

Review

Untangling the Multiple Ecological Radiations of Early Mammals

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The ecological diversification of early mammals is one of the most globally transformative events in Earth's history and the Cretaceous Terrestrial Revolution (KTR) and end-Cretaceous mass extinction are commonly hailed as catalysts. However, a confounding issue when examining this diversification is that it comprised nested radiations of mammalian subclades within the broader scope of mammalian evolution. In the past 200 million years, various independent groups experienced large-scale radiations, each involving ecological diversification from ancestral lineages of small insectivores; examples include Jurassic mammaliaforms, Late Cretaceous metatherians, and Cenozoic placentals. Here, we review these ecological radiations, highlighting the nuanced complexity of early mammal evolution, the value of ecomorphological fossil data, and the importance of phylogenetic context in macroevolutionary studies.

The Ecological Diversification of Mammals

Modern mammals are extraordinarily diverse, possessing body masses spanning eight orders of magnitude and occupying habitats on land, in water, and in air. By contrast, 200 million years ago (Ma) the earliest **mammaliaforms** (see *Glossary*) (i.e., mammals and their closest relatives) were mostly small, terrestrial insectivores persisting in reptile-dominated ecosystems. The evolutionary story of how mammaliaforms endured the Mesozoic Era (252–66 Ma), or the Age of Dinosaurs, and subsequently rose to ecological prominence has fascinated researchers for over 150 years [1–7]. Gaps in the fossil record and the lack of living representatives of many early mammaliaform groups have hindered our ability to examine some aspects of mammalian history, including the ecological diversity of many clades. However, recent fossil discoveries, advances in comparative techniques (e.g., morphometrics, micro-computed tomography), and the development of phylogenetic methods and molecular clock analyses have led to a much richer and more complex body of evidence for early mammaliaform diversification (e.g., [6–14]), which we critically review here.

Early mammaliaforms comprise multiple independent clades that came and went intermittently throughout the Mesozoic and early Cenozoic. Evolutionary success varied across these clades and several groups underwent major ecological radiations at different times [2–8,13–18]. Here, ecological radiation is defined as a geologically rapid diversification event that led to a broad array of ecologies. The ecological radiations of early mammaliaforms have become increasingly apparent as researchers consider the evolution of these groups in a phylogenetic context and with robust ecomorphological datasets [8,10,11,17–24]. The radiations originated independently from mostly small, insectivorous ancestors and many involved stem lineages of extant mammalian clades. The primary objectives of this review are to: (i) highlight the recent and growing evidence for these distinct radiations; and (ii) address confounding issues in assessing ecological diversity patterns in early mammaliaforms.

Multiple Radiations in Early Mammaliaforms

The observation that multiple mammaliaform groups have experienced large-scale ecological radiations is not new. For instance, paleontologist Henry Fairfield Osborn coined the term

Highlights

Multiple stem and early mammal groups experienced large-scale ecological radiations, including Jurassic mammaliaforms, Late Cretaceous multituberculates, Late Cretaceous metatherians, and Paleogene placentals.

Small insectivores or omnivores are the progenitors of each ecological radiation, which involve rapid diversifications of diets and modes of locomotion.

There are three main periods of ecological diversification (Early–Middle Jurassic, Late Cretaceous, and Paleogene), each involving radiations of multiple mammalian groups. The Late Cretaceous radiations may have been triggered by the KTR and the Paleogene radiations were to have been likely catalyzed by the end-Cretaceous mass extinction event.

Phylogenetic context and paleontological data are critical for examining ecological radiations in deep time, especially because many radiations involve stem lineages of modern clades that do not have living representatives.

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adaptive radiation in 1902 and noted six independent diversifications of early mammaliaform groups as examples of adaptive radiations [2]. These are temporally and geographically distinct diversifications that include some of the radiations highlighted in this review, such as the Jurassic (201–145 Ma) radiation of mammaliaforms, the Australian radiation of **marsupials**, and radiations of multiple eutherian groups, including **placentals**. Osborn argued that each radiation involved the diversification of diets and **locomotor modes** from an ancestral, small insectivore (although at the time there was minimal fossil evidence to support this claim for the earliest radiations). Considerable scientific progress has been made since Osborn's time and we now recognize additional independent radiations within Mammaliaformes. Further, the adaptive radiation concept has been refined by researchers [25–31] and the ecological radiations discussed in this review may not all qualify as adaptive radiations under modern definitions (hence, we refer to them as ecological radiations instead of adaptive radiations). Future studies can assess whether the ecological radiations of early mammaliaforms meet additional criteria that are often proposed for adaptive radiations, such as a greater speciation rate early in the radiation [26,31], monophyly of the radiating group [27], an 'early burst' of morphological evolution at the onset of the radiation [25], and the presence of novel ecological opportunities as catalysts for diversification [29,31].

Small Insectivores Give Rise to Mammalian Diversity

During the 320-million-year history of **synapsids**, there have been numerous examples of small insectivore or omnivore progenitors radiating into ecologically diverse clades [2,15,32]. This pattern recurred in early mammaliaforms and is highlighted in Figure 1 and in Table S1 in the supplemental information online. From these insectivorous or omnivorous forerunners, numerous dietary specialists have repeatedly evolved in mammalian clades, suggesting parallel ecological diversifications. In addition, derived locomotor modes repeatedly evolved from ground- or tree-dwelling (i.e., ambulatory, scansorial, or arboreal) ancestors. This includes convergent evolution of fossorial, semiaquatic, gliding, and saltatorial locomotion in the Mesozoic Era [6,8,19,33].

Below we review the lines of evidence that suggest each radiation involved significant ecological divergence from a small, ancestral insectivore or omnivore. We group the radiations into three distinct time periods of considerable ecological diversification: (i) Early–Middle Jurassic (201–163 Ma); (ii) Late Cretaceous (100–66 Ma); and (iii) Paleocene–Eocene (66–34 Ma).

Jurassic Radiations: Origins of Early Ecological Diversity

Tooth and jaw morphologies indicate insectivory or insect-based omnivory in most mammaliaforms from the Late Triassic and earliest Jurassic [6,11,34–37]. These early insectivores gave rise to ecologically diverse lineages, with evidence suggesting rapid ecological radiations of multiple groups during the Early and Middle Jurassic [6,8,18,20] (Figure 1 and 2). Recent fossil discoveries demonstrate that Jurassic mammaliaform groups such as docodonts and haramiyidans possessed greater ecological diversity than previously recognized [8,13,18,33,38–44]. Locomotor modes during this time include gliding, arboreal, terrestrial, semiaquatic, semifossorial, and fossorial (Table S1). Further, multiple mammaliaform groups experimented with mortar-and-pestle and multiple-cusp-row molars [6,8,43–45], indicating the evolution of a greater diversity of diets. Stem-mammal-dominated faunas of the Middle Jurassic transitioned to crown-mammal-dominated faunas of the Late Jurassic and Early Cretaceous [6,8,13] (Figure 1), but mammals continued to possess significant ecological diversity through this transition [6,8,11,24,46–48].

The **Cretaceous Terrestrial Revolution (KTR)** of the mid-Cretaceous (ca 125–80 Ma) resulted in considerable faunal turnover in terrestrial ecosystems, which is likely to have played a critical role in the origin of modern biodiversity [9,49–51]. Several mammaliaform groups went extinct

Glossary

Cretaceous Terrestrial Revolution (KTR):

a period (ca 125–80 Ma) in the mid-Cretaceous during which there was considerable taxonomic turnover and subsequent diversification of terrestrial clades that are now prominent in modern ecosystems, including flowering plants, social insects, squamates, turtles, birds, and therian mammals [49,50].

Diel activity pattern: when during the day or night an organism is active – diurnal, active during daytime; nocturnal, active during the night; cathemeral, equally likely to be active at any point during the day or night; and crepuscular, active at dawn and dusk.

End-Cretaceous mass extinction event:

the mass extinction event 66 million years ago that wiped out not only nonavian dinosaurs but up to 75% of all terrestrial and marine species worldwide.

Lagerstätten: sedimentary rock layers with exceptionally preserved fossils. The 'Lagerstätten' mentioned here are specifically 'Konservat-Lagerstätten', which preserve fossilized organisms (e.g., mammalian skeletons), whereas 'Konzentrat-Lagerstätten' are deposits with disarticulated organic parts (e.g., bone beds).

Locomotor mode: how an animal moves through the substrates in its environment. Examples include arboreal (tree using), scansorial (both ground and tree using), ambulatory (terrestrial walking), saltatorial (terrestrial hopping), and fossorial (digging).

Mammaliaforms: a group formed by the common ancestor of crown-group mammals and the Jurassic animal *Morganucodon* (e.g., [12]) or *Sinoconodon* (e.g., [6]) and all descendants of that ancestor. The group is morphologically diagnosed by the primary jaw joint being between the dentary and squamosal bones.

Mammaliaforms often exhibit some distinctly mammalian characteristics, but also retain some more basal characteristics (e.g., the mammaliaform *Morganucodon* had a dentary–squamosal jaw joint but also retained the secondary quadrate–articular jaw joint found in nonmammalian synapsids and reptiles).

Marsupials: crown-group metatherian mammals; that is, the common ancestor of all living metatherian mammals and all descendants of that ancestor whether

or experienced a significant decrease in abundance during the KTR [8,11,51], resulting in a mid-Cretaceous (ca 110–90 Ma) decrease in ecological diversity [11] (Figure 1 and 2). Historically, the mid-Cretaceous rock formations have been relatively poorly sampled [4,6,16], which might help to explain the observed decrease in diversity. However, considerable field collecting efforts in recent decades have begun to fill in the fossil record for this time interval (e.g., [52–56]) and a majority of fossils suggest that mid-Cretaceous mammals were ecologically limited as small insectivores and omnivores [9,11,21].

Late Cretaceous Radiations: Rebound in Diversity after the KTR

Therians, multituberculates, and dryolestoids all originated in the Jurassic [6,57], possibly as products of the Jurassic radiations (Figure 1). However, the fossil record suggests that members of these groups were primarily small insectivores or omnivores from the Late Jurassic through Early Cretaceous, a period that spans tens of millions of years (Figure 1). The earliest eutherians, metatherians, and dryolestoids all possess tooth and jaw morphologies indicative of insectivory or insect-dominated omnivory and most species are relatively small in size ([6,11,21,55,57–62]; Table S1). Similarly, the tooth shapes and small sizes of early (i.e., *plagiaulacidan*) multituberculates suggest an omnivorous diet with a considerable insect component [10].

After persisting through the Late Jurassic and Early Cretaceous as small insectivores/omnivores, the major mammalian groups of the Late Cretaceous each diversified ecologically after the KTR. Ecological radiations of cimolodontan multituberculates, metatherians, eutherians, and meridiolestid dryolestoids (Figure 1) are supported by quantitative analyses of teeth, jaws, and body sizes, which all suggest trends toward greater ecological diversity through the Late Cretaceous [10,11,21–23,63–66] (C.L. Gordon, PhD thesis, University of Oklahoma, 2003). Recent fossil discoveries also demonstrate greater ecological diversity in the latest Cretaceous than previously recognized [56,65–72]. The metatherian diversification may have been especially prolific because there is evidence of various specialized diets, including durophagy, carnivory, and omnivory-frugivory [21,64–66,68] (C.L. Gordon, PhD thesis, University of Oklahoma, 2003).

A majority of known Late Cretaceous fossils are from the Northern Hemisphere, but there is growing evidence of concurrent ecological diversification in the Southern Hemisphere [6,23,53,71,73]. For instance, tooth morphologies of meridiolestid dryolestoids from the latest Cretaceous of South America indicate omnivory and herbivory [23]. Gondwanatherians, which are known from the Cretaceous and Paleogene, are not highlighted in Figure 1 due to their limited fossil record, but they often possess features (e.g., hypodont dentition) that suggest the evolution of considerable dietary adaptations for herbivory by the latest Cretaceous [6,71].

Paleocene and Eocene Radiations: Rapid Rise of Extant Clades

In an extensive study on extant and fossil mammals, O’Leary *et al.* [12] reconstructed the last common ancestor of placentals as a small, scansorial insectivore (Figure 1). Additional studies of modern mammals also suggest insectivory in the earliest placentals [74,75]. Placentals are likely to have originated in the Late Cretaceous and were diversifying to some degree prior to the Cretaceous–Paleogene (K–Pg) boundary [9,21,64,69,72,74,76,77], possibly in concert with early eutherian lineages (Figure 1). However, paleontological and molecular genomic studies on this topic also show evidence of a Paleocene acceleration in placental ecological diversification, marked by rapid increases in mean body mass, dietary diversity, morphological disparity, diversity of **diel activity patterns**, and local and global taxonomic diversity [3,12,21,22,75,78–92] (J.P. Hunter, PhD thesis, State University of New York Stony Brook, 1997). A unique feature of this radiation is the appearance of especially large mammalian herbivores, which were not present in the Mesozoic.

extant or extinct. Metatherians have a relatively short gestation period and give birth to underdeveloped young, which often complete development in a pouch, also called a marsupium. With about 300 extant species, marsupials are less taxonomically diverse than placentals (with about 4000 extant species).

Monotremes: one of the three main groups of mammals with living representatives (along with placentals and marsupials). They lay eggs but also produce milk for their young. Living species include the echidnas (four species) and the platypus (one species).

Multituberculates: an extinct group of nontherian mammals named for their molar teeth, which exhibit multiple small cusps in rows. Multituberculates were numerically abundant and ecologically diverse on Mesozoic and early Cenozoic terrestrial landscapes for approximately 130 million years from the Jurassic to the Eocene. They are often considered morphologically and ecologically analogous to rodents, although the two groups are not closely related.

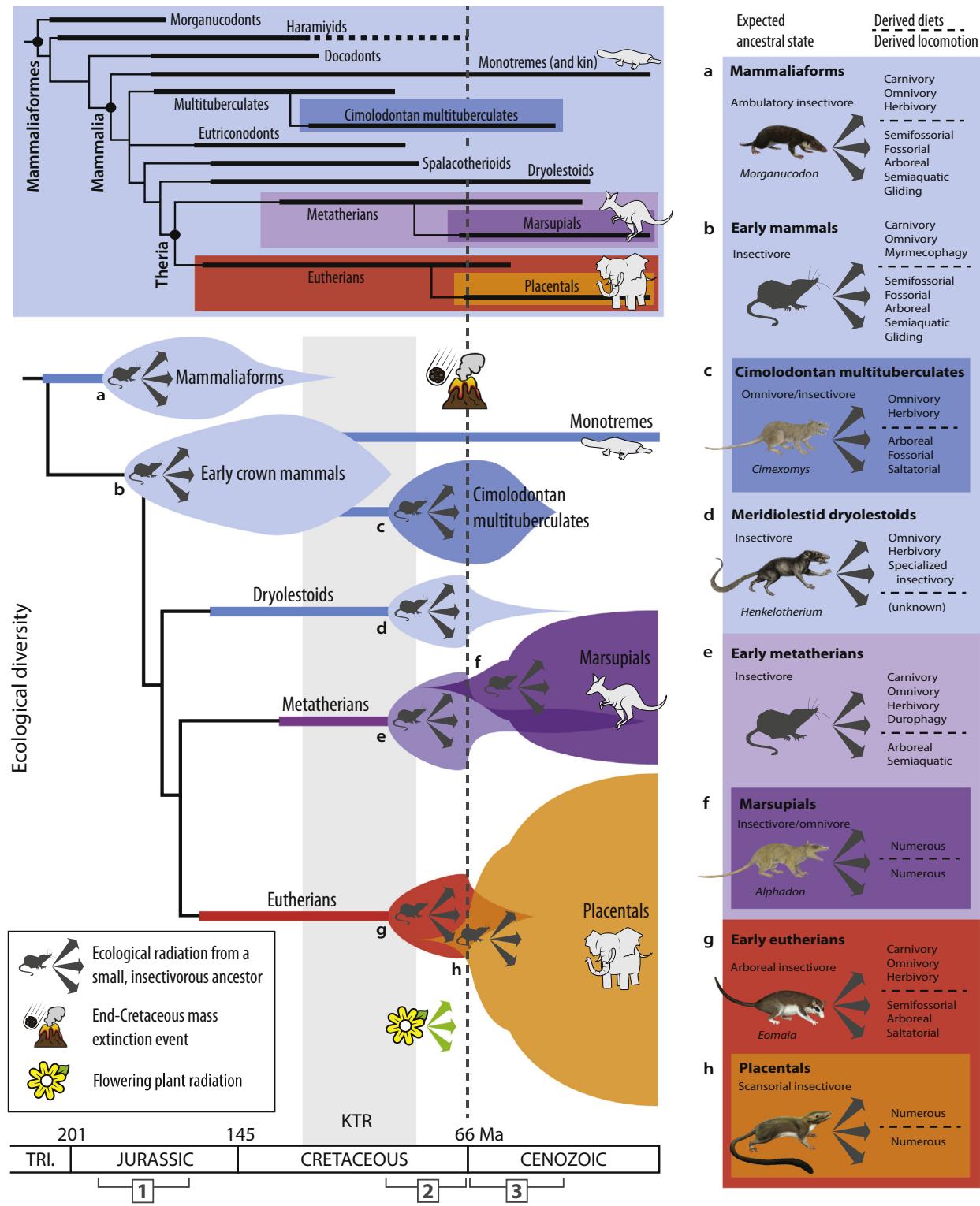
Paleocene–Eocene Thermal Maximum

Maximum: a major global warming event that occurred at the Paleocene–Eocene boundary approximately 56 million years ago. Global temperatures rose by 5–8°C; this change has been associated with dramatic species turnover, taxonomic diversification, and ecological change in a variety of organisms, especially mammals.

Placentals: crown-group eutherian mammals; that is, the common ancestor of all living placental mammals and all descendants of that ancestor whether extant or extinct. Placental mammals have a chorioallantoic placenta for nutrient exchange between mother and fetus during gestation. Placentals also generally have longer gestation periods and give birth to more-developed young than marsupials. Most extant mammals are placentals (e.g., rodents, bats, primates, carnivores).

Synapsids: the group of animals encompassing all amniote tetrapods with a synapsid pattern of skull fenestration (only lower temporal fenestra present). This group includes nonmammalian synapsids (e.g., *Dimetrodon*, *Cynognathus*) as well as all extant and extinct mammals and mammaliforms.

Therians: the group of mammals including Metatheria (marsupials and their extinct relatives) and Eutheria (placentals and their extinct relatives).



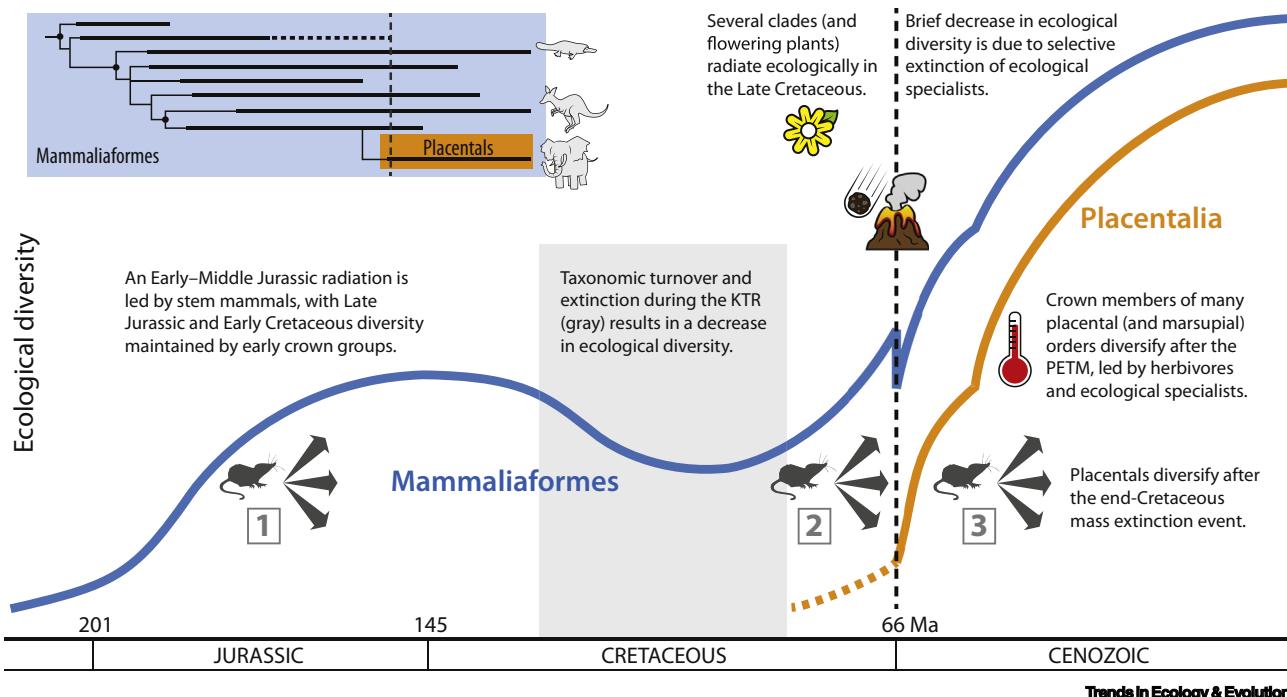


Figure 2. Ecological Diversity through Time in Mammaliaformes and Placentalia, Highlighting the Unique Patterns Between Clades of Varying Levels of Phylogenetic Scope. The numbered radiations correspond to the three periods of considerable diversification that are marked in Figure 1 and discussed in the text. Abbreviations: KTR, Cretaceous Terrestrial Revolution; PETM, Paleocene–Eocene Thermal Maximum.

In addition to the ancestor of all placentals, the earliest lineages of multiple placental subclades are thought to be small insectivores [2,7,74,75,93]. These subclades include Euarchonta, Afrotheria (in Africa), and Laurasiatheria (in the Northern Hemisphere), with early taxa from each group being morphologically similar to insectivorous living representatives, such as tree shrews, elephant shrews, and hedgehogs, respectively. Thus, the placental radiation in Figures 1 and 2 could be subdivided into multiple ecological radiations, each involving parallel ecomorphological diversification (e.g., [5]).

Metatherians and multituberculates also show paleontological evidence for ecological diversification in the Paleocene [10,94–97]. However, the multituberculate diversification in the aftermath of the **end-Cretaceous mass extinction event** may have been short lived [10,76,96,98] (Figure 1) and Cenozoic metatherians are primarily confined to the Southern Hemisphere (which is less sampled than the Northern Hemisphere), making the timing and dynamics of their diversification less clear. The Paleocene metatherian record of South America includes omnivorous–herbivorous polydolopimorphians and carnivorous borhyaenids [21,95], suggesting a metatherian radiation that was parallel to the placental radiation.

Although early placentals diversified in the Paleocene, the most diverse groups during this time are thought to be stem members of extant orders. These include plesiadapiforms (stem

Figure 1. Ecological Radiations of Early Mammaliaformes. Three periods of considerable diversification are labeled at the bottom. The progenitor of each radiation is thought to be a small insectivore or omnivore and examples of genera that may represent the ancestral states of these taxa are shown in the panel on the right. For each radiation, derived diets and locomotor modes that are known from the fossil record are listed. See Table S1 in the supplemental information online for citations and additional information. Mammaliaform reconstructions: *Morganucodon*, Michael B. H. (CC BY-SA 3.0); *Cimexomys*, courtesy Misaki Ouchida; *Henkelotherium*, courtesy Elke Gröning [58]; *Alphadon*, courtesy Misaki Ouchida; *Eomaia* [59], S. Fernandez (CC BY 2.5); reconstruction of the placental ancestor [12] by Carl Buell, courtesy of the National Science Foundation. Abbreviations: KTR, Cretaceous Terrestrial Revolution; Ma, million years ago; Tri, Triassic.

Primates), basal carnivoramorphans (stem Carnivora), leptictids (stem Eulipotyphyla), and archaic ungulates and pantodonts (stem Ungulata). By contrast, crown-group members of many placental orders (e.g., Chiroptera, Ungulata, Carnivora, Rodentia, Primates) diversified considerably in the Eocene (56–34 Ma), invading novel ecological niches (e.g., power-flying bats, aquatic whales) and achieving immense body masses [7,24,84,93,99–102]. Similarly, metatherians, including early marsupials, and notoungulate and litoptern placentals radiated in the Southern Hemisphere during the Eocene [94,95,97,103]. The Eocene radiations of crown placental and marsupial groups are highlighted in [Figures 1 and 2](#) by showing an acceleration in diversification rate 10 Ma after the K–Pg boundary. However, most clades that diversified in the Eocene are unlikely to have stemmed from ancestral, small insectivores, which is in contrast to the earlier radiations. Instead, many of these diversifications probably originated from members in taxonomic orders that already demonstrated ecological specialization (e.g., herbivorous ungulates, carnivorous carnivorans).

Challenges in Assessing Ecological Diversity in Deep Time

Ecological Diversity Patterns

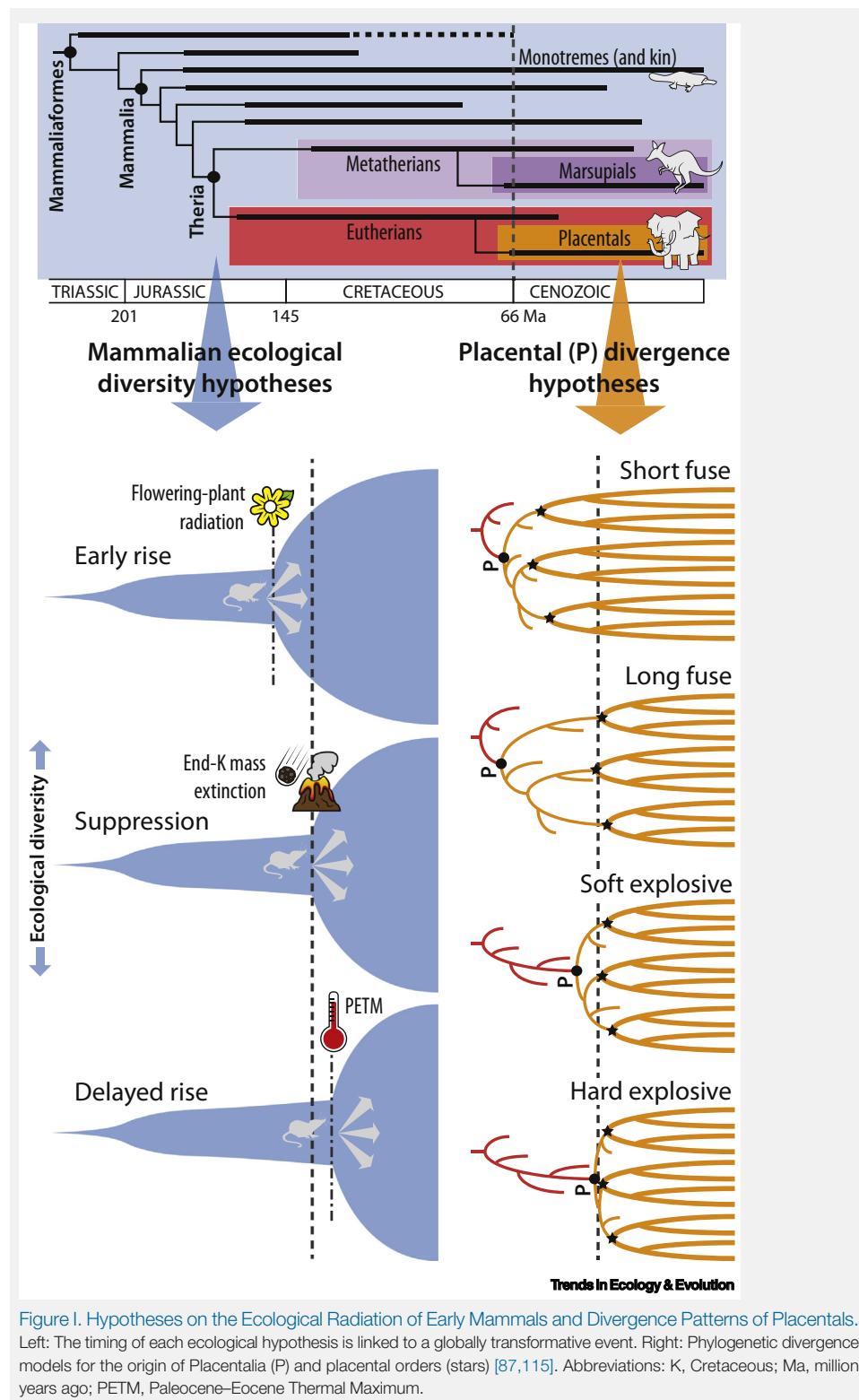
When examining diversification patterns in clades, a confounding issue is that there are many types of diversity that can be assessed, including taxonomic diversity (e.g., species richness), morphological disparity (i.e., anatomical variance), and ecological diversity, as well as phylogenetic divergence rates. For instance, in [Box 1](#) we highlight two sets of competing hypotheses that reflect different types of diversity patterns. One set of hypotheses centers on ecomorphological diversity and is often applied to Theria, Mammalia, or Mammaliaformes, whereas the second set emphasizes alternative phylogenetic divergence patterns in Placentalia. The type of diversity being studied can have a major impact on conclusions about macroevolu-

Box 1. Hypotheses on the Timing of Early Mammal Diversifications

Ecological hypotheses ([Figure 1](#), left) include the long-standing Suppression Hypothesis, which dates back to at least Osborn [80]. It implies that mammals experienced ecological release following the end-Cretaceous mass extinction event at 66 Ma. An earliest Paleocene recovery [21,64,76,113] quickly transitioned into an ecological radiation with rapid increases in mean body mass, dietary diversity, morphological disparity, diversity in diel activity patterns, and taxonomic diversity [3,12,22,75,78–92]. Recent fossil discoveries, quantitative ecomorphological studies, and molecular clock studies have led to alternative hypotheses that challenge the Suppression Hypothesis ([Figure 1](#)). The Early Rise Hypothesis implies that an ecological radiation of early mammals began prior to the K–Pg boundary, driven by broadly coincident ecological radiations of flowering plants and some insect groups. It is supported by Late Cretaceous increases in dietary, taxonomic, and body-mass diversity in some groups [10,11,21,23,63–72,77]. The Delayed Rise Hypothesis implies that an ecological radiation occurred in the Eocene [114], possibly spurred by the Paleocene–Eocene Thermal Maximum at 56 Ma. In contrast to previous faunas, the Eocene fauna included a greater proportion of crown taxa of mammalian orders, additional ecological specialists (especially herbivores), and greater body sizes [24,84,93,95,98–103].

Placental divergence hypotheses ([Figure 1](#), right) focus on the timing of clade origins that are not necessarily coupled with ecological diversification or causal mechanisms. Placentalia is the focus of many macroevolutionary studies because it comprises ~94% of extant mammals. The Long Fuse Model and Short Fuse Model include early branching of Placentalia in the Cretaceous followed by intraordinal diversification before (Short Fuse) or immediately after (Long Fuse) the K–Pg boundary [115]. These hypotheses are commonly supported by molecular data [9,14,114,116]. The explosive models involve a placental origin shortly before (Soft Explosive Model) or at (Hard Explosive Model) the K–Pg boundary followed by rapid diversification in the Paleocene [87,115]. These are often supported by paleontological data [12,83,89].

Although the ecological and placental hypotheses above are convenient tools for framing discussion on mammalian evolution, they can lead to confusion and a false dilemma when applied beyond the intended phylogenetic and macroevolutionary scope. For example, the 'competing' ecological hypotheses are likely to reflect temporally and geographically distinct patterns of radiations of multiple early mammaliaform groups rather than a single group. Various mammaliaform subclades radiated at different times and therefore provide support for all three ecological hypotheses (see main text).



tionary patterns. For instance, support for phylogenetic divergence of placentals in the Cretaceous (e.g., the Short Fuse Model in **Box 1**) does not necessarily provide evidence that placentals experienced a concurrent morphological or ecological diversification, which may have been delayed until after the K–Pg boundary (e.g., [90]).

In this review we focus on patterns of ecological diversity, which we believe are particularly informative because they more directly track adaptive evolutionary changes. However, because direct evidence of paleoecology (e.g., preserved gut contents) is rarely available in the fossil record and is not provided by extant mammals, measuring ecological diversity in deep time can be difficult. Recent paleontological studies have overcome that challenge by examining morphological traits that are strongly correlated with ecological traits. For example, tooth shape is associated with diet and therefore examining the diversity of dental morphologies through time provides a proxy for dietary diversity patterns [10,11,99,100]. In **Box 2**, we discuss the strengths and limitations of both fossil and modern mammal datasets in assessing the ecological diversity of early mammaliaforms.

A potential misconception that arises from the hypothesized evolutionary patterns in **Box 1** (and some citations within) is that each hypothesis suggests that there was a single, widespread radiation of mammals that began at a specific time, which conflicts with the evidence presented in this review that mammaliaforms have experienced many ecological radiations (**Figure 1**). In particular, the ecological hypotheses in **Box 1** present mammals as being ecologically depauperate for much or all of the Mesozoic before experiencing a single, rapid evolutionary radiation at or near the K–Pg boundary. This simplistic view of early mammals may be unintentionally propagated by comparative studies of living species that make inferences about early mammal traits. For example, data from modern mammals often support the ‘nocturnal bottleneck’ hypothesis, which posits that Mesozoic mammals were limited to nocturnal activity and that Cenozoic (66 Ma to current) mammals diversified to include taxa with diurnal (i.e., daytime) and cathemeral (i.e., day and night) activity [78,79]. A critical concern with this conclusion is that the majority of mammalian lineages from the Mesozoic and earliest Cenozoic do not have living representatives or are not

Box 2. Ecological Data in Mammalian Macroevolutionary Studies

Ecological diversity in deep time is challenging to assess, especially because behaviors of extinct species cannot be directly observed. Fossil and modern mammal datasets are used to infer ecological diversity in early mammals, but these two types of datasets possess unique strengths and limitations that can affect interpretations of evolutionary patterns (**Figure 1**).

Extant Mammal Datasets

Phylogenetic topologies resulting from molecular data of modern mammals are generally more robust and better resolved than those produced from morphological characters, including those of fossils. Ecological traits that are observed in extant mammals can be inferred at nodes of the phylogeny using ancestral-state reconstructions (e.g., [74,75,79]), thus providing estimates of the ecological traits of early mammals (**Figure 1**). However, modern-only phylogenies and comparative datasets become less powerful for inferring diversity patterns further back in time [111,117,118], especially because they struggle to account for extinct lineages. For instance, they exclude extinct, ecologically diverse crown mammalian clades (e.g., multituberculates, archaic ungulates) that provide information on the macroevolutionary history of mammals. Further, the ecological diversity of living representatives within a clade may not be indicative of the historical diversity of that clade (e.g., see the discussion of sloth evolution in [112]).

Fossil Mammal Datasets

Fossils provide direct evidence of the morphological and biogeographical traits of early mammals. However, ecological traits examined in extinct taxa are limited to those that can be inferred from fossils. Tooth and jaw shapes are strong indicators of diets and limb morphologies offer clues about locomotion. Thus, diet and locomotor mode are ecological traits commonly examined in early mammaliaforms [2,10,11,19,21,23,66,99,100,107]. Further, body-mass estimates can serve as ecological correlates because body size is associated with a variety of ecologically significant traits (e.g., [119]). Morphological disparity of an ecological correlate (e.g., variance in tooth shapes or body masses) can be calculated for large samples of fossils [10,11,21,24,82], providing a proxy for ecological diversity patterns through time. A major challenge in using paleontological data to assess macroevolutionary patterns is addressing the numerous sampling biases that are associated with the incomplete fossil record [112].

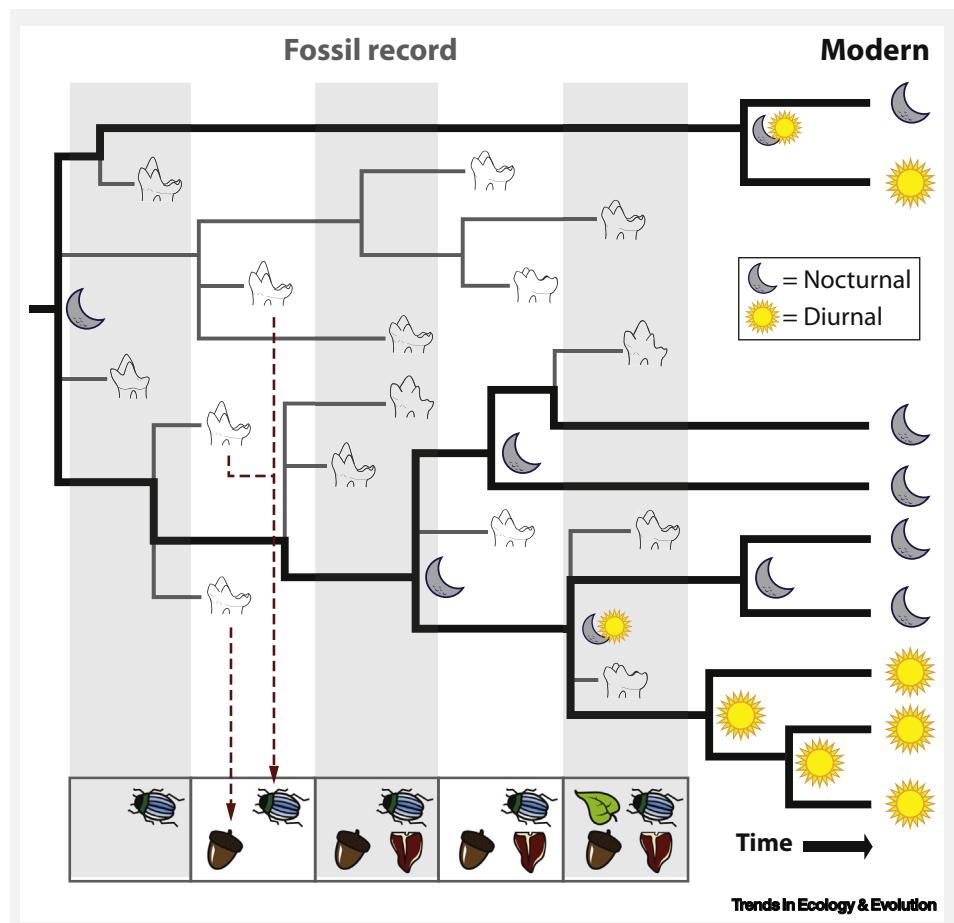


Figure 1. Conceptual Diagram Demonstrating How Comparative Datasets of Modern (Black Lines) and Fossil (Gray Lines) Mammals Are Used to Infer Ecological Diversity in Deep Time. The fossil record provides direct evidence of early mammals and includes a large sample size, but ecological information is limited to that which can be inferred from the fossils (e.g., tooth shape is indicative of diet). Molecular data from modern mammals produce more precise phylogenetic topologies and any ecological traits observed in living species (e.g., nocturnal and diurnal activity) can be reconstructed at ancestral nodes of the phylogenetic tree. However, modern-only datasets become less powerful for inferring ecological diversity further back in time because they cannot account for traits of extinct lineages.

phylogenetically bracketed by them in the comparative studies (Figure 1), and inferring diel activity patterns from mammalian fossils is challenging [104]. Thus, there is little or no direct evidence of diel activity patterns in Mesozoic mammals and comparative studies of modern mammals may inadvertently promote a biased and limited view of early mammalian ecological diversity (see Box 2 for additional discussion).

Phylogenetic Scope

The pattern of ecological diversity through time varies with the phylogenetic scale at which it is measured. For example, an explosive radiation in one subclade may be part of an iterative rise and fall of diversity measured across a larger clade. We emphasize this concept in Figure 2, which includes conceptualized summaries of ecological diversity patterns for two clades of varying levels of phylogenetic scope (i.e., Mammaliaformes and Placentalia). The differing macroevolutionary patterns highlight that the choice of clade(s) to study can have a considerable effect on the resulting conclusions about mammalian macroevolutionary patterns. For instance,

Mammaliaformes experienced significant ecological radiations in the Jurassic and Late Cretaceous, whereas Placentalia represents a nested diversification within Mammaliaformes that is largely confined to the Cenozoic (Figure 1 and 2). This emphasizes that different evolutionary patterns for mammaliaforms and placentals may not necessarily be in conflict, and varying levels of support for the ecomorphological hypotheses in Box 1 may be dependent on the clade of choice in studies.

Phylogenetic Uncertainty

During the Jurassic radiations of non-mammalian mammaliaforms and early crown mammals (i.e., *a* and *b* in Figure 1), rapid morphological changes accompanied the origination of multiple clades [6,8,13,20,44,60]. It is likely that these two radiations each encompass diversifications of several independent lineages [6,8,18]. However, there is uncertainty in the phylogenetic position of groups such as haramiyidans, australosphenidans, and eutrichodontontans [6,34,39,42–45,47,105,106], making it difficult to identify monophyletic clades and distinct diversification patterns. This is compounded by the limited fossil record of mammaliaforms during this time and the lack of living representatives in most groups. For instance, our understanding of postcranial adaptations for locomotion in Jurassic and Early Cretaceous clades is dominated by skeletons from the Middle–Late Jurassic Daohugou (Yanliao) Biota and Early Cretaceous Jehol Biota, which are ‘**Lagerstätten**’ in China [8,13,18,107]. These faunas are extremely informative, but they represent mere ‘snapshots’ of mammalian history and are separated in time by 40 million years. As additional fossils are discovered, it may be possible to identify unique diversification events in the Jurassic and Early Cretaceous. In contrast to the Jurassic radiations, the phylogenetic relationships and evolutionary patterns of crown mammalian clades of the Late Cretaceous and Cenozoic radiations are known with greater resolution (Figure 1). This is due in part to greater fossil sampling and the contributions of representatives of extant clades (**monotremes**, placentals, marsupials) to phylogenetic hypotheses.

What Triggered the Ecological Radiations?

Novel ecological opportunities are catalysts of adaptive (or ecological) radiations [28,29,31] and Erwin [27] notes that concurrent adaptive radiations of multiple monophyletic clades suggest ‘empty ecospace’ as a causal mechanism. Each of the three periods of diversification highlighted in this review involve multiple, independent radiations of monophyletic clades. The Jurassic radiations comprise several diversifying groups of stem and crown mammals, the Late Cretaceous radiations include four major clades (multituberculates, dryolestoids, metatherians, and eutherians), and the Paleocene–Eocene radiations include marsupial and placental groups (Figure 1 and 2). This suggests that ecological diversifications in each period were driven by ecological or environmental triggers that simultaneously benefited multiple mammaliaform groups.

Beyond recognizing the important role of ecological or environmental factors, unmasking more specific causal mechanisms of the mammaliaform radiations is challenging. Direct fossil evidence of trophic interactions is limited and the effects of environmental changes on macroevolutionary patterns of clades can be complex [50,102]. Studies commonly identify correlations between mammalian evolutionary patterns and major ecological/environmental changes, but whether these correlations equate to causal mechanisms is often unclear. Thus, there are many potential triggers for the ecological radiations of mammaliaforms, and we highlight some examples here.

The breakup of Pangea has been posited as a catalyst for the Jurassic radiations of mammaliaforms [20] and Luo *et al.* [43] note the possibility of herbivory in haramiyidans being associated with the evolution of diverse gymnosperm plants. Further, the evolution of key innovations associated with mammalian middle ears, jaws, and molars could have generated novel ecological opportunities by enhancing the hearing and mastication capabilities of early

mammaliaforms [6,8,15,32,37,60]. For the Late Cretaceous radiations, multiple studies suggest a link to the ecological diversifications of plants, specifically angiosperms, and some insect groups after the KTR [9,10,16,21,23,49,50,107] (Figure 1 and 2). This is in line with the Early Rise Hypothesis (Box 1). The angiosperm radiation could have directly benefitted omnivores and herbivores/frugivores by supplying novel food sources to diversifying clades (e.g., [108]). Further, angiosperms may have indirectly benefited mammals through: (i) coevolution with insect groups that provided additional food sources; and (ii) increasing the overall biodiversity of ecosystems [109], promoting increased niche partitioning at multiple trophic levels.

Flowering plants continued to diversify ecologically through the Paleocene and Eocene and it is commonly posited that therian mammals and angiosperms radiated in concert, possibly due to coevolutionary interactions [7,81,94,99,100,107,108,110]. The appearance of fleshy fruits may have been especially beneficial to omnivorous and herbivorous mammals. Further, the end-Cretaceous mass extinction event is often hypothesized to have created ecological opportunities for surviving lineages by eradicating numerous ecological competitors and predators, and this view is presented in Box 1 as the Suppression Hypothesis. Similarly, the **Paleocene–Eocene Thermal Maximum** may have triggered dispersal events and faunal turnovers that catalyzed the Eocene radiations of crown members of placental and marsupial orders (i.e., the Delayed Rise Hypothesis in Box 1).

Concluding Remarks

Mammalia constitutes one of most ecologically diverse clades on Earth and recent studies have shed new light on the origins and evolutionary patterns of early mammaliaforms. In this review, we focus on ecological diversity patterns, and we stress the importance of paleontological data and phylogenetic context when examining these patterns in deep time (Box 1 and 2). There is growing evidence that multiple early mammaliaform groups experienced independent ecological radiations (Figure 1). Each radiation stemmed from ancestral small insectivores or omnivores and each involved diversifications of diets, locomotor modes, and body masses. The diversifications of placental and marsupial groups in the Paleocene and Eocene were especially extensive, possibly catalyzed by the end-Cretaceous mass extinction event (66 Ma), the Paleocene–Eocene Thermal Maximum (56 Ma), and coevolutionary interactions with diversifying angiosperms. However, recent fossil discoveries indicate that early mammaliaforms and several Late Cretaceous crown mammal groups (i.e., multituberculates, early metatherians, early eutherians, dryolestoids) achieved greater ecological diversity than previously recognized. The timing of the Jurassic and Late Cretaceous radiations contradicts the hypothesis that all early mammaliaform groups were ecologically suppressed prior to the end-Cretaceous mass extinction event. This demonstrates that the evolutionary history of early mammaliaforms may be more complex than is often appreciated and illustrates the considerable impact that phylogenetic scope can have on interpretations of macroevolutionary patterns (Figure 1 and 2).

Despite intensive and ongoing study of early mammaliaform evolution, many topics remain unresolved (see Outstanding Questions). Improving our understanding of mammaliaform macroevolutionary patterns requires new fossil discoveries and therefore continued field collecting efforts are critical to this pursuit. Future work can also strive to better incorporate both paleontological and modern molecular data into analyses [12,85], which may be especially important for resolving conflicting phylogenetic hypotheses [111,112]. Further, continued research on ecological correlates in extant mammals will allow improved inferences of ecological patterns in fossil mammaliaforms [10,11,19,24,66,104,107] (Box 2). These efforts will lead to enhanced phylogenetic hypotheses and a greater understanding of the ecologies of fossil taxa, which in turn will permit novel comparative studies on the broad macroevolutionary patterns of early mammaliaforms.

Outstanding Questions

Resolving phylogenetic uncertainties of mammaliaforms: There is debate on the phylogenetic position of many early mammaliaform clades, including australosphenidans, haramiyidans, and eutriconodonts. This limits our understanding of the timing of clade origins (e.g., the age of the mammalian node varies considerably depending on the phylogenetic topology) and hinders the use of phylogenetic comparative methods. Future fossil discoveries and systematic studies can help to resolve these uncertainties.

Merging paleontological data and molecular genomic data: Phylogenies of fossil taxa are produced from morphological data, whereas phylogenies of extant mammals primarily rely on molecular genomic data. Several recent studies have utilized both types of data in analyses, but these often raise additional methodological questions (e.g., how should morphological data and molecular data be weighted?). Many potential research avenues can help to address these questions. Merging datasets of extinct and extant mammals will also be important for future analyses that utilize phylogenetic comparative methods.

Macroevolutionary patterns in the Southern Hemisphere: Most early mammal fossils are from the Northern Hemisphere, which biases our view of macroevolutionary patterns. Continued field collection efforts in southern continents will be critical for filling in the gaps in the evolutionary story of early mammals.

When did the ecological radiation of placentals begin? Many studies on early placentals focus on phylogenetic divergence patterns, not ecological patterns, and studies that have examined ecological patterns often come to very different conclusions about the timing of the placental ecological radiation. A confounding factor is that the phylogenetic placement of many early eutherian fossils remain uncertain, making it challenging to measure ecological diversity in early placentals using paleontological data. Continued efforts to resolve these phylogenetic questions are critical.

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