

Cenozoic Araucariaceae in the Northern hemisphere: decline and recovery

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Summary: Cenozoic extinct taxa of Araucariaceae from Europe, Asia and Northern America have been surveyed. The macrofossil and palynological records of Araucariaceae in the Northern hemisphere end in the Eocene. There are no convincing data on the occurrence of this family in the early Oligocene of Eurasia and North America. Two araucarioid fossil woods that have been reported (PRAKASH & DU 1995; FENG et al. 2015) from the late Oligocene to middle Miocene of China (*Araucarioxylon shandongense* Prakash & Du from Shandong province and *Agathoxylon* sp. from Hainan island) are the most recent fossil records of Araucariaceae in the Northern hemisphere. These woods may be considered as evidence of the dispersal of Araucariaceae from Australia to East Asia that gave rise to radiation of the genus *Agathis*.

Keywords: Araucariaceae, Cenozoic, Paleogene, Northern hemisphere, Oligocene, Miocene, *Araucarioxylon shandongense*, *Agathoxylon*, *Agathis*

The conifer family Araucariaceae comprising three recent genera *Araucaria*, *Agathis* and *Wollemia* is distributed now in South America, Malesia, Australia and Western Pacific. This family appeared in the early Triassic and widely expanded and diversified during the Mesozoic. In contrast to the present range, the Araucariaceae were widespread in both hemispheres throughout Jurassic and Cretaceous (STOCKEY 1982; KERSHAW & WAGSTAFF 2001; LESLIE et al. 2012). Their diversity in the Northern hemisphere declined, however, in the Paleogene up to their disappearance in the Eocene, with a brief reappearance in the late Oligocene to early Miocene. In this article, the Cenozoic extinct taxa from Europe, Asia and Northern America tentatively assigned to Araucariaceae are surveyed, and their role in the origin and diversification of recent genera of this family is discussed.

In the deposits of Europe, Araucariaceae are represented by sterile branches of *Araucarites sternbergii* and *Araucarites* sp. known from the Paleocene and Eocene of several localities in Austria, Denmark, England, Italy and Slovenia (SEWARD 1919; BRÜNNICH-NIELSEN 1926; CHANDLER 1960; JUNGWIRTH 2004). The foliage branches with male or female cones of *Doliosstrobilus taxiformis* (Sternberg) Z. Kvaček emend. Kunzmann occurring in the Eocene and Oligocene of Central and Western Europe as well as dispersed pollen of *Araucariacites europaeus* Krutzsch from the Eocene of these regions (SEWARD 1919; BUŽEK et al. 1968; WILDE & FRANKENHÄUSER 1998) were also assigned to Araucariaceae. Their affinity to this family has been questioned by KVAČEK (2002), who recognized these taxa as members of a new family Doliosstrobaceae.

In North America, Cenozoic Araucariaceae are known by foliage branches with cones of *Araucaria longifolia* (Lesquereux) Brown from the Paleocene of Wyoming and Montana (BROWN 1962). Besides that, three morphotypes of araucarioid woods have been reported from the Paleocene of Texas (WHEELER & LEHMAN 2005), and pollen of *Araucariacites* have been found in the late Paleocene of North Dakota (ZETTER et al. 2011).

In Asia, the seed scale of *Araucarites* sp. (MEHROTRA & SRIVASTAVA 1994) as well as the araucarioid woods belonging to several species of *Agathoxylon* (originally described as *Dadoxylon* and *Araucarioxylon*) have been reported from the early Paleogene deposits of India (CHITALEY 1949; HARSH & SHARMA 1988; TRIVEDI & SRIVASTAVA 1989, 1990; LAKHANPAL et al. 1977; SRIVASTAVA & GULERIA 2006) and Vietnam (VOZENIN-SERRA 1981). Pollen of Araucariaceae have been reported from the Paleocene and Eocene brown coal deposits of Amur region of the Russian Far East (KEZINA 2012) and from the early Paleocene of the Heilongjiang province in the neighbouring region of China (HAO et al. 2010).

However, the finding of fossil wood *Araucarioxylon shandongense* Prakash & Du in the middle Miocene deposits of the Shandong province in China (PRAKASH & DU 1995) is notable. Moreover, *Agathoxylon* sp., which has recently been reported from the late Oligocene to early Miocene of the Qiutangling Formation of Ledong, Hainan Island, is very similar to the former species (FENG et al. 2015). These fossil woods are the most recent records of Araucariaceae in the Northern hemisphere.

Therefore, the macrofossil and palynological records of Araucariaceae in the Northern hemisphere end in the Eocene with only two records of fossil woods from the late Oligocene to the middle Miocene. There are no convincing data on the occurrence of this family in the early Oligocene of Eurasia and North America, whereas the araucarioid fossils were reported in deposits of this age from Australia, New Zealand and South America (HILL & BRODRIBB 1999; KERSHAW 2001; JARAMILLO et al. 2013).

Araucarioxylon shandongense and *Agathoxylon* sp. from Ledong can be considered as representatives of a relict lineage of Araucariaceae that had been persisting in East Asia since the Eocene (KEZINA 2012). The paucity of fossil evidences for the presence of Araucariaceae in Asia during the late Paleogene suggests, however, that the occurrence of species in China can more likely be the result of the dispersal of Araucariaceae from Australia. This dispersal event would have occurred in the Oligocene or the early Miocene, after the emergence of Southeast Asia, caused by the collision of the Eurasian and Australian plates, and it gave rise to diversification of the genus *Agathis* (KERSHAW 2001; KERSHAW & WAGSTAFF 2001; BUEKI et al. 2013). Today, *Agathis* ranges through Malesia and extends east to the islands of Southwest Pacific, New Zealand and south Queensland. As almost all Malesian species of this genus are allopatric (WHITMORE & PAGE 1980), their radiation occurred following or in the course of the colonisation of this region (including the Malay peninsula, i.e. the mainland of Southeast Asia) by their ancestors.

It is not possible to confidently confirm the affinity of *A. shandongensis* and *Agathoxylon* sp. from Ledong to *Agathis* without SEM examination of these fossil woods, because Araucariaceae genera can be distinguished from each other only by fine details of warts (vestures) in their tracheids (HEADY et al. 2002). Nevertheless, these fossil woods give evidence of the presence of Araucariaceae in East Asia nearly coincidentally with the divergence age of *Agathis* in the early Neogene, as it was estimated by molecular dating (LESLIE et al. 2012). Therefore, the fossil woods of *A. shandongensis* and *Agathoxylon* sp. may well be the most ancient records of the dispersal of Araucariaceae from Australia to East Asia known to date. This interpretation of current data remains hypothetical until new researches confirm or reject it.

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