Timing and biogeography of the eutherian radiation: fossils and molecules compared

J. David Archibald*

Department of Biology, San Diego State University, 5500 Campanile Dr., San Diego, CA 92182-4614, USA

Received 20 August 2002; revised 6 December 2002

Abstract

Theria includes Eutheria and its sister taxon Metatheria. Placentalia includes extant eutherians plus their most recent common ancestor. The oldest eutherian is from 125 mya (million years ago). Molecular studies place this origin at about 130–185 mya. Older dates cannot be refuted based on fossil evidence as earliest eutherian remains are scarce. Earliest superordinal clades (hence Placentalia) range from 64–104 mya (median 84 mya) based on molecules, similar to 85–90 mya based on fossils. Superordinal clades Archonta, Ferungulata, Glires, and Paenungulata based on fossils are similar to molecularly based clades, except Afrotheria was not predicted by fossils. Both fossils and molecules recognize 16 of 18 extant placental orders. Fossils place the origins of orders around 65 mya as do some molecular studies, but others suggest ordinal diversification as old as 100 mya. Fossil evidence supports a Laurasian origin for Eutheria (and Metatheria) and Placentalia, although some molecular studies suggest a Gondwanan origin for both taxa.
© 2003 Elsevier Science (USA). All rights reserved.

1. Introduction

The oldest eutherian is from 125 mya in China (Ji et al., 2002) and the oldest metatherians are from 100 mya in North America (Cifelli, 1993). Eutheria and Metatheria comprise the taxon Theria. If both of these taxa are monophyletic, there is a ghost portion (Norell, 1992) of the metathere clade extending at least to 125 mya. The extant members of Eutheria and Metatheria are Placentalia and Marsupialia, respectively (Rougier et al., 1998). Placentalia is the more taxonomically diverse of the two with 4360 species versus 272 species for Marsupialia (Wilson and Reeder, 1993). This may in part be a biogeographic happenstance with marsupials today largely restricted to Central and South America and Australia. Placentals, however, are more ecologically and biogeographically diverse, with such ecomorphotypes as whales, bats, and hoofed herbivores, equivalents of which are unknown among marsupials. Placentals are found on all continents (except inland Antarctica) and many islands. This pattern is largely a developmental restriction caused by the specialization of the metatherian reproductive system that necessitates the embryo having clawed forelimbs to crawl to a nipple (and often a pouch) where it may remain attached for an extended period of time (Lillegraven, 1979).

2. Methods

Relationships among various clades of eutherians are only briefly discussed in this paper. The term "superordinal" as used here refers to any clade above that of the ordinal level within Eutheria.

The ordinal-level and above relationships as presented by Murphy et al. (2003) are accepted for the purposes of discussion in this paper as they represent very large (16.4 kb) molecular data sets incorporating 19 nuclear and three mitochondrial gene sequences. This study is also consistent with other studies (Delsuc et al., 2002; Eizirik et al., 2001; Madsen et al., 2001, Murphy et al., 2001a; Scally et al., 2001) that find the most basal split to be between Afrotheria and other placentals. In contrast, studies that find such taxa as a paraphyletic

* Fax: 619-594-5676.
E-mail address: darchibald@sunstroke.sdsu.edu.

Rodentia (Janke et al., 2002) or paraphyeletic (Eu)Lipotyphla (Arnason et al., 2002) as sister to other placental are based partially or exclusively on mitochondrial sequences.

The two main concerns of the present analysis are the timing and the biogeography of the eutherian radiation. Three important events or series of events for Eutheria are the origin of the taxon, the origin of Placentalia (as represented by the appearances of the earliest extant clades), and the origins of the extant orders of Placentalia. The biogeographic history of these three events is analyzed and discussed. Where possible, evidence from fossils and molecules for both the timing and biogeography of these events are compared and contrasted. For simplicity's sake in comparisons I group all molecularly based studies under molecular data and all anatomically studies under fossil data.

3. Results

3.1. Origin of Eutheria

With a few exceptions (Janke et al., 2002), Eutheria is regarded as the sister taxon of Metatheria (Rougier et al., 1998). The oldest known eutherian is from China at 125 mya. It is a nearly complete, but compressed individual that appears to be largely scansorial based on postcranial ratios, hence the name *Eomaia scansoria* ("climbing dawn mother") (Ji et al., 2002) (Fig. 1). Other, much less well-preserved species are known from

slightly younger beds in Russia, Mongolia, and the Unites States. The Russian taxon, *Murtoilestes abramovi* is known from a few isolated teeth (Averianov and Skutschas, 2001). *Montanalestes* from the US is based on a dentary with six teeth (Cifelli, 1999). The Mongolian taxon *Prokennalestes* includes two species, *P. trofimovi* and *P. minor*, that differ primarily in size and may be male and female of the same species (Averianov, personal communication, 1999). Considerable material is known of *Prokennalestes* (Kielan-Jaworowska and Dashzeveg, 1989). The described material includes dentaries and maxillae, both with teeth (Kielan-Jaworowska and Dashzeveg, 1989; Sigogneau-Russell et al., 1991), and an ear region (petrosal) (Wible et al., 2001). The most distinctive of these early eutherians is *Montanalestes*, which appears more closely related to later eutherians (Ji et al., 2002) (Fig. 1).

A variety of molecularly based dates have been calculated for the eutherian–metatherian split. A typical range for four dates are: 130 mya (Janke et al., 2002), 150 mya (Cooper and Fortey, 1998a,b), 160 mya $\pm$ 10 my (Nikaido et al., 2001), and 173 mya $\pm$ 12.3 my (Kumar and Hedges, 1998). The range of averages for these dates are 148–159 mya, with extremes of 130 and 185.3 mya. The general conclusion is that the oldest date based on fossils is younger than molecularly based dates by 5–50 million years. Without a clearer consensus on a molecularly based date, the possible discrepancy between fossil and molecularly based estimates for the origin of Eutheria is not known. Further, the record for early eutherians is taxonomically limited, thus an earlier time of
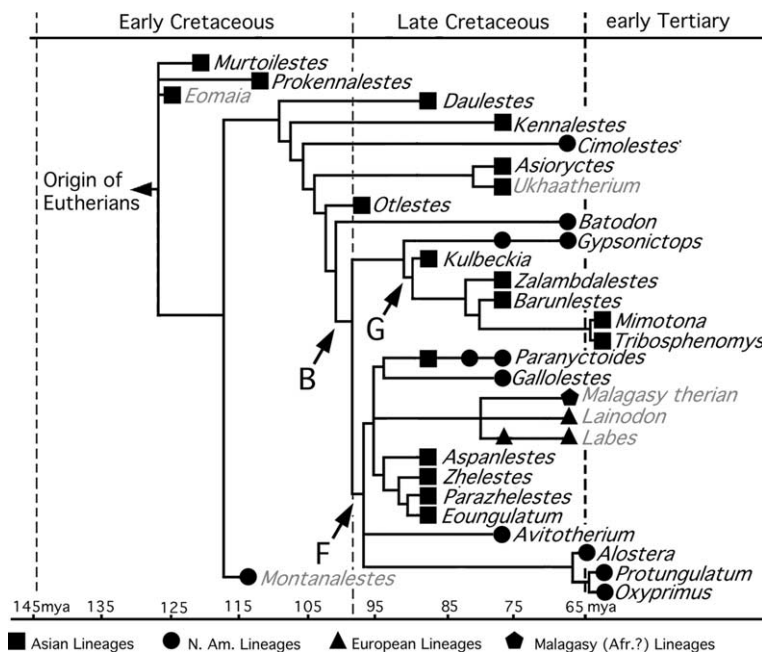

Fig. 1. Phylogeny of Cretaceous eutherians and some early Tertiary placentals based on Archibald et al. (2001) following the style of Ji et al. (2002). Taxa in gray are those hung on the phylogeny following Nessov et al. (1998), Ji et al. (2002), and Averianov et al. (2003). B, stem Boreoeutheria (also earliest Placentalia based on these fossil taxa); G, stem Glires; F, either stem Ferungulata or stem Laurasiatheria.

origin for Eutheria is possible. Because the earliest record of metatherians, the sister taxon of Eutheria, is 100 mya (Cifelli, 1993), this clade is of no help in setting a limit for an older eutherian–methatherian split.

The biogeographic history for Eutheria may be slightly better circumscribed than the timing of this event. A recent suggestion in a molecularly based study is that Eutheria is Gondwanan in origin (Murphy et al., 2003). With the exception of a fragmentary lower molar from the latest Cretaceous of Madagascar (Krause, 2001), however, no undisputed crown group therian, let alone eutherian, is known outside of Laurasia before the earliest Tertiary. Although there is some debate as to whether this Malagasy tooth fragment is a metatherian (Krause, 2001) or eutherian (Averianov et al., 2003), there is no disagreement that it is a crown group therian.

The only other recent claim of a pre-Tertiary eutherian from outside of Laurasia is that of *Ausktribosphenos* from the Early Cretaceous of Australia (Rich et al., 1997). This assessment has found little acceptance, with this taxon usually placed well outside both Eutheria and Theria (see discussion in Luo et al., 2002). Woodburne et al. (2003) have revived this controversy by arguing that a phylogenetic reanalysis of much of Luo et al.'s (2002) data shows that not only is *Ausktribosphenos* a eutherian, but also *Bishops* (Rich et al., 2001a) from the Early Cretaceous of Australia, *Ambondro* (Flynn et al., 1999) from the Middle Jurassic of Madagascar, and *Asfaltomylos* (Rauhut et al., 2002) from the Middle Jurassic of South America are eutherians as well. Although the analysis of Woodburne et al. (2003) was based on an extensive phylogenetic analysis, I argue that there is an underlying flaw in this analysis.

It is axiomatic that one should try to use only homologous characters in a phylogenetic analysis. One can argue that if there is uncertainty, homology should be assumed and then tested. The key point is that the four Gondwanan taxa in question are based *only* on lower dentitions, and yet the characters that are paramount in studying the origin of tribosphceny (the kind of molar common to therians) are mostly the very same characters used in the analysis. Establishing homology in this case is thus of paramount importance. A discussion of dental morphology of the relevant taxa is not within the scope of the present paper, but suffice it to say that a close inspection of the teeth of these Gondwanan taxa casts considerable doubt as to whether they possess a tribosphenic molar homologous to that seen in Theria. Interestingly, Woodburne et al. (2003) argued that monotremes lack a tribosphenic molar, thus rejecting a close tie to therians. The same concerns pertain to the other Gondwanan taxa.

The record of Cretaceous mammals is more extensive in Laurasia than in Gondwana. They are sufficiently well known in South America (Bonaparte, 1990; Bonaparte et al., 1993; Flynn and Wyss, 1998; Krause et al.,

1997) to conclude that it is unlikely that any crown group therians were present at the time. The only possible exception is *Asfaltomylos*, which the original authors (Rauhut et al., 2002) refer to the non-therian clade Australosphenida. As noted above, the assessment of Woodburne et al. (2003) that it is a eutherian is rejected. Australian (Rich et al., 1997; Rich et al., 2001a,b) and African (Sigogneau-Russell, 1991a,b, 1994, 1995, 1999) records are not as good, but none of the Cretaceous taxa from these two continents is a crown group therian. Again, the assessment of Woodburne et al. (2003) that the Australian *Ausktribophenos* and *Bishops*, and the Malagasy *Ambondro* are eutherians is rejected. This leaves only the Malagasy tooth fragment (Krause, 2001) as a widely accepted therian from Gondwana. If the reinterpretation of Averianov et al. (2003) is correct, it is a eutherian as well.

Eutherians are reported from India by latest Cretaceous (Prasad et al., 1994). Although Thewissen and McKenna (1992) feel that too much biogeographic weight has been given to these mammals, the preponderance of other faunal elements including discoglossid and pelobatid frogs, alligatorine crocodilians, ostrocods, and charophytes suggests that the Indian subcontinent was beginning to dock with Laurasia by the latest Cretaceous (see Prasad et al., 1994 and references therein).

3.2. Origin of Placentalia

Placentalia is the crown group of Eutheria, composed of all extant eutherians and their most recent common ancestor (Rougier et al., 1998). While the molecularly based range of dates of 130 and 185.3 mya discussed in the previous section refers to the time of the Eutheria–Metatheria split, recent calculations place the origin of Placentalia between 101 and 108 mya (Eizirik et al., 2001, Murphy et al., 2003). These dates correspond to the most basal split between the superordinal clade Afrotheria and other placentals (Murphy et al., 2003). The next split is between Xenarthra and Boreoeutheria, which is placed between 88 and 100 mya; and that of the boreoeutherian clades Laurasiatheria and Euarchontoglires at between 79 and 88 m mya.

The oldest known definite afrotherians belonging to extant clades are the early Eocene (55 mya) hyrax *Seggeurius* and the proboscidean *Phosphatherium*, both from north Africa (Gheerbrant et al., 2002). The extinct Embrithopoda from Africa, Asia, and Europe appears to be a member of Paenungulata, the taxon that includes the extant Hyracoidea, Proboscidea, and Sirenia (McKenna and Bell, 1997). The oldest embrithopod appears to be a phenacolophid, questionably known from the early Paleocene (61–65 mya) of Asia and definitely known from the late Paleocene (55–60 mya) of Asia (McKenna and Bell, 1997; McKenna and Manning, 1977). If these attributions are correct, then the

oldest known afrothere is from the early Paleocene of Asia. Because these taxa clearly belong to either recognizable extinct or extant afrotherian orders, it seems very likely that stem members of Afrotheria remain to be discovered.

The oldest known definite xenarthran is a dasypodid from the late Paleocene (60–65 mya) of South America (McKenna and Bell, 1997). Except for a possible sloth from the middle Eocene of Seymour Island, Antarctica, xenarthrans are not known outside of South America until the early Miocene (16–24 mya) when sloths are first known in the West Indies (McKenna and Bell, 1997). *Eurotamandua* from the middle Eocene of Europe was described as a myrmecophagid xenarthran by Storch (1981) but has been regarded as a pholidote by Rose and Emry (1993). The latter interpretation is followed here. To date, the earliest known xenarthrans already belong to extant xenarthran clades.

Finally, by far the most species rich superordinal clade of Placentalia, Boreoeutheria has also been known by taxa from the early Paleocene (61–65 mya) or very questionably from the latest Cretaceous (75 mya) (Archibald and Deutschman, 2001, Fig. 1). Recently, however, several stem representatives have been identified from the Late Cretaceous (85–90 mya). One of these was the "Zhelestidae," the oldest members of which are from Asia at 85–90 mya (Archibald, 1996; Nessov et al., 1998) (Fig. 2B). Zhelestids were included as members of Ungulatomorpha along with archaic ungulates, Artiodactyla, Cetacea, Perissodactyla, Proboscidea, Hyracoidea, Sirenia, and questionably Tubulidentata (Archibald, 1996; Nessov et al., 1998). The zhelestid–archaic ungulate
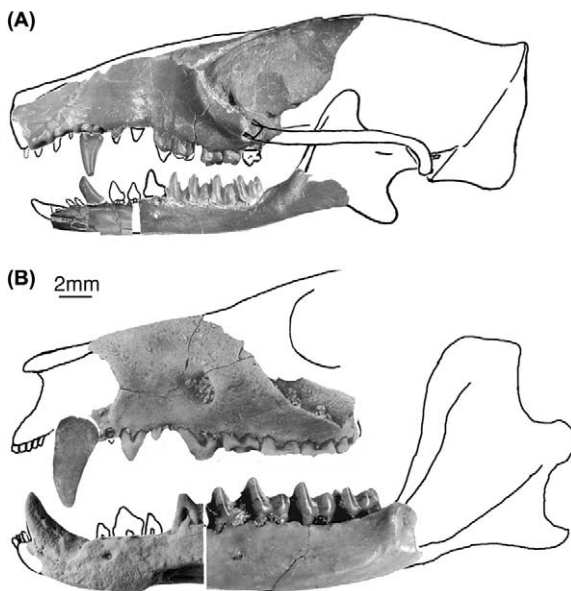
Fig. 2. (A) *Kulbeckia*, the oldest zalambdalestid, a probable stem Glires, and (B) a composite zhelestid, a probable stem ferungulate or stem laurasiathere, both from 85–90 mya, Dzharakuduk, Kyzylkum Desert, Uzbekistan (both left lateral views of skulls).

link (Fig. 1) remains supported by additional phylogenetic analyses (Archibald et al., 2001), as are some relationships between some archaic ungulates and the various extant "ungulate" clades. Such ungulate clades as Artiodactyla, Cetacea, and Perissodactyla are included in Ferungulata (along with Carnivora and Pholidota) within the boreoeutherian taxon, Laurasiatheria based on recent molecular studies, while the "ungulates" Proboscidea, Hyracoidea, Sirenia, and Tubulidentata are now referred to Afrotheria (e.g., Murphy et al., 2003). The recent work of Ji et al. (2002) suggested zhelestids might be related to lipotyphlans as well as ferungulates, thus zhelestids might be more basal (i.e., stem laurasiatheres) within Placentalia.

Archibald et al. (2001) in their analysis of another Cretaceous placental, the zalambdalestid *Kulbeckia*, presented data indicating that the other major clade of Boreoeutheria, Euarchontoglires is also present by 85–90 mya in Asia (Fig. 2A). In the most taxonomically inclusive phylogenetic analysis of Cretaceous eutherians (Fig. 1), which also included some basal members of extant placental clades, Archibald et al. (2001) found that the Late Cretaceous zalambdalestids (including *Kulbeckia*) group with members of Glires (Fig. 1). Thus, the fossil record indicates that the two clades of Boreoeutheria, Euarchontoglires (zalambdalestids) and Laurasiatheria (zhelestids), must have been present in Asia by 85–90 mya. This accords well with the Euarchontoglires—Laurasiatheria split between 79 and 88 mya, based upon molecular analyses (Janke et al., 2002; Murphy et al., 2003). Further, as zalambdalestids appear to be more closely related to the more inclusive Glires within Euarchontoglires, and zhelestids may be more closely related to the more inclusive Ferungulata within Laurasiatheria, an even older split (>90 mya) for Euarchontoglires—Laurasiatheria would not be unexpected based on the fossil record.

Meng and Wyss (2001) is the only other recent phylogenetic study to include some Late Cretaceous eutherians and more than one Tertiary or Recent placental taxon. In two of their three complete analyses they found that the Late Cretaceous zalambdalestids are the sister taxon to all the Tertiary and Recent placentals with exception of *Tupaia*, which was sister taxon to the zalambdalestid-placental clade. The relationships these authors found between Cretaceous, Tertiary, and Recent taxa differ from those found by Archibald et al. (2001), but in the latter study the support for the various relationships was stronger based on bootstrap values. Taken at face value, however, the Meng and Wyss (2001) study does suggest the presence of Late Cretaceous placentals.

The evidence that crown-group placentals were present in the Late Cretaceous is not universally accepted by paleontologists. Novacek et al. (1997) proposed five apomorphies of Placentalia that they suggest

are not seen in Late Cretaceous eutherians; thus, arguing that Placentalia would be a monophyletic taxon separate from known Cretaceous eutherians. These five apomorphies, which were not included in a phylogenetic analysis are: upper incisors four or fewer, nasals not posteriorly expanded, lacrimal without well-developed facial process, jugal not posteriorly extensive in the zygoma, and epipubics absent. These five characters are not well known for most eutherians. For example, Archibald et al. (2001) observed a well-developed facial process of the lacrimal among both extinct and extant Artiodactyla and Perissodactyla, and extinct archaic ungulates, all of which are placentals yet they retain the argued ancestral eutherian condition. The authors also noted that although less common, the nasals are posteriorly expanded in various clades in the above taxa, in some cases contacting the lacrimals. Finally, Archibald et al. (2001, and references therein) pointed out that the reduction or loss of epipubics and the reduction in number of upper incisors to four or fewer occurred in at least three different clades of metatherians. The likelihood is very high that such reductions and losses also

occurred more than once in eutherians and thus their reliability for uniting all Placentalia was questioned.

For now at least, the published phylogenetic analyses do support the presence of Late Cretaceous crown-group placentals; and also, fossil and molecular data show agreement, or at least are not at odds regarding timing of the origin of major superordinal clades. Fossil and molecular data do, however, differ on the biogeographic history of this radiation. Murphy et al. (2003) provided the most explicit description of the scenario for the early biogeographic history of placentals, borrowing the term "Garden of Eden" hypothesis from Foote et al. (1999). They reason that the placental radiation, at least in its early stages, occurred in Gondwana. They suggest that Eutheria may have established a Pangaean distribution some 173–176 mya ago after their split with metatherians (Fig. 3A). The sundering of Pangaea into Gondwana in the south and Laurasia in the north some 160 to 170 mya left stem eutherians in Laurasia such as the early eutherian *Prokennalestes*. The crown group Placentalia had its most recent common ancestry in Gondwana (Fig. 3B). The most basal split, Afrotheria in
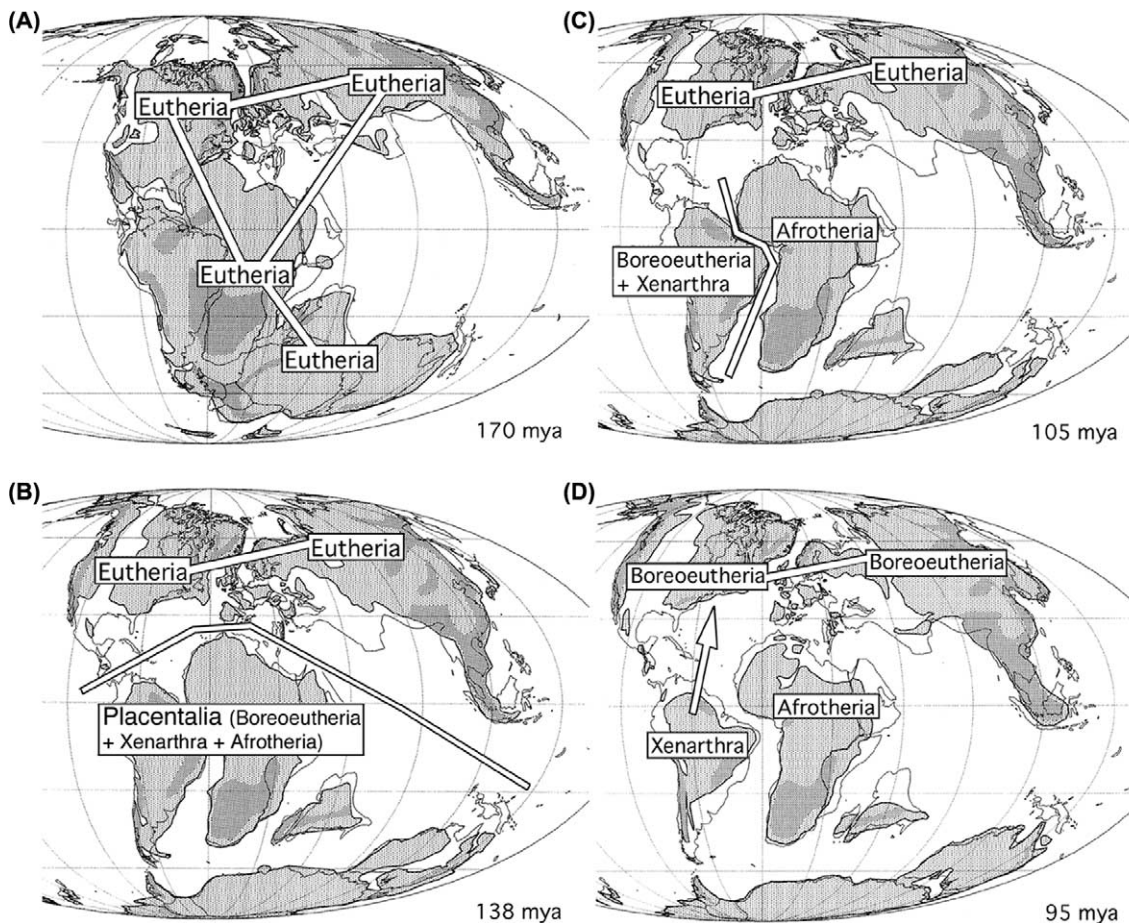

Fig. 3. Gondwanan biogeographic hypothesis for the origin of Eutheria and Placentalia following Murphy et al. (2003). See text for explanation. Base maps modified after Smith et al. (1994).

Africa and Xenarthra + Boreoeutheria in South America, occurred about 105 mya, which they say agrees with African–South American vicariance between 100 and 120 mya (Fig. 3C). Finally, there was a trans-hemispheric dispersal of Boreoeutheria after its split from Xenarthra between 88 and 100 mya (Fig. 3D).

First, the fossil record does not support this scenario. Second, some older, now largely discarded biogeographic theories of origination are implicit in this scenario. Third, there is a simpler biogeographic explanation for the pattern of splitting among the major eutherian clades.

As noted earlier, except for a Malagasy therian from the latest Cretaceous, no eutherians or metatherians are known from Gondwana until after the Cretaceous/Tertiary boundary. South American Cretaceous faunas all yield non-therians (Bonaparte, 1990; Bonaparte et al., 1993; Krause et al., 1997) with both metatherians and eutherians known in the Paleocene (e.g., Muizon and Cifelli, 2000). The Cretaceous record of Australia is not very good, but the taxa known are again non-therians. The earliest metatherians and eutherians (bats) are known from the Eocene of Australia (Godthelp et al., 1992), although earlier Tertiary records would not be unexpected. Africa, as noted, is devoid of Cretaceous therian mammal records, with the earliest eutherians known from the Paleocene according to McKenna and Bell (1997), but which are now regarded as Eocene by Gheerbrant et al. (2002).

Citing Foote et al.'s (1999) "Garden of Eden" hypothesis, Murphy et al. (2003) indicate that paleontological and molecular data may disagree on the timing of origin of crown-group placentals because it "postulates early placental diversification in regions with a poorly known fossil record." Implicit in such an assumption is that the place of such diversification equals the place or center of origin for the group in question. Following this logic, Africa would be the place or center of origin for Afrotheria. The idea that place of diversification should equal the center of origin of a taxon has been shown to be highly suspect (e.g., Brown and Lomolino, 1998). Such logic would suggest that Australia is the center of origin for metatherians because it is the place of greatest diversification. The 100 million year old metatherians from North America and the lack of metatherians in South America or the more poorly sampled Australia suggest otherwise. Similarly, stem afrotheres or even the clades within the crown group may well have originated elsewhere in the Cretaceous, and reached Africa much later in the latest Cretaceous or early Tertiary. For example, as noted earlier, the earliest recognized paenungulate is not known from Africa but is a Paleocene phenacolophid from Asia. When better known, however, Paleocene paenungulates might be recognized from Africa.

A related, but not independent issue with the "Garden of Eden" hypothesis is the implicit assumption that earliest (or most basaly) splitting lineages (Afrotheria versus Xenarthra + Boreoeutheria in Gondwana) should occur at their centers of origin. Again following this logic Hominoidea would have arisen in southeast Asia as the most basally splitting extant taxon, Hylobatidae, occurs in this region, yet the oldest fossils of Hominoidea are African (Fleagle, 1988; modified after McKenna and Bell, 1997).

The only evidence that seems to support the "Garden of Eden" hypothesis is the apparent similarity in the timing of the split between Afrotheria and Xenarthra + Boreoeutheria 105 mya, and the sundering of Africa and South America between 100 and 120 mya (Smith et al., 1994). Given the other problems with the "Garden of Eden" hypothesis, these two similarly timed events seem likely to be only coincidental.

A Laurasian origin of both Eutheria and Placentalia requires fewer biogeographic events and is supported by the fossil record. Eutheria originates on Laurasia before 125 mya (the age of the earliest eutherian) (Fig. 4A). Placentalia originates sometime between then and 85–90 million years ago also on Laurasia when we see the first probable placentals such as zhelestids and zalambdalestids (Archibald et al., 2001) (Fig. 2). As these taxa are boreoeutherians, the earlier splitting afrotheres must have also appeared, reaching Africa via dispersal by at least the early Tertiary (Fig. 4B). The xenarthrans split from the boreoeutherians slightly later, reaching South America at least by the Paleocene (Fig. 4C).

The "Garden of Eden" or Gondwanan hypothesis for the origin of Placentalia requires three biogeographic events. Eutheria was Pangaean in distribution with: (1) Placentalia arising vicariantly on Gondwana, (2) Afrotheria arising vicariantly in Africa, and Xenarthra + Boreoeutheria arising vicariantly in South America via the splitting of Africa and South America, and (3) Boreoeutheria arising by dispersal to Laurasia, presumably through North America. The Laurasian hypothesis for the origin of Placentalia requires only two biogeographic events, the dispersal of Afrotheria to Africa and the dispersal of Xenarthra to South America (Figs. 4B and C).

A final piece of evidence supports the Laurasian hypothesis. Although almost no crown therians are known from Gondwana before the Tertiary, tribosphenic mammals are known from the late Jurassic or early Cretaceous of Australia, South America, and Madagascar. Luo et al. (2002) concluded that although at a higher taxonomic level these Gondwanan taxa form a more distant sister clade to the Laurasian tribosphenic mammals, the tribosphenic condition arose separately in the north and in the south. Whether this is the case or the Gondwanan and the Laurasian clades form a (monophyletic) tribosphenic clade, mammals with a
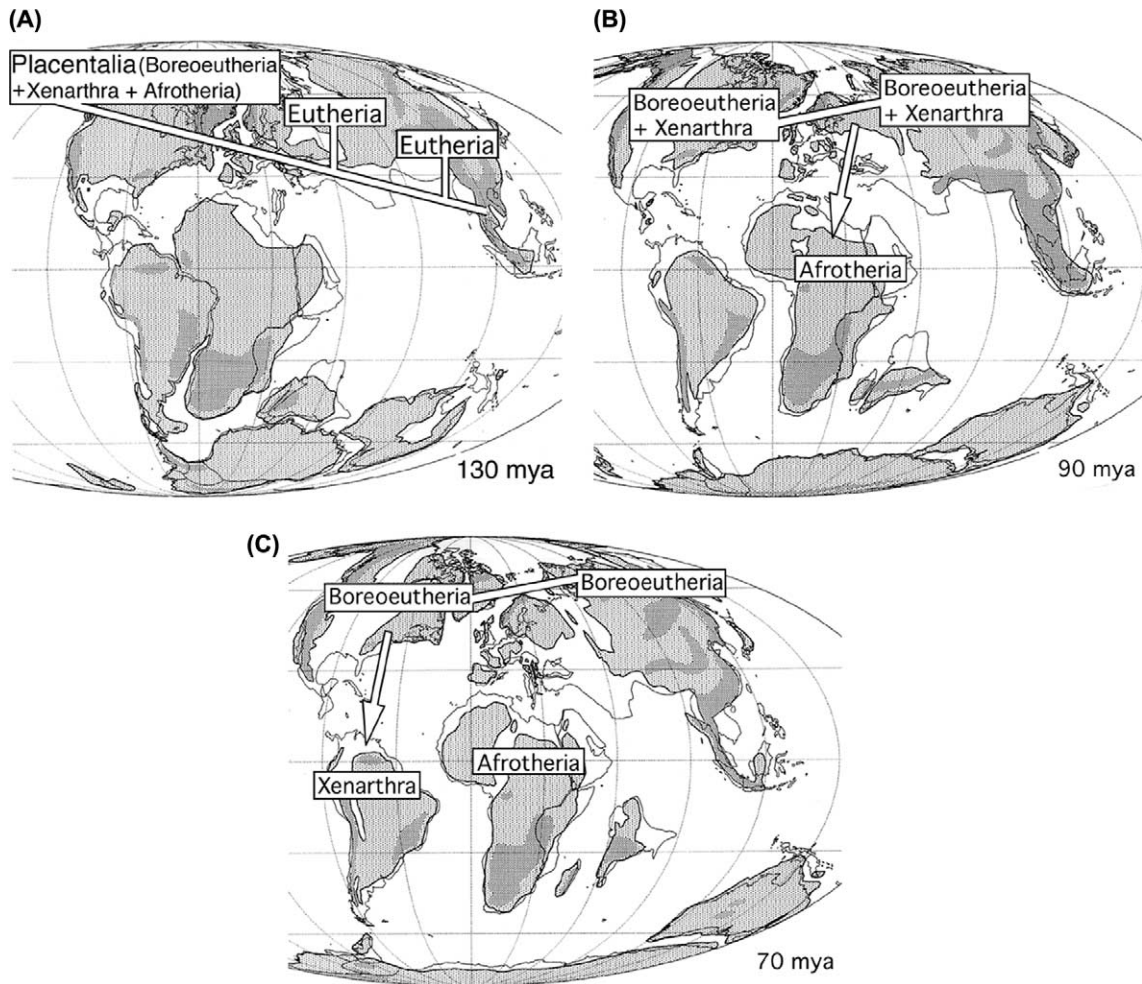
Fig. 4. Laurasian biogeographic hypothesis for the origin of Eutheria and Placentalia. See text for explanation. Base maps modified after Smith et al. (1994).

tribosphenic dentition appear to have had a Pangaean distribution with a later appearance of the tribosphenic Theria (including both Eutheria and Metatheria) in Laurasia.

3.3. Origin of placental orders

When we examine a molecularly based analysis such as that of Murphy et al. (2001a, 2003) and compare its results with those from traditional analyses we find there is less disagreement than is often portrayed (Fig. 5). The greatest disparity is at the superordinal level, where molecular studies have recognized some new and different combinations such as Laurasiatheria, Euarchontoglires, Afrotheria, and Boreoeutheria (Fig. 5). Even here, some traditionally defined superordinal taxa of some authors such as Glires and Paenungulata (e.g., Simpson, 1945), are identical to molecularly based taxa or are similar, such as Ferungulata (Simpson, 1945) and Archonta (Gregory, 1910). At the ordinal level the similarities between molecularly and anatomically based

phylogenies are even more striking. Murphy et al. (2001a, 2003) recognize 18 orders. Sixteen of these 18 were previously recognized based on fossils and anatomy. The major differences are that Cetacea is embedded within Artiodactyla and African insectivores are removed from Lipotyphla and grouped with macroscelidids and tubulidentates. Although in the case of Cetacea, recent fossil evidence was consistent with close ties to Artiodactyla.

In some recent molecular studies there has been an unfortunate tendency to name even slightly modified ordinal or superordinal clades. The International Code of Zoological Nomenclature (1999, fourth edition) does not specifically address taxa above the familial level. For the levels it does cover, however, one does not in most cases apply a completely new name each time there are modifications to the contents of an existing taxon, thus there is rationale for retaining old names while in other cases new names seem justified. For example, if in a study two taxa are newly found to be each other's sister taxon, then a new taxon is appropriate such as
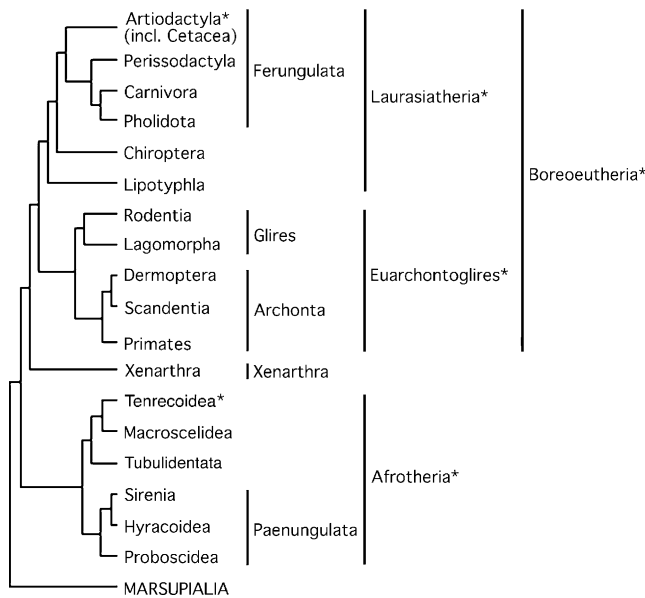
Fig. 5. Higher level phylogenetic relationships and taxonomy of Placentalia mostly after Murphy et al. (2001a, 2003), although some traditional names (see text) have been retained. An asterisk (*) denotes taxa that have been recognized almost exclusively through molecular studies. All other taxa are in general agreement between fossils and molecules.

Cetartiodactyla, if Cetacea and Artiodactyla are sister taxa. Most molecular studies now place Cetacea within Artidactyla probably as sister taxon to Hippopotamidae, thus a new name for these sister taxa is warranted, such as the whimsical Whippomorpha (Gatesy et al., 1996; Waddell et al., 1999b) but not a new name for Artiodactyla. Similarly, as it became ever clearer that Aves was within Dinosauria, the latter name was retained rather than naming a new taxon Avedinosauria. Similarly, if a taxon loses more inclusive taxa, there is no rationale for applying a new name. Hence, because Lipotyphla has lost Chrysochloridae and Tenrecidae to a new order Tenrecoidea (McDowell, 1958; Afrosoricida of Stanhope et al., 1998), it does not follow that the former taxon now should be Eulipotyphla (Waddell et al., 1999a,b). The same rationale pertains to rejecting Euarchonta in favor of Archonta, Fereuungulata in favor of Ferungulata (Waddell et al., 1999a,b).

It is reasonable to apply new names such as Laurasiatheria (Waddell et al., 1999b), Euarchontoglires (Murphy et al., 2003), Afrotheria (Stanhope et al., 1998), and Boreoeutheria (Murphy et al., 2003) (whether one finds them euphonious or not) that pertain to essentially new clades.

While there is considerable agreement between molecules and fossils over the composition of placental orders, there has been considerable disagreement as to the timing of ordinal originations. Some authors have used molecular dating to place the intraordinal diversification of at least some placental orders well back into the

Cretaceous, before the Cretaceous/Tertiary boundary at 65 mya. Rate-adjusted intraordinal divergence times of from 81.7 to 107.2 Ma within Lipotyphla, 70.7 Ma within Chiroptera, 85.9–108.8 Ma within Rodentia, 69.6 within Primates, and 85.0 within Xenarthra were reported by Springer (1997). Intraordinal divergence times of up to 66.2 Ma within Rodentia and 64.7 for Artiodactyla were reported by Kumar and Hedges (1998). Also, Kumar and Hedges (1998) placed the origin of Xenarthra at 129 Ma and Rodentia at between 109 and 112 Ma, while Cooper (1998a,b) indicated Rodentia and Lipotyphla appeared well before 100 Ma. Archibald and Deutschman (2001) termed this the "Short Fuse Model" because of the argument that some placental ordinal crown groups originated and began to diversify well back into the Cretaceous, before or shortly after the appearance of eutherians in the fossil record. More recently, some molecular studies have indicated that with a few exceptions the "Long Fuse Model" (Archibald and Deutschman, 2001) of placental diversification is supported, suggesting that interordinal diversification began before the K/T boundary while intraordinal diversification occurred after the K/T boundary (Springer, 2002). Specifically for rodents, Huchon et al. (2002) suggest that rodents radiated at about the Paleocene and Eocene transition. Further they found that the divergence between rodents and lagomorphs occurred at the K-T boundary and that splits among placentals occurred in the Late Cretaceous.

4. Summary

Both new molecularly based studies and new fossil finds are rapidly altering some of our perceptions of the origin and radiation of Eutheria. First is the question of timing of various events. Some agreements between the two approaches are that Eutheria originated before 125 mya and Placentalia (superordinal clades) arose before 85 mya. While the fossil data still strongly place ordinal diversification at around the K/T boundary 65 mya, some molecularly based studies suggest an older ordinal radiation, although some more recent molecular studies (Huchon et al., 2002; Springer, 2002) are more in accord with the dates supplied by the fossil record. Second is the question of biogeography of the eutherian radiation. Here there is less agreement. While some molecularly based studies suggest a Gondwanan origin for both Eutheria and Placentalia, the fossil record favors a Laurasian origin for both taxa. The latter hypothesis requires fewer biogeographic events, fewer assumptions regarding the center of origin, and agrees better with the fossil record. Third, there is far more agreement between fossil and molecules regarding ordinal-level relationships than is often appreciated. Only the placement of Cetacea within Artiodactyla and the

recognition of an African ordinal-level insectivore clade, Tenreoidea (= Afrosoricida) by molecular studies are substantially different from fossil-based orders. The most profound changes based upon molecular work are the recognition of a wholly African radiation (Afrotheria) and two Laurasian radiations (Laurasitheria and Euarchontoglires) including the great majority of placental taxonomic diversity. It will be in the areas of current disagreement between fossils and molecules that we will find the most fertile areas for future research.

Acknowledgments

References

Archibald, J.D., 1996. Fossil evidence for a Late Cretaceous origin of "hoofed" mammals. Science 272, 1150–1153.

Archibald, J.D., Averianov, A.O., Ekdale, E.G., 2001. Late Cretaceous relatives of rabbits, rodents, and other extant eutherian mammals. Nature 414, 62–65.

Archibald, J.D., Deutschman, D., 2001. Quantitative Analysis of the Timing of Origin of Extant Placental Orders. J. Mammal. Evol. 8, 107–124.

Arnason, U., Adegoke, J.A., Bodin, K., Born, E.W., Esa, Y.B., Gullberg, A., Nilsson, M., Short, R.V., Xu, X., Janke, A., 2002. Mammalian mitogenomic relationships and the root of the eutherian tree. PNAS 99, 8151–8156.

Averianov, A.O., Archibald, J.D., Martin, T., 2003. Placental nature of the alleged marsupial from the Cretaceous of Madagascar. Acta Palaeontol. Pol. 48, 149–151.

Averianov, A.O., Skutschas, P., 2001. A new genus of eutherian mammal from the Early Cretaceous of Tranbaikalia, Russia. Acta Palaeontol. Pol. 46, 431–436.

Bonaparte, J.F., 1990. New Late Cretaceous mammals from the Los Alamitos Formation, northern Patagonia. Natl. Geogr. Res. 6, 63–93.

Bonaparte, J.F., Van Valen, L.M., Kramartz, A., 1993. La fauna local de Punta Peligro, Paleoceno Inferior, de la Provincia del Chubut, Patagonia, Argentina. Evol. Monogr. 14, 1–61.

Brown, J.H., Lomolino, M.V., 1998. Biogeography, second ed. Sinauer Associates Inc., Sunderland, Mass.

Cifelli, R.L., 1993. Early Cretaceous mammal from North America and the evolution of marsupial dental. Proc. Natl. Acad. Sci. USA 90, 9413–9416.

Cifelli, R.L., 1999. Tribosphenic mammal from the North American Early Cretaceous. Nature 401, 363–366.

Cooper, A., Fortey, R., 1998a. Evolutionary explosions and the phylogenetic fuse. TREE 13, 151–156.

Cooper, A., Fortey, R., 1998b. Shortening the phylogenetic fuse, reply. TREE 13, 323–324.

Delsuc, F., Scally, M., Madsen, O., Stanhope, M.J., de Jong, W.W., Catzeflis, F.M., Springer, M.S., Douzery, E.J.P., 2002. Molecular phylogeny of living xenarthrans and the impact of character and taxon sampling on the placental tree rooting. Mol. Biol. Evol. 19, 1656–1671.

Eizirik, E., Murphy, W.J., O'Brien, S.J., 2001. Molecular dating and biogeography of the early placental mammal radiation. J. Hered. 92, 212–219.

Fleagle, J.G., 1988. Primate Adaptation & Evolution. Academic Press, San Diego.

Flynn, J.J., Parrish, M., Rakotosamimanana, B., Simpson, W.F., Wyss, A.R., 1999. A middle Jurassic mammal from Madagascar. Nature 401, 57–60.

Flynn, J.J., Wyss, A.R., 1998. Recent advances in South American mammalian paleontology. TREE 13, 449–454.

Foote, M., Hunter, J.P., Janis, C.M., Sepkoski Jr., J.J., 1999. Evolutionary and preservational constraints on origins of biologic groups: divergence times of eutherian mammals. Science 283, 1310–1314.

Gatesy, J., Hayashi, C., Cronin, M., Arctander, P., 1996. Evidence from milk casein genes that cetaceans are close relatives of hippopotamid artiodactyls. Mol. Biol. Evol. 13, 954–963.

Gheerbrant, E., Tassy, P., Domning, D., 2002. Origin, timing, and relationships of Paenungulata. J. Vertebr. Paleontol. 22 (suppl. to 3), 58A.

Godthelp, H., Archer, M., Cifelli, R.L., Hand, J.S., Gilkeson, C.F., 1992. Earliest known Australian Tertiary mammal fauna. Nature 356, 514–516.

Gregory, W.K., 1910. The orders of mammals. Bull. Am. Mus. Nat. Hist. 27, 1–524.

Huchon, D., Madsen, O., Sibbald, M.J.J.B., Ament, K., Stanhope, M.J., Catzeflis, F., de Jong, W.W., Douzery, E.J.P., 2002. Rodent phylogeny and a timescale for the evolution of Glires: evidence from an extensive taxon sampling using three nuclear genes. Mol. Biol. Evol. 19, 1053–1065.

Janke, A., Magnell, O., Wieczorek, G., Westerman, M., Arnason, U., 2002. Phylogenetic analysis of 18S rRNA and the mitochondrial genomes of the wombat, *Vombatus ursinus,* and the spiny anteater, *Tachyglossus aculeatus*, Increased support for the Marsupionta hypothesis. J. Mol. Evol. 54, 71–80.

Ji, Q., Luo, Z., Yuan, C., Wible, J.R., Zhang, J., Georgi, J.A., 2002. The earliest known eutherian mammal. Nature 416, 816–822.

Kielan-Jaworowska, Z., Dashzeveg, D., 1989. Eutherian mammals from the Early Cretaceous of Mongolia. Zool. Scr. 18, 347–355.

Krause, D.W., Prasad, G.V.R., von Koenigswald, W., Sahni, A., Grine, F.E., 1997. Cosmopolitanism among Gondwanan Late Cretaceous mammals. Nature 390, 504–507.

Krause, D.W., 2001. Fossil molar from a Madagacan marsupial. Nature 412, 497–498.

Kumar, S., Hedges, B., 1998. A molecular tree for vertebrate evolution. Nature 392, 917–919.

Lillegraven, J.A., 1979. Reproduction in Mesozoic mammals. In: Lillegraven, J.A., Kielan-Jaworowska, J.A.Z., Clemens, W.A. (Eds.), Mesozoic Mammals: the First Two-thirds of Mammalian History. University California Press, Berkeley, pp. 259–276.

Luo, Z., Kielan-Jaworowska, Z., Cifelli, R.L., 2002. In quest for a phylogeny of Mesozoic mammals. Acta Palaeontol. Pol. 47, 1–78.

Madsen, O., Scally, M., Douady, C.J., Kao, D.J., DeBryk, R.W., Adkins, R., Amrine, H.M., Stanhope, M.J., de Jong, W.W., Springer, M.S., 2001. Parallel adaptive radiations in two major clades of placental mammals. Nature 409, 610–614.

McDowell Jr., S.B., 1958. The Greater Antillean insectivores. Bull. Am. Mus. Nat. Hist. 115, 113–214.

McKenna, M.C., Bell, S.K., 1997. Classification of Mammals Above the Species Level. Columbia University Press, New York.

McKenna, M.C., Manning, E., 1977. Affinities and palaeobiogeographic significance of the Mongolian Paleogene genus *Phenacolphus*. Géobios, Mém. spécial 1, 61–85.

Meng, J., Wyss, A.R., 2001. The morphology of *Tribosphenomys* (Rodentiaforms, Mammalia): phylogenetic implications for basal Glires. J. Mammal. Evol. 8, 1–72.

Muizon, C.de, Cifelli, R.L., 2000. The "condylarths" (archaic Ungulata, Mammalia) from the early Palaeocene of Tiupampa (Bolivia): implications on the origin of the South American ungulates. Geodiv. 22, 47–150.

Murphy, W.J., Eizirik, E., O'Brien, S.J., Johnson, W.E., Zhang, Y.P., Ryder, O.A., O'Brien, S.J., 2001a. Molecular phylogenetics and the origins of placental mammals. Nature 409, 614–618.

Murphy, W.J., Eizirik, E., O'Brien, S.J., Madsen, O., Scally, M., Douady, C.J., Teeling, E., Ryder, O.A., Stanhope, M.J., de Jong, W.W., Springer, M.S., 2003. Resolution of the early placental mammal radiation using Bayesian phylogenetics. Science 294, 2348–2351.

Nessov, L.A., Archibald, J.D., Kielan-Jaworowska, Z., 1998. Ungulate-like mammals from the Late Cretaceous of Uzbekistan and a phylogenetic analysis of Ungulatomorpha. Bull. Carnegie Mus. Nat. Hist. 34, 40–88.

Nikaido, M., Kawai, K., Cao, Y., Harada, M., Tomita, S., Okada, N., Hasegawa, M., 2001. Maximum likelihood analysis of the a complete mitochondrial genomes of eutherians and a reevaluation of the phylogeny of bats and insectivores. J. Mol. Evol. 53, 508–516.

Norell, M.A., 1992. Taxic origin and temporal diversity: the effect of phylogeny. In: Novacek, M.J., Wheeler, Q.D. (Eds.), Extinction and Evolution. Columbia University Press, New York, pp. 89–118.

Novacek, M.J., Rougier, G.W., Wible, J.R., McKenna, M.C., Dashzeveg, D., Horovitz, I., 1997. Epipubic bones in eutherian mammals from the Late Cretaceous of Mongolia. Nature 389, 483–486.

Prasad, G.V.R., Jaeger, J.-J., Sahni, A., Gheerbrant, E., Khajuria, C.K., 1994. Eutherian mammals from the Upper Cretaceous (Maastrichtian) Intertrappean Beds of Naskal, Andhra Pradesh, India. J. Vertebr. Paleontol. 14, 260–277.

Rauhut, O.W.M., Martin, T., Ortiz-Jaureguizar, E., Puerta, P., 2002. A Jurassic mammal from South America. Nature 416, 165–168.

Rich, T.H., Vickers-Rich, P., Constantine, T.A., Flannery, T.F., Kool, L., van Klaveren, N., 1997. A tribosphenic mammal from the Mesozoic of Australia. Science 278, 1438–1442.

Rich, T.H., Flannery, T.F., Trusler, P., Kool, L., van Klaveren, N., Vickers-Rich, P., 2001a. A second placental mammal from the Early Cretaceous Flat Rocks site, Victoria, Australia. Records Queen Victoria Mus. 110, 1–9.

Rich, T.H., Vickers-Rich, P., Trusler, P., Flannery, T.F., Cifelli, R.L., Constantine, A., Kool, L., van Klaveren, N., 2001b. Monotreme nature of the Australian Early Cretaceous mammal *Teinolophos trusleri*. Acta Palaeontol. Pol. 46, 113–118.

Rose, K.D., Emry, R.J., 1993. Relationships of Xenarthra, Pholidota, and Fossil "Edentates": the Morphological Evidence. In: Szalay, F.S., Novacek, M.J., McKenna, M.C. (Eds.), Mammal Phylogeny: Placentasl. Springer-Verlag, New York, pp. 81–102.

Rougier, G.W., Wible, J.R., Novacek, M.J., 1998. Implications of *Deltatheridium* specimens for early marsupial history. Nature 396, 459–463.

Scally, M., Madsen, O., Douady, C.J., de Jong, W.W., Stanhope, J., springer, M.S., 2001. Molecular evidence for the major clades of placental mammals. J. Mammal. Evol. 8, 239–277.

Sigogneau-Russell, D., 1991a. Nouveaux Mammifères theriens du Crétacé inférieur du Maroc. C. R. Acad. Sci. Paris 313, 279–285.

Sigogneau-Russell, D., 1991b. Découverte du premier mammifère tribosphénique du Mésozoïque africain. C. R. Acad. Sci. Paris 313, 1635–1640.

Sigogneau-Russell, D., 1994. Further data and reflexions on the tribosphenid mammals (Tribotheria) from the Early Cretaceous of Morocco. Bull. Mus. Natl. Hist. Nat. 16, 291–312.

Sigogneau-Russell, D., 1995. Two possibly aquatic triconodont mammals from the Early Cretaceous of Morocco. Acta Palaeont. Pol. 40, 149–162.

Sigogneau-Russell, D., 1999. Réévaluation des Peramura (Mammalia, Theria) sur la base de nouveaux spécimens du Crétacé inférieur d'Angleterre et du Maroc. Geodiv. 21, 93–127.

Sigogneau-Russell, D., Dashzeveg, D., Russell, D.E., 1991. Further data on *Prokennalestes* (Mammalia, Eutheria *inc. sed.*) from the Early Cretaceous of Mongolia. Zool. Scr. 21, 205–209.

Simpson, G.G., 1945. The Principles of Classification and a Classification of Mammals. Am. Mus. Nat. Hist. Bull. 85, 1–350.

Smith, A.G., Smith, D.G., Funnell, B.M., 1994. Atlas of Mesozoic and Cenozoic Coastlines. Cambridge University Press, Cambridge.

Springer, M.S., 1997. Molecular clocks and the timing of the placental and marsupial radiations in relation to the Cretaceous-Tertiary boundary. J. Mammal. Evol. 4, 285–302.

Springer, M.S., 2002. A molecular perspective on higher level relationships and divergence times among placental mammals. Molecular Evolution: Evolution, Genomics, Bioinformatics, Sorrento, Abstracts, 525.

Stanhope, M.J., Waddell, V.G., Madsen, O., de Jong, W.W., Hedges, S.B., Cleven, G.C., Kao, D., Springer, M.S., 1998. Molecular evidence for multiple origins of Insectivora and for a new order of endemic African insectivore mammals. Proc. Natl. Acad. Sci. 95, 9967–9972.

Storch, G., 1981. *Eurotamandua joresi*, ein Myrmecophagide aus dem Eozän de "Grube Messel" bei Darmstadt (Mammalia, Xenarthra). Sencken. lethaea 61, 247–289.

Thewissen, J.G.M., McKenna, M.C., 1992. Paleobiogeography of Indo-Pakistan: a response to Briggs, Patterson, and Owen. Syst. Biol. 41, 248–251.

Waddell, P.J., Cao, Y., Hasegawa, M., Mindell, D.P., 1999a. Assessing the Cretaceous superordinal divergence times within birds and placental mammals by using whole mitochondrial protein sequences and an extended statistical framework. Syst. Biol. 48, 119–137.

Waddell, P.J., Okada, N., Hasegawa, M., 1999b. Towards resolving the interordinal relationships of placental mammals. Syst. Biol. 48, 1–5.

Wible, J.R., Rougier, G.W., Novacek, M.J., McKenna, M.C., 2001. Earliest eutherian ear region: a petrosal referred to *Prokennalestes* from the Early Cretaceous of Mongolia. Am. Mus. Novitates 3322, 1–44.

Wilson, D.E., Reeder, D.M. (Eds.), 1993. Mammal Species of the World. Smithsonian Inst. Press, Washington.

Woodburne, M.O., Rich, T.A., Springer, M.S., 2003. The Evolution of Tribosphony and the Antiquity of Mammalian Clades. MPE (in press).