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Cuticular micromorphology of *Pagiophyllum bladenensis*, comb. nov., from the Late Cretaceous of the North Carolina Coastal Plain, U.S.A.¹

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ABSTRACT

MICKLE, J. E. (Department of Botany, North Carolina State University, Box 7612, Raleigh, NC 27695). Cuticular micromorphology of *Pagiophyllum bladenensis*, comb. nov., from the Late Cretaceous of the North Carolina Coastal Plain, U.S.A. Bull. Torrey Bot. Club 120: 387-391. 1993—Abundant leaf and branch compressions referable *Araucaria bladenensis* Berry have been recovered from Late Cretaceous gray mudstones of the Tar Heel Formation along the Tar River in Pitt County, NC. Leaves are up to 21.2 mm long by 9.9 mm wide, flat, sessile, coriaceous, and fusiform, and have entire margins, acute tips, and numerous parallel, unbranched veins. Leaves are borne helically and are imbricate. Cuticle was recovered using 20% CrO₃ and is incompletely preserved. Epidermal cells are irregular to rectangular in shape with thin, straight anticlinal walls. Sunken stomata are in discontinuous rows with the long axis of guard cells typically parallel to that of the leaf. Stomata are encycloctic with a surrounding ring of three to five encircling cells. External stomatal wax plugs are commonly present. Florin rings are present but not observed consistently. Other stomatic features are indistinct due to incomplete preservation. Leaf morphology is similar to that seen in Araucariaceae and in *Nageia* sect. *Nageia* de Laubenfels (Podocarpaceae). Among cuticular features, the presence of Florin rings is consistent with *Agathis* Salisbury (Araucariaceae) and Podocarpaceae, and encircling cells are common in Araucariaceae and other conifers. It is concluded that this material shows its greatest affinities with Araucariaceae but does not fit precisely within any known taxa. Consequently, *A. bladenensis* is transferred from the form-genus *Pagiophyllum* Heer as *P. bladenensis* comb. nov.

Key words: *Pagiophyllum bladenensis*, conifer, plant cuticle, foliar morphology, micromorphology, paleobotany, Cretaceous, North Carolina, Atlantic Coastal Plain.

Recently some attention has been paid to conifer remains from the Upper Cretaceous of the Atlantic Coastal Plain of North Carolina. Conifers described by Hueber and Watson (1988) and Raubeson and Gensel (1991) from these sediments include *Androvetia statenis* Hollick and Jeffrey, *Brachypodium squamosum* (Velen.) Palibin, *Brachypodium sp.*, *Geinitzia reichenbachii* (Geinitz) Hollick and Jeffrey, and *Moriccia cyclotoxon* Debay and Ettinghausen. The present report examines an additional conifer, *Araucaria bladenensis* Berry (1908), from these sediments.

Berry (1908) erected the name *A. bladenensis* for flat-leaved foliar conifer remains. As the name implies, he believed that this material represented a North American occurrence of *Araucaria* (Araucariaceae). *Araucaria bladenensis* was reported as occurring at several localities in North Carolina, South Carolina, and Alabama. Indeed, Stephenson (1912) used this species as an index fossil for the Black Creek (=Bladen) Formation of North Carolina. Cuticular features of *A. bladenensis* were poorly defined by Berry (1908). Recently, abundant free leaves and shoots similar to Berry’s material have been discovered at one locality in Pitt County, North Carolina. This material provides an opportunity to expand our knowledge of morphological and cuticular features of this conifer and to compare these features with those of extant and fossil forms. This report demonstrates that the material does not represent a species of *Araucaria* but has a mosaic of characteristics shared by conifers in Araucariaceae and Podocarpaceae.

Materials and Methods. Specimens were preserved as coalified compressions and recovered

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from gray, silty sediments exposed on the southern bank of the Tar River near the boat landing, approximately 150 m downstream from the State Route 222 bridge. The locality is approximately ten miles upstream from Greenville, North Carolina (Greenville Northwest 7.5' Quadrangle, Pitt County, North Carolina, 1982, SW ¼ SW ¼ NW ½). Pertinent specimens are housed in the Paleobotanical Collections, Department of Botany, North Carolina State University.

Some specimens were removed from the matrix using fine-tipped dissecting needles, placed in 10% HCl overnight followed by 56% HF for a few hours to remove adhering mineral matter, and finally stored in 70% ethanol. These specimens were left whole or treated in 20% Cr₂O₃ to release cuticle (Alvin and Boulter 1974). Some cuticle fragments were dehydrated into absolute ethanol, stained in 1% ethanolic safranin, transferred to xylene by graded series, and mounted on microscope slides using Piccolyte. Other leaf and cuticle fragments were prepared for scanning electron microscopy (SEM) by washing in several changes of distilled water, mounting on aluminum stubs using double-sided tape, and coating to a thickness of 30 nm with gold-palladium alloy. Specimens were coated using a Technics Hummer V sputter coater and viewed with a Philips 505T SEM.

Matrix and specimens tended to crumble upon drying in air, so specimens that were retained on the matrix were stabilized by coating with one or two layers of clear, acetone-based fingernail polish.

Sohl and Owens (1991) discussed the age and interpretation of Upper Cretaceous sediments in North Carolina. The Tar River deposits have been correlated by Stephenson (1912) with the Black Creek Formation of Sloan (1907). The Black Creek Formation extends from North Carolina into South Carolina and has been assigned by various authors to dates ranging from middle Cenomanian to mid-Campanian (Sohl and Owens 1991). Sohl and Owens (1991) divided the former Black Creek Formation into three formations which they collectively recognize as the Black Creek Group. The basalmost of these three formations is the Tar Heel Fm. The Tar River sediments are approximately in the middle of the Tar Heel Fm. (R. Schoch, pers. comm.); Sohl and Owens (1991) interpret the age of the Tar Heel Fm. to be Early Campanian.

**Description of Specimens.** *Leaf Morphology.* Leaves from the Tar River locality are 8.2–18.9 mm long and 2.8–9.6 mm wide (Figs. 1, 2). [Berry (1908) reported a length of 10–28 mm, mean 16 mm, and a width of 5–12 mm, mean 8 mm.] The leaf is obovate in outline with the widest point about ⅓ (Fig. 2) to ⅛ (Fig. 1) the distance from the apex. The base of the leaf appears decurrent and sessile, and the point of attachment is generally about one-half the width of the widest point of the leaf (Figs. 1, 2). The blade is coriaceous. The distal apex is acute to caudate with a stiff, pointed tip. A keel is lacking. Fine parallel striations occur in the leaf, indicating positions of veins. The veins do not branch, but end blindly without converging toward the leaf tip as they reach the leaf margin. Leaves are borne helically on branches, and are imbricate (Fig. 1). The abundance of these fossils implies that these specimens represent adult leaves.

**Cuticular Features.** Cuticle tended to break into small pieces (ca. 0.5 mm diam.) upon treatment of leaf remains with CrO₃ and in general cuticular features were poorly preserved.

External cuticle surface shows some undulations that do not appear to indicate the epidermal cell outlines (Figs. 3, 4), possibly reflecting preservation state. No papillae, trichomes, hair bases, or platelets (Stockey and Ko 1986) were observed. Stomatal plugs occur in about half of the stomata observed (Figs. 4, 5, 8) and are round to oval in outline (Figs. 5, 8). Plugs consist of short rods or granular material (Fig. 5). Plug material appears to be fused on the outer surface, giving a smooth appearance. Florin rings are

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present (Figs. 3–5, 8), but this feature is not observed consistently.

Leaf stomatal apparatus distribution is difficult to ascertain. Abaxial/adaxial orientation of cuticular fragments could not be reliably traced during preparation. Leaves appear to be amphistomatic based on the observation that all cuticle fragments and whole mounts examined showed stomata. Stomata are typically oriented parallel to the long axis of the leaf and form discontinuous rows (Fig. 3). Stomata are sunken to the level of the hypodermis. Concise interpretation of the stomatal apparatus is difficult due to incomplete preservation. Cuticle of what appears to be the outer subsidiary wall shows a fluted and warty appearance (Fig. 7). The presence or absence of polar cells could not be ascertained. Surrounding the stomatal apparatus is a ring of three to five, most commonly four, cells that appear to be identical to epidermal cells (Fig. 8) that may represent perigenous encircling cells. Stomata are thus considered to be encycloctic (Baranova 1992).

Overall stomatal apparatus average 61.9μm long × 38.5μm wide and guard cell pairs have a mean of 32.7μm long × 18.4μm wide. While generally poorly preserved, cuticle between the guard cells and subsidiary cells appears to have been thick, with the flange having a warty appearance (Fig. 7). The flange between guard cells was robust (Fig. 7). Guard cell extensions were not observed, but these structures are typically quite delicate (Stockey and Ko 1988, 1989) and their absence could be due to incomplete preservation.

Epidermal cells are irregular to rectangular in shape, with straight anticinal walls (Figs. 6, 8). Epidermal cells average 22.8 × 16.6μm with the long axis generally parallel to the long axis of the leaf; no significant difference in size or shape was observed in cells between and within stomatal bands. Internal cuticle surface is generally smooth to slightly pitted (Fig. 6). Intercellular flanges between epidermal cells are thin and shallow, and buttresses are not present (Fig. 6).

Discussion. Berry’s (1908) justification for naming this material as an Araucaria rested on the outward similarity of these foilar remains with leaves and branches of A. bidwillii Hooker. While the Tar River conifer shows superficial similarities to A. bidwillii, the characteristics of the Tar River conifer actually represent a mosaic of features present in members of two families, the Araucariaceae and Podocarpaceae.

Leaf morphology of the Tar River conifer corresponds to Type IV of de Laubenfels (1953). Among living forms, Type IV morphology is found only in the Araucariaceae and in the podocarpaceous Nageia sect. Nageia (de Laubenfels 1953, 1988). The Tar River conifer leaves are sessile with a broad base. Both Agathis (Araucariaceae) and Nageia leaves possess a petiole, while in Araucaria leaves are sessile with a broad base (de Laubenfels 1953, 1988). The Tar River conifer falls within the general size range of and is similar in overall shape to A. bidwillii (Araucaria sect. Bunya) as noted by Berry (1908), but there is, however, no evidence of twisting of the leaf as occurs in A. bidwillii.

Venation in Nageia sect. Nageia and in Araucariaceae consists of several small, parallel veins without a defined midrib. In Nageia sect. Nageia, veins converge toward the apex (de Laubenfels 1988). In contrast, veins in Araucariaceae (Agathis) do not converge toward the apex but remain parallel to the leaf margin (de Laubenfels 1988). Pagiophyllum bladenensis is similar to Araucariaceae in this feature.

Leaf arrangement in the Tar River conifer is helical; that of Nageia sect. Nageia is opposite to subopposite (de Laubenfels 1988), while members of Araucariaceae bear helically-arranged leaves.

Florin rings (Buchholz and Gray 1948) are present in the cuticle of Agathis and most Podocarpaceae, but are absent in Araucaria (Stockey and Ko 1986, 1988, 1989; Stockey and Taylor 1981). Encycloctic stomata are characteristic of many conifers, including Araucaria, which has two rings of encircling cells, and Agathis, which has one ring (Baranova 1992). Other cuticular features of the Tar River conifer are too incompletely preserved for further detailed comparison with other taxa.

In summary, leaf morphology and attachment (both lack of a petiole and arrangement on the stem) are most similar to Araucaria, while cuticular features compare most closely with Agathis and Nageia sect. Nageia. This suggests that the affinities are closest to Araucariaceae; however, Podocarpaceae cannot be ruled out, and the features are not wholly consistent with either Araucaria or Agathis.

The cuticular features seen in the Tar River conifer clearly indicate that its taxonomic placement in Araucaria cannot be fully justified and accordingly, must be changed. Among fossil and living conifer genera, the form genus Pagiophyl-
Phylum with eraceous, 222 external at tion, to external having ing in straight, anticlinal Epidermal tures.

COLLECTING LOCALITY. East bank of Tar River about 150 m downstream of the State Route 222 bridge, Pitt Co., North Carolina.

STRATIGRAPHIC POSITION. Tar Heel Formation, Campanian, Upper Cretaceous.

Literature Cited


