

CHAPTER 5ON THE HYSTRICOMORPH AFFINITIES OF THE
BATHYERGIDAE AND THEIR TAXONOMIC 'ISOLATION'

Various authors (e.g. Romer, 1958, 501, and Simpson 1945, 212, amongst others) have commented on the taxonomic 'isolation' of the bathyergids. The former included them within the sciuriforms ".... for want of any better place to put them", while the latter 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, both these authorities state that they are sometimes associated with the hystricomorphs, and Simpson, in his well known work on the classification of mammals has included the mole-rats incertae sedis within the hystricomorphs.

In the more recent literature, Landry (1957) mentions a number of reasons (based on his own observations, and those of Tullberg (1899), Parsons (1894, 1896), and Dathe (1937) amongst others), why the bathyergids should be accepted as **hystricomorphs**. Landry furthermore states that the so-called isolation of the bathyergids may have been over-emphasized hitherto. This author also blames Thomas (1909) to a certain extent for this concept of isolation, especially when Thomas's article on tooth homologies of the bathyergids is taken into consideration./...

consideration.

It may therefore serve a useful purpose to consider briefly the various arguments, for and against the placing of the bathyergids with the hystricomorphs and why they are accepted as hystricomorphs in the present work. As far as some of these arguments are concerned, a number of them have been mentioned earlier on in this work but for the sake of clarity some recapitulation on a number of these aspects will be necessary in this chapter.

A. Hystricomorph affinities in the skull

In the preceding pages, a fairly detailed description of a skull of Bathyergus has been given, together with comments on the skull of Georychus and Cryptomys. However, as far as certain structural features are concerned, (e.g. the infraorbital foramen, the pterygoid fossa as well as aspects of tooth morphology), these structures justify a fuller discussion, not only in terms of Bathyergus, but also as far as the family Bathyergidae is concerned.

1. Teeth

Regarding the teeth of bathyergids, Landry (1957, 67) offers a number of interesting speculations which may be dealt with briefly at this point. Thomas (1909) speculated on the homologies of the cheekteeth 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" (p.67). 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/...

Consequently, there are seldom more than four cheek-teeth present simultaneously and in addition, the last tooth may never become functional. Thomas assumed that these teeth of Heliophobius represented premolars 2, 3 and 4 and molars 1, 2 and 3.

The $m \underline{3}$ 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 proximity to the roots of the incisors (e.g. in Cryptomys and Georychus). This led to a reduction of freedom, development and use. Thomas argued, that the next tooth i.e. the $m \underline{2}$ may be the next to have disappeared, but he prefers to consider,

".... without real proof", that the $pm \underline{2}$ 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 $pm \underline{3}$). However, in equally young Georychus specimens ".... the two anterior teeth are practically equal in size" (Thomas, 1909, 111). "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. p.111). This would therefore also apply to Cryptomys.

Landry (1957, 67) then states, quite rightly, 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/...

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".

It seems far more probable to Landry 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" (p. 68). This could be brought about by a persistent dental lamina budding off two extra tooth germs.

Furthermore, Landry also doubts Thomas' homologies of the cheekteeth. In order to follow the replacement of the teeth, he examined a series of Heliophobius skulls. Although he did not see absolutely unworn first cheekteeth, the youngest specimen he had available had only the first two teeth with very little difference in size between the two. 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/...

row of Heliophobius represents the tooth row of Georychus with two neomorphic teeth added to the back end" (Landry, 1957, 69). In the case of Bathyergus, Georychus and Cryptomys, Landry thus interprets the four molar elements to represent P4, M1, 2 and 3, based on the annotations of a figure of the cheekteeth of Heliophobius which Landry supplies on p. 68.

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, 69).

According to Landry (1957, 71), the cheekteeth of Bathyergus, in contrast to the other bathyergids, are deeply hypsodont. It is therefore possible that the bathyergids were derived from a hypsodont hystricomorph. The majority of the bathyergids are slightly hypsodont and this would imply that a hypsodont tooth evolved into a brachydont one, "... a decidedly unusual occurrence among mammals". However, Landry goes on to state that the teeth of the bathyergids do however 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 incisor to pass above them, as is the case in Georychus and Cryptomys. This lack of space in the skull could not accommodate both the deep alveolar part of the hypsodont molars as well as the long upper incisors. "If selection pressure for long incisors was strong enough, there would automatically/...

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, 71).

As was mentioned earlier on in this work, Tullberg (1899) stated that the motion of the lower jaw is propalinal in hystricomorphs, while this movement is prevented by cusps on the occlusal surfaces of the teeth in other groups e.g. the sciurognaths. The fact that bathyergids also show propalinal grinding may thus point to a hystricomorph affinity. It should however be pointed out that flat-crowned teeth are not limited to the hystricomorphs and for further information on this matter, the reader is referred to Landry (1957, 9-16).

An interesting bit of evidence pointing to the hystricomorphine nature of the bathyergids is found in the histology of the enamel of the incisor. Landry (p. 25) gives an excellent account of this aspect which will be paraphrased briefly at this point. Tomes (1850) investigated the possibility of obtaining useful taxonomic characters from the microscopic structure of the teeth of rodents and he found that the arrangement of prisms of enamel in the incisors was characteristic for each of the three classical suborders.

These enamel prisms run from the dentine to the surface of the tooth, arranged in lamellae next to the dentine, but towards the outside of the tooth these lamellae are broken up and the enamel prisms proceed uniformly to the surface, parallel to each other. According to Landry, in alternate lamellae the/...

the prisms are parallel. The differences between the different suborders are found in these lamellae. "In both the sciurormorphs 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, 25).

The histological structure of the hystri-comorph enamel is different however. In this case 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 hystri-comorph.

2. The pterygoid fossa

Returning once again to some aspects of features in the bathyergid skull, the question of the pterygoid fossa has to be raised.

The breaking down of the anterior wall of the pterygoid fossa so that it communicates with the orbit (see above) is an important hystricomorph character. The internal pterygoid muscle of the typical hystricomorph passes through the tunnel formed by the connection of the pterygoid fossa with the orbit (Landry, 1957, 9). In Bathyergus this muscle passes to the orbit in the normal hystricomorph manner (Landry, op.cit. p. 70). This is made possible by the fact that the incisors are short and their persistent pulp cavities are situated slightly in front of and dorsal to the first cheek teeth elements.

Landry (op.cit.) states that in most of the bathyergids however, the pterygoid fossa opens into the braincase (p. 9). 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 "... forcing the internal pterygoid muscle up into the brain case. The internal pterygoid thus takes origin from the posterior side of the incisor sheath" (p. 9). In Bathyergus the incisors are short and the pterygoid fossa opens into the orbit as in other hystricomorphs.

The most important character correlated with the fact that the pterygoid fossa breaks through into the orbit (as in Bathyergus), is, (according to/...

to Landry, p. 9), the propalinal chewing, a basic functional adaptation of the hystricomorphs. This in turn leads to the flat occlusal surfaces of the grinding teeth found in the bathyergids (i.e. absence of cusps). The lengthening of the internal pterygoid muscle which has occurred in the bathyergids gives a stronger 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". This movement, in fact, then leads 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..." and Landry (p. 9) agrees with Tullberg that this propalinal chewing is the basic functional adaptation of hystricomorphs.

These facts clearly point to the hystricomorph affinity of the bathyergids. In Bathyergus (which does not tunnel with the aid of its incisors and where the incisors are thus smaller) the usual hystricomorph condition is found; in Georychus and Cryptomys, who utilize their incisors during tunneling operations, these incisors have become enlarged causing an alteration in structure from the basic hystricomorph pattern.

3. The structure of the mastoid portion of the bulla

The possibility of an ancestral Petromys-like animal giving rise to the bathyergids as postulated by Landry (p. 75) has been mentioned above (see Chapter 2 of the present work). It will be recalled/...

recalled that 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 this form (as in the bathyergids) the mastoid covers a wider expanse at a deeper level between the lateral processes of the supraoccipital and the paroccipital processes of the exoccipitals. In the hystricids, the mastoid shows only a small surface between these processes. However, a long lateral process of the supraoccipital is not limited to the hystricomorphs, and, as has been stated above, 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 p. 75).

4. Structure of the infraorbital foramen

Landry (1957, 66, 67, 70) has mentioned a number of features as far as the small infraorbital foramen in the bathyergids is concerned and some of his arguments are to be paraphrased rather lengthily in this connection.

It is known that bathyergids possess all the characteristic hystricomorph features, with the exception of the enlarged infraorbital foramen. Winge (1887, 1924) postulated that this reduction could be secondary because he believed that this foramen was enlarged in primitive rodents and that a reduced infraorbital foramen was secondarily 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
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this foramen, at least in Cryptomys. Ellerman (1940, 44) states that in some bathyergids, especially in certain species of Cryptomys the infraorbital foramen is "starting to transmit muscle" through this foramen. In some cases, as in C. mellandi, this foramen may be as much enlarged as in the much reduced type of foramen found in the Rhizomyidae. Furthermore, Ellerman states that the size of the infraorbital foramen is evidently a variable character, for in Cryptomys the foramen may be larger on the one side of the skull than on the other in individual cases. Ellerman goes on to state (p. 44) 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 (p. 67) states 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 thus concludes that if we accept the fact that reduction has occurred in the rhizomyids, it can no longer be insisted that it could not have occurred in Cryptomys (and therefore in/...

in the bathyergids). On page 66 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, Landry (p.70) states that the small infraorbital foramen does not transmit a slip 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 very much reduced (see above) 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 rostrum".

Landry (1957, 71) gives further evidence and reasons for believing that the reduction of the infraorbital foramen is secondary and correlated with adaptation in the bathyergids for fossorial life by demonstrating a similar occurrence in the microtines, especially the genus Ellobius.

5. The fusion of the malleus and incus

One of the most important morphological characters of the 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 indicates their affinity with the hystricomorphs. What the significance of this fusion could be, is not easy to/...

to determine.

6. Structure of the lower jaw

The hystricomorphs all possess a peculiar type of angular process of the lower jaw, and Tullberg considered it to be the most important common feature of the Hystricognathi. Viewed from the ventral aspect, the 'origin' of the angular process is lateral to the incisor alveolus, while in the sciurognath type of jaw the angular portion arises from the ventral portion of 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, 6). This hystricomorphlike arrangement is encountered in the bathyergids and thus points once again to the hystricomorph nature of the mole-rats.

The facts briefly discussed above, indicate a definite hystricomorph affinity of the bathyergids, based on structural features of the skull. However, the postcranial skeleton also indicates a number of features, which are to be discussed briefly below.

B. Hystricomorph affinities in the postcranial skeleton

1. The limbs

According to Landry (1957, 67) 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/...

their distal ends. The former is apparently a genuinely primitive 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 and Landry does not doubt that it could have arisen among the hystricomorphs at any time. These aspects would be clarified considerably if the appropriate fossil forms could be found. In the mean-time, by means of this explanation, the taxonomic remoteness of the mole-rats is considerably decreased, although by themselves, these arguments do not place the bathyergids within the hystricomorphs.

Focussing our attention on the humerus however, the following may be mentioned: a character which all the hystricomorphs share (including the bathyergids) is the absence of the entepicondylar foramen on the distal humerus. This foramen usually forms a funnel through which the median nerve passes on its way to the zeugopodium. This characteristic however, is not restricted to the hystricomorphs alone: the earliest rodents (aplodontoids of Simpson, 1945) all possessed this foramen, as do most placental mammals. The sciuriforms tend to retain this foramen, the hystricomorphs to lose 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 in the early history of the group (Landry, p. 20). Again, this argument does not place the bathyergids definitely within the hystricomorphs, but taken on its face value/...

value, tends to strengthen the notion that they are to be placed within the hystricomorphs. Correlated with certain features of the skull described above (and with other features to be described below) the absence of this foramen in the bathyergids also points to their hystricomorph affinity.

C. Hystricomorph affinities in the reproductive organs and musculature

According to Landry (p. 17), Tullberg (1899) quoted another useful character which occurs in the hystricomorphs i.e. the sacculus urethralis. 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 titilatory effect during copulation. Dathe points out that there are many small spicules all over the penis except for a medial lane on the ventral surface which is free of them. This arrangement holds for all hystricomorphs. According to Landry, this arrangement is present only in the hystricomorphs and bathyergids and affords excellent evidence for placing the bathyergids with the hystricomorphs.

I have not seen an erect penis in any of the genera considered during the progress of this work, but on the flaccid penis the spicules on the surface of the penis in Bathyergus are clearly visible with/...

with the aid of a stereoscopic 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 worked on the comparative aspects of rodent myology. Landry (1957, 30) states, that all hystricomorphs (including the bathyergids) have a muscle called the 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 man innervates the subclavius".

Furthermore, Landry states that Bensley (1926) described the scapuloclavicularis in the rabbit under the name of pectoralis tertius, being a subdivision of the pectoral musculature. If, according to Landry, this 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." (p. 30).

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/...

hystricomorph character must be a primitive rodent feature.

The possible presence of this muscle in the bathyergids thus also places the mole-rats within the hystricomorphs and may also confirm the view that the Bathyergidae is an ancient offshoot from the basal hystricomorph 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 p. 30). However, this distinction is not absolute, for amongst the sciurognaths Cricetus, Microtus, Myodes and Hydromys (according to Parsons) show no tendon 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
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the midline" (Landry, 1957, 31).

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 (p. 31) could be pointed to as another primitive hystricomorph feature of the bathyergids.

Another feature mentioned by Parsons as being characteristic of the hystricomorpha 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 (p. 31) 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 mole-rats have come off from the early hystricomorph stock before the rest of the hystricomorphs began to lose this muscle.

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The muscle has undoubtedly been retained in terms of survival value and even Tullberg (1899, 349) 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 (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 break-away 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, 32) 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/...

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.

Summarizing the data discussed on the previous pages, it is clear that it may be grouped into four categories:

- a. Facts pointing to the apparent taxonomic isolation of the bathyergids;
- b. Facts pointing to their hystricomorph affinities;
- c. Facts which may point to their hystricomorph nature;
- d. Facts pointing to non-hystricomorph affinities.

a. As far as the first category is concerned, mention may be made of the homology of the teeth which is most likely based on a past misinterpretation of the facts. The size of the infraorbital foramen is satisfactorily explained by correlating it with the development of the incisors while the separate scaphoid and lunar elements in the manus may be due to the very ancient nature of the bathyergids. Seen from this point of view, the bathyergids may not be so isolated taxonomically as was thought at first.

b. The undoubted hystricomorph affinities are borne out by the following facts: the histological structure of the enamel of the upper incisors; the structure of the pterygoid fossa; features of the mastoid portion of the bulla; the fusion of the malleus and incus in the middle ear; the anatomical features/...

features of the lower jaw; the presence of the scapuloclavicularis muscle and the insertion of the musculus panniculus carnosus; and finally, the morphology of the male copulatory organ.

These are all relatively clearcut examples pointing to their hystricomorph nature.

c. On the other hand, a number of features may point to their hystricomorph affinity, but bearing in mind the fact that many of these aspects could be encountered in the sciurognaths (sciuiromorphs and myomorphs) as well. It seems that these features, although present or absent in the hystricomorphs, have undergone certain modifications in the bathyergids, which can be correlated to their fossorial mode of life and may thus have survival value. Examples of these aspects are:

the presence of the well developed transverse mandibular muscle; the structure of the digastric muscle; the insertion of the flexor digitorum longis; the absence of the entepicondylar foramen in the distal humerus and the propalinal grinding of the molars.

d. Finally there are some aspects pointing to non-hystricomorphine affinities, e.g. the presence of a well developed clavicle and the distally fused tibia and fibula. The former aspect has not been discussed in the previous pages but it may be mentioned that this element is widespread and well developed in the sciuiromorphs and myomorphs. In the hystricomorphs, this element is usually small, or virtually absent. It may be pointed out that a strong, well developed clavicle (as found in the bathyergids/...

bathyergids) is a common feature in all animals who need greater motility and manipulative ability of the forearm. Bathyergus, especially uses its forearms during tunneling, and this genus, as well as Georychus and Cryptomys, use their hands during feeding, in a similar fashion as mice and squirrels utilize it.

The distally fused tibia and fibula is also to be found in the majority of rodents and may also be interpreted as a habitus character, as has been mentioned above.

Based on the information presented above, I am virtually convinced about the hystricomorph affinities of the Bathyergidae. In the past they may have been associated rather dubiously with the hystricomorphs (with one noticeable exception i.e. the paper by Landry) but for the purposes of the present work they are accepted as highly specialized hystricomorphs.