PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

On the Tooth-Replacement in Theriodont Reptiles

F. R. Parrington

Phil. Trans. R. Soc. Lond. B 1936 **226**, 121-142
doi: 10.1098/rstb.1936.0005

IV—On the Tooth-replacement in Theriodont Reptiles

By F. R. PARRINGTON, M.A., *Assistant to the Director of the Museum of Zoology and Balfour Student, Cambridge*

(Communicated by J. STANLEY GARDINER, F.R.S.—Received July 31—Read November 14, 1935)

CONTENTS

	PAGE
I—INTRODUCTION	121
II—NOTE ON THE GENERA *Nythosaurus* AND *Thrinaxodon*	122
III—ON THE TOOTH-REPLACEMENT IN *Thrinaxodon liorhinus*, SEELEY	124
(*a*) MATERIAL	124
(*b*) TOOTH-REPLACEMENT	127
IV—ON *Parathrinaxodon proops* GEN. ET SPP. NOV.	132
V—NOTE ON *Tribolodon frerensis* SEELEY	137
VI—NOTE ON *Dimetrodon*	138
VII—DISCUSSION	139
VIII—REFERENCES	142

I—INTRODUCTION

In describing the very mammal-like dentitions of some of the advanced Theriodont reptiles various authors have identified premolars and molars (BROOM, 1913). Though there is some evidence for this differentiation in the form of the teeth of some of the gomphodont cynodonts, there is no satisfactory evidence that only two dentitions were present or that the replacement was of a mammalian type.

On the other hand SUSHKIN (1927) described the type of the primitive cynodont *Permocynodon sushkini*, SMITH WOODWARD, as having several molariform teeth "changing" and says "it may be established thus that the teeth are changing irregularly as usually in the reptiles and that there is no difference in this respect between the anterior and hindermost teeth; thus despite the difference of the form, no premolars and molars can be distinguished". Unfortunately he does not say which teeth are changing.

Other authors, uncertain of the manner of replacement, have avoided implying a mammalian succession by the use of such terms as "cheek" teeth or "post-canine" teeth.

The difficulties of analysing the dentitions of such fossil groups are due to the rarity of specimens in which replacement of the teeth is actually taking place, and also to the lack of developmental series. In this respect it is fortunate that there is a primitive cynodont, *Thrinaxodon liorhinus*, SEELEY, which is relatively abundant. One specimen of this animal, which is in the Museum of Zoology at Cambridge, seemed to show the method of tooth-replacement. An examination of all the available material of the species was made and this yielded sound evidence that the replacement is not of the mammalian type, but that alternate teeth are replaced at one stage and the others later. This condition is apparently present in other members of the group, and is an inheritance from the earliest tetrapods, a conclusion which is in accordance with BOLK's interpretation of the condition in living reptiles.

II—NOTE ON THE GENERA *Nythosaurus* AND *Thrinaxodon*

It has long been recognized that the cynodonts *Nythosaurus larvatus*, OWEN, and *Thrinaxodon liorhinus*, SEELEY, are very closely related. When describing the type of the latter SEELEY (1894) stated that it had six post-canine teeth each with three cusps, whereas OWEN's *Nythosaurus larvatus* had seven or eight post-canine teeth and several of them had four or possibly five cusps.

In a paper on *Thrinaxodon liorhinus* (PARRINGTON, 1933), the writer described one specimen in which a seventh post-canine tooth was present in one maxilla, and a specimen in which there were seven and eight post-canine teeth on the two sides respectively.* Subsequently two further skulls have been seen in which seven teeth are present, one in the British Museum (Natural History), R.5480, and one in the Transvaal Museum—the anterior of two skulls in a block numbered 80.

In regard to the question of tooth cusps, HAUGHTON (1924) reported a specimen of *Thrinaxodon liorhinus* in which one tooth had an additional cusp on the inside. BROOM (1932), however, states that he has never seen a specimen in which the teeth had more than three cusps. A specimen collected by the author in 1933 showed very plainly that the fourth tooth on either side had a fourth cusp, lying posterior and slightly lingual to the third. Careful preparation has shown the presence of additional cusps on the teeth of the maxillae of three other specimens, fig. 1. These cusps have been seen on the posterior inner edge of the fourth tooth in one specimen, C; on the anterior inner edge of the fifth tooth of two specimens, D and F; and on the anterior and posterior sides of the fourth tooth and the anterior of the fifth tooth of another, E. The apparent absence of these cusps in other specimens is probably due to the difficulty of cleaning between the teeth when they are set close together, particularly when the matrix is not relatively soft. The teeth of the left maxilla of specimen D were removed, the fourth being destroyed in the process. It could then be seen that the fifth tooth had only the additional anterior cusp, and that none was present on the first, second, third, or sixth tooth. The

* This second specimen has much smaller teeth than those of any other I have examined and, since it is too badly preserved to give any information on the question of tooth-replacement, it is omitted from this discussion.

dissection also exposed the teeth of the left dentary, fig. 1, and showed that the fifth and seventh teeth have five cusps as has, probably, also the eighth. The fact that the type of *Nythosaurus larvatus* consists largely of a negative mould makes it difficult to be certain of its detailed characters, and this further information on the teeth of *Thrinaxodon liorhinus* seemed to remove the justification for separating the two genera.

There are, however, sufficient fixed points shown in the type of *Nythosaurus larvatus* to enable a reconstruction to be made. These points are :—the position of

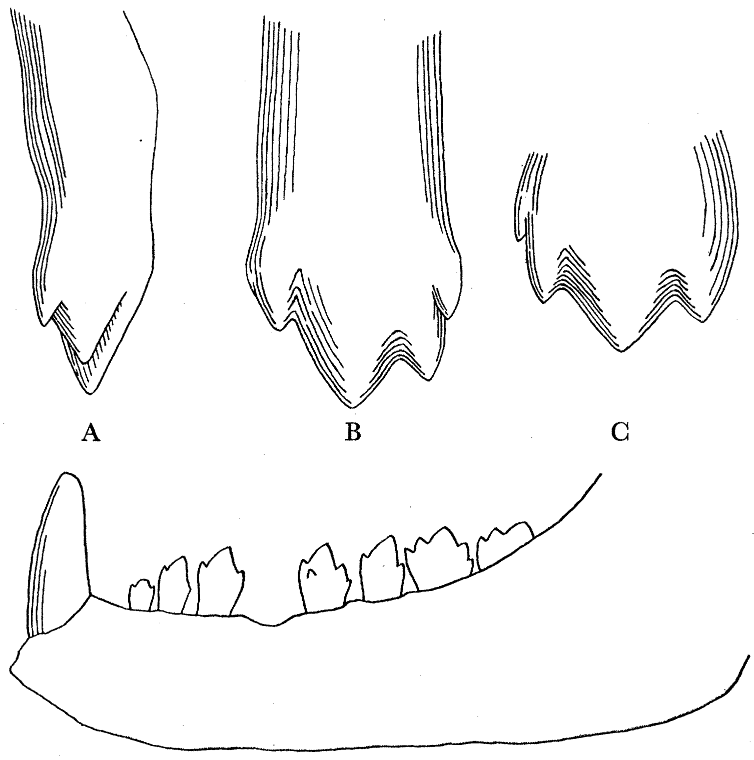


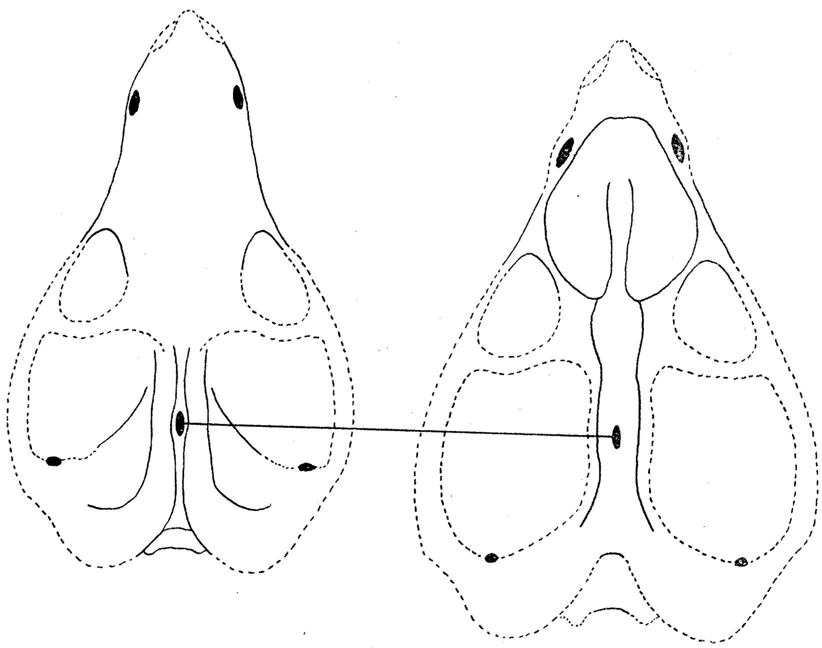
FIG. 1—Teeth of *Thrinaxodon liorhinus*, SEELEY. A, B, anterior and inner views of the fifth left post-canine of specimen D. X.12 ; C, outer view of right fourth post-canine of specimen C. X.12 ; D, left dentary of specimen D. X.3.

the canine tooth and the quadrate in the left side ; the anterior border of the orbits ; and the position of the pineal foramen ; the back of the parietal crest ; and of the foramen magnum as shown by the cast of the brain case. The position of the back of the parietal crest is given by the mould of the recess in the inter-parietal in the type compared with the section of a skull of *Thrinaxodon liorhinus* (PARRINGTON 1935).

When a reconstruction of *Nythosaurus larvatus* based on these points and on the mould of the nose is compared with one of *Thrinaxodon liorhinus* certain differences are at once apparent, fig. 2. The most obvious of these is the position of the quadrates,

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

which in *Thrinaxodon* are nearly in line with the pineal foramen while in *Nythosaurus* they are only just in front of the back of the parietal crest. In addition *Nythosaurus* has the occiput sloping much more, and is relatively shorter anterior to the pineal foramen. The reconstruction of a series of specimens of *Thrinaxodon liorhinus*, fig. 3, shows that the ratios of the distances between the back of the parietal crest and the pineal foramen, of the pineal to the front border of the orbits, and from the front border of the orbits to the tip of the snout vary between 1 : 1·83 : 2·25 in a small specimen to 1 : 1·76 : 2·11 in a large specimen, while the ratios in *Nythosaurus* are 1 : 1·6 : 1·86—the last figure being made on the estimated length of the snout. Another point of difference lies in the position of the post-canine teeth, the last



A B

FIG. 2—Restorations of A, *Thrinaxodon liorhinus*, SEELEY, and B, *Nythosaurus larvatus*, OWEN. Natural size. The positions of the canines, pineal foramina, and lower ends of the quadrates are marked in black.

three of which are situated below the orbit in *Nythosaurus*, whereas only the sixth and, when present, the seventh occupy this position in a *Thrinaxodon* of similar size. It seems quite clear therefore that the two genera are distinct.

III—On the Tooth-replacement in *Thrinaxodon liorhinus*, Seeley

(*a*) *Material*

Nine specimens of *Thrinaxodon liorhinus* are described in this paper, three the property of the British Museum (Natural History) (B.M.N.H.), and six belonging to the University Museum of Zoology at Cambridge (C.M.Z.). For convenience of discussion they have been arranged in order of their size and given a letter. This material is as follows :—

Specimen A, C.M.Z. R.2733 ;	Specimen F, C.M.Z. R.2734 ;
B, ,, R.2739 ;	G, B.M.N.H. R.5480 ;
C, ,, R.2737 ;	H, C.M.Z. R.2736 ;
D, ,, R.2738 ;	I, B.M.N.H. R.511*a*.
E, B.M.N.H. R.3731 ;	

All the Cambridge material was collected from the Lystrosaurus zone (*L. Trias*) at Harrismith in the Orange Free State, as was the British Museum specimen No. R.5480. The remaining two specimens are registered as Lower Trias, number R.511*a* from the Orange Free State and number R.3731 from Griqualand.

In order to establish the relative stages of growth of these specimens it was necessary to make reconstructions as far as this was possible. Though it is seldom that an absolutely complete or uncrushed specimen is found—the premaxillae and jugal arches are often missing—the presence of such parts as the septomaxillary foramen, the anterior borders of the orbits, the quadrates, and the occiputs enable restorations of six specimens to be made with fair accuracy. Unfortunately the three specimens A, D, and I, are too damaged in the region of the brain case to enable useful restorations to be made, but their growth stages are given by their dentaries. The growth series of the six specimens show a number of points of interest, fig. 3. If the drawings of the smallest and the largest specimens are placed with their pineal foramina on a line, and such points as the back of the parietal crest, the anterior border of the orbits, and the tip of the nose are joined, it will be found that the drawings of the remaining four skulls conform to these lines with only two exceptions. In specimen G the anterior border of the orbit falls somewhat short, but the specimen is distorted and the explanation of this may well lie in faulty reconstruction. A more interesting variation is found in specimen E, where the skull conforms perfectly only if the pineal is placed just behind the line of the other pineals. Also the nose of this specimen is a little broader than that of the slightly larger specimen F. Such differences may be due to natural variation or possibly sexual dimorphism.

This series shows the changes in proportion of the skull which take place during growth. The increase in the length of the skull is made up of about 42% in the increase in the nose anterior to the orbits, 35% in the region between the pineal foramen and the front of the orbits, and 23% between the pineal and the back of the parietal crest. Also while the length has increased by about 35% the width has increased by about 50%.

Restorations in side view are much less satisfactory owing to the fact that the majority of skulls have been crushed. Specimens H and F are very little distorted, however, and a fairly reliable restoration can be made of specimen C, fig. 4.

It will be seen from this series that the canine tooth occupies a constant position, and the post-canines remain close to it and do not occupy a much greater space in the old specimens than they do in the young. The result of this is that whereas in the

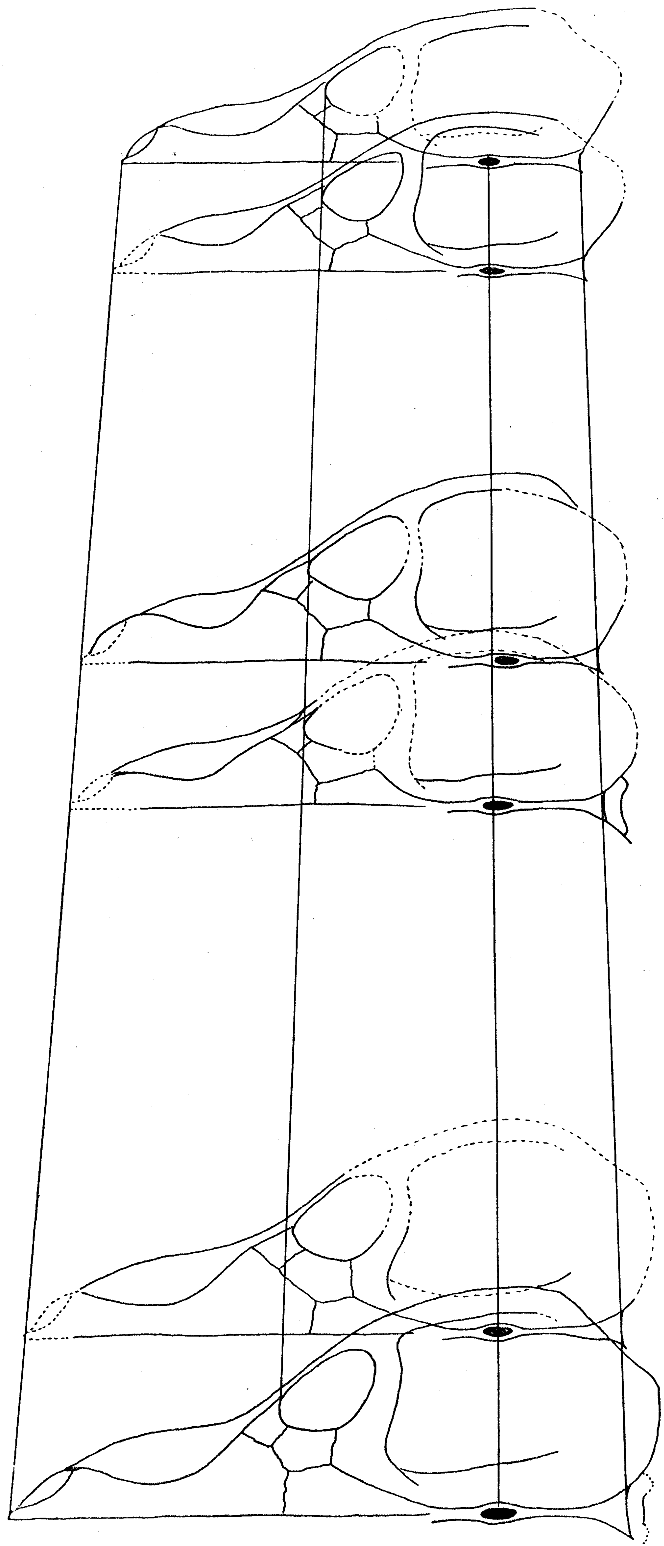


FIG. 3—Restorations of the skulls of *Thrinaxodon liorhinus*, SEELEY, to show the change in proportions during growth. Natural size.

young forms the posterior three teeth are situated below the orbit, only the last tooth occupies that position in the oldest. Another point of interest is in the position of the quadrates which occupy a much more posterior position in the young than they do in the older forms. This position of the quadrate, together with that of the last post-canines, and the fact that the young have a relatively small nose, suggests that it would be hard to distinguish them from the young of *Nythosaurus*.

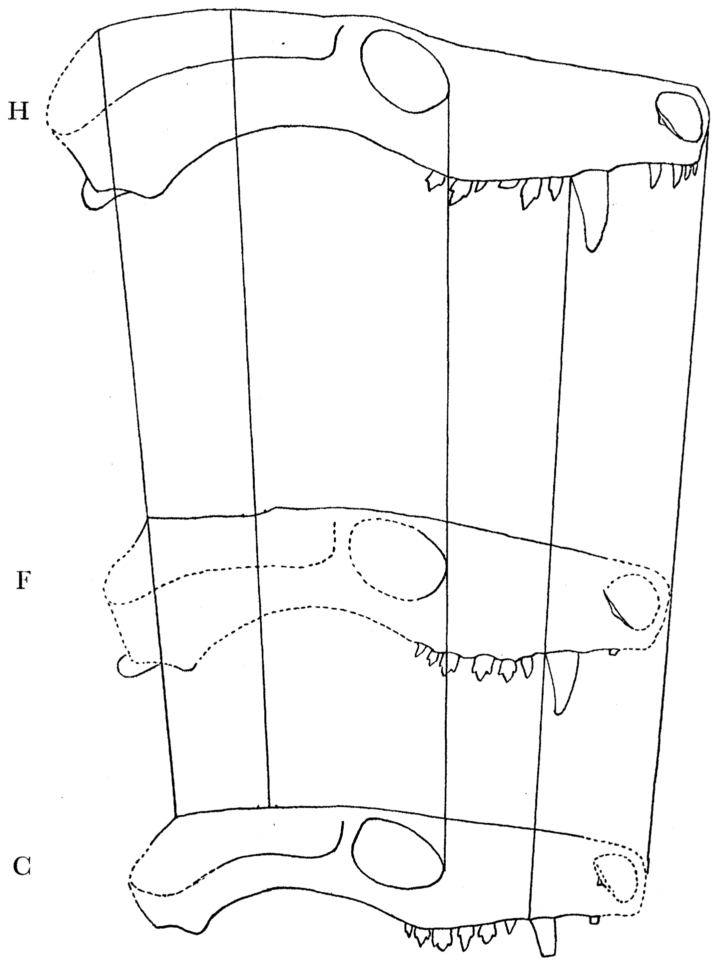


FIG. 4—Restorations of the skulls of *Thrinaxodon liorhinus*, SEELEY, in side view. Natural size.

(*b*) *Tooth-replacement*

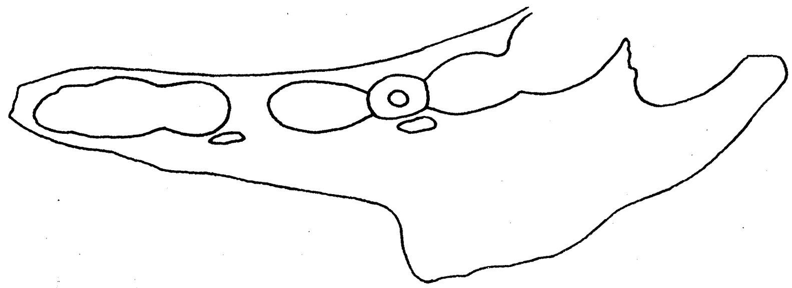
The first indication that the manner of the replacement of the post-canine teeth could be seen in these forms was noticed in specimen F. This is the second specimen that was described in 1933 when the presence of seven teeth in the left side was noted and the suggestion made that the extra tooth was actually the fourth. Comparison of the two sides shows that the anterior three teeth are almost identical with their fellows in the opposite side, as are the last three. The distance occupied is the same in both maxillae but in the right side there is a very marked gap in the middle of the series. The interpretation now suggested is that the real fourth tooth is missing from the right side, and that the true seventh is present in both maxillae. This is strongly supported by the fact that in every specimen examined—including a large number in various museums in South Africa—the fifth tooth is always relatively large, as in the left side, and is not of the small size of the actual fifth in the right maxilla. A similar condition may have been present in specimen A. Here the right maxilla is separate and has been cleaned in palatal view. The tip of the replacing canine, visible in its socket, and the root of the second post-canine tooth are all that is preserved, but it is seen that the alveoli of the three anterior post-canine teeth are confluent as are the last three, while the two series are separated by a distinct bridge of bone, fig. 5A. The left maxilla has the second, third and fifth teeth in place but there is no indication of a similar gap between the third tooth and the alveolus of the fourth. It is not possible to say whether or not a seventh tooth was present in this side. The explanation of the absence of the true fourth tooth in specimen F is not at all clear, but it is important to recognize that the teeth which are present in the right maxilla are the first, second, and third, and the fifth, sixth, and seventh. A further point in support of this interpretation, and the clue to the manner of the tooth replacement, is given by the alveoli. The nature of these is shown very clearly in this specimen, and there can be no doubt that their characters are true and not due to the preparation. The teeth and bone were very clear and distinct from the matrix which was sufficiently soft to enable a very satisfactory preparation to be made. In both sides the alveoli of the first, third, fifth, and seventh teeth are large and the teeth are only loosely implanted in them ; while the second, fourth, and sixth teeth in the left side and the second and sixth in the right side are held tightly, the bone coming closely round their roots, fig. 5B and C. The space of the missing fourth tooth in the right side is occupied by bone which reaches downwards between the large alveoli of the third and fifth teeth in the manner of the bone round the roots of the second and sixth teeth. The obvious interpretation of this difference in the nature of the alveoli of the odd and even numbered teeth is that those in the loose sockets are replacing-teeth that had erupted only a short time before the animal died.* The fact that the seventh teeth are implanted in a loose socket apparently means that they have been cut only a short time, but since there is no evidence of seven teeth being present in a smaller animal they are unlikely actually to have replaced teeth.

The examination of the remaining available material provided very satisfactory evidence in support of the foregoing interpretation. The main point of interest in the two smallest specimens lies in there being evidence of replacement of the canines and incisors. In specimen A the tip of a replacing canine is visible in the empty

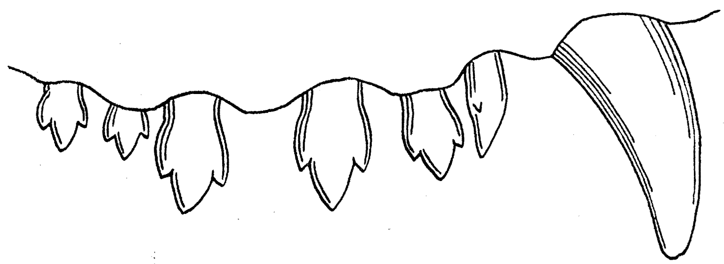
* The appearance in the left side suggests very strongly that the seventh tooth was not completely erupted. Furthermore, the teeth implanted in the loose sockets are rather larger than the others and have the centre cusp slightly larger in proportion.

socket of the right maxilla, and a small replacing-tooth is seen pressed against the root of the first incisor in the left dentary. The section cut through specimen B exposed a replacing-tooth which appears to be in the process of eruption just behind the first incisor of the right premaxilla. In neither specimen are the post-canine teeth well preserved but a point of interest in specimen B is the fact that the sixth tooth does not appear to have erupted in the right maxilla.

A



B



C

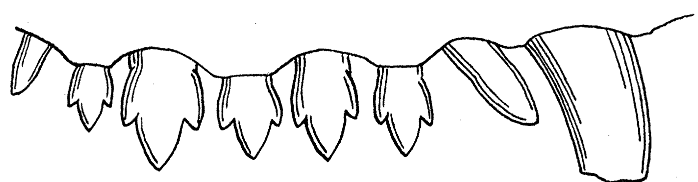


FIG. 5—*Thrinaxodon liorhinus*, SEELEY. A, right maxilla of specimen A, palatal view; B, teeth of right cheek of specimen F; C, teeth of left cheek of specimen F, drawing reversed for comparison; X, true fourth tooth missing in right maxilla. All × 4.

Specimen C has very large alveoli for the first post-canines and, while the tooth is missing in the right side, there is apparently a replacing-tooth half erupted in the left. Also the third teeth in both sides have the appearance of being incompletely erupted, and have their centre cusps rather larger in proportion to the main cusps in the adjacent teeth. The suggested interpretation of this dentition is that the

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

first post-canine teeth are being replaced while the third may have already been replaced, fig. 6.

The next specimen, D, is very poor. Its position in the series is given by the size

C

E

F

H

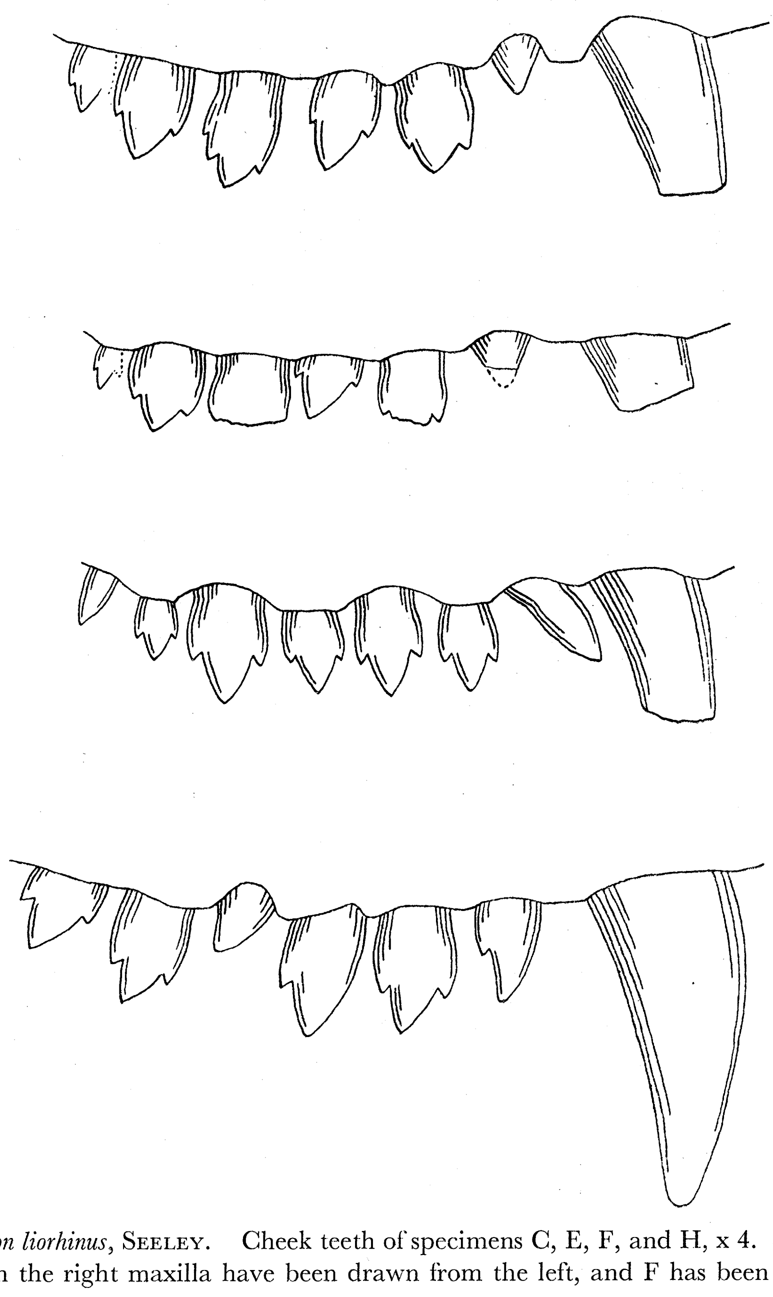


FIG. 6—*Thrinaxodon liorhinus*, SEELEY. Cheek teeth of specimens C, E, F, and H, x 4. Teeth missing or damaged in the right maxilla have been drawn from the left, and F has been reversed from the left side.

of the dentary which is slightly larger than that of specimen C. In neither case, however, is this bone well preserved. Here the post-canine teeth of the right side appear to show, though not so clearly, the same behaviour as that described for specimen F. The first and fifth teeth were certainly very loose and half out of their sockets. The teeth of the left maxilla were dissected out in the hope of finding replacing-teeth but no trace of these was found. The interpretation here is that the first, third, and fifth post-canine teeth have been replaced, and that the replacing-teeth of the second, fourth, and sixth teeth were not sufficiently calcified to be preserved.

Specimen E,* the next in order of size, is very interesting. It can be seen quite clearly in both sides that the first and third teeth are half erupted, the fifth teeth giving no convincing evidence of having been replaced. The crowns of the second and fourth teeth are not well preserved, but their appearance suggests that the cusps were subequal while the replacing third teeth have relatively large centre cusps, fig. 6. The sixth tooth has not erupted in the left side.

Specimen F has already been described, and the interpretation suggested that the first, third, fifth, and seventh teeth have just erupted.

Specimen G is an old one and the teeth have been prepared very badly. The following points are of interest, however. In the right side the fourth post-canine tooth seems to be more tightly clasped by the bone than the others, the sixth tooth (as shown in both sides) is small, and a seventh, also small, is present in the left maxilla.

Specimen H is of considerable importance. In both maxillae the fourth tooth is plainly just erupting—only the centre cusp being visible, fig. 6. Additional points are the fact that while the first three teeth are very similar to those of specimen F the six tooth is very much larger than in any of the smaller specimens. There is no evidence for a seventh tooth having been present. An important point in the dentition of this specimen is that the second incisor of the left premaxilla is smaller than that of the right, and may be erupting.

In the largest specimen, I, the post-canine teeth are rather damaged. The fourth and sixth teeth are seen to be as large as in specimen H and, what is of most importance, the second tooth of the right side has a relatively enormous cusp and has the appearance of being incompletely erupted.

This evidence of replacement may be summed up as follows:—The canine is being replaced in the first animal, which is certainly very young, and the first upper incisor in the next, an animal with a skull length of 61 mm.†

Of four skulls varying between 61 and 71 mm, C shows the first post-canine tooth replacing, and E the first and third post-canines, while D and F suggest that the first, third, and fifth have already been replaced.

In the three skulls between 79 and about 85 mm the smallest, G, suggests that the second, fourth, and sixth teeth, at least, are the same as those of the smaller specimens; the second, H, shows that the sixth teeth have been replaced (it is the

* This is the specimen mentioned by Watson (1920) as showing tooth change.

† The skull lengths are given from the premaxillae to the back of the parietal crest as this can be given with the greatest accuracy in most specimens.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

first specimen to have this tooth large), and the fourth are just erupting. In the largest, I, the second and sixth teeth have definitely been replaced.

There is sufficient positive evidence in these specimens to show that the canines, and at least one incisor, are replaced in the very young animal ; the first, third, and fifth post-canine teeth when the skull reaches a length of about 65 mm ; and the second, fourth, and sixth post-canines when it is about 82 mm.

The only evidence which suggests that more than one replacement occurs is the incompletely erupted second upper incisor in the adult specimen H. There is no evidence, however, to show that the second incisors were replaced at the same time as the first incisors, *i.e.*, in the very young animal, and it is possible, as will be pointed out later, that there was a considerable time interval between the replacement of the alternate incisor teeth as well as in the post-canines.

IV—On *Parathrinaxodon proops* gen. et spp. nov.

While investigating the Karroo rocks of the Ruhuhu valley in the south-west of Tanganyika in 1930, Mr. G. M. Stockley (1932), of the Tanganyika Geological Survey, discovered a number of bone localities at two distinct horizons. The remains collected were described by Haughton (1932) who concluded that the fauna of the lower horizon indicated an Upper Permian age, and that the beds were probably homotaxial with the middle part of the Lower Beaufort Beds of South Africa.

Among a series of Permian Theriodonts collected by the author from this horizon in 1933 was a new cynodont of particular interest for which the name *Parathrinaxodon proops* is suggested. The specimen, which was collected from Stockley's site B. 19, near Kingori mountain, consists of a skull which has lost the jugal arches, the top of the brain case, and the lower jaws. The right side of the face is somewhat distorted, and the state of preservation is also unsatisfactory in regard to the sutures, only a few of which can be identified.

The form of the face is unusual for the great depth of the snout, and the splaying out of the borders of the orbits which cause them to face more forwards than outwards, fig. 7.

The front of the premaxillae, with the internarial processes are missing. Weathering has worn the right side down to expose the sockets of four incisors with a replacing-tooth just erupting in the second. Restoration of the snout suggests that there must have been room for six incisors. As preserved it appears that the lower border of the bone curved upwards towards the front. The left premaxilla is so damaged that it yields no information.

The septomaxillae are partly preserved in both sides and show the presence of fairly large septomaxillary foramina below the back of the external nares.

The maxillae are very deep, somewhat swollen above the canines and extending posteriorly nearly to the orbits. They are pierced by six foramina, four above the base of the canines and two, rather larger, posteriorly.

The nasals slope upwards to meet at an angle in the midline and form a ridge which becomes very pronounced between the orbits where they meet the frontals posteriorly in a deeply crenulated suture. There are two foramina visible in the left nasal just posterior to the highest point of the overlap of the maxilla, and indistinct evidence of several smaller ones anteriorly.

The inner borders of the prefrontals are only distinguishable posteriorly where they lie halfway between the orbits and the midline. In this region the frontals slope downwards to meet the nasals and the frontals and form with them two distinct valleys. The anterior extension of the prefontals cannot be made out with any certainty, nor the borders of the lachrymals except where the left lachrymal meets the maxilla and the extension of the jugal below the orbit.

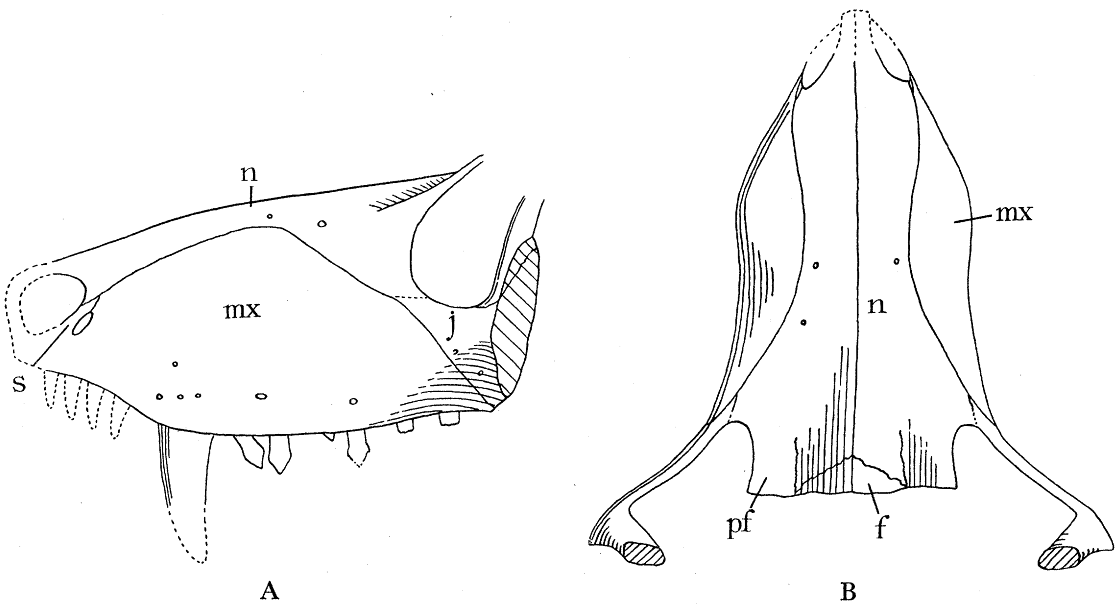


FIG. 7—*Parathrinaxodon proops* gen. et spp. nov. A, side view and B, dorsal view, x 1 ; f, frontal ; j, jugal ; mx, maxilla, n, nasal, pf, prefrontal, s, septomaxilla.

The anterior part of the left jugal is preserved. It forms the lower border of the orbit and apparently extends upwards round the back of the post-orbital nearly to the midline. Below the orbit there are two distinct, but small, foramina which face forwards and downwards.

Palate—The bones of the palate are badly fractured and it proved difficult to remove the matrix which will not part readily. Few sutures can be determined but the form is fairly clear.

There is a well-formed false palate, the left side of which has been cleaned, extending backwards nearly to the line of the orbits. Anteriorly there is some indication of palatal processes of the premaxillae, and there are the usual pits for the reception of the lower canines. The maxillae appear not to have joined completely in the midline opposite the canines and for a short distance posteriorly.

The posterior borders formed, presumably, by the palatines, meet at an angle of about 70° and extend backwards to join the ridges of the palatines and pterygoids which formed the walls of the naso-pharyngeal passage.

Part of the vertical plate of the fused vomers can be seen extending backwards to the middle of the skull, but its anterior extension and the outline of the bone is uncertain.

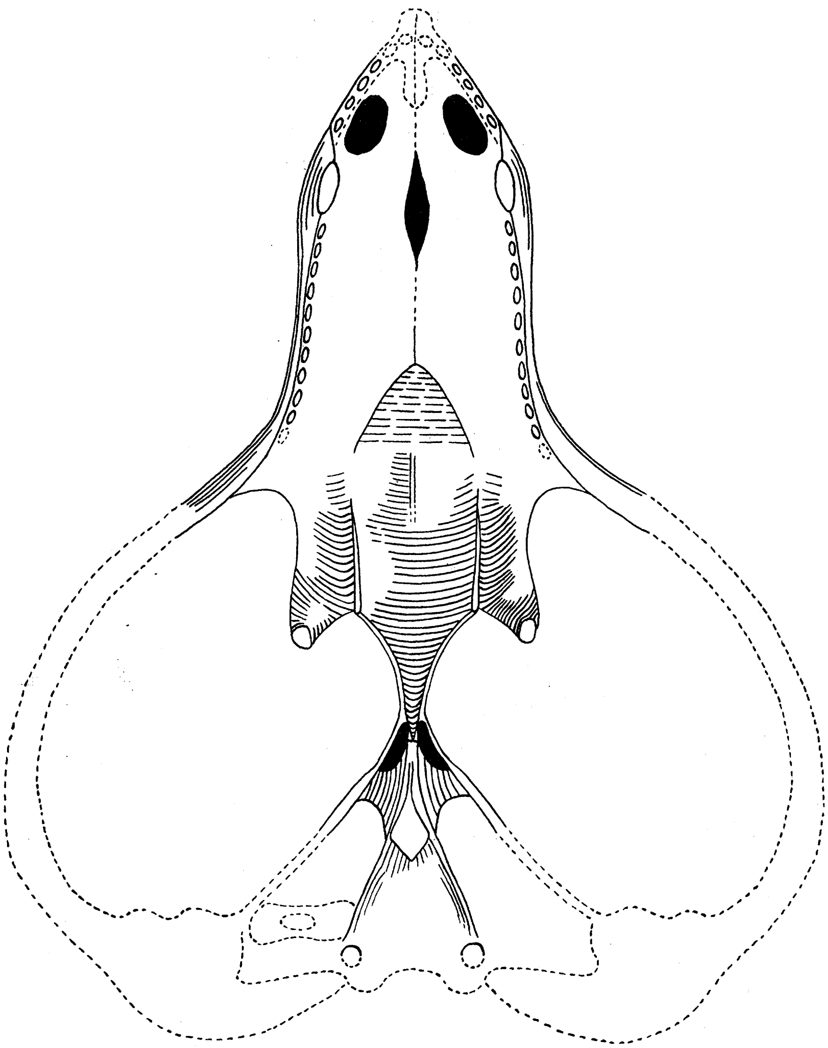


FIG. 8—*Parathrinaxodon proops* gen. et spp. nov. Palate natural size.

The pterygoids have strong transverse processes and form the well-developed walls of the naso-pharyngeal passage which are continued posteriorly into the two vertical plates of the pterygoid bar. There is an inter-pterygoid vacuity but posteriorly the pterygoids approach each other and finally meet in the region from which the quadrate rami are given off. This junction of the pterygoids, however, may be the result of the distortion of the right side of the skull. The quadrate ramus of the left pterygoid is missing and the right has been disturbed and its full extension cannot

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

be determined owing to the difficulty of cleaning such a thin strip of bone out of the hard, flinty matrix.

Sufficient of the left epipterygoid remains to show that it was flattened and similar to that of *Thrinaxodon*.

The basicranium is weathered and incomplete. Anteriorly there is a keel which passes forwards between the pterygoids and is continued backwards into a small triangular area which projects downwards from the main parasphenoid-basisphenoid complex, the posterior border of which, with the basioccipital, has been lost by weathering. The anterior border of the right foramen jugulare remains, however, to help to give the proportions of the skull.

On the left side the pleurosphenoid is visible fused to the front of the basisphenoid and rising upwards and outwards towards the epipterygoid.

Teeth—The teeth are, perhaps, the most interesting feature of the skull. The only incisor preserved is a replacing-tooth which is just erupting in the second of the preserved alveoli. The left canine is missing and the right badly damaged, but sufficient of the latter is preserved to give some indication of its size and to show that it was oval in shape.

In the left maxilla the first and third post-canine teeth are well preserved, the first being partly out of its socket, fig. 9. They are slightly compressed and spear shaped with a single cusp, the posterior border swelling out and having a crenulated edge running down towards the tip which in each tooth has been broken off. The second and fourth alveoli are empty but in the fifth is the tip of a replacing-tooth. The sixth tooth was fairly well preserved and the crown was removed for examination, fig. 9. In outer view is seen the remains of a large centre cusp with a small accessory cusp on either side. Internally there is a cingulum which carries a small accessory cusp anteriorly and apparently also a second accessory cusp posteriorly, but this latter was broken off and left in the matrix when the crown was removed.

There are the damaged remains of teeth in the eighth and tenth alveoli, but the seventh, ninth, and eleventh are empty. The eleven teeth occupied a length of 32 mm.

In the right maxilla the first four alveoli are empty. In the fifth, as in the left maxilla, is the tip of a replacing-tooth. The sixth post-canine is in place, but rather damaged, the seventh is missing, the eighth is present, but badly damaged, and the ninth just erupting. There are no teeth in the tenth or eleventh alveoli.

It seems quite plain that in this specimen the alternate post-canine teeth are being replaced in the manner found in *Thrinaxodon*; but that the replacement of the even numbered teeth had started in the front of the jaw before the replacement of the posterior odd numbered teeth had been completed. It might be argued that the absence of the first four post-canines in the right maxilla, and also the tenth, indicate that the loss of alternate teeth in the left maxilla and in the centre of the right was a post-mortem change. But the presence of replacing-teeth in both fifth aveoli and the right ninth alveolus, together with the presence of a replacing incisor, give fair evidence that the loss was due to replacement.

There are only three specimens of Cynodonts known from the Permian, *Cynosuchus suppostus*, OWEN, and *Cynosuchoides whaitsi* (HAUGHTON), from South Africa, and *Permocynodon sushkini*, SMITH WOODWARD, from Russia, and this new form at once recalls the latter. Unfortunately only a preliminary description of this has yet appeared (SUSHKIN, 1927) which, together with the incompleteness of the new form makes detailed comparison difficult. It is very similar, however, in the relatively small snout, the way in which the orbits face forwards, the dental formula and, in particular, the nature of the crowns of the post-canine teeth. It lacks, however, certain characters of the Russian form, in particular the perforation of the

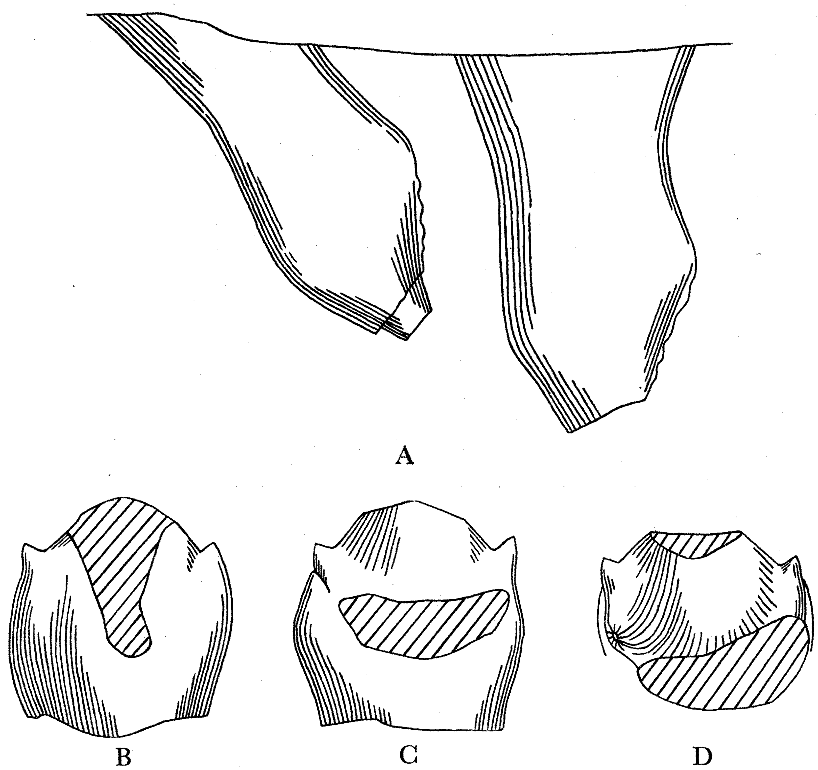


FIG. 9—Teeth of *Parathrinaxodon proops* gen. et spp. nov. A, first and third left post-canines, outer view ; B, outer view of sixth left post-canine ; C, inner view of same ; D, same viewed from inner side and below. All x 10.

pits for the lower canines between the premaxillae and the maxillae, the constriction of the snout behind the canines, and the hooking of the premaxillae. In this form, too, the nasals are unusual in meeting the frontals well behind the front borders of the orbits.

Both forms are very similar to the Lower Triassic cynodont *Thrinaxodon liorhinus*, particularly in regard to the teeth. The possession of post-canine teeth having a large centre cusp with a small accessory cusp on either side in outer view, and two small accessory cusps lingually is now known in the two Upper Permian cynodonts, *Permocynodon sushkini* and *Parathrinaxodon proops*, the Lower Triassic forms *Thrinaxodon* *liorhinus* and (probably) *Nythosaurus larvatus*, and the Middle Triassic form *Tribolodon frerensis*. The presence, in the first two forms, of single cusped teeth anteriorly, and in *Thrinaxodon liorhinus* of teeth with only the three outer cusps suggests that these forms may eventually prove to be closely related.

The maxilla which BROOM (1930) described as *Cyrbasiodon boycei*, and suggested was possibly a Scaloposaurid Therocephalian, is probably a related form.

V—NOTE ON *Tribolodon frerensis*, SEELEY

The cynodont *Tribolodon frerensis*, SEELEY, has been known until recently only by the type specimen, an incomplete dentary with three teeth, collected from the Cynoganthus zone at Lady Frere, Cape Province.

Recently, however, BROILI and SCHRÖDER (1934) have described further material and they reached the conclusion that, as in the allied genera *Permocynodon* and

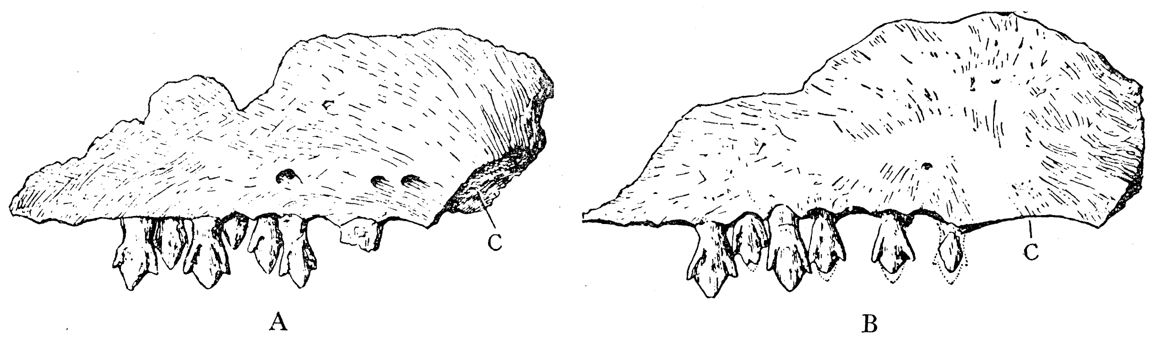


FIG. 10—Two maxillae of *Tribolodon frerensis*, SEELEY, to show replacement. x 2. From BROILI and SCHRÖDER, 1934.

Thrinaxodon, it was impossible to distinguish premolars and molars as tooth-change could be observed throughout the post-canine series. It is plain from their illustrations of two maxillae, fig. 10, that here also the post-canine teeth were in two series the members of which were replaced at different stages. In one figure, A, six consecutive postcanine teeth are well preserved. The penultimate of the series is incompletely erupted, the next but one anteriorly shows only the centre cusp while the anterior tooth is loose in its socket and may have been on the point of being replaced. In the second maxilla, B, the replacement is not so clear, but it may be seen that there are four teeth of much the same size in alternate sockets, the first two being followed by empty alveoli, and the second two by larger teeth the first of which is apparently loose.

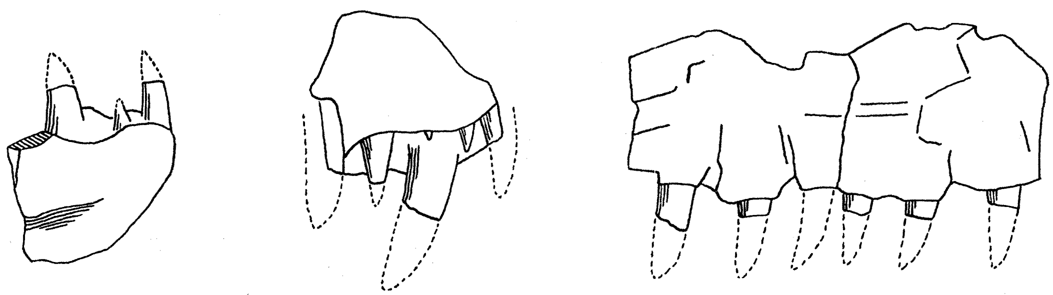
Though this evidence of alternate tooth-replacement is not by itself very clear yet taken in conjunction with the relationship of *Tribolodon* to *Parathrinaxodon* and *Thrinaxodon* it becomes fairly conclusive.

VI—Note on *Dimetrodon*

When the nature of the tooth replacement found in *Thrinaxodon* was described to Professor D. M. S. Watson he observed that he had seen similar replacement in some specimens of the Pelycosaur *Dimetrodon*, and very kindly placed at the author's disposal his collection of jaw fragments of this animal. In three of these the teeth are being replaced.

The first specimen, fig. 11A, consists of the anterior portion of a left mandible. The first and third teeth are in position though the crowns are damaged. In the second alveolus there is a replacing-tooth partly erupted, while the fourth alveolus, the last to be preserved, is apparently empty. This latter was ground down for about 3 mm and some small fragments were found which suggest that a damaged replacing-tooth may be present.

The second specimen, fig. 11B, is part of a left maxilla from the region in which this bone is swollen and carries the two enlarged canine-like teeth. Anteriorly



A B C

Fig. 11—Fragments of jaws of *Dimetrodon* spp. to show replacement of teeth. x $\frac{1}{2}$.

there are the remains of the root of a large tooth which is apparently fully erupted. The second alveolus is occupied by a tooth which must have been just erupting at the death of the animal. The third tooth is very large, lacks the tip of the crown, and has at its base, and on the lingual side, the tip of a replacing-tooth showing. In the fourth alveolus there is a tooth which is incompletely erupted and this is followed by the remains of a root of a tooth which appears to have been fully developed.

The third specimen, fig. 11C, consists of some four inches of a right maxilla which has been badly fractured. The anterior (broken) border passed through the back of a tooth but there is not sufficient of this tooth preserved to show whether or not it was completely erupted. Remains of teeth are preserved in the second, fourth, and sixth, and the seventh, ninth, and eleventh alveoli. No teeth were found in the third and fifth, or the eighth, tenth, and twelfth alveoli (the first four of which have been cleaned of matrix and the last of which has been ground down some 4 mm), except possibly in the tenth where some small fragment, apparently of a tooth, may be the tip of a replacing-tooth.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

These three specimens seem to indicate fairly clearly that, as in the described Cynodonts, the teeth in *Dimetrodon* belong in two series the members of which alternate and are replaced at somewhat different stages. If this is true, there are three points which call for some comment.

In the specimen B the first, third, and fifth teeth are well developed while the second and fourth are being replaced. There is, however, a replacing-tooth at the base of the third. The fact that this tooth is only just appearing while the second and fourth replacing-teeth are partly erupted suggests that the replacement of the, in this specimen, odd numbered teeth must have followed quickly on the replacement of the even numbered.

In the third specimen the most outstanding feature is the apparent absence of replacing-teeth from the empty alveoli, a condition which might be claimed to show that the loss of certain teeth was purely fortuitous and had nothing to do with replacement. We know, however, that during the replacement of a tooth the bone is resorbed around the roots and that the replacing-tooth moves down into an enlarged alveolus. In any animal which died during this process there would be a greater chance of the loss of a replacing-tooth than of those teeth which are held in the jaw in a normal manner.

It is also necessary to explain the fact that it is the odd numbered teeth which are being replaced in the anterior region, while the even numbered are being replaced in the posterior region. If, as seems to be indicated by the second specimen, the replacement of the second series follows very shortly after the first series, it is not unreasonable to suppose that the replacement of the first series (in this specimen the even numbered teeth) may not have been completed throughout the jaw before the replacement of the alternate series commenced.

VII—Discussion

The evidence on tooth replacement afforded by the material described may be summarized as follows :—

(1) In the cynodont *Thrinaxodon liorhinus* the first incisors and the canine teeth are replaced while the animal is young.

(2) In the cynodonts *Parathrinaxodon proops*, *Thrinaxodon liorhinus*, and *Tribolodon frerensis* the post-canine teeth belong to two series. The members are situated alternately in the jaw and are replaced at different stages. There is evidence of only one replacement of each tooth.

(3) The replacement of alternate teeth at different stages seems to have been present in the most primitive of the mammal-like reptiles (the Pelycosaurs) as is shown by three pieces of jaws of *Dimetrodon*.

That this " distichical " condition is typical of the non-mammal-like reptiles has already been shown by Bolk (1922). Bolk called attention to the fact that the tooth germs of living reptiles are situated alternately on the buccal side and at the base of the dental lamina, and called the two types "parietal" and "terminal". The row of parietal tooth germs he called the "exostichos", the row of terminal germs the "endostichos". He showed that the teeth of the exostichos always appeared in an embryo before those of the endostichos, but that they were not replaced by the latter, the teeth of the two rows being functional at the same time, each being replaced by further members of its own "family".

It is of interest at this point to consider the condition found in the earlier vertebrates. There is nothing known about the tooth-replacement in the Cotylosaurs, among which forms the common ancestors to the mammal-like and "true" reptiles may be sought. But for the forms which may be considered to be ancestral to all reptiles, the early amphibia, we have the work of Professor D. M. S. Watson.

In his description of the teeth of the Carboniferous Labyrinthodonts (the Embolomeri) Watson (1926) says "They are attached to their supporting bones by fusion, and are shed by resorption of the bone. When so lost they are replaced by a new tooth, which has been developing in a neighbouring emplacement. The whole dentition thus consists of a series of pairs of teeth which are functional alternately." Such a condition might be expected to occur in an animal in which the teeth were distichic if the development of the replacing-tooth was a very slow process, or if the life of a tooth was very short. The very great similarity between the dentitions of the primitive Crossopterygian fishes (the Osteolepids) and the Labyrinthodonts, in regard to both the structure of the teeth and the presence of large tusks by the side of which are pits for replacing-teeth (*idem*), make it almost certain that the Osteolepids also had the teeth in two alternating series.

It seems, therefore, that distichical arrangement of the teeth was inherited by both mammal-like reptiles and true reptiles from the earliest tetrapods and the primitive bony fishes. This conclusion supports Bolk's suggestion that the condition is inherited from very primitive ancestors and may be seen in the arrangement of the teeth in modern sharks.

The question of the origin of the mammalian type of tooth-replacement may now be considered.

Bolk claimed that the milk and permanent dentitions of mammals do not represent two surviving members of each reptilian tooth "family", as was commonly believed, but that the milk teeth are the sole surviving members of the exostichos while the permanent teeth represent the survivors of the endostichos. This condition, in which the members of the two rows were not functional at the same time, Bolk called "chorisstichic," and believed it to be the result of an increase in the time interval between the eruption of the two rows. In support of the view he pointed out that the time interval between the eruption of the two sets differed very greatly among various reptiles; and that in the mammals, while the interval is very considerable, the germs of both sets are formed very early.

The establishment of the distichical condition in the post-canines of the described cynodonts, together with the fact that there is a very considerable interval in time between the replacement of the two sets in *Thrinaxodon*, adds some confirmation to

Bolk's views. In the maxillae, at least, there appear to be only two members of each tooth family left in place of the large numbers typical of reptiles. Carried one stage further this reduction would mean that such an animal would erupt one set of teeth and then, later, another set between the members of the first. If at this stage the teeth became crowded, possibly by increase in size and complexity, the second set might well replace the first instead of erupting between them.

It is still necessary to account for the apparent double replacement in the incisors in *Thrinaxodon*. While this might well be explained by the retention of an extra member of each "family", it should also be remembered that the "reptilian" method of replacement, when the replacing-tooth appears from below and inside the older tooth, is only possible in a tooth in which the pulp cavity has remained widely open. The development of incisor teeth in which the root is nearly closed, as in *Thrinaxodon*, would mean that successive members of each tooth "family" would have to erupt at the side of their predecessors, a condition observed in this genus and also in *Galesaurus planiceps*, Owen (Parrington, 1934). It is thus impossible to distinguish members of the exostichos and endostichos in the incisors by the manner of their eruption. Now, while the first upper incisor is being replaced in the very young *Thrinaxodon*, specimen B, it is the second which is apparently erupting in the adult, specimen H, and this apparent double replacement in the incisors may well be due to a very considerable interval between the replacement of the exostichos, of which row the first incisor would be a member, and of the endostichos which would include the second incisor.

It is of interest at this point to consider the question of tooth replacement in the remaining Triassic Theriodonts.

The majority of the remaining Cynodonts have a gomphodont dentition (*Diademodon*, *Trirachodon*, etc.) and, as has already been pointed out, evidence of actual replacement in these forms is very rare. It is certain, however, that the teeth were subject to considerable wear, probably by an antero-posterior movement of the lower jaw. If the alternate teeth had been replaced at different times in the manner of *Thrinaxodon*, it would seem likely that some specimens would have been found by now which would have demonstrated this distichical condition by the different state of wear of alternate teeth. The absence of such specimens, and the occurrence of specimens which show a steadily progressive decrease in the amount of wear of the teeth towards the back of the jaw, seem to indicate that in these forms the mammalian chorisstichic condition had been reached, possibly as the result of the relatively large size of the teeth.

Watson (1931) has shown that in the early Bauriamorph *Ericiolacerta parva* the replacement is of the reptilian type, because damage to the crown of one of the cheek teeth exposed a successor immediately below it. He has also showed that there is reason to suppose that the whole of the Bauriamorpha were the descendants of the Scolaposaurid Therocephalia. However, while the condition in *Ericiolacerta* may have been typical of the group, a more advanced condition could have been present in the gomphodont forms as in the gomphodont cynodonts.

A further, and very important problem, on which some light has been thrown, is that of the possibly compound nature of mammalian teeth.

Bolk studied the structure of the enamel organs of mammalian and reptilian teeth, and came to the conclusion that the enamel organs of mammalian teeth are compound. He reasoned—against the weight of palaeontological evidence—that the teeth were therefore also compound, each being built up of two elements homologous with a reptilian tooth. The fact that in the early cynodonts there is a true reptilian succession of complex teeth seems evidence against such a view. But it is still possible to argue that the fusion of pairs of members of each family of reptilian teeth could have taken place at an earlier stage, and thus these reptiles also possessed " dimer " teeth.

I am greatly indebted to Dr. W. D. Lang and Dr. W. E. Swinton of the British Museum (Natural History) for the loan of the three specimens of *Thrinaxodon liorhinus* in their charge, and to Professor D. M. S. Watson for the generous loan of his *Dimetrodon* material and advice on the question of the restorations of *Nythosaurus* and *Thrinaxodon*. And finally I would like to take this opportunity of thanking the Balfour Managers for their sympathetic interest during my tenure of the Studentship, particularly in regard to my expedition to the Ruhuhu Valley in Tanganyika.

VIII—References

Bolk, L., 1922. 'J. Anat.,' vol. **77**, pp. 55–75.
Broill, F., and Schröder, J., 1934. 'S.B. Bay. Akad. Wiss.,' pp. 163–177.
Broom, R., 1913. 'Bull. Amer. Mus. Nat. Hist.,' pp. 465–468.
——, 1930. 'Phil. Trans.,' B, pp. 345–371.
——, 1932. "The mammal-like reptiles of South Africa." London.
Haughton, S. H., 1924. 'Ann. Transv. Mus.,' pp. 74–92.
——, 1932. 'Quart. J. Geol. Soc. Lond.,' pp. 634–671.
Parrington, F. R., 1933. 'Ann. Mag. Nat. Hist.,' pp. 617–24.
——, 1934. 'Ann. Mag. Nat. Hist.,' pp. 38–60.
——, 1935. 'Ann. Mag Nat. Hist.,' p. 400.
Seeley, H. G., 1894. 'Phil. Trans.,' B, vol. **185**, pp. 987–991.
Stockley, G. M., 1932. 'Quart. J. Geol. Soc. Lond.,' pp. 610–622.
Sushkin, P. P., 1927. 'Int. Cong. Zool.,' pp. 804–808.
Watson, D. M. S., 1920. 'Ann. Mag. Nat. Hist.,' pp. 506–524.
——, 1926. 'Phil. Trans.,' B, p. 193.
——, 1931. 'Proc. Zool. Soc. Lond.,' pp. 1164–1205.