SECOND TRICONODONT DENTARY FROM THE EARLY CRETACEOUS OF MARYLAND

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Previous authors have noted the general scarcity of Early Cretaceous vertebrate fossils, and mammals in particular (e.g., Clemens et al., 1979). The Arundel Clay facies of the Patuxent Formation (Potomac Group), Maryland, is one of a small number of Early Cretaceous units that has produced a vertebrate assemblage, and is the only vertebrate-producing unit of this age in eastern North America (Kranz, 1996, 1998). Isolated bones and teeth of dinosaurs have been known from the Arundel for more than a century (e.g., Marsh, 1888; Lull, 1911; Gilmore, 1921; Lipka, 1996, 1998; Chinnery et al., 1998), but only very recently did the deposit yield mammalian remains, a dentary of a new triconodont, *Arundelconodon hottoni* (Cifelli et al., 1999). Here we report a second mammal specimen from the Arundel Clay. The morphology of the dentary and its alveoli indicate that it also represents a triconodont, and it is tentatively referred to *A. hottoni* for reasons discussed below.

Triconodonts are primitive mammals distinguished by their simple, laterally compressed molars with three mesiodistally aligned primary cusps. This general molar structure provided the basis for recognition of the Order Triconodonta (Simpson, 1928a). The serially tricuspate molar pattern, long known for Amphilestidae and Triconodontidae (previously placed in the same family; Simpson, 1945), later proved to be shared by other Mesozoic mammal groups, such as Morganucodontidae, Sinoconodontidae, Gobiconodontidae, and Austroconodontidae, which were accordingly accommodated into the Triconodonta (Patterson and Olson, 1961; Kermack et al., 1973; Jenkins and Crompton, 1979; Bonaparte, 1990). However, this cusp pattern is plesiomorphic, being shared by certain non-mammalian cynodonts (Sigogneau-Russell and Hahn, 1994). Sinoconodontidae and Morganucodontidae are now widely regarded to be among the most plesiomorphous mammals or near mammals (mammaliaforms) (Rowe, 1988; Crompton and Luo, 1993; McKenna and Bell, 1997). On the other hand, cranial and postcranial anatomy of some later triconodonts is rather advanced. *Gobiconodon, Jeholodens,* and an undescribed triconodontid, for example, have unexpectedly derived, therian-like features of the shoulder girdle (Jenkins and Crompton, 1979; Jenkins and Schaff, 1988; Ji et al., 1999). Recent analyses suggest that the expanded Triconodonta is based on plesiomorphy; and even with the exclusion of Sinoconodontidae and Morganucodontidae, monophyly of remaining triconodonts, ''amphilestids'' and Triconodontidae, remains uncertain (Kermack et al., 1973; Rowe, 1988, 1993; Rougier et al., 1996; Ji et al., 1999). Fortunately, the Triconodontidae, to which the new specimen is referred, appear to be well-supported by synapomorphy (Jenkins and Crompton, 1979; Cifelli et al., 1998). Triconodontidae, which range from Late (or perhaps ?Early–Middle) Jurassic through Late Cretaceous, are the most diverse triconodonts, with some eight described genera (Table 1).

SYSTEMATIC PALEONTOLOGY

TRICONODONTIDAE Marsh, 1887
cf. *ARUNDELCONODON HOTTONI* Cifelli, Lipka, Schaff, and Rowe, 1999

Referred Specimen—USNM 497730, right edentulous dentary with alveoli of canine and five postcanine teeth (Fig. 1).

Locality—USNM locality 41615 (same as holotype), Cherokee-Sanford brick clay pit east of US route 1 and south of Contee Road, Muirkirk, Prince Georges County, Maryland (39°04′14″ N, 76°52′08″ W). Arundel Clay facies of the Patuxent Formation (Potomac Group), Ap-

tian, probably late-early to middle Aptian (Doyle, 1992, and pers. comm. to TRL). Collected by Michael McCloskey.

Comments—The specimen is tentatively referred to *Arundelconodon hottoni,* the only triconodont known from these beds, on the basis of close correspondence in size as judged from alveoli, as well as certain other features detailed below.

Description—The new dentary is in two pieces that have a limited contact at the lower margin, above which a section that contained the posterior alveolus of one tooth and the anterior alveolus of the next is largely missing (only edges of these alveoli remain). Dimensions of the alveoli are consistent with the interpretation that only the section with these two alveoli is missing, but a less likely possibility is that a longer section of jaw is missing in this gap. Assuming, however, that the two pieces have been correctly rejoined (as suggested by the precise fit of the limited contact between the two pieces), the preserved alveoli represent five postcanines. There are four complete alveoli in the anterior section and three in the posterior section. In addition there is a large hollow at the mesial end for the canine root, which appears to be continuous posteriorly with the mandibular canal (through a ventromedial opening), as it is in the holotype. The postcanine alveoli also appear to run inferiorly into the canal, as in the holotype (Cifelli et al., 1999:fig. 2).

The anteriormost complete alveolus probably held the posterior root of p2; the distal edge of the mesial alveolus is seen at the front of the preserved section. The canine alveolus extends to below the posterior root of p2, apparently farther back than in the holotype, but comparable to its extent in *Corviconodon* (Cifelli et al., 1998:fig. 2C); this may be related to the immature age of the individual represented by USNM 497730. The next two postcanine alveoli, for presumptive p3, are a little wider than the posterior p2 alveolus (Table 2), but slightly narrower than the next alveolus (for the mesial root of p4). The interalveolar septum is strongly elevated above the dorsal surface of the dentary. As far as can be judged, p3 and p4 would have been about the same length and a little longer than p2. These proportions accord well with the holotype, in which p3 and p4 are similar in length, and p4 is a little wider mediolaterally. Small sections of the edges of the two largely missing alveoli (for the posterior root of p4 and anterior root of m1) suggest that those sockets were at least as large as adjacent alveoli. The three complete alveoli in the posterior piece held molar teeth, probably the first two molars (or, less likely, more posterior ones if more of the jaw is missing than appears to be the case). All three are transversely narrower than the premolar alveoli (Table 2, Fig. 1A). They can be positively identified as molar alveoli by their shape, which reflects the distinctive tongue-and-groove interlocking between adjacent molar crowns and roots characteristic of all North American Cretaceous triconodontids (Cifelli and Madsen, 1998). The anteriormost complete alveolus (for the posterior root of m1) is transversely constricted distally, indicating a ridgelike distal margin of the tooth crown and root. The mesial border of the next alveolus (for the anterior root of m2) is divided by a median vertical ridge, which implies the presence of a groove on the mesial border of the root and crown. The last preserved alveolus, for the posterior root of m2, is transversely more compressed than the others and is directed somewhat posteroventrad. Ordinarily this might suggest that this was the last tooth present in the jaw, but there are no other indications that this is the end of the toothrow, such as deepening of the dentary as in other triconodontids, or evidence of the ascending

TABLE 1. Diversity and distribution of Triconodontidae*.

Genus	Age	Distribution	Species	Reference(s)
Indet.	?Early-Middle Jurassic	Mexico	1	(Montellano et al., 1998)
Alticonodon	early Campanian	Alberta	1	(Fox, 1969, 1976)
Arundelconodon	middle Aptian	Maryland	1	(Cifelli et al., 1999)
Astroconodon	Aptian-Albian to Albian-Cenomanian	Texas, Oklahoma, Utah	2	(Slaughter, 1969; Cifelli and Madsen, 1998)
Corviconodon	Aptian-Albian to Albian-Cenomanian	Utah, Montana	2	(Cifelli and Madsen, 1998; Cifelli et al., 1998)
Jugulator	Albian-Cenomanian	Utah	1	(Cifelli and Madsen, 1998)
Priacodon	Kimmeridgian-Tithonian to Berriasian	Wyoming, Utah, Portugal	5	(Simpson, 1929; Rasmussen and Callison, 1981; Krusat, 1989)
Triconodon	Berriasian	England	1	(Simpson, 1928a)
Trioracodon	Kimmeridgian-Tithonian to Berriasian	Wyoming, England	4	(Simpson, 1928a, 1929)

*The Moroccan genera *Dyskritodon* and *Ichthyoconodon,* which were included in Triconodontidae by McKenna and Bell (1997), are of enigmatic affinities (Sigogneau-Russell, 1995).

ramus or pterygoid crest as in *Corviconodon*. Furthermore, in at least some triconodontids, molars seem to be added at the back of the series (as in primitive forms like *Sinoconodon*), erupting from a crypt on the medial surface of the coronoid process, as in *Corviconodon* (Cifelli et al., 1998). These considerations suggest that there may have been more than two functioning molars in the individual represented by this specimen.

The dentary is shallower than the holotype (3.3–3.5 mm deep, compared to 4.4–5.6 mm deep in the holotype; Table 2, Fig. 2) and has a distinctive striated surface texture often seen in juvenile mammals, including other triconodontids (Jenkins and Cifelli, unpubl. data). USNM 497730 is also somewhat narrower mediolaterally than the holotype, but resembles it in being thicker mesially than distally (Table 2; the holotype is about 2.6 mm wide mesially and 2.4 mm wide distally), corresponding to the somewhat more robust premolars than molars. It is distinctly more robust than in *Corviconodon*. A mental foramen is present beneath the posterior alveolus of p2, as in *Astroconodon denisoni* (see Slaughter, 1969); this is slightly mesial of the position of the posterior mental foramen in *Corviconodon*. As in the holotype of *Arundelconodon hottoni,* there is a distinct Meckelian groove (called the internal mandibular groove or mylohyoid groove in older literature; Simpson, 1928b), which housed Meckel's cartilage and which is sometimes associated with some of the postdentary elements in early mammals (Kermack et al., 1973; Lillegraven and Krusat, 1991; Cifelli and Madsen, 1999). The groove is situated on the posteromedial aspect, running forward from the back of the preserved portion to the break (i.e., at least to a point below the anterior root of m1) and ambiguously continuing to the anterior root of p4. In either case, it is more distinct and extends farther forward than in the holotype, in which it fades below m2 and reappears weakly below the distal root of p4 and mesial root of m1. The clarity and anterior extent of the groove are probably related to the young ontogenetic age of USNM 497730. A Meckelian groove, in various forms, is present in many groups of early mammals (Luo, 1994), and appears to have been lost independently a number of times (Cifelli and Madsen, 1999). Among Triconodontidae, it is common among Jurassic taxa (Simpson, 1925a, b, 1928a, 1929), but it is lacking in *Corviconodon, Astroconodon,* and *Alticonodon* (Fox, 1969; Slaughter, 1969; Cifelli et al., 1998), the only other Cretaceous triconodontids whose dentaries are known. Hence, retention of the Meckelian groove in *Arundelconodon* represents a plesiomorphy with respect to other triconodontids from the Cretaceous of North America.

The new jaw is superimposed on the holotype in Figure 2 in order to illustrate their relative sizes. This comparison underscores its shallowness compared to the holotype, even though the estimated length of its p3–m2 (based on alveoli) is almost the same. The shallowness of the dentary in USNM 497730 is consistent with our interpretation that it represents an immature individual. The comparison also highlights the apparent close similarity in length of the posterior premolars in both specimens (note that crown length is typically longer than alveolar length for a given tooth). Whether m1 in the new jaw was shorter than the neighboring teeth, as in the holotype, would be difficult to confirm in the new jaw even if the alveoli were complete; however, the estimated lengths of the molars in the new jaw slightly exceed those of the holotype (Table 2). The difference is probably within normal intraspecific variation for triconodontids, judging from samples of *Triconodon mordax* (Simpson, 1928a) and a taxon similar to *Astroconodon denisoni* (Jenkins and Cifelli, unpubl. data).
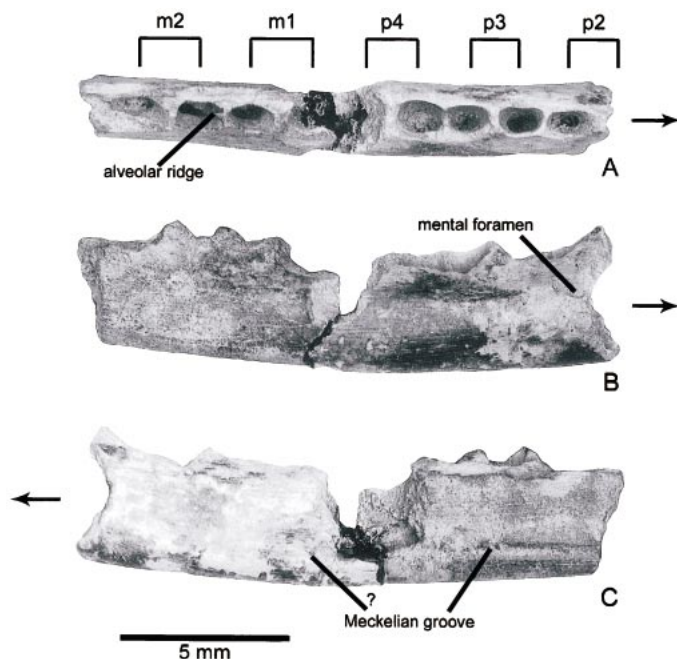

FIGURE 1. USNM 497730, cf. *Arundelconodon hottoni,* right dentary in superior (**A**), lateral (**B**), and medial (**C**) views. Arrows point anteriorly.

TABLE 2. Dimensions (to nearest 0.05 mm) of dentary and alveoli in USNM 497730.

Alveolus	Length	Width	Dentary depth (buccal)*	Dentary width
p2, distal	1.40	0.75	3.30	2.30
p3, mesial	1.35	0.80	3.30	2.20
p3, distal	1.35	0.85	—	2.25
p3, both	2.90	—	—	—
p4, mesial	1.40	1.00	~3.5	2.30
p4, both	~3.5	—	—	—
m1, distal	1.50	0.70	3.50	2.00
m1, both	~3.2	—	—	—
m2, mesial	1.40	0.75	3.50	2.00
m2, distal	~1.75	0.65	—	1.95
m2, both	~3.4	—	—	—

*Dentary depth was measured below alveoli; depths of 3.8–4.2 were measured at projecting points between alveoli.
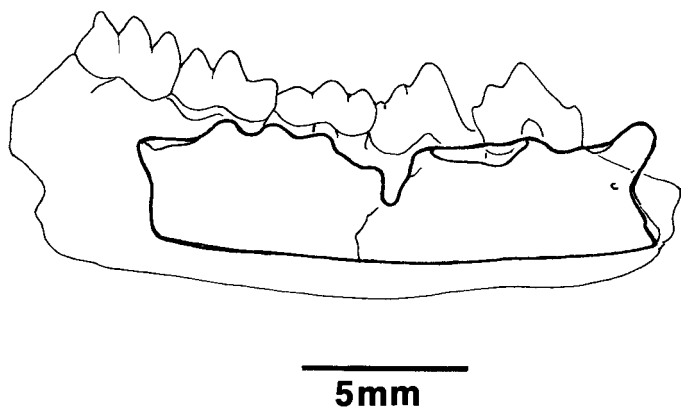
5mm

FIGURE 2.   Outline drawings of USNM 497730 superimposed on holotype of *Arundelconodon hottoni* (USNM 497729), drawn at the same scale.

TOOTH REPLACEMENT

Diphyodonty of the antemolar dentition, which may be related to determinate growth and precise occlusion (Crompton and Jenkins, 1973), is assumed to represent the ancestral pattern for Mammalia (Luckett, 1993; Martin, 1997). Unfortunately, the pattern and timing of tooth replacement is very poorly known for most groups of Mesozoic mammals (Cifelli, 1999). Because the new jaw referred to cf. *Arundelconodon* belonged to a juvenile or at least subadult individual, it provides additional insight concerning tooth replacement in triconodontids, about which there is virtually no information. The presence of deep alveoli extending inferiorly to the mandibular canal, together with the absence of radiographic evidence of any replacement teeth or germs within the dentary (Fig. 3), indicates that replacement was not underway at any of the preserved loci. Assuming the loci represented by the alveoli have been correctly identified, this leaves only two alternatives: (1) The permanent premolars were already erupted and functional; or (2) The deciduous premolars were still functional and permanent germs had not yet formed.

The second possibility seems most unlikely, given the state of the molars—erupted and functional at least as far back as m2. Furthermore, the ultimate deciduous premolars of Triconodontidae, at least, were elongate and narrow (Simpson, 1928a; Turnbull and Cifelli, 1999), as

are those of other mammals (Cifelli, 1999). The evidence from the antemolar alveoli of USNM 497730, suggests that they housed replacement premolars similar to those of other Triconodontidae. Therefore, it is probable that the premolars had already been replaced, despite the obvious immature state, as indicated by bone texture and jaw proportions (shallow depth and narrow breadth). A similar condition occurs in a taxon closely related to *Astroconodon denisoni* (Jenkins and Cifelli, unpubl. data), where there is no evidence for replacement of either premolars or molars and the permanent premolars are already functional, even in ontogenetically young individuals (with only the first two molars erupted).

In *Triconodon mordax,* by contrast, the last premolar was apparently not replaced until after m3 had fully erupted, and at least one specimen with three functioning molars still retained dp4 (= dm4) (Simpson, 1928a). *Gobiconodon ostromi* is unusual in replacing its molariform teeth: the holotype shows presumptive m1 and m2 in successive stages of eruption, with an unerupted m3 below a functional molariform at that locus (Jenkins and Schaff, 1988). Simultaneously, the anterior premolars appear to be in the process of erupting. Replacement of molariforms is known in other gobiconodontids, including *Gobiconodon borrissiaki* (Kielan-Jaworowska and Dashzeveg, 1998) and *Hangjinia chowi* (Godefroit and Guo, 1999), as well as in the primitive mammals *Sinoconodon* (Crompton and Luo, 1993; Zhang et al., 1998) and *Megazostrodon* (Gow, 1986). Whether molariform replacement in some or all of these taxa represents retention of a primitive condition, or an atavistic modification, cannot be determined (Jenkins and Schaff, 1988). The replacement pattern of Amphilestidae is unknown, so the significance of molariform replacement in gobiconodontids remains similarly unknown at present.

The evidence at hand suggests that tooth replacement in cf. *Arundelconodon* was similar to that in at least one other North American Cretaceous triconodontid, to the extent that they can be compared, and that it differed from the situation in either *Triconodon* or *Gobiconodon*. It is unclear why the North American triconodontids replaced their premolars at such an ontogenetically early age, but we provisionally regard this to be a derived pattern. Interestingly, the reverse pattern occurred in the contemporary North American spalacotheriid symmetrodonts (specifically Spalacolestinae), in which replacement of premolars is either delayed until late in ontogeny or suppressed entirely (Cifelli, 1999).
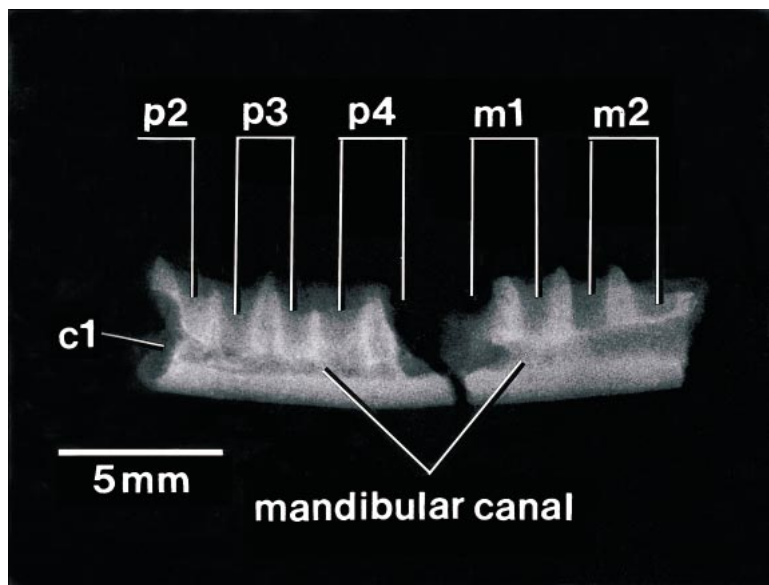
FIGURE 3.   Radiograph of USNM 497730 (medial view). Note that premolar alveoli descend into mandibular canal, with no evidence of replacing teeth or tooth germs.

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