THE STRATIGRAPHIC SEQUENCE OF NORTH AMERICAN RODENT FAUNAS

by

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CONTENT

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ABSTRACT

Rodents first appear in the latest Paleocene or earliest Eocene as very fragmentary specimens (Family Paramyidae) known largely from a single locality. After this sparse beginning, rodents are usually abundant in the North American record if proper recovery methods are used. Utilization of rodents for biostratigraphic purposes depends on 1/ extinction, and 2/ replacement by evolution of endemic groups and/or incursions of Old World rodents, and rarely and late by South American kinds. These incursions are separated by relatively long periods of isolation in the Paleogene, but more episodic in the Neogene. At least 10 rodent zones can be characterized by major distinctions, and these zones can be amplified into as many as 16 with little trouble. In general, rodent genera permit as refined a zonation as do genera of large mammals. Distinction at a specific level has not been attempted herein except in the Blancan and Post-Blancan.

ZUSAMMENFASSUNG

Nagetiere (Rodentia) treten erstmals am Ende des Paleozäns oder im frühesten Eozän auf, es sind Fragmente (Familie Paramyidae) von fast ausschliesslich einer einzigen Fundstelle bekannt. Nach diesem zögernden Beginn sind Nagetiere in Nordamerika gewöhnlich weit verbreite zu finden, sofern die geeigneten Sammlungsmethoden angewandt werden. Die Benutzung der Nagetiere für biostratigraphische Zwecke hängt vom 1/ Aussterben und 2/ Ersatz durch sich entwickelnde endemische Gruppen und/oder durch Einwanderung von Nagetiere aus der Alten Welt und selten und dies erst spät aus Südamerika ab. Relativ lange Perioden der Isolation liegen zwischen diesen Einwanderungen in Paläogen, während die Einwanderungen im Neogen mehr episodisch auftreten. Zumindest 10 Rodentia-Zonen können aufgrund von deutlichen Unterschieden charakterisiert werden, und manche Zonen können mit etwas Schwierigkeit weiter unterteilt werden, so dass man 16 Einheiten erhält. Im allgemeinen ist eine Zonierung nach Nagetiergattungen ebenso möglich wie nach Grossäugergattungen. Hierbei ist mit Ausnahme im Blancan und Post-Blancan nicht versucht worden bis zur Unterscheidung von Arten herunter zu gehen.

RESUME

Seuls quelques restes très fragmentaires provenant d'une unique localité, attestent de l'existence des Rongeurs dans le Paléocène terminal ou l'Eocène tout à fait inférieur. Après ce modeste début, les rongeurs sont habituellement abondants dans les faunes fossiles d'Amérique du Nord, chaque fois que l'on utilise des méthodes de récolte appropriées. L'emploi des rongeurs en biostratigraphie repose sur 1/ les extinctions, et 2/ les remplacements par suite d'évolution de groupes endémiques et/ou sur les incursions de rongeurs de l'ancien monde, et plus rarement et très tardivement, de types d'Amériques du Sud.

Ces incursions, séparées par des périodes d'isolement relativement longues durant le Paléogène, sont plus fréquentes dans le Néogène. Au moins dix zones peuvent être définies à partir de distinctions majeures dans les faunes successives de rongeurs et ce nombre peut être porté à seize sans difficulté. En général, les genres de rongeurs permettent une zonation aussi fine que celle définie à partir des genres de grands mammifères. Les espèces n'ont pas été employées jusqu'ici en biostratigraphie à l'exception des divisions les plus récentes, Blancan et post-Blancan.

INTRODUCTION

Rodents first appear in the latest Paleocene or earliest Eocene (see Gingerich, 1976, and A.E. Wood, 1977, for opposing views) as very fragmentary specimens, chiefly incisor fragments, of the Family Paramyidae, from the Eagle Coal Mine, Bear Creek, Montana, and a single incisor from beds of like age in the immediately adjacent part of Wyoming (Van Houten, 1944). A.E. Wood (1977, p. 96) has suggested that rodents ori-

ginated in the southeastern part of the United States, most probably from primates, and spread to this part of western North America at the close of the Paleocene. After this sparse beginning in the record, fossil rodents are usually abundant in North America if proper search procedures are followed. Recognition of the value of rodents for biostratigraphical purposes has been slow to develop, but this value is now accepted through recent work in Europe. In North America, various workers have argued for the value of rodents in stratigraphy (for example : Stirton, 1935 ; Wilson, 1937, 1968 ; Lindsay, 1972 ; Stout, 1975 ; and Schultz, Martin, Tanner and Corner, 1978), but work has not produced such an overall refinement as that of the zones of P. Mein, 1975.

Use of rodents for biostratigraphical purposes in North America depends on : 1/ extinctions, 2/ the evolution of certain endemic groups, and 3/ the periodic incursion of migrants, principally from the Old World. These incursions are separated by relatively long periods of isolation in the early rodent faunas (Eocene-Oligocene), but isolation becomes more episodic in the later Tertiary. A generalized summary follows, but it is obvious that precision is less than that implied by the zones of Mein. Approximate equivalents for North American mammalian ages (Wood, *et al.*, 1941), European mammalian ages (Fahlbusch, 1976), and Lyellian divisions are given for each rodent faunal stage discussed.

WASATCHIAN / NEUSTRIAN-EARLIEST RHENANIAN / EARLIER EOCENE

This age marks the first appearance of abundant, but largely undiversified rodents in the North American fauna. Most of this first wave represents the Family Paramyidae, and all are protrogomorphs. Near the end of the Wasatchian (Lysite-Lost Cabin levels) relatively rare sciuravids are present, presumably by development from native paramyids. It may be noted that North America is connected to Europe via a North Atlantic bridge in the earlier Wasatchian. Consequently, a strong resemblance exists among the rodents of the two continents. Later, and before the end of the Wasatchian, the connection with Europe, and Asia as well, is broken, and the rodent faunas become increasingly unlike each other with the development of endemic families, of which for North America the Sciuravidae is the most important.

Clarkforkian / Late Thanetian

First Appearance	Some Associated Genera
Paramys atavus	None known

Early Wasatchian / Neustrian

Franimus	*Pseudotomus*	*Paramys*
Lophiparamys	*Reithroparamys*	
Microparamys		

Late Wasatchian / Earliest Rhenanian

Leptotomus	*Knightomys*	*Lophiparamys*	*Pseudotomus*
Thisbemys	*Sciuravus*	*Microparamys*	*Reithroparamys*
Dawsonomys		*Paramys*	

BRIDGERIAN-UINTAN / MIDDLE AND LATE RHENANIAN-EARLY HEADONIAN / LATER EOCENE

This age is characterized by diversification of rodents at a protrogomorph level, with rare, chiefly late, native non-protrogomorph kinds. North America is clearly isolated from Europe and also from Asia until very late Eocene (Duchesnean) or earliest Oligocene (pre-Chadronian). A.E. Wood (1977) suggests that rodents did migrate to Asia by the middle Eocene, but if as late as middle Eocene, it was by a one-way street, and his suggestion is based on the American origin of rodents which is not necessarily the case.

In more detail, paramyids, sciuravids, and cylindrodontids (if *Mysops* is one) are all common in the Bridgerian, and the first two groups are diversified. An important development in the southwestern part of the United States is the presence of the first non-protrogomorph — the hystricognathus, and possibly hystricomorphous genus, *Prolapsus*. This genus seems to have had a sciuravine dental pattern.

In the Uintan, paramyids are still common, and sciuravids have become less common especially after the earlier Uintan, except in their possible descendants such as the first eomyids (*Protadjidaumo*), zapodids (?) (*Simimys*), and geomyoids (?) (*Griphomys*). *Pareumys* replaces *Mysops* among the cylindrodonts, and the genus *Protoptychus* is a rare rodent which is hystricomorphous and probably hystricognathous. The fauna in general is simply an increasingly diversified one of North American protrogomorph roots. The climate associated with these early rodents is one of high temperature and rainfall, probably of non-cyclonic circulation.

The terminal rodent fauna of the Eocene, the Duchesnean, suggests that climatic deterioration has already set in. The rodent fauna is not so well-known as earlier — perhaps in consequence of this — but contains no really new elements. In places, but seemingly not universally, a great decline in paramyids takes place. Thus in the Duchesnean part of the Sespe (Pearson Ranch local fauna, Wilson, 1949), but not in the Big Bend area of Texas (A.E. Wood, 1974), the paramyid fauna is impoverished. So far as can be determined, no rodent groups are introduced from outside the continent although migration occurs from the Old World as evidenced by such genera as *Pterodon*.

Bridgerian / Mid Rhenanian / Middle Eocene

First Appearance	Some associated Genera	
Ischyrotomus	*Leptotomus*	*Reithroparamys*
Pauromys	*Microparamys*	*Thisbemys*
Mysops	*Paramys*	*Sciuravus*
Prolapsus	*Pseudotomus*	

Uintan / Late Rhenanian-Early Headonian / Late Eocene

Mytonomys	*Protadjidaumo*	*Ischyrotomus*
Rapamys	*Simimys*	*Leptotomus*
Pareumys	*Griphomys*	*Pseudotomus*
Pseudocylindrodon	*Protoptychus*	*Reithroparamys*
Eohaplomys		*Thisbemys*

CHADRONIAN / LATE HEADONIAN-EARLY SUEVIAN / EARLY OLIGOCENE

In the earliest Oligocene, or in the immediately preceding latest Eocene, a new wave of migration took place, the strongest wave, probably the only, since the Wasatchian. Moreover, whether or not climatic deterioration took place in the Duchesnean, a comparison of typical late Eocene to earlier Oligocene indicates a drop of as much as 15 degrees centigrade in the mean annual temperature (Wolfe, 1978). Unfortunately, the rodent record for this long period of time, perhaps as much as six million years, is spotty. Most local rodent faunas are small, and only as a composite is the record abundant (the Cypress Hills may be an exception to this — see Russell, 1972, and Storer, 1978). Moreover, we cannot be certain which families of rodents are endemic and which are arrivals from outside the continent. For stratigraphic purposes this is an important consideration because a new arrival makes for a sharps boundary whereas otherwise we might expect an earlier record of an endemic group if conditions become favorable. The following rodent groups appear in the Oligocene for the first time : Sciuridae ; typical heteromyids (*Heliscomys*) ; Eutypomyidae-Castoridae (unless *Janimus* proves to be castoroid) ; and Cricetidae. Of these, the heteromyids appear almost certainly to be of American origin, sciurids might be, and castorids probably are not. Because of the uncertain taxonomic status of *Simimys*, the cricetids are ambivalent. A further characteristic of the Chadronian is the radiation of eomyids in North America. The Calf Creek local fauna, for example, contains five genera of these offshoots from *Protadjidaumo* (Storer, 1978). Surviving into the Chadronian are Eocene groups such as paramyids and cylindrodonts, but no sciuravines as such, only likely descendants from the stock (*e.g.*, geomyoids). The greatest change in the rodent fauna of North America occurs sometime between the typical Uintan and the Orellan, with the replacement of the older protrogomorph-dominanted fauna by one of modern families (Wilson, 1972). This change finds a parallel in Europe in the Grande Coupure. It may be suggested that

most of this faunal turnover occurred within the Duchesnean and the first part of the long Chadronian interval.

First Appearance		Some Associated Genera
Manitsha ?	*Eutypomys*	*Leptotomus*
Ardynomys	*Pipestoneomys*	*Mytonomys*
Cylindrodon	*Adjidaumo*	*Pseudocylindron*
Ischyromys	*Aulolithomys*	*Griphomys*
Titanotheriomys	*Centimanomys*	
Prosciurus	*Meliakrounomys*	
Pelycomys	*Namatomys*	
Protosciurus	*Paradjidaumo*	
Agnotocastor	*Yoderimys*	
	Heliscomys	
	Eumys ?	
	Subsumus	

ORELLAN-WHITNEYAN / LATE SUEVIAN-ARVERNIAN / LATER OLIGOCENE

The North American fauna is once again isolated, and the characteristic rodent fauna is simply an outgrowth of the Chadronian. Some groups that are rare in the Chadronian become common in the Orellan (*e.g.*, cricetids such as *Eumys*). The variety of eomyids becomes distinctly less. In the Whitneyan age, heteromyids start their diversification, cricetids start a decline numerically, and *Ischyromys* becomes, or is already, extinct. Beavers are common in the Whitneyan because of increase in suitable habitat in the known collecting areas, but both *Agnotocastor* and *Palaeocastor* are probably to be recorded as early as the Orellan. The first undoubted aplodontids appear (*Haplomys*) as kinds quite like *Prosciurus*, but with V-shaped paracone and metacone.

Orellan / Late Suevian / Middle Oligocene

First Appearance	Some Associated Genera	
? *Palaeocastor*	? *Manitsha*	*Eutypomys*
Diplolophus	*Ischyromys*	*Adjidaumo*
? *Proheteromys*	*Prosciurus*	*Paradjidaumo*
«*Eumys*» *planidens*	*Protosciurus*	*Heliscomys*
	Agnotocastor	

Whitneyan / Arvernian / Late Oligocene

Haplomys	*Prosciurus*	*Paradjidaumo*
Metadjidaumo	*Pelycomys*	*Heliscomys*
Scottimus	*Agnotocastor*	*Proheteromys*
	Adjidaumo	

ARIKAREEAN-HEMINGFORDIAN / AGENIAN-ORLEANIAN / LATEST OLIGOCENE-EARLIER MIOCENE

This period is characterized by renewed interchange between New and Old Worlds. The principal rodent to arrive is *Pseudotheridomys*, an eomyid, but *Anchitheriomys* may also have entered during this time as well as *Plesiosminthus*. Fairly early in the interval is a great radiation of geomyoids, mainly entoptychines and pleurolicines. Beavers are common, especially fossorial kinds of the *Palaeocastor* type. There are a large variety of aplodontids, and also the first mylagaulids. Relatively rare are cricetids, seemingly largely replaced by geomyoids and *Plesiosminthus* (Zapodidae). The North American-derived eomyids are largely of *Adjidaumo* type. Late in the interval, fossorial beavers decrease, *Monosaulax* becomes common, the relatively advanced *Mesogaulus* replaces primitive mylagaulids, sciurids increase in frequency of occurence, and the entoptychine-pleurolicine group becomes rare.

Early Arikareean / Agenian

First Appearance		Some Associated Genera	
Allomys	*Sanctimus*	*Prosciurus*	*Proheteromys*
Meniscomys	*Tenudomys*	*Eutypomys*	*Eumys*
Promylagaulus	*Plesiosminthus*	*Heliscomys*	*Scottimus*
Entoptychus	*Paciculus*		
Gregorymys			

Later Arikareean-Marsland / Orleanian

Mesogaulus	*Monosaulax*	*Plesiosminthus*
Miospermophilus	*Pseudotheridomys*	*Proheteromys*
Protospermophilus	*Dikkomys*	« *Leidymys* »
Anchitheriomys	*Schizodontomys*	*Paciculus*

BARSTOVIAN / ASTARACIAN / MIDDLE MIOCENE

Selective interchange between New and Old World continued during this interval. Among rodents this resulted in the arrival of the *Copemys-Democricetodon* group from the Old World, and cricetids once more become common in the North American record (derivation of this group from North American sources seems much less likely). Heteromyids are now of modern aspect. Advanced aplodontids (*Liodontia*) and mylagaulids (*Mylagaulus* and *Ceratogaulus*) occur. *Plesiosminthus* is still common, and *Macrognathomys* is present in addition among the zapodids. « *Monosaulax* » and rare *Anchitheriomys* probably are the only beavers.

First Appearance		Some Associated Genera	
Liodontia	*Megasminthus*	*Protospermophilus*	*Anchitheriomys*
Ceratogaulus	*Perognathoides*	*Plesiosminthus*	*Monosaulax*
Mylagaulus	*? Prodipodomys*	*Pseudotheridomys*	*Gregorymys*
Spermophilus (*s.l.*)	*Copemys*		
Macrognathomys			

CLARENDONIAN-HEMPHILLIAN / VALLESIAN-TUROLIAN-RUSCINIAN / LATE AND LATEST MIOCENE

In the earlier (Clarendonian) part of this interval, some migration occurred, but none is evident in the Rodentia. Consequently, the rodent fauna is much like that of the preceding Barstovian. Among beavers, *Eucastor* replaces « *Monosaulax* ».

In the later part of the interval (Hemphillian) some faunal interchange between New and Old World takes place, for example the first « microtoids » (*Microscoptes*, *Promimomys*) although one earlier fragment has been reported in North America (Shotwell, 1970), and the first *Castor**. *Dipoides* replaces *Eucastor*, and *Peromyscus* replaces *Copemys*, by continued development of their respective lines. The last known mylagaulids and eomyids are present.

Clarendonian / Vallesian

First Appareance		Some Selected Genera	
Tardontia	*Pliosaccomys*	*Mylagaulus*	*Perognathus*
Epigaulus	*Peromyscus*	*Protospermophilus*	*Prodipodomys*
Eucastor	*? Microscoptes*	*Macrognathomys*	
Leptodontomys			

Hemphillian / Turolian-Ruscinian

? Paenemarmota	*Ronquillomys*	*Liodontia*	*Microscoptes*
? Spermophilus (Spermophilus)	*Pliozapus*	*Macrognathomys*	*Peromyscus*
? Castor	*Pliotomodon*	*Pliosaccomys*	
Dipoides	*Promimomys*		
Kansasimys			

BLANCAN / VILLANYIAN / PLIOCENE

Interchange with the Old World is more significant than in the latest Miocene, with an abundance of microtines with rooted cheek-teeth as especially characteristic. Also a connection with South America is established, and erethizontids arrive from South

**Castor* seems to be of Old World origin, but a different view is held by T.M. Stout who visualizes parallel development of the « genus » in both Old and New World.

America. *Procastoroides* is present as a derivative of *Dipoides*. Rodent genera are largely Recent genera except for the microtines, and zonation of post-Hemphillian time can be quite precise as based on microtine evolution. In this regard, early Blancan is characterized by microtines with rooted teeth that lack cement, late Blancan my microtines with rooted cheekteeth but with cement.

Early Blancan

First Appearance		Some Associated Genera	
Procastoroides	*Ophiomys*	*Paenemarmota*	« *Dipoides* »
(with smooth incisor enamel)			
Cosomys	*Pliolemmus*	*Spermophilus*	*Perognathus*
Nebraskomys	*Pliopotamys*	*Castor*	*Peromyscus*

Late Blancan

Cynomys	*Synaptomys*	*Prodipodomys*
Procastoroides	*(Metaxomys)*	*Ophiomys*
(with grooved incisor enamel)		
Ondatra	? *Erethizon*	

IRVINGTONIAN / BIHARIAN / EARLIER PLEISTOCENE

This interval is marked by dominance of still extant genera of rodents although about fifty percent of the species are extinct. *Microtus* and *Microtus*-like microtines appear with molars of persistent growth. Extinct species of *Ondatra* are still present (*O. annectens* and *O. nebracensis*). « *Castoroides* » replaces *Procastoroides*. The Irvingtonian, as defined by Schultz, Martin, Tanner and Corner (1978) is a long stage, and seems capable of subdivision by means of fossil rodents. Some migration occurs, as for example *Allophiomys* (see Martin, 1973).

First Appearance		Some Associated Genera
« *Castoroides* »	*Ondatra annectens, O. nebracensis*	*Ondatra*
Allophiomys	*Synaptomys (Mictomys)*	*Synaptomys*
Microtus		

RANCHOLABREAN / LATER PLEISTOCENE

By this late time, rodents mostly represent still living species although the range may be somewhat different, and the morphology is sometimes somewhat atypical (subspecies different ?). South American-derived capybaras exist in the southern part of the United States. Migration from the Old World occurs in this time interval, but does not seem to affect the rodent fauna.

First Appearance	Some Associated Genera
Ondatra zibethica (and many other Recent species)	« *Castoroides* »

SUMMARY

The earlier Eocene (Wasatchian) witnessed a rapid expansion of rodents of paramyid type followed by a radiation from these stem rodents of a variety of protrogomorphs in the later Eocene (Bridgerian-Uintan). Modern families of rodents appear in the Oligocene, and largely replace the archaic families. The early Oligocene (Chadronian) is characterized by a large variety of eomyids. In the latest Oligocene and earlier Miocene (Arikareean-Marslandian) an expansion of geomyoids, aplodontids, and zapodids occur, largely at the expense of muroids. Later in the Miocene (Barstovian-Clarendonian-Hemphillian), cricetids become common once again, the first « microtoids » appear, coexisting with the last mylagaulids and eomyids. The Pliocene (Blancan) rodent fauna is dominated, at least in northern areas, by primitive Arvicolinae. In the Pleistocene, the rodent fauna is almost completely modern except for the presence of a few forms such as the giant beaver « *Castoroides* ». Throughout the Cenozoic, rodent genera are stratigraphically about as useful in the North American record as genera of the larger mammals.

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