Species differentiation among muroid rodents on the basis of their lower incisor size and shape : ecological and taxonomical implications

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Summary. – Incisors with continuous growth are a characteristic of rodents and fossiliferous deposits contain many of them. No significant sexual dimorphism in lower incisor size was observed among the analyzed samples. Prediction of skeletal measurements and body weight from lower incisor size in extant rodent species are studied. We show here that the lower incisor size is a good estimator of body length and skull length among rodents, whereas the prediction of body weight may be less accurate. Some morphometric indices are used to describe the shape of lower incisors among some selected living rodent species. The use of size, relative curvature, cross-sectional shape and relative cover onto the medial side of the lower incisor taken together, allows discrimination of some functional groups, in particular arboreal, terrestrial and burrower species. These results are then applied to Quaternary Japanese muroid rodent assemblages, permitting us to use isolated, fossil, lower incisors for paleocological analysis, thus largely increasing sample sizes of fossil rodent assemblages. In addition to this methodological contribution, the observed diversity of incisor morphology suggests that these rodents were capable of exploiting different resources, thereby providing a possible coexistence mechanism for the rodent assemblages.

Résumé. – Les incisives à croissance continue sont une des caractéristiques des rongeurs et les dépôts fossilifères en délivrent une très grande quantité. Aucun dimorphisme sexuel n'a pu être mis en évidence sur la taille de l'incisive inférieure pour les échantillons analysés. L'estimation de la taille et de la masse corporelle à partir de la taille de l'incisive inférieure est étudiée pour plusieurs espèces actuelles de rongeurs. Nous montrons que la taille de l'incisive inférieure est un bon estimateur de la longueur du crâne ainsi que de la taille du corps, tandis que l'estimation de la masse corporelle peut être moins précise. Des indices morphométriques sont utilisés pour décrire la forme de l'incisive inférieure pour certaines espèces actuelles de rongeurs. L'utilisation conjointe de la taille, de la courbure, de la forme de la section de l'incisive et de son recouvrement d'émail sur la face médiale a permis de différencier plusieurs groupes fonctionnels, en particulier les arboricoles, les terrestres et les fouisseurs. Ces résultats sont par la suite appliqués à des assemblages Quartenaires de rongeurs Muridae du Japon, permettant d'identifier les incisives inférieures isolées, et augmentant ainsi largement la taille des échantillons étudiés. En plus de cette contribution méthodologique, la diversité des morphologies observée sur les incisives inférieures suggère que ces rongeurs étaient capables d'exploiter des ressources différentes, ce qui est un des mécanismes probables permettant la coexistence des espèces de rongeurs au sein d'une communauté.

INTRODUCTION

Rodent species represent nearly the half of all mammalian species (Wilson and Reeder 1993), and since their origin they have risen to dominate, in number of species and biomass, mammalian herbivorous communities, developing various ecological adaptations. This diversity, both taxonomic and ecological, allows rodent species to be represented in various environments (Landry 1970), which makes this group a much favored material for both paleontological and ecological studies.

Body size in mammals has been correlated with many aspects of their physiology, morphology, ecology and behaviour (Barbault 1988 ; Peters 1983 ; Schmidt-Nielsen 1975, 1984), and estimates of fossil species body size can therefore be used for paleoecological considerations (Damuth and MacFadden 1990). Many studies have described the relationship between body length or body weight for various mammalian groups and other size parameters such as the area of the m1 (Conroy 1987 ; Creighton 1980 ; Gingerich et al. 1982), the dimensions of the M2 and m2 (Schwartz et al. 1995), the length of the humerus (Gingerich 1990), the diameter of long bones (Biknevicius et al. 1993), the metapodial diameters (Alberdi et al. 1995), or the area of the astragalus (Martinez and Sudre 1995). In addition, we recently established the relationship between body size and the size of the upper incisor among rodent species (Parra and Jaeger 1998). Here, we report a similar study, and show that the lower incisor size can be used to predict body size among rodents.

The presence of one upper and one lower ever-growing incisor in each quadrant of the skull and mandible is one of the characteristics of rodents, and possibly the main morphological trait responsible for the ecological success of this group. In addition, rodent incisors display great variation in size and shape. However, this variability is poorly known, and incisors are rarely used as a tool for studying the ecology or the taxonomy of living and fossil rodent species. Typically, most work on the systematics of living and fossil rodents is indeed based on their molar size and morphology.

The teeth are the preferred study material for the vertebrate paleontologist and fossil localities contain numerous rodents incisors, isolated or still associated with maxillary bones (upper incisors) or lower jaws (lower incisors). Upper incisors still in connection with maxillary bones are usually very scarce in the fossil material, making isolated upper incisors difficult to assign to a particular species. On the contrary, isolated lower incisors can be easily compared to those associated to lower jaws that are still quite abundant in fossil assemblages.

The purpose of this study is thus to demonstrate some of the taxonomic and ecological information inherent in lower incisors. This study is the first attempt to provide an overview of lower incisor variation in size and shape among extant muroid rodent species. This is obviously not an exhaustive review, given the large number of living rodent species (more than 2000 species ; Wilson and Reeder 1993). However, this review allows us to demonstrate some features of the lower incisor size and shape that are useful for the study of isolated fossil rodent incisors. Finally, these results will be applied to some Japanese Quaternary murid rodent assemblages, mostly respesented by isolated lower incisors.

MATERIAL

We followed the classification proposed by Wilson and Reeder (1993) for all the species studied. Only mature specimens were selected and the specimens were considered adults on the basis of the complete eruption of the M3.

Body size and body weight estimations from lower incisors. – This study was based on 844 specimens representing 61 species of muroid rodents that belong to four families : Muridae, Sciuridae, Heteromyidae and Dipodidae (Appendix I). The material examined is stored at the Muséum National d'Histoire Naturelle, Paris, and at the National Science Museum, Tokyo.

Morphological variability of lower incisors. – The comparative extant material represent 18 muroid rodent species that display great variation in habitat (Appendix II).

Our method was also applied to fossil rodent assemblages collected in several Quaternary caves from Japan (Table 1), among them the Ikumo, Ando and Locality 3-1 from Shiriya quarries. All the material from these three localities was collected by Y. Hasegawa and is stored at the National Science Museum, Tokyo (Kowalski and Hasegawa 1976). The Ikumo quarry is located at the south-eastern corner of the Paleo-

TABLE 1. – Number of lower incisors associated to lower-jaws and isolated incisors (in parentheses) sampled for seven Japanese muroid rodent species in some Quaternary localities.

	Ikumo Quarry	Ando Quarry	Ube Kosan Quarry (Loc. 3)	Shiriya Quarry (Loc. 2)	Shiriya Quarry (Loc. 3-1)
Location	Yamaguchi Pref.	Yamaguchi Pref.	Yamaguchi Pref.	Aomori Pref.	Aomori Pref.
Geological age (years ago) [b]	> 184 000		> 137 000		
Age	middle Middle Pleistocene	middle Pleistocene	late Middle Pleistocene	late Middle Pleistocene	early Late Pleistocene
Mammalian biozone [a]	QM4	QM4	QM5	QM5/QM6	QM6
C. japonicus	13 (33)	6 (7)	0 (10)	0 (7)	-
Clethrionomys-Phaulomys	-	-	-	-	28 (11)
Microtus sp.	5 (16)	0 (3)	-	-	-
M. montebelli	-	-	-	-	1 (44)
A. argenteus	14 (17)	0 (8)	4 (19)	24 (46)	2 (0)
A. speciosus	15 (24)	0 (42)	7 (47)	1 (12)	7 (4)
R. norvegicus	0 (1)	-	-	3 (34)	2 (1)
Total	47 (91)	6 (60)	11 (97)	28 (99)	40 (60)
Reference and location of specimens [c]	Kowalski & Hasegawa (1976) NSM	Kowalski & Hasegawa (1976) NSM	Kawamura (1988, 1989) AUE	Kawamura et al. (1988) NSM	Kowalski & Hasegawa (1976) NSM

a from Kawamura (1991)

b from Kawamura (1988)

c NSM: National Science Museum, Tokyo; AUE: Aichi University of Education

zoic « Zoneki Limestone Mass », west of Nakamura, Yamaguchi Prefecture (Kawamura 1988), and the fossil remains were found in fissure deposits. The Ando quarry is located at the Ofukudai karst plateau, Yamaguchi Prefecture and the sediments of Ando quarry are roughly contemporaneous with those of Ikumo quarry (Kawamura 1988). The Shiriya mammalian remains from locality 3-1 were collected in Quaternary limestone fissures, in Aomori Prefecture, Shimokita Peninsula. Two additional localities were included in this study, the Locality 3 from Ube Kosan quarry and the Locality 2 from Shiriya quarry. The Ube Kosan quarry is one of the largest limestone quarries in Japan, located at Isa-cho Mine, Yamaguchi Prefecture. The fossiliferous cave sediments of Locality 3 were excavated by Y. Kawamura in June 1978. The material studied was described by Kawamura and A. Sugimura in the Aichi University of Education, Japan. The material from Locality 2 of Shiriya quarry was collected in 1987 by Y. Hasegawa et al. and is stored at the National Science Museum, Tokyo (Hasegawa et al. 1988).

METHODS

Measurements. – For the study of interspecific size variation, four size parameters were considered for each specimen examined: (1) body weight in grams (BW); (2) head and body length in millimeters (HBL); (3) total skull length in millimeters (TLS); and (4) antero-posterior diameter of the lower incisor in millimeters (AP).

For the study of size and shape variability of the lower incisor, two additional characters of the lower incisors were considered: the transverse diameter in millimeters (T) and the radius of curvature in millimeters (R) (Fig. 1). In order to describe the position of the enamel layer, we also measured the extension of enamel on both lateral and medial sides of the incisor, expressed relatively to the antero-posterior diameter of the incisor (% lateral and % medial, respectively).
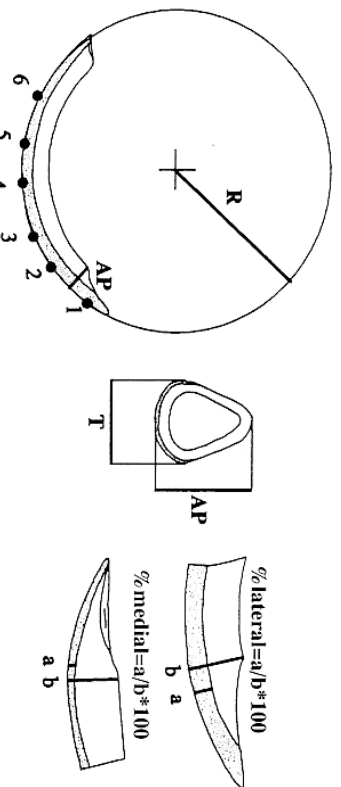

Fig. 1. – Lower incisor in lateral and cross-sectional views showing the fifth measurements taken: antero-posterior diameter (AP), transverse diameter (T), radius of curvature (R), and relative cover of enamel onto medial and lateral sides (% medial and % lateral) of the lower incisor. Points 1 to 6 located on the anterior edge of the incisor were used to estimate the radius of curvature.

We defined an index AP/T which describes the cross-sectional shape of the incisor and can be easily measured on both extant and fossil material. A round cross-section means that the antero-posterior diameter (AP) equals the transverse diameter (T) of the incisor, which can be expressed by the following equation: $AP/T = 1$. Similarly, an oval cross-section can be described by the following index: $AP/T > 1$. Finally, the relative curvature of each incisor was estimated by the index R/AP. The radius R was divided by the incisor diameter AP in order to eliminate the effect of size from the estimated curvature. All the measurements made on lower incisors were taken with a drawing tube coupled with a 2D digitizer to the 0.01 mm precision. The two measurements AP and T were taken at the level of the incisor gap, and the radius of curvature R was estimated from the coordinates of six points taken on the anterior edge of the incisor (Fig. 1). The total length of the skull was measured in dorsal view from the anterior edge of the upper incisor to the extremity of the condyle with a caliper to the nearest 0.1 mm. The data for head and body length and body weight were obtained from data given by the original collectors. When lacking, data for mean body weights were taken from the literature (Silva and Downing 1995).

Statistical analyses. – We first looked for the presence or the absence of sexual size dimorphism in the antero-posterior diameter (AP) of the lower incisor. For 18 selected populations representing seven species, we performed Student t-test mean comparison tests to compare the mean size of male and female populations.

All measurements were then transformed in natural logarithms to standardize scale before the following analyses were undertaken. The pairwise relationships between the size variables were fitted to an allometric model which can be expressed by a power function: $Y = a X^b$, where a is a constant and b the allometric coefficient. The transformation of this function to logs results in a linear relationship, $\text{Log } Y = \text{Log } a + b \text{ Log } X$, which was fitted to the data by a least-squares criterion (Smith 1984). Two additional parameters were computed: the percent standard error of the estimate: the percent coefficient of determination (% R = 100 r^2), and the percent standard error of the estimate (% SEE = 100 * standard error of estimate) which provides a comparative index of the accuracy of the different models computed (Smith 1984). All statistical analyses were performed using Systat software (version 5.2.1).

RESULTS

Intra-specific size variability : sexual dimorphism

Intra-specific variability, as expressed by CV values (Table 2) was comparable whether considering variability among males (from 0.02 to 0.15), among females (from 0.02 to 0.12) or among males and females together (from 0.04 to 0.12) within a given population, or between populations within a given species (from 0.05 to 0.12).

In nine cases out of the 18 considered, we found females to be larger than males in the lower incisor size, while the trend was the opposite in the nine remaining cases, where males were larger or similar in size to females (Table 2). The size difference between males and females was significant (P < 0.02) for only one population (*Phauhtomys smithii* from Fuji mountain, Table 2).

Inter-specific size variability : lower incisor size and body size

All the regression analyses computed, using the antero-posterior diameter of the lower incisor (AP) as the independent variable, were highly significant (all P < 0.0001).

TABLE 2. – Basic statistics (mean in mm, sample size and CV) for the antero-posterior diameter of the lower incisor for males (M), females (F), and males and females (M & F) from 18 selected populations of Japan, and for the 7 different species considered. Significant differences between males and females within each population are indicated at the 0.05 (*) level.

Species	Location	M	F	M & F	M:F	Statistics for sp
A. speciosus	Sado isl.	1.27 (19; 0.08)	1.31 (10; 0.04)	1.28 (29; 0.07)	0.96	1.30 (132; 0.10)
	Fuji Mt.	1.13 (6; 0.12)	1.19 (7; 0.10)	1.16 (13; 0.11)	0.95	
	Tsushima Isl.	1.27 (18; 0.08)	1.27 (11; 0.10)	1.27 (29; 0.08)	1.00	
	Poroshiri Mt.	1.43 (12; 0.05)	1.42 (6; 0.08)	1.43 (18; 0.06)	1.01	
	Tane Isl.	1.33 (12; 0.12)	1.30 (8; 0.09)	1.32 (20; 0.11)	1.03	
	Rishiri Isl.	1.35 (15; 0.06)	1.29 (8; 0.12)	1.33 (23; 0.08)	1.05	
A. argenteus	Nikko	1.05 (20; 0.07)	1.05 (17; 0.06)	1.05 (37; 0.07)	1.00	1.04 (119; 0.07)
	Odaigahara Mt.	1.05 (10; 0.05)	1.05 (4; 0.04)	1.05 (14; 0.05)	1.00	
	Fuji Mt.	1.01 (14; 0.06)	1.04 (14; 0.09)	1.03 (28; 0.07)	0.97	
	Tsushima Isl.	1.07 (10; 0.06)	1.04 (17; 0.05)	1.05 (27; 0.06)	1.03	
	Poroshiri Mt.	1.00 (7; 0.09)	1.05 (6; 0.05)	1.02 (13; 0.07)	0.95	
C. rutilus	Poroshiri Mt.	0.82 (10; 0.10)	0.91 (5; 0.09)	0.85 (15; 0.11)	0.97	0.85 (15; 0.11)
C. rufocanus	Rishiri Isl.	1.44 (8; 0.08)	1.47 (7; 0.04)	1.45 (15; 0.06)	0.98	1.45 (15; 0.06)
M. montebelli	Goyo Mt.	1.18 (6; 0.10)	1.16 (6; 0.08)	1.17 (12; 0.09)	1.02	1.17 (12; 0.09)
P. andersoni	Nikko	1.12 (10; 0.05)	1.13 (6; 0.06)	1.12 (16; 0.05)	0.99	1.04 (35; 0.12)
	Yatsugatake Mt.	0.95 (7; 0.15)	0.97 (12; 0.10)	0.97 (19; 0.12)	0.99	
P. smithii	Nikko	1.07 (2; 0.02)	1.00 (9; 0.06)	1.01 (11; 0.06)	1.07	1.00 (30; 0.05)
	Fuji Mt.	0.99 (13; 0.04)	1.03 (6; 0.02)	1.00 (19; 0.04)	0.96 *	

and we found high values for the three correlation coefficients r (Table 3). The lower incisor size appears to be a good predictor of the total length of the skull (% SEE = 8.3) and of head and body length (% SEE = 13.3). By contrast, even though the correlation coefficient is high (r = 0.93), the lower incisor size is a poor predictor of body weight with a percent standard error of the estimate % SEE = 39.8. The estimation of body weight from the variable AP of the lower incisor can thus vary within an interval of ± 40 % around its real value. Similar values for % SEE were computed when using the size of the upper incisor as a predictor of TLS, HBL and BW (10.6, 15.5 and 50.1 %, respectively ; Parra and Jaeger 1998), although the lower incisor size seems to be a more accurate predictor of body size than the upper incisor size.

The three regression equations raised to different values for the allometric coefficient, i.e. the slope of the regression line, depending on the size character estimated (Table 3). Under the hypothesis of an isometric increase of the incisor size with the length of the skull and with body length, that are linear measures, the slopes of the two

TABLE 3. – Values of the intercept, slope, coefficient of correlation (r), percent coefficient of determination (% R), percent standard error of the estimate (% SEE) and sample size (n) for the regression analyses performed with the antero-posterior diameter of the lower incisor (AP, in mm) as an independent variable. Significant differences between the slope and an isometric coefficient are indicated at the 0.05 (*) and 0.001 (***) levels.

Dependent variable	Intercept	slope	r	%R	%SEE	n
Total length of the skull (TLS, in mm)	3.10	0.75 ***	0.96	92.2	8.3	54
Head and body length (HBL, in mm)	4.42	0.93	0.93	86.3	13.3	42
Body weight (BW, in g)	3.19	2.58 *	0.93	85.9	39.8	51

regression lines computed should equal one. By contrast, the slope of the regression line between incisor size and body weight should equal three, since volumes should be proportional to the cube of lengths to keep the original shape (Schmidt-Nielsen 1975). The allometric coefficient was significantly different from one for the relationship between AP and TLS (P < 0.001), but not significantly different from one for the relationship between AP and HBL (P = 0.243). Lastly, the allometric coefficient was significantly different from three for the relationship between AP and BW (P < 0.015).

Inter-specific morphological variability

Morphological characters usually not preserved on fossil incisors. – Some characters of the lower incisor such as the color and ornamentation and even the microstructure of the enamel layer were not considered as appropriae tools to discriminate isolated fossil incisors. Previous systematic studies on extant rodent incisors were essentially based on the study of enamel microstructure which can be made with scanning electron microscope (SEM) observations (Escala and Galleco 1977 ; Martin 1992 ; Von Kœnigswald 1985 ; Von Kœnigswald et al. 1993). However, these studies revealed that rodent incisor enamel microstructure cannot be used for specific determination.

Despite the great range in the enamel color of extant rodents (from white for *Jaculus jaculus*, or yellow for *Eliomys quercinus* to very deep orange for *Rattus rattus*), the color is usually not preserved on fossil incisors, and thus cannot be used as a diagnostic character.

Ornamentation is very common on upper incisors (some species having one or several longitudinal grooves on the anterior surface of the enamel), however, lower incisors are almost always smooth. Such ornamentation was observed for only one single living taxon on the lower incisor, the genus *Otomys*, where both upper and lower incisors are deeply grooved.

Morphological and morphometrical characters still present on fossil incisors. – It was possible to find simple morphometric characters, such as the cross-sectional shape, the curvature of the incisor or the relative position of the enamel layer on the medial side of the incisor, that are much more varied among rodents and hence useful for the study of isolated fossil incisors.

The shape of the cross-section can be either roughly round, triangular or oval (Fig. 2). Interestingly, there is an increase in the index AP/T from fossorial species to terrestrial species adapted to forage in sandy habitats (Fig. 3). This index indeed allows us to discriminate between five functional groups among the species included in this study without any account for their phylogenetic relationships : (1) the fossorial species, here represented by *Tachyoryctes splendens* and *Otomys irroratus*, (2) the burrowers represented by the arvicolids (*Arvicola terrestris*, *Clethrionomys glareolus*, *Microtus montebelli* and *Phaulomys andersoni*), (3) the quadrupedal terrestrials species (*Tatera robusta*, *Acomys cahirinus*, *R. rattus*, *Praomys* sp. and *Apodemus argenteus*), (4) the arboreal species here represented by *E. quercinus*, and (5) the species that forage on sandy soils (*J. jaculus* and *Gerbillus nigeriae*). Finally, the two aquatic species *Ondatra zybethicus* and *Ichthyomys soderstromi* are included in the burrower and the quadrupedal terrestrial groups, respectively (Fig. 3). The adaptation to an exclusive aquatic life is not common among rodents, and this result could illustrate the progressive adaptation to new habits for these two species (from burrowing to aquatic and from terrestrial to aquatic life, respectively).

Rodents incisors are made up of dentine which is covered by a thick layer of enamel on its anterior side, and this layer can extend more or less onto the lateral and medial sides of the incisor. In order to estimate the extents of these layers, we used the two indices % lateral and % medial that represent the relative cover of enamel on both lateral and medial sides of the incisor. The variability of the % lateral is not important, with values ranging from 30 % (*Praomys* sp.) to 45 % (*A. cahirinus*). On the contrary, the % medial vary to a greater extent, with values ranging from less than 10 % (*A. cahirinus*) to more than 40 % (*M. montebelli*). The relative cover of enamel onto the medial side of the incisor seems thus to be a useful additional character to discriminate fossil isolated incisors (Fig. 3).

Lower incisors have a larger radius of curvature than upper ones. However, this radius is still very variable among lower incisors. The radius of curvature, R, divided by the antero-posterior diameter, AP, allows elimination of the effect of size on the curvature of the incisor. Interestingly, there is a general tendency for this index to decrease from fossorial and burrower species (from 6.56 to 8.75), to terrestrial species (from 5.28 to 7.85) up to arboreal species (from 5.20 to 5.65). As for the previous index AP/T which illustrates the cross-sectional shape of the incisor, the relative curvature R/AP seems to be related to the habitat of the species (Fig. 3). Arboreal species have a smaller radius of curvature than terrestrial species, and even smaller than burrower and fossorial species.

Observations made on occlusal view of the incisor, i.e. on the cutting edge, revealed a great variation (Fig. 4). The cutting edge area can be more or less elongated along the longitudinal axis, and the enamel layer more or less thick and symmetrical. Some species such as *A. cahirinus* or *T. robusta* have a relatively thick enamel layer when compared to other ones such as *A. terrestris* or *T. splendens*. Additionally, the position of the enamel is almost symmetrical for *T. robusta* and *T. splendens*, asymmetrical for *R. rattus* and *J. jaculus*, whereas it is highly asymmetrical for *A. cahirinus*, *G. nigeriae* and *Praomys* sp. (Fig. 4).

Otomys
AP/T = 0.98
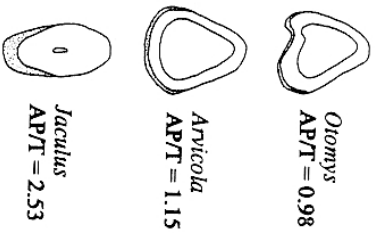
Arvicola
AP/T = 1.15

Jaculus
AP/T = 2.53

Fig. 2. — Three kinds of cross-sectional shape that can be observed on lower incisors : round (*O. irroratus*, CG 1913-215A), triangle (*A. terrestris*, CG 1996-2378) or oval (*J. jaculus*, CG 1995-570). For comparative purpose, the scale was not kept.
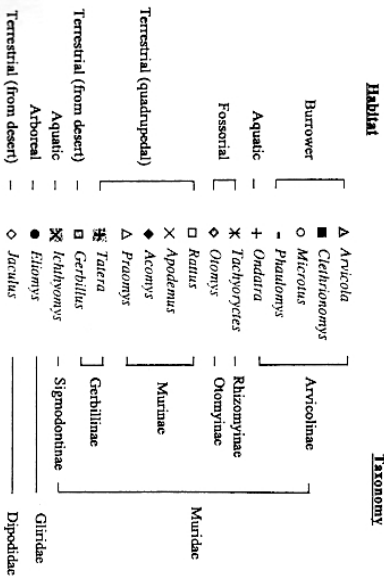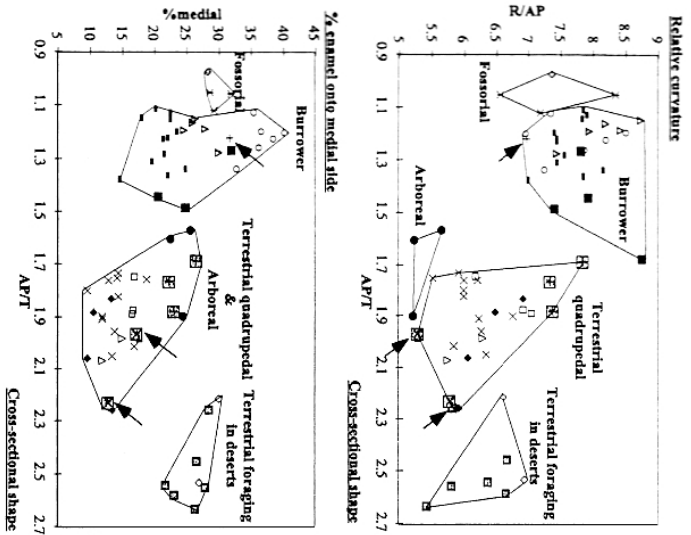
Habitat

- ▲ Arvicola — Burrower
- ■ Clethrionomys — Aquatic
- ○ Microtus — Fossorial
- - Phaulomys
- · Ondatra
- ✕ Tachyoryctes — Fossorial
- ◇ Otomys
- □ Rattus — Terrestrial (quadrupedal)
- ✕ Apodemus
- ◆ Acomys
- × Praomys — Terrestrial (from desert)
- ✳ Talera — Aquatic
- ⊡ Gerbillus — Arboreal
- ✕ Ichthyomys
- ● Eliomys
- ◇ Jaculus — Terrestrial (from desert)

Taxonomy

- Arvicola, Clethrionomys, Microtus, Phaulomys, Ondatra — Arvicolinae
- Tachyoryctes — Rhizomyinae
- Otomys — Otomyinae
- Rattus, Apodemus, Acomys, Praomys — Murinae
- Talera, Gerbillus — Gerbillinae
- Ichthyomys — Sigmodontinae
- Eliomys — Gliridae
- Jaculus — Dipodidae

Fig. 3. — Variation of the lower incisor shape among sixteen selected rodent species, top : relative curvature (R/AP) against the cross-sectional shape (AP/T) ; bottom : relative cover of the enamel layer onto the medial side (% medial) against the cross-sectional shape (AP/T) ; functional groups are well discriminated without any account for phylogenetic affinities, except for aquatic species that are indicated by an arrow.

In conclusion, we showed that lower incisors are a good predictor of body size among rodents, whereas the estimation of body weight may be less accurate. Furthermore, this study suggests that lower incisors might also be used to discriminate between coexisting rodent fossil species on the basis of their size differences and their differences in habitat utilization, which is reflected by the shape of the incisor.
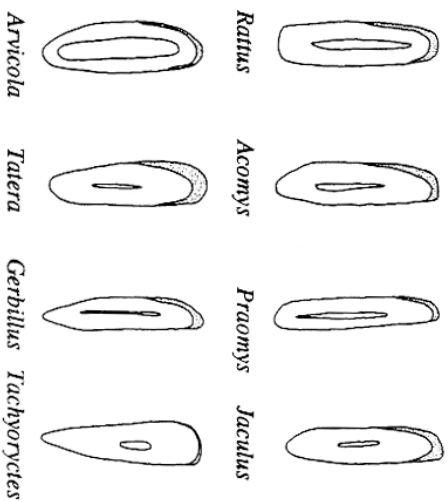

Fig. 4. — Representation in occlusal view of the tip of the lower incisor for the following species : *R. rattus* (CG 1981-551), *A. cahirinus* (CG 1997-1308), *Praomys* sp. (CG 1997-95), *A. terrestris* (CG 1996-2378), *T. robusta* (CG 1991-1373), *T. splendens* (CG 1992-2241), *J. jaculus* (CG 1995-570), *G. nigeriae* (CG 1997-1469), scale was not kept and left incisors were drawn as right ones.

Application to the muroid species from Japan

In order to test this hypothesis, we performed a comparison of fossil and extant lower incisors of rodent assemblages from Japan. The information contained in the isolated incisors will thus be added into the general fossil data, and bring more elements of knowledge to these faunas.

Taxonomical background. — The living muroid species from the Japanese islands belong to the murids (represented by the species *Apodemus argenteus, A. speciosus, Rattus norvegicus* and, only in the Ryukyu islands that were not included in this study, the genera *Tokudaia* and *Diplothrix*) and the arvicolids (represented by the species *Microtus montebelli, Clethrionomys rufocanus, C. rutilus, Phaulomys andersoni* and *P. smithii*). Introduced species such as *Mus musculus* and *Micromys minutus* that are not found as fossils in Japan were not included in the present study (Abe 1994 ; Dobson 1994). The systematics of fossil muroid species from Japan is still controversial, notably concerning the taxonomy of representatives of the genus *Microtus* (Kaneko and Hasegawa 1995 ; Kawamura 1989 ; Kowalski and Hasegawa 1976). However, we kept the most conservative hypothesis for the present study which is based on the following species list :
— murids : *A. argenteus, A. speciosus* and *R. norvegicus* ;

— arvicolids : *Microtus* sp. (as a fossil representative of this genus prior to Late Pleistocene) and *M. montebelli* (for specimens from the Late Pleistocene), *Clethrionomys japonicus* (for specimens prior to the Late Pleistocene), and *Clethrionomys-Phaulomys* transitional form (for specimens from the Late Pleistocene).

Variation of the lower incisor size and shape among extant Japanese muroid rodents. — The index AP/T (cross-sectional shape of the incisor) perfectly separates two groups (Fig. 5). The first is represented by the murids *Rattus* and *Apodemus* with values of AP/T > 1.62, while the second is represented by arvicolids *Microtus, Clethrionomys* and *Phaulomys*, with AP/T values < 1.51. Within this last assemblage, the
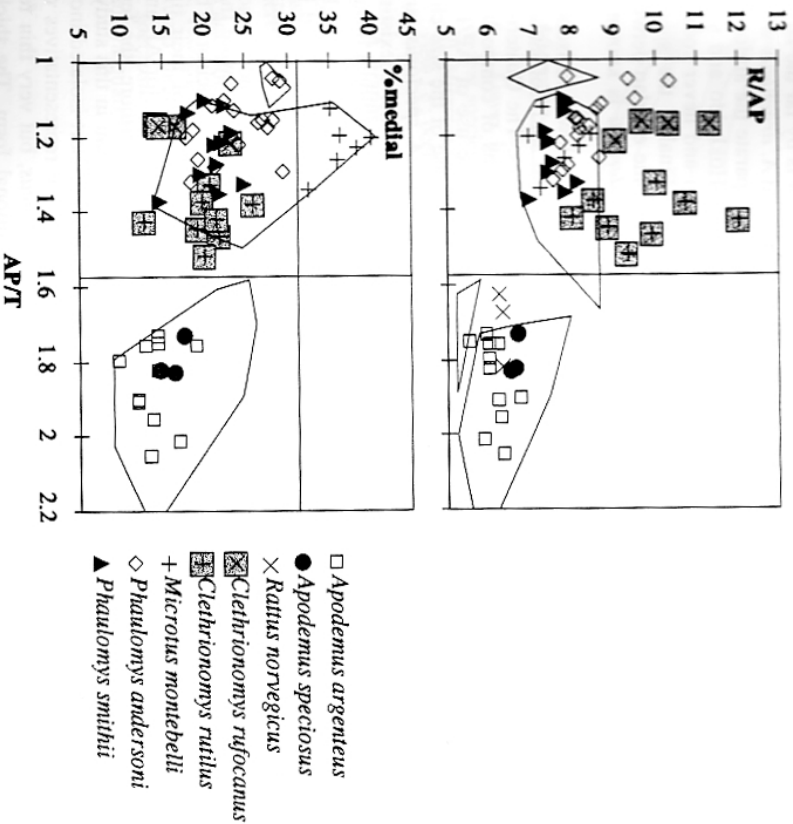

Fig. 5. — Variation of the lower incisor shape among the eight living muroid rodent species from the Japanese islands, top : relative cover of the enamel layer onto the cross-sectional shape (AP/T) ; bottom : relative cover of the enamel layer onto the medial side (% medial) against the cross-sectional shape (AP/T) : the areas evidenced on Fig. 3 are reported on the two graphs ; two groups are well discriminated based on the ratio AP/T : the quadrupedal terrestrial species (A. speciosus, A. argenteus and R. norvegicus) and the burrowers (genera Microtus, Clethrionomys and Phaulomys) ; the species M. montebelli has a relatively larger cover of enamel onto medial side (% medial) when compared to other arvicolid species.

□ *Apodemus argenteus*
● *Apodemus speciosus*
× *Rattus norvegicus*
▨ *Clethrionomys rufocanus*
▧ *Clethrionomys rutilus*
+ *Microtus montebelli*
◇ *Phaulomys andersoni*
▲ *Phaulomys smithii*

index AP/T is lower among C. rufocanus, with values ranging from 1.16 to 1.21, than among C. rutilus, with values ranging from 1.32 to 1.51. On the contrary, it is impossible to separate the two species P. andersoni and P. smithii that have a large overlap in their AP/T values.

Secondly, we used the value of the relative cover of enamel onto the medial side of the incisor, % medial. When compared to other arvicolids, the species M. montebelli shows larger values of this index, from 32.67 % to 38.45 %, whereas the values obtained for the other species (C. rufocanus, C. rutilus, P. andersoni and P. smithii) do not exceed 29.59 %.

Finally, the two characters AP and R were used to discriminate coexisting species by comparing their absolute size. Among the murids, R. norvegicus is by far the largest species, followed by A. speciosus which is intermediate in size, and A. argenteus which is the smallest species. We could not apply the same method to separate the arvicolids, however, the genus Clethrionomys is restricted to the island of Hokkaido and some small adjacent islands (Northern part of the Japanese archipelago) and never coexists with the genus Phaulomys which occurs more in the South. Finally, the species P. andersoni and P. smithii are different in size, even if there is some overlap between them. However these two species almost never coexist, as P. andersoni is known in Northern Japan and P. smithii in Southern Japan.

In conclusion, the observations and measurements made on the lower incisors of the Japanese extant muroid species can thus be very useful for the study of isolated fossil incisors, as it seems possible to assign each incisor to a species. The Quaternary rodent fauna from Japan is almost identical to the living one in terms of composition and we thus applied the same methodology to these faunas : (1) the use of AP/T to separate the murids from the arvicolids ; (2) among the murids, the use of the size characters AP and R to separate the three species R. norvegicus, A. speciosus and A. argenteus, and (3) The use of % medial to separate Microtus from other coexisting arvicolid species (whether C. japonicus or Clethrionomys-Phaulomys transitional form).

Application to the Quaternary fossil assemblages from Japan. – In order to validate our results, this method was applied to both fossil lower incisors that were still in connection with lower jaws and for which there was no doubt about their taxonomic affinity, and to fossil isolated lower incisors.

The fossil material studied was extremely well preserved, and we were aware that any kind of diagenesis could not alter the measurements taken on the incisor. The effect of diagenesis on incisors is mainly characterized by an alteration of their tip. However, all the measurements were taken at the level of the incisor gap (for AP and T), of from this level until the root extremity of the incisor (R). Furthermore, the few incisors that were considered too much altered were not taken into account in this study.

We also used some morphological characters of each species to sort isolated incisors (Fig. 6). On occlusal view, the enamel layer is thicker for the representatives of the genus Apodemus. This layer is still quite thick for R. norvegicus, but very thin for Microtus, Clethrionomys and Clethrionomys-Phaulomys transitional form. The thickness of the enamel layer can also easily be observed on cross-sectional view. The position of the enamel layer on occlusal view is highly asymmetrical among Apodemus, asymmetrical among Rattus and almost symmetrical among Microtus, Clethrionomys and Clethrionomys-Phaulomys transitional form. The cutting edge surface is more elongated along the murids than among arvicolids. A last interesting point is the occurrence of a wear facet on the medial side of the incisor of Apodemus which is marked from the extremity of the incisor to nearly half of the length of the cutting edge surface.
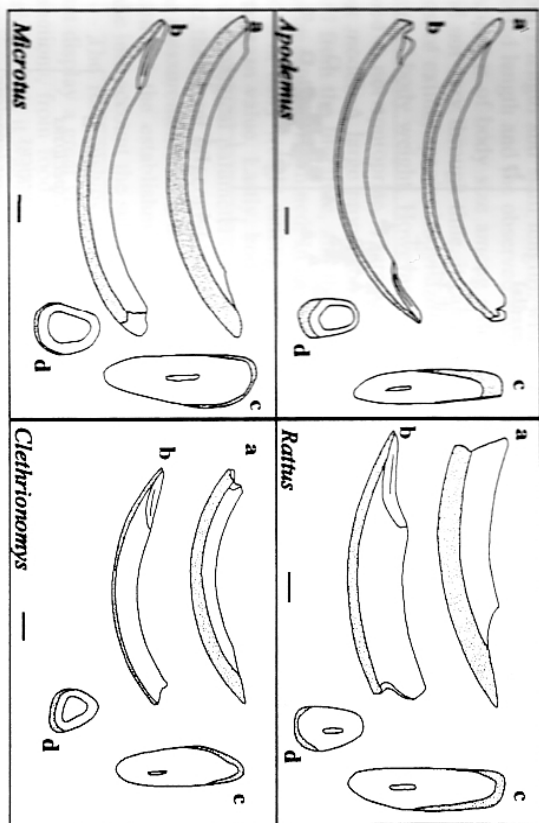
Fig. 6. – Lower incisor of four representative specimens of the Japanese Quaternary muroid rodent species from Ikumo Quarry. A. speciosus (NSM 9951-6), R. norvegicus (NSM 9951-9), Microtus sp. (NSM 9950-19), C. japonicus (NSM 9948-16), a : lateral view, b : medial view ; c : occlusal view ; d : cross-sectional view ; bar scale indicates 1 mm.

A graphical representation of the results obtained is given for the Ikumo locality (Fig. 7). These representations are very similar to those obtained for living assemblages, and we obtained a good discrimination of each species present in the fossil assemblages. The addition of isolated incisors to the fossil material can drastically increase total sample size (Table 1), sometimes by a factor 10 (from 6 lower incisors in connection with lower jaws to 60 isolated lower incisors, in the case of Ando quarry). In addition, some species that were not known by incisors associated to lower jaws can be recognized when isolated incisors are included, for example, R. norvegicus from Ikumo quarry, Microtus sp. from Ando and Ube Kosan quarries, A. argenteus and A. speciosus from Ando quarry, and C. japonicus from Ube Kosan and Locality 2 from Shiriya quarries (Table 1).

DISCUSSION

The general rule among mammals is that males are usually larger than females (Eisenberg 1981), although there are some exceptions. Reports of sexual size dimorphism among rodent species in the literature are more or less anecdotal, and in most studies that rely on tooth size variation, it is considered that intraspecific variability is larger than sexual dimorphism. In addition, when reported, the extent and direction of sexual size dimorphism among natural rodent population is much more variabe and concerns various size parameters (Biknevicius et al. 1993 ; Bondrup-Nielsen 1990 ;

□ *Apodemus argenteus*
● *Apodemus speciosus*
– *Rattus norvegicus*
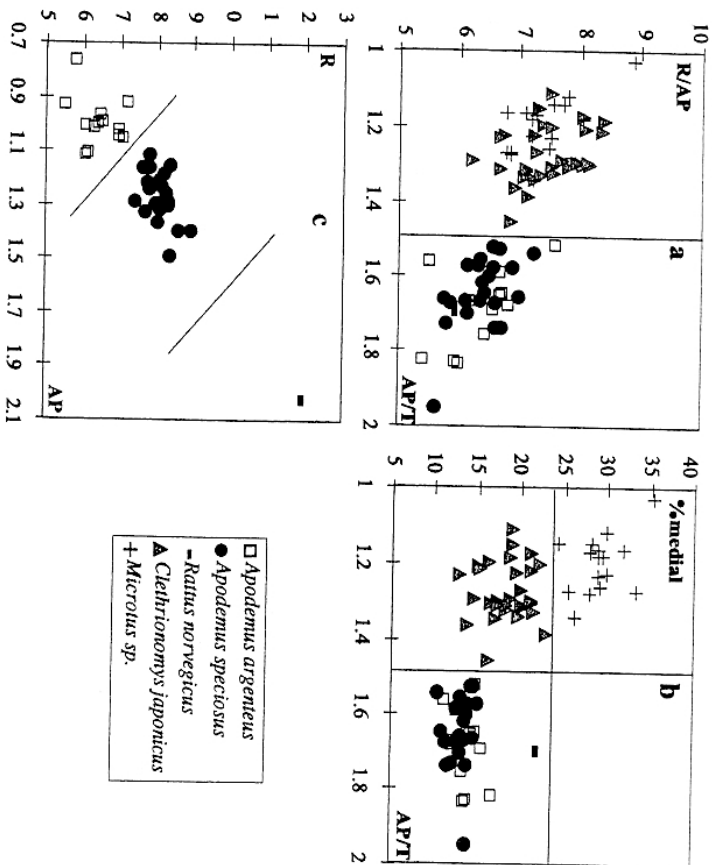▲ *Clethrionomys japonicus*
+ *Microtus sp.*

Fig. 7. — Graphical representation of the methodology used for the discrimination of isolated lower incisors from Ikumo Quarry ; a : the plot of the relative curvature (R/AP) against the cross-sectional shape (AP/T) separates the murid species (*R. norvegicus*, *A. speciosus* and *A. argenteus*) from the arvicolid species (*C. japonicus* and *Microtus* sp.) ; b : the plot of the relative cover of enamel onto the medial side (% medial) against the cross-sectional shape (AP/T) separates the species *Microtus* sp. from the species *C. japonicus* ; c : the plot of the absolute curvature (R, in mm) against the antero-posterior diameter (AP, in mm) separates the three murid species.

Boonstra *et al.* 1993 ; Leamy 1993 ; Mauk *et al.* 1999 ; Reiss 1986 ; Thorpe 1981 ; Xia and Millar 1987). Our results are in accordance with the general hypothesis that there is no sexual dimorphism among rodent for tooth size, an hypothesis demonstrated here for the lower incisor. Consequently, the investigation of phenotypic variability of fossil rodent species based on lower incisor size can be done without taking into account a possible sexual size dimorphism among species.

Since teeth are directly related to the function of food intake, it is not obvious *a priori* whether they scale isometrically with body size or with metabolic rate, the latter being correlated with body weight (Calder 1984 ; Fortelius 1990). The incisor size increases in direct proportion with body size (isometric scaling : slope = 0.9), whereas it increases proportionally to body weight (allometric scaling : slope = 2.6). Low values of the percent standard error of the estimate were recorded for prediction of lengths

(body length and skull length), which indicates a very low difference between the predicted length and the observed length (Smith 1984). The incisor size is thus an accurate estimator of body size among rodents. Under the hypothesis that the model computed did not vary through time, it can be applied to fossil rodent species, providing estimation of extinct species body size. By contrast, this difference is much larger for prediction of body weight. However, this result does not necessarily indicate that the model used is not appropriate. There are several explanations for the low predictive power of our model. A large proportion of data used for species mean body weight were obtained from the literature, and the values used are thus not accurate values for the specimens actually examined. In addition, it is well established that there are seasonal variations in body weight among rodents, which introduces an additional source of error in the mean value. Lastly, body weight is highly correlated with behavioral, physiological and ecological parameters (Barbault 1988 ; Peters 1983 ; Schmidt-Nielsen 1975 ; 1984) and the extent of geographical variation is much larger for body weight than for skeletal measurements such as body or skull lengths. As a result, the mean values that are used for the establishment of interspecific allometric relationships obviously do not take into account the substantial variability of body weight.

The relationships computed in this study involved several living rodent species that display a great variability in diet or locomotion. Since incisors are used for various functions, from food intake (seed husking) to locomotion (digging among some fossorial species), it was reasonable to look for some morphological aspects of these incisors that would reflect this variability in habitat. As a result, we showed that the morphology of the lower incisor, and particularly its cross-sectional shape, and its relative curvature, are mainly constrained by the species habitat. An alternative hypothesis, that could not be validated here, would suggest a close relationship between the morphology of the lower incisor and the evolutionary relationships among the rodent species studied. However, as the incisor is directly related to the food intake and locomotion, it is not surprising to find such high adaptive convergence of the size and shape of the incisor for species that are not closely related. Surprisingly, the relative cover of the enamel layer onto the medial side of the incisor was found to be related to functional adaptation as well.

Incisors are usually not used for taxonomic purpose since they are difficult to assign to a particular species. However, our study revealed that the incisors are much more varied in their shape than usually thought, and that this variability might be used as a tool for discriminating species. In particular, incisors might be of a precious source of information in the study of fossil assemblages that contain a large quantities of these incisors. As it has been demonstrated in the present study for some Japanese Quaternary assemblages, the incorporation into the fossil data of the information contained in incisors is likely to increase our taxonomic knowledge of these assemblages, by the increase of the faunal lists. In addition, the consideration of incisors might be a usefull tool for the characterization of rodent fossil species ecology.

CONCLUSION

Although the analyses are not exhaustive, this work clearly opens up a wide area of application in the field of fossil rodent paleobiology. The results are highly suggestive and indicate the substantial amounts of information that may be gleaned from fos-

sil incisors. First, the use of incisor size for body size estimations should increase our knowledge of the ecology of extinct rodent species and the evolution of fossil community structure. Secondly, the use of both morphological observations and morphometric approaches allowed us to include in small mammal fossil assemblages a large quantity of isolated incisors, thus increasing our sample size substantially. Lastly, it has been predicted that the coexistence of species within the same guild requires a regular community size structure, minimizing competition between species (Dayan and Simberloff 1994 ; Dayan et al. 1989 ; 1990). Some authors have tried to demonstrate such a regular size structure among rodent communities, and even proposed that the incisor size should be one of the characteristics of rodents which would allow the minimization of competition between species (Parra et al. 1999 ; Dayan and Simberloff 1994). However, the present study shows that, in addition to the absolute size, the shape of the lower incisor, and particularly its relative curvature and cross-sectional shape, could also be important factors involved in competitive interactions between species, since they might reflect the specialization of each coexisting species to a particular resource in the environment.

ACKNOWLEDGMENTS

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APPENDIX I

List of species examined for regression analyses. Number of specimens examined are indicated in parentheses :

Akodon amoenus (13) ; A. boliviensis (15) ; Allactaga elater (6) ; Apodemus argenteus (12) ; A. speciosus (11) ; A. sylvaticus (16) ; Arvicola terrestris (8) ; Auliscomys pictus (16) ; Calomys lepidus (9) ; C. sorellus (15) ; Chaetodipus penicillatus (3) ; Chinchillula sahamae (2) ; Chionomys nivalis (7) ; Clethrionomys glareolus (8) ; C. rufocanus (4) ; C. rutilus (6) ; Chroeomys jelskii (17) ; Desmodilliscus braueri (2) ; Dipodomys deserti (1) ; D. merriami (11) ; D. ordii (6) ; Discrostonyx groenlandicus (1) ; Eozapus setchuanus (1) ; Epixerus ebii (3) ; Funisciurus lemniscatus (12) ; F. pyrrhopus (13) ; Gerbillus campestris (19) ; G. hesperinus (3) ; Grammomys rutilans (14) ; Heliosciurus rufobrachium (17) ; Hybomys univittatus (14) ; Hylomyscus parvus (7) ; H. stella (14) ; Jaculus orientalis (7) ; J. jaculus (9) ; Lemniscomys barbarus (14) ; Massomys erythroleucus (13) ; Meriones shawi (14) ; Microtus arvalis (5) ; M. montebelli (9) ; Mus spretus (20) ; Myosciurus pumilio (3) ; Ondatra zybethicus (6) ; Pachyuromys duprasi (8) ; Paraxerus poensis (17) ; Perognathus longimembris (1) ; Peromyscus maniculatus (5) ; Phaulomys andersoni (10) ; P. smithii (8) ; Phyllotis osilae (15) ; Praomys tulbergi (15) ; Protoxerus stangeri (7) ;

Psammomys obesus (6) ; Pygeretmus pumilio (10) ; Rhombomys opimus (4) ; Stochomys longicaudatus (13) ; Stylodipus telum (1) ; Tatera robusta (9) ; Taterillus gracillis (6) ; Zapus hudsonius (3) ; Z. trinotatus (3).

APPENDIX II

List of species examined for morphological comparisons :

Acomys cahirinus, Apodemus argenteus, A. speciosus, Arvicola terrestris, Clethrionomys glareolus, C. rufocanus, C. rutilus, Eliomys quercinus, Gerbillus nigeriae, Ichthyomys soderstromi, Jaculus jaculus, Microtus montebelli, Otomys irroratus, Phaulomys andersoni, P. smithii, Praomys sp., Rattus rattus, R. norvegicus, Tachyoryctes splendens, Tatera robusta.