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CHRISTOPH OBERPRIELER

On the taxonomic status and the phylogenetic relationships of some unispecific Mediterranean genera of *Compositae-Anthemideae*
II. *Daveaua*, *Leucocyclus* and *Nananthea*

Abstract

Oberprieler, C.: On the taxonomic status and the phylogenetic relationships of some unispecific Mediterranean genera of *Compositae-Anthemideae* II. *Daveaua, Leucocyclus* and *Nananthea.* – Willdenowia 34: 341-350. – ISSN 0511-9618; © 2004 BGBM Berlin-Dahlem.

Sequences of the nrDNA internal transcribed spacer (ITS) region were analysed for 113 representative species of 59 genera of *Compositae-Anthemideae* to ascertain the systematic position of the three unispecific Mediterranean genera *Daveaua, Leucocyclus* and *Nananthea. Daveaua anthemoides* is found to be a member of a well supported clade of genera around the closely-knit *Leucanthemum* group, being a candidate (together with *Heteromera* and *Otospermum*) for a sister-group of this assemblage. For *Leucocyclus formosus,* which was considered to be closely related to *Anacyclus* due to its dorsiventrally flattened achenes, a position close to or even among representatives of *Achillea* is demonstrated, corroborating alleged relationships suggested by the flavonoid complements of these genera. *Nananthea perpusilla,* hitherto considered to be close to *Anthemis* due to its tetrasporic embryo sac development, is found to be more closely related to *Tripleurospermum,* which also shares the tetrasporic embryo sac and the indumentum of basifixed hairs.

Introduction

The present paper forms the continuation of a recent publication on three other unispecific genera (i.e. *Brocchia, Endopappus* and *Heliocauta;* Oberprieler 2004). It aims at a completion of the sequence information from the internal transcribed spacer region of the nuclear ribosomal repeat (nrDNA ITS) for all genera of *Compositae-Anthemideae* from the Mediterranean and adjacent Eurasian regions (Euro+Med area; Greuter & al. 2003) that form a monophyletic group characterised by a distinctive 15-17 bp deletion in ITS2 (Francisco-Ortega & al. 1997, Oberprieler & Vogt 2000, Oberprieler 2001, 2002). With the present publication on the last three remaining, unispecific genera *(Daveaua, Leucocyclus, Nananthea)* and an inclusion of a number of new sequences for the larger genera of the tribe in the area, a comprehensive discussion of the taxon-

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omy of the Mediterranean *Anthemideae* and their evolutionary history is facilitated. While the present paper focuses on the taxonomic implications, a further publication (Oberprieler, in prep.) will concentrate on the temporal and spatial diversification of this plant group as derived from sequence divergence rates and molecular clock reconstructions.

The genus *Daveaua* Willk. ex Mariz (1891) was based on the annual herb *D. anthemoides* Mariz from SW Europe (Spain, Portugal) and NW Africa (Morocco). It is characterised by glabrous, alternate and pinnatisect leaves, and solitary, pedunculate and radiate capitula with involucral bracts having dark brown, membranous margins. The receptacle is conical and epaleate, the white ray florets are either female and fertile or sterile, and the yellow disc florets are hermaphrodite with a regularly 5-lobed corolla. While the ray floret achenes are dorsiventrally flattened and bear, besides 3 adaxial ribs, lateral wings projecting into apical teeth, the disc floret achenes are obovoid, circular in cross-section, with 5 equal ribs and a marginally rounded apex. The pericarp is covered with myxogenic cells and has 3-5 resin sacs in the apical portion of the ribs.

Leucocyclus Boiss. was based by Boissier (1849) on the sole species *L. formosus* Boiss., a perennial herb endemic to Turkey with an indumentum of basifixed hairs. The species is characterised by alternate, 2-pinnatisect and vermiform leaves, solitary, long-pedunculate, radiate capitula and involucral bracts sometimes with dark brown tips. The receptacle is flat to convex and bears linear-elliptical receptacular scales. The ray florets are female and fertile; their corolla consists of an oblong to subrotund limb and a flattened tube, which is saccate basally and clasps the apex of the achene both adaxially and abaxially. The hermaphrodite, yellow disc florets also basally clasp the apex of the dorsiventrally flattened achenes. While the pericarp is thin on both faces, the lateral ribs are thick, sclerenchymatous and wing-like.

Nananthea DC. was based by Candolle (1838) on the small annual herb *Chrysanthemum perpusillum* Loisel., which is characterised by glabrous (rarely with some basifixed hairs), alternate, 3-5-lobed and slightly succulent leaves. The capitula are very small (only up to 7 mm in diameter), solitary, pedunculate, radiate or disciform. The receptacle is conical and epaleate. The ray florets are female, fertile and have a white (sometimes reduced) limb, while the disc florets are hermaphrodite and have a yellow, 4-lobed corolla. The achenes are obovoid, circular in cross-section and have c. 8 inconspicuous ribs; the achene apex is marginally rounded, the pericarp bears large myxogenic cells but no resin sacs or ducts. The species is endemic to the southern coasts of Corsica and the northern and western shores of Sardinia where it grows close to the sea.

Material and methods

Plant material. – One hundred and thirteen representatives from 59 genera of *Compositae-Anthemideae* were included in the present analysis. Sequence information for most of these taxa came from former publications (Oberprieler & Vogt 2000, Oberprieler 2001, 2002, 2004) and from published and unpublished EMBL/GenBank/DDBJ accessions (Table 1), while nrDNA ITS sequences for 18 taxa are new to science and published here for the first time. Following results of Watson & al. (2000), I used *Ursinia anthemoides* (L.) Poir. as outgroup in the present analysis.

DNA isolation, PCR amplification, sequencing. – DNA was extracted from herbarium specimens or silica gel dried leaf material using Qiagen DNeasy Plant Kit (Qiagen). PCR amplification followed the protocols given in Oberprieler & Vogt (2000). Amplification products were purified with a Qiaquick PCR cleaning column and filtration kit (Qiagen) or with Montage PCR Centrifugal Filter Devices (Millipore). Cycle sequencing of purified PCR products was performed using the CEQ Dye Terminator Cycle Sequencing Quick Start Kit (Beckman Coulter) and sequences were analysed on a CEQ 8000 automated sequencer (Beckman Coulter). All new nrDNA ITS sequences were submitted to the EMBL sequence data bank (Table 1).

Sequence alignment. – Sequences were aligned using CLUSTAL W (Thompson & al. 1994) and the alignment subsequently corrected manually. The alignment is deposited as electronic supplement at http://www.bgbm.org/bgbm/library/publikat/willd34/oberprieler-2.pdf.

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Table 1. List of taxa and sources of plant material analysed in addition to those given by Oberprieler (2004). Bold type denotes sequences new to science. Unless otherwise stated, the cited vouchers are (only) in the herbarium of the author; DB = DNA bank numbers at B.

Taxon	Accession	EMBL/GenBank/DDBJ accession number ITS1	ITS2
Achillea biebersteinii C. Afan.	Armenia, Echmiadzin, Zvarthnots, 11.6.2002, *Oberprieler 10031* (B-DB179)	AJ864573	AJ864593
A. filipendulina Lam.	Armenia, Urtsadzor - Azizkend, 20.6.2002, *Oberprieler 10115* (B-DB176)	AJ864574	AJ864594
A. tenuifolia Lam.	Armenia, Vedi, 18.6.2002, *Oberprieler 10094* (B-DB175)	AJ864575	AJ864595
A. vermicularis Trin.	Armenia, Yeghvard, 29.6.2002, *Oberprieler 10185* (B-DB178)	AJ864576	AJ864596
Anthemis alpestris (Hoffmanns. & Link) R. Fern.	Oberprieler (2001)	AJ312786	AJ312815
A. ammanthus Greuter	Oberprieler (2001)	AJ312800	AJ312829
A. arvensis subsp. *incrassata* (Loisel.) Nyman	Oberprieler (2001)	AJ312777	AJ312806
A. austroiranica Rech. f. & al.	Oberprieler (2001)	AJ312798	AJ312827
A. carpatica Willd.	Oberprieler (2001)	AJ312787	AJ312816
A. cotula L.	Oberprieler (2001)	AJ312794	AJ312823
A. gayana Boiss.	Oberprieler (2001)	AJ312799	AJ312828
A. gharbensis Oberprieler	Oberprieler (2001)	AJ312778	AJ312807
A. hyalina DC.	Oberprieler (2001)	AJ312779	AJ312808
A. maritima L.	Oberprieler (2001)	AJ312788	AJ312817
A. melampodina Delile	Oberprieler (2001)	AJ312780	AJ312809
A. orbelica Pančić	Oberprieler (2001)	AJ312790	AJ312819
A. pedunculata Desf.	Oberprieler (2001)	AJ312791	AJ312820
A. peregrina L.	Oberprieler (2001)	AJ312781	AJ312810
A. plutonia Meikle	Oberprieler (2001)	AJ312793	AJ312822
A. pseudocotula Boiss.	Oberprieler (2001)	AJ312795	AJ312824
A. rigida Boiss. & Heldr.	Oberprieler (2001)	AJ312782	AJ312811
A. tigreensis J. Gay ex A. Rich.	Oberprieler (2001)	AJ312796	AJ312825
A. urvilleana (DC.) Sommier & Caruana	Oberprieler (2001)	AJ312783	AJ312812
A. zaianica Oberprieler	Oberprieler (2001)	AJ312784	AJ312813
Cota tinctoria (L.) J. Gay	Oberprieler (2001)	AJ312802	AJ312831
C. triumfetti (L.) J. Gay	Oberprieler (2001)	AJ312803	AJ312832
Daveaua anthemoides Mariz	Morocco, Chefchaouene - Ouezzane, 14.5.1989, *Podlech 46709* (MSB)	AJ864577	AJ864597
Leucocyclus formosus Boiss.	Turkey, Taurus, Bulgar Dagh, 9.7.1853, *Kotschy 65* (M)	AJ864578	AJ864598
Nananthea perpusilla (Loisel.) DC.	Italy, Sardinia, 9.-20.4.1966, *Merxmüller 21023 & Oberwinkler* (M)	AJ864579	AJ864599
Pentzia monodiana Maire	Tschad, Tibesti, Trou au Natron, 18.12.1964, *Scholz 446* (B)	AJ864580	AJ864600
Soliva stolonifera (Brot.) Sweet	Spain, Tenerife, Anaga, Chinobre, 28.3.1999, *Oberprieler 9931*	AJ864581	AJ864601
Tanacetum abrotanifolium (L.) Druce	Armenia, Geghard, 19.6.2002, *Oberprieler 10108* (B-DB171)	AJ864582	AJ864602
T. balsamita L.	Armenia, Sevan - Dilijan, 15.6.2002, *Oberprieler 10073* (B-DB168)	AJ864583	AJ864603

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Taxon	Accession	EMBL/GenBank//DDBJ accession number	
		ITS1	ITS2
T. canescens DC.	Armenia, Vedi, 18.6.2002, *Oberprieler 10088* (B-DB173)	AJ864584	AJ864604
T. chiliophyllum (Fisch. & C. A. Mey.) Sch. Bip.	Armenia, Yeghegnadzor, Gnishik, 26.6.2002, *Oberprieler 10162* (B-DB174)	AJ864585	AJ864605
T. cinerariifolium (Trev.) Sch. Bip.	Francisco-Ortega & al. (2001)	AF155253	AF155290
T. coccineum (Willd.) Grierson	Armenia, Sevan - Tsovagyugh, 12.6.2002, *Oberprieler 10045* (B-DB167)	AJ864586	AJ864606
T. ferulaceum (Sch. Bip.) Sch. Bip.	Francisco-Ortega & al. (2001)	AF155255	AF155292
T. huronense Nutt.	Francisco-Ortega & al. (2001)	AF155256	AF155293
T. macrophyllum (Waldst. & Kit.) Sch. Bip.	Francisco-Ortega & al. (2001)	AF155257	AF155294
T. microphyllum DC.	Francisco-Ortega & al. (2001)	AF155258	AF155295
T. oshanahanii Marrero Rodr.	Francisco-Ortega & al. (2001)	AF155259	AF155296
T. parthenium (L.) Sch. Bip.	Armenia, Dilijan-Ijevan, 13.6.2002, *Oberprieler 10060* (B-DB170)	AJ864587	AJ864607
T. pinnatum Boiss.	Armenia, Urtsadzor - Azizkend, 20.6.2002, *Oberprieler 10116* (B-DB172)	AJ864588	AJ864608
T. pseudoachillea Winkler	Francisco-Ortega & al. (2001)	AF155260	AF155300
T. ptarmiciflorum (Webb) Sch. Bip.	Francisco-Ortega & al. (2001)	AF155262	AF155298
T. punctatum (Desr.) Grierson	Armenia, Yeghegnadzor, Eghegis, 27.6.2002, *Oberprieler 10164* (B-DB169)	AJ864589	AJ864609
T. vulgare L.	Francisco-Ortega & al. (2001)	AF155263	AF155299
Tripleurospermum caucasicum (Willd.) Hayek	Armenia, Aragats, 30.6.2002, *Oberprieler 10192* (B-DB162)	AJ864590	AJ864610
T. sevanense (Manden.) Pobed.	Armenia, Vajk - Gerger, 25.6.2002, *Oberprieler 10148* (B-DB164)	AJ864591	AJ864611
T. transcaucasicum (Manden.) Pobed.	Armenia, Sevan - Tsovagyugh, 17.6.2002, *Oberprieler 10043* (B-DB165)	AJ864592	AJ864612

Phylogenetic reconstructions. – Owing to the large scale of the present data set with 113 aligned sequences, I have omitted the time-consuming phylogenetic reconstructions based on maximum parsimony (MP) and maximum likelihood (ML). Instead, the data set was analysed with the model-based Bayesian Inference (BI) approach (Lewis 2001), which showed congruence over large parts of the resulting topologies and of clade support values with MP and/or ML analyses in the previous publication on Mediterranean *Anthemideae* (Oberprieler 2004). The program MODELTEST version 3.06 (Posada & Crandall 1998) was used to find the model (among the 56 models tested) that best fits the underlying sequence information. This resulted in the acceptance of the model of Tamura & Nei (1993) with a gamma distribution of substitution rates over the sites ($TrN + \Gamma$), the base frequencies being $freqA = 0.2722$, $freqC = 0.2026$, $freqG = 0.2095$ and $freqT = 0.3157$, a gamma distribution shape parameter of $\alpha = 0.6647$ and a substitution rate matrix of $R[A\text{-}C] = R[A\text{-}T] = R[C\text{-}G] = R[G\text{-}T] = 1.0$, $R[A\text{-}G] = 2.3549$ and $R[C\text{-}T] = 4.9650$.

These parameters were used in a Bayesian inference (BI) approach to phylogeny reconstruction with the software programme MRBAYES version 2.01 (Huelsenbeck & Ronquist 2001a-b). Four Metropolis-coupled Markov chain Monte Carlo (MCMC) chains with incremental heating temperature of 0.2 were run for 501 000 generations and sampled every 10th generation. The

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burn-in period was determined graphically, and the first 6000 of the 50 100 trees were discarded. Estimation of tree topology and posterior probabilities of clades were based on the remaining 44 100 trees.

Results

The alignment of all 113 nrDNA ITS sequences is 534 bp long (286 bp for ITS1 and 248 bp for ITS2, respectively) with 359 variable positions including 265 parsimony informative substitutions. The Bayesian analysis yielded the tree depicted in Fig. 1. The three unispecific Mediterranean genera under study are nested within a strongly supported (0.99 posterior probability [PP]) clade of genera with a Mediterranean and/or Eurasian centre of distribution (from *Anthemis maritima* to *Phalacrocarpum oppositifolium)* and a 17 bp deletion in ITS2. The only exception to this is *Brocchia cinerea,* which also shares the deletion but is not part of the strongly supported clade and appears merely as the sister group to it (see also Oberprieler 2004 for discussion). Additionally, there is also another monophyletic group characterised by a deletion but without any considerable support from the Bayesian analysis: it comprises the taxa between *Chrysanthoglossum deserticola* and *Lonas annua* in the present tree and shows the synapomorphy of a 5 bp deletion in the *trn*L-*trn*F intergenic spacer of the chloroplast genome (compare Oberprieler 2004).

Daveaua anthemoides is found as a member of a strongly supported clade (1.00 PP) between *Chrysanthoglossum deserticola* and *Daveaua.* Low support values for some of the subclades, however, render its phylogenetic relationships unsettled. The same is true for *Leucocyclus formosus,* which is found in close relationship with the five representatives of the genus *Achillea* in the present analysis. The position of *Nananthea perpusilla* as sister to the four representatives of the genus *Tripleurospermum,* in contrast, receives strong statistical support (1.00 PP).

Discussion

Daveaua Willk. ex Mariz – The phylogenetic position of *Daveaua anthemoides* in the present analysis is well settled. It is found to be a member of a clade including closely related genera of the so-called *Leucanthemum* group (i.e. from *Chrysanthoglossum* to *Chlamydophora*) with high statistical support (1.00 PP). However, its position within this clade is not solved because it seems not to be a member of the subclade of *Chrysanthoglossum* through *Coleostephus* (1.00 PP) nor of the subclade of *Heteromera* and *Chlamydophora* (0.95 PP).

In contrast to the genera united in the *Leucanthemum* group (i.e. *Chrysanthoglossum* through *Coleostephus* plus *Chlamydophora*), which are characterised by the possession of specialised achene walls with vallecular resin ducts and vallecular vascular strands (all of them members of a broader subtribe *Leucantheminae* sensu Bremer & Humphries 1993), *Daveaua* exhibits similarities in achene anatomy with *Heteromera* and *Otospermum* (all three genera being members of subtribe *Matricariinae* sensu Bremer & Humphries 1993), because of 5-ribbed achenes with vascular strands in the ribs (Reitbrecht 1974, Oberprieler & al. in press). Additionally, as in *Heteromera,* achenes of *Daveaua* are furnished with resin ducts in the apical portion of the ribs and the achenes of the ray florets are dorsiventrally flattened (Giroux 1930). The latter was considered as a synapomorphy for the sister-group relationship of the two genera by Bremer & Humphries (1993).

It is obvious from previous molecular analyses of the tribe (Watson & al. 2000, Oberprieler & Vogt 2000, Francisco-Ortega & al. 1997, 2001, Oberprieler 2001, 2002, 2004) that most of the subtribes erected by Bremer & Humphries (1993) on morphological, anatomical, cytological and phytochemical evidence are far from being monophyletic. This appears particularly obvious for their subtribe *Matricariinae,* whose members are found scattered all over the present phylogenetic tree, with the southern hemisphere genera *(Cotula, Soliva, Leptinella, Cymbopappus, Pentzia)* close to the base of the tree and the northern hemisphere genera *(Brocchia, Lonas, Endopappus, Aaronsohnia, Daveaua, Heteromera, Otospermum, Matricaria, Tripleurospermum)* throughout the clade

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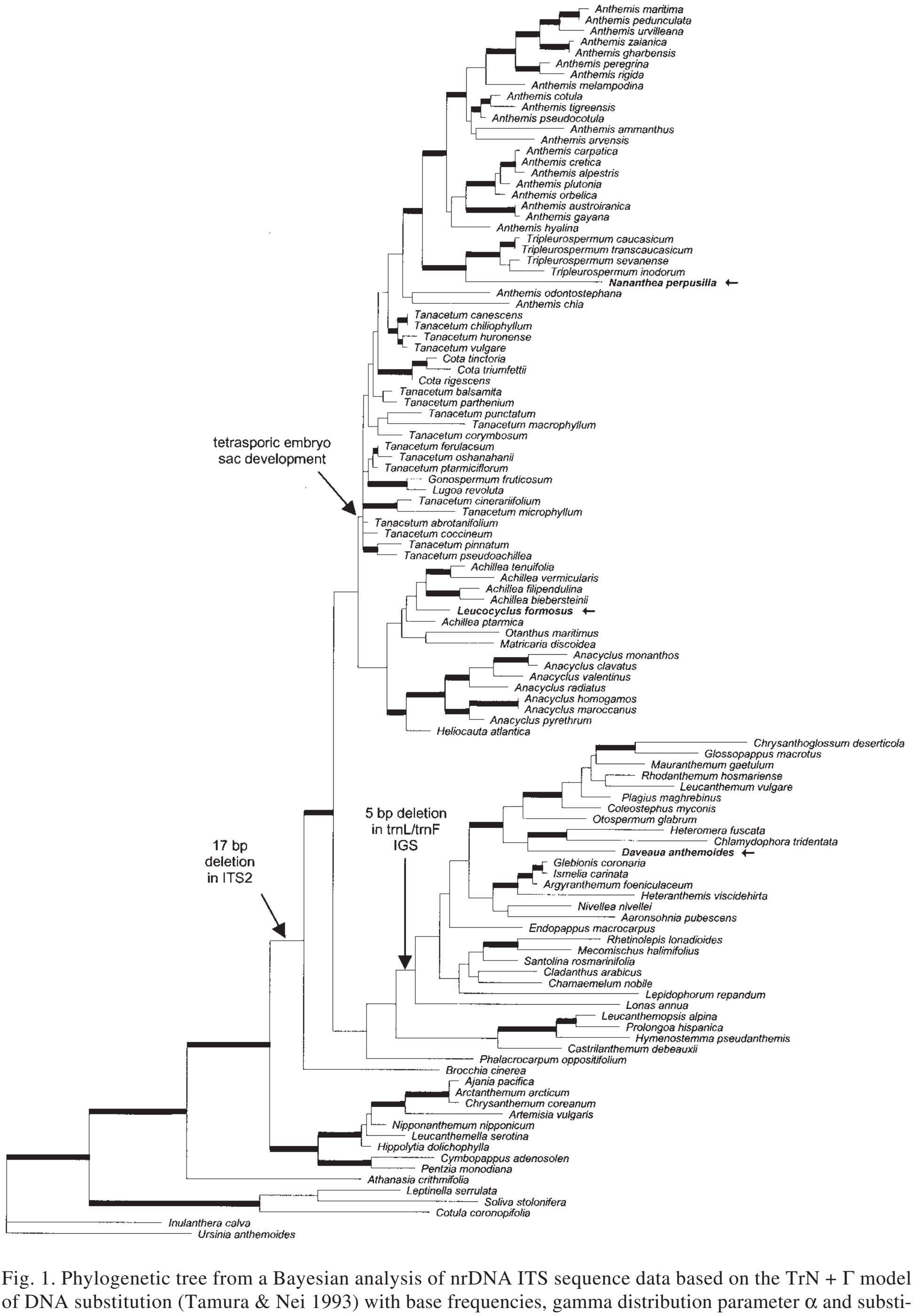

Fig. 1. Phylogenetic tree from a Bayesian analysis of nrDNA ITS sequence data based on the TrN + Γ model of DNA substitution (Tamura & Nei 1993) with base frequencies, gamma distribution parameter α and substitution rate matrix given in the text. Tree topology and posterior probabilities of clades were based on 44 100 trees from a MCMC chain run for 501 000 generations. Clades receiving posterior probabilities larger than 0.95 are shown with bold lines.

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characterised by the 17bp deletion in ITS2. The subtribe, therefore, appears to be highly polyphyletic and its alleged synapomorphies (achenes with myxogenic cells on abaxial surface and on ribs of the adaxial surface, corona adaxially long) extremely homoplasious.

The strong molecular support for the clade *Chrysanthoglossum* through *Daveaua* on the one hand and the strong evidence for the monophyly of the *Leucanthemum* group of genera from achene anatomy on the other hand, along with the still unsettled sister-group relationships of *Otospermum* and *Daveaua* and the equivocal sister-group relationships of *Heteromera* (sister to *Chlamydophora* according to nrDNA ITS sequence information, sister to *Daveaua* according to ray floret achene morphology) may indicate that *Daveaua, Heteromera* and *Otospermum* are a paraphyletic group that gave rise to the very distinct *Leucanthemum* group of genera with its specialised achene anatomy. For the time being, there seems to be not enough information available to decide on the sister genus of this group among the three candidates.

The transition between achenes with vascular strands and resin ducts in their ribs (as in *Daveaua, Heteromera* and *Otospermum)* and achenes with strands and ducts in the valleys between ribs (as in the *Leucanthemum* group of genera) may seem rather improbable, but there are observations in other groups of *Anthemideae* that this transition is rather easily realised. In the genus *Anthemis,* most of the species are characterised by achene walls in which the external ribs coincide with those of the mesocarpic sclerenchyma cylinder and (as a consequence) with the vascular strands in the mesocarpic ribs. However, in *Anthemis arvensis* and the close related *A. ruthenica* and *A. auriculata* the external ribs alternate with the ribs of the mesocarpic sclerenchyma cylinder due to the excessive growth of mesocarpic tissue above the valleys of the sclerenchymatic cylinder (Oberprieler 1998). The same process may have easily occurred at the transition between the normal achene type and the specialised one of the *Leucanthemum* group. The observation of Giroux (1930) that achenes of disc florets of *Otospermum glabrum* exhibit several cell layers of vallecular palisade parenchyma while a similar tissue is missing in the mesocarp of the ribs may point in this direction.

Leucocyclus Boiss. – In their cladistic analysis of *Compositae-Anthemideae* based on morphological, anatomical, phytochemical and cytological data, Bremer & Humphries (1993) considered the unispecific *Leucocyclus* as a member of their subtribe *Achilleinae,* which was based on the synapomorphies of paleate receptacles, at maturity thickened disc corolla tubes basally clasping the achene apex, and the lack of a corona in the achenes of both ray and disc florets. Within this subtribe, the authors found strong evidence for a sister-group relationship of *Leucocyclus* and *Anacyclus* because of the joint occurrence of laterally winged achenes in both genera (Bremer & Humphries 1993). The same was shown by Humphries (1979) who used *Leucocyclus* as an outgroup in a morphological cladistic study of the species of *Anacyclus.* The present analysis based on nrDNA ITS sequence variation shows in accordance with a former analysis (Oberprieler & Vogt 2000) that the subtribe *Achilleinae* sensu Bremer & Humphries (1993) is not monophyletic. While some genera *(Chamaemelum, Cladanthus, Mecomischus, Santolina, Rhetinolepis)* are found nested within a clade characterised by a 5 bp deletion in the cpDNA *trn*L-*trn*F intergenic spacer region, the rest of the subtribe *(Achillea, Anacyclus, Otanthus)* lacks this deletion and seems to be more closely related to the clade of genera with a tetrasporic embryo sac development *(Anthemis, Tripleurospermum, Nananthea, Cota, Tanacetum).* Though information on cpDNA *trn*L-*trn*F IGS sequence variation lacks for *Leucocyclus formosus,* ITS data point to the close relationship with the latter group of *Achilleinae* genera.

Within this group, achene morphological and anatomical characters stressed by Humphries (1979) and Bremer & Humphries (1993) support a close relationship between *Leucocyclus* and *Anacyclus*. However, there is also some evidence for a close relationship between *Leucocyclus* and *Achillea.* First, the leaves of *Leucocyclus formosus* are almost vermiform, with the small subopposite segments divided into spinulose-dentate lobes. In this respect they are more similar to leaves in some *Achillea* species (especially of *A.* sect. *Arthrolepis* and *Santolinoideae;* cf. Valant-Vetschera & Kästner 2000) than to all species of *Anacyclus* (cf. Humphries 1979). Sec-

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ond, it was demonstrated (Valant-Vetschera 1982) that both the tendency to produce C-glycosylflavones and 6-substituted polymethoxy flavones / flavonols unite *Achillea* and *Leucocyclus,* while the flavonoid complement of *Anacyclus* differs largely in this respect. Our present analysis supports the second scenario that *Leucocyclus* is more closely related to *Achillea* or parts of this genus than is to *Anacyclus:* Both the monophyly of *Anacyclus* and the sister-group relationship of this genus with the NW African endemic *Heliocauta* receive good statistical support in terms of posterior probabilities in the Bayesian analysis, while *Leucocyclus* is found nested within the five representatives of *Achillea* (however, with no statistical support: 0.64 PP). Therefore, while a sister-group relationship of *Leucocyclus* with the clade of *Heliocauta* and *Anacyclus* could not be ruled out completely, the above mentioned leaf morphological and phytochemical evidence may be a strong argument for a position of *Leucocyclus* close to (if not within) the genus *Achillea.* Consequently, the fruit compression typical for *Anacyclus* and *Leucocyclus* may have evolved in parallel in the two genera, as it has done in a number of different groups of the *Compositae-Anthemideae* (Humphries 1979, Bremer & Humphries 1993, Oberprieler & al. in press).

Nananthea DC. – Originally described as a member of the then very broadly defined genus *Chrysanthemum* and shortly afterwards as a member of the genus *Cotula* [*C. pygmaea* Poir.], this delicate, somewhat succulent, small annual was considered to belong to an independent genus by Candolle (1838). As in the equally unispecific genus *Brocchia,* the occurrence of 4-lobed tubular florets was considered to indicate a close relationship of *Nananthea* with the southern hemisphere genus *Cotula* and its segregates *Leptinella* and *Soliva.* However, as achene anatomical studies (Bruhl & Quinn 1990, Oberprieler unpubl.) and cladistic analyses based on morphology (Bremer & Humphries 1993) have shown, the similarities of *Nananthea perpusilla* with representatives of *Cotula* are very superficial and no synapomorphy is shared by the two entities. Following a suggestion by Reitbrecht (1974), Bremer & Humphries (1993) proposed the provisional placement of *Nananthea* as a sister of *Anthemis* based on the shared apomorphy of a tetrasporic embryo sac development. They even speculated about a probable placement within the latter genus because of its similarities with some deviating *Anthemis* species, such as the so-called *Ammanthus* group of the Aegean region.

The present analysis based on nrDNA ITS sequence variation definitively excludes a close relationship of *Nananthea perpusilla* with *Cotula* and its neighbour genera. While the latter are found close to the base of the tree among other representatives of *Anthemideae* of the southern hemisphere, *Nananthea* is a member of the monophyletic group of Mediterranean and western Eurasian genera characterised by the 17 bp deletion in ITS2 and is placed with high statistical support as a sister-group to the genus *Tripleurospermum* (1.00 PP). The same high statistical support receives the sister-group relationship of the clade of *Nananthea* and *Tripleurospermum* with the clade of *Anthemis* s.str. (i.e. without the deviating *A. odontostephana* and *A. chia* and those of *A.* subg. *Cota,* see Oberprieler 2001 for discussion).

All genera known to have a tetrasporic embryo sac development in the *Compositae-Anthemideae* (besides *Heteranthemis viscidehirta,* which is strongly supported as a member of the *Chrysantheminae* sensu Bremer & Humphries 1993 comprising *Argyranthemum, Glebionis, Ismelia* and *Heteranthemis*) form a clade in the present analysis which receives, however, no statistical support. Within this clade of *Tanacetum* (including also *Gonospermum* and *Lugoa*), *Cota, Anthemis, Tripleurospermum* and *Nananthea,* the sister-group relationship of the latter two is furthermore supported by the possession of basifixed hairs in contrast to medifixed or stellate hairs in the other genera (Oberprieler & al. in press). Therefore, though achenes of *Nananthea* and *Tripleurospermum* are very different from each other (those of the former genus being circular in cross-section with c. 8 ribs and bearing myxogenic cells but no resin sacs or ducts, while those of the latter are conspicuously triquetrous and furnished with large resin sacs) there is some morphological support for a closer relationship between the two entities. Further information from additional molecular markers will show whether this astonishing sister-group relationship is really unequivocal.

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Literature cited

Boissier, E. 1849: Diagnoses plantarum orientalium novarum **11.** – Paris.

Bremer, K. & Humphries, C. J. 1993: Generic monograph of the *Asteraceae-Anthemideae*. – Bull. Brit. Mus. (Nat. Hist.), Bot. **23:** 71-177.

Bruhl, J. J. & Quinn, C. J. 1990: Cypsela anatomy in the *'Cotuleae' (Asteraceae-Anthemideae)*. – Bot. J. Linn. Soc. **102:** 37-59.

Candolle, A.-P. de 1838: Prodromus systematis naturalis regni vegetabilis **6.** – Genève.

Francisco-Ortega, J., Barber, J. C., Santos-Guerra, A., Febles-Hernández, R. & Jansen, R. K. 2001: Origin and evolution of the endemic genera of *Gonospermineae (Asteraceae: Anthemideae)* from the Canary Islands: Evidence from nucleotide sequences of the internal transcribed spacers of the nuclear ribosomal DNA. – Amer. J. Bot. **88:** 161-169. [CrossRef]

— , Santos-Guerra, A., Hines, A. & Jansen, R. K. 1997: Molecular evidence for a Mediterranean origin of the Macaronesian endemic genus *Argyranthemum (Asteraceae)*. – Amer. J. Bot. **84:** 1595-1613. [CrossRef]

Giroux, M. 1930: Sur la carpologie de quelques Composées nord-africaines. – Bull. Soc. Hist. Nat. Afrique N. **21:** 161-188.

Greuter, W., Oberprieler, C. & Vogt, R. 2003: The Euro+Med treatment of *Anthemideae (Compositae)* – generic concepts and required new names. – Willdenowia **33:** 37-43.

Huelsenbeck, J. P. & Ronquist, F. 2001a: MRBAYES: Bayesian inference of phylogenetic trees. – BioInformatics **17:** 754-755. [CrossRef]

— & Ronquist, F. 2001b: MRBAYES: Bayesian inference of phylogenetic trees. Computer software available at http://brahms.biology.rochester.edu/software.html.

Humphries, C. J. 1979: A revision of the genus *Anacyclus* L. *(Compositae: Anthemideae)*. – Bull. Brit. Mus (Nat. Hist.), Bot. **7:** 83-142.

Lewis, P. O. 2001: Phylogenetic systematics turns over a new leaf. – Trends Ecol. Evol. **16:** 30-37. [CrossRef]

Mariz, J. de 1891: Subsdidios para o estudo da flora portugueza. – Bol. Soc. Brot. **9:** 144-243.

Oberprieler, C. 1998: The systematics of *Anthemis* L. *(Compositae, Anthemideae)* in W and C North Africa. – Bocconea **9:** 1-328.

— 2001: Phylogenetic relationships in *Anthemis* L. *(Compositae, Anthemideae)* based on nrDNA ITS sequence variation. – Taxon **50:** 745-762. [CrossRef]

— 2002: A phylogenetic analysis of *Chamaemelum* Miller *(Compositae, Anthemideae)* and related genera based upon nrDNA ITS and cpDNA *trn*L/*trn*F IGS sequence variation. – Bot. J. Linn. Soc. **138:** 255-273. [CrossRef]

— 2004: On the taxonomic status and the phylogenetic relationships of some unispecific Mediterranean genera of Compositae-Anthemideae. I. *Brocchia, Endopappus* and *Heliocauta*. – Willdenowia **34:** 39-57. [CrossRef]

— & Vogt, R. 2000: The position of *Castrilanthemum* Vogt & Oberprieler and the phylogeny of Mediterranean *Anthemideae (Compositae)* as inferred from nrDNA ITS and cpDNA *trn*L/*trn*F IGS sequence variation. – Pl. Syst. Evol. **225:** 145-170. [CrossRef]

— Vogt, R. & Watson, L. E. (in press): Tribe *Anthemideae* Cass. – In: Kadereit, J. W. (ed.), Families and genera of vascular plants – *Asteridae*. – Berlin, etc.

Posada, D. & Crandall, K. A. 1998: MODELTEST: testing the model of DNA substitution. Bioinformatics Application Note **14:** 817-818.

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Reitbrecht, F. 1974: Fruchtanatomie und Systematik der *Anthemideae (Asteraceae)*. – Thesis, Wien.

Tamura, K. & Nei, M. 1993: Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. – Molec. Biol. Evol. **10:** 512-526.

Thompson, J. D., Higgins, D. G. & Gibson, T. J. 1994: CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position specific gap penalties and weight matrix choice. – Nucleic Acids Res. **22:** 4673-4680. [CrossRef]

Valant-Vetschera, K. M. 1982: Flavonoid pattern and systematics of the genus *Leucocyclus*. – Phytochemistry **21:** 1067-1069. [CrossRef]

— & Kästner, A. 2000: Character analysis in *Achillea* sect. *Santolinoidea (Compositae-Anthemideae):* Part I. Leaf and floral morphology. – Edinburgh J. Bot. **57:** 189-208. [CrossRef]

Watson, L. E., Evans, T. M. & Boluarte, T. 2000: Molecular phylogeny and biogeography of tribe *Anthemideae (Asteraceae),* based on chloroplast gene *ndh*F. – Molec. Phylog. Evol. **15:** 59-69. [CrossRef]

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