

## Diet and dental morphology of two coexisting *Aethomys* species (*Rodentia*) in Mozambique. Implications for diet reconstruction in related extinct species from South Africa

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The examination of dental morphology of coexisting modern *Aethomys namaquensis* Smith, 1834 and *A. chrysophilus* de Winton, 1896 from Mozambique, whose diet has been studied in the field, shows that the development of stephanodont crests and the multiplication of supplementary cusps on labial side of the lower molars is associated with a mainly vegetarian diet. To the most specialized dentition corresponds the most specialized diet. The application of these results to two coexisting *Aethomys* species from the fossil site of Langebaanweg (Pliocene, South Africa) allows to conclude that their dental differences correspond to different paleodiets. Moreover, the *A. namaquensis* lineage shows during Plio- Pleistocene times a shift in dental morphology corresponding to an evolution toward a more vegetarian diet. The comparative tooth anatomy seems to be a reliable method for determining diet of extinct rodents species, their close or less close relatives, when diets of extant species are precisely known.

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### Introduction

Mammalian paleontologists have in many cases only the remains of teeth at their disposal. This is usually sufficient to determine their systematic position. Another aim of palaeontologists is to interpret paleodiets from dental morphology in order to reconstruct the way of life of past mammals, and also to find the significance of some evolutionary trends. For this purpose, comparative anatomy is one of the methods available. Although, it has been demonstrated, for some large mammals, that tooth morphology does reflect diet (Kay and Hylander 1978), this assertion has not yet been verified for many small mammals, and among them rodents. However, in an actualistic approach, van der Meulen and de Bruijn (1982) have attempted to extrapolate from dental morphology and ecology of the living, the diet and biotope of extinct Miocene *Gliridae* species. Such works are very rare, especially for tropical rodents whose habits and diet are poorly known, while the knowledge of the rodent fossil record is increasing in addition to its use in palaeo-

ecological interpretations of fossil sites. This has led to the description of numerous evolutionary dental trends, some being well known (Stehlin and Schaub 1951, Misonne 1969, Michaux 1971, Jaeger 1983). In most of these, hypothesis concerning the progressive acquisition of a more specialized diet has been proposed but not tested due to the extinct status of the concerned genera or species.

It is generally admitted that today the climatic conditions of tropical Africa approach those which prevailed in Europe during Cenozoic time. Therefore, the precise knowledge of diet and related dental patterns exhibited by some modern rodents of Africa would be of interest for the interpretation of some dental patterns exhibited by extinct rodents. Further, this could contribute to test hypotheses concerning evolutionary tendencies both in African and European rodents lineages during Neogene.

In Africa, very few field studies have been devoted to the diet of rodents. Gliwicz (1985, 1987) has conducted ecological study of a rodent community of an African dry savanna of Mozambique. This ecological study gave an interesting example of niche segregation between two species of the genus *Aethomys*: *A. namaquensis* Smith, 1834 and *A. chrysophilus* de Winton, 1896. Evidence was proposed for differences in habitat and diet, emphasized during the dry season. More than 50 skulls of these *Aethomys* were prepared. The careful examination of this material provides the opportunity to compare the diet and dental morphology in this genus. Moreover, many fossil species of *Aethomys* have been found in Plio-Pleistocene sites of East and South Africa (Denys 1990a, b). Two cohabiting fossil species of *Aethomys* have been described from the Langebaanweg site in South Africa by Denys (1990a). Their morphology places them very close to modern *Aethomys* species studied by Gliwicz (1985, 1987). Consequently, the aim of this paper is first to characterize the dental morphological features of the modern species of *Aethomys* related to their diet and second to apply the results to the fossil species of the Langebaanweg site. The latter results could provide further insights on the evolution of the genus in South Africa during Plio-Pleistocene times. The characterization of dental pattern related to diet in *Aethomys* could bring new elements to the interpretation of some of the extinct Miocene murid genera of Europe and Africa.

#### Systematics and phylogeny of the genus *Aethomys*

*Aethomys*, the bush rats are *Murinae* species spread all over tropical Africa in the savannah regions. Generally, they have the external aspect and size of *Rattus rattus*. According to the last revision of the genus (Davis 1975), there are at least 9 recognized species of *Aethomys* Thomas, 1915. The two species studied by Gliwicz (1985, 1987) and found in Mozambique both belong to the Zambezian savannah domain and have been characterized by Davis (1975). They are: *A. chrysophilus* and *A. namaquensis*. Davis (1975) has created a sub-genus *Micaelamys* to include species showing an accessory anterior cusp on the lower M<sub>1</sub> (e.g. *A. namaquensis*).

Denys (1990a, b) described the Langebaanweg Pliocene species and researched the phylogenetic relationships between fossil *Aethomys* species and modern ones.



*A. modernis* Denys, 1990 of Langebaanweg has relatively modern characters, and could have been the ancestor of *A. chrysophilus*. *A. adamanticola* Denys, 1990 from Langebaanweg retained more primitive characters, some of them being found both in *A. namaquensis* and *A. hindei*, a species from East Africa.

#### Diets in *Aethomys*

Previous studies on diet of *Aethomys* spp. were lacking in precision. In South Africa, *A. namaquensis* would be vegetarian (Shortridge 1934), omnivorous (Roberts 1951) or granivorous (Smithers 1971). In South Africa, Smithers (1971, 1983) reports *A. chrysophilus* as a seedeater, feeding on grass and seeds, but gnawing also on nuts, fruits. Shortridge (1934) states they subsist on grain but are omnivorous. According to Jacobsen (1977) they also feed on seeds of *Hibiscus engleri*. In central Transvaal, they feed on seeds of *Diodea natalensis* and *Pavonia transvaalensis* (Jacobsen 1977). In East Africa, Vesey-Fitzgerald (1966) reported *A. chrysophilus* feeding on the fallen fruits of *Combretum* and *Grevia*. More generally, for Kingdon (1974), *Aethomys* belongs to the ancestral group of omnivorous african murine ("Rattus division" of Misonne 1969) and among this group, *A. namaquensis* would be the species linking the ancestral group with a special african radiation of herbivorous murids (Misonne 1969).

Gliwicz (1985, 1987) has shown that in Mozambique, *A. namaquensis* was found in rocky slopes of the hills while *A. chrysophilus* was more widely associated with grassy lower zones. During the dry season, the diet of *A. namaquensis* was mostly composed of green parts of plants (no insects at all have been found) while *A. chrysophilus*, to the contrary, fed on starchy vegetarian food and insects. On average, during all the year *A. namaquensis* was more specialized in plants while *A. chrysophilus* ate in equal parts insects, starchy food, (deshy fruits, starch of seeds and bulbs), green plants (leaves and stems).

#### Material and methods

The dental morphology of the specimens attributed to *A. namaquensis* and *A. chrysophilus* that had been collected by Gliwicz in Mozambique has been studied. Their diet was studied in the field by analyses of the stomach contents under microscope of high magnification (Gliwicz 1985, 1987). Skulls of individuals collected and studied by Gliwicz are now housed at the Institute of Systematics and Evolution of Animals in Kraków (Poland). Comparisons have been made successively with modern *Aethomys* material from the Transvaal Museum, the Los Angeles County Museum, the Natural History Museum of London, the Natural History Museum of Paris and with fossils from the South African Museum (Cape Town, South Africa). The dental nomenclature is adapted here from Denys *et al.* 1992.

#### Results

##### *A. namaquensis* and *A. chrysophilus* from Mozambique

Young individuals (stages of molar wear 1 to 3), show a difference in size and surface of the molars between *A. namaquensis* and *A. chrysophilus* (Fig. 1). *A. na-*

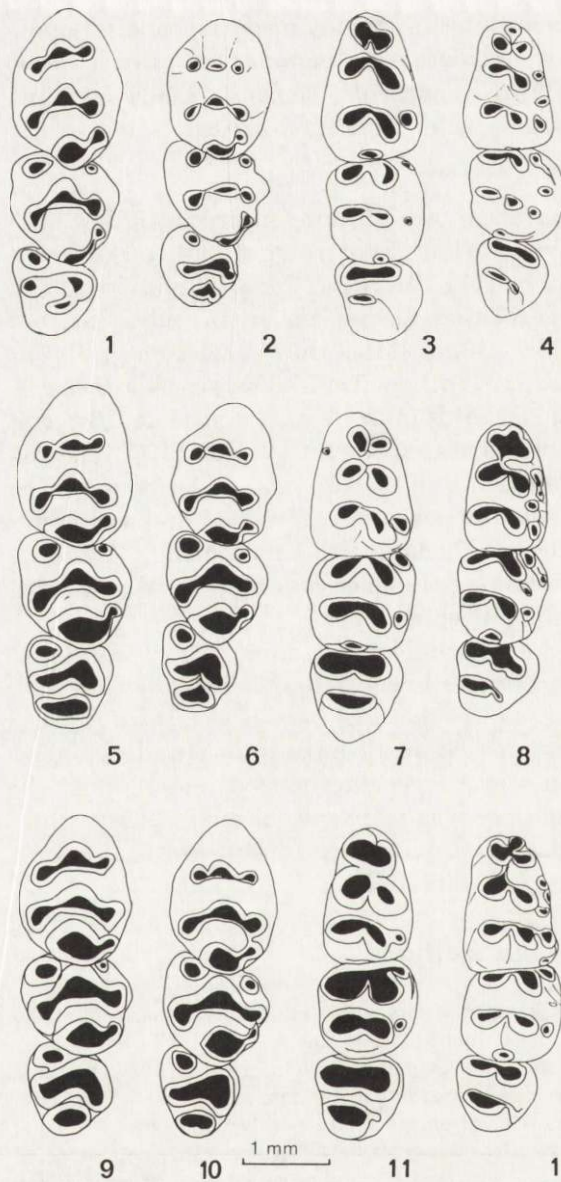


Fig. 1. Dental patterns of *Aethomys chrysophilus* and *A. namaquensis*. Specimens collected by Gliwicz (1985, 1987) housed at Inst. Syst. Evol. Kraków (Poland). Top row: molar rows of *A. chrysophilus* (1, 3, M/10177/90) and *A. namaquensis* (2, 4, M/10173/90) from Mozambique at wear stage 1 (the upper  $M^3$  are germs). Middle row: Wear stages 2-3, *A. chrysophilus* (5, 7, M/10151/90) and *A. namaquensis* (6, 8, M/10181/90). Bottom row: wear stages 4-5 *A. chrysophilus* (9, 11, M/10151/90) and *A. namaquensis* (10, 12, M/10181/90).

*namaquensis* has smaller molars than *A. chrysophilus*, but in stages of wear 4-5 the size difference decreases.

Another difference between both species is the disposition of the cusps. They are higher, more bented towards the back of the teeth, and more fused in *A. chrysophilus* than in *A. namaquensis*, in where they are better individualized. The cusps of the first lobe of the  $M^1$  are aligned in a transverse lamina in *A. namaquensis*, while in *A. chrysophilus* the more posterior t1 gives a convex outline to the first lobe.



In both *Aethomys* species examined here there is no strong development of stephanodont crests. The link between t6 and t9 may occur at very worn molars, earlier in *A. namaquensis* than in *A. chrysophilus*. On the M<sub>1</sub>, the longitudinal crest linking the prelobe to the first lobe, appears earlier in *A. namaquensis* (stage 2–3) than in *A. chrysophilus* (no link appearing or never before stage 5) (Fig. 1).

*A. namaquensis* is clearly different from *A. chrysophilus* in the lower molars. It has an accessory anterior cusp or tma, which gives a different disposition of the anterior main cusps of the prelobe and it has also a big labial cingulum upon which numerous cingular supplementary cusplets develop. *A. chrysophilus* has a less developed, more discontinuous cingulum, and shows only cusplet cv5 (Fig. 1). The development of the posterior cingulum on the M<sub>1-2</sub> is subject to high variability. The acquisition of numerous supplementary cusplets is considered as a derived character (Denys *et al.* 1992). By contrast, the fossil specimens from the Plio-Pleistocene sites of South Africa attributed to *A. cf. namaquensis* do not show so many supplementary cusplets.

#### Comparison with non-Mozambian *A. namaquensis* and *A. chrysophilus*

A comparison with other modern representatives of both species has been undertaken in order to verify whether the Mozambique populations of *Aethomys* show only local modifications of their molar structure or are similar to other ones. Comparison with other South African populations shows no important differences in the dental patterns. However, some *A. chrysophilus* representatives show more longitudinal crests in a population from Zimbabwe (MNHN collections). The systematics of the latter species has not been revised since more than 40 years, and the observed differences in the Zimbabwe population may point to the fact that they belong to another species. The development of the supplementary cingular cusplets on the lower molars of other *A. namaquensis* representatives is identical to the ones of the Mozambique population.

### Discussion

Differences in molar morphology are observed between the two *Aethomys* species living in the same community in Mozambique. These differences are similar to those observed between the same species in South Africa. The question now is which of these differences is related to diet?

*A. namaquensis* shows many supplementary cingular cusplets, bunodont cusps, and longitudinal crests appearing relatively early, all these characteristics are considered as derived (Misonne 1969, Michaux 1971). On the contrary, *A. chrysophilus* has retained a more primitive dental pattern. According to Gliwicz (1985, 1987) in Mozambique, *A. namaquensis* is primarily a folivore and grasseater. The latter feature could explain the existence of small "stephanodont" crests, occurring earlier, in *A. namaquensis* contrary to *A. chrysophilus*. During the dry season, *A. namaquensis* does not eat any insects in contrast to *A. chrysophilus*, which has a

wider spectrum of food. The development of longitudinal crests and of supplementary labial cingular cusps can be put in relation with a mainly vegetarian diet. As a matter of fact, the development of stephanodont crests reaches a maximum in another purely vegetarian murid of Africa: *Thallomys*, the diet of which being strictly vegetarian (Kingdon 1974). Similarly, *Thallomys* has a well developed labial cingular margin, but less supplementary cusplets on it.

*A. chrysophilus* has a standard murine dental pattern, which is rather close to the one of *Rattus rattus*, well known to be omnivorous. In Mozambique, Gliwicz (1987) found a less specialized diet for *A. chrysophilus* compared to *A. namaquensis*, especially during the dry season.

In summary, the present study shows that bunodonty associated with stephanodonty indicate a vegetarian diet.

#### Application to fossil *Aethomys* from Langebaanweg

The Langebaanweg site (Pliocene, 5 Myrs, Cape Region, South Africa) has yielded in the same levels well-preserved dental remains of two extinct *Aethomys* species (Denys 1990a, b) (Fig. 2). The two species show different molar morphology and probably belong to different lineages. The first species, *A. adamanticola*, is the larger of the two and is characterized by large and low cusps, relatively columnars. There is no tma on the lower molar, the cingular margin is discontinuous with two cusps. Longitudinal crests are absent on the lower molars at early stages of wear and there is no link t6-t9. This structure of the cusps is rather primitive and corresponds to a relatively generalized dental pattern. In regard to the previous results on modern *Aethomys*, it is highly probable that *A. adamanticola* would have been omnivorous like in the modern *A. chrysophilus*. The second fossil species of Langebaanweg is *A. modernis*. This smaller species shows more derived dental characters like the tma, the existence of a link prelobe – first lobe on M<sub>1</sub> and an early development of the crest between t6 and t9. *A. modernis* does not show such a developed labial cingular margin as the modern *A. namaquensis*. In *A. modernis*, the tma of the prelobe is rather small and the posterior cingulum on

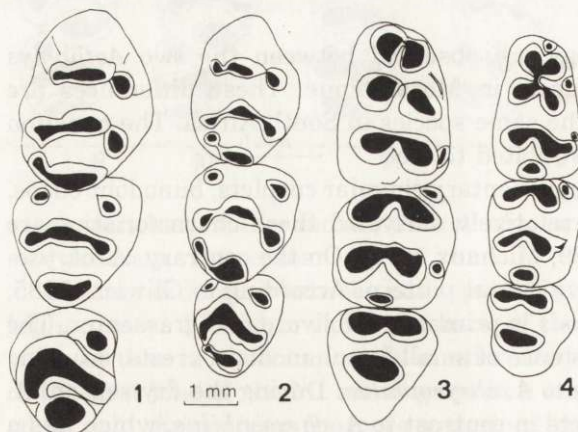


Fig. 2. Dental patterns of the two fossil species of Langebaanweg, reconstituted dental rows: (1) *A. adamanticola* (SAM PQL 14828 M<sup>1-2</sup>, 42570 M<sup>3</sup>), (2) *A. modernis* (SAMPQL 14828 M<sup>1</sup>, L33814 M<sup>2-3</sup>); (3): *A. adamanticola* (SAM PQL 50606), (4): *A. modernis* (SAM PQL 42987). All specimens come from the Pellet Phosphorit Member.



M<sub>1-2</sub> is important, while in *A. namaquensis* the latter is absent on M<sub>1</sub>. This could be an indication that the fossil *A. modernis* from Langebaanweg had a rather more generalized diet than is the case for the modern *A. namaquensis*, but was more vegetarian than *A. adamanticola*. It is possible to make derive modern *A. namaquensis* from both Langebaanweg species. The development of bunodonty, and of an enlarged cingular labial margin with many supplementary cusplets, among the *A. namaquensis* lineage could be the result of a shift toward a mainly vegetarian diet. The succession between the Plio-Pleistocene fossils of the Transvaal in South Africa and the modern forms is not continuous, and, in this region there is now an important gap in the fossil-record for the last 1.5–1 Ma. The first modern representatives of *A. namaquensis* and *A. chrysophilus* appears around 3.7 Ma (at Makapansgat, South Africa; Pocock 1987). None of the Plio-Pleistocene fossils of the well-documented faunas of South Africa show a similar development of the supplementary cusps of the cingular margin of the M<sub>1</sub> as the modern *A. namaquensis*. The trend toward the development of bunodonty in *A. namaquensis* could result from a late change in the diet, which occurred after 1.5–1 Ma.

### Conclusion

It is shown here that the ecologically most specialized *A. namaquensis* shows the most specialized dentition. The strong bunodonty of the dentition of *A. namaquensis* is related with mainly vegetarian diet. The presence of slightly developed stephanodont crests in *A. namaquensis* is also an indication of the vegetarian diet. *A. chrysophilus*, from Mozambique, do not show any longitudinal crests. The generalized dental pattern of *A. chrysophilus* can be related to an omnivorous diet similar to that found in *Rattus rattus*.

The two fossil *Aethomys* form Langebaanweg show different dental morphologies indicating different diets. One of the lineage leading to *A. namaquensis* shows a morphological shift that can be interpreted here has the acquisition of a mainly vegetarian diet.

For rodents, dental morphology can be a tool for a better understanding of paleodiets, as well as for the understanding of evolutionary differences in dental morphology between species. This method must be supplemented by other techniques, such as Sr content, or isotopes ratios, or microwear examination, despite some limitations noted elsewhere (Dauphin and Denys 1992). The African rodents diets have been very poorly investigated and further studies may provide important data for a better understanding of their extinct relatives and their evolution.

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