0 Introduction

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AIMS OF VOLUME 2

This enterprise was originally conceived of as a single volume. However, after a span of 10 years from its original conception, the current senior editor (Christine Janis), and the then junior editors (Kathleen Scott and Louis Jacobs) realized that it would be more realistic to proceed with chapters then in hand, which could more or less be assembled into the conceptually useful, if taxonomically paraphyletic, rubric of “Terrestrial Carnivores and Ungulates” (Janis, Scott, and Jacobs, 1998). This in part reflected the chapters that had been assembled to date, although it should be noted that some of the chapters in this current volume, most notably those by Darryl Domning on sirenians and desmostylians, were among the first ones received almost 20 years ago.

The mammals covered in this volume are thus those remaining from Volume 1, and they can more or less be grouped into two conceptual (and again paraphyletic) groupings: small mammals (aka “vermin”) and marine mammals. The only group of large terrestrial mammals considered in this volume are the xenarthrans, which do not appear until the latest Miocene. Also in this volume, new editors came on board (although Louis Jacobs continued as a co-author on two rodent chapters). Gregg Gunnell, who wrote the chapter on Hyaenodontidae in Volume 1, was a welcome addition as someone familiar with many of these small mammal groups, especially the primates. Mark D. Uhen, a mere teenager when this project was first conceived, was an essential addition as an expert in marine mammals.

As in Volume 1, the taxonomic level of interest in this volume is typically the genus, but locality information is (usually) provided at the level of the species. The faunal localities have been standardized throughout the chapters and are listed in Appendix I (see explanation below), and the locality references are available in Appendix II. For the purposes of standardization, and to provide equal quality of information across each chapter, the stratigraphic range charts in the chapter are presented according to a standardized format, and the institutional abbreviations have also been standardized and are listed in an appendix (Appendix III).

THE STANDARDIZED LAYOUT OF EACH CHAPTER

The chapters are laid out in a similar fashion to those in Volume 1. The contributors were requested to adhere to a common layout for each chapter, in order to provide uniform information throughout the book. The “Introduction” for each chapter introduces the group. The “Defining features” section lays out the basic cranial, dental, and postcranial features of the taxon. The term “defining features” was used, rather than the cladistically preferred term “diagnostic features,” as this section was intended to be a general introduction to the characters of the group as a whole, plesiomorphic as well as apomorphic. Due to the constraints of production costs, contributors were generally requested to limit their illustrations to one taxon for pictures of the skull, dentition, and skeleton.

The section on “Systematics” includes a “Suprataxon” section that deals with the history of the ideas of the relationships of the taxon in question among mammals in general, and an “Infrataxon” section that deals with interrelationships within the group, including a cladogram. Rather than have a more general “suprataxon” cladogram in each chapter, a single concensus cladogram is presented in the summary chapter for each section: Chapters 1 (non-eutherian mammals), 4 (insectivorous mammals), 8 (“Edentata”), 11 (Archonta), 16 (Glires), and 30 (marine mammals).

The “Included genera” section includes a brief description of each genus, including the listing of the type species and type specimen, and a listing of the valid species, including the localities at which each species was found. We also requested contributors to provide an average dental length measurement for each genus, m2 if it was available; if not, some other tooth. This was to provide some size

Evolution of Tertiary Mammals of North America, Vol. 2. ed. C. M. Janis, G. F. Gunnell, and M. D. Uhen. Published by Cambridge University Press.

Cambridge University Press
978-0-521-78117-6 - Evolution of Tertiary Mammals of North America, Volume 2: Small Mammals, Xenarthrans, and Marine Mammals
Christine M. Janis, Gregg F. Gunnell and Mark D. Uhen
Excerpt
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estimate for the taxon, as dental length measurements are a good proxy of body mass (see Damuth and MacFadden, 1990), and m2 length is the most reliable measurement, at least in ungulates (Janis, 1990). However, marine mammals have highly derived dentitions, and the link between molar size and body size is lost (as is often the ability even to identify a tooth as m2); so instead we have chosen to use occipital condyle breadth as an indicator for body size in pinnipeds and cetaceans, following Marino *et al.* (2000).

We have also retained the style, as in Volume 1, of putting "a" or "b" in the reference for taxonomic groups where appropriate (e.g., on p. 32, *Neoliotomus* Jepsen, 1930a). We acknowledge that, as the reference is actually part of the official taxonomic name, that the "a" does not strictly belong there. However, the problems that would ensue with other references, and the issue of the correct identification of the taxonomic reference in the bibliography, led us to decide to retain this style in this volume.

Finally, the "Biology and evolutionary patterns" section provides a synopsis of the paleobiology and evolutionary trends of the group. This section includes the standardized temporal range chart for each taxon. The biogeographic range charts (which may combine a number of taxa) are in the summary chapters (see below).

One difference from Volume 1 is that we no longer have reconstructions of extinct mammals in each chapter. This is partially because our previous artist, Brian Regal, has now changed careers. Additionally, it seemed that for many of the small mammals reconstructions were not known, and they would pretty much all look the same in any case! As we had to find funds to pay a new artist, Marguette Dongvillo, we decided to limit the art work to the summary chapters.

Another difference in the chapter layout is the way in which the synonyms have been handled. Stephen Walsh pointed out to us that the previous mode of noting taxonomic synonymies was phylogenetically suspect, and we have adopted a new standardized way of doing this, following his suggestions. In addition, we were not so anxious in this volume to note all of the known synonymies for each genus, as such information is now readily available in McKenna and Bell (1997).

THE UNIFIED LOCALITY LISTINGS

THE CREATION OF THE LISTING AND THE USE OF THE APPENDICES

The original unified listing in Volume 1 was created from the lists of localities supplied by the authors, supplemented with lists derived from Woodburne (1987). The localities in the individual chapters, (e.g., CP1, NP5), must be looked up in Appendix I. This saves space in the volume, as well as providing an overall unification. Despite extensive checking and cross checking by both editors and authors, it is impossible to have complete confidence that these listings are totally error free, but every attempt has been made to minimize errors.

A locality number (e.g., CP101) encompasses an entire formation. Subdivisions within that formation are then numbered A, B, C, etc., according to relative age. For the purposes of numbering, as well as for the creation of the biogeographic range charts, the localities are grouped into various biogeographic regions (see below). Within each biogeographic region, the localities are numbered according to stratigraphic position. The biogeographic regions are themselves ordered in a general west to east fashion, except for the Pacific Northwest and Northern Great Plains localities, which are listed after those of the Central Great Plains (see ordering in the figures in the summary chapters). A few localities appear to be slightly out of order; this is because information about the exact age was later revised after the creation of the list.

The unification of the localities necessitated a certain degree of grouping of sites. Sometimes this involved grouping of the quarries within a single time horizon in a formation (e.g., the quarries in the Miocene Valentine Formation, localities CP114A–CP114D). At other times, localities that were in a similar location at a similar time were grouped together (e.g., the North Coalinga Local Fauna and Domengine Creek, in the Temblor Formation of the Miocene of California, both contained within locality CC23). To list every single fossil-containing site as its own separate locality would have increased the number of individually listed localities by at least an order of magnitude. As references are provided for each locality, it should be possible in most cases for a concerned researcher to reconstruct finer detail.

Because the original numbering of the localities was accomplished before all final contributions were received, revisions had to be made to the listings that made the final more cumbersome than we would have preferred. In the case of new formations (primary locality numbers), additions were made by creating an intermediate locality between two existing ones, affixing the suffix II to the younger of the two localities (e.g., NP19, and NP19II). In the case of new subdivisions within formations, double letters were created (e.g., NP10B, NP10BB, NP10B2). This rather cumbersome mode of renumbering localities as "work in progress" proved to be more practical than renumbering localities throughout, which would have then necessitated renumbering the localities for the individual taxa that had already been processed (not only of the numbered locality itself, but of all younger localities within the region).

The locality list has grown dramatically over the past decade. Many new localities have been added, either ones that are completely new or ones that are new additions within existing localities. To maintain continuity with Volume 1, we have made the new localities fit in within the preexisting scheme. This, unfortunately, has only added to the cumbersome nature of the listing, but this could not be avoided: we considered that cumbersome was preferable to incompatible.

All new localities have been noted in boldface in Appendix I. Also noted in boldface are other changes that were made. In some instances, localities were moved and given different numbers (see discussion below about certain Mexican localities). In some instances, a locality became subdivided, and the original site contained within that locality was now given the suffix A or B, etc., depending on its age relative to the added sublocality. (For example, locality GC5 (Lower Fleming Formation) originally only contained

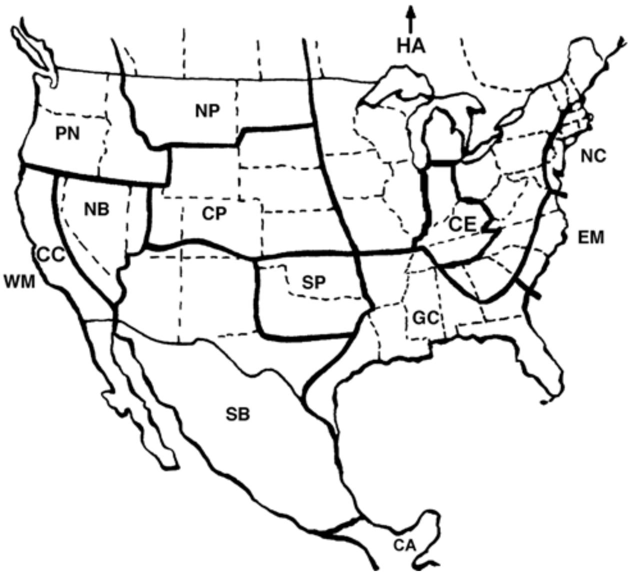

Figure 0.1. Map of North America showing the biogeographic regions employed in this volume. Key: CA, Central America; CC, California Central and Coastal Ranges; CE, Central East America; CP, Central Great Plains; EM, East Coast Marine; GC, Gulf Coast; HA, Canadian High Arctic; NB, Northern Great Basin; NC, Northern East Coast; NP, Northern Great Plains; PN, Pacific Northwest; SB, Southern Great Basin; SP, Southern Great Plains; WM, West Coast Marine.

the Carnahan Bayou Member; with the addition of the earlier Toledo Bend Local Fauna [now GC5A], the Carnahan Bayou Member now became GC5B.) Finally, some localities (fortunately only a few) have had their date changed since Volume 1: for example, the date of the Friars Formation (locality CC4) has been changed from early Uintan (Ui1) to middle Uintan (Ui2).

BIOGEOGRAPHIC REGIONS

ORIGINAL DIVISION OF THE REGIONS IN VOLUME 1

The localities were originally divided into biogeographic regions, so that biogeographical variation as well as stratigraphic ranges could be seen (see Figure 0.1). The biogeographic regions were originally based on those presented by Tedford *et al.* (1987). The division of the Mexican localities (as to inclusion with the Southern Great Basin, California Coast or the Central American region) followed distributional maps in chapters in MacFadden (1984) (but see later revisions for Volume 2).

The "West Coast Marine" localities (prefix WM) include coastal faunas of Washington, Oregon, and California. Terrestrial localities are placed into the "Pacific Northwest" (prefix PN; including Washington, Oregon, and Idaho) or "California Central and Coast" (prefix CC) sections according to latitude, the latter also including localities in Baja California, Mexico. The "Gulf Coast" (prefix GC) includes the Texas Gulf Coast, Florida, and the southern East Coast (Louisiana, Mississippi, Georgia, and North and South Carolina).

The "Northern Great Basin" (prefix NB) includes southeastern California, Nevada, and southwestern Utah. The "Southern Great Basin" (prefix SB) includes Arizona, New Mexico, Texas Big Bend area, southwestern Colorado (i.e., the Paleocene Animas Formation and the Eocene Huerfano Formation), and northern Mexico. The Texas Big Bend area includes all the Paleogene Texas localities (except for the Duchesnean Yegua Formation, grouped with the Gulf Coast), the Miocene Delaho, Rawls, and Banta Shut-In Formations, and the Pliocene Camp Rice and Love Formations.

The "Southern Great Plains" (prefix SP) includes the Texas/Oklahoma panhandles. The "Central Great Plains" (prefix CP) includes Nebraska, South Dakota, Wyoming, Kansas, most of Utah, and northern/northeastern Colorado (i.e., the Paleocene Denver and Wasatach Formations, the Eocene Wasatach, DeBeque, Uinta, and Washakie Formations, and all Oligocene and Neogene sites). The "Northern Great Plains" (prefix NP) includes Montana, North Dakota, western Canada (Alberta, Saskatchewan, and British Columbia). The "Northern East Coast" (prefix NC) includes the East Coast north of the Carolinas.

It is important to emphasize that, because all the individual information has been preserved in this volume (in the form of Appendices I and II), any scheme that we have used to lump together information, for the purposes of diagrams or discussion, has not been lost. The original information is retained for others to reconstruct their own biogeographic scheme.

CHANGES IN VOLUME 2

Some new biogeographic regions have been added, and some old regions have had some boundary changes (see Figure 0.1). Boundary changes include the following. The Gulf Coast region has now been extended to include northern Mississippi and western Tennessee, to include marine localities that form part of the Mississippi Embayment (see further discussion later about the nature of the marine localities). The East Coast Marine/Gulf Coast Region boundary has been more firmly delimited as the boundary between South Carolina and Georgia. A number of Mexican localities, previously included in the Central American region (prefix CA), have now been transferred to the Southern Great Basin region. Mexican localities remaining in the Central American region include the Mexican Gulf Coast – Oaxaca, Chiapas, and the Yucatan Peninsula.

The new biogeographic regions both contain relatively few faunas. They include the Canadian High Arctic (prefix HA) and Central East America (prefix CE). The Canadian High Arctic includes Ellesmere Island, Axel Heiberg Island, and Devon Island. In Volume 1 only a single site, Iceberg Bay Formation on Ellesmere Island, was included, and listed (for convenience more than anything else) with the Northern Great Plains localities. The Central East America region includes newly discovered late Tertiary sites from Tennessee (Gray Fossil Site) and Indiana (Pipe Creek Sinkhole).

Finally, we note that some sites in eastern Oregon that were included within the Pacific Northwest are in fact in close proximity to some of the northwestern Nevada sites included in the Northern Great Basin. Woodburne (2004) considered this to be a single biogeographic region, the Columbia Plateau. We have not made this a separate biogeographic region in this volume, but note in Appendix I which NB and PN sites this applies to.

THE SUMMARY BIOGEOGRAPHIC CHARTS

The biogeographic charts in the summary chapters represent the combined information from the authors' original contributions and information added (with consultation with the original authors) from the published literature and records from museum collections. These charts are presented in the summary chapters, rather than in the individual chapters, for the following reasons. First, space was saved by combining taxa. Second, overall diversity trends were more easily visible when closely related taxa were grouped together. Finally, the summary chapters proved to be a suitable venue in the book to discuss suprataxon evolutionary trends, and the biogeographic charts provide the appropriate illustrations.

THE GEOCHRONOLOGICAL TIME SCALE AND NALMA DIVISIONS

In Volume 1, the time scale and the divisions of the North American Land-Mammal Ages (NALMAs) were adopted from the first edition of Woodburne (1987). The Introduction in Volume 1 discussed the various controversies that existed with dating and NALMA boundaries at that time. In adjusting the time scale for this volume, we followed the second edition of Woodburne (2004) throughout. We acknowledge that there are controversies surrounding some of these changes, and some updates to epoch boundary ages in the past three years, but we decided to make our volume concordant with this publication. One specific issue, that of the division between early and late Blancan, is discussed below.

One profound change that has occurred since Volume 1 is the new division of the NALMAs into biochrons, or numbered units. At the time Volume 1 was published, the Paleocene had already been divided into biochrons rather than descriptive time periods (e.g., Puercan 1, 2, and 3, rather than early, middle, and late), but the other epochs had not yet received this treatment. During the past decade, the Wasatchian through Hemphillian epochs have received formal biochron subdivisions, which have been incorporated here, and we have also updated the ages of NALMA and NALMA subdivision boundaries. Table 0.1 lists the correspondence of these new biochrons with the descriptive units in Volume 1.

Shifts have also occurred in the position of the Oligo-Miocene and Mio-Pliocene boundaries. The Oligo-Miocene boundary, previously considered to fall between early and late Arikareean (i.e., between Ar2 and Ar3) is now considered to fall within late Ar2 (i.e., at 23.8 Ma rather than 23 Ma). Similarly, the Mio-Pliocene boundary, previously considered to fall between late and latest Hemphillian (i.e., between Hh3 and Hh4), is now considered to fall within Hh4, at 5.3 Ma. With regards to the Plio-Pleistocene boundary, we have included a few early Irvingtonian faunas in this volume as these faunas are now considered to be included within the Tertiary (although controversy remains). Our biogeographic charts now include these faunas in a "latest Blancan/earliest Irvingtonian" unit.

Table 0.1. *Equivalence of Wasatchian through Hemphillian (Eocene through Miocene) biochrons used in this volume (following Woodburne, 2004) with NALMA subdivisions in Volume 1*

Early early Wasatachian (Sandcouleean) = Wa0
Early Wasatchian (Greybullian) = Wa0–Wa5
Middle Wasatchian (Lysitian) = Wa6
Late Wasatchian (Lostcabinian) = Wa7
Early Bridgerian (Gardnerbuttian, Bridger A) = Br0–Br1
Middle Bridgerian (Blackforkian, Bridger B) = Br2
Late Bridgerian (Twinn Buttian, Bridger C, D) = Br3
Early Uintan (Shoshonian, Uinta A) = Ui1
Late Uintan (Uinta B, C) = Ui2–Ui3
Duchesnean = Du (no subdivisions)
Early Chadronian = Ch1
Middle Chadronian = Ch2–3
Late Chadronian = Ch4
Orellan = Or1–Or4
Whitneyan = Wh1–Wh2
Early early Arikareean = Ar1
Late early Arikareean = Ar2
Early late Arikareean = Ar3
Late late Arikareean = Ar4
Early Hemingfordian = He1
Late Hemingfordian = He2
Early Barstovian = Ba1
Early late Barstovian = Ba2
Late late Barstovian = Ba2
Barstovian–Clarendonian boundary = Cl1
Early Clarendonian = Cl1–Cl2
Late Clarendonian = Cl2–Cl3.
Early early Hemphillian = Hh1
Late early Hemphillian = Hh2
Late Hemphillian = Hh3.
Latest Hemphillian = Hh4

In Volume 1, we followed the scheme in the earlier edition of Woodburne (Woodburne, 1987) of setting the early/late Blancan boundary at 2.5 Ma, between the Gauss and Matuyama chrons. This meant that the early Blancan included the microtine rodent units Bl I to Bl IV, and the late Blancan included Bl V. We have followed this division in this volume, although the date of some faunas has been adjusted. Our usage of "early Blancan" includes the "middle Blancan" of many authors. The late Blancan, as defined in this fashion, is based on the appearance of certain Great American Interchange mammals, such as the xenarthrans *Dasypus* and *Holmensina*. Note that Flynn *et al.* (2005) discussed the fact that certain Interchange mammals appear earlier in central Mexico than in the United States, and discussed how this might affect the designation of the early/late Blancan boundary (although it is not surprising to us that these immigrants should appear sooner in more southern regions).

Robert Martin (personal communication) would prefer a division into early, middle, and late Blancan, based on his work on Meade Basin rodents (e.g., Martin, Honey, and Peláez-Campomanes, 2000) (see also discussion in Chapter 28). Bearing all these issues in mind, we have retained the early/late Blancan boundary at 2.5 Ma and would alert the reader to the fact that our way of noting individual localities means, as previously, that the position of individual taxa is tied to individual localities, not to particular time units.

FURTHER NEW ISSUES IN VOLUME 2

ISSUES WITH MARINE LOCALITIES AND MARINE MAMMALS

Inclusion of marine mammals in this volume posed some particular problems in that descriptions of marine deposits usually refer to marine time scales for placement in geologic time. Occasionally, terrestrial mammals have been found in these marine localities, providing a direct link to the NALMA time scale used elsewhere in this volume. In other cases, we had to rely on less direct means of relating marine and terrestrial time scales, including interfingering of marine and terrestrial deposits, dating of ash beds, and paleomagnetic dating.

In addition, many older specimens, including many type specimens of important taxa, are poorly placed in time and space. We have placed them into our locality listing system as best we can, but in some cases it was not possible to do so. These instances are clearly noted in each chapter.

THE ADDENDUM

A final contribution to this volume is the Addendum, which provides (minor) corrections from Volume 1 and updates information about taxa from Volume 1, including locality, systematic, and paleobiological information. This was originally planned to be the sole work of the senior editor, but Richard Hulbert was coopted to help with the extensive revision of equids, and Matt Mihlbachler was coopted to add his thesis work on revision of brontothere taxonomy and locality information. This Addendum proved to be an enormous undertaking, with a significant amount of new information, even though the search for new information was by no means exhaustive. New range charts and biogeographic charts are provided for those taxa that had the most revisions: borhyaenid canids, brontotheres, equids, and rhinocerotids.

ACKNOWLEDGEMENTS

A number of publications were indispensable in the production of this book. In addition to the edited volume by Woodburne (2004) already mentioned, we would have been lost without the books by Korth (1994) and McKenna and Bell (1997). We are also extremely grateful to Phil Gingerich for use of his office space and library at the University of Michigan for various editorial meetings during the production of this volume. The late Steve Walsh contributed much to this volume; his knowledge and wisdom will be missed.

The following people helped with reviewing individual chapters: Andrea Bair, Annalisa Berta, Doug Boyer, Bill Clemens, Richard Fox, Jonathan Geisler, Bill Korth, Nancy Simmons, Dale and Alisa Winkler, and Rick Zakrzewski. The following people helped with providing locality information: Tom Goodwin, Scott Foss, Richard Hulbert, Bob Martin, Don Prothero, and Steve Walsh. Mary Dawson, Don Prothero, Margaret Stevens, and Samantha Hopkins provided copies of preprinted papers for help with chapters. Julia Keller, Caitlyn Thompson, and Megan Dawson helped with editing details, and Jamie Lemon helped with obtaining figure permissions. CMJ thanks the Bushnell Foundation for help with some travel and editing costs.

We also acknowledge the extreme patience of certain authors who prepared manuscripts for inclusion close to two decades ago, notably Tom Bown, Daryl Domning, Larry Flynn, Howard Hutchinson, David Krause, Sam McLeod, and Ken Rose, although we are also delighted to have had the opportunity to work with many junior people who have come of age since Volume 1 was published. We also note the sterling contributions of Larry Flynn to this volume in writing the bulk of the rodent chapters, a truly stupendous task! Special thanks are owed to our copy editor, Jane Ward, whose diligence, patience, and extraordinary attention to detail meant that many embarrassing errors were caught and fixed, and she also greatly improved the consistency of the text.

Finally, we thank our own North American mammals for their company during the production of this volume: felines Diego, Sherman, Mimi, and Critter; canines Ronnie and Boswell; and equines Duster and Mel.

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Cambridge University Press
978-0-521-78117-6 - Evolution of Tertiary Mammals of North America, Volume 2: Small Mammals, Xenarthrans, and Marine Mammals
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Part I: Non-eutherian mammals

1 Non-eutherian mammals summary

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INTRODUCTION

"Non-eutherian mammals" is obviously a paraphyletic grouping. Metatheria (Huxley, 1880: extant marsupials and their extinct relatives that fall outside of the extant crown group) and Eutheria (Gill, 1872: extant placentals and their extinct relatives that fall outside of the extant crown group) have long been considered to belong in the Theria (Parker and Haswell, 1897), exclusive of both the multituberculates and the monotremes (although see below for discussion of past and present notions of the "Marsupionta", uniting marsupials and monotremes in a clade).

MULTITUBERCULATA

As discussed in Chapter 2, multituberculates have long been recognized as a distinctive group of mammals. Simpson (1945) ranked them as the subclass Allotheria (Marsh, 1880), one of three mammalian subclasses (the other two being Prototheria, or monotremes, and Theria). McKenna and Bell (1997), by comparison, recognized Allotheria as an infraclass within subclass Theriiformes; subclass Prototheria is retained, and subclass Theriiformes includes infraclasses Allotheria, Triconodonta, and Holotheria, the last including Theria as a supercohort (note that this classification differs from the one shown in Figure 1.2, below). Multituberculates are commonly known as "the rodents of the Mesozoic," and it is probable that they filled a rodent-like niche as small omnivores and herbivores prior to the evolution of the rodents in the early Tertiary. The probable paleobiology of multituberculates, including possible reasons for their extinction, is discussed in Chapter 2, this volume.

Multituberculates are usually considered as the order Multituberculata (Cope, 1884, originally proposed as a suborder of Marsupialia, now an order within the Allotheria). As such, they represent the longest-lived order of mammals, ranging from the Late Triassic (if the haramiyids are included, around 205 Ma) (Butler and Hooker, 2005) or the Middle Jurassic (if the haramiyids are excluded, around 160 Ma), to the late Eocene (around 35 Ma). The haramiyids are a paraphyletic and problematical group of mammals, with rather multituberculate-like cheek teeth, known from the Late Triassic to Late Jurassic (see further discussion below). Kielan-Jaworowska, Cifelli, and Luo (2004) considered the haramiyids to be a separate order, Haramiyida, within the Allotheria, rather than included within the Multituberculata. Kielan-Jaworowska, Cifelli, and Luo (2004) also rejected the notion that the rather multituberculate-like Gondwanatheria (known from the Late Cretaceous to early Paleocene of South America, Africa, India, and Madagascar) belong with the multituberculates, classifying them as Mammalia incertae sedis: the distribution of multituberculates is thus confined to the Northern Hemisphere, with the exception of a few fragmentary teeth referred from Morroco (Sigogneau-Russell, 1991) and Madagascar (Krause, *et al.*, 1999).

Kielan-Jaworowska, Cifelli, and Luo (2004; Chapter 8) provided a general summary of multituberculates, focusing primarily on the Mesozoic radiation, and the following text summarizes some of their major points. The main radiation of multituberculates was in the Cretaceous, with the earliest Tertiary multituberculates representing a diversity considerably reduced by the end Cretaceous extinctions. There are two major groups within the multituberculates: the paraphyletic "Plagiaulacidae," and the Cimolodonta, which are both composed of around 10 families (depending on the classification scheme). The plagiaulacids were less derived in their dentition than the cimolodonts, and are all of fairly small size; their major radiation was in the Late Jurassic of Eurasia and North America, although some lineages persisted into the Early Cretaceous (where one lineage is also found in Morocco). The cimolodonts include taxa of larger size (such as the wombat-sized taeniolabidids): they are more derived than plagiaulacids in a number of features, including the loss of the first upper incisor and the transformation of the lower fourth premolar into an arcuate, bladelike tooth. Cimolodonts first appeared

Evolution of Tertiary Mammals of North America, Vol. 2. ed. C. M. Janis, G. F. Gunnell, and M. D. Uhen. Published by Cambridge University Press.

Figure 1.1. Restoration of the early Tertiary marsupial *Peradectes* (by Marguette Dongvillo).

in the Early Cretaceous, were probably at their most diverse during the Late Cretaceous, and were known to occur throughout the Northern Hemisphere. Five families extend into the Tertiary: the Eucosmodontidae (North America and Europe), the Microcosmodontidae (North America), the Taeniolabididae (North America and Asia), the Ptilodontidae (North America, Europe, and Asia), and the Neoplagiaulacidae (North America, Europe, and Asia). The genus *Cimexomys*, placed incertae sedis within Cimolodonta, survived into the Paleocene of North America.

Hurum, Luo, and Kielan-Jaworowska (2006) noted that a monotreme-like os calcaris is present in several multituberculates from the Late Cretaceous of Mongolia. In the platypus, this bone is associated with the spur and poison gland of males, and an os calcaris is also seen in some other Mesozoic mammals such as *Gobiocon-odon* and *Zhangheotherium*. They, therefore, concluded that this is a primitive mammalian feature, not a monotreme autapomorphy as previously thought.

THERIA

MARSUPIAL/PLACENTAL SIMILARITIES AND DIFFERENCES

Extant therians are united by many morphological features. Osteological characteristics include tribosphenic molars, presence of a scapular spine and supraspinous fossa (see Sánchez-Villagra and Maier, 2003), middle ear bones fully enclosed (now determined to have occurred independently of the condition in monotremes [Rich *et al.*, 2005]) with a cochlea of two and a half coils, and numerous features of the basicranium (Wible and Hopson, 1993). Soft anatomy features include the presence of a dually innervated (cranial nerves V and VII) digastric jaw-opening muscle (as opposed to the detrahans muscle of monotremes, innervated by cranial nerve V, or the depressor mandibulae of other tetrapods, innervated by cranial nerve VII), scapular sling muscles derived from the hypaxial layer (e.g., rhomboideus and serratus muscles), an external ear (pinna), nipples, and various features of the urogenital system. Urogenital features include the rerouting of the ureters into the bladder (from the cloaca, evidently done convergently between marsupials and placentals as the position of the ureters relative to the reproductive ducts differs), separate openings for alimentary and urogenital systems (i.e., loss of the cloaca), descent of the testes into a scrotum (clearly accomplished convergently, as the scrotum, if present, is postpenile in marsupials and prepenile in [most] placentals), and a penis that is now used for urination as well as sperm transmission (see Renfree, 1993, for a summary of mammalian reproductive differences). Marsupials and placentals also share the derived feature of viviparity, but it is not clear if this condition arose once, or convergently between the two groups, because the formation of a uterus more derived than the monotreme condition was clearly evolved convergently (Renfree, 1993). Cifelli (1993) and Kielan-Jaworowska, Cifelli, and Luo (2004) have discussed the osteological attributes of extinct clades also considered to belong within the Theria.

Both placentals and marsupials possess unique features, and one general consideration about the original divergence, based on the postcranial skeleton, is that marsupials were originally more arboreal while placentals were more terrestrial (see Szalay, 1994). Placental apomorphies include the following features: the loss of the epipubic bones (although note the presence of these bones in some Cretaceous eutherians [Novacek *et al.*, 1997]), a corpus callosum linking the two cerebral hemispheres, the retention of the young in the uterus past a single estrus cycle, the fusion of the Müllerian ducts into a midline uterus, vasa deferentia that loop over the ureters, and a scrotum (if present) that is (usually) placed behind the penis (lagomorphs are an exception). Eutherians also possess various detailed derived features of the cranium, dentition, and postcranial skeleton (see Kielan-Jaworowska, Cifelli, and Luo, 2004), including the reduction of the number of molars to three, and (except for the most primitive forms) a reduced number of incisors with three or fewer in each jaw half. Additionally, although not all placentals have large brains, it is only among placental mammals that large brains (encephalization quotient significantly greater than one) have arisen (convergently, in many different clades).

Marsupials have a number of derived features relating to their unique mode of reproduction, including the presence of a pseudovaginal canal, and others that are discussed below. Marsupials are also unique in the possession of end arteries on the surface of the brain (Lillegraven, 1984). In addition, there are a diversity of derived features of the cranium, dentition, and postcranial skeleton (see Kielan-Jaworowska, Cifelli, and Luo, 2004). Extant marsupials have an auditory bulla, if present, made from the alisphenoid bone (the placental auditory bulla may be derived from a variety of sources, but never from the alisphenoid). A distinctive feature of almost all metatherians is the shelflike inflected angle of the dentary. However, this feature is absent from the supposed first metatherian, *Sinodelphys* (Luo *et al.*, 2003); a slight inflection is seen in early eutherians, and the angle is secondarily reduced in some extant marsupials, in the koala (*Phascolarctos*), the numbat (*Myrmecobius*), and the honey possum (*Tarsipes*). Other "typical" marsupial cranial features, used to distinguish extant forms from placentals, such as diamond-shaped nasals, palatal vacuities, and the exclusion of the jugal from the jaw glenoid, are all primitive therian features that may be variously observed among extant placentals. The marsupial dentition is apomorphic in the reduction of the number of premolars to three, and the condition of virtual monophyodonty, where the only tooth to be replaced is the last premolar.

Finally, despite the popularity of textbook figures showing ecomorphological convergence between extant marsupials and placentals (e.g., marsupial "wolf" etc.), marsupials exhibit some ecomorphological types not seen among placentals: no placental has evolved in a large (> 10 kg) ricochetal (hopping) form like the diversity of kangaroos, and there is no non-volant nectivore among placentals. All nectivorous placentals are bats, whereas the marsupial nectivore is the honey possum, or noolbenger (*Tarsipes rostratus*).

We discuss below the contribution of molecular biology to higher-level mammalian systematics. We also note here that molecular biology has also provoked controversy in the discussion of when the splits occurred between major mammalian lineages. For example, while the fossil record shows the earliest eutherians and metatherians to be in the Early Cretaceous, around 120 Ma (e.g., Ji *et al.*, 2002; Luo *et al.*, 2003), some molecular studies propose a split as early as the Late Jurassic (e.g., Kumar and Hedges, 1998). In addition, numerous authors have proposed the diversification of the major placental orders deep within the Cretaceous, in contrast to fossil record evidence that would place this diversification in the latest Cretaceous at the earliest (e.g., Hedges *et al.*, 1996; Eizirik, Murphy, and O'Brien, 2001; Madsen *et al.*, 2001; Murphy *et al.*, 2001a,b; but for estimates much closer to the K/T boundary, see Kitozoe [2007; molecular data] and Wible *et al.* [2007; morphological data]). This issue is further discussed in Kielan-Jaworowska, Cifelli, and Luo (2004: Chapter 15); Hunter and Janis (2006) also discussed this issue and the paleobiogeography of early placentals.

MARSUPIALS

Although marsupials are thought of as quintessentially Australian mammals, with perhaps a second outpost in South America, the first definitive metatherians are known from the Late Cretaceous of North America (Cifelli and Muizon, 1997; Cifelli, 1999). However, a candidate for the earliest metatherian, *Sinodelphys szalayi*, is known from the Early Cretaceous of Asia (Luo *et al.*, 2003), in the same deposits (the Yixian Formation of China) as the earliest known eutherian, *Eomaia scansoria* (Ji *et al.*, 2002). During the Tertiary, marsupials are found not only in North America but also during the Eocene and Oligocene in Europe, Asia, and Africa (possibly extending into the middle Miocene in Asia; see McKenna and Bell, 1997). However, these Old World marsupials were not a diverse radiation and are known by only a few individual fossils.

Present-day marsupials make up only 6% of mammalian species; however, marsupials exhibit a great degree of morphological diversity, and their low taxonomic diversity is explained, at least in part, by the area of land that they occupy today (Kirsch, 1977). Note, however, that the marsupials found in the Northern Hemisphere during the Tertiary were uniformly small to medium-sized, fairly generalized mammals, resembling Recent didelphids (opossums) in their ecomorphology.

Marsupials are usually distinguished from placentals by their mode of parturition. While placentals carry their young in the uterus past a single estrus cycle, marsupials all eject their young at the end of the estrus cycle. The neonates are highly altricial and make their way up their mother's ventral side to attach onto a nipple, which in more derived forms is enclosed within a pouch (or marsupium), where they complete their development. The marsupial form of reproduction was once thought to be some primitive intermediate stage between the oviparity of monotremes and the form of viviparity seen in placentals. Marsupials were reported to lack the chorioallantoic placenta of placentals, instead relying on the yolk sac (choriovitalline) placenta, which is also seen in the early stages of gestation in placentals; they are also primitive in retaining vestigies of the egg shell membrane. Marsupials have been assumed to be constrained in their taxonomic and morphological diversity by their reproductive mode (e.g., Lillegraven, 1975). However, in more recent years, this issue of "marsupial inferiority" has been reexamined (see Sears [2004] for a review).

For a start, the apparent lack of a chorioallantoic placenta in marsupials is not a primitive condition (indeed, this could hardly be the case as a chorioallantoic membrane is present in all amniotes). Some marsupials (e.g., bandicoots, koalas, and wombats) do indeed show evidence of a transitory chorioallantoic placenta at the end of gestation, and developmental studies show that the outgrowth of the chorioallantoic membrane is actually *suppressed* in marsupials (see Smith, 2001) (i.e., this apparent lack of a chorioallantoic membrane is a derived feature, not a primitive one). Furthermore, marsupial neonates are not merely undeveloped versions of placental neonates but show many derived features. In ontogeny, the development of the forelimb and craniofacial structures have been accelerated, at the expense of the later development of the nervous system (Smith, 1997), and marsupial neonates have a unique cartilaginous "shoulder arch," made up in part from retained interclavicle and coracoid elements (otherwise lost in adult therians), that aids in the crawl to the nipple (Sánchez-Villagra and Maier, 2003; Sears, 2004).

However, while it appears that marsupials should not be considered inferior to placentals because of their different mode of reproduction, it is likely that constraints on neonate forelimb anatomy have led to constraints on adult locomotor mode (see Sears, 2004). No marsupial has greatly reduced the numbers of fingers, as do many placental ungulates. Constraints on forelimb anatomy might also prevent the evolution of flippers in aquatic marsupials (Lillegraven, 1975), but it seems that the evolution of a fully aquatic marsupial might be more constrained by the need to carry young in a pouch, and to give birth on land. (Note that there is one semi-aquatic marsupial: the South American yapok, or water-opossum, *Chironectes minimus*, which can seal the pouch during brief underwater forays.)

Cambridge University Press
978-0-521-78117-6 - Evolution of Tertiary Mammals of North America, Volume 2: Small Mammals, Xenarthrans, and Marine Mammals
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SYSTEMATICS

MULTITUBERCULATES

Multituberculates are without close living relatives, and their placement within Mammalia is contentious. Most parsimony analyses place them within crown-group Mammalia (Rowe, 1988; Wible and Hopson, 1993; Rougier, Wible, and Novacek, 1996; Luo, Cifelli, and Kielan-Jaworowska, 2001; Woodburne, 2003; but see Wible [1991] and Miao [1993] for characters that would seem to place them outside). Among these, one school of thought is that multituberculates are more closely related to monotremes than to Theria. This hypothesis of relationship is supported by some braincase morphology (Kielan-Jaworowska, 1971), and the shape, position, and orientation of the ear ossicles (Meng and Wyss, 1995). It was also supported by a single character in Wible and Hopson's (1993) phylogeny of basicrania, although the authors thought that the relationship to monotremes was unlikely. The other, perhaps more widely accepted hypothesis, that Multituberculata is more closely related to Theria than to Monotremata, is the better supported when cranial and postcranial characters are combined (Rowe, 1988; Rougier, Wible, and Novacek, 1996; Luo, Cifelli, and Kielan-Jaworowska, 2001; Luo, Kielan-Jaworowska, and Cifelli, 2002) (as shown in Figure 1.2, below).

Both of these hypotheses seem problematic when basal mammalian dentitions are considered, because there are no identifiable cusp homologies between multituberculate teeth and tribosphenic teeth. The most common objection this raises is that multituberculate molars cannot be derived from a tribosphenic pattern. However, Krause (1982) noted that some murid rodents converge on the multituberculate pattern of longitudinal rows of cusps. Meng and Wyss (1995) pointed out that a similar molar form has evolved in the bat *Harpyionycteris* (illustrated in Nowak and Paradiso, 1983, p. 186); rodents and bats are placental groups with primitively tribosphenic molars. Moreover, recent phylogenies (Luo, Cifelli, and Kielan-Jaworowska, 2001; Luo, Kielan-Jaworowska, and Cifelli, 2002) have raised the possibility that tribosphenic molars arose separately in the monotreme and therian lineages (see discussion below). Alternatively, Woodburne (2003) argued that monotremes do not in fact have tribosphenic teeth. Either of these last hypotheses would obviate the need for any derivation of the multituberculate molar pattern from a tribosphenic morphology.

The significant problem posed is instead that, without identifiable homologies, many phylogenetic characters of the dentition are not applicable to multituberculates. For example, Luo, Kielan-Jaworowska, and Cifelli (2002) listed 55 molar morphology and 12 molar wear characters; this adds up to about one quarter of the 271 informative characters in their analysis of mammalian phylogeny, most of which are not applicable to multituberculates. The problem thus introduced is not resolvable by the analysis software used; the computer cannot distinguish between data that are missing (owing, for instance, to non-preservation) and characters that are inapplicable. As a result, the true most parsimonious trees may be rejected (Maddison, 1993). Any placement of Multituberculata on the tree of basal mammals should, therefore, be considered provisional and somewhat unreliable.

One precladistic classification of early mammalian relationships placed Multituberculata in the "Allotheria" with the Haramiyida. Haramiyids are known from the Late Triassic and until recently (Jenkins *et al.*, 1997) were known only from isolated teeth, on which multiple cusps are arranged in rows, similar to those of multituberculate teeth. The discovery of a dentary, premaxilla, and maxillary fragment in Greenland, however, revealed that haramiyids retained relatively substantial postdentary bones and dental specializations that preclude them from being directly ancestral to, or closely related to, multituberculates (Jenkins *et al.*, 1997). An experiment in which Multituberculata and Haramiyida were constrained to be related in phylogenetic analysis resulted in both "Allotheria" and eutriconodonts being pulled outside crown-group Mammalia. However, in phylogenetic analyses of the same matrix in which Multituberculata and Haramiyida were considered independently, haramiyids branch off far below crown-group Mammalia (Luo, Kielan-Jaworowska, and Cifelli, 2002).

MARSUPIALS

Kielan-Jaworowska, Cifelli, and Luo (2004; their Chapter 15) provided an extensive review of previous and current hypotheses and controversies concerning the interrelationships of various basal groups of mammals. Here we largely summarize their discussion of the relationship of marsupials to other mammals.

While tribosphenic molars were long considered to be a synapomorphy of therian mammals, various Mesozoic mammals have been found in the Southern Hemisphere since the mid 1990s that apparently possess tribosphenic molars (including an early monotreme, *Steropodon*), and there is considerable controversy about whether or not tribosphenic molars evolved once or convergently between Mesozoic mammals in Northern and Southern Hemispheres. A single evolution of the tribosphenic condition (e.g., Rich *et al.*, 1997, 2002; Woodburne, Rich, and Springer, 2003) would imply that monotremes are much more closely related to therians than previously supposed. In contrast, Luo and colleagues (Luo, Cifelli, and Kielan-Jaworowska, 2001; Luo, Kielan-Jaworowska, and Cifelli, 2002) considered that tribosphenic molars arose independently in the southern, monotreme-related group (their Australosphenida) and in the northern, therian group (their Boreosphenida), with monotremes and therians belonging to very separate clades that diverged from each other deep within the early mammalian radiation (see Figure 1.2).

The derived features uniting therians were discussed previously, and therian monophyly is strongly supported by a number of recent morphological analyses (e.g., Zeller, 1999; Szalay and Sargis, 2001; Luo, Kielan-Jarowoska, and Cifelli, 2002). Most molecular studies, either using nuclear DNA sequences (e.g., Retief, Winkfein, and Dixon, 1993; Kullander, Carlson, and Hallbrook, 1997; Lee *et al.*, 1999; Gilbert and Labuda, 2000; Killian *et al.*, 2001) or protein sequences (Messer *et al.*, 1998; Belov, Hellman, and Cooper, 2002), also support therian monophyly. However, studies of mitochondrial genomes (e.g., Janke, Xu, and Arnason, 1997; Kirsch,