



Review

Major mammalian clades: a review under consideration of molecular and palaeontological evidence

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Receipt of Ms. 30. 10. 2001
Acceptance of Ms. 05. 06. 2002

Abstract

Recent advances in mammalian higher-level molecular phylogenetics have generated support for the recognition of four fundamental superordinal clades of living placental mammals. These superordinal hypotheses are used as a framework for exploring patterns and trends that have occurred during mammalian evolution to give rise to the contemporary placental mammal fauna. Potential relationships of recent mammal groups not previously referred to one of these four clades are examined here. Patterns of comparative disparity and diversity, historical and modern biogeography, and morphological and ecological convergence between and within placental superorders are discussed.

Key words: Phylogenetics, eutherian, convergence, diversity, disparity

Introduction

“The stream of heredity makes phylogeny; in a sense, it is phylogeny. Complete genetic analysis would provide the most priceless data for the mapping of this stream...”

Simpson (1945)

Comprehensive molecular studies of higher-level mammalian phylogenetics (MADSEN et al. 2001; SCALLY et al. 2001; MURPHY et al. 2001 a, b) have recently infused fresh perspective into long-debated questions regarding relationships and radiations among the living placental mammal lineages. These studies, the first to employ very large molecular datasets (dominated by nuclear

exons) representing every eutherian order, have generated well-resolved phylogenies that suggest extant placental mammals can be partitioned into four superordinal clades. One of these fundamental superordinal groups is Afrotheria, a clade of probable African origin comprising six orders of mostly African and Madagascan mammals: Hyracoidea, Proboscidea, Sirenia, Tubulidentata, Macroscelidea, and Afrosoricida (tenrecs, otter shrews, and golden moles). The superorder Xenarthra, in turn, is a traditionally recognized assemblage comprising Folivora (sloths, see DELSUC et al. 2001), Vermilingua (vermilinguas), and Cingulata (armadillos) (all of which are recognized here as full orders) with greatest di-

versity and possible origin in South America (DELSUC et al. 2001; or possibly Antarctica, see VIZCAINO et al. 1998). A third clade was dubbed Euarchontoglires by MURPHY et al. (2001 b) to recognize that its membership consists of the apparently monophyletic clades Glires (Rodentia and Lagomorpha) and Euarchonta (Primates, Scandentia, and Dermoptera – i. e. Archonta sensu GREGORY 1910, minus bats and elephant shrews). The last of the four placental superorders was designated Laurasiatheria by MADSEN et al. (2001 a) (to denote the apparent origin of many of its member groups on northern continents); it includes the orders Lipotyphla (shrews, moles, and hedgehogs), Chiroptera, Carnivora, Pholidota, Perissodactyla, and Artiodactyla (including cetaceans; n. b. the name Cetartiodactyla, as currently employed by molecular systematists, should probably be considered a term of convenience rather than a valid superordinal name. Cetartiodactyla could be a valid name if cetaceans were considered the sister group of all other artiodactyls. However, cetaceans are properly nested within the order Artiodactyla as traditionally defined, which is otherwise paraphyletic – cf. ARNASON et al. 2000; LUM et al. 2000; SHIMAMURA et al. 1997 – thus, the name Artiodactyla can be retained for this assemblage, just as the order Carnivora, paraphyletic without pinnipeds, does not change its name upon their inclusion or exclusion).

This eutherian arrangement complements support previously generated from molecular and morphological studies for the recognition of two marsupial superorders (PHILLIPS et al. 2001; SZALAY 1982, 1994; TEMPLE-SMITH 1987): Australidelphia, including four Australasian orders as well as the enigmatic South American marsupial *Dromiciops* (in the monotypic order Microbiotheria); and Ameridelphia, comprising the American opossums (order Didelphimorphia) and shrew-mice (order Paucituberculata). Entertaining these superordinal hypotheses, a total of seven fundamental groupings can be recognized among living mammals: four placental superorders, two marsupial superorders, and monotremes.

Correct higher-level relationships among placental orders, among marsupial orders (PALMA and SPOTORNO 1999; PHILLIPS et al. 2001; SPRINGER et al. 1998), and between placentals, marsupials, and monotremes (JANKE et al. 1997, 2002; KILLIAN et al. 2001; KIRSCH and MAYER 1998), are currently the subject of very active molecular and morphological investigation. Researchers employing varied data sets have arrived at many conflicting hypotheses for placental relationships in particular (see LIU et al. 2001). In this light, the potential phylogenetic arrangements delineated by MURPHY et al. (2001 b) should be considered working hypotheses that will undergo additional refinement (see NOVACEK 2001). Notably, superordinal relationships supported by MURPHY et al. (2001 b) (and discussed here) strongly contradict the results of many morphology-based phylogenetic arrangements (e. g. SHOSHANI and MCKENNA 1998; FISCHER and TASSY 1993; NOVACEK 1992; NOVACEK and WYSS 1986). However, molecular phylogenetic studies can employ vastly larger datasets and potentially more powerful analytical methods, and are thus of fundamental utility in resolving relationships between taxa when morphological methods offer ambiguous results (cf. MURPHY et al. 2001 b; SHOSHANI and MCKENNA 1998). In addition to clarifying seemingly intractable phylogenetic problems, molecular phylogenetics acts in tandem to enrich macroevolutionary studies by pointing out anatomical convergences that would be difficult to conclusively identify otherwise (such as those used in the past to unite paraphyletic superorders such as Volitantia, Anagalida, Archonta, Altungulata, and Edentata; cf. SHOSHANI and MCKENNA 1998). This provides insight into the relationship between ecological similarity, homology, and homoplasy through time.

Assuming that there are four fundamental placental clades provides a fresh framework for exploring origins, comparative success, historical biogeography, and convergent adaptations of these major groups, and for addressing the unresolved relationships of

several poorly-known placental lineages within this framework. Some of these topics have been discussed elsewhere (EIZIRIK et al. 2001, MADSEN et al. 2001, MURPHY et al. 2001 a,b; NOVACEK 2001; SCALLY et al. 2001) but are explored in greater detail here.

Unresolved clade membership

Several poorly-known placental groups of uncertain affinity were not included in the collective analyses of MURPHY et al. (2001 b). While these are groups that appear only peripherally in the Holocene, their phylogenetic relationships have significant bearing on historical biogeography. The first of these are the solenodons and nesophonts, insectivore-grade mammals endemic to the Greater Antilles. Nesophonts have apparently become extinct in recent centuries and are known only by skeletal material, but solenodons survive as highly endangered species in Cuba and Hispaniola. The relationships of solenodons have never been very clear (McDOWELL 1958; VAN VALEN 1967; WHIDDEN and ASHER 2001). They are probably referable to the laurasiatherian order Lipotyphla (in the restricted sense, i.e. Eulipotyphla in recent literature) along with shrews, moles, and hedgehogs (see STANHOPE et al. 1998 b), but further study is needed in the context of the arrangement of MURPHY et al. (2001 b). The true affinities of nesophonts remain almost completely obscure; although commonly arranged as sister taxa, it remains to be demonstrated that nesophonts and solenodons are more closely related to each other than to any other insectivore-grade mammals (see WHIDDEN and ASHER 2001).

Another little-known group of insectivore-grade mammals are the Indomalayan gymnures and moonrats (Galericinae, formerly Hylomyinae). Morphological analyses conclusively place gymnures as the sister group to hedgehogs (Erinaceinae) (see CORBET 1988; FROST et al. 1991; NEVEU and GASC 2002), but apparently no molecular studies have included gymnures (NOVACEK 2001).

The recent sundering of insectivore-grade mammals to all branches of the placental mammal tree, the suggestion that erinaceids closely resemble tribosphenic mammals from the Early Cretaceous of Australia (RICH et al. 2001 b, 2002), and lingering argument over hedgehog relationships (CAO et al. 2000; MOUCHATY et al. 2000; NIKAIDO et al. 2001) all emphasize the need to further clarify the phylogenetic position of both gymnures and hedgehogs.

One last recent eutherian taxon omitted from molecular investigations of higher-level placental relationships (due to lack of samples) is the endemic Madagascan order Bibymalagasia. MACPHEE (1994) erected this order to house *Plesiorcyteropus*, an extinct genus of medium-sized mammals that survived late into the Holocene, probably until about 1000 ybp. The relationship between Bibymalagasia and other placental mammals is uncertain (MACPHEE 1994; MCKENNA and BELL 1997). However, *Plesiorcyteropus* was earlier classified as a tubulidentate (PATTERSON 1975; THEWISSEN 1985), and MACPHEE (1994) discussed morphological resemblances between *Plesiorcyteropus*, aardvarks, and hyraxes. In light of current knowledge about major placental groups, it seems highly possible that *Plesiorcyteropus* is part of the radiation of afrotheres, all of which share a traditionally enigmatic phylogenetic position and a distribution restricted to Africa and/or Madagascar. Interestingly, MACPHEE (1994) pointed out astragalar features shared (though not exclusively) by *Plesiorcyteropus*, elephants, hyraxes, aardvarks, and elephant shrews (but not sirenians, which of course lack hindlimbs), calling these “possible derived traits of a superordinal grouping that includes *Plesiorcyteropus*”, a point that deserves additional study. Despite overwhelming molecular evidence for Afrotherian monophyly (MADSEN et al. 2001; MURPHY et al. 2001 a,b; SPRINGER et al. 1997, 1999; STANHOPE et al. 1998 a,b; VAN DIJK et al. 2001), it is a commonly raised point that painstaking studies of comparative anatomy (e.g. SHOSHANI and MCKENNA 1998) have uncovered no mor-

phological synapomorphies coherently uniting this otherwise seemingly hodgepodge assemblage (ASHER 1999; HEDGES 2001, NOVACEK 2001). It is possible that the correct relationships of Bibymalagasiasia will only be resolved using methods for analyzing ancient DNA (reviewed by HOFREITER et al. 2001).

Comparative success of major mammalian clades

Extant diversity, disparity, and distribution are all potentially useful measures of current and historical success in cross-clade comparisons. Diversity is usually simply defined as the number of species in a clade (although here number of genera is used, because this measure is less dynamic over time, and assessments of species diversity in mammals have changed considerably since the most recent review volume was

published; WILSON and REEDER 1993). Disparity, a measure of gross morphological variation, is generally more difficult to quantify (NEIGE et al. 2001; WILLS et al. 1994). Nevertheless, disparity is probably more easily measured in living mammals than in some other taxonomic groups, as placental mammal orders (sensu MCKENNA and BELL 1997; with “insectivoran” groups as arranged by MURPHY et al. 2001 b) generally encompass species of similar morphotype often strikingly divergent in morphology from representatives of the most closely-related living order (a major reason why mammalian superordinal relationships have been so difficult to unravel). Thus, the number of orders within a mammalian superorder is considered here to be a reasonable proxy measurement of disparity. By these measures, laurasiatheres and euarchontoglires have been more successful than xenarthrans and afrotheres, especially

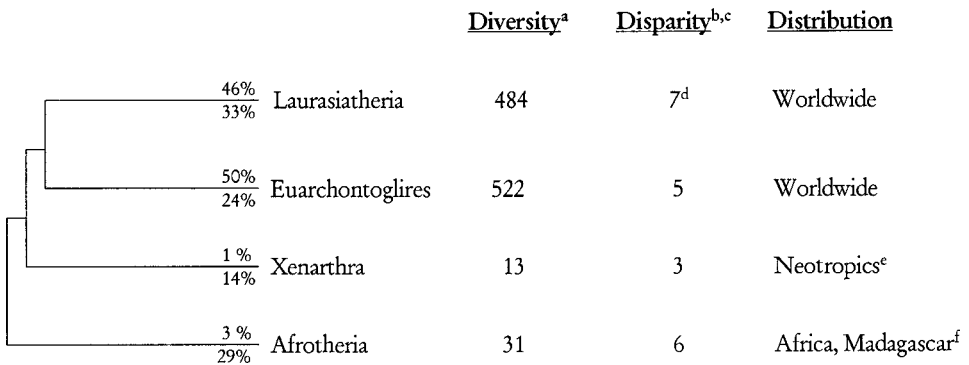


Fig. 1. Comparative success of major placental mammal clades. Diversity, disparity, and distribution of placental mammal superorders. Percentages of total placental mammal diversity and disparity in each superorder are shown above and below the branch for each clade, respectively. Figures are based on Recent mammals of the world (WILSON and REEDER 1993). Placental mammals constitute 93% of extant mammalian genera and 70% of extant mammalian orders.

a. Number of genera (less sensitive to taxonomic change than number of species).

b. Number of orders (proxy measurement for number of distinctive morphotypes; see text).

c. Orders recognized as follows: in Laurasiatheria: Lipotyphla, Chiroptera, Carnivora, Pholidota, Perissodactyla, Artiodactyla, (Cetacea); in Euarchontoglires: Rodentia, Lagomorpha, Scandentia, Dermoptera, Primates; in Xenarthra: Folivora, Cingulata, and Pilosa; in Afrotheria: Afrosoricida, Macroscelidea, Tubulidentata, Hyracoidea, Proboscidea, Sirenia.

d. Artiodactyla (including cetaceans and “traditional artiodactyls”) is counted twice for measuring disparity, because of the unusual morphological divergence of these two groups.

e. Includes one wide-ranging species in North America, the armadillo *Dasypus novemcinctus*.

f. Includes one terrestrial Asian representative, the elephant *Elephas maximus*.

Table 1. Modern distribution and generic diversity of major placental mammal clades. Figures are percentages of placental mammal totals. Current range is based on the approximate distributions given in figure 1; ranges of marine mammals are not considered. If A is the sum of the areas of all continents occupied by a clade, then range percentages are calculated as: $A/(\text{sum of the values of A for all four clades})$. Figures for continental size are taken from WORLD ALMANAC (2002).

	Superorder	Current range	Diversity
1	Xenarthra	5.6	1.2
2	Afrotheria	9.5	3.0
3	Euarchontoglires	42.5	49.7
4	Laurasiatheria	42.5	46.1

in terms of diversity and distribution (Fig. 1). These two superorders have high (and nearly equivalent) diversity and disparity, together accounting for 96% of extant placental mammal diversity and 51% of extant disparity. Living xenarthrans show the least diversity and disparity of the four major placental groups. Extant afrotheres also exhibit little diversity, but extremely high disparity (almost one-third of the placental total) nearly equivalent to that of Laurasiatheria. Interestingly, among placentals, disparity is rather equally distributed between “Gondwanan” (Xenarthra and Afrotheria) and “Laurasian” superorders (Laurasiatheria and Euarchontoglires) – a striking fact given the extremely unequal diversity of these two groups (a discrepancy of two orders of magnitude). This could suggest that these two large groupings are sister taxa and thus equally old assemblages, despite markedly uneven current success (see SCALLY et al. 2001; CAO et al. 2000; MADSEN et al. 2001; MURPHY et al. 2001 a); however, MURPHY et al. (2001 b) did not support this hypothesis. (Incidentally, a superordinal assemblage embracing afrotheres and xenarthrans [in part] dates to LINNAEUS [1758] who included elephants, sea cows, sloths, vermilings [and pangolins] in a group he named “Bruta”). Unbalanced diversity among placental superorders is due in part to the disproportionate success of two orders in particular: Chiroptera (bats) and Rodentia (rodents) (laurasiatheres and euarchontoglinans, respectively). Nevertheless, even with their exclusion, modern diversity of Euarchontoglires (79 genera excluding Rodentia) and

Laurasiatheria (307 genera excluding Chiroptera) greatly exceeds that of Afrotheria or Xenarthra (Fig. 1).

A classic tenet of ecology is that species richness increases with increasing area. A correlation might then be expected between the size of a higher taxon’s modern geographic range and its modern diversity. This is neatly demonstrated by comparisons between mammalian superorders. Distributional indices for each of the four placental superorders are good general predictors of modern diversity (Tab. 1), especially for Euarchontoglires and Laurasiatheria. The smaller modern ranges of xenarthrans and afrotheres are correlated with considerably lower diversity, although these groups appear to be even more depauperate in reality than expected on the basis of geography. Recent extinctions may partially explain this discrepancy. Compared to other superorders, xenarthrans and afrotheres suffered proportionally greater losses of diversity during late Quaternary extinctions (ANDERSON 1984), although these declines are partly accounted for already because the distributions of many such extinct species (e.g. North American taxa such as ground sloths and mastodons) lay outside the modern distributions of these clades.

Given congruence between number of lower-level taxa (i.e. diversity) and modern distribution within mammalian superorders, it is interesting to compare also number of higher taxa (i.e. disparity) and the estimated ancient distribution of each superorder at about the time they began to diversify (i.e. roughly 100 Mya, see MURPHY et al. 2001 b). Currently xenarthrans are posited

Table 2. Ancient distribution and modern disparity of major placental mammal clades. Figures are percentages of placental mammal totals. Distribution indices are calculated as in table 1.

1	Superorder	Cretaceous range A	Disparity	Cretaceous range B
1	Xenarthra	10.8	14.3	15.3
2	Afrotheria	18.3	28.6	29.1
3	Euarchontoglires	28.1	23.8	22.0
4	Laurasiatheria	42.8	33.3	33.6

to have been restricted to South America, afrotheres restricted to Africa, euarchontoglires restricted to Eurasia, and laurasiatheres to have been fully Laurasian in distribution (inhabiting Eurasia and North America) (ARCHIBALD et al. 2001; DELSUC et al. 2001; FLANNERY 2001; MURPHY et al. 2001 b; MCKENNA and BELL 1997), although evidence for some of these assumptions is slim. Cretaceous distribution calculations are approximations based on modern continental sizes (with the exception of Eurasia, from which the area of the Indian subcontinent was subtracted), although continental areas have fluctuated since the Middle Cretaceous with tectonic movements and shifting sea levels and coastlines (see SMITH et al. 1994).

Despite this impreciseness, this set of geographic assumptions approximately recovers the modern distribution of disparity among placentals (Tab. 2, "Cretaceous Range A"). These comparisons also suggest that afrotheres (and to a lesser extent, xenarthrans) exhibit disproportionately high modern disparity (with representatives as different as golden-moles, elephants, and sea cows) for having been restricted to Africa in the Middle Cretaceous. This discrepancy could have more to do with time than geography; if afrotheres are the sister group to all living placental mammals, they might exhibit disproportionately high disparity simply because they have been diversifying slightly longer than any one of the other three fundamental placental clades. However, molecular clock estimates of divergence times at each successive node early on the placental tree (corresponding to the fundamental superordinal splits) are similarly ancient (EIZIRIK et al. 2001), suggest-

ing a relatively rapid early radiation. Furthermore, xenarthrans (like afrotheres) are also thought to have split from the remainder of placentals relatively early, but as a group (both living and fossil) are considerably less morphologically variable than afrotheres.

Given that the early fossil record of afrotheres is essentially unknown, an alternate explanation for high afrothere disparity could be that the presumed early restriction of this group to Africa is not real. Perhaps some afrothere orders that survive only in Africa or Madagascar originated in other parts of Gondwanaland, dispersed to Africa prior to complete Gondwanan fragmentation, and subsequently became extinct on smaller Gondwanan fragments. Interestingly, if Cretaceous afrotheres (which occupy a basal phylogenetic position among living placentals according to MURPHY et al. 2001 b) are assumed to have originally ranged into parts of Gondwanaland that are today Antarctica, Australia, and the Indian subcontinent, and Cretaceous xenarthrans are assumed to have extended to Antarctica, these geographic assumptions recover the modern distribution of placental disparity much more accurately (Tab. 2, "Cretaceous range B"). Of course no such tight relationship need exist, and without additional fossil evidence (and a better understanding of the timing of Gondwanan fragmentation events), such conjectures about ancient distribution are practically baseless. These comparisons simply demonstrate that current ideas about the ancient geographic distribution of these groups are broadly concordant with patterns of disparity seen in placental clades today (with the possible exception of Afrotheria).

Gondwanan prodigal sons

In addition to Afrotheria and Xenarthra, Monotremata is a third major mammalian clade with low extant diversity and a limited modern range essentially limited to a Gondwanan fragment. Interestingly, all three of these groups are thought to have originated on the continents to which they are now restricted (however, future fossil discoveries on Gondwanan landmasses, especially Antarctica, may overturn these views; see VIZCAINO et al. 1998; SIMPSON 1978). Although none of these clades ever matched the diversity of modern Laurasiatheres or euarchontoglires, all have declined in diversity over time and have distributions considerably more limited than at some point in their past. For example, xenarthrans are known from the Eocene of Antarctica (VIZCAÍNO and SCILLATOYANÉ 1995; VIZCAINO et al. 2001) and achieved high diversity in the North American Pleistocene (ANDERSON 1984; MCKENNA and BELL 1997) but today are almost wholly restricted to the Neotropics. Afrotheres were likewise once more cosmopolitan in distribution, with proboscideans in particular inhabiting most of the world's land surface for much of the Cenozoic (SHOSHANI and TASSY 1996). Today, aside from the aquatic sirenians and one hyrax that extends into the Middle East, only a single afrothere, the Asian elephant (*Elephas maximus*), survives outside of Africa/Madagascar; coincidentally, the center of this species' historical distribution (the Indian subcontinent) was also originally a Gondwanan fragment. Monotremes, too, once ranged into South America and presumably Antarctica (PASCUAL et al. 1992), but are now found only in Australia and New Guinea. Although causal factors of extinction and range contraction in these three Gondwanan lineages have no doubt been varied and largely separate in space and time, coincidence of their modern and presumed ancient distributions (despite an interval of expansion, then contraction) raises an interesting question. Is there some underlying ecological factor, something

like a home field advantage, for their Gondwanan persistence? Is this analogous to a pattern commonly seen at much lower taxonomic levels, where, after initial or periodic expansion, species contract from more remote, marginal habitats to a central or core range? (See BROWN 1957.) Of course this pattern is far from universal among higher taxa, but a potential explanation for these particular cases may be that lineages originating on smaller landmasses are generally less successful than those from larger landmasses in colonizing and competing in new areas (MATTHEW 1915; JANIS et al. 1998), a phenomenon FLANNERY (2001: 78) claimed to be "one of biology's more iron-clad rules." Higher taxa that exhibit the pattern described here (i.e. wide expansion only to contract back to the point of origin) can be aptly labelled "prodigal son" taxa.

Convergent adaptations among major mammal groups

Debates involving mammalian phylogenetic relationships have frequently focused on establishing whether certain derived ecomorphological traits have evolved once (representing a unique synapomorphy) or multiple times (representing convergent evolution) during mammalian history. For example, in challenging chiropteran monophyly (and, thereby suggesting that powered flight originated not once but twice among mammals, i.e. separately in megachiropterans and microchiropterans), PETTIGREW (1986) excited considerable interest in bat relationships. Studies based on myriad systems, molecular and morphological, have since upheld chiropteran monophyly (see SIMMONS 1994), although "microchiropterans" are now thought to be a grade rather than a clade (HUTCHEON et al. 1998; TEELING et al. 2002). Given that gliding has evolved separately at least six times among mammals (JACKSON 2000; but note that these six events occurred only in Euarchontoglires and Australidelphia, three times in both lineages), it is rather surpris-

ing that powered flight evolved only once in mammals. The evolution of flight in other mammal lineages may have been precluded by complete domination of aerial guilds by both birds (especially in diurnal niches) and bats (especially in nocturnal niches), whose high geographic mobility may have rapidly granted them global monopolies after developing flight (see SPEAKMAN 2001). Bats are highly diverse, and it is tempting to call the evolution of flight a “key innovation” (as done for birds and insects; see CHATTERJEE 1997; KESEL 2001). However, this might be technically incorrect (see SLOWINSKI and GUYER 1993; de QUEIROZ 1999), because the sister group of Chiroptera (thought to comprise the carnivores, pangolins, perissodactyls, and artiodactyls including whales; MURPHY et al. 2001 b) is also quite diverse and successful (with more extant genera but fewer species than in bats). Therefore, rates of diversification may not be biased in favour of bats on account of their ability to fly. Whether or not flight is directly responsible for accelerated diversification in bats (an intuitive proposition nonetheless), it is certainly the source of their wide geographic success, which has ultimately allowed the superorder Laurasiatheria to match Euarchontoglires (with the spectacularly diverse order Rodentia, in which the small body size and generalist habits of many of its representatives promotes rapid dispersal) in nearly cosmopolitan distribution.

MADSEN et al. (2001) briefly discussed some notable convergent adaptations among different placental superorders (reviewed in additional detail by SCALLY et al. 2001), but these parallel radiations are even more spectacular than those authors note. For example, independently-acquired adaptations for insect- or worm-eating have resulted in the complete loss of teeth and extension of the tongue in three very distantly-related groups of mammals: echidnas (Tachyglossidae, Monotremata), pangolins (Manidae, Laurasiatheria), and vermilinguas (Myrmecophagidae, Xenarthra), as well as the evolution of a reduced or unspecialized dentition in numerous other mammals, including

numbats (*Myrmecobius*, Australidelphia), armadillos (*Oryzomys*, Afrotheria), and aardwolves (*Proteles*, Laurasiatheria). Marked adaptations for aquatic living have evolved multiple times among Laurasiatheres (whales, pinnipeds), Afrotheres (sirenians), and to a remarkable (albeit lesser) extent, even in the xenarthran *Thalassocnus* (a semi-aquatic sloth; see de MUIZON and McDONALD 1995). A notable adaptation for arboreality, the prehensile tail, has evolved many times within both marsupial superorders and within all placental superorders except Afrotheria (see EMMONS and GENTRY 1983). In fact, despite otherwise outstanding disparity in morphology and lifestyle (see above), and in contrast to other therian superorders, Afrotheres show almost no adaptations for arboreality (potentially an insight into competitive forces faced during early Afrotheria history), with only a single lineage (the tree shrews, i.e. the extant genus *Dendrohyrax*) living in trees. Finally, the many groups of small mammals adapted to a burrowing lifestyle underground, such as golden moles (Chrysochloridae, Afrotheria), true moles (Talpidae, Laurasiatheria), marsupial moles (*Notoryctes*, Australidelphia), and (albeit to a lesser extent) numerous lineages of subterranean rodents (Euarchontoglires) provide an especially remarkable example of morphological and ecological convergence. Another contemporary debate regarding the uniqueness of an important morphological trait involves tribosphenic molars (i.e. molars with a talonid basin that occludes with a large protocone, a functional complex allowing for grinding and shearing akin to a mortar-and-pestle; see BOWN and KRAUS 1979). This condition is considered synapomorphic for extant therian mammals and their close fossil relatives (tribosphenidans), and is traditionally held to have first appeared in early therians on northern continents (LUO et al. 2001). Within the last decade, a number of fully tribosphenic fossil mammals have been discovered on Gondwanan continents (e.g. SIGOGNEAU-RUSSELL 1991; FLYNN et al. 1999; RICH et al. 1997; RICH et al. 2001 a;

RAUHUT et al. 2002) that predate the appearance of Laurasian tribosphenic mammals. Most notably, two tribosphenic taxa from the Cretaceous of Australia, *Ausktribosphenos* and *Bishops* (together, the Ausktribosphenidae), have been identified as early placentals (RICH et al. 1997, 1998, 2001 a,b, 2002), although this arrangement has received little support from other authors (see KIELAN-JANWOROWSKA et al. 1998; LUO et al. 2001, 2002). LUO et al. (2001) instead argue that ausktribosphenids and other Gondwanan tribosphenid mammals share a more recent ancestor with monotremes (together comprising the clade "Australosphenida") than with extant therian mammals, suggesting separate origins of tribosphenic molars on northern and southern continents during the Mesozoic. This hypothesis has since been widely embraced (see RAUHUT et al. 2002; SIGOGNEAU-RUSSELL et al. 2001; LUO et al. 2002), but has been strongly criticized recently (RICH et al. 2002; see also BUTLER 2001), and whether the tribosphenic molars of tribosphenidans and "australosphenidans" are separately derived should probably be considered unresolved (RICH et al. 2002). Interestingly, current debate over whether placentals originated in Laurasia (particularly Far Eastern Eurasia) or Gondwanaland (particularly Australia) is currently paralleled by similar debates regarding the origins of modern birds (see COOPER and PENNY 1997) and angiosperms (see SUN et al. 2002), two other major groups that may have originated at about the same time.

Finally, in the context of distinguishing homology from homoplasy in mammalian history, a brief note about the unique organization of the mammalian middle-ear is in order, in response to a recent comment by RAUHUT et al. (2002). Incorporation of the "reptilian" postdentary bones (i.e. the quadrate and articular) into the middle-ear, such that the middle-ear contains three bones and the jaw comprises only the dentary, is generally acknowledged to be a synapomorphic arrangement uniting crown-group mammals (SHOSHANI and MCKENNA 1998; LUO et al. 2002; WANG et

al. 2001). This makes a claim by RAUHUT et al. (2002), who recently described a new tribosphenic mammal from the Jurassic of Argentina, more extraordinary than those authors alluded. RAUHUT et al. (2002) allied their new taxon *Asfaltomylos* with "australosphenidans" (see above), but noted of the holotype that "the subdivision of the post-dentary trough indicates the presence of distinct post-dentary bones". If this inference is correct, *Asfaltomylos* would be an example of a rather highly-derived mammal without the typical mammalian middle-ear arrangement, suggesting either a dual origin or a singular reversion of this condition. Given that a number of other Mesozoic mammals without post-dentary bones retain distinct (though not necessarily subdivided) post-dentary grooves (see LUO et al. 2002; RICH et al. 1998), it should probably be assumed (contra RAUHUT et al. 2002) that *Asfaltomylos* possessed the derived ear arrangement typical of other crown-group mammals, unless or until a specimen is discovered with post-dentary bones intact within the post-dentary groove.

Early placental biogeography

As MURPHY et al. (2001 b) noted, their well-resolved phylogeny of extant placental mammals provides an excellent framework against which biogeographic hypotheses about mammalian radiations can be tested. These authors developed an explicit hypothesis about the sequence of Cretaceous biogeographic events to explain the presence of afrotheres in Africa, xenarthrans in South America, and the remainder of living placentals (designated Boreoeutheria) in present-day North America and Eurasia. Given evidence that afrotheres split off from other placentals first, followed by xenarthrans, MURPHY et al. (2001 b) suggested that the root of the crown-group placental tree lay in Gondwanaland, that the split between afrotheres and all other living placentals corresponded to the vicariance event separating

Africa from South America, and that the next major subsequent split (between Xenarthra and Boreoeutheria) corresponded to a Laurasian invasion from South America. This scenario offers an intuitive link between the tree topology generated by MURPHY et al. (2001 b) and traditional assumptions about the geographic origins of these major groups (see above), and potentially corroborates both the Garden of Eden hypothesis of FOOTE et al. (1999 a) (but see FOOTE et al. 1999 b; ARCHER et al. 1999; RICH et al. 2001 b) and the discovery of putative Cretaceous placentals from Australia (see above). This scenario is also attractive in that the molecular clock date generated for the split between afrotheres and other mammals (101–108 Mya) is broadly concordant with the date attributed to the separation of Africa and South America (100–120 Mya) (SMITH et al. 1994; HAY et al. 1999).

One aspect of this hypothesis – a trans-hemipheric dispersal event from South America to Laurasia, is problematic given current fossil evidence. No placental mammals have been recorded from South America prior to the early Tertiary, when a diverse placental mammal fauna including xenarthrans, notoungulates, and a number of other enigmatic ungulate-forms appeared there (see MCKENNA and BELL 1997) (given this absence, it is difficult to imagine that South America played such a vital role in the taxonomic and geographic radiation of Cretaceous placentals). The key to understanding South America's Tertiary fauna may thus be an (as-yet undocumented) history of taxonomic and ecological differentiation that occurred in the Antarctic Cretaceous (see VIZCAINO et al. 1998; PASCUAL 1998). If this is the case, early placental mammal diversification may have proceeded by three

dispersal events out of a southern Gondwanan fragment that included Antarctica, Australia, and some contact with South America (see STOREY 1995): the first to an already-isolated Africa at roughly 100 Mya (EIZIRIK et al. 2001; also note that the afrotheres of Madagascar [i. e. tenrecs] arrived there during the Tertiary; see DOUADY et al. 2002); the second to Asia, perhaps either by transferral via the Indian subcontinent (see MURPHY et al. 2001 [supp. info.]; HAY et al. 1999) or by dispersal from Australia to southeastern Asia via mechanisms envisioned by RICH et al. (1998); and finally, that of an already well-differentiated fauna including xenarthrans from Antarctica to South America at the Cretaceous-Tertiary boundary (PASCUAL 1998). This model is extremely concordant with the presence of early placentals in Australia 115–120 Mya (RICH et al. 1998, 2002). Whether contemporary or slightly more ancient placental mammals from Laurasia (e. g. CIFELLI 1999; AVERIANOV and SKUTSCHAS 2000; KIELAN-JAWOROWSKA and DASHZEVEG 1989; including the 125 Mya *Eomaia*, JI et al. 2002) were close relatives or even direct ancestors of early Gondwanan placentals (whether ausktribosphenids are included or disregarded) remains to be clarified.

Acknowledgements

I thank T. FLANNERY for sharing many useful insights and reading several drafts of this manuscript. I also benefited from discussions with A. ROCA, E. EIZIRIK, and W. MURPHY (on molecular phylogenetics, divergence times, early biogeography, and nomenclature), T. RICH (on Mesozoic mammals), and M. LEE (on disparity). T. DIKOW assisted with German translation. I am supported in part by a grant from the Australian-American Fulbright Commission.

Zusammenfassung

Größere Taxa der Mammalia: eine Überprüfung nach Erwägung molekularer und paläontologischer Befunde

In der aktuellen Diskussion der Phylogenie der Mammalia werden vier Taxa als Überordnungen der rezenten Placentalia anerkannt. Anhand dieser Stammbaumhypothesen werden sowohl die Verteilung und Trends von Merkmalen innerhalb der Placentalia, als auch der Ursprung der Placentalia untersucht. Mögliche Beziehungen rezenter Säugetiertaxa, welche nicht in dieses System integriert werden konnten, werden diskutiert. Muster morphologischer und ökologischer Konvergenzen, historischer und rezenter Biogeographie und vergleichender Disparität und Diversität zwischen und unter den vier Taxa werden diskutiert. Die gegenwärtige Verteilung der Disparität innerhalb der Placentalia wird zu einer Analyse der geographischen Verteilung dieser Taxa während der Kreide herangezogen. Monotremata, Xenarthra und Afrotheria sind wichtige Säugetiertaxa, die auf Gondwanaland entstanden sind. Obwohl jedes dieser drei Taxa einst eine viel größere Verbreitung hatte, stimmt ihre rezente, eingeschränkte Verbreitung genau mit den Landmassen überein, auf denen sie entstanden sind.

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