

MOLERATS (BATHYERGIDAE, RODENTIA) IN
SOUTH AFRICAN NATIONAL PARKS: NOTES ON
THE TAXONOMIC “ISOLATION” AND
HYSTRICOMORPH AFFINITIES OF THE FAMILY

G. DE GRAAFF

Division of Research and Information

National Parks Board

P O Box 787

Pretoria

0001

Abstract – The history of classification of Afrotropical molerats is reviewed and an assessment is made of the supposed taxonomic “isolation” of the molerats (bathyergids) by considering morphological features in the skull, post-cranial skeleton, reproductive organs and myology which collectively point to hystricomorph affinities in contrast to a myomorph relationship which is often postulated.

Introduction

During the past two decades it has become increasingly clear that intensive taxonomic research on southern African mammals is a necessity. Our knowledge pertaining to many orders and families is often haphazard and scattered and this has led to taxonomic uncertainty in many groups. It is unlikely that many new species will be discovered in the area to the south of the Cunene River in the west and the Zambezi River in the east. A re-interpretation synthesis of faunistic data hitherto gained is now required.

Past research has predominantly been directed to the larger and more conspicuous mammal species which occur in southern Africa while the smaller mammals were neglected to a considerable extent. However, there has been a revival of interest in the smaller mammals since 1950 and the possibility of interesting, rewarding and important research has become evident. An example of this approach is afforded by the activities of the Medical Ecology Unit of the South African Institute for Medical Research in Johannesburg, in order to determine *inter alia*, the rodents which act as vectors in the distribution and transmission of plague (De Meillon, Davis & Hardy 1961). At the same time valuable taxonomic information is gained. On a more theoretical basis, the revision of shrews done by Meester (1963) on the southern African forms of *Crocidura* is a good example of the new research attitude towards the smaller mammals. Similar revisions of other species will eventually lead to a workable, practical taxonomy, a necessity which is still lacking for many small mammals in

southern Africa. It is understood that taxonomic revisions can not be undertaken for many mammalian groups as yet, due to the absence of available study material, lack of relevant information and other gaps in our knowledge.

This dearth in our apprehension, particularly as far as rodents are concerned, is probably due to the fact that the taxonomy of this order is also still in a fluid state. In addition, information pertaining to ecology, ethology and palaeontology of South African rodents is meagre. Absence of this kind of data is especially noticeable in the case of fossorial rodents such as the molerats also colloquially known as bathyergids.

The molerats (Order Rodentia, family Bathyergidae) are typical mammals of the Afrotropical Faunal Region. Their fossorial way of life has developed certain specializations which are also found in other unrelated fossorial rodent families including the murine Spalacidae and sciurid Geomyidae. These families all show suppressed development of the eyes, enlarged incisors and well developed claws adapted for digging (Ellerman 1940). As far as the molerats are concerned, they apparently have relatively unknown affinities (Simpson 1945) and it appears that they have become fossorial secondarily which has resulted in specific adaptive features.

External anatomical features which characterize the five living genera within the Bathyergidae are: the conspicuous incisors projecting beyond the closed lips; small eyes; the reduction of ear pinnae to a fringe of skin surrounding the external auditory meatus; short limbs and tail and a tendency for reduction in the pelage covering the body which reaches its culmination in the nearly naked sandpuppy *Heterocephalus*, presently occurring only in Somalia and Kenya. These features are modifications for a fossorial way of life which has been adopted by the genera *Bathyergus*, *Heliohobius*, *Heterocephalus*, *Georychus* and *Cryptomys*.

Sclater (1901) initially discussed the molerats occurring in southern Africa. Allen published his wellknown checklist for African mammals in 1939. Roberts (1951), in his already classical work, "The Mammals of South Africa" described the various genera, species and subspecies of molerats which he thought occurred in southern Africa, while this in turn was followed by other revisions of southern Africa mammals by Ellerman, Morrison-Scott & Hayman (1953), Meester, Davis & Coetzee (1964) and Meester & Setzer (1971). These publications all summarized and interpreted the then existing comprehension of southern African mammals from a taxonomic point of view. This has led to a diversity of interpretations, especially as far as the validity and status of the different species and subspecies are concerned.

Ellerman *et al.* (1953) lump seemingly different species of molerats together while Roberts (1951) has possibly oversplit the molerat species and subspecies to too great an extent. An interim assessment of the taxonomy of southern African mammals was attempted by Meester *et al.* (1964) and as far as the molerats are concerned, the interpretation given by Ellerman *et al.* (1953) was largely adopted. This gave rise to the compilation of "The Mammals of Africa: An Identification Manual" edited by Meester & Setz-

er (1971) and a taxonomic revision of the molerats based on Pan-African data was attempted and compiled by De Graaff as a contribution to the identification manual.

Three genera and four species of molerats are encountered in the Republic of South Africa. These are the Cape Dune Molerat *Bathyergus suillus*, the Namaqua Dune Molerat *B. janetta*, the Blesmol *Georychus capensis* and the Common Molerat *Cryptomys hottentotus*. Of these species *C. hottentotus* is ubiquitous in its occurrence throughout South Africa and consequently occurs in all national parks, with the possible exception of the Augrabies Falls National Park. Why this should be so, is not clear. As far as national parks go, *Bathyergus suillus* and *Georychus capensis* are encountered in the Tsitsikama Coastal National Park only. The distribution of *Bathyergus janetta* (limited to the South Western Cape Province) falls outside any area hitherto proclaimed a national park (De Graaff 1974).

This paper discusses some questions resulting from different interpretations of morphological features while contributing to taxonomic and phylogenetic uncertainties which pertain to the molerats. It is a useful exercise to review the history of classification of these rodents and to determine whether in fact they are "isolated" taxonomically as is often being claimed whilst their apparent hystricomorph affinities are reviewed and accentuated.

The classification of the Bathyergidae: a review

Wood (1955) states that the classification of rodents is inadequate and that there are two general philosophies underlying present arrangements:

- (i) A theoretical ideal, in which the classification should reflect interrelationships of the animals involved implying the use of certain criteria which are not agreed upon by all authorities on the species concerned. Consequently, forms of uncertain relationship are either grouped together and assigned to a position in a classification in a more or less arbitrary manner, or they are indicated as *incertae sedis*. The latter point of view has been advocated by Simpson (1945).
- (ii) The other alternative is a classification involving the use of key characters resulting in a system based on different criteria into which all the different forms can fit. This approach has been used extensively by Ellerman (1940). According to Wood (*op. cit.*) this solves the problem as to where to place all the various families of rodents, but leaves many of them in positions that do not seem to be correct from a phylogenetic point of view.

An obvious deficiency in evaluating the phylogenetic pathways of rodents in general is the paucity of palaeontological data, especially with a sharp break in rodent history at the Eocene-Oligocene boundary. This situation still holds, particularly for African rodents where the fossil histo-

ry of rodents is poorly known (De Graaff 1961). Resulting from his detailed palaeontological work, Wood stresses the fact that parallelism in rodents extends to the structure of the infraorbital region as well as to the teeth and these results indicate that the whole basis of rodent classification must be derived and that no classification based on key characters "... is likely to agree with one based on the phylogeny of the order". In his opinion one is not to rely on morphological criteria alone until it has been demonstrated by phylogenetic studies to be valid. In Wood's classification he stresses the occurrence and development of similar physical features independently in diverse and geographically isolated groups of rodents.

In a subsequent paper, Wood (1958) poses the question "Are there Rodent Suborders?", a problem which earlier on also interested other authorities like Kretzoi (1943). The latter author divides the rodents in but two suborders while at the other extreme the order is divided into seven suborders (Wood 1955) which could perhaps be increased to as many as eleven, according to a suggestion by Lavocat (1956). If this divergency of opinion is the position in the suprageneric ranks of rodents (for details the reader is referred to papers quoted above), the chances are that the correct systematic position of the molerats is also likely to be far from settled.

The affinity of the Bathyergidae with the hystricomorphs has often been questioned. Initially, the molerats were placed in a separate group under the Muridae (Myomorpha) by Waterhouse in 1838. In 1855 Brandt first proposed the subdivision of the simplicitate rodents into the three classical suborders also referred to as "waste-paper baskets" by Ellerman (1940). This subdivision into Sciuromorpha, Myomorpha and Hystricomorpha was based on the structure and insertion of the masseter muscle of the jaw musculature. This system has also been called the "classical" arrangement by Simpson (1945). Brandt referred to the molerats as "Spalaces subhystriciformes" and following Waterhouse also placed them under the Myomorpha.

This classification of Brandt was largely followed by Alston (1876) but he merged the molerats with the spalacids in a single family, also under the Myomorpha. Thomas (1896) placed the molerats as a separate family under the Myomorpha (as Waterhouse, Brandt and Alston have done previously) "... but divorced them from the spalacids" (Landry 1957), with whom they were provisionally placed by Alston. Landry points out that although Waterhouse, Brandt and Alston recognised the hystricognathid jaws of the bathyergids, they were apparently more impressed "... by the habitus resemblances of these forms to other burrowing rodents and also by the fact that the tibia and fibula of the bathyergids are fused distally as in the myomorphs", while these bones are separate in the sciuromorphs and hystricomorphs. These facts presumably also prompted Thomas to place them under the myomorphs. According to Ellerman (1940), this classification of Thomas was admittedly nothing more "... than a rearrangement and bringing up to date of an earlier classification of Alston," and that it may be discarded as unnatural as being based on the fusion or separation of the tibia and fibula.

Tullberg (1899) was the first to amass evidence in favour of placing the molerats with the hystricomorphs. Tullberg believed that the classical threefold arrangement of the rodent order was incorrect and he classified the rodents on a different basis to that of Alston or Thomas. He split the rodents into two major groups, the Tribus Sciurognathi and Tribus Hystricognathi respectively, based on the inflection or lack of inflection of the angle of the lower jaw. These categories were again divided into Subtribus Sciuiromorphi and Subtribus Myomorphi on the one hand and Subtribus Hystricomorphi and Subtribus Bathyergomorphi on the other based on the structure of the infraorbital foramen and the masseter muscle (Wood 1955). This is perhaps the best classification of the order that has been proposed (Ellerman 1940). Landry (1957) points out that Tullberg was the first person to provide sound evidence for placing the bathyergids with the hystricomorphs, for it "... was he who pointed out that these forms possess in common such important features as the fused malleus and incus, the sacculus urethralis, the extension of the internal pterygoid muscles through the pterygoid fossa into the orbit, as well as the hystricognath jaw". Since the scaphoid and lunar bones of the wrist are unfused in molerats (as in primitive sciuiromorphs) and since the infraorbital foramen is not enlarged, Tullberg concluded that the molerats must have originated near the very base of the hystricomorph line and hence deserved equal rank with the three "classical" suborders.

The next classification which may be considered at this point was the one proposed by Weber (1904/1928). In this case, the bathyergids are listed as a separate group, the "tribus" Bathyergoidea, together with nine others of equal rank (including the Haplodontoidea, Sciuroidea, Castoroidea, Geomyoidea, Anomaluroidea, "Myoxoidea", Dipodoidea, Myoidea and Hystricoidea. Ellerman (1940) finds that as far as the superfamily grouping is concerned, this is to be an acceptable classification. However, Weber indicates no closer affinities or possible relationships of the bathyergids with any other rodents.

Weber's classification was followed by a scheme proposed by Miller & Gidley (1918) who also abandoned the classical triple subdivision and divided the rodent order into five superfamilies, based on the zygomasseteric structure. The molerats were credited with superfamily rank, the Bathyergoidea, equal in rank to the Sciuroidea, Muroidea, Dipodoidea and Hystricoidea. Ellerman (1940) states that this classification attends much more to detail characters than either those of Winge or Weber. As was the case in Weber's classification Miller and Gidley also refrained from indicating possible affinities of the bathyergids.

In 1924 Winge proposed placing the molerats as a tribe "Bathyergini" under the Hystricidae (=Hystricomorpha). Apart from the Hystricidae, Winge proposed to divide the Order into eight other families, i.e. the "Haplodontidae", Anomaluridae, Dipodidae, "Myoxidae", Muridae, Sciuridae, "Sacomylidae" as well as the Leporidae (now placed under the suborder Duplicidentata or the Order Lagomorpha). Ellerman (1940) feels that Winge's classification of the Hystricidae is unnatural "... with the in-

clusion of the Bathyergidae". As a basis for his classification, Winge used the structure of the paroccipital process, which is a very variable character even within a genus. Winge also appreciated the virtual impossibility of dividing the rodents into three or four groups "... with any likelihood of the arrangement being correct" (Wood 1955) and so split them into nine groups (Ellerman *op. cit.*) attempting to avoid the difficulties of the classical approach (Wood *op. cit.*)

In his well known *Checklist of African Mammals*, Allen (1939) treated the molerats as a separate family. Shortly after the appearance of this work, Ellerman (1940) attempted to combine as far as possible various morphological criteria which appeared (to him) to be correct in the classifications of Thomas, Tullberg, Weber, Miller and Gidley and finally Winge, although he followed Tullberg in his major groupings. Consequently, by 1940 the molerats were interpreted as a major subdivision (Bathyergomorph series) together with the Hystricomorph series of the Hystricognathi co-ordinate, with the Sciurognathi as counterpart.

Simpson (1945) again classified the rodents according to the Brandtian three-fold scheme and he placed the bathyergids *incertae sedis* within the hystricomorphs. He points out that although these animals are fairly abundant and reasonably well known, there are few more doubtful points of classification than the affinities of the bathyergids. "Everyone agrees that they are extraordinarily isolated among rodents, and those who commit themselves further agree that if they have any special, though distant, affinity it is with the hystricomorphs."

Romer (1958) is the only authority who places the molerats under the Sciuromorphs and this proposal is conceivably based on the seemingly ischyromyid nature of the bathyergid-like Oligocene fossils, *Tsaganomys* and its companion genus *Cyclomytus* known from Mongolia. Landry (1957), however, states that as far as he was aware, no one has grouped the bathyergids with the sciuromorphs. Romer included them with the sciuromorphs "... for want of any better place to put them", but pointed out that they "... are sometimes associated, rather dubiously, with the hystricomorphs because they show an out-turned angular region of the lower jaw seen in characteristic members of that suborder". Romer states, however, that there are no other features suggesting such relationships and "... the diagnostic masseteric structures are of the primitive type seen only in the early sciuromorphs". Romer also points out that these animals are not closely related to any other group of rodent and they provisionally be interpreted as a superfamily Bathyergoidea within the suborder Sciuromorpha (Romer 1958).

Lavocat (1951) reverts back to the dual classification proposed by Tullberg and he emphasizes the structure of the mandible. Although "... he presents only a partial classification of the order, it is definitely an advance in separating the "Hystricognathes" into "Orthohystricognathes: Rongeurs sud-américains" and "Parahystricognathes: Formes palaearctiques et africains" (Wood 1955). The bathyergids are consequently placed under the latter group.

Roberts (1951) suggests separate suborder rank for the bathyergids, the Bathyergomorpha, equal to the Hystricomorpha, Sciuromorpha, Dipidomorpha and Myomorpha in status. Roberts gives no indication whether this term may have been used previously elsewhere (Wood 1955).

Schaub (1953) discussed the classification of rodents with emphasis on the hystricomorphs. He disagrees with other authorities who use characters like the infraorbital foramen and masseter muscle only as the basic criteria for classification. Schaub indicates that dental characters may also be used which may indicate relationships. He proposed the erection of a new suborder, the Pentalophodonta to include all forms with teeth having a five-crested ancestry. This suborder is in turn divided into two infra-orders, the Palaeotragomorpha and Nototrogomorpha. The Nototrogomorpha contains the South American hystricomorphs (=suborder Caviomorpha (suggested by Simpson in 1950) and erected by Wood & Patterson (1959) in a review of the South American rodents). The Palaeotrogomorpha contains the superfamilies Theridomyoidea, Hystricoidea and Castoroidea, together with a series of families, *incertae sedis*, including among others, the Bathyergidae, Spalacidae and Rhizomyidae (Wood 1955).

Another classification of rodents has been attempted by Wood (1955). Wood retains the classical suborders of Brandt, *i.e.* Sciuromorpha, Myomorpha and Hystricomorpha and adds the Theridomyomorpha and Caviomorpha as new suborders. Likewise the bathyergids are retained as a separate suborder, the Bathyergomorpha, as was suggested (possibly for the first time) by Roberts (1951).

Landry (1957) provided additional data on the classification of the bathyergids. He interprets them as hystricomorph rodents and accepts the splitting of rodents into sciurognath and hystricognath lineages as was proposed by Tullberg. Summarizing the Old World Hystricomorpha, he credits the molerats with superfamily rank (Bathyergoidea) containing a single family (Bathyergidae) with two subfamilies, the Bathyerginae (including *Bathyergus*, †*Cyclomytus* and †*Tsaganomys* as genera) and the Heterocephalinae (with *Cryptomys*, *Georychus*, *Heliophobius* and *Heterocephalus* as genera). The other Old World hystricomorph superfamilies which he considers of equal rank to the Bathyergoidea, are the Ctenodactyloidea, Petromyoidea, Thryonomyoidea and Hystricoidea.

It is clear that since 1838 three main tendencies can be traced relevant to molerat classification. They were either treated (i) as an isolated group or alternatively were placed (ii) either with the myomorphs, or (iii) with the hystricomorphs and in one isolated instance, with the sciuromorphs. Furthermore, even in the more recent literature there is still no general overall agreement where the molerats are to be placed taxonomically. It is not unreasonable to assume their stronger hystricomorph affinities and for the purposes of the present paper, they are considered as such (see below for a brief discussion of anatomical features pointing to their hystricomorph relationship). However, Simpson (1945) expressed the following warning which should also be borne in mind: "While awaiting better evi-

dence, it is considered inadvisable to base a major division of rodents on these few aberrant genera". (Table 1).

Table 1

Tendencies in the classification of moles

THE BATHYERGIDS CONSIDERED AS			
(a) An isolated group	(b) Sciuriforms	(c) Myomorphs	(d) Hystricomorphs
		Waterhouse (1838) Brandt (1855) Alston (1876) Thomas (1896)	Tullberg (1899)
Weber (1904) Miller and Gidley (1918)			Winge (1924)
Allen (1939)			Ellerman (1940) Simpson (1945) <i>inc. sedis.</i>
Roberts (1951)	Romer (1958)		Lavocat (1951) Ellerman <i>et. al</i> (1953) Schaub (1953) <i>inc. sedis.</i>
Wood (1955)			Landry (1957)

*Hystricomorph affinities of the Bathyergidae
and their taxonomic isolation*

Both Simpson (1945) and Romer (1958) have commented on the taxonomic "isolation" of the bathyergids. Romer included them within the sciuriforms "... for want of any better place to put them", while Simpson states that there "... are few more doubtful points in classification, concerning animals that are fairly abundant and quite well known, than the affinities of the bathyergids..." and that everyone "... agrees that they are extraordinarily isolated among rodents". However, these authorities also state that they are sometimes associated with the hystricomorphs, and Simpson, in his well known work on the classification of mammals has included the molerats *incertae sedis* within the hystricomorphs.

Landry (1957) examines evidence (based on his own observations, as well as those developed by Tullberg (1899)), Parsons (1894, 1896) and Dathe (1937) why the molerats are best interpreted as hystricomorphs. Landry asserts that the supposed taxonomic isolation of molerats may have been over-emphasized hitherto, especially if a paper by Thomas (1909) on tooth homologies of the bathyergids is considered.

The weight of evidence tips the scale heavily in favour of hystricomorph affinity of molerats and it serves a useful purpose to discuss the morphological criteria prompting a hystricomorph affinity on which such an interpretation is based.

Hystricomorph affinities in the skull

Teeth

Regarding the teeth of bathyergids, Landry (1957) offers a number of interesting speculations which may be reiterated briefly. Thomas (1909) speculated on the homologies of the cheek teeth of the bathyergids, especially the East African form *Heliophobius*. This genus possesses at one time or another "... six cheekteeth, the highest number known in any rodent or lagomorph". However, these teeth are not all present simultaneously and as the anterior tooth gets worn away another one forms at the posterior end of the toothrow. Consequently, there are seldom more than four cheekteeth present simultaneously and in addition, the last tooth may never become functional. Thomas assumed that the teeth of *Heliophobius* represented premolars 2, 3 and 4 and molars 1, 2 and 3. The M^3 is not always developed, and therefore Thomas felt that this tooth is the first one of the set to be depressed due to its position in close proximity to the roots of the upper incisors (as is also seen in *Cryptomys* and *Georychus*). This led to a reduction of the M^3 , its development and eventual use. Thomas argued, that the next tooth, i.e. the M^2 may be the next to have disappeared, but he prefers to consider, "... without real proof", that the Pm^2 is the next to be suppressed, for in young specimens with unworn teeth it is smaller than the

one next to it (*i.e.* the Pm³). However, in equally young *Georychus* specimens "... the two anterior teeth are practically equal in size" (Thomas 1909). "From this, therefore, cutting off a tooth at each end of the series, it would follow that in the 4-toothed members of the family, *Georychus* and *Bathyergus*, the formula is P 3-4, M 1-2" (Thomas, *op. cit.*). This would therefore also apply to *Cryptomys*.

Landry (1957) points out that if Thomas' assumptions are really true, then, "... of course, the bathyergids must be far removed from the rest of the rodents", leading to the concept of 'isolation' of the bathyergids among the rodents. "If *Heliophobius* really retains the primitive second upper premolar and the lower second and third premolars, it must have separated off from the rest of the rodent stock at least in the Paleocene, and probably in the Cretaceous. Indeed, if lagomorphs and rodents are descended from a common stock as implied by Simpson in grouping them together as "Cohort Glires", bathyergids must have come off the protogliroid stock before the rabbits did". In contrast, Landry argues that the extra teeth in *Heliophobius* represent new dental elements which have been added on to the posterior end of the usual mammalian molar series, such as has happened in the South African carnivore *Otocyon*. This seems plausible in view of the fact that the posterior teeth in *Heliophobius* "... push in from behind as the more anterior teeth are worn away". This could be brought about by a persistent dental lamina budding off two extra tooth germs. Furthermore, Landry also doubts Thomas' homologies of the cheek teeth. In order to follow the replacement of the teeth, he examined a series of *Heliophobius* skulls. Although he did not see absolutely unworn first cheek teeth, the youngest specimen he had available had only the first two teeth present with very little difference in size. All the teeth were shaped roughly like an inverted cone "... with a broad top and narrow base". As the teeth wear down, they decrease in size until, "... when the first tooth is almost gone, it is represented by a tiny peg. The disparity in size between the first and second tooth increases as the teeth are worn". Landry therefore doubts Thomas' notion that "... the tooth row of *Georychus* represents the tooth row of *Heliophobius* with one tooth lopped off from each end. Rather, the tooth row of *Heliophobius* represents the tooth row of *Georychus* with two neomorphic teeth added to the back end" (Landry 1957). In the case of *Bathyergus*, *Georychus* and *Cryptomys*, the four molar elements are interpreted to represent P4, M1, 2 and 3, if compared with an illustration of the cheek teeth of *Heliophobius* given by Landry. Once the additional teeth of *Heliophobius* is seen as a specialization of that particular genus, "... the taxonomic remoteness of the Bathyergidae considerably decreases" (Landry 1957).

According to Landry the cheek teeth of *Bathyergus*, in contrast to the other bathyergids, are pronouncedly hypsodont. Consequently, the bathyergids may have originated from a hypsodont ancestor. The majority of the bathyergids are but slightly hypsodont and this would imply that a hypsodont tooth evolved into a brachyodont one, a decidedly unusual occurrence among mammals. Landry is of the opinion that the teeth of ba-

thyergids tend to show a degenerate appearance suggesting that they are reduced hypsodont teeth. The posteriorly-directed extension of the incisors, combined with a narrowing of the anterior region of the snout may have necessitated a shortening of the length of the cheek teeth in order to allow the incisors to pass above them, as is found in *Georychus* and *Cryptomys*. Lack of space in the skull could not accommodate both the deep alveolar part of hypsodont molars as well as long upper incisors. "If selection pressure for long incisors was strong enough, there would automatically be strong selection pressure for a reduction in length of the molars, especially if the diet of the animal were changed to softer food" (Landry 1957).

Tullberg (1899) pointed out that the motion of the lower jaw is propalinal in hystricomorphs, while this movement is prevented by the presence of cusps on the occlusal surfaces of the teeth in some other groups e.g. the sciurognaths. The fact that bathyergids also show propalinal grinding may indicate a hystricomorph affinity. It should, however, be stressed that flat-crowned teeth are not limited to the hystricomorphs and Landry (1957) discusses this question at length.

Interesting evidence pointing to the hystricomorph affinity of bathyergids can be demonstrated in the enamel histology of the incisors. Landry (*op. cit.*) gives an excellent account which is paraphrased briefly. Tomes (1850) investigated the microscopic structure of rodent teeth in order to obtain useful taxonomic characters. He found the arrangement of enamel prisms in the incisor teeth to be characteristic for each of the three classical suborders. The prisms of enamel extend from the deeper lying dentine to the surface of the tooth. They are arranged in lamellae adjacent to the dentine, but towards the surface of the tooth. The lamellae are disrupted and the prisms are arranged uniformly in parallel fashion. The differences between the three suborders are found in the configuration of the lamellae. "In both the sciuromorphs and the myomorphs the lamellae are composed of transverse layers of single prisms running at right angles, or nearly so, to prisms in the subadjacent layer, so that a thin cross section of the incisor shows a diamond-shaped pattern in the region of the enamel where the prisms criss cross each other. In longitudinal section one can see the principal distinguishing characteristics of the suborders. The myomorphs are distinguished by their rugose lamellae, the projections from the prisms in one layer fitting into corresponding depressions in the next layer." (Landry 1957).

The histological structure of the hystricomorph enamel is markedly different. The lamellae are not just one prism deep but correspond to thick layers of prisms giving the enamel in longitudinal section a distinctive appearance.

"The prisms are thrown into transverse waves, and the prisms of adjacent layers are 180° out of phase; that is, at the position along a prism at which it swings farthest to the left, the prisms immediately below it and above it will be farthest to the right." Furthermore, in the outer part of the enamel, as usual, the ". . . prisms are straight and not arranged in lamellae and there is usually a sharp change in the angle of the direction of the

prisms at a point where the lamellae cease." According to Landry, the histology of the incisor enamel of the bathyergids is typically hystricomorph.

The pterygoid fossa

The breaking down of the anterior wall of the pterygoid fossa into the posterior part of the orbit is an important hystricomorph character. The internal pterygoid muscle of a typical hystricomorph passes through the tunnel formed by the connection of the pterygoid fossa with the orbit (Landry 1957). In *Bathyergus* this muscle passes to the orbit in the normal hystricomorph manner (Landry *op. cit.*) and is facilitated by the short incisors and the position of their persistent pulp cavities which are situated slightly in front of and dorsal to the first cheek teeth. Landry states that in most of the other bathyergids, however, the pterygoid fossa opens into the braincase. This is also related to the great development of the incisor, especially in *Georychus* and *Cryptomys*. In these cases, the incisors have pushed posteriorly into the pterygoid bone, shutting off the pterygoid fossa from the orbit and rerouting the internal pterygoid muscle. The internal pterygoid originates from the posterior side of the incisor sheath. In *Bathyergus* the incisors are short and the pterygoid fossa opens into the orbit as in other hystricomorphs.

An important character correlated with the fact that the pterygoid fossa breaks through into the orbit (as in *Bathyergus*), is the propalinal chewing, a basic functional adaptation of the hystricomorphs. This in turn implies flat occlusal surfaces of the grinding teeth found in the molerats (*i.e.* absence of cusps). The lengthening of the internal pterygoid muscle which has occurred in the bathyergids gives a strong pull to the jaw in an antero-posterior direction. If the forward extension of the masseter is of prime importance in producing a strong bite at the incisors, the pterygoid muscles are of prime importance in closing the cheek teeth against one another and rubbing anteroposteriorly. These combined movements lead to propalinal grinding. Tullberg (1899) states that in hystricognaths "... the movement of the jaw in chewing is always more definitely in a direction paralleling the zygomatic arch..." facilitating propalinal chewing. These facts point to a hystricomorph affinity of bathyergids. In *Bathyergus* (which does not tunnel with the aid of incisors and where the incisors are comparatively smaller) the usual hystricomorph condition is found. In *Georychus* and *Cryptomys*, who utilize its incisors for tunneling, the incisors are enlarged resulting in an altered morphology compared to the basic hystricomorph pattern.

The structure of the mastoid portion of the bulla

The possibility of an ancestral *Petromys*-like animal giving rise to the bathyergids has been postulated by Landry (1957). Landry finds *Petromys*

probably the most generalized of all Old World hystricomorphs and considers it as a type that could have been related to the bathyergid line. In *Petromys* (as in the bathyergids) the mastoid covers a wider area at a deeper level between the lateral processes of the supraoccipital and the paroccipital processes of the exoccipitals. In the hystricids, the mastoid shows narrower surface between these processes. However, a long lateral process of the supraoccipital is not limited to the hystricomorphs, and due to the otic specialization which has occurred in the Old World hystricomorphs, *Petromys* (an undoubted hystricomorph) is left as "... the closest relative of the bathyergids by default" (Landry 1957).

Structure of the infraorbital foramen

It can be demonstrated that bathyergids possess all the characteristic cranial hystricomorph features, with the exception of the enlarged infraorbital foramen. Winge (1887) postulated that the reduced foramen could be a secondary development because he believed that the foramen was enlarged in primitive rodents. He also reasoned that a reduced infraorbital foramen was a secondary condition in *all* rodents in which it is reduced. Tullberg (1899) and Parsons (1894) admitted that a slip of the anterior deep part of the masseter muscle (*i.e.* the musculus masseter medialis) does pass through this foramen, at least in *Cryptomys*. Ellerman (1940) states that in some bathyergids, especially in certain species of *Cryptomys* the infraorbital foramen is "... starting to transmit muscle". In some cases as in *C. hottentotus mellandi*, this foramen may be as enlarged as the somewhat reduced foramen found in Rhizomyidae. Furthermore, Ellerman states that the size of the infraorbital foramen is a variable character, for in some *Cryptomys* specimens the foramen may be larger on the one side of the skull than on the other. Ellerman continues by saying that it appears to him "... singularly unlikely that, having taken such a large step forward in evolution as the enlargement of this canal for muscle transmission (as it seems an unusual character among Mammalia to say the least), these families (e.g. Geomyidae, Sciuridae, Castoridae, Bathyergidae and Heteromyidae) should go even further in evolution and, so to speak, develop covering over this canal so that it does not transmit again".

Landry (1957) maintains that if Ellerman is following Tullberg, he follows blindly and not logically for in the same sentence in which he states that *Cryptomys* is beginning to transmit the muscle through the foramen, Ellerman also gives an example of a rodent which has reduced the foramen to the same size of that of *Cryptomys* (*i.e.* in some Rhizomyidae). Landry concludes that if it is accepted that reduction has occurred in the rhizomyids, it can no longer be insisted that it could not have occurred in *Cryptomys* (and therefore in the bathyergids). Landry then poses the question: why has no one made the obvious assumption that the bathyergids are hystricomorphs in which the infraorbital foramen has become reduced secondarily?

As far as *Bathyergus* is concerned, it appears that the small infraorbital foramen does not transmit any part of the masseter. Yet in spite of the small foramen and absence of the masseter from the rostrum, the rostrum of *Bathyergus* is enlarged. According to Landry, this enlargement is secondary and may be correlated with the broadening of the incisors which has occurred during the evolution of this genus, for the nasal cavity is much reduced compared to other rodents. This widening of the incisors has further encroached on the size of the infraorbital foramen and completed the exclusion of the masseter from the snout. Further evidence for accepting that reduction of the infraorbital foramen in bathyergids is secondary and correlated with adaptation for fossorial life, is demonstrated by a similar occurrence in the microtines, especially the genus *Ellobius*.

Fusion of the malleus and incus

One of the most important morphological characters of hystricomorphs mentioned by Tullberg (1899) is the fusion of the two outer ear ossicles, the malleus and incus. This condition is also found in the Bathyergidae and again accentuates their affinity with the hystricomorphs. What significance such fusion could have is hard to determine.

Structure of the lower jaw

The hystricomorphs all possess a typical angular process along the lower border of the mandible and Tullberg considered it to be the most important common feature of the Hystricognathi. Viewed from below the "origin" of the angular process is lateral to the incisor alveolus, while in the sciurognath type of jaw the angular portion arises ventrally to the incisor alveolus. The essential idea here is that in the "... sciurognaths the *inside* of the angular process of the sciurognath jaw is at the inside of the alveolar sheath, whereas in the hystricognath jaw the inside of the angular process is lateral to the outside of the incisor alveolar sheath" (Landry 1957). This hystricomorph like arrangement is encountered in bathyergids and points yet again to the hystricomorph nature of molerats.

Hystricomorph affinities in the postcranial skeleton

The limbs

According to Landry (1957) the only indication that the bathyergids are "extraordinarily isolated" amongst the rodents is the fact that the scaphoid and lunar elements of the manus are separate and that the tibia and fibula are fused at their distal ends. The former is apparently a genuinely primi-

tive character (*i.e.* implying that they may have split off from the basal rodent stock before these elements fused in the majority of rodents) while the latter is probably a habitus character related to digging. These aspects would be clarified considerably if appropriate fossil forms could be found. By themselves, these arguments do not place the bathyergids within the hystricomorphs.

When the humerus is considered, it appears that a character which all hystricomorphs share (including the bathyergids) is the absence of the entepicondylar foramen on the distal humerus. The earliest rodents (aplodontoids of Simpson 1945) all show this foramen and the sciurormorphs tend to retain it, while it occurs irregularly in the myomorphs. The fact that this foramen is almost never found in the hystricomorphs indicates that it was lost during the early history of the group. Taken on its face value absence tends to strengthen the notion that they are best placed within the hystricomorphs. Correlated with features of the skull described above (and with others to be described below) the absence of this foramen in the bathyergids also points to their hystricomorph affinity.

Hystricomorph affinities in the reproductive organs and musculature

Tullberg (1899) referred to the sacculus urethralis as yet another typical hystricomorph character. This feature was also studied extensively by Cole (1897), Pocock (1922) and Dathe (1937).

In the glans penis, just below (and communicating with) the urethral orifice, is an invagination. During erection of the penis this little sac everts, protruding a balloon-like extension which projects beyond the tip of the penis. In many hystricomorphs, there are two little horns at the bottom of this sac, which during copulation, are on the tip of the balloon and it may serve some titulatory effect during copulation. Dathe points out that there are many small spicules all over the penis except for a bare medial lane on the ventral surface. This arrangement holds for all hystricomorphs and is present only in the hystricomorphs and bathyergids. It affords strong evidence for placing the bathyergids with hystricomorphs. On a flaccid penis these spicules are clearly visible in *Bathyergus* with the aid of a dissection microscope.

As far as the myology of the bathyergids is concerned the reader is referred to the classical papers by Parsons (1894, 1896), who studied the comparative aspects of rodent myology. Landry (1957) states that all hystricomorphs (including the bathyergids) have a musculus scapuloclavicularis which "...runs from the clavicle, where it may be continuous with the subclavius, to the spine and vertebral border of the scapula, forming a sheet of muscle over the supraspinatus. This muscle is not found in any other rodent, but surprisingly enough it is well developed in lagomorphs". According to Parsons, this muscle is innervated by the same branch of the brachial plexus which in main innervates the subclavius. Landry also points out that Bensley (1926) described the scapuloclavicularis in the rab-

bit as the pectoralis tertius, being a subdivision of the pectoral musculature. If, according to Landry, this line of thought is to be accepted this muscle is not homologous to the scapuloclavicularis of rodents, but Bensley does not mention the innervation of this pectoralis tertius, nor "... does Parsons state whether or not he investigated the innervation of the scapuloclavicularis in rabbits. There is a possibility, therefore, that the two muscles are not homologous." Landry could not find a homologue of this muscle in other mammals, and while it is apparently only found in rodents and lagomorphs, this tends to confirm the notion that these two orders are related. He states, that if they are, this hystricomorph character must be a primitive rodent feature. The presence of this muscle in the bathyergids thus also confirms the view that the Bathyergidae is an ancient offshoot from the basal rodent stock.

Another myological character listed by Parsons for the hystricomorphs is the structure of the digastric muscle "... whose two bellies are continuous or at best separated only by a slight constriction. In myomorphs and sciurormorphs, on the other hand, there is a well marked tendon between the two bellies, as in man. Moreover, in myomorphs and sciurormorphs the anterior two bellies are joined across the midline by a tendinous arcade which is absent in hystricomorphs in which the anterior two bellies are widely separated" (Landry 1957). However, this distinction is not absolute, for amongst the sciurognaths *Cricetus*, *Microtus*, *Myodes* and *Hydromys* (according to Parsons) show no tendons between the two bellies but the anterior two bellies are still in close contact. Even in hystricomorphs, there is a constriction of the muscle between the two bellies "... and there is a flat tendinous reinforcement at this point so that a lack of a tendinous part in hystricomorphs is not immediately obvious. It seems to me that there could be, and probably are, all sorts of intermediate conditions between a completely tendinous interruption and a completely muscular one. The important difference between the two is whether or not the anterior belly of the digastric is attached to its fellow across the midline" (Landry 1957). The hystricomorphine structure has the two anterior bellies diverging from each other as they are traced backwards. In the bathyergids (*Bathyergus* and *Georychus*) the digastric is as in murids *i.e.* the anterior two bellies lie close besides each other but there is no tendinous cross connection between them *i.e.* corresponding to the hystricomorphs. This, according to Landry (1957) could be pointed to as another primitive hystricomorph feature of the bathyergids.

Another feature mentioned by Parsons as being characteristic of the hystricomorphs is the absence of the transverse mandibular muscle in the lower jaw. This muscle is peculiar to rodents and runs across the anterior ends of the two halves of the jaw. It is usually superficial to the mylohyoid in the Muridae, where it may be better developed than in other groups. It consists of a bundle of fibres running across the two hemi-jaws close to the symphysis and serves to diverge the tips of the lower incisors since the symphysis of the jaw is unfused in the majority of rodents. Amongst the hystricomorphs this symphysis is more tightly fused than usual (probably

correlated with the propalinal grinding motion) and consequently this transverse muscle is unimportant. However, Landry points out that the bathyergids have the most freely moveable jaws of any rodent and in these animals the muscle is consequently well developed. This may again point to the fact that the molerats have come off from the early hystricomorph stock before the rest of the hystricomorphs began to lose this muscle. The muscle has undoubtedly been retained in terms of survival value and even Tullberg (1899) remarked that the spreading of the incisors is important in the handling of small round objects and the handling of these during gnawing. This is especially true if it be kept in mind that the main diet of the bathyergids consists of bulbs and other subterranean roundish objects.

Another myological feature common to all hystricomorphs (see Parsons) is the uniting of the tendons of the flexor hallucis longis (flexor fibularis) with the flexor digitorum longis of the sole of the pes. An exception to this arrangement amongst the hystricomorphs are the bathyergids where the flexor digitorum longis is better developed than in other rodents, with its tendon inserting onto a sesamoid bone at the base of the first metatarsal and therefore it does not fuse with the flexor hallucis longis. This may again point to the early breakaway of the bathyergids from hystricomorph stock and I am inclined to interpret this as another habitus character: the hindfeet of the animals are used extensively to clear the passages and tunnels from excavated soil and a separation of these two muscles would allow greater flexibility of the pes and therefore greater manipulative effect.

Landry (1957) states that in all hystricomorphs which he has dissected the panniculus carnosus muscle takes origin, not from the inner side of the humerus next to the insertion of the latissimus dorsi as in most mammals, but from the outside of the scapula at the ventral end of the spine, the acromion process and the greater tuberosity and deltoid crest of the humerus. To him it seems likely that the attachment of the panniculus on the outside of the arm is a hystricomorph character. I have found that this condition also exists in *Bathyergus* and therefore, again points to their hystricomorph affinity.

REFERENCES

- ALLEN, G. M. 1939. A checklist of African mammals. *Bull. Mus. comp. Zool. Harv.* 83:1-736.
- ALSTON, E. R. 1876. On the classification of the order Glires. *Proc. zool. Soc. Lond.* 62-98.
- BENSLEY, B. A. 1926. *Practical anatomy of the rabbit*. Philadelphia: P Blakinston's Son & Co.
- BRANDT, J. F. 1855. Untersuchungen über die craniologischen Entwicklungsstufen und classification der Nager der Jetztwelt. *Mem. de l'Acad. Imp. de St. Petersbourg*, ser 6, 7:125-336.
- COLE, F. J. 1897. Structure and morphology of the intromittent sac of the male guinea-pig. *Jour. Anat. Physiol. Lond.* 32:141-152.

- DATHE, H. 1937. Über den Bau des männlichen Kopulationorganes beim Meerschweinchen und anderen hystricomorphen Nagetieren. *Gegenb. Morph. Jahrb.* 80:1–65.
- DE GRAAFF, G. 1961. A short survey of investigations of fossil rodents in African deposits *S. Afr. J. Sci.* 57:191–196.
- DE GRAAFF, G. 1974. Notes on the occurrence of rodents in South African National Parks. *Koedoe* 17:173–183.
- DE MEILLON, B., D. H. S. DAVIS and F. HARDY. 1961. *The Siphonaptera (excluding Ischnosyllidae)*. Pretoria: Staatsdrukker.
- ELLERMAN, J. R. 1940. *The families and genera of living rodents*. London: British Museum (Nat. Hist.).
- ELLERMAN, J. R., T. C. S. MORRISON-SCOTT and R. W. HAYMAN. 1953. *Southern African mammals 1758–1951: a reclassification*. London: British Museum (Nat. Hist.) publication.
- KRETZOI, M. 1943. Ein neuer Muscardinidae aus dem ungarischen Miozän. *Föld Közlöny.* 73:271–273.
- LANDRY, S. O. jr. 1957. The interrelationships of the new and old world hystricomorph rodents. *Univ. Calif. Publ. Zool.* 56:1,1–118.
- LAVOCAT, R. 1951. Révision de la faune des mammifères Oligocènes d'Auvergne et du Velay. Paris: *Editions Sciences et Avenir.* 1–153.
- LAVOCAT, R. 1956. Réflexions sur la classification des rongeurs. *Mammalia* 20: 49–56.
- MEESTER, J. A. J. 1963. A systematic revision of the shrew genus *Crocidura* in southern Africa. *Tvl Museum Mem.* 13. Pretoria.
- MEESTER, J., D. H. S. DAVIS and C. G. COETZEE. 1964. An interim classification of southern African mammals. Roneod. Zoological Society of southern Africa and Council for Scientific and Industrial Research.
- MEESTER, J. and H. W. SETZER. 1971. *The Mammals of Africa – an identification manual*. City of Washinton: Smithsonian Institution Press.
- MILLER, G. W. and J. W. GIDLEY. 1918. Synopsis of the supergeneric groups of rodents. *Jour. Wash. Acad. Sci.* 8:431–448.
- PARSONS, F. G. 1894. On the myology of the sciuromorphic and hystricomorphine rodents. *Proc. zool. Soc. Lond.* 251–296.
- PARSONS, F. G. 1896. Myology of rodents. *Proc. zool. Soc. Lond.* 159–192.
- POCOCK, R. I. 1922. On the external characters of some hystricomorph rodents. *Proc. zool. Soc. Lond.* 365–427.
- ROBERTS, A. 1951. *The Mammals of South Africa*. Johannesburg: Trustees “The Mammals of South Africa Book Fund.”
- ROMER, A. S. 1958. *Vertebrate Paleontology*. 2nd Ed. 7th Imp. Chicago: University of Chicago Press.
- SCHAUB, S. 1953. Remarks on the distribution and classification of the ‘Hystricomorpha’. *Verh. Naturf. Ges. Basel.* 64:389–400.
- SCLATER, W. L. 1901. *The Mammals of South Africa*. London: R. H. Porter.

- SIMPSON, G. G. 1945. The principles of classification and a classification of mammals. *Bull. Amer. Mus. nat. Hist.* 85:1–350.
- SIMPSON, G. G. 1950. History of the fauna of Latin America. *Amer. Scientist.* 38:361–389.
- THOMAS, O. 1896. On genera of the rodents: an attempt to bring up to date the current arrangement of the order. *Proc. zool. Soc. Lond.* 1012–1028.
- THOMAS, O. 1909. New African small mammals in the British Museum collection. *Ann. Mag. nat. Hist.* ser. 8 4:98–112.
- TOMES, J. 1850. On the structure of the dental tissues of the order Rodentia. *Phil. Trans. Roy. Soc. Lond.* 140:529–567.
- TULLBERG, T. 1899. Uber das system der Nagethiere: eine phylogenetische Studie. *Nov. Act. Reg. Soc. Sci. Upsal.* ser. 3, 18:1–514.
- WATERHOUSE, G. R. 1838. Observations on the Rodentia. *Mag. Nat. Hist.* New ser. 3:90–96, 184–188, 274–279, 539–600.
- WEBER, M. 1904/1928. *Die Säugetiere*. Jena: Gustav Fischer Verlag.
- WINGE, H. 1887. Jordfunde og nulevende Gnavere (Rodentia) fra Lagoa Santa Minas Geraes, Brasilien med undisgt over Gnavernes inbyrdes Slaegtskab E. Museo Lundii. Pattedyrslaegter Kobenhavn. H. Hagerup Forlag. *Publ. Univ. Zool. Mus.* 30, 31, 32 (Translated 1941 by E. Deichmann and G. M. Allen as “The interrelationships of the Mammalian Genera” Copenhagen: C. A. Reitzels Forlag).
- WOOD, A. E. 1955. A revised classification of the rodents. *J. Mammal.* 36:165–187.
- WOOD, A. E. 1958. Are there rodent suborders? *Syst. Zool.* 7:169–173.
- WOOD, A. E. and B. PATTERSON. 1959. The rodents of the Deseadan Oligocene of Patagonia and the beginnings of South American rodent evolution. *Bull. Mus. comp. Zool. Harv.* 120:297–428.