ribs of the achene, since the latter are formed above these bundles (Babcock and Stebbins 1937: 10; Kilian 1997: 47). The plesiomorphic constitution is thus an achene with five main ribs according to the originally five principal bundles of the ovary wall. The main ribs, however, are frequently differentiated, and each may be subdivided resulting in a less defined and smaller secondary rib on either side (Kilian 1997), which is a particularly frequent pattern in the tribe. Fusion of neighboring secondary ribs in the ontogeny of the achene explains the not infrequent pattern of ten equal ribs, as is the case, e.g., in *Ixeridium*, where five principal ovary wall bundles are also present (Pak and Kawano 1990a: 52–53). Rib numbers that are not a multiple of the number of principle ovary wall bundles or main ribs, occur not infrequently by incomplete differentiation into single main ribs, in particular when the achene body is not isodiametric in cross section.

The ribs, or single ribs, are transformed to (narrow) wings in several cases in the tribe, e.g., in the Crepidinae (*Ixeris* p.p., Pak and Kawano 1990a; *Youngia* p.p., Babcock and Stebbins 1937), Hyoseridinae (*Hyoseris*), Lactucinae (*Lactuca* p.p. = *Pterocypsela*), and Scorzonerinae (*Pterachaenia*, *Tourneuxia*).

In the *Lactuca* alliance (Jeffrey 1966; Tuisl 1968; Beliaeva and Boyko 1980; Kilian 2001; Kilian and Hand 2004) the number of main ribs is reduced from five down to the minimum of two in the tribe, corresponding to the reduction in the number of the principal ovary wall bundles; the achenes with only two main ribs are often strongly flattened (but see *Heteracia*; Voytenko 1989) and the ventral and dorsal surfaces show one or a few secondary ribs on each side.

Achene base. — The achene of Cichorieae is connected to the receptacle by a stipelike projection, usually from the centre of the achene base. As a rule, the peripheral achene wall is basally somewhat protruding and loosely attached to the receptacle. No in-depth survey of the achene base in Cichorieae is available, but in most cases only the main ribs somewhat protrude and they may be somewhat spreading, straight or incurved, and connate to different extents (Haque and Godward 1984). Such differences are usually of systematic value on the specific level only. However, there are at least two cases where the achene base is valuable on a higher systematic level: (1) the *Lactuca* alliance (Lactucinae) is characterized by an achene base forming a callose annulus or somewhat funnel-shaped carpodium; (2) the genus *Podospermum* (Scorzonerinae) is characterized by an extreme, tubular carpodium of up to 1/3 the achene body length.

Achene apex. — The achene apex is either truncate or variously attenuate (cuspidate) to rostrate. Both attenuation of a sculptured achene apex and formation of a beak (= rostrum), usually understood as a thin, unsculptured, distal part of the achene, are evidently functional for wind dispersal and have therefore evolved convergently in many genera and in seven of the eleven subtribes of Cichorieae. Presence or absence of beaks have been extensively used systematically but are actually of no systematic value unless at species level. Attenuate or beaked achenes are present in Chondrillinae (e.g., *Chondrilla*), Crepidinae (e.g., *Crepis*, *Heteracia*, *Ixeridium*, *Taraxacum*), Hyoseridinae (e.g., *Launaea*), Hypochaeridinae (e.g., *Hypochaeris*, *Leontodon*, *Urospermum*), Lactucinae (e.g., *Lactuca*) and Microseridinae (e.g., *Agoseris*, *Calycoseris*, *Picrosia*, *Pyrrhopappus*); Scorzonerinae (*Geropogon*, *Tragopogon*); no beaks are present in Cichoriinae, Hieraciinae, Scolyminae, and Warioniinae.

The achene apex in species of *Lapsanastrum*, where 2–4 main ribs are prolonged into apical hooks (Pak and Bremer 1995), is unique in Cichorieae. This also applies to the achenes in *Urospermum*, possessing a diaphragm separating the seed containing part from the hollow distal part of the achene.

Achene body shape. — The shape of the achene body shows considerable variation in the tribe. Cross sections range from isodiametric and terete or angled to a variety of anisodiametric shapes due to unilateral, median or dorsiventral flattening of the achenes. Bremer (1994: 166)

distinguished three types of cross sections, which appears rather simplistic, in particular since even within a single capitulum the cross section shape often varies from center to periphery. The shape is therefore one of the systematically least valuable feature of the achene, usually being of certain value on the specific level but already of much limited value on the generic level.

Ornamentation of the achene surface. — The achene surface may be glabrous, variously hairy, papillose or scaly. Conspicuously villous achenes are present in *Scorzonera* s.l. (Scorzonerinae) and in *Warionia* (Warioniinae), a considerable diversity of papillose achenes, ranging from short papillose over densely papillose to papillosely winged, is present in *Launaea* (Hyoseridinae); minutely scaly achenes are found, e.g., in *Lactuca* (Lactucinae). The sculpturing of the achene surface shows similar variation and includes striking hooks for epizoochorous dissemination in *Koelpinia* species (Scorzonerinae). In general the achene surface features are taxonomically valuable, mainly at species level, and more rarely concur with supraspecific delimitation.

Pericarp anatomy. — Pericarp cross sections have proven so far to be of some relevance for the circumscription of genera and infrageneric entities in Cichorieae and have been published in particular for Crepidinae (Pandey et al. 1978; Beliaeva and Boyko 1980; Pak and Kawano 1990a, b; Pak 1991, 1993; Pak and Bremer 1995; Sennikov and Illarionova 2007), Hyoseridinae (Lavalie 1912; Aldridge 1978; Pandey et al. 1978; Kilian 1997), and Lactucinae (Tuisl 1968; Pandey et al. 1978; Zhu et al. 2006). The data available cover only parts of the tribe and their analysis in a phylogenetic context is still lacking.

Testa epidermis. — Since the seed of Compositae is not exposed but covered by the pericarp, the testa has no protective function. Its micromorphological diversity is therefore potentially of phylogenetic and taxonomic relevance. A comparative morphological survey of the testa epidermis has been conducted by Tegel (2002), but a phylogenetic analysis of the considerable morphological diversity observed has still not been done. It merits attention that larger parts of the tribe are rather similar, possessing a “fenestrate type” of testa epidermis (most Chondrillinae, Crepidinae, Hyoseridinae, Hieraciinae, and Lactucinae), whereas in Crepidinae, *Taraxacum* shows a distinctly different type. A “reticulate type” is found in part of Hypochaeridinae and otherwise in *Krigia* sect. *Krigia* (Microseridinae). A “helicoid type” characterizes Scorzonerinae and is otherwise present in *Rothmaleria* (Cichoriinae). Other specialized types, as well as an unstructured type, exist and complicate the picture.

Pappus

No other morphological feature has received so much attention in the systematics of Cichorieae as the pappus, which had long been used as the key feature for

subdividing the tribe (see History, above). Since it is, in fact, of some systematic value at all ranks in the tribe, a brief comparative overview, not available so far, is given here.

The pappus of Cichorieae is either paleaceous or setaceous, or absent. If present, it may be homomorphic or heteromorphic. However, terminology is still unsatisfactory: “homomorphic” means both (1) the pappus of all achenes in a capitulum is homogeneous, and (2) all elements in the pappus of a single achene are equal or very similar; “heteromorphic” means (1) the pappus in the capitulum differs, which is a character often but not always correlated with heterocarpy (see above), and (2) the elements in a single pappus differ from each other. Heteromorphy involves differences in length, diameter, and/or structure of the pappus elements, or a combination of them. Heteromorphic pappuses have been studied in some detail in Hyoseridinae (*Launaea*; Kilian 1997) and Hypochaeridinae (*Picris*; Lack 1975). The largest pappus (up to 35 mm length) is found in *Tragopogon* (Borissova in Bobrov and Tzvelev 1964).

Paleaceous pappus. — A paleaceous pappus (Fig. 24.6) may resemble most the presumed homologues, the calyx lobes, and often also comprise five elements, which may be more or less keeled and/or aristate. Paleaceous pappuses are present in the subtribes Scolyminae (Fig. 24.6D–H, *Catananche*, *Hymenonema*), Cichoriinae (*Cichorium*, Kiers 2000: 12–15, fig. 2.1a–h; *Rothmaleria*, Lack et al. 1980; Fig. 24.6A–C) and Microseridinae, where the largest variety is present: in *Krigia*, predominantly with a setaceous pappus, the outer series may consist of small scales; in *Malacothrix* the pappus may consist of a scaly corona, or be otherwise either setaceous or missing; in the *Microseris* alliance (*Microseris*, *Nothocalais*, *Uropappus*) aristate scales are present apart from setaceous pappus, and in *Chaetadelpha* the pappus consists of bristles and awns. No attempts have been made yet to discuss possible homologies, in particular since it is unclear to what extent the pericarp is part of these structures.

The presence of the paleaceous pappus in three subtribes and two of the five major clades of the tribe, of which only the Scolyminae clade is among the basally branching ones, is inconclusive regarding its interpretation as plesiomorphic within Cichorieae (Stebbins 1974: 186). The same applies to the distribution of the paleaceous pappus within the subtribes and genera. The morphological similarity of, e.g., the aristate scaly pappus in Scolyminae with that of Microseridinae and with the non-aristate scaly pappus of *Rothmaleria* in Cichoriinae leaves little doubt that they represent homologous structures, and this may count for both their common origin and plesiomorphy. The distribution of a paleaceous pappus within the subtribes and genera provides strong indication for the homology of the paleaceous and the setaceous

pappus, and furthermore, that the genetic differences between both cannot be too large. The morphological differences between the paleaceous and the setaceous pappus elements are of rather minor nature, because both are built of largely the same cell types. The main difference between bristles and scales is the lateral extension of the latter. This also explains the morphological transitions, which occur particularly in Microseridinae. In subtribe Cichoriinae such morphological transitions can be seen in the line from *Rothmaleria* (with 5 large, keeled scales) to *Cichorium* (with mostly tiny, numerous irregular scales) and further to *Erythroseris* (with larger inner and an outer series of in part laterally fused minute bristles, see Fig. 24.7A and Kilian and Gemeinholzer 2007).

Setaceous pappus. — The setaceous pappus (Fig. 24.7) in Cichorieae is either (1) scabrid (= rough), denticulate (= toothed), or barbellate (= long-toothed), i.e., with lateral projections not or at most few times longer than the diameter of the seta (= bristle), see Fig. 24.7A, B, or (2) plumose (meaning feather-like), i.e., with side projections (= fimbriae) many times longer than the seta diameter (Fig. 24.7C). As first observed by Lack (1975, 1984) and much later applied to the whole tribe (Lack 2007: 82), three variants of the so-called plumose pappus exist in Cichorieae: (1) the *feather-like fimbriate pappus* (Fig. 24.7D) has the pinnae arranged in one plane as is the case in a true feather; (2) the *stiffly fimbriate pappus* (Fig. 24.7E) has stiff fimbriae pointing in all directions like a bottle-brush, each fimbria consisting of a single giant tubular cell resembling a macaroni; (3) the *softly fimbriate pappus* (Fig. 24.7F) has soft and often intertwined fimbriae pointing in all directions and consisting of a row of flattened cells resembling cotton fibers or knitting wool along the seta. The *feather-like fimbriate pappus* is exclusively present within the principally American Cichorieae clade of Microseridinae s.l., the *stiffly fimbriate pappus* is exclusively restricted to Hypochaeridinae, and the *softly fimbriate pappus* is exclusively restricted to Scorzonerinae. In all three subtribes, however, besides the respective plumose pappus variant, also other pappus types (non-plumose setaceous or even non-setaceous types) are present and the achenes may also lack a pappus altogether.

The diameter of the setae, its surface structure, and the number of cells involved varies and requires further study. The brittleness of the setae, e.g., in *Hieracium*, as well as the varying length and density of the fimbriae have long been known and used as traditional characters for rapid generic identification but have not been investigated further.

The setaceous pappus is usually homomorphic, i.e., all bristles are roughly of the same type, diameter and length. In several cases, however, a differentiation between outer and inner series of the pappus has occurred. In, e.g., *Hypochaeris radicata* L. and *Leontodon hispidus* L.

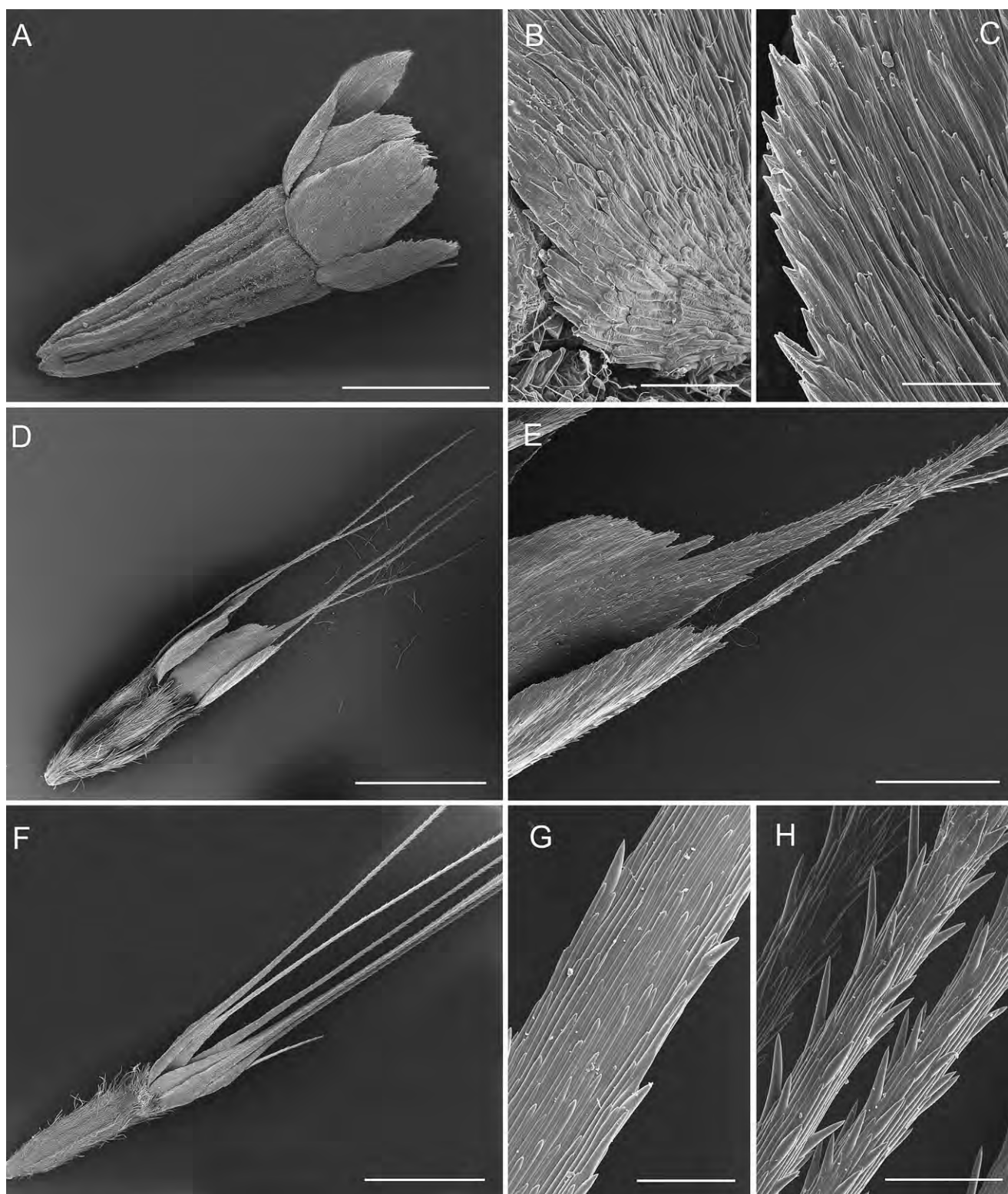


Fig. 24.6. Pappus types 1. **A–C** *Rothmaleria granatensis* (DC.) Font Quer, paleaceous pappus, overview (Spain, Bourgeau 1261, B), proximal portion (A), detail (B), distal portion, detail (C); **D, E** *Catananche caerulea* L., awned paleaceous pappus, overview (Morocco, Oberprieler 1845, B), median portion (D), detail (E); **F–H** *Hymenonema graecum* (L.) DC., lanceolate paleaceous-setaceous pappus, overview (Greece, Heldreich 1055, B), proximal paleaceous portion (F), detail (G), distal setaceous portion, detail (H). Scale bars: A = 2 mm, B, C, G = 100 μ m, D, F = 3 mm, E = 600 μ m, H = 200 μ m.

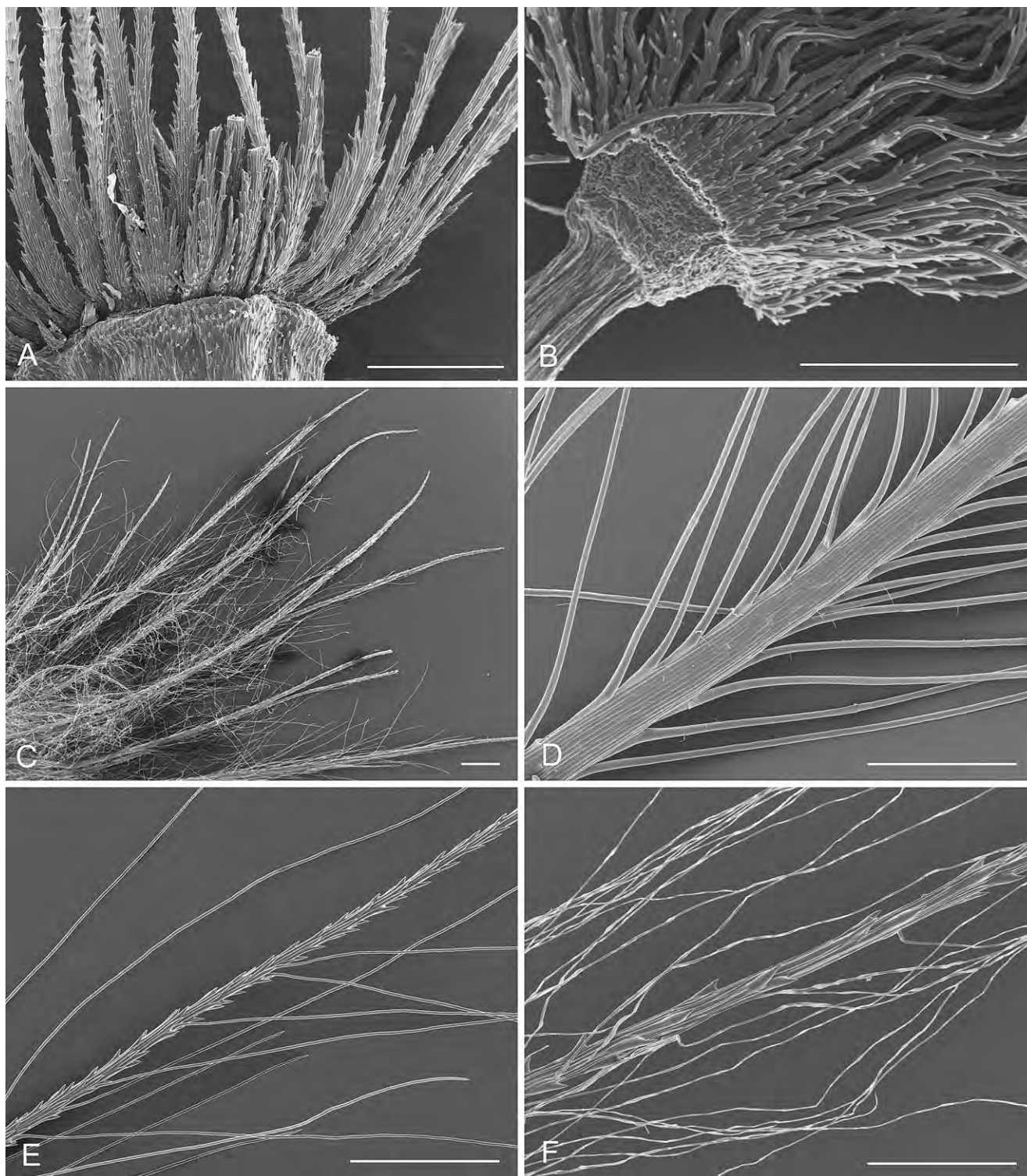


Fig. 24.7. Pappus types 2. **A** *Erythroseris somalensis* (R.E Fr.) N. Kilian & Gemeinholzer, scabrid setaceous pappus with basally partly fused bristles, proximal portion, detail (Somalia, *Thulin 4260*, UPS); **B** *Lactuca triquetra* (Labill.) Boiss., scabrid setaceous pappus, proximal portion, detail (Cyprus, *Buttler 32460*, B); **C** *Scorzonera ulrichii* Parolly & N. Kilian, proximally plumose, distally barbellate to scabrid setaceous pappus, overview (Turkey, *Ulrich 2/53*, B); **D** *Anisocoma acaulis* Torr. & A. Gray, feather-like fimbriate plumose pappus, detail (USA, *Rose 37071*, B); **E** *Hypochaeris achyrophorus* L., stiffly fimbriate plumose pappus (Greece, *R. et E. Willing 134.057*, B); **F** *Scorzonera mollis* M. Bieb., softly fimbriate plumose pappus (Greece, *R. and E. Willing 156.025*, B). Scale bars: A, D, F = 300 μ m, B = 500 μ m; C = 1 mm.

(Hypochaeridinae), only the inner pappus setae are plumose, whereas the marginal are denticulate (much shorter in the latter species). In many species of *Launaea* and *Sonchus* (Hyoseridinae), the inner bristles are stiff and strong, whereas the outer pappus elements are shorter, downy and flexible. In Lactucinae, besides the bristles of the inner series, frequently an outer series of tiny hairlike elements occurs.

Moreover, the setaceous pappus may be persistent or deciduous; in the latter case it either detaches as a single piece (e.g., in *Launaea* p.p. together with the pappus disk) or the bristles separate singly or in groups.

Absence of pappus. — The pappus is entirely absent in a number of taxa (*Arnosaris*, *Cichorium calvum* Asch. and *Phalacroseris* in Cichoriinae; *Acanthocephalus*, *Heteracia epapposa* (Regel & Schmalh.) M. Popov, *Lapsana*, *Lapsanastrum* and *Rhagadiolus* in Crepidinae; *Hispidella* in Hieraciinae; *Aposaris* in Hyoseridinae; *Atrichoseris* and *Krigia cespitosa* (Raf.) K.L. Chambers in Microseridinae; *Koelpinia* in Scorzonerinae); this is evidently a secondary trait, which has occurred repeatedly across the tribe.

Besides presumably having a protective property (providing a barrier for the immature fruit against predatory insects and water), the pappus is related to fruit dispersal. The assumption that in this function the pappus is a primary target of selection pressure and therefore subject of various modifications has been addressed by Carlquist (1966: 44–46) for Pacific Cichorieae. In the context of a loss of dispersability on oceanic islands, he noticed a tendency towards size reduction and deciduousness of pappus elements in the Juan Fernández taxa, the significance of which gained great support from the recent molecular data, identifying these taxa as close allies of the Old World *Sonchus* species (Kim et al. 2004). In *Hypochaeris oligocephala* (Hypochaeridinae; Lack 1978), a local endemic of Tenerife with somewhat succulent leaves, this is paralleled by the reduced number of fimbriae of its plumose pappus. The similar evolution of such antiteleochoric (= preventing long distant dispersal) properties, affecting both the achene and pappus, in arid environments with contracted vegetation is long known and was summarized, e.g., by Zohary (1950) and Voytenko (1989). It has been considered more recently by Lack (1975) in the case of *Picris*, where morphs with very short pappus and incurved outer achenes occur, and by Kilian (1997: 317) in case of *Launaea*, where morphs with deciduous pappus on long-beaked achenes occur. The dramatic short-term shifts in the achene and pappus morphology towards reduced dispersability found by Cody and Overton (1996) in weedy Cichorieae species on small Pacific near-shore islands in Canada strikingly prove the significance of selection pressure for the shaping of the pappus. Using the considerable variation in macromorphology of the pappus in Cichorieae uncritically in systematic analyses

consequently leads easily astray and is, in fact, responsible for numerous former artificial groupings or delimitations on the suprageneric as well as on the generic level.

CHROMOSOME NUMBERS

The chromosome numbers of Cichorieae range between the extremes of $2n = 14x = 126$ in *Sonchus novae-zelandiae* (Hyoseridinae; Beuzenberg and Hair 1984), which is one of the very few Cichorieae in New Zealand and the rare case of a high ploidy level in the tribe, and $2n = 2x = 6$ in a few species of *Crepis* (Crepidinae; for references see Watanabe 2008) and *Hypochaeris* (Hypochaeridinae; for references see Watanabe 2008). The report of an even lower number of $2n = 2x = 4$ (see Jeffrey 1966; Jeffrey and Beentje 2000; Lack 2007) allegedly found in *Dianthoseris schimperii* A. Rich. (according to our analyses a congener of *Crepis*, Crepidinae; see Enke et al. 2008) is erroneous, the only counts obtained and published for this species are $2n = 8$ (Hedberg and Hedberg 1977: 24; compare Watanabe 2008).

The basic number in the majority of the subtribes is $x = 9$ or a descending series starting with $x = 9$: Hypochaeridinae $x = 9, 8, 7, 6, 5, 4, 3$; Microseridinae $x = 9, 8, 7, 6, 5, 4$; Hyoseridinae $x = 9, 8, 7, 6, 5$; Lactucinae $x = 9, 8$ (basic numbers of 7 and 6 published seem erroneous); Hieraciinae and Cichoriinae $x = 9$. In the Chondrillinae only the numbers $x = 9, 7, 5$ are known. In contrast, in Crepidinae the series starts with $x = 8$ and runs to $x = 3$; in Scorzonerinae only $x = 7$ and 6 are known. Scolyminae with the basic numbers $x = 10$ and 9 and Warioniinae with its only species *Warionia saharae* having the basic number $x = 17$ (Reese 1957; Humphries et al. 1978; Oberprieler and Vogt 1993) are more strongly deviating.

The ancestral basic chromosome number of Cichorieae (and Compositae in general) has been assumed to be $x = 9$ by Stebbins et al. (1953: 416), Tomb (1977: 1076), and Tomb et al. (1978: 721), but $x = 5$ (or 4) and successive aneuploid reduction from the tetraploid level were suggested by Turner et al. (1961: 219, in adnot.) mainly for the reason that this would explain the frequent gaps in the series between $x = 4$ and 5 and $x = 8$ and 9 observed at that time. Since the numbers in Cichorieae known today do not exhibit such gaps and $x = 9$ is the number present in most genera and subtribes, and since a higher karyotype symmetry has been found in species with higher basic numbers compared to lower numbers in the same genus (e.g., in *Crepis* with $x = 6$ to 3, see Babcock 1947; in *Launaea* with $x = 9$ to 5, see Kilian 1997: 80), an original basic number of $x = 9$ appears to be the more parsimonious explanation. The case of *Warionia* ($x = 17$) may hypothetically be explained through dysploid reduction from

$2n = 18$ and subsequent autopolyploidization; the same number is also present in American species of *Lactuca* (e.g., *L. canadensis* L., *L. graminifolia* Michx.; see Tomb et al. 1978: 719), which otherwise have a basic number of $x = 9$ and 8. The basic number of *Scolymus* ($x = 10$) may be explained correspondingly and is paralleled by species of *Krigia* (*K. biflora* (Walt.) Blake, $x = 5, 10$; *K. montana* (Michx.) Nutt., $x = 10, 15$; see Tomb et al. 1978: 718; Kim and Turner 1992), which have as basic numbers $x = 9, 6, 5, 4$.

CHEMISTRY

Typical secondary chemical compounds within Cichorieae are glycosides of simple sesquiterpene lactone derivatives mainly of the lactucin type (Zidorn 2006, 2008), flavonoids (for review see Bohm and Stuessy 2001), phenolic acids and in particular derivatives of caffeic acid (Giner et al. 1993; Manez et al. 1994), simple coumarins, and triterpenes such as taraxasterol and their fatty acid esters. The latter compounds are frequently found in high amounts in the milky latex (Hegnauer 1964). Sugars and polysaccharides have extensively been studied in the economically important chicory (*Cichorium intybus*; e.g., Monti et al. 2005; Van Laere and Van den Ende 2002).

Only few studies deal with secondary metabolites in a chemosystematic context covering the tribe or individual subtribes (Bohm and Stuessy 2001; Zidorn 2006, 2008; Zidorn et al. 2006). In some cases chemical compounds have been used for intrageneric delimitations (e.g., in *Leontodon* and *Hieracium*; Zidorn and Stuppner 2001a, b; Zidorn et al. 2002) or findings on individual taxa have been discussed in a tribal context (e.g., Zidorn et al. 2005, 2006). More often the compounds of economically important taxa such as *Cichorium intybus*, *Lactuca sativa*, *Scorzonera hispanica* L. and *Tragopogon porrifolius* have been analyzed (e.g., Sessa et al. 2000; Bischoff et al. 2004; Kisiel and Zielinska 2001; Van Beek et al. 1990; Zidorn et al. 2000, 2005). Several publications deal with new chemical compounds isolated from different taxa (for review see Bohm and Stuessy 2001 and Zidorn 2006), while only few studies are concerned with phytochemical variation on the populational level (e.g., Grass et al. 2006).

Flavonoids have been comparatively well sampled throughout several groups of Cichorieae (for review see Bohm and Stuessy 2001). Common flavonoid compounds within most members of the tribe are derivatives of luteolin, apigenin, kampferol and quercetin or their simple *O*-methyl ethers. As presence and quantity of flavonoids often depend on the origin of the plant, time of collection, and method of analysis, González (1977) recommended the cautious application of this character for chemotaxonomic purposes. The phenolic compounds have been reported as

important characters for intraspecific, interspecific, and generic delimitation within Cichorieae (Crawford 1978; Zidorn et al. 2002), as the flavonoid structure can be altered by only few gene mutations (Fiasson et al. 1991). An exemplary evaluation of the efficacy of flavonoid data for Cichorieae systematics on higher taxonomic levels, provided in the context of a synopsis of the flavonoids in Asteraceae (González 1977; Bohm and Stuessy 2001), revealed, however, that the available data are of limited value for chemotaxonomic delimitations on the generic as well as on the subtribal level. This, for example, accounts for the presence of the “most unusual flavonoid in the tribe” (Bohm and Stuessy 2001), the 5,7,2',4',5'-pentahydroxyflavone (isoetin), which has been identified from *Crepis*, *Hedypnois*, *Hieracium*, *Hispidella*, *Hypochaeris*, *Leontodon*, *Picris*, *Reichardia*, and *Sonchus*, thus from genera throughout Cichorieae.

In contrast, clade 4 (Figs. 24.1–24.2), comprising Chondrillinae, Crepidinae, Hyoseridinae, Hypochaeridinae, and Lactucinae, seems to be characterized by (1) the flavonoid 6-hydroxyapigenin (scutellarein), which has up to now solely been detected in *Reichardia*, *Hedypnois*, *Hypochaeris* and *Leontodon* (Bohm and Stuessy 2001), (2) the occurrence of hypocretenolides in *Crepis aurea*, *Hedypnois cretica* (L.) Dum. Cours., *Hypochaeris cretensis* (L.) Bory & Chaub., *Leontodon hispidus* (Bohm and Stuessy 2001), and *L. rosani* (Ten.) DC. (Zidorn et al. 2007), and (3) in addition to the flavonoids, by the occurrence of the costus lactone type guaianolide β -D-glucopyranoside ixerin F (Zidorn 2006), which is known from species of, e.g., *Crepis*, *Lactuca*, *Picris* (Zidorn et al. 2006 and literature cited therein).

Zidorn (2006) established a hierarchical cluster analysis of sesquiterpene lactones (mainly of the guaiane type) from Hypochaeridinae sensu Bremer by summarizing phytochemical data. In concordance to our re-classification of Cichorieae, *Urospermum* turned out to be most dissimilar from all other taxa of Hypochaeridinae sensu Bremer (1994), a fact supported by the presence of *Urospermum*-type germacranolides, otherwise absent within the subtribe. *Scorzonera* and *Tragopogon* yielded numerous bibenzyl derivatives, including unique tyrolobibenzyls, which seem to be restricted to the genus *Scorzonera* (Zidorn et al. 2000, 2002, 2003, 2005; Paraschos et al. 2001).

BIOGEOGRAPHY

Cichorieae are mainly distributed in the temperate zone of the northern hemisphere, both in the Old and New Worlds (Fig. 24.8–24.10). Three main centers of diversity exist: Central to Eastern Asia, the Mediterranean Basin including SW Asia, and, to a lesser extent, western North America. Some genera are found native also in tropical and

southern Africa, (e.g., species of *Crepis*, *Lactuca*, *Launaea*, *Picris*, *Sonchus*, and *Tolpis*), tropical Asia (e.g., species of *Ixeridium*, *Ixeris*, *Launaea*, *Youngia*), Australia and New Zealand (few species of *Launaea*, *Microseris*, *Picris*, *Sonchus* s.l., and *Youngia*), South America (species of *Hypochaeris*, *Hieracium*, *Microseris*, *Picrosia*, and *Taraxacum*). Several genera have reached oceanic islands, radiated there and developed endemic taxa, some of them spectacular, indeed, notably the southeastern Pacific archipelagos of Juan Fernández and Desventuradas (*Sonchus*), but also the mid-Atlantic archipelagos (Azores, Madeira, Canary and

Cape Verde islands; *Lactuca*, *Launaea*, *Leontodon*, *Sonchus*, *Tolpis*). Most Cichorieae occur in moderately humid climates, some extend into semiarid to arid environments (e.g., *Lactuca*, *Launaea*), others inhabit mountains up to the alpine zone (e.g., *Soroseris*, *Taraxacum*), but they are almost absent from the humid tropics and from aquatic habitats.

Babcock (1947) was the first to address in more detail the question of the geographical origin of the tribe. He proposed an origin of Crepidinae sensu Stebbins (comprising genera from our Hieraciinae, Crepidinae, Hyoseridinae and Lactucinae) in the Angara region northeast of Lake

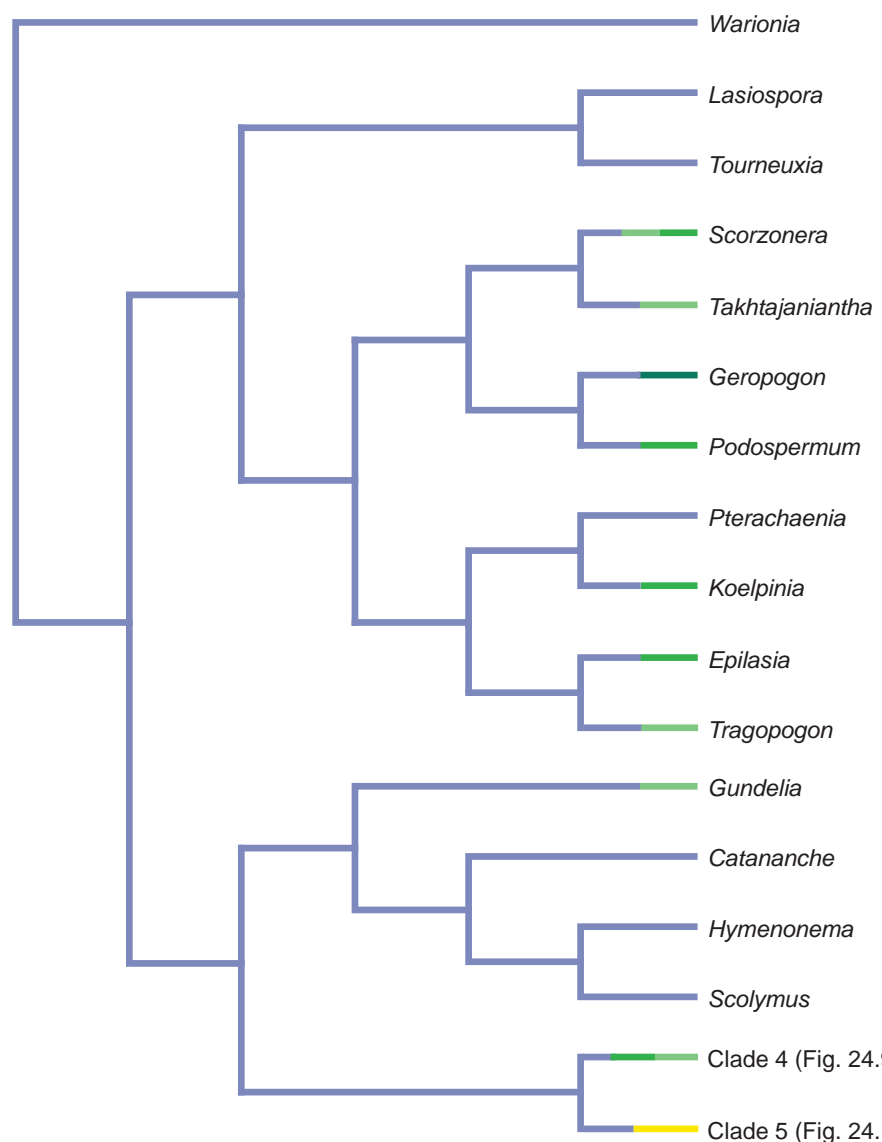


Fig. 24.8. Biogeography of the tribe Cichorieae mapped on the scheme of the ITS phylogeny in Fig. 24.1. Included are only genera for which molecular data are available. — Abbreviations: c1 = clade 1, Warioniinae; c2 = clade 2, Scorzonerinae; c3 = clade 3, Scolyminae; c4 = clade 4, including Crepidinae, Chondrillinae, Hypochaeridinae, Hyoseridinae and Lactucinae; c5 = clade 5, including Cichoriinae, Microseridinae and Hieraciinae. See Fig. 24.10 for color chart and Chapter 44 for the complete metatree.

Baikal and particularly in the Altai, where he presumed the origin of the angiosperms, although he stated that *Crepis*, *Launaea*, *Sonchus*, *Tolpis*, and *Taraxacum* have their most primitive species in the western Mediterranean region. Based on the latter assumption, Babcock proposed an alternative hypothesis of a western Eurasian origin with early migration of the Crepidinae of the pre-Tertiary arctic flora into the region of the northern Ural Mountains and subsequent migration into (1) northern Europe in the

early Eocene, where one line was driven southwards by the cooling climate in the Tertiary, whereas another line (2) migrated into North Central Asia and became established in the Altai-Tien Shan region.

Based on a morphological cladistic analysis, Bremer (1994) indicated an origin of the Cichorieae in the Mediterranean region or Central Asia, due to the highest distribution density of the basally branching genera. In a parsimony optimization analysis of the Asteraceae

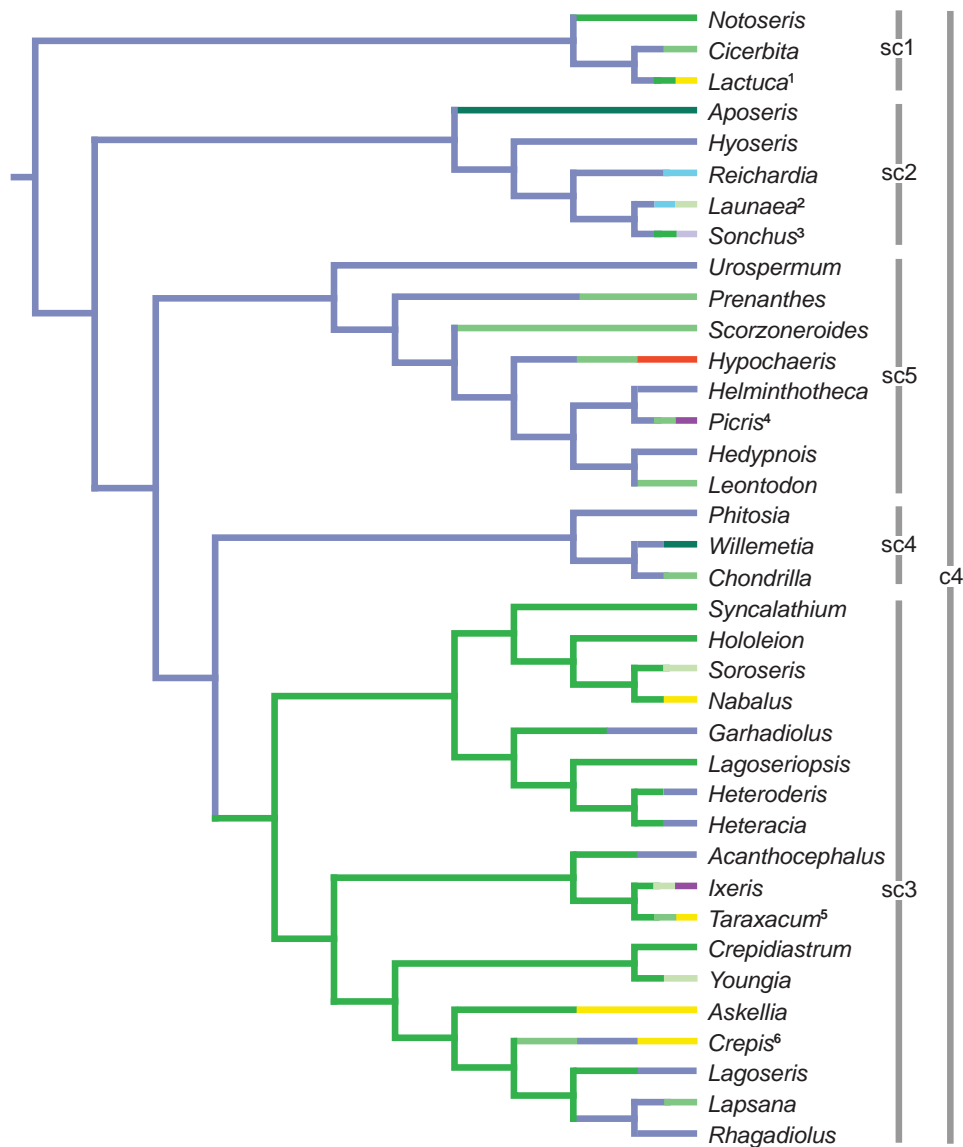


Fig. 24.9. Biogeography of clade 4 of the tribe Cichorieae mapped on the scheme of the ITS phylogeny in Fig. 24.2. Included are only genera for which molecular data are available. — Abbreviations: c4 = clade 4; sc1 = subclade 1, Lactucinae; sc2 = subclade 2, Hyoseridinae; sc3 = subclade 3, Crepidinae; sc4 = subclade 4, Chondrillinae; sc5 = subclade 5, Hypochaeridinae. — Notes: ¹also in tropical Africa and Eurasia; ²also in Central and East Asia and Western Australia; ³also in tropical Africa, South and Southeast Asia, Australia and New Zealand; ⁴also in tropical Africa; ⁵also in North and South America; ⁶also in tropical Africa, Central and East Asia and Mexico. See Fig. 24.10 for color chart.

supertree (=metatree), Funk et al. (2005) inferred a North African-Mediterranean origin of Cichorieae, as they form a clade together with the tribes Arctotideae, Liabeae and Vernonieae, which are thought to be of African origin, too (Funk et al. 2004, 2005). From North Africa and the Mediterranean, Cichorieae repeatedly spread into Eurasia and also reached North America where a monophyletic radiation took place (Lee et al. 2003; Funk et al. 2005).

Up to now, no ancestral area analysis for the tribe has been carried out. As for the distribution of the three basally branching subtribes, subtribe Warioniinae is restricted to northwestern Africa, Scolyminae to the Mediterranean region, while Scorzonnerinae to the Mediterranean and Eurasia (Fig. 24.8).

The distribution of the terminal-branching clade 4, including five subtribes, is predominantly Mediterranean and Central/Eastern Asian but frequently with extensions

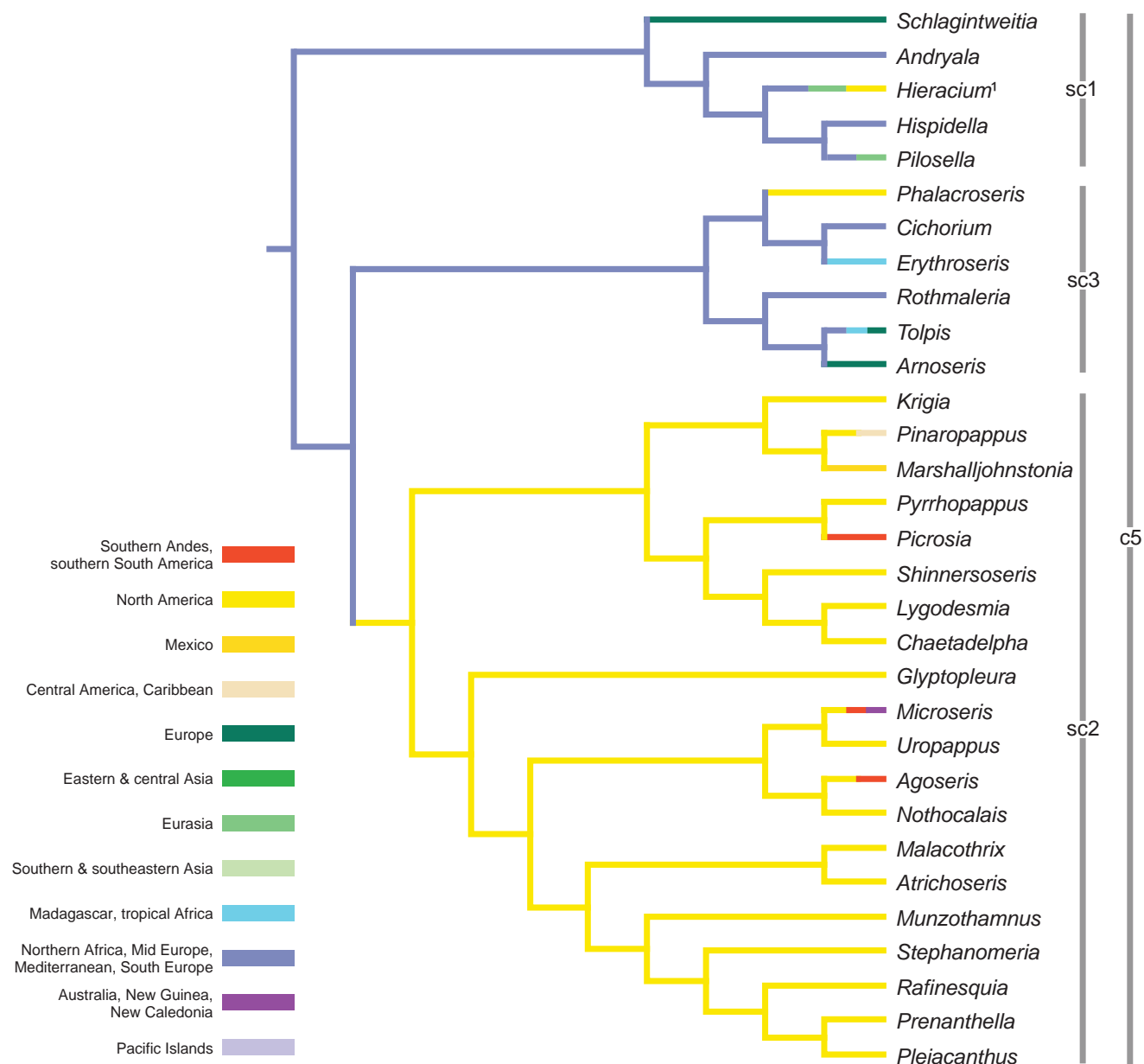


Fig. 24.10. Biogeography of clade 5 of the tribe Cichorieae mapped on the scheme of the ITS phylogeny in Fig. 24.3. Included are only genera for which molecular data are available. — Abbreviations: c5 = clade 5; sc1 = subclade 1, Hieraciinae; sc2 = subclade 2, Microseridinae; sc3 = subclade 3, Cichoriinae. — Notes: ¹also in tropical Africa, Central and East Asia and South America.

beyond this range (Fig. 24.9). Lactucinae have a Eurasian, African and North American distribution, commonly inhabiting montane to alpine, sub-boreal and boreal regions as well as steppe habitats, generally favoring cooler climatic conditions (Fries 1949; Meusel and Jäger 1992). Crepidinae have their highest species and generic diversity in Eurasia, with centers of distribution in Central/Eastern Asia and the Mediterranean region, but *Crepis* and *Taraxacum* extend to Africa and North America, the latter genus also to South America. Chondrillinae have a Eurasian distribution. Hyoseridinae have their centre of diversity in the Mediterranean region (*Aposeris*, *Hyoseris*, *Launaea*, *Reichardia*, *Sonchus*) extending to the mid-Atlantic Islands, Central and North-Eurasia, tropical Africa, Southwest and South-Asia, Australia/New Zealand, North America and the South Pacific Juan Fernández and Desventuradas Islands. Hypochaeridinae are centered in the Mediterranean region and Southwest Asia; only *Hypochaeris*, *Leontodon*, and *Picris* considerably extend beyond this area into the non-tropical part of Eurasia: *Leontodon* reaches the Ural Mountains (Meusel and Jäger 1992), *Hypochaeris* East Siberia (Vasilliev in Bobrov and Tzvelev 1964), and *Picris* extends even further eastwards to Kamchatka and Attu Island in the Aleutian archipelago but does not occur in North America (Stebbins 1971; Lack 1979). *Hypochaeris* (South America to Tierra del Fuego) and *Picris* (Australia, Tasmania and New Zealand; Holzapfel 1999) reached the southern hemisphere.

The distribution of the terminal-branching clade 5, including five subtribes, is chiefly Mediterranean/South West Asian and North American (Fig. 24.10). Cichoriinae are chiefly Mediterranean-Southwest Asian distributed but extend to North Europe, the mid-Atlantic Islands and South Africa, and with the exception of *Phalacroseris*, which occurs in western North America and traditionally has been treated as a member of the North American subtribes of Cichorieae (e.g., Lee et al. 2003; Bremer 1994). Microseridinae s.l., for which a single origin from their Old World ancestors has been supported by molecular analyses (Lee et al. 2003; Funk et al. 2005; and our results), are concentrated in southwestern North America, while species of some genera also occur in South America (e.g., *Microseris*, *Agoseris*). One genus is endemic to South America (*Picosia*) and *Microseris* also reached Australia and New Zealand via long distance dispersal and diversified there (Van Houten et al. 1993). Hieraciinae are mainly Eurasian distributed but also occur in Africa and the Americas.

Lactuca, although not being the largest genus of the tribe, has perhaps the widest distributional area, being natively spread across the temperate and warm regions of the northern hemisphere and extending south of the equator in Africa and Asia (the distribution given by Lebeda et al. 2004, however, is partly erroneous due to uncritical

inclusion of a number of species actually not belonging to *Lactuca* even in its widest sense). *Lactuca* is particularly species-rich and diverse in southern Eurasia, the African tropics, and in eastern North America (Meusel and Jäger 1992), with an altitudinal range from sea level to the alpine zone.

Also widely distributed is *Sonchus*, extending from the Mediterranean region to the mid-Atlantic Islands, temperate Eurasia, tropical Africa, Australia/New Zealand, North America and, apparently by long-distant dispersal, to the South Pacific Juan Fernández and Desventuradas Islands.

Hieracium and *Taraxacum*, the genera with the highest species number (if microspecies are considered) in the tribe, show distributional patterns similar to one another, occurring in Europe, Asia, North Africa and North and South America in boreal, temperate, humid, semiarid and arid regions, with a present center of diversity in Europe and the region between the Mediterranean and the eastern Himalaya, being synantropic in the southern parts of Africa, Australia and New Zealand. *Hieracium* has its center of diversity in the mountains of central and southern Europe in woody montane or alpine zones; in the Andes it can reach altitudes up to 4300 m. *Taraxacum* most often populates open habitats, reaching altitudes of up to 6000 m in the Himalayan region.

Genera with disjunct distribution in North America and Eurasia are *Askellia*, *Crepis*, *Hieracium*, *Lactuca*, *Nabalus*, and *Taraxacum*, with *Hieracium* also found in South America as far as Tierra de Fuego and the Falkland/Malvinas Islands. The species of *Agoseris* and *Microseris* are present in North and South America, while a remarkable South American-Eurasian disjunction occurs in *Hypochaeris*.

EVOLUTION

On a molecular base, Cichorieae are monophyletic if the variously placed genera *Gundelia* and *Warionia* are included; however, there is not a single morphological, anatomical or karyological autapomorphy characterizing Cichorieae. Wagenitz (1967) already referred to the convergent evolutionary traits of milky latex and flower symmetry in other tribes of Compositae allowing for two possible scenarios to explain the tribal evolution, either indicating a fast radiation in the early stage of the development of the tribes with incomplete lineage sorting, or hybridization events across lineages in the early stage of tribal development. The close relationships of Cichorieae within Compositae are weakly resolved as transitional characters indicative of relationships are scarce, pointing to adjacent independent evolutionary developments of the tribe with taxa of the basal lineages being descendants of this evolutionary scenario.

Despite that large amounts of molecular variation could be detected in the ITS region (478 characters in total of which 374 are parsimony informative), there is little resolution of relationships among major lineages within the tribe. Of five statistically well supported major lineages, two (clades 4 and 5) comprise more than 80% of the species of the tribes, indicating that repeated rapid radiation and diversification must have taken place in several evolutionary stages of Cichorieae.

Tremetsberger et al. (submitted) aimed at providing the best estimate of the age of Cichorieae and its subtribes based on available fossil evidence and DNA sequences. From the fossil record three different types of echinolate pollen, i.e., the *Cichorium intybus* type (age 22–28.4 Myr), the *Scorzonera hispanica* type (min. age 3.4 Myr), and the *Sonchus oleraceus* type (min. age 5.4 Myr) were used to calibrate the phylogenetic tree, and estimates were calculated by using an uncorrelated relaxed molecular clock approach (Drummond et al. 2006). The results indicate a most probable origin of the tribe in the Late Eocene or Oligocene (25.8–36.2 Ma) in North Africa with a subsequent divergence of the main groups during the Late Oligocene or Early Miocene (Scolyminae 18.9–23.6 Ma; Scorzonerae 17.4–21.2 Ma; and the core group of Cichorieae, comprising the species-rich clades 4 and 5, 19.9–24.9 Ma), which might be associated with the land bridge formation between the Afro-Arabian and Eurasian plates as result of northward drift of the Afro-Arabian plate. The subtribes of the core group diversified in the Middle and Late Miocene, a time of changing geological setting and climate in the Mediterranean region and Eurasia (e.g., uplift of the Alps, the Messinian Salinity Crisis and others; Mai 1995)

Four dispersal events to America seem to have occurred during the Miocene and Pliocene, the first resulting in a fast radiation and diversification of genera and species of Microseridinae in North America. Tremetsberger et al. (submitted) hypothesize that this radiation was associated with the uplift of mountain ranges along the west coast of North America and subsequent changes in climate and vegetation. Other dispersal events to America were restricted to genera that radiated at the specific level either in North America (*Crepis*), South America (*Hypochaeris*), or on both continents (*Hieracium*) involving hybridization, polyploidization and/or apomixis. Different distribution routes seem to have been involved; of these only those resulting in *Hypochaeris* on South America have been elucidated in detail (Samuel et al. 2003). Similar events led to the radiation of the otherwise Eurasian genus *Picris* in Australia. Only one tribe, Hyoseridinae, has an almost cosmopolitan distribution being present in Eurasia, Northern and Southern Africa, Australia, New Zealand and on some Pacific Islands, indicating accelerated molecular evolution, especially in the island endemics.

Parallel evolutionary trends of several characters suggest that hybridization across lineages and repeated rapid diversification played an important role in the evolution of and across several clades, which is indicated by first molecular analyses investigating maternal lineages and by comparison with nuclear data being bi-parentally inherited. Intergeneric hybridization events between ancestral lineages that resulted in cytoplasmic transfer from *Hieracium* subg. *Chionoracium* to *Pilosella* and from the introgressed *Pilosella* lineage to *Andryala* could be detected by Fehrer et al. (2007) and might also account for conflicting phylogenies of *Tolpis* (Kim et al. 1999b; Whitton et al. 1995; and this study), while it still needs to be examined for *Phytosia*, *Urospermum*, *Prenanthes* and possibly *Phalacroseris*.

Additional investigation within Cichorieae are still pending concerning their worldwide success, tendency to weediness, lack of apparent ability to move into tropical regions, and other factors that account for their present distribution and evolution.

ECONOMIC USES

Looking at Cichorieae as a whole, the number of agricultural species is rather small. *Mansfeld's Encyclopedia* (Jeffrey 2001) lists species belonging to *Chondrilla*, *Cichorium*, *Crepidiastrum*, *Gundelia*, *Hololeion*, *Ixeridium*, *Lactuca*, *Launaea*, *Pterocypsela* (= *Lactuca*), *Reichardia*, *Scolymus*, *Scorzonera*, *Sonchus*, *Taraxacum* and *Tragopogon*, all of them restricted in distribution to the Old World. For taxa occurring in the former Soviet Union an in-depth analysis lists a few more genera (Sokolov 1993). Only species of *Cichorium*, *Lactuca* and *Scorzonera* are cultivated widely; all other species seem to be of local importance only, although it is often difficult to get a clear view on the economic importance of plants used mainly as salads, potherbs, spinach and animal fodder, but rarely traded to any extent.

Basically Cichorieae are grown either for their leaves or their roots. Selection has led in some cases to cultivars with soft green leaves free of bitter substances, e.g., in lettuce (*Lactuca sativa*), or with colored leaves poor in bitter substances, e.g., in radicchio cultivars of chicory (*Cichorium intybus*). In other cases the ability to synthesize bitter substances persists, but is suppressed by keeping the plants during the development of their rosettes in the dark; this results in solid, blanched-leaf heads, e.g., the chicons in chicory. In other cases unblanched leaves are eaten as a cooked vegetable, e.g., in endive (*Cichorium endivia* L.) or only the soft innermost bleached leaves of the rosette are consumed, e.g., in dandelion (*Taraxacum officinale* Wigg. s.l.). The underground parts of several species are edible, but only Spanish salsify (*Scorzonera hispanica*) and salsify (*Tragopogon porrifolius*) are cultivated to any extent for this purpose. The use of the sweet roots of *Scorzonera deliciosa*

Guss. candied and eaten as confectionary is mentioned as a curiosity (Jeffrey 2001). The dried and roasted roots of chicory have been used historically as a substitute for roasted coffee beans, a habit made famous by the Viennese satirist Johann Nestroy, and are still used as an ingredient of caffeine-free instant coffee substitutes.

Diversification into cultivars is particularly marked in lettuce with considerable to hardly any heading, in chicory and in Indian lettuce (*Lactuca indica* L.; see Jeffrey 2001, as *Pterocypsela indica* (L.) S. Shih). Other plant parts are only occasionally used, e.g., juvenile flower heads of *Gundelia tournefortii* collected locally in the wild in the Near East and eaten as a cooked vegetable (Lev-Yadun and Abbo 1999).

In the Soviet Union under Stalin, during the period in which the political concept of economic autarky prevailed, the cultivation of perennial species of *Chondrilla*, *Scorzonera tau-saghyz* Lipschitz & Bosse and *Taraxacum kok-saghyz* Rodin as sources of milky sap for the production of rubber was a major issue. Not being in the position to grow tropical *Hevea brasiliensis* (A. Juss.) Müll. Arg. and at the same time needing large quantities of the commodity to develop the country further, great efforts were made both to better understand the taxa involved (e.g., Iljin 1930), all of them native in Central Asia, and to select and grow on a large scale variants with a high rubber content, the “Vavilon” in Leningrad acting as coordinating center (Rodin 1968). Nazi Germany under Hitler was equally focused on autarky and faced similar problems, but possessed no potential candidates for the production of rubber in its own flora. When parts of the Soviet Union were occupied by Nazi Germany, many *Taraxacum kok-saghyz* collections were therefore confiscated and subsequently grown and tested by researchers of the Kaiser-Wilhelm-Gesellschaft. Among others, prisoners from the concentration camp of Auschwitz did the work, with key political figures directly involved in the project (e.g., Heim 2003). The results being unsatisfactory, the cultivation of Cichorieae as a source for rubber has since been discontinued.

Whereas agricultural and horticultural species possess positive economic importance, weeds are best characterized as plants with negative economic importance. Among the 104 “world weeds” (Holm et al. 1997), no less than five belong to Cichorieae, all of them native in temperate Eurasia, but found today on all five continents. They are of no importance in their region of origin but only outside. Skeleton weed (*Chondrilla juncea* L.), introduced into Australia in the 1900s, may act as an example. It quickly infested huge areas of pastures and agricultural land reducing crop yields, regenerating from deep, branched taproots and seriously interfering with the wheat harvest. Other weedy Cichorieae, e.g., prickly sowthistle (*Sonchus asper* (L.) Hill), are pioneer species, invade disturbed sites, and infest the sites heavily due to copious seed production and

a root system with numerous root buds, which develop after fragmentation of the root system to root-born shoots and new, independent plants (Rauh 1937: 460–461). Rusts, e.g., *Puccinia chondrillina* Bubák, and gale mites, e.g., *Aceria chondrillae* Canestrini, have been shown to be the most effective organisms to control these most noxious plants, which under suitable conditions are reported to spread at considerable speed, e.g., an average of 24 km/yr has been indicated for skeleton weed in southeast Australia. Several other Cichorieae, among them *Cichorium intybus*, corn sowthistle (*Sonchus arvensis* L.) and prickly ox-tongue (*Helminthotheca echioides* (L.) Holub), behave also as aggressive weeds, notable in western North America and in Australia competing with crops and garden plants. Dandelion (*Taraxacum officinale*) seems to cause less economic loss than has been usually assumed, although it is a plant of some concern to those in search of a perfect lawn, with garden manuals recommending these weeds to be “cut out by hand using a knife or [be] killed by a herbicide applied with a ‘spot-weeder’” (Huxley 1992).

Even for the enthusiast, Cichorieae are not very spectacular plants and less so for the horticulturalist who tends to focus on bright contrasting flower colors, unconventional form, special texture of leaves and stems or other showy characters as well as pleasant scent. In addition, the uninitiated is inclined to regard members of this tribe simply as weeds, which may have lessened horticultural interest in the group. Considering further that the tribe is a predominantly northern hemisphere group with comparatively few strictly tropical species, it is no surprise that only a limited number of taxa are of major horticultural importance, and all of these in use only in gardens of the temperate zone. Brickell (1999), dealing with very important “plants suitable for growing in temperate gardens world wide”, lists only six genera of Cichorieae, i.e., *Catananche*, *Cicerbita*, *Cichorium*, *Crepis*, *Hieracium* and *Tolpis*. It seems that typical flower heads of the tribe with bright yellow ligules reminiscent of ubiquitous “weeds” such as *Taraxacum officinale* or *Picris hieracioides* L. were considered too trivial by the horticulturalist, who was and is attracted to species with (1) ligules in other colors, i.e., sky blue (*Catananche caerulea*; *Cicerbita alpina* (L.) Wall., *C. bourgaei* (Boiss.) Beauverd; *Cichorium intybus*), pink (*Crepis incana* Sm., *C. rubra* L.) or bright orange (*Crepis aurea*; *Pilosella aurantiaca* (L.) F.W. Schultz & Sch. Bip.), or (2) in flower heads with differently colored centers, e.g., in *Reichardia tingitana* or *Tolpis barbata*; a potential candidate with this character to further enrich gardens is *Hispidella hispanica*.

Although the much more comprehensive *New Royal Horticultural Society Dictionary of Gardening* (Huxley 1992) lists several more genera, e.g., the tomentose *Andryala* and the thistle-like *Scolymus*, as well as many more species of Cichorieae suitable for cultivation, the fact remains that the tribe comprises few ornamentals of any economic

importance. Extremely few genera restricted in distribution to North America, i.e., *Agoseris*, *Nabalus* and *Krigia*, have ever been used as ornamentals. Furthermore, anthropogenic differentiation of species into cultivars is quite limited in the tribe, present, e.g., in *Catananche caerulea* and *Tragopogon porrifolius*.

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Appendix 24.1. Subtribal classification of Cichorieae

Suprageneric nomenclature is essentially based on Reveal (1997). Genera are listed in alphabetical order within the subtribes; their synonyms are listed in chronological order. The types, so far designated, are given for all generic names, including synonyms; in certain cases where such clarification appeared helpful, synonyms are added for the typifying binomials.

(1) Warioniinae Gemeinholzer & N. Kilian, **subtr. nov.**

Subtribus monogenerica et monospecifica insignis, a subtribibus ceteris capitulis multifloris homogamis tubulifloris corollis luteis leviter zygomorphis differt. Typus: *Warionia* Benth. & Coss.

1 species/1 genus – NW Africa

Warionia Benth. & Coss. (1872) [type: *W. saharae* Benth. & Coss.], monospecific

(2) Scorzonerinae Dumort. (1827)

ca. 300 species/10 genera – Europe, N Africa, SW to Central and E Asia; several species introduced elsewhere

Note: The circumscription of *Scorzonera* is not yet fully settled and its revision in progress (Gemeinholzer, Kilian & Marhold, in prep.).

Epilasia (Bunge) Benth. (1873) [lectotype (designated by Lipschitz in Bobrov & Tzvelev, Fl. SSSR 29: 111. 1964): *E. hemilasia* (Bunge) C. Clarke]

Geropogon L. (1763) [lectotype (designated by Steudel, Nomencl. Bot., ed. 2, 1: 681. 1840): *G. glabrus* L. = *G. hybridus* (L.) Sch. Bip.], monospecific

Koelipinia Pall. (1776) [type: *K. linearis* Pall.]

Lasiospora Cass. (1822) [lectotype (designated by Tzvelev, Fl. Partis Eur. URSS 8: 45. 1989): *L. hirsuta* (Gouan) Cass.]

= *Pseudopodospermum* (Lipsch. & Krasch.) Kuth. [type: *P. molle* (M. Bieb.) Kuth.]

Podospermum DC. (1805) [type (cons.): *P. laciniatum* (L.) DC.]

Pterachaenia (Benth.) Lipsch. (1939) [type: *P. stewartii* (Hook. f.) R.R. Stewart], monospecific

Scorzonera L. s.str. (1753) [lectotype (designated by Green, Prop. Brit. Bot.: 177. 1929): *S. humilis* L.]

= *Gelasia* Cass. (1818) [type: *G. villosa* (Scop.) Cass.]

?= *Achyroseris* Sch.Bip. (1845) [type: *A. macrosperma* (DC.) Sch. Bip.]

?= *Avellara* Blanca & C. Díaz (1985) [type: *A. fistulosa* (Brot.) Blanca & C. Díaz]

Takhtajianantha Nazarova (1990) [type: *T. pusilla* (Pall.) Nazarova]

Tourneuxia Coss. (1859) [type: *T. variifolia* Coss.], monospecific

Tragopogon L. (1753) [lectotype (designated by Britton & Brown, Ill. Fl. N. U.S., ed. 2, 3: 313. 1913): *T. pratensis* L.]

(3) Scolyminae Less. (1832)

= Gundeliinae Benth. (1873), Catananchinae K. Bremer (1993)
12 species/4 genera – S Europe, N Africa, and SW Asia

Catananche L. (1753) [lectotype (designated by Green, Prop. Brit. Bot.: 178. 1929): *C. lutea* L.]

Gundelia L. (1753) [type: *G. tournefortii* L.]

Hymenonema Cass. (1817) [type: not designated]

Scolymus L. (1753) [lectotype (designated by Green, Prop. Brit. Bot.: 178. 1929): *S. maculatus* L.]

(4) Lactucinae Dumort. (1827)

ca. 230 species/3 genera – Europa, Africa, SW, Central and E Asia, North America; few species introduced elsewhere

Note: The generic arrangement provided here is still tentative and a revised classification (Kilian & Gemeinholzer, in prep.) in progress.

Cicerbita Wallr. (1822) [lectotype (designated by Kirpicnikov in Bobrov & Tzvelev, Fl. SSSR 29: 352. 1964): *C. alpina* (L.) Wallr.]

= *Mycelis* Cass. (1824) [type: *M. angulosa* Cass., nom. illeg. = *M. muralis* (L.) Dumort.]

= *Melanoseris* Decne. (1843) [lectotype (designated by Pfeiffer, Nomencl. Bot. 2: 259. 1874): *M. lessertiana* (DC.) Decne.]

= *Cephalorrhynchus* Boiss. (1844) [type: *C. glandulosus* Boiss.]

= *Chaetoseris* C. Shih (1991) [type: *C. lyriformis* C. Shih]

= *Zollikoferiastrum* (Kirp.) Kamelin (1993) [type: *Z. polycladum* (Boiss.) Kamelin]

Lactuca L. (1753) [type: *L. sativa* L.]

= *Mulgedium* F.W. Schmidt (1795) [lectotype (Shih in Acta Phytotax. Sin. 26: 390. 1988): *M. tataricum* (L.) DC.]

= *Scariola* F.W. Schmidt (1795) [type: *S. viminea* (L.) F.W. Schmidt] ≡ *Phaenioxopus* Cass. 1826 [lectotype (designated by Pfeiffer, Nomencl. Bot. 2: 659. 1874): *P. decurrens* Cass., nom. illeg. = *L. viminea* L.]

= *Steptorhamphus* Bunge (1852) [type: *S. crambifolius* Bunge]

= *Lactucopsis* Vis. & Pančić (1870) [lectotype (designated here): *L. aurea* Vis. & Pančić]

= *Lagedium* Soják (1961) [type: *L. sibiricum* (L.) Soják]

- = *Pterocypsela* C. Shih (1988) [type: *P. indica* (L.) C. Shih]
 = *Lactucella* Nazarova (1990) [type: *L. undulata* (Ledeb.) Nazarova], monospecific
- Notoseris** C. Shih (1987) [type: *N. psilolepis* Shih]
 = *Paraprenanthes* C. Shih (1988) [type: *P. sororia* (Miquel) C. Shih]
 = *Stenoseris* C. Shih (1991) [type: *S. graciliflora* (DC.) C. Shih]
 = *Kovalevskiella* Kamelin (1993) [type: *K. zerauschanica* (Kovalevsk.) Kamelin]
- (5) Hyoseridinae** Less. (1832)
- = Dendroseridinae Benth. (1873), Sonchinae K. Bremer (1993) ca. 150 species/5 genera – Europa, Africa, Asia, Australia, New Zealand, North America, S Pacific Juan Fernández and Desventuradas Islands off the coast of Chile; several species introduced elsewhere
 Note: A revision of *Sonchus* s.l. (see Phylogeny) aiming at the morphological delimitation of monophyletic entities (compare Kim et al. 2007) at generic or subgeneric rank is in preparation by Kim & Mejías (pers. comm., March 2007).
- Aposeris** Cass. (1827) [type: *A. foetida* (L.) Less.], monospecific
- Hyoseris** L. (1753) [lectotype (designated by Green, Prop. Brit. Bot.: 178. 1929): *H. radiata* L.]
- Launaea** Cass. (1822) [type: *L. bellidifolia* Cass.]
 = *Rhabdotheca* Cass. (1827) [type: *R. sonchoides* Cass.]
 = *Brachyrhamphus* DC. (1838) [lectotype (designated by Britton & Wilson, Bot. Porto Rico 2: 276. 1925): *Lactuca intybacea* Jacq.]
 = *Paramicrorhynchus* Kirp. (1964) [type: *P. procumbens* (Roxb.) Kirp.]
 = *Hexinia* H.L. Yang (1992) [type: *H. polydichotoma* (Ostenf.) H.L. Yang]
- Richardia** Roth (1787) [lectotype (designated by Britton, Fl. Bermuda: 382. 1918): *R. tingitana* (L.) Roth]
- Sonchus** L. (1753) [type: *Sonchus oleraceus* L.]
 = *Aetheorhiza* Cass. (1827) [type: *A. bulbosa* (L.) Cass.]
 = *Atalanthus* D. Don (1829) [lectotype (designated by Pfeiffer, Nomencl. Bot. 1: 321. 1873): *A. pinnatus* (L.f.) D. Don = *Prenanthes pinnata* L. f. = *Sonchus leptocephalus* Cass.] = *Taeckholmia* Boulos (1967), nom. illeg.
 = *Dendroseris* D. Don (1832) [type: *D. macrophylla* D. Don]
 = *Thamnosseris* Phil. (1895) [type: *T. lacerata* (Phil.) Johnst.]
 = *Sventenia* Font Quer (1949) [type: *S. bupleuroides* Font Quer]
 = *Kirkianella* Allan (1961) [type: *K. novae-zelandiae* (Hook.f.) Allan]
 = *Babcockia* Boulos (1965) [type: *B. platylepis* (Webb) Boulos]
 = *Embergeria* Boulos (1965) [type: *E. grandifolia* (Kirk) Boulos]
 = *Lactucosonchus* (Sch.Bip.) Svent. (1969) [type: *L. webbii* (Sch. Bip.) Svent.] = *Wildpretia* U. Reifent. & A. Reifent. (1996), nom. illeg.
 = *Actites* Lander (1976) [type: *A. megalocarpa* (Hook.f.) Lander]
 = *Chrysoprenanthes* (Sch.Bip.) Bramwell (2003) [type: *C. pendula* (Webb) Bramwell]
- (6) Crepidinae** Dumort. (1827)
- = Lapsaninae Dumort. (1829), Rhagadiolinae Benth. (1873), Sincalathinae Lipsch. (1956), Taraxacinae Tzvelev (2007), Ixeridinae Sennikov (2008)
 ca. 360 species apart from *Taraxacum* (with ca. 1600 apomictic species [Sterk 1987; IPNI 2007])/26 genera – Europe, Africa, Asia, North America; several species introduced elsewhere
 Note: The re-circumscription of *Crepis* as a monophyletic genus (see Phylogeny) is not settled yet: parts of the genus are sister to *Lapsana* and *Rhagadiolus* (see Enke & Gemeinholzer 2008) and would necessitate the recognition of a morphologically ill-circumscribed separate genus *Lagoseris*, or, inclusion of *Lapsana* and *Rhagadiolus* in *Crepis*, or acceptance of *Crepis*, *Lapsana* and *Rhagadiolus* as paraphyletic genera, the first solution certainly being the worst. Very recently three new genera from central Asia, *Crepidifolium*, *Sonchella* and *Tibetoseris*, have been published by Sennikov (in Tzvelev 2007 and Sennikov and Illarionova 2007); molecular analyses of their status and systematic position are under way (Kilian & Gemeinholzer, in prep.).
- Acanthocephalus** Kar. & Kir. (1842) [type: *A. amplexifolius* Kar. & Kir.]
- Askellia** W.A. Weber (1984) [type: *A. nana* (Richardson) W.A. Weber]
- Crepidiastrum** Nakai (1920) [lectotype (designated by Pak & Kawano in Mem. Fac. Sci. Kyoto Univ., Ser. Biol. 15(1-2): 50. 1992): *C. lanceolatum* (Houtt.) Nakai]
 = *Paraixeris* Nakai (1920) [lectotype (designated by Stebbins in J. Bot. (London) 75: 44. 1937): *P. denticulata* (Houtt.) Nakai]
- ?**Crepidifolium** Sennikov (2007) [type: *C. tenuifolium* (Willd.) Sennikov] = **Geblera** Kitag. (1937), nom. illeg., non Fisch & C.A. Mey. (1835)
- Crepis** L. (1753) [type: *C. biennis* L.]
 = *Zacintha* Mill. (1754) [type: *Lapsana zacintha* L.]
 = *Aracium* Neck. (1790) [type: *A. paludosum* (L.) Dulac]
 = *Barkhausia* Moench (1794) [lectotype (designated by Cassini, Dict. Sci. Nat. 48: 429. 1827): *B. scariosa* Moench, nom. illeg. = *C. alpina* L.]
 = *Wibelia* G. Gaertn. & al. (1801) [type: *W. foetida* (L.) Sch.Bip.] = *Hostia* Moench
 = *Berinia* Brign. (1810) [type: *B. andryaloides* Brign.]
 = *Rodigia* Spreng. (1820) [lectotype (designated by Steudel, Nomencl. Bot., ed. 2, 2: 462. 1841): *R. commutata* Spreng.]
 = *Psilochenia* Nutt. (1841) [type: *P. occidentalis* (Nutt.) Nutt.]
 = *Dianthoseris* A. Rich. (1848) [type: *Dianthoseris schimperi* A. Rich.] = *Nannoseris* Hedberg, nom. illeg. (1957)
- Dubyaea** DC. (1838) [lectotype (designated by Stebbins in Mem. Torrey Bot. Club 19(3): 9. 1940): *D. hispida* (D. Don) DC.]
- Faberia** Hemsl. (1888) [type: *F. sinensis* Hemsl.]
 = *Faberiopsis* C. Shih & Y.L. Chen [type: *F. nanchuanensis* (C. Shih) C. Shih & Y.L. Chen]
- Garhadiolus** Jaub. & Spach (1850) [lectotype (designated by Vassilczenko in Bobrov & Tzvelev, Fl. SSSR 29: 231. 1964): *G. angulosus* Jaub. & Spach]
- Heteracia** Fisch. & C.A. Mey. (1835) [type: *H. szovitsii* Fisch. & C.A. Mey.]
- Heteroderis** (Bunge) Boiss. (1875) [lectotype (designated by Leonova in Bobrov & Tzvelev, Fl. SSSR 29: 589. 1964): *H. pusilla* (Boiss.) Boiss.], monospecific
- Hololeion** Kitam. (1941) [type: *H. krameri* (Franch. & Sav.) Kitam.]
- Ixeridium** (A. Gray) Tzvelev (1964) [type: *I. dentatum* (Thunb.) Tzvelev]
- Ixeris** (Cass.) Cass. (1822) [type: *I. polycephala* Cass.]
 = *Choris* DC. (1838) [type: *C. repens* (L.) DC.]
- Lagoseriopsis** Kirp. (1964) [type: *L. popovii* (Krasch.) Kirp.], monospecific
- ?**Lagoseris** M. Bieb. (1810) [type: *L. crepoides* M. Bieb., nom. illeg. = *L. purpurea* (Willd.) Boiss.]
 = *Pterotheca* Cass. (1816) [type: *P. nemausensis* Cass.]
 = *Intybellia* Cass. (1821) [type: *I. rosea* Cass. = *C. purpurea* (Willd.) M. Bieb.] = *Myoseris* Link (1822)
 = *Trichocrepis* Vis. (1826) [type: *T. bifida* Vis.]
 = *Phaeacasium* Cass. (1826) [type: *P. lampsanoides* Cass., nom. illeg. =? *C. pulchra* L.] =? *Isianthes* Desvaux (1827) [type: *C. pulchra* L.] = *Sclerophyllum* Gaudin (1829)
 = *Cymboseris* Boiss. (1849) [type: *C. palaestina* Boiss.]

- Lapsana** L. (1753) [type: *L. communis* L.], monospecific
- Lapsanastrum** J.H. Pak & K. Bremer (1995) [type: *L. humile* (Thunb.) J.H. Pak & K. Bremer]
- Nabalus** Cass. (1825) [lectotype (designated by Britton & Brown, Ill. Fl. N.U.S., ed. 2, 3: 334. 1913): *N. trifoliolatus* Cass.]
- Rhagadiolus** Juss. (1789), nom. cons. [type: *R. edulis* Gaertn.]
- ?**Sonchella** Sennikov (2007) [type: *S. stenonema* (DC.) Sennikov]
- Sorosseris** Stebbins (1940) [type: *S. glomerata* (Decne.) Stebbins] = *Stebbinsia* Lipsch. (1956) [type: *S. umbrella* (Franch.) Lipsch.]
- Spirosaris** Rech. f. (1977) [type: *S. phyllocephala* Rech. f.], monospecific
- Syncalathium** Lipsch. (1956) [type: *S. sukaczewii* Lipsch. = *S. kawaguchii* (Kitam.) Y. Ling]
- Taraxacum** F.H. Wigg. (1780) [type: *T. officinale* F.H. Wigg.]
- ?**Tibetosaris** Sennikov (2007) [type: *T. depressa* (Hook. f. & Thomson) Sennikov]
- Youngia** Cass. (1831) [lectotype (designated by Sennikov in Komarovia 5: 108. 2008): *Y. lyrata* Cass.]
- (7) Chondrillinae** (W.D.J. Koch) Lamotte (1847)
28 species/3 genera – Central Europe, Mediterranean, SW, Central and E Asia; one species introduced elsewhere
- Chondrilla** L. (1753) [type: *C. juncea* L.]
- Phitosis** Kamari & Greuter (2000) [type: *P. crocifolia* (Boiss. & Heldr.) Kamari & Greuter], monospecific
- Willemetia** Neck. (1777–78) [type: *W. hieracioides* Neck., nom. illeg. = *W. stipitata* (Jacq.) Dalla Torre] = *Calycocorsus* F.W. Schmidt, nom. illeg.
- (8) Hypochaeridinae** Less. (1832)
= Leontodontinae Sch.Bip. (1834), Picridinae Sch.Bip. (1834)
ca. 150 species/8 genera – Europa, N, W and E Africa and Asia, with secondary evolutionary centers in Australia (*Picris*) and S South America (*Hypochaeris*).
Notes: For the time being *Prenanthes* s.str. has been placed with a question mark in this subtribe, based exclusively on data of the nuclear ITS region, while morphology does not provide any convincing support. Since the chloroplast marker furthermore indicates a basal position within Lactucinae, the ancestor of *P. purpurea* may most likely be hybridogenous, with one parent from Hypochaeridinae and the other from some other member of Clade 4 (see Phylogeny).
- Hedypnois** Mill. (1754) [lectotype (designated by Ferris in Abrams & Ferris, Ill. Fl. Pacific States 4: 587. 1960): *H. annua* Ferris] = *Hyoseris hedypnois* L. = *H. rhagadioloides* (L.) F.W. Schmidt]
- Helminthotheca** Zinn (1757) [type: *Picris echioides* L. = *H. echioides* (L.) Holub] = *Helminthia* Juss. (1789)
- Hypochaeris** L. (1753) [lectotype (designated by Britton & Brown, Ill. Fl. N. U.S., ed. 2, 3: 309. 1913): *H. glabra* L.] = *Achyrophorus* Adans. (1763)
= *Seriola* L. (1763) [lectotype (designated by Steudel, Nomencl. Bot., ed. 2, 2: 568. 1841): *S. laevigata* L.]
= *Trommsdorffia* Bernh. (1800) [type: *T. maculata* (L.) Bernh.]
= *Robertia* DC. (1815) non Scop. (1777) [type: *R. taraxacoides* (Loisel.) DC.]
= *Distoecha* Phil. (1891) [type: *D. taraxacoides* Phil.]
= *Heywoodiella* Svent. & Bramwell (1971) [type: *H. oligocephala* Svent. & Bramwell]
- Leontodon** L. (1753) [type (cons.): *L. hispidus* L.]
= *Apargia* Scop. (1772) [lectotype (designated by Britton & Brown, Ill. Fl. N. U.S., ed. 2, 3: 310. 1913): *A. incana* (L.) Scop.]
- Picris** L. (1753) [type: *P. hieracioides* L.]
= *Spitzelia* Sch.Bip. (1833) [*S. aegyptiaca* Sch.Bip., nom. illeg. = *P. asplenoides* L.]
= *Deckera* Sch.Bip. (1834) [lectotype (designated by Pfeiffer, Nomencl. Bot. 1(2): 1022. 1874): *D. asplenoides* (L.) Sch.Bip.]
- Scorzoneroides** Moench (1794) [type: *L. autumnalis* L. = *S. autumnalis* (L.) Moench] = *Oporinia* D. Don (1829)
= *Kalbfussia* Sch.Bip. (1833) [type: not designated]
- Urospermum** Scop. (1777) [type: *U. picroides* (L.) F.W. Schmidt] = *Tragopogon picroides* L.]
= *Daumailia* Arènes (1948) [type: *D. spinulosa* Arènes = *U. picroides* (L.) F.W. Schmidt]
- Inclusion questionable: **Prenanthes** L. (1753) [lectotype (designated by Cassini in Cuvier, Dict. Sci. Nat. 34: 96. 1825): *P. purpurea* L.], monospecific?
- (9) Hieraciinae** Dumort. (1827)
ca. 20 species besides *Hieracium* (with ca. 770 sexually reproducing species + 5200 apomictic microspecies) and *Pilosella* (with ca. 110 sexually reproducing species + ca. 700 apomictic microspecies and weakly competitive hybrids [pers. comm. G. Gottschlich, Tübingen, April 2007], see also Bräutigam & Greuter 2007)/5 genera – Eurasia and extending to Africa, North and South America
- Andryala** L. (1753) [lectotype (designated by Green, Prop. Brit. Bot.: 178. 1929): *A. integrifolia* L.]
= *Pietrosia* Nyár. (1999) [lectotype (designated by Sennikov in Komarovia 1: 77. 1999): *P. laevitomentosa* Sennikov]
- Hieracium** L. (1753) [lectotype (designated by Britton & Brown, Ill. Fl. N. U.S., ed. 2, 3: 328. 1913): *H. murorum* L.]
= *Stenotheca* Monnier (1829) [lectotype (designated by Garland in Taxon 39: 121. 1990): *S. subnuda* Monnier]
- Hispidella** Lam. (1789) [type: *H. hispanica* Lam.], monospecific
- Pilosella** Hill. (1756) [type: *Hieracium pilosella* L.]
- Schlagintweitia** Griseb. (1853) [type: *S. intybacea* (All.) Griseb.]
- (10) Microseridinae** Stebbins (1953)
= Stephanomeriinae Stebbins (1953), Malacothricinae K. Bremer (1993), Glyptopleurinae Joongku Lee & B.G. Baldwin (2004), Krigiinae Joongku Lee & B.G. Baldwin (2004), Lygodesmiinae Joongku Lee & B.G. Baldwin (2004), Pinaropappinae Joongku Lee & B.G. Baldwin (2004), Pyrrhopappinae Joongku Lee & B.G. Baldwin (2004)
ca. 115 species/22 genera – North and South America, one species (*Microseris*) in Australia and New Zealand
Note: The principally North American genera plus the South American *Picrosia*, excepting *Phalacosaris*, are treated as a single subtribe, considering their radiation from a single common ancestor (see Phylogeny). The suprageneric classification of the American clade by Lee & Baldwin (2004) should thus be applied at an informal subordinate rank. Generic circumscription is in several cases still disputable, affecting, e.g., *Malacothrix*, which has been shown to be polyphyletic (Lee et al. 2003).
- Agoseris** Raf. (1817) [lectotype (designated by Jones in Abrams & Ferris, Ill. Fl. Pacific States 4: 562. 1960): *A. glauca* (Pursh) Raf.]
- Anisocoma** Torr. & A. Gray (1845) [type: *A. acaulis* Torr. & A. Gray], monospecific
- Atrichoseris** A. Gray (1884) [type: *A. platyphylla* (A. Gray) A. Gray], monospecific
- Calycosaris** A. Gray (1853) [type: *C. wrightii* A. Gray]
- Chaetadelpha** S. Watson (1873) [type: *C. wheeleri* S. Watson], monospecific
- Glyptopleura** D.C. Eaton (1871) [type: *G. marginata* D.C. Eaton]
- Krigia** Schreb. (1791) [type (cons.): *K. virginica* (L.) Willd.]
- Lygodesmia** D. Don (1829) [lectotype (designated by Pfeiffer, Nomencl. Bot. 2: 183. 1874): *L. juncea* (Pursh) Hook.]

- Malacothrix** DC. (1838) [type: *M. californica* DC.]
- Marshalljohnstonia** Henrickson (1976) [type: *M. gypsophila* Henrickson], monospecific
- Microseris** D. Don (1832) [type: *M. pygmaea* D. Don]
= *Apargidium* Torr. & A. Gray (1943) [type: *A. boreale* (Bong.) Torr. & A. Gray]
= *Stebbinsoseris* K.L. Chambers (1991) [type: *S. heterocarpa* (Nutt.) K.L. Chambers]
- Munzothamnus** P.H. Raven (1963) [type: *M. blairii* (Munz & I.M. Johnst.) P.H. Raven], monospecific
- Nothocalais** (A. Gray) Greene (1886) [type: *N. troximoides* (A. Gray) Greene]
- Picrosia** D. Don (1832) [type: *P. longifolia* D. Don]
- Pinaropappus** Less. (1832) [type: *P. roseus* (Less.) Less.]
- Pleiacanthus** (Nutt.) Rydb. (1918) [type: *P. spinosus* (Nutt.) Rydb.], monospecific
- Prenanthesella** Rydb. (1906) [type: *P. exigua* (A. Gray) Rydb.], monospecific
- Pyrrhopappus** DC. (1838) [type: *P. carolinianus* (Walter) DC.]
- Rafinesquia** Nutt. (1841) [type: *R. californica* Nutt.]
- Shinnersoseris** Tomb (1973) [type: *S. rostrata* (A. Gray) Tomb], monospecific
- Stephanomeria** Nutt. (1841) [type (cons.): *S. minor* (Hook.) Nutt.]
- Uropappus** Nutt. (1841) [lectotype (designated by Chambers in Contr. Dudley Herb. 4: 276. 1955): *U. lindleyi* (DC.) Nutt.]
- (11) Cichoriinae** Dumort. (1829)
= Phalacroseridinae Joongku Lee & B.G. Baldwin (2004)
ca. 25 species/6 genera – Europe, N, E and S Africa, Middle Atlantic Islands, SW Asia, SW North America
Note: The placement of the enigmatic SW North American *Phalacroseris* in subtribe Cichoriinae according to the molecular data (see Phylogeny) deserves further consideration in the light of morphology and phytogeography.
- Arnososeris** Gaertn. (1791) [type: *A. pusilla* Gaertn., nom. illeg. ≡ *A. minima* (L.) Dumort.]
- Cichorium** L. (1753) [lectotype (designated by Green, Prop. Brit. Bot.: 178. 1929): *C. intybus* L.]
- Erythroseris** N. Kilian & Gemeinholzer (2007) [type: *E. amabilis* (Balf. f.) N. Kilian & Gemeinholzer]
- Phalacroseris** A. Gray (1868) [type: *P. bolanderi* A. Gray], monospecific
- Rothmaleria** Font Quer (1940) [type: *R. granatensis* (DC.) Font Quer] ≡ *Haensleria* DC. (1838), non Lag. (1816), nom. illeg.
- Tolpis** Adans. (1763) [type: *T. barbata* (L.) Gaertn.]
= *Chlorocephalus* Griseb. (1853) [type: *C. staticifolia* (All.) Griseb.]