

EVOLUTION OF TERTIARY MAMMALS OF NORTH AMERICA

VOLUME 2
SMALL MAMMALS, RENARTHRANS,
AND MARINE MAMMALS



Edited by CHRISTINE M. JANG,
GREGG F. GUNNELL AND MARK D. UHEN

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Evolution of Tertiary Mammals of North America

This second volume completes the unique survey of North American Tertiary mammals, and covers all the remaining taxa not contained in Volume 1. It provides a database of mammalian diversity over time and space, and evaluates the effect of biogeography and climatic change on evolutionary patterns and faunal transitions.

As with Volume 1, this book lays out, in a standardized format, the distribution in time and space of each taxon. It summarizes the current state of the systematics of the various mammal groups, and it discusses their paleobiology and evolutionary patterns. It contains six summary chapters that integrate systematic and biogeographic information for higher taxa, and provides a detailed account of the patterns of occurrence for different species at hundreds of different fossil localities, with the inclusion of many more localities than were contained in the first volume.

With over 30 chapters, each written by leading authorities, and an addendum that updates the occurrence and systematics of all of the groups covered in Volume 1, this will be a valuable reference for paleontologists and zoologists.

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*This volume is dedicated to our elders and betters
in the areas of small mammal and marine mammal paleontology:
Malcolm McKenna, Leigh Van Valen, and Charles Repenning*

Evolution of Tertiary Mammals of North America

Volume 2: Small Mammals, Xenarthrans,
and Marine Mammals

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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 consensus 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

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, Marguerite 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 Domingue 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

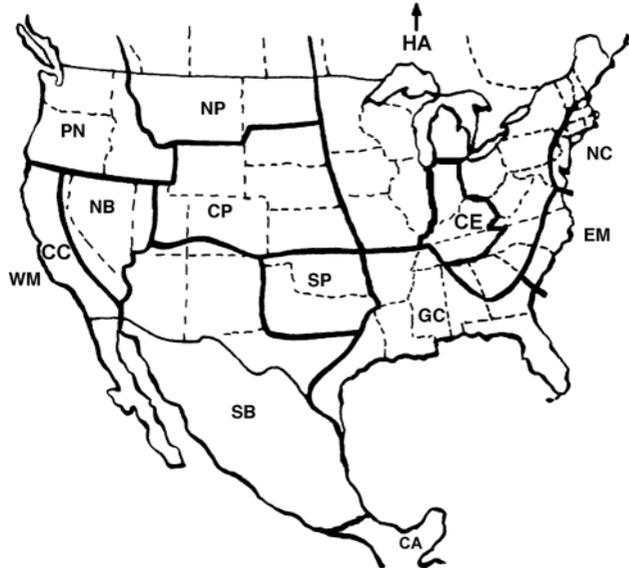


Figure 0.1. Map of North America showing the biogeographic regions employed in this volume. Key: CA, Central America; CC, California Central and Coastal Ranges; CE, Central East America; CP, Central Great Plains; EM, East Coast Marine; GC, Gulf Coast; HA, Canadian High Arctic; NB, Northern Great Basin; 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 (U1) to middle Uintan (U2).

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 Wasatch Formations, the Eocene Wasatch, 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

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 Wasatchian (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

controversy remains). Our biogeographic charts now include these faunas in a “latest Blancan/earliest Irvingtonian” unit.

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 BI I to BI IV, and the late Blancan included BI 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 *Dasyopus* 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 Muhlbachler 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.

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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

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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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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 infra-classes 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 Morocco (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



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 Neoplagiulacidae (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 *Gobiiconodon* 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 pseudo-vaginal 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) ricochetel (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 Kitzoe [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 diver-

sity, 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 (choriovitelline) placenta, which is also seen in the early stages of gestation in placentals; they are also primitive in retaining vestiges 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.)

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-Jaworowska, 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,

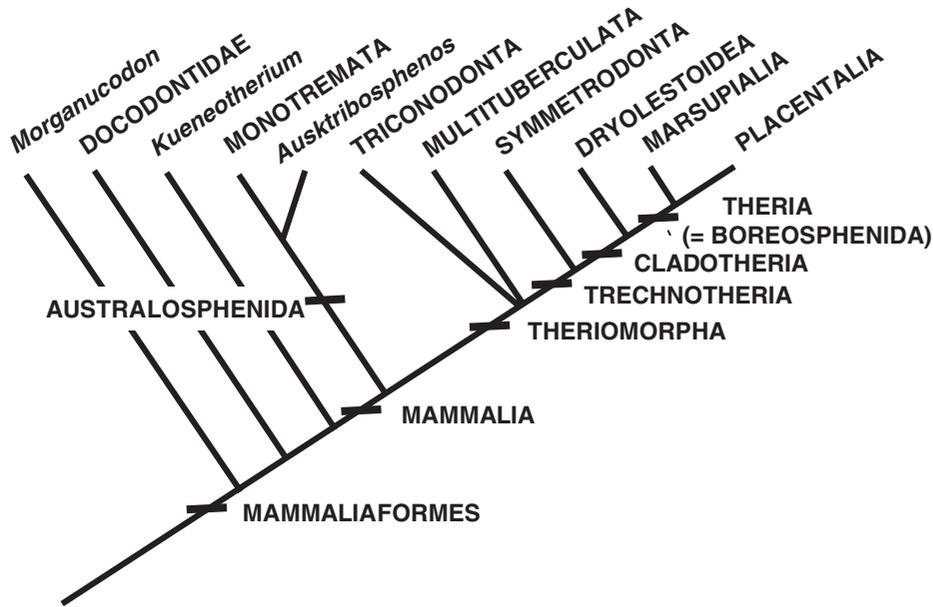


Figure 1.2. Interrelationships of the major lineages of mammals (modified from Rich *et al.* [2005] and Kielan-Jaworowska, Cifelli, and Luo [2004; their Figure 15.1]). Note that an alternative cladogram (displayed in Kielan-Jaworowska, Cifelli, and Luo [2004; their Figure 15.2]) would place *Kueneotherium* as the sister taxon of *Morganucodon*, below docodonts.

Lapointe, and Springer, 1997; Penny and Hasegawa, 1997; Kirsch and Mayer, 1998; Janke *et al.*, 2002) have instead supported the notion of a sister-group relationship between monotremes and marsupials, the old notion of the “Marsupionta” (Haeckel, 1898; Gregory, 1947). Springer *et al.* (2001) and Baker *et al.* (2004) both discussed this molecular controversy; they supported therian monophyly and advanced the notion that nuclear exon genes are more informative than mitochondrial genes for resolving deep branches within mammalian phylogeny. Baker *et al.* (2004) also provided a critique of some of the statistical methodologies applied by other workers.

Case, Goin, and Woodburne (2005) reviewed the higher-level classification of the Marsupialia, and the discussion below summarizes their work. Simpson (1945) originally classified marsupials (as order Marsupialia) into two major groups (superfamilies): the American Didelphoidea and the Australian Dasyuroidea. Ride (1964, 1970) raised marsupials to an equivalent taxonomic rank with placentals, including four orders: the Marsupicarnivora (including the North and South American, and Australian insectivorous taxa: didelphids, stagodontids, pediomyids, borhyenids, thylacines, and dasyurids), the Paucituberculata (the South American caenolestids, polydolopids, groeberiids, and argyrolagids), the Peramelina (the Australian bandicoots and bilbies), and the Diprotodontia (the Australian herbivores, including possums, koalas, wombats, kangaroos, etc.). The Didelphidae (including the North American Cretaceous and early Tertiary marsupials) was assumed to be the basal marsupicarnivoran family, from which all other marsupials were ultimately derived. However, within these early marsupials, Crochet (1979) distinguished between the South American Cenozoic Didelphidae and the predominately North American Peradectidae.

The work of Szalay (see Szalay, 1994) on tarsal morphology showed that the South American microbiotheres (including the extant genus *Dromiciops*) were actually united with the Australian

marsupials in what he termed the cohort Australidelphia, leaving the Ameridelphia as a paraphyletic American grouping; this proposition was later backed up by molecular evidence (e.g., Kirsch *et al.*, 1991; Springer *et al.*, 1998). Marshall, Case, and Woodburne (1990) proposed a third cohort to define the major clades of marsupials, the Alphadelphia, which distinguished the North American Cretaceous and early Cenozoic taxa from the Cenozoic South American Ameridelphia.

McKenna and Bell (1997) recognized the magnorder Ameridelphia (including orders Didelphimorphia and Paucituberculata [including polydolopids, see below]) and magnorder Australidelphia (including superorders Microbiotheria and Eometatheria [all Australian marsupials]). The taxa in the proposed Ameridelphia are dealt with as follows. The North American families Stagodontidae and Pediomyidae (which are confined to the Cretaceous) are left outside of this magnorder grouping, united in the suborder Archimetatheria. In contrast, alphadontids (Late Cretaceous of North America), peradectids, and herpetotheriids (both from the Late Cretaceous and Tertiary of North America) are now included as subfamilies within the Didelphidae. Thus the notion of a distinct grouping of Alphadelphia (whether paraphyletic or not) is abandoned. This is the classification essentially followed by Korth (Figure 3.1; see Chapter 3).

It was previously supposed that the alphadelphian marsupials dispersed to South America, giving rise to the ameridelphians (Case and Woodburne, 1986). However, recent discoveries of Cretaceous marsupials in North America (Case, Goin, and Woodburne, 2005) have led to a revision of this hypothesis. It appears that some ameridelphians were actually present in the latest Cretaceous of North America: thus the cohort must have had its origins on this continent. The Ameridelphia remains as a paraphyletic grouping, and at least two South American clades (Didelphoidea and Polydolopimorphia) originated in the Late Cretaceous of North America

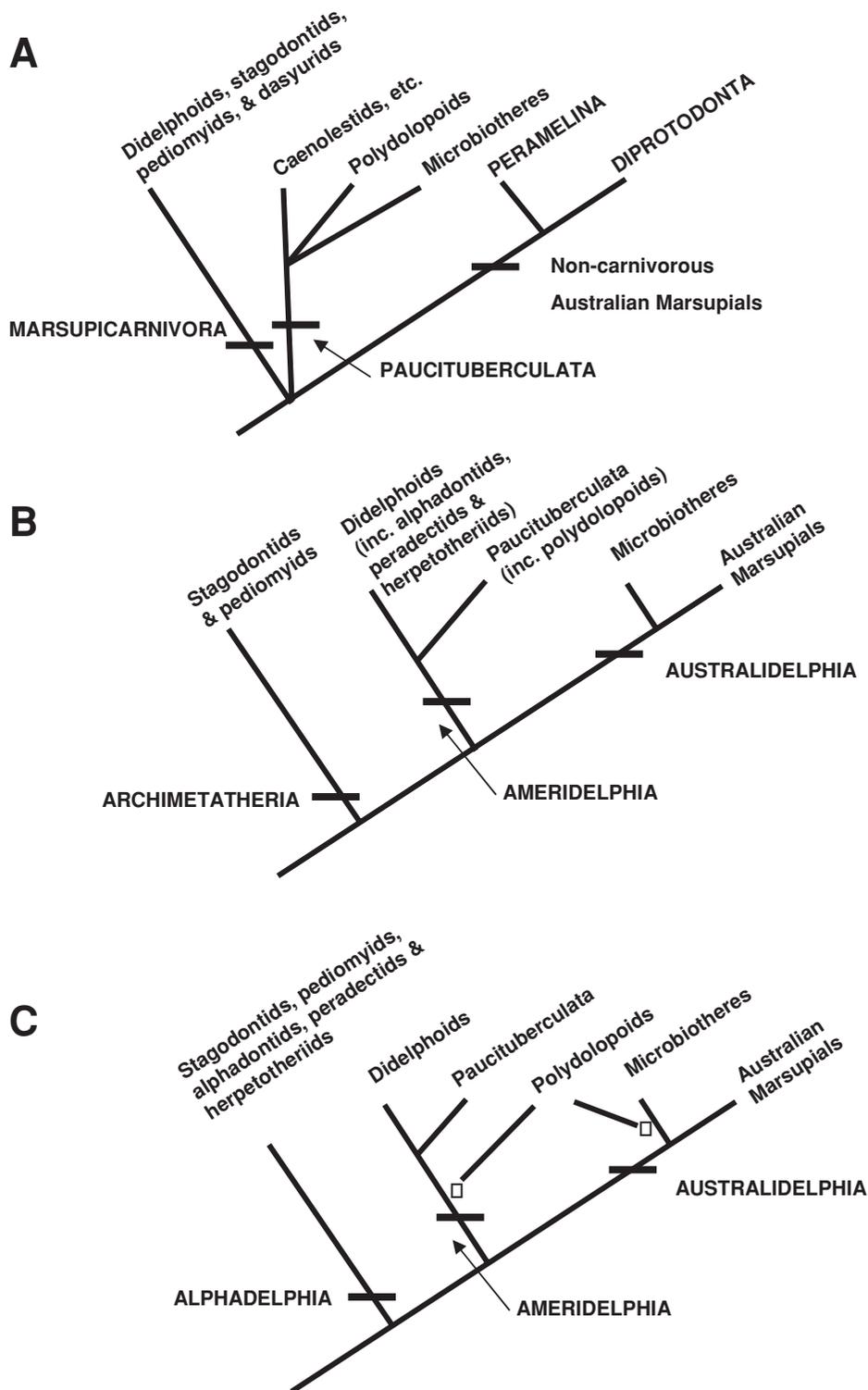


Figure 1.3. Interrelationships of major marsupial clades. A. Scheme of Ride (1964, 1970). B. Scheme of McKenna and Bell (1997). C. Scheme of Case, Goin, and Woodburne (2005).

(or were derived from taxa from that place and time) and subsequently migrated to South America. It has also been suggested that the polydolopimorphians (which are also known from Antarctica) might be related to the microbiotheres (and hence be members of the cohort Australidelphia) (Goin, 2003), which would further complicate hypotheses of marsupial dispersal and biogeography.

EVOLUTIONARY AND BIOGEOGRAPHIC PATTERNS

Non-eutherian mammals are essentially an early Tertiary radiation, with the exception of the reimmigration of the extant North American opossum, *Didelphis*, in the Pleistocene. However, there is a difference in the diversity patterns between multituberculates and

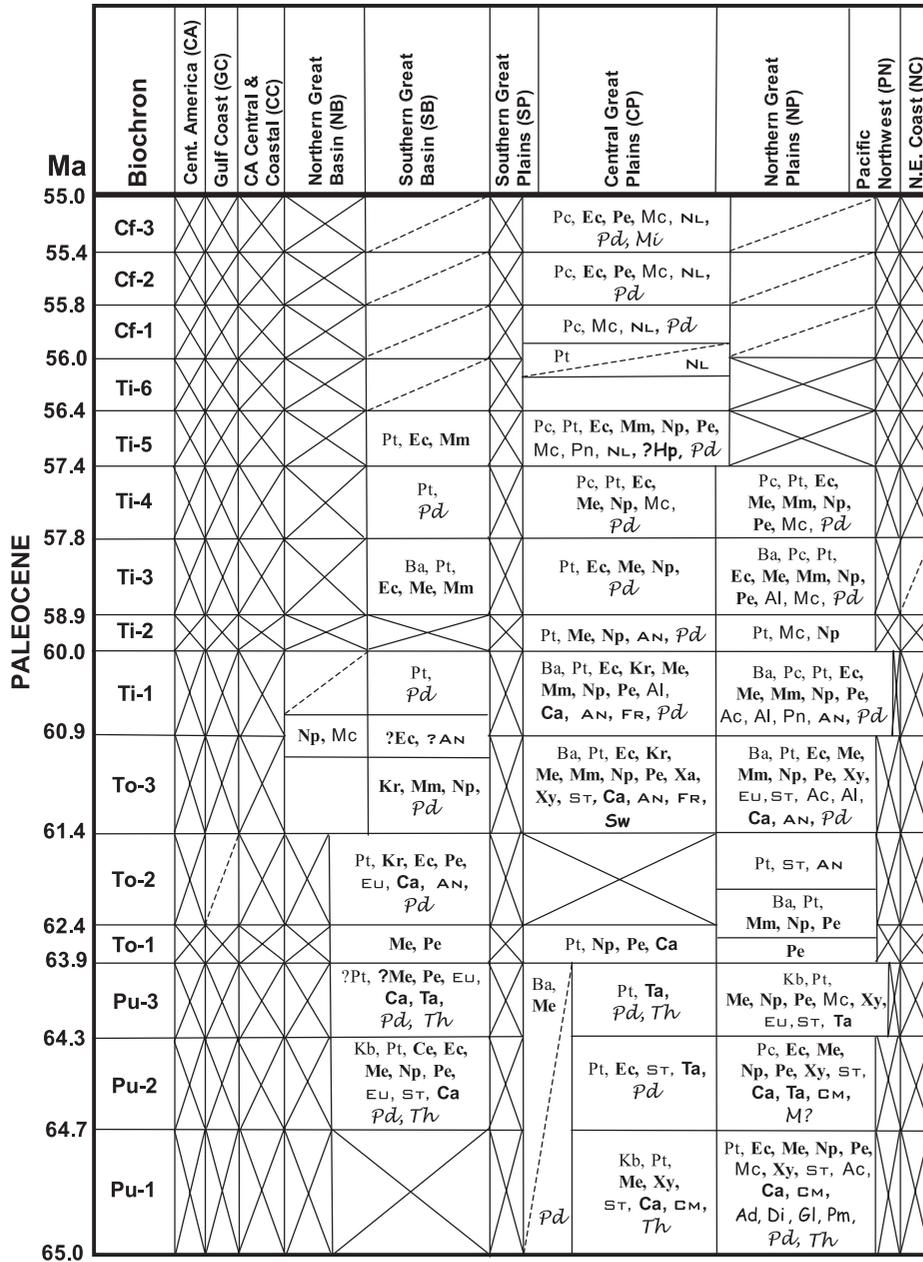


Figure 1.4. Biogeographic ranges of Paleocene multituberculates and marsupials. Key: A “box” (for a particular time period in a particular biogeographic region) that has a cross through it means no fossil mammal localities are known for that time period from that area; a single dashed line through the box means only scant fossil mammal information is available (usually only a single, small locality). MULTITUBERCULATA: PTILODONTIDAE (Times New Roman Plain): Ba, *Baiotomeus*; Kb, *Kimbetohia*; Pc, *Prochetodon*; Pt, *Ptilodus*. NEOPLAGIAULACIDAE (Times New Roman Bold): Ce, *Cernaysia*; Ec, *Ectypodus*; Kr, *Krauseia*; Me, *Mesodma*; Mm, *Mimetodon*; Np, *Neoplagiaulax*; Pe, *Parectypodus*; Xa, *Xanclomys*; Xy, *Xyronomys*. EUCOSMODONTIDAE (Bank Gothic Plain): EU, *Eucosmodon*; ST, *Stygimys*. MICROCOSMODONTIDAE (Arial Plain): AC, *Acheronodon*; Al, *Allocosmodon*; MC, *Microcosmodon*; Pn, *Pentacosmodon*. TAENIOLABIDIDAE (Arial Bold): Ca, *Catopsalis*; Ta, *Taeniolabis*. CIMOLODONTA INCERTAE SEDIS (Bank Gothic Bold): AN, *Anconodon*; CM, *Cimexomys*; FR, *Fractinus*; NL, *Neoliotomus*. MARSUPIALIA: MESOZOIC HOLDOVERS (Comic Sans MS Plain): Ad, *Alphadon*; Di, *Didelphodon*; Gl, *Glasbius*; Pm, *Pediomys*. HERPETOTHERIINAE (Comic Sans MS Bold): Sw, *Swaindelphys*. PERADECTINAE (Lucida Handwriting Bold): Mú, *Mimoperadectes*; Pd, *Peradectes*; Th, *Thylacodon*; M?, marsupial indet. (Lucida Handwriting Plain).

marsupials. Tertiary multituberculates reach their greatest diversity in the Paleocene; only three genera extend into the Eocene, and none extend past the end of the epoch. In contrast, marsupials are most diverse in the Eocene, three genera extend into the Oligocene, and there are a few occurrences in the Neogene.

PALEOCENE

The earliest Paleocene (Puercan 1) contains representatives of all of the surviving multituberculate families, and also some Mesozoic marsupial holdovers, as well as the marsupial peradectine taxa *Peradectes* and *Thylacodon*. *Thylacodon* does not persist past the

Puercan, while *Peradectes* is the longest-lived Tertiary marsupial genus, persisting until the end of the Eocene. Among the multituberculates, *Kimbetohia*, *Cernaysia*, *Taeniolabis*, and *Cimexomys*, are confined to the Puercan (Figure 1.4).

In terms of Puercan biogeographic patterns, marsupials are initially known primarily from the Northern Great Plains region, but past Puercan 1 are absent from this area, and are found in the Central Great Plains and Southern Great Basin regions. The multituberculates are more evenly distributed through these three regions, but the cimolodont incertae sedis *Cimexomys* and the neoplagiaulacid *Xyronomys* are not described from the Southern Great Basin (and both are confined to the Northern Great Plains after Puercan 1), whereas the eucosmodontid *Eucosmodon* is absent from the

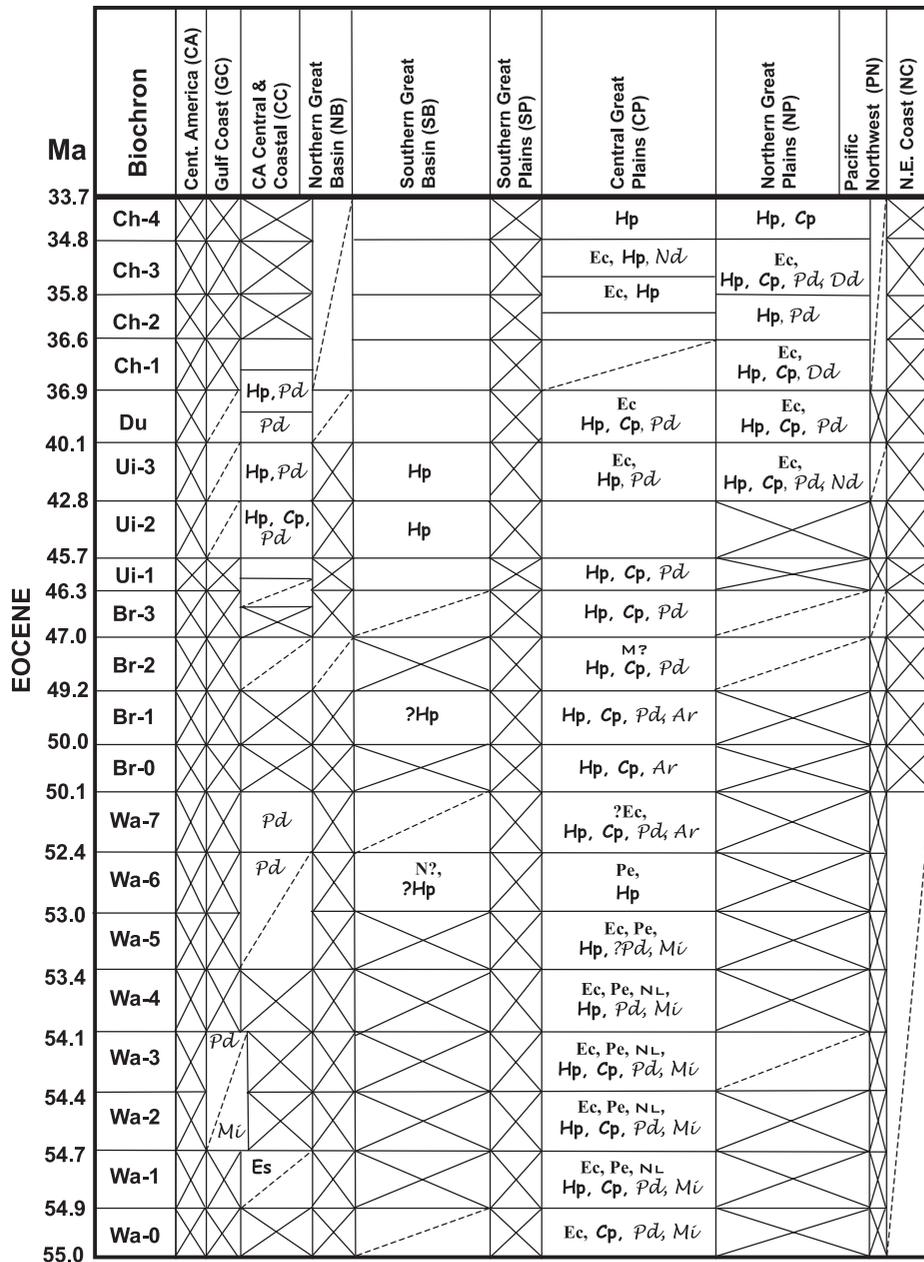


Figure 1.5. Biogeographic ranges of Eocene multituberculates and marsupials. Key as in Figure 1.4. MULTITUBERCULATA: NEOPLAGIAULACIDAE (Times New Roman Bold): **Ec**, *Ectypodus*; **N?**, neoplagiaulacid indet.; **Pe**, *Parectypodus*. CIMOLODONTA INCERTAE SEDIS (Bank Gothic Bold): **NL**, *Neoliotomus*. M?, multituberculate indet. (Times New Roman Plain). MARSUPIALIA: HERPETOTHERIINAE (Comic Sans MS Bold): **Cp**, *Copedelphys*; **Es**, *Esteslestes*; **Hp**, *Herpetotherium*. PERADECTINAE (Lucida Handwriting Bold): **Ar**, *Armintodelphys*; **Dd**, *Didelphidectes*; **Nd**, *Nanodelphys*; **Mi**, *Mimoperadectes*; **Pd**, *Peradectes*.

Central Great Plains. Several genera (*Kimbetohia*, *Stigymys*, *Catopsalis*, *Mesodma*) are known principally from the Central Great Plains in Puercan 1 but are absent from this region (although present in others) in the later Puercan. The pilodontid *Baiotomeus*, primarily a genus of the later Paleocene, is known only from an undifferentiated Puercan site in the Central Great Plains.

The marsupial *Peradectes* is briefly joined in the Torrejonian by the herpetotherine *Swaindelphys* (known only from Torrejonian 3), but otherwise marsupial diversity remains low. *Peradectes* is found throughout the known biogeographic regions in the Torrejonian, but *Swaindelphys* is known only from the Central Great Plains. Several new multituberculate genera appear in the Torrejonian: *Krauseia*, *Mimetodon*, *Xanclomys*, *Allocosmodon*, and *Fractinus*. With

the exception of *Xanclomys*, all of these taxa also range into the Tiffanian. However, several other genera go extinct at the end of the Torrejonian: *Xyronomys*, *Eucosmodon*, and *Stigymys*. *Baiotomeus*, *Xanclomys*, and *Xyronomys* are absent from the Southern Great Basin, and *Krauseia* is absent from the Northern Great Plains region.

Peradectes is the only marsupial genus known in the Tiffanian (aside from a possible occurrence of *Herpetotherium* in Ti5), and it retains a fairly cosmopolitan biogeographic distribution, although it is more rarely found in the Southern Great Basin than elsewhere. A couple of new multituberculate genera appear in the Tiffanian: *Pentacosmodon* at the start of this land mammal age (and confined to it), and *Neoliotomus* towards its end. However, the

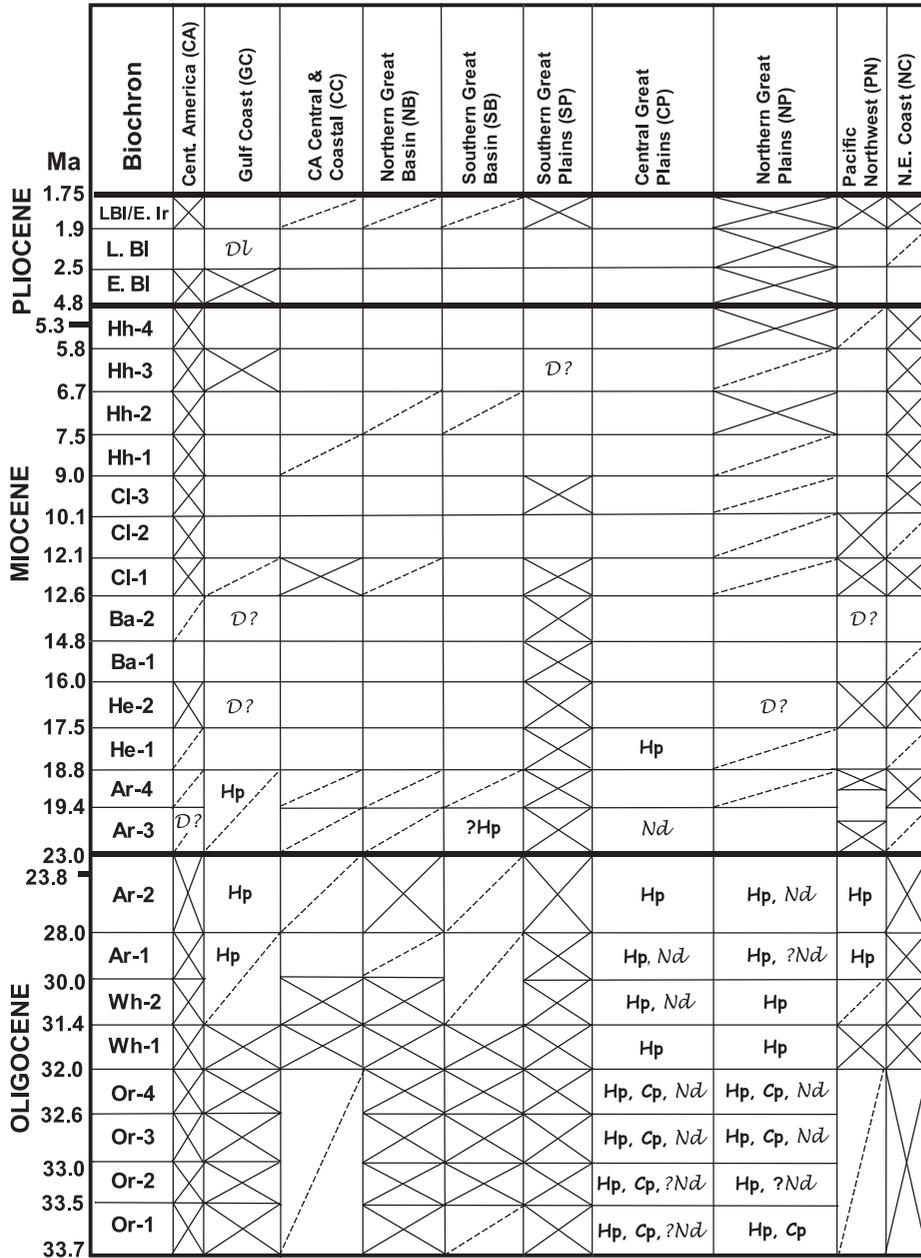


Figure 1.6. Oligocene–Pliocene marsupials: Key as in Figure 1.4. HERPETOTHERIINAE (Comic Sans MS Bold): **Cp**, *Copedelphys*; **Hp**, *Herpotherium*. PERADECTINAE (Lucida Handwriting Bold): **Nd**, *Nanodelphys*. DIDELPHINAE (Lucida Handwriting Plain): *Dl*, *Didelphis*; *D?*, didelphid indet.

majority of earlier multituberculate genera are extinct by the end of the Tiffanian, including such long-ranging and widely distributed taxa as *Ptilodus* and *Neoplagiaulax*, and all members of the families Eucosmodontidae and Taeniolabididae. In terms of Tiffanian biogeography, the microcosmodontids are absent from the Southern Great Basin, and neoplagiaulacids rare in this region. There appears to be little difference between Central Great Plains and Northern Great Plains regions, although *Mimetodon* is confined to the Northern Great Plains during the middle portion of the Tiffanian, (Ti2 to Ti4), and *Neoliotomus* is known only from the Central Great Plains.

The peradectine marsupial *Peradectes* is joined by the peradectine *Mimoperadectes* in the latest Clarkforkian. Only five multituberculate genera are known from the Clarkforkian. With the exception

of *Neoliotomus*, they are all taxa that first appeared in the Puercan (*Prochetodon*, *Ectypodus*, *Parectypodus*, and *Microcosmodon*). Two of these genera (*Prochetodon*, the last surviving ptilodontid, and *Microcosmodon*, the last surviving microcosmodontid) do not survive into the Eocene. All of these taxa are known only from the Central Great Plains during this time period, but fossil deposits from other areas are scarce.

EOCENE

Marsupial diversity increases in the early Eocene. In addition to the Paleocene peradectine survivors, *Peradectes* and *Mimoperadectes*, a number of herpotherines are known from the early Wasatchian (Wa): *Copedelphys* first appears in Wa0; *Herpotherium* makes its

first definitive appearance in Wa1; *Esteslestes* has a single appearance in the early Wasatchian of Baja California; and *Armintodelphys* appears in the late Wasatchian. Only three multituberculates are known in the Wasatchian, *Ectypodus*, *Parectypodus*, and *Neoliotomus*, and the latter two are confined to this interval. Most taxa are confined to the Central Great Plains during the Wasatchian, but, as with the Clarkforkian, fossil localities are rare in other regions. The marsupials apparently have a broader range than the multituberculates. *Peradectes* and *Mimoperadectes* are known from the early Wasatchian of the Gulf Coast region (Mississippi), *Peradectes* is known from the later Wasatchian of the California Coast region, and *Herpetotherium* is questionably known from the late middle Wasatchian of the Southern Great Basin (a questionable neoplagiaulacid multituberculate is known from the same Texas locality, SB24) (Figure 1.5).

Herpetotherium, *Copedelphys*, and *Peradectes* range through the Bridgerian, Uintan, and Duchesnean, but *Armintodelphys* is unknown after the early Bridgerian. The peradectid *Nanodelphys* makes a single appearance in the late Uintan of the Northern Great Plains (in Saskatchewan) but is otherwise unknown until the Chadronian. The only surviving multituberculate, *Ectypodus*, is absent from the fossil record during the Bridgerian and earlier Uintan but must have been present because it is known from the late Wasatchian and reappears in the late Uintan. *Herpetotherium* is known from the Southern Great Basin during the Uintan (although is absent from this region in the later Eocene), as well as from the other regions, and *Herpetotherium*, *Copedelphys*, and *Peradectes* are all known from the Gulf Coast region in the later Uintan and Duchesnean. Marsupials are strangely absent from Uintan 2 in the Central Great Plains, despite the number of fossil localities known from this region.

In the Chadronian, non-eutherian mammals are confined to the Central Great Plains and Northern Great Plains regions, despite the fact that localities are known from the Southern Great Basin during this time. The peradectine *Didelphidectes* is confined to the Chadronian of the Northern Great Plains, and the herpetotherine *Copedelphys* is also only known from the Northern Great Plains during this time. The herpetotherine *Nanodelphys* has a single appearance in Chadronian 3 of the Central Great Plains region, but is otherwise primarily an Oligocene taxon.

OLIGOCENE–PLIOCENE

No multituberculate survives past the end of the Eocene (the latest survivor is known from Chadronian 3). Three marsupial genera persist past the Eocene, although both are rarely known as fossils past the early Oligocene: the herpetotherine *Copedelphys* is confined to the Orellan, the peradectine *Nanodelphys* survives into the earliest Miocene (Ar3) and the herpetotherine *Herpetotherium* survives into the late early Miocene (He1). During the Orellan, all of these taxa are confined to the Central Great Plains and Northern Great Plains, although there are few fossil localities known from outside these regions at this time. *Herpetotherium* is more widely ranging during the Arikareean, being found in the Gulf Coast and Pacific Northwest regions during this time interval, with a possi-

ble appearance in the Southern Great Basin in Ar3, although its final (Hemingfordian) appearance is in the Central Great Plains (Figure 1.6).

Questionable occurrences of didelphids occur in the late Hemingfordian and Barstovian of Gulf Coast, Northern Great Plains, and Pacific Northwest regions. These are likely to represent surviving records of *Herpetotherium*. However, the record in the late Hemphillian of the Southern Great Plains is more problematical. Could this represent a surviving North American lineage, or an early immigrant from South America? As previously mentioned, no marsupials are known in the Old World Northern Hemisphere past the middle Miocene, and the first immigrants from South America (xenarthrans and rodents) appear in the latest Miocene. However, the first definitive record of *Didelphis* is a single Pliocene occurrence in the late Blancan of Florida, although the taxon is common in the North American Pleistocene record.

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2 Multituberculata

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INTRODUCTION

The Multituberculata are named for their unusual teeth, which have multiple molar cusps, or “tubercles,” arranged in longitudinal rows. Although now extinct, multituberculates were among the most successful of mammals by any criterion. Multituberculata is the longest-lived order within Mammalia, with a range extending from at least the Kimmeridgian (Late Jurassic) to the Chadronian (late Eocene). Multituberculates were widely distributed and are known from throughout Laurasia. Isolated teeth and tooth fragments suggest that they were also present in the Cretaceous of Africa (Sigogneau-Russell, 1991; Hahn and Hahn, 2003) and Madagascar (Krause *et al.*, 2006) and possibly from Argentina (Kielan-Jaworowska *et al.*, 2004). Multituberculates were diverse and common – so much so that they are commonly employed as stratigraphic index fossils in the Late Cretaceous and Paleocene of North America (Krause, 1982a; Savage and Russell, 1983; Lillegraven and McKenna, 1986; Sloan, 1987).

The greatest known diversity of multituberculates for any single area and time period is that of the North American middle Paleocene, but in recent years burgeoning numbers of newly described taxa from the Cretaceous of North America (Eaton, 1995; Eaton and Cifelli, 2001), and the Cretaceous of Asia (Kielan-Jaworowska and Nessov, 1992; Rougier, Novacek, and Dashzeveg, 1997) have suggested that our documentation of the group remains woefully incomplete. Where they occur in North America, multituberculates are common. They make up, on average, a little less than 50% of the individual mammals in Late Cretaceous localities, and at least 20% of the individuals in every well-sampled locality of the middle Paleocene. Multituberculates have been found in widely divergent facies and depositional systems, indicating that they were widespread across environments.

While articulated specimens are rare in North America, there is evidence that at least two Paleocene taxa were arboreal (Jenkins

and Krause, 1983), and abundant remains from the semi-arid areas of Asia have led to reconstructions of those animals as fossorial or desert adapted (Miao, 1988; Kielan-Jaworowska and Gambaryan, 1994). Most multituberculates were the size of a mouse or rat, but at least one genus, *Taeniolabis*, attained a size probably slightly larger than that of a modern-day beaver. Their dentition is specialized for herbivory, but they probably were not strictly herbivorous, and their tooth morphologies indicate a variety of dietary adaptations.

All Tertiary multituberculates belong to the derived clade Cimolodonta. Earlier, more primitive multituberculates are referred to the paraphyletic Plagiaulacida. The last known plagiaulacidans are about 100 million years old; they are not discussed here.

DEFINING FEATURES OF THE ORDER MULTITUBERCULATA (SUBORDER CIMOLODONTA)

CRANIAL

The only described, relatively complete skulls of Tertiary North American multituberculates are those of *Ptilodus* and *Taeniolabis*, studied in detail by Simpson (Simpson, 1937; see also Kielan-Jaworowska, 1971), and *Ectypodus* (briefly described by Sloan, 1979). Excellent cranial material of multituberculates is known from the Late Cretaceous and Paleocene of Asia (e.g., Kielan-Jaworowska, 1974a; Miao, 1988; Wible and Rougier, 2000) a single skull of a Cretaceous multituberculate is known from Europe (Rădulescu and Samson, 1996), and a single skull is known from the Late Cretaceous of North America (Weil and Tomida, 2001), but it is not yet fully described. Information from these other skulls, particularly the well-described Asian fossils, has been incorporated in the list of cranial features below.

The skull is dorsoventrally compressed and wide posteriorly. The snout is short (except in the European *Kogaionon*) and strongly

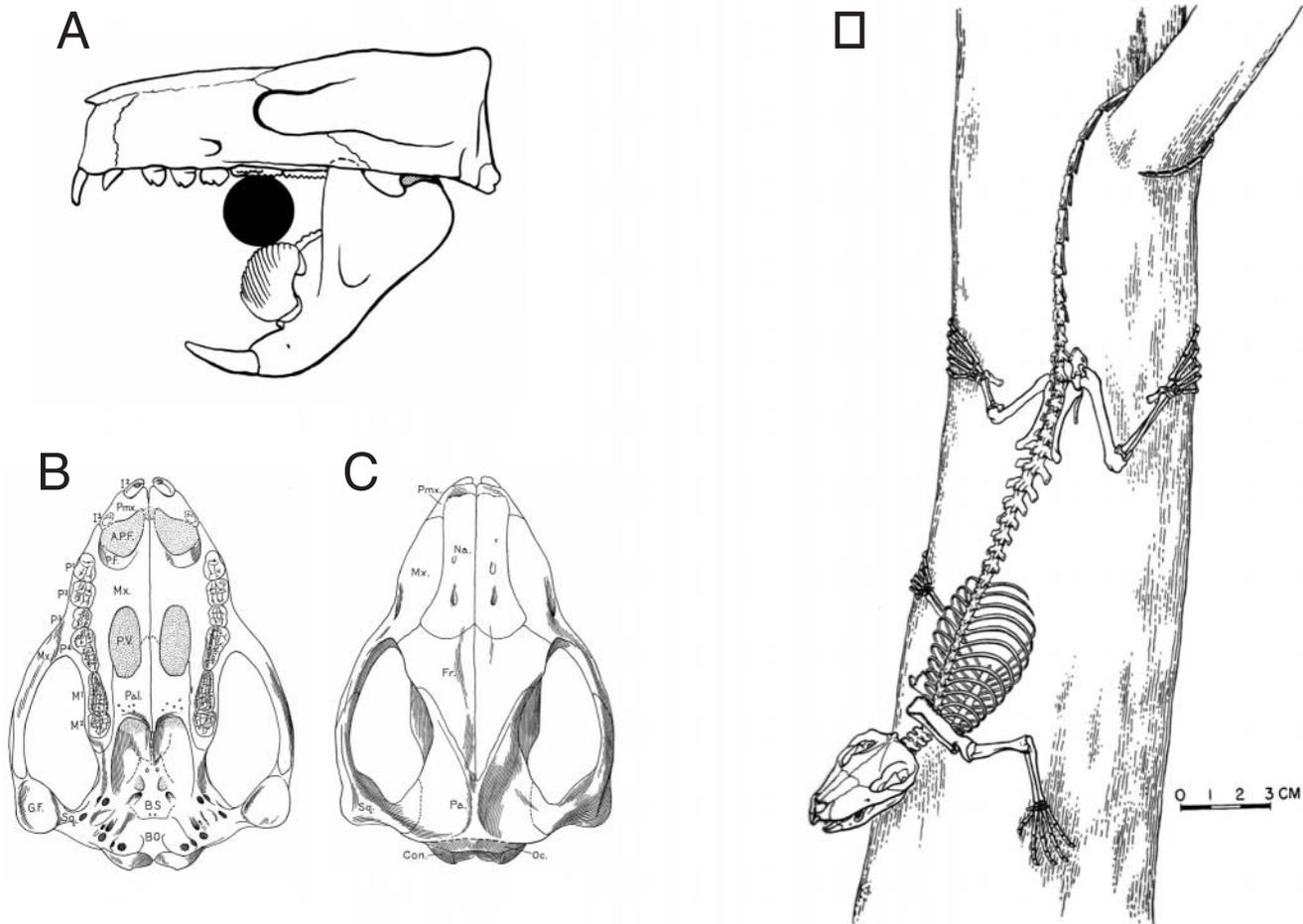


Figure 2.1. *Prilodus*. A. Lateral view of the skull, illustrating use of the p4 (modified from Wall and Krause, 1992). B. Ventral view of the skull and upper dentition (modified from Simpson, 1937). C. Dorsal view of the skull (modified from Simpson, 1937). D. Reconstruction of the skeleton (modified from Krause and Jenkins, 1983). (A: Courtesy of the Society of Vertebrate Paleontology.)

tapered anteriorly, giving the skull a triangular shape (Figure 2.1). The parietals are expanded to form the entire posterior cranial roof. Most of the lateral wall of the braincase is formed by the anterior lamina of the petrosal and the orbitosphenoid. The orbitosphenoid also forms part of the intraorbital wall, with the maxilla and frontal. In contrast to that of therian mammals, the laterally directed orbit does not have a floor but does have a roof (formed by the frontals and sometimes parietals). A postorbital process may be present or absent; an orbital pocket for pars anterior of the medial masseter (Gambaryan and Kielan-Jaworowska, 1995) is usually present anterior to the orbit (Wible and Rougier, 2000). The nasal bones are large and expanded posteriorly. The premaxilla has an extensive palatal process. Some taxa have large palatal vacuities; all have an incisive foramen. The infraorbital foramen is large and may have one or two exits. The zygomatic arch is robust. Contra Simpson (1937), a jugal is present (Hopson, Kielan-Jaworowska, and Allin, 1989). The cochlea is short, straight, and has a tiny hook at the end. The middle ear cavity is not enclosed ventrally by an ossified bulla, and three auditory ossicles are present. The auditory vestibule is large. The brain has large, anteriorly tapering olfactory bulbs (Krause and

Kielan-Jaworowska, 1993). The mandibular fossa is flat, shallow and ovoid, and it is situated lateral to the petrosal (rather than anterior to it, as in therians). The mandibular condyle is large, wide anteriorly and narrower posteriorly, and extends far inferiorly on the posterior surface of the dentary. The lower jaw consists entirely of the dentary and has a large and well-defined masseteric fossa. This masseteric fossa extends farther forward on the dentary than in any therian mammal (Gambaryan and Kielan-Jaworowska, 1995). The mandibular symphysis is unfused in smaller species but fused anteroventrally in *Taeniolabis* (Figure 2.2) and *Catopsalis*. The fossa for the medial pterygoid on medial and posteroinferior surfaces of the mandible is characteristically deep, and is bordered posteroventrally by a prominent flange that functions as an angular process (Miao, 1988).

DENTAL

The greatest number of teeth found in cimolodontan multituberculates are of the dental formula I2/1, C0/0, P4/2, M2/2; some Cenozoic taxa lose a number of premolars. The primitive

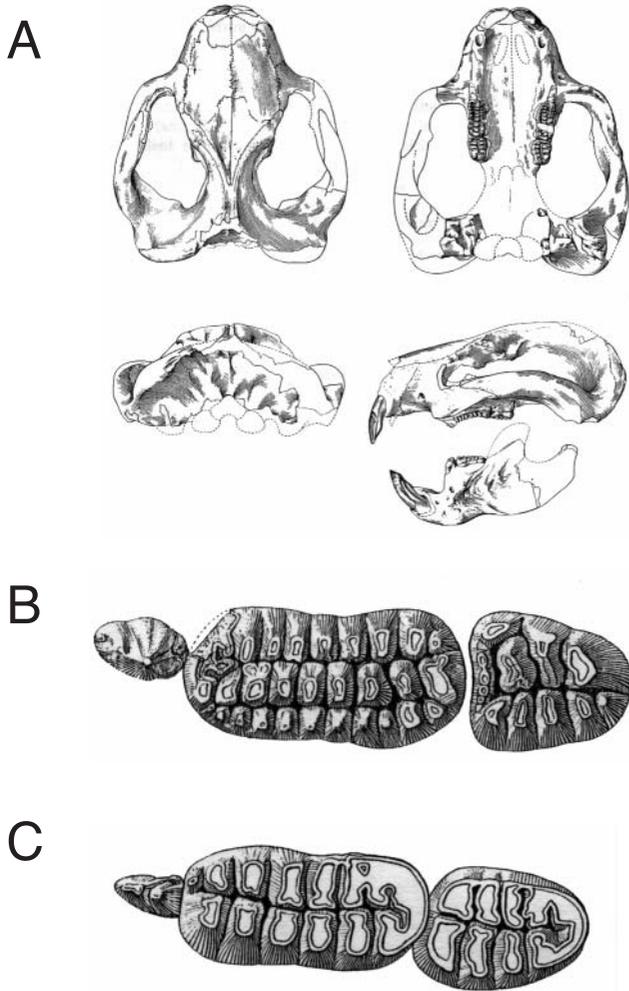


Figure 2.2. *Taeniolabis*. A. Dorsal, ventral, and posterior views of the skull, and lateral view of the skull and mandible (modified from Simpson, 1937). B. Occlusal view of upper cheek teeth (modified from Granger and Simpson, 1929). C. Occlusal view of lower cheek teeth (modified from Granger and Simpson, 1929). (Courtesy of the American Museum of Natural History.)

multituberculate dental formula of I3/1, C0/0, P4-5/3-4, M2/2 is present in Late Jurassic and Early Cretaceous taxa, but not in any Cenozoic multituberculate. The homologies of the anterior teeth of the more primitive Plagiaulacida to those of Cimolodonta are uncertain (see Kielan-Jaworowska and Hurum [2001] for discussion).

The upper central incisors (I2) may be unicuspid or bicuspid, and rarely even polycuspid. Position of the upper lateral incisor (I3) varies with the size of the incisive foramen; if the foramen is small, the I3 emerges from the anterior palate behind I2, but in taxa in which the incisive foramen is large, the I3 is situated on the palatal margin. The lower incisors are elongate, with roots extending below the roots of the second molar. Primitively the lower incisors are slender, tapered, and completely covered with enamel. Restriction of enamel to the ventrolabial surface of the lower incisor has evolved more than once within Multituberculata, however, and occurs in Tertiary North American Taeniolabidae, Eucosmodontidae, and Microcosmodontidae. There is a prominent diastema between the lower incisor

and the cheek teeth. The p3 is sometimes absent, particularly in later members of many lineages. When present it is proportionately small, single-rooted, and peg shaped, nestling under and perhaps supporting the anterior margin of the p4 crown. The p4 itself varies widely in shape and in size relative to the rest of the dentition; it may be large and bladelike with a serrate apical margin, small and rounded with cusplike serrations, or reduced to a triangular peg. The upper anterior premolars (P1-3) are small relative to P4 and usually bear two to four cusps, although the P3 has more in a few taxa. The P4 is longer than the P3 and invariably has more cusps. Multituberculates have only two upper and two lower molars. The first molars of Cenozoic taxa are always longer than the second molars, although ratios vary greatly. Molar cusps are approximately equal in height and are arranged in parallel or subparallel rows; the cusps vary in shape from conical to pyramidal to crescentic, sometimes on a single tooth. When crescentic or subcrescentic, lower molar cusps are concave posteriorly and upper molar cusps are concave anteriorly. The derived Cimolodonta is distinguished in part by the presence of three cusp rows on the upper molars. The derived or "added" row is the most lingual on the M1, and it may run the length of the tooth or be present only on the posterior portion. On the M2, the third row occurs anterolabially (Figure 2.3).

Primitively, molar wear occurs along the sides of the cusp rows, deepening and widening the valleys between cusps. Some groups, however, notably the Taeniolabidae, have bulbous cusps on which only the tips wear, creating enamel cross-lophs similar to those of some rodents. As in rodents, the length of the upper dentition (measured from incisor tip to the posterior end of the second molar) is greater than that of the lower dentition. Diphodonty has been demonstrated for lower incisors and some anterior upper premolars (e.g., Szalay, 1965), and Greenwald (1988) described a six-stage sequence of dental ontogeny. The permanent incisors erupt posterior

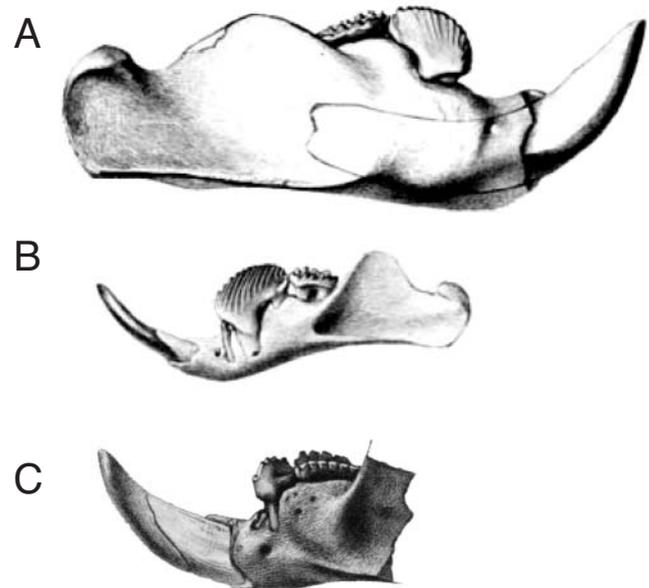


Figure 2.3. Mandibles of Paleocene multituberculates (modified from Jepsen, 1940). A. *Stygimys kuszmauli*. B. *Mesodma ambigua*. C. *Microcosmodon conus*. (Courtesy of the American Philosophical Society.)

to the deciduous incisors, and in the Paleocene Asian *Lambdopsalis* (the only cimolodontan for which an extensive growth series has been recovered), the distribution and color of enamel on the permanent lower incisor differ from those of the deciduous incisor (Miao, 1986). The p3 may be lost during ontogeny in some species (Weil, 1998), but it is not known whether it is mono- or diphodont. The upper and lower fourth premolars are monophodont (Clemens and Kielan-Jaworowska, 1979; Sloan, 1979; Miao, 1986) and are probably homologous to dP4/4 of diphodont plagiulacoids (Greenwald, 1988). The second molars erupt after the first molars, and in *Lambdopsalis* the lower molars move anteriorly with increasing age (Miao, 1986). Tooth enamel may have large, arcuate prisms, small circular prisms, or small prisms with a mixture of arcuate and circular prisms (Carlson and Krause, 1985; Krause and Carlson, 1986); large prisms appear to be primitive, and smaller prisms may have evolved more than once (Krause and Carlson, 1987).

POSTCRANIAL

The postcranium of Tertiary North American multituberculates is represented by only three incomplete specimens, two of *Ptilodus* and one questionably referred to *Eucosmodon* (or perhaps *Catopsalis*; see Williamson and Lucas, 1993). Additional isolated elements from Tertiary sediments have been attributed to *Ectypodus*, *Stygmymys*, *Taeniolabis* (Krause and Jenkins, 1983), and *Catopsalis* (Middleton, 1982). Detailed study of Late Cretaceous multituberculates of Asia has provided a wider perspective of morphological diversity within Cimolodonta and is incorporated here.

The scapulocoracoid has a shallow glenoid and a reduced coracoid and lacks a supraspinous fossa; the scapular spine lies along the anterior margin. A triangular interclavicle is present between the clavicles and the manubrium sternum (Serenio and McKenna, 1995). The sternbrae are ossified. The humerus has a large, hemispherical head, a well-developed deltopectoral crest, a large and spherical radial condyle, an elongate ulnar condyle, and an entepicondylar foramen. The humerus and the radius/ulna are about equal in length. The ulna has a laterally compressed olecranon, a prominent crest separating articular surfaces for the ulnar and radial condyles of the humerus, a prominent anconeal process, and a radial notch that is large and oval. The radius has an elliptical head, bearing a well-developed, strap-shaped (Krause and Jenkins, 1983) or semilunar (Kielan-Jaworowska and Gambaryan, 1994) facet for articulation with the ulna. Both manus and pes have five digits. The single described manus (Krause and Jenkins, 1983) has a divergent pollex, an enlarged and elongate prepollex, and recurved distal phalanges bearing well-developed extensor processes and flexor tubercles.

The pelvis has a long, rodlike ilium, dorsally emarginate acetabulum, keel-like ischiopubic symphysis with a narrow and V-shaped pelvic outlet, postoburator foramen within the ischiopubic symphysis, and epipubic bones. The femur has a robust greater trochanter, a small and narrow digital fossa, and a ventrally projecting and bulbous lesser trochanter. A patella is present. The tibia has a large, flat facet on the posterolateral margin of the head for articulation with the fibula, a deep excavation posteriorly beneath the proxi-

mal articular surface, a prominent medial malleolus, and a distal articular surface bearing an oval medial condyle and a spiral lateral condyle for articulation with the astragalus. The fibula is not fused to the tibia and has a long, slender reflected process arising from the posterolateral margin of the head and projecting distally. A large parafibula is present. The calcaneum has a robust, laterally compressed tuber calcanei, a bulbous astragalocalcaneal facet, a flat sustentacular facet, a deep peroneal groove, and a prominent peroneal tubercle. The astragalus has two shallow, concave facets for articulation with distal condyles of the tibia and a concave and anteroposteriorly elongate calcaneoastragalal facet. The pedal distal phalanges are similar to those of the manus, but more elongate.

There are seven cervical vertebrae, with dorsoventrally compressed centra and cervical ribs present on C3–C7; C7 has a transverse foramen (Kielan-Jaworowska and Gambaryan, 1994). The thoracic vertebral centra have their anterior epiphyseal surfaces recessed ventrally and bulbous dorsally. The lumbar vertebrae have centra that are dorsoventrally compressed; they lack anapophyses; and they possess well-developed spinous and transverse processes. There are four sacral vertebrae, with high spinous processes. The tail is long and the caudal vertebrae stout, with well-developed haemal spines and transverse processes.

SYSTEMATICS

SUPRAORDINAL

See the discussion in Chapter 1, the non-eutherian summary chapter.

SUBORDINAL

Relationships among the multituberculates are no more certain than those of multituberculates to other mammals (Figure 2.4). Within the last few years, the group has been the focus of many phylogenetic studies (Simmons, 1993; Kielan-Jaworowska and Hurum, 1997; Rougier, Novacek, and Dashzeveg, 1997; Weil, 1999; Wible and Rougier, 2000; Kielan-Jaworowska and Hurum, 2001) and has undergone repeated systematic revision (McKenna and Bell, 1997; Fox, 1999; Kielan-Jaworowska and Hurum, 2001). Because so many taxa are known only from isolated teeth, phylogenetic efforts focusing on North American taxa have produced little resolution. Perhaps the only thing that these authors agree on is that all multituberculates of Tertiary North America belong to the derived clade Cimolodonta. Cimolodontans are distinguished by a reduced number of lower premolars to a maximum of two, and by development of a third cusp row on the upper molars (Figure 2.2).

Cimolodonta was long divided into two suborders, the Taeniolabidoidea and Ptilodontoidea, differentiated by lower incisor structure; taeniolabidoids had enamel restricted to the ventrolabial surface, which produced a chisel-like cutting tip, as in rodents, while ptilodontoids had a long, slender, tapered incisor fully coated with enamel. As a result of both intense interest in multituberculate phylogeny and many fossil discoveries, it is recognized that

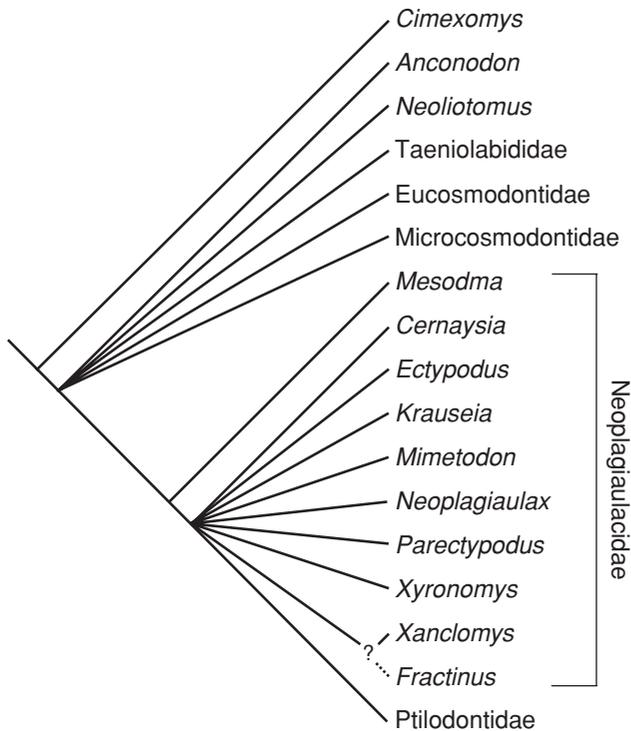


Figure 2.4. Highly hypothetical interrelationships of the Cenozoic multituberculate taxa. This tree represents a “best guess” rather than a strict phylogenetic analysis. Because many of the taxa are incomplete, limited mostly to isolated teeth or mandibles, the Cenozoic Multituberculata is not amenable to phylogenetic analyses, which can produce hundreds of thousands of shortest trees. Some genera may not be monophyletic.

this convenient division was an artifact of limited information that is disappearing as we learn more. In particular, we now recognize that restricted enamel evolved more than once within Multituberculata, including at least once in non-cimolodontan multituberculates (Engelmann and Callison, 1999) and in an endemic Asian superfamily, Djadochtheroidea (Kielan-Jaworowska and Hurum, 1997; Rougier, Novacek, and Dashzeveg, 1997). Also, many of the trees resulting from phylogenetic studies show Ptilodontoidea (sensu Hahn and Hahn, 1983) to be paraphyletic, polyphyletic, or both. The volume and pace of recent and ongoing work on multituberculates is high, as demonstrated by three substantial systematic revisions in five years. Higher-order relationships seem likely to remain unstable for some time to come. We, therefore, present multituberculate families without suprafamilial groupings and refrain from making formal revisions here.

PTILODONTIDAE

Ptilodontid multituberculates were among the first North American Paleocene mammals to be described (Cope, 1881). The family was first diagnosed in 1928 by Simpson, although the name had been listed without definition in at least two earlier works. The number of genera included within the family has varied greatly since its diagnosis and, at one time or another, included genera now assigned

to the families Eucosmodontidae, Cimolodontidae, Cimolomyidae, and Neoplagiaulacidae. Sloan and Van Valen (1965) considerably restricted the generic content of the family to include only *Ptilodus*, *Prochetodon*, *Kimbetohia*, *Essonodon*, *Cimolodon*, *Anconodon*, and *Liotomus*. The latter three genera were placed in the resurrected family Cimolodontidae by Sloan (in Van Valen and Sloan, 1966; their Fig. 2.4) and *Essonodon* was questionably allied with the Cimolomyidae by Archibald (1982). This left only *Ptilodus*, *Prochetodon*, and *Kimbetohia* until the addition of *Baiotomeus* (Krause, 1987b). McKenna and Bell (1997) considered the taxon to be of subfamilial rank, but Kielan-Jaworowska and Hurum (2001) restored it to familial rank.

NEOPLAGIAULACIDAE

Isolated teeth of neoplagiaulacids are among the most difficult to assign to lower taxa among Cenozoic multituberculates. The p4 is the easiest tooth to identify, but even in this case the purportedly diagnostic features are very subtle. There has been little attempt to define the genera on the basis of shared, derived characters, which renders phylogenetic analyses at the generic level (e.g., Simmons, 1993; Rougier, Novacek, and Dashzeveg, 1997) unreliable with respect to these taxa. Systematics of neoplagiaulacid species have been particularly dependent on typological definitions; the family remains in need of revision, with careful attention to both quantitative and qualitative morphological variability.

The generic content of the Neoplagiaulacidae was initially the result of work by R. E. Sloan. Sloan and Van Valen (1965) erected the family Ectypodidae, which was emended to Ectypodontidae by Van Valen and Sloan (1966) and was later replaced by the senior synonym Neoplagiaulacidae Ameghino, 1890 (see Clemens, 1973a, p. 77). Hahn and Hahn (1983) argued that the name Neoplagiaulacidae is a nomen oblitum, but it remains in use because of its general acceptance. The Neoplagiaulacidae initially included *Cimexomys*, *Ectypodus*, *Mesodma*, *Mimetodon*, *Neoplagiaulax*, and *Parectypodus*. To this list has been added *Xanclomys* (see Rigby, 1980) and *Xyronomys* (originally assigned to the Eucosmodontidae by Rigby [1980] but allied with the Neoplagiaulacidae by Johnston and Fox [1984] and Sloan [1987]). *Cimexomys* was recognized as more primitive and removed (Archibald, 1982). Vianey-Liaud (1986) made several reassignments within Neoplagiaulacidae, notably assignment of the species *Anconodon russelli*, *Parectypodus vanvaleni*, and probably *Parectypodus sinclairi* to the genus *Liotomus*; assignment of the species *Parectypodus clemensi* to the new genus *Krauseia*; and transfer of the P4 of *Parectypodus vanvaleni* to the new species *Cernaysia davidi*. While we regard these assignments as questionable, they have been adopted by some subsequent authors. McKenna and Bell (1997) revised the Neoplagiaulacidae to subfamily rank within Ptilodontidae and included the North American genera *Mesodma*, *Parectypodus*, *Ectypodus*, *Neoplagiaulax*, *Cernaysia*, *Krauseia*, *Xyronomys*, *Xanclomys*, *Ectypodus*, and *Mimetodon*, in addition to the Asian *Mesodmops*. Kielan-Jaworowska and Hurum (2001) did not examine relationships within Ptilodontoidea sensu McKenna and Bell (1997), and repeated this list.

EUCOSMODONTIDAE

The Eucosmodontinae was named by Jepsen (1940) as a subfamily of the Ptilodontidae but was elevated to familial rank within Taeniolabidoidea by Sloan and Van Valen (1965). The subfamilial name Eucosmodontinae was resurrected when Holtzman and Wolberg (1977) named a new subfamily, the Microcosmodontinae. Non-microcosmodontine eucosmodontids were placed in the Eucosmodontinae. More recently, Fox (1999) elevated Microcosmodontinae to familial rank, thus removing it from the Eucosmodontidae. He also removed the Eucosmodontidae from Taeniolabidoidea, a scheme that has been followed by Kielan-Jaworowska and Hurum (2001).

MICROCOSMODONTIDAE

Microcosmodon and *Pentacosmodon* were first recognized as differing substantially from other eucosmodontids by Holtzman and Wolberg (1977), who placed them in the subfamily Microcosmodontinae. *Acheronodon* was later described and recognized to be closely related by Archibald (1982). One result of Simmons' (1993) phylogenetic analysis was the assignment of *Pentacosmodon* and *Microcosmodon* to widely different clades, although they vary in only a single scored character. Following Simmons, McKenna and Bell (1997) placed *Pentacosmodon* in the otherwise Asian Chulsanbaatarinae, while retaining *Microcosmodon* and *Acheronodon* in the Microcosmodontinae. Weil (1998) reinstated *Pentacosmodon* in the monophyletic Microcosmodontinae, and Fox (1999, 2005) elevated the group to familial rank, removing it from the Eucosmodontidae. Fox (2005) made a differential diagnosis with the benefit of relatively complete specimens, and also named a fourth genus, *Allocosmodon*, to the family.

TAENIOLABIDIDAE

Taeniolabidids include the largest multituberculates known and are characterized by a highly derived dentition. The first taeniolabidids to be described were placed in the family Plagiaulacidae until Cope (1884a) named the Polymastodontidae. As reviewed by Hahn and Hahn (1983), the family name was changed to Taeniolabididae when it was recognized that the type genus *Polymastodon* Cope (1882b) was synonymous with *Taeniolabis* (Cope, 1882a). Again following Simmons (1993), McKenna and Bell (1997) included the genera *Buginbaatar*, *Meniscoessus*, *Prionessus*, *Lambdopsalis*, and *Sphenopsalis* in Taeniolabididae. More recent phylogenetic analyses (Kielan-Jaworowska and Hurum, 1997; Rougier, Novacek, and Dashzeveg, 1997) showed that *Buginbaatar* is not closely related to North American taeniolabidids, and Kielan-Jaworowska and Hurum (2001) tentatively removed it to Cimolomyidae. *Meniscoessus* is a cimolomyid, and McKenna and Bell's (1997) reassignment has not been accepted (Weil, 1999; Kielan-Jaworowska and Hurum, 2001). The major recent reclassifications of Multituberculata (McKenna and Bell, 1997; Kielan-Jaworowska and Hurum, 2001) have omitted the genus *Bubodens*, described by Wilson (1987) from the Late Cretaceous of South Dakota and placed by him in Multituberculata suborder and family incertae sedis. This taxon, represented thus far

by only a single tooth, is almost certainly a taeniolabidid, and in several respects is more derived than Paleocene genera (Weil and Clemens, unpublished data).

INCLUDED GENERA OF MULTITUBERCULATA COPE, 1884b

The locality numbers listed for each genus refer to the list of unified localities in Appendix I. The locality numbers may be listed more than one way. The acronyms for museum collections are listed in Appendix III.

Brackets around a locality (e.g., [CP101]) mean that the taxon in question at that locality is cited as an "aff." or "cf." the taxon in question. Parentheses are usually used for individual species, implying that the genus is firmly known from the locality, but the actual species identification may be questionable. Question marks in front of the locality (e.g., ?CP101) mean that the taxon is questionably known from that locality, implying some doubt that the taxon is actually present at that locality, either at the genus or species level. An asterisk (*) indicates the type locality.

PTILODONTIDAE SIMPSON, 1928 (INCLUDING CHIROGIDAE COPE, 1887; ECTYPODIDAE SLOAN AND VAN VALEN, 1965; AND ECTYPODONTIDAE SLOAN AND VAN VALEN, 1965)

Characteristics (modified from Krause, 1982b): Larger than most Neoplagiaulacidae and Cimolodontidae. Further differ from neoplagiaulacids and cimolodontids in presence of anterolabial bulge on P4 (this bulge may bear cusps, but usually does not); in having essentially straight ventral margin of P4 in lateral profile (the middle row of cusps is not elevated posteriorly as in many similar taxa); in having relatively large p4 (ratio between lengths of p4 and m1 is usually approximately 2.0 but ranges from 1.7 to 2.4).

Baiotomeus Krause, 1987a

Type species: *Baiotomeus douglassi* (Simpson, 1935) (originally described as *?Ptilodous douglassi*).

Type specimen: USNM 9795, right dentary with p4–m2 from the late Torrejonian of Montana.

Characteristics (from Krause, 1987a): Small genus of Ptilodontidae, equivalent in size to *Kimbetohia* and some species of *Ptilodus*, but much smaller than *Prochetodon*. Differs from *Kimbetohia* in having much narrower P4 with relatively small anterolabial bulge; p4 with higher first serration but lacking ventral bifurcations on labial ridges. Differs from *Ptilodus* in having relatively poorly developed anterolabial bulge but well-developed labial row of prominent cusps on P4. Differs from both *Ptilodus* and *Prochetodon* in having relatively low p4 that variably bears incipient serrations on anterior apical margin; in having prominent and angular anterolabial lobe on p4; in having m1 that is relatively longer compared with the length of

either p4. In addition, m1 appears to be relatively longer than m2 in *Baiotomeus* in comparison with *Ptilodus* and relatively shorter in comparison with *Prochetodon*.

Average length of p4: 6.36 mm.

Average length of m1: 3.80 mm.

Included species: *B. douglassi* (known from localities SB39B, CP13B, CP14A, NP19C*); *B. lamberti* Krause, 1987a (localities CP13IIA, B, NP20A*); *B. rhothonion* Scott, 2003 (localities NP1B, NP3A0*); *B. russelli* Scott, Fox, and Youzwshyn, 2002 (locality NP1C*).

Baiotomeus sp. is also known from localities CP13A, CP14B, NP2, NP3B, G.

***Kimbetohia* Simpson, 1936a**

Type species: *Kimbetohia campi* Simpson, 1936a.

Type specimen: UCMP 31305, fragmentary maxilla with broken P1, P2–P4 from the Puercan of New Mexico.

Characteristics (from Krause, 1982b): Small genus of ptilodontids, equivalent in size to *Baiotomeus* and some species of *Ptilodus*, but much smaller than *Prochetodon*. Differs from *Baiotomeus* in having much wider P4 with a well-developed anterolabial bulge; p4 with lower first serration and ventral bifurcations on some of the labial ridges; plane of occlusal surfaces of upper premolars of *Kimbetohia* forming dorsally concave arc in side view; in *Ptilodus* and *Prochetodon*, occlusal surfaces forming nearly straight line. Differs from *Ptilodus* and *Prochetodon* in having only three cusps (one labially and two lingually) and one root on P2 (*Prochetodon* occasionally has only three cusps on P2, but they are arranged in a different pattern with two labially and one lingually); relatively wide P4; p4 with relatively low crown and straight posterior slope; bifurcations on one to three of the labial ridges descending from serrations six to nine; relatively low first serration.

Average length of p4: 6.08 mm.

Average length of m1: unknown.

Included species: *K. campi* (known from locality SB23A*); *K. ? mziae* Middleton and Dewar, 2004 (locality CP61A*); *K. n. sp.* of Van Valen and Sloan (1966) (locality NP16C).

Comments: Krause (1992) removed specimens from the Late Cretaceous Lance Formation from *Kimbetohia campi* and erected a new genus and species, *Clemensodon megaloba*. It is questionable whether *Kimbetohia* occurs at all in the Late Cretaceous; although specimens have been mentioned (Clemens, 1973b), none have been described (Krause, 1992).

***Prochetodon* Jepsen, 1940**

Type species: *Prochetodon cavus* Jepsen, 1940.

Type specimen: YPM-PU 13925, right dentary with base of i1, p3, and fragmentary p4 from the Tiffanian of Wyoming.

Characteristics (from Krause, 1987b): Large ptilodontids, much larger than *Kimbetohia* and *Baiotomeus* but equivalent in size to some species of *Ptilodus*. Differ from *Kim-*

betohia, *Baiotomeus*, and *Ptilodus* in possession of lenticular, rather than conical, cusps labially on P1–3; arcuate arrangement of anterior and labial cusps on P2 (condition unknown in *Baiotomeus*); presence of eight to nine cusps on P3; relatively long and narrow P4 with persistent absence of cusps on anterolabial bulge; p4 with broad, flat anterior face, reduced anterolabial lobe, posteriorly canted shape in lateral view; presence of shallow vertical grooves labially on labial cusps of m1.

Average length of p4: 7.83 mm.

Average length of m1: 3.74 mm.

Included species: *P. cavus* (known from localities CP13F, G*); *P. foxi* Krause, 1987b (localities CP13F*, CP15B, [NP3C], NP7D, NP47B2); *P. speirsae* Scott, 2004 (localities NP1C*, NP3A, B, D); *P. taxus* Krause, 1987b (localities CP13H*, CP17A, B).

Prochetodon sp. is also known from localities? CP24B, NP3C, F, NP4, NP7C.

***Ptilodus* Cope, 1881 (including *Chirox* Cope, 1884b)**

Type species: *Ptilodus mediaevus* Cope, 1881.

Type specimen: AMNH 3019, isolated p4 from the ?Torrejonian of the San Juan Basin of New Mexico.

Characteristics (from Krause, 1982b): Differs from *Kimbetohia* in having four cusps and two roots on P2; relatively narrow P4; and p4 with relatively high crown and arched posterior slope; no bifurcations on labial ridges relatively high first serration. Differs from *Baiotomeus* in having well-developed anterolabial bulge on p4; relatively high-crowned p4 with a less angular anterolabial lobe almost never bearing pseudoserrations; an m1 that is short relative to the lengths of p4 and m2. Differs from *Prochetodon* in having conical rather than lenticular cusps on the labial sides of P1–3; cusps of P2 arranged in two longitudinal pairs; fewer cusps on P3 (there are a few instances of eight cusps on P3 of *Ptilodus*, however); relatively short and broad P4 with cusps occasionally present on anterolabial bulge; p4 with transversely rounded anterior margin, large anterolabial lobe, an uncanted lateral profile; m1 without grooved labial side of cusps in labial view.

Average length of p4: 6.99 mm.

Average length of m1: 3.38 mm.

Included species: *P. mediaevus* (known from localities SB23E*, SB39A-C, CP1C, CP13IIA, CP14A); *P. fractus* Dorr, 1952 (localities CP22B, CP26A); *P. gnomus* Scott, Fox, and Youzwshyn, 2002 (localities CP13IIA, CP16A, NP1C*, NP3A0); *P. kummae* Krause, 1977 (localities SB20A, CP13E, F, CP13IIA, CP14C, CP15B, CP24A, NP3F, NP7D*, NP47C, NP48B); *P. montanus* Douglass, 1908 (localities CP11IIA, [CP21A], [CP22A], NP3A0, NP19B, C*, NP20D, NP47B); *P. tsosiensis* Sloan, 1981 (localities SB23A*, [CP1A], [CP11IIA, G], [NP7B], NP16C); *P. wyomingensis* Jepsen, 1940 (localities CP13B, NP47B2, C); *Ptilodus* sp. “C” Krause 1982b (localities CP13E, EE, CP13IIA, CP16A, CP21B, CP22A, CP26A,

NP1C, NP3A, NP4, NP19IIC, NP20C, D, NP47A1, B, B2); *Ptilodus* sp. "T" Krause 1982b (localities CP13IIA, NP1C, NP3A, C, G, NP19IIA).

Ptilodus sp. is also known from localities SB39IIA, ?CPIC, CP11IIG, CP13C, D, CP15A, CP62A2, NP1C, NP2, NP3[A0, A], B–D, G, NP19IIA, C, NP20B, E, NP47C.

Indeterminate ptilodontids

Fossil material referred to Ptilodontidae has also been reported from localities SB23GG, CP22B, and CP26A.

NEOPLAGIAULACIDAE AMEGHINO, 1890

Characteristics (modified from Sloan and Van Valen [1965], Hahn and Hahn [1983], and Vianey-Liaud [1986]): Generally small; I1 pointed, gracile, and covered with enamel; tendency for labial cusp row of P4 to be reduced, but rarely altogether absent; lateral profile of P4 usually close to an isosceles triangle with the posterior edge shorter; p4 usually 1.4 to 2.0 times length of m1; lateral profile of p4 arcuate, anterior portion of profile curved, and highest point on profile occurring at midlength, above line of cusps of m1 and m2; first labial ridge of p4 begins at first serration; second through fifth ridges abut the first at an angle.

Cernaysia Vianey-Liaud, 1986 (including *Parectypodus*, in part)

Type species: *Cernaysia manueli* Vianey-Liaud, 1986.

Type specimen: CRL 897, right P4 from the late Paleocene (Cernaysian) of France.

Characteristics (modified from Vianey-Liaud, 1986): P4 low and compact; ultimate cusp highest; cusps of labial row well developed; posterobasal concavity and cingulum present; wear surface horizontal.

Average length of p4: not known for *C. davidi*.

Average length of m1: not known for *C. davidi*.

Included species: *C. davidi* (including *Parectypodus vanvaleni* Sloan 1981 in part) only; known from locality SB23A* only.

Comments: The type species, *C. manueli*, is known only from the late Paleocene of Europe. The formal diagnosis of *Cernaysia* does not effectively distinguish it from other neoplagiulacids and does not accurately encompass specimens referred to *C. davidi*. Nevertheless, validity of the taxon has not been formally challenged, and recent systematic revisions of Multituberculata (McKenna and Bell, 1997; Kielan-Jaworowska and Hurum, 2001) included it as a valid taxon.

Ectypodus Matthew and Granger, 1921 (including *Charlesmooria* Kühne, 1969)

Type species: *Ectypodus musculus* Matthew and Granger, 1921.

Type specimen: AMNH 17373, maxilla from the Tiffanian of the San Juan Basin of Colorado.

Characteristics (modified from Sloan, 1981): Ultimate cusp in lingual row of P4 highest on crown; P4 very trenchant with both anterior and posterior slopes straight in profile; posterior basal cuspule usually weak or absent. Early species have p3; crown of p4 relatively low, fourth serration highest; relative height of first serration between one-third and one-half length of p4; height of enamel at anterolabial lobe of p4 less than crown length; posterior angle between plane of occlusion of molars and anterior face of p4 approximately a right angle.

Average length of p4: 3.22 mm.

Average length of m1: 1.90 mm.

Included species: *E. musculus* (known from localities SB20A*, SB39B, C, [CP16A]); *E. aphronorus* Sloan, 1987 (localities CP13B, CP15A, NP19C*); *E. childei* (Kuehne, 1969; originally described as *Charlesmooria childei*) (European, but may occur in localities CP27D, CP63); *E. elaphus* Scott, 2005 (localities NP3B, C*, D); *E. lovei* Sloan, 1966 (localities CP29C, D, CP39B, CP44, CP98B, NP8, NP9A, B, NP10B, Bi, NP23A, NP49II); *E. powelli* Jepsen, 1940 (localities CP13[E], G*, H, [CP14C, E], CP17B, CP21A, CP22B, [CP24A], CP26A, [NP3B], [NP7D], [NP19IIC], [NP20E]); *E. szalayi* Sloan, 1981 (localities SB23F, CP13IIA, CP14A, [NP1C], [NP3A0], NP19C*); *E. tardus* Jepsen, 1930a (localities CP15B, CP19AA–C, CP20A, BB, [CP27A], CP63).

Ectypodus sp. is also known from localities ?SB23H, CP11IIE, CP44, NP3C, G, NP7B, NP17, NP20D, NP47B.

Comments: *Ectypodus* is also known from the late Paleocene to early Eocene of Europe.

Krauseia Vianey-Liaud, 1986 (including *Parectypodus*, in part; *Ectypodus*, in part)

Type species: *Krauseia clemensi* (Sloan, 1981) (originally described as *Parectypodus clemensi*).

Type specimen: KU 16001, crushed rostrum with P1–M2, right dentary with broken i1, p3–m1, and fragmentary left dentary from the Puercan of New Mexico.

Characteristics (modified from Vianey-Liaud, 1986): P4 large; lingual side very steep and labial side vertical to labially inclined; ultimate cusp highest; posterior edge abrupt but more inclined than that of *Ectypodus*, bearing slight posterobasal cingulum; mandible shorter and thicker than that of *Mimetodon*, with raised horizontal ramus; mental foramen below p3 alveolus; short diastema; robust i1 completely covered with enamel, although enamel thinner on dorsolingual side; anterior edge of p4 gently rounded; height at first serration 38–40% of crown length, crest of p4 highest between third and fifth serrations.

Average length of p4: 3.4 mm.

Average length of m1: 2.7 mm.

Included species: *K. clemensi* (also including *Ectypodus* sp. C of Rigby, 1980) only (known from localities SB23F*, GG, CP13IIA, CP14A).

Mesodma Jepsen, 1940

Type species: *Mesodma ambigua* Jepsen, 1940.

Type specimen: YMP-PU 14414, left dentary with i1–m1 from the Puercan of Wyoming.

Characteristics (modified from Clemens, 1963; Sloan, 1981; Hahn and Hahn, 1983): As in *Ectypodus* and *Mimetodon*, the ultimate cusp of P4 highest; p3 present; p4 crown relatively low (height of blade at first serration less than one-third crown length), rising anteriorly, then declining gradually until level with occlusal surface of m1; molar cusps semi-crescentic or crescentic. Includes the smallest species of Tertiary multituberculate, *M. pygmaea*.

Average length of p4: 3.46 mm.

Average length of m1: 2.32 mm.

Included species: *M. ambigua* (known from localities CP11IIA, IIB, CP12A*, [CP61A], [NP16C]); *M. formosa* Marsh, 1889 (localities SB23A, CP11IIB, NP7B, C, NP16C, NP17 and additional Late Cretaceous localities); *M. garfieldensis* Archibald, 1982 (localities SB39IIA, [CP11IIA], NP16A*); *M. hensleighi*: Lillegraven, 1969 (locality CP11IIB, and additional Late Cretaceous localities); *M. pygmaea* Sloan, 1987 (localities [SB39B], CP13B, ?C, CP13IIA, CP14C, CP15A, CP16A, NP1C, NP3A0, C, D, F, NP4, NP7D, NP19C*, NP19IIA, C, NP20A, NP47B); *M. thompsoni* Clemens, 1963 (localities SB23A, SB39IIA, NP6, NP7A–C, NP17 and additional Late Cretaceous localities).

Mesodma sp. is also known from localities CP11IIB, CP13A, CP15B, CP24A, NP7C, NP15A–C, NP16A, B, NP47A0, ?B.

Comments: In addition to Late Cretaceous occurrences of *M. hensleighi*, *M. formosa*, and *M. thompsoni*, there are two species (*M. primaeva* and *M. senecta*) that are entirely Cretaceous. *Mesodma* may be paraphyletic. Sloan (1981, 1987) hypothesized that *Neoplagiaulax*, *Parectypodus*, and *Mimetodon* arose from different species of *Mesodma*, and this hypothesis has not been ruled out by phylogenetic analyses. *Mesodma* molars retain several primitive characteristics, and where *Mesodma* species co-occur with *Cimexomys* of similar size, m1, m2, and M2 of the two genera cannot be reliably distinguished.

Mimetodon Jepsen, 1940

Type species: *Mimetodon churchilli* Jepsen, 1940.

Type specimen: YPM-PU 14525, left dentary with i1, p3–m1 from the Tiffanian of Wyoming.

Characteristics (modified from Jepsen, 1940; Hahn and Hahn, 1983): As in *Ectypodus* and *Mesodma*, ultimate cusp on P4 highest; P4 bearing three posteroventrally directed grooves on posterolabial surface; lower incisor disproportionately robust compared with those of other neoplagiaulacids; dentary deep below p4 to accommodate i1; p3 present.

Average length of p4: 4.16 mm.

Average length of m1: 2.71 mm.

Included species: *M. churchilli* (known from locality CP13G*); *M. krausei* Sloan, 1981 (locality SB23GG*); *M. silberlingi* Simpson, 1935 (localities SB39B, C, CP13[B], C, [CP15A], NP1C, NP3A0, A, C, D, NP7D, NP19C*, NP20E, NP48B).

Mimetodon sp. is also known from localities NP2, NP19IIA.

Comments: *Mimetodon* is also questionably known from the late Paleocene of Europe (McKenna and Bell, 1997).

Neoplagiaulax Lemoine, 1882 (including Plagiaulax, in part)

Type species: *Neoplagiaulax eoacenus* (Lemoine, 1880) (originally described as *Plagiaulax eoacenus*).

Type specimen: CRL 936, fragmentary left dentary with p4–m2 from the late Paleocene (Cernaysian) of France.

Characteristics (modified from Sloan, 1981): Includes the largest species of Neoplagiaulacidae. As in *Parectypodus*, penultimate or antepenultimate cusp highest on crown of P4; posterior slope of middle cusp row (between ultimate cusp and crown base) short and straight, rather than concave as in *Parectypodus*; p3 present in all species except *N. eoacenus*; anterior profile of p4 less convex than that of *Ectypodus*; serrations five to seven highest on p4; relative height of first serration 0.30–0.45 times crown length.

Average length of p4: 4.58 mm.

Average length of m1: 2.65 mm (not known from all spp.).

Included species: *N. cimolodontoides* Scott, 2005 (known from localities NP3B, C*); *N. grangeri* Simpson, 1935 (localities CP13C, ?CP21A, NP19C*); *N. hazeni* Jepsen, 1940 (localities CP13G*, CP24A, [NP3[A], B–D, F], [NP7D], NP47C, NP48B); *N. hunteri* Simpson, 1936b (localities CP13E, CP24A, NP1C, NP3A0, [C, D], F, NP4, NP7D, NP19IIA, C*, NP20D, NP47A1, B, B2, [C]); *N. jepi* Sloan, 1987 (localities CP13E*, CP13IIA); *N. kremnus* Johnston and Fox, 1984 (localities NP7B*, NP17, [NP17IIA]); *N. macintyreii* Sloan, 1981 (localities SB23A*, CP1C); *N. macrotomeus* Wilson, 1956 (locality SB23GG*); *N. mckennai* Sloan, 1987 (localities CP13F, CP26A*, NP20E, NP47C); *N. nanophus* Holtzman, 1978 (localities [NP2], NP47B2*); *N. nelsoni* Sloan, 1987 (localities CP13IIB, CP14A, CP15A, NP1C, NP2, NP3A0, NP16C*, NP19IIA); *N. paskapooensis* Scott, 2005 (localities NP3A–C*, NP4); *N. serrator* Scott, 2005 (localities NP3A–C*, D, NP4).

Neoplagiaulax sp. is also known from localities NB1A, CP13C, D, CP14C, NP3E, NP17, NP17IIA, NP19IIA, NP20B, NP47B, B2.

Comments: One species questionably referred to *Neoplagiaulax* (?*N. burgessi*) is known from the Late Cretaceous of North America. Five species (*N. annae*, *N. eoacenus*, *N. copei*, *N. nicolae*, and *N. sylvani*) are known from the late Paleocene of Europe.

Parectypodus Jepsen, 1930a

Type species: *Parectypodus simpsoni* Jepsen, 1930a.

Type specimen: YPM-PU 13242, fragmentary left dentary with i1–m1 from the Wasatchian of Wyoming.

Characteristics (modified from Sloan, 1981): Antepenultimate cusp of P4 usually highest; posterobasal cusp usually absent; posterior slope of middle cusp row between ultimate cusp row and crown base of P4 short, steep, and slightly concave; anterior slope convex; p3 absent in later species; relative height of first serration greater than 0.45 times crown length of p4; height of enamel at anterolabial lobe of p4 approximately equal to or greater than crown length; posterior angle between plane of occlusion of molars and anterior face of p4 a right or (usually) acute angle; third or fourth serration of p4 highest.

Average length of p4: 3.74 mm.

Average length of m1: 2.28 mm (not known from all species).

Included species: *P. simpsoni* (known from localities CP19B, C, CP20A*, BB); *P. armstrongi* Johnston and Fox, 1984 (locality NP7B*); *P. corystes* Scott, 2003 (localities NP1C, NP2*, NP3A0); *P. laytoni* Jepsen, 1940 (localities CP13G*, H, CP17B, [NP20D]); *P. lunatus* Krause, 1982a (localities CP19A, CP20A, CP25B, CP27A, CP28A, CP63*); *P. sinclairi* Simpson, 1935 (localities CP13IIA, CP15A, NP1C, NP4, NP19A, C*); *P. sloani* Schiebout, 1974 (localities SB39B, C); *P. sylviae* Rigby, 1980 (localities CP13C, CP13IIA, B, CP14A*, CP15A, [NP1C], [NP3A0]); *P. trovessartianus* Cope, 1882b (locality SB23F*); *P. vanvaleni* Sloan, 1981 (locality SB23A*).

Parectypodus sp. is also known from localities CP1C, CP25A, NP2, NP3A0, NP7C, NP16C, NP17, NP47B, B2.

Comments: One species, *P. foxi*, is known only from the Late Cretaceous. *P. pattersoni* was synonymized with *P. sylviae* by Secord (1998). This synonymy was ignored without any explanation by Higgins (2003a), and we have followed Secord here.

***Xanclomys* Rigby, 1980**

Type species: *Xanclomys mcgrewi* Rigby, 1980.

Type specimen: AMNH 87859, fragmentary dentary with p3–p4 from the Torrejonian of Wyoming.

Characteristics (modified from Rigby, 1980): P4 with subquadrate to triangular occlusal outline; ultimate cusps of P4 fused and highest; anterolabial row form two sides of triangle and with single major elevation of one or two cusps at most laterally extended portion, with cusps descending anteriorly and posteriorly; p3 present. Differs from all other multituberculate genera in shape of p4; crown of p4 triangular or sickle shaped in lateral outline, with long, flat, gently inclined anterior slope bearing one to three serrations near apex, and short, nearly vertical posterior slope with serrations.

Average length of p4: 4.90 mm.

Average length of m1: unknown.

Included species: *X. mcgrewi* only; known from locality CP14A only.

Comments: It is unclear on what basis Rigby referred *Xanclomys* to Neoplagiaulacidae. The fourth premolars are unique. The molars, which are all isolated teeth, are questionably referred and seem not to differ from those of *Neoplagiaulax*.

***Xyronomys* Rigby, 1980**

Type species: *Xyronomys swainae* Rigby, 1980.

Type specimen: AMNH 87897a, isolated right p4 from the Torrejonian of Wyoming.

Characteristics (modified from Rigby, 1980; Middleton, 1983; Johnston and Fox, 1984): p4 lower than those of comparably sized *Mesodma*, with little or no anterolabial lobe. Lower molars similar to those of *Mesodma* but proportionally narrower.

Average length of p4: 3.05 mm.

Average length of m1 (known only from *X. robinsoni*): 2.15 mm.

Included species: *X. swainae* (known from locality CP14A*); *X. robinsoni* Middleton and Dewar, 2004 (locality CP61A*).

Xyronomys sp. is also known from localities NP3A0, NP7B, C, NP16B.

Comments: Rigby (1980) had only isolated premolars and placed *Xyronomys* in the Eucosmodontidae on the basis of its low p4, which is similar in shape to that of *Stygimys*. Middleton's (1983) discovery of a fragmentary dentary with p4–m2 of a second species confirmed the suspicion of Johnston (mentioned in his 1980 M.Sc. dissertation, and published in Johnston and Fox [1984]) that *Xyronomys* is a neoplagiaulacid. Unlike the eucosmodontids *Eucosmodon* and *Stygimys*, *Xyronomys* has small, circular tooth enamel prisms (Carlson and Krause, 1985; Krause and Carlson, 1986).

Indeterminate neoplagiaulacids

Fossil material referred to Neoplagiaulacidae has also been recovered at localities SB24, CP13B, CP61B, NP3A0, NP7C, and NP19C.

EUCOSMODONTIDAE JEPSEN, 1940 (INCLUDING BOFFIDAE HAHN AND HAHN, 1983)

Characteristics: I2 with two cusps; I3 palatal; P1 (when present), P2, and P3 single-rooted; i1 strongly laterally compressed, with enamel restricted to ventrolabial side; p3 absent; p4 proportionally large and elongate, as long or longer than m1 and with at least seven serrations; crest of p4 continuous with occlusal surface of m1.

***Eucosmodon* Matthew and Granger, 1921 (including *Neoplagiaulax*, in part)**

Type species: *Eucosmodon americanus* (Cope, 1885) (originally described as *Neoplagiaulax americanus*).

Type specimen: AMNH 3028, fragmentary left dentary with p4 and broken i1 from the Puercan of the San Juan Basin of New Mexico.

Characteristics: Very similar to *Stygmymys* but larger; P1 absent; i1 less compressed than that of *Stygmymys*; p4 often over 1 cm in length, about twice as long as m1; anterolabial lobe of p4 not pronounced.

Average length of p4: 11.53 mm.

Average length of m1: 5.6 mm.

Included species: *E. americanus* (known from locality SB23B*); *E. molestus* (Cope, 1886) (originally described as *Neoplagiaulax molestus*) (localities SB23A, NP1B); *E. primus* Sloan, 1981 (locality SB23A*).

Eucosmodon sp. is also known from localities SB23E and NP16B (Weil, 1999).

***Stygmymys* Sloan and Van Valen, 1965**

Type species: *Stygmymys kuszmauli* Sloan and Van Valen, 1965.

Type specimen: UMVP 1478, fragmentary left dentary with i1 from mixed Cretaceous–Tertiary sediments of Montana.

Characteristics (modified from Sloan and Van Valen, 1965): I2 bicuspid; P1 present; i1 more laterally compressed than that of *Eucosmodon*; lateral profile of posterior portion of p4 nearly straight; p4 slightly longer than m1; p4 roots large, the anterior one being larger and curved forward.

Average length of p4: 4.65 mm.

Average length of m1: 4.24 mm (but not known from the larger species.).

Included species: *S. kuszmauli* (including *S. cupressus* Fox, 1989; see Lofgren *et al.*, 2005) (known from localities CP1A, CP12A, NP7A, NP15A*, B, C, NP16A); *S. camptorhiza* Johnston and Fox, 1984 (localities NP7B*, [NP17]); *S. jepseni* Simpson, 1935 (localities NP19B, C*); *S. teilhardi* Granger and Simpson, 1929 (locality SB23A); *S. vastus* Lofgren *et al.*, 2005 (locality CP39IIB).

Stygmymys sp. is also known from localities CP13B, [NP3A0], NP7C, NP16A-C.

Comments: Lofgren (1995) recognized that the type of *Stygmymys gratus* belonged to *Cimexomys "hausoi"* and assigned the remaining specimens of *Stygmymys* from Harbicht Hill (locality NP15C), and Mantua Lentil (locality CP12A) to *S. kuszmauli*. Fox (1989) described a new species, *S. cupressus*, from the Ravenscrag Formation (locality NP4), which Lofgren *et al.* (2005) synonymized with *S. kuszmauli*.

Indeterminate eucosmodontids

Fossil material referred to Eucosmodontidae has also been recovered at localities SB23GG and NP15C.

MICROCOSMODONTIDAE HOLTZMAN AND WOLBERG, 1977

Characteristics: Tooth i1 proportionally large and strongly laterally compressed, with enamel restricted to ventrolabial surface for

most of incisor length (enamel cap, quickly worn away, may be present on unworn incisors); root extending posterior to p4; crown of p4 with three to six serrations; anterior serration (lost in *Microcosmodon rosei*) strong; posterior serrations cusplike; m1 and m2 both with notch posterior to last cusp of internal cusp row. In some species, first molars with accessory roots. In the three species for which dentaries are known, pterygoid fossa very large and deep.

***Allocosmodon* Fox, 2005**

Type species: *Allocosmodon woodi* (Holtzman and Wolberg, 1977) (originally described as *Microcosmodon woodi*).

Type specimen: MCZ 19963, right p4 from Ti1 of Wyoming. Characteristics (based on Holtzman and Wolberg, 1977; Weil, 1998; Fox, 2005): I2 bicuspid with thick anterior enamel, exposed dentine medially, labial groove separating cusps; P4 large with five or six large cusps, ultimate cusp highest; M1 cusps conical to pyramidal, accessory roots present i1 laterally compressed, with enamel engulfing tip but not covering the entire dorsolingual surface; p3 present; p4 longer than m1, with five or six serrations, lingual and labial ridges that are short but strong, differs from other microcosmodontids in long, low blade.

Average length of p4: 3.1 mm.

Average length of m1: 2.4 mm.

Included species: *A. woodi* only (known from localities CP15A*, NP3A–C, NP19IIA, NP20D, NP47B).

Comments: Holtzman and Wolberg (1977) placed this species in *Microcosmodon*. Weil (1998) removed it from *Microcosmodon* and Microcosmodontinae (= Microcosmodontidae Fox 1999, 2005) but did not give it a new generic name or refer it to any named genus. Fox (2005), working with considerably better specimens, replaced it within Microcosmodontidae, named the new genus, and provided a revised, differential diagnosis.

***Acheronodon* Archibald, 1982**

Type species: *Acheronodon garbani* Archibald, 1982 (emended by Fox, 2005).

Type specimen: UCMP 116953, fragmentary p4 from the Puercan of Montana.

Characteristics (modified from Archibald [1982] with reference to Fox [2005]): The p4 has a very distinct, cusplike, ultimate serration and a wide posterolabial shelf.

Average length of p4: 1.90 mm.

Average length of m1: 2.3 mm (not known for *A. garbani*).

Included species: *A. garbani* (known from locality NP16A*); *A. vossae* Fox, 2005 (localities NP1C*, [NP3A]).

Acheronodon sp. is also known from locality NP3A0.

Comments: The type of, and for a long time the only specimen referred to, this genus is a fragmentary p4, and it may well be that the name *Acheronodon* is a nomen nudum. The type species was named *A. garbani*, by Archibald (1982), but the Latin was emended to *garbanii* by Fox (2005). Scott

(2003) refer an m1 with length of 1.7 mm from locality NP3A0 to *Acheronodon*, on the basis of a personal communication with Fox, apparently concerning the specimens described in Fox (2005).

***Microcosmodon* Jepsen, 1930b**

Type species: *Microcosmodon conus* Jepsen, 1930b.

Type specimen: YPM-PU 13331, left dentary with i1 and p4 from the Tiffanian of Wyoming.

Characteristics (modified from Weil, 1998; Fox, 2005): The p3 may be present in all species but *M. rosei*; p4 posterior crown wider than anterior; p4 shorter than m1, with high, arcuate, serrated edge; molar cusps semi-crescentic to strongly recurved; molars with more cusps than those of *Pentacosmodon*; enamel prisms a mix of small, circular and large, arcade shaped.

Average length of p4: 2.05 mm.

Average length of m1: 2.11 mm.

Included species: *M. conus* (known from localities CP13G*, CP14E, [CP15B], NP3C, F, G, NP4, NP7D) “*M.*” *arcuatus* Johnston and Fox, 1984 (locality NP7B*); “*M.*” *harleyi* Weil, 1998 (locality NP16B); *M. rosei* Krause, 1980 (localities CP13H, CP17A, B*).

Microcosmodon sp. is also known from localities NB1A, NP47A1.

Comments: Fox (2005) removed “*M.*” *arcuatus* Johnston and Fox, 1984 and “*M.*” *harleyi* Weil, 1998 from *Microcosmodon* but did not refer them to another genus or create a new generic name. *Microcosmodon* is also known from the early Eocene of Europe (McKenna and Bell, 1997).

***Pentacosmodon* Jepsen, 1940**

Type species: *Pentacosmodon pronus* Jepsen, 1940.

Type specimen: YPM-PU 14085, left dentary with broken i1, p4, and m1–2 from the Tiffanian of Wyoming.

Characteristics (modified from Jepsen, 1940; Hahn and Hahn, 1983): The p3 absent; p4 less reduced than those of later species of *Microcosmodon*, and with strong lateral ridges, crown shape appears truncated posteriorly; molars with fewer cusps than those of *Microcosmodon*, molar cusps subcrescentic with anteroposteriorly elongated bases; large, arcade-shaped enamel prisms.

Average length of p4: 1.9 mm.

Average length of m1: 5.4 mm.

Included species: *P. pronus* (known from locality CP13G*); *P. bowensis* Fox, 2005 (locality NP1C*).

Indeterminate microcosmodontines

Fossil material referred to Microcosmodontinae has been recovered from localities NP3G and NP7A.

TAENIOLABIDIDAE GRANGER AND SIMPSON, 1929

Characteristics: Tooth enamel gigantoprismatic. Large in size relative to multituberculate genera with which they co-occur. P1–3

absent; P4 extremely reduced; i1 enamel ridged and restricted to ventrolabial side of tooth; i1 not laterally compressed as in Eucosmodontidae and Microcosmodontidae; p3 absent; p4 extremely reduced, altered from slicing tooth in more primitive members of family to single-pointed tooth in more derived members; molar cusps bulbous or transversely expanded, wearing first on apices rather than on sides as in other North American multituberculates; M1 tending to develop lingual cusp row running entire length of tooth.

***Catopsalis* Cope, 1882c**

Type species: *Catopsalis foliatus* Cope, 1882c.

Type specimen: AMNH 3035 from the Nacimiento Formation of New Mexico.

Characteristics: *Catopsalis* is paraphyletic (Simmons and Desui, 1986) and it is difficult to distinguish larger species of *Catopsalis* from smaller species of *Taeniolabis*. Simmons (1987) found m1 and M1 of *C. calgariensis* to overlap in size with those of *Taeniolabis*; however, she found i1, I2, m2, and M2 of *Catopsalis* spp. to be smaller in all cases than those of *Taeniolabis*. Buckley (1995) described an even larger species of *Catopsalis*, and distinguished it from *Taeniolabis* on the basis of low cusp count.

Average length of p4: 4.3 mm (not known from all species).

Average length of m1: 11.8 mm.

Included species: *C. foliatus* (known from localities SB23A, NP7A); *C. alexanderi* Middleton, 1982 (localities CP12A, CP61A*, NP15C, NP16A); *C. calgariensis* Russell, 1926 (localities CP13IIA, CP15A, NP1B*); *C. fissidens* Cope, 1884a (localities SB23E, CP1C, CP13IIA); *C. joyneri* Sloan and Van Valen, 1965 (localities CP11IIA, NP6, [NP7A], NP15A*, B, NP16A); *C. waddleae* Buckley, 1995 (locality NP17*).

Catopsalis sp. is also known from localities SB23B, CP13B, NP7B, C, NP16A.

***Taeniolabis* Cope, 1882b**

Type species: *Taeniolabis taoensis* Cope, 1882b.

Type specimen: AMNH 3036, fragmentary right maxilla with M1–2 and skull fragments from the Puercan of New Mexico.

Characteristics (modified from Simmons, 1987): Includes the largest known multituberculate species; i1, I2, m2, M2 larger than those of any other genus, although M1/1 dimensions may overlap those of some species of *Catopsalis*; M1 with nine or more cusps in labial and lingual cusp rows; M2 with four or more cusps in medial cusp row; m1 with seven or more cusps in labial row and six or more cusps in lingual row; m2 with four or more cusps in lingual row. Length ratio of p4/m1 less than 0.40.

Average length of p4: 6.2 mm.

Average length of m1: 17.9 mm.

Included species: *T. taoensis* (known from localities SB23B*, [CP1A], CP11IF, NP7C); *T. lamberti* Simmons, 1987 (locality NP16B*).

Taeniolabis sp. is also known from localities CP1B, NP16C, NP18.

CIMOLODONTA INCERTAE SEDIS

Anconodon Jepsen, 1940 (including *Ptilodus*, in part)

Type species: *Anconodon gidleyi* (Simpson, 1935) (originally described as *?Ptilodus gidleyi*).

Type specimen: USNM 9763, left dentary with p4 and fragmentary m1 from the Torrejonian of Montana.

Characteristics (modified from Jepsen, 1940; Hahn and Hahn, 1983): Lingual cusp row of P4 more strongly developed into cutting edge than in *Cimolodon* and less so than in *Liotomus*, the two other genera that historically have been included in Cimolodontidae. The p4 highly arched; distance between anterior “beak” and first serration straight and greater than one-half length of tooth; p4 “squared” above basal concavity in anterior view; anterior ridges on lingual side tend to branch.

Average length of p4: 5.31 mm.

Average length of m1: 2.70 mm.

Included species: *A. gidleyi* (known from localities SB23F, CP13B, NP1B, C, NP19B, C*); *A. cochranensis* Russell, 1929 (localities CP13B, [C], D, CP13IIA, CP16A, NP1B*, C, NP3A0, NP19C, NP19IIA); *A. lewisi* Sloan, 1987 (localities CP13IIA, CP15A*, NP19IIA).

Anconodon sp. is also known from localities ?SB23H, CP13C, CP13IIB, NP20B.

Comments: *Anconodon* is generally considered to belong to the Cimolodontidae, a family that was never formally diagnosed and is hazily united in having a slender i1 that is completely covered with enamel, and a round, high arch of the cutting edge of p4. Hahn and Hahn (1983) included *Anconodon* and *Cimolodon* from the Late Cretaceous of North America, and *Liotomus* from the late Paleocene of Europe. Vianey-Liaud (1986) assigned the species *A. russelli* to *Liotomus*, but we have followed Sloan (1987) in synonymizing *A. russelli* with *A. cochranensis*. Simmons' (1993) parsimony analysis did not include *Anconodon* but found *Cimolodon* and *Liotomus* to be phylogenetically disparate. Accordingly, McKenna and Bell (1997) removed *Liotomus* to the Eucosmodontidae (they also followed Vianey-Liaud and listed an early Paleocene North American occurrence of *Liotomus*) and retained *Anconodon* in Cimolodontidae. Kielan-Jaworowska and Hurum (2001) included all three genera in Cimolodontidae. The difficulty with all these assignments is that the type genus, *Cimolodon*, is non-monophyletic (Weil, 1999). Characters used to diagnose *Cimolodon* (Clemens, 1963) are widely distributed among Cimolodonta, and many are primitive. Considering that the type genus is polyphyletic and that

the only analysis to test monophyly of the Cimolodontidae indicated that it was also non-monophyletic, we have listed *Anconodon* as Cimolodonta incertae sedis.

Cimexomys Sloan and Van Valen, 1965

Type species: *Cimexomys minor* Sloan and Van Valen, 1965.

Type specimen: SPSM 62-2115, fragmentary left dentary with p3–4 from mixed Cretaceous–Tertiary sediments of Montana.

Characteristics (from Archibald, 1982; Montellano, 1992): Height of P4 lower than in comparably sized species of *Mesodma*. M1 cusp formula greater than that of *Paracimexomys*, with which it co-occurs in the Cretaceous, but less than that of *Mesodma*; M1 cusp rows not divergent anteriorly; lingual cusp row 50% or less of M1 length, and tending to be ridgelike with indistinctly divided cusps; p4 with fewer serrations (8–10) than in comparably sized species of *Mesodma*, arcuate in outline, last two or three serrations formed into distinct cusps without lingual or labial ridges; m1 cusp formula (5–7:4–5) greater than that of *Paracimexomys*, and less than or equal to that of *Mesodma*; molar cusps tending to be subcrescentic to crescentic; molars not waisted.

Average length of p4: 3.53 mm.

Average length of m1: 3.27 mm (but does not include *C. minor*).

Included species: *C. minor* (known from localities CP61A, NP7A, B, NP15A*, B, C, NP16A and additional Late Cretaceous localities); *C. arapahoensis* Middleton and Dewar, 2004 (locality CP61A*); *C. gratus* (Jepsen [1930b], originally described as *C. hausoi* see Lofgren, [1995]) (localities CP12A*, [NP7A, B, C], NP15A, C, NP16A).

Cimexomys sp. may also be present at locality NP17.

Comments: Three species (*C. antiquus*, *C. gregoryi*, and *C. judithae*) are exclusively Late Cretaceous. Sloan and Van Valen (1965) placed *Cimexomys* in the Neoplagauiacidae, but Archibald (1982) removed it to Cimolodonta incertae sedis because it is more primitive than those multituberculates that have been placed in Taeniolabidoidea and Ptilodontoidea. Isolated teeth of *Cimexomys* can be difficult to distinguish from those of other genera that have retained some primitive characters. The M1 is the only molar of *Cimexomys* that is consistently differentiable from those of co-occurring *Mesodma* of similar size (Lofgren, 1995; Montellano, Weil, and Clemens, 2000). However, the M1 of *Cimexomys* is very similar to (and perhaps indistinguishable from) M1s attributed to *Microcosmodon* (Krause, 1980; Weil, 1998) and to the Cenomanian *Dakotamys* (Eaton, 1995).

Fractinus Higgins, 2003b

Type species: *Fractinus palmorum* Higgins, 2003b.

Type specimen: UW 27063, left p4 from the Tiffanian of Wyoming.

Characteristics: Very distinct from any other multituberculate. p4 with five serrations, serrations rounded in unworn state, first serration at highest point on arc of p4 in profile; anterior edge of crown only slightly convex. Differs from *Xanclomys* in having all serrations except the first in a straight line when viewed in profile. Differs from other taxa with similarly low numbers of serrations in having a prominent anterolabial lobe.

Average length of p4: 4.92 mm.

Average length of m1: unknown.

Included species: *F. palmorum* only, known from locality CP13IIA* only.

Comments: Known from only the type and the anterior half of a second p4.

***Neoliotomus* Jepsen, 1930a**

Type species: *Neoliotomus conventus* Jepsen, 1930a.

Type specimen: YPM-PU 13297, fragmentary left dentary with broken i1, root of p3, and p4 from the Clarkforkian of Wyoming.

Characteristics: Relatively large size, with p4 greater than 1 cm in length; I2 unicuspid; P1–4 present; all have two roots; i1 laterally compressed, with enamel restricted to ventrolabial surface; p3 present; p4 longer than m1, and in unworn state higher than m1; enamel prisms small and circular.

Average length of p4: 12.52 mm.

Average length of m1: 6.99 mm.

Included species: *N. conventus* (known from localities CP13G, H, CP14E, CP17A, B, CP22B, CP62A2, B); *N. ultimus* Granger and Simpson, 1928 (localities CP19A, B, CP20A, CP25B, CP63).

Comments: Because of its laterally compressed, gliriform incisor, in combination with its relatively large p4, *Neoliotomus* was long considered to belong in Eucosmodontidae. It differs, however, from Eucosmodontidae in the following respects: enamel prisms are small and circular; p3 is present; p4 crest is higher than the occlusal surface of m1–2; I2 has only one cusp; and P1–3 are all present and have two roots. As a result of her phylogenetic study, Simmons (1993) removed *Neoliotomus* from Eucosmodontidae. McKenna and Bell (1997) placed it in the Boffiidae sensu Hahn and Hahn, 1983, but changed the rank to that of tribe (and the taxon name to Boffiini) within the family Eucosmodontidae. Following the result of their parsimony analysis, Kielan-Jaworowska and Hurum (2001) placed *Neoliotomus* in Ptilodontoidea incertae sedis.

INDETERMINATE MULTITUBERCULATES

Fossil material referred to Multituberculata has also been recovered from localities SB39IIA, CP17B, CP31E.

BIOLOGY AND EVOLUTIONARY PATTERNS

Multituberculates have for a long time been referred to as the ecological vicars of rodents. Comparisons with rodents are inviting: multituberculates and rodents evolved numerous similar cranial and dental adaptations convergently, multituberculates were the most common small mammals of the early Tertiary as rodents are today, and the size range of multituberculates was about the same as that of living rodents. The smallest known North American Cenozoic multituberculate is *Mesodma pygmaea*, which was similar in size to small shrews living today; its lower first molar is only about 1.5 mm long. By contrast, *Taeniolabis taoensis*, the largest known multituberculate with a lower first molar about 20 mm long (skull length about 160 mm), was probably slightly larger than a modern beaver (notwithstanding that Cope [1884a] described it as being the same size as a large kangaroo) (Figure 2.5).

Despite characterizations of multituberculates as the first mammalian herbivores, it is likely that most were not strictly herbivorous. Most multituberculates were small, and living mammals of comparable size require more protein than is provided in a herbivorous diet (Krause, 1982c; Wing and Tiffney, 1987). Since there are no close living relatives of multituberculates, their diet is difficult to infer from their relationships. The closest living structural analogs are some small phalangeroid marsupials (e.g., *Aepyprymnus*, *Bettongia*, *Burramys*, *Hypsiprymmodon*), all of which are omnivorous (Clemens and Kielan-Jaworowska, 1979; Krause, 1982c), and it has been suggested that the pointed lower incisors of some taxa may have been used to stab insects, as are the incisors of living caenolestid marsupials.

One trend among Tertiary North American multituberculates is that of proportionate enlargement of the p4 to an exaggerated degree not seen in the Late Cretaceous. Those multituberculates that had enlarged lower fourth premolars may have ingested hard food items (Krause, 1982c; Wall and Krause, 1992), perhaps fruits and seeds. After a food item was ingested, it could have been held against the multicusped upper premolars (primarily P4) and sliced or wedged apart by the enlarged, laterally compressed and serrated p4 as the jaw closed. Following this slicing action, food passed posteriorly to the grinding molars. The molar chewing cycle of multituberculates is noteworthy because the power stroke was directed posteriorly, a unique or nearly unique condition among mammals. The two rows of lower molar cusps, which tend to be concave posteriorly, fit between the three rows of upper molar cusps, which tend to be concave anteriorly. This arrangement provided for a highly efficient mechanism of en-echelon shear as the lower molars were drawn posteriorly along the uppers (Krause, 1982c; Wall and Krause, 1992).

Taeniolabidids elaborated a different set of dental specializations: chisel-shaped lower incisors, reduction of the p4 and P4, and molars with large, often bulbous or transversely expanded cusps, on which wear did not occur in the valleys between cusps, but on the cusp apices. Cusp-tip-wearing multituberculates appear first in North America in the latest Cretaceous. Interestingly, both the Late Cretaceous and Paleocene taxa are the largest multituberculates in their faunas. Their dental morphology and large size suggest an increased

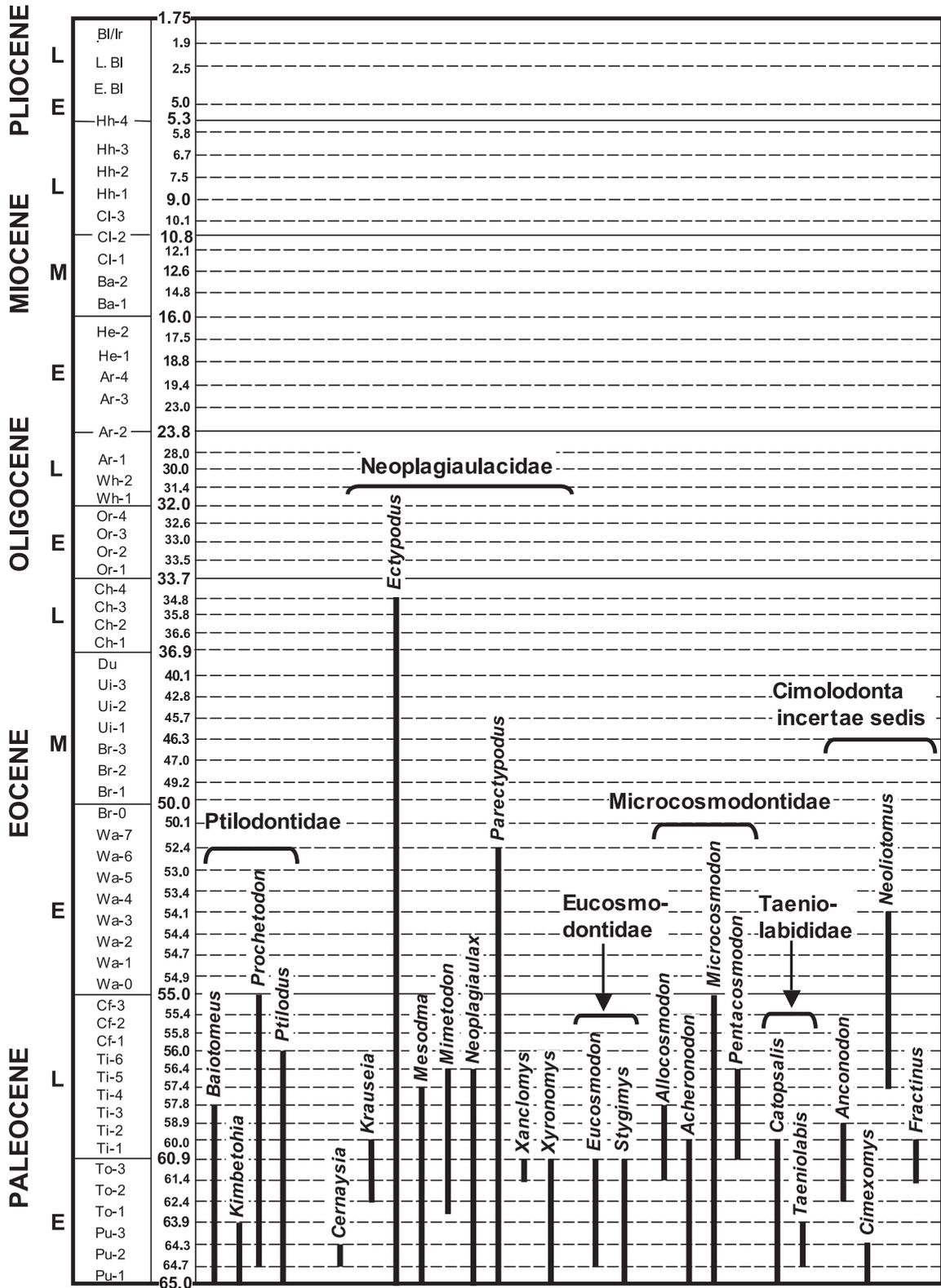


Figure 2.5. Temporal ranges of North American Tertiary multituberculate genera.

dependence on vegetation; they may have been more folivorous than other multituberculates.

Gliriform lower incisors evolved at least twice, and quite probably more times, within multituberculates. Among the Cenozoic multituberculates of North America, taeniolabidids evolved robust lower incisors with enamel restricted to the ventrolabial surface, while the lower incisors of eucosmodontids, microcosmodontids, and *Neoliotomus* are strongly laterally compressed, and thus very narrow. The restriction of enamel causes the incisor to wear in a chisel shape and provides a self-sharpening mechanism. This same mechanism has evolved several times within the Mammalia and is particularly well developed in rodents. It appears, however, that the lower incisors of multituberculates were not ever-growing as they are in rodents. As indicated by the discrepant lengths of the upper and lower tooth rows, the tips of the incisors can only be approximated if the lower jaw is substantially protruded.

By comparison with rodents, it is reasonable to assume that taeniolabidids, eucosmodontids, microcosmodontids, and *Neoliotomus* used their incisors for snipping and gnawing. Indirect evidence that this is the case comes from gnawed bones in the Nacimiento Formation of the San Juan Basin (Sinclair and Granger, 1914; Simpson and Elftman, 1928). The gnaw marks fit exactly the conformation of the lower incisors of *Eucosmodon*, and there is no other reasonable candidate in the same deposits. Eucosmodontids, microcosmodontids, and *Neoliotomus* differ from taeniolabidids not only in the shape of their incisors, but also in retaining a slicing p4, which is quite large in eucosmodontids and *Neoliotomus*. Their molars wear along the sides of the cusps, a condition that seems to be primitive for Cimolodonta. This suggests that, although they may have gnawed on bones, their diet included a substantial amount of plant material, such as seeds.

Multituberculate locomotion varied with environment. The first described multituberculate skeleton, that of *Ptilodus*, possesses specializations that would have allowed it to move headfirst down trees. These are a hallucal metatarsal divergent from those of digits II–V and with a saddle-shaped proximal articular facet, and a specialized tarsal structure for abduction, plantarflexion, and eversion of the pes (Jenkins and Krause, 1983; Krause and Jenkins, 1983). This is the only anywhere near complete multituberculate skeleton described from North America, but a foot questionably referred to *Eucosmodon* and tarsal elements referred to *Stygimys* and questionably to *Mesodma* possess similar features (Krause and Jenkins, 1983). Extant animals with this kind of adaptation are scansorial or arboreal (Jenkins and McClearn, 1984). Multituberculates from more xeric paleoenvironments (notably in Asia) lack these features. Kielan-Jaworowska and Gambaryan (1994) found that the Cretaceous Asian *Nemegtbaatar* and *Chulsanbaatar* had tarsi differently constructed from those of *Ptilodus*, and they interpreted those taxa to be terrestrial and possibly ricochetal. The Paleocene Asian *Lambdopsalis*, included within Taeniolabididae, is interpreted as fossorial (Miao, 1988).

Multituberculate reproduction is also a subject of speculation. Kielan-Jaworowska (1979) thought that the narrow, V-shaped pelvis of multituberculates, with its long, keeled symphysis, was too nar-

row and inflexible for the passage of either eggs or young as far developed as those of living placentals. It would, therefore, seem most likely that multituberculates had very altricial young, nourished through most of their development in a way similar to that of living marsupials.

At the end-Cretaceous extinction, multituberculate diversity plunged by perhaps 50% (Archibald and Lofgren, 1990; Archibald, 1996). A few species survived into the earliest Paleocene, but earliest Paleocene mammalian assemblages of the North American Western Interior differ taxonomically from those of the Late Cretaceous. Especially notable among Multituberculata are the first appearances of the Microcosmodontidae and of the genus *Catopsalis*, as well as the sudden abundance of *Stygimys*. Within 400 000 years (by Puercan 2), North American multituberculate diversity seems not only to have rebounded, but to have surpassed Late Cretaceous diversity. Where did the new multituberculates come from? Faunal interchange with Asia has been invoked to explain the appearance of new lineages in the northern Western Interior at the beginning of the Cenozoic (Kielan-Jaworowska, 1974b; Kielan-Jaworowska and Sloan, 1979; Beard, 1998). Although there is evidence for Asian mammalian influx about 100 million years ago (Cifelli *et al.*, 1997; Eaton and Cifelli, 2001) there is no phylogenetic evidence to support an Asian influx at the Cretaceous–Tertiary boundary; the genus *Catopsalis* was formerly thought to have occurred on both continents (Kielan-Jaworowska and Sloan, 1979), but this is now recognized to have been a misidentification (Kielan-Jaworowska and Hurum, 1997). It is more likely that, as initially proposed by Fox (1968), these “new” Paleocene multituberculates were present in the Late Cretaceous of North America, but during that period were living in upland environments that were not preserved. This hypothesis has been supported by recent reconsideration of phylogeny and biogeography (Weil, 1999).

Very little has been written about multituberculate migration after the mid-Puercan. Vianey-Liaud (1986) suggested that four North American taxa (*Neoplagiaulax hazeni*, *Neoplagiaulax cf. hunteri*, *Anconodon russelli*, and *Cernaysia davidi*) dispersed to Europe at the Dano–Montian/Cernaysian boundary (roughly corresponding to the Torrejonian/Tiffanian boundary) and gave rise to several European neoplagiaulacid species. She conducted no analysis, so the specifics of this interchange are speculative, but it is clear that neoplagiaulacid species are present in Cernaysian localities. She also speculated that the European *Hainina* was derived from North American Cretaceous Cimolomyidae, but subsequent authors (Kielan-Jaworowska and Hurum, 2001) have more convincingly placed *Hainina* in the strictly European Kogaionidae. The genus *Ectypodus* occurs in both North America and Europe during the late Paleocene and early Eocene; presumably it dispersed from North America to Europe, considering that the Neoplagiaulacidae (as taxonomically problematic as they are) seem to have originated in North America.

This is not to say that dispersal between continents played no role in multituberculate evolution; the immigration of rodents may have played a key role in multituberculate extinction. The similarities between multituberculates and rodents led several early workers (e.g., Matthew, 1897) to suggest that the decline and extinction of

multituberculates was related to the adaptive radiation of rodents. More recent attempts to test this hypothesis of competitive exclusion and taxonomic displacement have, in fact, found more evidence in support of it (Van Valen and Sloan, 1966; Krause, 1986). High taxonomic diversity was reestablished by the middle Paleocene. However, North American multituberculates underwent a decline in diversity in the latest Paleocene and earliest Eocene, at the time during which rodents are thought to have dispersed from Asia into North America. Competitive exclusion of multituberculates by rodents can be inferred from inverse correlations of relative abundance and generic richness between the two groups. Although multituberculates lived on into the Chadronian Land-Mammal Age, they were a minor component of North American faunas during the Eocene.

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3 Marsupialia

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INTRODUCTION

Marsupials have been identified first in North America beginning in the Cretaceous (Clemens, 1979; Johanson, 1996; Cifelli and Muizon, 1997; Cifelli, 1999). The Tertiary record begins in the Paleocene and extends to the early middle Miocene (Barstovian – locality GC4C; Slaughter, 1978). There is no further record of marsupials until the late Pliocene (Kurtén and Anderson, 1980).

North American Tertiary marsupials were never very diverse either morphologically or taxonomically. Although marsupials are included in nearly all Paleocene through Oligocene faunal samples, they represent only a small percentage of the collected specimens from any fossil locality. Nearly all of the Tertiary record of marsupials consists of dental elements. By the early Miocene, marsupials are extremely rare. The early middle Miocene (Barstovian) record consists of only a single isolated molar (Slaughter, 1978; Korth, 1994). The latest reviews of North American marsupials were presented by Krishtalka and Stucky (1983a) for the Paleocene and Eocene species (Tiffanian–Duchesnean) and Korth (1994) for the Oligocene and Miocene (Chadronian–Hemingfordian).

DEFINING FEATURES OF THE COHORT MARSUPIALIA

There are a number of major differences in physiology and overall morphology of the skeleton and body between the marsupials and all placental mammals (e.g., Lillegraven, 1969; Nowak, 1991; Szalay, 1993). However, the fossil record of marsupials in North America consists almost entirely of dental elements. For this reason, the features discussed here will be limited to teeth and jaws (Figure 3.1). All of these taxa probably had a generalized type of terrestrial or scansorial postcranial morphology, like that of extant didelphid marsupials.

The dental formula for all North American marsupials, as far as it is known, is the primitive formula for all marsupials: $I5(?)/4, C1/1, P3/3, M4/4$. This is easily distinguishable from even the most primitive eutherian mammals (primitive dental formula $I3/3, C1/1, P4/4, M3/3$), which have fewer molars and incisors and more premolars. All North American marsupials retain pointed cusped cheek teeth with little or no modification from the primitive condition. The crowns of the teeth never become lophate or hypsodont in any species. The premolars never attain the level of molarization of many eutherians, maintaining a conservative premolariform shape.

The lower molars of marsupials can be distinguished from those of eutherians by the close positioning of the entoconid and hypoconulid on the talonids, often referred to as “twinning.” The upper molars of marsupials differ from those of eutherian mammals in having a much wider stylar shelf (generally with an ectoflexus) and well-developed stylar cusps. Marsupial upper molars also lack a hypocone. The mandible is generally very slender with multiple mental foramina and a characteristic medial flange of the angle of the dentary.

SYSTEMATICS

SUPRAFAMILIAL

North American Tertiary marsupials are all very small-sized species and show very conservative changes throughout their fossil record occurrence. They can be divided into three recognizable groups based on dental morphology: herpetotheriines, peradectines, and didelphines. These groups either have been classified as tribes or subfamilies of the family Didelphidae (Crochet, 1980; McKenna and Bell, 1997); or the peradectines have been included in their own family Peradectidae (Reig, Kirsch, and Marshall, 1985), or even as a superfamily (Marshall, Case, and Woodburne, 1990) (see also discussion in Case, Godin, and Woodburne, 2005).

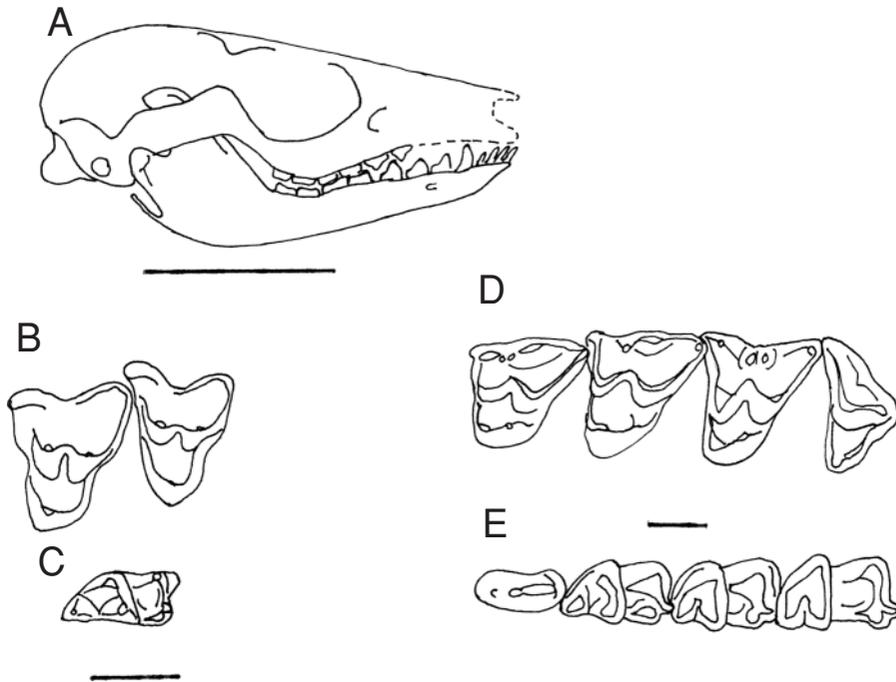


Figure 3.1. Skull and dentitions of Tertiary marsupials. A. Reconstruction of the skull of Orellan peradectine *Nanodelphys hunti* (based on USNM 11955, as per description by Gazin [1935]). B. Left M2–3 of the Orellan peradectine *Nanodelphys hunti* (from McGrew, 1937, his Fig. 3.4). C. Right m1 of the Duchesnean peradectine *Peradectes californicus* (from Rothecker and Storer, 1996, their Fig. 3.1Q). D. Left M1–4 of the Orellan herpetheriine *Herpetotherium fugax* (redrawn from Green and Martin, 1976, their Fig. 3.2). E. Right p3–m3 of *H. fugax* (redrawn from Korth, 1994, his Fig. 3.3). All figures not to same scale. Scale bar below A = 1 cm. Others = 1 mm. B and C to same scale (below left), D and E to same scale. (A, E: courtesy of the Society for Sedimentary Geology. B: courtesy of the University of Chicago Press. C: courtesy of the Society of Vertebrate Paleontology.)

The systematics of North American marsupials above the family level recently has been in question. The variation in the systematics has been based on the allocation of the peradectines and Cretaceous genera rather than the distinction between the recognizable Tertiary subfamilies (or families). The herpetheriines and didelphines have been considered as subfamilies of the Didelphidae by all authors.

When first proposed, the Peradectinae was intended only to include the Tertiary genus *Peradectes* (Crochet, 1979). Reig, Kirsch, and Marshall (1985, 1987) raised the rank of the peradectines to the family level and included the Cretaceous genera *Alphadon* and *Albertatherium*. Marshall, Case, and Woodburne (1990) erected a superordinal rank (cohort), Ameridelphia, which included most of the marsupials from North and South America and Eurasia, but excluded the peradectines *Alphadon* and *Albertatherium*. The Cretaceous genera were included with the Tertiary peradectines in the cohort Alphadelphia. Johanson (1996) demonstrated that there were shared, derived morphologies of the peradectines and didelphids that separated the former from the Cretaceous alphadontines, and included the peradectines along with the didelphids in the Ameridelphia, leaving the Cretaceous species as a separate group, the Alphadelphia. The most recent classification of marsupials (McKenna and Bell, 1997) included the alphadontines, peradectines, didelphines, and herpetheriines as subfamilies of the Didelphidae.

INFRAFAMILIAL

Crochet (1979) demonstrated a number of dental morphologies that separated herpetheriines from peradectines. On the upper molars: (1) herpetheriines have a wider stylar shelf with more pronounced stylar cusps; (2) herpetheriines have a V-shaped centrocrista

(dilambdodonty) that is lacking in peradectines; (3) the conules are larger on herpetheriines; (4) the metacone is taller than the paracone (cusps subequal in peradectines on lower molars); and (5) the hypoconulid is posteriorly projecting on herpetheriines and nearly vertical on peradectines (Figure 3.2).

In addition to the different morphologies of the cheek teeth, there may also be some differences in the anterior dentitions of peradectines and herpetheriines. The lower incisors of *Herpetotherium* and *Copedelphys* are specialized over those of the peradectines. In both of the former herpetheriines, the first two lower incisors are greatly enlarged (compared with i3 and i4) and procumbent (Fox, 1983; Korth, 1994). In *Peradectes*, the first two incisors are the largest but are closer in size to the last two incisors and nearly vertically implanted (Fox, 1983). Also, in another peradectine, *Nanodelphys*, the first three lower incisors are subequal in size (not greatly enlarged) and also nearly vertically oriented (Gazin, 1935). However, the enlargement and horizontal orientation of the first two incisors of the North American herpetheriines is not necessarily the same in European didelphids, where these incisors are enlarged but not procumbent (Crochet, 1980).

Herpetheriines and peradectines appear to be separate throughout their occurrence in the Tertiary. Species of these subfamilies commonly co-occur, but peradectines, although they appear first in the fossil record (Cretaceous), become extinct by the latest Oligocene (Arikarean [Martin, 1973]), before the last occurrence of didelphids in the Barstovian (Slaughter, 1978).

INCLUDED GENERA OF MARSUPIALIA ILLIGER, 1811

The locality numbers listed for each genus refer to the list of unified localities in Appendix I. The locality numbers may be listed more

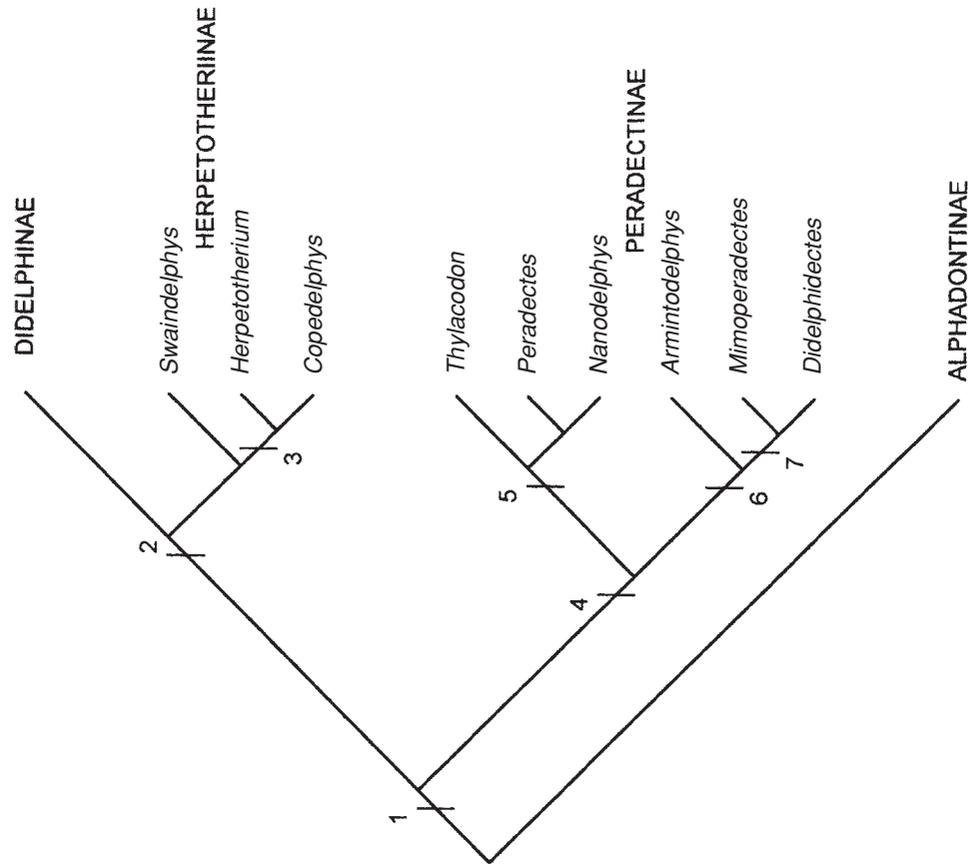


Figure 3.2. Suggested generic relationships of North American Tertiary marsupials. 1. Paracone lower than metacone, styler cusp A smaller and more closely approximated to B at level of styler shelf; preparamacrista running from paracone to a point anterior to cusp B; conules and internal conular cristae reduced in size; absence of postmetaconular crista; cristid obliqua meeting posterior wall of trigonid labial to protocristid notch (Johanson, 1996, his Fig. 3.3). 2. V-shaped centrocrista on upper molars (dilambdodonty); metacone markedly larger than paracone; hypoconulid projecting posteriorly on lower molars. 3. First two lower incisors enlarged and procumbent. 4. Reduction of styles and conules on upper molars; entoconid on lower molars vertically oriented and closely appressed to hypoconulid. 5. Further progressive reduction of styler cusps and conules on upper molars. 6. Entoconid on lower molars reduced. 7. Cheek teeth and mandible more massive, premolars crowded.

than one way. The acronyms for museum collections are listed in Appendix II.

Brackets around a locality (e.g., [CP101]) mean that the taxon in question at that locality is cited as an “aff.” or “cf.” the taxon in question. Parentheses are usually used for individual species, implying that the genus is firmly known from the locality, but the actual species identification may be questionable. Question marks in front of the locality (e.g., ?CP101) mean that the taxon is questionably known from that locality, implying some doubt that the taxon is actually present at that locality, either at the genus or species level. An asterisk (*) indicates the type locality.

HERPETOTHERIINAE

The changes in *Herpetotherium* and *Copedelphys* through their Tertiary record is mainly in overall size and relative size of the styler cusps of the upper molars (Korth, 1994). In both, their overall size is reduced through time. In *Herpetotherium*, styler cusp B (primitively the largest) is progressively reduced and the central styler

cusp becomes dominant. It is likely that *Copedelphys* was ultimately derived from an Eocene species of *Herpetotherium*.

Another genus of herpetotheriine, *Swaindelphys*, appears much earlier in the fossil record and is distinct from later herpetotheriines in the more primitive condition of the molars: shorter talonid, hypoconulid not directed posteriorly, no dominant styler cusp on upper molars (Johanson, 1996). There is no morphology of *Swaindelphys* that would bar it from an ancestral position with either *Herpetotherium* or *Copedelphys*.

***Herpetotherium* Cope, 1873 (including *Peratherium*, in part; *Didelphis* [including *Didelphys*], in part; *Entomacodon*; *Centraconodon*)**

Type species: *Herpetotherium fugax* Cope, 1873.

Type specimen: AMNH 5254.

Characteristics: Central, dominant styler cusp on upper molars (cusp D on M1–2, cusp C on M3–4); styler cusps C and D progressively fuse on M1–2; styler cusp B progressively reduced; i1–2 enlarged and procumbent.

Average length of m2: 1.92 mm.

Included species: *H. fugax* (including *Herpetotherium* [= *Peratherium*] *scalare*, *Herpetotherium* [= *Peratherium*] *tricuspis*, *Didelphys pygmaea*, *Didelphys tricuspis*, *Didelphys scalare*, *Didelphys pygmaea*, *Peratherium* sp. cf. *P. spindleri*, *Peratherium* [*Herpetotherium*] *fugax*) (known from localities CP46, CP68[B], C*, [D], [CP84A-C], CP98B, C, NP10B2, BB, NP24C, D, NP27C1, D, NP32B, C, NP37, [NP49II]); *H. comstocki* (Cope, 1884) (including *Peratherium comstocki*, type locality unknown) (localities ?SB22C, ?SB24, SB42, SB43A, CP20A, BB, CP25A, CP27E, CP34D); *H. edwardi* (Gazin, 1952) (including *Peratherium edwardi*) (locality CP25G*); *H. knighti* (McGrew, 1959) (including *Entomacodon minutus*, *Centracodon delicatus*, *Peratherium knighti*, *Peratherium morrisi*) (localities GC8AA, [CC4], [CC7E], [CC9A, AA], CP25I, J, [CP29C, D], CP31E, CP34A, D*, [CP36A], [CP38A, B], [CP63], CP65, CP101, NP8, NP9A, [NP22]); *H. merriami* (Stock and Furlong, 1922) (including *Peratherium merriami*) (localities [GC7], PN6C1*); *H. marsupium* (Troxell, 1923) (localities SB42, SB43A, B, CP5A, CP25I2, CP27B, D, E, [CP29C, D], [CP31E], [CP32], CP34A, [B, C], D, NP8, NP9A); *H. valens* (Lambe, 1908) (including *Didelphys valens*, *Peratherium valens*, *Peratherium donahoei*) (localities [CC8IIB], NP10B, B2, NP24D, NP25B, C, NP27C, C1, D, NP49II); *H. youngi* (McGrew, 1937) (including *Peratherium youngi*, *Peratherium spindleri*) (localities CP85C, CP86B, CP101, CP103B*, NP10CC).

Herpetotherium (including *Peratherium*) sp. is also known from a large number of localities including GC8A, AB, CC6A, CC7A, B, CC8, CC9IVC, ?SB39IIA, SB44A, ?SB46, ?CP13G, CP25A, GG, J2, CP31A, C, CP32B, CP34C, E, CP35, CP36B, ?CP38C, CP39?B, C, ?F, CP64A, ?CP83C, CP84B, C, CP88, CP99C, NP9B, NP10Bi, Bii, C, C2, CC, NP23A, NP25A, NP34A, NP36A, B, D, PN6D3.

Comments: Cope (1873) first named *Herpetotherium* but considered it an insectivore. Later, Cope (1884) recognized that it was a marsupial and referred all of the species he had proposed to the previously named European genus *Peratherium* Aymard (1846), an allocation followed by most later authors for nearly a century. Crochet (1977, 1980) referred all of the North American "*Peratherium*" to Cope's original genus, leaving only the European species in *Peratherium*. Fox (1983) described the anterior dentition of *Herpetotherium*, noting its difference from the European species and allocated only the type species to *Herpetotherium*. This practice was followed by a number of authors (Krishtalka and Stucky, 1983a; Reig, Kirsch, and Marshall, 1985). Korth (1994) described the anterior dentition of a number of North American species, demonstrating that the characters used by Fox (1983) were consistent with several post-Duchesnean (early late

Eocene) species, thus referring all of these species to *Herpetotherium*, but retaining all earlier Eocene and Paleocene species in *Peratherium*.

More recently, Rothecker and Storer (1996) demonstrated that the distinctions between the cheek teeth of *Peratherium* and *Herpetotherium* cited previously (Crochet, 1977; Korth, 1994) were also recognizable in the earliest Tertiary didelphids, and referred these early species to *Herpetotherium*. Most recently, in their classification of all mammals, McKenna and Bell (1997) followed Crochet and others by including all of the North American species in *Herpetotherium* and European species in *Peratherium*. It should be noted that the European taxon *Peratherium constans* has been recognized at locality GC21II (Beard and Dawson, 2001).

***Esteslestes* Novacek *et al.*, 1991**

Type species: *Esteslestes ensis* Novacek *et al.*, 1991.

Type specimen: IGM 3688.

Characteristics: Relatively large size; dentary relatively deep; lower molars with relatively weak entoconid notch and labially positioned hypoconulid; m3 talonid relatively broad; p3 relatively tall and trenchant.

Average length of m3: 3.10 mm.

Included species: *E. ensis* only, known from locality CC50 only.

Comments: *Esteslestes* is known from Baja California and is represented by the type specimen only. Novacek *et al.* (1991) originally placed it in the tribe Didelphini but their concept of that tribe is similar to what is recognized here as Herpetotheriinae (these authors also included North American *Herpetotherium* within their Didelphini). *Esteslestes* does differ from other known herpetotheriines in having a much deeper and more robust dentary and more labially positioned lower molar hypoconulids, both features that are in common with extant *Didelphys*. Novacek *et al.* (1991) also noted some character states that are similar to South American marsupials, especially *Mirandotherium*. It is possible that *Esteslestes* belongs in a separate subfamily from other North American herpetotheriines but this determination must await the discovery of more complete material.

***Copedelphys* Korth, 1994 (including *Peratherium* [including *Herpetotherium*], in part; *Herpetotherium*, in part; *Nanodelphys*, in part)**

Type species: *Copedelphys titanelix* (Matthew, 1903) (originally described as *Peratherium titanelix*).

Type specimen: AMNH 9603.

Characteristics: Small size; stylar cusps B, C, and D on upper molars equal in size; stylar cusp D elongated and obliquely oriented; M1 wider relative to length; conules on upper molars minute; p2 and p3 subequal in size; p3 markedly smaller than m1; trigonid of m1 more widely

open lingually; i1 and i2 enlarged and procumbent as in *Herpetotherium*.

Average length of m2: 1.26 mm.

Included species: *C. titanelix* (Matthew, 1903) (including *Peratherium titanelix*, *Peratherium titanohelix*) (known from localities NP10B, NP24C*, D, [NP25B, C], NP27D); *C. innominata* (Simpson, 1928) (including *Peratherium innominatum*, *Peratherium mcgrewi*) (localities [CC4], CP5A, CP5II, CP20AA, CP25I1, CP27D, E, CP29C, D, [CP31E], CP33B, CP34A–B, C, D, CP63, CP65, NP8, NP9A); *C. stvensoni* (Cope, 1873) (including *Herpetotherium stvensonii*, *Peratherium huntii*, in part, *Didelphis huntii*, in part, *Herpetotherium stvensoni*, *Nanodelphys* n. sp., in part) (localities CP46, CP68C*, [NP32B, C]).

Copedelphys sp. is also possibly known from locality CP67.

Comments: The Cedar Ridge Fauna of Setoguchi (1978) (locality CP46), which contained referred specimens of *Copedelphys stvensoni*, is not Whitneyan in age as originally cited but is rather Orellan (Korth, 1989). Although *Peratherium innominatum* Simpson (1928) has been allocated exclusively to the European genus *Peratherium*, Rothecker and Storer (1996) demonstrated that it was a more primitive species of *Copedelphys*, thus extending the record of the genus into the Duchesnean.

***Swaindelphys* Johanson, 1996**

Type species: *Swaindelphys cifellii* Johanson, 1996.

Type specimen: AMNH 100417C, right m3.

Characteristics: Upper molars with greater transverse width to length ratio on M2 and M3; ectoflexus present on M2, small and symmetrical ectoflexus present on M3; anterior stylar shelf wider on M2 and M3; posterior stylar shelf more posterolabially directed than posteriorly directed on M2 and M3; stylar cusps A and B separated by a distinct notch; stylar cusps C and D approximately equal in size; cusp B larger than C and D but no stylar cusp clearly dominant on M1–3; talonid anteroposteriorly short on lower molars; hypoconulid lower than other herpetotheriines and directed posterolabially (talonid basin not open posteriorly).

Average length of m2: 2.05 mm.

Included species: *S. cifellii* only, known from locality CP14A only.

Comments: *Swaindelphys* is the earliest and most primitive species of herpetotheriine from North America. It occurs in the Torrejonian (Johanson, 1996) whereas the earliest occurrence of any other herpetotheriine in North America is Wasatchian (Krishtalka and Stucky, 1983a).

PERADECTINAE

Unlike the herpetotheriines, there is little difference in the size of peradectines throughout their Tertiary occurrence. One lineage or

clade of peradectines includes *Thylacodon*, *Peradectes*, and *Nanodelphys*. Among these genera, there is a reduction in the development of stylar cusps and conules on the upper molars. *Thylacodon*, the early Paleocene genus, has much more distinct stylar cusps and conules (Archibald, 1982), whereas these features are progressively reduced in Eocene *Peradectes* (Krishtalka and Stucky, 1983a) and nearly completely lost in Oligocene *Nanodelphys* (Korth, 1994). There is also a change in the proportions of the upper molars. In *Nanodelphys*, the upper molars are much more transversely elongated than in earlier genera.

Three distinctive genera of peradectines, *Didelphidectes*, *Arminotodelphys*, and *Mimoperadectes*, share the unique feature of a reduced entoconid on m4. Both *Didelphidectes* and *Mimoperadectes* are also characterized by more robust cheek teeth and dentaries, features that are lacking in *Arminotodelphys* (Bown and Rose, 1979; Krishtalka and Stucky, 1983b; Korth, 1994). These three genera are clearly distinct and separable from the *Thylacodon*–*Peradectes*–*Nanodelphys* clade, but it is uncertain whether they form a distinct clade of their own.

***Peradectes* Matthew and Granger, 1921 (including *Peratherium* [including *Herpetotherium*], in part; *Nanodelphys*, in part)**

Type species: *Peradectes elegans* Matthew and Granger, 1921.

Type specimen: AMNH 17376.

Characteristics: Talonids on m1–3 short; labially positioned cristid obliqua; entoconid and hypoconulid subequal in height on lower molars; M1–3 paracone and metacone subequal in size; stylar cusps and conules on upper molars weak; posterolingual part of the base of protocone not expanded on upper molars.

Average length of m2: 1.82 mm.

Included species: *P. elegans* (known from localities SB20A*, CP13E, G, CP16A, CP24A, CP63, NP3A, C, D, NP4, NP15C, NP16A, NP47B); *P. californicus* (Stock, 1936) (including *P. californicum*, *Nanodelphys californicus*) (localities CC4, CC6B, CC7B, D, E, CC8, CC8IIA, CC9A*, [AA], B2, CC9IVA, CC10, CP29C, D, NP8, NP9A); *P. chesteri* Gazin, 1952 (localities CP5A, [CP18B], CP20A, ?D, CP25G*, ?I, CP27D, CP34A, B, D); *P. pauli* Gazin, 1956 (localities CP16A*, [NP19IIA]); *P. protinnominatus* McKenna, 1960 (including *Peradectes chesteri*, in part, *Peradectes* cf. *chesteri*) (localities CP14E, CP15B, CP17B, CP20AA, [BB], CP25B, CP27A, CP63*, NP4, [NP20E]).

Peradectes sp. is known from localities CC1, CC4, CC6A, CC7A, CC8IIB, CC9A, SB23A, B, F, H, CP13A, [CP14D], [CP15A], [CP17A], CP20BB, CP25GG, J2, CP31C, CP34C, E, CP36B, NP1C, [NP20B], NP47C, NP49II.

Comments: *Peradectes* is also known from the Late Cretaceous to early Paleocene of South America, from the early Eocene of Europe, and also possibly from the Late Cretaceous of North America (some of these instances may be of *Thylacodon*, see below) (McKenna and Bell, 1997).

***Thylacodon* Matthew and Granger, 1921 (including *Peradectes*, in part)**

Type species: *Thylacodon pusillus* Matthew and Granger, 1921.

Type specimen: AMNH 16414.

Characteristics: Large size for a peradectine; conules and stylar cusps on upper molars large; stylar cusp B is the largest, cusps C and D small to absent; entoconid on lower molars more posterior than in other peradectines, closer to the hypoconulid.

Average length of m2: 2.47 mm.

Included species: *T. pusillus* only (including *Peradectes* cf. *P. pusillus*) (known from localities SB23A*, B, [CP11IIB, G], CP12A, [NP16A]).

Comments: Archibald (1982) considered *Thylacodon* a synonym of *Peradectes*. This suggested synonymy has been followed by some later authors (Marshall, Case, and Woodburne, 1990; McKenna and Bell, 1997) and not by others (Krishtalka and Stucky, 1983a; Johanson, 1996). Krishtalka and Stucky (1983a) felt that the difference between *Thylacodon* and *Peradectes* was so great that they suggested that the former was likely referable to a different subfamily.

***Nanodelphys* McGrew, 1937 (including *Herpetotherium*, in part; *Miothen* [= *Domnina*] in part; *Domnina*, in part; *Peratherium* [= *Herpetotherium*], in part; *Peradectes*, in part)**

Type species: *Nanodelphys huntii* (Cope, 1873) (originally described as *Herpetotherium huntii*).

Type specimen: AMNH 5266.

Characteristics: Small size; upper molars relatively wider than long; stylar cusp B only major distinguishable stylar cusp on upper molars, remainder reduced to a low rim along buccal edge of stylar shelf; conules minute to absent on upper molars; trigonids of lower molars narrower and more elongated; entoconids of lower molars not reduced.

Average length of m2: 1.48 mm.,

Included species: *N. huntii* only (including *Herpetotherium huntii*, *Miothen gracile*, *Domnina gracilis*, *Peratherium huntii*, *Didelphis huntii*, *Nanodelphys minutus*, *Herpetotherium fugax*, in part, *Peradectes minutus*) (known from localities CP46, CP68C*, CP84C, CP98B, CP99A, B, [NP8], [NP10BB], NP32C, NP36?A, ?B, D).

Nanodelphys sp. is also known from localities CP41B, CP101 (Martin, 1973), NP10CC.

***Mimoperadectes* Bown and Rose, 1979**

Type species: *Mimoperadectes labrus* Bown and Rose, 1979.

Type specimen: UM 66144.

Characteristics: Large size; cheek teeth more robust than other North American marsupials; paraconids on lower molars larger than metaconids; paraconid less removed anteriorly; metaconid posterolingual to protoconid; trigonid both longer and wider than talonid; talonid width

decreases from m2 to m4; entoconids reduced on lower molars; stylar cusp B largest on upper molars, all others small; conules reduced.

Average length of m2: 2.97 mm.

Included species: *M. labrus* only (known from localities GC21II, ?CP18B, CP19A*, A, CP20AA, A, CP62C, CP64B).

***Armintodelphys* Krishtalka and Stucky, 1983b**

Type species: *Armintodelphys blacki* Krishtalka and Stucky, 1983b.

Type specimen: CM 41159.

Characteristics: Entoconid lower and smaller than hypoconulid; talonid narrower than the trigonid on m1–2.

Average length of m2: 2.0 mm.

Included species: *A. blacki* (known from localities CP27D*, E); *A. dawsoni* Krishtalka and Stucky, 1983b (localities CP5A, CP27D, E).

Cf. *Armintodelphys* sp. is also known from locality CP34A.

***Didelphidectes* Hough, 1961**

Type species: *Didelphidectes pumilis* Hough, 1961.

Type specimen: USNM 20084.

Characteristics: Cheek teeth more robust than alphadonines, less robust than *Mimoperadectes*; trigonids on lower molars subequal in width to talonids; entoconids on lower molars reduced; trigonid cusps subequal in size; lower premolars massive, p2 longer than p3; m4 longest of the lower molars.

Average length of m2: 1.65 mm.

Included species: *D. pumilis* only (known from localities NP10B, NP24C*).

Comments: McKenna and Bell (1997) recently considered *Didelphidectes* a junior synonym of *Nanodelphys*. However, the more robust nature of the cheek teeth and reduction of the entoconid on the lower molars of *Didelphidectes* is not present in species of *Nanodelphys*, making the former a distinct genus (Korth, 1994).

MISCELLANEOUS DIDELPHIDAE

Typically Mesozoic marsupials, including *Alphadon rhaisiter*, *Pediomys hatcheri*, *Pediomys elegans*, *Pediomys florencae*, *Pediomys krejci*, *Glasbius twitchelli*, and *Didelphodon vorax*, have been recognized from earliest Paleocene localities (NP15C, NP16A) in Montana (Lofgren, 1995).

Unidentified didelphids have been reported from Tertiary localities GC4C, GC8DB, CC1, ?CC9BB, ?SP1D, NP6, NP17, NP34D, PN9B. Other than its numerous occurrences in the Pleistocene and widespread extant distribution, the only Tertiary record of *Didelphis virginiana* in North America is from late Blancan deposits in Florida (locality GC14A).

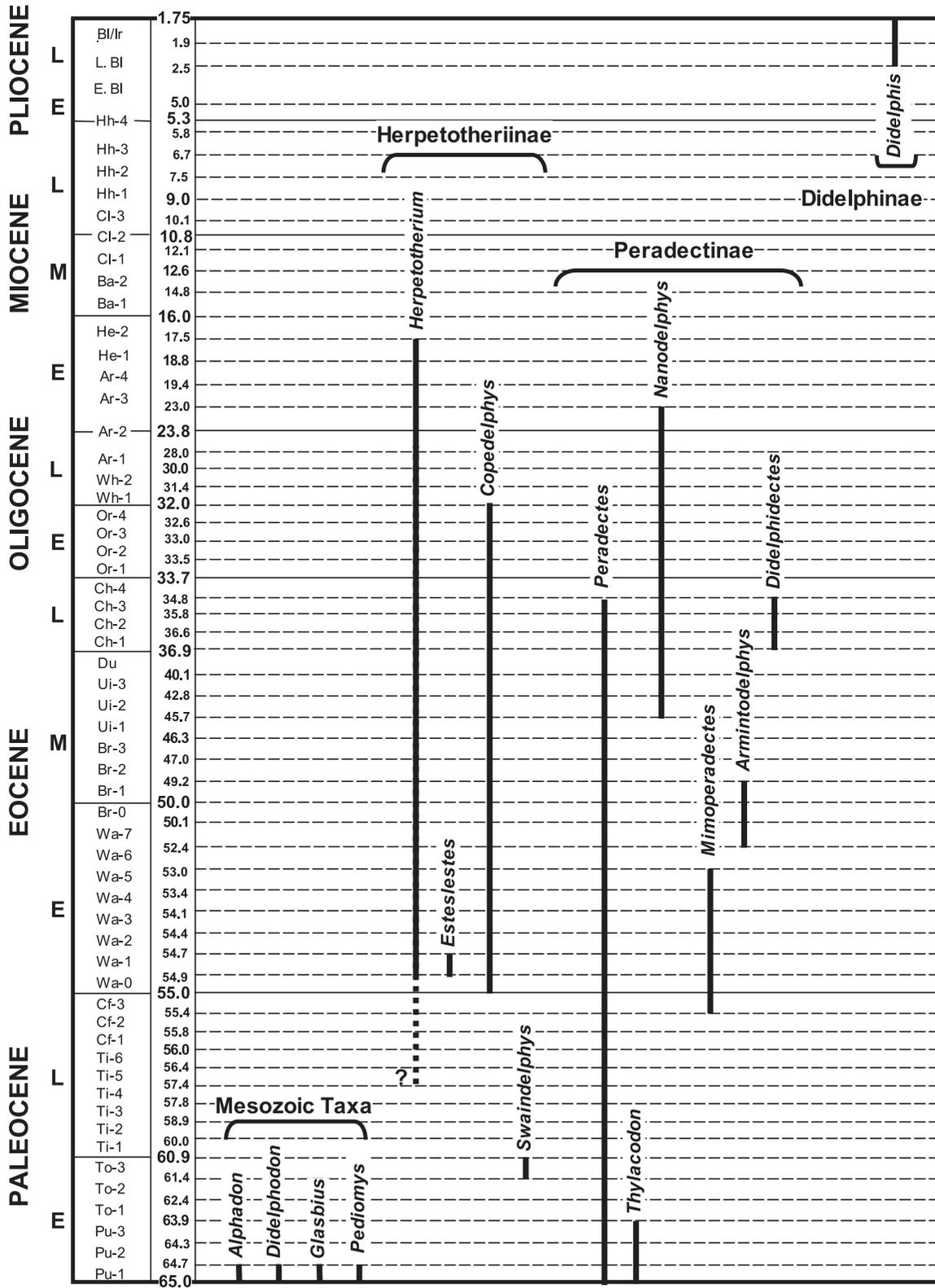


Figure 3.3. Temporal ranges of North American marsupial genera.

BIOLOGY AND EVOLUTIONARY PATTERNS

The fundamental differences between metatherian and eutherian reproductive biology have been well documented (see Lillegraven [1979] for an overview) and there is no need for further discussion here. Generally speaking, most North American Tertiary marsupials were quite small with even the largest known taxon (*Mimoperadectes labrus*) barely attaining half the size of extant North American *Didelphis virginiana*.

The relatively primitive and generalized nature of Tertiary marsupial dentitions indicate that most taxa were probably opportunistic omnivorous species that fed on a variety of plants, insects, invertebrates, eggs, and small vertebrates (Clemens, 1979) (Figure 3.3). *Mimoperadectes* is characterized by somewhat more robust teeth, suggesting that this taxon may have utilized more fruits in its diet while *Didelphidectes* has relatively enlarged premolars, indicating that it may have specialized on harder food objects such as small shellfish, tough-skinned fruits, and nuts. What little is known of early marsupial postcranial anatomy indicates that most taxa were terrestrial, generalized quadrupeds; however, some peradectines may have been scansorial or arboreal.

North American marsupials first appeared in the Cretaceous (Cifelli, 1993, 1999; Cifelli and Muizon, 1997) and most of their diversification occurred before the Tertiary. Lineages that crossed the Cretaceous–Tertiary boundary had their origins in the late Mesozoic. There was surprisingly little subsequent taxonomic diversification and increased morphological disparity was limited to subtle changes in dental characters (few cranial or postcranial specimens of Tertiary marsupials are known – additional morphological diversification may have manifest itself in these character complexes). Marsupials are essentially absent from the North American fossil record by the end of the Oligocene and do not make a reappearance until the latest Pliocene in the form of *Didelphis virginiana*, an immigrant from South America. The demise of marsupials in the early Miocene may have been a result of the invasion of North America (from Europe) by procyonine carnivores in the Hemingfordian (Baskin, 1998). Extant North American procyonines (raccoons, ringtails, coatis) are scansorial or arboreal omnivores. Their ancestral populations likely would have been in direct ecomorphospace competition with marsupials.

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Part II: Insectivorous mammals

4 Insectivorous mammals summary

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INTRODUCTION

GENERAL CONSIDERATIONS

The idea of “Insectivora” serving as a waste-basket taxon for a variety of extinct and extant small, insectivorous mammals has had a relatively long history (Symonds, 2005). For the purposes of this book, we have chosen to recognize three groups of North American insectivorous mammals: the potentially monophyletic Leptictida and Lipotyphla, and the clearly polyphyletic “Proteutheria.” Leptictids and proteutherians are only represented by extinct taxa, while lipotyphlans are abundant and diverse from the Paleocene to the Recent. It is nearly certain that these three groups do not share common ancestry except perhaps at a very basal level within the mammalian tree where insectivore-grade stem lineages may have given rise to a number of different mammalian groups (Asher, 2005).

Modern lipotyphlans are represented by nearly 400 species included in four families, Erinaceidae, Solenodontidae, Soricidae, and Talpidae. We consider the families Tenrecidae, Potamogalidae, and Chrysochloridae to be members of Afrotheria and distinct from Lipotyphla (Asher, Novacek, and Geisler, 2003; Springer *et al.*, 2005). Among living mammals, lipotyphlan diversity is eclipsed only by bats (approximately 1000 species) and rodents (over 2000 species). Lipotyphlans are common on all of the northern continents, have modest representation in Africa and Madagascar, and have recently colonized South America (represented by the soricid *Cryptotis*). Lipotyphlans are lacking in Australia and Antarctica but are present on the islands of the Philippines and the Greater Antilles (Symonds, 2005).

FEATURES UNITING INSECTIVOROUS MAMMALS

Butler (1972, p. 254) noted that there is no way to define an order Insectivora “except by exclusion of the specializations which distin-

guish the other orders.” In gross anatomical terms, living insectivorous mammals can be described as being relatively small (ranging from 2 g to about 1 kg), having elongate snouts (often extremely mobile), relatively small eyes and ears, relatively small brains with smooth cerebral hemispheres, pentadactyl and plantigrade feet, and rudimentary endothermy (Eisenberg, 1980; Symonds, 2005).

However, searching for shared and derived characters that unite insectivorous mammals is a difficult task. Asher (2005), in a comprehensive review of the morphological similarities that have been used to define an order Insectivora, found only two characters that were potentially consistent with insectivore monophyly (including lipotyphlans, tenrecs, chrysochlorids, and potamogalids): a reduced pubic symphysis and a simplified intestinal tract including absence of the cecum. Yet both of these characters can be found in other mammals (in a variety of groups for the former and in some bats, pangolins, and some dolphins for the latter), although the absence of a cecum may well represent a shared and derived character of Lipotyphla (and convergently Afrosoricoidea [also known as Tenrecoidea] as well). An additional potential synapomorphy for Lipotyphla is a posteriorly expanded maxilla found in conjunction with a ventrally restricted palatine (Asher, Novacek, and Geisler, 2003; Asher, 2005).

The addition of fossil taxa makes any definition of insectivorous mammals even more difficult, especially since so many early fossil forms are represented only by a handful of teeth and jaws. In some cases, fossil taxa have simply been referred to the insectivoran-grade taxa Soricomorpha or Erinaceomorpha based on phenetic similarity in tooth and dental patterns. In other cases, it is not possible to assign fossil taxa to any living higher-level grouping either because they lack characters linking them with any extant group or because they represent clades that left no living descendants.

FEATURES DISTINGUISHING LIPOTYPHILA, LEPTICTIDA, AND “PROTEUTHERIA”

BODY SIZE

In general, all insectivorous mammals are quite small (500 g or less). However, some fossil groups attained relatively larger body sizes, especially within the proteutherian families Pantolestidae and Pentacodontidae, some members of which probably having reached body weights of 4–5 kg. The largest living insectivorans are *Erinaceus* and *Solenodon*, both of which may range up to 3 kg while the smallest living forms (*Suncus*) barely reach 2 g and are among the smallest known living mammals. Interestingly, at least one fossil insectivore seems to have achieved a relatively smaller body size within the lipotyphlan family Geolabididae, with a body mass of about 1.3 g (Bloch, Rose, and Gingerich, 1998).

LOCOMOTION AND POSTCRANIAL SPECIALIZATIONS

All living lipotyphlans are pentadactyl, plantigrade, and quadrupedal, and they usually have forelimbs shorter than hindlimbs. Most talpids and some shrews have extremely specialized forelimbs and pectoral musculature adapted for efficient digging. Most shrews have distally fused tibiae and fibulae. Proscalopids have a number of postcranial specializations reflecting extreme digging adaptations (including head digging). These specializations include a shortened neck with some co-ossification of cervical vertebrae, fusion of the first rib and manubrium, elevated deltoid crest of scapula, long clavicle, rotary burrowing modifications of the humerus and forelimb, a laterally compressed humeral head, a broad distal humerus, pectoral crest of humerus terminating in a spike or plate, teres tubercle extending distally beyond midshaft, transversely expanded ulnar olecranon process, and tibia and fibula unfused (Barnosky, 1982).

Lipotyphlans practice terrestrial, fossorial, or semi-aquatic locomotor patterns. Where known, fossil lipotyphlans are similar to their living relatives except perhaps in the case of the soricomorph family Nyctitheriidae. Hooker (2001) has suggested that at least some nyctitheriids were arboreal, based on the structure of isolated tarsal elements from the late Eocene of England.

Leptictids have shorter forelimbs than hindlimbs and have distally fused tibiae–fibulae. They were probably terrestrial mammals that were capable of rapid running and quadrupedal jumping (Rose, 1999). The structure of the forelimb indicates that leptictids may have been accomplished diggers as well (Cavigelli, 1997; Rose, 1999).

In general, most proteutherians are poorly represented by postcranial material. A single partial forelimb is known of a palaeoryctid and indicates that these animals may have been fossorial diggers although not nearly as specialized as talpids (Van Valen, 1966).

Pantolestids are small to moderate in size and in general, larger than other proteutherians. In overall limb proportions, *Pantolestes* resembles extant otters and was probably otter-like in habits (Matthew, 1909). Pfretzchner (1999) noted aquatic adaptations in the European pantolestid *Buxolestes piscator*. Following Koenigswald (1980), he noted osteological features indica-

tive of strong neck and tail musculature including a long spinous process on C2, broad and enlarged vertebral mammillary processes, and spinous processes that expanded craniocaudally. Rose and Koenigswald (2005) described a nearly complete skeleton of *Palaeosinopa*, the oldest known pantolestid skeleton, from the Eocene Green River Formation of Wyoming. They noted strong similarities to *Buxolestes* and suggested that pantolestids as a group were semi-aquatic mammals with a propensity for digging, most similar among extant mammals to river otters (*Lutra* and *Lontra*) and beavers (*Castor*). They hypothesized that during swimming, *Palaeosinopa* propelled itself by hindlimb paddling and dorsoventral tail undulation.

Apatemyids such as *Apatemys* (Koenigswald *et al.*, 2005) and *Labidolemur* (Bloch and Boyer, 2001, Bloch, Boyer, and Houde, 2004) are known by nearly complete skeletons. They document the arboreal nature of apatemyids and also indicate that these taxa have specialized finger elongation like that seen in the European apatemyid *Heterohyus*. Apatemyids may have been similar to extant *Dactylopsila* (the striped possum) and *Daubentonia* (the aye-aye lemur), which utilize elongate hand digits for percussive feeding in search of tree-boring insects (Koenigswald and Schierner, 1987; Koenigswald, 1990; Fleagle, 1999; Bloch and Boyer, 2001; Bloch, Boyer, and Houde, 2004; Kalthoff, Koenigswald, and Kurz, 2004; Koenigswald *et al.*, 2005). These mammals have been perceived as taking a similar ecological niche to woodpeckers: it is interesting to note that apatemyids did not survive past the appearance of woodpeckers (birds) in the mid Cenozoic, but places where the striped possum and the aye-aye are found (Australia and Madagascar, respectively) are islands where there have never been woodpeckers.

DIET AND CRANIODENTAL SPECIALIZATIONS

Lipotyphlan skulls indicate animals that rely predominantly on olfaction for locating insect prey. The skulls are generally low with laterally facing small orbits, small braincases, and long snouts. Auditory bullae range from unossified to solidly ossified with minor inflation. Proscalopid skulls appear to be functionally convergent on Chrysochloridae (Barnosky, 1981), animals that use their heads in burrowing. Proscalopid skulls have fused cranial bones (in adults), a long rostrum, broad and deep cranium with ventrally placed condyles, premaxillae with prominent lateral shelves, and slightly inflated tympanic bullae. Unlike proscalopids, talpids do not use their heads in digging. Their skulls are relatively long and shallow with unfused cranial bones and thin and low zygomatic arches and they lack jugals. Geolabidid skulls have a very long, tubular rostrum and lack zygomatic arches. Apternodontids have well-developed sagittal crests and develop lambdoid plates on the posterolateral braincase (Asher *et al.*, 2002). Soricids tend to have inflated braincases, have either weak or absent zygomatic arches, lack jugals, and have relatively large ectotympanics that lie horizontally. Erinaceids have complete zygomatic arches and relatively large orbits.

Teeth vary from acutely cusped to more flattened with rounded, low cusps. In some forms, posterior premolars become specialized for crushing and grinding while in others anterior incisors become



Figure 4.1. Restoration of the early Tertiary leptictid, *Leptictis* (by Marguette Dongvillo).

enlarged for specialized food acquisition. In general, insectivoran teeth indicate dietary specializations predominantly for invertebrate prey, although the teeth in some forms indicate a more omnivorous diet (many erinaceomorphs) or other specializations (fruit and fish feeding in pantolestids; Koenigswald, 1980; Richter, 1987; Rose and Koenigswald, 2005).

Erinaceomorphs have quadritubercular upper molars and lower molars with distinct trigonids and well-developed talonids. Many erinaceomorphs have molars that reduce in size from first to last. Proscalopids have enlarged anterior incisors and exhibit loss of anterior cheek teeth in more derived taxa. Proscalopid molars range from brachydont to hypsodont in derived forms. Talpids are dilambdodont, with primitive forms retaining all teeth but later forms losing anterior cheek teeth and often having enlarged incisors. Apternodontids, parapternodontids, and oligoryctids all have very specialized zalambdodont dentitions. Apternodontids have enlarged anterior incisors while oligoryctids have extremely reduced lower molar talonids. In plesiosoricids, the second lower incisor is enlarged and procumbent and upper molars lack dilambdodonty. Soricids have dilambdodont upper molars, a distinct, enlarged, hooklike upper incisor, simple unicuspid teeth between the first upper incisor and the upper fourth premolar, and an enlarged and procumbent anterior lower incisor.

In general cranial proportions, leptictids were similar to extant tupaiids and macroselidians and probably had elongate, mobile noses (see Figure 4.1) (Novacek, 1986). Dentitions indicate that leptictids were primarily insectivorous and omnivorous.

Palaeoryctids have relatively low and elongate skulls with distinct but low sagittal crests, incomplete zygomatic arches, and ossified auditory bullae (Thewissen and Gingerich, 1989; Bloch, Secord, and Gingerich, 2004). Upper molars were protozalambdodont with closely appressed, connate paracones and metacones, while lower

molars had high trigonids and narrow talonids. Shearing crests were well developed on cheek teeth indicating an insectivorous diet.

Cimolestids are poorly represented by cranial material. What little is known indicates that these animals are characterized by low skulls with broad nasals, small lacrimal exposure on the face, a single sagittal crest, flaring nuchal crests, and lacking an ossified bulla (Van Valen, 1966). Cimolestids have small and procumbent incisors, enlarged canines, premolariform premolars, upper molars lacking hypocones, and lower molars with high trigonids. Lower molars increase in size posteriorly.

Pantolestid skulls are generally characterized by having a short rostrum, an elongate and low neurocranium, a distinct postorbital constriction, a single sagittal crest, and flaring nuchal crests. The basicranium is broad, with pantolestines lacking, and pentacodontines having, ossified auditory bullae (Matthew, 1909; Gingerich, Houde, and Krause, 1983; Pfretzchner, 1999; Rose and Lucas 2000; Boyer and Bloch, 2003). Pantolestids have an enlarged and blade-like upper third incisor, large and massive canines, fourth premolars either premolariform (pantolestines) or semimolariform and enlarged (pentacodontines), and molars with relatively low and massive cusps. (Matthew, 1909; Simpson, 1937a,b; Gazin, 1959, 1969; Van Valen, 1967; Gingerich, Houde, and Krause, 1983; Pfretzchner, 1999; Rose and Lucas 2000; Boyer and Bloch, 2003).

Apatemyids have skulls that lack ossified auditory bullae, possess a groove on the promontorium marking the course of the internal carotid artery, and have a large, free ectotympanic ring, an infraorbital foramen placed above the first molar, and small foramina on the skull roof (Jepsen, 1934; McKenna, 1963; Koenigswald, 1990; Bloch, Boyer, and Houde, 2004). Apatemyid dentitions are specialized in possessing an enlarged and procumbent first lower incisor that has a root extending posteriorly to the last molar, in lacking canines, in having a lower third premolar blade-like and single rooted, lower molars low crowned with labial paraconids, simple upper molars lacking mesostyles, and a very large mental foramen placed below the lower first molar.

OTHER ANATOMICAL FEATURES

Living insectivorans exhibit some features that are uncommon in most other groups of mammals. Pinnae (external ears) are often very small or absent and eyes are always small, and sometimes very small and essentially non-functional.

Among erinaceids, hedgehogs have spiny guard hairs and specialized “drawstring muscles” that allow them to roll into a defensive ball, but gymnures have neither spines nor *panculus carnosus* muscles (Feldhamer *et al.*, 2004). Some hedgehog species that live in relatively harsh, seasonal habitats may estivate or even practice true hibernation, unlike any other known insectivoran.

Several species of living insectivorans practice rudimentary forms of echolocation. Desmans actively use echolocation for hunting and maneuvering in water (Richard, 1973). Solenodons emit high-pitched clicking noises, which may be used for prey detection, while many species of shrews emit high-frequency sounds, which presumably are used for communication, orientation, and hunting (Feldhamer *et al.*, 2004).

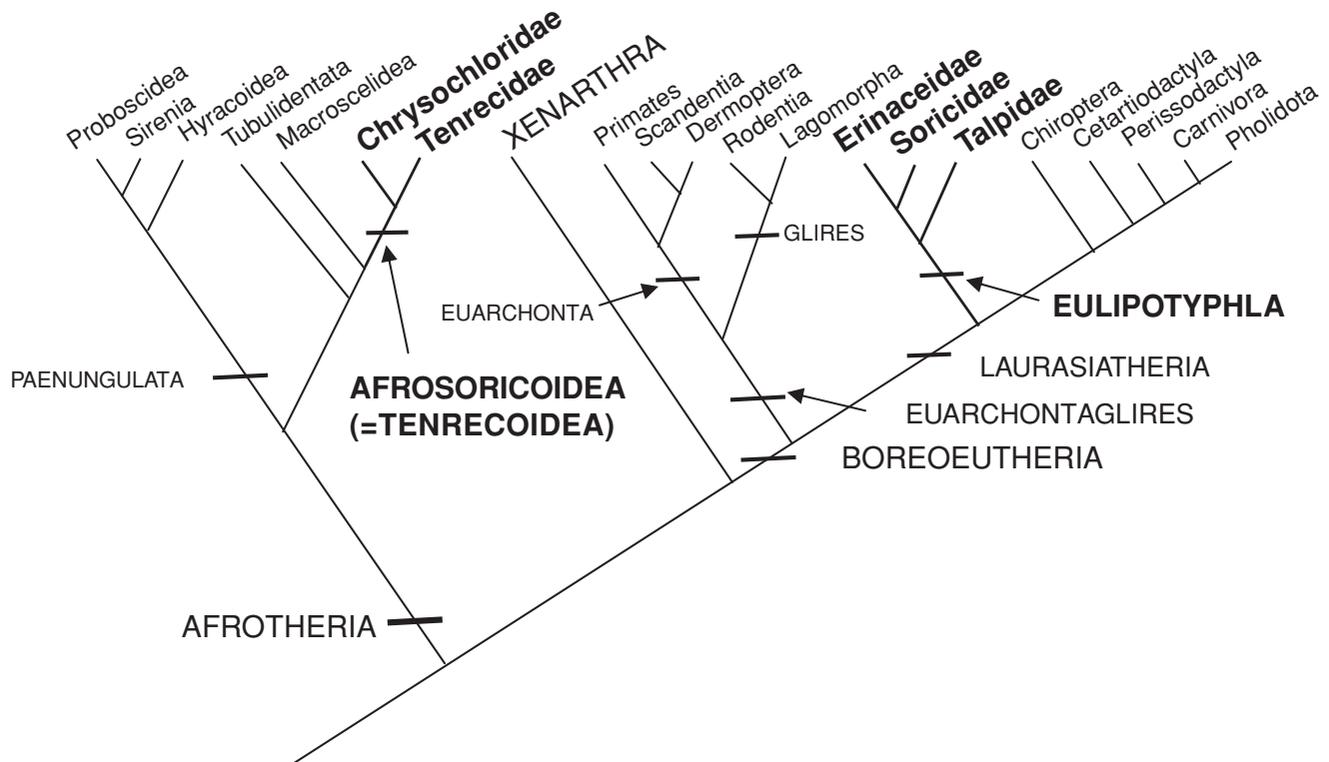


Figure 4.2. Cladogram showing the interrelationships of extant insectivorous mammals with other placental mammals. “Insectivorans” are indicated by bold face type.

Solenodons and some shrews are the only extant mammals (in addition to the platypus) that produce toxins to immobilize prey (Churchfield, 1990; Feldhamer *et al.*, 2004). In the case of *Solenodon*, there is a deep groove along the inner surface of the enlarged i2 that accommodates toxins produced by the submaxillary gland. Recently, Fox and Scott (2005) described a specimen of *Bisonalveus* (pentacodontine) from the Paleocene of Canada that potentially has a venom-delivery system via a groove in the upper canine.

SYSTEMATICS

ORIGIN AND AFFINITIES OF LIPOTYPHILA, LEPTICTIDA, AND “PROTEUTHERIA”

EXTANT FORMS

Extant animals included in this summary are represented only by the lipotyphlan families Erinaceidae, Soricidae, Talpidae, and Solenodontidae. Among these families, most authorities would agree that talpids and soricids share sister-group status while the relationships of the other two families are less clear (Figure 4.2). Based on morphological evidence alone, Butler (1956) placed erinaceids as the basal clade in his concept of Insectivora which also included tenrecs (Tenrecidae) and golden moles (Chrysochloridae). He grouped solenodontids with tenrecids as a sister clade to chrysochlorids, and that clade as sister group to a soricid–talpid clade. Butler (1988) changed his insectivore topology slightly by moving solenodontids

to sister-group status with soricids and talpids but maintained the other relationships as before. Other variations on these arrangements based on interpretation of morphological evidence were offered by McDowell (1958), Van Valen (1967), Eisenberg (1980), and MacPhee and Novacek (1993).

Shortly after the landmark study of MacPhee and Novacek (1993) had questioned the status of “Insectivora” and the position of Chrysochloridae within that “order,” Springer *et al.* (1997) and Stanhope *et al.* (1998) published papers based on mitochondrial gene sequence data indicating that golden moles and tenrecs were not closely related to soricids, talpids, erinaceids, and solenodontids, but instead were members of an African endemic mammalian radiation referred to as Afrotheria (also including aardvarks, elephant shrews, elephants, sirenians, hyraxes, and potentially some fossil groups such as ptolemaiids). In nearly every subsequent molecular phylogenetic analysis since 1998, Afrotheria has been supported, although it has proven difficult to find any morphological synapomorphies that unambiguously support this African clade (Seiffert and Simons, 2001; Asher, Novacek, and Geisler, 2003; Asher, 2005).

Recent molecular phylogenies normally support the sister-group status of soricids and talpids (Arnason *et al.*, 2002), but erinaceids and solenodontids appear in a variety of different places on phylogenetic trees (Emerson *et al.*, 1999; Douady *et al.*, 2002; Waddell and Shelley, 2003). Roca *et al.* (2004) presented molecular evidence that indicated a very early (Late Cretaceous) divergence for the extant Greater Antillean *Solenodon*. These studies suggest that there is at least a biphyletic “Insectivora” if not a triphyletic or multiphyletic “Order Insectivora” (Symonds, 2005).

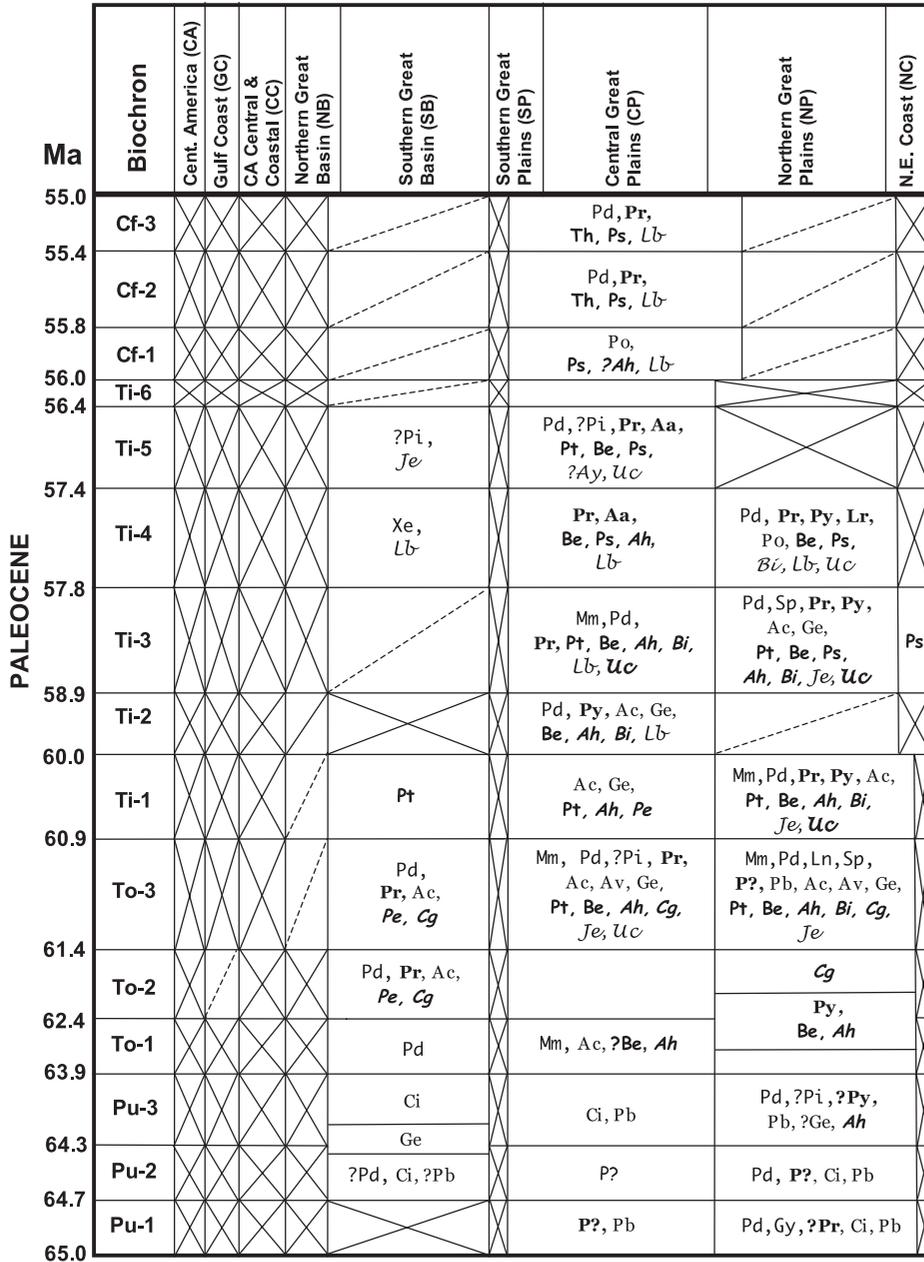


Figure 4.3. Biogeographic ranges of Paleocene proteutherians. Key: A “box” (for a particular time period in a particular biogeographic region) that has a cross through it means no fossil mammal localities are known for that time period from that area; a single dashed line through the box means only scant fossil mammal information is available (usually only a single, small locality). LEP-TICTIDA: LEPTICTIDAE (Monaco Plain): Ln, *Leptonysson*; L?, Leptictid indet.; Mm, *Myrmecoboides*; Pd, *Prodiacodon*; Pi, *Palaeictops*; Xe, *Xenacodon*. GYPSONICTOPIIDAE (Monaco Bold): Gy, *Gypsonictops*; Sp, *Stilpnodon*. PALAEOXYCTIDAE (Georgia Bold): Aa, *Aaptoryctes*; Lr, *Lainoryctes*; Pr, *Palaeoryctes*; Py, *Pararyctes*; P?, *Palaeoryctid indet.* CIMOLESTIDAE and CIMOLESTA INDET. (Georgia Plain): Ac, *Acmeodon*; Av, *Avunculus*; Ci, *Cimolestes*; Ge, *Gelastops*; Pb, *Procerberus*; Po, *Protentomodon*. PANTOLESTA: PANTOLESTIDAE: PANTOLESTINAE (Comic Sans MS Bold): Be, *Bessoecetor*; Ps, *Palaeosinopa*; Pt, *Paleotomus*; Th, *Thelysia*. PENTACODONTINAE (Comic Sans MS Bold Italics): Ah, *Aphronorus*; Bi, *Bisonalveus*; Cg, *Coriphagus*; Pe, *Pentacodon*. PANTOLESTA INCERTAE SEDIS (Comic Sans MS Plain): P?, *Pantolestid indet.* APATEMYIDAE (Lucida Handwriting): Ay, *Apatemys*; Je, *Jepsenella*; Lb, *Labidolemur*; Uc, *Unuchinia*.

FOSSIL RELATIVES

The fossil record of insectivorous mammals is ancient, abundant, diverse, geographically widespread and fraught with incompleteness and complexities. Lipotyphlans (both erinaceomorphs and soricomorphs) are known beginning in the earliest Tertiary and almost certainly originated in the Cretaceous from uncertain basal placental lineage(s). The fossil record of solenodontids is not temporally deep (Pleistocene and Recent), but extant solenodonts, both morphologically and genetically, appear to be relicts of an ancient (perhaps even Cretaceous) radiation.

Insectivorous groups only known by fossils, including proteutherians, leptictids, and a variety of early lipotyphlans, are difficult to place taxonomically. The origins of most can be traced in a vague

way to the archaic roots of the mammalian tree but few (if any) can be traced to specific ancestral lineages. Nearly all probably had their origins in the Cretaceous of Laurasia, either in North America or Asia.

EVOLUTIONARY AND BIOGEOGRAPHIC PATTERNS

GENERAL TRENDS

Figures 4.3–4.9, below, summarize the biogeographic ranges of insectivorous mammals in the North American fossil record. Most of the earliest appearances in the Cenozoic are represented by

proteutherians or leptictids with only the Late Cretaceous holdover taxon *Batodon* and relatively sparse records of *Adunator*, *Leptacodon*, and *Litocherus* representing lipotyphlans before the late Paleocene. It is not until the latest Paleocene (middle Clarkforkian onward) that lipotyphlan diversity began to outstrip that of proteutherians and leptictids, a trend that continued through the Eocene. By the end of the Eocene, proteutherian and leptictid diversity was greatly reduced but both groups survived into the late Oligocene. Leptictids had their last known occurrence in the late Whitneyan, represented by *Leptictis*, while proteutherians hung on until the early Arikarean, represented by the enigmatic apatemyid *Sinclairiella*.

The lipotyphlan radiation can be usefully divided into Erinaceomorpha (Erinaceidae, Sespedectidae, Amphilemuridae, and a variety of erinaceomorphs of uncertain placement), Soricomorpha (Geolabididae, Nyctitheriidae, Micropternodontidae, Apternodontidae, Parapternodontidae, Oligoryctidae, Plesiosoricidae, Soricidae, and various soricomorphs of uncertain placement), and Talpoidea (Proscalopidae and Talpidae).

The earliest records of North American Tertiary lipotyphlans include both erinaceomorphs (*Adunator* and *Litocherus*) and soricomorphs (*Batodon*). These earliest lipotyphlans are sufficiently primitive that it is not easy to assign them to any known lower taxonomic grouping, although *Batodon* may be a very early geolabidid. Beginning in the late Paleocene (middle Tiffanian, biochronological zone Ti3) lipotyphlan diversity increases from localities scattered along the Rocky Mountain corridor. In the early Eocene, lipotyphlan generic diversity reached a maximum of 18 genera documented from the Central Great Plains and representing both soricomorphs and erinaceomorphs. By the end of the middle Eocene (biochronological zones Ui3 and Du), lipotyphlans are common elements of faunal assemblages from California across both the Southern and Northern Great Plains.

Erinaceomorphs are represented early in the North American Tertiary record by sespedectids, three possible erinaceids, one amphilemurid, and a number of taxa of uncertain placement. True Erinaceidae do not appear until late early Oligocene, represented by *Ocajila* and *Proterix*. Erinaceomorphs last occurred in North America in the early late Hemphillian (Hh3) represented by *Untermannerix* in the Central Great Plains.

The early record of soricomorphs in North America is dominated by primitive families such as Geolabididae, Nyctitheriidae, Micropternodontidae, Parapternodontidae, Apternodontidae, and Oligoryctidae. More advanced soricids make their first appearance in the late middle Eocene (Uintan biochronological zone Ui3) represented by *Domnina* and then later by *Pseudotrimylus*, first appearing at the beginning of the Oligocene (Orellan biochronological zone Or1). Soricids underwent diversification through the Miocene with four of those genera (*Sorex*, *Notiosorex*, *Cryptotis*, and *Blarina*) surviving to the present.

Talpids have their earliest occurrence in North America in the latest Eocene (Chadronian biochronological zone Ch3), represented by the proscalopids *Oligoscalops* and *Proscalops*. Proscalopids disappear from the North American record by the end of the Barstovian. Talpids are first represented in the earliest Arikarean (Ar1) by

Quadrodens, *Mystipterus*, and *Scalopoides*, but the major diversification of talpids does not occur until the middle Miocene. Talpids are represented in North America today by *Scalopus*, *Condylura*, and *Scapanus* along with several taxa lacking fossil records.

CHRONOFAUNAL CHANGES

The notion of North American Tertiary “chronofaunas” was employed in Volume 1, and is discussed further in this volume in the Glires summary chapter (Chapter 16).

PALEOCENE

Leptictids and proteutherians are common elements of Paleocene faunal samples from North America (Figure 4.3). Among leptictids, *Prodiacodon* is present throughout the Paleocene and is most common in the Central and Northern Great Plains faunal provinces. *Prodiacodon* is also relatively common in the Southern Great Basin in the early Paleocene but is not present there after the Torrejonian. *Myrmecophaga* is present in the Central Great Plains and Northern Great Plains from the early Torrejonian through middle Tiffanian. Leptictid diversity peaks in the late Torrejonian with three genera in the Central Great Plains and four in the Northern Great Plains. At no other time in the Paleocene are leptictids as diverse.

No group of proteutherians dominates during the Paleocene, with pentacodontids, cimolestids, and pantolestids being relatively diverse and common. Cimolestids and pentacodontids tend to be more diverse and abundant during the early Paleocene, with pantolestids becoming more so in the later Paleocene. Apatemyids and palaeoryctids maintain relatively low diversity throughout but may be locally abundant at certain localities.

The Paleocene record of lipotyphlans consists of decent samples from the Central Great Plains and the Northern Great Plains, mainly from the late Torrejonian onward and a few records from the Southern Great Basin (Figure 4.4). The early records from before Ti3 are either primitive erinaceomorphs like *Adunator* or *Litocherus* or equally primitive soricomorphs like *Leptacodon*. A more diverse group of erinaceomorphs makes their first appearance in Ti3, including *Cedrocherus* and *Diacocherus* along with *Adunator* and *Litocherus*. Soricomorphs do not become especially diverse until the middle Clarkforkian (Cf2) when *Leptacodon*, *Pontifactor*, *Plagiocetenodon*, *Limaconyssus*, *Wyonycteris*, and *Ceutholestes* all co-occur. This soricomorph diversity, consisting of nyctitheriids only, persists to the end of the Paleocene, while erinaceomorphs maintain lower diversity, represented by only two genera in Cf3.

EARLY TO MIDDLE EOCENE

As in most of the Paleocene, leptictids maintain a relatively low diversity through the early and middle Eocene, never having more than two co-occurring genera in any biochron. From the earliest Wasatchian (Wa0) through Ui2, the only leptictids in the record are *Prodiacodon* and *Palaictops*. *Leptictis* makes its first appearance near the end of the Uintan in Ui3 along with *Palaictops*. *Prodiacodon* makes its last appearance in the latest Wasatchian (Wa7).

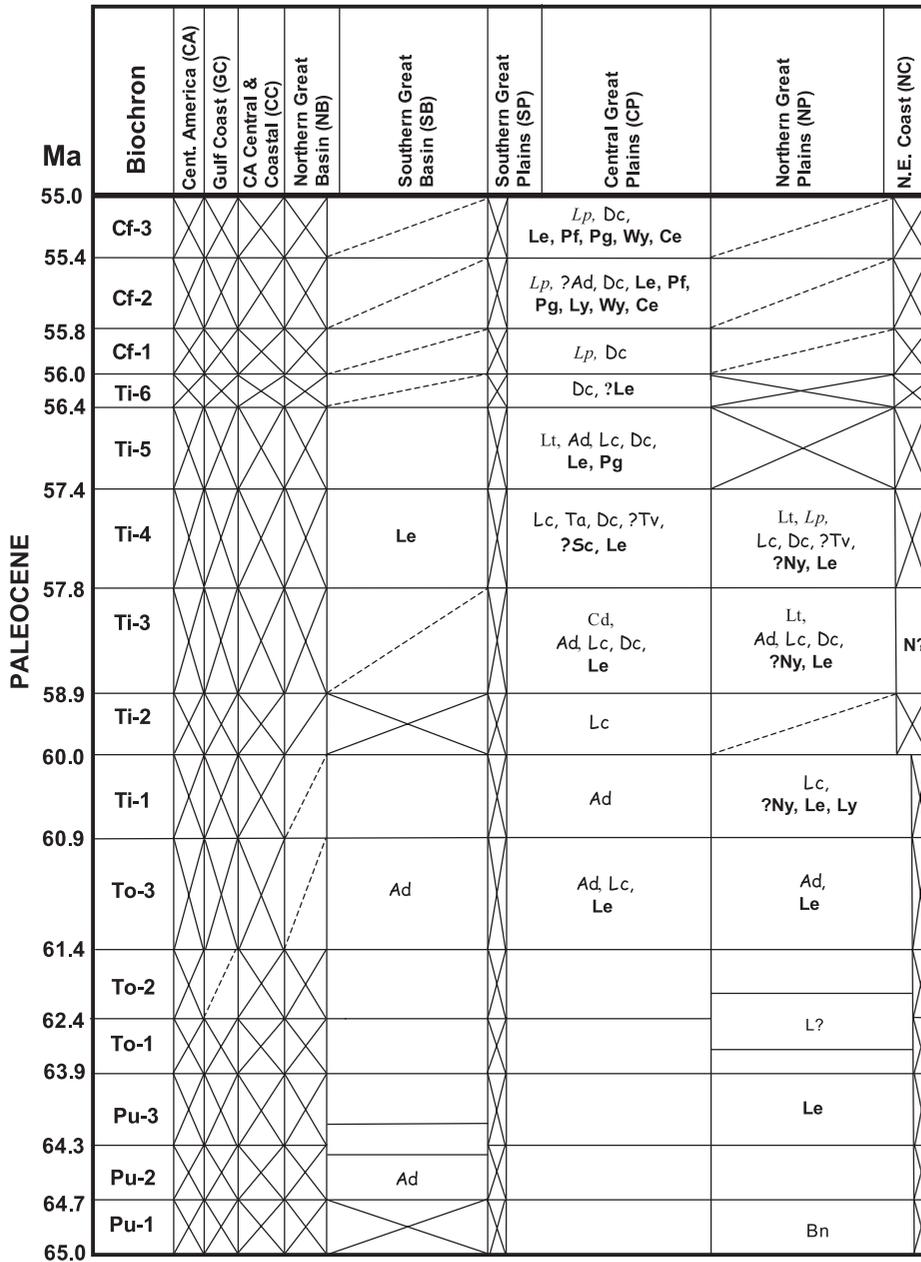


Figure 4.4. Biogeographic ranges of Paleocene lipotyphlans. Key as in Figure 4.3. ERINACIDAE INCERTAE SEDIS (Times New Roman Plain): Cd, *Cedrocherus*; Lt, *Litolestes*. ERINACEOIDEA INSERTAE SEDIS (Times New Roman Italics): Lp, *Leipsanolestes*. ERINACEOMORPHA INCERTAE SEDIS (Comic Sans MS Plain): Ad, *Adunator*; Dc, *Diacocherus*; Lc, *Litocherus*; Ta, *Talpavoides*; Tv, *Talpavus*. SORICOIDEA: GEOLABIDIDAE (Arial Plain): Bn, *Batodon*. NYCTITHERIIDAE (Arial Bold): Ce, *Ceutholestes*; Le, *Leptacodon*; Ly, *Limaconyssus*; Ny, *Nyctitherium*; N?, *Nyctitheriid* indet.; Pf, *Pontifactor*; Pg, *Plagiogtenodon*; Wy, *Wyonycteris*.

Unlike the Paleocene where pentacodontids and cimolestids were well represented, the former is gone by the Eocene and the latter is only represented by a single, yet persistent genus, *Didelphodus*. The best samples of Eocene proteutherians come from the Central Great Plains and are dominated by palaeoryctids until the beginning of Wa6, when palaeoryctids essentially disappear from the record (Figure 4.5). Pantolestids and apatemyids maintain low but nearly constant diversity throughout the early and middle Eocene, fluctuating between one and two genera through the entire sequence.

Early and middle Eocene lipotyphlans are well represented in the Central Great Plains and, in the middle and late Uintan, in California Central and Coast and the Northern Great Plains as

well (Figure 4.6). There are also a few records from the Southern Great Basin and one locality with lipotyphlans in the Gulf Coast Faunal Province that spans Biochrons Wa2/3. Nyctitheriids are diverse early in the Eocene and maintain moderate diversity through the Bridgerian but are only represented by *Nyctitherium* by the end of the Uintan. Other soricomorphs such as paraptornodontids and geolabidids are less diverse than nyctitheriids through Wa4 but are equally as persistent. Paraptornodontids disappear after Wa4 and nyctitheriid and geolabidid diversity evens out through the Bridgerian. In the Uintan, geolabidids remain modestly diverse while oligoryctids, apternodontids, and micropternodontids are all present

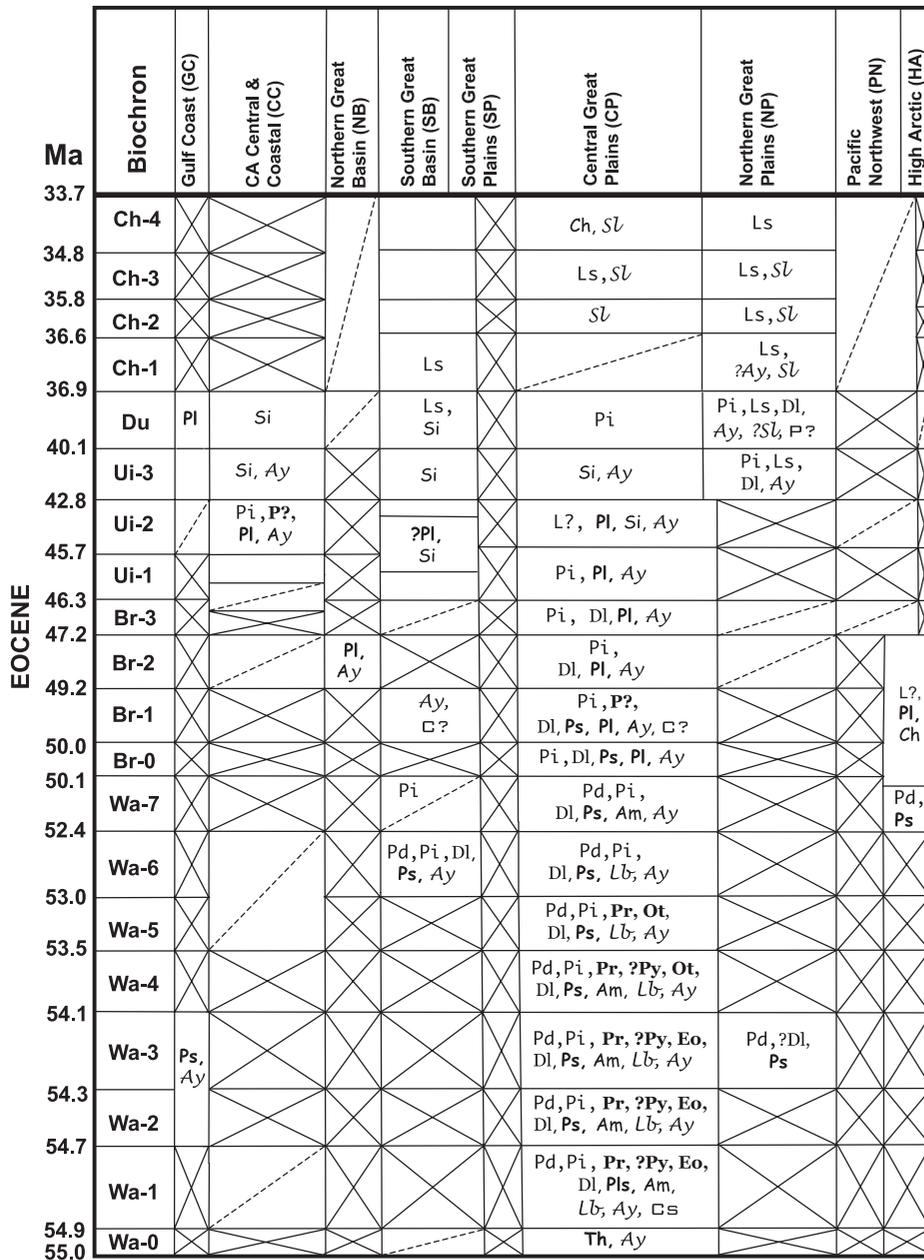


Figure 4.5. Biogeographic ranges of Eocene proteutherians. Key as in Figure 4.3. LEPTICTIDAE (Monaco Plain): *Ls*, *Leptictis*; L?, Leptictid indet.; Pd, *Prodiacodon*; Pi, *Palaeictops*. PALAEOORYCTIDAE (Georgia Bold): **Eo**, *Eoryctes*; **Ot**, *Ottoryctes*; **Pr**, *Palaeoryctes*; **Py**, *Pararyctes*; **P?**, Palaeoryctid indet. CIMOLESTIDAE & CIMOLESTA INDET. (Georgia Plain): Dl, *Didelphodus*. PANTOLESTA: PANTOLESTIDAE: PANTOLESTINAE (Comic Sans MS Bold): **Ps**, *Palaeosinopa*; **Pi**, *Pantolestes*; **Th**, *Thelysia*. PANTOLESTA INCERTAE SEDIS (Comic Sans MS Plain): **Am**, *Amaramnis*; **Ch**, *Chadronia*; **Si**, *Simidectes*. APATEMYIDAE (Lucida Handwriting): *Ay*, *Apatemys*; **Lb**, *Labidolemur*; **Sl**, *Sinclairrella*. PROTEUTHERIA INDET. (Bank Gothic): □s, *Creotarsus*; □?, *Creotarsine* indet.; P??, Proteutherian indet.

at low diversities, especially in California Central and Coast, Central Great Plains, and Northern Great Plains localities. Erinaceomorphs are diverse through the Wasatchian, being represented by sespedectids like *Macrocranion* and *Scenopagus* and a variety of taxa of uncertain placement within Erinaceomorpha. By the late Uintan, the first records of heterosoricine shrews (represented by *Domnina*) appear in the Central Great Plains and Northern Great Plains.

WHITE RIVER CHRONOFAUNA

Leptictids and proteutherians are present in the White River Chronofauna but are gone from the North American record by the end of Ar1. In the Duchesnean, leptictids are represented by both *Palaeic-*

tops and *Leptictis*, but *Palaeictops* disappears from the record after the Duchesnean while *Leptictis* survives into the early Arikarean in the Central Great Plains (Figure 4.7).

Proteutherian diversity is greatly diminished through this period as well. In the Duchesnean, pantolestids are represented by *Simidectes* in Central and Coastal California (California Central and Coast) and in the Southern Great Basin, while the cimolestid *Didelphodus*, the apatemyids *Apatemys*, and ?*Sinclairrella*, and a possible palaeoryctid, still survive in the Northern Great Plains. There is a single occurrence of the possible pantolestid *Chadronia* in Ch4 in the Central Great Plains representing the last occurrence of North American pantolestids. *Sinclairrella* remains a small part of mammalian faunal samples until the end of the early Arikarean in

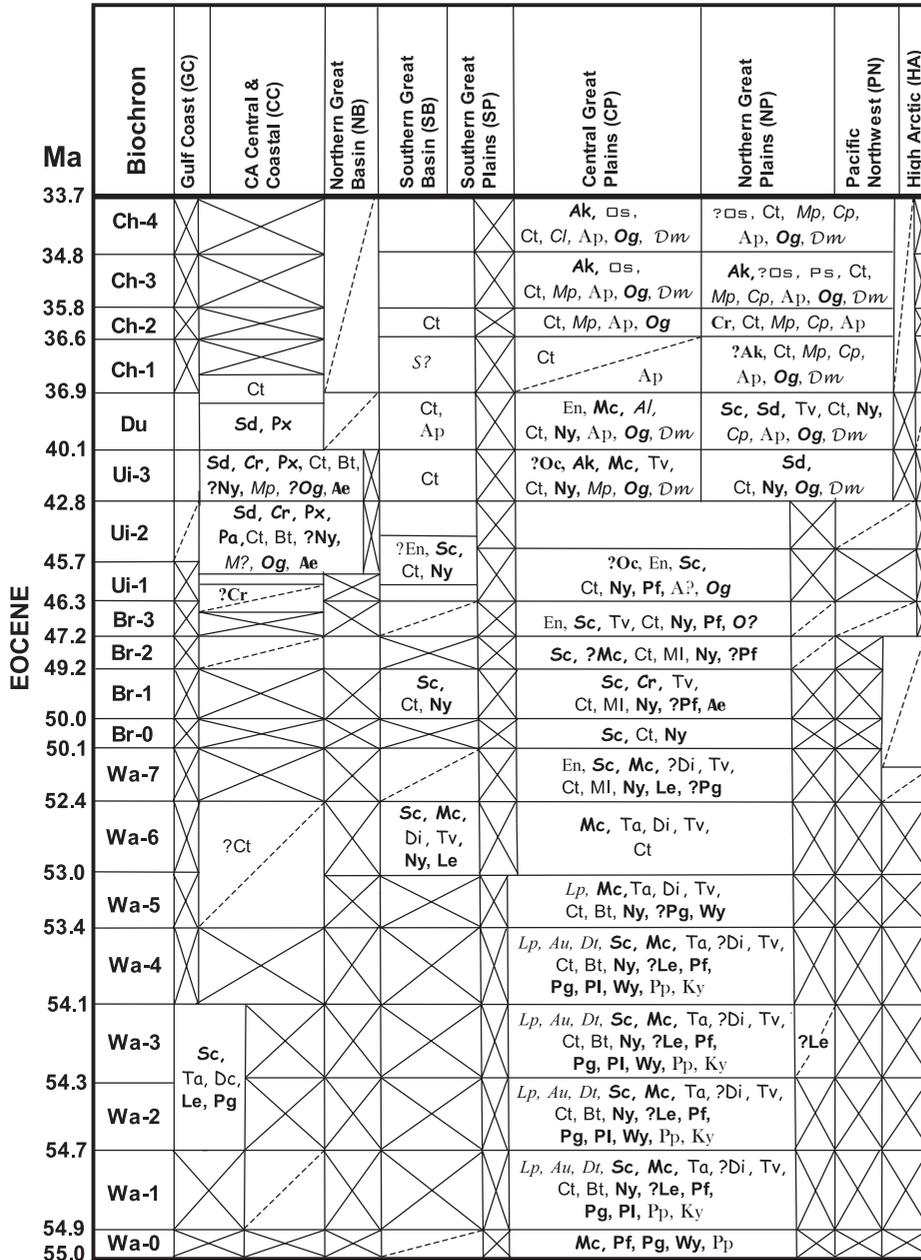


Figure 4.6. Biogeographic ranges of Eocene lipotyphlans. Key as in Figure 4.3. ERINACEOMORPHA: ERINACIDAE INCERTAE SEDIS (Times New Roman Plain): *En*, *Entomolestes*. ERINACEOIDEA INCERTAE SEDIS (Times New Roman Italics): *Au*, *Auroralestes*; *Dt*, *Dartoni*; *Lp*, *Leipsanolestes*. SESPEDECTIDAE (Comic Sans MS Bold): **Ak**, *Ankylo*; **Cr**, *Crypholestes*; **Mc**, *Macrocranion*; **Pa**, *Patriolestes*; **Px**, *Proterixoides*; **Sc**, *Scenopagus*; **Sd**, *Sespedectes*. AMPHILEMURIDAE (Comic Sans MS Italics): *Al*, *Amphilemur*. ERINACEOMORPHA INCERTAE SEDIS (Comic Sans MS Plain): *Dc*, *Diacocherus*; *Di*, *Diacodon*; *Ta*, *Talpavoides*, *Tv*, *Talpavus*. TALPOIDEA: PROSCALOPIDAE (Bank Gothic). □s, *Oligoscalops*; Ps, *Proscalops*. SORICOIDEA: GEOLABIDIDAE (Arial Plain): Ct, *Centetodon*; Bt, *Batodonoides*; Mi, *Marsholestes*. NYCTITHERIIDAE (Arial Bold): **Le**, *Leptacodon*; **Ny**, *Nyctitherium*; **Pf**, *Pontifactor*; **Pg**, *Plagioctenodon*; **Pl**, *Plagioctenoides*; **Wy**, *Wyonycteris*. MICROPTERNODONTIDAE (Arial Italics): *Cl*, *Clinopternodus*; *Cp*, *Cryptoryctes*; *Mp*, *Micropternodus*; *M?*, *Micropternodontid* indet. APTERNODONTIDAE (Baskerville Old Face Bold): **Ap**, *Apternodus*; **A?**, *apternodontine* indet. PARAPTERNODONTIDAE (Baskerville Old Face Plain): *Ky*, *Koniaryctes*; *Pp*, *Parapternodus*. OLIGORYCTIDAE (Arial Bold Italics): *Og*, *Oligoryctes*; *O?*, *oligoryctid* indet. LIPOTYPHLAN INCERTAE SEDIS (Brittanic Bold): **Ae**, *Aethomylos*.

the Central Great Plains and represents the last surviving proteutherian in North America.

Lipotyphlans are dominated by soricomorphs from the Duchesnean through the end of the Chadronian mostly represented by several species of *Centetodon* and a variety of apternodontids, micropternodontids, and oligoryctids, all of which survive through the Orellan in the Central Great Plains and Northern Great Plains. Nyctitheriids have disappeared from the North American record by the beginning of the Chadronian while *Centetodon* survives into the early late Arikarean (Ar3) in the Central Great Plains and California Central and Coast. Oligoryctids are present until the end of the Orellan in the Northern Great Plains and through the Whitneyan

in the Central Great Plains, while micropternodontids make a late appearance in the early Arikarean (Ar1/2) in the Pacific Northwest.

Erinaceomorphs are never very diverse after the Duchesnean but are present through the entire White River Chronofauna, mostly represented by *Ankylo* early and then by *Ocajila* and *Proterix* later. Erinaceomorphs in general are more common from the Central Great Plains than the Northern Great Plains throughout the White River Chronofauna.

Soricids first appear in North America in Ui3, represented by *Domnina*, which is present throughout the White River Chronofauna in the Central Great Plains, Northern Great Plains, and Pacific Northwest. *Pseudotrimylus* and *Limnoecus* join *Domnina* in the Central

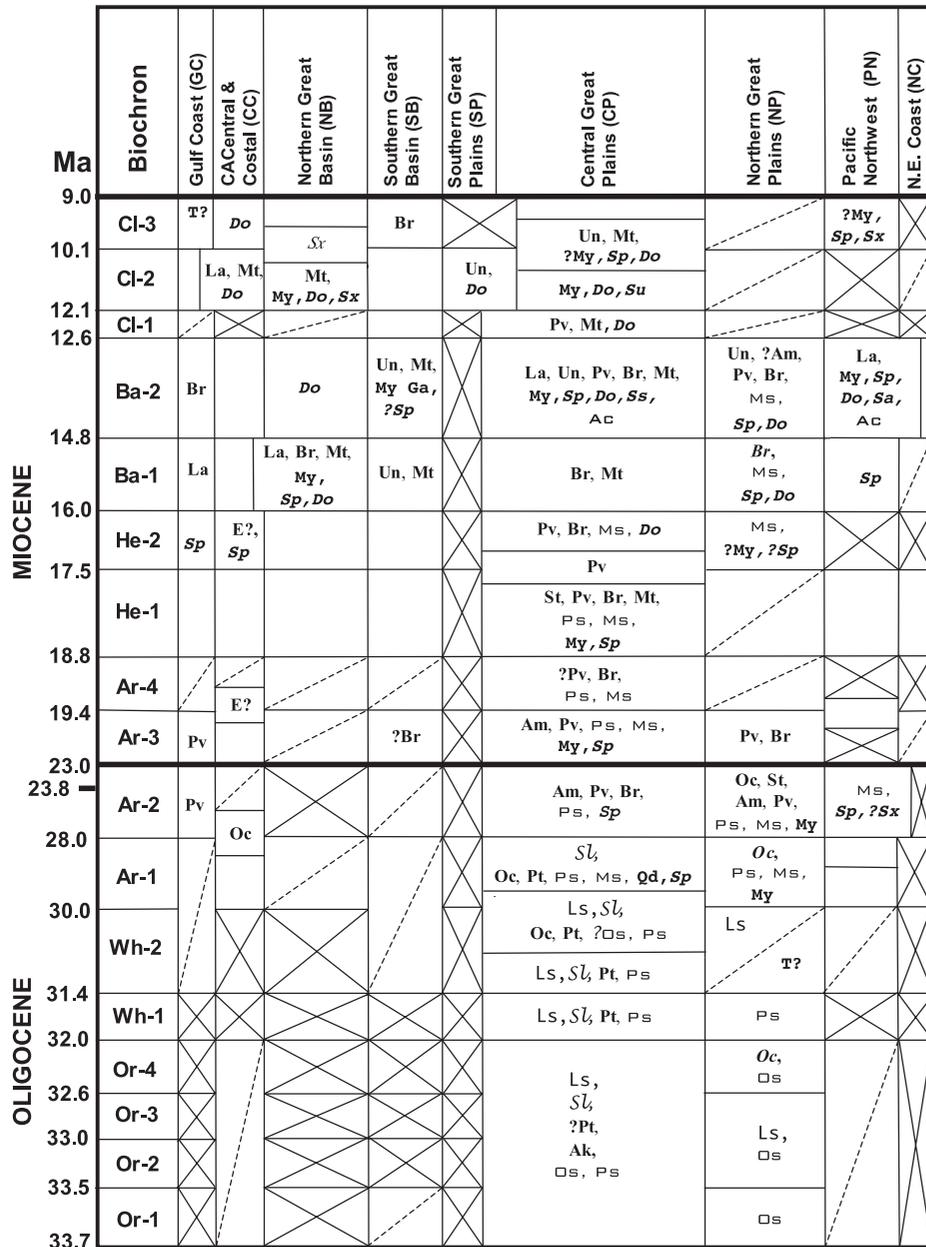


Figure 4.7. Biogeographic ranges of Oligo-Miocene insectivores (less soricoids). Key as in Figure 4.3. LEPTICTIDAE (Monaco Plain): *LS*, *Leptictis*. APATEMYIDAE (Lucida Handwriting): *Sl*, *Sinclairiella*. ERINAECOMORPHA: ERINACEIDAE: GALERICINAE: (Times New Roman Bold): **La**, *Lantanothorium*; **Oc**, *Ocajila*; **Pt**, *Proterix*. ERINACEINAE: **Am**, *Amphechinus*; **Pv**, *Parvericius*; **St**, *Stenoechinus*; **Un**, *Untermannex*. BRACHYERCINAE: **Br**, *Brachyerix*; **Mt**, *Metechinus*. SESPEDECTIDAE (Comic Sans MS Bold): **Ak**, *Ankyledon*. TALPOIDEA: PROSCALOPIDAE (Bank Gothic Plain): **os**, *Oligoscalops*; **ms**, *Mesoscalops*; **ps**, *Proscalops*. TALPIDAE (Courier Bold): **Ga**, *Gailardia*; **My**, *Mystipterus*; **Qd**, *Quadrodens*. TALPINAE: SCALOPINI (Courier Bold Italics): **Do**, *Dominoides*; **Sa**, *Scapanoscapter*; **Sp**, *Scalapoides*; **Ss**, *Scapanus* (*Scapanus*); **Su**, *Scalopus*; **Sx**, *Scapanus* (*Xereoscapanus*). TRIBE UNCERTAIN (Bank Gothic Bold): **Ac**, *Achlyoscapter*. **E?**, erinacid indet. (Times New Roman Bold). **T?**, Talpid indet. (Courier Plain).

Great Plains in the Orellan and early Arikareean, respectively, and *Pseudotrimylus* in the early Arikareean.

Talpoids first appear in Ch3 in the Central Great Plains and Northern Great Plains, represented by *Oligoscalops* (Central Great Plains, Northern Great Plains) and *Proscalops* (Northern Great Plains only). These taxa are present through most of the White River Chronofauna and are joined by *Mesoscalops*, *Quadrodens*, *Scalopoides*, and *Mystipterus* in the early Arikareean. In general, talpid and soricid diversity is relatively low through the White River Chronofauna until the late Whitneyan or early Arikareean, when modest diversification happens in both groups.

RUNNINGWATER CHRONOFAUNA

The Runningwater Chronofauna is the first to be dominated by modern lipotyphlan groups as the last geolabidids and micropternodontids are gone from the North American record by the end of the early late Arikareean (Ar3). *Plesiosorex* makes its first appearance in the late Arikareean in the Central Great Plains and also appears in the Pacific Northwest and Northeast Coast in the early Hemingfordian. Among soricids, *Domnina* persists until Ar3 in the Central Great Plains and into the early Hemingfordian from California Central and Coast along with *Limnoecus*, which is also known from the Gulf Coast in He1. The highest diversity of soricids in the

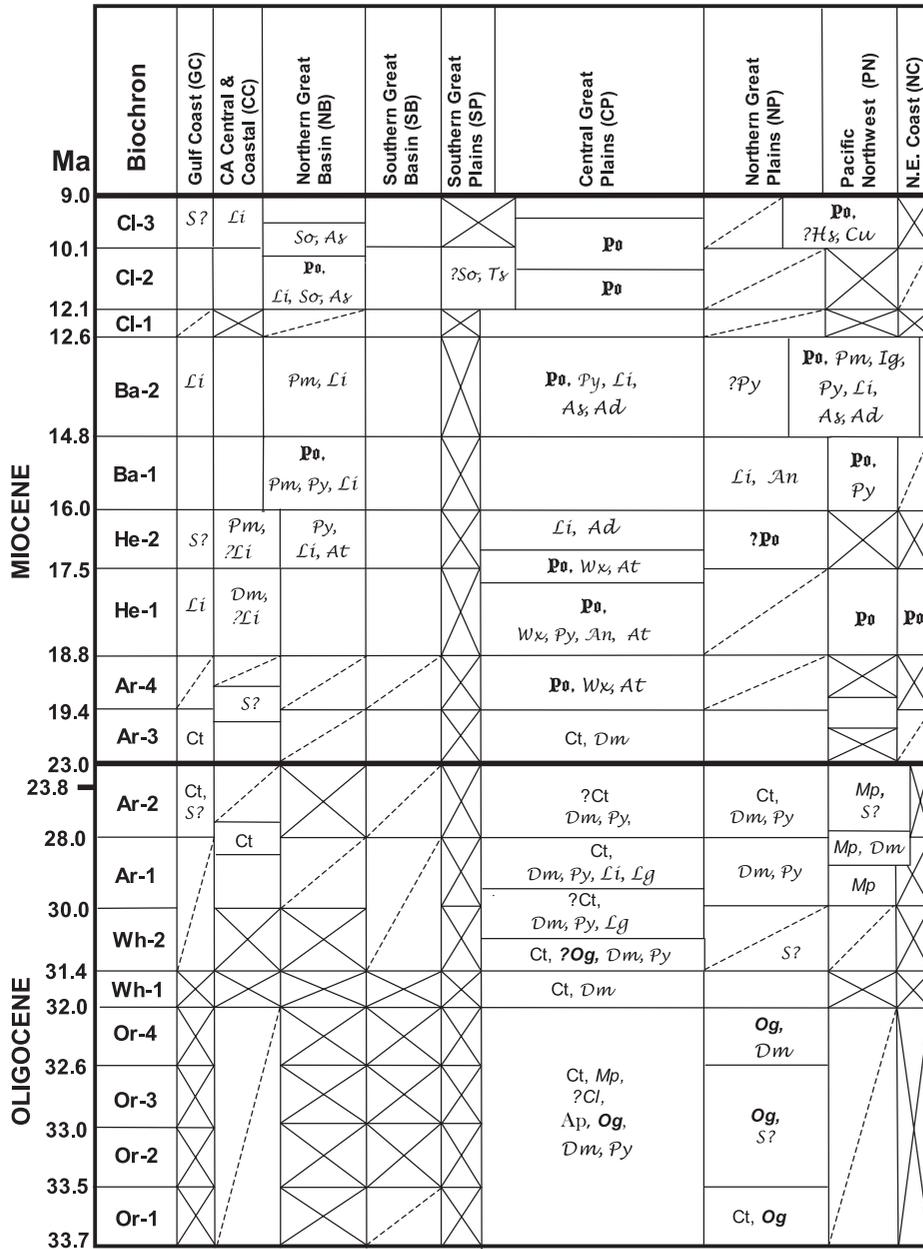


Figure 4.8. Biogeographic ranges of Oligo-Miocene soricoids. Key as in Figure 4.3. GEOLABIDI-DAE (Arial Plain): *Ct*, *Centetodon*. MICROPTERNODONTIDAE (Arial Italics): *Cl*, *Clinopternodus*; *Mp*, *Micropternodus*. APTERNODONTIDAE (Baskerville Old Face Bold): **Ap**, *Apterodonta*. OLIGORYCTIDAE (Arial Bold Italics): **Og**, *Oligoryctes*. PLESIOSORICIDAE (Blackmore Let): **Po**, *Plesiosorex*. SORICIDAE: HETEROSORICINAE (Lucida Handwriting Plain): *Dm*, *Domnina*; *Ig*, *Ingentisorex*; *Pm*, *Paradomnina*; *Py*, *Pseudotrimylus*; *Wx*, *Wilsonosorex*. LIMNOECINAE (Lucida Calligraphy): *An*, *Angustidens*; *Lg*, limnoecine new genus; *Li*, *Limnoecus*. SORICINAE (Lucida Handwriting Bold): *Ad*, *Adeloblarina*; *Ax*, *Allvisorex*; *At*, *Antesorex*; *Cu*, *Crusafontina*; *Hx*, *Hesperosorex*; *Sx*, *Sorex*; *S?*, *Soricid* indet.; *Tx*, *Tregosorex*.

Runningwater Chronofauna occurs in He1 in Central Great Plains, where four genera (*Wilsonosorex*, *Pseudotrimylus*, *Angustidens*, and *Antesorex*) are present.

Talpids are well represented from the Runningwater Chronofauna in the Central Great Plains, with two to four genera being present throughout (*Proscalops*, *Mesoscalops*, *Mystipterus*, and *Scalopoides*). The only other talpid records from the Runningwater Chronofauna are those from the Pacific Northwest and Northeast Coast where three mole genera are present in the late early Arikarean (Ar2).

Erinaceomorphs have a relatively widespread distribution during the Runningwater Chronofauna with records known throughout the Arikarean from Gulf Coast, California Central and Coast, Southern Great Basin, Central Great Plains, and Northern Great

Plains. The only Hemingfordian records of erinaceomorphs are from the Central Great Plains, where *Stenoechinus*, *Parvericius*, *Brachy-erix*, and *Metechinus* occur.

CLARENDONIAN CHRONOFAUNA

Proscalopidae disappear during the Clarendonian Chronofauna, with *Mesoscalops* last appearing in the late Barstovian (Ba2) in the Northern Great Plains. The only non-Hemphillian occurrence of *Gaillardia* is also recorded in this chronofauna from Ba2 in the Southern Great Basin. The late Barstovian also has the highest diversity of talpids from this time period, with five genera being found in the Central Great Plains and Pacific Northwest. The first appearance of the modern genus *Scalopus* is recorded from the middle

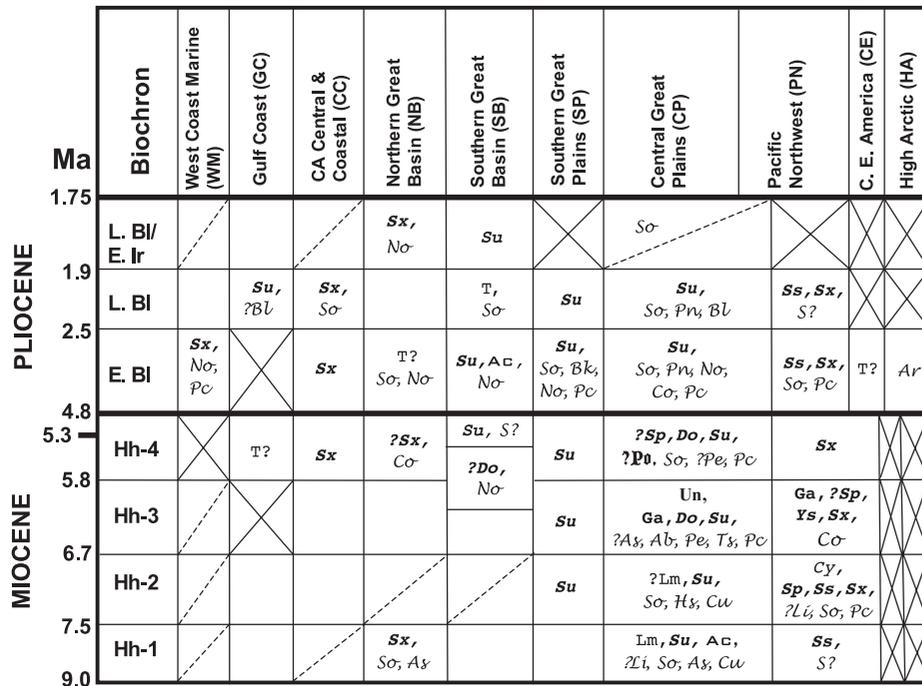


Figure 4.9. Biogeographic ranges of Mio-Pliocene lipotyphlans. Key as in Figure 4.3. ERINACEIDAE (Times New Roman Bold): ERINACEINAE: **Un**, *Untermannerix*. TALPOIDEA: TALPIDAE (Courier Bold): **Ga**, *Gailardia*. TALPININAE: DESMANINI (Courier Plain). **Lm**, *Lemoynea*. CONDYLRINI (Courier Italics). **Cy**, *Condylura*. SCALOPINI (Courier Bold Italics): **Do**, *Dominoides*; **Sp**, *Scalopoides*; **Ss**, *Scapanus* (*Scapanus*); **Su**, *Scalopus*; **Sx**, *Scapanus* (*Xereoscapanus*); **Ys**, *Yanshuella*. TRIBE UNCERTAIN (Bank Gothic Bold): **Ac**, *Achlyoscapter*. **T?**, Talpid indet (Courier Bold). SORICOIDEA: PLESIOSORICIDAE (Blackmore Let): **Po**, *Plesiosorex*. SORICIDAE: LIMNOECINAE (Lucida Calligraphy): **Li**, *Limnoecus*. SORICINAE (Lucida Handwriting Bold): **Ab**, *Anchiblarinella*; **Ar**, *Arcitorex*; **As**, *Alluvisorex*; **Bk**, *Beckiasorex*; **Bl**, *Blarina*; **Co**, *Cryptotis*; **Cu**, *Crusafontina*; **Hs**, *Hesperosorex*; **No**,

Notiosorex; **Pc**, *Paracryptotis*; **Pe**, *Petenya*; **Pn**, *Planisorex*; **So**, *Sorex*; **S?**, Soricid indet.; **Ts**, *Tregosorex*.

Clarendonian in the Central Great Plains and the last appearance of *Mystipterus* occurs near the C12/3 boundary in the Central Great Plains.

Erinaceomorphs are relatively common throughout the Clarendonian Chronofauna. They are especially diverse in the late Barstovian of the Central Great Plains, with five genera being present (*Lantanotherrium*, *Untermannerix*, *Parvericius*, *Brachyerix*, and *Metechinus*). Except for a late occurrence of *Untermannerix* in Hh3 of the Central Great Plains, erinaceomorphs disappear from North America by the end of the Clarendonian Chronofauna.

Plesiosorex, except for a questionable occurrence in Hh4 in the Central Great Plains, disappears at the end of the Clarendonian. Heterosoricine and limnoecine shrews also have their last appearances in the Clarendonian Chronofauna (there is a questionable record of *Limnoecus* from the earliest Hemphillian in the Central Great Plains). Soricid diversity is relatively stable through this time period with two or three genera normally being represented from any given biochron (Figure 4.8). However, as was the case with erinaceomorphs and talpoids, soricid diversity peaks in the late Barstovian with four genera being known from the Central Great Plains and five from the Pacific Northwest.

MIO-PLIOCENE CHRONOFAUNA

The Mio-Pliocene North American Tertiary lipotyphlans are represented by talpids and soricine shrews. The most complete temporal sample is from the Central Great Plains, where shrews are more diverse throughout except in the latest Hemphillian where both shrews and moles are represented by three genera (Figure 4.9).

The highest diversity of moles is recorded in the middle Hemphillian (Hh2/3) of the Pacific Northwest, while shrew diversity is highest (five genera) in both Hh3 and early Blancan in the Central Great Plains. By the end of the Blancan into the Irvingtonian, only the extant genera *Scalopus*, *Scapanus*, *Sorex*, and *Notiosorex* are represented in the fossil record of North America.

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5 “Proteutheria”

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INTRODUCTION

Romer (1966) proposed a new suborder, “Proteutheria,” for insectivorous mammals that had no clear relationship to living insectivorans. Romer’s concept of “Proteutheria” included leptictids, zalambdalestids, anagalids, paroxyclaenids, pantolestids, ptolemaidids, tupaiids, pentacodontids, apatemyids, and macrosclidians. “Proteutheria” as constituted by Romer is an unnatural grouping and cannot be sustained phylogenetically. According to McKenna and Bell (1997), the lowest-level grouping that contains all of the mammals discussed in this chapter is the Magnorder Epitheria (cohort Placentalia). Within the Epitheria, Romer’s “proteutherians” are distributed unevenly in the Superorders Leptictida (leptictids) and Preprotheria.

“Proteutheria” is perhaps still best thought of as a paraphyletic group of archaic insectivorous mammals traditionally not placed in Lipotyphla. Bloch, Rose, and Gingerich (1998) showed that taxa included in this group generally exhibit larger body size than those grouped in Lipotyphla and argued that the term was still useful in representing an ecologically coherent subset of Paleogene faunas. We include Palaeoryctidae, Cimolestidae, Pantolestidae, and Apatemyidae as members of this informal group.

Palaeoryctidae are known from the early Paleocene through early Eocene in North America. Some species from the Late Cretaceous of Asia and Europe, and from the late Paleocene to early Eocene of Africa, may also be palaeoryctids (McKenna and Bell, 1997).

Cimolestids first appear in the Late Cretaceous in North America, represented by *Cimolestes*, and survive through the Duchesnean, last represented by *Didelphodus*. Cimolestids are otherwise known from the late Paleocene of Europe and Africa and the early Eocene of Europe and Asia and may be represented in the early Paleocene in South America (McKenna and Bell, 1997).

Pantolestids are a geographically widespread group with representatives from North America, Europe, Asia (e.g., Dashzeveg

and Russell, 1985), and Africa (Gheerbrant, 1991). Pantolestids are known from the Torrejonian through the end of the Eocene (Chadronian) in North America but survive to the end of the Oligocene in Asia (*Oboia*; Gabunia, 1989).

Apatemyids range from the late Paleocene into the early Arikarean in North America. They are also represented in the Paleocene and Eocene in Europe but remain unknown from elsewhere (McKenna and Bell, 1997).

DEFINING FEATURES OF ‘PROTEUTHERIANS’

FAMILY PALAEORYCTIDAE

CRANIAL

Skull relatively low and elongate; rostrum and neurocranium of approximately the same size; postorbital constriction moderate; single sagittal crest distinct but low; incomplete zygomatic arches; auditory bulla ossified; rostral tympanic processes of petrosal that contribute to bulla to varying degrees; intrabullar annular ectotympanic; no pyriform fenestra; large epitympanic recess (Thewissen and Gingerich, 1989; Bloch, Secord, and Gingerich, 2004).

DENTAL

Upper molars protozalambodont (Figure 5.1) with closely appressed, connate paracones and metacones; lower molars with high trigonids and narrow talonids; shearing crests well developed on cheek teeth; three upper and lower premolars except in *Pararyctes* (Fox, 2004).

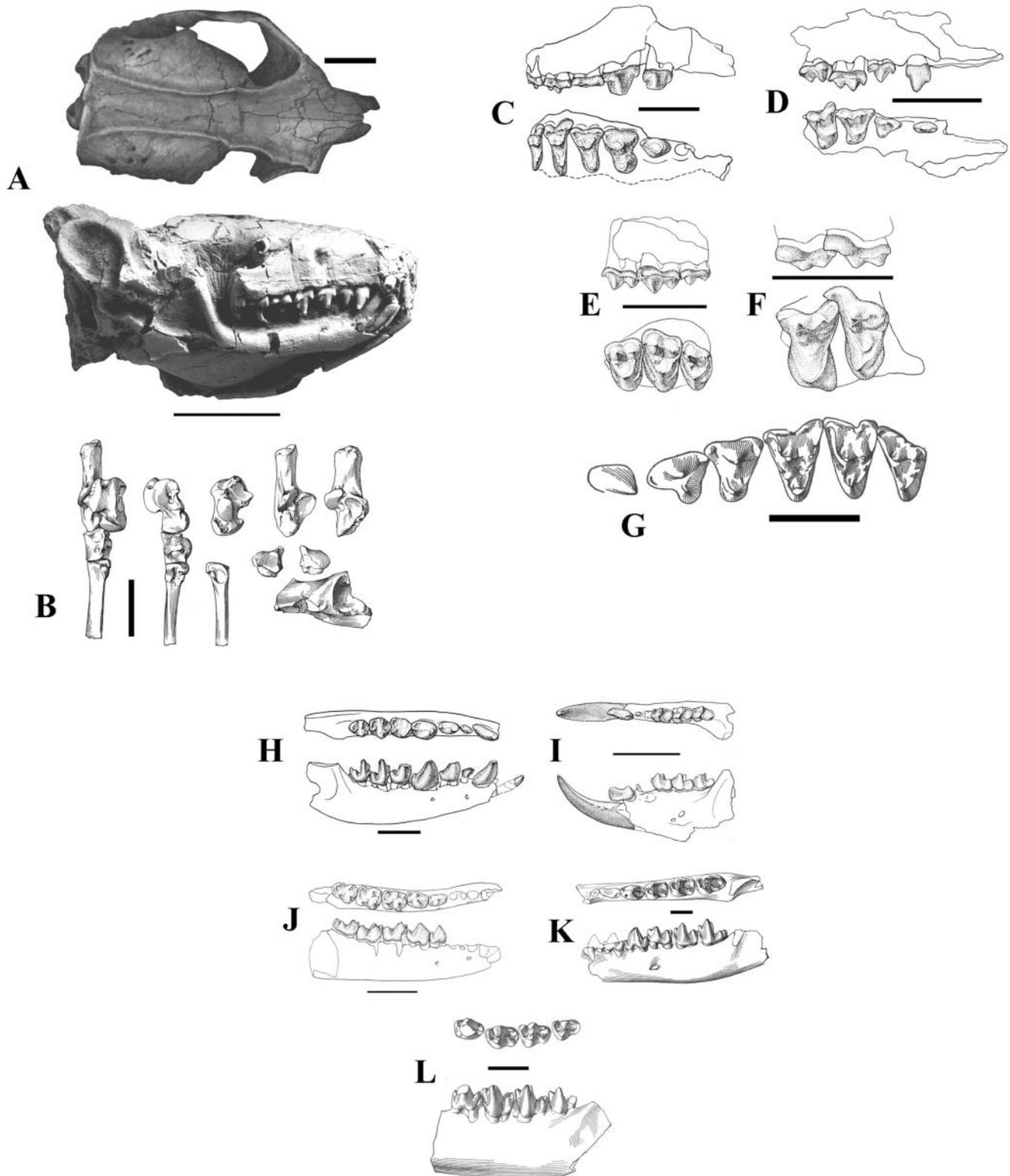


Figure 5.1. A. Skulls of apatemyid *Sinclairella dakotensis* (top, from Jepsen, 1934) and of palaeoryctid *Ottoryctes winkleri* (below, from Bloch, Secord, and Gingerich, 2004). B. Postcrania of creotarsine *Creotarsus lepidus* (from Matthew, 1918). Scale bars for A and B = 1 cm. C–G. Upper dentitions of selected “proteutherians;” C. Palaeoryctid *Aaptoryctes ivyi* (from Gingerich, 1982a). D. Apatemyid *Labidolemur kayi* (from Gingerich and Rose, 1982). E. Pentacodontine *Bisonalveus browni* (from Krause and Gingerich, 1983). F. Pantolestid *Bessoecetor septentrionalis* (from Krause and Gingerich, 1983). G. Cimolestid *Didelphodus absarokae* (from Matthew, 1918). Scale bars = 5 mm. H–L. Lower dentitions of selected “proteutherians;” H. Palaeoryctid *Aaptoryctes ivyi* (from Gingerich, 1982a). I. Apatemyid *Labidolemur kayi* (from Gingerich and Rose, 1982). J. Pentacodontine *Bisonalveus browni* (from Krause and Gingerich, 1983). K. Pantolestine *Palaeosinopa veterrima* (from Matthew, 1918). L. Cimolestid *Didelphodus absarokae* (from Matthew, 1918). Scale bars = 5 mm. (A (top): courtesy of the American Philosophical Society. A (bottom), C–F, H–J: courtesy of the University of Michigan. B, G, K, L: Courtesy of the American Museum of Natural History.)

POSTCRANIAL

The only known postcranial material for the group is that associated with *Palaoryctes punctatus*, represented by a distal humerus and proximal ulna: humerus with prominent medial epicondyle that is proximally inflected with a hook; trochlea mediolaterally broad with a small arc of curvature; lacks fossa seen in talpids; ulna with shallow trochlea, truncated coronoid, and anteriorly inflected olecranon process of moderate length (Van Valen, 1966).

FAMILY CIMOLESTIDAE

CRANIAL

Broad nasals that may contact lacrimals; lacrimal with small exposure on face and prominent foramen; possible palatine–lacrimal contact; palatine extends to P4, lacks postpalatine spine, and has large tori; low, single sagittal crest; occipital condyles dorsally shielded by flaring nuchal crests; infraorbital foramen large, situated at level of P3–4; parietal foramina for tributaries of sagittal venous sinuses present; no evidence for ossified bulla; no development of caudal tympanic process of petrosal – foramen rotundum exposed; promontorium with three grooves for “auricular nerve” (running mediolateral), promontory branch of internal carotid artery (running anterolaterally) and entocarotid artery (running antero-posterior on medial aspect of promontorium); tympanohyal element fused to posterolateral wall of stapedius fossa as well as to small mastoid process; facial canal closed by crista parotica; pyri-form fenestra present; glenoid fossa flat with prominent postglenoid and entoglenoid processes; postglenoid foramen present posterior to postglenoid process; no separate vidian foramen or groove preserved (based on *Puercolestes* [= *Cimolestes*] and *Didelphodus*; Van Valen 1966).

DENTAL

Dental formula I[?]/3, C[?]/1, P[?]/4, M3/3; incisors small, peglike and procumbent; canine large and slightly procumbent; premolars premolariform; upper molars very transverse with expanded stylar shelves and no hypocones; lower molars with high trigonids; m1 < m2 < m3.

POSTCRANIAL

Astragalus with posteriorly extensive, grooved tibial facet exhibiting sharp medial and lateral margins with lateral half wider than medial half, fibular facet with dorsally facing shelf, superior astragalal foramen absent, neck relatively long, distinctly separate navicular and sustentacular facets; calcaneum with reduced calcaneofibular facet, peroneal tuberosity and plantar tubercle distally positioned, no distinct groove between cuboid facet and plantar tuberosity marking calcaneocuboid ligament insertion; ungual phalanx straight and flat (based on *Didelphodus* [Van Valen, 1966] and *Procerberus* and *Cimolestes* [Szalay, 1977]).

FAMILY PANTOLESTIDAE

Only pantolestine members of the Pantolestidae are currently known to exhibit aquatic adaptations. Several nearly complete pantolestid skeletons have been recovered from lacustrine limestones and oil shales (Pfretzchner, 1993).

CRANIAL

Pantolestidae: Facial portion of skull short; neurocranium elongate and low; marked postorbital constriction; infraorbital foramen relatively large; no postpalatine spine on palate; basicranium broad; single sagittal crest; occipital condyles dorsally shielded by flaring nuchal crest; anterior nares very large and posteriorly extensive (based on *Pantolestes*, Matthew, 1909; *Buxolestes*, Pfretzchner, 1993; Rose and Lucas 2000; *Aphronorus*, Gingerich, Houde, and Krause, 1983; Boyer and Bloch, 2003).

Pantolestinae: Nares extends to level of M2; auditory bulla unossified; basioccipital mediolaterally broad (based on *Pantolestes*, Matthew, 1909; *Buxolestes*, Pfretzchner, 1993).

Pentacodontinae: Promontorium with bifurcating groove on lateral aspect; ossified bulla lacking contribution from basisphenoid (*Aphronorus*, Boyer and Bloch, 2003)

DENTAL

Pantolestidae: Dental formula I3/3, C1/1, P4/4, M3/3; I3 enlarged and bladelike; canines large and massive; p4 premolariform; premolars and molars with low, massive cusps; stylar shelves reduced or absent; external cingula on lower molars reduced or absent; mandibular angle robust and blunt (Matthew, 1909; Simpson, 1937a; *Buxolestes*: Pfretzchner, 1993; Rose and Lucas 2000; *Aphronorus*: Gingerich, Houde, and Krause, 1983; Boyer and Bloch, 2003).

Pantolestinae: Upper incisors peglike, separated, except for I3, which is enlarged and bladelike; distinct mental foramen below m1 (Matthew, 1909; Simpson, 1937a; *Buxolestes*, Pfretzchner, 1993).

Pentacodontinae: P4/p4 semimolariform and greatly enlarged in most taxa; p4 with very heavy, posteriorly angled protoconid, well-developed metaconid, and basined heel; P4 with massive, conical, paracone, smaller but sharply distinct metacone, styles small or lacking, and large, low protocone with widely expanded anterior and posterior cingula; trigonids relatively low; m3 trigonid smaller than m1–2 (Simpson, 1937b; Gazin, 1959, 1969; Van Valen, 1967; Gingerich, Houde, and Krause, 1983).

POSTCRANIAL

Pantolestidae: Humerus with strong deltoid, pectoral, and supinator crests and wide distal end; radius and ulna not fused; tibia and fibula united distally; astragalus with short, deeply grooved

trochlea, and convex, pyriform head; superior astragalar foramen present, but small and located on tibial facet; pes habitually everted (based on *Pantolestes*: Matthew, 1909; *Buxolestes*: Pfretzchner, 1993; Rose and Lucas 2000; *Aphronorus*: Boyer and Bloch, 2003).

Pantolestinae: Craniocaudally extensive spinus process on C2; lumbar zygapophyses flat; tail vertebrae massive, tail long; humerus with deltoid crest that is sharp and faces laterally, and wide distal end; radius and ulna not fused; manus and pes with elongate, flattened claws; femur with flattened shaft, possessing third trochanter, short and broad patellar trochlea; tibia very curved with cnemial crest reduced to process and placed nearly at mid shaft; fibular–calcaneal articulation large; astragalus with short neck, confluent navicular and sustentacular facets; forelimbs and especially metacarpals much shorter than hindlimbs and metatarsals, respectively (based on *Pantolestes*: Matthew, 1909; *Buxolestes*: Pfretzchner, 1993; *Palaeosinopa*: Rose and Von Koenigswald, 2005).

Pentacodontinae: Humerus with prominent deltoid tuberosity expanded into shelflike projection that is concave and facing anteriorly; ulna with deep shaft strongly grooved on lateral aspect; radius with elliptical head, shaft flattened mediolaterally towards distal end, and arcuate ridge on posterolateral aspect marking origin of deep digital flexors; tibial shaft mediolaterally flattened; astragalus with distinctly separate navicular and sustentacular facets (Boyer and Bloch, 2003).

FAMILY APATEMYIDAE

CRANIAL

Lack ossified bulla; groove on promontorium marking course of internal carotid artery; large, free ectotympanic ring; infraorbital foramen above M1; small foramina on skull roof (Jepsen, 1934; McKenna, 1963; Koenigswald, 1990; Bloch, Boyer, and Houde, 2004).

DENTAL

First lower incisor enlarged and procumbent with root extending posteriorly to m3; I1 lacking lateral enamel; canines absent; p3 blade-like and single-rooted; lower molars low, crowned with labial paraconids; P3–4 double-rooted but unicusate; upper molars simple, lacking mesostyles; depression on mandible under p4 or m1, posterior mental foramen generally very large below m1.

POSTCRANIAL

Distal femora anteroposteriorly deep; astragalus grooved; metatarsals elongate; unguals mediolaterally narrow; elongate second and third hand digits (Koenigswald and Schierring, 1987; Koenigswald, 1990; Bloch and Boyer, 2001; Bloch, Boyer, and Houde, 2004; Kalthoff, Koenigswald, and Kurz, 2004; Koenigswald *et al.*, 2004, 2005).

SYSTEMATICS

PALAEORYCTIDAE

The systematic position of Palaeoryctidae is uncertain. Van Valen (1966) included the subfamilies Deltatheridiinae, Palaeoryctinae, and Micropternodontinae in Palaeoryctidae and classified the family in the Deltatheridia. Later publications removed deltatheridiines (Butler and Kielan-Jaworowska, 1973) and micropternodontines (Butler, 1972) from Palaeoryctidae. McKenna (1975) classified Palaeoryctidae in Kennalestida, Szalay (1977) in Leptictimorpha, and Butler (1972), Novacek (1976), Kielan-Jaworowska (1981), and Bown and Schankler (1982) in Proteutheria. While Gingerich (1982a) and Thewissen and Gingerich (1989) placed Palaeoryctidae in Insectivora, and McKenna, Xue, and Zhou (1984) placed it in Soricomorpha, others have argued that Palaeoryctidae are not directly related to Lipotyphla (McDowell, 1958; Van Valen, 1966, 1967; Lillegraven, 1969; Szalay, 1977; Butler, 1988). Thewissen and Gingerich (1989) included palaeoryctids in Insectivora (*sensu* Novacek, 1986) in order to recognize a close relationship between taxa included in Palaeoryctidae, Leptictidae, and Lipotyphla. This broad classification is at least supported by the recent phylogenetic hypotheses published by Asher *et al.* (2002) in which “Lipotyphla” is paraphyletic with respect to a number of fossil taxa, including the palaeoryctids *Eoryctes* and *Pararyctes*.

Palaeoryctidae as recognized here includes four species of *Palaeoryctes* (Matthew, 1913; Van Valen, 1966; Gunnell, 1994; Bloch, Secord, and Gingerich, 2004), two species of *Pararyctes* (Van Valen, 1966), one species of *Aptoryctes* (Gingerich, 1982a), one species of *Eoryctes* (Thewissen and Gingerich, 1989), one species of *Ottooryctes* (Bloch, Secord, and Gingerich, 2004), and one species of *Lainoryctes* (Fox, 2004). This is similar to the classification of McKenna and Bell (1997) except that it includes *Pararyctes* (also excluded by Kellner and McKenna, 1996) in order to recognize, given our current state of phylogenetic resolution, that excluding taxa like *Pararyctes* that appear closely related will only complicate later phylogenetic studies and classification (Bloch, Secord, and Gingerich, 2004) (Figure 5.2).

CIMOLESTIDAE

Cimolestids include some of the most primitive members of Tertiary “proteutherians” as recognized here. *Cimolestes* includes several Late Cretaceous species and cimolestids have been proposed as possible ancestral or sister taxa for a variety of other groups including Taeniodonta, Carnivora, Creodonta, Apatemyidae, Palaeoryctidae, and Condylarthra (Kielan-Jaworowska, Bown, and Lillegraven, 1979). We follow McKenna and Bell (1997) in recognizing Cimolestidae as a family of the suborder Didelphodonta. Except for *Paleotomus*, which we consider to be a pantolestine, the North American members of Cimolestidae recognized here are the same as those included by McKenna and Bell (1997).

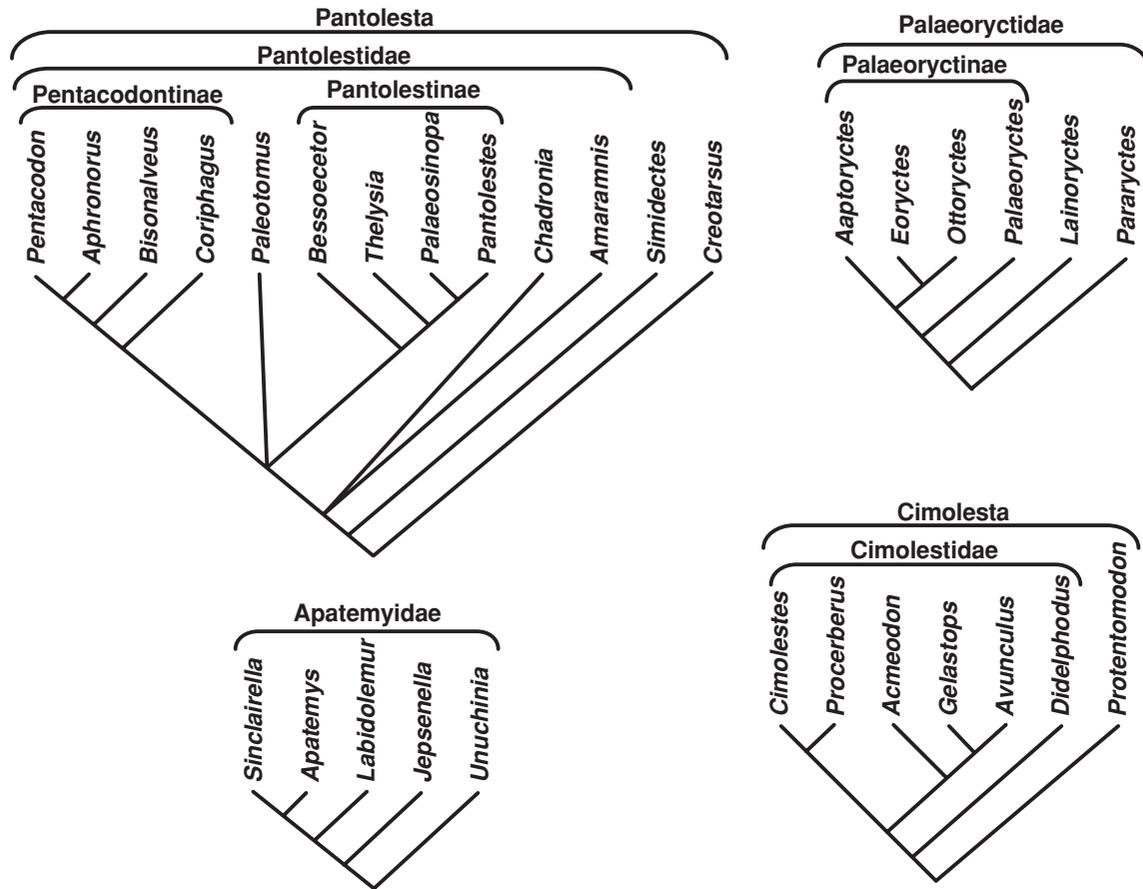


Figure 5.2. Proposed relationships of Pantolestida, Palaeoryctidae, Apatemyidae, and Cimolestida. See text for characters supporting labeled clades.

PANTOLESTIDAE

Matthew (1899) initially suggested a primate or creodont affinity for pantolestids. Following his description of a relatively complete specimen of *Pantolestes natans*, Matthew (1909) rejected all previous hypotheses of relationship and asserted that pantolestids were “insectivores of a peculiar type.” He noted that *Pentacodon* probably belonged in the Pantolestidae, partly because of the position of the mental foramen (below m1). He did, however, also suggest a broader relationship of pantolestids to aquatic carnivores, stating: “the arrangement of the fronto-nasal maxillary sutures, the large infraorbital foramen, the arrangement of the upper incisors and canines, the form of the astragalus, etc. compare with the walrus . . . in such a way as to suggest some degree of actual affinity.” However, Matthew also suggested that other features of *Pantolestes* were probably convergent on Pinnipedia. He noted “flattening of the distal part of the femur, reduction of the cnemial crest and internal malleolus of the tibia and the facet for the tibia on the neck of the astragalus, the elongate pisiform, elongation of the metapodials and especially of proximal phalanges, thickening of the metapodials and proximal phalangeal shafts, flattening of the distal phalangeal shafts and unguals and above all, the conversion of the ball-and-socket joints of the metapodials and phalanges into hinge-joints” as “probably

adaptive.” Why he felt that some features were “synapomorphies,” while regarding other shared features as convergences, is unclear. He also noted that the odd wear of the teeth in combination with the body size probably indicated a diet consisting of fish, turtles, and clams.

The Pentacodontinae (Simpson, 1937b) is a fairly diverse group recognized here as a subfamily of Pantolestidae, which is as Simpson (1937b) originally conceived it (see also McKenna and Bell, 1997). Their fossils are known from Torrejonian (*Coriphagus*) through middle Tiffanian (*Bisonalveus*). Pentacodontines were originally differentiated from pantolestines on the basis of a hypertrophied submolariform fourth premolar, as well as by relatively lower molar trigonids. Doubt regarding the precise relationships of this group began to accrue, leading Van Valen (1966) to elevate it to the family level. Previously, Gazin (1959) suggested that the condition of the premolars was phylogenetically significant and indicated that some hypsodontid condylarths (*Phenacodaptes* and *Apheliscus*) should be considered closer relatives of pentacodontids than to other condylarths. Other researchers (Saban, 1954, 1958; McKenna, 1960; Van Valen, 1966) agreed with this interpretation, although Van Valen believed the premolar similarity to be convergent. Rose (1978) noted the possibility of a close relationship to palaeoanodonts on the basis

of very general similarities in tooth shape, relative tooth size, and dental wear pattern, but cautioned that these shared features could easily be convergent. The fact that a diversity of taxa have been suggested to be relatives of pentacodontids is a reflection of the very fragmentary preservation and generalized tooth morphology (save the premolar) of this group.

Boyer and Bloch (2003) reported on newly discovered, semi-articulated specimens of early Tiffanian *Aphronorus orieli*, recovered from limestone nodules of the Fort Union Formation. They represent a new skull and the first postcrania known for the Pentacodontidae. The new morphology appears similar to that known for pantolestines and, therefore, consistent with the hypothesis, based on dental features, that pentacodontines are closely related to this group. Postcranial similarities to the primitive palaeonodont *Escavadodon zygus* and other palaeonodonts hint that Palaeonodonta may have arisen from Pantolestidae, as implied by Rose (1978), and Rose and Lucas (2000).

APATEMYIDAE

Marsh (1872) described the first North American apatemyids (two species of *Apatemys*) and placed them in his broadly construed "Insectivora." Since then, apatemyids have been assigned to a number of different groups including rodents (Matthew, 1899), insectivores (Matthew, 1909; Jepsen, 1934), plesiadapiforms (Matthew, 1918), in their own order Apatotheria (Scott and Jepsen, 1936; Carroll, 1988), primates (Simpson, 1945), and proteutherians (Romer, 1966; Rose, 1981). Most recently, McKenna and Bell (1997) recognized Apatotheria as a suborder of Cimolesta.

INCLUDED GENERA OF "PROTEUTHERIANS"

The locality numbers listed for each genus refer to the list of unified localities in Appendix I. The locality numbers may be listed more than one way. The acronyms for museum collections are listed in Appendix III.

Parentheses around the locality (e.g., [CP101]) mean that the taxon in question at that locality is cited as an "aff." or "cf." the taxon in question. Parentheses are usually used for individual species, implying that the genus is firmly known from the locality, but the actual species identification may be questionable. Question marks in front of the locality (e.g., ?CP101) mean that the taxon is questionably known from that locality, implying some doubt that the taxon is actually present at that locality, either at the genus or species level. An asterisk (*) indicates the type locality.

CIMOLESTA MCKENNA, 1975

PALAEORYCTIDAE WINGE, 1917

Palaeoryctes Matthew, 1913

Type species: *Palaeoryctes puercensis* Matthew, 1913.

Type specimen: AMNH 15923.

Characteristics: Dental formula I[?]/3, C1/1, P3/3, M3/3; temporal bone expanded into lambdoid plates; no evidence of vasculature on promontorium; upper molars narrow and transversely wide, protozalambdodont, lacking precingula and postcingula; M3/m3 unreduced; lower premolars simple; p2–3 larger than p4; lower molars with tall trigonids (Van Valen, 1966; Bloch, Secord, and Gingerich, 2004).

Average length of m2: 1.4 mm (*P. puercensis*).

Included species: *P. puercensis* (known from localities SB23[F], G*, H, CP14A); *P. cruoris* (locality CP24A*); *P. jepseni* (localities CP13F, G*); *P. punctatus* (localities [CP13G], [CP14E], CP17B, CP18*, [CP20A], [CP24A], [CP25B], [NP1C], [NP3B], [NP47B, B2]).

Palaeoryctes sp. is also known from localities CP13(E), G, CP14B, C, CP18B, CP19A, CP20A, (BB), NP7B, NP20D, (NP47C).

Comments: *Palaeoryctes* is also known from the late Paleocene to late Eocene of Morocco (McKenna and Bell, 1997).

Pararyctes Van Valen, 1966

Type species: *Pararyctes pattersoni* Van Valen, 1966.

Type specimen: UW 2002.

Characteristics: Dental formula I[?]/? , C1/1, P5/5, M3/3; upper molars with distinct precingulum and postcingulum (Van Valen, 1966; Fox, 1983).

Average length of m1: 1.6 mm.

Included species: *P. pattersoni* (known from localities CP16A*, NP1C, NP3B–D, NP4, NP19IIC, NP47B); *P. rutherfordi* (locality NP1C*).

Pararyctes sp. is also known from localities (CP20A), NP1C, NP2, NP3A–C, F, NP7D, (NP16C), (NP47C).

Aptoryctes Gingerich, 1982a

Type species: *Aptoryctes ivyi* Gingerich, 1982a.

Type specimen: UMMP 77291.

Characteristics: Dental formula I[?]/3, C1/1, P3/3, M3/3; upper molars simple, protozalambdodont with broad stylar shelf, connate paracone and metacone, no precingulum or postcingulum; lower molars with broad high trigonids and narrow talonids; premolars enlarged and inflated (especially P4/p4) (Gingerich, 1982a).

Average length of m2: 2.5 mm.

Included species: *A. ivyi* only (known from localities CP13F, G*).

Aptoryctes sp. is also known from locality CP22B.

Eoryctes Thewissen and Gingerich, 1989

Type species: *Eoryctes melanus* Thewissen and Gingerich, 1989.

Type specimen: UM 68074.

Characteristics: Dental formula I[?]/? , C[?]/1, P[?]/3, M3/3; temporal bone expanded into lambdoid plates; middle ear

arteries enclosed in bony tubes; bulla ossified; retroarticular foramen small; P4 uninflated, transversely elongate with relatively small parastyle; upper molars with strongly inflected labial cingulum and weak lingual cingula; p1 absent; p4 uninflated and lacking paraconid; lower molars with relatively high trigonid and labially placed hypoconid (Thewissen and Gingerich, 1989).

Average length of m1: 2.3 mm.

Included species: *E. melanus* only (known from localities CP19A, B).

Lainoryctes Fox, 2004

Type species: *Lainoryctes youzwyshyni* Fox, 2004.

Type specimen: UALVP 43003.

Characteristics: Dental formula I?/? , C1/? , P3/? , M3/? ; relatively large size; P3 lacking protocone; P4 lingually slender; M1 paracone and metacone moderately connate; upper molars with conules (Fox, 2004).

Average length of M2: 2.6 mm.

Included species: *L. youzwyshyni* only, known from locality NP3E only.

Ottoryctes Bloch, Secord, and Gingerich, 2004

Type species: *Ottoryctes winkleri* Bloch, Secord, and Gingerich, 2004.

Type specimen: UM 72624.

Characteristics: Dental formula I3/3, C1/1, P3/3, M3/3; temporal bone expanded into lambdoid plates; C1 double-rooted with distinct anterior and posterior accessory cusps; P2 double-rooted; P3 lacking protocone; P4 with metacone; M3 metacone reduced; c1 relatively small but larger than p2; p3 with anterior cuspule; p4 with narrow and pointed protoconid and bladeli-like unbasined talonid; m1–3 with relatively expanded talonids (Bloch, Secord, and Gingerich, 2004).

Average length of m2: 1.95 mm.

Included species: *O. winkleri* only, known from locality CP19C* only.

Indeterminate palaeoryctids

In addition to the taxa above, indeterminate or undescribed palaeoryctids are known from localities CC4, CP5A, CP11IIA, CP15B, NP1C, NP3A0, D, NP7B, NP16C, NP17, NP19IIA, NP48B.

CIMOLESTA INCERTAE SEDIS

Protentomodon Simpson, 1928

Type species: *Protentomodon ursivalis* Simpson, 1928.

Type specimen: AMNH 22164.

Characteristics: m2–3 trigonid elevated well above heel, cusps acute and angulate, metaconid anterointernal to protoconid, large, and not as high as protoconid, paraconid

distinct, acute, low and median on tooth, united by sharp ridge to protoconid; m2 talonid short, low, about as wide as trigonid, basin surrounded by continuous, sharp, raised rim with entoconid, hypoconulid, and hypoconid as elevations of equal prominence, hypoconulid somewhat closer to hypoconid; m3 talonid narrower and longer, hypoconulid median and elevated above other more indistinct cusps; m2–3 with cingulum running sharply downward and externally from near paraconid around the external base of protoconid; dentary very slender and elongate, with posterior mental foramen below m1 (Simpson, 1928).

Average length of m2: 2.0 mm.

Included species: *P. ursivalis* only (known from localities CP17A*, NP20E).

Comments: Simpson originally placed *Protentomodon* in a new family, Nyctitheriidae (which it does not at all resemble) while Van Valen (1967) suggested affinities with Pentacodontidae. McKenna (1960) suggested that the genus might have apatemyid affinities while McKenna and Bell (1997) placed it in Cimolestidae. The genus is too poorly known to ascertain its relationship positively, but the idea of an affinity with apatemyids may have merit given the presence of elevated trigonids that are canted somewhat posteriorly, the medial paraconid, talonid structure, mental foramen beneath m1, and the extension of the symphysis posteriorly to a point beneath the p3–4 boundary.

DIDELPHODONTA MCKENNA, 1975

Cimolestes Marsh, 1889 (including Nyssodon; Puercolestes)

Type species: *Cimolestes incisus* Marsh, 1889.

Type specimen: YPM 11775.

Characteristics: Dental formula I?/2, C?/1, P?/4, M3/3; P3–4 with protocones; P4 lacks or has a small metacone; upper molars with relatively broad stylar shelves, small stylar cusps, closely approximated, high, connate paracone and metacone, postparaconule and premetaconule wings extending from conules to bases of paracone and metacone, and precingula and postcingula absent or small; p4 trenchant with small anterior accessory cusp, unicuspid talonid, and lacking metaconid; lower molar paraconids lingual positions; metaconids slightly lower and smaller than protoconids (Clemens, 1973).

Average length of m2: 3.4 mm (*C. incisus*).

Included species: *C. incisus* (known from localities NP15A, [NP17]); *C. cerberoides* (localities [NP6], [NP7A]); *C. magnus* (locality NP15A); *C. simpsoni* (localities SB23A*, B, [NP7B]); *C. stirtoni* (locality [NP7A]).

Cimolestes sp. is also known from localities SB23A, B, CP11IIG, NP7C, NP17.

Comments: The holotypes of *C. incisus*, *C. magnus*, and *C. stirtoni* are from the Late Cretaceous Lance Formation in Montana, that of *C. cerberoides* is from the Late Cretaceous Scollard Formation in Alberta. *Cimolestes* is

also known from the Paleocene of Africa and questionably from the Paleocene of South America (McKenna and Bell, 1997).

***Procerberus* Sloan and Van Valen, 1965**

Type species: *Procerberus formicarum* Sloan and Van Valen, 1965.

Type specimen: UMVP 1460.

Characteristics: Relatively small size; P3–4 submolariform with shearing metacristae, lingual cingula and conules absent; upper molars not transverse, lingual cingula small to absent, paracone and metacone connate, conules small; p3 simple with paraconid and single-cusped talonid; p4 submolariform, narrow with anterior paraconid, weak parolophid, metaconid slightly posterior to protoconid; lower molars with large, lingual paraconids, paraconid and metaconid of subequal height, and trigonid only moderately higher than talonid (Sloan and Van Valen, 1965).

Average length of m2: 2.8 mm.

Included species: *P. formicarum* (known from localities [NP7A], NP15A*-C, NP16A); *P. plutonis* (locality NP16C*).

Procerberus sp. is also known from localities ?SB23A, CP11IIG, CP61A, NP3, NP7B, C, NP16A, NP17.

Comments: When originally described by Sloan and Van Valen (1965), the type locality of *P. formicarum*, Bug Creek Anthills (locality NP15A), was thought to be in the Late Cretaceous, as were the other two localities (Bug Creek West and Harbicht Hill, localities NP15B and NP15C, respectively) where *P. formicarum* was recognized. All of these localities are now placed in the early Paleocene (Lofgren *et al.*, 2004).

***Acmeodon* Matthew and Granger, 1921**

Type species: *Acmeodon secans* Matthew and Granger, 1921.

Type specimen: AMNH 16599.

Characteristics: p4 low with deeply basined postvallid and talonid; m1 hypoconulid close to hypoconid.

Average length of m2: 3.0 mm (*A. secans*).

Included species: *A. secans* (known from localities SB23F, G, H*, CP13C, D, CP13IIA, CP14B); *A. hyoni* (localities CP14A*, [B]).

Acmeodon sp. is also known from localities CP1C, NP19IIA, NP20B, D.

***Avunculus* Van Valen, 1966**

Type species: *Avunculus didelphodontidi* Van Valen, 1966.

Type specimen: AMNH 35297.

Characteristics: c1 alveolus about half as long as that of p4; p1 single-rooted; p3 much shorter and smaller than p4 with relatively prominent paraconid; p4 protostylid and metaconid absent and talonid unbasined; m1 metacristid absent from at least m1 (Van Valen, 1966).

Average length of m1: 2.8 mm.

Included species: *A. didelphodontidi* only (known from localities [CP13C], NP19C*).

***Gelastops* Simpson, 1935 (including *Emperodon*)**

Type species: *Gelastops parvus* Simpson, 1935.

Type specimens: USNM 6148.

Characteristics: Dental formula I?/? , C?/1, P?/4, M3/3; M2 metaconule vestigial, hypocone absent; c1 erect; lower premolars crowded; p4 with distinct and subequal paraconid and metaconid; m1 trigonid long relative to talonid; m2–3 trigonids shorter and more elevated; m2 and particularly m3 smaller relative to m1 (Simpson, 1935; Van Valen, 1966).

Average length of m2: 2.5 – 2.9 mm (*G. parvus*).

Included species: *G. parvus* (including *Emperodon acmeodontoides* Simpson, 1935) (known from localities CP13B, [C, D], [CP14B], NP19C*); *G. joni* (localities [CP13IIB], CP14A*).

Gelastops sp. is also known from localities SB39IIA, CP15A, NP3A0, C, (NP16C).

***Didelphodus* Cope, 1882 (including *Didelphyodus*; *Phenacops*; *Deltatherium*, in part)**

Type species: *Didelphodus absarokae* (Cope, 1881) (originally described as *Deltatherium absarokae*).

Type specimen: AMNH 4228.

Characteristics: Dental formula I?/3, C1/1, P4/4, M3/3; lower premolars simple and uncrowded; p3 moderately reduced relative to p4; m1 trigonid short relative to talonid; m2–3 moderately reduced relative to m1 (Matthew, 1909; Van Valen, 1966).

Average length of m2: 3.8 mm (*D. absarokae*).

Included species: *D. absarokae* (including *Didelphodus ventanus* Matthew, 1918) (known from localities SB24, CP19A, CP20A-D, CP25B, CP27C, D, CP63, CP64A-C); *D. altidens* (including *Phenacops incerta* Matthew, 1909) (localities CP27C, [D, E], CP34B, D*, CP63, CP64C); *D. rheos* (locality NP9A*); *D. serus* (locality NP8*).

Didelphodus sp. is also known from localities CP25F, G, CP27B, D, E, CP31E, NP9B, (NP49).

Comments: The precise locality of Cope's holotype of *Didelphodus absarokae* is unknown. The specimen was collected by Jacob Wortman in 1881. According to Gingerich (1980), Wortman's work in the Bighorn Basin that summer was probably concentrated around the Dorsey Creek area south of the Greybull River. If the holotype of *D. absarokae* was collected from this area it was found somewhere in the CP20 sequence.

Didelphodus is also known from the Eocene of Europe (McKenna and Bell, 1997).

Indeterminate didelphodontids

An indeterminate didelphodontid is known from locality NP1C.

PANTOLESTA MCKENNA, 1975

PANTOLESTIDAE COPE, 1884

PANTOLESTINAE COPE, 1884

***Paleotomus* Van Valen, 1967 (including *Niphredil*;
Palaeosinopa, in part)**

Type species: *Paleotomus senior* (Simpson, 1937a) (originally described as *Palaeosinopa senior*).

Type specimen: AMNH 33990.

Characteristics: Lower molar paraconid moderately high and sectorial but not shifted forward, trigonid high, labial border of protoconid forms circular arc, protoconid considerably higher than metaconid, paralophid and protolophid with deep carnassial notches, talonid narrower than trigonid, entoconid distinct and higher than hypoconid, prevalid and postvallid shear well developed; $p4 \sim m1 < m2 \sim m3$; $m3$ trigonid higher than that of $m1-2$ (Van Valen, 1967).

Average length of $m3$: 5.0 mm (*P. senior*).

Included species: *P. senior* (including *Palaeosinopa simpsoni* Van Valen, 1967) (known from localities SB39A, CP22B, NP1C, NP19IIA, C*, [NP47A, B]); *P. carbonensis* (localities CP13IIA, B*); *P. junior* (localities NP1C*, NP3A0); *P. milleri* (locality CP14A*); *P. radagasti* (Van Valen, 1978) (originally described as *Niphredil radagasti*) (localities CP13E*, [CP22B]).

Paleotomus sp. is also known from localities CP13IIA–B, CP24A, NP1C.

Comments: McKenna and Bell (1997) placed *Paleotomus* in Cimolestidae along with *Procerberus* and *Cimolestes* while Scott, Fox, and Youzwysyn (2002) assigned *Paleotomus* to family incertae sedis. We choose to retain it as a pantolestid because of the similarities between it and *Palaeosinopa*.

***Bessoecetor* Simpson, 1936 (including *Propalaeosinopa*;
Thylacodon, in part; *Palaeosinopa*, in part; *Palaeictops*, in part; *Diacodon*, in part)**

Type species: *Bessoecetor septentrionalis* (Russell, 1929) (originally described as *Diacodon septentrionalis*).

Type specimen: UALVP 126.

Characteristics: Upper molars relatively transverse, anterolingual cingulum weak, hypocone moderate to small; $M3$ only slightly reduced with distinct metacone; $p4$ elongate with distinct anterior basal cusp, talonid short and weakly basined; lower molars with low paraconid shelf, talonid cusps distinct, especially on $m3$; $p4 \sim m1 < m2 \sim m3$; $m3$ trigonid higher than that of $m1-2$ (Simpson, 1936).

Average length of $m2$: 2.3 mm.

Included species: *B. septentrionalis* (including *Propalaeosinopa diluculi* Simpson, 1935; *Propalaeosinopa thomsoni* Simpson, 1936; *Thylacodon* sp. nov. Russell [in Rutherford, 1927]; *Palaeictops septentrionalis*, Van Valen, 1967)

only (known from localities CP13C, D, [E], CP14A, C, D, [CP24A], CP26A, NP1C*, NP3A0, NP3B, D, NP4, NP14D, NP19C, NP19IIA, C, NP20D, E, NP47A, B, BB).

Bessoecetor sp. is also known from localities?CP1B, NP2, NP3A0, F, NP7D, NP20B, NP47C.

Comments: Scott, Fox, and Youzwysyn (2002) noted that Simpson’s (1927) holotype of *Propalaeosinopa albertensis* is non-diagnostic, rendering the genotype species a nomen dubium and leaving the genus *Propalaeosinopa* unavailable. These authors also recognized that Russell’s (1929) holotype of *Diacodon septentrionalis* represents the same species as Simpson’s (1935) “*Propalaeosinopa diluculi*,” giving it priority over the latter species. Since *Propalaeosinopa* has no taxonomic status, Scott, Fox, and Youzwysyn (2002) referred Russell’s taxon to *Bessoecetor* as the type species, placing both “*Propalaeosinopa diluculi*” and “*Propalaeosinopa thomsoni*” in synonymy with *Bessoecetor septentrionalis*.

Bessoecetor is also questionably known from the late Paleocene of Europe (McKenna and Bell, 1997).

***Thelysia* Gingerich, 1982a**

Type species: *Thelysia artemia* Gingerich, 1982a.

Type specimen: UMMP 68281.

Characteristics: Dentary shallow; lower molars with antero-posteriorly short, high trigonids, reduced paraconids, and narrow talonids (especially on $m2-3$) lacking entocristids and open lingually (Gingerich, 1982a).

Average length of $m2$: 3.9 mm.

Included species: *T. artemia* only, known from locality CP17B* only.

Thelysia sp. is known from locality CP19AA.

***Palaeosinopa* Matthew, 1901**

Type species: *Palaeosinopa veterrima* Matthew, 1901.

Type specimen: AMNH 95.

Characteristics: Dental formula I3/3, C1/1, P4/4, M3/3; P3–4 simple with small P3 protocone and strong P4 protocone; P4 anterobuccal and posterobuccal basal cusps small to tiny; $M1$ metastyle rudimentary, moderately extended on $M2$; upper molars tritubercular with strong posterolingual cingular ledge, protocone high and crescentic, paracone and metacone conical, sharp, somewhat inset from buccal border, well-developed buccal cingular shelf, crest curving anterobuccally from paracone apex to posterobuccal angle, narrow anterior cingulum; $M3$ transverse with vestigial metacone; $m1-3$ trigonid cusps subequal, paraconid distinct, talonid larger than trigonid, hypoconid and entoconid strong, hypoconulid present but strong only on $m3$ (Matthew, 1901, 1918).

Average length of $m2$: 5.4 mm (*P. didelphoides*).

Included species: *P. veterrima* (known from localities CP20A*, B, BB, D, CP27D); *P. didelphoides* (localities SB24, [CP25H, I], CP26C, CP27D, E*, [NP20E]);