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NOTES ON SOME WHAITSIIDS AND MOSCHORHINIDS

By A. S. Brink

Abstract

This paper contains descriptions of five genera. The first is a redescription of the type specimen of *Notosollasia boonstrai*, which has been additionally cleaned since it was first introduced. It has, lodged in its "throat", the crushed skull of a *"Dicynodon"* and circumstances indicate that the *Notosollasia* died while devouring its prey. The second specimen is recognised as perhaps representing the doubtful genus *Notaelurops*. It was earlier identified as a small *Notosollasia longiceps*. The third specimen is not a Whaitsiid, but being a contemporary form with some vague affinities to *Moschorhinus*, it is taken into consideration. It is named *Hewittia albanensis* gen. et sp. nov. A snout of *Moschorhinus kitchingi*, also mentioned in a previous publication, is redescribed and figured. The fifth specimen is a beautiful and complete skull of a new species, *Moschorhinus natalensis*, the first specimen of this genus that has the whole of the posterior half of the skull preserved and it is peculiar in that it dates from the *Lystrosaurus*-zone. An interesting new arrangement in the replacement of the canines in this family is analysed.

Introduction

Mr. J. W. Kitching recently recovered from *Lystrosaurus*-zone beds in northern Natal the complete skull of a *Moschorhinus*. It struck him immediately that this specimen is unique in being the first of this genus which includes the whole of the posterior half of the skull, and also that it was found in *Lystrosaurus*-zone beds. There can be no doubt about the age, because Mr. Kitching also recovered a *Lystrosaurus* specimen a few yards away.

The total thickness of the beds of this zone is still quite appreciable in the area concerned, while the higher zones virtually disappear as they thin out northwards. Had this been the case with the *Lystrosaurus* zone, it may be considered that at a particular level, relative to the total thickness, the actual age could be earlier than a similar relative level farther south where the zone is appreciably thicker. However, the zone is extremely thick in northern Natal and the fact that the specimen was discovered alongside with *Lystrosaurus* specimens show that the difference in age between the new specimen and its *Cistecephalus*-zone relatives is very significant indeed.

At the time of the discovery of this specimen, the Bernard Price Institute had on loan from the Albany Museum, Grahamstown, the anterior half of a Therocephalian skull, recovered from *Cistecephalus*-zone beds. It is a rather interesting specimen and as it is a contemporary of the Whaitsiids and shows some vague relationship to *Moschorhinus*, an account of it is included here. It is, however, not a member of the family Whaitsiidae.

In the meantime some other Whaitsiids, which have already been featured in a previous description, were additionally cleaned and a better interpretation of three of them is now offered.

Notosollasia boonstrai Brink

(Figs 7, 8, 9, 10, 11)

1951, BRINK, A. S., *Trans. Roy. Soc. S. Afr.*, xxxiv, 1, p. 43, fig. 6.

Type: A complete skull with lower jaw in situ, No. 147 in the collection of the Bernard Price Institute, from middle *Cistecephalus*-zone beds on the farm Milton in the Murraysburg district.

Diagnosis: Orbits large and completely round; postorbital bars roundly curved backward; parietal crest extending far back and occipital crests turning sharply outward; skull exceptionally short and broad; snout well constricted in front of orbits, with the anterior portion round and massive.

In 1954 I introduced the name *Notosollasia boonstrai* as a new species, for a rather good skull in the collection of the Bernard Price Institute. Unfortunately, through lack of proper facilities and equipment at the time, our preparation techniques were rather primitive and the specimen could not be properly cleaned in view of the extreme hardness of the matrix and the fragile nature of the bone. As it happened, the specimen suffered unnecessary damage and although some fractures showed interesting structural detail, the inclination was to leave the specimen partly cleaned and merely record it as a new species based on some superficial characteristics.

A few years ago we acquired the services of an assistant preparator who, with some training, became so expert that we trusted this type specimen in his care and the results he achieved demand that the specimen should be redescribed. However, previous damage and the hardness of the matrix, which could not be removed in certain strategic areas, still obscure some important structural details.

A very interesting feature about this specimen is that it has, lodged between the rami of the lower jaw, in the position of the "throat", the skull of a small *"Dicynodon"*. This region was so unsatisfactorily cleaned when the skull was first described, that these foreign bones could not be identified. They were regarded as some skeletal bones belonging to the specimen. Now it is not only clear that this foreign element is the skull of a *"Dicynodon"*, with its lower jaw approximately in situ, but that it suffered some considerable pre-fossilization damage. There can be no doubt that this *"Dicynodon"* was actually being swallowed when the *Notosollasia* died and that death was evidently due to suffocation, judging from the size of the prey.

The *"Dicynodon"* skull could hardly have landed in this peculiar position after the death of the *Notosollasia,* because it is too intimately thrust against the posterior palate and between the rami of the lower jaw. If this had happened by accident, some forces must have been responsible for bringing the two skulls into such intimate association and these forces would certainly have dislodged the lower jaws of both specimens. However, although the *"Dicynodon"* lower jaw is somewhat dislocated as part of its general damage, the lower jaw of *Notosollasia* is firmly in situ.

The damage that the *"Dicynodon"* skull suffered is not merely crushing. The posterior portions of both skull and lower jaw are missing and this is not due to weathering, because the more pronounced damaged regions are on the inside, closest to the palate of *Notosollasia*. The snout of the *"Dicynodon"* is directed forward and somewhat ventrally, protruding below the ventral margins of the lower jaw of *Notosollasia*. It is peculiar, for example, that the left ramus of the *"Dicynodon"* lower jaw extends across the otic-basioccipital region of the *Notosollasia* skull, that is, through the "throat", but the right ramus, if it had been present, would then have extended through the temporal fossa. The temporal vacuities could be cleaned on the dorsal side down to the level of the palate and no trace of the *"Dicynodon"* skull could be found. The position of the latter skull is such that had it landed in its peculiar position by accident, some portions of it must have penetrated into the temporal vacuities.

There can be no doubt whatsoever that this *Notosollasia* died while it was in the act of swallowing its prey and that the most likely cause of death was suffocation.

The posterior portion of the *"Dicynodon"* skull had apparently already been swallowed, as was evidently the case with the rest of the body, while the more rigid and bulky anterior portions offered some resistance. This procedure in devouring prey is mammal-like and not reptile-like. Reptiles normally start at the head and swallow this first. The specimen also supports the view that Whaitsiids masticated their food to some extent. It is also possible that this portion of the *"Dicynodon"* skull was left over by another carnivore and that *Notosollasia* afterwards salvaged it, thus indicating scavenger habits in this animal.

With the specimen in its previously rather unsatisfactorily cleaned state, little more could be recorded about it than the above diagnosis and a list of measurements. Although the specimen is now very much better cleaned, a good many structural details are still rather obscure. The figures do not indicate the actual condition of preservation and the extent to which the matrix could be removed. All the figures in this paper are idealistic, distortion being corrected, damaged portions reconstructed and obscure details added from information obtained from other specimens, but only in so far as no risk is taken by crediting one specimen with characteristics peculiar to a different species. Matrix is eliminated by tracing, in the case of dorsal and ventral views, the relevant information from the one to the other.

The basioccipital forms the greater part of the occipital condyle and the posterior half of the area between the fenestrae ovales. The latter appear to have had insubstantially ossified borders as in *Aneugomphius* (Brink, 1956).* The suture extending between these two fenestrae is extensive and clear, unlike the typically obscure unions between two cartilage bones. This suture therefore marks the union of the basioccipital directly with dermal parasphenoid, so that the basisphenoid is not exposed medianly. The latter bone could have been slightly exposed laterally between the parasphenoid and the pro-otics.

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* Brink, A. S., Palaeont. Afr., 4, p. 97.

The exoccipitals are like those of *Aneugomphius*. However, they do not approach one another so closely on the dorsal side of the foramen magnum and they also contribute less to the borders of the jugular foramina. Their lobes contributing to the occipital condyle are not properly fused to that of the basioccipital. The spaces between these three lobes had apparently been cartilaginous, illustrating the juvenility of the specimen.

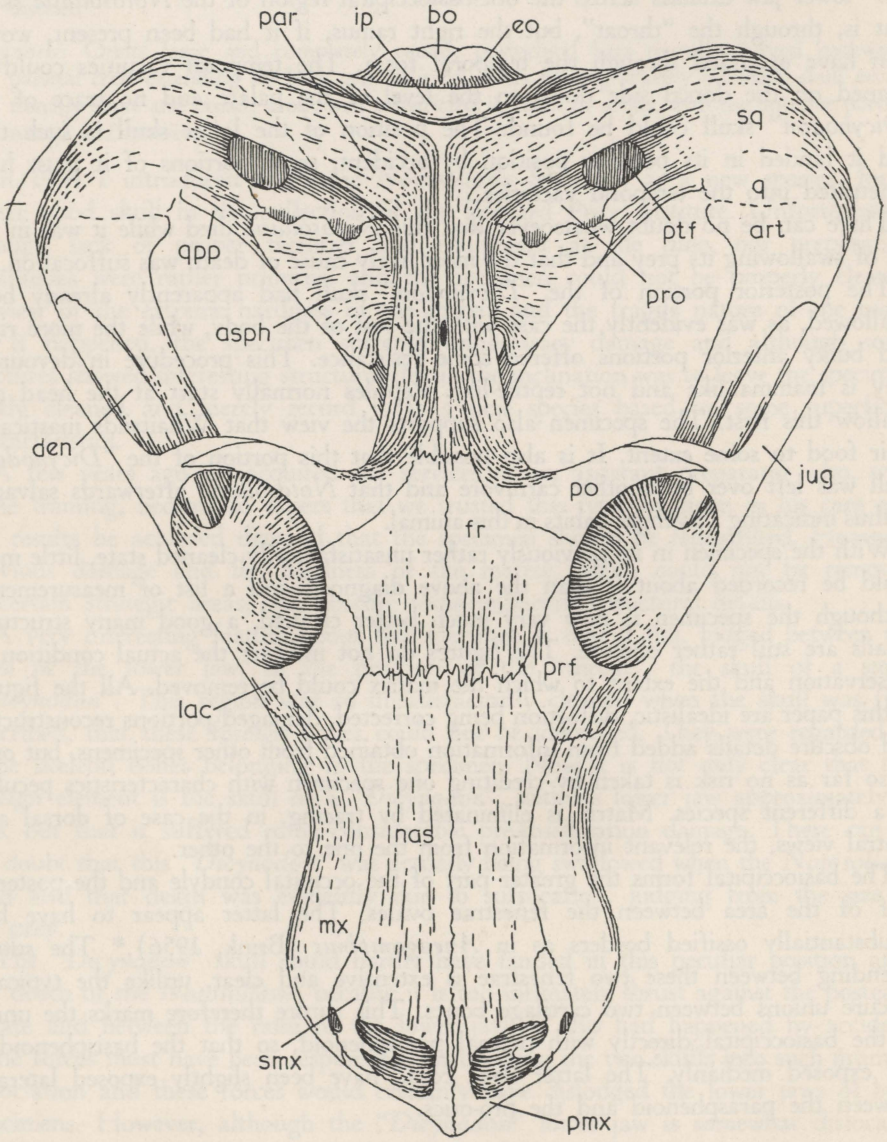

Fig. 7—Dorsal view of the skull of *Notosollasia boontsrai,* natural size. For abbreviations see end of article.

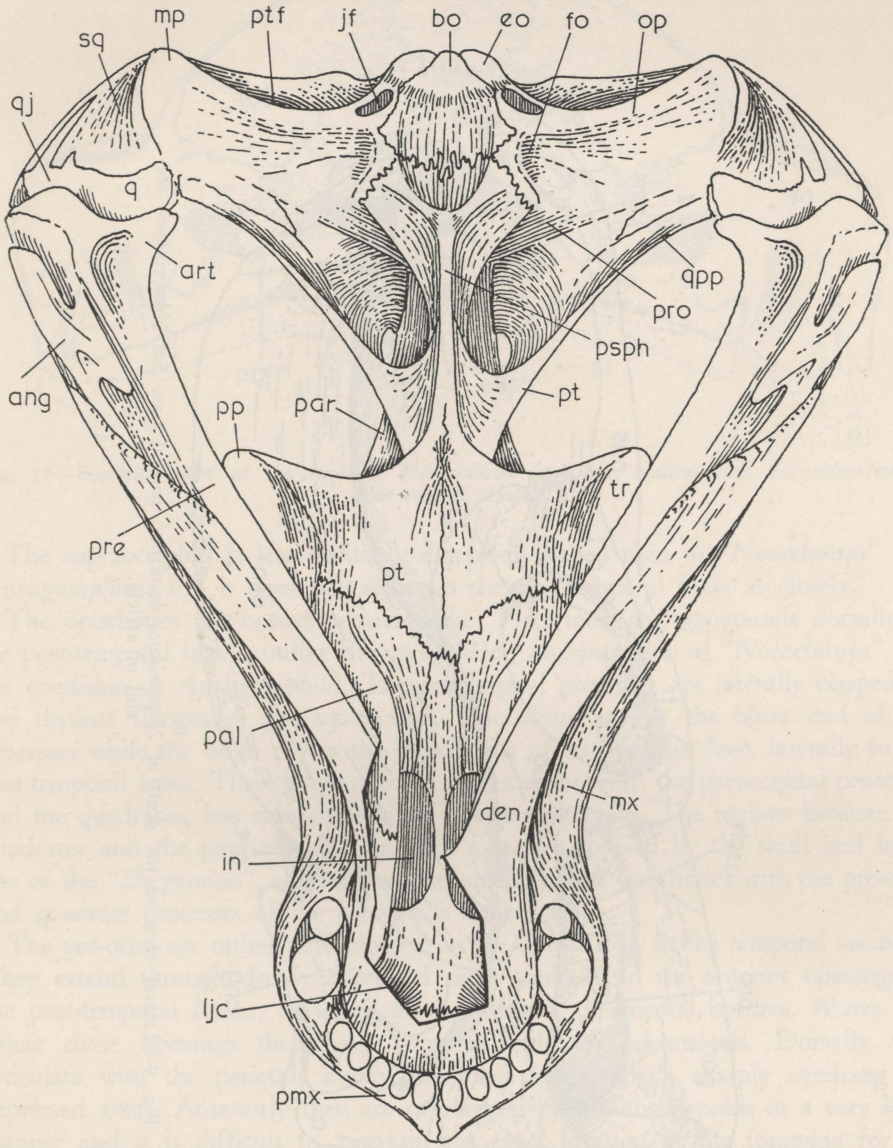

Fig. 8—Ventral view of the skull of *Notosollasia boonstrai,* natural size. For abbreviations see end of article.

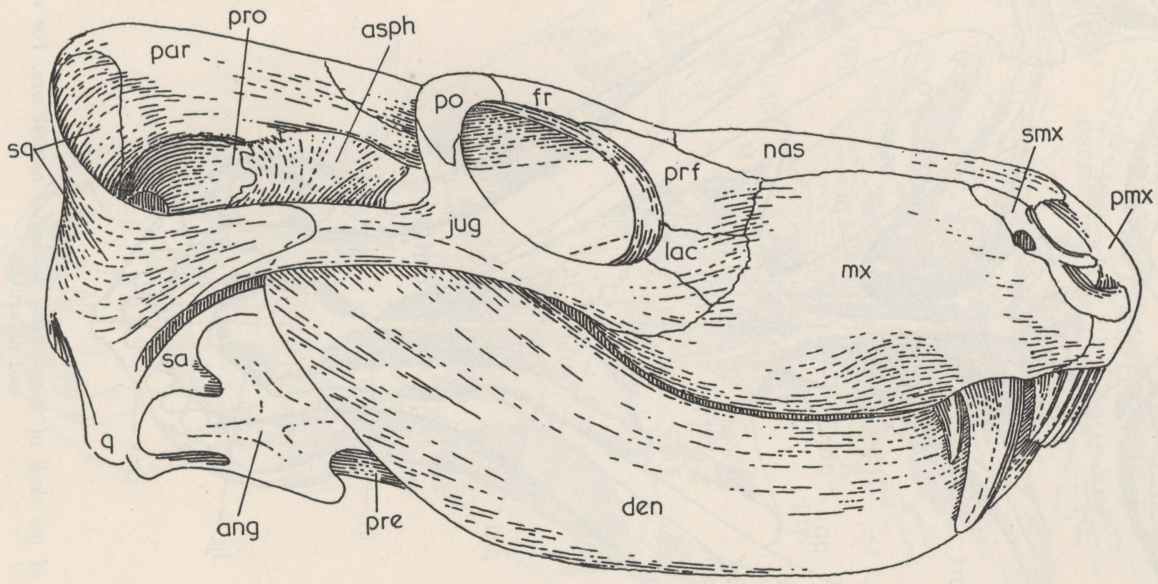

Fig. 9—Lateral view of the skull of *Notosollasia boonstrai,* natural size. For abbreviations see end of article.

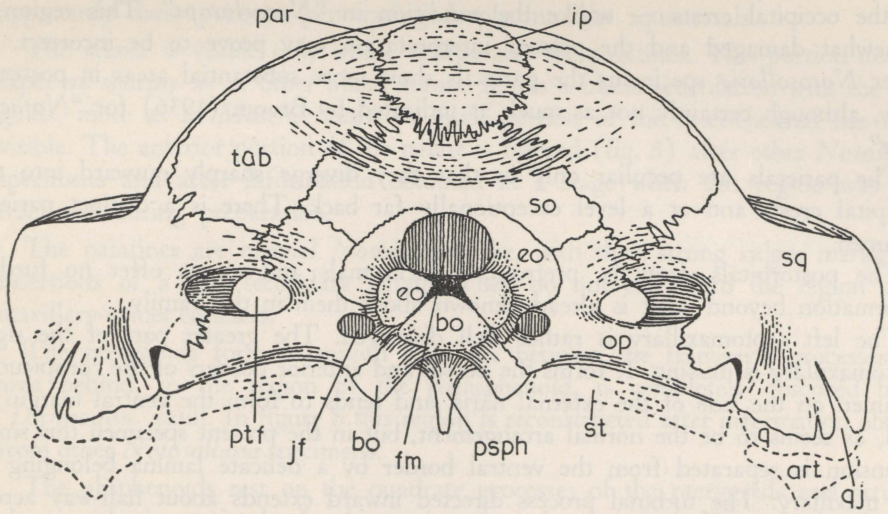

Fig. 10—Posterior view of the skull of *Notosollasia boonstrai,* natural size. For abbreviations see end of article.

The supraoccipital is less distinctly dumb-bell-shaped than in *"Notaelurops"* and *Aneugomphius,* and it does not approach the post-temporal fossa as closely.

The opisthotics are normal whaitsiid-like. They meet the squamosals dorsally to the post-temporal fossae, unlike Broom's (1936) interpretation of *"Notaelurops"* and the condition in *Aneugomphius.* The paroccipital processes are laterally clasped by two distinct flanges of the squamosals. One abuts against the blunt end of the processes while the other covers the dorsal part of its posterior face, laterally to the post-temporal fossa. There appears to be a contact between the paroccipital processes and the quadrates, less substantial than in *Aneugomphius.* The regions between the quadrates and the parasphenoid, on each side, are covered by the skull and lower jaw of the *"Dicynodon",* so that the relationship of the opisthotics with the pro-otics and quadrate processes of the pterygoids is not clear.

The pro-otics are rather well exposed on the dorsal side, in the temporal vacuities. They extend through deeply depressed areas medially to the anterior openings to the post-temporal fossae, to which they contribute the medial borders. Above and below these openings they have contacts with the squamosals. Dorsally they articulate with the parietals along prominent ledges which sharply overhang the depressed areas. Anteriorly they are overlapped by the alisphenoids in a very loose manner and it is difficult to ascertain the exact location of the foramina for the different branches of the fifth nerve. This can be due to preparation damage.

The tabulars are excluded from the borders of the post-temporal fossae. They form elaborately interdigitated sutures with the supraoccipital. This extensive penetration of one bone into another all along their suture is quite characteristic of unions between dermal and cartilage bones.

The interparietal is small and round, and apparently reaches to the dorsal margins of the occipital crests — unlike the condition in *"Notaelurops"*. This region is somewhat damaged and the present interpretation may prove to be incorrect. In other *Notosollasia* specimens the parietals show more substantial areas in posterior view, although certainly not as much as indicated by Broom (1936) for *"Notaelurops"*.

The parietals are peculiar only in that they diverge sharply outward into the occipital crests and at a level exceptionally far back. There is a distinct parietal foramen.

The postorbitals, frontals, prefrontals, lachrymals and nasals offer no further information beyond what is already known about them in this family.

The left septomaxillary is rather well displayed. The greater part of the right septomaxillary is missing. It forms the dorsal and anterior borders of the conspicuous foramen on the side of the external naris, and tends to form the ventral margin as well, as seems to be the normal arrangement, but in the present specimen this small extension is separated from the ventral border by a delicate lamina belonging to the maxillary. The turbinal process directed inward extends about half-way across to the internarial bridge. The septomaxillary forms the ventral border of the external naris and apparently much of the floor of this opening. A fragment of the right septomaxillary indicates that these bones also fold over the premaxillaries to cover portions of their anterior faces.

The premaxillaries have five incisors each and the internarial processes penetrate into the nasals, not between them as is more often interpreted as the normal condition. The nasals separate these processes for a considerable distance, at least 10 mm.

The maxillaries bulge very prominently sideward in the region of the canines. On both sides the anterior canines are large but still loosely situated in their sockets. The posterior canines had recently started to erupt. They are distinctly situated within the same sockets as the larger anterior teeth. There are no postcanine teeth.

The transverse bones form the bulk of the processes guiding the lower jaw. Unfortunately the *"Dicynodon"* skull is thrust against the pterygoid processes so that it is difficult to establish the extent to which the pterygoids contribute to these processes. They may form substantial portions of the lateral faces guiding the lower jaw, but the exact condition cannot be ascertained as a result of the presence of the lower jaw.

The jugals have been damaged on both sides and their relationship with neighbouring bones, as figured, could only be deduced indirectly.

The squamosals form the lateral halves of the borders of the post-temporal fossae, in both posterior and anterior aspects. Anteriorly, above these fossae, the squamosals overlap the parietals elaborately. There seem to be good contacts between the squamosals and the quadrate processes of the pterygoids, leaving no pterygo-paroccipital foramen. The quadrates are in loose articulation with the squamosals, in spite of the fact that the quadratojugals penetrate these bones very deeply. The external auditory meatus grooves are small and shallow.

The quadrates are obscure, being covered by the articulars. The quadratojugals are apparently those portions penetrating deeply into the squamosals.

The vomer is visible only where it separates the palatines. This portion does not taper as sharply as in other allied forms. It has a blunt articulation with the pterygoids, more as in *Moschorhinus*. A small portion of the inter-choanal bar is also visible. The anterior portion of the palate is figured (fig. 8) after other *Notosollasia* specimens and after information obtained at a stage when this region was badly fractured during preparation.

The palatines are normal *Notosollasia*-like, with their strong ridges marking the insertions of a soft secondary palate. They do not extend to the region of the maxillary-vomer contacts.

The pterygoids form a smooth flat area between the transverse processes. The area behind, in the region of the parasphenoid, is completely obscured by the "*Dicynodon*" skull. In figure 8 this region is reconstructed after information obtained from other *Notosollasia* specimens.

The alisphenoids rest on the quadrate processes of the pterygoids and articulate above with the parietals. In this region there is a marked difference between the present specimen and the one described below as a possible "*Notaelurops*". In the present specimen the ventral margins of the parietals along the alisphenoid contacts are raised. The alisphenoids have a strong articulation posteriorly along these margins, while anteriorly the contacts seem to be rather loose. In "*Notaelurops*" these margins drop to meet the alisphenoids and the latter have their firm contacts anteriorly.

The parasphenoid is visible between the fenestrae ovales and just in front of this region it shows a very deep keel.

The dentaries are large and massive. The coronoid processes extend far back, but not very high through the temporal fossae. Anteriorly the roots of the four canines are exposed through preparation damage. The posterior roots are larger than the anterior ones and are situated very loosely in their sockets. Ventrally, at the ends of the roots, the anterior and posterior canines have distinctly separate sockets, divided by a substantial wall of bone. Upwards the two teeth converge and at the level of the alveolar border they seem to share one socket, as can be seen in a small section cut by a dental emery wheel. It appears, therefore, that *Notosollasia boonstrai* has one canine on each side in the lower jaw, which in the present specimen is in the act of being replaced. The distinctly separate origins of the erupting and deciduous teeth indicate that the presence of two separate canines on each side was a recent ancestral condition and that one functional canine in this and other Whaitsiids did not develop through the loss of one of the two, but by the two joining together in such a manner that the one functioned alternately to the other.

This arrangement would imply that the erupting canine will appear alternately in front and behind the deciduous tooth, which seems to be exactly what happened. In the present specimen the smaller new canine appears behind the larger anterior

tooth in the upper jaw, while in the lower jaw it is distinctly the anterior tooth which is the younger, endeavouring to replace the posterior one, which had already loosened. In another specimen of *Notosollasia* (*N.longiceps?, No.* 139) the new upper canine is situated anteriorly.

From the Whaitsiid material at the author's disposal it is quite clear that the newly erupting canine does not emerge consistently on the same side of the deciduous canine, which can be regarded as the normal condition, but alternately in front and behind the predecessor, apparently according to a standard pattern.

This peculiar arrangement can best be explained with the aid of the accompanying diagram (see fig. 11). The original condition as it is found in some earlier Therocephalians like *Trochosaurus, Lycosuchus* and *Hyaenosuchus,* is illustrated in figure 11A, where two canines on both sides and in both jaws are equally strongly developed and functional at the same time. To clarify the subsequent diagrams, new tooth buds representing the replacers for each canine are indicated, each so situated that it will erupt in a normal fashion on the same side of the functional tooth.

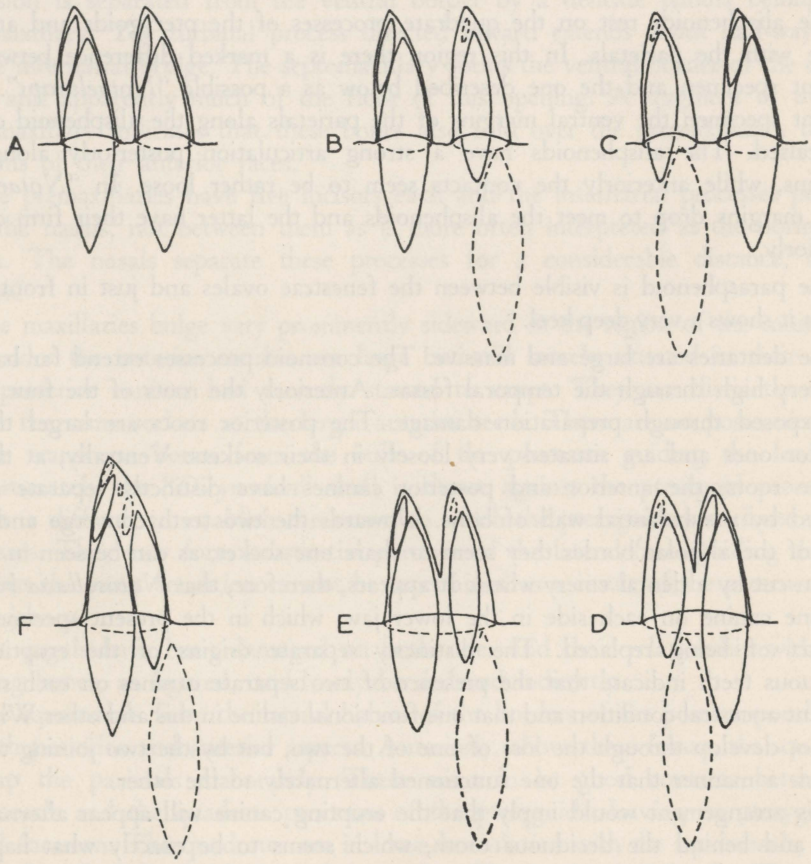

Fig. 11—Diagrammatic representation of the replacement of the canines in the Whaitsiidae.
See text page 33.

From this stage there are two distinct directions of subsequent evolutionary development. In the one direction the tendency developed to sacrifice one of the two canines in favour of the other, double canines having no particular advantage over a single canine. From the available material representing subsequent stages of Therocephalian evolution it appears that the anterior canine had been the one that had become reduced and finally disappeared. In some forms there were more than one canine in front of the large canine; in others like *Moschorhinus* the one anterior canine had reduced to a size inferior to that of the incisors. Finally total loss of the superfluous canine paved the way for the eventual further development in the direction of true mammals. This circumstance adds to the doubt the author has expressed before (1956)* about *Moschorhinus* being a member of the Whaitsiid family.

The Whaitsiids form a natural group in which a second line of evolutionary development occurred. Rather than sacrificing the one tooth in favour of the other, the tendency here was to allow the one to be functional alternatively to the other. The first step in this direction is illustrated in Fig. 11B, where it is shown how the one canine remained functional while the other was being replaced. In this case the new tooth emerges in front of the tooth that remains functional. At a later stage in the life of the particular individual the anterior tooth will remain functional while the new canine will appear posteriorly, as shown in fig. 11C. This seems to have been still the condition in *Alopecopsis, Hofmeyria* and perhaps *"Notaelurops"*. In more advanced Whaitsiids this co-operation between the two canines was apparently enhanced by a tendency to share one socket, as illustrated in figure 11D and E. The ultimate condition, which may not have been reached by the most advanced Whaitsiids, would be the one illustrated in figure 11F, where both canines came to share a single communal socket, not semi-subdivided as in the previous stage.

This condition is naturally unique. It implies that the deciduous canine is not being replaced by its own successor, but by a different tooth altogether, while the successor to this latter tooth is in actual fact the replacer of the tooth previous to the one it is replacing. It explains why it is that a new tooth can emerge either in front of or behind the deciduous tooth, and it indicates that this could have occurred in a regularly alternating manner. The major implication of this strange condition is that apparently the greater part of the range of stages illustrated in figure 11 can occur within the life-span of a single individual. It would appear from the material at the author's disposal that a very juvenile specimen of a *Notosollasia* species may indicate the condition illustrated in figure 11B or C, while later in the life of the same individual stage D is reached. In all likelihood the same individual may even reach stage F at a very advanced age. Thus, when examining these specimens, one would be inclined to consider a juvenile specimen with two separate canines as belonging to a distinctly separate genus, if not a new family, to another specimen with a single canine, which may in fact have been the mother of the former specimen! For this reason the two canines of *Aneugomphius* can no longer be regarded as a

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* Brink, A. S., Palaeont. Afr., 4, p. 97.

generic distinguishing feature, leaving only the pterygoid teeth to support its recognition as a separate genus. The specimen described below as possibly a *"Notaelurops"* is characterised mainly by having two separate canines. If the above interpretation is correct, *"Notaelurops"* cannot continue to enjoy recognition and it must thus be regarded as a juvenile *Notosollasia longiceps.*

The space between the anterior erupting canines and the symphysis is very small. This region was excavated with a dental emery wheel to a level a short distance above the tips of the upper incisors, but no lower incisor roots could be traced. From other available material it is clear that the *Notosollasia* lower jaw had only three incisors, these being considerably smaller than their upper fellows. In the present specimen the space occupied by the lower incisors is very small indeed and although it is to be expected that the region becomes wider at a higher level, it is nevertheless clear that it could not accommodate more than three teeth on each side, even if they are half the size of the upper teeth.

The rest of the bones in the lower jaw are not well exposed and the portions that could be exposed have been damaged, so that it is not safe to base any conclusion on what they tend to convey in the line of structure and relationship. In the accompanying figures these bones are superficially restored after information obtained from other specimens, within the limits of some general outlines visible in the present specimen.

Notaelurops paucidens Broom 1936.

(Figs. 12, 13)

1936, BROOM, R., *Ann. Transv. Mus.*, xviii, p. 367.

1954, BRINK, A. S., (*Notosollasia longiceps,* No. 142) *Trans. roy. Soc. S. Afr.*, xxxiv, p. 52.

1954, BRINK, A. S., Idem, p. 57.

Type: A "beautiful" small skull, believed to have been discovered in lower or middle *Cistecephalus*-zone beds on Dr. S. H. Rubidge's farm Wellwood in the Graaff-Reinet district and presented to the Transvaal Museum where it is now housed. No number supplied.

Diagnosis: From Broom's (1936) description and figures it appears that the following are the only features of this specimen in which it differs from nearly related forms like *Alopecopsis* and *Notosollasia*: The pineal foramen is more distinct and more posteriorly situated than in *Alopecopsis;* the parietals are well exposed in posterior view; the interparietal is small and low; the tabulars are small and short; the supraoccipital extends to the post-temporal fossae (doubtful); the dentaries are long and slender (the only substantial feature if age is disregarded).

Present specimen: A small skull with both temporal arches missing, the right side being additionally damaged (prefossilization); only the left mandible is in position. It was discovered in middle *Cistecephalus*-zone beds on the farm Suurplaas in the Graaff-Reinet district, and is numbered 142 in the collection of the Bernard Price Institute. In 1954 the author referred this specimen to the genus and species *Notosollasia longiceps.*

Revised diagnosis: None of the above distinguishing features is substantially confirmed by the present specimen, other than the smallness of the interparietal and the slenderness of the dentary, both being likely juvenile characteristics. However, the present specimen has two separate canines in the upper jaw, their sockets being well separated by a bony partition up to the level of the alveolar border. There is no indication as to which of the two is the older. The snout is missing in the type.

If the author's interpretation about the nature of the replacement of the canines, as explained above, is correct, especially if it is considered possible that the various stages illustrated in figure 11 can occur through the life-span of a particular individual, then it is doubtful whether this specimen is a *Notaelurops paucidens*. In fact, it is doubtful whether even the type specimen should enjoy this recognition. In all likelihood these two specimens are juvenile idividuals of *Notosollasia longiceps*.

Broom's (op. cit.) description of the type gives no convincing indication as to why he recognised it as a separate genus and species. There is no feature about the shape and structure of the type, in which it differs from *Notosollasia longiceps,* which cannot be accounted for in terms of age. As hinted above, the only substantial difference lies in the shape of the dentary, which could change with increase in age. The difference in the shape of the dentary between the present specimen and *Notosollasia boonstrai* is quite substantial. Besides the fact that the latter is much more robust, the outline of the coronoid process is conspicuously different and it is most unlikely that this can be due to age. However, *N.boonstrai* is certainly a distinct species. No lower jaw of *N.longiceps* has so far been described, but another specimen at hand (No. 139 referred to *N.longiceps* by the author in 1954) has a beautiful lower jaw. There is no difference between the lower jaw of this specimen and the one evaluated here as a possible *"Notaelurops"*. The skull of this *N.longiceps* (No. 139) does not differ in any respect from three other specimens in this collection, which could be identified as *N.longiceps* without the slightest degree of doubt. Even more conspicuous is the absolute similarity between this specimen and the present *"Notaelurops"*. The latter differs from No. 139 only in size, and in the anterior snout region being less bulged. Otherwise, even the degree of distortion and the amount of damage are similar. The only other difference is that the *"Notaelurops"* has two very distinctly separate canines, while the *Notosollasia longiceps* has one canine on each side. The left is an old tooth firmly lodged in its socket; the right is a smaller young tooth well erupted, with a space posteriorly in the socket indicating the recent loss of the predecessor. There is distinctly one socket on the alveolar border, but a section cut across the region of the roots indicates two separate sockets at a higher level. In *"Notaelurops"* the sockets are separated up to the level of the alveolar border with a substantial bony partition.

In view of the otherwise absolute similarity between these two specimens, the one being undoubtedly a *Notosollasia longiceps,* it is very likely indeed that the above explanation (not only of how the two canines co-operate, but also that one individual could illustrate the whole range of these stages through its life span) is substantially correct. Thus the present specimen is most unlikely a *Notaelurops paucidens* and it is doubtful whether the type should continue to enjoy generic status.

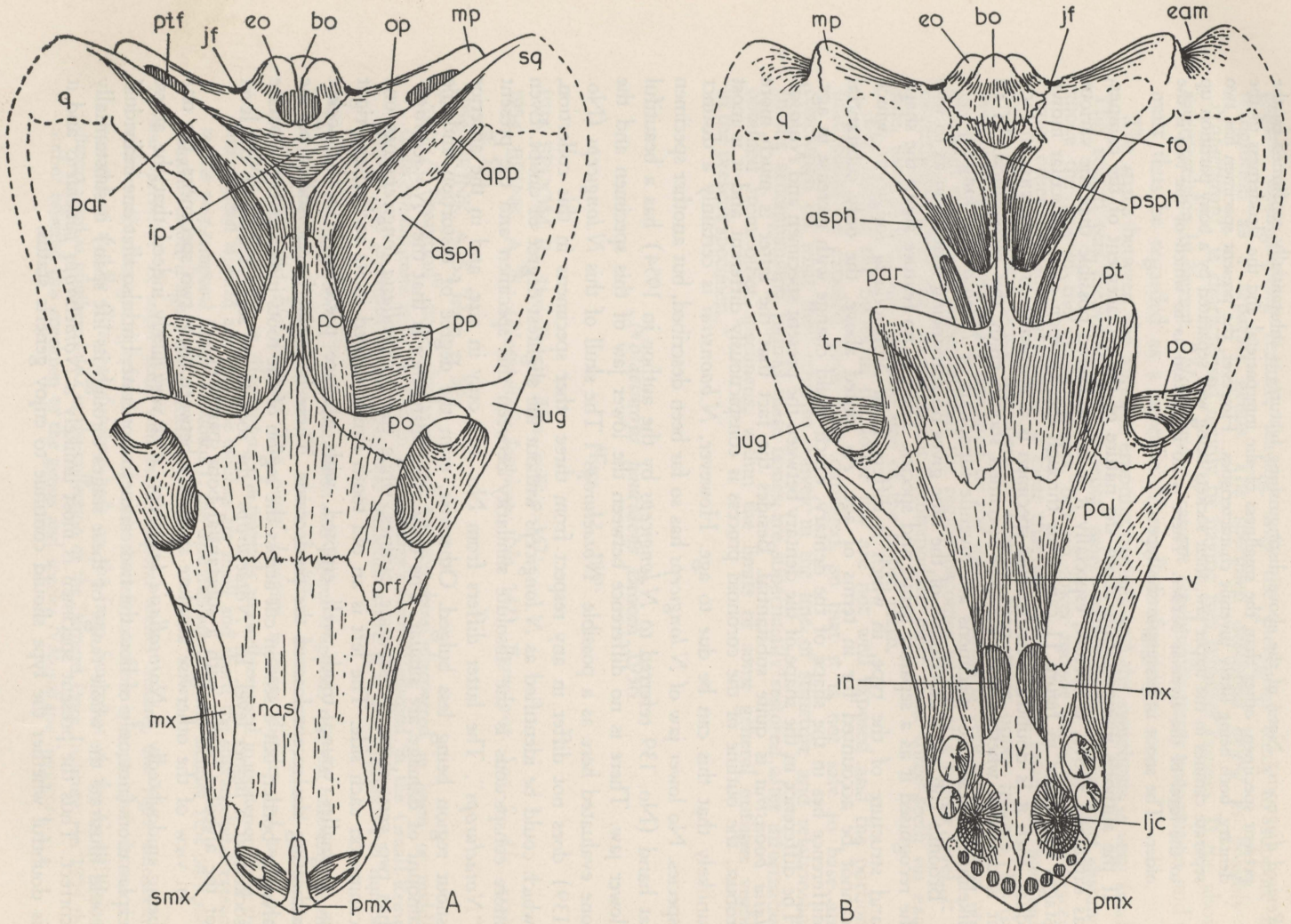

Fig. 12—A, Dorsal and B, Ventral view of the skull of *"Notaelurops paucidens,"* natural size.
For abbreviations see end of article.

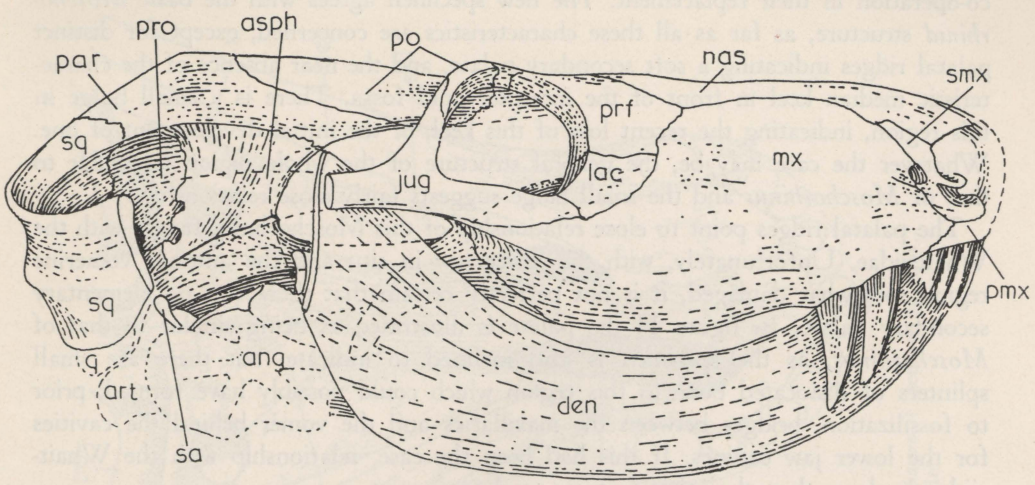

Fig. 13—Lateral view of the skull of *"Notaelurops paucidens,"* natural size. For abbreviations see end of article.

Hewittia albanensis gen. et sp. nov.

(Figs. 14, 15)

Type: Anterior two-thirds of a skull with lower jaw, No. 4206 in the Albany Museum, Grahamstown, from upper *Cistecephalus*-zone beds in the Cradock district.

Diagnosis: Snout broad and low, nasals peculiarly depressed in the middle of their lengths; dentaries slender; symphysial region high, with the broad anterior face sloping strongly backward and the ventral margin forming a sharp Gorgonopsid-like angle; palate basically Moschorhinid-like, with sub-orbital vacuities situated in deep excavations; palatines forming Whaitsiid-like ridges indicating the presence of a soft palate; apparently no elementary secondary hard palate; small bulge in the position of the median keel in front of the interpterygoid vacuity, characteristic of *Moschorhinus;* dental formula apparently i5, c2, pc4 for the upper jaw, with four incisors in the lower jaw.

The present specimen is not a Whaitsiid, but it could be classed in the same family with *Moschorhinus* if the latter is removed from the Whaitsiidae. The Whaitsiidae is quite a unique natural family, the members being characterised by the complete loss of postcanine teeth, the development of an elementary secondary palate, the presence of an extensive soft secondary palate, the absence of suborbital and interpterygoid vacuities and, as has become evident from the material described above, the peculiar co-operation of the two canines on each side and in both jaws. *Moschorhinus,* in addition to its completely different building, differs from the Whaitsiidae in each of the above characteristics. There are postcanine teeth; there is no elementary secondary palate and only vague indications that a soft secondary palate was present; the suborbital openings are large and there is an interpterygoid fossa; there are two separate canines but the anterior ones are highly reduced and there is no sign of

co-operation in their replacement. The new specimen agrees with the basic *Moschorhinid* structure, as far as all these characteristics are concerned, except for distinct palatal ridges indicating a soft secondary palate, and the near absence of the characteristic median keel in front of the interpterygoid fossa. There is a small bulge in this region, indicating the recent loss of this keel, or the initial development of one. Whatever the case may be, the general structure of the whole region is similar to that of *Moschorhinus* and the small bulge suggests fairly close relationship.

The palatal ridges point to close relationship of this Moschorhinid family with the Whaitsiidae. Unfortunately, with the lower jaw in situ and the anterior vomerine region somewhat damaged, it is not perfectly certain that there was no elementary secondary palate. In figure 14 the palate is illustrated as being similar to that of *Moschorhinus,* as the specimen is also inclined to indicate, but there are small splinters of dislocated bone in this region which could possibly have formed, prior to fossilization, bridges between the maxillaries and the vomer behind the cavities for the lower jaw canines. If this had been the case, relationship with the Whaitsiidae is closer than the other features tend to suggest.

In the new specimen the snout is low, broad and short, but not as markedly as in *Moschorhinus.* The peculiar depression of the nasals could be exaggerated as a result of distortion.

The upper incisors are large as in *Moschorhinus.* The two canines on both sides are damaged, but it is clear that the posterior ones are the larger, the anterior ones being in the size range of the incisors, not so markedly smaller as in *Moschorhinus.* The postcanine teeth decrease sharply in size backward, as is characteristic of *Moschorhinus.*

The lower teeth are not clearly displayed. The anterior face of the symphysial region is badly weathered so that the roots of the lower incisors are exposed. There appear to be four incisors on each side. They are long and quite as large as those of the upper jaw, quite unlike the Whaitsiid condition where the lower incisors are reduced in size and number. The incisors of this specimen, both upper and lower, are also flattened transversely as in *Moschorhinus* and unlike the condition in the Whaitsiidae.

In the light of the new information presented by this specimen, it is proposed that the Moschorhinidae be accepted as a family distinct from the Whaitsiidae, to accommodate *Moschorhinus, Hewittia* and *Euchambersia.* It is likely that the Whaitsiidae may prove to include only the forms *Hofmeyria, Aneugomphius, Alopecopsis, Whaitsia* and *Notosollasia,* the latter including *Notaelurops.* The author is also inclined to doubt whether there is any substantial difference between *Notosollasia* and *Whaitsia.* It would appear that *Notosollasia* merely represents juvenile specimens of the genus *Whaitsia,* in which case the latter name should be used as it has priority. The aberrant *Whaitsia pricei* may turn out to be a *Moschorhynchus* and this genus, with *Promoschorhynchus,* could then be included in the Moschorhinidae. The genera *Hyaenasuchus* and *Theriognathus* will have to remain incertae sedis between these two families.

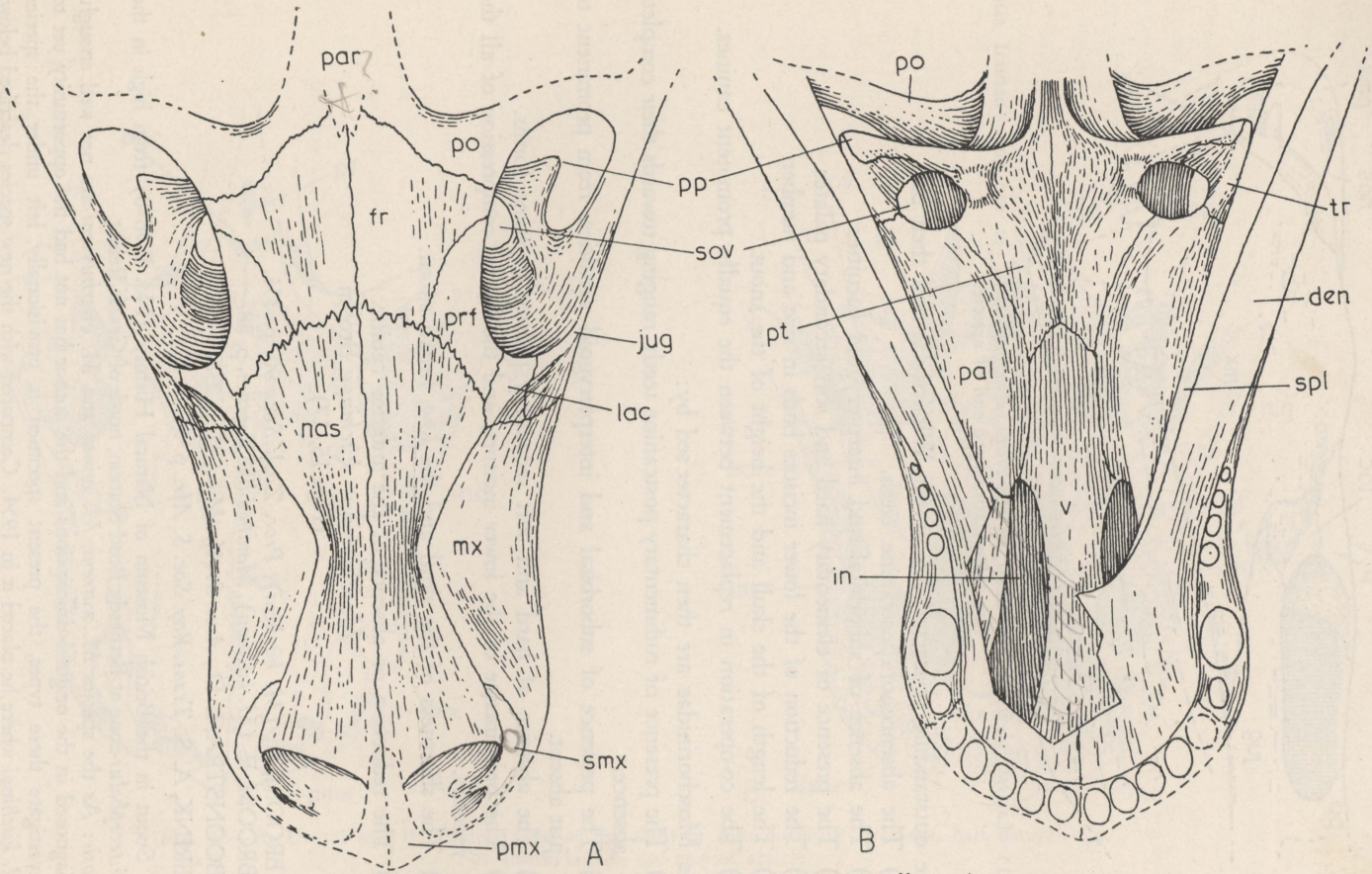

Fig. 14—A, Dorsal and B, Ventral view of the skull of *Hewittia albanensis* gen. et sp. nov., natural size. For abbreviations see end of article.

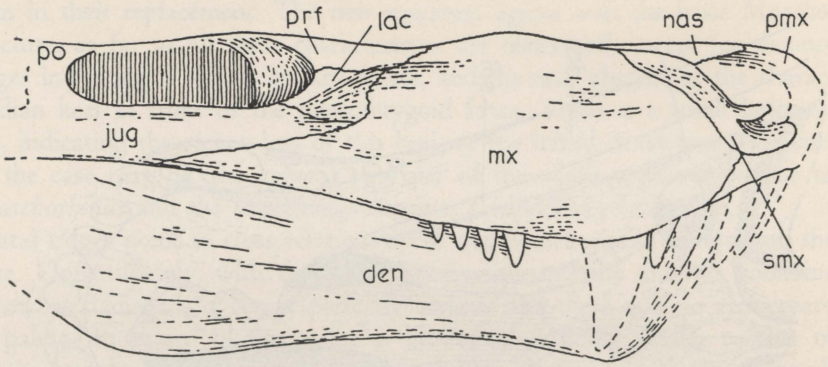

Fig. 15—Lateral view of the skull of *Hewittia albanensis* gen, et sp. nov., natural size. For abbreviations see end of article.

The outstanding characteristics of the Whaitsiidae will then be:

(1) The absence of postcanine teeth.
(2) The absence of suborbital and interpterygoid vacuities.
(3) The presence of elementary hard and soft secondary palates.
(4) The reduction of the lower incisors both in size and number.
(5) The length of the skull and the height of the snout.
(6) The co-operation in replacement between the equally prominent canines.

The Moschorinidae are then characterised by:

(1) The presence of rudimentary postcanine teeth, ranging towards their complete absence.
(2) The presence of suborbital and interpterygoid vacuities, from prominent to just absent.
(3) The absence of hard and soft secondary palates in some forms.
(4) The prominence of the lower incisors, and the lateral compression of all the incisors.
(5) The shortness of the skull and the low, broad snout.
(6) The reduction or absence of the anterior canine.

Moschorhinus kitchingi Broom
(Figs 16, 17)

1920, BROOM, R. (*M. kitcheni*), *Proc. Zool. Soc.*, 90, p. 351.
1932, BROOM, R. (*M. kitcheni*), *Mammal-like Reptiles*, p. 88.
1934, BOONSTRA, L. D., *Ann. S. Afr. Mus.*, 31, p. 238.
1954, BRINK, A. S., *Trans. Roy. Soc. S. Afr.*, p. 54.

Type: Snout in the British Museum of Natural History (No. R.5698) from high in the *Cistecephalus*-zone at Bethesda Road Station, north of Graaff-Reinet.

Diagnosis: As the species *M. warreni, M. minor* and *M. esterhuyseni* are not well enough diagnosed in the original descriptions and the author has not had the opportunity yet to investigate these types, the present specimen is provisionally left under the species *M. kitchingi* where he placed it in 1954. Compared with the new species described below,

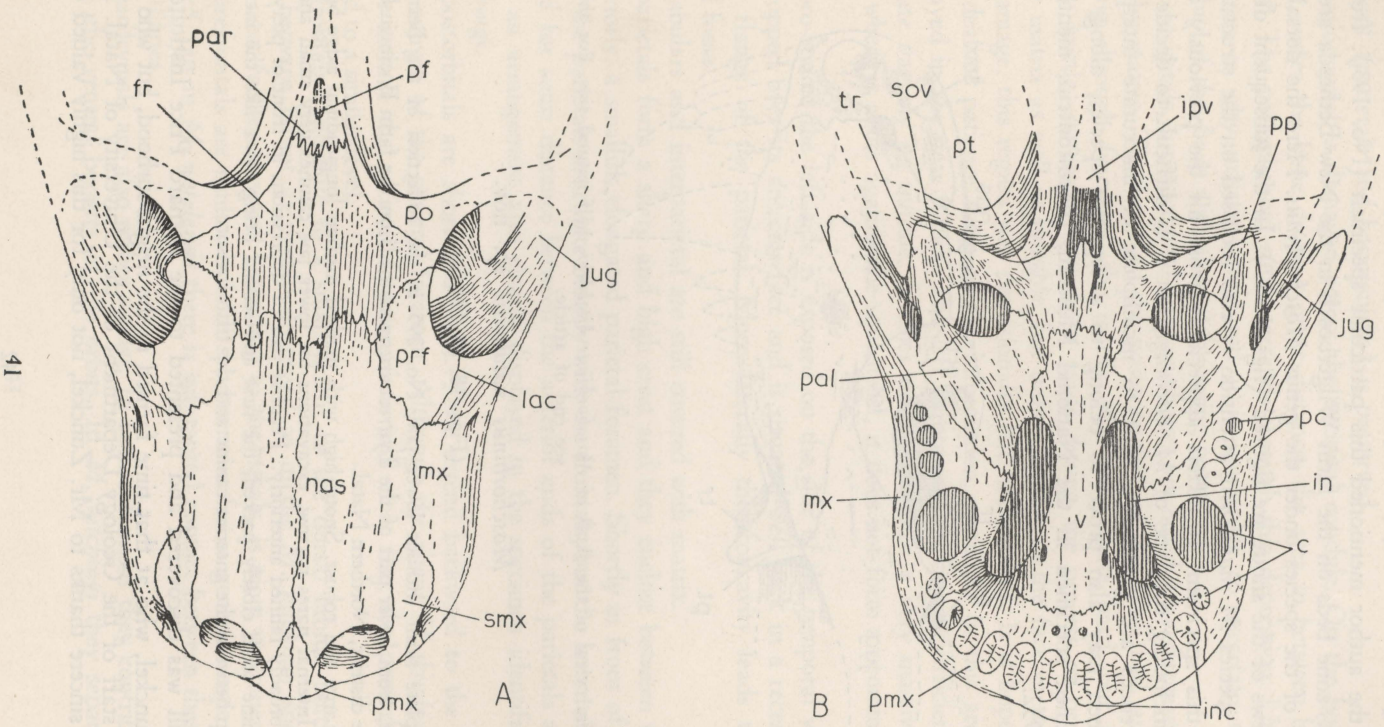

Fig. 16—A, Dorsal and B, Ventral view of the skull of *Moschorhinus kitchingi,* half natural size. For abbreviations see end of article.

the snout is small and low, interorbital region more depressed, vomer narrower anteriorly, depressions in front of pterygoid keel not well defined, and there is no gap between the anterior canine and the fifth incisor.

In 1954 the author mentioned this particular specimen (No. 193), from upper *Cistecephalus*-zone beds on the farm Wilgerbosch in the New Bethesda area, in his brief survey of the species under the genus *Moschorhinus*. Here the dorsal, ventral and side views of the snout are figured (figs. 16-17). In the subsequent description of the new species *M. natalensis* attention is also focussed on the structural peculiarities of this specimen. It differs appreciably from all the previously described specimens, including the type of *M. kitchingi,* but it is difficult to decide whether these differences are genuine or due to incomplete or inaccurate interpretation. This specimen may also prove to belong to a separate species, along with the so-far unnamed specimen in the National Museum, Bloemfontein, mentioned by Broom in 1932.

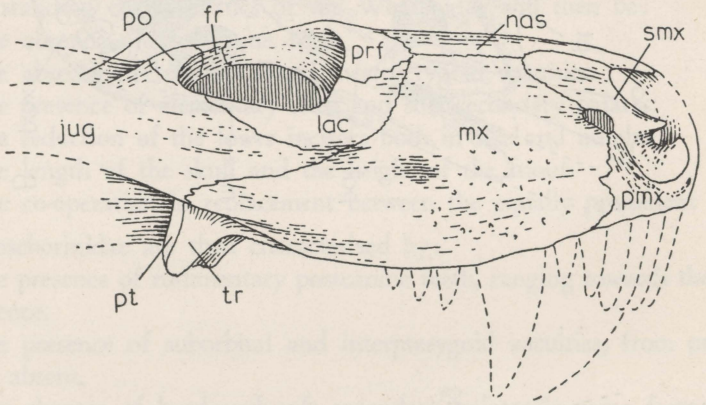

Fig. 17—Lateral view of the skull of *Moschorhinus kitchingi,* half natural size. For abbreviations see end of article.

Moschorhinus natalensis sp. nov.

(Figs. 18, 19, 20)

Type: Complete skull without lower jaw, No. 295 in the collection of the Bernard Price Institute, from lower part of the *Lystrosaurus*-zone beds on the farm Boesmansklip in the Bergville district, Northern Natal.

Diagnosis: Large and robust. Snout high with marked median longitudinal ridge between the orbits. Internal nares narrow, excavations for lower jaw canines very small and shallow. Vomer broadly fanned anteriorly. Peculiar pair of depressions in front of pterygoid keel. Post-canine teeth closely packed, the first and second being ovate like the incisors. Distinct gap between the anterior canine and the fifth incisor.

This skull was discovered and presented to the Bernard Price Institute by Mr. Maurice Zunckel, who at that time farmed in the neighbourhood, but who has since joined the staff of the Geology Department of the University of Natal. I wish to extend my sincere thanks to Mr. Zunckel, not only for this highly valued donation,

but also for his previous and continued co-operation. The specimen is valuable both for being the first Moschorhinid from the *Lystrosaurus*-zone and for its completeness. So far in only one other specimen, *M. esterhuyseni,* a portion of the posterior half of the skull (parietals and basicranium) is preserved.

The basioccipital is damaged across the occipital condyle. On the borders of the fenestrae ovales the bone drops a great distance, the area in between being deeply excavated. The parasphenoid suture extends through this depression. Unfortunately preservation is very unsatisfactory and it is impossible to ascertain the detailed relationship of this bone with the neighbouring bones.

The exoccipitals, supraoccipital and opisthotics are not displayed, these areas being covered by matrix. The bone on the posterior face of the skull had suffered some weathering through fractures, the matrix still being quite hard, but the bone is extremely brittle. Attempts have been made during the process of preparation to clear the matrix as well as possible, but unfortunately, in the face of the danger of undue damage, this region was provisionally left undisturbed. It is hoped that with a great deal of patience some of the information contained in this area may still be displayed in the near future. The left paroccipital process is sufficiently exposed to indicate vaguely its outline. It does not seem to be a very massive bone and distally, where it abuts against the squamosal, it does not form a prominent mastoid process.

The pro-otic of the left side is exposed on the side of the temporal vacuity. It is deeply cupped over its anterior face and is situated well back in a recess below the occipital flange of the parietal. More laterally this concavity leads to the post-temporal fossa.

The tabulars and interparietal are still covered with matrix.

The parietals form a sharp and high crest and they enclose between them, rather far anteriorly, a smallish elongated parietal foramen. Shortly in front of the parietal foramen the parietals articulate bluntly with the frontals, but the latter also penetrate backward for some distance between the anterior ends of the parietals and the post orbitals, an arrangement also clearly displayed in the specimen identified above as *M. kitchingi.*

The postorbitals are short and stout. They extend backward to the level of the anterior margin of the parietal foramen. Although the above *M. kitchingi* specimen does not include the parietal foramen, it is still clear that the postorbitals extend backward to a similar level.

The frontals contribute to a small extent to the dorsal orbital borders and the area in between is not as deeply depressed as in the *M. kitchingi* specimen. The median crest farther forward, extending to the nasals, is more prominent.

The prefrontals are similar in both specimens as far as general shape and size are concerned, but in *M. natalensis* there is substantial contact between these bones and the maxillaries.

The lachrymals are also rather similar. In both specimens they contribute substantially to the ventral borders of the orbits. In *M. kitchingi* they separate the pre-

frontals from the maxillaries, while in *M. natalensis* they form sharp crests on the orbital borders in the region of the lachrymal duct opening.

The nasals are relatively longer and narrower in *M. natalensis* and are not so distinctly broader at the level of their contacts with the maxillaries. These contacts are also shorter than in the *M. kitchingi* specimen.

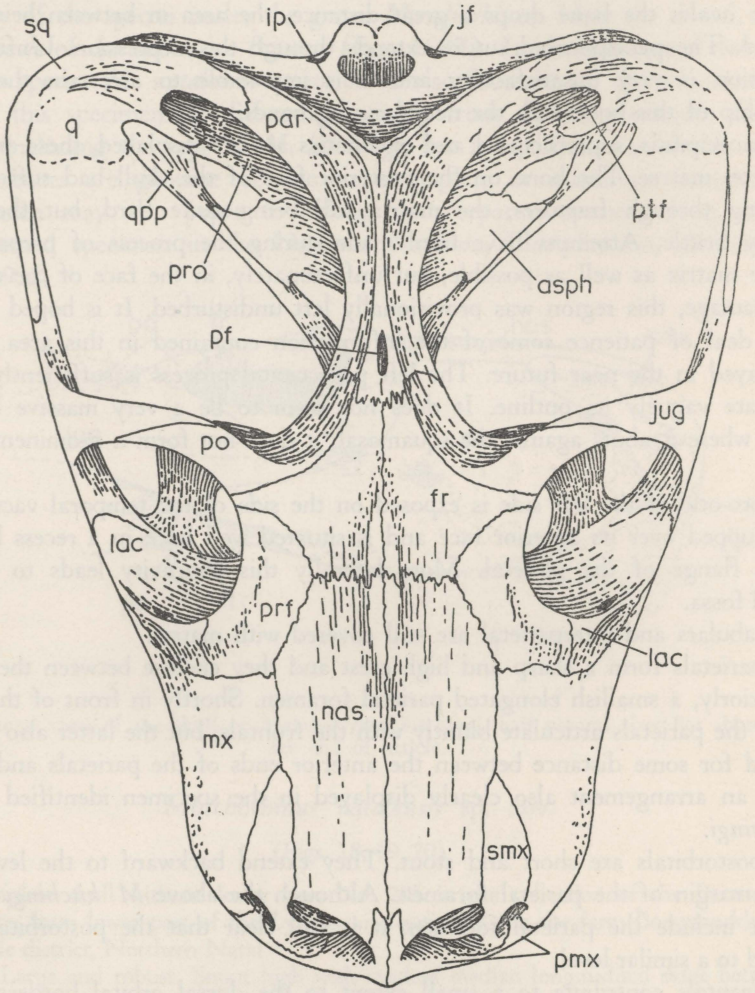

Fig. 18—Dorsal view of the skull of *Moschorhinus natalensis* sp. nov., half natural size. For abbreviations see end of article.

The septomaxillaries do not reach close to the midline below the external nares. In both specimens it can clearly be seen that the turbinal process is not a lamella extending inward and tending to divide the external naris into two separate passages. The structure is better interpreted as the true ventral margin of the external naris, the anterior face of the snout below this margin, on either side of the internarial

bridge, being deeply excavated. This excavation communicates with the nasal cavity, not straight backward as the impression is often created when a specimen is not sufficiently cleaned, but sharply inward towards the midline immediately behind the internarial bridge. The ventral margin of the naris is built by the septomaxillary and it forms a prominent shelf extending forward over this depression. The septo-

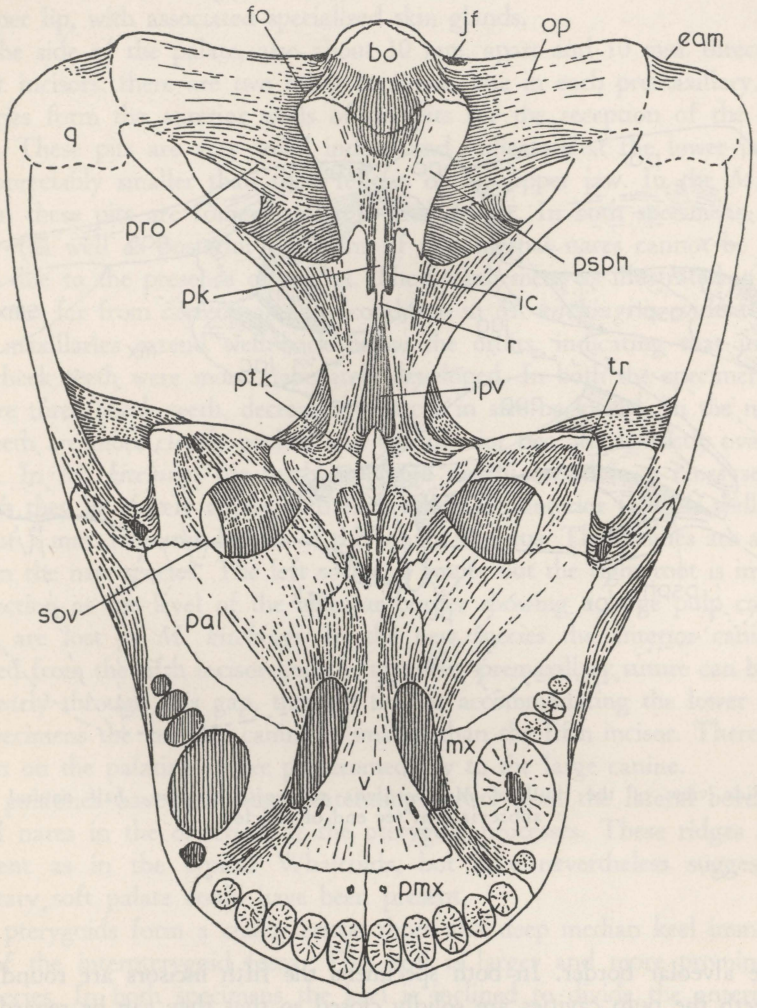

Fig. 19—Ventral view of the skull of *Moschorhinus natalensis* sp. nov., half natural size. For abbreviations see end of article.

maxillary-premaxillary suture extends upward and inward through the centre of this depression to the foramen leading to the nasal cavity. Immediately below the shelf in the deepest part of the excavation, there are two foramina for blood vessels. They are equidistant on either side of the septomaxillary-premaxillary suture.

There is no difference of diagnostic value in the nature of the septomaxillaries between the two specimens at hand.

The premaxillaries have five large ovate incisors each, all broken off at the alveolar border. In the *M. kitchingi* specimen the fifth incisor on the left side is complete, while the third and fourth of the same side are broken off about 10 mm.

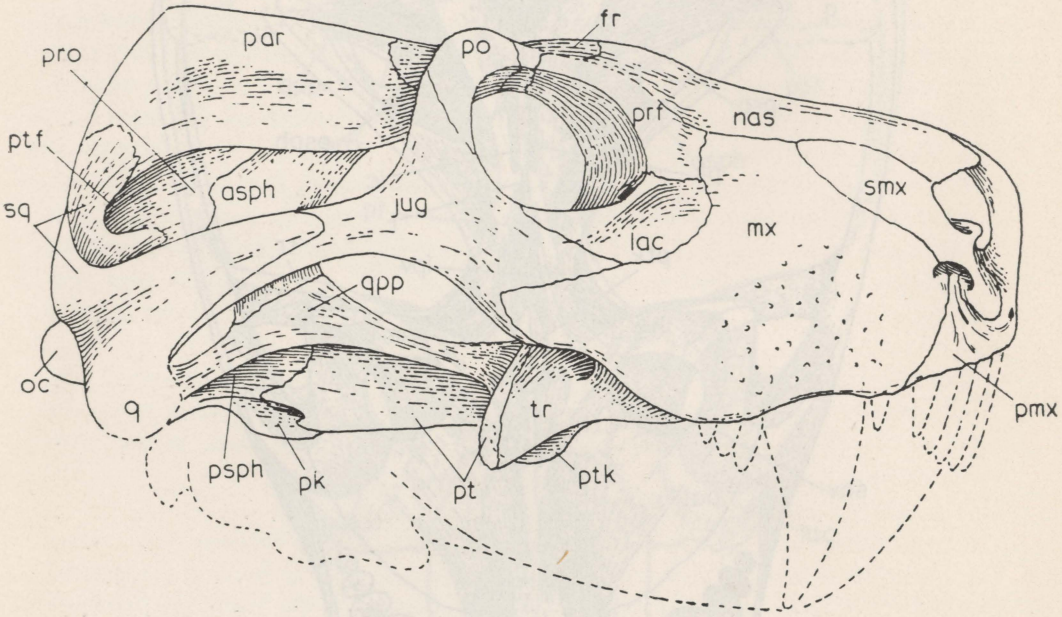

Fig. 20—Side view of the skull of *Moschorhinus natalensis* sp. nov., half natural size. For abbreviations see end of article.

below the alveolar border. In both specimens the fifth incisors are round, and in all the teeth the pulp cavities are solidly closed so that they can be regarded as of a more or less similar advanced age.

There are two foramina, one in each premaxillary, about 10 mm. apart and 10

mm. above the alveolar border on the anterior face of the snout, opposite the first incisors. Very distinct grooves, especially in the *M. kitchingi* specimen, extend from these foramina outward below the septomaxillary sutures and upward to the large foramina in the lateral margins of these bones. There are also indications of grooves extending from these latter foramina down to the alveolar border. The whole arrangement in this area is strikingly indicative of richly innervated and vascularised nostrils and upper lip, with associated specialized skin glands.

On the side of the palate, also about 10 mm. apart and 10 mm. directly behind the first incisors, there are two other foramina, one in each premaxillary. The premaxillaries form the anterior walls of the pits for the reception of the lower jaw canines. These pits are very small indeed and indicate that the lower jaw canines were appreciably smaller than their fellows of the upper jaw. In the *M. kitchingi* specimen these pits are somewhat larger and deeper. In both specimens the actual anterior (as well as posterior) margins of the internal nares cannot be accurately defined due to the presence of matrix. The arrangement as illustrated in figure 19 may be not far from correct, and the condition in *M. kitchingi* is evidently similar.

The maxillaries extend well back below the orbits, indicating that in ancestral forms cheek teeth were more elaborately developed. In both the specimens at hand there are three cheek teeth, decreasing sharply in size backward. In the new species these teeth are more closely packed and the anterior two are distinctly ovate like the incisors. In *M. kitchingi* the teeth are more nearly round in a cross section and although they lie closely adjacent to each other, the anterior tooth is well separated by about 5 mm. from the border of the canine alveolus. The canines are appreciably larger in the new species. The left socket is empty but the right root is in place, the cross section at the level of the alveolar border showing a large pulp cavity. Both canines are lost in *M. kitchingi.* In the new species the anterior canine is well separated from the fifth incisor and the maxillary-premaxillary suture can be followed very clearly through this gap, through the pit accommodating the lower canine. In both specimens the anterior canine is smaller than the fifth incisor. There is a large foramen on the palatine suture posteromedially to the large canine.

The palatines have low ridges extending across from the lateral borders of the internal nares in the direction of the pterygoid processes. These ridges are not as prominent as in the typical Whaitsiids, but they nevertheless suggest that an elementary soft palate could have been present.

The pterygoids form a characteristic short and deep median keel immediately in front of the interpterygoid fossa. This keel is larger and more prominent in the new species. In both specimens the keel is inclined to divide the anterior part of the interpterygoid fossa. The area in front of the keel, including the posterior end of the vomer, is generally concave in the *M. kitchingi* specimen, but in the new species there are two peculiar depressions tapering forward on to the vomer and broadly rounded posteriorly on either side of the keel. In *M. kitchingi* there is a tuberosity some 20 mm. from the keel on the ventral margin of the portion of the pterygoid extending to the process guiding the lower jaw. In the new species this

prominence is more in the shape of a fold. In both specimens the pterygoid processes do not incline backward as much as in *M. esterhuyseni.*

The pterygoids do not meet on the midline posteriorly to the interpterygoid fossa. They are separated by the parasphenoid rostrum, the condition being comparable with that of *Aneugomphius.* Farther back the parasphenoid forms a keel, only for a short distance and less prominent than the typical Whaitsiid keel. Closely on either side of this keel there is an elongated opening for the internal carotid artery. The pterygoid sends an elaborate fold backward on the outside of this opening.

The quadrate process of the pterygoid swings sharply outward and also upward to the point where it meets the alisphenoid. From here it continues outward, but downward to the quadrate. Below the alisphenoid the process is high and narrow. Posteriorly and anteriorly it is low and broad.

The alisphenoid of the left side is exposed, but it suffered considerable prefossilization damage. Its actual shape and relationship seems to be true Whaitsiid-like, as figured. It rests below on an elevated portion of the quadrate process of the pterygoid and there seems to have been a wide opening ventrally between the alisphenoid and the squamosal.

The transverse bones cover the pterygoid processes anteriorly and they form the bulk of the surfaces guiding the lower jaw. There is a large foramen within the trough between the transverse process and the jugal.

The jugals penetrate more deeply forward between the lachrymals and the maxillaries in *M. kitchingi* than in the new species. They do not contribute greatly to the borders of the orbits. Posteriorly on the zygomatic arches they are quite slender.

The squamosals overlap the jugals dorso-laterally on the zygomatic arches. In the otic region each squamosal sends two wings inward, one above the post-temporal fossa, overlapping the parietals anteriorly, and one below the fossa, communicating with the pro-otic. On the posterior face of the skull the relationship of the squamosal with neighbouring bones is obscure.

The quadrates are also completely undefinable.

The vomer is rather different in the two specimens at hand. In the new species it is broadly fanned anteriorly. Posteriorly it also has a prominent median ridge while in *M. kitchingi* this region is quite smooth. The type of *M. kitchingi* apparently has a short median ridge on the vomer at the level of the posterior borders of the internal nares. The arrangement in the new species agrees fairly well with that of *M. esterhuyseni,* where the vomer is also well fanned anteriorly and where the median ridge posteriorly is long and prominent.

There are two elongated foramina, 25 mm. apart, on the anterior fan-shaped portion of the vomer. In the *M. kitchingi* specimen they are 15 mm. apart.

The parasphenoid forms very prominent bulges on the borders of the fenestrae ovales. The latter are not visible in ventral view. It is likely that the basisphenoid is exposed on these bulges, but medially the suture extending through the deep depression evidently marks the contact of the parasphenoid directly with the basisoccipital.

The following are some useful measurements of the two Moschorhinid specimens:

	M. natalensis	*M. kitchingi*
Greatest length of skull (in millimeters)	257	
Greatest breadth of skull	198	
Breadth across canines	111	94
Height of snout at level of canines	82	60
From premaxillaries to pineal foramen	162	154?
From premaxillaries to anterior borders of orbits	97	92
Interorbital width	75	63
Distance between lateral borders of external nares	52	49
Length of row of five incisors	45	41
Distance across pterygoid processes	118	90
Distance between medial borders of suborbital vacuities	40	39
From premaxillaries to posterior end of pterygoid keel	154	128

ang	Angular.
art	Articular.
asph	Alisphenoid.
bo	Basioccipital.
c	Canine.
den	Dentary.
eam	External auditory meatus.
eo	Exoccipital.
fm	Foramen magnum.
fo	Fenestra ovalis.
fr	Frontal.
ic	Foramen for internal carotid artery.
in	Internal naris.
inc	Incisivi.
ip	Interparietal.
ipv	Interpterygoid vacuity.
jf	Jugular foramen.
jug	Jugal.
lac	Lachrymal.
ljc	Cavity for lower jaw canine.
mp	Mastoid process.
mx	Maxillary.
nas	Nasal.
oc	Occipital condyle.
op	Opisthotic.
pal	Palatine.
par	Parietal.
pc	Postcanine teeth.
pf	Parietal foramen.
pk	Parasphenoid keel.
pmx	Premaxillary.
po	Postorbital.
pp	Pterygoid process.
pre	Prearticular.
prf	Prefrontal.
pro	Pro-otic.
psph	Parasphenoid.
pt	Pterygoid.
ptf	Post-temporal fossa.
ptk	Pterygoid keel.
q	Quadrate.
qj	Quadratojugal.
qpp	Quadrate process of the pterygoid.
r	Rostrum.
sa	Surangular.
smx	Septomaxillary.
so	Supraocciptal.
sov	Suborbital vacuity.
spl	Splenial.
sq	Squamosal.
st	Stapes.
tab	Tabular.
tr	Transverse bone.
v	Vomer.