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

Abstract

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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. *Osmiopsideinae*, *Phymasperminae*, *Pentziinae* and *Leucanthemopsidineae*) are described as new to science, for a further subtribe a new name (*Glebionidineae*, replacing the illegitimate *Chrysantheminae*) is validated.

Key words: *Asteraceae*, nrDNA 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 & Cavillier 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 Reitbrecht (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 '*Cotuleae*' 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, Vallès & 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) Ghaffoor, *Handelia trichophylla* (Schrenk) Heimerl, *Phaeostigma salicifolium* (Mattf.) Muldashev, *Picrothamnus desertorum* Nutt., *Richteria pyrethroides* Karelin & Kir., *Sclerorhachis 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 ITS5A (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.bgbm.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

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[A-C] = R[A-T] = R[C-G] = R[G-T] = 1.0, R[A-G] = 2.8158, and R[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 *Matricariinae* 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 *Anthemis* (*Matricaria* through *Nananthea*, PP 1.0), *Leucanthemum* (*Otospermum* through *Heteromera*, PP 1.0), *Leucanthemopsis* (*Castrilanthemum* through *Leucanthemopsis*, 100 % BS / PP 1.0) and *Argyranthemum* (*Heteranthemis* through *Glebionis*, PP 0.98).

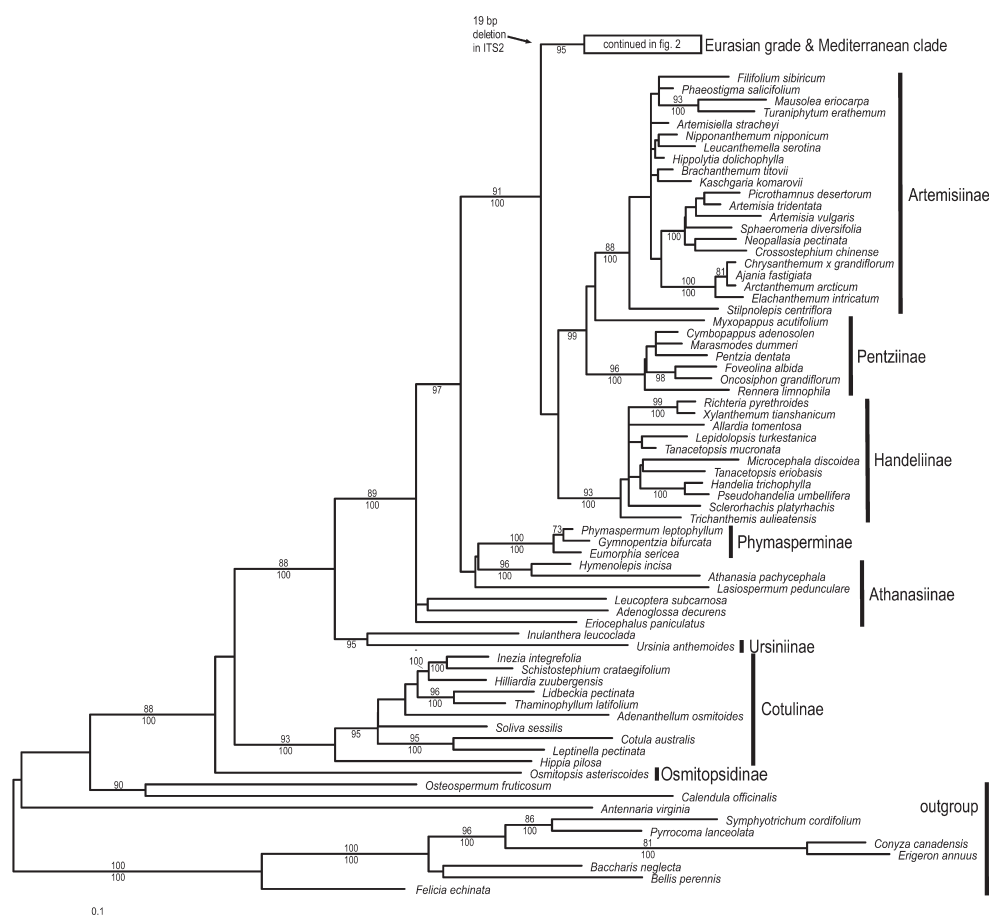


Fig. 1. Basal part of a phylogenetic tree from a maximum-likelihood (ML) analysis of nrDNA ITS sequence variation data based on the TrN + Γ model of DNA substitution (Tamura & Nei 1993) with base frequencies, gamma distribution parameter α and substitution rate matrix given in the text. Values above 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.

Taxonomic consequences

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 *Osmitsopsis*, (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

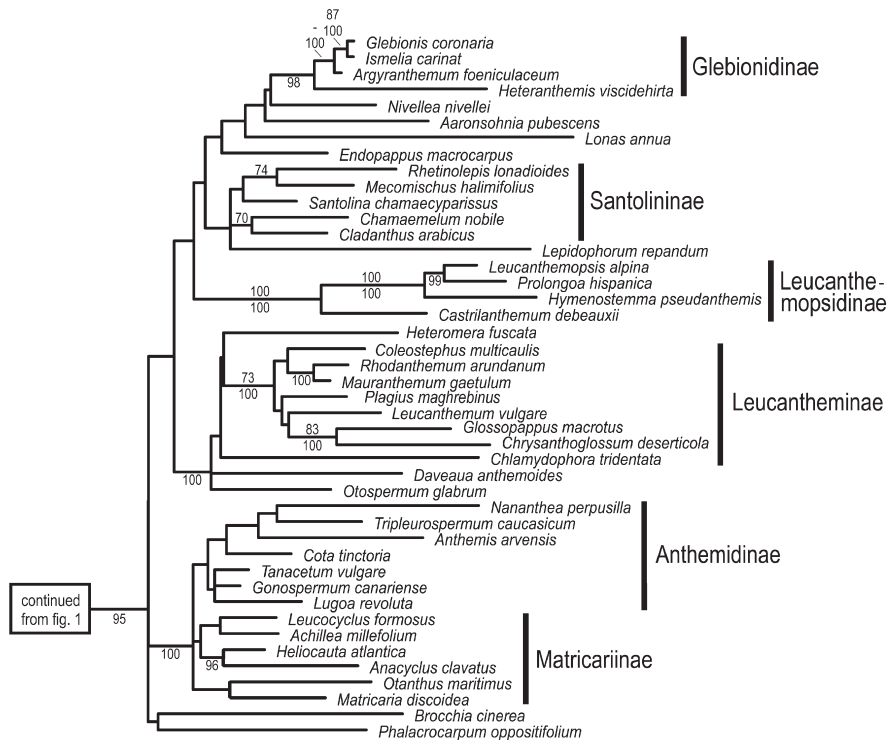


Fig. 2. Apical part of a phylogenetic tree from a maximum-likelihood (ML) analysis of nrDNA ITS sequence variation data based on the TrN + Γ model of DNA substitution (Tamura & Nei 1993) with base frequencies, gamma distribution parameter α , and substitution rate matrix given in the text. Values above 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.

but not so in the cpDNA *ndhF* data set) and (b) the position of *Phymaspermatae* relative to *Athanasiae* (closely related in the nrDNA ITS tree but closely related with *Artemisiae* and *Pentziae* 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. *Osmitopsidinae* 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-

tum. *Involucris phylla* imbricata, 2-4-seriata, scariose marginata. *Receptaculum* planum vel conicum, paleaceum; paleae anguste ellipticae vel obovatae, canaliculatae et flores amplexantes. *Flores marginales* ligulati, foeminei vel neutri, albi, in latere abaxiali pilosi, tubo piloso. *Flores centrales* hermaphroditi vel masculi, corollis quinquelobatis luteis; antherae basi caudatae, endothecio non polari, filamenta infra antheras tenuia; stylopodium amplum et ad maturitatem fructus persistens. *Achaenia* obovoidea vel ellipsoidea 3-4-angulata vel costata, squamis subulatis vel triangularibus vel rotundatis coronata. *Chromosomatum numerus basicus*: $x = 10$.

Shrubs or subshrubs. *Indumentum* absent or of basifixed hairs. *Leaves* alternate, entire to lobed. *Capitula* solitary or in lax corymbs, 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; limb white, occasionally pilose abaxially, tube occasionally pilose. *Disc florets* hermaphrodite or male; corolla 5-lobed, yellow; anthers basally caudate, with non-polarised endothecial tissue and a slender filament collar; stylopodium sometimes large and persistent in fruit. *Achenes* obovoid 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 involucre 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 (epaleate) genera *Adenanthellum*, *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 endothecial 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).

2. *Cotulinae* Kitt., Taschenb. Fl. Deutschl., ed. 2, 2: 609. 1844.

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

= *Thaminophyllinae* Bremer & Humphries in Bull. Nat. Hist. Mus. London, Bot. 23: 144. 1993.

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 corymbs, radiate, disciform, or discoid. *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*), epaleate 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 endothelial 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*, *Schistostephium*, *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 endothelial 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 epaleate 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 venation, 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 zuubergenin 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*.

3. *Ursiniinae* Bremer & Humphries in Bull. Nat. Hist. Mus. London, Bot. 23: 91. 1993.
Type: *Ursinia* Gaertn. [*Ursinia paradoxa* (L.) Gaertn.].

Shrublets, 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 endothecial tissue and a balusterform filament collar. *Achenes* cylindrical 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 *Asaemia*), *Eumorphia*, *Gymnopentzia*, *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 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 polarised endothecial 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 achenes 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 *Inulanchera* (*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 nrDNA 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 *Inulanchera* into the *Ursiniinae* in the present circumscription.

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

equal rows, the outer phyllaries with very wide scarious margins, the inner ones connate and hairy). *Receptacle* flat, hemispherical to conical, paleate or epaleate (*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 endothelial 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.

Members. – *Adenoglossa* B. Nord. (1), *Athanasia* L. (39), *Eriocephalus* L. (32), *Hymenolepis* Cass. (7), *Lasiospermum* Lag. (4), *Leucoptera* B. Nord. (3).

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 *Athansiinae* 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 *Phymaspermatae* and the *Pentziinae* northern hemisphere clade (*Trichanthemum* through *Glebionis*). (b) The *Phymaspermatae* appear to be closely related to *Athanasia*, *Hymenolepis* and *Lasiospermum*, making *Athansiinae* 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 *Phymaspermatae* possess a chloroplast type that is more closely related to members of the *Pentziinae*/northern hemisphere clade than with all other members of *Athansiinae*. 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 *Phymaspermatae* (with the plastid donor to be found among the members of the *Pentziinae*/northern hemisphere clade) or may indicate a sister group relationship between *Phymaspermatae* 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 *Eumorphia*, *Gymnopentzia* and *Phymaspermum* as a subtribe independent of *Athansiinae* despite the paraphyly of the latter because inclusion would not change its paraphyletic nature.

With the exception of *Eriocephalus* all members of *Athansiinae* (together with *Phymaspermatae*) are characterised by the possession of anthers with a polarised endothelial tissue. Since this character expression is apomorphic relative to the unpolarised endothecium found in the more basal *Cotulinae* and *Osmiopsideae*, 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 *Phymaspermatae*). For the time being, however, we prefer to treat the *Phymaspermatae* as an independent subtribe because of its consistent monophyletic nature and leave all other genera with polarised endothelial 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.].

Frutices vel subfrutices. *Indumentum* nullum vel e pilis basifixis formatum. *Folia* alterna vel opposita, integra vel lobata. *Capitula* solitaria vel in corymbum laxum disposita, radiata vel discoidea. *Involucrum* hemisphaericum vel sphaericum, raro cylindricum vel obconicum. *Involucris phylla* imbricata, 2-4-seriata, scarioso-marginata, raro ciliata. *Receptaculum* planum vel conicum, epaleaceum, raro paleaceum; paleae lineares, canaliculatae. *Flores marginales* ligulati, foeminei, albi, lutei vel purpurei. *Flores centrales* hermaphroditi, corolla quinquelobata; antherae endothecio polari, filamenta infra antheras tenuia. *Achaenia* cylindracea vel ellipsoidea, 10-12(-18)-costata, apice truncata vel toro incrassato papilloso coronata, sine cellulis myxogenis vel canalibus resiniferis.

Shrubs or shrublets. *Indumentum* absent or of basifixed hairs. *Leaves* opposite or alternate, entire to lobed. *Capitula* solitary or in lax corymbs, 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, epaleate, sometimes paleate (*Eumorphia*, occasionally in *Gymnopentzia*); paleae linear canaliculate. *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 (in *Phymaspermum* with ovoid myxogenic trichomes and resin sacs in some of the ribs). *Embryo sac development* and *base chromosome number* unknown.

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

Members. – *Eumorphia* DC. (6), *Gymnopentzia* Benth. (1), *Phymaspermum* Less. (19).

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 endothecial tissue the closest relationships are found with members of the *Athanasinae*. 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.]

Frutices, suffrutices vel herbae annuae vel perennes. *Indumentum* nullum vel e pilis basifixis vel medifixis formatum. *Folia* alterna, raro opposita, integra vel lobata vel 1-2-pinnatisecta. *Capitula* solitaria vel in corymbum laxum, raro densum disposita, radiata vel disciformia vel discoidea. *Involucrum* hemisphaericum vel cylindraceum, raro urceolatum. *Involucris phylla* imbricata, 3-5-seriata, interdum scarioso-marginata. *Receptaculum* planum vel convexum vel conicum, epaleaceum. *Flores marginales* ligulati, foeminei, albi vel purpurei. *Flores centrales* hermaphroditi, corolla 4-5-lobata; antherae endothecio non polari, filamenta infra antheras tenuia. *Achaenia* obovoidea vel ellipsoidea, (3-)4-5-costata, apice rotundata vel toro vel squamis coronata, canalibus secretoriis carentia, plerumque in latere abaxiali (nec adaxiali) et in costis cellulis myxogenis instructa. *Formatio megagametophyti* monosporica. *Chromatosomatum numerus basicus*: x = 6, 7, 8 vel 9.

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 corymbs, 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, epaleate. *Ray florets* female; limb white or pinkish. *Disc florets* hermaphrodite; corolla 4-5-lobed, sometimes tube swollen and brittle (*Oncosiphon*) or with thick vascular strands (*Cymbopappus*, *Marasmodes*, *Pentzia*); anthers with non-polarised endothecial tissue and a slender filament collar. *Achenes* oblong to obovoid, 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.

Members. – *Cymbopappus* B. Nord. (3), *Foveolina* Källersjö (5), *Marasmodes* DC. (4), *Myxopappus* Källersjö (2), *Oncosiphon* Källersjö (8), *Pentzia* Thunb. (23), *Rennera* Merxm. (4).

Notes. – This strongly supported monophyletic group of six genera (with the seventh genus, *Myxopappus*, being included due to results from nrDNA ITS and cpDNA *ndhF* analyses of Himmelreich & al., in press) contains further southern African members of subtribe *Matricariinae* as circumscribed by Bremer & Humphries (1993). It forms a closely-knit group of genera that is characterised by epaleate receptacles, anthers with unpolarised endothecial 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 *Matricariinae* 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.

7. *Handeliinae* Bremer & Humphries in Bull. Nat. Hist. Mus. London, Bot. 23: 108. 1993.

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

=? *Cancriniinae* Bremer & Humphries in Bull. Nat. Hist. Mus. London, Bot. 23: 96. 1993.

Subshrubs or annual, biennial (hapaxanthic) or perennial (pollacanthic) herbs. *Indumentum* absent or of basifixed, rarely of medifixed hairs (some species of *Tanacetopsis* and *Xylanthemum*). *Leaves* alternate, lobed or apically trifid, 1-2-pinnatifid to 3-4-pinnatisect. *Capitula* solitary, in lax to dense corymbs, or in a long panicle (*Lepidolopsis*), discoid or radiate. *Involucre* hemispherical to spherical or obconical (*Trichanthemis*, *Xylanthemum*), sometimes umbonate (*Scleorrhachis*). *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 endothelial tissue and a balusterform 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 lacinate 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 & Schmalh. (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*), *Matricariinae* (*Microcephala*) and *Tanacetinae* (*Tanacetopsis*, *Xylanthemum*). Unfortunately, sequence information for the type of *Cancriniinae* [*Cancrinia* Karelin & 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 involucre 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.

8. *Artemisiinae* Less. in Linnaea 5: 163. Jan 1830.

Type: *Artemisia* L. [*Artemisia vulgaris* L.].

= *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 2-3-pinnatisect. *Capitula* solitary, in lax to dense corymbs, or in panicles, rarely in dense glomerules (*Turaniphytum*), 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 endothelial tissue and a slender filament collar. *Achenes* ellipsoid to obovoid 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 (*Crossostephium*, *Nipponanthemum*, *Spheromeria*); 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.

Members. – *Ajania* Poljakov (39), *Arctanthemum* (Tzvelev) Tzvelev (3), *Artemisia* L. (522, incl. *Seriphidium* Fourr.) [incl. *Crossostephium* Less. (1), *Filifolium* Kitam. (1), *Mausolea* Poljakov

(1), *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), *Kaschgaria* Poljakov (2), *Leucanthemella* 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 *Leucanthemeinae* genera (*Leucanthemella*, *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 (plesiomorphic in some *Ajania*, *Artemisia*, *Brachanthemum*, *Chrysanthemum*, *Leucanthemella* and *Turaniphytum* species 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).

Following pollen morphological studies by Martín & al. (2003) the molecularly not yet studied genus *Ajaniopsis* 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.

Unassigned to a subtribe: *Ajaniopsis* C. Shih (1), *Cancrinia* Kar. & Kir. (4), *Cancriniella* Tzvelev (1), *Hulteniella* Tzvelev (1), *Lepidolopha* C. Winkl. (9), *Opisthopappus* C. Shih (2), *Polychrysium* (Tzvelev) Kovalevsk. (1), *Tridactylina* (DC.) Sch. Bip. (1), *Ugamia* Pavlov (1).

III. Eurasian grade

9. *Matricariinae* Willk. in Willk. & Lange, Prodr. Fl. Hispan. 2: 92. 1870.

Type: *Matricaria* L. [*Matricaria recutita* L.].

= *Achilleinae* Bremer & Humphries in Bull. Nat. Hist. Mus. London, Bot. 23: 126. 1993.

Subshrubs, perennial or annual herbs. *Indumentum* of basifixed, in *Achillea* sometimes asymmetrically medifixed hairs. *Leaves* alternate or in a basal rosette (*Heliocauta*), rarely entire, usually dentate to 4-pinnatisect, sometimes vermiform. *Capitula* solitary or in lax to dense corymbs, radiate, disciform or discoid. *Involucre* hemispherical to cylindrical or obconical. *Phyllaries* in 2-3 rows, with narrow to broad scarious margins. *Receptacle* flat, hemispherical or conical, paleate or epaleate (*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* obovoid, terete 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.

Members. – *Achillea* L. (115), [incl. *Leucocyclus* Boiss. (1), *Otanthus* Hoffmanns. & Link (1), see Guo & al. (2004), Ehrendorfer & Guo (2005, 2006)], *Anacyclus* L. (12), *Heliocauta* Humphries (1), *Matricaria* L. (6).

Notes. – This subtribe consists of members of Bremer & Humphries' (1993) *Achilleinae* (*Achillea*, *Anacyclus*, *Leucocyclus*, *Otanthus*), *Tanacetinae* (*Heliocauta*) and *Matricariinae* (*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 *Matricariinae* over *Achilleinae*) is further supported by cpDNA *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 *Matricariinae* and *Anthemidinae* together. However, while *Anthemidinae* could be defined as monophyletic by the apomorphic character expression of a tetrasporic embryo sac development (see below), *Matricariinae* 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 amides (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 *Matricariinae*, *Chamaemelum* and *Cladanthus* of the *Santolininae*, *Leucanthemum* of the *Leucantheminae*, *Argyranthemum* 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.

= *Tanacetinae* Bremer & Humphries in Bull. Nat. Hist. Mus. London, Bot. 23: 99. 1993.

= *Gonosperminae* Bremer & Humphries in Bull. Nat. Hist. Mus. London, Bot. 23: 106. 1993.

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-pinnatisect. *Capitula* solitary or in lax to dense corymbs, radiate, disciform or discoid. *Involucre* hemispherical or obconical, sometimes umbonate. *Phyllaries* in 1-5 rows, with scarious 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 ecoronate 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.

Members. – *Anthemis* L. (175), *Cota* J. Gay (40), *Nananthea* DC. (1), *Tanacetum* L. (154) [incl. *Gonospermum* Less. (4), *Lugoa* DC. (1)], *Tripleurospermum* Sch. Bip. (40).

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 *Argyranthemum* and *Heteranthemis* of the *Glebionidinae*). As described above, the *Anthemidinae* are closely related to subtribe *Matricariinae* 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 alpina* (L.) Heywood].

Herbae annuae vel perennes. *Indumentum* e pilis medifixis formatum. *Folia* alterna, serrato-dentata ad bipinnatisecta. *Capitula* solitaria, radiata. *Involucrum* hemisphaericum. *Involucris phylla* imbricata, 4-seriata, scarioso-marginata. *Receptaculum* convexum, epaleaceum. *Flores marginales* ligulati, foeminei vel neutri, albi vel lutei. *Flores centrales* hermaphroditi, corollis 5-lobatis; antherae endothecio non polari, filamenta infra antheras tumida. *Achaenia* obovoidea, (3-)5-10-costata, apice margine scarioso coronata vel rotundata, canalibus sectretoriis carentia, in costis cellulis myxogenis instructa. *Formatio megagametophyti* monosporica. *Chromosomatum numerus basicus*: $x = 9$.

Annual or perennial herbs. *Indumentum* of medifixed hairs. *Leaves* alternate, serrate-dentate to 1-2-pinnatisect. *Capitula* solitary, radiate. *Involucre* hemispherical. *Phyllaries* in 4 rows, with broad scarious margins. *Receptacle* convex, epaleate. *Ray florets* female or neuter; limb white or yellow. *Disc florets* hermaphrodite; corolla 5-lobed; anthers with non-polarised endothelial tissue and a balusterform filament collar. *Achenes* obovoid, round in cross-section and with (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 (only known in *Leucanthemopsis*). *Base chromosome number* $x = 9$.

Distribution. – Southwestern Europe, northwestern Africa.

Members. – *Castrilanthemum* Vogt & Oberprieler (1), *Hymenostemma* Willk. (1), *Leucanthemopsis* (Giroux) Heywood (9), *Prolongoa* Boiss. (1).

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

12. *Leucantheminae* Bremer & Humphries in Bull. Nat. Hist. Mus. London, Bot. 23: 136. 1993. Type: *Leucanthemum* Mill. [*Leucanthemum vulgare* (Vaill.) Lam.].

Annual or perennial herbs, rarely subshrubs (*Leucanthemum*, *Plagius*, *Rhodanthemum*). *Indumentum* absent or of basifixed hairs, rarely of medifixed hairs (*Rhodanthemum*). *Leaves* alternate or basally opposite, entire, serrate-dentate, lobed, or up to 3-pinnatisect. *Capitula* solitary, discoid or radiate. *Involucre* meniscoid to hemispherical. *Phyllaries* in 3-5 rows, with narrow to broad scarious margins. *Receptacle* hemispherical to conical, epaleate. *Ray florets* female or sterile; limb white, yellow, or red (*Rhodanthemum*). *Disc florets* hermaphrodite; corolla (4-)5-lobed, ba-

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.

Members. – *Chlamyphora* Less. (1), *Chrysanthoglossum* B. H. Wilcox & al. (2), *Coleostephus* Cass. (3), *Glossopappus* Kunze (1), *Leucanthemum* Mill. (43), *Mauranthemum* Vogt & Oberprieler (4), *Plagius* DC. (3), *Rhodanthemum* (Vogt) B. H. Wilcox & al. (14).

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 *Chlamyphora*, 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 (*Daveaua*, *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 *Daveaua*, *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.

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

Type: *Santolina* L. [*Santolina chamaecyparissus* L.].

Shrubs, subshrubs, perennial or annual herbs. *Indumentum* of basifixed or of medifixed or stellate hairs. *Leaves* alternate, entire, lobed, or dentate to 2-3-pinnatisect, sometimes vermiform. *Capitula* solitary or in lax corymbs, radiate, disciform or discoid. *Involucre* hemispherical or obconical to urceolate (*Rhinolepis*), sometimes umbonate (*Mecomischus*, *Santolina*). *Phyllaries* in 3 rows, with narrow to broad scarious 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* obovoid, 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 *Chamaemelum* and *Cladanthus*). *Base chromosome number* $x = 9$.

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

Members. – *Chamaemelum* Mill. (2), *Cladanthus* Cass. (5), *Mecomischus* Benth. & Hook. f. (2), *Rhinolepis* Coss. (1), *Santolina* L. (13).

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 *Rhadinolepis*. A morphological or anatomical synapomorphy for the clade suggested by the molecular analyses is still lacking.

14. *Glebionidinae* Oberpr. & Vogt, **nom. nov.**

Type: *Glebionis* Spach [*Glebionis coronaria* (L.) Spach, *Chrysanthemum coronarium* L.]. = *Chrysantheminae* Bremer & Humphries in Bull. Nat. Hist. Mus. London, Bot. 23: 136. 1993, nom. illeg.

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 endothelial 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.

Members. – *Argyranthemum* Webb (24), *Glebionis* Cass. (2), *Heteranthemis* Schott (1), *Ismelia* Cass. (1).

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*.

Unassigned to a subtribe: *Aaronsohnia* Warb. & Eig (2), *Daveaua* Mariz (1), *Endopappus* Sch. Bip. (1), *Heteromera* Pomel (2), *Lepidophorum* DC. (1), *Lonas* Adans. (1), *Nivellea* B. H. Wilcox & al. (1), *Otospermum* Willk. (1).

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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.

Aaronsohnia pubescens (Desf.) Bremer & Humphries, AJ3296408/AJ3296443 (Oberprieler & Vogt 2000); *Achillea millefolium* L., AY603186 (Guo & al. 2004); *Adenanthellum osmitoides* (Harvey) B. Nord., AM774445 (Himmelreich & al., in press); *Adenoglossa decurens* (Hutch.) 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); *Arcantherum arcticum* (L.) Tzvelev, L777756 (Francisco-Ortega & al. 1997); *Argyranthemum foeniculaceum* (Willd.) Sch. Bip., AF155270/AF155307 (Francisco-Ortega & al. 1997); *Artemisia (Serephidium) tridentata* Nutt. AF060460/AF061376 (Kornkven & al. 1998); *Artemisia vulgaris* L., AJ3296389/AJ3296424 (Oberprieler & Vogt 2000); *Artemisiella 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; *Athanasia pachycephala* DC., AM774447 (Himmelreich & al., in press); *Brachanthemum titovii* Krasch., AF504142/AF504169 (Vallès & al. 2003); *Brocchia cinerea* (Del.) Vis., AJ748778/AJ748779 (Oberprieler 2004a); *Castrilanthemum debeauxii* (Degen) Vogt & Oberprieler, AJ3296390/ AJ3296425 (Oberprieler & Vogt 2000); *Chamaemelum nobile* (L.) All., AJ3296382/AJ3296417 (Oberprieler & Vogt 2000); *Chlamydochora tridentata* (Del.) Less., AJ3296391/AJ3296426 (Oberprieler & Vogt (2000)); *Chrysanthemum xmorifolium* Ramat., AF314599 (Zhao & al., unpubl.); *Chrysanthoglossum deserticola* (Murb.) B. H. Wilcox & al., AJ3296392/ AJ3296427 (Oberprieler & Vogt 2000); *Cladanthus arabis* (L.) Cass., AJ3296383/ AJ3296418 (Oberprieler & Vogt 2000); *Coleostephus multicaulis* (Desf.) Durieu, AJ296393/ AJ296428 (Oberprieler & Vogt 2000); *Cota tinctoria* J. Gay, AJ312802/ AJ312831 (Oberprieler 2001); *Cotula australis* (Spreng.) Hook. f., AM774448 (Himmelreich & al., in press); *Crossostephium chinense* (L.) Makino, AY127685/AY127686 (Watson & al. 2002); *Cymbopappus adenosolen* (Harv.) B. Nord., AM774449 (Himmelreich & al., in press); *Daveaua anthemoides* Mariz, AJ864577/ AJ864597 (Oberprieler 2004b); *Elachanthemum intricatum* (Franch.) Y. Ling & Y. R. Ling, AY127683/AY127684 (Watson & al. 2002); *Endopappus macrocarpus* Sch. Bip., AJ748780/AJ748781 (Oberprieler 2004a); *Eriocephalus paniculatus* DC., AM774450 (Himmelreich & al., in press); *Eumorphia sericea* J. M. Wood & M. Evans, AM774451 (Himmelreich & al., in press); *Filifolium sibiricum* (L.) Kitam., AY127687/AY127688 (Watson & al. 2002); *Foveolina albida* (DC.) Källersjö, AM774452 (Himmelreich & al., in press); *Glebionis coronaria* (L.) Spach, L777741 (Francisco-Ortega & al. 1997); *Glossopappus macrotus* (Darieu) Briq., AJ3296394/AJ3296429 (Oberprieler & Vogt 2000); *Gonospermum canariense* (DC.) Less., AF155243/AF155280 (Francisco-Ortega & al. 2001); *Gymnopentzia bifurcata* Benth., AM774453 (Himmelreich & al., in press); *Handelia trichophylla* (Schrenk) Heimerl, Tian-shan, montes Kirgiski khrebet, 10 km NE Frunze (Pishpek), 1000-1200 m, 29.5.1974, *Vasak* (B), AM774422; *Heliocauta atlantica* (Litard. & Maire) Humphries, AJ748782/ AJ748783 (Oberprieler 2004a); *Heteranthemis viscidhirta* Schott, L777761 (Francisco-Ortega & al. 1997); *Heteromera fuscata* (Desf.) Pomel, AJ3296409/AJ3296444 (Oberprieler & Vogt 2000); *Hilliardia zuurbergensis* (Oliv.) B. Nord., AM774454 (Himmelreich & al., in press); *Hippia pilosa* (P. Bergius) Druce, AM774455 (Himmelreich & al., in press); *Hippolytia dolichophylla* (Kitam.) Bremer & Humphries, AJ748784/AJ748785 (Oberprieler 2004a); *Hymenolepis incisa* DC., AM774456 (Himmelreich & al., in press); *Hymenostemma pseudanthemis* Willk., L77762 (Francisco-Ortega & al. 1997); *Inezia integrefolia* (Klatt) E. Phillips, AM774457 (Himmelreich & al., in press); *Inulanthera leucoclada* (DC.) Källersjö, AM774458 (Himmelreich & al., in press); *Ismelia carinata* (Schousb.) Sch. Bip., L777764 (Francisco-Ortega & al. 1997); *Kaschgaria komarovii* (Krasch. & N. Rubtsov) Poljakov, AY127689/ AY127690 (Watson & al. 2002); *Lasiospermum pedunculare* Lag., AM774459 (Himmelreich & al., in press); *Lepidolopsis*

turkestanica (Regel & Schmalh.) Poljakov, AF504190/ AF504163 (Vallès & al. 2003); *Lepidophorum repandum* (L.) DC., AJ3296395/AJ3296430 (Oberprieler & Vogt 2000); *Leptinella pectinata* (Hook.f.) D. G. Lloyd & C. J. Webb, AM774460 (Himmelreich & al., in press); *Leucanthemella serotina* (L.) Tzvelev, L77766 (Francisco-Ortega & al. 1997); *Leucanthemopsis alpina* (L.) Heywood, AJ3296396/ AJ3296431 (Oberprieler & Vogt 2000); *Leucanthemum vulgare* (Vaill.) Lam., AJ3296398/ AJ864598 (Oberprieler & Vogt 2000); *Leucocyclus formosus* Boiss., AJ864578/AJ864598 (Oberprieler 2004b); *Leucoptera subcarnosa* B. Nord., AM774461 (Himmelreich & al., in press); *Lidbeckia pectinata* P. Bergius, AM774462 (Himmelreich & al., in press); *Lonas annua* (L.) Vines & Druce, AJ3296411/ AJ3296446 (Oberprieler & Vogt 2000); *Lugoa revoluta* (Link) DC., AF155252/AF155289 (Francisco-Ortega & al. 2001); *Marasmodes dummeri* Hutch., AM774463 (Himmelreich & al., in press); *Matricaria discoidea* DC., AJ3296412/AJ3296447 (Oberprieler & Vogt 2000); *Mauranthemum gaetulum* (Batt.) Vogt & Oberprieler, AJ3296399/ AJ3296434 (Oberprieler & Vogt 2000); *Mausolea eriocarpa* (Bunge) Poljakov, AF504164/ AF504191 (Vallès & al. 2003); *Mecomischus halimifolius* (Munby) Hochreutiner, AJ3296384/ AJ3296419 (Oberprieler & Vogt 2000); *Microcephala discoidea* (Ledeb.) Bremer & al., AY127677/AY127678 (Watson & al. 2002); *Myxopappus acutifolium* (DC.) Källersjö, AM774464 (Himmelreich & al., in press); *Nananthea perpusilla* DC., AJ864579/AJ864599 (Oberprieler 2004b); *Neopallasia pectinata* (Pall.) Poljakov, AY127691/ AY127692 (Watson & al. 2002); *Nippoanthemum nipponicum* (Maxim.) Kitam., L77772 (Francisco-Ortega & al. 1997); *Nivellea nivellei* (Braun-Blanq. & Maire) B. H. Wilcox & al., AJ3296400/AJ3296435 (Oberprieler & Vogt 2000); *Oncosiphon grandiflorum* (Thunb.) Källersjö, AM774465 (Himmelreich & al., in press); *Osmitopsis asteriscoides* (P. Bergius) Less., AM774466 (Himmelreich & al., in press); *Otanthus maritimus* (L.) Hoffmanns. & Link, AJ3296385/AJ3296420 (Oberprieler & Vogt 2000); *Otospermum glabrum* (Lag.) Willk., AJ3296413/AJ3296448 (Oberprieler & Vogt 2000); *Pentzia dentata* Kuntze, AY127681/ AY127682 (Watson & al. 2002); *Phalacrocarpum oppositifolium* (Brot.) Willk., AJ3296401/ AJ3296436 (Oberprieler & Vogt 2000); *Phaeostigma salicifolium* (Mattf.) Muldashev, China, Sze-ch'uan, reg. bor., Dongrergo, in prato herboso-fruticoso, 4200, 8.8.1922, Smith [S], AM774423; *Phymaspermum leptophyllum* (DC.) Benth. ex B. D. Jackson, AM774467 (Himmelreich & al., in press); *Picrothamnus desertorum* Nutt., USA: Idaho, Owyhee Co, 8 miles southwest of Marsing, 19.4.1959, Cronquist 8121 (S), AM774424; *Plagiis maghrebinus* Greuter & Vogt, AJ3296403/AJ3296438 (Oberprieler & Vogt 2000); *Prolongoa hispanica* G. López & C. E. Jarvis, L77776 (Francisco-Ortega & al. 1997); *Pseudohandelia umbellifera* (Boiss.) Tzvelev, AJ880330/AM774468 (Gemeinholzer & al. 2006, Himmelreich & al., in press); *Rennera limnophila* Merxm., AM774469 (Himmelreich & al., in press); *Rhadinolepis lonadioides* Coss., AJ3296386/ AJ3296421 (Oberprieler & Vogt 2000); *Rhodanthemum arundanum* (Boiss.) B. H. Wilcox & al., AJ3296405/AJ3296440 (Oberprieler & Vogt 2000); *Richteria pyrethroides* Karelin & Kir., Tian-shan, montes Chatkalski khrebet, mons Chimgan, 1900-2600 m, 17.7.1973, Vasak (B), AM774425; *Santolina chamaecyparissus* L., AF155276/ AF155313 (Francisco-Ortega & al. 2001); *Schistostephium crataegifolium* Harv. & Sond., AM774470 (Himmelreich & al., in press); *Sclerohachis platyrhachis* (Boiss.) Podlech, Iran, Khorasan, in saxosis serpentinicis ditionis Robat-I Safid 82-90 km S Mashhad, 70 km N Torbat-e Heydariyeh, 1520 m, Rechinger 51325 (B), AM774426; *Soliva sessilis* Ruiz Lopez & Pavon, AM774471 (Himmelreich & al., in press); *Sphaeromeria diversifolia* Rydb., AY127693/ AY127694 (Watson & al. 2002); *Stilpnolepis centriflora* (Maxim.) Krasch., AY127695/ AY127696 (Watson & al. 2002); *Tanacetopsis eriobasis* (Rech.f.) Kovalevsk., Afghanistan, in valle Maidan, 2400 m, Rechinger 36000 (B), AM774427; *Tanacetopsis mucronata* (Regel & Schmalh.) Kovalevsk., Montes Karatau et Talas-Aiatau, 5.7.1931, Pavlov 539 (B), AM774428; *Tanacetum vulgare* L., AF155263/ AF155299 (Francisco-Ortega & al. 2001); *Thaminophyllum latifolium* Bond, AM774472 (Himmelreich & al., in press); *Trichanthemis aulieatensis* (B. Fedtsch.) Krasch., Kazachstania, jugum Kirghizicum, in angustis fl. Alamaly-Saj, in declivibus austro-orientalibus schistosis, Fisjun (no 4448), 22.5.1961 (B), AM774429; *Tripleurospermum caucasicum* (Willd.) Hayek, AJ864590/AJ864610 (Oberprieler 2004b); *Turaniphytum eranthemum* (Bunge) Poljakov,

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.) Cronqist, 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); *Symphotrichum cordifolium* (L.) G. L. Nesom, DQ005972 (Kress & al. 2005)

Calenduleae. – *Calendula officinalis* L., AF422114 (Wagstaff & Breitwieser 2002).

Gnaphalieae. – *Antennaria virginia* Stebbins, L40851/L40930 (Bayer & al. 1996).