A CORRELATION OF THE FEEDING HABITS, JAW MUSCULATURE AND TYPE OF TEETH OF SOME SOUTH AFRICAN GOLDEN MOLES.

BY

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Thesis presented to the Faculty of Science,
Rhodes University, for the Degree of
Master of Science.

With 15 Text-Figures.

APRIL, 1957.

ABSTRACT.

The jaw musculature and its innervation in the Chrysochloridae studied is typically mammalian except that the m. temporalis occupies the whole of the orbito-temporal fossa. The antemolar teeth are specialized, while the molars are simple and primitive. Normally the diet of Golden Moles consists of earthworms, insects in all stages of development and millipedes. The firm implantation of the antemolar teeth can be correlated with their function of catching the prey, while the molars are adapted for a worm-like diet. The available evidence indicates that the genera Bematiscus and Chrysospalax are more primitive than the other Golden Moles. Since Golden Moles feed on insects in all stages of development and millipedes, they can be considered as being of economic importance.

CONTENTS

INTRODUCTION

Though some authors have studied the dentition, jaw musculature and the diet of Golden Moles, a correlation of the feeding habits of these animals with their type of teeth and jaw musculature has not as yet been done. This aspect, therefore, will form the main body of this investigation.

There still appears to be some doubt as to the systematic position of the Golden Mole. Some authors consider that they should be included with the Insectivora, while others feel that they should have ordinal rank.

The first specimen of a Golden Mole was described by Linnaeus (1766), who named it Talpa Asiatica and included it with the Insectivora. The generic name was subsequently changed to Chrysochloris by Lacépéde (1799). Dobson (1883) also included the Golden Moles in the Insectivora, but suggested an early phylogenetic separation of the Golden Moles from other Insectivora.

Those authors who still include the Golden Moles in the Insectivora, have ranked them differently. Hewitt ('18) and Ellerman, Morrison-Scott and Hayman ('53) placed the Golden Moles in a family, the Chrysochloridae, while Simpson ('31 and '45) gave them superfamily rank - Chrysochloroidea. Parker and Haswell ('47) considered the Golden Moles as being a sub-order of the Insectivora.

There are, however, a number of systematists who consider that the Golden Moles should not be included in the order Insectivora, and some have even discarded this order. Broom

('15 and '16), Hewitt ('31), Shortridge ('34), Roberts ('37 and '51) and Roux ('47) have given the Golden Moles ordinal rank under the name *Chrysochloridea*. Butler ('56) has, however, classified the Golden Moles as a superfamily of the suborder *Soricomorpha* which he places under the order *Lipotyphla*. Shortridge (34), Roberts ('51) and Butler ('56) discarded the order *Insectivora*. Roberts' ('51) classification of Golden Moles appears to be more orderly than the others and it will be followed in this investigation.

Three species of Golden Moles were used for the present investigation - *Amblysomus hottentotus hottentotus, Bematiscus villosus pratensis* and *Chrysospalax trevelyani*. *Amblysomus hottentotus hottentotus* was first described by Smith (1829) who called it *Chrysochloris hottentotus*, and *Bematiscus villosus pratensis* was first described by Roberts ('13) under the name *Chrysospalax pratensis*. The nomenclature of both species was changed to their modern form by Allen ('39). As for *Chrysospalax trevelyani*, Günther (1875 a and b) was the first to describe it under the name *Chrysochloris trevelyani*. Roberts ('13) revised the generic name to its present form.

Judging from the available literature only two authors have worked on the jaw musculature of some Golden Moles. Dobson (1883) described the muscles of the head and neck of some species of *Chrysochloridae*. Fiedler ('53) studied the muscles of mastication of some insectivores including *Chrysochloris obtusirostris*.

Dobson (1883), and Broom ('07 a and b, and '09) studied the dentition of some species of Chrysochloridae. Romer ('45), Parker and Haswell ('47) and Gregory ('51) place the Golden Moles in the zalambdodent group of insectivores, because of the presence of an amphicone (paracone of Butler ('37 and '39)). Gregory ('20) studied the molars of Chrysochloris and only mentioned points of evolutionary significance. Systematists have used the number of teeth found in the various Golden Moles as a taxonomic character.

Scott (1892) gave the nomenclature for the premolar cones. Osborn ('07), however, suggested that the nomenclature for the lower premolar cones should be the same as that of the lower molar cones since there is evidence of serial homology between the cusps of the two types of teeth. Although some authors have challenged the validity of the Cope-Osborn theory, the osbornian nomenclature for the molar cones has been generally accepted. Because Scott's (1892) nomenclature for the upper premolars and Osborn's ('07) nomenclature for the lower premolars and the upper and lower molars are in current use, they will be followed in this investigation.

Fitzsimons ('20, p.42-43) in making a study of the diet of Golden Moles states that he " ... examined the stomachs of large numbers of Moles, and have not once found any vestige of vegetable substance therein. The contents of the stomachs consisted of beetles, worms and the larvae and eggs of a variety of insects and other creatures which prey upon the roots of plant life." Haagner ('20) appears to be of the same opinion about the diet of the Golden Moles.

Hewitt ('31 p.30) records that *Bematiscus villosus leschae* " ... comes out at night to search for insects on the surface of the ground, which it roots up in pig-like fashion". Ranger ('27 p.489) in describing the feeding habits of the Giant Golden Mole - *Chrysospalax trevelyani*, states that it is " ... partly diurnal in habit, is a surface feeder, and in searching for its food (insects in all stages of development, and pillmillipedes) stirs up the floor of the forest, employing mainly its snout ... ." Roberts ('51 p.106) sums up the position as follows :- "Most of them seek their food, which consists of larvae of insects and worms, under the surface of the soil, but two at least (of the genera *Bematiscus* and *Chrysospalax*) seek their food mainly on the surface at night".

MATERIAL AND TECHNIQUE

Amblysomus hottentotus hottentotus was chosen for the present investigation because it is common in Alice and district. *Bematiscus villosus pratensis* and *C. trevelyani* though not obtainable in this area, were also used for purposes of comparison, because their feeding habits, as far as could be established from the available literature, differ from those of *A. hottentotus hottentotus*.

The material of A. *hottentotus hottentotus* was collected in Alice. Some of the heads of these specimens were fixed and left in Bouin's fluid for about a year. After the initial regular changes of this fluid, it was changed after every month. The picric acid and acetic acid in conjunction with formic acid liberated by the formalin served as decalcifying agents. The remainder of the material was fixed in 10 per cent formalin containing 4 per cent sodium chloride, and was decalcified in 5 per cent nitric acid in 70 per cent alcohol. All the specimens treated in both ways were found to be too hard to section, although various dehydrating and clearing agents were used. The sectioning of the adult material was therefore abandoned. A macrodissection of the muscles of mastication was undertaken, and drawings were done on graph paper with the aid of a projection microscope fitted with a micrometer grid. The micrometer grid was so fitted that the light went through it, thus focussing the lines on the object to be drawn.

Holy Cross, Eastern Pondoland is one of the localities where

B. villosus pratensis is plentiful, and the specimens of this species were collected from this area. Those of C. trevelyani were collected in the Pirie Forests, Kingwilliamstown district, the area from which the first specimen in this genus was collected and described. Since the material of B. villosus pratensis and C. trevelyani was limited, no attempt was made to prepare it for sectioning. This had already proved impossible in the case of the adult material of A. hottentotus hottentotus. Macrodissection of the jaw musculature was performed, and drawings on graph paper were made with the aid of a projection microscope fitted with a micrometer grid.

In the adults of Golden Moles the sutures are fused, and as a result the individual bones could not be determined. Two embryos, a 30 mm. and a 45 mm. embryo of A. hottentotus hottentotus were therefore used for this investigation in order to determine the extent of the skull bones to which the various muscles of mastication are attached. The head of the younger embryo was fixed in Bouin's fluid, bulk stained in alcoholic borax carmine, sectioned at 10μ and counter stained with good results in a mixture of aniline blue, orange G and acetic acid. The older embryo which was taken from the laboratory collection of embryos, had been preserved in formalin for about 4 years. This preservative appeared to have decalcified the embryo. The head was bulk stained in alcoholic borax carmine and then treated in the same way as was the 30 mm. embryo. A graphic reconstruction of the skull and jaw muscles of the 45 mm. embryo was made according to a method described by Pusey ('39). The slides of the 30 mm. embryo were observed but no reconstruction was made as they differed little with the slides of the 45 mm. embryo.

For purposes of studying the dentition, 5 skulls of A. hottentotus hottentotus, 3 skulls of B. villosus pratensis and one skull of C. trevelyani were boiled to facilitate the removal of the flesh. The teeth were extracted and drawings of them were made with the aid of a dissection microscope fitted with a micrometer grid in the ocular. In addition to this material 50 skulls of each of the following species; Amblysomus hottentotus hottentotus, Chrysochloris asiatica minor and Eremitalpa granti, and 16 skulls of Chrysospalax trevelyani were studied in the Kaffrarian Museum, Kingwilliamstown. Other than the study of the skulls of the species of Chrysochloridae mentioned above, some skulls of Aethechinus frontalis frontalis and Elephantulus myurus myurus, also in the mammalian skull collection of the Kaffrarian Museum, were examined with the view to gaining a general idea of the dentition in the insectivorous mammals.

Four specimens of A. hottentotus hottentotus which were collected alive were kept in a glass container half filled with soil. After starving these specimens for about a day in each case, they were fed alternately on earthworms, insect larvae and relatively small lizards. An examination of the stomach contents of the specimens of A. hottentotus hottentotus, which were found dead in the traps, was done. This examination was extended to the specimens of B. villosus pratensis and C. trevelyani which were dead by the time of collection.

Fig. Ia.

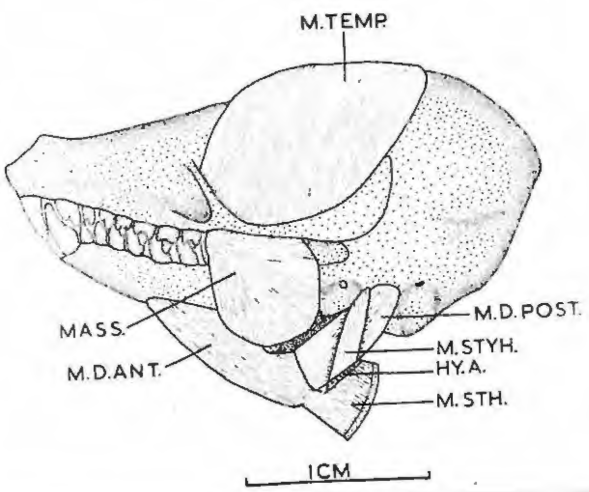

Fig. Ib.

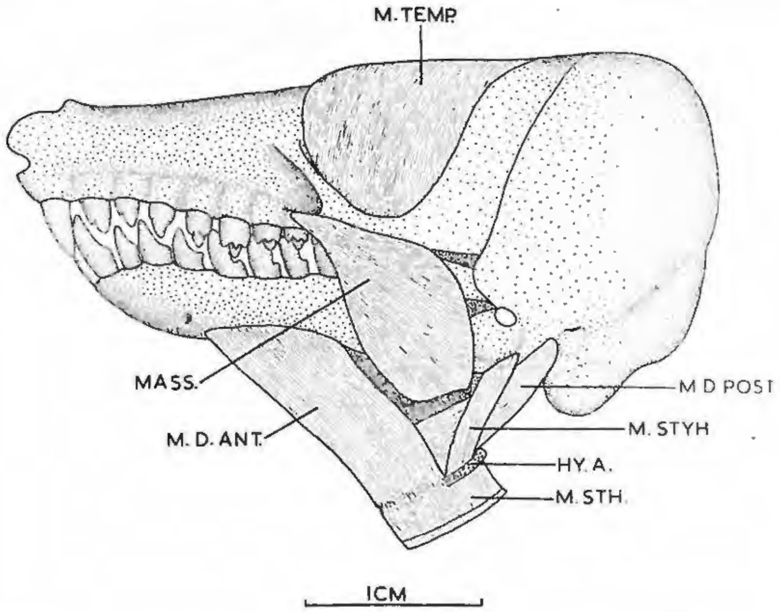

Diagram of the lateral view of the skull and the jaw musculature of (a) *A. hottentotus hottentotus* and (b) *B. villosus pratensis*. HY.A., hyoid apparatus; MASS., masseter; M.D.ANT., m. digastricus anterior; M.D.POST., m. digastricus posterior; M.STH., m. sternohyoideus; M. STYH., m. stylohyoideus; M.TEMP., m. temporalis.

Fig. 3a.

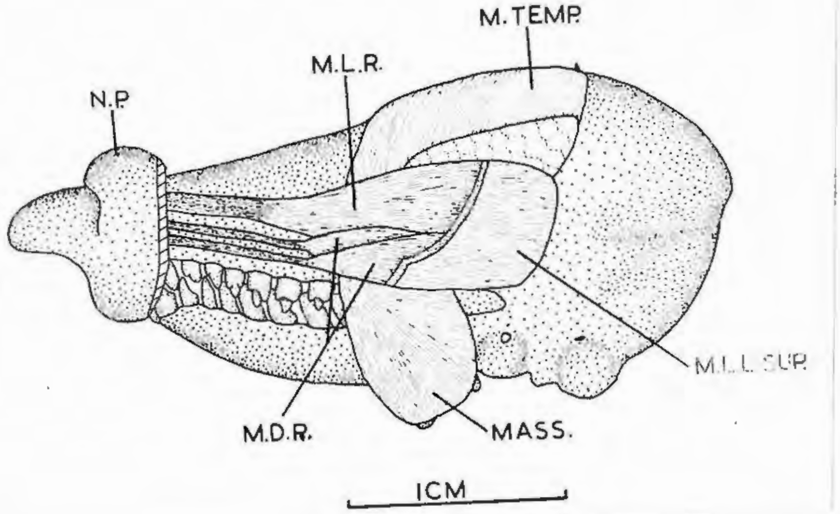

Fig. 3b.

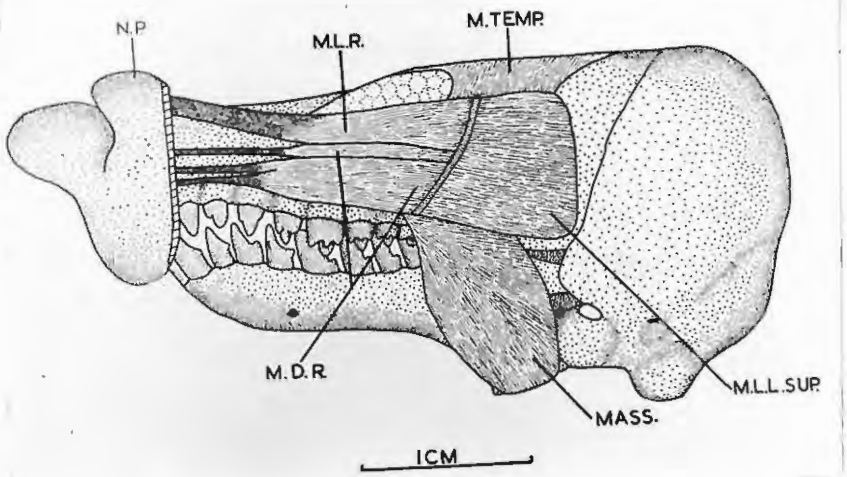

Diagram of the lateral view of the skull, the jaw musculature and the musculi rostrii of (a) <u>A. hottentotus hottentotus</u> and (b) <u>B. villosus pratensis</u>. MASS., masseter; M.D.R., m. depressor rostrum;M.L.L.SUP., m. levator labii superioris; M.L.R., m. levator rostrum; M.TEMP., m. temporalis; N.P., nose pad.

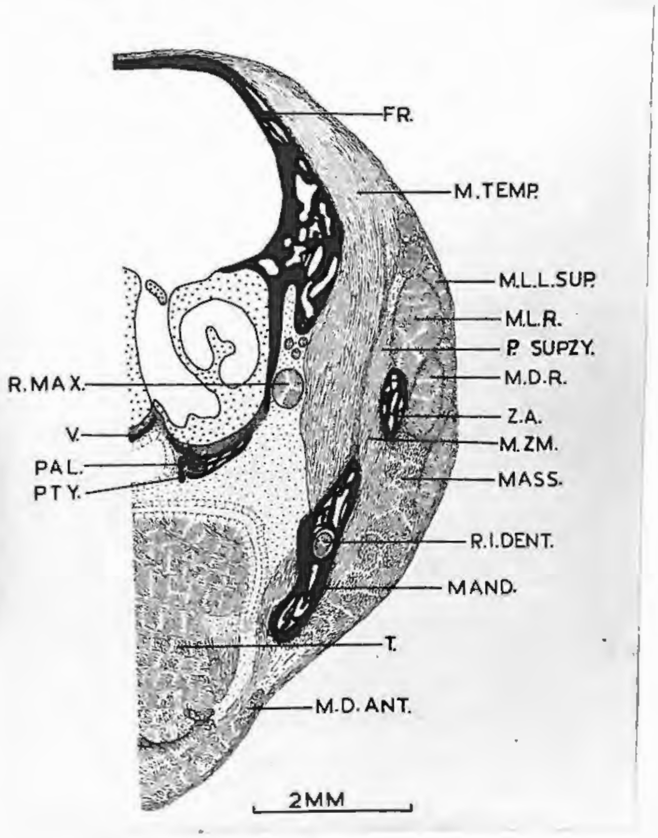

Fig.4.

Transverse section through the jaw musculature of a 45mm. embryo of A. hottentotus hottentotus. FR., frontal; MAND., mandible; MASS., masseter; M.D.ANT., m. digastricus anterior; M.D.R., m. depressor rostrum; M.L.L.SUP., m.levator labii superioris; M.L.R., m. levator rostrum; M.TEMP., m. temporalis; M.ZM., m. zygomaticomandibularis; PAL., palatine; P.SUPZY., pars suprazygomatica; PTY., pterygoid; R.I.DENT., r. inferior dentalis; R.MAX., r. maxillaris; T., tongue; V., vomer; Z.A., zygomatic arch.

THE JAW MUSCULATURE AND THE MUSCULI ROSTRII OF AMBLYSOMUS HOTTENTOTUS HOTTENTOTUS

A. The Jaw Musculature

The masseter (the superficial portion of the masseter of Johnston and Whillis ('38)) (figs. 1a, 3a and 4). The masseter arises from the ventro-lateral and ventral surfaces of the zygomatic arch. The fibres pass posteroventrally to become inserted onto the lateral and ventral surfaces of the angular process of the mandible.

The main function of the masseter is to close the jaws. However, the arrangement of the fibres is such that the contraction of this muscle also causes the mandible to be displaced anteriorly as the mouth is being closed.

The m. zygomaticomandibularis (the deep portion of the masseter of Johnston and Whillis ('38)) (fig. 4). This muscle lies between the masseter and the m. temporalis, and is separated from the m. temporalis by an aponeurosis. Though no aponeurosis separates the masseter from the m. zygomaticomandibularis, the distinction between these two muscles is easily determined by the direction of the fibres. The fibres of the masseter, as described above, are postero-ventrally disposed, while those of the m. zygomaticomandibularis pass ventrally and slightly anteriorly. ? The pars suprazygomatica (fig. 4), which is the part of the m. zygomaticomandibularis, arises from the aponeurosis above the zygomatic arch and forms a thin layer covering the anterior half of the m. zygomaticomandibularis. The m. zygomaticomandibularis arises from the medial surface of the zygomatic arch and the

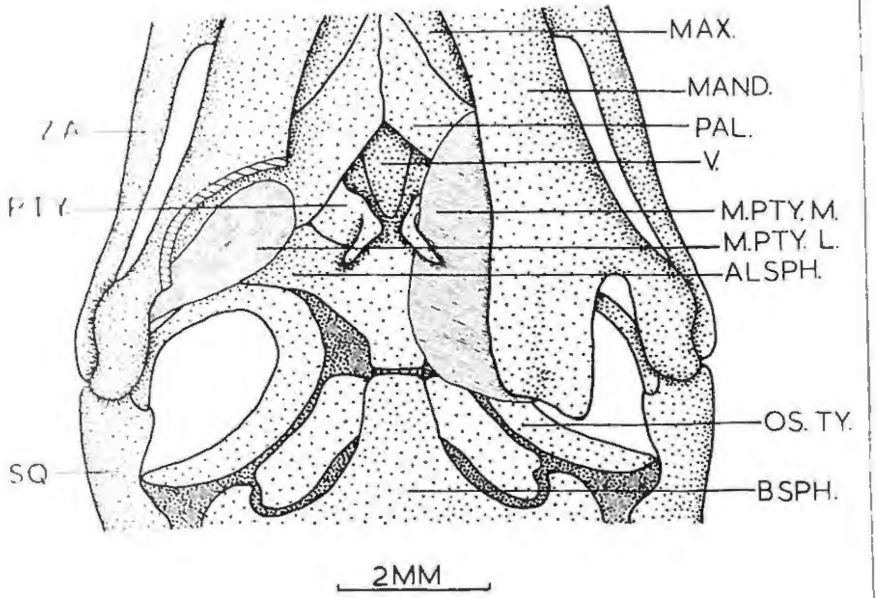

Fig. 2.

Graphic reconstruction of the ventral view of theskull and the musculi pterygoidei of a 45 mm. embryo of A. hottentotus hottentotus. ALSPH., alisphenoid; BSPH., basisphenoid; MAND., mandible; MAX., maxillary; M.PTY.L., m. pterygoideus lateralis; M.PTY.M., m. pterygoideus medialis; OS.TY., os tympanicum; PAL., palatine; PTY., pterygoid; SQ., squamosal; V., vomer; Z.A., zygomatic arch.

aponeurosis surrounding the m. levator rostrum above the zygomatic arch. The m. zygomaticomandibularis is inserted on the aponeurosis separating this muscle from the m. temporalis, and on the dorso-lateral surface of the lower jaw, a short distance behind the last molar to the end of the coronoid process.

The contraction of the m. zygomaticomandibularis also serves to approximate the lower jaw against the upper, and perhaps helps in withdrawing the lower jaw to its normal position after it had been displaced anteriorly.

The m. temporalis (figs. 1a, 3a and 4). This muscle is large and occupies the whole of the orbito-temporal fossa and is lateral to the r. maxillaris. The m. temporalis arises from the frontal, temporal, squamosal, orbitosphenoid and the medial surface of the expanded part of the zygomatic arch. The fibres pass ventrally and slightly anteriorly to be inserted on the medial surface and dorsal margin of the coronoid process of the lower jaw. It is interesting to note that the two muscles on either side of the skull almost meet dorsally.

The m. temporalis, like the masseter, closes the jaws. However, the arrangement of the fibres is such that the m. temporalis also helps in restoring the lower jaw to its normal position after it has been displaced anteriorly.

[illegible]

The m. pterygoideus medialis (fig. 2). This muscle is relatively thick and lies ventral to the r. mandibularis (V). The m. pterygoideus medialis arises from the ventro-lateral surface at the posterior end of the palatine, the lateral surface of the pterygoid and the tympanic process of the basisphenoid. The fibres pass laterally and slightly ventral to become inserted on the medial surface of the angular process of the mandible.

By the contraction of the m. pterygoideus medialis, the lateral movement of the jaw is effected.

The m. pterygoideus lateralis (fig. 2). This muscle is somewhat conical in shape and arises from the lateral surface of the pterygoid and the ventro-lateral surface of the posterior end of the alisphenoid. The fibres pass postero-laterally and slightly dorsally to become inserted on the medial surface of the condyloid process just anterior to the head of the mandible.

Because of the contraction of the m. pterygoideus lateralis, the lower jaw is pulled anteriorly causing the lower incisors to assume a position in front of the corresponding upper incisors.

The m. digastricus. This muscle is relatively thin. As in other mammals, it is composed of two bellies, the m. digastricus anterior (figs. 1a and 4), and the m. digastricus posterior (fig. 1a). The m. digastricus anterior arises from the ventral surface of the mandible just anterior to the masseter. Its fibres pass posteriorly, the deeper ones inserting on the hyoid, while the superficial fibres intermingle with those of the m. sternohyoideus. The m. digastricus posterior lies medial to the m. stylohyoideus and extends from a point lateral to the occipital condyle to a point just posterior to the masseter. At the latter point some of its fibres intermingle with those of the m. digastricus anterior, and some insert on the hyoid, like those of the m. digastricus anterior.

By its contraction the m. digastricus anterior depresses the anterior part of the lower jaw, thus opening the mouth. The m. digastricus anterior has an additional function, that of elevating the hyoid when it acts in conjunction with the m. digastricus posterior. This occurs if the jaws of the animal are kept closed and both bellies of the m. digastricus contract simultaneously.

B. The Musculi Rostrii

To gain a better understanding of the feeding habits of these Golden Moles a description of the muscles which are responsible for the movements of the nose pad will be given. The nose pad, which is adapted for digging, is composed of dense connective tissue covered externally by horny tissue.

The m. levator rostrum (fig. 3a). The m. levator rostrum and the m. depressor rostrum are covered by the m. levator labii superioris. The musculi rostrii are joined posteriorly, and arise from the posterior expansion of the zygomatic arch. They separate a short distance from their origin. The fibres of the m. levator rostrum pass anteriorly and in the region of the foramen infraorbitale, the muscle is continued as a relatively long tendon which inserts in the dorsal part of the nose pad (fig. 3a). This insertion is in the form of a flattened tendon whose fibres intermingle with the connective tissue fibres of the nose pad.

The contraction of the m. levator rostrum causes the elevation of the nose pad.

The m. depressor rostrum (fig. 3a). This muscle as already stated, arises with the m. levator rostrum, but lies ventral to it. After the musculi rostrii have separated the m. depressor rostrum divides into two parts. The fibres of the m. depressor rostrum pass anteriorly and in the region of the foramen infraorbitale the two parts of the muscle are continued as numerous relatively long, thin tendinous fibres which are roughly divided into two bundles, one being dorsal to the other. The dorsal bundle has its insertion in the nose pad latero-ventral to the external nares, while the ventral bundle inserts ventro-medially to the external nares.

Both portions of the m. depressor rostrum serve to depress the nose pad, and the fibres which are continued as the dorsal bundle of tendons may possibly assist in widening the nares as well.

THE JAW MUSCULATURE AND THE MUSCULI ROSTRII OF BEMATISCUS VILLOSUS PRATENSIS AND CHRYSOSPALAX TREVELYANI

The jaw musculatures of *A. hottentotus hottentotus*, *B. villosus pratensis* and *C. trevelyani* are similar though there are slight differences in detail. The m. temporalis (figs. 1b and 3b) of *B. villosus pratensis* and *C. trevelyani* has, however, a relatively wider area of origin than in *A. hottentotus hottentotus*, because of its attachment to almost the entire medial surface of the greatly expanded posterior portion of the zygomatic arch. The m. temporalis appears to be more developed in *B. villosus pratensis* and *C. trevelyani* than it is in *A. hottentotus hottentotus*.

The following are the noticeable differences between the

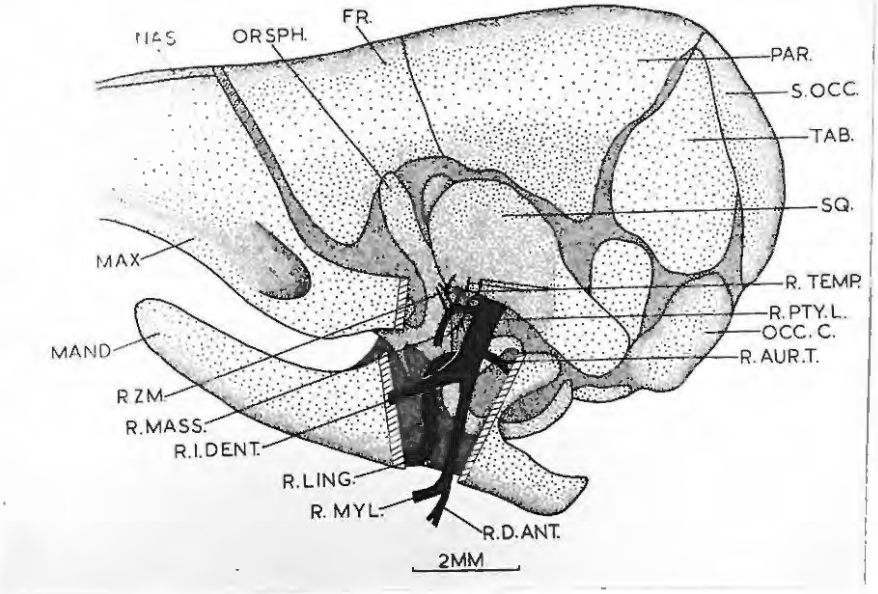

Fig. 5.

Graphic reconstruction of the lateral view of the skull and the nerves supplying the jaw musculature of a 45 mm. embryo of _A. hottentotus hottentotus_. FR., frontal; MAND. mandible; MAX., maxillary; NAS., nasal., OCC.C., occipital condyle; ORSPH., orbitosphenoid; PAR., parietal; R.AUR.T., r. auriculotemporalis; R.D.ANT., r. digastricus anterior; R.I.DENT., r. inferior dentalis; R.LING., r. lingualis; R.MASS., r. masseter; R.MYL., r. mylohyoideus; R.PTY.L., r. pterygoideus lateralis; R.TEMP., r. temporalis; R.ZM., r. zygomaticomandibularis; SQ., squamosal; S.OCC., supraoccipital; TAB., tabular.

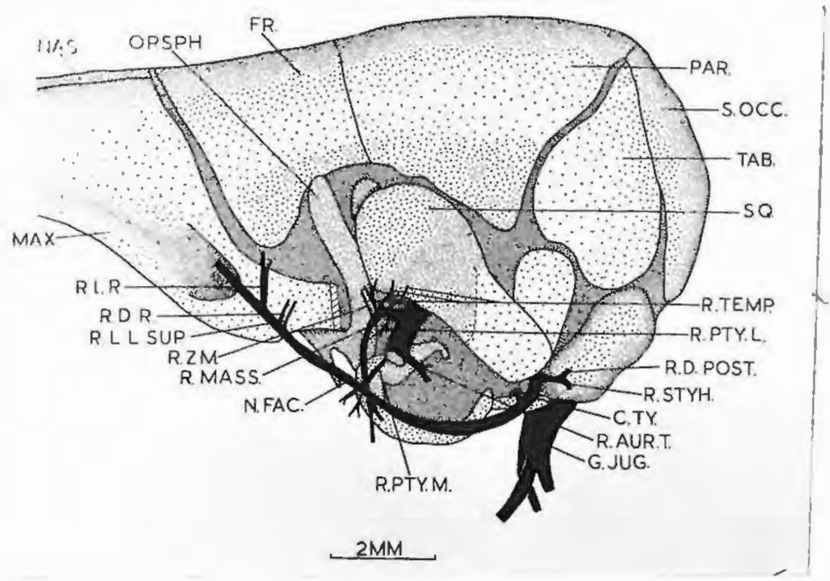

Fig. 6.

Graphic reconstruction of the lateral view of the skull and the nerves supplying the jaw musculature of a 45mm. embryo of *A. hottentotus hottentotus*. C.TY., chorda tympani; FR., frontal; G.JUG., ganglion jugulare; MAX., maxillary; NAS., nasal; N.FAC., n. facialis; ORSPH., orbitosphenoid; PAR., parietal; R.AUR.T., r. auriculotemporalis; R.D.POST., r. digastricus posterior; R.D.R., r. depressor rostrum; R.L.L.SUP., r. levator labii superioris; R.L.R., r. levator rostrum; R.MASS., r. masseter; R.PTY.L., r. pterygoideus lateralis; R.PTY.M., r. pterygoideus medialis; R.STYH., r. stylohyoideus; R.TEMP., r. temporalis; R.ZM., r. zygomaticomandibularis; SQ., squamosal; S.OCC., supraoccipital; TAB., tabular.

musculi rostrii of *A. hottentotus hottentotus* and those of *B. villosus pratensis* and *C. trevelyani*. The tendons of these muscles in the latter two species join the bellies anterior to the region of the foramen infraorbitale. Further, the m. depressor rostrum is continued to its insertion by three tendons (fig. 3b).

THE ACTION OF THE JAW MUSCULATURE AND THE MUSCULI ROSTRII

The action of the masseter, the m. temporalis and the m. zygomaticomandibularis is antagonistic to that of the m. digastricus anterior. As already stated the former muscles close the jaws, whilst the latter muscle opens the jaw. The m. pterygoideus lateralis is helped in its action of displacing the lower jaw anteriorly by the masseter. By replacing the lower jaw to its normal position after being displaced anteriorly, the m. temporalis and the m. zygomaticomandibularis have an action antagonistic to that of the m. pterygoideus lateralis and the masseter. The musculi pterygoidei mediales are antagonistic in action to each other. The action of the m. levator rostrum is antagonistic to that of the m. depressor rostrum.

THE INNERVATION OF THE JAW MUSCULATURE AND THE MUSCULI ROSTRII OF AMBLYSOMUS HOTTENTOTUS HOTTENTOTUS (figs. 5 and 6)

The nerves supplying the jaw musculature and the musculi rostrii of *A. hottentotus hottentotus* were reconstructed from serial sections of a 45 mm. embryo.

The jaw musculature in mammals is referred to as the trigeminal musculature. These muscles are innervated by branches of the r. mandibularis of V. Immediately after leaving the foramen ovale the r. mandibularis gives off a branch which passes dorsally to the m. pterygoideus lateralis and gives off 5 rami, after which this branch continues as the r. masseter. These 5 rami are the r. pterygoideus lateralis which enters the muscle of the same name dorsally, the three rami temporales and the r. zygomaticomandibularis. The latter 4 rami enter their respective muscles antero-ventrally. The r. masseter crosses the mandible anterior to the head of the mandible to ramify in the masseter.

The r. pterygoideus medialis branches from the r. mandibularis just after the latter has given off the r. auriculotemporalis. The r. mandibularis then continues forwards to enter the foramen mandibularis of the mandible as the r. inferior dentalis. The r. pterygoideus medialis enters the muscle of the same name dorsally near its origin.

The m. digastricus anterior is supplied by a branch from the r. mylohyoideus of Vc. The r. mylohyoideus branches from the r. mandibularis just before the latter enters the foramen mandibularis. The r. mylohyoideus descends between the m. pterygoideus medialis and the mandible. The ramus to the m. digastricus anterior branches from the r. mylohyoideus just below the ventral margin of the mandible.

The m. digastricus posterior is supplied by the r. digastricus posterior, a visceral motor component of the n. facialis. The r. digastricus posterior and the r. stylohyoideus are given off from the n. facialis as a single branch which divides into the two rami just after leaving the foramen stylohyoideus.

The musculi rostrii belong to the facial musculature. The branch to the m. levator rostrum is given off from the n. facialis a short distance posterior to the foramen infraorbitale. The r. depressor rostrum is given off posteriorly to the point of origin of the r. levator rostrum. Both rami are visceral motor components of the n. facialis.

Due to the scarcity of material the innervation of the jaw musculature of B. villosus pratensis and C. trevelyani could not be investigated.

The similarity of the cranial nerves in the different species of Golden Moles studied here should be great, judging from the similarity exhibited by the jaw musculature and the musculi rostrii. Furthermore, Fiedler ('53) has shown that in mammals the innervation of the various regions of the body is on the whole uniform. It may, therefore, be taken that the description of the innervation of the jaw musculature and the musculi rostrii given for A. hottentotus hottentotus is equally valid for B. villosus pratensis and C. trevelyani.

DISCUSSION

Johnston and Whillis ('38) consider only the masseter, the m. temporalis, the m. pterygoideus medialis and the m. pterygoideus lateralis to be muscles of mastication. These authors exclude the m. digastricus from this group. Fiedler ('53) correctly regards the m. digastricus as a muscle of mastication. Apart from the fact that this muscle is concerned with mastication the m.

digastricus anterior of mammals is supplied by the r. digastricus anterior of V. The m. digastricus anterior, therefore, belongs to the trigeminal musculature which in mammals includes all muscles of mastication.

According to Weichert ('51) the masseter, the m. temporalis, the m. pterygoideus medialis and the m. pterygoideus lateralis were derived from the m. adductor mandibulae, or constrictor I dorsalis of elasmobranchs. He also showed that the m. intermandibularis is derived from the constrictor I ventralis and that the former gives rise to the m. mylohyoideus and part of the m. digastricus in mammals. Weichert ('51) further showed that the constrictor ventralis of the hyoid arch gave rise to the rest of the m. digastricus.

So what ?

After studying the muscles of mastication of some insectivorous mammals and some primates, Fiedler ('53, p. 172) stated that, "Für den Mass.[1] ist die einzige für alle berücksichtigten Ordnungen gültige Gliederung die von der Mehrzahl der neueren Autoren verwendete in einen oberflächlichen und einen tiefen Mass. ohne Berücksichtigung des ZM.[2]" Fiedler ('53, p. 166) also showed that the m. zygomaticomandibularis " ... ist als selbständiger Muskel nach Lage, Innervation und vielfach auch Funktion unbedingt anzuerkennen." Apart from the different arrangement of the fibres of the m. zygomaticomandibularis as compared with those of the masseter, the former muscle in Golden Moles receives a nerve branch of its own. Furthermore, other than the function of closing the

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[1] Fiedler ('53) uses Mass. for masseter

[2] Fiedler ('53) uses ZM. for zygomaticomandibularis

jaws, the function of the masseter as shown in the description differs from that of the m. zygomaticomandibularis. These findings appear to agree with Fiedler's ('53) contention. Allen (1880), as quoted by Fiedler ('53, p. 117) distinguished the pars suprazygomatica and referred to it as a " ... suprazygomatic slip of the masseter." It cannot be doubted, as shown in the case of the Golden Moles investigated here, that the pars suprazygomatica is a part of the m. zygomaticomandibularis because it receives its nerve supply from the same nerve branch as the m. zygomaticomandibularis. Fiedler ('53) reached a similar conclusion in the case of some insectivorous mammals like *Solenodon paradoxum* and the primate, *Tarsius philippinensis*.

The extent of the m. temporalis in mammals is usually limited to the area within the temporal fossa. In Golden Moles, however, this muscle covers the whole of the orbito-temporal fossa. This arrangement of the m. temporalis is possible because there is no postorbital process, and the orbit and the temporal fossa form one uninterrupted fossa. Further, the eyes are vestigial and situated under the skin. It would appear that this arrangement of the m. temporalis in Golden Moles represents an extreme condition in mammals.

Clark ('24) has shown that in the tree shrew the fibers of the m. pterygoideus medialis blend anteriorly with those of the masseter. In Golden Moles , however, the insertions of these muscles are only close to each other along the lower margin of the lower jaw.

Johnston and Whillis ('38) have shown that in man, the m.

pterygoideus lateralis has two heads. Fiedler ('53) found the same arrangement in Solenodon paradoxum and Tenrec ecaudatus. In some mammals, as in the case of Chrysochloridae, the m. pterygoideu lateralis has a single head. The significance of the possession by the m. pterygoideus lateralis of two heads in some mammals and one in others is not clear.

Because of its innervation from a branch of the r. mylohyoideus it is clear that the m. digastricus anterior of mammals was derived together with the m. mylohyoideus from the m. intermandibularis. The m. digastricus posterior derives its innervation from the n. facialis, thus showing that this is the part of the m. digastricus thought by Weichert ('51) to have been derived from the constrictor ventralis of the hyoid arch. The innervation of the m. digastricus clearly shows that the m. digastricus is composed of two muscles, the m. digastricus anterior which belongs to the trigeminal musculature and the m. digastricus posterior which belongs to the facial musculature. Huber ('23 p.360) actually referred to the m. digastricus as " ... ein zusammengesetzter Muskel ... ".

The upward expansion of the posterior part of the zygomatic arch in Golden Moles, more noticeable in the genera Bematiscus and Chrysospalax than in other Chrysochloridae, can be correlated with the development of the musculi rostrii which are thus provided with a wider area of attachment. The fact that these muscles are well developed may be associated with their function of moving the nose pad during digging operations. The way Golden Moles dig with their nose pads is similar to pigs.

Fig. 7a.

Fig. 7b.

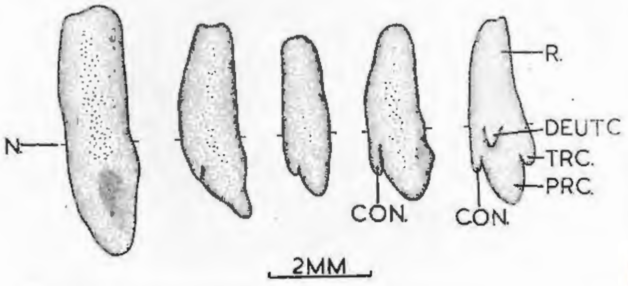

Diagram of the lingual surface of the upper right incisors, canines and premolars of (a) A. hottentotus hottentotus and (b) B. villosus pratensis. CON., conule; DEUTC., deuturocone; N., neck; PRC., protocone; R., root; TRC., tritocone.

Fig.8a.

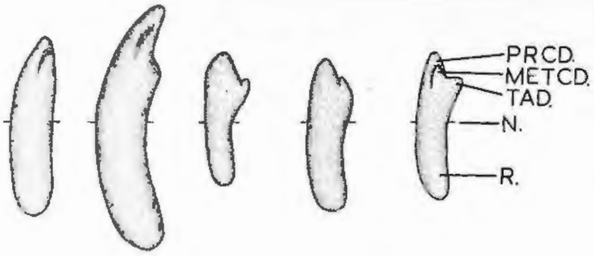

Fig. 8b.

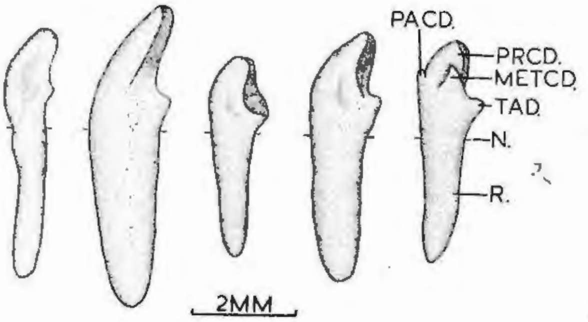

Diagram of the lingual surface of the lower right incisors, canines and premolars of (a) A. hottentotus hottentotus and (b) B. villosus pratensis. METCD., metaconid; N., neck; PACD., paraconid; PRCD., protoconid; R., root; TAD., talonid.

Fig. 9a.

Fig. 9b.

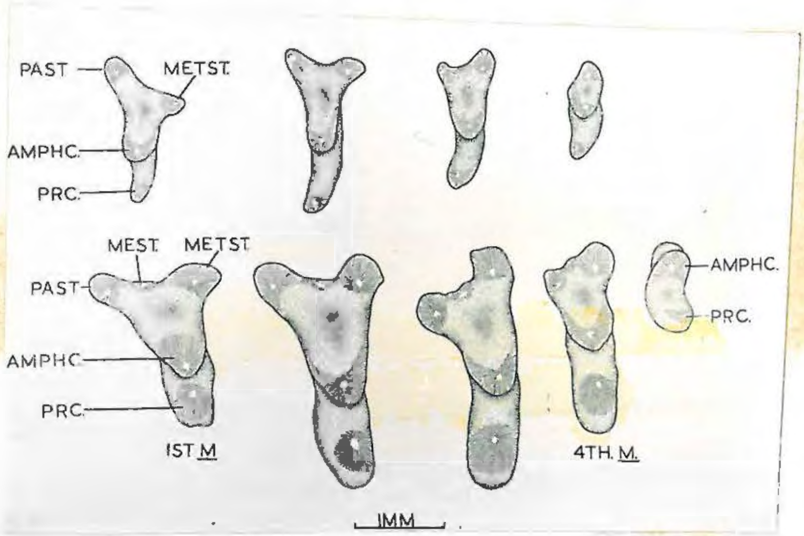

Diagram of the crown surface of the upper right molars of (a) A. hottentotus hottentotus and (b) B. villosus pratensis.
AMPHC., amphicone; MEST., mesostyle; METST., metastyle; PAST., parastyle; PRC., protocone.

Fig. I0a.

Fig. I0b.

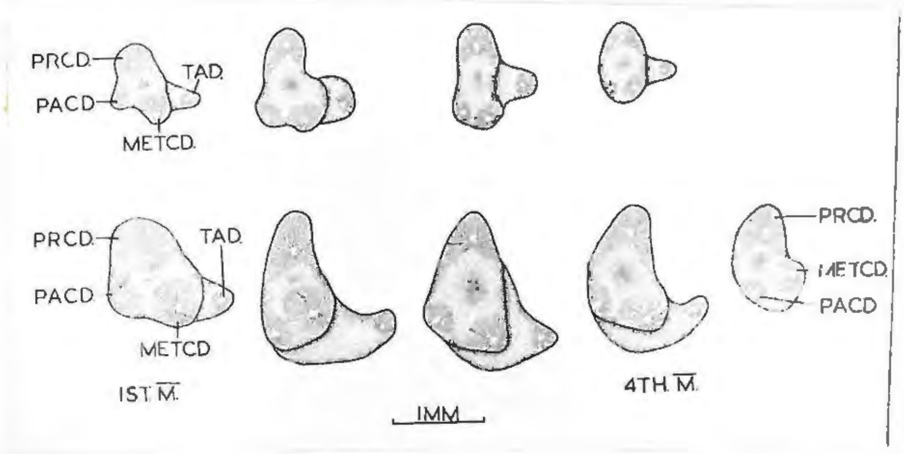

Diagram of the crown surface of the lower right molars of (a) A. hottentotus hottentotus and (b) B. villosus pratensis.
METCD., metaconid; PACD., paraconid; PRCD., protoconid; TAD., talonid.

THE DENTITION OF AMBLYSOMUS HOTTENTOTUS HOTTENTOTUS

The dentition of A. hottentotus hottentotus is heterodont and [illegible]yodont. There are 36 teeth which have sharp pointed cones and the necks of the various types of teeth are indistinct. The usually accepted dental formula is represented by $i\,^{3}/$[illegible] $c\,^{1}/1$, [illegible]. But it will be suggested here that the correct formula is $i\,^{2}/2$, $c\,^{1}/1$, $p\,^{2}/2$, $m\,^{4}/4$.

The first i (fig. 7a) is longer and broader than the second, while in the lower jaw (fig. 8a) the reverse is true. The labial surfaces of the crowns of the upper and lower incisors are slightly convex. The lingual surface of the first i shows slight wear which is possibly due to the action of the first and second lower incisors against it. There is in the second incisor of both jaws a conule, which in the case of the upper tooth is anterior to the protocone, and in the case of the lower tooth is posterior to the protocone. Broom ('09) called the above mentioned conule of the second $\bar{\text{I}}$, a talonid.

In both upper and lower jaws the canines (figs. 7a and 8a) are smaller than the incisors and premolars. There is a conule anterior to the protocone in the C while the $\bar{\text{C}}$ has a talonid posterior to the protocone.

There is a conule (fig. 7a) anterior to the protocone in the upper premolars. A tritocone (fig. 7a) is only present in the second p. In addition to the protoconid the crown of the first and second lower premolars has a talonid (fig. 8a). The second $\bar{\text{p}}$ also possesses a metaconid.

The crowns of the upper and lower molars (figs. 9a and 10a) are more complicated than those of the premolars. In the upper

Fig. 11a.

Fig. 11b.

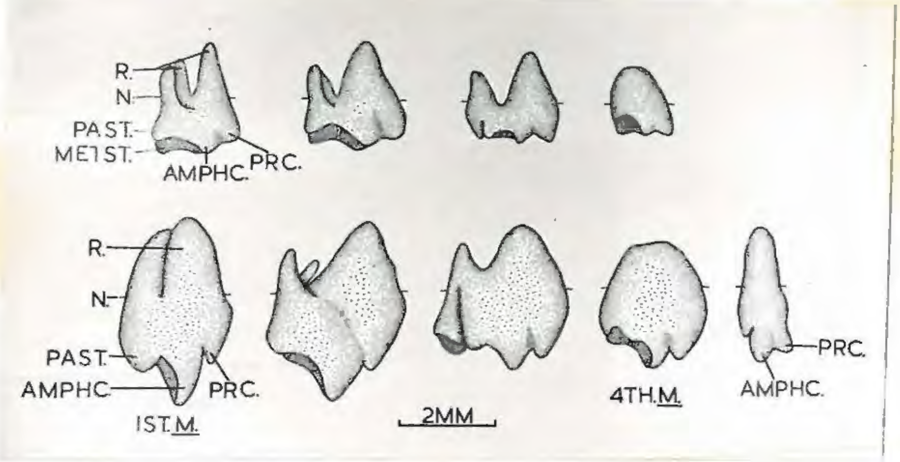

Diagram of the anterior view of the upper right molars of (a) A. hottentotus hottentotus and (b) B. villosus pratensis. AMPHC., amphicone; METST., metastyle; N., neck; PAST., parastyle; PRC., protocone; R., roots.

Fig. 12a.

Fig. 12b.

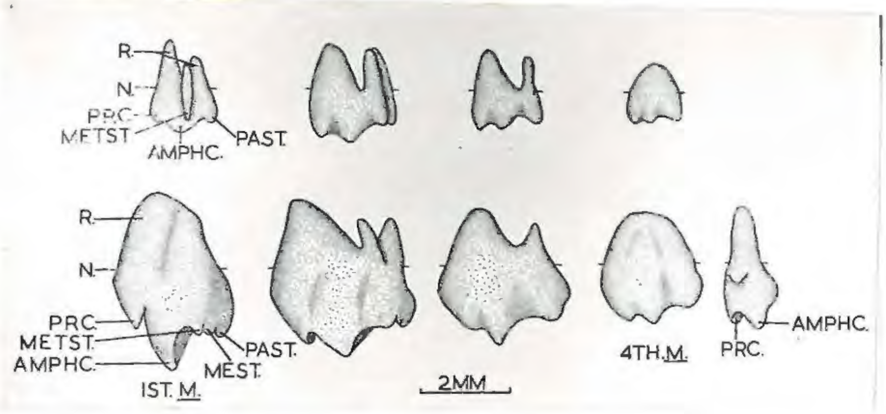

Diagram of the posterior view of the upper right molars of (a) A. hottentotus hottentotus and (b) B. villosus pratensis. AMPHC., amphicone; MEST., mesostyle; METST., metastyle; N., neck; PAST., parastyle; PRC., protocone; R., roots.

Fig. I3a.

Fig. I3b.

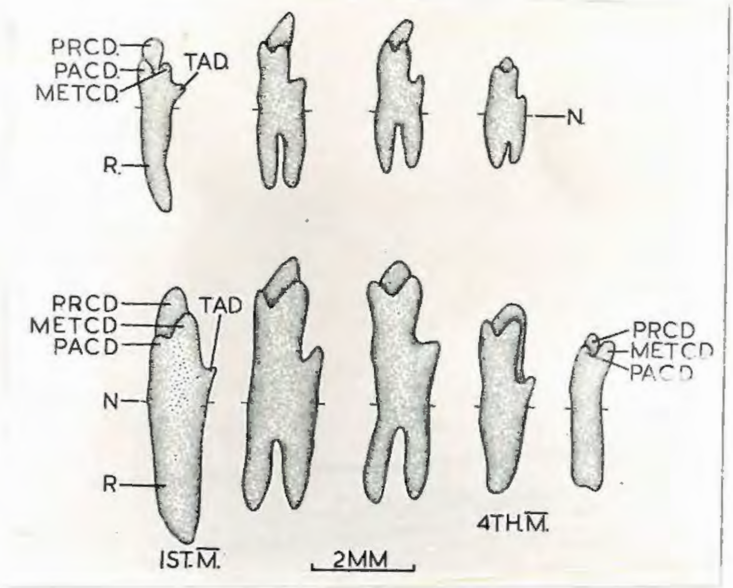

Diagram of the lingual view of the lower right molars of (a) A. hottentotus hottentotus and (b) B. villosus pratensis. METCD., metaconid; N., neck; PACD., paraconid; PRCD., protoconid; R., roots; TAD., talonid.

Fig. I4a.

Fig. I4b.

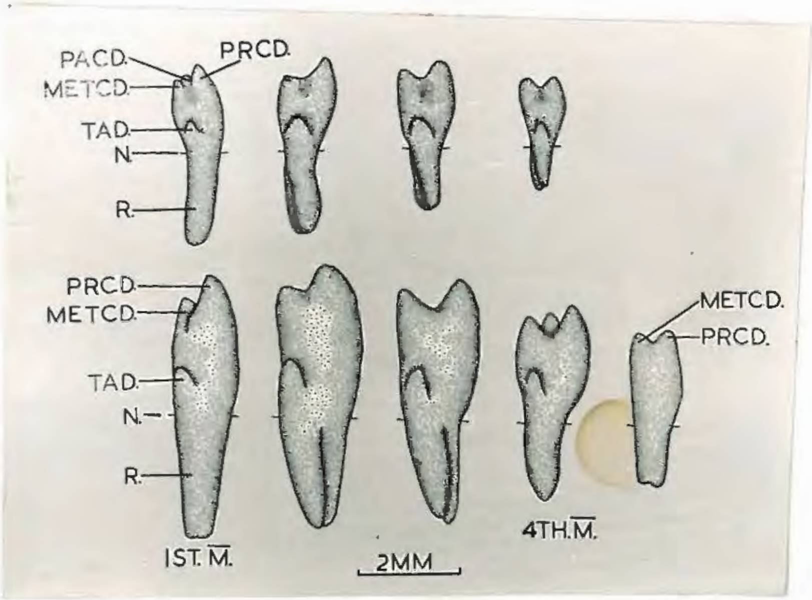

Diagram of the posterior view of the lower right molars of (a) A. hottentotus hottentotus and (b) B. villosus pratensis. METCD., metaconid; N., neck; PACD., paraconid; PRCD., protoconid; R., roots; TAD., talonid.

molars, the smaller protocone is lingual to the larger amphicone (figs. 9a, 11a and 12a). In the last $\underline{m}$ the protocone and the amphicone are approximately equal in size. The parastyle and the metastyle (fig. 9a) form the sharp pointed cusps on the labial margins of the upper molars. In the lower molars (figs. 10a, 13a and 14a) the protoconid is longer and broader than the other cones, and the paraconid and the metaconid are approximately equal in size. All the lower molars have a talonid which has a single cone, the hypoconulid.

The roots of the incisors, canines and premolars, in both jaws are single, cylindrical and longer than their respective crowns. The roots of the incisors are open.

There are three roots in the first and second upper molars (figs. 11a and 12a), a lingual root which is larger than the others, an anterior labial root and a posterior labial root. The third $\underline{m}$ and the second, third and fourth lower molars (figs. 11a, 12a, 13a and 14a) have two roots, the arrangement of which is, however, different. In the third $\underline{m}$ there is a lingual and a labial root while in the lower molars there is an anterior and a posterior root. The fourth $\underline{m}$ and the first $\overline{m}$ have single roots.

THE DENTITION OF BEMATISCUS VILLOSUS PRATENSIS AND CHRYSOSPALAX TREVELYANI

Except in size the dentition of *B. villosus pratensis* and *C. trevelyani* is similar. The dentition of these Golden Moles is also similar to that of *A. hottentotus hottentotus* except for the following differences:

1. There is a total of 40 teeth as compared with 36 in *A. hottentotus hottentotus*, and the dental formula is as follows:

$$\mathrm{i}\ ^{2}/2 \quad \mathrm{c}\ ^{1}/1 \quad \mathrm{p}\ ^{2}/2 \quad \mathrm{m}\ ^{5}/5$$

2. The first $\overline{\mathrm{i}}$ (fig. 8b) of *B. villosus pratensis* and *C. trevelyani* has a talonid.

3. A deuterocone (fig. 7b) is present in the second $\underline{\mathrm{p}}$. There is a talonid in the first $\overline{\mathrm{p}}$, and a paraconid is present in the second $\overline{\mathrm{p}}$.

4. The mesostyle (fig. 9b) is present in the upper molars, and is situated between the parastyle and the metastyle. These cusps are wanting in the fifth $\underline{\mathrm{m}}$ and the cingulum is represented by a cone which is smaller than the amphicone and protocone. The paraconid of the first, second and last molars is smaller than the metaconid (figs. 10b, 13b and 14b) while the two cones in the third and fourth lower molars are nearly equal. The fifth $\overline{\mathrm{m}}$ lacks a talonid. In some specimens of *C. trevelyani*, however, the talonid of the fifth $\overline{\mathrm{m}}$ is either vestigial or well developed.

5. Only the second $\underline{\mathrm{m}}$ has three roots (figs. 11b and 12b) in *B. villosus pratensis* and *C. trevelyani*, while the third $\underline{\mathrm{m}}$ and the second and third lower molars have two roots. The first, fourth and last upper and lower molars (figs. 11b, 12b, 13b and 14b) have single roots. The first $\underline{\mathrm{m}}$, however, shows an incision which almost divides the root into lingual and labial components.

DISCUSSION

In a footnote Thomas and Schwann ('05, p.259) stated that in *Amblysomus iris* " ... the broadly triangular premolars ...

are the milk teeth". Broom ('07 b) added that the teeth of the second set in Chrysochloris asiatica asiatica are all smaller than those of the first set. The conclusions arrived at by these authors were based on measurements of the teeth taken from different specimens of Golden Moles, all belonging to the same species. An examination of the skulls of Chrysochloridae in the Kaffrarian Museum was undertaken with a view to determining the validity of the concept suggested by Broom ('07 b) that the size of teeth is a means of distinguishing the deciduous from the permanent dention. It was found that in all the species studied by the present author the size of the teeth relative to the size of the skull was constant for the members of each species. This strongly suggests that size alone cannot be used as a criterion for distinguishing the deciduous from the permanent set.

According to Broom ('07 b) the first set in Golden Moles persists for the greater part of the animal's life, and replacement takes place with the approach of old age. If this is in fact common in Golden Moles it should be possible to find a replacement of the first by the second set in a fairly big collection of adult skulls. The majority of skulls examined in the Kaffrarian Museum had their teeth intact, and only those skulls in which the jaws were damaged during collecting together with old dry skulls collected from owl haunts, had lost some teeth. Furthermore in the 30 mm. and 45 mm. embryos of A. hottentotus hottentotus only one set of teeth was observed. The occurrence of replacement at any age is therefore doubtful in Golden Moles.

Roux ('47 p.314, fig. 54) labelled a structure in a sectional drawing of Eremitalpa granti as a "milk molar tooth". In a study of the serial sections of A. hottentotus hottentotus embryos, no suppressed deciduous set or anlagen of the permanent set was observed. It was therefore impossible to ascertain whether the set of teeth present is deciduous or permanent.

According to Broom ('16) A. hottentotus hottentotus has three incisors, the socket for the third incisor being formed by both the premaxillary and the maxillary. In the 30 mm. and 45 mm. embryos of A. hottentotus hottentotus and in the adult chrysochlorid skulls examined, the socket for the third tooth, especially clear in C. trevelyani, lies between the premaxillary and the maxillary. In some insectivorous mammals such as Aethechinus frontalis frontalis and Elephantulus myurus myurus there is no tooth embedded in the premaxillo-maxillary suture. In Talpa, Peake ('15 p.99) states that the canine " ... appears to be implanted in the intermaxillary suture". It is important to note that in those insectivores having no tooth in the premaxillo-maxillary suture, the canine lies behind this suture and the sockets of the incisors are all in the premaxillary. Parker and Haswell ('47 p.653) describe the canine in mammals as " ... the most anterior tooth of the maxilla, situated on or immediately behind the premaxillo-maxillary suture ... ". As has been seen, the socket for the canine in some mammals including Talpa is situated in the premaxillo-maxillary suture. It may therefore be suggested here that the tooth lying in the premaxillo-maxillary suture, and the corresponding tooth in the lower jaw, should be regarded as a canine. According to this contention Golden Moles have 4 incisors in each jaw not 6 as previously thought by Broom ('16).

Weichert ('51 p.223) suggested that the molars can be distinguished from the premolars because they " ... have no predecessors in the milk dentition". This method, however, cannot be used in the case of Golden Moles because the dentition of these animals is monophyodont. A method suggested by Romer ('55) has been used here. This is based on the assumption that molars develop a more complex crown pattern than that which occurs in the other teeth. This criterion has its draw-backs, as any distinction between the premolars and molars is difficult in those mammals where molarization of the premolars has occurred. In the specimens under investigation, however, the crowns of the upper molars are practically uniform in structure and are more complex than those of the upper premolars. The difference between the crowns of the lower premolars and molars is not as great as in the upper teeth. The teeth corresponding to the upper premolars and molars in the lower jaw should, therefore, be regarded as lower premolars and molars. It follows, therefore, that the dental formula of Amblysomus should be represented as follows:

$$i\ {}^{2}/_{2}\quad c\ {}^{1}/_{1}\quad p\ {}^{2}/_{2}\quad m\ {}^{4}/_{4}\qquad 3/1/3/2$$

and that of Bematiscus and Chrysospalax as:

$$i\ {}^{2}/_{2}\quad c\ {}^{1}/_{1}\quad p\ {}^{2}/_{2}\quad m\ {}^{5}/_{5}\qquad 3/1/3/3$$

Crowcroft ('56) showed that in shrews the severe tooth wear provides a rough guide to the age of the individual. An examination of a large collection of chrysochlorid skull material in the Kaffrarian Museum showed that Crowcroft's ('56) finding in the shrews cannot be applied to the Golden Moles. The cones of the various teeth in all the skulls of Golden Moles examined showed no tooth wear.

The posterior conule of the second $\overline{I}$ and $\overline{c}$ of A hottentotus hottentotus, and the lower incisors and $\overline{c}$ of B. villosus pratensis and C. trevelyani appears to correspond in position to the talonid of the premolars and molars. For this reason Broom's ('09) contention that this conule of the incisors and canines is a talonid, has been confirmed.

Romer ('45), Parker and Haswell ('47) and Gregory ('51) agree with the concept that the main cone of the upper molars in zalambdodonts should be called the amphicone. According to this view the ancestral placental form, the fossil zalambdodonts, had an amphicone, which is still present in the modern zalambdodonts. The amphicone according to Romer ('45 p.327) appears to be the " ... homologue of paracone and metacone ... " of later forms. The Cretaceous form Deltatheridium is regarded by Romer ('45) as intermediate in its molar structure between the Jurassic pantotheres which had an amphicone and the typical placentals having widely separated paracone and metacone. Romer ('45 p.327) arrived at this conclusion because the paracone and metacone in Deltatheridium were situated almost in the centre of the tooth and " ... were only barely separated at their tips". Butler ('37 and '39), however, doubts that the amphicone ever existed and proposes that the paracone is the main cone of the upper molars of zalambdodonts, the metacone having arisen from the slopes of the main cone. According to Butler ('37) the structure of the molars of Oryzoryctes and Nesoryctes supports his view. It is beyond the scope of this investigation to ascertain which of the two concepts is correct, because only palaeontological evidence in conjunction with embryological observations, perhaps of insectivorous mammals, can throw light on this problem. The term amphicone, however, has been used in this investigation because the majority of authors favour its use.

Having studied the dentition of *Centetes* and other zalambdodonts, including some specimens of *Chrysochloridae*, Butler ('37) came to the conclusion that in zalambdodonts a molar tooth, in occupying a posterior position in a series undergoes some reduction, which is not exactly the same in all zalambdodonts. This reduction occurs to some extent in all the species of the zalambdodonts, and the culmination of this process occurs in *Amblysomus* and *Chrysotricha* amongst the *Chrysochloridae* where the 5th molar tooth is lost completely. *Bematiscus villosus pratensis* and *C. trevelyani* were examined in the light of this conclusion and the following was observed. The parastyle, mesostyle and metastyle is lacking in the last $\underline{m}$ of *B. villosus pratensis* and *C. trevelyani*. The talonid of the last $\overline{m}$ is absent in *B. villosus pratensis* and in some specimens of *C. trevelyani*, while in other specimens of *C. trevelyani* it is either vestigial or quite distinct. These observations in these two genera appear to agree with Butler's ('37) conclusion cited above.

According to Woodward (1896) the dentition of the insectivorous mammals cannot be regarded as primitive except the molars, because the antemolar teeth are obviously specialised in form and number. This is supported by the following observations.

There is present in some genera of Golden Moles a conule anterior to the protocone in the upper incisors, canines and premolars, and a talonid in the lower incisors and canines. These cones are absent in the incisors and canines of most mammals. Furthermore, the incisors in the species studied here have been reduced to two; the same applies to the premolars.

According to Parker and Haswell ('47), the small cusps (the styles) on the external cingulum are frequently present in small primitive placental mammals with zalambdodont or dilambdodont molars. According to this view the molars of Golden Moles have retained these cusps which are primitive structures, in that they were present in primitive placental forms, and have been lost by most modern forms of mammals. The mesostyle, though not as developed as the other styles, is present in B. villosus pratensis and C. trevelyani, while in other Golden Moles it is absent. The presence of more styles in B. villosus pratensis and C. trevelyani as compared with the other Chrysochloridae , agrees with the idea that these two genera are more primitive than the other genera of the Chrysochloridea.

The talonid of the lower molars of Centetes as described by Butler ('37) has a hypoconid, a hypoconulid and an entoconid. The talonid of Golden Moles on the other hand, has only one cusp, possibly a hypoconulid judging by its position. Roberts ('51) has shown that amongst Golden Moles the genera Chlorotalpa, Amblysomus, Neamblysomus, Bematiscus and Chrysospalax have a talonid which is lacking in the other genera. This possibly suggests that at least two evolutionary lines were followed by this order of

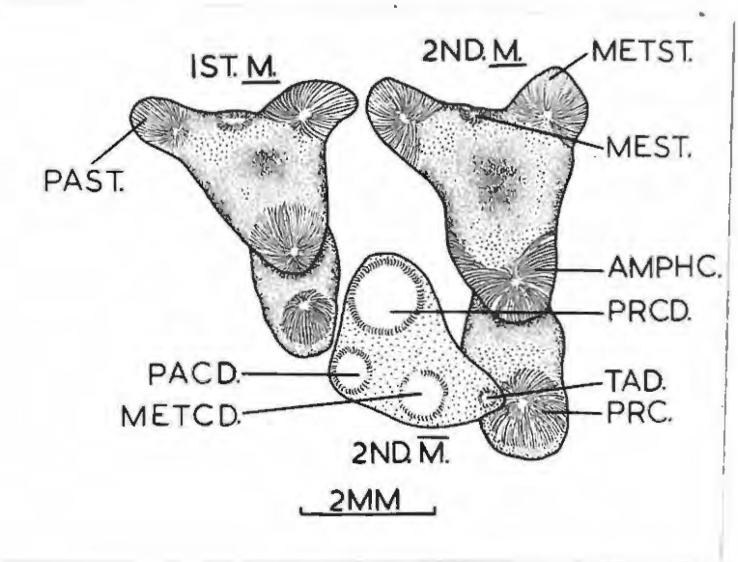

Fig. 15.

Diagram to illustrate occlusion of the molars in Golden Moles. AMPHC., amphicone; MEST., mesostyle; METCD., metaconid; METST., metastyle; PACD., paraconid; PAST., parastyle; PRC., protocone; PRCD., protoconid; TAD., talonid.

mammals. One line was followed by these forms which have no talonid, and the other by those with a talonid.

There is closer resemblance between the molar structure of the Jurassic *Pantotheria* and that of the Golden Moles whose molars possess a talonid, than there is between the *Pantotheria* and those Golden Moles without a talonid. The resemblance of the molar structure of the *Pantotheria* with that of Golden Moles supports Richie's ('44 p.896) view that the *Chrysochloridae* are " ... probably the most primitive of all Eutheria ... ".

OCCLUSION

The following account of occlusion applies equally well to *A. hottentotus hottentotus*, *B. villosus pratensis* and *C. trevelyani*.

Except for the first and second lower incisors, the teeth of the lower jaws bite on the lingual side between two consecutive teeth of the upper jaw. The first and second lower incisors bite on the lingual side of the first *i*. When the jaws are closed, the first $\bar{I}$ remains opposite the first *i*, while the second $\bar{I}$ comes to lie between the first and second upper incisors. The second $\bar{I}$ is long and its tip fits into a small cavity on the premaxillary just lingual to the *i*, thus limiting the upward movement of the lower jaw.

During a bite, the protoconids of the lower molars are received in the interdental spaces between every two consecutive upper molars (fig. 15). The protocone and the talonid of the molars do not meet in these animals and therefore do not assist in limiting the movement of the lower jaw towards the upper.

DISCUSSION

In mammals generally, the movement of the lower jaw towards the upper is limited by the crown surfaces of the upper and lower molars, and of the upper and lower premolars in some mammals coming together. In the Golden Moles, however, this is not the case as shown in the description of occlusion. Even the protocone and the talonid of the molars which lie opposite each other when the jaws are closed, do not meet. This contention is supported by the observations made on the chrysochlorid skull material in the Kaffrarian Museum. In all the specimens examined, the lower molars of which possess a talonid, the protocone and the talonid were found to be sharp even in the skulls of old animals.

The method of limiting the upward movement of the lower jaw as employed by Golden Moles would be painful to the animal if it were not for the following reasons. The tissue lining the hard palate is horny, while the animal's prey is slow moving and consists mainly of soft material. There is thus no need for snapping.

SOME OBSERVATIONS ON THE FEEDING HABITS OF AMBLYSOMUS HOTTENTOTUS HOTTENTOTUS AND CHRYSOSPALAX TREVELYANI

An observation was made whilst collecting the specimens of A. hottentotus hottentotus that when these animals are searching for food in wet soil, they make elevations in the surface layers of the soil. This is done in the following manner. Using the front limbs as fulcra, the snimal pushes itself forwards, head first, in such a way that the nose pad is the most anterior part. The head is constantly jerked upwards as the animal forces itself forwards. During the dry season, they simply dig for their prey using their forelimbs.

It was observed whilst feeding the specimens of A. hottentotus hottentotus in captivity that they ate earthworms and insect larvae rather greedily while they merely killed lizards and adult insects without eating them. However, if the A. hottentotus hottentotus specimens were starved for more than a day, they ate the lizards and adult insects. It is important to note that all the specimens used for the above observation were collected from a lucern field rich in earthworms. Insect larvae were also present although not as abundantly as earthworms. It is possible, therefore, that the behaviour of these Golden Moles towards the prey given to them in captivity was conditioned by the plentiful supply of earthworms and insect larvae in their natural environment.

An observation of the behaviour of A. hottentotus hottentotus specimens inhabiting a lucern field measuring about 120 yards by 60 yards at Lovedale, was made over the wet summer and dry winter months. Earthworms were plentiful in this field and insect larvae were also present though in much smaller numbers than earthworms. Big mounds, about 4 times as large as the usual summer mounds, were made during the dry winter months by these Golden Moles, though they were not working as regularly as in the summer months. The main tunnels were found to be about a foot below the surface in contrast to the usual main tunnels made in summer, which are about 4 inches below the surface. Specimens which had just fed on earthworms were caught during these dry winter months. These Golden Moles migrated to the neighbouring trees when the field was flooded with water.

The stomach contents of the collected specimens of A. hottentotus hottentotus which were found dead in the traps consisted of insect larvae, millipedes and earthworms. An interesting observation was made, that the prey before being swallowed had only been chopped into pieces and showed no signs of being crushed.

In B. villosus pratensis, the stomach contents could not be identified with certainty. The food had already been acted upon by the digestive juices of the stomach by the time of collecting.

The stomach contents of C. trevelyani specimens consisted of the remains of beetles, millipedes and earthworms. The beetles and millipedes had been roughly broken down into bits while the earthworms ranged from about one inch lengths to entire worms. As in A. hottentotus hottentotus the stomach contents showed no signs of having been crushed.

DISCUSSION

Fitzsimons ('20) stated that the sense of smell in Golden Moles is well developed. He showed that they depend on smell when locating their prey.

The presence of earthworms in the stomachs of two species of Chrysochloridae; A. Hottentotus hottentotus an underground feeder and C. trevelyani a mainly surface feeder, implies that earthworms are a part of the main diet of the Chrysochloridae. Furthermore, throughout the present investigation it was continually observed that A. hottentotus hottentotus prefers environments where there are earthworms and insect larvae. Since movements underground are not as easy as above ground, burrowing animals like Golden Moles cannot be too specific in the choice of their diet. Setting aside their preference for a certain type of diet it is not surprising therefore, that the specimens of A. hottentotus hottentotus fed on all the types of prey they were given in captivity.

The observations made on the lucern field at Lovedale, suggest that A. hottentotus hottentotus works just under the surface during the wet season because earthworms have come to the surface layers of the soil. It may further be suggested that during the dry months these Golden Moles follow the earthworms as the latter withdraw deeper into the soil. This perhaps shows that A. hottentotus hottentotus, and possibly other Golden Moles as well, do not become wholly dormant during the dry winter months. Until a thorough investigation has been done on the behaviour of the Golden Moles we may meanwhile accept the suggestion of Shortridge ('34) that the Chrysochloridae become dormant to some extent during the dry winter months.

Roberts ('51) fed a Bematiscus specimen kept in a box, with grasshoppers, and stated that it emerged when it heard him or smelt the grasshoppers. Under natural conditions Roberts ('51) states that he has never known Bematiscus to come to the surface except after rains. This was also noticed during the present investigation while collecting Bematiscus specimens, when they were never seen on dry days but were found dead on the meadows after rains perhaps killed by herdboys or dogs.

Ranger ('27) has shown that C. trevelyani is a surface feeder in the forest. This observation is supported by the presence of the remains of beetles in the stomachs of these specimens. Though earthworms do come to the surface, their presence in such a bulk in the stomachs of the specimens of C. trevelyani examined here, suggests that these Golden Moles may also burrow for the earthworms.

Romer ('45) suggested that insects, worms and grubs presumably formed part of the diet of the primitive placental forms. When the ancestors of A. hottentotus hottentotus and the closely related forms took to burrowing, perhaps in order to exploit the underground food material and escape from enemies, earthworms and insect larvae probably became the main part of their diet. Bematiscus villosus pratensis and C. trevelyani in addition to earthworms and insect larvae include adult insects as the main part of their diet. The diet of B. villosus pratensis and C. trevelyani therefore, probably approximates more to that of the primitive placental form than does that of the other Golden Moles.

The vestigial eyes of Golden Moles suggest that their ancestors were above-ground forms, with possibly well developed eyes which became vestigial when these animals took to burrowing. Taking this contention to be true it may be assumed that the genera *Bematiscus* and *Chrysospalax*, because they lead an above-ground as well as an underground life, have not changed much from the ancestral form of Golden Moles as the wholly underground smaller forms. Broom ('09) is of the same opinion. Furthermore, Roberts ('51 p.107) states that " ... judging by the teeth *Bematiscus* and *Chrysospalax* would appear to be the oldest genera ... ".

It may, on the contrary, be argued that the vestigial eyes of *Bematiscus* and *Chrysospalax* show that these two genera must at one stage have been complete underground dwellers. The partly above ground habits they display may therefore, mean a partial reversion to their original state, but they would probably not be successful in becoming complete surface dwellers unless they regain their eyes. This would therefore mean that they may have changed more from the original ancestors than the other forms. If, however, the number of teeth and the form of the molars are considered in *Bematiscus* and *Chrysospalax* it becomes clear that these two genera are nearer to the ancestral form than the other Golden Moles.

Judging from the similarity of the molars of Golden Moles with those of the *Pantotheria*, it is likely that the ancestors of Golden Moles took to burrowing at some time during the Jurassic and since then the Golden Moles have continued feeding on the same diet as that of the ancestral form. The Oligocene form *Apternodus* which is regarded by Gregory ('20) as a forerunner of Golden Moles was possibly a burrower. As far as can be ascertained ever since the ancestors of Golden Moles took to burrowing they met with little or no competition from other predators for their subterranean diet, which they have therefore continued eating. Also, even in those few forms which live on adult insects (as well as on earthworms and insect larvae) the plentiful supply of the insects precluded any pressure for changing their diet. It is not surprising, therefore, that there is little or no change in the molar structure of Golden Moles as compared with that of the Jurassic placental forms. The specialisation of the antemolar teeth is probably correlated with an improvement in their form and arrangement to serve as efficient grasping organs.

Other important factors for mammals which have to burrow for their existance are the nature of the hair and the size of the animal. In the genus Amblysomus the texture of the hair is smooth, while in the genera Bematiscus and Chrysospalax it is coarse. In Amblysomus it is clear that the soil particles detached from the sides of the burrow cannot easily be lodged in between the hair, while in Bematiscus and Chrysospalax this is possible and thus cause some inconvenience. The size of the members of the genus Amblysomus also show that they are more adapted for burrowing than those of the genera Bematiscus and Chrysospalax because the bigger the animal the more work it has to perform in making its burrow. Furthermore, the claws of the forelimbs in Bematiscus and Chrysospalax relative to body size, are poorly developed as compared with those of Amblysomus.

THE CORRELATION OF THE FEEDING HABITS OF AMBLYSOMUS HOTTENTOTUS HOTTENTOTUS, BEMATISCUS VILLOSUS PRATENSIS AND CHRYSOSPALAX TREVELYANI WITH THEIR JAW MUSCULATURE AND THEIR TYPE OF TEETH

As already shown, the head is so held that the nose pad is the most anterior part when A. hottentotus hottentotus makes elevations in the surface layers of the soil as it searches for food. The nose pad is kept in the desired position by the musculi rostrii. The great development of the musculi rostrii of B. villosus pratensis and C. trevelyani as compared with A. hottentotus hottentotus can be associated with the surface feeding habits of the two former genera. In. B. villosus pratensis and C. trevelyani the nose pad is directly used in stirring up the relatively hard surface. The nose pad in Golden Moles is used for placing the prey in such a position that biting will be effective. This is done by moving the nose pad in various directions as is necessary, after the fashion of a pig.

The articulation of the head of the mandible with the glenoid fossa is such that both up and down, and side to side movements as well as the anterior displacement of the lower jaw, are possible. The upward movement of the lower jaw which is the result of the contraction of the masseter, m. zygomaticomandibularis and the m. temporalis, is mainly involved in the catching and cutting of the prey into bits. It was difficult to make a comparison of the masseter and the m. zygomaticomandibularis in the species studied here. The m. temporalis is, however, more developed in B. villosus pratensis and C. trevelyani than in A. hottentotus hottentotus, perhaps because part of the main diet of the two former genera contains chitin which is somewhat hard.

The side to side movement of the lower jaw is important for two reasons, firstly it ensures that the tips of the cones of the upper and lower teeth come close to each other during a bite. Secondly, if any food particles adhere to the cones, the brushing effect of the cones caused by the movement of the one jaw against the other, probably serves to remove the sticking particles. The muscle responsible for this movement is the greatly developed m. pterygoideus medialis.

The effect of the side to side movement is similar to that of the anterior displacement of the lower jaw. The muscle mainly responsible for the anterior displacement of the lower jaw, the m. pterygoideus lateralis, is poorly developed, perhaps because this movement does not need much force, or because this muscle is helped by the masseter in its action.

As in other mammals the m. digastricus anterior in Golden Moles depresses the lower jaw. This muscle is generally feebly developed in mammals because normally slight force is needed to open the jaws. Furthermore, in the Golden Moles the food is not sticky.

Tomes (1897) pointed out that feeble implantation of teeth militates against the idea that they are put to very hard work. Examining the dentition of these Golden Moles in this light, the following was observed. The roots of the incisors are longer than their respective crowns in the Golden Moles here investigated. This condition may be correlated with the use of these teeth for catching the prey and their consequent need for firm support. Further, the upper incisors slant posteriorly and the lower incisors incline anteriorly. This arrangement of the incisors, also found in the marsupial mole Notoryctes, perhaps improves the efficiency of the incisors in their function of catching the prey. The arrangement of the incisors in these animals also suggest that they may cut the prey in a rodent-like fashion. Gregory ('20) has shown that Notoryctes also feeds on earthworms. The length of the roots of the canines and premolars shows that these teeth also have the same function as incisors. The specialisation of the antemolar teeth may, therefore, be correlated with their function as a prey-seizing apparatus. The roots of the molars are short compared with those of the antemolar teeth, suggesting that they are adapted for cutting soft food material.

The cusps of the teeth in Golden Moles remain sharp throughout the animal's life. This is understandable in A. hottentotus hottentotus because the members of this species feed mainly on soft food material. The hard chitinous covering of adult insects could be expected to cause tooth wear in B. villosus pratensis and C. trevelyani. Perhaps the absence of tooth wear in these two species of Golden Moles is either because chitin is not hard enough to cause tooth wear or because the crown surfaces of the upper and lower teeth do not act against one another. Possibly the occlusal relations of the upper and lower teeth and the fact that the Golden Moles do not grind their prey, also account for the absence of tooth wear which might be expected to be caused by sand grains in the gut of earthworms or sand grains sticking to the prey, especially in those forms which feed under the ground surface.

The complicated premolar and molar structures of herbivores is associated with the presence of cellulose in their diet while the premolars and molars in carnivores are adapted for the carnivorous diet. In Golden Moles, however, the molars are adapted for cutting the worm-like food material. The upper molars are thus broad transversely. The lower molars, as shown in the description of occlusion fit in the interdental spaces between the upper molars thus forcing the food against the edges of the upper molars as the animal chews. Since the food is soft, it is easily cut into pieces in this way.

As already shown, the simple structure of the molars can be correlated with a diet consisting of earthworms, millipedes and insects. This diet was inherited by Golden Moles from their Jurassic ancestors, and because the diet has not changed much, the molars too have changed very little.

THE ECONOMIC IMPORTANCE OF AMBLYSOMUS HOTTENTOTUS HOTTENTOTUS, BEMATISCUS VILLOSUS PRATENSIS AND CHRYSOSPALAX TREVELYANI

Earthworms, which formpart of the main diet of Golden Moles, are generally regarded as of economic importance because they bring the subsoil to the surface and aerate the soil. It may, therefore, be thought that Golden Moles are a pest by destroying the earthworms. Fitzsimons ('20) suggested that the Golden Moles also do the same good to the soil and perhaps on a larger scale compared with earthworms.

The members of the genus Amblysomus may be considered as economically important because they eat insect larvae and millipedes which inhabit the cultivated lands. Insect larvae such as cutworms, which live underground, are of great economic importance to farmers and gardeners because of their destructive habits. Richie ('44) has shown that the millipedes are vegetarians, feeding on the underground parts of plants, thus doing a great deal of harm to crops such as potatoes.

The available literature indicates that the members of the genera Bematiscus and Chrysospalax destroy millipedes and insects in all stages of development.

SUMMARY

1. The jaw musculature as well as its innervation in the Golden Moles used for this investigation is typically mammalian, except that the m. temporalis occupies the whole of the orbito-temporal fossa.
2. Fiedler's ('53) contention that the m. zygomaticomandibularis is a separate muscle is confirmed by the present investigation.
3. The musculi rostrii are responsible for the movements of the nose pad when the animal is feeding.
4. The dentition of A. hottentotus hottentotus, and possibly other Golden Moles as well, is monophyodont.
5. The antemolar teeth are specialized, while the molar teeth exhibit a very simple molar structure similar to that of primitive placental mammals.
6. The dental formula of Amblysomus is

$i\ ^{2}/2\ \ c\ ^{1}/1\ \ p\ ^{2}/2\ \ m\ ^{4}/4$ and that of Bematiscus and Chrysospalax is

$$i\ ^{2}/2\ \ c\ ^{1}/1\ \ p\ ^{2}/2\ \ m\ ^{5}/5.$$

7. The second $\bar{I}$ limits the movement of the lower jaw towards the upper.

8. Although the Golden Moles investigated here show some differences in their feeding habits, the worm diet is common to all of them.

9. The molars of Golden Moles are adapted for cutting the worm-like food material.

10. The simple molar structure can be correlated with the earthworm and insect diet which the Golden Moles inherited from their ancestors.

11. All the available evidence indicates that the members of the genera Bematiscus and Chrysospalax are unspecialized as regards burrowing, and more primitive than the other Golden Moles.

12. Because Golden Moles eat millipedes and insects in all stages of development, they are considered as being of considerable economic importance.

ACKNOWLEDGEMENTS

I wish to express my indebtedness to the following persons for their assistance in connection with this investigation: Dr. M. Webb, Dr. W.J. Steyn and Mr. J.W.T. Dandy of the University College of Fort Hare, for their invaluable advice and helpful criticism in the preparation of this manuscript.

The Director and Staff of the Kaffrarian Museum, Kingwilliamstown for the supply of the Giant Golden Mole material, and for putting the insectivore skull material at my disposal for purposes of study.

My colleagues, Mr. C.R. Dennis and Mr. N.N. Sishuba for their advice and encouragement.

I am further deeply indebted to the Council for Scientific and Industrial Research for financial aid which made it possible for me to carry out this research.

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