Artemisia Systematics and Phylogeny: Cytogenetic and Molecular Insights

Joan Vallès
E. Durant McArthur

Abstract—The genus *Artemisia* (Asteraceae, Anthemideae, Artemisiinae) is a large genus, one of the largest genera in its family. It is comprised of about 500 taxa at the specific or subspecific level, distributed in 5 sections or subgenera. Most species are perennial and many are landscape dominants of arid or semiarid regions. *Artemisia* is widely distributed in the Northern Hemisphere but poorly represented in the Southern Hemisphere. It is more richly represented in Eurasia than it is in North America. A number of *Artemisia* species have a high economic value for food, medicine, forage, ornamentals, and other uses. Some taxa are invasive weeds, which can adversely affect harvests. Even though some features (carpological and palynological ones) are quite constant and characteristic of the genus, a high degree of morphological variation exists. *Artemisia* has two basic chromosome numbers, with ploidy levels ranging from diploid to dodecaploid for x = 9 and from diploid to hexaploid for x = 8. Polyploidy and dysploidy are two very relevant evolutionary mechanisms in the genus, particularly the first one, which is present in all its major groups. The classical systematics of *Artemisia* have been refined by molecular methods, for example, internal transcribed spacer (ITS) sequences of nuclear ribosomal DNA, chloroplast DNA restriction site (cpDNA) data, and randomly amplified polymorphic DNA (RAPD) analysis but in the main hold well. This presentation provides a general introduction and characterization of *Artemisia* with particular emphasis on its systematics and evolution as illuminated by cytogenetic and molecular data.

Introduction

Artemisia, one of the larger genera in the family Asteraceae and the largest genus in the tribe Anthemideae, comprises from 200 to more than 500 taxa at the specific or subspecific level (depending on the authors, for example, Bremer and Humphries 1993; Ling 1991a,b, 1995a,b; Mabberley 1990; McArthur 1979), which are distributed in 5 sections or subgenera (Torrell and others 1999b). Many *Artemisia* species have a high economic value in several fields. Some examples are as food plants (absinth–*A. absinthium*–and other taxa, such as *A. genipi*, used in preparation of liquors); as spices (tarragon or estragon–*A. dracunculus*); in medicine, as an antihelminthic (*A. santonicum* and related taxa) and a new promising source of anti-malaria biochemicals (*A. annua*); as forage (*A. herba-alba* and related species in African and Asian steppes and semideserts and *A. tridentata* and its allies in North American shrublands); as ornamentals (*A. absinthium*, *A. caucasica*, and *A. stelleriana* among many others); and as soil stabilizing agents in badly disturbed habitats, for example, highways, railroads, and mines (*A. ludoviciana* and *A. vulgaris*)—see Bailey Hortorium Staff (1976) and Turner and Wassen (1999) for general reference. On the other hand, some taxa, such as *A. verlotiorum*, are invasive weeds, which can adversely affect harvests. Some others may be toxic (*A. absinthium*, for instance) or causative of pollen-induced allergies (the Iberian endemic *A. barrelieri* among others; Giner and others 1999). Marco and Barberá (1990) give a conspectus of the chemical composition of *Artemisia*, and revisions of applied aspects of the genus can be found in Pareto (1985) and Tan and others (1998). The high number of taxa, the dominance of some of them in landscapes, and the usefulness of many of them have attracted the interest of the researchers, who have produced a considerable amount of literature concerning *Artemisia* in many disparate fields of study (systematics in all its approaches, ecology, chemistry, pharmacology, and so forth). This paper provides a general review of different systematic and evolutionary aspects of the genus, with special emphasis on cytogenetic and molecular data.

Life Form and Morphology

Artemisia species are most commonly shrubs, rarely perennial herbs and more rarely annual or biennial herbs. Thus, perennial plants largely dominate the genus; only 5 percent of the taxa (approximately 10 species) are annual or biennial species. Leaves are alternate or sparse, usually more or less divided (exceptionally entire, such as in *A. dracunculus* and *A. cana*), with extremely variable shapes and dimensions. Flower heads are small, basically ovoid, cylindrical or hemispheric in shape, constituted by a rather small number (4–40) of flosculose florets (lacking ligulate ones), and grouped in racemose or paniculate synflorescences. Fruits are pappus-lacking achenes or cypselas, characteristic of the genus (Korobkov 1981; Ouyahya and Viano 1985, 1990; Persson 1974; Vallès and Seoane 1992). Palynological characters are useful markers for the genus *Artemisia*. The weak (verrucose) exine ornamentation contrasts with the higher (spinulose) one of the other members of the tribe Anthemideae, as already pointed out by Wodehouse (1926) and confirmed by later authors (Dimon 1971; Vallès and others 1987). Some of the morphological traits of *Artemisia* (non-opposite leaves, absence of radial florets, non-paleate head receptacle, many capitula with few florets in each

In: McArthur, E. Durant; Fairbanks, Daniel J., comps. 2001. Shrubland ecosystem genetics and biodiversity: proceedings; 2000 June 13–15; Provo, UT. Proc. RMRS-P-21. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Joan Vallès is Professor, Laboratori de Botànica, Facultat de Farmàcia, Universitat de Barcelona, Av. Joan XXIII, s/n, 08028 Barcelona, Catalonia, Spain. E. Durant McArthur is research geneticist and project leader, Shrub Sciences Laboratory, Rocky Mountain Research Station, Forest Service, United States Department of Agriculture, Provo, Utah 84606, USA.

synflorescence, achenes without pappus) are considered phylogenetically derived characters, within the phylogenetically advanced family Asteraceae (Cronquist 1977).

Phenology and Reproductive Biology

Phenology is a good distinctive trait for *Artemisia* in respect to the remaining Anthemideae or Asteraceae genera. Most *Artemisia* species flower in autumn; however, a few taxa start flowering in summer and others flower in the winter. In the Northern Hemisphere, the flowering period ranges from June to January and fruiting period from August to March. Pollination is basically anemogamous; *Artemisia* and closely related genera are the only tribe Anthemideae genera that have this kind of pollination (Heywood and Humphries 1977; Leppick 1970), evidently related to the pollen ornamentation; nevertheless, frequent insect visits have been reported in different species of the genus, which makes it reasonable to think that a certain percentage of entomogamous pollination occurs (Garnock-Jones 1986; Vallès 1989). Even though they lack the pappus (except for the distinctive *A. papposa*), the achenes of *Artemisia* are at least partly anemochorous due to their very small dimensions and low weight. Zoochory and hydrochory also have significance in the genus. *Artemisia* shows a relatively low capability of fruit dispersion far from mother plants and a relatively high seedling mortality index. These dispersal disadvantages are compensated for and plants are efficiently propagated due to high fruit productivity, germination rates, and general plant vigor (Bostock and Benton 1979; Oliva and others 1997; Vallès 1989; Walton and others 1986).

Ecology and Geographical Distribution

Artemisia species are found in many ecosystems: from desert communities (*A. santolina* in Uzbekistanian and Iranian deserts, for instance) to humid environments (*A. molinieri*, an endemic species to southeastern France and *A. cana* ssp. *bolanderi*, endemic to the Oregon area of the United States, the only taxa in the genus to live in temporarily inundated soils); from near sea level (*A. caerulescens* from European marine salt marshes) to the top of high mountains, at almost 4,000 m (the Iranian *A. melanolepis* and the North American *A. pattersonii* and *A. scopulorum*); some species are ruderal (as *A. vulgaris*). The genus is widely distributed in the Northern Hemisphere but uncommon in the Southern Hemisphere (only about 10 species). Most *Artemisia* species grow sparsely or form small populations, but several taxa form large, expansive populations and characterize landscapes. Different steppe and semidesert shrubby communities are dominated by species belonging to the subgenera *Seriphidium* (Mediterranean region, Central Asia) or *Tridentatae* (North America).

Classification

In such a large genus, it is to be expected that many attempts have been made to establish an infrageneric classification. The main proposals are compared in Table 1, where we can see that some large infrageneric groups are more or less present in all *Artemisia* classifications. Besser (1829, 1832, 1834, 1835) and Candolle (1837) established these groups as sections. They follow and are based on a few morphological characters:

Artemisia (originally named *Abrotanum* Besser). Heterogamous capitula with outer florets female and central florets hermaphrodite, and fertile and glabrous receptacle.

Absinthium DC. Heterogamous capitula with outer florets female and central florets hermaphrodite and fertile and hairy receptacle. Some authors merge this section into the precedent one.

Dracunculus Besser. Heterogamous capitula with outer florets female and central florets hermaphrodite but female-sterile and glabrous receptacle. Cassini (1817) transferred the species of this section to a new genus, *Oligosporus* Cass.

Seriphidium Besser. Homogamous capitula with all florets hermaphrodite and fertile and glabrous receptacle.

Table 1—Comparison among different infrageneric classifications of *Artemisia*.

Category	Infrageneric taxa					Reference
Genera	*Absinthium*	*Abrotanum*	*Artemisia*			Tournefort (1700)
Genus	*Artemisia*					Linné (1735)
Genera	*Artemisia*				*Oligosporus*	Cassini (1817); Lessing (1832)
Sections	*Absinthium*	*Abrotanum*	*Seriphidium*		*Dracunculus*	Besser (1829, 1832, 1834, 1835); De Candolle (1837)
Subgenera	*Euartemisia*		*Seriphidium*		*Euartemisia*	Rouy (1903)
Subgenera Sections	*Absinthium*	*Abrotanum*	*Seriphidium* *Seriphidium*	 *Tridentatae*	*Dracunculus*	Rydberg (1916)
Subgenera	*Artemisia*		*Seriphidium*		*Dracunculus*	Polyakov (1961b)
Subgenera	*Absinthium*	*Artemisia*	*Seriphidium*		*Dracunculus*	Persson (1974)
Sections	*Artemisia*				*Dracunculus*	Tutin and others (1976)
Subgenera	*Artemisia*		*Seriphidium*	*Tridentatae*	*Dracunculus*	McArthur and others (1981)
Subgenera	*Artemisia*		*Seriphidium*		*Dracunculus*	Podlech (1986)
Genera Subgenera	*Artemisia* *Artemisia*		*Seriphidium* *Seriphidium*		*Artemisia* *Dracunculus*	Ling (1991a,b)

Rydberg (1916) created the new section *Tridentatae* Rydb. to include the main part of North American *Seriphidium*, which he treated as a subgenus. McArthur (McArthur and others 1981) elevated this section to the subgeneric level. Ling (1982, 1991a,b, 1995a,b) proposed separation of one of the main *Artemisia* sections (or subgenera) as a large (almost 150 species) independent genus, *Seriphidium* (Besser ex Hook.) Fourr. (table 1). Bremer and Humphries (1993) and Bremer (1994) have accepted this segregation in their cladistic revisions of the tribe Anthemideae and the family Asteraceae, respectively.

Some small (even monotypic) genera have also been removed from *Artemisia*, such as *Filifolium* Kitam., *Kaschgaria* Poljakov, *Neopallasia* Poljakov, *Turaniphytum* Poljakov, *Elachanthemum* Y. Ling & Y.R. Ling, *Artemisiella* A. Ghafoor, *Artemisiastrum* Rydb., *Mausolea* Poljakov and *Picrothamnus* Nutt. (Bremer and Humphries 1993; Ghafoor 1992; Ling and Ling 1978; Poljakov 1961a; Rydberg 1916). However, many current treatments retain these proposed segregates within *Artemisia*. Most of the genera included in the subtribe Artemisiinae contain some species previously described as members of *Artemisia*.

Cytogenetics

Artemisia chromosomes are rather small (2–8 μm). Karyotypes tend to be symmetric, considering both the interchromosomal and the intrachromosomal asymmetry (McArthur and Plummer 1978; McArthur and Pope 1979; McArthur and others 1981; Mendelak and Schweizer 1986; Oliva and Vallès 1994; Schweizer and Ehrendorfer 1983; Vallès and Siljak-Yakovlev 1997); they fit into 2A and 2B classes (Stebbins 1971). The use of Giemsa C-banding and chromomycin and bisbenzimide fluorochrome banding (Mendelak and Schweizer 1986; Oliva and Vallès 1994; Schweizer and Ehrendorfer 1983; Vallès and Siljak-Yakovlev 1997; Torrell and Vallès, unpublished data on file at Laboratori de Botànica, Facultat de Farmàcia, Universitat de Barcelona) provide the opportunity to use heterochromatic chromosome segments banding patterns—called banding style by Schweizer and Ehrendorfer (1983)—for systematic study. There is a predominance of telomeric bands over intercalary and centromeric bands. Chromomycin-positive (GC-rich) bands appear often linked to the nucleolus organizing regions in satellited chromosomes. Preliminary studies using fluorescent *in situ* hybridization (FISH) show that 18S rDNA tends to be located in the chromomycin-positive regions (Torrell and others, unpublished data on file at Laboratori de Botànica, Facultat de Farmàcia, Universitat de Barcelona). The general pattern basically characterized by telomeric bands is also found in other genera of the tribe Anthemideae (Schweizer and Ehrendorfer 1983). B chromosomes have been reported in different numbers (1–5) in some species and populations of the genus (McArthur and others 1981; McArthur and Sanderson 1999a; Torrell and others 1999a, 2000; Vallès and Siljak-Yakovlev 1997; Torrell and Vallès, unpublished data on file at Laboratori de Botànica, Facultat de Farmàcia, Universitat de Barcelona).

The genus has two basic chromosome numbers, the largely predominating x = 9 and the less extended x = 8. X = 9 is not only the most common basic number in the genus *Artemisia*, but in the tribe Anthemideae and the family Asteraceae as well (McArthur and Sanderson 1999; Oliva and Vallès 1994; Schweizer and Ehrendorfer 1983; Solbrig 1977; Vallès and Siljak-Yakovlev 1997). A single species has been reported at x = 7 (*Artemisia pattersonii*—Wiens and Richter 1966). We do not believe this isolated circumstance warrants consideration as a basic chromosome number for the genus; rather, we believe this must have been an aneuploid reduction. Two phenomena have been basic in the chromosome evolution in the genus: polyploidy and dysploidy.

Polyploidy

Apart from being a common evolutionary mechanism in plants, it has been widely recognized as particularly active in *Artemisia* (Ehrendorfer 1964, 1980; Estes 1969; Koul 1965; McArthur and Pope 1979; McArthur and others 1981; McArthur and Sanderson 1999; Oliva and Vallès 1994; Persson 1974; Torrell and others 1999b, 2000; Vallès 1987a, 1987b; Vallès and Siljak-Yakovlev 1997). A high percentage of *Artemisia* species are polyploid. This phenomenon is present in all the major groups into which the genus is divided. Both basic chromosome numbers show polyploidy, with levels up to 12x for x = 9 and 6x for x = 8. The circumboreal, but largely Eurasian, *Artemisia dracunculus*, for which the chromosome numbers 2n = 18, 36, 54, 72 and 90 have been reported (Kawatani and Ohno 1964; Rousi 1969) constitutes a good example of a complete series from diploid to decaploid levels, based on x = 9. The large, western North American subgenus *Tridentatae* (= sagebrush), also based on x = 9, provides another robust example of polyploidy from diploid (2n = 18) to octoploid (2n = 72) levels (McArthur and Sanderson 1999). The dodecaploid level has been reported to now only for one species, *A. macrantha* (Malakhova 1990). For x = 8, the *Artemisia vulgaris* group shows a series from diploid to hexaploid levels (Vallès 1987a; Vallès and Torrell, unpublished data on file at Laboratori de Botànica, Facultat de Farmàcia, Universitat de Barcelona). Recent studies (Torrell and Vallès 2001) show that nuclear DNA content (ranging approximately from 3 to 27 pg) is well correlated with ploidy level, and that evolutionary trends in genome size in the genus comprise both decreases and increases in DNA content, as it has been reported to happen in other groups belonging to the family Asteraceae (Cerbah and others 1999; Price and Bachmann 1975).

Dysploidy

The existence of two basic numbers shows *Artemisia* as a dysploid genus. Dysploidy is present in three of the main groups in the genus (*Artemisia*, *Absinthium* and *Dracunculus*); *Seriphidium* and *Tridentatae* display only one basic number, x = 9. Kawatani and Ohno (1964) inferred that x = 9 was the original basic number from the fact that it is the most common one in the genus. Vallès and Siljak-Yakovlev (1997) found evidence for a chromosomal fusion in *A. vulgaris*, which experimentally supported the hypothesis that descending dysploidy in the genus is derived. This 2n = 16 species has a chromosome pair much longer than the remaining 7 pairs. This long pair of chromosomes is almost perfectly metacentric and includes a centromeric

heterochromatic region. In addition to that, this chromosome pair shows a high centromeric fragility, so that both arms of every chromosome often appear distinctly separated after squashing. These traits are evidence of a chromosomal fusion. This can explain the appearance of a number of x = 8 based species, as well as the existence of some erroneous x = 9 based counts for some of these taxa. Subsequent research has confirmed the same fusion syndrome in other species, such as *A. judaica*, *A. lucentica,* and *A. reptans* (Torrell and Vallès, unpublished data on file at Laboratori de Botànica, Facultat de Farmàcia, Universitat de Barcelona), and *A. incana* and *A. splendens* (Torrell and others 2000), representing different groups in which dysploid processes have occurred. Polyploid x = 8 taxa (for example, *A. splendens*, 2n = 32) have two larger metacentric chromosome pairs, confirming the likelihood of a fusion event prior to polyploidization (Torrell and others 2000). The idea of descending dysploidy as an evolutionary trend is consistent with what is known in different genera in the family Asteraceae (Siljak-Yakovlev 1996; Solbrig 1977). Other examples of dysploid processes are known in the tribe Anthemideae (Heywood and Humphries 1977), even though this is not a common mechanism in the tribe (Mitsuoka and Ehrendorfer 1972; Schweizer and Ehrendorfer 1983).

Chromosome Number Evolution

Figure 1 presents a scheme of the putative chromosome number evolution in *Artemisia*. The examples described above illustrate almost all changes in chromosome number and ploidy level. There is only one point left: the appearance of 2n = 34 populations or taxa. This chromosome number may be reached from 2n = 18 through 2n = 36 or from 2n = 16 through 2n = 32. In the first case we cite the example of *A. umbelliformis*, with one 2n = 18 subspecies (ssp. *eriantha*) and another one (ssp. *umbelliformis*) for which 2n = 36 and 2n = 34 have been reported (Oliva and Vallès 1994). Chromosome morphology suggests an allotetraploid origin for *A. umbelliformis* ssp. *umbelliformis*, with ssp. *eriantha* as one of the ancestors (Ehrendorfer 1980; Gutermann 1979; Oliva and Vallès 1994); 2n = 34 populations seem stabilized enough to discard a simple case of aneuploidy and to consider a dysploid-polyploid origin of a new secondary basic number, x = 17. Some populations of the *A. vulgaris* complex may also have reached this number from 2n = 16 by means of polyploidy and duplication of one chromosome pair (Vallès and Torrell, unpublished data on file at Laboratori de Botànica, Facultat de Farmàcia, Universitat de Barcelona).

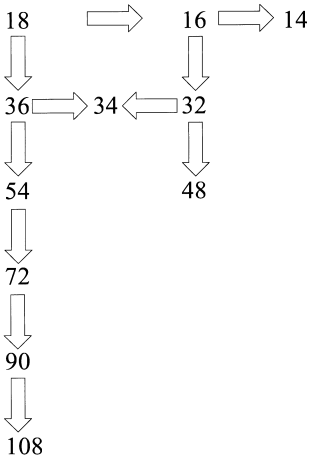

Figure 1—Chromosome number evolution in the genus *Artemisia*.

Molecular Biology

Working on *Artemisia* it is easy to be convinced that, as Persson (1974) stated, the currently accepted main groups within the genus do not represent natural groups. So, different attempts have been made in recent years to refine or redefine the systematics of the genus to the light of molecular data (Kornkven and others 1998, 1999; McArthur and others 1998a,b; Torrell and others 1999b). Two main questions (generic delimitation and infrageneric classification) concerning classification may be addressed by molecular studies.

Generic Delimitation

As stated above (see Classification section), different authors proposed to segregate some of the main infrageneric groups in *Artemisia*, namely *Oligosporus* (Cassini 1817) and *Seriphidium* (Bremer 1994; Bremer and Humphries 1993; Ling, 1982, 1991a,b, 1995a,b), as independent genera. Phylogeny based on the nuclear ribosomal DNA internal transcribed spacers (ITS-1 and ITS-2) sequences does not support these segregations and shows a monophyletic genus in its broad, classical sense (Torrell and others 1999b). Molecular data support morphological ones. Only minor morphological-physiological traits (receptacle indumentum and sex of peripheral florets) separate *Dracunculus* (the basis for the genus *Oligosporus*) and *Seriphidium* from other main groups in the genus, whereas major characters, such as pollen and cypsela morphology, clearly define them as members of the genus *Artemisia*.

Infrageneric Classification

ITS sequencing data define five major clades within *Artemisia*, which are similar, but not identical, to the five main groups discussed in the Classification section (above) (table 1). Figure 2 shows these clades, which have the following links with the classically recognized groups:

Tridentatae and *Dracunculus* are delimited as traditionally conceived. *Absinthium* and *Seriphidium* are resolved in clades with the addition of some species up to now included in *Artemisia*, a completely fragmented group in the ITS phylogeny (which agrees with the extraordinary morphological variation within the group).

Finally, a clade is constituted by the taxa of the group of *A. vulgaris*, the type species of the genus.

The analysis of molecular data shows the monophyly of subgenus *Tridentatae* (RAPD: McArthur and others 1998a;

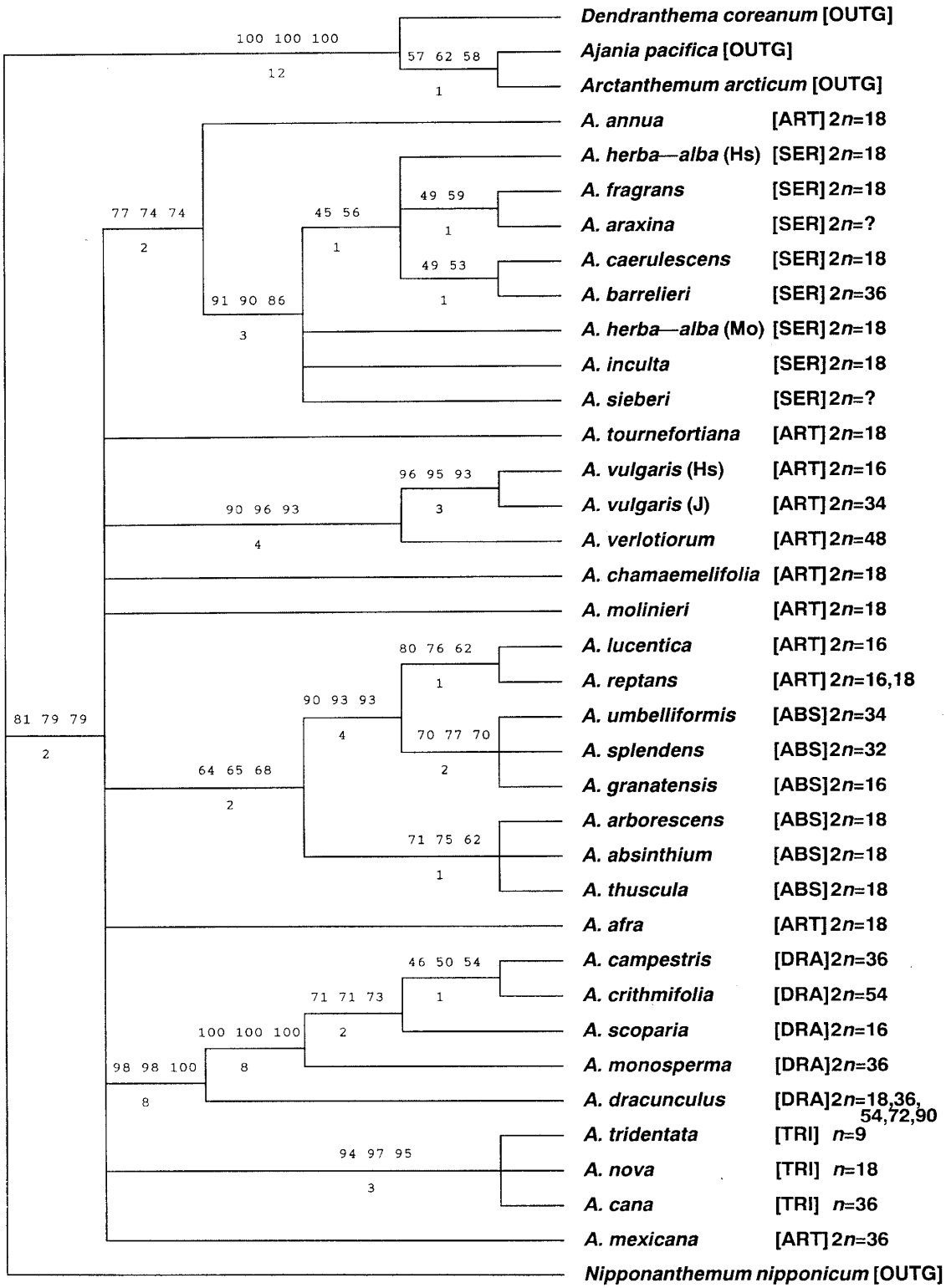

Figure 2—Cladogram showing the hypothetical ITS phylogeny of *Artemisia* (adapted from Torrell and others, 1999b). Consistency index excluding uninformative characters (CI) = 0.471; retention index (RI) = 0.740. Numbers above branches are bootstrap percentages and parsimony jackknife results: first, Lidén and others (1997) bootstrap method; second, Plunkett and others (1996) bootstrap method; third, parsimony jackknife values. Numbers below branches are decay indices. ART = Section/Subgenus *Artemisia*, SER = Section/Subgenus *Seriphidium*, ABS = Section/Subgenus *Absinthium*, DRA = Section/Subgenus *Dracunculus*, TRI = Section/Subgenus *Tridentatae*, OUTG = Outgroup.

ITS sequencing: Kornkven and others 1998; Torrell and others 1999b; chloroplast DNA: Kornkven and others 1999) and clearly supports the independence of this North American endemic group from *Seriphidium* (Torrell and others 1999b). Bremer and Humphries (1993) and Ling (1995b) included the members of *Tridentatae* in the genus *Seriphidium*, even though different authors had suggested, on the basis of morphological, karyological or chemical characters, the independence and the convergent evolution of both subgenera or even a closer relationship between *Tridentatae* and *Artemisia* than between *Tridentatae* and *Seriphidium* (Jeffrey 1995; McArthur 1979; McArthur and others 1981, 1998a,b; McArthur and Plummer 1978; Seaman 1982; Shultz 1986).

Perspectives in the Study of *Artemisia*

The present article has summarized a significant part of the considerable amount of research carried out in different fields about the genus *Artemisia*. We can conclude that it is a rather well-studied genus, but some of its systematic and phylogenetic aspects remain unsolved as, for example, the placement of *A. filifolia, A. palmeri,* and *A. californica*, see Hall and Clements (1923) and McArthur and Sanderson (1999), or the infrageneric classification (Torrell and others 1999b). Apart from research about applied aspects that are very relevant in this genus, even though they are not the main object of this paper, many biosystematic studies—in morphology, population biology, cytogenetics, and molecular biology, among others—are suitable in order to obtain a better knowledge of the genus. We believe that karyological (from chromosome counts to molecular cytogenetics) and molecular (combining different techniques in as many taxa as possible) studies in *Artemisia* and the subtribe to which it belongs (Artemisiinae) will be effective tools in better systematic definition.

These further studies may support or contradict the present evidences and nuances. They may demonstrate that a new revision of the genus is necessary or contrariwise they may confirm our present understanding in regard to both the infrageneric classification and the relationships between *Artemisia* and its closely related genera (subtribe Artemisiinae). However, we believe that it is certain that multidisciplinary systematic and phylogenetic studies will continue on this interesting and important group of plants.

Acknowledgments

We thank Montserrat Torrell (Barcelona) for critically reading the first version of this paper. The research by JV that permitted a part of the present review has been subsidized by the following institutions: Generalitat de Catalunya (Catalan autonomous government: AR83-210, 1983–1984; 1998BEAI400180, 1999), Universitat de Barcelona (AIUB, 1985–1986), and Spanish government (DGICYT: PB-88-0033, 1989–1991; PB-93-0032, 1994–1996; PB-97-1134; 1999–2001). Research by EDM that lead to this review has been facilitated by a USDA CSREES grant (91-98300-6157) and by Pittman-Robertson Agreement W-82-R (Rocky Mountain Research Station and Utah Division of Wildlife Resources, cooperating).

References

Bailey Hortorium Staff, L. H. 1976. Hortus third. New York: Macmillan Publishing Company.

Besser, W. S. J. G. 1829. Synopsis Absinthiorum. Bulletin de la Société Impériale des Naturalistes de Moscou. 1: 219–265.

Besser, W. S. J. G. 1832. Tentamen de Abrotanis seu de sectione IIda Artemisiarum Linnaei. Bulletin de la Société Impériale des Naturalistes de Moscou. 3: 1–92.

Besser, W. S. J. G. 1834. De Seriphidiis seu de sectione IIIa Artemisiarum Linnaei. Bulletin de la Société Impériale des Naturalistes de Moscou. 7: 1–46.

Besser, W. S. J. G. 1835. Dracunculi seu de sectione IVta et ultima Artemisiarum Linnaei. Bulletin de la Société Impériale des Naturalistes de Moscou. 8: 1–95.

Bostock, S. J.; Benton, R. A. 1979. The reproductive strategies of five perennial Compositae. Journal of Ecology. 67: 91–107.

Bremer, K. 1994. Asteraceae: cladistics and classification. Portland, OR: Timber Press.

Bremer, K.; Humphries, C. J. 1993. Generic monograph of the Asteraceae–Anthemideae. Bulletin of the Natural History Museum of London (Botany). 23(2): 71–177.

Candolle, A. P. de. 1837. Prodromus systematis naturalis regni vegetabilis, pars VI. Paris.

Cassini, A. H. G. 1817. Aperçu des genres formés par M. Cassini dans la famille des Synantherées. Troisième fascicule. Bulletin Scientifique, par la Société Philomatique de Paris. 3: 31–34.

Cerbah, M.; Coulaud, J.; Brown, S. C.; Siljak-Yakovlev, S. 1999. Evolutionary DNA variation in the genus *Hypochaeris*. Heredity. 82: 261–266.

Cronquist, A. 1977. The Compositae revisited. Brittonia. 29: 137-153.

Dimon, M. T. 1971. Problèmes généraux soulevés par l'étude pollinique de Composées méditerranéennes. Naturalia Monspeliensia, série Botanique. 22: 129–144.

Ehrendorfer F. 1964. Notizen zur Cytotaxonomie und Evolution der Gattung *Artemisia*. Oesterreichische Botanische Zeitschrift. 111: 84–142.

Ehrendorfer F. 1980. Polyploidy and distribution. In: Lewis W. H., ed. Polyploidy: Biological relevance. New York-London: Plenum Press: 45–60.

Estes J. R. 1969. Evidence for autoploid evolution in the *Artemisia ludoviciana* complex of the Pacific Northwest. Brittonia. 21: 29–43.

Garnock-Jones, P. J. 1986. Floret specialization, seed production and gender in *Artemisia vulgaris* L. (Asteraceae, Anthemideae). Botanical Journal of the Linnean Society. 92: 285–302.

Ghafoor, A. 1992. *Artemisiella*, a new genus of Compositae based on *Artemisia stracheyii* Hook. F. & Thoms. ex Clarke. Candollea. 47: 635–643.

Giner, M.; García, J. S.; Sellés, J. 1999. Aerobiology of *Artemisia* airborne pollen in Murcia (SE Spain) and its relationship with weather variables: annual and intradiurnal variations for three different species. Wind vectors as a tool in determining pollen origin. International Journal of Biometeorology. 43: 51–63.

Gutermann, W. 1979. Systematik und evolution einer alten, dysploid-polyploiden Oreophyten-Gruppe: *Artemisia mutellina* und ihre Verwandten (Asteraceae: Anthemideae). University of Vienna. Dissertation,

Hall, H. M.; Clements, F. E. 1923. The phylogenetic method in taxonomy, the North American species of *Artemisia, Chrysothamnus,* and *Atriplex*. Publication no. 326. Washington, DC: Carnegie Institution of Washington.

Heywood, V. H.; Humphries, C. J. 1977. Anthemideae. Systematic review. In: Heywood, V. H., Harborne, J. B., Turner, B. L., eds. The biology and the chemistry of the Compositae. London-New York-San Francisco: Academic Press: 851–898.

Jeffrey, C. 1995. Compositae systematics 1975–1993. Developments and desiderata. In: Hind, D. J. N.; Jeffrey, C.; Pope, G. V., eds. Advances in Compositae Systematics. Kew, Royal Botanic Gardens: 7–21.

Kawatani, T.; Ohno, T. 1964. Chromosome numbers in *Artemisia*. Bulletin of the National Institute of Hygienic Sciences, Tokyo. 82: 183–193.

Kornkven, A. B.; Watson, L. E.; Estes, J. R. 1998. Phylogenetic analysis of *Artemisia* sect. *Tridentatae* (Asteraceae) based on sequences from the internal transcribed spacers (ITS) of nuclear ribosomal DNA. American Journal of Botany. 85: 1787–1795.

Kornkven, A. B.; Watson, L. E.; Estes, J. R.. 1999. Molecular phylogeny of *Artemisia* sect. *Tridentatae* (Asteraceae) based on chloroplast DNA restriction site variation. Systematic Botany. 24: 69–84.

Koul M. L. H. 1965. Cytogenetics of Polyploids. II. Cytology of polyploid *Artemisia maritima* L. Cytologia. 30: 1-9.

Korobkov, A. A. 1981. Polyni severo-vostoka SSSR. Leningrad, Nauka.

Leppick, E. E. 1970. Evolutionary differentiation of the flower head of the Compositae II. Annales Botanici Fennici. 7: 325–352.

Lessing, C. F. 1832. Synopsis generum Compositarum. Berlin.

Lidén, M.; Fukuhara, T.; Rylander, J.; Oxelman, B. 1997. Phylogeny and classification of Fumariaceae, with emphasis on *Dicentra* s. l. based on the plastid gene *rps*16 intron. Plant Systematics and Evolution. 206: 411–420.

Ling, Y. R. 1982. On the system of the genus *Artemisia* L. and the relationship with its allies. Bulletin of the Botanical Laboratory of the North-East Forest Institute. 2: 1–60.

Ling, Y. R. 1991a. The Old World *Seriphidium* (Compositae). Bulletin of Botanical Research, Harbin. 11(4): 1–40.

Ling, Y. R. 1991b. The Old World *Artemisia* (Compositae). Bulletin of Botanical Research, Harbin. 12(1): 1–108.

Ling, Y. R. 1995a. The New World *Artemisia* L. In: Hind, D. J. N., Jeffrey, C., Pope, G. V., eds. Advances in Compositae Systematics. Kew, Royal Botanic Gardens: 255–281.

Ling, Y. R.1995b. The New World *Seriphidium* (Besser) Fourr. In: Hind, D. J. N., Jeffrey, C., Pope, G. V. Advances in Compositae Systematics. Kew, Royal Botanic Gardens: 283–291.

Ling, Y.; Ling, Y. R. 1978. *Elachanthemum*, genus novum familiae Compositarum. Acta Phytotaxonomica Sinica. 16(1): 61–65.

Linné, C. 1735. Systema naturae. Leiden. 1st ed.

Mabberley, D. J. 1990. The plant-book. Cambridge: Cambridge University Press.

Malakhova, L. A. 1990. Kariologicheskii analiz prirodnykh populyatsii redkykh i ischezayushchykh rastenii na yuge Tomskoi oblasti. Byulletin Glavnogo Botanicheskogo Sada. 155: 60–66.

Marco, J. A.; Barberá, O. 1990. Natural products from the genus *Artemisia* L. In: Atta-ur-Rahman, ed. Studies in natural products chemistry. Amsterdam: Elsevier. 7A: 201–264.

McArthur, E. D. 1979. Sagebrush systematics and evolution. In: Sagebrush ecosystem symposium. Logan: Utah State University: 14–22.

McArthur, E. D.; Mudge, J.; Van Buren, R.; Andersen, W. R.; Sanderson, S. C.; Babbel, D. G. 1998a. Randomly amplified polymorphic DNA analysis (RAPD) of *Artemisia* subgenus *Tridentatae* species and hybrids. Great Basin Naturalist. 58: 12–27.

McArthur, E. D.; Plummer, A. P. 1978. Biogeography and management of native western shrubs: a case study, section *Tridentatae* of *Artemisia*. Great Basin Naturalist Memoirs. 2: 229–243.

McArthur, E. D.; Pope, C. L. 1979. Karotypes of four *Artemisia* species: *A. carruthii, A. filifolia, A. frigida,* and *A. spinescens*. Great Basin Naturalist. 39: 419–426.

McArthur, E. D.; Pope, C. L.; Freeman, D. C. 1981. Chromosomal studies of subgenus *Tridentatae* of *Artemisia*: evidence for autopolyploidy. American Journal of Botany. 68: 589–605

McArthur, E. D.; Sanderson, S. C. 1999. Cytogeography and chromosome evolution of subgenus *Tridentatae* of *Artemisia* (Asteraceae). American Journal of Botany. 86: 1754–1775.

McArthur, E. D.; Van Buren, R.; Sanderson, S. C.; Harper, K. T. 1998b. Taxonomy of *Sphaeromeria*, *Artemisia*, and *Tanacetum* (Compositae, Anthemideae) based on randomly amplified polymorphic DNA (RAPD). Great Basin Naturalist. 58: 1–11.

Mendelak, M.; Schweizer, D. 1986. Giemsa C-banded karyotypes of some diploid *Artemisia* species. Plant Systematics and Evolution. 152: 195–210.

Mitsuoka, S.; Ehrendorfer, F. 1972. Cytogenetics and evolution of *Matricaria* and related genera (Asteraceae-Anthemideae). Oesterreichische Botanische Zeitschrift. 120: 155–200.

Oliva M.; Vallès J. 1994. Karyological studies in some taxa of the genus *Artemisia* (Asteraceae). Canadian Journal of Botany. 72: 1126–1135.

Oliva, M.; Torrell, M.; Vallès, J. 1997. Data on germination rates and germinative vigour in *Artemisia* (Asteraceae). Bocconea. 5: 679–684.

Ouyahya, A.; Viano, J. 1984. Contribution à l'étude morphologique et biométrique des akènes de taxons endémiques marocains du genre *Artemisia*. Lagascalia. 12: 223–228.

Ouyahya, A.; Viano, J. 1990. Étude au MEB du test des akènes du genre *Artemisia*. Boletim da Sociedade Broteriana, Série 2. 63: 99–113.

Pareto, G., ed. 1985. Artemisie. Ricerca ed applicazione. Quaderni Agricoli, supplemento 2: 1–261.

Persson, K. 1974. Biosystematic studies in the *Artemisia maritima* complex in Europe. Opera Botanica (Lund). 35: 1–188.

Plunkett, G. M.; Soltis, D. E.; Soltis, P. S. 1996. Evolutionary patterns in Apiaceae: inferences based on *mat*K sequence data. Systematic Botany. 21: 477–495.

Podlech, D. 1986. *Artemisia*. In: K. H. Rechinger, ed., Flora Iranica. Graz, Academische Druck Verlagsansalt: 159–223.

Poljakov, P. P. 1961a. Materialy k sistematike roda polyn—*Artemisia* L. Trudy Instituta Botaniki Akademii Nauk Kazakhskoi S.S.R. 11: 134–177.

Poljakov, P. P. 1961b. Rod 1550. Polyn - *Artemisia* L. In: Shishkin, B. K., Bobrov, E. G., eds. Flora SSSR. Leningrad, Nauka: 425-631.

Price, H. J.; Bachmann, K. 1975. DNA content and evolution in the Microseridinae. American Journal of Botany. 62: 262–267.

Rousi, A. 1969. Cytogenetic comparison between two kinds of cultivated tarragon (*Artemisia dracunculus*). Hereditas. 62: 193–213.

Rouy, G. C. C. 1903. Flore de France, tome 8. Asnières-Paris-Rochefort.

Rydberg, P. A. 1916. *Artemisia* and *Artemisiastrum*. North American Flora. 34: 244–285.

Schweizer, D.; Ehrendorfer, F. 1983. Evolution of C-band patterns in Asteraceae-Anthemideae. Biologisches Zentralblatt. 102: 637–655.

Seaman, F. C. 1982. Sesquiterpene lactones as taxonomic characters in the Asteraceae. Botanical Review. 48: 121–595.

Shultz, L. M. 1986. Taxonomic and geographic limits of *Artemisia* subgenus *Tridentatae* (Asteraceae). In: McArthur, E. D., Welch, B. L., comps. Proceedings. Symposium on the biology of *Artemisia* and *Chrysothamnus*. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 20–29.

Siljak-Yakovlev, S. 1996. La dysploïdie et l'évolution du caryotype. Bocconea. 5: 211–220.

Solbrig, O. T. 1977. Chromosomal cytology and evolution in the family Compositae. In: Heywood, V. H., Harborne, J. B., Turner, B. L., eds. The biology and chemistry of the Compositae. London-New York-San Francisco: Academic Press. 1: 269–281.

Stebbins, G. L. 1971. Chromosomal evolution in higher plants. London: E. Arnold.

Tan, R. X.; Zheng, W. F.; Tang, H. Q. 1998. Biologically active substances from the genus *Artemisia*. Planta Medica. 64: 295–302.

Torrell, M.; Bosch, M.; Martín, J.; Vallès, J. 1999a. Cytogenetic and isozymic characterization of the narrow endemic species *Artemisia molinieri* (Asteraceae, Anthemideae): implications for its systematics and conservation. Canadian Journal of Botany. 77: 51–60.

Torrell, M.; Garcia-Jacas, N.; Susanna, A.; Vallès, J. 1999b. Infrageneric phylogeny of the genus *Artemisia* L. (Asteraceae, Anthemideae) based on nucleotide sequences of nuclear ribosomal DNA internal transcribed spacers (ITS). Taxon. 48: 721–736.

Torrell, M.; Vallès, J.; Garcia-Jacas, N.; Mozaffarian, V.; Gabrielian, E. 2000. New or rare chromosome counts in the genus *Artemisia* L. (Asteraceae, Anthemideae) from Armenia and Iran. Botanical Journal of the Linnean Society. 135: 51–60

Torrell, M.; Vallès, J. 2001. Genome size in 21 *Artemisia* L. species (Asteraceae, Anthemideae): systematic, evolutionary, and ecological implications. Genome. 44: 231–238.

Tournefort, J. P. de. 1700. Institutiones Rei Herbariae. Paris.
Turner, R. J.; Wasson, E., eds. Botanica. 1999. Hong Kong: Barnes and Noble, Inc.
Tutin, T. G.; Persson, K.; Gutermann, W. 1976. Artemisia L. In: Tutin, T. G., Heywood, V. H., Burges, N. A., Moore, D. M., Valentine, D. H., Walters, S. M., Webb, D. A., eds. Flora Europaea. Cambridge: Cambridge University Press. 4: 178–186.
Vallès J. 1987a. Aportación al conocimiento citotaxonómico de ocho táxones ibéricos del género *Artemisia* L. (Asteraceae-Anthemideae). Anales del Jardín Botánico de Madrid. 44: 79–96.
Vallès J. 1987b. Contribución al estudio de las razas ibéricas de *Artemisia herba-alba* Asso. Boletim da Sociedade Broteriana. Série 2. 60: 5–27.
Vallès, J. 1989. Dades sobre la biologia d'espècies ibèrico-baleàriques d'*Artemisia* L. Collectanea Botanica (Barcelona). 17: 237–245.
Vallès, J.; Seoane, J. A. 1992. Estudis carpològics en el gènere *Artemisia* L. a la Península Ibèrica i les Illes Balears. In: Conesa, J.A., Recasens, J., eds. Actes del Simposi Internacional de Botànica Pius Font i Quer. Lleida, Institut d'Estudis Ilerdencs. 2: 211–215.
Vallès, J.; Suárez, M.; Seoane, J.A. 1987. Estudio palinológico de las especies ibérico-baleáricas de las secciones *Artemisia* y *Seriphidium* Bess. del género *Artemisia* L. Acta Salmanticensia, Ciencias. 65: 167–174.
Vallès, J.; Siljak-Yakovlev S. 1997. Cytogenetic studies in the genus *Artemisia* L.: fluorochrome banded karyotypes of five taxa, including the Iberian endemic species *Artemisia barrelieri* Besser. Canadian Journal of Botany. 75: 595–606.
Walton, T. P.; White, R. S.; Wambolt, C. L. 1986. *Artemisia* reproductive strategies: a review with emphasis on plains silver sagebrush. In: McArthur, E. D., Welch, B. L., comps. Proceedings-Symposium on the biology of *Artemisia* and *Chrysothamnus*. Ogden, UT: Intermountain Research Station, Forest Service, U.S. Department of Agriculture: 67–74.
Wiens, D.; Richter, J. A. *Artemisia pattersonii*: a 14-chromosome species of alpine sage. American Journal of Botany. 53: 981–986.
Wodehouse, R. P. 1926. Pollen grain morphology in the classification of the Anthemideae. Bulletin of the Torrey Botanical Club. 53: 479–485.