Chromosome numbers and karyotypes within the genus Achillea (Asteraceae: Anthemideae)

Authors: Baltisberger, Matthias, and Widmer, Alex

Source: Willdenowia, 46(1) : 121-135

Published By: Botanic Garden and Botanical Museum Berlin (BGBM)

URL: https://doi.org/10.3372/wi.46.46110

The BioOne Digital Library (https://bioone.org/) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (https://bioone.org/subscribe), the BioOne Complete Archive (https://bioone.org/archive), and the BioOne eBooks program offerings ESA eBook Collection (https://bioone.org/esa-ebooks) and CSIRO Publishing BioSelect Collection (https://bioone.org/csiro-ebooks).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commmercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Willdenowia on 19 May 2025
Terms of Use: https://complete.bioone.org/terms-of-use

Willdenowia
Annals of the Botanic Garden and Botanical Museum Berlin-Dahlem

MATTHIAS BALTISBERGER[1] & ALEX WIDMER[1*]

Chromosome numbers and karyotypes within the genus *Achillea* (*Asteraceae*: *Anthemideae*)

Abstract: We investigated 28 taxa of the genus *Achillea* from 85 natural populations. The chromosome numbers of 75 populations are presented for the first time, all showing a basic number of 9 chromosomes. The chromosome numbers of *A. alexandri-regis* and *A. lucana* have not previously been reported (both diploid with $2n = 2x = 18$). New ploidy levels are reported for *A. ageratifolia* subsp. *ageratifolia* (tetraploid with $2n = 4x = 36$) and for *A. stricta* (octoploid with $2n = 8x = 72$). B-chromosomes were observed in one population each of *A. fraasii* and *A. holosericea*. There are confirmed indications in literature for the other chromosome numbers. The karyotype was investigated for 27 taxa from 79 natural populations. Haploid karyotypes in all taxa of *Achillea* are highly homogeneous with seven metacentric and two submeta- to subtelocentric chromosomes, the latter with satellites. Karyotypes are indicated for the first time for ten taxa, viz. *Achillea alexandri-regis, A. atrata*, *A. erba-rotta*, *A. grandifolia*, *A. lucana*, *A. macrophylla*, *A. moschata*, *A. nana*, *A. pindicola* subsp. *integrifolia*, *A. ptarmica* and *A. tomentosa*. A deviating karyotype was found in plants from one single *A. holosericea* population. The phylogenetic relevance of cytological data for *Achillea* is discussed.

Key words: chromosome number, hybridization, karyotype, karyology, phylogenetic relevance, polyploidy, *Asteraceae*, *Compositae*, *Anthemideae*, *Achillea*

Article history: Received 17 November 2015; peer-review completed 27 January 2016; received in revised form 8 February 2016; accepted for publication 9 February 2016.

Citation: Baltisberger M. & Widmer A. 2016: Chromosome numbers and karyotypes within the genus *Achillea* (*Asteraceae*: *Anthemideae*). – Willdenowia 46: 121–135. doi: http://dx.doi.org/10.3372/wi.46.46110

Introduction

Cytological data within a taxon (e.g. family, genus or species) may vary with respect to the number of chromosomes (including ploidy level and aneuploidy), but may also show variation in absolute and relative size, in morphology, and in staining properties of the respective chromosomes (Sharma & Sen 2002). The position of the centromere is the most important feature to characterize morphological differences of chromosomes (Levan & al. 1964). Information on chromosome morphology is a powerful tool to characterize genomes. For any organism, karyological data represent essential information and provide important characters for plant systematics and evolutionary analysis (Baltisberger & Widmer 2009; Baltisberger & Hörandl 2016).

The genus *Achillea* L. comprises 110–140 species and has a rather wide geographic distribution spanning Europe, Asia and N Africa (Ehrendorfer & Guo 2006; Oberprieler & al. 2007). Its centre of diversity is located in SE Europe and SW Asia, and the taxa vary broadly in morphology, life cycle and ecology (Guo & al. 2004). Polyploidy is rather frequent, and evidence for natural hybridization has been reported (Guo & al. 2005). Recent investigations including molecular methods show that *Achillea* has to be newly circumscribed and the two related and monotypic genera *Leucocyclus* Boiss. and *Otanthus* Hoffmanns. & Link have to be included in *Achillea* (Guo & al. 2004; Ehrendorfer & Guo 2005; 2006). Based on available molecular data, four sections are currently accepted within *Achillea*, viz. *A.* sect. *Achillea* s.l., *A.* sect. *Anthemoideae* (DC.) Heimerl s.l., *A.* sect. *Babounya* (DC.) O. Hoffm.

---

[1] ETH Zürich, Plant Ecological Genetics, Institute of Integrative Biology, Universitätstr. 16, CH-8092 Zürich, Switzerland; *e-mail: alex.widmer@env.ethz.ch (author for correspondence).

and *A.* sect. *Ptarmica* (Mill.) W. Koch (Guo & al. 2004).

Similar to *Achillea*, the genus *Ranunculus* L. (*Ranunculaceae*) is highly diverse and also varies broadly in morphology, life cycle and ecology. *Ranunculus* shows pronounced cytological variation that supports the phylogeny of the genus (Baltisberger & Hörandl 2016). To investigate whether cytology is also variable in *Achillea* and reflects phylogenetic relationships, we evaluate novel cytological information (chromosome numbers and karyotypes) within *Achillea* using our own data, as well as data from literature, and we discuss the phylogenetic relevance of such data.

Material and methods

Living plants were sampled at 85 natural populations (32 from Switzerland, 22 from Greece, 15 from Italy, four each from Austria and Slovenia, three from France, two each from Bulgaria and Macedonia, and one from Kosovo). The plants were transferred to Zurich and cultivated in the greenhouse.

The taxa are arranged alphabetically. Geographic indications are given for each site. The sites are arranged according the country and then the year of sampling; indications of Greek sites have been adapted to the new organization of Greece that was part of the "Kallikratis" administrative reform starting on 1 Jan 2011 (for information and maps see https://en.wikipedia.org/wiki/Regional_units_of_Greece). The identification numbers refer to the herbarium specimens in the collection of Matthias Baltisberger, deposited in the herbarium Z+ZT (herbarium codes follow Thiers [continuously updated]).

The cytological investigations were carried out on root tips (for method see Baltisberger & Widmer 2009). Five to ten metaphases were counted for each investigated individual to determine chromosome numbers. Numbers of investigated individuals (N) are indicated in Table 1.

Table 1. Alphabetical list of investigated *Achillea* taxa with the year of sampling. – Voucher: number associated with vouchers deposited in the herbarium Z+ZT; N: number of individuals investigated for chromosome numbers; 2*n*: chromosome number in somatic cells; KT: number of metaphases investigated for karyotype analysis.

Achillea	**Year**	**Voucher**	**N**	**2*n***	**KT**
ageratifolia subsp. *ageratifolia*	1990	12543	2	18	–
ageratifolia subsp. *ageratifolia*	1990	12251	9	36+	1
ageratifolia subsp. *aizoon*	1987	11368	4	18	1
alexandri-regis	1990	12278	11	18*	1°
atrata	1988	11742	6	18	2°
atrata	1992	12623	9	18	1
atrata	1992	12647	7	18	1
atrata	1992	12661	10	18	1
atrata	1992	12674	7	18	1
atrata	1992	12681	9	18	1
atrata	1993	12728	10	18	1
atrata	1994	12986	9	18	1
atrata	1997	13411	7	18	1
atrata	1998	13467	4	18	1
atrata	2000	13627	7	18	3
atrata	2000	13766	2	18	1
barrelieri	1987	11533	–[1]	18[1]	1
barrelieri	1995	14408	9	18	1
chrysocoma	1990	12309a	7	54	1
chrysocoma	2011	14876	4	54	–
clavennae	1988	10992	–[1]	18[1]	2
clavennae	1992	12622	15	18	1
clavennae	1992	12673	11	18	1
clavennae	1992	12682	15	18	1
clavennae	1998	13493	6	18	2
clavennae	2000	13619	6	18	3
clavennae	2000	13631	6	18	4
clavennae	2000	13647	6	18	2
clavennae	2000	13684	6	18	2
clypeolata	2011	14873	6	18	2
coarctata	1987	11423	6	18	1
coarctata	1990	12316	11	18	1
coarctata	1993	12771	–[3]	18[3]	1
crithmifolia	1990	12248	6	18	1
distans	2011	14878	5	54	–
erba-rotta	1997	14446	7	18	1°
fraasii	1987	11312	14	18	3
fraasii	1990	12522	9	18 + 2–4B	4
grandifolia	1992	12611	9	18	3°
holosericea	1990	12317	20	18	1
holosericea	1990	12329	5	18	1
holosericea	1992	13596b	5	18	8Δ
holosericea	1990	12520	4	18 + 1B	2
holosericea	1990	12307	12	36	1
lucana	1999	13826	9	18*	1°
macrophylla	1988	11840	9	18	4°
macrophylla	1989	12978	6	18	1
macrophylla	1994	12936	6	18	4
macrophylla	1989	13452	6	18	1
millefolium s.l.	1990	12322	8	18	1
millefolium s.l.	1988	11890	9	54	1
millefolium s.l.	1989	12357	–[2]	54[2]	1
millefolium s.l.	1993	14214	8	54	1

(Table 1 continued on next page)

(Table 1 continued from previous page)

Achillea	Year	Voucher	N	2*n*	KT
moschata	1987	11630	7	18	6°
moschata	1988	11666a	5	18	1
moschata	1989	11881	–[2]	18[2]	1
moschata	1991	12545	–[2]	18[2]	1
moschata	1994	12935	9	18	1
moschata	1997	13416	11	18	1
moschata	1998	13459	6	18	1
multifida	1987	11418	4	18	1
multifida	1993	12747	15	18	–
multifida	2011	14877	4	18	3
nana	1988	11833	10	18	1°
nana	1989	12143	8	18	1
nana	1991	12546	–[2]	18[2]	1
nana	1997	13408	7	18	2
nana	1998	13458	6	18	–
nana	1998	13469	6	18	2
nobilis	1989	11453	–[2]	18[2]	2
nobilis	1990	12330	4	18	1
oxyloba	1988	10993	–[1]	18[1]	1
oxyloba	2000	13609	6	18	1
oxyloba	2000	13630	6	18	4
oxyloba	2000	13649	6	18	2
pindicola subsp. *integrifolia*	1987	11337	15	18	3°
ptarmica	1989	12977	10	18	1°
ptarmica	1992	12709	4	18	3
ptarmica	1993	14267	7	18	1
ptarmica	1994	12970	6	18	1
ptarmica	1997	13285	7	18	1
setacea	1987	11401	4	18	2
stricta	2001	13774	6	72+	–
tomentosa	1988	11660	11	18	1°
tomentosa	1989	11454	–[2]	18[2]	1

* chromosome number not previously reported
+ new ploidy level
° karyotype given for the first time
Δ deviating karyotype
Chromosome numbers published earlier: [1] Baltisberger (1990); [2] Huber & Baltisberger (1992); [3] Baltisberger (2006).

Chromosome numbers in literature were checked with Goldblatt & Johnson (1979+). To investigate karyotypes, good metaphases were drawn with a camera lucida. The number of analysed metaphases per population is given in Table 1. The nomenclature for chromosome morphology follows Levan & al. (1964). The chromosomes are named according to the position of the centromeres. This is expressed with the ratio "long arm to short arm". We used the following terms: metacentric (arm ratio 1–1.7), submetacentric (ratio 1.7–3), subtelocentric (ratio 3–7); further chromosome types have not been observed in *Achillea*. As there are several polyploids, we indicate the haploid karyotype to more easily compare the indications of the respective taxa. In Fig. 1 metaphases are shown for taxa of which the chromosome number has not been previously reported, for taxa with B-chromosomes and for the deviating karyotype found in some plants of one population of *A. holosericea*. Searching in literature for karyotype information, it turned out that papers with figures of good metaphases were very helpful. We therefore offer illustrations of one metaphase of each investigated taxon for which the chromosome number was known but no karyotype information was found in literature (Fig. 2).

Based on indications in Richardson (1976), Hess & al. (1980), Pignatti & Ehrendorfer (1982), Franzén (1991) and Aeschimann & al. (2004), geographic distributions and interesting systematic aspects are discussed within the respective taxon including further literature if needed. A general discussion concerning *Achillea* and its cytological data (chromosome numbers, ploidy levels and karyotypes) follows the treatment of the taxa.

Results and Discussion

Achillea ageratifolia (Sm.) Benth. & Hook. f. subsp. ***ageratifolia***

2*n* = 2*x* = 18: Greece, West Macedonia, ESE of Grevena, Mt Kamvounia, near Deskati, calcareous rocks and scree SW of Mt Vounassa, 1500–1615 m, 9 Aug 1990, *M. Baltisberger & U. Schäppi 12543*.

2*n* = 4*x* = 36: Macedonia, 10 km W of Tetovo, Popova Sapka, rocky meadow, 1830–1845 m, 2 Aug 1990, *M. Baltisberger & U. Schäppi 12251, 12500*.

The rather variable *Achillea ageratifolia* occurs in the S parts of the Balkan Peninsula and comprises three subspecies (Franzén 1986, 1988). We investigated the two mountain subspecies, viz. subsp. *ageratifolia* (growing throughout the range of the species) and subsp. *aizoon* (occurring in N Greece). The lowland subspecies *A. ageratifolia* subsp. *serbica* (Nyman) Heimerl was not investigated here.

All three taxa are known to be diploid with 2*n* = 2*x* = 18 chromosomes (Franzén 1988), as we found in one population of subsp. *ageratifolia* as well as in subsp. *aizoon*. But in subsp. *ageratifolia* one population (Macedonia, *12251*) proved to be tetraploid with 2*n* = 4*x* = 36 chromosomes, which was not known up to now. Both subspecies showed the same haploid karyotype with seven metacentric and two submeta- to subtelocentric chromosomes, the latter with satellites as it was indicated also by Baltisberger (2006) for subsp. *ageratifolia* as well as by Međedović

(1976, and repeated 1984) and Baltisberger (1994) for subsp. *aizoon*.

Achillea ageratifolia subsp. ***aizoon*** (Griseb.) Heimerl

2*n* = 2*x* = 18: Greece, Central Macedonia, SSW of Katerini, E side of Mt Olympus, near Refugio A, E-exposed steep rocky slope, 1900–2200 m, 23 Jun 1987, *M. Baltisberger & U. Meili 11368*, *11679*, *12064*.

See comments under *Achillea ageratifolia* subsp. *ageratifolia*.

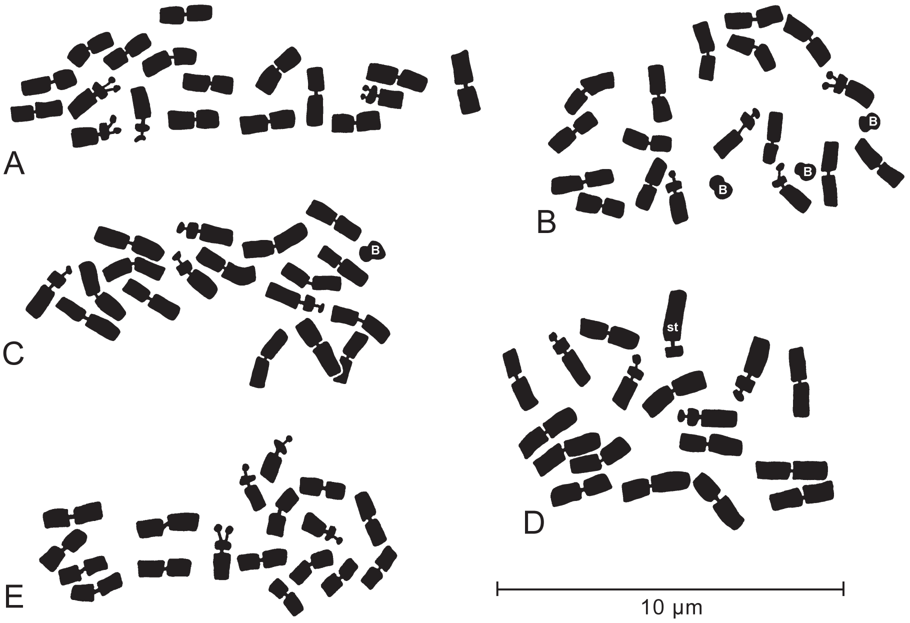

Fig. 1. Somatic metaphases of *Achillea* species, all with 2*n* = 2*x* = 18 chromosomes. – A: *A. alexandri-regis* (*12278*); B: *A. fraasii* (*12522*) with three additional B-chromosomes (marked with B); C: *A. holosericea* (*12520*) with one additional B-chromosome (marked with “B”); D: *A. holosericea* (*12596b*), one metacentric chromosome with deviating morphology, changed into a submeta- to subtelocentric chromosome (marked with “st”), the long arm distinctly longer than the arms of the metacentric chromosomes; E: *A. lucana* (*13826*).

Achillea alexandri-regis Bornm. & Rudski

2*n* = 2*x* = 18: Kosovo, 55 km SSW of Pristina, E of Prizren, Mt Ošljak, rocky meadow on limestone, 2200 m, 5 Aug 1990, *M. Baltisberger & U. Schäppi 12278*, *12512*.

Achillea alexandri-regis is a narrow-endemic taxon known only from Mt Ošljak in Kosovo (Gaijic 1975). Mt Ošljak is the northernmost part of Šar Planina, which spans the joint borders of NE Albania, NW Macedonia and S Kosovo. *Achillea alexandri-regis* grows in alpine meadows on limestone. It is characterized by yellow flowers and undivided (rarely shallowly pinnate), dentate and sericeous leaves. Despite its rarity and restricted geographic range, it was subject of several pharmacobotanical investigations (Kovačević & al. 2005; Kundaković & al. 2000, 2004, 2005a, 2005b).

The chromosome number of this species was not known until now. With 2*n* = 2*x* = 18 chromosomes (Fig. 1A) it is diploid. The haploid karyotype consists of seven metacentric and two submeta- to subtelocentric chromosomes, the latter with satellites.

Achillea alexandri-regis combines some taxonomically relevant morphological characters of two other mountain *Achillea* species: *A. holosericea* with pinnatifid, sericeous leaves and yellow flowers is also calcicole and grows on gravel and stony meadows in the S part of the Balkan Peninsula (Albania, Kosovo, Macedonia and Greece). *Achillea lingulata* Waldst. & Kit. with undivided, glabrous to pubescent leaves and white flowers is calcifuge and occurs on meadows and rocky slopes in the E and C Carpathians as well as scattered in mountains of the Balkan Peninsula southwards to N Greece. Based on the somewhat intermediate morphology and the fact that these two species grow not far away from Mt Ošljak, Diklić & al. (1991) suggested that *A. alexandri-regis* is of hybrid origin with these two species as putative parents. They also proposed to investigate the karyology of these three species to support or reject this hybrid hypothesis. All three species are fully or at least mostly diploid and show the same haploid karyotype (for *A. alexandri-regis* see above; for *A. holosericea* see below; for *A. lingulata* see Međedović & Siljak 1978, Međedović 1984 and Baltisberger & Widmer 2009). Consequently, caryological data do not allow to support or reject the hybrid origin hypothesis for *A. alexandri-regis*.

Mt Ošljak is situated on the border of the geographic areas of both potential parent species (Diklić & al. 1991): the mountain is located on the N border of the geographic range of *Achillea holosericea*, the northernmost sites of *A. holosericea* being in Šar Planina S and SE of Mt Ošljak. Concerning the geographic distribution of *A. lingulata*, Mt Ošljak is in the range of the S and SW border of the respective geographic area. This restricted and peripheral distribution of *A. alexandri-regis* concerning the geographic areas of both widespread species suggests another scenario of speciation than the hybrid origin of *A. alexandri-regis*: It may have originated from one of these species by quantum speciation. Quantum speciation is defined as the occurrence of a new daughter species from a semi-isolated (mostly peripheral) population of the ancestral species (Grant 1971). As *A. alexandri-regis* is closer to *A. holosericea* (shape and hairiness of leaves, colour of flowers, ecology) it seems more likely that it was separated by quantum speciation from *A. holosericea*.

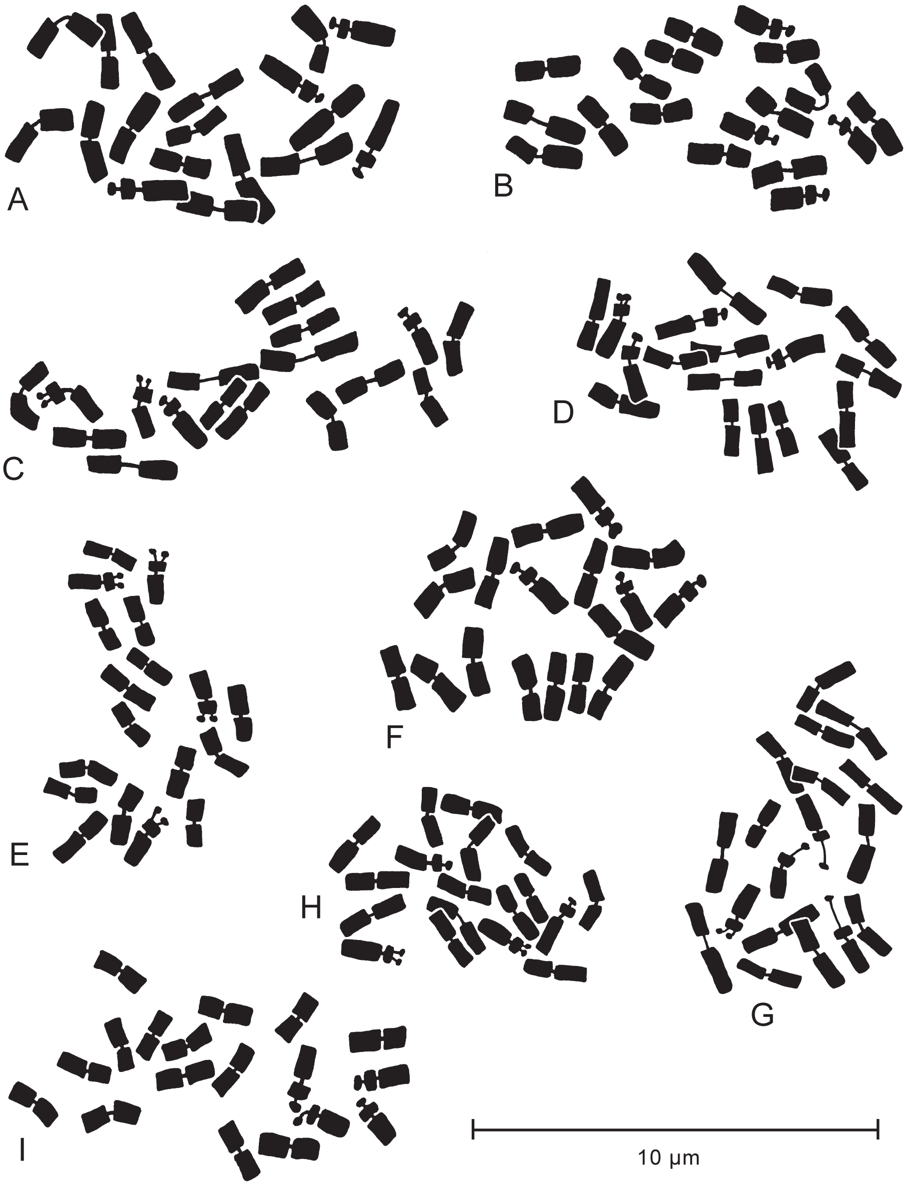

Fig. 2. Somatic metaphases of *Achillea* taxa (all with 2*n* = 2*x* = 18 chromosomes) for which no karyotype information was found in literature. – A: *A. atrata* (*12623*); B: *A. erba-rotta* (*14446*); C: *A. grandifolia* (*12611*); D: *A. macrophylla* (*1840*); E: *A. moschata* (*11630*); F: *A. nana* (*11833*); G: *A. pindicola* subsp. *integrifolia* (*11337*); H: *A. ptarmica* (*12709*); I: *A. tomentosa* (*11454*).

Achillea atrata L.

2*n* = 2*x* = 18: Austria, Carinthia, Mt Karawanken, SSW of Bleiburg, N of pass Knieps, scree and sparse meadow on limestone, 1950 m, 23 Jul 1992, *M. Baltisberger & A. Widmer 12623*; Austria, Carinthia, Mt Karawanken, 20 km SE of Klagenfurt, E side of Hochobir, N- to NW-exposed ledges and scree on limestone, 1800–1830 m, 24 Jul 1992, *M. Baltisberger & A. Widmer 12647*; Austria, Carinthia, Mt Karawanken, 20 km SSE of Klagenfurt, S of Zell Pfarre, NW of Koschuta-Turm, N-exposed scree on limestone, 1650 m, 24 Jul 1992, *M. Baltisberger & A. Widmer 12661*, *13258*, *13785*; Italy, South Tirol, 7 km S of pass Brenner, 1.5 km N of Rollspitze, near Schlüsseljoch, NW-exposed meadow and ledges, 2100 m, 27 Jul 2000, *M. Baltisberger & A. Widmer 13627, 13820*; Italy, Alpi Dolomitiche, 35 km E of Bolzano, 4 km NE of Canazei, N of Passo Pordoi, between Rif. Forcla Pordoi and Sass Pordoi, rocks and scree, 2880–2920 m, 29 Jul 2000, *M. Baltisberger & A. Widmer 13766*; Slovenia, NE of Bovec, W of pass Vrsic, N-exposed calcarous scree, 1870 m, 25 Jul 1992, *M. Baltisberger & A. Widmer 12674*; Slovenia, NNW of Bovec, Mt Mangart, N side of Cima Piccola, meadow on limestone, 1890 m, 25 Jul 1992, *M. Baltisberger & A. Widmer 12681*, *13289*; Switzerland, ct. Grisons, Lower Engadine, Val Schombrina, 2.5 km S of S-charl, NE-exposed scree, 2500 m, 17 Aug 1988, *G. Eich 11742*; Switzerland, ct. Grisons, S of Samnaun, Val Maisas, scree, 14 Jul 1993, *M. Baltisberger 12728, 13124*; Switzerland, ct. Grisons, 3 km NW of Davos Platz, pass Strela, scree on dolomite, 2350 m, 26 Aug 1994, *M. Baltisberger 12986, 13088*; Switzerland, ct. Grisons, Val Müstair, 6 km S of Sta. Maria, NW of Piz Umbrail, calcarous scree, 2800–2850 m, 30 Aug 1997, *M. Baltisberger & M. Ring 13411*; Switzerland, ct. Grisons, Upper Engadine, 2 km NW of Maloja, on the path from Maloja to Piz Lunghin, near Lake Lunghin, sparse meadow on limestone, 2350–2400 m, 2 Sep 1998, *M. Baltisberger & M. Ring 13467, 13517*.

Achillea atrata is a widespread species on calcarous soils in the Alps. We investigated plants from twelve sites from four different countries (Austria, Italy, Slovenia and Switzerland). All plants proved to be diploid with 2*n* = 2*x* = 18 chromosomes and with the same haploid karyotype of seven metacentric and two submeta- to subtelocentric chromosomes, the latter chromosomes with mostly visible satellites. As no karyotype information was found in literature, we present a metaphase of this species (Fig. 2A).

Achillea barrelieri (Ten.) Sch. Bip.

2*n* = 2*x* = 18: Italy, C Appennini, Mgna. della Maiella, Mt Amaro, stony meadow, 2000–2250 m, 14 Aug 1987, *M. Baltisberger & M. Jeker 11533, 11729*; Italy, C Appennini, Monti Sibillini, between Rif. Tito Zilioli and top of Mt Vettore, N-exposed meadow on limestone, 2190 m, 27 Jul 1995, *M. Soliva & A.-B. Utelli 14408*, *13261*.

Achillea barrelieri is a diploid endemic mountain species with 2*n* = 2*x* = 18 chromosomes occurring only in Italy in C and S Appennini. The species is known to be diploid, which was confirmed by the plants from Mt Vettore (*14408*; the chromosome number of the other site [*11533*] was published earlier, see Baltisberger 1990). Plants from both sites showed a haploid karyotype of seven metacentric and two submeta- to subtelocentric chromosomes, the latter with satellites. The same karyotype was indicated by Baltisberger & al. (1996) for plants from three different mountains.

Achillea chrysocoma Friv.

2*n* = 6*x* = 54: Greece, West Macedonia, NE of Grevena, Mt Vourinos, SW of Kataphygion E of Paleokastron, SE- to SW-exposed rocky slope, 1350–1550 m, 9 Aug 1990, *M. Baltisberger & U. Schäppi 12309a*; Greece, Central Macedonia, WNW of Edhessa, Mt Kajmakčalan, near Voras Ski Resort, meadow, 2100–2200 m, 2 Aug 2011, *B. Baltisberger & M. Baltisberger 14876*, *17618*.

Achillea chrysocoma is closely related to the diploid lowland species *A. tomentosa* (see below). *Achillea chrysocoma* is a species of mountain grasslands in the Balkan Peninsula growing in Albania, Macedonia, Bulgaria and N Greece. Plants from E Albania, Macedonia and Bulgaria are hexaploid with 2*n* = 6*x* = 54 chromosomes (Baltisberger 1992, 2006), whereas plants from mountains in S Albania are octoploid with 2*n* = 8*x* = 72 chromosomes (Baltisberger & Baltisberger 1995; Baltisberger 2002). The plants from N Greece investigated here proved to be hexaploid with 2*n* = 6*x* = 54 chromosomes. This fits well with the separation of the geographic areas of the respective cytotypes, with hexaploid plants occurring in more eastern areas than the octoploid ones (Baltisberger 2002).

The haploid karyotype shows seven metacentric and two submeta- to subtelocentric chromosomes. The 12 submeta- to subtelocentric chromosomes probably all have satellites, but these are not always visible. This has been observed earlier in several *Achillea* species, especially in plants with higher ploidy levels (e.g. Baltisberger & Baltisberger 1995; Baltisberger 2002; Baltisberger & Widmer 2009). The haploid karyotype found in plants from Mt Vourinos (*12309a*) is the same as that indicated for plants from other localities (Baltisberger 1992, 2002; Baltisberger & Baltisberger 1995).

Achillea clavennae L.

2*n* = 2*x* = 18: Austria, Carinthia, Mt Karawanken, SSW of Bleiburg, N of pass Knieps, scree and sparse meadow on limestone, 1950 m, 23 Jul 1992, *M. Baltisberger & A. Widmer 12622*, *12785*; Italy, Alpi Dolomitiche, ENE of Cortina d'Ampezzo, S of Tre Cime, near the hut Auronzo, scree on limestone, 2310 m, 20 Aug 1988, *G. Huber & W. Huber 10992, 11850*; Italy, Alpi Dolomitiche, 35 km E of Bolzano, 8 km SE of Canazei, Marmolada, between Rif. Contrin and Passo Ombretta, sparse meadow, 2150 m, 26 Jul 2000, *M. Baltisberger & A. Widmer 13619*, *13809*; Italy, Alpi Dolomitiche, 15 km ESE of Predazzo, NW side of Cimon della Pala, N- to W-exposed scree, 2250 m, 28 Jul 2000, *M. Baltisberger & A. Widmer 13631*, *13819*; Italy, Alpi Dolomitiche, 35 km E of Bolzano, 4 km NE of Canazei, N of Passo Pordoi, between rocks in open meadow, 2350–2400 m, 29 Jul 2000, *M. Baltisberger & A. Widmer 13647*; Italy, Alpi Bergamasche, 13 km WSW of Riva del Garda, S of Passo di Tremalzo, top of Cno. della Marogna, 1940–1953 m, 31 Jul 2000, *M. Baltisberger & A. Widmer 13684*, *13808*; Slovenia, NE of Bovec, W of pass Vrsic, N-exposed calcarous scree, 1870 m, 25 Jul 1992, *M. Baltisberger & A. Widmer 12673*, *13196*; Slovenia, NNW of Bovec, Mt Mangart, N side of Cima Piccola, meadow and scree on limestone, 1880–1900 m, 25 Jul 1992, *M. Baltisberger & A. Widmer 12682*, *12788*; Switzerland, ct. Ticino, 10 km SSE of Lugano, N of top of Monte Generoso, SW-exposed calcarous ledges, 1600 m, 21 May 1998, *M. Baltisberger 13493*.

The group of *Achillea clavennae* consists of five species growing in stony meadows, screes and ledges on limestone mostly on mountains (Franzén 1986). Two species are rather widespread, viz. *A. clavennae* in the Alps and the Balkan Peninsula (southwards to Mt Korab on the border between Albania and Macedonia) and *A. fraasii* (Balkan Peninsula from Montenegro to Greece and W Anatolia, see below). Three species have rather narrow distribution areas, viz. *A. ambrosiaca* (Boiss. & Heldr.) Boiss. (endemic on Mt Olympus), *A. pindicola* (endemic to C and S Pindhos in Greece, see below), and *A. umbellata* Sm. (endemic to C and S Greece).

Achillea clavennae is highly variable (Heimerl 1926), but, as the characters show weak correlations and many intermediate plants can be found, no infraspecific subdivision seems useful (Franzén 1986). We counted the chromosome number of plants from eight sites from four countries (Austria, Italy, Slovenia and Switzerland; the chromosome number of one Italian site [*10992*] was published earlier, see Baltisberger 1990). All plants were diploid with 2*n* = 2*x* = 18 chromosomes. Plants from all nine sites investigated showed the same haploid karyotype of seven metacentric and two submeta- to subtelocentric chromosomes, the latter with satellites. The same karyotype was indicated by Međedović (1976, 1984) and Baltisberger & al. (1996).

Achillea clypeolata Sm.

2*n* = 2*x* = 18: Greece, West Macedonia, island Agios Achilleios in lake Mikri Prespa, rocky slope, 860–900 m, 30 Jul 2011, *B. Baltisberger & M. Baltisberger 14873*, *15579*.

Achillea clypeolata shares several important characters and is therefore rather similar to *A. coarctata* (see below). Both grow in dry, rocky meadows in the Balkan Peninsula. They mainly differ in the density of the indumentum and the dissection of the leaves. *Achillea clypeolata* is less densely hairy, and the leaves are less dissected (1- to 2-pinnatisect) and mostly flat. *A. clypeolata* is known to be a diploid species with 2*n* = 2*x* = 18 chromosomes, as was found in the plants investigated here. The haploid karyotype consists of seven metacentric and two submeta- to subtelocentric chromosomes, the latter with satellites. The same karyotype was indicated in Kuzmanov & Kozuharov (1973), Baltisberger (1993, 2006), and Nedelcheva (1995).

Achillea coarctata Poir.

2*n* = 2*x* = 18: Bulgaria, SE part of Mt Pirin, W of Goce Delcev, near Popovi livadi, roadside, 1500 m, 29 Jul 1993, *M. Baltisberger 12771*, *12926*; Greece, Central Macedonia, NW of Edhessa, SE side of Mt Kajmakčalan, roadside, 900 m, 25 Jun 1987, *M. Baltisberger & U. Meili 11423*, *11690*; Greece, West Macedonia, NE of Grevena, Mt Vourinos, SW of Kataphygion E of Paleokastron, SE- to SW-exposed rocky slope, 1350–1550 m, 9 Aug 1990, *M. Baltisberger & U. Schäppi 12316*, *12538*.

Achillea coarctata is rather similar to *A. clypeolata* (see above), but in contrast to *A. clypeolata* the indumentum of *A. coarctata* is denser and the leaves are more dissected (2- to 3-pinnatisect) and subterete. Two ploidy levels are known, viz. diploid with 2*n* = 2*x* = 18 and tetraploid with 2*n* = 4*x* = 36 chromosomes. With 2*n* = 2*x* = 18 chromosomes all plants from both Greek sites proved to be diploid (the chromosome number of the Bulgarian site was published earlier, see Baltisberger 2006). The haploid karyotype of plants of all three sites shows seven metacentric and two submeta- to subtelocentric chromosomes, the latter with satellites. The same karyotype was given in Kuzmanov & Kozuharov (1973) and Baltisberger & Baltisberger (1995).

Achillea crithmifolia Waldst. & Kit. (det. Wolfgang Lippert, Munich, 1991).

2*n* = 2*x* = 18: Macedonia, 10 km W of Tetovo, Popova Sapka, rocky meadow, 1830–1845 m, 2 Aug 1990, *M. Baltisberger & U. Schäppi 12248*, *12498*.

Achillea crithmifolia grows in meadows and shrubby areas mostly on mountains in the Balkan Peninsula. Diploid plants with 2*n* = 2*x* = 18 as well as tetraploid plants with 2*n* = 4*x* = 36 chromosomes are known. The plants from Macedonia investigated here were diploid with 2*n* = 2*x* = 18 chromosomes and showed a haploid karyotype with seven metacentric and two submeta- to subtelocentric chromosomes, the latter with satellites, which corroborates the indications in Kuzmanov & al. (1989), Baltisberger (1994, 2002, 2006) and Baltisberger & Baltisberger (1995).

Achillea distans Waldst. & Kit. ex Willd.

2*n* = 6*x* = 54: Greece, Central Macedonia, WNW of Edhessa, Mt Kajmakčalan, near Voras Ski Resort, meadow, 2100–2200 m, 2 Aug 2011, *B. Baltisberger & M. Baltisberger 14878*, *14932*.

Achillea distans occurs in rocky meadows in the Alps, the Carpathians, as well as in the mountains of the Balkans. It is a member of the highly polymorphic and difficult *A. millefolium* group (see below), with diploid to highly polyploid taxa, or is at least closely related to that group (Danihelka & Rotreklova 2001). *Achillea distans* is known to be mostly hexaploid with 2*n* = 6*x* = 54 chromosomes, as were the plants from Greece investigated here. No suitable metaphases for an analysis of the karyotype were obtained from the material investigated here. Nevertheless the haploid karyotype of seven metacentric and two submeta- to subtelocentric chromosomes was indicated in Baltisberger (1992) and Baltisberger & Widmer (2009).

Achillea erba-rotta All.

2*n* = 2*x* = 18: Italy, Alpi Marittime, 60 km NNW of Nizza, N side of Col de la Lambarde, siliceous scree, 2300 m, 2 Aug 1997, *P. Senn & A.-B. Utelli 14446*.

Achillea erba-rotta belongs to a group of taxa growing on rocks and screes and in stony meadows in the Alps, the Appennini, as well as on Mt Olymbos in Greece. The taxa are treated at species or subspecies levels. We investigated three taxa of the group, viz. *A. erba-rotta* (here) as well as *A. moschata* and *A. lucana* (see below).

In the Alps three taxa of this group are indicated, all being calcifuge (Richardson 1976; Aeschimann & al. 2004): *Achillea erba-rotta* occurs in the SW Alps (France and Italy), *A. moschata* (see below) is widespread in the C and E Alps (from France to E Austria), and *A. erba-rotta* subsp. *ambigua* (Heimerl) Richardson growing in the SW Alps (France and Italy) is morphologically intermediate between the other two species.

Only diploid plants of *Achillea erba-rotta* are known, and the plants investigated here corroborate this ploidy level with 2*n* = 2*x* = 18 chromosomes with the haploid karyotype of seven metacentric and two submeta- to subtelocentric chromosomes, the latter chromosomes with satellites. As no karyotype information was found in literature, we present a metaphase of this species (Fig. 2B).

Achillea fraasii Sch. Bip.

2*n* = 2*x* = 18: Greece, Thessalia, N of Karditsa, NNE of Mt Karava, stony meadow, 1900–2000 m, 20 Jun 1987, *M. Baltisberger & U. Meili 11312*, *12355*, *12544*.

2*n* = 2*x* = 18 + 2–4B: Greece, Thessalia, WSW of Trikala, Mt Loupata, S of Petroulion, SE- to SW-exposed steep slope, 1950–2000 m, 10 Aug 1990, *M. Baltisberger & U. Schäppi 12522*.

Achillea fraasii belongs to the *A. clavennae* group (see above). It is highly variable (Heimerl 1926), but, as no subunit merits recognition, no infraspecific taxa are recognized (Franzén 1986). *Achillea fraasii* occurs in the W part of the Balkan Peninsula (Montenegro, Albania, Kosovo, Macedonia and Greece) as well at one site in W Anatolia (Mt Ida, Franzén 1991). Most plants are diploid with 2*n* = 2*x* = 18 chromosomes, but tetraploid plants with 2*n* = 4*x* = 36 chromosomes also exist. All plants investigated here showed 2*n* = 2*x* = 18 chromosomes and proved to be diploid, but in one of the two populations (Mt Loupata, *12522*) additionally two to four B-chromosomes were observed in every plant investigated (Fig. 1B). Neglecting the B-chromosomes, the haploid karyotype of plants from both sites consists of seven metacentric and two submeta- to subtelocentric chromosomes, the latter with satellites. The same haploid karyotype was indicated in Baltisberger (1993 [on tetraploid plants], 2002) and Baltisberger & Baltisberger (1995). Additional B-chromosomes have also been indicated for other species of the *A. clavennae* group: for *A. pindicola* see below; for *A. umbellata*, Contandriopoulos & Martin (1967) indicated B-chromosomes in plants from Mt Parnassos, and Tzanoudakis & Iatrou (1981) found one to three B-chromosomes in all plants of their five investigated Greek sites.

Achillea grandifolia Friv.

2*n* = 2*x* = 18: Greece, Epirus, NNW of Ioannina, SW side of Mt Timphi, Vikos gorge, between Aristi and Monodendrion, shrubbery, 700–800 m, 27 Jun 1992, *M. Baltisberger 12611*, *12980*.

Achillea grandifolia grows in mountain woods in the Balkan Peninsula and in Turkey. Only diploid plants with 2*n* = 2*x* = 18 chromosomes are known, as we found in the plants investigated here. The haploid karyotype shows seven metacentric and two submeta- to subtelocentric chromosomes, the latter with satellites. As no karyotype information was found in literature, we present a metaphase of this species (Fig. 2C).

Achillea holosericea Sm.

2*n* = 2*x* = 18: Greece, West Macedonia, NE of Grevena, Mt Vourinos, surroundings of Kataphygion E of Paleokastron, SE- to SW-exposed rocky slope, 9 Aug 1990, *M. Baltisberger & U. Schäppi 12317*, *12519*, *13091*; Greece, Thessalia, WSW of Trikala, Mt Loupata, S of Petroulion, SE- to SW-exposed steep rocky slope, 1950–2000 m, 10 Aug 1990, *M. Baltisberger & U. Schäppi 12329*, *12893*; Greece, Epirus, NNW of Ioannina, SW side of Mt Timphi, Vikos gorge, between Aristi and Monodendrion, calcarous rocks and scree, 700–750 m, 27 Jun 1992, *M. Baltisberger & W. Huber 13596b*, *12792*, *12981*, *13080*, *13081*.

2*n* = 2*x* = 18 + 1B: Greece, West Macedonia, ESE of Grevena, Mt Kamvounia, near Deskati, calcarous rocks and scree SW of Mt Vounassa, 1500–1615 m, 9 Aug 1990, *M. Baltisberger & U. Schäppi 12520*.

2*n* = 4*x* = 36: Greece, Thessalia, W of Karditsa, NNW of Mt Karava, rocks and stony meadow on limestone, 1980–2007 m, 7 Aug 1990, *M. Baltisberger & U. Schäppi 12307*, *12517*.

Achillea holosericea grows on gravel and stony meadows from lowlands to the mountains in the S part of the Balkan Peninsula (Albania, Kosovo, Macedonia and Greece). It is mostly diploid with 2*n* = 2*x* = 18 chromosomes, but tetraploid plants with 2*n* = 4*x* = 36 chromosomes are also known. We investigated plants from five Greek sites. Four of them proved to be diploid with 2*n* = 2*x* = 18 chromosomes. From one of these sites with diploids (Mt Kamvounia, *12520*) all four investigated plants constantly showed one additional B-chromosome (Fig. 1C). Plants with one to three B-chromosomes were also reported by Persson (in Franzén 1991) from two mountains on Peloponnisos (S Greece). All plants from one site (Mt Karava, *12307*) were tetraploid with 2*n* = 4*x* = 36 chromosomes.

Neglecting the B-chromosomes, the haploid karyotype found in the plants from four sites always proved to consist of seven metacentric and two submeta- to subtelocentric chromosomes, the latter with satellites. The same haploid karyotype was indicated in Baltisberger (1984, 1991, 1993, 1994). Five plants were investigated from the fifth site (Vikos gorge, *13596b*) and all proved to be diploid with 2*n* = 2*x* = 18 chromosomes. One of these plants showed the typical haploid karyotype, as do the plants from the other sites. But four plants had a deviating karyotype with one of the 14 metacentric chromosomes changed into a submeta- to subtelocentric chromosome. The short arm of this chromosome was similar to the short arm of the other four satellited submeta- to subtelocentric chromosomes, but the long arm of this chromosome was distinctly longer than the arms of the metacentric chromosomes. The diploid karyotype of these four plants therefore consisted of 13 metacentric chromosomes, one submeta- to subtelocentric chromosome without satellites and four submeta- to subtelocentric chromosomes with satellites. These findings suggest that a change within one metacentric chromosome took place and a substantial part of one arm has been translocated to the other arm of the same chromosome (Fig. 1D).

In 1992 we sampled six living rosettes of young plants in the Vikos gorge (from where the plants with the deviating karyotype originate). Five individuals survived, four of them showed the deviating karyotype, and only one plant proved to have the "regular" karyotype. As we sampled six rosettes by chance and got at least four with the deviating karyotype, those plants seem to be rather frequent and viable within that natural population and their survival is not just the result of protection in culture. We checked important morphological characters comparing the five plants from the Vikos gorge all flowering in the greenhouse (shape and indumentum of the leaves, hairs on the stems, number of capitula per corymb, size and hairs of the involucres). No significant morphological difference could be detected. We stained pollen grains of the respective plants with carmine acetic acid, and all five plants proved to have well-developed and well-staining pollen. It seems that the deviating karyotype has no negative impact on the fitness of the individuals. Nevertheless we do not currently know whether plants with the deviating karyotype are able to successfully reproduce and produce viable offspring.

Achillea lucana Pignatti

2*n* = 2*x* = 18: Italy, Calabria, 6 km SW of Castrovillari, Saracena, scree, 900 m, July 1999, *G. Pellegrino, 13826*.

The calcicole *Achillea lucana* belongs to the group of *A. erba-rotta* (see above). It is a taxon of a cluster of plant populations from screes and mountains scattered in C and S Italy (Richardson 1976; Pignatti 1979; Pignatti & Ehrendorfer 1982). Several names on various taxonomic levels have been assigned to the populations of this cluster [e.g. *A. erba-rotta* var. *ambigua* Heimerl, *A. erba-rotta* subsp. *ambigua* (Heimerl) Richardson, *A. erba-rotta* subsp. *calcarea* (Porta) Richardson, *A. moschata* var. *calcarea* Porta, *A. lucana* Pignatti, *A. rupestris* Huter vel Porta, *A. erba-rotta* subsp. *rupestris* (Porta) Richardson]. The delimitations of the respective entities is unresolved, and further investigations (including molecular methods) studying plants from as many origins as possible are needed.

Mt Pollino is mentioned in Pignatti & Ehrendorfer (1982) as the southernmost site with plants of this group. These plants from Mt Pollino are named as *Achillea rupestris* Huter, a taxon with undivided leaves and bracts with narrow margins (less than 0.2 mm). The plants investigated here originate from Saracena, which is situated about 20 km S of Mt Pollino. As the plants from Saracena show pinnatifid leaves and bracts with rather broad margins (more than 0.3 mm), they best fit with *A. lucana* even though this species has only been reported from sites N of Mt Pollino (Pignatti 1979). The chromosome number of *A. lucana* was not known until now. With 2*n* = 2*x* = 18 (Fig. 1E) the chromosome number is the same as that indicated for plants from Mt Pollino [Cesca & Morrone 1981, named as *A. erba-rotta* subsp. *calcarea* (Porta) Richardson]. The plants investigated here show a haploid karyotype of seven metacentric and two submeta- to subtelocentric chromosomes, the latter with satellites.

Achillea macrophylla L.

2*n* = 2*x* = 18: Switzerland, ct. Valais, N of pass Simplon, N-exposed wet slope, 1850 m, 9 Jul 1988, *M. Baltisberger 11840*; Switzerland, ct. Valais, S of Sierre, Val d'Anniviers, S of Zinal, E-exposed wet slope, 1820 m, 9 Jul 1989, *M. Baltisberger & N. Tonascia 12978*; Switzerland, ct. Valais, Val d'Hérens, S of Sion, SE of Arolla, Les Places, NW-exposed wet slope, 2050 m, 27 Jul 1994, *M. Baltisberger & A.-B. Utelli 12936*, 13082; Switzerland, ct. Grisons, Upper Engadine, 0.5 km S of Sils-Maria, in gorge Fedacla, wet slope, 1810 m, 29 Aug 1998, *M. Baltisberger & M. Ring 13452, 13503*.

Achillea macrophylla grows in the Alps and in the N Appennini. We investigated plants from four Swiss sites. All plants proved to be diploid with 2*n* = 2*x* = 18 chromosomes, corroborating the indications in literature. The haploid karyotype shows seven metacentric and two submeta- to subtelocentric chromosomes, the latter with satellites. As no karyotype information was found in literature, we present a metaphase of this species (Fig. 2D).

Achillea millefolium L. s.l.

2*n* = 2*x* = 18: Greece, West Macedonia, ESE of Grevena, Mt Kamvounia, near Deskati, calcarous rocks and scree SW of Mt Vounassa, 1500–1615 m, 9 Aug 1990, *M. Baltisberger & U. Schäppi 12322, 12359*.

2*n* = 6*x* = 54: France, N of Grenoble, Massif de la Chartreuse, N of St Pierre-de-Chartreuse, Mt Petit Som, SW-exposed slope, 1725 m, 9 Aug 1988, *A. Bosshard & M. Jeker 11890*; Norway, Oppland, Dovre, Grimsdalen, Verkenseter, roadside, 1000 m, 23 Jul 1993, *W. Huber & Ö. Nilsson 14214*, *13167*; Switzerland, ct. Valais, S of Sierre, Val de Zinal, L'Ar Pitteta, stony meadow, 2050 m, 9 Jul 1989, *W. Huber 12357*.

The polyploid complex of *Achillea millefolium* occurs in Europe, W Asia and North America, and diploid to octoploid plants are known. Hybridization and introgressions seem to be frequent, and identification of a given plant is therefore often difficult. Plants of this complex that could be determined are presented under the respective name (viz. *A. distans*, *A. setacea* or *A. stricta*). Plants summarized here under *A. millefolium* s.l. could not be assigned to a specific taxon within the complex.

The plants from Greece proved to be diploid with 2*n* = 2*x* = 18 chromosomes, and the plants from France and

Norway were hexaploid with 2*n* = 6*x* = 54 (the chromosome number of the Swiss site was published earlier, see Huber & Baltisberger 1992). All plants from all four sites showed the same haploid karyotype with seven metacentric and two submeta- to subtelocentric chromosomes, the latter with satellites (in hexaploid plants not always with all satellites visible).

Achillea moschata Wulfen

2*n* = 2*x* = 18: Switzerland, ct. Grisons, Upper Engadine, 10 km SE of St Moritz, between Morteratsch and the hut Boval, scree, 2100–2300 m, 4 Oct 1987, *M. Baltisberger 11630, 11731*; Switzerland, ct. Valais, S of Brig, W of pass Simplon, Hopsche, siliceous scree, 2000 m, 9 Jul 1988, *M. Baltisberger 11666a*; Switzerland, ct. Valais, S of Sierre, Val d'Anniviers, 2 km SSE of Zinal, SW-exposed steep meadow, 2450 m, 9 Jul 1989, *W. Huber 11881*, *12117*; Switzerland, ct. Valais, S of Brig, S of Gamsen in the Nanz valley, ENE-exposed stony slope, 2300–2350 m, 10 Sep 1991, *M. Baltisberger & W. Huber 12545*; Switzerland, ct. Valais, Val d'Hérens, S of Sion, N of Arolla, 750 m WSW of Satarma, rocky place near Lac Bleu, 2090 m, 26 Jul 1994, *M. Baltisberger 12935, 13085*; Switzerland, ct. Grisons, Val Müstair, 6 km S of Sta. Maria, pass Umbrail, meadow, 2520 m, 30 Aug 1997, *M. Baltisberger & M. Ring 13416*; Switzerland, ct. Grisons, Upper Engadine, 1.5 km NE of Pontresina, between hut Segantini and Piz Languard, SW-exposed rocky siliceous slope, 2650 m, 30 Aug 1998, *M. Baltisberger 13459, 13491*.

The calcifuge *Achillea moschata* belongs to the group of *A. erba-rotta* (see above) and is sometimes treated on the subspecies level as *A. erba-rotta* subsp. *moschata* (Wulfen) Richardson. It occurs in the C and E Alps (from France to E Austria). It is diploid with 2*n* = 2*x* = 18 chromosomes, which was confirmed by plants from five sites from Switzerland (the chromosome numbers of two sites [*11881*, *12545*] were published earlier, see Huber & Baltisberger 1992). The plants from all seven sites showed the same haploid karyotype consisting of seven metacentric and two submeta- to subtelocentric chromosomes, the latter with satellites. As no karyotype information was found in literature, we present a metaphase of this species (Fig. 2E).

Achillea multifida DC.

2*n* = 2*x* = 18: Bulgaria, 60 km SSE of Sofija, Mt Rila, surroundings of the lakes NNE of Moussala, meadow, 2400 m, 25 Jul 1993, *M. Baltisberger 12747*, *12885*; Greece, Central Macedonia, NW of Edhessa, SE side of Mt Kajmakčalan, stony meadow, 2220 m, 25 Jun 1987, *M. Baltisberger & U. Meili 11418*, *11699*; Greece, Central Macedonia, WNW of Edhessa, Mt Kajmakčalan, near Voras Ski Resort, meadow, 2100–2200 m, 2 Aug 2011, *B. Baltisberger & M. Baltisberger 14877*, *14928*.

Achillea multifida occurs in the S parts of the Balkan Peninsula (Albania, Macedonia, Bulgaria and Greece) and on Uludağ in NW Turkey. It is closely related or even conspecific with *A. clusiana* Tausch, which has a distribution area restricted to the E Alps. The separation of plants from the Balkans and Turkey as *A. multifida* is therefore not generally accepted, but it seems that the two entities are not conspecific and might be treated as distinct taxa (Ehrendorfer 2005, in litt.).

Diploid with 2*n* = 2*x* = 18 chromosomes (Turkey: Martin-Noguet 1969; Bulgaria: Kuzmanov & Kozuharov 1970; Baltisberger 2006) and decaploid plants with 2*n* = 10*x* = 90 chromosomes (Mt Korab and Šar Planina in Albania and Macedonia; Baltisberger 1992) are known. The plants from Bulgaria and Greece investigated here showed 2*n* = 2*x* = 18 chromosomes and proved to be diploid. The haploid karyotype consists of seven metacentric and two submeta- to subtelocentric chromosomes, the latter with satellites. The same or at least a rather similar karyotype was indicated for diploid (Kuzmanov & Kozuharov 1973; Baltisberger 2006) as well as for decaploid plants (Baltisberger 1992).

Achillea nana L.

2*n* = 2*x* = 18: Switzerland, ct. Valais, W of pass Simplon, S of Mt Tochuhorn, E-exposed siliceous slope, 2250–2300 m, 9 Jul 1988, *M. Baltisberger 11833*; Switzerland, ct. Valais, S of Sierre, Val d'Anniviers, 2.5 km NNE of Zinal, SW-exposed siliceous scree, 2550 m, 13 Jul 1989, *M. Baltisberger 12143*; Switzerland, ct. Valais, S of Brig, S of Gamsen in the Nanz valley, ENE-exposed stony slope, 2300–2350 m, 10 Sep 1991, *M. Baltisberger & W. Huber 12546*; Switzerland, ct. Grisons, Val Müstair, 6 km S of Sta. Maria, SE of Piz Umbrail, sparse meadow, 2700 m, 30 Aug 1997, *M. Baltisberger & M. Ring 13408*; Switzerland, ct. Grisons, Upper Engadine, 1.5 km NE of Pontresina, between hut Segantini and Piz Languard, SW-exposed rocky siliceous slope, 2650 m, 30 Aug 1998, *M. Baltisberger 13458*; Switzerland, ct. Grisons, Upper Engadine, 2.5 km WNW of Maloja, W of Piz Lunghin, siliceous scree, 2700–2750 m, 2 Sep 1998, *M. Baltisberger & M. Ring 13469, 13519*.

Achillea nana is calcifuge and grows in screes and on rocks in the W and C Alps. The chromosome number was investigated on plants from five Swiss sites. They all proved to be diploid with 2*n* = 2*x* = 18 chromosomes (the chromosome number of one site [*12546*] was published earlier, see Huber & Baltisberger 1992). The haploid karyotype proved to be with seven metacentric and two submeta- to subtelocentric chromosomes, the latter with satellites. As no karyotype information was found in literature, we present a metaphase of this species (Fig. 2F).

Achillea nobilis L.

2*n* = 2*x* = 18: Greece, Thessalia, WSW of Trikala, Mt Loupata, S of Petroulion, SE- to SW-exposed steep rocky slope, 1950–2000 m, 10 Aug 1990, *M. Baltisberger & U. Schäppi 12330* (det. Wolfgang Lippert, Munich, 1991); Switzerland, ct. Valais, NNW of Visp, between Ausserberg and Eggerberg, S-exposed dry rocky slope, 1000 m, 19 Jun 1989, *M. Baltisberger & W. Huber 11453*, *12356*.

Achillea nobilis is a variable species and belongs to a difficult group of species (Bässler 1963). It grows in dry habitats in C and S Europe, in Turkey and further eastwards. It is a mostly diploid species with $2n = 2x = 18$ chromosomes, as confirmed here by our investigations on Greek plants (the chromosome number of the Swiss site was published earlier, see Huber & Baltisberger 1992). The haploid karyotype in plants from both sites investigated consists of seven metacentric and two submeta- to subtelocentric chromosomes, the latter with satellites. The same karyotype was indicated by Međedović (1984) in *A. nobilis* as well as by Kuzmanov & Kozuharov (1973) and Baltisberger & Baltisberger (1995) in *A. neilreichii* A. Kerner [= *A. nobilis* subsp. *neilreichii* (A. Kerner) Velen.], which is closely related and probably even conspecific with *A. nobilis*.

Achillea oxyloba (DC.) Sch. Bip.

2*n* = 2*x* = 18: Italy, Alpi Dolomitiche, ENE of Cortina d'Ampezzo, S of Tre Cime, near the hut Auronzo, scree on limestone, 2310 m, 20 Aug 1988, *G. Huber & W. Huber 10993, 11851*; Italy, Alpi Dolomitiche, 35 km E of Bolzano, 8 km SE of Canazei, Marmolada, between Rif. Contrin and Passo Ombretta, scree, 2500–2600 m, 26 Jul 2000, *M. Baltisberger & A. Widmer 13609*, *13825*; Italy, Alpi Dolomitiche, 15 km ESE of Predazzo, NW side of Cimon della Pala, N- to W-exposed scree, 2250 m, 28 Jul 2000, *M. Baltisberger & A. Widmer 13630*, *13768*; Italy, Alpi Dolomitiche, 35 km E of Bolzano, 4 km NE of Canazei, N of Passo Pordoi, between Rif. Forcla Pordoi and Sass Pordoi, rocks and scree, 2880–2920 m, 29 Jul 2000, *M. Baltisberger & A. Widmer 13649*, *13765*.

The *Achillea oxyloba* group consists of three mountain taxa, which are treated as species or subspecies. The three taxa have clearly disjunct geographic areas, viz. *A. mucronulata* Bertol. [= *A. oxyloba* subsp. *mucronulata* (Bertol.) Richardson] in the C and S Appennini, *A. oxyloba* in the SE Alps and *A. schurii* Sch. Bip. [= *A. oxyloba* subsp. *schurii* (Sch. Bip.) Heimerl] in the E and S Carpathians. All three taxa are known to be diploid with $2n = 2x = 18$ chromosomes, as we found in plants of *A. oxyloba* from three sites from the Alpi Dolomitiche (the chromosome number of one site [*10993*] was published earlier, see Baltisberger 1990). The haploid karyotype of plants from all four sites consists of seven metacentric and two submeta- to subtelocentric chromosomes, the latter with satellites. All three taxa of the group show the same haploid karyotype, viz. Brullo & al. (1991) for *A. mucronulata*, Maffei & al. (1986) for *A. oxyloba*, and Tacina (1979) and Baltisberger & Widmer (2009) for *A. schurii*.

Achillea pindicola subsp. ***integrifolia*** (Halacsy) Franzén

2*n* = 2*x* = 18: Greece, Thessalia, WSW of Trikala, Mt Loupata, rocks and scree, 1800–2066 m, 21 Jun 1987, *M. Baltisberger & U. Meili 11337*, *12523*.

Achillea pindicola is an endemic species of C and S Pindhos in Greece and belongs to the group of *A. clavennae* (see above). It is divided into two subspecies differing in shape and indumentum of the leaves (Franzén 1986). Both subspecies are diploid with $2n = 2x = 18$ chromosomes (Contandriopoulos & Martin 1967; Franzén 1986), sometimes additional B-chromosomes are indicated (Franzén 1986). All plants investigated here proved to be diploid without any B-chromosomes and with a haploid karyotype of seven metacentric and two submeta- to subtelocentric chromosomes, the latter with satellites. As no karyotype information was found in literature, we present a metaphase of this species (Fig. 2G).

Achillea ptarmica L.

2*n* = 2*x* = 18: Norway, Troms, Tromsö, Mt Flöjfjell, near the funicular station, roadside, 50 m, 29 Jul 1993, *W. Huber & Ö. Nilsson 14267*, *13286*; Switzerland, ct. Basle, Riehen, near the bridge Weil across the river Wiese, meadow, 270 m, 14 Aug 1989, *B. Merz 12977*; Switzerland, ct. Zürich, S end of lake Greifensee, Aaspitz, roadside, 436 m, 25 Aug 1992, *M. Baltisberger & X. Jutz 12709*, *12790*; Switzerland, ct. Aargau, N of Gippingen, W of the dam of the power station Klingnau, roadside, 320 m, 20 Aug 1994, *M. Baltisberger & A.-B. Utelli 12970*, *13130*; Switzerland, ct. Valais, N of Brig, on the path from Naters to Geimen, meadow, 800 m, 15 May 1997, *M. Baltisberger 13285*.

Achillea ptarmica is widespread in Europe and grows in damp meadows and ruderal places. The species is known to be diploid with $2n = 2x = 18$ chromosomes, which was confirmed by plants from all five sites investigated. The haploid karyotype consists of seven metacentric and two submeta- to subtelocentric chromosomes, the latter with satellites. As no karyotype information was found in literature, we present a metaphase of this species (Fig. 2H).

Achillea setacea Waldst. & Kit. (det. Arne Strid, Copenhagen, 1991)

2*n* = 2*x* = 18: Greece, West Macedonia, E of Kozani, Mt Pieria, S of Kataphygion, sparse forest, 1400–1600 m, 24 Jun 1987, *M. Baltisberger & U. Meili 11401*, *11683*.

Achillea setacea is a member of the polyploid complex of *A. millefolium* (see above). It is mostly diploid with $2n = 2x = 18$ chromosomes, as are the plants investigated from Greece. The haploid karyotype consists of seven metacentric and two submeta- to subtelocentric chromosomes, the latter with satellites. The same or at least rather similar karyotypes were indicated by Međedović (1984), Kuzmanov & al. (1989) and Danihelka & Rotreklova (2001).

Achillea stricta Schleich. ex Gremli

$2n = 8x = 72$: Switzerland, ct. Grisons, S of Thusis, 0.5 km NE of Campsut, open places under W-exposed rocks, 1800 m, 30 Jul 2001, *M. Baltisberger & U. Müller 13774*, *13818*.

Achillea stricta belongs to the polyploid complex of *A. millefolium* (see above). It grows in grasslands and ruderal places in the Carpathians, the Alps, as well as in the Appennini. It is a hexaploid species with $2n = 6x = 54$ chromosomes. All six plants investigated here proved to be octoploid with $2n = 8x = 72$ chromosomes, which is a new ploidy level for this species. As no suitable metaphases have been obtained on the material investigated here, nothing can be said about the karyotype.

Achillea tomentosa L.

$2n = 2x = 18$: Switzerland, ct. Valais, Goms, NW of Grengiols, SE-exposed dry slope, 850–900 m, 15 Jul 1988, *M. Baltisberger & G. Eich 11660*, *11889*; Switzerland, ct. Valais, NNW of Visp, between Ausserberg and Eggerberg, S-exposed dry rocky slope, 1000 m, 19 Jun 1989, *M. Baltisberger & W. Huber 11454*, *12535*.

Achillea tomentosa grows in dry habitats in the lowlands of SW Europe (Spain, France, Switzerland and Italy) and is closely related to *A. chrysocoma* (see above). The plants from Grengiols (*11660*) are diploid with $2n = 2x = 18$ (the chromosome number of the other site [*11454*] was published earlier, see Huber & Baltisberger 1992). The haploid karyotype of plants from both sites shows seven metacentric and two submeta- to subtelocentric chromosomes, the latter with satellites. As no karyotype information was found in literature, we present a metaphase of this species (Fig. 2I).

General discussion

All taxa of *Achillea* investigated to date show the basic chromosome number $x = 9$ on diploid as well as on polyploid levels. The haploid karyotype within *Achillea* is rather uniform with seven metacentric and two submeta- to subtelocentric chromosomes, the latter with (mostly visible) satellites, as observed in 27 taxa representing three sections, *A.* sect. *Achillea*, *A.* sect. *Anthemoideae* and *A.* sect. *Ptarmica* (we could not investigate any taxon from the fourth section, *A.* sect. *Babounya*). Besides the 27 taxa investigated and discussed here, the same karyotype is given in literature for several additional taxa. From *A.* sect. *Achillea*: *A. collina* Rchb. (Baltisberger 2006), *A. lingulata* Waldst. & Kit. (Baltisberger & Widmer 2009) and *A. neilreichii* A. Kerner (Baltisberger & Baltisberger 1995); from *A.* sect. *Anthemoideae*: *A. abrotanoides* (Vis.) Vis. (Baltisberger 1993; Baltisberger & Baltisberger 1995), *A. ambrosiaca* (Boiss. & Heldr.) Boiss. (Baltisberger 1994), *A. schurii* Sch. Bip. (Baltisberger & Widmer 2009) and *A. umbellata* Sm. (Tzanoudakis & Iatrou 1981; Baltisberger 1994); and from *A.* sect. *Babounya*: *A. fragrantissima* (Forssk.) Sch. Bip. (Baltisberger 2012). Thus, taxa from all sections currently recognized in *Achillea* show the same haploid karyotype. The genus therefore is rather uniform with respect to the chromosome morphology. This might be an important prerequisite to allow even morphologically strongly divergent taxa to hybridize, as is the case in *Achillea* (Heimerl 1884, 1926; Halacsy 1902; Hayek 1928–1931; Wagenitz 1979; Richardson 1976; Hess & al. 1980; Franzén 1991; Afanas'ev & Bochantsev 1995).

Most *Achillea* species are diploid with $2n = 2x = 18$ chromosomes, but polyploid species up to $2n = 14x = 126$ have been reported (Dabrowska 1989). Polyploidy is frequent and occurs throughout the genus (Guo & al. 2004). Despite this extensive variation in ploidy levels, all species show the same haploid karyotype. The chromosomes within *Achillea* are rather large, but it is interesting that in plants with higher ploidy levels the chromosomes generally are smaller than in diploids, as is also the case in *Ranunculus* (Baltisberger & Hörandl 2016). As the size of chromosomes varies, we do not consider the size of chromosomes for our analysis.

Ranunculus (*Ranunculaceae*) shares several interesting aspects with *Achillea*: with about 600 species, *Ranunculus* is rather species-rich, has a broad geographic distribution and shows substantial variation in morphology, life cycle and ecology (Tamura 1995; Emadzade & al. 2010; Hörandl & Emadzade 2012). In marked contrast to *Achillea*, however, *Ranunculus* shows significant variability in karyotypes, and karyotype evolution mirrors the molecular phylogeny of the genus (Baltisberger & Hörandl 2016).

The splitting of *Achillea* into four sections is based on molecular data, but the morphology of the chromosomes and therefore the karyotype within *Achillea* is homogenous. This is in contrast to *Ranunculus* with eight different karyotypes reflecting the phylogenetic structure of the genus. In general, hybrids between taxa with differing karyotypes are not viable or at least sterile, as pairing of the not or not fully homologous chromosomes in meiosis is problematic or even impossible. This is also reflected by the behaviour of the two genera: in *Ranunculus*, fertile hybrids have only been reported between species sharing the same karyotype (Baltisberger & Hörandl 2016), but hybrids in *Achillea* frequently occur (Heimerl 1884), even between morphologically clearly separated taxa and different ploidy levels (e.g. *A. clypeolata* [2x] and *A. collina* J. Becker ex Heimerl [4x; member of *A. millefolium* s.l.]; Saukel & al. 2003). This contrast suggests that karyotype variation has played an important role in the evolution of reproductive barriers in *Ranunculus* but not in *Achillea*.

Acknowledgements

We thank Johannes Saukel (WUP) and an anonymous reviewer for comments on an earlier version of this paper.

References

Aeschimann D., Lauber K., Moser D. M. & Theurillat J.-P. 2004: Flora alpina. – Bern.

Afanas'ev K. S. & Bochantsev V. P. 1995: *Achillea* L. – Pp. 76–142 in: Shishkin B. K. & Bobrov E. G. (ed.), Flora of the U.S.S.R. **XXVI**. – Dehra Dun: Bishen Singh, Mahendra Pal Singh & Koeltz Scientific Books.

Baltisberger M. 1984: Zytologische Untersuchungen an einigen Pflanzen aus Albanien. – Ber. Geobot. Inst. ETH, Stiftung Rübel, Zürich **51:** 63–77.

Baltisberger M. 1990: Zytologische Untersuchungen an einigen Arten aus Italien. – Arch. Bot. Ital. **66:** 153–65.

Baltisberger M. 1991: Cytological investigations of some Greek plants. – Fl. Medit. **1:** 157–173.

Baltisberger M. 1992: Botanische Notizen und zytologische Untersuchungen an einigen Pflanzen (insbesondere aus den Gattungen *Ranunculus* und *Achillea*) aus dem albanisch-jugoslawischen Grenzgebiet (Korab, Sar Planina). – Ber. Geobot. Inst. ETH, Stiftung Rübel, Zürich **58:** 192–211.

Baltisberger M. 1993: Zytologische Untersuchungen an Compositen aus Albanien. – Candollea **48:** 437–448.

Baltisberger M. 1994: Chromosome numbers in some species from Greece. – Bot. Chron. (Patras) **11:** 15–29.

Baltisberger M. 2002: Cytological investigations on some Albanian plant species. – Candollea **56:** 245–259.

Baltisberger M. 2006: Cytological investigations on Bulgarian phanerogams. – Willdenowia **36:** 205–216.

Baltisberger M. 2012: IAPT/IOPB chromosome data. – Taxon **61:** 889 + E2–5.

Baltisberger M. & Baltisberger E. 1995: Cytological data of Albanian plants. – Candollea **50:** 457–493.

Baltisberger M. & Hörandl E. 2016: Karyotype evolution supports the molecular phylogeny in the genus *Ranunculus* (*Ranunculaceae*). – Perspect. Pl. Ecol. Evol. Syst. **18:** 1–14.

Baltisberger M., Krug K. & Widmer A. 1996: Cytological data of some plant species from Italy. – Archiv. Geobot. **2:** 133–142.

Baltisberger M. & Widmer A. 2009: Karyological data of angiosperms from Romania. – Willdenowia **39:** 353–363.

Bässler M. 1963: Zur Taxonomie der Gattung *Achillea* 1. Die Formenkreise um *A. nobilis* L. und *A. virescens* (Fenzl) Heimerl. – Feddes Repert. **68:** 139–162 (+1 Tafel).

Brullo S., Guglielmo A., Pavone P. & Terrasi M. C. 1991: Numeri cromosomici per la Flora Italiana: 1251–1266. – Inform. Bot. Ital. **23:** 39–46.

Cesca G. & Morrone M. 1981: Cariologia di *Achillea erba-rotta* All. subsp. *calcarea* (Porta) I. B. K. Richardson, del M. Pollino. – Giorn. Bot. Ital. **115:** 388.

Contandriopoulos J. & Martin D. 1967: Contribution à l'étude cytotaxinomique des *Achillea* de Grèce. Irrégularités de la méiose. – Bull. Soc. Bot. France **114:** 257–275.

Dabrowska J. 1989: Problematic octaploid forms and a new chromosome number in the genus *Achillea* L., $2n = 126$. – Acta Soc. Bot. Polon. **58:** 179–184.

Danihelka J. & Rotreklova O. 2001: Chromosome numbers within the *Achillea millefolium* and the *A. distans* groups in the Czech Republic and Slovakia. – Folia Geobot. **36:** 163–191.

Diklić N., Stevanović V. & Niketić M. 1991: The taxonomic status of *Achillea alexandri-regis* Bornm. & Rudski. – Bot. Chron. (Patras) **10:** 729–735.

Ehrendorfer F. & Guo Y.-P. 2005: Changes in the circumscription of the genus *Achillea* (*Compositae – Anthemideae*) and its subdivision. – Willdenowia **35:** 49–54.

Ehrendorfer F. & Guo Y.-P. 2006: Multidisciplinary studies on *Achillea* sensu lato (*Compositae – Anthemideae*): new data on systematics and phylogeography. – Willdenowia **36:** 69–87.

Emadzade K., Lehnebach C., Lockhart P. & Hörandl E. 2010: A molecular phylogeny, morphology and classification of genera of *Ranunculeae* (*Ranunculaceae*). – Taxon **59:** 809–828.

Franzén R. 1986: Taxonomy of the *Achillea clavennae* group and the *A. ageratifolia* group (*Asteraceae*). – Willdenowia **16:** 13–33.

Franzén R. 1988: Differentiation pattern in *Achillea ageratifolia* (*Asteraceae*). – Willdenowia **18:** 47–62.

Franzén R. 1991: *Achillea* L. – Pp. 431–450 in: Strid A. & Tan K. (ed.), Mountain flora of Greece **2.** – Edinburgh: Edinburgh University Press.

Gaijic M. 1975: *Asteraceae* Dumortier. – Pp. 1–465 in: Josifovic M. (ed.), Flora SR Srbije **VII**. – Beograd: Srpska akademija nauka i umetnosti.

Goldblatt P. & Johnson D. E. (ed.) 1979+: Index to plant chromosome numbers (IPCN). – Published at: http://www.tropicos.org/Project/IPCN [accessed 21 Jul 2015].

Grant V. 1971: Plant speciation. – New York: Columbia University Press.

Guo Y.-P., Ehrendorfer F. & Samuel R. 2004: Phylogeny and systematics of *Achillea* (*Asteraceae – Anthemideae*) inferred from nrITS and plastid *trnL-F* DNA sequences. – Taxon **53:** 657–672.

Guo Y.-P., Saukel J., Mittermayr R. & Ehrendorfer F. 2005: AFLP analyses demonstrate genetic divergence, hybridization, and multiple polyploidization in the evolution of *Achillea* (*Asteraceae – Anthemideae*). – New Phytol. **166:** 273–290.

Halácsy E. von 1902: Conspectus florae graecae. **2.** – Lipsiae: Guilelmi Engelmann.

Hayek A. von 1928–1931: Prodromus florae peninsulae balcanicae. Band 2. Dicotyledoneae Sympetalae. – Repert. Spec. Nov. Regni Veg. Beih. **30(2).**

Heimerl A. 1884: Monographia sectionis "*Ptarmica*" Achilleae generis: Die Arten, Unterarten, Varietäten und Hybriden der Section *Ptarmica* des Genus *Achillea*. – Denkschr. Kaiserl. Akad. Wiss. Wien, Math.-Naturwiss. Kl. **48:** 113–192.

Heimerl A. 1926: Achilleen-Studien I–IV. – Österr. Bot. Zeitschr. **75:** 133–153.

Hess H. E., Landolt E. & Hirzel R. 1980: Flora der Schweiz und angrenzender Gebiete **3:** *Plumbaginaceae* his *Compositae*, ed. 2. – Basel: Springer.

Hörandl E. & Emadzade K. 2012: Evolutionary classification: A case study on the diverse plant genus *Ranunculus* L. (*Ranunculaceae*). – Perspect. Plant Ecol. Evol. Syst. **14**, 310–324.

Huber W. & Baltisberger M. 1992: IOPB chromosome data. – IOPB Newsletter **18/19:** 6–8.

Kovačević N. N., Ristić M. S., Tasić S. R., Menković N. R., Grubišić D. V. & Đoković D. D. 2005: Comparitive study of essential oil of three *Achillea* species from Serbia. – J. Essent. Oil Res. **17:** 57–60.

Kundaković T., Dobrić S., Bokonjić D., Dragojević-Simić V., Kilibarda V. & Kovačević N. 2000: Anti-inflammatory and anti-ulcer activity of *Achillea alexandri-regis*. – Pharmazie **55:** 866–867.

Kundaković T., Fokialakis N., Magiatis P, Kovačević N. & Chinou I. 2004: Triterpenic derivatives of *Achillea alexandri-regis* Bornm. & Rudski. – Chem. Pharm Bull. **52:** 1462–1465.

Kundaković T., Mimica-Dukić N. & Kovačević N. 2005a: Free radical scavenging activity of *Achillea alexandri-regis* extracts. – Fitoterapia **76:** 574–576.

Kundaković T., Stanojković T., Juranić Z. & Kovačević N. 2005b: Cytotoxic and antioxidant activity of *Achillea alexandri-regis*. – Pharmazie **60:** 319–320.

Kuzmanov B. & Kozuharov S. 1970: IOPB chromosome number reports. – Taxon **19:** 265–266.

Kuzmanov B. & Kozuharov S. 1973: Karyological study of Bulgarian *Compositae*. 2. – Izv. Bot. Inst. (Sofia) **24:** 125–137.

Kuzmanov B. A. Zdravkova M. A. & Georgieva S. B. 1989: Variability of the Bulgarian yarrow species from the group *Achillea millefolium* and *A. crithmifolia*. I. Morphological and karyological study. – Fitologija **36:** 26–43.

Levan A., Fredga K. & Sandberg A. A. 1964: Nomenclature for centromeric position on chromosomes. – Hereditas **52:** 201–220.

Maffei M., Deirino L. & Codignola A. 1986: Numeri cromosomici per la Flora Italiana**:** 1064–1069. – Inform. Bot. Ital. **18:** 153–158.

Martin-Noguet D. 1969: Contribution à l'étude cytotaxinomique des *Achillea* et des *Pyrethrum* de Turquie. – Bull. Soc. Bot. France **116:** 197–206.

Međedović S. 1976: Ecological and cytogenetic characteristics of the *Achillea clavenae* L. and *Achillea ageratifolia* (S.S.) Boiss. subsp. *aizoon* (Gris.) Heim. – God. Biol. Inst. Univ. Sarajevo **29:** 69–77.

Međedović S. 1984: Cytogenetic variability and possible directions of karyotype evolution in the genus *Achillea* L. on the Dinarids. – God. Biol. Inst. Univ. Sarajevo **37:** 61–78.

Međedović S. & Siljak S. 1978: Interpopulational variability of some chromosome complement characteristics in *Achillea lingulata* W. K. from the mountains of the central and western Bosnia. – Glas. Zem. Muzeja, Sarajevo **17:** 169–177.

Nedelcheva A. M. 1995: Mediterranean chromosome number reports. – Fl. Medit. **5:** 320–323.

Oberprieler C., Vogt R. & Watson L. E. 2007: Tribe *Anthemideae* Cass. (1819). – Pp. 342–374 in: Kadereit J. W. & Jeffrey C. (ed.), The families and genera of vascular plants **VIII**. – Berlin & Heidelberg: Springer.

Pignatti S. 1979: Note critiche sulla Flora d'Italia. VI. Ultimi appunti miscellanei. – Giorn. Bot. Ital. **113:** 359–368.

Pignatti S. & Ehrendorfer F. 1982: *Achillea* L. – Pp. 77–85 in: Pignatti S., Flora d'Italia **3**. – Bologna: Edagricole.

Richardson I. B. K. 1976: *Achillea* L. – Pp. 159–165 in: Tutin T. G., Heywood V. H., Burges N. A., Moore D. M., Valentine D. H., Walters S. M. & Webb D. A. (ed.), Flora europaea **4.** – Cambridge: Cambridge University Press.

Saukel J., Anchev M., Guo Y.-P., Vitkova A., Nedelcheva A., Goranova V., Konakchiev A., Lambrou M., Nejati S., Rauchensteiner F. & Ehrendorfer F. 2003: Comments on the biosystematics of *Achillea* (*Asteraceae – Anthemideae*) in Bulgaria. – Phytol. Balcan. **9:** 361–400.

Sharma A. & Sen S. 2002: Chromosome botany. – Enfield: Science Publishers.

Tacina A. 1979: Recherches caryologiques sur l'*Achillea schurii* Schultz-Bip. – Rev. Roumaine Biol., Sér. Biol. Vég. **24:** 7–9.

Tamura M. 1995: *Angiospermae*. Ordnung *Ranunculales*. Fam. *Ranunculaceae*. II. Systematic part. – Pp. 223–519 in: Hiepko P. (ed.), Die natürliche

Pflanzenfamilien, ed. 2, **17aIV.** – Berlin: Duncker & Humblot.

Thiers B. [continuously updated]. Index Herbariorum: a global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. – Published at http://sweetgum.nybg.org/science/ih/ [accessed 21 Mar 2016].

Tzanoudakis D. & Iatrou G. 1981: New combinations for two endemic taxa of the greek Flora. – Bot. Chron. (Patras) **1:** 22–28.

Wagenitz G. 1979: *Achillea* L. – Pp. 310–349 in: Hegi G. (ed.), Illustrierte Flora von Mitteleuropa, ed. 2, **VI(3)**. – Berlin & Hamburg: Verlag Paul Parey.

Willdenowia

Open-access online edition www.bioone.org/loi/will BioOne

Online ISSN 1868-6397 · Print ISSN 0511-9618 · Impact factor 0.721

Published by the Botanic Garden and Botanical Museum Berlin, Freie Universität Berlin