



Structure and affinities of *Athrotaxites yumenensis* sp. nov. (Cupressaceae) from the Lower Cretaceous of northwestern China

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ABSTRACT

Compressions of leafy twigs, pollen cones and seed cones of *Athrotaxites yumenensis* C. Dong et B.N. Sun sp. nov. (Cupressaceae) are abundant in certain layers of the Lower Cretaceous Zhonggou Formation in western Gansu Province, northwestern China. The leafy branches are stiff and ascending. The leaves are scale-like, spirally arranged and closely appressed to the stem. The seed cones are located terminally, globular, with 8–11 helically arranged bract-scale complexes. The bracts are intimately fused with, and more massive than, the seed-bearing portion, and each scale has two seeds. The seeds are oval, 0.9–1.1 mm long and 1 mm wide with two wings derived from the seed coat. A single pollen cone occurs at the ends of the ordinary branches with 10–16 microsporophylls. The microsporophylls are wedge-shaped and spirally arranged. Terminal microsporophylls fall away from the cone axis after pollen dispersal. The pollen sacs are ovate and produced more than 20 pollen grains per sac. The pollen grains are spherical, lack air bladders and have small germinal papilla and pores. Compared to the extant Tasmanian genus *Athrotaxis* in morphological, structural and cuticular features of leafy shoots, as well as seed cones and pollen cones, the study fossil consistently shares many characteristics with the extant genus, especially the extant species *Athrotaxis cupressoides*, but differs from it in other aspects; thus, it has been placed in a new genus. The similar characteristics, however, suggest that the fossil has the closest affinity with the extant *Athrotaxis cupressoides*. A detailed comparison of leaf morphology and the macro- and microstructure of the pollen and seed cones with related fossil species of *Athrotaxis* and *Athrotaxis*-like species reveals that the present fossil is a new species. Additionally, the occurrence of the fossil in the Zhonggou Formation and its similar characteristics with another fossil species, *Athrotaxites berryi*, suggests that *Athrotaxites yumenensis* sp. nov. might be an intermediate between *Athrotaxites berryi* and the extant *Athrotaxis* and that the new species is more closely aligned with extant *Athrotaxis* than with *Athrotaxites berryi*.

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1. Introduction

The Tasmanian montane and rainforest conifer *Athrotaxis* D. Don 1838 is the only living genus of Southern Hemisphere Cupressaceae with a spiral adult arrangement and consists of only three extant species: *Athrotaxis cupressoides*, *Athrotaxis selaginoides* and *Athrotaxis laxifolia* (Silba, 1986; Jordan et al., 2004; Eckenwalder, 2009). The genus comprises small to moderately large evergreen plants and has a distinctive combination of foliar, pollen cone and seed cone characteristics (Farjon, 2005; Schulz et al., 2005). The dense branches are spirally arranged with scale-like to broad claw-like leaves. The terminal microsporophylls fall away from the cone axis after pollen dispersal. The seed cones are rarely globular, with

15–25 spirally arranged seed scales. The cone scales are characterized by the fusion of the bract scales and the ovuliferous scales, with the apex of the bract scales forming thin, triangular or spinuous distal ends. Each scale bears three to six inverted seeds (Farjon, 2005; Schulz et al., 2005; Eckenwalder, 2009). Although restricted to Tasmania today, fossils of *Athrotaxis* are found in mainland eastern Australia, New Zealand, South America, and perhaps in North America (Spegazzini, 1924; Florin, 1940, 1960; Archangelsky, 1963; Townrow, 1965, 1967; Hill and Macphail, 1985; Hill et al., 1993; Srinivasan, 1995; Del Fueyo et al., 2008). The oldest representative record of the genus was dated to be from the Lower Cretaceous of Ticó, Santa Cruz Province, Argentina (Archangelsky, 1963).

Additionally, there are numerous fossils in the Northern Hemisphere that are similar to *Athrotaxis*, particularly from the Early Cretaceous. These species belong to the related extinct genera *Athrotaxites* and *Athrotaxopsis* (Fontaine, 1889; Florin, 1940; Bell,

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1956; Zheng and Zhang, 1982; Miller and LaPasha, 1983; Krassilov, 1967; 1973; Chen and Deng, 1990; Wan, 1996; Sun et al., 2001; Deng and Lu, 2008; Volynets, 2009). *Athrotaxites* was described by Unger (1849) from a branched cone-bearing shoot from the Upper Jurassic of Solenhofen, and *Athrotaxopsis* was described by Fontaine (1889) from fertile shoots from the Potomac Formation, USA. The type species of these two genera are *Athrotaxites lycopodioides* and *Athrotaxopsis grandis*. Vegetative shoot characteristics of *Athrotaxites* and *Athrotaxopsis* have similar leafy branches with spirally arranged and scale-like leaves that are appressed to the stem. There is only one seed at the bottom of the cone scale in *Athrotaxopsis grandis*, whereas the cones of *Athrotaxites lycopodioides* are incomplete and nothing is known of the seeds (Seward, 1919). Miller and LaPasha (1983) described *Athrotaxites berryi* based on leafy twigs, pollen and seed cones that were preserved both attached to twigs and separately. The cones of *Athrotaxites berryi* are large, and there is at least one seed produced at the base of the ovuliferous scale (Miller and LaPasha, 1983). Both Unger (1849) and Fontaine (1889) indicated that their genera were similar and were related to the Tasmanian genus *Athrotaxis*. Miller and LaPasha (1983) re-examined Fontaine's materials and indicated that the number of seeds per scale of *Athrotaxopsis grandis* was more than one and the differences separating *Athrotaxites* from *Athrotaxopsis* were insufficient. Thus, Miller and LaPasha (1983) proposed that there was no basis for maintaining two genera for the same types of fossil and that *Athrotaxites* Unger had priority. Fossil records of these three genera have not been comprehensively summarized and reviewed. Hence, there is a poor understanding concerning the origin of their extant distribution, an incorrect understanding of their past distribution and an unsubstantial interpretation of the phylogenetics of this genus.

Conifers dominate the megafossil flora from the Lower Cretaceous Zhonggou Formation in western Gansu Province, northwestern China (Deng and Lu, 2008; Du et al., 2013). The most common of these conifers is *Athrotaxites*. These fossils consist of leafy twigs and seed and pollen cones that are preserved both attached to twigs and separately. In this study, we described a new fossil species of *Athrotaxites* from recently discovered foliage and cone compressions from the Lower Cretaceous Zhonggou Formation. These comprehensive materials include morphological and

microstructural characteristics of leafy shoots, leaves, female cones and seeds, and male cones and pollen, which could provide new evidence that this Tasmanian conifer occurred in northwestern China during the Early Cretaceous. The phylogeographic history of *Athrotaxis* and *Athrotaxis*-like plants is also summarized, incorporating the new fossil evidence to outline the distribution patterns of these genera in the geological record.

2. Locality and stratigraphy

More than 30 specimens including leafy shoots, pollen cones and seed cones of *Athrotaxites yumenensis* sp. nov. were collected from lower part of the Zhonggou Formation in the western Jiuquan Basin, northwestern China (Fig. 1). The geological age of the Zhonggou Formation is considered to be Aptian to Albian of the Early Cretaceous based on plant fossil assemblages and spore-pollen assemblages (Liu, 2000; Deng et al., 2005; Deng and Lu, 2008; Du et al., 2013). The Lower Cretaceous stratum is well exposed in Jiuquan Basin. The exposed part of Zhonggou Formation is up to 200 m thick, composes of red mudstones and argillaceous sandstones in the lower part and finely laminated dolomitic limestones, dark-gray mudstones in the mid-upper part. The Zhonggou Formation conformably overlies the lower Cretaceous Xiagou Formation and is unconformably overlain by the Liugouzhuang Formation of the Paleogene. Abundant fossils were preserved as compressions mainly in the dark-gray mudstones of the upper part (Deng et al., 2005; Deng and Lu, 2008), including *Athrotaxites yumenensis* sp. nov.

3. Material and methods

The specimens were photographed first. Hydrogen peroxide (5%) was dripped evenly on the surface of the selected vegetative compressions in order to disaggregate the matrix below. Distilled water flooded on the surface when the foliage cuticle fragments were detached from the matrix, then removed them from the fossil using a small soft brush. Selected coalfield leaves and microsporophyll fragments were cleaned with hydrofluoric acid and hydrochloric acid, followed by maceration with Schulze's solution and a short time treatment with 5% ammonia. At last, the processed

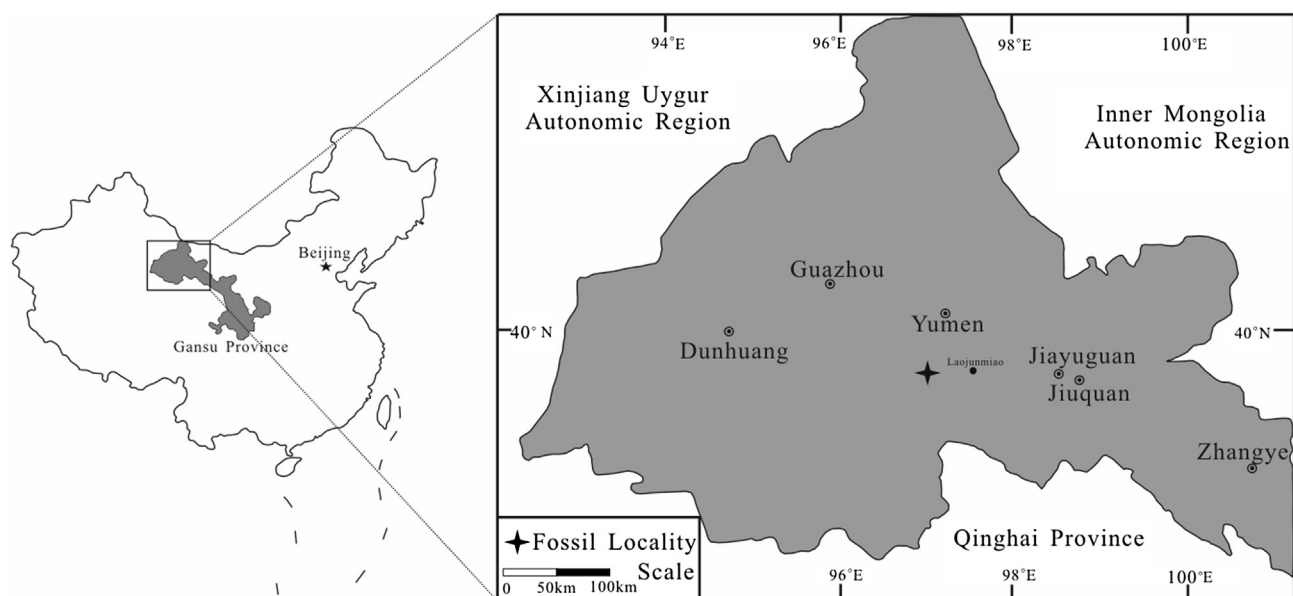


Fig. 1. Map showing the fossil locality (black star) of *Athrotaxites yumenensis* sp. nov.

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