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The First Tertiary Monotreme from Australia

MICHAEL O. WOODBURN¹ AND RICHARD H. TEDFORD²

ABSTRACT

Remains of a new genus and species of fossil, ornithorhynchid monotreme are described. The specimens were recovered from Miocene deposits in South Australia and are part of the Ngapakaldi and equivalent aged faunas in this region. The

fossil genus represents the oldest record of the group in Australia and begins to fill a large gap in our understanding of the evolution of the Monotremata.

INTRODUCTION

In this article we report a new genus and species of mammal that represents the first Tertiary record of the Monotremata in Australia. *Ektopodon serratus* (Stirton, Tedford, and Woodburne, 1967) was tentatively accorded that position, but has been shown to be a phalangeroïd marsupial (Woodburne and Clemens, in preparation). The specimens described in the present work were recovered from two localities in South Australia about 200 miles apart (fig. 1). The first discovery of this new species was made by the joint American Museum-Queensland Museum field party in 1971, working at Lake Namba in the northern Frome Embayment. The second specimen, the holotype, was recovered in 1972 at Lake Palankarinna, east of Lake Eyre, by the joint University of California, Riverside-South Australian Museum field party. The two specimens appear to represent different, perhaps

serially adjacent, upper teeth. From geological and biostratigraphical considerations, the specimens appear to have been approximately contemporaneous, and are part of the Ngapakaldi and equivalent aged faunas in interior Australia.

ACKNOWLEDGMENTS

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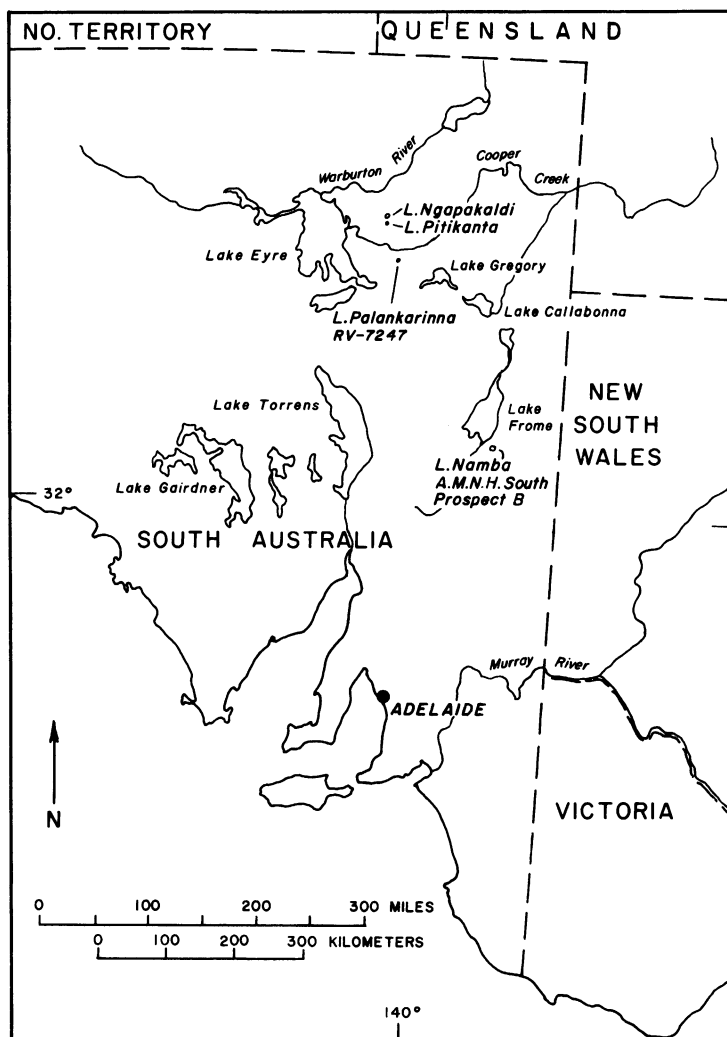


FIG. 1. Portion of southern Australia showing localities mentioned in text.

work in South Australia and provided facilities and personnel without whose help our expeditions could not have succeeded. In addition we gratefully acknowledge the help of the members of our field parties who worked so strenuously to bring these and other fossil specimens to light. Special appreciation is offered Mr. and Mrs. Bryan Oldfield, of Etadunna Station, and Mr. and Mrs. Buddy Napier, of Frome Downs Station who graciously permitted us to work on land under their jurisdiction and warmly gave of their hospitality. The illustrations used here were pre-

pared by Mr. Chester Tarka of the American Museum of Natural History and Mr. Karoly Fogassy of the Department of Earth Sciences, University of California, Riverside.

ABBREVIATIONS

AMNH, Department of Vertebrate Paleontology, the American Museum of Natural History, New York

SAM P, Paleontological collections, South Australian Museum, Adelaide

RV-, fossil vertebrate locality number, De-

partment of Earth Sciences, University of California, Riverside
 V-, fossil vertebrate locality number, Museum of Paleontology, University of California, Berkeley

DESCRIPTION AND COMPARISON

SUBCLASS PROTOTHERIA

ORDER MONOTREMATA

FAMILY ORNITHORHYNCHIDAE

OBDURODON, NEW GENUS

Etymology. From the Latin *obduros* + *don*, enduring tooth, in reference to the larger, more robust and probably longer lasting nature of these teeth, in contrast with those of *Ornithorhynchus*.

Diagnosis. Upper teeth larger, higher crowned, relatively shorter, and less complex than in *Ornithorhynchus* Blumenbach, 1800, with an anteriorly narrower and less labially emarginate transverse valley than in the Recent form.

Type. *Obdurodon insignis*, new species.

Obdurodon insignis, new species

Etymology. From the Latin *insignis*, distinguishing mark, in reference to the importance of the species' Tertiary record.

Holotype. SAM P18087; right upper molar slightly worn, complete.

Referred Specimen. AMNH 97228, right upper molar, worn and broken.

Specific Diagnosis. That of the genus until other species are described.

Distribution. For the holotype; University of California, Riverside Loc. RV-7247, SAM Quarry North, Etadunna Formation, west side of Lake Palankarinna, South Australia, grid zone 5, reference 656431, Kopperamanna topographic series SH 54-1, 1:250,000, 1965: in white to pale gray quartz sandstone at local base of member 6 of Stirton, Tedford, and Miller (1961) about 10 feet stratigraphically below the calcareous mudstone of member 8.

For AMNH 97228, South Prospect B, unnamed formation, grid zone 6, reference 320135, Cumamona topographic series SH 54-14, 1:250,000, 1965: A float specimen but

probably from thin-bedded black claystone with lenses of very fine sand overlying green claystone and white weathering dolomitic claystone exposed near the base of the low bluffs just south of the track to Billeroo waterhole, west side of Lake Namba, South Australia.

Age. SAM P18087 was collected from beds of the stratotype of the Etadunna Formation that contains elements of the Ngapakaldi fauna (Stirton, Tedford, and Woodburne, 1968). The sparse mammalian remains collected from RV-7247 include a *Ngapakaldia*-type diprotodontid, and a relatively primitive pseudocheirine phalangerid. The beds occur about 5 feet stratigraphically below mammal-bearing deposits at Tedford Quarry (RV-7230 = V-5375) and about 23 feet stratigraphically below Lungfish Locality, V-5766, situated about 385 feet north of V-5375.

The Etadunna Formation at Lake Ngapakaldi, about 35 miles north of Lake Palankarinna, contains the type locality of the Ngapakaldi Fauna (Stirton, Tedford, and Woodburne, 1968). The diprotodontid *Ngapakaldia* is abundant in the deposits at Lake Ngapakaldi, and also at Lake Pitikanta, about 4 miles to the south of it. Fossil dasyurid species recovered from Tedford Quarry, Lake Palankarinna, are comparable with those found in Etadunna deposits at Lake Pitikanta, and fossil macropodids from Lungfish Locality, Lake Palankarinna, are conspecific with those found at lakes Pitikanta and Ngapakaldi. On these bases, the remains from SAM Quarry North are referred to the Ngapakaldi Fauna.

The Ngapakaldi Fauna is the oldest such entity in the fivefold biochronologic succession in northern South Australia (Stirton, Tedford, and Woodburne, 1968), and is one of the oldest vertebrate faunas in interior Australia. Fossil pollen assemblages recovered from the Etadunna Formation in Lake Eyre (W. K. Harris, personal commun., 1974) suggest that those strata may correlate with marine deposits in coastal southern Australia of Batesfordian or Balcombian age. If this correlation can be extended to the vertebrate-bearing portion of the Etadunna Formation, these fossils may be that old. Foraminiferal and molluscan faunas indicate (Ludbrook, 1973) that the Batesfordian and Balcombian stages are approximately middle Miocene in age.

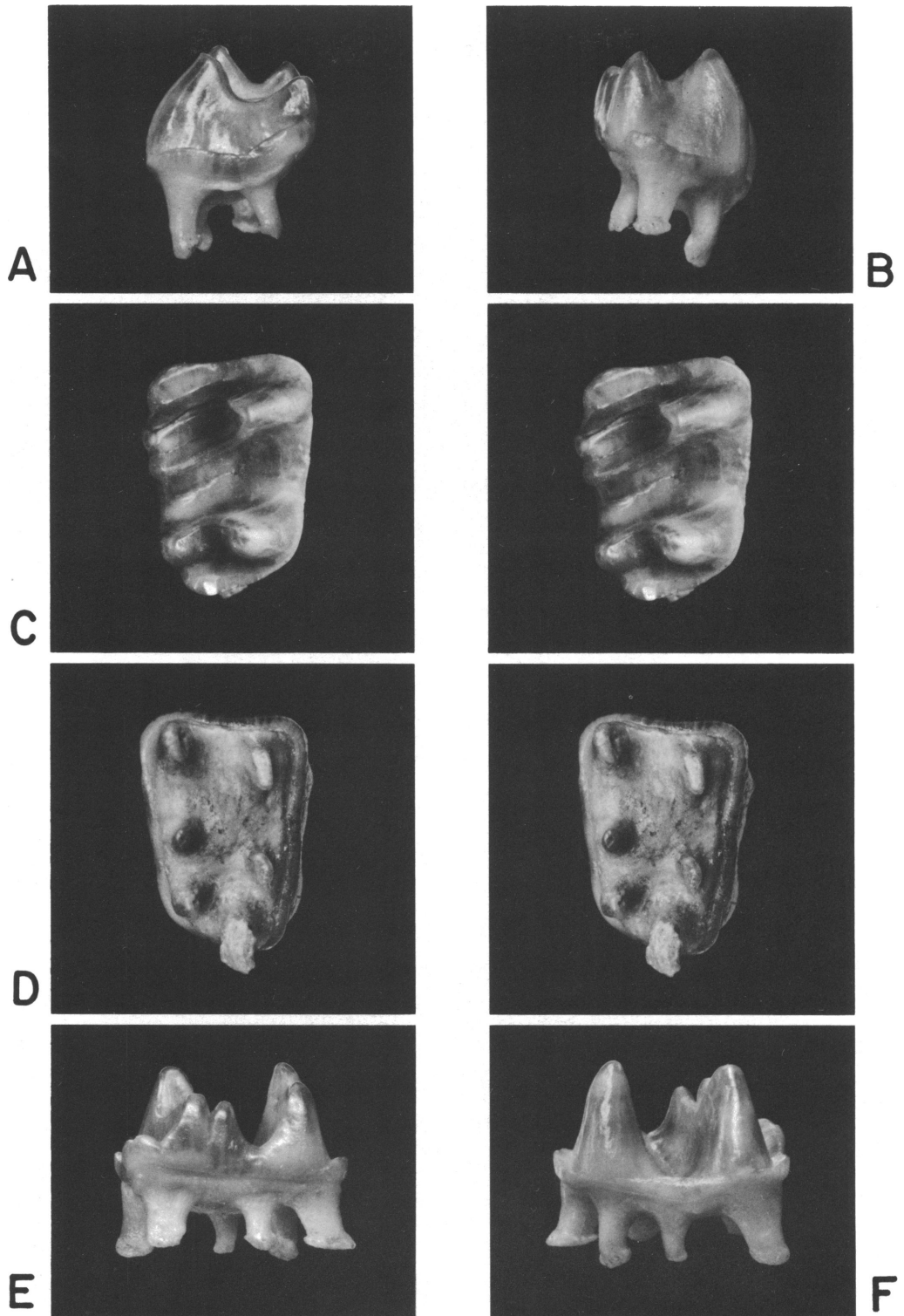


FIG. 2. *Obdurodon insignis*, holotype right posterior upper molar, SAM P18087. A. Anterior view. B. Posterior view. C. Stereopair of occlusal view, anterior side at top, lingual side at right. D. Stereopair of view of base of crown showing roots, anterior side at top, lingual side at left. E. Labial view, anterior side at left. F. Lingual view, anterior side at right. $\times 5$.

The Frome Embayment deposits that yielded AMNH 97228 share the following taxa with the Lake Palankarinna succession: the new monotreme reported herein, the relatively primitive pseudocheirine mentioned above, and a *Ngapakaldia*-like diprotodontid. In addition, a fossil pollen flora similar to that from the Etadunna Formation has been reported (W. K. Harris, personal commun., 1974) from well cuttings taken from strata correlated with those that produce the fossil vertebrates in the Frome Embayment. The vertebrates from South Prospect B and its stratigraphic equivalent at the nearby Ericmas Quarry, constitute the Ericmas Fauna, and based on the evidence summarized above, are considered approximately equivalent in age to the Ngapakaldi Fauna.

Description. As oriented in figure 2, the holotype has an elongate, subrectangular occlusal outline that narrows posteriorly. The crown is composed of two transversely oriented lophs separated by a longitudinally wide, deep, transverse valley. A broad anterior cingulum and a narrower posterior cingulum are present. Both cingula are broadest labially and diminish in width lingually. The tooth is slightly worn. Whereas the posterior cingulum is unworn and lightly dentate, the anterior cingulum shows slight wear in its labial quarter, and in subcircular abraded areas near its longitudinal axis and lingual quarter respectively. If the subcircular areas represent worn cusps, as seems probable, the anterior cingulum was also somewhat dentate in its original state. The apices of the two labial cusps of the anterior loph are worn, but the enamel is not breached. Dentine is exposed along the two transverse crests of that loph and at the apex of its lingual cusp. The posterior loph is either completely unworn or possibly very slightly worn.

In occlusal view, the anterior loph is directed anterolingually. It is composed of a single, high, lingual cusp and two lower labial cusps. Each of the latter is connected to the lingual cusp by a continuous crest. Each crest is lowest, relative to the base of the crown, in the labial third. The configuration of the crests, in anterior view, is broadly V-shaped. As defined by their respective

outer surfaces, the labial and lingual cusps slant labially from base to tip rather than being vertically aligned. The anterior of the two labial cusps is slightly taller, and has a greater areal diameter than the posterior cusp. The anterior and posterior surfaces of the anterior loph are steep and smooth; the anterior being steeper than the posterior.

The posterior loph is simpler than the anterior, is composed of a single labial and lingual cusp, and bears only a single transverse crest. The apices of these cusps are closer together than in the anterior loph, so that the profile of the transverse crest is a narrower "V" than its anterior counterparts. Both cusps of the posterior loph are higher than their anterior counterparts, and the labial cusp of the posterior loph is distinctly more massive than either of those anterior to it. A sulcus is present on the posterior surface of the posterior loph. The sulcus is most strongly expressed apically and blends into the posterior base of the loph. The posterior loph is directed more transversely than the anterior so that the transverse valley broadens lingually. The lingual half of the valley, as well as corresponding parts of the cingula, are lower relative to the base of the crown than their labial counterparts. The base of the crown thus rises apically in its labial half, but in spite of this, the labial cusps are still distinctly lower relative to the occlusal plane than the lingual ones. Whereas the lingual cusp slants labially, as in the anterior loph, the labial cusp is oriented nearly vertically. There is no labial cingulum, but a weak lingual cingulum is present at the base of the lingual cusps, and becomes better defined at the transverse valley.

One of the more unusual features of this specimen is the presence of six roots, three on each side of the coronal base. All but the posterolabial root are longitudinally elongate; the latter has a stout subquadrate cross section. There are no interradicular crests. On the lingual side, the anterior root is the best developed, the middle root the least. All have a slightly expanded distal tip. That of the anterior and posterior roots is also recurved labially. The middle root is straighter. The anterior and posterior roots support the lingual cusps; the middle

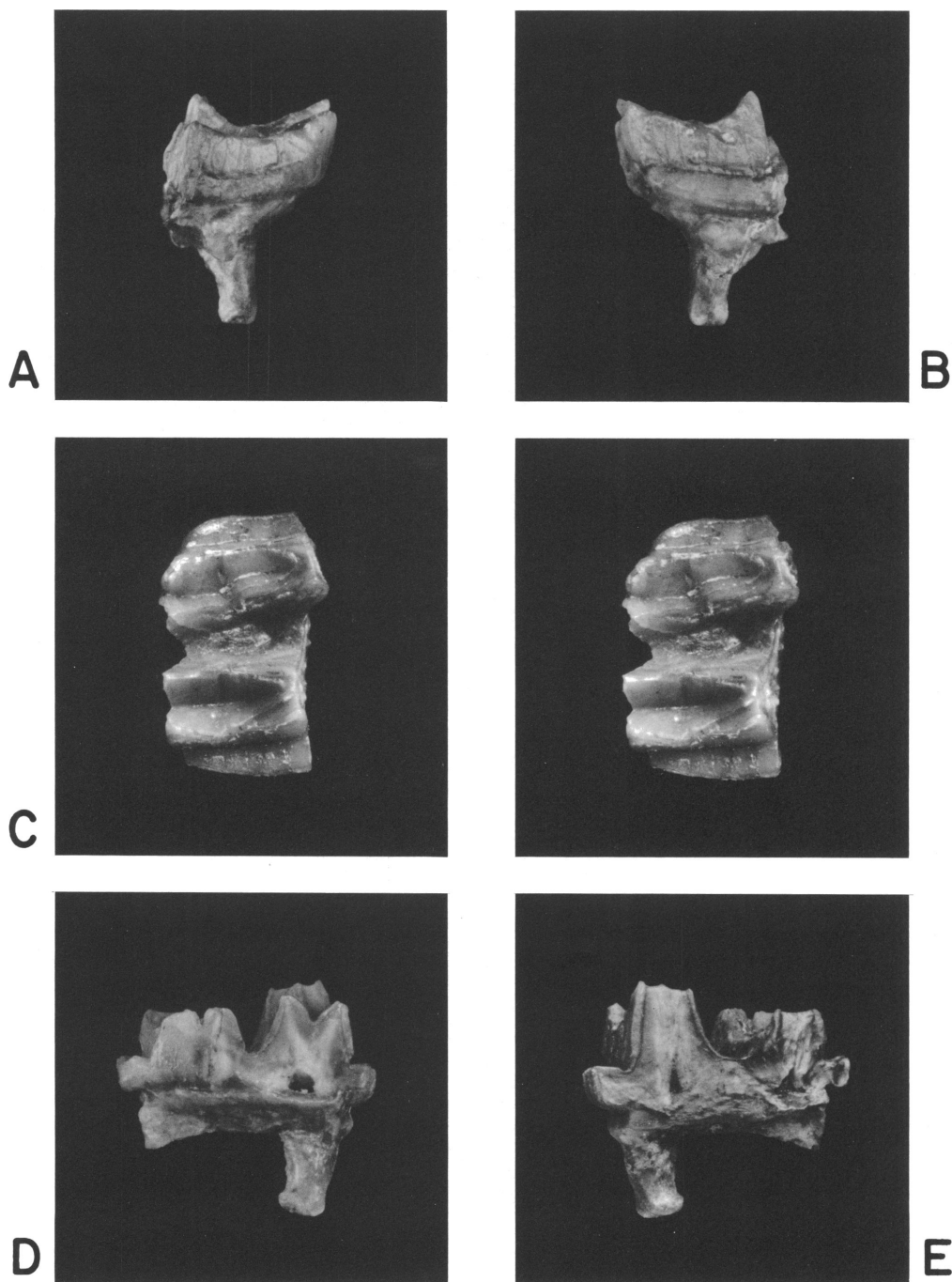


FIG. 3. *Obdurodon insignis*, referred right anterior upper molar, AMNH 97228. A. Anterior view. B. Posterior view. C. Stereopair of occlusal view, anterior side at top, lingual side at right. D. Labial view, anterior side at left. E. Lingual view, anterior side at right. $\times 5$.

root supports the lingual exit of the transverse valley.

On the labial side, the roots are not so closely associated with the major cusps. The roots arise well internal to the labial edge of the tooth, aligned beneath the labial third of the crown. The anterior root is aligned slightly anterior to the foremost labial cusp, the middle root occurs slightly posterior to the transverse valley, and the posterior root occurs well behind the vertical axis of the posterior labial cusp. The anterior two roots project distally and slightly labially; the posterior root is more vertically oriented in posterior view, but projects posteriorly in labial aspect. The distal tips of the two posterior roots are expanded. The tips of all six roots are irregularly roughened and punctate, as though they bore a syndesmotic articulation with the maxillary bone, possibly in addition to alveolar sockets resembling those of other mammals and thecodont reptiles. Another possibility, that the roots were in the process of being resorbed, appears unlikely, as the tooth is in a very early stage of wear. In addition, occlusal wear is well advanced in AMNH 97228 and the best preserved root, the posterolabial, is comparable in size and structure with SAM P18087. A syndesmotic tooth to bone articulation might represent a modified acrodont (reptilian) condition, but without knowing more about the phyletic history of *Obdurodon*, the situation described here could be a secondary development. Tomes (1923, p. 359) described a generally similar situation in *Ornithorhynchus*. In the living genus an unspecified number of roots pierce a dense, thick, cuplike layer of epithelium and fit into depressions in the underlying bone. When the teeth are shed, the epithelial layer coalesces to form the horny plates that serve as the animal's masticatory battery for the rest of its life.

AMNH 97228 is less well preserved and much more worn than the holotype. It appears to represent a more anterior tooth of the upper molar series and is of somewhat more regular construction. It also appears to have been larger and more robust than SAM P18087. Its morphology is basically that of the holotype with the following conspicuous exceptions: The anterior cingulum, as preserved, is slightly narrower than the posterior; the posterior loph is

bifid and thus similar to the anterior; the transverse valley is narrower longitudinally, and the posterior cingulum narrows labially rather than linguallly. These differences are interpreted as being due to AMNH 97228 representing a different tooth in the molar series, pending further evidence.

AMNH 97228 is broken linguallly and as much as the lingual third of the tooth may be missing including the presumed lingual roots. Enamel is also missing from part of the labial surface of the anterior loph and all of that surface on the posterior loph. As mentioned above, the tooth is also much more heavily worn than SAM P18087 and shows apical wear along the crests of both lophs. The enamel is breached along nearly the full length of the posterior crest of the anterior loph and the lingual halves of the other crests. As in the holotype, the anterior loph is oriented anterolingually, whereas the posterior loph is directed more transversely. Anterior and posterior cingula of the Namba specimen are heavier in anterior and posterior view than in the holotype. Also, the cusps and crests of the lophs appear to be more robust as compared with the holotype. The posterior crest of the anterior loph bulges slightly anteriorly in the labial third of the tooth, in contrast to the more smoothly arcuate, anteriorly concave configuration of its counterpart in SAM P18087. Although incompletely preserved, the labial cusps of the posterior loph appear to slant labially in contrast to the vertical orientation of the single labial cusp in the holotype. The narrower transverse valley has been mentioned above. As expected, the cingula are more heavily worn than in SAM P18087. An interdental wear facet is present on the anterior and posterior cingular surfaces. Breakage and wear reveals that a very uneven thickness of enamel covers the crown of this tooth. Marked thickening of the enamel occurs on the anterior and posterior surfaces of the transverse lophs and to a lesser extent over the anterior and posterior cingula.

Only two roots are preserved in AMNH 97228. These appear to be the anterior and posterior roots of the labial row and, as in the holotype, they occur well lingual to the labial surface of the tooth. Only the posterior of these is well preserved. It has the same robust, sub-

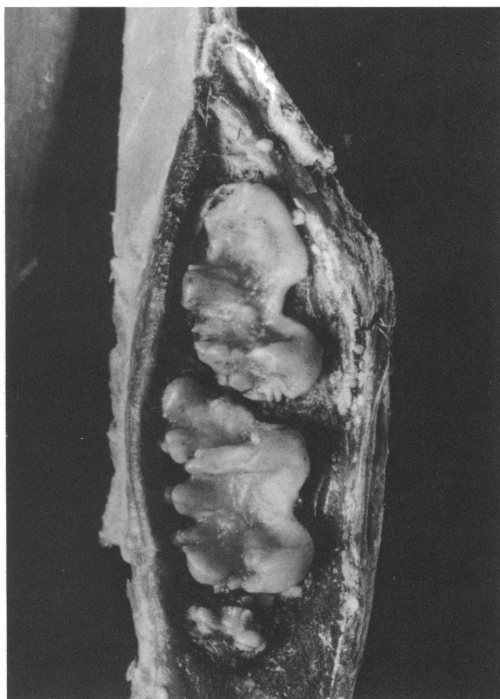
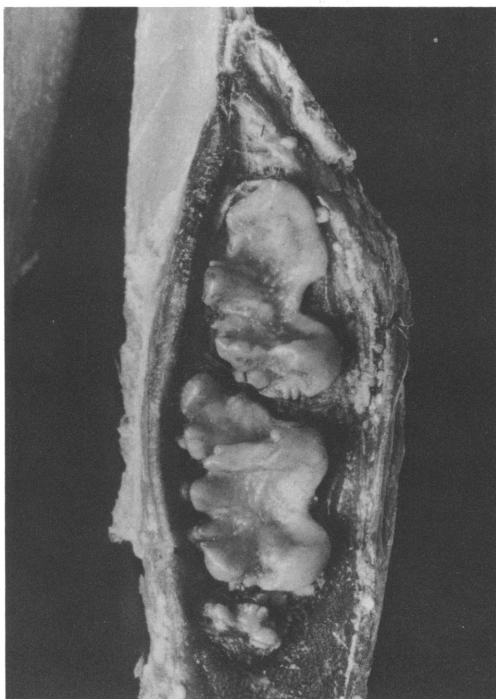
A**B**

FIG. 4. *Ornithorhynchus anatinus*, AMNH 1303. A. Stereopair of occlusal view of right upper molars. B. Stereopair of occlusal view of right lower molars. $\times 6$.

quadrate cross section and expanded, roughened tip as seen in the holotype. The root is much more massive in the Namba tooth, however, and although cracked, appears to be directed anteriorly in contrast to that of the holotype. There is no evidence that a middle labial root was present, in distinct contrast to SAM P18087. The lingual series of roots is not preserved and appears to have been lost along with the lingual third of the crown.

Comparison. Simpson (1929) and Green (1937) have described and illustrated the short-lived teeth of *Ornithorhynchus*. The following comments are based on these observations and direct comparison with a specimen of *Ornithorhynchus* (AMNH 1303, Simpson, 1929, fig. 1B, 1B¹). The basic morphology of the upper teeth of the platypus is sufficiently like that of *Obdurodon* to strongly suggest affinity between these genera. Green (*op. cit.*) indicated that the complete dental formula for the living genus is $\frac{0}{5}, \frac{1}{1}, \frac{2}{2}, \frac{3}{3}$ and that the fully erupted teeth are the last premolar and first two molars above, and three molars below. For the purpose of discussion the large upper teeth of *Ornithorhynchus* are designated as M¹ and M².

The following comments are given by way of comparison with those of *Obdurodon*. As is apparent in figure 4, and as discussed by Simpson (*op. cit.*) and Green (*op. cit.*), upper teeth of *Ornithorhynchus* are much smaller and more complex than in the fossil form. There is a greater proliferation of labial cusps and conules in the living genus and, where present, the anterior and posterior cingula are more dentate. Also, the teeth are relatively more elongate, and lower crowned, and the transverse valley is longitudinally wider in *Ornithorhynchus*. The paired transverse crests seen in *Obdurodon* are traceable but less sharply developed in *Ornithorhynchus*, and the teeth of the latter are strongly emarginated lingually at the transverse valley. Particularly for M¹ the lophs of *Ornithorhynchus* are more obliquely oriented than in either specimen of *Obdurodon*. Simpson (*op. cit.*) noted that although variable, most of the lophs of the teeth of *Ornithorhynchus* are crescentic, with a pair of crests extending labially from the lingual cusp.

TABLE 1
Measurements (in Millimeters) of Upper Teeth of
Obdurodon insignis, New Genus and Species

	SAM P18087	AMNH 97228
Length	7.15	7.35
Width, anterior loph	5.45	(4.70)
Width, posterior loph	4.45	(4.35)
Height, anterolingual cusp	4.00	—
Height, posterolingual cusp	4.25	—
Height, anterolabial cusp, anterior loph	2.55	—
Height, posterolabial cusp, anterior loph	2.50	—
Height, posterolabial cusp	3.25	—

() = measurement on broken specimen; actual dimension probably 30 percent greater.

Simpson indicated that the number and arrangement of the labial cusps are variable and present no definite pattern. Green (*op. cit.*) suggested that the basic pattern is for two labial cusps to be opposite each lingual cusp, at least for M¹. In AMNH 1303, M¹ shows two main labial cusps opposite each lingual cusp (fig. 4). However, the anterior loph has only a single transverse crest; a possible second crest posterobasal to the first, is less well developed and connects to a conule between the two large labial cusps. The posterior loph bears two well-developed transverse crests, each of which connects to a labial cusp. In contrast to *Obdurodon*, each of these transverse crests in AMNH 1303 becomes progressively dentate labially. There is no anterior cingulum on M¹. The posterior cingulum of M¹ is broadest labially in AMNH 1303 and smaller than the anterior cingulum of M². The morphology of M² is less well defined than for M¹ of AMNH 1303, but the relatively broad anterior loph bears several poorly defined transversely oriented structures that extend toward three or four labial cusps. The posterior loph is longitudinally broader than the anterior, appears to have a single main transverse crest, and is labially bounded by four major and three smaller cusps. The labially expanded anterior cingulum is better developed than the posterior.

The holotype of *Obdurodon* is tentatively considered to be homologous with the tooth here designated as M^2 in *Ornithorhynchus*. M^2 of *Ornithorhynchus* resembles SAM P18087 in having a labially expanded anterior cingulum, a less well-developed posterior cingulum, and the probable presence of only a single transverse crest in the posterior loph. The posterior cingulum of AMNH 97228 is not exactly comparable with that of M^1 in *Ornithorhynchus* but, as in the latter, this cingulum is less expanded labially than the anterior cingulum of M^2 . The well-developed, double-crested posterior loph and the possibility that the basic pattern for the anterior loph includes the presence of two labial cusps in *Ornithorhynchus* (Green, *op. cit.*) provide evidence for tentatively designating AMNH 97228 as a homologue. Wear facets are present on the anterior and posterior cingula of AMNH 97228, indicating the presence of an adjoining large and functional tooth. Green (*op. cit.*) designated this tooth as a premolar in *Ornithorhynchus* and indicated that it passes through a developmental stage in which it is three-cusped, and much larger than the tooth that is finally erupted. The presence of a large, functional, last premolar in *Obdurodon* is conceivable and reasonable. It is also possible, however, that the tooth homologies proposed above are in error, that, for instance AMNH 97228 actually is M^2 , with a well-developed molar anterior to it, and SAM P18087 is a more posterior molar. According to Green (*op. cit.*) this would be the third molar in the series. Depending on what evolutionary level is reflected in the ontogenetic history of dental anlagen in *Ornithorhynchus*, it is possible that the molar formula of Tertiary monotremes, such as *Obdurodon*, was different from that inferred for the platypus.

Green (*op. cit.*) summarized information on the multiple degenerate roots of the teeth of *Ornithorhynchus* and illustrated (fig. 14) the configuration of the basal opening of the enamel organs of the large lower molars. The pattern indicates the presence of a large, generally transversely oriented opening into the pulp cavity at the posterior end of each tooth. Anteriorly there is a more irregular array of smaller openings. Although it is difficult to interpret from these openings the size, length, shape, etc., of the roots

they represent, there is little doubt that each tooth was supported by more than four roots. In this sense, the teeth of *Ornithorhynchus* further resemble those of *Obdurodon*, especially as exemplified by the holotype.

DISCUSSION

Based on the overall similarities between the teeth of *Obdurodon* and *Ornithorhynchus*, there is little doubt that the two genera are related and that the fossil form represents the first Tertiary record of the Monotremata in Australia. There is sufficiently close and detailed morphological resemblance between *Obdurodon* and *Ornithorhynchus* to justify assignment of the fossil to the Ornithorhynchidae. However, inasmuch as the teeth of *Ornithorhynchus* are degenerate, it is not possible to state whether the obviously simpler construction of the teeth of *Obdurodon* represents an annectant pre-*Ornithorhynchus* stage of evolution, or whether the two genera were derived along collateral lineages.

Obdurodon and *Ornithorhynchus* appear to share a basically similar root morphology and method of tooth implantation, therefore it is conceivable that the larger teeth of the fossil form were shed during life as in the Recent genus. Tomes (1923, p. 360) indicated that, prior to being shed, the teeth of *Ornithorhynchus* are "worn as thin as paper," and those of *Obdurodon* likewise show occlusal wear. Nevertheless, *Obdurodon* does appear to have teeth of more regular, less degenerate construction and it is tempting to maintain that the fossil form is dentally more representative of Tertiary, or at least Neogene, monotremes than is the living genus. Assuming, for purposes of discussion, that this is the case, to what extent does the morphology of *Obdurodon* modify or support previous statements as to the origin of the Monotremata?

Based upon cranial and postcranial considerations as recently summarized by Kermack and Kielan-Jaworowska (1971), monotremes are best grouped with the nontherian mammals. If true, it is unlikely the monotremes would prove to have teeth whose cusps are homologues of those developed by therians. Simpson (1929) indicated that the teeth of *Ornithorhynchus* are

developed in such a way that the dental battery consists of a longitudinal row of cusps flanked by a series of accessory structures, labially for the uppers and lingually for the lowers. This arrangement is retained in the upper teeth of *Obdurodon*, except that the accessory structures are fewer and the transversely oriented connecting crests are stronger. Labial cusps are relatively, as well as actually, more robust in *Obdurodon* than in *Ornithorhynchus*. However, inasmuch as the labial roots in *Obdurodon* are situated well lingual to the apically reflected labial edge of the tooth, we interpret this area to represent the labial cingulum. The labial cusps are thus cingular cusps, albeit very well-developed ones, and occur opposite a pair of large, primary lingual cusps. Morphologically, although certainly not phylogenetically, the teeth of *Obdurodon* resemble the labial half of upper molars of the Peramelidae, wherein the paracone and metacone bear a pair of transverse crests that connect to labial styler cusps, and the anterior and posterior pairs are separated by a transverse cleft. *Obdurodon* is also reminiscent of various symmetrodonts in which the labial styler cusps, supported by roots, are joined by transverse crests to the paracone. However, all the known symmetrodonts lack the dilambdodont crest array shown by AMNH 97228. Docodonts show no particular resemblance to *Obdurodon*, even though their teeth are transversely crested. In docodonts (cf. Hopson and Crompton, 1969, fig. 6) the reduced styler area and great lingual expansion are fundamentally different from *Obdurodon*. Triconodonts show no close similarities to *Obdurodon*, although Mills (1971) presented evidence which he believed favored derivation of the monotremes from morganucodonts. However, the modifications necessary to transform the longitudinally shearing morganucodont triconodont dentition to the transverse shearing dilambdodont tooth of *Obdurodon* seem radical but perhaps not outside the realm of possibility. In the absence of much important information the possibility remains that the dental morphology of the fossil and living platypus could have been ultimately derived from a triconodont ancestor.

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