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Paleogene rodents of Eurasia

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Soon after their Asian origin in the Late Paleocene, rodents began a morphological radiation and geographic expansion that extended across the entire Holarctic and at least northern Africa. Following this initial dispersal, a relatively high degree of endemism developed among Eocene rodents of both Europe and Asia. Only the family Ischyromyidae was shared by Europe and Asia, but the ischyromyid genera of the two areas were highly divergent. Eocene endemic development appears to have been complete among the glirids and theridomyids of Europe and the ctenodactylids of Asia. The evolution of Cylindrodontidae, Eomyidae, Zapodidae, and Cricetidae in Asian Eocene faunas occurred independently of contemporary rodent faunal developments in Europe. Following the latest Eocene or early Oligocene regression of the marine barrier between Europe and Asia, marked faunal changes occurred as a result both of the evolution of new rodent families (e.g., Aplodontidae, Castoridae, Sciuridae) that accompanied climatic changes of the later Eocene and of changes in rodent distribution across the Holarctic. Within Europe, the theridomorphs were at last negatively impacted, but the glirids appear not to have been adversely affected. In the Asian Oligocene, the ctenodactylids continued to be a prominent part of rodent faunas, although they were diminished in morphologic diversity.

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INTRODUCTION

The 33 million years of rodent evolution that occurred during the Paleogene witnessed the origin of the Rodentia from among the small Asian herbivores that are recognized as early Glires, primitive mammals in many ways but in which a set of anterior incisors became lengthened and expanded into relatively large, chisel-like teeth. In the rodents and lagomorphs, and presumably in the earlier Glires, the enlarged teeth are $dI2/2$. The loss of the canine tooth and of several premolars results in a more-or-less pronounced diastema separating the incisors from the next tooth in the maxilla and mandible. Within a relatively short time after their Asian origin in the Late Paleocene, rodents expanded their range into North America, Europe, and at least northern

Africa. Early in this history of expansion, which took place during a time of marked global climatic warming, the rodents faced competition for food sources from a variety of other herbivores that included non-rodent Glires, multituberculates, primates, and probably smaller artiodactyls.

Even at the time of their first appearance in the fossil record, there was morphological differentiation within rodents, particularly in premolar structure and occlusal pattern of the cheek teeth. By the late Early or early Middle Eocene, evolutionary changes had occurred also in the zygomaseteric structure (Hartenberger 1969, Dawson *et al.* 1990) and the incisor enamel (Martin 1992). Although rodents did experience some crises, such as their reduction in variety in the early Middle

Eocene of Europe (Hartenberger 1989), their diversity continued to increase during the Paleogene. The climatic cooling of the later Eocene and accompanying changes in vegetation, which may have been critical limiting factors for some of their earlier herbivore competitors and which were probably factors in extinction of some of the primitive rodent families, did not hinder the remarkably adaptive Rodentia as a whole and, indeed, the Oligocene was a time of more phylogenetic diversification and geographic expansion, now into South America. This led into the role in the Neogene of rodents as the most abundant and diverse mammals in existence.

Even within the geographically mobile Paleogene rodents, there are instances of their strongly endemic development. In Asia this can be seen most clearly in the array of ctenodactyloids and in Europe of glirids and theridomyids. The theridomyids did not flourish after the influx of allochthonous rodents that flowed into Europe early in the Oligocene, following the Grande Coupure, whereas the glirids became very successful. The Asian endemic ctenodactyloids were reduced in morphological diversity in the Oligocene, became increasingly restricted in distribution during the Neogene, and survive today only in northern and eastern Africa.

THE FRAMEWORK

There are at least three basic requirements for a review of this sort to have any validity, even short lasting. The first is to have a sound temporal framework within which to arrange the continental deposits from which the rodent fossil record mostly stems. The second is to have a solid taxonomic base on which to work. And the third is to build on some concept of the geographic and, if possible, environmental constraints to the distribution of primarily terrestrial mammals at the time under consideration. Although intracontinental correlation of Paleogene terrestrial deposits of Eurasia must still be regarded as 'work in progress', it is essential here to arrive at and adhere to a temporal framework for

this discussion. This framework will affect interpretations of the fossil record in numerous ways, and is especially interesting for intervals that seem to correspond to critical biotic, climatic, and distributional events. A good deal of attention has been given to events such as the Paleocene-Eocene boundary and its associated global warming, the timing of the Grande Coupure, following the onset of global cooling, and enough closing of the marine Turgai Strait to promote rodent distribution across Eurasia. The accurate timing of these events is particularly vital.

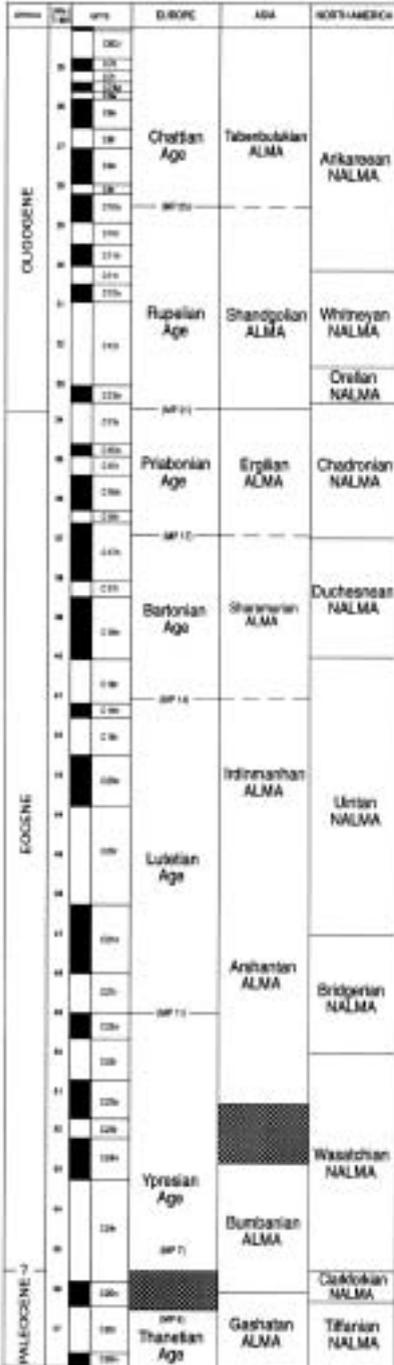
The temporal framework here utilized (Table 1) was established in the following manner:

(1) The foundation on which it stands is the Paleogene time scale built from marine biostratigraphy that has been correlated to the global polarity time scale and with the addition of radiometric calibration points (Berggren *et al.* 1995); to this information can be added the calibration of the Paleocene/Eocene thermal maximum at about 55 Ma (Norris & Röhl 1999).

(2) For Europe the usually accepted Paleogene mammal reference levels (Schmidt-Kittler 1987) were followed. Under this system, European terrestrial mammal sites were assigned to reference localities that are both named and sequentially numbered as reference levels, MP1 to 30 for the Paleogene (MP1-5 were assigned without precise reference localities due to the inadequate earlier Paleocene record in Europe). The reference levels were, in turn, tied to boundaries of marine stages. This system is especially applicable to localities in western Europe.

(3) The vast central, eastern and southern Asian record is a weaker link in Paleogene terrestrial correlation. In most cases, biostratigraphy provides the sole evidence for correlation. Carefully applied, this can be relatively accurate, but in a geographic area where several groups of mammals originated, 'first appearances' and related biostratigraphic tools can be very misleading. Few localities in the Paleogene of north-central and eastern

Table 1 The Paleogene time scale followed here for Europe, Asia and North America, with radiometric time (MA, millions of years) and chronozones of the Global Polarity Time Scale (GPTS). Abbreviations: **MP**, reference levels; **ALMA**, Asian Land Mammal Age; **NALMA**, North American Land Mammal Age.



Asia have marine associations, few types of sediment appropriate for radiometric study are available, and, so far, few magnetostratigraphic studies have been completed. The correlation attempted here is derived from the biostratigraphic discussions of Russell & Zhai (1987), Dashzeveg (1988), Tong *et al.* (1995), Meng *et al.* (1998), Emry *et al.* (1998), Meng & McKenna (1998), Ting (1998), Wang Y. *et al.* (1998), Marivaux *et al.* (1999); from the biostratigraphic and magnetostratigraphic work of Benammi *et al.* (2001); and from the biostratigraphic, radiometric, and magnetostratigraphic work of Höck *et al.* (1999). Nonetheless, major intervals remain problematic for correlation, especially the Arshantan-Sharamurunian and the later Shandgolian-early Tabenbulukian. Until these times can be more precisely correlated on a worldwide basis, interpretations of the phylogenetic significance of rodents from these intervals must remain somewhat problematic.

(4) The fossil record from North America has been consulted in cases where origin of a group of rodents might be traced in that continent. It must not be forgotten, even in a discussion of the rodents of Eurasia, that the North American fossil rodents were there in the Eocene, lurking on the edge of the Beringia, which was an operational land corridor throughout the Paleogene, and in the North Atlantic terrestrial province (Dawson 2001), which appears to have been habitable at least until the end of the Early Eocene. The relatively well-established North American land mammal ages have been indicated in Table 1 (Prothero 1995, Woodburne & Swisher 1995, Beard & Dawson 1999).

Taxonomic framework

The taxonomic foundation on which this review is based is the compilation by McKenna & Bell (1997) for genera and their ranges, although not for higher categories; questionable genera have been examined and included or rejected according to my judgement of their taxonomic validity, phylogene-

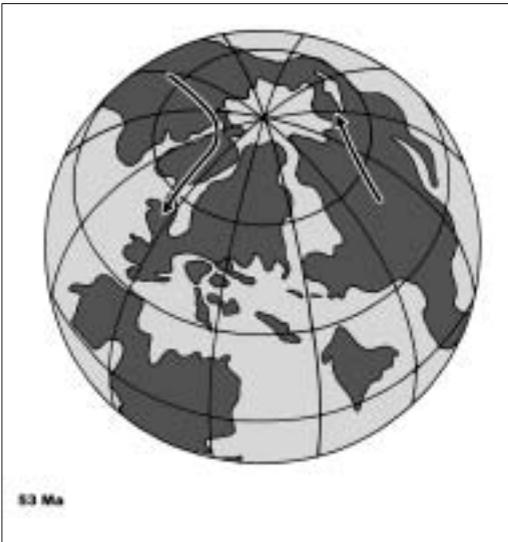
tic impact and/or stratigraphic accuracy. Attempts were also made to keep up with new taxa and range changes from the end of 1996 until the end of 2000. The importance of sound systematic work to a review of this sort cannot be overemphasized. It is also remembered that paleontological exploration continues to bring new discoveries that can be expected to have considerable impact on interpretations of Paleocene rodent evolution. This is particularly true of the Asian record. Forty years ago Eocene ctenodactyloids were not even recognized! What might the next forty bring?

Paleogene paleogeography presents us with a different Holarctic world. For a time in the Late Paleocene and beginning of the Eocene, there must have been an uninterrupted North Atlantic terrestrial province between North America and Europe south of Scandinavia (McKenna 1983, Knox 1998), although some details of the position (Map 1) and timing of this connection are still not entirely clear. Beringia was a widely open habitat bridging Asia and North America throughout the

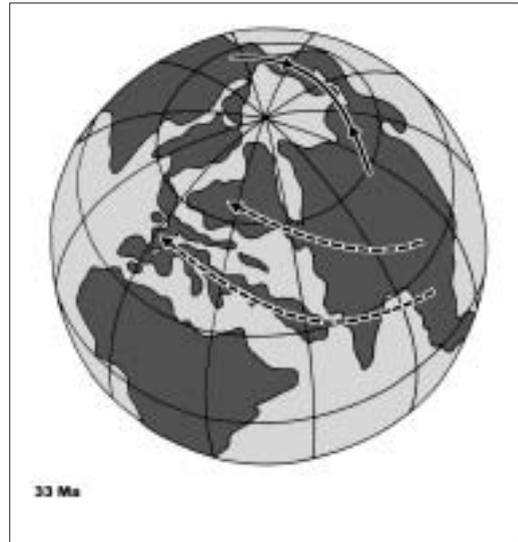
Paleogene (Marincovich & Gladenkov 1999). Within Eurasia, on the other hand, the Turgai Strait, an only incomplete marine barrier during the Paleocene, restricted free interchange of terrestrial animals between Asia and Europe during most of the Eocene. This barrier to interchange was gone, following marine regression, by the Late Eocene or Early Oligocene (Map 2). Rodents of the Late Paleocene through Late Oligocene (Map 3) also witnessed strong environmental perturbations, including the thermal maximum at the Paleocene-Eocene border, cooling that affected mid- and high-latitudes in the later Eocene, and still further cooling, marked by transient Antarctic glaciation, at the Oligocene-Miocene border (Zachos *et al.* 2001).

THE ORIGIN AND EARLY DIVERSIFICATION OF RODENTS IN ASIA

The Early to Middle Paleocene Wanghudun Formation in the Qianshan Basin of Anhui Province, east central China, has yielded specimens that document an early radiation



Map 1 Early Eocene (53MA) continental positions; the rodent record supports an interpretation of closer proximity of India to Asia at the time. Arrows indicate directions of rodent migrations. (Sources for map construction: <http://www.ods.de/odsn/services/paleomap/paleomap.html> (Hay *et al.* 1999), Heissig 1979b, Smith *et al.* 1994)



Map 2 Early Oligocene (33MA) continental positions; arrows indicate directions of rodent migrations. The rodent record suggests the proximity of India to Asia and more possibilities of island hopping in the northern Tethys.

of the mammalian order Anagalida, and the first appearance of their close relatives, *Heomys* and *Mimotona* (Li 1977), two genera that provide the earliest known information on the origin of the Rodentia and the Lagomorpha respectively. This differentiation into two highly successful mammalian lineages appears to have occurred prior to the radiation of the non-rodent, non-lagomorph Glires that is characteristic of the Late Paleocene and Early Eocene of Asia (Dashzeveg & Russell 1988, Dashzeveg *et al.* 1998).

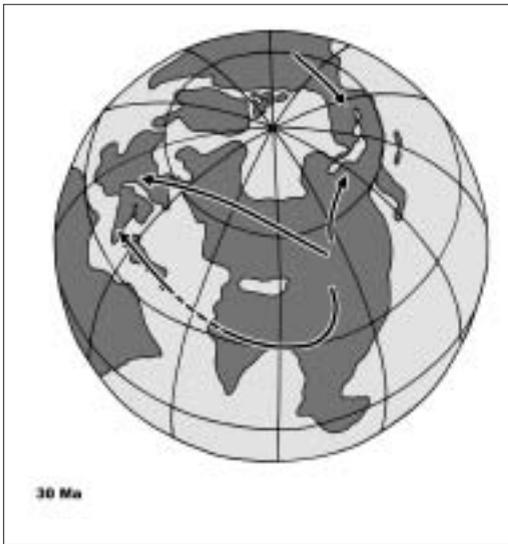
The Late Paleocene (Gashatan) Bayan Ulan fauna of Inner Mongolia provides the next record of a rodent, or rodent relative, from Asia. This is *Tribosphenomys*, a relatively well-represented genus that has been regarded as a sister group of the Rodentia, or as a rodent of the family Alagomyidae (Meng & Wyss 1994, Meng *et al.* 1994). The slightly younger first appearances of rodents (*sensu stricto*) in Asia are in three faunas that represent the latest Paleocene or earliest Eocene (Beard 1998) in Asia. These are the Wutu (Tong & Wang 1998) and Hengdong (Ting

1998) faunas of China and the Bumban fauna of Mongolia (Dashzeveg 1990a,b, Dashzeveg *et al.* 1998). From these occurrences, the Wutu rodent fauna of Shandong Province includes two species of Ischyromyidae, one of Alagomyidae (Fig. 1), and one ctenodactyloid questionably of the family Yuomyidae (Tong & Dawson 1995). Only Cocomyidae (Fig. 2) have been reported from the Hengdong fauna. Four genera of ctenodactyloids (Family Cocomyidae) have been reported from the Bumban fauna as well as one alagomyid and the peculiar *Ivanantonia*, the affinities of which are presumed to be with the Rodentia on the basis of the Hunter Schreger bands in the *portio interna* of the two layered incisor enamel (Hartenberger *et al.* 1997). *Ivanantonia* is, however, peculiarly derived for a rodent and may be an enigmatic non-rodent member of the Glires.

A high degree of endemism has been noted among Chinese Paleogene mammals (Wang Y. *et al.* 1998), among which the rodents appear to be no exception. During the Paleocene and Early Eocene two climatic zones were present in China, a semiarid to arid subtropical zone in central and south China and a more humid zone in eastern China (Tong & Wang 1998). Of the three Early Eocene localities in central and eastern Asia that have produced rodents, only the Wutu locality is in the eastern zone and it is a highly carbonaceous deposit indicative of a warm, moist environment. It is probably no coincidence that the oldest known, Clarkforkian, rodents of North America occur at two localities, Bear Creek in Montana and Big Multi in Wyoming, that also are characterized by highly carbonaceous deposits, indicative of similarly warm, moist environments (Dawson & Beard 1996).

The earliest recorded rodents from the Indian subcontinent are a few teeth of ischyromyid and ctenodactyloid rodents from the Early (? earliest) Eocene at Barbora Banda, Pakistan (de Bruijn *et al.* 1982, Leinders *et al.* 1999).

From an Early Eocene diversity of four families, Ischyromyidae, Alagomyidae,



Map 3 Later Oligocene (30Ma) continental positions; arrows indicate direction of rodent migrations.

Table 2 Temporal ranges of Asian Paleogene rodent genera by Asian Land Mammal Age. **G**, Gashatan; **B**, Bumbanian; **A**, Arshantan; **I**, Irldinmanhan; **S**, Sharamurunian; **E**, Ergilian; **Sh**, Shandgolian; **T**, Tabenbulukian. ? indicates that age is not precisely known; > indicates that range extends into the Miocene.

	G	B	A	I	S	E	Sh	T	>
ALAGOMYIDAE									
Talocaphonyx	■								
Alagomyx		■							
ISCHYROMYIDAE									
Tatshkonys		■							
†Mortgusanyx		■							
Artonys			■						
Anatolomyx				■					
Evactyonyx					■				
Halgaya						?	■		
†paranyx T		■							
CTENODACTYLOIDEA									
Cocomyx		■							
Shanomyx		■							
Adalomyx		■							
Taiga†huatunys		■							
Blundersonys		■							
Bandaomyx		■							
Hohomyx		■							
Tampanomyx			■	■	■				
Adventinus			■	■	■				
Yuomyx						■			
Stenomys					■				
Beromyx					■				
Xuxunys						■			
Zyphlotyris					■				
Zhalomyx						■			
Anadromys					■				
Dianomyx							■		
Vilomyx					■				
Tanigomyx					■				
Chaukuentzi					■				
Hannanomyx			■						
Petrokobaia			■	■					
CTENODACTYLIDAE									
Protalomyx					■				
Bouromyx							■		
Karakomyx							■		
Tatanomyx							■	■	▶
Hindomyx								■	▶
Dialomyx								■	▶
Prochytomyx								■	▶
Euryochromys							■		
CHAPATTIMYIDAE									
Chapatimys		■	■						
Gibbatimys		■	■						
Gumbatimys		■							
?CHAPATTIMYIDAE									
Falsona								■	

	G	B	A	I	S	E	Sh	T	>
BALUCHIOMYINAE									
Baluchimys						■	■		
Lindamys							■		
Lophobactha							■		
Hodotatbaia								■	
TSAGANOMYIDAE									
Tsaganomys								■	
Cyrtomys								■	
CYLINDRODONTIDAE									
†Cylindrodontob				■					
Prochytomyx				■					
Pseudocylindrodont						■	■		
Arcynomys						■	■		
Anomomys							■		
APLODONTIDAE									
Pastapemophilus								■	
Haplomys								■	
Prosenecomyx								■	
SCURIDAE									
“Sclurus”								■	
CASTORIDAE									
Agrotocaster								■	■
Propaleocaster								■	■
Aleocaster								■	▶
COMYIDAE									
new genus				■					
Zalomyx						■			
Symplocomyx							■		
Echimyx							■		
Pseudopentacomys								■	▶
Comysodon								■	
CRICETIDAE									
Euryzodion								■	
Pappocricetodon					■	■			
Palaeomyx					■				
Ranocricetodon					?	■			
Zhongxianomyx					■				
Quercocricet							■	■	▶
Shanomyx							■	■	
Cricetops							■	■	
Pseudocricetodon							■	■	
Akakricetodon							■		
Tactyocricetidae								■	▶
Argyromys								■	
ZAPOCIDAE									
Ptilomythos					■	■			
Baryomythos						■			
Siroomythos							■		
Meosomythos							■		
Alzomythos							■		
Paromythos								■	▶
Malykomyx					■				

Coomyidae, and Yuomyidae (Fig. 3), the Asian record quickly became dominated by the ctenodactyloid rodents (Table 2), which apparently diversified markedly at the generic level. The alagomyids have not been reported from Asia after the Early Eocene. Ischyromyids never had a position of prominence

among Asian rodents, whether northern or southern, but they did persist through the end of the Eocene, usually as relatively derived members of the rodent faunas (Dawson 1968, Qi 1987, Wang B. *et al.* 1998, Dawson & Wang 2001).

OUT OF ASIA: THE FIRST RODENT RANGE EXTENSIONS

Although the first faunal expansions for rodents out of Asia took place well before the end of the Paleocene, it was not ctenodactyls that moved. Rather, it was ischyromyids and alagomyids that had migrated into North America by the Early Clarkforkian (Dawson & Beard 1996). A rodent radiation began, and by the Early Wasatchian four rodent genera, of which two were endemic, were present in North America (Ivy 1990). There is no Cernaysian occurrence of rodents in Europe, where their record begins in the Early Eocene, MP7 (Table 3), with ailuravine, pseudoparamyine, microparamyine and ?paramyine ischyromyids all represented (Escarguel 1999), suggesting an interval of earlier rodent presence in the post-Cernaysian, pre-Spurnacian interval. *Corbarimys*, a very primitive rodent from the Silveirinha locality in Spain, may represent another line of rodent development but is still of uncertain affinities; the genus and its possible Middle Eocene relative *Zamoramys* may be allied with the theridomyids (Vianey-Liaud *et al.* 1994, Escarguel 1999).

Although the marine Turgai Strait created a considerable faunal barrier in the Eocene, especially between northern parts of Asia and Europe, the question still arises of the origin of the European rodents (Fig. 4), whether they stem directly from Asia or indirectly via North America (Escarguel 1999). This question has also been raised in regard to other members of the Early Eocene European fauna (Godinot 1996). At least for the rodents, some fossil evidence supports the interpretation of a dispersal route into Europe via North America. The first indication in favor of this route comes from the North American origin for the microparamyines, which are absent in the known Asian record. Microparamyines are an important part of the rodent fauna in Early Eocene deposits of the High Arctic, an area that was part of the North Atlantic province bridging the gap between North America and Europe. Thus,

the abundant microparamyines of western Europe are here interpreted as a colonization from across the North Atlantic terrestrial province. Although paramyines are known from all across the Holarctic in the Early Eocene, their presence in the Arctic Eocene also adds some support to the concept of a North American origin for Early Eocene European ischyromyids (Dawson 2001). Although relationships between the European ailuravines and the Asian Alagomyidae have been suggested (Hartenberger 1995, 1998), this cannot be supported on any available morphological evidence, and ailuravines are here considered to be a distinct, European endemic subfamily of Ischyromyidae (Michaux 1968, Wood 1976).

LATER EOCENE RODENT EVOLUTION IN ASIA

Ischyromyids were a persistent, though never dominant, element of later Eocene Asian rodent faunas. The oldest of these is *Asiomys* from the Middle Eocene Arshanto fauna of Inner Mongolia (Qi 1987). *Eoischyromys* is a Late or latest Middle Eocene rodent recognized from one jaw collected in the Changxindian Formation of northern China and one from upper red beds (?Shara Murun Formation) of Inner Mongolia (Wang *et al.* 1998). *Hulgana*, a relatively derived ischyromyid, is known by several upper and lower jaws from the Late Eocene Ulan Gochu Formation of Nei Mongol (Dawson 1968). A few other occurrences from the Middle and Late Eocene (Li 1963, Dawson 1964, Shevyreva 1984, Tong, 1997), mostly of isolated teeth, are the only additional ischyromyids from the Asian Eocene, outside of several taxa from the Middle Eocene fissure fillings of southern Jiangsu Province, China (Dawson & Wang 2001).

Following their appearance as an already diverse group of rodents in the Bumbanian, the ctenodactyls continued to be the characteristic, and endemic, Asian rodents of the Middle and Late Eocene. Their endemic radiation presumably involved differentiation

Table 3 Temporal ranges of European Paleogene rodent genera by MP reference level, based in part on Hartenberger (1989). ? indicates that MP level is not precisely known; > indicates that range extends into the Miocene.

	7	8-9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	▶	
ISCHYROMYIDAE																									
"Paratmys" woodi		■	■																						
Alurmys		■	■	■	■	■	■	■	■	■															
Meldmys		■																							
Eurotys	■																								
Pseudoparomya	■	■																							
Plesarcomya		■	■	■	■	■	■	■	■	■	■	■	■	■											
Spanacomya		■																							
Pantogna		■	■																						
Hartenbergeromya		■	■	■																					
Maulamys		■	■	■	■	■																			
GLIRIDAE																									
Eglinvius			■			■																			
Glirivus								■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	▶
Parodyromys																■					■	■	■	■	▶
Glirivus																						■	■	■	▶
Oligodyromys																■									
Bransatoglis														?	■	■								■	▶
Pseudodyromys																			?					■	▶
Minglis										■	■														
Tenaglis													■	■	■										
Glirivus									■	■	■	■	■	■	■	■									
Microdyromys														?				■				■	■	■	▶
Parodyromys																	■					■	■	■	■
THERIDOMYIDAE																									
Protodelomys					■	■																			
Banardis										■															
Solurodes								■	■	■	■	■	■	■											
Paradelomys								■	■	■	■	■	■	■											
Suaveolentis										■	■	■	■	■		■	■	■							
Tropocricus										■	■	■													
Pseudocricus												■	■	■	■	■	■								
Tamomys																									
Estelomys											■														
Olinomys												■	■												
Elomys								■	■	■	■		■	■	■	■									
Pseudolinomys								■	■	■			■	■	■	■	■								
Asiodromys																					?	■	■	■	■
Taeniodus																									
Sauromya																■	■	■							
Colombomys																								■	■
Theridomys										■	■	■	■	■	■	■	■				?				
Patriohelidomys													■	■	■										
Bialvillomys													■	■	■	■	■	■	■	■	■	■	■	■	■
Thalomya														■											
Archaeomys																		■	■	■	■	■	■	■	■
Romya										■	■														
Palromys																									
Estropomys																									
?THERIDOMYIDAE																									
Corbaromys	■	■																							
Zanomya																									?

Table 3 Temporal ranges of European Paleogene rodent genera by MP reference level, based in part on Hartenberger (1989). ? indicates that MP level is not precisely known; > indicates that range extends into the Miocene. (continued)

	?	8-9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	>	
AFLODONTIDAE																									
<i>Ephemeromya</i>															■										
<i>Plesiopermophilus</i>														■	■	■					■			■	▶
<i>Solurodon</i>														■			■	?							
<i>Paralomya</i>																								■	
SCIURIDAE + PETAURISTIDAE																									
<i>Palaeosciurus</i>														■	■	■								■	▶
<i>Paradellus</i>														■											
<i>Heterosceus</i>																■	■				■			■	▶
<i>Oligoperus</i>														■											
<i>Trigonomys</i>														■											
CASTORIDAE																									
<i>Steneofiber</i>														■							■	■	■	■	▶
RHIZOSPALACIDAE																									
<i>Rhizospalax</i>																							■	■	
EDMYIDAE																									
<i>Eomyia</i>														■		■					■	■	■	■	▶
<i>Pseudotheridomys</i>																					■			■	▶
<i>Rhodanomys</i>																								■	▶
<i>Riteneta</i>																								■	▶
<i>Eomyodon</i>																								■	
CRICETIDAE																									
<i>Atavocricetodon</i>														■	■	■	■								
<i>Eucricetodon</i>														■	■	■	■	■	■	■	■	■	■	■	▶
<i>Pseudoborbocetodon</i>															■	■	■	■	■	■	■	■	■	■	▶
<i>Alloborbocetodon</i>																								■	
<i>Karsaria</i>																									
<i>Heterocricetodon</i>																				?	■				
<i>Cheamysion</i>																									?
<i>Paracricetodon</i>														■			■	■	■	■	■				
<i>Trakymys</i>																									
<i>Edimella</i>																									
<i>Adelomyson</i>																								■	
<i>Melissiodon</i>															■	■	■	■	■	■	■	■	■	■	▶
ZAPOIDAE																									
<i>Plescomitrus</i>																	■				■	■	■	■	
THRYONOMYIDAE																									
<i>Sacaresia</i>																								■	

into several families although the content of these groups is not yet convincingly established (Tong 1997, Wang 1997). The ctenodactyloids suffered a major decrease in diversity at the end of the Sharamuronian, none are reported from the Ergilian, and only relatively derived Ctenodactylidae are known from the Oligocene of central Asia (Wang 1997).

The Middle Eocene chapattimyids appear to have been endemic to the Indian subcontinent, though possibly derived from ctenodactyloids of central Asia (Sahni & Khare 1973, Hartenberger 1982). Later affinities of the chapattimyids have been suggested to be with the African phiomyids (Hussain *et al.* 1978, de Bruijn *et al.* 1982), with the baluchimyines (Flynn *et al.* 1986), or still unclear (Wang

1997). The south Asian endemic baluchimyines appear first in the Late Eocene Krabi Basin of Thailand (Marivaux *et al.* 2000), and later in the Early Oligocene of Pakistan (Flynn *et al.* 1986, Marivaux *et al.* 1999). Phylogenetic position of the baluchimyines, which have a highly lophate occlusal pattern of the cheek teeth and multiserial incisor enamel, is far from well established but may have been somewhere in the ctenodactyloid-chapattimyid-phiomyid radiation of rodents that had a southern Asia-northern Africa distribution in the Paleogene.

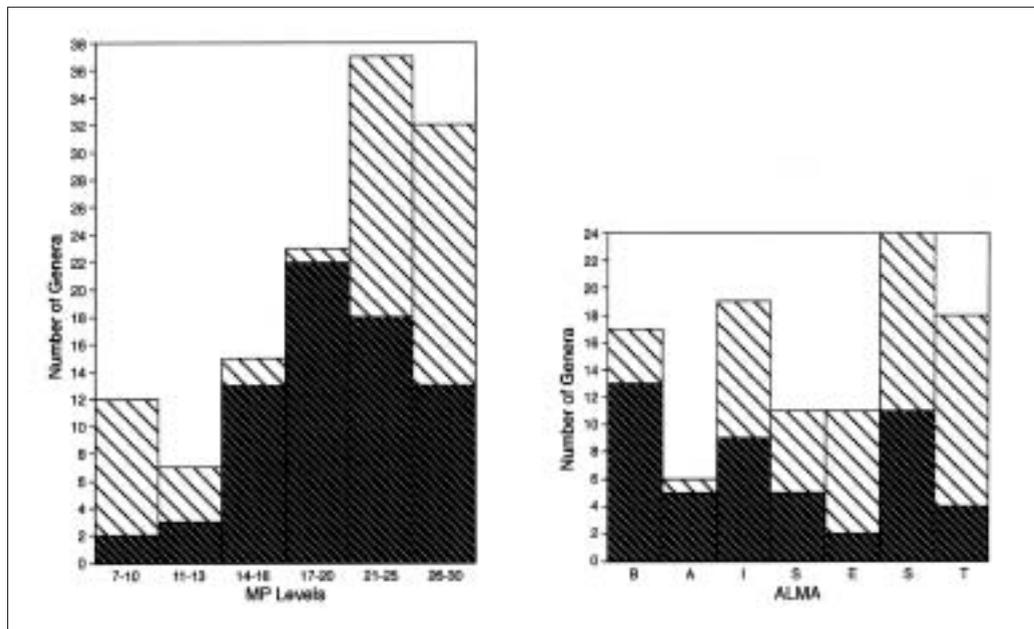
Four other rodent families, the Cylindrodontidae, Eomyidae, Cricetidae, and Zapodidae, also were present in the Asian Middle and Late Eocene. All of these families are shared with North America in the Eocene. The Family Cylindrodontidae is an old family that appears to be of North American origin, based on rodents now under study from the Paleocene-Eocene boundary in the Gulf Coastal Plain that may be the earliest representatives of this family. A questionable cylindrodontid *Dawsonomys* is known from the Wasatchian, and the primitive cylindrodontid *Mysops* is a common rodent in Bridgerian faunas. The family persists in North America through the Chadronian. The Asian record commences with two genera reported from the Irдинmanhan, *Orientocylindrodon* (Fig. 5) from China (Tong 1997) and *Proardynomys* from Mongolia (Dashzeveg & Meng 1998). Beringia appears to have been a hospitable habitat for these rodents in the later Eocene, shown by an Asian-North American sharing of the genera *Ardynomys* (Ergilian and Chadronian) and *Pseudocylindrodon* (Ergilian and Duchesnean-Chadronian).

The Eomyidae are also shared by North America and Asia, appearing in North America in the Middle Eocene (Uintan). The oldest known Asian eomyid is the Ergilian *Symplokeomys* of Kazakhstan. This genus has highly derived dental characteristics for an eomyid, shown by complexities of cusps and lophes of its cheek teeth (Emry *et al.* 1997).

Although the Ergilian *Zelomys* (Wang & Li 1990) has been referred to the Eomyidae because of some presumed dental similarities with the North American eomyid *Namatomys* (Korth 1994), the zygomaseteric structure of *Zelomys* indicates that it is not an eomyid and it may represent a new Asian endemic family.

Cricetids and zapodids both have Asian records back to the Irдинmanhan, a time when the two families are morphologically very similar and some cricetids still retain P4 (Wang & Dawson 1994). The two families probably share a common origin, but whether this occurred in North America or Asia is still not clear. Evidence for the former comes from North American occurrences of the late Early Eocene *Armitomys* in which there is evidence of some development of hystri-comorphy and the incisor enamel is transitional to uniserial (Dawson *et al.* 1990) and of the primitive zapodid *Elymys* from the early Middle Eocene of Nevada (Emry & Korth 1989). These genera predate the Asian zapodids, and may help to bridge the gap between the North American sciuravids and the earliest myomorphs. Whatever their place of origin, early zapodids were more diverse in Asia than in North America. One of the oldest zapodids, known from numerous isolated teeth, is *Primisminthus yuenus* from the Irдинmanhan Hetaoyuan Formation of Henan Province, which ranges into the Sharamur-nian Zhaili Formation of Shanxi Province, where it occurs with another zapodid, *Banyusminthus* (Tong 1997). A second Irдинmanhan genus, *Aksyiromys*, is known by isolated teeth from the Kolpak Formation in eastern Kazakhstan (Emry *et al.* 1998). The Ergilian Caijiachong fauna of Yunnan shows even greater diversity, with three genera, *Allosminthus*, *Heosminthus*, and *Sinosminthus*, of which *Heosminthus* may be related to *Banyusminthus* on the one hand and *Plesiosminthus* on the other. *Sinosminthus* has been allied to *Parasminthus* (Wang 1985).

Table 4 Number of genera of Paleogene rodents in Europe (left) and Asia (right). Darker shading indicates number of genera belonging to families that are endemic to Asia or Europe. Arranged by MP reference levels for Europe. Abbreviations for Asian Land Mammal Ages: **B**, Bumbanian; **A**, Arshantan; **I**, Irudinmanhan; **S**, Sharamurunian; **E**, Ergilian; **S**, Shandgolian; **T**, Tabenbulukian.



THE EUROPEAN EOCENE RECORD

Endemism is the strongly documented characteristic of European rodent faunas after the Early Eocene (Hartenberger 1973). In a fairly restricted geographic area, bounded by the sea where the North Atlantic terrestrial province formerly existed, and a well-developed Turgai marine barrier, the European later Eocene rodents developed in isolation. They even suffered a mini-diversity crisis early in the Middle Eocene after the extinction of small to medium-sized ischyromyids but prior to the initial radiation of the Theridomyidae (Hartenberger 1993). The ischyromyids *Ailuravus*, *Plesiarctomys*, and *Masillamys* persisted after the Early Eocene.

The endemic rodent family Theridomyidae is known only from Europe from origin to extinction. The oldest known theridomyid, *Protadelomys*, is first recognized in MP13 and MP14; this suggested to Hartenberger (1990) an allochthonous origin and migration into Europe at the Early-Middle Eocene boundary. He attributed local extinction of

the small and middle-sized Ischyromyidae at that time to the development of the theridomyids. A more recent investigation (Escarguel 1999), however, derives the theridomyids from European Microparamyini, particularly *Hartenbergeromys*. The later Eocene record of theridomyids is one of generic diversity and dominance, from only the genus *Protadelomys* in MP13-14, to four additional genera in MP15 and 10 genera in MP20.

One of the best-documented histories of any rodent family is the lineage of the glirids (Fig. 6), which have been shown to be derived before the Middle Eocene from European microparamyines (Hartenberger 1971). The oldest, *Eoglravus wildi*, occurs in MP10 of western Europe (Daams 1999). The fossil record of this family provides a strong example of endemic development in rodents, for throughout the Eocene and most of the Oligocene glirids were restricted to western Europe.

BREAKING THROUGH THE BARRIERS: EURASIA AFTER THE GRANDE COUPURE

The major faunal changes in Europe identified as the Grande Coupure were pronounced for rodents as well as for the ungulates on which the concept was originally established (Stehlin 1909, Heissig 1979b), being marked especially by the first appearances in Europe of rodent families Aplodontidae, Cricetidae, Eomyidae, Castoridae, Petauristidae, and Sciuridae. During the Oligocene Eurasia became one enormous geographic province within which there are great environmental differences. Across Eurasia, rodent faunas go from sharing one family (Ischyromyidae) and no genera in the late Eocene to sharing four families (Aplodontidae, Castoridae, Eomyidae, and Cricetidae) and five genera in MP21 immediately after the Grande Coupure. It is interesting, however, that endemism remains important among Oligocene Eurasian rodents. For example, in Europe the theridomyids continued through the Oligocene without venturing into Asia, as did the glirids until the latest Oligocene into northwestern China (Wu *et al.* 2000). The ctenodactylids avoided Europe, although they reached westward into Turkey, and the tsaganomyids are known only from central Asia.

Eight theridomyid genera persisted in Europe through the faunal perturbations marked by the Grande Coupure. During the Oligocene, the family (Fig. 7) continued with both originations and extinctions, but their generic diversity was reduced by the late Oligocene and no theridomyids persisted after the Oligocene. Although the western European late Eocene rodents are still varied at the generic level, their lack of morphological diversity, having only the three families, Ischyromyidae, Gliridae, and Theridomyidae, was one of the several factors contributing to the success of immigrant rodents after the Grande Coupure (Hartenberger 1973, 1989). The generic diversity of the European endemic glirids approximately doubled from the Eocene to the Oligocene (Hartenberger

1994), when the family was evidently highly successful and showed no adverse effects following immigration of the eomyids and cricetids. Their decline was a later Miocene event (Daams 1999), apparently not related to the Early Oligocene rodent incursions from Asia.

On the Asian side, the ctenodactylids remained Asian endemics during the Oligocene, with a diversity of seven genera, but all in the family Ctenodactylidae (Fig. 8). Their species diversity remained relatively constant through the Oligocene in central Asia (Wang 1997). Baluchimyines are persistent in southern Asia (Flynn *et al.* 1986), and a recently discovered diversity of ctenodactylids is present in Turkey (de Bruijn pers. comm. 2000). The endemic Tsaganomyidae, highly derived burrowing rodents of the central Asian Oligocene, have provoked a great deal of speculation about their phylogenetic position (Burke, 1935, Wood 1980), but most probable is the interpretation of these rodents, which are hystricognathous and have multiseptate incisor enamel, as early Bathyergidae (Matthew & Granger 1923, Martin 1992), a family otherwise known from Africa. The Tachyoryctoididae were another short lasting Asian endemic family, first appearing in the late Oligocene (Bohlin 1946) but, although variously referred to the Rhizomyidae and Spalacidae, of problematic phylogenetic affinities (Klein Hofmeijer & de Bruijn 1985, Huguency & Mein 1993).

Although some rodents are known from the Oligocene of the Arabian Peninsula, these have significance for African rather than Eurasian faunal distributions. The Oligocene rodents from Oman have clear African affinities, as would be expected from the Paleogene geographic position of the area as part of Africa. Two faunal levels have produced, in the lower level, the phiomyids *Phiomys* and *Metaphiomys*, added to which are anomalurids and cricetids in the upper level (Thomas *et al.* 1999).

Of the rodent families that expanded into western Europe after the Grande Coupure, the

eomyids (Emry *et al.* 1997) and cricetids (Tong 1992, Wang & Dawson 1994) are known from older fossil records in Asia. The appearance of *Eomys* in MP21 was considered by Fahlbusch (1973) to represent derivation from the North American *Adjidaumo*, which is first reported from the Duchesnean. This interpretation remains valid on the basis of the currently known Asian record. The oldest known Asian eomyid is the Late Eocene *Simplokeomys*, which has a tooth pattern that is much too derived to suggest affinities with *Eomys*. Later Oligocene European eomyids (Fig. 9) present a great diversity of dental (Fahlbusch 1970) and skeletal adaptations, including those shown by *Eomys quercyi*, a glider of the late (MP28) Oligocene (Storch *et al.* 1996). Eomyids are often abundant in European Oligocene small mammal faunas (Engesser 1999).

Although *Eomys* experienced a species level radiation during the earlier Oligocene, other eomyid genera (including *Pseudotheridomys* and *Eomyodon* (MP28) and *Rhodanomys* (MP29)) are not known until later in the epoch. Of these *Pseudotheridomys* and *Eomyodon* are also known from probable late Oligocene deposits of Asia, showing a pan-Eurasian distribution for at least some eomyid genera (Wang & Emry 1991). Time and place of origin for these genera is difficult to establish due to uncertainties of correlation within Eurasia. *Pseudotheridomys* had a Holarctic Early Miocene distribution. *Rhodanomys* appears to have replaced *Eomys* in the later Oligocene faunas. *Apeomys*, first appearing in the latest Oligocene (MP30) of Europe, may have been autochthonously derived from *Pseudotheridomys* (Engesser 1999). At their first appearance in western Europe (MP21) after the Grande Coupure cricetids are already diverse, being represented by *Eucricetodon*, *Paracricetodon*, *Pseudocricetodon*, and *Atavocricetodon*. Of these genera, *Eucricetodon* has been reported from the late Eocene and Oligocene of China, indicating a possible place of origin for this taxon. Evidence for a pre-Grande Coupure expan-

sion of the range of cricetids into eastern Europe comes from the late Eocene (Priabonian) of Romania, where *Pseudocricetodon* and *Atavocricetodon* have been found (Baciu and Hartenberger 2001). A recent discovery of cricetids in the Early Oligocene of Pakistan adds to the intriguing evidence for a more southerly fauna shared between Asia and Europe. Of the two genera represented there, *Pseudocricetodon* and *Atavocricetodon*; the former is plesiomorphous compared to the first European *Pseudocricetodontinae*, which first occur in Europe in MP23; the Pakistan *Atavocricetodon* has some characters that are intermediate between those of the Asian *Eucricetodon leptaleos* and the more derived European species of *Atavocricetodon* (Marivaux *et al.* 1999). The family (Fig. 10) continued to prosper in its new European habitats, with three genera, *Eucricetodon*, *Pseudocricetodon*, and *Melissiodon* ranging into the Miocene (Hartenberger 1989, Hugueney 1999).

Zapodids had a long and varied record in Asia well before the arrival of the family in Europe. Outside of considerable diversity in the Asian Oligocene, interrelationships of taxa are not clear, and indeed, some authorities (McKenna & Bell, 1997) have synonymized *Parasminthus*, *Heosminthus*, *Sinosminthus*, *Gobiosminthus*, and *Shanosminthus* with *Plesiosminthus*. However, the North American and Eurasian *Plesiosminthus* do share such characters as the grooved incisor, absent in *Parasminthus*. *Plesiosminthus promyarion*, the first zapodid to appear in Europe, is from MP26, well after the Grande Coupure. The genus appears in North America (Engesser 1979, Korth 1994) and in Asia (Höck *et al.* 1999) at approximately the same time. *Plesiosminthus* (Fig. 11) may have had a Beringian migration into North America on the one hand, and dispersal into Europe via a northern migration route, which was only available in the later Oligocene (Heissig 1979b), on the other.

Two of the families newly arrived in Europe after the Grande Coupure, Aplodon-

tidae (Fig. 12) and Sciuridae (Fig. 13), are known from older representatives in North America but not in Asia. The Chadronian North American *Prosciurus*, an aplodontid, and *Douglasia*, a sciurid (Emry & Korth 1996), suggest that the origins for these families may be outside of Eurasia. The currently known record of the aplodontids documents a good deal of Holarctic interchange. The oldest known European aplodontid, *Plesispermophilus* (MP21) also occurs in the late Oligocene of Asia. *Ephemeromys*, a European prosciurine (MP22), has been considered to indicate a European origin for the Allomyinae, with later Oligocene (Arikarean) migration into North America (Wang & Heissig 1984, Korth 1992, 1994). In the case of *Parallomys*, the genus is first known from the late Oligocene of Europe, and later from North America (Korth 1992). The prosciurine *Haplomys* has late Oligocene records in Asia and North America. An Asian origin for the Mniscomiinae is indicated by the late Oligocene *Promeniscomys* (Wang 1986); this genus has a more brachydont dentition than others in the subfamily, which underwent a considerable later radiation in North America (Korth 1994).

The Sciuridae are an interesting case. The North American Chadronian *Douglasia*, with its primitive protrogomorphous zygomasstetic structure, is more primitive as well as apparently older than the post-Grand Coupure appearance of sciurids in Europe, *Palaeosciurus* in MP21 (Brunet & Vianey-Liaud 1987). Later in the Oligocene, sciurids exhibited some diversity in Europe and North America but interrelationships across the Holarctic are unclear (de Bruijn 1999), in part because of an inadequate Asian record of the family. The only sciurid reported from the Asian Oligocene is based on two small teeth referred to *Sciurus* from the late Oligocene of Taben-buluk, China (Bohlin 1946). Did the sciurids migrate between North America and Europe via a northern route, as suggested by de Bruijn & Ünay (1989), crossing areas where there is no known Paleogene rodent

record, or by the more southerly route advocated by Heissig (1979b) for some other mammals? The present diversity of sciurids in southeastern Asia and Africa does not appear to have its roots in any known Paleogene fossil record.

The flying squirrels, Petauristidae, are known in Europe from the Grande Coupure, with *Oligopetes* (Fig. 14) in MP21 and 22 (Heissig 1979a). The genus has also been reported from the Early Oligocene of Pakistan (Marivaux this volume). Interrelationships among the flying squirrels united as Petauristidae are inadequately understood (de Bruijn 1999).

The oldest known Castoridae are North American, with the Chadronian genus *Agnotocastor*, which is first known in Asia from the Early Oligocene along with *Propaleocastor*. The beaver *Steneofiber* (Fig. 15) is recorded in Europe after the Grande Coupure in MP21 (Hugueney 1975). *Agnotocastor* and *Propaleocastor* persist through the Oligocene in Asia, where beaver diversity increases in the late Oligocene with the first appearance of *Asiacastor* (Lytschev 1970, 1978). By the late Oligocene *Palaeomys* has joined *Steneofiber* in Europe. The burrowing castoroid *Rhizospalax* is a European endemic, presumably locally derived (Hugueney & Mein 1993) and limited to the European late Oligocene (MP29-30).

PALEOGENE RODENTS: SURVIVAL OF THE FITTEST

The Paleogene record of the Rodentia attests to a remarkable evolutionary adaptability that led to a highly successful role in terrestrial mammalian faunas. Shaped early in their existence by the late Paleocene-Eocene thermal maximum, stressed by cooling later in the Eocene, adapting to the pressures of faunal migrations, the rodents responded by a wide array of dental, musculo-skeletal, and presumably behavioral and physiological adaptations that insured their survival.

The early division of Asian rodents into the ischyromyids and their kin on the one hand

and the ctenodactyls on the other had phylogenetic results that can be traced past the temporal limits of the Paleogene. Following their Asian origin, rodents quickly entered the migratory mode, colonizing the Holarctic and Africa by the beginning of the Eocene, but also showing strong endemism in both Europe and Asia (Table 4). During the Eocene the European endemic glirids and theridomyids developed in geographic isolation, whereas the Asian endemic ctenodactyls shared their habitats with several invaders that seemed to have come from Beringia and the American part of the Asian-American biotic province. Reduction in diversity of the old endemic natives in Asia occurred prior to the faunal changes that took place in Europe following the Grande Coupure.

Rodent migrations in the Oligocene included not only invasions into western Europe from the east but also multidirectional movements across the Holarctic. Routes appear to have been both southerly, as shown by the rodent records from Pakistan and Turkey, and northern, as implied by the lag in dispersal of the zapodids into Europe, the absence of sciurids in the earlier Oligocene of Asia, and frequent crossings of Beringia between Eurasia and America by other rodents.

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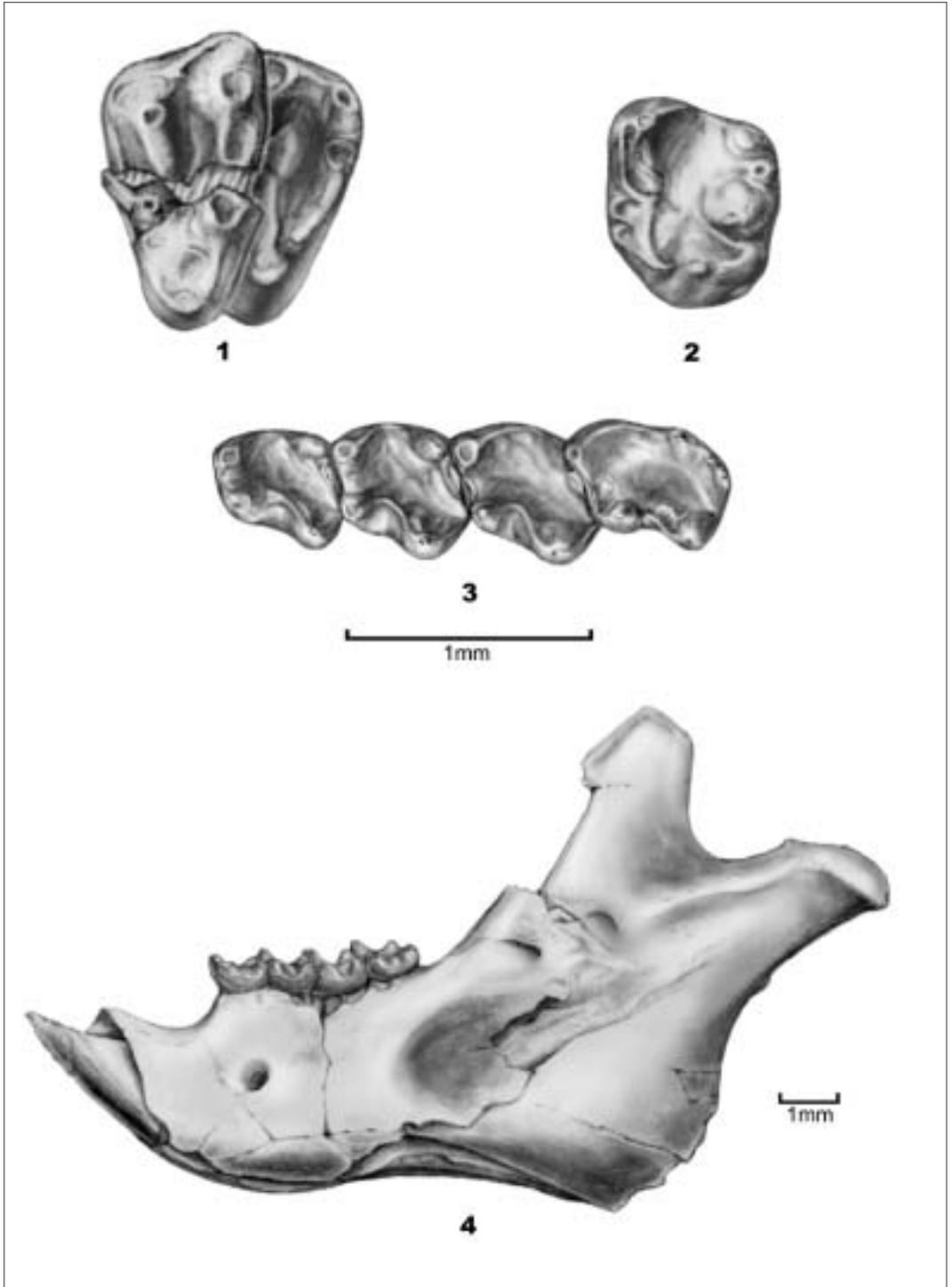


Figure 1 Family Alagomyidae: *Alagomys oriensis*, Wutu fauna, China, Bumbanian. **1**: occlusal view of M1 overlying M2; **2**: M3; **3**: occlusal view of p4-m3; **4**: lateral view of mandible (after Tong & Dawson 1995). Note: For consistency, all figures have the jaws and teeth positioned to show the upper right side and lower left side.

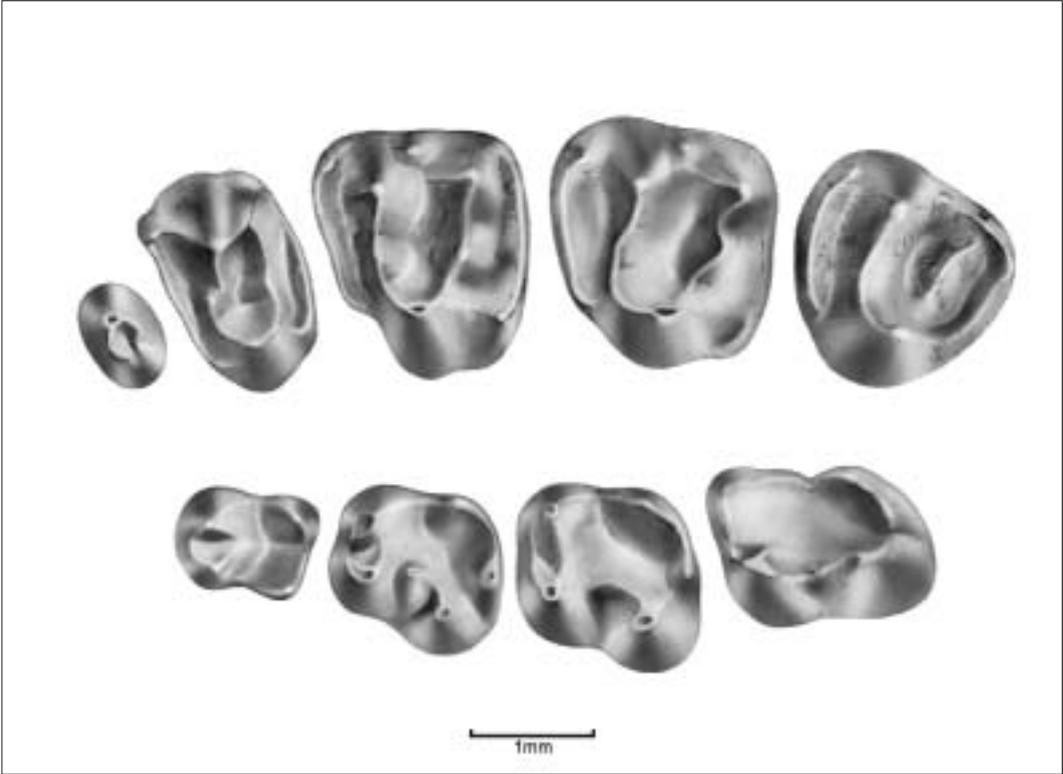


Figure 2. Family Cocomyidae: *Cocomys lingchaensis*, Hengdong fauna, China, Bumbanian. Occlusal views of above, P3-M3 and below, p4-m3 (after Li *et al.* 1989).

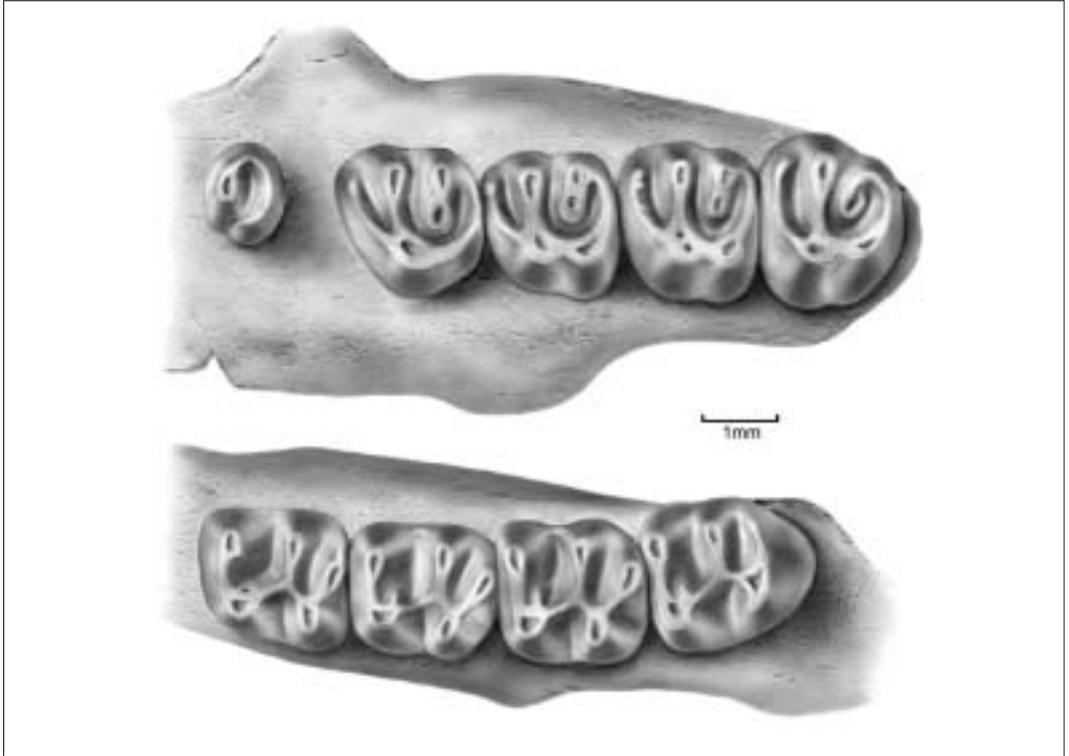


Figure 3 Family Yuomyidae: *Yuomys cavioides*, Rencun fauna, China, Sharamunian. Occlusal views above, maxilla with P3-M3 and below mandible with p4-m3 (after Li 1975).

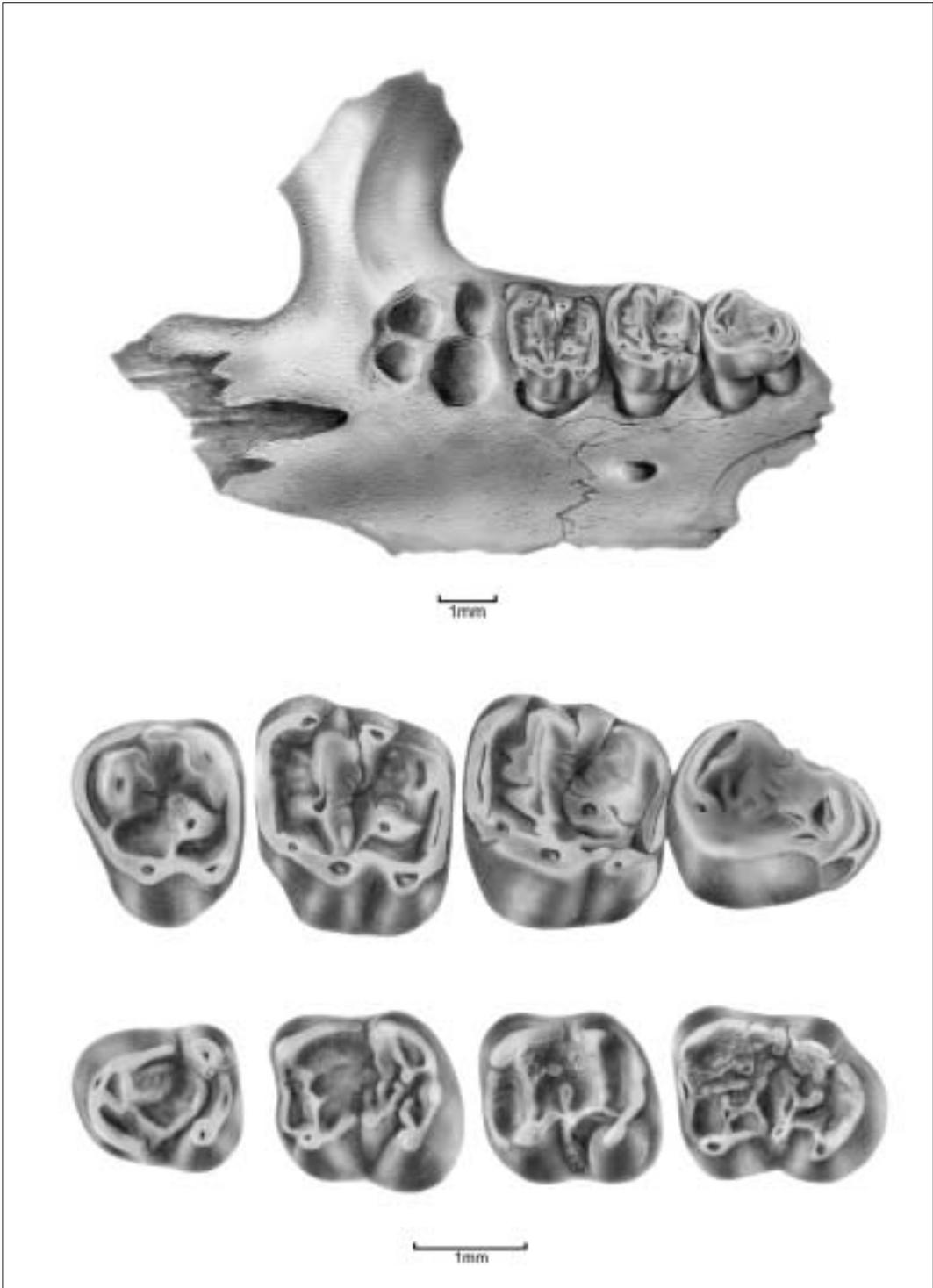


Figure 4 Family Ischyromyidae: *Pantogna marandati*, Prémontré, France, lower Eocene (MP10). Occlusal views of above, maxilla with M1-3; center, P4-M3; and below p4-m3 (after Escarguel 1999).

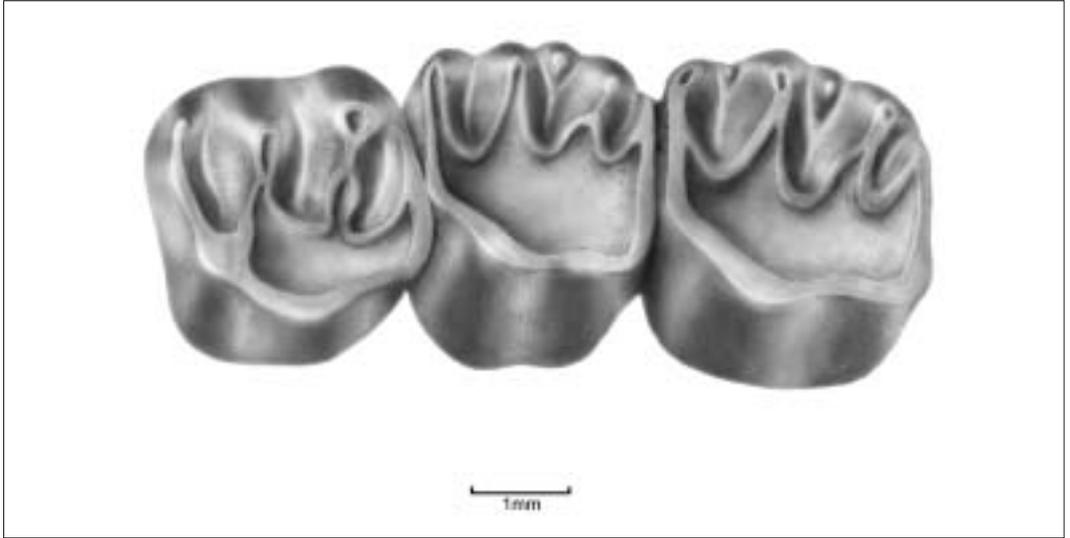


Figure 5 Family Cylindrodontidae: *Orientocylindron liguanqiaoensis*, Shipigou fauna, China, Irдинmanhan. Occlusal view of P4-M2 (after Tong 1997).

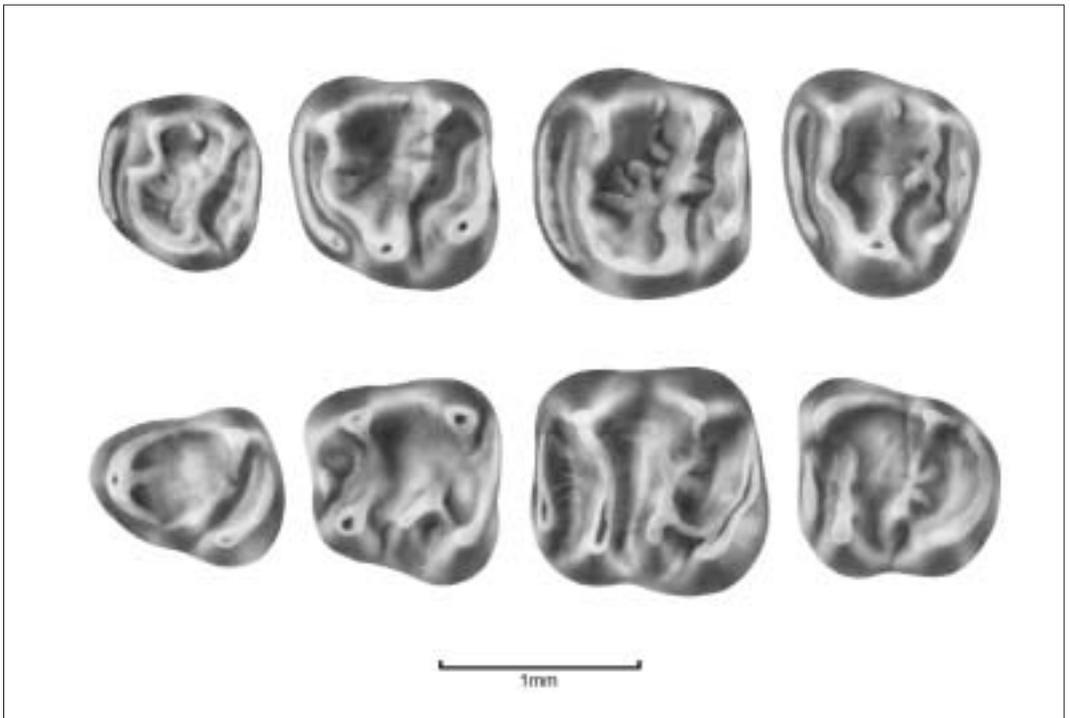


Figure 6 Family Gliiridae: *Eogliravus hammeli*, Bouxwiller, France, Middle Eocene (MP13). Occlusal views of above, P4-M3 and below, p4-m3 (after Hartenberger 1971).

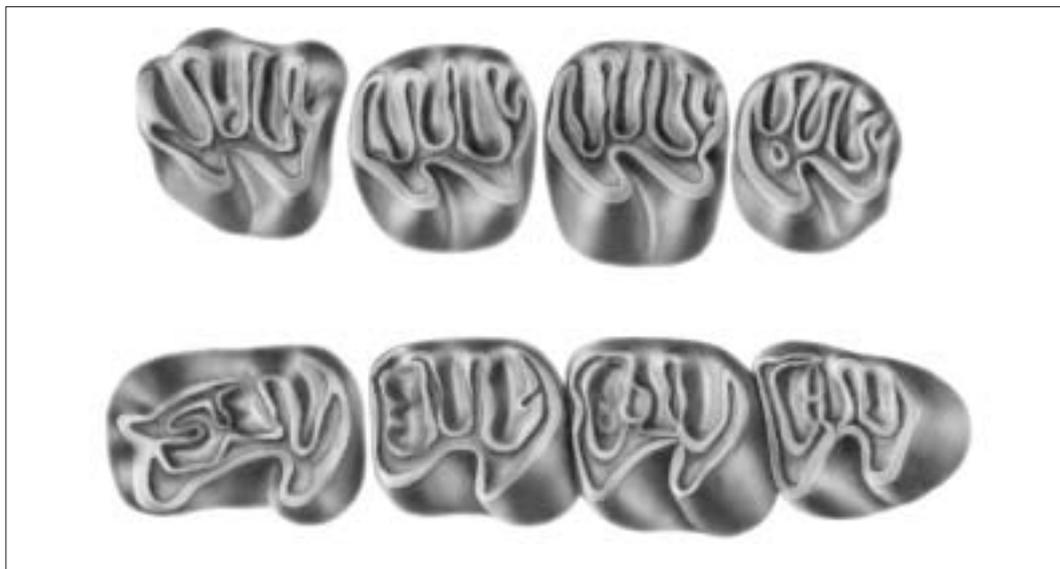


Figure 7 Family Theridomyidae: *Theridomys aquatilis*, Ronzon, France, lower Oligocene (MP21). Occlusal views of above, P4-M3 and below, p4-m3 (after Vianey-Liaud 1972).

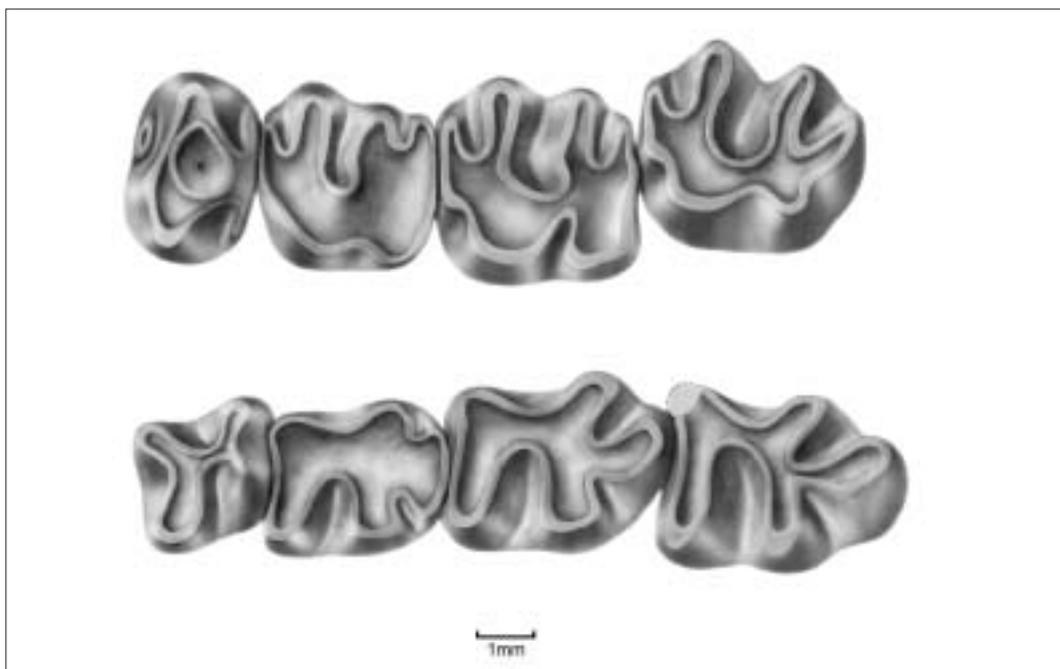


Figure 8 Family Ctenodactylidae: *Tataromys plicidens*, Hsanda Gol, Mongolia, lower Oligocene, Shandgolian. Occlusal views of above, P4-M3 and below, p4-m3 (after Wang 1997).

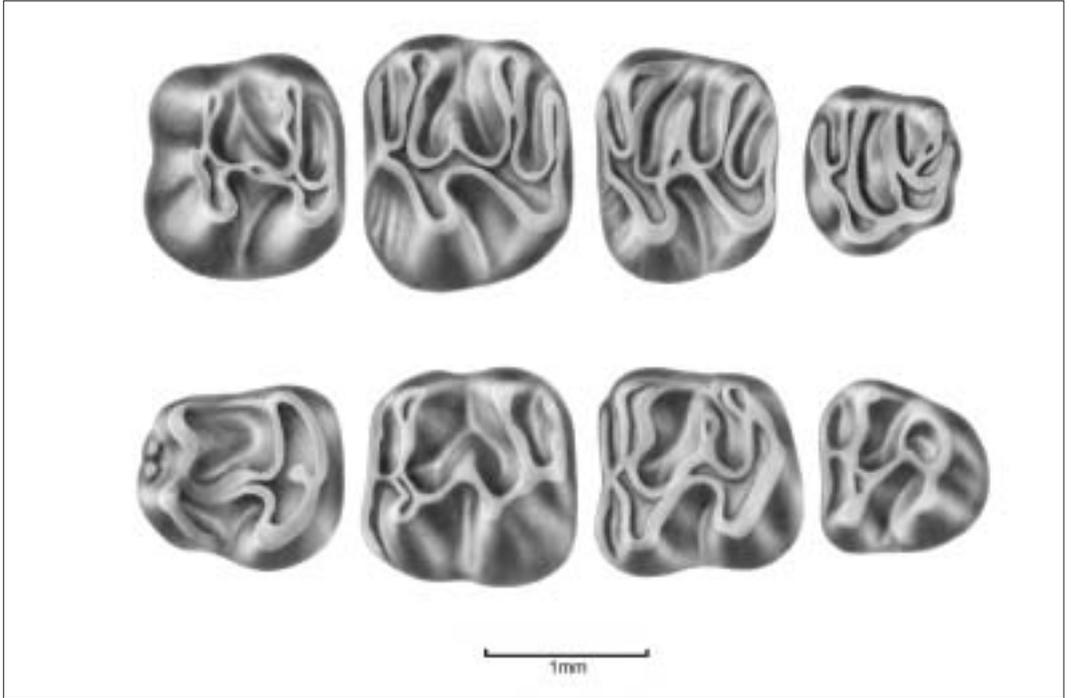


Figure 9 Family Eomyidae: *Eomys huerzeleri*, Rances, Switzerland, upper Oligocene (MP29). Occlusal views of above, P4-M3 and below, p4-m3 (after Engesser 1999).

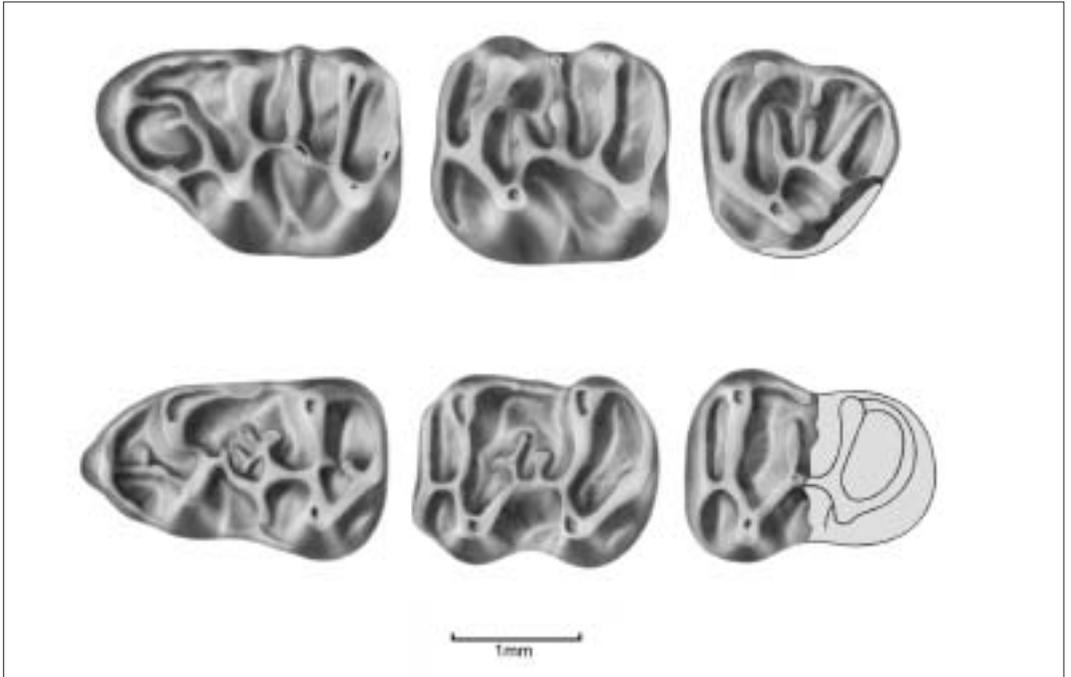


Figure 10 Family Cricetidae: *Heterocricetodon hausi*, Bumbach, Switzerland, Middle Oligocene (MP25). Occlusal views of above, M1-3 and below, m1-3 (after Engesser 1987).

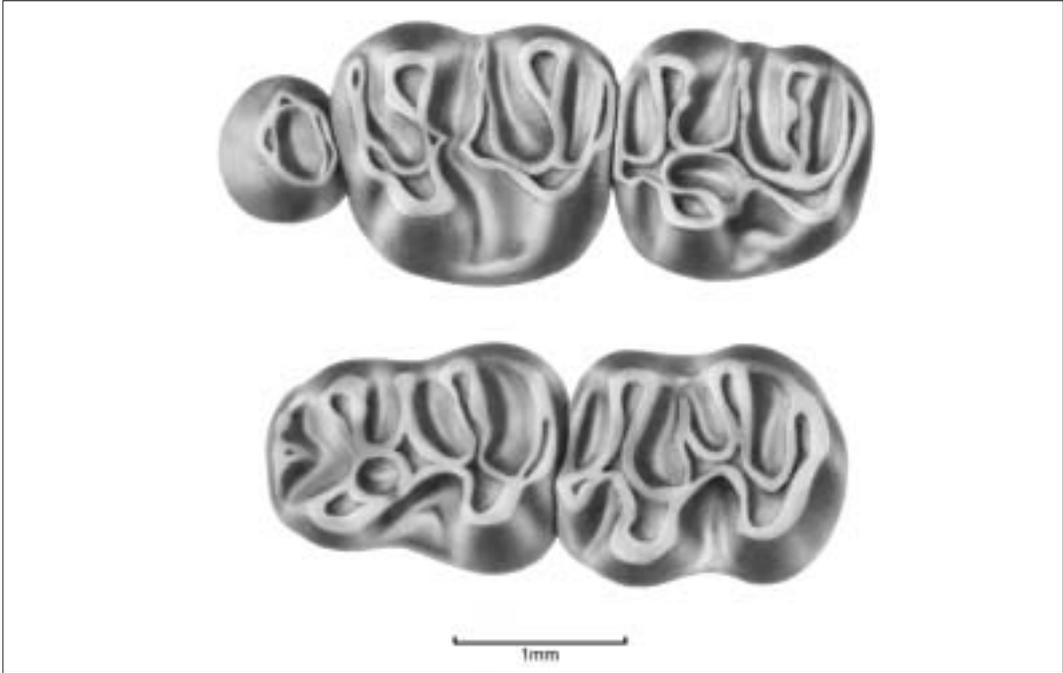


Figure 11 Family Zapodidae: *Plesiosminthus schaubi*, Coderet, France, Upper Oligocene (MP30). Occlusal view of above, P4-M2 and below, m1-2 (after Engesser 1979).

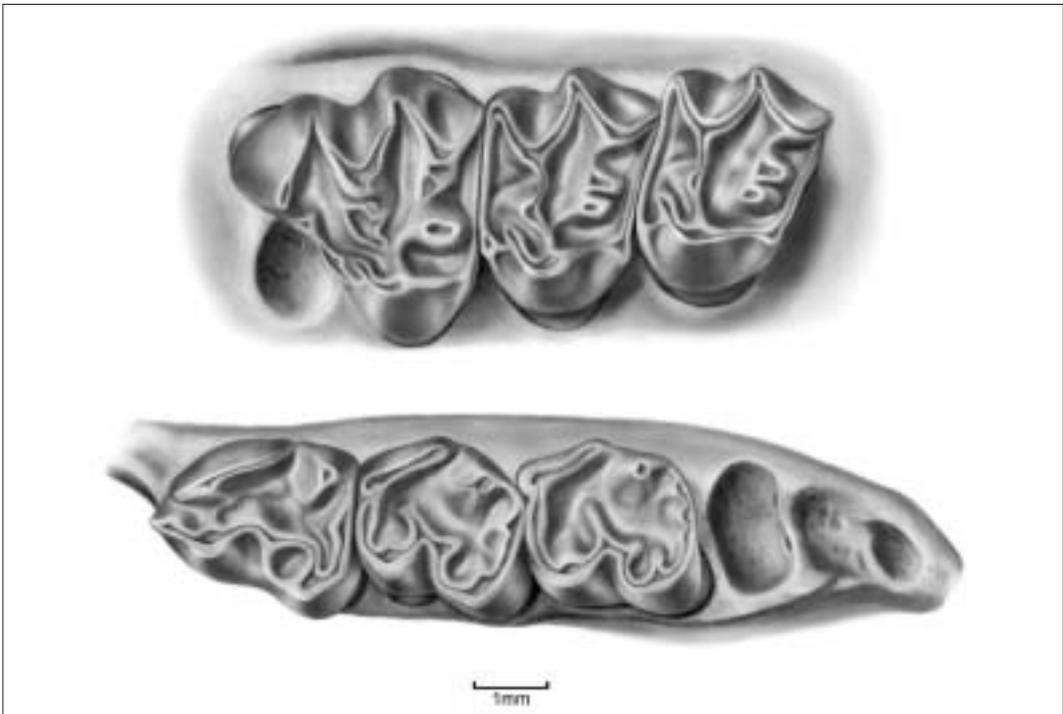


Figure 12 Family Aplodontidae: *Plesispermophilus emii*, Coderet, France, Upper Oligocene (MP30). Occlusal view of above, maxilla with P4-M2 and below, mandible with p4-m2 (after Viret & Casoli, 1961).

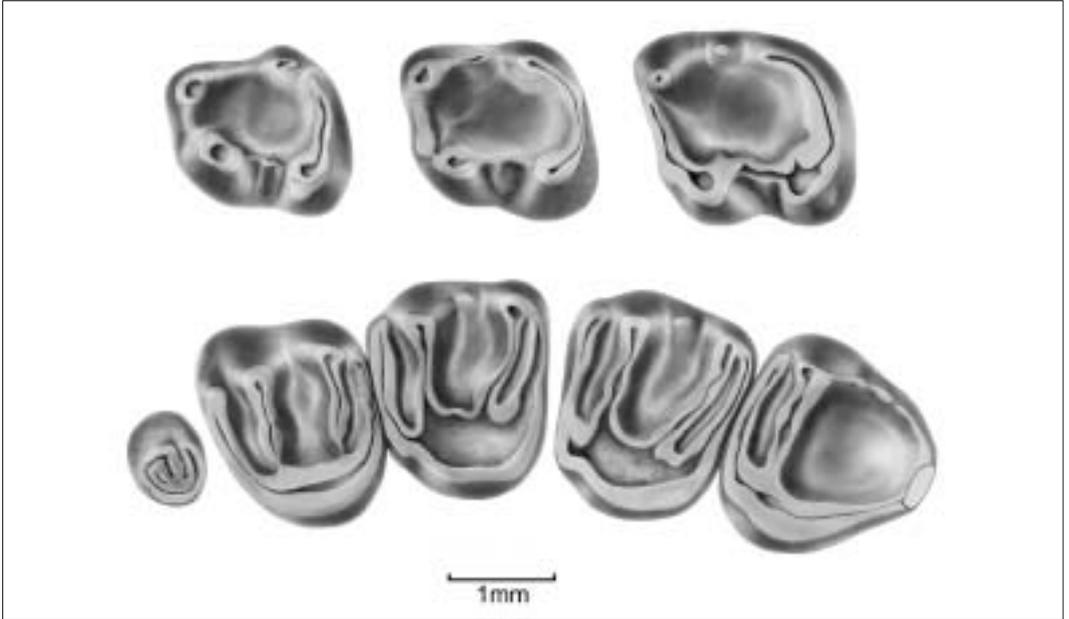


Figure 13 Family Sciuridae: *Palaeosciurus goti*, Mas de Got, France, lower Oligocene (MP22). Occlusal view of above, p4, m1, m2 and below P3, P4-M3 (after Vianey-Liaud 1974).

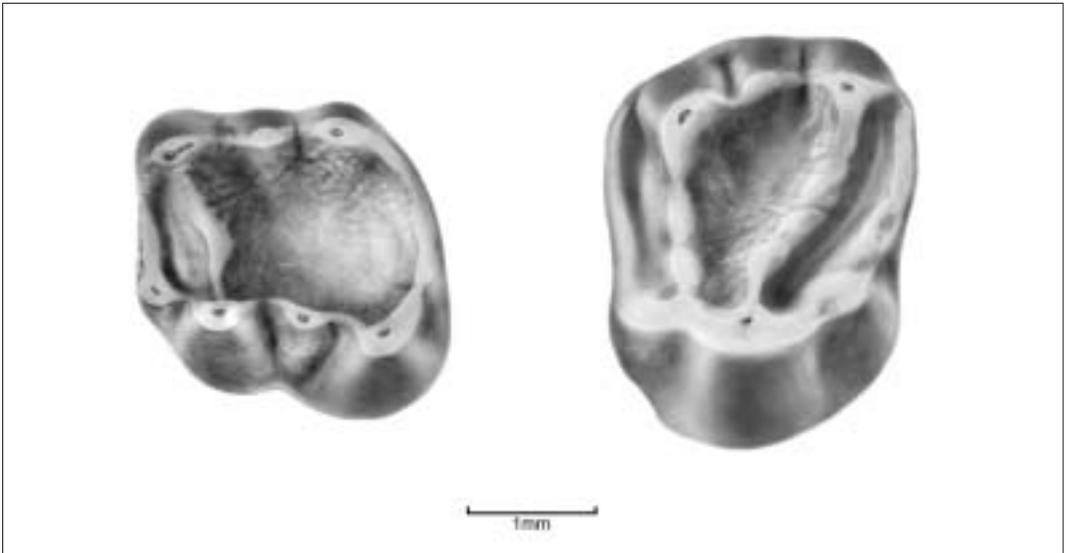


Figure 14 Family Petauristidae: *Oligopetes obtusus*, Möhren 13, Germany, lower Oligocene (MP22). Occlusal view of left, m1 or 2 and right, M1 or 2 (after Heissig 1979a).

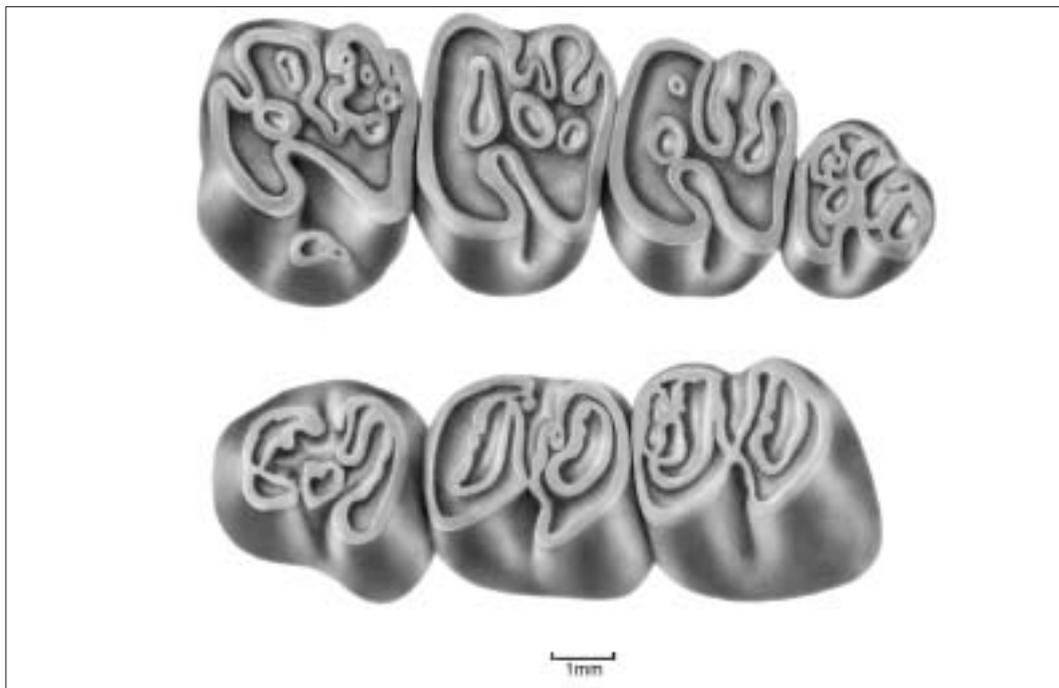


Figure 15 Family Castoridae: *Steneofiber butselensis*, Hoogbutsel-Hoeleden, Belgium, lower Oligocene (MP21). Occlusal view of above, P4-M3 and below, p4-m2 (after Hugueney 1975).