

# Anthemideae

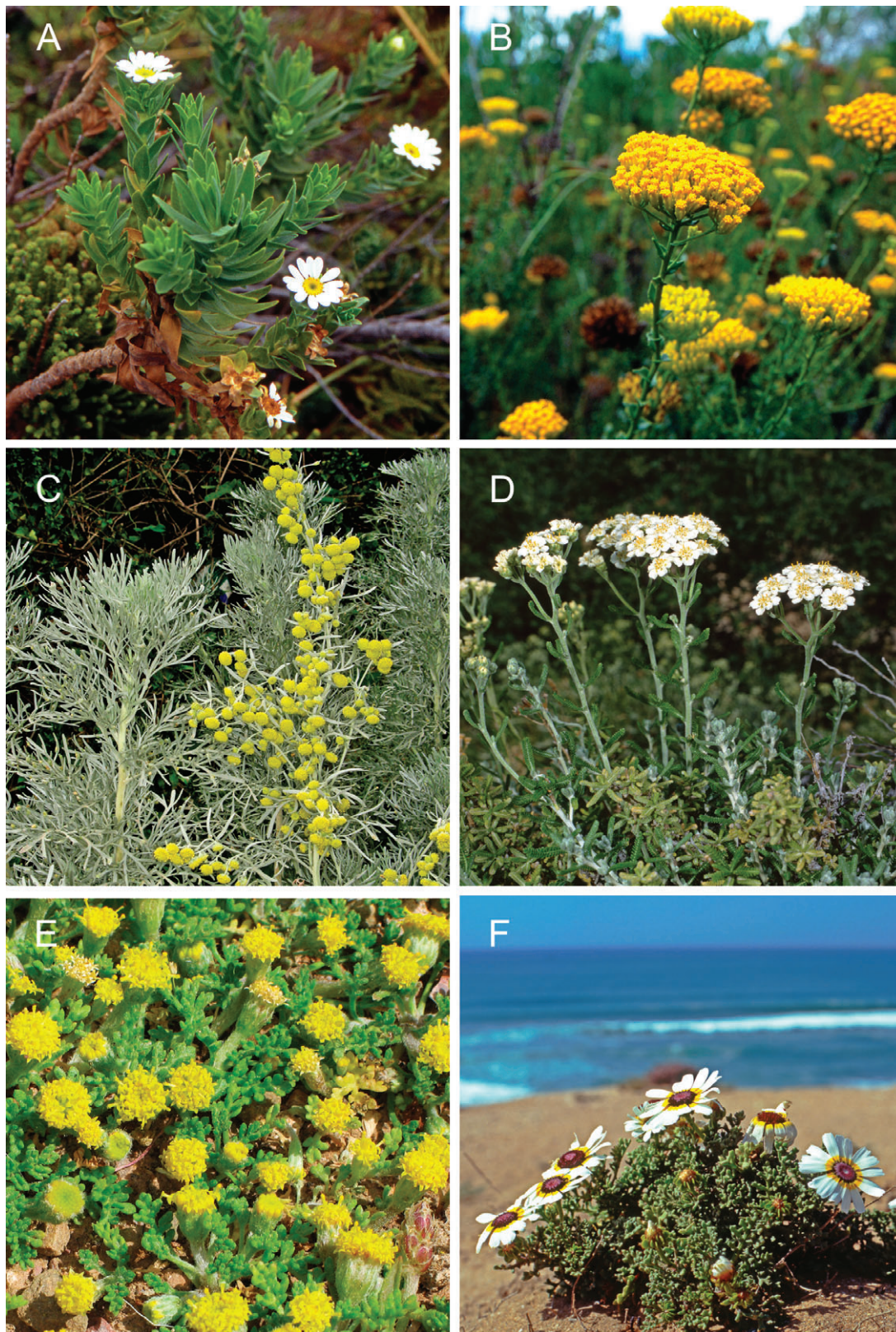
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## HISTORICAL OVERVIEW

According to the most recent generic conspectus of Compositae tribe Anthemideae (Oberprieler et al. 2007a), the tribe consists of 111 genera and ca. 1800 species. The main concentrations of members of Anthemideae are in Central Asia, the Mediterranean region, and southern Africa. Members of the tribe are well known as aromatic plants, and some are utilized for their pharmaceutical and/or pesticidal value (Fig. 38.1).

The tribe Anthemideae was first described by Cassini (1819: 192) as his eleventh tribe of Compositae. In a later publication (Cassini 1823) he divided the tribe into two major groups: “Anthémidéés–Chrysanthémées” and “Anthémidéés–Prototypes”, based on the absence vs. presence of paleae (receptacular scales). These two subtribes, later validly named Chrysantheminae Less. and Anthemidinae Dumort., were used by most systematists concerned with the infratribal taxonomy in the following decades (e.g., Candolle 1838; Boissier 1875; Hoffmann 1890–1894). The artificiality of this subdivision was clearly stated by Merxmüller (1954) and Wagenitz (1964), and demonstrated by Greuter (1968) when he found that in *Ammanthus*, previously classified as Chrysantheminae, the presence or absence of paleae “does not even suffice to distinguish species”. Hybridization experiments among members of Anthemideae made by Mitsuoka and Ehrendorfer (1972) have shown that the inheritance of paleae is probably under simple oligogenic control.

The circumscription of Anthemideae remained relatively unchanged since the early artificial classification systems of Lessing (1832), Hoffmann (1890–1894), and Bentham (1873), and also in more recent ones (e.g., Reitsebrecht 1974; Heywood and Humphries 1977; Bremer and Humphries 1993), with *Cotula* and *Ursinia* being included in the tribe despite extensive debate (Bentham 1873; Robinson and Brettell 1973; Heywood and Humphries 1977; Jeffrey 1978; Gadek et al. 1989; Bruhl and Quinn 1990, 1991; Bremer and Humphries 1993; Kim and Jansen 1995). Subtribal classification, however, has created considerable difficulties throughout the taxonomic history of the tribe. Owing to the artificiality of a subtribal classification based on the presence vs. absence of paleae, numerous attempts have been made to develop a more satisfactory taxonomy for the tribe. In this endeavour, carpological characters proved to be the most important source of phylogenetically relevant features. Despite some early findings on the relevance of carpological characters in delimitating natural genera (e.g., Schultz 1844, 1860; and in Schnitzlein 1854), the full merit for the exploitation of achene anatomy for taxonomic questions in Anthemideae is attributed to J. Briquet who used characters of the pericarp to circumscribe Mediterranean genera in the tribe (Briquet 1916a–c; Briquet and Cavillier 1916). In the following decades, detailed carpological studies have been made in the so-called “*Chrysanthemum* complex” (Giroux 1930, 1933; Horvatic 1963; Borgen 1972; Alavi 1976; Humphries 1976), the *Anthemis* complex (Humphries 1977; Benedí i González and Molero i Briones 1985), and in a more geographically



**Fig. 38.1.** Representative members of Anthemideae. **A** *Osmitopsis asteriscoides* (P. Bergius) Less.; **B** *Athanasia dentata* (L.) L.; **C** *Artemisia arborescens* (Vaill.) L.; **D** *Achillea cretica* L.; **E** *Anthemis rigida* Heldr.; **F** *Ismelia carinata* (Schousb.) Sch.Bip. [Photographs: A, B, Ch. Oberprieler; C–F, P. Schönfelder.]



focused study by Kynčlová (1970). The carpological survey of Reitbrecht (1974) deserves consideration as the first comprehensive tribal evaluation of achene anatomical features for the elaboration of a more natural subtribal classification, utilizing as many genera with suitable study material as possible but with a clear focus on the northern hemisphere representatives of the tribe. The latter study yielded a subdivision into seven provisional groups which were also accepted for the (informal) subtribal treatment of Anthemideae in Heywood and Humphries (1977). Triggered by these surveys, studies of achene anatomy in the following decades contributed to a better understanding of the taxonomy and phylogenetic classification of southern hemisphere genera: Källersjö (1985, 1988) used mainly carpological characters for generic circumscriptions in the *Athanasia* and *Pentzia* complexes, respectively, while Bruhl and Quinn (1990) added fruit anatomical evidence for the exclusion of several genera of “Cotuleae” from Anthemideae and the retention of *Cotula*, *Leptinella*, *Nananthea*, and *Soliva* in the tribe.

The tribe was monographed and a subtribal classification with twelve subtribes was proposed by Bremer and Humphries (1993) based on a mostly morphological phylogenetic study. However, the proposed classification showed little congruence with any of the previous classifications and with molecular phylogenies for the whole tribe (Watson et al. 2000), for the Mediterranean genera alone (Francisco-Ortega et al. 1997, Oberprieler and Vogt 2000, Oberprieler 2002, 2004a, b, 2005), or for Asian genera (Watson et al. 2002). As a consequence of these findings, Oberprieler et al. (2007a) rejected the subtribal classification of Bremer and Humphries (1993) in their recent treatment of Anthemideae in Kubitzki's *The Families and Genera of Vascular Plants*, volume 8, *Asterales* (Kadereit and Jeffrey 2007) and arranged the genera in a linear manner according to the results of Watson et al. (2000), i.e., in a primarily geographic representation of the tribe members beginning with the (basal) southern African representatives, followed by the central and eastern Asian ones, and ending with the Eurasian/Mediterranean genera; within these major biogeographical groups, genera were arranged alphabetically and/or into putative monophyletic generic groups. In the present treatment, we adopted a new subtribal classification proposed recently by Oberprieler et al. (2007b) based on phylogenetic analyses of nrDNA ITS and cpDNA *ndhF* sequence variation.

## PHYLOGENY

Reconstructions of the evolutionary history of Anthemideae presented and discussed here are based on two molecular datasets: The first comprises sequence information for cpDNA *ndhF* for 62 representatives of 61 genera of

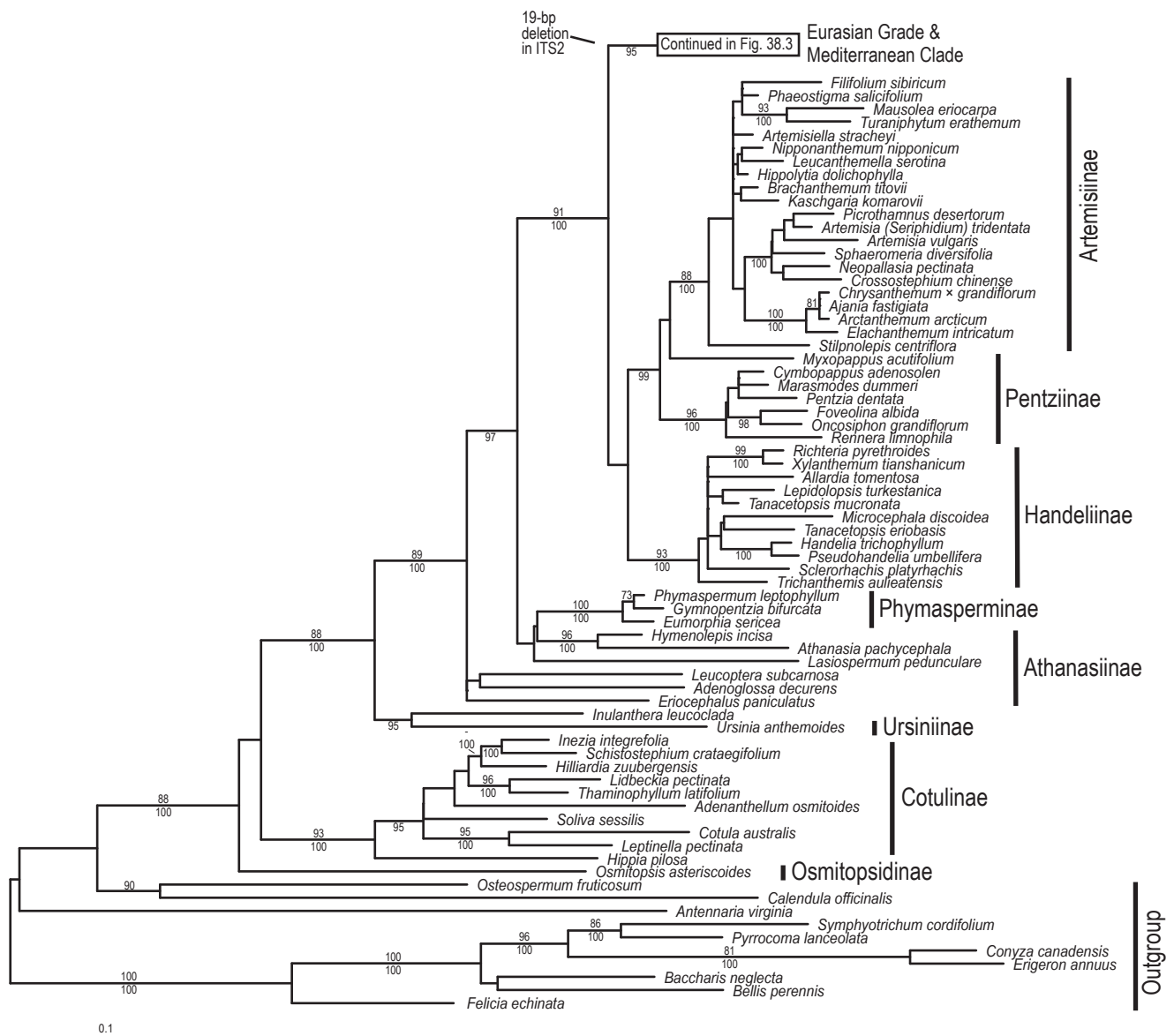
the tribe (Himmelreich et al. 2008), while the second is more complete and provides sequence information for the nrDNA ITS marker for 103 of the 111 accepted genera (Oberprieler et al. 2007b). Both datasets were analyzed using maximum parsimony (MP), maximum likelihood (ML), and Bayesian Inference (BI) as tree-constructing tools and representatives of tribes Astereae, Calenduleae, Gnaphalieae, and (in the case of *ndhF*) Inuleae as outgroups. The resulting tree topologies of the ML analyses are depicted in Figs. 38.2–38.4, along with support values from bootstrap (BS) analyses (MP and ML in the *ndhF* dataset, MP in the ITS dataset) and with posterior probabilities (PP) of the BI analyses.

Despite some minor incongruence between the phylogenetic reconstructions based on the two markers (that will be discussed in detail below), there are a seven features supported by both analyses:

1. The tribe Anthemideae in the circumscription of Bremer and Humphries (1993) and Oberprieler et al. (2007a) is strongly supported as monophyletic in both analyses (*ndhF*: BS: 87% MP, 90% ML; PP: 1.00; ITS: BS: 88% MP; PP: 1.00). Therefore, it is now clear that the tribe includes the genera *Cotula* and *Ursinia* for which a classification as independent tribes has been previously debated (Bentham 1873; Robinson and Brettell 1973; Heywood and Humphries 1977; Jeffrey 1978; Gadek et al. 1989; Bruhl and Quinn 1990, 1991; Bremer and Humphries 1993; Kim and Jansen 1995).
2. Both datasets are congruent with each other in the basal split within the tribe into three independent monophyletic lineages: (a) the isolated position of the genus *Osmitopsis* from southern Africa (i.e., subtribe Osmitopsidinae), (b) the well supported clade around *Cotula* (i.e., subtribe Cotulinae) with members showing their distributional range in southern Africa and/or the southern hemisphere (*ndhF*: BS: 100% MP, 100% ML; PP: 1.00; ITS: BS: 93% MP; PP: 1.00); and (c) the well supported clade comprising the rest of the tribe with further southern African genera and all Asian and Eurasian/Mediterranean representatives (*ndhF*: BS: 91% MP; PP: 1.00; ITS: BS: 88% MP; PP: 1.00).
3. A further common feature of phylogenetic trees based on both markers is a paraphyletic assemblage of southern African genera around the two genera *Athanasia* and *Ursinia* (i.e., subtribes Athanasiinae and Ursiniinae) at the base of the above-described clade (c) as opposed to the strongly supported monophyletic group (*ndhF*: BS: 90% MP, 91% ML; PP: 1.00; ITS: BS: 91% MP; PP: 1.00) comprising all northern hemisphere representatives and a closely-knit, southern African generic group around *Pentzia* (i.e., subtribe Pentziinae, see below). This is also where

the main discrepancies are found between the two datasets: in the *ndhF* analyses the clade of *Eumorphia*, *Gymnopentzia*, and *Phymaspermum* (i.e., subtribe Phymasperminae) is nested within members of the Pentziinae/northern hemisphere clade, whereas in the ITS analyses these three genera are excluded from the latter clade and form a lineage in the paraphyletic assemblage around *Athanasia* and *Ursinia*. Himmelreich et al. (2008) provide two possible explanations for

this incongruence between nuclear and plastid dataset: (a) The progenitor of Phymasperminae may have been formed by a hybridization event between a member of the phylogenetically basal southern African group of genera as a paternal partner and either a member of the Asian groups around *Artemisia*, *Microcephala*, or *Pseudohandelia* or a member of southern African Pentziinae as the maternal (chloroplast contributing) partner, whereby the latter event seems

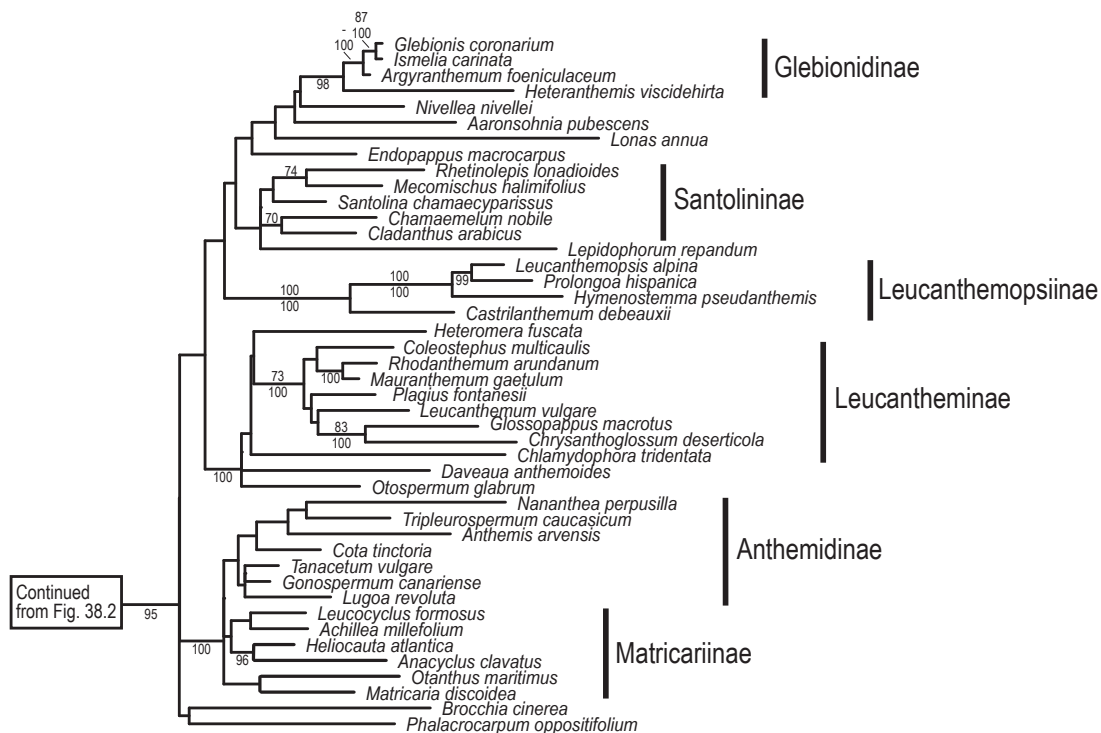


**Fig. 38.2.** Basal part of a phylogenetic tree from a maximum-likelihood (ML) analysis of nrDNA ITS sequence variation data based on the TrN +  $\Gamma$  model of DNA substitution (Tamura and Nei 1993) with base frequencies, gamma distribution parameter  $\alpha$ , and substitution rate matrix given in Oberprieler et al. (2007b). Values above branches indicate bootstrap support values from a maximum-parsimony (MP) analysis based on 100 replicates and values below branches give posterior probability (PP in percent) of clades gained from a Bayesian analysis (BI) of data.

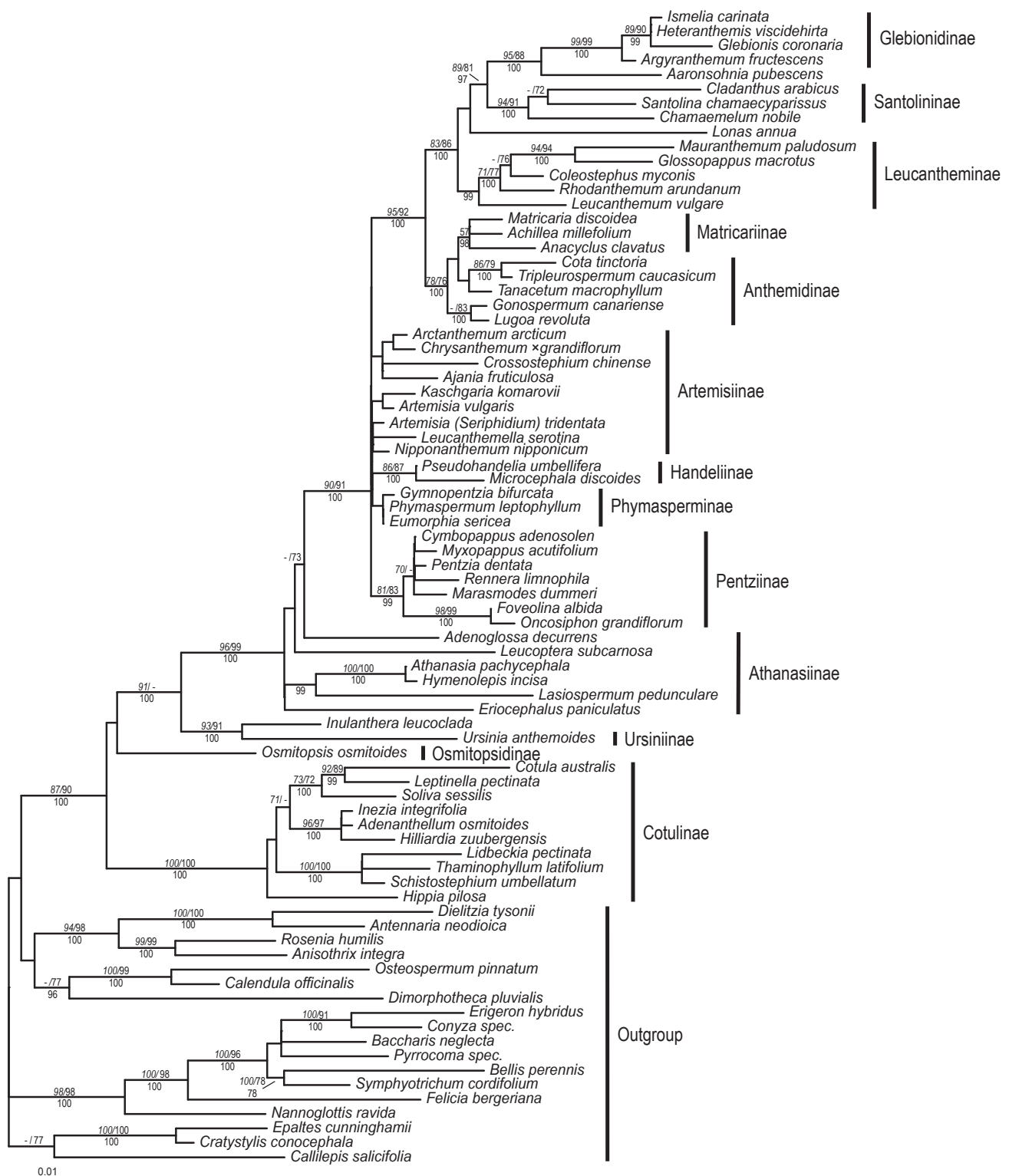
- geographically more reasonable. (b) Phymasperminae may hold a phylogenetically intermediate and bridging position between the more basal southern African members of the tribe and the more advanced crown group consisting of Pentziinae and all Asian and Eurasian Anthemideae, sharing the rather apomorphic chloroplast type with the latter but a relatively plesiomorphic ITS sequence with the former. As a consequence of this scenario, Phymasperminae may be a good candidate for the sister group to the clade of Pentziinae + Asian + Eurasian Anthemideae, while Pentziinae itself may exhibit a sister group-relationship to the Asian (or the Asian + Eurasian) members of the tribe.
- Besides monophyletic Phymasperminae (no significant support for *ndhF*, but for ITS: BS: 100% MP; PP: 1.00) and Pentziinae (*ndhF*: BS: 81% MP, 83% ML; PP: 0.99; ITS: BS: 96% MP; PP: 1.00, excluding *Myxopappus*), there is also support for two generic assemblages with an Asian center of diversity. While the clade around *Handelia* (i.e., subtribe Handeliinae) receives high support values in analyses of both markers (*ndhF*: BS: 86% MP, 87% ML; PP: 1.00; ITS: BS: 93% MP; PP: 1.00), subtribe Artemisiinae is only

supported by the reconstructions based on ITS (BS: 88% MP; PP: 1.00).

- A further corresponding topological feature of all analyses is the strongly supported clade of Eurasian and Mediterranean genera comprising subtribes Anthemidinae, Glebionidinae, Leucantheminae, Leucanthemopsidinae, Matricariinae, and Santolininae. In addition to the high support values from the different sequence-based analyses (*ndhF*: BS: 95% MP, 92% ML; PP: 1.00; ITS: PP: 0.95), the monophyly of this generic assemblage is further corroborated by the synapomorphy of a 19-bp deletion in ITS2 found in all of the members of the clade.
- Within the Eurasian + Mediterranean clade, corresponding topological features are (a) the sister group relationship between generic groups around *Anthemis* (i.e., subtribe Anthemidinae) and *Matricaria* (i.e., subtribe Matricariinae) (*ndhF*: BS: 78% MP, 76% ML; PP: 1.00; ITS: PP: 1.00) and (b) the monophyletic group formed by members of Glebionidinae, Leucantheminae and Santolininae. The latter, however, is only supported by *ndhF*-based analyses (BS: 83% MP, 86% ML; PP: 1.00). According to the ITS-based analyses, the generic assemblage around *Leucanthemopsis* (i.e.,



**Fig. 38.3.** Apical part of a phylogenetic tree from a maximum-likelihood (ML) analysis of nrDNA ITS sequence variation data based on the TrN +  $\Gamma$  model of DNA substitution (Tamura and Nei 1993) with base frequencies, gamma distribution parameter  $\alpha$ , and substitution rate matrix given in Oberprieler et al. (2007b). Values above branches indicate bootstrap support values from a maximum-parsimony (MP) analysis based on 100 replicates, and values below branches give posterior probability (PP) in percent) of clades gained from a Bayesian analysis (BI) of data.



**Fig. 38.4.** Phylogenetic tree from a maximum-likelihood (ML) analysis based on cpDNA *ndhF* sequence information. Numbers above the lines are bootstrap values of the MP and ML analyses; numbers below the lines are posterior probabilities of the Bayesian inference (BI) approach (adapted from Himmelreich et al. 2008).

subtribe Leucanthemopsidinae), that shows strong support (BS: 100% MP; PP: 1.00) as a monophyletic group, may also belong to this clade, but there is evidence that the latter subtribe may be more basal within the Eurasian + Mediterranean clade. In previous analyses based on the cpDNA *trnL-trnF* intergenic spacer, Oberprieler and Vogt (2000) observed that members of Glebionidinae, Leucanthemeinae and Santolininae share an apomorphic 5 bp deletion while members of Anthemidinae, Matricariinae and Leucanthemopsidinae show the plesiomorphic condition.

7. Both datasets in the present study unequivocally show a clear biogeographic pattern with a basal position of southern hemisphere representatives of the tribe. This is in accordance with previous studies based on *ndhF* sequence variation (Watson et al. 2000; Himmelreich et al. 2008) and on ITS sequences (Oberprieler 2005).

### SUBTRIBAL TAXONOMY

Based on our analyses of ITS and *ndhF* sequence variation, Oberprieler et al. (2007b) proposed a new subtribal classification of Compositae-Anthemideae. Discussion of the molecular phylogenetic analyses in conjunction with morphological, anatomical, cytological, embryological, and phytochemical evidence resulted in the recognition of 14 subtribes. Table 38.1 provides information about the subtribal placement of most genera, although some genera are missing or have equivocal molecular evidence. Following their biogeographical pattern in the phylogenetic reconstructions, the subtribes are arranged into (1) a southern hemisphere grade, (2) an Asian-southern African grade, (3) an Eurasian grade, and (4) a Mediterranean clade.

#### I. Southern hemisphere grade

**Osmitopsidinae** Oberprieler & Himmelreich in Willdenowia 37: 94. 2007

The subtribe consists of the single genus, *Osmitopsis*, that holds a basal and isolated position in the molecular analyses of ITS and *ndhF* sequence variation. It contains nine southern African species of shrubby habit with alternate and entire to lobed leaves and an indumentum of basifixed hairs. It is further characterized by radiate capitula with a paleate receptacle, ray florets with a white, many-veined limb and a pilose tube, and disc florets with a 5-lobed corolla, basally caudate anthers with non-polarized endothelial tissue and a slender filament collar. The achenes are obovoid to ellipsoid, 3–4-angled or -ribbed, and have an apex with a corona made of subulate to triangular, basally fused scales that is sometimes lacking.

The main characteristic of *Osmitopsis* is its possession of tailed anthers that led some authors (Bentham 1873; Hoffmann 1890–1894) to consider an inulean affiliation for the genus, whereas others (e.g., Cassini 1823) included it in their concept of Anthemideae. Palynological evidence (Stix 1960) and additional characters like odor, the occurrence of pluriseriate involucre bracts with scarious margins, together with the truncate style and the tendency towards the reduction of the pappus also support its inclusion in Anthemideae. This membership is also strongly supported by our present analyses based on ITS and *ndhF* sequence data.

While membership in Anthemideae is supported in both analyses, its relationship to either of the two highly supported subclades of the tribe (subtribe Cotulinae on the one hand and the remainder of the tribe on the other) remains unresolved. This corroborates observations made by Bremer (1972) and Nordenstam (1987) who already noted that the genus is systematically isolated in the tribe. The inclusion of the paleate genus *Osmitopsis* in the subtribe Thaminophyllinae by Bremer and Humphries (1993), together with the alleged closely related (epaleate) genera, *Adenanthellum*, *Inezia*, *Lidbeckia*, and *Thaminophyllum*, was mainly based on a similar habit and foliage, the occurrence of many-veined rays and a large stylopodium, the tendency towards the loss of a pappus in some species, and the (still not yet fully corroborated) base chromosome number of  $x = 10$ . Alternative affiliations were proposed by Reitbrecht (1974) and Baagøe (1977) who considered closer relationships of the genus to *Lasiospermum* (paleate,  $x = 9$ ) based on morphological and ligule micromorphological grounds, respectively, and by Watson et al. (2000) who found a strongly supported sister group relationship of *Osmitopsis* with *Athanasia* (paleate,  $x = 8$ ) in their molecular study based on *ndhF* sequence variation. Since both *Lasiospermum* and *Athanasia* are characterized, however, by deviating base chromosome numbers and anthers with polarized endothelial tissue (unpolarized in *Osmitopsis*), these alleged relationships seem unjustified. The same is true for any relationship with other genera of Anthemideae characterized by tailed anthers: neither *Inulanthera* nor *Hippolytia* are confirmed by our present analyses as closely related to *Osmitopsis*.

**Cotulinae** Kitt., Taschenb. Fl. Deutschl., ed. 2, 2: 609.

1844 = Thaminophyllinae Bremer & Humphries in Bull. Nat. Hist. Mus. Lond. (Bot.) 23: 144. 1993

Cotulinae are formed by ten genera with approximately 137 species of the southern hemisphere with its center of diversity in southern Africa but also distributed and species-rich in Australia, New Guinea and New Zealand, and some species widespread and naturalized also in the northern hemisphere. While strongly supported as a monophyletic group in our molecular phylogenetic



**Table 38.1.** List of accepted genera of Compositae-Anthemideae, with information on number of species, distributional area, and subtribal relationships.

	Number of species	Distribution
<b>I. SOUTHERN HEMISPHERE GRADE</b>		
<b>1. Osmitopsidinae</b> Oberprieler & Himmelreich		
<i>Osmitopsis</i> Cass.	9	South Africa
<b>2. Cotulinae</b> Kitt.		
<i>Adenanthellum</i> B. Nord.	1	South Africa, Swaziland
<i>Cotula</i> L.	55	Africa, Australia, South America, Mexico, New Zealand, southern oceanic islands
<i>Hilliardia</i> B. Nord.	1	South Africa
<i>Hippia</i> L.	8	South Africa
<i>Inezia</i> E. Phillips	2	South Africa, Swaziland
<i>Leptinella</i> Cass.	33	New Guinea, Australia, New Zealand, South America, Falkland Islands, subarctic islands
<i>Lidbeckia</i> P.J. Bergius	2	South Africa
<i>Schistostephium</i> Less.	12	South Africa, Mozambique, Zimbabwe, Swaziland
<i>Soliva</i> Ruiz & Pav.	8	South America
<i>Thaminophyllum</i> Harv.	3	South Africa
<b>3. Ursiniinae</b> Bremer & Humphries		
<i>Ursinia</i> Gaertn.	39	South Africa, Namibia, Botswana, Ethiopia
<b>4. Athanasiinae</b> (Less.) Lindl. ex Pfeiff.		
<i>Adenoglossa</i> B. Nord.	1	South Africa
<i>Athanasia</i> L.	39	South Africa, Namibia
<i>Eriocephalus</i> L.	32	South Africa, Namibia, Botswana, Lesotho
<i>Hymenolepis</i> Cass.	7	South Africa
<i>Lasiospermum</i> Lag.	4	South Africa, Namibia, Lesotho, Egypt (Sinai)
<i>Leucoptera</i> B. Nord.	3	South Africa
<b>5. Phymaspermatae</b> Oberprieler & Himmelreich		
<i>Eumorphia</i> DC.	6	South Africa, Lesotho, Swaziland
<i>Gymnopentzia</i> Benth.	1	South Africa, Lesotho
<i>Phymaspermum</i> Less.	19	South Africa, Swaziland, Zimbabwe, Namibia
<b>Genera of the Southern hemisphere grade unassigned to a subtribe</b>		
<i>Inulanthera</i> Källersjö <sup>a</sup>	10	South Africa, Swaziland, Lesotho, Angola, Zimbabwe, Madagascar
<b>II. ASIAN-SOUTH AFRICAN GRADE</b>		
<b>6. Pentziinae</b> Oberprieler & Himmelreich		
<i>Cymbopappus</i> B. Nord.	3	South Africa
<i>Foveolina</i> Källersjö	5	South Africa, Namibia
<i>Marasmodes</i> DC.	4	South Africa
<i>Myxopappus</i> Källersjö	2	South Africa, Namibia
<i>Oncosiphon</i> Källersjö	8	South Africa, Lesotho, Namibia



Table 38.1. Continued.

	Number of species	Distribution
<i>Pentzia</i> Thunb.	23	South Africa, Namibia, Morocco, Algeria, Chad, Somalia, Yemen
<i>Rennera</i> Merxm.	4	Namibia, South Africa, Botswana
<b>7. Handeliinae</b> Bremer & Humphries		
<i>Allardia</i> Decne.	8	Afghanistan, Central Asia, Mongolia, China
<i>Handelia</i> Heimerl	1	Afghanistan, Pakistan, Central Asia, China
<i>Lepidolopsis</i> Poljakov	1	Iran, Afghanistan, Central Asia
<i>Microcephala</i> Pobed.	5	Central Asia, Afghanistan, Iran, Pakistan, Mongolia, China
<i>Pseudohandelia</i> Tzvelev	1	Iran, Afghanistan, Central Asia, China
<i>Richteria</i> Kar. & Kir.	6	Iran, Afghanistan, Central Asia, Mongolia, China, Himalaya
<i>Sclerorhachis</i> (Rech. f.) Rech. f.	4	Iran, Afghanistan
<i>Tanacetopsis</i> (Tzvelev) Kovalevsk.	21	Iran, Afghanistan, Central Asia
<i>Trichanthemis</i> Regel & Schmalh.	9	Central Asia
<i>Xylanthemum</i> Tzvelev	8	Iran, Afghanistan, Central Asia
<b>8. Artemisiinae</b> Less.		
<i>Ajania</i> Poljakov	39	Central Asia, China, Japan
<i>Arctanthemum</i> (Tzvelev) Tzvelev	3	Arctic Eurasia, Siberia, Japan, Arctic North America
<i>Artemisia</i> L. (incl. <i>Seriphidium</i> Fourr.)	522	Northern hemisphere, South America, South Africa, Pacific Islands
<i>Crossostephium</i> Less.	1	Philippines, Taiwan, South Japan, China
<i>Filifolium</i> Kitam.	1	Siberia, Mongolia, China, Korea
<i>Mausolea</i> Poljakov	1	Iran, Afghanistan, Central Asia
<i>Neopallasia</i> Poljakov	3	Central Asia, South Siberia, Mongolia, China
<i>Picrothamnus</i> Nutt.	1	North America
<i>Sphaeromeria</i> Nutt.	9	North America, Mexico
<i>Turaniphytum</i> Poljakov	2	Turkmenistan, Iran, Afghanistan, Kazakhstan
<i>Artemisiella</i> Ghaffoor	1	Ladakh, Tibet, Nepal, Bhutan, South China
<i>Brachanthemum</i> DC.	10	Central Asia, Mongolia, China
<i>Chrysanthemum</i> L.	37	Asia (Mongolia, Russia, China, Japan, Korea), East Europe
<i>Elachanthemum</i> Y. Ling & Y.R. Ling	1	Mongolia, China
<i>Hippolytia</i> Poljakov	19	Central Asia, Mongolia, China, Himalaya
<i>Kaschgaria</i> Poljakov	2	Mongolia, Kazakhstan, China
<i>Leucanthemella</i> Tzvelev	2	East Europe, Far East (Mongolia, China, Korea, Japan)
<i>Nipponanthemum</i> Kitam.	1	Japan
<i>Phaeostigma</i> Muldashev	3	China
<i>Stilpnolepis</i> Krasch.	1	Mongolia, China
<b>Genera of the Asian-South African grade unassigned to a subtribe</b>		
<i>Ajaniopsis</i> C. Shih <sup>b</sup>	1	China, Tibet
<i>Cancrinia</i> Kar. & Kir. <sup>c</sup>	4	Central Asia, Mongolia, China
<i>Cancriniella</i> Tzvelev <sup>c</sup>	1	Central Asia

Table 38.1. Continued.

	Number of species	Distribution
<i>Hulteniella</i> Tzvelev <sup>b</sup>	1	Arctic Eurasia, Arctic North America
<i>Lepidolopha</i> C. Winkl. <sup>c</sup>	9	Central Asia
<i>Opisthopappus</i> C. Shih <sup>b</sup>	2	China
<i>Polychrysum</i> (Tzvelev) Kovalevsk. <sup>c</sup>	1	Afghanistan, Central Asia
<i>Tridactylina</i> (DC.) Sch.Bip. <sup>b</sup>	1	East Siberia
<i>Ugamia</i> Pavlov <sup>c</sup>	1	Central Asia
<b>III. EURASIAN GRADE</b>		
<b>9. Matricariinae</b> Willk.		
<i>Achillea</i> L.	115	Europe, Asia, North Africa, North America
<i>Leucocyclus</i> Boiss.	1	Turkey
<i>Otanthus</i> Hoffmanns. & Link	1	South Europe, North Africa, Southwest Asia
<i>Anacyclus</i> L.	12	South Europe, North Africa, Southwest Asia
<i>Heliocauta</i> Humphries	1	Morocco
<i>Matricaria</i> L.	6	Europe, North Africa, Asia, North America
<b>10. Anthemidinae</b> (Cass.) Dumort.		
<i>Anthemis</i> L.	175	Europe, Southwest Asia, North and East Africa
<i>Cota</i> J. Gay	40	Europe, Southwest Asia, North Africa
<i>Nananthea</i> DC.	1	South Europe (Corsica, Sardinia)
<i>Tanacetum</i> L.	154	Europe, Asia, North Africa, North America
<i>Gonospermum</i> Less.	4	Canary Islands
<i>Lugoa</i> DC.	1	Canary Islands
<i>Tripleurospermum</i> Sch.Bip.	40	Europe, North Africa, Asia, North America
<b>11. Leucanthemopsidinae</b> Oberprieler & Vogt		
<i>Castrilanthemum</i> Vogt & Oberprieler	1	Spain
<i>Hymenostemma</i> Willk.	1	Spain
<i>Leucanthemopsis</i> (Giroux) Heywood	9	Europe, Northwest Africa
<i>Prolongoa</i> Boiss.	1	Spain
<b>Genera of the Eurasian grade unassigned to a subtribe</b>		
<i>Brocchia</i> Vis. <sup>d</sup>	1	North Africa, Southwest Asia
<i>Phalacrocarpum</i> (DC.) Willk. <sup>e</sup>	2	Southwest Europe
<b>IV. MEDITERRANEAN CLADE</b>		
<b>12. Leucantheminae</b> Bremer & Humphries		
<i>Chlamydophora</i> Ehrenb. ex Less.	1	North Africa, Cyprus
<i>Chrysanthoglossum</i> B.H. Wilcox & al.	2	North Africa
<i>Coleostephus</i> Cass.	3	Mediterranean region, Macaronesia
<i>Glossopappus</i> Kunze	1	Southwest Europe, North Africa
<i>Leucanthemum</i> Mill.	43	Europe, Siberia
<i>Mauranthemum</i> Vogt & Oberprieler	4	North Africa, Southwest Europe

Table 38.1. Continued.

	Number of species	Distribution
<i>Plagiurus</i> L'Hér. ex DC.	3	South Europe (Corsica, Sardinia), North Africa
<i>Rhodanthemum</i> (Vogt) B.H. Wilcox & al.	14	Northwest Africa, Southwest Europe
<b>13. Santolininae</b> Willk.		
<i>Chamaemelum</i> Mill.	2	South and West Europe, Northwest Africa
<i>Cladanthus</i> Cass.	5	South Europe, North Africa, Southwest Asia
<i>Mecomischus</i> Coss. ex Benth. & Hook. f.	2	Northwest Africa
<i>Rhetinolepis</i> Coss.	1	Northwest Africa
<i>Santolina</i> L.	13	South Europe, Northwest Africa
<b>14. Glebionidinae</b> Oberprieler & Vogt		
<i>Argyranthemum</i> Webb	24	Macaronesia
<i>Glebionis</i> Cass.	2	South Europe, North Africa, Northwest Asia, Macaronesia
<i>Heteranthemis</i> Schott	1	Northwest Africa
<i>Ismelia</i> Cass.	1	Northwest Africa
<b>Genera of the Mediterranean clade unassigned to a subtribe</b>		
<i>Aaronsohnia</i> Warb. & Eig	2	North Africa, Southwest Asia
<i>Daveaua</i> Willk. ex Mariz <sup>f</sup>	1	Northwest Africa, Southwest Europe
<i>Endopappus</i> Sch.Bip.	1	North Africa
<i>Heteromera</i> Pomel <sup>f</sup>	2	North Africa
<i>Lepidophorum</i> Neck. ex DC.	1	Southwest Europe
<i>Lonas</i> Adans.	1	North Africa, South Europe
<i>Nivellea</i> B.H. Wilcox & al.	1	Morocco
<i>Otospermum</i> Willk. <sup>f</sup>	1	North Africa, Southwest Europe

<sup>a</sup> Suggested placement in Ursiniinae, <sup>b</sup> Artemisiinae, <sup>c</sup> Handeliinae, <sup>d</sup> Matricariinae, <sup>e</sup> Leucanthemopsidinae, <sup>f</sup> Leucantheminae.

reconstructions, the subtribe is morphologically diverse and consists of members of subtribes Matricariinae (*Cotula*, *Hilliardia*, *Hippia*, *Leptinella*, *Schistostephium*, *Soliva*) and Thaminophyllinae (*Adenanthellum*, *Inezia*, *Lidbeckia*, *Thaminophyllum*) in the sense of Bremer and Humphries (1993).

In the present circumscription, the subtribe contains mainly shrubs and perennial herbs (with annuals occurring in *Cotula*, *Leptinella*, and *Soliva*) with a plesiomorphic, basifixed indumentum. The capitula, which are arranged solitarily or in lax to dense corymbs, are radiate, disciform, or discoid. The receptacle is usually epaleate, but sometimes hairy (*Lidbeckia*, *Thaminophyllum*) or marginally paleate (*Schistostephium*). The ray florets (when present) are either white or yellow, and in *Adenanthellum*, *Inezia*, and *Thaminophyllum* confluent with the achene. In *Cotula* the ray florets or marginal female disc florets are stalked.

The disc florets are usually hermaphroditic or functionally male in *Hippia*, *Leptinella*, *Schistostephium*, and *Soliva* with a 3–4- or sometimes 5-lobed (*Adenanthellum*, *Hippia*) corolla, and anthers with non-polarized endothelial tissue and a slender filament collar. The achenes of Cotulinae are highly polymorphic, with a tendency towards the reduction of rib number from 3–4 (as in *Osmitopsis* of the Osmitopsidinae) towards 2, and the transition between terete to dorso-ventrally flattened cross-sections. As an exception to this, 10-ribbed and only slightly compressed achenes are observed in *Adenanthellum*. The subtribe shows the presumably plesiomorphic base chromosome number of  $x = 10$  (with descending dysploidy in *Cotula* [ $x = 8, 9, 10$ ] but ascending dysploidy in the closely related genus *Leptinella* [ $x = 13$ ]). The monophyly of this subtribe suggested by our molecular results may be corroborated in morphological respects by the apomorphies of epaleate

receptacles and 4-lobed corollas of tubular florets (with exceptions to this in *Adenanthellum* and *Hippia*).

Evidence for the unification of members of Bremer and Humphries's (1993) two subtribes into a single subtribe was suggested by Nordenstam (1987) when describing the new genus *Hilliardia* (Matricariinae in the sense of Bremer and Humphries 1993) and connecting it with *Adenanthellum* and *Inezia* (Thaminophyllinae). These genera possess ray florets with a bifid or emarginated limb, a branching venation, a papillate upper surface, a reduced tube, and large sessile glands. Additionally, there is further support from phytochemical investigations made by Bohlmann and Zdero (1972a, 1974, 1977, 1982) who found that the guaianolide called zuobergenin from *Hilliardia* is closely related to guaianolides that have been found in *Lidbeckia* and *Inezia* (both Thaminophyllinae), and that *Thaminophyllum* is phytochemically related to *Schistostephium* (sub *Peyrousea*, Matricariinae).

**Ursiniinae** Bremer & Humphries in Bull. Nat. Hist. Mus. Lond. (Bot.) 23: 91. 1993

Ursiniinae in the sense of Bremer and Humphries (1993), comprising the genera *Athanasia* (including *Asaemia*), *Eumorphia*, *Gymnopentzia*, *Hymenolepis*, *Lasiospermum*, *Phymaspermum*, and *Ursinia*, are not supported as monophyletic in our molecular phylogenetic reconstructions where we observe a deep split between *Ursinia* on the one hand and the remainder of the mentioned genera on the other hand. The circumscription of Ursiniinae in the sense of Bremer and Humphries (1993) was based mainly on phytochemical evidence, with a number of publications made by Bohlmann and co-workers (Bohlmann and Rao 1972; Bohlmann and Zdero 1972b, 1974, 1978a, b; Bohlmann et al. 1973; Bohlmann and Grenz 1975) indicating that representatives of these genera possess furanosesquiterpenes rather than the common polyacetylenes. This, in conjunction with morphological and anatomical evidence (paleate receptacles, ray floret limbs with tabular epidermis cells, anthers with partly or totally polarized endothelial tissue) was considered sufficient to suggest the monophyly of the subtribe (Källersjö 1985; Bremer and Humphries 1993), which also included *Ursinia*, a carpologically and palynologically distinct genus. However, due to its anthers with broad ovate apical appendages and baluster-shaped filament collars (Meiri and Dulberger 1986), its pollen exine without columnar structure, and its achenes with a biseriate pappus formed of scales, this genus had been formerly considered to hold a very isolated position within Anthemideae (Cassini 1816; Beauverd 1915), or as an independent tribe Ursinieae (Robinson and Brettell 1973), or even as a member of Arctoteae (Bentham 1873).

Treated here as an independent subtribe, Ursiniinae, with its sole member *Ursinia*, is a mainly southern African subtribe (with one species reaching Ethiopia) of perennial

(sometimes annual) herbs or shrublets characterized by basifixed hairs and alternate, entire to 2-pinnatisect, sometimes succulent leaves, radiate or discoid capitula arranged solitarily or in lax corymbs with a paleate receptacle, yellow, orange, white or reddish ray florets and 5-lobed disc florets with polarized endothelial tissue and a baluster-shaped filament collar. The achenes are cylindrical or obovoid, straight or curved, circular in cross-section, with five ribs and a basal tuft of hairs or glabrous; their apex is furnished with a uniseriate pappus of 5–10 ovate or circular scales, or a biseriate pappus of five outer such scales and five inner subulate ones, or is rarely epappose. The genus shows a descending dysploidy with base chromosome numbers of  $x = 5, 7, 8$ .

Our present molecular phylogenetic reconstructions suggest a close relationship of *Ursinia* with the small, southern African genus *Inulanthera*, which was treated as a member of the polyphyletic subtribe Gonosperminae by Bremer and Humphries (1993). Since *Inulanthera* differs from *Ursinia* morphologically (anthers caudate and with slender filament collar, achenes with a pappus of small scales terminating each of the 8–10 ribs), we have refrained from including it in Ursiniinae to emphasize the isolated phylogenetic position of *Ursinia*. On the other hand, we also consider it premature to erect an independent subtribe for *Inulanthera* due to the apparently clear position of this genus as sister to *Ursinia* in the molecular phylogenetic reconstructions.

**Athansiniinae** (Less.) Lindl. ex Pfeiff., Nomencl. Bot. 1(1): 323. ante 12 Jul 1872

This subtribe is comprised of genera that were formerly classified as members of Matricariinae (*Adenoglossa*, *Eriocephalus*, *Leucoptera*) or Ursiniinae (*Athanasia*, *Hymenolepis*, *Lasiospermum*) sensu Bremer and Humphries (1993). Since the distinction of this group of genera from *Ursinia* is strongly supported, unification under a single subtribe Ursiniinae seems unjustified. However, the assemblage of genera around *Athanasia* is by far the most problematic in our present classification because in the ITS tree (1) the group appears to be paraphyletic with *Adenoglossa*, *Eriocephalus*, and *Leucoptera* being sister group to a well-supported clade of *Athanasia*, *Hymenolepis*, *Lasiospermum* plus Phymasperminae and the Pentziinae–northern hemisphere clade (*Trichanthemum* through *Glebionis*), and (2) Phymasperminae appear to be closely related to *Athanasia*, *Hymenolepis*, and *Lasiospermum*, making Athansiniinae even more paraphyletic. While the former findings are also supported by the analyses based on *ndhF* sequence variation, the three Phymasperminae genera hold a different position in the plastid phylogenetic reconstruction, supporting their treatment as an independent subtribe (see discussion below).

While molecular evidence is (at best) equivocal with respect to the monophyly of Athansiniinae, there is one



morphological character that appears to support a close relationship among these genera: with the exception of *Eriocephalus*, all members of Athanasiinae (together with Phymasperminae) are characterized by the possession of anthers with polarized endothelial tissue. Since this character expression is apomorphic relative to the unpolarized endothecium found in the more basal Cotulinae and Osmitopsidinae, and in the more advanced subtribes, this morphological evidence may argue for a monophyly of the subtribe (and, as a consequence, the inclusion of Phymasperminae).

As circumscribed here, Athanasiinae are comprised of six mainly southern African genera with approximately 86 species (only one *Lasiospermum* species reaching the northern hemisphere). The plants are mainly shrubs or shrublets, but rarely also perennial and annual herbs (*Adenoglossa*, *Lasiospermum*). They are characterized by alternate or opposite, entire to 2-pinnatisect leaves and radiate, disciform or discoid capitula arranged in a solitary fashion or in lax to dense corymbs with a paleate or epaleate (*Adenoglossa*, *Leucoptera*) receptacle, yellow, white or reddish ray florets, and 5-lobed, hermaphroditic (functionally male in *Eriocephalus*) disc florets with anthers with polarized endothelial tissue (unpolarized in *Eriocephalus*) and a slender filament collar. The achenes are cylindrical to obovate, either terete and with 5–12(–18) ribs or dorsiventrally flattened with lateral wings (*Adenoglossa*, *Leucoptera*); their apex is marginally rounded, with a short, thickened rim (*Athanasia*), or furnished with a corona or scales (*Adenoglossa*, *Hymenolepis*, *Leucoptera*); the pericarp is glabrous or densely hairy (*Eriocephalus*, *Lasiospermum*). Base chromosome numbers are  $x = 8, 9$ .

**Phymasperminae** Oberprieler & Himmelreich in Willdenowia 37: 99. 2007

This small subtribe comprises three South African genera with only 26 species. While its monophyly is strongly supported in our phylogenetic analyses based on molecular data, its position in the tribe is rather unclear. Analyses based on ITS show a close relationship to members of Athanasiinae, while analyses based on *ndhF* consistently indicate that Phymasperminae possess a chloroplast type that is more closely related to members of the Pentziinae–northern hemisphere clade than to members of Athanasiinae. Himmelreich et al. (2008) argue that this conflict between results based on nuclear and plastid sequences is either due to a hybrid origin of the ancestor of Phymasperminae (with the plastid donor among members of the Pentziinae–northern hemisphere clade) or may indicate a sister group relationship between Phymasperminae and the Pentziinae–northern hemisphere clade that is unresolved in the ITS trees due to a lack of parallel evolution of the two markers examined.

According to Källersjö (1985) and Bremer and Humphries (1993), the monophyly of the subtribe seen in the molecular phylogenies is also strongly supported by morphology because the three genera share the apomorphies of achenes with 10–12(–18) ribs and a papillose pericarp. The possession of anthers with polarized endothelial tissue indicates a close relationship to Athanasiinae but contrasts markedly with the plastid phylogeny.

Phymasperminae are shrubs or shrublets with basifixed hairs, opposite or alternate, entire to lobed leaves, and radiate or discoid capitula arranged solitarily or in lax corymbs and with epaleate or paleate (*Eumorphia*, occasionally in *Gymnopentzia*) receptacles, white, yellow, or purplish ray florets, and hermaphroditic, 5-lobed disc florets. The achenes are cylindrical or ellipsoid, terete with 10–12(–18) ribs. The apex is truncate or furnished with an entire to dentate, thickened rim or corona. The pericarp is papillose, usually without myxogenic cells or resin sacs, but in *Phymaspermum* with ovoid myxogenic trichomes and resin sacs in some of the ribs.

**II. Asian-South African grade**

**Pentziinae** Oberprieler & Himmelreich in Willdenowia 37: 99. 2007

This strongly supported clade of six genera (with the seventh genus, *Myxopappus*, being included due to *ndhF* support) contains further southern African members of subtribe Matricariinae in the sense of Bremer and Humphries (1993). It forms a close-knit group of genera that is characterized by epaleate receptacles, anthers with unpolarized endothelial tissue and slender filament collars, basifixed hairs (medifixed in *Pentzia*), and a base chromosome number of  $x = 9$  (with descending dysploidy in *Myxopappus*, *Oncosiphon*, and *Pentzia*). It unites genera of shrubby habit (*Cymbopappus*, *Marasmodes*, *Pentzia*) and annuals (*Foveolina*, *Myxopappus*, *Oncosiphon*, *Rennera*) that were all once united under a broad concept of *Pentzia*, which has been dismembered by Källersjö (1988). According to Bremer and Humphries (1993), this group may be supported as monophyletic by achenes with myxogenic cells on the abaxial surface and on the ribs of the adaxial surface (with exceptions in *Oncosiphon* and *Rennera*) and with an adaxially long auricle (with a secondary loss of a corona in *Oncosiphon*, *Rennera* and some *Pentzia* species). Despite considerable similarity in achene characters (oblong to obovoid, with 4–5 ribs, in *Myxopappus* triquetrous in cross-section and with one adaxial and two lateral ribs), putative close relationships with the northern hemisphere Matricariinae genera, *Matricaria*, *Otospermum*, or *Tripleurospermum*, were not supported by the molecular data. On the other hand, a sister group relationship with subtribe Artemisiinae receives some support (PP 0.99 in the ITS analysis, but not in the

*ndhF* analysis), and may be of great importance for the further understanding of the biogeography of the whole tribe, forming a link between the strictly southern hemisphere genera of other subtribes and the northern hemisphere representatives. The occurrence of some species of *Pentzia* in northern Africa or in southwest Asia may add further evidence to this biogeographic pattern, but may, on the other hand, be interpreted equally justified as an example of independent expansion towards the north at a different time.

**Handeliinae** Bremer & Humphries in Bull. Nat. Hist. Mus. Lond. (Bot.) 23: 108. 1993 ?= Cancriniinae Bremer & Humphries in Bull. Nat. Hist. Mus. Lond. (Bot.) 23: 96. 1993

This subtribe is well supported as monophyletic in the ITS analysis (93% BS; PP 1.0) and consists of at least ten genera that have been members of Handeliinae (*Handelia*, *Lepidolopsis*, *Pseudohandelia*, *Sclerorhachis*), Cancriniinae (*Allardia*, *Richteria*, *Trichanthemis*), Matricariinae (*Microcephala*), and Tanacetinae (*Tanacetopsis*, *Xylanthemum*) in the sense of Bremer and Humphries (1993). Unfortunately, sequence information for the type of Cancriniinae (*Cancrinia* Karelin and Kir. [*Cancrinia chrysocephala* Karelin and Kir.]) is still lacking and inclusion of this subtribe in Handeliinae in the present circumscription is preliminary. However, since other members of Cancriniinae in the sense of Bremer and Humphries (1993) are well nested in this clade and appear to be closely related to *Cancrinia* (synapomorphies of Cancriniinae being the compact, scapoid habitus and involucre bracts with dark brown margins; Bremer and Humphries 1993), inclusion of this subtribe in a broad subtribe Handeliinae seems to be justified.

In its present circumscription, the subtribe Handeliinae is considerably diverse, and synapomorphies from morphology or anatomy are lacking. It contains annual, biennial (hapaxanthic) or perennial (pollacanthic) herbs or subshrubs with basifixed, rarely (in some species of *Tanacetopsis* and *Xylanthemum*) medifixed hairs, alternate, lobed to 3–4-pinnatisect leaves, and discoid or radiate capitula arranged solitarily, in lax to dense corymbs, or in a long spike-like panicle (*Lepidolopsis*). While in most members receptacles are epaleate, *Handelia* and *Sclerorhachis* have paleate receptacles. Ray florets have white, yellow, pink or violet limbs and disc florets are usually 5-lobed (4–6-lobed in *Lepidolopsis*), are sometimes hairy (*Tanacetopsis*, *Trichanthemis*, *Xylanthemum*), and possess anthers with non-polarized endothelial tissue and a baluster-shaped filament collar (slender in *Allardia* and some *Tanacetopsis* species). Achenes are cylindrical to obconical, circular to elliptical in cross-section, with 4–10 ribs, sometimes with 3–5 adaxially arranged ribs (*Microcephala*); their apex is furnished with a corona

formed by 25–50 bristle-like scales (*Allardia*), a short rim, consists of lacinate scales of various shapes, or is rarely ecoronate (*Pseudohandelia*, *Sclerorhachis*); the pericarp is usually glabrous and with or without myxogenic cells, but is densely hairy in *Trichanthemis*. While  $x = 9$  prevails as the base chromosome number, the dysploid number  $x = 7$  is reported for a member of *Microcephala*.

Generic groupings among members of Handeliinae are largely unresolved in the molecular trees, but the similar habit of *Handelia*, *Lepidolopsis*, *Pseudohandelia*, and *Sclerorhachis*—with rather thick, basally villous stems, a soft pith, and strongly dissected leaves with filiform lobes (as apomorphic characters used by Bremer and Humphries 1993 to define their smaller Handeliinae)—may argue for a closer relationship of these entities and for an inclusion of the not yet sequenced *Polychrysum* into this monophyletic group. In addition to that, further members of the Cancriniinae sensu Bremer and Humphries (1993), i.e., *Cancrinia*, *Cancriniella*, and *Ugamia*, may be further candidates for inclusion into Handeliinae in the broad sense proposed here.

**Artemisiinae** Less. in Linnaea 5: 163. Jan 1830 = Chrysantheminae Less. in Linnaea 6: 167. 1831

With the exception of the recently described genus *Artemisiella* (Ghafoor 1992), the genus *Hippolytia* (from Tanacetinae in the sense of Bremer and Humphries, 1993) and two of their Leucantheminae genera (*Leucanthemella*, *Nipponanthemum*), the members of the strongly supported clade around *Artemisia* (88% BS; PP 1.0 in the ITS analysis) all belong to subtribe Artemisiinae in the sense of Bremer and Humphries (1993). This corroborates findings of Kornkven et al. (1998, 1999), Torrell et al. (1999), Watson et al. (2002), Vallès et al. (2003), and Sanz et al. (2008) who have concentrated on the phylogeny of this subtribe and, therefore, comprehensively sampled it. These studies also demonstrated that *Artemisia*, in the circumscription of Bremer and Humphries (1993), is highly paraphyletic and that *Crossostephium*, *Filifolium*, *Mausolea*, *Neopallasia*, *Picrothamnus*, *Seriphidium*, *Sphaeromeria*, and *Turaniphytum* should be sunk into its synonymy to arrive at a monophyletic genus, which is the largest in the whole tribe.

According to the cladistic analyses by Bremer and Humphries (1993), morphological evidence for the monophyly of the subtribe is considered to be the possession of medifixed or stellate rather than basifixed hairs (plesiomorphic in some species of *Ajanina*, *Artemisia*, *Brachanthemum*, *Chrysanthemum*, *Leucanthemella*, and *Turaniphytum*, and in *Arctanthemum*), the anthers with triangular-linear-lanceolate apical appendages of rather thick-walled cells, and the tendency towards ecoronate, marginally rounded achenes (with exceptions in *Crossostephium*, *Nipponanthemum* and one species of *Sphaeromeria* where a pappus of small scales is observed, and in *Artemisiella* and *Hippolytia* where the

achene apex is a more or less distinct rounded rim). With base chromosome numbers of  $x = 7, 8, 9, 10, 11, 17$ , the subtribe Artemisiinae shows an impressive and comprehensive example of descending and ascending dysploidy in Anthemideae.

The phylogeny of Artemisiinae is marked by a transition between the more basal genera with solitary to laxly corymbose arrangements of radiate, disciform or discoid capitula with insect-pollinated, hermaphroditic disc florets and spiny pollen of the so-called *Anthemis*-type, towards the advanced genera of the *Artemisia* group with densely corymbosely or paniculately arranged disciform or discoid capitula with wind-pollinated, often unisexual florets and smooth pollen of the *Artemisia*-type. In a recent molecular phylogenetic study based on nrDNA ITS and ETS sequence variation, Sanz et al. (2008) found that at the very base of the subtribe a generic group of *Brachanthemum*, *Hippolytia*, and *Nipponanthemum* receives high support as a monophyletic group. This group may also include *Leucanthemella*, and then would consist of shrubs and perennial herbs with either radiate or discoid capitula with white, female or sterile ray florets, hermaphroditic, 5-lobed disc florets, and achenes with 5–10 ribs and a pericarp without myxogenic cells (with myxogenic cells in *Brachanthemum*). A further well-supported generic assemblage is formed by the perennial genera *Ajania*, *Arctanthemum*, and *Chrysanthemum*, along with the annual *Elachanthemum*, and may also comprise two other annual, unispecific genera: the morphologically similar genus *Tridactylina* that shares involucre bracts with dark brown margins with *Arctanthemum* and *Chrysanthemum*, and the enigmatic genus *Ajaniopsis* from China and Tibet. The unispecific genus *Elachanthemum*, which has been united with *Stilpnolepis* by Bremer and Humphries (1993), was corroborated by Watson et al. (2002) and Sanz et al. (2008) as an independent genus. It shows, despite its firm position in the *Chrysanthemum* group of genera and in contrast to the yet ungrouped unispecific *Stilpnolepis*, an *Artemisia*-like pollen type with a smooth exine also shared with *Ajaniopsis* (Martín et al. 2003). Finally, Sanz et al. (2008) also succeeded in pinpointing the sister group of *Artemisia* (including all the derivatives mentioned above) to the small Central Asian genus *Kaschgaria*, which also possesses the *Artemisia* pollen type (Martín et al. 2001).

### III. Eurasian grade

**Matricariinae** Willk. in Willk. & Lange, Prodr. Fl. Hispan. 2: 92. 1870 = Achilleinae Bremer & Humphries in Bull. Nat. Hist. Mus. Lond. (Bot.) 23: 126. 1993

This subtribe consists of members of Achilleinae (*Achillea*, *Anacyclus*, *Leucocyclus*, *Otanthus*), Tanacetinae (*Heliocauta*), and Matricariinae (*Matricaria*) in the sense of Bremer and Humphries (1993). The group was resolved in

previous molecular phylogenetic studies based on ITS sequences (Oberprieler and Vogt 2000: “Achilleinae I”; Oberprieler 2004a, b). The inclusion of *Matricaria* in this subtribe (with its nomenclatural consequences due to the priority of Matricariinae against Achilleinae) is further supported by *ndhF* sequence information, as is the exclusion of *Tripleurospermum* that was considered closely related to *Matricaria* (e.g., Applequist 2002). In our present ITS dataset, the subtribe lacks support in both the MP bootstrap and the BI analyses. There is only high support (PP = 1.0) for a monophyletic group consisting of Matricariinae and Anthemidinae together. However, while Anthemidinae could be defined as monophyletic by the apomorphic character expression of a tetrasporic embryo sac development, and this is supported at least by the topology of the nrDNA ITS phylogeny (see below), Matricariinae with their monosporic development possibly constitute a paraphyletic group relative to Anthemidinae.

The members of Matricariinae are subshrubs or perennial to annual herbs with an indumentum of basifixed hairs (in *Achillea* sometimes asymmetrically medifixed), alternate or basally rosulate, usually dentate to 4-pinnatisect, rarely entire, sometimes vermiform leaves, and radiate, disciform or discoid capitula arranged solitarily or in lax to dense corymbs. The medium to small capitula have a paleate or epaleate (*Matricaria*) receptacle, white, yellow, or pink ray florets with more or less flattened tubes, and hermaphroditic disc florets with a (4–)5-lobed, basally saccate corolla clasping the top of the achene, and anthers with non-polarized endothelial tissue and a baluster-shaped filament collar. The achenes are obovoid, terete with 3–5 weak ribs or dorsiventrally flattened and with two lateral ribs or wings; their apex is marginally rounded or with a narrow marginal corona (*Anacyclus*, *Matricaria*), and their pericarp is furnished or lacks myxogenic cells and sometimes possesses longitudinal resin ducts (*Achillea*, *Heliocauta*). All members of the subtribe show a base chromosome number of  $x = 9$ . The subtribe is distributed in Europe, Asia, northern Africa, and western North America.

Following results of Guo et al. (2004), the genera *Leucocyclus* and *Otanthus* should be included in a broader genus *Achillea* to achieve monophyly. Oberprieler (2004a) demonstrated that the northwestern African, unispecific genus *Heliocauta* is the sister group to the western Mediterranean genus *Anacyclus*, despite the alleged relationships (Bremer and Humphries 1993) of the former with the Asian genus *Hippolytia* of Artemisiinae (in their present circumscription). Another northern African-southwestern Asian, unispecific genus, *Brochia*, with a single species, *B. cinerea*, which was treated as a member of *Cotula* by Bremer and Humphries (1993), is clearly a member of the Eurasian/Mediterranean clade of Anthemideae (Oberprieler 2004a). Despite its very isolated position

in the molecular analyses, it may be closely related to *Matricaria* due to its achenes with four inconspicuous lateral and adaxial ribs, a marginally rounded apex, and a pericarp of elongated myxogenic cells without resin sacs.

**Anthemidinae** (Cass.) Dumort., Fl. Belg.: 69. 1827 = Pyrethrinae Horan., Char. Ess. Fam.: 90. 1847 = Tanacetinae Bremer and Humphries in Bull. Nat. Hist. Mus. Lond. (Bot.) 23: 99. 1993 = Gonosperminae Bremer and Humphries in Bull. Nat. Hist. Mus. Lond. (Bot.) 23: 106. 1993

The Anthemidinae are easily characterized as monophyletic by the joint possession of a tetrasporic embryo sac development that constitutes an apomorphic character expression in the otherwise monosporic Anthemideae (with exceptions in *Argyranthemum* and *Heteranthemis*, Glebionidinae). As described above, Anthemidinae are closely related to the subtribe Matricariinae with which they form a well supported monophyletic clade in our ITS-based analysis (PP 1.0).

Containing the species-rich genera *Anthemis* (175 spp.) and *Tanacetum* (154 spp.), the subtribe is the second largest in Anthemideae. It comprises annuals, biennials, or short- to long-lived perennial herbs and subshrubs with an indumentum of medifixed or basifixed (*Tanacetum*, *Tripleurospermum*) hairs, radiate, disciform, or discoid capitula arranged solitarily or in lax to dense corymbs and with paleate or epaleate receptacles, white, yellow or pink ray florets, and hermaphroditic, 5-lobed (4-lobed in *Nananthea*) disc florets with anthers with non-polarized endothelial tissue and a baluster-shaped filament collar. The achenes are obovoid to obconical, either circular in cross-section and possessing 5–10(–15) ribs, or dorsiventrally flattened with 3–10 ribs on each surface (*Cota*), or sometimes triquetrous and with 3(–5) ribs (*Tripleurospermum*); their apex is furnished with a corona or an auricle, but is also sometimes ecoronate and/or marginally rounded; the pericarp usually carries myxogenic cells that are lacking in *Tanacetum*, and are devoid of resin sac or ducts, except in *Tripleurospermum* where (1–)2(–5) abaxial-apical resin sacs are observed. With a base chromosome number of  $x = 9$  the subtribe is cytologically homogeneous.

While the circumscription of the subtribe as monophyletic is rather clear based on the embryological findings, the generic delimitations and the phylogenetic relationships within the subtribe remain unresolved. Despite the assessment of Bremer and Humphries (1993: 99) that “there are several segregate genera and groups of genera, possibly even whole subtribes, which are related to parts of *Tanacetum*” making it a highly paraphyletic genus, molecular phylogenetic studies thus far based on ITS sequence variation with a number of *Tanacetum* species included (Oberprieler 2005) have shown that the Mediterranean and southwestern Asian representatives of the genus are

all closely related. More comprehensive, but yet unpublished, analyses (Stroka and Oberprieler, in prep.) demonstrate that only a few central Asian representatives of the genus (all of them with phylogenetic connections to Artemisiinae or Handeliinae, respectively) will have to be removed and transferred to other genera to arrive at a monophyletic genus *Tanacetum* around the type species *T. vulgare* L. Preliminary analyses based on small samples of *Tanacetum* species (Francisco-Ortega et al. 2001; Oberprieler 2005; Oberprieler and Vogt 2006), however, have already clearly shown that the Canary Island endemics, *Gonospermum* and *Lugoa*, represent derivatives closely related to the *Tanacetum* species found on this archipelago and, therefore, should be included in a monophyletic genus *Tanacetum*, and that the generic distinction between *Tanacetum* (with disciform, discoid or yellow-rayed capitula) and *Pyrethrum* (with white- or pink-rayed capitula) may not be very helpful to achieve monophyletic genera in this subtribe.

Molecular phylogenetic studies based on ITS and focussing on the delimitation and infrageneric classification of *Anthemis* (Oberprieler 2001, 2004a, 2005; Oberprieler and Vogt 2006) have demonstrated that *A.* subg. *Anthemis* is more closely related to *Tripleurospermum* and the unispecific *Nananthea* than to species formerly treated under *A.* subg. *Cota*. This has led to the acknowledgement of *Cota* as an independent genus and the transfer of a number of *Anthemis* species to this genus (Greuter et al. 2003). Again, more detailed analyses are underway (Lo Presti and Oberprieler, in prep.) to provide a better understanding of the phylogenetic relationships for the species formerly treated under *Anthemis* and other members of subtribe Anthemidinae.

**Leucanthemopsidinae** Oberprieler & Vogt in Willdenowia 37: 104. 2007

This small subtribe consists of the small perennial genus *Leucanthemopsis* with nine species in southwestern and Central Europe (one species in northern Africa) and the three unispecific, annual segregate genera *Castrilanthemum*, *Hymenostemma*, and *Prolongoa*, all of which are endemic to Spain and formerly treated under the subtribe Leucantheminae in the sense of Bremer and Humphries (1993; cf. Vogt and Oberprieler 1996). The members are characterized by an indumentum of medifixed hairs, solitary and radiate capitula with epaleate receptacles, yellow or white ray florets, and hermaphroditic, 5-lobed disc florets with anthers with non-polarized endothelial tissue and a baluster-shaped filament collar. The achenes are obovoid, round in cross-section and with (3–)5–10 ribs, rarely dorsoventrally compressed and with one adaxial, two lateral and two abaxial ribs (*Prolongoa*); their apex is furnished with a scarious corona or is marginally rounded (*Castrilanthemum*); the pericarp possesses



myxogenic cells along the ribs and is devoid of resin sacs. The base chromosome number is  $x = 9$ .

As Bremer and Humphries (1993) and Vogt and Oberprieler (1996) have shown in cladistic analyses based on morphological and anatomical characters, the members of this subtribe lack the specialized achene anatomy of the *Leucanthemum* group of genera. Furthermore, molecular studies (Oberprieler and Vogt 2000, Oberprieler 2005) have shown that the monophyly of Leucanthemopsidinae is strongly supported and that they are not closely related to the *Leucanthemum* group of genera (that is treated here as subtribe Leucantheminae). Despite its well-supported monophyly in studies based on molecular characters, the subtribe is not yet well-defined by morphological or anatomical synapomorphies: while Bremer and Humphries (1993) considered the reduced number of pericarp ribs and the occurrence of a scarios, flimsy corona as possible synapomorphies for *Hymenostemma*, *Leucanthemopsis*, and *Prolongoa*, the addition of *Castrilanthemum* by Vogt and Oberprieler (1996) with its 10-ribbed and ecoronate achenes changed the circumscription enormously. In fruit morphology and anatomy, *Castrilanthemum* shows similarity to the southwestern European endemic genus *Phalacrocarpum* that has an unresolved position in the ITS analyses. However, following our present phylogenetic reconstructions, the closer relationship of the former with *Hymenostemma*, *Leucanthemopsis*, and *Prolongoa* is strongly supported.

#### IV. Mediterranean clade

**Leucantheminae** Bremer & Humphries in Bull. Nat. Hist. Mus. Lond. (Bot.) 23: 136. 1993

Leucantheminae are a group of eight genera with approximately 71 species distributed mainly in the western Mediterranean region, Macaronesia, Europe, and Asia. It consists of annual or perennial herbs and subshrubs (*Leucanthemum*, *Plagiis*, *Rhodanthemum*) with an indumentum of basifixed, rarely medifixed (some *Rhodanthemum* species) hairs, entire, lobed or up to 3-pinnatisect leaves, discoid or radiate, solitarily arranged capitula with epalate receptacles, white, yellow or red ray florets, and disc florets with a (4–)5-lobed, basally often saccate corolla clasping the top of achenes, and anthers with non-polarized endothecial tissue and a baluster-shaped filament collar. The main distinctive feature to circumscribe this subtribe is the fruit anatomy of its members: the achenes are ellipsoid and circular in cross-section, with 5–10 ribs, a marginally rounded apex sometimes furnished with a scarios and adaxially longer corona, and a pericarp with myxogenic cells along the ribs and with resin canals and vascular strands in the furrows between ribs. The apomorphic nature of these vallecular resin canals and vascular strands had been clearly worked out by Bremer

and Humphries (1993). They used it to circumscribe their *Leucanthemum* group of genera, which formed the centre of their larger subtribe Leucantheminae, but also including now some unrelated generic elements (e.g., *Leucanthemella* and *Nipponanthemum* of Artemisiinae and *Hymenostemma*, *Leucanthemopsis*, and *Prolongoa* of Leucanthemopsidinae).

Despite that the subtribe Leucantheminae in the present circumscription is well-defined morphologically, there is less support provided by molecular analyses. While most of its members form a moderately to well-supported monophyletic clade in the analyses based on ITS sequences, the genus *Chlamydochloa*, which shares the apomorphic achene anatomy of valecular resin canals and valecular vascular strands, is consistently found outside this clade (Oberprieler and Vogt 2000; Oberprieler 2004a, b, 2005; Vogt and Oberprieler 2006; Oberprieler et al. 2007b). Alternatively, the next, more inclusive and well-supported clade in the present analysis (PP 1.0) also contains genera (*Daveaua*, *Otospermum*, *Heteromera*) of Matricariinae in the sense of Bremer and Humphries (1993) devoid of the characteristic achene anatomy of Leucantheminae but with similarity to each other in achene anatomical respects (5-ribbed achenes with vascular strands in the ribs). As Oberprieler (2004b) has argued, this controversial morphological and molecular evidence may indicate that *Daveaua*, *Heteromera* and *Otospermum* are a paraphyletic group that gave rise to the very distinct *Leucanthemum* group of genera with its specialized achene anatomy. Due to the unclear generic relationships in the ITS analyses and the incomplete sampling in the *ndhF* analysis, Oberprieler et al. (2007b) have refrained from inclusion of these three genera in the well-circumscribed Leucantheminae and treated them as genera unassigned to subtribe.

**Santolininae** Willk. in Willk. & Lange, Prodr. Fl. Hispan. 2: 76. 1870

This subtribe comprises those genera of Achilleinae in the sense of Bremer and Humphries (1993) that also were found to be characterized by an apomorphic 5-bp deletion in cpDNA *trnL-trnF* spacer that they share with Glebionidinae, Leucantheminae, and a number of unassigned Mediterranean genera (*Aaronsohnia*, *Endopappus*, *Lepidophorum*, *Lonas*, *Nivellea*), but not with *Achillea*, *Anacyclus*, or *Matricaria* (Oberprieler and Vogt 2000; Oberprieler 2002). Therefore, in Oberprieler and Vogt (2000) this group was called “Achilleinae II” in contrast to “Achilleinae I”, the latter being here treated as the subtribe Matricariinae (see above).

Members of Santolininae are perennial or annual herbs, subshrubs or shrubs with an indumentum of basifixed, medifixed or stellate hairs, entire or lobed up to 2–3-pinnatisect, sometimes vermiform leaves, and radiate,

disciform or discoid capitula arranged solitarily or in lax corymbs. The capitula are characterized by paleate receptacles, white, yellow or orange ray florets, and hermaphrodite, 5-lobed disc florets with distinct basally saccate or spurred corollas clasping the top of achenes either laterally or adaxially, and anthers with non-polarized endothelial tissue and a baluster-shaped filament collar. Most of the members of the subtribe are characterized by achenes with a very thin pericarp that mainly consists of an epidermis formed by longitudinal rows of large mucilage cells that is devoid of resin sacs or ducts. The only exception is found in *Santolina* where some species are lacking mucilage cells altogether and the pericarp is thicker and sclerenchymatous. Since the latter condition is considered plesiomorphic, the thin pericarp is a synapomorphy that unites the four genera *Chamaemelum*, *Cladanthus*, *Mecomischus*, *Rhadinolepis*, and some of the species of *Santolina*. Putative close relationships to other genera with reduced pericarp (e.g., *Achillea* or *Matricaria* of Matricariinae or members of Artemisiinae) were not confirmed by analyses based on nuclear or plastid markers.

**Glebionidinae** Oberprieler & Vogt in Willdenowia 37: 106. 2007 = Chrysantheminae Bremer & Humphries in Bull. Nat. Hist. Mus. London, Bot. 23: 136. 1993, nom. illeg.

Glebionidinae consist of four mainly western Mediterranean and Macaronesian genera of 28 species of which the majority are found in the shrubby Macaronesian endemic genus *Argyranthemum* and the remainder being annual species. The close relationship of these four genera had been previously described by Heywood and Humphries (1977) and received subtribal status by Bremer and Humphries (1993) under the name “Chrysantheminae”. However, since the conserved type of *Chrysanthemum* L. is now *Ch. indicum* L. (= *Dendranthema indicum* (L.) Des Moul.) the two Mediterranean annuals *Ch. coronarium* and *Ch. segetum* are now treated as members of *Glebionis* Spach, and the subtribal name Chrysantheminae Bremer and Humphries, validly published with a Latin description and designation of type, became an illegitimate later homonym of Chrysantheminae Less. As a consequence, the name of the subtribe was changed to Glebionidinae (Oberprieler et al. 2007b).

The monophyly of this group is well-supported due to the occurrence of distinctly heteromorphic achenes with achenes of ray florets being triquetrous and winged and achenes of disc florets being terete or laterally flattened. Early studies of ITS sequence variation in Mediterranean and Macaronesian Anthemideae by Francisco-Ortega et al. (1997), and more comprehensively sampled studies, revealed this generic group as a well-supported clade (Oberprieler 2005), as did studies based on *ndhF* sequence variation (Watson et al. 2000; Himmelreich et al. 2008).

The latter analysis also suggested a close relationship of Glebionidinae with the northwestern African endemic, annual genus *Aaronsohnia* and may serve as an argument that the annual life-form may be plesiomorphic in the subtribe, and that the perennial life form observed in *Argyranthemum* may be best interpreted as an adaptation to the insular habitat (“insular woodiness”; Carlquist 1974). Close phylogenetic relationships of Glebionidinae to members of Anthemidinae, as suggested by Bremer and Humphries (1993) based on the alleged apomorphy of thick-walled achenes, did not receive support from the molecular analyses.

## MORPHOLOGY

### Habit and life form

Anthemideae comprise annual, biennial or perennial, hapaxanthic or pollacanthic herbs, subshrubs or shrubs. All presently accepted subtribes (besides basal Osmitopsidinae and more advanced Phymaspermatae, which contain only shrubs or subshrubs) are characterized by transitions between perennials and annuals, either within genera or in the phylogenies of closely related genera. In *Anthemis*, for example, Oberprieler (2001) demonstrated that the distinction of perennial and annual sections within the genus was highly artificial since the annual habit evolved several times independently. The same observation was also made in a more comprehensive molecular phylogenetic study of Eurasian and Mediterranean representatives of Anthemideae (Oberprieler 2005), where it was suggested that the annual habit in this group appeared around 5 to 10 million years ago in conjunction with a progressive aridification in the area (Van Dam 2006) and the onset of a Mediterranean climate type at 3 Ma (Suc 1984). Analogous results should be expected from comparable comprehensive species-based phylogenetic analyses of the southern African representatives of the tribe, where the onset of a Mediterranean climate in the Cape Floristic Region is also dated to 5 Ma (Midgley et al. 2001; Linder 2003).

The two Asian-centered subtribes Artemisiinae and Handeliinae are mainly perennial herbs, subshrubs or shrubs. Annual representatives constitute only a minority in these groups (e.g., *Ajaniopsis*, *Microcephala*, *Elachanthemum*, *Tridactylina*, *Neopallasia*, *Stilpnolepis*, and some *Artemisia* species), which may be interpreted as adaptations to steppe habitats evolving during the Tertiary (Oligocene to late Miocene, 34–10 Ma; Willis and McElwain 2002).

### Indumentum

The indumentum of Anthemideae frequently consists of short glandular hairs formed by two parallel rows of

cells (biseriate) and an apical pair of enlarged cells capped with an acellular vesicle. This hair type is very common in all subtribes and seems to be of minor taxonomic and evolutionary significance (Ciccarelli et al. 2007). In contrast, eglandular hairs of Anthemideae are far more interesting phylogenetically (see reconstruction of character evolution in Fig. 38.5). While the basal subtribes Osmitopsidinae, Cotulinae, and Ursiniinae are characterized by an indumentum of basifixed hairs formed by a few basal stalk cells and a long apical cell, more advanced subtribes (especially Artemisiinae, Anthemidinae, Leucanthemopsidinae, and Santolininae) are partly or completely formed by genera characterized by medifixed or so-called dolabriform hairs (Napp-Zinn and Eble 1980; Bremer and Humphries 1993). These usually comprise a few stalk cells and a transversely arranged apical cell. In some cases (e.g., *Athanasia*, *Hymenolepis*, *Artemisia*, *Mecomischus*) stellate hairs are encountered that may be interpreted as derived from medifixed ones.

In a recent publication, Herman (2001) reported on septate hairs with oblique (or sometimes perpendicular) walls observed on fruits or paleae of *Eriocephalus*, *Lasiospermum*, *Lidbeckia*, and *Ursinia* (Athansiniinae, Cotulinae, and Ursiniinae, respectively) and also described the occurrence of hairs with spiral wall thickenings in *Ursinia*. Since Bremer and Humphries (1993) also reported on hairs with spiral thickenings on the achenes of the Asian genus *Microcephala* (Handeliinae) this may emerge as another feature of phylogenetic significance if studied in a more comprehensive sampling of genera.

### Leaves

Leaves of Anthemideae are usually alternate and only a few genera have opposite leaves. While sometimes entire, or in some cases (mainly from South African representatives) ericoid and needle-like, in the majority of the tribe dentate or moderately to extremely dissected leaves are observed. As extremely dissected foliage the 3–4-pinnatisect leaves with hair-like pinnae of *Sclerorhachis* (Handeliinae) and the strongly dissected, sometimes 3-dimensional and vermiform leaves of some *Achillea* species may serve as impressive examples. While in most genera leaves are covered with glandular hairs and basifixed or medifixed trichomes, Bremer and Humphries (1993) describe secretory cavities that are otherwise only found in floral structures of a number of genera in the leaves of *Eumorphia*, *Gymnopentzia*, and *Phymasperma* (Phymasperminae) and of *Athanasia* and *Hymenolepis* (Athansiniinae).

Napp-Zinn and Eble (1978) surveyed the stomatal apparatus of species of *Eriocephalus* and a number of northern hemisphere genera and documented a number of different types. These findings, however, are very hard to utilise due to the very sporadic sampling.

### Inflorescence

Capitula are arranged either solitarily or in lax to dense corymbose capitulescences. The heads are usually distinctly pedunculate, but in some cases (e.g., *Cladanthus* or *Soliva*; Weberling and Reese 1988) sessile capitula or syncephalia (clustered capitula) are observed. In subtribe Artemisiinae and in some representatives of Handeliinae, panicle- or raceme-like capitulescences with numerous, small capitula are formed.

### Floral arrangement

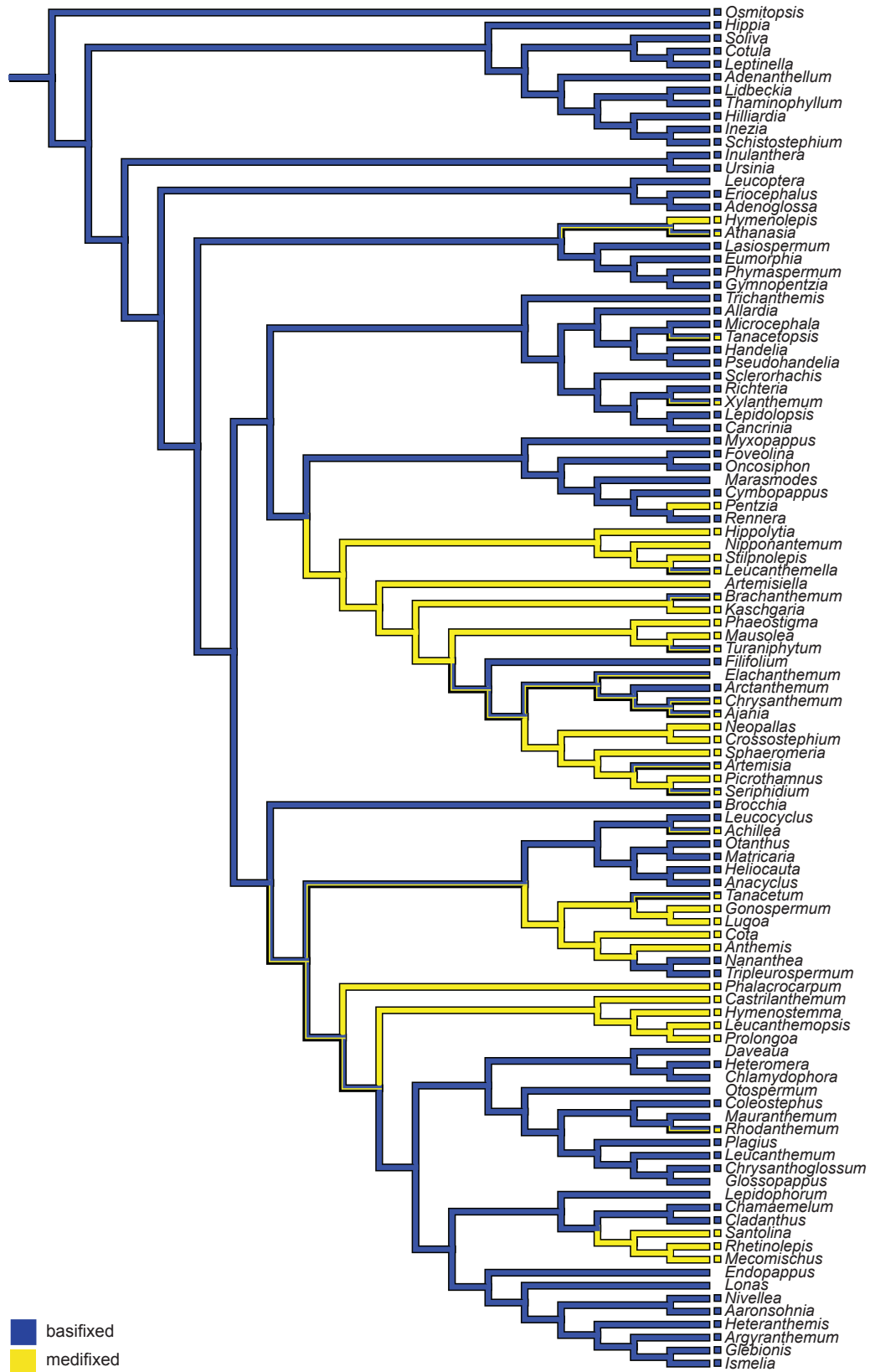
In all presently accepted subtribes, the plesiomorphic condition of radiate, heterogamous capitula with hermaphroditic disc florets and female (or sometimes sterile or neuter) ray florets is encountered. The occurrence of capitula with reduced ray florets leading to discoid, homogamous capitula and of disciform, heterogamous flower heads with female marginal and hermaphroditic central disc florets in many of the subtribes demonstrate the plasticity of Anthemideae in this respect, and even within single species the transition between radiate and discoid capitula is often observed (e.g., *Anthemis*; Oberprieler 1998).

In subtribe Artemisiinae, the reconstruction of character evolution based on a molecular phylogeny made by Watson et al. (2002) demonstrates that homogamous discoid capitula have arisen several times in parallel from heterogamous, either radiate or disciform ones. Here, namely in the genera *Artemisia*, *Filifolium*, *Mausolea*, *Picrothamnus* and *Turaniphytum*, central disc florets with reduced female fertility leading to functionally male florets are observed. In some cases (*Elachanthemum*, *Neopallasia*) the inner tubular florets are even completely sterile.

The *Cotula* group of genera (*Cotula*, *Leptinella*, *Soliva*) in subtribe Cotulinae exhibits even more complex floral arrangements in the flower heads. While in *Cotula* capitula are either radiate, disciform, or discoid with outer female ray or tubular florets and a central mass of hermaphroditic florets, the derivative genera *Leptinella* and *Soliva* show outer female disc florets and functionally male inner disc florets. In *Leptinella*, subdioecious or even dioecious conditions are observed, while Heywood and Humphries (1977) report the gynodioecious condition in *Achillea* and the occurrence of dioecy in *Artemisia*.

### Involucre and involucre bracts

The involucre encountered in Anthemideae are often hemispherical or obconical, but may (especially in smaller capitula) tend to be more cylindrical or even urceolate. The phyllaries are usually arranged in two to seven imbricate rows and almost always possess scarious margins and a scarious apex that are reduced only in a minority of genera. In *Eriocephalus* the rows of involucre bracts



**Fig. 38.5.** Evolution of indumentum type (basifixed vs. medifixed hairs), as reconstructed based on the nrDNA ITS maximum likelihood tree topology shown in Figs. 38.1 and 38.2.



are reduced to two very unequal types, the outer scarious with very wide brown to reddish scarious margins, and the inner connate and hairy that subtend the outer florets.

### Receptacle

In Anthemideae the receptacles are either paleate or epaleate. This character had been used by Cassini (1823) to divide the tribe into two subtribes, later validly named *Chrysantheminae* Less. and *Anthemidinae* Dumort. The artificiality of this subdivision was clearly stated by Merxmüller (1954) and Wagenitz (1964), and demonstrated by Greuter (1968) when he found that in *Ammanthus* (now included in *Anthemis*) the presence or absence of paleae “does not even necessarily suffice to distinguish species”. Hybridization experiments among members of Anthemideae made by Mitsuoka and Ehrendorfer (1972) have shown that the inheritance of pales is probably under simple oligogenic control. The observation of sporadic paleate capitula in *Glebionis* (Napp-Zinn and Eble 1978, under *Chrysanthemum*) and inclusion of paleate and epaleate species into *Athanasia* by Källersjö (1991) point in the same direction.

A reconstruction of character evolution based on the present phylogeny of the tribe is equivocal with respect to the plesiomorphy of paleate or epaleate receptacles (Fig. 38.6). With *Osmitopsidinae* assumed to be basal and sister to the rest of the tribe, the presence of paleae may be the plesiomorphic condition, arguing for a epaleate receptacle to constitute a synapomorphy of *Cotulinae* and a number of Asian, Eurasian, and Mediterranean subtribes, with reversals to the paleate conditions occurring in *Anthemidinae*, *Matricariinae*, *Santolininae*, and a number of other genera or infrageneric entities.

The paleae are either persistent or readily deciduous and may be flat or canaliculate, sometimes even enclosing the florets. Paleae may be also hairy or may be furnished with resin canals along their midvein.

The shape of the receptacles varies from flat or convex to conical or even narrowly conical. Usually the receptacle is filled with pith, but in some cases (e.g., *Matricaria*) it is hollow. In some cases (e.g., *Inezia*, *Eriocephalus*, and some *Artemisiinae*) the receptacles are pilose or densely hirsute.

### Ray florets

The ray florets in Anthemideae are either female and fertile or sterile, or neuter. Their limb is usually white or yellow, but also red, orange, or pink colors are found in some genera. In some genera of *Cotulinae* (e.g., *Adenanthellum*, *Hilliardia*, *Inezia*) the limbs of ray florets are apically emarginate or bifid, possess a branching venation, and are characterized by a reduced tube. While most of the genera have ray florets with a helianthoid epidermal cell type (following

the definitions of Baagøe, 1977), *Osmitopsis* and some representatives of *Athanasinae* (*Lasiospermum*), *Ursiniinae* (*Ursinia*), and *Phymaspermatae* (*Eumorphia*, *Phymaspermum*) possess the senecioid cell type with tabular cells.

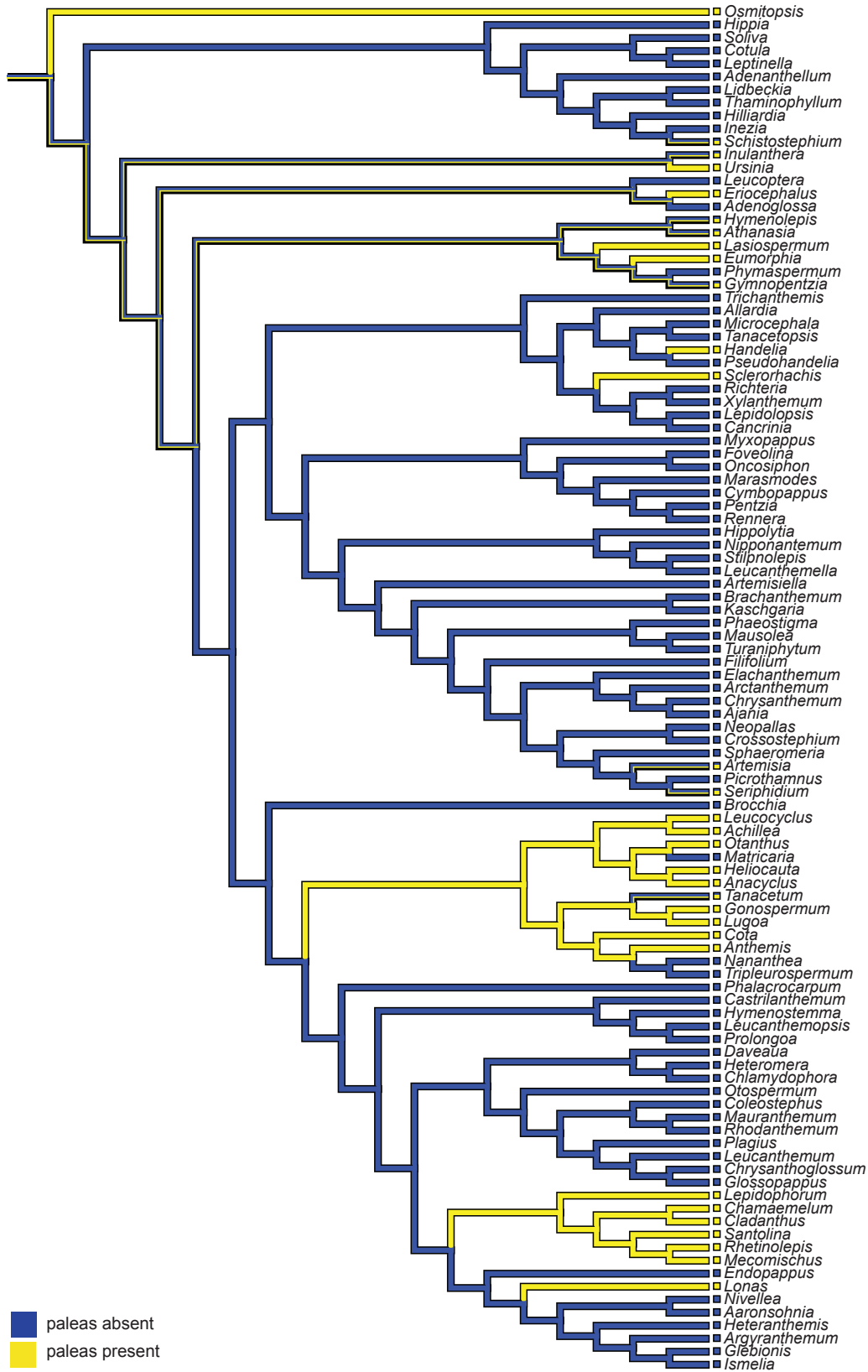
### Disc florets

Following Bremer and Humphries (1993) and our present phylogenetic reconstructions, the plesiomorphic type of tubular florets in Anthemideae is characterized by an unswollen, non-saccate tube and a 5-lobed limb. In *Pentziinae*, *Anthemidinae*, *Leucantheminae*, and *Glebionidinae* many representatives have basally swollen tubular florets, being conspicuously inflated and spongy at maturity. Sponginess is caused by the excessive growth of subepidermal tissue, with the cells forming long interwoven and repeatedly branched rows and large intercellulars, while the epidermal cells become indurate by sclerification of their walls. However, as observed in *Anthemis* (Oberprieler 1998), inflation of disc floret bases is often not consistently realized throughout a genus and florets with a slender base or with a base pressed flat and appearing laterally winged at maturity are found.

In *Matricariinae*, *Leucantheminae*, and *Santolininae* the disc florets have a more-or-less conspicuously saccate tube with either lateral or abaxial spurs clasping the top of achenes. This character expression is often correlated with the occurrence of achenes with marginally rounded apices and the lack of a pappus or corona. In a number of genera the tube is confluent with the achene and may persist on top of the mature fruits. While hairy corollas are encountered in several genera of Anthemideae, some species of *Athanasia* in *Athanasinae* bear unique, long-stalked glands at the base of the disc corolla tubes that have the appearance of a bristly pappus, although not connected with the achenes.

In some subtribes the corolla has only four lobes. This is often observed in *Cotulinae* where only two genera (*Adenanthellum*, *Hippia*) are characterized by 5-lobed corollas, and the 4-lobed condition may be a synapomorphy of the subtribe or of a generic group within. However, corollas with reduced lobe numbers also occur in other, unrelated subtribes such as *Pentziinae* (*Myxopappus*, *Oncosiphon*), *Handeliinae* (*Lepidolopsis*), *Artemisiinae* (*Ajania*, *Filifolium*, *Artemisiella*), *Matricariinae* (*Matricaria*), *Anthemidinae* (*Nananthea*), and *Leucantheminae* (*Chlamydo-phora*), mainly in connection with capitula of small size and the reduction of tubular florets. In disciform capitula the outer female, tubular florets are often further diminished and provided with a reduced, sometimes slender limb without apical teeth. In *Cotula* these peripheral florets are usually stalked, while in the closely related genus *Soliva* they form several rows.

The disc floret corolla lobes are often of the same size, but in several genera (e.g. *Anacyclus* in *Matricariinae*)



**Fig. 38.6.** Evolution of receptacle type (paleas absent vs. present), as reconstructed based on the nrDNA ITS maximum likelihood tree topology shown in Figs. 38.1 and 38.2.

characteristic appendages on the abaxial side are found and may lead to asymmetrical corollas. However, Oberprieler (1998) found in *Anthemis* that these appendages are too variable to characterise species or species groups. The vascularization of corolla lobes seems to provide some useful characters, with the majority of Anthemideae genera devoid of vascular bundles along the margins of lobes but with an anastomosing vascular system in *Athanasia* (Athansiinae). This feature, however, has been studied very fragmentarily.

### Anthers

In the majority of Anthemideae the anther thecae are obtuse to slightly pointed at the base. However, in some genera of different subtribes (*Osmitopsis* [Osmitopsidinae], *Inulanthera* [unassigned to a subtribe], and *Hippolytia* [Artemisiinae]), they are tailed. The apical anther appendage is usually ovate in outline and obtuse to round apically. In Artemisiinae, however, triangular, linear, or elliptical appendages are observed that consist of rather thick-walled cells and may constitute an apomorphy of the subtribe (Bremer and Humphries 1993). The endothelial tissue is usually not polarized, i.e., its cells have wall thickenings evenly distributed over their whole length, while in the genera of Ursiniinae, Athansiinae (with the exception of *Eriocephalus*), and Phymasperminae cells of the endothelial tissue have thickenings only apically and basally. The filament collar is either slender or widens gradually towards its proximal end (“baluster-shaped”, Meiri and Dulberger 1986). It consists of cells with thickened walls and its margins are involute in cross-section. The filament proper is usually formed by large, unthickened, elongated cells.

### Styles

The styles in Anthemideae are very uniform and represent the so-called senecioid type: two vascular bundles run through the cylindrical and glabrous style shaft and end in the stigmatic branches, which are truncate-penicillate, bearing two separate lines of stigmatic papillae on the inside and obtuse sweeping hairs at their apex. Usually the stigmatic branches contain elongate resin ducts with a brown or orange content. The base of the style usually becomes swollen and hardened due to enlarged and sclerified cells. In the functionally male florets of *Artemisia*, *Cotula*, *Filifolium*, *Leptinella*, *Mausolea*, *Picrothamnus* and *Turaniphytum*, the style branches are undivided and lack a stigmatic area. In *Soliva* the styles of the marginal female florets become spinescent in fruit.

### Achenes

Dating back to the studies of Cassini (1823) and Schultz-Bipontinus (in Schnitzlein 1854, Schultz 1860), the paramount importance of achene morphology for the taxonomy and for the delimitation of genera in Anthemideae

is well known. Achenes are often either cylindrical, ellipsoid or obovoid in outline and more or less circular in cross-section. In a number of genera or generic groups, flattened achenes are encountered. In some genera of Cotulinae, Athansiinae, Artemisiinae, Matricariinae, and Anthemidinae dorsiventrally compressed, sometimes even laterally winged, achenes are found, while in Glebionidinae laterally compressed fruits occur.

The presence, number, shape, and arrangement of ribs are variable. In the most basal representative of the tribe (*Osmitopsis* in Osmitopsidinae), achenes are 3–4-angled or ribbed. Four or five evenly arranged ribs may therefore be the plesiomorphic condition in the tribe. In dorsiventrally or laterally flattened achenes, the number of ribs may be reduced and 1–2 wing-like ribs are formed. In other cases, the number of ribs is increased and achenes with up to 18 (in *Cota* even more) ribs are encountered.

The achene apex in Anthemideae is usually furnished with a relatively large, bowl-shaped discus called either coronet, nectary, or stylopodium, respectively (Kynčlová 1970; Vogt 1991; Bremer and Humphries 1993). In *Lidbeckia* and *Thaminophyllum* (Cotulinae) this discus is very large and persistent in fruit. The apical plate is either ecoronate and truncate or marginally rounded, or it is coronate. Only in Ursiniinae and in some Handeliinae is this corona pappus-like and formed of ovate scales (*Ursinia*) or subulate to bristle-like scales (*Allardia*, *Ursinia*), but never formed of true bristles. In many cases the corona is formed by basally fused scales or is an adaxial auricle or a more-or-less thickened rim.

### ANATOMY

Owing to the artificiality of a subtribal classification once based on the presence vs. absence of paleae, numerous attempts have been made to elaborate a more satisfactory taxonomy of the tribe. In this endeavour, carpological characters proved to be the most important source of phylogenetically relevant features. Despite some early findings on the relevance of carpological characters in the elaboration of naturally delimited genera (e.g., Schultz 1844, 1860, and in Schnitzlein 1854), the full merit for the exploitation of achene anatomy for taxonomic questions in Anthemideae goes to J. Briquet who used characters of the pericarp for the demarcation of Mediterranean genera of the tribe (Briquet 1916a–c; Briquet and Cavillier 1916). In the following decades, detailed carpological studies have been made in the so-called *Chrysanthemum* complex (Giroux 1930, 1933; Horvatic 1963; Borgen 1972; Alavi 1976; Humphries 1976), in the *Anthemis* complex (Humphries 1977; Benedí i González and Molero i Briones 1985), or in a more geographically focused study by Kynčlová (1970). The carpological survey of Reitbrecht

(1974) deserves consideration as the first comprehensive tribal-wide evaluation of achene anatomy for the elaboration of a more natural subtribal classification, utilizing as many genera with suitable study material as possible but with a clear focus on the northern hemisphere representatives of the tribe. The latter study yielded a subdivision into seven provisional groups, which were also accepted for the (informal) subtribal treatment of Anthemideae in Heywood and Humphries (1977). Triggered by these studies, anatomical studies of achenes in the following decades contributed to a better understanding of the taxonomy and the phylogenetic classification of southern hemisphere genera: Källersjö (1986, 1988) used mainly carpological characters for generic circumscriptions in the *Athanasia* and *Pentzia* complexes, respectively, while Bruhl and Quinn (1990) added fruit anatomical evidence for the exclusion of several genera of “Cotuleae” from Anthemideae and the retention of *Cotula*, *Leptinella*, *Nananthea*, and *Soliva* in the tribe.

The achene wall is often several cell layers thick and partly or completely sclerified. In other cases, especially in Santolininae, the pericarp is very thin and consists only of a single cell layer that is made up of longitudinal rows of mucilage cells. In the majority of the genera of the tribe, the pericarpic ribs coincide with vascular bundles through the mesocarp. However, in some genera (e.g., in a few *Anthemis* species; Oberprieler 1998) or generic groups (such as Leucantheaminae), the vascular bundles are found in the furrows between ribs, and the external ribs of the achene seem to result from the outgrowth of intervascular mesocarpic tissue.

The pericarp of achenes in Anthemideae is frequently furnished with myxogenic cells of different dimensions and different shapes. Very often these mucilage cells are localized on the ridges of achene ribs and consist of transversely compressed cells in longitudinal rows, but in other cases these specialized cells are solitarily interspersed among normal epidermal cells. In most representatives of the tribe the epicarp is furnished with short glandular hairs formed by two parallel rows of cells (biseriate) and an apical pair of enlarged cells capped with an acellular vesicle. Besides these glands, several genera of Cotulinae, Athanasiinae, Handeliinae, and Artemisiinae are characterized by normal, eglandular hairs. Extremely villous achenes are found in *Lasiospermum* (Athanasiinae) and *Trichanthemum* (Handeliinae), while achenes with a conspicuously papillose pericarp are typical for subtribe Phymaspermia.

Additionally, the pericarp of many Anthemideae representatives is furnished with resin canals or resin sacs. These may be either scattered over the whole pericarp or are found in more characteristic positions (longitudinal resin canals in or between ribs, round or ellipsoid resin sacs near the achene apex). As Oberprieler (1998) has demonstrated when discussing the differences between

*Anthemis* and *Cota*, further useful characters may be found when analyzing the shape and number of calcium oxalate crystals in the epicarpic cells.

The testa epidermis of nearly half of the presently accepted genera of the tribe was studied in a comparative manner by Kneißl (1981) who classified them into three different testa epidermis types (epidermal, sclerenchymal, and parenchymal type) and a number of genera unassigned to these groups. While the parenchymal type was found to be restricted to members of the present Cotulinae, and other members of the southern hemisphere subtribes (together with members of subtribes Anthemidinae, Glebionidinae, Leucanthemopsidinae, Matricariinae, and Santolininae) are characterized by the epidermal type, the sclerenchymal type is restricted to some northern hemisphere subtribes (Anthemidinae, Artemisiinae, Handeliinae, Leucantheaminae).

## POLLEN

The first detailed light microscopic studies of Anthemideae pollen were made by Wodehouse (1926, 1935) on *Anthemis cotula* and *Chamaemelum nobile*. He described the pollen as tricolporate, echinate, having a coarse-granular, two-layered exine. The thicker inner layer appeared to him to be built of coarse radial striae, and the outer, much thinner layer was found to have very fine radial striae. He considered the exine sculpturing as a main difference within the tribe, with echinate pollen grains with sharply pointed spines characterizing *Anthemis* together with other insect-pollinated genera (*Leucanthemum*, *Glebionis*, *Tanacetum*) and non-echinate pollen grains with vestigial or entirely absent spines being typical for generally wind-pollinated genera like *Artemisia* (Wodehouse 1935).

Stix (1960), in her comprehensive light microscopical work on pollen morphology of Compositae, described her “*Anthemis*-type”, to which she also assigned representatives of *Achillea*, *Chamaemelum*, *Glebionis*, *Leucanthemum*, *Cotula*, and *Matricaria*, as having a tegillate sexine. She found the inner, coarsely striate layer of the sexine to consist of rather thick and distantly branched infrategillary baculae, while the outer, finer striate layer is formed of fine pila with heads mostly fused together (“intertegillary baculae”). Her findings were later corroborated by transmission electron microscopy (TEM) and scanning electron microscopy (SEM) (e.g., Skvarla et al. 1977; Vezey et al. 1994; the latter authors use the term “double tectum” for the outer layer of baculae that they erroneously call “infratectal columellae”, while the infrategillary baculae are called “basal columellae”).

In further studies of pollen in Anthemideae by Čigurjaeva and Tereškova (1983), Benedí i González (1987), Fedorončuk and Savitskii (1988), and De Leonardis et al.



(1991), pollen grains of the “*Anthemis*-type” were found to be rather uniformly sphaeroidal, trizonocolporate and spiny, with tenuimarginate, sharply pointed colpi, and lalongate, tenuimarginate, sharply pointed ora. Detailed SEM studies by Vezey et al. (1994) demonstrated that pollen grains of *Ursinia* are qualitatively different from the common “*Anthemis*-type” because grains lack the infrategillary baculae (“basal columellae”) leading to so-called caveate pollen (Skvarla and Larson 1965; Skvarla and Turner 1966; Skvarla et al. 1977). They also found that pollen grains from *Artemisia* are characterized by infrategillary baculae (“basal columellae”) with complex and interwoven branches. Both conditions were interpreted as being apomorphic relative to the common “*Anthemis*-type” with vestigial infrategillary baculae observed in *Ursinia* being a reversal towards the plesiomorphic condition. A further exceptional case in Anthemideae is observed in *Adenanthellum* (Cotulinae), where the pollen is hexa-panto-colporate rather than tricolporate (Bremer and Humphries 1993).

Gadek et al. (1989) were able to provide light and electron microscopical (SEM, TEM) evidence for the dismembering of the former “Cotuleae”, with *Cotula*, *Leptinella*, *Nananthea*, and *Soliva* having anthemoid pollen, but *Abrotanella*, *Ischnea*, and *Centipeda* having senecioid, and *Ceratogyne*, *Dimorphocoma*, *Elachanthus*, *Isoetopsis*, *Minuria*, and *Plagiocheilus* having helianthoid exines, leading to their exclusion from Anthemideae. Detailed pollen morphological studies (LM, SEM) in Artemisiinae made by Martín et al. (2001, 2003) demonstrated that besides *Artemisia* and the closely related genera *Crossostephium*, *Filifolium*, *Mausolea*, *Neopallasia*, *Picrothammus*, *Seriphidium*, *Sphaeromeria*, and *Turaniphytum*, the more distantly related genera *Ajaniopsis*, *Kaschgaria*, and *Phaeostigma* are also characterized by smooth or microechinate pollen grains, while *Arctanthemum*, *Chrysanthemum*, *Hulteniella*, *Stilpnolepis*, and *Tridactylina* show the normal long-spined “*Anthemis* type”.

## EMBRYOLOGY

Anthemideae have been thoroughly, but not comprehensively, studied embryologically by Harling (1950, 1951, 1960), who concentrated mainly on northern hemisphere representatives of the tribe. Sparse information on embryo sac formation for southern hemisphere, i.e., the basal genera of the tribe (*Cotula* [Harling 1951], *Ursinia* [Ahlstrand 1978], *Lasiospermum* [Harling 1950], *Oncosiphon* [Harling 1951]), suggest that a monosporic embryo sac development is the plesiomorphic condition in the tribe (see reconstruction of character evolution in Fig. 38.7), and that the bisporic and tetrasporic modes of development are apomorphic. While the bisporic condition has been

solely reported for *Argyranthemum* of Glebionidinae, the tetrasporic embryo sac development observed in *Anthemis* (Harling 1950, 1960), *Cota* (Harling 1950, 1960), *Nananthea* (Martinoli 1940), *Tanacetum* (Harling 1951), and *Tripleurospermum* (Harling 1951) constitutes an important argument for the monophyly of Anthemidinae with a parallelism found in *Heteranthemis* (Harling 1951) of Glebionidinae. As in the case of chromosome numbers and karyotypes, more extensive and taxonomically complete studies on this character are needed (especially for the southern hemisphere representatives of the tribe) to fully appreciate the power of embryology for the phylogenetic classification of Anthemideae.

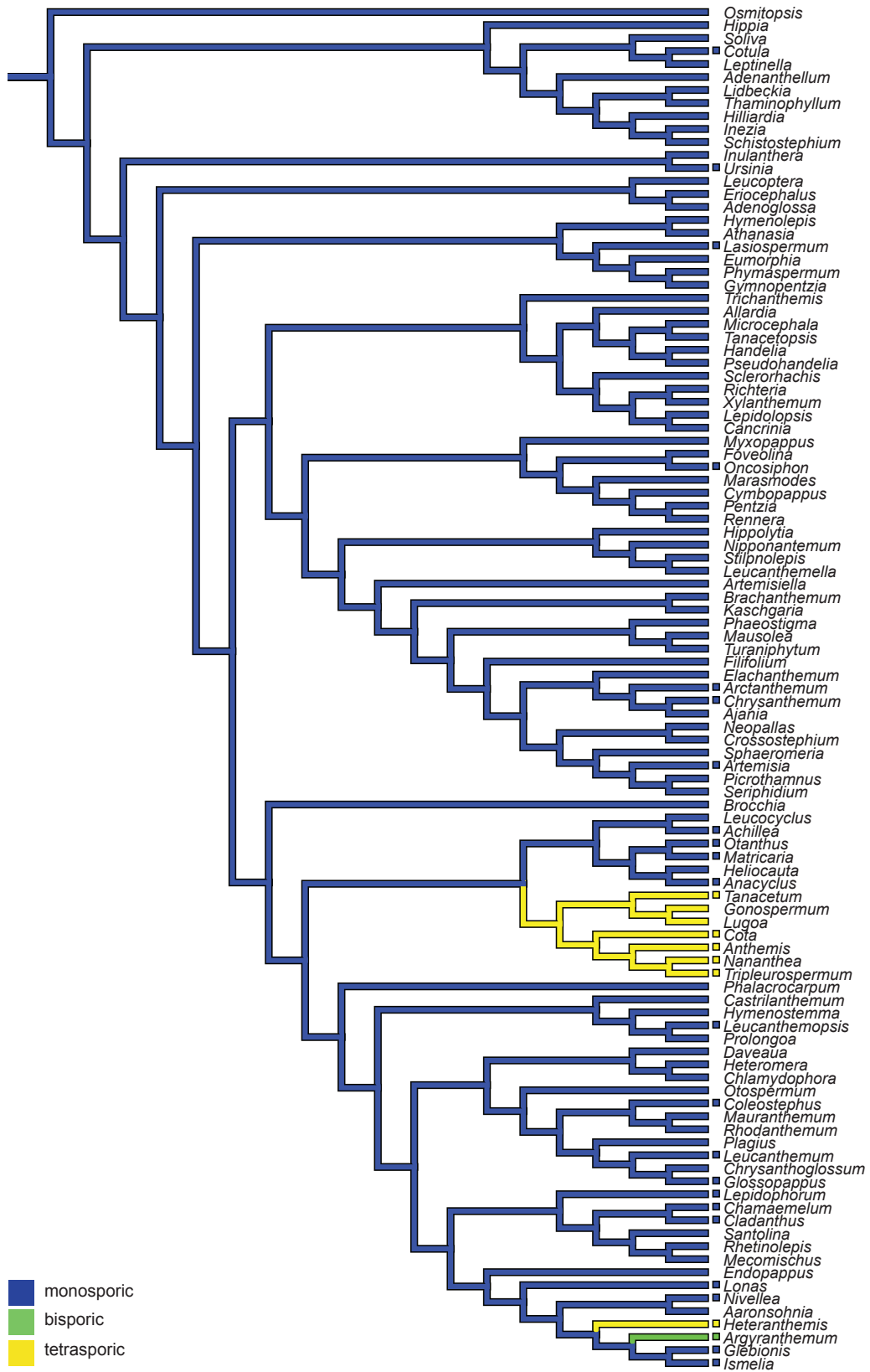
## CHROMOSOME NUMBERS

According to Heywood and Humphries (1977) and Bremer and Humphries (1993),  $x = 9$  is the most common base chromosome number in Anthemideae. Other base numbers occur only in a few genera. Based on our present phylogenetic reconstructions with the basal position of *Osmitopsis* (Osmitopsidinae) and Cotulinae and the base chromosome number of  $x = 10$  found in *Osmitopsis* (cf. Bremer and Humphries 1993) and a number of genera of Cotulinae (*Cotula*, *Hilliardia*, *Inezia*, *Soliva*, *Thaminophyllum*), the reconstruction of character evolution shown in Fig. 38.8 indicates that  $x = 10$  is the most reasonable base chromosome number for the common ancestor of the tribe. A transition to  $x = 9$ , however, is observed very close to the base of the tree and this base chromosome number is reconstructed for most of the subtribes above Athanasiinae.

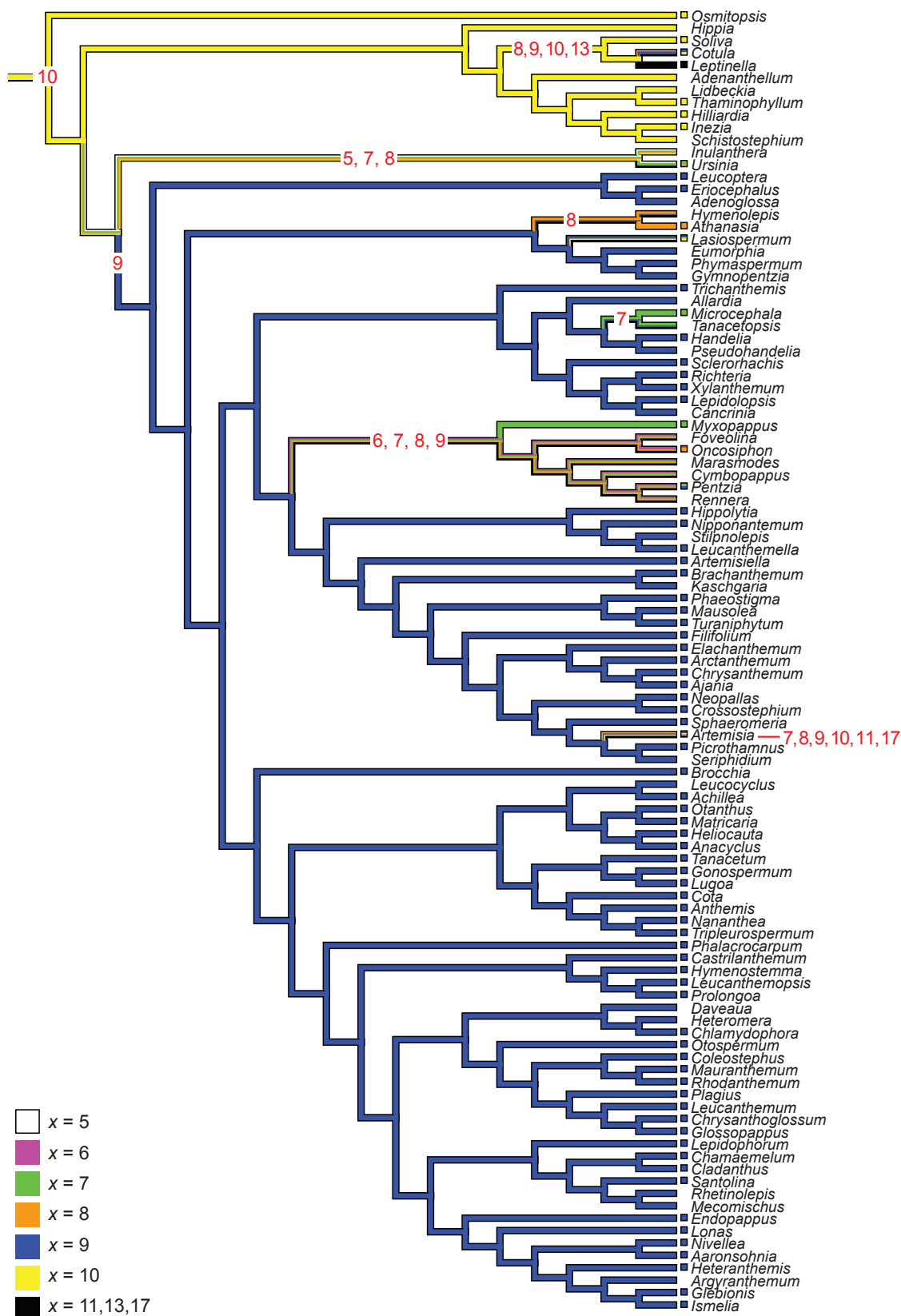
Descending dysploidy is found in *Cotula* ( $x = 8, 9, 10$ ; Cotulinae), *Ursinia* ( $x = 5, 7, 8$ ; Ursiniinae), *Athanasia* ( $x = 8$ ; Athanasiinae), *Myxopappus*, *Oncosiphon*, *Pentzia* ( $x = 6, 7, 8$ ; Pentziinae), *Microcephala* ( $x = 7$ ; Handeliinae), and to a considerable extent in *Artemisia* ( $x = 7, 8, 9$ ; Artemisiinae), while ascending dysploidy occurs more rarely in *Leptinella* ( $x = 13$ ; Cotulinae) and again in *Artemisia* ( $x = 8, 9, 10, 11, 17$ ; Artemisiinae).

Polyploidy is common in the tribe. Extensive polyploid complexes are found in *Achillea* ( $2x-10x$ ), *Artemisia* ( $2x-16x$ , Pellicer et al. 2007), *Dendranthema* ( $2x-10x$ ), *Leptinella* ( $4x-12x$ ), and *Leucanthemum* ( $2x-22x$ , Vogt 1991).

Uitz (1970) found prominent differences in structure and total size of karyotypes among Anthemideae. However, these observations were only based on northern hemisphere representatives of the tribe. Despite the lack of a more comprehensive study on the cytogenetics of the tribe, also including representatives of the southern hemisphere and Asian subtribes, some interesting evolutionary patterns of karyotype modification were observed (Uitz 1970). The low recombination rate



**Fig. 38.7.** Evolution of embryo sac development type, as reconstructed based on the nrDNA ITS maximum likelihood tree topology shown in Figs. 38.1 and 38.2.



**Fig. 38.8.** Evolution of base chromosome numbers, as reconstructed based on the nrDNA ITS maximum likelihood tree topology shown in Figs. 38.1 and 38.2.

caused by long generation times in perennials seems to be compensated for by the prevalence of allogamy and polyploidy. The relatively high recombination rates in annuals, due to their short generation times, are compensated by the tendency towards autogamy and structural heterozygosity, along with higher cross-over frequencies during meiosis. With the exception of a cytogenetic study by Mitsuoka and Ehrendorfer (1972), who included *Pentzia* as a southern hemisphere Anthemideae member in their study, more detailed surveys on karyotype evolution in the whole tribe are lacking. Only some studies at the generic level have been made in the last three decades, e.g., Ehrendorfer et al. (1977) in *Anacyclus*, Oberprieler (1998) in *Anthemis* s.l., or Mendelak and Schweizer (1986), Oliva and Vallès (1994), Vallès and Siljak-Yakovlev (1997), Torrell et al. (2003) and Garcia et al. (2007) in *Artemisia*.

## CHEMISTRY

As Christensen (1992) pointed out, the tribe Anthemideae is one of the chemically best investigated tribes of Compositae. According to Greger (1977), polyacetylenes, sesquiterpene lactones, and flavonoids are the three main classes of interest to systematists. However, as Bremer and Humphries (1993) also noted, information on micromolecular substances are still difficult to utilise in a taxonomic or phylogenetic context because these data have often been collected in a rather unsystematic, uncomprehensive and sporadic manner. Further, these studies often do not indicate the absence of a particular chemical compound in a taxon. The hardly accessible, and in many cases unknown, background information on biochemical pathways further complicates exploitation of micromolecular data for systematic studies. Nevertheless, in the following we will try to give a short review of important groups of secondary compounds in the tribe.

### Acetylenes and related compounds

Acetylenes and related compounds were reviewed for the tribe by Christensen (1992), who noted that a wide array of acetylenic compounds are present, including aromates, lactones, isocoumarins, cumulenes, pyrones, spiroacetal enol ethers, furans, thiophenes, thioethers, sulphoxides, alkamides, and straight chain acetylenes. Only in some southern hemisphere representatives of the tribe, namely in *Athanasia* and *Lasiospermum* of Athanasiinae, *Eumorphia*, *Gymnopentzia*, and *Phymaspermum* of Phymasperminae and *Ursinia* of Ursiniinae, acetylenes seem to be completely absent and are found substituted for by characteristic furanosesquiterpenes (see below).

An additional main pattern of chemical variation in the tribe is the predominance of C<sub>17</sub>-acetylene dehydro-

falcarinone and its derivatives in the southern hemisphere genera of *Cotula*, *Inezia*, *Lindbeckia*, *Schistostephium*, *Thaminophyllum* (all Cotulinae), and *Eriocephalus* (Athanasiinae) and in the northern hemisphere genus *Artemisia* (Artemisiinae). Most of the northern hemisphere representatives (including *Artemisia*) also contain acetylenes of the C<sub>13</sub> or C<sub>14</sub> pathways (Greger 1977; Marco and Barberá 1990; Christensen 1992). It is interesting to note that the mainly southern hemisphere genus *Pentzia* (Pentziinae), which is found closely related to the northern hemisphere portions of the molecular phylogenetic tree, is also characterized by acetylenes of the C<sub>14</sub> rather than the C<sub>17</sub> pathway.

Other groups of acetylenes have been observed (or studied) mainly in northern hemisphere representatives of the tribe. These show only restricted phylogenetic and/or taxonomic significance. For example, thiophenes (consisting mainly of C<sub>10</sub>-, C<sub>12</sub>- and C<sub>13</sub>-monothiophenes) are found regularly in *Artemisia* of Artemisiinae, in *Anthemis*, *Tanacetum*, and *Tripleurospermum* of Anthemidinae, in *Anacyclus* and *Matricaria* of Matricariinae, and in *Argyranthemum* of Glebionidinae. Aromatic acetylenes and furan acetylenes are mainly restricted to some Mediterranean genera of the tribe (*Anthemis* of Anthemidinae, *Leucanthemum* of Leucantheminae, *Santolina* of Santolininae, *Argyranthemum* and *Glebionis* of Glebionidinae, and in the unassigned *Lonas*), but also occur in *Artemisia* (Artemisiinae).

The presence of amides, which are frequently responsible for insecticidal activity, was considered significant for the circumscription of Achilleinae in Bremer and Humphries (1993), but it now seems that these secondary compounds are characteristic of a broader array of Mediterranean genera (*Achillea*, *Anacyclus*, *Leucocyclus*, and *Otanthus* of Matricariinae, *Chamaemelum* and *Cladanthus* of Santolininae, *Leucanthemum* of Leucantheminae, *Argyranthemum* and *Glebionis* of Glebionidinae, and the unassigned *Aaronsohnia*).

### Terpenoids

The strong aromatic odors found in members of Anthemideae are caused by the presence and high concentrations of monoterpenes. In several members of the tribe (e.g., *Achillea*, *Artemisia*, *Tanacetum*) essential oils from leaves and/or flowers are used medicinally or industrially (Greger 1977). The "pyrethrins", responsible for the insecticidal properties of some Anthemideae species (especially of *Tanacetum cinerariifolium*), also belong to this group of secondary compounds. A comprehensive study of monoterpenes and their bearing on the infrageneric classification of *Artemisia* was conducted by Stangl and Greger (1980). Oberprieler and Vogt (1999) used a gas chromatographic survey of essential oils to study species delimitation in *Anthemis* from Cyprus.

Of the sesquiterpenes, bisabolol from *Matricaria recutita* has gained some pharmaceutical attention due to its anti-



phlogistic activity, while the occurrence of furansesquiterpenes instead of polyacetylenes in *Athanasia*, *Lasiospermum* (Athansiinae), *Eumorphia*, *Gymnopentzia*, *Phymaspermum* (Phymasperminae), and *Ursinia* (Ursiniinae) was considered an important character to circumscribe the subtribe Ursiniinae in the sense of Bremer and Humphries (1993), which now appears to be highly polyphyletic.

Sesquiterpene lactones in Anthemideae were reviewed by Seaman (1982) in the course of his study on this group of secondary compounds as taxonomic markers in Compositae. The simplest sesquiterpene lactones are the germacranolides that are converted into more derived guaianolides and santanolides (Greger 1977). Sesquiterpene lactones are very common in the genus *Artemisia*, in which they constitute the most characteristic chemical markers (Marco and Barberá 1990). While the santanolides are only known from *Artemisia*, the other two groups are found both in the basal subtribe Cotulinae and in the more advanced ones (Pentziinae, Artemisiinae, Anthemidinae, Matricariinae, and Santolininae). Most important in phylogenetic respects is the observation reported by Seaman (1982) that many genera of the tribe are linked together by the presence of C<sub>6</sub> trans-lactonized guaianolides, and that these constituents are missing in the southern hemisphere genera *Osmitopsis* (Osmitopsidinae) and *Ursinia* (Ursiniinae).

### Flavonoids

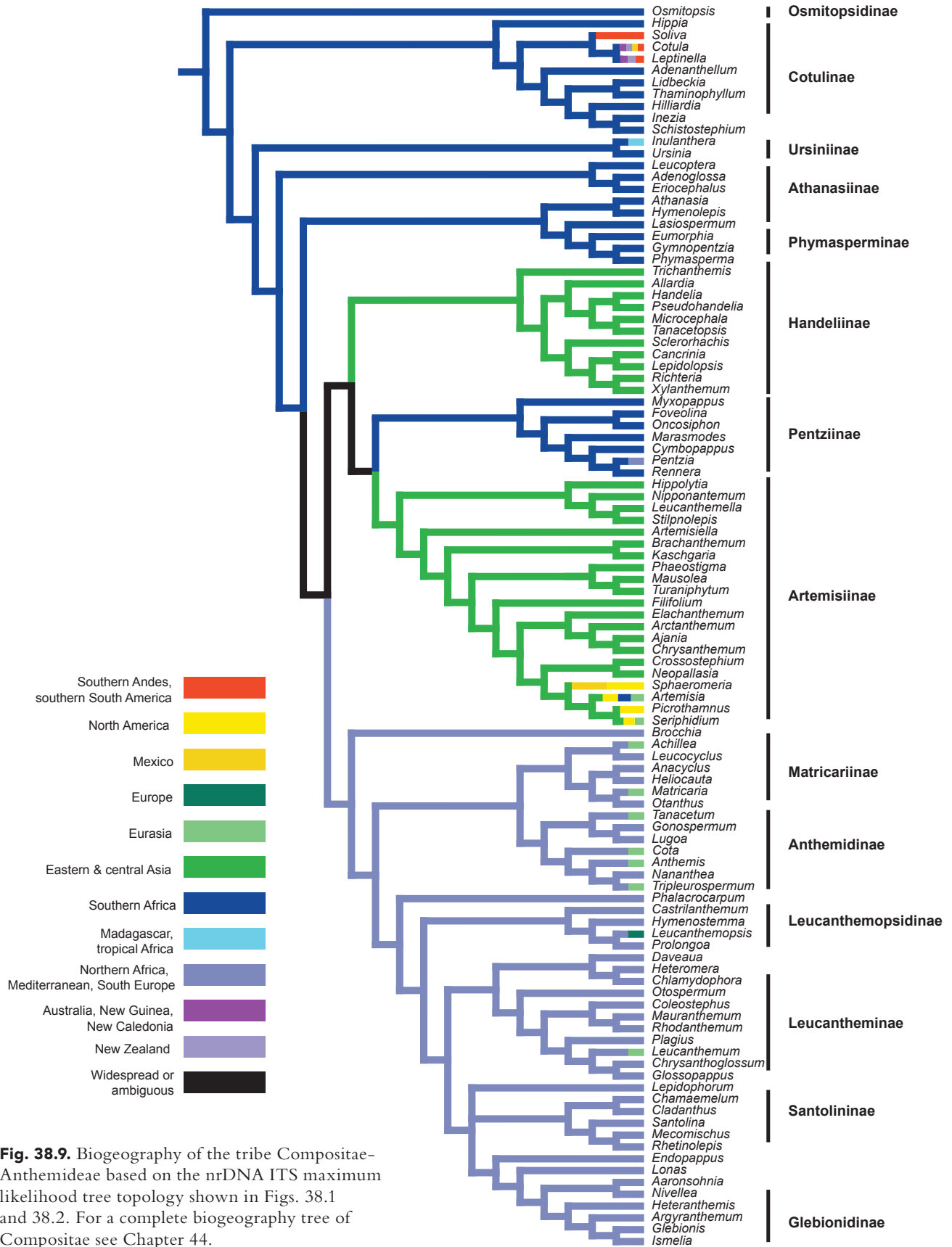
Information on flavonoids in Anthemideae was reviewed recently by Bohm and Stuessy (2001) in their comprehensive treatment of this group of secondary compounds for the whole family. These authors consider the tribe as moderately complex in its flavonoid chemistry and find that flavones and flavonols are about equally represented in the larger genera (Bohm and Stuessy 2001). While anthochlors (aurones and chalcones) and isoflavones have never been reported from the tribe (with the exception of a chalcone derivative reported by Huneck et al., 1985, as quoted in Marco and Barberá, 1990), only a few members were found to possess dihydrochalcones, flavanones, dihydroflavonoles, and C-glycosylflavones. When information available from Bohm and Stuessy (2001) is compared with the presently suggested subtribal classification only two interesting distribution patterns emerge. Firstly, it seems that a 4'-hydroxylation with extra oxygenation at C<sub>6</sub>, while present in at least some genera of the other surveyed subtribes, is completely lacking from Leucantheminae, Leucanthemopsidinae, and Glebionidinae. Secondly, flavanones are absent from both the basal and the advanced subtribes and characterise the intermediate Athansiinae (*Eriocephalus*), Phymasperminae (*Gymnopentzia*), Pentziinae (*Oncosiphon*, *Pentzia*), and Artemisiinae (*Arctanthemum*, *Artemisia*, *Filifolium*).

### BIOGEOGRAPHY

Anthemideae show a mainly Old World-centered, extra-tropical distributional range. Primary concentrations of genera and species are observed in the steppe and semi-desert vegetation of middle and southwest Asia and the areas with a winter rain, Mediterranean climate type in southern Africa, and the Mediterranean region ("etesian climate"). While both the boreal and arctic zone is inhabited by numerous species of the large genera *Artemisia* and *Achillea*, other members of the tribe (*Cotula*, *Leptinella*, and *Soliva* of Cotulinae) occur in the southern hemisphere (Jäger 1987). In addition, representatives of the tribe are also characteristic at high altitudes (Meusel and Jäger 1992). The adaptation to a winter-green and often annual growth rhythm in the Mediterranean climate types has led to the enlargement of distributional areas of numerous taxa due to their co-migration with humans as members of a segetal or ruderal flora (Meusel and Jäger 1992).

The biogeographic signal in the evolutionary history of the entire tribe is apparent (Fig. 38.9). Members of the basal subtribes Osmitopsidinae, Cotulinae, Ursiniinae, Athansiinae, and Phymasperminae form a mainly southern hemisphere grade with a concentration of genera and species in South Africa. Only some members of Cotulinae and Athansiinae occur outside of southern Africa. Members of *Cotula* are found also in northeastern Africa (*C. abyssinica* Sch.Bip. ex A. Rich., *C. cryptocephala* Sch. Bip. ex A. Rich.), Australia (*C. alpina* (Hook. f.) Hook. f., *C. cotuloides* (Steetz) Druce), Java (*C. elongata* B. Vogel), Central and southern America (*C. mexicana* (DC.) Cabrera), and the southern oceanic islands (*C. goughensis* R.N.R. Brown, *C. moseleyi* Hemsl.) or have conquered vast areas as widespread weedy species (*C. anthemoides* L., *C. australis* (Spreng.) Hook. f., *C. coronopifolia* L.). *Leptinella*, a derivative of *Cotula*, has a center of diversity in Australia and New Zealand, and *Soliva* is mainly American and Australian with two species widespread as weeds (*S. sessilis* Ruiz & Pav., *S. stolonifera* (Brot.) Loudon). Finally, *Ursinia* of Ursiniinae and *Lasiospermum* of Athansiinae have an extended distributional range to northeastern Africa (Ethiopia) and southwestern Asia (Sinai), respectively.

Subtribes of the intermediate Asian-southern African grade clearly demonstrate that the evolutionary history of the tribe obviously passed through phases of migrations out of Africa into Asia and/or the Mediterranean region. Pentziinae are mainly southern African, but some species of *Pentzia* are also found in northern Africa (*P. hesperidum* Maire & Wilczek, *P. monodiana* Maire) and in the Horn of Africa region (*P. somalensis* E.A. Bruce ex Thulin, *P. arabica* Thulin; Thulin 2001). Handeliinae are strictly Asian with most genera stretching their area between Iran and Afghanistan and China, while Artemisiinae (headed by *Artemisia* and its allied genera) have conquered



**Fig. 38.9.** Biogeography of the tribe Compositae-Anthemideae based on the nrDNA ITS maximum likelihood tree topology shown in Figs. 38.1 and 38.2. For a complete biogeography tree of Compositae see Chapter 44.

areas of the northern hemisphere beyond central Asia (e.g., *Arctanthemum* in arctic Eurasia and arctic America, *Chrysanthemum* and *Leucanthemella* in Japan and eastern Europe, or *Artemisia*, *Picrothamnus*, and *Sphaeromeria* in America) and made their way to the Mediterranean (*Artemisia*), South America (*Artemisia copa* Phil., *A. echegrayi* Hieron., *A. mendozana* DC.), and even back into Africa south of the Sahara (*Artemisia afra* Jacq.).

The Eurasian/Mediterranean clade of the tribe which comprises the most advanced subtribes Anthemidinae, Glebionidinae, Leucantheminae, Leucanthemopsidinae, Matricariinae, and Santolininae shows a strictly northern hemisphere distribution with a main concentration in southwestern Asia and the circum-Mediterranean region, and only four species of *Tanacetum* reaching the New World via Siberia (*T. camphoratum* Less., *T. douglasii* DC., *T. huronense* Nutt., *T. bipinnatum* Sch.Bip.). This monophyletic group of subtribes is the only part of the tribe for which detailed statistical biogeographic analyses have been carried out (Oberprieler 2005). Based on a combination of dispersal–vicariance analysis (Ronquist 1997) and molecular clock dating of calibrated, rate-smoothed maximum-likelihood trees based on ITS sequence information, Oberprieler (2005) demonstrated that the ancestor of this clade diverged from the basal African lineages in the late Early Miocene (18 Ma), presumably in conjunction with the collision of the African and Eurasian platforms. Recurrent dispersal/vicariance events during the Middle and Late Miocene (16–11 Ma), both between the eastern and western Mediterranean region and (in the latter region) between the northern and southern Peri-Tethys platforms, caused the further diversification of the clade. This led to the paramount role of the North African platform and the Anatolian region in the radiation of the tribe, causing the present-day generic richness in the western Mediterranean subclade and richness of species in the large genera *Achillea*, *Anthemis*, *Cota*, *Tanacetum*, and *Tripleurospermum* of the eastern Mediterranean subclade.

## EVOLUTION

As Ehrendorfer (1970) pointed out, the main changes in evolutionary patterns and processes in Anthemideae have been observed in connection with the switch from a perennial to an annual life form. According to the survey made by Uitz (1970), perennials of the tribe are mostly self-incompatible, while annuals are nearly all self-compatible, more or less autogamous, and much more variable in karyotype length, symmetry, and chiasma frequency. In these respects, the finding made in a systematic study of *Anthemis* in northern Africa by Oberprieler (1998) may be roughly generalized to most Eurasian/Mediterranean representatives of the tribe, if not for all members of

Anthemideae. Variation in perennials occurs on a larger geographical scale, and morphologically divergent forms are geographically isolated but often connected by morphological intermediates, which results in clinal patterns of morphological variation. In contrast, annual taxa show more restricted, allopatric distributional areas, and morphological variation within taxa is rather small as compared to the variation among taxa. Evolutionary divergence appears to be more rapid in the annual representatives than in the perennial ones. However, exceptions to these rules exist, and we often find narrowly restricted perennials (often paleoendemics with remnant populations or neoendemics due to polyploidization), as well as widely distributed annuals (especially weedy species that followed the human dispersal as members of a segetal or ruderal flora).

Anthemideae provide several impressive and fascinating examples of polyploid complexes in Compositae. Without exception, these are confined to perennial taxa (whole genera as in *Achillea*, *Leucanthemum*, or *Leptinella* or perennial members of polymorphic genera, e.g., as in *Anthemis*). As noted above, the most comprehensive series of polyploid chromosome numbers exist in *Achillea* ( $2x-10x$ ), *Artemisia* ( $2x-16x$ , Pellicer et al. 2007), *Dendranthema* ( $2x-10x$ ), *Leptinella* ( $4x-12x$ ), and *Leucanthemum* ( $2x-22x$ , Vogt 1991). In *Achillea*, the best studied genus of the polyploid complexes in Anthemideae, various studies have demonstrated numerous cases of polyploidy, transition zones between species, hybridization, and excessive polymorphism (Ehrendorfer 1959; Vetter et al. 1996a, b; Saukel et al. 2004) leading to the conclusion that reticulate evolution was not only involved in recent radiations but must have been already active in the early diversification of the genus (Guo et al. 2005). On the other hand, however, studies presently underway in *Leptinella* (Himmelreich, unpub.) and *Leucanthemum* (Höbl, unpub.) demonstrate that the present polyploid species evolved mainly from their diploid ancestors during the Pleistocene. Using AFLP analyses, Guo et al. (2005) were able to decipher some relationships in the *Achillea millefolium* complex which contains species with diploid and up to hexaploid chromosome numbers.

The Macaronesian genus *Argyranthemum* of subtribe Glebionidinae with its 24 endemic species provides a spectacular example of adaptive radiation at the diploid level (Francisco-Ortega et al. 1996, 1997). Using evidence from phylogenetic analyses based on nrDNA and cpDNA, along with the characterisation of the ecology of each species, Francisco-Ortega et al. (1996, 1997) demonstrated that the primary avenue of taxonomic diversification in this group was extensive inter-island colonization between similar ecological zones, and that hybridization and diploid hybrid speciation played an important role in the evolution of the genus. In other genera of the tribe, diversification through hybrid speciation is often

hypothesized on morphological grounds (e.g., in *Anthemis* by Oberprieler, 1998) but remains unproven using molecular techniques. Since intergeneric crosses between and among different genera of the tribe produce fertile or semifertile offspring (cf. experiments of Mitsuoka and Ehrendorfer, 1972, with representatives of *Anthemis*, *Chamaemelum*, *Cota*, *Matricaria*, and *Tripleurospermum*), the prerequisite for diploid hybrid speciation is highly plausible and may be responsible not only for speciation events within genera but also for the reticulate combination of characteristic morphological features of different genera of the tribe.

### ECONOMIC USES

Members of Anthemideae are used and cultivated for a broad variety of purposes, mainly as ornamentals, but also for their medicinal and culinary importance, as well as other economic uses. For the southern hemisphere representatives of the tribe, cultivation as ornamentals is known for species of *Athanasia*, *Eriocephalus*, *Oncosiphon*, and *Ursinia*, while members of *Cotula* and especially of *Leptinella* are well-known carpeting plants also in the northern hemisphere. From the Asian subtribe Artemisiinae, the autumn flowering garden chrysanthemums derived from *Chrysanthemum grandifolium* (probably a complex hybrid group raised in China from *Ch. indicum*) are of high economic importance as ornamentals, followed by members of *Ajania*, *Arctanthemum*, *Artemisia*, *Leucanthemella*, and *Nipponanthemum*. Ornamentals from the Eurasian/Mediterranean clade are found in *Tanacetum* (*T. coccineum*, the garden pyrethrum), *Leucanthemum* (*L. ×superbum*, the oxeye daisy or marguerite), *Mauranthemum* (*M. paludosum*), and the Paris daisy *Argyranthemum frutescens*. To a lesser extent, members of *Achillea*, *Otanthus*, *Cota*, *Heteranthemis*, *Ismelia*, *Glebionis*, *Chamaemelum*, *Santolina*, and *Lonas* are also found in ornamental gardens.

Medicinal importance of Anthemideae species is mainly restricted to members of *Artemisia* and *Matricaria*, where, for example, vermifugal or antimalarian usages

are described for *A. abrotanum* and *A. annua*, respectively. *Matricaria recutita* is known for its antibacterial and anti-inflammatory chemical compounds. To a lesser extent, members of *Achillea* (*A. millefolium* as an herbal treatment of arthritis), *Anacyclus* (*A. pyrethrum* as the source of ‘Radix Pyrethri’, pellitory), and *Tanacetum* (*T. corymbosum* providing an antibacterial oil) may be similarly used. *Artemisia* is also an important source for plant species with high culinary importance. *Artemisia absinthium* (absinth), *A. genipi*, *A. glacialis* and *A. umbelliformis* (genepi liqueur), and *A. pontica* (flavour of vermouth) are used to flavour alcoholic beverages; *A. dracuncululus* (tarragon, estragon) and *A. vulgaris* are important spices.

Additional economic importance is reported for the two species of *Glebionis* that are cultivated in China and Japan due to their edible leaves and flowers, for *Crossostephium chinense* as a source of cotton-like wool that is obtained from the hairs on young leaves, for *Cota tinctoria* that produces a yellow dye, and for *Chamaemelum nobile*, the source of the ‘‘Roman Chamomile’’ oil that is mainly used in the cosmetics industry. Some members of Anthemideae are known for their insecticidal potential. This is mainly exploited in the case of *Tanacetum cinerariifolium*, the important source of ‘‘pyrethrum’’ insecticide. Some Asiatic, North African and North American species of *Artemisia* are relevant for pastures and fodder. *Pentzia* has also been introduced (with little success) in North America as a fodder plant in arid areas.

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