PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Tooth Replacement in Mammal-Like Reptiles of the Suborders Gorgonopsia and Therocephalia

K. A. Kermack

Phil. Trans. R. Soc. Lond. B 1956 **240**, 95-133
doi: 10.1098/rstb.1956.0013

TOOTH REPLACEMENT IN MAMMAL-LIKE REPTILES OF THE SUBORDERS GORGONOPSIA AND THEROCEPHALIA

By K. A. KERMACK
Department of Zoology, University College London

(*Communicated by P. B. Medawar, F.R.S.—Received* 3 *January* 1956—
Revised 7 *March* 1956)

[Plates 6 to 8]

CONTENTS

The Mammalia are characterized by a limited degree of tooth replacement. This condition must have arisen from that typical of primitive reptiles, where the teeth are continually replaced throughout the animals' life. The therapsid reptiles include the ancestors of the mammals, and it is here that the origin of the mammalian mode of tooth succession is to be sought. The present paper describes an investigation of two groups of the more primitive therapsids, the Gorgonopsia and the Therocephalia, which lie close to the main line of synapsid evolution. The investigation involved the use of the recently developed methods of chemical preparation, along with X-ray examination of the material so prepared.

In the Gorgonopsia and in the Therocephalia all the teeth were replaced at least once. Thus, none of their teeth can be equated with the molars of placental mammals, which are never replaced. Replacement of the incisors occurred at least twice and of the upper canines at least four times. Thus the condition in the mammals, where no tooth is replaced more than once, had not yet been achieved.

Except in the upper canines there was no *functional* distichial replacement, each tooth being immediately replaced in function by the next generation of its own tooth family. The only sign of distichism is the tendency of the functional teeth to fall into two alternating groups in some cases,

the members of each such group being replaced at about the same time. There are two alveoli in each maxilla for the upper canines. In the most primitive Therocephalia, and in the Gorgonopsia, there is only one functional canine on each side of the upper jaw, and this tooth is borne alternately by each of the pair of alveoli. Thus there is functional distichial replacement, since each canine is immediately replaced by a member of the tooth family of the other alveolus. This distichism is secondary, the ancestral Pelycosauria having two functional canines in each maxilla, each being immediately replaced by the next member of its own tooth family. Thus in the ultimate descendants of these theriodonts, the Mammalia, the deciduous and permanent teeth are almost certainly members of the same tooth family, with a possible exception in the case of the upper canines. The theory of Bolk (1922), that the two dentitions of the mammals are homologous with the alternating dentitions of primitive tetrapods, is unacceptable.

The upper, and in one genus at least (*Notosollasia*) the lower, canines are shed by the erosion of the tooth through its cervix, the root being retained within the alveolus. The root is then penetrated by spongy bone and resorbed, the resorption starting at the cervix and proceeding along to its apex. This method of shedding the teeth appears to be unique.

In the majority of the specimens the functional canine lies in the anterior alveolus, the posterior alveolus being filled with a plug of spongy bone, which often contains the remains of an old root undergoing resorption. In these examples there are no replacing canines, and replacement in the other teeth is limited or absent. This suggests that after a certain time in the animal's life tooth replacement ceased, the permanent upper canines being always borne by the anterior alveoli.

In this limited tooth replacement the Gorgonopsia and the Therocephalia show an analogy with the mammals. The number of teeth is not fixed; for example, there may be seven incisors on one side and six on the other, or four cheek teeth on one side and five on the other. Thus tooth number is not a good taxonomic character.

I. Introduction

The limited and definite tooth replacement found in mammals is one of their most characteristic features. The placentals replace all except the molars, the marsupials only the third milk molar, and in each of those subclasses replacement takes place once and once only during the life of the animal. Jepson (1940) has shown that in the multituberculates there was probably no tooth replacement, while Kühne (1956) has shown the same to be true in the Tritylodontidae—a family of advanced mammal-like reptiles.

Until about thirty years ago it was assumed without question that the deciduous and permanent teeth of a mammal were formed by the abbreviation of the continuous series of teeth which follow one another in each alveolus of a typical reptile.

Bolk (1922) challenged this. From the study of the embryology of recent reptiles, he concluded that the tooth germs in these animals are situated alternately at the base of the dental lamina and on its buccal side. He called the former 'endostichos' and the latter 'exostichos'. Each set of tooth germs gave rise to functional teeth. Parrington (1936*a*, *b*) showed that the teeth were replaced in alternate pairs along the jaw in some mammal-like reptiles (a pelycosaur and three cynodonts) and in two mosasaurs. This he interpreted as the replacement of the exostichos and endostichos occurring at different times, and this interpretation is probably the correct one. Alternate or 'distichial' replacement is common to many rather primitive vertebrates, being found in the labyrinthodont Amphibia and in the osteolepid fish (Watson 1926) as well as in primitive reptiles.

Bolk carried his theory further. He postulated that the mammalian deciduous teeth were the sole surviving members of the exostichos, whilst the permanent teeth were the survivors of the families of endostichos. Thus, each deciduous tooth with its permanent successor formed a distichial pair and the mammalian type of dentition has evolved by the effective halving of the reptilian dentition. If this change took place after the teeth had become differentiated into incisors, canines and cheek teeth one would expect to find somewhere in the fossil record an animal with a dental formula of $\frac{8.2.16}{8.2.16}$ as a minimum. The differentiation of the teeth had occurred by the middle Permian, after which no mammal-like reptile had as many teeth as this dental formula would require. This important argument against the extension to Bolk's theory is due to Parrington (1936*b*), who showed distichial replacement still taking place in the Triassic cynodonts. He also mentions that the occurrence of two functional upper canines on each side in some mammal-like reptiles (pelycosaurs and early Therocephalia) may offer some support to the theory. However, I know of no skull of a mammal-like reptile with more than one functional canine on each side of the lower jaw.

Clearly, more information as to the mode of tooth replacement of mammal-like reptiles was needed. The preparation of the fossil material produces the main difficulties as the bones and teeth are often found in a very hard and intractable matrix, in which the preparation of fine detail by mechanical means is difficult, while to examine the dentition properly, the lower jaw needs to be taken off the skull. Recently, an important and fundamental advance in the techniques of preparation available to the vertebrate palaeontologist has been made by Rixon (1949) and Toombs (1948). Weak acids are used to break down the matrix, and the bone, consequently exposed, is strengthened by impregnation with a suitable plastic.

This paper confines itself to accounts of tooth replacement in the more primitive theriodont reptiles, the Gorgonopsia and Therocephalia, and in a later paper I hope to describe that found in their more advanced successors, the Cynodontia and Bauriamorpha.

II. Material and methods

(1) *Material*

Sixteen specimens were examined: ten gorgonopsids and six therocephalians. Of these sixteen specimens, nine were specially prepared for this work, eight chemically (R 339, R 855 and R 2581 by Mr Rixon, and R 855*a*, 337, 79, R 393 and 100 by myself) and one (R 256) by sectioning. Of the remaining seven, three (R 121, R 49396 and R 4097) had previously been sectioned, and two (R 5747 and R 5699) had been extensively broken up at some time and yielded valuable information on being unstuck.

The ten gorgonopsids were:

(*a*) Three snouts in the collection of the British Museum. Two (R 339 and R 855*a*) are examples of *Aelurosaurus felinus*, one (R 855) is the closely related *Aelurosauroides watsoni*. They came from the Gouph district, Beaufort West, South Africa (probably *Endothiodon* zone) and were obtained by purchase from T. Bain Esq., in 1880.

(*b*) The complete skull of a small, unnamed gorgonopsid, allied to *Aelurosaurus*, lent by the Transvaal Museum (serial number 337), and probably an *Endothiodon* zone form. There is no locality data, beyond the fact that it was found in South Africa.

(*c*) The snout of a large gorgonopsid from the collection of Mr F. R. Parrington. He tells me (1954) that he has identified it as *Dixeya quadrata* (Haughton 1926). It bears the reference number 79, and came from Kingori, Tanganyika—probably from the *Cistecephalus* zone.

(*d*) The type of *Gorgonops torvus* (registered number R1647) in the British Museum. It comes from the *Endothiodon* zone of Mildenhalls, near Fort Beaufort.

(*e*) The type of *Cynariops robustus* (Broom 1925). This is in the British Museum (R5743). It comes from the top of the *Endothiodon* zone, at Biesjespoort Station, South Africa.

(*f*) The skull of a gorgonopsid allied to *Scylacops capensis*. This is in the collection of Professor D. M. S. Watson, and bears the number R121. It was collected at Wellwood, Graff Reinet, South Africa (*Cistecephalus* zone).

(*g*) A skull of *Scymnognathus whaitsi* in the British Museum (R49396). It comes from the *Endothiodon* zone of Beaufort West, South Africa. This specimen is described by Watson (1921) and Boonstra (1934*a*) under the number R49369. This was incorrect, and the catalogue number is as given above.

(*h*) Part of the right side of the snout and lower jaw of a large gorgonopsid from the collection of Professor D. M. S. Watson. This specimen was collected from Murraysborg commonage, South Africa, in the *Cistecephalus* zone. It bore the reference number R256.

The six therocephalians were:

(*i*) A skull of the large therocephalian *Trochosaurus major* in the British Museum (R5747). There are no locality data for this specimen, except that it came from South Africa. However, *Trochosaurus* is one of the most primitive of the Therocephalia, and other specimens are known which have come from the *Tapinocephalus* zone (Broom 1915).

(*j*) Two snouts of *Pristerognathus polyodon* (Seeley 1894). One (R2581) is the type in the collection of the British Museum, and it comes from the *Tapinocephalus* zone of Cypher, near Tamboerfontein, South Africa. The other specimen, which is almost certainly the same species, had been presented to Professor Watson with no locality data. It bears the number R393.

(*k*) The snout of *Cynariognathus platyrhinus* Broom, in the British Museum (R4097). It comes from the *Tapinocephalus* zone of Uitkyk, Prince Albert, South Africa.

(*l*) The skull of *Notosollasia laticeps* (Broom 1925). This specimen is in the British Museum with the number R5699. It was collected by Dr Broom from the *Cistecephalus* zone near Bethesda Railway Station, South Africa.

(*m*) The snout of a large therocephalian collected by Mr Parrington. It may be referred provisionally to the genus *Whaitsia*, and comes from the same locality and zone as the *Dixeya* (79) mentioned above. It bears the number 100.

(2) *The technique of preparation*

The only novel technique employed was the preparation of some of the specimens chemically. A brief description of the method will be given.

The technique of preparation was basically the same for all the eight specimens successfully treated. The superficial dirt was first removed by washing in a solution of a synthetic detergent ('Teepol'), and the specimen was thoroughly dried. All exposed bone was coated with a solution of the impregnating plastic. At first a thin solution of polystyrene dissolved in ethyl acetate was used, but later this was replaced by polybutylmethacrylate dissolved in methyl ethyl ketone.* The latter substance gave a tougher, less brittle film than the polystyrene. The plastic was thoroughly dried out in an oven at a temperature not exceeding 80° C. The specimen was then immersed in the acid bath. This was originally a 20 % solution of acetic acid in water, but, as a 10 % solution of formic acid was found to be more active and to have a less unpleasant smell, the latter is now used. The time of immersion in the acids varied, but was normally 24 hours. The specimen was then thoroughly washed, either in running water or in constant changes of water. Less washing seems necessary if formic acid is used rather than acetic. Inadequate washing was shown by the appearance of a white deposit when the specimen dried. The appearance of this deposit necessitated further washing. When this was complete the specimen was thoroughly dried in an oven at between 50 and 80° C.

Further treatment depended on the nature of the matrix in each individual case. This varied considerably, specimens 337 and R 393 being at one extreme. In these the matrix was composed partly of sandstone, which broke up in the acid slowly and with difficulty; and partly of a very hard grey shale which remained unattacked by the acid. This shale had to be removed by means of a Stensio hammer, assisted by the cautious use of diamond-cutting wheels and burrs. In some cases the shale actually adhered to the surface of the bone, and here it was impossible to preserve the surface of the latter. Specimen R 393 was treated with hot acetic acid on a water-bath, this treatment being continued for many days at a time. This broke up matrix which was unaffected by the cold acid, possibly due to a solvent action of the hot acid upon iron salts.

Specimen 79 was the exact opposite of the above two. Here the matrix was an homogeneous brown sandstone, which broke up readily in the cold acid. All the mechanical preparation needed was the gentle scraping away, with a needle, of the residual sand left after the acid had done its work. It thus proved possible to preserve in this specimen the thin vertical bony septum rising from the vomer, although it is no thicker than a piece of writing paper.

The other five specimens were intermediate in difficulty between the first two and specimen 79. Along with a greyish brown sandstone, readily attacked by the acid, a hard grey shale was present. Although this was unattacked by the acid, it did not adhere to the actual surface of the bone, and so could be removed mechanically without damage to the latter.

After mechanical preparation was complete, all exposed bone was cleaned with a brush dipped in ethyl acetate or dichlorethylene, and then coated with a thin solution of the plastic used initially. Small breaks were repaired with a thicker solution of the same plastic, and larger ones with a solution of polymethylmethacrylate ('Perspex') in chloroform or dichlorethylene. The specimen was again placed in the oven to allow the plastic to harden thoroughly, this taking considerably longer for polybutylmethacrylate than for polystyrene. The specimen was then replaced in the acid bath and the process repeated. This went on until no more matrix could be safely removed—ideally until no more matrix was left.

The specimens treated with polystyrene were then brushed over with the following

* The polystyrene used was the Monsanto Chemicals Limited's 'Lustrex'; the polybutylmethacrylate was obtained from Vinyl Products Limited as a thick solution—Vinalak 5909 M.E.K.

solution: 2 g of celluloid dissolved in 100 ml. of the following solvent—60 % acetone, 30 % benzene and 10 % amyl acetate. This replaces some of the polystyrene by celluloid as the impregnating plastic. This was thought necessary owing to the rather brittle nature of the polystyrene film, and its uncertain ageing properties. The specimens prepared with polybutylmethacrylate required no after-treatment.

The chemically prepared specimens could be X-rayed by the usual medical techniques. They were more opaque than similar recent material, but gave fairly good pictures.

III. Description of specimens

In the descriptions of teeth in this paper the terms used in human anatomy will be employed, being unambiguous. The surface of the tooth which is directed outwards, towards the lips, is the *buccal* surface, and that which is directed inwards, towards the tongue, the *lingual*. The interstitial surface which faces towards the symphysis between the premaxillae or the dentaries (generally facing more or less forwards) is the *mesial* surface of the tooth; while that which faces backwards towards the jaw articulation is its *distal* surface. The surface of the tooth which opposes its fellow in the other jaw in biting is its *occlusal* surface. Root and crown join at the *cervix*, while the *apex* is the end of the root furthest from the crown.

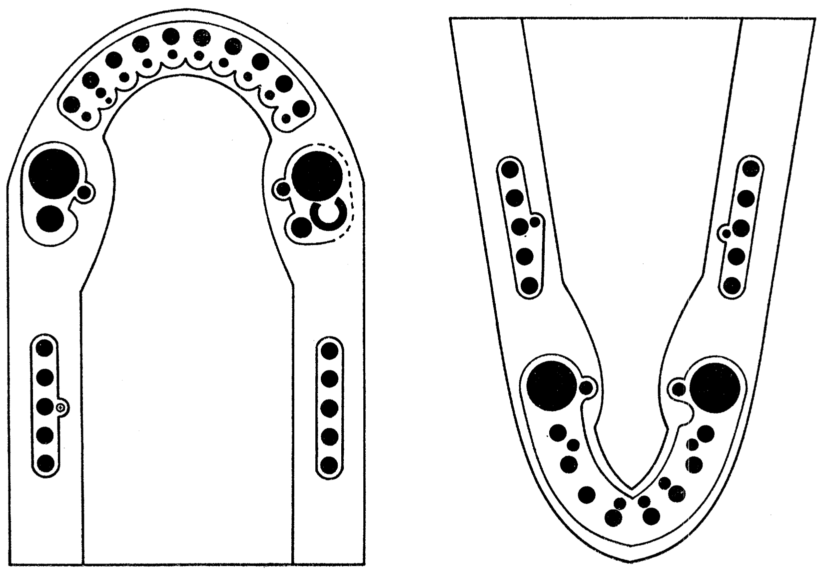
(a) *Gorgonopsia*

(1) *Aelurosaurus felinus* Owen (R 339)

This specimen is the type (Owen 1881) and consists of a snout and associated lower jaw, and shows the complete dentition. There are five upper incisors on each side of the jaw, laterally compressed and with probably a serrated edge only along their distal margins. All have replacement teeth coming through on the lingual side of those now functional. These replacement teeth are set in the same alveoli that bear the functional teeth, each alveolus being considerably extended lingually to make this possible (figure 1 *a*). This enlargement of the alveoli results in the functional teeth being set loosely in their sockets. The replacements to the fourth incisor on each side are much larger than the rest, and lingual to the fourth right replacement incisor can be seen the tiny tip of its successor, still within the same alveolus. It is therefore possible to see, not only the immediate replacement to the tooth now functional, but also the next member of the same tooth family, which will succeed in its turn the first replacement tooth.

There is only one functional canine on each side of the upper jaw. The canines are long, laterally compressed teeth, with a marked backward curvature. The distal edge of each is sharp and serrated. The right canine is more worn than the left, and probably erupted some time before the latter. Behind the alveolus that bears the functional tooth, there is another of the same size, on both sides of the jaw, although there seems to be no dividing wall of bone between the two alveoli. On the right this second alveolus bears the tip of a tooth which must be the replacing canine. X-ray photographs show that the root of this tooth extends up dorsally behind the root of the functional canine, both roots being of the same size. But, while the root of the functional canine is closed at its apex, that of its replacement is wide open, showing that it is the root of an actively growing tooth. Figure 1 *a* shows the tip of another tooth in a little lingual extension of the alveolus which bears the functional tooth. This is much smaller than that of the replacing canine in the posterior alveolus and can only be the successor to the posterior replacing canine.

On the left-hand side of the skull a considerable amount of damage was done by Owen's preparator when he opened up the root of the functional canine, fortunately, without destroying any vital structure. Lying in the posterior alveolus is the root of a tooth. The crown of this tooth appears to have been shed naturally and not broken off accidentally. This is, to some extent, confirmed by the use of X-rays; the functional tooth has a root which is wide open apically, while that of the old tooth behind it is completely closed. This



R L R L

a *b*

FIGURE 1. (*a*) Upper, and (*b*) lower dentitions of specimen R 339 (*Aelurosaurus felinus*). The following symbols are employed throughout: ● = tooth actually present in specimen; ⊕ = empty alveolus from which tooth presumably fell after death; **O** = old canine root; ▧ = spongy bone.

condition would be expected if the functional canine had only just erupted at the time of the animal's death. Lingual to the old root, and in the same alveolus, can be seen the tip of a replacement canine. This tooth is smaller than that which is coming through in the posterior alveolus on the right. Lingually to the left functional canine, and breaking through the medial wall of its alveolus, can just be seen the tip of a still smaller tooth.

The story is here quite clear: these upper canines are showing the 'distichial replacement' of Bolk. There are two alveoli, the one behind the other, each with its own tooth family, and the functional canine is borne by these alveoli alternately. In each alveolus the members of its tooth family replace one another in exactly the same way as in the incisors—a tooth's successor appearing lingually to it. In the present specimen the anterior alveolus bears the functional canine on both sides of the jaw. On the right the immediate replacement to the functional canine can be seen in the posterior alveolus. Lingually to the functional tooth is the next member of its own tooth family, which will replace the tooth of the posterior alveolus in its turn. On the left the picture is essentially similar.

In the posterior alveolus is the remains of the tooth which was replaced by that now functional. Lingually to this old root can be seen the next member of the posterior tooth family, which will move buccally and replace the functional canine when the old root has been completely resorbed. Lingually to the functional tooth in the anterior alveolus can be seen the next member of its own tooth family, which will become functional in its turn, after the next tooth of the posterior family. The differences between the degree of development of the replacing teeth on the two sides of the jaw would be explained if the left functional canine had only just come into use on the death of the animal, while that on the right had been functional for a considerable time.

There are five functional cheek teeth on each side of the upper jaw. They are conical, sharply pointed teeth, rather transversely flattened and with serrations along their distal borders. The two most posterior are shorter than the rest, and give the appearance of having only recently erupted. This is particularly striking on the left. On this side there is no sign of any replacement teeth, while on the right there is a small lingual extension of the alveolus of the third tooth, which may have borne a replacement tooth.

The lower incisors, of which there are four on each side of the jaw, are well-flattened, leaf-shaped teeth, with serrations along both their mesial and distal edges (figure 1*b*). There appear to be no distinct alveoli at all, all the teeth lying rather loosely in a single trough. On the right, the first has a replacement tooth coming through lingually, and there is another lingual to the third and fourth; while on the left, the first and second have similar replacement teeth, and another lies lingual to the third and fourth.

There is one functional canine on each side of the lower jaw. Both are unworn, and therefore erupted only shortly before the death of the animal. They are long, pointed teeth with a slight backward curve, and they bear a serrated edge both linguo-mesially and distally. They show marked lateral flattening. Lingual to each, and in the same alveolus, can be seen the tip of a replacing tooth.

There are five functional cheek teeth on each side of the lower jaw. They are flattened, sharply pointed teeth, with a serrated border both mesially and distally. On the right the crown of the third has been broken off, and there is the tip of a replacement tooth coming through lingually to it in the same alveolus. On the left the tip of a replacement tooth can be seen coming through between and lingually to the second and third functional teeth. It lies in the same general alveolus.

Thus there is clear evidence of replacement in all except the upper cheek teeth, where it is probable but not certain. In the upper canines this replacement is distichial, two adjacent alveoli being responsible for a single functional tooth. In the case of all the other teeth the functional tooth is replaced directly by a member of its own tooth family, and distichial replacement does not take place.

(2) *Aelurosaurus felinus* Owen (R 855 *a*)

This specimen, referred by Lydekker (1890) to the genus *Aelurosaurus* (with no specific attribution) is almost certainly *Aelurosaurus felinus*. It consists of a snout and associated lower jaw and shows the complete dentition.

There were five functional upper incisors on each side. These teeth are so damaged by weathering that little can be said about their shape, but there is no reason to suppose that

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

they differed from those of the other specimen of *A. felinus* (R 339). On the right the tips of replacing teeth are visible lingually to the first, third and fifth (figure 2*a*; figure 18; figure 20, plate 6). These replacement teeth are borne in the usual lingual extensions of the alveoli which bear the functional teeth. Behind the second and fourth functional teeth, which are still in process of eruption, are two such alveolar extensions, from which the successional teeth probably dropped out subsequent to the animal's death. On the left there are similar replacement teeth situated lingually to the second, third and fifth functional teeth. The alveolus of the first tooth is very badly damaged, and may have borne a replacement tooth, while there is a large, empty alveolar extension lingual to the fourth, from which the replacement tooth probably has fallen out.

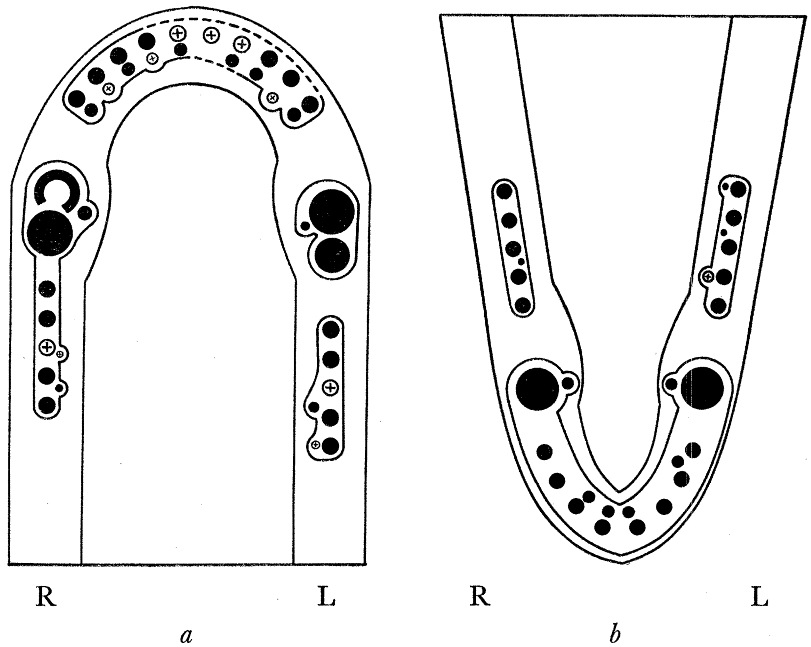


FIGURE 2. (*a*) Upper, and (*b*) lower dentitions of specimen R 855*a* (*Aelurosaurus felinus*).

There is only one functional canine on each side of the upper jaw. On both sides, however, there are two alveoli, one posterior to the other, just as in the preceding specimen (R 339). On the right it is the posterior alveolus which bears the functional canine. This tooth is compressed and slightly curved, with a serrated distal edge. X-ray photographs show that its root is wide open apically, and from its generally unworn appearance it is probably only recently erupted. The anterior alveolus contains the root of a tooth of which the crown has been shed. The lower end of this root is dorsal to the lower border of its alveolus, thus making it improbable that the crown was broken off accidentally. The root has suffered considerable resorption posteriorly, and X-rays show that the pulp cavity is quite closed at the apex. Lingually to this root, and lying within the same alveolus, can be seen the tip of a replacing tooth. On the left the functional canine is in the anterior alveolus, and the X-ray shows a root in process of closing. Therefore this tooth probably erupted before its fellow on the right. The posterior alveolus contains a well-developed replacement tooth. Lingual to the functional canine can be seen another replacement tooth, much smaller than that in the posterior alveolus (figure 21, plate 6).

There were five functional cheek teeth on each side of the upper jaw. These teeth seem to have been implanted rather loosely in their sockets, and lie in a trough as the bony septa between the individual alveoli are absent. The teeth are sharply pointed and laterally compressed, and with a serrated distal margin. On the right the tip of a replacement tooth can be seen lying between, and lingual to, the fourth and fifth functional teeth. Lingually to the third was a circular extension of its alveolus from which the replacement tooth had probably fallen out. The tip of a replacement tooth is visible lying lingual to the fourth and in an extension of the alveolus of the latter; and there is a similar extension lingual to the fifth. This is now empty, the replacement tooth having fallen out.

There are four lower incisors on each side of the jaw (figure 2*b*; figure 22, plate 7). They are rather flattened, pointed teeth, with serrations along their mesial and distal margins. They all lie in an open trough, no individual alveoli being visible. On the right of the jaw replacement teeth are visible lingual to the first and second functional teeth; and from the large open space behind the third and fourth, others may have dropped out. On the left there is a replacement tooth lingual to the first functional tooth, and another between and lingual to the third and fourth. Replacement teeth for the other left incisors may have fallen out after the death of the animal. There is ample room for them in the large alveolar space.

There is one functional canine on each side of the lower jaw. They are long, compressed and backwardly curved teeth, and bear a serrated edge both linguo-mesially and distally. The right tooth is fresh and quite unworn, and can only recently have erupted. This is confirmed by X-ray photographs of its root—the latter being wide open apically. The left tooth is worn, and shows that the wear took place across the anterior face of its tip. X-rays show its root to be almost closed. Thus this left tooth must have erupted a considerable time both before the eruption of its fellow on the right and before the death of the animal. On each side of the lower jaw the tip of a replacement tooth can be seen coming through lingual to the functional canine, and lying within the same alveolus (figure 2*b*; figure 22, plate 7). The replacement tooth on the left is slightly larger than its fellow on the right.

There were five functional cheek teeth on each side of the lower jaw. They are pointed and slightly flattened teeth, with a mesial and a distal serrated edge. There appear to be no

---

Description of plate 6

Figure 20. Palatal view of specimen R 855*a* (*Aelurosaurus felinus*). 1, functional canine; 2, root of old canine; 3, replacement incisors; 4, lingual extension of alveolus from which a replacement tooth has probably fallen out; 5, functional canine; 6, tooth which will immediately succeed the canine now functional; 7, deep channel formed by vomer and palatine.

Figure 21. Lingual view of left upper canine of specimen R 855*a*. 1, functional canine in anterior alveolus; 2, replacement canine *A*. This is the oldest member of the tooth family of the posterior alveolus and would have been the successor to the functional canine; 3, empty lingual extension of alveolus from which a replacement tooth has almost certainly fallen out after death; 4, replacement cheek tooth; 5, floor of respiratory channel formed by palatines and vomer; 6, replacement canine *B*. This is the next tooth of the family of the anterior alveolus and would succeed replacement canine *A* as the functional canine.

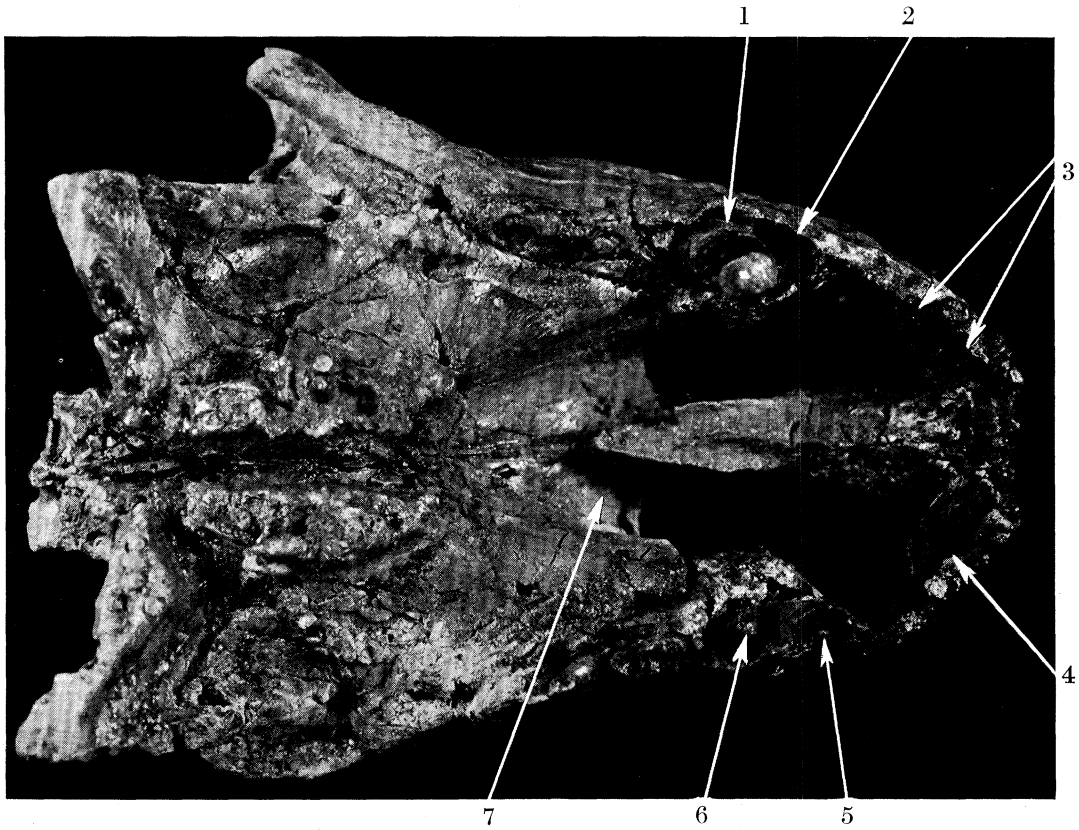


FIGURE 20

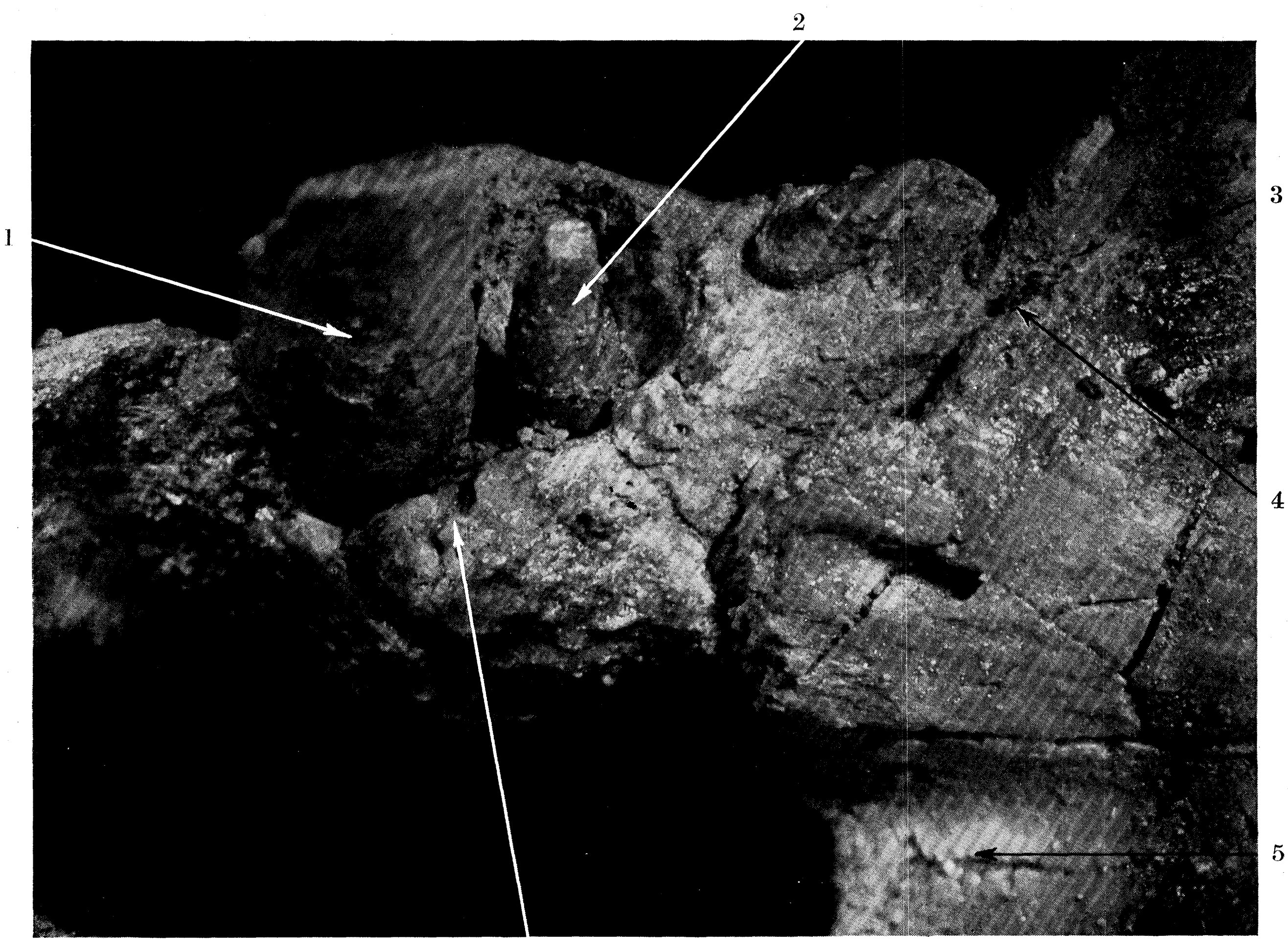


FIGURE 21

(*Facing p.* 104)

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

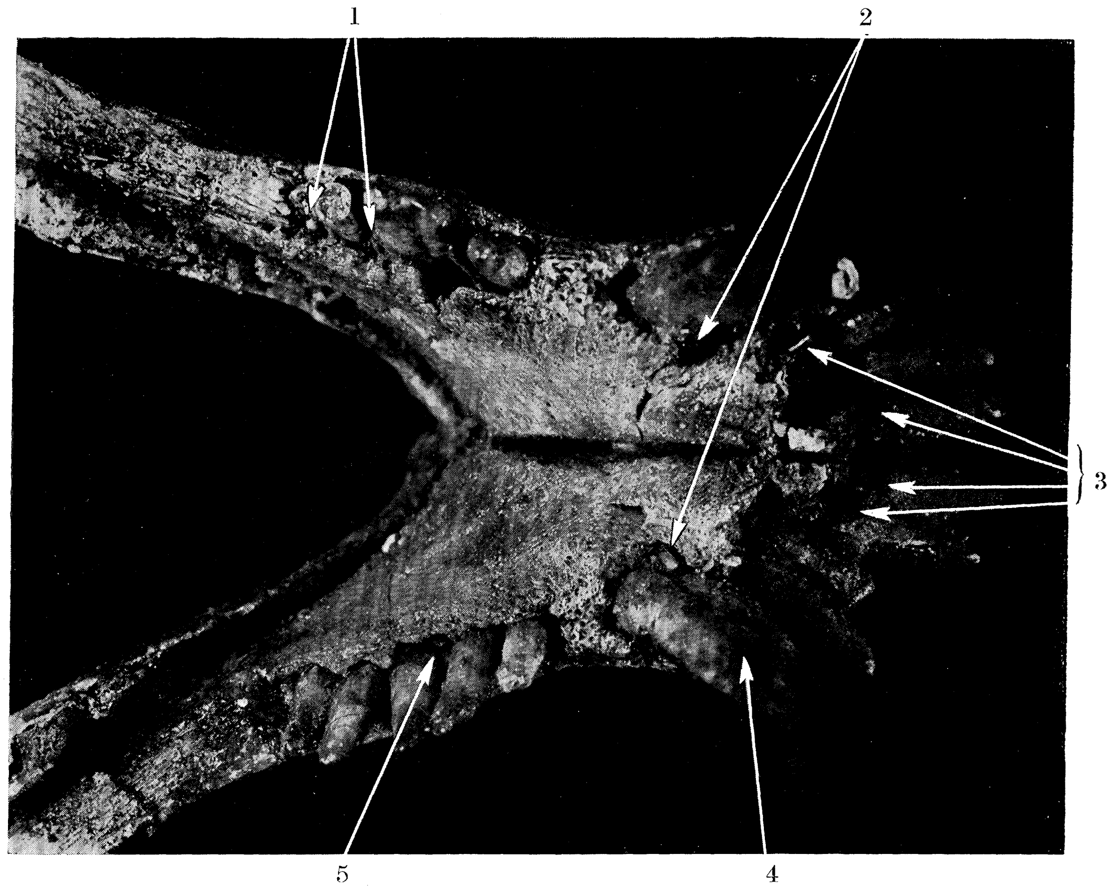


FIGURE 22

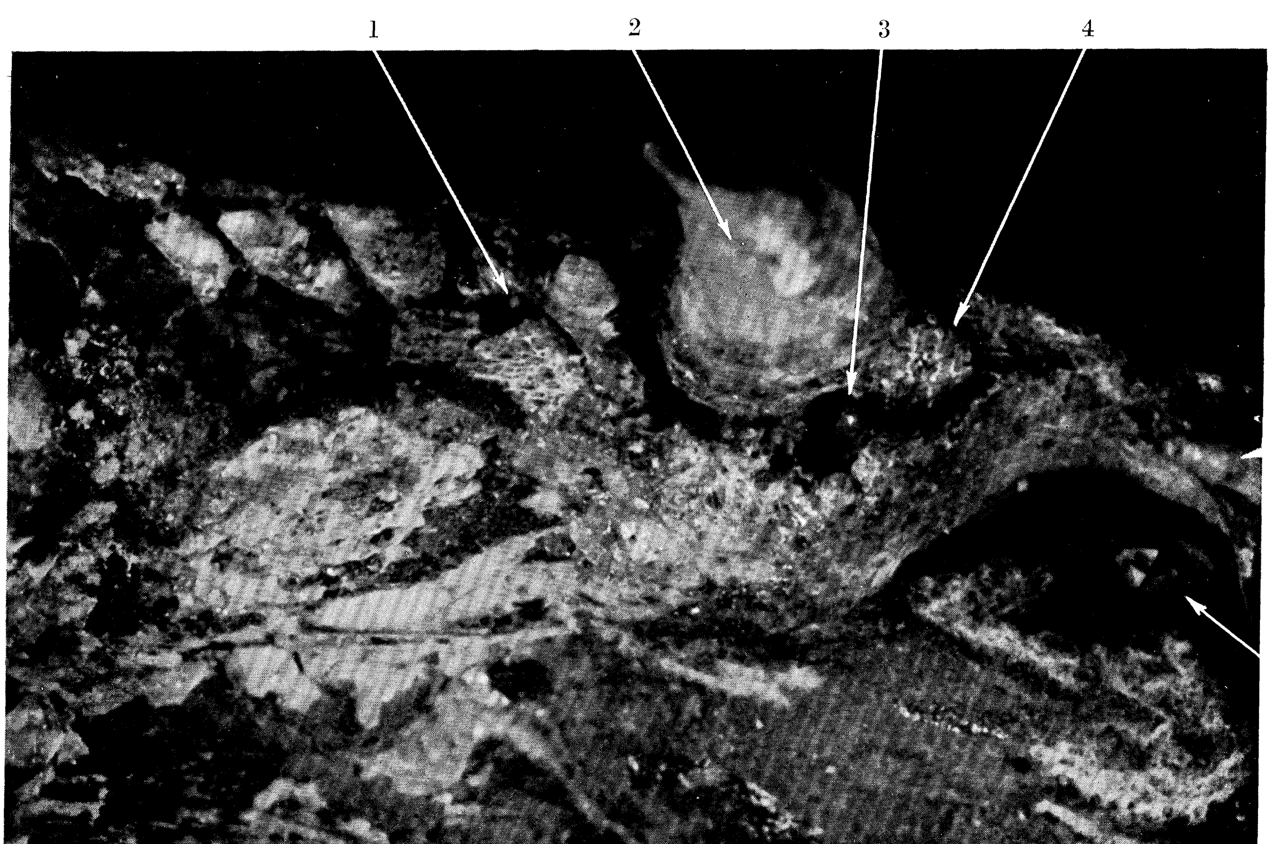


FIGURE 23

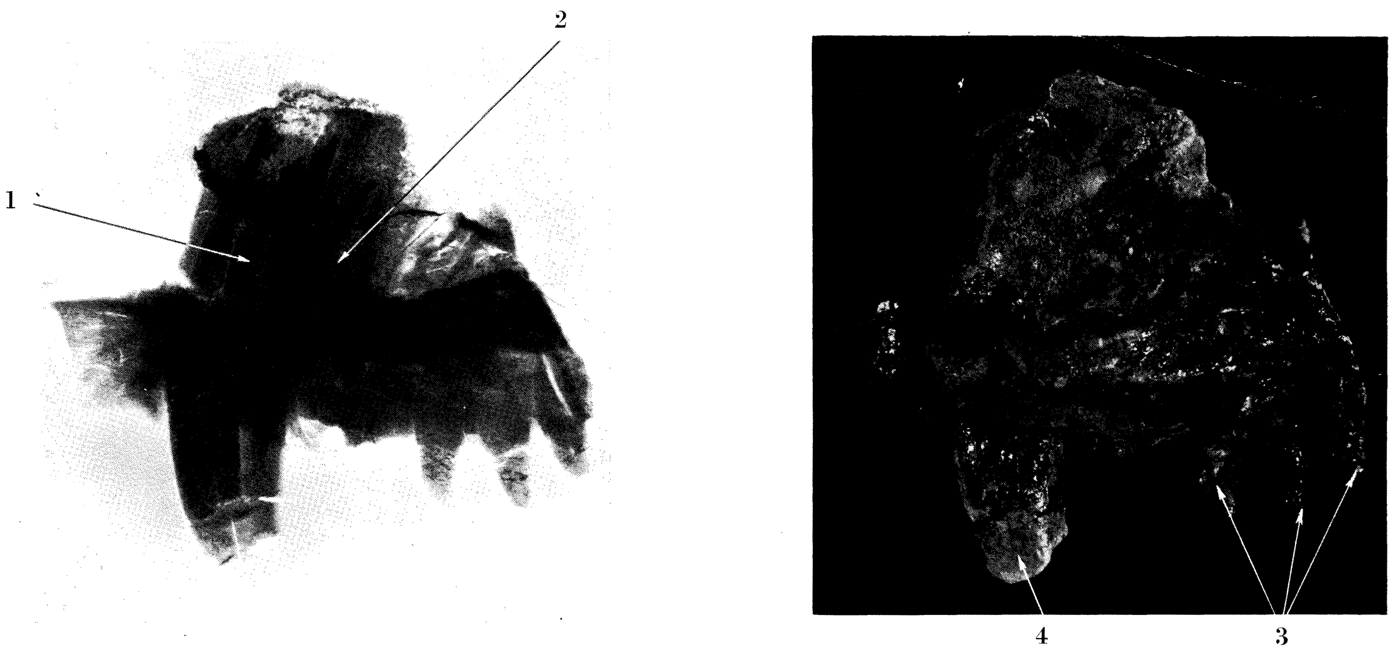
PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Description of plate 7

Figure 22. Dorsal view of lower jaw of specimen R855*a* to show pair of replacement canines. 1, replacement cheek teeth; 2, replacement canines; 3, replacement incisors; 4, functional canine; 5, replacement cheek tooth.

Figure 23. Lingual view of right upper canine of specimen 337 (unnamed aelurosaurid) to show plug of spongy bone and replacing teeth. 1, replacement cheek tooth; 2, functional canine; 3, tip of replacement canine; 4, plug of spongy bone covering old root; 5, crown of most distal incisor; 6, detached tip of lower canine.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES



a *b*

FIGURE 24

FIGURE 25

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

individual alveoli, the teeth on each side lying within a single open groove. On the right the tip of a replacement tooth can be seen coming through lingually and between the second and third functional teeth. On the left, two replacement teeth are visible, one lingual to the third and fourth functional teeth, and the other lingual to the most posterior tooth of the row. In addition, there is a space, from which the replacement tooth has probably fallen out, lingual to the second functional tooth on this side of the jaw.

The specimen shows almost exactly the same picture as the other example of *A. felinus* (R 339). The functional teeth are directly succeeded by members of the same tooth family to which they themselves belong, except in the case of the upper canines. Here there are two alveoli on each side and distichial replacement. This specimen shows in addition that

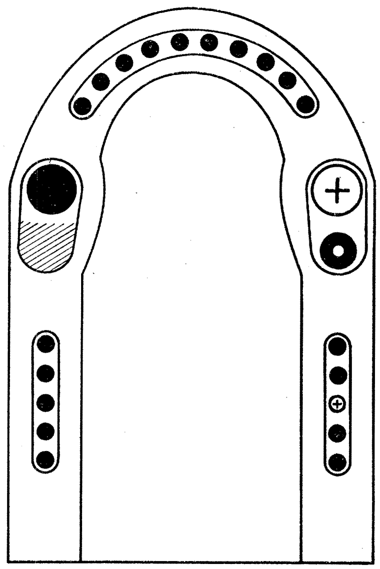


FIGURE 3. Upper dentition of specimen R 855 (*Aelurosauroides watsoni*).

all the teeth are replaced, and that this replacement includes the most posterior members of both upper and lower cheek teeth. In other words, it is wrong to apply the terms *molars* and *premolars* to these animals.

(3) *Aelurosauroides watsoni* Boonstra (R 855)

This specimen is the type (Boonstra 1934 *a*) and consists of a snout without the lower jaw. There are five functional upper incisors (figure 3). These are long, rather curved teeth, showing little or no flattening.

DESCRIPTION OF PLATE 8

FIGURE 24. (*a*) Lingual view of right upper canine of specimen R 393 (*Pristerognathus polyodon*). (*b*) X-ray photograph of same to show closed root of old canine behind functional tooth. 1, open pulp cavity at root of functional canine; 2, closed pulp cavity of root of old canine; 3, cheek teeth; 4, functional canine.

FIGURE 25. Palatal view of specimen 100 (*Whaitsia* sp.) to show plug of spongy bone behind each canine. 1, functional canine; 2, plug of spongy bone covering old root; 3, palatal process of maxilla.

On the right there is a single functional canine. It is broken off just above the gum-line, so that little can be said about its shape; but it appears to have had the usual sharp distal edge. There is no sign of any serrations, which is not surprising under the circumstances. The tooth is firmly grasped by the walls of its alveolus and by a lightly fitting plug of spongy bone lying distally to it. The closed end of its root can be seen dorsally through an accidental break in the maxilla. This observation is confirmed by X-rays, and it is clear that this tooth must have erupted long before the death of the animal. There is no sign of any replacement canine.

On the left side of the upper jaw is a large, empty alveolus, from which the functional canine must have fallen out after the death of the animal. Distally to this is a large root, broken off cleanly along the gum-line. This root is undergoing resorption and was the root of the penultimate functional canine on the left-hand side. There is no evidence of any replacement canines on this side either. The loss of the functional canine on the left means that it was not firmly held by the walls of its alveolus, suggesting that it had not erupted long before the animal's death. This is confirmed by the excellent state of preservation of the root of its predecessor.

There were five cheek teeth on both sides. They are all broken off close to the gum; and all that can be said about their shape is that they were approximately circular in cross-section. There are no replacement teeth.

The striking thing about this specimen is the complete absence of any tooth replacement, and the way in which the teeth are firmly implanted. In both respects it makes a sharp contrast with the two preceding specimens (R 339 and R 855 *a*) to which it is undoubtedly closely related.

(4) Unnamed aelurosaurid (337)

This specimen is related to *Aelurosaurus* and consists of the complete skull and lower jaw, along with the atlas and the axis. Some very intractable grey shale was included in the matrix in which the specimen was embedded. This was not attacked by acetic or formic acid, so it was not possible to prepare the specimen as completely as had been hoped; but, despite this, it has yielded much useful information.

On each side of the upper jaw there were five functional incisors (figure 4 *a*). These are laterally compressed recurved teeth, serrated along their distal edges. They all have replacement teeth coming through lingually, on both sides of the jaw.

There is one functional canine on each side of the upper jaw. These are laterally compressed and recurved, with a serrated distal border. In front, on each side of the jaw, there is another alveolus with a plug of spongy bone closing it ventrally. On the right the tip of a replacing canine can be seen just breaking through, lingually to this plug (figure 23, plate 7). X-ray photographs show that, buccally to this replacing tooth, and therefore directly above the plug, is the root of an old canine whose crown has been shed. This root is suffering erosion distally.

On the left a replacement canine is not visible externally. However, a fortunate break through the maxilla shows here an exactly similar state of affairs to that on the right. Above the bony plug is the root of an old canine, and lingually to this is the root of the replacing canine, which in this case has not yet broken through the jaw.

On the right there were five functional upper cheek teeth. These are conical, and slightly laterally compressed. They probably had a serrated edge bucco-distally. There is a replacement tooth lying between the first and second functional teeth, in a lingual extension of the common alveolus.

Four functional upper cheek teeth are present on the left. There is the tip of a replacement tooth coming through into a large linguo-mesial extension to the alveolus of the first tooth, and another, in a lingual extension of their common alveolus, between the second and third functional teeth. In addition, there is a tiny alveolus lying lingually and between the first and second functional teeth. This is now filled with hard shale, but in life it almost certainly bore another replacement tooth, although the shale filling makes it

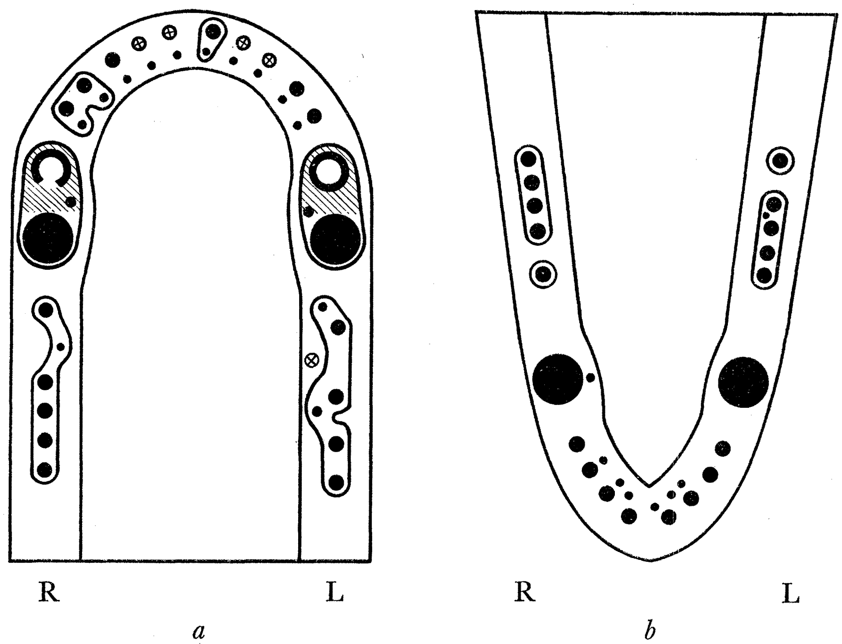


FIGURE 4. (*a*) Upper, and (*b*) lower dentitions of specimen 337 (an unnamed aelurosaurid).

impossible to clear it out and be certain. When these three teeth had erupted fully, and the first and second of the present series shed, there would have been five functional cheek teeth on the left as well as on the right. This would suggest that the present specimen was probably young, and had not acquired its full complement of cheek teeth at the time of its death.

There are four functional lower incisors on each side of the jaw (figure 4*b*). These are backwardly curved teeth, rather compressed, and with mesial and distal serrated cutting edges. The presence of shale makes it impossible to expose fully the jaw behind these teeth. On the right three incisors (1st, 2nd and 3rd) are being replaced, while on the left there are three replacing teeth visible—one lingual to each of the first and second functional teeth, and the third lying between this pair. As complete preparation is impossible, these may not be all the replacing teeth actually present.

There is a single functional lower canine on each side of the lower jaw. These are long, backwardly curved and laterally compressed teeth, with certainly a serrated cutting edge distally, and probably with another linguo-mesially. X-ray photographs show that the root of the right-hand tooth is closed off apically, so that the tooth must have erupted some considerable time before the animal's death. This is confirmed by the worn nature of the tooth. The left functional canine is unworn, and its root is wide open ventrally. Thus it can only have erupted just before the end of the animal's life.

On the right the functional canine has a replacement, the tip of its crown just penetrating the dentary lingually to the functional tooth, and X-rays show that its root already extends to the bottom of the dentary. On the left hard shale makes it impossible to prepare down to the dentary lingually to the functional tooth. In addition, this shale makes the evidence of X-rays inconclusive. It is possible that there is a young replacement canine lingually to the functional tooth; but, if so, it has not grown to anything like the same size

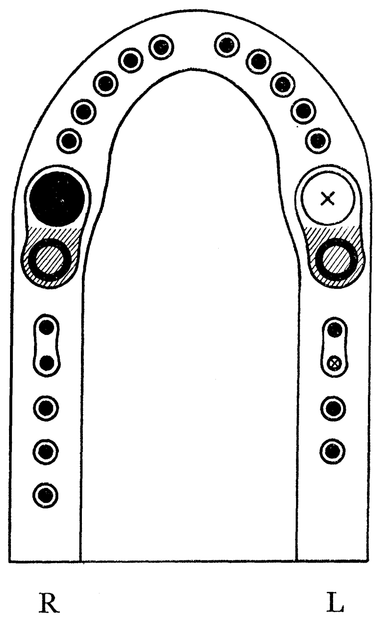


FIGURE 5. Upper dentition of specimen 79 (*Dixeya quadrata*).

as its fellow on the right. This difference in development would be consistent with the different times of eruption of the functional teeth.

There are five functional lower cheek teeth visible on each side of the jaw. These are cylindrical, sharply pointed teeth, with mesial and distal serrated cutting edges. On the right there are no replacement teeth; on the left there is one, situated lingually between the third and fourth functional teeth.

(5) *Dixeya quadrata* Haughton (79)

This specimen consists of a snout without the lower jaw.

There are five incisors on each side (figure 5). They are approximately circular in cross-section, and no serrated edge is visible. As the teeth are poorly preserved this does not mean very much. These incisors are firmly set in their alveoli, and there are no replacement teeth.

There was a single functional canine on each side of the jaw, that on the left being now represented by an empty alveolus. Behind each socket is a plug of bone, and above this plug is the remains of a closed root. On the right the old root could not be detected by

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

X-rays, but was found by cutting a window into the maxilla; on the left the old root can still be seen in an X-ray photograph. A radiograph of the root of the single functional canine remaining (right) shows that it is closed apically, so that this tooth must have erupted a considerable time before the death of the animal.

The surface of the upper jaw behind the canines had been ground down well below the gum-line before its examination by the author. This makes interpretation very difficult. There were probably five cheek teeth on the right; and there were certainly three on the left, with, in addition, one empty alveolus. No replacing teeth can be seen.

This specimen compares closely with the last but one (*Aelurosauroides* R 855). In both, replacing teeth are absent, whilst the functional teeth are firmly set in their sockets; and behind the upper canines there is a plug of spongy bone.

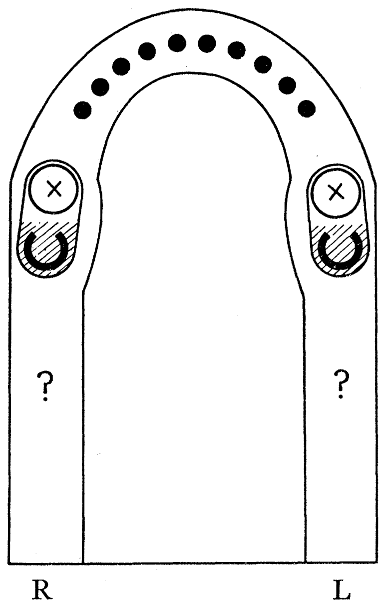


FIGURE 6. Upper dentition of specimen R 1647 (*Gorgonops torvus*).

(6) *Gorgonops torvus* Owen (R 1647)

This specimen is the type (Owen 1876) and consists of a skull lacking the lower jaw. The palate and jaw margin have been ground down at some time.

There were five functional incisors on each side of the upper jaw (figure 6). These were large, cylindrical teeth, slightly compressed transversely. No replacement teeth are visible.

There was one functional upper canine on each side, but both have fallen out, leaving the empty alveoli. Behind each is part of an old canine root, embedded in spongy bone, and showing mesial erosion. In addition, both the pulp cavities are filled with spongy bone. No replacing canines are visible.

No cheek teeth can be seen.

(7) *Cynariops robustus* Broom (R 5743)

This is a damaged, but reasonably complete skull, lacking the lower jaw (figure 7). The edges of the premaxillae and of the maxillae are broken and worn down along the tooth-line. There are still present the remains of two of the functional incisors on the right and one on the left. Originally there were probably four functional incisors on each side, not five as suggested by Broom (1925) and Boonstra (1934*a*). Both the functional incisors on the right have replacing teeth lingual to them, and between these two replacing teeth lies a third, corresponding to the position of the third functional incisor. There is a small shale-filled alveolus in a position lingual to that which would be occupied by the first functional incisor on this side. A replacement tooth has probably fallen out of this alveolus. On the left there are replacing teeth corresponding in position to the second and third incisors.

There is one functional canine on each side. The one on the right has a replacing tooth lying mesially and lingually to it, while on the left there are the remains of the root of an

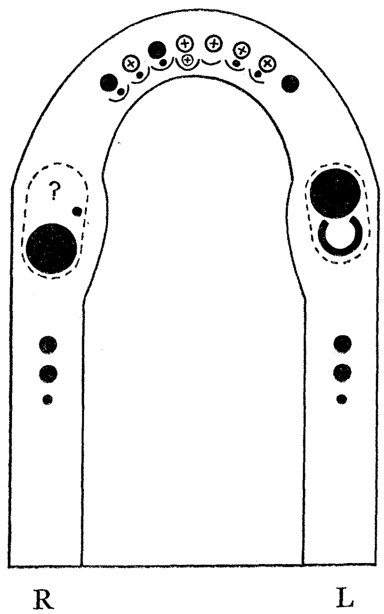


FIGURE 7. Upper dentition of specimen R 5743 (*Cynariops robustus*).

old canine, eroded mesially and lying distally to the functional tooth. No replacement canine can be seen on this side, which is not surprising in view of the state of preservation of the specimen. Thus this animal has the functional canine in the anterior alveolus on the left, and in the posterior on the right.

There are three cheek teeth visible on each side. No replacements can be seen.

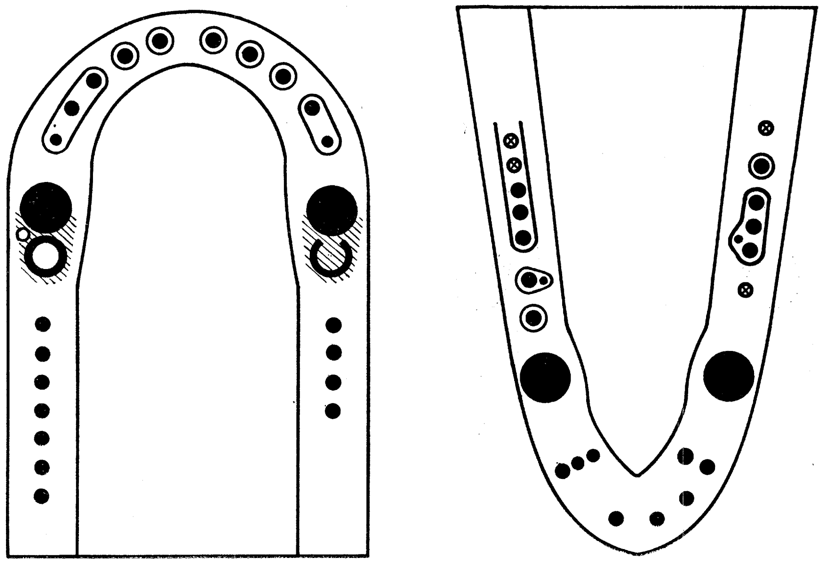
(8) Cf. *Scylacops capensis* Broom (R 121)

This specimen consists of a complete skull with the associated lower jaw. Three horizontal slices have been cut which pass through the anterior part of the lower jaw and through the roots of the anterior teeth of the upper jaw.

There are five functional incisors on each side of the upper jaw (figure 8*a*). These were long, rather cylindrical teeth, the last on each side being smaller than the other four. Their state of preservation is poor, and no serrated edges are discernible. Their roots as seen in section vary in diameter, as do the sizes of their pulp cavities, but there are apparently no replacement teeth.

There is a single functional canine on each side of the upper jaw. These are rather laterally compressed teeth with a sharp posterior edge. No serrations are visible, probably owing to the damaged condition of the teeth. The roots of these functional canines narrow down as they pass upwards in the jaw. Thus they are closed, or nearly so, apically, and the teeth must have erupted some considerable time before the end of the animal's life.

Behind each functional canine is a plug of spongy bone which passes upwards into an old root. These last are showing much resorption, and are heavily invaded by the spongy bone. The root of the right functional canine lies rather lingually within its alveolus, and buccally to it lies a small piece of the root of another tooth. This is definitely not a replacement tooth, and is almost certainly the remains of the root of the antepenultimate canine.



R L R L

a *b*

FIGURE 8. (*a*) Upper, and (*b*) lower dentitions of specimen R 121 (*Scylacops capensis*?).

On the right seven cheek teeth can be seen in section. Their diameters, and those of their pulp cavities, vary considerably. On the left, parts of four cheek teeth are visible. No replacement cheek teeth seem to be present on either side of the jaw.

Four lower incisors are visible in section on each side (figure 8*b*). They have been displaced, probably due to the lower incisors of gorgonopsids lying in a wide open trough on each side, and they vary considerably, both in diameter and in the relative size of the pulp cavity. No replacements can be seen, and the four teeth visible on each side are the usual number of functional lower incisors for a gorgonopsid.

There is one functional canine on each side of the lower jaw. These are laterally compressed teeth and there are clearly no replacement canines.

On the right there are traces of five of the seven functional lower cheek teeth; the two most distal ones have fallen out of their alveoli. A replacement tooth can be seen lingually to the second cheek tooth. On the left there were at least six functional teeth, with a replacement tooth lying lingually and between the second and third cheek teeth.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

(9) *Scymnognathus whaitsi* Broom (R 49396)

This specimen—an associated snout and lower jaw—had been previously cut into transverse sections. There are ten of these, including the two ends, each about 1 cm thick.

None of the upper incisors can be seen (figure 9*a*). There is one functional canine on each side, with a plug of spongy bone behind it. In each plug is embedded an old root, the spongy bone having even penetrated into its pulp cavity. This pair of old roots can only have belonged to the immediate predecessors of the canines functional at the animal's death. The roots of the functional teeth become markedly reduced in diameter as they pass upward in the maxilla, and must have been closed, or nearly so, at their apices. They must therefore have completed their eruption some considerable time before death. Replacing canines are absent.

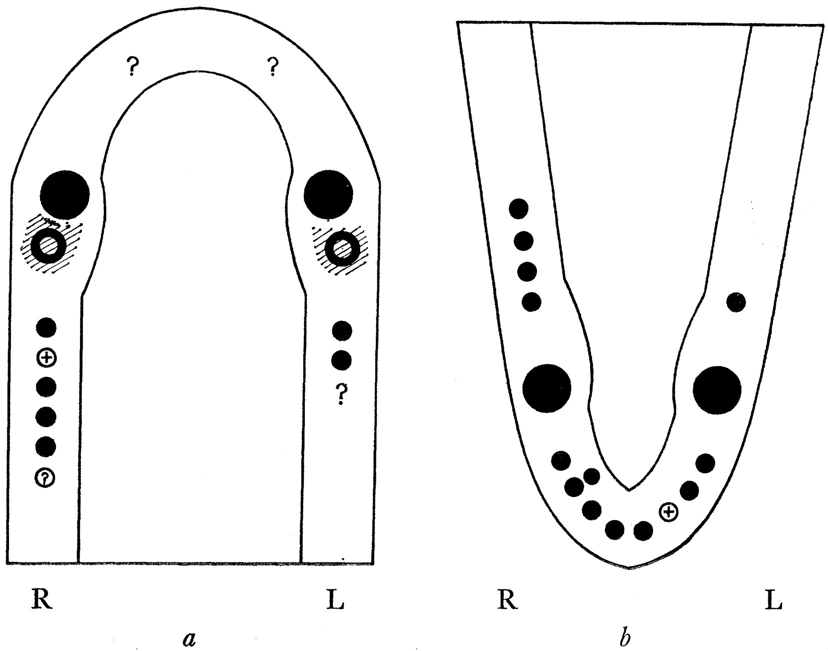


FIGURE 9. (*a*) Upper, and (*b*) lower dentitions of specimen R 49396 (*Scymnognathus whaitsi*).

There are four functional upper cheek teeth visible on the right and two on the left. On the right one is missing between the first and second teeth, and there is room for one more behind the last tooth visible. Thus the animal would have had five or six upper cheek teeth. There are no replacements visible.

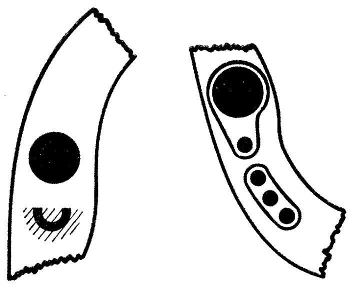
There are four lower incisors on the right (figure 9*b*), and this is apparently the full number. The third incisor may have been very recently replaced, as there seem to be pieces of the root of its predecessor lying buccally to it. An alternative explanation is that there are five incisors on the right which have become rather displaced in position. On the left there are three teeth visible with space for a fourth. There are no replacements visible on either side.

There is a single lower canine on each side, and definitely no replacement teeth, while four cheek teeth are visible on the right and one on the left. There is no evidence of replacement teeth.

(10) Unknown gorgonopsid (R 256)

This specimen is part of the right maxilla and lower jaw of an unknown gorgonopsid. An attempt was made to prepare this specimen by acetic acid. This proved unsuccessful, and what was left of the specimen was cut and ground down to give a series of transparent, horizontal sections. Five of these were obtained from the upper jaw, and five from the lower.

The sections through the maxilla showed simply the canine (figure 10*a*). In each section the root of the functional tooth could be clearly seen, and behind this the remains of another root. In the most dorsal pair of sections this shows a complete ring, although



a *b*

FIGURE 10. (*a*) Upper, and (*b*) lower dentitions of specimen R 256 (an unidentified gorgonopsid).

this is much invaded by spongy bone. Passing ventrally, in the next two sections this invasion by bone has become more severe, and the root no longer forms a complete ring. In the last section of this series, which passes just above the line of the gum, this posterior root has completely disappeared, and its place has been taken by spongy bone.

The five sections through the dentary show the four distal of the original five incisors, and the canine. There is no tooth replacement (figure 10*b*). Two lower cheek teeth were lost during preparation. They are shown in table 1 but not in figure 10 *b*.

(*b*) *Therocephalia*

(11) *Trochosaurus major* (Broom) (R 5747)

This British Museum specimen has at some time been broken into a number of separate pieces. The skull was unstuck into its component parts at my request, and due to the fortunate location of the breaks, a considerable amount of information can be obtained about the dental succession, although this information is, of necessity, less than would be obtained from a properly prepared specimen. The degree of damage made it undesirable to attempt chemical preparation. The specimen is important, as it is one of the most primitive Therocephalia known, having two functional canines on each side of the upper jaw.

The specimen consists of a fairly complete skull, with part of the associated lower jaw. On the right side of the upper jaw four incisors are visible, and on the left five (figure 11*a*). They appear to have been long, slightly curved teeth, with serrated edges both mesially and distally. On the left the second incisor is only half erupted, and has a large open pulp cavity, while the fifth has a replacement tooth lingual to it.

The two functional canines on each side of the upper jaw are borne in a pair of alveoli arranged antero-posteriorly. Nothing can be said about the shape of these teeth, except that they had serrated edges both mesially and distally. On the right-hand side a fracture passes through the alveoli above the gum-line. In this section the root of a replacement tooth can be seen lying lingually to each of the pair of functional canines. The anterior of this pair of replacement teeth is in a considerably more advanced stage of development than the posterior one.

On the left-hand side the fracture is below the gum-line, and does not pass through the alveoli. The anterior of the pair of functional canines was still in process of eruption at the death of the animal, and has a wide open pulp cavity. No replacement canines can be seen, which is not unexpected in view of the position of the fracture.

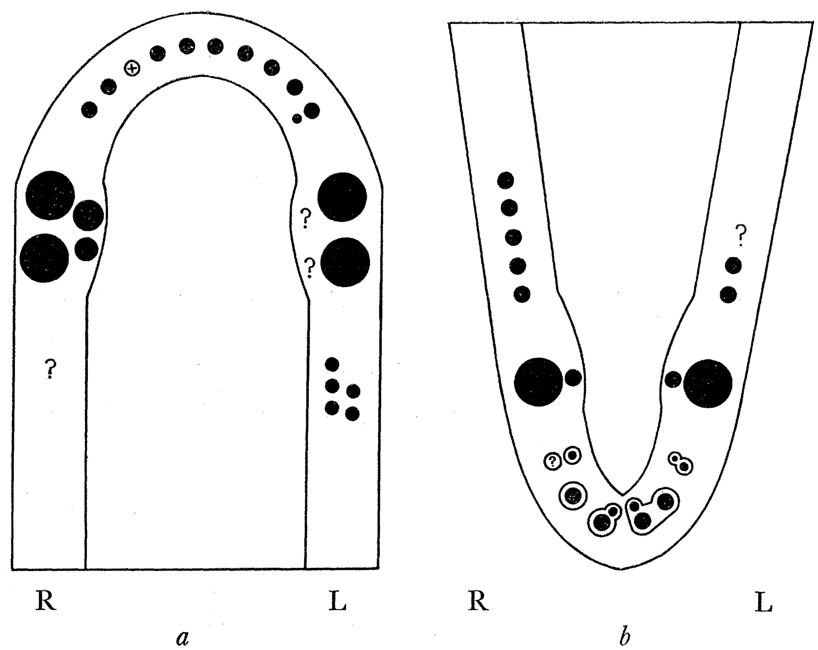


Figure 11. (*a*) Upper, and (*b*) lower dentitions of specimen R 5747 (*Trochosaurus major*).

As there is no fracture in the required place, the cheek teeth on the right-hand side of the jaw are invisible. On the left a total of five can be seen, but their interpretation is not easy. They seem to lie roughly in two rows: two with almost closed pulp cavities in the buccal row, and three with large pulp cavities in the lingual row. Those in the lingual row have well-erupted crowns, and so are not replacement teeth. The two roots in the buccal row may be the remains of teeth whose crowns have been shed. This is not inconsistent with their general appearance. Such retention of the roots of teeth, other than canines, can possibly be seen in the fourth left lower incisor of *Scymnognathus whaitsi* (R 49396).

In the lower jaw there were three functional incisors on each side—two large teeth with another smaller one distally (figure 11 *b*). The first on the right and the first and third on the left have replacement teeth coming through lingually to them. The third on the right seems to be just commencing eruption, and there is no sign of the definitive third tooth at all. These teeth were approximately circular in cross-section, and had serrated edges both mesially and distally.

Two replacement canines are clearly visible in the lower jaw. That on the right is just breaking through, while that on the left has erupted considerably further. Both these teeth have wide open roots. The right functional tooth is now represented only by its crown, the rest of the tooth having been lost when the specimen was broken up. It is clear, however, that the position of this functional tooth in the jaw was buccal to its replacement. Similarly on the left, only the crown of the functional canine is preserved, and, again, it must have lain buccally to its replacement.

All that can be seen of the lower cheek teeth are parts of five on the right and two crowns on the left-hand side. It is therefore impossible to say whether any tooth replacement was going on here.

This specimen compares closely with the two specimens of *Aelurosaurus* (R 339 and R 855 *a*). The only essential difference is that, in the two gorgonopsids, the pair of alveoli in the maxilla each alternately bears the functional canine, while in the therocephalian each bears a functional tooth simultaneously. The difference is one of timing only.

(12) *Pristerognathus polyodon* Seeley (R 2581)

This specimen consists of the snout and associated lower jaw showing the complete series of incisors and canines in both upper and lower jaws, although the row of cheek teeth is complete only in the lower jaw.

There are six upper incisors on the right, and seven on the left. On both sides the most distal tooth is considerably smaller than the rest. These incisors are cylindrical teeth, slightly flattened bucco-lingually. No serrations can be seen, but owing to the low level at which the teeth have been truncated, no importance can be attached to this observation. The incisors are not being replaced.

There is a single functional upper canine on each side. These are large, laterally compressed teeth, with the distal edge serrated. Each canine is gripped firmly by the bone of its alveolus mesially and laterally, but distally there is a large space containing spongy bone. On each side, X-ray photographs indicate the presence of an old root within this plug. These are the remains of the last canine on each side to occupy these posterior alveoli, the functional canine occupying the anterior alveolus on each side.

The upper cheek teeth, three on each side with, in addition, one empty alveolus on the left, are so badly preserved that nothing can be said about their shape. There is a replacement lying lingually and between the second and third teeth on the left.

There are three functional incisors on each side of the lower jaw (figure 12 *b*). These are long, curved, laterally compressed teeth, with serrations along their distal edges. Their mesial edges are too badly damaged to show whether they bore serrated edges. In each ramus the lower incisors lie in a wide open trough. There is probably a replacement lingual to the second and third functional teeth on the left. On the right there is something in the same position, which may be a tooth, but, on the other hand, may be just a loose piece of bone.

There is a single functional canine on each side of the lower jaw. These are transversely compressed teeth, with a serrated edge visible distally. Each tooth is firmly held in its alveolus, and there are no replacements for these canines.

There were seven functional post-canines on the right and eight on the left. These are sharply pointed and laterally compressed teeth, with serrated edges both mesially and distally. A single replacement tooth lies lingually and between the fifth and sixth functional teeth on the left.

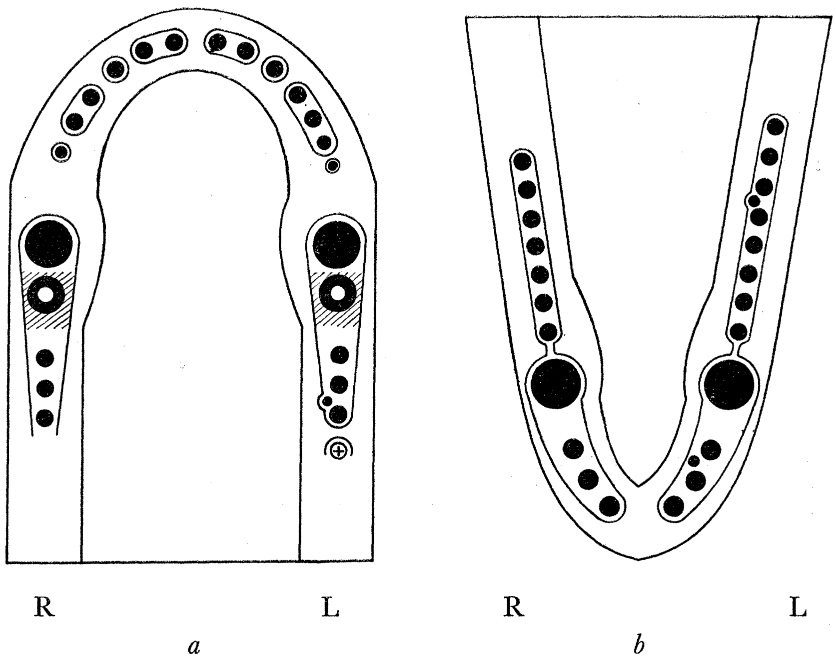


FIGURE 12. (*a*) Upper, and (*b*) lower dentitions of specimen R 2581 (*Pristerognathus polyodon*).

(13) *Pristerognathus polyodon* Seeley (R 393)

This specimen is the snout and lower jaw of a therocephalian, probably *Pristerognathus polyodon* Seeley. As preserved, it shows the complete series of incisors and the canines in both upper and lower jaws; but the row of cheek teeth is only complete on the right side in the lower jaw. The others have been lost, being left behind when the snout broke off the rest of the skull. In the upper jaw there are six incisors, the last on each side being considerably smaller than the others, one canine and three cheek teeth remaining on the right and two on the left.

The incisors (figure 13*a*) are flattened transversely to the long axis of the tooth, and bear serrations on their lateral edges. There are two replacing incisors visible, one on the right of the jaw, and one on the left. The one on the right is lingual to the first functional tooth on that side, and is partly erupted, while the one on the left is lingual to the second functional incisor. These two replacement teeth are borne in a small lingual extension of the same alveolus that bears the functional tooth. Except for these two, the incisors are very firmly set in their alveoli, the bone of the jaw clasping the teeth tightly. The third right incisor is unworn, and clearly recently erupted.

The upper canines are large teeth, truncated due to weathering. They are laterally compressed, with the bucco-distal margin forming a serrated edge. Each canine lies in an alveolus considerably greater than its own diameter. In front, and on both sides, the bone grasps the tooth fairly tightly, but behind there is a large space which is loosely filled by a plug of spongy bone. In this respect the canine teeth of both sides are identical. On examination by X-rays, the remains of the root of a tooth can be seen lying above the plug on both sides of the upper jaw (figure 24*a*, *b*, plate 8). The presence of this root was confirmed on the left side by an accidental fracture. The root is similar in size to the root of the functional canine which can be seen lying in front of it in the radiograph, and only differs from it in having its pulp cavity almost completely closed at the apex. The pulp cavity of the functional canine is wide open, as can be seen. The closed root is that of the canine which immediately preceded the one which was functional at the time of the animal's death. Further, the tooth must have been shed by the crown breaking off at the line of the gum, the root remaining to be resorbed.

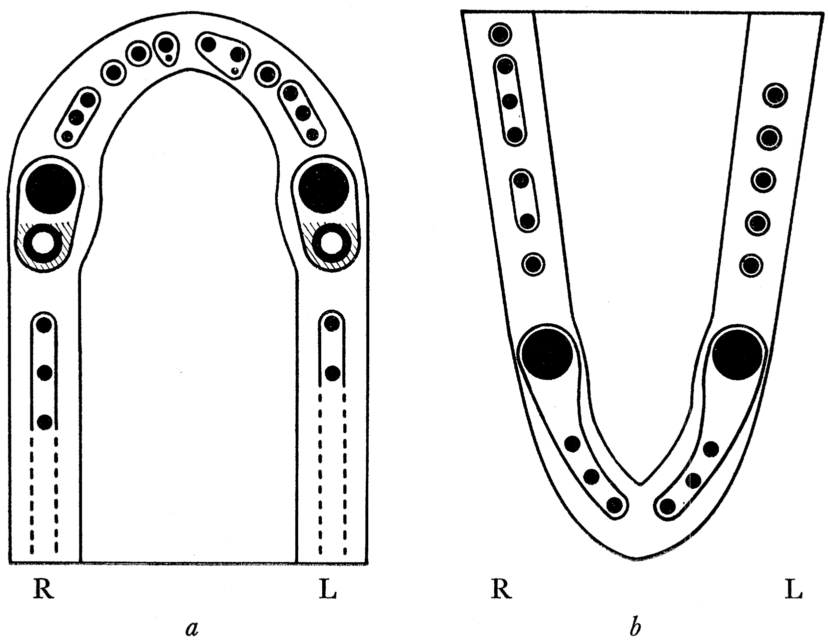


FIGURE 13. (*a*) Upper, and (*b*) lower dentitions of specimen R 393 (*Pristerognathus polyodon*).

The anterior cheek teeth preserved are small, sharply pointed teeth, laterally compressed, and with serrations running down both their mesial and distal borders. There is no sign of replacing teeth for either the upper canines or the upper cheek teeth.

The lower incisors (figure 13*b*), of which there are three on each side, are rather elongate, conical teeth, with their adjacent edges serrated. These teeth are all firmly clasped by the bone of the jaw; and there is no sign of any replacement going on—either by inspection under a binocular microscope or in X-ray photographs.

There is a single lower canine on each side of the jaw. This is a long, pointed tooth, slightly curved, and with a crown length of some 2·5 cm. The teeth are transversely compressed, and bear serrated edges both mesially and distally. The roots of these canines are long, and extend ventro-posteriorly for a considerable distance on the dentary. X-ray pictures show that these roots are closed and that there are no replacing canines. There is no marked difference in the state of wear of the two teeth, both seemingly having erupted just before the death of the animal. Each tooth is firmly set in its alveolus, as is confirmed by a fortunate fracture through both rami, while the same fracture confirms the absence of any replacing canines.

There are seven lower cheek teeth on the right-hand side, the series being here complete; and five on the left, the series being truncated distally. They resemble the upper cheek teeth closely, being laterally compressed and sharply pointed, with serrations on their mesial and distal borders. They are firmly set in their sockets, and there is no sign of any replacing teeth.

(14) *Cynariognathus platyrhinus* Broom (R 4097)

Three transverse slices had previously been cut off the back of this specimen (Boonstra 1934*b*), which is a very badly weathered snout and lower jaw. The upper dentition is preserved only on the left-hand side.

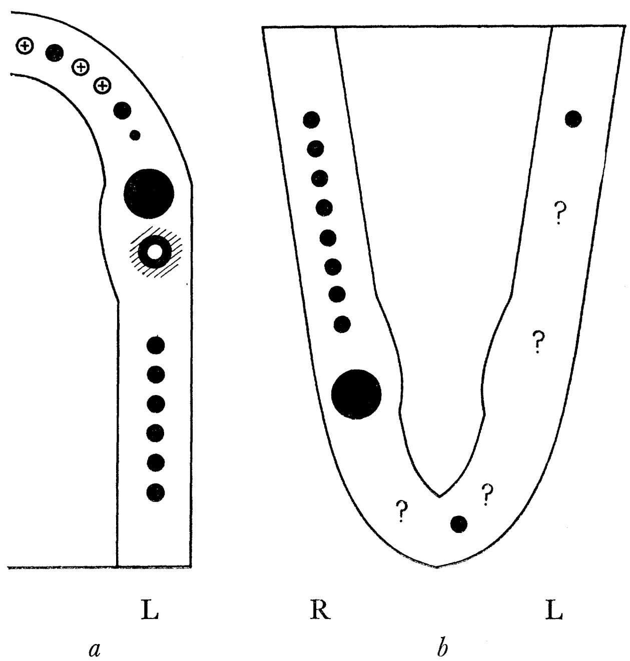


FIGURE 14. (*a*) Upper, and (*b*) lower dentitions of specimen R 4097 (*Cynariognathus platyrhinus*).

Three upper incisors are visible (figure 14*a*), the most posterior being considerably smaller than the other two. This suggests that it is the last incisor; and, if so, there would have been room for a total of six upper incisors. These teeth are strongly laterally compressed, with a serrated distal cutting edge. No replacements are visible.

There is a single functional upper canine, a laterally compressed tooth, with a serrated distal cutting edge. The tooth appears in the most anterior section, where its large open root is showing high up in the maxilla. Below it, in the section, is another, slightly smaller and with a narrow pulp cavity. This is the root of the penultimate canine, whose crown has been shed.

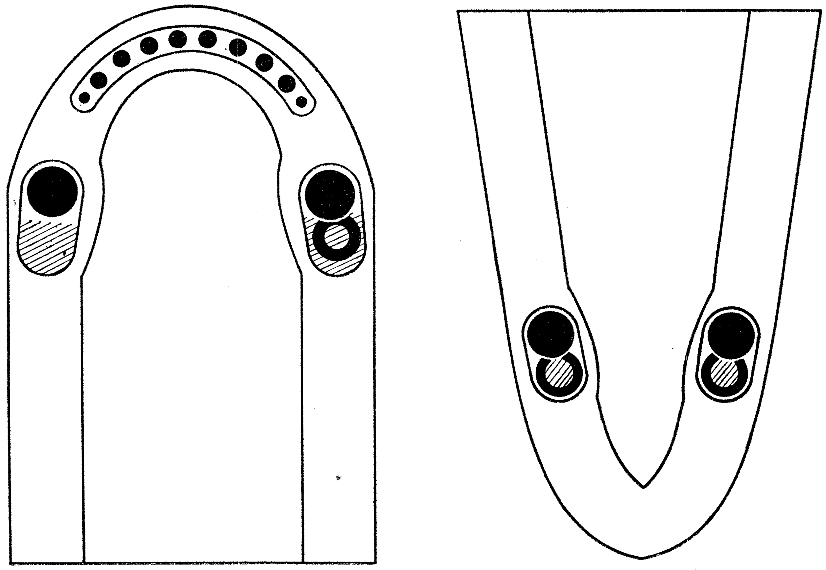
Six upper cheek teeth are visible, but there are no replacements.

On the left-hand side of the lower jaw only one incisor and one cheek tooth remain (figure 14*b*). No right incisors can be seen, but the remains of a lower canine along with eight cheek teeth are present. Replacements could not be found for any of the lower jaw teeth.

(15) *Notosollasia laticeps* Broom (R 5699)

This specimen consists of a skull and lower jaw. The specimen has fractured at some time, and was subsequently stuck together with Seccotine. After unsticking by immersion in hot water, it yielded much valuable information.

The upper incisors are long, well-rounded teeth (figure 15*a*). No sign of serrated edges can be seen, but, in view of the state of preservation of the teeth, this observation does not mean very much. There are five incisors on each side of the jaw, the last being much smaller than its neighbours, as is common in the Therocephalia. The first tooth on the right, and the second and fourth on the left may still be in process of eruption.



R L R L

a *b*

FIGURE 15. (*a*) Upper, and (*b*) lower dentitions of specimen R 5699 (*Notosollasia laticeps*).

There is a single upper canine on each side of the jaw. Relative to the size of the skull these are rather small smooth teeth, cylindrical in cross-section. On the right a plug of spongy bone lying distally to the functional canine has been cut through. On the left the break passes through at a rather higher level, and shows the root of another canine lying distally to that now functional. This cannot be a replacement tooth as it is suffering erosion mesially, and its pulp cavity is full of spongy bone. It is therefore the root of the tooth which preceded that now functional, and which is undergoing resorption.

There are no upper cheek teeth in *Notosollasia*.

No lower incisors can be seen and there almost certainly were none in this species.

There is a single lower functional canine on each side (figure 15*b*). The roots of these teeth can be seen due to a number of breaks across the lower jaw, and were wide open apically, so that the teeth had only recently erupted before the death of the animal.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Another large root can be seen on each side mesial to that of the functional canine. These are suffering erosion distally, and the pulp cavities contain spongy bone. They may be observed in the same three sections as the functional tooth roots, and, unlike the latter, both they, and their pulp cavities, rapidly contract in diameter as they pass towards their apices. Thus these roots were closed, unlike those of the functional canines, and so they are the roots of the penultimate lower canines, the crowns of which have been shed.

There are no lower cheek teeth in *Notosollasia*.

This specimen is important as it shows that in some species the lower canines could be shed in the same way as the upper, by the crown dropping off and the root being penetrated by spongy bone and absorbed.

(16) *Whaitsia* sp. (100)

This is a very well-preserved snout, the lower jaw being missing.

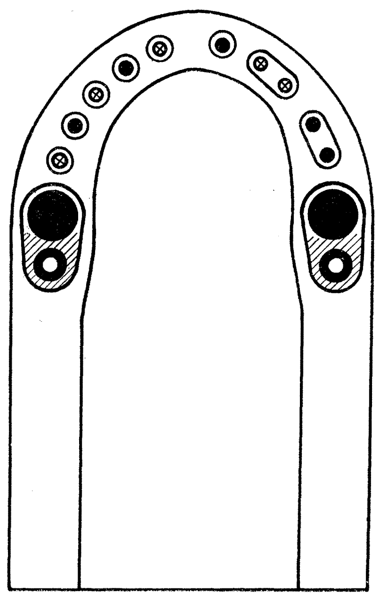


FIGURE 16. Upper dentition of specimen 100 (*Whaitsia* sp.).

There were five incisors on each side (figure 16). Of these the first, third and fifth are missing on the right, and the second and third on the left. These missing teeth are represented by their empty alveoli. The incisors are round in cross-section. No replacing incisors are visible, and even supposing that these had dropped out, the characteristic lingual notch in the alveolus of the functional tooth would have betrayed their former presence. There are no such notches in this specimen, and so it may be confidently asserted that there were no replacing incisors present at the time of its death.

There is a single functional canine on each side. Both teeth have been broken off at the gum-line, and again no serrations are visible. Behind each functional tooth there is another alveolus filled with spongy bone (figure 25, plate 3). Radiographs show that there are the remains of an old root above this plug on each side of the jaw. These must be those of the last functional canines to occupy the posterior alveoli.

There are no cheek teeth in this genus.

IV. Discussion

In the early tetrapods the tooth replacement is distichial. When a tooth is shed its function is taken over by the pair of teeth in the two adjacent alveoli, the next member of its own tooth family (using the terminology of Bolk (1922)) remaining in the alveolus for some time before its eruption is completed. When this tooth does complete its eruption, however, the teeth in the two neighbouring alveoli are shed in their turn. Thus one series of alveoli bear the functional teeth, while the other series, alternating with them, bear their immediate replacements* (Parrington 1936*a*, *b*). This is shown diagrammatically in figure 17.

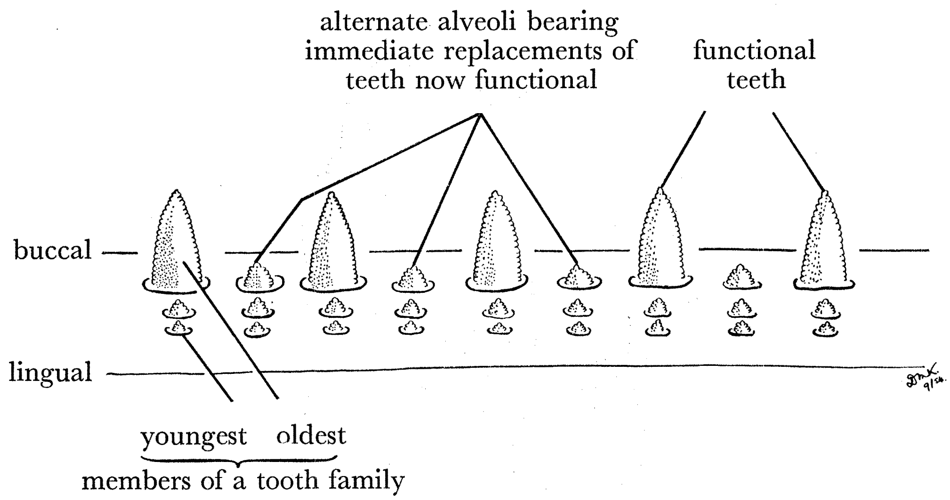


Figure 17. Diagrammatic representation of tooth replacement in a primitive reptile.

This functional distichial replacement has been almost completely lost in the Gorgonopsia and Therocephalia. It is completely absent in some of the more primitive Therocephalia, and in the rest of the Therocephalia and in the Gorgonopsia it is confined to the upper canines. In all the other teeth the immediate replacement of a tooth comes from its own tooth family, borne in a lingual extension of the alveolus of the functional tooth.

In the Gorgonopsia and Therocephalia with distichially replaced upper canines, only one is functional on each side at any one time. But as there were two alveoli in each maxilla, each bore the functional upper canine alternately. Replacement probably took place independently on each side of the jaw. The members of the tooth family of each alveolus of the pair succeeded each other in exactly the same way as for the other alveoli, each member of the family appearing lingually to its predecessor.

This functional distichial replacement in the upper canines of gorgonopsids and of most therocephalians is not primitive, but has arisen to meet a definite mechanical need. In the sphenacodont pelycosaurs, such as *Dimetrodon* (Romer & Price 1940), and in the most primitive Therocephalia (for example, *Trochosaurus*, described above), there are two functional canines on each side of the upper jaw. Thus both of the pair of canine alveoli in each maxilla bore a functional tooth simultaneously. These canines were replaced in

* The immediate replacement of a tooth is that tooth which takes over the other's function *as soon as the latter is shed.*

exactly the same way as the rest of the animal's teeth, the immediate successor to each tooth being a member of its own tooth family.

It seems that there were selective advantages in having but a single functional canine on each side of the upper jaw. This condition is found in all succeeding mammal-like reptiles and in their successors the mammals. In the ancestral gorgonopsids and therocephalians this was achieved, not by a suppression of one alveolus, but by an alternation of the timing of the replacement of the pair of canines in each maxilla. In the pelycosaurs and those therocephalians with two functional upper canines in each maxilla, the time

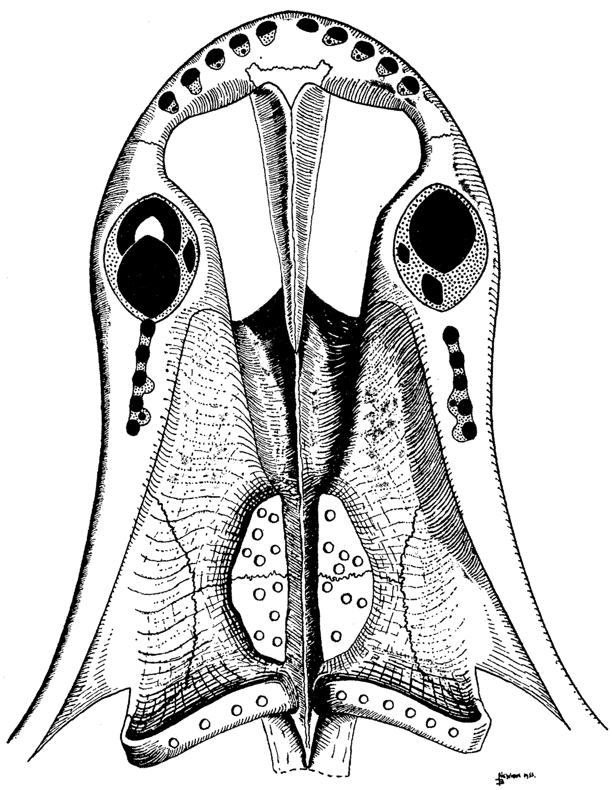


FIGURE 18. Palatal view of specimen R855*a* (*Aelurosaurus felinus*) to show the dentition and the anterior dorsal extensions of the palatine. For clarity, the teeth have been represented diagrammatically.

between the shedding of one of these teeth and the completion of the eruption of its successor in the same alveolus was short. Thus they normally had two functional canines on each side of the upper jaw.* In the gorgonopsids and therocephalians this time lengthened until it equalled the life of the functional tooth. These animals thus had only one functional canine at a time on each side of the upper jaw, and this tooth was borne alternately in the two alveoli.

Why the change from two pairs of upper canines to one took place in this way becomes clear after consideration of the structure of the palate. An incidental result of the chemical preparation carried out for the present work was the complete development of the palates

* A specimen of *Dimetrodon limbatus* (MCZ 1347), figured by Romer & Price (1940), was replacing its anterior right upper canine at the time of its death, and hence only has one such tooth functional on this side of its jaw.

of four of the gorgonopsids (*Aelurosaurus felinus*, R 339 and R 855 *a*; *Aelurosauroides watsoni*, R 855; and *Dixeya quadrata*, 79). These showed that the previous descriptions of the gorgonopsid palate were incomplete.* In the four specimens mentioned there are two deep channels, lying one on each side of the vomer, bounded laterally by an anterior extension of the palatines, and separated from one another in the median plane of the head by the dorsal lamina of the vomer (figure 18; figure 20, plate 6). The internal nares must have been situated at the posterior ends of these channels, which were very probably converted in life into a true secondary palate by a sheet of soft tissue ventrally, as first suggested by

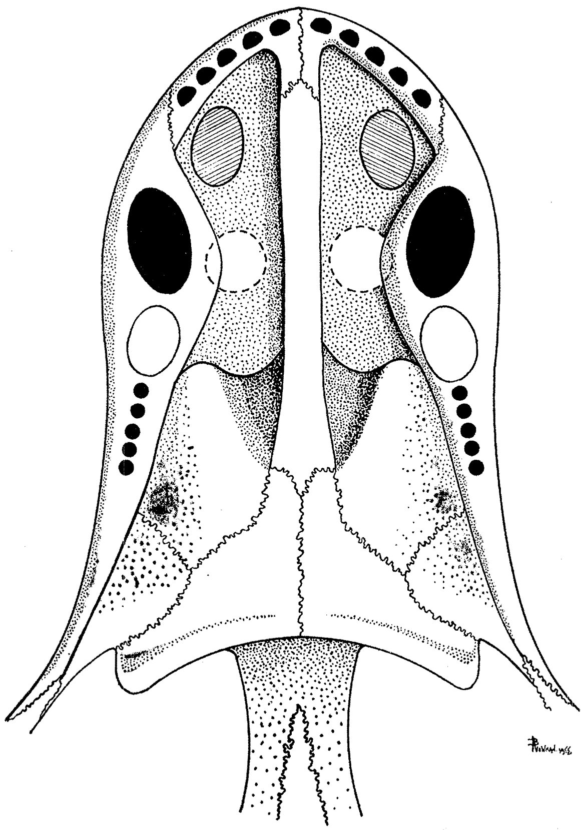


FIGURE 19. Diagrammatic view of gorgonopsid palate—explained in the text below.

Watson (1921). The therocephalian palate is less well known owing to the inferior state of preservation of the material I have worked on, but I have little doubt that at any rate in some forms (the whaitsids, for example) there was a functionally similar partial secondary palate formed by soft tissue. The lower canine's pushed up into the channels when the jaw was shut. Their position is indicated by the diagonally shaded areas in figure 19. These teeth entered the channels where they were broadest, and so left a free passage for the air medially. Now let us consider the effect of the replacement of the upper canines on these air passages, as it would be embarrassing for either to become blocked at any stage.

* Exceptions are Watson's description of *Scymnognathus whaitsi* (1921), Broom's description of *Cynaroides gracilis* (1930) and Parrington's description of the palate of *Dixeya* (1955)—based in this particular on specimen 79. There is no doubt that the latter author is right when he says that these channels are typical of the gorgonopsid palate, and have hitherto not been seen due to the impossibility of preparing them by mechanical means (Broom's *Cynaroides* was sectioned).

The upper canines must have been by far the most important weapons in the capture of prey, growing as they do in some gorgonopsids to a size which rivals that of the upper canines of the sabre-toothed cats. Such large teeth could only have grown slowly, and the animal could not afford to be without a functional canine on one side while replacement took place; or, in other words, the crown of the replacement tooth must have grown almost to its full size before the functional tooth was shed. But, if the functional canine and its immediate successor were members of the same tooth family, the replacement tooth must have grown almost to its full size while in a lingual extension of the alveolus of the functional tooth. Figure 19 shows that this would have been quite impossible, the hypothetical replacement canines being indicated by broken lines; the resultant lingual extension of the alveolar wall would have blocked the internal air passages on that side.

By the secondary re-establishment of functional distichial replacement this difficulty was overcome. The immediate successor to the functional canine could move buccally into its alveolus, as soon as the preceding member of its own tooth family had ceased to function; and there it could grow to the required size without causing any difficulty.

It is of interest to note that there is a similar functional distichial replacement in the maxillary teeth (the poison fangs) of the vipers and some other snakes (Tomes 1894). The functional fang is borne on one side of the maxilla, and it is replaced by a tooth borne on the other side of this bone. Thus there are two families of teeth on each maxilla, which alternately give rise to the functional poison fang. The explanation given by Tomes is the same as that given above for the development of secondary distichism in the theriodonts, namely, these poison fangs are essential to the life of the snake, and as soon as one is lost another must be ready to replace it immediately. This is not possible if the functional tooth and its replacement are members of the same tooth family; but, in the arrangement adopted, the replacing tooth of the other family can move forward and become ankylosed on to the maxilla (the teeth are here acrodont) before the functional tooth is shed.

It is now necessary to consider the way in which the upper canines are shed. In all except one specimen (R5747) the roots of old canine teeth, whose crowns have been lost, can be seen still lying within their alveoli. In some cases these roots are being penetrated by spongy bone, which fills the pulp cavity, and are also undergoing resorption. It is unlikely that these are the roots of teeth which have been broken off by accident, for the following reasons:

(i) they are very common;

(ii) the surface where the crown was lost is a regular cut normal to the long axis of the tooth;

(iii) in all cases where it can be seen, the apex of the root is closed, showing that the tooth was already old when its crown was shed.

This suggests that the upper canines in the Gorgonopsia and in the Therocephalia were regularly shed in this manner, the tooth being cut through just below the gum-line, the crown shed, and the root retained and absorbed from below upwards. This would be advantageous to the animal in reducing the loss of calcium salts—the replacement of these great teeth must always have been a heavy drain on the animal—and in preventing infection of the empty alveolus. One specimen (*Notosollasia laticeps*, R5699) shows that the lower canines could sometimes be shed in the same manner. This form of tooth loss was first noted by Broom (1925, 1930, 1936), but only in the upper canines. It is, as far as I know, peculiar to the Theriodontia.

Table 1 shows that it is possible for all the teeth to be replaced. Replacement of the upper incisors is shown in six (R339, R855*a*, 337, R5743, R5747 and R393) of the sixteen specimens in the table; and of the lower incisors in five certainly (R339, R855*a*, 337, R5747 and R2581) and possibly in one more (R49396). Replacement of the upper canines is again taking place in five specimens (R339, R855*a*, 337, R5743 and R5747), and replacement of the lower canines in four (R339, R855*a*, 337 and R5747). The upper cheek teeth are being replaced in three specimens (R855*a*, 337 and R2581) and the lower cheek teeth in five (R339, R855*a*, 337, R121 and R2581).

In this connexion specimen R855*a* (referred to *Aelurosaurus felinus*) is of importance. It shows that even the last post-canines can be replaced in these theriodonts (figure 2*a*), and thus it is impossible to divide their cheek teeth into premolars which were replaced, and molars which were not. Broom (1936) expressed the opinion that in both the Gorgonopsia and the Therocephalia the cheek teeth, to which he applied the term 'molars', were never replaced. This is not so, and any use of the terms 'molars' and 'premolars' in connexion with the teeth of these animals is to be deprecated. Their cheek teeth form a short row, and are all functionally equivalent, being simple teeth lacking cusps. The terms 'cheek teeth' or 'post-canines' should be used to describe them.

Specimen R339 (the type of *A. felinus*) shows that there were at least three sets of upper incisors (figure 1*a*), and from table 1 it is clear that all the other teeth were replaced at least once. In the Gorgonopsia the upper canines were replaced at least three times, as is shown by specimens R339 and R855*a*. In the Therocephalia examined there is no evidence that the upper canines were replaced more than once; but, in view of the similarity of the method of tooth replacement in the two orders, it would be surprising if the Therocephalia did not replace their upper canines as often as the Gorgonopsia.*

The most complete evidence of tooth replacement can be obtained from the upper canines, due to their great size and consequent slow replacement. Table 2 shows that, of the sixteen specimens examined, nine certainly show no replacing upper canines (R855, 79, R1647, R121, R49396, R2581, R393, R5699 and 100), five show at least one upper canine in process of being replaced (R339, R855*a*, 337, R5743 and R5747), and two are doubtful, due to the loss of the maxilla on one side (R256 and R4097). These last two specimens show no replacement on the side which is preserved.

In the specimens which show replacement in progress in the upper canines, one (R339) has both the functional canines in the anterior pair of alveoli, two (R855*a* and R5743) have the functional canine in the anterior alveolus on one side and in the posterior on the other, and one (337) has both in the posterior alveoli.† Specimen R5747 (*Trochosaurus major*), having two functional canines on each side of the upper jaw, is not relevant here. If the times of replacement of the upper jaw canines on each side are independent of each other,

* Although Parrington (1936*b*) describes a therocephalian in which the upper canines are replaced at least four times, he now informs me (1953) that this specimen could just as well be a gorgonopsid.

† A gorgonopsid in Munich (no. 1262, *Aelurognathus* cf. *serratideus* Haughton) shows a replacing canine behind the functional upper canine on the right, and in front of it on the left. Buccal to the right replacement is the remains of an old root (Broili & Schröder 1934).

TABLE 1

GORGONOPSIA

		Aelurosaurus felinus (R 339)	*Aelurosaurus felinus* (R 855*a*)	*Aelurosauroides watsoni* (R 855)	an aelurosaurid (337)	*Dixeya quadrata* (79)	*Gorgonops torvus* (R 1647)	*Cynariops robustus* (R 5743)	*Scylacops capensis* (R 121), partly sectioned	*Scymnognathus whaitsi* (R 49396), sectioned specimen	large unidentified gorgonopsid (R 256), sectioned specimen. Right side only preserved
UPPER DENTITION											
dental formula ...		5.1.5	5.1.5	5.1.5	5.1.5	5.1.4 and 5	5.1.?	4.1.3	5.1.7	?.1.5 or 6	?.1.?
teeth in process of replacement: incisors	R	all	1, 3, 5	none	all	none	none	2, 3, 4	none	—	—
	L	all	2, 3, 5	none	all	none	none	2, 3	none	—	—
canines	R	yes	yes	no	yes	no	no	yes	no	no	no
	L	yes	yes	no	yes	no	no	obs.	no	no	—
cheek teeth	R	none	4	none	1	none	none	none	n.v.	n.v.	—
	L	none	4	none	1, 2	none	none	none	n.v.	n.v.	—
position of plug of spongy bone in the pair of canine alveoli on each side	R	abs.	abs.	post.	ant.	post.	post.	obs.	post.	post.	post.
	L	abs.	abs.	abs.	ant.	post.	post.	abs.	post.	post.	—
position of root of old canine in pair of canine alveoli	R	abs.	ant.	abs.	ant.	post.	post.	obs.	post.	post.	post.
	L	post.	abs.	post.	ant.	post.	post.	post.	post.†	post.	—
LOWER DENTITION											
dental formula ...		4.1.5	4.1.5	—	4.1.5	—	—	—	4.1.7	4.1.4	5.1.2+
teeth in process of replacement: incisors	R	1, 4	1, 2	—	1, 2, 3	—	—	—	none	3 (poss.)	none
	L	1, 2, 3	1, 3	—	1, 2, 3	—	—	—	none	n.v.	—
canines	R	yes	yes	—	yes	—	—	—	none	none	none
	L	yes	yes	—	obs.	—	—	—	none	none	—
cheek teeth	R	3	2	—	none	—	—	—	2	none	—
	L	3	3, 5	—	3	—	—	—	3	none	—
roots of old canines		none	none	—	none	—	—	—	none	none	none

THEROCEPHALIA

		Trochosaurus major (R 5747)	*Pristerognathus polyodon* (R 2581)	*Pristerognathus polyodon* (R 393)	*Cynariognathus platyrhinus* (R 4097), sectioned specimen	*Notosollasia laticeps* (R 5699)	*Whaitsia* sp. (100)
UPPER DENTITION							
dental formula ...		5.2.3?	6 and 7.1.4+	6.1.3+	6?.1.6	5.1.0	5.1.0
teeth in process of replacement: incisors	R	none	none	1	—*	none	none
	L	5	none	2	none	none	none
canines	R	both	no	no	—*	no	no
	L	obs.	no	no	no	no	no
cheek teeth	R	obs.	none	none	—*	—	—
	L	?	3	none	none	—	—
position of plug of spongy bone in the pair of canine alveoli on each side	R	abs.	post.	post.	—*	post.	post.
	L	obs.	post.	post.	post.	post.	post.
position of root of old canine in pair of canine alveoli	R	abs.	post.	post.	—*	obs.	post.
	L	obs.	post.	post.	post.	post.	post.
LOWER DENTITION							
dental formula ...		3.1.5	3.1.7 and 8	3.1.7	1+.1.8	0.1.0	—
teeth in process of replacement: incisors	R	1	none	none	n.v.	—	—
	L	1, 3	2	none	n.v.	—	—
canines	R	yes	none	none	n.v.	none	—
	L	yes	none	none	n.v.	none	—
cheek teeth	R	not known	none	none	n.v.	—	—
	L	not known	6	none	n.v.	—	—
roots of old canines		none	none	none	n.v.	one on each side	—

Key. abs. = absent, post. = posterior, ant. = anterior, obs. = obscured, n.v. = none visible, poss. = possibly.

* Upper jaw dentition preserved on left side only.

† Small piece of root of another canine lies buccal to right functional tooth.

Note. This table is a record of replacement teeth actually present in the specimens. No mention has been made here of empty alveoli from which replacement teeth may have fallen after the death of the animal.

TABLE 2

		anterior canine alveolus: functional teeth R.	functional teeth L.	replacing teeth R.	replacing teeth L.	plug of spongy bone R.	plug of spongy bone L.	old root R.	old root L.	posterior canine alveolus: functional teeth R.	functional teeth L.	replacing teeth R.	replacing teeth L.	plug of spongy bone R.	plug of spongy bone L.	old root R.	old root L.
THEROCEPHALIA	*Whaitsia* sp. (100)	+	+	0	0	0	0	0	0	0	0	0	0	+	+	+	+
	Notosollasia laticeps (R 5699)	+	+	0	0	0	0	0	0	0	0	0	0	+	+	?	+
	Cynariognathus platyrhinus (R 4097) sectioned specimen	–	+	–	0	–	?	–	0	–	0	–	0	–	+	–	+
	Pristerognathus polyodon (R 393)	+	+	0	0	0	0	0	0	0	0	0	0	+	+	+	+
	Pristerognathus polyodon (R 2581)	+	+	0	0	0	0	0	0	0	0	0	0	+	+	+	+
	Trochosaurus major (R 5747)	+	+	+	?	0	?	0	?	+	+	+	?	0	?	0	?
GORGONOPSIA	large unidentified gorgonopsid (R 256)	+	–	0	–	0	–	0	–	0	–	0	–	+	–	+	–
	Scymnognathus whaitsi (R 49396), sectioned specimen	+	+	0	0	0	0	0	0	0	0	0	0	+	+	+	+
	Scylacops capensis (R 121), partly sectioned	+	+	0	0	0	0	+	0	0	0	0	0	+	+	+	+
	Cynariops robustus (R 5743)	0	+	+	?	?	0	?	0	+	0	?	?	?	0	?	+
	Gorgonops torvus (R 1647)	+	+	0	0	0	0	0	0	0	0	0	0	+	+	+	+
	Dixeya quadrata (79)	+	+	0	0	0	0	0	0	0	0	0	0	+	+	+	+
	an aelurosaurid (337)	0	0	+	+	+	+	+	+	+	+	0	0	0	0	0	0
	Aelurosauroides watsoni (R 855)	+	+	0	0	0	0	0	0	0	0	0	0	+	0	0	+
	Aelurosaurus felinus (R 855*a*)	0	+	+	+	0	0	+	0	+	0	0	+	0	0	0	0
	Aelurosaurus felinus (R 339)	+	+	+	+	0	0	0	0	0	0	+	+	0	0	0	+

then, in a random sample, we would expect on the average one-quarter of the specimens to have both the functional canines in the anterior alveoli, half to have one in the anterior alveolus and one in the posterior, and a quarter to have them both in the posterior alveoli. This is, in fact, exactly what we have in our small sample of four specimens. The size of this sample is, of course, so small that any test of significance would be valueless. This sample does show, however, that the time of replacement of the upper canines on each side of the jaw was not strictly synchronized, as it would be if either the anterior or the posterior pair bore the functional teeth, and the simplest hypothesis, which is therefore to be preferred, is that both sides were replaced independently.

The nine specimens in which there are certainly no replacing canines have both the functional teeth in the anterior alveoli. In two cases (R 256 and R 4097) doubt arises because

Table 3

	any replacement canines present in either of the pair of alveoli	no such replacement canines present	
functional canine in anterior alveolus	3	20	23
functional canine in posterior alveolus	4	0	4
	7	20	27

the maxilla of one side is absent. Taking as our unit the alveolar pair on one side, as we are justified in doing if the replacement on the two sides is independent, table 3 can be constructed. This table shows that the functional canine is in the anterior alveolus in the twenty alveolar pairs in which there is no replacement canine, while of the seven alveolar pairs in which canine replacement was going on at the animal's death, the functional tooth is in the anterior alveolus in three, and in the posterior in four. Application of the χ^2 test, making Yates' correction for continuity in view of the small size of the expected numbers, shows that this difference is significant ($P<0{\cdot}01$).* Table 1 further shows that in those specimens (R 855, 79, R 1647, R 121, R 49396, R 256, R 2851, R 393, R 4091, R 5699 and 100) in which there are no replacing upper canines, the replacement of the other teeth is limited or absent (seven give no evidence of tooth replacement, one is replacing three teeth, two are replacing two teeth, and one is doubtfully replacing one). Only one of the seven specimens giving no evidence of any tooth replacement shows the full dentition; and from this it may be argued that some of these specimens were, in fact, replacing teeth at the time of their death. Three (R 855, 79 and 100), however, show the whole upper dentition clearly, and here there is definitely no tooth replacement. In any case, the whole picture shown by these eleven specimens is in striking contrast to that shown by the four specimens with replacing upper canines. Here brisk replacement is going on all over the place. The three specimens prepared with acid (R 339, R 855*a* and 337) were each replacing about half of

* In this case it is possible to calculate the exact probability of obtaining the arrangement of table 3, without reference to χ^2. This can be done by the method of Yates (1934) and gives a probability of 0·002. The two methods of approach lead here to the same conclusion.

their teeth at the time of their death; and even R 5743, a very imperfectly prepared specimen, is definitely replacing seven of the eleven teeth visible, and may well be replacing more.

The following hypothesis is put forward to explain these observations. Let us suppose that during the early part of the animal's life tooth replacement went on briskly. The pair of canine alveoli in each maxilla bore the functional tooth alternately, the two sides of the jaw being independent as far as the timing of the replacement was concerned. Then, as the animal approached its full size, the rate of tooth replacement diminished, finally ceasing altogether. The cessation always occurred with the functional upper canine in the anterior alveolus. This invariable occurrence of the permanent upper canine in the anterior alveolus suggests that these teeth were replaced a definite, fixed number of times. This may be true for the other teeth as well. In this case the animals had a number of deciduous dentitions, not perhaps the same number for all the teeth, followed by a final, permanent dentition.

In favour of the suggestion that tooth replacement occurred during growth of the animal in size, it should be noted that the diameter of the old root often shows that the functional upper canine is larger than its predecessor (Broom (1936) in *Pristerognathus vanderbyli*, and the same may be observed in many specimens of the present series). Broom (1925) had observed that the functional upper canine sometimes lay anterior to an old root, and he states that this anterior upper canine formed the permanent tooth.

The evidence for the eventual cessation of tooth replacement comes largely from the upper canines; and, from the very nature of the case, it can only be negative, i.e. no replacement teeth can be seen in any specimen. It might therefore be argued that replacement of these teeth went on throughout the life of the animal. With advancing age, this argument would continue, replacement slowed down so much that, in those twenty alveolar pairs in which no replacement canines can be seen, the germs of the latter, although present, had not calcified sufficiently to be preserved in the fossil state.

This argument can be shown to be untenable for the following two reasons:

(1) Following acid preparation it is possible to detect replacement teeth at a very early stage of their development. Specimens R 339 and R 855*a* clearly show two sets of replacement upper canines, of which the smaller would have supplied the next-but-one functional teeth. The replacement canines must have grown slowly to their ultimate large size, and thus in these two specimens the second replacement canines could not have become functional for a long time. In addition, specimens 79 and R 855, which show no replacement canines, also show the roots of the penultimate canines quite resorbed on one side of R 855 and almost completely resorbed on both sides of 79. This resorption was, in itself, a very slow process; specimen R 121 shows the root of the ante-penultimate canine still present, although the root of the penultimate tooth is already showing considerable resorption. Those specimens in which no replacing upper canines can be seen must have been replacing these teeth very slowly indeed if, in fact, they were not the permanent dentition.

(2) The second reason, however, is decisive. If replacement of the upper canines were still going on, no matter how slowly, the pair of alveoli in each maxilla would bear the functional canine alternately. Supposing replacement to be taking place, in a random sample of such alveolar pairs, half, on the average, will bear the functional canine in the

anterior alveolus, half in the posterior. All the twenty pairs in which replacing teeth were absent had the functional canine in the anterior position, as we have already seen (p. 128). It is easy to calculate the probability of this arrangement having arisen by chance on the hypothesis of continued slow replacement. The probability of the tooth being in the anterior position in any one alveolar pair on this hypothesis being $\frac{1}{2}$, the probability of its being in the anterior position in twenty such pairs is $(\frac{1}{2})^{20} = 9{\cdot}5 \times 10^{-7}$ or about one to a million against. The hypothesis of continued slow replacement is untenable.

The general story of the evolution of tooth replacement in the mammal-like reptiles seems to be as follows. In the earliest and most primitive forms (e.g. *Varanosaurus*) there is a long row of maxillary teeth, of which two, about a third of the way back from the front of the maxilla, are rather enlarged and may be called 'canines'. In the more primitive ophiacodonts the replacement of the teeth is strictly distichial, each tooth being functionally replaced by a member of the tooth family of the adjacent alveolus (figure 17), and not much more than half the alveoli bore functional teeth at any one time (Romer & Price 1940).

In the more advanced ophiacodonts (edaphosaurs) and in the sphenacodonts, there are only occasional gaps in the tooth row, most of the alveoli bearing functional teeth at any given time. In an advanced sphenacodont, such as *Dimetrodon*, the two enlarged maxillary teeth (canines) have become so large that the pre-canine maxillary teeth are reduced in number to three or less. The post-canines (cheek teeth) are also reduced in number to about a dozen. The majority of the teeth are functional at any one time, although, as Parrington (1936*b*) has shown, it is still possible to demonstrate distichism in them. Despite this, the tooth which is the *functional* replacement is a member of the tooth family of the replaced tooth, and *functional* distichial replacement has vanished.

The pair of upper canines in each maxilla are replaced alternately, but most of the time the animal has two pairs of functional upper canines. Each canine was functionally replaced by a member of its own tooth family; but this replacement was quite a slow process, specimens being known in which only one of the alveolar pair bears a functional canine, the other alveolus showing the tip of a replacement canine (Romer & Price 1940).

The most primitive of the Therocephalia (e.g. *Trochosaurus*) are not dissimilar in this matter from *Dimetrodon*. All that has happened is that the number of the cheek teeth has been reduced from about a dozen to six or eight. Owing to the small number, no trace of distichism can be seen, and the functional replacement was always by a member of the same tooth family. As in *Dimetrodon* there was a pair of functional upper canines on each side in these primitive Therocephalia, and they were replaced alternately. The functional replacement for each of the pair was the next member of its own tooth family. Like *Dimetrodon*, when one of the upper canines was being replaced, these Therocephalia must have had but one functional canine on that side of the jaw.

The only difference between these primitive forms and the more advanced members of the Therocephalia and the whole of the Gorgonopsia is that in the latter, where the number of cheek teeth tends to be still further reduced, there is only one functional canine on each side of the upper jaw. This single maxillary canine is also to be found in the carnivorous Deinocephalia (contemporaries of the early Therocephalia); and it persists in all subsequent carnivorous synapsids, including the mammals. The change from a pair of canines in each maxilla to only one must therefore have conveyed some selective advantage, and it is not hard to see what this was. A single enlarged tooth on each side of the upper jaw would be a much more efficient instrument for stabbing and grasping than a pair of such teeth. This change was brought about by the establishment of a secondary distichial mode of replacement, for the reasons already discussed on p. 122.

These Gorgonopsia and Therocephalia almost certainly had a definite limited tooth replacement. This would have had the selective advantage that when the animal was fully grown it could dispense with the exhausting and inconvenient process of tooth replacement. A further advantage can be seen in those specimens showing brisk tooth replacement (e.g. R855*a*) and comparing them with those in which none is visible (e.g. 79). In the former the teeth are held but loosely in their alveoli, while in the latter the bone grasps the teeth firmly. These firmly held teeth would function more efficiently than the loosely held teeth of the former group.

I know of no evidence suggesting a limited tooth replacement in the Pelycosaurs; and I have no evidence at all for the Deinocephalia.

The successors of the Gorgonopsia and the Therocephalia were the Cynodontia and the Bauriomorpha. As far as the latter group is concerned I know nothing which is relevant to the discussion; but in the cynodonts the upper canines were replaced in the same way as in the earlier Theriodontia. This is shown by the observations of Seeley (1895) on *Cynognathus* and those of Broom (1932) on *Trirachodon*, together with my own observations on *Cynognathus*, *Thrinaxodon* and *Procynosuchus*. Work on tooth replacement in these later theriodonts is now in progress.

The present work suggests that, while Bolk is generally incorrect in postulating that the deciduous and permanent dentitions of the Mammalia are members of different tooth families, he may well be correct as far as the upper canines are concerned. This very difficult problem of the change from the condition found in the mammal-like reptiles to the condition found in the mammals may be solved by work on the advanced theriodonts.

Finally, the danger of defining species or genera of these Karroo reptiles on dental formulae has now been clearly demonstrated. The actual number of teeth is indefinite and may even differ on opposite sides of the same individual. Specimens 337 (an unknown aelurosaurid) and R855 (*Aelurosauroides watsoni*), both gorgonopsids, have four upper post-canines on one side and five on the other, while the therocephalian R2581 (Seeley's type of *Pristerognathus polyodon*) has eight lower post-canines on the left and seven on the right. This last specimen is still more disturbing as it has seven upper incisors on the left and six on the right.

It must also be remembered that in the past the number of teeth was often simply assumed. For example, this specimen R2581, the type of its genus, has the rows of upper cheek teeth on both sides truncated posteriorly owing to damage. Thus, the true number of upper cheek teeth is unknown. Broom assumed this number to be six, and separated off those forms with eight into another closely related genus, *Alopecognathus*. Now that the type has been fully prepared, however, it is known to have seven or eight lower cheek teeth, and is unlikely to have had less than seven or eight in the upper jaw. So the status of the genus *Alopecognathus* is very doubtful. This is not an isolated example, and it must be realized that the detailed classification of the Gorgonopsia and Therocephalia is not in a satisfactory state. This is due, as much as anything, to inadequate preparation before description.

In conclusion, I wish to thank all those who have assisted me in this work, and the following in particular: Professor P. B. Medawar, F.R.S., Professor D. M. S. Watson, F.R.S., Mr W. N. Edwards, Dr E. I. White, F.R.S., Mr F. R. Parrington, Dr W. E. Swinton, Mr J. T. Robinson, Dr D. W. Seth-Smith, Mr A. E. Rixon, Mr P. Venning, Mr B. H. Newman, Miss R. Birbeck and my wife.

References

Bolk, L. 1922 Odontological Essays. No. 5. On the relations between reptilian and mammalian dentition. *J. Anat., Lond.*, **57**, 55.

Boonstra, L. D. 1934*a* Additions to our knowledge of the South African Gorgonopsia preserved in the British Museum (Natural History). *Ann. S. Afr. Mus.* **31**, 175.

Boonstra, L. D. 1934*b* A contribution to the morphology of the mammal-like reptiles of the suborder Therocephalia. *Ann. S. Afr. Mus.* **31**, 215.

Broili, F. & Schröder, J. 1934 Beobachtungen an Wirbeltieren der Karrooformation. III. Ein Gorgonopside aus den unteren Beaufort-Schichten. *S.B. bayer Akad. Wiss.*, p. 179.

Broom, R. 1915 Catalogue of types and figured specimens of fossil vertebrates in the American Museum of Natural History III—Permian, Triassic and Jurassic reptiles of South Africa. *Bull. Amer. Mus. nat. Hist.* **25**, 105.

Broom, R. 1925 On some carnivorous therapsids. *Rec. Albany Mus.* **3**, 309.

Broom, R. 1930 On the structure of the mammal-like reptiles of the suborder Gorgonopsia. *Phil. Trans.* B, **218**, 345.

Broom, R. 1932 *The mammal-like reptiles of South Africa.* London: Witherby.

Broom, R. 1936 On the structure of the skull in the mammal-like reptiles of the suborder Therocephalia. *Phil. Trans.* B, **226**, 1.

Haughton, S. H. 1926 On Karroo vertebrates from Nyasaland. *Trans. Geol. Soc. S. Afr.* **29**, 69.

Jepson, G. L. 1940 Palaeocene faunas of the Polecat Bench formation, Park County, Wyoming. Part I. *Proc. Amer. Phil. Soc.* **83**, no. 2, 217.

Kühne, W. G. 1956 (in press). *The Liassic Therapsid* Oligokyphus. London: British Museum.

Lydekker, R. 1890 *Catalogue of the fossil Reptilia and Amphibia in the British Museum (Natural History)*, Part 4. London: British Museum.

Owen, R. 1876 *Descriptive and illustrated catalogue of the fossil Reptilia of South Africa in the collection of the British Museum.* London: British Museum.

Owen, R. 1881 On the order Theriodontia, with a description of a new genus and species (*Aelurosaurus felinus* Owen). *Quart. J. Geol. Soc. Lond.* **37**, 261.

Parrington, F. R. 1936*a* On the tooth replacement in Theriodont reptiles. *Phil. Trans.* B, **226**, 121.

Parrington, F. R. 1936*b* Further notes on tooth replacement. *Ann. Mag. Nat. Hist.* (10), **18**, 109.

Parrington, F. R. 1953 Private communication.

Parrington, F. R. 1954 Private communication.

Parrington, F. R. 1955 On the cranial anatomy of some gorgonopsids and the synapsid middle ear. *Proc. Zool. Soc. Lond.* **125**, 1.

Rixon, A. E. 1949 The use of acetic and formic acids in the preparation of fossil vertebrates. *Mus. J., Lond.*, **49**, 116.

Romer, A. S. & Price, L. I. 1940 Review of the Pelycosauria. *Spec. Pap. geol. Soc. Amer.* **28.**

Seeley, H. G. 1894 Researches on the structure, organisation and classification of the fossil reptiles. ix (1). On the Therosuchia. *Phil. Trans.* B, **185**, 987.

Seeley, H. G. 1895 Researches on the structure, organisation and classification of the fossil reptiles. ix (5). On the skeleton in new Cynodontia from the Karroo rocks. *Phil. Trans.* B, **186**, 59.

Tomes, C. S. 1894 *A manual of dental anatomy, human and comparative.* 4th Edition. London: Churchill.

Toombs, H. A. 1948 The use of acetic acid in the development of vertebrate fossils. *Mus. J., Lond.*, **48**, 54.

Watson, D. M. S. 1921 The bases of classification of the Theriodontia. *Proc. Zool. Soc. Lond.* p. 35.

Watson, D. M. S. 1926 The evolution and origin of the Amphibia. *Phil. Trans.* B, **214**, 189.

Yates, F. 1934 Contingency tables involving small numbers and the χ^2 test. *Suppl. J.R. Statist. Soc.* **1**, 217.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

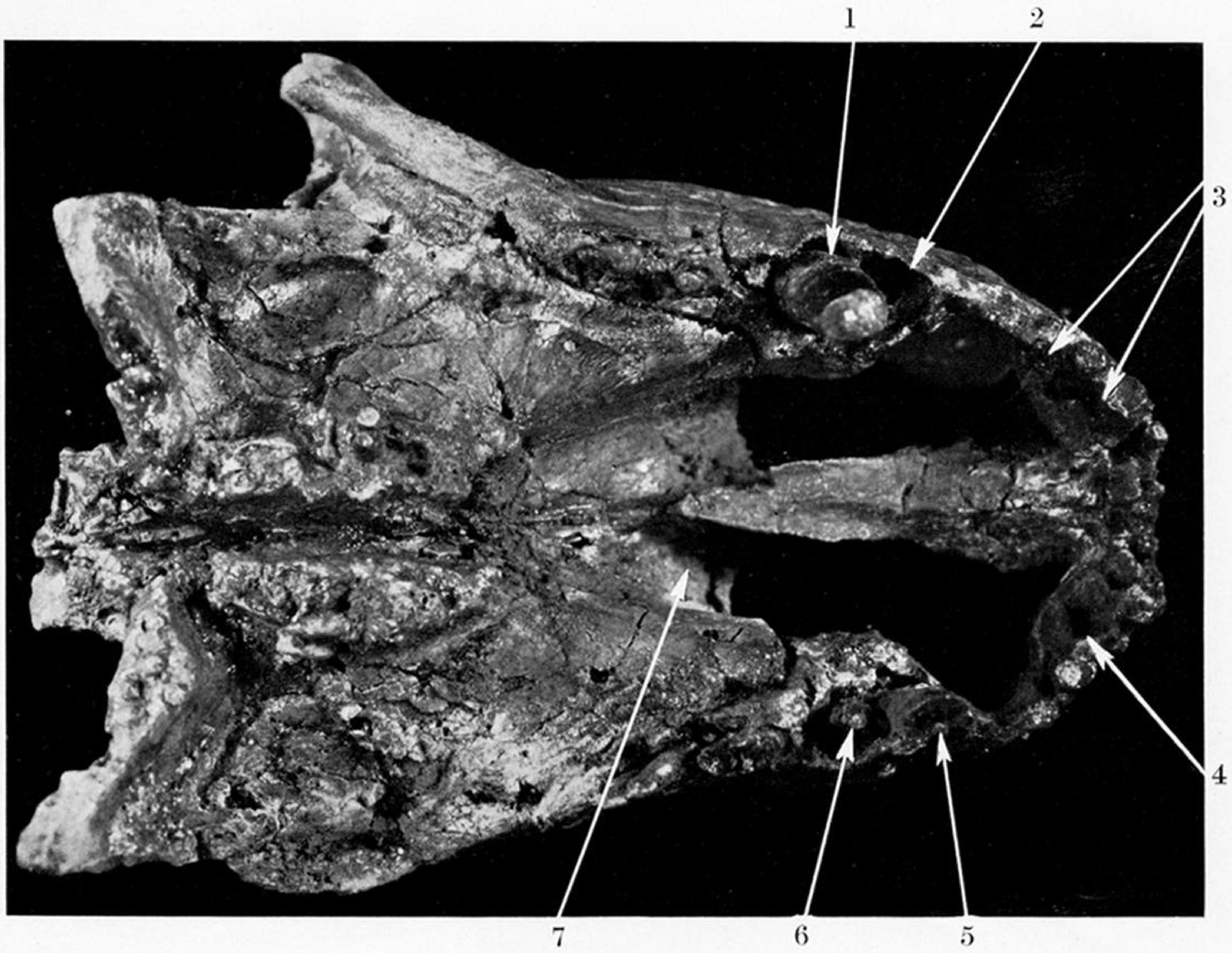


FIGURE 20

FIGURE 21

DESCRIPTION OF PLATE 6

FIGURE 20. Palatal view of specimen R 855*a* (*Aelurosaurus felinus*). 1, functional canine; 2, root of old canine; 3, replacement incisors; 4, lingual extension of alveolus from which a replacement tooth has probably fallen out; 5, functional canine; 6, tooth which will immediately succeed the canine now functional; 7, deep channel formed by vomer and palatine.

FIGURE 21. Lingual view of left upper canine of specimen R 855*a*. 1, functional canine in anterior alveolus; 2, replacement canine *A*. This is the oldest member of the tooth family of the posterior alveolus and would have been the successor to the functional canine; 3, empty lingual extension of alveolus from which a replacement tooth has almost certainly fallen out after death; 4, replacement cheek tooth; 5, floor of respiratory channel formed by palatines and vomer; 6, replacement canine *B*. This is the next tooth of the family of the anterior alveolus and would succeed replacement canine *A* as the functional canine.

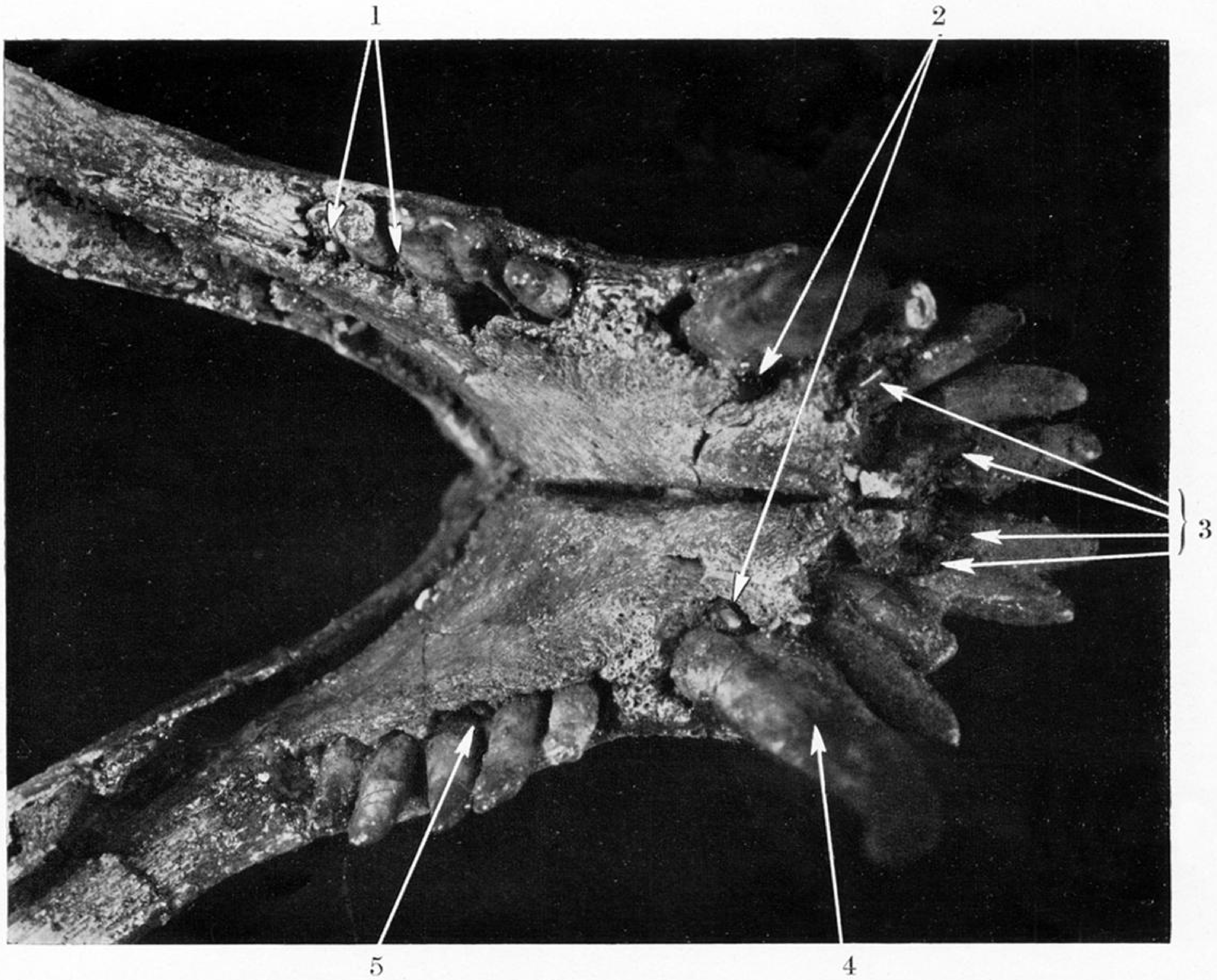


FIGURE 22

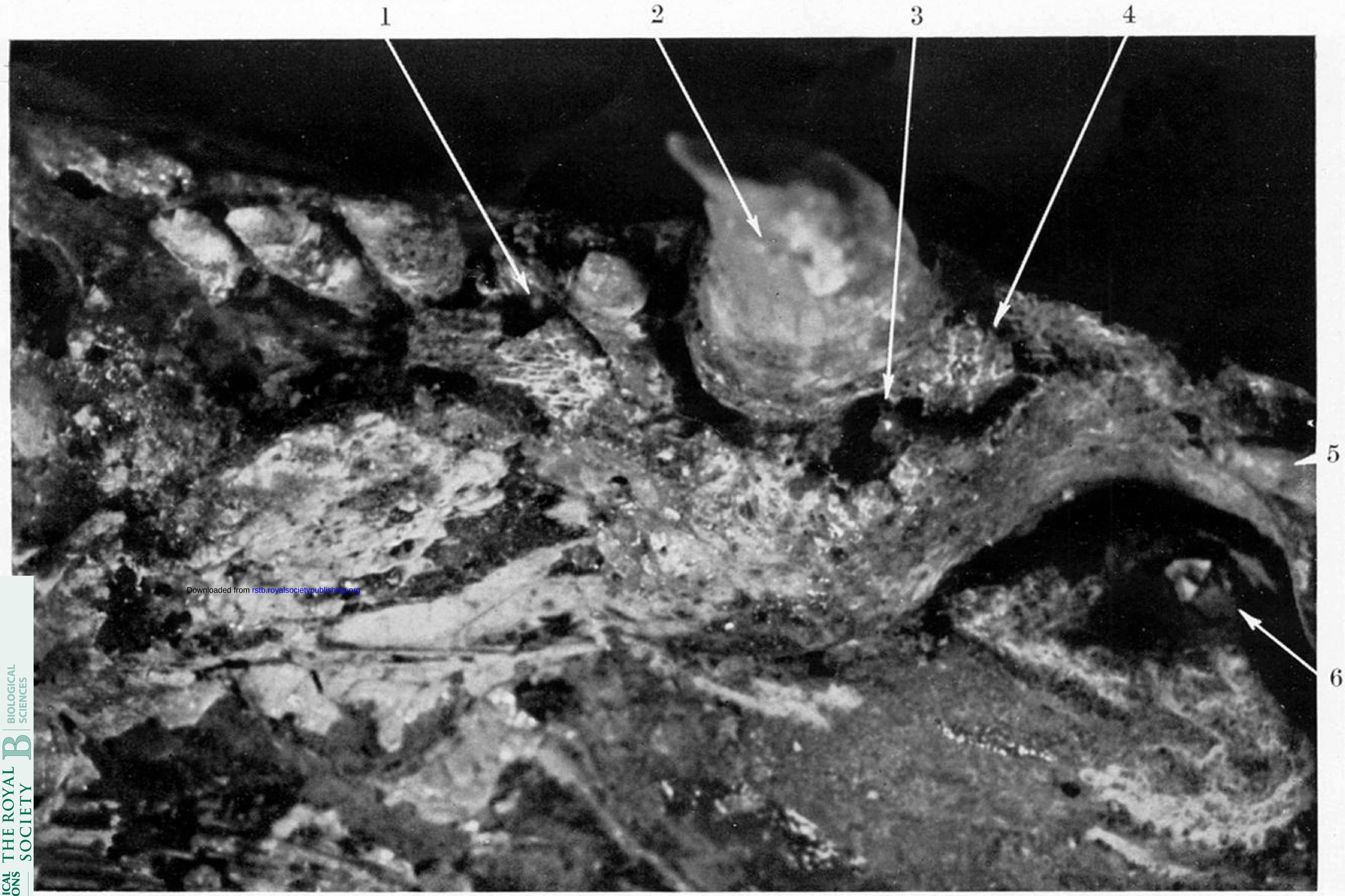


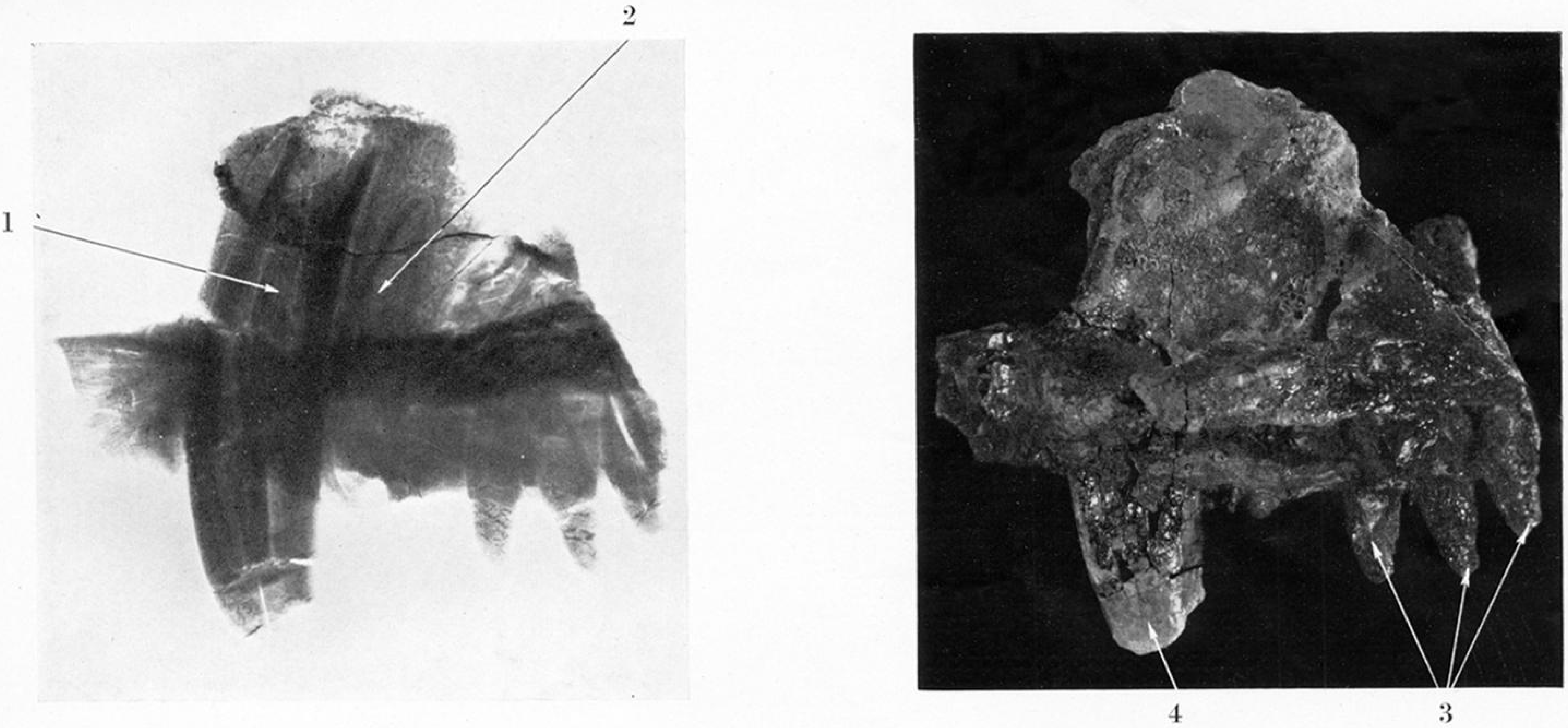
FIGURE 23

DESCRIPTION OF PLATE 7

FIGURE 22. Dorsal view of lower jaw of specimen R855*a* to show pair of replacement canines. 1, replacement cheek teeth; 2, replacement canines; 3, replacement incisors; 4, functional canine; 5, replacement cheek tooth.

FIGURE 23. Lingual view of right upper canine of specimen 337 (unnamed aelurosaurid) to show plug of spongy bone and replacing teeth. 1, replacement cheek tooth; 2, functional canine; 3, tip of replacement canine; 4, plug of spongy bone covering old root; 5, crown of most distal incisor; 6, detached tip of lower canine.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES



a *b*

FIGURE 24

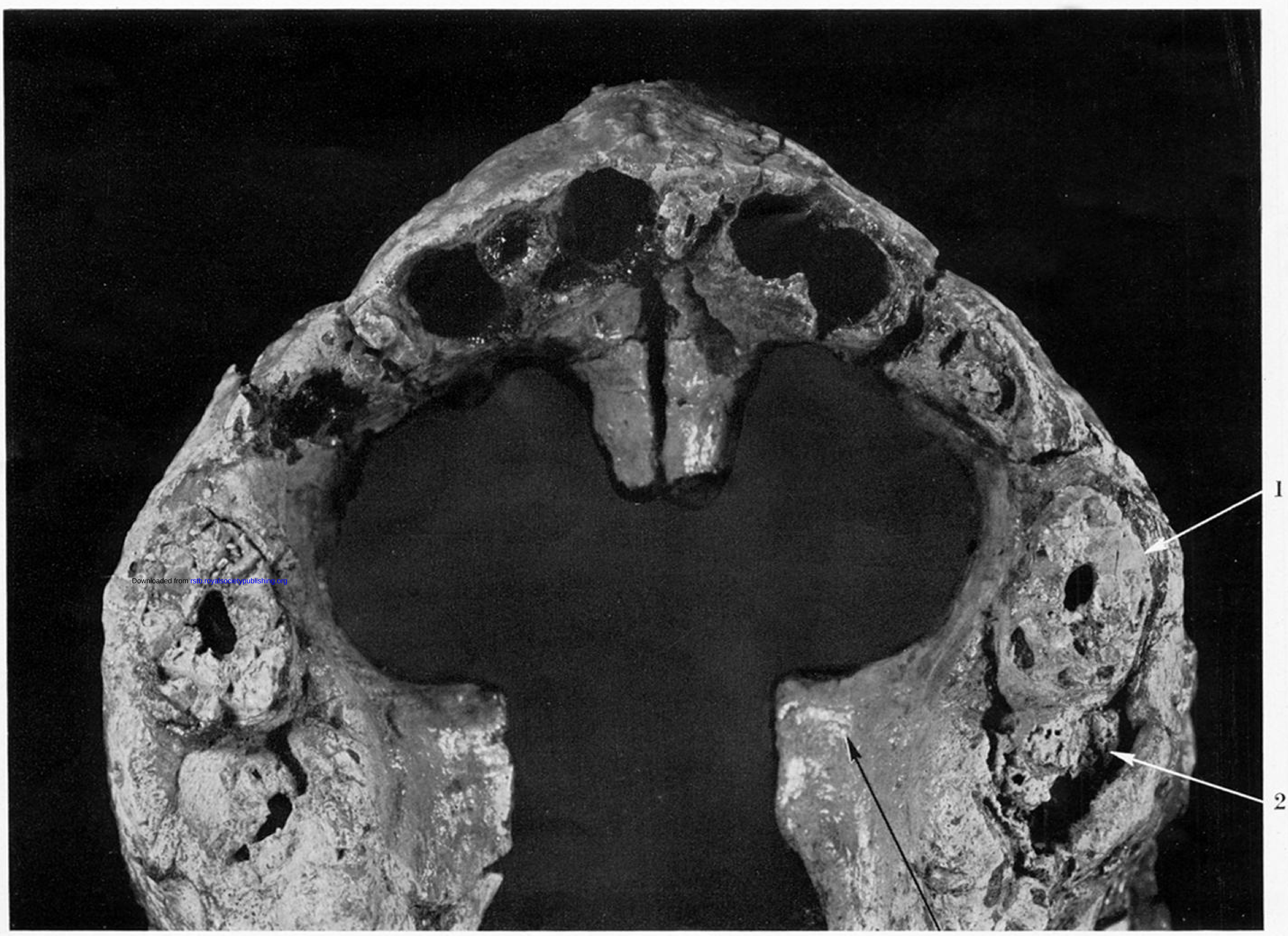


FIGURE 25

DESCRIPTION OF PLATE 8

FIGURE 24. (*a*) Lingual view of right upper canine of specimen R 393 (*Pristerognathus polyodon*). (*b*) X-ray photograph of same to show closed root of old canine behind functional tooth. 1, open pulp cavity at root of functional canine; 2, closed pulp cavity of root of old canine; 3, cheek teeth; 4, functional canine.

FIGURE 25. Palatal view of specimen 100 (*Whaitsia* sp.) to show plug of spongy bone behind each canine. 1, functional canine; 2, plug of spongy bone covering old root; 3, palatal process of maxilla.