INVESTIGATIONS INTO THE EVOLUTION OF AUSTRALIAN MAMMALS WITH A FOCUS ON MONOTREMATA

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ABSTRACT

This thesis began as an investigation into evolution of the platypus family (Ornithorhynchidae, Monotremata), now known from both Australia and South America. The thesis broadened its scope with inclusion of non-ornithorhynchid Mesozoic monotremes from Lightning Ridge, NSW. This change in direction brought an unexpected result: a fossil mammal from Lightning Ridge investigated for this thesis (presumed to be monotreme: Flannery et al., 1995) appears to be a new and unique type of mammal. Specimens were procured through Queensland Museum (Riversleigh material); Australian Museum (Lightning Ridge material); and Museum of Victoria and the South Australian Museum (fossil ornithorhynchids). Specimens were examined under a light microscope and scanning electron microscope; specimens were photographed using light photography and a scanning electron microscope; and illustrations and reconstructions were done with a camera lucida microscope attachment and photographic references. Parsimony analysis utilised the computer programs PAUP and MacClade. Major conclusions: 1) analysis and reconstruction of the skull of the Miocene platypus *Obdurodon dicksoni* suggest this robust, large-billed platypus was a derived northern offshoot off the main line of ornithorhynchid evolution; 2) the well-preserved skull of *Obdurodon dicksoni* shows aspects of soft anatomy previously unknown for fossil ornithorhynchids; 3) two upper molars from Mammalon Hill (Etadunna Formation, late Oligocene, central Australia) represent a third species of *Obdurodon*; 4) the South American ornithorhynchid *Monotrematum sudamericanum* from the Paleocene of Argentina is very close in form to the Oligocene-Miocene *Obdurodon* species from Australia and should be considered congeneric; 5) a revised diagnosis of the lower jaw of the Early Cretaceous monotreme *Steropodon galmani* includes the presence of two previously undescribed archaic features: the probable presence of postdentary bones and a meckelian groove; 6) morphological evidence is presented supporting a separate family Steropodontidae; and 7) analysis of new fossil material for *Kollikodon ritchiei* suggests that this taxon is not a monotreme mammal as originally identified but is a basal mammal with close relationships to allotherian mammals (Morganucodonta; Haramiyida). *Kollikodon* is provisionally placed as basal allotherian mammal (*Allotheria sensu* Butler 2000) and is unique at the ordinal level, being neither haramiyid nor multituberculate. A new allotherian order – Kollikodonta – is proposed.
ORIGINALITY STATEMENT

‘I hereby declare that this submission is my own work and to the best of my knowledge it contains no materials previously published or written by another person, or substantial proportions of material which have been accepted for the award of any other degree or diploma at UNSW or any other educational institution, except where due acknowledgement is made in the thesis. Any contribution made to the research by others, with whom I have worked at UNSW or elsewhere, is explicitly acknowledged in the thesis. I also declare that the intellectual content of this thesis is the product of my own work, except to the extent that assistance from others in the project’s design and conception or in style, presentation and linguistic expression is acknowledged.’

Anne Marie Musser
31 August 2005
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INTRODUCTION TO THE THESIS

This thesis presents a series of investigations into mammalian evolution in Australia from the Mesozoic to the present. The primary focus is on Monotremata (the platypus and echidnas and their extinct relatives); the origins of these unusual and archaic mammals have been obscure since their discovery by the western world over 200 years ago. The thesis also examines the affinities of the recently discovered Early Cretaceous mammal *Kollikodon ritchiei*, originally described as a monotreme mammal (Flannery *et al.*, 1995) but whose relationships are reinterpreted here. The thesis is primarily in the form of published papers (Chapters 1-4) but includes an unpublished manuscript (Chapter 5). Additional studies (reported as abstracts) are included in appendices.

The purpose of this thesis was to investigate the available fossil monotreme material or material deemed to be monotreme (much of which is recently discovered and highly significant); to compare these fossils to mammals and near-mammals from both southern and northern continents; and to formulate hypotheses on relationships and origins. The origin of mammals - and of southern hemisphere mammals in particular - is a dynamic and contentious area of palaeontology. Mesozoic mammals from Gondwanan continents have only recently been recovered and figure prominently in current debates on mammalian origins (see below).

Methods employed include analysis of fossil material using a binocular microscope and scanning electron microscope; comparison of this material to that of non-mammalian cynodonts and basal mammals (taken from the literature); and parsimony analysis utilising the computer programs PAUP and MacClade. Specimens were photographed using light photography and a scanning electron microscope; and illustrations and reconstructions were done with a camera lucida microscope attachment and photographic references.

Fossil taxa studied (or in some cases restudied) for this thesis include the Early Cretaceous *Steropodon galmani*, the first Mesozoic mammal from Australia (Archer *et al.*, 1985; Kielan-Jaworowska *et al.*, 1987; Musser, in press; Luo *et al.*, 2001, 2002; abstract, Musser, 2005); the Early Cretaceous *Kollikodon ritchiei*, described as a monotreme based on the lower jaw and dentition (Flannery *et al.*, 1995; Chapter 5, this thesis); the first non-Australian monotreme, the Paleocene South American platypus *Monotrematum sudamericanum* (Pascual *et al.*, 1992 a, b; abstract, Musser and Archer, 1998; Pascual *et al.*, 2002; Forasiepi and Martinelli, 2003); Tertiary ornithorhynchids in the genus *Obdurodon* (Woodburne and Tedford, 1975; Archer *et al.*, 1978, 1992, 1993a; Musser and...
Archer, 1998; abstract, Musser, 1999); Pleistocene platypus material referable to the living Platypus *Ornithorhynchus anatinus* (De Vis, 1885; Archer *et al.*, 1978; Musser, 1998; Musser, in press); Tertiary echidnas in the genus *Megalibgwilia* (Dun, 1895; Murray, 1978a, b; Griffiths *et al.*, 1991; Musser, in press); and the living Short-beaked Echidna *Tachyglossus aculeatus* (Jenkins and Musser, unpub.; Musser and Jenkins, 1992; Musser, in press).

**Mammalian evolution in the southern hemisphere**

Mesozoic mammals from the southern hemisphere are exceedingly rare. Most of what is known about the earliest mammals has come from evidence found in the northern hemisphere, in part because of more extensive work on northern continents and in part because of lack of exposure of fossil-bearing outcrops of the right age (Triassic-Early Jurassic) on southern continents. Mammals evolved from advanced mammal-like reptiles (cynodonts) near the close of the Triassic and radiated into the earliest types during the first part of the Jurassic (e.g., Hopson and Crompton, 1969; Clemens *et al.*, 1979; Crompton and Jenkins, 1979; Miao, 1991; Kielan-Jaworowska, 1992; Cifelli, 2001).

The oldest mammals are about 225 million years old (Late Triassic of North America: Lucas and Luo, 1993). These archaic, non-therian mammals (early mammals not closely related to Theria: marsupials and placentals and their extinct relations) comprised early mammalian faunas, which generally gave way to more advanced types as these evolved. Marsupial and placental mammals (advanced therians) have only been in existence since the Early Cretaceous (e.g., Ji *et al.*, 2002; Luo *et al.*, 2003). Although debated (e.g., Rich *et al.*, 1997, 1999a, Woodburne *et al.*, 2003) the current consensus is that advanced therians evolved on northern continents, replacing older mammal faunas during the latter part of the Mesozoic.

In recent years there have been several key discoveries of Mesozoic mammals and near-mammals from the southern hemisphere: Australia (Archer *et al.*, 1985; Flannery *et al.*, 1995; Clemens *et al.*, 2003); South America (Bonaparte 1986a, 1986b, 1987, 1990; Bonaparte and Rougier 1987; Kielan-Jaworowska and Bonaparte, 1996; Pascual *et al.*, 2000; Rauhut *et al.*, 2002; Rougier *et al.*, 2000); Madagascar (Krause *et al.*, 1994, 1997a, b, 1999; Krause and Grine 1996; Flynn *et al.*, 1999); India (Datta 1981; Yadagiri 1985; Prasad and Sahni 1988; Prasad *et al.*, 1995; Datta and Das 2001; Rana and Wilson 2003); and Africa (Heinrich 1998, 1999; Sigogneau-Russell *et al.*, 1998; Krause *et al.*, 2003). No Mesozoic mammals have yet been found in either Antarctica or New Zealand although they were certainly present in those regions (early Tertiary mammals are now known from Antarctica: e.g., Woodburne and Zinsmeister, 1982). Archaic mammals remained on southern continents well past the point at which they disappeared from more northern areas and these relict groups had in many cases become highly
specialised (e.g., Bonaparte, 1990; Heinrich, 1999; Pascual et al., 2000). Late Cretaceous Gondwanan mammals are overwhelmingly non-therian, non-tribosphenic or pre-tribosphenic (e.g., Bonaparte, 1990; Pascual et al., 2000; Krause et al., 1997a, b).

At least one group of Jurassic-Cretaceous Gondwanan mammals with primitive lower jaws developed advanced, therian-like tribosphenic teeth (*Ausktribosphenos nyktos* and *Bishops whitemorei*: Rich et al., 1997, 1999a, 2001a; *Ambondro mahabo*: Flynn et al., 1999; and *Asfaltomylos patagonicus*: Rauhut et al., 2002; Martin and Rauhut, 2005). Although their relationships to other mammals are contested (Rich et al., 1997, 1999a; Kielan-Jaworowska et al., 1998; Musser and Archer, 1998; Archer et al., 1999; Luo et al., 2001, 2002; Rich et al., 2002; Woodburne et al., 2003) these southern tribosphenic mammals (‘Australosphenida’ of Luo et al., 2001, 2002 [who include monotremes in this group]) have generated great interest in Gondwanan Mesozoic mammals and the part they may have played in mammalian evolution.

**Australia’s role: a key player**

Today Australia is home to all three groups of living mammals: monotremes, marsupials and placental mammals. It is the only continent to have such a fauna, the result of past geographical position, long since obliterated polar dispersal routes, and long periods of isolation during which relict types (monotremes) persisted and emigrants (predominantly marsupials) flourished in the absence of more extreme competition faced on other continents.

Monotreme mammals have traditionally been seen by many palaeontologists as sole Australian survivors of the Triassic-Jurassic early radiation of mammals (see Musser, 2003 for a review). The highly specialised living monotremes have undoubtedly diverged in many ways from what must have been a more generalised ancestor (e.g., Musser, in press) and their origins are a source of great interest as well as debate. The 1985 discovery of *Steropodon*, described by Archer et al. (1985) as a possible tribosphenic therian mammal because of its therian-like molars, galvanised debate about monotreme origins because this suggested a much more advanced position for monotremes than previously believed. Subsequent studies place monotremes in more basal positions (e.g., Kielan-Jaworowska et al., 1987; Rowe, 1988; Wible, 1991; Meng and Wyss, 1995; Luo et al., 2001, 2002; Pascual et al., 2002; Rich et al., 2005) but without consensus about relationships.

Prior to the discovery of *Steropodon galmani* from Lightning Ridge in New South Wales (Archer et al., 1985) there was no record of any Australian mammal older than the late Oligocene (Rich et al., 1991). Australia lacks Late Cretaceous and earliest Tertiary vertebrate sites (aside from some fragmentary remains from the early Late Cretaceous; see below), leaving a 'black hole' of over
50 million years from the Early Cretaceous (110-115 myo) to the early Eocene (the approximately 55 myo Murgon fossil site in southeast Queensland: Godthelp et al., 1992). Murgon records the first known Australian marsupials, several of which have ties to South American types (e.g., Archer et al., 1993b) and which were descendants of the mainly arboreal South American marsupials that spread across Antarctica to Australia during the latest Cretaceous-earliest Tertiary (e.g., Case, 1989).

Australian Mesozoic mammals have now been recovered from three Early Cretaceous sites: Lightning Ridge; Flat Rocks, Victoria; and the Toolebuc Formation (abstract, Godthelp, 2005) as well as from the early Late Cretaceous Winton Formation (abstract, Salisbury, 2005). Lightning Ridge deposits are middle Aptian in age (approx. 110 mybp: Burger, 1988) and have produced Steropodon galmani (Archer et al., 1985); Kollikodon ritchiei (Flannery et al., 1995); and an edentulous maxilla (Rich et al., 1989). Several edentulous jaws that appear to be monotreme have also been recovered (Musser, in prep.). Remarkably, a single tooth has recently been described that may either be that of a traversodont cynodont or dryolestoid mammal (Clemens et al., 2003). Flat Rocks is roughly 115 million years of age (the base of the Aptian: Rich et al., 1997) and has produced a diverse Mesozoic fauna, including the oldest known monotreme (Teinolophos trusleri: Rich et al., 1999, 2001a, 2005) as well as Ausktribosphenos nyktos and Bishops whitmorei, two new mammals described as archaic placentals and assigned to the newly erected order Ausktribosphenida (Rich et al., 1997, 1999, 2001a; see above).

Tertiary Australian mammals come from several sites, including the late Oligocene central Australian Etadunna Formation and the Oligocene-Miocene Riversleigh World Heritage Fossil Deposits in northwest Queensland. The first toothed fossil ornithorhynchid (Obdurodon insignis: Woodburne and Tedford, 1975) was recovered from Etadunna Formation sediments. The early Miocene platypus Obdurodon dicksoni (Archer et al., 1992, 1993; Musser and Archer, 1998) and thylacine Nimbacinus dicksoni (Wroe and Musser, 2001) were both produced from Riversleigh limestones; their exceptional preservation as well as taxonomic importance are testament to the outstanding nature of the material being recovered at this site.

**General aims and approach of this thesis**

The original aim of this thesis was an investigation of Tertiary platypus material; it has since grown into a much broader project as new fossil material has come to hand. In particular, several Mesozoic mammalian specimens from Lightning Ridge, NSW have recently been recovered and added to this study: a maxilla with upper dentition of the bunodont mammal Kollikodon ritchiei Flannery et al., 1995 and a series of edentulous monotreme jaws (abstract, Musser, 2003a; Musser in
prep.). In addition, the holotype lower jaw of the Early Cretaceous *Steropodon galmani* has been reexamined, revising the original diagnosis of Archer *et al.* (1985). *Steropodon* is compared to the recently discovered Victorian Early Cretaceous monotreme *Teinolophos trusleri* (abstracts, Musser, 2003, 2005), recently shown to possess a very archaic lower jaw with trough for possible accessory jaw bones (Rich *et al.*, 2005). This thesis also examines the biogeography, palaeoecology and distributions of monotremes (Musser, 1998).

The aims of these investigations were to 1) describe and identify fossil material provided for the thesis; 2) analyze and assess affinities and intrafamilial relationships of fossil platypuses within Ornithorhynchidae; 3) determine relationships of the Early Cretaceous mammal *Kollikodon ritchiei*; and 4) put the evolution, palaeoecology and biogeography of these fossil mammals into a regional and global context.

**Chapter aims and results**

All thesis chapters except for Chapter 5 have been or are about to be published in peer-reviewed scientific journals or books. Chapter 5 is presented as an unpublished manuscript.

Chapter 1 (Musser, 2003) reviews the monotreme fossil record, the literature on monotreme anatomy and palaeontology, and the debates – historical and ongoing – over monotreme relationships. Estimates of divergence times between monotremes and other mammals and relationship hypotheses as determined by molecular studies are compared with the monotreme fossil record. This paper was published as part of the conference proceedings of a symposium on monotreme biology (a Satellite Symposium of the International Congress of Comparative Physiology and Biochemistry) held at Lemonthyme Lodge, Tasmania in February 2003 (*Comparative Biochemistry and Physiology Part A [Molecular and Integrative Physiology], Volume 136A, 2003*).

Chapter 2 (Musser, in press) is a chapter in a forthcoming book on Australasian vertebrates, *Evolution and Biogeography of Australasian Vertebrates*, due to be published later this year (2005). It is a comprehensive overview of both extant and extinct monotremes and includes discussion of monotreme anatomy (internal, external and skeletal), physiology, ecology, biogeography, and the fossil record. Original investigations presented here but otherwise unpublished include comparison of ornithorhynchid dentitions and a preliminary, revised diagnosis of the lower jaw of *Steropodon galmani*.

Chapter 3 (Musser and Archer, 1998) presents a study of the skull of the Miocene platypus *Obdurodon dicksoni*. This paper was part of a special volume on platypus biology published in *Philosophical Transactions of the Royal Society of London, Series B* (Volume 353, 1998). An
osteological reconstruction of the skull and dentary is described and illustrated along with a description of the cranial and mandibular foramina. Comparisons are made with the skull of the living platypus, *Ornithorhynchus anatinus*. This study synonymises the major foramina of the skull and dentary for both *Ornithorhynchus* and *Obdurodon* using as a guide the landmark study of the skull of *Ornithorhynchus* by Zeller (1989a). The phylogenetic importance of features of the skull, dentary and dentition is discussed and possible differences between the diets and lifestyles of *Obdurodon* and *Ornithorhynchus* are proposed.

Chapter 4 (Musser, 1998) discusses evolutionary trends within the platypus family, putting this into a biogeographical and palaeoecological context. This paper was published as part of a special issue of *Australian Mammalogy* (Volume 20, Number 2) following the first National Symposium of Platypus Biology held at Charles Sturt University, Bathurst NSW in November, 1996. Keystone discoveries (*Obdurodon dicksoni* and the South American platypus *Monotrematum sudamericanum*) are used to illustrate morphological change as ornithorhynchids evolved from toothed forms to the edentate and highly specialised living platypus *Ornithorhynchus anatinus*.

Chapter 5 (unpublished manuscript) describes new material for the enigmatic Early Cretaceous mammal *Kollikodon ritchiei*, known initially from a fragmentary lower jaw with bunodont molar teeth and described as a highly specialised monotreme (Flannery et al., 1995). Flannery et al. (1995) base their identification on perceived similarities between the lower molars of *Kollikodon* and monotremes. Newly acquired material (a maxillary fragment with four upper molariform teeth and a single premolar) is studied for this thesis and an alternative interpretation of the affinities of *Kollikodon* is presented.

Results of these investigations are summarised (Thesis Conclusions) and conclusions drawn on the evolutionary trends, relationships, ecology and biology of the taxa studied.

Thesis appendices contain 1) additional papers in which I was either author or co-author (Rich et al., 2005; Wroe and Musser 2001; Musser, 1999; Archer et al., 1999); and 2) conference abstracts from papers or posters presented at palaeontological meetings. Announcement of the first occurrence of possible postdentary bones in a fossil monotreme, the Early Cretaceous *Teinolophos trusleri*, is made by in a groundbreaking paper by Rich et al. (2005), a discovery of global importance. In Wroe and Musser (2001) the well-preserved skull of a comparatively basal marsupial carnivore, the Miocene thylacinid *Nimbacinus dicksoni* (the only fossil thylacine known from a nearly complete skeleton) is described. A short summary of the monotreme fossil record is presented by Musser (1999) as part of a series of papers on the evolution of the Australian mammal faunas (Archer et al.,
1999). Archer et al. (1999) is a jointly authored paper on Australian fossil mammals of uncertain affinities.

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CHAPTER 1

Review of the monotreme fossil record
and comparison of palaeontological and molecular data

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CHAPTER 1

Chapter 1 (‘A review of the monotreme fossil record and comparison of palaeontological and molecular data’) reviews the palaeontological history of fossil monotremes and compares morphological data on monotremes to results of molecular studies. It grew out of a special symposium on monotreme biology held at Lemonthyme Lodge, Tasmania in February, 2003. Participants were invited to prepare papers for publication in a special volume of *Comparative Biochemistry and Physiology* (Part A: Vol. 136; 2003, edited by Stewart Nicol).

In the past decade molecular systematics has grown from an almost unknown field into one of the most dynamic disciplines in biological sciences. Biochemical techniques have been utilised to study phylogenetic relationships of many organisms, particularly those whose relationships are poorly understood or contentious. Monotremata has been of special interest because of the differences and similarities between this group and other living mammals and because of the archaic features that monotremes possess. This paper, primarily aimed at a non-palaeontologist audience, reviews and condenses the literature on monotreme anatomy and palaeontology and discusses how the current molecule-based theories fit with morphological data and the fossil record from the Early Cretaceous to the present. The morphology of living monotremes, the fossil record, and the relationship between the platypus and echidnas are discussed.

Since this paper was written a significant new monotreme fossil has been described, certain to fuel debate and perhaps alter opinions of some molecular biologists on monotreme relationships. The Early Cretaceous monotreme *Teinolophos trusleri* from Flat Rocks, Victoria has been identified as having a trough for possible accessory jaws bones (a postdentary trough, as in cynodonts and basal mammals) (Rich *et al.*, 2005). This discovery supports the independent origin of the ear ossicles from the lower jaw in therian mammals and in monotremes, putting the split between monotremes and therians well back in time – perhaps to the Early Jurassic or earlier.


Review

Review of the monotreme fossil record and comparison of palaeontological and molecular data

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Abstract

Monotremes have traditionally been considered a remnant group of mammals descended from archaic Mesozoic stock, surviving to the present day on the relatively isolated Australian continent. Challenges to this orthodoxy have been spurred by discoveries of ‘advanced’ Cretaceous monotremes (*Steropodon galmani*, Archer, M., et al., 1985. First Mesozoic mammal from Australia—an Early Cretaceous monotreme, Nature. 318, 363–366) as well as by results from molecular data linking monotremes to therian mammals (specifically to marsupials in some studies). This paper reviews the monotreme fossil record and briefly discusses significant new information from additional Cretaceous Australian material. Mesozoic monotremes (including *S. galmani*) were a diverse group as evidenced by new material from the Early Cretaceous of New South Wales and Victoria currently under study. Although most of these new finds are edentulous jaws (limiting dental comparisons and determination of dietary niches), a range of sizes and forms has been determined. Some of these Cretaceous jaws exhibit archaic features—in particular evidence for the presence of a splenial bone in *S. galmani*—not seen in therian mammals or in post-Mesozoic (Tertiary and Quaternary) monotreme taxa. Tertiary monotremes were either archaic ornithorhynchids (toothed platypuses in the genera *Monotrema*um and *Obdurodon*) or tachyglossids (large echidnas in the genera *Megalibgwilia* and *Zaglossus*). Quaternary ornithorhynchid material is referable to the sole living platypus species *Ornithorhynchus anatinus*. Quaternary echidnas, however, were moderately diverse and several forms are known (*Megalibgwilia* species; *Zaglossus*‘*hacketti*; *Zaglossus* species and *Tachyglossus aculeatus*).

Keywords: Echidna; Evolution; Gondwana; Mesozoic mammals; Monotreme; Platypus; Prototheria

1. Introduction

Living monotremes are represented by two somewhat dissimilar families: Ornithorhynchidae and Tachyglossidae. The only extant ornithorhyn-
species generally prefer a diet of insect larvae. Both families share unique specializations (synapomorphies) as well as primitive features (synapomorphies), making this group an interesting study in mosaic evolution.

Mosaic evolution describes a phenomenon seen in many organisms: archaic features occur alongside highly specialised or advanced features in the same plant or animal. Although monotremes have many mammalian features (e.g., a dentary-squamosal jaw joint), many aspects of monotreme anatomy, particularly the skeletal and reproductive systems, are primitive in comparison to these systems in marsupial and eutherian mammals. Monotremes are the only mammals that lay eggs (the probable mode of birth of the earliest mammals); they have retained ‘reptilian’ bones in the skull and shoulder girdle; and share many other archaic features. Recognition of the comparatively primitive (plesiomorphic) nature of these features has led most scientists to consider monotremes—in spite of their specialisations—to be primitive mammals far removed from marsupial and eutherian mammals (Theria).

The monotreme fossil record has grown steadily over the past few decades. Monotreme fossils have been recovered from many parts of Australia as well as from a single site in southern South America (confirmation of Gondwanan affinities for the group; Pascual et al., 1992a,b). Of particular interest are Mesozoic (Early Cretaceous) sites in both New South Wales and Victoria that are producing material of great potential (e.g., Archer et al., 1985; Flannery et al., 1995; Rich et al., 1997, 1999, 2001a,b). Mesozoic monotremes are key to determining ancestral monotreme features and relationships to other mammals because of extreme specialisation in living monotremes as well as an exceptionally long history for the group, allowing a great deal of time in which to lose ancestral features and develop new characteristics.

The taxonomic status of monotremes has recently been revised by McKenna and Bell (1997) in an updated classification of all known mammal taxa. Monotremes have formally been elevated in rank from an order (Monotremata) to a subclass (Prototheria); platypuses have been raised from a family (Ornithorhynchidae) to an order (Platypoda), composed of the single family Ornithorhynchidae and S. galmani; and echidnas are likewise raised from a family (Tachyglossidae) to an order (Tachyglossidae). This reclassification recognises that monotremes deserve greater taxonomic status than the level of order (as proposed by Hopson, 1970). Adopting the term Prototheria, however, dispenses with the well-known and descriptive taxon name Monotremata. Prototheria as proposed by Hopson (1970) includes other non-therian mammals (Triconodonta, Docodonta and Multituberculata) in addition to monotremes. Monotremata includes only monotreme mammals and additionally is the older of the two names (Monotremata was proposed by Bonaparte in 1837 and Prototheria was coined by Gill in 1872).

This review presents a broad overview of mammalian evolution as it relates to understanding of the position of monotremes; a brief description of known fossil monotreme taxa; and a discussion on conflicting results between molecular phylogenetics and palaeontological studies. For a recent review of fossil monotreme taxa see Musser (1999). For a more detailed discussion of morphology of fossil monotremes, palaeohabitats and associated faunas see Musser (in press). Terms highlighted in bold type are defined in Table 1 (glossary). Geological time periods are charted in Fig. 1 (geological time scale and the monotreme fossil record).

2. Early mammalian evolution

Although controversy rages over the exact definition of a mammal and over which taxa are included within the Class Mammalia (e.g., Rowe, 1988; Miao, 1991; Wible, 1991; McKenna and Bell, 1997), some general points can be made about timing and origins of the group. Mammals evolved from a group of reptiles (synapsids) that originated not long after stem reptiles first appear in the fossil record (Late Carboniferous, over 300 million years ago). These basal mammal-like reptiles, originally not dissimilar to stem reptiles, gave rise to taxa that progressively acquired ‘mammalian’ features. Mammal-like reptiles flourished during the Permian and Triassic periods and were the dominant large land vertebrates before evolution of the dinosaurs.

Therapsids (Advanced mammal-like reptiles) appear at the base of the Late Permian (about 270 million years ago). Advanced therapsids survived until the middle Jurassic, overlapping with early mammals for over 50 million years. The most mammalian of the therapsids were the cynodonts
cynodonts see Hopson and Kitching

from one or more of the cynodonts that mammals
that originated during the latest Permian, and it is
through Middle Jurassic) and the group from which mammals evolved (Kermack and Kermack, 1984).

Gondwana: the southern continents (previously called ‘Gondwanaland’), originally part of the giant supercontinent of Pangaea in the early part of the Mesozoic. Gondwana included South America, Africa, Madagascar, India, Antarctica, New Zealand and Australia and had probably separated from the northern continents (Laurasia) by the late Jurassic (Carroll, 1988).

Laurasia: the northern continents, composed of North America, Greenland and Eurasia, originally part of the supercontinent Pangaea in the early Mesozoic. Laurasia and Gondwana were separated by the Tethys Sea, a barrier for faunal interchange (Carroll, 1988).

Paraphyletic: a group containing a hypothetical common ancestor and some, but not all, of its descendants (Schuh, 2000).

Plesiomorphic: primitive, as opposed to advanced (apomorphic); the quality of being group-defining only at a higher level (Schuh, 2000).

Polyphyletic: a group that does not include the most recent common ancestor of all its members; it may be based on convergent or homoplasic characters and, therefore, not indicative of a shared ancestry (Kitching et al., 1998).

Symplesiomorphy: shared, primitive traits defining groups only at higher levels (Schuh, 2000).

Synapomorphy: an apomorphy (shared derived character) that unites two or more taxa into a monophyletic group (Kitching et al., 1998).

Synapsid: a skull with a single opening in the cheek area; this opening (fossa) primitively is bounded above by the squamosal and postorbital bones and below by the jugal and squamosal bones and is only known in mammal-like reptiles and mammals. Synapsida includes mammal-like reptiles as well as mammals (Kermack and Kermack, 1984).

Talonid: in the basic therian lower molar pattern, the talonid is the posterior part of the molar (or the ‘heel’) formed by a small cusp (the hypoconulid) and an extension of the cingulum (shelf-like base of the tooth). Enlargement of the talonid and formation of a basin for the occluding upper protocone is characteristic of more advanced therian mammals (Kermack and Kermack, 1984).

Taxon (pl. taxa): a named group of two or more organisms (Kitching et al., 1998).

Therapsid: the more advanced and diverse of the two types of mammal-like reptiles (the other being the more primitive Pelycosauria) characterised by more mammalian skulls (non-kinetic) and progressively more mammalian postcranial skeletons. A subgroup of the therapsids, the cynodonts, were the ancestors of mammals (Hotton, 1991).

Triosphenic: traditionally defined as the distinctive, tritubercular tooth form possessed by basal Marsupialia, Placentalia and Theria of metatherian-eutherian grade. Triosphenic molars have a cusp (protocone) on upper molars that occludes with the talonid basin of lower molars (a mortar-and-pestle action) acting in concert with the alternating, shearing action of the trigon (triangulated cusps of upper molars) and trigonid (triangulated cusps of lower molars) (Bown and Kraus, 1979).

Trigonid: in the basic therian lower molar pattern, the trigonid is the anterior part of the molar and is triangular in shape with three main cusps: a protoconid, paraconid and metaconid (Kermack and Kermack, 1984).

‘dog toothed’ therapsids with mammal-like teeth) that originated during the latest Permian, and it is from one or more of the cynodonts that mammals evolved. For a recent review of non-mammalian cynodonts see Hopson and Kitching (2001).

The oldest mammals date from the end of the Late Triassic, the first period of the Mesozoic (the Triassic, Jurassic and Cretaceous periods). These archaic Mesozoic forms—morganucodontids, docodonts and sinoconodonts among others—are known mostly from lower jaws and teeth, and are distinguished in part from later mammals by possession of a more reptilian type of lower jaw (e.g., McKenna and Bell, 1997). Although palaeontologists have traditionally included these early representatives within the class Mammalia, some place these taxa outside of Mammalia as near relatives (e.g., Rowe, 1988; McKenna and Bell, 1997). In the present account, all post-cynodont mammal-like forms are referred to as mammals.

The Mesozoic was a time of experimentation and incremental advancement for mammals as they diversified and spread across the joined supercontinents of Laurasia (northern continents) and
Fig. 1. The geological timescale and the monotreme fossil record. The geological timescale plotted against the monotreme fossil record (timescale not drawn to scale, e.g. the Mesozoic period is condensed for brevity and the Pleistocene is enlarged in order to accommodate taxon names). Source: AGSO Phanerozoic Timescale 1995. Numbers on the left indicate age in millions of years. Halocene fossils and living monotreme taxa are not included.
Gondwana (southern continents, including Australia). From the Late Triassic through Middle Jurassic (the middle part of the Mesozoic), mammals were to varying degrees primitive in form, and it appears from many aspects of their anatomy that many of these early mammals were not closely related to or ancestral to later Theria.

Therian mammals and their immediate ancestors appear to have had their origins in the northern hemisphere (Laurasia) from the Middle Jurassic to earliest Cretaceous, based on extrapolation from the fossil record. Theria comprises crown therians Marsupialia (metatherians) and Placentalia (eutherians), which are characterised by possession of tribosphenic teeth, as well as several more archaic taxa (pre-tribosphenic therians or Theria of metatherian-eutherian grade, e.g. Kielen-Jaworska et al., 1979). Holotheria, a more inclusive grouping, includes all mammals along the line leading to and including Theria: Kuehneotherium, symmetrodonts, dryolestoids, pre-tribosphenic therians and crown Theria (McKenna and Bell, 1997).

The oldest holotherian, Kuehneotherium, is known from the Late Triassic—Early Jurassic of Europe and was contemporaneous with basal mammals such as Morganucodon (McKenna and Bell, 1997). The fossil record for crown therians extends back to the Early Cretaceous. The oldest marsupials are known from the late Early Cretaceous of North America (approx. 100 myo; Cifelli, 1993). The oldest known eutherian (the beautifully preserved Eomaia scansionis) is older in age, from the middle Early Cretaceous of China (approx. 125 myo; Ji et al., 2002). If metatherians and eutherians are a monophyletic group, a ‘ghost lineage’ for metatherians would extend back at least to 125 mya and a common ancestor to crown Theria prior to that (Archibald, 2003). Diversification into most marsupial and eutherian orders appears, from the fossil record, to have occurred at about the Cretaceous/Tertiary boundary (65 mya, e.g. Archibald, 2003).

Although non-therian Mesozoic mammals had a wide range of dental forms, basal therians and immediate outgroups are characterised by possession of a tribosphenic tooth: both upper and lower molars have triangulated cusps that shear precisely (creating distinctive wear facets) and interlock when the jaw occludes (e.g. Crompton, 1971; Bown and Kraus, 1979). Possession of a similar tribosphenic pattern by the Early Cretaceous monotreme S. galmani prompted Archer et al. (1985) to describe it as a tribosphenic therian, against the prevailing view that monotremes were non-therian mammals. Mesozoic mammals can thus be more or less divided into middle Mesozoic non-therian mammals and later Mesozoic therians. Although at least one group of non-therian mammals persisted into the early Cainozoic (the rodent-like multituberculates), most were extinct by the end of the Late Cretaceous. The vast majority of post-Mesozoic (Cainozoic) mammals, therefore, were therians (marsupials and eutherians).

The classification of mammals by McKenna and Bell (1997), although contentious, is comprehensive and serves as a baseline reference for all described mammals or ‘near-mammals’. Mammalia (defined by McKenna and Bell as including the last common ancestor of living mammals plus all its descendants) includes monotremes, multituberculates, triconodonts and holotherians (McKenna and Bell, 1997). Taxa that have reached a post-cynodont level of organization but which lie just outside of Mammalia as defined above (retaining features such as accessory jaw bones in the lower jaw) are classed as basal Mammaliaformes (a clade inclusive of these base taxa plus Mammalia). Included in this category are Adelobasileus, Tricuspes, Kollikodon ritchiei (described as a monotreme by Flannery et al., 1995), sinoconodontids, morganucodontids, docodonts and haramiyids. Not included in McKenna and Bell (1997) are several recently discovered mammals from the southern hemisphere (all described after publication of the above volume) that are of great interest in the debate over monotreme affinities.

3. Mesozoic mammals from the southern hemisphere

In the past few years there have been several small mammal jaws with tribosphenic dentitions recovered from southern hemisphere Mesozoic fossil sites. These finds have sparked a wave of debate over their affinities and of the role of the southern hemisphere in Mesozoic mammalian evolution. Ambondro mahabo (Middle Jurassic, Madagascar: Flynn et al., 1999); Asfaltomylos patagonicus (Middle to Late Jurassic, Argentina: Rauhut et al., 2002); Ausktribosphenos nyktos (Early Cretaceous, Australia; Rich et al., 1997, 1999); and Bishops whitmorei (Early Cretaceous, Australia; Rich et al., 2001a) all possess the
distinctive, three-cornered molar teeth characteristic of tribosphenic mammals.

Analyses of these rather fragmentary fossils raise many questions, the most obvious being whether these taxa are therian or close to the therian line or whether they developed tribosphenic dentitions independently of therian mammals. All were originally described as holotherian taxa; A. nyktos and B. whitmorei were further identified as probable early members of Placentalia (Rich et al., 1997, 1999). The designation of A. nyktos and B. whitmorei as early eutherians, in particular, has been contentious. Several authors have expressed doubt over these proposed affinities. Possible links to monotremes (Musser and Archer, 1998; Archer et al., 1999; Luo et al., 2001) peramurids (Musser and Archer, 1998; Archer et al., 1999) and symmetrodonts (Kielan-Jaworowska et al., 1998) have been put forth, although strong evidence for affinities may be lacking.

Luo et al. (2001) combined all of these southern taxa into a new clade within Holotheria defined by possession of tribosphenic teeth with similar dental features (e.g. a ‘wrapping cingulum’ on the molar teeth). Australosphenida as conceived by Luo et al. includes the above taxa, Shuotherium (Kielan-Jaworowska et al., 2002) plus monotremes (based on the tribosphenic dentition of S. galmani). Northern tribosphenic mammals are likewise grouped together, as the clade Boreosphenida. Luo et al. (2001) argue for separate origins within each clade of similar (tribosphenic) molar forms: an earlier southern hemisphere radiation and later radiation of related mammals in the northern hemisphere. This taxonomy, however, has not had ready acceptance (e.g. Rich et al., 2002; Woodburne et al., 2003).

If these southern mammals are not close to or within Theria (i.e. if they are either ancient holotherians or unrelated to Holotheria), independent evolution of tribosphenic dentition must have occurred. This may not be as radical a notion as once thought (tribosphenic teeth having traditionally been considered the exclusive ‘hallmark’ of therian mammals). A recent study on the mechanics of producing appropriate dental forms found that ‘tribosphenic’ (three-cornered) teeth developed repeatedly in their trials (Evans and Sanson, 2003). Independent development in unrelated mammal groups of such a useful tooth form, one able to both slice and crush food, suggests that possession of tribosphenic dentition may not be a strong indicator of shared relationships as has traditionally been thought.

It must be noted that all of the above taxa apart from monotremes are only known from lower jaws and that the jaws of both A. mahabo and A. patagonicus are damaged. Resolution of the question of affinities of these southern taxa may have to await further discoveries, particularly of skull and skeletal material.

4. Mesozoic monotremes

The monotreme fossil record prior to the Cainozoic is sparse but significant. The first Mesozoic monotreme—in fact the first Mesozoic mammal from Gondwana—is the Early Cretaceous Steropodon galmani (Archer et al., 1985). S. galmani is Albian-Aptian in age (approx. 110 myo) and was recovered from opal-bearing sediments at Lightning Ridge in New South Wales. S. galmani is known only from a partial lower jaw that retains three molars (the complete molar row) and an alveolus for the last premolar.

Molar form in S. galmani is similar in some ways to that of Cainozoic toothed ornithorhynchids (Obdurodon species) as well as to tribosphenic therians. Both S. galmani and Obdurodon species have three lower molars; compressed trigonids; large talonids, and transverse shearing crests (Archer et al., 1985). On this basis, S. galmani was initially placed in Ornithorhynchidae (Archer et al., 1985). However, S. galmani has now been put into its own family, Steropodontidae, (Flannery et al., 1995) primarily because molecular data suggests a split between Ornithorhynchidae and Tachyglossidae postdating the Early Cretaceous occurrence of S. galmani (e.g. Westerman and Edwards, 1992 [Late Cretaceous–early Tertiary]; Retief et al., 1993 [mid-tertiary]; Kirsch and Mayrer, 1998 [mid-tertiary]). Morphologically, a family-level distinction is warranted (Musser, in press). Differences in molar form, jaw form and, therefore, in jaw function distinguish S. galmani from ornithorhynchids.

A second mammal from Lightning Ridge with uniquely bunodont teeth, K. ritchiei, has been described as a derived monotreme (Flannery et al., 1995). A partial maxilla referable to the species, currently under study, has features that suggest K. ritchiei may in fact not be monotreme but may instead represent a new type of mammal (Musser, in press; Musser et al., in prep.). For the present,
it may be best to consider *K. ritchiei* a basal mammal of uncertain affinities.

A series of toothless jaws from Lightning Ridge has also been recovered and is currently under study (Musser et al., in prep.). These jaw fragments range in size from rat-sized to cat-sized, with few close matches between the various specimens (suggesting a diversity of taxa).

An Early Cretaceous monotreme from a slightly older deposit, *Teinolophos trusleri*, has been recovered from coastal Victoria (the Flat Rocks locality; approx. 115 myo) (Rich et al., 2001b). *T. trusleri* was initially described as a eupantothere (Rich et al., 1999) but was redescribed as monotreme after subsequent cleaning of a tiny molar (the only tooth preserved) revealed similarities to the molars of *S. galmani* (Rich et al., 2001b). The Flat Rocks site has also produced the *A. nyktos* and *B. whitmorei* material (Rich et al., 1997, 1999, 2001a).

Comparatively high taxonomic diversity of Cretaceous monotremes suggests that the Early Cretaceous was a time of diversification for monotremes rather than a time of origin. This radiation, in concert with archaic anatomical features, suggests that monotreme origins were almost certainly deep in the Jurassic or even Late Triassic. Lack of rock outcrops of the right age hampers the search for the oldest monotremes. There are almost no Late Triassic, Jurassic, Late Cretaceous or early Tertiary vertebrate fossil sites known from Australia and there are only a handful of Early Cretaceous terrestrial vertebrate sites known. The critical Jurassic era—a period of approximately 150 million years—is almost a blank. Fossils from these transitional periods are needed in order to understand the depth and scope of the Mesozoic/early Tertiary monotreme radiation.

5. Cainozoic monotremes

The end of the Mesozoic period, marked by the extinction of the dinosaurs, ushered in the Cainozoic period. This period, from 65 mya to the present, includes the Tertiary (Paleocene, Eocene, Oligocene, Miocene and Pliocene epochs) and Quaternary eras (the Pleistocene and Holocene [present] epochs).

From the earliest Tertiary to the present, there are only two monotreme families known: Ornithorhynchidae and Tachyglossidae. Fossil material for both families—the semi-aquatic platypuses and the insectivorous echidnas—shows that all members of both families were highly specialised (although not to the extent seen in living monotremes) and that Cainozoic monotremes represent ‘variations on a theme’ within the families. Neither Cainozoic family, therefore, should be seen as representative of the subclass Prototheria any more than a whale should be seen as a representative member of Placentalia.

Based on anatomy as well as on evidence from the fossil record, Ornithorhynchidae is the older of the two families. Comparatively plesiomorphic features in ornithorhynchids lost in tachyglossids include dentition (albeit vestigial); greater development of the jaw and masticatory musculature; and certain skull features such as form of the ectopterygoid bone in the skull. Recovery of the South American platypus Monotrematum suggests that platypus-like monotremes have been part of the southern mammal fauna for at least 65 million years. The oldest echidna fossils recovered are only middle Miocene in age (15 myo; see below) at which point they had already developed specialised features (edentate beak; large, hemispherical cranium) characteristic of the family today. All Tertiary fossil ornithorhynchids had functional adult dentition, in contrast to *O. anatinus* that loses its vestigial molars at maturity. Most of the fossil ornithorhynchid material consists of isolated molar teeth although some cranial and postcranial material has been recovered.

The oldest known ornithorhynchid, *Monotrematum sudamericanum*, is a large, robust platypus from the early Paleocene of Patagonia, Argentina (Pascual et al., 1992a,b). The Paleocene date—approximately 62 mybp—postdates the end of the Mesozoic by a mere 3 million years. This Patagonian ornithorhynchid provides unequivocal evidence for terrestrial connections between South America, Antarctica and Australia through the end of the Mesozoic and into the Tertiary, suggesting that ornithorhynchids evolved within Australia or perhaps Antarctica, crossing to South America at some point during the latter part of the Cretaceous. Although only known from three molar teeth and the distal end of a femur (Pascual et al., 1992a,b; Pascual and Goin, 2002; Forasiepi and Martinelli, in press), *M. sudamericanum* clearly resembles later Tertiary *Obdurodon* species and there are no doubts as to its familial identity.

Subsequent to the record for *M. sudamericanum*, all ornithorhynchids are Australian. The oldest Australian ornithorhynchids are recorded from late
Oligocene deposits (approx. 25 myo; Woodburne et al., 1993) from the Lake Eyre region of central Australia. Two *Obdurodon* species have been recovered from this area: *Obdurodon insignis* (the first fossil platypus discovered: Woodburne and Tedford, 1975); and a second species (*Ob. sp. A*) from the Mammalon Hill locality. *Ob. insignis* is known from isolated teeth, a lower jaw fragment and partial pelvis (ilium) (Woodburne and Tedford, 1975; Archer et al., 1978) while *Ob. sp. A* is known from two upper molars. Both species are small in comparison to *M. sudamericanum* and to a younger *Obdurodon* species from Riversleigh in northern Australia, *Ob. dicksoni*. *Ob. dicksoni*, early to middle Miocene in age (20–15 myo), is known from a beautifully preserved skull in addition to isolated molars, premolars and dentary fragments (Archer et al., 1992, 1993; Musser and Archer, 1998). This large, sturdy platypus had a proportionately huge bill and flattened skull; these possibly derived features suggest that this platypus was not ancestral to later *Or. anatinus* but was perhaps a specialised northern offshoot (Musser and Archer, 1998).

Miocene ornithorhynchid fossils (all referred to the living *Or. anatinus*) are known from several sites in southeastern Australia (listed by Musser (1998). Interestingly, *Or. anatinus* fossils are known from several Tasmanian cave deposits recording human occupation and food consumption, suggesting that fat-rich platypuses may have formed an important part of aboriginal diets during glacial times in Pleistocene Tasmania (Marshall, 1992).

The echidna fossil record begins, as stated above, in the middle Miocene. Echidnas and their direct ancestors were certainly around well before this time but the edentate echidnas have left few clues to their origin. There are arguments suggesting echidnas may have been derived off the platypus lineage (primarily taken from genetic distance studies, see below) but an opposing argument could be raised on morphological and palaeontological grounds that echidnas evolved from an as yet unrecognised, more generalised monotreme type. The diversity of Cretaceous monotrems—one of which may have been ancestral to echidnas—lends support to this view.

The Miocene *Z. robustus* is known from a partial skull and associated humerus (originally described as the humerus of a giant platypus, *Or. maximus*) (Dun, 1895). The fossil site (a deep lead gold mine at Gulgong, NSW, now collapsed) was originally believed to be Pleistocene in age but has been redated as middle Miocene (13–14 myo; Woodburne et al., 1985). *Z. robustus* is missing the distal part of the snout, but in size and form the skull resembles that of Pleistocene long-beaked echidnas. A modest radiation of echidnas during the Pliocene and Pleistocene resulted in three distinct types: a large form with an upright stance (‘Z.’ hacketti from Western Australia); medium-to large-sized long-beaked echidnas similar to those found in New Guinea today (*Megalibgwilia* and *Zaglossus* species) and the smaller, somewhat more specialised Short-beaked Echidna, *T. aculeatus* (Murray, 1984; Griffiths et al., 1991).

*T. aculeatus* is known primarily from Pleistocene cave deposits (e.g. Naracoorte; Western Australia). Some Pleistocene *T. aculeatus* were up to 10% larger than living representatives; the species, therefore, experienced post-Pleistocene dwarfing, as did many other Australian mammals (such as the Grey Kangaroo, *Macropus giganteus*) (Murray, 1984). In all other respects *T. aculeatus* fossils are indistinguishable from the living species. *T. aculeatus* is today one of the most widely distributed Australian mammals, in part due to the abundance of its favoured prey of ants and termites.

6. The relationship between platypus and echidnas

The exact relationship between platypuses and echidnas is by no means clear. There are two possibilities, neither of which has solid evidence of support. Firstly, platypuses and echidnas may be only distantly related and echidnas may have been derived from an as yet unknown monotreme ancestor (a view given some support from the previously unrecognised diversity of Cretaceous monotrems). Secondly, it has been proposed that echidnas may be secondarily terrestrial, derived off the platypus line, making Ornithorhynchidae paraphyletic (e.g. Gregory, 1947; Pascual et al., 1992a,b; Archer et al., 1993). Many of the striking features shared between ornithorhynchids and tachyglossids are plesiomorphies (e.g. septomaxilla; ectopterygoid in the skull; most aspects of the shoulder girdle) while certain shared, derived features may have been present in Mesozoic monotrems as well (e.g. specialisations of the shoulder girdle; early fusion of skull bones; possibly electroreceptive capabilities). Therefore, many char-
acters are of little use in determining relationships between these two families.

As discussed, platypuses are almost certainly Cretaceous in origin while echidnas, on the basis of their fossil record, appear to be a mid-Tertiary group. The gap separating the oldest fossil records for the two families—a period of roughly 50 million years—may be an artefact of sampling or preservational bias (particularly for the edentate echidnas). However, it probably reflects the much greater age of ornithorhynchids. According to the fossil record (discounting for the moment the possibility that echidnas are derived platypuses), a family-level split must have occurred during the mid-Cretaceous or perhaps as long ago as the Early Cretaceous.

Most estimates of divergence times between ornithorhynchids and tachyglossids based on molecular data roughly agree on a Tertiary split. Estimates range from the end of the Mesozoic (Late Cretaceous-early Tertiary: Westerman and Edwards, 1992); latest Eocene (34 mybp; Janke et al., 2002) to late Oligocene-early Miocene (21–25 mybp, e.g. Kirsch and Mayer, 1998; Belov and Hellman, 2003a). Several of these divergence times are fairly close to each other in spite of the techniques employed (mitochondrian protein-coding genes; DNA–DNA hybridisation; immunoglobulin genes). If these dates reflect cladogenesis between families, echidnas must have split from Ornithorhynchidae because of the latter’s undoubtedly great age.

How difficult would it be to derive an echidna from an ornithorhynchid ancestor and how long might such a process take? Echidnas are superficially quite dissimilar to the platypus: to derive an echidna from an ornithorhynchid you would need to jettison aquatic specialisations (e.g. waterproof fur; wide bill; flattened form) before subsequently developing insectivorous, terrestrial specialisations (narrow, toothless beak; robust build; protective spines). Tertiary platypuses (as proposed echidna ancestors) certainly had most ornithorhynchid specialisations; they differ in degree but not in basic form from the living Or. anatinus (e.g. Musser and Archer, 1998). Some morphologists believe certain features in echidnas could have been derived from those in platypuses (e.g. the otic region of the skull; Gregory, 1947). Others believe that, in spite of their synapomorphies, differences between ornithorhynchids and tachyglossids are so profound that separation between the two must have occurred at a comparatively early point in monotreme phylology (e.g. Zeller, 1989, in a comparative study of development of the skull). This view supports the observation that highly specialised animals seldom give rise to new taxa, particularly those that then develop novel but dissimilar specialisations of their own. As with so many other questions about monotreme relationships, determination of the relationship between Tachyglossidae and Ornithorhynchidae may have to await discovery of additional fossil material.

7. ‘Molecules vs. morphology’: consensus or disagreement?

The advent of molecular systematics over the past decade has broadened the debate over monotreme relationships and added a potentially powerful tool to phylogenetic analyses. Data from genetics studies have been combined with new fossil discoveries, outlined above, to split researchers roughly into four camps: those that believe that monotremes do not share a close relationship to therians and that Theria forms a natural group to the exclusion of monotremes (a prototherian-therian dichotomy); those that believe monotremes are closely related to therian mammals (nested within Holotheria); those that believe monotremes have a special relationship to marsupials within Theria (the Marsupionta hypothesis); and those that feel the split between all three groups happened so close together in time that teasing apart their relationships will prove to be difficult (a trichotomous split).

7.1. Prototherian-therian dichotomy

Most mammals known from the Late Triassic through Early Cretaceous, as discussed, were not therian mammals; some are considered to be on the line leading to Theria (Holotheria sensu Wible, 1991) while the rest arguably have no close connection to therians (e.g. morganucodontids; docodonts; multituberculats). A dichotomous division between therian and non-therian mammals was proposed by Hopson (1970), who suggested a subclass (Prototheria) exclusive of therians and inclusive of Monotremata, Multituberculata, Triconodonta and Docodonta. These taxa were united by a synapomorphy of the braincase, a favourite region for taxonomic studies because it is a rela-
tively conservative part of the body (Hopson, 1970).

This traditional view—that monotremes had an origin remote from that of therians—takes into account the numerous plesiomorphic features retained by monotremes as listed above (e.g. Simpson, 1945, 1959; Kermack, 1963, 1967; MacIntyre, 1967; Hopson and Crompton, 1969; Hopson, 1970; Kermack and Kielan-Jaworowska, 1971; McKenna, 1975). Simpson (1945, 1959) considered it possible that monotremes originated from a separate therapsid line to that giving rise to therian mammals, in other words, a polyphyletic origin of mammals. MacIntyre (1967) proposed that monotremes be studied not as mammals but as therapsids and coined the term ‘quasi-mammals’ for monotremes and other basal mammals to emphasise their distance from ‘true or therian, mammals’. Possible links to multituberculates based on skull structure and ear region have been proposed (Kielan-Jaworowska, 1971; Wible and Hopson, 1993; Meng and Wyss, 1995; but see Miao, 1993). Although relationships between these poorly-known non-therian taxa and monotremes remain vague, there are strong morphological indications—such as jaw form and shoulder girdle morphology—that suggest monotremes belong to this basal group of mammals.

Losses of archaic features in crown-group therians are considered synapomorphies of these later taxa. A partial list of therian synapomorphies includes loss of the ectopterygoid bone in the skull; loss of the post-temporal canal in the skull; differing paths for the course of the trigeminal nerve (V); and possession of a fully coiled cochlea in the inner ear (e.g. Kermack and Kielan-Jaworowska, 1971). Possession of a fully tribosphenic tooth, with occluding protocone and specific wear patterns, is also characteristic of advanced therians (basal marsupials and eutherians). Many other characters—reproductive, cytological, internal and myological—separate living therians from monotremes (e.g. Griffiths, 1978; Renfree, 1993).

Several molecular studies support the view that there is a great genetic distance between monotremes and therians (e.g. McKenna, 1987; Retief et al., 1993; Kullander et al., 1997; Messer et al., 1998; Lee et al., 1999; Killian et al., 2001a,b; Belov et al., 2002a,b; Belov and Hellman, 2003b, summarised by Phillips and Penny, 2003). Methods include the use of amino acid sequences and large nuclear genes (including immunoglobulin genes). These large nuclear genes offer the strongest support to date for separation of therians from monotremes (Phillips and Penny, 2003).

7.2. Monotremes included within Holotheria

Some palaeontologists believe that, in spite of their many plesiomorphies, monotremes share a close relationship to therians as members of the infraclass Holotheria sensu Wible et al. (1995) (e.g. Kemp, 1982; Kielan-Jaworowska et al., 1987; Jenkins, 1990; Bonaparte, 1990; Kielan-Jaworowska, 1992; Archer et al., 1993; Luo et al., 2001, 2002). Kemp (1982) used the development of the chain of ear ossicles from the bones of the reptilian jaw as a synapomorphy linking monotremes and therians. His justification was based on the complexity of the ossicular system and his belief that such specific structures could only have evolved once. Kielan-Jaworowska et al. (1987) based their placement of monotremes on the dentition of *S. galmani*, which in some respects is similar to that of pre-tribosphenic therians. Bonaparte (1990) and Archer et al. (1993) thought certain South American dryolestoids might have dentitions similar to that of *S. galmani*. Arguing against holotherian affinities are the advanced features of symmetrical (early holotharian) skeletons as described above (Hu et al., 1997), and the archaic nature of the monotreme cranial and postcranial skeleton.

The only recent morphological study positioning monotremes within Theria itself (but not linking monotremes with marsupials) is that of Archer et al. (1985) based on the tribosphenic-like teeth of *S. galmani*. In addition to objections raised by Kielan-Jaworowska et al. (1987) on dental grounds, subsequent reanalysis of jaw structure in *S. galmani* (possible retention of a splenial along with a meckelian groove) argues against close therian affinities for this taxon (Musser, in press).

Some molecular studies support a close link between monotremes and therians (perhaps as basal therians or holotherians) without supporting Marsupionta (e.g. Phillips and Penny, 2003). Using mitochondrial DNA but recoding data and improving the fit of models to data, Phillips and Penny (2003) found that, contrary to other studies using mtDNA that support Marsupionta, a link to therians but not to Marsupionta was found.

7.3. The marsupionta hypothesis

A close relationship between monotremes and Australasian marsupials was first outlined by Greg-
ory (1947) in a lengthy anatomical study opposing the prevailing view that monotremes were archaic non-therian mammals. Gregory compares skeletal anatomy as well as internal or soft anatomy, finding many similarities between monotremes and Australian diprotodontian marsupials. He lists a number of features as synapomorphic (e.g. presence of a single deciduous premolar in upper and lower jaws; number and form of vertebrae; temporomandibular joint; embryonic chondrocranium; form of the malleus and incus; pouch; pelvis; manus and pes; and brain structure). He emphasises that these features are ‘diverse and disconnected fragments’ of a shared body plan (later specialisations in both groups obscuring the basic shared structural plan: his ‘palimpsest’ theory). On the basis of these supposed synapomorphies, he proposed that a new subclass of mammals be erected (Marsupionta, comprised of orders Marsupialia and Monotremata), to be the sister-group to eutherians (Subclass Monodelphia or Placentalia).

Kühne (1973) supports Marsupionta primarily on the basis of a cladistic analysis he performed on dental replacement patterns in various mammal groups (including Or. anatinus). Kühne claims that both marsupials and Or. anatinus share (1) replacement of only a single postcanine tooth (the single deciduous premolar of Gregory (1947) and the tooth designated as ‘dv’ by Green (1937)) and (2) a molar count of four. He contrasts this with tooth replacement in basal eutherians that primitively have three molars. Kühne bases his support on this single ‘synapomorphy’, a decision criticised by, among others, Parrington (1974) and Luckett and Zeller (1989), but declines to discuss other synapomorphies proposed by Gregory (1947).

Other morphological studies provide little support for Marsupionta; most studies testing the ideas put forth by Gregory (1947) instead offer strong support for a more distant relationship between monotremes and therians (e.g. Kuhn, 1971; Parrington, 1974; Marshall, 1979; Kuhn and Zeller, 1987; Zeller, 1987; Luckett and Zeller, 1989). Marshall (1979) conducted a cladistic analysis of numerous marsupial and eutherian characters (including features of both skeletal and internal anatomy, physiology and behaviour), finding no close links between monotremes and therians and no justification for the Marsupionta theory. Parrington (1974), in a critique of Marsupionta, discussed fundamental differences in jaw-opening musculature between monotremes and therians. Parrington’s argument, that the jaw-opener in monotremes (the m. detrahens) must have been developed in non-therians as the jaw joint was reorganising from the reptilian jaw joint, is of special interest in light of the possibly quite archaic jaw of S. galmani.

Luckett and Zeller (1989) investigated dental development in Or. anatinus specifically to test the Marsupionta theory, finding that the developmental pattern of tooth replacement was essentially very different in monotremes and marsupials and that ‘dv’ was not replaced in Or. anatinus (contra Kühne, 1973, 1977). Additionally, the dental formula of Or. anatinus is not known with certainty; Green’s dental formula is not universally accepted (it may be no more than ‘a reasonable guess’ (Marshall, 1979)). Finally, no toothed fossil monotreme with more than three molars has yet been recovered, discounting Kühne’s belief that monotremes, like marsupials, possess four molar teeth.

Several genetics studies have supported the Marsupionta hypothesis, albeit with varying degrees of confidence (Penny and Hasegawa, 1997; Zar doya and Mayer, 1998; Kumazawa et al., 1998; reviewed by Phillips and Penny, 2003). Strongest support for Marsupionta is given by Janke et al. (1996, 1997, 2002) using mitochondrial protein-coding genes. Weak support for Marsupionta is given using other techniques (e.g. amino acid sequences (Toyosawa et al., 1998) and DNA to DNA hybridisation (Kirsch and Mayer, 1998)).

Some of the divergence estimates between monotremes and therians using techniques that support Marsupionta appear to be especially at odds with the fossil record. Janke et al. (1997, 2002) predict divergence times in the Early Cretaceous, where the fossil record records a diversity of monotreme taxa. One estimate by Janke et al. (2002)—the base of the Aptian (115 mybp)—is the stated age of an already specialised monotreme, Trusleri (Rich et al., 1999, 2001).

7.4. A trichotomy

Few palaeontologists discuss the possibility that a split between monotremes, marsupials and eutherians happened almost simultaneously (a trichotomous split) and that it is difficult to differentiate between these taxa on morphological grounds. Most morphology-based phylogenetic analyses instead suggest links to particular taxonomic
groups, many of which have hotly-debated affinities and obscure origins themselves. Conceptually, a hypothesis based on such a trichotomy appears to be more of a topic of debate within genetic ranks, where chronological estimates of divergence times are highly significant.

The advent of genetics-based phylogenies raises several questions that palaeontologists and morphologists need to address. How important are morphological constraints? How robust is morphological data and how subject is any area of morphology to convergence or independent acquisition of key traits? How closely does the fossil record need to be taken into account? Where are its weaknesses?

In turn, molecular scientists need to be informed about the breadth and volatility of the morphology-based debate over relationships. It can be seen from this discussion that results from morphological investigations vary considerably depending on which anatomical systems are being investigated. Results are also dependent on individual beliefs about convergence, independent evolution or relative importance of specific features. New fossil discoveries may shift the balance in favour of one hypothesis or another and debate is sure to arise over any new discovery. However, it does appear that solid progress is being made on all fronts: morphological, palaeontological and molecular.

8. Future directions

These are exciting times for monotreme palaeontology, debate notwithstanding. The success of the excavations at Flat Rocks and Lightning Ridge are providing impetus to continue work at these very promising fossil localities. Work is also continuing at other potential mammal-bearing deposits of Early Cretaceous age, particularly in Queensland. The search for critical Late Triassic, Jurassic and early Tertiary localities will be a priority; these ‘black holes’ in the monotreme fossil record need addressing. Finally, comparisons of monotreme fossil material need to be made with Mesozoic mammals from both the northern hemisphere and from non-Australian components of the old Gondwana (South America, Madagascar, India, Africa and Antarctica).

9. Summary

1. Analysis of recent fossil monotreme material strongly suggests that monotremes are an ancient group more closely allied with Late Triassic and Early Jurassic mammals than with Late Jurassic–Early Cretaceous mammals (in particular, therian mammals). Living monotremes are highly derived, relict members of what had been a more generalised and more diverse subclass of mammals, with an origin possibly as distant as the Late Triassic but almost certainly not later than the Middle Jurassic. The two surviving monotreme families—Ornithorhynchidae and Tachyglossidae—are far removed from their origins, have undoubtedly lost or altered many ancestral features and should not be seen as representative of basal monotremes.

2. Monotremes are morphologically distant from therian mammals; the suite or mosaic of primitive, ‘mammalian’ and derived features that are unique to monotremes are far removed from comparable features in therians and suggest a remote separation between these two lineages. Development of tribosphenic dentition in monotremes, in other southern hemisphere Mesozoic mammals and in therian mammals may have been a convergent development not indicative of shared ancestry.

3. The monotreme fossil record illustrates that, at the very least, Mesozoic monotremes spread from Australia through Antarctica to southern South America (the landmasses known as East Gondwana from the Early Cretaceous through early Tertiary). Relationships to newly discovered Mesozoic mammals from the southern hemisphere (Asfaltomylos from the Jurassic of Patagonia; Ambondro from the Cretaceous of Madagascar; Ausktribosphenos and Bishops from the Cretaceous of Australia: (Rauhut et al., 2002; Flynn et al., 1999; Rich et al., 1997, 1999, respectively) are unclear and subject to debate, but offer emerging insights into a uniquely southern radiation of mammals during the Mesozoic of which monotremes were an important part.

4. Based on both the fossil record and morphology, platypuses appear to be a much older family than echidnas. Platypuses may have found their ‘niche’ as semi-aquatic insectivore/carnivores during the Mesozoic, and thus are one of the...
most ancient of living mammalian families. Although much of the genetic evidence suggests that a platypus/echidna split occurred comparatively recently (middle Tertiary), this would make echidnas ‘derived platypuses’. Morphological constraints make it difficult (although perhaps not impossible) to derive tachyglossids from an ornithorhynchid ancestor.

5. The longevity of monotreme mammals is extraordinary: if anatomical and palaeontological evidence for a basal position for monotremes is supported, this subclass of mammals is conceivably close to 200 million years of age (late Triassic–Early Jurassic). Closest competitors would be the multituberculates, which have a record spanning 160 million years (before becoming extinct in the early Tertiary). Theria, whose level of organization is similar to that of other Late Jurassic–Early Cretaceous mammals, is by far a much younger group. Monotrems may have survived in the comparatively isolated, ‘peninsular’ eastern limit of Gondwana in part because of lack of competition and in part because of successful specialisations that enabled utilisation of habitats and resources under-utilised by marsupial and/or other vertebrate taxa.

6. Genetics data using certain techniques (in particular, large nuclear genes) agree roughly with evidence from the fossil record but, conversely, results using other techniques (e.g. mitochondrial DNA) are in disagreement with palaeontological data. It is imperative for molecular biologists and palaeontologists to understand results from both disciplines and acknowledge that new techniques, fossil discoveries and reanalyses of described materials will continue to challenge orthodoxies, assumptions and the phylogenetic position of monotremes.

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References


CHAPTER 2

Furry egg-layers: Monotreme relationships and radiations

A. M. Musser

Published in:


A manuscript of the published paper follows.
Chapter 2 (‘Furry egg-layers: Monotreme relationships and radiations’) was written as a book chapter for *Evolution and Biogeography of Australasian Vertebrates* (in press; edited by J. Merrick and G. Hickey). This book is a revision of *Vertebrate Zoogeography and Evolution in Australasia* (1984) and will be a comprehensive reference on the biology and evolution of all Australasian vertebrate groups. Authors (recognised specialists in their fields) were invited to contribute chapters to this edited, peer-reviewed text. Editors requested a format that limited citation of references to those deemed especially significant; references for many statements of fact are therefore not cited, as is done for papers published in scientific journals.

This paper provides a detailed synopsis of the anatomy (skeletal and soft anatomy), physiology, taxonomy and field biology of living monotremes; a review of the fossil record for all known monotremes (Ornithorhynchidae; Tachyglossidae and ‘Steropodontidae’ [including *T. trusleri*]); a discussion of the biogeography of the Australian region through the known temporal range of Monotremata; and a discussion on other gondwanan mammals and how these relate to Monotremata.

Although this chapter is generally a review of what is known to date about Monotremata from previously published sources, several original observations on material investigated for this thesis have been included (some points taken from abstracts of papers given at conferences but not yet published as papers).

This account was written in 1999-2000; however, there have been delays in publication and the book is still ‘in press’. This therefore means that some of the information presented in this paper will be out of date or superceded by new or revised information by the time it is published. Significant new fossil discoveries that are not covered in this paper include XX and the discovery of possible accessory jaw bones (=compound lower jaw) in an archaic monotreme (*Teinolophos trusleri*: Rich *et al.*, 2005).


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INTRODUCTION

Living monotremes - the egg-laying platypus and echidnas - have intrigued and confounded zoologists and palaeontologists since they were first brought to the attention of western science in the late 1700s. No other living mammals are oviparous, and none share other monotreme features that include a bony bill or beak, the ability to detect electrical fields of prey, and an ancient type of shoulder girdle that would be at home in long-extinct reptiles (cynodonts) that were the ancestors of living mammals. Monotremes today survive only in Australia, New Guinea and some offshore islands, but they have an ancient history that almost certainly predates the Cretaceous and, geographically, spans at least the eastern part of the great supercontinent of Gondwana.

'Monotremata' comes from the Greek 'mono', meaning 'one', and 'tremos', or 'hole, referring to the single orifice (cloaca) in monotremes for passage of both reproductive products (sperm and eggs) and excretory products (urine and faeces). Although there are other mammals that can be considered cloacate, none have the comparatively primitive 'reptilian' reproductive system that monotremes do. Living monotremes share numerous primitive ('plesiomorphic') characters; however, monotremes can't be said to represent primitive, or Mesozoic, mammals in any general way. Both the amphibious platypus and terrestrial, insectivorous echidnas are so specialised for their particular niches that they bear little resemblance to an archetypal Mesozoic mammal.

At present three monotreme families are recognized: an extinct Early Cretaceous family (Steropodontidae) that includes Steropodon galmani from Lightning Ridge and (provisionally) Teinolophos trusleri from Flat Rocks, Victoria; the platypuses (Ornithorhynchidae); and the echidnas (Tachyglossidae). A second Early Cretaceous mammal, Kollikodon ritchiei (Kollikodontidae; Flannery et al. 1995), is described as a highly derived bunodont monotreme; however, further analysis casts doubt on this interpretation and suggests that, for the present, K. ritchiei should be considered a basal mammal of uncertain affinities (Musser et al. in prep.).

In a recent classification of all mammals above the species level, extant or extinct, monotremes were elevated from an order (Monotremata) to a subclass (Prototheria). Platypus-like monotremes are grouped together at the ordinal level (order Platypoda; families Steropodontidae and Ornithorhynchidae) as are the echidnas (order Tachyglossa; family Tachyglossidae) (McKenna and Bell 1997).

This recent revision has not yet been incorporated by many researchers in the field and, unfortunately, dispenses with the well-known term Monotremata - using the term Prototheria. While an elevation in rank is justified, my objection to Prototheria rests on the fact that Monotremata is recognized as a monophyletic group and is a widely-used, descriptive term; Prototheria is not descriptive and has traditionally included a wide range of unrelated, non-therian mammals. The term Monotremata is used in this account.
There are many questions raised by the enigmatic monotremes. How ancient are they? How far did they roam? Without a dental record, can we determine where the edentate echidnas came from? To which of the known mammal groups living or extinct are monotremes most closely related? In fact, there is debate as to whether monotremes are really mammals at all, and about their phylogenetic position; placement in the mammalian family tree differs greatly depending on the researcher's particular focus. This chapter discusses the morphology and palaeontology of monotremes, reviews the historical debates on phylogenetic affinities and considers developments of the past fifteen years.

Many aspects of monotreme morphology, relationships and biogeography have been studied previously. For example, Griffiths (1978) discussed morphology and physiology in detail, while Grant (1995) and Augee and Gooden (1997) provide excellent summaries of anatomy, physiology and lifestyles of extant species.

LIVING MONOTREMES

The platypus, Ornithorhynchus anatinus, is the only surviving member of the Ornithorhynchidae. Ornithorhynchids are considered to be more plesiomorphic than tachyglossids because they have a much longer palaeontological record and appear to have more ancestral character states for a number of features - see Musser and Archer (1998).

The geographical range of Or. anatinus extends along the east coast of Australia from Cooktown (south of Cape York) to Tasmania. The platypus primarily feeds on a range of aquatic invertebrates, sifted from bottom sediments, but will on occasion take larger prey such as frogs. Platypuses are generally crepuscular, usually feeding at dawn, dusk or through much of the night. They shelter and raise their young in burrows dug into banks along rivers and streams.

The platypus has often been described as an odd collection of disparate animal parts. No one that has ever held a living platypus or watched one swim in a stream or billabong, however, could fail to be impressed by the natural beauty and elegant design of this small, amphibious mammal. The body is streamlined, almost torpedo-shaped, with short but powerful limbs, a flat, tapered tail and, of course, the inimitable bill. Propulsion is accomplished by alternate strokes of the forelimbs while the hindlimbs and tail act as rudders. Each hand, or manus, is equipped with extensive, fan-shaped webbing that aids in swimming but which is retracted under the forepaw when the platypus is moving overland or burrowing. Short, dense, waterproof fur, ranging from light to very dark brown, covers the body. Adult males have hollow ankle spurs connected to venom glands over the thighs although female platypuses lose their spurs on reaching adulthood. The sharp spurs are primarily used by males in combat during the breeding season.

The bill of the platypus is an extraordinary sense organ. The underlying structure is formed by the bones of the snout and shape is given to the bill by an extensive sheet of cartilage. The bill is covered by soft, sensitive skin. Platypuses, which feed and mate underwater, habitually keep normal senses 'shut down.' The eye and ear are housed together in a horizontal groove that can be tightly shut, keeping water from entering but effectively rendering the platypus blind and deaf. Flaps of skin seal the dorsally located nostrils when swimming, shutting down the normal mammalian sense of smell (although the platypus does have Jacobson's Organ in the roof of the mouth, a more reptilian odour-detecting system). The bill is imbued with thousands of tiny specialized pores (or rod organs) that are either electroreceptors or touch (mechano-) receptors and together create a unique dual
sensory system (Pettigrew et al., 1998). Using these cutaneous receptors, the platypus can react to both touch and to the small electric stimuli given off by active prey like a crayfish. This highly sophisticated system - shared with echidnas but most developed in the platypus (Scheich et al. 1986) - has been perfected over millions of years and has surely been instrumental in the success of this ancient group. It is a completely different sensory system from those of living therian mammals, which have developed vibrissae (or whiskers) on the face but have not developed electoreceptive capabilities.

Like the edentate echidnas, the platypus has developed a unique solution to the loss of true teeth in the adult. Juvenile platypuses have vestigial molar teeth that are retained until the platypus begins to feed on its own soon after leaving the burrow. Adults masticate their food with flat dental pads of keratin that form over the molar toothbeds. The dental pads mimic the teeth they've replaced: the upper dental pads are subdivided into two sections, corresponding to the two upper molars in Tertiary ornithorhynchids (Figure 5I), while the lower dental pads additionally have a small posterior segment that corresponds to the small, button-like lower third molar in Tertiary platypuses. The platypus has an unusual tongue structure; two keratinous spikes, at the anterior end of a round pad at the base of the tongue, assist mastication. Two anterior, longitudinal keratinous ridges substitute for an anterior dentition, acting as grasping structures to hold active prey.

Platypuses are still fairly common over their range (Figure 5M) although there have been local declines and extinctions since European settlement. Much of their habitat has been altered or destroyed through clearing and grazing, however, and they are currently classed as 'potentially vulnerable'.

**Echidnas**

Echidnas (family Tachyglossidae), sometimes called spiny anteaters or porcupines, have taken a much different evolutionary path. They have lost all vestiges of a dentition (lacking even a dental lamina). Their rounded, bird-like crania end in tubular bony beaks and their long tongues are coated with sticky saliva to trap their invertebrate prey. Echidnas are covered by keratinous spines as well as fur. They have dome-like bodies and their skeletons are much more robust than that of the platypus. The forefeet have wide, spade-like claws used in digging. The hind feet are rotated outward, giving the echidnas a peculiar stance. Long claws on the hind feet are used for grooming between the spines rather than for digging. Echidnas have spurs on the ankles, but the venom apparatus is non-functional and distribution of the spurs between males and females is less consistent (female echidnas occasionally have spurs while they are sometimes absent in males). Like the platypus, echidnas have both electoreceptors and touch receptors in the skin of their beaks.

The phenomenon of morphological convergence can be seen in the way tachyglossids have independently evolved many of the specializations seen in placental anteating mammals. Particularly striking are the elongation of the rostrum into a bony, toothless beak and the correlated reduction of the lower jaw seen in both tachyglossids and in South American anteaters (xenarthrans). Both groups have long, extensible tongues coated with saliva and large front claws to dig into ant and termite mounds. In an interesting parallel, both monotremes and some xenarthrans have retained the septomaxilla on the snout, a small, splint-like bone otherwise seen only in reptiles and some early mammals.

Echidnas use their tongues for both the capture and mastication of prey. The short-beaked echidna, *Tachyglossus aculeatus*, feeds primarily on ants and termites. The distal portion of the sticky tongue is highly mobile, darting in and out of termite mounds or ant nests at lightning speed. *Zaglossus* species, long-beaked echidnas from New Guinea, feed primarily on oligochaete worms and
insect larvae although they also feed occasionally on ants and termites. *Zaglossus* species have spines in a deep groove on the distal end of the tongue; these sharp hooks are used to snare worms. The long palates in both types of echidna have transverse keratinous spines that work against opposing spines on the posterior part of the tongue to grind the invertebrate prey into a paste, which is then swallowed.

FIGURE 2A: The eastern New Guinea long-beaked echidna *Zaglossus bartoni* illustrates the basic monotreme body plan. Monotremes have bony beaks or bills covered by sensitive skin, small eyes, compact bodies with short, splayed limbs and hind feet that are rotated outwards. Echidnas have long, tubular beaks, vertical aural slits rather than external ear pinnae, and spines covering the body. Living long-beaked echidnas have long, downcurved beaks and a sparse covering of spines on the body.

The two living genera are distinguished primarily by the length and shape of the beak and by the distribution of spines covering the body. *T. aculeatus* is found in both Australia and New Guinea. It has, as its name implies, a relatively short beak that may be either straight or slightly upturned but which does not have a marked downward curvature. Its spines are long, sharp and usually black-tipped, and cover the back and tail. Long-beaked echidnas today are found only in New Guinea (Flannery and Groves, 1998) although similar echidnas are known as fossils from the Australian mainland. *Zaglossus* species have proportionately longer beaks with downward curvatures of varying degrees, and have smaller, less numerous spines than *T. aculeatus*. In some *Zaglossus* the spines do not cover the back and some *Z. bruijnii* have spines on the belly as well as on the back. *T. aculeatus* is a small echidna of about 40 cm in length. *Zaglossus* species are much more variable: the single known specimen of *Z. attenboroughi* is about the size of a typical *T. aculeatus*; *Z. bruijnii* is of medium size; and the variable *Z. bartoni* reaches nearly 1 metre in length in the eastern part of its range (Flannery and Groves, 1998).
*T. aculeatus* is quite possibly the most widely distributed mammal on the Australian continent. It is found in suitable habitat throughout Australia (including Tasmania) and also occurs on offshore islands such as Kangaroo Island and King Island. In New Guinea, unfortunately, neither its range nor its habits are well documented. The status of the several named subspecies is also questionable; Augee and Gooden (1997) believe that two forms - the mainland form (which includes New Guinean *Tachyglossus*) and the distinctive Tasmanian form - probably deserve subspecific status.

Taxonomy of New Guinea *Zaglossus* has recently been revised by Flannery and Groves (1998), who base their study on reexamination of disputed features (e.g., the number of claws on the feet and certain cranial features) and on statistical analyses of these features plotted against the geographical ranges of the known specimens. Prior to this study it was generally accepted that *Z. bruijnii* was the sole living, although variable, species of *Zaglossus*. In a nutshell, the species from western New Guinea (including Salawati) that normally has three clawed digits on each forefoot is considered to be *Zaglossus bruijnii*, the type species for the genus. *Z. bruijnii* occurs from mountain peaks to sea level (on the low-lying island of Salawati) although *Zaglossus* is usually considered a mountain-dweller. A second species of *Zaglossus*, normally with five clawed digits on each forefoot, has been put into the resurrected species *Z. bartoni*, with four subspecies (distinguished on size and proportional differences along the east-west morphocline) proposed by Flannery and Groves (1998). *Z. bartoni* occupies the mountain summits of the central cordillera and the Huon Peninsula. The rarest *Zaglossus*, the newly discovered *Z. attenboroughi* from the high, remote peaks of the Cyclops Mountains, differs from *Z. bruijnii* and *Z. bartoni* in having: a relatively short, straight beak; small size, and fur of a different colour and texture. It has five claws on the forefoot. Superficially *Z. attenboroughi*, with its small size and short, straight beak form, resembles a cross between *Zaglossus* and *Tachyglossus*.

*T. aculeatus* appears to be an echidna success story; the ants and termites it usually feeds on occur all over the Australian continent, and its numbers currently appear to be stable. Its status in New Guinea is not known, although it may be hunted for food. Species of *Zaglossus*, however, are in greater danger and *Z. attenboroughi* may already be extinct. *Z. bruijnii* and *Z. bartoni* are often taken by hunters and some subspecies of *Z. bartoni* in particular should be considered endangered. Much of New Guinea, however, remains as wilderness, raising hopes for survival of these unique mammals.

**MONOTREME MORPHOLOGY**

Monotremes have a mix of primitive features in combination with very specialised features called, appropriately, a mosaic; this confounding but fascinating situation in the monotremes has made the phylogenetic placement of these 'living fossils' an ongoing and hotly debated exercise. The concept of mosaic evolution is intriguing: a group of mammals may have branched off the tree at a very early stage but may have evolved highly sophisticated adaptations. In addition, they may have convergently acquired traits that define more advanced mammal groups. Certain recent fossil discoveries display such mosaic complexes; for example, the eutriconodont *Jeholodens jenkinsi* (described by Ji et al., 1999) has an advanced shoulder girdle but a primitive pelvis and hindlimb.

The phenomenon of mosaic evolution underscores the need to look at monotreme morphology as a unit, not limiting examinations to any single system such as dental structure or genetic data. Investigations on specific areas such as the ear region (Meng and Wyss, 1995), basicranium (Wible and Hopson, 1993) and braincase (e.g., Kielan-Jaworowska, 1971) in addition to molecular studies (e.g., Westerman and Edwards, 1992) have been of enormous help in clarifying the relative placement of these features in comparison to other mammal groups. However, these studies have also
resulted in a blizzard of cladograms with placement of monotremes in every conceivable position along the line (see Johanson, this volume). Complicating matters, many of the earliest mammals are known primarily from teeth and jaws -
critical features such as the development of the skull or shoulder girdle are unknown for many key groups.

**Skull structure**

Ornithorhynchids and tachyglossids share many cranial features although they differ in details such as bill or beak shape. The majority of these characteristics are primitive features although certain specializations are shared between the two. To explain the many plesiomorphic features in monotremes, a palaeontologist must see these as either retained (never lost) within the lineage, or as ‘reversions’ – features secondarily reverted back to after having been dispensed with by the group.

A partial list of plesiomorphic cranial features in living monotremes includes: a post-temporal canal linking the temporal fossa to the area above the ear (also present in stem reptiles, mammal-like reptiles and in some extinct mammals); an open ear region without an auditory bulla, but with primitive configurations of the incus, malleus and stapes; a semi-coiled cochlea (about 270º; in contrast to the cochlea of living therians, which is fully coiled at 360º); a septomaxilla in the snout (a large bone on the rostrum that is found in reptiles, therapsids, some early mammals and some living xenarthrans); and ectopterygoid bones on the ventral surface of the skull (possibly remnants of the reptilian pterygoids). Specializations include: the early fusion (and obliteration) of skull sutures; elongation of the snout into a bony bill or beak; extensive development of the trigeminal nerve to service the sensitive, electroreceptive beak (reflected in numerous foramina through the skull and rostrum); and loss of functional teeth in adult living monotremes.

Features of the jawbone (dentary) in living monotremes are difficult to assess because of their extreme specializations. The angular and coronoid processes are either reduced or absent. An internal mylohyoid process just above the mandibular foramen, however, appears to be a unique development in ornithorhynchids. The dental canal carrying nerves to the snout is large although it is more developed in ornithorhynchids than in tachyglossids.

The skull of the platypus (Figure 2) does not look like that of any other mammal, past or present. The wide, flat bill is formed by rostral projections of the septomaxilla, maxilla and premaxilla. A small, dumbbell-shaped bone (os paradoxum) is sandwiched between the prongs of the bill. Its purpose isn't clearly understood and it isn't present in any other mammal, but the bilateral openings of Jacobson's Organ lie in the constriction between the expanded sections of this odd bone. The dorsal nostrils open anterolaterally to the os paradoxum. Large foramina on the bill carry branches of the trigeminal nerve that service the electroreceptors and mechanoreceptors. The braincase is large and inflated although proportionately it is smaller than in echidnas. The zygomatic arches are thin and close to the skull, reflecting the reduced jaw musculature in this ‘edentulous’ mammal. Flat, perforated ‘toothbeds’ formed by expansion of the maxillae form the bases of the dental pads.
The ventral aspect of the platypus skull illustrates a number of specialized features. The palate is very long and perforated by large foramina for the trigeminal nerve, as is the basicranium. Keratinous dental pads substitute for a functional molar row. Two longitudinal ridges of hardened epithelium, midway between the dental pads and the tip of the bill, take the place of an anterior dentition and are used to hold and masticate prey. Some skull features are plesiomorphic: the tympanic region is completely open and no bulla is formed; in life, a cartilaginous ear funnel terminates over the horse-shoe-shaped tympanic bone supporting the tympanum as it may have in therapsid reptiles (Crompton, 2001, personal communication). Thin, plate-like ectopterygoids, sutured to the palatines, abut the tympanic bones.

The ephemeral molars of *Or. anatinus* were first described by Simpson (1929) and in greater detail by Green (1937). Green determined the dental formula to be I0/1-?5 C1/1 P1-2/1-2 M1-3/1-3 and that the last premolar, first upper molar and all three lower molars erupt. The small molars, which do not fill the tooth bed, vary in structure between individuals. The unique triangular blade systems, cuspule development and shallow roots seen clearly in fossil ornithorhynchids can just be discerned in the degenerate *Or. anatinus*, which is distinguished from Tertiary ornithorhynchids by its lower crowns, greater development of cuspules, more obliquely-oriented lophs, more dentate cingula and loss of the anterior cingulum on M1/ (Woodburne and Tedford, 1975).

In lateral view (Figure 5B (iii)) the flattening of the skull and the downward deflection of the bill are clearly seen. The dentary has both anterior epithelial ridges and posterior dental pads that ‘occlude’ with their counterparts on the skull. The articular condyle is fairly well-developed, but the coronoid process has been lost and the angular process may or may not be present in *Or. anatinus*. The masseteric fossa is developed into a deep pocket. The small eye is placed high on the skull, an adaptation common in aquatic animals that float at the water’s surface. The reptilian post-temporal canal passes between the skull and the posteriormost part of the zygomatic arch.

The short-beaked echidna (*Tachyglossus aculeatus*, Figure 5C) has a comparatively short, straight beak without a marked curvature, while long-beaked echidnas have proportionately longer and more recurved beaks. The dorsal nostrils open through the median space (interseptomaxillary fenestra) between the rostral prongs. The foramina for branches of the trigeminal nerve to the skin of the bill are more numerous than in the platypus but much smaller because of the reduced role that electro- and mechanoreceptors play in the sensory apparatus of echidnas. The surprisingly large braincase is usually teardrop-shaped in *T. aculeatus*. (Figure 5C).

The palate in echidnas is even longer than in the platypus; the palate of *Z. bruijnii* is said to be the longest palate known in mammals. Robust ectopterygoids fused to the posterior palatines overhang the ear regions to create a protective shelf although this can’t be considered a substitute for an auditory bulla. Tympanic bones connected to the ear ossicles (missing from Figure 3) complete the middle ear. The footplate for the stapes is circular in monotremes, a plesiomorphic feature. There is no postglenoid process since the weak lower jaws have no need for buttressing.

The small, subterminal mouth opens ventrally and the mandible is bound to the upper jaw by ligaments in life, creating a ‘tunnel’ for the extensible tongue. The jaws cannot open any wider than the circumference of the tongue. The echidna mandible, perhaps comparatively the weakest lower jaw in Mammalia, has been reduced to two thin, tapered rods joined loosely at the symphysis. The angular process and articular condyle are poorly developed and the coronoid process is vestigial. The masseteric fossa has been lost entirely; the lower jaws do not operate in an up-and-down orthal movement. Instead, they twist about their long axes to open the mouth in a unique jaw-opening mechanism known only in echidnas (Murray, 1978a).
Postcranial skeleton

The postcranial skeletons of the platypus and echidnas are similar in many ways. Most of the shared features are plesiomorphic, although living monotremes share specializations for digging (fossorial adaptations). The platypus is a more lightly-built animal with some aquatic specialisations (especially in the flattened, streamlined body form) while the echidnas are robustly built diggers.

Monotremes have a sprawling stance where the limbs extend horizontally from the body. The humerus projects from the body at least 45° and the hand (manus) normally contacts the ground lateral to the shoulder girdle (Sereno and McKenna, 1995). This posture is probably a fossorial adaptation developed from a primitive mammalian body plan rather than a reptilian stance (Jenkins, 1973). Limbs held at such an angle do result in a more reptilian mode of locomotion where the body undulates from side to side. In contrast, many Mesozoic mammals and all modern mammals (unless specialised) hold their limbs closer to the midline of the body (a parasagittal posture) which permits a faster, more 'mammalian' gait.

The monotreme vertebral column is plesiomorphic in several respects: the cervical vertebrae bear ribs (as in reptiles); the vertebrae are variable in number; and more of the dorsal vertebrae bear ribs than in therian mammals. The ribs do not have a head or tubercle but attach directly to the bodies of the vertebrae. Monotremes have large, flat, overlapping sternal ribs (ossified as in birds) that are separated by cartilage from the ribs attaching to the vertebrae. The sternal ribs, therefore, do not attach to the sternum by cartilage, as in other quadrupeds, but by bone. Echidnas have a xiphisternum while the platypus does not.

The shoulder girdle in monotremes (Figure 5E) is basically similar to that of therapsid forebears and basal mammals (mammaliaformes) although some elements (i.e., the bones of the sternum) are similar to those of more advanced mammals (Klima, 1973). A series of extra bones - a median, T-shaped interclavicle, procoracoids (also called precoracoids or epicoracoids, derived from the anterior coracoid of therapsids) and metacoracoids (derived from the posterior coracoid of therapsids) - are present. These bones buttress the clavicle and scapula, the only elements of the therapsid shoulder girdle still retained by other living mammals (at least as adults; the chondral part of the interclavicle can be seen during embryological development in marsupials and placentals) (Klima, 1973). The scapula is plesiomorphic in that the flat anterior plate of bone (the supraspinous fossa) for origin of m. supraspinatus and a central spinous process, as in therian mammals, has not been developed. The addition of the supraspinous fossa and its attached musculature in therians keeps the shoulder stable when running, an asymmetrical gait not possible with the rigid shoulder structure of monotremes (Bramble and Jenkins, 1989). The lateral orientation of the glenoid and the buttressing of the coracoid, interclavicle and clavicle are considered to be fossorial specializations.
FIGURE 2D: The skeleton of the Short-beaked Echidna *Tachyglossus aculeatus*. The robustly-built *T. aculeatus* has a bird-like skull, compact, domed body, large hands with spatulate digging claws, short tail, and an opening in the acetabulum. Like the platypus, echidnas have cervical ribs (on the vertebrae of the neck), a splayed posture, a therapsid-like shoulder girdle, sternal (costal) plates, epipubic bones, and outwardly-rotated hind feet. Abbreviations: cerv. r., cervical rib; cl., clavicle; ep., epipubic bone; fib., fibula; hum., humerus; ob. f., obturator foramen; pat., patella; perf. acet., perforated acetabulum; rad., radius; scap., scapula; ul., ulna. From Augee & Gooden 1997.

Interclavicle, procoracoids and metacoracoids appear to have been lost or greatly reduced in nearly every mammal group for which the shoulder girdle is known. Recently discovered skeletal material for certain key early mammal groups have shown surprisingly advanced shoulder girdle morphologies (Sereno and McKenna, 1995; Hu *et al.*, 1997; Ji *et al.*, 1999). Although details differ, all of these mammals have jettisoned most of the extra bones and rigid structure retained in monotremes. Loss of these bones allows for a more mobile shoulder girdle articulation. The monotreme shoulder girdle is probably their most perplexing anatomical feature. However, it has been a useful retention in the fossorial monotremes: the extra bones provide extensive areas for attachment of pectoral musculature that assists in both digging and swimming, and the rigidity of the girdle helps keep the animal stable during these activities.

The forelimbs in both living monotreme families are well-developed, particularly in tachyglossids. The short, broad humerus is twisted across the shaft and is expanded at both ends for the attachment of robust forelimb musculature, as in therapsids, many archaic mammals and placental moles. The proximal end of the ulna is expanded and the ulna articulates with the humerus via a condyle; this structure, modified from the spiral ulnar condyle of cynodonts, is most similar to the elbow of some Jurassic mammals (Jenkins, 1973). Therian mammals have developed a groove between the ulnar and radial condyles, forming a trochlea (an indication of parasagittal posture). A humerus of Early Cretaceous age - the first mammal from the Victorian Cretaceous - appears to be that of a monotreme; interestingly, the as yet undescribed humerus appears to have a pit (olecranon fossa) at the base of the humerus for the ulna, which would indicate that this monotreme, at least, may have had a more upright stance (Rich and Rich, 2000).
The pelvis in monotremes, although short and broad, is basically like that of primitive therian mammals and some advanced therapsids but with some specializations. Monotremes have epipubic bones, along with advanced therapsids, many early mammals, marsupials and archaic placentals (Novacek et al., 1997). Oddly, echidnas have a perforation in the acetabulum through which the head of the femur projects. Many features of the hindlimb are plesiomorphic while other features are specializations (the knee joint structure, elongation of the fibular process).

![Diagram](image)

**FIGURE 2E:** Shoulder girdle of the Short-beaked Echidna *Tachyglossus aculeatus*. Abbreviations: cl., clavicle; gl. f., glenoid fossa; intercl., interclavicle; meta., metacoracoid; mst., manubrium sterni; pro., procoracoid; scap., scapula. Revised from Augee & Gooden 1993.

The fibula is twisted posteriorly, which accounts in part for the posterolateral orientation of the hindfeet. The tarsus (ankle) is a very specialised version of the plesiomorphic mammalian (non-therian) tarsus.

The ankle (crural) spurs have traditionally been considered a uniquely monotreme feature. However, recent discoveries of well-preserved Mesozoic mammals with similar crural spurs (Jenkins and Schaff, 1988; Hu et al., 1997) suggest that these structures are plesiomorphic.

**Soft anatomy and physiology**

The most ‘reptilian’ anatomical system in monotremes is the reproductive system, designed, as in reptiles, for the very ‘un-mammalian’ purpose of laying eggs. The female reproductive tract is basically lizard-like: monotremes have paired oviducts, paired uteri and an unpaired urogenital sinus but no median uterus in which young develop. The eggs, which are coated by shell glands, pass through the urogenital sinus and out through the cloaca. The monotreme egg is meroblastic; this large yolked egg is similar to bird and reptile eggs but not to those of other mammals, which have eggs with small yolks.
Unlike most other mammals the males have internal testes and the penis is held internally, only everted when the occasion demands. The penis in both platypus and echidnas is subdivided at the head (bifid in the platypus and divided into four ‘rosettes’ in the echidnas). The penis is only used for copulation as urine passes out through the cloaca in both sexes.

A hatchling monotreme must extricate itself from its egg, and does so in a very reptilian way. A sharp egg tooth, shed after birth, is used to pick through the parchment-like shell with the aid of a pointed bump on the snout made of hardened epithelium (the os caruncle). Monotremes have functional mammary glands that can reach enormous size when the female is lactating. However, monotremes have no teats, an interesting and arguably primitive feature. The young suck the milk directly from special mammary hairs from an areolar patch on the mother’s belly.

Does such a seemingly archaic system fundamentally separate monotremes from other living mammals? Oviparity was undoubtedly the mode of birth for the earliest mammals (e.g., Jenkins, 1990). Although the marsupial neonate is at a similar stage of development as the monotreme hatchling when born, the reproductive apparatus in monotremes - without development of a placenta, birth canal or teats - does appear to differ at a very basic level from the reproductive systems of living therian mammals.

Body temperature (TB) in monotremes is low for mammals, about 32°C (compared to 35-38° for marsupials and placentals respectively). This low TB may be similar to that of Jurassic mammals and is probably a primitive condition retained by monotremes (Jenkins, 1990). It had been believed that, like reptiles, monotremes could not regulate their TBs efficiently but TBs do remain constant under normal circumstances. Echidnas may hibernate in colder regions, dropping their TBs to a little above ambient temperature (just as in therians) although platypuses are not known to hibernate. Neither platypus nor echidnas tolerate high temperatures well. Basal metabolism differs between the platypus and echidnas; the metabolic rate of the platypus approaches that of therian mammals while the echidnas, subsisting on low-energy insect diets, have the low metabolic rates seen in other insectivores (Jenkins, 1990).

Like other living mammals (and possibly advanced therapsids), monotremes have a four-chambered heart, muscular diaphragm and non-nucleated red blood cells although, as always, they have their own peculiarities. The kidneys are basically mammalian in structure, as are the lungs.

The monotreme brain is therian-like and is proportionately quite large (the echidna brain is proportionately similar to that of the rat). The platypus has a lissencephalic (smooth-surfaced) brain like an opossum (Didelphis) without creases, or convolutions, on its surface. In contrast, the surface of the echidna cerebrum is highly convoluted. Interestingly, the pattern of convolutions on the echidna brain differs from the pattern of convolutions on the brains of therian mammals (Griffiths, 1978). The platypus neocortex (site of higher mental activities) is quite large, reflecting the role it plays in use of the bill. However, the neocortex of the echidnas is hugely expanded and is the largest of any mammal, including humans. Although echidnas do not lack in intelligence (at about the level of the rat in standard tests), the exact purpose of this impressive neural apparatus is one of life's little mysteries.

The musculature of monotremes, built on their mosaic body plan, reflects the primitive/specialised skeletal structure. The detrahens mandibulae is a single-bellied slip of the jaw-closing muscle group that has migrated to the underside of the jaw to become the jaw-opener in monotremes. It is innervated by the trigeminal nerve. The presence of the detrahens in monotremes has been used as an argument for an ancient origin and that the detrahens may be a holdover from the
time, far back in mammalian history, when the jaw joint was evolving from the articular-quadrate joint to the dentary-squamosal joint.

The facial musculature in monotremes is also distinctly different from that of living therians. The well-developed superficial facial musculature extends over the head and back and, remarkably, inserts onto the forelimbs in monotremes; this specialised musculature contrasts with the superficial musculature of therian mammals, which share the plan seen in both primitive marsupials and placentals (Hüber, 1930).

The shoulder girdle musculature is almost certainly close in form to the pectoral musculature of the cynodonts and the earliest mammals with a similar shoulder girdle arrangement. Certain developments are fossorial specializations to create powerful musculature for digging and some muscles appear to be reptilian holdovers. The unique arrangement of the musculature in monotremes makes it difficult to homologize the muscles of the pectoral girdle with those in living mammals and suggests a separate line of evolution (Shrivastava, 1962).

**FOSSIL MONOTREMES**

*Cretaceous forms*

The first Mesozoic mammal from Australia - in fact from Gondwana – was ‘discovered’ by palaeontologist Alex Ritchie in a tray of opalised Early Cretaceous fossils from Lightning Ridge, N.S.W. Perhaps not surprisingly, it was a monotreme. The specimen is a jaw fragment with three molars *in situ* and an alveolus for the last premolar (Figure 5F) (Archer et al., 1985). It has been christened *Steropodon galmani* because of its opalized nature (‘sterope’ is Greek for ‘flash of lightning’) and to honour the Galman brothers who procured the jaw.

The dentition of *S. galmani* is a more plesiomorphic version of the distinctive blade/cusp structure found in ornithorhynchids (Figure 5I). The rectangular molars of *S. galmani* differ from ornithorhynchids in that diakidrepanids, rather than triakidrepanids, occur on the posterior halves of M/1 and M/2; M/3 is well-developed (and not vestigial); the ridges between cusps are weakly developed (incipient) rather than well-developed shearing crests as in ornithorhynchids; and buccal cingula are present. The presence of three well-developed lower molars in *S. galmani* suggests that there were three well-developed, occluding upper molars in *S. galmani*.

When *S. galmani* was described, Archer et al. (1985) interpreted the teeth as tribosphenic (and therefore therian) rather than non-therian, upsetting the prevailing view of monotreme affinities. They cited loss of postdentary bones, tribosphenid-like cusp patterns and wide talonid basins that would indicate the presence of an occluding protocone (a defining tribosphenic feature) to link monotremes to tribosphenic therians (Archer et al., 1985). Kielan-Jaworowska et al. (1987) reexamined the evidence and proposed that *S. galmani*, because it had no wear on the talonid to positively indicate it had an occluding protocone and probably had no protocone or entoconid, had not reached the tribosphenic level of organisation. However, they did consider *S. galmani* therian, possibly derived from a form similar to the pre-tribosphenic therian *Peramus*, which has a talonid with a hypoconid and hypoconulid but no protocone (and so no basined talonid).

The fragmentary dentary of *S. galmani* is missing almost all normally diagnostic features: coronoid process, articular condyle, angular (or pseudangular) process, mandibular foramen, and all of the dentary anterior to the posterior alveolus for the ultimate premolar. However, *S. galmani*
retains several archaic features including a faint meckelian groove and what appear to be comparatively large facets for one or more postdentary bones (at least a splenial bone) anterior to where the mandibular foramen would have been located. Postdentary bones are additional bones on the inside of the jaw present in archaic mammals and their therapsid forebears but lost in therian mammals, which have only a single jaw bone, the dentary. Although detailed comparisons are not yet complete, the presence of relatively large postdentary bones in a comparatively forward position suggests that S. galmani had a jaw form more archaic than that of therian mammals or in fact holotherians (mammals included in the lineage leading to therians).

FIGURE 2F: Steropodon galmani: right dentary fragment with M/1-M/3 in place and an alveolus for the last premolar (anterior is to the right). M/1 has diakidrepanid-like structures anteriorly and posteriorly; M/2 and the smaller M/3 have triakidrepanid-like structures anteriorly and diakidrepanid-like structures posteriorly. M/1 and M/2 have well-developed anterior, posterior and buccal cingula; M/3 has a prominent anterior and buccal cingula but the posterior cingulum is not well-developed. Variably developed cingular cuspules are present on all molars. Scale bar equals 10 mm. From an unpublished study by Musser, 2001.

Luo et al. (2002) illustrate a mandibular foramen and possible postdentary trough posterior to it in their interpretation of a cast of the S. galmani jaw. In basal mammals (mammaliaformes) and cynodonts this groove, at the back of the inside of the lower jaw behind the mandibular foramen, houses several postdentary bones. However, since a mandibular foramen in S. galmani is not present (and therefore neither is a postdentary trough posterior to it), this depression may instead be a recessed, faceted area for postdentary bones as described above. The meckelian groove in S. galmani is faint and incomplete, not a deep sulcus as suggested by Luo et al. (2002). Any suggestion of postdentary bones or remains of a meckelian groove or sulcus is missing in the more derived jaw of Ornithorhynchus although there is a faint meckelian groove and what appears to have been a facet for a coronoid bone in Ob. dicksoni (Musser, unpub.). Additionally, several other features distinguish the jaw of S. galmani from that of ornithorhynchids. The dentary is proportionately deeper and more compressed in S. galmani than it is in ornithorhynchids, which have a shallower dentary and widened areas for the large, rectangular teeth. The dental canal is large in S. galmani, but not as capacious as it is in ornithorhynchids because of the deeper molar roots in S. galmani, which extend into the dental canal.

S. galmani was placed in Ornithorhynchidae because of its platypus-like molars and the large mandibular canal suggesting a bill-like structure (Archer et al., 1985). But S. galmani is now in its own family, Steropodontidae, because according to some molecular evidence, the split between the platypus and echidna lineages probably happened close to the Cretaceous-Tertiary boundary (e.g., Westerman and Edwards, 1992), which would exclude an Early Cretaceous monotreme from membership in the family (Flannery et al., 1995). Results from other molecular studies (e.g., Messer et al., 1998) give an earlier date for divergence; it is suggested that morphological differences -
primarily in jaw structure and possibly function - may also be great enough for separation of S. galmani from ornithorhynchids at the family level. These are discussed in detail below.

In addition to the archaic features of the jaw described above, the deeper and more compressed jaw in S. galmani differs considerably in form from the shallower and wider dentary in later ornithorhynchids. The shallow, boat-shaped jaw in ornithorhynchids is correlated with the flattening of the skull and reduction in length of the molar roots, shown in the *Obdurodon dicksoni* skull, which is a specialisation within the Ornithorhynchidae (and synapomorphy for the family) to the probable exclusion of steropodontids. The dentition in S. galmani certainly shares many features with ornithorhynchids, but the much stronger development of transverse shearing crests in ornithorhynchids, the loss of buccal cingula, and the possible inclusion of hardened epithelial tissue in the dental battery suggests that platypuses were using their dentition in a fundamentally different way from earlier steropodontids.

S. galmani was extraordinarily large for a Mesozoic mammal, measuring about 35 cm from head to tail (similar in size to female *Or. anatinus* in the more northerly parts of its range). This large size can be attributed to the cool-to-cold climate of Lightning Ridge that, at the time of deposition, was close to the inland Eromanga Sea just north of the Antarctic Circle. Lightning Ridge deposits are Aptian-Albian in age (about 110 m.y.a.).

One of Australia's most surprising fossil finds was that of its second Mesozoic mammal, *Kollikodon ritchiei* (Fig. 5G; Flannery et al. 1995). *K. ritchiei*, also found at Lightning Ridge, was described as a very specialised, bunodont monotreme on the basis of the holotype lower jaw (Flannery et al. 1995). However, recovery of a partial maxilla and reanalysis of the lower jaw strongly suggest that *K. ritchiei* is not monotreme but instead represents a hitherto-unknown type of mammal.

*Teinolophos trusleri*, a tiny Early Cretaceous mammal from Flat Rocks in Victoria, was found as a lower jaw fragment with a single molar (Figure 5H) covered by hard matrix (Rich et al., 1999). *T. trusleri* was originally described as a eupantothere based on what could be seen of the molar structure, but when the single, delicate tooth was more thoroughly cleaned the uniquely monotreme triakidirepanid structure could be seen (Rich et al., 2001). With a head length of about 25 mm, *T. trusleri* might have been about the size of a small dasyurid marsupial.
FIGURE 2G: *Kollikodon ritchiei*, right maxillary fragment with last premolar and M/1-M/4 in place; and right dentary fragment with M/1-M/3 in place (the anterior alveolus for M/4 has been preserved but the molar is missing). (a) occlusal view, maxillary fragment. (b) occlusal view, dentary fragment. The wide, crescentic upper molars are pitted on the mamelonated cusps. The rectangular lower molars are simpler in form but also exhibit pitting. From an unpublished study by Musser *et al.* 2001.

which makes it by far the smallest monotreme known. At about 115 million years of age, it is also the oldest known monotreme.

*T. trusleri* has provisionally been assigned to Steropodontidae because of similarities in molar structure. The preserved molar has a triakidrepanid (trigonid) anteriorly and a diakidrepanid (talonid) posteriorly, as in *S. galmani*, but both trigonid and talonid are very compressed and angled obliquely. Anterior and posterior cingula are present in *T. trusleri*, but are more poorly developed than in *S. galmani*.

The articular condyle is well above the horizontal ramus of the dentary, suggesting a deep (rather than flat) face. The well-developed angular (or pseudangular) process, anterior to the condyle, has both medial and lateral flanges. This contrasts with ornithorhynchid and tachyglossid jaws where the small, variably developed angular process, when present, projects only medially. Possible dietary preferences for *T. trusleri* haven’t been proposed, but Rich *et al.* compare the jaw structure to that of some triconodonts and spalacotheriids as well as to Geomyidae (the placental pocket gophers). The raised condyle suggests a more powerful bite than in the primarily insectivorous ornithorhynchids or tachyglossids. Further study may show what sort of dietary specializations *T. trusleri* had.

*Ornithorhynchids*

Ornithorhynchids are the ‘true’ platypuses. Three genera are currently included in the family: *Monotrematum*, *Obdurodon* and *Ornithorhynchus*. Ornithorhynchid fossil material dates from the earliest Tertiary and consists primarily of isolated molar teeth referred to *Obdurodon*. However, a beautifully preserved skull was found in 1985 which gives us a clear look at an archaic, toothed platypus (Archer *et al.*, 1992; 1993; Musser and Archer, 1998); lower jaw fragments and part of an ilium have also been found.

An incomplete dental formula for *Obdurodon* species can be inferred from the skull and dentaries. The *Obdurodon dicksoni* skull is missing all molar teeth but has alveoli for M1/ and M2/ in addition to retaining P1/ and P2/ in the skull, which gives us the number of teeth in the adult skull. There are no canines or incisors, or alveoli for them. Unfortunately, none of the dentary fragments (referred to *Ob. dicksoni* and *Ob. insignis*) are complete anteriorly and the number of lower premolars and presence of incisors or canines in the jaw can’t be determined. This is of interest in part because of Green’s (1937) determination that *Or. anatinus* has toothbuds for five lower incisors although there are no anlages (buds) for upper incisors. There is no indication in this adult skull of Green’s third upper molar and no molar fitting this position is known. Both *Ob. dicksoni* and *Ob. insignis* have a small, single root for a very reduced third lower molar. The dental formula for *Obdurodon* species, as far as can be determined, is therefore I0/? C0/?0 P1-2/?1-2 M1-2/1-3.
Premolars have only been recovered for *Ob. dicksoni* and are briefly discussed by Musser and Archer (1998) although not figured. These premolars are unicusp and well-developed, with basal cingula that nearly encircle the base of the teeth. The second upper premolar has three roots, which is unusual in mammals where two premolar roots are the norm. Like multiple molar roots, multiple roots in the premolars may be a specialisation in *Obdurodon* species (Musser and Archer, 1998). There are almost certainly only two lower premolars, matching the uppers, although confirmation must wait until additional material is procured.

**FIGURE 2H:** *Teinolophos trusleri:* (a) comparison between the penultimate molar of *T. trusleri*, left and the M/2 of *S. galmani*, right, illustrating the basic similarities in molar form between the two molar teeth. (b), lateral view of left mandibular fragment with condyle, base of the ascending ramus, angular process, and the penultimate molar; (c) occlusal view; (d) medial view showing the angular process and large medial mandibular foramen; (e) posterior view; and (f) oblique-labial view of penultimate molar. From Rich *et al.* 2001.
Molar teeth have been recovered for all fossil ornithorhynchid taxa although no species has a complete set of upper and lower molars (Figure 5I). Ornithorhynchid molars, like those of *S. galmani*, have triakidrepanon (id) and diakidrepanon (-id) blade systems and embrasures between the blade systems. They differ from the (lower) molars of *S. galmani* in elaboration of the blades into transverse shearing crests; addition of triakidrepanids to M/1 and M/2 (replacing the posterior diakidrepanids); loss of buccal cingula; reduction of M/3; and development of shallow, multiple roots. The multiple roots are interesting; because they are not set deeply into the dentary or skull, flattening of the skull and dentary in ornithorhynchids was possible (not an option for an animal with a deeper skull and jaws). The teeth sit in flat toothbeds, possibly buttressed by hardened gum tissue, and may have been shed during life (as the shallow-rooted vestigial molars are in *Or. anatinus*). Upper molars are less elongate (rectangular) than lower molars, and both lingual and buccal cuspules are more prominent. The two small, button-like M/3s recovered for *Ob. dicksoni* differ in form (to be expected in a vestigial tooth) and functionally would have contributed very little to the molar row.

The oldest known ornithorhynchid (and only early Tertiary monotreme) is not Australian. *Monotrematum sudamericanum* (Figure 5i) was first described from a single upper molar (M2/) recovered from early Paleocene deposits in Patagonia, Argentina (Pascual *et al.*, 1992a, b). Subsequently, a second fragmentary M2/ and lower M/1 have been described (Pascual *et al.*, 2002). The importance of these finds cannot be exaggerated; they confirm the Gondwanan nature of monotremes as well as the antiquity of Ornithorhynchidae. Based on the molar teeth recovered to date, the robust *M. sudamericanum* would have been the largest member of the family (Pascual *et al.*, 2002).

Molar morphology is typically ornithorhynchid and although *M. sudamericanum* has been given separate generic status, there are few differences of any consequence between *M. sudamericanum* and species of *Obdurodon*. This is a striking example of dental conservatism considering that these taxa are separated by about 35 million years.

The molars of *M. sudamericanum* are larger and more robust than those of *Obdurodon* species, but other features that were originally thought to separate the two genera are either variable in *Obdurodon* species or present in both taxa. *M. sudamericanum* was recovered from the Banco Negro site just west of Golfo de San Jorge in central Patagonia. The fossil site today is a bleak and windswept rocky plain but when *M. sudamericanum* was alive it was a lush lowland rainforest near the widening Atlantic Ocean (Pascual *et al.*, 1992a). The early Paleocene site, dated at 63.2 - 61.8 mya, supported a very un-Australian fauna (Pascual *et al.*, 1992a; Archer, 1995).

The oldest Australian ornithorhynchid, *Obdurodon insignis*, was originally described from two molar teeth discovered separately near Lake Eyre (Etadunna Formation) and Lake Frome (Namba Formation) in central Australia (Woodburne and Tedford, 1975). These late Oligocene sites (26-24 m.y.a.) are part of one of the oldest and best-known Tertiary vertebrate fossil assemblages in Australia. Prior to these discoveries, no fossil monotremes older than the Pliocene and no fossil monotremes with functional dentition were known. However, because molars of the living platypus are vestigial, it had been assumed by palaeontologists that ancestral platypuses did have functional teeth. Woodburne and Tedford, therefore, took an educated guess regarding the identity of the molars, tracing the distinctive blade structures in *Ob. insignis* back to the same structures on the ephemeral molar teeth of *Or. anatinus*.

The relatively unworn holotype of *Ob. insignis* (Figure 5I) is a small, exceptionally well-preserved molar with six roots. It was described as an upper second molar but on discovery of additional material it became clear that the holotype was a lower first molar. The paratype, an M/2, is
also small but is very well worn and heavily damaged. To date it is the only known M/2 for *Obdurodon* species and is the only molar, upper or lower, to have equally well-developed, dual triakididrepanid (-on) blade systems.

On a subsequent trip to the Lake Eyre type locality a partial ilium and a dentary fragment were recovered and assigned to *Ob. insignis* (Archer et al., 1978). The small dentary fragment, missing the articular condylar area as well as its anterior section, roughly correlates in size with the *Ob. insignis* molars. There is a small projecting angular process (broken at the tip) on the lingual side of the jaw but no additional development of the process laterally, as there is in *T. trusleri*. If steropodontids prove to have lateral development of the angular process, the reduction or loss of this projection would characterise ornithorhynchids. The internal mylohyoid process above the mandibular foramen, present as well in *Ob. dicksoni* and *Or. anatinus*, is moderately developed. Loss of a ventrolateral process and acquisition of a more anterior ventromedial process implies a fundamental change in jaw function and muscle origins in ornithorhynchids, which may correlate with changes in molar morphology.

There is no mention of the presence of an ascending coronoid process in the original description of the *Ob. insignis* jaw (Archer et al., 1978). This plate-like process is a feature of most mammalian dentaries but is absent in the derived jaw of *Or. anatinus*. However, it is present in a jaw fragment recovered for *Ob. dicksoni*, suggesting that *Obdurodon* species had not yet lost this process. On close inspection of the *Ob. insignis* jaw, a broken edge along the dorsal edge of the jaw posterior to the toothbed can be seen that may represent the base of an ascending coronoid process. Molar alveoli open directly into the dental canal, as they do in *Ob. dicksoni*. The mandibular foramen and canal are smaller than that in *Or. anatinus*, which suggests to Archer et al. (1978) that the bill in *Ob. insignis* was less well-developed and innervated than the bill in the living platypus.

The ilial fragment is also small but is from a juvenile animal (as indicated by breakage that occurs along suture lines where the pubis and ischium would attach). The distal end of the ilium is less expanded than in *Or. anatinus*, possibly a more primitive condition indicating that *Ob. insignis* was less efficient at digging than the modern platypus (Archer et al., 1978).

Interestingly, a second species of *Obdurodon* has been recovered from a single locality in the Lake Eyre basin Etadunna Formation (Mamallon Hill). Dated at 25 m.y.a. (Woodburne et al., 1994), it would have been roughly contemporaneous with *Ob. insignis*. This species, *Ob. sp. A*, is known from two upper right second molars (therefore representing two individuals) found a scant five metres apart. These molars have a strongly developed pit between the blade systems and in this respect appear to be closer in form to *M. sudamericanum* than the slightly older *Ob. insignis*.

*Obdurodon dicksoni*, from Riversleigh in northwestern Queensland, was initially known only from isolated molar teeth. In 1985, however, a nearly perfect skull (Figure 5J) was recovered from Ringtail Site (dated 15 m.y.a.: Archer et al., 1992; 1997). It is the only pre-Pleistocene ornithorhynchid skull known and, as such, it is a highly significant find. Two dentary fragments have also been recovered, providing the information for an accurate reconstruction of the skull and dentary (Musser and Archer, 1998).

The large, robust *Ob. dicksoni* skull revealed a surprising array of features, some of them unexpected in an ancestral platypus. The remarkable extent of the bill in *Ob. dicksoni* is stunning. No other mammal has developed the rostrum to such an extent. Proportionately the bill is well over 2/3 the length of the face. While the bill in *Or. anatinus* is somewhat rectangular, the bill in *Ob. dicksoni* would have been spoon-shaped when the marginal cartilage is added. The dorsal septomaxilla, difficult to see in adult living monotremes, clearly overlies the ventral premaxilla.
Paired foramina anterior to the eyes, similar to those in *Or. anatinus* that innervate the frontal shield, indicate that such a sensory shield was present in *Ob. dicksoni*. The rounded zygomatic arches accommodated the robust masticatory musculature needed for the well-developed teeth and jaws.

**FIGURE 21:** Molar teeth of *Steropodon galmani* and Ornithorhynchidae (not to scale, with some teeth reversed to aid comparisons). Upper left: diagram of left lower first molar, holotype of *Obdurodon insignis* illustrating the blade systems of molars (from Musser 1998). Triakidirepanans (triakidirepanids on the lower teeth) have dual blade systems subtended by three cusps, forming a triangular blade system. Diakidirepanans (diakidirepanids on the uppers) have two cusps connected by a single blade. True triakidirepanons (-ids) and diakidirepanons (-ids)
are only formed in ornithorhynchids. A wide occluding basin is formed between all blade systems.

Ventrally the most obvious difference between *Ob. dicksoni* and *Or. anatinus* is in the presence of functional premolars and molars in the adult *Ob. dicksoni*. The somewhat square, transversely ridged molars are much larger than the premolars. The shallow-rooted molars were probably stabilised by hardened gum tissue in life, an evolutionary precursor to the development of the epithelial dental pads in *Or. anatinus*. The anterior half of the skull is edentate but the fossil skull bore deep bilateral depressions roughly in the position of the epithelial ridges in *Or. anatinus*. Comparatively enormous epithelial ridges filling the concavities, therefore, have been reconstructed. These ridges are the sole ‘dental’ structures for the anterior half of the skull and have replaced the lost upper canines and incisors of ancestral monotremes.

In lateral view the flattened nature of the skull and dentary is striking. It is quite possible that this toothed platypus did not forage through bottom sediments as *Or. anatinus* does, using its downwardly-deflected bill. *Ob. dicksoni* may have been more like a miniature crocodile, feeding on unwary invertebrates and small vertebrates (perhaps fish or frogs) near the water’s surface. The combination of occluding keratinous ridges in combination with fully enamelled cheekteeth appears odd, but the dental battery would have been more of a ‘unit’ if epithelial tissue were part of the premolar-molar apparatus.

Both the anterior and posterior (condylar) parts of the dentary have been reconstructed based on the dentary in *Or. anatinus*. The two complementary dentary fragments recovered for *Ob. dicksoni* indicate the following features: a moderately well-developed ascending coronoid process, a projecting, rod-like angular process, a deep masseteric ‘pocket’, a distinct medial mylohyoid process just above the mandibular foramen, and large mandibular foramen and canal. The dentary is quite flat, corresponding to the flattened nature of the skull. It is proportionately deeper than in *Or. anatinus* but not as deep as in *S. galmani*. The presence of both an ascending coronoid process and an internal coronoid process in *Ob. dicksoni* is proof that the internal process is not the vestigial ascending coronoid process, as had been presumed (Musser and Archer 1998).

It had been thought that bill size in ornithorhynchids gradually increased through time and that the wide, rectangular bill of the living *Or. anatinus* developed from the smaller bill of a platypus like *Ob. insignis*. The large size and extreme shape of the bill in *Ob. dicksoni* led Musser and Archer (1998) to suggest that the Riversleigh platypus might actually have been even more specialised than *Or. anatinus* at least in development of the bill and that perhaps *Ob. dicksoni* was well off of the main evolutionary line leading to *Or. anatinus*. *Ob. insignis*, with a smaller bill and lighter build, may have been closer to the ancestor of today's lightly-built *Or. anatinus*.

The only ornithorhynchid material reported from the Pliocene is that of a limb bone from the Bow Local Fauna of N. S. W. referred to the genus *Ornithorhynchus* (Rich et al., 1991). Numerous platypus cranial and postcranial elements from the Pleistocene and Holocene have been recovered, the majority of this material from cave deposits in Tasmania (Marshall, 1992). Pleistocene platypus material appears to be identical to *Or. anatinus* and all Pleistocene ornithorhynchid material recovered is assigned to this species (e.g., Archer et al., 1978; Marshall, 1992).

The oldest Pleistocene record, from Bunya Siding, NSW, dates from about 100,000 ypb (Davis, 1996). All Pleistocene sites fall within the range of the living *Or. anatinus* except for a record
from Lake Tandou west of the Darling River (J. Hope, personal communication). An edentulous jaw and tibia from King's Creek, Qld (Archer et al., 1978), an undescribed shoulder girdle element from the Darling Downs, Qld. (J. Wilkinson, 2001, personal communication) and a juvenile skull from the Snowy River, NSW (Marshall, 1992) represent natural deposition in streams, rivers or caves. Two archaeological sites have produced fossil platypus material: the late Holocene Brisbane River Platypus Rock Shelter site and the late Pleistocene cave deposits from Tasmania, dating from 14-29,000 ybp (see Marshall, 1992). The large number of skeletal elements from the Tasmanian deposits suggest that the platypus may have been used as a source of dietary fat during glacial periods when Tasmanian aborigines were using the caves (Marshall, 1992).

**Tachyglossids**

Animals without true teeth are at a disadvantage in the fossilisation process because teeth, with an outer coat of durable enamel, are often preserved when other elements are not. The edentate echidnas are no exception to this general rule. The echidna fossil record is almost unknown prior to the relatively recent Pleistocene. The oldest known echidna, possibly as old as middle Miocene ('Zaglossus' robusta), is edentate and can tell us nothing about dental evolution in tachyglossids.

Traditionally, classification of fossil echidnas was relatively simple: small, short-beaked echidnas were assigned to the genus *Tachyglossus* and a more diverse group of larger, long-beaked echidnas (known from both New Guinea and Australia) were put into the genus 'Zaglossus'. However, Griffiths et al. (1991) suggest that the story may be more complex and that the diversity of long-beaked echidnas should be recognised at the generic level, reflecting differences in feeding strategies and, therefore, in niche partitioning.13-14 myo; Woodburne et al., 1985). The argument over the age of the site - a difference of over 10 million years - depends in part on whether the associated fauna found in the mine shaft is archaic or is more recent in age. Woodburne et al. (1985) describe the assemblage from the mine as taxonomically similar to Miocene faunas, while the marsupial fauna and the type of preservation suggest to Murray (1978b) that the material may be Pliocene or Pleistocene in age. Preservation is similar to that of the nearby Wellington Caves Bone Cave deposits, which have a 'rubbery' date of about 250,000 ybp (M. Augee, 2001, personal communication).

A partial skull, complete humerus, atlas vertebra and clavicular fragment were recovered from the mineshaft (*Echidna (Proechidna) robusta* Dun, 1895). The skull is typically tachyglossid and is similar to that of the more well-known Pleistocene long-beaked echidna *Megalibgwilia ramsayi*. Unfortunately, the anterior section of the beak is missing which prevented Griffiths et al. from formally reassigning 'Z.' robusta to the genus *Megalibgwilia* (Griffiths et al. 1991). The humerus was originally described by Dun (1895) as that of a giant platypus and given the name *Ornithorhynchus maximus*. It is undoubtedly tachyglossid, however, and is most likely from the same animal as the skull (Mahoney and Ride, 1975).

There are no Pliocene cranial remains but there are a few postcranial elements. Two well-preserved, complementary tibiae were found near Cooma, N.S.W. and a partial humerus and scapular fragment were recovered from Chinchilla in southeast Queensland. The humerus ('Echidna' owenii Krefft, 1868) was the first record of a large, long-beaked echidna from either Australia or New Guinea; this discovery predated the description of the living New Guinea long-beaked echidna by eight years ('Tachyglossus' bruijnii Peters and Doria, 1876). The form of the humerus closely resembles that of *Megalibgwilia ramsayi*, described below. Although Krefft described the Chinchilla Sands deposit as Pleistocene, most material from this deposit is now believed to be Pliocene in age.
The vast bulk of fossil tachyglossid material is Pleistocene and most of this has been excavated from various cave and swamp deposits in eastern and southern Australia. Henschke's Cave, at Naracoorte in South Australia, is particularly rich in tachyglossid material, with three contemporaneous species of echidna recovered to date (J. Barrie, personal communication).
There are at least three distinct genera of Pleistocene echidnas: the long-beaked *Megalibgwilia* or *Zaglossus* species and the huge *Zaglossus* 'hacketti' as well as the living Short-beaked Echidna *Tachyglossus aculeatus*. These three types are separated by size, by differences in the beak and palate (indicating differences in dietary preferences) and by proportional differences in the limbs. By the Pleistocene, then, echidnas had successfully radiated out into various niches, much like the anteaters of South America, reflecting the patchwork of wet and dry environments (and their respective invertebrate faunas) that continue to characterise Australia today.

Taxonomy of mainland long-beaked echidnas has long been confusing. There are many synonyms, with specific status given to limb bones and other fragmentary remains. The first comprehensive study of fossil long-beaked echidnas was by Peter Murray (1978b). Most of the material, from the Naracoorte cave deposits and from Tasmania, appeared to represent a single, variable species that he assigned to *Zaglossus ramsayi* (the name *Z. ramsayi* having priority over other names given to some of the fossil material). *Z. ramsayi* (figure 11) was described as a large, robustly built echidna with a fairly straight, strong beak and long, well-muscled limbs. These features indicated a powerful digger with a beak that could act as a lever in prying up logs and rocks in search of insect larvae. Murray thought *Z. ramsayi* might have been less specialised than either *Z. bruijnii* or *T. aculeatus*; skull morphology suggests *Z. ramsayi* probably lacked the acanthid groove on the tongue of *Z. bruijnii* and probably had not developed the complex tongue musculature of *T. aculeatus*. In a twist on the debate over relationships, Murray thought that *Z. ramsayi* was actually closer in form to *T. aculeatus* than to *Z. bruijnii*, although *Z. bruijnii* had probably evolved from *Z. ramsayi* or an echidna very much like it.

Restudy of *Zaglossus* cranial material prompted Griffiths *et al.* (1991) to propose a separate genus (*Megalibgwilia*) for *Zaglossus* *ramsayi*. Its relatively short, straight, untapered beak and the shape and conformation of its palate suggested a difference in diet, a distinction that in many mammal groups is considered fundamental enough to separate taxa at the generic level. The diet of *M. ramsayi* was probably not primarily oligochaete worms, as is usually the case in New Guinea *Zaglossus*, but perhaps large insect larvae such as that of beetles or moths. These grubs would have been plentiful in the cool, moist grasslands of Pleistocene southeastern Australia. To Griffiths *et al.*, the cranial morphology of *M. ramsayi* appeared to be intermediate between that of *Tachyglossus* and *Zaglossus* and they proposed that a species of *Megalibgwilia* may have been the ancestral form for these later genera.

Fossil echidnas resembling the New Guinea *Zaglossus* forms are known from the late Pleistocene of mainland Australia (Murray, 1978b) and from Pleistocene deposits in New Guinea (Flannery, 1995). Both *Z. robusta* and *M. ramsayi* are described as being larger and more robust than these *Z. bruijnii*-like forms (Murray, 1984) although since Murray’s diagnosis, larger New Guinea *Zaglossus* species (up to 1 metre in length) have been recorded (Flannery, 1995). Murray sees the *Z. bruijnii/Z. bartoni* species, with their long, recurved beaks and less robust build, as the
specialised, wet-forest end-forms of the *M. ramsayi* lineage. The slender, recurved beak is perfectly designed for probing leaf litter of rainforests for worms but is ill-equipped to pry up the rocks or logs that litter the drier woodlands that were the habitat for *M. ramsayi*.

FIGURE 2K: Skulls of fossil Australian long-beaked echidnas. The Pleistocene long-beaked echidna *M. ramsayi*, known from complete skulls as well as from postcranial material, had a long, fairly straight beak and flattened, *Zaglossus*-like cranium. (i), dorsal view; (ii) lateral view; and (iii) ventral view. *Zaglossus' robusta*, possibly a much older tachyglossid of Miocene age, is only known from a single specimen but appears to have been very similar to *M. ramsayi* in most respects. (iv) dorsal view; (v) lateral view; and (vi) ventral view. Scale bars equal 50 mm. *Z.' robusta* drawn from holotype AMF51451 (*Echidna (Proechidna) robusta* Dun), Australian Museum. *M. ramsayi* drawn from P20488 (South Australian Museum) (Griffiths et al. 1991).

There would have been intermittent land connections between Australia and New Guinea up until at least 20,000 y.b.p. and possibly later, allowing ancestral *Zaglossus* types from northern Australia to reach this now-isolated island. The unique landscape of New Guinea, with its high mountain peaks clothed in ancient remnant vegetation, has served as a refuge for many Australian marsupials. For *Zaglossus* species, the mountainous terrain preserved ideal habitat. During climate fluctuations the vertical zonation that characterises mountain slopes would have ensured access to suitable habitat regardless of climate shifts (e.g., Murray, 1978b).

The middle Miocene *Z.' robusta* is similar to *M. ramsayi*. Both Murray (1978b) and Griffiths *et al.* (1991) believe that it should either be included in *M. ramsayi* or be considered as an ancestral species. However, as mentioned, the rostrum of the skull, which would help in positive identification, is missing. A femur of a long-beaked echidna, described as a separate species (*Z. harrisoni*) is
indistinguishable from the *M. ramsayi* material and should be assigned to that species (Murray, 1978b).

Some researchers feel that there isn't a generic-level distinction between the New Guinea species of *Zaglossus* and the forms assigned to *Megalibgwilia*. I've examined the 'Z.' *robusta* material and tend to agree, especially in light of the morphological diversity within New Guinea *Zaglossus*. If the taxonomy proposed by Griffiths *et al.* is upheld, the genus *Megalibgwilia* would include most of the Miocene to Pleistocene/Holocene mainland long-beaked echidnas and the genus *Zaglossus* would be confined to Pleistocene to present forms close to the living New Guinea species. If the forms now assigned to *Megalibgwilia* are reassigned back to the genus *Zaglossus*, most long-beaked types would be considered species of *Zaglossus*. The fossil history of the genus *Zaglossus*, then would date from the ?Miocene to the present and distribution would include both mainland Australia and New Guinea. A wealth of recently excavated tachyglossid material from Naracoorte, S. A. may help to settle the debate.

The most distinctive Pleistocene echidna, 'Zaglossus' *hacketti* (Figure 5L) is an enormous echidna recovered from two caves in Western Australia. Pelvic fragments, hindlimb bones, a partial shoulder girdle, front limb elements and vertebrae were recovered but, unfortunately, there was no cranium that would help to answer questions about its relationships to other echidnas. A complete cranium would also allow a taxonomist to assign 'Z.' *hacketti* to a new genus, a status it almost certainly deserves. The skeletal elements recovered indicate this echidna was about 1 metre long and had a mix of both *Tachyglossus* and *Zaglossus/Megalibgwilia* features. A fragment of a large humerus recovered from Western Australian cave deposits may belong to 'Z.'
hacketti (Murray, 1984). The entepicondylar area is more like that of the older 'Z.' robusta than either M. ramsayi or Z. bruijnii although Murray describes this part of the humerus as variable in echidnas (Murray, 1978b).

Limb proportions of 'Z.' hacketti, surprisingly, are closer to those of T. aculeatus than to any of the long-beaked echidnas. The lengths of the tibia and femur are nearly equal in 'Z.' hacketti and in T. aculeatus, while in both M. ramsayi and in the New Guinea Zaglossus species the tibia is much longer than the femur. Perhaps the proportionately longer limbs aided in navigation over logs and litter in forest environments (Murray, 1984). Some of the Naracoorte tachyglossid fossils resemble the 'Z.' hacketti material although these elements are not especially large (J. Barrie, 2001, personal communication). It is probable that this giant among echidnas was either a rare form or that it was part of an earlier radiation that had largely disappeared by the Pleistocene.

Long-beaked echidnas from the Australian mainland have a much longer pedigree than the Short-beaked Echidna, T. aculeatus, which only dates back to the Pleistocene. The 'Z.' robusta record is evidence that long-beaked echidnas may have been present at least in New South Wales from the middle Miocene to the Pleistocene. Records from Pleistocene deposits in western, southern and eastern Australia indicate that long-beaked echidnas had a wide distribution during this period. These Pleistocene environments were primarily woodlands or mosaic grasslands (Murray, 1978b). Speciation into Tachyglossus and Zaglossus types may have resulted as the Miocene and Pliocene forests retreated. Drier environments, with their new suites of invertebrate prey (particularly ants and termites), would have favoured T. aculeatus while Zaglossus species would have become increasingly restricted to remnant forest habitats.

Long-beaked echidnas appear to have survived into the Holocene on mainland Australia. Extinction times can be guessed at from the spotty fossil record as well as from some interesting but circumstantial evidence. The latest record for M. ramsayi comes from Holocene deposits in Tasmania. This island state may have been a refuge for M. ramsayi as well as for a number of other Australian mammals like the thylacine. The single record for 'Z.' hacketti from the late Pleistocene indicates the species became extinct at some point after this (Pledge, 1980). Intriguingly, Holocene rock art (possibly as old as Pleistocene) from western Arnhem Land appears to depict a long-beaked echidna (Murray, 1984). Northern Australia and New Guinea, Murray believes, may have, like Tasmania, been refugia for long-beaked echidnas as the interior dried out.

What caused long-beaked echidnas to disappear from mainland Australia? Short-beaked echidnas are commonly eaten by aborigines in Australia and long-beaked echidnas are a favourite food item in New Guinea now that taboos against eating them have broken down. Murray (1984) suggests that hunting pressure may have been responsible for the demise of at least 'Z.' hacketti and overhunting may have contributed to the extinction of M. ramsayi as well. Loss of the extensive inland forests and of the moist grasslands may have been a factor in the reduction of scarab beetle numbers (with their fat-rich larvae).
*Tachyglossus aculeatus* had a wide distribution during the Pleistocene, as it does today, with records from Wombeyan Caves, N.S.W., Lake Menindee, N.S.W., Naracoorte, S.A. and Mammoth Cave, W.A. However, it is not as common in fossil deposits as long-beaked echidnas are. Some *T. aculeatus* from Naracoorte were around 10% larger than their living counterparts, overlapping in size with some of the smaller long-beaked echidnas at the site (Pledge, 1980).

The relationship between echidnas and other monotremes remains a mystery. The lack of a dental 'trail' means that there are no echidna teeth to compare to the teeth of any of the other monotremes. The platypus and echidnas are similar to each other at the molecular level (e.g., Westerman and Edwards, 1992; Gemmell and Westerman, 1994). Pascual *et al.* (1992a) proposed that echidnas may have diverged from the platypus line, an idea also proposed by Gregory (1974). Pascual *et al.* base their hypothesis on genetic data suggesting the platypus and echidna lines diverged from each other at some point near the Cretaceous-Tertiary boundary (e.g., Westerman and Edwards, 1992). Oddly, this would make echidnas derived platypuses, which are themselves highly specialised. If the genetic data is an underestimate (e.g., Messer *et al.*, 1998) and if the echidna-platypus split dates from the early to middle Cretaceous, it is quite probable that echidnas descended from an as-yet-unknown monotreme. In this scenario, the ancestors of echidnas might have been terrestrial and more generalised than ornithorhynchids.

**BIOGEOGRAPHY**

The discovery of an ornithorhynchid monotreme in South America confirmed that monotreme mammals were Gondwanan and not uniquely Australian. The Gondwanan continents - South America, India, Africa, Antarctica and Australia - were joined throughout the Mesozoic, breaking up sequentially from west to east before the final breach between Antarctica and the South Tasman Rise at about 30 mybp (e.g., Lawver *et al.*, 1992). With this history, it is reasonable to assume that monotremes may have been widespread over Gondwana when travel between the landmasses was possible.

To construct a biogeographical scenario, we have to make some assumptions about evolutionary paths and dispersal opportunities. Because the earliest monotremes hail from Australia it is probable (but by no means certain) that they originated either on this continent or perhaps in Antarctica. *T. trusleri* and *S. galmani* are both specialised, suggesting that their lineages had been evolving for a long time. Many researchers, myself included, are quite comfortable with the possibility of a Jurassic origin for the monotremes. The Jurassic mammalian fossil record for Gondwanan continents is minute. There are only a handful of Jurassic mammal sites for the Gondwanan continents (none from Australia) and the Cretaceous record is not much better.

By 120 mybp, West Gondwana (Africa, Madagascar and India) had separated from the East Gondwanan landmasses (South America, Antarctica, New Zealand and Australia) clustered around the South Pole (Lawver *et al.*, 1992). During the Aptian and Albian, Victoria lay within the Antarctic Circle and Lightning Ridge, on the shores of the inland Eromanga Sea, was situated just to the north. Temperatures were low although there is debate about whether the climate was actually polar (with development of permafrost) or merely cool-to-cold, perhaps like the cooler parts of Tasmania today. However, it is clear that Victoria and Lightning Ridge would have experienced the long winter nights and summer days of higher latitudes.

Ornithorhynchid monotremes may have spread across Antarctica to southern South America during the latter part of the Cretaceous. By the Late Cretaceous, temperatures had warmed
considerably and even the most southerly regions were traversable. From the Late Cretaceous to Eocene, southeastern Australia, New Zealand (up to 80 mybp), Antarctica and southern South America formed a continuous and fairly homogeneous cool-temperate forest environment dominated by southern beech (*Nothofagus*) (Case, 1989). This corridor would have been the dispersal route for, among other taxa, Late Cretaceous ornithorhynchids travelling from Australia to South America as well as for South American marsupials entering Australia from South America via Antarctica. Pascual *et al.* (1992a) believe that ornithorhynchids, along with gondwanatheres, may have been in South America since the Early Cretaceous and that southern South America may have been isolated from the Early Cretaceous to the early Tertiary. Some geological evidence, however, indicates that South America remained connected to Antarctica through an archipelagic connection throughout this period (Lawver *et al*., 1992).

*M. sudamericanum*, recovered from deposits that date from just 2-3 million years after the end of the Cretaceous, may represent either a single dispersal of ornithorhynchid monotremes to South America or a relict of a greater South American monotreme radiation. Pascual *et al.* (1992a, b) surmise that *M. sudamericanum* and the gondwanatheres represent the 'last stand' for archaic, non-therian mammals in South America. Contemporaneous faunas further to the north have neither monotremes nor gondwanatheres but do record diverse marsupial and placental mammals, immigrants and competitors from North America (Pascual *et al*., 1992b). Monotremes, perhaps surprisingly, haven't been recorded from the late Cretaceous Los Alamitos.
FIGURE 2M: Map of Australia showing the present and historic distribution of ornithorhynchids plus *S. galmani*. Inset: southern South America, Antarctica and Australia (the ‘Weddellian Province’) at 60 mybp (adapted from Lawver et al. 1992). Crosshairs indicate position of the South Pole at 60 mybp. The shaded area along the Australian coast indicates the present distribution of the living Platypus *Ornithorhynchus anatinus* (Grant 1995). RV, Riversleigh World Heritage Fossil Deposits (Miocene; *Obdurodon dicksoni*); LR, Lightning Ridge opal fields (early Cretaceous, *Steropodon galmani*); EF, Etadunna Formation (late Oligocene, *Obdurodon insignis, O. sp. A*); NF, Namba Formation (late Oligocene, *Obdurodon insignis*); BNI, Banco Negro Inferior, Patagonia (early Paleocene; *Monotrematum sudamericanum*). From Musser 1998.

site to the south of Banco Negro (many other non-tribosphenid mammals have been found; however, no advanced therian mammals have yet been recovered (Bonaparte, 1990). Ornithorhynchids probably went extinct in South America as marsupial and placental mammals became established and faunal compositions changed. Australia, entering a long period of isolation, provided a less competitive environment for continued survival of ornithorhynchids.

Marsupial and placental mammals have been recorded from Seymour Island, an Eocene site off the Antarctic Peninsula (dated to ~ 40 mya). The mammals are endemic Antarctic forms of South American taxa, suggesting that Antarctica by this time was isolated from South America. Ornithorhynchids have not yet been recorded from Antarctica and, conversely, none of the distinctive
Antarctic mammals have been found in Australia. Current estimates for the onset of glaciation over the Antarctic continent and for the complete separation of Antarctica from Australia vary. Antarctic floral records suggest that most terrestrial plant life (and, by inference, the animal life dependant on it) had become extinct by the late Oligocene or earliest Miocene (25-20 mya) (Askin, 1992). This agrees with an estimation for establishment of a strong circumpolar current around Antarctica (30-20 mya), effectively isolating the continent from ameliorating climatic influences (Lawver et al., 1992).

The oldest Australian ornithorhynchid fossils are late Oligocene in age (about 25 m.y.o.). As Australia drifted north the continent experienced many climatic fluctuations; however, the onset of arid conditions is a comparatively recent event (White 2003). This drying had a devastating effect on inland river systems, most of which have now disappeared along with the vast inland forests.

These events have reduced the range of ornithorhynchids to a considerable extent, and platypuses are 'out on a limb' in evolutionary terms. During the early Tertiary they occupied three continents; during the middle to late Tertiary they ranged from central and northern Australia to eastern Australia, far to the west of their present range; and today they cling to the eastern coast. Although platypuses are not classified as either threatened or endangered, their numbers are not well-documented, there is increasing pressure on waterways, and there is growing evidence that at the local level platypus numbers are declining (e.g., Grant, 1995). The continued survival of this ancient mammal from the age of dinosaurs can not be taken for granted and care must be taken to preserve its fragile habitat.

MONOTREME RELATIONSHIPS

Relationships within Monotremata

Prior to the discovery of T. trusleri, the link between S. galmani and ornithorhynchids seemed clear; the molar form of S. galmani was a precursor to the molar form in ornithorhynchids and the deeper dentary in S. galmani was a more 'normal' form that evolved into the shallower, more derived jaw of ornithorhynchids. Since both T. trusleri and S. galmani share the distinctive monotreme molar structure, this form might represent the primitive monotreme molar form and not a molar form unique to the S. galmani/ornithorhynchid line. The corollary to this is that ornithorhynchids, rather than developing a unique molar structure, may have retained and modified an ancient monotreme molar pattern to suit their own needs.

Although tachyglossids are wonderfully complete, the lack of dentition and the absence of a likely fossil predecessor make it difficult to carry the search for relationships to other monotremes any further than Pascual et al. (1992a) have done by suggesting that tachyglossids may be derived platypuses.

Relationships with other mammals

The crux of the debate over monotreme relationships is primarily whether monotremes should be placed on the line leading to the living therian mammals or be considered as non-therian mammals with no close ties to therians. Some comparative anatomists (e.g., MacIntyre, 1967) have seen monotremes, with their many primitive features, as surviving therapsid reptiles but most researchers have traditionally viewed monotremes as basal, non-therian mammals, specialised types allied with Mesozoic mammals such as triconodonts or multituberculates (e.g., Hopson and Crompton, 1969; Kielan-Jaworowska, 1971; Crompton and Jenkins, 1973; Woodburne and Tedford, 1975). The
possibility that monotremes might be pre-tribosphenic therian mammals was discussed by Kemp (1983), who cited the structure of the ear ossicles and correlated loss of post-dentary bones.

Among living therians, marsupials are regarded to be generally more plesiomorphic than placental mammals. Gregory (1947) focused on similarities between marsupials and monotremes, grouping them together as a new subclass Marsupionta; however, the features cited by Gregory that are common to both monotremes and marsupials are now generally regarded as shared primitive features, and thus are of no use in determining relationships.

The discovery of the lower jaw and molars of *Steropodon galmani* focused the debate on dental affinities. The wide, enclosed talonid basins and well-developed tribosphenic-like triangular cusp and crest systems (suggested as being homologous to the entoconids, pre-entocristids and cristid obliqua in tribosphenic mammals) suggested a close relationship between monotremes and advanced therian mammals such as peramurids (Archer et al., 1985). Kielan-Jaworowska et al. (1987), taking a second look at *S. galmani*, placed monotremes as basal to tribosphenic mammals but kept them within the therian camp, basing their conclusions on occlusion (the lack of wear on the talonid basin for a protocone - the tribosphenic hallmark) and the probable absence of the protocone and entoconid. They proposed that monotremes were survivors of an early therian radiation before the development of the tribosphenid molar. Bonaparte (1990), working with the specialised dryolestoid mammals of Los Alamitos, thought that, if Kielan-Jaworowska et al. were correct, monotremes might have been part of a greater dryolestoid (early therian) radiation in Gondwana. However, as discussed above, the jaw structure of *S. galmani* may in fact be more archaic than that of any therian mammal. Tribosphenic-like monotreme teeth may also have been independently derived from those of therian mammals (Pascual et al., 2002; Musser, 2003) rather than from archaic therian stock.

Questions over the primitive nature of the monotreme skeleton have refused to disappear. Spectacular recent discoveries of skeletal remains of Mesozoic mammals, especially from China, have fuelled the debate. Results from these fossil finds are surprisingly consistent. Investigations of cranial, basicranial and postcranial features place monotremes either between early Jurassic mammals and multituberculates or group monotremes (somewhat cautiously) together with multituberculates (Rowe, 1988, 1993; Wible, 1991; Wible and Hopson, 1993; Hopson and Rougier, 1993; Meng and Wyss, 1995; Wible et al., 1995; Rougier et al., 1996). 'Triconodonts' (Ji et al., 1999), multituberculates (Sereno and McKenna, 1995) and archaic therians (Krebs, 1991; Rougier, 1993; and Hu et al., 1997) all have a more modern postcranial skeleton than monotremes (particularly in the shoulder girdle), placing monotremes on the basis of postcranial characters in a position basal to the majority of known mammalian groups.

Although molecular techniques are new and useful tools to investigate phylogenetic questions, some recent molecular findings are in conflict with morphological data and with the palaeontological record. Some recent studies have strongly suggested that monotremes and marsupials share a close relationship; these investigations (e.g., Janke et al., 1996, 1997 and Penny et al. 1999 using mtDNA; Kirsch and Mayer, 1998 using DNA hybridization) are in agreement that an early divergence of monotremes from the stem leading to living therian mammals is the least likely outcome (Penny and Hasegawa, 1997). Alternative techniques have supported great genetic distance between monotremes and other living mammals (e.g., Westerman and Edwards, 1992; Retief et al., 1993; Killian et al., 2000; Belov et al. 2002). Of interest at this writing are the conclusions of a study using nuclear, rather than mitochondrial, DNA, which unambiguously support the morphological conclusion that monotremes form a group far removed from therian (marsupial and placental) mammals (Killian et al., 2001).
Molecular genetics can be used to estimate the point chronologically where one group may have diverged from another. This is especially helpful where there are gaps in the fossil record. However, divergence times estimated in this way vary greatly depending on the techniques used. Estimates of a split between monotremes and the line leading to living therians range from the early Jurassic (Messer et al., 1998) to the Early Cretaceous (Janke et al., 1996, 1997; Kirsch and Mayer, 1998), a difference of about 60 million years.

**Gondwanan radiation**

Fossil mammals of Jurassic and Cretaceous age are now appearing on the southern continents and evidence is mounting for an endemic southern mammalian radiation during the Mesozoic. This was first suggested by Jose Bonaparte (1990) who excavated the late Cretaceous Los Alamitos site in Argentina and was struck by the unusual nature of the mammalian fauna, most of them unique, non-tribosphenic mammals with older northern hemisphere relatives. He proposed that the northern hemisphere (Laurasia) had been dominated by tribosphenic mammals during the later Mesozoic but that the southern hemisphere (Gondwana) had been predominantly dominated by these derived non-tribosphenic types.

Luo et al. (2001, 2002) take a different approach, prompted by the discovery of Mesozoic mammals from Madagascar (Ambondro mahabo Flynn et al. 1999; Patagonia (Asfaltomylos patagonicus Rauhut et al. 2002), and Australia (Ausktribosphenos nyktos Rich et al. 1997, 1999; Bishops whitmorei Rich et al. 1999). The Middle Jurassic Am. mahabo is described as the oldest tribosphenic mammal to date (older by 25 million years than any of the northern tribosphenic mammals) and is considered by Flynn et al. (1999) to be the first Jurassic Gondwanan holothere known (Flynn et al., 1999). Au. nyktos, from the Early Cretaceous Victorian locality that produced T. trusleri, has been described as an archaic placental mammal by Rich et al. (1997) although its affinities are controversial (e.g., Musser and Archer, 1998; Kielan-Jaworowska et al., 1998). Luo et al. group Au. nyktos, Am. mahabo and monotremes together as part of an endemic radiation of Gondwanan mammals with tribosphenic dentitions (or dentitions derived from this pattern in the case of monotremes) separate from the northern tribosphenic radiation (but see, for example, Pascual et al., 2002). Characters of the teeth and jaws (the only material recovered for Am. mahabo and Au. nyktos) were analysed together with craniodental and postcranial characters for monotremes and all other known mammalian taxa. Results suggested a division of 'tribosphenic' mammals into two morphologically and geographically distinct groups - a northern group and a southern group. Luo et al. have proposed a new classification: a southern subclass Australosphenida (including Am. mahabo, Au. nyktos and monotremes) and a northern subclass Boreosphenida (including the northern hemisphere tribosphenic therians). This concept counters a northern origin for tribosphenic mammals and suggests that mammals with advanced, tribosphenic teeth appeared independently in the southern hemisphere before they appeared and radiated in the northern hemisphere.

**Evolutionary trends**

What are we to make of the basic monotreme body plan: ‘tribosphenic’ teeth, primitive shoulder girdle and lower jaw, but somewhat more advanced pelvic girdle? The total monotreme design is a complex of features, some of which have probably developed convergently with those of therian mammals. There is no consensus among researchers about which anatomical systems are so unique and complex that they can only have evolved once. The middle ear ossicular system, a mobile shoulder girdle and tribosphenic dentition have all been called too complex to have arisen more than once in mammalian evolution. However, Ji et al. (1999) have concluded that homoplasies are common in the postcranial skeleton (especially in the pectoral girdle and forelimbs but less so in the
pelvic girdle and hindlimb) and that many seemingly shared, specialised features may be convergent, evolving at least twice in Mesozoic mammals. Several studies are in general agreement that dental characters may be more highly homoplasic than those of the postcranium, which may explain the 'reinvention' of a tribosphenid-like tooth form.

A modern shoulder appears to have had an ancient origin; monotremes in this respect are at a very basal level, along with cynodonts and the earliest mammals, as discussed above. On morphological grounds, evidence points to an ancient origin – from the early to middle Jurassic - for monotremes. Their unique combination of features is most likely the result of early branching, a specific suite of inherited features, and a long period in which to refine specializations.

Summary

Is it possible to come to a consensus about relationships and origins? The short answer may be 'no' at present, but for some very interesting reasons. Firstly, the conflicting results between morphological and molecular studies should not be dismissed, but should be seen as a catalyst for further investigations. Secondly, the relationships of Mesozoic mammals need further resolution; taxonomy of Early to Middle Jurassic mammals, 'triconodonts' and multituberculates are currently in flux. New fossil finds will help to determine the suites of features in these early groups, which will in turn help to clarify the position of monotremes. Thirdly, we need to keep an open mind about biological evolutionary processes that may have combined to create the unique combinations of features found in a number of mammalian groups. If reversions rather than retentions can explain the primitive features of monotremes, there must be an evolutionary mechanism to account for this reinvention and perhaps to allow a close relationship between monotremes and more recent mammals, particularly marsupials. Studies into such mechanisms - the switching on of hox genes, as a pertinent example - are ongoing and may help to provide answers.

We may find that the most satisfying answer to the question of monotreme origins is the view promoted for most of the last 200 years, since their discovery by western science. Living monotremes may be the last surviving representatives of the earliest mammals that have miraculously persisted for perhaps well over 150 million years. The long-term survival of these ancient mammals can only be assured by addressing the issues of habitat preservation, hunting pressures and protection of populations from disease or predation.

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CHAPTER 3

New information about the skull and dentary of the Miocene platypus *Obdurodon dicksoni* and a discussion of ornithorhynchid relationships

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Chapter 3

Chapter 3 (‘New information about the skull and dentary of the Miocene platypus *Obdurodon dicksoni*, and a discussion of ornithorhynchids relationships’) was written as a contribution to ‘Platypus biology: recent advances and reviews’, a special issue of *Philosophical Transactions of the Royal Society of London (B)*, Vol. 352 [1372], 1998 edited by P. R. Manger and J. D. Pettigrew. Authors were invited to submit papers on all aspects of platypus research: field biology, anatomy, genetics or evolution.

Chapter 3 presents a detailed investigation and reconstruction of the skull and mandible of *Obdurodon dicksoni* from the Riversleigh World Heritage Fossil Deposits in northwest Queensland. Material includes a beautifully preserved skull (the only fossil ornithorhynchid skull older than the Pleistocene), partial dentaries and isolated molar teeth. A reconstruction of the skull and lower jaw was made possible by the completeness of the fossil material and by its exemplary preservation. Comparisons are made with the living platypus *Ornithorhynchus anatinus*; cranial foramina are described; and skull structures synonymised with the work of Zeller (1989a) on *Ornithorhynchus*. Some features of ‘soft’ anatomy – markings or foramina on the skull and dentary for nerves, blood vessels or, in this case, the bill of the platypus – are investigated. This is often not the case in many fossil mammals since abrasion and preservation can obliterate such anatomical detail. Comparisons are also made between *Obdurodon* and non-monotreme fossil mammals in order to determine if some of the more plesiomorphic features of *Obdurodon* shed light on monotreme relationships. Differences in palaeoecology, distribution, diet and lifestyle are also discussed.
New information about the skull and dentary of the Miocene platypus Obdurodon dicksoni, and a discussion of ornithorhynchid relationships

A. M. Musser and M. Archer

A reconstruction of the skull, dentary and dentition of the middle Miocene ornithorhynchid Obdurodon dicksoni has been made possible by acquisition of nearly complete cranial and dental material. Access to new anatomical work on the living platypus, Ornithorhynchus anatinus, and the present comparative study of the cranial foramina of Ob. dicksoni and Or. anatinus have provided new insights into the evolution of the ornithorhynchid skull. The hypertrophied bill in Ob. dicksoni is seen here as possibly apomorphic, although evidence from ontogenetic studies of Or. anatinus suggests that the basic form of the bill in Ob. dicksoni (where the rostral crura meet at the midline) may be ancestral to the form of the bill in Or. anatinus (where the rostral crura meet at the midline in the embryonic platypus but diverge in the adult). Differences in the relative positions of cranial structures, and in the relationships of certain cranial foramina, indicate that the cranium may have become secondarily shortened in Or. anatinus, possibly evolving from a more elongate skull type such as that of Ob. dicksoni. The plesiomorphic dentary of Ob. dicksoni, with well-developed coronoid and angular processes, contrasts with the dentary of Or. anatinus, in which the processes are almost vestigial, as well as with the dentary of the late Oligocene, congeneric Ob. insignis, in which the angular process appears to be reduced (the coronoid process is missing). In this regard the dentary of Ob. insignis seems to be morphologically closer to Or. anatinus than is the dentary of the younger Ob. dicksoni.

Phylogenetic conclusions differ from previous analyses in viewing the northern Australian Ob. dicksoni as possibly derived in possessing a hypertrophied bill and dorsoventrally flattened skull and dentary, perhaps being a specialized branch of the Obdurodon line rather than ancestral to species of Ornithorhynchus. The presence of functional teeth and the robust, flattened skull and dentary in Ob. dicksoni argue for differences in diet and lifestyle between this extinct ornithorhynchid and the living Ornithorhynchus.

Keywords: Obdurodon; Ornithorhynchus; platypus; Monotremata; Riversleigh; Miocene

1. INTRODUCTION

The platypus family, Ornithorhynchidae, is one of four in the order Monotremata, the egg-laying mammals that are today restricted to the Australo-Papuan region. Monotremes are considered to be the most primitive of living mammals because of the retention of ‘reptilian’ characteristics such as oviparity and a therapsid-like shoulder girdle that have been lost in marsupial and placental mammals.

From the time of their discovery in Australia, by Europeans two centuries ago, until 1995, only two monotreme families had been recognized: the semi-aquatic Ornithorhynchidae (the platypus-like monotremes), and the terrestrial Tachyglossidae (the ant-, termite- and worm-eating echidnas). The Early Cretaceous monotreme Steropodon galmani, recovered as a lower jaw fragment with three molars in situ from opal-bearing deposits at Lightning Ridge in New South Wales, Australia, had been included within Ornithorhynchidae when first described because its molar teeth are strikingly similar to the lower molars of known ornithorhynchids (Archer et al. 1985). However, in order to reconcile Steropodon’s great age (approximately 110 million years (Ma) old) with evidence from molecular studies indicating divergence dates between Ornithorhynchidae and Tachyglossidae that possibly postdate the Cretaceous (the latest Cretaceous at the earliest (Westerman & Edwards 1992), Steropodon was placed in its own family, Steropodontidae (Flannery et al. 1995), rather than accept a significantly paraphyletic Ornithorhynchidae. The decision to remove Steropodon from Ornithorhynchidae was taken in a paper describing Kollikodon ritchiei (Flannery et al. 1995), an extraordinarily derived, new monotreme with bunodont molars from the same Lightning Ridge locality that produced Steropodon galmani. The addition of Steropodontidae and Kollikodonidae brings the number of known families within Monotremata to four.

The earliest undoubted ornithorhynchid, Monotrematum sudamericanum, is known from late Early Palaeocene deposits of Patagonia, Argentina (Pascual et al. 1992). The oldest Australian ornithorhynchid, Obdurodon insignis, comes from the late Oligocene central Australian Etadunna Formation and was the first pre-Pleistocene ornithorhynchid found, identified by comparison with Ornithorhynchus anatinus, which retains vestigial molar teeth in the juvenile (Woodburne & Tedford 1975). A second, undescribed Obdurodon species has been recovered from the Mammalon Hill locality of the Etadunna Formation. Obdurodon dicksoni,
from early and middle Miocene limestone deposits at Riversleigh, Queensland, Australia, is by far the most complete fossil ornithorhynchid known. Beautifully preserved cranial material as well as isolated molars and premolars have been recovered. The Pliocene ornithorhynchid record is minuscule, with only a limb element of an Ornithorhynchus species recovered (Rich 1991). Pleistocene Ornithorhynchus material, much of it found in conjunction with archaeological sites, appears to be identical to that of the living species *Or. anatinus* (Archer et al. 1978; Marshall 1992; Davis 1996).

The amphibious ornithorhynchids have been considered to be the most plesiomorphic living monotreme family because of their more generalized dietetic niche and longer list of plesiomorphic features (e.g. formation of the secondary lateral wall of the braincase and contents of the cavum epiptericum (Zeller 1989c), and certain features of the middle ear such as the lack of a cochlear aqueduct in *Or. anatinus* (Zeller 1993)). The palaeontological record supports this placement; whereas, the ornithorhynchid fossil record stretches back to the early Palaeocene (Pascual et al. 1992), the first tachyglossid does not appear in the fossil record until possibly the middle Miocene (Griffiths et al. 1991; Archer et al. 1995).

This study presents a reconstruction of the skull, dentary and dentition of *Ob. dicksoni*, the only pre-Pleistocene ornithorhynchid for which the skull is known. The skull, previously described by Archer et al. (1992, 1993), was found with all premolars present but all molars absent. It provides our best look at a relatively plesiomorphic ornithorhynchid as well as a functional morphic ornithorhynchid as a functional morphic ornithorhynchid. The present work describes and identifies cranial foramina in the skull and compares these with the foramina in *Or. anatinus*. Features of the soft anatomy that can be inferred from the fossil skull are discussed.

Skull nomenclature is primarily that of Zeller (1989c). Dental terminology is that of Archer et al. (1993).

2. MATERIALS AND METHODS

The *Ob. dicksoni* holotype (QM F20568) is an almost complete skull with both left and right first and second premolars in place. The major damage is to the cranial roof where a narrow oblique section of the skull is missing. The basioccipitum sustains slight damage on the left side but is essentially complete. The left lateral side of the rostrum and parts of the palate are incomplete. No os paradoxum, ectopterygoids or tympanic bones (fragile, loosely attached structures in *Or. anatinus*) have been preserved.

The skull was recovered from freshwater carbonate deposits from Ringtail Site, Ray’s Amphitheatre, Gag Plateau, Riversleigh World Heritage property. Ringtail Site is low in the System C sequence interpreted by Archer et al. (1995) to be middle Miocene in age. Because molars were absent from the skull, isolated molars from the same site (QM F18973, QM F16888, QM F18983 and QM F23994) were used to complete the reconstruction. Two dentary fragments (also edentulous) have been recovered: a section of a left dentary that includes the anterior part of the molar tooth bed with alveoli for a six-rooted M/1 (QM F18977 from Neville’s Garden Site, System B sequence; early Miocene *vide* Archer et al. (1995)); and a more posterior fragment (also of a left dentary) that includes the posterior part of the tooth bed with alveoli for a five-rooted M/2 and single-rooted M/3 (QM F18981 from Quentin’s Quarry, System C). The second fragment preserves most of the coronoid process, mylohyoid process, angular process and ascending ramus of the dentary.

(a) Referred specimens

QM F18978 from Neville’s Garden (System B); QM F30249, F30716 and 30717 from Dirk’s Towers (System B); QM F18976, F18979, F18980, F18982, F18983, F18986, F18987, F18988, F18989, F20755 and F23722 from Ringtail Site (System C); QM F18974, F18975 and F18977 from Quentin’s Quarry (System C); QM F18984 from Bob’s Boulders Site (System C).

Congeneric comparisons were made with late Oligocene (Woodburne et al. 1993). *Ob. insignis* material from central Australia (QM F1627, left dentary fragment; SAM P18087, lower left molar (holotype)). Comparisons with fossil Ornithorhynchus were made from Pleistocene *Or. anatinus* (QM F707, edentulous left dentary fragment). Comparisons with modern *Or. anatinus* involved a juvenile skull and mandible from Queensland (QM J25753); a series of juvenile and adult skulls from Victoria (C5569, C25089, C25093 and C26491); and an os paradoxum from New South Wales (AM M26638).

(b) Abbreviations


3. RESULTS

Because general descriptions of the *Ob. dicksoni* skull appear in Archer et al. (1992, 1993), the present work focuses on detailed descriptions of features pertinent to the reconstruction presented herein and to the cranial foramina, which are described here for the first time. The reconstructed skull and dentary of *Ob. dicksoni* (figure 1a–c) are compared with those of an adult male *Or. anatinus* (figure 2a–c).

To review Archer et al. (1992, 1993), the main features distinguishing *Ob. dicksoni* from *Or. anatinus* include: a hypertrophied rostrum in *Ob. dicksoni* that is both wider and longer than the rostrum in *Or. anatinus*; lack of fusion of the component rostral bones in *Ob. dicksoni*, clearly showing the septomaxillae separate from and overlying the premaxillae and contrasting with the relatively well-fused rostrum in adult *Or. anatinus*; a remarkably flat table in *Ob. dicksoni* with no downward deflection of the rostrum as in *Or. anatinus*; expanded zygoma on the skull and well-developed angular and coronoid processes on the dentary in *Ob. dicksoni* for robust jaw adductor musculature; an ovoid, enclosed interseptomaxillary fenestra (a narial interspace through which the dorsal nostrils open) in *Ob. dicksoni*, a space which is open and V-shaped in *Or. anatinus*; prominent anterolateral maxillary processes.
Figure 1. Reconstruction of the skull and dentary of *Obdurodon dicksoni*. Based on QM F20568 (holotype), and QM F18977 and QM F18981 (dentary fragments). (a) Dorsal view, (b) ventral view and (c) lateral view. For abbreviations, see table 1.
formed by extensions of the maxillae in *Ob. dicksoni* (processes that are absent in *Or. anatinus*; and well-developed, functional teeth (albeit with shallow roots) in *Ob. dicksoni*, in contrast to the keratinous pads that take the place of true teeth in the adult *Or. anatinus*).

With only a single *Ob. dicksoni* skull, it cannot be said with certainty where within the size range for the species this skull falls. However, because some of the teeth in the sample are larger than ones that would have fit into the alveoli of this skull, this specimen would not have been at the top end of the size range for the species (assuming for the present that all Riversleigh material represents a single taxon [Archer et al. 1992, 1993]).

(a) Dorsal view (figure 1a)

The left premaxilla, septomaxilla, lateral aspect of the rostrum, anterior section of the zygomatic arch and the missing diagonal section of the skull roof have been restored in the illustration of the skull. The os paradoxum, the median dumb-bell-shaped bone anterior to the vomer and maxilla and flanked by the rostral prongs of the premaxillae in *Or. anatinus* (figure 2a), has been reconstructed for *Ob. dicksoni* because the construction of the snout is basically similar in both ornithorhynchs. The origin of this interesting bony element, known to date only in *Or. anatinus*, is not known. Hypotheses have variously suggested that it is homologous with the premaxal of the pig (Turner 1883); that it is the fused rudiment of the 'reptilian' anterior vomer or prevomer (Wilson 1894; Broom 1932); or that it a vestige of the palatal processes of the premaxillae (Parrington & Westoll 1940). Zeller (1989a) could not positively identify this bone as either a prevomer or as part of the premaxilla but he does believe that it is a very specialized feature in *Or. anatinus* and is not a 'reptilian' retention. Its scroll-like posterior-dorsal flanges support the medial part of Jacobson's cartilage housing the vomeronasal, or Jacobson's, organ in *Or. anatinus* (Symington 1891).

The bones of the rostrum in this adult skull are comparatively unfused, allowing for examination of the sandwiching of component bones that form the rostrum. The right premaxilla and septomaxilla are complete showing that the shorter septomaxilla terminates lateral to the underlying premaxilla, which meets its opposite at the midline. This contrasts with the rostrum in adult *Or. anatinus* where the premaxilla and septomaxilla are fused together in the adult and the resulting prongs of bone do not meet at the midline. However, in foetal *Or. anatinus*, illustrated by Zeller (1989a), the premaxillae are fused ventrally and the septomaxillae, overlying the premaxillae and separated from them by the developing marginal cartilage, terminate lateral to the midline (in part to accommodate the os carunculae) as they do in *Ob. dicksoni*.

The septomaxilla in monotremes has been recognized by some authors as being homologous with the septomaxilla in 'reptiles', therapsids and some early mammals such as *Docodon* (e.g. Watson 1916; de Beer 1937; Goodrich 1958; Kermack & Kielen-Jaworowska 1971; Kuhn 1971; Zeller 1989a; Archer et al. 1992, 1993), but has been misidentified as the premaxilla (e.g. van Bemmelen 1901; Wilson 1901; Kesteven & Furst 1929). Recent studies have confirmed that a septomaxilla is retained in monotremes and in some edentates among living mammals (Zeller et al. 1993). The huge, discrete septomaxilla in *Ob. dicksoni* clearly illustrates the unequivocal delineation of this splint-like bone from the premaxilla in an adult monotreme. The septomaxilla, comparatively large in both *Ob. dicksoni* and in *Or. anatinus*, is especially well developed in *Ob. dicksoni* because of the hypertrophy of the snout. This bone helps to support and retain the marginal cartilage sandwiched in between the septomaxillae and maxillae dorsally, and the premaxillae and maxillae ventrally, in *Or. anatinus*, and would have done so in *Ob. dicksoni* (Archer et al. 1992, 1993).

The widened area on the dorsolateral surface of the maxilla dorsal to the insertion of M1 in *Ob. dicksoni* is quite thin, and it appears as if the shallow roots of the molars breached the bone in life; this condition is not seen in *Or. anatinus* skulls examined. Posteriorly the molar alveolus open ventral to the eye socket. In *Or. anatinus*, fenestrations occur in the approximate positions of the missing molar alveoli.

The cranial bones in *Ob. dicksoni* are well fused (unlike the bones of the rostrum), a feature also seen in multituberculates (Kermack & Kielen-Jaworowska 1971). The *Ob. dicksoni* skull shows moderately developed temporal muscle scars (for Mm. temporalis, trapezius anterior, rhomboideus and pterygoideus [Schulmann 1906], that are also evident on *Or. anatinus* (figure 2a). Development of these scars is related to age and sex in *Or. anatinus*, being much more evident and elaborate in adult males.

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**Table 1. Abbreviations for figures 1a–c and 2a–c**

| a. d. nl. | aditus ductus nasolacrimalis |
| a. p. mx. | anterior process of maxillare |
| c. io. | canalis infraorbitalis |
| c. temp. | canalis temporalis |
| cr. par. | crista parotica |
| ect. | ectopterygoid |
| f. V3 | foramen for V3 |
| f. V4 | foramen for V4 |
| f. car. | foramen caroticum |
| f. ethm. | foramen ethmoideum |
| f. jug. | foramen jugulare |
| f. mag. | foramen magnum |
| f. mand. | fossa mandibularis |
| f. mand. m. | foramen mandibulare medium |
| f. mf. | foramen maxillofaciale |
| f. mm. a. | foramen maxillopalatinum anterius |
| f. mm. p. | foramen maxillopalatinum posterius |
| f. pal. | foramen palatinum |
| f. pmx. a. | foramen premaxillare anterius |
| f. sph. | foramen sphenopalatinum |
| f. orb. | fissura orbitonasalis |
| ju. | jugale |
| k. d. pd(s). | keratinized dental pad(s) |
| ismx. f. | interseptomaxillary fenestra |
| mx. | maxillare |
| na. | nasale |
| o. par. | os paradoxum |
| pmx. | premaxillare |
| pr. ang. | processus angularis |
| pr. cor. | processus coronoideus |
| s. rds. | secateuring ridges |
| s. temp. | canalis temporalis |
| s. io. | canalis infraorbitalis |

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Figure 2. The skull and dentary of *Ornithorhynchus anatinus* (skull and dentary, C25089 with supplemental information from C25093 and C26491; os paradoxum, M26638). (a) Dorsal view, (b) ventral view and (c) lateral view. For abbreviations, see table 1.
and better developed in *Or. anatinus* than in tachyglossoids, which have a reduced masticatory apparatus. Because the jaw musculature was more robust in *Oh. dicksoni* (a necessary corollary of a more functional dentition as evidenced by a more well-developed mandible and wider zygoma), it might be assumed that muscle scars would be prominent in larger/male *Oh. dicksoni*.

The small, triangular jugal, reconstructed on the left side, angles medially in *Oh. dicksoni* as in *Or. anatinus*, but there is no shallow notch along the dorsal margin of the zygoma posterior to the jugal, in contrast to the situation in *Or. anatinus*. Fusion has obscured any indication of sutures. The jugal (erroneously reported as absent in Monotremata (Kermack & Kielen-Jaworowska 1971), but which is absent only in tachyglossoids (Griffiths 1978), is reduced in the two ornithorhynchids compared here.

(b) *Ventral view (figure 1b)*

Ventrally, the rostrum and palate in *Oh. dicksoni* exhibit a complex lamination of the maxillae and premaxillae. Neither side of the central palatal region is complete in this specimen (the right side being more intact than the left).

The palate has deep embrasures anteriorly in approximately the same position that longitudinal epithelial ridges occur in *Or. anatinus* (the anterior horny plates of Poulton (1889)) (figure 2b). These ridges are formed from thickenings in the oral epithelium of the stratum corneum and are penetrated by long, thin papillae that create an irregular surface along the plates (Poulton 1889). They function as grasping and holding devices in the absence of anterior dentition, aiding in securing and manipulating prey and growing throughout the life of the animal to combat wear caused by grit and sand ingested during feeding (Poulton 1889). A small sulcus indicates the presence of these ridges in *Or. anatinus*. In *Oh. dicksoni* these pits are exceptionally deep, presumably for greatly enlarged epithelial ridges of the same type (Archer et al. 1993), and such epithelial ridges have been reconstructed here.

The ectopterygoids and ectotympanics have been reconstructed here as they appear in *Or. anatinus*. Although the function of the ectopterygoids in *Or. anatinus* is not known, Griffiths (1978) suggests that they offer resistance to upward movements of the posterior part of the tongue and could aid in transferring food from the cheek pouches to the oral cavity. Ectopterygoids (incorrectly identified as alisphenoids Kesteven & Furst 1929) are retained in all living monotremes (although morphologically dissimilar in the two families (Griffiths 1978)), and are also present in multituberculates and possibly in docodonts, although absent in therians (Kermack & Kielen-Jaworowska 1971). They may represent remnants of ‘reptilian’ pterygoids (Goodrich 1958). Facets on the palatines for the ectopterygoids are comparatively large and broad in *Oh. dicksoni* and, although they have been reconstructed as they appear in *Or. anatinus*, the ectopterygoids may have been more robust in *Oh. dicksoni*.

The monotreme car region is plesiomorphic in that it is open ventrally, with no osseous floor for the epitympanic recess, although there is a slight overhang in tachyglossoids formed by the ectopterygoid. Absence of an osseous floor is also a feature of several plesiomorphic marsupials including some borhyaenids and several Triassic didelphimorphians. In some features, particularly the tight connection between the ectotympanic and malleus, the tympanic region of monotremes resembles that of therapsids (Zeller 1993) and multituberculates (Meng & Wyss 1995). The horseshoe-shaped ectotympanic in *Or. anatinus* is morphologically similar to the angular bone (from which it was derived) of some Mesozoic synapsids (Zeller 1993) and the multituberculate *Lambdopalis bulla* (Meng & Wyss 1995). The horizontal orientation of the ectotympanic in all living monotremes is a derived condition related to enlargement of the cranial cavity; the ectotympanic of *Lambdopalis bulla* is similarly oriented, a feature regarded by Meng & Wyss (1995) to be a possible synapomorphy linking the two groups.

The basisphenoid forms a prominent crest in *Oh. dicksoni*, extending well beyond the posterior margin of the palate. It is a thick ridge of bone slightly bulbous at its caudal end, in contrast to the thin plate of bone that forms this crest in *Or. anatinus*. The orientation of the glenoid fossa is much more oblique in *Oh. dicksoni* than in *Or. anatinus*, where the fossae are oriented nearly perpendicular to the long axis of the skull. The postero medial border of the fossa forms a lip in *Oh. dicksoni*, whereas in *Or. anatinus* there is little indication of a discrete termination of the fossa. This may reflect a tighter jaw articulation in *Oh. dicksoni* as occlusion of the triangular blades of the molars would have necessitated a more vertical or vertical oblique masticatory stroke. This contrasts with a more transverse stroke in *Or. anatinus* where the wide, flat, keratinous pads may move back and forth against each other in a more horizontal plane.

The most fundamental difference between *Oh. dicksoni* and *Or. anatinus* is the presence of rooted premolars and molars, apparently functional throughout life, in *Oh. dicksoni*. Teeth are absent in adult *Or. anatinus* (figure 2b), although juveniles retain vestigial molars until about one month after leaving the burrow (Griffiths 1978). Dental terminology used here is that of Archer et al. (1993) adapted from Every (1972, 1974) (table 2). This thegotic terminology is used rather than that developed for tribosphenic mammalian teeth both because monotreme molar cusps may not be homologous to those of tribosphenic mammals (Archer et al. 1992, 1993), and because this terminology emphasizes function rather than homology.

The upper molar row depicted (figure 1b), was drawn using left teeth (LM1/1=QM F16888 and LM2/2=QM F18973) and reversed to create the right molar row. Molars chosen from among paratypes from Ringtail Site have been sized to fit and ‘reinserted’ into the molar alveoli.

The adult dental formula for *Oh. dicksoni* is apparently P1-2/1-2, M1-2-1/1-3 (the upper dentition has been mislabelled as P3-4/ and M1-3/ in Archer et al. (1993)). This differs from the postcanine dental formula established for *Or. anatinus* (Green 1937) in having only two, rather than three, upper molars. An abrupt change in tooth morphology distinguishes the uncusped premolariform teeth from the wide molariform teeth, a monotreme characteristic evident in the earliest taxa known, *Stenodonen galmani* and *Kallikodon ritchiei* (Archer et al. 1983; Flannery et al. 1993). Although questions remain about the identity of the premolariform teeth (Luckett & Zeller 1989,
Table 2. Abbreviated table of thecotic terms relevant to dental structure in ornithorhynchids

<table>
<thead>
<tr>
<th>structure</th>
<th>upper dentition</th>
<th>lower dentition</th>
</tr>
</thead>
<tbody>
<tr>
<td>crest(s) or loph(s)</td>
<td>drepanon(s)</td>
<td>drepanid(s)</td>
</tr>
<tr>
<td>cusp(s)</td>
<td>akis(s)</td>
<td>akid(s)</td>
</tr>
<tr>
<td>paracone(s); paraconid(s)</td>
<td>parakis(es)</td>
<td>parakid(s)</td>
</tr>
<tr>
<td>a blade subtended by two alises</td>
<td>diakididrepanon(s)</td>
<td>diakididrepanid(s)</td>
</tr>
<tr>
<td>two blades sharing an akis, creating a V-shaped blade system</td>
<td>triakididrepanon(s)</td>
<td>triakididrepanid(s)</td>
</tr>
</tbody>
</table>

Archer et al. 1993), we have interpreted the premolariform teeth to be premolars and molariiform teeth to be molars.

The upper premolars are single crowned, with a primary akis (presumably the parakis) and well-developed, rugose basal cingula on both teeth except beneath the lingual base of the parakises. P1/ is smaller than P2/.

The first premolar is double rooted, whereas the second premolar appears to have three roots (a small accessory root evident from the lingual side), a feature that could cause problems with its identification as a premolar. The premolariform morphology and contrast in size and shape with the molar teeth, however, suggest that the multiple-rooted condition is autapomorphic (Archer et al. 1993; but see Lockett & Zeller 1989).

Ornithorhynchid molars are distinguished by triakididrepanos (three-cusped, two-blade structures) with the junctions of the blades lingual on the upper jaw and buccal on the lower jaw. This apparently autapomorphic dental morphology, with a reversed system of triangular blades, mimics with two teeth the function of four tribosphenid molars (Archer et al. 1993). M1/ is square in shape, with both anterior and posterior triakididrepanon bladder systems; lingual and buccal cusps are present; and a wide occluding basin is present between the triakididrepanos. The anterior cingulum is small but the posterior cingulum is quite well developed. M2/ is wider than long, with a large triakididrepanon anteriorly and a smaller triakididrepanon posteriorly. Lingual and buccal cusps are likewise present. The anterior cingulum is well developed (although the posterior cingulum is not), and together with the posterior cingulum of the M1/ it forms a large interdental basin not unlike that formed between the triakididrepanos of M1/ (Archer et al. 1993).

The molars have multiple, shallow roots (less than one-third the height of the crowns (Archer et al. 1993)) that may have been only loosely held in the alveoli in life, a condition most certainly responsible for the lack of molar teeth not only in the skull but also in the edentulous dentary fragments recovered. Many of the Riversleigh molars have lost or damaged roots (as do both of the upper molars—QM Fl6888 and QM Fl8973—used in this reconstruction) or are enamel caps. The roots may have been buttressed by supportive gum tissue in life in order to maintain stability. The skull has alveoli for a six-rooted M1/ and four-rooted M2/.

(e) Lateral view (figure 1c)

It is in the lateral view that the comparative robustness of the *Ob. dicksoni* skull is most obvious. The relatively unreduced dentary with well-developed coronoid and angular processes correlates with the heavier skull and contrasts with the more gracile form of *Or. anatinus* (figure 2c).

Noted by Archer et al. (1992, 1993), the flattened nature of the skull and dentary differs from the skull of *Or. anatinus*, where the rostrum is ventrally deflected from the basi-cranium and the dentary angles cranially in a comparatively sharp fashion, making the profile in *Or. anatinus* comparatively deeper than the profile in *Ob. dicksoni*.

A deep groove between the lamination of the septomaxilla and maxilla dorsally and that of the premaxilla and maxilla ventrally for the insertion of the marginal cartilage runs anteroposteriorly from the anterior tip of the rostrum to the f. maxillariaceae. In proportion, the depth of this groove quite exceeds that in *Or. anatinus*, an indication that the marginal cartilage was much more well developed in *Ob. dicksoni* than in *Or. anatinus* (Archer et al. 1992, 1993).

The zygomatic arch is robust; the arch is especially deep ventral to the eye socket and dorsal to the ear region in comparison to *Or. anatinus* (figure 2c). There appears to be no evidence of a lacrimal in *Ob. dicksoni*, which is absent from both living monotreme families (Watson 1916; De Beer 1937; Zeller 1989a; contra Kesteven & Furst 1929).

The two dentary fragments, both of the left side, provide complementary information. The more anterior fragment, extending from just in front of the origin of the molar tooth bed and terminating posterior to the alveoli for M1/1, retains the alveoli for M1/1 and a remnant of the mandibular foramen. The alveolar pattern indicates that M1/1 had six roots, as does the holotype, a left M1/1, of *Ob. insignis* (none of the M1/1s recovered from Riversleigh have complete sets of roots). The more posterior fragment (described in Archer et al. (1993)), missing the body of the dentary anterior to the alveoli for M1/2 as well as the proximal part of the ascending ramus (including the articular condyle), preserves the alveoli for a five-rooted M1/2 and a single-rooted M3. All alveoli open into the lumen of the dentary.

Before the discovery of the posterior jaw fragment assigned to *Ob. dicksoni*, the extent of development of the coronoid and angular processes in extinct ornithorhynchids was not known. The fragile, plate-like coronoid process has been lost on the jaw fragment recovered for *Ob. insignis*, the only other pre-Pleistocene ornithorhynchid jaw fragment known, and is also missing from the Steropodon galmani jaw fragment.

In *Ob. dicksoni* the coronoid process is well developed, reflecting the need for a wide area of attachment for the strong temporalis muscles that would have been present in the Riversleigh taxon. There is a fairly long, medially inflected angular process in *Ob. dicksoni* (broken at the tip in this specimen), which contrasts with the dentary of *Or. anatinus*, where this process is either absent or much reduced. It appears to contrast as well with the dentary of *Ob. insignis*, where the angular process, although also broken at the tip, appears more reduced than in *Ob. dicksoni*. The *Ob. dicksoni* dentary possesses a well-developed
internal ‘mylohyoid’ process (broken just past the origin), confirmation that this process in ornithorhynchids does not represent a vestige of the coronoid process. The ascending ramus of the jaw curves smoothly upward to the condylar region in Ob. dicksoni, rather than exhibiting an angled bend as the ramus does in both Ob. insignis and Or. anatinus; this would correlate with the flattening of the skull base and lack of a deflected bill in Ob. dicksoni.

As in the upper dentition, there is a sharp change in morphology in the lower dentition from premolariform to molariform teeth. The single-cusped lower (presumptive) premolars (found as isolated teeth and not yet described) both have only two roots (Archer et al. 1993). P/1 is long and narrow, whereas P/2 is shorter and wider (Archer et al. 1993). The basal cingulid is complete in P/1 but incomplete lingually in P/2 (Archer et al. 1993).

Except for its larger size, the M/1 of Ob. dicksoni is nearly identical to the M/1 of Ob. insignis, originally interpreted as an upper-right second molar (Woodburne & Tedford 1975). The anterior blade is a diakidirepanid and the posterior blade is a triakidirepanid. As with the corresponding upper molar, the posterior cingulum is well developed, as is the anterior cingulum of M/2, creating an occlusal basin for the posterior triakidirepanon of the M1/ (Archer et al. 1993). No M/2 has been found among Riversleigh molars to date, so our reconstruction relies on extrapolation from the morphology of the M/2 of Steropodon galmani and the worn M/2 recovered for Ob. insignis. Both anterior and posterior halves of M/2 apparently had well-developed triakidirepanid blade systems (Archer et al. 1993).

The posterior-most alveolus in both the Ob. dicksoni and Ob. insignis dentaries indicates that a single-rooted, extremely reduced M/3 was present. Such a vestigial tooth could be expected from an animal that had already lost any trace of a third molar from the upper toothrow. Two undescribed Riversleigh teeth that appear to be M/3s have been recovered from Ringtail Site. The M/3 would have played only a minor functional role in the occlusion of the upper and lower molar rows.

**Foramina**

The extensive network of cutaneous nerves that innervate the electro- and mechanoreceptors of the upper and lower bill in Or. anatinus are the ophthalmic (V₂), maxillary (V₂), and mandibular (V₃) branches of the sensory part of the trigeminal nerve (Manger 1994). Edgeworth (1935) describes the trigeminal nucleus as single, a feature shared with Dipnoi, Holoccephali, Plagiostomi, Ganoidei and Amphibia, although he declines to call this plesiomorphic. These branches exit through 14 large, distinct foramina on the skull and dentary, a remarkably high number of trigeminal foramina within Mammalia (Huber 1930). The foramen innervating the dermal dorsal shield (the asterisk (*) of Zeller (1989a)) and the foramen for V₂ in Or. anatinus are larger than those of any other mammal, highlighting the extreme specialization of the platypus bill (Zeller 1988).

In therian mammals, the trigeminal system innervates the region around the vibrissae, the acquisition of vibrissae being considered a synapomorphy of therian mammals (Huber 1930). The elaboration of the electrical sense, however, may be a monotreme synapomorphy (Manger 1994). The trigeminal system, interestingly, is enlarged in some semi-aquatic placental mammals such as *Micropotamogale* to innervate the well-developed vibrissae important in underwater navigation (Stephan & Kuhn (1982), cited in Zeller (1988)).

The unique arrangement of the rostral foramina for the trigeminal nerve in monotremes differs fundamentally from the arrangement of these foramina in marsupials and placentals (Huber 1930). The placement of the rostral foramina is essentially the same in all living monotremes (Huber 1930). Although there are marked differences between the two families in the arrangement of the foramina of the braincase, the course of the cranial nerves relative to the vestiges of the primary wall of the braincase are also the same in both families (Zeller 1989a).

There have been many arguments over the homologies of the cranial foramina in monotremes (see table 3). Zeller (1989a) refrains from using terminology that implies homology if there is doubt or error (e.g. the controversy over the homology of the ‘foramen ovale’), preferring to define the foramen in question by its contents. The present account follows Zeller in this decision. In addition, Huber (1930) cites the misinterpretation of the anterior rostral foramina as vestigial alveoli for incisors and canines by Abel (1922) and Weber (1927).

The structure and placement of the cranial foramina in Ob. dicksoni are basically similar in position to the matching foramina in Or. anatinus. Therefore, it is assumed here that the innervation and vasculature would be essentially the same for both taxa.

**Cranial foramina**

In Ob. dicksoni there is a small foramen on the ventral surface of the premaxilla close to the midline where the distal ends of the premaxillae meet. This foramen is not present in post-foetal Or. anatinus and is not seen in the foetal Or. anatinus modelled in Zeller (1989a). It resembles a small foramen in the anterior premaxilla in Morganucodon (Kermack et al. 1981) and the tritylodont *Oligokyphus* (Kuhne 1956), which, according to Kuhne, is also present in *Thrinaxodon loricatus* and *Gomphognathus cl. mastacus*. We call this foramen in Ob. dicksoni the foramen premaxillare anterius.

The foramen maxillopalatinum anterius carries the branches of V supplying the anterolateral aspect of the bill in Or. anatinus (Manger 1994). In Ob. dicksoni this foramen appears as a notch bounded by the premaxilla ventromedially, the anterolateral process of the maxilla laterally and the septomaxilla dorsomedially. In Or. anatinus, where these large anterolateral maxillary processes do not develop, the anterior maxillopalatine foramen is a slit-like canal formed by the premaxilla medially and the maxilla laterally, terminating anteriorly at the anterolateral junction of the septomaxilla and maxilla. A similar foramen through the septomaxilla near the junction of the premaxillary–maxillary suture is seen in both *Sinoconodon* (Crompton & Lao 1993) and in the Upper Permian gorgonopsid *Disaea quadra* (Kermack & Kermack 1984). Because the maxilla forms a greater part of the dorsal surface of the bill in Ob. dicksoni, this foramen more closely resembles the septomaxillary foramen in these earlier taxa than does the foramen in Or. anatinus.
Table 3. Table of synonyms for the major foramina of the skull and dentary in Ornithorhynchus anatinus and Obdurodon dicksoni

(The terminology used by van Bemmelen (1901), Kesteven & Furst (1929), Jollie (1962), and Zeller (1989a, 1993) refers to foramina in *Or. anatinus*. Terminology of Archer et al. (1993) refers to foramina in *Ob. dicksoni*. The dorsal foramina for egress of the ethmoid nerve are of uncertain homology and thus are identified by an asterisk as in Zeller (1989a))

<table>
<thead>
<tr>
<th>foramina</th>
<th>synonyms</th>
<th>reference</th>
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<tbody>
<tr>
<td>foramen maxillopalatinum anterius</td>
<td>foramen infraorbitale anterius</td>
<td>van Bemmelen (1901), Kesteven &amp; Furst (1929)</td>
</tr>
<tr>
<td></td>
<td>infraorbital canal</td>
<td>Jollie (1962)</td>
</tr>
<tr>
<td></td>
<td>infraorbital foramen</td>
<td>Zeller (1989a)</td>
</tr>
<tr>
<td>foramen maxillopalatinum posterius</td>
<td>foramen infraorbitale inferius</td>
<td>van Bemmelen (1901), Kesteven &amp; Furst (1929)</td>
</tr>
<tr>
<td></td>
<td>infraorbital canal</td>
<td>Jollie (1962)</td>
</tr>
<tr>
<td></td>
<td>foramen maxillopalatinum posterius</td>
<td>Zeller (1989a)</td>
</tr>
<tr>
<td></td>
<td>infraorbital foramen</td>
<td>Archer et al. (1993)</td>
</tr>
<tr>
<td>foramen palatinum</td>
<td>foramen palatinum</td>
<td>van Bemmelen (1901), Kesteven &amp; Furst (1929),</td>
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<tr>
<td></td>
<td>anterior palatine foramen</td>
<td>Zeller (1989a)</td>
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<td>greater palatine foramen</td>
<td>Archer et al. (1993)</td>
</tr>
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<td>foramen maxillofaciale</td>
<td>foramen infraorbitale laterale</td>
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</tr>
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<td></td>
<td>foramen infraorbitale</td>
<td>Kesteven &amp; Furst (1929)</td>
</tr>
<tr>
<td></td>
<td>infraorbital canal</td>
<td>Jollie (1962)</td>
</tr>
<tr>
<td></td>
<td>foramen maxillofaciale</td>
<td>Zeller (1989a)</td>
</tr>
<tr>
<td></td>
<td>infraorbital foramen</td>
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<tr>
<td>*</td>
<td>foramen supraorbitale</td>
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<td>foramen ophthalmicum superius</td>
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<td></td>
<td>infraorbital canal</td>
<td>Jollie (1962)</td>
</tr>
<tr>
<td>*</td>
<td>infraorbital foramen</td>
<td>Zeller (1989a)</td>
</tr>
<tr>
<td>aditus ductus nasolacrimalis</td>
<td>foramen lacrymale</td>
<td>van Bemmelen (1901)</td>
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<td></td>
<td>foramen lachrymale</td>
<td>Kesteven &amp; Furst (1929)</td>
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<td></td>
<td>lacrimal canal</td>
<td>Jollie (1962)</td>
</tr>
<tr>
<td></td>
<td>aditus ductus nasolacrimalis</td>
<td>Zeller (1989a)</td>
</tr>
<tr>
<td>canalis infraorbitalis</td>
<td>foramen infraorbitale</td>
<td>van Bemmelen (1901)</td>
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<tr>
<td></td>
<td>foramen infraorbitale posterior</td>
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<td>canalis infraorbitalis</td>
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<tr>
<td></td>
<td>infraorbital canal</td>
<td>Archer et al. (1993)</td>
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<td>foramen ethmoidicum</td>
<td>foramen ethmoidicum (pro nervo ophthalmico)</td>
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<td></td>
<td>ethmoid foramen</td>
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<td>fissura orbitonasalis</td>
<td>fenestra sphen-o-ethmoida</td>
<td>van Bemmelen (1901)</td>
</tr>
<tr>
<td></td>
<td>fenestra ethmoidalis</td>
<td>Kesteven &amp; Furst (1929)</td>
</tr>
<tr>
<td></td>
<td>orbital fissure—f. rotundum</td>
<td>Jollie (1962)</td>
</tr>
<tr>
<td></td>
<td>fissura orbitonasalis</td>
<td>Zeller (1989a)</td>
</tr>
<tr>
<td>foramen sphenopalatinum</td>
<td>foramen sphenopalatinum</td>
<td>van Bemmelen (1901)</td>
</tr>
<tr>
<td></td>
<td>foramen palatinum posterius</td>
<td>Kesteven &amp; Furst (1929)</td>
</tr>
<tr>
<td></td>
<td>sphenopalatine foramen</td>
<td>Jollie (1962)</td>
</tr>
<tr>
<td></td>
<td>sphenopallatine foramen</td>
<td>Zeller (1989a)</td>
</tr>
<tr>
<td></td>
<td>spenopalatine foramen</td>
<td>Archer et al. (1993)</td>
</tr>
<tr>
<td>foramen for II, III, IV, V₁ &amp; VI</td>
<td>foramen sphen-o-orbitale + opticum</td>
<td>van Bemmelen (1901)</td>
</tr>
<tr>
<td></td>
<td>foramen sphenopticum</td>
<td>Kesteven &amp; Furst (1929)</td>
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<tr>
<td></td>
<td>optic foramen</td>
<td>Jollie (1962)</td>
</tr>
<tr>
<td></td>
<td>foramen for II, III, IV, V₁ &amp; VI</td>
<td>Zeller (1989a)</td>
</tr>
<tr>
<td></td>
<td>sphenorbital foramen</td>
<td>Archer et al. (1993)</td>
</tr>
<tr>
<td>foramen for V₂</td>
<td>foramen rotundum</td>
<td>van Bemmelen (1901), Kesteven &amp; Furst (1929),</td>
</tr>
<tr>
<td></td>
<td>foramen for V₂</td>
<td>Jollie (1962)</td>
</tr>
<tr>
<td></td>
<td>foramen pseudorotundum</td>
<td>Zeller (1989a)</td>
</tr>
<tr>
<td>foramen for V₃</td>
<td>foramen ovale (Ram. III trigeminii)</td>
<td>van Bemmelen (1901)</td>
</tr>
<tr>
<td></td>
<td>foramen ovale</td>
<td>Kesteven &amp; Furst (1929), Jollie (1962)</td>
</tr>
<tr>
<td></td>
<td>foramen for V₃</td>
<td>Zeller (1989a)</td>
</tr>
<tr>
<td></td>
<td>foramen pseudovale</td>
<td>Archer et al. (1993)</td>
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(Cont.)
Table 3. (Cont.)

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<thead>
<tr>
<th>foramen</th>
<th>synonyms</th>
<th>reference</th>
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<tr>
<td>foramen caroticum</td>
<td>foramen caroticum externum</td>
<td>van Bemmelen (1901)</td>
</tr>
<tr>
<td></td>
<td>foramen arteriae carotis internae</td>
<td>Kesteven &amp; Forst (1929)</td>
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<tr>
<td></td>
<td>carotid canal</td>
<td>Jollie (1962)</td>
</tr>
<tr>
<td></td>
<td>foramen caroticum</td>
<td>Zeller (1989a)</td>
</tr>
<tr>
<td></td>
<td>internal carotid canal</td>
<td>Archer et al. (1993)</td>
</tr>
<tr>
<td>foramen vasculare externum medium</td>
<td>foramen vasculare externum medium</td>
<td>van Bemmelen (1901)</td>
</tr>
<tr>
<td>foramen vasculare externus laterale</td>
<td>foramen vasculare externum laterale, foramen vasculosum externa</td>
<td>Archer et al. (1993)</td>
</tr>
<tr>
<td>foramen jugulare</td>
<td>fenestra occipitalis (For, vagi + For. jugulare + For. praecordioideum)</td>
<td>van Bemmelen (1901)</td>
</tr>
<tr>
<td></td>
<td>foramen jugulare</td>
<td>Kesteven &amp; Forst (1929); Zeller (1993)</td>
</tr>
<tr>
<td></td>
<td>foramen for IX, X, XI &amp; XII</td>
<td>Zeller (1989a)</td>
</tr>
<tr>
<td></td>
<td>jugular foramen</td>
<td>Jollie (1962), Archer et al. (1993)</td>
</tr>
<tr>
<td>foramen magnum</td>
<td>foramen magnum</td>
<td>van Bemmelen (1901)</td>
</tr>
<tr>
<td></td>
<td>foramen occipitale magnum</td>
<td>Zeller (1993)</td>
</tr>
<tr>
<td>canalis temporalis</td>
<td>canalis temporalis</td>
<td>van Bemmelen (1901), Zeller (1989a)</td>
</tr>
<tr>
<td></td>
<td>temporal canal (post-temporal fenestra)</td>
<td>Jollie (1962)</td>
</tr>
<tr>
<td></td>
<td>posterior temporal canal</td>
<td>Archer et al. (1993)</td>
</tr>
<tr>
<td>foramen mandibulare medium</td>
<td>foramen mandibulare medius</td>
<td>Zeller (1989a)</td>
</tr>
<tr>
<td>fossa mandibularis</td>
<td>fossa mandibularis</td>
<td>Zeller (1989a)</td>
</tr>
</tbody>
</table>

The foramen maxillopalatinum posterior, a foramen on the palate through the maxilla, is much smaller and more anterior in relation to the posterolateral maxillary process in Ob. dicksoni than it is in Or. anatinus. In Or. anatinus it carries the numerous fibres of the middle superior alveolar nerve (V₃), which extend to the anterior margin of the bill (along with fibres of the external nasal nerve, V₁) (Manger 1994). Two paired foramina through the maxilla anterior to the palatine foramen occur in Oligokyphus (Kühne 1956).

The large foramen maxillofaciale in Ob. dicksoni, transporting the nerves to the lateral aspect of the bill posterior to the f. maxillopalatinum anterius, opens between the dorsal and ventral laminae of the maxilla. Its posterior border is formed by the anterior margin of the projecting posterolateral maxillary process as in Or. anatinus.

The foramen palatinum, a bilateral foramen in Ob. dicksoni with a smaller auxiliary foramen anterior to it, runs through the palate just anterior to the posterior border of the toothbed. This position is substantially more posterior to that in Or. anatinus, where the single foramen is just posterior to the anterior limit of the toothbed. In both taxa the foramen is just cranial to the maxillo-palatine suture, although the suture lines in Ob. dicksoni are very faint.

The foramen sphenopalatinum apparently runs through the palatine posterior to the infraorbital canal in Ob. dicksoni, with a much more posterior course in this taxon both in relation to the palatine foramen and to the molar toothbed than in Or. anatinus (where it appears to share an opening with the palatine foramen).

In Or. anatinus a large canal for the n. ethmoidalis, a branch of V₃, pierces the nasal postero medial to the f. maxillofaciale (Zeller 1989a; Manger 1994). It is not homologous to any foramen in therians, probably being best identified with the ‘vascular foramen’ of Simpson (1937, cited in Zeller 1989a) as seen in the rostrums of multituberculates and possibly of Morganucodon (Zeller 1989a). This foramen has a long phylogenetic history, being present in theriodonts and lacerilians as well as the mammals discussed above; however, it is absent in therians (Zeller 1989a). This foramen is unusually large in Or. anatinus because of the thickness of the fibres of the r. lateralis of the n. ethmoidalis that travel through the large canalis nervus ethmoidalis (Zeller 1989a). Two foramina in the nasal posterior to the maxillary processes are present on the right side of this specimen of Ob. dicksoni (identified by an asterisk, *), the anterior foramen being larger. The left side of this specimen is damaged, and as there can be either one or two foramina through the nasal in Or. anatinus, the number could be variable in Ob. dicksoni as well (although the reconstruction depicts them as bilaterally symmetrical). The fibres of the ethmoid nerve passing through these foramina innervate the dorsal shield of the bill and the postero medial section of the skin of the upper bill in Or. anatinus (Manger 1994), and the presence of these foramina in Ob. dicksoni indicates that a dermal dorsal shield may have been present in this taxon as well.

The bones through which the foramina of the braincase pass are difficult to identify in Ob. dicksoni because of the extent of fusion. Nevertheless, relative positions and orientations provide a basis for comparison with Or. anatinus.

The aditus canalis ductus nasolacrimalis, or tear duct, appears to be a small slit posterodorsal to the angle of the orbit in Ob. dicksoni; the frontal/maxillary suture is just visible posteriorly. The nasolacrimal duct opens more dorsally in Ob. dicksoni than it does in Or. anatinus.

The infraorbital canal in Or. anatinus is proportionately larger than in any other mammal (Zeller 1988), and is even larger in relative terms in Ob. dicksoni. It runs
rostrally through the maxilla carrying a large branch of \( V_2 \) (the superior alveolar nerve) to the bill in \textit{Or. anatinus}, which branches at the maxillofacial foramen (Manger 1994). In \textit{Ob. dicksoni} the bulk of the nerve fibres presumably would have exited through this latter large foramen while the remainder would have continued anteriorly to exit through the anterior maxillopalatine foramen, as in \textit{Or. anatinus}.

The fissura orbitonasalis opening into the supracricibrous recess anterior to the cranial cavity (de Beer 1937) appears to be similar in position to the orbitonasal fissure in \textit{Or. anatinus}, running through the frontal bone dorsal to the f. sphenopalatinum and ventral to the orbital process.

The foramen in the side wall of the braincase for exit of the optic (II), oculomotor (III), trochlear (IV), \( V_1 \) and abducens (VI) nerves in adult \textit{Or. anatinus} is a large, discrete foramen bordered by the pila praepaetica and the lamina obturans (Zeller 1989a). In young \textit{Or. anatinus}, this opening is confluent with the foramen for \( V_2 \) but a strut of bone forms to separate these foramina in the adult (Kesteven & Forst 1929). This foramen in monotremes apparently is not homologous with the f. opticum and f. sphenoprotorbitale in therians (see table 3), both because the aperture for the ganglia are on different planes in both groups and because the relations with the bones differ (Zeller 1989a). The f. opticum of placental opens between the pila praepaetica and pila metopica (the p. metopica being absent in monotremes although the pila antotica is present) and the f. sphenoprotorbitale opens between the pila metopica and alisphenoid (Zeller 1989a). The foramen for II–VI differs in \textit{Tachyglossus aculeatus}, with an auxiliary foramen pseudophenoorbitale, but the trochlear nerve (IV) leaves the cavum epippticum through the f. proucticum in both monotremes, indicating that the primary wall of the braincase is homologous and synapomorphic for the two (Zeller 1989b).

The foramen for II–VI in \textit{Ob. dicksoni} resembles that of \textit{Or. anatinus} but, between fusion and breakage of the cranium in this section, the identification of the component bones and understanding of the structure is difficult. According to Zeller (1989a), the foramen for the exit of the maxillary branch of the trigeminal nerve \( V_2 \) from the cavum epippticum, called the foramen rotundum or the f. pseudorotundum in monotremes (see table 3), is homologous with neither the f. rotundum nor the f. pseudorotundum because of the aberrant conditions in both monotreme families. In \textit{Or. anatinus} the exit for \( V_2 \) is bordered by the lamina obturans, alisphenoid and basi-sphenoid (Zeller 1989a). Zeller (1989a) sees the extent of variation in the relations of this foramen in therians as evidence that an f. rotundum was not present in the common ancestor of recent therians (and thus not in an ancestor shared with monotremes) and that separate derivations of an f. rotundum occurred independently within different therian lineages. The foramen for \( V_2 \) is a large ovoid foramina in \textit{Ob. dicksoni} with two auxiliary foramina anterodorsal to the foramen (the posterior one being larger), a condition not seen in \textit{Or. anatinus} skulls examined.

There has also been controversy over the terminology of the foramen for exit of the mandibular branch of the trigeminal, \( V_3 \), called by most authors the foramen ovale in monotremes (table 3). It is not homologous with either the f. ovale (through the alisphenoid) or the f. pseudovale (between the alisphenoid and petrosal) in therians (Zeller 1989a; but see Griffiths 1978), and is not identically formed in the two living monotreme families (Griffiths 1978; Zeller 1989a). It appears that in therians, a completely closed f. ovale through the alisphenoid is a derived condition and independently arrived at many times, and as such is not a homologous structure. In addition, it appears that a branching of \( V_3 \) prior to the aperture (as in \textit{Or. anatinus}) negates the homology of the foramen. In \textit{Or. anatinus} this huge foramen is bordered by the alisphenoid, the lamina obturans, the petrosal and the basisphenoid (Zeller 1989a).

In \textit{T. aculeatus} this foramen is bordered by the ectopterygoid and lamina obturans and is more rostral in position (Zeller 1989a). Fusion in this region of the \textit{Ob. dicksoni} skull makes delineating the borders of the foramen impossible, but in position this foramen is more caudal in relation to the posterior margin of the palate in \textit{Ob. dicksoni} than in \textit{Or. anatinus}. The lamina obturans forms an enlarged rim on its lateral border.

The foramen caroticum for passage of the internal carotid artery is a small bilateral foramen lateral to the posterior base of the basisphenoid crest and posterior to the caudal margin of the palate in \textit{Ob. dicksoni}. The foramina open into the cranium anteromedially and are more posterior in relation to the foramen for \( V_3 \) in \textit{Ob. dicksoni} than they are in \textit{Or. anatinus}.

The ‘foramen lacerae anterius’ of van Bemmelen (1901) is a variably developed opening or series of perforations on the roof of the sulcus posterior to the f. caroticum and leading from it in \textit{Or. anatinus}, but these openings are absent in \textit{Ob. dicksoni}. According to Zeller (1989a), the naming of these as separate foramina is incorrect because bone is resorbed on both sides of the base of the skull, with a sulcus caroticus formed from the caudal part of the f. caroticum. The bony roof of the sulcus is solid in \textit{Ob. dicksoni}, perhaps owing to the overall robustness of the cranial bone. Zeller suggests that degeneration of bone in \textit{Or. anatinus} may be related to its aquatic lifestyle as a similar phenomenon occurs in sea lions (Stark (1967), cited in Zeller (1989a)); its absence in \textit{Ob. dicksoni} may indicate that the Riversleigh animal was less specialized in this regard.

The fenestra vestibuli (the foramen for the footplate of the stapes, a circular footplate in monotremes, which is plesiomorphic for Mammalia) lies in the floor of the petrosic (petrosal), posteroventral to the foramen for \( V_3 \). In both ornithorhynchids it is partly overhung by a shelf of bone formed by the crista paroticia and the tympanohyal process. This foramen is slightly more posterior and closer to the tympanohyal process in \textit{Ob. dicksoni} than it is in \textit{Or. anatinus}.

Foramina for VII and VIII, best seen from the interior of the skull, are similarly placed in both ornithorhynchids but are difficult to see clearly in \textit{Ob. dicksoni}.

The foramen jugulare for the glossopharyngeal (IX), vagus (X), accessory (XI) and hypoglossal (XII) nerves is enormous in both ornithorhynchids and is more obliquely angled in \textit{Ob. dicksoni} than in \textit{Or. anatinus} owing to the longer skull base and greater occipital slope in \textit{Ob. dicksoni}.

The sizeable foramen magnum in \textit{Ob. dicksoni}, for passage of the lower end of the medulla oblongata and other structures, has a dorsal notch that in \textit{Or. anatinus} is
the remnant of a deep embayment in the chondrocranium accommodating the projecting median lobe of the cerebellum (de Beer 1937). This notch is covered in young *Or. anatinus* by a membrane separating the median lobe from the ligamentum nuchae (Gregory 1947). The shape of this arched foramen is variable in *Or. anatinus*, and the foramen in *Ob. dicksoni* appears to be within this range of variation. It is more posterior in position in *Ob. dicksoni*, because of the greater occipital slope and more elongate cranium. The opening is more dorsal (thus slightly more horizontally directed), reflecting the flatter skull and presumably more horizontal body alignment in *Ob. dicksoni*.

Of particular interest in monotremes is the presence of the canalis temporalis (post-temporal canal), believed to be the remnant of the well-developed post-temporal fenestra or fossa in the 'reptilian' skull (Goodrich 1938). The post-temporal canal, relatively small in monotremes compared with earlier 'reptilian' forms, links the temporal fossa with the region dorsal to the ear capsule (Romer 1956). Running between the petrosal and squamosal, it occurs in stem 'reptiles' such as *Seymouria* (Romer 1956) through the earliest mammals including multituberculates (Kermack & Kielen-Jaworowska 1971). This canal, however, is absent in other living mammals (de Beer 1962).

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(ii) *Mandibular foramina*

The mandible in ornithorhynchids is exceptionally well innervated by the mandibular branch of the trigeminal nerve (the inferior alveolar nerve), which gives off several branches, the largest of these exiting from the foramen mandibulare medium (Manger 1994). Laterally, only the barest indication of the f. mandibulare medium is preserved in the *Ob. dicksoni* anterior dentary fragment; it is just a notch-like remnant at the posteroentral margin along the line of breakage of the fragment. This notch, just anteroventral to the anterior limit of the toothbed, appears to be roughly similar in position (perhaps slightly more anterior) and in configuration to this foramen in *Or. anatinus*, although its position is variable in the platypus.

The fossa mandibularis of the posterior dentary fragment is a uniformly rounded basin forming a deep, elongate trough that tapers smoothly up the ascending ramus. The lateral face of the dentary fragment has a section missing that would have included the anterior margin of the fossa; therefore, the reconstruction borrows information from the similar dentary of *Ob. insignis*. Because of this breakage it is not possible to ascertain whether or not the anterior margin of the lip rounded over the fossa as it does in *Ob. insignis*, or whether there were protuberances for attachment of the m. temporalis atop a well-developed prominence as there is in *Or. anatinus*. However, because the mandibular fossa is similar in other respects to the *Ob. insignis* dentary, and because the coronoid process for the temporals is well developed in *Ob. dicksoni*, the assumption is made at present for the purpose of the reconstruction that no prominences or muscle attachments were present dorso-lateral to the mandibular fossa in *Ob. dicksoni*.

There is a foramen that passes between the buccal and lingual sides of the dentary in both *Ob. dicksoni* and in some *Or. anatinus* (the masseteric canal is infilled in the *Ob. insignis* dentary and the presence or absence of this foramen at this stage cannot be determined). In *Ob. dicksoni* the dorsal margin is preserved although the ventral margin has been broken. The foramen opens just posteroventral to the single alveolus for M/3 and is anterioventral to the origin of the mylohyoid process. In *Or. anatinus* the foramen is posteroventral to where the alveolus for M/3 would have been, as in *Ob. dicksoni*, but the origin of the mylohyoid process is much more posterior in *Or. anatinus* than it is in *Ob. dicksoni* and the relationship between this foramen and the origin of the mylohyoid process is correspondingly more distant. An analogous but much larger foramen, the masseteric foramen, passes between both sides of the dentary in kangaroos (Macropodoidea). A much smaller foramen in phalangeridan possums (e.g. pseudocheirids) also passes transversely through the dentary in this region. However, in neither case is there evidence that these are homologous with the foramen in monotremes.

4. DISCUSSION OF THE DIFFERENCES IN CRANIAL MORPHOLOGY SEPARATING *OB. DICKSONI* FROM *OR. ANATINUS*

The similarities in skull form between the Miocene *Ob. dicksoni* and the living *Or. anatinus* are striking despite the fact that the two are approximately 15 Ma apart. Clearly, by at least the middle Miocene, the basic pattern—flattened skull with prominent, splayed bill—had been attained (Archer et al. 1993). Because of the similarities between the molar teeth of all ornithorhynchids, it is likely that members of the family shared at least a general skull morphology with a wide bill being a definitive feature.

Postcranial material for *Ob. dicksoni* has not yet been recovered from any of the Riversleigh sites (although an ilial fragment has been assigned to *Ob. insignis* (Archer et al. 1978)). However, both by inference from the platypus-like cranial morphology of *Ob. dicksoni*, and by the fact that much of the postcranial anatomy of *Or. anatinus* appears either plesiomorphic (in particular, the shoulder girdle) or specialized for aquatic life (e.g. the dorsoventrally flattened body form), it seems reasonable to assume that the body plan of *Ob. dicksoni* would have been similar.
Development of the bill in ornithorhynchids

The bill in *Or. anatinus* is used both as a sense organ and as a tool for breaking the ground when burrowing (Burrell 1927). The hypersensitivity of the bill and the presence of mechano-, or touch, receptors in the bill have been known since the late 1800s (Poulton 1889). Electoreceptors, however, which are unique among mammals to monotremes and which are apparently able to detect small electromygogenic impulses given off by certain aquatic prey such as freshwater shrimp (Taylor et al. 1992), were not detected until 1986 (Scheich et al. 1986).

Huber (1990) believes that the platypus bill, as a navigational instrument, within its environment is superior to a rostrum with vibrissae. Although Huber’s observations were made before knowledge of electoreceptive ability in *Or. anatinus*, he cites its extraordinary ‘oral sense’ as an important factor in the evolution of the ornithorhynchid neopallium.

Dorsal and ventral dermal extensions that continue the skin of the bill over the front of the face and throat (also called frontal shields) augment the sensory surface area of the bill. These immobile dermal shields (absent from the simpler beak of the echidnas) were first thought to protect the eyes from mud and debris when burrowing or foraging along muddy stream beds (Bennett 1860) and Oldfield Thomas (1888) cited in Burrell (1927), but they actually emarginate just in front of the eye and would, therefore, be relatively inefficient as protective devices. It is probable that at least the dorsal dermal shield was present in *Ob. dicksoni*, because the foramina on the dorsum of the skull (*) are similar in position to those that supply the dorsal shield in *Ob. anatinus*. It is unclear whether there was a ventral shield in *Ob. dicksoni*, although it is probable that one was present.

The contours of the bill in *Or. anatinus* are formed by an extensive cartilaginous plate, the cartilago marginalis, that fills the interseptomaxillary space (through which the dorsal nostrils open) and continues well beyond the bony limits of the rostrum. Only a remnant of the marginal cartilage is present during ontogeny in *T. aculeatus* (Wilson 1901). The marginal cartilage may be homologous with the anterior end of the palatal process, which would be an unusual instance of the reversion of bone to cartilage (Edgeworth 1935). A well-developed (possibly hypertrophied) marginal cartilage in *Ob. dicksoni* (indicated by the comparatively deep insertional area along the lateral aspect of the bill) and an exceptionally wide, flared bill (exaggerated in *Ob. dicksoni* by anterolateral maxillary processes absent in *Or. anatinus*), suggest that the bill in *Ob. dicksoni* was an important and highly sensory structure.

The rostral crura meet at the midline of this adult specimen of *Obdurodon dicksoni*, whereas the rostral crura diverge as bony prongs in adult *Or. anatinus* (Archer et al. 1992, 1993). However, Zeller (1989a) illustrates a foetal *Or. anatinus* in which the rostral crura meet at the midline as they do in *Ob. dicksoni*. The shape of the interseptomaxillary fenestra in foetal *Or. anatinus* also resembles the more ovoid shape of this fenestra in *Ob. dicksoni*, a consequence of the crura meeting at the midline. The ovoid shape contrasts with the V-shape of the fenestra in adult *Or. anatinus*. This ontogenetic evidence suggests that an *Obdurodon*-type bill, with the crura meeting at the midline, may have been ancestral to the bill form seen in *Or. anatinus*.

Reduction and osteological fusion appear to be entrenched monotreme features as all living monotremes exhibit these characteristics to some extent. Reduction and streamlining of the bill form is especially noticeable in *Or. anatinus* when compared to the form of the bill in *Ob. dicksoni*; the anterior maxillary processes have apparently been lost and the bill form has become more linear in *Or. anatinus*. The comparative lack of fusion of the rostral bones of *Ob. dicksoni* contrasts with the condition in living monotremes where, in adults, rostral suture lines are often difficult to see. The tendency towards fusion (particularly in the cranium), probably present in a common monotreme ancestor, seems either to have reversed itself at least in the rostral bones of *Ob. dicksoni* or to have evolved to the degree seen in the bills of all modern monotremes independently, given that the tendency towards fusion had established itself in the common ancestor.

Until discovery of the *Ob. dicksoni* skull, there were few clues as to the origin of the ornithorhynchid bill; reduction and fusion in the rostrum of *Or. anatinus* obscured traces of its ancestry. The structure of the rostrum in *Ob. dicksoni* and placement of rostral foramina (e.g. the foramina through the premaxilla and septomaxilla, which appear to be similar to foramina in some Mesozoic mammals and therapsids such as *Oligokyphus*, but which are missing in therian mammals), indicates that ornithorhynchids have retained these as plesiomorphic features. Taking these observations one step further, it is not inconceivable that the distinctive ornithorhynchid bill shape may have derived from a rostrum such as that of *Oligokyphus* in which the incisive foramina fused to form a single opening through the premaxillae; enlargement of such an arrangement may have resulted in a bill form like that of *Ob. dicksoni* (and thus of monotremes) in which this ovoid space bounded anteriorly by the conjoined premaxillae became progressively enlarged.

Development of a wide, flattened bill distinguishes ornithorhynchids from tachyglossids; the extent of bill development in fossil monotremes, therefore, is of great interest. *Steropodon* and *Kollikodon* both possess large mandibular canals, presumably for the innervation of a sensitive bill. The presence of both mechano- and electro-receptors in the bills of *T. aculeatus* (Gregory et al. 1989) and of *Zaglossus bruijni* (Manger et al. 1997), suggests that they were present in a common ancestor and possibly that these senses were also present in Steropodon and Kollikodon.

Hypertrophy of the bill in *Ob. dicksoni* was surprising because ornithorhynchids were assumed to have gradually elaborated the snout from the more generalized form of a common monotreme ancestor (Murray 1984). Evidence for extensive innervation of the rostrum in *Ob. dicksoni* comes from the presence of the numerous large foramina along the bill with the same relative placement as the foramina in *Or. anatinus*.

Arguing against derivation of the bill of *Or. anatinus* from that of *Ob. dicksoni* is parsimony. The late Oligocene *Ob. insignis* possesses what appears to be a relatively small bill, *Ob. dicksoni* from the early Miocene possesses a hypertrophied bill, whereas the modern *Or. anatinus* possesses a much-reduced bill. If *Ob. insignis* gave rise to *Ob. dicksoni* which gave rise to *Or. anatinus*, the bill first enlarged and then reduced. Alternatively, some another species within
the genus with a less hypertrophied snout gave rise to the genus *Ornithorhynchus*. The extent of hypertrophy of the bill of *Obdurodon* may then represent a derived condition.

(b) **Comparisons involving the crania and dentaries**

Possibly correlated with reduction of the bill in *Or. anatinus* is shortening of the cranium in this species. The cranium appears more elongate in *Ob. dicksoni* and less so in *Or. anatinus*, an observation supported by quantification of morphological features and relative positions of the cranial foramina. The maxillary toothed in *Or. anatinus* extends posteriorly, which may be a correlate to shortening of the cranium. Differences in cranial shapes are reflected in the relative positions of the cranial foramina, with many foramina closer together or closer to certain cranial structures in *Or. anatinus* than in *Ob. dicksoni*.

Flattening of both the skull and dentary in *Ob. dicksoni* represents an extreme in monotreme skull morphology, a group already noted for the unusual flatness of the skull (Owen 1868). In *Ob. dicksoni* the rostrum is not down-turned, the foramen magnum is slightly more dorsal (indicating a more horizontal body alignment) and the dentary is not sharply angled. These are features that suggest a difference in lifestyle. *Ob. dicksoni*, with a flatter skull and body form, possibly foraged higher in the water column or perhaps even at the surface rather than in the benthic substrate where the modern platypus finds most of its food. It may have taken insects from the water’s surface, a behaviour occasionally observed in the living platypus (Grant 1995). The downwardly deflected bill in *Or. anatinus* may reflect its habit of shovelling through benthic debris in search of aquatic invertebrate prey.

A trend towards reduction can be seen in the evolution of the dentary. In respect of morphology, the dentary of *Ob. dicksoni* resembles other mammals in having well-developed coronoid and angular processes. The dentary of *Or. anatinus* exhibits reduction of the angular and coronoid processes. The mastiatory stroke would have become progressively less vertical (with reduction in height and subsequent loss of the high-crowned, interlocking molars) and progressively more horizontal. The more horizontal mastiatory musculature was correspondingly reduced as evidenced by the flat zygoma of *Or. anatinus* as well as by loss of major muscle attachment sites, in particular the coronoid process. Dentary reduction appears then to reflect overall reduction in skull morphology in *Or. anatinus*.

Few confident conclusions can be reached about differences between dentary structure in *Ob. insignis* and *Ob. dicksoni* because of breakage. However, although the tip of the angular process in this *Ob. insignis* specimen is broken, it appears to have been more reduced in the Oligocene ornithorhynchid (thus resembling more closely the angular process of *Or. anatinus*, where it is either reduced or absent). In addition, the *Ob. insignis* dentary does not curve gently upward as does the *Ob. dicksoni* dentary, but instead angles upward more sharply, as in *Or. anatinus*. Lack of an obvious angle in the *Ob. dicksoni* dentary corresponds to the flatness of the skull in this taxon, additional evidence that this skull conformation may be a derived rather than a plesiomorphic condition.

(c) **Dental evolution in ornithorhynchids**

Three correlated trends in dental evolution leading to and within the ornithorhynchid line can be seen: (i) elaboration and multiplication of the transverse shearing blades; (ii) progressive reduction of the roots of the molars; and (iii) increased role of the oral epithelium in dental function through production of horny pads.

The combination of wide, multiple-rooted molars with dual triakidirepano blade systems is unique among mammals. Archer et al. (1983, 1992, 1993), Kielan-Jaworowska et al. (1987), Jenkins (1990), Kielan-Jaworowska (1992) and Flannery et al. (1995), have variously compared monotreme dentitions to those of tritubercular mammals, pretritubercular therians such as the advanced eucaninotherian *Peramus*, and mesungulatid dryolestoids. The possibility that monotremes might be related to Early Cretaceous eucaninotheres such as *Vincelestes* was challenged by an analysis of *Vincelestes*, which revealed fundamental differences in the formation of the sidewall of the braincase (Rougier et al. 1992). Recovery of more fossil material, particularly the missing upper molars of *Steropodon galmani*, would be invaluable to the debate.

Although *Ob. dicksoni* apparently retained functional teeth throughout life, the molar roots are much shallower than those of *S. galmani*, which also had a much deeper jaw. As the molars widened and the jaw became less deep, the number of molar roots increased to four to six in the anterior two molars of species of *Obdurodon*. The shallowness of the roots and the case of loss of molars from both skull and dentary fragments suggest that molars may have been fairly loosely held in the alveolar cavities by periodontal fibres. Hardened or built-up gum tissue may have helped to buttress the teeth in *Ob. dicksoni* or hold them more securely in their alveoli. This intermediate condition could have been a precursor to the evolution of horny epithelial pads as alternatives to functional teeth in *Or. anatinus*.

Elaboration of palatal epithelium occurs in all living monotremes. Tongues in both families have spines of keratinized tissue that work against the palate to assist further mastication (Griffiths 1978). Epithelial ridges on the palate in *Or. anatinus* aid in securing and dissecting prey in the absence of an anterior dentition. The possible presence of comparatively huge epithelial ridges as well as interlocking triangular blades on the teeth suggest that *Ob. dicksoni* may have fed on larger prey than *Or. anatinus*, perhaps small vertebrates such as frogs or snakes.

5. **RELATIONSHIPS WITHIN MONOTREMA**

Phylogenetic affinities of monotremes are uncertain despite a significant increase in understanding about early mammals (e.g. Lillegraven & Krusat 1994; Krebs 1991; Rougier et al. 1992; Crompton & Luo 1993; Hu et al. 1997). Recent reviews of monotremes have tentatively linked them to early therians (Jenkins 1990; Kielan-Jaworowska 1992), dryolestoids (Bonaparte 1990; Archer et al. 1993), and multituberculates (Wible & Hopson 1993; Meng & Wyss 1995; but see Miao 1993). Results of molecular studies vary greatly, some suggesting a close relationship to marsupials (Janke et al. 1997; Kirsch & Mayer, this issue) with a revival of Gregory’s (1947) Marsupionta, whereas others suggest that monotremes are genetically distant from thrian mammals (e.g. Westerman & Edwards 1992; Retief et al. 1993).

On the basis of molar morphology, there appear to be four clades among monotremes: (i) kollkokodontids with
four bunodont molars; (ii) stenodontids with three molars, triakididreponan blade systems and deep tooth roots; (iii) ornithorhynchids with three (or four) elaborated triakididreponans and shorter but more numerous molar roots; and (iv) tachyglossids with complete loss of teeth. Among forms with high-crowned teeth, all share wide, rectangular molars with double V-shaped blade systems that have apparently converged on tribosphenid dental morphology (Archer et al. 1993). Because this unique pattern in toothed monotremes persists over a period of more than 110 Ma, it is the most striking example of dental conservatism known among mammals.

_Steinodon galmani_ was included within Ornithorhynchidae when first described because it shared many features with the Oligo-Miocene species of _Obdurodon_ (i.e. the distinctive double triakididreponan blade systems, a diakidreponan on the anterior half of the first lower molar and an enlarged mandibular canal) and because the mandibular canal suggested that a bill was present (Archer et al. 1985). Exclusion of _S. galmani_ from Ornithorhynchidae was prompted by molecular studies (e.g. Westerman & Edwards 1992; Retief et al. 1993; Messer et al. 1995) that agree to a family split between Ornithorhynchidae and Tachyglossidae either near the Cretaceous–Tertiary boundary or postdating the Cretaceous (Flannery et al. 1995). Accepting this, Ornithorhynchidae in the sense of Archer et al. (1985) would be paraphyletic. Reference of _S. galmani_ to a distinct family of its own resolved the problem (Flannery et al. 1995).

That monotremes were once far more diverse and that the line is capable of extreme specialization is demonstrated by _Kollikodon ritchiei_ (Flannery et al. 1995). The highly specialized echidnas have either lost or are in the process of losing features considered platypus-like, in particular teeth and the marginal cartilage that might have supported a wider, more platypus-like bill.

**a) Relationships within Ornithorhynchidae**

Archer et al. (1993) suggest that the middle Miocene _Ob. dicksoni_ might be ancestral to species of _Ornithorhynchus_. Many features of the Miocene taxon may be plesiomorphic (e.g. the structure of the bill and development of the dentary). In development of the angular and coronoid processes of the dentary, _Ob. dicksoni_ may even be more plesiomorphic than the late Oligocene _Ob. insignis_, whose small dentary with its apparently reduced angular process suggests a trend towards reduction in this lineage.

Other features of _Ob. dicksoni_ are not clearly plesiomorphic. Although the basic bill structure (with rostral crura meeting at the midline) may be plesiomorphic in _Ob. dicksoni_, it is possible that the extreme development (hypertrrophy) of the bill represents an autapomorphic specialization in the Riversleigh animal. The flat skull and low angle of the dentary in _Ob. dicksoni_ may also be an autapomorphic condition because the dentary of _Ob. insignis_ appears to have been relatively ‘normal’ (i.e. with an upwardly angled ascending ramus). Specialization in the bill and skull of _Ob. dicksoni_ may therefore preclude it from being ancestral to species of _Ornithorhynchus_. _Ob. insignis_, with its smaller bill and less flattened skull, may have been closer to the ancestral form for species of _Ornithorhynchus_. Both the Paleocene _Monotrematum sudamericanum_ and the Miocene _Ob. dicksoni_ appear to have been large and robust animals. All of the _Ob. insignis_ material suggests a more gracile animal which, in this regard, more closely resembles _Or. anatinus_.

The nature of the sediments in the central Australian and Riversleigh fossil deposits supports this interpretation. The Etadunna and Nambja Formations (containing _Ob. insignis_) consist primarily of claystones and mudstones and some fine-grained sandy lenses, evidence that the palaeoenvironments were dominated by fluvio-lacustrine conditions (Woodburne et al. 1993), probably surrounded by cool, scrubby wet forest (Archer et al. 1993). The benthic substrate in these waters would probably have been silted, bordered by banks of semi-consolidated clay and mud. In this regard, these central Australian environments would have been closer to those that today support _Or. anatinus_. At Riversleigh, although much of the area was lacustrine, the lime-rich waters would have produced limey muds rather than clays or gravels and possibly carbonate-cemented banks (Archer et al. 1994, 1995).

**ADDENDUM**

After the present paper was sent for review a new Early Cretaceous mammal from southeastern Australia was reported, _Austrotherium nyktos_, described by Rich et al. (1997) as an early placental mammal. Rich et al. (1997) cite similarities in molar count, tooth and mandibular morphology between _A. nyktos_ and early placentalts such as _Prokennalestes_ in making their case for inclusion of _A. nyktos_ within the infraclass Placentalia. However, one of us (M.A.) has seen the specimen and is convinced that this small jaw is not that of a placental mammal but instead may share a relationship with peramurids or possibly with monotremes.

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**REFERENCES**


A fossil ornithorhynchid


CHAPTER 4

Evolution, biogeography and palaeoecology of the Ornithorhynchidae

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CHAPTER 4

Chapter 4 (‘Evolution, biogeography and palaeoecology of the Ornithorhynchidae’) is a short paper written as part of the proceedings of the first National Symposium on Platypus Biology held at Charles Sturt University, Bathurst, NSW in 1997. Contributions were compiled as a special issue of Australian Mammalogy (Journal of the Australian Mammal Society): Vol. 20 [2]; June 1998, edited by D. Goldney and T. R. Grant.

Chapter 4 outlines the fossil record of ornithorhynchids, giving ages, localities and fossil material; discusses the anatomy of both fossil and living ornithorhynchid species; gives past ornithorhynchid distributions from Australia to southern South America and puts this information into a contemporary context; presents data on past climates and land connections; and investigates the palaeoecology of fossil ornithorhynchids.

Since this paper was written in 1998 additional fossil material of the Paleocene South American platypus, Monotrematum sudamericanum from Patagonia, has been recovered. A second fragmentary upper molar and the first known lower molar of Monotrematum are described by Pascual et al. (2002). The additional molar teeth are larger than in Obdurodon species (as is the holotype M2 of M. sudamericanum) (Pascual et al., 2002). Strong similarities are noted to the molars of Obdurodon, also discussed in an abstract by Musser and Archer (1998) who consider the Australian and South American species congeneric. Distal portions of two large ornithorhynchid femora have been recovered from the Banco Negro Inferior locality that produced the molar teeth (Pascual et al., 1992a, b; Pascual et al., 2002) and tentatively assigned to Monotrematum by Forasiepi and Martinelli (2003). Forasiepi and Martinelli estimate the total length of the South American platypus at 70 cm, relatively close in length to a large Tasmanian platypus (males can reach 60 cm in length: e.g., Grant, 1998) but much larger than a Queensland platypus (average length of males: 44 cm).


EVOLUTION, BIOGEOGRAPHY AND PALAEOECOLOGY OF THE
ORNITHORHYNCHIDAE

A.M. MUSSER

147-162.

This paper reviews present understanding of the evolution of the ornithorhynchids, an
ancient family within the mammalian order Monotremata. Ornithorhynchidae today is represen-
ted only by the living platypus Ornithorhynchus anatinus but has a history that
probably predates the Tertiary and a past distribution that spanned at least three conti-
ents. Analysis of the palaeontological record has focused on the distinctive ornitho-
 rhynchid dentition, which in species of Monotremata and Obdurodon was probably
functional throughout life. The retention of functional dentition in concert with the great
age of Ornithorhynchidae gives the platypus family a much larger role in analysis of the
biogeographic and phylogenetic history of the monotremes than is given to the more
specialised, edentate tachyglossid, or echidnas. A complete ornithorhynchid skull, recov-
ered from Miocene deposits at Riversleigh in northwestern Queensland, has allowed com-
parison between the cranium of a generally more plesiomorphic platypus and that of
the living Or. anatinus, a study that answers some of the morphological questions posed
by this enigmatic group while raising others. This review concludes with a discussion of the
biogeography and palaeoecology of the family.

Key words: platypus, Ornithorhynchidae, Ornithorhynchus, Obdurodon, Monotremata,
Steropodon, morphology, biogeography, palaeoecology.

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ORNITHORHYNCHIDS are the amphibious, large-billed platypuses, one of two extant families
(the second being the edentate Tachyglossidae, or echidnas) within Monotremata, the egg-laying
mammals that today occupy Australia and New Guinea. Ornithorhynchidae today is represented
only by the living platypus Ornithorhynchus anatinus, a semi-aquatic insectivore/carnivore
found in waterways of eastern Australia from south of Cooktown, Queensland to Tasmania (Grant

Both living monotreme families are very specialised for their particular niches in spite of being
considered quite primitive in many other features, such as retention of an egg-laying habit and pos-
session of a shoulder girdle that resembles that of the earliest mammals. Advanced specialisations
alongside such primitive retentions have been used to illustrate the concept of mosaic, or patch-
work, evolution within the monotreme line, and have made teasing apart these character states in a
search for relationships a complex task.

FOSSILS AND EVOLUTIONARY
RELATIONSHIPS

Although fossil ornithorhynchid material is still quite scarce (primarily consisting of isolated molar
teeth but including a complete skull), enough has been recovered within the past decade to allow for
definition of key characters common to members of the family. Ornithorhynchids share a distinctive
molar morphology (Fig. 1) with the following characteristics: V-shaped blade systems on wide,
rectangular molars forming blades (apparently convergent with the interlocking triangular teeth of
triosphenid tharian mammals: Archer, Jenkins, Hand, Murray and Godthelp 1992; Archer,
Murray, Hand and Godthelp 1993); anterior, pos-
terior and buccal cingula are prominent; and mol-
ers have shallow, multiple roots. In addition to
this unique dental morphology ornithorhynchids
possess a large, flattened, well innervated bill
formed by the bones of the snout (as in Or.
anatinus) and all members of the family presumably
would have been to some degree semi-aquatic,
using the sensitive bill to detect underwater prey.
Fig. 1. Left lower first molar, holotype of *Obrurodon insignis* (SAM P18087), illustrating the blade structures of ornithorhynchid molars. Abbreviations: dkd'id, digitidispersid (single blade); tkd'id, tridentidispersid (V-shaped blade); a. cing., anterior cingulum; p. cing., posterior cingulum. Terminology from Ever (1974).

<table>
<thead>
<tr>
<th>SPECIES</th>
<th>AGE</th>
<th>LOCALITY</th>
<th>MATERIAL</th>
</tr>
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<tbody>
<tr>
<td><em>Monotrematum sudamericanum</em></td>
<td>early Paleocene (63.2-61.8 mybp)</td>
<td>Banco Negro Inferior, Patagonia, southern Argentina</td>
<td>two upper molars and fragment of a lower molar</td>
</tr>
<tr>
<td><em>Obrurodon insignis</em></td>
<td>late Oligocene (26-25 mybp)</td>
<td>Lakes Palankarina, Pinpa and Namba, Etadunna Fmm. and Namba Fmm., central Australia</td>
<td>dentary fragment, ilial fragment and isolated molars</td>
</tr>
<tr>
<td><em>Obrurodon sp. A</em></td>
<td>late Oligocene (approx. 24 mybp)</td>
<td>Mammelon Hill (Lake Palankarina), Etadunna Fmm., central Australia</td>
<td>2 molars</td>
</tr>
<tr>
<td><em>Obrurodon dicksoni</em></td>
<td>middle Miocene (approx. 15 mybp)</td>
<td>Riversleigh Station, northwestern Qld.</td>
<td>skull, 2 dentary fragments and isolated molars and premolars</td>
</tr>
<tr>
<td><em>Ornithorhynchus sp.</em></td>
<td>early to middle Pliocene (4-4.5 mybp)</td>
<td>Bow Local Fauna, Bow, NSW</td>
<td>undescrbed limb element</td>
</tr>
<tr>
<td><em>Ornithorhynchus anatinus</em></td>
<td>middle Pleistocene to present (100,000 ybp to present)</td>
<td>King's Creek and Brisbane River, Qld.; Bunyan Siding and Lake Tandou, NSW; Snowy River, Vic.; and southwestern Tasmania</td>
<td>numerous cranial and postcranial elements</td>
</tr>
</tbody>
</table>

Table 1. The present composition of Ornithorhynchidae, with estimated ages, localities and a listing of recovered material. Fmm., Formation.

Ornithorhynchidae (Table 1) is comprised of early Paleocene of Patagonia, Argentina (Pascual, *Monotrematum sudamericanum* from the late Archer, Ortiz Jaureguizar, Prado, Godthelp and
Although *M. sudamericana* is presently considered to be the earliest ornithorhynchid, an older platypus-like monotreme is known from a lower jaw fragment with three molar teeth (*Steropodon galmani*) recovered from early Cretaceous opal deposits at Lightning Ridge in New South Wales (Archer, Flannery, Ritchie and Molnar 1985). *S. galmani* was originally included within Ornithorhynchidae both because it possesses the distinctive ornithorhynchid-like tooth morphology (although more plesiomorphic in both blade structure and development of the third molar, which is reduced in later taxa) and because the presence of a large mandibular canal indicates that a bill may have been present at the front of the face (Archer et al. 1985). However, *S. galmani* is currently placed in its own family (Flannery, Archer, Rich and Jones 1995) to reconcile its great age (over 100 mybp) with divergence dates between ornithorhynchids and tachyglossids estimated by molecular techniques that have been no earlier than the Cretaceous-Tertiary boundary (eg. Relict, Winkfield and Dixon 1993; Westerman and Edwards 1992). Whatever its current classification, *S. galmani* must be considered in any discussion of the ornithorhynchid lineage since, if not technically an ornithorhynchid, it certainly appears to have been along the evolutionary line leading to ornithorhynchids.

The position of *S. galmani* remains problematical since in dental morphology this taxon is very close to the ornithorhynchid level of organisation in spite of molecular evidence excluding it from the family. Positioning *S. galmani* as ancestral to Ornithorhynchidae places the time of origin for platypus-like monotremes to at least the pre-Albian early Cretaceous. In determining place of origin, the existence of an ornithorhynchid-like monotreme in eastern Australia during the Cretaceous supports an ornithorhynchid origin either on the Australian continent or possibly Antarctica, whose palaeontological history is poorly known but which appears to have been the place of origin for certain higher Gondwanan taxa such as the southern beech *Nothofagus* (Hill 1996).

Pascal et al. (1992a) suggest that the *Monotremata* lineage may have reached southern South America by the early Cretaceous since South America may have been isolated geographically from the early Cretaceous to the early Paleocene; presence of *M. sudamericana* in Paleocene Banco Negro Inferior Formation therefore suggests to them that this taxon was established in Patagonia prior to the early Paleocene, possibly from a lineage that entered South America during the early Cretaceous. However, some geological evidence indicates that South America
AUSTRALIAN MAMMALOGY

retained close connections to Antarctica through the early Cretaceous, only severing connections with the opening of the Drake Passage in the Oligo-Miocene (Luuwer, Galagahan and Coffin 1992).

Analyses of intrafamilial relationships are primarily limited to dental comparisons since only a single pre-Pliocene cranium is known to compare to the skull of the living Or. anatinus. The remarkable conservatism of ornithorhynchid molar morphology has made separation of taxa on dental grounds alone difficult although progressive elaboration of the blade systems and a general trend towards more shallow-rooted molars (culminating in the lack of teeth in adult Ornithorhynchus) can be seen (Messer and Archer 1998). Further complicating matters is that taeniolatid ss have no apparent ancestral type in the (admittedly poor) fossil record, leading some to wonder if they might not be derived ornithorhynchids, which would make Ornithorhynchidae paraphyletic (Pascual et al. 1992b).

Hypotheses about monotreme origins prior to the 1985 publication of S. galmani focused primarily on comparisons between the monotreme skull and skulls of other mammal groups, most often linking monotremes to non-therian mammals such as triconodonts or multituberculates based on construction of the side wall of the braincase (e.g., Hopson and Crompton 1969; Kielen-Jaworowska 1971). Less-favoured hypotheses linked monotremes to either marsupials (Gregory 1947; Kühne 1973, 1977) or non-mammalian synapsids (MacIntyre 1967).

Discovery of S. galmani prompted a series of hypotheses based on ornithorhynchid-type dentition since its molars were less derived than those of the Oligo-Miocene Oxdudron species. Initial analysis of S. galmani described the molars as tribosphenic and therefore therian with a clear pattern of reversed triangular blades resembling those of therian mammals (there are up to two V-shaped blades on the large, rectangular ornithorhynchid molars) (Archer et al. 1985). A subsequent paper considered the molars to be pre-tribosphenic but with therian affinities (related to eucapantotheres, possibly peramurids or vince- lestids) (Kielen-Jaworowska, Crompton and Jenkins 1987). Affinities with South American me- singulatid dryolestoids were suggested when the South American M. sudamericanum was described (Pascual et al., 1992a). In describing the skull and dentition of Oxdudron dicksoni, Archer et al. (1992, 1993a) proposed that monotreme molars may in fact be autapomorphic, with few or none of the cusps homologous to those of therian mammals and with the triangular molar pattern convergent on the pattern of tribosphenic teeth. This view may move the discussion away from dentition for the present and again towards features of the cranium and postcranium.

The early Cretaceous ?eupantofothere Vince- lestes neoventus from Argentina is the first therian mammal for which the skull is known and factors into the debate over whether monotremes are therian or non-therian mammals. A description of the cranial vasculature of V. neoventus has found no close relationship between this taxon and monotremes (Rougier, Wible and Hopson 1992). Recent work on the tympanic region of multituberculates (Meng and Wyss 1995) and on the braincases of early mammals (Wible and Hopson 1993) suggest similarities (possibly synapomorphic) between the rodent-like multituberculates and monotremes in a return to the concept of a monotreme-multituberculate sister group relationship as proposed by Kielen-Jaworowska in 1971. Two recent molecular studies using mitochondrial DNA (Jantke, Xu and Arnaud 1997) and DNA hybridisation (Kirsch and Mayer 1998) find genetic relationships between monotremes and marsupials, revising Gregory's (1947) Marsupionta theory. Additionally, the side wall of the braincase in both living monotreme families may be an independent ossification (Kuhn 1971; Zeller 1989 but see Wible and Hopson 1993), making comparisons of this region difficult at present since fossil taxa lack this ontogenetic information. No relationship hypothesis has yet been universally accepted, highlighting the need for a better understanding of early mammal taxa and of the need for caution in dealing with a group like the monotremes that exhibit such a mosaic of anatomical traits.

MORPHOLOGY

Ornithorhynchus anatinus is beautifully adapted to its niche, feeding and mating in the water and burrowing into the banks of rivers and streams for shelter. It is basically nocturnal, foraging from dusk to dawn, but can be seen during the day in most parts of its range (Grant 1995). Specialisations primarily relate to its amphibious lifestyle: the form is dorso-ventrally flattened and streamlined; the short, powerful limbs are adapted for both swimming and burrowing; manus and pes are webbed (the manus with enormous fan-shaped webbing that aids in swimming); and the fur is dense and waterproof.

The sensitive bill in all living monotremes is covered by numerous mechan- and electroreceptors (Schleich, Langer, Tideman, Coles and Guppy 1986; Andrus, von Daring, Iggo and Proskie 1991;
Manger, Collins and Pettigrew 1997). Electroreceptors need an aqueous environment in which to function, presumably why the tip of the snout is perennially wet in the terrestrial echidnas. The presence of sensory receptors in fossil taxa is inferred by large mandibular canals that would have served as conduits for extensive innervation of the skin of the bill. Understanding the evolutionary development of such unique features as electroreception in fossil forms has been hampere by the dearth of cranial material and lack of postcranial material for nearly all taxa, but some conclusions can be drawn, as discussed below.

**DENTAL MORPHOLOGY**

The thegotic terminology of Every (1974) is used to describe the morphology of ornithorhynchid teeth because it emphasises structure rather than homology, appropriate in the case of the possibly autopomorphic monotreme dentition where structural homologies are unclear (Fig. 1).

The major trend in dental evolution of ornithorhynchid-like monotremes has been a gradual change from the deep-rooted, relatively narrow tooth form of S. galmani to the wide, keratinous tooth pad in Or. anatina, with intermediate forms showing progressive degeneration and multiplication of roots and widening of the molar base.

In Or. anatina, nestlings retain vestigial molar teeth until approximately one month after leaving the burrow (Griffiths 1978). These milk teeth display the characteristic ornithorhynchid double-V pattern, albeit in degenerate form, but are replaced by keratinous pads in adult Or. anatina that take over the task of mastication (Simpson 1929; Green 1937). It had been predicted (eg. Thomas 1889) that ancestral platypuses must have had functional teeth because the molars in Ornithorhynchus are clearly vestigial and the dentition, therefore, must have had a functional predecessor. Comparison with the morphology of young Or. anatina molars enabled identification of the first Tertiary ornithorhynchid, Obdurodon insignis (Woodburne and Tedford 1975).

The single blade (diakidrepanon) on the posterior half of the M1 of S. galmani and the presence of a well-developed M3 are two principal dental features separating the Cretaceous taxon from the Palaeocene M. sudamericanum and the Oligo-Miocene Obdurodon species, all of which have a V-shaped blade (triakidrepanon) on the posterior half of M1 (Archer et al. 1992, 1993a; Musser and Archer 1998; pers. obs.). The size and development of M3 is not known for M. sudamericanum, temporo-superiorly between S. galmani and the earliest Obdurodon species, but both Or. insignis and Or. dicksoni must have had very reduced M3s as evidenced by a single posterior alveolus for a small M3 in the dentaries assigned to these taxa and by a small, undescribed M3 recovered for Or. dicksoni.

**CRANIAL MORPHOLOGY**

The recovery of Or. dicksoni from the middle Miocene of Riversleigh, a complete adult ornithorhynchid skull with premolars in place, has allowed comparisons between the crania of Or. anatina and this species of Obdurodon (Fig. 2; Table 2) (Archer et al. 1992, 1993a; Musser and Archer 1998). Most of the distinctive morphological features present in Or. anatina also appear in the Miocene taxon (eg., a large, flattened bill formed by both cartilage plate and the bones of the snout) and it must have been similarly amphibious (Archer et al. 1992; 1993a; Musser and Archer 1998). Although molars were missing from the specimen (no doubt because of the shortness of the molar roots) ornithorhynchid molars recovered from the same site as the skull have been identified as belonging to Or. dicksoni (Archer et al. 1992; 1993a; Musser and Archer 1998).

Many of the features in Or. dicksoni appear to be ancestral states (Archer et al. 1992, 1993a; Musser and Archer 1998). The robustness of the skull and dentary are certainly plesiomorphic, reflecting the presence of functional dentition and correlated muscularity musculature. The dentary has well-formed coronoid and angular processes for this musculature (the coronoid process is missing in Or. anatina and the angular process is reduced in Or. insignis and Or. anatina). The bones of the rostrum are unfused, in contrast to the state in Or. anatina as well as in the echidnas where fusion of the rostral bones obliterates suture lines. The sutures of the cranium itself, however, are well fused. The flatter skull base in Or. dicksoni (in contrast to the downwardly-deflected skull in Or. anatina) suggests that Or. dicksoni forged higher in the water column rather than sifting through bottom sediments as Or. anatina does, a behaviour correlated with change in morphology that is most likely derived. Some of the differences, however, are not easily categorised. The surprisingly large, spoon-shaped bill in Or. dicksoni was quite unexpected. The much-rewarded upon bill in Or. anatina has no counterpart among living mammals for its size and it is much larger than the bill in the echidnas. The expectation, therefore, was that an earlier platypus temporally between these two taxa would have had an intermediate-sized bill. The hypertrophied bill in Or. dicksoni is perhaps the largest snout proportionally within Mammalia.
Fig. 2 Comparison of the bill and marginal cartilage between *Odoburodon dicksoni* and *Ornithorhynchus anatinus*, illustrating hypertrophy of the bill and cartilage in *Ob. dicksoni*. A, *Ob. dicksoni*; B, *Or. anatinus*. Abbreviation: M. ca., marginal cartilage.

<table>
<thead>
<tr>
<th><em>Odoburodon dicksoni</em></th>
<th><em>Ornithorhynchus anatinus</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>cranium large and robust</td>
<td>cranium small and gracile</td>
</tr>
<tr>
<td>rostrum relatively straight with respect to cranial table</td>
<td>rostrum downwardly deflected</td>
</tr>
<tr>
<td>rostral bones unfused</td>
<td>rostral bones fused</td>
</tr>
<tr>
<td>anterior processes of premaxilla, septomaxilla meet at midline</td>
<td>anterior processes of premaxilla, septomaxilla widely separate</td>
</tr>
<tr>
<td>fossae on palate deep, wide and oval</td>
<td>fossae on palate shallow, narrow</td>
</tr>
<tr>
<td>zygomatic arches bowed laterally reflecting robust masticatory musculature</td>
<td>zygomatic arches straight, reflecting more weakly-developed masticatory musculature</td>
</tr>
<tr>
<td>glenoid fossa broad, deep and oblique</td>
<td>glenoid fossa narrow, transverse</td>
</tr>
<tr>
<td>'mucal' crest prominent</td>
<td>'mucal' crest weak</td>
</tr>
</tbody>
</table>

Table 2: A list of some of the differences between the crania of *Odoburodon dicksoni* and *Ornithorhynchus anatinus* (modified from Archer et al. 1992, 1993a).
This poses one of the more interesting questions for this lineage: does the hypertrophied bill in *Ob. dicksoni* reflect a plesiomorphic condition or a derived one?

While absolute skull length in *Ob. dicksoni* is considerably greater than in the average *Or. anatina*, the difference in the functional length of the cranium (inclusive of the tooth row) is not as great. In fact, this length in *Ob. dicksoni* overlaps the same measurement in larger *Or. anatina* (pers. obs.) which may reach 60 cm in total length (Grant 1995). These proportional differences emphasise the hypertrophy of the snout in *Ob. dicksoni*. Whether the bill in *Or. anatina* was reduced from a large-billed ancestor such as *Ob. dicksoni* or whether its bill instead represents an enlargement of an *Ob. ingens*-type smaller bill is still conjecture, although the most parsimonious explanation at present is that species of *Ornitohyracodon* descended from an *Obdurodon* species closer in form to the more gracile *Ob. ingens* than to the larger, more robust *Ob. dicksoni* (Musser and Archer 1998). It is impossible at present, in the absence of cranial material from other known ornithohyracoids, to know the extent of hypertrophy within the line.

The exquisite preservation of the *Obdurodon dicksoni* skull has permitted reconstruction of parts of the soft anatomy. The results of this study (Musser and Archer 1998) indicate that 1) dorsal and possibly ventral frontal shields (extensions of the skin of the bill) would have been present in *Ob. dicksoni* (as in *Or. anatina*), evidenced by the presence and placement of foramina for a branch of the large trigeminal nerve that in *Or. anatina* innervates the dorsal shield; 2) a relatively larger marginal cartilage formed the contours of the bill in *Ob. dicksoni*, indicated by the proportionately deeper lateral margins of the bill (Fig. 2); and 3) deeply dished areas on the palate in the region of the epithelial ridges in *Or. anatina* may have housed comparatively huge, ridge-like epithelial structures in *Ob. dicksoni*, taking the place of the missing anterior dentition (the incisors and canines) as do the much smaller epithelial ridges in *Or. anatina*. Outgrowths of epithelium possibly helped to hold the shallow-rooted molars in place. The trend towards elaboration of oral epithelium, seen at its most extreme in the replacement of true teeth by epithelial pads in *Or. anatina*, seems to have thus been underway by the Miocene (Musser and Archer 1998).

Palaeontological evidence, then, indicates that the distinctive platypus cranial form had appeared by at least the early Miocene (Archer et al. 1995a). Although there is no cranial material for earlier ornithohyracodont taxa aside from the *Ob. ingens* jaw fragment, because of the similarities in molar morphology it is difficult not to assume that *Monotrematum* and the central Australian *Obdurodon* species shared at least a general skull form, bringing this skull morphology at the least to the earliest Tertiary.

As the conundrum over the question of hypertrophy illustrates, the platypus line may have had a few evolutionary dead ends. In spite of its very platypus-like morphology, *Ob. dicksoni* may have been off the direct line leading to species of *Ornitohyracodon* as part of a specialised northern population of large-billed platypuses (Musser and Archer 1998). The distant Patagonian population may have been a remnant as well, having left no known descendants in South America (Pascual et al. 1992a).

**POSTCRANIAL MORPHOLOGY**

The most strikingly plesiomorphic structure in monotremes is the shoulder girdle, which retains 'reptilian' bony elements - interclavicle, prococaroids (epiconaroids) and separate metacocaroids (anterior conaroids) - that were still present in some early mammal taxa but which have been lost in more advanced groups such as marsupials and placentals (in which rudiments of the prococaroid, metacocaroid and chondral part of the interclavicle appear in ontogeny but where no bony interclavicle or prococaroid develop: Klima 1987). There are few complete shoulder girdles known for early mammal taxa, which are usually recovered as isolated teeth or jaws. However, the shoulder apparatus has been described for the triconodont *Morganucodon* (Europteryxodon), *Megarachyodon* and *Erythrotherium* (material which may have included shoulder girdle elements of the ?early symmetrodont *Kuelneotherium* (Jenkins and Par- rington 1976); the late Jurassic dryolestoid *Helenkeleratherium* (Kreib 1991); a late Cre- taceous tenuilabidoid multituberculate *Bulgana- thex* (Sereno and McKenna 1995) and a newly-discovered late Jurassic symmetrodont, *Zhangheotherium* (Hu, Wang, Luo and Li 1997). The *Helenkeleratherium*, *Bulgana- thex* and *Zhangheotherium* girdles are more advanced than the monotreme shoulder girdle in reduction of the interclavicle and mobility of the shoulder joint while the triconod- on*?Kuehneotherid* girdles appear to be more plesiomorphic (Jenkins and Par- rington 1976), placing the monotreme shoulder girdle morphologically between the earliest mammal types such as *Morganucodon* and later symmetrodonts such as *Zhangheotherium*, i.e., between the triconodont and later symmetrodont levels of organisation.
This indicates a point of origin for at least the shoulder girdle temporally between the early and late Jurassic, which agrees with an early Jurassic origin for monotremes proposed by Kielan-Jaworska (1992).

A feature usually cited as unique to monotremes is the presence of a hollow cranial spur which is vestigial in tachyglossids but which conducts poison in *Or. anatinus* (Griffiths 1978). However, both the symmetrodont *Zalmoxes lata* and tektroodont *Gobiconodon australis* (Lamin and Schaff 1988) were equipped with pedal spurs making the character plesiomorphic rather than apomorphic in monotremes.

**BIOGEOGRAPHY, DISTRIBUTION AND PALAEOECOLOGY**

Monotremes, specifically ornithorhynchids, had been distributed across at least southern South America, Antarctica and Australia during the late Cretaceous through the earliest Tertiary (Pascual et al. 1992a, b) in a continuous biogeographic realm of southern Gondwana termed the Weddelian Province, a region that also included New Zealand (Case 1989). Prior to the discovery of ornithorhynchids in southern South America (Pascual et al. 1992a, b) proof that monotremes were a Gondwanan group was lacking, although their apparent antiquity suggested that they may have been widely distributed across the southern continents when these land masses were still joined.

Changes in ornithorhynchid distribution over time have involved a complex mix of geographic configurations of the southern land masses, the effects of crustal plate movements, and the aridification and warming of Australia brought about by its northward drift. These factors have combined to progressively reduce ornithorhynchid distribution to that of its sole surviving representative *Ornithorhynchus anatinus* in eastern Australia.

Although parts of its range have contracted since European settlement, most populations of *Or. anatinus* appear to be in no imminent danger (Grant 1995). The present distribution of *Or. anatinus* only begins to appear fragile and resilient when compared to prehistoric ornithorhynchid distribution. This Gondwanan distribution is coupled with a temporal span from at least the Cretaceous/Tertiary boundary to the present, a record unequalled by any living mammalian family.

The three Mesozoic mammals now known from Australia are all from the early Cretaceous (Aptian-Albian) of southeastern Australia - the Lightning Ridge monotremes *Sieropus galmani* (Archer et al. 1985) and *Kollikodon richiei* (Flannery et al. 1993) and the newly-discovered, slightly older *Australobisphodon nyktos* from Victoria in southeastern Australia, described as an early placental mammal (Rich, Vickers-Rich, Constantine, Flannery, Kool and van Klaveren 1997).

Lightning Ridge is considered Albian (about 110 mybp), by which time India and Madagascar had severed their connection to Antarctica via Sri Lanka and were moving north, leaving a gap closer to South America. Antarctica and Australia effectively isolated from Africa, India and Madagascar (Lawver et al. 1992). A shallow seaway had opened from the west between Australia and Antarctica by the Albian although the two continents remained contiguous across southeastern Australia (Lawver et al. 1992). West Antarctica would not become amalgamated with East Antarctica until the late Cretaceous although there was extensive continental shelf in the region (Lawver et al. 1992) which may have been periodically emergent.

During the Albian Lightning Ridge lay just north of the Antarctic Circle (Archer et al. 1985; Flannery et al. 1995) and Victoria lay within the Antarctic Circle itself (Rich et al. 1997). *S. galmani*, *K. richiei* and *A. nyktos*, therefore, were all members of polar or near-polar faunas and subject to the environmental stresses at these high latitudes. The early Cretaceous was one of the coolest periods in Australian history and southeastern Australia, because of its orientation, lay closer to the South Pole than did the rest of Australia (Froese 1997). Mean annual temperature in this region (between 70° and 80° latitude) would have been about 4°, with frigid conditions possible year-round and formation of extensive winter ice (Froese 1997). The near-polar localities would have experienced long winter nights and summer days.

Lightning Ridge (Fig. 3) was situated close to the shores of the great inland Eromanga Sea at a time (Aptian/Albian) when sea level had reached a peak and marine transgression was at a maximum (Fig. 3) (Archer et al. 1985; White 1990). Glaciers were present on high ground and parts of the Eromanga Sea would have frozen during the winter (White 1990) although the climate would not have been as extreme as in polar regions today (Froese 1997). The depositional environment at Lightning Ridge was estuarine as evidenced by the presence of plesiosaur teeth in the deposit (Archer et al. 1985; Flannery et al. 1995). The Lightning Ridge Local Fauna reflects the antiquity of stereopodids and kollikodontids: dinosaur remains found with *S. galmani* and *K. richiei* include the
large theropod *Rapator ornitholestoides*, the ornithopod *Pulgarotaurus australis* and the iguanodontid *Mutaburrasaurus longidoni* as well as a small crocodile, two types of lungfish, pleosauurs and turtles (Archer et al. 1985; Flannery et al. 1995).

The large size of both *S. galmani* and *K. ritchiei* is extraordinary for Mesozoic mammals, a feature attributed to the near-polar climate. However, *A. nyktos* found further south was shrew-sized (Rich et al. 1997) and thus is closer in size to most Mesozoic mammals than are *S. galmani* and *K. ritchiei* suggesting greater diversity among near polar Cretaceous Australian mammals than previously recognised.

Global temperatures had warmed considerably by the late Cretaceous with a thermal maximum at about 90 mybp (Prates 1997). The cool temperate Weddellian Province served as a corridor for taxa such as arboreal marsupial mammals dispersing between southern South America and Australia through Antarctica (Case 1989). This region may have also been an important centre of origin and diversification for taxa such as *Nothofagus* (Hill 1996) and an area where the marsupial fauna, closely associated with the relatively homogenous *Nothofagus*-dominated forest environment, did not generally diversify before entering Australia in the early Tertiary. The many new habitats created as Australia moved north provided the catalyst for the explosive Australian marsupial radiation that subsequently took place (Case 1989).

Patagonia during the Paleocene would have been part of the Weddellian Province (Fig. 3), possibly isolated from the rest of South America by river systems while it was connected, via Antarctica, to Australia (Ramos 1989; Crisci, Cigliano, Moronne and Roig-Jumet 1991). Studies that suggest separate biogeographic histories for northern and southern South America and their bivalves support the belief that southern South America has closer ties to Antarctica, Australia, New Zealand and New Caledonia than to northern South America (Ramos 1989; Crisci et al. 1991).

New Zealand, New Caledonia and other continental fragments (eg., Campbell Plateau and Lord Howe Rise) were accreted along the eastern margin of Gondwana throughout the Cretaceous, rifting from Antarctica at about 85 mybp (Lawver et al. 1992) and thus conceivably could have carried ornithorhynchids with them as they moved to the northeast.

What little is known about the Paleocene environment of Patagonia indicates lowland rainforest, the site representing a freshwater lagoon close to the widening South Atlantic Ocean (Pascual et al. 1992a, b; Archer 1995). Three of the mammals from the Banco Negro Inferior Local Fauna - the derived multituberculate *Sudamerica ameghinoi* and at least two primitive placental 'condylarths' - are of special interest: *S. ameghinoi* and *M. sudamericanum* are both relic taxa from archaic lineages that survived into the Paleocene although their fates beyond their appearance in the BNI Local Fauna are unknown (Pascual et al. 1992a). The condylarths represent elements of faunal invasions from North America (Pascual et al. 1992b). Also recovered from the Patagonian site are a single marsupial, five types of crocodiles, four species of chelid turtles and a huge, metre-long frog (Pascual et al. 1992a; Archer 1995).

As South America moved north into lower latitudes, intermittent land connections were made with both North America and Africa enabling placental mammals and other non-mammalian groups to invade; such competition may have been responsible for extinction of ornithorhynchids on that continent (Pascual et al. 1992b). No ornithorhynchid material has been recovered from either the Bolivian or Peruvian mammal assemblages of approximately the same age (collectively representing the Tiupampaan Land Mammal Age of South America) and it is probable that ornithorhynchids were never a part of the more northern South American mammal fauna (Pascual et al. 1992b).

The early Eocene Tingamarra faunal assemblage from southeastern Queensland (55 mybp; Godthelp, Archer, Cifelli and Gilkeson 1992) offers the closest temporal comparison to the Patagonian site although no monotremes have yet been found in this deposit. The Tingamarra Local Fauna includes an archaic microchiropteran (Hand, Novacek, Godthelp and Archer 1994), a possible condylarth (Godthelp et al. 1992), primitive marsupial carnivores (Godthelp, pers. comm.), primitive nondiprotodontid marsupials with bunodont teeth (eg., Archer, Hand and Godthelp 1993b), other undetermined marsupial taxa, bird taxa including passerines (Boles 1997), two species of crocodile (Willis, Molnar and Scanlon 1993; Salisbury and Willis 1996), a trionychid turtle (Gaffney 1991), madasooid snakes (Scanlon 1993), and 3 types of frog (Tyler and Godthelp 1993).
No subsequent fossil ornithorhynchids are known until the late Oligocene of Australia, by which time Australia and Antarctica had severed connections, effectively isolating Australia biogeographically for the next 25 million years prior to docking with southeast Asia. Timing of the disruption of passage between southern South America through Antarctica to Australia remains contentious; terrestrial migration would have been dependant on emergence of the of the archipelagic connections between southern South America and the Antarctic Peninsula and between Antarctic and Australia via the Tasman Rise. Clearance at about 30 mybp of the South Tasman Rise from Antarctica as Australia moved north (Veevers 1991; Lawver et al. 1992) broadly coincided with a period of lowered sea level from the end of the Eocene to the middle Oligocene (probably due to Antarctic glaciation and formation of sea-ice) (Quilty 1994), suggesting that terrestrial migration may have been possible although difficult to the early to middle Oligocene (contrary to Woodburn and Case 1996). A strong circumpolar current developed only when the Drake Passage opened up between southern South America and the Antarctic Peninsula at about 20 mybp (Lawver et al. 1992).
Floral records indicate that the Antarctic Peninsula (the only rein of Antarctica for which early Tertiary floral records are available) had probably become inhospitable to most terrestrial flora and fauna by the late Oligocene or early (Aaskin 1992).

As Australia moved north the continent experienced alternating periods of icehouse (cool, dry) conditions and greenhouse (warm, moist) conditions (McGowan and Li 1994). The Oligocene, late Miocene and late Pliocene-Pleistocene were characterised by icehouse conditions while the early Eocene, early middle Miocene and early Pliocene were greenhouse periods (McGowan and Li 1994).

All Tertiary fossil sites producing ornithorhynchid material appear to have been lacustrine, riverine, freshwater lagoon, or rainforest springs and pools (some with cave connections). The late Oligocene Etadunna Formation of the eastern Lake Eyre region and Nambha Formation of the Freme Embayment (Obdurodon insignis and Ob. sp. A localities), far west of the present distribution of Ot. anatinus (Fig. 3), were large, permanent lakes supporting diverse vertebrate faunas. Associated faunas include fish (including lungfish), crocodiles, flamingoes and freshwater dolphins, with possums, palorchestids, kangaroos and koalas on the forested periphery (Rich et al. 1991; Woodburne, MacFadden, Case, Springer, Pledge, Power, Woodburne and Springer 1994). The river systems of the Channel Country - principally the ancestral Diamantina River and Cooper Creek systems - would have had permanent flows during the late Oligocene, draining southwest into Lake Eyre North, while the rivers from what is now the arid centre would have flowed to the southeast into the lake basin (White 1990). Whether the eastern systems alone supported ornithorhynchids or whether the distribution extended west to include the rivers from the centre is unknown.

Australia had come to within 15° south of its present geographic position by the middle Miocene (approx. 15 mybp) (Veever 1991). Riversleigh during the middle Miocene was predominantly rainforest marked by a series of freshwater springs, pools and braided streams, with many of the fossil sites being cave deposits (Archer, Hand and Godthelp 1994; Creaser 1997). Climate was warm, wet, and probably aseasonal, this period marking the end of greenhouse conditions before deterioration of temperatures through the late Miocene (McGowan and Li, Archer et al. 1995).

Obdurodon dicksoni was recovered from eroded sediments in the watershed of the modern Gregory River which drains into the Gulf of Carpentaria, a system which today at least does not support platypuses (Grant 1992, 1995). Although the Riversleigh deposits are close to the Gregory River, during the Miocene the freshwater springs forming the deposits were part of an internal drainage system that did not open to the sea (Archer et al. 1994). Evidence for this comes from the absence of any saltwater-tolerant taxa in any of the sedimentologically diverse Riversleigh deposits spanning the late Oligocene to late Miocene such as file snakes (family Acrochordidae) which might be expected given that they were present in the Indian Ocean region prior to the middle Miocene (Archer et al. 1994).

Loss of ornithorhynchid habitat since the middle Miocene was almost certainly related to increasing drying and its consequent effects on the continent's river systems. Sclerophyllous vegetation had replaced rainforest in the centre of the continent by the early Miocene (Martin 1998); river systems progressively dried out and much of the habitat available to platypuses was gradually eliminated. The Lake Eyre Basin is the only one of the great internal drainage basins of Tertiary Australia to have retained a degree of permanency (White 1990), although today it is dry most of the time and only fills periodically after heavy rains. The continued movement north of the Australian continent and the inevitable contact with Asia, causing deformation of the northern edge of the continent (resulting in the rise of the New Guinea highlands), brought some relief from the general trend towards aridification as Australia entered the hot, humid tropics (Veever 1991). Refugia were created for both flora and fauna in areas such as the Atherton Tablelands in Queensland (Archer et al. 1995) and the mountains of New Guinea (Flannery 1995). During this long and changeable period it is possible that platypuses speciated in isolated regions such as Riversleigh.

The Pliocene climate fluctuated greatly, beginning with a warm interval but gradually cooling, a trend that culminated in the cold regimes of the late Pliocene and Pleistocene (Kershaw, Martin and McEwen Mason 1994). Many Miocene mammalian families had become extinct by the Pliocene, the diverse Miocene mammalian faunas in Australia reflecting the creation of more arid habitats (Archer et al. 1995). Pliocene Ornithorhynchus material from the Bow Local Fauna in eastern New South Wales was found with the still-extant genera Macropus, Perameles and Dasyurus as well as with extinct genera such as Thylacoleo and Palorchestes (Rich et al. 1991).

By the Pleistocene Australia appeared much as
it does today although the climate was generally much cooler and at times even drier than at present (Martin 1994; Kersevay et al. 1994). Periodic glaciation caused great climatic swings together with changes in sea level that both created and eliminated habitat. As an example, King Island, which has retained a platypus population, would have been periodically separated from Tasmania during interglacial periods before its present isolation from the Tasmanian mainland from about 6,000 ybp (White 1990).

The earliest occurrence of Ornithorhynchus anatinus dates from about 100,000 ybp from the Bunyan Siding site in New South Wales (Davis 1996). All Pleistocene fossil sites fall within the present range of O. anatinus with the exception of the Lake Tandou site (Hope, pers. comm.), which is now a dry lake bed to the west of the Darling River in New South Wales. The King's Creek, Brisbane River, Bunyan Siding and Snowy River sites all appear to be deposition in a natural environment, primarily creek or riverine deposits (De Vol 1885; Marshall 1992; Davis 1996). However, the Lake Tandou and southern Tasmanian sites are archaeological and platypuses from these sites may have been used as a food item by Aborigines (J. Hope, pers. comm.; Marshall 1992). The Tasmanian material in particular provides compelling evidence for Aboriginal hunting, with numerous cranial and postcranial skeletal elements recovered from cave deposits (Marshall 1992). The Tasmanian cave sites were in use, apparently, only while Tasmania lay in the grip of glaciation; such a nutritious supply of dietary fat, along with the warmth provided by the platypus thick, insulated fur, may have been essential for survival (Marshall 1992).

FACTORS LIMITING DISTRIBUTION OF ORNITHORHNCHIDS

Platypuses today only occur on the far eastern fringe of their previous distribution, a collapse in range of great magnitude. Since present distributional patterns generally follow relatively permanent river systems, loss of permanence correlated with drying of the continent is probably a critical factor that contributed to the geographic decline of ornithorhynchids. However, one plausible reason for the absence of platypuses from the Carpentaria region today is that the long northern wet season with attendant flooding of habitat would also create conditions untenable for platypuses (Grant 1995).

Ornithorhynchids are as yet unknown from either Western Australia or the Northern Territory and it is not known whether the western half of the continent supported ornithorhynchids; the rivers of Western Australia (now chains of saline lakes) flowing into the Great Australian Bight to the south and into the Indian Ocean to the west ceased to be perennial in the middle Miocene (White 1990).

Possible predation by crocodiles across the north of the continent has been suggested as a factor limiting the northern distribution of O. anatinus, but the ranges for the saltwater crocodile (Crocodylus porosus) and O. anatinus do overlap near Cooktown (with reports of crocodiles feeding on platypus: Grant 1995). The fossil evidence indicates that platypus-like monotremes have co-existed with crocodiles for millions of years, the first instance being the co-occurrence of S. galbani and of small crocodiles at Lightning Ridge over 100 million years ago (Archer et al. 1985). Diverse assemblages of crocodiles (including small forms) in Patagonia (Pascual et al. 1992a), central Australia (Woodburne et al. 1994) and Riversleigh (Archer et al. 1992) share their habitat with platypuses. Although the presence of crocodiles in the environment may not have excluded platypuses, co-existence with such efficient predators may well have had an influence on the retention or development of defences such as the poisonous spur of the platypus.

Other predators in faunas associated with earlier platypus-like monotremes were quite different from any living today. Some of the Cretaceous dinosaurs would certainly have been predators on small mammals, and even such unlikely predators as the giant frog of the Patagonian Patagonia might have been a danger. Although the crural spurs in O. anatinus are used primarily by male platypuses during the mating season (spurs are vestigial in female O. anatinus) (Griffiths 1978) perhaps these weapons were used against such predators during the early evolution of ornithorhynchids.

A CONSERVATION MESSAGE

It seems certain that the monotreme fossil record will continue to grow and, quite possibly, to surprise students of monotreme and mammalian evolution. The discovery of a new tachyglossid in New Guinea suggests that even among living monotremes there may yet be unexpected discoveries (Flannery, 1995). The status of the Australian short-beaked echidna T. aculeatus appears to be secure; however, the status of the long-beaked Zaglossus species in New Guinea may be fragile. Reloading tribal restrictions against eating of echidnas in New Guinea coupled with growing population pressures does not bode well for their future, and they are becoming locally extinct in
parts of their range (Flannery 1995). The status of *Oro- anatina*, protected in Australia but not considered threatened, must be considered in light of the pressures being currently exerted on the waterways of eastern Australia, in particular pollution, land degradation and unpredictable climate change. The fossil record unequivocally demonstrates 1) that monotremes are the most archaic group of living mammals; 2) that they were previously much more diverse and 3) that ornithorhynchids at least were historically much more widespread than at present, their range now contracted to the far eastern corner of the original extent. Palaeontologically it is a lineage in decline. It is imperative that all efforts be made to consider the welfare of both the platypus and echidnas in any conservation plan both for Australia and for New Guinea.

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CHAPTER 5

Reassessment of the affinities of *Kollikodon ritchiei*:
An ?allotherian mammal from the Cretaceous of Australia

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A copy of the manuscript follows.
CHAPTER 5

Chapter 5 (‘Reassessment of the affinities of Kollikodon ritchiei: An ?allotherian mammal from the Cretaceous of Australia’) is an unpublished manuscript describing the first upper molars and fragmentary maxilla of the Early Cretaceous mammal Kollikodon ritchiei. Phylogenetic analysis was conducted to assess its relationships to other mammals. This unusual mammal is only otherwise known from the holotype lower jaw (Flannery et al., 1995). The new specimen represents the first upper molars of a Mesozoic mammal recovered from Australia and is a highly significant discovery.

This extended paper is intended to follow a shorter (co-authored) paper announcing the discovery of the maxilla. Contributions of co-authors to this paper are listed in the Acknowledgements. The format is that of the Journal of Vertebrate Paleontology, to which the long version of the paper will most likely be submitted.

This paper includes discussion of the palaeogeography of the Lightning Ridge area (where the fossil material was recovered); a complete description of the maxilla, upper molariform row and ultimate premolariform tooth; a revised description of the holotype lower jaw and dentition; comparisons between Kollikodon and other Mesozoic mammals or near relatives; a model for derivation of the multicuspid molar teeth of Kollikodon; and a phylogenetic analysis of the relationships of Kollikodon to those of other Mesozoic mammals.

Analysis of the maxilla, lower jaw and dentition has cast doubt on the original interpretation by Flannery et al. (1995) that Kollikodon is a derived monotreme; several lines of evidence (primarily dental) suggest that although Kollikodon has some monotreme-like features, it falls outside of Monotremata based on presently agreed-upon synapomorphies for the group. It instead appears to be related to allotherian mammals (Haramiyida + Multituberculata) with which it shares a multicuspid dentition arranged in parallel rows.
Reassessment of the affinities of *Kollikodon ritchiei*: An ?allotherian mammal from the Cretaceous of Australia

ANNE M. MUSSER

ABSTRACT -- The first upper cheekteeth of a Mesozoic mammal from Australia have been recovered from Early Cretaceous deposits at Lightning Ridge, New South Wales (Musser et al., in prep.). The specimen is a partial, opalised maxillary fragment with complete molar row and ultimate premolariform. It has been referred to the highly derived *Kollikodon ritchiei* (family *Kollikodontidae*: Flannery et al., 1995) because it has unique features otherwise only combined in the holotype lower jaw including: 1) longitudinal rows of bunodont cusps; 2) convex curvature of the tooth row; and 3) abrupt size disjunction between the ultimate premolar and first molar (Flannery et al., 1995). Molar form – multiple cusps arranged in parallel rows - is remarkably similar to that of tritylodontid cynodonts, theroteinids, haramiyids and multituberculates. Multicusped dentitions arranged in rows have thus evolved several times during the Mesozoic. The holotype lower jaw is re-examined, providing evidence of a well-developed meckelian groove and small mandibular canal. The small size of the mandibular canal in *K. ritchiei*, together with a longitudinally arranged (rather than triangulated) dentition, suggests that *K. ritchiei* is not a monotreme, as previously suggested (Flannery et al., 1995). Monotremes have enlarged mandibular canals that carry a large trigeminal nerve to sensory receptors on the snout (a synapomorphy for the group: Musser, 2003; Rich et al., 2005) and all toothed monotremes have molars with a reversed-triangle pattern (e.g., Archer et al., 1985; Pascual et al., 1992a, b, 2002; Archer et al. 1992, 1993; Musser and Archer, 1998; Rich et al., 2001b, 2005). Although certain features of the maxillary region suggest a relationship to monotremes, parsimony analysis based primarily on dental features suggests a much closer relationship to theroteinids and haramiyids (order Haramiyida) and to Multituberculata (together comprising the subclass Allotheria *sensu* Butler, 2000). A model is presented for derivation of the molar pattern in *K. ritchiei* based on the hypothesis that haramiyid and multituberculate molars may have evolved from the ‘cusps-in-line’ pattern of morganucodontids (reviewed by Patterson, 1956). Relationships between morganucodontids, haramiyids, multituberculates, monotremes and *Kollikodon* are investigated. *K. ritchiei* has a mosaic of plesiomorphic and derived characters that in combination place it as a unique, highly specialised taxon within Mammalia (provisionally within Allotheria). A new monotypic order, Kollikodonta, is proposed.
INTRODUCTION

Opalized fossils of Early Cretaceous age have been known from Lightning Ridge, New South Wales, for nearly one hundred years (e.g., Etheridge, 1917). Opal miners recover the fossilised remains of dinosaurs and other Mesozoic vertebrates, plants and invertebrates in a search for precious opal. However, mammal remains are rare and have only been known since the mid-1980s. The first mammal from Lightning Ridge – in fact, the first Mesozoic mammal from Australia – was the monotreme *Steropodon galmani* (Archer et al., 1985). A second described mammal, *Kollikodon ritchiei*, was subsequently discovered and described as a new type of highly derived monotreme (Flannery et al., 1995).

Although the molar pattern of *Steropodon* (rectangular molars with triangulated cusps) is similar to that of Tertiary platypuses (*Obdurodon* species), the molars of *Kollikodon* are not triangulated and are remarkably and uniformly bunodont. The name ‘*Kollikodon*’ combines the Greek ‘kollix’ (bun or bread roll) with ‘odon’ (tooth), in reference to the rounded shape of the molar cusps (Flannery et al., 1995). In the analysis of the lower jaw by Flannery et al. (1995), monotreme affinities appear to have been the only options considered and detailed comparisons were made only with monotremes. The decision to place *Kollikodon* within Monotremata – an assumption based primarily on dental characters (Flannery et al., 1995) – is reassessed in the present study. The discovery of an upper jaw with cheekteeth provides a great deal of new information on dental pattern, palatal structure and orbital region, enabling a much more detailed analysis. A new interpretation of affinities and relationships of *Kollikodon* is presented here.

The new material is a partial maxilla with part of the palate, four molariform teeth and ultimate premolariform preserved. The specimen was found on a mullock heap (mine tailings) on the edge of Lightning Ridge Township and was subsequently purchased by Andrew Cody. Preservation of the maxilla differs slightly from that of the *K. ritchiei* holotype (there is less internal structure on the maxilla). Like the holotype, the maxilla is comprised of amber potch (non-precious opal).

GEOLOGICAL AND PALAEONTOLOGICAL SETTING

During much of the Mesozoic the present continent of Australia was part of the southern supercontinent of Gondwana. Gondwana began to fracture into the present landmasses of South America, Africa, Madagascar, India-Sri Lanka, Antarctica, New Zealand and Australia beginning in the Late Triassic (shortly after the breakup of Pangaea: Lawver et al., 1992; Veevers, 2000). After progressive rifting, the component landmasses completed separation in the early Tertiary, with Australia completely isolated from Antarctica at about 35 mybp (through establishment of the Circum-Antarctic Current and buildup of polar ice: Veevers,
2000). The southern and eastern regions of Gondwana, with Antarctica in a central position, were clustered around the South Pole. This high-latitude geographical position had profound effects on the flora and fauna, including that of Lightning Ridge. Mesozoic connections to Pangaeauan and subsequently Gondwanan landmasses were also highly significant in determining the composition, relationships and evolution of Australian biotas.

The Lightning Ridge fossil-bearing sediments are middle Aptian in age (approx. 110 mybp: Burger, 1988; Morgan, 1988). At that time Lightning Ridge lay between 50º and 60º south, just north of the Antarctic Circle (Fig 1; adapted from Lawver et al., 1992). The climate was probably seasonal and cool-temperate conditions would have prevailed (Rich and Rich, 1989). Evidence from other Early Cretaceous sites in southeastern Australia indicate a strongly seasonal climate and perhaps even winter freezing (Rich et al., 1988).

FIGURE 1. Geographical position of Lightning Ridge during the middle Aptian (110 mybp) relative to the continents that comprised the supercontinent Gondwana at that time. Clockwise from left: South America; Africa; Madagascar-India-Sri Lanka; Australia; New Zealand (bottom right); and Antarctica. Concentric lines indicate latitude at 10 degree intervals to 30º South; lines of longitude are at 30º intervals and converge at the South Pole. Lightning Ridge during the middle Aptian lay between 50 and 60 degrees South. Redrawn from Lawver et al. (1992).

Much of central Australia during the Early Cretaceous was covered by a vast inland sea (the Eromanga Sea) that flowed in from what is now the north of the continent (e.g., Veevers,
The Eromanga Sea was in existence from the Neocomian to Aptian (140.5 to 116.5 mybp) and reached its maximum extent at about 116 mybp (Barremian) before retreating (Veevers, 2001). At the time of deposition of the Lightning Ridge fossil-bearing sediments (middle Aptian), the area that is now the Ridge would have been close to the shores of the Eromanga Sea as evidenced by the mix of predominantly freshwater species and estuarine or possibly marine taxa.

**FIGURE 2.** Extent of maximum incursion of the Eromanga Sea (116 mybp). Much of the Australian continent was inundated by this shallow sea during the Early Cretaceous (Neocomian to Aptian) and emergent land was limited to a series of large islands. At the time of deposition of the Lightning Ridge sediments the sea had begun its retreat, which was complete by 99 mybp (latest Early Cretaceous). Contours of the present continent of Australia are outlined in black. Redrawn from Veevers (2001).

Lightning Ridge fossils are found within volcanically derived clay facies (the ‘Finch claystone’) of the Wallangulla Sandstone Member of the Griman Creek Formation (e.g., Smith, 1999). The Wallungalla Sandstone represents estuarine or shallow marine deposits (Byrnes, 1977, Molnar, 1980). The Lightning Ridge environment during the middle Aptian is believed to have been brackish (estuarine) or freshwater (lakes and streams) (Molnar, 1980a; Dettman et al.,
1992). Evidence for freshwater accumulation includes a distinctive assemblage of viviparids, thiarids and other non-marine gastropods (e.g., McMichael, 1957 [mussels]; Dettman et al., 1992; Smith, 1999; Hamilton-Bruce et al., 2002, 2004 [gastropods]). The coastal plain facies overlie extensive sequences of marine rocks: Surat Siltstone (Albian) and Wallumbilla Formation (Aptian-Albian) (Hamilton-Bruce et al., 2004). The period of inundation from epiereic sea(s) lasted from the late Neocomian to the early Albian (Burger, 1988).

**Opalization: processes, timing, and preservation of fossils**

All fossils from Lightning Ridge are opalized; preservation ranges from gem-quality opal through low-grade ‘potch’ (Smith, 1999). Most of the fossils (although not all) are small, perhaps because the size of opal seams is limited by processes of silica deposition (e.g., Smith, 1999).

The process of opalization is not well understood. There are three primary models for the genesis of opal. In the ‘weathering’ model of Watkins (1985), heavy Late Cretaceous weathering of silicates in the overlying sandstone led to mobilization of the silica and subsequent filling of cavities by silica solution. A second model, by Behr et al. (2000), proposes activity by Cretaceous microbes in an estuarine environment prior to deposition of the overlying Tertiary sandstone; evidence for this comes from the presence of microbes in both the host rock and opal. A third model, the ‘syntectonic’ model of Pecover (1996) posits an upward movement of hydrothermal fluid through faults and cracks into the claystone during the Tertiary. Dowell and Mavrogenes (abstract, 2003) support the claim for a biological origin of opal because both carbon (present in black opal) and casts of micro-organisms are found in opal.

The age at which opal formed in the fossils or casts is disputed. Opal deposits in Australia are associated with potassium-bearing minerals (potassium-argon and hollandite grains, the latter commonly associated with opal at Lightning Ridge) (Newberry, 2004). Dating of sediments using $^{40}\text{Ar}/^{39}\text{Ar}$ geochronology gives a Miocene age (29 mybp +/-2 to 4.7 +/-0.5 mybp) for silicification and opal precipitation at Lightning Ridge (Newberry, 2004). Similar dates using this technique are recorded for other Australian opal-producing areas (Coober Pedy and Andamooka, South Australia: Newberry, 2004) and support K-Ar dates of Bird et al. (1990). The first three models are based on Late Cretaceous/early Tertiary events; Dowell and Mavrogenes’ (2003) model, using C$^{14}$ dating, proposes a surprisingly recent date (Quaternary: between 1740 and 7790 ybp) for opalization.

Some fossils are preserved as pseudomorphs, whereby silica solution filled in a cavity in the fine-grained opal dirt left by a fossil that had disintegrated; such fossils may retain surface detail but no internal structure (Smith, 1999). Other fossils may have been formed through slow molecule-by-molecule replacement of internal and external structures via chemical alteration.
prior to silica deposition (Smith, 1999); the lower jaw of K. ritchiei, with fine detail seen through the translucent opal, is an excellent example of this type of preservation. Many fossils show a combination of both processes (Smith, 1999).

**Associated flora and fauna**

Fossil plant material is abundant in the Lightning Ridge deposits. Small pinecones, wood, stems and roots of archaic conifers, and cycads have been preserved, sometimes in exquisite detail (Smith, 1999). Many specimens are flattened or compressed, suggesting that they fossilized while they were either unripe or soft (Smith, 1999). However, although work is in progress, the Lightning Ridge palaeoflora has not yet been thoroughly studied.

Molluscs – far and away the most common invertebrate fossils - are also very common at Lightning Ridge. Most of the mollusc fossils found at the Ridge are freshwater mussels, clams or snails although the remains of crustaceans are also found (in particular, the gastroliths of freshwater crayfish, or ‘yabbies’) (Smith, 1999). Non-marine gastropods in the families Viviparidae (the most common type) and Thiaridae comprise the snail fauna (Hamilton-Bruce et al., 2004). Living Thiaridae has a global distribution with many living species; most are freshwater taxa with some found in brackish water; the genus *Melanoides* (known from Lightning Ridge) is still extant (Hamilton-Bruce et al., 2004).

In addition to *K. ritchiei*, the Lightning Ridge vertebrate fauna includes undescribed chondrichthyans and teleosts (Smith, 1999); lungfish (material referable to the living Queensland lungfish *Neoceratodus forsteri*; also *Ceratodus* spp.: Kemp and Molnar, 1981; Kemp, 1991); turtles (possibly primitive cryptodires: Molnar, 1980), small crocodyliforms (Etheridge, 1917; Smith, 1999); dinosaurs (several types of ornithopods: Molnar and Galton, 1986; sauropods: Molnar, 1991; theropods: von Huene, 1932; Smith, 1999); plesiosaurs (Smith, 1999); possibly pterosaurs (Smith, 1999); crow-sized, non-enantiornithine birds (Molnar, 1980a-b, Molnar and Galton, 1986; Smith, 1999); and mammals (the monotreme *Steropodon galmani*: Archer et al., 1985; an unidentified and edentulous but probably mammalian maxillary fragment: Rich et al., 1989; and a possible dryolestoid mammal [alternatively, a traversodontid cynodont]: Clemens et al., 2003) (Table 1). The holotype lower jaw of *K. ritchiei* was found in situ with small dinosaur bones, theropod teeth, a fragment of turtle shell, turtle vertebrae, lungfish toothplates, freshwater teleost vertebrae, yabby buttons, mussels and gastropods (Smith, 1999).

Little is known of the taphonomy of the Lightning Ridge Local Fauna, in part because the fossils are seldom retrieved within the mines themselves. Fossils are usually collected during the mining process: the raw clay matrix is put through a tumbling tank (or ‘puddler’) to separate opal from matrix, a system that, while a necessary evil, can be quite damaging to fragile fossils.
and which removes them from their original context. Few of the Lightning Ridge fossils show signs of transport prior to burial but there may be some bias towards small elements such as phalanges that could be easily transported (pers. obs., by R. Molnar, from Clemens et al., 2003).
TABLE 1. Vertebrate fauna of the Griman Creek Formation, Lightning Ridge, N.S.W. (updated from Kemp and Molnar, 1981; additions indicated in brackets []).

<table>
<thead>
<tr>
<th>Class</th>
<th>Subclass</th>
<th>Order</th>
<th>Family</th>
<th>Species/Genus</th>
<th>Author/Year</th>
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<tbody>
<tr>
<td>Chondrichthyes</td>
<td>Elasmobranchi</td>
<td></td>
<td></td>
<td>Undetermined sharks, indet. ray/skate</td>
<td>Smith, 1999</td>
</tr>
<tr>
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<td>Actinopterygii</td>
<td>Teleostei</td>
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<td>Two undetermined taxa</td>
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</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>?Anguilliformes [Smith, 1999]</td>
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<tr>
<td>Sarcopterygii</td>
<td>Dipnoi</td>
<td></td>
<td></td>
<td>Ceratodontidae</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Ceratodus wollastoni</td>
<td>Chapman, 1914</td>
<td></td>
</tr>
<tr>
<td>Reptilia</td>
<td>Anapsida</td>
<td></td>
<td></td>
<td>Pleurodira indeterminate [Smith, 1999]</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Cryptodira</td>
<td>[Molnar 1980; Smith, 1999]</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Euryapsida</td>
<td>Sauropterygia</td>
<td>Plesiosauria</td>
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<tr>
<td></td>
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</tr>
<tr>
<td>Archosauaria</td>
<td>Crocodilia</td>
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<td>?'Crocodylus’ selasphensis (Etheridge, 1917)</td>
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<td>undetermined crocodyliform [Smith, 1999]</td>
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<td>von Huene, 1932</td>
<td>Rapator ornitholestoides von Huene, 1932</td>
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<td>Dromaeosauridae</td>
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<td></td>
<td>Indeterminate theropods [Smith, 1999]</td>
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<tr>
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<td></td>
<td>Unnamed hysilophodontids [Smith, 1999]</td>
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<td></td>
<td>Large ornithopod tracks [Molnar, 1991]</td>
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<tr>
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<td>Muttaburrasaurus sp. [Molnar, 1991]</td>
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<td>Indeterminate pterosaur [Smith, 1999]</td>
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<tr>
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<td>Monotremata</td>
<td>Steropodon galmani</td>
<td>[Archer et al., 1985]</td>
<td>Steropodon galmani [Archer et al., 1985]</td>
<td></td>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Fragmentary lower jaws [several specimens; Musser in prep.]</td>
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<tr>
<td></td>
<td></td>
<td>Mammalia incertae sedis</td>
<td>Kollikodon ritchiei</td>
<td>Kollikodon ritchiei [Flannery et al., 1985; this paper]</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Undetermined postcranials [Smith, 1999]</td>
<td></td>
</tr>
<tr>
<td>Class uncertain: synapsid tooth</td>
<td>[Clemens et al., 2003]</td>
<td></td>
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</table>
MATERIALS AND METHODS

The new specimen is a right maxillary fragment retaining four molariform cheekteeth (the complete molariform row) and ultimate premolariform tooth. For descriptive purposes it is assumed that the cheekteeth represent M1-4 although it is possible that the first molariform tooth is a molariform premolar (see Description and Discussion). The specimen has combined pseudomorph/replacement features, the fossil comprised of ‘silica that has replaced the original bone. The maxilla is from the private collection of Andrew Cody and is represented in the Australian Museum Palaeontological Collection by cast AMF119740.

The holotype lower jaw, re-examined for this study, is a right dentary fragment (AMF96602) with three molariform teeth. There are four alveoli anteriorly for two premolars and an alveolus for a posterior (ultimate) molariform (Flannery et al., 1995). The lower jaw preserves a greater degree of interior detail than the maxilla, in particular a network of fine nerve channels through the jaw ramus. The holotype is held in the palaeontological collection of the Australian Museum, Sydney and was collected by miner Bob Sutherland, where it was found in situ within his mine at Lightning Ridge (Flannery et al., 1995).

Because of the translucent nature of both maxilla and dentary, conventional light photography was not effective. Single image scanning electron microscope images (SEMs) were generally not feasible because of the large size of the specimens. Composite SEM images were therefore done by ‘marrying up’ sequential single image SEMs using the graphic imaging program Photoshop. Interpretive drawings (pencil renderings and ink line drawings) were done using a camera lucida. Andrew Cody, owner of the maxilla, kindly allowed a cast of the maxilla to be made by the Australian Museum. Measurements were made to the nearest millimetre and were taken with a metric rule.

Terminology -- Terminology for maxillary, palatal and mandibular structures is taken from Kermack et al. (1973, 1981) unless otherwise noted. Molar cusp terminology is adapted from Jenkins et al., 1997/Butler, 2000; because the dentition of K. ritchiei is not tribosphenic or pre-tribosphenic, dental terminology used to describe tribosphenic dentitions (e.g., Patterson, 1956; Crompton, 1971) is not employed. Superscript numbers designate upper teeth (e.g., M1 is the first upper molar) and subscript numbers designate lower teeth (e.g., M1 is the first lower molar).

DESCRIPTION

The new specimen is a fragmentary right maxilla retaining four molars (the complete molar row) and a small, ultimate premolar. Part of the palatine is also preserved although other
bones of the palatal, zygomatic and orbital regions - premaxilla, lachrymal or jugal - are missing. Part of the bony secondary palate is preserved medial to the tooth row but the preserved portion of the palate has been broken prior to the midline. The palate extends posteriorly to just past the last molar, although there is damage in this area. However, it appears that the secondary palate extended at least to the posterior end of the tooth row if not beyond it. Much of the sutural connection between the maxilla and palatine is preserved. The anterior root of the zygomatic arch has been preserved although it is difficult to interpret facets or scars for component bones because of damage and/or poor preservation in this area. The maxilla has been sheared off dorsally just above the toothrow, fortuitously exposing the course and structure of the infraorbital canal. There is some delamination evident on the molar teeth, especially on the lingual aspects of M\textsuperscript{1} and M\textsuperscript{2}.

For descriptive purposes the upper cheekteeth are described as M\textsubscript{1-4} and lower cheekteeth as M\textsubscript{1,3} although it is possible that the first molariform teeth in both upper and lower jaws are molariform premolars (see below).

**Maxilla**

In occlusal (ventral) view (Fig. 3A, C) the maxilla preserves the ultimate premolar, complete molar row, anterior root of the zygomatic arch and part of the secondary palate (with the palatine). The molar row forms a uniform crushing surface of considerable width. There is a distinct disjunction in size between the transversely wide molar teeth and the small premolar. The maxilla expands around the molar row, forming a lip along the lateral margin of the tooth row, but narrows markedly at the premolar/molar boundary. This expansion of the maxilla is an unusual feature in mammals but one that is seen in ornithorhynchid monotremes (e.g., Musser and Archer, 1998; Musser, in press) and possibly docodonts (Lillegraven and Krusat, 1991). There is a slight flaring of the maxilla anteriorly that may indicate the beginnings of a rounded snout, but there is damage to this area and the contours are not certain.

The anterior root of the zygomatic arch (the zygomatic process of the maxilla: zpm) originates between the posterior half of the second molar and anterior half of the third molar and projects at an angle of about 45\textdegree. This lateral projection suggests that the zygoma in *K. ritchiei* were wide and flaring.

The palate is arched, more so anteriorly than on the more posterior part of the palate. The palate is also comparatively more arched laterally (near the tooth row), flattening towards the horizontal as the palate becomes more medial.

The maxillo-palatine suture originates posteriorly within the crease of a 'lip' of bone (the palatine tubercle) extending the length of M\textsuperscript{1} (described with the palatine; see below). The suture makes a lateral bend at the posterior half of M\textsuperscript{3}, then angles medially to the midline of M\textsuperscript{3}.
before becoming parallel to the midline. It continues its course in an anteromedial direction before becoming transverse at the anterior half of $M^2$. Small nutrient foramina pierce the maxilla lingual to $M^{1-3}$ and there is a small foramen through the maxilla close to the alveolar border of the anterior third of $M^4$.

The lateral half of the major (greater) palatine foramen (mpf) in its usual anterior position has been preserved; the maxilla and palatine are broken off approximately at the midline of the foramen. There is a second, posterior opening of the major palatine foramen through the palatine onto the palate, described with the palatine below. The (anterior) major palatine foramen appears to be primarily (if not wholly) within the palatine, opening via a deep notch just past the midline of $M^2$ (described with the palatine). There is no evidence of a major (or greater) palatine groove running anteriorly or diagonally from the major palatine foramen - the surfaces of both maxilla and palatine are flat - but the absence of this phylogenetically significant feature cannot be unequivocally determined (G. W. Rougier, pers. comm.).

In lateral view (Figs. 4A, 5A) the molar row forms a curved, convex occlusal plane (in Fig. 4A the specimen has been tipped slightly in a lateral direction so that the course of the infraorbital canal can be seen). The lip or rounded margin of the maxilla forms dorsal to $M^1$; anterior to this the sides of the maxilla are flat. This lip continues to the posterior end of $M^2$; is not developed dorsal to $M^3$; but reforms over $M^4$. There is a tiny foramen dorsal to $M^2$.

The course of the infraorbital canal (ioc) is preserved from its posterior opening dorsal to $M^3$ (Fig. 6) to the premolar (the point of breakage: Fig. 4A). The infraorbital canal carries the infraorbital nerve (the main trunk of the maxillary branch [V2] of the trigeminal nerve) and associated infraorbital artery and vein to the front of the face (Kermack et al., 1981). The infraorbital canal in *Kollikodon* is floored by the maxilla along its length but the canal is sheared off laterally just above the floor. It is difficult, therefore, to determine if there were lateral branches off the canal at any point along the preserved course. There is a minute notch (n) dorsal to the space between the premolar and $M^1$; the exposed edges of the canal narrow at this point, also suggesting that a structure was present. This may be the remnant of a lateral foramen opening onto the face. The presence or absence of lateral branches onto the face, and where they are located, is an important assessment. If there were no lateral branches opening onto the face between the posterior entrance of the canal and the last premolar, *Kollikodon* would have an unusually lengthy, unbranched infraorbital canal. Such a conformation might be of phylogenetic significance because of its rarity. It might be best, given the damage to the canal, to say that there may be a lateral branch in the position described but that the specimen is too damaged for confident determination of size or importance.
FIGURE 3. Upper and lower jaws of *K. ritchiei*; molar rows are shown opposite each other as in occlusion. Although upper and lower jaws were not found in association, they are of comparable size, allowing a degree of comparison. A and C, occlusal view of maxilla (sp. No.) (SEM); B and D, occlusal view of lower jaw (AMF96602). A and B are composite scanning electron microscope images; C and D are interpretive drawings done using a camera lucida. Abbreviations: Table 2.
As the canal courses anteriorly it becomes quite narrow and is smaller than the infraorbital canals of monotremes (*Ornithorhynchus* and *Obdurodon*). There is no egress for the maxillo-palatine branch of the infraorbital nerve (the maxillo-palatine foramen) as there is in *Ornithorhynchus* (G. W. Rougier, pers. comm.).

The orbital platform is robust and quite deep (Figs. 4A, 6). In both lateral (Fig. 4A) and posterior views (Fig. 6; occlusal side down) the relative depth of the orbital platform and the width of the posterior opening of the infraorbital canal are evident.

There are three small foramina posteroventral to the infraorbital canal along the anterior margin of the orbit floor medial to the base of the zygomatic arch. The presence of these foramina (which open into the maxilla) as well as inflation of the orbital floor may suggest a maxillary sinus in *Kollikodon* (as described in *Haldanodon*: Lillegraven and Krusat, 1991). The infraorbital canal does not enter the maxillary sinus as it does in cynodonts (e.g., Kühne, 1956; Sues, 1985).

The zygomatic arch is relatively deep and narrow, its width exposed by a clean break through the opalized maxilla. The dorsal edge of the arch may be a contact facet for the jugal - the lateral half appears to be a natural edge and the bone here is stepped along its length – but this is a tentative determination.

The medial view of the maxilla (Fig. 5A) illustrates the remarkably uniform medial cusp row of the molars. The lingual cusp row is obliquely angled and the cusps are somewhat higher than those of the medial cusp row, but in this view (done with a series of SEM images) the lingual row was not captured on film and thus is not seen.

The course of the anterior major palatine foramen can be seen running posterodorsally from the palate; its posterior margin is delineated by a thin ridge of bone. The large, oblique channel angling posterodorsally from the palate to the orbit is the sphenopalatine foramen (G. W. Rougier, pers. comm.). Posterior to this is the posterior major palatine foramen, whose edges are not clearly defined due to poor preservation. The protruding bone on the posterventral palate is the posteriormost part of the palatine (broken at the tip).

**Palatine**

The palatine is clearly sutured to the maxilla along the palate; however, sutural connections on the medial side of the specimen are hard to determine and can’t be followed confidently. As described above, an anterior major palatine foramen opens onto the palate through the palatine, through what appears to be a notch (although it is possible this is an artefact of damage). The major palatine foramen transmits the greater palatine nerves and blood vessels to the gums and roof of the mouth (Kermack et al., 1981). In addition to the anterior foramen there is a posterior groove (pmpf) on the palatine just past the midline of M₃ and continuous with it on the dorsal surface of the palatine. This is interpreted as a second opening onto the palate of the major palatine foramen (posterior major palatine foramen), which to date appears to be unknown in other groups for which the palate is known (G. W. Rougier, pers. comm.).
FIGURE 5. Medial view of upper and lower jaws. A, maxilla (A. Cody) and B, dentary (AMF96602). The flat, striated surface on the lower jaw dorsal to the meckelian groove may represent a contact surface for a splenial; alternatively, the splenial may not have been present. The ledge on the maxilla midway between the tooth row and the dorsal edge of the specimen is the broken edge of the palate. Abbreviations: Table 2.

The palatine tubercle (pt: Figs. 4A; 6; and 7A, B and C) is similar to that described for Morganucodon, where a raised portion of the posterolateral palatine is formed by the juncture of the palatal, orbital and posterior palatine plates (Kermack et al., 1981).

Two small channels are delimited by three knob-like protuberances at the posterior margin of the lip of the tubercle (Figs. 6; 7A, C): one course runs in an anteroposterior direction and a second course in a transverse direction. A series of pits runs through the palatine on the medial side of the lip of the tubercle in an indistinct groove. Similar pits and groove (the lesser palatine groove: lpg) are seen on the posterior part of the palate in Morganucodon (Kermack et al., 1981: Figs. 46, 47, 48) and larger foramina in a similar position are seen in the palate of Probainognathus (from Kemp, 1982). A small foramen through the dorsal surface of the palatine is present just posterior to the maxillo-palatine suture at the level of the anterior root of M\(^2\). There is no evidence of palatal fenestrae (although the better part of the palate is missing).
FIGURE 6. Posterior view of maxilla (turned slightly to the left). The entrance to the infraorbital canal (ioc) is a large, single posterior opening floored by the maxilla. The orbital platform (op) is deep, accommodating the roots of the last molariform tooth. Small foramina open onto the orbital platform.

TABLE 2. Abbreviations used in Figures 3-10.

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
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<tbody>
<tr>
<td>ampf</td>
<td>anterior major palatine foramen</td>
</tr>
<tr>
<td>appm</td>
<td>alveolus for penultimate premolar</td>
</tr>
<tr>
<td>aupm</td>
<td>alveolus (alveoli) for ultimate premolar</td>
</tr>
<tr>
<td>aM₄</td>
<td>alveolus for M₄</td>
</tr>
<tr>
<td>fop</td>
<td>foramina through orbital platform</td>
</tr>
<tr>
<td>idc</td>
<td>inferior dental canal</td>
</tr>
<tr>
<td>ioc</td>
<td>infraorbital canal</td>
</tr>
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<td>meckelian groove</td>
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<td>maxilla</td>
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<td>M¹-₄</td>
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<td>pt</td>
<td>palatine tubercle</td>
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<td>sphenopalatine foramen</td>
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Lower jaw

The holotype lower jaw, AMF96602, is a dentary fragment retaining three molar teeth (M1-M3). In the description of the holotype by Flannery et al. (1995) there is no mention of markings or depressions on the jaw for accessory jaw bones or a meckelian cartilage. Re-examination of the holotype finds that these landmarks or structures may in fact be present. A revised and expanded description is therefore presented here.

The lower jaw of K. ritchiei (Figs. 3B, D; 4B; 5B; 8) is narrow (compressed) anteriorly prior to the molar row. A vertical-sided ridge is formed through the dorsal third of the
jaw (in the vertical dimension) through which several premolar alveoli open. There are three complete premolar alveoli and part of a fourth anterior to the molars, almost certainly for two premolars in close succession (without a diastema between them) (alveoli described below with the dentition). Seen in cross-section, the contours of the jaw subsequently expand medially and laterally to round the ventral margin of the dentary (damaged in this area). Ventral to the premolar alveoli there is a cavity through the centre of the jaw formed only by the comparatively thin walls of the dentary at this point. The premolar alveoli open into this cavity, which is plugged posteriorly by the pinkish sediment that fills the inferior dental canal (see Fig. 8A and description below). The conformation and apparent large size of this cavity may suggest that a procumbent lower incisor occupied this space (G. W. Rougier, pers. comm.). Alternatively, it may be the anterior continuation of the dental canal that appears enlarged because it is traveling through a constricted part of the dentary (where the walls are thin and where there is a good deal of diagonal breakage distorting the limits of the cavity). The dentary is translucent and the ventral course of the dental canal seen through the dentary appears to be continuous to the point of breakage, supporting the second interpretation.

The preservation of the jaw is exquisite; fine nerve fibres can be seen branching off the dental canal laterally, traveling along the jaw in an anteroposterior direction, and surrounding the roots of both premolars and molars. The dorsal part of the dental canal is obscured by the network of fibres and by the roots of the molars.

M1-M3 are preserved in situ (described below) and there is a wide, shallow anterior alveolus for a subsequent lower molar posterior to M1. Occlusal relations with the maxilla, in which M4 is reduced, suggest M4 would likewise have been reduced in size.

The inferior dental (mandibular) canal is clearly exposed through a clean break at the posterior end of the specimen (Fig. 8; comparison is made with the dentary of the monotreme *Steropodon galmani*). The dental canal at this point (ventral to the anterior alveolus for M4) runs through the centre of the dentary fragment, its dorsal margin at about the vertical midline of the dentary. It occupies roughly about 1/4 of the depth of the dentary and about 1/3 of the width. The alveolus for M4 does not reach the dental canal (the ventral margin of the alveolus clearly terminates above the dorsal margin of the canal). The dental canal in *Kollikodon* is thus of comparatively moderate size, larger than that of *Morganucodon* (Kermack et al., 1973: Fig. 28) but much smaller than that of monotremes, where the dental canal occupies the whole of the interior of the dentary. Flannery et al. (1995) describe a large dental canal in *Kollikodon* but they may have limited their observations to the space at the anterior end of the jaw fragment (in this account interpreted as either a space for an incisor or artificially enlarged through breakage; see above).
FIGURE 8. Comparative views in cross-section of the dentaries of *K. ritchiei* and the Early Cretaceous monotreme *Steropodon galmani* (both are from the right side). A, *K. ritchiei*, posterior to the third (‘penultimate’) molar. B, *S. galmani*, posterior to the third (ultimate) molar. The diameter of the inferior dental (mandibular) canal is much greater in *S. galmani* (a large cavity occupying most of the interior of the dentary) than in *K. ritchiei* (a much smaller, discrete channel running through the centre of the dentary).

The medial aspect of the jaw has several features of interest that have not yet been described. There is a distinct, gently bevelled ridge on the ventral margin of the medial side of the jaw at the posteroventral end that converges toward the ventral margin of the jaw and extends forward to the anterior root of M₃ before fading away (Figs. 5B; 8). This is here interpreted as a well-developed meckelian groove (mg). A meckelian groove convergent on the ventral border of the mandible is both common and primitive (G. W. Rougier, pers. comm.; but see Luo et al., 2002).

Dorsal to this ridge the jaw is distinctly flattened (and very slightly depressed). The jaw resumes its rounded appearance about 2/3 of the distance to the alveolar margin (unfortunately, the medial side of the dentary fragment is broken along its posterodorsal corner and the contours of the jaw here can’t be seen in cross-section). The flattened zone fades out beyond these parameters and the jaw resumes a more ‘normal’ shape. This area is scored by numerous grooves that run parallel to the meckelian groove (i.e., convergent with the ventral border of the jaw), many of which continue anteriorly beyond the flattened area. The planed surface suggests contact between the dentary and another (accessory) jaw bone; the location of the faceted surface (anterior to the mandibular foramen) indicates this bone would have been the splenial.
The presence and depth of the horizontal striations suggests that if the splenial were present, it would have been embedded in the jaw in life and not merely a vestigial marking on the jaw for a long-absent bone (J. A. Hopson, pers. comm.). If a splenial were present it may have been a large, plate-like splenial as in *Haldanodon* (Lillegraven and Krusat, 1991) although larger, or as in *Diademodon* (per Kühne, 1956). Alternatively, the flattened area on the ramus of the jaw may be an artifact; there are horizontal grooves as mentioned elsewhere along the medial side of the jaw, possibly weakening the case for a splenial (G. W. Rougier, pers. comm.)

There does not appear to be a groove for the replacement dental lamina on the dorsomedial margin of the jaw, as reported for cynodonts, *Sinoconodon*, *Morganucodon* and *Megazostrodon* (summarised by Luo et al., 2002) although there is delamination of the bone where such a groove would be expected.

The lateral side of the jaw is unfortunately missing the region of the masseteric fossa although there is a slight but distinct lateral angle to the dentary along the posterodorsal aspect of the jaw.

**Upper dentition**

The transversely wide upper molars overlap the root of the zygomatic arch (as in cynodonts: Lillegraven and Krusat, 1991) (Fig. 3A, C). The upper tooth row is not aligned medial to the root of the zygomatic arch, as in Tritylodontoidea (e.g., Kühne, 1956). The central (median) row of cusps on the molar teeth is aligned with the primary cusp of the premolar. This suggests that the median molar cusps can be homologised with the primary cusp of the premolar. The upper tooth row is strongly convex (Figs. 4A; 5A; 10A, B), matching the concave curvature of the lower molar row (Figs. 4B; 5B; 10A, B). Upper molars occlude just posterior to the lower molars, in opposite (rather than alternate) occlusion (Fig. 10A, B).

**Ultimate upper premolar** -- A small premolar is preserved anterior to the four much larger molar teeth. The maxillary fragment is sheared off immediately anterior to the premolar, exposing its anterior root, and no additional premolar alveoli are preserved. The premolar is much smaller and simpler in form than M^1^, which it abuts. Because the dental formula is not known in *Kollikodon* the premolar is designated here as the ultimate premolar; however, as discussed below, it is possible that ‘M^1^’ is instead a molarized premolar and that the ultimate upper premolariform tooth is actually the penultimate premolar.

The premolar is irregularly pear-shaped in outline with three main cusps forming a triangular pattern: the primary cusp is anterior to two smaller, transversely-aligned cusps (thus the posterior half of the tooth is proportionately much wider than the anterior half). Of the two posterior cusps the buccal cusp is taller; both cusps have a slight posterior inclination. A deep
groove separates the anterior cusp from the two posterior cusps. There are no lingual, labial or posterior cingula although there is an indistinct, somewhat cuspidate shelf on the anterior margin of the tooth.

The upper premolar is double-rooted, the posterior root being more robust than the anterior root. The anterior root (which is partially exposed at the break) appears to about twice as long as the posterior root. The much shorter length of the posterior root (visible through the translucent maxilla) may be an artifact of the preservation process. Although roots appear to be short, they may have been only partially preserved. In contrast to the preservation seen in the holotype lower jaw, where all detail is exquisitely preserved, the maxilla appears to have had internal structures filled in by opal (see Discussion) and the length and internal detail of all roots (premolar and molar) as seen through the translucent maxilla may be misleading.

The apices of the principal cusp have been flattened through wear and bear two conjoined, pitted wear facets that are transversely aligned. There is a slight wear facet on the posterobuccal cusp but no appreciable wear on the lower, posterolingual cusp. All three cusps occluded with and presumably thegosed the anterior face of M1. The small size of the premolar, the lack of wear on the anterior flank of the premolar, and the occlusal relationships of upper and lower molars (Fig. 10) indicate that the upper and lower ultimate premolars would not have occluded.

**Upper molariforms** -- Upper molars are transversely wider than long and are roughly crescentic in shape. Each molar is characterised by three longitudinally aligned cusp rows: a lingual row of 1-2 cusps (wholly or incipiently divided); a median row of 2 cusps per tooth; and an arcuate buccal row of 2-3 cusps. Cusp rows are roughly parallel to each other with deep grooves (vertical fissures or near-vertical-sided troughs) separating the rows. Transverse grooves separate anterior from posterior cusps. M1<M2<M3>M4. M1 is transversely ovoid. M3-4 are crescent-shaped with convex posterior flanks, concave anterior margins and bowed lingual and buccal margins. The median margin of the molar row forms a straight line parallel to the probable long axis of the palate. Each molar is locked tightly in place through imbrication of the flanks of adjacent molars.

All molar cusps are low and dome-shaped (bunodont). No vertical shearing blades exist in the dentition; the battery of low, multiple cusp rows forms a nearly uniform occlusal surface (the only exceptions being the comparatively high anterior cusp of M1 and correspondingly low anterior half of M1; see Fig. 10).

Several cusps sustain cone-shaped depressions or pits with rounded bases (Fig. 9A, D). These pits are primarily apical in position, exceptions being those developed on the posterior flanks of the posterior and posterobuccal cusps of M1 (where it occludes with the fairly
prominent posterolingual cusp of M1). Other cusps have deep, excavated areas (Fig. 9B, C). Not all cusps bear apical pits or depressions; they are present on most of the more anterior and more buccal cusps but are generally absent on the more posterior and more lingual cusps. Wear (masticatory and/or thegotic: Fig. 9A) is evident around the periphery of the pits and over the apices of the cusps if pits are missing. The only unambiguous thegotic facet appears to be on the apex of the posteriormost cusp of M1.

These apical pits and excavated areas appear to be the result of heavy wear; the dentine seems to have been scoured out from the apices of the cusps, perhaps in the way described for tritylodontids (Kühne, 1956). The crushing action of the molar row (see below) would have exerted great force on individual cusps and the hard, brittle nature of the presumed food items - bivalve and gastropod molluscs and crustaceans – would have abetted the process. Apical wear is not obvious on the median and lingual cusps of M3 and M4, which may mean that these more posterior teeth erupted later than the more anterior molars.

The occlusal plane is ventrally convex, buccally concave and lingually rectilinear, reflecting the fact that M2–3 are markedly wider than M1 or M4 (which are of approximately equal size). In centric occlusion, the buccal rows of M2–3 overhang the buccal edges of the corresponding lower molars. Wear facets are not precise and not consistently developed.

M1 is roughly ovoid in outline. There is a cuspidate anterior cingulum extending from the anterior margin of the anterolateral cusp to the anterolateral margin of the anteromedial cusp. This low, shelf-like cingulum has several small basal cuspules of roughly equal size along its anterior margin. This structure is the only one on any of the molars that could be considered a cingulum unless the buccal and lingual cusp rows were derived from cuspidate cingula (see Discussion). M1 has six domed cusps. There are two lingual cusps of roughly equal size (the anterior cusp being just slightly larger). The mesiolingual cusp has a deep apical pit but the apical area on the posterolingual cusp has just an irregular impression rather than a defined pit. There are two central cusps of unequal size; the larger posterior cusp is the largest cusp on M1.

The anteromedial cusp is wedge-shaped (wider anteriorly) and bears no pit at the apex. The posteromedial cusp has a large U-shaped excavation (half the length of the cusp) at its posterior margin. The angle formed at the labial limit of this fossa forms a tongue-in-groove joint with the opposing M2. There are two labial cusps, the anterior cusp again being slightly larger than the posterior cusp. There is a large, shallow apical pit on the anterolabial cusp and an excavation similar to that on the posterior margin of the posterolabial cusp. It is not certain whether this first upper molar-like tooth is a premolar or molar; root number (double) suggests this tooth may be a molarised premolar, which if true would give *Kollikodon* an upper molar count of three rather than four. Molarization of premolars, unusual in Mesozoic mammals, is known in haramiyids, multituberculates and ungulates (see Butler and Clemens, 2001). Tooth
form may thus not be a reliable character in identification (Butler and Clemens, 2001). According to Rowe (1988), simpler premolars and more complex molars are distinct from each other in all known Mesozoic mammals (except for multituberculates and haramiyidans, as mentioned). Premolars are not usually conscripted for molar function (in this case, crushing); they tend to do the primitive tasks of grasping and puncturing (Butler and Clemens, 2001).

FIGURE 9. Scanning electron microscope images of pits on the apices of upper molar cusps. Pits appear to be formed through cusp-on-cusp wear. a, the apex of the cusp has been pounded flat through wear and the dentine has been breached, forming a small pit. b, a larger pit, exposing dentine, is developed through more extensive wear. c, a large, open pit. d, a small pit on the apex of a cusp, illustrating an apical pit in the early stages of wear.

One criterion used to distinguish premolars from molars in extinct mammals is that the ultimate premolar has a taller main cusp than the first molar and is simpler morphologically; exceptions to this include multituberculates and the triconodont Gobiconodon (Butler and Clemens, 2001). In Kollikodon the first lower molarized tooth has a higher cusp than the second and third molars although this does not hold for the upper teeth, where the first molar-like tooth lacks a high cusp. However, the morphology of the first molarized teeth in both upper and lower jaws differs from the succeeding molars. Tooth replacement, the means by which premolars and
molars of placental mammals or mammals with an extensive sample size can be identified, is not possible to determine in *Kollikodon* (with only two known specimens). In the well-sampled early mammal *Morganucodon*, as in therians, the last premolariform replaced a molariform tooth (Mills, 1971; Parrington, 1978; from Butler and Clemens, 2001). The possibility therefore should be raised that the first molarized teeth in upper and lower jaws in *Kollikodon* may in fact be molarized premolars.

M2 is much larger than M1 (M1 being about 2/3 the width of M2). M2 is somewhat ovoid but approaching the crescentic form of M3 and M4. There appear to be no traces of cingula. M2 has seven cusps. The two lingual cusps are imperfectly divided by a short groove running transversely then angling anteromedially; the cusps are otherwise confluent. The larger anterolingual cusp has a large ovoid depression oriented in an anteroposterior direction. The smaller posterolingual cusp has a round, moderately deep pit. There are two central cusps, the anterior cusp being just slightly smaller than the posterior cusp. The anterior cusp bears a distinct, round, slightly crenulated pit at its centre. The posterior cusp has a deep ovoid pit that is on the posterior flank (not apical) but which does not extend to the posterior margin of the cusp. There are three labial cusps: the central cusp is largest; the anterior cusp is next in size; and the posterior cusp is smallest. There is a large, circular pit on the anterolabial cusp and, in addition, a flat, faceted area medial to the pit. The mediolabial cusp has a smaller but still substantial apical pit. The posterolabial cusp has a comparatively small, not quite apical pit and the suggestion of a second pit posteromedial to it.

M3 is the largest upper molar; although it is wider than M2, it is marginally shorter in length anteroposteriorly. M3 is crescentic in outline with a fairly flat anterior margin and convexly curved, continuous labial to lingual margin. M3 has seven cusps. As in M2, the two lingual cusps are imperfectly divided (a small transverse groove originating midway along the lingual groove of the posteriormost central cusp transects the cusps). The anterolingual cusp is by far the larger of the two.

There are several cusps on M3 and M4 that have no distinct apical pits. The general lack of pitting on the posterior cusps suggests that the posterior teeth may be more recently erupted. Lack of wear on posterior molars may indicate that these teeth may have erupted later in life than more anterior molars, as in *Morganucodon* (*M. watsoni*: from Butler and Clemens, 2001). However, unlike *Morganucodon* (Crompton and Luo, 1993) and *Megazostrodon* (Gow, 1986), molars in *Kollikodon* may not have been replaced, as this would have disrupted the function of a unified molar row. It is possible that molars erupted sequentially from anterior to posterior (as in tritylodontids: Kühne, 1956) with the most posterior molar erupting last; this would account for the observation that the more posterior molars in *Kollikodon* are less worn than anterior ones.
Neither lingual cusp has a definite apical pit although there is a tiny indentation on the posterolinguval cusp that may be an incipient pit. There are two central cusps with the anterior cusp the larger of the two. This cusp is rhomboidal in shape and shows no apical pitting. The posteromedial cusp has a minute pit at its apex. There are three labial cusps that decrease in size from anterior to posterior. The anterolabial cusp has a large 'stepped' depression that flattens out to a planed surface (rather than a more conventional pit). There do not appear to be apical pits on either the mediolabial cusp or posterolabial cusp.

M^4 is proportionately the most elongate of the molar teeth but is much smaller than M^3. Like M^1, the anterior margin is transverse and the lingual, posterior and labial margins merge to form a continuous convex curve. M^4 has five main cusps along with a very small cusp sandwiched between the mediolabial and posteromedial cusps. Lingually, there is only a single large, crescentic cusp without an apical pit. There are two central cusps: a larger, rhomboidal anterior cusp (without a pit) and a smaller, transversely elongate posterior cusp. This cusp appears to be the only one of the molars that exhibits a distinctly planed surface, possibly formed by thegotic wear against the lower M_4. There are three labial cusps, a large anterolabial cusp, a smaller mediolabial cusp and the tiny posterolabial cusp previously mentioned.

Upper molars have very robust, multiple roots. The comparatively small M^1 may have only two roots: an abnormally wide posterior root (as on the lower molars: Fig. 8A: aM_4) and a narrower anterior root (strengthening the case for this being a premolar rather than molar). There appear to be at least two poorly divided buccal roots and one large lingual root on M^2-4. However, the exact number of roots, particularly on M^1 buccally, are hard to distinguish. It would seem that the exceptionally wide M^{2-3} would be multiply-rooted, as in tritylodontids and toothed ornithorhynchids.

Lower dentition

Lower molars are aligned anteroposteriorly on the occlusal surface of the dentary (and not diagonally across the dentary, as in multituberculates).

Lower molariform teeth -- Although the lower dentition of Kollikodon has been previously described, as mentioned above, an alternative to certain of the interpretations of Flannery et al. (1995) is presented here. A more extensive description of the molariform teeth is warranted, given the luxury of space, and a few points made in the original description by Flannery et al. (1995) need revising.

The first molariform tooth is the smallest of the three preserved cheekteeth. It is obliquely ovoid, narrower anteriorly and wider posteriorly. There is a weakly developed, cuspidate
anterior cingulum, the only cingulum present on the tooth. It wraps around the anterior and buccal aspects, originating on the anterior flank (ventral to the apex of the anteromedial cusp), wrapping to the buccal side of the tooth and merging into a large mediobuccal cusp on the buccal cusp row. The cusp and cingulum appear to be a single continuous structure, the mediobuccal cusp therefore developed from the cingulum.

There are two anterior cusps and three unevenly divided posterior cusps; the two sets of cusps (anterior and posterior) divide the occlusal surface in half. The anterolingual cusp is the highest on the tooth (perhaps suggesting it might be the original primary cusp). The anterobuccal cusp is shorter but still higher than any other cusp on the tooth. The two anterior cusps are flattened and obliquely angled (the flattened posterior flank of the cusp), with the medial side highest. Wear on the cusps is varied. On the anterolingual cusp there is a longitudinal groove rather than an apical pit. On the anterobuccal cusp there is a distinct pit near the apex. On the posterolingual cusp no pit is developed although the cusp is flattened. On the posteromedial cusp there are two facets: a distinct central pit and a wear facet more lingually. On the small posterobuccal cusp there is a clear pit. The tooth is about 5mm long and 4mm wide at its posterior end.

This tooth, like the upper first molariform tooth, may be a specialized premolar rather than the first molar. Unlike the upper first molariform, root number is not informative; lower molars and premolars in most mammals have double roots. However, it differs morphologically from the more posterior molars, which are remarkably alike. Its cusp pattern might be homologized with that of the uncontested upper premolar: the anterolingual, posterolingual and posteromedial cusps possibly homologous with the three cusps of the premolar and the buccal cusps developed from cuspidate cingula.

The second and third molariform teeth are very similar. They are both nearly square; however, the last molar is narrower posteriorly, probably because the succeeding tooth (not preserved) was reduced (as in the upper teeth). There are four low, uniformly bunodont cusps on each molar, irregularly subdivided into four quarters apiece by clearly defined grooves (contained on the occlusal surface). There are no cingula except for tiny ‘ledges’ that wrap around the anterobuccal cusps anteriorly (possibly helping link successive molars). The occlusal surface of the molars is oblique (slightly higher on the lingual side).

Roots are double, proportionately wide and robust. The anterior root of the first tooth is smaller than the succeeding roots. The wide, single, empty alveolus at the rear of the jaw suggests that even though the teeth are wide the roots are not further divided.

Wear -- Many cusps, as mentioned, show apical wear on posterior flanks (some of which is substantial). It is probable that unerupted or newly-erupted molars of Kollikodon had rounded
cusps and that apical pits, wear facets/planed surfaces evident on molars were the result of heavy use and a powerful masticatory stroke. Substantial wear may be a consequence of a postcanine dentition lacking precise occlusion; in animals without precise occlusal relationships the contacts between opposing teeth often show heavy wear (Butler and Clemens, 2001). It may be that, as in Morganucodon but not as in therian mammals (Crompton and Jenkins, 1968), comparatively accurate occlusal relationships in Kollikodon developed through wear rather than through molar teeth that matched upon eruption.

**Occlusion and dental function**

In Kollikodon the upper molars are nearly opposite the lower molars during occlusion, upper molars occluding just posterior to lower molars (Fig. 10). The two cusp rows on the lowers occlude the lingual and central cusp rows on the uppers in centric occlusion. It appears that the jaw, however, could move transversely so that the buccal cusp row of the lowers could contact the buccal cusp row of the uppers. This might best be described as a primarily orthal jaw action with a transverse component. The upper buccal row slants medially, possibly trapping fragments of hard shell and thus protecting the cheek. Wear is present on the upper buccal cusp row, most likely from a combination of contact with the lower buccal cusp row and abrasion from hard food items (mollusc shells).

Wear facets on upper molars have been examined using a scanning electron microscope (Fig. 9). Longitudinal striations were not found on the wear facets examined, suggesting that there was no strong backward motion to the masticatory stroke. The height of the primary cusps of the upper premolar and M1 (Fig. 10) would prevent forward motion of the lower jaw or backward motion of the upper jaw.
COMPARISONS AND DISCUSSION

Comparisons are made with Mesozoic mammals or near-mammals that are potential ancestors or sister-taxa to Kollikodon; this list includes cynodonts with transversely wide molariform teeth (gomphodonts and tritylodonts); basal mammals with some shared derived features similar to those of Kollikodon (Morganucodonta and Docodonta); mammals with multicusped dentitions similar to that of Kollikodon (haramiyids and multituberculates); and
monotremes, to which Kollikodon has been referred (Flannery et al., 1995). Haramiyids and multituberculates, placed together in the suborder Allotheria by Butler (2000), are compared separately in this account.

Cynodonts and basal mammals without features that relate to characters in Kollikodon are not considered here. Mammals within the infraclass Holotheria sensu McKenna and Bell (1997) have been eliminated from consideration because all of the basal members of this higher-level taxon have reversed triangle (therian-like) dentitions that are incipiently, partially or fully tribosphenic; the dentition of Kollikodon does not appear to be derived from such a pattern. Results are summarised in Appendix I, Table 1 (craniomandibular comparisons) and Table 2 (dental comparisons).

**Tritylodontoidea**

The Early to Late Triassic gomphodont (broad-toothed, or traversodont) cynodonts and the latest Triassic to Late Jurassic tritylodontids are thought to be related in an ancestor-descendant relationship, tritylodontids being derived from traversodontid gomphodonts (Watson, 1942; Kühne, 1956; Crompton and Ellenberger, 1957; Crompton, 1972; Hopson and Kitching, 1972; Hopson and Barghusen, 1986). Together these herbivorous advanced cynodonts comprise the superfamily Tritylodontoidea, the largest group of nonmammalian cynodonts (Hopson and Kitching, 1972; Hopson and Barghusen, 1986). Tritylodontoidea have multiple cusp rows and/or transversely wide molars (dental patterns that could be comparable to that of Kollikodon). The early cynodont Dvinia, although it has transversely wide, multicusped teeth (from Kemp, 1982), is otherwise too archaic as well as too specialised to be considered here.

Traversodont gomphodonts (Diademodontidae, Trirachodontidae and ‘Traversodontidae’) were a diverse group of mainly herbivorous cynodonts whose taxonomy is still uncertain (e.g., Hopson and Barghusen, 1986). They ranged temporally from the Lower to Late Triassic and had a strong Gondwanan distribution (Africa, Argentina, Brazil, Madagascar, India) although they are now known from several Laurasian sites as well (Europe, China, North America) (see Hopson, 1984; Sues et al., 1999; Flynn et al., 2000). Gomphodonts are characterized by having buccolingually expanded, molariform cheekteeth with well-developed crown-to-crown occlusion (Crompton, 1972; Hopson and Barghusen 1986; Battail, 1991; Hopson, 1991).

Tritylodontids first appear in Upper Triassic deposits and had a global distribution (southern Africa, China, western Europe, North America and South America) (Kemp, 1982). They are also characterized by molariform teeth transversely wider than long that meet in crown-to-crown occlusion (a shared derived feature with traversodont gomphodonts: Hopson and Barghusen, 1986). The latest record for a tritylodontid is from the Early Cretaceous
(Tatarinov and Matchenko, 1999), tritylodontids surviving alongside early mammals for most of their tenure. Sizes ranged from forms that were quite small (Oligokyphus had a head length of about 8cm) to larger forms (e.g., Tritylodon maximus, with a skull length of about 22 cm) (from Kemp, 1982).

Tritylodontids were thought to be mammals when they were first discovered because of a raft of mammal-like features (Broom 1905; Simpson 1928, 1929a but see Simpson 1937, 1938). Some palaeontologists grouped tritylodontids with multituberculates (Woodward, 1925; Simpson, 1928 but see Simpson 1937, 1938, 1943) while others disagreed (Simpson, 1945; Bohlin, 1946; Young, 1947).

Reptilian affinities were recognised with the discovery that Tritylodon had a quadrate-articular jaw joint (Kühne, 1943) although this is also the case in near-mammals such as Morganucodon (Kermack et al., 1973). The changes required to derive a multituberculate from a tritylodontid are numerous (see Kühne, 1956; p.139). In spite of the ‘mammalian’ features of tritylodontids (especially in the postcranial skeleton), tritylodontids are not mammals; these features appear to be convergences (Hopson and Barghusen, 1986 but see Kemp 1982, 1983) and tritylodontids are not believed to have given rise to any known group of cynodonts or mammals (Watson, 1942; Young, 1947; Kühne, 1956; Sues, 1983; Sun and Li, 1985).

Maxillo-palatal region: In Tritylodontoidea the palate terminates forward of the tooth row and the zygomatic arch is deep (Kemp, 1982; Hopson and Barghusen, 1986; Hopson, 1994). The postcanines are medially positioned (left and right postcanine rows are close together) and the maxilla has a wide exposure lateral to the tooth row in traversodonts (Kemp, 1982). The palatines terminate at about the level of the fourth molariform in Oligokyphus and Bienotherium yunnanense and more posteriorly, to the fifth molariform, in B. elegans (Young, 1947; Kühne, 1956).

In Oligokyphus the jugal is large and is carried forward to a point anterior to the first molariform where it meets the large lachrymal dorsally; the maxilla therefore lies internal to the lateral side of the face and the jugal is sandwiched between the lacrimal and maxilla (Kühne, 1956). In Bienotheroides, Stereognathus, Dinnebitodon and a Mexican tritylodontid (Clark and Hopson, 1985), the maxilla is excluded from the face by an enlarged premaxilla and lachrymal; the jugal overlaps the maxilla completely; and the maxilla is excluded from the secondary palate by the premaxilla and palatine (Sues, 1986b). This is not the case in Kollikodon, where the maxilla appears to have a large exposure on the face, zygomatic arch and palate. In Bienotherium the jugal terminates more posteriorly and abuts the maxilla (?and lachrymal) via a diagonal suture about where the maxilla is broken in Kollikodon. The maxilla therefore has a zygomatic process on the lateral side of the face (a more mammalian conformation) (Young,
1947). The orbit in *Bienotherium* is bordered by the jugal, lachrymal and frontal (Young, 1947). The greater palatine foramen in *Oligokyphus* opens on the maxilla just anterior to the palatine (Kühne, 1956). There is a ridged diastema anterior to the cheekteeth and posterior to the canine in *Bienotherium* (Young, 1947: Fig. 3).

An infraorbital canal is unknown in theriodonts (Lillegraven and Krusat, 1991). When present in cynodonts, several smaller canals branch off the main canal to open laterally onto the face (Fourie, 1974; Kemp, 1982). In *Oligokyphus* the infraorbital canal is floored by the maxilla and roofed by the lacrimal and palatine; its posterior entry is primarily within the lacrimal; the canal runs obliquely through the sutural surfaces of the lacrimal and maxillary; and its course is laterally convex (Kühne, 1956) unlike the anteroposterior course of this canal in *Kollikodon*.

**Mandible:** In cynodonts the mandible is still compound to varying degrees. The dentary was enlarged and accessory jaw bones reduced in advanced cynodonts (Kemp, 1982) as in the earliest mammals (e.g., Kermack et al., 1973). The symphysis of the lower jaw is usually fused in traversodonts (Hopson, 1984) but unfused in tritylodontids, and occlusion was bilateral (e.g., Young, 1947; Hopson and Kitching, 2001). The anterior border of the coronoid process is lateral to the posteriormost postcanines in all Triassic cynodonts, continuing anteriorly as a ridge that forms the anterodorsal margin of the masseteric fossa (Hopson, 1984). Depressed areas or contact facets for accessory jaw bones are well marked (e.g., Kemp, 1982).

The lower jaw in *Oligokyphus* and *Bienotherium* is slightly convex (less so than in *Kollikodon*) (Young, 1947; Kühne, 1956). In *Oligokyphus* the deepest point of the jaw is below the first cheektooth and the jaw narrows ventral to the mandibular foramen (Kühne, 1956) (in contrast to *Kollikodon*, where the deepest point on the jaw is posterior). The alveolar border is sharp anterior to the cheekteeth (through the diastema) as in *Kollikodon*, where the alveolar border narrows to a ridge anterior to the cheekteeth. The posteriormost cheekteeth in *Oligokyphus* and *Bienotherium* are medial to the ascending ramus of the jaw (Young, 1947; Kühne, 1956), probably not the case in *Kollikodon* (although the jaw is broken anterior to the ultimate molar).

The meckelian groove in *Oligokyphus* is shallow but distinct (as in all cynodonts) and is double, with a narrower dorsal and wider ventral course (Kühne, 1956). Both grooves run parallel to the ventral border of the mandible, the dorsal groove curving upward at the symphysis and the ventral groove coursing downward to meet the symphysis; this is very similar to the course of the meckelian groove in *Docodon* as well as many other Mesozoic mammals (Simpson 1928a; Kühne, 1956).
The size of the mandibular canal is described as small and elongate in *Bienotherium* (Young, 1947). The inferior dental canal is also moderate in size in *Cynognathus* (an older and less specialised cynodont) (Kermack et al., 1973: Fig. 28).

In most respects the jaw of *Oligokyphus* and other cynodonts differs in construction from the jaw of *Kollikodon*, with the exception of a slight convexity and a sharp edge along the anterior alveolar border; and possibly in the large size of the splenial as is possibly the case in the *Kollikodon* holotype.

**Dentition:** Both traversodonts and tritylodontids have undifferentiated dentitions; like other cynodonts, the postcanine teeth are not divisible into premolars or molars (hence the term ‘cheekteeth’: Kühne, 1956). This separates even the most advanced cynodonts from the earliest mammals, which have morphologically distinct premolar and molar teeth (except for *Sinoconodon*; see Luo et al., 2002).

In most traversodonts the upper cheekteeth are wider than long; primitively have three cusps (buccal, central and lingual) aligned transversely; a well-developed longitudinal ridge; and a large central basin with narrower posterior basin (e.g., Kemp, 1982; Sues, 1999). Lower postcanines are usually longer than wide (near-crescentic and imbricating in some advanced traversodonts: Kemp, 1982; Sues et al., 1999; Flynn et al., 2000); they usually have two high, transversely aligned cusps on the anterior half of the crown; a transverse crest anteriorly; and a basined posterior heel (Kemp, 1982; Hopson, 1984). Opposing transverse crests formed pairs of shearing edges to cut vegetation, and the basins enabled crushing or pounding of food; enamel is thin and wear is correspondingly heavy (Kemp, 1982). *Dadadon*, from Madagascar, has strong external cingula; these are otherwise lacking in traversodontids (Flynn et al., 2000) except for *Scalenodon angustifrons*, *Massetognathus* and *Luangwa*, which have external cingula (Hopson, pers. comm.). Some traversodonts have obliquely-oriented postcanines (e.g., Flynn et al., 2000) as *Kollikodon* does.

In some traversodonts the teeth in the postcanine series enlarge in size then reduce (e.g., *Diademodon*; from Kemp, 1982) while in others the postcanine teeth progressively enlarge posteriorly (e.g., *Dadadon*: Flynn et al., 2000). The number of postcanine teeth ranges from 8/6-7 to 15 upper postcanines (see Flynn et al., 2000). As mentioned, upper and lower tooth rows are set in from the snout in all but the most primitive traversodonts; this suggests to Hopson (1984) that they may have had an oral vestible and therefore a cheek. At least one traversodont appears to have a slight convex curvature to the lower and upper jaws (*Pascualgnathus*; from Kemp, 1982). Roots of both upper and lower postcanines are single, as in most cynodonts except tritylodontids (e.g., Hopson and Barghusen, 1986).
Tritylodontid cheekteeth bear a remarkable similarity to the molar teeth of *Kollikodon*. There are three well-developed, parallel rows of longitudinally aligned cusps on the upper cheekteeth and two rows on the lower cheekteeth separated by deep grooves (e.g., Young, 1947; Kühne, 1956; Hopson and Kitching, 1972; Sues, 1983; Sues, 1986b); in many respects this is the closest match dentally to *Kollikodon* amongst known mammals or near-mammals. Upper postcanines are wide (slightly longer than wide in smaller *Oligokyphus* and *Bienotherium minor*: Kühne, 1956; Young, 1947 and wider than long in all other Tritylodontidae: Savage, 1971). Molars imbricate in some species (e.g., *Bienotherium*: Young, 1947) as they do in *Kollikodon*. Cusp number varies: there are from two to three buccal, two to four median and two to four lingual cusps per row on the uppers; and lower cheekteeth usually have two cusps and an accessory cuspule in each row (excepting *Oligokyphus* and some juvenile *Tritylodon* [J. A. Hopson from Sues, 1986b] that have three cusps per row [see Sues, 1986b]).

The upper cheekteeth in *Bienotherium* first increase in size (the largest teeth are the fourth and fifth postcanines) then decrease (Young, 1947), as in *Kollikodon*. Upper molars of *Bienotherium* have a distinct, mediolateral oblique slant (Young, 1947), not dissimilar to the oblique slant of molars in *Kollikodon*. Lower teeth are rectangular, with three well-defined cusps in each row in *Oligokyphus* (Kühne, 1956) and two per row in *Bienotherium* (Young, 1947).

Wear on individual cheekteeth in *Oligokyphus* suggests they erupted sequentially from first to last (Kühne, 1956). Although the penultimate cheektooth is always worn, the ultimate upper cheektooth (even when fully erupted) does not show wear; the number of cusps is also greatly reduced, suggesting disuse of the last cheektooth (Kühne, 1956). As in *Kollikodon*, the battery of cheekteeth would have functioned as a unit (Kühne, 1956). The position of the ultimate upper cheektooth lies below that of the others, reminiscent of the way the upper molar row curves dorsally in *Kollikodon*. The ultimate lower molar remains permanently unerupted in *Oligokyphus* (Kühne, 1956). There is no sign of replacement of cheekteeth in *Oligokyphus* (Kühne, 1956) although Young (1947) argues a case for replacement in *Bienotherium*. Teeth are heavily worn in mature individuals and wear facets are horizontally striated, indicating propalinal movement of the jaw (Kühne, 1956). Apical cusp wear forms when the dentine has been ‘scooped’ out between high ridges of enamel (Kühne, 1956); perhaps a similar form of wear could explain the apical pits seen in *Kollikodon*. Enamel shows wrinkling on anterior upper teeth (Kühne, 1956).

As in some mammals (but not other cynodonts), tritylodontids have cheek teeth with multiple roots (as many as five in the upper postcanines: Kühne, 1956; Cui and Sun, 1987). The multiple roots of upper teeth are set in two transverse rows beneath the crown; the (usually)
double roots of the lowers are recurved and set one behind the other anteroposteriorly (Kühne, 1956); as described above, lower molar roots are slightly recurved in *Kollikodon*.

In summary, the differences between *Kollikodon* and both traversodonts and tritylodontids appear to be profound in spite of the many similarities in dentition. Dental differences between *Kollikodon* and tritylodontids appear significant, and include 1) interlocking, crescentic cusps on upper and lower postcanines that meet in precise occlusion in tritylodontids (Sues 1986b, although cusps are less crescentic and more peg-like in *Bienotherium*: Young, 1947); 2) cusps almost never of equal height (Kühne, 1956); 3) a file-like action of uppers against lowers to shred (rather than crush) food (Young, 1947; Kühne, 1956); 4) propalinal jaw action and a significant, backwardly directed powerstroke (Sues 1986b); and 5) high postcanine (molariform) number, which varies from 6 to 8 in tritylodontids (Young, 1947; Kühne, 1956). These differences, as well as significant differences in jaw, orbital and palatal structure described above, appear to preclude a close relationship between *Kollikodon* and Tritylodontidae (see also General Discussion).

**Morganucodonta**

Morganucodons are diminutive early mammals or near-mammals from the Late Triassic of Europe, Africa and Asia (see Crompton and Jenkins, 1968; Jenkins and Crompton, 1979). The most well-known genus, *Morganucodon* (e.g., Kermack et al., 1973; Kermack et al., 1981) is known from a wealth of fossil material including skulls and skeletal material, mainly from the Rhaetic fissure deposits of Great Britain (Kermack et al., 1981 and references therein). Once included in Triconodonta as basal members (Parrington, 1967; Crompton and Jenkins, 1968; Jenkins and Crompton, 1979) as well as in Docodonta (Patterson, 1956; Kermack and Mussett, 1958; Kermack, 1967), morganucodonts are currently placed in a separate order Morganucodontidae (suborder: Kermack et al., 1973; order: McKenna, 1993, McKenna and Bell, 1997).

The comprehensive monographs of the skull and mandible of *Morganucodon* (Kermack et al., 1973; Kermack et al., 1981) are required reading for any investigation of early mammal material. This account relies heavily on these references in part because they provide the only detailed information about certain parts of the palatal and orbital regions for mammals of this grade.

**Maxillo-palatal region:** The skull of *Morganucodon* (*M. oehleri* and *M. watsoni*; Kermack et al., 1981) is elongate, with a generally mammalian appearance in spite of the fact that it has a compound (=reptilian) lower jaw (Kermack et al., 1973, 1981). The skull broadens gradually posterior to the canine and the maxilla does not expand around the molar row as in *Kollikodon*. 

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The zygomatic arch is delicate and thin (Kermack et al., 1981). The anterior root of the zygomatic arch is formed by the lacrimal anterolaterally, the maxilla medially and the jugal sandwiched in between (Kermack et al., 1956: Fig. 42). The cornu of the maxilla is wrapped around both lachrymal and jugal, joining these three bones (Kermack et al., 1981). Although it is hard to determine relations of the maxilla in this area in Kollikodon, the maxilla seems to form the root of the arch alone; the anterior root of the zygomatic arch does not seem to be formed as in Morganucodon, where the jugal, maxilla and lachrymal meet and overlap.

The palate in Morganucodon is markedly vaulted (to accommodate the high-cusped lower molars) (Lillegraven and Krusat, 1991; Kermack et al., 1981). There are pits for reception of some of the cusps of the lower teeth (excepting M³ and M⁴ where the palate is arched) (Kermack et al., 1981). The lower teeth in Morganucodon occlude inside of the uppers (Kermack et al., 1981), as in most early mammals (Crompton and Jenkins, 1968) but not as in Kollikodon, haramiyids (Jenkins et al., 1997) or multituberculates (Clemens and Kielan-Jaworowska, 1979).

The maxillo-palatine suture in Morganucodon takes a diagonal course from the distal end of the molar row to the entrance onto the palate of the greater palatine foramen (at the posterior margin of the fifth postcanine tooth, the first molariform) before becoming transverse (Kermack et al., 1981). The greater palatine foramen opens through a deep notch in the palatine (as in Kollikodon). It does not open a second time onto the palate as in Kollikodon. A well-developed greater palatine groove marks the maxilla anterior to the foramen (Kermack et al., 1981; Lillegraven and Krusat, 1991), a phylogenetically important feature that appears to be absent in Kollikodon.

The maxillo-palatine suture at the posterolateral corner of the hard palate is simple but there is a palatine tubercle (a raised lip formed where the palatal, orbital and posterior plates of the palate meet) along the posterolateral margin of the suture (Kermack et al., 1981). The palatine tubercle in Morganucodon is variable in detail between specimens but agrees in general form with this part of the palate in Kollikodon. A well-developed lesser palatine groove is present in Morganucodon leading to the lesser palatine foramen (via the lesser palatine canal); small foramina open through the palatine lateral to this groove or through it carrying branches of the lesser palatine nerve (e.g., Kermack et al., 1981: Fig. 47A, 48A, 49B). The lesser palatine groove is more distinct in Morganucodon than in Kollikodon; the formation of the lesser palatine canal or foramen, however, can’t be assessed in Kollikodon because the specimen is broken at this point. Differences between Morganucodon and Kollikodon include the following: the lip of the palatine tubercle does not wrap laterally in Morganucodon (as it does in Kollikodon) but joins the maxilla ventrolaterally; and the small, aligned tubercles and ‘rolled
lip’ of the edge of the tubercle seen in *Kollikodon* may be absent in *Morganucodon* (they are not figured).

The infraorbital canal in *Morganucodon* has a double posterior opening - a large medial opening and smaller, more lateral entrance (Kermack et al., 1981; Lillegren and Krusat, 1991). A posterior (rather than interior or medial) opening anterior to the orbit is a derived feature of post-cynodont taxa (Lillegren and Krusat, 1991). The infraorbital canal is floored by the maxilla; the lacrimal forms the side walls and roof (Kermack et al., 1981).

**Mandible:** The lower jaw in *Morganucodon* is long, slender and straight, without convex curvature (Kermack et al., 1973). The tooth row runs diagonally across the jaw and the posterior molars are not shielded laterally by the coronoid process (Kermack et al., 1973: Fig. 8).

A full complement of accessory jaw bones is present, similar to those of advanced cynodonts (Kermack et al., 1973). *Morganucodon* has a dual jaw articulation (both the reptilian articular-quadrate and mammalian dentary-squamosal articulations) between the lower jaw and skull (Kermack and Mussett, 1958; Kermack et al., 1973). There is a long, splint-like splenial (misinterpreted as the prearticular by Kermack et al., 1973) whose anterior limit is reconstructed as ventral to the posterior root of M₂ (Kermack et al., 1973: Fig. 7).

The meckelian groove is well-developed in morganucodontids (Kermack et al., 1973; Luo et al., 2002). In *Morganucodon* this groove is distinct and comparatively deep, converging on the ventral margin of the mandible ventral to the anterior root of M₁ (Kermack et al., 1973). This conformation of the meckelian groove – convergent rather than parallel – is similar to the course in *Kollikodon*, but this groove is more well-developed, with a deeper imprint of the groove on the jaw, in *Morganucodon*. A groove for the dental lamina is present along the dorsal margin of the jaw, best seen in juvenile specimens (Kermack et al., 1973: Fig. 24) (apparently absent in *Kollikodon*).

A cut-away view of the reconstructed lower jaw of *Morganucodon* shows the size and position of the dental canal at approximately the point where the jaw in *Kollikodon* is broken (Kermack et al., 1973: Figs. 20, 29); the diameter of the dental canal is smaller than in *Kollikodon*, which is more moderate in size (Fig. 8).

**Dentition:** The elongate upper and lower molars of morganucodonts have a linear arrangement of cusps: there are three main cusps on both upper and lower molars (B/b, A/a, C/c respectively with smaller cusps D/d, from anterior to posterior), a pattern retained from cynodont ancestors such as *Thrinaxodon* (Crompton and Jenkins, 1968; Mills, 1971). The ultimate premolar (P₄) in *Morganucodon* is enlarged on both upper and lower dentitions (Kermack et al., 1973). Upper molars of the morganucodontid *Eozostrodon* have a prominent
cuspidate cingulum on both buccal and lingual faces of the crown (Crompton and Jenkins, 1968; Mills, 1971). Lower molars of *Eozostrodon* have a distinct, cuspidate lingual cingulum but lack any trace of a buccal cingulum (Crompton and Jenkins, 1968; Mills, 1971). Cingular cusps that are large enough to be distinguished by name include cusps E (anterolingual) on upper molars and cusps e (anterolingual) and g (just posterior to the midline) (Crompton and Jenkins, 1968). Cusp g is also termed the Kühnecone (Parrington, 1967). Roots of both upper and lower molars in *Morganucodon* are double (Mills, 1971; Kermack et al., 1973, 1981).

In *Eozostrodon* the upper molars occlude opposite to the lowers rather than being alternately arranged: principal cusp A of the uppers occludes between lower cusps a and c of the opposite lower molar rather than in the valley between adjacent lower molars, as in mammals or near-mammals with alternate molar position (Crompton and Jenkins, 1968). The position of the upper molars of *Eozostrodon* in occlusion is just posterior to the lowers (Crompton and Jenkins, 1968), much as it is in docodonts (Crompton and Jenkins, 1968), haramiyids (Jenkins et al., 1997) and *Kollikodon* (see Discussion).

Dental function in morganucodonts is limited to vertical shearing; shear facets are created through wear rather than being present on eruption of the molars (Crompton and Jenkins, 1968). Lower molars are medial to the uppers (there is no overlap of upper and lower molars) so that uppers shear laterally to lowers; wear is along the sides of the molars rather than on the occlusal surface (Crompton and Jenkins, 1968). This arrangement is similar to that of most Triassic-Jurassic mammals; exceptions include docodonts, haramiyids, multituberculates and *Kollikodon*. There is no crushing component to the masticatory stroke in morganucodonts (Crompton and Jenkins, 1968). Dental function, therefore, is significantly different between morganucodonts and *Kollikodon*. However, the basic bauplan of morganucodont molars – a central row of cusps with cuspidate cingula – may serve as a possible model for derivation of the molar pattern in *Kollikodon* (see Discussion). The Late Triassic mammal *Megazostrodon*, which has large external cingula (a character of interest in this investigation) has alternate rather than opposite occlusion of molars (Crompton and Jenkins, 1968) and therefore is not considered.

**Docodontidae**

Docodonts were Jurassic mammals (order Docodontida) known primarily from the northern hemisphere (see Kron, 1979) although there is a possible docodont from the Late Cretaceous of Patagonia (Pascual et al., 2000) and Middle/Late Jurassic of India (Prasad and Manhas, 2001). Docodonts are characterised by unusual, complex, specialized molar teeth and by plesiomorphic skull and mandibular features (Lillegraven and Krusat, 1991). Docodonts are thought by many to have been derived from morganucodontid stock (Kühne/Butler, 1950;
Patterson, 1956; Kermack and Mussett, 1958; Kermack, 1965; Crompton and Jenkins, 1968, 1979; Hopson and Crompton, 1969; Hopson, 1970; Kermack and Kermack, 1984; Butler, 1988; Rowe, 1988) and some believe morganucodonts are docodonts (Patterson, 1956; Kermack, 1965).

Analysis of the skull of the comparatively primitive Late Jurassic fossorial docodont *Haldanodon exspectatus* suggests that docodonts may be more basal than morganucodontids (Lillegraven and Krusat, 1991). Further challenges to the traditional interpretation have come from recovery of docodont teeth from the Rhaetic of France that suggests a close relationship between docodonts and kuehneotheriids (Sigogneau-Russell, 1983; Sigogneau-Russell and Hahn, 1995; Butler, 1997).

**Maxillo-palatal region:** The skull of *Haldanodon* is flat, wedge-shaped in dorsal view, with a pointed snout (Lillegraven and Krusat, 1991: Figs. 1, 2 and 3). The palate is exceptionally long and not well arched (the latter feature a plesiomorphic cynodont retention: Lillegraven and Krusat, 1991); there are deep pits between molars for the lower cusps; and deep corrugations run anteroposteriorly across the maxilla in some specimens (Lillegraven and Krusat, 1991); all of these palatal features are absent in *Kollikodon* (although the length of the palate – at least past the molar row – can’t be determined).

In *Haldanodon* the maxillopalatine suture runs parallel and comparatively close to the tooth row (although not as close as it does in *Kollikodon*). As in *Morganucodon*, the transverse part of the maxillary-palatine suture in *Haldanodon* is at the anterior margin of the fifth postcanine tooth (in *Haldanodon* it is the second molariform: Kermack et al., 1981; Lillegraven and Krusat, 1991). The part of the palate that might have formed a palatal tubercle (had it been present) as well as the orbital process and the medial flange of the palatine is missing in *Haldanodon* (Lillegraven and Krusat, 1991). There is no lesser palatine groove present (perhaps the primitive state: Lillegraven and Krusat, 1991), a structure seen in both *Morganucodon* (Kermack et al., 1981) and *Kollikodon*.

The major (greater) palatine foramen is close to the palatal midline. The posterior two-thirds of the foramen open through a deep notch in the palate and the anterior third opens through the maxilla (Lillegraven and Krusat, 1991: Fig. 2). There is no visible greater palatine groove; the possible lack of this groove in *Kollikodon* and *Haldanodon* is of interest since absence of this groove may be a plesiomorphic cynodont retention (Lillegraven and Krusat, 1991).

It appears from the description that the maxilla may be expanded around the molar teeth: ‘The ascending process of the maxilla has its ventral edge immediately lateral to the cheekteeth along the entirety of the postcanine dental series’ (Lillegraven and Krusat, 1991; p. 63). This
may be similar to the expansion of the maxilla around the cheekteeth in *Kollikodon*, an unusual morphology not seen in many Mesozoic mammals (G.W. Rougier, pers. comm.) but seen as well in ornithorhynchid monotremes. The sinus system within the maxillary in *Haldanodon* is described as unique, and absent in *Morganucodon* and cynodonts (Lillegraven and Krusat, 1991). Lillegraven and Krusat (1991) describe small foramina (the posterior maxillary sinus foramina) perforating the bone in this area; small foramina are also seen in *Kollikodon* in this general area (and the maxilla is inflated), perhaps indicating the presence of a maxillary sinus.

The infraorbital canal in *Haldanodon* opens posteriorly, is single, concave, and floored by the maxilla posteriorly (Kermack et al., 1981; Lillegraven and Krusat, 1991). The infraorbital canal enters the maxillary sinus at the level of the middle of M2 (Lillegraven and Krusat, 1991).

The zygomatic arch in *Haldanodon* is formed by a process of the maxilla anteriorly and ventrally (extending past the tooth row); by a lachrymal process dorsally; and by the jugal laterally (Lillegraven and Krusat, 1991). This differs from the construction in *Morganucodon* (see above) but may be closer in form to the structure of the arch in *Kollikodon*, where it appears that a process of the maxilla extends posteriorly to form the root of the arch. The root of the zygomatic arch originates anteriorly between M2 and M4 and is fairly deep in lateral view (Lillegraven and Krusat, 1991).

**Mandible:** The lower jaw in docodonts is similar to that of morganucodonts: it is long and slender, accessory jaw bones and a distinct meckelian groove are present; the angular process is forwardly-placed and jaw articulation is double (e.g., Lillegraven and Krusat, 1991; Luo et al., 2002). The meckelian groove runs parallel to the ventral border of the jaw in *Haldanodon* (Lillegraven and Krusat, 1991).

A reconstruction of the lower jaw of *Haldanodon* depicts a deep but short splenial (indicated by a facet on the dentary); its anterior extent is the anterior margin of the ultimate molar. (Lillegraven and Krusat, 1991: Fig. 14). Lillegraven and Krusat (1991) report that a large splenial is not retained in morganucodontids or more advanced mammals although it is typical for cynodonts. If *Kollikodon* retained the splenial it may have been larger than in *Haldanodon* (the anterior end of the possible splenial facet terminating ventral to the penultimate molar in *Kollikodon* and ventral to the ultimate molar in *Haldanodon*).

**Dentition:** Docodonts have a unique molar form incorporating a huge cingular lobe developed on the lingual side that overlaps the lower teeth rather than shearing past them as in most early mammals (e.g., Crompton and Jenkins, 1968; Jenkins, 1969; Butler, 1997). This development created crushing areas in addition to shearing (e.g., Butler, 1997), a rare occurrence in Mesozoic
mammals and one that may be relevant to *Kollikodon*. The expanded cingular lobe partially opposes the crowns of the lowers on the occlusal surface (Butler, 1997). Opposition of upper and lower molars is a pattern shared only by docodonts, haramiyids and multituberculates among Jurassic mammals [and by the Early Cretaceous *Kollikodon*]; all other early mammals had molars in which lower teeth passed lingually to uppers and occlusal surfaces of opposing molars did not make contact (Butler, 1997).

In *Haldanodon* there were normally three premolars and four molars although occasionally a fifth, very reduced upper molar has been reported (Lillegraven and Krusat, 1991). The cheektooth rows (upper and lower) in lateral and ventral views are straight and the basal crowns in lateral and ventral views form an almost perfectly straight line (as in morganucodontids; a plesiomorphic feature seen in cynodonts: Lillegraven and Krusat, 1991). P₃ may be molariform, with a well-developed medial lobe supported by a separate root (Lillegraven and Krusat, 1991).

Molar function in docodonts is the subject of debate; Jenkins (1969) proposed that function was primarily shearing rather than crushing. Mills (1971) suggests that a grinding phase might follow the shearing phase although opposing teeth in docodonts overlap to produce crushing surfaces (Butler, 1997).

Docodonts have multiple-rooted upper molars (at least triple), probably as a consequence of the widening of the upper molars; *Haldanodon* had medially expanded, triply-rooted upper molars (Lillegraven and Krusat, 1991). Lillegraven and Krusat (1991) consider this a unique specialization in *Haldanodon*. However, multiple upper (and lower) molar roots are also known in monotremes. Interestingly, archaic monotremes have a jaw form similar to that of docodonts (Rich et al., 2005) and derivation of monotreme molars from those of docodonts has been proposed (Patterson, 1956; Pascual and Goin, 1999).

Wear facets in *Haldanodon* are consistent, suggesting that the molars were not replaced (Lillegraven and Krusat, 1991).

### Haramiyida

Haramiyida is an enigmatic order of primarily Late Triassic to Early Jurassic Laurasian mammals or near-mammals that were known until recently solely on the basis of isolated teeth (e.g., Plieninger, 1847; Hahn, 1973; Freeman, 1976; Jenkins et al., 1983; Clemens, 1988; Butler and MacIntyre, 1994; Kermack et al., 1998). They are among the oldest mammals known, with a record from the Norian of Germany (Hahn, 1973). There is a late survivor from Gondwana (a Middle Jurassic haramiyid from Tanzania: Heinrich, 1999). Associated upper and lower jaws and skeleton of a haramiyid have recently been described from the Late Triassic of Greenland (*Haramiyavia clemmenseni*: Jenkins et al., 1997).
Members of Haramiyida (suborders Theroteinida and Haramiyoidea: Butler, 2000) share a distinctive pattern of multiple cusps arranged in rows similar to that of multituberculates, with whom they are often linked (see Butler, 2000). Origins of Haramiyida are obscure and the subject of much debate. Theories include independent origins from cynodons (Simpson 1928, 1929, 1937, 1945, 1971; from Miao 1988); specifically, traversodont cynodons (Butler and MacIntyre, 1994); or Triassic mammals (as incertae sedis, allied with or members of Multituberculata: Marsh, 1887; Osborn, 1888; Gregory, 1910, Heinrich, 1999; Hahn, 1969; Hahn, 1973; Hahn et al., 1989; Butler 2000). ‘They may be either or neither’ (Simpson, 1947; p.497). Several others share this uncertainty (Simpson, 1928; Kermack and Mussett, 1958; Clemens and Kielan-Jaworowska, 1979).

Haramiyids are now generally regarded as mammals (see Clemens and Kielan-Jaworowska, 1979). Mammalian characters include a dentition differentiated into premolars and molars; and pre-prismatic enamel (as in morganucodontids and kuehneotheriids: Frank et al., 1984). Simpson (1971, p. 191) says an origin from morganucodontids is possible.

Haramiyida is comprised of two suborders proposed by Butler (2000): Haramiyoidea (families Haramiaviidae [Butler, 2000], Haramiidae [Simpson, 1947] and Eleutherodontidae [Kermack et al., 1998]) and Theroteinida (comprised of a single genus, Theroteinus, from the early Rhaetic of France: Sigogneau-Russell 1986; Hahn et al. 1989). Theroteinids were at first recognized only as being mammals or near-mammals but affinities with Allotheria Marsh 1880 have been proposed (Hahn et al. 1989).

Maxillo-palatal region: There is very little described for the only haramiyid known from cranial material; recovered to date is the partial upper jaw of Haramiyavia clemmenseni (Jenkins et al., 1997). Very little of what is preserved can be sensibly compared with Kollikodon.

Mandible: The lower jaw of H. clemmenseni is long and slender, with a trough at the rear for accessory jaw bones (Jenkins et al., 1997). The meckelian groove is described as well-developed and parallel to the ventral border of the mandible (Luo et al., 2002). The size of the mandibular canal has not been described or figured for Haramiyavia.

Dentition: Molar teeth of Haramiyida are distinguished by multiple rows of cusps (2-3 on uppers, 2 on lowers) of unequal height; ‘reversed symmetry’ of upper and lower molars so that uppers are highest posteriorly, lowers mesially; differing number of lingual, buccal cusp rows bordering a central basin; a U-shaped posterior rim of tooth crown; and there is always an orthal component to the jaw action not present in multituberculates. (Heinrich, 1999; Butler, 2000) (Figure 10).
In Haramyoidea lower molars are nearly opposite to uppers; the median valley is longer than in Theroteinida except on anterior lower molariforms (not known in Eleutherodontidae) where it is distal; palinal movement is developed to varying degrees (incipient in Haramiyaviidae and most developed in Eleutherodontidae) (from Butler, 2000).

Theroteinida have fully orthal occlusion, upper molars are alternate to lower molars; the highest cusps are more central than in Haramyoidea; and longitudinal valleys are short (from Butler, 2000). There may be three rows of multiple cusps on the upper molars (rather than two as in Haramyoidea); lingual cusps may be developed; there are tubules in the enamel (lacking in Haramyiidae: Sigogneau-Russell et al., 1986); and, interestingly, theroteinid molariforms have low rounded cusps (from Butler, 2000). Wear patterns, cusp pattern (irregular), and number of cusps differ from that in Kollikodon and, unlike Kollikodon, Theroteinida have wrinkled enamel (there is the tiniest suggestion of folded enamel on the base of one cusp in Kollikodon).

**Multituberculata**

Multituberculates were a diverse group of rodent-like herbivores known from the Late Jurassic to early Tertiary (see Miao 1988; Clemens and Kielan-Jaworowska, 1979). The oldest and most primitive undoubted multituberculates are basal Paulchoffatiidae (suborder Plagiaulacida: Hahn and Hahn, 2003) from the Late Jurassic (Kimmeridgian) of Portugal (Hahn, 1969; Hahn, 1971; Krause and Hahn, 1990) although there are possible Late Rhaetic and Middle Jurassic paulchoffatiids (Hahn and Hahn, 2003). A possible early paulchoffatiid is described from the Late Triassic of Belgium (Mojo: Hahn et al., 1989). Although most multituberculates have been described from Laurasia (see Clemens and Kielan-Jaworowska, 1979; Hahn and Hahn, 1983), multituberculates are now known from the Early Cretaceous of Morocco (Sigogneau-Russell, 1991; Hahn and Hahn, 2003) and from the Late Cretaceous of Madagascar (Krause and Grine, 1996).

Haramiyids (discussed above) may be related to multituberculates. Gondwanatheres (from the Late Cretaceous and early Tertiary of South America, Madagascar, India, Antarctica and possibly Africa: see Krause et al., 2003) have been thought to be either edentates (Scillato-Yané and Pascual, 1984, 1985; Bonaparte, 1986a,b; Mones, 1987; Bonaparte, 1990) or multituberculates (Krause and Bonaparte, 1990, 1993; Krause et al., 1992; Bonaparte et al., 1993; Kielan-Jaworowska and Bonaparte, 1996). The current view seems to be that they are a unique group of uncertain affinities (Mammalia incertae sedis, Pascual et al., 1999; Koenigswald et al., 1999).

Multituberculates are generally considered mammalian because of advanced skull and postcranial features (see Miao, 1988). An early divergence from other mammals is favoured by
most palaeontologists (see Miao, 1988). However, although there is a great deal of fossil material available for study, their relationships are by no means clear. Comparisons here are made primarily with primitive Jurassic multituberculates (Paulchoffatiidae) and with some advanced multituberculates (e.g., Lambdopsalis: Miao, 1988; Kamptobaatar and Sloanbaatar: Kielan-Jaworowska, 1971) that are known from well-described cranial material.

Maxillo-palatal region: Multituberculate cranial material is rare and often poorly preserved (Miao, 1988). The palatal region – presence/absence and shape of palatal vacuities, origin of zygomatic arch and shape of the muzzle - varies considerably between various multituberculate genera, probably in relation to feeding habits (Hahn, 1977b).

The maxillo-palatine suture in Lambdopsalis runs parallel to the tooth row and the transverse suture between these bones is about at the level of the posterior one-third of M\(^1\) (Miao, 1988). The secondary palate is posterior to the last molar in Kamptobaatar (Kielan-Jaworowska, 1970).

The origin of the zygomatic arch in multituberculates is generally much more anterior than it is in Kollikodon relative to the tooth row. The root of the zygomatic arch originates lateral to the premolars rather than molars (as in paulchoffatiids: Hahn, 1969, 1977; and Kamptobaatar: Kielan-Jaworowska, 1970). There is no floor to the orbit in multituberculates (e.g., Kielan-Jaworowska, 1970). The lateral face of the maxilla curves medially towards the distal end of the tooth row in paulchoffatiines (Hahn, 1987: p. 189; from Krause and Hahn, 1990).

The infraorbital canal in Lambdopsalis bulla (Taeniolabidae) is a single posterior opening at the bottom of the orbit, passing anteriorly through the root of the zygomatic process of the maxilla (Miao, 1988). Because of the conformation of the skull and posterior position of the molars, the canal entrance in Lambdopsalis is dorsal to the anterior tip of M\(^1\) (Miao, 1988). In Ornithorhynchus and Lambdopsalis (among other mammals) the infraorbital canal enters the maxilla only, rather than being roofed by the lachrymal bone (lachrymals at that time were believed to be absent in both groups) (Miao, 1988). Some paulchoffatiids and Meniscoessus have double (subdivided) foramina, suggesting variability in this feature and lack of phylogenetic utility as a character (see Miao, 1988).

The major (greater) palatine foramen in Lambdopsalis lies along the suture between the maxilla and palatine (Miao, 1988) as in Kollikodon, Ornithorhynchus, the multituberculate Kamptobaatar and many therian mammals (Miao, 1988). Lambdopsalis does not have a posterior continuation of the greater palatine foramen as Kollikodon does although it has two separate minor palatine foramina within the palatine (as do some other multituberculates and many modern mammals) (Miao, 1988). In some multituberculates there is a foramen through
the posterior part of the palate in the suture between the maxilla and palatine lateral to the postpalatine torus (the palatonasal foramen: Kielan-Jaworowska 1970) that is suggestive. However, judging from the terminology employed it does not appear to be homologous. There is a single, large sphenorbital fissure in both primitive and advanced multituberculates (Hahn, 1977b).

**Mandible:** The mandible in multituberculates is highly derived and does not invite detailed comparisons with the mandible of *Kollikodon*. The rodent-like multituberculate lower jaw is usually comprised only of the dentary (e.g., Clemens and Kielan-Jaworowska, 1979; Miao, 1988) although a rudimentary coronoid similar to that of the contemporaneous docodont *Haldanodon* has been reported in Guimarota Paulchofatiidae (Hahn, 1977). Other than this single instance, all markings on the jaw for accessory jaw bones or Meckel’s cartilage are absent.

The short, robust jaw is highly derived: the pterygoid fossa is large and deep; the masseteric fossa extends a considerable distance anteriorly (as origin for the large m. masseter that drives the posteriorly directed masticatory stroke); the anterior of the jaw is ventrally (rather than horizontally) directed; and the angular process has been reduced to a flange on the medial side of the jaw (e.g., Kielan-Jaworowska, 1971; Clemens and Kielan-Jaworowska, 1979; Miao, 1988). Although the lower jaw of *Kollikodon* is fragmentary, it is fairly gracile rather than massive, does not have an anterior extension of the masseteric fossa, has a well-developed meckelian groove and possible splenial facet. Other differences include a slight medial inclination of the alveolar border in multituberculates (Miao, 1988); in *Kollikodon* the alveolar border inclines somewhat laterally. However, there is a suggestion of the concave curve and posterior deepening of the dentary of *Kollikodon* in the jaw of multituberculates (e.g., *Lambdopsalis bulla*: curved to below P₄ before straightening out although this curvature is ventrally directed: Miao 1988, Fig. 32). The mandibular canal is described as large in at least some multituberculates (e.g., *Sloanbaatar mirabilis*), with a single opening (Kielan-Jaworowska, 1971).

**Dentition:** Multituberculate molars have longitudinal rows of cusps, as in Tritylodontidae, Haramiyida and *Kollikodon*. There are two upper and two lower molars (e.g., Hahn, 1971; Clemens and Kielan-Jaworowska, 1979). Premolar numbers vary between taxa, the more primitive members having higher premolar counts (Hahn, 1971). Some paulchofatiid and plagiaulacid molars have low, blunt or bunodont cusps (Hahn, 1971). As in *Kollikodon*, cingula are absent (e.g., Luo et al., 2002). Roots of molars are robust in paulchofatiids (Hahn, 1971: Fig. 17-18) and roots of second molars (upper and lower) may grow together or become
confluent (Hahn, 1971). Molars are double-rooted (Hahn, 1971; 1977b; Clemens and Kielan-Jaworowska, 1979).

The distinction between multituberculate premolars and molars is on morphological grounds rather than on evidence of tooth replacement, as in placentals (Hahn, 1971). Posterior upper premolars in Paulchoffatiinae and Pinheirodontidae have two to three longitudinal rows of cusps and are molariform (e.g., Hahn, 1977b; Hahn and Hahn, 2003, who consider this autapomorphic). Lower premolars in most multituberculates are specialised for cutting but in Kimmeridgian Paulchoffatia and Kuehneodon upper premolar morphology suggests the lower premolars were used for chewing or grinding (Hahn, 1969; Hahn, 1971). The blade-like premolars of plagiaulacoid multituberculates may have been derived from molar-like, cuspidate teeth (Hahn, 1971).

Anterior upper premolars in Paulchoffatiidae are round in outline with 3-4 cusps; Bolodon and Ctenacodon species are tricuspid and cusps are arranged in a triangular pattern but the more basal Paulchoffatia and Kuehneodon are tetracuspid (Hahn, 1971). In paulchoffatiids the posterior upper premolars resemble molars (Hahn, 1971). The P5 in Paulchoffatia is molariform with three rows of cusps and both P4 and P5 are molariform in Pseudobolodon (Hahn, 1977b). Posterior upper premolars are roughly similar in size to the first designated molar and anterior premolars are not markedly smaller (Hahn, 1971: Fig. 12), not the case in Kollikodon where the ultimate upper premolariform tooth is much smaller than the first molariform. A third cusp row is developed on P6 of Paulchoffatia, a unique development within Plagiaulacoidea to increase surface area for chewing and not homologous with the third row on the upper molars of later multituberculates (Hahn, 1971).

Multituberculates are unique in that upper molars are offset from lowers so that the anteroposterior midline of M2 is lingual to the midline of M1 (M2 is distolingual rather than directly dorsal to M1) (e.g., Krause and Hahn, 1990). Cusp rows, therefore, cannot be described as being parallel, as they are in Kollikodon. The absence of upper/lower molar offset described in Paulchoffatiidae (Hahn, 1969, 1971, 1987) has been shown to be in error; like all other multituberculates, uppers are offset from lowers (Krause and Hahn, 1990).

The Plagiaulacida (including Paulchoffatiidae) have two cusp rows on upper molars (Hahn, 1969; Hahn, 1971; Krause and Hahn, 1990; Hahn and Hahn, 2003) with a small ridge sometimes developed on M2 (Krause and Hahn, 1990). A third upper row – lingual on M1 and buccal on M2 - is variably added in the later multituberculate suborders Taeniolabidoidea and Ptilodontoidea (Hahn, 1971; Krause and Hahn, 1990). In Plagiaulacida the buccal row of cusps on the upper cheekteeth is elevated (as in the buccalmost row in Kollikodon) but is reversed in the lower teeth (the lingual row is elevated) (Hahn, 1971). The lingual rows of both M1 and M2
have more cusps than the buccal rows (Hahn, 1971) in contrast to Kollikodon, where the buccal row has the most cusps.

Lower cheekteeth of paulchoffatiids also have two cusp rows and vary in shape from oblong to rectangular (Hahn, 1971: Fig. 19). The lower tooth row is relatively straight in Paulchoffatiidae (as in Kollikodon) but in non-paulchoffatiid multituberculates the tooth row runs diagonally across the lower jaw (anterior premolars being buccal and molars being lingual) to allow for enlargement of the lower incisor and accommodation of the roots of the lower premolars (Hahn, 1971). In paulchoffatiid lower molars the buccal row has more cusps than the lingual row, while in plagiaulacids the number of cusps is either equal (as in Kollikodon lower molars) or higher for the lingual row (Hahn, 1971). M1 with its multiple cusp rows does not resemble the basined M2 in Paulchoffatiidae, a possible specialization (Hahn, 1971).

Multituberculate molars were used for grinding plant matter (such as hard seeds: Hahn, 1971; Krause, 1982) rather than for crushing hard or brittle objects. The masticatory stroke in multituberculates such as *Ptilodus* had a slicing-crushing cycle (as premolars cut orthally into food items) and a grinding cycle in which the lower jaw was retracted, engaging the molars in tight occlusion while grinding (i.e., jaw action was palinal, the jaw moving from anterior to posterior) (Krause, 1982). There was no transverse, triangular component as in therians (Krause, 1982). Heavy wear reduced the crown to the base in paulchoffatiids (Hahn, 1977b). Wear in all plagiaulacoid molars shows a horizontal orientation (Krause and Hahn, 1990). Wear may be extreme as in Paulchoffatiidae, where the crowns may be eroded to their bases (Hahn, 1977b).

Occlusion in multituberculates is opposite: upper teeth do not alternately bite between lower teeth but are nearly opposed (e.g., Krause and Hahn, 1990). However, the molar offset described above creates a pattern of buccal-lingual shift in upper/lower dental relations that differs significantly from occlusion in Kollikodon.

**Monotremata**

Monotremata includes the platypuses (Ornithorhynchidae), echidnas (Tachyglossidae) and their extinct relatives *Steropodon galmani* (Archer et al., 1985) and *Teinolophos trusleri* (Rich et al., 2001, 2005). *Kollikodon ritchiei* was initially described as a highly derived monotreme (Flannery et al., 1995). Monotremes (fossil and recent, excluding Tachyglossidae) are distinguished primarily by a pseudo-tribosphenic dentition and an enlarged mandibular canal (to accommodate an exceptionally large trigeminal nerve to a sensitive bill or beak) (e.g., Musser, in press; Pascual and Goin 1999; Rich et al., 2005). An archaic Early Cretaceous monotreme from Victoria, the abovementioned *Teinolophos*, was described with a postdentary trough (and presumably a complement of accessory jaw bones) and jaw form is similar to that of *Morganucodon* and *Docodon* (Rich et al., 2005). This primitive feature – along with
numerous other plesiomorphies – places Monotremata near the base of Mammalia, only distantly related to therian mammals (Rich et al., 2005).

The descriptions and comparisons below have been made from personal observation (Obdurodon species; Ornithorhynchus; Tachyglossus and Zaglossus) as well as from the literature where noted.

Maxillo-palatal region: In Ornithorhynchidae the maxilla is expanded to accommodate the wide upper molars in a similar fashion to Kollikodon (the edentate echidnas do not invite comparison). The tooth bed is extremely shallow (paper thin in young Ornithorhynchus) but in Kollikodon this part of the maxilla is exceptionally deep.

The anterior origin of the zygomatic arch in ornithorhynchids projects posteriorly. Its position is concealed by the wide molar bed. In both Obdurodon and Ornithorhynchus the zygomatic arch originates laterally to the posterior half of the first ‘molar’ (M1 in Obdurodon and the impression on the dental pad in roughly the same spot in Ornithorhynchus). The zygomatic arch is deep but very narrow.

In Ornithorhynchus the maxillo-palatine suture is close to the molar row, turning medially at the level of what would have been the first molariform tooth. The maxillo-palatine suture in Obdurodon dicksoni is unfortunately fused. In Tachyglossus the palatines angle anteromedially from the lateral margins of the palate.

In monotremes the secondary palate is exceptionally long (one of the longest palates known in mammals: see Musser and Acher, 1998). The palate is less vaulted in monotremes than it is in Kollikodon; the edentate Ornithorhynchus and Tachyglossus have only moderately vaulted palates but the palate in the toothed ornithorhynchid Obdurodon dicksoni is flatter still. In the premolar region the palate shows no suggestion whatsoever of vaulting. Neither a palatine tubercle nor the series of small channels seen in Kollikodon are present in ornithorhynchids or tachyglossids.

The positions of the foramen palatinum and other palatal foramina are variable in monotremes. In Obdurodon dicksoni the major palatine foramen appears to be quite posterior and there is a hole-like foramen anterior to it (Musser and Archer, 1998: Fig. 1). The lack of readable maxillo-palatine sutures in Ob. dicksoni makes interpretation of the position of the major palatine foramen difficult. Although it is suggestive in regard to the posterior palatal foramen in Kollikodon, there is no anteriorly positioned major palatine foramen in Ob. dicksoni to compare to that of Kollikodon.

The infraorbital canal in monotremes is exceptionally large, as is the dental canal (Zeller, 1998). The infraorbital canal, large in tachyglossids, is massive in ornithorhynchids, carrying branches of the trigeminal nerve to the electroreceptors and mechanoreceptors of the bill (see
Musser and Archer, 1998). Although variable, in all of the ornithorhynchid specimens examined
the posterior opening of the infraorbital canal was much larger than in \textit{Kollikodon}. This canal
in \textit{Ornithorhynchus} is larger than that of any living mammal (Zeller, 1988) and is
proportionately even larger in \textit{Ob. dicksoni} (Musser and Archer, 1998). The much reduced
‘beak’ in echidnas seems to be a secondarily derived morphology (see Musser, in press).

\textit{Mandible:} Although living monotremes have lost all suggestion of accessory jaw bones or a
meckelian groove in the adult, Mesozoic monotremes have retained some of these
plesiomorphic mandibular features in various configurations (Musser 2003; Rich et al., 2005;
Musser in press; abstract, Musser 2005). The lower jaws of the Early Cretaceous Australian
monotremes \textit{Teinolophos trusleri} (Rich et al., 2005) and \textit{Steropodon galmani} (Musser in press;
abstract: Musser, 2005) show Mesozoic monotremes may have retained postdentary bones: the
splenial, angular and coronoid in \textit{Teinolophos} (Rich et al., 2005) and probably the splenial in
\textit{Steropodon} (Musser, in press; abstract, Musser, 2005). These two monotremes differ in the
configuration of the probable postdentary bones. In addition, \textit{Steropodon} has retained a faint,
discontinuous meckelian groove parallel to the ventral border of the mandible (Musser in press;
abstract: Musser, 2005) although a meckelian groove is not detectable in \textit{Teinolophos} (Rich et al.,
2005). Neither \textit{Steropodon} nor \textit{Teinolophos} (Rich et al., 2005) have a large, depressed area
on the medial side of the jaw for a large splenial, or striations on the surface of the jaw as seen
in \textit{Kollikodon}.

An exceptionally large mandibular canal through the lower jaw is considered a
monotreme synapomorphy (Musser, in press; Rich et al., 2005). The massive mandibular canals
in \textit{Steropodon} (Fig. 8), \textit{Obdurodon} and \textit{Ornithorhynchus} occupy most if not all of the interior of
the dentary. This is in contrast to the dental canal in \textit{Kollikodon}, which is similar in size to
known Mesozoic mammals.

\textit{Dentition:} The basic dental pattern of toothed monotremes is comprised of a reversed-triangle
dentinion with transverse shearing blades. Reversed triangle morphology is also seen in therian
mammals although it may be convergent to the pattern in monotremes (see Pascual and Goin,
1999). The mode of occlusion is unilateral, with a very well-developed transverse component
to the masticatory stroke. This dental pattern differs fundamentally from that of \textit{Kollikodon} and
is one of the primary reasons that this investigation suggests \textit{Kollikodon}, with multicusped
dentition and orthal, crushing occlusion, is not monotreme. However, there may be certain
similarities (e.g., upper molars in monotremes are wider than long), and derivation of both
molar patterns from similar stock is discussed below, as is the comparison by Flannery et al.
(1995) of the lower molars of monotremes and \textit{Kollikodon} (see General Discussion below).
There are no known upper molars for Cretaceous monotremes. Tertiary ornithorhynchids appear to have had two upper molars (Archer et al., 1992, 1993; abstract, Musser and Archer, 1998; Musser and Archer, 1998 but see Pascual et al., 1992 for *Monotrema*). *Steropodon* and *Obdurodon* species have three lowers molars (the third being much reduced in *Obdurodon*; Archer et al., 1992, 1993; Musser and Archer, 1998). If the dental formula for *Kollikodon* is four molars (upper and lower) it differs from known monotreme dental formulas, but if there are three molars with a molarised premolar in *Kollikodon* (the preferred hypothesis presented here) the molar formulas are similar. Premolar number is unknown in *Kollikodon* as well as in Mesozoic monotremes.

Roots are multiple in both upper and lower molars of Tertiary ornithorhynchids (Archer et al., 1992, 1993; Musser and Archer, 1998; Luo et al., 2002). Roots of the lower molars are double in *Steropodon* (Archer et al., 1985) and are slightly recurved (personal observation). Roots of at least some premolars may be triple in *Obdurodon* (personal observation).

**Other Gondwanan Mesozoic mammals**

Mesozoic mammals have only been reported from the southern continents in fairly recent times. Several new finds from the Jurassic and Early Cretaceous have greatly expanded our knowledge of these pre Late Cretaceous mammals or near-mammals. Most of these southern mammals appear to have little in common with *Kollikodon*, being tribosphenic or pseudo-tribosphenic: the Australian Ausktribosphenidae (Rich et al., 1997, 1999, 2001), *Ambondro* from Madagascar (Flynn et al., 1999); and the Patagonian *Asfaltomylos* (Rauhut et al., 2002).

Some features of gondwanatheres merit discussion: molar teeth have been interpreted as having three rows of anteroposteriorly aligned cusps on the uppers and two on lowers (Krause et al., 1992). Arguing against gondwanathere affinities: gondwanathere molars have well-developed transverse ridges and furrows (cusp rows connected by ridges: Krause et al., 1992); cheekteeth are hypsodont and not divisible into premolars or molars (von Koenigswald et al., 1999); molars are longer than wide (Kielan-Jaworowska and Bonaparte, 1996); cusp number per row is high (Krause et al., 1992); enamel is grooved at the bases of the cusps, as in multituberculates (Krause et al., 1992); the posterior lower premolars are enlarged (Kielan-Jaworowska and Bonaparte, 1996) rather than presumably reduced in *Kollikodon* (as in the upper dentition); M1 is large relative to M2 (Krause et al., 1992); and wear is anteroposterior, indicating propalinal jaw action (Krause et al., 1992). A recently discovered, poorly preserved unnamed taxon from Tanzania is a possible gondwanathere: like other gondwanatheres it has hypsodont teeth and a large, angled, procumbent lower incisor (Krause et al., 2003). However, there are even greater differences between this form and *Kollikodon*: in addition to hypsodonty,
the posterior cheekteeth (of which there are five) appear to be single-rooted (Krause et al., 2003).

PHYLOGENETIC ANALYSIS

Data sets and character coding

In order to test relationships between Kollikodon and other mammals, parsimony analysis was conducted using PAUP. The analysis performed here employs the large data set for Mesozoic mammals of Luo et al. (2002) because it is by far the most comprehensive database available. It includes 46 Mesozoic taxa and 275 osteological and dental characters using parsimony analysis (Swofford, 2000; Luo et al., 2000).

Luo et al.’s (2002) data matrix for an unconstrained search was used in this analysis. Luo et al.’s results using an unconstrained search separated Haramiyida and Multituberculata (their Fig. 1, p. 14). Multituberculata was found to be closely related to Trechnotheria (spalacotheriids + crown therians) and Haramiyida formed a basal clade with tritylodontids in Luo et al.’s most parsimonious tree (Fig. 1). In a constrained search based on dental characters (Fig. 2), Luo et al. (2002) found that Haramiyida and Multituberculata formed a clade. The two trees obtained by Luo et al. (2002) did not differ significantly from each other; Luo et al. chose the optimum tree (Fig. 1) but state that tree lengths between the two resultant cladograms were close (differing by only about 0.6% of total tree length).

The only changes to the characters used by Luo et al. (2002) other than the inclusion of Kollikodon are the addition of new (uniquely derived) character states for Kollikodon (characters 43, 88, 91 and 92). Although there have been challenges to some characters in the original database of Luo et al. (2002) (e.g., Woodburne et al., 2003), it is used in its original form in this analysis in order to test Kollikodon against the results obtained by Luo et al. (2002).

Mandible

Four characters of the mandible from the data set of Luo et al. (2002) have been coded for Kollikodon; these include characters 4 (curvature of Meckel’s groove); 5 (degree of development of Meckel’s groove); 7 (presence or absence of the groove for the dental lamina); and 14 (splenial as a separate element). This information is either present on the holotype or may be inferred from the information present on the holotype. Characters 3 (ridge above postdentary trough); 6 (mandibular symphysis); 8-10 (characters for the angular process); 11 (coronoid); 12 (mandibular foramen); and 13 (fossa for reflected lamina of
angular) are not coded for because this information is missing from the *Kollikodon* lower jaw.

**Character 4:** curvature of Meckel's groove (under tooth row) in adult (sensu Luo 1994). This is coded as (1) ‘present and convergent to the ventral border of the mandible’ in *Kollikodon*.

**Character 5:** degree of development of Meckel's groove in adults. This character has been coded as (0) ‘well developed’ in *Kollikodon*.

**Character 7:** groove for replacement dental lamina (Crompton and Luo 1993; Luo 1994). This feature appears to be absent in *Kollikodon* (1) and is scored as such. As mentioned in the Description (see above), there is some delamination of the bone near the alveolar border on the medial side of the jaw in *Kollikodon* but it was probably not present on this specimen.

**Character 14:** the splenial as separate element (as indicated by its scar on dentary) in adult. The flattened area on the medial side of the jaw is a prominent feature and a decision has been made for this analysis to code *Kollikodon* as having had a separate splenial bone (0). However, there is difference of opinion on this feature (see Description) and it may be that the alternative interpretation – that the splenial was absent – is the correct one.

**Character 20:** anteroventral extension of the masseteric fossa. This is coded (0) in *Kollikodon* because the jaw shows no extension of the mandibular fossa anterior to where the ultimate molar would have been had it been present.

### Molar morphology

The first set of characters below (characters 38, 39, 42, 43, 51, 52, 55, 57, 58, 76, 84, 87, 88) pertain to general molar morphology exclusive of whether the dentitions are multicuspid or otherwise.

**Character 38:** alignment of cusps on lower molars. *Kollikodon* is coded as having (3) multiple longitudinal muticuspatate rows on the lower molars.

**Character 39:** alignment of main cusps of M₁. *Kollikodon* is coded as possessing (2) multiple longitudinal rows wherein the main cusps of M₁ are aligned anteroposteriorly.

**Character 42:** presence or absence of precise occlusion. *Kollikodon* has been coded (1) ‘present (one-to-one or occluding at opposing embrasure or talonid’ rather than (2) ‘present: one molar sequentially contacts more than one upper molar’ (as in tritylodontids, *Haramiyavia* and multituberculates) because I have interpreted (2) to mean a degree of posterior movement of the jaw, which does not appear to be present in *Kollikodon*. 

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Character 43: occlusal relations between upper and lower molars. This is a new character state (5) added to the analysis: ‘lower multicuspate rows occlude opposite upper multicuspate rows.’ The upper molars occlude just posterior to the lower molars (rather than alternately) in Kollikodon, similarly to the occlusion of morganucodontids, docodonts and triconodonts (whereby molars are closer to being opposite than alternate: Crompton and Jenkins, 1968) but differs in that tooth form – multicusped rows – differs and cusp homologies in Kollikodon can’t be determined with absolute certainty.

Character 51: labiolingual compression of the primary functional cusps of the lower molars. This is coded (0) absent in Kollikodon because there is no compression of the primary functional cusps; in fact the opposite is true: cusps are expanded.

Character 52: posterior lingual cingulid of lower molars. Kollikodon is coded (0) ‘absent or weak’ for this character because the lower molars lack posterior lingual cingulids.

Character 55: mesial transverse cingulid above gum. A mesial transverse cingulid above the gum is not developed in Kollikodon so is therefore coded (0) ‘absent.’

Character 57: distal transverse cingulid. There is likewise no distal transverse cingulid on the lower molars of Kollikodon and this character is therefore coded (0) ‘absent.’

Character 58: interlocking mechanism between two adjacent lower molars. This character, interlocking of adjacent lower molars, is coded (0) ‘absent’ in Kollikodon. Although the lower molars are tightly imbricated they do not interlock in the manner described.

Character 76: morphology of labial cingulum of upper molars. There is no labial cingula on the labial upper cusp row in Kollikodon and it is therefore coded (0) ‘absent.’ The labial and lingual cusp rows in Kollikodon may have been derived from cingula but that is an hypothesis and not able to be accounted for here.

Character 83: upper molars cuspule E. Kollikodon is coded (1) ‘absent’ for this character (as are tritylodontids, Priacodon, Trioracodon, Haramiyavia and multituberculates) because, like the other taxa with multicuspid dentitions, cusp homologies are uncertain in Kollikodon.

Character 84: upper molars interlock. As with character 58 (interlocking mechanism between two adjacent lower molars), upper molars in Kollikodon are imbricated but not interlocked, so this is coded (0) ‘absent’. This character is one that separates Priacodon and Trioracodon from all other taxa because they show a ‘tongue-in-groove’ interlock absent in other mammals or near-mammals.

Character 87: outline of M1. The lower molars of Kollikodon are nearly square (marginally longer than wide). The character state (5) ‘(M1) rectangular (or slightly rhomboidal)’ should accommodate the description of the lower molar shape in Kollikodon because they are slightly elongate rather than perfectly square (=rectangular).
Character 85: \( M^1 \) - number of cusps within the main functional straight cusp row. There are either two or three cusps in upper molar rows in Kollikodon so it is coded (0) ‘three main functioning cusps or fewer within a row.’

Character 86: multicuspate \( M^1 \) - number of cusps within the main functional straight multicusp row. Lower molars in Kollikodon have two cusps per row so it is coded (0) ‘three main functioning cusps or fewer within a row.’

Character 89: cusp height gradient in the upper molars. Upper molar cusps of Kollikodon are almost uniformly equal in height (particularly in the lingual and median rows) so Kollikodon is coded (0) ‘cusps in a row with more or less equal height.’

Character 90: presence or absence of U-shaped ridge on lower molars. Possession of a U-shaped ridge is a uniquely derived feature of Haramiyida (e.g., Butler, 2000) and is used by Luo et al. (2002) to distinguish Haramiyida or their relations from taxa without this feature. Kollikodon is coded (0) ‘U-shaped ridge (anterior crest) absent at mesial end of lower molar with open valley-basin between longitudinal cusp rows.’ The longitudinal grooves separating cusp rows in Kollikodon are here considered to be the essentially the same as ‘open valleys’; the semantic differences between ‘groove’ and ‘open valley’ do not seem significant enough to warrant a separate character state.

Character 91: multicuspate \( M^2 \) with lingual offset with \( M^1 \). This character has been included in the database of Luo et al. (2002) because it is considered a unique feature setting Multituberculata apart from other taxa with multicusped rows. Kollikodon is given a new character state (2) ‘upper \( M^2 \) labial row occludes to medial side of \( M^2 \) labial row.’

Tritylodontids and Haramiyavia are coded [0] ‘upper \( M^2 \) lingually offset from \( M^1 \) so that the lower \( M^2 \) lingual row occludes the lingual side of the \( M^2 \) upper labial row’ but in Kollikodon the cusps on the molar rows more or less oppose each other (‘positive-on-positive’).

Character 92: cusp height ratio within the labial longitudinal row on lower molars. This character has been given a new state for Kollikodon: (2) ‘both cusps equal’ because neither the first state (0) ‘second cusp highest’ or (1) ‘second cusp highest’ is applicable to
One of the most striking things about the molar morphology in *Kollikodon* is the uniform height of the cusps, which appears to be uniquely specialised.

Many of the dental characters analysed by Luo et al. (2002) are relevant only to taxa with dentitions characterised by reversed triangulation of molar cusps with well differentiated trigonids and talonids: characters 40 (presence or absence of postvallum/prevallid shearing); 41 (development on postprotocrista on upper molar for double rank postvallum shear); 44 (relative height of protoconid to metaconid of anterior lower molars); 45 (relative size/heights of paraconid to metaconid based on M₂); 46 (elevation of cingulid base of paraconid relative to that of metaconid); 47 (presence, absence and orientation of cristid obliqua); 48 (‘pre-entocristid’ or ‘pre-hypoconulid’ on talonid heel); 49 (labial curvature of primary cusp a of lower molars relative to that of cusps b and c); 50 (labial curvature of main cusps A, B, C); 53 (presence or absence of mesiolingual cingular cusp (e) on lower molars); presence or absence of mesiolabial cingular cuspule (f) [homologies uncertain for *Kollikodon*]; 56 (presence or absence of wrapping cingulum around anterointernal corner of molar and degree of development); 60 (trigonid configuration on lower molars [as for Tritylodontidae, Haramiyida and Multituberculata, the posterior halves of the lower molars in *Kollikodon* may not be true talonids and talonid characters are therefore coded ‘non-applicable’]); 61 (orientation of paracristid relative to long axis of molars); 62 (conformation of mesiolingual surface of paraconid); 63 (lower molar trigonid/talonid width ratio); 64 (lower molar hypoflexid); 65 (talonid morphology); 66-69 (hypoconulid characters); 70-71 (entoconid characters); 72 (alignment of triangulated cusps); 73-74 (proportions of talonid); 75 (stylar shelf); 78 (width of protocone); 79 (distances between triangulated cusps); 80 (conules); 81 (relative heights of paracone, metacone); and 82 (centrocrista). For these characters *Kollikodon* is given (-) ‘non-applicable’ as for tritylodontids, haramiyids, ‘plagiaulacidans’ and cimolodontans (multituberculates) (Luo et al., 2002).

**Molar wear patterns**

**Character 93:** functional development of occlusal facets on individual molar cusps. *Kollikodon* is coded (1) ‘(occlusal facets) absent at eruption but developed later by wearing of the crown’ because occlusal facets are present in *Kollikodon* but do not appear to have been present upon eruption; these wear facets were almost certainly formed through cusp-on-cusp wear after eruption of the molars.

**Character 94:** topographic relationship of wear facets to the main cusps. *Kollikodon* is coded as (3) ‘multicuspathe series, each cusp may support two wear facets’; most cusps in
Kollikodon support only a single, apical wear facet but some cusps do have two facets (the posteromedial cusp on the lower first molariform ?premolar).

Other dental features

This section of the analysis includes additional dental characters not coded for in the sections above.

Character 110: number of lower molars or molariform postcanines. As discussed above (see Description), there is a strong likelihood that the first molar-like teeth in both upper and lower jaws in Kollikodon are molarised premolars rather than true molars. This character, therefore, has been given the coding (2) ‘three molars or fewer’ although the possibility remains that there are four molars rather than three.

Character 111: lower postcanine roots. The presence of two or more roots on the lower postcanines (rather than a single root) is a mammalian character used to distinguish cynodont teeth from those of near-mammals (some of which have incipient root division: Character (0)) and those of ‘true’ mammals (which have at least two, completely divided roots per postcanine: ref). The lower postcanines in Kollikodon appear to have two very robust roots apiece; Kollikodon is therefore coded as (1) ‘roots divided’ for this character.

Palatal, orbital and zygomatic characters

Most of the cranial characters in Luo et al. (2002) can’t be coded for Kollikodon because of lack of information or material. However, the section of maxilla described above does have a few palatal and orbital characters in this section of Luo et al.’s analysis that can be assessed (characters 237; 238; 243; 249; 250). Characters that cannot be coded for in this section includes characters 239 (presence or absence of pterygopalatine ridges); 240 (presence or absence and relative size of the transverse process of the pterygoid); 241 (conformation of the basisphenoid costricture); 242 (morphology of the vault of the naso-oral pharyngeal passage near the pterygoid-basisphenoid junction); 244 (pattern of the orbital mosaic as exposed externally); 245 (presence or absence of the overhanging roof of the orbit); 246 (outline of the facial part of the lacrimal); 247 (presence or absence of the pila antotica in the adult); and 248 (contact of the frontal-parietal suture on the alisphenoid). The maxilla has not preserved assessable or codable material for these characters.

Character 237: bony secondary palate. This character has been used to differentiate cynodonts from Mammalia (mammals excluding multituberculates with secondary palates extending at least to the end of the molar row: e.g., Luo et al., 2002) and has generally been
a reliable indicator of mammalian status. However, an advanced cynodont (a South American ictidosaur) has recently been found with a secondary palate reaching the end of the molar row (Bonaparte et al., 2001). In *Kollikodon* the palatine is broken at a point just posterior to the molar row; it therefore must have continued past the end of the molar row. It is therefore coded as (2) ‘extending posterior to the tooth row’.

**Character 243:** complete ossification of the orbital floor. The maxilla in *Kollikodon* forms the orbital floor in *Kollikodon* (and is exceptionally deep) so this is coded (1) present.

**Jaw characters**

**Character 274:** direction of jaw movement during occlusion. *Kollikodon* has been coded (0) ‘dorsomedial movement (as inferred from teeth)’. This is deduced by the conformation of the wear facets on the apices of the cusps of the molars; by the apparent lack of striations on the wear facets indicating a propalinal or strongly transverse component to the masticatory stroke; and by occlusion of the upper and lower molars: they are in centric occlusion when the two cusp rows on the lowers occlude with the lingual and median cusp rows of the uppers. This indicates a primarily orthal (or dorsal) masticatory stroke (see Description above). This is usually correlated with bilateral (rather than unilateral) jaw action, a feature coded for in Character 275 (bilateral vs unilateral occlusion, correlated with either a rigid or a mobile symphysis). However, the symphysis of the jaw in *Kollikodon* is not preserved and it would be premature to code *Kollikodon* for this character in this analysis.

**Equivocal characters and characters coded as ‘not preserved’**

Character 2 (separate scars for surangular-prearticular in Meckel’s groove and postdentaly trough) was not included in the analysis of *Kollikodon* although there is a groove on the mandible that may be for the prearticular in Meckel’s groove. This has not been firmly established (the groove in question may simply be a groove in the vicinity of Meckel’s groove) so character 2 is not used.

*Kollikodon* was coded (?) ‘not preserved’ for the following sections because either *Kollikodon* has not preserved the information being assessed; or the dental, craniomandibular or postcranial elements have not been recovered: *Lower premolars* (characters 27-37) (although Character 35 is for the upper premolar, which *Kollikodon* has preserved, character 35 is non-applicable because it is for taxa with triangulated dentitions); *Vertebrae* (characters 119-127); *Shoulder girdle* (characters 128-143); *Forelimb* (characters 144-155); *Pelvic girdle* (characters 156-158); *Hind limb* (characters 159-169); *Ankle joint* (characters 170-179); *Other postcranial characters* (characters 180-181); *Basicranium* (characters 182-227); *Incus (quadrates)* (characters 228-236); Palatal, orbital and zygomatic characters (characters
238-242; 244-250); Occipital and other skull characters (characters 251-263); and Cranial vault and brain endocast characters (characters 264-273).

Results

PAUP Version 4.0b (Swofford 2000) was used to replicate the original results of Luo et al. (2002) using the data matrix provided online (Acta Palaeontologica Polonica archives: Luo et al. 2002(1)). Luo et al. (2002) used unordered characters to obtain their preferred trees, the benefit being that these involve no a priori assumptions about the direction of the evolution of characters. The tree presented here (Fig. 11) was first run without the addition of Kollikodon (to ensure the results obtained matched those of Luo et al.) and the program rerun with Kollikodon included. Fig. 11 shows a strict consensus of 252 most parsimonious trees, with tree topology based on 100 replicates of an heuristic search (random addition sequence; TBR branch swapping).
Fig. 11: Phylogenetic relationships of Kollikodon as determined by parsimony analysis using the data matrix of Luo et al. (2002) (strict parsimony from unconstrained search). Statistics for the 252 most parsimonious trees: length = 897; CI = 0.4715; RI = 0.7615. Multistate characters unordered; PAUP 4.0b5 heuristic search (stepwise addition) 100 replicates. Bars indicate
Monotremata; and 2) a clade comprised of Kollikodon + Haramiyida-Multituberculata (Allotheria sensu Butler, 2000).

The cladogram obtained here unites Kollikodon in a clade with other mammalian taxa with multicusp dentitions, Haramiyida + Multituberculata, to the exclusion of cynodonts (Tritylodontidae) with such dentitions. It also retrieves a monophyletic Allotheria comprised of Haramiyida and Multituberculata, as sister taxon to Kollikodon. These results 1) place Kollikodon as a near relation of Allotheria sensu Butler 2000 or as a member of Allotheria (pending a revision of the diagnosis used by Butler 2000; see Discussion); 2) support the concept of Allotheria (sensu Butler 2000) and a close relationship between Haramiyida and Multituberculata; and 3) cast doubt on a close relationship between Kollikodon and monotremes or placement of Kollikodon within Monotremata.

GENERAL DISCUSSION

Acquisition and analysis of the maxilla and upper dentition of Kollikodon ritchiei has greatly improved knowledge of this Early Cretaceous mammal. Detailed comparisons of the palatal region, dental morphology and molar occlusion are now possible. It must be emphasized, however, that discovery of additional new material could alter the interpretation presented here, compiled on the basis of a limited amount of material.

Unique derived features of Kollikodon not seen in other Mesozoic mammals include 1) three well-developed cusp rows on upper molars separated by longitudinal grooves; 2) extreme bunodonty on molar teeth; 3) distinct curvature of upper and lower molar rows; 4) a second (posterior) opening of the greater (major) palatine foramen onto the palate; 4) crescentic upper molars; and 5) primarily orthal, positive-on-positive crushing (positive-on-positive action differing from negative-positive crushing in Haramiyida: Butler, 2000; puncture-crushing as proposed for the haramiyid Haramiyavia: Jenkins et al., 1997; or grinding or shearing of other Mesozoic mammals: e.g., Jenkins et al., 1997). The functional significance of this suite of apomorphic characters – a bunodont crushing dentition capable of exerting great force – supports the contention by Flannery et al. (1995) that Kollikodon was a specialist on molluscs.

Dental morphology

The distinctive molar teeth of Kollikodon share many features with Tritylodontoidea, Haramiyida and Multituberculata: multiple rows of cusps aligned in an anteroposterior direction separated by grooves or valleys; generally wide uppers and narrower lowers; and weak or absent cingula. Unique features of the dentition of Kollikodon include crescentic upper molars; an unusual degree of bunodonty, as mentioned; the strong development of the buccal cusp row (not seen in Haramiyida or Multituberculata); and a convex/concave curvature of the jaws. The
main cusp of the single preserved upper premolariform tooth is aligned with the centre row of cusps in the molariform tooth row, suggesting cusp homologies between the median upper cusp row and the primary cusp of the premolar.

The first upper molariform in *Kollikodon*, as described above, may be a specialized molariform premolar. Specialization of the ultimate premolar is very uncommon in Mesozoic mammals; most early mammals have generalized premolars even if the molars are specialized (e.g., Heinrich, 1999). Haramiyids (*Thomasia* [tooth group II]: Sigogneau-Russell 1989; and *Staffia*: Heinrich, 1999) have molarized lower posterior premolars, with cusps in two parallel longitudinal rows.

Possession of more than two roots on the uppers of *Kollikodon* may represent convergence with forms that have wide upper molariform teeth; alternatively, it may suggest phylogenetic relationship. Tritylodontids and docodonts (e.g., Kron, 1979) in addition to Tertiary monotremes (Woodburne and Tedford, 1975; Archer et al., 1992, 1993; Musser and Archer, 1998) also have more than two roots on the upper teeth. It seems probable that multiple roots developed at least in part in concert with wide upper molars to provide adequate support.

**Occlusion and dental function**

The occlusal pattern in *Kollikodon* in which upper molars close opposite (or nearly so) to lower molars is very unusual in early mammals; most Late Triassic-Early Jurassic mammals have upper molars that alternately occlude between lower molars (Crompton and Jenkins, 1968). Alternate occlusion (intermolar occluding position) was present in cynodonts (e.g., *Thrinaxodon*) and inherited by cynodont descendants including symmetrodont (and subsequently therian) mammals (Crompton and Jenkins, 1968). Opposite occlusion is seen in the morganucodontid *Eozostrodon*; to a lesser extent in docodonts (*Haldanodon* and *Docodon*) (Crompton and Jenkins, 1968); in haramiyids (Jenkins et al., 1997; Butler, 2000); and multituberculates (Krause and Hahn, 1990).

Crown-to-crown occlusion (occlusal contact between upper and lower molar surfaces) is also rare in early mammals. In almost all vertebrates (including early mammals such as *Morganucodon*) upper molars bite buccally to lower molars (e.g., Butler and MacIntyre, 1994). Crown-to-crown occlusion developed in tritylodontids, docodonts, haramiyids, multituberculates, monotremes, tribosphenic therians (e.g., Butler, 1988) and *Kollikodon*. Crown-to-crown occlusion occurs with expansion of upper molar area so that upper molars overlap lowers, establishing contact. Docodonts accomplished this through internal (lingual) expansion of the internal cingulum of upper molars, which in turn led to complex relationships (adding shearing surfaces) as in therian molars (Mills, 1966; Crompton and Jenkins, 1968). In much the same way, additional shearing surfaces were added to the molars of gomphodont
cynodonts where internal expansion of the upper postcanines completely overlapped lower postcanines (Crompton, 1968b).

Determination of jaw motion is an important factor in assessing phylogenetic affinities. Bilateral jaw action, whereby both left and right jaws occlude in unison, is the primitive reptilian mode of jaw closure usually accomplished with an up-and-down action (orthal jaw action) (e.g., Butler and MacIntyre, 1994). Jaw motion in *Kollikodon* was almost certainly bilateral and primarily orthal (the molar rows crushing more or less in unison) with a small transverse component to allow contact with the buccal cusp rows. Bilateral jaw movement is often correlated with fusion of the symphysis of the lower jaw (e.g., Luo et al., 2002), as in the majority of advanced cynodonts (Hopson and Kitching, 2001). Discovery of additional material will hopefully determine if this were the case in *Kollikodon*.

There do not appear to be anteroposteriorly directed striations on the molars in *Kollikodon* indicating propalinal motion (see Description and Fig. 9); in addition, the curvature of upper and lower jaws and height of the primary cusp a on the first lower molariform would have prohibited fore-and-aft movement. Flattened wear facets also indicate a powerful up-and-down force on the molars (Fig. 9). The need for optimum power or leverage when crushing hard materials suggests that orthal/bilateral rather than transverse movement would be the primary masticatory stroke (with possibly some transverse action causing wear on the buccal cusp row, perhaps when teeth were not in occlusion but separated by food). This could be a secondarily derived condition for the crushing of shells; alternatively, it could represent a plesiomorphic retention in *Kollikodon* utilized in a specialized way.

Unilateral jaw movement, whereby the upper jaw moves across the lower jaw in a transverse direction, allows more complex jaw movements and evolved with the development of triangulated dentitions (e.g., Kermack and Kermack, 1984). *Morganucodon* (and related forms), *Docodon* (Crompton and Jenkins, 1968) and haramiyids generally lack transverse motion: in haramiyids, ‘the longitudinal cusp rows would prevent any significant transverse movement’ (Butler, 2000: p. 323). Transverse movement in Haramiyida was only possible when teeth were not in occlusion (Butler and MacIntyre, 1994), as may have been the case with *Kollikodon*. Sigogneau-Russell (1989) noted that abrasion at the tops of cusps A and B in Haramiyida is sometimes inclined marginally (= in opposite directions), which may imply transverse movement could occur when teeth were separated by bulky food.

Apical cusp wear, creating pits on molar cusps, is a distinctive feature in *Kollikodon*. It differs from the shear facets on the lateral flanks of teeth that developed in mammals like *Morganucodon* (Crompton and Jenkins, 1968; Mills, 1971) and from the shearing surfaces developed on tribosphenic teeth (Crompton, 1971). Apical wear on the tops of cusps is seen in haramiyids, where tooth-on-tooth contact produces flat or cylindrically concave surfaces that
are usually smooth but often have parallel striations (indicating backward motion) (Butler and MacIntyre, 1994). There is also abrasive wear from contact with food, producing the rounding and eventual removal of cusps (Butler and MacIntyre, 1994). Wear in haramiyids is not consistent, as it is in therians (Butler and MacIntyre, 1994); wear in *Kollikodon* is likewise inconsistent. Abrasive wear at apices of cusps leads to removal of the outer enamel to expose dentine (Butler and MacIntyre, 1994; Sigogneau-Russell, 1989), as seems to be the case in *Kollikodon*. Haramiyids also have non-horizontal wear (40° to the base of the enamel) (Butler and MacIntyre, 1994) as in *Kollikodon*. Apical wear is seen in the haramiyid *Staffia aenigmatica* from Tanzania: ‘apices of all cusps lack their enamel’ and there are ‘triangular or rounded facets on tips’ (Heinrich, 1999). Some multituberculates also show apical pitting (e.g., *Loxaulax*: Clemens and Lees, 1971).

Precise occlusion appears to be lacking in *Kollikodon*: upper cusps do not match lower cusps on a cusp-by-cusp basis. In some cynodonts, *Morganucodon* and possibly *Sinoconodon*, precision was attained through wear: matching shearing planes were developed as the teeth were used and triangulated planes developed; shear was consequently not well developed in unworn teeth (Crompton and Jenkins, 1968). Occluding teeth with matching shear facets were not present until the appearance of early therians and Late Jurassic triconodonts, occlusal surfaces of the teeth matched on eruption (Parrington, 1967; Crompton and Jenkins, 1968). In acute-angled symmetrodonts and therians (as well as advanced gomphodont cynodonts) the pattern of facets (=shear) was therefore genetic rather than mechanical and was thus a major advancement (Crompton and Jenkins, 1968). The molar cusps of *Kollikodon* do not appear to be precisely matched even if worn; upper and lower cusps do not match (although the maxilla and lower jaw were not found in association, it nonetheless is probable that the cusp pattern on both is fairly representative for the species).

**Palatal and maxillary form**

The maxilla in *Kollikodon* resembles that of monotremes, with an expansion around the molar row. This might not be a unique morphology; *Haldanodon* is described as having the lateral edge of the maxilla close to the wide molar row (Lillegraven and Krusat, 1991). The maxilla is not expanded in either multituberculates (e.g., Kielan-Jaworowska, 1971; Miao, 1988) or *Morganucodon* (Kermack et al., 1981). A maxillary sinus, which (if interpreted correctly) may be present in *Kollikodon*, is considered a unique feature in *Haldanodon* that is absent in *Morganucodon* (Lillegraven and Krusat, 1991) and monotremes (pers. obs.). A maxillary sinus is either not described or not present in most Mesozoic mammals (Lillegraven and Krusat, 1991).
The position of the root of the zygomatic arch in *Kollikodon* appears to be similar to that in several early mammals (e.g., *Morganucodon*: Kermack et al., 1981; *Haldanodon*: Lillegraven and Krusat, 1991), projecting laterally from between the middle of the molar row. It is in contrast to multituberculates, where the zygoma project lateral to the premolars (e.g., Kielan-Jaworowska, 1971) or between the premolar and first molar (e.g., Miao, 1988) because of the posterior position of the molar teeth. In monotremes (Ornithorhynchidae) the zygomatic arch is directed posteriorly rather than laterally, appearing in ventral view to project posterior to the molar teeth (e.g., Musser and Archer, 1998). The zygomatic arch in *Kollikodon* is deep and narrow, a difficult character to assess but which seems substantial and therefore primitive: a robust zygomatic arch is considered plesiomorphic for Mammalia (Wible, 1991).

The moderately vaulted palate in *Kollikodon* differs from the flat palates in monotremes (pers. obs.), *Haldanodon* (Lillegraven and Krusat, 1991) and probably multituberculates (judging from stereo photographs of *Kamptobaatar* and *Sloanbaatar*: Kielan-Jaworowska, 1971). *Morganucodon* has a fairly well vaulted palate (Kermack et al., 1981).

Some details of the palate in *Kollikodon* are like that in *Morganucodon* (i.e., the presence of a well-developed palatine tubercle and presence of a lesser palatine groove) (Kermack et al., 1981) but most early mammals are either not described in such minute detail or have not preserved complete palates. The palates in monotremes (Ornithorhynchidae and Tachyglossidae) show no signs of palatal tubercles or grooves.

**Conformation of lower jaw**

The lower jaw of *Kollikodon* appears to be quite primitive in form; a large splenial comprising a separate element on the lower jaw in adults is a plesiomorphic feature in mammals (e.g., Luo et al., 2002). Jaw development might have been similar to that of *Haramiyavia*, where accessory jaw bones were somewhat larger than in *Morganucodon* (Jenkins et al., 1997; Luo et al., 2002).

The course of the meckelian groove has been considered phylogenetically useful (e.g., Luo et al., 2002). The plesiomorphic condition (found in cynodonts) is one in which it runs parallel to the ventral border of the mandible (per Luo et al., 2002). Cynodonts, primitive stem mammals (*Sinoconodon; Haldanodon*), ‘triconodonts,’ ‘symmetrodonts’ and other holotherians have a meckelian groove parallel to the lower margin of the mandible (Luo et al. 2002) as does *Steropodon* (Luo et al., 2002; abstract, Musser 2005) and *Haramiyavia* (Luo et al., 2002). A meckelian groove convergent on the ventral border of the mandible is considered derived by Luo et al. (2002) and is seen in *Morganucodon*, the docodonts *Megazostrodon* and *Dinnetherium*, the primitive ?holotherian *Kuehneotherium*, the ‘triconodont’ *Amphilestes*, the ‘symmetrodont’ *Tinodon*, the pseudo-tribosphenic *Shuotherium* and *Ausktribosphenos*, and the
‘eupantheres’ Amphitherium and Peramus (Luo et al., 2002). According to some (G.W. Rougier, pers. comm.), convergence may be primitive and is common. Although of interest, therefore, perhaps this character is not significant.

Kollikodon has a dental canal of moderate size, comparable to that of most Mesozoic mammals for which this feature is described or illustrated (e.g., Morganucodon: Kermack et al., 1973). The size of the mandibular canal running through the centre of the dentary is a significant character when assessing affinities with monotremes. An enlarged mandibular canal is a key synapomorphy for Monotremata (with the exception of echidnas, which have a very reduced lower jaw) (Musser, 2003; Rich et al., 2005). The absence of a large mandibular canal in Kollikodon suggests that it is not closely related to monotremes (see below).

Body size

Kollikodon ritchiei is comparatively large for a Mesozoic mammal. Judging from the size of its molars (the upper molar row measures 19mm in length), Kollikodon would have had a head length of (very) roughly 5cm (head-body length estimate: less than 20 cm). Non-eutherian mammals are considered ‘large’ if either the length or width of crowns of the cheek teeth exceed 5.0mm (Clemens et al., 2003); the widest molar crown in Kollikodon, M3, measures about 9.0mm across its widest point.

When Kollikodon was described in 1995 it was one of the largest Early Cretaceous mammals known (Flannery et al., 1995). Other large Early Cretaceous mammals include Steropodon galmani (Archer et al., 1985), which was roughly the size of a small platypus (Musser, 2003; not ‘cat-sized’ as has been described); the triconodonts Gobiconodon (an opossum-sized mammal from the Early Cretaceous of Montana: Clemens et al., 2003) and the recently discovered Repenomamus giganticus (a badger-sized mammal from the Early Cretaceous of China: Hu et al., 2005).

The relatively large size of Kollikodon (as with Steropodon) is attributed to the cool temperate environment of Lightning Ridge at the time of deposition (Flannery et al., 1995). Large size is often equated with cooler habitats (Bergman’s Rule). A mammal the size of Kollikodon would be able to take advantage of the molluscs found at Lightning Ridge, many of which would have been of a good size for a mammal the size of Kollikodon.

Mammalian characteristics

Several features of the dentition and orbito-palatal region suggest that Kollikodon had reached a post-cynodont or basal mammalian level: 1) premolars differentiated from molars (Hopson and Barghusen, 1986; Rowe, 1988); 2) postcanine teeth with divided roots (convergent with Tritylodontidae: Hopson and Barghusen, 1986; also Hopson and Crompton, 1969;
Crompton, 1974; Crompton and Jenkins, 1979; Crompton and Sun, 1985); 3) a bony secondary palate either level with or posterior to the posterior end of the upper tooth row (Rowe, 1988; Luo et al., 2002); 4) orbit floored by maxilla (Rowe, 1988); 5) well-developed infraorbital canal with posterior opening (from Miao, 1988); and 6) a meckelian sulcus forming a medial groove in the adult (Rowe, 1988). Mode of occlusion, form of the lower jaw and certain palatal features shared between basal mammals such as morganucodontids and Kollikodon are not seen in more advanced mammals. Kollikodon is therefore most likely at a basal position within Mammalia (‘Mammaliaformes’ of some authors [e.g. Rowe, 1988; Wible, 1991]; basal Mammalia of others [e.g., Miao, 1991; Luo et al., 2002]). The dental pattern of Kollikodon has few if any similarities to the triangulated molar pattern of basal therian mammals; plesiomorphic jaw and palatal features also suggest Kollikodon is not derived from an advanced, therian lineage. Therian relationships, therefore, are not considered further.

Some characters seen in Kollikodon are somewhat cynodont-like and are of interest given the basal position proposed for Kollikodon. These include 1) lack of consistently developed wear facets (although this may be a specialization); 2) possibly a large splenial present on the medial side of the lower jaw in life. Results of this study suggest, however, that in spite of some remarkable dental similarities between Kollikodon and tritylodontid or traversodontid cynodonts, Kollikodon is not closely related to or probably descended from these reptiles. Differences between Kollikodon and tritylodontids, aside from the abovementioned mammalian characteristics, include mode of mastication (‘filing’ or grinding in tritylodontids vs. crushing in Kollikodon) and several features of the palatal and mandibular region (see Comparisons and Discussion).

RELATIONSHIP HYPOTHESES

Within Mammaliaformes or non-therian Mammalia, possible sister taxa to Kollikodon include Haramiyida and Multituberculata (as suggested by the results of the phylogenetic analysis presented here) and Monotremata (as originally proposed by Flannery et al., 1995). Docodonta is of interest because of several features that might have phylogenetic significance to this study (see below) but its uniquely derived dentition seems to preclude an ancestor-descendant or sister-group relationship.

Monotreme affinities

The question of monotreme affinities in regard to Kollikodon is not a simple one. Some features in Kollikodon are monotreme-like and otherwise unusual in Mesozoic mammals: a sharp break in size between molar and premolar teeth (as noted by Flannery et al., 1995); the
correlated expansion of the maxilla around the molar row, seen in monotremes (pers. obs.) and possibly *Haldanodon* (Lillegraven and Krusat, 1991); and certain details of the dentition (e.g., degree of development of cusps or cuspules in the buccal molar row, also seen in theroteinids: e.g., Sigogneau-Russell et al., 1986; Butler, 2000). Crown-to-crown occlusion is rare, occurring in Haramiyida, Multituberculata, Docodonta and Monotremata (as stated above). Other features, particularly of the dentition, seem almost impossible to reconcile between *Kollikodon* and monotremes given the importance placed on shared, derived dental characters as indicators of relationship.

Cranial comparisons between *Kollikodon* and Monotremata must rely solely on the highly derived ornithorhynchids and tachyglossids since no earlier monotremes (i.e., *Steropodon* or *Teinolophos*) are known from skull material. Numerous morphological changes must have occurred in Monotremata since its origin; the discovery of possible accessory jaw bones in an archaic monotreme, lost in living monotremes (Rich et al., 2005) illustrates this point. Dental and mandibular comparisons can be made with *Teinolophos*, *Steropodon* and species of *Obdurodon*, all of which had a functional dentition and which are known from at least partial lower jaws (Rich et al., 2001, 2005; Woodburne and Tedford, 1975; Archer et al., 1985, 1992, 1993a; Musser, 2003, 2005 [abstract]; Musser and Archer, 1998; Pascual et al., 1992a, b; 2002).

All toothed monotremes have a dental pattern of reversed triangles characterized by V-shaped transverse lophs; unilateral occlusion; and a transverse component to the masticatory stroke (transverse shear is most well developed in ornithorhynchids). Orthal occlusion and a crushing dentition, as mentioned, might be seen as the plesiomorphic state for mammals (although crushing may also be considered derived). This appears to be a fundamental difference between monotremes and *Kollikodon* regardless of how and when monotremes developed transverse shear and unilateral occlusion.

Flannery et al. (1995) list several features of *Kollikodon* they consider to be monotreme-like: 1) an anteroposteriorly compressed $M_1$ trigonid that lacks a paraconid (‘autapomorphic among Mesozoic mammals’); 2) high, transverse loph-like trigonid and talonid blades (‘autapomorphic’); 3) a very large talonid (‘autapomorphic among pre-tribosphenic mammals’); 4) prominent anterior, posterior and buccal cingula (‘symplesiomorphic in mammals’); 5) abrupt discontinuity in size between the small ‘$P_2$’ (=ultimate premolar) and large $M_1$ (‘autapomorphic among Mesozoic mammals’) and 6) wide talonids without entoconids (‘autapomorphic among Mesozoic mammals’). They state that all of these features are present in *Kollikodon* (except transverse, loph-like blades) and infer from this that *Kollikodon* is monotreme. Assessing the characters individually, 1), 2), 3) and 6) presume that the molar pattern of *Kollikodon* was derived from the reversed triangle pattern of toothed monotremes. Additionally, it is difficult to see how the bunodont molars of *Kollikodon* could be described as
loph-like or blade-like. 4) is incorrect; *Kollikodon* lacks well-developed cingula on both upper and lower molariform teeth. Flannery et al. (1995) state further that ‘all cusps…are remnants of prominent buccal cingula with associated cingular cuspules on at least M1:2’; however, both cusp rows on lower molars – buccal and lingual - could not have been derived from buccal cingula. 5), change in size from large molariform teeth to smaller premolariform teeth is seen in docodonts (e.g., Lillegraven and Krusat, 1991) and therefore cannot be considered a monotreme synapomorphy.

Lower jaw form differs significantly between *Kollikodon* and Monotremata. Monotremes possess the following two synapomorphies of the lower jaw: 1) a large mandibular canal (Musser, 2003; Rich et al., 2005); and 2) a posterointernal process on the medial side of the jaw (Rich et al., 2005). The mandibular canal is not enlarged in *Kollikodon* (contra Flannery et al., 1995) which as described has a moderately sized mandibular canal. Presence of a posterointernal angle on the jaw cannot be determined in *Kollikodon* because the holotype lower jaw is missing that part of the mandible where this process would be expected. There do not appear to be any phylogenetically informative, undoubted maxillary, mandibular or dental synapomorphies shared exclusively by *Kollikodon* and monotremes, casting doubt on the identification of *Kollikodon* as a derived monotreme as proposed by Flannery et al. (1995).

Flannery et al. (1995) state that: ‘the conclusion that *Kollikodon ritchiei* is a monotreme depends on dental morphology’. I would suggest alternatively that, in light of the insights gained by study of the new material, the conclusion that *Kollikodon* is not a monotreme depends heavily on dental morphology. The dentition of *Kollikodon* is much more similar to that of multicusped forms – haramiyids, multituberculates or even tritylodontids - than it is to toothed monotremes in which the molar cusps are triangulated. However, unusual features of skull and dentition shared by *Kollikodon* and known monotremes may suggest a relationship between them at a deeper level, perhaps through a common ancestor shared with morganucodontids, docodonts and haramiyids (see below).

**Haramiyida**

Amongst basal mammals, dental similarities are strongest between *Kollikodon* and Haramiyida (in some cases closer to Haramiyoidea; in some features closer to Theroteinidae; see below). Cusp pattern of *Kollikodon* can tentatively be homologized with that of haramiyids (as proposed by Butler and MacIntyre, 1994) (Fig. 12). The lower jaw recovered for *Haramiyavia* is plesiomorphic, with comparatively unreduced accessory jaw bones (Jenkins et al. 1997), as proposed here for *Kollikodon*.

Shared derived features for the order Haramiyida not present in *Kollikodon* include 1) molars in which the highest cusp is towards the distal end in the upper lingual row and towards
the mesial end in lower rows (reversed buccolingually and anteroposteriorly as in many rodents: a very derived pattern: Butler and MacIntyre 1994); 2) a high distal lingual upper cusp that occludes in the longitudinal valley of the lower molar and a high mesial buccal lower cusp that occludes in the longitudinal valley of the upper molar; and 3) a U-shaped ridge (Butler 2000).

There are some similarities between Haramiyoida and *Kollikodon* to the exclusion of Theroteinidae: occlusion (alternate in *Theroteinus*) (Butler, 2000) is nearly opposite in Haramiyoida (Butler, 2000). Some features are shared with Theroteinidae to the exclusion of Haramiyoida include development of bunodonty/apical wear (Butler and MacIntyre, 1994; Hahn et al. 1989; Sigogneau-Russell et al. 1986); and possibly a dentition specialized for crushing of hard objects (hard, brittle seeds; probably not soft fruits per Hahn et al. 1989 according to Butler and MacIntyre, 1994).

Derived characters present in *Kollikodon* but absent in Haramiyida include possession of well-developed third (buccal) rows of cusps; crescentic (rather than oblong) molars; and curvature of the upper and lower jaws. There are few characters other than dental ones that can be compared between *Kollikodon* and Haramiyida, as discussed. Certain characters known in Haramiyida cannot be determined in *Kollikodon*, in part because of the nature of its preservation. Enamel microstructure, a key difference between Theroteinidae and Haramiyidae (Butler 2000) can’t be determined in *Kollikodon* because of the nature of its preservation (enamel microstructure is not preserved in an opal pseudomorph).

**Multituberculata**

Multituberculates share several derived dental features with *Kollikodon*, as with Haramiyida. In addition to possession of multiple, longitudinal cusp rows, some multituberculates, like *Kollikodon*, have cusps of equal height (all multituberculates except Paulchoffatiidae: Butler, 2000); occlusion is opposite in ?centric occlusion (e.g., Krause and Hahn, 1990; Fig. 1); and there are similarities in the palatal and orbital regions (deep zygoma; palatine foramina).

Differences between *Kollikodon* and Multituberculata include 1) lower molars are in many cases wider than corresponding uppers in multituberculates (Sigogneau-Russell, 1989) (in contrast to *Kollikodon* where upper molars are markedly wider than lowers); 2) the dental formula in multituberculates is reduced to two upper and lower molars even in Paulchoffatiidae, the most primitive multituberculates (Hahn, 1969); 3) the lower jaw differs in shape and form: in multituberculates the jaw is massive, with a forward extension of the masseteric fossa, and the jaw is comprised solely of the dentary (with the single xception of a rudimentary coronoid in Paulchoffatiidae: Hahn, 1977a) (e.g., Clemens and Kielan-Jaworowska, 1979; Miao, 1988); 4) the orbit (floored by the maxilla in *Kollikodon*) is unfloored in Multituberculata (Clemens and
Kielan-Jaworowska 1979, Miao 1988); 5) jaw movement is propalinal in multituberculates (Clemens and Kielan-Jaworowska, 1979; Miao, 1988) but primarily orthal in *Kollikodon*; and 6) cusp rows on $M^1$ and $M^2$ are lingually offset in Multituberculata (e.g., Clemens and Kielan-Jawaorowska, 1979; Miao, 1988).

**Allotheria**

Haramiyida, thought by most to be a very early, divergent lineage (e.g., McKenna 1987; Hahn et al. 1989; Miao 1993), are considered by many to be either basal multituberculates or allied with Multituberculata in the subclass Allotheria (Hahn, 1973; Hahn et al., 1989; Wible, 1991; Sigogneau-Russell, 1989b; Butler and MacIntyre, 1994; Butler, 2000).

Butler (2000) has proposed that Haramiyida and Multituberculata form a natural group (the subclass Allotheria Marsh, 1880) based on derived dental features, and that allotherian and non-allotherian mammaliaform clades separated before Mammaliaformes developed a shearing dentition with unilateral occlusion and transverse jaw movements (the clades evolving in parallel). An allotherian/mammaliaformes split possibly happened as long ago as the mid-Triassic; differences between morganucodontids and Haramiyida suggest a long period of separate evolution during the Triassic (Butler and MacIntyre, 1994).

FIGURE 12. Comparison between the upper and lower molariform teeth of *Kollikodon*, Haramiyida (Haramiyoidea + Theroteinidae) and Monotremata.  

molariform, *Ob. insignis*. c, d redrawn from X; position in row not known. e, f redrawn from X. g, h drawn from Musser, 1998 and Musser and Archer, 1998.

Proponents of the Allotheria hypothesis believe that the pattern of multiple cusps in parallel rows shared by haramiyids and multituberculates is such a strong indicator of relationship that it can override other character sets (e.g., profound differences in postcranial and mandibular characters between haramiyids and the more advanced multituberculates: see Butler, 2000). Butler (2000) suggests that the development of multicusped dentitions is a ‘highly improbable transformation of dentition’ that would not tend to develop in parallel in unrelated groups.

Doubts over a close relationship between Haramiyida and Multituberculata, however, increased with the discovery of *Haramiyavia*, particularly because of the primitive structure of the lower jaw and postcranium (Jenkins et al. 1997). This argument is somewhat muted by the presence of a rudimentary coronoid in Late Jurassic Paulchoffatiidae (Hahn 1977), suggesting basalmost multituberculates or multituberculate ancestors may have retained at least some accessory jaw bones. It is worth noting that monotremes appear to have independently lost accessory jaw bones within the lineage (Rich et al., 2005), which might factor into arguments over whether the plesiomorphic jaw of haramiyids could have evolved into the advanced, specialized jaw of multituberculates, particularly given the great chronological distance between Late Triassic haramiyidans and later Jurassic (Kimmeridgian) multituberculates.

If Haramiyida and Multituberculata are not related, the similar dental patterns must be convergent. All hypotheses of multituberculate relationships require a huge number of convergences or reversals (see Miao, 1988). Determining relationships is complicated by the sometimes extreme specializations for herbivory in multituberculates.

There are many derived features of *Kollikodon* shared by both haramiyids and multituberculates, lending support to the ‘Allotheria’ hypothesis: mammals with multiple cusp rows; absence or weak development of cingula on molar teeth; shape of molariforms; development of apical cusps on molar crowns; tendency towards molarization of ultimate premolars (e.g., Heinrich 1999; Sigogneau-Russell 1989); small penultimate premolars (Sigogneau-Russell, 1989); and orthal, crushing component in some Allotheria (Butler and MacIntyre 1994).

Many characters shared by *Kollikodon*, Haramiyida and Multituberculata, in addition to multicusped dentitions, are plesiomorphic for Mammalia and relate to development of cingula: 1) absent/weak posterior lingual cingulid of lower molars [ch 52 of Luo]; 2) mesial transverse cingulid above gum absent [ch 55 of Luo]; 3) distal transverse cingulid on lower molars absent
Butler (2000) diagnoses Allotheria as follows: 1) mammals in which upper, lower molariform teeth have basically two longitudinal rows of cusps (additional rows may develop on upper teeth); 2) occlusion is such that the buccal lower row bites into the valley between upper rows; 3) occlusion is bilateral and jaw movement is either orthal or palinal or combination of these, but not significantly transverse. The features that define *Kollikodon* fit this definition of Allotheria fairly well; taking the specializations of *Kollikodon* into consideration and emending Butler’s (2000) diagnosis to accommodate a slightly different occlusal pattern (positive-on-positive cusp contact) in *Kollikodon*.

**Results of cladistic analysis**

Results of phylogenetic analysis support placement of *Kollikodon* close to or within the subclass Allotheria; dental characters are either remarkably convergent or indicative of shared ancestry. *Kollikodon* is neither a haramiyid nor a multituberculat as these groups are now defined, although it shares phylogenetically significant, synapomorphic characters with both groups.

One interpretation of the data would be to include *Kollikodon* within the subclass Allotheria given the present material. Another would be to consider *Kollikodon* the sister-group to Allotheria *sensu* Butler (2000). Outstanding problems include resolution of the relationship between Haramiyida and Multituberculata, and a better understanding of the morphology of *Kollikodon*, pending acquisition of more material. This study of the *Kollikodon* material does not support a tritylodontid-haramiyid-multituberculat relationship, in agreement with Hahn (1969) who felt that a relationship between tritylodontids and multituberculates was unlikely and the result of convergence.

Parsimony analysis using the database provided by Luo et al. (2002 [1]: archives, Acta Palaeontologica Polonica) and the computer programs PAUP and MacClade placed *Kollikodon* in a clade with Haramiyida/Multituberculata (Fig. 11) to the exclusion of all other mammals. Results obtained by Luo et al. (2002) without the addition of *Kollikodon* to the database give two alternative cladograms, one (unconstrained) that separates multituberculates and haramiyidans on the basis of the derived cranial and postcranial characters of multituberculates, and one (constrained; using dental characters) that links the two. Luo et al. (2002) found that their large data set did not resolve ‘Allotheria’; the results from both searches are statistically similar (the difference in tree lengths being small). Luo et al. (2002) ‘imposed a topological constraint that excludes the allotherian clade from that of living mammals, and retained only those trees compatible with constraint’ (p.33) so the tree linking Haramiyida and
Multituberculata is suboptimal but with only a small statistical difference from their more preferred tree separating Allotheria (Fig. 1, Luo et al., 2002). Arguments against a multituberculate-haramiyidan relationship include the advanced nature of the multituberculate skeleton and the plesiomorphic nature of the jaw of the Late Triassic Haramiyavia.

Luo et al.’s database is generally weighted towards dental characters. There are compelling reasons for accepting a bias towards dentition, mostly to do with the fact that teeth are often the only part of an extinct animal fossilized, and dentitions are generally seen to be conservative anatomical systems. Limitations of Luo et al.’s database are mainly due to this bias; although the authors have attempted to identify dental synapomorphies that lessen the chance of bias, the database may not in all cases be able to distinguish between convergence and phylogenetic relationship in dental form. Some features that may be significant in Kollikodon are not assessed by Luo et al. (2002).

Results of the analysis performed here are significant both because Kollikodon forms a fairly well-defined clade with both Haramiyida and Multituberculata, with several characters in common other than simply a multicusped dentition set in rows. This analysis also results in a monophyletic Allotheria without putting constraints into the database, which lends strong support to the Allotheria hypothesis championed by so many palaeontologists (see Butler, 2000).

A MODEL FOR DERIVATION OF MOLAR FORM

It is difficult to see how the dentitions of Kollikodon, haramiyids and multituberculates could have been derived from an ancestor characterized by 1) a shearing, triangulated dentition; 2) upper molars positioned alternate to lower molars; 3) a strong transverse component to mastication; and 4) molar teeth that had precise wear facets determined at birth, features that characterize the dentitions of most Mesozoic mammals and all therian mammals and their ancestors.

It has previously been suggested that the molar patterns of mammals with multicusped dentitions in anteroposterior rows – allotherians - may have been derived from an ancestor or ancestors without advancements related to the development of precisely occluding, triangulated molars, hallmarks of therian mammals, possibly mammals like morganucodontids with cusps arranged in an anteroposterior, linear fashion (e.g., Bohlin 1945; Simpson [quoted by Patterson, 1956; no year given]; Patterson, 1956 but see Butler and MacIntyre, 1994). Although this hypothesis is speculative (e.g., Patterson, 1956), and although the clade comprised of Kollikodon and allotherians presented here (Fig. 11) is distant from the position of morganucodontids, it is worth revisiting because of the linear arrangement of cusps on Kollikodon molars.
The molars of *Eozostrodon* may provide a model (Fig. 13): this Late Triassic morganucodontid had a mix of primitive dental characters (linearly arranged cusps on its molar teeth; mainly orthal jaw action; cuspidate cingula) and derived features of interest in relation to haramiyids, multituberculates and *Kollikodon* (upper and lower molar rows set opposite to each other) (Crompton and Jenkins, 1968). In *Eozostrodon*, as in other morganucodontids, the original reptilian cusp row (retained from cynodonts) is only somewhat modified: cusps are aligned anteroposteriorly (upper cusps B, A, C and D and antero-internal cingulum cusp E; lower cusps b, a, c, d) as in carnivorous cynodonts like *Thrinaxodon* (Crompton and Jenkins, 1968). The crowns of unworn upper molars have a continuous cuspidate cingulum around the base (the lingual part of this cingulum is lost through wear on worn teeth: Crompton and Jenkins, 1968). The crowns of the lower molars have no external (buccal) cingula but do have an internal (lingual) cuspidate cingulum that wraps to the

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**FIGURE 13. Hypothesis of possible derivation of multicusped teeth in *Kollikodon*.**  
*a*, lower molariforms (left) and upper molariform (right), *Eozostrodon*. Redrawn from Crompton and Jenkins 1968.  
*b*, lower molariforms (left) and upper molariforms (M¹, M²), *Kollikodon ritchiei*. Possible cusp homologies as suggested in the text. Cusps B, A and C on the upper molariforms and cusps b, a and c (=metaconid) on the lower molariforms are the original ‘reptilian’ cusp row in *Eozostrodon*. Cusp g of Crompton and Jenkins (1968) is homologous with the Kühnecone of Parrington (1971). The central row of cusps in *Kollikodon*, possibly developed from the buccal and lingual cingula of a form like *Eozostrodon*, align with the principal cusp ‘A’ of the ultimate premolariform, and most likely represent the original cusp row B-A-C of *Eozostrodon*. Abbreviations: Table 1.
anterior aspect (Crompton and Jenkins, 1968). There are two prominent cingular cusps on the lower molars: e and g (=Kühnecone of Parrington, 1967) (from Crompton and Jenkins 1968). Opposition in Eozostrodon may have developed from an ancestor (a hypothetical, more generalized morganucodontid) with alternate occlusion by shifting either the upper teeth forward or lower teeth back, or both, so that the main cusp a of lower molars occluded between the upper cusps B and A, and the main cusp A of the upper molars was external to the depression between cusps a and c of the lowers (Crompton and Jenkins, 1968). All British Morganucodon specimens have the same occlusal this stage; therefore, constant occlusal relations had developed (Crompton and Jenkins, 1968).

A dentition in which cusps are arranged in rows (‘cusps-in-line’ as in Morganucodonta) is plesiomorphic for Mammaliaformes or Mammalia. A dentition with triangulated cusps is considered derived (Rowe, 1988) and a shearing-type dentition with pre-tribosphenic or tribosphenic molar teeth characterizes most early, mostly insectivorous mammals. MacIntyre (1967) defined Mammalia as being ‘amniote craniate Chordata with …tribosphenic or pre-tribosphenic cheek teeth’. A dentition in which multiple cusps are arranged in parallel rows is a derived pattern common to Tritylodontidae, Haramiyida, Multituberculata and Kollikodon.

Patterson (1956) suggests that such multicusped dentitions may have arisen from an ancestor with cusps arranged in a linear, anteroposterior direction (‘cusps-in-line’, the original reptilian cusp row) as well as from a mammal with cuspidate cingula on molar teeth, from which additional cusp rows could be derived. Derivation of the multiple cusp rows of haramiyids from the cuspidate cingula of ‘triconodonts’ (morganucodonts) was discussed by Butler and MacIntyre (1994), who cite the ‘major change from unilateral, transverse chewing to presumably bilateral, longitudinal chewing’ as a possible obstacle to an ancestor-descendant relationship between morganucodontids and haramiyids. A row developed from the original cusp row of ‘triconodonts’; B row developed from lingual cingulum (Crompton 1974: B row from buccal cingulum; compared with Megazostrodon).

In Kollikodon the arrangement of cusps, as mentioned, are linear and central cusps are in line with the primary cusp of the premolar. This lends additional support to the ‘cusps-in-line’ theory because, unlike Haramiyida, the pattern of cusp homologies or relations between premolar and molars in Kollikodon is evident. However, if Kollikodon is closely related to Haramiyida and if Butler and MacIntyre (1994) are correct in their view that haramiyids could not have evolved from morganucodont-like mammals, the above model for evolution of the dentition of Kollikodon would not be a possibility.
‘PROTOTHERIA’ REVISITED

Although results of this phylogenetic analysis place the Kollikodon-Haramiyida-Multituberculata clade within Mammalia (with ‘Australosphenida’ as outgroup), some similarities between Kollikodon, ‘allotherians,’ morganucodonts, docodonts and monotremes suggest the possibility of a more distant relationship between these taxa. Kollikodon has allotherian features, a few monotreme-like features, and characteristics in common to both (as well as possibly to morganucodonts and docodonts).

This is an interesting result in light of the historic debate (going into its third century) over relationships of non-therian mammals. Each of the above groups has at some point in time been linked to the others. Morganucodonts and docodonts have been regarded as related (or of a similar evolutionary grade) on the basis of jaw form and dentition (docodont molars possibly derived from the triconodont molars of Morganucodonta: Patterson, 1956). A close relationship between Morganucodonta and Monotremata was proposed by Kermack and Mussett, 1958 (citing specialization of the petrosal: Kermack et al., 1956) as a side branch of mammalian evolution. Monotremes and multituberculates have been linked in several studies: Cope, 1888; Broom, 1914, Winge, 1923; Kermack and Kielan-Jaworowska, 1971; Kermack and Kermack, 1998; Kemp, 1982, 1983 (summarized by Miao, 1988). Most recently, the multituberculate skull and ear region have been shown to be similar to that of monotremes (Kielan-Jaworowska, 1970, 1971; Meng and Wyss, 1995 respectively).

This study lends support to a relationship at some level between morganucodontids, haramiyidans, multituberculates, monotremes and Kollikodon. A common stem? Before or after development of a shearing dentition? Opposite occlusion, shared by all, seems to be a strong character (but could it be convergent?)

One observation stands out: if these taxa are not closely related, the independent acquisition or evolution of similar characteristics – a carrying forward of a ‘mixed bag’ of character suites from common ancestors – is pervasive at the ‘mammaliaform’ level. Similarities have been previously noted in Late Triassic and Early Jurassic mammals (e.g., Crompton and Jenkins, 1968). This phenomenon is termed ‘mosaic evolution’ and seems to have been common in many mammals and near-mammals early in mammalian evolution. Examples of such ‘mosaic evolution’ cited in the literature include the haramiyid Haramiyavia (Jenkins et al., 1997); the triconodont Jeholodens jenkinsi (Hu et al., 1997) and many others.

TAXONOMIC RELATIONSHIPS

Kollikodon is provisionally placed as a basal allotherian (Allotheria sensu Butler 2000) pending discovery of more complete material. Kollikodontidae (comprised of the monotypic Kollikodon ritchiei) is put into a new order, Kollikodonta, reflecting the belief that Kollikodon
does not fit either into Haramiyida or Multituberculata and is thus distinct at the ordinal level.

The following diagnosis is proposed:

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA
Subclass ALLOTHERIA
KOLLIKODONTA ord. nov.
KOLLIKODONTIDAE Flannery et al., 1995
Kollikodon ritchiei Flannery et al., 1995

Revised diagnosis. Derived features shared with other mammals: a bony secondary palate; posterior opening of the infraorbital foramen; and differentiated, multirooted teeth. Distinguished from all known mammals by the following combination of features: transversely wide, crescent-shaped upper molars with three parallel rows of cusps; square to rectangular lower molars with two parallel rows of cusps; bunodont morphology; curvature of upper and lower tooth rows; and imbricating cheekteeth that form a continuous crushing surface. Differs from Monotremata in: multicusped, bunodont molariforms arranged in parallel rows; crushing rather than shearing dental function; primarily orthal jaw movement; lack of well-developed cingula; four (rather than three) molariform teeth; well-developed meckelian groove; and comparatively small mandibular canal. Differs from Multituberculata in: parallel (rather than offset) cusp rows; non-propalinal jaw motion; well-developed orbital platform; and prominent meckelian groove (absent in multituberculates). Differs from Haramiyida in: lacking a U-shaped ridge on upper and lower molars; lacking reversed symmetry of upper and lower molars; and possibly in having a transverse component to the masticatory stroke.

CONCLUSIONS

1) On the basis of distinctive dental and mandibular characters, and in recognition that Kollikodon appears to be mammalian, this study finds that Kollikodon most closely resembles Haramiyida amongst basal mammals or mammaliaformes (plesiomorphic lower jaw features suggest that Kollikodon, like Haramiyavia, is at the mammaliaform or basal mammalian level). Kollikodon also shares many dental features with Multituberculata (Haramiyida and Multituberculata together comprising ‘Allotheria’ of Butler, 2000).

2) Results of parsimony analysis utilising PAUP find Kollikodon to be sister taxon to a clade comprised of Haramiyida and Multituberculata (‘Allotheria’ of Butler, 2000).
Shared derived characters uniting *Kollikodon* and ‘Allotheria’ include possession of multicuspid, longitudinal cusp rows on upper and lower teeth (a dental pattern otherwise only shared with tritylodontid cynodonts) (Butler, 2000). *Kollikodon*, on the basis of these shared derived dental characters, is tentatively placed within Allotheria *sensu* Butler (2000) and a revised diagnosis is given for Allotheria (based on that of Butler, 2000) to incorporate *Kollikodon* within the subclass.

3) As *Kollikodon* does not fit within either Haramiyida or Multituberculata as defined by Butler (2000), a new order provisionally within Allotheria – *Kollikodonta* – is proposed; *Kollikodon ritchiei* is sole known taxon within the order.

4) *Kollikodon* shares some unusual features (such as the form of the maxilla) with Monotremata. This may lend support to studies that suggest a relationship between monotremes and multituberculates and suggests that *Kollikodon* may be a possible link between these groups. However, this study finds that *Kollikodon* does not appear to be a derived monotreme, as suggested by Flannery et al. (1995).

5) *Kollikodon* does not have molars that resemble those of basal therian mammals. The suggestion is made here that *Kollikodon* 1) never passed through a reversed triangulation molar stage; and 2) may have developed multiple rows from cuspidate cingula as seen in morganucodontids (also proposed for allotherians by some workers). Morganucodontids were comparatively generalised basal mammals with opposition of molars in some forms (e.g., *Eozostrodon*), and may provide a model for the development of multicuspid dentition in *Kollikodon*.

6) Molar form in *Kollikodon* is bunodont, with a crushing stroke. This suggests a specialised diet of hard, brittle material, such as the shells of molluscs that would require crushing. Nothing about the dentition of *Kollikodon* suggests a shearing ability (or derivation from a form with such molar function).

7) *Kollikodon* was part of a Mesozoic-earliest Tertiary Gondwanan radiation of non-therian mammals and near-mammals that included morganucodontids, docodonts, monotremes, multituberculates, triconodonts, Haramiyida and gondwanatheres (see Introduction). Most of these taxa appear to be descended from ancestors that evolved during the Late Triassic-Early Jurassic and survived into the Cretaceous or beyond in Gondwana, long after extinctions of most of these groups in the Northern Hemisphere.
Such may also be the case for *Kollikodon*, if closely related to the primarily Late Triassic to Early Jurassic Haramiyida.

8) Results of this study show that multicusped dentitions (mammalian and non-mammalian) have evolved several times during the Mesozoic and may have been an alternative to shearing, triangulated dentitions during this period.

FUTURE DIRECTIONS

Results of this initial analysis suggest that the highly specialized Early Cretaceous *Kollikodon ritchiei* may provide a link between several early mammalian taxa. *Kollikodon* has a mosaic of unusual characters with close affinities to Haramiyida and Multituberculata. The ‘allotherian’ hypothesis would be interesting to pursue at greater length: potential synapomorphies – some of these not yet described in the existing literature and beyond the scope of this project - should be identified and examined in order to test relationship hypotheses. Further comparisons between *Kollikodon*, monotremes, haramiyidans and multituberculates may offer a unique opportunity to contribute to the long-standing debates on relationships between these mammalian groups.
ACKNOWLEDGEMENTS

I am indebted to Andrew Cody for loan of the maxilla, without which this study would not have been possible. M. Archer (University of New South Wales) and G. W. Rougier (University of Louisville) contributed to aspects of the description of the maxilla (where noted); my thanks to them both. Ernie Lundelius and Carole Burrow provided comparative information on dental form and structure. I thank Ian Graham, Robert Jones, Alex Ritchie and Tony Smallwood for information on and discussion of the geology and sedimentology of the Lightning Ridge opal fields. Zerina Johanson and Shane Ahyong provided assistance with the PAUP analysis. Zerina additionally provided invaluable guidance, comment and critique. Sue Lindsay (Australian Museum) produced the scanning electron microscope photographs and Carl Bento (Australian Museum) assisted in compositing the SEM photographs.

LITERATURE CITED


**TABLE 1: CRANIOMANDIBULAR COMPARISONS**

<table>
<thead>
<tr>
<th>feature</th>
<th>Kollikodon</th>
<th>Tritylodontidae</th>
<th>Morganucodon</th>
<th>Haldanodon</th>
<th>Haramiyavia</th>
<th>Multituberculata</th>
<th>Monotremata</th>
</tr>
</thead>
<tbody>
<tr>
<td>maxillo-palatine area</td>
<td>maxilla expanded around molar row</td>
<td>maxilla not expanded; tooth row internally positioned$^{1,2}$</td>
<td>maxilla expanded around molar row$^6$</td>
<td>maxilla not expanded around molar row$^7$</td>
<td>maxilla not expanded around molar row$^6,10$</td>
<td>maxilla expanded around molar row in ornithorhynchids$^{11}$</td>
<td></td>
</tr>
<tr>
<td>maxilla has convex curvature in lateral view</td>
<td>maxilla straight in lateral view$^{1,2}$</td>
<td>maxilla straight in lateral view$^{3,6}$</td>
<td>maxilla straight in lateral view$^7$</td>
<td>maxilla straight in lateral view$^7$</td>
<td>maxilla straight in lateral view in <em>Lambdopsalis</em> but slightly curved in <em>Kamptobaatar</em></td>
<td>maxilla straight in lateral view$^{1,11}$</td>
<td></td>
</tr>
<tr>
<td>maxillary sinus may be present</td>
<td>maxillary sinus not described$^{1,2}$</td>
<td>maxillary sinus absent$^{1,6}$</td>
<td>maxillary sinus present$^6$</td>
<td>not preserved$^7$</td>
<td>maxillary sinus not described$^{8,10}$</td>
<td>maxillary sinus absent</td>
<td></td>
</tr>
<tr>
<td>root of zygomatic arch between 2nd and 3rd molars</td>
<td>root of zygomatic arch extends from 1st cheektooth to 4th cheektooth$^{1,2}$</td>
<td>root of zygomatic arch from just ant’r to 3rd molariform to 5th molariform$^3$</td>
<td>root of zygomatic arch posterior to M$^1,3$</td>
<td>root of zygomatic arch in <em>Lambdopsalis</em> from last premolar to first third of first molar$^{10}$; in <em>Sloanbaatar</em> between P$^2$ and P$^4$</td>
<td>root of zygomatic arch between anterior and posterior M$^2$ in <em>Obdurodon</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>palate vaulted</td>
<td>palatal vaulting not described for <em>Oligokyphus</em> but in <em>Bienotherium</em> the area posterior to incisors is deeply concave$^2$</td>
<td>palate vaulted to P$^4$, after which it flattens$^2$</td>
<td>palate not well arched (deep pits receive lower cusps)$^6$</td>
<td>not described$^7$</td>
<td>palate not well vaulted (from stereo photos of <em>Kamptobaatar</em>, <em>Sloanbaatar</em>)</td>
<td>palate not well vaulted in ornithorhynchids and Tachyglossus; V-shaped in <em>Zaglossus</em></td>
<td></td>
</tr>
<tr>
<td>maxillo-palatine suture close to tooth row but angled; becomes transverse at ant’r end of M$^2$</td>
<td>maxillo-palatine suture roughly parallel to tooth row; becomes transverse at middle of M$^2$ $^1$</td>
<td>maxillo-palatine suture at oblique angle to tooth row; becomes transverse at anterior end of M$'(5^{th}$ postcanine)$^3$</td>
<td>maxillo-palatine suture roughly parallel to tooth row; becomes transverse at ant. end of M$'(5^{th}$ postcanine)$^5$</td>
<td>not preserved$^7$</td>
<td>maxillo-palatine suture not preserved: <em>Obdurodon</em>; parallel to tooth row in <em>Ornithorhynchus</em> and transverse at ant’r of M$^1$ $^{11}$</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 1 continued

<table>
<thead>
<tr>
<th>Kollikodon</th>
<th>Tritylodontoidea</th>
<th>Morganucodon</th>
<th>Haldanodon</th>
<th>Haramiyavia</th>
<th>Multituberculata</th>
<th>Monotremata</th>
</tr>
</thead>
<tbody>
<tr>
<td>palatine tubercle and lesser palatine groove at posterior junction of maxilla, palatine</td>
<td>not described for Oligokyphus or Bienotherium but complete palatines not recovered</td>
<td>palatine tubercle and lesser palatine groove at posterior junction of maxilla, palatine</td>
<td>area of palatine tubercle missing but probably present; no lesser palatine groove</td>
<td>not preserved</td>
<td>postpalatine torus in Kamptobaatar with longitudinal, fisure-like foramen (palato-nasal) described</td>
<td>palatine tubercle and lesser palatine groove absent</td>
</tr>
<tr>
<td>lesser palatine foramina present</td>
<td>not described for Oligokyphus or Bienotherium but complete palatines not recovered</td>
<td>lesser palatine foramina present</td>
<td>single large lesser palatine foramina present</td>
<td>not preserved</td>
<td>small foramina (minor palatine foramina) in multituberculates but probably not homologous</td>
<td>lesser palatine foramina absent</td>
</tr>
<tr>
<td>single posterior opening for infraorbital canal</td>
<td>infraorbital canal in Oligokyphus runs obliquely through lacrimal; does not appear to have posterior opening</td>
<td>double opening for infraorbital canal posteriorly; an additional side branch passes through lacrimal</td>
<td>single posterior opening for infraorbital canal; maxillary sinus between f1 and post’r part of canal</td>
<td>not preserved</td>
<td>single posterior opening for infraorbital canal in most</td>
<td>single posterior opening for infraorbital canal</td>
</tr>
<tr>
<td>posterior opening on palate of greater palatine foramen</td>
<td>(?) ventral opening on palatine for greater palatine nerve; posterior opening on maxilla: groove above cheektooth</td>
<td>absent</td>
<td>absent</td>
<td>not preserved</td>
<td>minor palatine foramina in some multituberculates; palatoanosal foramen in Kamptobaatar</td>
<td>double openings for f. palatinum in Ogdobodon but anterior opening not a true major palatine foramen</td>
</tr>
<tr>
<td>greater palatine groove absent (?)</td>
<td>?gutter on maxillary near sagittal suture described in Oligokyphus</td>
<td>well-developed greater palatine groove present</td>
<td>greater palatine groove absent</td>
<td>not preserved</td>
<td>palatine groove absent in Kamptobaatar</td>
<td>greater palatine groove absent</td>
</tr>
<tr>
<td>secondary palate extends posteriorly at least to end of tooth row</td>
<td>secondary palate extends only to 4th cheektooth</td>
<td>secondary palate ends at level of posterior-most molars</td>
<td>palatine extends posteriorly to tooth row and beyond</td>
<td>not preserved</td>
<td>secondary palate anterior to toothrow but toothrow very posterior</td>
<td>palatine extends well beyond tooth row</td>
</tr>
<tr>
<td>orbit floored by maxilla (deep)</td>
<td>orbit floored by lacrimal</td>
<td>orbital platform floored by maxilla but not deep</td>
<td>orbit floored by maxilla (?not deep)</td>
<td>not preserved</td>
<td>orbit not floor by maxilla; roofed by maxilla and frontal</td>
<td>orbit floored by maxilla but not deep (extremely shallow)</td>
</tr>
<tr>
<td>zygomatic arch deep vertically and thin transversely</td>
<td>zygomatic arch not deep vertically in Oligokyphus; deeper in Bienotherium</td>
<td>zygomatic arch not deep</td>
<td>zygomatic arch complex; medial and lateral walls</td>
<td>not preserved</td>
<td>zygomatic arch deep vertically and thin transversely</td>
<td>zygomatic arch deep vertically and thin transversely</td>
</tr>
</tbody>
</table>
Table 1 continued

<table>
<thead>
<tr>
<th></th>
<th>Kollikodon</th>
<th>Tritylodontoidea</th>
<th>Morganucodon</th>
<th>Haldanodon</th>
<th>Haramiyavia</th>
<th>Multituberculata</th>
<th>Monotremata</th>
</tr>
</thead>
<tbody>
<tr>
<td>dentary</td>
<td>mandibular canal small</td>
<td>mandibular canal not described for <em>Oligokyphus</em>; size of mandibular foramen is small in <em>Bienotherium</em></td>
<td>mandibular canal small</td>
<td>mandibular canal appears to have moderate opening (foramen)</td>
<td>size of mandibular canal not described for <em>Haramiyavia</em></td>
<td>opening of mandibular canal large but size of canal not described</td>
<td>mandibular canal large</td>
</tr>
<tr>
<td></td>
<td>meckelian groove convergent with ventral border of mandible</td>
<td>meckelian groove parallel with ventral border of mandible</td>
<td>meckelian groove convergent with ventral border of mandible</td>
<td>meckelian groove parallel with ventral border of mandible</td>
<td>meckelian groove lost in adults</td>
<td>meckelian groove parallel to ventral border of mandible</td>
<td>meckelian groove</td>
</tr>
<tr>
<td></td>
<td>meckelian groove weakly developed</td>
<td>meckelian groove well developed</td>
<td>meckelian groove well developed</td>
<td>meckelian groove well developed</td>
<td>meckelian groove well developed</td>
<td>meckelian groove absent</td>
<td>meckelian groove</td>
</tr>
<tr>
<td></td>
<td>masseteric fossa does not extend forward below molars</td>
<td>masseteric fossa does not extend forward below molars</td>
<td>masseteric fossa does not extend forward below molars</td>
<td>masseteric fossa does not extend forward below molars</td>
<td>masseteric fossa extends forward below molars</td>
<td>masseteric fossa does not extend forward below molars</td>
<td>masseteric fossa</td>
</tr>
<tr>
<td></td>
<td>groove for dental lamina absent</td>
<td>groove for dental lamina present</td>
<td>groove for dental lamina absent</td>
<td>groove for dental lamina absent</td>
<td>groove for dental lamina absent</td>
<td>groove for dental lamina absent</td>
<td>groove for dental lamina</td>
</tr>
<tr>
<td></td>
<td>postdentary bones comparatively unreduced</td>
<td>postdentary bones comparatively unreduced</td>
<td>postdentary bones comparatively unreduced</td>
<td>postdentary bones comparatively unreduced</td>
<td>postdentary bones absent</td>
<td>postdentary bones reduced in <em>Teinolophos</em></td>
<td>postdentary bones</td>
</tr>
</tbody>
</table>

Sources (see Literature Cited)

1Kühne, 1957  
2Young, 1947  
3Kermack et al., 1981  
4Kermack et al., 1973  
5Luo et al., 2002  
6Lillegraven and Krusat, 1991  
7Jenkins et al., 1997  
8Clemens and Kielan-Jaworowska, 1979  
9Kielan-Jaworowska, 1971  
10Miao, 1988  
11Musser and Archer, 1998  
12Rich et al., 2005  
13Musser, 2005  
14Butler, 2000
**TABLE 2: COMPARISONS OF DENTAL CHARACTERS (UNFINISHED)**

<table>
<thead>
<tr>
<th>feature</th>
<th>Kollikodon</th>
<th>Tritylodontoidea</th>
<th>Morganucodon</th>
<th>Docodonta</th>
<th>Haramiyoida</th>
<th>Theroteinida</th>
<th>Multituberculata</th>
<th>Monotremata</th>
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</thead>
<tbody>
<tr>
<td>last upper</td>
<td>3 cusps:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>premolariform</td>
<td>1 anterior</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2 posterior, transv</td>
<td></td>
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<td>checkteeth not differentiated?</td>
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<td></td>
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<tr>
<td>1 principal cusp</td>
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<td>+ distal cuspule</td>
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<tr>
<td>3 cusps:</td>
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<td>1 anterior</td>
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<tr>
<td>2 posterior, transv</td>
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<tr>
<td>(in Docodon?)</td>
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<td></td>
</tr>
<tr>
<td>unknown for Haramiyavia</td>
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<td>?unknown</td>
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<tr>
<td>some paulhoff. are tricuspid</td>
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<tr>
<td>(varies but can have 1 ant’r, 2 post’r cusps)?</td>
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<tr>
<td>no cingula (tiny shelf anteriorly)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>roughly continuous cingulum around premolars (Obdurodon)</td>
</tr>
<tr>
<td>lingual cingulum and narrow buccal</td>
<td>Check Jenkins</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>cingulum?</td>
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</tr>
<tr>
<td>no premolariform teeth (ref)</td>
<td></td>
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<td></td>
<td></td>
<td></td>
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<td></td>
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<tr>
<td>no buccal cingula</td>
<td>no buccal cingula</td>
<td></td>
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</tr>
<tr>
<td>upper molars or molariforms</td>
<td>3 rows of cusps aligned antero-</td>
<td></td>
<td></td>
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<td></td>
<td>posteriorly</td>
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<td></td>
</tr>
<tr>
<td></td>
<td>3 rows of cusps aligned antero-</td>
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<td></td>
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<tr>
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<td>posteriorly</td>
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</tr>
<tr>
<td></td>
<td>1 row of cusps aligned antero-</td>
<td></td>
<td></td>
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<td></td>
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<tr>
<td></td>
<td>posteriorly</td>
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<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>2 rows of cusps</td>
<td></td>
<td></td>
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<td>(reversed triangles)?</td>
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<td>(Obdurodon)</td>
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<td>buccal row overhangs lower</td>
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<td>buccal halves of uppers is lateral</td>
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<td>to lower in occlusion?</td>
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<td>buccal row overhangs in Eleutherodon (has BB cusps) and Staffia [H]</td>
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<td>no buccal cingula</td>
<td>no buccal cingula</td>
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<td></td>
<td></td>
<td></td>
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<td>buccal cingulum present?</td>
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<td>buccal cingulum on M¹; less dev’d on M²; absent on M¹</td>
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<td>no buccal cingula</td>
<td>buccal cingula present</td>
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<td>buccal cingula present</td>
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### Table 2 continued

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<tr>
<th>Kollikodon</th>
<th>Tritylodontoidea</th>
<th>Morganucodon</th>
<th>Docodonta</th>
<th>Haramiyoidae</th>
<th>Therotoeidae</th>
<th>Multituberculata</th>
<th>Monotremata</th>
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<tbody>
<tr>
<td>no lingual cingula</td>
<td>no lingual cingula</td>
<td>lingual cingulum present¹,⁴</td>
<td>lingual cingulum developed into lobe¹</td>
<td>no lingual cingula</td>
<td>no lingual cingula</td>
<td>lingual cingulum present; cusps developed (Obdurodon)</td>
<td></td>
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<tr>
<td>small anterior cingulum on first molariform</td>
<td>continuous cingulum around unworn tooth⁵,⁶</td>
<td>pm with 'indentation' on ant. face but no shelf [H]</td>
<td>well-developed anterior cingulum (Obdurodon)</td>
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<tr>
<td>apical pits (wear)</td>
<td>n/a; wear is mostly shear⁷,⁸</td>
<td>apical pits (Thomasia, Haramiyia)¹¹</td>
<td>apical pits (e.g., Loxaulax)</td>
<td>wear mainly transverse shear (Obdurodon)</td>
<td></td>
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<tr>
<td>four upper molariforms (?3 molars)</td>
<td>usually four upper molariforms (sometimes five)⁹</td>
<td>three upper molariforms in Docodon? but maybe four In Thomasia²</td>
<td>unknown</td>
<td>two upper molars¹², two upper molars in Obdurodon and probably three in Steropodon</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>multiple rows</td>
<td>multiple rows</td>
<td>two rows; cusps in line³</td>
<td>multiple rows</td>
<td>multiple rows</td>
<td>multiple rows</td>
<td>reversed triangles</td>
<td></td>
</tr>
<tr>
<td>no U-ridge</td>
<td>no U-ridge</td>
<td>no U-ridge⁵</td>
<td>u-ridge mesially where B joins A³</td>
<td>u-ridge mesially where B joins A [B]</td>
<td>no U-ridge</td>
<td>n/a</td>
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<tr>
<td>valleys between rows (upper and lowers)</td>
<td>valleys between rows (upper and lowers)</td>
<td>n/a; single row³,⁴</td>
<td>basins between rows</td>
<td>basins between rows (as for lowers)</td>
<td>n/a</td>
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<tr>
<td>cusps of equal height (except M¹ where anterior cusp tallest)</td>
<td>cusps of varied height; anterior cusps are tallest¹⁴</td>
<td>unequal height; highest cusps distal; diagnostic for Haramiyida²</td>
<td>unequal height; highest cusps distal; diagnostic for Haramiyida [B]</td>
<td>unequal height (however, all other multis have cusps of equal height but ‘derived’) [B]</td>
<td>n/a</td>
<td></td>
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<tr>
<td>cusps low, bunodont</td>
<td>not bunodont¹³</td>
<td>not bunodont¹⁴</td>
<td>not bunodont⁶</td>
<td>not bunodont¹⁷</td>
<td>some (e.g., Loxaulax) partly bunodont</td>
<td>not bunodont</td>
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<tr>
<td>enamel not grooved (also for lowers)</td>
<td>enamel not grooved¹</td>
<td>enamel not grooved¹⁴</td>
<td>enamel not grooved¹⁴</td>
<td>enamel not grooved¹⁴</td>
<td>enamel grooved¹⁴</td>
<td>enamel not grooved</td>
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<tr>
<td></td>
<td>Kollikodon</td>
<td>Tritylodontoidea</td>
<td>Morganucodon</td>
<td>Docodonta</td>
<td>Haramiyoida</td>
<td>Theroteinidae</td>
<td>Multituberculata</td>
</tr>
<tr>
<td>--------------------------</td>
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<td>--------------</td>
<td>-----------</td>
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<tr>
<td>lower molars or molariforms</td>
<td>longer than wide (rectangular)</td>
<td>longer than wide (rectangular)</td>
<td>longer than wide (oblong)</td>
<td>longer than wide (rectangular)</td>
<td>longer than wide (oblong)</td>
<td>longer than wide (oblong)</td>
<td>longer than wide (rectangular)</td>
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<tr>
<td>multiple rows</td>
<td>multiple rows</td>
<td>multiple rows</td>
<td>cusps-in-line</td>
<td>modified cusps-in-line</td>
<td>multiple rows</td>
<td>multiple rows</td>
<td>multiple rows</td>
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<tr>
<td>four lower molariforms (?) molars</td>
<td>usually four; sometimes five</td>
<td>three upper molariforms in Haramiyavia</td>
<td>not known</td>
<td>not known</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2 rows of cusps</td>
<td>2 rows of cusps</td>
<td>1 row of cusps + lingual cingulum</td>
<td>2 rows of cusps</td>
<td>2 rows of cusps</td>
<td>2 rows of cusps</td>
<td>2 rows of cusps</td>
<td>2 rows of cusps</td>
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<tr>
<td>2 lingual cusps, 2 buccal cusps</td>
<td></td>
<td>3 main cusps in line</td>
<td>2 lingual cusps (g/h)</td>
<td>4 lingual cusps in Haramiyavia</td>
<td>2 lingual cusps</td>
<td>several buccal cusps [B]</td>
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<tr>
<td>vestigial buccal cingula</td>
<td>slight buccal cingulum in M. oehleri; otherwise absent</td>
<td>no buccal cingula</td>
<td>no buccal cingula</td>
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<td>no lingual cingula</td>
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<td>always a lingual cingulum</td>
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<td>no lingual cingula</td>
<td>no lingual cingula</td>
<td>no lingual cingula</td>
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<tr>
<td>vestigial anterior, posterior cingula</td>
<td>anterior cingulum (’C’) and posterior cingulum (’d’) present</td>
<td>no anterior or posterior cingula</td>
<td>no anterior or posterior cingula</td>
<td>no anterior or posterior cingula</td>
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<td>no u-ridge</td>
<td>no u-ridge</td>
<td>no u-ridge</td>
<td>u-ridge or transverse ridge except in Eleutherorodon</td>
<td>u-ridge distally</td>
<td>no u-ridge</td>
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<tr>
<td>cusps of equal height (on M1 mesial cusps highest)</td>
<td>cusps of varied height; anterior cusps tallest</td>
<td>highest cusps mesial</td>
<td>highest cusps mesial</td>
<td>most multis have cusps of equal height</td>
<td>cusps of varied height, buccal cusps highest</td>
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</tr>
<tr>
<td>roots</td>
<td>multiple on uppers; double on lowers; upper premolar double-rooted</td>
<td>multiple on uppers; double on lowers</td>
<td>upper and lower molars double rooted</td>
<td>Multiple on uppers (at least triple) (LK)</td>
<td>X for uppers double for lowers [J]</td>
<td>Steropodon: double for lowers; Obdurodon: multiple for uppers and lowers</td>
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<tr>
<td>root form</td>
<td>molars slightly recurved</td>
<td>premolars, molars have straight roots</td>
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<td>roots recurved in Steropodon</td>
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### Table 2 continued

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<tr>
<th>Monotremata</th>
<th>Kollikodon</th>
<th>Tritylodontoidea</th>
<th>Morganucodon</th>
<th>Docodonta</th>
<th>Haramiyidea</th>
<th>Theroteinidae</th>
<th>Multituberculata</th>
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<tbody>
<tr>
<td>pattern of opposing teeth</td>
<td>no reversal</td>
<td>no reversal$^1$</td>
<td>no reversal$^{1,2}$</td>
<td>no reversal</td>
<td>reversed buccolingually and mesio-distally$^9$</td>
<td>reversed buccolingually and mesio-distally$^{11}$</td>
<td>n/a; triangulated</td>
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<td>molar-pm boundary</td>
<td>disjunction between pm, molars</td>
<td>cheeckteeth not differentiated$^1$</td>
<td>last upper premolar is larger than first molar$^{12}$</td>
<td>distinct in uppers; gradual in lowers$^7$</td>
<td>not described for Haramiyavia</td>
<td>unknown</td>
<td>disjunction between pm, molars</td>
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<tr>
<td>occlusion: position of molar rows</td>
<td>nearly opposite</td>
<td>nearly opposite$^{3,4}$</td>
<td>alternate$^5$</td>
<td>nearly opposite$^{3,10}$</td>
<td>alternate$^{11}$</td>
<td>?alternate</td>
<td></td>
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<tr>
<td>occlusion: molar contact</td>
<td>crown-to-crown</td>
<td>uppers shear past lowers$^{3,4}$</td>
<td>crown-to-crown$^6$</td>
<td>crown-to-crown$^{11}$</td>
<td>?crown-to-crown</td>
<td></td>
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</tr>
<tr>
<td>dental function and diet</td>
<td>crushing hard food (shellfish)</td>
<td>grinding or cutting (plant fibre)$^1$</td>
<td>shearing (insectivorous)$^{1,4}$</td>
<td>shearing/crushing$^{8,9}$</td>
<td><em>puncture-crushing</em> for Haramiyavia$^{10}$</td>
<td>crushing hard, brittle food$^7$ or soft food (Het al.89)</td>
<td>grinding [J]</td>
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<td>occlusal precision</td>
<td>precision through wear</td>
<td>precision through wear$^1$</td>
<td>precision through wear$^1$</td>
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<td>precision through wear$^1$</td>
<td>no cusp-cusp relations; not precise$^1$</td>
<td>precise wear facets [K-J et al.]</td>
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<td>action</td>
<td>orthal/some transverse; bilateral occlusion</td>
<td>orthal/transverse$^4$</td>
<td>orthal/transverse$^4$</td>
<td>some ant-post movement of lower jaw and complex masticatory movements$^9$</td>
<td>orthal$^8$ but see $^9$ ?bilateral</td>
<td>orthal (fully orthal; no sliding contact)$^9$</td>
<td>propalinal (fully horizontal) [xx]</td>
</tr>
</tbody>
</table>

**Sources (see Literature Cited):**

$^1$Kühne, 1956  
$^2$Another trit. Ref  
$^3$Mills, 1971  
$^4$Kermack et al., 1981  
$^5$Kermack et al., 1981  
$^6$Kron, 1979  
$^7$Jenkins, 1969  
$^8$Butler, 2000  
$^9$Jenkins et al., 1997  
$^{10}$Sigogneau-Russell, 1989  
$^{11}$Hahn, 1971  
$^{13}$Hahn, 1971  
$^{14}$Clemens and Kielan-Jaworowska, 1979  
$^{15}$Krause and Hahn, 1990
Crompton and Jenkins, 1968  
Butler, 1997  
Hahn et al., 1989  
Musser and Archer, 1998
APPENDIX II: PAUP ANALYSIS

TAXON: Kollikodon ritchiei (Early Cretaceous, Australia)

ADDITIONAL TAXA (from Luo et al. 2002): Probainognathus (non-mammalian, derived cynodont; used as outgroup for rooting tree by phylogenetic algorithms); tritylodontids (possible sister-taxon to mammals: Rowe 1993; Wible 1991); tritheledontids (possible sister-taxon to mammals: Hopson & Barghusen 1986; Shubin et al. 1991; Crompton & Luo 1993; Luo 1994; Crompton 1995; Sidor & Hopson 1998); Adelobasileus (intermediate between cynodonts and primitive mammals); Sinoconodon (one of most primitive mammalian stem taxa) Morganucodon (one of best-known early mammals); Megazostrodon (docodont); Dinnotherium (docodont); Haldanodon (docodont known from skull, dental and postcranial material); Hadrocodium (taxon between stem lineages and crown Mammalia) Gobiconodon ('amphilestid' eutriconodont known from skull, dental and postcranial material); Amphilestes (plesiomorphic 'triconodont'); Jeholodens (triconodont known from complete skeleton); Priacodon (Late Jurassic N.Am. Triconodontidae); Trioracodon (earliest Cretaceous European Triconodontidae); Kuehneotherium (one of earliest mammals with reversed triangle dentition); Tinodon ('obtuse-angled symmetrodont'); Shuoatherium (taxon with pseudo-tribosphenic dentition); Ambondro (earliest known mammal with 'tribosphenic' dentition); Ausktribosphenos (early, unusual 'tribosphenic' mammal of debated affinities); Bishops (as for Ausktribosphenos); Steropodon, Teinolophos (oldest known monotremes); Obtusodon (earliest ornithorhynchid; known from dentition, skull, mandible); Ornithorhynchus (extant monotreme); Haramiyavia (?early allotherian); Plagiaulacida (oldest multituberculates); Cimolodonta (advanced multituberculates); Zhangheotherium (spalacotheriid ['acute-angled' symmetrodont known from skeleton); Henkelotherium (paurodontid 'eupantothere' known from skeleton); Dryolestes (representative of Dryolestidae: diverse group of 'eupantotheres'); Amphitherium (amphiletherid 'eupatothere') Vincelestes (pre-tribosphenic therian known from skull and postcranial material); Peramus (advanced 'eupantothere') Kielanterium (plesiomorphic tribosphenic therian ['boreosphenid'] Aegialodon (one of earliest 'boreosphenids') Deltheridium (possible stem marsupial) Pappotherium (taxon close to base of crown Theria) Kokopellia (earliest accepted marsupial) Asiatitherium (earliest marsupial known from skeleton); Pucadelphys (best-known Paleocene marsupial); Didelphis (extant plesiomorphic marsupial); Prokennalestes (best-represented Early Cretaceous placental) Montanalestes (earliest placental from N.Am); Asioryctes (Late Cretaceous Asian placental); Erinaceus (extant plesiomorphic placental).

CHARACTERS FROM LUO ET AL. (2002)

Mandible (26 characters used)
1. postdentaly trough (behind tooth row): (0) present, or (1) absent, or (?) not preserved
2. separate scars for surangular-prearticular in Meckel's groove and postdentaly trough: (0) present, or (1) absent, or (?) not preserved
3. overhanging medial ridge above postdentaly trough (behind tooth row): (0) present, or (1) absent, or (?) not preserved
4. curvature of Meckel's groove (under tooth row) in adult (sensu Luo 1994): (0) present and parallel to the ventral border of the mandible, or (1) present and convergent to the ventral border of the mandible, or (?) unknown or not preserved
5. degree of development of Meckel's groove in adults: (0) well developed, or (1) weakly developed, or (2) vestigial or absent, or (?) unknown or not preserved
6. mandibular symphysis: (0) fused, or (1) unfused, or (2) unfused and reduced, or (?) not preserved
7. groove for replacement dental lamina (Crompton and Luo 1993; Luo 1994): (0) present, or (1) absent, or (?) not preserved
8. angular process of dentary - presence vs absence: (0) present, or (1) reduced or weakly developed, or (2) present and transversely flaring, or (3) present and slightly inflected, or (4) present, strongly inflected, and continuing anteriorly as a mandibular shelf, or (5) absent, or (?) not preserved
9. angular process of dentary - anteroposterior position relative to the dentary condyle: (0) an anterior position (the angular process is below the main body of the coronoid process, separated widely from the dentary condyle), or (1) a posterior position (the angular process is positioned at the same level at the posterior end of the coronoid process; either close to or directly under the dentary condyle), or (?) not applicable
10. angular process of the dentary - vertical elevation relative to the molar alveolar line: (0) angular process is low, at or near the level of the ventral border of the mandibular horizontal ramus, or (1) angular process is high, at or near the
level of molar alveolar line (and far above the ventral border of the mandibular horizontal ramus), or (?) not applicable

11. coronoid (or its attachment scar) in adults: (0) present, or (1) absent, or (?) not visible

12. mandibular foramen (posterior opening of the mandibular canal) for inferior alveolar nerve and vessels: (0) located within the postdentary trough (the depression around the foramen is a part of Meckel's sulcus-postdentary trough), or (1) the foramen is not associated with either postdentary trough or the Meckel's groove, or (?) not preserved

13. medial concavity (fossa) for the reflected lamina of the angular bone on the medial side of the dentary process: (0) medial concavity (excavated fossa) for the reflected lamina of the angular bone on the medial side of the dentary angular process (Crompton and Luo 1993), or (1) angular region has no fossa for the angular bone, or (?) not preserved

14. the splenial as separate element (as indicated by its scar on dentary) in adult: (0) present, or (1) absent, or (?) not preserved

15. relationship of the surangular to craniomandibular joint (CMJ): (0) participates in CMJ either as a separate bone, or fused with the articular, or (1) surangular as bony element is lost in adults, or (?) unknown

16. the pterygoid fossa on the medial side of the mandible: (0) absent, or (1) present, or (?) not preserved

17. medial pterygoid ridge (shelf) along the ventral border of the coronoid part of the mandible: (0) absent, or (1) present, or (2) pterygoid shelf present and reaching the dentary condyle via a low crest, or (?) not preserved

18. ventral border of masseteric fossa: (0) absent, or (1) present as a low and broad crest, or (2) present as a well defined and thin crest, or (?) not exposed; not preserved

19. crest of the masseteric fossa along anterior border of coronoid process: (0) absent or weakly developed, or (1) present, or (2) present and laterally flaring, or (?) not preserved

20. anteroventral extension of masseteric fossa: (0) below the ultimate molar or posterior to it, or (1) anterior extension below the ultimate premolar, or (?) not preserved

21. orientation of dentary peduncle and condyle: (0) dentary peduncle is posteriorly directed, or (1) dentary condyle is continuous with the semicircular posterior margin of the dentary; condyle is facing up due to the upturning of the posteriormost part of the dentary, or (2) dentary articulation extends vertically for the entire depth of the horizontal ramus of the mandible; it is confluent with the horizontal ramus and lacks a peduncle; the dentary articulation is posteriorly directed, or (3) vertically directed dentary peduncle, or (?) not preserved

22. shape and relative size of dentary articulation: (0) small and dorsoventrally compressed, or (1) condyle is massive and bulbous, transversely broad in its dorsal aspect, or (2) condyle mediolaterally narrow and vertically deep, forming a broad arc in lateral outline, either ovoid or triangular in posterior view, or (?) not preserved

23. ventral (inferior) border of dentary peduncle: (0) posteriorly tapering, or (1) columnar and with lateral ridge, or (2) ventrally flaring, or (3) robust and short, or (4) ventral part of peduncle and condyle becoming continuous with the ventral border of the mandible, or (?) not applicable; not preserved

24. position of dentary condyle relative to vertical level of postcanine alveoli: (0) below or about the same level as the postcanine alveoli, or (1) above the level of the postcanine alveoli, or (?) not applicable; not preserved

25. tilting of coronoid process of dentary (measured as the angle between the imaginary line of the anterior border of the coronoid process and the horizontal alveolar line of all molars): (0) coronoid process is strongly reclined and the coronoid angle is obtuse (>\(= 150^\circ\)), or (1) coronoid process less reclined (135-145\(^{\circ}\)), or (2) coronoid process is less than vertical (115-125\(^{\circ}\)), or (3) coronoid process is near vertical and the coronoid angle small (95-105\(^{\circ}\)), or (?) not preserved

26. alignment of the erupting ultimate molar (or postcanine) to the anterior margin of the dentary coronoid process (and near the coronoid scar if scar is present): (0) ultimate functional molar erupts medial to the coronoid process, or (1) ultimate functional molar erupting in alignment with the anterior margin of coronoid process, or (?) not preserved

Lower premolars (11 characters)

27. ultimate lower premolar - symmetry of the main cusp (=protoconid). This character measured by the length ratio of the anterior and posterior cutting edges extending from cusp: (0) asymmetrical (anterior edge of cusp a is more convex in outline than the posterior edge), or (1) symmetrical (anterior and posterior cutting edges are equal or subequal in length; neither edge is more convex or concave than the other in lateral profile), or (?) not applicable; not preserved

28. the ultimate lower premolar - anterior cusp b (=paraconid) (absence or reduction of anterior cusp b tends to make the premolar appear more asymmetrical): (0) present (at least subequal to cusp c of the same tooth), or (1) small (much smaller than cusp c of the same tooth), or (2) present; not preserved; not applicable

29. ultimate lower premolar - arrangement of principal cusp a, cusp b (if present) and cusp c (we assume the cusp to be c if there is only one cusp behind the main cusp a): (0) aligned straight or at a slight angle, or (1) distinctive triangulation, or (2) premolar with multicusps in longitudinal row(s), or (3) premolar multicuspate and blade-like, or (?) not preserved; not applicable

30. ultimate lower premolar - posterior (distal) cingular or cingular cuspule d (in addition to main cusp c): (0) absent, or (1) posterior cingular cusp present, or (2) presence of the continuous posterior (distal) cingular, or (?) premolar not preserved

31. ultimate lower premolar (outline): (0) laterally compressed (or slightly angled), or (1) blade-like, or (2) transversely wide, or (?) premolar not preserved
32. labial cingulid of the ultimate lower premolar: (0) absent or vestigial, or (1) present (along more than half the crown
length). Or (?) not preserved
33. lower premolar lingual cingulid: (0) absent or vestigial, or (1) present, or (?) premolar not preserved, not applicable
34. relative height of the primary cusp a to c of the ultimate lower premolar (measured as the height ratio of a and c from
the bottom of the valley between the two adjacent cusps): (0) posterior cusp c is indistinctive, or (1) posterior cusp c
is distinctive but less than 30% of primary cusp a, or (2) posterior cusp c and primary cusp a are equal or subequal in
height (c is 40-100% of a), or (?) not preserved, not applicable
35. ultimate upper premolar - functional protocone (character applicable to mammals with reversed triangulation of
molar cusps): (0) absent, or (1) present, or (?) not preserved
36. penultimate lower premolar - anterior cusp b (=paraconid): (0) vestigial (much smaller than cusp c of same tooth) to
absent, or (1) distinctive, or (2) multicuspate row(s), or (?) not preserved, not applicable
37. penultimate lower premolar - arrangement of principal cusp a, cusp b (if present) and cusp c (we assume the cusp to
be c if there is only one cusp behind main cusp a): (0) cusps in straight alignment (for tooth with single cusp, the
anterior and posterior crests from the main cusp are in alignment, or (1) cusps in triangulation, or (2) premolar with
multiple cusps in longitudinal row(s), or (?) not preserved, not applicable

Molar morphology (55 characters)
38. alignment of main cusps of the posterior lower molar(s) (m3 or more posterior if present): (0) single longitudinal row,
or (1) obtuse angle (>/=95°), or (2) acute angle (</=90°), or (3) multiple longitudinal multicuspate rows, or (?) not
preserved, not applicable
39. alignment of main cusps of anterior lower molar (m1) (see justification on character 38 and note below): (0) single
longitudinal row, or (1) acute angle, or (2) multiple longitudinal rows, or (?) not applicable
40. postvallum/prevallid shearing (angle of main trigonid shear facets): (0) absent, or (1) present, weakly developed,
slightly oblique, or (2) present, strongly developed, and more transverse, or (?) not preserved, not applicable
41. development of postprotocrista on the upper molar for double rank postvallum shear (applicable to molars with
reversed triangulation of molar cusps): (0) postprotocrista is short and does not extend labially beyond metacone, or
(1) postprotocrista is long and extends labially beyond metacone, or (?) not preserved, not applicable
42. precise opposition of upper, lower molars (either one-to-one, or occluding at opposing embrasure or talonid): (0)
absence of precise occlusion of upper and lower molars, or (1) present (either one-to-one, or occluding at the
opposing embrasure or talonid), or (2) present, one lower molar sequentially contacts more than one upper molar, or
(?) not preserved
43. relationships between the cusps of the opposing upper and lower molars: (0) absent, or (1) present, lower primary
cusp a occludes in the groove between upper cusps A, B, or (2) present, lower primary cusp a occludes in front of
upper, or (3) present, parts of the talonid occluding with the lingual face (or any part) of the upper molar, or (4) lower
multicuspate rows alternatively occlude between the upper multicuspate rows, or (?) not preserved, not applicable
44. relative height of primary cusp a (protoconid) to cusp c (metaconid) of anterior lower molars (measured as the height
ratio of a and c from the bottom of the valley between the two adjacent cusps, on m1): (0) posterior cusp c is less
than 40% of the primary cusp a (protoconid), or (1) posterior cusp c and primary cusp a are equal or subequal in
height (c is 50-100% of a), or (?) not applicable, not preserved
45. relative size/height of anterior cusp b (paraconid) to posterior cusp c (metaconid) (based on m2): (0) c taller than b, or
(1) b taller than c, or (2) b and c are more or less equal in height, or (?) incomplete; not applicable
46. elevation of the cingulid base of paraconid (cusp b) relative to the cingulid base of metaconid (cusp c) on lower
molars: (0) absent, or (1) present, or (?) not preserved; not applicable
47. the cristid obliqua (sensu Fox 1975: defined as the oblique crest anterior to, and connected with, a labialmost cusp on
the talonid heel, the leading edge of facet 3): presence vs absence and orientation (applicable only to the molar with
at least a hypoconid on the talonid or a distal cingulid cuspule): (0) absent, or (1) present, and oriented lingual of the
metaconid-protoconid notch, or (2) present, hypertrophied, and directed to posterior (distal) part of metaconid, or (3)
present, short and pointed anteriorly between the metaconid-protoconid notch and the protoconid (labial of the
notch), or (?) not applicable
48. lower molar - medial and longitudinal crest (='pre-entocristid' or 'pre-hypoconulid') on the talonid heel (only
applicable to taxa with talonid or at least cusp d): (0) talonid (or cusp d) lacks medial and longitudinal crest, or (1)
medialmost cristid (‘pre-entocristid’) of talonid in alignment with the metaconid or with the postmetacristid if the
latter is present, or (2) medialmost cristid of talonid (‘prehypoconulid’ cristid, based on cusp designation of KielanJaworowska et al. 1987) is hypereetrophied and in alignment with the postmetacristid and abuts the latter by a Vshaped notch, or (3) ‘pre-entocristid’ crest is offset from the metaconid (and postmetacristid if present) and the ‘preentocristid’ extends anterolingually past the base of the metaconid, or (?) not preserved; not applicable
49. labial curvature of primary cusp a of lower molars (at the base level) relative to the curvature of cusps b and c: (0)
cusp a and cusps b, c have the same degree of bulging, or (1) cusp a is far more bulging than cusps b, c, or (?) not
applicable
50. labial curvature of the main cusps A, B, C at the level of the cusp valley of the penultimate and ultimate upper
molars: (0) cusps A, B and C have about the same degree of curvature, or (1) cusp A is slightly concave (or far less
convex than either cusp B or cusp C), or (?) not applicable
51. labiolingual compression of the primary functional cusps of the lower molars (at the level of the cusp base but above
the cingulid): (0) absent, or (1) present

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52. posterior lingual cingulid of lower molars: (0) absent or weak, or (1) distinctive, or (2) strongly developed, crenulated with distinctive cuspules, or (?) not exposed; not applicable

53. anterior internal (mesiointernal) cingular cusple (e) on the lower molars: (0) present, or (1) absent, or (?) not applicable

54. anterior and labial (mesiolabial) cingular cusple (f): (0) absent, or (1) present, or (?) not preserved; not applicable

55. mesial transverse cingulid above gum: (0) absent, or (1) present below the trigonid but weak and discontinuous (as individual cusple e, or f, or both, but e and f are not connected), or (2) present in a continuous shelf below the trigonid (with no relations to protoconid and paraconid) and without occlusal function, or (3) cingular area present, and has occlusal contact with the upper molar, or (?) not preserved

56. cingulid shelf wrapping around the anteroexternal corner of the molar to extend to the lingual side of the trigonid below the paraconid: (0) absent, or (1) present, weakly developed, and its lingual part without occlusal function to upper molars, (2) present, strongly developed, and its lingual part without occlusal function to upper molars, or (3) present, weakly developed, and with occlusal function to upper molars, or (?) not preserved; not applicable

57. postcingulid (distal transverse cingulid) on lower molars: (0) absent, or (1) present, oblique, and connected to hypoconulid, or (2) present, horizontal above the gum level, or (?) not preserved

58. interlocking mechanism between two adjacent lower molars: (0) absent, or (1) present, posterior cingular cusple d (or the base of the hypoconulid) of the preceding molar fits in between cingular cusple e and f of the succeeding molar, or (2) present, posterior cingular cusple d fits between cingular cusple e and cusple b of the succeeding molar, or (3) present, posterior cingular cusple d of the preceding molar fits into an embayment or vertical groove of the anterior aspect of cusple b the succeeding molar, or (?) not preserved

59. size ratio of the posterior lower molars: (0) last three postcanines form a series of decreasing size: the penultimate molar is larger than the ultimate molar but smaller than the preceding molar, or (1) penultimate molar is the largest of the molars, or (2) ultimate molar is the largest, or (?) not preserved, not applicable

60. trigonid configuration on lower molars: (0) paraconid in anterointernal position and the paraconid-protocloid line forming an oblique angle to longitudinal axis of tooth, or (1) paraconid lingually positioned and the paraconid-protocloid line forming a more transverse triangle to the longitudinal axis of the tooth, or (2) paraconid linguually positioned and appressed to the metaconid ("twinned"). or (?) not preserved; not applicable

61. orientation of the paracristid (crest between cusps a and b) relative to the longitudinal axis of the molars (separate from character 60 because of different distribution of the a-b crest among mammals with non-triangulated molars): (0) longitudinal orientation, or (1) oblique, or (2) nearly transverse, or (?) not applicable; not preserve

62. mesiolingual surface of paraconid on lower molars (applicable only to taxa with triangulation of molar cusps): (0) rounded, or (1) forming a keel, or (?) not preserved; not applicable

63. molar (m2) trigonid/talonid width ratio: (0) narrow (talonid <=40% of trigonid), or (1) wide (talonid 40-70% of the trigonid width), or (2) talonid is equal to or wider than trigonid, or (?) not applicable

64. lower molar hypoflexid (the labial embayment between trigonid part and the talonid or the posterior heel located between the protoconid and hypoconid above the cingulid level: (0) absent or shallow, or (1) deep (but less than 50% of the talonid width), or (2) very deep (>=60% of the width of the talonid), or (?) not applicable

65. morphology of the talonid (posterior heel) of the molars: (0) absent, or (1) present as an incipient heel or a cingulid, or cingular cusple (d), or (2) present as a heel (with at least one functional cusp), or (3) present as a transverse V-shaped basin with two functional cusps, or (4) present as a functional basin, rimmed with three functional cusps (if the entoconid is vestigial, there is a functional crest to define the medial rim of the basin), or (?) not preserved; not applicable

66. hypoconulid (revised from Luo et al. 2002: they designate the distal cingulid cusple d as the homolog to hypoconulid in teeth with linear alignment of main cusps; they assume the cusp to be the hypoconulid if there is only single cusp on the talonid in teeth with reversed triangulation): (0) present, but not elevated above the cingulid level, or (1) present, elevated above the cingulid level, labially positioned, (2) present and larger, with occlusal contact to the upper molar (elevated above the cingulid level, lingually positioned), or (?) not preserved; not applicable

67. hypoconulid (distal cuspule d, after Crompton 1971): (0) absent, or (1) present, posterior, median and equal distant to entoconid and hypoconid, or (2) present and placed on the lingual rim of the talonid basin, or (?) not preserved; not applicable

68. hypoconulid anteroposterior orientation: procumbent versus reclined (applicable to taxa with at least twp cusps on talonid): (0) cusp tip reclined and posterior wall of hypoconulid is slanted and overhanging the root, or (1) cusp tip procumbent and the posterior wall of the cusp is vertical, or (2) cusp tip procumbent and the posterior wall is gibbous, or (?) not applicable

69. hypoconulid labial postcingulid (shelf) on lower molars (non-homologous with postcingulid of character 57 because of different relationship to talonid cusps; applicable to taxa with identifiable hypoconid and hypoconulid only: (0) absent, or (1) present as a crest descending mesiolabially from apex of hypoconulid to base of hypoconid, or (?) not preserved; not applicable

70. morphology of entoconid: (0) absent, or (1) present, or (2) present and twinned with hypoconulid, or (?) not preserved; not applicable

71. height of entoconid as compared to other cusps of talonid (applicable only to taxa with triangulated molar cusps and a talonid or cusp b): (0) absent on the talonid, or (1) lower than the hypoconulid (or even vestigial), or (2) subequal height as the hypoconulid, or (?) not preserved; not applicable
72. alignment of paraconid, metaconid, and entoconid on lower molars (applicable only to taxa with triangulation of trigonid cusps and entoconid present on talonid): (0) cusps not aligned, or (1) cusps aligned, or (?) not preserved; not applicable
73. aspect ratio in occlusal view (length versus width) of the functional talonid basin at cingulid level (based on m2): (0) longer than wide (or narrows posteriorly), or (1) length equals width, or (2) wider than long, or (?) not preserved; not applicable
74. elevation of the talonid (measured as the height of hypoconid from the cingulid on the labial side of the crown) relative to the trigonid (measured as the height of protoconid from the cingulid) (applicable only to teeth with reversed triangles): (0) hypoconulid/protoconid height ratio less than 20% (hypoconulid or cusp d is on the cingulid), or (1) hypoconulid/protoconid height ratio between 25-35% (talonid cusp elevated above the cingulid level), or (2) hypoconulid/protoconid height ratio between 40-50%, or (3) hypoconulid/protoconid height ratio between 50-60%, or (4) hypoconulid/protoconid height ratio between 60-70%, or (?) not applicable
75. width of upper stylar shelf (the area labial to the paracone-metacone): (0) absent, or (1) present and narrow, or (2) present and broad, or (3) present, broad and with a hypertrophied ectoflexus, or (?) unknown; not applicable
76. morphology of labial cingulum of upper molars: (0) absent or weak, or (1) distinctive cingulum, straight, or (2) distinctive cingulum with strong ectoflexus (but without hypertrophied stylar cusps), or (3) wide cingulum with ectoflexus, plus individualized and hypertrophied stylar cusps, or (4) cingulum crenulated with distinctive and even-sized multiple cuspules, or (?) not preserved
77. upper molars with a functional lingual protocone or pseudoprotocone that grinds against a basin on the lowers: (0) absent, or (1) present, or (?) not preserved; uncertain
78. transverse width of the protocone on upper molars (applicable only to taxa with protocone present: M2 measured where possible): (0) narrow (distance from protocone apex to paracone apex less than 0.60 of total tooth width), or (1) strongly transverse (distance from protocone apex to paracone apex greater than 0.60 of total tooth width), or (?) not preserved; not applicable
79. anteroposterior development of the lingual region on the upper molars (applicable only to taxa with triangulation of molar cusps and ocluding lingual portion of the upper molar; for the taxa with conules, this is measured between the paraconule and metaconule; for those taxa without conules, this is measured as the length of the tooth labial to the base of paracone; M2 measured where possible): (0) narrow (anteroposterior distance medial to the paracone and metacone less than 0.30 of total tooth length), or (1) moderate development (distance between position of conules = 0.31-0.50 of total tooth length), or (2) long (distance between conules greater than 0.51 of total tooth length), or (?) not preserved; not applicable
80. conules on the upper molars (character applicable to mammals with triangulation of molar cusps and a functional lingual cusp): (0) absent, or (1) present but weak and without cristae, or (2) conules distinctive, with cristae, or (?) not preserved; not applicable
81. relative height and size of the paracone (cusp B) and metacone of the upper molars: (0) paracone higher than metacone, or (1) metacone is higher and larger than paracone, or (?) not preserved; not applicable
82. centrocrista between the paracone and metacone of upper molars (applicable only to taxa with well-developed metacone and distinctive wear facets 3 and 4): (0) straight, or (1) V-shaped, with labially directed postparacrista and premetacrista, or (?) not preserved; not applicable
83. upper molars cuspule E (an enlarged version of E would be the metastyle, after Crompton 1971): (0) present, or (1) absent, or (?) not preserved; not applicable
84. upper molars interlock: (0) absent, or (1) tongue-in-groove interlock, or (?) not preserved
85. M1 - number of cusps within the main functional straight cusp row (if there are multiple rows, the labial row is designated): (0) three main functioning cusps, or (1) four main functioning cusps or more, or (?) not preserved; not applicable
86. multicuspate m1 - number of cusps within the main functional straight multi-cusp row (if there are multiple rows, the labial row is designated): (0) three main functioning cusps, or (1) four main functioning cusps or more, or (?) not preserved; not applicable
87. outline of m1: (0) oval-shaped, or (1) laterally compressed, or (2) oblong with a slight labial bulge, or (3) oblong with a strong labial bulge, or (4) triangular or tear-drop shaped, or (5) rectangular (or slightly rhomboidal)
88. aspect ratio of M1: (0) longer than transversely wide (oval-shaped or spindle-shaped), or (1) transversely wider than long (triangular outline), or (2) transversely wide (dumb-bell shaped), or (3) rectangular or nearly so, or (?) not preserved
89. multi-cuspatc row in the upper molars: cusp height gradient within the individual longitudinal rows of cusps: (0) cusps in a row with more or less equal height, or (1) distal cusp highest, with a gradient of anteriorly decreasing height, or (?) not preserved; not applicable
90. lower molars with multicuspate rows - U-shaped ridge: (0) U-sha ed ridge (anterior crest) absent at the mesial end of lower molar with open valley-basin between longitudinal cusp rows, or (1) presence of the U-shaped ridge (anterior crest) at mesial end of lower molars enclosing the valley-basin between longitudinal cusp rows, or (?) not applicable
91. multicuspate M2 with longitudinal multicuspate rows - lingual offset with M1: (0) upper M2 lingually offset from M1 so that the lower m2 lingual row occludes the lingual side of the M2 upper labial row, or (1) m2 labial row occludes to the labial side of the M2 labial row, or (?) not preserved; not applicable
92. multicuspate lower molars: cusp height ratio within the labial longitudinal row: (0) the first cusp (b1 by the designation of Butler 2000) is the highest so that the labial cusp row forms a series of decreasing height posteriorly,
Molar wear patterns (12 characters)

93. functional development of occlusal facets on individual molar cusps: (0) absent for lifetime, or (1) absent at eruption but developed later by wearing of crown, or (2) wear facets match upon eruption of teeth (inferred from the flat contact surface upon eruption), or (?) not preserved; not applicable
94. topographic relationship of wear facets to the main cusps: (0) wear facet absent or a simple longitudinal facet that extends the entire length of crown, or (1) lower cusps a, c support two different wear facets (facets 1 and 4) that contact the upper primary cusp A, or (2) lower cusps a, c support a single wear facet (4) that contacts the upper primary cusp B, or (3) multicuspate series, each cusp may support two wear facets, or (?) not preserved; homology uncertain
95. development and orientation of the prevallum/postvallid shearing: (0) absent, or (1) present and obtuse, or (2) present, hypertrophied and transverse, or (?) not preserved; not applicable
96. wear facet 1 (a single facet supported by cusp a and cusp c) and facet 2 (a single facet supported by cusp a and cusp b): (0) absent, or (1) present, or (?) not preserved, not applicable
97. upper molars - development of facet 1 and preprotocrista on upper molar (applicable to molars with reversed triangulation of molar cusps): (0) facet 1 (prevallum crest) is short, and does not extend to the stylocone area, or (1) wear facet 1 extends beyond into the hook-like area near the stylocone, or (2) a long preprotocrista (below the paracone-stylocone crest) is added to the prevallum shear and extends labially beyond paracone, or (?) not preserved; not applicable
98. differentiation of wear facet 3 (on the anterolabial aspect of talonid) and facet 4 (on the posterolabial aspect of the talonid): (0) absent, or (1) present, or (2) facets 3 and 4 hypertrophied on the flanks of the strongly V-shaped talonid, or (?) not preserved, not applicable
99. orientation of facet 4 (on the posterior aspect of the hypoconid): (0) present and oblique to long axis of tooth, or (1) present and forming a more transverse angle to long axis of tooth, or (?) not preserved; not applicable
100. morphology of the posteroslabial aspect of the talonid (the labial face of the hypoconid, applicable to taxa with fully basined talonids): (0) gently rounded, or (1) angular, or (?) not preserved; not applicable
101. wear pattern on talonid: (0) absent, or (1) present, or (?) not preserved
102. development of the distal metacristid (applicable only to taxa with triangulation of molar cusps): (0) distal metacristid present, or (1) distal metacristid absent, or (?) not preserved, not applicable
103. differentiation of wear facets 5 and 6 on the labial face of the entoconid: (0) absent, or (1) present, or (?) not preserved; not applicable
104. surficial features on the occluding surfaces of facets 5 and 6 in the talonid (only applicable to taxa with triangulation of molar cusps): (0) smooth surface on the talonid, or (1) multiple ridges within talonid basin, or (?) not preserved; not applicable

Other dental features (14 characters)

105. number of lower incisors: (0) three or more, or (1) two or fewer, or (?) not preserved
106. upper canine, presence versus absence, and size: (0) upper canine present and large, or (10 present and small, or (2) absent, or (?) not preserved
107. lower canine size, presence versus absence: (0) present and large, or (1) present and small, or (2) absent, or (?) not preserved
108. total number of lower premolars: (0) five or more, or (1) four premolars, or (2) three, or (3) two or fewer, or (?) not applicable (premolars not differentiated); not preserved
109. diastema separating P1 from P2: (0) absent, or (1) present, or (?) not applicable; not preserved
110. number of lower molars or molariform postcanines: (0) 6 or more, or (1) 4 to 5 molariforms, or (2) 3 molars or fewer, or (3) 2 molars, or (?) uncertain (postcanines undifferentiated); incompletely preserved
111. lower postcanine roots: (0) root division incipient or incomplete, or (1) roots divided, or (2) multiple roots (more than 3), or (?) not preserved
112. replacement of incisors and canines: (0) alternating and multiple replacement, or (1) diphyodont replacement or none, or (?) not preserved; not applicable
113. replacement of the premolariforms: (0) multiple replacement, or (1) one replacement or none, or (?) not preserved; not applicable
114. replacement of at least some functional molariforms: (0) present, or (1) absent, or (?) unknown
115. procumbent and enlargement of the anteriormost lower incisors: (0) absent, or (1) both procumbent and enlarged (at least 50% longer than second functional incisors), or (?) not preserved; not applicable
116. bicuspate second upper incisor: (0) absent, or (1) present, or (?) not preserved; not applicable
117. enlarged diastema in the lower incisor-canine region (better developed in older individuals): (0) absent, or (1) present and behind the canine, or (2) present and behind the posterior incisor, or (?) not preserved; not applicable
118. enamel microstructure: (0) synapsid columnar enamel (prismless), or (1) ‘transitional’ character state, or (2) plesiomorphic prismatic enamel, or (?) unknown

Vertebrae (9 characters)
119. proatlas neural arch as a separate ossification in adults: (0) present, or (1) absent, or (?) not preserved
120. fusion of atlas neural arch and intercentrum in adults: (0) unfused, or (1) fused, or (?) not preserved
121. atlas rib in adults: (0) present, or (1) absent, or (?) not preserved
122. prezygapophysis on axis: (0) present, or (1) absent, or (?) not preserved
123. fusion of dens to axis: (0) unfused, or (1) fused, or (?) not preserved
124. rib of axis in adults: (0) present, or (1) absent, or (?) not preserved
125. postaxial cervical ribs in adults: (0) present, or (1) absent, or (?) not preserved
126. thoracic vertebrae: (0) 13 thoracic vertebrae, or (1) 15 or more, or (?) unknown
127. lumbar ribs: (0) unfused to vertebrae, or (1) syntosed to vertebrae to form transverse processes, or (?) not preserved

Shoulder girdle (16 characters)
128. interclavicle in adults: (0) present, or (1) absent, or (?) not preserved
129. contact relationships in adults between the interclavicle (embryonic membranous element) and the sternal manubrium (embryonic endochondral element) (assuming the homologies of these elements by Klima): (0) two elements distinct from each other, posterior end of interclavicle abuts anterior border of manubrium, or (1) two elements distinct from each other, the interclavicle broadly overlaps the ventral side of the manubrium, or (2) complete fusion of the embryonic membranous and endochondral elements, or (?) not preserved
130. cranial margin of the interclavicle: (0) anterior margin is emarginated or flat, or (1) with a median process, or (?) not preserved
131. claviculo-sternal apparatus joint (assuming that homologous elements of interclavicle and manubrium are fused to each other in therians): (0) immobile, or (1) mobile, or (?) not preserved
132. acromioclavicular joint: (0) extensive articulation, or (1) limited articulation, or (?) not preserved
133. curvature of the clavicle: (0) boomerang-shaped, or (1) slightly curved, or (?) not preserved
134. scapula - supraspinous fossa: (0) absent, or (1) weakly developed, or (2) fully developed and present along the entire dorsal border of scapula, or (?) not preserved
135. scapula - acromion process: (0) short stump (level with the glenoid, or behind the glenoid), or (1) hook-like and extending below the glenoid, or (?) not preserved
136. scapula - a distinctive fossa for the teres major muscle on the lateral aspect of the scapular plate: (0) absent, or (1) present, or (?) not preserved
137. procoracoid (as a separate element in adults): (0) present, or (1) fused to the sternal apparatus and absent in adult, or (?) not preserved
138. procoracoid foramen: (0) present, or (1) absent, or (?) unknown
139. coracoid: (0) large, with posterior process, or (1) small, without posterior process, or (?) not preserved
140. size of the anteriormost sternal element ('manubrium') relative to the succeeding sternebrae in the sternal apparatus in adults: (0) large, or (1) small, or (?) not preserved
141. orientation ('facing' of articular surface) of the glenoid (relative to the plane or axis of the scapula): (0) nearly parallel to the long axis of scapula and facing posterolaterally, or (1) oblique to the long axis of scapula and facing more posteriorly, or (2) articular surface of glenoid is perpendicular to main plane of the scapular plate, or (?) not preserved
142. shape and curvature of the glenoid: (0) saddle-shaped, oval and elongate, or (1) uniformly concave and more rounded in outline, or (?) not preserved
143. medial surface of the scapula: (0) convex, or (1) flat, or (?) not preserved

Forelimb (12 characters)
144. humeral head: (0) subspherical, weakly inflected, or (1) spherical and strongly inflected, or (?) not preserved
145. intertubercular groove that separates deltopectoral crest from lesser tubercle: (0) shallow and broad intertubercular groove, or (1) narrow and deep intertubercular groove, or (?) not preserved
146. size of the lesser tubercle of humerus (relative to greater tubercle): (0) wider than the greater tubercle, or (1) narrower than the greater tubercle, or (?) not preserved
147. torsion between the proximal and distal ends of the humerus: (0) strong (>=30º), or (1) moderate (30-15º) or (2) weak (< 15º), or (?) not preserved
148. ventral extension of the deltopectoral crest or position of deltoid tuberosity: (0) not extending beyond the midpoint of the humeral shaft, or (1) extending ventrally (distally) past the midpoint of the shaft, or (?) not preserved
149. ulnar articulation on the distal humerus: (0) bulbous ulnar condyle, or (1) cylindrical trochlea (in anterior view) with vestigial ulnar condyle (in anterior view), or (2) cylindrical trochlea without ulnar condyle (cylindrical trochlea has extended to anteriorventral side), or (?) not preserved

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150. radial articulation on the distal humerus: (0) distinct and rounded condyle in both anterior (ventral) and posterior (dorsal) aspects of the structure that does not form continuous synovial surface with the ulnar articulation in anterioventral view, or (1) radial articulation forms a rounded condyle anteriorly but its posterior surface is nearly cylindrical, or (2) capitulum (radial articulating structure that forms continuous synovial surface with ulnar trochlea; the surface is cylindrical in both anterior and posterior aspects), or (?) not preserved

151. entepicondyle and ectepicondyle of the humerus: (0) robust, or (1) weak, or (?) not preserved

152. rectangular shelf for the supinator ridge extended from the ectepicondyle: (0) absent, or (1) present, or (?) not preserved

153. styloid process of the radius: (0) weak, or (1) strong, or (?) not preserved

154. enlargement of the scaphoid with a distomedial projection: (0) absent, or (1) present, or (?) not preserved

155. size and shape of the hamate (unciform) on wrist: (0) anteroposteriorly compressed (wider than long in dorsal view), or (1) mediolaterally compressed (longer than wide) or (?) not preserved

Pelvic girdle (3 characters)

156. acetabular dorsal emargination (cotyloid notch of Kühne 1956): (0) open (emarginated), or (1) closed (with a complete rim), or (?) not preserved

157. suture of the ilium, ischium and pubis within the acetabulum in adults: (0) unfused, or (1) fused, or (?) not preserved

158. ischiatic dorsal margin and tuberosity: (0) dorsal margin concave (emarginated) and ischiatic tuberosity present, or (1) dorsal margin concave and ischiatic tuberosity hypertrophied, or (2) dorsal margin straight and ischiatic tuberosity small, or (?) not preserved

Hind limb (11 characters)

159. head of femur is inflected and set off from the shaft by a neck: (0) neck absent (and head oriented dorsally), or (1) neck present and head inflected medially; head spherical and inflected, or (?) not preserved

160. fora for the acetabular ligament on femoral head: (0) absent, or (1) present, or (?) unknown

161. greater trochanter: (0) directed dorsolaterally, or (1) directed dorsally, or (?) not preserved

162. orientation of the lesser trochanter: (0) on medial side of shaft, or (1) on ventromedial or ventral side of shaft, or (?) not preserved

163. size of the lesser trochanter: (0) large, or (1) small, or (?) not preserved

164. patellar facet ('groove') of the femur: (0) absent, or (1) shallow and weakly developed, or (2) well developed, or (?) not preserved

165. proximaltubercle or tuberosity of the femur: (0) large and hook-like, or (1) indistinctive, or (?) not preserved

166. distal tibial malleolus: (0) weak, or (1) distinct, or (?) not preserved

167. fibula contacting distal end of femur: (0) present, or (1) absent, or (?) not preserved

168. distal fibular styl oid process: (0) weak or absent, or (1) distinct, or (?) not preserved

169. fibula contacting calcaneus (= 'tricontact upper ankle joint' of Szalay): (0) extensive contact, or (1) reduced, or (2) mortise and tendon contact of fibula to ankle, or (?) not preserved

Ankle joint (10 characters)

170. superposition (overlap) of the astragalus over the calcaneus (lower ankle joint): (0) little or absent, or (1) weakly developed, or (2) present, or (?) not preserved

171. orientation of the sustentacular facet of the calcaneus with regard to horizontal plane astragalus over (lower ankle joint): (0) nearly vertical, or (1) oblique (<70°) to nearly horizontal, or (?) not preserved

172. astragalar neck: (0) absent, or (1) weakly developed, or (2) present, or (?) not preserved

173. astragalar trochlea: (0) absent, or (1) present, or (?) not preserved

174. calcaneal tubercle: (0) short, without terminal swelling, or (1) elongate, vertically deep, and mediolaterally compressed, with terminal swelling, or (?) not preserved

175. peroneal process and groove of the calcaneus: (0) forming laterally directed shelf; and without a distinct process, or (1) weakly developed with shallow groove on lateral side of process, or with a distinct peroneal process, or (?) not preserved

176. contact of the cuboid on the calcaneus (following the orientation identified by Lewis 1983; Szalay 1993b): (0) on the anterior (distal) end of calcaneus (cuboid aligned with long axis of calcaneus), or (1) on the anteromedial aspect of the calcaneus, or (?) not preserved

177. orientation and placement of the sustentacular facet on the calcaneus: (0) the sustentacular facet is vertically oriented on the medial edge of the calcaneus, or (1) the sustentacular facet is on the dorsal aspect of the calcaneus and positioned medial to anteromedial to the astragalar facet on the calcaneus, or (2) the sustentacular facet is on the dorsal aspect of calcaneus and positioned anterior to the astragalar facet on the calcaneus, or (?) not preserved

178. relationships of the proximal end of metatarsal V to the cuboid: (0) metatarsal V is offset from the cuboid, or (1) metatarsal V is far offset from the cuboid, so that it contacts the calcaneus, or (2) metatarsal V is aligned with the cuboid, or (?) not preserved
179. angle of metatarsal III to the calcaneus (which indicates how much the sole of the foot is 'bent' from the long axis of the ankle): (0) metatarsal III is aligned with (or parallel to) an imaginary line through the long axis of the calcaneus, or (1) metatarsal III is oriented obliquely to an imaginary line through the long axis of the calcaneus, or (?) not preserved

Other postcranial characters (2 characters)
180. sesamoid bones in flexor tendons: (0) absent, or (1) present and unpaired, or (2) present and paired, or (?) not preserved
181. external pedal (tarsal) spur in male: (0) absent, or (1) present, or (?) not preserved

Basicranium (46 characters)
182. external size of the cranial moiety of squamosal: (0) narrow, or (1) broad, or (?) not preserved
183. participation of the cranial moiety of the squamosal to the braincase: (0) does not participate in the endocranial wall of the braincase, or (1) participates in the endocranial wall of the braincase, or (?) not preserved
184. entoglenoid constriction (neck) between the craniomandibular joint (or glenoid) and the cranial moiety of the squamosal (only applicable to taxa with the dentary-squamosal joint; this character is best seen in the ventral view): (0) absent, or (1) present, or (?) not preserved
185. postglenoid depression on squamosal (= 'external auditory meatus'): (0) present as the post-craniomandibular joint sulcus, or (1) absent, or (2) present, or (?) not preserved
186. position of the craniomandibular joint: (0) posterior or lateral to the level of the fenestra vestibuli, or (1) anterior to the level of fenestra vestibuli, or (0/1 polymorphic), or (?) not preserved
187. orientation of the glenoid on the squamosal for the craniomandibular joint: (0) on the inner side of the zygoma and facing ventromedially, or (1) on platform of the zygoma and facing ventrally, or (0/1 polymorphic), or (?) not applicable
188. postglenoid process: (0) absent, or (1) present as a distinctive process, or (0/1 polymorphic), or (?) not applicable; not preserved
189. postglenoid foramen within the squamosal bone: (0) absent, or (1) present, or (?) not preserved
190. basisphenoid wing on the ventral aspect of the skull: (0) present, overlapping a part of or the whole cochlear housing, or (1) basisphenoid wing is absent, the bone does not overlap the petrosal cochlear housing, or (?) not preserved or not visible
191. relationship of the pars cochlearis to the lateral lappet of basioccipital: (0) pars cochlearis is entirely covered by basioccipital, or (1) pars cochlearis is partially covered by basioccipital,. or (2) pars cochlearis fully exposed as promontorium, or (?) not preserved
192. the medial flat facet of the promontorium of the pars cochlearis: (0) medial flat face is present on pars cochlearis, or (1) medial aspect of the promontorium is inflated and convex, or (?) not preserved
193. external outline and morphology of the promontorium: (0) triangular, with steep and slightly concave lateral wall, or (91) elongate and cylindrical petrosal cochlear housing, or (2) bulbous and oval-shaped promontorium, or (?) not preserved
194. cochlea: (0) short and uncoiled, or (1) elongate and partly coiled, or (2) elongate and coiled to about 360º, or (?) not preserved
195. morphology of the internal acoustic meatus: (0) the region for VII and VIII cranial nerves is poorly ossified and no clearly developed internal auditory meatus is present, or (1) the floor is well ossified and meatus is a deep tube, or (2) present as a shallow depression, or (3) present and the floor is developed as the cribiform foramina for auditory nerve, or (1/2 polymorphic), or (?) not preserved
196. primary bony lamina within the cochlear canal: (0) absent, or (1) present, or (?) preserved but not exposed; not preserved
197. secondary bony lamina for the basilar membrane within the cochlear canal: (0) absent, or (1) present, or (?) unknown (in the intact specimens); not preserved
198. crista interfenestralis: (0) horizontal and extending to base of paroccipital process, or (1) vertical, delimiting the back of the promontorium, or (?) not preserved
199. post-tympanic recess: (0) absent, or (1) present, or (?) not preserved
200. caudal tympanic process of the petrosal: (0) absent, or (1) present, or (2) caudal tympanic process notched, or (0/1 polymorphic), or (?) not preserved
201. the prootic canal: (0) prootic canal absent, or (1) prootic canal present, and its tympanic aperture is a distinct foramen (and separated from the pterygoparoccipital foramen if the latter is present), or prootic canal is present, and its tympanic aperture is confluent with the pterygoparoccipital foramen, or (1/2 polymorphic), or (?) not preserved
202. lateral trough floor anterior to the tympanic aperture of the prootic canal and/or the primary facial foramen: (0) open lateral trough but no bony floor, or (1) present, or (2) lateral trough absent, or (?) not preserved
203. enclosure of the geniculate ganglion by bony floor of the petrosal: (0) absent, or (1) present, or (?) unknown
204. anterovelventral opening of the cavum epiptericum: (0) present, or (1) present with a reduced size, or (2) present and partially enclosed by the petrosal, or (3) enclosed by both the alisphenoid and petrosal, or (?) not preserved
205. the anterior lamina of the petrosal and ascending process of the alisphenoid and their relationships to the exit of the mandibular branch (V3) of the trigeminal nerve: (0) V3 trigeminal foramen placed at the suture of the alisphenoid ascending process and the anterior lamina of petrosal, or (1) V3 trigeminal foramen placed within the enlarged anterior lamina of the petrosal, or (2) double trigeminal foramina within the anterior lamina in addition to the trigeminal foramen at anterior border with alisphenoid, or (3) V3 trigeminal foramen within the ascending process of the alisphenoid, or (2/3 polymorphic), or (?) not preserved

206. the 'quadrate ramus' of the alisphenoid: (0) forming a rod overlapping with the anterior part of the lateral flange, or (1) quadrate ramus absent, or (?) not preserved

207. orientation of the anterior part of the lateral flange: (0) horizontal shelf, or (1) ventrally directed, or (2) medially directed and contacting the promontorium, or (3) vestigial or absent, or (?) not exposed; not preserved

208. vertical component of the lateral flange ('L-shaped' and forming a vertical wall to pterygoparoccipital foramen): (0) present, or (1) absent, or (?) not preserved

209. vascular foramen in the posterior part of the lateral flange (and anterior to the pterygoparoccipital foramen or the 'ramus superior foramen'): (0) present, or (1) absent, or (?) unknown

210. relationship of the petrosal lateral flange to the valve process (or the anterior paroccipital process that bears the crista): (0) widely separated, or (1) narrowly separated, or (2) continuous bone formed by petrosal, or (?) uncertain; not preserved

211. morphotype of the pterygoparoccipital foramen (for the ramus superior of the stapedial artery): (0) laterally open notch, or (91) foramen enclosed by the petrosal or squamosal or both, or (?) not preserved

212. position of the pterygoparoccipital foramen relative to the fenestra vestibuli: (0) the pterygoparoccipital foramen is posterior or lateral to the level of the fenestra vestibuli, or (1) the foramen is anterior to the level of the fenestra vestibuli, or (0/1 polymorphic), or (?) not applicable; not preserved

213. bifurcation of paroccipital process - presence versus absence (modified from character used in previous studies): (0) bifurcation absent, or (91) bifurcation present, or (?) not preserved

214. posterior paroccipital process of petrosal: (0) no ventral projection below the level of its surrounding structures, or (1) projecting below the surrounding structures, or (?) uncertain; not preserved

215. morphological differentiation of the anterior paroccipital region: (0) anterior paroccipital region is indistinct from surrounding structures, or (1) anterior paroccipital region is bulbous and distinctive from the surrounding structures, or (2) anterior paroccipital region has a distinct crista parotica, or (?) not preserved

216. epitympanic recess lateral to the crista parotica: (0) absent, or (1) present (as a large depression on the crista parotica), or (0/1 polymorphic), or (?) not applicable; not preserved

217. relationship of the squamosal on the paroccipital process: (0) squamosal covers the entire paroccipital region, or (1) no squamosal cover on anterior paroccipital paroccipital region, or (2) squamosal covering a part of the paroccipital region, but not on the crista parotica, or (?) not preserved

218. medial process of the squamosal reaching towards the foramen ovale: (0) absent, or (1) present, or (?) not preserved

219. stapedial artery sulcus on the petrosal: (0) absent, or (1) present, or (0/1 polymorphic), or (?) not preserved

220. transpromontorial sulcus for internal carotid artery on the pars cochlearis: (0) absent, or (1) present, or (?) not preserved

221. site for the attachment of the tensor tympani muscle on the petrosal: (0) absent, or (1) present on a shallow anterior embayment of the lateral trough, or (2) present as a longitudinal groove on the lateral trough, or present on an oval-shaped fossa, or (?) not preserved; not exposed

222. bullar process of the alisphenoid: (0) absent, or (1) present, or (?) not preserved

223. hypotympanic recess in the junction of the alisphenoid, squamosal and petrosal: (0) absent, or (1) present, or (?) not preserved

224. separation of the fenestra cochlea from the jugular foramen: (0) fenestra cochlea and jugular foramen within the same depression, or (1) separate, or (?) not preserved

225. channel of the perilymphatic duct: (0) open channel and sulcus, or (1) channel partially or fully enclosed, or (0/1 polymorphic), or (?) not preserved

226. stapedial muscle fossa: (0) absent, or (1) present and in alignment with the crista interfenestralis, or (2) present and lateral to the crista interfenestralis, or (?) uncertain; not preserved

227. hypoglossal foramen: (0) indistinct, either confluent with the jugular foramen or sharing a depression with the jugular foramen, or (1) separated from the jugular foramen, or (?) not preserved

**Incus (quadrate) characters (9 characters)**

228. geometry (shape) of the incudo-mallear contact: (0) trochlear (convex and cylindrical) surface of the incus, or (1) trough- or saddle-shaped contact on the incus, or (2) flat surface, or (?) unknown

229. alignment of the incus and malleus by the 'centre of mass': (0) anteroposterior, or (1) posteroanterior to anterior, or (2) dorsoventral, or (?) unknown

230. presence of a quadrate-incus neck (separation of the dorsal plate and the trochlea; this represents the differentiation between the "body" and crus brevis of the incus): (0) absent, or (1) present, or (?) unknown

231. stapedial process (cresus longum) of the incus-quadrate: (0) absent, or (1) present, or (?) unknown

232. dorsal plate (= crus brevis) of the quadrate-incus: (0) broad plate, or (1) pointed triangle, or (2) reduced, or (?) unknown
233. incus: angle of the crus brevis to crus longum: (0) alignment of stapedial process (crus longum) and the dorsal plate (crus brevis) (or an obtuse angle between the two structures), or (1) perpendicular, or (2) acute angle of the crus brevis and crus longum, or (?) unknown

234. primary suspension of the incus-quadrate on the basicranium: (0) by squamosal and quadratejugal, or (1) by squamosal only, or (2) by petrosal, or (?) not preserved

235. quadratejugal notch in squamosal: (0) present as an independent element in the adult, or (1) absent, or (?) not preserved

236. morphology of the stapes: (0) columniform-macroperforate, or (1) columniform-imperforate (or microimpergorate), or (2) bicornuate-perforate, or (?) not preserved

Palatal, orbital and zygomatic characters (14 characters)

237. bony secondary palate: (0) ending anterior to the posterior end of the tooth row, or (1) level with the posterior end of the tooth row, or (2) ending posterior to the tooth row, or (?) not preserved

238. relationship of the maxilla to subtemporal margin of orbit: (0) participating in the rounded subtemporal margin of the orbit, or (1) forming a well defined edge along the subtemporal margin, or (?) not preserved

239. pterygopalatine ridges: (0) present, or (1) absent, or (?) not preserved

240. transverse process of pterygoid: (0) present and massive, or (1) present but reduced (as the hamulus), or (2) greatly reduced or absent, or (0/1 polymorphic), or (1/2 polymorphic), or (?) not preserved

241. basiphysial constriction (= palatal width anterior to the basisphenoid): (0) strongly developed (very narrow anterior to the basisphenoid), or (1) intermediate (wide anterior to the basisphenoid), or no constriction (palatal width is as broad at the basisphenoid as the internal choanae), or (?) not preserved

242. vault of the naso-oral pharyngeal passage near the pterygoid-basisphenoid junction: (0) roof of the pharynx is V-shaped in transverse section, narrowing towards the basisphenoid, or (1) roof of the pharynx is U-shaped in transverse section, or (?) not preserved

243. complete ossification of the orbital floor: (0) absent, or (1) present, or (?) not preserved

244. pattern of orbital mosaic as exposed externally: (0) alisphenoid contacts the frontal and parietal, thereby separating the petrosal anterior lamina from the orbitosphenoid in external view of the orbit, or (1) the petrosal anterior lamina contacts the orbitosphenoid thereby separating the alisphenoid from the frontal and parietal, or (0/1 polymorphic), or (1/2 polymorphic), or (?) not preserved

245. overhanging roof of orbit: (0) overhanging roof of orbit formed by prefrontal, or (1) overhanging roof of orbit absent, or (2) overhanging roof of orbit formed by frontal, or (?) not preserved

246. outline of facial part of lacrimal: (0) large, triangular, and pointed anteriorly, or (1) small and rectangular or crescentic, or (2) excluded from the facial (and pre-orbital) part of the skull, or (?) not preserved

247. pila antotica: (0) present, or (1) absent in adult, or (?) unknown

248. frontal-parietal suture on the alisphenoid: (0) dorsal plate of the alisphenoid contacting the frontal by the anterior corner, or (1) dorsal plate of alisphenoid has more extensive contact to the frontal, or (?) not applicable; not preserved

249. jugal on the zygoma: (0) anterior part of jugal extends on the facial part of the maxillary and forming a part of the anterior orbit, or (1) anterior part of jugal does not reach the facial part of the maxillary and is excluded from the anterior part of the orbit, or (?) not preserved

250. maximum vertical depth of the zygomatic arch relative to the length of the skull (this character is designed to indicate the robust versus gracile nature of the zygomatic arch): (0) between 10-20%, or (1) between 5-7%, or (?) not preserved

Occipital and other skull characters (13 characters)

251. the posterior opening of the post-temporal canal: (0) at the junction of petrosal, squamosal and tabular, or 91) between the petrosal and squamosal, or (?) not preserved

252. the anterior ascending vascular channel (for the arteria diploëtica magna) in the temporal region: (0) open groove, or (1) partially enclosed in a canal, or (2) completed enclosed in a canal or endocranial, or (?) not preserved

253. the lambdoidal crest: (0) crest overhanging the concave or straight supraocciput, or (1) weak crest with convex dorsal part of the occipitalplate, or (0/1 polymorphic), or (1/2 polymorphic), or (?) not preserved

254. the sagittal crest: (0) prominently developed, or (1) weakly developed, or (2) absent, or (1/2 polymorphic), or (?) unknown

255. the tabular bone: (0) present, or (1) absent, or (?) unknown

256. shape of the occipital condyles: (0) bulbous, or (1) ovoid, or (2) subcylindrical, or (1/2 polymorphic), or (?) not applicable

257. the occiput slope: (0) occiput slopes posterodorsally (or is vertically oriented) from the occipital condyles, or (1) occiput slopes anterodorsally from the occipital condyles, or (?) not preserved

258. foramina on the dorsal surface of the nasal bone: (0) absent, or (1) present, or (?) not preserved

259. septomaxilla: (0) present and with a ventromedial shelf, or (1) present and without the septomaxillary shelf, or (3) absent, or (?) unknown
premaxillary internarial process: (0) present, (1) absent, or (?) uncertain

facial part of premaxillary borders on nasal: (0) absent, or (1) present, or (0/1 polymorphic), or (?) uncertain

ossified ethmoidal cribiform plate of nasal cavity: (0) absent, or (1) present, or (?) unknown

posterior excavation of the nasal cavity into the bony sphenoid complex: (0) absent, or (1) present, or (2) present and partitioned from the nasal cavity, or (?) unknown

Cranial vault and brain endocast characters (10 characters)

external bulging of braincase in the parietal region: (0) absent, or (1) expanded, or (2) greatly expanded, or (1/2 polymorphic), or (?) not preserved

the interparietal: (0) present as a separate element in the adult, or (1) absent, or (?) not preserved

bony tentorium septum: (0) present, or (1) absent, or (?) unknown

anterior expansion of the vermis (central lobe of cerebellum): (0) absent, or (1) present, to cover and conceal mesencephalon on endocast, or (?) unknown

overall size of vermis: (0) small, or (1) enlarged, or (?) unknown

lateral cerebellar hemisphere (excluding the paraflocculus): (0) absent, or (1) present, or (?) unknown

lateral extension of the paraflocculus: (0) less than 30% of total cerebellar width, or (1) more than 30% of cerebellar width, or (?) unknown

external division of the endocast between the olfactory lobe and cerebral hemisphere (presence versus absence of the circular sulcus that defines the external aspect of the olfactory lobe): (0) absent, or (1) present, or (?) unknown

anterior expansion of cerebral hemisphere: (0) absent, or (1) developed, or (?) unknown

cerebral hemisphere (for each hemisphere, not the combined width of the posterior hemispheres): (0) absent, or (1) present, or (?) unknown

Jaw characters (2)

direction of jaw movement during occlusion: (0) dorsomedial movement, or (1) dorsomedial movement with a significant medial component, or (2) dorsoposterior movement, or (0/2 polymorphic), or (?) not preserved

mode of occlusion as inferred from the mandibular symphysis: (0) bilateral (with more or less rigid symphysis), or (1) unilateral (with mobile symphysis) or (?) not preserved

Following pages: data matrix of Luo et al. (2002) taken from Archives, Acta Palaeontologica Polonica website
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Tritheledontids
Adelobasileus
Sinoconodon
Morganucodon
Megazostrodon
Dinnetherium
Haldanodon
Hadrocodium
Kuehneotherium
Shootherium
Ambondro
Ausktribosphenos
Bishops
Steropodon
Teinolophos
Obdurodon
Ornithorhynchus
Gobiconodon
Amphilestes
Jeholodens
Priacodon
Trioracodon
Haramiyavia
Plagiaulacidans
Cimolodontans
Tinodon
Zhangheotherium
Peramus
Amphitherium
Dryolestes
Henkelotherium
Vincelestes
Kielantherium
Aegialodon
Deltatheridium
Asiatherium
Kokopellia
Pucadelphys
Didelphis
Pappotherium
Erinaceus
Asioryctes
Prokennalestes
Montanalestes;
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END;

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6 Morganucodon,
7 Megazostrodon,
8 Dimetrodon,
9 Haldanodon,
10 Hadrocodium,
11 Kuehneotherium,
12 Shuotherium,
13 Ambydoros,
14 Auskribosphenos,
15 Bishops,
16 Steropodon,
17 Thrinolophos,
18 Odburodon,
19 Ornithorhynchus,
20 Gobiconodon,
21 Amphilestes,
22 Jeholodens,
23 Priacodon,
24 Trioracodon,
25 Haramayavia,
26 Plagiaulacidans,
27 Cimolodontans,
28 Tinodon,
29 Zhangwetherium,
30 Peramus,
31 Amphitherium,
32 Dryolestes,
33 Wenklotherium,
34 Vincelestes,
35 Kielantherium,
36 Aegialodon,
37 Deltatheridium,
38 Asiatherium,
39 Kokopellia,
40 Pucadelphys,
41 Didelphys,
42 Pappotherium,
43 Erinaceus,
44 Asioryctes,
45 Prokennalestes,
46 Montanalestes

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This thesis explores several lines of enquiry into the evolution, anatomy, palaeoecology and biogeography of monotreme mammals. It also presents a revised description of the Early Cretaceous mammal *Kollikodon ritchiei*, originally interpreted as a monotreme but which is identified in this thesis as a possible allotherian mammal. Conclusions have been drawn from the fossil material provided for the thesis and revised as new material has been discovered and incorporated into the investigations.

**MONOTREME MORPHOLOGY AND PALAEOONTOLOGY**

Tertiary and Cretaceous fossil monotremes (*Obdurodon* species; *Megalibgwilia ramsayi*; *Steropodon galmani*; *Teinolophos trusleri*) as well as the living platypus (*Ornithorhynchus anatinus*) and echidnas (*Tachyglossus aculeatus* and *Zaglossus bruijni*) were examined for this thesis. A musculo-skeletal study (done in collaboration with Prof. Farish A. Jenkins, Jr. of Harvard University) laid the anatomical groundwork for subsequent osteological studies.

**Tertiary ornithorhynchids**

Tertiary platypuses (Ornithorhynchidae: *Obdurodon* and *Monotrema* species) are similar in many ways to the living platypus, *Ornithorhynchus anatinus*. The very platypus-like skull of *Obdurodon dicksoni* from the early to middle Miocene of Riversleigh, Queensland was almost surprising in its likeness to *Ornithorhynchus* (although differences of the skull and dentary, along with possession of functional teeth in Tertiary platypuses, are noteworthy). It is remarkable that platypuses have actually changed so little over the known span of their temporal range (62 million years to the present). Differences include retention of a functional dentition in Tertiary ornithorhynchids and plesiomorphic features of the skull and dentary. The following conclusions about morphology and biology have been taken or revised from studies presented in this thesis.

Analysis and reconstruction of the skull of the Miocene platypus from Riversleigh, Obdurodon dicksoni, suggest that this robust, large-billed platypus was a derived northern side branch off the main line of ornithorhynchid evolution. A reconstruction of the skull, dentary and dentition of *Obdurodon dicksoni* was completed, based on nearly complete cranial and dental material. Detailed
comparisons of proportional differences suggest that the large, robust Obdurodon dicksoni differed from the living Ornithorhynchus in relative size and shape: Ornithorhynchus is distinguished by gracile proportions and reduction of many bony features. Perhaps another Obdurodon species, one more lightly built than the Riversleigh platypus, was ancestral to Ornithorhynchus.

Phylogenetic conclusions differ from previous analyses (Archer et al., 1992, 1993) in considering the northern Australian Ob. dicksoni to be derived in having a hypertrophied bill and dorsoventrally flattened skull and dentary. Well-developed coronoid and angular processes are identified on the dentaries of both Obdurodon dicksoni and Obdurodon insignis (where the coronoid process appears to have been broken at its root). Conversely, in Ornithorhynchus the mandibular processes are almost vestigial. The presence of functional teeth and the robust, flattened skull and dentary in Ob. dicksoni suggest differences in diet and lifestyle between this extinct ornithorhynchid and the living Ornithorhynchus (Musser & Archer 1998).

Certain features in the skull of Ob. dicksoni are more plesiomorphic than in Ornithorhynchus; these features help clarify the evolution of the bill structure in ornithorhynchids. A recent comprehensive study of the skull of Ornithorhynchus anatinus (Zeller, 1989a, b) was the basis for comparison of the skulls of Obdurodon dicksoni and Ornithorhynchus. A comparative study of the cranial foramina of Ob. dicksoni and Ornithorhynchus presented here provides insight into the evolution of the ornithorhynchid skull. Form seen in ontogeny in Ornithorhynchus suggests that the basic form of the bill in Ob. dicksoni (where the rostral crura meet at the midline) could be a model for the form of the bill in Ornithorhynchus (where the rostral crura meet at the midline in the embryonic platypus but diverge in the adult). Differences in the relative positions of cranial structures and in the relationships of certain cranial foramina indicate that the cranium may have become secondarily shortened in Ornithorhynchus, possibly evolving from a more elongate cranial base such as that of Ob. dicksoni (Musser & Archer 1998).

Aspects of soft anatomy previously not known for fossil ornithorhynchids are studied in Obdurodon. Exquisite preservation of the Obdurodon dicksoni skull has permitted reconstruction of parts of the soft anatomy. Results suggest that 1) dorsal and possibly ventral frontal shields (sensory extensions of the skin of the bill) were probably present in Ob. dicksoni (as in Ornithorhynchus), evidenced by the presence and placement of foramina for a branch of the large trigeminal nerve that in Ornithorhynchus innervates the dorsal shield; 2) a larger marginal cartilage formed the contours of the bill in Ob. dicksoni, indicated by the proportionately deeper lateral margins of the bill (Fig. 2);
and 3) deeply dished areas on the palate in the region of the epithelial ridges in *Ornithorhynchus* may have housed comparatively huge, ridge-like epithelial structures in *Ob. dicksoni*, taking the place of the missing anterior dentition (the incisors and canines) as do the much smaller epithelial ridges in *Ornithorhynchus*. Outgrowths of epithelium possibly helped to hold the shallow-rooted molars in place. The trend towards elaboration of oral epithelium, seen at its most extreme in the replacement of true teeth by epithelial pads in *Ornithorhynchus*, seems to have thus been underway by the Miocene (Musser and Archer, 1998).

Two upper molars from Mammalon Hill (Etadunna Formation, late Oligocene, central Australia) represent a new species of *Obdurodon*. Two left upper second molars have been recovered from the Mammalon Hill locality, Etadunna Formation, central Australia. These molars represent a second species of fossil ornithorhynchid (*Obdurodon griffithsi* sp. nov.) from this region. In some features (e.g., extent and pattern of wear), this new species appears to be intermediate between the Paleocene ornithorhynchid *Monotrematum sudamericanum* from Patagonia and the early to middle Miocene ornithorhynchid *Ob. dicksoni*. One of the most remarkable features of ornithorhynchid molars is conservatism of form; surprisingly, however, the two molars of *Ob. griffithsi* differ in number and structure of buccal cuspules as well as root number (the occurrence of multiple roots being an ornithorhynchid specialisation), suggesting that these features are more plastic than had been previously thought. The presence of two distinct ornithorhynchid species within a single geological formation suggests that this lineage was somewhat speciose at least in central Australia during the late Oligocene (Abstract, Musser 1999).

Note: naming a new species without publishing a description constitutes a nomen nudem; a paper describing and naming *Ob. griffithsi* is in preparation [Musser and Pledge in prep.]).

The Paleocene ornithorhynchid *Monotrematum sudamericanum*, now known from three molar teeth (Pascual et al. 1992a, b; Pascual & Goin 2000; Pascual et al., 2002) and the distal end of a femur (Forasiepi & Martinelli 2003) is very close in form to the Oligocene-Miocene *Obdurodon* species from Australia and perhaps should be considered congeneric. *Monotrematum sudamericanum* (Pascual et al., 1992a, b) the first non-Australian monotreme and oldest described fossil platypus, was described as an ornithorhynchid monotreme based on a worn, upper second molar that was distinctively ornithorhynchid in form. Shared features include dual triakididrepanons (three-cornered blade systems) with lingual midvalley cuspules between them at the base; large anterior cingulum; and multiple upper molar roots.
Erection of a new genus for the South American platypus was justified primarily on grounds that *Monotrematum* appeared to have a third upper molar based on the shape of the posterior margin of the tooth. An upper molar count of three would be significant; it is the number probably present in the early Cretaceous *Steropodon galmani*, while in contrast species of *Obdurodon* have only two. Differences in size (*Monotrematum* being exceptionally large) and morphology (e.g., the shape of the base of the lingual cusps) are cited as additional reasons for distinct taxonomic status.

Recovery of a second (also worn) M₂ and of the relatively unworn posterior half of an M₁ allows closer comparison between these two genera. Analysis suggests *Monotrematum* probably had only two upper molars as in species of *Obdurodon* (the posterior margin being similar in shape to at least some *Obdurodon* M₂ s) (Musser and Archer 1998; Pascual *et al.*, 2002). The lower molar fragment has a triakididrepanid (three-cornered blade on lower teeth) posteriorly, as in species of *Obdurodon* but not as in *Steropodon*, a feature probably formed by ‘twinning’ the posterolingual cusp of a *Steropodon*-like M₁. The buccal cingulum of M₁, well-formed in *Steropodon*, has been greatly reduced in *Monotrematum* as in species of *Obdurodon*. Other differences (e.g., morphology of the midvalley cuspule) appear to be either relatively minor or variable within *Obdurodon*. It is suggested, therefore, that 1) *Monotrematum* be considered congeneric with *Obdurodon* (reassigned to the genus as *Obdurodon sudamericanum*) and that 2) together with *Ornithorhynchus* these genera comprise Ornithorhynchidae. The genus *Obdurodon* would have temporally spanned at least 50 million years and geographically spanned at least three continents, a remarkable record for any mammalian genus (revised from Musser & Archer 1998).

**Cretaceous monotremes**

New fossil monotreme material from Lightning Ridge supports the suggestion (Rich *et al.*, 2005; Musser in press) that the lower jaws in Cretaceous monotremes were primitive in configuration, possibly retaining postdentary bones as well as a distinct meckelian groove in the adult in some taxa. Mesozoic monotremes were a diverse group as evidenced by new material from the Early Cretaceous of New South Wales and Victoria (Musser, in prep., Rich *et al.*, 2001b, 2005). Although most of these finds are edentulous jaws (limiting dental comparisons and determination of dietary niches), a range of sizes and forms has been determined. Some of these Cretaceous jaws exhibit archaic features - in particular evidence for the presence of accessory jaw bones in *Teinolophos* and *Steropodon* - not seen in therian mammals or in post-Mesozoic (Tertiary and Quaternary) monotreme taxa (excepting a possible coronoid bone in the Miocene *Obdurodon dicksoni*, as inferred from a partial lower jaw: Musser, in prep.)
Steropodon galmani Archer et al. 1985, the first Mesozoic mammal from Australia, is known only from a fragmentary lower jaw with three molar teeth. Steropodon was initially described as a possible tribosphenic therian - a phylogenetically advanced position - based on its therian-like (reversed-triangle) dentition (Archer et al., 1985). Although subsequent analyses have suggested a more basal position for Steropodon (e.g., Kielan-Jaworowska et al. 1987; Luo et al. 2001, 2002), none of these studies identified the specific (and very primitive) conformation of the lower jaw (Luo et al., 2002 incorrectly attribute a postdentary trough, mandibular foramen and meckelian sulcus in Steropodon based on examination of a cast).

The dentary of Steropodon (Archer et al. 1985) is missing almost all normally diagnostic features: coronoid process, articular condyle, angular (or pseudangular) process, mandibular foramen, and all of the dentary anterior to the posterior alveolus for the ultimate premolar. Steropodon retains archaic features including a weakly developed meckelian groove; and what appear to be comparatively large facets for one or more postdentary bones (at least a splenial bone) anterior to the mandibular foramen (as in mammal-like reptiles, mammaliaforms and archaic mammals). There are recessed areas in that part of the jaw just anterior to the mandibular foramen that resemble facets for accessory jaw bones described in other taxa, including Teiinolophos and Morganucodon. If these recessed areas are in fact facets for accessory jaw bones, the most likely candidates would have been the prearticular (the more dorsal facet) and splenial (the more ventral facet). The prearticular (along with the articular) becomes the malleus of the mammalian middle ear; the splenial, however, is either vestigial or lost in most mammals. In addition to these faceted areas on the jaw of Steropodon, there is a weak but distinct meckelian groove present running parallel to the ventral border of the mandible. It is of interest that the jaws of Steropodon and Teiinolophos differ in detail; Teiinolophos, as mentioned in this thesis, has a probable trough for postdentary bones in a slightly different configuration to that of Steropodon, but no meckelian groove (Rich et al., 2005) (revised from Musser in press).

Several features of the dentary and dentition distinguish Steropodon from ornithorhynchids. Most suggestions of postdentary bones or remains of meckelian grooves/sulci are missing in the more derived ornithorhynchids (although Ob. dicksoni may have had a coronoid, as mentioned, and has a faint meckelian groove: Musser, in prep.). The deeper and more compressed jaw in Steropodon differs in form from the shallower and wider dentary in later ornithorhynchids. The shallow, boat-shaped jaw in ornithorhynchids is correlated with the flattening of the skull and reduction of length of the molar roots, as seen in the skull of Obdurodon dicksoni, which is a specialisation within Ornithorhynchidae (and thus a synapomorphy for the family) to the probable exclusion of
steropodontids. The dental canal is large in Steropodon, but not as capacious as it is in ornithorhynchids because of the deeper molar roots in S. galmani that extend into the dental canal. The dentition of Steropodon certainly shares many features with ornithorhynchids, as discussed, but the much stronger development of transverse shearing crests in ornithorhynchids, the loss of buccal cingula, and the possible inclusion of hardened epithelial tissue in the dental battery suggest that platypuses were using their dentition in a fundamentally different way from the earlier steropodontids. This morphological evidence supports molecular evidence (Flannery et al., 1995) for a family-level distinction between Steropodon and ornithorhynchids (revised from Musser in press; and abstract, Musser 2003b).

Molar structure in monotremes

Derivation of monotreme molar structure and relationship between steropodontids and ornithorhynchids: Prior to the discovery of the oldest known monotreme, Teinolophos trusleri from Victoria (Rich et al., 1999, 2001b; 2005 the link between Steropodon and ornithorhynchids seemed clear; the molar form of Steropodon was antecedent to the molar form in ornithorhynchids and the deeper dentary in Steropodon was a more 'normal' form that evolved into the shallower, more derived jaw of ornithorhynchids. However, if Teinolophos (with a distinctive monotreme molar pattern) turns out to be closely related to Steropodon (as suggested by Rich et al., 2001b), and if the jaw of Steropodon resembled that of Teinolophos (Rich et al., 2001b, 2005), jaw structure would differ greatly between Cretaceous monotremes and later ornithorhynchids (the molar form therefore shared by Steropodon and Teinolophos and subsequently inherited and modified by ornithorhynchids). If this is the case, the distinctive monotreme molar plan in these monotremes might represent the primitive monotreme molar form and not a molar form unique to the Steropodon/ornithorhynchid line. Ornithorhynchids, rather than developing a unique molar structure, may have retained and modified an ancient monotreme molar pattern to suit their own needs (revised from Musser in press).

Several theories have been put forth in recent times on derivation of the monotreme molar pattern (e.g., Kielan-Jaworowska et al., 1987; Luo et al., 2002; Pascual et al., 2002). Sense can be made of this debate by determining the deeper phylogenetic relationships of monotremes: are they derived therians or descended from very basal, pre-tribosphenic stock? Are they part of a radiation of ‘pseudo-tribosphenic’, possibly non-therian southern mammals, as proposed by Luo et al., 2001; 2002; Rauhut et al., 2002; Martin and Rauhut, 2005)? Are they, like ‘Australosphenida’, ‘pseudo-tribosphenic’ (Martin and Rauhut, 2005) but not related? These questions should not be tackled
without investigation of the actual fossil material for the taxa in question, which I have not yet done. However, it is my current belief that monotreme molars are not tribosphenic or descended from a tribosphenic ancestor (e.g., Musser and Archer, 1998); the monotreme molar pattern lacks the hallmarks of tribosphenic teeth (e.g., Kielan-Jaworowska et al., 1987) and molar form may be convergent on, rather than related to, the molars of therians (as may the molars of mammals like Asfaltomylos (Martin and Rauhut, 2005), Ambondro (Flynn et al., 1999), Ausktribosphenos and Bishops (Rich et al., 1997, 1999, 2001a). A suggestion by Pascual et al. (2002) deserves mention: that monotreme molars may have been derived from docodonts or near relatives. Given the docodont-like jaw of Teinolophos, their revival of Patterson’s (1956) suggestion of relationship between monotremes and docodonts bears thinking about.

ORIGINS OF MONOTREMES

Evidence from new fossil discoveries suggests a Jurassic or earlier origin for monotremes: Analysis of recent fossil monotreme material showing archaic jaw form in monotremes (Rich et al., 2005; Musser in press; abstract, Musser, 2005; Musser, in prep.) strongly suggests that monotremes are an ancient group more closely allied with Late Triassic and Early Jurassic mammals or near-mammals than with Late Jurassic-Early Cretaceous mammals (in particular, therian mammals), as has been suggested by many authors (see Musser, 2003 for a review). Living monotremes appear to be highly derived, relict members of what had been a more generalised and more diverse subclass of mammals, with an origin possibly as distant as the Late Triassic but almost certainly not later than the Middle Jurassic. The two surviving monotreme families – Ornithorhynchidae and Tachyglossidae – are far removed from their origins, have undoubtedly lost or altered many ancestral features, and should not be seen as representative of basal monotremes. Monotremes may have survived in the comparatively isolated, ‘peninsular’ eastern limit of Gondwana in part because of lack of competition and in part because of successful specialisations that enabled utilisation of habitats and resources under-utilised by marsupial and/or other vertebrate taxa (revised from Musser, 2003).

Based on morphology and on the palaeontological record, Ornithorhynchidae appears to be a much older family than Tachyglossidae. Based on both the fossil record and morphology, platypuses (Ornithorhynchidae) appear to be a much older family than echidnas (Tachyglossidae). Platypuses may have found their ‘niche’ as semi-aquatic insectivore/carnivores during the Mesozoic, and thus are one of the most ancient of living mammalian families. Although much of the genetic evidence
suggests that a platypus/echidna split occurred comparatively recently (middle Tertiary), this would make echidnas ‘derived platypuses’. Morphological constraints make it difficult (although perhaps not impossible) to derive tachyglossids from an ornithorhynchid ancestor (from Musser, 2003).

**BIOGEOGRAPHY AND PALAEOECOLOGY**

Biogeography of southern hemisphere mammals has been a topic of great interest for several decades as mammalian fossils from the Gondwanan continents have been recovered. Monotreme mammals are of special interest since this group, with a record dating to the Early Cretaceous, is still extant. The fossil record of non-monotreme mammals in Australia during the Cretaceous (Kollikodon ritchiei [Flannery et al., 1995 and Chapter 5, this thesis]; Ausktribosphenida: Rich et al., 1997, 1999a, 2001a, b; and unnamed forms from the Toolebuc and Winton Formations: abstracts Godthelp, 2005; Salisbury, 2005) is rapidly growing, putting paid to the notion that only monotreme mammals were found in Australia during the Mesozoic. Palaeoecology is likewise of great interest; for much of their early evolution, Mesozoic Australian mammals lived in polar or near-polar environments that, regardless of climate, had extremes of day length, light and temperatures because of Australia’s southern geographical position.

Monotremata during the Early Cretaceous was a fairly diverse group probably endemic to East Gondwana: Discoveries of several monotreme lower jaws from the Early Cretaceous of Australia (Musser in prep; Rich et al., 2005) suggest that Monotremata was a fairly diverse group and formed an important component of the Early Cretaceous Australian mammal fauna. The monotreme fossil record illustrates that, at the very least, Mesozoic ornithorhynchids spread from Australia through Antarctica to southern South America (the landmasses inclusive of the nascent New Zealand known as East Gondwana from the Early Cretaceous through early Tertiary) (revised from Musser 2003c).

Ornithorhynchid monotremes, probably descended from archaic monotreme stock within Australia, may have spread across Antarctica to southern South America during the latter part of the Cretaceous. By the late Cretaceous, temperatures had warmed considerably and even the most southerly regions were traversable. Through most of the late Cretaceous, southeastern Australia, New Zealand, Antarctica and southern South America formed a continuous and fairly homogeneous cool-temperate forest environment dominated by southern beech (Nothofagus) (Case, 1989). This corridor
would have been the dispersal route for, among other taxa, ornithorhynchids travelling from Australia to South America as well as for ancestral South American marsupials entering Australia from South America via Antarctica (revised from Musser 1998).

Palaeoecology of fossil sites yielding monotreme material illustrates tremendous change throughout the extraordinarily long history of this enigmatic mammalian group.

i) Early Cretaceous sites: Lightning Ridge was situated close to the shores of the great inland Eromanga Sea at a time (Albian/Aptian) when sea level had reached a peak and marine transgression was at a maximum (Figure 3) (Archer et al. 1985; White 1990). Glaciers were present on high ground and parts of the Eromanga Sea would have frozen during the winter (White 1990) although the climate would not have been as extreme as in polar regions today (Frakes 1997). The depositional environment at Lightning Ridge was estuarine as evidenced by the presence of plesiosaur teeth in the deposit (Archer et al., 1985; Flannery et al., 1995). The Lightning Ridge Local Fauna reflects the antiquity of steropodontids and kollikodontids: dinosaur remains found with *S. galmani* and *K. ritchiei* include the large theropod *Rapator ornitholestoides*, the ornithopod *Fulgurotherium australis* and the iguanodontid *Muttaburrasaurus langdoni* as well as a small crocodile, two types of lungfish, plesiosaurs and turtles (Archer et al. 1985; Flannery et al. 1995) (Musser 1998).

ii) Tertiary Australian sites: all Tertiary fossil sites producing ornithorhynchid material appear to have been either lacustrine, riverine, freshwater lagoonal, or rainforest springs and pools (some with cave connections). The late Oligocene Etadunna Formation of the eastern Lake Eyre region and Namba Formation of the Frome Embayment (*Obdurodon insignis* and *Ob*. sp. A localities), far west of the present distribution of *Or. anatinus* (Figure 3), were large, permanent lakes supporting diverse vertebrate faunas (Rich et al., 1991; Woodburne et al., 1994). Associated faunas include fish (including lungfish), crocodiles, flamingoes and freshwater dolphins, with possums, palorchestids, kangaroos and koalas on the forested periphery (Rich et al., 1991; Woodburne et al., 1994). The river systems of the Channel Country - principally the ancestral Diamantina River and Cooper Creek systems - would have had permanent flows during the late Oligocene, draining southwest into Lake Eyre North, while the rivers from what is now the arid centre would have flowed from the southeast into the lake basin (White, 1990). Whether the eastern systems alone supported ornithorhynchids or
whether the distribution extended west to include the rivers from the centre is unknown (from Musser, 1998).

*Distribution of ornithorhynchids, originally extensive, has markedly declined:* In Australia, ornithorhynchids are known from the Oligocene to the present day; the sole surviving ornithorhynchid, *Ornithorhynchus anatinus*, is restricted to the well-watered eastern fringe of the continent. The contraction in range for ornithorhynchids was driven by 1) aridification of the Australian continent, causing loss or reduction of inland waterways; 2) change in faunal composition and competition in southern South America as northern faunas moved progressively south; and 3) the isolation and subsequent chilling of the Antarctic continent, making it uninhabitable for almost all terrestrial animals (revised from Musser 1998).

**KOLLIKODON RITCHIEI: A NEW ?ALLOTERIAN MAMMAL**

*Analysis of new fossil material for Kollikodon ritchiei suggests that this taxon is not a monotreme mammal (contra Flannery et al. 1995) but instead represents a mammal more closely related to Haramiyida and Multituberculata (‘Allotheria’ of some authors).* This unusual bunodont mammal from the Early Cretaceous of New South Wales was initially known only from a lower jaw, and on this basis was described as a new type of monotreme (Flannery et al., 1995). Analysis of new material - a partial maxilla with four molar teeth and a single preserved premolar - sheds doubt on monotreme affinities. There do not appear to be any unequivocal synapomorphies in either the holotype jaw or the maxilla linking *K. ritchiei* to Monotremata.

The holotype lower jaw is re-examined, providing evidence for comparatively unreduced accessory jaw bones as in very basal mammals such as *Haramiyavia* (Jenkins et al., 1997). Several features, such as possession of a well-formed premolar differentiated from subsequent molariform teeth, suggest that *Kollikodon* had reached a post-cynodont level of organisation. Parsimony analysis groups *Kollikodon* with Haramiyida and Multituberculata (‘Allotheria’ of Butler, 2000) and *Kollikodon* is provisionally included in Allotheria as its basalmost member (noting that *Kollikodon* is only known from fragmentary material and diagnosis could change given more information). A new ?allotherian order – Kollikodontida – is proposed.
Kollikodon ritchiei was part of a Gondwanan radiation of mammaliaforms and archaic non-therian mammals during the Mesozoic that also included monotremes, morganucodontids, docodonts and gondwanatheres (revised from Musser, this thesis; Musser et al. in prep.).

SUMMARY

This thesis has attempted to bring together analyses and observations on fossil monotremes as well as other Cretaceous Australian mammals in order to define and discuss morphologies, evolutionary trends and relationships both within Monotremata and with other Mesozoic mammals or near-mammals. It must be mentioned (as it invariably is for so many fossil mammals) that the fossil record of archaic monotremes – *Steropodon*, *Teinolophos* and the unnamed edentulous Early Cretaceous forms – is still very fragmentary and limited to partial jaws with lower dentitions. That said, several discussion points, clarifications and insights have come from study of the recent material (particularly the work of Rich et al., 2005) as well as from restudy of previously described material. The study by Rich et al. (2005) brings the argument over monotreme relationships almost full circle from proposals (based on the dentition of *Steropodon*) that monotremes are highly derived, therian mammals (e.g., Archer et al., 1985). Although new fossil material might alter the direction of consensus yet again, it seems clear that monotremes derive from a very basal root on the mammalian tree and that over many millions of years their specializations have obscured many (but not all) of their archaic features.

FUTURE WORK

The subject of monotreme biology, evolution and anatomy is a large one, and although this thesis covers a great deal of ground there is still much work to do. Future plans include conducting a comprehensive phylogenetic analysis of Monotremata based on the database of Luo et al. (2002) with the aim of independently testing results (beyond the scope of this thesis); continuing work on the Early Cretaceous Australian mammal material, certain to provide new information and insights into mammalian evolution in Australia; and ongoing work on an illustrated atlas of monotreme anatomy and palaeontology (several of the illustrations in this thesis have in part been prepared for that project).

ADDENDUM
The above conclusions have been drawn from the body of work that I have produced over the course of this thesis. I have not included discussion of the recent discovery of the very archaic lower jaw of an Early Cretaceous monotreme (provisionally referred to *Teinolophos trusleri*) (Rich *et al.*, 2005) because I am third author on that paper and because it appears in the Appendix (I) rather than in the body of the thesis. However, this paper is of enormous significance to the story of monotreme evolution, and merits discussion here.

The lower jaw of well-preserved specimens of *T. trusleri* exhibit a recessed area at the back of the jaw that we have interpreted as a trough for accessory jaw bones, as in morganucodontids, docodonts and other basal mammals with this mandibular morphology (Rich *et al.*, 2005). On the most complete specimen, NMV P212933, there is a well-defined trough with what appears to be a facet for the angular, which has been found as part of a rod of bones (with the prearticular and articular) within this trough or recess in morganucodontids (Kermack *et al.*, 1973). The angular, prearticular and articular are transformed in living mammals into the ectotympanic (angular) and malleus (fused prearticular and articular) of the mammalian middle ear. There are additional facets on the *T. trusleri* jaws interpreted as being for coronoid and splenial bones (with evidence for fusion of the coronoid to the dentary in some specimens) (Rich *et al.*, 2005).

This remarkably primitive morphology in the oldest known monotreme provides strong evidence for independent origin of the middle ear bones in monotremes and therian mammals: all living mammals – monotremes, marsupials and placentals – have a middle ear configuration in which incus, malleus and stapes form a chain of ear ossicles in the adult (summarised by Rich *et al.*, 2005). Presence of an angular (and, by inference, prearticular and articular) in an adult monotreme leads to the conclusion that these bones were lost or transformed into middle ear ossicles independently in the lines leading to living monotremes and to therian mammals (Rich *et al.*, 2005). Morphological analysis of the conformation, depth and position of the angular facet in *T. trusleri* suggests that transformation of the ear ossicles was entrained (the angular in a more medial position than in morganucodontids and docodonts and thus in the process of detaching from the dentary) (Rich *et al.*, 2005). This suggests that this Early Cretaceous monotreme was more derived in mandibular morphology than morganucodontids and docodonts but less derived than Theriiiformes (Triconodonta, Multituberculata and Holotheria), placing Monotremata at the base of the mammalian tree (Rich *et al.*, 2005). This is a phylogenetic position advocated by several authors on the basis of other anatomical systems (see Rich *et al.*, 2005 for a review). This conclusion contributes significant new information to the debate over the origins of the auditory complex that has been ongoing for
decades, and lends strong support to a polyphyletic (rather than monophyletic) origin of the ‘definitive’ mammalian middle ear (Rich et al., 2005).

Results presented by Rich et al. (2005) have likewise generated controversy. Bever et al. (2005) have questioned whether the material described by Rich et al. (2005) can be confidently referred to T. trusleri given proportional differences between specimens and the fact that a postdentary trough was not described on the holotype lower jaw (Rich et al., 1999; 2001b). Rich et al. (2005a, b) counter this by considering attribution to T. trusleri as provisional, given these minor but noticeable differences; they also cite extensive damage on the holotype, making thorough description of this area difficult. The material does, however, appear to be monotreme (possessing monotreme synapomorphies of 1) a large mandibular canal; 2) a posterointernal process on the medial side of the jaw; and 3) a bilophodont molar pattern on a molar found in association with the most well preserved dentary). Whether or not all of the material can be referred specifically to T. trusleri, it appears that the jaws are indeed those of archaic monotremes, rendering the conclusions of Rich et al. (2005) valid. Rougier et al. (2005) question the identification of the faceted areas of the jaws; the senior author independently inspected the T. trusleri jaws and disagrees with the contention by Rich et al. (2005) that clearly defined facets for the angular and splenial are present. Rougier et al. (2005) suggest, therefore, that the material lacks unequivocal evidence for the freeing of the prearticular and articular (=malleus) from the lower jaw. Both Bever et al. (2005) and Rougier et al. (2005) lament the lack of a comprehensive phylogenetic analysis. Rich et al. (2005b) have answered this criticism by running a computer-based analysis (with the aid of M. Woodburne) including characters relating to the presence of a postdentary trough and accessory jaw bones, with results identical to those presented by Rich et al. 2005a.

The results obtained by Rich et al. (2005a, b) will undoubtedly catalyse further debate on monotreme origins, a subject of great interest to students of mammalian evolution. It is hoped that both the Flat Rocks and Lightning Ridge fossil localities will continue to yield Mesozoic monotreme material; it is through the study of early monotremes that new information on their origins will emerge.
THESIS REFERENCES

References used in thesis chapters 1-5; for papers given as abstracts (Appendix); and as general background for the thesis.

Rich et al. (2005); Wroe and Musser (2001); Musser (1999) and Archer et al. (1999) are printed in Appendix I as published papers; Musser (1999; 2003; 2005); and Musser and Archer (1998) are printed in Appendix II as abstracts.


DE PLATER, G., 1993. Characterisation of biologically active components from the venom of *Ornithorhynchus anatinus* (the platypus). Bachelor of Science (Hons) thesis, Australian National University, Canberra.


GLAUERT, L., 1914. The mammoth cave (continued). Records of the Western Australian Museum 1, 244-251.


HINES, M., 1929. The brain of Ornithorhynchus anatinus. Philosophical Transactions of the Royal Society of London (B) 217, 155-287.


JURD, R.D., 1994. ‘Not proper mammals’: Immunity in monotremes and marsupials. *Comparative Immunology, Microbiology and Infectious Diseases* 17, 41-52.


ROUGIER, G.W., WIBLE, J.R. & NOVACEK, M.J., 1996a. Middle-ear ossicles of the multituberculate *Kryptobaatar* from the Mongolian Late Cretaceous: Implications for mammaliamorph


APPENDIX I

Additional publications as either author or co-author


Abstracts from papers or posters given at conferences
AN ILLUSTRATED ANATOMY OF THE MONOTREMATA

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The results of a study of the musculoskeletal system of monotremes are presented as anatomical illustrations. Monotremes exhibit both plesiomorphic characteristics and unique specializations. Clear illustrative material is scant in the existing literature. Part I illustrates the crania of *Tachyglossus aculeatus* (the Short-beaked Echidna) and of *Ornithorhynchus anatinus* (the Platypus). Plesiomorphic features include the retention of an open tympanic region, ectopterygoids and post-temporal foramina. Derived features include the bone structure underlying the distinct bills of both monotremes and the reduction and fusion of the cranial bones. Part II illustrates dissections of the postcranial musculature of *Tachyglossus aculeatus*. Insight into the anatomy of this ancient group will lead to a better understanding of the evolution of the mammalian appendicular structure. Although the pattern of both the shoulder and pelvic muscles reflects a primitive mammalian plan, fossorial specializations (such as the massive development of the antebrachial flexors and the distal migration of insertions of both shoulder and hip muscles) are clearly evident.
(a) dissection, superficial musculature; (b) dissection, deeper layers of musculature
(c) deep dissection of head and forelimb
(d) dorsal view, forearm; (e) ventral view, forearm
(f) side view, pelvic region
(g) ventral view showing cloacal region
(h) dorsal view, lower hind limb; (i) ventral view, lower hind limb
PLATE 7

(j) ventral view
A reconstruction of the skull, mandible and non-vestigial dentition of the middle Miocene platypus *Obdurodon dicksoni*, from Riversleigh, northwestern Queensland, is illustrated. Comparisons are made with the dentitions of other fossil ornithorhynchids: the early Cretaceous *Steropodon galmani*, the Paleocene *Monotrematum sudamericanum* from Patagonia, Argentina and the Oligo-Miocene *Obdurodon insignis* from South Australia. Results from a musculoskeletal study of the living Platypus *Ornithorhynchus anatinus* allow reconstruction of parts of the soft anatomy of *O. dicksoni*. Conclusions include 1) an extensive marginal cartilage was present, forming the contours of the spoon-shaped bill; 2) sensory receptors and possibly electroreceptors in the epidermis of the bill would have been well-developed, as evidenced by the large foramina for egress of the trigeminal nerve (sensory nerve to the bill); 3) the size and placement of foramina for branches of the trigeminal nerve indicate the presence of dorsal and ventral frontal shields as in *O. anatinus* and 4) the presence of functional teeth and the large area of attachment for the masticatory musculature indicate well-developed jaw adductor muscles. The presence of plesiomorphic characters of soft anatomy in monotremes such as the m. detrahens mandibulae as jaw opener and a cartilaginous ear tube are discussed as they relate to the hypothesized state in *O. dicksoni*. The disjunct distribution of fossil ornithorhynchids in Australia and in Patagonia and the most recent theories concerning the origin of the monotremes are reviewed.
The acquisition of nearly complete cranial material for the Middle Miocene ornithorhynchid Obdurodon dicksoni allows for a reconstruction of the skull, mandible and dentition illustrating plesiomorphic features not evident in the Platypus Ornithorhynchus anatinus. The retention of clearly-delineated sutures between component bones in Ob. dicksoni shows the presence of a large septomaxilla and identifies this bone as such in Ornithorhynchus; the large rostrum and proportionately small braincase indicate a hypertrophied bill in Ob. dicksoni and a secondarily reduced bill in Ornithorhynchus; the robust skull and dentary and the presence of functional teeth argue for differences in diet and lifestyle between the two taxa. Two complementary dentary fragments provide evidence for the presence of a six-rooted M/1, five-rooted M/2 and single-rooted, vestigial M/3 as well as for the presence of a large ascending process and angular process that are but poorly developed in the more apomorphic Ornithorhynchus. The dentition is complete but for M/2 and derivation from the Early Cretaceous Steropodon galmani - the most plesiomorphic ornithorhynchid known and the only fossil ornithorhynchid for which the complete molar row is in situ - is examined. Ob. dicksoni, with its shallow-rooted molars, illustrates that while quite conservative, ornithorhynchid dentition does show a marked trend towards the edentate condition of living monotremes.

Reconstruction of elements of the soft anatomy again shows comparative hypertrophy in Ob. dicksoni: the palate is deeply dished anteriorly for large secateuring ridges that would aid in securing prey; an extensive marginal cartilage was present, forming the contours of a comparatively large and spoon-shaped bill; and the extreme shape of the bill coupled with the presence of large foramina for sensory innervation indicate a bill, with both dorsal and ventral frontal shields, that was highly sensitive and most certainly electroreceptive.

The concept of neoteny in Ornithorhynchus is discussed. The palaeoenvironments of Riversleigh's aquatic sites and the disjunct distribution of fossil ornithorhynchids put this study of Ob. dicksoni into a biogeographical context. Recent works on the morphology of both Or. anatinus and of relevant early mammalian groups are reviewed.
EVOLUTION OF THE ORNITHORHYNCHIDAE

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Recent acquisition and analysis of fossil ornithorhynchid material has prompted a revision of the family and has suggested a possible evolutionary mechanism that may help to explain retention in the group of many primitive features. At present Ornithorhynchidae is comprised of Monotrematum sudamericanum from the Paleocene of Patagonia; Obdurodon insignis from the Oligocene of central Australia; Obdurodon dicksoni from the Miocene of northern Australia; and Ornithorhynchus anatinus from the Pleistocene (several localities) to its present distribution along the eastern coast of Australia. With the 1992 discovery of two additional Monotrematum teeth from Patagonia - an upper right second molar and lower right first molar - the suggestion is made that Monotrematum should be included within the genus Obdurodon for two reasons: 1) it is now probable that both genera had two upper molar teeth (rather than Monotrematum having the more plesiomorphic number of three upper molars as first thought); and 2) it appears that there are only minor differences between the lower molar teeth of both genera, distinctions not significant enough to warrant a generic distinction between the two. This would provide an example of extraordinary dental conservatism with the genus Obdurodon spanning over 40 million years, with a distribution over three continents that included not only South America and Australia but, by inference, Antarctica as well. Evidence for greater diversity within the Obdurodon clade is provided by two teeth of an undescribed species referable to Obdurodon. Differences in the cranial morphology between Obdurodon dicksoni from the Miocene of Riversleigh in northwestern Australia and the living Ornithorhynchus argue a case for the possibility of neoteny as an evolutionary mechanism within Ornithorhynchidae and possibly, by extension, within the order Monotremata as well.
MONOTREME EVOLUTION WITH A FOCUS ON THE PLATYPUS FAMILY

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This review synthesizes the knowledge to date about the evolution of monotremes, the egg-laying mammals which today are represented by the platypus and echidnas but which have a history that predates the Cretaceous and a distribution that once included at least South America and Antarctica as well as Australia and New Guinea. While the palaeontological history of both living monotreme families is presented, it is the Ornithorhynchidae (the platypus family) that is the focus for most of monotreme palaeontology because of the lengthy record for platypus-like animals (primarily of dentition) and because in most respects platypuses appear to be less derived than the edentate, ant-eating echidnas. *Kollikodon ritchiei*, a very specialised Cretaceous monotreme represented by a partial jaw with bunodont molars, was recently excavated from the same locality deposits that also produced the earliest platypus-like monotreme, *Steropodon galmani*; this brings the number of monotreme families to four (*Steropodon* at present placed in its own family) and indicates a greater past diversity for this enigmatic group than had been assumed.

Ornithorhynchid morphology is examined here primarily for resolution of intrafamilial relationships, with the caveat that, although the past decade has seen an exponential increase in the collection of fossil ornithorhynchid material, remains are still quite fragmentary and scarce. The distinctive ornithorhynchid double-bladed molar morphology is followed chronologically from the Cretaceous to the present (juvenile Platypuses retaining degenerate molar teeth). The meaning of such apparent monotreme synapomorphies as multiple molar roots in monotremes is discussed. Through fortuitous preservational bias, dentaries have been recovered for most taxa; these show a progressive flattening of the jaw beneath the tooth row in concert with the trend towards loss of functional teeth in ornithorhynchids, illustrated in part by gradual reduction of molar root length. Explorations in skull evolution have been limited to comparisons between the Miocene *Obdurodon dicksoni* and the living *Ornithorhynchus anatinus* because of the absence of other cranial material. However, the excellent state of preservation in the *Obdurodon* skull has allowed for detailed comparisons between the two taxa that lead to some interesting questions, notably whether or not this possibly derived platypus might have been a specialised offshoot of the ornithorhynchid line rather than directly ancestral to *Ornithorhynchus*. The review concludes with a discussion on the biogeographical and palaeoecological factors that have figured heavily in the evolutionary history of the group.
EXAMINING RELATIONSHIPS OF THE MONOTREMES
IN A BIOGEOGRAPHICAL CONTEXT

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Monotremes are the egg-laying mammals - the platypus and echidna families - that today are found only in Australia and New Guinea. However, this ancient subclass was previously much more diverse, and so far as is known at least the platypus family (Ornithorhynchidae) occupied a much more extensive range than does the living representative, Ornithorhynchus. Monotremata is comprised of four families: the semi-aquatic, carnivorous Steropodontidae and Ornithorhynchidae; the possibly semi-aquatic shellfish specialist Kollikodontidae; and terrestrial ant-, termite- and worm-eating echidnas, or Tachyglossidae. The monotypic Steropodontidae and Kollikodontidae are known only from early Cretaceous (110mybp) opal-bearing deposits at Lightning Ridge in New South Wales, Australia. The oldest known ornithorhynchid, Monotrematum sudamericanum, was recovered from early Paleocene (61-63mybp) deposits from Patagonia, Argentina, a find that confirms the Gondwanan nature of the monotremes and indicates that ornithorhynchids occupied Antarctica as well. In Australia ornithorhynchids are known from the Oligocene to the present, with Ornithorhynchus restricted to the green eastern fringe of the continent. Tachyglossids are known from the Miocene to the present, and are found in both Australia (Tachyglossus) and New Guinea (Tachyglossus and Zaglossus). The historical distribution of the monotremes is plotted and potential dispersal routes, vicariance events and the effects of drift on monotreme populations are examined. The contraction in range for ornithorhynchids, driven by aridification of the Australian continent and the isolation and subsequent chilling of the Antarctic continent, is put into a contemporary perspective urging conservation measures to protect the living species from further habitat loss. Palaeoecology of fossil sites yielding monotreme material illustrates tremendous change throughout the extraordinarily long history of this enigmatic mammalian group. Theories on higher-level monotreme relationships are reviewed and distributions of proposed sister taxa - therian mammals, multituberculates and marsupials - are compared to that of the monotremes.
COMPARISON OF THE ORNITHORHYNCHID GENERA

MONOTREMATUM AND OBDURODON

AND A REVISION OF THE GENUS OBDURODON

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The South American ornithorhynchid genus Monotrematum (the monotypic M. sudamericanum Pascual et al. 1992) was erected on discovery of a single, worn, upper second molar from late early Paleocene sediments in Patagonia, Argentina. This taxon, the first non-Australian monotreme and earliest recognised ornithorhynchid, was classified as ornithorhynchid based on possession of an upper second molar with dual triakididrepanons (three-cusped blade systems on upper molars in thegotic dental terminology, triakididrepanids being the same structures on lower molars) with lingual midvalley cuspule(s) between the triakididrepanons, large anterior cingulum and multiple roots, this combination of features being unique to members of Ornithorhynchidae. Erection of a new genus was primarily justified on grounds that M. sudamericanum appeared to have had a third upper molar (based on shape of the posterior margin of the tooth), the upper molar number probably present in the early Cretaceous platypus-like monotreme Steropodon galmani. Species of Obdurodon have only two upper molars. Differences in size (M. sudamericanum being exceptionally large) and morphological detail (e.g., the shape of the base of the lingual cusps) were cited as additional reasons for distinct taxonomic status. Recovery of a second M2/ (also worn) and of the relatively unworn posterior half of a first lower molar has enabled closer comparisons between these two genera. Analysis of this new material suggests that M. sudamericanum probably had only two upper molars (the posterior margin being similar in shape to at least some Obdurodon specimens), as in species of Obdurodon. The lower molar fragment has a triakididrepanid as its posterior blade system, as in species of Obdurodon but not as in S. galmani, a feature probably formed by ‘twinning’ the posterolingual cusp of a Steropodon-like M1/. The buccal cingulum of M/1, well-formed in S. galmani, has been greatly reduced in M. sudamericanum as in species of Obdurodon. Other differences (e.g., morphology of the midvalley cuspule) appear to be either relatively minor or variable within Obdurodon. It is suggested, therefore, that Monotrematum be considered congeneric with Obdurodon (reassigned to the genus as Obdurodon sudamericanum), and that together with Ornithorhynchus these two genera comprise Ornithorhynchidae. The genus Obdurodon would have temporally spanned at least 50 million years and geographically spanned at least three continents, a remarkable record for any mammalian genus.
**OBDURODON GRIFFITHSI SP. NOV. (MONOTREMATA, ORNITHORHYNCHIDAE), A LATE OLIGOCENE PLATYPUS FROM CENTRAL AUSTRALIA**

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Two left upper second molars have been recovered from the Mammalon Hill locality, Etadunna Formation, central Australia, representing a second species of fossil ornithorhynchid (*Obdurodon griffithsi* sp. nov.) from this region. In some features (e.g., extent and pattern of wear), this new species appears to be intermediate between the Paleocene ornithorhynchid *Monotrematum sudamericanum* from Patagonia (now known from two upper second molars as well as from a fragmentary lower first molar) and the early to middle Miocene ornithorhynchid *Ob. dicksoni* (known from numerous isolated teeth and from a nearly complete skull). One of the most remarkable features of ornithorhynchid molars is conservatism of form; surprisingly, however, the two molars of *Ob. griffithsi* differ in number and structure of buccal cuspules and in root number (the occurrence of multiple roots being an ornithorhynchid specialisation), suggesting that these features are more plastic than had been previously thought. The presence of two distinct ornithorhynchid species within a single geological formation suggests that this lineage was somewhat speciose at least in central Australia during the late Oligocene.
UPPER MOLARS OF A BIZARRE MESOZOIC MAMMAL FROM AUSTRALIA (MONOTREMATA; KOLLIKODONTIDAE)

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The first upper cheekteeth of a Mesozoic mammal from Australia appear to represent the bizarre Cretaceous monotreme family Kollikodontidae. The specimen, from early Cretaceous sediments at Lightning Ridge, NSW, is a partial maxilla with four molars and a premolar referred to the early Cretaceous Kollikodon ritchiei Flannery et al. 1995. In addition to having unique moon-shaped and mamelonated molar crowns, it is also unique among mammals in exhibiting large, hemispherical depressions in the enamel that may have assisted securing and fragmentation of food which may have been hard-shelled crustaceans or molluscs. The specimen, which also represents the first-known upper molars for a non-ornithorhynchid monotreme, does not support evidence from DNA hybridisation that monotremes are tribosphenidan mammals or that, among them, they are the sister-group of marsupials.
UPPER MOLARS OF A BUNODONT MESOZOIC MAMMAL FROM AUSTRALIA
(MONOTREMATA; KOLLIKODONTIDAE)

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The first upper cheekteeth of a Mesozoic mammal from Australia appear to represent the bizarre Cretaceous monotreme family Kollikodontidae. The specimen, from early Cretaceous sediments at Lightning Ridge, NSW, is a partial maxilla with four molars and a premolar referred to the early Cretaceous *Kollikodon ritchiei* Flannery et al. 1995. *K. ritchiei* is unique among mammals in having moon-shaped and mamelonated molar crowns and in exhibiting large, hemispherical depressions in the enamel that may have aided in securing and fragmenting food. These unusual apical depressions, or pits, appear to be part of the intrinsic enamel surface of the teeth rather than formed through wear (either masticatory or thegotic), suggesting that these pits in *K. ritchiei* are primary rather than secondary structures, a condition not found in other mammals. The dentition is suited to crushing, rather than shearing, and *K. ritchiei* may have specialised in hard-shelled invertebrates including molluscs (abundant in the Lightning Ridge Local Fauna), crustaceans and perhaps aquatic insects. This specimen also represents the first known upper molars for non-ornithorhynchid monotremes. Monotreme-like features of the maxilla include a large infraorbital canal; marked disjunction between molars and premolars; and laterally expanded molar toothbed. The presence of an apparent trough on the medial side of the dentary, previously unreported for this taxon, is noted. Monotreme and australosphenidan affinities will be discussed; extreme specialisation in this taxon and the fragmentary nature of the fossil material, however, limit comparisons and phylogenetic interpretations.
**EVOLUTION OF THE MONOTREME JAW**

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**Key words:** monotremes; Mesozoic; mammals; evolution  
Monotremes are traditionally thought of as a relict group descended from ancient stock. In the past few decades there have been challenges to this 'orthodoxy' based on recovery of Mesozoic monotreme fossils and advances in molecular phylogenetics. A series of edentulous monotreme jaws from Flat Rocks, Victoria and Lightning Ridge, New South Wales are currently under study and preliminary results are presented here (Hopson *et al.* in prep; Musser *et al.* in prep). Jaw fragments referable to *Teinolophos trusleri* (the oldest known monotreme) in addition to jaws that represent new taxa have been recovered from these Early Cretaceous mammal-bearing sites. Although none of the jaws is complete and some features of interest vary between taxa, certain observations can be made. Jaw structure is archaic, with evidence of retention of postdental bones (coronoid, splenial and angular). A transversely expanded angular process on *T. trusleri* provides information on the position and action of the m. detrahens (jaw-opener) in Early Cretaceous monotremes. The edentulous jaws are compared with that of the undisputed monotreme *S. galmani* that has a faint meckelian groove and possible facet for a splenial. Of special interest is a jaw from Lightning Ridge that appears to be platypus-like. Few of the jaws can confidently be matched with one another, suggesting a diversity of monotremes during the Early Cretaceous. Size estimates range from the mouse-sized *T. trusleri* to the cat-sized *S. galmani*. Comparisons to early to middle Mesozoic mammals are currently in progress. Comparisons to fossil and extant ornithorhynchids and tachyglossids illustrate the morphological changes in jaw form as these two specialised monotreme families evolved and diverged from each other. Results do not support a close relationship between monotremes and therians; taxa within Theria have 'modern' jaws that have lost traces of depressions or grooves for postdental bones. These results also argue against a close relationship between monotremes and multituberculates, which have also lost any indication of postdental bones on the mandible. Possession of such an archaic jaw supports the placement of monotremes at a basal level within Mammalia.
Living monotremes are comprised of two families of very different appearance: the semi-aquatic Ornithorhynchidae (Platypus) and the terrestrial, anteating Tachyglossidae (echidnas). Although the Platypus and echidnas are superficially dissimilar, they share many plesiomorphic features (e.g., 'reptilian' bones in the shoulder girdle and skull) and unique specialisations (perhaps the most extraordinary is the 'sixth sense' of electrorception). Monotreme origins have been debated since their discovery by western science in the late 1790s. The consensus of most 19th and 20th century comparative anatomists and palaeontologists was that monotremes represented a relict group descended from archaic Mesozoic stock surviving on the relatively isolated Australian continent, free from the competition and predation of continents with more 'modern' faunas.

This 'orthodoxy' has been challenged over the past few decades, beginning in 1985 with the discovery of the Early Cretaceous monotreme *Steropodon galmani*. *Steropodon* possessed a dentition that appeared to have advanced, tribosphenic characteristics and, therefore, affinities to therians - marsupial and placental mammals. Research using certain molecular techniques also suggested close links between monotremes and therian mammals although results from other molecular techniques supported the placement of monotremes far from therians. Recent discoveries of skeletal remains of early Mesozoic mammals more advanced than monotremes, however, have rekindled the debate and have pointed to an early origin - perhaps early to middle Jurassic - for monotremes. It must be emphasised that the fossil record is heavily biased and incomplete and that there are huge chronological gaps for which little or nothing is known (e.g., Late Triassic; Jurassic; Late Cretaceous; Paleocene and Eocene).

Two sites in Australia have produced Mesozoic mammals; these Early Cretaceous deposits formed when Australia lay far to the south of its present position and was still joined to Antarctica as part of East Gondwana. The near-polar Flat Rocks and Dinosaur Cove sites along the Victorian coast (115 myo and 106 myo respectively) represent stream channel deposits emptying into the rift valley forming between Australia and Antarctica as these continents separated. The more northerly Lightning Ridge site in north-central New South Wales, about 110 myo, represents an estuarine environment on the shores of the vast inland Early Cretaceous Eromanga Sea. Faunas from both the Victorian and New South Wales sites include plesiosaurs, dinosaurs, pterosaurs, turtles and lungfish. The Victorian sites also include the world's last labyrinthodont amphibians as well as ausktribosphenid mammals. Most of the fossil monotreme material consists of either edentulous jaws or, more rarely, jaws with molar teeth. The oldest known monotreme, the mouse-sized *Teinolophos trusleri* from Flat Rocks, is represented by at least one well-preserved partial dentary although only a single molar is known. The slightly younger *S. galmani* is known from a partial, opalised dentary with three molars that share general form with Tertiary ornithorhynchids. A series of edentulous jaws currently under study (a lower jaw of *Teinolophos* but, additionally, several jaws not referable to either *Steropodon* or
Teinolophos: Hopson et al.; Musser et al.) shed additional light on the evolutionary level that Cretaceous monotremes had reached. Facets on some of the jaws for postdentary bones (probable coronoids, splenials and possibly additional bones) support the view that monotremes are much closer in form to Jurassic mammals or mammaliaforms than to therian mammals. One edentulous jaw of particular interest appears to be platypus-like in form. These discoveries suggest that a fairly diverse Monotremata formed an important component of the Early Cretaceous Australian mammal fauna and that, because of contiguous land connections to Antarctica (and through Antarctica to South America and to what would become New Zealand), monotremes may have been widespread across East Gondwana.

By the end of the Cretaceous (earliest Tertiary) most Mesozoic monotremes may have become extinct. Interestingly, the only fossil monotreme known from this period is a toothed platypus from the Paleocene of South America (Monotrematum sudamericanum, approx. 62 myo), evidence that platypus-like monotremes, at the least, were present across East Gondwana prior to the end of the Mesozoic. Platypuses of the genus Obdurodon, also characterised by the possession of true teeth in the adult, are known from the Oligocene and Miocene of central and northern Australia (30-15mybp) and were moderately diverse in size and form. However, by the Pleistocene only the living platypus Ornithorhynchus anatinus is recorded. Echidnas make their appearance in the middle Miocene (the long-beaked 'Zaglossus' robusta, about 15 myo from central New South Wales). This may reflect preservational bias (the edentate echidnas would not have left fossilised teeth that would be preferentially preserved) or it may suggest that echidnas are a comparatively young group. No 'proto-echidnas' or intermediate, toothed forms are as of yet known. A modest radiation of echidnas during the Pliocene and Pleistocene resulted in several species in at least three genera (the long-beaked Zaglossus species [possibly incorporating Megalibgwilia], the smaller short-beaked Tachyglossus aculeatus and a large echidna from Western Australia, 'Z.' hacketti, that probably represents a separate genus). The older, more plesiomorphic Zaglossus types most likely fed on insect larvae but the more adaptable T. aculeatus specialised on ant and termite prey, spreading across the Australian continent as drier environments dominated the landscape. Today T. aculeatus is the most widely distributed Australian mammal species, occurring in all states and in many environments. There are currently three Zaglossus species now restricted to New Guinea (although the most recently described species, Z. attenboroughi, may already have become extinct).

In summary, there seems to be little doubt that monotremes are an ancient group, a theory strongly supported by the abovementioned Early Cretaceous discoveries and evidence from the lower jaw for retention of 'reptilian' postdentary bones. The survival of monotremes from the early Mesozoic to the present may have resulted in part from development of unique specialisations and in part from lack of competition and predation due to isolation. A previously unrecognised diversity of monotremes during the Mesozoic suggests that monotremes played a significant role in Gondwanan mammalian faunas. Although platypuses have a long pedigree, echidnas appear to be a comparatively recent family; neither family may be representative of this extraordinarily long-lived group. Continued survival of both ornithorhynchids and tachyglossids - particularly Zaglossus species - is dependent on conservation of habitat and recognition of the specific requirements of highly specialised animals.
The lower jaw of the Early Cretaceous monotreme *Steropodon galmani*

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*Steropodon galmani*, a Mesozoic mammal from the Early Cretaceous Lightning Ridge fossil locality, is known from a single opalised lower jaw with three molar teeth. *S. galmani* is an undoubted monotreme as evidenced by the large mandibular canal and distinctive molar form it shares with other toothed monotremes. However, there is ongoing debate over details of molar morphology and conformation of the lower jaw. In this report I present a revised description of the holotype lower jaw.

One commonly-cited diagnostic feature uniting Mammalia has been the presence of a single bone – the dentary – in the lower jaw. Placement of Monotremata within Mammalia depends in part on whether evidence could be found for retention of accessory jaw bones on the medial side of the dentary; the presence of some or all of these bones is a plesiomorphic feature of the earliest mammals (or mammaliaforms) generally absent in more advanced mammals. An Early Cretaceous monotreme from Victoria, *Teinolophos trusleri*, shows clear evidence of a trough on the posterior part of the jaw that presumably housed a rod of postdentary bones, as well as a facet for a splenial bone anterior to the mandibular foramen. *S. galmani* is missing the posterior section of the jaw where the mandibular foramen and trough would have been located had they been present. However, there are recessed areas in that part of the jaw just anterior to the mandibular foramen that resemble facets for accessory jaw bones described in other taxa, including *T. trusleri* and *Morganucodon*. If these recessed areas are in fact facets for accessory jaw bones, the most likely candidates would have been the prearticular (the more dorsal facet) and splenial (the more ventral facet). The prearticular (along with the articular) becomes the malleus of the mammalian middle ear; the splenial, however, is either vestigial or lost in most mammals. In addition to these faceted areas on the jaw of *S. galmani*, there is a weak but distinct Meckelian groove present running parallel to the ventral border of the mandible.


To get an idea of the temperatures and time scales involved, we considered a 100-μm-diameter sphere at a temperature of 3500 K. The formation of a thin, amorphous carbon skin occurs at the globule surfaces, where the thermal quenching rates are very high. This material is liquid on well-formed nanotubes without dissolving or otherwise distorting the nanotubes. Furthermore, the material has a density that is close to that of liquid carbon. Both the processes leading to the amorphous material and the properties that we can ascribe to it are characteristic of a glass: It is almost certain that this material is in fact carbon glass.

References and Notes
8. The nanotube deposits were generated in an arc (20 V, 100 A) between a 7-mm-diameter graphite anode and a 2.5-cm-diameter graphite cathode in a 500 mb He atmosphere. The samples were analyzed with scanning microscopy (SEM 6330F) and high-resolution TEM (SEM-3010 URJ, 0.17-nm point resolution) at Campinas, Brazil; low-resolution TEM images were analyzed with a JEOL 100CX II at Georgia Tech. Individual nanotube-containing carbon columns were glued with silver paint on conventional TEM copper grids and suspended over the grid holes. It must be emphasized that the sample must be prepared with extreme care to minimize the manipulation of the individual carbon columns and conserve the pristine surface where the beaded NTS are present.
10. The physical constants for liquid carbon are from (20).
18. The evaporation rate is estimated from the vapor pressure by noting that, in thermodynamic equilibrium with the vapor (and a unit sticking coefficient), the rate of atoms arriving on the surface is balanced by an equal rate of evaporated atoms (21).
22. This work was supported by NSF grants 9971412 and 0404084; we acknowledge P. C. Silva, the Georgia Institute of Technology Electron Microscopy Facility, and particularly Z. L. Wang for assistance.

Independent Origins of Middle Ear Bones in Monotremes and Therians
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A dentary of the oldest known monotreme, the Early Cretaceous Teinolophus trusteri, has an internal mandibular trough, which in outgroups to mammals houses accessory jaw bones, and probable contact facets for angular, coronoid, and splenial bones. Certain of these accessory bones were detached from the mandible to become middle ear bones in mammals. Evidence that the angular (homologous with the mammalian ectotympanic) and the articular and prearticular (homologous with the mammalian malleus) bones retained attachment to the lower jaw in a basal monotreme indicates that the definitive mammalian middle ear evolved independently in living monotremes and therians (marsupials and placentals).

In the evolutionary transition from primitive synapsids (the so-called mammal-like reptiles) to extant mammals, the dentary bone of the lower jaw established a neomorphic articulation with the squamosal bone of the skull, and three of the accessory lower jaw bones...
were transformed to sound-transmitting elements of the middle ear (1). The articular and prearticular bones became the mammalian malleus, and the angular bone became the ectotympanic (or tympanic ring), which supports the eardrum (Fig. 1A). An additional synapsid element, the quadrate (which with the articular forms the primitive synapsid jaw joint), became the mammalian incus. A controversy exists as to whether the transformation of jaw bones to middle ear bones occurred independently in the two clades of living mammals: the Monotremata (platypuses and echidnas) and Theria (marsupials and placentals). In other words, did the accessory jaw bones that gave rise to the ear ossicles and ectotympanic become detached from the lower jaw only once (2–7) in the common ancestry of monotremes and therians (a monophyletic origin), or did they become detached from the jaw independently in the two living groups subsequent to their evolutionary divergence from a common ancestor (a polyphyletic origin) (1, 8–10)? Assertions of fundamental differences in development and morphology between monotreme and therian ears are no longer supported (4, 11), so the primary argument for a polyphyletic origin lies in the existence of mammal-like dentaries from the Late Triassic to Early Cretaceous (12–16) that show evidence of a persisting contact of putative ear bone homologs with the lower jaw. Unfortunately, the contentious nature of the phylogenetic relations of Mesozoic mammals has until now prevented the establishment of a reliable link between fossil mammals with accessory jaw bones and living and fossil mammals with true ear ossicles. Here we present evidence of such a link between a fossil monotreme with accessory jaw bones (Fig. 2) and living monotremes in which certain of those bones are entirely within the middle ear.

The transformation of jaw bones to ear bones was first documented embryologically, when it was recognized that the reptilian articular bone and the greater part of the mammalian malleus were both formed by ossification of the posterior portion of Meckel’s cartilage, the embryonic cartilage of the lower jaw (17) (Fig. 1B). With the establishment of an embryonic (or neonate) contact of the mammalian dentary bone with the squamosal of the skull, the middle portion of Meckel’s cartilage atrophies, leaving the incus (= reptilian quadrate), malleus (= articular + prearticular), and ectotympanic (= angular) ligamentously attached to the ear region of the skull (1).

One of the most compelling pieces of fossil evidence for the transformation of jaw to ear bones is seen in Morganucodon (Fig. 1C), a Late Triassic/Early Jurassic near-mammal (mammaliaform), in which the lower jaw consists of a greatly enlarged dentary and six highly reduced accessory bones, with the primitive articular-quadrate jaw joint lying adjacent to a newly evolved mammalian dentary-squamosal jaw joint (18). The rod of accessory jaw bones that includes the homologs of the ear bones of living mammals lies in a prominent trough on the posteromedial side of the dentary (Fig. 3A). It is the presence of such a trough in the dentaries of presumed mammals [such as Sphenodon (13) and Asfaltoylos (16)] thought to be closely allied either to monotremes (19) or to therians (20, 21) (Fig. 4) that provides the principal evidence for a possible multiple origin of the definitive mammalian ear bones. However, the presence of a mandibular trough in an Early Cretaceous monotreme provides what we consider to be the most compelling evidence for the polyphyletic origin of the definitive mammalian middle ear.

Teinolophos trusleri (22–24) is known from six mandibular fragments, of which the most informative are the holotype (Museum Victoria specimen number NMV P208231) (Fig. 2, A and B) and the most complete referred dentary (NMV P212933) (Fig. 2, C to H). The latter is in much better condition than the holotype, which is crushed and distorted (22, 23), and preserves fine surface detail absent in the type. All were found at the Early Cretaceous (Early Aptian) Flat Rocks fossil vertebrate locality [38°39′40″ ± 0°2′S, 145°40′52″ ± 0′3″E (World Geodetic Standard 1984)] in the Wonthaggi Formation on the shore platform of the Bunurong Marine Park, Victoria, Australia (22).

A striking feature of the medial surface of the referred dentary of T. trusleri is the prominent mandibular trough (m.t, Figs. 2D and 3C) that extends forward from the notch above the angular process (a.p) to the large mandibular foramen (m.f, damaged because of a V-shaped break). A similar trough in Morganucodon (Fig. 3A), docodontids (Fig. 3B) (25, 26), and other basal mammaliaforms houses a rod of accessory jaw bones including the articular (that is, the ossified posterior end of Meckel’s cartilage) and three dermal bones, the dorsal and lateral surangular, the ventral and lateral angular, and the medial prearticular (Fig. 1C). Together the three dental elements form a hollow cylinder that presumably enclosed a persistent anterior extension of Meckel’s cartilage.

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Fig. 1. (A) Middle ear ossicles (malleus, incus, and stapes) and tympanic ring (ectotympanic) of an adult opossum Didelphis marsupialis in lateral view. (B) Medial view of the lower jaw of a pouch-young opossum, showing that the malleus (formed from the fusion of the ossified posterior end of Meckel’s cartilage with a dermal bone, the prearticular) and ectotympanic are components of the lower jaw in early development. The middle portion of Meckel’s cartilage atrophies in early post-hatching stages of monotremes, post-birth stages of marsupials, and late fetal stages of placentals, severing the connection of the malleus and ectotympanic to the dentary. (C) Diagrammatic view of the mandible of the near-mammal (mammaliaform) Morganucodon. Present are both the primitive tetrapod jaw joint, which lies between the articular fossa (ar.f) and the quadrate of the upper jaw, and the neomorphic mammalian jaw joint between the dentary condyle (co) and the squamosal bone of the skull. The angular, which bears a hooklike ventral process, the reflected lamina, is homologous with the ectotympanic of mammals; and the articular and prearticular are homologous with the malleus of mammals. The bone covering the meckelian groove is interpreted as a splenial, following (39). The surangular, coronoid, and splenial are absent in living mammals. Abbreviations: an, angular; ar.f, articular fossa; c, coronoid; co, dentary condyle; d, dentary; e, ectotympanic; i, incus; m, malleus; m.c., Meckel’s cartilage; mg, meckelian groove; p, prearticular; s, stapes; sp, splenial; su, surangular. [(A) and (B) are after (1); (C) is redrawn from (18)].
lage, as it does in living reptiles ([27], p. 199). Because it was unossified, the more anterior portion of Meckel’s cartilage is not usually preserved in fossils, but a narrow trough on the dorsal surface of the angular in nonmammalian synapsids indicates its former presence in the living animal ([18], figure 35; [27], figure 106; [28], figures 31 and 32). In many Mesozoic mammals, a narrow groove, usually called the meckelian groove ([18], on the medial surface of the dentary below the tooth row is thought to contain the most anterior portion of Meckel’s cartilage ([6, 7, 18]).

The nature of the postdental bones in *Teinolophos* cannot be known with certainty, but the morphology of the mandibular trough implies that it housed a rod of accessory jaw bones enclosing an unossified Meckel’s cartilage. The lateral wall and roof of the anterior part of the mandibular trough are smoothly curved, forming in cross section the arc of a circle (Fig. 2C). However, the floor of the mandibular trough, from a point about mid-way along its length forward into the mandibular canal, is a flat surface that meets the curved lateral wall of the trough at a distinct angle (a.f, Fig. 2, C and D). The observation that the floor of the trough is flat and clearly set off from the trough’s curved lateral wall suggests that it was a contact surface for an accessory jaw bone. Comparison with *Morganucodon* (18) and the docodont Haldanodon (25, 26) indicates that this element would be the angular, which contacts the floor of the mandibular trough nearly as far forward as, and somewhat ventral to, the opening of the mandibular foramen. An identifiable facet for the surangular on the lateral and dorsal walls of the trough cannot be distinguished, but such a contact may have existed. The medially located prearticular, however, would not be expected to leave evidence of its former presence on the dentary, except perhaps in the area just anteromedial to the mandibular foramen, which, however, is damaged in this specimen.

The extension of the presumed angular contact of *Teinolophos* into the mandibular canal is not seen in early mammaliaforms but occurs in nonmammalian cynodonts; in the Early Triassic cynodont *Thrinaxodon*, the angular, which bears a dorsal groove for Meckel’s cartilage, extends forward within the mandibular canal to the level of the last tooth (28). The extension of the angular into the mandibular canal is presumably a secondary condition in *Teinolophos*, possibly associated with the great enlargement of the mandibular foramen.

Evidence for the retention of two additional accessory jaw bones, sometimes referred to

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**Fig. 2.** (A) Medial view of holotype of *T. trusleri*, specimen NMV P208231. (B) Diagrammatic medial view of NMV P208231; the stippled area indicates the position of the fused coronoid bone. (C) Cross section of mandible of referred specimen of *T. trusleri*, NMV P212933; position of cross section is indicated in (D) and (E) by lines terminated with asterisks. (D) Diagrammatic medial view of NMV P212933. The stippled area indicates the position of the contact facet for the coronoid bone. Diagonal lines indicate the flat facet interpreted as a contact surface for the angular bone. (E) Diagrammatic dorsal view of NMV P212933. Traces of roots of a molar can be seen in alveoli three and four. (F) Medial view of NMV P212933, rotated slightly medially toward the viewer. (G) Occlusal and (H) medial views of isolated lower molar associated with dentary, NMV P212933. Traces of roots of the lower molar found close to alveoli three and four of dentary NMV P212933 and the remnants of roots in those alveoli suggest that is where the tooth was located in the jaw. The presence of a prominent wear facet across the entire width of the tooth on the anterior lophid of the lower molar implies that there was an upper molar anterior to this lower molar and thus the latter cannot be the m1. So the preserved first and second alveoli on the dentary must be for a molar, behind which were four additional molars. Abbreviations: a.f, angular facet; a.p, angular process; c, coronoid; c.f, coronoid facet; m.f, mandibular foramen; m.t, mandibular trough; p.a, posterointernal angle; s.f, splenial facet.

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**Fig. 3.** Comparison of the dentary of *T. trusleri* (C) with selected nonmammalian mammaliaforms (A and B) and mammals (D and E). (A) *Morganucodon*. (B) *Docodon*. (C) *Teinolophos*. (D) The amphilestid triconodont *Phascolotherium*. (E) The primitive cladothere *Amphitherium*. The angular process of *Amphitherium* (E) and other members of the Cladotheria (40), including therians, lies below the condyle rather than well anterior to it and may not be homologous with the angular process of monotremes, basal mammaliaforms, and nonmammalian cynodonts ([14, 40, 41]). Abbreviations: a.p, angular process; c, coronoid facet; m.f, mandibular foramen; m.g, meckelian groove; m.t, mandibular trough; p.c, pterygoid crest; r, ridge; s.f, splenial facet. ([A] is after [18]; [B] and (C) are original; [D] and [E] are after [30])
as parodontal bones (1, 6, 10), is seen on the most complete referred dentary. On the anteromedial edge of the ascending ramus is a flat facet (c.f. Fig. 2, D to F) in the position of the coronoid bone and its underlying facet in Morganucodon (c, Figs. 1C and 3A) and the coronoid facet seen in many early mammaliaforms (c, Fig. 3, B, D, and E). On the holotype and the fragmentary referred specimen NMV P208526, a medially directed flange of bone occupies the same area (c, Fig. 2, A and B). This flange is interpreted here as a coronoid that has fused to the dentary. In the large available sample of Morganucodon, some dentaries preserve only the contact facet for the coronoid, whereas others have a bulbous coronoid in place [(18), figure 34]. In some cases, the coronoid of Morganucodon is fused to the dentary without the trace of a suture (18).

In referred specimen NMV P212933 of T. trusleri, a shallow bifaceted groove (s.f., Fig. 2, C and D) lies below the anterior part of the mandibular trough, being separated from the trough by a sharp lip, and extends forward nearly to the anterior end of a V-shaped break. The dorsal two-thirds of this groove is formed by a flat surface that faces ventromedially, whereas the lower one-third is formed by a flat medially facing surface. The fragmentary juvenile specimen NMV P212811 preserves a single flat facet in the same position below the mandibular trough. This faceted surface appears to be homologous with a similarly located facet on the dentary that served as a contact for the splenial in Triassic cynodonts, such as Cynognathus [(18), figures 10 and 26] and, by inference, in the Late Jurassic docodontids, such as Docodon (s.f., Fig. 3B) and Haldanodon [(25), figure 4 and plate 1]. The facet for the presumed splenial in Teinolophos extends for a short distance anterior to the mandibular foramen, unlike the usual condition in nonmammalian cynodonts, where it extends to the symphysis, or in Morganucodon, where it occupies the entire meckelian groove (29). However, Teinolophos lacks an anterior extension of the meckelian groove and therefore may have lost the anterior part of the splenial usually associated with this groove. The anterior portion of Meckel’s cartilage, considered to lie within the groove (6, 7, 18), may have been ossified as part of the dentary.

Teinolophos shares with morganucodonid and docodont mammaliaforms the following primitive features of the lower jaw (Fig. 3, A to C): a prominent mandibular trough bordered above by a well-developed ridge (implying that the middle ear ossicles and ectotympanic of early monotremes retained an adult contact with the lower jaw); a mandibular foramen lying at the anterior end of the trough below the ridge; and an angular process directed posteroventrally and lying below the lower margin of the jaw well anterior to the articular condyle. The failure of the facet for the angular to extend posteriorly as far as the angular process suggests that the posterior part of the postdentary rod in Teinolophos was shifting medially, away from close proximity to the dentary condyle to the more medially located middle ear cavity, a condition to be expected in a transitional form in which the ear bones are beginning to separate from the jaw. In most Mesozoic Mammalia other than monotremes (in triconodonts, multituberculates, symmetrodonts, dryolestoids, and Amphitetherium), the internal mandibular trough and its overlying ridge are absent and the mandibular foramen opens backward into a broad, flat or slightly concave area bounded ventrally by a prominent ridge (Fig. 3, D and E): the “pterygoid crest” of Simpson (30). This ridge extends from the lower margin of the mandibular foramen back either on to the medial side of the angular process (for example, in dryolestoids) or on to the medial side of the condylar process (for example, in triconodonts (Fig. 3D), multituberculates, symmetrodonts, and Amphitetherium (Fig. 3E)). The absence of the mandibular trough and its overlying ridge implies that in these taxa the ear ossicles and ectotympanic bone were no longer connected to the lower jaw via a complete Meckel’s cartilage. This is known to be the case in living monotremes and therians and in the extinct multituberculates, where definitive ear ossicles are preserved (5) and probably in goblinodontid triconodonts, where an ossified middle portion of Meckel’s cartilage appears to be detached from the malleus (6, 7).

The phylogenetic position of monotremes with respect to marsupials and placentals (crown group therians) has long been a point of contention. Both molecular and morphological evidence has been mustered to support either a sister group relationship of monotremes with marsupials (Marsupionta hypothesis) (Fig. 4) or, alternatively, a distant relationship between monotremes and crown group therians [reviewed in (20, 31, 32)]. The current consensus of molecular and morphological analyses places monotremes outside of a monophyletic Theria (31).

As shown in Fig. 4, uncertainty surrounds the relationships of monotremes to other, primarily Mesozoic, mammalian taxa [views summarized in (20, 21)]. It is generally agreed that monotremes are more derived than morganucodonids and docodonts, which are thus excluded from Mammalia and classified as nonmammalian Mammaliaforms (33, 34) (Fig. 4). A number of studies place Monotremata as the outgroup to a clade comprising Triconodontata, Multituberculata, and Therotheria (19, 34–36), unequivocal members of which lack evidence of middle ear elements attached to the lower jaw (Fig. 3, D and E). This higher-level clade, the Therimorpha (Fig. 4), is defined by Rowe as a monophyletic taxon that includes therians and all extinct taxa closer to therians than to monotremes (34). We provisionally accept this phylogenetic position of monotremes because it is in accord with the polyphyletic origin of the definitive mammalian middle ear but requires the least amount of homoplaspy in com-

Shell Composition Has No Net Impact on Large-Scale Evolutionary Patterns in Mollusks

Susan M. Kidwell

A major suspected bias in the fossil record of skeletonized groups is variation in preservability owing to differences in shell composition. However, despite extensive changes in shell composition over the 500-million-year history of marine bivalves, genus duration and shell composition show few significant relationships, and of those, virtually all are contrary to bias from preferential loss of highly reactive shell types. Distortion of large-scale temporal patterns in marine bivalves owing to preservability is thus apparently weak or randomly distributed, which increases the likelihood that observed patterns in this and other shell groups carry a strong biological signal.

In the sedimentary record, biological hard parts, inorganic grains, and cements originally composed of calcite are typically better preserved than their aragonitic counterparts (1, 2). This calcite bias, along with experimental evidence that skeletal microstructure can also strongly influence preservation (3–6), is of concern because of the potential to distort paleoecological patterns among shelled invertebrates, which constitute the bulk of the marine metazoan
Response to Comments on “Independent Origins of Middle Ear Bones in Monotremes and Therians”

We stand by our assessment of the taxonomic identity of Teinolophos trusleri and maintain that this specimen shows features that support an independent evolution of the middle ear in living monotremes and therians. Bever et al. (1) question whether the lower jaw that we (2) provisionally referred to T. trusleri (NMV P212933) can be conspecific with the holotype jaw (NMV P208231), in part because the latter appears to lack the mandibular trough preserved in the referred specimen. Our reexamination of the holotype (Fig. 1A), in light of knowledge gained from NMV P212933 (Fig. 1B) and other more fragmentary specimens, indicates the presence of an indentation bounded above by a slight ridge in the position of the internal trough seen in other specimens. Therefore, we are confident that the type also possesses a mandibular trough, although it has been nearly obliterated by diagenetic crushing and distortion. This was implicit in our statement about the damaged (hence, unreliable) nature of the type with regard to this feature (2). The suggestion by Bever et al. (1) that the holotype is a mature individual in which the trough was not laterally, so it does not explain the existence of the posterior part of the trough in Teinolophos.

Rougier et al. (4) do not challenge the identification of Teinolophos as a monotreme, but do question our interpretation (2) of its mandibular trough as housing postdental bones homologous with mammalian middle ear bones. They argue that (i) the mandibular trough does not possess the features characteristic of mammaliforms with known postdental bones; (ii) the flat surface on the floor of the trough lacks features expected of a contact facet for the angular bone (homolog of mammalian ectotympanic); and (iii) our preferred phylogenetic hypothesis regarding the position of monotremes with respect to other mammals lacks supporting data.

The molar tooth associated with the referred specimen, although heavily worn, closely resembles that of the holotype in having the characteristic derived bilophodont pattern present in Steropodon and ornithorhynchids but notably absent in other Mesozoic mammals. The association of this tooth with the referred jaw was made because it was found next to the mandible, close to the alveoli containing broken roots, into which it fits perfectly. Furthermore, only one other isolated mammalian tooth has been found at Flat Rocks since 1997, although 37 mammalian jaw fragments have been collected. Thus, we are confident that the referred specimen NMV P212933 is a monotreme congeneric with Teinolophos and that it very likely pertains to T. trusleri.

Rougier et al. (4) do not challenge the interpretation of Teinolophos as a monotreme, but do question our interpretation (2) of its mandibular trough as housing postdental bones homologous with mammalian middle ear bones. They argue that (i) the mandibular trough does not possess the features characteristic of mammaliforms with known postdental bones; (ii) the flat surface on the floor of the trough lacks features expected of a contact facet for the angular bone (homolog of mammalian ectotympanic); and (iii) our preferred phylogenetic hypothesis regarding the position of monotremes with respect to other mammals lacks supporting data.

Our interpretation of the mandibular trough in Teinolophos as the site of a rod of postdental jaw bones is based entirely on its resemblance to a similar trough in the geologically older mammaliaforms Morganucodon, in which postdental bones have been found in place (5), and Haldanodon, to which an isolated postdental rod is convincingly attributed (6). The trough in all three taxa extends between the mandibular foramen and the notch above the angular process and is bounded above by a distinct ridge, more prominent in the basal mammaliaforms than in Teinolophos. The ridge in all three taxa also has a low area just behind the raised facet for the coronoid bone, thought to allow the mandibular branch of the trigeminal nerve to pass into the anterior part of the trough and forward into the mandibular canal. This nerve would not normally contact the mandible farther posteriorly, so it does not explain the presence of the posterior part of the trough in Teinolophos.

Rougier et al. (4) do not comment on these resemblances. Rather, they argue that the trough in Teinolophos is not homologous with that in basal mammaliaforms because it does not continue posteriorly on to the condylar process as a well-defined groove bounded above by a continuation of the medial ridge [see figure 3, A and B, in (2)]. However, whereas the grooved condylar process in Morganucodon and Haldanodon lies directly behind the trough (5, 7), the preserved base of the condylar process in the undistorted NMV P212933 [figure 2E in (2)] curves laterally from the plane of the trough; consequently, the postdental rod appears to have lost its primitive contact with the condylar process. This evidence of increased transverse separation of the middle ear bones from the jaw joint...
TECHNICAL COMMENT

is to be expected in the transition to free ear bones, as we argued with respect to the presumed angular facet (2). Thus, we do not consider the differences noted by Rougier et al. to be valid arguments against the trough in *Teinolophos* being homologous with that of basal mammaliaforms.

We interpreted a flat longitudinal surface on the floor of the trough in *Teinolophos* as a possible contact facet for an accessory jaw bone. Rougier et al. deny that this surface is a contact facet inasmuch as “[i]t has no limits, no textural changes, and no indication of a conspicuous area for articulation” (4). In fact, the surface is delimited medially by the sharp ventromedial border of the trough and laterally by a distinct angle with the curved lateral wall of the trough, seen in all well-preserved specimens. Its posterior termination is also marked by a change in surface contour. We do not think that such a surface needs to show a distinct texture or conspicuous area for articulation to be a contact facet. Nor do we accept that the surface “is merely the floor of the large mandibular canal” (4), for we fail to see how the mandibular nerve or other soft tissues could create such a distinctly flattened area. We think that a bone with a flat ventral surface is its most likely cause, which, based on comparison with early mammaliaforms, would be the angular.

That the putative angular facet extends forward into the mandibular canal of the dentary is unlike the angular facet of known mammaliaforms, and we cannot explain why it does so in *Teinolophos*. Our suggestion that it was “possibly associated with the great enlargement of the mandibular foramen” (2) was meant to indicate how such a configuration might have been permitted, not what its functional or developmental cause might have been. These remain unknown.

Rougier et al. (4) consider our statement regarding the position of monotrems with respect to other mammals to lack supporting data and imply that our choice of cladograms was made to fit our prior conclusion of an independent origin of free ear bones in monotrems and therians. The evidence we adduced for a polyphyletic origin of the definitive mammalian middle ear bones, i.e., ear bones freed from the lower jaw, was based on *Teinolophos* being a monotrete, which is generally accepted, and on marsupials and placentals being more distantly related to living monotrems than is *Teinolophos*. We noted in our original report that “[t]he current consensus of molecular and morphological analyses places monotrems outside of a monophyletic Theria” (2). These relations, as expressed in figure 4 in (2), are the basis for our claim of a polyphyletic origin of free middle ear bones in mammals. Our reason for selecting the phylogeny advocated by Rowe (8), in which all other Mesozoic mammals lie closer to Theria than to Monotremata, was that it “requires the least amount of homoplasies in comparison with other proposed phylogenetic placements of monotrems” (2).

Finally, Rougier et al. state that our tree does not support our claim of a polyphyletic origin of free ear bones, “because upon optimization, the character ‘free middle ear bones’ is equivocal at the base of Monotremata and present at the root of Mammalia” (4). This is incorrect, because this character is also equivocal at the root of Mammalia. Two equally parsimonious outcomes (each involving two evolutionary steps) are possible: Either free ear bones originated once, at the base of Mammalia, with a subsequent reversal to the attached state in *Teinolophos*, or free ear bones originated independently in post-*Teinolophos* monotrems and other mammals (Therimorpha) [figure 4 in (2)]. We consider it unlikely on functional grounds that ear bones once freed from attachment to the mandible would revert to the primitive attached condition. Discovery of new Mesozoic monotrems will test this hypothesis.

When the problems in interpreting the damaged holotype specimen are taken into account, we are confident that our conclusions on the taxonomic identity and jaw morphology of *T. trusleri* are substantially correct and that our interpretation of a polyphyletic origin of the definitive mammalian middle ear best explains the available evidence.

References and Notes


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The skull of *Nimbacinus dicksoni* (Thylacinidae : Marsupialia)

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Abstract

The exceptionally well preserved skull and mandible of the Miocene thylacinid *Nimbacinus dicksoni* is described. Phylogenetic analysis supports the contention that, within the family, the dentition of *N. dicksoni* is unspecialised, less derived than the recent *Thylacinus cynocephalus* for at least 12 features. However, relatively few cranial specialisations evident in *T. cynocephalus* clearly distinguish it from *N. dicksoni*. These two taxa share at least three derived cranial features not present in the most generalised thylacinid known from significant cranial material, the late Oligocene *Badjcinus turnbulli*. On the other hand, where comparison is possible, even the most specialised thylacinid, *T. cynocephalus*, is plesiomorphic for at least 10 cranial features common to modern dasyurids and five present in the Miocene dasyurid, *Barinya wangala*. Two character states found in thylacinids are more derived than in *B. wangala*. Relative to the remaining dasyuromorphian family, *Myrmecobius fasciatus*, thylacinids are derived for five cranial features and plesiomorphic for five. It appears that despite considerable anatomical diversity among the dentitia of thylacinids and the presence of many highly specialised dental features in some species, the crania of thylacinids have remained remarkably conservative. Even with respect to dentitia, in terms of overall similarity, the Miocene *Thylacinus macknessi* and late Oligocene material referred to *Thylacinus* does not differ greatly from the recently extinct *T. cynocephalus*. It now also seems probable that *T. macknessi* was also very similar to *T. cynocephalus* with respect to cranial anatomy. Numerical parsimony analysis incorporating this new material produced moderate bootstrap and Bremer support for a monophyletic Thylacinidae–Dasyuridae clade, but bootstrap and Bremer support was lacking. Both of these results are contra those of the most recent attempt to resolve dasyuromorphian relationships using numerical parsimony and anatomical data. In the present analysis, the early Eocene Australian taxon, *Djarthia murgonensis*, fell outside a clade including all other Australian taxa and was monophyletic with the borhyaenoid, *Mayulestes ferox*. This latter relationship is based on limited material, poorly supported and considered highly unlikely, but it does strengthen the argument that formal placement of *D. murgonensis* beyond the level of Marsupialia incertae sedis is unwarranted at present.

Introduction

Until recently, Australia’s fossil record of marsupicarnivores has been poor. However, new discoveries over the last decade have greatly advanced our understanding (Wroe 2002). Prominent among these have been the first pre-Pleistocene skulls referred to Thylacinidae and Dasyuridae by Muirhead and Wroe (1998) and Wroe (1999), respectively. A major and unexpected revelation has been that Thylacinidae, monotypic at the time of European colonisation, was once a relatively diverse clade. Prior to 1990 the pre-Pliocene record for the family consisted of a single species, *Thylacinus potens*, from the late Miocene Alcoota Local Fauna (Woodburne 1967). However, since 1990 the fossil record of the family has grown from one to 11 (Muirhead and Archer 1990; Wroe 1996; Muirhead 1997; Murray...
Six of these new species have come from the late Oligocene to early–late Miocene deposits of Riversleigh in northwestern Queensland (Muribacinus gadiyuli, Badjcinus turnbulli, Wabulacinus ridei, Ngamalacinus timmulvaneyi, Thylacinus macknessi and Nimbacinus dicksoni). The remaining four were discovered in three deposits from the Northern Territory of middle to late Miocene age (Thylacinus megiriani, Mutpuracinus archibaldi, Nimbacinus richi and Tyarrpecinus rothi). While this newly discovered material has obviously enriched our understanding of thylacinid diversity and evolution, it has to date included only one species represented by significant cranial remains (Badjcinus turnbulli). Below is the description of a second and exceptionally well preserved thylacinid fossil specimen referred to the Miocene species Nimbacinus dicksoni (Muirhead and Archer 1990).

Incorporating new data from the study of this skull and some additional taxa, the cladistic investigation of Wroe et al. (2000) is re-run. To date relatively few anatomy-based numerical parsimony treatments inclusive of Australian marsupicarnivores have been undertaken (Kirsch and Archer 1982; Springer et al. 1997; Rougier et al. 1998; Wroe et al. 2000). Results of the first three of these are reviewed by Wroe et al. (2000) and only the latter is considered here. The analysis of Wroe et al. (2000) included a variety of extant and extinct marsupicarnivore species, both Australidelphian and Ameridelphian, achieving resolution in some important respects. These included monophyly for Dasyuromorpha and placement of the Barinya wangala as sister taxon to a monophyletic clade containing representatives of each of the three extant dasyurid subfamilies. However, Wroe et al. (2000) found Thylacinidae to be paraphyletic and did not resolve the positions of dasyuromorphian families with respect to one another.

Methods

Terminology and institutional abbreviations

Dental nomenclature follows Flower (1867) and Luckett (1993) regarding the molar–premolar boundary, such that the adult (unreduced) post-canine cheektooth formula of marsupials is P1–3 and M1–4. Morphological terminology follows Archer (1976a, 1976b), as modified by Wroe (1997a). Systematic terminology follows that used by Wroe (1996, 1997a) and Wroe et al. (2000), adapted from Marshall et al. (1990) and Krajewski et al. (1994). Institutional abbreviations are: QMF (Queensland Museum Fossil) and NTM (Northern Territory Museum).

General methods

The new specimen of Nimbacinus dicksoni (QMF 36357; see Figs 1–7) has been directly compared with all described thylacinid material from Riversleigh deposits and the holotype of Thylacinus potens. We have not observed the holotypes of Thylacinus megiriani, Mutpuracinus archibaldi, Tyarrpecinus rothi or Nimbacinus richi at first hand and any comparisons with these species are based on the comments and figures provided in the descriptions by M urray (1997) and M urray and M egirian (2000).

A primary objective of the numerical parsimony analysis was to study effects of including new data, from the skull of N. dicksoni, on the placement of thylacinids with respect to other dasyuromorphians. This is because only three thylacinids are currently represented by significant cranial material and consequently any investigation using both cranial and dental features would have been based on a data set dominated by missing characters for most taxa. Analyses of intrafamilial relationships based primarily or exclusively on dental features have been performed by M urray and W roe (1998), M urray and M egirian (2000) and W roe (2001).

Taxa included in the present analysis are as used by Wroe et al. (2000), but with five additions. These were the peradectid Alphadon marshii, the possible microbiotherian Mirandatherium alplopi, Australia’s oldest marsupicarnivore Djarthia margonensis (Marsupialia incertae sedis) and two thylacinids, Muribacinus gadiyuli and Nimbacinus dicksoni. Alphadon marshii was included because, historically, species of Alphadon have been treated as generalised, if not stem, marsupials (Clemens 1979) and, within
The skull of *Nimbacinus dicksoni* is relatively well represented and unspecialised (Johanson 1996). Inclusion of *Mirandatherium alipioi* was considered appropriate given that it was treated as a microbiotherian with links to the Australian radiation by Marshall (1987). *Alphadon marshii* constituted the outgroup to all remaining taxa. Of these five fossil species, all excepting *N. dicksoni* were known on the basis of dental material only. However, each was represented by complete upper and lower molar rows at least.

A number of significant fossil taxa were not included because they are known only from incomplete molar material and would not have fulfilled minimum requirements for the realistic elucidation of phylogeny (Novacek et al. 1988). Among excluded taxa were seven thylacinids: *Thylacinus macknessi* (Muirhead 1992), *Wabulacinus ridei* (Muirhead 1997), *Ngamalacinus timmalvaneyi* (Muirhead 1997), *Nimbacinus richi*, *Yarreepsicus rothi* and *Mutpuracinus archibaldi* (Murray and Megirian 2000). Other fossil Australian marsupicarnivore taxa that likewise failed to meet this requirement included *Mayigriphus orbis* (Wroe 1997b), *Ganbulanyi djadinguali* (Wroe 1998), *Ankotarinja tirarensis* (Archer 1976c) and *Keeuna woodburnei* (Archer 1976c).

Character scoring largely follows Wroe et al. (2000) with character states given in Appendix 1 for 44 dental and 33 cranial features. Altogether, 29 taxa were included in the input data matrix (Table 1). An additional three thylacinids known from incomplete upper and/or lower molar rows were also scored in this table but were not included in the phylogenetic analysis. Notoryctidae, a possible sister taxon to Dasyuromorphia, was excluded because specialisation in *Notoryctes* is so extreme that for most features it would have been scored either as unknown or as autapomorphic. Diprotodontians were not included for the same reasons.

The analysis employed PAUP 3.1.1 (Swofford 1993), a heuristic search, ACCTRAN character optimisation and TBR branch swapping. The relative stability of clades was assessed using Bremer support (Bremer 1988, 1994) and bootstrap analysis (Felsenstein 1985). Bremer support indices were determined by studying suboptimal trees. Only species that we have examined at first hand were included. Bootstrapping was based on 100 replicates.

**Description of new material**

**Background**

The description of *Nimbacinus dicksoni* by Muirhead and Archer (1990) was based on a left M1 (QM F16802), the holotype and the following paratypes: QMF 16803, a right maxillary fragment containing P3 – M1; QMF 16804, a right maxillary fragment containing M1–3; QMF 16805, a right M3; QMF 16806, a left M3; QMF 16807, a right M4; QMF 16809, a broken right M3; and NTM P85553–3, a right dentary fragment containing P1,2, 3 and M1. Excepting NTM P85553–3 and QMF 16809 all material is from Henk’s Hollow Site, Riversleigh, north-western Queensland. This deposit is thought to be middle Miocene in age (Creaser 1997). QMF 16809 is from D-Site, Riversleigh and NTM P85553–3 is from the Bullock Creek Local Fauna. Respectively, these deposits are considered to be late Oligocene and middle Miocene in age (Black 1997).

**General description**

The cranium and mandible QMF 36357 are from AL90 Site, Riversleigh, north-western Queensland. Black (1997) considers this site to be middle Miocene in age. Overall, the quality of preservation is exceptional. Fine detail is present, including parts commonly not recovered in fossil material such as the pterygoid processes and alisphenoid tympanic processes. There is little distortion, although dorsally the nasals and anterior regions of the frontals are crushed. RI2 is retained; all other incisors are absent; only the bases of both canines are present; and RP2 has been lost. From the degree of tooth wear it is clear that the specimen represents a mature adult. QMF 36357 is referred to *Nimbacinus dicksoni* because it differs in no way from the holotype or paratypes from the type locality that can not be ascribed to differences in wear. Dental and cranial measurements are given in Table 2.
Table 1. Data matrix showing the distribution of 77 characters among 29 taxa subject to parsimony analysis (PAUP 3.1) in the present study.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Character</th>
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<tr>
<td>*Thylacinus macknessii</td>
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</tr>
</tbody>
</table>

0 = the plesiomorphic state; P = polymorphic; n = not applicable; u = state unknown; and ? = missing; three thylacinids denoted by asterisks are shown here for comparative purposes but were not included in the analysis because they were represented by insufficient material.
The skull of *Nimbacinus dicksoni* 491

Skull

Cranium

Nasal. The nasal flares posteriorly before angling sharply towards the midline at the naso-maxillo-frontal suture. The bone's posterior limit lies just beyond the anterior-most margin of the orbit and the naso-premaxillo-maxillary suture is dorsal to the anterior margin of P³ and the naso-maxillo-frontal suture is approximately dorsal to M². Anteriorly the nasal tapers slightly towards the midline as in *Badjcinus turnbulli*, but not in *Thylacinus cynocephalus* and *Dasyurus maculatus*, where the anterolateral border of the nasal is straight, or in *Barinya wangala* and *D. viverrinus* where this bone is angled laterally. Because of damage, it can not be determined whether the nasal extends beyond the point of contact with the premaxillae. The posterior margin of the right nasal is intact although marginally displaced; it angles obliquely towards its posterior junction with the maxilla, as it does in *T. cynocephalus*, *B. turnbulli* and *B. wangala*, rather than as in *Dasyurus* (in particular *D. viverrinus*), where this suture tends to be more transverse.

Premaxilla. Laterally the premaxilla and maxilla form a near-linear suture, as in *Thylacinus cynocephalus*, *Barinya wangala* and *Dasyurus maculatus*; in *Dasyurus viverrinus* the lateral margin of the premaxilla has a distinct sigmoid curve. The state of this feature can not be ascertained in *Badjcinus turnbulli*. The dorsomedial border of the premaxilla is formed by the nasal and the ventrolateral and ventral borders are formed by the maxilla. Laterally, the premaxillo-maxillary suture is anterior to the canine as in *T. cynocephalus*, *Badjcinus turnbulli*, *B. wangala* and *Dasyurus*. As in *B. turnbulli*, *B. wangala* and *Dasyurus*, but not *T. cynocephalus*, the premaxilla does not contribute to the anteromedial border of the canine alveolus. Ventrally the premaxillo-maxillary suture extends posteromedially from the anteromedial third of the canine alveolus before angling anteromedially to meet the anterolateral border of the premaxillary vacuity (palatal fissure). Medially, the premaxilla runs transversely from the posteromedial margin of the premaxillary vacuity to the median line of the skull. In occlusal view the curvature of the incisal arcade is very slightly convex, as in *T. cynocephalus*, *B. turnbulli* and *D. maculatus*, contrasting with the more obviously convex and V-shaped arcades of *D. viverrinus* and *B. wangala*, respectively. Alveoli for I¹-⁴ are contained in the premaxilla and R¹² is retained. A well developed depression for the reception of C¹ is present. The paired incisive foramina are bordered anterolaterally and medially by the premaxilla and posterolaterally by the maxilla.

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Table 2. Dental measurements of *Nimbacinus dicksoni* (QMF36357)

Dental measurements are given for the dentition of the left side for upper teeth and right side for lowers. All measurements are in millimetres. Further measurements are as follows: skull length, 132.4 mm; maximum width across zygomatic arches, 80.8 mm; length of upper molar row, 27.4 mm; length of lower molar row, 30.3 mm

<table>
<thead>
<tr>
<th>Tooth</th>
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<th>Upper jaw Width</th>
<th>Lower jaw Length</th>
<th>Lower jaw Width</th>
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<td>2.7</td>
<td>P²</td>
<td>7.8</td>
</tr>
<tr>
<td>P³</td>
<td>7.7</td>
<td>4.2</td>
<td>P³</td>
<td>8.1</td>
</tr>
</tbody>
</table>
Fig. 1. *Nimbacinus dicksoni*, QM F36357; cranium. (a), lateral view; (b), ventral view; (c), dorsal view. Scale = 2 cm.
Maxilla. Although damage to the skull has obscured some of the relationships of the maxilla, where comparison is possible it appears to have the same borders as in *Thylacinus cynocephalus*, *Badjcinus turnbulli*, *Barinya wangala* and *Dasyurus*. On the rostrum the maxilla is bordered anterodorsally by the premaxilla, posterodorsally by the nasal and briefly by the frontal, and posteriorly by the lachrymal and jugal, the suture between these two bones meeting posterior to the slit-like infraorbital canal. The maxilla floors the orbit and the suture between the maxilla and palatine medial to the orbit floor extends posteriorly before wrapping ventrally onto the palate. In palatal view the maxilla, bordered anteriorly by the premaxilla, forms the postero-lateral border of the premaxillary vacuity. C1, P1–3, and M1–4 are contained within this bone; the anterior border of the canine alveolus is confluent with its antero-lateral border. Posteromedially the maxilla abuts the palatine at the postero-lateral margin of the conjoined maxillary vacuity. The maxillary vacuities are large and contained mostly within the maxilla, but are bordered posteriorly by the palatine. Where comparable, these vacuities are similar in structure to those of *T. cynocephalus* and *B. turnbulli* (only the lateral border is preserved). They differ from those of *Dasyurus*, where the vacuities are small and variable (*B. wangala* is damaged in this area but the maxillary vacuities appear to have been large and conjoined). A rostral opening of the infraorbital canal, situated anterior to the lachrymal/jugal suture and dorsal to the posterior limit of M1, is surrounded by the maxilla as in *B. turnbulli*, *Dasyurus* and *B. wangala*. In *T. cynocephalus* the infraorbital canal is much larger and anteriorly the canal runs through the maxilla, while posterolaterally its margin is formed by the jugal with the maxillo-jugal suture running through its roof. The roughly triangular orbital (posterior) opening of the canal in *Nimbacinus dicksoni* opens dorsal to the posterior root of M2. This canal appears to be bordered dorsally by the lachrymal and is floored by the maxilla, which forms the lateral, ventral and medial borders. The palatine has no contact with the infraorbital canal, terminating posterior to the orbital opening. An incomplete postero-lateral palatine foramen is present entirely within the palatine and has no border with the maxilla. No accessory postero-lateral palatine foramen is evident.

Palatine. Although sutures are somewhat obscured, relationships of the palatine to other bones appear to largely follow the pattern in *Thylacinus cynocephalus* and *Barinya wangala* (because the maxillary vacuities are small in *Dasyurus* the contribution of the palatine to the secondary palate is greater). The palatine is only partially preserved in *Badjcinus turnbulli*. In palatal view the palatine is bordered laterally by the maxilla, the sutures running posterolaterally from the maxillary vacuities at about a 45° angle as in *T. cynocephalus* and *B. wangala*. Anteriorly the palatine forms the posterior margin of the maxillary vacuity; medially the palatines project to form a median process. Posterior to the palate the palatine meets the pterygoid just anterior to the pterygoid wings. In the orbital region the palatine is bordered laterally by the maxilla, anteriorly by the lachrymal, dorsally by the frontal and posteriorly by the alisphenoid, extending to a point just anterior to the foramen rotundum. The orbitosphenoid may make a small contribution between the frontal and the alisphenoid. A distinct transverse bar of bone, the postpalatine torus, forms the posterior margin of the palate. This torus is thickened and rugose and terminates laterally in small, sharp spines. It is generally similar to that in *Dasyurus*, but is better developed than in *B. wangala* (where a smooth lip is formed). In the *T. cynocephalus* examined a torus, as such, is absent, although there is a raised ridge of bone. The palatal spines are larger in *T. cynocephalus* and are displaced posteriorly. The vomerine/presphenoid region is obscured and interpretation is difficult. On the orbital face just posterior to the palatine–lachrymal suture is an elliptical sphenopalatine foramen, similar in position to that
Fig. 2. *Nimbacinus dicksoni*, QMF 36357: right and left dentaries. Right dentary: (a), occlusal view (b), lingual view (c), buccal view. Left dentary: (d), occlusal view (e), lingual view (f), buccal view. Scale = 2 cm.
The skull of *Nimbacinus dicksoni* of *B. wangala* and *Dasyurus*. In *T. cynocephalus* the sphenopalatine foramen is proportionately slightly larger and lies closer to the maxillopalatine suture.

**Lachrymal.** The lachrymal, forming the anterior rim of the orbit, is bordered anteriorly by the maxilla, dorsally and posteriorly by the frontal, ventrally by the palatine and maxilla and ventrolaterally by the jugal. Three small lachrymal foramina are present; on the rostral part of the lachrymal just anterior to the rim of the orbit are superior and inferior foramina and a third foramen lies within the orbit. The lachrymal extends onto the face to a greater extent than in *Dasyurus* or *Barinya wangala*, but not to the extent seen in *T. cynocephalus*, in which the rostral extension of the lachrymal overlaps the infraorbital foramen. This bone is not preserved in *Badjcinus turnbulli*.

**Jugal.** The anterior border of the jugal is formed by broad contact with the maxilla. Dorsal to this the jugal contacts the lachrymal and continues posteriorly to form the remainder of the ventral margin of the orbit, ending in a well developed postorbital process of the jugal (inferior postorbital process). This process terminates just in front of the anterior junction with the squamosal. The squamosal overlies the jugal to form its posterodorsal border. The sulcus for origin of the masseter is well developed. Ventrally the jugal forms the lateral border of the glenoid fossa to produce a preglenoid process of the jugal as in *Dasyurus* and *Barinya wangala*, but not *Thylacinus cynocephalus*, where the jugal terminates prior to the fossa with no distinct process formed. This region is damaged in *B. turnbulli*. The zygomatic arch is relatively deep, as in *D. maculatus*, in contrast to the more slender zygoma in *B. wangala*, *D. viverrinus* and *T. cynocephalus*. A gain, damage prohibits direct comparison with *Badjcinus turnbulli* here.

**Frontal.** Damage to the anterior part of the frontal obscures much of its precise relationships to the nasal and maxilla, and some of the sutural connections, particularly in the orbital region and side wall of the braincase, are damaged or obscured. However, the following relationships are clear. Anteriorly the frontal abuts the nasal at an oblique angle. Anterolaterally the frontal makes brief contact with the maxilla; just posterior to this the frontal is bordered anterolaterally to anteroventrally with the lachrymal, forming the
anterior region of the orbit. Posteriorly the orbital region is formed by the frontal and orbital part of the palatine, the palatine forming the ventral border of the frontal. On the side wall of the braincase the frontal is bordered posterovertrally by the small orbitosphenoid and, dorsal to this, by the alisphenoid, although portions of the alisphenoid–squamosal–frontal region are damaged. In *Thylacinus cynocephalus* the frontal is bordered posterovertrally by the squamosal, which is probably the case in *Nimbacinus dicksoni*, although there is breakage and flaking of bone in this region. The frontal–squamosal suture is not clear, but the relatively minor contribution of both the parietal and alisphenoid to the braincase excludes the possibility of alisphenoid–parietal contact, in contrast to both *Barinya w angala* and *Dasyurus* where the alisphenoid contacts the parietal dorsally (feature not preserved in *Badjcinus turnbulli*). Posteriorly the frontal is bordered by the parietal. The dorsal fronto-parietal suture in both *N. dicksoni* and *T. cynocephalus* lies more posteriorly than it does in *Dasyurus* and *B. wangala*. A distinct orbital process of the frontal (supraorbital process, zygomatic process of frontal bone) is present. There is a tiny foramen posterior to the orbital process of the frontal, preceded by a narrow sulcus. Both features are present in *T. cynocephalus* examined and this foramen is variably present in *Dasyurus* (absent in *B. w angala*), but is not accompanied by a sulcus or groove. A V-shaped ethmoid foramen is present at the juncture of the frontal, alisphenoid and orbitosphenoid.

**Parietal.** The paired parietals roof the brain case and form a moderate sagittal crest where they meet along the dorsal midline. The parietal is bordered by the frontal anteriorly at the origin of the sagittal crest. Laterally the parietal is overlain by the squamosal, but damage to this part of the skull makes interpretation difficult. In *Thylacinus cynocephalus* the parietal is bordered ventrally by the squamosal before abutting the frontal, with no parietal–alisphenoid contact, which also appears to be the case in *Nimbacinus dicksoni*. In *Dasyurus* and *Barinya w angala* the parietal contacts the alisphenoid anteovertrally between the squamosal and frontal. The relationships of these bones can not be determined in *Badjcinus turnbulli*. The parietal broadly contacts the postparietal, or interparietal,
posteriorly. Ventral to the postparietal the parietal briefly abuts the supraoccipital, contributing in a minor way to the nuchal crest.

**Postparietal (interparietal).** The postparietals, contacting the parietals across their anterior margins, form the terminus of the dorsal surface of the skull and contribute to the sagittal crest. The nuchal crest is formed by the posterior margin of the postparietal fused to the anterior border of the supraoccipital (described as part of the fused basioccipital–exoccipital–supraoccipital complex [BES] below). A median V-shaped notch is formed along the posterior margin and is more developed than in *Thylacinus cynocephalus, Barinya wangala* or *Dasyurus*.

**Orbitosphenoid.** The orbitosphenoid is exposed on the skull at the rear of the orbital region, sandwiched between the frontal anteriorly and the alisphenoid posterodorsally. It briefly contacts the palatine ventrally and forms the medial wall of the optic orbital foramen. This foramen is completed by the alisphenoid laterally. A minute foramen communicates with the opposite side of the skull. The orbitosphenoid makes no significant contribution to the orbit.

**Alisphenoid.** The alisphenoid is bordered anterodorsally by the frontal, anteroventrally by the palatine, and ventromedially by the basisphenoid. Its posterodorsal border is formed by the squamosal, which also delimits the alisphenoid's lateral extent on its ventral surface where it is confluent with the glenoid fossa (forming the medial margin of the glenoid fossa). The dorsal margin of the alisphenoid forms a natural edge and its margin meets the frontal (as in *Thylacinus cynocephalus* but not *Barinya wangala* and *Dasyurus*, where the alisphenoid contacts the parietal). A complete secondary foramen ovale (*sensu* Wroe 1997a) is present, as in *T. cynocephalus, B. turnbulli, some Dasyurus* and *Sarcophilus*. It is formed by an anteriorly directed strut emanating from the alisphenoid tympanic process. The alisphenoid also forms at least the anteriormost boundary of the primary foramen ovale. A moderately well developed alisphenoid tympanic process is present, enclosing an alisphenoid hypotympanic sinus. This process is proportionately larger and more inflated than in *T. cynocephalus* and *B. turnbulli*, but somewhat smaller than in *D. maculatus*. Posteriorly, the alisphenoid tympanic process is fused to the ectotympanic. Ventromesially, a deep and extensive sulcus is formed at the alisphenoid–basisphenoid boundary. This almost certainly conducted a branch of V3 as in other dasyuromorphians (Wroe 1997a). The transverse canal is contained within this sulcus.

**Basisphenoid.** The unpaired basisphenoid floors the anterior two-thirds of the neurocranium. It is roughly triangular in ventral view, with the apex formed anteriorly by articulation with the presphenoid and the base formed by contact with the unpaired basioccipital. The basisphenoid makes a minor contribution to the internal carotid foramen. Bilaterally it is bordered by thin flanges of the alisphenoids.

**Squamosal.** The dorsal margin of the squamosal is delimited by the parietal. The squamosal meets the frontal anteriorly (as in *Thylacinus cynocephalus*) and not the alisphenoid as in most dasyurids. Anterodorsally the squamosal overlies the alisphenoid; the ventral squamosal–alisphenoid suture runs anteroposteriorly along the medial limits of the glenoid fossa. The squamosal abuts the occipital region posteriorly to form the anteroventral margin of the nuchal crest before terminating in lateral occipital wings. There is a well developed posterior glenoid process. The transverse orientation of the glenoid fossa resembles that of *T. cynocephalus* and *Dasyurus* (but not *Barinya wangala*, where its orientation is more oblique). Laterally the squamosal overlies the jugal, terminating just posterior to the postorbital process of the jugal on the lateral face of the zygomatic arch. The anterior terminus of the squamosal on the zygomatic arch varies within *Dasyurus*—
**B. wangala** and **Badjcinus turnbulli** are damaged in this area and cannot be assessed, and in **T. cynocephalus** the squamosal extends anteriorly below the infraorbital process. The zygomatic arch is robust, contrasting with the more slender zygomatic arch in **T. cynocephalus** and **B. wangala** and resembling the more robust zygoma in **Dasyurus**. Damage in **B. turnbulli** again precludes comparison. The zygomatic arch is roughly horizontal, terminating posteriorly and somewhat dorsally on the skull (similar to the condition in **Dasyurus**). In **T. cynocephalus** the zygomatic arch curves ventrally to terminate at a more ventral point on the skull, as it does in **B. wangala**. A small subsquamosal foramen is present at the point where the dorsal ridge of the zygomatic arch runs into the skull wall. A distinct squamosal epitympanic sinus is also present.

**Basoccipital, exoccipital, and supraoccipital.** Sutural boundaries between these bones cannot be distinguished and they are described here as a single unit (BES). The BES is bordered anteriorly by a transverse suture with the basisphenoid. A distinct basoccipital keel is present on the ventral surface anterior to the occipital condyles. On either side of the occipital condyles are paired paroccipital processes whose anterolateral borders are formed by the pars mastoidea of the periotic. The internal jugular canal is not fully enclosed although a sulcus for the internal jugular is present, as is an incomplete posterior lacerate foramen. A large condylar foramen is positioned at the base of the ventral condylar lobe, with a smaller foramen immediately anterior to this. In posterior view the BES is bordered by the pars mastoidea of the periotic laterally and is fused with the postparietal dorsally.

**Periotic.** The periotic is composed of two parts: the **pars petrosa** and **pars mastoidea**. The **pars petrosa** contains the inner ear and internal acoustic meatus, while the **pars mastoidea** contributes to the lateral occipital region. Only the external features are described because no isolated periotics are known to reveal endocranial detail. The **pars petrosa** does not abut the basioccipital ventromedially. A small periotic tympanic process is present, but does not contact the alisphenoid tympanic process or the ectotympanic. Neither the **pars mastoidea** nor the paroccipital are contacted posteriorly. No distinct tubal
The skull of *Nimbacinus dicksoni*.

Foramen for the Eustachian tube is formed. Whether the *pars petrosa* contributes to the posterior rim of the primary foramen ovale cannot be determined. Neither a secondary facial canal nor stylomastoid foramen are evident. The fenestra ovalis is not visible in ventral view. The *pars mastoidea* contains no epitympanic recess, nor is there a paroccipital epitympanic sinus. Anteroventrally, a well defined sulcus may be for transmission of the facial nerve. Ventromedially the *pars petrosa* forms the base of the paroccipital process.

**Upper dentition**

\( P^3 \) and \( M^{1-4} \) are described in detail by Muirhead and Archer (1990). The morphology of these teeth in QMF36357 does not differ in any significant way from that of the material considered by these authors. Consequently, only those elements of the upper dentition not previously described are treated here. All molars, as well as the \( P^3 \), show moderate wear.

\( I^2 \) is present in the right premaxilla. This tooth is spatulate. From the alveoli it is clear that no diastema are formed between any of the upper incisors. In ventral view the incisal arcade has only a slight convex curvature. The alveoli of \( I^{1-3} \) are similar in size and shape and it seems unlikely that \( I^4 \) was procumbent, as in *Barinya wangala*. The alveolus of \( I^4 \) is the largest of the incisal arcade as in *Thylacinus cynocephalus*, but not *Badginus turnbulli*, *Dasyurus maculatus* or *D. viverrinus*. Although \( C^1 \) is not fully preserved, from its occlusal outline in the less badly damaged left \( C^1 \), it was evidently compressed on the transverse axis. It is contained within the maxilla. \( P^1 \) is separated from \( C^1 \) by a short diastema. It is double rooted, transversely compressed, roughly triangular in lateral view and slightly recurved along the posterior face (although not to the extent evident in *T. cynocephalus*). A poorly developed heel is apparent. \( P^2 \) is preserved in the left side of the skull. It is separated from \( P^1 \) by a small but distinct diastema. It differs from \( P^1 \) in being higher crowned with a more strongly developed heel. No diastema separates \( P^2 \) and \( P^3 \).

**Dentary**

Both dentaries are well preserved although neither is complete posteriorly; the angular processes are not fully preserved and neither of the mandibular condyles is present. The right
dentary retains all of the teeth excepting the incisors; the left dentary retains the canine, P2, and M2. In lateral view the dentary is long and slender, similar proportionately to the dentaries of *Badjcinus* *turnbulli* and *Daspyurus maculatus*, but not as elongate and gracile as in *Thylacinus cynocephalus*. The masseteric fossa is shallow, resembling that of *T. cynocephalus* and *B. turnbulli*, and contrasting with that of *D. maculatus* and *D. viverrinus*, where a distinct lip rimming the fossa is present. The posterolateral shelf of the masseteric fossa is wide, as in *D. maculatus* and *D. viverrinus*; this shelf is less pronounced in *T. cynocephalus* (incompletely preserved in *B. turnbulli*). Two mental foramina are present. On both dentaries the anterior foramina (the larger) are ventral to the posterior roots of P1. The more posterior foramina differ in position: the foramen through the left dentary is tiny and lies ventral to the posterior root of P3 while on the right dentary a more well developed foramen lies ventral to the posterior root of M1. In the Bullock Creek specimens, assigned to *N. richi* by Murray and Megirian (2000), the posterior mental foramen is larger and positioned more posteriorly, below the anterior alveolus of P3 in P85553–3, but present ventral to the posterior root of P3 in P9612–4. Intraspecific and within-individual variation regarding size, number and position of mental foramina is evident in *D. maculatus*, *D. viverrinus*, *B. turnbulli* and *T. cynocephalus*. On the medial aspect of the dentary the mandibular foramen (inferior alveolar foramen) lies beneath the most dorsal point on the anterior margin of the coronoid process, as it does in *T. cynocephalus*, *D. maculatus*, and *D. viverrinus*. The mandibular foramen is well developed as in *T. cynocephalus* and larger than in *D. maculatus* and *D. viverrinus* (not preserved in *B. turnbulli*). The coronoid process rises from the dentary at an angle of about 80°, which is similar to the inclination of the coronoid process in *D. maculatus* and *D. viverrinus* and more steeply inclined than in *T. cynocephalus*. The angular process is broken away.

**Lower dentition**

Muirhead and Archer (1990) have described P1, P3 and M1 (M2 of these authors) from Riversleigh and Bullock Creek material; P3 and M2,4 (M3,5 of these authors) present in the

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**Fig. 7.** *Nimbacinus dicksoni*, QMF36357; stylised occipital view. See Appendix 3 for legend to abbreviations.
The skull of *Nimbacinus dicksoni* specimen described here, had not been recovered for *Nimbacinus dicksoni* at that time. Differences between M1 of the holotype and material referred to *Nimbacinus richi* by Murray and Megirian (2000) are discussed above. Because we have not seen the holotype of *N. richi* at first hand we do not attempt detailed comparisons with this specimen, but reiterate that, based on the description provided by Murray and Megirian (2000), there are no clear differences regarding premolar or molar morphology other than entoconid size.

From the alveoli of the incisal arcade it is inferred that I3 was crowded or staggered (*sensu* Hershkovitz 1995, 1999). C1 is large, recurved and transversely compressed. It is separated from P1 by a diastema almost 3 mm in length. On both the right and left C1, a distinct wear facet is present, probably formed by occlusion with C1. P1 is recurved, twin rooted, low crowned and shows considerable wear. A well developed heel is evident. P2 differs from P1 in being larger, higher crowned and more distinctly recurved, with a poorly defined cristid running from the protoconid to the base of the heel. P3 is separated from P2 by a very small diastema of less than 1 mm. In the Bullock Creek dentary described by Muirhead and Archer (1990), the size of the P3 alveoli suggest that P3 in *N. dicksoni* was approximately equal in size to P2, but P3 is larger in all dimensions than P2. P3 is only slightly worn in both the right and left dentaries. Although the crown has been somewhat diminished by wear, P3 in *N. dicksoni* lacks the higher, more triangular cutting blade of the P3 in *T. cynocephalus*. Its lower crown resembles that of the P3 in *Dasyurus maculatus* although the P3 of *N. dicksoni* is probably transversely compressed. M1 is missing from the left dentary. The right M1 is heavily worn, as is the M1 in the Bullock Creek dentary (M2 of Muirhead and Archer 1990). Its talonid is wider than its trigonid. Neither a paraconid (present but poorly developed in the holotype: Muirhead and Archer 1990) nor entoconid (present in holotype: Muirhead and Archer 1990) appear to be present, but this may be the product of wear. M2 shows less wear than M1 and can be further distinguished as follows: it is larger in anteroposterior, dorsoventral and transverse dimensions; both a small entoconid and a distinct paraconid are apparent as is an anterior cingulid; the protoconid is more massive and displaced buccally; the metaconid is not positioned as posteriorly relative to the protoconid; the trigonid is only very slightly shorter than the talonid transversely; and the cristid obliqua runs into the posterior face of the protoconid at a point level with the protoconid's centre. M3 is similar to M2 but differs in the following ways: the talonid is smaller on both the long and transverse axes of the dentary and is not as wide as the trigonid; the protoconid and paraconid are higher crowned; the entoconid is smaller; and the cristid obliqua terminates anteriorly in a more lingual position. M4 differs from M3 as follows: the tooth is less worn; the entoconid is absent; and the talonid is further reduced in overall size relative to the trigonid.

**Remarks**

As conceded by Muirhead and Archer (1990) and extrapolated upon by Murray and Megirian (2000), there are differences between the holotype of *Nimbacinus dicksoni*, the Bullock Creek paratype and QMF16809 that may be of phylogenetic consequence. In particular, Murray and Megirian (2000) question the status of paratype QMF16809, a broken M3 now thought to be from a considerably older site than the holotype. This tooth fragment is characterised by marked reduction of the metaconid, leading Murray and Megirian (2000) to suggest that it may not represent *N. dicksoni*. When Muirhead and Archer described *N. dicksoni* it was then only the third thylacinid known. Certainly the species richness of *Thylacinidae* attested to by subsequent discoveries was then unanticipated. With the benefit of hindsight and new material, we concur with Murray and
Megirian (2000) regarding the taxonomic status of QMF1609, which must now be considered uncertain. However, the basis of the argument advanced by Murray and Megirian (2000) to dispute whether QMF1609 represented *N. dicksoni* eats into the validity of their own distinction between this species and the new taxon, *N. richi*. When described, the lower molar morphology of *N. dicksoni* was known only from two first lower molars and the partial M₂ that Murray and Megirian (2000) suggest is another species. As stated by Murray and Megirian (2000, p. 153) their ‘... proposed revision leaves the states of the M₂ metaconids of *N. dicksoni* in some doubt’. But the presence of relatively well developed metaconids on M₂ in conjunction with a reduced metaconid on M₁ in *N. richi* was one of the two diagnostic features used to distinguish it from *N. dicksoni*. The second feature was the presence of large conical entoconids on M₁–3. In QMF36357 the M₂ metaconids are distinct, although clearly reduced on the plesiomorphic dasyuromorphian condition. Comparison with the figures provided by Murray and Megirian (2000) yields no obvious differences with respect to metaconid morphology between QMF36357 and the holotype of *N. richi*. This brings us to another issue, i.e. whether metaconid reduction for these two specimens should be scored as differential (sensu Muirhead and Wroe 1998). Confusion over this matter may be attributable to misinterpretation of the character-state descriptions given by Muirhead and Wroe (1998), so here we will attempt clarification. Plesiomorphically, in dasyuromorphians the metaconid of M₁ is smaller than that of M₂–4. However, uniquely among thylacinids in *Badjcinus turnbulli* the M₁ metaconid is lost while the M₂–4 metaconids are only slightly reduced. This character state was treated as a dasyuromorphian apomorphy by Muirhead and Wroe (1998). Despite significant to very heavy wear on all M₁ metaconids referred to *Nimbacinus*, a distinct metaconid is present in each. While the metaconid on M₁ is clearly smaller than that of M₂–4 in the only two *Nimbacinus* specimens wherein a full molar row is preserved (i.e. QMF36357 and the holotype of *N. richi*), this difference is within the range exhibited by other thylacinids, excepting *B. turnbulli*. In short, *N. dicksoni* and *N. richi* can not be distinguished from each other on the basis of metaconid morphology and neither possesses differential reduction of the metaconids sensu Muirhead and Wroe (1998). This leaves one diagnostic feature separating the two species of *Nimbacinus*: M₁–3 entoconid size. We do not question the fact that in both the holotype of *N. dicksoni* and QMF36357 the entoconids appear to be smaller than in the holotype of *N. richi* and P85553-3. P85553-3 was considered to represent *N. dicksoni* by Muirhead and Archer (1990), but *N. richi* by Murray and Megirian (2000). However, the question here is whether differences in entoconid size alone, particularly given such a small sample size, should be accepted as a basis for the erection of a new taxon. The value of entoconid morphology as a stand-alone diagnostic character among dasyurids has been questioned by Dickman et al. (1998). Even the presence or absence of entoconids has been shown to be highly variable among unworn teeth of juvenile *Sminthopsis griseoventor* and *Antechinus flavipes* (Crowther et al. 1999). Consequently, we consider the status of *N. richi* to be debatable at present.

**Phylogenetic analysis**

Numerical parsimony analysis produced 10 shortest trees of 275 steps. Excluding uninformative characters CI = 0.379, HI = 0.621, RI = 0.647, and RC = 0.254. The strict consensus tree is provided in Fig. 8 along with bootstrap and Bremer support indices for resolved nodes. Character-state reconstructions for the first of the 10 most-parsimonious trees are provided in Appendix 2 for the nodes in Fig. 9.
Fig. 8. Strict consensus of 10 most-parsimonious trees of 275 steps. Excluding uninformative characters CI = 0.379, HI = 0.621, RI = 0.647 and RC = 0.254. Bremer support is given above and bootstrap below branches.

In the strict consensus tree the monophyly of Thylacinidae received moderate bootstrap and Bremer support as did that of Dasyuridae (however, among extant dasyurid subfamilies only Sminthopsinae was monophyletic). While both the position of Myrmecobius fasciatus as sister taxon to a thylacinid–dasyurid clade and a monophyletic Dasyuromorphia were
resolved, neither of these results were supported by analysis of suboptimal trees or bootstrap values of over 50. Similarly, the early Eocene Murgon taxon, *Djarthia murgonensis*, and the generalised Palaeocene borhyaenoid, *Mayulestes ferox*, were found to be monophyletic, but this relationship was unsupported.

Within Thylacinidae *Nimbacinus dicksoni* was plesiomorphic for most dental features analysed here. With respect to the generalised *Muribacinus gadiyuli* it was apomorphic for
The skull of *Nimbacinus dicksoni*

only one dental feature (absence of an anterior cingulum on M\(^1\), C 24), but it lacked the following 12 apomorphies of the dentition that were present in the specialised *T. cynocephalus*: M\(^1\) preparacrista oriented anterobuccally relative to long axis of tooth (C 12), protoconule absent (C 14), metaconule absent (C 15), styal cusp B absent on M\(^3\) (C 17), styal cusp D absent on M\(^3\) (C 18), posterior cingulum on M\(^1\) absent (C 25), metaconids absent on M\(^2\) (C 33), posterior cingulid absent on M\(_{1,3}\) (C 36), presence of carnassial notch in cristid obliqua (C 38), entoconid reduced (C 41), length of M\(_4\) exceeds that of M\(_3\) relative to the long axis of the dentary (C 42) and number of cusps on M\(_4\) talonid reduced to one (C 44).

In contrast to its relatively generalised dentition, the crania of *N. dicksoni* lacked only one apomorphy evident in *T. cynocephalus* (fossa for the lower canine bordered by anterolateral processes of premaxilla and maxilla, C 46). Together, *N. dicksoni* and *T. cynocephalus* shared three derived cranial character states absent in *B. turnbulli*: a primary foramen ovale delimited by the alisphenoid only (C 50), a complete secondary foramen ovale (C 51) and presence of a squamosal epitympanic sinus (C 55).

Relative to *Myrmecobiidae*, thylacinids were apomorphic for five cranial features: presence of palatal vacuities (C 47), loss of posterolateral palatine foramen (C 48), presence of a complete secondary foramen ovale formed by a mesial fold in the alisphenoid tympanic process (C 52), a laterally extensive U-shaped ectotympanic (C 58) and frontal squamosal contact. While five derived cranial features in *Myrmecobius fasciatus* distinguish it from thylacinids: a tympanic wing of the periotic that contacts the alisphenoid tympanic process (C 65), presence of a paroccipital tympanic process that does not contact any other tympanic elements (C 66), a mastoid tympanic wing that contacts the alisphenoid tympanic process (C 67) and a small antorbital fossa (C 76).

Modern dasyurids were distinguished from thylacinids by the presence of 10 cranial specialisations: a ventral facial nerve canal (C 54), an alisphenoid hypotympanic sinus enclosed wholly within the alisphenoid (C 56), an internal jugular canal that extends to the basisphenoid (C 60), a well developed posteroventral lip in the pars petrosa enclosing the internal jugular ventrally (C 61), an internal jugular canal that is fully enclosed dorsally (C 62), a tympanic wing of the periotic that contacts the alisphenoid tympanic process and floors the periotic hypotympanic sinus (C 65), a paroccipital that is fused to the pars petrosa anteriorly and mastoid tympanic process laterally (C 66), a mastoid tympanic process that contacts the pars petrosa (C 67), a foramen lacerum medium that is confluent with the primary foramen ovale (C 69) and a tubal foramen formed by a sulcus in the pars petrosa (C 70).

All thylacinid cranial synapomorphies were also found in at least some modern dasyurids. However, two shared derived cranial features present in thylacinids were not found in *Barinya wangala*: a laterally extensive, U-shaped ectotympanic (C 58) and frontal–squamosal contact (C 64). Five features in the cranium of *B. wangala* were derived with respect to *Thylacinidae*. These specialisations in characters 65, 66, 67, 69 and 70 were shared with the three extant dasyurid subfamilies.

**Discussion**

**Phylogeny**

Overall, the inclusion of new thylacinid material and additional fossil taxa in the analysis improved on the resolution of dasyuromorphian phylogeny provided by Wroe *et al.* (2000), but in general, consistency was low and homoplasy high. Support was weak at most nodes,
but there were exceptions, particularly within Dasyuromorphia. Many possible synapomorphies identifying specific clades were in agreement with those determined in previous analyses. Dasyuromorphia was united by the reduction of upper (C 1) and lower (C 26) incisor numbers (Marshall et al. 1990; Wroe et al. 2000), while Dasyuridae was unified by the acquisition of basicranial features largely as found by Wroe (1999) and Wroe et al. (2000). However, as also found by Wroe et al. (2000), clades were often denoted by additional possible synapomorphies not predicted in earlier investigations. For example, at node 13 (Fig. 9) the reduction of upper and lower incisor numbers accounts for only two of 10 synapomorphies that supported monophyly for dasyuromorphians.

Regarding thylacinid phylogeny and evolution, the finding of monophyly for Thylacinidae is in agreement with results of the numerical parsimony analysis performed by Muirhead and Wroe (1998), but contra that of Wroe et al. (2000). Thylacinidae was united by possession of character states that included previously suggested synapomorphies such as a laterally extensive, tubular ectotympanic (C 58) and squamosal–frontal contact (C 64) (Archer 1982; Muirhead and Wroe 1998). However, homoplasy among middle ear features complicates any interpretation. Of 10 potential synapomorphies for Thylacinidae at node 15 (Appendix 2), two are reversals in middle ear characters (C 65 2⇒1, C 66 1⇒0), while at node 13 another middle ear feature is reversed (C 52 1⇒0). Reversals in this region are treated as most improbable (MacPhee 1981) and consequently, although monophyly for Thylacinidae is supported, it is difficult to take all character-state transformations at face value.

Within Thylacinidae a point of interest borne out in this study is that although considerable variation is apparent among the dentitions of thylacinid species, the family’s skull anatomy appears to be have been characterised by marked conservatism. Thus, despite a prevalence of relatively plesiomorphic dental features, the cranium of Nimbaucinus dicksoni is remarkably similar to that of the recent Thylacinus cynocephalus. Among characters analysed, N. dicksoni lacks only one apomorphy present in T. cynocephalus, i.e. a fossa for the lower canine bordered by an anterolateral process of the premaxilla (C 46). Because dentally generalised Nimbaucinus and dentally specialised Thylacinus are both now known from late Oligocene deposits (Wroe 2002), it now appears likely that much of the gamut of thylacinid specialisation, both cranial and dental, had appeared prior to the earliest Miocene.

As regards higher-level relationships among dasyuromorphians, placement of Myrmecobius fasciatus as the immediate outgroup to a clade comprising thylacinids and dasyurids is in agreement with two previous studies based on morphology (Archer 1984; Aplin and Archer 1987), but not Wroe (1997a). Of three molecular investigations addressing this issue two concur with this interpretation, Lowenstein et al. (1981) and Krajewski et al. (2000a), while another places M. fasciatus within Dasyuridae (Krajewski et al. 1997). However, the results of neither the present nor any previous investigations have received strong support.

With respect to the position of dasyuromorphians within Marsupialia, results differ from those of Wroe et al. (2000) in that potential sister taxa are reduced from seven to three (Lestodelphys halli, Dromiciops australis and Peramelemorphia). Both Dromiciops australis (Rougier et al. 1998) and peramelemorphians (Kirsch 1968; Bavestock et al. 1990; Westerman 1991) have been advanced as possible sister taxa to Dasyuromorphia. But while historically Didelphidae has been considered as possibly ancestral to Australian marsupicarnivores (Archer 1976a), this is not a position accepted by any recent authors including ourselves. In this context, the placement of the relatively derived didelphid L. halli as a potential sister taxon to dasyuromorphians seems unlikely in the extreme.
The position of Australia’s oldest marsupicarnivore, *Djarthia murgonensis*, as monophyletic with the generalised borhyaenoid *Mayulestes ferox* appears most improbable. However, this result does highlight the need for circumspection regarding both the classification of *D. murgonensis* beyond the level of *Marsupialia incertae sedis* and decisions over whether Australian and South American marsupial radiations are fundamentally disjunct (excepting microbiotheriids), as has been suggested by Woodburne and Case (1996).

**Trends in thylacinid evolution**

Three thylacinids are now known to have existed in the late Oligocene (Wroe 2002), while as many as 10 are known from Miocene sites. All of these have been collected within a somewhat restricted geographical area including Riversleigh, north-western Queensland, and three sites in the Northern Territory. By way of contrast, only one species is widely recognised in Pliocene and Pleistocene deposits. At present, no more than two species have been shown to have existed sympatrically, but given the species richness evident in Riversleigh in particular, it is probable that as many as five, thylacinids coexisted in late Oligocene–Miocene times (Murray and Megirian 2000). Exactly how sympatric thylacinids may have carved out niche space in these northern Australian habitats is at present unclear. Moreover, Tertiary thylacinid ecology must be seen against a backdrop of increasingly complex interaction and competition with other marsupial carnivores. For example, in Riversleigh sites these now include four thylacoleonids, two giant rat-kangaroos and at least one bone-cracking dasyurid (Wroe 2002). Detailed, quantitative analyses are needed to more accurately predict the ecology of different thylacinid species. However, it is already apparent that considerable variation existed, although all share at least some apomorphies associated with a carnivorous habitus. The smallest, *Muribacinus gadiyuli*, is about the size of *Dasyurus maculatus* (Wroe 1996), while the biggest, *Thylacinus megiriani* and *Thylacinus potens*, are significantly larger than the recently extinct *Thylacinus cynocephalus* (Murray 1997). On the basis of both dentition and body size it is likely that smaller, less specialised species, such as *M. gadiyuli* and *Badjcinus turnbulli*, took small to medium-sized vertebrate prey and probably supplemented their diets with invertebrates. The near total dominance of vertical shear and extreme reduction of stylar cusps in the molars of more specialised *Thylacinus* and *Wabulacinus* suggests that these taxa were fully carnivorous.

A combination of evolutionary stagnation with respect to cranial anatomy and specialisation of the dentition among thylacinids stands in marked contrast to the emerging picture of dasyurid evolution, characterised by the retention of dental plesiomorphies (in most taxa) stacked against a plethora of new adaptations in the middle ear region. Wroe (1997a) speculates that the development of key adaptations of the middle ear in dasyurids may at least partly account for the apparent reversal of thylacinid and dasyurid fortunes in the late Tertiary. Expansion and full enclosure of the middle ear can significantly enhance the reception of low-frequency sound (Webster and Webster 1975, 1980). However, this is an allometric function and there is an absolute maximum size beyond which further increases impart no advantage (Webster and Webster 1975, 1980). This may have produced differential selection in favour of larger thylacinids, with smaller members of the family being out-competed by large, carnivorous dasyurids (Wroe 1997a; Krajewski et al. 2000b). Similarly, in the middle Miocene, small dasyurids may have attained an adaptive edge over diminutive peramelemorphian insectivores such as *Yarala burchfieldi* (Muirhead 2000).
Acknowledgments

We are indebted to C. de Muizon, M. Archer, H. Godthelp and W. D. L. Ride, as well as three anonymous reviewers, for their constructive criticism and comment on drafts of this manuscript. Funding has been provided to S. Wroe through grants from the following institutions: University of Sydney (U2000 Postdoctoral Research Fellowship), French Ministry of Foreign Affairs, Linnean Society of New South Wales, Australian Geographic Society, Institute of Wildlife Research, and the University of New South Wales. Support has also been given by the Australian Research Council (to M. Archer); the National Estate Grants Scheme (Queensland) (grants to M. Archer and A. Bartholomai); the Department of Environment, Sports and Territories; the Queensland National Parks and Wildlife Service; the Commonwealth World Heritage Unit (Canberra); ICI Australia Pty Ltd; the Queensland Museum; the Australian Museum; Century Zinc Pty Ltd; Mt Isa Mines Pty Ltd; Surrey Beatty and Sons Pty Ltd; the Riversleigh Society Inc.; the Royal Zoological Society of New South Wales and many private supporters.

References


### Appendix 1. Character states (character analysis given by Wroe et al. 2000)

1. Upper incisor number. 5 (0); 4 (1).
2. Shape of upper incisors. Peg-shaped (0); spatulate (1).
3. Height of I\(^1\). Not hypsodont (0); hypsodont (1).
4. Morphology of C\(^1\). Caniform (0); premolariform (1).
5. Height of P\(^3\). Higher crowned than P\(^2\) (0); lower crowned than P\(^2\) (1); absent (2).
6. Shape of P\(^3\). Laterally compressed in occlusal view (0); bulbous and ovate in occlusal view (1).
7. Posterolingular cuspule present or absent on P\(^3\). Absent (0); present (1).
8. Relative size of paracone and metacone M\(^1\)–M\(^3\). Paracone and metacone equal or almost equal in size (0); metacone much larger than paracone (1).
9. M\(^1\) on M\(^4\). Present and distinct from metastylar corner of tooth (0); present but not distinct from metastylar corner of tooth (1); absent (2).
10. Shape and orientation of the centrocrista (unordered). Centrocrista straight, with apex of postparacrista and premetacrista oriented dorsoventrally terminating dorsally at or almost level with the talon basin (0); apex of centrocrista oriented buccally and well above talon basin, with an acute angle evident between the postparacrista and premetacrista, and a distinct V-shape in occlusal view (1); apex of centrocrista oriented buccally and well above protocone basin, with an oblique angle apparent between the postparacrista and premetacrista (2); and apex of centrocrista positioned well above protocone basin with linear centrocrista (3).
11. Proximity of apex of centrocrista to ectoloph in dilambdodont taxa. Does not approach or breach ectoloph (0); approaches or breaches ectoloph (1).
12. Orientation of preparacrista on M\(^1\). M\(^1\) preparacrista forms a near perpendicular angle with respect to the long axis of the tooth (0); M\(^1\) preparacrista oriented anterobuccally relative to long axis of the tooth (1); M\(^1\) preparacrista runs postero- buccally relative to long axis of the tooth (2); M\(^1\) preparacrista absent (3).
13. Relative lengths of M\(^3\) and M\(^4\) preparacristae. M\(^4\) preparacristae shorter than or equal to that of M\(^3\) (0); M\(^4\) preparacristae longer than that of M\(^3\) (1).
14. Protoconule present or absent. Present (0); absent (1).
15. Metaconule present or absent. Present (0); absent (1).
16. Stylar cusp A distinct or indistinct from parastylar corner of tooth. Distinct (0); indistinct (1).
17. Size of stylar cusp B on M\(^3\). Large (0); small (1); absent (2).
18. Size of stylar cusp D on M\(^3\). Large (0); small (1); absent (2).
19. Relative size of stylar cusp B and stylar cusp D on M\(^3\). Stylar cusp B > stylar cusp D (0); stylar cusp D > stylar cusp B (1).
20. Relationship of stylar cusp D to metacone. Not appressed (0); appressed (1).
21. Presence or absence of stylar cusp C. Stylar cusp C absent (0); stylar cusp C present (1).
22. ‘Central cusp’. Absent (0); present (1).
23. Twinned cusps in the ‘C’ position. Absent (0); present (1).
24. Presence or absence of anterior cingulum on M\(^1\). Present (0); absent (1).
25. Presence or absence of posterior cingulum on M\(^3\). Present (0); absent (1).
26. Lower incisor number. 4 (0); 3 (1).
27. I\(_3\) bilobed or not bilobed. Not bilobed (0); bilobed (1).
28. Position of hypoconulid. Hypoconulid positioned posterolingual to entoconid (0); positioned posterior to entoconid (1).
29. I\(_3\) morphology. Not staggered (0); staggered (1).
30. Presence or absence of hypoconulid notch. Present (0); absent (1).
31. Presence or absence of well developed sulcus formed by anterior cingulum. Absent (0); present (1).
32. Size of metaconid on M\(_1\) relative to that of M\(_2\). M\(_1\) metaconid not reduced relative to M\(_2\) (0); reduced relative to M\(_2\) (1).
33. Size of metaconid in M\(_3\). Large (0); reduced (1); absent (2).
34. Size of paraconid in M\(_3\). Large (0); reduced (1); absent (2).
35. Orientation of postprotocristid with respect to long axis of dentary. Transverse (0); oblique (1).
36. Size of posterior cingulid in M\(_1\). Posterior cingulid present and well developed on M\(_1\) (0); reduced (1); absent (2).
<table>
<thead>
<tr>
<th>Feature</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>37.</td>
<td>Posterior cingulid in M₄ present or absent. Present (0); absent (1). This feature has been treated as separate from character 36 because loss of a posterior cingulid on M₄ occurs in many taxa without concomitant reduction or loss of the posterior cingulid in M₁-₃.</td>
</tr>
<tr>
<td>38.</td>
<td>Posterior cingulid in M₄ present or absent. Present (0); absent (1).</td>
</tr>
<tr>
<td>39.</td>
<td>Presence or absence of carnassial notch in cristid obliqua. Absent (0); present (1).</td>
</tr>
<tr>
<td>40.</td>
<td>Morphology of postprotocristid in M₃. Postprotocristid continuous with metacristid (0); oriented posteriorly and almost continuous with cristid obliqua (1); oriented posteriorly and continuous with cristid obliqua (2).</td>
</tr>
<tr>
<td>41.</td>
<td>Anterior point of termination of the cristid obliqua in M₃ with respect to carnassial notch formed by postprotocristid and metacristid (unordered). Beneath carnassial notch (0); lingual to carnassial notch (1); buccal to carnassial notch (2).</td>
</tr>
<tr>
<td>42.</td>
<td>Entoconid size. Large (0); reduced (1); absent (2).</td>
</tr>
<tr>
<td>43.</td>
<td>Anteroposterior dimension of M₄ relative to that of M₃. M₄ &lt; M₃ (0); M₄ &gt; M₃ (1).</td>
</tr>
<tr>
<td>44.</td>
<td>Height of P₃ relative to P₂. P₃ higher crowned than P₂ (0); smaller than P₂ (1); absent (2).</td>
</tr>
<tr>
<td>45.</td>
<td>Morphology of ventral facial nerve canal (unordered). Absent (0); present but incomplete anteriorly (1); present and complete (2).</td>
</tr>
<tr>
<td>46.</td>
<td>Size of squamosal epitympanic sinus. Absent (0); present (1).</td>
</tr>
<tr>
<td>47.</td>
<td>Size of alisphenoid hypotympanic sinus (unordered). Absent (0); present with periotic component (1); present wholly within alisphenoid, i.e. separated from alisphenoid hypotympanic sinus by distinct petrosal ridge (2); present with alisphenoid, periotic and squamous contributions (3).</td>
</tr>
<tr>
<td>48.</td>
<td>Shape of ectotympanic (unordered). Simple ‘U-shape’ (0); laterally extensive, but simple ‘U-shape’ in lateral view (1); laterally extensive, complex ‘saddle-shape’ (2).</td>
</tr>
</tbody>
</table>

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67. Morphology of mastoid tympanic process (unordered). Absent (0); present (1); present and contacts *pars petrosa* (2); present and contacts alisphenoid tympanic process (3).

68. Presence or absence of mastoid contribution to occiput. Present (0); absent (1).

69. Morphology of foramen lacerum medium. Distinct from primary foramen ovale (0); confluent with primary foramen ovale (1).

70. Morphology of tubal foramen (unordered). Absent (0); present but slit-like and incomplete anteroventrally (1); present and ovoid, with sulcus in *pars petrosa* (2); present, with sulcus in alisphenoid tympanic process (3).

71. Shape of nasals. Nasals posteriorly expanded (0); not posteriorly expanded (1).

72. Maxilla–nasal contact. Maxilla–nasal contact longer than premaxilla–nasal contact (0); premaxilla contact longer than maxilla–nasal contact (1).

73. Posterior extension of nasals. Nasals extend posteriorly beyond the anterior rim of the orbit (0); do not extend posteriorly beyond the orbit (1).

74. Frontal–maxillary contact. Present (0); absent (1).

75. Morphology of jugal. Jugal not Y-shaped (0); jugal Y-shaped (1).

76. Morphology of foramen lacerum medium. Distinct from primary foramen ovale (0); confluent with primary foramen ovale (1).

77. Presence or absence of prootic canal. Present (0); absent (1).

Appendix 2. Character-state changes for Nodes 1–27 in the first of 10 most-parsimonious trees

See Fig. 9

| Node 1: C6 1 ⇒ 0; C13 0 ⇒ 1; C25 0 ⇒ 1; C37 0 ⇒ 1; C40 0 ⇒ 2 |
| Node 2: C8 0 ⇒ 1; C10 0 ⇒ 1; C36 0 ⇒ 1 |
| Node 3: C45 0 ⇒ 1; C59 0 ⇒ 1; C65 0 ⇒ 1 |
| Node 4: C40 2 ⇒ 0; C43 0 ⇒ 1; C74 0 ⇒ 1; C77 0 ⇒ 1 |
| Node 5: C47 0 ⇒ 1; C63 0 ⇒ 1 |
| Node 6: C9 0 ⇒ 1; C21 1 ⇒ 0; C31 0 ⇒ 1; C56 0 ⇒ 2; C57 0 ⇒ 1; C59 1 ⇒ 0 |
| Node 7: C36 1 ⇒ 2; C66 0 ⇒ 1 |
| Node 8: C19 0 ⇒ 1; C44 0 ⇒ 1; C53 1 ⇒ 0; C57 1 ⇒ 2; C67 0 ⇒ 1; C77 0 ⇒ 1 |
| Node 9: C14 0 ⇒ 1; C15 0 ⇒ 1; C45 1 ⇒ 0 |
| Node 10: C20 0 ⇒ 1; C3 0 ⇒ 1; C12 0 ⇒ 1; C46 0 ⇒ 3; C64 0 ⇒ 1; C66 1 ⇒ 0 |
| Node 11: C12 1 ⇒ 2; C26 0 ⇒ 1; C27 0 ⇒ 1; C28 0 ⇒ 1; C30 0 ⇒ 1; C52 1 ⇒ 2; C56 2 ⇒ 0; C57 2 ⇒ 1; C75 0 ⇒ 1; C76 0 ⇒ 1 |
| Node 12: C4 0 ⇒ 1; C9 1 ⇒ 0; C11 0 ⇒ 1; C25 1 ⇒ 0; C40 2 ⇒ 1; C71 0 ⇒ 1; C72 0 ⇒ 1; C73 0 ⇒ 1 |
| Node 13: C1 0 ⇒ 1; C16 0 ⇒ 1; C26 0 ⇒ 1; C31 1 ⇒ 0; C33 0 ⇒ 1; C35 0 ⇒ 1; C46 0 ⇒ 1; C52 1 ⇒ 0; C55 0 ⇒ 1; C65 1 ⇒ 2 |
| Node 14: C25 1 ⇒ 0; C36 2 ⇒ 1; C43 0 ⇒ 1; C48 0 ⇒ 1; C56 2 ⇒ 1 |
| Node 15: C10 1 ⇒ 2; C17 0 ⇒ 1; C18 0 ⇒ 1; C34 0 ⇒ 1; C52 0 ⇒ 1; C58 0 ⇒ 1; C64 0 ⇒ 1; C65 2 ⇒ 1; C66 1 ⇒ 0; C69 1 ⇒ 0 |
| Node 16: C43 1 ⇒ 0; C50 0 ⇒ 1; C51 0 ⇒ 3; C67 1 ⇒ 0 |
| Node 17: C7 0 ⇒ 1; C26 1 ⇒ 0 |
| Node 18: C33 1 ⇒ 0; C61 0 ⇒ 1; C65 2 ⇒ 3; C66 1 ⇒ 2 |
| Node 19: C54 0 ⇒ 2; C56 1 ⇒ 2; C60 0 ⇒ 1; C62 0 ⇒ 1; C66 2 ⇒ 3; C67 1 ⇒ 2; C70 0 ⇒ 2 |
| Node 20: C5 0 ⇒ 1; C12 0 ⇒ 3; C32 0 ⇒ 1; C36 0 ⇒ 1; C43 1 ⇒ 2 |
| Node 21: C3 0 ⇒ 1; C9 1 ⇒ 2; C10 1 ⇒ 2; C20 0 ⇒ 1; C25 0 ⇒ 1; C36 1 ⇒ 2; C38 0 ⇒ 1; C44 1 ⇒ 2; C51 0 ⇒ 1; C52 0 ⇒ 1; C58 0 ⇒ 1 |
| Node 22: C45 1 ⇒ 0 |
| Node 23: C44 1 ⇒ 0 |
| Node 24: C2 0 ⇒ 1; C54 2 ⇒ 3 |
| Node 25: C44 1 ⇒ 2; C46 1 ⇒ 2; C71 0 ⇒ 1; C72 0 ⇒ 1 |
| Node 26: C2 0 ⇒ 1; C25 0 ⇒ 1; C35 1 ⇒ 0; C46 2 ⇒ 3; C64 0 ⇒ 1 |
| Node 27: C14 0 ⇒ 1; C17 0 ⇒ 1; C41 0 ⇒ 2 |
Appendix 3. Abbreviations for cranial features

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
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<tbody>
<tr>
<td>AL, a.t.p.</td>
<td>alisphenoid, alisphenoid tympanic process</td>
</tr>
<tr>
<td>BES</td>
<td>basioccipital–exoccipital–supraoccipital complex</td>
</tr>
<tr>
<td>bo.k.</td>
<td>basioccipital keel</td>
</tr>
<tr>
<td>BS</td>
<td>basisphenoid</td>
</tr>
<tr>
<td>c.f.</td>
<td>condylar foramina</td>
</tr>
<tr>
<td>eth.f.</td>
<td>ethmoid foramen</td>
</tr>
<tr>
<td>et.s.</td>
<td>eptympanic sinus</td>
</tr>
<tr>
<td>f.l.c.</td>
<td>fossa for lower canine</td>
</tr>
<tr>
<td>f.m.</td>
<td>foramen magnum</td>
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<tr>
<td>fo</td>
<td>foramen ovale</td>
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<tr>
<td>FR</td>
<td>frontal</td>
</tr>
<tr>
<td>f.rot.</td>
<td>foramen rotundum</td>
</tr>
<tr>
<td>g.f.</td>
<td>glenoid fossa</td>
</tr>
<tr>
<td>i.c.c.</td>
<td>internal carotid canal</td>
</tr>
<tr>
<td>i.o.c.</td>
<td>infraorbital canal</td>
</tr>
<tr>
<td>i.o.f.</td>
<td>infraorbital foramen</td>
</tr>
<tr>
<td>JU</td>
<td>jugal</td>
</tr>
<tr>
<td>LA</td>
<td>lacrimal</td>
</tr>
<tr>
<td>l.f.</td>
<td>lacrimal foramen</td>
</tr>
<tr>
<td>l.o.w.</td>
<td>lateral occipital wings</td>
</tr>
<tr>
<td>lpps</td>
<td>lateral postpalatine spine</td>
</tr>
<tr>
<td>mp</td>
<td>mastoid process</td>
</tr>
<tr>
<td>mpt</td>
<td>middle palatine foramen</td>
</tr>
<tr>
<td>mpps</td>
<td>medial postpalatine spine</td>
</tr>
<tr>
<td>max.v.</td>
<td>maxillary vacuity</td>
</tr>
<tr>
<td>MX</td>
<td>maxilla</td>
</tr>
<tr>
<td>NA</td>
<td>nasal</td>
</tr>
<tr>
<td>nuc.c.</td>
<td>nuchal crest</td>
</tr>
<tr>
<td>o.c.</td>
<td>occipital condyles</td>
</tr>
<tr>
<td>o-o.f.</td>
<td>optic–orbital foramen</td>
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<td>o.p.f.</td>
<td>orbital process of frontal</td>
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<td>ORB</td>
<td>orbital</td>
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<tr>
<td>PA</td>
<td>parietal</td>
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<tr>
<td>PM</td>
<td>palatine</td>
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<td>pal.f.</td>
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<td>pgf</td>
<td>postglenoid foramen</td>
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<td>PL</td>
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<tr>
<td>PM(pm)</td>
<td>pars mastoidea of petromastoid</td>
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<tr>
<td>PM(pp)</td>
<td>pars petrosa of petromastoid</td>
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<td>pg.p.j.</td>
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<td>pg.p.s.</td>
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<td>prgpp</td>
<td>preglenoid process of squamosal</td>
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<td>pterygoid canal</td>
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<td>sulcus for origin of masster</td>
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TWO early Cretaceous monotremes have been described from the Griman Creek Formation, Lightning Ridge, New South Wales. The platypus-like *Steropodon galmani* (family Steropodontidae) was Australia's first known Mesozoic mammal (Archer et al. 1985). A second taxon, *Kollikodon richiei* (family Kollikodontidae), characterised by unique bunodont teeth, may have specialised in eating crustaceans (Flannery et al. 1995). An edentulous maxillary fragment from Lightning Ridge has been described as possibly that of a monotreme (Rich et al. 1989). Edentulous lower jaw fragments of a monotreme-like mammal from Lightning Ridge have also been recovered.

The oldest undoubted ornithorhynchid is *Monotrematum sudamericanum*, from late early Paleocene sediments in Patagonia, Argentina (Pascual et al. 1992). This species demonstrates that at least ornithorhynchids had a Gondwanan distribution (Pascual et al. 1992). Two species referable to the genus *Obdurodon* have been recovered from the late Oligocene central Australian Etundra and Namba Formations: *Obdurodon insignis* (Woodburne and Tedford 1975; Archer et al. 1978) and the undescribed *O. sp. A*. *Ob. dicksoni*, a third *Obdurodon* species, has been recovered from the World Heritage fossil deposits in northwestern Queensland (Archer et al. 1992, 1993; Musser and Archer 1998). The only known Pliocene ornithorhynchid material consists of a limb fragment from the Bow Local Fauna, near Merriwa, NSW referred to the genus *Ornithorhynchus* (Rich et al. 1991b). Pleistocene ornithorhynchid material appears to represent the living *Ornithorhynchus anatinus* (e.g., Archer et al. 1978; Marshall 1992).

Echidnas of the genus *Megaligwilia*, characterised by a beak shape intermediate between that of the living *Tachyglossus* and *Zaglossus*, are known from Pleistocene swamp and cave deposits from Tasmania, New South Wales and South Australia. This recently erected genus supersedes the assignment of several long-beaked types (e.g., *ramsayi*) to the genus *Zaglossus* (Griffiths et al. 1991). A middle Miocene echidna, *Echidna (Proechidna) robusta* Dun. 1895 from Chalrong, New South Wales, is probably a species of *Megaligwilia* (Griffiths et al. 1991). A humerus found with the partial cranial of this specimen, originally described as ornithorhynchid (*Ornithorhynchus maximus* Dun. 1895), is tachyglossid and probably belongs to the individual represented by the cranium (Mahoney and Ride 1973). The huge *Zaglossus* hacketti from Western Australia may represent a distinct genus (I. Mahoney cited in Griffiths et al. 1991). Zaglossus material from the Pleistocene of New Guinea probably represents the living *Z. bruijnii* (Murray 1991). The living Short-beaked Echidna (*Tachyglossus aculeatus*) is known from many Pleistocene to Holocene deposits in southern Australia (Murray 1978, 1991).

The cladogram (Fig. 1) reflects the uncertain phylogenetic relationships of tachyglossids as well as the unresolved position of the very derived *K. richiei*. Some genetic studies infer that tachyglossids separated from ornithorhynchids near the end of the Cretaceous or early in the Tertiary (e.g., Westerman and Edwards 1992; Messer et al. 1998 but see Retief et al. 1993). Given the early Cretaceous age of the platypus-like *S. galmani*, such findings suggest that tachyglossids may have been derived from a platypus-like ancestor thus making the platypus lineage paraphyletic. However, Messer et al. (1998) suggest that such dates may be underestimates of divergence times because evolution of at least the milk protein α-lactalbumin appears to be slower in monotremes than in living therians.

Much of the monotreme fossil material is fragmentary and vast temporal gaps separate taxa. However, some tentative conclusions about historical diversity can be drawn. The presence of *S. galmani* in the early Cretaceous is testimony to the antiquity of platypus-like monotremes (Archer et al. 1985), while the presence of the contemporaneous, specialised *K. richiei* argues for far greater intradental diversity than previously anticipated (Flannery et al. 1995).

However, from the early Tertiary to the present, only ornithorhynchids and tachyglossids are represented. Ornithorhynchids may have been more diverse during the early to middle Tertiary (four species are known) while tachyglossids appear to have radiated during the Pleistocene, with at least five Pleistocene species recognised (Murray 1978; Griffiths et al. 1991).
Fig. 1: Monotreme diversity through time: a cladogram of probable relationships (see text) within Monotremata. Uncertain relationships are indicated by dashed lines. Each block represents a distinct species. Blocks that extend without breaks through more than one time period indicate apparently long-surviving species.

Phylogenetic affinities of monotremes to other groups remain contentious. Dental structure, diagnosed as therian based on the triangular molar blades of S. galmani (Archer et al. 1985; Kielan-Jaworowska et al. 1987), may be autapomorphic with independent acquisition of therian-like triangular blade systems (Archer et al. 1992, 1993). Basiliaran anatomy appears to link monotremes most closely with multituberculates (e.g., Wible and Hopson 1993; Meng and Wyss 1995). Several key Mesozoic taxa known from postcranial material exhibit advanced shoulder girdle morphology (e.g., Hu et al. 1997), placing the plesiomorphic shoulder girdle of monotremes between archaic morganucodonids or triconodontids and the more derived multituberculates (Hu et al. 1997), and suggesting an early to late Jurassic origin for the monotreme shoulder girdle (Musser 1998). Genetic evidence is equivocal: Messer et al. (1998) support a middle Jurassic divergence of monotremes from therian mammals, although Westerman and Edwards (1992) place this split at the earliest Cretaceous. A close relationship between monotremes and marsupials to the exclusion of placental mammals has recently been suggested (Janke et al. 1997; Kirch and Mayer 1998 in revisions of Gregory's 1947 Marsupialia hypothesis), although results from other molecular techniques argue against this.
on the basis of DNA-DNA hybridisation studies other Australian marsupials, that peramelemorphians are distinct from all

THE EVOLUTIONARY HISTORY OF NOTORYCTIDS, YINGABALANARIDS, YALKAPARIDONTIDS AND OTHER ENIGMATIC GROUPS OF AUSTRALIAN MAMMALS

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There are several highly autapomorphic Australian mammals whose relationships to other groups remain unclear. These include: notoryctids, yingabalani, yalkaparidonts, Tingamarra porterorum, Thylacocinga bartholomaei, microbiotheriods, Auskribosphenos nyctos and other inadequately represented or unassessed taxa (Fig. 1).

Living notoryctids, or marsupial moles, include one or two species (depending on authority) in the genus Notoryctes. Aplin and Archer (1987), recognizing the distinction of notoryctids as well as long-standing disagreements about their phylogenetic relationships, elevated them to ordinal status as notoryctemorphians, a view generally accepted. For example, Westernman (1991), on the basis of DNA-DNA hybridisation studies, supports the view that they should be a distinct order. At least one distinct genus of notoryctids is present in the early Miocene sediments of Riversleigh (Gott 1988; Archer et al. 1994, 1997). In terms of postcranial and dental remains, it is unmistakably notoryctid but it is much more plesiomorphic than the living taxa with a pre-zalambdodont molar morphology that clarifies the otherwise enigmatic structure of the upper molars of species of Notoryctes. There is no reason known to us why the Miocene taxon could not be ancestral to the species of Notoryctes.

Yingabalana richardsoni (Archer et al. 1990), known so far from two isolated lower molars found in early Miocene sediments of the Riversleigh World Heritage area, was conservatively placed in its own family, Yingabalaniidae. The bizarre molar morphology of this animal has made it impossible to determine with confidence its inter-ordinal affinities. Discovery of the second molar (currently under study by one us, Y.W.) may help to narrow the range of possibilities considered by Archcr et al. (1990) which included marsupials, nectilionid bats, primates, simmirodonts, zalambdodonts and tribotheres.

Yalkaparidones colelii and Y. jonex (Archer et al. 1988), from the late Oligocene to middle Miocene sediments of the Riversleigh World Heritage area, are among the most specialised of any known Australian mammals. They combine unique and completely zalambdodont molars with an enormous, curved, hystelodont first incisor which extends below the whole of the cheektooth row. A skull of the former suggests marsupial affinities but beyond this nothing is certain. Szalay (1994) regards them to be aberrant diprotodontians presumably on the basis of the incisor formula which is 1-3/1. Archer et al. (1988) referred this genus to its own order, the Yalkaparidontida, based on its suite of very distinctive autapomorphic features and lack of undoubted synapomorphies with other orders of marsupials.

Tingamarra porterorum (Godthelp et al. 1992) was originally described, on the basis of a single lower molar, as a possible condylarth placental from the early Eocene Tingamarra Local Fauna from Murgon, southeastern Queensland. While a second, larger but otherwise similar taxon has since been recovered from the same deposit, it does not clarify the relationships of this puzzling mammal. It remains a less parsimonious possibility that this is a very distinctive group of marsupials that has converged on placental tooth morphology.
Fig. 1. Diversity through time of notoryctids, yingabalanarids, yalkaparidens and other enigmatic groups of Australian mammals. Most of these are distinct from each other at the ordinal level. The interordinal relationships of all except (arguably) the microbiotherids and notoryctids are unclear. Each block represents a distinct species. Blocks that extend without breaks through more than one time period indicate apparently long-surviving species.

Thylacotinga barbholomai (Archer et al. 1993) was described, on the basis of isolated teeth from the early Eocene Tingamara Local Fauna, as a semi-bunodont marsupial with uncertain ordinal affinities. Although the morphology of this animal is distinctive, bunodont molar morphology in general has been developed independently in several families of didelphimorphian, polydolopimorphian and diprotodontian marsupials. Similarities to possibly early Paleocene marsupials from Peru are most striking and the subject of ongoing research.

Since microbiotherids were first hypothesised by Szalay (1982), on the basis of tarsal bone morphology, to have been the sister group (or ancestral) to Australian marsupials,
many other soft-tissue studies have corroborated this broad hypothesis. The details of the relationship are, however, controversial with other authors alternatively suggesting that microbiotheroids are the sister group to a combined dasyuroid/perameloid clade or the sister group of a combined dasyuroid/diprotodontian clade. Discovery of at least two microbiotherid-like marsupials in the early Eocene Tingamarra Local Fauna may be seen as further support for this intercontinental connection.

Other enigmatic early Eocene taxa in the Tingamarra Local Fauna are less well represented. These range from bunodont to dilambdodont marsupials, most of which are known only from isolated teeth. Some resemble early Eocene groups known from Argentina such as carlosedomorphs. Continuing work on this deposit will almost certainly enable their relationships to be better assessed and these assessments published.

Austrabiosphanea nyktos (Rich et al. 1997) was described, on the basis of a dentary with four teeth, from early Cretaceous (~115 million-year-old) sediments at Flat Rocks, Victoria. Its authors suggest that it is most parsimoniously interpreted as a placental mammal. If so, it would be as old as any previously known in the world (e.g., Prokananastes from Mongolia) and would challenge conventional understanding about the time of arrival of placentals into Australia. This interpretation has prompted spirited debate. Examination of the specimen by one of us (M.A.) suggests that A. nyktos may represent either an archaic monotreme,autopomorphic peramurid or a unique ordinal-level group that has converged on therian mammals. Some features of A. nyktos cited by Rich et al. (1997) as indicative of placentat affinities (e.g., molar number, decrease in size posteriorly of molars, possession of wide talonids and possibly the presence of a submolariform last premolar) are also characteristic of monotremes. Peramurid affinities are suggested by the trigonid-like nature of the posterior premolar as in other peramurids including Peramus and the putative peramurid Vinealestes. Kielan-Jaworowska et al. (1998) have suggested that A. nyktos may have been derived from early symmetrodont stock based on certain primitive features of the mandible (including the probable presence of attached postdental bones), the dentition being convergent on a tribosphenic pattern (as may be the case in monotremes: Archer et al. 1992). Discovery of additional materials will help to clarify the relationships of this very curious and oldest-known Australian mammal.

A somewhat mammal-like taxon from Lightning Ridge, New South Wales was described, on the basis of an edentulous maxillary fragment, by Rich et al. (1989) and Alveoli indicate that the teeth were multi-rooted. Although this may well represent a mammal if not a monotreme (Musser, above), it might also represent a derived but non-mammalian synapom. Until better material is found, this specimen will remain a tantalising mystery.

Several mammalian taxa described as fossils from Australia are even more problematical. Undoubtedly elephants were described by Richard Owen as Mastodon australis (Owen 1844) and Notolephas australis (Owen 1882). While it is possible (perhaps even probable) that these fossils were not collected in Australia, collection data indicate otherwise which leaves these records as provocative mysteries.

Other enigmatic mammal fossils include: Cucurcus proctorii DeVis, 1889 probably from the early Pliocene Chinchilla Local Fauna; Archizomatus securus DeVis, 1889 probably from the Chinchilla LF; and Chronizomus australis DeVis, 1883 from the Chinchilla LF. It is possible that C. australis represents a sirenian but the relationships of the other two DeVis taxa which are each represented by a single incomplete postcranial element, are unclear. Details of these descriptions are compiled in Mahoney and Ride (1975).