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An updated subtribal classification of *Compositae* tribe *Anthemideae* based on extended phylogenetic reconstructions

Christoph Oberprieler¹, Alisha Töpfer¹, Marco Dorfner¹, Miriam Stock¹ & Robert Vogt²

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Abstract: An updated subtribal classification of the *Compositae*–*Anthemideae* is presented based on gene- and species-tree reconstructions considering sequence variation from the plastid (cpDNA *ndhF*, *trnL-trnF*) and nuclear genome (nrDNA ITS1–5.8S–ITS2, ETS; nDNA dual specificity phosphatase *DSP*, plus-3 domain-containing protein of the vernalization independence 5 complex *VIP5*, major facilitator superfamily protein of the Nitrate Transporter1/Peptide Transporter *NPF3.1*) for 113 of the 115 hitherto accepted genera of the tribe. As a result, six subtribes are newly circumscribed, i.e. *Anthemidinae* (including also *Xylanthemum*), *Artemisiinae* (including also *Hulteniella*, *Lepidolopha*, *Opisthopappus* and *Tridactylina*), *Glebionidinae* (including also *Otoglyphis*, *Endopappus* and *Nivellea*), *Handeliinae* (including *Cancrinia*, *Polychrysum* and excluding *Xylanthemum*), *Leucantheminae* (including also *Daveaua*, *Heteromera* and *Otospermum*) and *Leucanthemopsidinae* (including *Phalacrocarpum*). Additionally, five unigeneric subtribes (i.e. *Brocchiinae*, *Inulantherinae*, *Lepidophorinae*, *Lonadinae* and *Vogtiinae*) are described as new to science due to their phylogenetically isolated positions, resulting in 19 subtribes accepted for *Compositae*–*Anthemideae*. Three new combinations are proposed to accommodate the former *Aaronsohnia factorovskyi* Warb. & Eig and *A. pubescens* subsp. *maroccana* (Ball) Fennane & Ibn Tattou in the genus *Otoglyphis* Pomel (1874), which was found to have priority over *Aaronsohnia* Warb. & Eig (1927), and to accommodate the former *Tanacetum paleaceum* Podlech in the genus *Xylanthemum* Tzvelev.

Keywords: *Anthemideae*, *Asteraceae*, *Compositae*, gene trees, multispecies coalescent, species trees, phylogeny, subtribes, taxonomy

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Introduction

The chamomile tribe of the sunflower family (*Compositae*–*Anthemideae*) comprises more than 100 genera and around 1800 species (Oberprieler & al. 2006, 2009). A subtribal classification of the tribe was proposed by Bremer & Humphries (1993) in a generic monograph of the *Anthemideae* and was mainly based on morphological characters. However, in subsequent molecular phylogenetic studies, many of the subtribes erected by Bremer & Humphries (1993) turned out to be non-monophyletic, and a new subtribal classification was proposed by Oberprieler & al. (2007, 2009) based on nrDNA ITS and cpDNA *ndhF* sequence variation. Due to the lack of plant material for a number of genera or their unresolved positions in the mentioned phylogenetic analyses, the subtribal classification of Oberprieler & al. (2007, 2009) still comprised a number of orphan genera, for which a subtribal assignment was not possible. For some of these,

the present contribution tries to determine their subtribal placement and their generic relationships based on adding sequence information from an additional nuclear multi-copy (nrDNA ETS), three low-copy nuclear markers and from the faster evolving cpDNA intergenic spacer region *trnL-trnF*.

Material and methods

Plant material and DNA sequencing — The selection of taxa and specimens studied in the present contribution was based on the previous circumscription of genera of the *Anthemideae* (Oberprieler & al. 2007, 2009), with the addition of representatives of the hitherto subtribally unclassified genera (Appendix 1). Total genomic DNA was extracted following the modified protocol of the CTAB method (Doyle and Doyle 1987; Doyle and Dickson 1987).

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PCR amplicons of nrDNA ITS were gained using the following primers: ITS2, ITS4, ITS5 (White & al. 1990), ITS5 (Downie & Katz-Downie 1996), ITS-18SF, ITS-26SR (Rydin & al. 2004), P1 (Ochsmann 2000), ITS-D (Blattner 1999) and ITS-SR (Blattner & al. 2002). For the amplification of nrDNA ETS, we used the primers L-ETS (Lee & al. 2002) and 18S-ETS (Baldwin & Markos 1998). The plastid gene *ndhF* was amplified with the primers *ndhF*-1260, *ndhF*-3'Forward and *ndhF*-3'Reverse (Eldenäs & al. 1999) and the intergenic spacer region *trnL-trnF* with the primers *trnL*(e) and *trnF*(f) (Taberlet & al. 1991). The three novel single- or low-copy nuclear markers used in the present contribution were designed with the help of *Leucanthemum* Mill. consensus sequences (from the four species *L. vulgare* Lam., *L. gaudinii* Dalla Torre, *L. monspeliense* (L.) H. J. Coste and *L. rotundifolium* DC.) generated from clusters of Nanopore sequence reads, which were obtained during a previous target enrichment experiment (Scheunert & al. unpublished). For this purpose, particularly exon-rich consensus sequences were blasted against the genomes of *Helianthus annuus* L. (NCBI gene bank assembly accession: GCA_002127325) and *Artemisia annua* L. (NCBI gene bank assembly accession: GCA_003112345) and resulting alignments were used for primer design. Sequence sections that appeared to be suitable were analysed with Primer3Plus (Untergasser & al. 2012), and the primer sequences were checked for suitability with OligoCalc (Kibbe 2007) and Multiple Primer Analyzer (Thermo Fisher Scientific Inc., Waltham, MA, U.S.A.). Primer information and NCBI (National Center for Biotechnology Information) GenBank information on primer positions on the *Artemisia annua* L. genome are given in Table 1. The different marker names are based on the *Arabidop-*

sis thaliana (L.) Heynh. genome (At), where they were annotated as At1g18593 coding for the dual specificity phosphatase (*DSP*), At1g61040 coding for the plus-3 domain-containing protein, which is part of the vernalization independence 5 (*VIP5*) complex, and At1g68570 coding for the major facilitator superfamily protein, which is part of the Nitrate Transporter1/Peptide Transporter (*NPF3.1*).

After purification of PCR amplicons with AMPure (Agencourt Bioscience Corp., Beverly, MA, U.S.A.) or AmpliClean (Nimagen, Nijmegen, The Netherlands) magnetic beads, Sanger sequencing was carried out by a contract sequencing company (MacroGen Europe, Amsterdam, The Netherlands). Electropherograms were edited with CHROMAS v2.6.6 (Technelysium Pty Ltd 1998–2018) with usage of the IUPAC code for polymorphisms, and marker-wise alignments were done with BioEDIT v7.2.5 (Hall 1999) and the MAFFT algorithm (Katoh & Standley 2013; Katoh & al. 2019).

Phylogenetic analyses — As outgroups for the analyses of both nrDNA ITS and cpDNA *ndhF* and *trnL-trnF*, we used nine species of the tribes *Astereae*, *Calenduleae* and *Gnaphalieae* (Appendix 1). In the phylogenetic reconstructions based on the combined datasets (both in the concatenated and in the coalescent-based species-tree reconstructions), the lack of complete sequence information for any of these outgroup taxa impeded rooting of the resulting species trees. Since the present phylogenetic reconstructions mainly aimed at the analysis and circumscription of subtribes in terms of monophyletic groups, we considered the placement of a tree root of secondary importance and rooted the species trees on the longest internal branch (i.e. the branch leading to *Inulanthera* and *Ursinia*).

Table 1. Description of and primer information for the three nuclear single- or low-copy markers used in the present study. All three markers were gained by comparing genomic information for *Helianthus annuus* L. and *Artemisia annua* L. with reads from a target-enrichment experiment in *Leucanthemum* Mill. Selected loci are characterized by their positions on the *Artemisia annua* genome.

	<i>DSP</i>	<i>VIP5</i>	<i>NPF3.1</i>
Protein	Dual specificity phosphatase	Plus-3 domain-containing protein	Major facilitator superfamily protein
NCBI GenBank assembly accession	<i>Artemisia annua</i> L.: GCA_003112345		
Locus	LBNU01013331	LBNU01034717	LBNU01021142
WGS Project/Scaffold	PKPP01000597	PKPP01010419	PKPP01019732
Forward primer sequence	CAT CCA ACG AAG AGG CTC AAC	GGT TTA TGG AGC CTT TCT TTG AGG	CAG GGG TAG AAA GGG GAG TTT C
Melting temperature	61.2°C	63.6°C	64.2°C
Primer position	25904–25924	47505–47528	10187–10208
Reverse primer sequence	CCG TGG AGA GAA AAT TGA TAG CAC	TAT TTC CTC AGT AAA CAT GT	AGC AAT CTC AAG GGG TTT AAA AGT G
Melting temperature	63.6°C	65.2°C	62.5°C
Primer position	26172–26195	47291–47314	10671–10695
Calculated/sequenceable sequence length	297 bp/264 bp	240 bp/205 bp	512 bp/458 bp

For gene-tree reconstructions in MRBAYES v3.2.7 (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003; Ronquist & al. 2012), the General Time-reversible (GTR+I+G) model was found to be the best-fit sequence evolution model by using the “Automated Model Selection” option in PAUP* v.4.0a169 (Swofford 2021). Each gene-tree reconstruction was performed both with and without a coding of indels (done with GAPCODER v.4; Young & Healy 2003) and the splitting of data into a DNA and a “coded gaps” partition. The latter partition was modelled with an equal-rates parameter. The gene-tree analyses for individual markers and the species-tree analysis based on the concatenated dataset were run in MRBAYES for 4 million to 150 million generations in two parallel runs with four chains each and a temperature of 0.02–0.1 on a workstation with ten cores until convergence of runs was attained (average standard deviation of split frequencies < 0.01).

Species-tree reconstruction based on a multispecies-coalescent model was performed with BEAST v2.6.6 (Bouckaert & al. 2014, 2019) after creating the input file comprising the three nDNA markers of *DSP*, *VIP5* and *NPF3.1*, the two cpDNA markers *ndhF* and *trnL-trnF* and the concatenated nrDNA ITS/ETS alignment with BEAUTI (Drummond & al. 2012) using the STARBEAST template. Substitution models assigned to the individual markers were the same as those used for the gene-tree analyses (GTR+I+G). For all partitions, the “Relaxed clock Log Normal” clock type, a Yule tree prior and a random starting tree were chosen. Priors were left at the default values, except for the uncorrelated lognormal relaxed clock means (“uclMean”), which were modelled as a gamma distribution with the Alpha value at 0.2 and the Beta at 5.0. The chain length was set to 150 million and every 5000th generation was recorded. Runs were repeated until all operators were adjusted according to the suggestions given after each run was finished. The finalized BEAUTI setup was run nine times using BEAST v2.6.6. The convergence of independent runs was checked using TRACER v1.7.2. (Rambaut & al. 2018). Five of the resulting log and tree files that had converged best based on their “Effective Sample Size” values were combined using LOGCOMBINER v2.6.6 with a burn-in of 20% and 30% until all ESS values of the finalized files were >200. TREEANNOTATOR v2.6.6 was then used to combine the 117,005 post-burn-in trees into a maximum-clade-credibility tree. TREEGRAPH v2.15.0-887beta (Stöver & Müller 2010) was used to edit the tree files.

Results and Discussion

Gene-tree reconstructions — The alignment of the traditionally Sanger sequenced plastid gene *ndhF* and the intergenic spacer region *trnL-trnF* is 1685 bp long (Online Resource S1; including gap-coding information) and resulted in a phylogenetic tree with some well-sup-

ported monophyletic groups (Fig. 1). When compared with the phylogenetic tree based on *ndhF* information alone and comprising far fewer representatives of the tribe (Oberprieler & al. 2009), many topological features observed in this former phylogenetic reconstruction with its 62 taxa receive corroboration by being congruent to the present reconstruction based on 107 *Anthemideae* generic representatives: (1) the monophyly of subtribe *Cotulinae*; (2) the isolated position of *Osmitopsis*; (3) the sister-group relationship of *Ursinia* (*Ursiniinae*) and *Inulanthera* (hitherto unassigned to a subtribe); (4) the paraphyly of subtribe *Athansiiinae*; (5) the monophyly of all remaining subtribes comprising both subtribes centred in the S hemisphere (*Pentziinae*, *Phymasperminae*) and N hemisphere; (6) the lack of resolution among the subtribes of the “Asian-southern African grade” (Oberprieler & al. 2009; i.e. *Artemisiinae*, *Handeliinae*, *Pentziinae* and *Phymasperminae*); (7) the monophyly of the subtribes of the “Eurasian grade” and the “Mediterranean clade” (Oberprieler & al. 2009); (8) the lack of a clear demarcation between *Anthemidinae* and *Matricariinae* in the former; and (9) the clear monophyly of the latter (i.e. *Glebionidinae*, *Leucantheminae* and *Santolininae*). Additionally, many orphan genera missing from the previous analysis and hitherto unassigned to a subtribe now show well-supported subtribal affiliations that were only speculated upon by Oberprieler & al. (2009): (1) *Cancrinia*, *Polychrysum* and *Ugamia* in *Handeliinae*; (2) *Phalacrocarpum* in *Leucanthemopsidinae*; (3) *Daveaua*, *Heteromera* and *Otospermum* in *Leucantheminae*; and (4) *Endopappus*, *Nivellea* and *Otoglyphis* (the former *Aaronsohnia*, see below) in *Glebionidinae*. In contrast to this, other genera unassigned to a subtribe in our previous study are also found to be phylogenetically isolated here (i.e. *Brocchia*, *Lepidophorum*, *Lonas* and *Vogtia*).

The length of the alignment of the nuclear ribosomal repeat (nrDNA ITS) is 710 bp long (Online Resource S2), comprising ITS1 (alignment positions 1–293), the 5.8S gene (294–462) and ITS2 (463–710). The resulting phylogenetic reconstruction (Fig. 2) was found to be largely in accordance with the one based on plastid DNA sequence variation. It corroborates: the early divergence of *Cotulinae* and *Osmitopsidinae*; the paraphyly of *Athansiiinae* (with *Phymasperminae* nested within this anyway non-monophyletic generic assemblage); the inclusion of the S hemisphere subtribe *Pentziinae* into the large monophyletic group of all N hemisphere-centred subtribes; the close relationship among the circum-Mediterranean subtribes (*Anthemidinae*, *Glebionidinae*, *Leucantheminae*, *Leucanthemopsidinae*, *Matricariinae* and *Santolininae*); and the monophyly of the vast majority of previously described subtribes (except the already mentioned *Athansiiinae*). Additionally, most of the above-mentioned subtribal affiliations of hitherto unclassified genera seen in the phylogenetic tree based on the two plastid markers receive further support from the nrDNA ITS tree; the exceptions being *Endopappus* and *Phalacrocarpum*, which

lack supported placement in *Glebionidinae* and *Leucanthemopsidinae*, respectively.

The alignments of the three single-copy nuclear markers *DSP*, *VIP5* and *NPF3.1* are 264 bp (and additional 12 coded indels), 205 bp (without indels coding) and 458 bp long (without indels coding), respectively (Online Resources S3–S5). Phylogenetic trees based on these three markers individually received much less-supported topologies (Online Fig. S1–S3) but contained some strongly supported backbone and terminal branches. We hoped these would contribute additional support to the subtribal classification of orphan genera and the phylogenetic relationships among subtribes in the total-evidence approaches of the downstream species-tree reconstructions (see below). Owing to the patchy sampling of sequence information from the multi-copy nrDNA ETS marker (see Appendix 1), we decided to include it only in the species-tree reconstructions, in which only accessions with the majority of markers sampled were taken into account.

Species-tree reconstructions — The concatenated alignment of the total dataset is 3860 bp long (Online Resource S6), comprising markers *DSP* (alignment positions 1–241), *VIP5* (positions 242–446), *NPF3.1* (positions 447–904), ITS+ETS (positions 905–2389), *ndhF* (positions 2390–3401) and *trnL-trnF* (positions 3402–3860), and resulted in the phylogenetic tree shown in Fig. 3. The corresponding species tree received from the coalescent-based analysis of the same data set is depicted in Fig. 4. Owing to

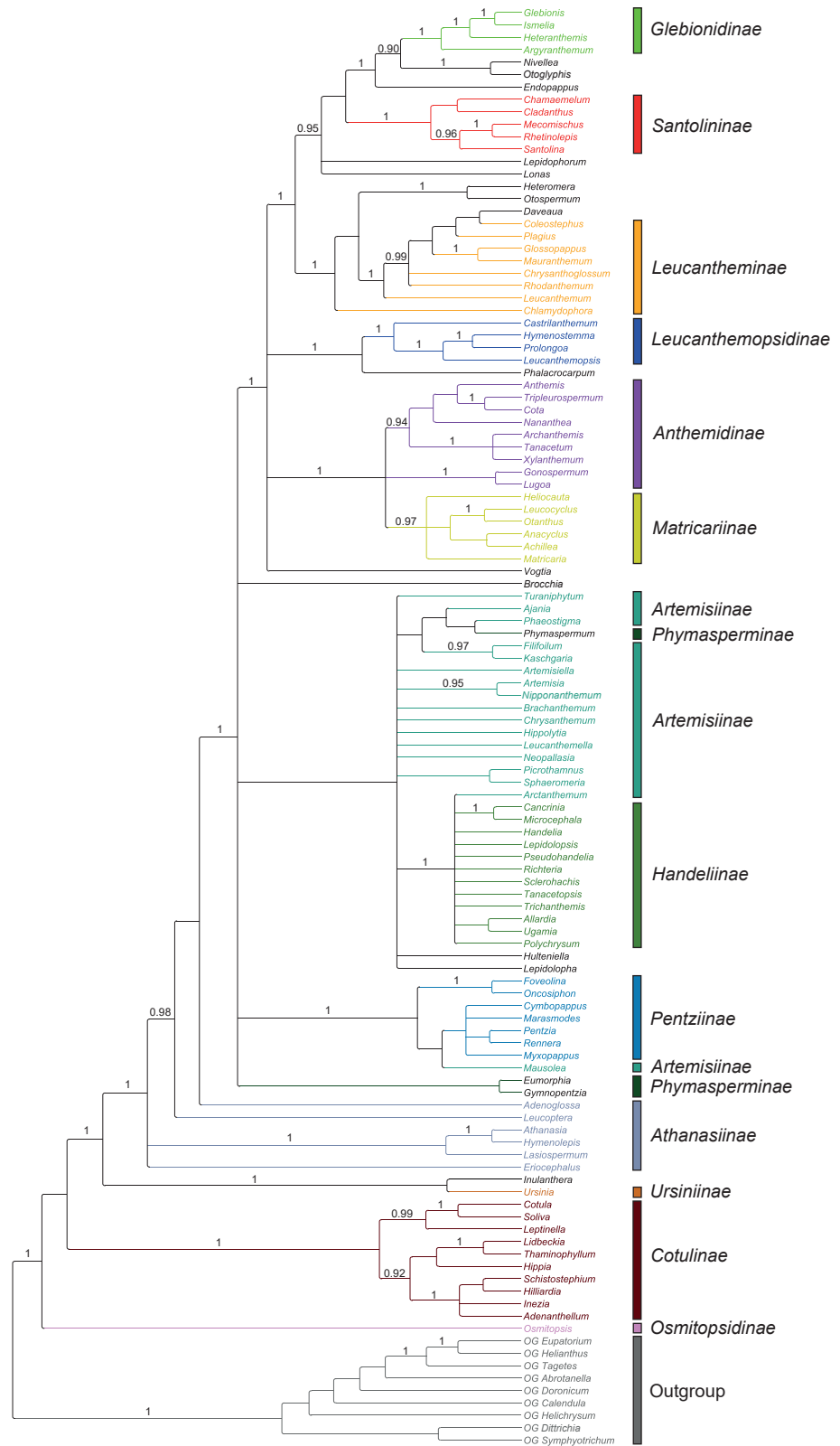


Fig. 1. Phylogeny (gene tree) of *Compositae–Anthemideae* based on combined cpDNA sequences (*ndhF*, *trnL-trnF*) with subtribal assignment according to Oberprieler & al. (2007, 2019), Sonboli & Oberprieler (2010) and Sonboli & al. (2012). Clade support values (posterior probabilities > 0.9) are indicated.

the lack of sequence information for all members of the outgroup and a considerable number of ingroup taxa, the

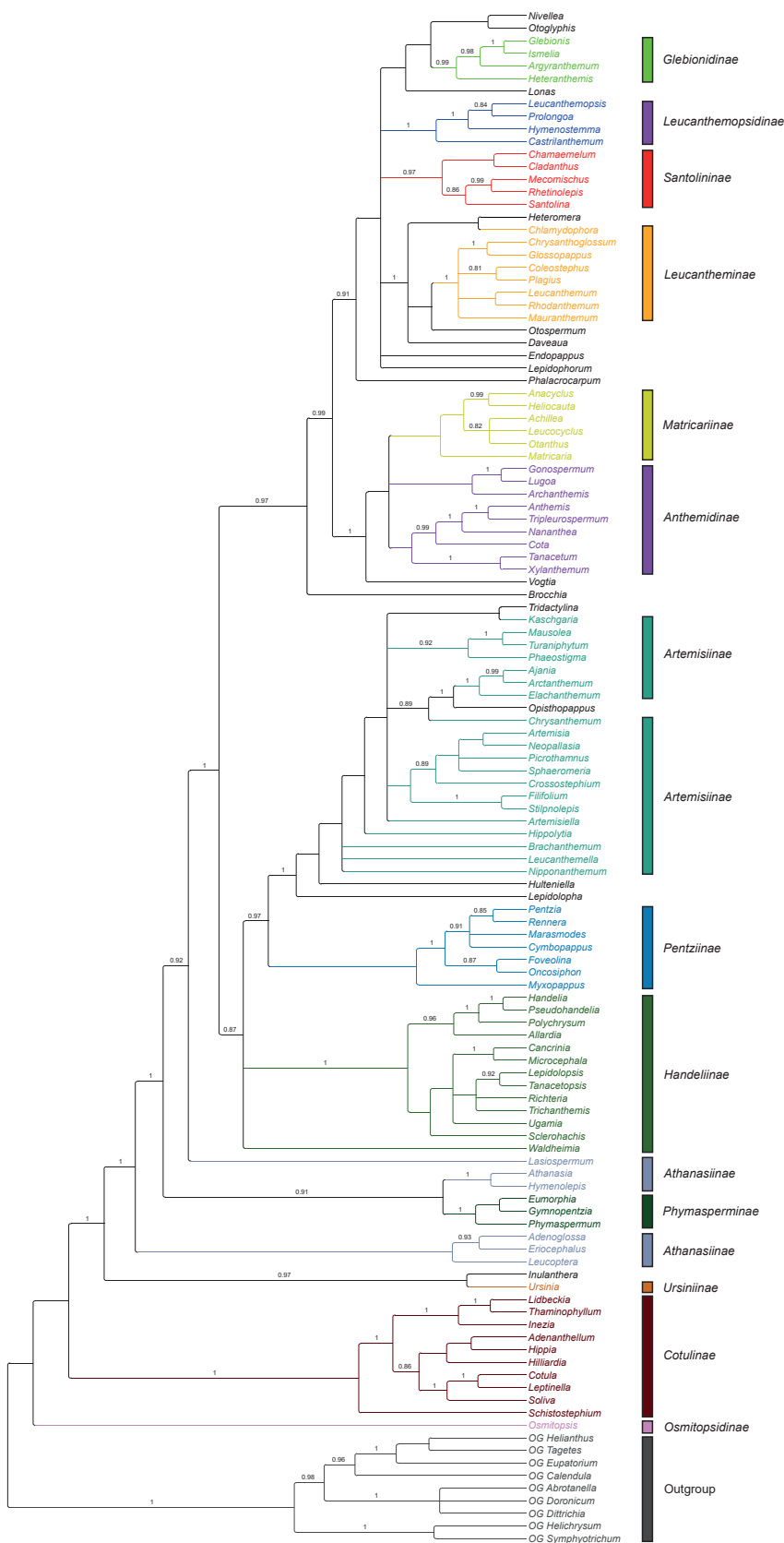


Fig. 2. Phylogeny (gene tree) of *Compositae-Anthemideae* based on combined nrDNA sequences (ITS1, 5.8S, ITS2) with subtribal assignment according to Oberprieler & al. (2007, 2019), Sonboli & Oberprieler (2010) and Sonboli & al. (2012). Clade support values (posterior probabilities > 0.9) are indicated.

two species-tree reconstructions differ from the gene trees mostly concerning the position of the root of the trees and the relationship among the early-diverging lineages of the tribe. However, when posterior probabilities along the backbone of the tree are considered, it becomes clear that there is only support from the analysis based on concatenated sequences (Fig. 3) that the earliest diverging lineage has to be found among the *Cotulinae*, the *Osmitopsidinae* and the clade of *Inulanthera* and *Ursinia*.

In general, support values of monophyletic groups appear to be much higher in the analyses of concatenated sequences (Fig. 3) than in the coalescent-based species-tree reconstruction (Fig. 4). Owing to the comprehensive topological correspondence observed between the plastid phylogeny (Fig. 1) and the tree reconstruction based on nrDNA ITS (Fig. 2), we think that this is a consequence of the incongruence among the three single-copy nuclear markers (Online Fig. S1–S3), which has led to the diminishing posterior probabilities in the coalescent-based reconstruction (Fig. 4), while in the concatenated analysis (Fig. 3) these information-poor and contradicting markers are overridden by the more information-rich and less contradicting signals from cpDNA and nrDNA ITS.

Nevertheless, the subtribal classification in general and the affiliation of hitherto unassigned genera in particular receive support from both reconstructions in many cases: (1) the sister-group relationship between *Ursinia* (*Ursiniinae*) and *Inulanthera*; (2) the lack of support for the *Athansiiinae*; (3) the monophyly of the *Phymasperminae*; (4) the monophyly of the *Handeliinae*; (5) the monophyly of the *Artemisiinae* including *Hulteniella* and *Lepidolopha*; (6) the monophyly of the *Leucanthemopsidinae* including *Phalacrocarpum*; (7) the monophyly of the *Leucanthemeinae* including *Daveaua*, *Hetero-*

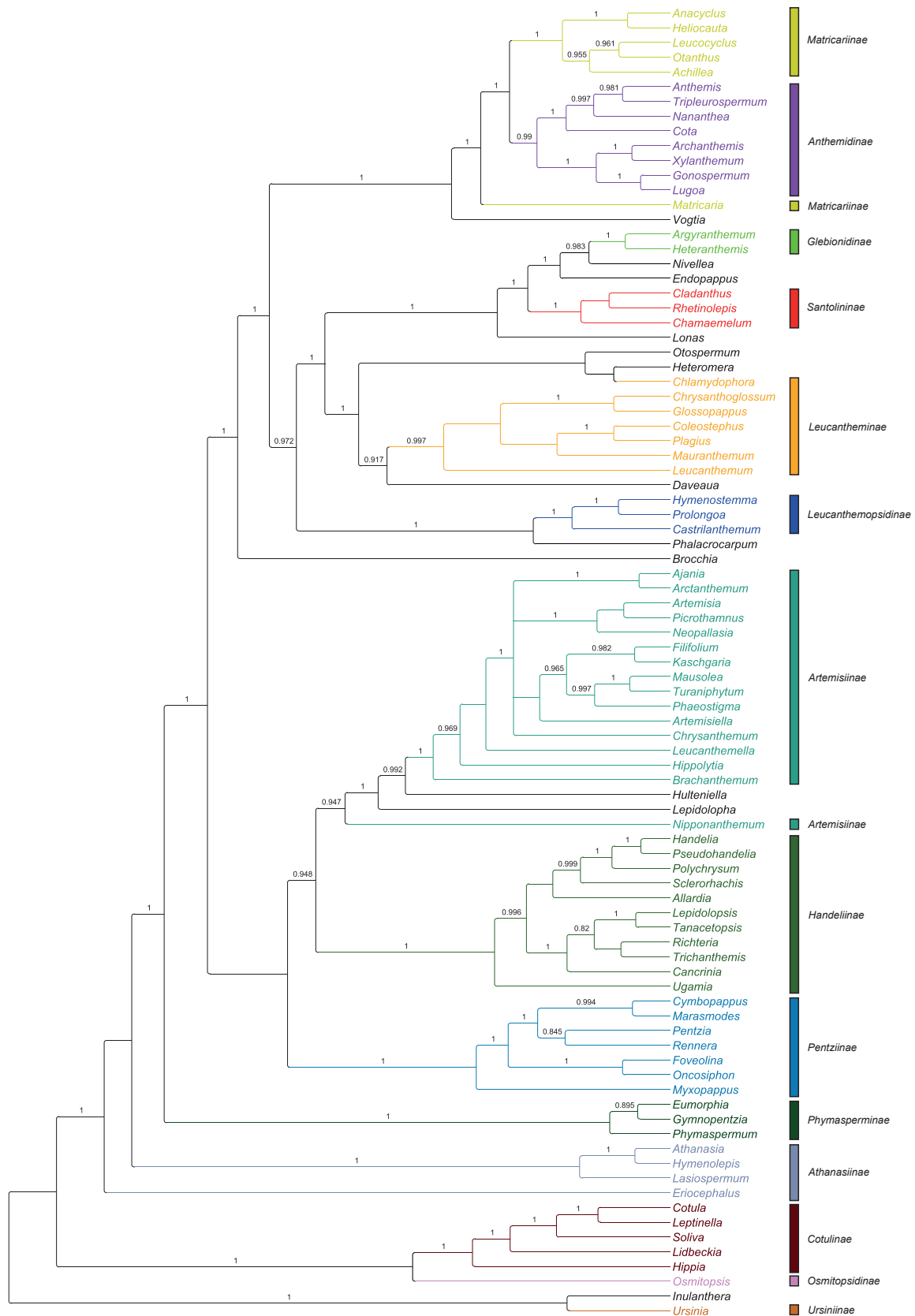


Fig. 3. Phylogeny of *Compositae–Anthemideae* based on a species-tree reconstruction with concatenated plastid and nuclear markers (cpDNA *ndhF*, *trnL-trnF*; nrDNA ITS1-5.8S-ITS2, ETS; nDNA *DSP*, *VIP5*, *NPF3.1*). Subtribal assignment of genera according to Oberprieler & al. (2007, 2019), Sonboli & Oberprieler (2010) and Sonboli & al. (2012). Clade support values (posterior probabilities > 0.9) are indicated.

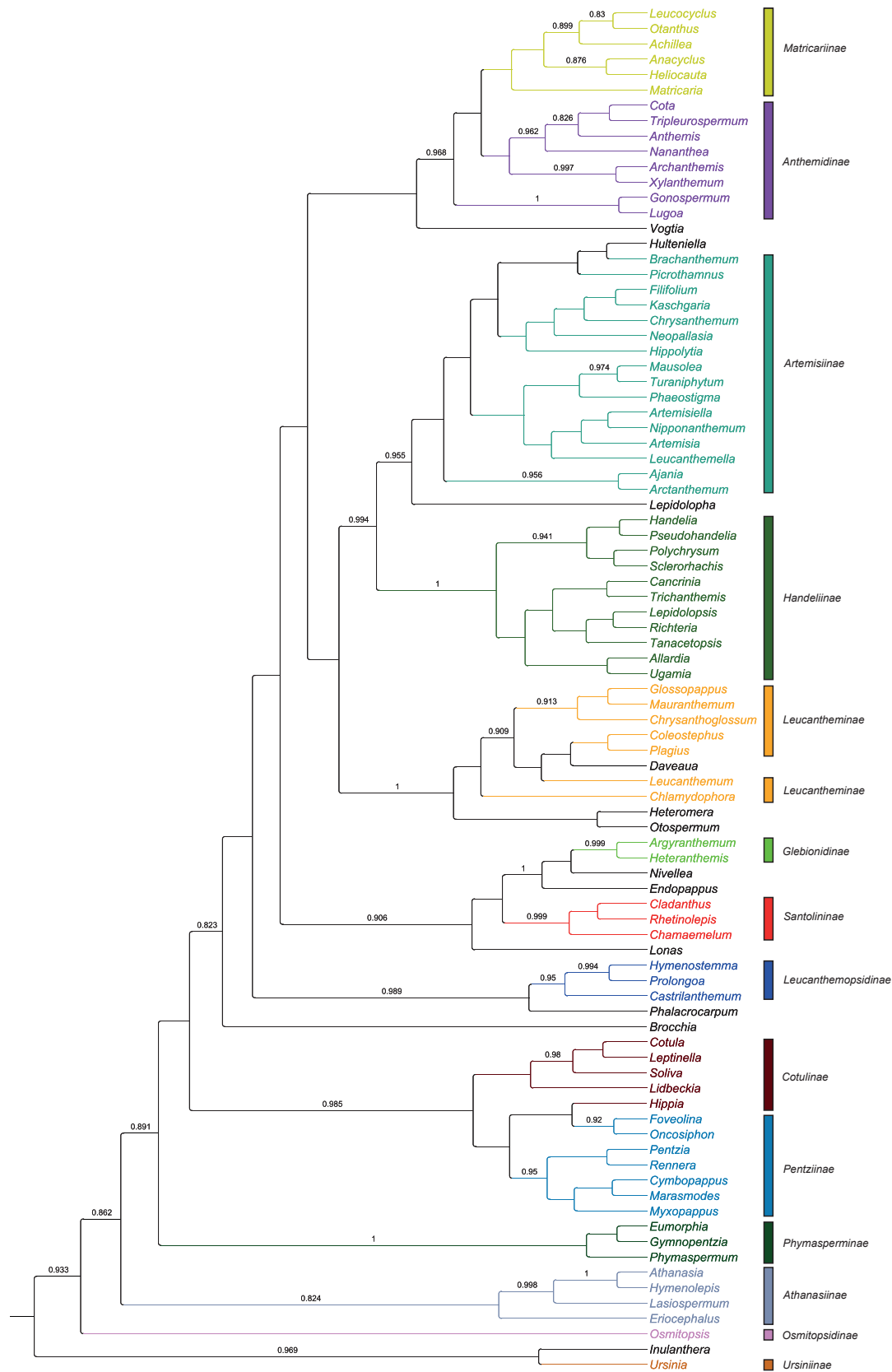


Fig. 4. Phylogeny of *Compositae*–*Anthemideae* based on a coalescent-based species-tree reconstruction with plastid and nuclear markers (cpDNA *ndhF*, *trnL-trnF*; nrDNA ITS1-5.8S-ITS2, ETS; nDNA *DSP*, *VIP5*, *NPF3.1*). Subtribal assignment of genera according to Oberprieler & al. (2007, 2019), Sonboli & Oberprieler (2010) and Sonboli & al. (2012). Clade support values (posterior probabilities > 0.9) are indicated.

mera and *Otospermum*; (8) the monophyly of the *Santolininae*; (9) the monophyly of the *Glebionidinae* including *Endopappus* and *Nivellea*; (10) the sister-group relationship of the *Anthemidinae* and *Matricariinae*, but with the lack of support for the monophyly of both subtribes; and (11) the isolated positions of *Brocchia*, *Lonas* and *Vogtia*.

Discrepancy between the two species-tree reconstructions mostly concern (1) the *Cotulinae* (monophyletic in the concatenated, but not in the coalescent-based reconstruction); (2) the position of *Osmitopsis* (sister to the *Cotulinae* in the concatenated, but with unclear relationships in the coalescent-based analysis); (3) the monophyly of the *Pentziinae* (supported in the concatenated, but not in the coalescent-based analysis); (4) the sister-group relationship of *Glebionidinae* and *Santolininae* (supported in the concatenated, but not in the coalescent-based analysis); and (5) the monophyly of the *Anthemidinae* (supported in the concatenated, but not in the coalescent-based analysis).

Taxonomic consequences

The previously proposed subtribal classification of *Compositae*–*Anthemideae* (Oberprieler & al. 2007, 2009) was based on sequence information from nrDNA ITS and cpDNA *ndhF* for 103 and 62 species of the tribe, respectively, and resulted in the acknowledgement of 14 subtribes, but left a considerable number of genera unassigned to a subtribe due to missing sequence information or unresolved positions in the phylogenetic reconstructions. Our present contribution managed (at least for the most comprehensive tree based on nrDNA ITS sequence variation; Fig. 2) to include all presently accepted genera of the tribe with the exception of two unispecific ones, *Ajaniopsis* (from China and Tibet) and *Cancriniella* (C Asia). Enlargement of the taxonomic sampling for the mentioned molecular markers and addition of further sequence information from the chloroplast (*trnL-trnF* intergenic spacer region) and the nuclear genome (*DSP*, *VIP5* and *NPF3.1*) allow us now to propose an updated subtribal classification of the *Anthemideae*, in which all of the genera with hitherto unsecure subtribal placement are either assigned to one of the already existing subtribes or form the basis of subtribes newly described. Our treatment presented here therefore consists of 19 subtribes that are arranged in grades or clades based on biogeographical patterns in the following. The description of subtribes is based on descriptions given in Oberprieler & al. (2007) but updated wherever required by a new circumscription.

New to science are the five unigeneric subtribes *Brocchiinae*, *Inulantherinae*, *Lepidophorinae*, *Lonadinae* and *Vogtiinae*. While the erection of four of these independent subtribes is the consequence of the isolated positions of *Brocchia*, *Lepidophorum*, *Lonas* and *Vogtia* in the phylogenetic reconstructions presented here, the

constant and well-supported grouping of *Inulanthera* as sister to *Ursinia* would have also allowed inclusion of this orphan genus into *Ursiniinae*. However, we refrain from this assignment because of considerable morphological differences between the two genera, which would have made the resulting subtribe extremely diverse and lacking of predictive information. *Inulanthera* differs from *Ursinia* most distinctly by the possession of basally caudate anthers; a character expression that is shared in the whole tribe only by the genera *Osmitopsis* (subtribe *Osmitopsidinae*) and *Hippolytia* (subtribe *Artemisiinae*). Additionally, the densely arranged, discoid capitula (laxly arranged and mostly radiate in *Ursinia*) and the achenes with a corona of small, entire to toothed scales terminating each rib (in contrast to the uni- or biseriolate pappus exhibited by *Ursinia*) argue for acceptance of an independent subtribe *Inulantherinae*.

I. Southern hemisphere grade

1. *Osmitopsidinae* Oberpr. & Himmelr. in Willdenowia 37: 94. 2007. – Type: *Osmitopsis* Cass. (*Osmitopsis asteriscoides* (L.) Less.).

Description — 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 conic, paleate; paleae narrowly elliptic to obovate, canaliculate and enclosing 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-polarized endothelial tissue and a slender filament collar; stylopodium sometimes large and persistent in fruit. *Achenes* obovoid to ellipsoid, 3- or 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 position of the genus in the tribe already mentioned by Bremer (1972) and Nordenstam (1987) and acknowledged by classification in a unigeneric subtribe by Oberprieler & al. (2007) is unequivocally supported by the present phylogenetic reconstructions. The similarity with *Inulanthera* (subtribe *Inulantherinae*) and *Hippolytia* (*Artemisiinae*) due to the possession of basally caudate anthers does not correspond to a close evolutionary relationship to these genera.

2. *Cotulinae* Kitt., Taschenb. Fl. Deutschl., ed. 2, 2: 609. 1844. – Type: *Cotula* L. (*Cotula coronopifolia* L.).

= *Thaminophyllinae* K. Bremer & Humphries in Bull. Nat. Hist. Mus. London, Bot. 23: 144. 1993. – Type: *Thaminophyllum* Harv. (*Thaminophyllum mundtii* Harv.).

Description — Shrubs, subshrubs, perennial or annual herbs (*Cotula*, *Leptinella*, *Soliva*). *Indumentum* of basifixed hairs or absent. *Leaves* alternate or opposite, entire, lobed, pinnatifid to 1- or 2-pinnatisect. *Capitula* solitary or in lax to dense corymbs, radiate, disciform or discoid. *Involucre* broadly campanulate, hemispheric to cylindrical or obconic, 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 hemispheric or conic, 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 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-polarized endothelial tissue and a slender filament collar; stylopodium sometimes large and persistent in fruit (*Lidbeckia*, *Thaminophyllum*). *Achenes* oblong to obovoid, terete with 2 or 3 adaxial or 3–10 ribs, sometimes 3- or 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 numbers* $x = 8, 9, 10, 13$.

Distribution — S and E Africa, Australia, New Guinea, New Zealand, South America, S oceanic islands; some species widespread and naturalized as weeds.

Members — *Adenanthellum* B. Nord. (1), *Cotula* L. (58), *Hilliardia* B. Nord. (1), *Hippia* L. (8), *Inezia* E. Phillips (2), *Leptinella* Cass. (33), *Lidbeckia* P. J. Bergius (3), *Schistostephium* Less. (12), *Soliva* Ruiz & Pav. (8), *Thaminophyllum* Harv. (3).

Notes — The circumscription of this subtribe with its ten genera proposed by Oberprieler & al. (2007) is corroborated by all present phylogenetic reconstructions except the coalescent-based species-tree reconstruction (Fig. 4), where *Hippia* is associated with members of subtribe *Pentziinae*. Since this position and the reciprocal monophyly of each of both subtribes (*Cotulinae* and *Pentziinae*) is not supported by posterior probabilities, we think that any hypothesis of a non-monophyly of the subtribe is unsubstantiated. Species numbers given for *Cotula* and *Leptinella* are only approximations due to the

lack of recent and/or comprehensive revisions of the two genera (*Leptinella*: Lloyd & Webb 1987; Himmelreich & al. 2012, 2014; *Cotula*: Powell & al. 2014; Jakoet & al. 2019).

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

Description — Annual or perennial herbs or shrublets. *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* hemispheric. *Phyllaries* in 3–7 rows, with narrow to broad scarious margins. *Receptacle* hemispheric, paleate; paleae canaliculate, elliptic or narrowly linear with an apical limb. *Ray florets* usually neuter, sometimes female and fertile; limb yellow, orange, white or reddish. *Disc florets* hermaphrodite, fertile; corolla 5-lobed, yellow, purplish. *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, a biseriata 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 numbers* $x = 5, 7, 8$.

Distribution — South Africa, Namibia, Botswana, Ethiopia.

Members — *Ursinia* Gaertn. (43).

Notes — The present results support our previous findings (Oberprieler & al. 2007) that the circumscription of *Ursiniinae* sensu Bremer & Humphries (1993) with the inclusion of genera classified in subtribes *Athansiniinae* (*Athansia*, *Hymenolepis*, *Lasiospermum*) and *Phymasperminae* (*Eumorphia*, *Gymnopentzia*, *Phymaspermum*) is not supported as a monophyletic assemblage. Conversely, all gene- and species-tree reconstructions unequivocally indicate the close phylogenetic relationship with the S African genus *Inulanthera*. However, due to the considerable morphological differences between *Ursinia* and *Inulanthera* described in detail in the following subtribal account, we have refrained from uniting the two genera in *Ursiniinae*. A preliminary molecular phylogenetic study of *Ursinia* by Swelankomo (2008) based on nrDNA ITS sequence information revealed some support for the infrageneric classification of *Ursinia* species into *U.* subg. *Ursinia* (with a biseriata pappus of five outer scales and five inner subulate awns) and *U.* subg. *Sphenogyne* (Aiton) Prassler (with a uniseriate pappus of 5–10 ovate or circular scales) but did not provide any justification for the acknowledgement of the two monophyletic groups as independent genera. As a consequence, four newly discovered species of this plant group

were all described in the broadly circumscribed genus *Ursinia* (Magee & al. 2014).

4. *Inulantherinae* Oberpr. & Töpfer, **subtrib. nov.**

Type: *Inulanthera* Källersjö (*Inulanthera calva* (Hutch.) Källersjö).

Description — Shrubs or subshrubs. *Indumentum* absent or of basifixed hairs. *Leaves* alternate, entire to lobed. *Capitula* in dense corymbs, discoid. *Involucre* hemispheric to spheric. *Phyllaries* in 3 rows, with narrow, pale to light brown scarious margins. *Receptacle* flat, paleate, rarely epaleate; paleae linear, flat to shallowly canaliculate, with a central resin duct. *Florets* hermaphrodite, fertile; corolla 5-lobed, yellow; anthers basally caudate, with polarized endothelial tissue. *Achenes* obovoid, circular in cross-section, with (8–)10 ribs; apex with a corona of small, entire to toothed scales terminating each rib; pericarp smooth, sometimes papillose, without myxogenic cells or resin sacs, but with protruding, light brown glands. *Embryo sac development* and *base chromosome number* unknown.

Distribution — South Africa, Swaziland, Lesotho, Angola, Zimbabwe, Madagascar.

Members — *Inulanthera* Källersjö (9; see Magoswana & al. 2016).

Notes — A close evolutionary relationship between *Inulanthera* and the two genera *Gonospermum* Less. and *Lugoa* DC. from the Canary Islands was suggested by the treatment of these genera under a subtribe *Gonosperminae* (Bremer & Humphries 1993) but was demonstrated as being unsupported in molecular phylogenetic analyses (Oberprieler & al. 2007, 2009; Sonboli & al. 2012), hence the subtribal placement of *Inulanthera* remained unresolved. Despite the consistent sister-group relationship of *Inulanthera* and *Ursinia* in the previously mentioned and present molecular phylogenetic studies, distinct differences between the two genera in morphological respects rather suggest the erection of an independent, unigeneric subtribe than the merging of the two genera into an extremely heterogeneous one: *Inulanthera* differs from *Ursinia* by its discoid capitula in dense corymbs, its caudate anthers and its achenes devoid of a well-developed, scaly pappus. Within the whole tribe, the caudate anthers are shared only by *Osmitopsis* (*Osmitopsidinae*) and *Hippolytia* (*Artemisiinae*; Oberprieler & al. 2007, 2009), but close phylogenetic relationships to these three genera have never been substantiated.

5. *Athansiinae* Pfeiff., Nomencl. Bot. 1: 323. 1872. – Type: *Athanasia* L. (*Athanasia crithmifolia* (L.) L.).

Description — 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- or 2-pinnatisect. *Capitula* solitary or in lax to dense corymbs, radiate, disciform or discoid. *Involucre* hemispheric, spheric to urceolate. *Phyllaries* in 2–5 rows, without or with scarious margins, with central resin canals or sacs (in *Eriocephalus* in 2 unequal rows, outer phyllaries with very wide scarious margins, inner ones connate and hairy). *Receptacle* flat, hemispheric to conic, 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 polarized endothelial tissue, rarely non-polarized (*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 (Sinai), Israel, Jordan.

Members — *Adenoglossa* B. Nord. (1), *Athanasia* L. (41), *Eriocephalus* L. (32), *Hymenolepis* Cass. (7), *Lasiospermum* Lag. (4), *Leucoptera* B. Nord. (3).

Notes — The subtribe *Athansiinae* in its present circumscription is surely the most problematic generic assemblage in the subtribal classification of the tribe presented here. The present circumscription corresponds completely with the one proposed in our former treatment (Oberprieler & al. 2007, 2009), where its non-monophyletic nature was discussed to some extent. Our present phylogenetic reconstructions do not support a monophyly of the *Athansiinae*—neither the gene trees with representatives of all six mentioned genera (Fig. 1, 2) nor the species trees with the reduced set of those four genera, for which a complete data matrix was achieved (Fig. 3, 4). This is paralleled by the quite diverse morphological circumscription of the subtribe in itself. Nevertheless, we presently refrain from a decomposition of this possibly paraphyletic subtribe until a more complete sampling and a more reliable phylogenetic reconstruction is available. Species numbers of the present account were updated following taxonomic work done by Powell & Magee (2013) in *Athanasia* and by Magoswana & Magee (2014) and Magoswana & al. (2015) in *Hymenolepis*.

6. *Phymasperminae* Oberpr. & Himmelfr. in Willdenowia 37: 99. 2007. – Type: *Phymaspermum* Less. (*Phymaspermum junceum* Less.).

Description — 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- or 2-pinnatisect. *Capitula* solitary or in lax to dense corymbs, radiate, disciform or discoid. *Involucre* hemispheric, spheric to urceolate. *Phyllaries* in 2–5 rows, without or with scarious margins, with central resin canals or sacs (in *Eriocephalus* in 2 unequal rows, outer phyllaries with very wide scarious margins, inner ones connate and hairy). *Receptacle* flat, hemispheric to conic, 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 polarized endothelial tissue, rarely non-polarized (*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 (Sinai), Israel, Jordan.

Members — *Adenoglossa* B. Nord. (1), *Athanasia* L. (41), *Eriocephalus* L. (32), *Hymenolepis* Cass. (7), *Lasiospermum* Lag. (4), *Leucoptera* B. Nord. (3).

Notes — The subtribe *Athansiinae* in its present circumscription is surely the most problematic generic assemblage in the subtribal classification of the tribe presented here. The present circumscription corresponds completely with the one proposed in our former treatment (Oberprieler & al. 2007, 2009), where its non-monophyletic nature was discussed to some extent. Our present phylogenetic reconstructions do not support a monophyly of the *Athansiinae*—neither the gene trees with representatives of all six mentioned genera (Fig. 1, 2) nor the species trees with the reduced set of those four genera, for which a complete data matrix was achieved (Fig. 3, 4). This is paralleled by the quite diverse morphological circumscription of the subtribe in itself. Nevertheless, we presently refrain from a decomposition of this possibly paraphyletic subtribe until a more complete sampling and a more reliable phylogenetic reconstruction is available. Species numbers of the present account were updated following taxonomic work done by Powell & Magee (2013) in *Athanasia* and by Magoswana & Magee (2014) and Magoswana & al. (2015) in *Hymenolepis*.

Description — 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* hemispheric to spheric, rarely cylindrical to obconic. *Phyllaries* in 2–4 rows, with scarious, sometimes ciliate margins. *Receptacle* flat to conic, 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 polarized endothelial 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 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. (17).

Notes — Apart from the strange but unsupported position of one of its members (i.e. *Phymaspermum*) in the cpDNA gene tree (Fig. 1), the monophyly of this subtribe is corroborated by the other phylogenetic reconstructions (Fig. 2, 3, 4). Closer relationships appear to exist with the *Athansiinae*, with which the *Phymasperminae* share the possession of anthers with polarized endothelial tissue and a slender filament collar. However, since even inclusion of its three members into a broader circumscribed *Athansiinae* would not make the latter subtribe monophyletic, we suggest keeping this small generic assemblage in a subtribe of its own. Revisionary work done by Swelankomo (2011) for *Eumorphia* and Ruiters & al. (2016) for *Phymaspermum* updated the species numbers given in the present account.

II. Asian-southern African grade

7. *Pentziinae* Oberpr. & Himmelr. in Willdenowia 37: 99. 2007. – Type: *Pentzia* Thunb. (*Pentzia crenata* Thunb., nom. illeg.).

Description — 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- or 2-pinnatisect. Capitula solitary or in corymbs, rarely closely aggregated (*Marasmodes*), discoid or disciform, sometimes radiate (*Cymbopappus*, *Foveolina*, *Oncosiphon*). *Involucre* hemispheric to cylindrical, sometimes urceolate (*Marasmodes*). *Phyllaries* in 3–5 rows, with or without scarious margins. *Receptacle* flat or convex to conic, epaleate. *Ray florets* female; limb white or pinkish. *Disc*

florets hermaphrodite; corolla 4- or 5-lobed, sometimes tube swollen and brittle (*Oncosiphon*) or with thick vascular strands (*Cymbopappus*, *Marasmodes*, *Pentzia*); anthers with non-polarized endothelial tissue and a slender filament collar. *Achenes* oblong to obovoid, with 4- or 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 ribs and 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. (13), *Myxopappus* Källersjö (2), *Oncosiphon* Källersjö (8), *Pentzia* Thunb. (27, incl. *Rennera* Merxm.).

Notes — While in the analysis based on concatenated sequences the subtribe *Pentziinae* received strong support for being monophyletic (Fig. 3), this signal is less clear in the other phylogenetic reconstructions. In the tree based on cpDNA sequence variation, a monophyletic *Pentziinae* is found comprising also the representative of *Mausolea* from the *Artemisiinae* (Fig. 1), while in the nrDNA tree (Fig. 2) only a group excluding *Myxopappus* receives strong support, and in the coalescent-based species tree (Fig. 4) a strongly supported relationship with subtribe *Cotulinae* emerged. These equivocal circumscriptions and relationships may be a consequence of either hybridization events or incomplete lineage sorting connected with the intermediary role of the *Pentziinae* in biogeographical respects between the S hemisphere-based subtribes on the one hand and the Asian-based subtribes *Artemisiinae* and *Handeliinae* on the other. This is additionally supported by the occurrence of some species of *Pentzia* in N Africa and SW Asia (Oberprieler & al. 2007).

Delimitation of genera in the *Pentziinae* is highly problematic. Phylogenetic analyses based on nrDNA ITS and cpDNA markers by Magee & al. (2015) revealed considerable discrepancies between tree topologies based on the two datasets with little support for the monophyly of the hitherto accepted genera; exceptions being *Marasmodes* (well supported by both datasets), *Myxopappus* (supported in the cpDNA tree) and *Rennera* (well supported by both datasets but nested in a paraphyletic genus *Pentzia*). Except for the transfer of the four *Rennera* species to *Pentzia* proposed by Magee & al. (2015), no further nomenclatural consequences were drawn from the

mentioned analyses, and a further discussion of generic limits in this subtribe must await more comprehensive genetic/genomic datasets and analyses. However, due to the extremely productive revisionary work of A. R. Magee (Compton Herbarium, Cape Town, South Africa) and his collaborators, the taxonomy of some genera is now well understood (*Marasmodes*, Magee & al. 2017; *Oncosiphon*, Kolokoto & Magee 2018; the *Pentzia incana* group, Magee & Tilney 2012).

8. *Handeliinae* K. Bremer & Humphries in Bull. Nat. Hist. Mus. London, Bot. 23: 108. 1993. – Type: *Handelia* Heimerl (*Handelia trichophylla* (Schrenk) Heimerl).

= *Cancriniinae* K. Bremer & Humphries in Bull. Nat. Hist. Mus. London, Bot. 23: 96. 1993. – Type: *Cancrinia* Kar. & Kir. (*Cancrinia chrysocephala* Kar. & Kir.).

Description — 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- or 2-pinnatifid to 3- or 4-pinnatisect. *Capitula* solitary, in lax to dense corymbs or in a long panicle (*Lepidolopsis*), discoid or radiate. *Involucre* hemispheric to spheric or obconic (*Trichanthemis*), sometimes umbonate (*Sclerorhachis*). *Phyllaries* in 2–4 (or 5) rows, with narrow to broad scarious margins. *Receptacle* hemispheric, 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*); anthers with non-polarized endothelial tissue and a balusterform filament collar (slender in *Allardia* and some *Tanacetopsis* species). *Achenes* cylindrical to obconic, circular to elliptic in cross-section, with 4–10(–15) ribs, sometimes with 3–5 adaxially arranged ribs (*Microcephala*); apex with a corona formed by 5–20 (*Cancrinia*, *Ugamia*) or 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, glabrous or rarely sparsely to densely hairy (*Allardia*, *Cancrinia*, *Trichanthemis*, *Ugamia*). *Embryo sac development* unknown. *Base chromosome number* $x = 7$ (*Microcephala*), 9.

Distribution — Iran, Afghanistan, Pakistan, C Asia, Mongolia, China.

Members — *Allardia* Decne. (4), *Cancrinia* Kar. & Kir. (4), *Cancriniella* Tzvelev (1), *Handelia* Heimerl (1), *Lepidolopsis* Poljakov (1), *Microcephala* Pobed. (5), *Polychrysum* (Tzvelev) Kovalevsk. (1), *Pseudohandelia* Tzvelev (1), *Richteria* Kar. & Kir. (6), *Sclerorhachis*

(Rech. f.) Rech. f. (4), *Tanacetopsis* (Tzvelev) Kovalevsk. (21), *Trichanthemis* Regel & Schmalh. (9), *Ugamia* Pavlov (1), *Waldheimia* Kar. & Kir. (4).

Notes — The phylogeny of the subtribe was studied in detail by Oberprieler & al. (2019) in a multi-locus approach based on both plastid and nuclear markers. Incongruence among the marker-wise gene-tree reconstructions was interpreted there as a result of ample hybridization having occurred in the evolutionary history of the members of *Handeliinae*. While generic circumscriptions were unaddressed by the mentioned study due to the limited sampling of representatives from the species-rich genera, the exclusion of *Xylanthemum* from the subtribe and its transfer to *Anthemidinae* as proposed earlier by Sonboli & al. (2012) and the polyphyly of *Allardia* and its classification as two independent genera (*Allardia* and *Waldheimia*) received good support from these phylogenetic reconstructions. There is still a lack of information for the subtribal placement of the unispecific genus *Cancriniella* Tzvelev. However, the close relationship to *Cancrinia* and *Trichanthemis karataviensis* (the type of *Trichanthemis*), as proposed by Poljakov (1959) by uniting them under a more comprehensive genus *Cancrinia*, argues for the classification of *Cancriniella* in *Handeliinae* and awaits support from a molecular phylogenetic analysis of this C Asian endemic.

9. *Artemisiinae* Less. in Linnaea 5: 163. 1830. – Type: *Artemisia* L. (*Artemisia vulgaris* L.).

= *Chrysantheminae* Less. in Linnaea 6: 167. 1831. – Type: *Chrysanthemum* L. (*Chrysanthemum indicum* L., typ. cons.).

Description — Shrubs, subshrubs, perennial or annual herbs, sometimes with basally woody, virgate and sometimes leafless stems (*Lepidolopha*). *Indumentum* absent, of basifixed or medifixed (sometimes stellate) hairs. *Leaves* rosulate or alternate, entire, lobed, serrate to 1–3-pinnatisect. *Capitula* solitary, in lax to dense corymbs or in panicles, rarely in dense glomerules (*Turaniphytum*), radiate, disciform or discoid. *Involucre* hemispheric to cylindrical, obconic or urceolate. *Phyllaries* in 1–7 rows, with narrow to broad scarious margins. *Receptacle* flat to conic, 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- or 3(–5)-lobed. *Central disc florets* hermaphrodite or male (rarely neuter); corolla (4 or) 5-lobed; anthers basally rounded, rarely caudate (*Hippolytia*), with non-polarized endothelial tissue and a slender filament collar. *Achenes* ellipsoid to obovoid without or with 3–8(–12) ribs, sometimes flattened; apex marginally rounded, sometimes with a rounded rim (*Artemisiella*, *Hippolytia*, *Hulteniella*), a lacerate corona with small scales (*Crossostephium*, *Nipponanthemum*, *Opisthopappus*, *Spheromeria*) or a corona

formed by 8–10 linear-elliptic scales (*Lepidolopha*); 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 in *Arctanthemum*, *Artemisia* and *Chrysanthemum*). *Base chromosome number* $x = 6, 7, 8, 9, 10, 11, 17$.

Distribution — Worldwide, with a centre of diversity in C Asia.

Members — *Ajania* Poljakov (39), *Ajaniopsis* C. Shih (1), *Arctanthemum* (Tzvelev) Tzvelev (3), *Artemisia* L. (522, incl. *Seriphidium* Fourr.), *Artemisiella* Ghafoor (1), *Brachanthemum* DC. (10), *Chrysanthemum* L. (37), *Crossostephium* Less. (1), *Elachanthemum* Y. Ling & Y. R. Ling (1), *Filifolium* Kitam. (1), *Hippolytia* Poljakov (19), *Hulteniella* Tzvelev (1), *Kaschgaria* Poljakov (2), *Lepidolopha* C. Winkl. (9), *Leucanthemella* Tzvelev (2), *Mausolea* Poljakov (1), *Neopallasia* Poljakov (3), *Nipponanthemum* Kitam. (1), *Opisthopappus* C. Shih (2), *Phaeostigma* Muldashev (3), *Picrothamnus* Nutt. (1), *Sphaeromeria* Nutt. (9), *Stilpnolepis* Krasch. (1), *Tridactylina* (DC.) Sch. Bip. (1) *Turaniphytum* Poljakov (2).

Notes — As in the previous subtribe, delimitation of genera in this extremely species-rich subtribe was beyond the aims of the present study. However, representatives of all mentioned 24 genera were found forming a strongly supported monophyletic group in the nrDNA ITS tree (Fig. 2). The subtribal circumscription and the inclusion of the formerly unassigned genus *Lepidolopha* was additionally supported both by the multi-locus analysis of Oberprieler & al. (2019) and the species-tree reconstructions presented here (Fig. 3, 4). The unispecific genus *Ajaniopsis* C. Shih, endemic to Tibet and China, still lacks a phylogeny-based subtribal classification. However, as discussed by Bremer & Humphries (1993) based on morphological evidence, membership of this annual in the *Artemisiinae* is beyond doubt.

III. Eurasian grade

10. *Brocchiinae* Oberpr. & Töpfer, **subtrib. nov.**

Type: *Brocchia* Vis. (*Brocchia cinerea* (Delile) Vis.).

Description — Annual herbs. *Indumentum* of basifixed hairs. *Leaves* alternate, pinnatipartite to pinnatisect, sometimes entire to lobed. *Capitula* solitary or in lax corymbs, discoid, pedunculate. *Involucre* hemispheric. *Phyllaries* in 2 rows, with narrow, pale membranous margins. *Receptacle* hemispheric to conic, epaleate. *Disc florets* hermaphrodite, fertile; corolla yellow, apically 4-lobed. *Achenes* obovoid, circular in cross-section, with c. 4 inconspicuous lateral and adaxial ribs; apex slanting, marginally rounded; pericarp with large, elongated myxogenic cells, without resin sacs. *Embryo sac devel-*

opment unknown. *Base chromosome number* $x = 9$.

Distribution — N Africa, SW Asia.

Members — *Brocchia* Vis. (1).

Notes — As discussed in detail by Oberprieler (2004a), there are a number of morphological, anatomical and cytological characters that argue against the close relationship of *Brocchia cinerea* with *Cotula*, in which this primarily N African species was described by Delile (1813). The superficial similarity with *Cotula* due to the 4-merous disc florets is paralleled both by a number of other genera from *Cotulinae* (*Hilliardia*, *Inezia*, *Lep tinella*, *Lidbeckia*, *Schistostephium*, *Soliva*, *Thamino phyllum*), but also from *Anthemidinae* (*Nananthea*), *Artemisiinae* (*Artemisiella*, *Filifolium*, *Phaeostigma*), *Handeliinae* (*Lepidolopsis*), *Matricariinae* (*Matricaria*) and *Pentziinae* (*Foveolina*, *Myxopappus*, *Oncosiphon*). A close evolutionary relationship of *Brocchia* and any of those generic assemblages, however, is excluded by the present phylogenetic reconstructions (gene trees based on cpDNA, nrDNA ITS, nDNA *NPF3.1*, Fig. 1, 2, Online Fig. S3; species trees, Fig. 3, 4) and the groupings seen with *Matricaria* in nDNA *DSP* (Online Fig. S1) and *Nananthea* in nDNA *VIP5* (Online Fig. S2) are not supported by any significant posterior probability values.

11. *Vogtiinae* Oberpr. & Töpfer, **subtrib. nov.**

Type: *Vogtia* Oberpr. & Sonboli (*Vogtia microphylla* (DC.) Oberpr. & Sonboli).

Description — Annual herbs. *Indumentum* of long and slender, appressed, medifixed hairs mixed with sessile glands. *Leaves* alternate and in axillary fascicles, simple and linear-lanceolate to 1- or 2-pinnatisect. *Capitula* in dense corymbs with up to 40 capitula, shortly pedunculate to sessile, discoid. *Involucre* hemispheric. *Phyllaries* in 2 or 3 rows, with yellowish or whitish, scarios, apically rounded and reflexed or subacute margins. *Receptacle* epaleate. *Disc florets* hermaphrodite, fertile; corolla 4- or 5-lobed, yellow, basally not clasping top of achene. *Anthers* with pointed, triangular apical appendages; pollen of “*Anthemis* type” with distinct spines. *Achenes* obovoid, with 8–10 very thin and narrow ribs; apex with a very short corona of protruding ribs forming teeth, c. 0.1 mm; pericarp without myxogenic cells and without resin sacs or ducts. *Testa* epidermis of an epidermal type (i.e. with undulating anticlinal walls). *Embryo sac development* unknown. *Base chromosome number* $x = 9$.

Distribution — Europe (France, Spain, Portugal), N Africa (Morocco).

Members — *Vogtia* Oberpr. & Sonboli (2).

Notes — The genus *Vogtia* with its two members, *V. annua* and *V. microphylla*, was erected as a result of a phylogenetic analysis of the genus *Tanacetum* based on nrDNA ITS and cpDNA *trnH-psbA* sequence variation done by Sonboli & al. (2012), who found the latter of the two species consistently and significantly excluded from a clade formed by further members of *Anthemidinae* (*Anthemis*, *Archanthemis*, *Cota*, *Nananthea*, *Tanacetum*, *Tripleurospermum*, *Xylanthemum*) and *Matricariinae* (*Achillea*, *Anacyclus*, *Heliocauta*, *Matricaria*). Originally described as members of *Tanacetum*, the two species are distinctly deviating from all other species of this genus by their annual life form. The unique phylogenetic position of *Vogtia* corroborated by the present gene- and species-tree reconstructions is morphologically supported by the pointed apical appendages of the anthers and the testa epidermis with undulating anticlinal walls. While the latter is unique in the whole tribe, the former is observed in all members of *Artemisiinae*, “though variously expressed” (Bremer & Humphries 1993).

12. *Matricariinae* Willk. in Willkomm & Lange, Prodr. Fl. Hispan. 2: 92. 1870. – Type: *Matricaria* L. (*Matricaria recutita* L., typ. cons.).
= *Achilleinae* K. Bremer & Humphries in Bull. Nat. Hist. Mus. London, Bot. 23: 126. 1993. – Type: *Achillea* L. (*Achillea millefolium* L.).

Description — Subshrubs or perennial or annual herbs. *Indumentum* of basifixed, sometimes asymmetrically medifixed (*Achillea*) 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* hemispheric to cylindrical or obconic. *Phyllaries* in 2 or 3 rows, with narrow to broad scarious margins. *Receptacle* flat, hemispheric or conic, 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 or)5-lobed, basally ± saccate and clasping top of achene; anthers with non-polarized 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, N Africa, W North America.

Members — *Achillea* L. (115), [incl. *Leucocyclus* Boiss. (1), *Otanthus* Hoffmanns. & Link (1), see Guo & al. (2004), Ehrendorfer & Guo (2005, 2006)], *Anacyclus* L. (9), *Heliocauta* Humphries (1), *Matricaria* L. (6).

Notes — The reciprocal monophyly of the two closely related subtribes *Anthemidinae* and *Matricariinae* is not supported by our present analyses. Only when *Matricaria* is excluded from both subtribes do they receive strong support in the phylogenetic reconstruction based on concatenated sequence information (Fig. 3). As discussed earlier (Oberprieler & al. 2007), the main difference between the two subtribes is found in the embryo sac development, which follows a monosporic type in *Matricariinae* and a tetrasporic one in *Anthemidinae*. Since a tetrasporic embryo sac development constitutes an apomorphic condition in the otherwise monosporic tribe (with exceptions in *Argyranthemum* and *Heteranthemis* in the *Glebionidinae*), we cannot exclude the possibility that a monophyletic subtribe *Anthemidinae* is nested in a paraphyletic *Matricariinae*. This situation already described in Oberprieler & al. (2007) based on nrDNA ITS sequence information has not been resolved by adding more markers in the present analysis. However, we still refrain from uniting these two embryologically well-separated generic assemblages without an unequivocal phylogenetic signal.

In contrast to former enumerations, the genus *Anacyclus* has been reduced in its species number due to the transfer of three species to the genus *Cota* in the *Anthemidinae* (Vitales & al. 2018). Both genera share the character of dorsio-ventrally flattened achenes, but the mentioned sequence-based phylogenetic analysis (nrDNA ITS, cpDNA *psbA-trnH*) revealed that the three E Mediterranean representatives, *A. anatolicus*, *A. latealatus* and *A. nigellifolius*, do not belong to the W Mediterranean lineage of *Anacyclus*.

13. *Anthemidinae* Dumort., Fl. Belg.: 69. 1827. – Type: *Anthemis* L. (*Anthemis arvensis* L.).
= *Pyrethrinae* Horan., Char. Ess. Fam.: 90. 1847. – Type: *Pyrethrum* Zinn. (*Pyrethrum corymbosum* (L.) Willd.).
= *Gonosperminae* K. Bremer & Humphries in Bull. Nat. Hist. Mus. London, Bot. 23: 106. 1993. – Type: *Gonospermum* Less. (*Gonospermum fruticosum* Less.).
= *Tanacetinae* K. Bremer & Humphries in Bull. Nat. Hist. Mus. London, Bot. 23: 99. 1993. – Type: *Tanacetum* L. (*Tanacetum vulgare* L.).

Description — Subshrubs, short- to long-lived perennial herbs, biennials or annuals; sometimes shrublets with basally woody, virgate and sometimes leafless stems (*Xylanthemum*). *Indumentum* absent or of medifixed and/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* hemispheric or obconic, sometimes umbonate. *Phyllaries* in 1–5 rows, with scarious margins. *Receptacle* hemispheric or conic, paleate or epaleate; 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*), sometimes hairy (*Xylanthemum*); anthers with non-polarized endothelial tissue and a balusterform filament collar. *Achenes* obovoid to obconic, circular in cross-section, with 5–10(–15) ribs or dorsiventrally flattened with 2 lateral ribs and 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, sometimes (*Xylanthemum*) with 3–6 adaxial, elliptic scales shorter than achene body; pericarp with myxogenic cells, sometimes without (*Tanacetum*), usually without resin sac or ducts, in *Tripleurospermum* with (1 or)2(–5) abaxial-apical resin sacs. *Embryo sac development* tetrasporic. *Base chromosome number* $x = 9$.

Distribution — Europe, SW Asia, N and E Africa, Canary Islands, North America.

Members — *Anthemis* L. (175), *Archanthemis* Lo Presti & Oberpr. (4), *Cota* J. Gay (43), *Nananthea* DC. (1), *Tanacetum* L. (154) [incl. *Gonospermum* Less. (4), *Lugoa* DC. (1), see Sonboli & al. (2012)], *Tripleurospermum* Sch. Bip. (40), *Xylanthemum* Tzvelev (8).

Notes — The subtribe received a new circumscription due to the establishment of the genus *Archanthemis* for four phylogenetically deviating *Anthemis* species (Lo Presti & al. 2010) and the transfer of the genus *Xylanthemum* from *Handeliinae* to *Anthemidinae* (Sonboli & al. 2012; Oberprieler & al. 2019). Following the phylogenetic analyses by Sonboli & al. (2012) based on nrDNA ITS and cpDNA *trnH-psbA* sequence information, *Xylanthemum* could even be sunk into synonymy with *Tanacetum* (like the two Canarian genera *Gonospermum* and *Lugoa*), but this must await a better-resolved molecular phylogeny of the latter genus.

As discussed under subtribe *Matricariinae*, the close relationship of *Anthemidinae* and *Matricariinae* is consistently supported by our present analyses. However, their reciprocal monophyly is questionable and their classification as two subtribes is only supported by a differing embryo sac development realized by those representatives surveyed for this character.

As representative of the genus *Xylanthemum*, we included a specimen labelled “*Xylanthemum paradoxum*” by Podlech, who never validly published that name when including *Xylanthemum* into *Tanacetum* (due to the existence of the older homonym *T. paradoxum* Bornm.) but described the species as *T. paleaceum* Podlech in his treatment of *Compositae–Anthemideae* in *Flora iranica* (Podlech 1986). Sonboli & al. (2012) demonstrated that *T. paleaceum* is closely related with the type of *Xylanthemum* (i.e. *X. fisherae* (Aitch. & Hemsl.) Tzvelev), but refrained from proposing a new combination due to uncertainties connected with the demarcation of *Xylanthemum*

against *Tanacetum*. However, in order to accommodate *Xylanthemum* in the present subtribal classification, we herewith propose the new combination:

Xylanthemum paleaceum (Podlech) Oberpr. & Vogt, **comb. nov.** = *Tanacetum paleaceum* Podlech in Rechinger, Fl. Iran. 158: 143. 1986.

14. *Leucanthemopsidinae* Oberpr. & Vogt in Willdenowia 37: 104. 2007. – Type: *Leucanthemopsis* (Giroux) Heywood (*Leucanthemopsis alpina* (L.) Heywood).

Description — Annual or perennial herbs. *Indumentum* of medifixed hairs. *Leaves* alternate or sometimes opposite (*Phalacrocarpum*), serrate-dentate to 1- or 2-pinnatisect. *Capitula* solitary, radiate. *Involucre* hemispheric. *Phyllaries* in 4 rows, with broad scarious margins. *Receptacle* convex, epaleate, sometimes hairy (*Phalacrocarpum*). *Ray florets* female or neuter; limb white or yellow, sometimes reddish (*Phalacrocarpum*). *Disc florets* hermaphrodite, rarely (*Phalacrocarpum*) functionally male; corolla 5-lobed; anthers with non-polarized 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*, *Phalacrocarpum*); pericarp with myxogenic cells along ribs (without myxogenic cells in *Phalacrocarpum*), without resin sacs. *Embryo sac development* monosporic (only known in *Leucanthemopsis*). *Base chromosome number* $x = 9$.

Distribution — SW Europe, NW Africa.

Members — *Castrilanthemum* Vogt & Oberpr. (1), *Hymenostemma* Willk. (1), *Leucanthemopsis* (Giroux) Heywood (9), *Phalacrocarpum* (DC.) Willk. (1), *Prolongoa* Boiss. (1).

Notes — In contrast to the phylogenetic reconstructions based on nrDNA ITS (Fig. 2), both the gene tree based on plastid markers (Fig. 1) and the two species trees (Fig. 3, 4) strongly support the sister-group relationship of the Iberian endemic genus *Phalacrocarpum* and the closely knit generic assemblage of subtribe *Leucanthemopsidinae*. Tomasello & al. (2015) dated the divergence between *Phalacrocarpum* and the three other genera to c. 20 Ma and the further differentiation among the latter to the range between 7 Ma (divergence of *Hymenostemma* and *Prolongoa*) and 17 Ma (divergence of *Castrilanthemum*). Caused by the extremely long periods of evolutionary independence exhibited by the five lineages, the morphological diversity of the subtribe is considerable and gains even more heterogeneity by inclusion of *Phalacrocarpum*. However, erection of an independent, unigeneric subtribe for the latter genus would immediately question the treatment of the remaining genera as a single subtribal entity.

The infrageneric taxonomy of both the enigmatic *Phalacrocarpum* and the much younger genus *Leucanthemopsis* is complicated by evolutionary reticulations due to homoploid and polyploid hybrid speciation, respectively. Molecular-based analyses on species delimitations in the two genera were done by Criado Ruiz & al. (2021) and Tomasello & Oberprieler (submitted) and partially question the morphology-based taxonomic treatments proposed in *Flora iberica* (Pedrol 2019; Nieto Feliner 2019).

IV. Mediterranean clade

15. *Lonadinae* Oberpr. & Töpfer, **subtrib. nov.**

Type: *Lonas* Adans. (*Lonas annua* (L.) Vines & Druce).

Description — Glabrous annual herbs. *Leaves* alternate, pinnatisect. *Capitula* in a dense corymb, discoid. *Involucre* hemispheric to cylindrical. *Phyllaries* in 3 or 4 rows, with narrow, pale scarious margins. *Receptacle* narrowly conic, paleate; paleae narrowly obovate, flat to slightly canaliculate, with a central resin canal. *Florets* hermaphrodite, fertile; corolla 5-lobed, yellow. *Achenes* narrowly obovoid, round in cross-section or slightly dorsiventrally flattened, with 1 adaxial and 2 lateral ribs; apex with a scarious corona; pericarp with myxogenic cells abaxially and on ribs and with a resin sac apically in adaxial rib. *Embryo sac development* monosporic. *Base chromosome number* $x = 9$.

Distribution — NW Africa, Sicily.

Members — *Lonas* Adans. (1).

Notes — The unispecific genus *Lonas* was assigned to the extremely polyphyletic subtribe *Matricariinae* sensu Bremer & Humphries (1993), who acknowledged that the position of the genus “is difficult to assess” (l.c.: 155). The species *L. annua* was described by Linnaeus (1753) as a member of the genus *Santolina* and a close relationship with *Santolina* and other members of the *Santolininae* is reasonable both on morphological (receptacular paleae with a central resin duct) and molecular phylogenetic grounds. However, none of the gene and species trees presented here revealed a strongly supported position within the *Santolininae*; conversely, in the concatenated sequence analysis (Fig. 3), it is strongly supported as a sister-group to a monophyletic *Santolininae*+*Glebionidinae* lineage.

16. *Lepidophorinae* Oberpr. & Töpfer, **subtrib. nov.**

Type: *Lepidophorum* Neck. ex Cass. (*Lepidophorum repandum* (L.) DC.).

Description — Annual, glabrous herbs. *Leaves* alternate, serrate. *Capitula* solitary, pedunculate, radiate. *Involucre* meniscoid to hemispheric. *Phyllaries* in 3 or 4 rows, with

narrow, brown scarious margins. *Receptacle* convex, paleate; paleae flat to canaliculate, narrowly elliptic to obovate, with a central resin duct. *Ray florets* female or neuter, sterile; limb yellow. *Disc florets* hermaphrodite, fertile; corolla 5-lobed, yellow. *Achenes of ray florets* flat; apex with c. 4 free or basally connate scales. *Achenes of disc florets* narrowly obovoid, 5-ribbed; apex marginally rounded; pericarp with myxogenic cells along ribs, without resin sacs. *Embryo sac development* monosporic. *Base chromosome number* $x = 9$.

Distribution — SW Europe.

Members — *Lepidophorum* Neck. ex Cass. (1).

Notes — As in the previous case of *Lonas*, the annual, unispecific genus *Lepidophorum* was considered “difficult to place” on morphological and anatomical grounds by Bremer & Humphries (1993: 139), who classified it in their highly polyphyletic subtribe *Leucantheminae*, which contained also genera presently arranged in subtribes *Artemisiinae* (*Leucanthemella*, *Nipponanthemum*), *Glebionidinae* (*Nivellea*) and *Leucanthemopsidinae* (*Hymenostemma*, *Leucanthemopsis*, *Phalacrocarpum*, *Prolongoa*). Based on the possession of receptacular paleae with a central resin duct, the genus shows some morphological affinity to *Lonadinae* and *Santolininae*. However, both gene trees of the present study (Fig. 1, 2) do not support either affinity, while the genus is unfortunately missing in the species-tree reconstructions due to missing sequence information from the other nuclear markers.

17. *Leucantheminae* K. Bremer & Humphries in Bull. Nat. Hist. Mus. London, Bot. 23: 136. 1993. – Type: *Leucanthemum* Mill. (*Leucanthemum vulgare* Lam.).

Description — Annual or perennial herbs, rarely subshrubs (*Leucanthemum*, *Plagiis*, *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 or in a lax corymb, discoid or radiate. *Involucre* meniscoid to hemispheric. *Phyllaries* in 3–5 rows, with narrow to broad scarious margins. *Receptacle* hemispheric to conic, epaleate. *Ray florets* female or sterile; limb white, yellow or red (*Rhodanthemum*). *Disc florets* hermaphrodite; corolla (4 or)5-lobed, basally often saccate and clasping top of achene; anthers with non-polarized endothelial tissue and a balusterform filament collar. *Achenes of ray florets* ellipsoid, circular in cross-section, with 5–10 ribs, sometimes dorsiventrally flattened, with 3 adaxial ribs and lateral wings (*Daveaua*). *Achenes of disc florets* ellipsoid, circular in cross-section, with 5–10 ribs, rarely dorsiventrally flattened and with 1 abaxial, 2 lateral and 1–3 adaxial ribs (*Otospermum*); apex marginally rounded or with a scarious and adaxi-

ally longer corona, sometimes (*Heteromera*) with a short and basally callose corona or with 5–9 obovate scales; pericarp with myxogenic cells along ribs and with resin canals between ribs, sometimes (*Daveaua*, *Heteromera*) with 3–5 resin sacs apically in ribs, rarely (*Otospermum*) without any resin ducts. *Embryo sac development* monosporic. *Base chromosome number* $x = 9$.

Distribution — Mediterranean region, Macaronesia, Europe, Asia.

Members — *Chlamydochora* Ehrenb. ex Less. (1), *Chrysanthoglossum* B. H. Wilcox & al. (2), *Coleostephus* Cass. (3), *Daveaua* Mariz (1), *Glossopappus* Kunze (1), *Heteromera* Pomel (2), *Leucanthemum* Mill. (43), *Mauranthemum* Vogt & Oberprieler (4), *Otospermum* Willk. (1), *Plagiatus* L'Hér. ex DC. (3), *Rhodanthemum* B. H. Wilcox & al. (14).

Notes — Dating back to analyses of nrDNA ITS sequence variation in Oberprieler (2004b), the inclusion of *Daveaua*, *Heteromera* and *Otospermum* into subtribe *Leucantheminae* has been evident but was never formalized thereafter (Oberprieler & al. 2007, 2009). This was mainly due to the distinctness of the achene-anatomically well-circumscribed generic assemblage around the core genus *Leucanthemum* with its apomorphic character state of achenes with resin canals and vascular bundles between the ribs, which is lacking in the three mentioned genera. Here, achenes are 5-ribbed and ribs contain vascular bundles, while *Daveaua* and *Heteromera* also share the possession of resin ducts in the apical portions of ribs and of dorsiventrally flattened achenes of ray florets (Giroux 1930; Oberprieler 2004b). With the inclusion of *Daveaua*, *Heteromera* and *Otospermum* in the *Leucantheminae*, as suggested again by our phylogenetic analyses based on the now more comprehensive dataset, the morphological circumscription of the subtribe becomes more heterogeneous; however, it avoids the erecting of uninformative, unigeneric subtribal units where there is a clear evolutionary pattern.

18. *Santolininae* Willk. in Willkomm & Lange, Prodr. Fl. Hispan. 2: 76. 1870. – Type: *Santolina* L. (*Santolina chamaecyparissus* L.).

Description — Shrubs, subshrubs, perennial or annual herbs. *Indumentum* of basifixed, medifixed or stellate hairs. *Leaves* alternate, entire, lobed or dentate to 2- or 3-pinnatisect, sometimes vermiform. *Capitula* solitary or in lax corymbs, radiate, disciform or discoid. *Involucre* hemispheric or obconic to urceolate (*Rhedinolepis*), sometimes umbonate (*Mecomischus*, *Santolina*). *Phyllaries* in 3 rows, with narrow to broad scarious margins. *Receptacle* hemispheric to conic, paleate; paleae flat to canaliculate, often with a central resin duct. *Ray florets* female or neuter; limb white, orange or yellow. *Disc florets* hermaphro-

dite; corolla 5-lobed, basally often saccate and clasping top of achene; anthers with non-polarized endothelial 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 in *Chamaemelum* and *Cladanthus*). *Base chromosome number* $x = 9$.

Distribution — W and S Europe, N Africa, SW Asia.

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

Notes — The circumscription of *Santolininae* of Oberprieler & al. (2007) is well-supported both in the cpDNA (Fig. 1) and nrDNA ITS gene trees (Fig. 2), as well as (for a reduced generic sample comprising *Chamaemelum*, *Cladanthus* and *Rhedinolepis*) in the species-tree reconstructions (Fig. 3, 4).

19. *Glebionidinae* Oberpr. & Vogt in Willdenowia 37: 106. 2007. – Type: *Glebionis* Cass. (*Pyrethrum indicum* Roxb. ex Sims. [= *Glebionis coronaria* (L.) Cass. ex Spach]).

Description — 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, rarely (*Otoglyphis*) discoid or disciform. *Involucre* meniscoid to hemispheric. *Phyllaries* in 3–5 rows, with broad scarious margins. *Receptacle* convex to conic, epaleate. *Ray florets* female; limb white or yellow. *Disc florets* hermaphrodite; corolla 5-lobed, rarely (*Otoglyphis*) lobes with a central resin sac; anthers with non-polarized endothelial tissue and a balusterform filament collar. *Achenes* of ray florets triquetrous and 2- or 3-winged; achenes of disc florets laterally compressed and 1- or 2-winged, sometimes terete and 10-ribbed; apex marginally rounded or with a corona; pericarp without myxogenic cells or resin sacs, rarely (*Nivellea*) with myxogenic cells along ribs; in *Otoglyphis*, circular to only slightly flattened in cross-section, apex marginally rounded or with an adaxial auricle, pericarp with myxogenic cells and sometimes with 2 lateral resin canals; in *Endopappus*, dorsiventrally flattened, 3-angled with 1 adaxial and 2 lateral ribs; apex with a corona; pericarp with myxogenic cells abaxially and along ribs, without resin sacs. *Embryo sac development* monosporic, bisporic (*Argyranthemum*) or tetrasporic (*Heteranthemis*). *Base chromosome number* $x = 9$.

Distribution — Macaronesia, Europe, N Africa, SW Asia.

Members — *Argyranthemum* Webb (24), *Endopappus* Sch. Bip. (1), *Glebionis* Cass. (2), *Heteranthemis* Schott (1), *Ismelia* Cass. (1), *Nivellea* B. H. Wilcox & al. (1), *Otoglyphis* Pomel (2) [incl. *Aaronsohnia* Warb. & Eig (1)].

Notes — In its previous circumscription, the subtribe *Glebionidinae* comprised the four genera *Argyranthemum*, *Glebionis*, *Heteranthemis* and *Ismelia* and formed a well-supported monophyletic and morphologically well-characterized generic assemblage due to the occurrence of distinctly heteromorphic achenes (achenes of ray florets triquetrous, those of the disc florets terete or laterally flattened). Our present phylogenetic analyses, especially the gene tree based on cpDNA sequence variation (Fig. 1) and the total-evidence tree based on concatenated markers (Fig. 3), indicate that three annual genera [*Endopappus*, *Nivellea* and *Otoglyphis* (the former *Aaronsohnia*)] are closely related with this core group. In order to keep the number of subtribes in the *Anthemideae* at a reasonable level, we suggest inclusion of these three genera into the *Glebionidinae*, which then becomes inevitably more heterogeneous and less characteristic in its circumscription.

The close relationship between the SW Asian species *Aaronsohnia factorovskyi* Warb. & Eig and the N African *Chlamydophora pubescens* (Desf.) Coss. & Durieu (based on *Cotula pubescens* Desf.) led Bremer & Humphries (1993) to transfer the latter taxon to *Aaronsohnia*. However, by doing so, the two authors did not realize that there is an older generic name available for *Cotula pubescens*. It was discovered by A. Dobignard (in Dobignard & Chatelain (2011) that Pomel (1874) had described the genus *Otoglyphis* based on *Chlamydophora pubescens* and he consequently transferred the subspecies *Aaronsohnia pubescens* subsp. *maroccana* (Ball) Fennane & Ibn Tattou to *Otoglyphis* as an independent species (*O. maroccana* (Ball) Dobignard). If *Aaronsohnia* is considered as being congeneric with *Otoglyphis* following the reasoning of Bremer & Humphries (1993), the latter has priority over the former. Owing to the observation of very similar nrDNA ITS1 sequences of *Aaronsohnia factorovskyi* and *Otoglyphis pubescens* (Desf.) Pomel (Gemeinholzer & al. 2006) and the treatment of *Matricaria maroccana* Ball (= *Aaronsohnia pubescens* subsp. *maroccana*) as a subspecies of *O. pubescens*, we propose the following two new combinations:

Otoglyphis factorovskyi (Warb. & Eig) Oberpr. & Vogt, **comb. nov.** ≡ *Aaronsohnia factorovskyi* Warb. & Eig in Leaflet Agric. Exp. Sta. Zionist Organ. Inst. 6: 40. 1927.

Otoglyphis pubescens subsp. *maroccana* (Ball) Oberpr. & Vogt, **comb. nov.** ≡ *Matricaria maroccana* Ball in J. Bot. 11: 367. 1873 ≡ *Aaronsohnia pubescens* subsp. *maroccana* (Ball) Fennane & Ibn Tattou in *Bocconea* 8: 18. 1998 ≡ *Otoglyphis maroccana* (Ball) Dobignard, Index Syn. Fl. Afrique N. 2: 333. 2011.

Author contributions

Christoph Oberprieler and Robert Vogt initiated and conveyed the present study and discussed its results and its nomenclatural consequences. Miriam Stock contributed nrDNA ITS, ETS and cpDNA sequences in the course of a post-doctoral engagement with the Evolutionary and Systematic Botany Group at Regensburg University. Alisha Töpfer completed the dataset during her Master thesis in 2021, while Marco Dorfner helped with phylogenetic reconstructions. Christoph Oberprieler wrote the manuscript and Alisha Töpfer drew the phylogenetic trees.

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Appendix 1. List of taxa and sources of plant material used for the current molecular study. When two accession numbers are given under ITS, these represent the ITS1 and ITS2 regions, respectively. **Boldface** denotes sequences new to science.

Taxa	Source and voucher data		GenBank accession number						
	ITS	ETS	<i>ndhF</i>	<i>trnL-trnF</i>	DSP	VIP5	<i>NPF3.1</i>		
<i>Aaronsohnia pubescens</i> (Desf.) K. Bremer & Humphries (<i>Otologyphis pubescens</i> (Desf.) Pomel)	AJ296408 AJ296443		ON089900	ON089795	ON089989	ON090092			
<i>Achillea ptarmica</i> L.	AJ296380 AJ296415	ON089706	ON089901	ON089796	ON089990	ON090093	ON090195		
<i>Adenanthellium osmitoides</i> (Harv.) B. Nord.	AM774445		AM900445	ON089797					
<i>Adenoglossa decurrens</i> (Hutch.) B. Nord.	AM774446		AM900446	ON089798					
<i>Ajania achilleoides</i> Poljakov ex Grubov	ON100515	ON089707	ON089902	ON089799	ON089991	ON090094	ON090196		
<i>Allardia tomentosa</i> Decne.	ON100516	ON089708	ON089903	ON089800	ON089992	ON090095	ON090197		
<i>Anacyclus radiatus</i> Loisel. subsp. <i>radiatus</i>	AJ296381 AJ296416	ON089709	ON089904	ON089801	ON089993	ON090096	ON090198		
<i>Anthemis arvensis</i> subsp. <i>incrassata</i> (Loisel.) Nyman	AJ312777 AJ312806	ON089710	ON089905	ON089802	ON089994	ON090097	ON090199		
<i>Arctanthemis marschalliana</i> subsp. <i>pectinata</i> (Boiss.) Lo Presti & Oberpr.	FM957698	ON089711	ON089906	ON089803	ON089995	ON090098	ON090200		
<i>Arctanthemum arcticum</i> (L.) Tzvelev					ON089996	ON090099	ON090201		
<i>Arctanthemum arcticum</i> (L.) Tzvelev	EF577286	AB359864	AF153671						
<i>Arctanthemum arcticum</i> subsp. <i>polare</i> (Hult.) Tzvelev		ON089712	ON089907						

<i>Argyranthemum adauctum</i> subsp. <i>canariense</i> (Sch. Bip.) Humphries	Spain, Canary Islands, Gran Canaria, Cruz de la Tejada, Ayacata – Pozo de las Nieves, 6 Apr 1990, <i>Kilian 2438 & Willerding</i> (B 10 0271410)	ON100517	ON089713	ON089908	ON089804	ON089997	ON090100	ON090202
<i>Artemisia vulgaris</i> L.	Germany, Regensburg, 16 Sep 2010, <i>Konowalik s.n.</i> (WRSL)	ON100518	ON089714	ON089909	ON089805	ON089998	ON090101	ON090203
<i>Artemisiella stracheyi</i> (Hook. f. & Thomson ex C. B. Clarke) Ghafoor	China, Xizang (Tibet), Nagqu – Siling, 4580 m, 16 Aug 1993, <i>Miethe 9488/OJ</i> (B 10 0144871)	AM774421	ON089715	ON089910	ON089806	ON089999	ON090102	ON090204
<i>Athanasia dentata</i> (L.) L.	South Africa, Eastern Cape, Van Staden's Flower Reserve, 17 Jan 2003, <i>Ueckert & Oberprieler 10269</i> (B 10 0112584)	ON100519	ON089716	ON089911	ON089807	ON090000	ON090103	ON090205
<i>Brachanthemum kirghisorum</i> Krasch.	Kyrgyzstan, Yssyh-Kul, Ak-Saji, 1600 m, 10 Aug 2000, <i>Rost s.n.</i> (B 10 0673692)	ON100520	ON089717	ON089912	ON089808	ON090001	ON090104	ON090206
<i>Brochia cinerea</i> (Delile) Vis.	Tunisia, Tozeur, 30 Mar 1998, <i>Bauke & al.</i> 509 (B 10 1172518)	ON100521	ON089718	ON089913	ON089809	ON090002	ON090105	ON090207
<i>Cancerina chrysocephala</i> Kar. & Kir.	China, Xinjiang Prov., Dzungaria, Tian Shan, Urumqi – Korla, 3850 m, 14 Aug 1986, <i>Dickoré 0081</i> (MSB)	ON100522	ON089719	ON089914	ON089810	ON090003	ON090106	ON090208
<i>Castrilanthemum debeauxii</i> (Degen & al.) Vogt & Oberpr.	Spain, Sierra Guillamona, Pinar de Araceli, 1820 m, 10 Jun 2011, <i>Alvares & Tomasello IA2170-4</i> (MA)	ON100523	ON089720	ON089915	ON089811	ON090004	ON090107	ON090209
<i>Chamaemelum nobile</i> (L.) All.	Germany, Hort. Bot. Jena, <i>Oberprieler 9761</i> (B 10 0018369)	AJ296382 AJ296417	ON089721	ON089916	ON089812	ON090005	ON090108	ON090210
<i>Chlamydo-phora tridentata</i> Ehrenb. ex Less.	Cyprus, Larnaka, Meneou, 13 Apr 1991, <i>Vogt 8120</i> (B 10 0550374)	ON100524	ON089722	ON089917	ON089813	ON090006	ON090109	ON090211
<i>Chrysanthemum sinuatum</i> Ledeb.	Russia, Altay Republic, Ongudayskiy Rayon, SE of Onguday, 1120 m, 3 Aug 2008, <i>Martins 2381</i> (B 10 0274585)	ON100525	ON089723	ON089918	ON089814	ON090007	ON090110	ON090212
<i>Chrysanthoglossum trifurcatum</i> (Desf.) B. H. Wilcox & al.	Tunisia, Tataouine – Remada, 450 m, 13 May 1994, <i>Vogt 13038 & Oberprieler 7343</i> (B 10 0673083)	AJ296392 AJ296427	ON089724	ON089919	ON089815	ON090008	ON090111	ON090213
<i>Cladanthus arabicus</i> (L.) Cass.	Morocco, Beni Snassen, Gorges du Zegzel, 10 May 1993, <i>Vogt 11650 & Oberprieler 6098</i> (B 10 1158040)	AJ296383 AJ296418	ON089725	ON089920	ON089816	ON090009	ON090112	ON090214
<i>Coleostephus myconis</i> (L.) Rech. f.	Italy, Reggio Calabria, Gallico – Gambarie, 27 May 1994, <i>Vogt 13976 & Oberprieler 8281</i> (B 10 1172523)	ON100526	ON089726	ON089921	ON089817	ON090010	ON090113	ON090215

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	ITS	ETS	<i>ndhF</i>	<i>trnL-trnF</i>	DSP	VIP5	<i>NPF3.1</i>		
<i>Cota tinctoria</i> (L.) J. Gay	AJ312802 AJ312831	ON089727	ON089922	ON089818	ON090011	ON090114	ON090216		
	Italy, Pescara, Passo di San Leonardo – Caramanico, 29 May 1994, <i>Vogt 14055 & Oberprieler 8360</i> (B 10 1172519)								
<i>Cotula australis</i> (Spreng.) Hook. f.	AM774448	ON089728	AM900448	ON089819					
	New Zealand, Canterbury, South Branch Waimakariri, 29 Sep 1998, <i>Wagstaff 98.086</i> (CHR)								
<i>Cotula australis</i> (Spreng.) Hook. f.					ON090012	ON090115	ON090217		
	Spain, Tenerife, Anaga, Chinobre, 28 Mar 1999, <i>Oberprieler 9931</i> (B 10 0029776)								
<i>Crossostephium chinense</i> (L.) Makino	EF577293								
	Zhao & al. (2010)								
<i>Cymbopappus adenosolen</i> (Harv.) B. Nord.	AM774449	ON089729	ON089923	ON089820	ON090013	ON090116	ON090218		
	South Africa, Boesmansrivier, McGregor – Stormsvlei, 17 Nov 1985, <i>Källersjö 208</i> (S)								
<i>Daveaua anthemoides</i> Mariz	ON100527	ON089730	ON089924	ON089821					
	Spain, Caceres, Logrosán, Las Chamizas, 26 Jun 1993, <i>Rico s.n.</i> (SALA 135877, B 10 1172520)								
<i>Daveaua anthemoides</i> Mariz					ON090014	ON090117	ON090219		
	Spain, Caceres, Logrosán, Las Chamizas, 425 m, 26 May 2012, <i>Rico ER-8082</i> (SALA 143862, B 10 1172521)								
<i>Elachanthemum intricatum</i> (Franch.) Y. Ling & Y. R. Ling	EF577313								
	Zhao & al. (2010)								
<i>Endopappus macrocarpus</i> (Coss. ap. Kralik) Sch. Bip.	AJ748780 AJ748781	ON089731	ON089925	ON089822	ON090015	ON090118	ON090220		
	Algeria, Ghardaia – El Golea, 400 m, 28 Mar 1981, <i>Podlech 35512</i> (MSB)								
<i>Eriocephalus paniculatus</i> Cass.	AM774450	ON089732	AM900449	ON089823	ON090016	ON090119	ON090221		
	South Africa, Western Cape, Citrusdal, 13 Jun 1998, <i>Hanekom 3033</i> (S)								
<i>Eumorphia sericea</i> J. M. Wood & M. S. Evans	AM774451	ON089733	AM900450	ON089824	ON090017	ON090120	ON090222		
	South Africa, Eastern Cape, Barkly East District, 3 Feb 1963, <i>Hilliard & Burtt 16369</i> (S)								
<i>Filifolium sibiricum</i> (L.) Kitam.	ON100528	ON089734	ON089926	ON089825	ON090018	ON090121	ON090223		
	Mongolia, Zünmod, 1400–1500 m, 29 Aug 1966, <i>Soják s.n.</i> (S)								
<i>Foveolina albida</i> (DC.) Källersjö	ON100529	ON089735	ON089927	ON089826	ON090019	ON090122			
	South Africa, Lüderitz-Süd, Spitskop, Witpiits – Rosh Pinah, 1 Jul 1974, <i>Nordenstam & Lundgren 432</i> (S)								
<i>Foveolina albida</i> (DC.) Källersjö							ON090224		
	South Africa, Northern Cape, Namaqualand, 43 km ENE of Springbok along the road to Pofadder, 930 m, 11 Oct 1989, <i>Greuter 21630</i> (B 10 1154363)								

<i>Glebionis coronaria</i> (L.) Cass. ex Spach	Morocco, Nador, Selouane – Zaïto, 120 m, 12 Apr 1987, <i>Bayón, Oberprieler 2015 & Vogt</i> (B 10 1172504)	ON100530	ON089928	ON089827	ON090020	ON090123
<i>Glossopappus macrotus</i> subsp. <i>hesperius</i> (Maire) Jahand. & Maire	Morocco, Ifrane – Fez, Immouzer du Kandar, 1090 m, 29 May 1993, <i>Vogt 12028</i> (B 10 0550375)	ON100531	ON089929	ON089828	ON090021	ON090124 ON090225
<i>Gonospermum fruticosum</i> Less.	Spain, Tenerife, Teno, Punta de Teno, Casa Blanca, 23 Mar 1999, <i>Oberprieler 9877</i> (B 10 0029773)	ON100532	ON089930	ON089829	ON090022	ON090125 ON090226
<i>Gymnopentzia bifurcata</i> Benth.	South Africa, Eastern Cape, Barkly East District, <i>Hilliard & Burt 16384</i> (S)	ON100533	ON089931	ON089830	ON090023	ON090126 ON090227
<i>Handelia trichophylla</i> (Schrenk) Heimerl	Iran, Khorazan Razavi, Dargaz, <i>Amiri s.n.</i> (MPH-1689)	ON100534	ON089932	ON089831		ON090024 ON090127 ON090228
<i>Handelia trichophylla</i> (Schrenk) Heimerl	Kyrgyzstan, Tian-shan, montes Kirgiski khrebet, 10 km NE of Frunze (Pishpek), 1000–1200 m, 29 May 1974, <i>Vasak s.n.</i> (B 10 0144853)					
<i>Heliocaula atlantica</i> (Litard. & Maire) Humphries	Morocco, Toubkal, 3850 m, 23 Aug 1992, <i>Kreisch 92/0589</i> (B 10 0469570)	ON100535	ON089933	ON089832	ON090025	ON090128 ON090229
<i>Heteranthemis viscidhirta</i> Schott	Morocco, Kenitra, Kenitra – Allal Tazi, 3 May 1987, <i>Bayón, Oberprieler & Vogt 6131</i> (B 10 1172505)	ON100536	ON089934	ON089833	ON090026	ON090129 ON090230
<i>Heteromera fuscata</i> (Desf.) Pomel	Tunisia, Tozeur, Kariz – Gafsa), 65 m, 23 Mar 2009, <i>Vogt 16585, Oberprieler 10528 & Gsöthl</i> (B 10 0216212)	ON100537	ON089935	ON089834	ON090027	ON090130 ON090231
<i>Hilliardia zaarbergensis</i> (Oliv.) B. Nord.	South Africa, Natal, near Mt Alida, Eweka Estates, 16 Sep 1991, <i>Hilliard & Burt 19118</i> (S)	AM774454	AM900452	ON089835		
<i>Hilliardia zaarbergensis</i> (Oliv.) B. Nord.	South Africa, 2930 AB, near Mt Alida, Eweka Estates, growing in hort. R. Mackellar, Howick, 16 Apr 1991, <i>Hilliard & Burt 19118</i> (M)				ON090028	ON090131
<i>Hippia pilosa</i> (P. J. Bergius) Druce	South Africa, Cape Province, Rooiberg mountain, 2 Nov 1988, <i>Vlok 2041</i> (S)	AM774455	ON089936	ON089836		
<i>Hippia pilosa</i> (P. J. Bergius) Druce	South Africa, Vamrhynsdorp Div., 4 miles N of Vamrhynsdorp, 1 Nov 1963, <i>Rechinger A-4764</i> (M)				ON090029	ON090132 ON090232

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	ITS	ETS	<i>ndhF</i>	<i>trnL-trnF</i>	DSP	VIP5	<i>NPF3.1</i>		
<i>Hippolytia dolichophylla</i> (Kitam.) K. Bremer & Humphries	AJ748784 AJ748785	ON089744	ON089937	ON089837	ON090030	ON090133	ON090233		
<i>Hulteniella integrifolia</i> (Richardson) Tzvelev	ON100538	ON089745	ON089938	ON089838	ON090031	ON090134	ON090234		
<i>Hymenolepis incisa</i> DC.	AM774456	ON089746	AM900453	ON089839	ON090032	ON090135	ON090235		
<i>Hymenostemma pseudanthemis</i> (Kunze) Willk.	ON100539	ON089747	ON089939	ON089840					
<i>Hymenostemma pseudanthemis</i> (Kunze) Willk.					ON090033	ON090136	ON090236		
<i>Inezia integrifolia</i> (Klatt) E. Phillips	AM774457		AM900454	ON089841		ON090137			
<i>Inulanthera leucoclada</i> (DC.) Källersjö	AM774458	ON089748	AM900455	ON089842	ON090034	ON090138	ON090237		
<i>Ismelia carinata</i> (Schousb.) Sch. Bip.	ON100540		ON089940	ON089843	ON090035	ON090139			
<i>Kaschgaria komarovii</i> (Krasch. & Rubtzov) Poljakov	ON100541	ON089749	ON089941	ON089844	ON090036	ON090140	ON090238		
<i>Lastospermum pedunculare</i> Lag.	AM774459	ON089750	AM900456	ON089845	ON090037	ON090141	ON090239		
<i>Lepidolopha mogoltavica</i> (Krasch.) Krasch.	ON100542	ON089751	ON089942	ON089846	ON090038	ON090142	ON090240		
<i>Lepidolopsis turkestanica</i> (Regel & Schmalh.) Poljakov	ON100543	ON089752	ON089943	ON089847	ON090039	ON090143	ON090241		
<i>Lepidophorum repandum</i> DC.	ON100544		ON089944	ON089848	ON090040	ON090144			
<i>Lepinella pectinata</i> subsp. <i>villosa</i> (D. G. Lloyd) D. G. Lloyd & C. J. Webb	HE860639	ON089753	AM900457	ON089849		ON090145	ON090242		

<i>Leptinella pectinata</i> subsp. <i>villosa</i> (D. G. Lloyd) D. G. Lloyd & C. J. Webb	Germany, Bot. Garten Regensburg (ex Arktisch-Alpiner-Garten Chemnitz, ex New Zealand, The Remarkables), 28 Jul 2004, <i>Himmelreich 5</i> (CHR)	ON090041							
<i>Leucanthemella serotina</i> (L.) Tzvelev	Romania, Banatus, distr. Caras-Severin, locis paludosis insulae Ostrov prope pag. Moldova Veche, 20 Sep 1967, <i>Moraria & al. s.n.</i> (B 10 0267975)	ON100545	ON089754	ON089945	ON089850	ON090042	ON090146		ON090243
<i>Leucanthemella serotina</i> (L.) Tzvelev	Germany, Bayern, MTB 8230/3, Feuchtwiese südöstlich Heggen, 26 Sep 1995, <i>Dörr s.n.</i> (M)								
<i>Leucanthemopsis alpina</i> (L.) Heywood	France, Vallouise, Glacier Blanc, 2380 m, 18 Jul 2010, <i>Tomaseilo 40</i> (PAL)	KM589814 KM589837		ON089946	ON089851				
<i>Leucanthemopsis alpina</i> (L.) Heywood	Spain, Huesca, Valle de Pio Esero – Puerto de Benasque, 2 Aug 1985, <i>Vogt 4041</i> (B 10 1172507)					ON090043	ON090244		
<i>Leucanthemum vulgare</i> Lam.	Germany, Regensburg, Deuerling, Pittmannsdorf – Neuhausl, 450 m, 8 Jun 2004, <i>Eder & Oberprieler s.n.</i> (B 10 0550249)	ON100546	ON089755	ON089947	ON089852	ON090044	ON090147	ON090245	
<i>Leucocyclus formosus</i> Boiss.	Turkey, Taurus, Bulgar Dag, 6000 ft., 9 Jul 1853, <i>Kotschy 65</i> (M)	AJ864578 AJ864598	ON089756	ON089948	ON089853	ON090045	ON090148	ON090246	
<i>Leucoptera subcarcosa</i> B. Nord.	South Africa, Cape Province, Vamrhynsdorp Div., 3 Sep 1974, <i>Nordenstam & Lundgren 1615</i> (S)	AM774461		AM900458	ON089854	ON090046	ON090149	ON090247	
<i>Lidbeckia pectinata</i> P. J. Bergius	South Africa, Cape, Tulbagh, Roodsandberg, 400 m, 23 Oct 1983, <i>Rourke 1812</i> (S)	AM774462	ON089757	AM900459	ON089855	ON090047	ON090150	ON090248	
<i>Lonas annua</i> Vines & Druce	Tunisia, Zaghouan, Tebourba – Mateur, 200–250 m, 2 May 1994, <i>Vogt 12069 & Oberprieler 6374</i> (B 10 1158042)	AJ296411 AJ296446	ON089758	ON089949	ON089856	ON090048	ON090151	ON090249	
<i>Lugoa revoluta</i> (Buch) DC.	Spain, Tenerife, Anaga, Benijo, 26 Mar 1999, <i>Oberprieler 9919</i> (B 10 0029775)	FN827337 FN827338	ON089759	ON089950	ON089857	ON090049	ON090152	ON090250	
<i>Marasmodes polycephala</i> DC.	South Africa, Cape Province, Malmesbury Dist., Malmesbury road, 19 Mar 1971, <i>Esterhuysen 32584</i> (S)	ON100547	ON089760	ON089951	ON089858				
<i>Marasmodes polycephala</i> DC.	South Africa, Cape Province, Paarl District, 10 Jun 1975, <i>Esterhuysen 33883</i> (S)								ON090251
<i>Matricaria discoidea</i> DC.	Germany, Jena, 10 Jul 1997, <i>Oberprieler 9762</i> (B 10 0018500)	AJ296412 AJ296447	ON089761	ON089952	ON089859	ON090051	ON090154	ON090252	

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	ITS	ETS	<i>ndhF</i>	<i>trnL-trnF</i>	DSP	VIP5	NPF3.1
<i>Mauranthemum paludosum</i> (Poir.) Vogt & Oberpr. subsp. <i>paludosum</i> (WRSL)	ON100548	ON089762	ON089953	ON089860	ON090052	ON090155	ON090253
<i>Mausolea eriocarpa</i> (Bunge) Poljakov ex Podlech	ON100549	ON089763	ON089954	ON089861	ON090053	ON090156	ON090254
<i>Mecomischus halimifolius</i> (Munby) Hochr.	AJ296384 AJ296419		ON089955	ON089862	ON090054	ON090157	
<i>Microcephala lamellata</i> (Bunge) Pobed.	ON100550		ON089956	ON089863			
<i>Microcephala lamellata</i> (Bunge) Pobed.					ON090055	ON090158	
<i>Myxopappus acutilobus</i> (DC.) Källersjö	AM774464		AM900461				
<i>Myxopappus acutilobus</i> (DC.) Källersjö		ON089764		ON089864	ON090056	ON090159	ON090255
<i>Nananthea perpusilla</i> DC.	ON100551	ON089765	ON089957	ON089865	ON090057	ON090160	ON090256
<i>Neopallasia pectinata</i> (Pall.) Poljakov	ON100552	ON089766	ON089958	ON089866	ON090058	ON090161	ON090257
<i>Nipponanthemum nipponicum</i> (Franch. ex Maxim.) Kitam.	ON100553	ON089767	ON089959		ON090059	ON090162	ON090258
<i>Nivellea nivellei</i> (Braun-Blanq. & Maire) B. H. Wilcox & al.	ON100554	ON089768	ON089960	ON089867	ON090060	ON090163	ON090259
<i>Oncosiphon grandiflorus</i> (Thumb.) Källersjö	AM774465	ON089769	ON089961	ON089868	ON090061	ON090164	ON090260
<i>Opisthopappus taihangensis</i> (Ling) C. Shih	EF577318						
<i>Osmitopsis asteriscoides</i> (L.) Less.	AM774466	ON089770	ON089962	ON089869	ON090062	ON090165	ON090261

<i>Otanthus maritimus</i> (L.) Hoffmanns. & Link	Spain, Cádiz, Tarifa, 28 May 1992, Prem-Vogt & Vogt 9268 (B 10 1172510)	AJ296385 AJ296420	ON089771	ON089963	ON089870	ON090063	ON090166	ON090262
<i>Otospermum glabrum</i> (Lag.) Willk.	Morocco, Fès, Moulay-Yakoub, 400 m, Bayán, Oberprieler & Vogt 5984 (B 10 1172511)	ON100555	ON089772	ON089964	ON089871			
<i>Otospermum glabrum</i> (Lag.) Willk.	Tunisia, Jendouba, Kroumirie, Ain Draham – Tabarka, Oued El Kabir, 5 m, 20 May 1994, Vogt 13741 & Oberprieler 8046 (B 10 1158045)					ON090064	ON090167	ON090263
<i>Pentzia</i> sp.	South Africa, Eastern Cape, Addo Elephant National Park, 16 Jan 2003, Ueckert & Oberprieler 10268 (B 10 1172526)	ON100556	ON089773	ON089965	ON089872	ON090065	ON090168	ON090264
<i>Phaeostigma salicifolium</i> (Mattf.) Muldashev	China, Sze-ch'uan, Dongrengo, 4200 m, 8 Aug 1922, Smith s.n. (S)	ON100557	ON089774	ON089966	ON089873	ON090066	ON090169	ON090265
<i>Phalacrocarpum oppositifolium</i> (Brot.) Willk.	Portugal, Serra de Estrela, Manteigas – La Torre, 1000 m, 10 May 2011, Tomasello 281 (MA)	KM589820 KM589843	ON089775	ON089967	ON089874			
<i>Phalacrocarpum oppositifolium</i> (Brot.) Willk.	Portugal, Sierra de Estrela, Manteigas, Poco de Inferno, 18 Jul 1986, Vogt 4653 & Bayon (B 10 1172512)					ON090067	ON090170	ON090266
<i>Phymaspermum leptophyllum</i> (DC.) Benth. & Hook. f. ex B. D. Jacks.	South Africa, Western Cape, Oudtshoorn – Robinson Pass, 23 Jan 2003, Ueckert & Oberprieler 10274 (B 10 0112580)	ON100558	ON089776	ON089968	ON089875	ON090068	ON090171	ON090267
<i>Picrothamnus desertorum</i> Nutt.	USA, Idaho, Owyhee Co., Marsing, 19 Apr 1959, Cronquist 8121 (S)	ON100559	ON089777	ON089969	ON089876	ON090069	ON090172	ON090268
<i>Plagius maghrebinus</i> Vogt & Greuter	Tunisia, Jendouba, Kroumirie, Col des Ruines NW of Ain Draham, 950 m, 20 May 1994, Vogt 13696 & Oberprieler 8001 (B 10 0114201)	AJ296403 AJ296438	ON089778	ON089970	ON089877	ON090070	ON090173	ON090269
<i>Polychrysium tadshikorum</i> (Kudr.) Kovalevsk.	Afghanistan, Kataghan, Pul-i Khumri, Surkhab, 700 m, 4 May 1967, Reehinger 33659 (S)	ON100560	ON089779	ON089971	ON089878	ON090071	ON090174	ON090270
<i>Prolongoa hispanica</i> G. López & C. E. Jarvis	Spain, Puente Duero, 695 m, 23 Apr 2011, Tomasello 221 (MA)	KM589818 KM589842	ON089780	ON089972	ON089879			
<i>Prolongoa hispanica</i> G. López & C. E. Jarvis	Spain, Málaga, Tolox – Sierra de las Nieves, 26 May 1992, Vogt 9233 (B 10 1158046)					ON090072	ON090175	ON090271
<i>Pseudohandelia umbellifera</i> (Boiss.) Tzevelev	Iran, Khorasan Razavi, Mashhad, Joharchi 37712 (MPH-1745)	ON100561	ON089781	ON089973	ON089880			

Taxa	Source and voucher data	GenBank accession number						
		ITS	ETS	<i>ndhF</i>	<i>trnL-trnF</i>	DSP	VIP5	NPF3.1
<i>Pseudohandelia umbellifera</i> (Boiss.) Tzvelev	Afghanistan, Kataghan, inter Pul-i Khumri, 35°55'N, 68°45'E et Ribat, 36°09'N, 68°25'E, 700–1200 m, <i>Rechingher 33840_b</i> (B 10 0144858)					ON090073	ON090176	ON090272
<i>Rennera limnophila</i> Merxm.	South Africa, Distr. Groofofontein, 3 Aug 1974, <i>Volk 01402</i> (S)	AM774469	ON089782	AM900463	ON089881	ON090074	ON090177	ON090273
<i>Rhadinolepis lonadioides</i> Coss.	Morocco, Charis, Goulmina, 12 May 1993, <i>Vogt 11692</i> & <i>Oberprieler 6140</i> (B 10 0268417)	AJ296386 AJ296421	ON089783	ON089974	ON089882	ON090075	ON090178	ON090274
<i>Rhodanthemum catananche</i> (Ball) B. H. Wilcox & al.	Morocco, Oukaimeden, 2650 m, 6 Jun 1996, <i>Gomiz FG-489J</i> (LEB)	ON100562		ON089975	ON089883		ON090179	ON090275
<i>Richteria djilgense</i> (Franch.) K. Bremer & Humphries	Tajikistan, Gorno-Badakhshan, Uch Kul lake mts, 17 Sep 2002, <i>Dickoré 18288</i> (MSB)	ON100563	ON089784	ON089976	ON089884	ON090076	ON090180	ON090276
<i>Santolina rosmarinifolia</i> L.	Morocco, Tounfite – Boumia, 1 Jul 1989, <i>Oberprieler 1950</i> (cult. in Hort. Bot. Berol. 071-52-91-10; B 10 0268584)	AJ296387 AJ296422		ON089977	ON089885		ON090181	ON090277
<i>Schistostephium crataegifolium</i> (DC.) Fenzl ex Harv.	South Africa, Natal, Lions River District, Fort Nottingham Commonage, 4 May 1977, <i>Hilliard & Burt 10331</i> (S)	ON100564		ON089978	ON089886	ON090077	ON090182	
<i>Sclerorhachis platyrachis</i> (Boiss.) Podlech ex Rech. f.	Iran, Khorasan Razavi, Torbat-e Heydariyeh, <i>Hassanpour & Shahi-Shavvon s.n.</i> (MPH-2363)	ON100565	ON089785	ON089979	ON089887		ON090183	ON090278
<i>Sclerorhachis platyrachis</i> (Boiss.) Podlech ex Rech. f.	Iran, Khorasan, in saxosis serpentinicis ditomis Robat-I Safid 82–90 km S of Mashhad = 70 km N of Torbat-e Heydariyeh, 1520 m, <i>Rechingher 51325</i> (B 10 0144856)					ON090078	ON090183	ON090278
<i>Soliva sessilis</i> Ruiz & Pav.	USA, California, San Francisco, Golden Gate Park, 100 ft, 6 May 1970, <i>Rose 70037</i> (S)	AM774471	ON089786	AM900464	ON089888	ON090079	ON090184	ON090279
<i>Sphaeromeria potentilloides</i> (A. Gray) A. Heller	USA, California, Sierra Nevada, Plumas Co., Chilcoot, 5000 ft, 19 Jun 1962, <i>Howell s.n.</i> (B 10 0657836)	ON100566		ON089980	ON089889	ON090080		ON090280
<i>Stilpnolepis centiflora</i> (Maxim.) Krasch.	Masuda & al. (2009)	AB359695 AB359781						
<i>Tanacetopsis goloskokovii</i> (Poljakov) Karmysch.	Kazakhstan, Alatau Dshungarici, Belgain, Dshelanaschkul, 12 Jun 1959, <i>Goloskokov 4447</i> (B 10 0144810)	ON100567	ON089787	ON089981	ON089890	ON090081	ON090185	ON090281

<i>Tanacetum corymbosum</i> (L.) Sch. Bip.	Germany, Jena, Kunitz-Kunitzburg, 2 Jul 1997, Oberprieler 9752 (B 10 0018499)	AJ296414 AJ296449	ON089982	ON089891	ON090082	ON090186
<i>Thaminophyllum latifolium</i> Bond	South Africa, Cape Province, Caledon Div., Hermanus, Voelklip, 6 Sep 1974, Esterhuysen 33604 (S)	AM774472	AM900465	ON089892	ON090083	
<i>Trichanthesis karataviensis</i> Regel & Schmalh.	Kazakhstan, Alatau Dshungarici, Czulak mts, Terekty-Saj, 30 May 1995, Goloskokov 4297 (S)	ON100568	ON089788	ON089893	ON090084	ON090187 ON090282
<i>Tridactylina kirilowii</i> Sch. Bip.	Masuda & al. (2009)	AB359694 AB359780				
<i>Tripleurospermum caucasicum</i> (Willd.) Hayek	Armenia, Aragatsothn Province, Ashtarak Distr., Mt Aragats, c. 20 km N of Ashtarak, c. 1 km SE of observatory, 30 Jun 2002, Oberprieler 10192 (B 10 0066671)	AJ864590 AJ864610	ON089789	ON089894	ON090085	ON090188 ON090283
<i>Turanophytum codringtonii</i> (Rech. f.) Podlech	Afghanistan, Bamian, Band-e Amir, 3000 m, 28 Jun 1952, Volk 2742 (S)	ON100569	ON089790	ON089895	ON090086	ON090189 ON090284
<i>Ugamia angrenica</i> (Kirasch.) Pavlov	Kyrgyzstan, Pskemski ridge, 3000 m, 25 Aug 2006, Lazkov s.n. (W 2007-0014400)	ON100570	ON089791	ON089896	ON090087	ON090190 ON090285
<i>Ursinia anthemoides</i> (L.) Poir.	South Africa, Cape Province, Namakwaland Div., Kamieskroon, 800–1000 m, 12 Sep 1993, Strid & Strid 37382 (S)	AM774473	ON089792	ON089897	ON090088	ON090286
<i>Ursinia nana</i> DC.	Lesotho, Thaba-Taeka Province, Malibamatso river near Paray, 29°29'52"S, 28°39'04"E, 2928 CB, 25 Nov 1997, Boucher 6232 (S)					ON090191
<i>Vogelia microphylla</i> (DC.) Oberpr. & Sonboli	Spain, Córdoba, Comarca de Los Pedroches, Belalcázar – Sta. Eufemia, 510 m, 25 Oct 2016, Vogt 17566 & Prem-Vogt (B 10 0673627)	ON100571	ON089793	ON089898	ON090089	ON090192 ON090287
<i>Waldheimia tridactylites</i> Kar. & Kir.	India, Ladakh, Jammu & Kashmir, Ladakh, Likir Phulu, S-face, high altitude dry rocky slopes, 34°20'N, 77°15'E, 4600 m, 8 Aug 1999, Beck 208 (MSB)	ON100572				
<i>Waldheimia tridactylites</i> Kar. & Kir.	Kazakhstan, jugum Alatau Transiliensis, systema fl. Almaatinka Malaja, in morenis glaciei Tujuksu, 28 Aug 1963, Filatova & Vassiljeva 4865 (S)				ON090090	ON090193 ON090288

Taxa	Source and voucher data		GenBank accession number						
	ITS	ETS	<i>ndhF</i>	<i>trnL-trnF</i>	DSP	VIP5	NPF3.1		
<i>Xylanthemum paleaceum</i> (Podlech) Oberpr. & Vogt ("Xylanthemum <i>paradoxum</i> " Podlech, in sched.) (S)	ON100573	ON089794	ON089988	ON089899	ON090091	ON090194	ON090289		
Outgroup taxa									
<i>Abrotanella emarginata</i> (Gaudich.) Cass. (<i>Senecioneae</i>)	EF538143		AJ012679	EF538089					
<i>Calendula arvensis</i> L. (<i>Calenduleae</i>)	GU818507		GU817838	GU817981					
<i>Doronicum pardalianches</i> L. (<i>Doronicaceae</i>)	EF538188		EF537962	EF538098					
<i>Eupatorium serotinum</i> Michx. (<i>Eupatorieae</i>)	AB032050		GU817857	GU818001					
<i>Helianthus tuberosus</i> L. (<i>Heliantheae</i>)	AF047953		GU817867	GU818008					
<i>Helichrysum stoechas</i> (L.) Moench (<i>Gnaphaliteae</i>)	AY445193		GU817868	GU818009					
<i>Inula viscosa</i> L. (= <i>Dittrichia</i> <i>viscosa</i> (L.) Greuter) (<i>Inuleae</i>)	GU818558		GU817874	GU818017					
<i>Symphotrichum novae-angliae</i> (L.) G. L. Nesom (<i>Astereae</i>)	GU818492		GU817797	GU817970					
<i>Tagetes</i> sp. (<i>Tageteae</i>)	GU818722		GU817934	GU818097					

Supplemental content online

See <https://doi.org/10.3372/wi.52.52108>

Online Fig. S1. Phylogeny (gene tree) of *Compositae–Anthemideae* based on nDNA *DSP* sequences with subtribal assignment according to Oberprieler & al. (2007, 2019), Sonboli & Oberprieler (2010) and Sonboli & al. (2012). Clade support values (posterior probabilities > 0.9) are indicated.

Online Fig. S2. Phylogeny (gene tree) of *Compositae–Anthemideae* based on nDNA *VIP5* sequences with subtribal assignment according to Oberprieler & al. (2007, 2019), Sonboli & Oberprieler (2010) and Sonboli & al. (2012). Clade support values (posterior probabilities > 0.9) are indicated.

Online Fig. S3. Phylogeny (gene tree) of *Compositae–Anthemideae* based on nDNA *NPF3.1* sequences with subtribal assignment according to Oberprieler & al. (2007, 2019), Sonboli & Oberprieler (2010) and Sonboli & al. (2012). Clade support values (posterior probabilities > 0.9) are indicated.

Online Resource S1. Alignment of the plastid gene *ndhF* and the intergenic spacer region *trnL-trnF*, including gap-coding information.

Online Resource S2. Alignment of the nuclear ribosomal repeat (nrDNA ITS), without gap-coding information.

Online Resource S3. Alignment of the single-copy nuclear marker *DSP*, including gap-coding information.

Online Resource S4. Alignment of the single-copy nuclear marker *VIP5*, without gap-coding information.

Online Resource S5. Alignment of the single-copy nuclear marker *NPF3.1*, without gap-coding information.

Online Resource S6. Concatenated alignment of the total dataset, comprising markers *DSP*, *VIP5*, *NPF3.1*, ITS+ETS, *ndhF* and *trnL-trnF*, without gap-coding information.

Willdenowia

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