A new subtribal classification of the tribe *Anthemideae* (*Compositae*)

Abstract


A new subtribal classification of the *Compositae-Anthemideae* is presented based on phylogenetic reconstructions for sequence information of the internal transcribed spacer (ITS) region of the nuclear ribosomal DNA (nrDNA) for 103 of the 111 accepted genera of the tribe. Results of the present analyses are compared with results from phylogenetic analyses based on cpDNA ndhF sequence variation and discussed in conjunction with morphological, anatomical, cytological, embryological and phytochemical evidence. As a result, 14 subtribes are circumscribed and described in detail, with information provided concerning the generic members and the geographical distribution of these entities. Four subtribes (i.e. *Osmitopsidinae*, *Phymasperminae*, *Pentziinae* and *Leucanthemopsidinae*) are described as new to science, for a further subtribe a new name (*Glebionidinae*, replacing the illegitimate *Chrysantheminae*) is validated.

Key words: *Asteraceae*, mtDNA ITS, phylogeny, taxonomy.

Introduction

According to the most recent generic conspectus of *Compositae* tribe *Anthemideae* (Oberprieler & al. 2006), that tribe consists of 111 genera and c. 1800 species. Main concentrations of members of the *Anthemideae* are in Central Asia, the Mediterranean region and southern Africa. Members of the tribe are well known as aromatic plants, and some are utilised for their pharmaceutical and/or pesticidal value. While the circumscription of the tribe remained relatively unchanged since the early artificial classification systems of Lessing (1832), Hoffmann (1890-94) and Bentham (1873) and more recent ones (e.g., Reitbrecht 1974, Heywood & Humphries 1977, Bremer & Humphries 1993) with *Cotula* and *Ursinia* included in the tribe despite considerable debate (Bentham 1873, Robinson & Brettell 1973, Heywood & Humphries 1977, Jeffrey 1978, Gadek & al. 1989, Bruhl & Quinn 1990, 1991, Bremer & Humphries 1993, Kim & Jansen 1995), the subtribal classification caused 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 (receptacular scales), 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 the Anthemideae goes to John Briquet who used characters of the pericarp for the demarcation of Mediterranean genera of the tribe (Briquet 1916a-c, Briquet & Cavilleri 1916). In the following decades, detailed carpological studies were made in the so-called Chrysanthemum complex (Giroux 1930, 1933, Horvatic 1963, Borgen 1972, Humphries 1976, Alavi 1976), in the Anthemis complex (Humphries 1977, Gonzál & Brion 1985) and in a more geographically focussed study by Kynčlová (1970). The carpological survey of Reithbrecht (1974) deserves consideration as the first comprehensive tribe-wide 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 by Heywood & Humphries (1977). Triggered by these studies, achene anatomical studies in the following decades contributed to a better understanding of the taxonomy and the 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 & Quinn (1990) added fruit anatomical evidence for the exclusion of several genera of ‘Cotulae’ from the Anthemideae and the retention of Cotula, Leptinella, Nananthea and Soliva in the tribe.

As Christensen (1992) has pointed out, the tribe Anthemideae is one of the chemically best investigated tribes of the Compositae. Following Greger (1977), polyactylenes, sesquiterpene lactones and flavonoids are the three main classes of interest to systematists. However, as also Bremer & Humphries (1993) have 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 and because these studies often lack the communication of the absence of a particular chemical compound in a taxon. Additionally, the hardly accessible and in many cases unknown background information on biochemical pathways further complicates exploitation of micromolecular data for systematic studies.

The tribe was recently monographed and a subtribal classification elaborated by Bremer & 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 & al. 2000) or for the Mediterranean genera alone (Francisco-Ortega & al. 1997, Oberprieler & Vogt 2000, Oberprieler 2002, 2004a-b, 2005). As a consequence of these findings, Oberprieler & al. (2006) refused to accept the subtribal classification of Bremer & Humphries (1993) in their recent treatment of Anthemideae in Kubitzki’s The Families and Genera of Vascular Plants, Vol. 8 Asterales (Kadereit & Jeffrey 2006) and arranged the genera in a linear manner according to the results of Watson & 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, while within these major groups genera were arranged alphabetically and/or into alleged monophyletic generic groups.

Over the last decade sequence information, especially for the internal transcribed spacer (ITS) region of the nuclear ribosomal repeat (nrDNA), has been collected for representatives of nearly all genera of Anthemideae. With the publication of Oberprieler (2004b), at least one member of all accepted genera in the Eurasian/Mediterranean clade had been sequenced for this marker. The further contribution of nrDNA ITS sequence information for all genera of the southern hemisphere genera by Himmelreich & al. (in prep.) and the addition of yet unpublished se-
quences for the Asian representatives of the tribe allows it now to present a complete molecular analysis with nearly all genera accepted by Bremer & Humphries (1993) or Oberprieler & al. (2006). The present publication, therefore, aims at a new proposal of a subtribal classification of the Anthemideae based on nrDNA ITS sequence information and discussed with the morphological, anatomical, cytological and phytochemical evidence at hand.

Material and methods

**Plant material.** – One hundred and five representatives from 103 genera of Anthemideae were included in the present analyses. Sequence information for most of the taxa came from former publications (Francisco-Ortega & al. 1997, 2001, Kornkven & al. 1998, Oberprieler & Vogt 2000, Oberprieler 2001, 2002, 2004-b, 2005, Watson & al. 2002, Vallés & al. 2003, Guo & al. 2004, Gemeinholzer & al. 2006, Himmelreich & al., in press) and from published and unpublished EMBL/GenBank accessions (Appendix 1). The sequences for Allardia tomentosa Decne., Artemisiella stracheyi (Clarke) Ghafoor, Handelia trichophylla (Schrenk) Heimerl, Phaeostigma salicifolium (Mattf.) Muldashev, Picrothamnus desertorum Nutt., Richteria pyrethroides Karelin & Kir., Scherorhachis platyrhachis (Boiss.) Podlech, Tanacetopsis eriobasis (Rech. f.) Kovalevsk., Tanacetopsis mucronata (Regel & Schmalh.) Kovalevsk., Trichanthemis aulieatensis (B. Fedtsch.) Krasch. and Xylanthemum tianschanicum (Krasch.) Muradyan are new to science and were obtained from herbarium specimens (see Appendix 1). We used 10 species of the tribes Astereae, Calenduleae and Gnaphalieae as outgroup representatives in the analyses.

**DNA isolation, PCR amplification, sequencing.** – DNA was extracted from leaves taken from herbarium specimens. Specimens were extracted following a modified protocol based on the method by Doyle & Doyle (1987). PCR amplifications of the nrDNA ITS marker were performed using primers 18SF and 26SR (Rydin & al. 2004) or ITS5A (Funk & al. 2004) and ITS4 (White & al. 1990). In some cases ITS1 and ITS2 were amplified separately using primers ITSSA (Funk & al. 2004), ITS2, ITS3 and ITS4 (White & al. 1990). PCR amplifications were performed with 0.2 µM dNTP's, 0.02 µM of each primer, 0.2 U Taq polymerase (Qbiogene) in 10 µl 1x Buffer and the following temperature profile: 2-5 min at 95 °C, then 35 to 40 cycles of 30 s at 95 °C, 30 s at 50 °C, 60 s at 72 °C, with a final extension of 8 min at 72 °C. Cycle sequencing of purified PCR products was performed using the CEQ Dye Terminator Cycle Sequencing Quick Start Kit (Beckman Coulter) and sequences were analysed on a CEQ 8000 automated sequencer (Beckman Coulter). The new nrDNA ITS sequences (ITS1 and ITS2) were submitted to the EMBL sequence data bank.

**Sequence alignment and phylogenetic reconstructions.** – Sequences were aligned with BioEdit version 7.0.5.2 software (Hall 1999) and the alignment subsequently corrected manually. Gaps in the alignments were treated as missing data. The alignment is provided in the electronic supplement to this paper at www.bgsm.org/willdenowia/willd37/Oberprieler+al.htm.

Maximum parsimony (MP) analyses of the data sets were performed using the heuristic search algorithm of PAUP* version 4.0b10 (Swofford 2002) with ACCTRAN, MULPARS and TBR branch swapping in action. Character states were specified unordered and unweighted. Support for clades was evaluated using a bootstrap analysis (Felsenstein 1985). Bootstrap analyses were performed using the following settings: 100 bootstrap replicates, 10 random addition sequence replicates per bootstrap replicate, with a time limit of 10 s per random addition sequence replicate, and ACCTRAN, TBR and MULPARS in action.

In addition to the above described cladistic (MP) analyses, the data set was also analysed with two model-based approaches to phylogenetic inference, the Maximum-Likelihood (ML) method (Felsenstein 1981, Kishino & Hasegawa 1989) and a Bayesian inference (BI) approach (Lewis 2001). Since both methods are dependent on assumptions about the process of DNA substitution (a model of DNA evolution), we used the program MODELTEST version 3.06 (Posada & Crandall...
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1998) to find the model (among the 56 models tested) that best fits the underlying sequence information. This resulted in the acceptance of the model of Tamura & Nei (1993) with a gamma distribution of substitution rates over the sites (TrN + Γ), the base frequencies being freqA = 0.2562, freqC = 0.2128, freqG = 0.2000 and freqT = 0.3309, a gamma distribution shape parameter of α = 0.7540, and a substitution rate matrix of $R[\text{A-C}] = R[\text{A-T}] = R[\text{C-G}] = R[\text{G-T}] = 1.0, R[\text{A-G}] = 2.8158$, and $R[\text{C-T}] = 4.0621$. Using these parameters, a ML search was performed with Treefinder (Jobb 2004).

The same parameters of the TrN + Γ model were also used in the BI approach performed with the software programme MRBAYES version 2.01 (Huelsenbeck & Ronquist 2001). Four Metropolis-coupled Markov chain Monte Carlo (MCMC) chains with incremental heating temperature of 0.2 were run for 2 000 000 generations and sampled every 100th generation. The burn-in period was determined graphically, and the first 1000 of the 20 000 sampled trees were discarded. Estimation of tree topology and posterior probabilities of clades were based on the remaining 19 000 trees.

Results

The alignment of all 115 nrDNA ITS sequences was 527 bp long with 412 variable positions including 323 parsimony informative characters. The heuristic MP search (results not shown) yielded 7716 equally most parsimonious trees with a length of 2599 steps, a consistency index (CI with autapomorphies excluded) of 0.2756, and a retention index (RI) of 0.6185. The ML tree (lnL = -13 044.994) is shown in Fig. 1 and 2, together with bootstrap values from the MP search and posterior probabilities gained from the model constrained BI analysis.

The monophyly of the Anthemideae was confirmed in all analyses with high statistical support (88 % bootstrap support BS / posterior probability PP 1.0). The monophyletic tribe was found to include also those genera of the Anthemideae sensu Bremer & Humphries (1993) for which an independent tribal classification had been discussed, i.e. Ursinia (Ursinieae Robinson & Brettell 1973: 83) and Cotula (Cotuleae Lowe 1857-68: 415. 1868). In correspondence to a number of former analyses based on nrDNA ITS (Francisco-Ortega & al. 1997, 2001, Oberprieler & Vogt 2000, Oberprieler 2004a-b, 2005) or cpDNA ndhF (Watson & al. 2000, Himmelreich & al., in press) sequence variation, the results of the present analyses again demonstrate that most of the subtribes circumscribed by Bremer & Humphries (1993) are not monophyletic. Exceptions are the ‘Chrysantheminae’ (now Glebionidinae) consisting of Argyranthemum, Glebionis, Heteranthemis and Ismelia (0.98 PP) and the Artemisiinae (after inclusion of Hippolytia of the ‘Tanacetinae’ and Leucanthemella and Nipponanthemum of the Leucantheminae: 88 % BS / PP 1.0), while an example for an extremely polyphyletic subtribe are the Mattricariinae as defined by Bremer & Humphries (1993) with members found scattered throughout the cladogram from Hippia and Cotula at the base to Aaronsohnia, Endopappus and Lonas at the very top of the phylogenetic tree.

As far as the main features of the trees are concerned, the phylogenetic reconstructions received from the different methods applied are consistent and comprise (a) the basal split into the isolated genus Osmitopsis plus the generic group around Cotula (93 % BS / PP 1.0) and the rest of the tribe (88 % BS / PP 1.0), (b) a grade of southern African representatives of the tribe (Ursinia through Phymaspermum), (c) the clade of further southern African genera around Pentzia (96 % BS / PP 1.0), together with a clade of Asian genera (Trichanthemis through Richteria, 93 % BS / PP 1.0), the Artemisiinae (88 % BS / PP 1.0) and the monophyletic Mediterranean/Eurasian group of genera (91 % BS / PP 1.0), (d) the latter clade (Phalacrocarpum through Glebionis, PP 1.0) that is additionally supported by a deletion of 19 bp in ITS2), and (e) smaller clades around the genera Anthenis (Mattricaria through Nananthea, PP 1.0), Leucanthemum (Otospermum through Heteromera, PP 1.0), Leucanthemopsis (Castilanthemum through Leucanthemopsis, 100 % BS / PP 1.0) and Argyranthemum (Heteranthemis through Glebionis, PP 0.98).

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As discussed in detail by Himmelreich & al. (in press), the main topological features of the here presented phylogenetic analysis based on nrDNA ITS sequence information is in agreement with phylogenetic reconstructions based on cpDNA ndhF sequences for representatives of 61 genera of the tribe. To shortly summarise these results here, the phylogenetic trees from the chloroplast marker also indicate (a) the isolated and basal position of *Osmitopsis*, (b) the monophyly of the generic group around *Cotula*, (c) the paraphyletic nature of the generic assemblage around *Athanasia*, (d) the rather isolated position of *Ursinia*, (e) the clade of further southern African genera around *Pentzia*, (f) the monophyly of the group made of by *Eumorphia*, *Gymnopentzia* and *Phymaspermum*, (g) the monophyly of the group of genera characterised by the mentioned deletion of 19 bp in ITS2, and (h) the monophyly of several genetic groups in the Mediterranean clade (i.e. the present *Glebionidinae*, *Santolininae*, *Leucantheminae*). On the other hand, the two analyses contrast in (a) the support of *Artemisiinae* (well supported in the nrDNA ITS data set).
but not so in the cpDNA ndhF data set) and (b) the position of Phymasperminae relative to Athanasiinae (closely related in the nrDNA ITS tree but closely related with Artemisiinae and Pentziinae in the cpDNA topology).

Based on the two mentioned molecular studies we present here a new subtribal classification for the Anthemideae. The subtribes are described morphologically and (when possible) cytologically, their type, their geographical distribution and their generic members are stated, and they are discussed in terms of their phylogenetic nature (monophyly vs. para- or polyphyly) using evidence from morphology, anatomy, embryology, cytology and phytochemistry. Genera with unknown (due to the lack of sequence information) or equivocal affiliation (due to unsupported positions in the phylogenetic reconstructions) are indicated as unassigned to a subtribe at the end of each of the four geographical groups of subtribes described below. For each genus, the number of species is given in brackets.

I. Southern hemisphere grade

1. Osmitopsisinae Oberpr. & Himmelreich, subtrib. nov.
Type: Osmitopsis Cass. [Osmitopsis asteriscoides (L.) Less.].
Frutices vel suffrutices. Indumentum nullum vel e pilis basifixis formatum. Folia alterna, integra vel lobata. Capitula solitaria vel in corymbum laxum disposita, radiata. Involucrum campanula-

Shrubs or subshrubs. *Indumentum* absent or of basifixed hairs. *Leaves* alternate, entire to lobed. *Capitula* solitary or in lax corymbbs, radiate. *Involucre* campanulate. *Phyllaries* in 2-4 rows, often with scarious margins. *Receptacle* flat to conical, paleate; paleae narrowly elliptical to obovate, canaliculate and enclosing the florets. *Ray florets* female or neuter; limbus white, occasionally pilose abaxially, tube occasionally pilose. *Disc florets* hermaphrodite or male; corolla 5-lobed, yellow; anthers basally caudate, with non-polarised endothelial tissue and a slender filament collar; stylopodium sometimes large and persistent in fruit. *Achenes* obvoid to ellipsoid, 3-4-angled or -ribbed; apex with a corona of subulate to triangular, basally fused scales, or marginally rounded. *Embryo sac development* unknown. *Base chromosome number* $x = 10$.

**Distribution.** – South Africa.

**Members.** – *Osmitopsis* Cass. (9)

**Notes.** – The isolated and basal position of *Osmitopsis* is not only demonstrated by the present results based on nrDNA ITS sequence variation but was also found in phylogenetic analyses based on cpDNA *ndhF* (Himmelreich & al., in press). The main characteristic of *Osmitopsis* is the possession of tailed anthers, which led some authors (Bentham 1873, Hoffmann 1890-94) to consider an inulean affiliation for the genus, while others (e.g. Cassini 1823) included it into their concept of *Anthemideae*. Palynological evidence (Stix 1960) and further characters such as odour, the occurrence of pluriseriate involucral bracts with scarious margins, together with the truncate style and the tendency towards the reduction of the pappus also argue for its inclusion into the *Anthemideae*.

As Bremer (1972) and Nordenstam (1987) already noted, the genus is systematically isolated in the tribe. The inclusion of the paleate genus *Osmitopsis* in their subtribe *Thaminophyllinae*, together with the more closely related (paleate) genera *Adenenthellum, Inezia, Lidbeckia* and *Thaminophyllum* (Bremer & Humphries 1993), was mainly based on a similar habit and similar foliage, the occurrence of many-veined rays and a large stylopodium, the tendency towards the loss of a pappus in some species, and the (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 & al. (2000), who found a strongly supported sister-group relationship of *Osmitopsis* with Athanasia (paleate, $x = 8$) in their molecular study based on cpDNA *ndhF* sequence variation. Since more recent analyses based on *ndhF* sequence variation (Himmelreich & al., in press) did not corroborate the close relationship of *Osmitopsis* and *Athanasia* and both *Lasiospermum* and *Athanasia* are characterised by deviating base chromosome numbers and anthers with polarised endothelial tissue (unpolarised in *Osmitopsis*), these alleged relationships seem unjustified. The same is true for any relationship with other genera of *Anthemideae* characterised by tailed anthers: neither *Inulanthera* nor *Hippolytia* are confirmed by our present analyses as closely related with *Osmitopsis*. This is in accordance with findings by Bremer & Humphries (1993) and corroborated by phylogenetic reconstructions based on cpDNA *ndhF* sequence variation (Himmelreich & al., in press).


*Type: Cotula L. [*Cotula coronopifolia* L.].

Shrubs, subshrubs, perennial or annual herbs (Cotula, Leptinella, Soliva). Indumentum of basifixed hairs or absent. Leaves alternate or opposite, entire, lobed, pinnatifid to 1-2-pinnatisect. Capitula solitary or in lax to dense corymb, radiate, disciform, or disoid. Involucre broadly campanulate, hemispherical to cylindrical or obconical, sometimes (Leptinella) umbonate. Phyllaries in 2-4 rows, without (Lidbeckia) or with narrow to broad scarious margins, sometimes (Cotula) with central resin ducts. Receptacle flat to hemispherical or conical, glabrous or hairy (Lidbeckia, Thaminophyllum), epleate or with few marginal paleae (Schistostephium). Ray florets and outer disc florets (when present) female, rarely sterile or neuter (Lidbeckia), sometimes stalked (Cotula); limb white or yellow, rarely pilose (Inezia), sometimes confluent with the achene and tube short or absent (Adenanthellum, Inezia, Thaminophyllum). Disc florets hermaphrodite or functionally male (Hippia, Leptinella, Schistostephium, Soliva); corolla 3-4- or sometimes 5-lobed (Adenanthellum, Hippia); anthers with non-polarised endothecial tissue and a slender filament collar; stylopodium sometimes large and persistent in fruit (Lidbeckia, Thaminophyllum). Achenes oblong to obovoid, terete with 2-3 adaxial or 3-10 ribs, sometimes 3-4-angled, often dorsiventrally compressed with 2 lateral, wing-like ribs; apex truncate or marginally rounded, ecoronate, rarely with minute scales (Inezia); pericarp with or without myxogenic cells and/or resin canals in ribs, sometimes papillose or hairy (Cotula, Hippia). Embryo sac development monosporic (only known in Cotula). Base chromosome number \( x = 8, 9, 10, 13 \).

**Distribution.** – Southern and eastern Africa, Australia, New Guinea, New Zealand, South America, southern oceanic islands; some species widespread and naturalised as weeds.

**Members.** – Adenanthellum B. Nord. (1), Cotula L. (55), Hilliardia B. Nord. (1), Hippia L. (8), Inezia E. Phillips (2), Leptinella Cass. (33), Lidbeckia P. J. Bergius (2), Schistostephium Less. (12), Soliva Ruiz & Pav. (8), Thaminophyllum Harv. (3).

**Notes.** – This strongly supported monophyletic group of genera consists of members of Bremer & Humphries’ (1993) subtribes Matricariinae (Cotula, Hilliardia, Hippia, Leptinella, Soliva) and Thaminophyllinae (Adenanthellum, Inezia, Lidbeckia, Thaminophyllum). Comprising mainly shrubs and perennial herbs (with annuals occurring in Cotula, Leptinella, and Soliva) with a plesiomorphic, basifixed indumentum, anthers with unpolarised endothecial tissue and slender filament collars (both conditions plesiomorphic), and the 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 clade suggested by our molecular results may be corroborated by the apomorphies of epleate receptacles and the formation of 4-lobed corollas in tubular florets (with exceptions to this in Adenanthellum and Hippia).

Further evidence for the unification of members of Bremer & Humphries’ (1993) two subtribes into a single subtribe was suggested by Nordenstam (1987) when describing the new genus Hilliardia (Matricariinae) and connecting it with Adenanthellum and Inezia (Thaminophyllinae): these genera share ray florets with a bifid or emarginate limb, a branching vena
tion, a papillate upper surface, a reduced tube, and large sessile glands. Additionally, there is further support from phytochemical investigations made by Bohlmann & Zdero (1972a, 1974, 1977, 1982), who found that the guaianolide called zuubergerin 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).

In fruit-anatomical respects the Cotula clade as circumscribed in our present contribution is highly polymorphic, with a tendency towards the reduction of the number of achene ribs from 3-4 (as in Osmitopsis) towards 2 and the transition between terete to dorsi-ventrally flattened cross sections. As an exception to this, 10-ribbed and only slightly compressed achenes are observed in Adenanthellum.

Type: *Ursinia* Gaertn. [*Ursinia paradoxa* (L.) Gaertn.]

Shrubs, or perennial to annual herbs. *Indumentum* absent or of basifixed hairs. *Leaves* alternate, entire to 2-pinnatisect, sometimes succulent. *Capitula* solitary or in lax corymbs, radiate or discoid, pedunculate. *Involucre* hemispherical. *Phyllaries* in 3-7 rows, with narrow to broad scarious margins. *Receptacle* hemispherical, paleate; *paleae* canaliculate, elliptical or narrowly linear with an apical limb. *Ray florets* usually neuter, sometimes female; limb yellow, orange, white, or reddish. *Disc florets* hermaphrodite; corolla 5-lobed, yellow, purplish; *anthers* with polarised endotheial tissue and a balusterform filament collar. *Achenes* cylindric or obovoid, straight or curved, circular in cross section, with 5 ribs and a basal tuft of hairs or glabrous; *apex* with a uniseriate pappus of 5-10 ovate or circular scales, or a biseriate pappus of 5 outer such scales and 5 inner subulate ones, or rarely epappose; pericarp rarely with myxogenic cells. *Embryo sac development* monosporic. *Base chromosome number* *x* = 5, 7, 8.

**Distribution.** – South Africa, Namibia, Botswana, Ethiopia.

**Members.** – *Ursinia* Gaertn. (39).

**Notes.** – The *Ursiniinae* sensu Bremer & Humphries (1993), comprising the genera *Athanasia* (including the genus *Asaeamia*), *Eumorpha*, *Gynnopentzia*, *Hymenolepis*, *Lasiospermum*, *Phymaspermum* and *Ursinia*, are not supported as a monophyletic group in our present analysis. This is corroborated by findings of Himmelreich & al. (in prep.) based on cpDNA *ndhF* sequence variation where also a deep split between *Ursinia* on the one hand and the rest of the mentioned genera on the other hand was observed.

The circumscription of *Ursiniinae* sensu Bremer & Humphries (1993) was mainly based on phytochemical evidence, with a number of publications made by Bohlmann and co-workers (Bohlmann & al. 1973, Bohlmann & Rao 1972, Bohlmann & Zdero 1972b, 1974, 1978a-b, Bohlmann & Grenz 1975) indicating that representatives of these genera possess furosesquiterpenes rather than the common polycyclytelenes. This in conjunction with morphological and anatomical evidence (paleate receptacles, ray floret limbs with tabular epidermis cells, anthers with partly or totally polarised endotheial tissue) was considered to sufficiently underpin the monophyly of the subtribe (Källersjö 1985, Bremer & Humphries 1993), which should even include the carpologically and palynologically deviating, but name-giving genus *Ursinia*. Due to its anthers with broadly ovate apical appendages and balusterform filament collars, the pollen exine without columnar structure and the achene with a biseriate pappus formed of scales, this genus had been formerly considered to hold a very isolated position within the tribe *Anthemideae* (Cassini 1816, Beauverd 1915), or had been even suggested as an independent tribe *Ursinieae* (Robinson & Brettell 1973) or a member of the *Arctoteae* (Bentham 1873).

In our present analysis we find a rather well supported (PP 0.95) sister-group relationship of *Ursinia* with the genus *Inulanthera* (Gonosperminae sensu Bremer & Humphries 1993). But since this support seems to be highly equivocal in alternative analyses (no support at all in MP and ML analyses based on nDNA ITS, but strong support of 93 % MP-BS, 91 % ML-BS, BI-PP 1.0 in analyses based on cpDNA *ndhF*; Himmelreich & al., in press), we refrain from inclusion of *Inulanthera* into the *Ursiniinae* in the present circumscription.


Type: *Athanasia L.* [*Athanasia crithmifolia* (L.) L.]

Shrubs or shrublets, rarely perennial to annual herbs (*Adenoglossa*, *Lasiospermum*). *Indumentum* absent or of basifixed or stellate (*Athanasia*, *Hymenolepis*) hairs. *Leaves* alternate or opposite, entire or lobed to pinnatifid or 1-2-pinnatisect. *Capitula* solitary or in lax to dense corymbs, radiate, disciform or discoid. *Involucre* hemispherical, spherical to urceolate. *Phyllaries* in 2-5 rows, without or with scarious margins, with central resin canals or sacs (in *Eriocephalus* in two un-

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equal rows, the outer phyllaries with very wide scarious margins, the inner ones connate and hairy). Receptacle flat, hemispherical to conical, paleate or epanate (Adenoglossa, Leucoptera); paleae flat or canaliculate, rarely villous (Eriocephalus). Ray florets female; limb yellow, white or reddish. Disc florets hermaphrodite (male in Eriocephalus); corolla 5-lobed; tube sometimes with long stalked hairs (Athanasia); anthers with polarised endothecial tissue, rarely unpolarised (Eriocephalus), and a slender filament collar. Achenes cylindrical to obovate, either terete and with 5-12(-18) ribs or dorsiventrally flattened and laterally winged (Adenoglossa, Leucoptera); apex marginally rounded, with a short, thickened rim (Athanasia), or with a corona or scales (Adenoglossa, Hymenolepis, Leucoptera); pericarp glabrous or densely hairy (Eriocephalus, Lasiospermum), with or without myxogenic cells and/or resin sacs. Embryo sac development monosporic (only known in Lasiospermum). Base chromosome number \( x = 8, 9 \).

Distribution. – South Africa, Namibia, Botswana, Lesotho, Egypt.


Notes. – This subtribe comprises genera that were classified as members of Matricariinae (Adenoglossa, Eriocephalus, Leucoptera) or Ursiniinae (Athanasia, Hymenolepis, Lasiospermum) in the circumscription by Bremer & Humphries (1993). Since the distinction of this group of genera from Ursinia is strongly supported by our present and further analyses (Himmelreich & al., in press), unification under a single subtribe Ursiniinae does not seem justified. However, support for the monophyly of the Athanasiinae as presently circumscribed is admittedly far from significance: (a) In the present analysis based on nrDNA ITS sequence variation the group appears to be paraphyletic with Adenoglossa, Eriocephalus, and Leucoptera being sister-group to a well-supported clade (PP 0.97) of Athanasia, Hymenolepis, Lasiospermum plus Phymasperminae and the Pentziinae northern hemisphere clade (Trichanthemum through Glebionis). (b) The Phymasperminae appear to be closely related to Athanasia, Hymenolepis and Lasiospermum, making Athanasiinae even more evidently paraphyletic.

However, while analyses of Himmelreich & al. (in prep.) based on nrDNA ITS show the same results with only marginal deviations, analyses based on cpDNA ndhF consistently indicated that the Phymasperminae possess a chloroplast type that is more closely related to members of the Pentziinae/northern hemisphere clade than with all other members of Athanasiinae. Himmelreich & al. (in prep.) 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 to be found among the members of the Pentziinae/northern hemisphere clade) or may indicate a sister group relationship between Phymasperminae and the Pentziinae/northern hemisphere clade that is not resolved in the nrDNA ITS trees due to the lack of parallel evolution of the two markers used. Irrespective of which of the two scenarios is right, it appears appropriate to treat the strongly supported clade of Eumorpha, Gymnopentzia and Phymaspernum as a subtribe independent of Athanasiinae despite the paraphyly of the latter because inclusion would not change its paraphyletic nature.

With the exception of Eriocephalus all members of Athanasiinae (together with Phymasperminae) are characterised by the possession of anthers with a polarised endothecial tissue. Since this character expression is apomorphic relative to the unpolarised endothecium found in the more basal Cotulininae and Osmotispidinae, along with the more advanced genera of the rest of the tribe, this morphological evidence may argue for a monophyly of the subtribe (and, as a consequence, the inclusion of Phymasperminae). For the time being, however, we prefer to treat the Phymasperminae as an independent subtribe because of its consistent monophyletic nature and leave all other genera with polarised endothecial tissue (together with Eriocephalus) in an alleged paraphyletic subtribe until our understanding of the topology in this crucial part of the Anthemideae phylogeny is better resolved by inclusion of more morphological and/or molecular markers.
5. **Phymasperminae** Oberpr. & Himmelreich, subtrib. nov.

Type: *Phymaspermum* Less. [*Phymaspermum junceum* Less.].

Shrubs or shrublets. *Indumentum* absent or of basifixed hairs. *Leaves* opposite or alternate, entire to lobed. *Capitula* solitary or in lax corymb, radiate or discoid. *Involucre* hemispherical to spherical, rarely cylindrical to obconical. *Phyllaries* in 2-4 rows, with scarious, sometimes ciliate margins. *Receptacle* flat to conical, ephalaceous, sometimes leafy (in *Eumorphia*, occasionally in *Gymnopentzia*); paleae linear canalicolate. *Ray florets* female; limb white, yellow, or purplish. *Disc florets* hermaphrodite; corolla 5-lobed; anthers with polarised endothecial tissue and a slender filament collar. *Achenes* cylindrical or ellipsoid, terete with 10-12(-18) ribs; apex truncate or with an entire to dentate, thickened rim or corona; pericarp papillose, without myxogenic cells or resin sacs. *Embryo sac development* and *base chromosome number* unknown.

**Distribution.** – South Africa, Lesotho, Swaziland, Zimbabwe, Namibia.


**Notes.** – This small subtribe is strongly supported as monophyletic in our present analysis based on nrDNA ITS sequence variation, while its position in the phylogeny of the tribe is rather unclear (see discussion above and in Himmelreich & al., in prep.). Following Källersjö (1985) and Bremer & Humphries (1993), the monophyly of the subtribe is also strongly supported by morphology because the three genera share the apomorphies of achenes with 10-12(-18) ribs and a papillose pericarp. Being characterised by the possession of anthers with polarised endotheelial tissue the closest relationships are found with members of the *Athanasiinae*. However, its inclusion into the latter subtribe is not supported by chloroplast sequence data (Himmelreich & al., in press).

**Unassigned to a subtribe:** *Inulanthera* Källersjö (10).

**II. Asian-southern African grade**

6. **Pentziinae** Oberpr. & Himmelreich, subtrib. nov.

Type: *Pentzia* Thunb. [*Pentzia crenata* Thunb., nom. illeg.]

Shrubs, subshrubs, or perennial to annual herbs. *Indumentum* of basifixed hairs or absent, rarely of medifixed hairs (*Pentzia*). *Leaves* alternate or rarely opposite (*Pentzia, Rennera*), entire, lobed, or 1-2-pinnatisect. *Capitula* solitary or in corymb, rarely closely aggregated (*Marasmodes*), discoid or disciform, sometimes radiate (*Cymbopappus, Foveolina, Oncosiphon*). *Involucre* hemispherical to cylindrical, sometimes urceolate (*Marasmodes*). *Phyllaries* in 3-5 rows, with or without scarious margins. *Receptacle* flat or convex to conical, eplaleate. *Ray florets* female; limb white or pinkish. *Disc florets* hermaphroditic; corolla 4-5-lobed, sometimes tube swollen and bitty (*Oncosiphon*) or with thick vascular strands (*Cymbopappus, Marasmodes, Pentzia*); anthers with non-polarised endothelial tissue and a slender filament collar. *Achenes* oblong to obvoid, with 4-5 ribs, sometimes triquetrous in cross-section and with 1 adaxial and 2 lateral ribs (*Myxopappus*); apex marginally rounded, with an entire or toothed rim, an oblique, adaxially longer entire corona, a corona of 3-10 scales, or with a large adaxial and a smaller abaxial scale; pericarp sometimes spongy (*Myxopappus*), with myxogenic cells on the ribs and the abaxial surface, without resin sacs, rarely without myxogenic cells (*Oncosiphon, Rennera*). *Embryo sac development* monosporic (only known in *Oncosiphon*). *Base chromosome number* $x = 6, 7, 8, 9$.

**Distribution.** – South Africa, Lesotho, Namibia, Botswana, Morocco, Algeria, Chad, Somalia, Yemen.


**Notes.** – This strongly supported monophyletic group of six genera (with the seventh genus, *Myxopappus*, being included due to results from nrDNA ITS and cpDNA adhF analyses of Himmelreich & al., in press) contains further southern African members of subtribe *Matricariae* as circumscribed by Bremer & Humphries (1993). It forms a closely-knit group of genera that is characterised by epaleate receptacles, anthers with unpolarised 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*), which were all once united under a broad concept of *Pentzia* until dismembered by Källersjö (1988) into the presently acknowledged entities. Following Bremer & 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 a considerable similarity concerning these achene characters, alleged close relationships with the northern hemisphere *Matricariae* genera *Matricaria, Otospermum*, or *Tripleurospermum* were not supported by our present analyses. On the other hand, a sister-group relationship with subtribe *Artemisiinae* receives some support (PP 0.99) and may be of great importance for the further understanding of the biogeography of the 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 N Africa or SW Asia may further enhance the phylogeographical importance of this subtribe.

**Type:** *Handelia* Heimerl [*Handelia trichophylla* (Schrenk) Heimerl].


Subshrubs or annual, biennial (hapaxanthic) or perennial (pollacanthic) herbs. *Indumentum* absent or of basifixed, rarely of medifixed hairs (some species of *Tanacetopsis* and *Xylanthenum*). *Leaves* alternate, lobed or apically trifid, 1-2-pinnatiapartite to 3-4-pinnatisect. *Capitula* solitary, in lax to dense corymb, or in a long panicle (*Lepidolopsis*), discoid or radiate. *Involucre* hemispherical to spherical or obconical (*Trichanthes, Xylanthenum*), sometimes umbonate (*Sclerorrhachis*). *Phyllaries* in 2-4(-5) rows, with narrow to broad scarious margins. *Receptacle* hemi-
spherical, epaleate or paleate (Handelia, Sclerorhachis); paleae subulate to linear, flat to canaliculate, sometimes readily deciduous (Sclerorhachis). Ray florets female or neuter; limb white, yellow, pink or violet. Disc florets hermaphrodite; corolla 5-lobed, sometimes 4-6-lobed (Lepidolopsis), sometimes hairy (Tanacetopsis, Trichanthemis, Xylanthemum); anthers with non-polarised endothecial tissue and a balusteriform filament collar (slender in Allardia and some Tanacetopsis species). Achenes cylindrical to obconical, circular to elliptical in cross section, with 4-10 ribs, sometimes with 3-5 adaxially arranged ribs (Microcephala); apex with a corona formed by 25-50 bristle-like scales (Allardia), a short rim, or of laciniate scales of various shapes, rarely ecoronate (Pseudohandelia, Sclerorhachis); pericarp with or without myxogenic cells, without resin sacs, rarely densely hairy (Trichanthemis). Embryo sac development unknown. Base chromosome number x = 7 (Microcephala). 9.

Distribution. – Iran, Afghanistan, Pakistan, central Asia, Mongolia, China.

Members. – Allardia Decne. (8), Handelia Heimerl (1), Lepidolopsis Poljakov (1), Microcephala Pobed. (5), Pseudohandelia Tzvelev (1), Richteria Kar. & Kir. (6), Sclerorhachis (Rech. f.) Rech. f. (4), Tanacetopsis (Tzvelev) Kovalevsk. (21), Trichanthemis Regel & Schmal. (9), Xylanthemum Tzvelev (8).

Notes. – This subtribe is well supported as a monophyletic group in our present analysis (93 % BS / PP 1.0) and consists of members of Bremer & Humphries’ (1993) Handeliinae (Handelia, Lepidolopsis, Pseudohandelia, Sclerorhachis), Cancriniinae (Allardia, Richteria, Trichanthemis), Matricarinae (Microcephala) and Tanacetinae (Tanacetopsis, Xylanthemum). Unfortunately, sequence information for the type of Cancriniinae (Cancrinia Karel & Kir. (C. chrysocephala Karelin & Kir.)) is still lacking and our inclusion of this subtribe in the Handeliinae is preliminary. But since other members of Bremer & Humphries’ Cancriniinae are well nested in this clade and seem to be closely related to Cancrinia (synapomorphies of Cancriniinae being the compact, scaphoid habit and involucral bracts with dark brown margins; Bremer & Humphries 1993), inclusion of this subtribe in a broad subtribe Handeliinae seems to be justified. In its present circumscription, the subtribe Handeliinae is fairly diverse, and synapomorphies from morphology or anatomy are lacking.

  = Chrysantheminae Less. in Linnaea 6: 167. 1831.

Description. – Shrubs, subshrubs, perennial or annual herbs. Indumentum absent, of basifixed or medifixed (sometimes stellate) hairs. Leaves rosulate or alternate, entire, lobed, serrate to 3-5-parallel. Capitula solitary, in lax to dense corymbs, or in panicles, rarely in dense glomerules (Taranaphyllum), radiate, disciform, or discoid. involucre hemispherical to cylindrical, obconical or urceolate. Phyllaries in 1-7 rows, with narrow to broad scarious margins. Receptacle flat to conical, epaleate or paleate, sometimes pilose. Ray florets (when present) female or neuter; limb white, yellow or pink. Outer disc florets (in disciform capitula) female, corolla absent or slender, 2-3- rarely 4-5-lobed. Central disc florets hermaphrodite or male (rarely neuter); corolla (4-)5-lobed; anthers basally rounded, rarely caudate (Hippolytia), with non-polarised endothecial tissue and a slender filament collar. Achenes ellipsoid to ovoid without or with 4-8(-12) ribs, sometimes flattened; apex marginally rounded, sometimes with a rounded rim (Artemisiella, Hippolytia) or a lacerate corona with small scales (Crososstephiun, Nipponanthemum, Spheronemia); pericarp with or without myxogenic cells in rows, without resin sacs (with longitudinal resin canals in Hippolytia), sometimes pilose. Embryo sac development monosporic (only known from Arctanthemum, Artemisia and Chrysanthemum). Base chromosome number x = 7, 8, 9, 10, 11, 17.

Distribution. – Worldwide, with a centre in central Asia.

Neopallasia Poljakov (3), Picrothamnus Nutt. (1), Sphaeromeria Nutt. (9), Turaniphytum Poljakov (2), Artemisiella Ghafoor (1), Brachanthemum DC. (10), Chrysanthemum L. (37), Elachanthemum Y. Ling & Y. R. Ling (1), Hippolytia Poljakov (19), Kasczkaria Poljakov (2), Leucanthelemella Tzvelev (2), Nipponanthemum Kitam. (1), Phaeostigma Muldashev (3), Stilpnolepis Krasch. (1).

Notes. – With the exception of the only recently described (and newly sequenced) genus Artemisiella, the genus Hippolytia (from Tanacetinae as defined by Bremer & Humphries 1993) and two Leucantheleminae genera (Leucanthelemella, Nipponanthemum), the members of the strongly supported clade (88 % BS / PP 1.0) around Artemisia all belong to subtribe Artemisiinae as delimited by Bremer & Humphries (1993). Our present analysis corroborates findings of Torrell & al. (1999), Watson & al. (2002), Vallès & al. (2003) and Sanz & al. (in press), who have concentrated on the phylogeny of this subtribe and, therefore, comprehensively sampled it. According to the cladistic analyses by Bremer & Humphries (1993), morphological evidence for the monophyly of the subtribe is considered to be the possession of medifixed or stellate rather than basifixed hairs (pleisomorphic in some Ajania, Artemisia, Brachanthemum, Chrysanthemum, Leucanthelemella and Turaniphytum species and in Arctanthemum), the anthers with triangular-linear-lanceolate apical appendages of rather thick-walled cells and the tendency towards ecororate, marginally rounded achenes (with exceptions in Crossostephium, Nipponanthemum and one species of Spherochrysa, 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).

Following pollen morphological studies by Martín & al. (2003) the molecularly not yet studied genus Ajanioptis may be included in the Artemisiinae due to the occurrence of the smooth and spineless pollen typical for Artemisia and its close relatives (Artemisia type). The same authors include also Hulteniella and Tridactylina, two segregate genera morphologically close to Chrysanthemum with spiny Anthemis type of pollen, in the subtribe. Since we presently lack information from molecular studies, we presently leave these genera unclassified.


III. Eurasian grade
Type: Matricaria L. [Matricaria recutita L.].

Subshrubs, perennial or annual herbs. Indumentum of basifixed, in Achillea sometimes asymmetically medifixed hairs. Leaves alternate or in a basal rosette (Heliocauta), rarely entire, usually dentate to 4-pinnatisect, sometimes vermiciform. Capitula solitary or in lax to dense corymbs, radiate, disciform or discoid. Involucrum hemispherical to cylindrical or obconical. Phyllaries in 2-3 rows, with narrow to broad scarious margins. Receptacle flat, hemispherical or conical, paleate or e widest (Matricaria); paleae flat to convex or canaliculate. Ray florets female; limb white, yellow or pink; tube ± flattened. Disc florets hermaphrodite; corolla (4-)5-lobed, basally ± saccate and clasping top of achene; anthers with non-polarised endothecial tissue and a balusterform filament collar. Achenes obvoid, vertere with 3-5 weak ribs or dorsiventrally flattened and with 2 lateral ribs or wings; apex marginally rounded or with a narrow marginal corona (Anacyclus, Matricaria); pericarp with or without myxogenic cells, sometimes with longitudinal resin ducts (Achillea, Heliocauta). Embryo sac development monosporic. Base chromosome number x = 9.

Distribution. – Europe, Asia, northern Africa, western North America.

Notes. – This subtribe consists of members of Bremer & Humphries’ (1993) Achilleinae (Achillea, Anacyclus, Leucocyclus, Otanthus), Tanacetinae (Heliocauta) and Matricarinae (Matricaria). The group was also found in molecular phylogenetic studies based on nrDNA ITS sequence variation by Oberprieler & Vogt (2000: ‘Achilleinae’ I) and Oberprieler (2004a-b). Following results of Guo & al. (2004), the genera Leucocyclus and Otanthus should be included into a broader genus Achillea to make this genus monophyletic. The inclusion of Matricaria in this subtribe (with its nomenclatural consequences due to the priority of Matricarinae over Achilleinae) is further supported by cDNA ndhF sequence information (Himmelreich & al., in press). In our present data set the subtribe lacks support from both the MP bootstrap and the BI analyses. There is only high support (PP = 1.0) for a monophyletic group consisting of Matricarinae and Anthemidinae together. However, while Anthemidinae could be defined as monophyletic by the apomorphic character expression of a tetrasporic embryo sac development (see below), Matricarinae with their monosporic development constitute possibly a paraphyletic group relative to Anthemidinae as long as no other synapomorphy for the subtribe is found or a better resolution with another molecular marker is achieved.

The presence of amids (Greger 1977), that are frequently responsible for an insecticidal activity, was considered significant for the circumscription of Achilleinae in the sense of Bremer & Humphries (1993), but it now seems that these secondary compounds are characteristic to a broader array of Mediterranean genera (Achillea, Anacyclus, Leucocyclus and Otanthus of the Matricarinae, Chamaemelum and Cladanthus of the Santolininae, Leucanthemum of the Leucantheminae, Argyanthemum and Glebionis of the Glebionidinae, and the unassigned Aaronsohnia).

10. Anthemidinae (Cass.) Dumort., Fl. Belg.: 69. 1827.
Type: Anthemis L. [Anthemis arvensis L. (see Oberprieler 1998)].
= Pyrethrinae Horan., Char. Ess. Fam.: 90. 1847.

Subshrubs, short- to long-lived perennial herbs, biennials or annuals. Indumentum absent or of medifixed or basifixed (Tanacetum, Tripleurospermum) hairs. Leaves alternate, dentate to lobed or 1-3-pinnatisept. Capitula solitary or in lax to dense corymb, radiate, disciform or discoid. involucrum hemispherical or obconical, sometimes umbonate. Phyllaries in 1-5 rows, with scarios margins. Receptacle hemispherical or conical, paleate or epaliate; paleae flat, sometimes subulate (Anthemis). Ray florets female or neuter; limb white, yellow, or pink; tube sometimes hairy. Disc florets hermaphrodite; corolla 5-lobed, rarely 4-lobed (Nananthea); anthers with non-polarised endothecial tissue and a balusterform filament collar. Achenes obovoid to obconical, circular in cross-section, with 5-10(-15) ribs, or dorsiventrally flattened with 3-10 ribs on each surface (Cota), sometimes triquetrous and with 3(-5) ribs (Tripleurospermum); apex with a corona or auricle, sometimes econorate and/or marginally rounded; pericarp with myxogenic cells, sometimes without (Tanacetum), usually without resin sac or ducts, in Tripleurospermum with (1-2)(5) abaxial-apical resin sacs. Embryo sac development tetrasporic. Base chromosome number x = 9.

Distribution. – Europe, southwestern Asia, northern and eastern Africa, Canary Islands, North America.


Notes. – The Anthemidinae are easily characterised as a monophyletic group of genera by the joint occurrence of a tetrasporic embryo sac development that constitutes an apomorphic character expression in the otherwise monosporic Anthemideae (with exceptions in Argyanthemum and Heteranthemis of the Glebionidinae). As described above, the Anthemidinae are closely related to subtribe Matricarinae with which they form a well supported monophyletic group in our present analysis (PP 1.0). Demarcation of genera in this subtribe is not yet well settled but at least the inclusion of Gonospermum and Lugoa in Tanacetum is indicated by studies of Francisco-Ortega & al. (2001) and Oberprieler (2005) based on nrDNA ITS sequence variation.
11. **Leucanthemopsidinae** Oberpr. & Vogt, subtrib. nov.

Type: *Leucanthemopsis* (Giroux) Heywood 

**Leucanthemopsis** (Giroux) Heywood 

- *Leucanthemopsis alpina* var. *alpina* (Sibth. & Sm.) Heywood, an alpine species with hermaphrodite flowers. 
- *Leucanthemopsis limosula* (Desf.) Heywood, a species with a scarious margin on the receptacle.

**Notes.** – This new subtribe consists of the larger perennial genus *Leucanthemopsis* and the three annual unispecific segregate genera *Castrilanthemum*, *Hymenostemma* and *Prolongoa*, all of them (cf. Vogt & Oberprieler 1996) formerly treated under the subtribe *Leucantheminae* by Bremer & Humphries (1993). As Bremer & Humphries (1993) and Vogt & Oberprieler (1996) have shown in cladistic analyses based on morphological and anatomical characters, the members of the subtribe lack the specialised achene anatomy of the *Leucanthemum* group of genera (see below). Molecular studies (Oberprieler & Vogt 2000, Oberprieler 2005) have shown that the monophyly of the *Leucanthemopsidinae* is strongly supported and that they are not closely related to the *Leucanthemum* group of genera (i.e. subtribe *Leucantheminae* as here circumscribed). 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 & Humphries (1993) considered the reduced number of pericarp ribs and the occurrence of a scarious, flimsy corona in *Hymenostemma*, *Leucanthemopsis* and *Prolongoa* as possible synapomorphies for this group, the addition, by Vogt & Oberprieler (1996), of *Castrilanthemum* with its 10-ribbed and ecoronate achenes changed the circumscription enormously.

**Unassigned to a subtribe:** Brocchia Vis. (1), Phalacrocarpum (DC.) Willk. (2).

**IV. Mediterranean clade**


Type: *Leucanthemum* Mill. 

**Leucanthemum vulgare** (Vaill.) Lam.

Annual or perennial herbs, rarely shrubs. *Indumentum* of medifixed hairs. *Leaves* alternate, serrate-dentate to 1-2-pinnatisect. *Capitula* solitaria, radiata. Involucre hemisphaericum. *Involucrums* phyllarys in 4 rows, with broad scarious margins. *Receptacle* convex, epealeaceum. *Ray florets* female or neuter; limb white or yellow. *Disc florets* hermaphrodite; corolla 5-lobed; anthers with non-polarised endothecial tissue and a balusterform filament collar. *Achenes* ovovoid, (3-)5-10 ribs, rarely dorsiventrally compressed and with 1 adaxial, 2 lateral and 2 abaxial ribs (*Prolongoa*); apex with a scarious corona or marginally rounded (*Castrilanthemum*); pericarp with myxogenic cells along the ribs, without resin sacs. *Embryo sac development* monosporic. *Base chromosome number* $x = 9$.

**Distribution.** – Southwestern Europe, northwestern Africa.


**Notes.** – This new subtribe consists of the larger perennial genus *Leucanthemopsis* and the three annual unispecific segregate genera *Castrilanthemum*, *Hymenostemma* and *Prolongoa*, all of them (cf. Vogt & Oberprieler 1996) formerly treated under the subtribe *Leucantheminae* by Bremer & Humphries (1993). As Bremer & Humphries (1993) and Vogt & Oberprieler (1996) have shown in cladistic analyses based on morphological and anatomical characters, the members of the subtribe lack the specialised achene anatomy of the *Leucanthemum* group of genera (see below). Molecular studies (Oberprieler & Vogt 2000, Oberprieler 2005) have shown that the monophyly of the *Leucanthemopsidinae* is strongly supported and that they are not closely related to the *Leucanthemum* group of genera (i.e. subtribe *Leucantheminae* as here circumscribed). 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 & Humphries (1993) considered the reduced number of pericarp ribs and the occurrence of a scarious, flimsy corona in *Hymenostemma*, *Leucanthemopsis* and *Prolongoa* as possible synapomorphies for this group, the addition, by Vogt & Oberprieler (1996), of *Castrilanthemum* with its 10-ribbed and ecoronate achenes changed the circumscription enormously.

**Unassigned to a subtribe:** Brocchia Vis. (1), Phalacrocarpum (DC.) Willk. (2).
sally often saccate and clasping top of achene; anthers with non-polarised endothecial tissue and a balusterform filament collar. *Achenes* ellipsoid, circular in cross section, with 5-10 ribs; apex marginally rounded or with a scarious and adaxially longer corona; pericarp with myxogenic cells along the ribs and with resin canals between the ribs. *Embryo sac development* monosporic. Base chromosome number \( x = 9 \).

**Distribution.** – Mediterranean region, Macaronesia, Europe, Asia.


**Notes.** – In contrast to the *Leucanthemopsidinae*, the subtribe *Leucantheminae* in the present circumscription is well defined morphologically but less so from the results of molecular analyses. While most of the genera form a moderately to well supported (73 % BS / PP 1.0) monophyletic group, the genus *Chlamydotrichum*, which shares the apomorphic achene anatomy with vallecular resin canals and vallecular vascular strands, is consistently found outside this clade. On the other hand, the next, more inclusive and well supported clade (PP 1.0) also contains genera (*Daveaea, Otospermum, Heteromera*) of Bremer & Humphries’ (1993) *Matricariinae* that are devoid of the characteristic achene anatomy of *Leucantheminae* but show great similarity to each other in achene anatomy (5-ribbed achenes with vascular strands in the ribs). As Oberprieler (2004b) has argued, these controversial morphological and molecular evidences may indicate that *Daveaea, Heteromera* and *Otospermum* are a paraphyletic group that gave rise to the very distinct *Leucanthemum* group of genera with its specialised achene anatomy. For the time being, we refrain from including these three genera in the well circumscribed *Leucantheminae* and do not assign them to any subtribe.


Shrubs, subshrubs, perennial or annual herbs. *Indumentum* of basifixed or of medixed or stellate hairs. *Inflorescence* solitary, in lax corymb, radiate, disciform or discoid. *Capitula* solitary or in lax corymb, radiate, disciform or discoid. *Involucral bracts* hemispherical or obconical to urceolate (*Rhetinolepis*), sometimes umbonate (*Mecomischus, Santolina*). *Phyllaries* in 3 rows, with narrow to broad scarios margins. *Receptacle* hemispherical to conical, paleate; paleae flat to canaliculate, often with a central resin duct. *Ray florets* female or neuter; limb white, orange or yellow. *Disc florets* hermaphrodite; corolla 5-lobed, basally saccate and clasping top of achene; anthers with non-polarised endothecial tissue and a balusterform filament collar. *Achenes* obvoid, circular in cross section, with 3 flimsy ridges (in *Santolina* 3-5-angled or slightly dorsiventrally flattened); apex marginally rounded; pericarp consisting of large myxogenic cells in longitudinal rows, without resin sacs (in *Santolina* sometimes without myxogenic cells). *Embryo sac development* monosporic (only known from *Chamaelemum* and *Cladanthus*). Base chromosome number \( x = 9 \).

**Distribution.** – Southern and western Europe, northern Africa, southwestern Asia.


**Notes.** – This subtribe comprises those genera of *Achilleinae* sensu Bremer & Humphries (1993) that were found to be characterised by an apomorphic 5bp-deletion in cpDNA *trnL-trnF*, which 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 & Vogt 2000). Therefore, in Oberprieler & Vogt (2000) this group was called ‘*Achilleinae II*’ in contrast to ‘*Achilleinae I*’, the latter being here treated as subtribe *Matricariinae* (see above). Members of the present subtribe are characterised by achenes
with a very thin pericarp that mainly consists of longitudinal rows of large mucilage cells but that is devoid of any resin sacs or ducts. The only exception to that feature is found in the genus *Santolina* where some species are lacking mucilage cells at all and the pericarp is thicker and sclerenchymatic. Since the latter condition is considered plesiomorphic, the thin pericarp unites as a synapomorphy the four genera *Chamaemelum*, *Cladanthus*, *Mecomischus* and *Rhetinolepis*. A morphological or anatomical synapomorphy for the clade suggested by the molecular analyses is still lacking.


Subshrubs (*Argyranthemum*) or annual herbs. *Indumentum* absent or of basifixed hairs (in *Heteranthemis* with glandular hairs). *Leaves* alternate, serrate-dentate to 2-pinnatisect. *Capitula* solitary or in lax corymbs, radiate. *Involucre* meniscoid to hemispherical. *Phyllaries* in 3-4 rows, with broad scarious margins. *Receptacle* convex to conical, epaleate. *Ray florets* female; limb white or yellow. *Disc florets* hermaphrodite; corolla 5-lobed; anthers with non-polarised endo-thecial tissue and a balusterform filament collar. *Achenes* of ray florets triquetrous and 2-3-winged; achenes of disc florets laterally compressed and 1-2-winged, sometimes terete and 10-ribbed; apex marginally rounded or with a corona; pericarp without myxogenic cells or resin sacs. *Embryo sac development* monosporic, bisporic (*Argyranthemum*), or tetrasporic (*Heteranthemis*). Base chromosome number *x* = 9.

**Distribution.** – Macaronesia, Europe, northern Africa, southwestern Asia.


**Notes.** – This subtribe corresponds in its circumscription completely to the subtribe *Chrysantheminae* Bremer & Humphries (1993) which was considered a well-supported monophyletic group due to the occurrence of distinctly heteromorphic achenes (achenes of ray florets triquetrous and winged, achenes of disc florets terete or laterally flattened). Since the conserved type of *Chrysanthemum* L. is now *C. indicum* L. [formerly *Dendranthema indicum* (L.) Des Moul.], the two Mediterranean annuals *C. coronarium* and *C. segetum* are now treated as members of *Glebionis* Spach, and the subtribal name *Chrysantheminae* Bremer & Humphries, validly published with a Latin description and designation of type, became an illegitimate later homonym of *Chrysantheminae* Less. As a consequence, we have changed the name of the subtribe to *Glebionidinae*.


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Appendix 1: Information on nrDNA ITS sequences used in the present analysis. Published sequences are characterised by their EMBL/GenBank accession number(s), while for newly established sequences information on herbarium vouchers is given.

Aaronsosiphia pubescens (Desf.) Bremer & Humphries, AJ3296408/AJ3296443 (Oberprieler & Vogt 2000); Achillea millefolium L., AM774445 (Himmelreich & al., in press); Adenanthellum adensolens (Harvey) B. Nord., AM774446 (Himmelreich & al., in press); Ajania fastigiata (C. Winkl.) Poljakov, AF504169/AF504142 (Vallès & al. 2003); Allardia tomentosa Decne., Pakistan, Northern Areas, oberes Kosto-Tal, alpine Matten, 4300 m, 11.7.1994, Nüsser 1414 (B), AM774420; Anacyclus clavatus (Desf.) Pers., AJ748762/AJ748763 (Oberprieler & Vogt 2004a); Anthemis arvensis L., AJ312777/AJ312806 (Oberprieler 2001); Arcanthenium arcticum (L.) Tsvelev, L777756 (Francisco-Ortega & al. & al. 1997); Argyranthemum foeniculaceum (Willd.) Sch. Bip., AF155270/AF155307 (Francisco-Ortega & al. & al. 1997); Artemisia (Serephidium) tridentata Nutt. AF060460/AF061376 (Kornkven & al. 1998); Artemisia vulgaris L., AJ3296391/AJ3296426 (Oberprieler & Vogt 2000); Artemisia stracheyi (Clarke) Ghafoor, China, Xizang, Central Plateau, Nagqu-Siling Co, 31°28'N, 91°00'E, 4580 m, 16.8.1993, Miehe 9488/01 (B), AM774421; Athonasia pachycephala DC., AM774447 (Himmelreich & al., in press); Brachanthemum titovii Krusch., AF504142/AF504169 (Vallès & al. 2003); Brocchia cinerea (Del.) Vis., AJ748778/AJ748779 (Oberprieler 2004a); Castrilanthenum debeaunixii (Degen) Vogt & Oberprieler, AJ3296390/AJ3296425 (Oberprieler & Vogt 2000); Chamaemelum nobile (L.) All., AJ3296382/AJ3296417 (Oberprieler & Vogt 2000); Chlamyrophora tridentata (Del.) Less., AJ3296391/AJ3296426 (Oberprieler & Vogt 2000); Chrysanthemum ×morifolium (Desf.) Pomel, AJ3296409/AJ3296444 (Oberprieler & Vogt 2000); Coleostephus multicaulis (Desf.) Durieu, AJ296393/AJ296428 (Oberprieler & Vogt 2000); Cotula tinctoria (L.) Cass., AJ3296383/AJ3296418 (Oberprieler & Vogt 2000); Cypripedium calceolus (L.) Bl., AM774448 (Himmelreich & al., in press); Cynoglossum deserticola (Franch.) Y. Ling & Yu. Ling, AM774449 (Himmelreich & al., in press); Cytisus scoparius (L.) Tzvelev, L77766 (Francisco-Ortega & al. & al. 1997); Daurania glandulosa (Oberprieler & Vogt 2000); Diancephalus anthemoideus Mairz, AJ865477/AJ865497 (Oberprieler 2004b); Elachanthemum intricatum (Franch.) Y. Ling & Yu. Ling, AJ127683/AJ127684 (Watson & al. 2002); Endopappus macrocarpus Sch. Bip., AJ748780/AJ748781 (Oberprieler 2004a); Eriogonum integrifolium DC., AM774450 (Himmelreich & al., in press); Eupatorium sericeum J. M. Wood & M. Evans, AM774451 (Himmelreich & al., in press); Filifolium sibiricum (L.) Spach, L777741 (Francisco-Ortega & al. 1997); Foveolina albida (DC.) Källersjö, AM774452 (Himmelreich & al., in press); Glediosia coronaria (L.) Sch. Bip., L777741 (Francisco-Ortega & al. & al. 1997); Glossopappus macrostachys (Darieu) Briq., AJ3296394/AJ3296429 (Oberprieler & Vogt 2000); Gymnopus centauriense (DC.) Less., AF155243/AF155280 (Francisco-Ortega & al. 2001); Heliocauta atlantica (Litard. & Maire) Humphries, AJ748782/AJ748783 (Oberprieler 2004a); Heteranthenis visechehirta Schott, L777761 (Francisco-Ortega & al. 1997); Heteromera fuscata (Desf.) Pomel, AJ3296409/AJ3296444 (Oberprieler & Vogt 2000); Hippophae rhamnoides (L.) Tzvelev, L77765 (Himmelreich & al., in press); Inula chumii (Oliv.) B. Nord., AM774445 (Himmelreich & al., in press); Ischemia carinata (Schoubr.) Sch. Bip., L777764 (Francisco-Ortega & al. & al. 1997); Kaschgaria komarovi (Krasch. & N. Rubtsov) Poljakov, AM774457 (Himmelreich & al., in press); Krasch. & N. Rubtsov) Poljakov, AM774457 (Himmelreich & al., in press); Lepidolopsis arvensis L., AJ312777/AJ312806 (Oberprieler 2001); Lasiospermum pedunculare (Franch.) Bremer & Humphries, AJ748784/AJ748785 (Oberprieler 2004a); Lophocereus selenicus (Hüll.) Sch. Bip., L777765 (Himmelreich & al., in press); Nymphaea pumiliformis Willk., L77762 (Francisco-Ortega & al. 1997); Inezia integrefolia (Klatt) E. Phillips, AM774454 (Himmelreich & al., in press); Inulanthera leucoclada (Källersjö) Himm.
turkestanica (Regel & Schmalh.) Poljakov, AF504190/AF504163 (Vallès & al. 2003); Lepido-
phorum repandum (L.) DC., ... Hayek,
AJ864590/AJ864610 (Oberprieler 2004b); Turaniphytum eranthemum (Bunge) Poljakov,
Willdenowia 37 – 2007 113

Sphaeromeria diversifolia

Stilpnolepis centriflora

Rennera limno-

Pseudohandelia umbellifera

36000 (B), AM774427;

sus
Boiss., AJ864578/AJ864598 (Oberprieler 2004b);

alpina
(Vaill.) Lam., AJ3296398/AJ864598 (Oberprieler & Vogt 2000);

vulgare
(Taun.) Lam., AJ3296398/AJ864598 (Oberprieler & Vogt 2000);

canthemella serotina

m,
serpentinicis ditionis Robat-I Safid 82-90 km S Mashhad, 70 km N Torbat-e Heydariyeh, 1520

Sclerohachis platyrhachis

& al., in press);

Tanacetopsis eriobasis

Karelin & Kir., Tian-shan, montes Chatkalski khrebet, mons Chimgan, 1900-2600 m, 17.7.1973,

Wilcox & al., AJ3296405/AJ3296440 (Oberprieler & Vogt 2000);

Rhodanthemum arundanum

AJ3296386/AJ3296421 (Oberprieler & Vogt 2000);

Merxm., AM774469 (Himmelreich & al., in press);

phila

Nippoanthemum nipponicum

AY127692 (Watson & al. 2002);

Pavlov 539

Tanacetum vulgare

AF155299 (Francisco-Ortega & al. 2001);

Thaminophyllum latifolium

Wettst. & al., in angustiis fl. Alamaly-Saj, in declivibus austro-orientalibus schistosis,

Plagius maghrebinus

(Vaill.) Lam., AJ3296398/AJ864598 (Oberprieler & Vogt 2000);

Mecomischus halimifolius

Link) DC., AF155252/AF155289 (Francisco-Ortega & al. 2001);

Lugoa revoluta

dummeri

Hutch., AM774429;

Tripleurospermum caucasicum

Fisjun (no 4448), 22.5.1961 (B), AM774424;

Rydb., AY127693/AY127694 (Watson & al. 2002);

Phalacrocarpum oppositifolium

(Brot.) Willk., AJ3296401/AJ3296436 (Oberprieler & Vogt 2000); Paeostigma salicifolium

Mattf.) Muldasev, China, Sze-ch’uan, reg. bor., Dongrergo, in prato herboso-fruticoso, 4200, 8.8.1922, Smith [S], AM774423; Phynas-

pseudum leptophyllum

(Regel & Schmalh.) Krasch., Kazachstania,

Himmelreich & al., in press); Rictanthemis aulieatensis

(Himmelreich & al., in press);

Leucocyclus formosus

(Thunb.) B. D. Jackson, AM774467 (Himmelreich & al., 1997); Nivellia nivellei

(Pall.) Poljakov, AY127691/AY127692 (Watson & al. 2002); Neopallasia pectinata

(Boiss.) D. G. Lloyd & C. J. Webb, AM774460 (Himmelreich & al., in press);

L. Willcox & al., AJ3296400/AJ3296435 (Oberprieler & Vogt 2000); Oncosiphon grandisflorum

(Thunb.) Källersjö, AM774465 (Himmelreich & al., in press); Osmotopsis asteriscoidea

(P. Bergius) Less., AM774466 (Himmelreich & al., in press); Otanthus maritimus

(L.) Hoffmanns. & Link, AJ3296385/AJ3296420 (Oberprieler & Vogt 2000); Otoaspernum glabrum

(Lag.) Willk., AJ3296413/AJ3296448 (Oberprieler & Vogt 2000); Pentzia dentata

Kuntze, AJ127681/AJ127682 (Watson & al. 2002); Phalacrocarpum oppositifolium

(Brot.) Willk., AJ3296401/AJ3296436 (Oberprieler & Vogt 2000); Paeostigma salicifolium

Mattf.) Muldasev, China, Sze-ch’uan, reg. bor., Dongrergo, in prato herboso-fruticoso, 4200, 8.8.1922, Smith [S], AM774423; Phynas-

pseudum leptophyllum

(Regel & Schmalh.) Krasch., Kazachstania,
AF504195/AF504168 (Vallès & al. 2003); *Ursinia anthemoides* (L.) Poir., AM774473 (Himmelreich & al., in press); *Xylanthemum tianshanicum* (H. Kraschen.) Muradyan, Kirgisistan, Tien-Shan, Naryn-Gebiet, Son-Köl, Berghänge, Schotter, ca. 3800-4000 m, 23.7.2002, *Dürbye 1742* (B), AM774430.

Outgroup genera:
- *Astereae*. – *Baccharis neglecta* Britton, U97604 (Morgan 1997); *Bellis perennis* L., AF046950 (Noyes & Rieseberg 1999); *Conyza canadensis* (L.) Cronquist, AF046987 (Noyes & Rieseberg 1999); *Erigeron annuus* Pers., AF118489 (Noyes 2000); *Felicia echinata* Nees, AY193797 (Eastwood & al. 2004); *Osteospermum fruticosum* (L.) Norl., AF422131 (Wagstaff & Breitwieser 2002); *Pyrrocoma lanceolata* Greene, AF251574 (Markos & Baldwin 2001); *Symphyotrichum cordifolium* (L.) G. L. Nesom, DQ005972 (Kress & al. 2005)