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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 *Monotrematum* 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 ornithorhynchid is the Australian platypus *Ornithorhynchus anatinus*. Extant tachyglossids include *Tachyglossus aculeatus* (the short-beaked echidna of Australia and New Guinea) and *Zaglossus bruijnii* (the long-beaked echidna of New Guinea). Two additional *Zaglossus* species, *Z. bartoni* and the possibly extinct *Z. attenboroughi*, are recognised by Flannery and Groves (1998). The platypus is a semi-aquatic mammal that feeds on freshwater benthic invertebrates. Echidnas are edentate insectivores variably covered with spines: *T. aculeatus* specialises on ants and termites while *Zaglossus*

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species generally prefer a diet of insect larvae. Both families share unique specializations (**synapomorphies**) as well as primitive features (**symplesiomorphies**), 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 (Tachyglossa, which includes the single family 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**

Table 1
A glossary of terms highlighted in boldface in the text, taken from the sources cited. Words in italics are defined elsewhere in the glossary

Cynodonts: carnivorous mammal-like reptiles, the largest and most advanced group of *therapsids* (known from the Late Permian 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 homoplastic 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).

Tribosphenic: traditionally defined as the distinctive, tritubercular tooth form possessed by basal Marsupialia, Placentalia and Theria of metatherian-eutherian grade. Tribosphenic 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 as 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

		PERIOD	EPOCH	MONOTREME FOSSIL RECORD
0	C A I N O Z O I C	**Quaternary**	Holocene	
			Pleistocene	***Ornithorhynchus anatinus*** ***Megalibgwilia ramsayi*** ***'Zaglossus' hacketti*** ***Zaglossus* species** ***Tachyglossus aculeatus***
1.78		**Tertiary**	Pliocene	
			Miocene	***'Zaglossus' robustus*** ***Obdurodon dicksoni***
			Oligocene	***Obdurodon insignis*** ***Obdurodon* sp. A**
			Eocene	
			Paleocene	***Monotrematum sudamericanum***
65	M E S O Z O I C	**Cretaceous**	Late	
			Early	***Steropodon galmani*** ***Teinolophos trusleri***
141		**Jurassic**	Late	
			Middle	
			Early	**evolutionary grade of ancestral monotremes as indicated by jaw form, shoulder girdle**
205		**Triassic**	Late	
			Middle	
			Early	
251	**P A L A E O Z O I C**			

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. Kielan-Jaworowska 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 scansoria*) 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 Mayer, 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 *Or. 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).

Pleistocene 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 monotremes—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 monotremes). 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 monotremes as well (e.g. specialisations of the shoulder girdle; early fusion of skull bones; possibly electroreceptive capabilities). Therefore, many characters 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 phylogeny (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; multituberculates). 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 relatively 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 symmetrodont (early holotherian) skeletons as described above (Hu et al., 1997), and the archaic nature of the monotreme cranial and posteranial 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 Gregory (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; temporo-mandibular 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; Zardoya 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, *T. 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 montotremes is supported, this subclass of mammals is conceivably close to 200 million years of age (latest 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. 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.
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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