



Multidisciplinary studies on *Achillea sensu lato* (Compositae-Anthemideae): new data on systematics and phylogeography

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Abstract

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On the basis of extended DNA sequences (nrITS, *cptrnL-F*) and other new evidence present knowledge on the differentiation of the northern hemisphere *Compositae-Anthemideae* genus *Achillea* in time and space is surveyed. Evidence is presented for a wide circumscription of the genus with 110-140 species. This includes the former unispecific genera *Otanthus* and *Leucocyclus*, which have originated from ancestors of the basalmost clade of *Achillea*, the xerophytic *A.* sect. *Babounya* s.l. (incl. sect. *Arthrolepis* and *Santolinoideae*). Maps show the predominantly SW Asian distribution of the section and its derivative, *A.* (sect. *Otanthus*) *maritima*, a psammophyte of the Mediterranean and Atlantic coasts. Through taxa from the Caucasus differentiation has proceeded from *A.* sect. *Babounya*-like ancestors to the Eurasian and more meso- and hygrophytic 2x members of *A.* sect. *Parmica* s.s. They are linked with 2x *A. asiatica* (*A. millefolium* agg.) by the hybrid 4x *A. alpina* agg., which has expanded across northern North America. *A.* sect. *Anthemioideae* s.l. consists of several distinct clades distributed in the mountain systems of NW Anatolia, the Balkans, Carpathians, Alps, Apennines and E Pyrenees. This section was formerly combined with *A.* sect. *Parmica* but is closer to the following section and may be polyphyletic. *A.* sect. *Achillea* includes closely related taxa with white and yellow(ish) ligulate flowers (the latter formerly separated as *A.* sect. *Filipendulinae*). Members of the section have differentiated from a centre of diversity in dry habitats of SE Europe, partly into uniform 2x species, partly into polymorphic and polyploid species groups. “Crown group” of the genus and section is *A. millefolium* agg., a strongly diversified polyploid complex. Its basal 2x species exhibit a vicarious and sometimes relic differentiation pattern. They are connected in a complex way to several parallel and reticulate lines of 4x, 6x and 8x taxa, which are partly very expansive. From 4x *A. asiatica*-like ancestors in E Siberia the 4x and 6x *A. borealis* has successfully radiated into many ecological niches in North America and 6x *A. millefolium* s.s. has become a cosmopolitan weed.

Key words: nr + cpDNA, polyploidy, ecological radiation, *Asteraceae*, *Leucocyclus*, *Otanthus*.

Introduction

Within the framework of a multidisciplinary research project the genus *Achillea* s.l. (*Compositae-Anthemideae*) is currently being studied with respect to morphology, karyology, phytochemistry, DNA polymorphisms, ecology and distribution in order to further clarify its evolution, systematics and nomenclature (Guo 2004, Guo & al. 2004, 2005, 2006, Ehrendorfer & Guo 2005,

Saukel & al. 2004). Here, we present additional DNA sequence data and conclusions relevant for the systematics and phylogeography of the genus. As a token of gratitude for decades of good friendship, stimulating scientific cooperation and remarkable scientific as well as organizational achievements, we dedicate this contribution to Prof. Werner Greuter at the occasion of his 68th birthday and his retirement from decades of successful activities as First Director of the Botanic Garden and Botanical Museum Berlin-Dahlem.

Members of *Achillea* L. are suffruticose to herbaceous perennials, entomophilous and predominantly outbreeding. The basic diploid karyotype ($2x, 2n = 18$) is quite uniform throughout the genus but polyploid taxa have originated in many clades, often $4x$, but sometimes $6x$ and even $8x$ taxa. The genus exhibits an extraordinary ecological amplitude and ranges from deserts to water-logged habitats and from sea coasts to the nival zone of high mountains. In its present circumscription and depending on species definition *Achillea* includes about 110-140 species, which are centred in SW Asia and SE Europe, have extended throughout the Mediterranean and Eurasia into North America, and *A. millefolium* L. s.s. even has become a cosmopolitan weed.

Material and methods

The DNA analyses (nrITS, *cptrnL-F*) presented here are based on 96 accessions from 77 different taxa or cytotypes. From the latter, 7 constitute the outgroup, 1 [*Anacyclus clavatus* (Desf.) Pers.] represents the sister genus and 69 are members of *Achillea* s.l. Taxa from all traditional sections of this genus and also from the former genera *Otanthus* Hoffmanns. & Link and *Leucocyclus* Boiss. (Ehrendorfer & Guo 2005) were studied. Many of the relevant provenances have already been listed with taxa names and authorities in Guo & al. 2004, 2005, 2006) and are not repeated in the present contribution. The following important additional samples have been studied (with references to genera, sections, species and subspecies, accepted and synonym names, authorities, accession numbers, localities, collectors and GenBank accession numbers); vouchers at the herbarium of the Institute of Botany, University of Vienna (WU):

Achillea sect. *Babounya* (DC.) O. Hoffm. s.l.:

A. formosa (Boiss.) Sch. Bip. subsp. *formosa* (\equiv *Leucocyclus formosus* Boiss. subsp. *formosus*) – access. no. 396: Turkey, C6 Adana, Amanus near Yarpuz, E. Hübl & al. 1978/7-21-1, DQ267610 (ITS), DQ267615 (*trnL-F*).

A. membranacea (Labill.) DC. [ad *A. sect. Arthrolepis* (Boiss.) Boiss.] – access. no. 397: Turkey, C7 Urfa, near Birecik transplanted into hort. bot. Vienna (no. A-1626), 14.7.1980, F. Sorger & K. Valant, DQ267611 (ITS), DQ267616 (*trnL-F*).

A. pseudoaleppica Hausskn. ex Hub.-Mor. [ad *A. sect. Santolinoidea* (DC.) Heimerl] – access. no. 400: Turkey, B7 Elaziğ, 19.7.1978, F. Ehrendorfer 68-14, DQ267612 (ITS), DQ267618 (*trnL-F*).

A. vermicularis Trin. [ad *A. sect. Santolinoidea* (DC.) Heimerl] – access. no. 399: hort. bot. Erevan 75/13, cult. hort. bot. Vienna (no. A-1321), 14.6.1976, K. Valant, DQ267613 (ITS), DFQ267618 (*trnL-F*).

A. sect. Achillea s.l.:

A. latiloba Ledeb. ex Nordm. – access. no. 414: Georgia, Adjara, Sari-chair, $141^{\circ}29'57''\text{N}$, $42^{\circ}31'46''\text{E}$, 2006 m, subalpine meadow, 18.7.2004, D. Kharazishvili, DQ267614 (ITS), DQ267619 (*trnL-F*)

For methods of DNA extraction, amplification, sequencing and phylogenetic analyses the reader is referred to Guo & al. (2004, 2005, 2006).

Results and discussion

The results of our phylogenetic reconstructions are based on nrITS and *cptrnL-F* DNA sequences from all genera considered close to *Achillea* and from all traditional sections of the genus with more than half of its species. They are shown in two strict consensus trees (Fig. 1 A+B) and two corresponding phylograms (Fig. 2A+B). The phylogenetic and phylogeographical interpretation

of these results and their systematic relevance for an improved taxonomic classification is presented in the following chapters.

1. Relationships and circumscription of *Achillea*

All available evidence, from research groups in Vienna (Guo 2004, Guo & al. 2004, 2005, 2006, Ehrendorfer & Guo 2005) as well as Regensburg (Oberprieler 2004, 2005), is in favour of a wide circumscription of the Linnean genus *Achillea*. This is relevant for rejecting recent efforts to revive the old concept of separating the genus *Ptarmica* Mill. from *Achillea* (e.g., Klokov & Krytzka 1984, Sytnik & Androshchuk 1984, Barkalov 1992). According to these authors, *Ptarmica* should include the taxa here classified under *Achillea* sect. *Ptarmica* (Mill.) W. D. J. Koch s.s. and sect. *Anthemoideae* (DC.) Heimerl. Such generic splitting of *Ptarmica* from *Achillea* is contradicted by several findings illustrated in Fig. 1-2. First, there are very close affinities between Caucasian members of *A.* sect. *Ptarmica* s.s. and *A.* sect. *Babounya* (DC.) O. Hoffm. s.l. [e.g., *A. biserrata* M. Bieb., *A. ptarmicifolia* (Willd.) Rupr. ex Heimerl]. Furthermore, and as discussed below, *A.* sect. *Anthemoideae* and *A.* sect. *Achillea* exhibit considerable overlap and the latter and *A.* sect. *Ptarmica* s.s. are linked by allopolyploid taxa (Guo & al. 2006).

Is it justified to maintain the traditional unispecific genera *Otanthus* Hoffmanns. & Link [*O. maritimus* (L.) Hoffmanns. & Link] and *Leucocyclus* Boiss. (*L. formosus* Boiss.)? Relevant taxa are included in the present data set and in our phylogenetic reconstructions together with members of *Achillea* s.s. In Fig. 1-2 these taxa are framed and listed under *Achillea* (Ehrendorfer & Guo 2005) and Fig. 3 shows their distribution. In the nrITS tree (Fig. 1A) *Otanthus* [as *A. maritima* (L.) Ehrend. & Y.-P. Guo] and *Leucocyclus* [as *A. formosa* (Boiss.) Sch. Bip.] are embedded in clade 2, in the *trnL-F* tree (Fig. 1B) in clade I. The obvious and exclusive affinities of these taxa with members of *A.* sect. *Babounya* s.l. are clearly demonstrated. For *Otanthus* (*A. maritima*) a relatively isolated position is indicated by its long branch in Fig. 2A and its separation in Fig. 1B and 2B. In contrast, *Leucocyclus* (*A. formosa*) always appears closely integrated among members of *A.* sect. *Babounya* s.l. This is most clearly shown in Fig. 2B, where these taxa are separated as a group from all others on a very long branch, demonstrating numerous changes in this region of the plastid DNA. The ITS data recently presented by Oberprieler (2004, 2005) on *Anthemideae* are well in line with our results, particularly with respect to *Leucocyclus*. Only *Otanthus* occupies a sister position relative to *Achillea* in his trees, a fact that may be due to the smaller number of his *Achillea* samples. Rather unexpectedly, his data suggest additional, close affinities between *Otanthus* and *Matricaria discoidea* DC., a finding that urgently needs verification.

The differential characters of *Otanthus* and *Leucocyclus* against *Achillea* are very weak. *Otanthus* has no female ligulate flowers, but this feature also occurs in *A. fragrantissima* (Forssk.) Sch. Bip., the type of *A.* sect. *Babounya*. Both genera also share undivided and \pm serrate leaves, features that reappear in other taxa of *Achillea* (e.g., in *A.* sect. *Ptarmica* s.s.). In *Otanthus* the base of the corolla is inflated, spongy and develops appendages on both lateral sides of the achene which partly enclose it. Nevertheless, somewhat inflated and pouched corolla bases, covering the upper part of the achene, are typical for all taxa of *Achillea* (see Fig. 7: 8 and 3 in Davis 1975). *Leucocyclus* is believed to differ from *Achillea* by its vermiform, linear leaves with minute, \pm divided, transverse and imbricate segments, single flower heads and particularly by more clearly winged achenes. But very similar leaves and single flower heads occur also in species of *A.* sect. *Babounya* s.l., and there is a gradual transition from the achenes with narrow wings (0.25 mm) in *Leucocyclus formosus* subsp. *formosus* via the even narrower winged ones in subsp. *amicus* (Rech. f.) Hub.-Mor. to the \pm thin margins of the compressed achenes in *Achillea* (see Fig. 7: 4-5 and 3 in Davis 1975). Furthermore, phytochemical analyses of various groups of constituents (e.g., Greger 1978 for *Otanthus* and Valant-Vetschera & Wollenweber 1989 for *Leucocyclus*) have not shown any significant differences between these genera and *Achillea*, and the alkalamides even demonstrate their relatively close affinities with *A.* sect. *Babounya* s.l. (Greger 1988).

Taking together all the evidence presented, it becomes imperative to include the traditional genera *Otanthus* and *Leucocyclus* into *Achillea* s.l., the former as a unispecific *A.* sect. *Otanthus*,

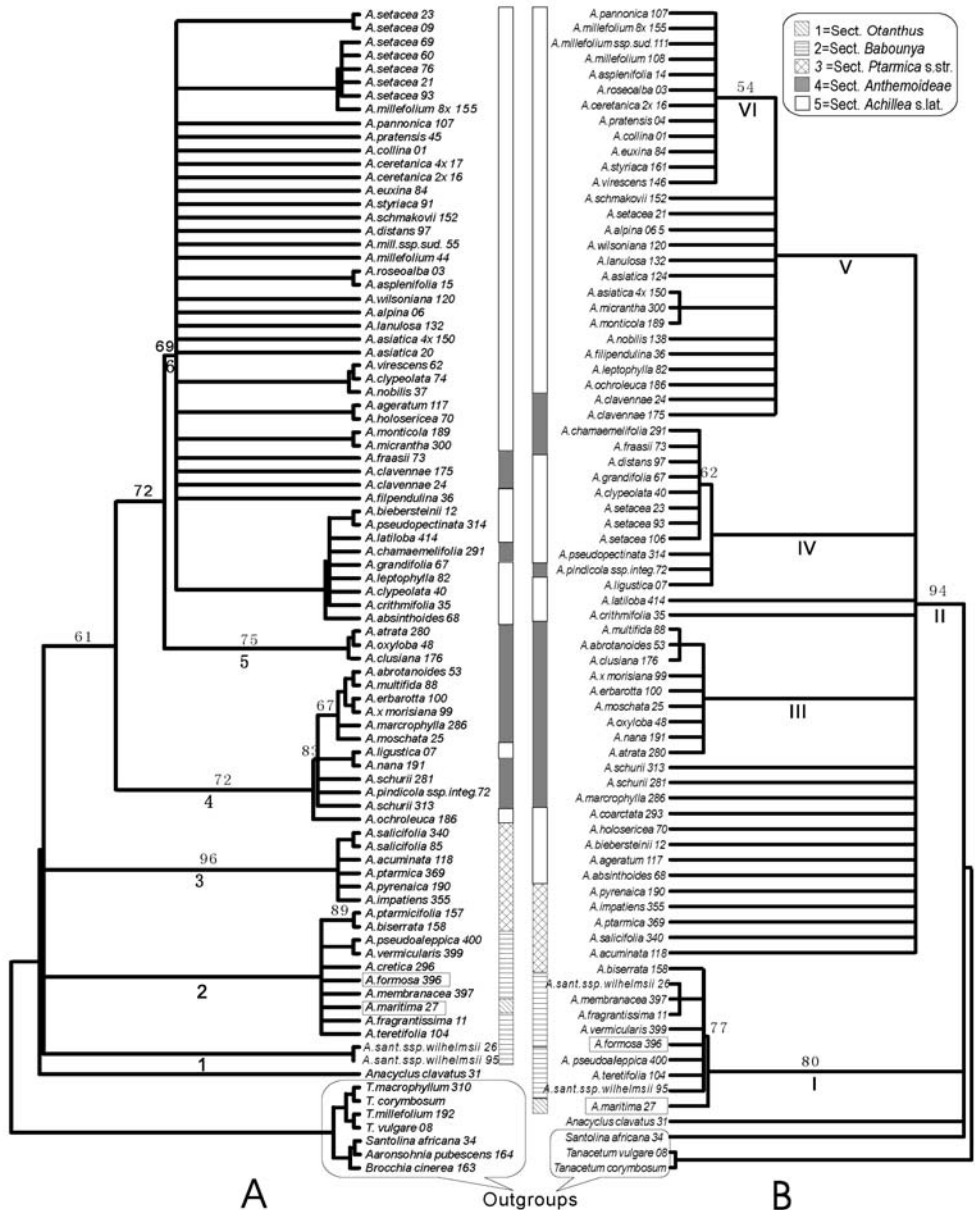


Fig. 1. Strict consensus trees for *Achillea* s.l. (taxa from all sections) and related *Anthemideae* genera from nrITS data (A: tree length = 397, CI = 0.48, RI = 0.75) and cp $trnL$ - F data (B: tree length 101, CI = 0.88, RI = 0.97) in juxtaposition. Bootstrap percentages (>50%) are shown above branches. Important clades are designated by arabic numerals below branches in A and by roman numerals in B. Taxa names with accession numbers correspond to Appendix 1 in Guo et al. (2004) and those listed in 'Material and methods'. Up-to-date assignment of taxa to *Achillea* sections is shown by two vertical reference bars in the middle, signatures are explained in the insert.

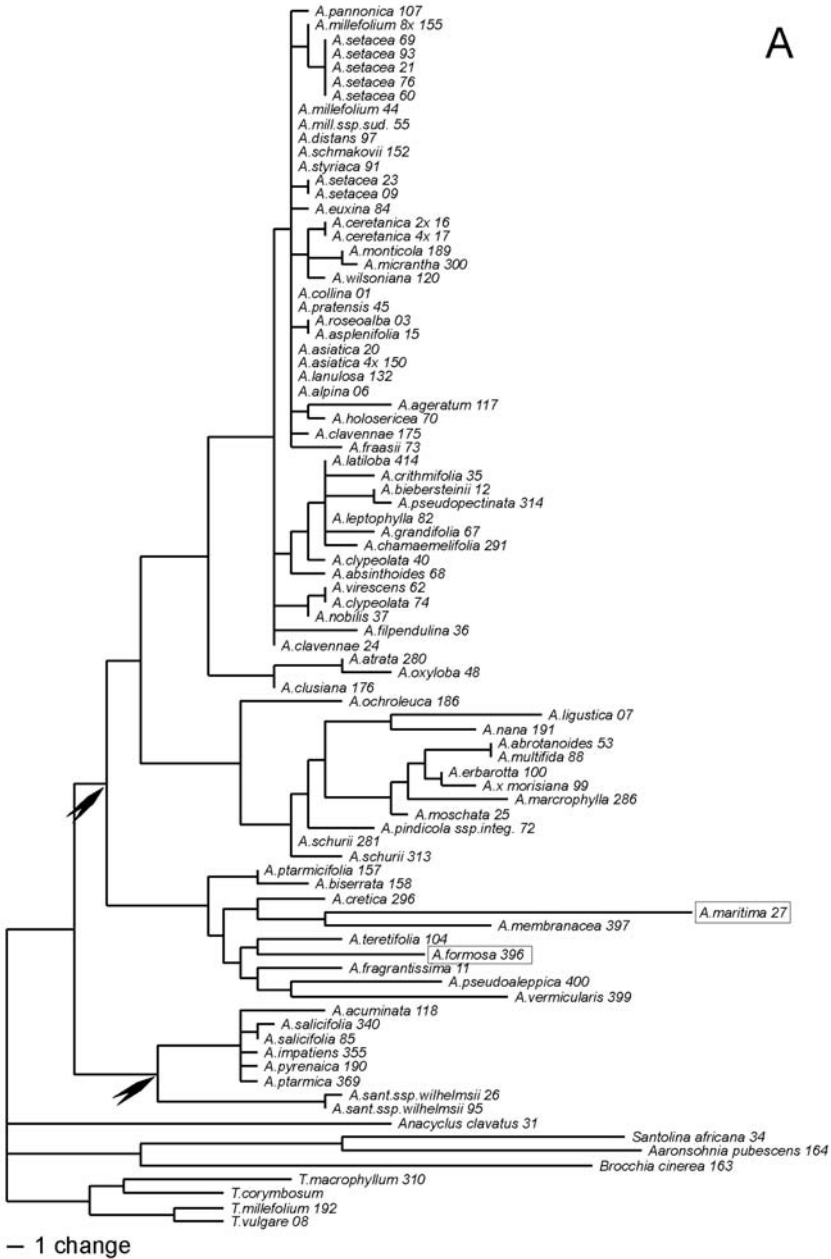


Fig. 2A. One of the 9670 equally most parsimonious phylograms from nrITS data for the same taxa and clades as in Fig.1A, showing branch lengths. Branches that collapse in the >50 % majority rule consensus tree are marked by arrows.

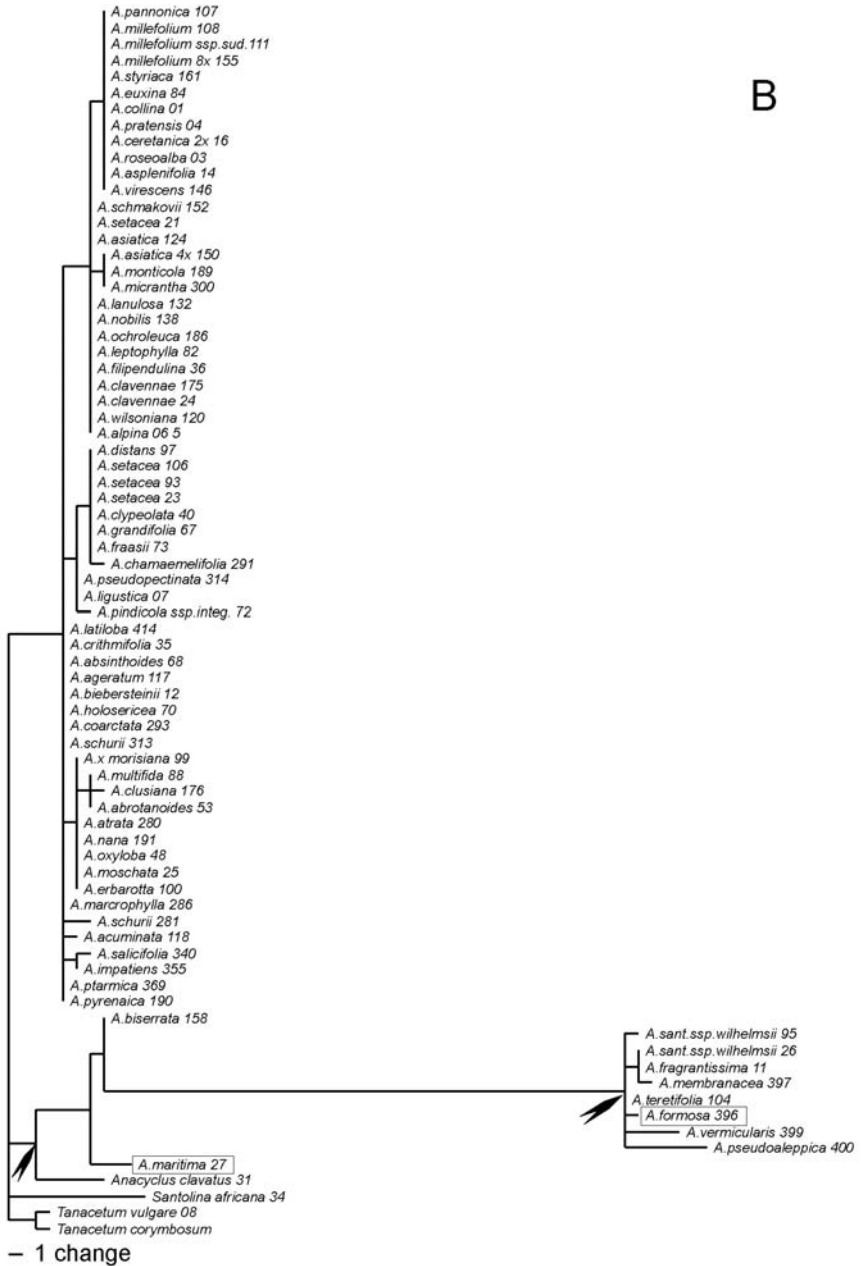


Fig. 2B. One of the 237 equally most parsimonious phylograms from *cptrnL-F* data for the same taxa and clades as in Fig. 1B, showing branch lengths. Branches that collapse in the >50% majority rule consensus tree are marked by arrows.

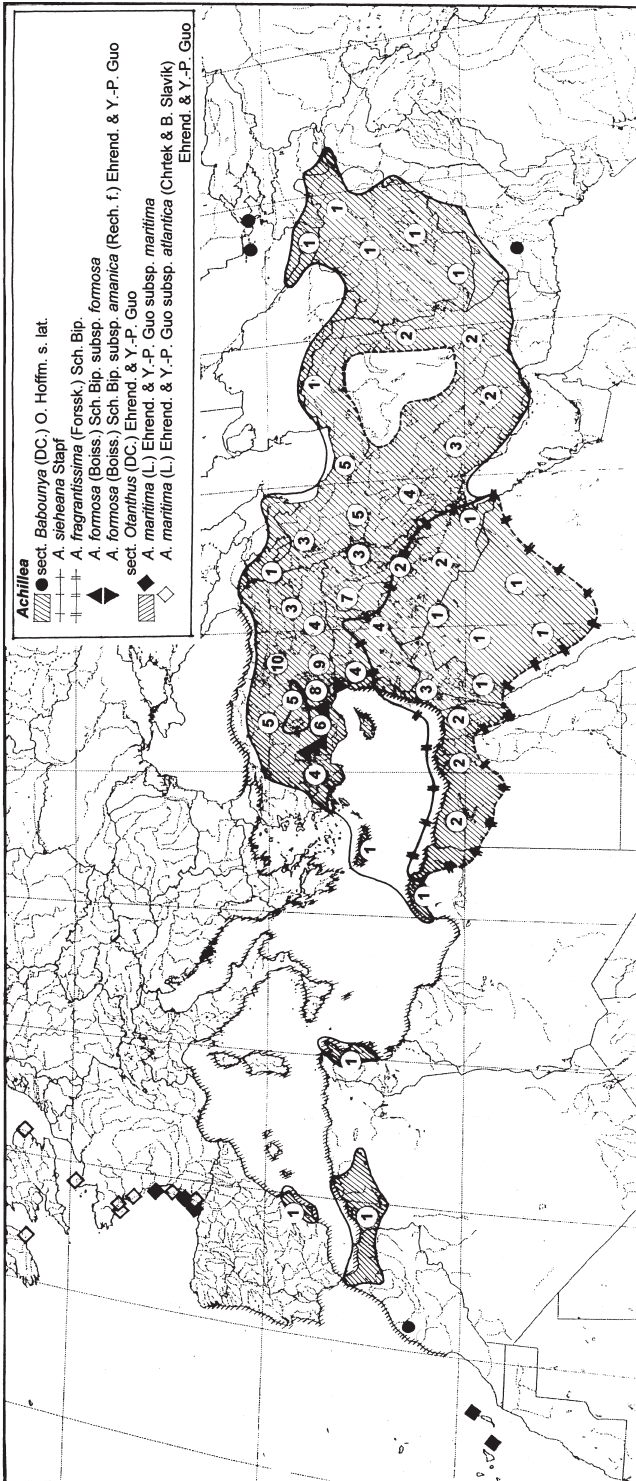


Fig. 3. Distribution map of *Achillea* sect. *Babounya* s.l. and *A. sect. Otanthus*. Numbers refer to species density of *A. sect. Babounya* s.l. in different areas, the species pair *A. sieheana* + *A. fragrantissima* (≡ *A. sect. Babounya* s.s.) and the two subspecies of *A. formosa* (≡ *Leucocyclus formosus*) are shown separately. For *A. sect. Otanthus*, *A. maritima* (≡ *Otanthus maritimus*), different symbols mark the two subspecies.

and the latter as part of *A.* sect. *Babounya* s.l. The necessary nomenclatural changes have already been made (Ehrendorfer & Guo 2005). But do these changes result in a monophyletic genus *Achillea* s.l.? The trees shown in Fig. 1-2 make such an interpretation likely and suggest *Anacyclus* L. to be the sister genus of *Achillea* s.l. Support for such conclusions comes from the independent DNA analyses of Oberprieler & Vogt (2000) and Oberprieler (2004, 2005), which in addition demonstrate the unispecific genus *Heliocauta* Humphries from the Moroccan Atlas to be even closer to *Anacyclus* than to *Achillea*. The three genera form an obviously monophyletic core clade within *Anthemideae-Achilleinae* as described by Bremer & Humphries (1993) and Bremer (1994). We agree with Oberprieler (2001) that this subtribe *Achilleinae* is polyphyletic and has to be much reduced with respect to its original circumscription. That means to exclude *Chamaemelum* Mill., *Cladanthus* Cass., *Mecomischus* Coss. ex Benth., *Rhedinolepis* Coss. and *Santolina* L., and to include only the three genera mentioned above. These *Achilleinae* s.s. (= *Achilleinae* I sensu Oberprieler 2002, *Achillea* clade sensu Oberprieler 2005) exhibit a clear geographical E/W Mediterranean differentiation: *Achillea* s.l. with its centre of diversity in SE Europe, the E Mediterranean and SW Asia versus *Anacyclus* + *Heliocauta* centred in the W Mediterranean (Meusel & Ehrendorfer 1987, Oberprieler 2005).

2. The basal clade of *Achillea*: *A.* sect. *Babounya* s.l. and its distribution

The ITS and *trnL-F* trees from our data set (Fig. 1-2) tend to place taxa of the *Achillea* sections *Babounya* s.l., *Otanthus* and *Ptarmica* s.s. into basal positions within the genus, suggesting that these clades were the first to differentiate. This corresponds to the topology reported in Guo & al. (2004). Members of *A.* sect. *Babounya* s.l. (together with the former *Otanthus* and *Leucocyclus*) form the majority of clade 2 and clade 1 [containing *A. santolinoides* subsp. *wilhelmsii* (K. Koch) Greuter only] in the ITS strict consensus tree (Fig. 1A), whereas most of the *A.* sect. *Ptarmica* s.s. members constitute clade 3. Only two Caucasian taxa (*A. biserrata* and *A. ptarmicifolia*) appear in clade 2. In the *trnL-F* strict consensus tree (Fig. 1B) all taxa of *A.* sect. *Babounya* s.l. are found in clade I, whereas those of *A.* sect. *Ptarmica* s.s. mostly appear in the large clade II with the exception of the Caucasian *A. biserrata*, which again affiliates with the taxa of *A.* sect. *Babounya* s.l. Thus, nuclear ribosomal and plastid DNA sequences are congruent (Fig. 1-2) and suggest that the Caucasian members of *A.* sect. *Ptarmica* s.s. form an intermediate element linking the xerophytes of *A.* sect. *Babounya* s.l. centred in SW Asia (Fig. 3) with the widespread meso- to hygrophytes of *A.* sect. *Ptarmica* s.s. in temperate and northern Eurasia (Meusel & Jäger 1992: maps 478c-d).

Molecular data, numerous apomorphic features and the ecology of the single representative of *Achillea* sect. *Otanthus*: *A. maritima* (\equiv *Otanthus maritimus*) suggest that this is a very specialized derivative of *A.* sect. *Babounya*-like progenitors, possibly related to the somewhat similar *A. fragrantissima*. *A. maritima* is a long-lived pioneer of maritime sand dune habitats with a creeping rhizome, densely lanate shoots and capitula without ligulate flowers. Its achenes remain united in fruit with the inflated corolla whose spongy tissue forms a lifebelt-like structure. This specialization appears to increase the buoyance of the diaspores and to facilitate their dispersal in sea water. Our map (Fig. 3) demonstrates that *A. maritima* has expanded from the E over the whole W Mediterranean and beyond along the Atlantic coasts of SW Europe to Ireland and England and exhibits a geographical S/N differentiation, corresponding to two subspecies (Chrtek & Slavík 1993). There are several parallel examples for the origin of Mediterranean Sea coast pioneers from Irano-Turanian progenitors, as *Beta maritima* L., *Crucianella maritima* L. or *Artemisia caerulescens* L. and *A. maritima* L.

From the traditional *Achillea* sections *Babounya* s.s. (= B, 2 sp.), *Arthrolepis* (Boiss.) Boiss. (= A, 4 sp.) and *Santolinoideae* (DC.) Heimerl (= S, about 24-29 sp.) (cf. Ehrendorfer & Guo 2004) samples of *A. fragrantissima* (B), *A. membranacea* (Labill.) DC. (A) and *A. pseudoaleppica* Hausskn. ex Hub.-Mor., *A. santolinoides* subsp. *wilhelmsii*, *A. teretifolia* Willd., *A. vermicularis* Willd. and *A. formosa* (\equiv *Leucocyclus formosus*) (all S) have been available for our DNA analyses. The trees (Fig. 1-2) demonstrate that all these taxa are closely related and exhibit no significant resolution, particularly not with the cp *trnL-F* data (Fig. 1B and 2B). Only *A. santolinoides* subsp.

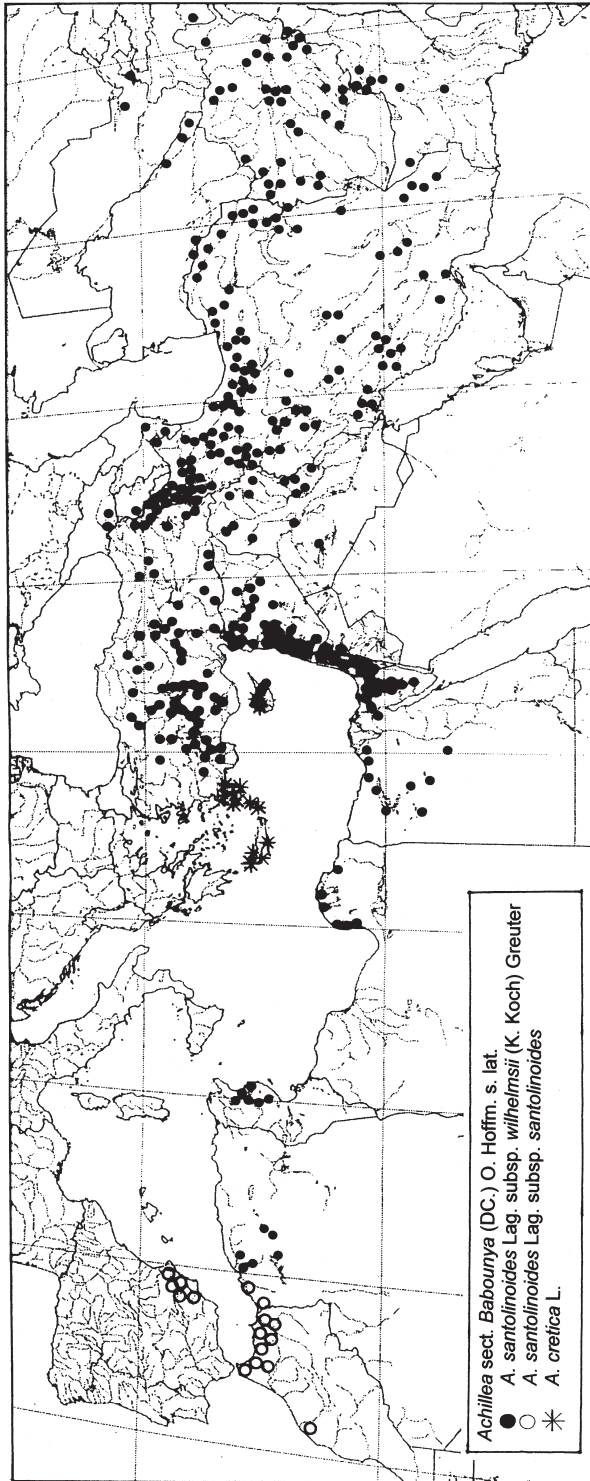


Fig. 4. Distribution map of *Achillea cretica* and *A. santolinoides* (with subspecies), two contrasting species from *A. sect. Babounya* s.l.

wilhelmsii appears somewhat separated with respect to its nrITS (Fig. 1A and 2A). There are morphological differences, e.g., the undivided leaves in *A. sect. Babounya*, the \pm articulate phyllaries and numerous large ligulate flowers in *A. sect. Arthrolepis* or the formation of root suckers in *A. santolinoideae* subsp. *wilhelmsii* of *A. sect. Santolinoideae*. Nevertheless, there are transitions between all these character states and the general similarities of xerophytic habit, leaf structures and capitula prevail (Valant-Vetschera & Kästner 2000). Karyological data, as far as available, show a dominance of diploids and occasional tetraploids. Flavonoid profiles are also similar (Valant-Vetschera 1999). All these findings support the inclusion of all three traditional *Achillea* sections discussed above under a more broadly defined *A. sect. Babounya* s.l. (Ehrendorfer & Guo 2005).

The general ecogeographical differentiation of *Achillea* sect. *Babounya* s.l. is shown in Fig. 3 and reveals a predominantly Irano-Turanian distribution. The greatest diversity with respect to morphology, ecological position and species number is found in southern and central Anatolia. It is in this area that the distribution of taxa of the former *Achillea* sections *Santolinoideae*, *Babounya* s.s. and *Arthrolepis*, and of the former genus *Leucocyclus* overlap. *A. sieheana* Stapf and *A. fragrantissima*, the only members of the former *A. sect. Babounya* s.s., are closely related salt tolerant desert plants. The first is limited to the central Anatolian surroundings of the salt lake Tuz Gölü, the second, more of Saharo-Sindian distribution, extends from Syria into Iraq and Arabia and from Sinai into N Egypt and NE Libya.

The distribution of two other remarkable and contrasting species of *Achillea* sect. *Babounya* s.l. (formerly sect. *Santolinoideae*) is outlined in Fig. 4. *A. cretica* L. has a deep-reaching taproot, reproduces only by seeds and is possibly related to the Anatolian *A. teretifolia*. It is limited to limestone rocks of the lower Mediterranean zone and has a relatively restricted and disjunct distribution from the Marmaris Peninsula of SW Anatolia to the islands of Simi, Rhodos, a few of the southeasternmost Cyclades, Karpathos and Saria, Amoi and to E and W Crete. Populations reported from NW Cyprus (Meikle 1985) seem to deviate from the western populations and are in need of critical study with respect to their taxonomic status. This suggests that *A. cretica* could have reached its present distribution already prior to the tectonic isolation of the continental S Aegean islands and Cyprus already before the end of the Miocene (see Greuter 1970, 1979, Meulenkaamp & Sissingh 2003).

Achillea santolinoideae subsp. *wilhelmsii* (Valant-Vetschera & Kästner 1998, Greuter & al. 2003) appears somewhat isolated in this section with respect to its nrITS sequence. It grows on fine-grained soils and has reached an enormous distribution area from Central Asia to NW Africa, often coinciding with the limits of *A. sect. Babounya* s.l. This remarkable expansion appears to be related to its enormous capacity for vegetative reproduction and gregarious clonal growth due to the abundant formation of root suckers. In contrast, the typical *A. santolinoideae* subsp. *santolinoideae* is possibly limited to gypsum soils in SE Spain and adjacent N Morocco. It seems to tend towards an abbreviated (sometimes apparently annual) life cycle, a trend otherwise rare in *Achillea* but widespread in many other *Anthemideae* genera. Further studies could show that the two taxa merit specific status.

3. The expansion of *Achillea* sect. *Ptarmica* s.s. and its hybrid derivatives

We circumscribe the traditional *Achillea* sect. *Ptarmica* in a narrowed sense, corresponding to *A. sect. Euptarmicae* (DC.) Heimerl (1884). This follows earlier considerations (Guo & al. 2004, Saukel & al. 2004, Ehrendorfer & Guo 2005) and is supported by the DNA data presented here (Fig. 1-2). *A. sect. Ptarmica* s.s. includes relatively tall, herbaceous hemicryptophytes with creeping rhizomes, growing in wet to mesic habitats of the temperate to boreal zone of the northern hemisphere. About 8-14 diploid species are recognized. The Caucasian taxa *A. ptarmicifolia* and *A. biserrata* morphologically are undisputed 2x members of this section but exhibit nrITS and cp*trnL-F* sequences that suggest a closer affinity to representatives of *A. sect. Babounya* s.l., the most basal clade in the genus (see Fig. 1-2 and the previous chapter). This supports the hypothesis that the progenitors of *A. sect. Ptarmica* s.s. were related to these species and had a SW Asian/Caucasian distribution.

Further divergent speciation of *Achillea* sect. *Ptarmica* s.s. on the 2x level starting from temperate SW Asia apparently has led to the differentiation of \pm allopatric additional taxa throughout Eurasia (Meusel & Jäger 1992: maps 478c and d): *A. ptarmica* L. and *A. pyrenaica* Sibth. ex Godr. in Europe and the E Pyrenees, *A. salicifolia* Besser s.l. (incl. *A. cartilaginea* Ledeb. ex Rchb.) from E Europe, NE Anatolia and the Caucasus to Siberia, partly overlapping with *A. impatiens* L. in the area from Altai to Lake Baikal and northward, *A. acuminata* (Ledeb.) Sch. Bip. on the E Asian mainland and *A. macrocephala* Rupr. from Japan to Kamchatka. With the exception of *A. impatiens* with pectinate leaves, all these taxa are characterized by undivided leaves with dentate to serrate margins and relatively large capitula (diam. >10 mm), usually with more than 8 ligulate flowers and long ligules (>4 mm).

Only recently (Nishikawa 1980, 1984, 1988, Barkalov 1992, Guo & al. 2004, 2005, 2006) it became clear that a very polymorphic 4x complex overlies this basic 2x pattern of *Achillea* sect. *Ptarmica* in E Asia. It includes populations with \pm pinnate to pinnatisect leaves, smaller capitula (diam. <10 mm), usually with less than 8 ligulate flowers and shorter ligules (<4 mm). From a combination of AFLP, plastid haplotype (cpDNA RFLP), DNA sequence and morphological data, it was possible to show that this 4x complex has originated by allopolyploidy from 2x ancestral taxa close to *A. acuminata* (*A. sect. Ptarmica*) and *A. asiatica* Serg. (*A. sect. Achillea: A. millefolium* agg.) in N China (Guo & al. 2006). We have proposed to call this 4x complex *A. alpina* L. agg., according to the oldest species name available, of which the formerly widely used *A. sibirica* Ledeb. is a synonym. In addition to *A. alpina* s.s. and the closely related *A. wilsoniana* (Heimerl) Heimerl ex Hand.-Mazz., this aggregate includes a number of other taxa of dubious specific or rather infraspecific status, in particular *A. mongolica* Fisch. ex Spreng., *A. multiflora* Hook., *A. ptarmicoides* Maxim., *A. pulchra* Koidz., *A. sinensis* Heimerl ex Hand.-Mazz., *A. sibirica* subsp. *camtschatica* Heimerl, subsp. *japonica* Heimerl, subsp. *subcartilaginea* Heimerl, var. *angustifolia* (Hara) Ohwi, var. *brevidens* (Makino) Ohwi, etc. This 4x *A. alpina* agg. has expanded from China far beyond the parental 2x taxa to Tibet and Nepal, to Mongolia, Central and E Siberia, Korea, Japan, Alaska and through northern North America eastward to the Gaspé Peninsula.

4. The differentiation of *Achillea* sect. *Anthemoideae* s.l. in the Central and S European mountain systems

Already Candolle (1838) and Heimerl (1884) have separated within *Ptarmica* or *Achillea* sect. *Ptarmica* s.l. the typical “*Euptarmicae* DC.” with taller stems and mostly undivided leaves, growing at lower elevations in the northern hemisphere, from the “*Anthemoideae* DC.” with more condensed growth and mostly divided leaves, centred in the montane to alpine zone of the Balkan mountains and the Alps. The subsequent recognition of the *Achillea* sections *Ptarmica* s.s. and *Anthemoideae* s.l. (incl. *A. sect. Montanae* Heimerl) (Guo & al. 2004, Saukel & al. 2004, Ehrendorfer & Guo 2005) is justified by the available DNA data (Fig. 1-2). They clearly show that all members of *A. sect. Anthemoideae* studied so far are much more closely affiliated with taxa of *A. sect. Achillea* than with taxa of *A. sect. Ptarmica* s.s. The only possible exception is *A. lingulata* Waldst. & Kit., for which DNA data are not yet available. It has undivided leaves and forms a morphological link from *A. sect. Anthemoideae* to *A. sect. Ptarmica*.

As can be seen from Fig. 1-2, a core group of *Achillea* sect. *Anthemoideae* taxa is kept together in the nrITS clades 4 and 5 and in the *cptrnL-F* clade III: *A. abrotanoides* (Vis.) Vis., *A. erbarotta* All., *A. xmorisiana* Rchb. f., *A. moschata* Wulfen, *A. multifida* (DC.) Boiss., *A. clusiana* Tausch, *A. atrata* L., *A. oxyloba* (DC.) Sch. Bip. and *A. nana* L. The taxa *A. macrophylla* L., *A. schurii* Sch. Bip. and *A. pindicola* Hausskn. deviate only in *cptrnL-F* and only by 1 or 2 changes. But other traditional members of *A. sect. Anthemoideae* differ considerably with respect to both nrITS and *cptrnL-F* from this core group and appear among clades of *A. sect. Achillea*. This applies to *A. chamaemelifolia* Pourr. and particularly to parts of the *A. clavennae* L. group. Thus, in spite of its morphological and ecogeographical coherence, the monophyly of *A. sect. Anthemoideae* remains questionable. That makes future studies on the critical taxa obligatory. In its present and provisional circumscription the section includes about 21-25 nearly exclusively diploid species.

The origin of *Achillea* sect. *Anthemoideae* obviously has been stimulated by the lifting of the high mountain systems in Central and S Europe since the late Tertiary. With respect to the ancestors of the section and related extant taxa one could think of *A. ligustica* All. (and *A. ochroleuca* Ehrh.). These species are placed into *A. sect. Achillea* but constantly affiliate with the core group taxa of *A. sect. Anthemoideae* in the DNA trees. Its step-wise adaptation from montane to high alpine conditions becomes apparent from a comparison of *A. abrotanoides* and *A. barbeyana* Heldr. & Heimerl in the Balkans or of *A. macrophylla* and *A. nana* in the Alps. Thus, the isolated and relatively plesiomorphic montane taxa *A. abrotanoides*, *A. macrophylla* and possibly *A. chamaemelifolia* in the E Pyrenees could be regarded as relicts from an early phase of high mountain species differentiation in *A. sect. Anthemoideae*.

Available new data and the information presented by Meusel & Jäger (1991-92: 81-83, 252-253, maps 477a-478b) allow some additional phylogeographic comments on the clades of *Achillea* sect. *Anthemoideae*. Their greatest diversity is found in the Central and S Balkan mountains with 11 species, followed by the Alps with 7, the Apennines with ± 5 , the Carpathians with 2 and the E Pyrenees with 1 species. Endemic to the Balkans are the isolated species *A. abrotanoides*, *A. barbeyana*, the remarkable new *A. occulta* Constantin. & Kalpoutz. from the SE Peloponnisos (Constantinidis & Kalpoutzakis 2005) and the *A. ageratifolia* (Sm.) Boiss. complex with three subspecies (Franzén 1986, 1988, 1991). Three other groups of *A. sect. Anthemoideae* are clearly centred in the Balkan mountains but extend either to the Carpathians as *A. lingulata* with its 2x and 4x cytotypes (Saukel & al. 2004) or to the E Alps as the *A. atrata* group and the *A. clavennae* group.

The *Achillea atrata* group includes *A. multifida*, *A. clusiana* and *A. atrata*, all represented in our trees (Fig. 1-2), and is obviously related to the SE Illyric-Albanian-N Greek *A. abrotanoides*. There are considerable differences in nrITS and cp*trnL-F* between *A. multifida* and *A. clusiana*. Therefore we suggest not to lump the two species (as proposed by Richardson 1976 and Franzén 1991). Instead, we provisionally use the name *A. multifida* for the populations reaching from Albania, Macedonia, Bulgaria and adjacent NE Greece to the Bithynian Olymp, and *A. clusiana* for the populations limited to the NE limestone Alps (Saukel & al. 2004). That further analyses are obligatory in this group is obvious from the report by Baltisberger (1992) on 10x populations (with $2n = 90$) from the Korab Mts at the border of Albania and FYR Makedonija which are morphologically similar to *A. multifida*. All other data on chromosome numbers available for the *A. atrata* group are 2x ($2n = 18$). *A. atrata* appears as the sister to *A. clusiana* but is more widespread in the E Alps and partly overlaps with it. Their close relationships are well supported by our DNA sequence data, but there are also affinities with *A. oxyloba*, traditionally regarded as a member of the group of *A. barrelieri* (Ten.) Sch. Bip. (discussed below).

The following groups of *Achillea* sect. *Anthemoideae* have no representatives in the Balkan mountains. Taxa with large, single capitula form the *A. barrelieri* group with a very disjunct distribution: *A. schurii* is endemic in the E Carpathians, *A. oxyloba* endemic in the SE limestone Alps and the closely related species (? or better subspecies) pair *A. barrelieri* and *A. mucronulata* (Bertol.) Sch. Bip. is limited to the Central and S Apennines. The phylogenetic coherence of this group remains uncertain in the light of nrITS and cp*trnL-F* sequence differences between *A. schurii* and *A. oxyloba* (which do not support their treatment under one species: Richardson 1976) and because of the close affiliation of the latter with the *A. atrata* group (see above). More data are needed to clarify these questions.

The *Achillea erba-rotta* group has its main centre of distribution on siliceous substrates in the Alps: *A. moschata* in the E and *A. erba-rotta* in the W, linked by transitional populations (*A. xmorisiana*). In addition, the limestone mountains of S Italy harbor an allopatric group of populations called *A. rupestris* Huter, *A. lucana* Pign. and the transitional “*A. calcarea* Huter” (not validly published). For the alpine populations nrITS and cp*trnL-F* demonstrate only minor genetic differences, for the S Italian taxa relevant data are lacking. There is not yet a clue whether all taxa of the group should be treated as members of one (Richardson 1976) or of several species (Pignatti & Ehrendorfer 1982). Moreover, the direction of the phylogeographic differentiation (S→N?) is still uncertain.

Another unispecific group of *Achillea* sect. *Anthemoideae* is made up of the relatively isolated and uniform *A. nana*, mostly confined to the high alpine to nival zone of the central and western silicate Alps. Morphology and available DNA data support its inclusion in the core group of the section but give no clear hints as to affinities and origin.

Among the traditional members of *Achillea* sect. *Anthemoideae* the *A. clavennae* group is the most critical with respect to its relationships and taxonomic placement. In continuation of the monographic treatment of the section by Heimerl (1884), multidisciplinary studies were done on the group by Franzén (1986, 1987, 1991). He characterized the group by the occurrence of T-shaped hairs, a differential character unique among members of *A. sect. Anthemoideae*. Nevertheless, the available nrITS and *cptrnL-F* data (Fig. 1-2) do not correspond with this treatment. Whereas *A. pindicola* subsp. *integrifolia* (Halácsy) R. Franzén is quite well integrated with the core group taxa of *A. sect. Anthemoideae*, *A. fraasii* Sch. Bip. and *A. clavennae* appear far removed among representatives of *A. sect. Achillea*. Ongoing AFLP and cpDNA studies could either demonstrate hybrid impacts from *A. sect. Achillea* or suggest a taxonomic separation of the group from *A. sect. Anthemoideae*.

With respect to the phylogeography of the *Achillea clavennae* group, one has to consider *A. umbellata* Sm., *A. ambrosiaca* (Boiss. & Heldr.) Boiss. and *A. pindicola*, all endemic in the Greek mountains, *A. fraasii* extending from Greece to FYR Makedonjia, Albania, Bosnia and Mt Ida in W Anatolia, and *A. clavennae* with an area from FYR Makedonjia and Albania through the Dinarids to the E Alps. This apparent S→N extension of the group is reflected in the flavonoid pattern: the flavonol-3-O-glycosides in *A. umbellata* and the forms of *A. clavennae* with glandular achenes in the S Dinarids are replaced by flavon7-O-glycosides in the forms with glabrous achenes in the E Alps (Valant-Vetschera 1981).

5. Diversification of *Achillea* sect. *Achillea* in W Eurasia

As we have already shown in earlier publications (Guo 2004, Guo & al. 2004, Saukel & al. 2004, Ehrendorfer & Guo 2005), the traditional *Achillea* sect. *Filipendulinae* (DC.) Afan. has to be united with *A. sect. Achillea* [= *A. sect. Millefoliatae* (DC.) Klok. & Krytzka] because it is characterized by yellow(ish) ligules only and appears as clearly polyphyletic according to our nrITS and *cptrnL-F* sequences (Fig. 1-2). This enlarged circumscription corresponds to the traditional concept, already established by Candolle (1838). Separation from other sections of the genus is easy with the exception of two instances already discussed (allopolyploid links with *A. sect. Ptarmica* s.s. and some critical taxa of *A. sect. Anthemoideae*). Furthermore, two groups considered traditionally as representatives of *A. sect. Achillea* usually affiliate with members of *A. sect. Anthemoideae* in our nrITS and *cptrnL-F* trees. This applies to *A. ochroleuca* Ehrh. + *A. pseudopectinata* Janka and to *A. ligustica* All.

Achillea ochroleuca and closely allied taxa (*A. pseudopectinata*, *A. depressa* Janka) form a small group, isolated with respect to morphology (suffruticose, pectinate middle stem leaves, very short ligules) and phytochemistry (sesquiterpene coumarin ethers: Greger & al. 1983, Hofer & Greger 1984). This has been correctly recognized by Klovok & Krytzka (1984) and is also indicated by available DNA data, in spite of differences among taxa. No hybrids with other clades of the genus are known. There is considerable variation within the group, but relationships between the taxa (1-3 species?) are not yet understood (Saukel & al. 2004). *A. ochroleuca* and allies occupy very xeric, rocky to sandy habitats in SE Europe and extend from N Greece, Bulgaria and FYR Makedonjia to Serbia, Hungary and S Slovakia in the NW and to E Romania, Moldova and the Ukraine in the NE. From the DNA data available, one could speculate that the *A. ochroleuca* group represents a relatively basal clade in the differentiation towards typical groups of *A. sect. Achillea*, still somewhat reminiscent of *A. sect. Babounya* s.l.

Up to now, *Achillea ligustica* has been regarded as part of the informal group of *A. nobilis* L. (Bässler 1963, Richardson 1976, Meusel & Jäger 1991-92: map 479a), a placement clearly contradicted by morphology as well as nrITS and *cptrnL-F* (Figs. 1-2). The species is quite uniform, does not hybridize and occupies a disjunct area from Crete and the W Balkans to Italy, Sicily, the

Tyrrhenian islands and the W Mediterranean to Morocco. All this and recent AFLP data (Guo & al. 2005: fig.1) indicate that it constitutes a unispecific, relic and relatively early clade (late Tertiary?) of *A. sect. Achillea* with affinities to *A. sect. Anthemoideae*.

The core groups of *Achillea sect. Achillea* correspond widely with the distal clade 6 in the nrITS trees (Fig. 1A, 2). In the *cprrnL-F* trees, which suffer from much less resolution (Fig. 1B, 2B), the members of the section appear not only in the distal clades IV, V and VI, but partly also in clade II. A clearer picture only emerges together with new AFLP data, available for a limited number of taxa (Guo & al. 2005: fig.1). This allows the separation of a heterogeneous group of basal taxa from a tightly interconnected and very polymorphic distal complex. The first group consists of often less variable, better isolated, more plesiomorphic and predominantly diploid taxa (about 26-35 species), centred in SE Europe. The second forms an extremely variable, strongly reticulate, more apomorphic and predominantly polyploid complex extending throughout the northern hemisphere. This *A. millefolium* agg. is discussed in the following chapter.

The relationships among the more basal taxa of *Achillea sect. Achillea* with yellow to white ligules is still badly understood and the DNA sequences available up to now are not of great help in this respect. Nevertheless, a few comments based on morphology, karyology, ecology and chorology may stimulate further studies.

Achillea absinthoides Halácsy is an isolated diploid and narrow endemic from rock fissures of the subalpine zone of the S Pindhos Mts (Franzén 1991). *A. clypeolata* Sm. and *A. filipendulina* Lam. are the core species of a nearly exclusively diploid and morphologically rather coherent group of tall herbs with taproot and rootstock, which occupy open and dry to mesic habitats. *A. clypeolata* ranges from the Greek mainland to S Albania, FYR Makedonjia, Serbia, Bulgaria, SE Romania and European Turkey, and exhibits considerable genetic (Fig. 1B, 2) as well as morphological variability (Richardson 1976). The occasional formation of fertile hybrid swarms with 4x members of *A. millefolium* agg. is possible through unreduced gametes (Saukel & al. 2004, Guo & al. 2005). The related *A. coarctata* Poir. has an even wider distribution, reaching from SE Hungary to the W Ukraine and Anatolia. Its vicarious sister species *A. taygetea* Boiss. & Heldr. and *A. aegyptiaca* L. extend into S Greece and the S Aegean. The central Balkan endemics *A. baldaccii* Degen and *A. thracica* Velen. form a link to the often cultivated *A. filipendulina*, a rather stable species with a wide range from SE Anatolia and the Iraq through W Iran and the Caucasus, to Afghanistan and Central Asia. Members of the *A. clypeolata-A. filipendulina* group hybridize with each other and with other taxa of *A. sect. Achillea*.

Among the basal taxa of *Achillea sect. Achillea* with yellow to white ligulate flowers are two very distinct, uniform and diploid species in the Mediterranean region. In the east, *A. grandifolia* Friv. inhabits ± shady forests and woodlands from Albania through the Balkan Peninsula to N, W and S Anatolia, in the west, *A. ageratum* L. occupies open and humid to wet localities, extending from Italy, Sardinia and Corsica to the Iberian Peninsula and NW Africa. The two species are not closely related, quite isolated (for *A. ageratum* even a separate section was established) and evidently old relic taxa. Another isolated diploid is *A. latiloba* Ledeb. ex Nordm. from subalpine, tall herb communities of the Euxinian mountains from NW Anatolia to adjacent Georgia. Morphologically it is reminiscent of *A. distans* Waldst. & Kit. ex Willd. (6x) in the *A. millefolium* agg., but the available sequences and AFLP data exclude closer affinities with this polyploid complex.

In contrast to the above taxa, the following four groups (a-d) of *Achillea sect. Achillea* are more closely related with each other and include 2x, 4x and even 6x taxa. They are more polymorphic and still insufficiently studied. Most are xerophytes of open grassland from lower to montane elevations.

- a) *Achillea tomentosa* L. (2x) extends from the southern regions of the Alps and northern Apennines to NE Spain, the obviously related *A. chrysocoma* Friv. (6x) is limited to the E Balkan (Meusel & Jäger 1991-92: map 480a).
- b) The group of *A. leptophylla* M. Bieb. (2x), *A. biebersteinii* Afan. and *A. micrantha* Willd. (2x/4x) reaches from a centre of diversity in SE Europe to SW and Central Asia (Meusel & Jäger 1991-92: map 480a), and apparently exhibits polyploid links with *A. millefolium* agg.

(as shown by morphology and nr and cpDNA sequences: see topology of *A. micrantha* and *A. monticola* Martrin-Donos in Fig. 1-2). *A. micranthoides* Klok. (4x) from the Ukraine may represent a similar link to *A. nobilis* (2x).

- c) *A. crithmifolia* Waldst. & Kit. forms a polymorphic group with 2x, 3x and 4x cytotypes in SE Europe.
- d) The basal taxa of the *A. nobilis* group (exclusive of *A. ligustica*; see Bässler 1963, Meusel & Jäger 1991-92: map 479a.), i.e. *A. kotschyi* Boiss., *A. nobilis* (2x) and *A. odorata* L. (2x), have differentiated \pm vicariously from SW and Central Asia through Europe to the W Mediterranean region. For *A. virescens* (Fenzl) Heimerl (4x) (probably inclusive of *A. tenorii* Grande) in the NW Balkan and the Italian Peninsula the ambivalent morphology and DNA sequences (Fig.1-2; in the nrITS tree affiliation with *A. nobilis*, in the *cprrnL-F* tree affiliation with *A. millefolium* agg.) as well as the AFLP data (Guo & al. 2005) clearly indicate an allopolyploid origin, linking the groups of *A. nobilis* and *A. millefolium*.

6. Eco-geographical radiation of the polyploid complex *Achillea millefolium* agg. throughout the northern hemisphere

DNA sequences (Fig. 1-2) and particularly AFLP fingerprinting data (Guo & al. 2005), combined with other information, allow to characterize the *Achillea millefolium* species aggregate and to separate it from hybrids and polyploids, which link it with various other clades of the *Achillea* sections *Ptarmica* and *Achillea* as discussed above. By morphological, phytochemical, DNA-analytical and ecogeographical criteria *A. millefolium* agg. appears as the most apomorphic, polymorphic, diverse and wide-spread, highly polyploid (2x, 4x, 6x, 8x) but nevertheless monophyletic “crown group” of the genus. Taxonomic treatments of this group have differed dramatically, from the extreme splitting of up to 40 (micro)species to their lumping into a single monstrous *A. millefolium* (sensu latissimo). The following brief survey of our present interpretation of the aggregate considers about 20 species. Their distribution is still badly known and available maps (e.g., Meusel & Jäger 1991-92: maps 479b-d) need corrections because they often have been based on erroneous literature references.

According to AFLP data (Guo & al. 2005: fig.1, 2, 6) the 2x ancestors of *Achillea millefolium* agg. must have been closely related to the *A. sect. Achillea* groups of *A. nobilis*, *A. crithmifolia* and *A. clypeolata*. Thus, one can assume a 2x “basal substrate” of this polyploid complex in SE Europe. A first differentiation step has produced *A. setacea* Waldst. & Kit., today distributed in Pontic steppes from SE Europe (W of Dnepr) and NE Anatolia to Central Europe and interior valleys of the Alps. A second step has resulted in the separation of a western European and an eastern Asiatic group, each with three extant 2x taxa. The first group includes *A. asplenifolia* Vent., an endemic of wet Pannonian grasslands from Bulgaria and Hungary to Austria and the Czech Republic. The closely related *A. roseoalba* Ehrend. (2x), vicarious and widespread in anthropogenous meadows in N Italy, may have originated from it by hybrid introgression on the 2x level (Ehrendorfer 1959). Finally, there is *A. ceretanica* Sennen (2x), an endemic of subalpine grassland in the E Pyrenees. This latter taxon is close to the second group of still insufficiently known Asiatic 2x taxa, mostly found in mesic to dry, montane to alpine grasslands. The best documented is *A. asiatica* Serg. (2x) (? = *A. sergievskiana* Shaulo & Shmakov), which extends from the Altai through Mongolia to NE China. Genetically quite different 2x populations from NW China (Xingjiang) may not belong to *A. asiatica* 2x but rather to *A. bucharica* C. Winkl., more widespread in the mountains of Central Asia. A third 2x taxon from the western Himalayas has been described as *A. cuspidata* Wall. All these taxa of the 2x “basal substrate” of *A. millefolium* agg. discussed above exhibit a clear allopatric and vicarious differentiation pattern.

An even greater variability and species diversity is found on the 4x level of *Achillea millefolium* agg. in Eurasia. The close links between the 2x, 4x and higher polyploid taxa are evident from phenetic comparisons but even more obvious from the distribution of specific AFLP markers (Guo & al. 2005: fig. 8) and plastid haplotypes (van Loo, pers. comm.). From these data several parallel hybridization and polyploidization events have to be postulated. New variation and re-

combination have occurred on the 4x and on higher polyploid levels as well as “horizontal” hybrid contacts between different taxa on the same level. But “vertical” hybridizations between different ploidy levels are also possible through unreduced gametes and/or by anorthoploid progenies and backcrosses. All this contributes to the more complex reticulate relationships and much less clear differentiation of polyploid as compared to 2x taxa. So far one can recognize on the 4x level of *A. millefolium* agg. from W to E the following taxa (with their genetically closest 2x relatives in brackets): in central France *A. ceretanica* (4x) (*A. ceretanica* 2x), in Central Europe *A. pratensis* Saukel & Länger (*A. roseoalba*), from Styria to the Czech Republic *A. styriaca* Saukel & Danihelka ined. (2x relative uncertain), from Central to SE Europe *A. collina* J. Becker ex Heimerl (*A. asplenifolia* + *A. setacea*), in the Ukraine *A. euxina* Klok. (*A. asplenifolia*), *A. inundata* Kondr. (4x) (2x relative unknown) and E of the Dnepr *A. stepposa* Klok. & Krytzka (*A. setacea*), from E Europe to Siberia *A. submillefolium* Klok. & Kratzka (2x relative uncertain) and from central to E Siberia *A. asiatica* (4x) (*A. asiatica* 2x).

Multiple processes of polyploidization and cycles of differentiation and hybridization (Ehrendorfer 1959) similar to those from 2x to 4x, also have occurred from 4x to 6x and to 8x (Guo & al. 2004, 2005). In Eurasia and on the 6x level this has led to the origin of *Achillea millefolium* s.s., most closely related to *A. submillefolium* (4x) and *A. asiatica* (4x). With its remarkable ecotypic variation it has reached a natural distribution throughout N Eurasia from Iceland to Kamchatka and world-wide as a weed. Another 6x taxon, possibly influenced by *A. styriaca* (4x), is the more thermophilous *A. distans* from the region of the Alps, Carpathians, N Balkans and the Apennines. Hybrid links with *A. millefolium* s.s. have been called *A. stricta* (W. D. J. Koch) Schleicher ex Gremli. A third, obviously independent, local 6x taxon from the Altai has recently been described as *A. schmakovii* Kupr. References for 6x *A. inundata* in the Ukraine (Sytnik & Androshchuk 1984) are in need of verification (so far only 4x and 8x cytotypes of this species have been located). For *A. millefolium* agg. not only local 8x individuals but three independent 8x taxa have been documented so far: *A. monticola* Martrin-Donos in the Iberian Peninsula, the Pyrenees and adjacent France, *A. pannonica* Scheele, an element of the Pontic forest steppes extending from SE to Central Europe (Meusel & Jäger 1991-92: map 479b) and a still undescribed taxon “8x *A. millefolium*” (? = *A. millefolium* subsp. *elbursensis* Hub.-Mor.) reaching from the Caucasus region into the mountains of N Iran. For the remarkable plasticity of all these high polyploid taxa of *A. millefolium* agg. it is most relevant that in zones of contact between 4x and 6x or 6x and 8x ± fertile 5x or 7x F₁ and backcrosses are produced, which allow gene flow between the different ploidy levels (e.g., Schneider 1958).

What do we know about the remarkable expansion of *Achillea millefolium* agg. throughout North America? Here, the complex has developed an enormous secondary ecological radiation of 4x and 6x (and even 8x) populations (Clausen & al. 1948, Hiesey & Nobs 1970, Ehrendorfer 1973, Tyrl 1975). Available AFLP data (Guo & al. 2005 and unpubl.; J. Ramsey, pers. comm.) strongly suggest that this remarkable diversity has originated from ancestors similar to *A. asiatica* (4x) and their relatively recent (Pleistocene) immigration across Beringia. One has to assume several independent origins of 6x from 4x populations in North America and their intimate hybrid contacts. Thus, it may be most appropriate to use only *A. borealis* Bong. (the first of 17 species described from the New World) with several subspecies for the North American populations.

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