

## Review

# Phylogeny of *Artemisia* L.: Recent developments

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In this review, classification and phylogeny of genus *Artemisia* L. is discussed. Its centers of diversity lie in the temperate and cold temperate regions of the Eurasia, North America and Asia. *Artemisia* has two basic chromosome numbers, with ploidy levels  $x=9$  and  $x=8$ . Chromosome number in diploid is most often  $2n=18$  or 16. The genus is divided into five large groups *Absinthium* DC., *Artemisia* L., *Dracunculus* Besser, *Seriphidium* Besser and *Tridantatae* (Rydb.) McArthur. Its phylogeny was based on the two hypothesized evolutionary trends, loss of fertility in the disc florets and loss of ray florets. Recently its molecular phylogeny based on internally transcribed spacer (ITS), externally transcribed spacer (ETS) regions of the DNA and chloroplast DNA suggested that the genus *Artemisia* is a monophyletic but it could not resolve the problem of infra-generic classification. This study revealed that there is need to search new genome regions to establish a natural classification based on modern molecular techniques.

**Key words:** *Artemisia*, phylogeny, pollen, polyploidy.

## INTRODUCTION

*Artemisia* L. of the family Asteraceae is a genus with enormous economic importance. From last five to six decades taxonomists are trying to solve the problem of its classification and phylogeny but its natural classification still has not been achieved. It is the largest and diverse genus of the tribe Anthemideae of Asteraceae (Martin et al., 2001; Watson et al., 2002; Martin et al., 2003). It is consisted of more than 500 taxa at specific or subspecific levels (the number differs in different reports) (McArthur, 1979; Mabberley, 1990; Ling, 1982, 1991a-b, 1994, 1995a-b; Bremer and Humphries, 1993; Oberprieler, 2001; Valles and McArthur, 2001; Valles and Garnatge, 2005). It is a well known wind pollinated cosmopolitan genus, mainly distributed in temperate areas of mid to high latitudes of the northern hemisphere, colonizing in arid and semiarid environments landscape, and has only few representatives in southern hemisphere. Central Asia is its center of diversification, while the Mediterranean region and North West America are two secondary speciation areas (McArthur and Plummer, 1978; Valles and McArthur, 2001). Few species are also reported in Africa and Europe (Ling, 1994; Tutin et al., 1976; Shultz,

2006). Majority of the members of this genus have a high economic value and they have been used in medicines, food, forage, ornamentals or soil stabilizers in disturb habitats; some taxa are toxic or allergenic and some others are invasive weeds which can adversely affect harvests (Pareto, 1985; Tan et al., 1998). Most of the species of this genus are perennial; only 10 species are annuals or biannual (Valles et al., 2003). *Artemisia* is considered to be an indicator of steppe climate (Erdtman, 1969) and moderate precipitation (El-Moslimany, 1990).

Because of high number of taxa, ecological and economic importance, the genus *Artemisia* has been the object of many diversity focused studies (Valles et al., 2003). In spite of all this, the global system for its classification and phylogeny has not yet been cleared. Extensive studies on the genus are going on to unveil its evolutionary and taxonomic relationships. The primary objective of this review is to investigate the recent developments in the study of genus *Artemisia* and to present a current picture of its phylogeny and classification.

## CENTER OF DIVERSITY

Like most herbaceous plants fossil records of *Artemisia* are so far largely confined to pollen data (Wang, 2004). A

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summary of the fossil record reveals that this plant group has been originated in temperate Asia in the mid-tertiary period of Cenozoic era, possibly within the early arid or subarid habitats (Wu, 1980; Shackleton, 1984).

The centers of diversity of the genus are in the temperate and cold temperate regions of the Eurasia, North America and Asia (Ling, 1982). It has been proposed that the center of origin of *Artemisia* was in the mountain regions of north-western Asia, possibly from the mesothermic subarctic or semihumid forest steppe environments near the Ural Mountains (Ling, 1982).

## CLASSIFICATION

Taxonomic treatments for *Artemisia* over the past 50 years range from maintaining a single, large genus of over 500 species (Cronquist, 1955, 1988; Kornkven et al., 1998, 1999; Torrell et al., 1999; Martin et al., 2001; Watson et al., 2002) to the recognition of six to eight genera within its taxonomic boundaries (Bremer and Humphries, 1993; Poljakov, 1961a; Ling, 1994). *Artemisia* of antiquity was divided into three genera (*Artemisia*, *Absinthium* and *Abrotanum*) by Tournefort (1700). However, the concept of a more inclusive genus was resurrected by Linnaeus (1735), hereinafter, refer to as *Artemisia* L. After reunion of these all genera, they were considered as sections of *Artemisia*. Section *Artemisia* and *Absinthium* were later united by Gray (1884). Then all sections were raised to level of subgenus (Rouy, 1903; Rydberg, 1916).

Afterwards, Poljakov (1961b) and Ling (1982, 1991a-b, 1995a-b) proposed the segregation of *Seriphidium* (Besser ex Hook) Fourr. as an independent genus along with several small genera from within the boundaries of *Artemisia* which was accepted by Bremer and Humphries (1993) and Bremer (1994) in their cladistic revisions of the Anthemideae and Asteraceae, respectively. However molecular studies based on chloroplast DNA (cpDNA) restriction site variation and internal transcribed spacers (ITS) of nuclear ribosomal DNA (Kornkven et al., 1998; Torrell et al., 1999; Watson et al., 2002; Valles et al., 2003) have refuted this separation (Pellicer et al., 2007).

In addition, a number of authors (McArthur and Plummer, 1978; McArthur et al., 1981; Kornkven et al., 1998, 1999; Rydberg, 1916; Beetle, 1960) consider the American woody sagebrushes to an independent origin from the woody Asian species (subgenus *seriphidium*), and recognize section *Tridentatae* (Watson et al., 2002).

In the case of subgenus *Dracunculus* the demarcation of the group is variable depending on the authors consulted (Shishkin and Bobrov, 1995; Ling et al., 2006). The subgenus is spread across Eastern Europe and Asia, where the genus is native from (Wang, 2004), and reaches North Africa and North America. Cassini (1817) treated this subgenus as a new genus, *Oligosporus* Cass., which was latterly returned to *Artemisia* (Besser, 1829, 1832, 1834, 1835; Candolle, 1837). The inclusion

of this group with in *Artemisia* has been conformed by molecular phylogenetic data (Torrell et al., 1999; Watson et al., 2002; Valles et al., 2003).

After various taxonomic rearrangements, the genus was divided into five large groups which have been considered at sectional or subgeneric level; *Absinthium* DC., *Artemisia* (= *Abrotanum* Besser), *Dracunculus* Besser, *Seriphidium* Besser and *Tridentatae* (Rydb.) McArthur (Torrell et al., 1999). Even so, this classification is not accepted by all authors. A general agreement exists concerning the idea that this infrageneric division does not represent natural groups (Persson, 1974; McArthur et al., 1981; Valles and McArthur, 2001; Valles and Garnatje, 2005). Similarly, the most recent molecular analysis carried out by Sanz et al. (2008), Tkach et al. (2007), Valles et al. (2003) and Watson et al. (2002). They clearly indicated that the five groups within the genus may need more revisions and scientific evidences to produce a global treatment of the genus at specific and infra specific levels as a natural assemblage.

## POLLEN EVOLUTION

Pollen grains of this genus are more or less distinct, easily recognized and are characterized by short spines or no spines (Bremer and Humphries, 1993). Martin et al. (2001, 2003) carried out a palynological study of the tribe Anthemideae including *Artemisia*, its allies and segregate genera, and determined that ornamentation with short spinules is good taxonomic marker for *Artemisia* and its allies. It seems that the pollen morphology of *Artemisia* has remained unchanged throughout its documented history, as indicated by morphological comparisons between fossils and modern pollen grains (Wang, 2004). Wang (2004) also demonstrated that *Artemisia* type pollens with short spinules evolve from ones with long spines (*Anthemis* type) based on the order of their occurrences in the geological past. Jiang et al. (2005), based on exine sculptures, divide the pollen grains of *Artemisia* into two types: (a) Myriantha type and (b) Mongolica type, which possesses 4 subtypes according to the distribution forms of spinules: (1) Sacrorum subtype, (2) Oligocarpa subtype, (3) Lavandulaefolia, subtype (4) Anomale subtype. It shows that every type (subtype) of *Artemisia* in their evolution developed more and more degenerative small thorns along with less and less or even no granules between spinules sharing evolve regular arrangement from dense to lose. The types (subtypes) of *Artemisia* pollen above are also related to their distribution, i.e., the primitive group defined to Myriantha type is generally dispersed in the high-latitude high elevation arid regions while low-latitude low elevation moist region are more likely to have the advanced categories defined to Oligocarpa subtype and Anomale subtype. The possible pollen morphological evolution of each type (subtype) is from Myriantha type to Sacrorum subtype which further evolves to Oligocarpa subtype or Myriantha type to La-

vandulaefolia subtype which further evolves to *Anomale* subtype.

Jiang et al. (2005) investigated that in the primitive group of *Artemisia*, pollen usually has a broader colpus. The evolved spaces and those widely distributed or those in the east and south generally have thinner groove and narrower polar region, minor thinner colpus, demonstrating that *Artemisia* is originated in temperate zone and shifted southward in the third and forth glacial epoch leaving the primitive spaces in the north temperate zone or high latitude regions and the advanced one in the low latitude and low elevation regions, hypothesis according the conclusion and results of Lin (1982, 1993) and Jiang and Lin (1992, 1993, 1997) experiments.

Many specie of *Artemisia* are clearly wind pollinated (Korobkov, 1981; Wang, 2004). However, there is evidence for a transition to insect pollination because of colorful capitula and sticky pollen in some species (Hesse, 1979; Wagenitz, 1987; Valles et al., 2001). Self compatibility has been observed in the few species tested thus for Estes (1969), Ferreira et al. (1997).

## CHROMOSOME COUNTS AND POLYPLOIDY

In addition of simple chromosome counts, various taxonomic or geographical groups within *Artemisia* have been studied karyologically at some depth (Arano, 1963; Ehrendorfer, 1964; Estes, 1969; Filatova, 1971, 1974a-b; Korobkov, 1972, 1981; Persson, 1974; McArthur and Plummer, 1978; McArthur et al., 1981; Ouyahya and Viano, 1981, 1988; Mendelak and Schweizer, 1986; Valles, 1987a-b; Valles and Seoane, 1987; Oliva and Valles, 1994; Valles and Torrell, 1995; Valles and Siljak-yakovlev, 1997). These studies have led to new hypothesis on evolutionary relationships among taxa. Clearly polyploidy and dysploidy have played a major role in the karyological evolution of the genus (Torrell et al., 1999).

*Artemisia* has two basic chromosome numbers, with ploidy levels ranging from diploid to dodecaploid for  $x=9$  and from diploid to hexaploid for  $x=8$  (Valles and McArthur, 2001). Chromosome number in diploid is most often  $2n=18$  or 16, the highest chromosome number known is 144 (Pellicer et al., 2007), and aneuploidy is frequent. Within several species, different ploidy levels have been observed that were considered to rest on autopolyploidy (McArthur and Sanderson, 1999). However, based on characters such as intermediate morphology and geographical distribution, Ehrendorfer (1964) suggested that several Eurasian polyploids were in fact allopolyploids. Although much cytological work has been done in *Artemisia* (McArthur and Sanderson, 1999), Valles and Garnatge (2005) definite evidence for allopolyploidy is scarce (Clausen et al., 1940; Estes, 1969; Persson, 1974). The distribution of ploidy levels in *Artemisia* on a large geographical scale has not been analyzed, but appears especially interesting in view of the general hypothesis on plant evolution (Tkach et al., 2007).

In five major groups of *Artemisia*, two (*Seriphidium* and *Tridentatae*) are characterized by  $x=9$  and the other three (*Artemisia*, *Absinthium* and *Dracunculus*) have both  $x=8$  and  $x=9$  representatives. Despite the reasonably good cytogenetic knowledge of the genus and the conclusion drawn from it so far, we concur with the statement of Yuan et al. (1996), that before evaluating the phylogenetic significance of the karyological data one must consider to what they reflect the phylogeny (Torrell et al., 1999).

## EVOLUTION OF FLORAL CHARACTERS

Traditionally the taxonomic and phylogenetic relationships have been inferred on the bases of floral and capitular morphology. In *Artemisia s.l.*, the typical limb of the Anthemideae-type ray florets are reduced to a membranous vestige, giving the impression that the small capitula are composed only of disk florets, referred to as disciform capitula (inflorescence) by Bremer and Humphries (1993). In other members of the genus, the ray florets are absent, thus the capitulum is composed only of disk florets, i.e., discoid. In addition, plants with discoid capitula are considered homogamous since all florets are of one sexual form (perfect-bisexual disk florets), and plants with disciform capitula are considered heterogamous with two or more sexual forms (i.e., pistillate rays and perfect disks, or pistillate rays and staminate disks) (Watson et al., 2002).

The first phylogenetic treatment (Hall and Clements, 1923) recognized four sections with in broadly defined *Artemisia s.l.*, with section *Artemisia* proposed as the progenitor to section *Absinthium*, *Dracunculus*, *Seriphidium*. This phylogeny was based on the two hypothesized evolutionary trends:

1. Loss of fertility in the disc florets
2. Loss of ray florets

According to Bremer and Humphries (1993), the *Artemisia*-group is monophyletic and defined by heterogeneous disciform capitula (disc florets usually bisexual and fertile, ray florets pistillate) or homogamous discoid capitula (disc florets usually bisexual and fertile, ray florets absent) and also confirmed by Watson et al. (2002).

## MOLECULAR PHYLOGENY

Advancements in more significant and reliable molecular phylogenetic techniques have prompted many authors to undertake the studies of the genus. There are many papers concerning its molecular phylogeny. Torrell et al. (1999) reviewed seven papers on *Artemisia* DNA, which had been published at that time: Francisco-Ortega et al. (1997) give the ITS sequence of one species in a work

concerning 32 genera of Anthemideae and centered on the endemic Macaronesian genus *Argyranthemum*; McArthur et al. (1992) studied the control of hybridization in “*Tridentatae*” using randomly amplified polymorphic DNA (RAPD) pattern; Watson (1996) made a chloroplast DNA restriction site study of one species of *Artemisia*, in work on Anthemideae; McArthur et al. (1998a-b) published two papers using RAPD, the first concerning *Artemisia*, *Sphaeromeria* and *Tanacetu*, the second of the “*Tridentatae*” with in *Artemisia*; finally, Kornkven and Watson (1997) and Kornkven et al. (1998) investigated the molecular systematics of the “*Tridentatae*”, based on ITS sequences and chloroplast DNA restriction site.

Torrell et al. (1999) using internally transcribed spacer (ITS) sequences for phylogenetic analysis clearly supports the monophyly of the genus *Artemisia* in its classical, broad sense, i.e. comprising the five major groups, including “*Seriphidium*” and “*Tridentatae*”. These two major groups in *Artemisia* with homogamous capitula, but planological and carpological features, were now supported by their study.

The ITS sequence analysis presented by Valles et al. (2003) clearly supports changes in *Artemisia* delimitation, they also showed that structure of *Artemisia* and that of Artemisiinae are too not satisfactorily solved questions. This notwithstanding, from their first study (Torrell et al., 1999) on ITS phylogeny, dealing with 31 *Artemisia* species and latter study (Valles et al., 2003) including 44 *Artemisia* species and 11 species of related genera, represent a first approach to the solution of these systematic and phylogenetic problems. They on the one hand indicated some groups clearly established within *Artemisia* may point out toward the proposal of an infragenic classification. On the other hand, different levels are defined in the relationships between *Artemisia* and its segregate and/or related genera included in subtribe Artemisiinae or in other subtribes of Anthemideae, which means a first step in the redefinition of the subtribe.

Cladogram, constructed by Tkach et al. (2007) based on ITS and externally transcribed spacer (ETS) sequences of the DNA, topology does not support the traditional classification in several details. For example, subgenus *Seriphidium* was shown to consist of two independent groups and three of the four section analyzed within subgenus *Artemisia* were polyphyletic. The placement of some segregate genera within *Artemisia* also points to shortcomings of the traditional taxonomy and details of character evolution and the major relationships within *Artemisia*.

On the bases of nuclear ribosomal DNA ETS and ITS sequences, Sanz et al. (2008) show the combined phylogeny of *Artemisia* and allies, which highly supports the monophyly of the genus *Artemisia* including sex of the twelve segregated or related genera considered. Their analysis also suggested that a subgenus *Artemisia*-type taxon (species with heterogamous capitula with all hermaphrodite florets fertile) should be the progenitor of the remaining lineages within *Artemisia*.

## Conclusion

Torrell et al. (1999) and Valles et al. (2003) have revealed the limits of the ITS resolution power in the phylogeny of Artemisiinae. The high level of homoplasy and the low number of informative characters by the sequences of the ITS region suggested that other regions should be explored for a better understanding of the limits and phylogeny of the genus *Artemisia*. It is also obvious from their research that the chloroplast DNA trnL-F spacer is not useful at this level. There is a need to look for new genome regions for further research and it is need to include representatives of all the remaining genera in the subtribe in future studies in order to clarify a subtribal classification that over molecular analysis have weakened. The results will surely allow them to present more specific well-founded proposals for a natural classification of the genus *Artemisia* and subtribe Artemisiinae. Similarly, the classification, based on morphology should also need to be revived and more morphological characters should be included to remove conflicts between the taxa of *Artemisia*.

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