CHAPTER 4

DESCRIPTION OF THE SKULL OF BATHYERGUS, CRYPTOMYS AND GEORYCHUS

In order to facilitate comparisons of the features of skulls referred to in this work it may serve a useful purpose to describe the skull of Bathyergus to a greater extent. Apart from brief descriptions of some salient features, there is no virtually complete account of a bathyergid skull available in the existing literature. The terminology used in this chapter corresponds to the accepted nomenclature without implying rigid homologies between the different elements of the skull compared with similar elements in skulls of other animals. This aspect can only be put in proper perspective by a detailed study of these elements during ontogenetic development and this embryological information is not available to date.

The description which follows is based on a skull of Bathyergus suillus (Schreber) and the reasons for choosing this species are two-fold:

(i) in this species, the largest bathyergid skull is encountered, facilitating easier identification of the various units of the skull. B. janetta, the only other species within the genus is a far smaller animal;

(ii) B. suillus has a fairly wide geographical distribution in the south-western Cape Province and is therefore the most likely to be encountered.

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The description of the skull of Bathyergus which follows below, will then be supplemented by short notes about the skulls of Georychus and Cryptomys, especially emphasizing those aspects of their crania which differ from Bathyergus. Where no further comments are offered, it is inferred that what has been said for Bathyergus, is also applicable to both Georychus and Cryptomys.

General Appearance:

The skull of Bathyergus is rather elongate, (Fig. 4.1), the average length from gnathion to the posterior dorsal rim of the occipital region being approximately 50.0 mm. Seen from the lateral aspect, it is more or less flattened dorsally, tapering with a small angle downwards towards the muzzle. The skull is robust and strongly built as would be expected in fossorial animals. The greatest width is across the zygomatic arches.

In contract to Bathyergus, the skulls of Georychus and Cryptomys are much smaller: the average length as defined above being approximately 42.0 mm. and 32.0 mm. for Georychus and Cryptomys respectively. Seen from the lateral aspect, both these skuls have a definite convex curvature dorsally, compared with the flat dorsal aspect of the skull in Bathyergus. Furthermore, the skulls of Georychus and Cryptomys are not as robust and sturdily constructed as is the case in Bathyergus. (Fig. 4.2, 4.3).

Naso-maxillary region:

In Bathyergus the nasals to a certain extent protrude dorsally above the underlying premaxillaries, tapering to a point posteriorly on reaching the frontals, while anteriorly they terminate bluntly after widening slightly before the anterior rim is reached. There seems to be no special structure for the attachment of the nose pad, as is found in many chrysochlorids. The lateral edges of the nasal elements are limited

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by the well developed premaxillaries except for the most posterior portion where they are bound and fused to the frontals. Anteriorly, the nasals form the dorsal edge of the aperture of the external nares.

The foramen of the external nares (seen from the front of the skull), is almost square in appearance being wider dorsally than ventrally and narrower transversely than its height. The ventral rim, formed by the premaxillaries (which incidentally also forms the lateral walls) is narrower than the dorsal rim made up by the anterior portions of the nasal elements.

The premaxillaries are strong and well developed bulging out laterally to house the strong upper incisors. On the dorsal surface of the premaxillaries are small openings (irregularly spaced), probably for exit of small branches of the olfactory nerve innervating the sensitive nose and snout. The premaxillaries taper down laterally and medially and fuse in the midventral line to form the strong diastemic region of the snout. Anteriorly, they are also in contact with each other just above the upper incisors (forming the lower rim of the external nares) and each premaxilla sends down a wedgelike protrusion between the two incisors extending to about half-way down the length of the exposed incisors. Where the two premaxillaries meet medially dorsal to the incisors there is a small elevation which may present a clear gnathion. Posteriorly, the premaxillary elements make contact with the frontals by means of a wedgelike structure, while laterally and ventrally they fuse with the

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maxillaries by means of a clearly defined suture. On this suture, in the midventral line of the skull are two small, elongate (but nevertheless well developed) anterior palatine foramina.

The muzzle protrudes and is relatively narrow in comparison to the rest of the skull.

As far as the naso-maxillary region of Georychus and Cryptomys is concerned, the following may be pointed out: in Georychus the contact made by the anterior rim of the frontals with the posterior rim of the nasals are not as sharply pointed as in Bathyergus. In Cryptomys the posterior portions of the nasals terminate a short distance before reaching the main body of the frontal elements and the latter send out a rostrally directed process, meeting the posterior rim of the nasals. Although there is a certain degree of variation in this character, this aspect may be used as a criterium to distinguish between skulls of Georychus and Cryptomys.

Furthermore, in Georychus and Bathyergus the nasal elements tend to bulge out laterally to a certain extent (more or less in the middle portion of these elements) while this is not the case in Cryptomys. In this instance, the outer edges of the nasals form a more or less straight line from the front to the back.

Looking at the skulls of Georychus and Cryptomys from the norma anterior it will be seen that the shape of the exterior nasal foramen looks something like an inverted triangle, compared to the more "squared" condition in Bathyergus. This also seems to be a feature in which individual variation will be encountered.

Finally, in Cryptomys the large incisors housed in the premaxillaries underlying the nasals do not seem to bulge out laterally to such an extent as is the case in both Bathyergus and Georychus. Comparatively speaking, the muzzle in Cryptomys is far less robust compared to the other two genera, which may seem to be surprising, in view of the fact that the muzzle is an important portion of the skull during burrowing activities.

The orbital region and zygomatic arches:

In Bathyergus the frontals are strongly developed, fusing with the posterior tapered points of the nasals and the wedgelike protrusions of the posterior premaxillaries antero-dorsally. Antero-dorsolaterally and dorso-laterally they fuse with the ascending

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portion of the maxilla and lachrymals as well as the orbitosphenoid respectively. Near its point of contact with the lachrymals (which are very small elements), the frontals widen out laterally to a certain extent. Postero-laterally, they are limited by the squamosal process of the zygomatic arch while medio-posteriorly they make contact with the parietal elements. The two frontal elements are separated by a small medial ridge, which is a forward extension of the sagittal crest between the parietals. This ridge forks into two near the broadening of the frontal elements as described above. There is a marked interorbital constriction across the frontals slightly anterior to the suture of the squamosal process of the zygoma. There is no indication whatsoever of a postorbital process on the frontals. Consequently, the orbits are in open contact with the temporal region.

Within the orbit there is a lachrymal element present in addition to a large, orbitally situated lachrymal foramen. This foramen is situated dorso-laterally more or less on the suture between the anterior part of the lachrymals and the perpendicularly ascending portion of the maxilla (through which passes the infraorbital foramen). In juvenile or adult specimens, the sutures limiting the lachrymal elements can not be distinguished easily due to a very strong ankylosis with the surrounding elements. Ventrally and postero-ventrally the lachrymal is connected to the maxilla and orbitosphenoid respectively.

The orbitosphenoid element has the usual mammalian position and also has a number of distinct

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foramina. The functions of these various foramina have not yet been determined, and the following nomenclature is therefore tentative. On its anterior border, there is a spheno-palatine foramen. Posteriorly, the orbitosphenoid is depressed medially resulting in a groove which is limited dorsally by the frontals, posteriorly by the pterygoid fossa breaking through into the orbit (see below) and ventrally mainly by the maxillaries. Within this groove is a small optic foramen followed by an equally small more posteriorly situated anterior lacerum foramen.

Seen from the dorsal aspect the zygomatic arches are rather wide, consisting of the usual elements, i.e. a maxillary complement anteriorly, a separate jugal element in the middle and a squamosal portion posteriorly. The jugal element extends ventrally slightly beyond the squamosal contribution so that seen from the norma dorsalis it can be seen as a small piece of bone jutting posteriorly from below the squamosal contribution to the zygoma. The maxilla is joined to the jugale anteriorly by means of a dove-tail joint while posteriorly the jugal is overlain by the squamosal contribution.

The jugal arches are solidly constructed; the maxilla forms a more or less perpendicular transverse plate through which a small, nearly circular infraorbital foramen passes. This maxillary portion of the zygoma does not form an antero-posteriorly directed perpendicular plate in front of the orbits as is found in many murids. Just ventral to each infraorbital foramen near the suture

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between this element and the jugal, the maxilla shows a flattened, horizontal surface which may serve as an insertion point for the muscles closing the diastema (zygomatic plate).

The squamosal portion of the zygoma forms the elongated anteriorly-posteriorly directed glenoid fossa for articulation with the condyle of the mandible. Its lateral edge is supplied by the jugal element itself, and on the whole, the fossa is wide allowing a certain laterally-directed movement of the lower jaw in addition to the usual front- and backward movements.

As is the case in both _Bathyergus_ and _Cryptomys_, the frontal elements in _Georychus_ are limited postero-laterally by the squamosal process of the zygoma and postero-medially by the parietals. However, the distance between these two squamosal processes on either side is greater in _Georychus_ than in _Bathyergus_ or _Cryptomys_.

In view of the fact that the roots of the upper incisors are situated in the pterygoidal region in both _Cryptomys_ and _Georychus_, a number of differences are bound to be present in the orbital region compared to _Bathyergus_. In the former two genera the lachrymal foramen is situated at a slightly higher (more dorsal) level in order to allow the incisor to pass below it. As is the case in _Bathyergus_, the infraorbital foramen within the orbit is small and Landry (1957, 66) ascribed this condition (i.e. the reduction) of the infraorbital foramen as secondary.

As in the case of _Bathyergus_, the precise role played by the different foramina in the orbital region of _Cryptomys_ and _Georychus_ is tentatively named and presented below. However, due to the large incisors, there is no sphenolateral foramen in either _Georychus_ or _Cryptomys_ and the optic foramen shares a common aperture with the anterior lacerum foramen, in the shape of a well developed groove (above the incisor sheath) through which one can see more or less into the braincase.

The jugal element in _Georychus_ and _Bathyergus_ meets the maxillary component anteriorly by means of a dove-tail joint. In _Cryptomys_, however, the jugal bone fits into a long groove on the maxillary component. This feature has been used by Roberts (1951, 382) to distinguish between members of the subfamily Georychinae (i.e. containing the genera _Georychus_ and _Cryptomys_).

The thickened, horizontal surface below the infraorbital foramen on the maxillary portion of the zygoma as described for Bathyergus is present in both Georychus and Cryptomys but is the least developed in the latter genus. In some skulls of this genus, it may virtually be said to be absent altogether.

The glenoid fossa in Georychus and Cryptomys is comparatively speaking shallower and broader than in Bathyergus. This may be correlated with the fact that the former two animals utilize their incisors during tunneling and this would imply a greater degree of moveability and motility of the mandibles in relation to the cranium, than is needed in Bathyergus.

The braincase:

The parietals, forming the dorso-medial section of the braincase are bound anteriorly and dorso-laterally as well as laterally by the posterior frontals and squamosal elements respectively. A conspicuous feature is the presence of a well developed sagittal crest, the posterior portion of which is formed by the supra-occipitals and not by the parietals. This ridge also extends rostrally between the frontals (although not as high and pronounced as between the parietals) as related above. Posteriorly the parietals are limited by the supra-occipitals, i.e. they do not reach the posterior rim of the skull.

In Georychus and Cryptomys the posterior rim of the parietals are more or less on the edge of the nuchal crest, compared to the condition in Bathyergus where the supra-occipitals contribute to the dorsal surface of the skull to a certain extent. In other words, in Georychus and Cryptomys the posterior edge of the parietals extend caudally to a greater extent than in Bathyergus.

The squamosal units, forming the dorso-lateral complement of the braincase are rather elongate structures extending backwards from about the posterior third of the frontals to the nuchal crest of the supra-occipitals. Near the posterior portion of the squamosal process of the jugal arch, is a small foramen apparently leading directly into the braincase, via the squamosal. Immediately anterior to the external auditory meatus the squamosals have a marked medially directed constriction, more or less mid-way between the squamosal portion of the zygoma and the posterior portion of the squamosals butting against the lateral extensions of the supraoccipitals. Seen from the dorsal side, the impression is created that the braincase is hereby constricted - this however, is not the case.

The constriction of the squamosals in _Georychus_ corresponds to a greater degree to that found in _Bathyergus_, while in _Cryptomys_ the hind (caudal) portion of this lateral notch is not so long as in either _Bathyergus_ or _Georychus_. The length of the braincase in _Cryptomys_ accordingly seems to be shorter.

The squamosals are limited antero-laterally by the descending frontals, and ventrally by the alisphenoid and tympanic bullae while posteriorly they are limited by the supraoccipitals. Anterior to the external auditory meatus, just below the constriction made by the squamosals (see above) and just posterior to the squamosal portion of the zygomatic arch, there is a large foramen of which the antero-ventral and dorsal walls are furnished by the squamosals while the posterior edge is supplied by the auditory bullae. This foramen leads directly into the dorso-lateral portion of the braincase but it could not be established what its possible function is. A similar situation is encountered in many murids which correspond to the postglenoid foramen. It may therefore be assumed that this is the equivalent foramen in the bathyergids.

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The antero-latero-ventral section of the braincase is constructed to a great extent by the alisphenoid. In bathyergids the alisphenoid elements are largely ventral to the squamosals. Dorsally, the alisphenoid meets the squamosal, antero-dorsally the frontals while it makes contact with the palatine and maxillary elements antero-ventrally. Postero-ventrally, it tapers to a point, meeting the basisphenoid close to the mid-line of the skull.

In _Bathyergus_ the alisphenoid makes contact with the palatine and maxillary elements by means of a thin sheet of bone which forms a lateral wall to a canal which in actual fact is the pterygoid fossa which has broken through from its original posterior position anteriorly into the orbit.

In both _Georychus_ and _Cryptomys_ the pterygoid fossa has not broken through into the orbit (i.e. below the alisphenoid as described above) due to the presence of the roots of the incisors in the pterygoid region.

Posteriorly, the alisphenoid is separated from the tympanic bulla by a large foramen lacerum medius. The medial edge of the alisphenoid forms part of the pterygoid fossa.

In neither _Georychus_ or _Cryptomys_ is the foramen lacerum medius so well developed as in _Bathyergus_ and it is the least developed in _Cryptomys_.

On looking into the pterygoid fossa from its posterior opening, it will be seen that there is a small bony canal on the outer wall of the pterygoid fossa. This canal is very flimsy, and may be complete or present in part, or in some cases, absent altogether. If present, this small

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canal leads into the orbit in Bathyergus and into the braincase in Georychus and Cryptomys.

On the alisphenoid, lateral to the pterygoid fossa and anterior to the foramen lacerum medius, is a well developed foramen ovale. Anterior to this foramen are three smaller apertures, all leading into the braincase and which may or may not all be present simultaneously or even symmetrically on both sides. The anterior two lie more or less dorso-ventrally to one another (the dorsal one being larger) and both occur more or less in line with the anterior rim of the glenoid fossa. In the absence of ontogenetical data, it can not be stated specifically what their possible functions are.

In Georychus and Cryptomys a well developed foramen ovale is also present. The distance between the hindrim of this foramen and the anterior part of the bulla is very small in Cryptomys in comparison to Bathyergus. In Georychus, the apertures referred to above in Bathyergus are also variable and this also applies to Cryptomys, where the largest dorsally situated foramen (more or less on the anterior rim of the glenoid fossa) is often the only one present.

The ventral portion of the braincase is made up by the following elements: a strong, well developed basioccipital which is separated from the bulla by a slitlike foramen lacerum posterius. Immediately anterior to the exoccipital condyles, within the exoccipital, is a well developed foramen condylare. Anteriorly, the basioccipital meets the basisphenoid (near the pointed antero-medial portion of the bullae) which in turn is bound laterally by the palatines and makes contact anteriorly with the presphenoid. The sutures between the basisphenoid and palatine elements are not clear, while the vomer can be seen within the nares interni. Dorsal to the medially-directed anterior point of the tapering bulla, on the basisphenoid (near the point of fusion of this element with the posteriorly pointed alisphenoid), is a small but distinct foramen, the Eustachian aperture.

In Cryptomys the basioccipital is a relatively narrow element in comparison to Georychus or Bathyergus, while the distance between the bullae and exoccipitals is also very slight so that the foramen lacerum posterius as well as the condylar foramen is not easily seen in Cryptomys. In this respect Georychus corresponds reasonably well to the condition found in Bathyergus.

Posteriorly, the walls of the braincase are constructed by the supraoccipitals dorsally and the exoccipitals ventrally. The suture between these elements can not be detected with ease in adult specimens. Postero-dorsally, the supraoccipitals form a strong nuchal crest which folds over dorsally and posteriorly on the vertical surface of the occipital region. The supraoccipitals encroach a small distance on to the dorsal surface of the skull, contributing to the structure of the posterior part of the sagittal crest, as related above. Furthermore, they consequently fuse with the posterior edges of the parietals and squamosals. The nuchal crest of the supraoccipitals send out laterally directed flanges strengthening the auditory bulla postero-dorsally. This flange bends ventrally, just posterior to the external auditory meatus. On the occipital surface of the supraoccipitals one finds a varying number of small foramina. The median portion of the dorsal rim of the foramen magnum is also supplied by the supraoccipital element.

In both Georychus and Cryptomys the nuchal crest does not fold over dorsally and posteriorly on the surface of the occipital region as in Bathyergus. In these genera, the nuchal crest is not as well developed.

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The dorso-lateral, lateral and ventral portions of the foramen magnum are supplied by the exoccipitals. The midventral portion however, is made up by the posterior part of the basioccipital. The foramen magnum has a more or less squarish appearance with the ventral rim semi-circular.

Ventro-lateral to the foramen magnum the exoccipitals supply two strong, well developed condyles for articulation with the atlas. Laterally, the exoccipital elements also strengthen the posterior-lateral parts of the bullae by means of two strongly developed paroccipital processes. These paroccipital processes do not reach beyond the level of the dorsal portions of the exoccipital condyles and terminate rather bluntly, with a similar type of thickened bony surface as was found on the maxillary portion of the zygoma, as related above. These may serve as areas for attachment of the neck muscles.

The paroccipital processes in Georychus and Cryptomys are not as big as in Bathyergus. In Bathyergus they are broad and blade-like while in the former two genera they are much narrower. In Cryptomys the distal ends of these processes end in a thickened notch, to a far greater degree than is found in Georychus.

The surface of the occipital region is more or less scalloped, i.e. not smooth. The occipital region does not slope forwards and this feature is assumed to be primitive in Bathyergus (Landry, 1957, 71). Seen from the norma posterior the skull of Bathyergus is relatively flat and wide.

On the other hand, the occipital regions of Georychus do slope or slant rostrally to a certain degree and seen from the posterior aspect, the skull of Georychus is not as flat and wide as in Bathyergus. In the case of Cryptomys, the skull seems to have been "flattened" on the lateral sides giving this skull a more "rounded" appearance.

The anterior inner wall of the braincase is constructed by a strongly developed cribriform plate (more or less on the inner (medial) side of the orbitosphenoid) and possesses the usual number of small apertures for exit of branches of the olfactory nerve .

<u>The palatal region</u>:

The presence of a pair of anterior palatine foramina has already been mentioned (see above). Behind this point (if seen from the ventral aspect of the skull), the strong and well developed maxillary elements are raised to a certain extent to house the two rows of molar teeth (Fig. 4.4).
On the anterior surface of this 'elevation' the ridges made by the roots of the first cheekteeth can be seen clearly. From this point laterally, the maxillae give rise to the maxillary complement of the zygoma (where the flattened bony surface on the ventral anterior portion of the zygoma is to be seen) and also to the transversely directed horizontal plate through which the infraorbital canal passes from the outer side of the snout to the orbit. Immediately in front of this plate, the maxilla fuses with the premaxillaries, dorsally with the frontals and posteriorly with the lachrymals.

The maxilla, dorsal to the toothrows, fuses with the orbitosphenoid. Behind the last molar, it fuses with the palatine elements. Medially, between the two toothrows, the two maxillae are separated by a small elevated ridge.

The distance between the toothrows is very narrow indeed, not wider than the width of a single toothrow.

In Georychus (Fig. 4.5) and Cryptomys (Fig. 4.6) there is a small bulge or elevation immediately behind the last molar element and lateral to the palatal elements, housing the pulp cavities of the caudally developed incisors. This point also corresponds to the most anteriorly situated portion of the pterygoids. In Bathyergus, the palate is flat, with a small medial ridge while a pronounced medial ridge is present in Georychus, and also to a certain extent in Cryptomys. The palatal region of Cryptomys is more rounded than in either of the two other genera. The toothrows in Georychus and Cryptomys are much more convergent posteriorly than in Bathyergus, where they are more or less parallel.

The palatines, (merging anteriorly with the posterior maxillary-palatal elements) are not very broad and provide the ventral rim of the internal choanae. Laterally, they fuse with the alisphenoid (which then forms the pterygoid fossa) while dorsally they meet the basisphenoid and vomer elements to form the 'roof' of the internal nasal passage, which is relatively large.

The internal choanae are relatively smaller in Georychus and Cryptomys compared to Bathyergus. Consequently the distance between the vertical parts of the pterygoids is much narrower in Georychus and Cryptomys. In Georychus, these vertical pterygoid plates tend to diverge to a certain extent, while they are parallel in Bathyergus and Cryptomys.

The perpendicular portion of the palatines (which meets the alisphenoid to form the pterygoid fossa) are accentuated and extended posteriorly by fusion with the pterygoids. The pterygoidal elements thus fuse with the palatines anteriorly and the basisphenoid dorsally, while the posterior perpendicular margin of the pterygoids make contact with the antero-medial portions of the auditory bullae.

The auditory region:

The auditory bullae in Bathyergus are strong and well developed. Landry (1957, 71) even calls them large and thus finds another primitive

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feature in the skull of Bathyergus. The bullae taper to a point antero-medially, meeting the posterior portion of the basisphenoid and the posteriorly directed perpendicular portions of the pterygoids (already described above). The ventro-medial edge of the bulla is limited by the basioccipital (between which the slit-like foramen lacerum posterius is found) while the posterior end of the bulla is strengthened by the exoccipital paroccipital process (see above). Postero-laterally, the bulla extends between the paroccipital process ventrally and the supraoccipital flange dorsally and this portion consists of the mastoid element of the skull. In other words, the mastoid unit also takes part in the formation of the tympanic bulla. The supraoccipital portion lying dorsal to the mastoid complement extends ventrally to about the same level as the more posterior paroccipital process. Anterior to this flange, below the level of the ventral rim of the external auditory meatus, is a small stylomastoid foramen.

The external auditory meatus is more or less oval in shape, while the length of the ear passage is about 6 mm.

Dorsally and antero-laterally, the bulla is connected to the squamosal while the ventral portion is separated from the alisphenoid by means of the large foramen lacerum medium. The dorsal portion of the bulla provides the posterior part of the rim of the postglenoid foramen.

In Georychus and Cryptomys, the bullae are also, relatively speaking, large. In these genera, the posterior lacerum foramen is not as clear as in Bathyergus and in Cryptomys, the paroccipital processes are not so enlarged.

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The external auditory meatus is also oval shaped in Georychus and is virtually circular in Cryptomys. As would be expected, the length of the outer ear canal is far shorter in these genera. Similarly, the foramen lacerum medium is not as clear as is the case in Bathyergus.

The middle ear region, containing the ear ossicles, has received a considerable amount of attention in the past. One thinks immediately of the classic work on ear bones by Doran (1876) in which the ear bones of Bathyergus are also discussed. The following brief account of the ear ossicles in Bathyergus has been paraphrased from Doran's paper. The genus Bathyergus exhibits in its ossicles a feature which distinctly allies it to the cavies and porcupines. The head of the malleus is much elongated anteriorly (though not as much as in the hystrids): the neck is thin and constricted with a distinct laminar expansion below it. The manubrium is rather short and relatively wide near the base, getting very narrow towards the tip with a distinct processus brevis present. A small stout tubercle occurs on its inner border representing the processus muscularis, as in squirrels. The head of the body is completely fused to that of the incus by their articular surfaces, the contour of which is deeply marked all round the seat of ankyloses. This bony union involves the neck and a part of the inner border of the manubrium, from the root to close above the tubercle of the tendon of the tensor tympani. The manubrium is fused to the processus longus of the incus, nearly down to the point where it turns inwards to the head of the stapes. According to Doran, this ankyloses was observed by Hyrtle. "Whilst the malleus differs from the hystricine

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malleus in the head being less produced forwards, the incus is distinguished from that of the porcupines in having the very shallow body and proportionally large crura seen in the rest of these fossorial animals. The posterior crus is particularly long. The processus brevis is as well developed as in Spalax or Ellobius, and hence different from the same in Rhizomys".

The stapes is a large bone, though not proportionally as great as in Spalax. In both these animals the crura are straight, not very long and widely divergent, the base being very broad and extremely convex towards the vestibule. The crura are inserted some distance from both extremities. "There does not appear to be any bony canal between the crura; at least such does not exist in the skulls of Bathyergus in the college collection " (Doran, 1876, 413).

The description of the ear ossicles in Bathyergus has been given at some length above, for very often in the existing literature it is only stated that in all bathyergids the malleus and incus within the middle ear are fused, without any indication as to how these elements are fused.

Cockerell, Miller and Printz (1914, 440) state that in Tachoryctes (an extra-limital bathyergid-like rodent as far as this work is concerned), the arrangement is essentially similar to that of Bathyergus as described and figured by Doran. In the former genus however, the malleus and incus are not completely fused.

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The lower jaw:

The lower jaw is solidly and stockily built (Fig. 4.1). There is an obvious correspondence in structure to the typical hystricognath type of jaw.

In Bathyergus the symphysis between the two hemi-jaws ankylose at an early age (Roberts, quoted in Shortridge, 1934, 318) but this fusion is evidently not very strong.

As is well known, this symphysis is not fused in Georychus and Cryptomys, allowing a certain degree of freedom of movement between the two lower incisors (see later) which is effected by the transverse muscle.

Seen from the ventral aspect, each hemi-jaw has a conspicuous alveolar sheath for its incisor and this sheath leads virtually into the condyle where the open roots of the lower incisors are situated.

The ascending ramus of the jaw is relatively low resulting in an anteriorly situated coronoid process and a well developed rounded condyle. The coronoid process is a small, sharp, dorso-posteriorly pointing element.

In Georychus (Fig. 4.2) the ascending ramus ascends at a slightly larger angle and this portion of the lower jaw is slightly higher than in Bathyergus. This impression is further strengthened in the case of Cryptomys. Comparitively speaking, the coronoid process in Cryptomys is much higher than in Georychus and Bathyergus so that the "valley" between the coronoid process and the condyle of the mandible is much deeper in Cryptomys. The longer coronoid process in Cryptomys curves caudally to a greater extent than in either Georychus or Bathyergus, the latter having a very short coronoid process (Fig. 4.3).

It is especially the angular portion of the jaw which creates the strong hystricognath impression. The angular portion springs from the outer side of the bony alveolar incisor sheath, so that, when seen from the ventral aspect, there is a deep linear groove

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(immediately lateral to the incisor) between the angular and dental portions. Seen from the lateral aspect, the angular portion reaches far beyond the condyle. The inner edge of the angular is scalloped and more or less flattened on its lower border.

Seen from the ventral aspect, the groove between the angular portion of the jaw and the incisor alveolus is not as deep in _Cryptomys_ or _Georychus_ as is the case in _Bathyergus_. Furthermore, seen from the lateral aspect, the angular portion does not extend caudally beyond the condyle of the jaw to such an extent in _Georychus_ and _Cryptomys_ as is the case in _Bathyergus_. Still seen from the lateral aspect, the angle the angular portion of the jaw makes with the main axis of the jaw is far more pronounced in _Georychus_ and _Bathyergus_ in comparison to _Cryptomys_ where this point of departure from the main body of the jaw is far more gradual.

There is a small but definite mental foramen on the anterior outer side of the lower jaw (below the posterior portion of the first molar) more or less on the same level where the angular portion leaves the main body of the lower jaws. A small mandibular foramen (on the inner posterior part of the ascending ramus) is also present, more or less behind the level of the fourth molar element, some distance dorsally on the ascending ramus (inner surface).

The dentition:

As far as the teeth are concerned, the incisors will first be discussed briefly which will be followed by a short discussion of the molar complement.

The upper incisors are very long, and as Beddard (1902, 480) has mentioned, stand out in front of the closed lips in all the bathyergids. Sclater (1901, 72) also relates the fact that the incisors are so long that they are always visible, the lips not being large enough to cover them. The upper incisors are more heavily curved than the lower incisors, and the former pair lie anterior to the lower incisors when the mouth is in the normal closed position.

In Bathyergus these teeth (in contrast to the lower incisors) are heavily grooved and these grooves run down the middle of the teeth. Their colour is usually white and they arch posteriorly with a gentle curvature to "a point situated above the anterior grinding teeth..." (Roberts, quoted in Shortridge, 1934, 319). Owen (1868, 296) already remarked that the incisors are broader than the occlusal surfaces of the molars.

Comparing the upper incisors of Bathyergus to the other bathyergids, Landry (1957, 70) has pointed out that they are short and broad, not reaching farther back than the infraorbital foramen itself. This foramen is reduced in size and does not (or scarcely) transmit a slip of the masseter (see below). In spite of this the rostrum is greatly enlarged (described below) and Landry interprets this enlargement as secondarily correlated with the enlargement of the incisors, for the nasal cavity is still much reduced in comparison to that of other rodents. As a comment on Landry's remarks, it may be added that a widened nasal passage would probably be a greater hinderance to fossorial animals. Landry furthermore states that this widening of the upper incisors has further encroached on the size of the infraorbital foramen and completed the exclusion of the masseter muscle from the muzzle (p. 70).

The/...

The upper incisors in Bathyergus have been termed scalpriform. They grow from persistent pulps (as do all incisors in the Rodentia) while the anteriorly situated enamel of the tooth does not extend to its posterior surface.

In contrast to the upper incisors of Bathyergus, these teeth are not grooved, in Georychus and Cryptomys. Although the infra-orbital foramen is small in these forms, it is relatively larger than encountered in Bathyergus and this may be due to the fact that the pulp cavities of these teeth are situated in the pterygoidal region, as related above. It is likely that a small slip of the masseter passes through this aperture in Georychus and Cryptomys. The upper incisors are comparitively speaking not as wide as in Bathyergus (although still broader than the molars) and consequently these incisors have not encroached on the size of the infraorbital foramen as is the case in Bathyergus, thus not effecting the exclusion of the masseter muscle from the muzzle.

Sclater (1901, 72) has remarked that the incisors in the case of Bathyergus may sometimes be over 3" (76.2 mm.) in length of which half protrudes beyond the alveolus. These two teeth are separated in the lower jaw by a small hiatus.

The incisors of Georychus measures up to 2" (50.8 mm.) in length, while those of Cryptomys can attain 1½" (38.1 mm.)

The lower incisors are also big structures but are not grooved on their anterior surface. They are rather long, also growing from persistent pulps which are situated ventrally to the condyle of the jaw. These large incisors are thus partially responsible for the deep fissure which is present between the edge of the incisor sheath and the angular process (see above).

The incisors are separated from the molars by a well developed diastema, which is shorter than the premaxillary-maxillary diastema of the skull.

The/...

The molar teeth of Bathyergus are rooted, and, according to Landry (1957, 71) deeply hypsodont, if not actually evergrowing. There are four teeth in each maxilla, as well as in each hemi-jaw, and in all cases they decrease in size from the front to the back.

The molars are simple structures with re-entering folds in juveniles only (Sclater 1901, 72) while Weber (1928, 269) describes them as having had outer and inner enamel folds originally. The molars are somewhat oval in section surrounded by a ring of well developed enamel, gradually disappearing with age. (Sclater, op. cit.). The central portions of the teeth are built up by dentine.

The first upper grinding tooth has a protocone, which fuses with a hypocone posteriorly. Buccally, the anterior paracone is separated from the posteriorly situated metacone by an enamel groove. The second tooth is essentially the same except that the lingual anterior protocone is separated from the hypocone by an enamel fold. This arrangement is also found in the third molar element and in this case the outer (buccal) and inner (lingual) enamel folds are much clearer. The posterior tooth of the maxillary grinding teeth, is the smallest element of the tooth row and in this case the metacone is present while the hypocone is absent.

The lower molar elements also decrease in size from the front to the back and the first tooth has an enamel fold on the buccal side, separating the anteriorly situated protoconid from the posterior

hypoconid/...

hypoconid. The second tooth has enamel folds on both inner and outer surfaces (i.e. lingual and buccal) which is better developed on the buccal side separating the protoconid from the hypoconid. In the first tooth the metaconid and endoconid tend to fuse and this applies to the second molar element as well. The third tooth has a strong buccal enamel fold separating the protoconid from the hypoconid while the last element is provided with a protoconid, hypoconid and metaconid, the endoconid being absent or under-developed.

The upper toothrow is usually shorter in its total length than the lower toothrow.

The homology of these grinding teeth is at present in a state of confusion. Sclater (1899, 225, 1901, 71) and Weber (1928, 269) suggest the following dental formula:

$$i\,\frac{1}{1} : c\,\frac{0}{0} : pm\,\frac{1}{1} : m\,\frac{3}{3} = 20.$$

On the other hand, Thomas (1909, 111) and Roberts (1951, 379) propose the following scheme:

$$i\,\frac{1}{1} : c\,\frac{0}{0} : pm\,\frac{2}{2} : m\,\frac{2}{2} = 20.$$

The two premolars in this scheme would correspond (according to Thomas) to the third and fourth pre-molars, while the molars would be the first and second molars of the original mammalian dental formula.

Landry (1957, 14) mentions the fact that Tullberg (1899) stated that the motion of the jaw in hystricomorphs is propalinal and that in other groups (e.g. the sciurognaths) this movement is pre-vented by the cusps of the teeth. This propalinal

grinding/...

grinding is also possible in bathyergids, and consequently in <u>Bathyergus</u>, due to the occlusal surfaces of the molars being plane (Landry, 1957, 12). Landry (<u>op. cit</u>. p. 9) states that <u>Petromys</u> is the only hystricomorph that he has examined whose teeth are not flat-crowned.