

# Interpretation of the dental pattern of the South African fossil *Euryotomys* (Rodentia, Murinae, and origin of otomyine dental morphology

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## Introduction

Otomyinae, the grooved toothed rats, include two genera: *Parotomys* and *Otomys*. Both are semi-hypsodont and their jugal teeth have plane occlusal surfaces characterized by transverse laminae. The third upper molar and the first lower one show a high number of laminae (3 to 10) in comparison to the other molars. Concerning *Parotomys*, 3 complete laminae and a posterior pillar constitute the third upper molar, the first lower one being composed by 4 laminae, the anterior two ones being linked together in a kidney shape structure. The number of transverse laminae is much more variable in *Otomys*: for the third upper molar it can vary from 4 to 10 and from 4 to 6 for the first lower molar. Otomyinae are exclusively African. *Parotomys* is restricted to the west of South Africa and Namibia; it inhabits semi-arid to arid environments while *Otomys* has a wider distribution, from savannas and mountain grasslands to semi-arid areas. Both are completely vegetarian with a diet mainly composed of seeds, grasses and shoots of shrubs (DE GRAAFF, 1981; SKINNER and SMITHERS, 1990).

For years, many authors (for example ELLERMAN, 1941; SIMPSON, 1945; MEESTER and SETZER, 1971; CHALINE and MEIN, 1979; DE GRAAFF, 1981; LAVOCAT and PARENT, 1985; MUSSER and CARLETON, 1993) have debated about the position of this group within the Muroids because of the particular characteristics of their skull and jugal teeth. The description of *Euryotomys pelomyoides* by POCOCK (1976) from the Mio-Pliocene locality of Langebaanweg (West of South Africa) brought evidence of a close relationship with the Murinae. The recently described *E. bolti* (SÉNÉGAS and AVERY, 1998) from the Early Pliocene locality of Waypoint 160 (Bolt's Farm area, Gauteng Province, South Africa) strengthened the hypothesis of a close affinity of otomyine rodents to Murinae, while several molecular investigations support similar conclusions (CHEVRET *et al.*, 1993; WATTS and BAVERSTOCK, 1995; DUCROZ, 1998). With the discovery of *E. bolti* which appears as a clear missing link between *Euryotomys pelomyoides* and the oldest *Otomys* species, it was confirmed (SÉNÉGAS and AVERY, 1998) that the Otomyinae should not be considered a subfamily but rather a tribe of the Murinae, the Otomyini.

The dental patterns of the jugal teeth of the two species of *Euryotomys* are clearly intermediate between the one of the murines and the peculiar one of the otomyines. *Euryotomys pelomyoides* has a less derived dental pattern than the one of *Euryotomys bolti* (fig. 1). *E. pelomyoides* has a Late Miocene or very Early Pliocene age and *E. bolti*, according to its stage of evolution is dated from Early Pliocene. In the former, there is a weak variability of crown morphology contrary to the latter. The most important characteristics of *E. bolti* are the weak development or the absence of the accessory cusps t1 and t3 on the second and third upper molars and the posterior cingulum (pc) on the first and second lower molars; the laminated pattern is also more developed, and the number of laminae of the third upper molar is variable (fig. 2). If DENYS (1990) has correctly emphasized the fact that there are few lineages of rodents recognized in South Africa, *Euryotomys* and the modern Otomyini nevertheless illustrate one good example of such a lineage. Basically, in murine jugal teeth, cusps are linked together by more or less developed transverse ridges but one can still observe the trace of the murine cusps even at pronounced wear stages. Cusps are much less individualized in the two *Euryotomys* species and, in *Otomys* and *Parotomys*, cusps have completely disappeared, the crown only showing transverse laminae.

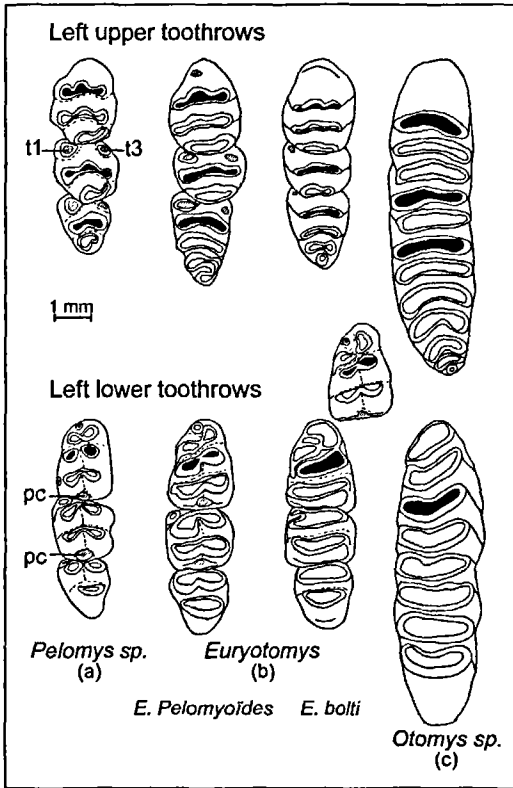


Figure 1  
Dental pattern in Murinae (top: upper tooththrows, bottom: lower tooththrows). a) cusp pattern of *Pelomys* sp., b) intermediate pattern of the two fossil species (*Euryotomys pelomyoides* and *Euryotomys bolti*), c) laminar pattern of a true Otomyini (*Otomys* sp.)

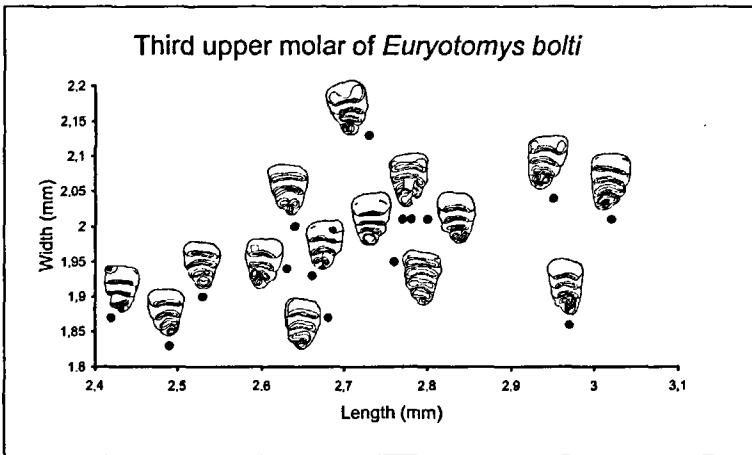


Figure 2  
Morphological variability of the third upper molar in *Euryotomys bolti* (Waypoint 160) superimposed on a length and width diagram.

Some transformations of the dental pattern in rodents can be put in relation with an adaptation to a grazing diet, as for instance the development of hypsodonty and lamination (HERSHKOVITZ, 1962). This question has been recently assessed by VAN DAM (1997) for extant and fossil Murinae. This author used a morphometric analysis to describe and compare dental patterns in order to infer if the diet of extinct species involved grazing adaptation. Considering the above, our primary aim was to use such an approach to determine how the dental morphology of the two species of *Euryotomys* bridges the gap between the patterns of some Murinae already adapted to an abrasive diet and the more derived pattern of Otomyini.

## Material and methods

An analysis has been conducted following VAN DAM's (1997) morphometric approach. Three indices are calculated to quantify differences in dental patterns for extant and extinct Murinae (fig. 3): 1)  $b/a$ : index of relative width of the first upper molar; 2)  $e/d$ : index of relative width of the second lower molar; 3)  $\delta$ : the angle measuring the curvature of the chevrons. This latter index gives at the same time a measure of the degree of development of the posterior cingulum. Such a definition is more appropriate to this work. In VAN DAM's (1997) work, the material was composed by 5 first upper molars and 5 second lower molars for each species. The standardized calculated indices were treated by Principal Component Analysis (PCA). This is a method of graphic representation of the variables (here the indices), where the axes are recalculated in order to express the maximum of variation. In the present analysis, the first component explains more than 80% of the total variation. VAN DAM (1997) precised that this first component is calculated and used as a summary index. The latter analysis indicates that the diminution of relative size of the posterior cingulum associated with the increase of hypsodonty and with the straightening of the chevrons are a good indication of grazing in Murinae.

We are aware that the use of PCA on indices could reduce the amount of information get in processing the raw data. Nevertheless we did so in order to compare our data with those of VAN DAM (1997) who

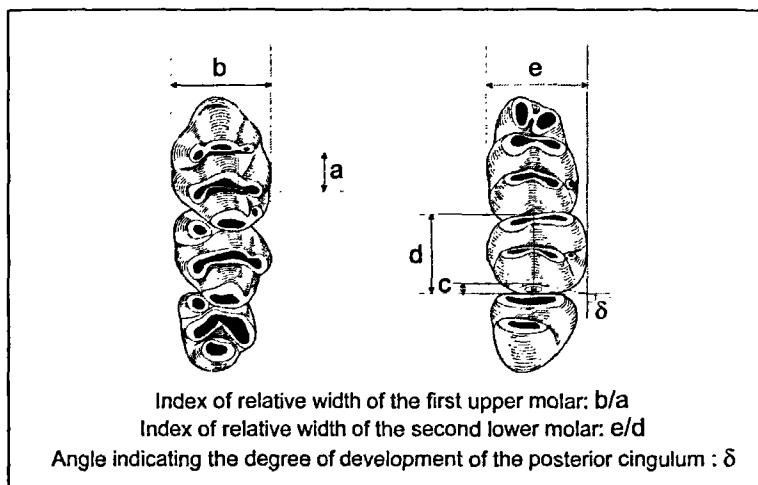


Figure 3  
 Representation of the three indices used ( $e/d$ ,  $b/a$  and  $2\delta$ ) on upper and lower toothrows of *Aethomys* sp. (Murinae), according to Van Dam (1997).

published only indices. We have calculated the three indices for three extinct taxa: *E. pelomyoides*, *E. bolti* and the more recent *Otomys gracilis*. Our sample is as follows: *Eurytomys pelomyoides*, 8 unbroken first upper molars and 12 unbroken second lower molars; *Eurytomys bolti*, 11 unbroken first upper molars and 6 unbroken second lower molars; *Otomys gracilis*, 6 unbroken first upper molars and 5 unbroken second lower molars. A PCA was conducted using the program Statistica v. 4.3 (1993). Henceforth, we adopt the convention by which upper molar is represented by M and lower molar by m.

## Results

The main results are summarized in table 1. Only the first principal axis is represented as it explains most of the variation (with the 3 new taxa included, it reaches 90%). In fig. 4, the score of the first principal component for each species is reported from the lowest to the highest. We note an increase of this value from *E. pelomyoides* to

species	locality	e/d	2δ	b/a	PC1
extant:					
<i>Aethomys kaiseri</i>	Wangeregeze Forest, Uganda	0,94	144	2,4	- 0.10
<i>Apodemus mystacinus</i>	Scalita, Turkey	0,96	130	2	- 0.68
<i>Apodemus sylvaticus</i>	Ethe, Belgium	0,94	131	2	- 0.71
<i>Arvicanthis niloticus</i>	Nakuru, Kenya	1,09	157	2,7	0.89
<i>Daysmys incomtus</i>	Chaya, Nr. Ruchuru	1,2	179	2,8	1.81
<i>Grammomys dolichurus</i>	Namaganga Forest, Uganda	0,95	130	2	- 0.71
<i>Hybomys univittatus</i>	Wangeregeze Forest, Uganda	0,97	129	2,5	- 0.28
<i>Lemniscomys striatus</i>	Queen Elizabeth Park, Uganda	1,11	146	2,7	0.69
<i>Lenothrix canus</i>	Kepong, Malaysia	0,88	120	2,2	- 0.99
<i>Oenomys hypoxanthus</i>	Namaganga Forest, Uganda	0,94	135	2,4	- 0.31
<i>Thallomys paedulus</i>	Stampriet, Namibia	0,96	129	2,1	- 0.62
<i>Thamnomys rutilans</i>	Ghana	0,94	131	2,1	- 0.63
fossil:					
<i>Apodemus gudrunae</i>	Valdecebro 3, Spain	0,89	129	2,1	- 0.83
<i>Huerzelerimys turolensis</i>	Concud 3, Spain	0,89	134	2,2	- 0.64
<i>Huerzelerimys vireti</i>	Puente Minero, Spain	0,96	137	2	- 0.51
<i>Occitanomys adroveri</i>	Los Mansuetos, Spain	0,99	152	2,5	0.32
<i>Occitanomys alcalai</i>	Valdecebro 3, Spain	0,97	139	2,3	- 0.20
<i>Occitanomys sondaari</i>	Tortajada A, Spain	0,96	142	2,3	- 0.16
<i>Parapodemus barbarae</i>	Los Mansuetos, Spain	0,94	129	2	- 0.76
<i>Parapodemus lugdunensi</i>	Lefkon, Greece (M1) and Crevillente 2, Spain (m2)	0,89	132	1,9	- 0.92
<i>Progonomys cathalai</i>	Masia del Barbo 2B, Spain	0,88	127	2,2	- 0.83
<i>Progonomys hispanicus</i>	Masia del Barbo 2B, Spain	0,93	137	2,2	- 0.45
<i>Stephanomys donnezari</i>	Layna, Spain	1,04	144	2,6	0.36
<i>Stephanomys ramblensis</i>	Valdecebro 3, Spain	1,01	143	2,5	0.17
<i>Euryotomys pelomyoides</i>	Langebaanweg, South Africa	1,17	143,54	2,98	1.03
<i>Euryotomys bolti</i>	Waypoint 160, Bolt's Farm, South Africa	1,35	166,68	3,21	2.29
<i>Otomys gracilis</i>	Bridge Cave, Bolt's Farm, south Africa	1,22	180	3,95	2.78

Table 1

Mean values for the 3 indices (e/d, 2δ and b/a) and their first principal component (PC1) for extant and fossil murines. The Van Dam sample (1997) is composed for each species of 5 M1 and 5 m2. For *Euryotomys pelomyoides* we had 8 M1 and 12 m2, for *E. bolti* 11 M1 and 6 m2 and for *Otomys gracilis* 6 M1 and 5 m2.

*E. bolti* and *O. gracilis* with the last two ones having the highest values of all the species studied. Such an increase is interpreted as indicating a diet including more and more grazing and we can associate to this changes in the modifications of the dental pattern in the lineage, the loss of accessory cusps and the disappearance of cusps within the laminae. It can be noted that 3 genera of the tribe Arvicanthini (*Dasymys*, *Arvicanthis* and *Lemniscomys*), thought to be the sister group of the Otomyini (DUCROZ, 1998) have also high values for the first component of the PCA.

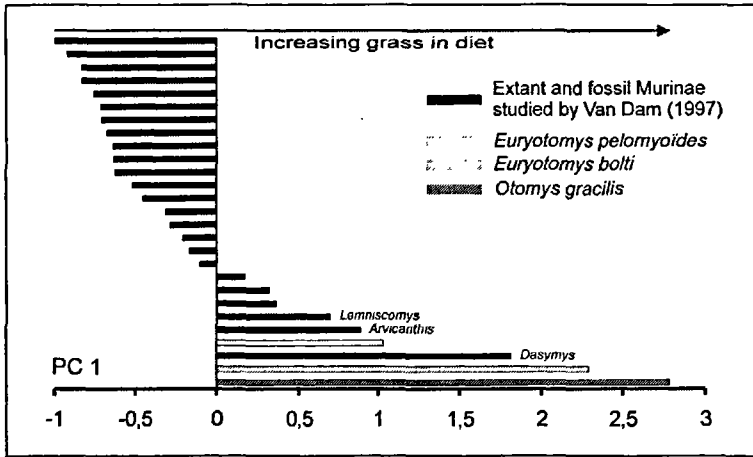


Figure 4  
Ranked values of the first principal component of an analysis on the standardized indices ( $b/a$ ,  $e/d$  and  $2\delta$ ).

## Discussion and conclusion

What drives the evolution towards the *Otomys* pattern? A classical interpretation would advocate an environmental determinism: an environment which became more open offered the opportunity to a murine pre-adapted to a relatively abrasive diet to go further in such a direction as it is shown by the above biometric analysis (fig. 4). As several authors have shown, there were some important climatic events in the period considered here. During the Late Miocene, there was a cooling (KENNETT, 1995), a drying and a progressive replacement of C3 by C4 plants (CERLING *et al.*, 1997). This climatic modification could have induced changes in the vegetation and a possible adaptation of the lineage to an abrasive diet through transformations in the dental pattern. Indeed, we know that the adaptation towards a more grazing diet can result at the dental level in several modifications, as observed in different groups of mammals in particular with the development of hypsodonty in ungulates (VRBA, 1978; JANIS, 1988), associated with a lamellar pattern in some small mammals including rodents (JANIS and FORTÉLIUS, 1988). Chronological data do not

contradict such an hypothesis: Langebaanweg with *Euryotomys pelomyoides* is Late Miocene or Early Pliocene, Waypoint 160 with *E. bolti* is younger but older than Makapansgat Member 1 (about 3.7-3.5 Ma) (PARTRIDGE, 1973; MC FADDEN and BROCK, 1984). Inferred dating based on molecular clock (TAYLOR *et al.*, 1989) indicated that the separation between the Arvicanthini and the Otomyini may have occurred between 8 and 9 Ma (DUCROZ, 1998) or around 7 Ma (CHEVRET *et al.*, 1993) and that the dichotomy (*Parotomys* + *Otomys unisulcatus*)/*Otomys* may have occurred between 5.5 and 6.4 Ma. So the early differentiation of the lineage leading to the Otomyini may have occurred during the Late Miocene. Based on the findings in the two sites of Langebaanweg and Waypoint 160 (Bolt's Farm area), we can also hypothesize that at least at one time, *Euryotomys* was widespread in a large portion of South Africa. Later, some populations could have been restricted to the more arid western part of South Africa. This could have stabilized the morphological variability and led to the group of *Parotomys*. The others, with a wider distribution, could have occupied a more diversified environment and led to the group of *Otomys*. In this case, the wider geographic distribution would have allowed a more important radiation.

We need, of course, more Early Pliocene sites both in West and in East of South Africa to appraise more precisely how this group was distributed during these periods and at what rhythm the dental morphology has changed. We also need more specimens for the different species considered in order to solve the problem of small sample sizes and intraspecific variability. We are now completing the sample for recent material; as for extinct material, we depend on the discovery of new fossils. We also lack fossil *Parotomys*. But the hypothesis we propose could be a basis of work to explain how the group of Otomyini has differentiated.

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