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The conifer *Araucaria bladenensis* and associated large pollen and ovulate cones from the Upper Cretaceous Ingersoll shale (Eutaw Formation) of Alabama

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ABSTRACT

Araucarian conifer remains from the Upper Cretaceous Ingersoll shale Konservat-Lagerstätte (Eutaw Formation) of Alabama include shoots of *Araucaria bladenensis*, an associated pollen cone, an ovulate cone, and an isolated bract-scale complex that were probably produced by the same plant species. Well-articulated *A. bladenensis* specimens with preserved cuticles reaffirm the original generic determination and show similarity to branches of the extant species *A. bidwillii*. The large pollen cone is remarkable as the earliest example comparable in size and pollen sac number to those of the largest extant *Araucaria* species. The co-occurrence of this cone with *Upatoia barnardii* in the Eutaw Formation also demonstrates that typical, small araucarian fossil pollen cones coexisted during the Late Cretaceous with modern appearing, large-coned species. The intact ovulate cone is large and ovoid but poorly preserved. An associated bract-scale complex displays lateral wings and a ligule. Comparisons with other fossil and extant araucarian conifers indicate affinity with section *Bunya*, making this the first North American record of the section. These fossils reaffirm that araucarian conifers were a significant component of the southeastern US Cretaceous flora, and provide a temporal and biogeographic context for the currently unexplained transition from small to large pollen cones in the family.

1. Introduction

The Araucariaceae is one of the earliest of the extant conifer families to appear in the fossil record, as it has been identified from Late Triassic sediments and is commonly reported in Jurassic and Cretaceous deposits from both the northern and southern hemispheres (Kunzmann, 2007). Today the family includes three genera (i.e., *Araucaria* de Jussieu, *Agathis* Salisbury, *Wollemia* Jones, Hill and Allen) with approximately 40 species that are restricted to Southern Hemisphere localities (Farjon, 2008; Taylor et al., 2009). The genus *Araucaria* includes 19 species that occur in widely separated areas: South America, Australia, and several southern Pacific islands (Kunzmann, 2007). Four extant sections and one extinct section are formally recognized: *Araucaria* (= *Columbea* Endlicher), *Bunya* Wilde and Eames, *Eutacta* Endlicher, *Intermedia* White, and *Yezonia* (Ohsawa et al., 1995; Setogushi et al., 1998; Kershaw and Wagstaff, 2001; Kunzmann, 2007). Currently, section *Eutacta* is the largest with 15 species found in New Caledonia and other South Pacific islands; section *Araucaria* contains two species native to South America; section *Intermedia* contains one species found in New Guinea; and section *Bunya* with one species found in Australia (Setogushi et al., 1998; Farjon, 2001; Kershaw and Wagstaff, 2001; Eckenwalder, 2009).

Reliable araucarian records that include reproductive remains are known from several North American sites (Tidwell, 1990; Tidwell and Ash, 2006; Axsmith et al., 2008; Gee and Tidwell, 2010). Early records also include descriptions of probable araucarian vegetative remains (Hollick, 1898). Berry (1908) described shoots with flattened, parallel-veined, cuspidate leaves from Upper Cretaceous deposits in Alabama, Georgia, North Carolina, South Carolina, and Tennessee. They are similar to the leaves of the extant species *A. bidwillii*, and he assigned them to the extinct species *A. bladenensis* (Berry, 1908, 1910a, b, 1921). Large numbers of isolated bract-scale complexes (*A. jeffreyi*) were also found in association with *A. bladenensis* at the North Carolina locality. Mickle (1993) presented an emended diagnosis of *A. bladenensis* based on newly collected specimens from the Tar Heel Formation of North Carolina, and transferred the species to the morphogenus *Pagiophyllum*. This transfer was based on poorly preserved specimens that displayed inconsistently present structures on the cuticles that

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were interpreted as Florin rings. As Florin rings do not occur on any known leaves of *Araucaria*, but do occur on leaves of *Agathis* species (Araucariaceae) and *Nageia* (Podocarpaceae), Mickle (1993) concluded that definitive generic and familial assignment would have to await the discovery of reproductive material. The known association of *A. bladenensis* and abundant *A. jeffreyi* was apparently not considered in this nomenclatural transfer.

Here we describe well-articulated leafy shoots of *A. bladenensis* from the Upper Cretaceous Ingersoll shale (part of the Eutaw Formation in eastern Alabama) Konservat-Lagerstätte (Knight, 2007; Bingham et al., 2008; Savrda et al., 2009; Knight et al., 2010), including analysis of the cuticles that reaffirm the original generic determination. An associated ovulate cone, an isolated bract-scale complex, and a very large pollen cone (15.5 cm long) support this conclusion. The pollen cone is particularly remarkable, as it is comparable in size to the large pollen cones seen in extant representatives of Araucariaceae generally and the genus *Araucaria* in particular. Although the cones are not found physically connected to the vegetative branches, this material occurs in an outcrop that represents a short depositional period (i.e., approximately one year) (Bingham et al., 2008). This, along with the level of articulation of the organs and their similarity to those of extant species of *Araucaria*, indicates that they were probably produced by the same parent plant species that lived fairly close to the site of deposition.

2. Geological context

The Eutaw Formation is of Santonian age (85.5–83.5 Ma) and crops out in a belt from southwestern Tennessee, northeastern Mississippi, northwestern through central Alabama, and ends in central western Georgia. The Ingersoll shale is a thin (<1 m) clay lens of the Eutaw Formation located in eastern Alabama that has been interpreted as a shallow tidal channel deposit formed during a marine transgression (Bingham et al., 2008). The rich fossil floral assemblage includes ferns, horsetails, conifers, and angiosperms. The fauna includes mollusks, insects and other terrestrial arthropods (some in amber), fish scales, abundant feathers, and many other components (Bingham et al., 2008).

3. Material and methods

All the fossils described here are impression-compression remains collected from the basal portions of the Ingersoll shale, an informal unit of the Eutaw Formation in Alabama (Bingham et al., 2008). While the Ingersoll shale is rightly considered an important Konservat-Lagerstätte, the preservation of the plant fossils in this lowermost interval is highly variable. In some cases, including most of the fossils described here, the quality is somewhat compromised by oxidation from groundwater infiltration and the presence of oxidized pyrite. Nevertheless, the fossils are well articulated and provide useful new information.

3.1. Fossil preparation and examination

Light microscopy with a dissecting microscope was utilized to identify components of the ovulate cone, pollen cone, and leaves. Efforts to image leaf epidermal features on the cuticles and discern pollen on the pollen cone with epifluorescence microscopy were unsuccessful. Although preservational quality of the leaf cuticles was variable, enough cuticle was removed so that small areas of the epidermis could be cleared with Schulze's reagent and mounted on slides for study with light microscopy. Initial efforts at macerating microsporophyll cuticle and associated pollen sacs to retrieve pollen were unsuccessful. Additional attempts were not made, as only one pollen cone specimen is currently available. However, a small section of pollen sac was removed, mounted on a stub, and sputter coated with gold for SEM analysis. This allowed documentation of two poorly preserved pollen grains imbedded in tapetal membrane. The ovulate cone degraded considerably shortly after collection and before detailed study was possible, mainly due to pyrite oxidation, so only the gross morphology was visible. However, a single isolated bract-scale complex provided some morphological detail.

3.2. Specimen numbering and repository

Specimens examined for this study are deposited in the Paleobotany and Palynology Collection at the Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA under the locality prefix UF19310 (Ingersoll shale, Russell County, Alabama). Original field numbers designated by the KIS (Cretaceous Ingersoll shale) prefix are listed in the systematic paleontology section below following the UF numbers.

3.3. Nomenclatural considerations

From a strict nomenclatural standpoint, the name *Araucaria bladenensis* refers to the leafy shoots as originally named by Berry (1908). The case is made here that the same plant produced the shoots and cones, and the evidence for this conclusion is strong. However, the cones are not formally named separately or as *A. bladenensis* in the absence of unequivocal attachment or cuticular evidence. Berry's (1908) names for isolated cone scales, *A. jeffreyi* and *A. clarkia*, are also not applied to the fossils here, as the original descriptions are not detailed or provided with clear diagnoses, and the preservation of the Ingersoll shale specimens precludes detailed comparisons.

4. Systematic paleontology

Order: Coniferales
Family: Araucariaceae
Genus: *Araucaria* de Jussieu, 1789

Leafy shoots

Araucaria bladenensis Berry, 1908
Fig. 1A–E

Material. UF19310-55065 (KIS 246), UF19310-55066 (KIS 244), and UF19310-55067 (KIS 223).

Description and comparison. Leafy branches of *A. bladenensis* from the Ingersoll shale are represented by articulated segments up to 20.0 cm long (Fig. 1A–C). Leaves are helically arranged with lengths of up to 3.0 cm and widths between 0.8 and 2.0 cm (Knight, 2007). Most commonly, however, the leaves are around 2.0 cm long and less than 1.0 cm wide. Leaves are lanceolate to obovate, commonly apetiolate, with spiny apices (cuspidate). Most of the leaves are spread out and rather flattened along the branch, although much shorter imbricate leaves can be found below longer leaves on the same branch (Fig. 1B). These alternating regions probably represent growth increments like those of the extant species *A. bidwillii* (Eckenwalder, 2009). Veins are somewhat difficult to discern because the leaves were coriaceous and many are now covered by thick organic material (Fig. 1C); however, some impression specimens show evidence of closely