FAUNA of AUSTRALIA

14. DIAGNOSIS OF THE CLASS MAMMALIA

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INTRODUCTION

These days, the production of new definitions of the Class Mammalia appears to be a healthy cottage industry. The products vary according to the different philosophies of classification espoused by their authors and the applications for which they are intended. Here, I shall discuss classifications that may be appropriate for two different types of inquiries:

First are definitions of the Class for the purposes of comparing members of the Mammalia with members of other groups of comparable rank, especially Reptilia or Aves. Assessment of the fidelity with which a classification represents patterns and rates of evolution is particularly important when studies emphasise comparison of characters of modern members of the classes.

Second, other definitions have been proposed for the purpose of circumscribing the Mammalia and distinguishing its membership from the animals that usually are dubbed the 'mammal-like reptiles'. These commonly are based on a foundation made up of the living mammals – monotremes, marsupials and eutherians. Then, on different criteria, related prehistoric species are included. In some, membership is strictly defined to include only modern mammals, their last common ancestor and members of all extinct lineages derived from that common ancestor. Other definitions have been variously designed to recognise the origin of a mammalian grade of evolution, typus or Bauplan with a specific character or suite of characters arbitrarily chosen to define membership. A survey of the classifications produced by these different approaches shows that in both the apparent common ancestors of all living mammals usually are included in the Class. Frequently, however, those based on recognition of a mammalian grade of evolution also incorporate some closely related, extinct groups that have achieved this grade of evolution in some characters, but are side branches from lineages leading to the common ancestor of modern mammals. Although these attempts differ significantly in approach, the number of species of which membership in the Mammalia is debated is relatively small.

Our current understanding of the phylogenetic relationships of the major groups of amniote tetrapods – reptiles, birds and mammals – is presented diagrammatically in Fig. 14.1. Although one recent comparative study has led to the suggestion of a closer relationship between birds and mammals (Gardiner 1982), the weight of evidence, particularly that from the fossil record, supports the interpretation given in the diagram (Gauthier 1984; Gauthier & Padian 1985).

The basal dichotomy between the group including modern reptiles and birds on one hand and that including modern mammals on the other now appears to date back to the late Carboniferous, some 300 mybp (Kemp 1982). Time of origin of Aves from their reptilian ancestors has long been placed within the Late Jurassic (some 135 mybp).

Turning to the other major branch of the diagram, the discovery in Australia of *Steropodon* has extended the record of Monotremata back to the later part of the Early Cretaceous, about 100 mybp (Archer *et al*. 1985). The oldest records of mammals clearly identifiable as members of the Marsupialia and Eutheria (therian mammals) come from rocks of Late Cretaceous age, some 70–80 mybp. Some fragmentary material, however, indicates these groups might have evolved earlier in the Cretaceous (Clemens & Lillegraven 1986; Clemens 1986). Current research suggests that the monotreme lineage might have diverged from the therian during the Late Triassic, some 200 mybp, or more recently, in the Early Jurassic. The 'stem' of this branch, leading from the basal 'reptile-bird vs.

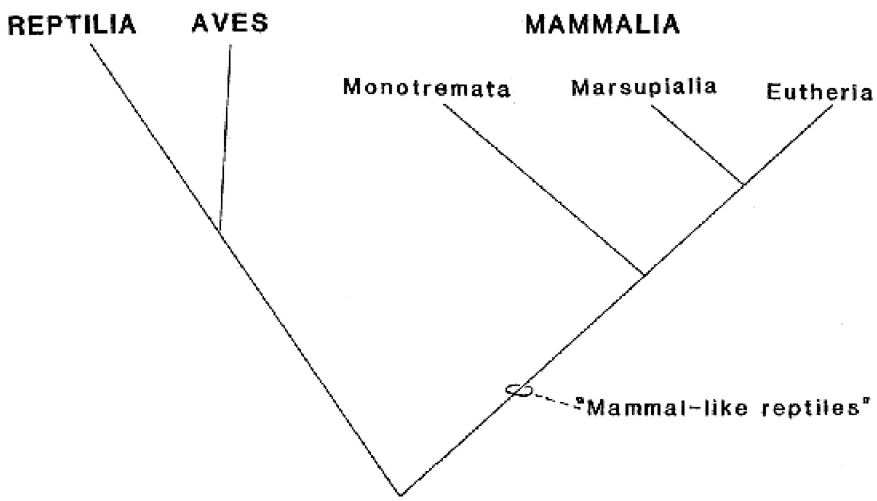

Figure 14.1 Diagrammatic representation of phylogenetic relationships of some major groups of amniote vertebrates.

mammal' dichotomy to the first members of the mammals, includes a wide range of late Paleozoic and early Mesozoic forms that unfortunately have been dubbed the 'mammal-like reptiles'.

THE THEROPSID–SAUROPSID DICHOTOMY

Goodrich's (1916) classic study, synthesising information from comparative anatomical and palaeontological studies recognised that, as traditionally used, Reptilia was an 'artificial group' containing three major units. The first, and geologically oldest, included the Protosauria, 'early amphibian-like' amniotes. Goodrich stressed that the interrelationship of the higher Amniota constituted a major evolutionary dichotomy of the second and third groups: reptiles and birds (the Sauropsida) and mammals (the Theropsida).

The traditional pattern of classification, based on the theropsid-sauropsid dichotomy, clearly recognises the great antiquity of the evolutionary divergence of the last two major groups of amniotes. The oldest known members of the Theropsida were those Carboniferous amniotes that first evolved a single opening low on the posterior part of their skull behind the orbit, the synapsid type of skull (Kemp 1982). It must be stressed that the 'reptile-like' similarities of theropsid skeletal morphology that have been used to justify description of primitive synapsids as 'mammal-like reptiles' are either primitive characters present in the last common ancestor of sauropsids and theropsids or products of parallel evolution.

In his influential classifications of vertebrates, A.S. Romer (1966 and earlier editions) included in the Class Mammalia all the theropsid amniotes having a dentary-squamosal jaw joint and, possibly, a few other characters (for example, reduction or loss of other bones of the mandible). Theropsids lacking this character were designated 'mammal-like reptiles' and classified as members of the Class Reptilia. Several authors (for example, see the exchange of views between Reed 1960; Van Valen 1960; Simpson 1960) have suggested that various groups of early theropsids also should be included in the Class Mammalia.

The inertia of the traditional taxonomy probably will prevent redefinition of the Mammalia to include all theropsids. In terms of naming levels within the hierarchy of a classification, the question is really semantic; it matters little

whether the 'mammal-like reptiles' are included in the Class Mammalia or these groups are joined in a higher category, dubbed the Theropsida or Synapsida, for example.

In contrast, in comparative studies addressing similarities or differences of Mesozoic or Cainozoic reptiles and mammals recognition of phylogenetic relationships is more than a semantic exercise. Although the first records of animals now usually classified as mammals come from deposits of the Late Triassic, some 200 mybp, this is not the calibration point, the time of last common ancestry, for these studies. Investigations of differences in rates and patterns of evolution of reptiles and mammals must be set to the time of differentiation of the sauropsids and theropsids, an event now thought to have occurred about 300 mybp.

MAMMALIA, A GRADE OR A CLADE?

Although not always expressed in such terms, the history of the concept of Mammalia, in part, has been a quest to bring together at least the modern monotremes, marsupials and eutherians, their last common ancestor and all intermediate lineages. The goal has been to isolate this crown of the theropsid phylogenetic tree. A large suite of characters (presence of hair, mammary glands, a dentary-squamosal jaw articulation and three bones in the middle ear, to cite but a few) unites the modern members of the Mammalia. Most likely, they are characters inherited from their last common ancestor.

A second theme underlying attempts to define Mammalia focuses on the origin of this peculiar mammalian 'adaptive grade' or Bauplan. Depending upon the authors' choices of 'significant' characters, origin of some 'adaptive grades' apparently preceded significantly the differentiation of the major groups of modern mammals from the basal synapsid stock.

In recent decades, students of both patterns of phylogenetic relationships and origins of adaptive grades, have increasingly adopted cladistic methods of analysis and classification. These taxonomists are directing their attention to defining strictly monophyletic groups and insisting that only such groups be used in evolutionary studies.

Outside the specialised palaeontological literature, the widely used diagnosis of the Class Mammalia is based on the presence of a dentary-squamosal articulation as the key, if not the sole, diagnostic character required for membership in the Class (Romer 1966, for example). This diagnostic criterion appeared to satisfy, or at least not be in open defiance, of the goals of: including monotremes and therians in the Mammalia; designating a diagnostic character that is clearly associated with origin of a mammalian grade of evolution, and; defining a relatively monophyletic group.

In spite of some dissent and modification by expansion to include other characters, this diagnosis by the late G.G. Simpson and others, was used by most specialists during the 1950s and 1960s. In his analysis of papers presented at a symposium on Mesozoic mammals held at the Linnean Society in 1970 and evaluation of the general status of studies of Mesozoic mammals, Simpson mused: 'It is interesting and significant that in this symposium no one attempted a formal definition of the class, in the usual sense of 'definition', and the problem was no more than mentioned' (Simpson 1971, p. 193). In the following decade, this consensus within the field was shattered.

The evolutionary transition from the advanced non-mammalian Cynodonta – the most derived of the 'mammal-like reptiles' – to early mammals has long been described as one of the best documented segments of vertebrate history. A continuing flood of new material adds justification for this assessment. For example, *Morganucodon*, which usually is classified as a mammal, is now

known from large samples of fossils from broadly contemporaneous deposits in Western Europe and China (Clemens 1986). Research on the skull by Kermack and associates (Kermack, Mussett & Rigney 1981) and jaws (Kermack, Mussett & Rigney 1973), on the dentition by Mills (1971) and Parrington (1971) and on the postcranial skeleton by Jenkins & Parrington (1976) have made *Morganucodon* one of the best known of the theropsids involved in the transition from 'mammal-like reptile' to mammal (Fig. 14.2).

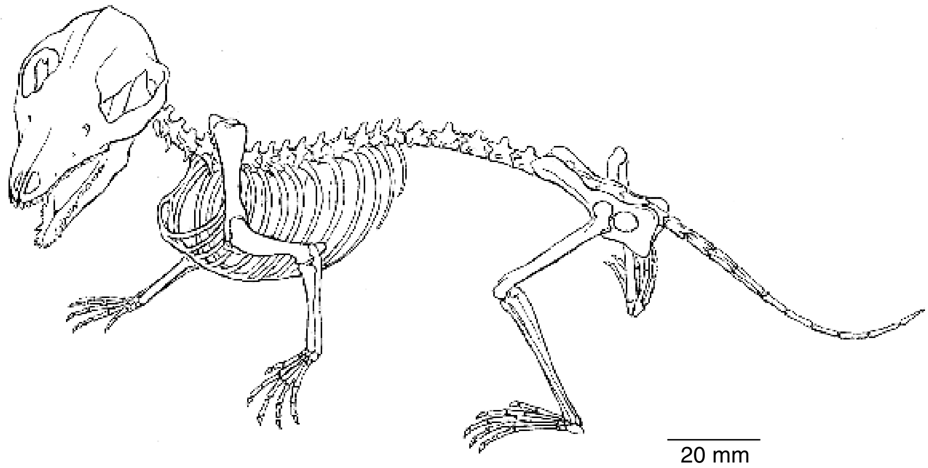

Figure 14.2 Composite skeletal reconstruction of a morganucodont based on isolated bones of *Morganucodon* selected and associated according to the body proportions of *Megazostrodon*. (After Jenkins & Parrington 1976; © ABRS) [F. Knight]

No longer do gaps in the fossil record allow 'mammal-like reptiles' with the primitive quadrate-articular jaw articulation to be clearly distinguished from mammals in which the dentary and squamosal exclusively form the jaw articulation. In *Morganucodon* and other recently discovered genera, articulations between the jaws and skull are complex, involving both pairs of bones or others (Crompton & Jenkins 1979; Kemp 1982). Should Mammalia be defined on the origin of a dentary-squamosal joint, the loss of the quadrate and articular from the jaw articulation or some other feature? This new material fills gaps in the fossil record and the problem of choice of the character or characters to adopt as diagnostic of mammals becomes increasingly complex.

Increasing application of cladistic analysis in study of the 'mammal-like reptiles' (for example, Hopson & Barghusen 1986; Kemp 1982, 1983, 1985; Rowe 1986) and Mesozoic mammals (for example, McKenna 1975; Prothero 1981) has contributed constructively to the current, unsettled situation. Because of the demand for data on homologous characters of all forms analysed, these studies have revealed major biases in the fossil record available for study. Until recently, most of the advanced 'mammal-like reptiles' were known from skulls and partial skeletons. In comparison to those of marsupials and eutherians, the dentitions of these forms are made up of relatively simple postcanine teeth that show little morphological variation – hardly subjects of detailed investigation. In contrast, the most primitive groups included in the Mammalia are known almost exclusively from isolated teeth or, at best, fragments of jaws.

Because of the absence of material or appropriate studies of available fossils, analyses of the evolutionary transition were greatly impaired. Recent work is diminishing this bias. The dentitions of 'mammal-like reptiles' are receiving much more attention (for example, Crompton 1974). In the last decades, skulls and skeletons of some of the early mammals have been discovered and more knowledgeably studied.

As research on cranial and postcranial anatomy of advanced cynodonts and early mammals progresses, it is revealing a mosaic pattern of evolution. Kemp (1983) has noted that if Tritylodonta, which are usually classified as 'mammal-like reptiles', were known only from their postcranial skeletons, they probably would be included in the Mammalia. Although they processed their food with highly specialised dentitions, their mandibles moved on a quadrato-articular hinge.

Finally, a major disquieting event has been the challenge and probable falsification of a dominant hypothesis of relationships within the Mammalia. Until recently, the argument has been that very early in their differentiation a basic dichotomy occurred (Hopson 1970; Kermack & Kielan-Jaworowska 1971). One lineage was characterised by cheek teeth on which the cusps are arranged in linear (antero-posterior) patterns. The lateral wall of the expanding braincase was formed by enlargement of an anterior lamina of the petrosal. Monotremes, as was argued, are the only living representatives of this group, the Atheria, Prototheria or non-therian mammals.

Members of the other lineage, including the marsupials and eutherians, were characterised by cheek teeth with cusps arranged in triangular patterns and enlargement of the alisphenoid to form a significant part of the braincase. Studies by Griffiths (1978), Presley (1981) and Presley & Steel (1976) have challenged previous interpretations of the embryology and anatomy of the mammalian skull and definitely discredit the neat therian vs. non-therian dichotomy. Kemp (1983) argued that the linear pattern of organisation of cusps on the cheek teeth is a primitive pattern inherited from 'mammal-like reptiles' and thereby cannot be treated as compelling evidence of close relationship.

In consequence, current perceptions of the interrelationships of early mammals are in disarray. The groups of mammals characterised by a triangular pattern of symmetry of the cusps of the cheek teeth and a derived pattern of distribution of bones forming the lateral side of the braincase still appear to be a natural, monophyletic clade, the Theria. The dentition of *Steropodon*, the Early Cretaceous monotreme, shows a triangular pattern of symmetry suggesting that this group might be related more closely to therian mammals than previously suspected. The interrelationships of the other so called non-therian mammals (morganucodontids, triconodontids and multituberculates, for example) remain unknown.

CLASS MAMMALIA – QUEST FOR A DIAGNOSIS

Gone are the days when there was a consensus among systematists on an appropriate definition of the Mammalia; probably, this is good riddance. Where do we stand now? A new, widely accepted view has yet to emerge. Some taxonomists appear to regard this situation as a normal state of affairs, '... it is not surprising that there have been varied opinions on defining the Class Mammalia ...' (Jenkins 1984, p. 38). Others are far from content: 'It is a considerable irony that an operational osteological definition remains elusive for Mammalia ...' (Kirsch 1984, p. 21).

In his excellent monograph on the 'mammal-like reptiles', Kemp (1982; 1983) provided a thorough review and analysis of previous attempts to refine the diagnosis of the Mammalia, but he stopped short of providing a full revision. The available spectrum of choices is broad. At one extreme we could include only therians (marsupials and eutherians) in the Mammalia. A possibly broader definition might be to include all the descendants of the last common ancestor of monotremes and therians, but the interrelationships of these groups are not clearly understood.

A specific character, such as the origin of an articulation between the dentary and squamosal or the shift of the quadrate (incus) and articular (malleus) from the functional jaw articulation into the middle ear, could be used to diagnose a mammalian grade of evolution. This would probably cast the net farther and result in the inclusion of forms that are related to, but not descendants of the last common ancestor of modern mammals. Without an external standard, however, such as a requirement that the character be a specialisation (apomorphy) of the last common ancestor of the group, the choice of diagnostic characters will still vary greatly. For example, Crompton & Sun (1985) argued that the origin of a dentary-squamosal articulation should be only one of several diagnostic characters of the Mammalia; consequently, they included *Sinoconodon* and *Morganucodon* in the Mammalia. In contrast, Zhang & Cui (1983) argued that inclusion of the quadrate and articular in the middle ear should be the diagnostic character of the Mammalia; consequently, they removed these genera to the 'mammal-like reptiles'.

Obviously, these and other suggestions will vary according to their author's method of classification. What is appropriate for a cladistic classification might be rejected by those favouring neo-Darwinian or phenetic methods of classification. Of the groups shown in Fig. 14.3, almost certainly the therians and monotremes will be included in any definition of the Class Mammalia. The bevelled end of the horizontal bar labelled 'Mammalia' in Fig. 14.3 lies opposite taxa whose reference to the class is currently being contested. Likewise, the bevelled end of the bar labelled 'Theria' lies opposite many of the taxa once classified as non-therian or atherian mammals of which the taxonomic allocation also is being debated. Here, recent discoveries loom large in their contribution to the discussions. For example, the cusps of the cheek teeth of *Steropodon* show a distinct triangular pattern of arrangement suggesting closer relationship of monotremes and therians than previously expected (Archer *et al.* 1985). Discovery of three ear-ossicles in the multituberculate *Lambdopsalis* also raises questions concerning the relationships of this group (Maio & Lillegraven 1986).

SUMMARY

Although long celebrated as the best documented and understood evolutionary history of the origin of a new class of vertebrates, the transition from the 'mammal-like reptiles' to mammals does not coincide with the time when modern members of the Reptilia and Mammalia shared their last common ancestor. The division between these lineages occurred much earlier, in the late Carboniferous, some 300 mybp. The reptile-like characters of the 'mammal-like reptiles' are either the retention of primitive characters inherited from their common ancestor or the product of parallel evolution.

The simple, traditional consensus diagnosis of the Mammalia, based on the presence of an articulation between the dentary and squamosal bones and, in some cases, supported by a few other characters, is being challenged. Likewise the hypothesis that very early in mammalian evolution there was a differentiation of the group into non-therians (including the monotremes) and therians (including the marsupials and eutherians) has been seriously weakened. The therian mammals, including Marsupialia and Eutheria, characterised by a triangular pattern of organisation of the cusps on their molars, still appear to be a monophyletic group which possibly might be enlarged to include the Monotremata. The phyletic relationships of groups formerly classified as non-therian mammals, Atheria or Prototheria, remain poorly understood. Currently, there is debate over which, if any, of these non-therian groups should be included in the Mammalia.

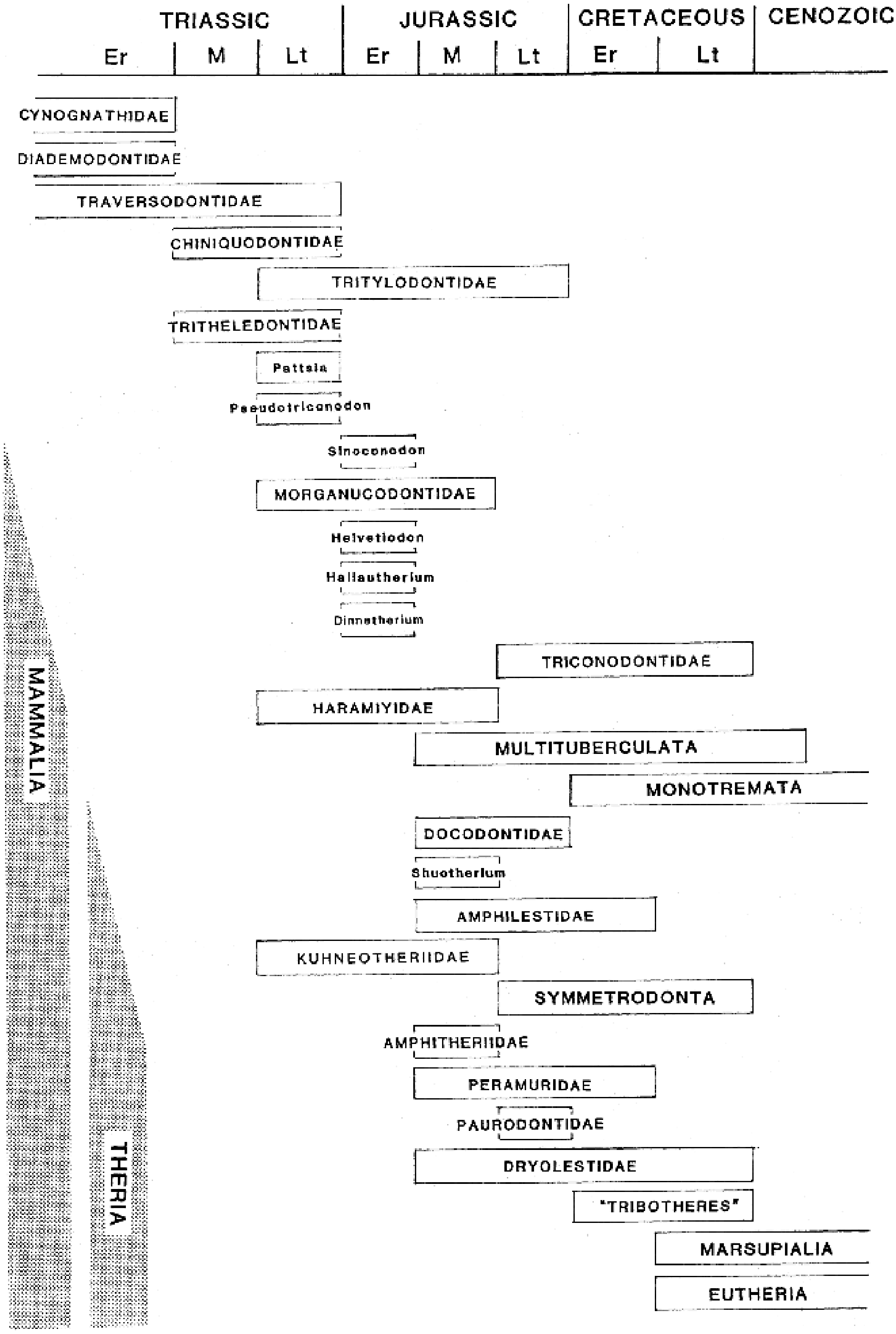

Figure 14.3 Stratigraphic ranges of some groups of advanced 'mammal-like reptiles' and early mammals. Divisions are not proportional to duration of the geological periods. Bevelled end of the horizontal bar labelled 'Mammalia' lies opposite taxa whose reference to the class currently is contested. Likewise, bevelled end of the bar labelled 'Theria' lies opposite taxa once classified as non-therian or atherian mammals, the taxonomic allocation of which is also debated.

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