



Monotreme nature of the Australian Early Cretaceous mammal *Teinolophos*

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The morphology of the single preserved molar of the holotype of the Australian Early Cretaceous (Aptian) mammal *Teinolophos trusleri* shows that it is a monotreme and probably a steropodontid, rather than a 'eupantothere' as originally proposed. The structure of the rear of the jaw of *T. trusleri* supports the molecular evidence that previously formed the sole basis for recognising the Steropodontidae as a distinct family.

When the holotype of *Teinolophos trusleri* was first described from the Early Cretaceous (Aptian) Strzelecki Group of southern Victoria, Australia (Rich *et al.* 1999), it was regarded as a member of the Order Eupantotheria Kermack & Mussett, 1958 (= Legion Cladotheria McKenna, 1975 – Infralegion Tribosphenida McKenna, 1975) of uncertain family. This interpretation was based in large part on the inferred structure of the penultimate lower molar, the only tooth preserved on the severely crushed holotype. The crown of that tooth was largely obscured by a hard matrix. As a consequence of that, a critical misidentification of the cusp in the posterolingual region of the tooth as the metaconid rather than the hypoconulid was made. It was this erroneous interpretation and the consequent corollaries that the trigonid was anteroposteriorly expanded and the talonid unbasined that led Rich *et al.* (1999) to interpret the specimen as a 'eupantothere'.

In September 1999, Mr. Charles Schaff of Harvard University successfully cleared the obscuring matrix from crown of the tooth (Fig. 1). Upon his doing so, it became immediately obvious that this tooth, although much smaller, bore a remarkable resemblance to the m2 in the somewhat younger Early Cretaceous (Albian) monotreme *Steropodon galmani* Archer, Flannery, Ritchie, & Molnar 1985 from Lightning Ridge, New South Wales, Australia. There is also a significant resemblance to two species of the Cainozoic ornithorhynchid monotreme *Obdurodon*: *Obdurodon insignis* Woodburne & Tedford, 1975 from South Australia and *Obdurodon dicksoni* Archer, Jenkins, Hand, Murray, & Godthelp, 1992 from Queensland. To date, no specimen has been described or figured of the lower dentition of the Paleocene Argentine ornithorhynchid *Monotrematum sudamericanum* Pascual, Archer, Jaureguizar, Prado, Godthelp, & Hand, 1992.

Abbreviations. — MSC, Monash Science Centre, Monash University, Clayton, Victoria, Australia; NMV P, Palaeontology collections, Museum Victoria, Melbourne, Australia.

Dental nomenclature. — The names given to structures on the lower molars (Fig. 2) follows the usage of Kielan-Jaworowska *et al.* (1987) with the names of the lophids after Van Valen (1966). Implicit in the use of this nomenclature, but not necessarily always the case, is the assumption that dental structures in monotremes are homologous to those with the same names in therians. However, the familiarity of these terms and the ease with which they can be applied to the teeth of monotremes recommend their use for descriptive purposes in this case.

Musser & Archer (1998) recently reviewed the varied opinions expressed during the past decade regarding the affinities of monotremes. In many of those hypotheses, monotremes were widely sepa-

rated from therians. In describing the dentition of monotremes, Musser & Archer (1998) reflected this uncertainty by utilising the thegotic terminology of Every (1972). Their doing so has the advantage of avoiding any implication of homology of dental structures with therians. The trigonid as used here would be described as a triakididrepanid in that system while the talonid as used here would be described as a diakididrepanid.

Class Mammalia Linnaeus, 1758

Subclass Monotremata Bonaparte, 1837

Family ?Steropodontidae Flannery, Archer, Rich, & Jones, 1995

Diagnosis. — Distinguished from kollikodontids by the fact that the trigonid and talonid support high (rather than bunodont) cusps and blades; from the ornithorhynchids in having only two elongated roots below the lower molars; from the tachyglossids by having teeth; from both tachyglossids and ornithorhynchids by a deep mandible with a condyle well above the dorsal margin of the horizontal ramus, a prominent ascending ramus with both medial and lateral flanges on its anterior border, a more dorsally placed masseteric fossa, and the lack of a distinct coronoid process, internal coronoid process, and a mandibular fossa.

***Teinolophos* Rich, Vickers-Rich, Constantine, Flannery, Kool, & van Klaveren, 1999**

Type species: *Teinolophos trusleri* Rich *et al.*, 1999.

Diagnosis. — That of *Teinolophos trusleri* until other species are described.

***Teinolophos trusleri* Rich, Vickers-Rich, Constantine, Flannery, Kool, & van Klaveren, 1999**

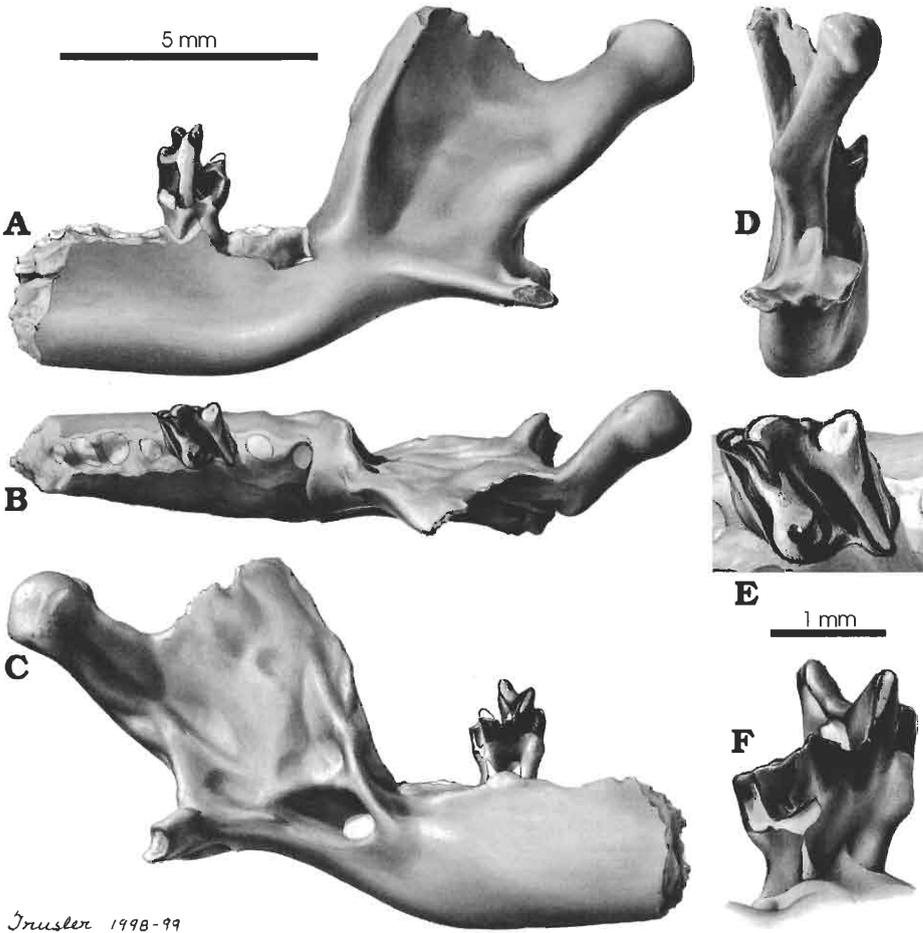
Holotype: MSC 148 [= NMV P208231]. Left mandible fragment significantly crushed but preserving the condyle, base of ascending ramus, angular process, and the penultimate molar (Fig. 1).

Diagnosis. — Distinguished from other monotremes by markedly smaller size; from other toothed monotremes by the marked difference in the angle formed between the major axis of the trigonid (that is, the bisector of the trigonid lophids) with respect to both the lingual and labial margins of the tooth, the greater degree of anteroposterior compression of both the trigonid and talonid and the length and width of the penultimate molar being subequal rather than the length being noticeably greater than the width; and from *Steropodon galmani* by the much weaker anterior and posterior molar cingula.

Measurements of molar of holotype of *Teinolophos trusleri*. — (mm; all length measurements parallel to long axis of jaw; width measurements perpendicular to long axis of jaw): length, paraconid-hypoconulid, 1.3; length, paraconid-hypoconid, 1.5; length, trigonid, 0.5; width, trigonid, 1.2; width, talonid, 1.3.

Discussion. — The principal reason that *Teinolophos trusleri* is here regarded as a monotreme is the similarity of the crown pattern of the penultimate molar to that of *Steropodon galmani* (Fig. 2), and to a slightly lesser degree, the species of *Obdurodon*. In particular, the anteroposteriorly compressed nature of the trigonid and talonid, which sets the teeth of these other unquestioned monotremes apart from most other mammals, is manifested to an even greater degree in *T. trusleri*. In addition, the wear pattern on the trigonid and talonid is similar to that of *S. galmani* as outlined by Kielan-Jaworowska *et al.* (1987). That is, it is a non-tribosphenic pattern of wear in which there is no evidence of a protocone having occluded within a talonid basin. Rather, wear facets on the talonid face away from its centre instead than forming the inwardly sloping walls of a basin.

In *Steropodon galmani* and *Obdurodon insignis*, and presumably *O. dicksoni*, the major axis of the trigonid is nearly perpendicular to the medial and labial sides of the tooth and the long axis of the jaw (Fig. 2A). In contrast, in *Teinolophos trusleri*, this line forms an angle of 77° (Fig. 2B). That angle and the 73° angle formed by the major axis of the talonid both being markedly less than 90° means there could have been no significant mediolateral motion of the jaw after the occlusal surfaces of the upper and lower teeth met unless the jaws were completely dislocated or the mandibular articulation



Trusler 1998-99

Fig. 1. *Teinolophos trusleri* Rich *et al.* 1999, crushed left mandible fragment with condyle, base of the ascending ramus, angular process, and the penultimate molar, MSC 148 (=NMV P208231), holotype. A. Lateral view. B. Occlusal view. C. Medial view. D. Posterior view. E. Occlusal view of penultimate molar. F. Oblique-labial view of penultimate molar. Left scale bar is for A–D, right for E, F.

sufficiently loose to make possible oblique transverse shear. Likewise, the relatively great height of the trigonid coupled with the vertical or near vertical nature of some of the wear facets would have precluded significant propalinal motion once the teeth were in occlusion. Therefore, the motion of the jaw would necessarily seem to have been almost strictly orthal after the teeth occluded. The wear facets of *S. galmani* are likewise nearly vertical.

Ornithorhynchids and tachyglossids are characterised by relatively weak jaws adapted for diets of insects, particularly ants in the case of echidnas; and small, soft aquatic invertebrates in the case of the platypus (and presumably, despite their fully enameled teeth, the species of *Obdurodon* as well). In marked contrast, what is known of the lower jaw of *Teinolophos trusleri* suggests it was an animal with a relatively more powerful bite. Evidence for this is seen in (1) the position of the condyle well above the level of the dorsal edge of the horizontal ramus instead of level with it, (2) a relatively much higher ascending ramus with (3) prominent flanges extending both laterally and lingually along the anterior edge of the masseteric fossa, and (4) a prominent angle with (5) flanges extending both labi-

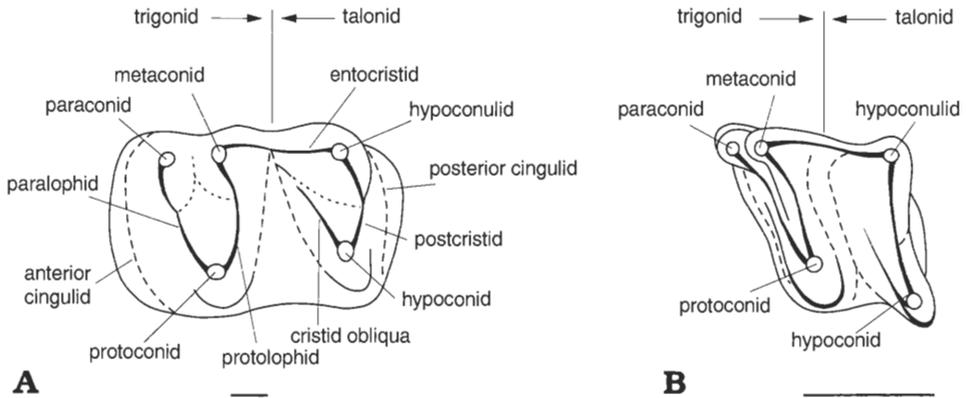


Fig. 2. Diagrammatic drawings of (A) the m2 of *Steropodon galmani* (reversed) and (B) the penultimate molar of *Teinolophos trusleri*, in occlusal view, showing terminology used for describing *Teinolophos*, and structures regarded as homologous. Anterior is to the left. Scale bars 1 mm.

ally and lingually. Features (3) and (5) suggest that the *mm. masseter* and *pterygoideus*, respectively, were prominent. Although labial flanges on the mandibular angle are rare in mammals, they do occur in groups such as the Geomyidae (pocket gophers), which also have the more common condition of lingual flanges on the mandibular angle as well. Radinsky (1985) noted that features (1) and (4) were characteristic of ungulates with their powerful bite rather than of carnivores and primitive mammals generally. Most early mammals, by contrast, have a lower condyle (at about the level of the tooth row) and a more poorly developed angle, in correlation with emphasis on *m. temporalis*. Intriguingly, an efflected masseteric flange and well-developed attachment sites for *m. pterygoideus* are found on the angular region of the jaw in certain Mesozoic mammals such as triconodontids (Simpson 1928) and spalacotheriids (Cifelli & Madsen 1999), despite the fact that the condyle is located near the level of the tooth row.

Turnbull (1970) recognised four classes of mammalian masticatory apparatus. Of the nine modern mammalian species considered by him, the jaw of *Echinosorex gymnurus* in his 'Generalized Group' most closely resembles that of *Teinolophos trusleri*. However, the likely greater relative prominence of the *mm. masseter* and *pterygoideus* in *T. trusleri*, inferred from the nature of the angle as outlined in the previous paragraph, suggests that functionally, the jaw of *T. trusleri* was intermediate between the Turnbull's 'Generalised Group' and his "Specialized Group II – The 'ungulate-grinding' or 'mill' type".

Turnbull (1970) regarded the platypus and echidnas as falling outside of his four-fold classification of the mammalian masticatory apparatus. Differences between the mandible of *Teinolophos trusleri* on the one hand and those of living monotremes and species of *Obdurodon* on the other, are so great that if these taxa could not be linked together on the basis of dental evidence, these sharply contrasting features of the lower jaw would rationalise placing these taxa in widely separated groups.

Several character states of the posterior region of the jaw which separate the echidna and platypus from *Teinolophos trusleri* are derived features shared by these living monotremes. *T. trusleri* exhibits the plesiomorphic character states for these features. However, it exhibits derived features in the strong development of the angle, high coronoid process, and features related to attachment of the *mm. pterygoideus* and *masseter*. As *T. trusleri* appears to be a steropodontid, this morphological evidence accords with the hypothesis initially put forward by Flannery *et al.* (1995), solely on the basis of molecular evidence and geological age, that the platypus and echidnas are sister groups, with the Steropodontidae lying outside of the crown group Monotremata. Specifically, the molecular evidence (e.g., Messer *et al.* 1995; Retief *et al.* 1993; Westerman & Edwards 1992) suggests that the ornithorhynchids and tachyglossids split either near the Cretaceous–Tertiary boundary or subse-

quently, and thus was an event significantly postdating the Early Cretaceous age of *T. trusleri* and *Steropodon galmani*.

As far as the two are known, *Steropodon galmani* and *Teinolophos trusleri* are more like one another than either is to any other monotreme. However, the assignment of *T. trusleri* to the Steropodontidae must be regarded as provisional. This is because of both the limited number of comparable features of the two taxa available for study and the fact that none of the known shared character states are necessarily apomorphic.

Unfortunately, the condition of the rear of the jaw is unknown in both *Steropodon galmani* and *Kollikodon ritchei*. However, the depth and robust nature of their jaws beneath their cheek teeth suggests that the unknown regions of their jaws may well have been closer to that of *Teinolophos trusleri* than to tachyglossids or ornithorhynchids.

Conclusions. — The similarity of the only known tooth of *Teinolophos trusleri* to *Steropodon galmani* makes a persuasive case that *T. trusleri* belongs within the monotremes and, within that group, probably to the Steropodontidae.

Previously, the structure of the rear of the jaw of steropodontids was unknown. The rear of the jaw of *Teinolophos trusleri* is primitive in a number of features common to both ornithorhynchids and tachyglossids, while derived in a number of others. This supports the hypothesis initially put forward by Flannery *et al.* (1995) based solely on molecular evidence and geological age, that the platypus and echidnas are sister groups, with the Steropodontidae being a primitive outgroup.

The features of the one preserved molar regarded as linking *Teinolophos trusleri* with 'eupantotheres' by Rich *et al.* (1999) are now known to have been misinterpreted. Only the well-defined mandibular angle remains to suggest such a relationship. A mandibular angle may have been developed independently in 'eupantotheres' and monotremes, or could have been lost in crown Monotremata (Tachyglossidae + Ornithorhynchidae), in correlation with other modifications of the masticatory apparatus.

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Addendum

After the present paper was submitted for publication, the paper by Luo *et al.* (2001) appeared. In that paper the authors erect two new infraclasses: Australosphenida, in which they include Monotremata, Ausktribosphenida, and *Ambondro*; and Boreosphenida for all the remaining mammals with tribosphenic molars. Hence these authors have proposed that tribosphenic molars arose twice in mammalian evolution. The paper appeared too late to be commented herein.

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