

Historical biogeography of the genus *Chamaecyparis* (Cupressaceae, Coniferales) based on its fossil record

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Abstract The megafossil record of *Chamaecyparis* (Cupressaceae) in the Northern Hemisphere, especially that in Europe, is reviewed with the aim of gaining a better understanding of the biogeographic history of this genus and providing an explanation of the causes of eastern Asian and western and eastern North American intercontinental disjunction of extant members. The fossil data available favor the hypothesis that earlier members of *Chamaecyparis* were widely distributed in the mid to high latitudes of North America and Europe during the Paleogene and that they spread via the North Atlantic land bridges. During a period of successive global climatic coolings in the Neogene, the distribution of the genus was gradually restricted until *Chamaecyparis* ultimately disappeared from Europe in the Plio-Pleistocene. Eastern Asian *Chamaecyparis* most likely came from North America via Beringia during the Paleogene or migrated from Europe eastwards after the Oligocene, when the Turgai Strait retreated. Eastern North American *Chamaecyparis* appears to have originated either from northern high latitudes or western North America.

Keywords *Chamaecyparis* · Disjunction distribution · Dispersal · Fossil record · Historical biogeography · Land bridge

Introduction

For nearly two centuries, the distinctive disjunction of taxa between eastern Asia and eastern North America has remained a classic phytogeographical phenomenon (Gray 1846; Mai 1995; Wen 1999, 2001). Recently, however, comparative analyses of molecular sequences from nuclear, mitochondrion, and chloroplast DNA and RNA have contributed not only to our understanding of phylogenetic relationships, but also to that of biogeographic patterns of dispersal (Manos and Donoghue 2001), adding to an already substantial body of data based on the more traditional fields of botany and paleobotany.

In this context, *Chamaecyparis* (Cupressaceae) is considered to have a typical disjunct distribution (Li et al. 2003; Wang et al. 2003). Two independent studies on the historical biogeography of all extant *Chamaecyparis* species, both based on the analysis of DNA, have been recently published (Li et al. 2003; Wang et al. 2003), with each proposing explanations for the intercontinental disjunction of *Chamaecyparis*. The two studies share one common aspect: Europe, due to the lack of any living *Chamaecyparis* species, was completely excluded from the biogeographic analyses. Nevertheless, in the paleobotanical literature it has been well documented that Europe, among the three major landmasses of the Northern Hemisphere, played a crucial role in past plant migrations, including *Chamaecyparis* (Kotyk et al. 2003; Mai 2004).

It is admittedly difficult for phylogeographers to include in their analysis a region from which taxa are

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currently absent. While phylogeography provides us with a framework (Donoghue et al. 2001), it apparently becomes less useful in the face of local extinctions, as is the case for *Chamaecyparis* (Li et al. 2003; Wang et al. 2003) and *Thuja* (Li and Xiang 2005). For a better understanding of biogeography, it is therefore essential to integrate a careful review of fossil data with phylogenetic information in order to reconstruct the most parsimonious cladistic trees. These trees will in turn yield the most informative evidence that can then be used to deduce the phytogeographic history (Manchester and Tiffney 2001; Tiffney and Manchester 2001).

The aim of this paper is to construct biogeographical scenarios for *Chamaecyparis* on the basis of reliable megafossil evidence.

Review of the fossil record of *Chamaecyparis*

Because cupressaceous pollen and wood are more or less indistinguishable at the generic level, our review of the fossil record of *Chamaecyparis* focuses on megafossils only. The megafossil record of *Chamaecyparis* has been briefly discussed and tabulated by Kotyk et al. (2003), and while their list provides a good starting point for our understanding of the fossil history of *Chamaecyparis*, especially for the fossil record in North America and Asia, it is incomplete in terms of the European record. Furthermore, the list includes a number of taxa that may not be attributable to *Chamaecyparis* because reliable generic determination based exclusively on the external morphology of vegetative organs of Cupressaceae is very difficult (McIver 1994). Consequently, the identification of fossil vegetative remains, such as twigs, leaves, or branches, to an extant genus is typically unreliable. We have therefore excluded these taxa from our biogeographical analysis.

A recent proposal to revise the genus *Chamaecyparis* and to remove *Chamaecyparis nootkatensis* from the genus (Jagel and Stützel 2001; Farjon et al. 2002; Little et al. 2004; Xiang and Li 2005) will influence our interpretation of the fossil record of *Chamaecyparis* s.s. For example, the oldest report of *Chamaecyparis*, *Ch. corpulenta* (Bell) McIver 1994, from the Upper Cretaceous of Vancouver Island, British Columbia, Canada, will have to be removed from the fossil record of the genus, as noted by Kotyk et al. (2003), because the seed cones of *Ch. corpulenta* are most similar to those of the living *Ch. nootkatensis*. In the following discussion, all fossils assignable to the *Ch. nootkatensis* lineage will be excluded, and the designation of *Chamaecyparis* will be used in the strictest sense.

Three fossil species of *Chamaecyparis* have been reported from China, including one piece of wood (*Chamaecyparioxylon chinense* Du) from the Paleocene of

Liaoning, northeast China (Du 1987) and two leaves with no specific determinations (*Ch. sp.*) from the Eocene of Sichuan, southwestern China (Guo 1986), and the Eocene and Pliocene of Hunan, central China (Sze and Lee 1954; WGCPC 1978). The fossil leaves have no cuticles preserved, and their generic determinations are dubious, while fossil wood is not known to exhibit diagnostic characters for *Chamaecyparis* (Kotyk et al. 2003).

Europe has yielded a diversity of remains of *Chamaecyparis*, as reported by Mai (2004), who provides a key for the determination of most European fossil species of the genus based on external morphology. The reported oldest occurrence for Europe, *Chamaecyparis belgica* Saporta et Marion, is a twig from the Paleocene of Gelinden in Belgium (Saporta and Marion 1873). The holotype of this species has been lost (D.H. Mai, personal communication). Based on the description and published figure (Plate 1, Fig. 3 of Saporta and Marion 1873), however, its morphological characters are found not in *Chamaecyparis*, but in the extant species *Calocedrus formosana* (Florin) Florin, *Calocedrus macrolepis* Kurz, and *Thujaopsis dolabrata* (Thunb. ex L.f.) Sieb. et Zucc. (Schulz et al. 2005). Only with additional material from this site, which is of particular interest to researchers in terms of gaining an understanding of plant migration routes between Europe and Asia (Kovar-Eder 1994), will the true nature of these cupressaceous fossils be understood. Other fossils of a similar uncertain affinity from the Paleogene of Europe—and excluded from this biogeographical analysis—include *Chamaecyparis mengeana* (Goeppert et Berendt) Goeppert and Berendt 1845, *Ch. breyniana* (Goeppert et Berendt) Goeppert and Berendt 1845, *Ch. ehrenswaerdii* Heer 1870, *Ch. europaea* (Saporta) Saporta 1889, *Ch. massiliensis* (Saporta) Saporta 1889, *Ch. argesensis* Givulescu 1971, and *Ch. obtuse* Sieb. et Zucc. *fossilis* Chochieva 1975. An exception may be made, however, for fossil twigs assigned to *Chamaecyparis* cf. *Ch. lawsoniana fossilis* from the Pliocene of Willershausen (central Germany), for which putatively diagnostic leaf cuticles are preserved (Straus 1952).

The European fossil remains of *Chamaecyparis* preserved as seed cones or seeds may be identified with more certainty and include *Chamaecyparis europaea* (Saporta) Saporta from the Upper Oligocene of France (Saporta 1889), *Ch. salinarum* Zabłocki emend. Mai of the Neogene in Central Europe (Zabłocki 1930; Mai 2004), *Ch. uralensis* Dorofeev from Miocene strata of Ural area in Siberia (Dorofeev 1970), *Ch. pisifera* Sieb. et Zucc. *fossilis* Szafer from the Pliocene of Poland (Szafer 1947), *Ch. sp.* from the Pliocene of Germany (van der Burgh and Zetter 1998), and *Ch. sp.* from the Plio-Pleistocene of northern Italy (Martinetto and Ravazzi 1997). Among these, *Ch. salinarum* has received particular attention due to its

common occurrence throughout Central European Middle Miocene to Pliocene strata. It is considered to closely resemble extant *Ch. obtusa* Sieb. et Zucc. of Japan and Taiwan (Mai 2004).

Fossil records from North America, as reviewed by Kotyk et al. (2003), include *Chamaecyparis eureka* Kotyk from the Eocene of Axel Heiberg Island, *Ch. linguaeifolia* (Lesq.) MacGinitie from the Oligocene of Colorado, and Miocene and Pliocene material considered indistinguishable from extant *Ch. lawsoniana* (Axelrod 1962; MacGinitie 1962; Wolfe 1964). The leafy twig fossils from the middle Eocene of Idaho, which were attributed to *Ch. edwardsii* Axelrod 1998, were recently revised and recognized as an unidentifiable species (Erwin and Schorn 2005). Most recently, leafy twigs and cones resembling those of *Chamaecyparis* from the upper Lower Eocene of British Columbia, Canada were reported as *Chamaecyparis* sp. by Dillhoff et al. (2005), although without formal taxonomic treatment this record will be considered as tentative.

Table 1 summarizes these megafossils and other important records from the Northern Hemisphere. It is worth mentioning that the older fossils of *Chamaecyparis* appear to be generally similar to the living *Ch. pisifera* from Japan and *Ch. lawsoniana* of western North America, while younger fossils resemble extant *Ch. obtusa* of Japan and Taiwan. More fossils are needed to test if this observation has any evolutionary relevance.

Biogeographic history of *Chamaecyparis*

The current geographic distribution of *Chamaecyparis* displays a classical eastern Asia and western and eastern North America disjunct pattern (Fig. 2), thereby representing one of the most remarkable phytogeographical phenomena of the boreal temperate flora (Xiang et al. 1998; Wen 1999; Kotyk et al. 2003; Li et al. 2003; Wang et al. 2003). It is generally accepted that the disjunct pattern is a relic of the maximum development of temperate forests in the Northern Hemisphere during the Cenozoic and that it has multiple origins involving interchange across either the North Atlantic (linking eastern North America and Europe via Greenland and/or the Arctic Islands) or Beringia (connecting western North America and eastern Asia) corridors, or both (Figs. 1, 2) (Wen 1999; Liu and Basinger 2000; LePage 2002). Despite the similarity of the geographical distribution patterns found for numerous groups, the involved extant plant taxa may have originated at different geological times, may have followed various dispersal routes, and may have quite different histories of extinction and survival (Xiang et al. 1998).

Chamaecyparis includes just five living species widely distributed along the eastern margin of East Asia and in western as well as eastern North America (Fig. 2) (Kotyk et al. 2003; Li et al. 2003; Wang et al. 2003; Farjon 2005). All species are restricted to humid environments (Farjon 2005).

Table 1 Selection of reliable fossil records of *Chamaecyparis* from Asia, Europe, and North America used in this study^a

| Age | Fossil | Comparable extant | Locality | Reference |
|-------------------------------|---------------------------------------|---------------------------------------|--------------------------|-------------------------------------------|
| Late Early Eocene | <i>Chamaecyparis</i> sp. | ? | British Columbia, Canada | Dillhoff et al. 2005 |
| Middle Eocene | <i>C. eureka</i> | <i>Chamaecyparis pisifera</i> | Arctic, Canada | Kotyk et al. 2003 |
| Early to Mid-Oligocene | <i>C. linguaeifolia</i> | <i>C. lawsoniana</i> | Colorado, USA | MacGinitie 1953 |
| Upper Oligocene | <i>C. europaea</i> | ? | France | Saporta 1889 |
| Miocene | <i>C. sp.</i> | <i>C. cf. lawsoniana</i> | USA | Smiley and Rember 1981 |
| | <i>C. uralensis</i> | <i>C. obtusa</i> | Ural, Russia | Dorofeev 1970 |
| Mid Miocene to Lower Pliocene | <i>C. salinarum</i> | <i>C. obtusa</i> | Central Europe | Mai 2004 |
| Mid Miocene to Pleistocene | <i>C. pisifera fossilis</i> | <i>C. pisifera</i> | Poland | Szafer 1947 |
| Upper Miocene to Pliocene | <i>C. lawsoniana</i> | <i>C. lawsoniana</i> | Western USA. | Axelrod 1962; MacGinitie 1962; Wolfe 1964 |
| Pliocene | <i>C. lawsoniana fossilis</i> | <i>C. lawsoniana</i> | Germany | Straus 1952 |
| | <i>C. sp.</i> | ? | Germany | van der Burgh and Zetter 1998 |
| | <i>C. pisifera</i> & <i>C. obtusa</i> | <i>C. pisifera</i> , <i>C. obtusa</i> | Japan | Miki 1958 |
| Lower Pleistocene | <i>C. salinarum</i> | <i>C. obtusa</i> | Caucasus | Chochieva 1975 |
| Pliocene to Pleistocene | <i>C. pisifera</i> | <i>C. pisifera</i> | Caucasus | Chochieva 1975 |
| | <i>C. sp.</i> | ? | Northern Italy | Martinetto and Ravazzi 1997 |

^a For more details, see Kotyk et al. 2003

Fig. 1 Generalized paleogeographic reconstruction of the Northern Hemisphere, polar projection, during the Paleogene (approx. 45 million years ago), showing the occurrence of *Chamaecyparis* macroremains in the Eocene (solid circles) and Oligocene (solid squares). Star North Pole. Modified from LePage and Basinger (1995)

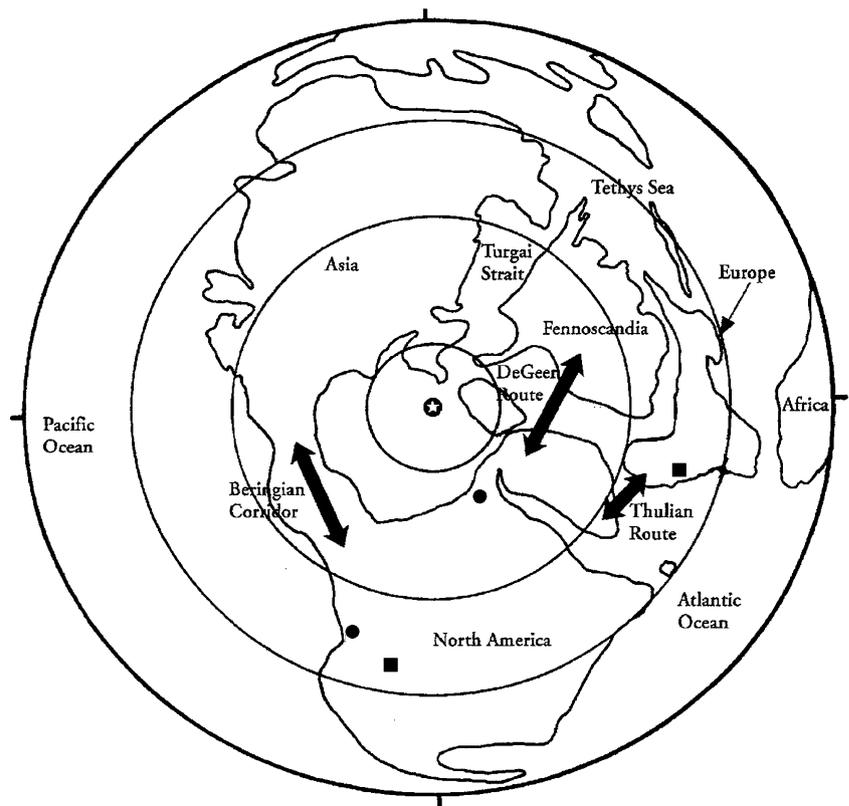
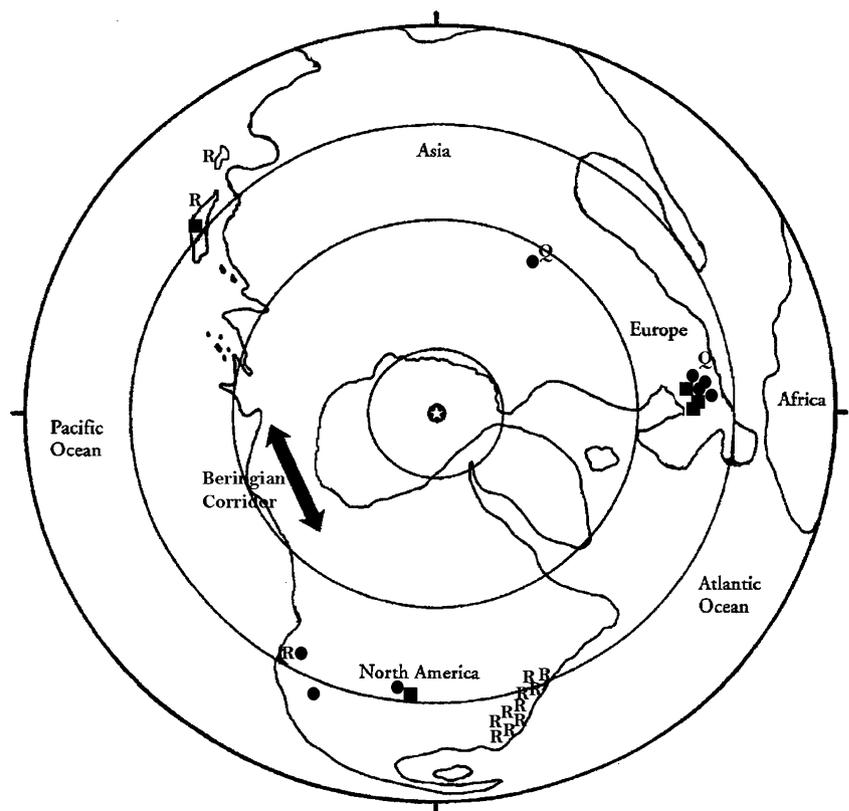


Fig. 2 Generalized paleogeographic reconstruction of the Northern Hemisphere, polar projection, during the Neogene (approx. 15 million years ago), showing the occurrence of *Chamaecyparis* macroremains in the Miocene (solid circles) and Pliocene (solid squares). Quaternary remains (Q) and recent distributions of *Chamaecyparis* (R) are also plotted. Star North Pole. Modified from LePage and Basinger (1995)



The phylogeny and biogeography of *Chamaecyparis* have been studied intensely using molecular data of either the nuclear ribosomal intergenic transcribed spacer (nrITS) or chloroplast (cp)DNA intergenic spacer *petG-trnP* for all living *Chamaecyparis* species by Li et al. (2003) and Wang et al. (2003), with both sets of authors contributing phylogenetic trees inferred from their specific molecular data. These authors then used these trees to construct area cladograms by replacing terminal taxon names with the distribution area of the respective taxon (Humphries and Parenti 1999). Based on these resulting area cladograms, Li et al. (2003) explained the cause of inter-continental disjunct distribution of *Chamaecyparis* in two alternative biogeographic scenarios with a minimum of two dispersal events between eastern Asia and North America, while Wang et al. (2003) concluded that *Chamaecyparis* may have originated in North America first and then dispersed to eastern Asia via Beringia.

It is beyond the scope of our paper to review the phylogeny of *Chamaecyparis*. We therefore focus on the biogeographical analysis. When discussing the historical biogeography of *Chamaecyparis*, both Li et al. (2003) and Wang et al. (2003) propose that *Chamaecyparis* may have exploited Beringia for inter-continental dispersal. As no living *Chamaecyparis* species occur in Europe, this continent was consequently excluded from their historical biogeographic analyses. Nevertheless, this dismissal of the relevance of Europe to the biogeographical evolution of *Chamaecyparis* appears to have been inappropriate. The documentation of *Chamaecyparis* fossils from European Tertiary strata (Mai 2004) leaves no doubt that Europe must have played a critical role in the biogeographical distribution of the genus. Although the current fossil record of *Chamaecyparis* is not extensive, the data are sufficient to enable us to outline a history of the genus.

With the removal of *Chamaecyparis nootkatensis* from the genus, and therefore the removal of the Cretaceous *Ch. corpulenta* as well, the oldest reliable fossil record of *Chamaecyparis* s.s. is *Ch. eureka* from the Canadian Arctic Archipelago (Table 1). This does not necessarily imply that this region must be the center of origin for the genus. Nevertheless, when additional data are considered, the distribution of Paleogene *Chamaecyparis* appears to be confined to mid- to high-latitude regions in North America and Europe (Fig. 1). During this time, North America and Western and Northern Europe were to a greater or lesser extent connected via two land bridges, i.e., the northern DeGeer Route bridging North America to Fennoscandia through northern Greenland, and the southern Thulian Route linking North America to Europe through southern Greenland (Fig. 1) (LePage 2002; Scotese 2004). Given the mild polar climate of the Paleogene, these routes would have allowed taxa such as *Chamaecyparis* to exchange

freely (Fig. 1). During the later Paleogene, *Chamaecyparis* extended its range southward to occupy western North America, as shown by the occurrence of *Chamaecyparis* in the Oligocene of Colorado (Fig. 1) (MacGinitie 1953). Westward extension of the range across the high latitude Beringian Corridor appears to have allowed the genus to reach eastern Asia, where *Chamaecyparis* later became established in Japan and Taiwan. While there is little fossil evidence to support the Beringian Corridor scenario (only a single Pliocene occurrence of *Chamaecyparis* is known from Japan) (Miki 1958) (see Table 1 and Fig. 2), entry directly into eastern Asia from Europe, or vice versa, was precluded by the epicontinental seaway barrier of the Turgai Strait and/or a climatic barrier (R.A. Spicer, personal communication) (Fig. 1). Exchange between Europe and East Asia would have been difficult until at least the Oligocene, when the Turgai Strait finally closed (Fig. 2) (Scotese 2004), which is consistent with the limited similarities of the Eocene floras of China and Central Europe. For example, several elements, such as *Metasequoia*, *Alnus*, and *Platanus*, are common elements of the Chinese Eocene floras but are absent from Central European coeval floras (Manchester et al. 2004).

The Neogene witnessed profound global climatic cooling and active tectonic activities, which must have strongly limited the availability of the North Atlantic land bridges and floral exchange between North America and Europe (Fig. 2) (LePage 2002; Scotese 2004). With the loss of the Turgai Strait in the Oligocene, however, plant exchange within Eurasia became easier, and *Chamaecyparis* made its appearance in the Ural regions in the Miocene (Fig. 2) (Dorofeev 1970). Nevertheless, with the uplift of the Tibetan Plateau in the mid-Tertiary (An et al. 2001) and the increasingly dry continental climate in north-central Asia, this route did not longer remain available to plants adapted to high humidity levels (LePage 2002; Scotese 2004). This may explain the absence of fossils of *Chamaecyparis* in the Russian Far East (Fig. 2).

Quaternary glaciations in Europe appear to have been the ultimate cause of extinction for *Chamaecyparis* in Europe. The Caucasus and northern Italy appear to have become a refugium for a number of plants into the Pleistocene (Fig. 2) (Chochieva 1975; Martinetto and Ravazzi 1997). There is as yet no reliable fossil record of *Chamaecyparis* from Central Asia and continental eastern Asia (Table 1), which argues against an eastward dispersal to Japan and Taiwan, where three living species of *Chamaecyparis* survive (Fig. 2).

Manchester (1999) reviewed North American Tertiary floras and proposed four main patterns of geographic distribution of taxa in the Northern Hemisphere: circum-boreal, Euro-American, Amer-Asian, and endemic patterns. The biogeographical history of *Chamaecyparis* matches

Manchester's pattern 2, i.e., Euro-American distribution, whereby the Eocene interchange between North America and Europe via the North Atlantic land bridges occurred prior to dispersal into Asia. Subsequent dispersal into eastern Asia could have involved either Beringia and/or post-Eocene migration within Eurasia. Disjunct distribution of extant species in East Asia and North America, with the extinction of European populations, is a pattern shared by many flowering plants, including, for example, *Carya* (Juglandaceae), *Gordonia* (Theaceae), and *Hydrangea* (Hydrangeaceae) (Manchester 1999).

As Paleogene and Neogene floras are rare in northeastern North America (Graham 1999), the origin of the populations of living *Chamaecyparis* in eastern North America is unclear. A dispersal hypothesis, rather than vicariance events, may better correspond with the fossil data available, such that either of two dispersal routes may have contributed to the current distribution of the genus in eastern North America. During the Paleogene and Neogene, the exchange of plants, such as *Chamaecyparis*, between western and eastern North America became limited by temperature (increasing seasonality in the Cordillera in the Paleogene and cooling in the late Neogene and Quaternary), moisture (drying in the Cordillera in Paleogene times and the development of grassland in the central plains), and physical continuity (the Cordilleran barrier from the Eocene onwards) (Tiffney and Manchester 2001). Consequently, it is unlikely that a dispersal route from western to eastern North America was available to *Chamaecyparis*, a drought-intolerant plant, if it is accepted that climatic tolerance in the genus has not substantially changed through time. Thus, one possibility is that the current eastern North American *Chamaecyparis* populations may have originated from the retreat of ancient *Chamaecyparis* into the high latitude regions, as represented by the Arctic fossil *Chamaecyparis* (Kotyk et al. 2003). New fossil data from eastern North America will be needed to either prove or disprove this hypothesis.

Future research

Phylogeographical analyses of several extant flowering plant taxa with endemic species in eastern Asia, western North America, and eastern North America indicate that eastern North American and western North American species are more closely related to one another than they are to the species from eastern Asia (Xiang et al. 1998, 2000). Further phylogenetic work on the living species of *Chamaecyparis* as well as a more detailed investigation of the fossil record of the genus are required in order to establish if this pattern is also seen in *Chamaecyparis*. Although Kotyk et al. (2003) have indicated that the Arctic

fossil is morphologically most similar to extant *Ch. pisifera* of Japan, its phylogenetic relationship remains uncertain. Clarification of the phylogenetic relationships among the living species of *Chamaecyparis*, the inclusion of well-preserved fossils, especially Arctic fossils, and the incorporation of the fossils into cladistic analysis will lead to more refined phylogenetic cladograms (Manchester and Tiffney 2001, compare Manen et al. 2002). This will, in turn, provide for a better working hypothesis on the origin, biogeographic evolution, and evolutionary differentiation within the *Chamaecyparis* lineage.

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