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RAPID COMMUNICATION

FIRST EARLY CRETACEOUS MAMMAL FROM THE EASTERN SEABOARD OF THE UNITED STATES

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Early Cretaceous terrestrial vertebrates are poorly known on a worldwide basis (e.g., Clemens et al., 1979; Weishampel, 1990). Of the few units in North America that have yielded them, only those in the West—the Cloverly Formation of Montana and Wyoming (Jenkins and Crompton, 1979; Jenkins and Schaff, 1988; Cifelli et al., 1998) and the Trinity Group of northern Texas and southern Oklahoma (Winkler et al., 1990; Cifelli et al., 1997)–have yielded substantial faunas including mammals and other microvertebrates. As a result, continent-wide comparisons, evaluation of biogeographic provinciality, and interpretation of other aspects of vertebrate history for this time interval are constrained by the paucity of available data. The Lower Cretaceous Arundel Clay of the Patuxent Formation, exposed in the mid-Atlantic region of the United States, has produced a modest vertebrate fauna, mainly dinosaurs of enigmatic affinities, based on isolated bones and teeth (e.g., Marsh, 1888; Lull, 1911; Gilmore, 1921; Ostrom, 1970). In this context, any morphologically informative specimen is noteworthy. Herein we report the discovery of a remarkably complete jaw of a new triconodontid mammal from the Arundel Clay of Maryland, and discuss the relationships of this taxon to other members of the family and its implications for biogeography and biostratigraphy. The Arundel Clay is considered to be a facies, representing oxbow swamp deposits, within the Potomac Group (Kranz, 1998); its age is discussed more fully below. The specimen is from the Cherokee-Sanford brick clay pit, Muirkirk, Prince Georges County, Maryland; this is the main site now yielding fossil vertebrates from the Arundel Clay (Kranz, 1996).

Abbreviations

Terminology—Molar cusp terminology follows established convention (Crompton and Jenkins, 1968; Jenkins and Crompton, 1979); **L**, maximum mesiodistal length; **W**, maximum labiolingual width.

Institutional—**BMNH**, The Natural History Museum, London; **SMP-SMU**, Shuler Museum of Paleontology, Southern Methodist University, Dallas, Texas; **USNM**, National Museum of Natural History, Smithsonian Institution, Washington, DC; **YPM**, Yale Peabody Museum, Yale University, New Haven, Connecticut.

SYSTEMATIC PALEONTOLOGY

Family TRICONODONTIDAE Marsh, 1887
ARUNDELCONODON, gen. nov.

Etymology—Arundel, in reference to the fossil-yielding unit; conodon (Greek, "cone-tooth") is a commonly-used suffix for genera of triconodontids and primitive mammals in general, in allusion to the pattern of cusps on molariforms.

Type and Only Known Species—*Arundelconodon hottoni*, sp. nov.

Known Distribution—Arundel Clay (Lower Cretaceous), Maryland.

Diagnosis—As for the type and only known species.

ARUNDELCONODON HOTTONI, sp. nov.
(Figs. 1, 2)

Etymology—For Nicholas J. Hotton, in recognition of his lifelong contributions to vertebrate paleontology.

Holotype and Only Specimen—USNM 497729, right mandibular ramus with two ultimate premolars (perhaps p3–4) and m1–3.

Locality and Horizon—USNM locality 41615, Cherokee-Sanford brick clay pit east of US route 1 and south of Contee Road, Muirkirk, Prince Georges County, Maryland; Arundel Clay Facies of the Potomac Group (Aptian, Lower Cretaceous).

Diagnosis—Differs from Jurassic and earliest Cretaceous members of the family (*Triconodon, Trioracodon, Priacodon*) in having higher crowned lower molars with primary cusps (a–c) that are posteriorly recumbent and asymmetrical, with slightly curved labial and more angulate lingual faces, in having a cusp d that does not overhang the posterior root, and in having an extensive interlocking system between molars, whereby mesial and distal faces have a groove and ridge, respectively, that extend from the crown along the length of the root. Differs, where known, from the most comparable Cretaceous taxa (*Astroconodon, Corviconodon, Jugulator*) in having a meckelian groove on the medial side of the mandible, a much smaller cusp d on lower molars, and a weaker, occasionally discontinuous lingual cingulid on molars.

Measurements (mm)—Penultimate p L = 3.42, W = 1.13; ultimate p L = 3.27, W = 1.30; m1 L = 2.89, W = 1.03; m2 L = 3.03, W= 1.19; m3 L = 3.43, W = 1.23.

Description—The dentary (Fig. 1A, B) preserves no alveoli save those for the teeth present; it is relatively more robust than that of *Priacodon* and deepens posteriorly to a greater extent than in *Astroconodon* (e.g., Slaughter, 1969:fig. 1Q). The dentary has a meckelian groove; as it extends anteriorly, it fades out below the middle of m2 and reappears below the anterior root of m1 and the posterior part of the last premolar. The meckelian groove is placed low on the dentary and parallels its ventral margin. The dentition (Figs. 1, 2) is well preserved, save for the loss of a few cusp apices, and is lightly worn by com-

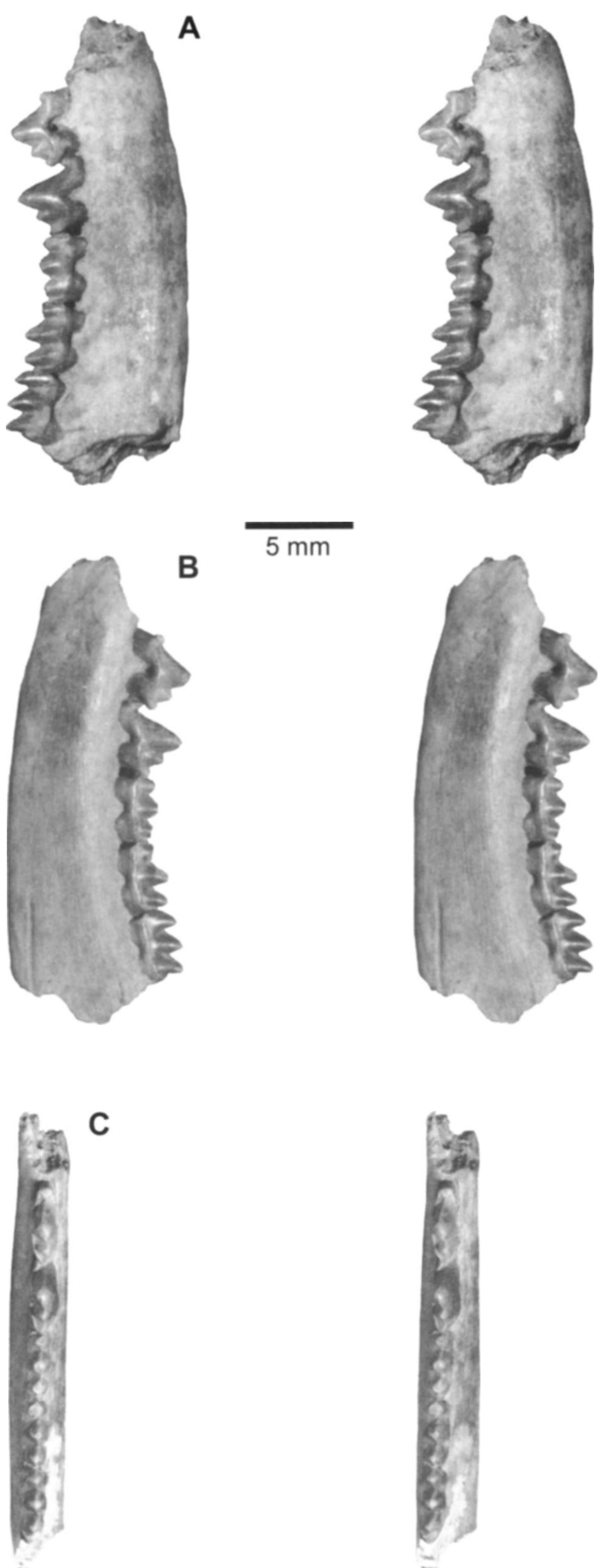

FIGURE 1. *Arundelconodon hottoni*, gen. et sp. nov., holotype, USNM 497729, right mandibular ramus with last two premolars and m1–3; stereopairs. **A**, labial view; **B**, lingual view; **C**, occlusal view.

parison to many specimens of Cretaceous triconodontids (see, e.g., Patterson, 1951; Cifelli et al., 1998). The complete dental formula is unknown. However, *Arundelconodon* is similar to an unnamed triconodontid from the Lower Cretaceous Cloverly Formation (Jenkins and Crompton, 1979) and to *Astroconodon* from the approximately equivalent Trinity Group (Slaughter, 1969); both have four premolars, suggesting that the preserved premolars in USNM 497729 may be p3–4. These are of interest in that well-preserved, associated premolars have not been described for any triconodontid from the Cretaceous of North America. Both premolars are large relative to the molars, and each bears four cusps. The penultimate premolar is lower-crowned, longer, and narrower than the ultimate premolar, with an anterior cuspule (cusp b) that is not placed nearly as low as on the last premolar. This pattern suggests that the isolated premolars used by Slaughter (1969:fig. 1Q) in his restored dentition of *Astroconodon* probably are reversed, with SMP-SMU 61989 representing p3 and SMP-SMU 61984 representing p4. Both premolars of USNM 497729 bear prominent lingual cingula; on the penultimate premolar a labial cingulum, discontinuous at the base of cusp b, also is present, whereas on the ultimate premolar there is only a trace of a labial cingulum, adjacent to cusp d. A sharp, mesiodistally aligned crest joins all cusp apices on each premolar. The ultimate premolar differs from the penultimate in its lower placement of cusp b, relatively steeper anterior face of cusp a, somewhat taller cusp c, and better developed, more mesiodistally expanded cusp d. The molars increase in length, width, and crown height from m1–3. Cusps a–c are subequal in height and are posteriorly recumbent; a sharp crest joins all cusp apices. Cusps a–c are asymmetrical in occlusal view, with labial faces being slightly rounded and inner cusp faces being more sharply angulate. The mesial face of cusp b forms a pronounced, inferomesially facing concavity. Cusp d, which is considerably smaller than the remaining cusps, fits within this cavity on the succeeding tooth, to the point that it is nearly obscured from view. A lingual cingulum is present on each molar, but it is weakly developed or variably absent at the base of cusp a.

All teeth bear two, well-divided roots; those for the premolars extend through the mandibular canal, terminating on its ventral margin, whereas the molar roots invade only the dorsal roof of the mandibular canal (Fig. 2A, B). The premolar roots are more robust than those of the molars, with the roots of the ultimate premolar being notably the largest in cross section (Fig. 2C–E). The mesial root of the penultimate premolar is labiolingually compressed, whereas the distal root is oval in cross section. The roots of the ultimate premolar are oblong in cross section, with the apex of the mesial root facing straight down and the apex of the distal root pointing distally. The mesial root of the molars bears a distinct, U-shaped groove mesially; this groove extends the length of the root. Likewise, the distal root bears a prominent distal keel that also extends the length of the root.

DISCUSSION

Triconodontidae are believed to be a monophyletic Jurassic–Cretaceous group characterized by generally primitive, serially cusped molars (e.g., Jenkins and Crompton, 1979; Cifelli et al., 1998). Taxa from the Cretaceous of North America include *Astroconodon,* from the Trinity Group of Texas and the Cedar Mountain Formation of Utah; *Corviconodon,* from the Cloverly Formation of Montana and the Cedar Mountain Formation of Utah; *Jugulator,* from the Cedar Mountain Formation of Utah; *Alticonodon,* from the Milk River Formation of Alberta; and two unnamed taxa from the Cloverly Formation (Patterson, 1951; Fox, 1969; Slaughter, 1969; Fox, 1976; Jenkins and Crompton, 1979; Cifelli and Madsen, 1998; Cifelli et al., 1998).

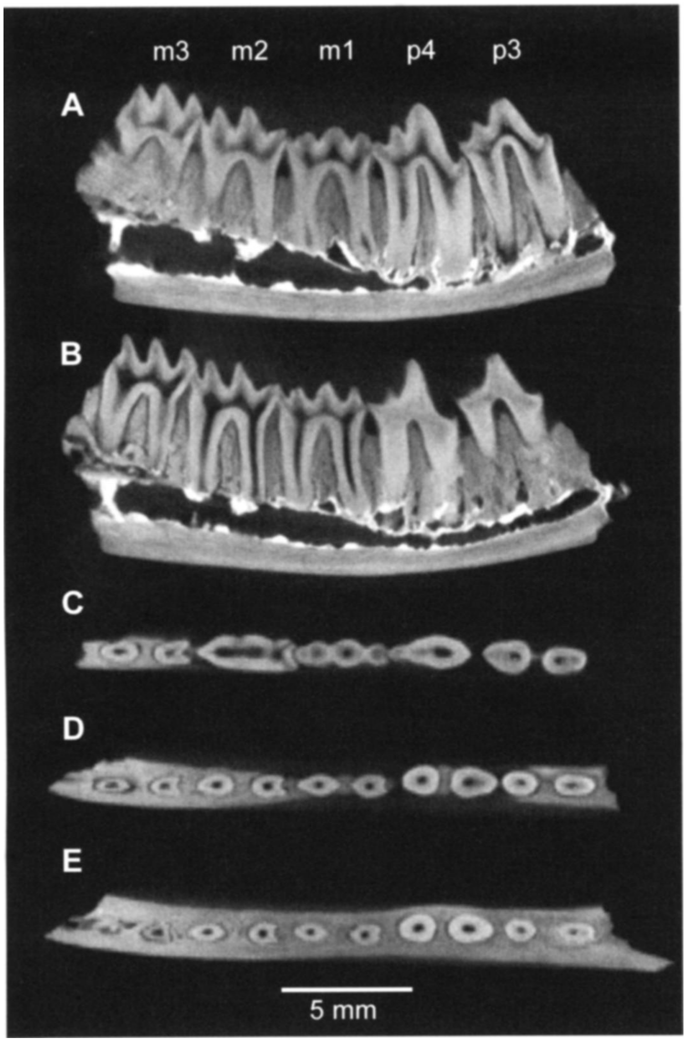

FIGURE 2. *Arundelconodon hottoni,* gen. et sp. nov., holotype, USNM 497729, right mandibular ramus; high-resolution x-ray CT images showing internal structures. Identity of two ultimate premolars is uncertain; they may be p3–4 (as labeled) if the dental formula was similar to that of comparable taxa from the Cretaceous of North America. **A**, **B**, parasagittal sections (section in B is labial to that of A); **C**–**E**, frontal sections. **C** represents a slice through the roots of p3, just above the dentary, through the crowns of p4–m2, and cutting through the dorsal part of the dentary at the roots of m3; **D** represents a slice immediately above the alveolar border adjacent to m1; **E** is a slice just dorsal to the mandibular canal adjacent to m3.

These appear to form a monophyletic cluster within the family (Cifelli et al., 1998); we made comparisons to these taxa, as well as to triconodontids from the Jurassic of North America and earliest Cretaceous of Europe (*Trioracodon, Priacodon, Triconodon*), and to the dentally more primitive amphilestids (for taxonomy see McKenna and Bell, 1997).

One noteworthy feature of the dentary in *Arundelconodon* is the presence of a meckelian groove, a primitive retention as judged by its widespread presence in early mammals and mammal-like reptiles (Luo, 1994). In Jurassic (Morrison Formation) and earliest Cretaceous (Purbeck Limestone) triconodontids (e.g., Simpson, 1928a, 1928b, 1929), the meckelian groove is generally placed low on the dentary and is parallel with its lower border, as it is in *Arundelconodon,* a condition judged by Luo (1994) to be primitive. The condition is variable in amphilestids: in *Amphilestes,* the groove converges with the ventral border of the ramus anteriorly, whereas in *Phascolotherium* it may be either subparallel to the ventral margin (see Osborn, 1888:pl. 8, fig. 3) or descends to that border, running anteriorly along the inferior margin of the dentary (Simpson, 1928a:76). The meckelian groove is lacking in all North American Cretaceous triconodontids in which the dentary is sufficiently well known (*Astroconodon, Corviconodon, Alticonodon*).

The premolars of *Arundelconodon* are generally similar to those described for Jurassic and earliest Cretaceous triconodontids, but appear to differ in proportions: the penultimate premolar is noticeably longer than the ultimate in the taxon from the Arundel Clay, whereas in other triconodontids for which the premolars have been described and illustrated, all dimensions increase sequentially through the premolar series (Simpson, 1928a, 1929). Indeed, in *Priacodon* and *Trioracodon* (the condition in *Triconodon* is unclear), the penultimate premolar is noticeably smaller than the ultimate (Simpson, 1925:fig. 5, 1928a:pl. 5, fig. 6). Comparison to amphilestids suggests that the conditions in *Arundelconodon* on the one hand and *Priacodon–Trioracodon* on the other are both derived. The possibility that *Astroconodon* may be similar to *Arundelconodon* in this respect suggests that this character may be of systematic utility when its distribution is better understood.

Lower molars of *Arundelconodon* are similar to those of medial Cretaceous triconodontids of North America (*Astroconodon, Corviconodon, Jugulator*) but differ in having a much smaller d cusp—presumably a primitive condition. Cusp d is generally quite small in Jurassic–earliest Cretaceous triconodontids, although it varies among taxa and according to tooth position: the condition in *Arundelconodon* is approximated on m3 of *Priacodon ferox* (YPM 606) and *Trioracodon ferox* (BMNH 47775). Advanced features seen on lower molars of *Arundelconodon* and other taxa from the North American Cretaceous (*Astroconodon, Corviconodon, Jugulator*), but not Jurassic or earliest Cretaceous taxa (*Triconodon, Trioracodon, Priacodon*), are the posteriorly recumbent primary cusps (a–c) with asymmetrical labial and lingual faces, greater crown height, and extension of the tongue-and-groove system onto tooth roots (Cifelli and Madsen, 1998; Cifelli et al., 1998). These derived features show that *Arundelconodon* agrees with structure in the clade of triconodontids from the Cretaceous of North America. The condition of other characters (e.g., presence of a meckelian groove, small cusp d), however, suggest that *Arundelconodon* is more primitive than other taxa in this clade. Indeed, *Arundelconodon* is morphologically intermediate between Jurassic and Cretaceous taxa, and available evidence suggests that it represents the sister taxon to remaining triconodontids from the Cretaceous of North America.

Age relationships among the few Early Cretaceous vertebrate faunas known from North America are not well established. The main evidence for age of the Arundel Clay comes from palynomorphs, including the monosulcate angiosperms *Brenneripollis* and *Schrankiopollis,* which indicate it to be Aptian, probably middle Aptian, in age (Doyle, 1992). Although a number of fossil vertebrates is known from the Arundel Clay, most are represented by remains that are of dubious biostratigraphic value. Most compelling in our view are teeth possibly belonging to *Tenontosaurus* (Ornithopoda), *Deinonychus* (Maniraptora), and *Acrocanthosaurus* (Theropoda) (see Galton and Jensen, 1979; Lipka, 1998). Of these, the first two are known both from the Trinity Group (Oklahoma and Texas) and the Cloverly Formation, (Wyoming and Montana); the latter is otherwise known only from the Trinity Group (Ostrom, 1970; Langston, 1974; Winkler et al., 1997; Brinkman et al., 1998; Harris, 1998). The Trinity Group includes the terrigenous Twin Mountains and Paluxy formations, where the intervening Glen Rose Limestone is present, and the terrigenous Antlers Formation where it is not (Winkler et al., 1990). Combined evidence from interbedded marine invertebrates and from stable carbon isotopes indicates that the Twin Mountains Formation is Aptian and the Paluxy Formation early in Albian age; most of the fossil-bearing part of the Antlers Formation is thought to be of early Albian age (Jacobs et al., 1991; Jacobs and Winkler, in press). The bulk of the diverse vertebrate fauna of the Trinity Group is from the upper part of the sequence (Winkler et al., 1990) and is probably of Albian age. Hence, the fauna of the Arundel Clay is older than that of the Paluxy Formation and, probably, the Antlers Formation; it is thought to be roughly equivalent in age to that of the Twin Mountains Formation (Jacobs and Winkler, in press). *Acrocanthosaurus* and *Tenontosaurus* range through the terrestrial part of the Trinity Group, whereas *Deinonychus* is definitively recorded only from the Antlers Formation of Oklahoma, presumably in the Albian part of the sequence (Brinkman et al., 1998). The age of the Cloverly Formation is not well understood, except that it is older than the overlying Thermopolis Shale, which is of late Albian age (Jacobs and Winkler, in press). The vertebrate fauna of the Cloverly has long been noted to be similar to that of the Trinity Group (Ostrom, 1970), but detailed correlation with the Trinity Group is not yet possible (Jacobs et al., 1991; Brinkman et al., 1998). Both the Trinity Group and Cloverly Formation have produced *Astroconodon* or a closely similar form (Patterson, 1951; Slaughter, 1969; Jacobs et al., 1991; Cifelli et al., 1998), and the genus extends into the Albian–Cenomanian of Utah (Cifelli and Madsen, 1998). In Texas, *A. denisoni* ranges through the sequence, including the Aptian Twin Mountains Formation (Winkler et al., 1990). Given the equivocal nature of available data, the distinction of *Arundelconodon* from other triconodontids of the North America Early Cretaceous could be biogeographic, chronologic, or both.

Recent work on dinosaurs has suggested continuity of terrestrial faunas of North America, Europe, and the gondwanan continents of Africa and South America until nearly the end of the Early Cretaceous (e.g., Sereno et al., 1996). Mammals of the Purbeck and overlying Wealden of western Europe are considerably older than the Arundel Clay: the former is probably of earliest Cretaceous age (Kielan-Jaworowska and Ensom, 1994) and its triconodontids have long been noted to be similar to those of the Kimmeridgian Morrison Formation of the western US (Simpson, 1928a, 1929). The Wealden fauna is probably Valanginian to Hauterivian in age (Clemens et al., 1979) and has not yet yielded remains of triconodontids. Two mammals with triconodont cusp pattern have been described from the earliest Cretaceous (?Berriasian) of Morocco; *Dyskritodon amazighi* and *Ichthyoconodon jaworowskorum*. Neither is closely comparable to *Arundelconodon*; indeed, the familial assignment of both Moroccan taxa is highly uncertain (Sigogneau-Russell, 1995). Similarly, two triconodonts (in a descriptive, not taxonomic sense, see Cifelli et al., 1998) are known from the Campanian Los Alamitos fauna of Argentina (Bonaparte, 1986, 1992); they are placed in the endemic South American family Austrotriconodontidae and are dissimilar to *Arundelconodon*. Evidence from the mammalian assemblages of Argentina suggest a prolonged period of endemicity, perhaps extending to the Jurassic (Bonaparte, 1990). In sum, the new taxon from the Arundel Clay shows no evidence for a hypothesized faunal tie with Europe or the southern continents.

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