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AN ENIGMATIC (SYNAPSID?) TOOTH FROM THE EARLY CRETACEOUS OF NEW SOUTH WALES, AUSTRALIA

WILLIAM A. CLEMENS[1], GREGORY P. WILSON[1], and RALPH E. MOLNAR[2]
[1]Museum of Paleontology and Department of Integrative Biology, University of California Berkeley, California 94720-4785,
bclemens@uclink4.berkeley.edu;
[2]Queensland Museum, P.O. Box 3300, South Brisbane QLD 4101, Australia, and Museum of Northern Arizona,
Flagstaff, Arizona 86011

ABSTRACT—Largely fragmentary fossils from sites in New South Wales, Victoria, and Queensland, Australia document terrestrial and marine vertebrate faunas of Aptian–Albian age. The natural cast of a large tooth from the Griman Creek Formation, Lightning Ridge, New South Wales, records the presence of a hitherto unknown member of the fauna. Although reference to one of the groups of crocodyliforms that evolved complex, mammal-like postcanine teeth cannot be excluded, the fossil more likely represents a species of synapsid. In some respects it is similar to lower postcanines of traversodontids. Greater morphological similarities to upper molars of dryolestids make reference of this tooth to this group more likely. Current Mesozoic Laurasian and Gondwanan fossil records include mammals with cheek teeth of similar large size.

INTRODUCTION

Early Cretaceous terrestrial faunas from Australia are known primarily from fragmentary specimens of Albian age. Discoveries at Lightning Ridge and several other localities in New South Wales, Australia, document the presence of dipnoans, teleosts, chelonians, crocodyliforms, ornithopods, saurischians, birds, and monotremes (Dettmann et al., 1992; Willis, 1993; Flannery et al., 1995). Approximately contemporaneous (Aptian–Albian) sites along the southern coast of Victoria have produced remains of actinopterygians, lungfish, temnospondyls, turtles, plesiosaurs, crocodyliforms, pterosaurs, theropods, ornithopods, birds, and mammals (Rich et al., 1999; Rich and Vickers-Rich, 2000). Marine Cretaceous rocks in central Queensland have yielded pterosaur, ornithopod, ankylosaur, sauropod, bird, and mammal material (Molnar, 1991).

In 1991, Mrs. Elizabeth Smith showed one of the authors (REM) an opalized cast of a tooth. The specimen had been found that year by Mr. Edward Long in the Albian opal-bearing rocks of the Griman Creek Formation exposed in a mine at ‘‘Vertical Bill’s’’ claim in the Three-Mile Field, Lightning Ridge, New South Wales (Smith, 1999). Analysis of its characters indicates that it is the replica (natural cast) of a tooth of a vertebrate, hitherto unrecognized in Australian, Aptian–Albian terrestrial faunas. Nor does it appear to belong to any aquatic vertebrate, either fish (elasmobranchs, actinopterygians, or sarcopterygians) or marine reptile (ichthyosaurs or sauropterygians), known from Australia at this time. Comparisons described below suggest it is most likely the tooth of a synapsid. Its greatest similarities in derived characters are to upper molariform teeth of dryolestid mammals.

MATERIALS AND METHODS

Initially, its discoverer, Edward Long, kindly permitted casts to be made of the fossil and distributed for study (e.g., Queensland Museum, Brisbane, fossil collection, QM F33564). Elizabeth Smith (1999:23) published a photograph of the specimen (‘‘Vertical Bill’s Beastie’’). The original specimen was curated in the collections of the Australian Museum, Sydney (AMF 118621). Although the specimen apparently represents a new taxon, we refrain from assigning it a formal binomial because of the uncertainties surrounding its identification and our limited knowledge of the Australian Early Cretaceous fauna. Measurements made to the nearest 0.1 millimeter (mm) were obtained with dial calipers.

SYSTEMATIC PALEONTOLOGY

Preservation

AMF 118621 (Fig. 1) is a fully opalized cast of a tooth of a vertebrate. The surface texture of its crown varies from smooth to a lightly textured or pitted pattern resembling rugose areas of some kinds of teeth (Fig. 2). Small areas of its surface are abraded. Few of the opalized bones from the Griman Creek Formation show evidence of transport prior to final burial, however, they exhibit a clear bias towards small, equi-dimensional elements (such as centra and phalanges) that could be transported easily (unpublished analysis by REM). Also, the fossil might have suffered slight abrasion during collection for it was recovered after being separated from the clay matrix in a tumbling tank. Smith (1999:48) noted that surface detail of many of the larger bone specimens from Lightning Ridge is ‘‘. . . poorly preserved, pitted and corroded.’’ Some of the pitting in the surface of the tooth might be the result of transport prior to burial or reworking. Acid attack from ground water or passage through a carnivore’s gut also might have damaged some areas of the tooth. We conclude that the pitted areas on the crown probably reflect the general morphology but not the original surface pattern, and that only a few areas appear to have been modified by abrasion.

Description

The cast of the occlusal surface of the crown has a triangular outline (Fig. 1). On the basis of comparisons with dentitions of a variety of vertebrates, detailed below, we find the closest resemblance of this tooth are to upper molars of dryolestid mammals and use them to provide a basis for orientation of AMF 118621. Following this working hypothesis, the two large cusps define the transverse axis of the crown with the largest cusp buccal. From the lingual side of the large buccal cusp a low ridge extends to the base of the smaller lingual cusp. If reference to the dryolestids proves correct, the buccal cusp would be the stylocone and the lingual cusp the paracone. A weak

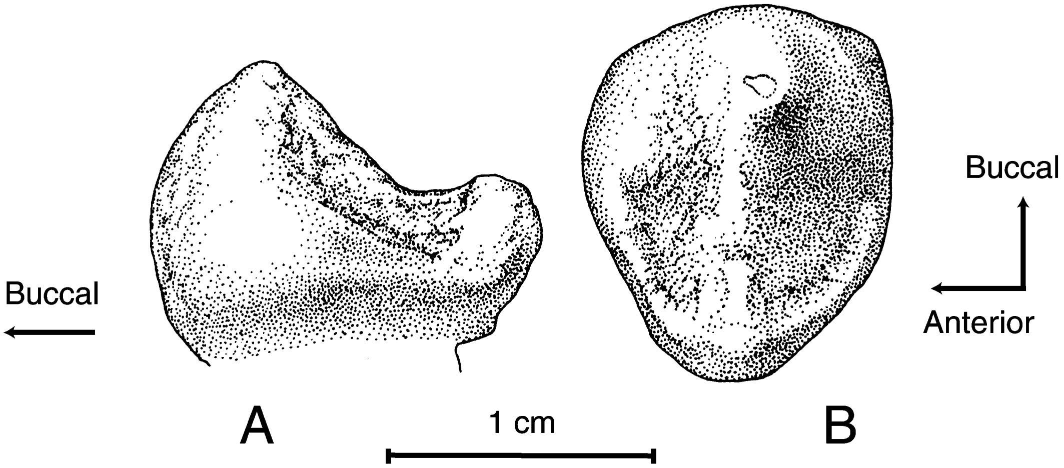

FIGURE 1. Natural cast of AMF 118621 from Lightning Ridge, New South Wales, Australia. **A**, anterior view; **B**, occlusal view. Illustrations based on a cast of the specimen.

crest extending from the paracone toward the presumed metastylar region bounds a posterior basin. A deeper basin is present anterior to the main transverse ridge and is bounded anteriorly by a low crest. Clear evidence of a parastylar cusp is lacking, but the surface of the specimen in this area appears to have been slightly abraded.

When viewed laterally, the walls of the base of the crown are convex with, apparently, a distinct boundary between the crown and root(s). Below the crown there is a small, irregular pyramidal projection, which is interpreted as a postmortem artifact and not a trace of the root(s). The morphology of the rim of the base of the crown suggests that at the time of death either the root(s) had not been formed or had been resorbed.

In the orientation assumed here, AMF 118621 is 12.2 mm in maximum anteroposterior length, and 14.0 mm in maximum width.

Comparisons

Vertebrates Other than Synapsids—The specimen was compared with teeth of elasmobranchs, actinopterygians, sarcopterygians, temnospondyls, and reptiles, particularly those groups that have been documented in the Mesozoic faunas of Australia and other southern continents (by REM and GPW). Similarities were found only with the dentitions of ‘‘notosuchian’’ crocodyliforms. These taxa either possess simple, caniniform teeth or multicusped teeth that can be mistaken for those of synapsids (Wu and Sues, 1996; Gomani, 1997; Buckley and Brochu, 1999). In fact, one taxon based on teeth originally identified as mammaliaform was later shown to be a crocodyliform (Carvalho, 1994). In view of these morphological similarities, the possibility that AMF 118621 derives from a crocodyliform must be explored.

If the ridge connecting the main cusps of AMF 118621 was not oriented transversely but oriented anteroposteriorly, the specimen shows some similarities to molariform teeth of *Malawisuchus mwakasyungutiensis* from Malawi (Gomani, 1997) and *Candidodon itapecuruense* from Brazil (Carvalho, 1994), both of Early Cretaceous age. Specifically, the molariform teeth of these ‘‘notosuchians’’ have a single major central cusp, a very small posterior cusp, and a minor anterior cusp, aligned approximately anteroposteriorly. Although AMF 118621 has two obvious cusps, each situated at an end of the crown, a third

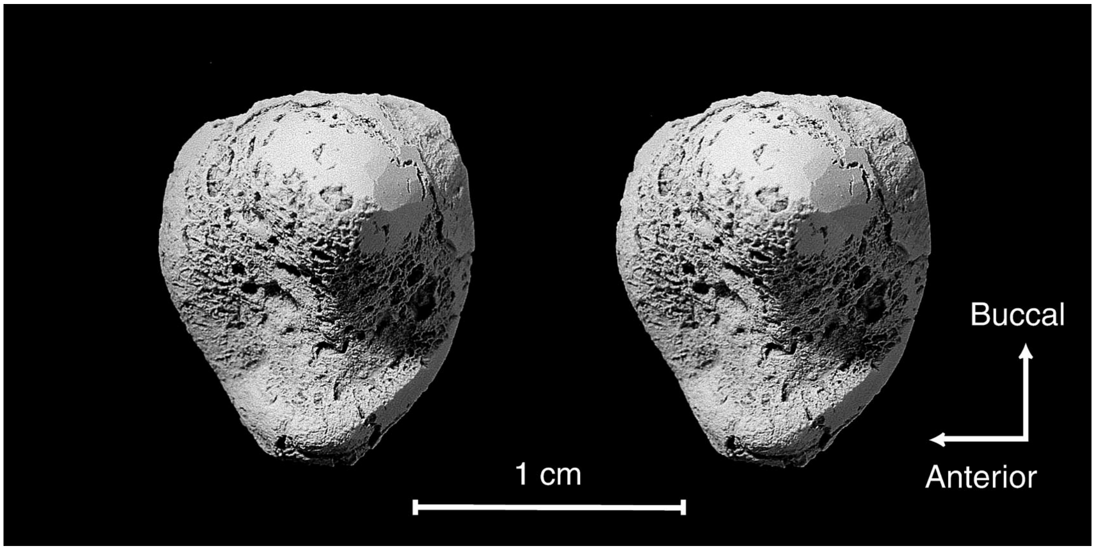

FIGURE 2. Stereophotograph of AMF 118621 in occlusal view from Lightning Ridge, Australia.

minor anterior cusp is not evident. Likewise, the low crests described above could be interpreted as marginal cingula as described for ‘‘notosuchian’’ teeth, but the low crests in AMF 118621 are not multicusped and do not extend anterior to the principal cusp, as they do in ‘‘notosuchian’’ teeth. Furthermore, its crown is far more inflated than the laterally compressed molariform teeth of these ‘‘notosuchians.’’ Finally, these crocodyliform teeth are substantially smaller—about half the size—than AMF 118621. Other molariform ‘‘notosuchian’’ teeth of more comparable size, such as those of *Chimaerasuchus paradoxus* from the Cretaceous of China (Wu and Sues, 1996), are ovoid rather than triangular in occlusal view and contain three, anteroposterior rows of cusps, unlike AMF 118621.

As far as we can determine, none of the known ‘‘notosuchians’’ has complex cheek teeth closely resembling AMF 118621. However, in view of the limitations of our knowledge of the species diversity of Gondwanan, Jurassic and Cretaceous terrestrial vertebrate faunas, the possibility that AMF 118621 represents a new kind of ‘‘notosuchian’’ cannot be dismissed.

Nonmammalian Synapsids—Members of this paraphyletic group are abundantly represented in Triassic faunas of most southern continents. However, with the exception of fragmentary records of dicynodonts (fragmentary bones and possibly trackways; Retallack, 1996) and forms tentatively identified as ‘‘probably cynodont’’ (Thulborn, 1990), nonmammalian synapsids have yet to be recorded in the few known Mesozoic faunas of Australia (Molnar, 1991). This absence is peculiar in light of paleogeographic reconstructions (Scotese, 1997) that suggest a high potential for intercontinental dispersal in Gondwana during the Triassic. It most likely reflects the current incompleteness of the known Australian Triassic fossil record.

AMF 118621 resembles the postcanines of some nonmammalian synapsids, particularly members of the Gomphodontia (Hopson and Kitching, 2001). Gomphodonts, including members of the Trirachodontidae, Diademodontidae, Traversodontidae, and Tritylodontidae, are characterized by laterally expanded postcanines with two (lower) or three (upper) cusps oriented in transverse rows.

Some postcanine teeth of trirachodontids have both a single transverse ridge formed by three cusps and a set of lesser anterior and posterior transverse rows formed by strings of small cuspules (Crompton, 1972). Although AMF 118621 is transversely expanded and includes a main transverse ridge and smaller crests, it has only two distinct cusps, both of which are larger and more inflated than those in trirachodontid postcanines. In addition, the transverse ridge extending between these two cusps is less pronounced than that in trirachodontids. Low anterior and posterior crests are present in AMF 118621 but show no evidence that they are formed by strings of cuspules. Finally, in occlusal view, trirachodontid cheek teeth have a rectangular to ovoid outline with a length/width ratio of approximately 1:2, whereas AMF 118621 tapers lingually to give it a triangular outline.

Although the cheek teeth of diademodontids have a subtle tranverse ridge connecting buccal and lingual principal cusps, unlike AMF 118621, they have a variable number of smaller cusps that form a ring around the perimeter of the tooth (Crompton, 1972). Furthermore, the occlusal outlines of their postcanine crowns are ovoid, not triangular.

The lower cheek teeth of some traversodontids (i.e., *Massetognathus* and *Scalenodon*) have a length/width ratio and an occlusal outline similar to AMF 118621 (Crompton, 1972). However, the arrangement of their cusps is quite different. The buccal margin of a traversodontid lower postcanine can have multiple sharp cusps forming an anteroposterior crest. The lingual margin has a sharp principal cusp situated anteriorly and one or more accessory cusps that do not form an anteroposterior crest. A pronounced transverse ridge stretches between the labial crest and the principal lingual cusp, posterior to which lies a concavity. In contrast, the bulbous inflated cusps of AMF 118621 show no evidence of anteroposterior crests or a large central concavity.

A recently described traversodontid from the Late Triassic of Belgium, *Habayia halbardieri*, resembles AMF 118621 in general morphology and the bulbous morphology of its cusps (Godefroit, 1999). A striking dissimilarity of this and some other European, Late Triassic traversodonts is their minute size; the transverse widths of the postcanines of *Habayia* are less than one millimeter.

Of the gomphodonts, the tritylodonts were the only clade known to have diversified during the Jurassic, particularly in eastern Asia and North America. Recently, Early Cretaceous occurrences of tritylodonts were discovered in Siberia (Tatarinov and Matchenko, 1999) and Japan (Matsuoka and Setaguchi, 2000). Although approximately contemporaneous and relatively large, the postcanines of these tritylodonts with their transverse rows of crescentic cusps are clearly distinguishable from AMF 118621.

Although exhibiting morphologic similarities to postcanine teeth of various gomphodonts, AMF 118621 cannot be referred to a currently recognized taxon. We cannot, however, eliminate the possibility that it represents an unknown gomphodont or other nonmammalian synapsid.

Australian Mesozoic Mammals—In the past two decades, five remarkable mammals have been described from the Early Cretaceous of Australia, *Steropodon*, *Kollikodon*, *Ausktribosphenos*, *Bishops*, and *Teinolophos*. Only elements of their lower dentitions are known. The lower molariform teeth of the monotreme *Steropodon galmani* are characterized by multiple transverse ridges. They range from 5.0 to 7.3 mm long and 2.8 to 4.3 mm wide (Archer et al., 1985). Similarly, *Kollikodon richiei* is known from an opalized fragment of a lower jaw containing one premolariform and two molariform teeth (Flannery et al., 1995). All the teeth are bunodont, and the cusps of the quadritubercular molariforms are inflated and tightly packed. The teeth range between 5.5 to 5.7 mm in length and 4.1 to 5.7 mm in width. Both the morphology of its crown and its larger size argue against reference of AMF 118621 to either *Steropodon* or *Kollikodon*.

Dental dimensions of the other currently recognized Australian, Early Cretaceous mammals are smaller than those of *Steropodon* and *Kollikodon*. *Ausktribosphenos nyktos* is known from lower jaws from Flat Rocks, Victoria, a local fauna approximately contemporaneous with the Lightning Ridge local fauna (Rich et al., 1999). The lengths of its tribosphenic-like molariform teeth range from 1.2 to 1.8 mm. A dentally similar form, *Bishops whitmorei*, has molariform teeth in the same size range (Rich et al., 2001). A third, small monotreme-like species, *Teinolophos trusleri*, is based on a fragmentary dentary containing one molariform tooth (ca. 1.2 mm in length) found at the Flat Rocks locality (Rich et al., 2001). Again, on the basis of differences in morphology of its crown and much larger size, AMF 118621 is not referable to these taxa.

Other Gondwanan Mammals—Comparisons of the compositions of Early Cretaceous Australian and Late Cretaceous South American mammalian faunas with contemporaneous faunas from the Laurasian continents highlight their distinctly different memberships. Stressing the limited number of available samples, several authors have noted that Cretaceous mammalian faunas of Australia and South America consisted of a variety of non-tribosphenic and pre-tribosphenic mammals (e.g., Bonaparte, 1996; Pascual, 1998).

One possible exception to this generalization is *Ausktribosphenos nyktos*. The authors of this taxon argue that it represents an unexpectedly early record of a eutherian lineage; one that might have special affinities to the erinaceomorph lipotyphlans

(Rich et al., 1997, 1999). This interpretation has been challenged by others who argue that *A. nyktos* represents a lineage characterized by independent evolution of a tribosphenic-like dentition (e.g., Luo et al., 2001). Whatever the outcome of this debate, it probably will add support to the interpretation of the markedly different patterns of mammalian evolution in the Laurasian and Gondwanan continents during the Cretaceous.

The South American record includes a second possible exception. All the mammals composing currently known Campanian faunas of South America represent non-tribosphenic lineages. Previously reported occurrences of Cretaceous marsupials and eutherians in Peru and Bolivia are now regarded as being Paleocene (Sempere et al., 1997, and references cited therein). Recently, Gayet et al. (2001) analyzed a new Bolivian local fauna of Maastrichtian age. The small sample of mammals (three isolated teeth) from this site apparently includes representatives of both non-tribosphenic and tribosphenic mammals.

Among South American Cretaceous lineages, several species referred to the Dryolestidae or other families within the Dryolestoidea (see Bonaparte, 1996) are of particular importance in attempts to determine the phylogenetic relationships of the AMF 118621. A majority of the species of dryolestids, recently reviewed by Martin (1999), is known from the Late Jurassic and Early Cretaceous of North America and Western Europe. Supporting the conclusions of earlier workers, Martin (1999) recognized the presence of three species of dryolestids—*Leonardus cuspidatus*, *Groebertherium stipanicici*, and *G. novasi*—in the Campanian Los Alamitos fauna of Argentina. *Leonardus cuspidatus* was assigned to a dryolestid clade with *Phascolestes*, *Guimarotodus*, and *Laolestes* (including *Melanodon*). Because of the paucity of material, *Groebertherium* was not included in his analysis. Of these genera, currently only partial upper dentitions of *Laolestes* and *Leonardus* and isolated upper molariforms of *Groebertherium* are known.

The hypothesis that AMF 118621 represents a dryolestid is supported by its morphological resemblance to upper molars of *Laolestes*, known from North America and Europe, and the South American genus, *Groebertherium*. Like AMF 118621, the crowns of the upper molars of *Laolestes* and *Groebertherium* are dominated by two cusps, the stylocone and paracone, which are linked by a transverse ridge. This ridge separates anterior and posterior basins. Upper molars of *Groebertherium* differ from those of *Laolestes* and AMF 118621 in their asymmetrically high lingual and low labial crown heights.

Size—''Common knowledge'' holds that Mesozoic mammals, suffering under the tyranny of the dinosaurs, were very small creatures. Although the morphology of AMF 118621 suggests it represents a new dryolestid, its large size (length 12.2 mm; width 14.0 mm) does not. A survey of Jurassic and Cretaceous mammals indicates that the ''common knowledge'' concerning their maximum size (mass) is open to revision.

Because the vast majority of Jurassic and Cretaceous mammals are only known from isolated teeth or fragmentary jaws, comparisons of their body masses can only be based on estimates derived from the sizes of individual molariform teeth. Correlations of size of molars and body mass have been analyzed in many groups of eutherian mammals (see Bloch et al., 1998, and references cited therein); we cannot assume, however, that the same correlations apply to non-eutherian mammals. To provide an admittedly arbitrary but precise definition, non-eutherian mammals will be described as large if either the length or width of the crowns of their cheek teeth exceeds 5.0 mm.

Dimensions of molars of several North American Cretaceous mammals exceed or almost reach this arbitrarily chosen 5.0 mm boundary. Jenkins and Schaff (1988) described partial skeletons of the triconodontan *Gobiconodon ostromi* from the Early Cretaceous of Montana. This species was almost twice the size of the approximately contemporaneous *Gobiconodon borissiaki* from Mongolia and, in size of its skeleton, rivaled the modern North American opossum, *Didelphis virginiana*. Lower molars of *G. ostromi* range from 4.20 mm to 4.90 mm in length and 2.05 mm to 2.75 mm in width, and the upper molars vary from 3.75 mm to 4.10 mm in length and 2.65 mm to 3.15 mm in width. Li et al. (2001) described *Repenomamus robustus* from the Yixian Formation (Early Cretaceous) Liaoning, China, which, on the basis of dimensions of their mandibles, was slightly larger than *Gobiconodon ostromi*. The dental dimensions of *R. robustus* were not reported. Although not quite large by our arbitrary standard, among Early Cretaceous mammals *R. robustus* currently holds the record as the largest mammal known from the Northern Hemisphere.

During the Late Cretaceous, North American mammals of both multituberculate and metatherian lineages evolved molariform teeth that are large by our criterion. Among the multituberculates, molars of *Meniscoessus robustus* reached lengths of 9.88 mm and widths of 6.95 mm (Clemens, 1963; Archibald, 1982). The species with the largest molars is *Bubodens magnus*, in which the m1—the only known molar—is 12.8 mm long and 6.0 mm wide (Wilson, 1987). *Cimolodon nitidus* and *Cimolomys gracilis*, although smaller, also had cheek teeth that exceeded 5.0 mm in length (Clemens, 1963; Archibald, 1982). The metatherian *Didelphodon vorax*, found in many of the same faunas as these multituberculates, had lower molars ranging from 4.1 mm to 7.9 mm in length and 2.9 mm to 5.6 mm in width; upper molars vary from 4.3 mm to 6.2 mm in length and 5.8 mm to 9.3 mm in width (Clemens, 1966). Some molars of the largest species of the marsupial *Pediomys*, *P. florencae*, also exceed 5.0 mm in length (Clemens, 1966).

Through the Jurassic and Cretaceous, the continents of the Southern Hemisphere evolved greater degrees of faunal provincialism as connections to Laurasia were attenuated and then sundered. The Late Cretaceous, Campanian, Los Alamitos Formation of Argentina has yielded specimens of a wide variety of non-tribosphenic mammals. The teeth of most of these fall within the size range of small Northern Hemisphere mammals (Bonaparte, 1996). *Mesungulatum houssayi*, thought to represent a highly modified dryolestoid lineage, is one exception (Bonaparte, 1990). A referred, isolated upper molar figured by Bonaparte (1990:fig. 15) has a length of ca. 4.3 mm, and a width of 5.8 mm (measurements taken from the figure). Rougier et al. (2000) report a large mesungulatid from the La Colonia local fauna of Argentina that had an estimated jaw length of 8.0 cm making it one of the largest Mesozoic mammals. *Gondwanatherium patagonicum*, also from the Los Alamitos Formation, represents a highly derived group of mammals of uncertain affinities. A hypsodont molar figured by Bonaparte (1990:fig. 18) has a crown length of ca. 6.3 mm and a width of 6.0 mm (measurements taken from figure).

Krause et al. (1994) described a fragment of part of a mammalian lower cheek tooth found in beds of latest Cretaceous (Maastrichtian) age in the Mahajunga Basin, Madagascar. The anteroposterior length of this specimen, which probably approximates the length of the whole tooth, is 7.55 mm.

Currently, no known Jurassic or Cretaceous mammals have cheek teeth as large as AMF 118621. However, during this interval mammals with relatively large detentions and, presumably, body masses evolved independently in both hemispheres. The differences in size of their cheek teeth and AMF 118621 are not great. Therefore, we conclude that its large size is not, in itself, a reason for rejecting an identification of AMF 118621 as a natural cast of a mammalian tooth.

CONCLUSIONS

We offer the following hypotheses for future testing. Analysis of the morphology of the natural cast from Lightning Ridge indicates that it is most probably a replica of an isolated, molariform tooth. Among known Mesozoic vertebrates other than synapsids, the closest morphological similarities of AMF 118621 are with cheek teeth of ''notosuchian'' crocodyliforms. Although reference to this group cannot be excluded, because of the roughly triangular outline of the occlusal surface of AMF 118621 (a configuration unknown in ''notosuchians''), it is ranked as unlikely. Among Mesozoic synapsids, AMF 118621 resembles the teeth of gomphodont nonmammalian synapsids in a number of derived characters. The crowns of their cheek teeth tend to be transversely widened and multicusped. AMF 118621 is comparable in size to the cheek teeth of many gomphodonts, but its triangular occlusal outline, a morphological pattern more frequently encountered among mammals, argues against reference to this group. AMF 118621 exhibits a number of derived characters that are typical, but not diagnostic, of the teeth of mammals in general and of dryolestoid cladotherians in particular. Cheek teeth of some Gondwanan and Laurasian mammals were of similarly large size. Provisional allocation to the dryolestids receives additional support from the documented Late Cretaceous diversity of this group in South America. Finally, we must offer the hypothesis that none of the three hypotheses of phylogenetic affinity is correct. Given the evidence of increasing biogeographic isolation of Australia during the Cretaceous there is a distinct possibility that the intriguing new fossil represents an otherwise unknown, endemic group of vertebrates. Whatever the outcome, AMF 118621 demonstrates that the diversity of vertebrates in the Lightning Ridge fauna has yet to be fully documented.

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