

https://dspace.org/

Struthiocephalus kitchingi sp. nov.

Brink, A. S.

1958-06-01
http://hdl.handle.net/10539/16102
Bernard Price Institute for Palaeontological Research

Downloaded from a DSpace repository. https://dspace.org/

STRUTHIOCEPHALUS KITCHINGI sp. nov.

By A. S. Brink

Abstract

In this paper a new species of the Tapinocephalid Dinocephalian *Struthiocephalus* (*S. kitchingi*) is described, based on a good skull without lower jaw, adding not only to our knowledge of the structure of the skull of this genus, but also exhibiting more pronounced features on the strength of which some idea may be formed regarding the mode of living of the animal. This specimen differs appreciably from the known species, *S. whaitsi, S. rheederi, S. milleri,* and *S. akraalensis,* but where some of the differences appear even to transgress the generic boundary, it is considered that previous descriptions are not based on absolutely perfect material. Even the present specimen does not exhibit its structural detail so clearly that a wrong interpretation should be considered as excluded.

Introduction

The generic name *Struthiocephalus* (genotype *S. whaitsi*) was introduced by Haughton in 1915 for a fair skull in the collection of the South African Museum. In 1916 the same author reported on a badly crushed but nevertheless mountable skeleton which belongs to this genus and which Broom in 1932 thought could actually belong to the type skull, but at present this skeleton still bears a catalogue number different from that of the type. Broom (op. cit.) also offered a restoration of the skeleton of this animal in the form of a free hand sketch.

In 1937 two new species were assigned to this genus, *S. rheederi* introduced by Broom, and *S. milleri* introduced by Olson and Broom. A fourth species, *S. akraalensis,* was introduced by Boonstra in 1952, while elsewhere, in the same year, he redescribed the type *S. whaitsi.* In the following year (1953) the same author published a comprehensive paper on this genus, in which he described in detail the genotype, based on two good specimens in addition to the type, after he succeeded in exposing more clearly sutural patterns with the aid of hydrochloric acid. He also listed very useful generic and specific distinguishing characteristics.

Material and Technique

The present description is based on a complete skull without lower jaw, discovered by Mr. J. W. Kitching in *Tapinocephalus* zone beds on the farm De Bad, near Fraserburg Road, south of Beaufort West in the Karroo. It is numbered 284 in the collection of the Bernard Price Institute.

The skull is appreciably larger than any of the previously described specimens and could not be excavated in one piece. In its fairly badly disarticulated condition Mr. Kitching was able to remove virtually all the matrix manually (excluding the matrix within the brain case and nasal cavities) and after thorough treatment with hydrochloric acid he assembled all the pieces, reinforcing the skull internally with metal dowels. Thus, although the skull is particularly large and of great weight due to the pronounced pachyostosis, while it appears fragile on account of the amount of matrix removed it can nevertheless be handled with little fear of damage.

While in its disarticulated condition little structural information could be gathered from fracture surfaces. These fractures were all initiated by weathering, which tended to obscure sutural detail more badly than on outer surfaces, and the tendency was to avoid development of such surfaces for fear of effecting imperfect fits on assembling the pieces.

The skull is virtually complete and not badly distorted. The snout is bent to the right and the roof of the skull inclines somewhat over to the left. In the accompanying figures this distortion is corrected. The quadrates could have been pressed closer to the skull, but apparently not much.

The dorsal surface of the skull suffered some weathering in particular areas where sutures are not easily traceable. In other areas the sutures are beautifully displayed. The ventral surface is very good but some sutures are obscured by fractures.

Small portions of the postorbital bars and the occipital margin are damaged to an extent where reconstructions were necessary, but these areas are so local that they do not affect the structural interpretation and the genuine contours can be followed accurately.

Other damage affects the alveolar margin, but again the actual margin can easily be traced. The proximal halves of both stapes are missing, but their shape and extent can be judged from margins around the fenestrae ovales where they had apparently rather intimate contact.

Most of the teeth are missing, only some sockets containing fragmentary roots.

Build and Posture of the Skull

The general build of the skull is that of a typical *Struthiocephalus*. The posterior portion appears to be less high than in *S. whaitsi* and *S. akraalensis,* while the snout seems also flatter and more pointed, both in side and dorsal views. The occipital plate is almost in the same plane as the general ventral surface of the skull, so that the occipital condyle is situated relatively farther forward than in previously described specimens.

There is a very large frontonasal boss, larger than in *S. rheederi* which, according to published information, has the largest boss in the known species. This boss towers high above the general dorsal surface of the skull and is virtually confined to the nasals. It has steeply sloping side walls and a generally flattened dorsal

surface, the plane of which slopes forward. There can be little doubt that this boss is actually the core of a horn structure, ideally situated for the purpose of defence.

For several reasons the author is convinced that the head was posed with the snout directed sharply downward, at least as much as indicated in figure 11. These reasons are:

(1) With the skull at this inclination the plane of the occipital plate is vertical. With the snout pointing forward, the occiput extends so nearly horizontally that it is difficult to visualise how the muscles of the neck could keep the skull thus orientated.

(2) The occipital condyle points nearly ventrally when the snout is horizontal.

(3) The floor of the cerebellum also extends horizontally only when the skull is inclined as illustrated.

(4) With the skull horizontal, the quadrates are so far forward that it is difficult to visualise how the lower jaw could operate effectively. With an inclination as illustrated, the quadrates are situated ventrally, in perfectly normal relationship relative to other occipital structures.

(5) At this inclination the jaw muscles extend vertically and they have the effect of swinging the lower jaw to and fro. With the head horizontal, the muscles would also extend horizontally and, judging from the space available to them, they could not have been strong enough to keep the relatively long lower jaw in a closed position, let alone lift it in an effective bite.

(6) The horn structure points forward at this inclination and is thus a more effective weapon in an animal which certainly could not have had the agility of a mammal. Horned mammals rely to a large extent on agility to outmanoeuvre their foes, while in all horned reptiles (Ceratopsia especially) these weapons are normally directed forward to offer resistance to an adversary directly in the line of its approach, without demanding much manoeuvrability on the part of the head and neck, relative to the body.

This inclination of the head, the nature of the jaw articulation, and the peculiar dental arrangement, appear to indicate a specialised diet not uncommon in a great variety of animals. A near parallel may be found in the not too distantly related and reasonably near contemporary form, *Lystrosaurus*. Although the dentition is elaborate, the lower jaw could not have been very effective in a horizontal attitude, judging from the size of the jaw muscles and the direction in which they exerted their force. Nevertheless, in spite of this weak articulation arrangement, the very foremost teeth are the strongest, their size decreasing backward till they disappear at the level of the middle of the length of the snout and well forward of the posterior ends of the maxillaries. With the teeth in addition inclined forward, there can be little doubt that the anterior ones fulfilled the more important function.

Taking all these pecularities into consideration it would appear that this animal

fed under water, like a duck, the platypus, or *Lystrosaurus,* which may also account for the general shape of the snout. The animal then either drove its snout downward into the mud, nibbling around for embedded food, or it would feed directly on subaquatic weeds. The downward inclined upper teeth would then rather have been used for digging, gathering and grasping than for biting purposes. With a mouthful of weeds it then apparently lifted its head and strained the material in a higher level of cleaner water to wash out the excess mud. This habit of feeding does not demand strong jaw musculature and the general shape of the skull and mechanism of the lower jaw are thus quite effectively adapted.

The following are some useful measurements for comparison with the previously described species:

Greatest length	700 mm
Greatest width	442 mm
Interorbital width	144 mm
Intertemporal width	203 mm
Pineal foramen to occipital edge	82 mm
Anterior margin of external nares to premaxillary edge	122 mm
Posterior margin of occipital condyle to occipital edge, in the plane of the axis of the skull	112 mm

The Structure of the Skull

The author would like to emphasise that the structural detail of the present skull is not as distinctly displayed in the specimen as the figures would tend to suggest. In the subsequent descriptions it will be stipulated where interpretations are based on what appear to be "likely", but by no means "clear", arrangements. Where the structure of the present specimen differs in places rather appreciably from that of the previously described species, the tendency should not be to regard it as generically distinct. While the chances are not excluded that the present author has misinterpreted this specimen, it is perhaps as likely that previous authors have also encountered similar difficulties in view of the problematic nature of this *Tapinocephalus* zone material. It is therefore considered more advisable to state what this specimen appears to convey than to be influenced by previous descriptions.

The *basioccipital* (bo, fig. 12) forms a single rounded condyle directed more ventrally than posteriorly*. The upper surface is cleaned for some distance into the brain case and this surface (the floor of the cerebellum) extends sharply upward in a direction opposite to that assumed by the condyle (see fig. 11). The basioccipital does not contribute to the lateral margins of the foramen magnum. It articulates with the exoccipitals at the level of the ventral margin, where the latter expand into small bosses (see *exoccipitals*). In front of these contacts are

* Relative directions here and subsequently are to be interpreted with the long axis of the skull horizontal.

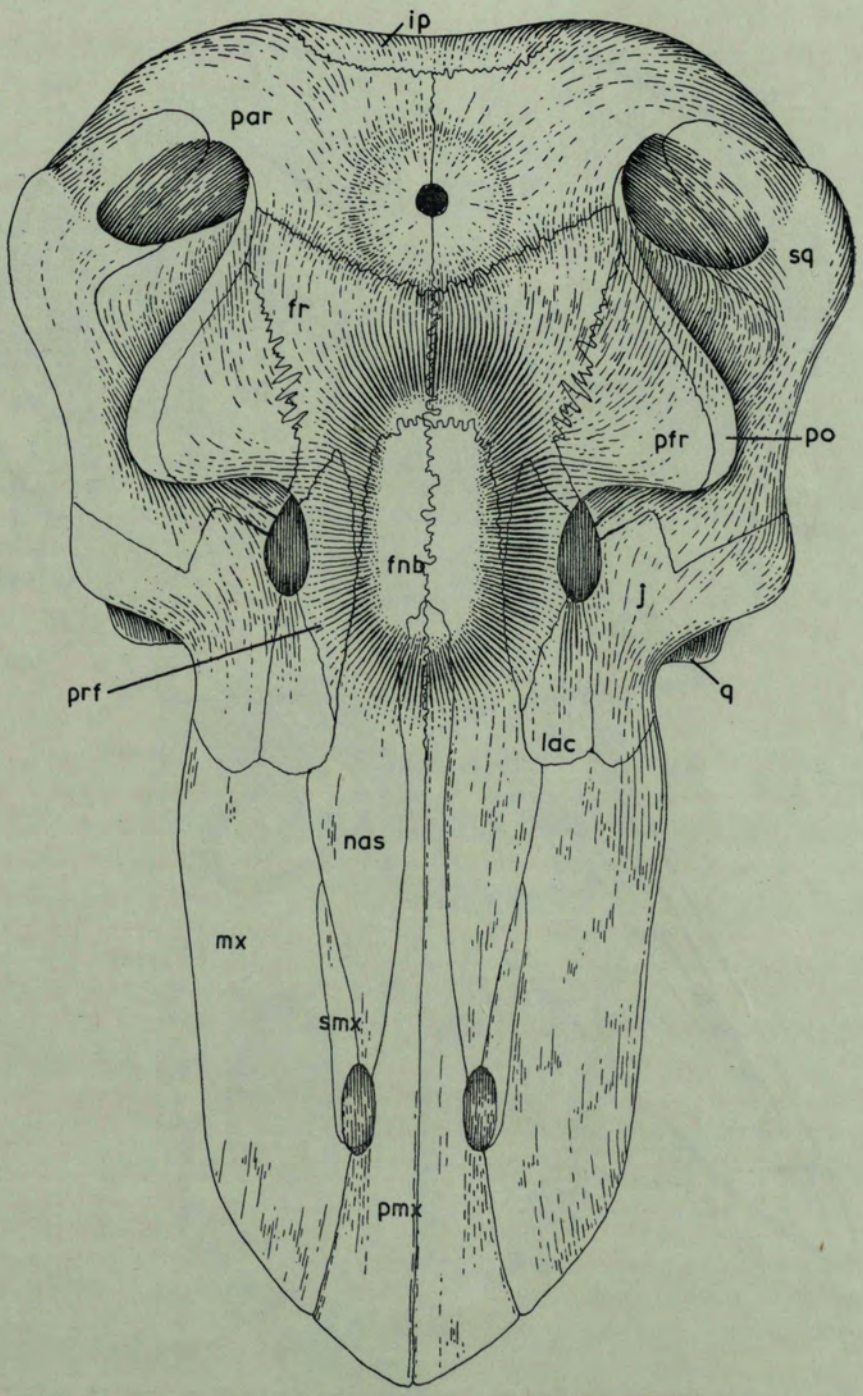


Fig. 10—Dorsal view of the skull of *Struthiocephalus kitchingi* sp. nov. (¼ natural size).

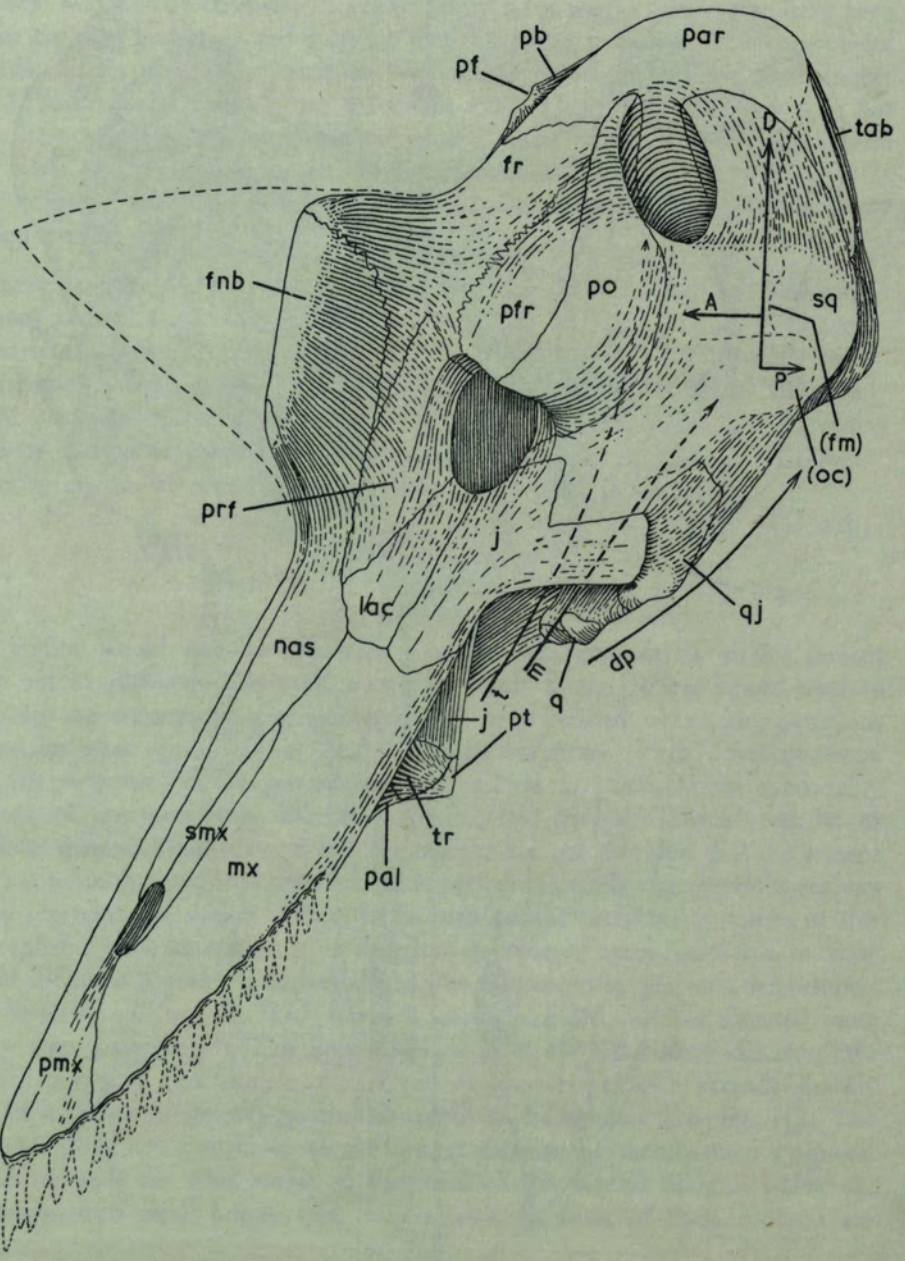


Fig. 11—Side view of the skull of *Struthiocephalus kitchingi* sp. nov. ($\frac{1}{4}$ natural size).

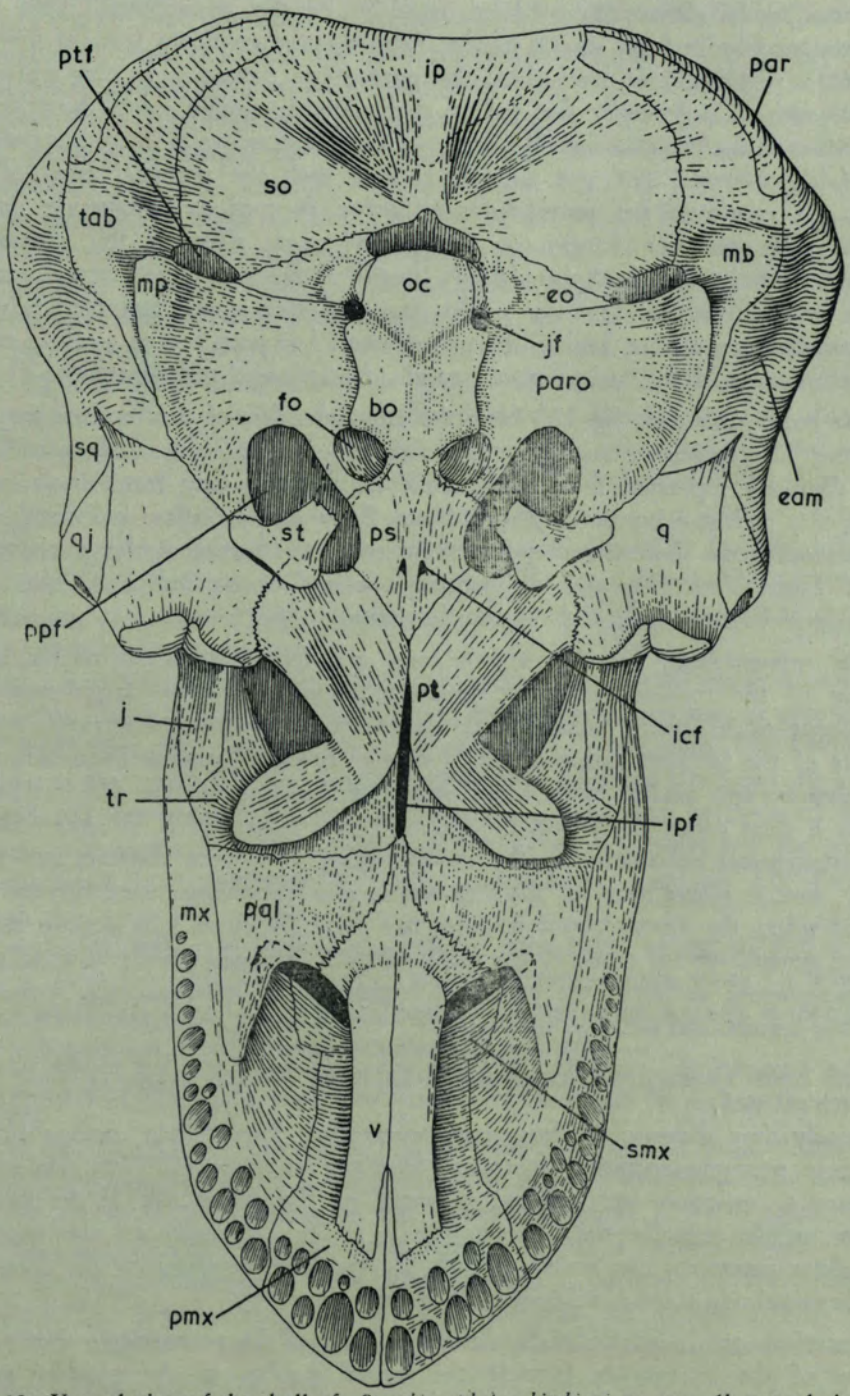


Fig. 12—Ventral view of the skull of *Struthiocephalus kitchingi* sp. nov. (¼ natural size).

the two jugular foramina, bordered medially by the basioccipital. This bone expands laterally in front of the jugular foramina and continues forward between, and at a slightly lower level than, the paroccipital processes. In this region its ventral surface is generally flat with a slight, broad, median ridge. Anteriorly it contributes to the posterior-medial margins of the fenestrae ovales where it apparently had fairly intimate, but not sutural, contact with the proximal ends of the stapes. It continues for some distance farther forward as a tapering process between the posterior flanges of the parasphenoid, although this portion is almost certainly the basisphenoid. A vague indication of a suture extends across between the two fenestrae ovales, but this effect could have been achieved if a portion of a median keel to the parasphenoid had been broken away to expose a small triangle of the basisphenoid (see also *basisphenoid* and *parasphenoid*).

The *exoccipitals* (eo, fig 12) form the lateral borders of the foramen magnum and they also contribute slightly to the occipital condyle. Immediately laterally to, and distinctly separated from, these condylar portions they form small bosses. Posteriorly to these bosses they spread out flatly and articulate indistinctly with the supraoccipital. Laterally they appear to reach the border of the post-temporal fossa. Their relationship with the paroccipitals is also very indistinct. The bosses form the posterior margins of the jugular foramina.

The *supraoccipital* (so, fig. 12) is large and forms the whole of the dorsal border of the foramen magnum. From the middle of this margin two very prominent ridges extend outward and backward. They start so abruptly on the border of the foramen magnum that a median notch is formed. From this notch a rather massive median ridge arises, extending backward to the occipital border, across a deep concavity behind the postero-lateral ridges. It is not clear whether the interparietal contributes to this median ridge. It is even possible, and rather likely, that it covers most of the area within this depression. Anteriorly to these lateral ridges the supraoccipital occupies two large flat areas very slightly inclined to the general ventral plane of the skull, where it articulates with the exoccipitals. Antero-laterally it forms the posterior borders of the post-temporal fossae and laterally it articulates with the tabulars.

The *paroccipitals* (paro, fig. 12) are extremely wide and flat in the plane of the ventral surface of the skull. Posteriorly they have some vertical thickness, but anteriorly they decrease to thin plates where they form deeply concave margins to large pterygo-paroccipital foramina. Medially to these foramina they extend forward to articulate with the parasphenoid, on the dorsal side of the fenestrae ovales, while laterally they swing widely around, medially to the quadrates (quadrate processes), to articulate with the quadrate processes of the pterygoids on the dorsal side of the distal ends of the stapes.

Posteriorly to the quadrates the lateral margins of the paroccipitals abut against ridges of the squamosals forming the medial borders to the auditory meatus grooves. Still farther back, these ridges expand into prominent mastoid bosses,

formed largely by the tabulars, on the inside of which the paroccipitals form distinct but not very significant mastoid processes, bending ventrally, not posteriorly. Medially to these processes, the post-temporal fossae are enclosed between the paroccipitals anteriorly, the supraoccipital posteriorly, with the tabulars contributing, apparently not insignificantly, to the lateral margins. These fossae, although they face ventrally, penetrate the skull in a sharply anterior direction above the paroccipitals.

The paroccipitals form the lateral borders of the jugular foramina.

The general arrangement is not unlike that described by Boonstra for *S. whaitsi*. The detailed differences are: (a) in the present specimen the quadrate processes are stronger and extend farther forward; (b) the mastoid processes are weaker and not inclined backward; (c) the contact between the paroccipital and pterygoid is at the level of the distal end of the stapes; (d) due to the shorter quadrates, the paroccipitals articulate with the squamosals farther forward, so that they have more significant contact with the tabulars. These differences, although rather pronounced, could pass as specific variations, with the exception of the paroccipital-pterygoid-stapes relationship, which could be regarded as a generic distinction, but distortion or insufficiently clear preservation could account for this difference. If this is the case, *S. whaitsi* is more likely to be at fault, because the structure and relationship of the paroccipitals are rather well displayed in the present specimen.

The *prootics* are not exposed.

The *tabulars* (tab, fig. 12) are peculiarly wedged between the squamosals and the mastoid processes of the paroccipitals, where they appear to penetrate to some appreciable depth, while they are little exposed on the surface. In this region they extend some 30 mm. farther ventrally than the mastoid processes. Behind the latter the tabulars expand and are exposed over greater areas where they form pronounced mastoid bosses. Still farther back they taper between the supraoccipital and the parietals, curving inward to articulate with the interparietal. They are not visible in dorsal view.

The major difference between the tabular relationship in the present specimen and *S. whaitsi* is that in the latter it is situated farther back so that it is wedged to a lesser extent between the mastoid process and the squamosal and its contribution to the mastoid boss therefore appears to be less significant.

In the present specimen the tabular sutures are, in general, very distinctly displayed.

The *interparietal* (ip, figs 10, 12) is very indistinct and its position and extent is judged by the relationship of the surrounding bones. Ventrally it could contribute to the median ridge extending to the foramen magnum, or even cover most of the depression that this ridge traverses, but this region is badly damaged. Dorsally there are vague indications of a suture with the parietals in the position as figured (fig. 10), so that the interparietal builds the middle portion of the vertically thickened, well rounded, and horizontally slightly concave occipital border. It is visible in dorsal view.

The *parietals* (par, fig. 10) are well fused along the midline so that the median suture is extremely difficult to trace. Between them they enclose a large, perfectly round, pineal foramen, situated on a low, but nevertheless distinct circular boss. Their sutures with the frontals extend through slight depressions extending transversely, but slightly forward from the dorsal borders of the temporal fossae to a point on the midline of the skull between the pineal boss and the fronto-nasal boss. Laterally they form the dorsal borders of the temporal fossae, where they are overlapped for some distance from front to back by the posteriorly extending processes of the postorbitals. Behind the temporal fossae they articulate with the squamosals, where they penetrate deeply down between the long tapering processes of the latter anteriorly and the tabulars posteriorly.

The parietals in the present specimen differ from those of *S. whaitsi* as described and figured by Boonstra (op. cit.) in that they have no contact with the post-frontals. In this respect they agree with *S. akraalensis*. The overlaps between the parietal flanges and the squamosal processes are also more extensive. They differ from *S. akraalensis* in being more extensively flanked by the postorbitals along the antero-dorsal borders of the temporal fossae. The latter species is also figured as though there is little, if any, articulation between the parietals and squamosals, the tabulars apparently reaching the borders of the temporal fossae. The general build of this region in the present specimen is inclined to create a similar impression but, fortunately, on the right side enough of a tabular-parietal suture is discernable to show that the actual structure is more like that of *S. whaitsi*. On account of the difficulty in tracing sutures in *Tapinocephalus*-zone material, this difference in *S. akraalensis* should not be regarded as a "specific" variation; it could be a wrong impression created by the specimen.

The *frontals* (fr, fig. 10) are not unlike those of *S. whaitsi* and *S. akraalensis*. They build the posterior slopes of the fronto-nasal boss and contribute only slightly to the dorsal flattened surface. They differ from *S. whaitsi* in that they articulate with the postorbitals, as in *S. akraalensis*. Their delicate extensions to the dorsal borders of the orbits appear to reach the latter farther posteriorly than in the described specimens. The processes flanking the nasals are also longer. The main difference, however, is that they build much steeper posterior slopes to the fronto-nasal boss.

The *postfrontals* (pfr, fig. 10) have a similar structural relationship to those of *S. akraalensis*, but they agree more with those of *S. whaitsi* in general shape, that is in their greater breadth and in being more laterally situated. As the postorbital bosses form more pronounced protrusions on the orbital borders, their orbital margins extend more perpendicularly to the axis of the skull.

The *postorbitals* (po, fig. 11) form pronounced bosses (jointly with the post-frontals) which appear to extend more forward than in the described species. The resultant protrusions on the orbital borders can be considered as a distinguishing characteristic of this species.

These bones extend backward dorsally to the temporal fossae, where they flank

the parietals. They contribute to the ventral borders of the orbits. They are separated from the anterior margins of the temporal fossae by short extensions of the squamosals.

The postorbitals are almost thrice as long (antero-posteriorly) as they are high (vertically). In *S. whaitsi* the length is apparently equal to the height, while in *S. akraalensis* the height appears to be twice the length. Extremely broad and short postorbital bars, added to the forward protruding postorbital bosses, furnish a rather prominent distinguishing characteristic for this species.

The *prefrontals* (prf, figs. 10, 11) are situated more directly above the orbits than in the previously described species. They contribute substantially to the dorsal borders of the orbits and extend from there backward as well as forward as they rise, almost vertically, to add to the lateral sloping walls of the fronto-nasal boss. Their greater size and these backward extensions, penetrating the frontals more deeply than in the existing species, provide a further distinguishing characteristic.

The *lachrymals* (lac, fig. 11) are not different from those of the previously described species.

The *nasals* (nas, figs. 10, 11) form the bulk of the fronto-nasal boss. They form a great deal of the lateral sloping walls and their median suture is restricted to the dorsal flattened surface. The size and shape of this fronto-nasal boss could be the most conspicuous characteristic of this new species, but it could also be subject to sex and age.

The nasals taper gradually forward from a level shortly in front of the orbits, where their combined breadth is greatest, to the posterior borders of the external nares.

The *septomaxillaries* (smx, figs. 10, 12) form "floors" to the external nares, which enter the snout sharply inward and backward. The external nares are small and narrow transversely. The greater portions of the septomaxillaries extend backward between the nasals and maxillaries. These extensions appear to be superficial posteriorly, where the maxillaries and nasals meet below them.

Ventrally, in the palate, the portions of the septomaxillaries forming the "floors" to the external nares articulate with the premaxillaries anteriorly and with the maxillaries laterally. Actually, these portions lying within the external nares and visible in dorsal view lie intimately above the posterior ends of the premaxillaries, seen in the palatal view on either side of the vomer. The portions of the septomaxillaries seen in ventral view are posterior extensions of the "floor" portions, not visible in dorsal view. The areas in front of the internal nares slope evenly inward and backward, while they grow narrower between the palatines and the vomer. The choanae are broadly oblong in the vertical plane, and face forward and outward over the fan-like excavation. They are bordered dorsally by the septomaxillaries, medially by the vomer, laterally by the palatines and maxillaries, and ventrally by the vomer and palatines. The dorsal septomaxillary border is a free edge over which the cavity passes forward to the external nares.

This arrangement, where both external and internal nares open forward, gives support to the view that these animals fed under water and that their teeth were largely used for straining muddy vegetation. Water caught in the nasal cavity would, on lifting the head above the water, run down and forwards through the internal nares and through the teeth, thus additionally washing the food.

The *premaxillaries* (pmx, figs. 10, 12) form the inter-narial bridge and send extremely long tapering processes backward between the nasals. At about the level where the nasals are broadest, in front of the orbits, these processes are narrowest, but from here they expand again slightly, where they extend up the anterior slope of the fronto-nasal boss. They terminate somewhat abruptly after extending some short distance on to the upper flattened surface of the boss.

From the level of the anterior margins of the external nares the premaxillaries fan out forward to the alveolar margin, the dorsal outer surfaces not bending down. Ventrally they taper backward, not as evenly, and a short distance from the choanae they articulate with the septomaxillaries along transverse sutures. From shortly behind the front teeth, up to this level, they articulate medially with the vomer, which forms a prominent median beam situated at a level appreciably lower than the areas on either side.

Boonstra (1953) illustrates the premaxillaries as being confined to the area in front of the vomer in the palatal aspect in *S. whaitsi,* but this impression could be created by imperfect preservation. However, with the additional specimens at his disposal, his interpretation of narrower premaxillaries in this species is accepted as genuine, and the fact that each covers in breadth only three teeth is considered here as a rather serious difference. In the present specimen each premaxillary covers in breadth the equivalent of approximately five teeth, as is also the case in *S. rheederi.* This difference could nevertheless pass as a specific and not generic distinction, because the dentition as a whole in this genus appears to be inconstant (see maxillaries). In the present specimen there are five large teeth in a row on the right side, with three occasional teeth, smaller in size, behind in a second row, while on the left there are four teeth in the front row, one exceptionally large, with five in a very distorted second row.

The *maxillaries* (max, fig. 12) articulate with the premaxillaries medially, in the palatal aspect, in the surfaces sloping backward to the choanae. Behind these sutures they articulate with the septomaxillaries to where they contribute themselves to the dorso-lateral margins of the choanae. The ventro-lateral and ventral margins are formed by the palatines, which send tapering processes forward on the inside of the teeth, to continue the ventral margins of the choanae as fairly prominent ridges across the maxillaries. Laterally to the palatines the maxillaries extend backward as a plate, exposed more on the lateral surface of the snout, but sufficiently represented in the palatal aspect to be of significance to a more elaborate dentition, but these extensions behind the level of the choanae are free of teeth. The posterior ends are intimately clasped by the jugals.

The right maxillary contains sockets of about 16 teeth (some damage in one area makes it difficult to be sure of the exact number). These teeth are arranged very roughly in two rows, in fact, so indistinctly that had it not been for the more recognisable two rows of the premaxillaries, they could not be interpreted in terms of rows. All the teeth on the right side occupy a distance of 150 mm. which could as well be covered by about 10 teeth of similar size.

The left maxillary has 17 sockets, also roughly distributed in two rows, and occupy a distance of 190 mm, which could be covered by 13 similarly sized teeth. On both sides these sockets decrease in size backward, although some sockets are appreciably larger than others farther forward. Posteriorly the "two rows" of each side merge into one.

This arrangement is not due to tooth replacement. All the sockets are distinctly separate. Boonstra (1953) mentions the presence of additional teeth behind the main row in *S. whaitsi* and interprets them as replacing teeth, but in the light of the new specimen, they may also prove to be regular teeth.

Judging from the difference in the distribution of the sockets between the left and right sides, the difference in number and the different distances they cover, it is to be expected that there could be even greater variations from individual to individual, so that it is not advisable to select any feature in this dentition as a distinguishing characteristic for the new species.

The *transverse* bones (tr, fig. 12) appear to be longer and narrower in the new species than in *S. whaitsi*. They are more clearly locked between the pterygoids ventrally and the maxillaries dorsally. It appears as if the pterygoids extend farther laterally in forming their processes for guiding the lower jaw, so that they cover more of the transverse bones in ventral view. Laterally the jugals cover them for some distance and posteriorly they extend for a longer distance backward, intimately on the inside of the jugals, than in *S. whaitsi*. In ventral view their extreme posterior ends are obscured from view by the quadrates which, in this specimen, are also situated farther forward.

The *jugals* (j, figs. 11, 12) are rather small and mainly build the suborbital bars, where they are fairly flat. Anteriorly they form two distinct flat and blunt processes, one articulating with the maxillaries on the outer face of the snout, the other articulating mainly with the transverse bones, but also supporting the posterior ends of the maxillaries below with considerable overlaps. Dorsally and medially they have substantial contact with the lachrymals. Posteriorly, still generally within the suborbital bars, they articulate with the squamosals, allowing the latter to penetrate forward into them with broad wedges. Postero-laterally they overlap the quadrato-jugals, but the articulation appears to be somewhat feeble.

Both jugals display their sutures very clearly.

The *squamosals* (sq, fig. 11) contribute with very small, slender processes to the ventral borders of the orbits, over which extend forward projections of the postorbitals. They have long massive contacts with the postorbitals all the way back to the temporal fossae, to which they contribute the ventral, posterior, and the

lower halves of the anterior borders. Posteriorly they overlap extensively the lateral occipital flanges of the parietals. Ventrally the squamosal-tabular sutures extend across the prominent mastoid bosses, laterally to the mastoid processes of paroccipitals. Immediately laterally to these bosses the broad, shallow external auditory meatus grooves extend forward and slightly inward across the ventral surfaces of the squamosals, from levels where the latter bones form prominent bosses directed outward. These bosses merge upward, on the outer face of the skull, into the anterior borders of the temporal fossae. On the ventral surface the external auditory meatus grooves extend forward, widening, and disappearing as distinct concavities at the level where the squamosals have their contacts with the paroccipitals medially and the quadrates and quadratojugals anteriorly. The squamosals clasp the blunt posterior ends of the quadratojugals (laterally) within broad notches.

The external auditory meatus grooves start distinctly farther forward than in *S. whaitsi* and the general arrangement of the sutures between the squamosals, quadrates and quadratojugals is also different. Once again this may be due to incorrect interpretation of either specimen. The squamosal-parietal relationship in *S. akraalensis* is completely different but, as stated above (under *parietals*), this difference is most likely due to a misinterpretation.

The *quadrates* (q, fig. 12) are broad, long and very flat in the horizontal plane, and their articulation surfaces are rather small compared with the size of the skull, although not when compared with the size of the lower jaw. The cavities between the quadrates below and the jugals above are very flat (between 30 and 40 millimeters high in a skull with a total length of 700 millimeters) and with the articulars in position the space on either side for the masseter and temporal muscles is extremely restricted. These muscles could obviously not have been very strong. Even their apparent restricted lengths are out of proportion to the size and shape of the skull. The general structure and build of the surrounding areas show no indication of distortion. Had the quadrates been pressed closer to the jugals, the amount could not have been much and it would make little difference to the size of the jaw muscles, while their lengths and the directions in which they extended would not have been altered.

The pterygoid processes to the quadrates articulate firmly with the latter along fairly broad and blunt contacts. Behind these contacts the distal ends of the stapes are lodged in very intimate contact with both bones, more with the quadrates than with the pterygoids, and more posteriorly also with the quadrate processes of the paroccipitals. On the right side the stapes-paroccipital contact appears to be a firm suture. On the whole both stapes appear to have been virtually immovable. The general arrangement is again completely different in *S. whaitsi,* but allowance should be made for an incorrect interpretation.

Posteriorly, the quadrates have blunt articulations with the squamosals, that is, they do not taper into sharp points as in *S. whaitsi.* Laterally the quadratojugals extend far back, also unlike the condition displayed in *S. whaitsi.*

The quadrates are separated from the posterior ends of the jugals by only a few millimeters.

The *quadratojugals* (qj, figs. 11, 12) separate the posterior ends of the jugals from the quadrates. Posteriorly they are wedged bluntly into the squamosals, as seen in the lateral face of the skull. A process of the squamosal extends forward laterally to the quadratojugal of the left side. Both quadratojugals are damaged so that their surface topography is not clear. On the left side sutures are nevertheless well displayed.

The *stapes* (st, fig. 12) are each represented only by the distal end. These ends are well locked in fixed positions behind the pterygo-quadrate suture. Proximally they also appear to have been well held in position by prominent margins around the fenestrae ovales. It is not clear at all how and where a tympanum could have been located and how it could have functioned.

The *vomer* (v, fig. 12) is very distinctly paired. The premaxillaries send processes backward medially between the left and right portions. It forms a solid median beam in the palate, extending backward well below the level of the choanal excavations on either side. Its flat ventral surface is even at a lower level than the plane of the alveolar borders. As it extends backward it increases in vertical thickness, apparently solidly. Deep notches in the lateral vertical faces form the medial borders of the choanae. Behind this level the palatal surface rises to join the general plane of the palatines, while the vomer fans out to build the medial halves of the postero-ventral borders of the choanae. Posteriorly it tapers to a point and terminates on the anterior border of the interpterygoid fossa.

The *palatines* (pal, fig. 12) build the postero-ventral free margins of the choanae. These margins are directed forward with the choanae entering the nasal cavity backward and inward above them. More medially these margins are formed by the vomer, but the palatines still extend intimately above, inward to within the vomerine notches forming the medial borders of the choanae. Laterally the palatines swing forward as ridges forming lateral borders to the general choanal excavations and also supporting the maxillaries below.

The pterygo-palatine sutures are indistinct, but traceable. The left and right palatines do not meet in the midline, the vomer intervening. *S. whaitsi* displays in this area two short and sharp longitudinal ridges, but in the present specimen the two equivalent ridges are so slight that they would not have been recognised as such if they had not been demonstrated in a previous description. More laterally than in *S. whaitsi* there are also slight bulges, but definite miniature teeth can not be recognised.

The *pterygoids* (pt, fig. 12) enclose between them a long and very narrow interpterygoid fossa. In front of this fossa, without meeting medially, they articulate with the palatines and laterally they swing outward to build buttresses for guiding the lower jaw. These processes do not project strongly in a ventral direction. The ventral surfaces of these portions of the pterygoids are concave. Behind the palatine sutures they build strong transverse ridges increasing gradually in size laterally

to where they overlap the transverse bones. Medially these ridges swing backward and join the lateral margins of the inter-pterygoid fossa at about the middle of its length. The posterior margins of these depressed areas are free and swing sharply back and outward again at the level where the anterior ridges join the inter-pterygoid fossa, to form the anterior free edges of the quadrate processes. These edges incline sharply downward, with deep troughs medially, extending from the pterygo-paroccipital fossae to the inter-pterygoid fossa. For a short distance behind the latter fossa the pterygoids form a median suture, where they cover the parasphenoid.

The quadrate processes of the pterygoids appear to meet the quadrate processes of the paroccipitals above the distal ends of the stapes.

The *alisphenoids* are not exposed.

The *parasphenoid* (ps, fig. 12) forms a broad, flat bridge extending between the pterygoids and basioccipital. Its lateral edges form the medial borders of the pterygo-paroccipital foramina, where it has contact with the paroccipitals above the fenestrae ovales. Anteriorly it extends flatly over the pterygoids, disappearing between them, in ventral view, in a tapering point. A low median ridge extends over the parasphenoid, the areas on either side being broadly and slightly concave. Just forward of the middle of the length of this ridge the internal carotid foramina enter the skull in a backward direction. The ridge appears to have been more prominent posteriorly between the fenestrae ovales and, being damaged, a small portion of the basisphenoid is exposed. The parasphenoid forms the anterior borders of the fenestrae ovales, where the basisphenoid is also apparently slightly exposed.

The *basisphenoid* is interpreted here as lying above the basioccipital and parasphenoid and is only slightly exposed between them as a result of damage. The bone described by Boonstra (op. cit.) as the basisphenoid for *S. whaitsi* is here interpreted as a parasphenoid, because posteriorly this bone has a suture with the basioccipital (and portions of the basisphenoid) in typically dermal bone fashion. Normally the basioccipital-basisphenoid suture is indistinguishable in Therapsids, especially in old specimens, and in this *Tapinocephalus*-zone material one would expect this to be more definitely the case, but in the present specimen the suture in this region is exceptionally well displayed.

Distinguishing Characteristics

The present specimen is recognised as a distinct species (*Struthiocephalus kitchingi*) on the strength of the following characteristics.

From *S. whaitsi* it differs in the following respects:

(1) The snout is narrower and more pointed, both horizontally and vertically, and is narrower posteriorly across the jugals than across the pterygoid processes.

(2) The posterior portion of the skull is broader and flatter, with the occipital condyle situated farther forward. The occipital plate is broader and lower, and its dorsal border extends farther backward so that the greatest breadth of the skull is at a level farther forward, although this level is still across the squamosals and

occipital condyle. The articular surfaces of the quadrates are virtually at the level of the middle of the length of the skull.

(3) The fronto-nasal boss is considerably more prominent. This may, however, be subject to sex and age.

(4) Although the present skull is reasonably larger, the interorbital width is smaller, while the intertemporal width is, out of proportion, twice that of *S. whaitsi.*

(5) The external nares are smaller and narrower.

(6) The premaxillaries are broader.

(7) The pterygoid processes swing farther outward.

(8) The postorbital bosses incline more forward so that the posterior borders of the orbits extend more transversely. The postorbital bars are shorter and stouter.

(9) The prefrontals extend farther backward, contributing more to the dorsal borders of the orbits.

(10) The post-temporal fossae are more laterally situated.

(11) The quadrate processes of the pterygoids are shorter and articulate differently with the quadrates, especially relative to the stapes.

(12) The quadrate processes of the paroccipitals are longer.

(13) The tabulars and squamosals partake more significantly in forming the mastoid bosses.

(14) The tabulars are not visible in dorsal view.

Other structural differences mentioned above are regarded as being possibly due to incorrect interpretations as a result of the problematic nature of this *Tapinocephalus*-zone material. In this respect, although the present author has described what appears to be most likely the correct structural arrangement, the present specimen is not so perfectly preserved and its structure so clearly displayed that *S. whaitsi* should invariably carry the blame.

From *S. akraalensis* it differs in the following respects:

(1) The snout is shorter, narrower and more pointed, but it agrees in being slightly constricted across the jugals.

(2) The posterior portion of the skull is less high and apparently also inclines more backward over the occipital region.

(3) Although the skull is some 45 mm. larger, the interorbital width is less.

(4) The external nares are smaller and more posteriorly situated.

(5) The prefrontals are situated more posteriorly, more directly above the orbits and contribute more significantly to their dorsal borders.

(6) The postfrontals are broader and more laterally situated, contributing to the postorbital bosses.

(7) These bosses incline more forward so that the posterior margins of the orbits extend more transversely.

(8) The occipital margin across the interparietal is concave.

(9) The tabulars do not show in dorsal view.

Again some structural differences, especially the tabular-squamosal-parietal relationship, are considered to be due to incorrect interpretation.

From *S. rheederi* it differs as follows:

(1) There is a sharper demarcation between snout and skull.
(2) The snout is shorter, smaller and more pointed.
(3) The temporal openings and pineal foramen are situated farther forward.
(4) The postorbital bosses incline more forward.
(5) The intertemporal width is greater.

On account of the unsatisfactory description of *S. rheederi* it is not possible to give a more detailed list of differences. The above list is nevertheless sufficient to show that *S. kitchingi* is distinct from *S. rheederi.*

From *S. milleri* it differs as follows:

(1) The external nares are situated farther back.
(2) The postorbital bars are more stout.
(3) The pineal foramen is smaller.
(4) The snout is smaller.

Otherwise the new specimen agrees with *S. milleri* in the shape of the fronto-nasal boss and the general flatness of the skull.

Because *S. whaitsi* is the only other species sufficiently well known for detailed comparison, and while it is not safe at present to accept certain structural interpretations in the described forms as perfectly reliable, it is preferable not to be too definite on the matter of finer relationship, either between the species, or to add to what is already indicated as the likely relationship of this genus with other near forms.

Acknowledgements

I wish to record my sincere thanks to Mr. J. W. Kitching for not only procuring this specimen under difficult circumstances, but especially for the magnificent preparation work he has done to expose sutural detail.

Literature Cited

BOONSTRA, L. D., 1952. 'n Nuwe soort van Tapinocephalide Deinocephaliër, *Struthiocephalus akraalensis* sp. nov. *S. Afr. J. Sci.*, xlviii, 247.

BOONSTRA, L. D., 1952. *Ann. Mag. Nat. Hist.* (12) 5, p. 455.

BOONSTRA, L. D., 1953. The cranial morphology and taxonomy of the Tapinocephalid genus *Struthiocephalus. Ann. S. Afr. Mus.*, xlii, 32.

BROOM, R., 1932. The Mammal-like Reptiles of South Africa (p. 37, figs. 12C, 13). H. F. & G. Witherby, London.

BROOM, R., 1937. A further contribution to our knowledge of the fossil reptiles of the Karroo. *Proc. Zool. Soc. Lond.*, Ser. B., p. 299.

HAUGHTON, S. H., 1915. A new Dinocephalian from the Gouph. *Ann. S. Afr. Mus.*, xii, 52.

HAUGHTON, S. H., 1916. Report of the South African Museum for 1915, p. 4.

OLSON, E. C. & BROOM, R., 1937. New genera and species of tetrapods from the Karroo beds of South Africa. *J. Palaeont.*, xi, 613.