

CHAPTER 2THE ORIGIN OF THE BATHYERGIDAE AND  
THE PALEONTOLOGICAL RECORD

The origin of the Bathyergidae, and problems relating thereto, is shrouded in a mist of many uncertainties. To a large extent this is due to the absence of sufficient paleontological data. A number of fossil forms (to be discussed briefly below) are known from Asian deposits (especially in Mongolia) and from various African localities, but it has to be emphasized that the possible bathyergid nature of the Mongolian finds is still open to debate. Consequently, phylogenetic relationships are still largely unknown both from an overall phylogenetic point of view and as far as the interrelationships of the different genera are concerned.

Simpson (1945, 213) correctly maintains that any decisive indications of their ancestry ".... are overlain and obscured by specializations for a highly specific and peculiar mode of life, and a definitive arrangement cannot be expected until less specialized ancestral forms are found. Supposed ancient allies, like Tsaganomys (now believed to be sciurormorph), have been claimed, but it now seems improbable that any are true bathyergoids." Simpson accordingly treats the Mongolian forms Tsaganomys and Cyclomylyus as sciurormorphs in his well known classification of mammals. (See below).

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It is probable that the bathyergids have a pronounced affinity with the hystricomorphs (see below), but a number of other authorities do not accept the mole-rats as hystricomorphs. Schaub (1953, 399) finds that the bathyergids are so highly specialized that closer affinities are entirely unknown. Romer (1958, 501) regards them as an early specialized offshoot of primitive sciuromorph stock, not closely related to any other group. Wood (1955, 185) states that the best guess is perhaps that these animals separated from the Paramyidae (i.e. Sciuromorpha) in the early or middle Eocene. On the other hand, one has the opinion of Burke (1936, 137, 138) who concluded that the Mongolian Tsaganomys was related to Ardynomys, an early Oligocene semi-fossorial cylindrodontid (i.e. sciuromorph). This interpretation was also accepted by Wilson (1949, 93), who called them specialized cylindrodontines.

Tullberg (1899) was the first to place the bathyergids with the hystricomorphs (Landry, 1957, 66), concluding that these forms must have split off at the very base of the hystricomorph line and hence deserved equal rank with the three classical suborders (see below). Landry also accepts the late Oligocene Mongolian forms (Tsaganomys and Cyclomytus) to be true bathyergids. Furthermore, he maintains that these Mongolian specimens were as highly specialized as the living forms, and that consequently the family must have split off from the hystricomorph-types during the early part of the Tertiary. This conclusion fits in with  
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the fact (as mentioned by Tullberg) that in the bathyergids the scaphoid (radiale) and lunar bones of the wrist are unfused, a primitive rodent characteristic.

Furthermore, Landry (p. 74) states that a decision as to which of the living Old World hystricomorphs are related to the bathyergids is not easy, for the former are all highly specialized. The hystrids as such are far too specialized although some are known as fossils from the late Miocene. The hystricids are really the adaptive antithesis of bathyergids in that the trend among hystricids is toward larger and larger nasal cavities, well illustrated in extreme forms such as Hystrix africae-australis and Hystrix cristata, where the nasal cavity is as large as the brain case. However, the most primitive porcupine, Trichys, does not show this nasal expansion, and it is possible that such an unspecialized hystricid could have given rise to the bathyergids. However, there is no evidence at all that it did so.

Landry (1957, 74) also discussed certain points of similarities between the cane rat Thryonomys and Bathyergus. Both forms possess grooved upper incisors, recurved lower incisors and a short diastema in the lower tooth row. He then continues to give reasons for believing that the rostrum of Bathyergus is not primitive among the bathyergids and this reduces the similarities to the presence of grooved incisors - which in itself is hardly impressive evidence for classifying the bathyergids with the Thryonomyidae. The grooved incisors may have developed by means of evolutionary/...

evolutionary parallelism.

An interesting line of thought as to the possible origin of the bathyergids is given by Landry, when he discusses a very generalized Old World hystricomorph, Petromys. This form is known as the African rock "rat". Landry (p. 74) states that it is to such a form as this that we would expect a primitive hystricomorph to be related. Paraphrasing Landry rather lengthily, his line of thought runs more or less as follows: Among the Old World hystricomorphs the otic region of Petromys resembles that of the bathyergids rather closely. In these forms, as in many other rodents, the mastoid part of the bulla bulges backward between the lateral process of the supra-occipital and the paroccipital processes of the exoccipitals so that there is a wide expanse of mastoid surface at a deeper level than at the occipital fingers which surround it. In Thryonomys and the hystricids the paroccipital process is much closer to the lateral process of the supra-occipital so that only a little of the mastoid shows between the processes. This seating of the mastoid in a notch of occipital bone is apparently a primitive rodent character for it is found in many rodents. A long lateral process of the supra-occipital is not limited to the hystricomorphs, nor is it even found most frequently among them. The specialization of the otic region (i.e. the paroccipital process being closer to the lateral process) in all other Old World hystricomorphs besides Petromys leaves it the closest relative of the bathyergids by default.

Landry (p. 75) furthermore postulates  
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then that some primitive rat-like hystricomorph, more or less similar in general appearance to the living Petromys gave rise to the Bathyergidae. Such a form however, was still more primitive than Petromys in that the scaphoid and lunar elements were not fused and that it certainly possessed less specialized cheekteeth.

Although Burke (1936, 137, 138) has concluded that the Mongolian fossils are cylindrodontid in nature, (i.e. sciuromorph) Landry (1957, 73) can not accept the possibility that the highly specialized hystricognath jaw could possibly be derived from the jaw of cylindrodonts. Yet one does find a typical hystricomorphine jaw structure in the bathyergids. Landry maintains that in fossorial rodents which have come from sciurognath stock (e.g. Spalax occurring in the Mediterranean region, Ellobius which is found in Eastern Europe and Asia and Rhizomys, another Asiatic form) and whose crania have become modified as that of Tsaganomys for fossorial life, the typical sciurognath lower jaw is retained. According to him, an exaggerated hystricognath jaw is, therefore, not part of the adaptation to a fossorial mode of life.

As has been indicated above, the meagre paleontological data available concerning the bathyergids come from Asian and African deposits. The Asian finds are much older geologically speaking and will be discussed briefly below.

Matthews and Granger (1923) described Tsaganomys altaicus and Cyclomytus lohensis as bathyergids from Hsanda Gol (Late Oligocene) in Mongolia/...

Mongolia. According to Landry (1957, 72) the greater part of a skull and jaws are figured, but from these drawings it cannot be ascertained whether the jaws were hystriocognath. On the other hand, Teilhard de Chardin (1926) also described T. altaicus from Upper Oligocene deposits in western Kansu (Mongolia) and figures an almost complete lower jaw, which in ventral view is decidedly hystriocognath (Landry, p. 72), with the angular portion curving up at the posterior end exactly as in the bathyergids. From these illustrations it is clear that the infraorbital foramen is small while the roots of the upper incisors apparently do not reach back beyond the first premolar. Landry (p. 72) states however, that it can not be ascertained from Teilhard de Chardin's figures whether the pterygoid fossae are broken through to the orbits, a point which would be crucial in deciding its hystriocomorph or bathyergid character.

In 1937, Bohlin also reported Tsaganomys altaicus from Upper Oligocene deposits in Western Kansu, and these finds are beautifully illustrated in his paper. In these specimens the enamel does not surround the tooth prism entirely as Matthews and Granger have stated to be the case in their specimens. In the  $m \bar{3}$  only the posterior outer half of the tooth possesses enamel while in the other molars the anterior portions are all devoid of encircling enamel. The upper molars are partially encircled by enamel and this corresponds to the Hsanda Gol specimens. From Bohlin's figures, the lower jaws look decidedly hystriocognath.

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In addition to the above mentioned finds, Young and Chow (1956, 456) described some Oligocene mammals from Lingwu, Northern Kansu (Mongolia) which included some broken incisors and a fragment of a lower jaw which they referred to as Cyclomytus lohensis. They state that these fossils resemble Tsaganomys but that they are smaller and that the roots of the cheekteeth are constricted and tend to be closed at the lower ends. The crowns are comparatively low while there is a trace of an external fold on the antero-external side of the fourth lower premolar. The incisors are relatively large, with flat enamel surfaces and ornamented with "barely visible fine striae". These authors state that Teilhard de Chardin's smaller forms correspond more or less in size to theirs. (Teilhard de Chardin divided his fossil specimens into two groups, based on size: i.e. larger and smaller forms). C.lohensis has also been reported from Tatal-Gol, Mongolia by Vinogradov and Gambarian (1952).

The differing interpretations as to the possible phylogenetic and taxonomic position of these Mongolian finds has briefly been commented upon above, e.g. the opinions held by Burke (1936), Wood (1955) and Wilson (1949). These authors all interpret these finds as semifossorial specialized cylindrodontid sciuriforms. On the other hand, some of Landry's (1957) arguments have also been listed above where he argues for the hystricomorph, and consequently bathyergid nature of these fossils. As has been related above, he cannot see how the hystriognath jaw could have developed from the sciuriform/...

sciuromorph lower jaw and he furthermore maintains, quite rightly, that the following information is necessary before the correct nature of these fossils can finally be settled:

- (i) the tympanic bullae of Tsaganomys and Cyclomylus should be opened, in order to ascertain whether the malleus and incus are fused (as they are in the bathyergids) and
- (ii) that sections of the incisors should be made and the patterns of the enamel prisms checked (for they have a definitive arrangement in the hystricomorphs) and finally
- (iii) to find out whether the pterygoid fossa communicates with the orbit.

In his work, Landry did not investigate these aspects (probably due to the fact that the specimens were not available) and he concludes that Matthews and Granger were probably right in accepting the genera Tsaganomys and Cyclomylus as bathyergids and in his own work Landry treats and accepts these fossils accordingly.

If this interpretation is accepted (and in the present work a number of facts are briefly discussed pointing to the hystricomorph nature of the bathyergids - see Chapter 5 - one can agree with Landry in stating that the earliest possible records of hystricomorphs in the Old World has been yielded by Oligocene deposits of Mongolia when the ctenodactylids and bathyergids first appear.

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It is interesting to note that the late Dr. Robert Broom also accepted these Mongolian fossils as bathyergids. Broom (1934, 476) states that although these forms are not at all closely related to the South African Pleistocene giant rodent mole Gypсорhynchus (see below) "... they are interesting in showing that the giant rodent moles occur as far back as Oligocene.... times and (that they were) widely distributed over the Old World."

I have not seen these controversial fossils personally and it may seem wise to refrain from any further comments about their interpretation and the possible validity of such an interpretation. If an opinion may be voiced, it may be well to point out, that apart from the clearly hystri-comorph jaw, the essential morphological criteria as far as the cranium is concerned, are still missing, as listed by Landry. Furthermore, the fact that Ardynomys (a definite cylindrodont) has also been found in Late Oligocene Asian deposits (and bearing Burke's (1936) opinion in mind) it may well be that these animals are not bathyergids, as assumed by Matthews and Granger, as well as by Landry. The facts pertaining to these fossils were discussed rather lengthily in the above paragraphs, as to allow the reader to draw his own conclusions about the possible taxonomic position of these scantily represented fossils.

When the attention is focussed on Africa for paleontological data, the fossils seem to offer firmer ground. The different fossil finds will be discussed briefly below, in a sequence corresponding to the geological strata and age of the deposits.

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The earliest African bathyergid is known from the Oligocene-Miocene boundary from South West Africa and has been named Bathyergoides neotertianus. Stromer (1924) reported this fossil from deposits south of Luderitz Bay. This preliminary notification was followed in 1926 by a fuller description (Stromer, 1926). (Hopwood and Hollyfield, 1954, 132).

Bathyergoides neotertianus is only known from a few fragmentary jaws and Broom (1934, 475) states that judging from Stromer's figures, these fossils are considerably nearer to Georychus than to Bathyergus, and that the molars are short rooted teeth with folded enamel, quite different to the type of tooth structure found in Gypsoorychus. He thus concludes that these South West African fossils are not closely allied to the Pleistocene form, Gypsoorychus, nor to the Mongolian genera as already related above.

Apart from this lower Miocene genus (which apparently is unquestionably bathyergid in its nature) there is a pronounced gap in African paleontological data as far as the bathyergids are concerned, for all the other bathyergid fossils have been found in Pleistocene deposits. Incidentally, this paucity of material from deposits ranging from Miocene to Upper Pliocene formations applies to other rodents as well.

Starting with the extralimital fossil bathyergids (i.e. north of the Cunene and Sambezi rivers), Heterocephalus quenstedti is to be mentioned. This fossil species of the extant 'sand puppy' from Somaliland was discovered by

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the Kohl-Laren'schen expedition to Central and Eastern Africa in 1937-1939 and was described in a preliminary note by Dietrich (1941). This find from Lower Pleistocene deposits in Tanganyika was described more fully in a subsequent paper by Dietrich (1942, 66) together with illustrations. It evidently points to the presence of these bathyergids in the early Quaternary of East Africa. The overall resemblance to the extant Heterocephalus glaber of Abyssinia and Somaliland is great.

It is interesting to note that this genus has had a far greater geographical distribution in the past. Lavocat (1957, 133) reported this genus from the Makapansgat breccias of the Central Transvaal. Furthermore, the presence of another form, also from this locality, Heterocephaloides darti, has also been recorded by Lavocat (personal communication). The elements representing this genus are a few isolated teeth and portions of lower jaws. As far as I am aware, no description of these fossils has yet been published.

From Pleistocene deposits in South Africa, an interesting form of a giant rodent mole has been recorded, viz. Gypsorhynchus. According to Broom, three species, darti, minor and makapani are represented in Southern African breccias.

In 1930, Broom announced the discovery of the first specimen in breccias associated with the ape-man Australopithecus africanus found at Taung in 1925. This type was named Gypsorhynchus darti, after Prof. R.A. Dart, who first described the australopithecine Taung "child". The specimens were sufficiently preserved to be identified and it appeared that/...

that they are rather larger than skulls possessed by Bathyergus. The remains consisted of the following:

- (i) the anterior half of one skull with both upper and lower jaws preserved in part (type specimen);
- (ii) much of a second snout with most of the frontal region present as well as an imperfect palate.

The present author was unable to trace the type specimen needed for closer, more detailed inspection.

Broom (1934, 474) described these fossils in greater detail and provided illustrations of the dorsal and lateral views as well as the occlusal surfaces of the upper molars. In the same paper he postulated that Gypсорhynchus is allied to Georychus for the following reasons:

- (i) The upper incisors project forward as in Georychus;
- (ii) there are no grooves on the upper incisors;
- (iii) in Bathyergus the anterior portions of the nasals widen out in front near the nostrils, while in Georychus this widening does not occur and the latter condition is also found in Gypсорhynchus;
- (iv) the arrangement of the sutures in the posterior nasal region of the skull, as well as the structure of the lateral walls of the frontals and maxillae, correspond in Georychus and Gypсорhynchus.

There are a number of morphological aspects in which the fossil Gypсорhynchus differs from

Georychus/...

Georychus and which may be tabulated as follows:

- (i) there is no incisor bulge or ridge below the optic foramen in the fossil form as is the case in Georychus;
- (ii) the frontal region in Bathyergus and Georychus is narrower than in Gypсорhychus;
- (iii) the snout of Gypсорhychus is about twice as long compared to the extant Georychus.

The teeth of Gypсорhychus are interesting: they are not like those found in Bathyergus or Georychus. The maxillary teeth consist of four molariform molars, the first three broad and flat with unfolded enamel, while the fourth molar is triangular with (probably) folded enamel. Broom thought it possible that the molars were permanently growing and the flattened nature and persistent growth also applied to the teeth of the mandible (Broom, 1934, 475). Although only the front half of the lower jaw has been preserved, the lower jaw probably had a similar structure to that of Georychus.

These specimens were also illustrated (norma dorsalis) by Broom (1948, 48). Additional information about dimensions were also supplied: "basal length" of skull probably 70 mm., while the length of the nasals in the type was 26.5 mm.

Another Gypсорhychus specimen was discovered in 1937 in Hrdlicka's Cave, Buxton near Taung and was first described and referred to by Broom (1939, 315) as G.darti, (later renamed G.minor - see below). This find consisted of a practically complete skull without a mandible and illustrations of the dorsal and ventral/...

ventral aspects accompanied the description. The right incisor was missing, as well as the premolar and three molars of the left side in addition to the premolar of the right maxilla. All the tooth sockets were well preserved. The incisors were not grooved as in Bathyergus and as in the case of G.darti the maxillary teeth differed from all the living species, in being flattened, permanently growing, consisting of flattened dental plates. The dimensions of the first molar on its worn surface was 5.2 mm. x 1.2 mm., with the second molar having similar dimensions. The third molar was folded on its inner surface and the teeth "..... differ very greatly from those not only of other known Bathyergids, but apparently from all other rodents" (Broom, 1939, 316).

As is the case in G.darti, this specimen could also not be traced.

On page 316 Broom states that the general shape and structure of the skull agrees well with that of Cryptomys and other living allied genera, with the size of the skull comparable to that of Bathyergus and Cryptomys ansorgei. The length of the skull from the gnathion to the top of the occipital crest was 54 mm. while the width across the zygoma was 40 mm. The nasals are as long as in C.ansorgei and the facial portion of the maxilla resembles Bathyergus to a greater extent due to its small infra-orbital foramen as well as the flat palatal portion in front of the premolars. On the other hand, "the little hard palate formed by the palatines resemble that of Cryptomys more than of Bathyergus". This Gypsorychus specimen had large air sinusses in its frontal/...

frontal region but in other respects the "agreement with the giant Cryptomys is close." Furthermore, "the parietal and squamosal regions are also similar to those in Cryptomys and this also applies to the posterior part of the base of the skull" (Broom, 1939, 316). The premaxillaries are similar to those of the three extant living genera in South Africa. In the fossil the upper incisors project a little more than in Cryptomys but not much more than in Georychus. An important point of resemblance is that the posterior growing root of the incisor is situated a little behind and above the last molar, as is found in Cryptomys. According to Broom, "... it thus differs from Cryptomys, Georychus and Heliophobius, but of course it resembles these genera in this character more than it does Bathyergus".

This specimen, described in 1939, was also figured in Broom and Schepers (1946, 26-27) as G.darti but in 1948 Broom changed the name of the specimen to G.minor. The reason for doing this was that he found this specimen to be considerably smaller than the type specimen of G.darti, on which this species was originally founded. The basal length of G.minor is about 54 mm. (in G.darti about 70 mm.), while the length of the nasals in G.minor equals about 19 mm., (compared to 26.5 mm. in G.darti). Apart from size, the two specimens agreed fairly closely, but Broom finds that the difference in size is too great to accept these fossils as representing one species. Furthermore, he supplies the following points of difference:

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G.minorG.darti

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| (i) snout relatively narrower  | (i) snout wider  |
| (ii) a deeper groove on the premaxilla above the incisors                          | (ii) groove shallower  |
| (iii) temporal muscles smaller, for the muscular impressions are further backwards | (iii) temporal muscles larger, for impressions are further forward (Broom, 1948, 49) |
| (iv) infraorbital canal smaller  | (iv) infraorbital canal larger   |
| (v) teeth smaller  | (v) teeth larger judged by the sockets of the third upper molar                      |
| (vi) the tooththrows of the molars more divergent.                                 | (vi) tooththrows of molars more convergent.  |

Broom concludes (1939, 316) that this giant rodent mole (i.e. Gypsorychus) is a specialized and not primitive type, closely related to Cryptomys.

During 1946 the anterior part of a lower jaw of another Gypsorychus specimen was found at Makapansgat, in the Central Transvaal. It consisted of a perfect incisor "with the three molars in nearly perfect condition and the socket of the 4th premolar" (Broom, 1948, 48).

Although the mandible is imperfect Broom attached a new specific name to this find, i.e. G. makapani. According to him, the shape of the anterior part of the mandible differs considerably from G.darti, especially the symphysis which is

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deeper while the jaw seems to be more powerfully built.

The type specimen is housed in the Division of Physical Anthropology and Paleontology of the Transvaal Museum, Pretoria.

The lower incisor is large, its undamaged and exposed portion measuring 32 mm., whilst near the base its width is 5 mm., "with the thickness slightly more" (Broom, loc. cit.). As is evident from the brief description of the Taung material given in the preceding paragraphs, the lower molars of Gypсорhynchus are not satisfactorily known. The first upper molar of G.darti measures 5.8 x 1.8 mm. and 5.2 x 1.3 (1.2) mm. in G. minor. Broom states that it is unlikely that the first upper and lower molars would differ much in size. The socket of the fourth lower premolar of G. makapani is a broad oval, measuring 5.2 x 2.4 mm. The first lower molar in this specimen, being well preserved, measures, according to Broom, 7.0 x 1.9 mm., the second molar 6.8 x 2.0 mm. and the third lower molar 6.8 x 1.5 mm. I have remeasured the first lower molar of G. makapani and found it to be 6.4 x 1.7 mm. (compared to 7.0 x 1.9 mm. which Broom obtained). From these figures it may be deduced that the molars of G. makapani are considerably larger than the molars found in the other two species.

During 1959 a virtually complete skull (although badly damaged in some sections) was extracted from the Makapansgat breccias and the authorities of the Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, kindly allowed me to investigate and describe this skull/...

skull. (Fig. 1.1, 1.2). This description has not yet been completed but a number of morphological aspects may be enumerated. The two rows of molars are present, with the occlusal surfaces of the left side damaged. The  $m_1$  measures 5.9 x 1.6 mm. and the  $m_2$  5.5 x 1.4 mm. The molars are also platelike, molariform, without folded enamel while the third molar is triangular, also without a folded posterior-medial portion. There is a pronounced incisor ridge present below the optic foramen. The distance between the anterior points of the nasals and the posterior rim of the occiput is approximately 55 mm. - this figure could not be determined accurately, for the nasal elements are missing. Similarly, the jugals are missing, and the estimated width across the zygomatic arches is about 44 mm. The rightsided tympanic bulla is present.

The correct identification of this specimen is considerably hampered by the absence of the Taung specimens which are not available for detailed comparison. The only other alternative is to compare this specimen with the natural size drawings which accompanied the different descriptions by Broom. Furthermore, many structural elements which Broom uses for comparative purposes, are missing in this specimen, e.g. the nasals.

This specimen has a number of features common to both G.darti and G.minor as well as a few which do not correspond to either. The skull shows a general overall agreement in structure to Georychus, as Broom has remarked for G.darti, but in both cases the fossils are much larger than the extant genus.

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As in G.darti, the frontals are wide and the snout is reasonably long. The first upper molar of this specimen measures 5.9 x 1.6 mm. which corresponds very well with the similar tooth in G.darti (i.e. 5.8 x 1.8 mm.). However, here the resemblance to G.darti ends. According to Broom, G.darti probably had folded enamel on the third molar: this feature is definitely lacking in this specimen. Furthermore, G.darti had no incisor bulge below the optic foramen while in this specimen there is a very clear ridge visible. Broom did not define his 'basal length' measurement, obtained for G.darti, which he gave as "about 70 mm." On looking at the natural size illustration (Broom, 1948, 48) this length probably represents the distance between the anterior points of the nasals to the dorsal posterior rim of the occipital region. (It may be pointed out that the posterior part of the drawing illustrating the skull of G.darti was "reconstructed" after the structure of the occiput in G.minor). The equivalent distance in the specimen under consideration is estimated to be 55 mm. (due to the absence of the nasal elements as related above), which corresponds reasonably well with the value Broom obtained (apparently based on the same points of measurement) for G.minor i.e. 54 mm.

Comparing the natural size drawing of G. minor (Broom 1939, 315) with this specimen, the overall size is more or less comparable. As far as the incisor bulge below the optic foramen is concerned, there is no information available for G.minor and this also applies to the width of the frontals and length of the snout. Morphologically, there are

no obvious differences in the structure of the molars between the Makapan specimen and G.minor (i.e. molariform, platelike, etc.) but one point of difference relating to the posterior third upper molar is evident however: Broom stated that this tooth had an enamel fold on its postero-medial rim, which is absent in this specimen. Although there is a very marked resemblance in size between the Makapansgat fossil and G.minor, it is also evident that the individual molar teeth of the maxillae are far larger in the newer find than in G.minor which is evident from the following comparison:

<u>G.minor</u>	<u>Makapansgat specimen</u>
right m <u>1</u> : 5.2 x 1.2 (1.3) mm.	5.9 x 1.6 mm.
right m <u>2</u> : 5.2 x 1.2 mm.	5.5 x 1.4 mm.

In recent genera (especially in Bathyergus) it is a fairly general rule that the length of the lower toothrow (as well as the individual teeth) is longer than the upper toothrow. In the lower jaw found in 1946, it seems that the dimensions of the m I (6.4 x 1.7 mm.) could possibly form a reasonably acceptable counterpart for the Makapansgat skull and the impression is gained that the erection of the species makapani may have been premature, when based on overall size alone. On the other hand, the difference in size between the molars of the Makapan skull and G.minor are very pronounced indeed, which may justify the acceptance of G.makapani as a valid species.

As far as the evidence goes (related briefly above), I am prepared to accept the Makapansgat skull tentatively as an example of G.makapani

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(hitherto unknown), but this assumption has to allow for the following facts:

- (i) that the original specimens of G.darti and G.minor were not available for direct comparison;
- (ii) that the skull has a strong size resemblance to G.minor (apart from the size of the molar teeth); and
- (iii) that actual points of comparison, which could be gleaned from the published accounts, could often not be used, due to the damaged nature of the Makapansgat specimen.

The foregoing paragraphs have related somewhat lengthily, various aspects of the giant fossil rodent moles or mole-rats which occur in the South African Pleistocene deposits. This has been done purposely because these finds are examples of bathyergids which are known as fossils from Southern Africa, and it serves to illustrate how little material is available for possible conclusions. Secondly, it is also clear that the interpretations which may be held at present are bound to be changed in future when (possibly) more material becomes available. Thirdly, this information has been given to illustrate and possibly justify Broom's remarks concerning G.darti and G.minor respectively: "It will be seen that we have in this fossil form a new genus of Bathyergid mole allied to Georychus but.... (which) cannot be ancestral to Georychus, nor is it likely to have evolved from Georychus as we have it today. But very probably Georychus and the giant fossil/...

fossil mole have had a common ancestor" (Broom, 1934, 475), and that G.minor is a specialized and not primitive type, "closely related to Cryptomys" (Broom, 1939, 316).

Apart from the fossil genus Gypsorhynchus which occurs in australopithecine deposits (where they may have served as additional titbits for the Australopithecus diet (Broom and Schepers, 1946, 31), the extant genus Cryptomys also occurs in Pleistocene breccias (de Graaff, 1960, 88).

Cryptomys robertsi (Broom, 1937, 1) is a fossil species based on a type housed in the Transvaal Museum, Pretoria. According to Broom, the type site is probably Schurveberg, near Pretoria. It is a moderately large species, with one mandible measuring "from the front of the incisor to the back part of the angular portion of the jaw 40 mm." The shape of the hind portion of the jaw is different to any species Broom was able to compare it with (de Graaff, op.cit.), having a distinct ridge passing forward on the outer side of the jaw from the condyle, a peculiarity which is not entirely attributable to the roots of the lower incisors. The teeth are relatively small. In one specimen the pm, m  $\bar{1}$  and m  $\bar{2}$  together measured 5.2 mm., with the tooth crowns low "and each tooth has the enamel of the upper half folded in on both the outer and inner sides" (Broom, op.cit.).

The distribution of this fossil is interesting: it has been identified in all the Pleistocene fossiliferous localities hitherto analysed (de Graaff, 1960, 104). The material is scantily represented however: the frequency of these fossils

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tend to decrease in abundance as the younger Pleistocene deposits (e.g. Makapansgat compared to the older Taung) are approached. The versatility of this species is illustrated by its presence in all Pleistocene breccias hitherto investigated (de Graaff, 1960, 110).

When the later Pleistocene fossiliferous breccias are considered, one finds that there are quite a number of localities (e.g. along the Vaal river, Transvaal, Vlakkraal in the Orange Free State, etc.) but that their mammalian microfaunal element is not satisfactorily known. Some information on the Hopefield area (where the neanderthaloid Saldanah man was found) is available however. Amongst the microfaunal mammalian fossils found in this vicinity, a number of mole-rat fossils have come to light. This material is housed in the South African Museum, Cape Town. According to Prof. R. Singer (personal communication), the extant genera Bathyergus sp. (cf. suillus) and Georychus sp. (cf. capensis) have tentatively been diagnosed from Elandsfontein, a few miles to the west of Hopefield. Today both these species occur mainly in the south-western Cape and from this data it may be deduced firstly, that they are already resident in that area for a considerable span of time; secondly, that the fossils are not more (if anything) than subspecifically distinct from the living forms. This is the only evidence hitherto where the extant Bathyergus and Georychus are known to be represented in the fossil or sub-fossil state.

From what has been briefly discussed above regarding the paleontological data of the bathyergids

in Africa, the only definite fact emerging is that they are all definitely bathyergid (compared to the uncertain status of the Mongolian finds). Some interesting historical zoogeographical facts have also emerged (e.g. the Pleistocene distribution of Heterocephalus and Cryptomys) but it is clear that, based on fossil evidence alone, very little information has come to light about the possible phylogenetic relationships between the extant and fossil forms. I have none the less attempted a possible provisional phylogenetic scheme (based on very little information) and it is offered here for what it may be worth, bearing in mind its very tentative nature (Fig. 2.3).