THE ANATOMY OF THE THECODONT REPTILE *EUPARKERIA CAPENSIS* BROOM

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[Plates 31 to 34]

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The South African Museum specimens of *Euparkeria* originally described by Broom (1913 *a, b*) and later studied by Haughton (1922) have been further prepared using the dental mallet. In addition, material in Professor D. M. S. Watson's collection has been prepared and studied.

As a result of inquiries made at Aliwal North, it is suggested that all the material may represent a single find and a small exposure of *Cynognathus* zone shale close to the town is considered to be the most probable location of the site.

On the basis of the specimens already mentioned a detailed description of most of the skeleton is given, the only parts remaining unknown, or incompletely known, being the carpus and manus, the braincase and the caudal vertebrae.

The following features are discussed in functional terms: skull architecture; the limbs and their girdles; the vertebral column and ribs. The skull, although showing some adaptation to predacious habits, is relatively unspecialized and a subsequent reversal of trend towards a more omnivorous

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or even vegetarian diet is not impossible. A consideration of the probable arrangement of the jaw muscles suggests that the antorbital fenestra of the archosaurs was not originally evolved in relation to the development of the pterygoideus D musculature.

A study of the limbs and their girdles indicates that *Euparkeria* was facultatively bipedal and that when this gait was adopted the femora were brought into a vertical position, although they must have been held horizontally while at rest or moving slowly.

It is suggested that the alteration in position of the rib articulations along the length of the vertebral column is related to efficiency of pulmonary ventilation. Expansion of the tips of the neural spines is shown to be related not to the development of dermal armour but to the arrangement of the muscles of the transversospinalis system. The term 'scute tables' used to designate these expansions is therefore abandoned and they are referred to simply as spine tables.

The relationships of *Euparkeria* to other groups is briefly discussed. *Euparkeria* shows a number of progressive features related to a highly carnivorous habit and increased locomotor efficiency combined with retention of several primitive characters. Previous authors have tended to lay emphasis on one or other of these types of characteristic and accordingly classify *Euparkeria* either as an advanced form or as a very primitive one: the consequent variation in proposed systematic position ranges from inclusion in the Sphenosuchidae (v. Huene 1962) to the Erythrosuchidae (Hughes 1963). It is concluded that *Euparkeria*, although a progressive form, is closely related to the latter family with which it may be convenient, for the time being, to classify it. It could well have been directly ancestral to advanced pseudosuchians such as *Ornithosuchus* and *Hesperosuchus* and possibly to the prosauropods and sauropods but not to the ornithischians or the birds and was a trifle too advanced to have been directly ancestral to the Aëtosauridae, to which it is, however, closely related.

I. INTRODUCTION

Euparkeria was first described by Broom (1913*a*, *b*) on the basis of material then in the collection of Mr A. Brown of Aliwal North. After Brown's death, his collection was acquired by the South African Museum and Haughton (1922) did some further work on the *Euparkeria* specimens. Both of these workers had at their disposal only very crude means of mechanical preparation and were therefore not able to extract all the information available from the specimens. It was thus clearly necessary for the material to be re-studied, using modern preparative techniques, so that a more complete description might be given. In order to do this, it was desirable to examine all the available specimens. In addition to the Brown collection, the South African Museum in 1924 and 1925 received further material from Aliwal North, from the collection of A. W. Higgins. A few *Euparkeria* specimens were presented in 1926 to Tübingen, where they are now in the collection of the Institut und Museum für Geologie und Paläontologie. In addition, Brown presented a slab containing *Euparkeria* remains to Professor D. M. S. Watson of University College London. This material was only partly developed and has not been described. A grant from the Royal Society and Nuffield Foundation enabled me to visit Tübingen and examine the material there, and also London, where Professor Watson's material was prepared and studied.

Although all the *Euparkeria* specimens are from Aliwal North, the exact details of the site, or sites, from which they came are not known. The South African Museum specimens are catalogued as 'A. Brown collection, Krielfontein, Aliwal North' and 'A. W. Higgins collection, Quarry, Commonage, Aliwal North', while the single Higgins collection specimen received in 1924 is listed as 'Higgins collection, Krielfontein, Aliwal North'. There are also a few unnumbered pieces.

A visit was made to Aliwal North in 1960 in order to try to identify the localities. The municipal authorities, although anxious to assist in every possible way, could find no record of Krielfontein anywhere in the neighbourhood and the commonage consisted of two separate areas on neither of which was there then, or was there known previously to have, been, a quarry. A preliminary survey of the commonages failed to disclose any deposits from which the specimens might have come. I was, however, fortunate enough to be introduced to the late Colonel D. N. de Wet, who as a youth had known Brown. He told me that there was only one place in the immediate neighbourhood where Brown had collected fossils and gave me directions where to find it. He also informed me that Higgins had done a great deal of collecting for Brown.

The area indicated by Colonel de Wet is situated on one of the commonages over the brow of a hill on the left of the road to Lady Grey just outside Aliwal North. A search here brought to light a small exposure of *Cynognathus* zone shale, with its typical large labyrinthodont remains. At the heads of several dongas the shale was overlain by sandstone of the same type as the *Euparkeria* matrix. Where the underlying shale had weathered away the sandstone had fallen down and broken into slabs and blocks, much like those containing the *Euparkeria* remains. Watson (1913) says that the specimens 'were found near Aliwal North in the *Cynognathus* zone of the Karroo system'. It thus seems extremely probable that this exposure is a *Euparkeria* locality. It is even possible that, despite the two localities listed in the South African Museum catalogue, all the specimens are from this single site. The 'Brown collection' contains all the best specimens, and it is known that Higgins collected for Brown. Thus Higgins may actually have found the material and presented all the most promising pieces to Brown, the ones he himself retained being those which Brown did not consider of much value. The fact that no quarry could be located on the commonage and that the name Krielfontein did not appear to be locally known, suggests the possibility that these were never official designations but may have been Higgins's and Brown's private names for the same collecting ground. The specimens could thus all represent a single find, originally made by Higgins, consisting of a group of individuals lying in close proximity. Certainly Watson's slab and specimen S.A.M. 6047 each contain two animals lying in close contact. Such an occurrence of a number of adult specimens lying in close contact is by no means unique. A group of *Trirachodon*, as yet undescribed, discovered by Mr S. Fourie in the *Cynognathus* zone lay together and Mr J. Kitching has also found similar groups of individuals in the same zone. The eight *Millerosaurus* described by Watson (1957) were also all close together, and Watson states that, in his opinion, the animals must have been together when they died, but does not discuss how this might have come about. There is no doubt that the *Euparkeria* specimens have been preserved on the spot where they died: the presence of dorsal scutes and even sclerotic bones in position is clear evidence that very little post mortem disturbance occurred. The most reasonable suggestion as to why a number of animals came to be killed in association would seem to be that they were buried alive while hibernating together in a single retreat. Plumstead (1963), on the basis of botanical evidence, has shown that throughout the period represented by the Karroo deposits seasonal changes were considerable, so that a small, probably largely insectivorous form like *Euparkeria* could hardly have survived the winter without hibernating. Indeed, she has suggested that both the pupal stage in insects and the habit of hibernating in terrestrial animals may have been first evolved in adaptation to the severe winters of lower Karroo times.

The specimens which have been utilized in preparing the description which follows are listed at the end of this section. Haughton (1922) studied six of these, referring to them as 1 to 6 and giving the Museum numbers of only the first three. It has, however, been possible to identify the others and Haughton's numbering is included in the list.

One of the specimens, number S.A.M. 6047, requires some discussion. The block so numbered contains the pelvis, femur and posterior dorsal vertebrae illustrated by Broom (1913*b*, Fig. 21) and described by him as belonging to a related but distinct genus, which he named *Browniella africana*. Broom also mentioned a shoulder girdle of *Browniella*, which he apparently thought belonged to another individual, but he gave no details, apart from a measurement of the length of the coracoid. It has been possible to identify this coracoid in one of a number of unlabelled fragments which were stored together in a box. Further development of this piece has brought to light in addition to the coracoid and some other parts of the shoulder girdle, a series of vertebrae, identifiable as numbers 7 to 13. Although half a vertebra is missing between these and the posterior dorsal series in the block numbered 6047 there is no doubt that they in fact belong to a single animal and Broom's two specimens of *Browniella* thus are one.

'*Browniella*' is somewhat larger than the *Euparkeria* specimens and, according to Broom, 'the ischium differs in shape in being constricted near its middle, and the pubis, besides being much broader and stouter, differs in having only a single pubic foramen'. These differences he regarded as sufficient to justify placing this specimen in a separate genus. Haughton (1922) pointed out that the apparent constriction of the ischium is really the result of damage and that the absence of a second pubic foramen is doubtful, since the pubis in this region is so thin that it is extremely difficult to determine the details of its structure either in this or in most of the *Euparkeria* specimens. He therefore came to the conclusion, with which I am entirely in agreement, that the '*Browniella*' specimen is simply a rather large *Euparkeria*, any differences between it and the other specimens being sexual rather than specific or generic.

The situation is complicated by the fact that there is an undoubted *Euparkeria* skull which originally lay close to the pelvis of specimen 6047. Haughton (1922) did not express his opinion very clearly, but seemed inclined to believe that this skull might belong to the same individual as the pelvis. This, however, cannot be the case. Close to the point where the skull contacts the numbered block containing the pelvis, further preparation of the latter has revealed the first three vertebrae belonging to the skull while in the box of unlabelled fragments is one which contacts the numbered block and contains the 4th to 13th vertebrae continuing this series.

It is thus clear that specimen 6047 is part of a once bigger block which contained remains of two animals. The smaller animal is represented by the skull and the vertebrae 1 to 3 and 4 to 13. Of the larger ('*Browniella*') the parts preserved are portions of the shoulder girdle, vertebrae 7 to 13 together with the posterior dorsals, pelvis and femur in the original numbered block. Since they clearly were once part of this block, the number 6047 has also been given to the skull, to the piece containing the coracoid and vertebrae 7 to 13 and to the piece containing vertebrae 4 to 13. For convenience, parts belonging to the small and to the large animal have been distinguished as 6047A and 6047B respectively.

The matrix in which the specimens are embedded is a somewhat irregularly calcified sandstone. It yields to treatment with acetic acid but the specimens are too delicate to be satisfactorily prepared by this method. Although acid was used to a slight extent, mainly for the cleaning of isolated bones, most of the preparation has been done mechanically, using a dental mallet.

The material used in the description which follows comprises the following specimens:

South African Museum Collection

S.A.M. 5867	the type specimen (Haughton's specimen 1).
S.A.M. 6047	several pieces of a single block containing parts of two animals. 6047A, skull, vertebrae 1 to 13 and some limb fragments. 6047B, vertebral column, pelvis and femur, parts of shoulder girdle. (Haughton's specimen 2)
S.A.M. 6048	six pieces including a maxilla in external view, the posterior end of another from the internal side, part of a skull roof showing the interparietal, a pelvis and some post-sacral vertebrae. (Haughton's specimen 3)
S.A.M. 6049	posterior dorsal, sacral and anterior caudal vertebrae, pelvis and right hind limb and portions of coracoids and interclavicle. (Haughton's specimen 4)
S.A.M. 6050	crushed incomplete skull. (Haughton's specimen 6)
S.A.M. 7696	large block with almost complete specimen including damaged posterior portion of skull
S.A.M. 7700	damaged scapula, humerus and proximal end of radius
S.A.M. 7702	posterior end of ilium and damaged post-sacral vertebrae
S.A.M. 7713	gastralia (dorsal aspect), with impression of vertebral centra and a few rib fragments
S.A.M. 13664	right pterygoid and ectopterygoid and part of left palatine. (This is the specimen mentioned by Haughton (1922) at the bottom of p. 83)
S.A.M. 13665	three pieces including crushed and somewhat disarticulated skull. (Haughton's specimen 5)
S.A.M. 13666	large block in four pieces, including part of a skull and some metacarpals
S.A.M. 13667	large block including crushed skull and some metacarpals
S.A.M. 7698	ilium, hind limb and tail fragments. (Now in the collection of the Institut und Museum für Geologie und Paläontologie of the University of Tübingen)

D. M. S. Watson Collection, University College London

R 527	a slab containing remains of two animals. A, Skull showing part of the braincase and vertebrae 1 to 16. B, Disarticulated skull fragments and vertebrae 1 to 16

II. Description

(1) *The skull*

The type specimen gives a good external view of the skull. In specimen 6047A the bones are slightly disarticulated and it thus gives some information about the shapes of individual bones and the way in which they are linked together.

(*a*) *External features* (figures 1*a*, 2*a* and *b*)

Broom (1913*b*) has figured restorations of lateral and dorsal views of the skull, made from the type specimen (figure 20, plate 31). In general features, there is little to add to or modify in his restoration, although some of the contacts shown between individual bones are not quite accurate. The skull is relatively high, with the snout not elongated. Although the top of the occiput is rounded, the skull table is almost flat, making a sharp angle with the lateral walls, so that in transverse section the skull is somewhat trapezoidal for most of its length. In construction it is typically archosaurian: the nostril is large and behind it lies a well-developed antorbital fenestra: the orbit is large and contains a ring of sclerotic bones: behind the orbit lie the two temporal fossae, the smaller, superior one facing dorsally; the larger, inferior fossa looking sideways and with the characteristic indentation of its posterior wall. There is no trace of a pineal opening. As in modern crocodiles, wherever the bones lie close under the skin the surface is sculptured. On the surangular and angular the sculpturing takes the form of fine roughly horizontal lines but elsewhere it forms a more irregular pattern of faint rugosities.

Premaxilla. In the type the anterior end of the snout is damaged and only the posterior part of the premaxilla is preserved. In specimen 6047A, however, the left premaxilla is complete except for the dorsal region where it meets the anterior end of the nasal (figure 21, plate 32). Anteriorly it forms a narrow, slightly forward sloping pillar, rounded on the external surface but flat internally where it meets its fellow in the midline. The alveolar border is deep and strong to accommodate the roots of the teeth. Its upper margin is gently convex, so that the lower border of the nostril is slightly scalloped. The thickened alveolar border abuts against the maxilla behind in a broad edge-to-edge contact. Above the level of the tooth sockets the posterior vertical ramus thins away to a flat plate of bone which is underlain by a flange extending forward from the maxilla, while its dorsal end fits into a depression in the descending anterior end of the nasal. The external line of contact between the premaxilla and the nasal runs with a downward slope from front to back, not an upward one as shown in Broom's Fig. 5.

Nasal. The nasal is a large bone, forming about half the length of the skull table. It forms a flat horizontal plate roofing the skull above the antorbital fenestra, while in front of the fenestra its edge is bent downwards sharply to meet the top of the maxilla. Anteriorly it extends forwards and downwards to form the postero-dorsal wall of the nostril and a slip of it underlies the top of the maxilla. The bone is thickest (about 1·5 mm) above the anterior border of the antorbital fenestra, but becomes thinner further back. The type skull is somewhat laterally compressed, but the full width of the bone is shown in specimen 6047A. From this it is clear that the skull table above the fenestra is distinctly wider than it appears in the type and Broom's restoration is thus too narrow in this region. The junctions with other bones are complex (figure 22, plate 32). The descending anterior wing bordering the nostril lies under the tip of the premaxilla and bears a depression to receive the tip of the latter. The posterior margin of this descending facial portion forms a groove into which fits a flange on the anterior edge of the maxilla, while a little higher up the upper wall of the groove vanishes and its lower wall is continued as a broad depression which receives the upper margin of the latter bone. Above the dorsal margin of the antorbital fenestra the groove is reconstituted and into it fits a projection on the upper edge of the lachrymal. Anteriorly the nasal is damaged and it is not possible to see how it joins the premaxilla above the nostril. Postero-laterally, the nasal meets the pre-frontal and posteriorly, the frontal, while in the midline it meets its fellow in a grooved suture. Thus, braced strongly against its fellow mesially and against the frontal behind, the nasal,

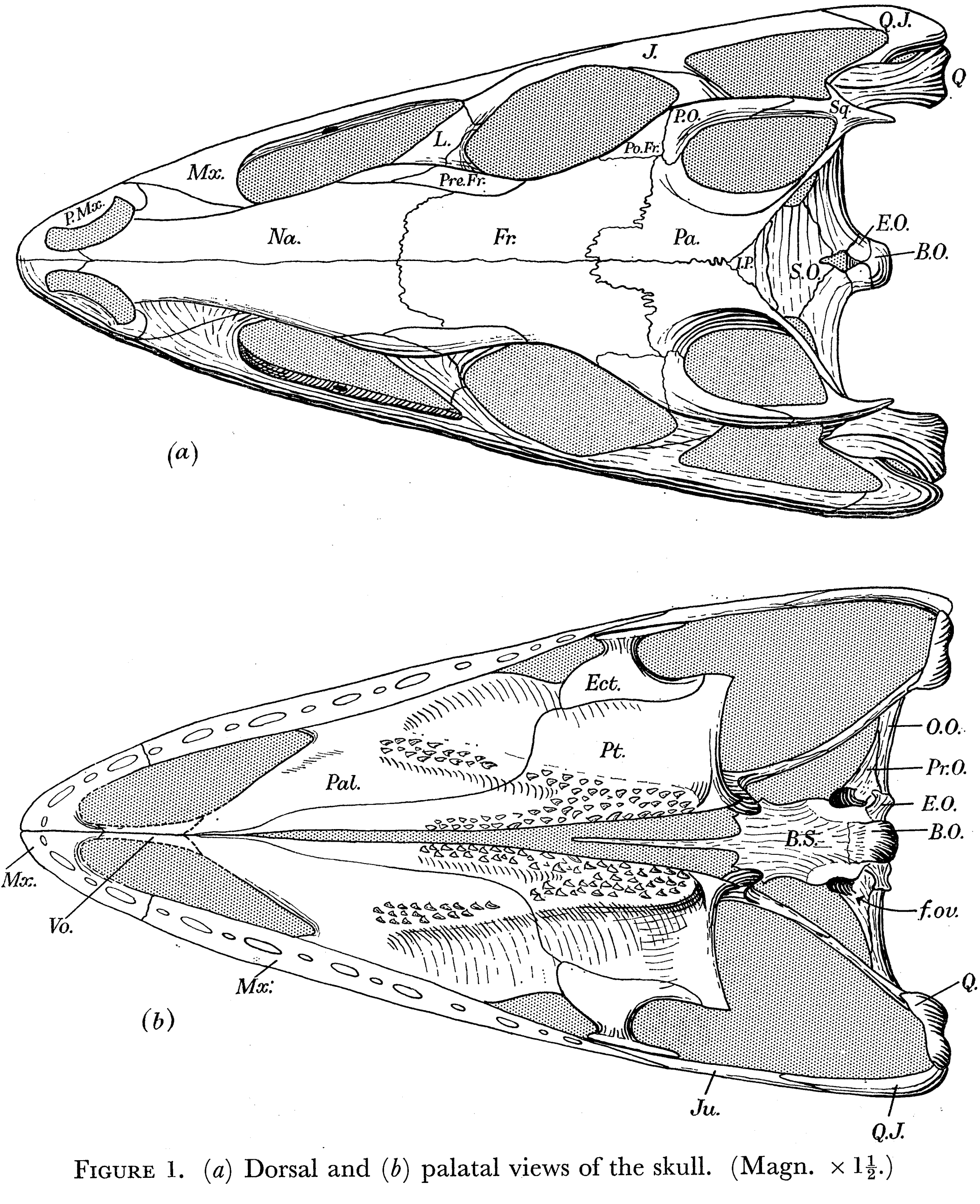

FIGURE 1. (*a*) Dorsal and (*b*) palatal views of the skull. (Magn. × $1\frac{1}{2}$.)

by means of its descending facial portion, gives firm support to the tooth-bearing elements of the upper jaw.

Frontal. The frontal forms the skull table from near the back of the antorbital fenestra to the back of the orbit, abutting in front against the nasal and uniting behind with the parietal

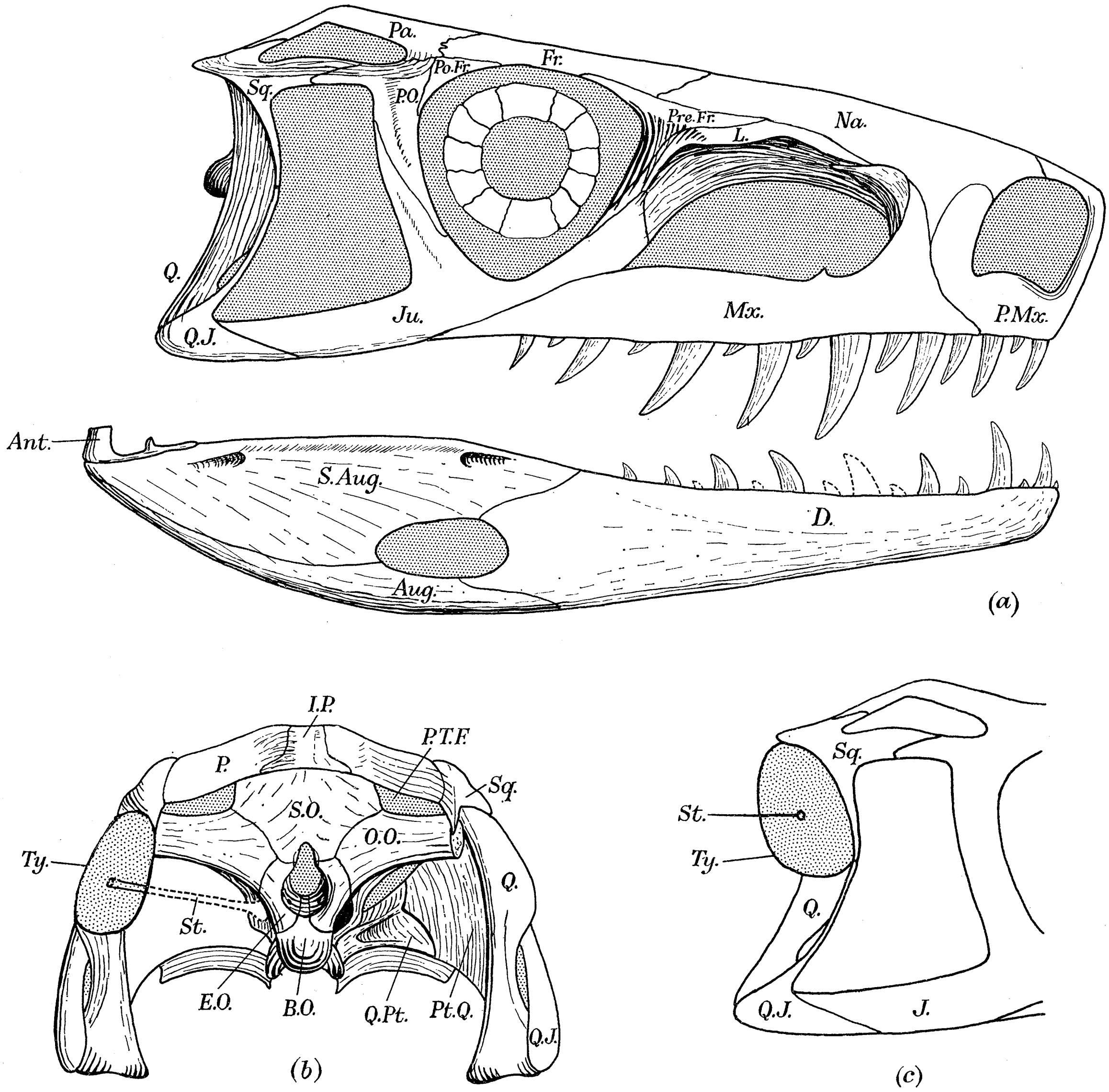

FIGURE 2. (*a*) Lateral view of skull and lower jaw. (*b*) Occipital view of skull. On the left the suggested arrangement of tympanum and stapes is shown. (*c*) Posterior end of skull showing suggested position of tympanum. (Magn. × 1½.)

by a sloping interdigitating suture. Antero-laterally and postero-laterally the frontal meets the pre- and post-frontals so that it borders the orbit only for a short distance. From specimen 6048 it can be seen that at the junction with the pre-frontal the two bones overlap, the frontal extending beneath the posterior wing of the pre-frontal in a surface which is longitudinally splined to prevent lateral dislocation of the latter bone.

Parietal. The parietal is of somewhat complex shape. A flat expansion, meeting the frontals and post-frontals anteriorly, in an interdigitating suture, forms the posterior part

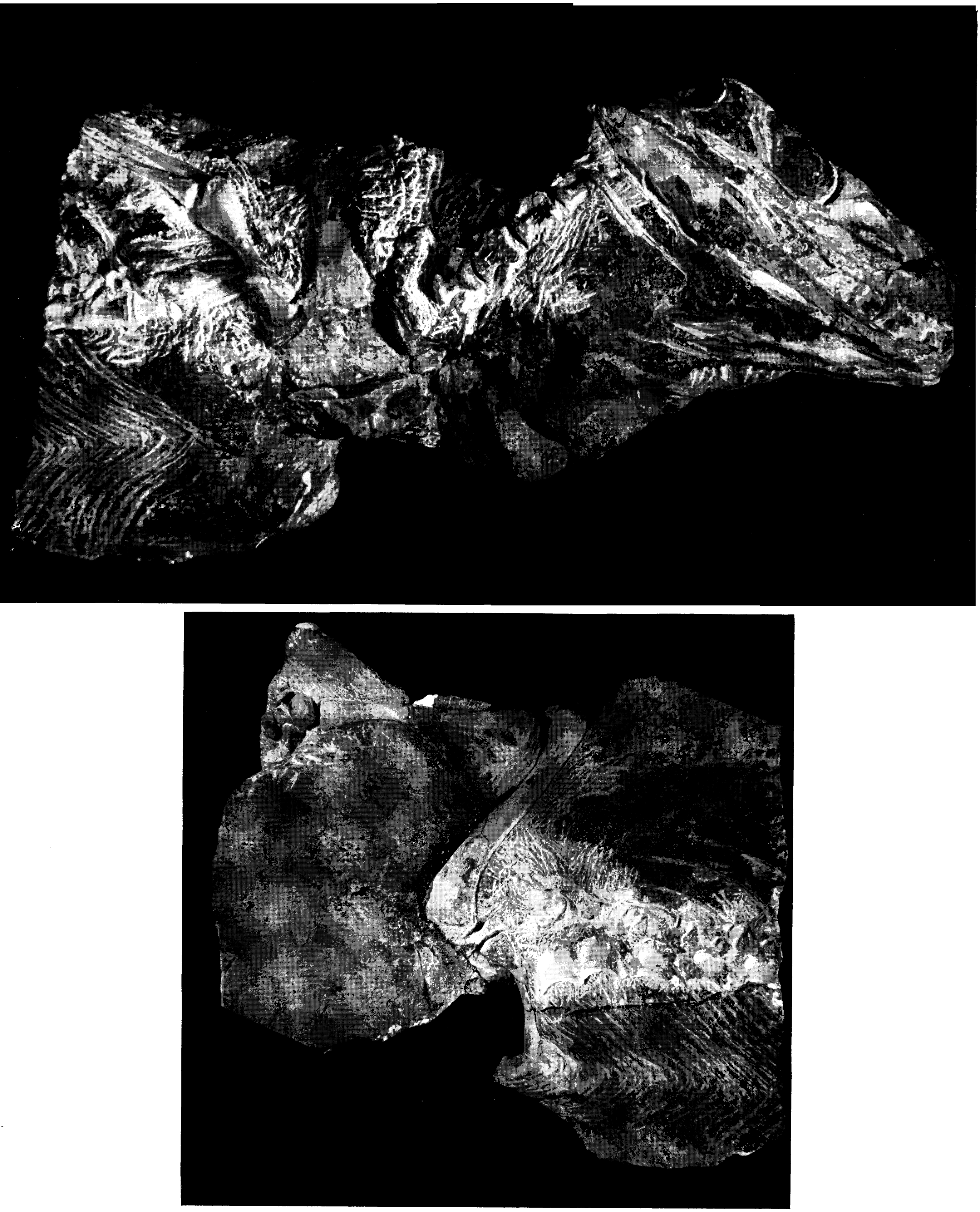

FIGURE 20. The type specimen (S.A.M. 5867). The counter-slab shows that there is one vertebra missing between the two pieces. (Natural size.)

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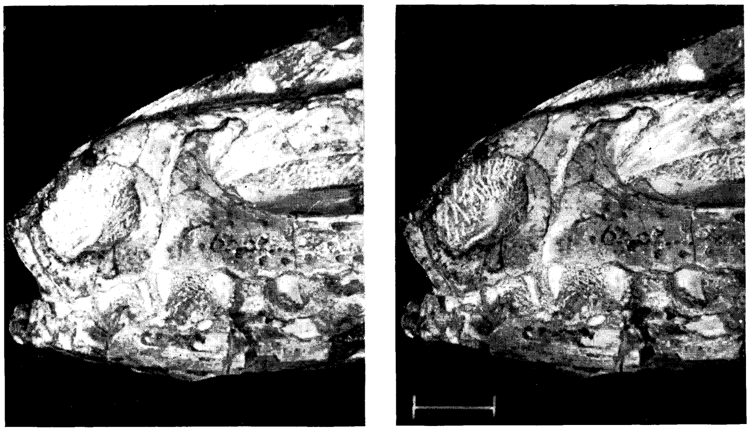

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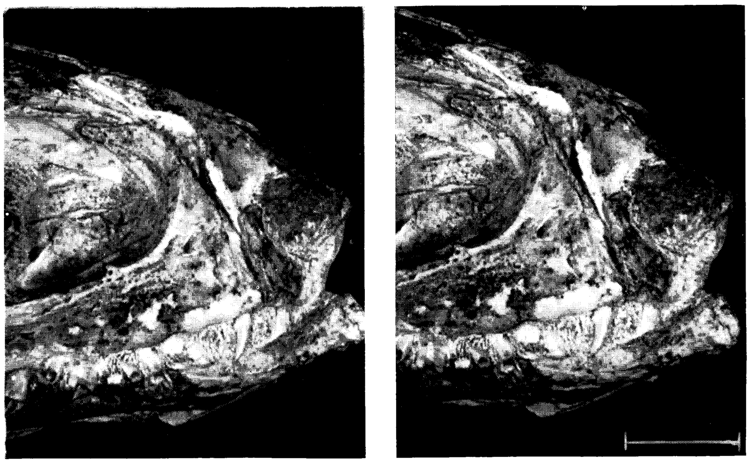

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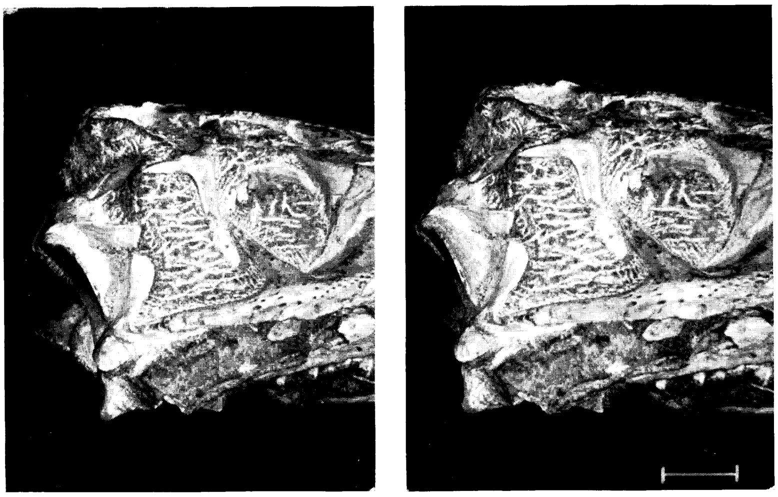

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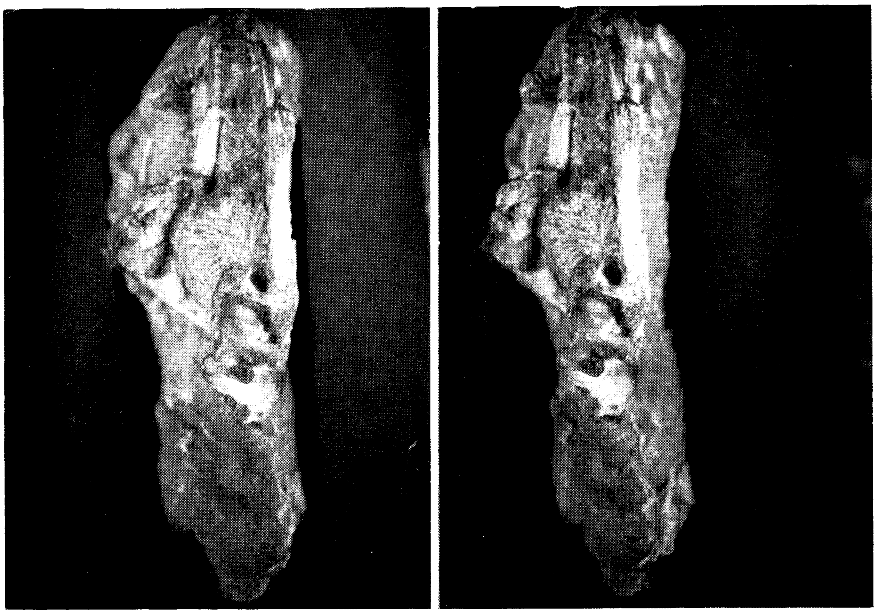

FIGURES 21–24. For description see facing page.

DESCRIPTION OF PLATE 32

FIGURE 21. Specimen S.A.M. 6047 A, anterior region of skull showing left premaxilla. (Scale 10 mm.)

FIGURE 22. Right side of the same skull, showing junction of descending flange of nasal with premaxilla and maxilla. (Scale 10 mm.)

FIGURE 23. Posterior end of same skull, showing junction of squamosal with quadrate and postorbital. (Scale 10 mm.)

FIGURE 24. Specimen R 527 B. Dorsal surface of posterior end of lower jaw, showing glenoid.

Description of plate 33

Figure 25. Specimen S.A.M. 13664. Posterior end of right pterygoid, showing the quadrate wing on the right and, on the left, the median vertical flange of the palatal wing. (Scale 10 mm.)

Figure 26. Palatal view of the same specimen with the ectopterygoid (slightly dislocated) on the left. (Scale 10 mm.)

Figure 27. Specimen S.A.M. 13664. Anterior end of right palatine (actually left, printed reversed so as to match the pterygoid shown in figures 25 and 26). (Scale 5 mm.)

Figure 28. Specimen S.A.M. 6047A. Vertebrae 4 to 13. Below, lateral view; above, seen from a slightly more dorsal position. On the left side all but the first three paramedian scutes have been removed. (Scale 10 mm.)

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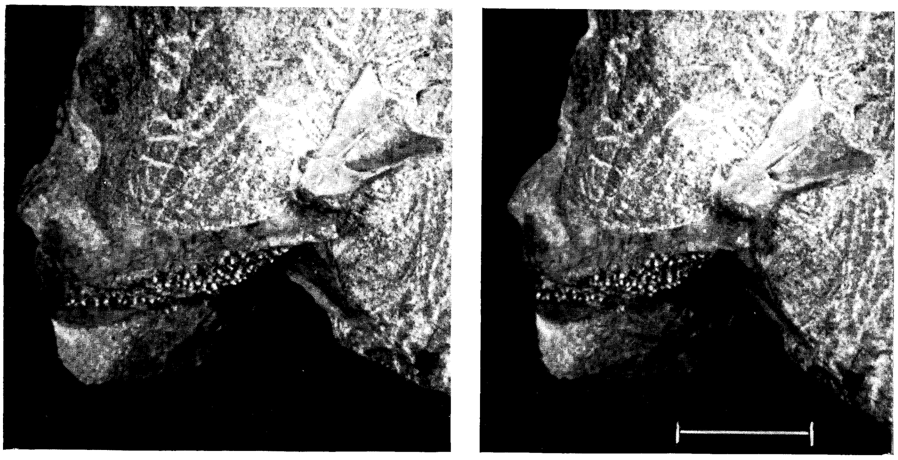

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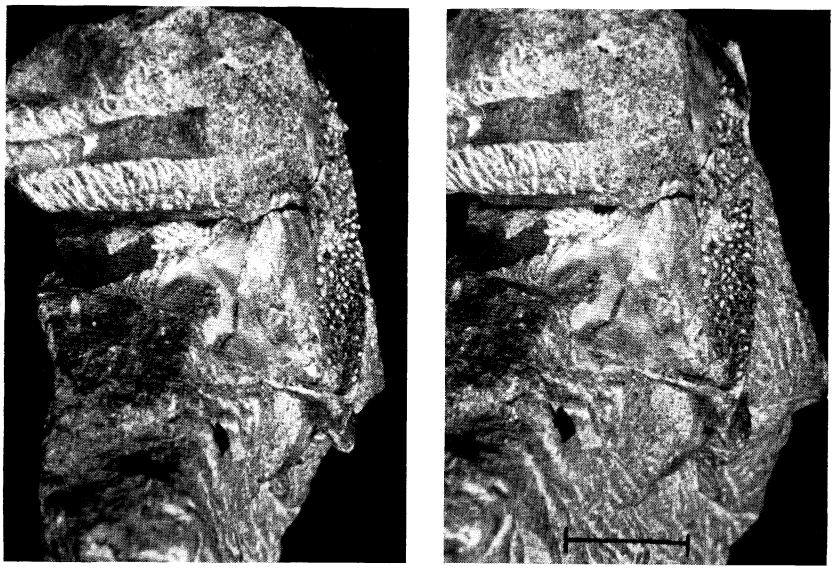

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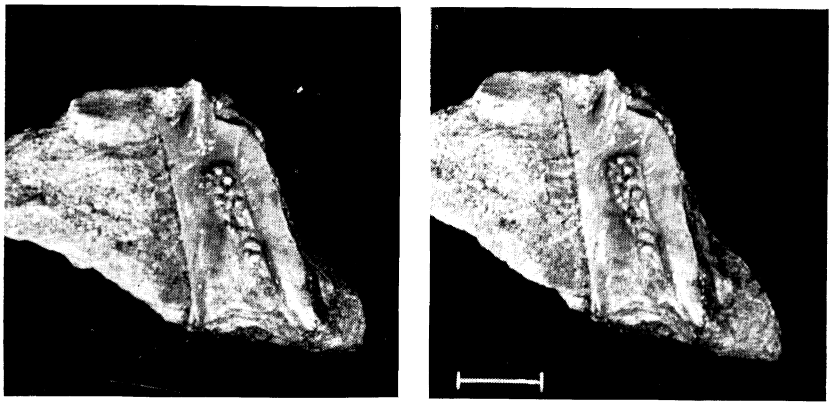

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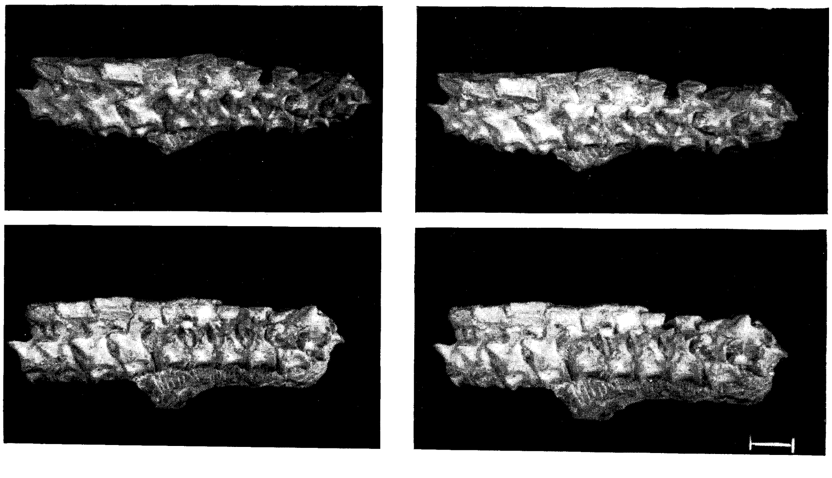

FIGURES 25–28. For description see facing page.

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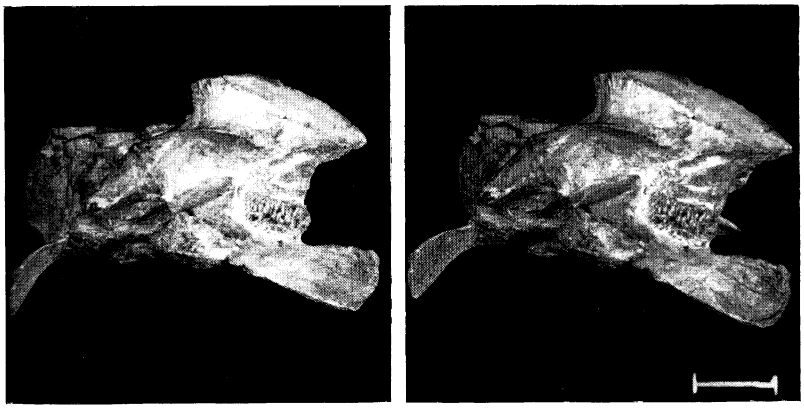

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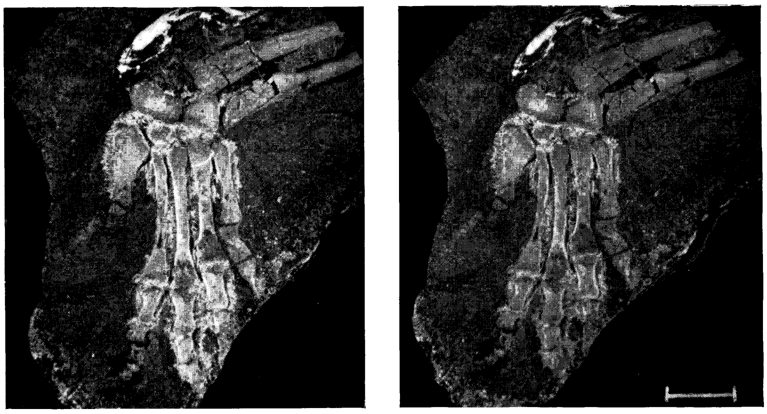

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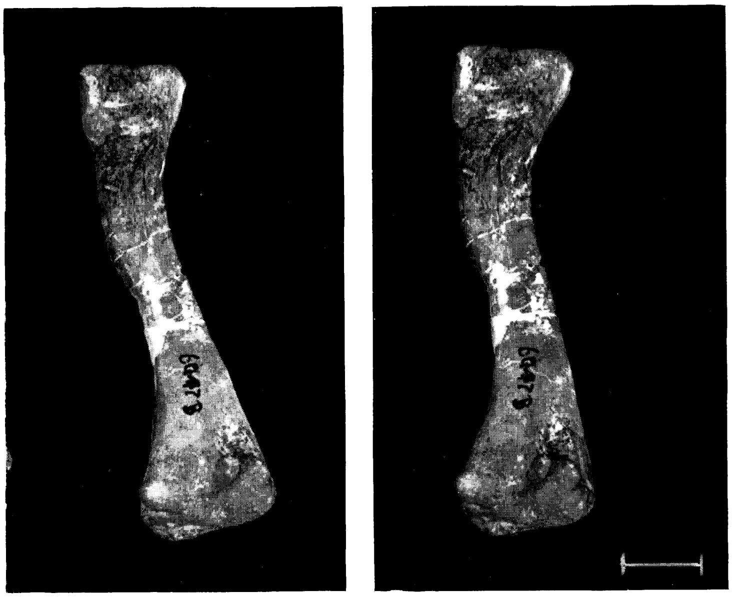

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FIGURES 29–32. For description see facing page.

of the skull table between the superior temporal fossae. A flange of bone turns downwards to form the mesial wall of the fossa and then curves postero-laterally to form an almost vertical strip, the anterior face of which forms the posterior wall of the fossa and the posterior face the upper portion of the occiput. At its distal end this postero-lateral ramus of the parietal is closely applied against the posterior wing of the squamosal. The parietal meets its fellow in the midline in an interdigitating suture and there is no trace of a pineal foramen.

Interparietal. Between the posterior ends of the two parietals the apex of the single median triangular interparietal is inserted. It extends outwards on either side between the lateral wings of the parietals and its lower margin meets the supraoccipital. It is somewhat larger than it is appears in Broom's Fig. 6 (1913*b*).

Maxilla. The maxilla forms the whole of the lower and anterior margins of the antorbital fenestra. The union of its anterior process with the premaxilla and nasal has already been described. The posterior part of the dorsal tip of the anterior process overlies the lachrymal and below this the posterior wall of the process is turned in to form the anterior wall of the fenestra. This inturning is continued on the lower margin of the fenestra to form a horizontal shelf about 4 mm wide which meets the lateral edge of the palatine and contains the sockets of the teeth. Watson's specimen *A* includes a maxilla seen from the lingual side and S.A.M. 6048 the posterior end of another. From these, the details of the union with the jugal can be made out. As can be seen from the external surface, the posterior part of the vertical external wall of the maxilla overlaps the anterior end of the jugal and slopes downwards to end below the orbit. The internal shelf of the maxilla, however, lies beneath the jugal so that the latter is supported from below.

Jugal. The jugal is a three-pronged bone. The anterior prong curves up to meet the lachrymal above and rests on the maxillary shelf below; the two posterior rami diverge to unite with the postorbital and the quadratojugal. In its contact with the lachrymal the jugal lies upon a slightly depressed face on the ventral end of the descending process of the latter, backward slip being resisted by a slight step. Where the postorbital process of the jugal meets the descending limb of the post-orbital its anterior edge is extended into a flange which fits into a corresponding groove on the posterior face of the postorbital. The tapering posterior ramus of the jugal lies over the anterior end of the quadratojugal but there is no specimen in which the internal details of this union can be made out.

Lachrymal. The lachrymal is a large bone forming the upper wall of the antorbital fenestra and the major part of the pillar dividing the latter from the orbit. Above the fenestra it

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Description of plate 34

Figure 29. Specimen S.A.M. 6049. Pelvis viewed from the left side. The downturned anterior flange of the pubis is missing from the left side of the specimen. (Scale 10 mm.)

Figure 30. Right pes. Un-numbered specimen. The astragalus has been rotated so that the calcaneum now meets the distal tarsal facet. (Scale 10 mm.)

Figure 31. Specimen S.A.M. 6047B. Ventral surface of left femur. (Scale 10 mm.)

Figure 32. Specimen S.A.M. 6049. Right tibia and distal part of fibula with astragalus and calcaneum. The spot on the astragalus marks the facet for articulation with the distal tarsal. (Scale 10 mm.)

forms a narrow rim flush with the surface of the skull. The descending portion, dividing the antorbital fenestra from the orbit, is also slightly depressed below the level of the other skull bones. The result is that the fenestra is not a mere opening in the skull, but a basin-like depression, giving the impression of having housed some soft structure. Anteriorly the lachrymal underlies the tip of the dorsal process of the maxilla and unites with the nasal as already described. Posteriorly it overlaps the prefrontal on a splined surface and its descending process carries a stepped facet to receive the tip of the jugal, as already mentioned. Walker (1961) describes a posterior contact of the lachrymal with the maxilla in *Stagonolepis*. If any such contact occurs in *Euparkeria* it can be no more than a meeting of the end of the descending limb with the internal shelf of the maxilla, for on the skull surface the jugal is inserted between the two bones.

Prefrontal. The prefrontal is an angled bone, lying immediately behind the lachrymal, forming the antero-dorsal wall of the orbit. The main part of the bone is a horizontal plate with a sculptured surface, which forms part of the skull table. It is united anteriorly with the lachrymal and mesially with the nasal and frontal by the grooved overlaps already mentioned. In front of the orbit the bone is sharply bent down through almost 90° and extends behind the lachrymal to form part of the pre-orbital bar. Externally it disappears from view somewhat dorsal to the level of the tip of the jugal but beneath, a thin slip descends considerably further internal to the lachrymal. Whether it extends far enough to contact the palate cannot be determined, but it is clear that the process is comparable with the similar descending process of the prefrontal of *Sphenodon* and quite unlike the medially situated process of the crocodilian prefrontal. In the type specimen the limits of this bone cannot be made out and Broom shows only its horizontal dorsal portion.

Postfrontal. The postfrontal is a small, roughly triangular bone bordering the postero-dorsal part of the orbit and forming part of the skull roof between the frontal, parietal and squamosal.

Postorbital. The postorbital is a three-pronged bone forming the back wall of the orbit, much of the anterior walls of the two temporal fossae and the anterior half of the upper temporal arcade. It is sharply angled, so that its three prongs extend approximately at right angles to each other mesially, posteriorly and ventrally. The mesial prong contacts the parietal and postfrontal; the posterior one is tapered and fits into a groove on the squamosal while the long ventral process is itself grooved behind to receive the flange on the ascending process of the jugal.

Squamosal (figure 23, plate 32). The squamosal is a bone of complex shape and is extremely important mechanically since it not only forms the posterior part of the upper temporal arcade but is also responsible for supporting both the quadratojugal, which stabilizes the posterior end of the upper jaw, and the quadrate, which carries the lower jaw articulation. It consists essentially of a relatively heavy centre piece from which four processes arise. One of these runs directly forwards and is deeply hollowed out on its external face to receive the posterior prong of the postorbital. A second extends mesially and forms a flange underlying the posterior wing of the parietal. A third process extends posteriorly, approximately continuing the line of the upper temporal arcade. In only one case is this posterior process preserved intact, in all the other specimens available the tip is missing. In the type specimen the left squamosal is somewhat displaced ventrally. Its posterior process is complete and shows a tapering point which must have extended out at the back of the skull well clear of the paroccipital process. The fourth prong of the squamosal extends ventrally with a slight forward slope to form the upper part of the posterior wall of the inferior temporal fossa. The central portion between the posterior and ventral prongs is deeply excavated to receive the thickened rounded head of the quadrate and the descending external face of the latter lies against the posterior wall of the descending squamosal process. On the surface of the skull this process appears to end in a point but this is deceptive. The descending process is in fact a broad strap-like structure extending inwards almost at right angles to the surface and with a flat termination.

Quadratojugal. The quadratojugal consists of two limbs enclosing an angle of approximately 40°. The horizontal limb is a simple bar, extending forwards and overlapped by the posterior end of the jugal. The internal surface of the junction of the two rami of the quadratojugal is hollowed out to fit over the outer surface of the lower end of the quadrate. The vertical limb is more complex. On the left-hand side of the type the bone has become disarticulated and its inner surface is visible, while in specimen 6047 A most of its external face can be seen. It is somewhat flattened and expanded with a slight twist just above the angle, where it meets an indentation in the quadrate. Here the two bones change relative positions so that although the angle of the quadratojugal lies on the postero-external surface of the quadrate, the upper part of the ascending limb of the former lies against the anterior wall of the latter. The externally visible part of the ascending limb of the quadratojugal ends where it meets the descending process of the squamosal, but the part overlapped by the quadrate extends further upwards, forming a sort of tab held in place between the quadrate and the flat internally extending plate of the descending process of the squamosal. Thus although in external view the quadratojugal looks as though its attachment to the skull is very weak, it is in fact held in place quite firmly above.

(*b*) *The quadrate, pterygoid and palate*

Quadrate. The quadrate is both more extensive and more massive than can be seen from the type specimen which shows little of its structure. It forms a vertical pillar, running from a thickened head above, which articulates with the squamosal, to the lower jaw articulation almost vertically beneath. The latter has the form of two condyles, a large internal and a smaller external one, separated by a groove which slopes outwards and backwards. Above the external condyle the bone flares out laterally, narrows abruptly and again flares out to form an antero-laterally directed wing. The first expansion underlies the angle of the quadratojugal, the pinched-in central region is the point where the ascending wing of the latter twists round to lie in front of the quadrate, overlapped behind by the second outflaring of the edge of the latter. At this cross-over point there is a slight gap between the two bones forming the quadrate foramen. Above the internal condyle the quadrate passes up vertically to the level of the quadratojugal cross-over and then expands to form a strong, triangular pterygoid wing which extends anteromesially. On the anterior face of the bone the pterygoid wing sweeps round in a curve to unite with the antero-laterally facing dorsal flange.

There is no specimen in which the whole of the palate can be seen. The posterior part is shown in a number of specimens, but the anterior end remains unknown. Watson's specimen *A* shows some details of the pterygoid and palatine; in S.A.M. 6047A and 6050 some of the dorsal surface is visible; S.A.M. 13664 consists of an isolated right pterygoid incomplete at the front, a right ectopterygoid and part of a left palatine, all seen from the ventral surface while S.A.M. 13667 also shows much of the palate in ventral view, rather flattened dorsoventrally.

Pterygoid (figures 25 and 26, plate 33). The pterygoid is extremely large. It consists of a relatively small quadrate wing lying in a vertical plane, united by a strong hooked basipterygoid process with the much larger palatal wing. The quadrate wing is shaped rather like a fish's tail and the lower part of its mesial surface is slightly hollowed out and separated from the dorsal part by a ridge of bone. Anteriorly this hollowed lower part extends forwards as a slight excavation in the thickened area of bone above the basipterygoid articulation. The bony ridge will, on the principle of the T-girder, give rigidity to the whole quadrate wing and possibly this is its sole function. The hollowed area below it, however, strongly suggests a muscle attachment. If a muscle did originate on this surface, its only possible insertion would seem to be on the vertical ramus of the quadrate. The possible function of such a muscle will be discussed in the section dealing with skull kinesis.

The basipterygoid articulation consists of a depression facing upwards and backwards, guarded below by a hook of bone. Into the depression the basipterygoid process of the basisphenoid articulates. The palatal portion of the pterygoid is complex. Mesially it is sharply bent up to form a vertical plate of bone bordering the interpterygoid vacuity. This vertical portion extends far forward, almost to the front of the antorbital fenestra. Posteriorly the palatal portion forms a wide flange bent downwards ventrally. On its outer surface this flange unites with the ectopterygoid and at the anterior end of the latter bone it narrows abruptly where it joins the posterior edge of the palatine. In front of this point the palatal portion of the pterygoid extends forward as a narrow strip of bone whose anterior end cannot be made out with certainty. This strip of bone, immediately adjacent to the upturned vertical flange, bears an extensive armature of small, conical, slightly recurved teeth. These extend forwards at least as far as the posterior end of the antorbital fenestra and backwards to just in front of the basipterygoid articulation. At its widest point, near the back, the tooth-bearing region is 5 mm wide but anteriorly it narrows. At the level of the union of the ectopterygoid and jugal the tooth-bearing area divides, the main part continues straight forward along the edge of the vertical flange, while a smaller branch diverges laterally. There are no teeth on the posterior edge of the palatal wing and no visible signs of a palatal fenestra at or near the union with the palatine.

Ectopterygoid (figure 26, plate 33). The ectopterygoid is a small, elongated bone, united with the lateral edge of the posterior part of the palatal wing of the pterygoid. Passing laterally it narrows abruptly to form a neck and then swells out somewhat to a broad flattened end, butting against the inner wall of the jugal.

Palatine (figure 27, plate 33). The palatine is large and forms most of the roof of the mouth from immediately in front of the ectopterygoid to the margin of the internal nares. A slight notch in its antero-lateral end marks the posterior end of the choana: from this point the anterior wall of the palatine runs forwards and inwards to form the mesial wall of the choana and terminates at approximately the same level as the vertical flange of the pterygoid. The edge of the bone bordering the nostril is turned upwards. Running back and mesially from a point a few millimetres behind the choana there is a row of small teeth which continues the line formed by the diverging outer branch of the pterygoid tooth row. Between this line of teeth and the jaw margin both the palatine and the pterygoid are arched, so that the palate in this region is distinctly vaulted.

The structure of the anterior end of the palate is not clear. There is no specimen showing the extent of the premaxilla on the palate and the only evidence of a vomer is a small strip of bone visible through the external nostril of specimen 6047A. The shapes of the vomer and premaxilla as shown in figure 1*b* are therefore largely conjectural.

(*c*) *The occiput and braincase* (figure 2*b* and 3)

The occiput is well exposed in the type, although it is undoubtedly somewhat displaced and would have been more nearly vertical in life: specimen S.A.M. 7696 also shows part of the occiput and otic region. Watson's specimen *A* shows something of the braincase, but it is incomplete and its structure is therefore not fully clear.

Supraoccipital. The foramen magnum is pear-shaped and lies at a level considerably above the lower end of the quadrate. Its upper margin is formed by the broad plate-like supraoccipital which at its dorsal edge unites mesially with the interparietal and laterally with the posterior wings of the parietal. On its lateral face the supraoccipital unites with the paroccipital process. Immediately ventral to the parietal flange bordering the superior temporal fossa there is a vertical plate of bone, forming part of the side wall of the braincase and passing backwards to form the lower border of the post-temporal fossa. This may represent an anterior extension of the supraoccipital.

Exoccipital. The pillar-like exoccipitals border the lower part of the foramen magnum, almost meeting below, so that the basioccipital is all but excluded from the foramen. In the type the margin of the foramen is damaged on the left side, but on the right, just below its union with the supraoccipital, there is a small facet for articulation with the proatlas and on the internal surface the foramen for the exit of nerve XII is visible. Laterally, the exoccipital unites with the opisthotic which extends out horizontally to form the paroccipital process, above which lies the small post-temporal fossa. The relations of the distal end of the process with other bones are not fully clear, owing to displacement, but apparently it lay against the lower end of the squamosal, between its mesial and posterior processes, immediately below the point where the latter bone is overlapped by the parietal, the arrangement being very much as in *Sphenodon.*

Basioccipital. The occipital condyle is convex and formed almost entirely from the basioccipital, the exoccipitals barely being involved. On the ventral surface of the skull the basioccipital extends downwards and forwards for a short distance to unite laterally with the opisthotics and anteriorly with the basisphenoid. In the region of its union with the latter there is, on either side, a small basal tuber.

Basisphenoid. Watson's specimen *A* shows part of the braincase in lateral view (figure 3). The basisphenoid appears to be virtually complete. From its union with the basioccipital it slopes downwards and forwards to a hollowed out basipterygoid process. Dorsally, it forms two expanded wings, separated by an incurved concave area directly beneath the foramen for the palatine branch of nerve VII (see figure 3). Anteriorly a small portion of the cultriform process is preserved. Specimen 7696, a large individual, shows its complete length. It extends forward to approximately the level of the anterior end of the ectopterygoid.

Prootic. Uniting with the dorsal edge of the basisphenoid lies the prootic. The middle part of its anterior wall is rounded and concave, presumably representing the point at which nerve V emerged, but above and below this the anterior wall is incomplete. Down the middle of the bone, directly above the concave depression in the basisphenoid, runs a deep, curved groove in which there are two foramina, one at the point of union with the basisphenoid, the other a little higher up (see figure 3). The latter is probably the foramen through which nerve VII emerges from the braincase, while the groove marks the course of its chorda tympani branch upwards and backwards and its palatine branch downwards to reach the roof of the mouth by passing through the lower foramen. Dorsally the margin of the prootic lies against the anterior wall of the paroccipital process, but its posterior limits cannot be made out in Watson's specimen. Specimen 7696, however, shows that its posterior border lay along the antero-ventral margin of the paroccipital process. Both the prootic and opisthotic are incomplete anteriorly in Watson's specimen and there is a gap between them and the broken end of the parietal. On the left side of the type, however, it has been possible to excavate the superior temporal fossa sufficiently to expose the top of the braincase directly below the downturned margin of the parietal. The bone in this region runs back to form the floor and inner wall of the post-temporal fossa and unites with the supraoccipital and opisthotic. Sutures in this region are uncertain, but it seems most likely, as already mentioned, that the bone directly below the parietal is a forward extension of the supraoccipital. What appears to be the junction with the upper wall of the prootic is visible lower down, and possibly the latter bone extends upwards along the anterior vertical edge to meet the parietal. Watson (1957) declared that in *Euparkeria* 'the anterior part of the brain is surrounded by laterosphenoids which articulate with the skull roof'. No trace of a laterosphenoid ossification was visible in the specimen when I examined it in 1961, but since the prootic is incomplete it may previously have been visible anterior to the point where nerve V emerges from the braincase and have been lost in the process of preparation. Since a laterosphenoid is present in *Stagonolepis* (Walker 1961) the presence of a similar ossification in *Euparkeria* would not be surprising.

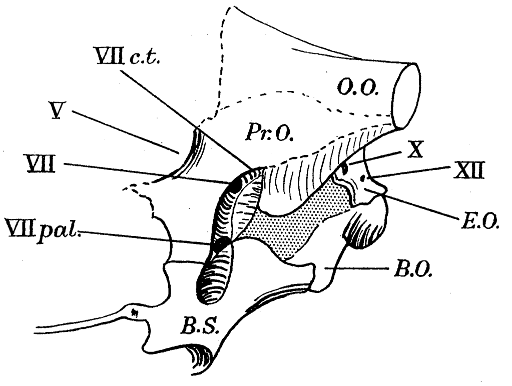

FIGURE 3. Specimen R 527 A. Braincase seen from the left side. V, VII, X, XII, points of emergence of cranial nerves from braincase; VII, *c.t.*, course of chorda tympani branch of nerve VII; VII *pal.*, foramen transmitting palatine branch of nerve VII. (Magn. × 2.)

No trace of an epipterygoid has been found but this cannot be taken to prove that it was not present, since there is no undamaged specimen in which it has been possible to prepare the relevant region of the skull. *Chasmatosaurus* certainly possesses an epipterygoid and Walker (1961) is of the opinion that it also exists in *Stagonolepis*: if this is correct, it is likely to have been present in *Euparkeria* also.

Opisthotic. The opisthotic forms the large, horizontally directed paroccipital process united mesially with the exoccipital and supraoccipital. In Watson's specimen *A*, the area lying directly beneath the paroccipital process appears to be damaged and no details can be made out: it is even possible that this region was incompletely ossified. The fenestra ovalis must have lain close to this area. In the type, beneath the left paroccipital process a rounded foramen is visible, which is presumably the fenestra. The bones surrounding it are somewhat crushed and few details can be made out, but specimen 7696 shows this region clearly. The fenestra ovalis is large and lies in the angle between the paroccipital process and the exoccipital and basioccipital. It is bounded antero-dorsally by the prootic, which extends outwards laterally and lies against the antero-ventral margin of the paroccipital process.

No stapes has been found but it is not unlikely that one was present. The curvature of the lower border of the posterior process of the squamosal, with its line continued along the anterior margin of the quadrate, is suggestive of the presence of a tympanum, supported by these two bones. If a tympanum did exist in this position, the stapes would most probably have been a slender bone, running inwards almost horizontally from the membrane to a slightly expanded footplate in the fenestra ovalis. The suggested arrangement is shown in figures 2*b* and 2*c*.

(*d*) *The lower jaw* (figure 2*a*)

The type shows much of the external surface and some further details are visible in S.A.M. 6050, while Watson's specimen *B* shows an articular end. No specimen shows much of the internal surface of the posterior part and very little is therefore known of the structure of the pre-articular, although Watson's *B* shows that it was present. The other lower jaw bones are the dentary, angular, surangular, articular and splenial.

Dentary. The dentary is large and extends for rather more than half the total length of the jaw. At its posterior end it forks to surround the anterior end of the mandibular fenestra. The lower branch overlaps the anterior end of the angular, while the upper one appears to pass underneath the anterior end of the surangular.

Surangular. On the external surface the surangular forms the greatest part of the posterior region of the jaw. It borders the upper and posterior ends of the fenestra and runs back to the end of the retro-articular process, where it is closely applied to the ventral face of the articular. Its surface is delicately sculptured with fine, approximately horizontal lines, as is the external face of the angular below it. On the external face, just anterior to the glenoid, there is a deep groove, ending anteriorly in a foramen leading to the interior of the jaw, presumably transmitting a blood vessel: further forward, close to the upper margin of the surangular, a second foramen and groove mark the position of its re-emergence on the outer surface of the jaw. The upper margin of the bone is somewhat thickened and extends inwards to form the antero-external corner of the glenoid and a small hook-like projection extends across mesially in front of the anterior end of the articular to meet the pre-articular on the mesial surface.

Angular. On the external face the angular forms only a small part of the lower margin of the posterior half of the jaw, but its extent on the internal surface is unknown. Anteriorly it forms the lower margin of the mandibular fenestra and then runs forward as a long spike beneath the lower border of the dentary.

Splenial. The inner wall of the anterior half of the jaw is formed by the splenial which enters into the symphysis in front and then runs back to the level of the mandibular fenestra. Its posterior end is not visible.

Articular (figure 24, plate 32). The articular is a small bone of complex shape. At the front a hammer-like projection buts against the posterior end of the pre-articular mesially and against the internal hook of the surangular labially. The upper surface of this hammer head is hollowed out to form the major part of the glenoid, receiving the large inner condyle of the quadrate. The posterior wall of the glenoid is raised to form a post-glenoid process. Behind this the upper surface of the retro-articular process is excavated to form a deep concavity extending the whole width of the bone. Its surface is extremely smooth and there is a small foramen behind the post-glenoid process. Owing to distortion and crushing it is difficult to be certain of the exact orientation of this concavity. In Watson's specimen *B* it appears to lie almost horizontally, but in 6047A and in the type it has a distinct downward slope mesially. The extreme posterior tip of the articular is drawn up into a pillar like projection shaped like the heel of a lady's shoe. Presumably the depressor mandibuli muscle was inserted over the whole of the concave area as well as on this projecting heel.

Beneath the jaw in the type specimen (see plate 31) lies a long thin bone, clearly part of the hyoid apparatus.

(*e*) *The dentition*

(i) *Marginal teeth*. Specimens S.A.M. 5867 (type), 6047A and 6050 show labial views of the teeth. Watson's specimen *A* (figure 4) provides a lingual view of the teeth on a maxilla and a dentary lacking its anterior end, while S.A.M. 13665 and 13666 show these borne on parts of a dentary and maxilla, also from the lingual side. From these specimens a considerable amount can be learnt not only of the structure of the teeth but also of their mode of attachment and replacement.

The teeth are laterally compressed, blade-like structures with sharp posterior and rather less distinct anterior keels. Both keels are finely serrated but, while the serrations on the posterior keel are easily visible in most of the teeth, those on the anterior edge are more difficult to make out and can be clearly seen in only a few cases.

Stromer (1934) notes that in *Compsognathus* there is slight heterodonty: the upper and lower cheek teeth are blade-like and serrated whereas the premaxillary teeth and anterior mandibulars are more conical and are unserrated. In *Euparkeria* the situation is less clear. On the left side of specimen 6047A two premaxillary teeth are visible: these are less flattened than the succeeding maxillary teeth and no serrations can be made out. On the right side, however, where a single premaxillary tooth can be seen, although serrations are again not visible, the tooth is blade-like. In the type the single premaxillary tooth visible on the right side is indistinguishable from a typical maxillary tooth, having the characteristic flattened shape and a clearly serrated posterior keel. On the other hand, the most anterior mandibular tooth directly below it is not flattened but conical and serrations cannot be seen. In specimen 6050, the anterior mandibular tooth is missing, but its impression in the matrix shows clear traces of posterior serrations and the anterior mandibular of 13665 is also serrated. It is thus rather difficult to decide what importance should be attached to the few cases in which anterior teeth appear to show slight differentiation. It is not possible to determine whether the age of the individual affects the issue, since the specimens involved are not very different in size and, unfortunately, the skull is not preserved in either the very large specimen (6047B) or the very small one (6049). Possibly in *Euparkeria* we have a very early stage in the evolution of the type of differentiation into gripping incisors and cutting cheek teeth which is shown in *Compsognathus*. The complex morphogenetic field which is required to produce this heterodonty may be very poorly developed in its initial stages and still rather unstable.

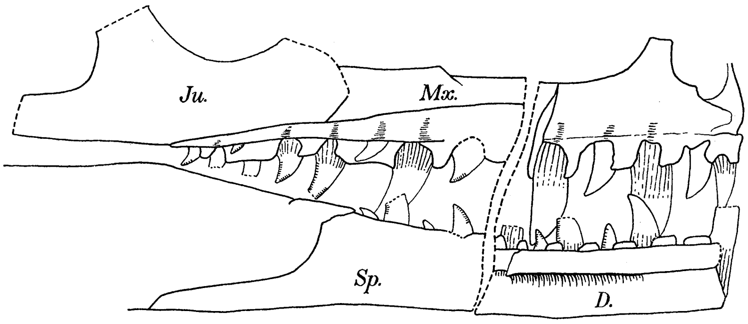

FIGURE 4. Specimen R527A. Lingual view of maxilla and dentary. (Magn. × 1½.)

The teeth have well-developed roots embedded in the bone of the jaw, and are thus fully thecodont. On the lingual side, the root is surrounded by somewhat spongy bone of attachment. In many cases this bone of attachment has been resorbed on the lingual side in the midline of the tooth so that a narrow channel is formed through which almost the whole depth of the root is visible. In three cases (S.A.M. 13665, S.A.M. 13666 and Watson's specimen *A* (figure 4)) a replacement tooth can be seen in position next to the functional tooth which it was due to replace. It is situated on the lingual side of the functional tooth, separated from it by a thin layer of attachment bone. In other cases a small partly erupted tooth occupies the middle of the alveolus from which a large tooth has clearly been recently shed. The outer face of a tooth which is fully erupted lies almost flush with the outer surface of the jaw bone, whereas incompletely erupted teeth are situated slightly more lingually. It is thus clear that the replacing teeth develop lingually to the functional ones. The attachment bone between the two is then resorbed and the replacing tooth moves over labiad to take the place of its predecessor once the latter has been shed. Although in a few cases there appears to be slight resorbtion of the root of an old tooth on its lingual face, so that it becomes slightly hollowed out in the area immediately adjoining the resorbtion channel in the bone of attachment, no case of such resorbtion proceeding far enough to perforate the pulp cavity has been found and the replacing tooth does not enter the pulp cavity of its predecessor. The two replacement teeth visible in parallel with their predecessors are orientated approximately at right angles to the jaw but many of the young teeth in the process of erupting have a very pronounced backward slope. Since at this stage they are very loosely held in an alveolus much too big for them, I am inclined to interpret their backward slope as being unnatural, the result of post mortem displacement, rather than as indicating rotation during eruption.

In reptiles it is usual for tooth replacement to be alternate. It is, however, relatively rare for all the teeth of one series (odd or even numbered) to be shed and replaced simultaneously: more commonly the teeth of each series are shed progressively from back to front of the jaw or sometimes from front to back. Edmund (1960) has shown that all these variations in replacement pattern are simply explicable in terms of tooth ontogeny. In the embryo, teeth develop progressively from front to rear of the jaw. Furthermore, each tooth differentiates, erupts and becomes functional and is finally shed and replaced by a new tooth developing at the same position in the jaw. The ultimate replacement pattern of the adult depends on the relative lengths of two time intervals: (i) the time between the eruption of new teeth at successive positions along the jaw and (ii) the time between successive eruptions of teeth at a single position. If the second tooth at position n erupts synchronously with the first at position $(n+2)$, then the end result is synchronous alternate replacement. On the other hand, if the second tooth at position n erupts a little in advance or a little after the first at position $(n+2)$, then apparent waves of replacement from front to back or back to front respectively will result.

In *Euparkeria* the replacement pattern is not very easily determined. The tooth number is relatively small: there are 17 teeth in the upper jaw, 13 maxillary and 4 premaxillary. There is no complete lower jaw series, but, judging from specimens in which the posterior part of the dentary appears to be in its natural position relative to the maxilla the teeth on the dentary appear to end a little in advance of the posterior end of the maxillary row so that the number of teeth in the lower jaw may have been less than 17. Since the teeth towards the back of the jaw are smaller than those more anteriorly situated and there are not sufficient specimens to determine the maximum height attained at each tooth position, it is not always easy to be certain whether a tooth is or is not fully erupted, particularly towards the back of the jaw. Furthermore, many of the teeth are damaged or missing. Nevertheless, an analysis of the teeth in the type, 6047A, 6050, 13666 and Watson's specimens *A* and *B* has been attempted. For this purpose the following six stages of tooth development are recognized:

(1) tooth just erupting but not yet projecting beyond the jaw margin;
(2) tooth projecting slightly above jaw margin;
(3) tooth approximately half erupted;
(4) tooth not quite fully erupted;
(5) fully erupted functional tooth;
(6) tooth about to be shed.

The results of the analysis are shown in table 1. All specimens show clear evidence of alternate replacement, but the details of the process are a trifle confused. On the left side specimen 6047A shows a distinct back to front wave of the usual reptilian type, while the right side of the same specimen gives indications of the same situation. On both sides the teeth of the odd-numbered series are functional, while replacement is in progress in the even-numbered series. Specimens 13666 and 6050 also show back to front replacement. On the left side of the latter specimen, tooth No. 4, which is clearly old and due to be shed, interrupts the series. It seems probable that its replacement tooth is in fact well developed behind it and its failure to be shed as early as its neighbours is of no great significance. In the type replacement is virtually simultaneous, with only the merest indication of a back to front gradient, while Watson's specimen *A* shows a clear front to back wave and his *B* shows indications of the same thing. In figure 5 the data for specimens S.A.M. 6047 A and Watson's *A* are plotted as examples of the opposite types of replacement wave. Such irregularities are not without precedent. Edmund (1962) has shown that in *Crocodilia* replacement at first shows a pattern of waves of replacement passing along alternate tooth series from back to front but with increasing age there is a reversal in direction and increasing irregularity. In *Euparkeria* although the discrepancies may well relate to age, this is not demonstrable in the small sample of specimens available, for 6050 and 6047 A are the largest and smallest and both show a back to front replacement wave. However, since the size range covered is not very great, individual variability and possibly also sexual size differences may well be obscuring the issue.

TABLE 1. STAGES OF ERUPTION OF TEETH AT VARIOUS POSITIONS ALONG THE JAW

tooth position	specimen 5867 (upper jaw)		specimen 6047 A (upper jaw)		specimen 6050 (upper jaw)		Watson's *A* (left side)		Watson's *B* (left side) maxilla	S.A.M. 13666 (right dentary)
	right	left	right	left	right	left	maxilla	dentary		
premaxilla										
a	—	—	—	—	—	—	—	—	—	—
b	—	—	—	5	—	—	—	—	—	—
c	5	—	5	—	—	—	—	—	—	—
d	3	4	1	5	—	—	—	—	—	—
maxilla/dentary										
1	1	6	5	5	5	5	5	5	$4\frac{1}{2}$	—
2	—	4	—	—	2	2	4	—	6	—
3	—	5	4	4	5	4	5	5	$4\frac{1}{2}$	—
4	5	4	—	—	—	6	4	3	5	3
5	1	5	5	4+	5	5	5	5	$3\frac{1}{2}$	5
6	5	4	4	1	2	—	3	2	5	$4\frac{1}{2}$
7	2	—	5	5	5	5	5	5	3	2
8	5	—	—	2	3	3	1	—	—	5
9	—	—	5	5	2	5	5	4	—	4
10	5	—	—	3	5	5	4	2	—	5
11	—	—	—	5	4	—	—	4	—	5
12	5	—	—	—	—	—	—	2	—	3
13	—	—	—	—	—	—	—	—	—	—

A few other anomalies occur. On the right side of 6047 A the third premaxillary tooth is functional, the 4th just erupting and the 1st maxillary functional, so that alternation proceeds unaffected by the junction between premaxilla and maxilla. On the left side, however, the 2nd and 4th premaxillary teeth are functional, as is the first maxillary, so that here the successive teeth on either side of the suture are functional and regular alternation is interrupted. In the type there seems to be asymmetry between left and right sides: on the right the functional teeth belong to the even-numbered on the left to the odd-numbered series. Admittedly the statement that the first tooth preserved on the right maxilla is 4th depends on the correctness of the estimate of three vacant spaces in front of it. It is, however, difficult to make any other interpretation: not only do there appear to be three slight scallopings, indicating three tooth positions, in front of the 1st tooth, but the distance of the latter behind the premaxillary suture is exactly the same as that of the 4th tooth on the left side of the specimen.

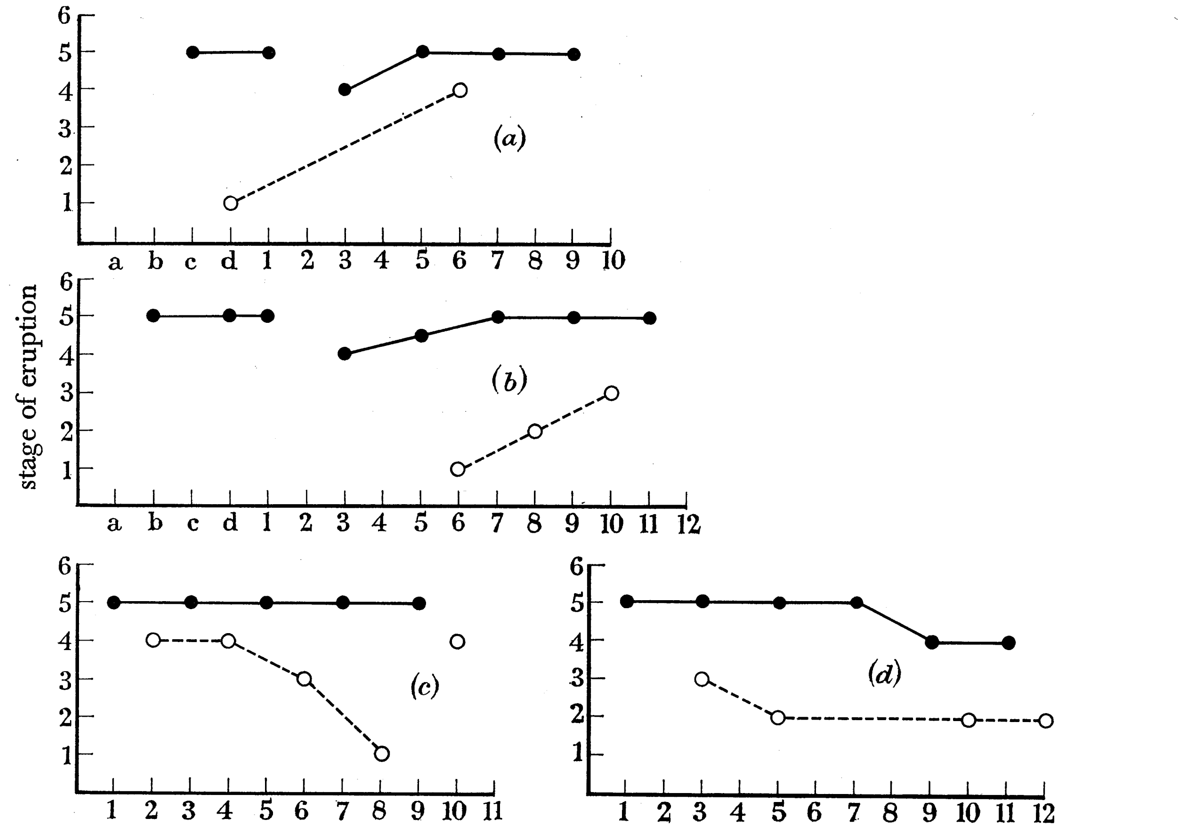

Figure 5. Stages of eruption of teeth in two of the specimens. S.A.M. 6047A (*a*) right upper; (*b*) left upper: R527A; (*c*) left upper, (*d*) left lower. Abscissa, tooth positions reading from front to rear. Numbers refer to maxilla or dentary, letters to premaxilla. Filled circles, teeth of the functional series; open circles, teeth of the replacing series. For definition of stages of eruption, see text.

(ii) *Palatal teeth.* As mentioned above, teeth occur on the pterygoid and palatine, forming together an elongated Y-shaped dentigerous area. The palatal teeth are extremely small, conical without any lateral flattening and somewhat recurved. Their greatest height is a little less than 1 mm. They do not appear to be socketed, but attached directly to the somewhat thickened area of bone supporting them.

At the anterior end of the palatine field, the teeth are arranged in rows of three, sloping forwards and mesially. Further back the field narrows and the arrangement is less regular (figure 27, plate 33). On the pterygoid, the widest part of the tooth field lies a little anterior to the basipterygoid articulation. Here there is a tendency for the same arrangement in slanting rows, but there is considerable irregularity (figure 26, plate 33). There is no clear evidence of replacement: no tooth shows a resorbtion pit near its base or appears to be about to be shed. On the other hand, that replacement did occur is suggested by the following facts. First, the teeth are not all of the same size: some are very much smaller than their neighbours but no regularity could be seen to govern the positions of the small teeth. Secondly, although many of the teeth are needle sharp, others appear to be worn. It should, however, be pointed out here that the teeth are extremely delicate and in preparing them the tips of several were knocked off. It is not easy in every case to distinguish between wear and preparative damage.

The evidence for replacement is thus equivocal. Certainly if the teeth were functional, replacement must have been active, for such fine points could not have remained sharp for long, had they been in use. On the other hand, the teeth are so small that it is natural to question whether they ever perforated the lining of the buccal cavity. An examination of some extant lizards possessing palatal teeth, however, suggests that they probably did so. In *Gerrhosaurus grandis* (Boul.) there are 2 pterygoid teeth on either side which do perforate the skin. In a specimen with a head length of 41 mm the largest tooth was a little less than 1 mm in height. In the much smaller *G. typicus* Smith there are on each pterygoid 6 much smaller teeth which again project just clear of the skin. It thus seems likely that the palatal teeth of *Euparkeria* also did so and if this is the case, then replacement probably occurred, although evidence as to the details of the process is lacking.

(2) *The vertebral column and ribs*

(*a*) *General features of the vertebral column*

Many of the specimens include vertebrae, but none shows a complete column. In the type only fragments of the atlas and pro-atlas remain, but the axis and the 5 following cervicals are present. Behind the girdle a series of 9 dorsals is present, all in approximately natural position and there is nothing immediately apparent to indicate that the intervening vertebrae are not also in position but obscured by the shoulder girdle (see figure 20, plate 31). It has, however, been possible to excavate behind the 7th cervical and in front of the first visible dorsal sufficiently far to show that in neither case is the neighbouring centrum present in the natural position. Apparently in the region of the shoulder girdle a whole section of the column has been displaced without disturbing the vertebrae lying in front and behind. It is not possible to locate the missing vertebrae without damaging the girdle but their position is indicated by the distal ends of a set of ribs, projecting behind the right fore-limb. Six ribs are present in this series, 4 of which are visible in plate 31, overlaid by the humerus. The gap between the two sections of the column *in situ* corresponds to a length of 6 centra, and it therefore seems safe to conclude that the displaced section consisted of 6 vertebrae. The total number of presacrals thus appears to be 22, of which 7 may be regarded as cervicals. Behind the pelvis 5 post-sacrals are preserved.

Specimen 6049 shows that there are two sacral vertebrae. No complete tail exists, but a number of specimens show sufficient to indicate that it was long. Specimen S.A.M. 7698 shows tail fragments lying in the same block with an ilium and hind limb and these suggest that there were between 30 and 40 caudal vertebrae.

The presacral vertebrae are relatively short and high. The centra are gently amphicoelous and constricted in the middle. The neural arch is high and the articular facets of the zygapophyses are not horizontal but slope inwards and downwards. The neural spines are relatively low and do not change very much in height along the length of the column. In the posterior cervical and anterior dorsal regions the top of the spine is expanded to form a wide flat surface. Such an expansion has been called (e.g. Walker 1961) a 'scute table', implying that its function was to provide a support for overlying dermal osteoscutes. Reasons will be given later for concluding that this is not the case and the expansions will be referred to by the more noncommittal name of spine tables. Figure 19 and table 2 give the maximal widths of the tables wherever measurement is possible.

TABLE 2. LENGTHS OF VERTEBRAL CENTRA (L) AND MAXIMUM WIDTHS OF SPINE TABLES (S) WHEREVER THESE ARE MEASURABLE

	S.A.M. 5867		S.A.M. 6047A		S.A.M. 6047B		S.A.M. 6049		S.A.M. 6048	
vertebra no.	L	S	L	S	L	S	L	S	L	S
cervical										
1	—	—	—	—	—	—	—	—	—	—
2	—	2·5	8·6	—	—	—	—	—	—	—
3	—	2·3	9·0	—	—	—	—	—	—	—
4	9·0	2·5	9·5	3·4	—	—	—	—	—	—
5	9·7	3·0	9·6	—	—	—	—	—	—	—
6	9·0	3·2	9·4	—	—	—	—	—	—	—
7	9·0	3·7	9·0	—	—	4·5	—	—	—	—
dorsal										
8	—	—	9·0	—	9·8	5·0	—	—	—	—
9	—	—	8·6	—	10·2	5·0	—	—	—	—
10	—	—	8·6	4·9	10·7	5·8	—	—	—	—
11	—	—	9·0	5·4	10·3	—	—	—	—	—
12	—	—	9·4	4·5	10·7	4·3	—	—	—	—
13	—	—	9·7	4·4	11·0	—	—	—	—	—
14	9·7	—	—	—	—	—	—	—	—	—
15	9·6	—	—	—	11·0	—	—	—	—	—
16	9·6	—	—	—	11·6	—	—	—	—	—
17	—	—	—	—	11·4	—	—	—	—	—
18	—	2·0	—	—	11·7	—	—	—	—	—
19	9·8	—	—	—	11·7	2·0	—	—	—	—
20	10·2	—	—	—	11·7	—	—	—	—	—
21	9·9	—	—	—	11·5	—	8·8	—	—	—
22	10·0	—	—	—	11·4	—	—	1·5	—	—
sacral										
S1	—	—	—	—	—	—	—	1·5	10·2	2·1
S2	10·7	—	—	—	—	2·9	—	—	—	1·4
caudal										
1	9·6	—	—	—	—	—	8·3	1·4	9·4	—
2	9·3	—	—	—	—	—	8·3	1·5	8·9	1·3
3	9·1	—	—	—	—	—	—	1·3	8·6	—
4	9·3	—	—	—	—	—	—	—	8·5	—
5	9·1	—	—	—	—	—	—	—	—	—

In a few damaged vertebrae the neural canal is exposed. In each of these the canal is expanded ventrally to form a deep depression in the dorsal wall of the centrum (figure 7*i*). This condition is visible in one isolated unidentified dorsal, in a 13th (specimen 6049), a 16th and 2nd sacral (6907B) and a 1st post-sacral (7702). Since in every case where the canal is exposed, the ventral expansion is present, it cannot be attributed to some abnormality and clearly it existed over the whole lumbar region, if not over the entire length of the column.

Specimen 7702, a few much damaged caudal vertebrae, also shows that both the centrum, the neural arch and the base of the spine were highly porous.

As far as can be judged, there was no very great difference in the size of the presacral vertebrae along the length of the column. Table 2 and figure 6 show the lengths of such centra as can be measured. Minor irregularities are almost certainly reflections of the difficulty of making accurate measurements but in spite of these, figure 6 suggests a slight shortening of the centra at the shoulder and a lengthening in the lumbar region. Although the size difference is slight, the vertebrae show considerable regional differentiation, particularly in the progressive changes in the rib articulation facets along the length of the column.

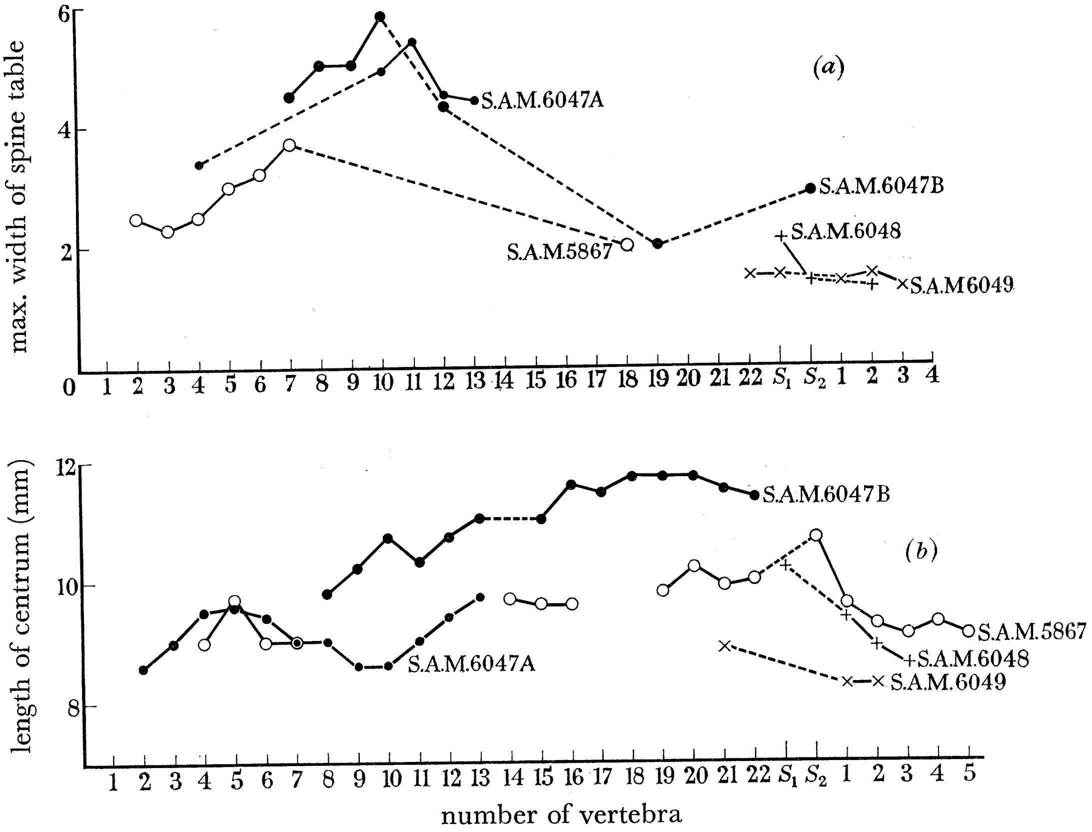

FIGURE 6. (*a*) Widths of spine tables and (*b*) lengths of centra in various specimens.

(*b*) *The pro-atlas, atlas and axis* (figure 7)

Although the anterior part of the column is not complete in any one specimen, almost the whole of its structure can be made out by combining various specimens. S.A.M. 6047 A shows the pro-atlas, the atlas neural arch and much of the axis; Watson's specimen *A* shows the first intercentrum, forming the base of the atlas, while his specimen *B* shows the centrum of the axis and the type, its neural arch. A displaced, rounded piece of bone lying close to the anterior end of the axis appears to be the odontoid, which cannot therefore have been very firmly fused to the axis. The suture uniting it with the axis centrum is clearly visible in 6047.

The pro-atlas consists of a little slip of bone approximately 5 mm long, narrow and rounded at one end and expanded and flattened at the other and not joined anteriorly to its fellow from the other side. It lies slightly displaced in specimen 6047 A, but the rounded end appears to have articulated with the atlas and the spatulate one against the facet already mentioned on the side of the foramen magnum.

The atlas intercentrum is a small piece of bone shaped like a single segment from an orange, with the two ends clipped off to form facets for articulation with the neural arches (figure 7*a*). The neural arch consists of a slightly bifurcated, horizontally placed dorsal portion roofing the neural canal, supported by a lateral column which is slightly narrowed in the middle and abuts below on the intercentrum. The posterior part of the dorsal portion bears a depression, presumably for the attachment of the obliquus capitis superior muscle, and anterior to this a flattened area on which the posterior end of the pro-atlas must have rested.

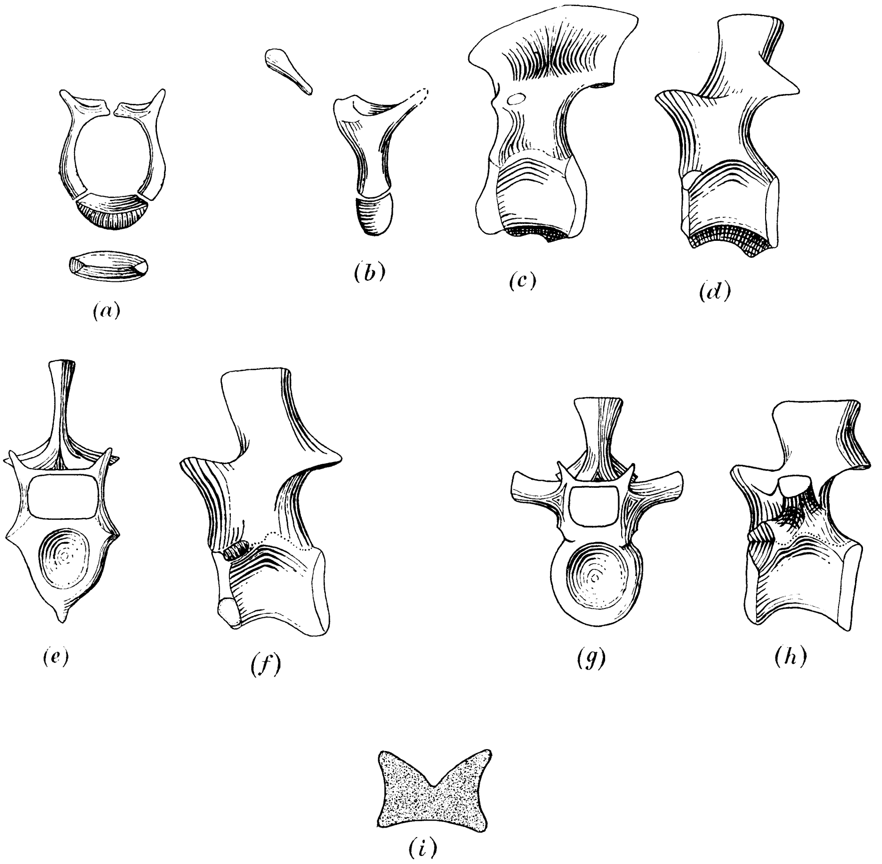

FIGURE 7. (*a*) Anterior view of atlas, (*b*) lateral view of pro-atlas and atlas, (*c*) axis, (*d*) 3rd vertebra, (*e*, *f*, *g*, *h*) anterior and lateral views of vertebrae 5 (on left) and 12 (on right), (*i*) longitudinal section of vertebral centrum to show the ventral expansion of the neural canal. (Magn. × 1½.)

The axis has an extremely long and high neural spine, indicating a well-developed obliquus capitis magnus muscle. The spine is slightly widened at the top posteriorly, forming an incipient spine table, but this is presumably correlated with the development of a large posterior division of the rectus capitis posterior muscle, which normally originates in this position. The anterior zygapophysis does not project forwards, but consists of a flat facet on the shoulder of the neural arch, against which the posterior limb of the dorsal Y-shaped part of the atlas neural arch rests: the posterior zygapophysis is large. At the posterior end of the vertebra the centrum is produced into a distinct keel midventrally.

(*c*) *Cervical vertebrae* 3 *to* 7

The general character of the cervical vertebrae may be seen in figure 7*d*, *e*, *f*. Along the length of the neck a number of progressive changes occur. The most anterior vertebrae are distinctly keeled ventrally, continuing the line of the keel on the axis, but the keeling becomes progressively weaker and there is only a trace of it on the 7th vertebra. On the other hand, the neural spines become progressively more expanded dorsally, to form larger and larger spine tables along the length of the neck (see figure 6*a*). On the 3rd vertebra, both the rib articulations are situated at the anterior end, the diapophysis on the neural arch just where it joins the centrum, the parapophysis low down on the centrum near the ventral surface. Along the length of the neck the tubercular facet shifts dorsally and posteriorly and becomes raised on a slight prominence, while the capitular facet moves dorsally up the front of the centrum: by the 7th vertebra the former lies on the neural arch, its posterior margin approximately midway along the length of the vertebra and the latter lies a little less than half way up the anterior edge of the centrum.

(*d*) *Dorsal vertebrae*

Apart from the changes in the size of the spine tables, shown in figure 6*a*, the main changes which occur in the vertebrae in the dorsal region concern the articular facets for the ribs. In specimen 6047A (see figure 28, plate 33) there is an abrupt change between the 7th and 8th vertebrae. In the former, as already mentioned, the tubercular facet lies on the slight knob-like prominence: in the latter, it lies at the end of a well-marked transversely projecting apophysis situated in the middle of the neural arch and well above the level of the suture with the centrum. Dorsally this transverse process is rounded but antero-ventrally a thin ridge of bone unites it with the anterior margin of the centrum, immediately above the parapophysis. Proceeding backwards along the column, the transverse process becomes longer and slightly more posterior in position and the antero-ventral bony ridge becomes more marked: at the same time the parapophysis continues to migrate dorsally, so that on the 12th vertebra it is half on the neural arch and half on the centrum and is now linked with the transverse process by the bony ridge (figure 7*g*, *h*). On the 13th vertebra the parapophysis is predominantly on the neural arch but its ventral margin is still on the centrum. In Watson's specimen *B* the 14th vertebra shows the parapophysis fully on the neural arch, close to the transverse process but distinct from it and linked with it by the ridge of bone previously mentioned.

In specimen 6047B and in Watson's specimen *B* the transition between vertebra 7 and 8 is less abrupt than in 6047A. In both the former specimens the tubercular facet is borne on a small but distinct apophysis on vertebra 7 and on a larger one on vertebra 8. From the 8th vertebra onwards the same progressive changes as are shown in 6047A occur and again it is on the 12th vertebra that the parapophysis is half on the neural arch. In Watson's specimen such fragments of the skull roof as remain seem rather thicker than those of 6047A and of the type and it had been concluded that the former was probably a male and the latter two were females before the difference in the vertebral columns had come to light. Similarly the large size of 6047B suggests that it was a male. Thus the supposed female shows an abrupt transition and the two supposed males a more gradual one at the 7th to 8th vertebrae. There are, however, not sufficient specimens to decide whether this difference is merely a matter of individual variation or is indeed sexual. Its significance, if so, remains obscure.

Unfortunately the posterior dorsals of 6047B are damaged and the rib articulations are missing: they are also much damaged in the type. The only specimen preserving complete posterior dorsals is thus 6049, the smallest of all the animals represented in the material. Assuming that there are 22 presacral vertebrae, then the most anterior preserved in this specimen is number 14. As in Watson's *B*, this shows the tubercular facet on the end of a well-marked transverse process and the parapophysis on the neural arch, anterior and slightly ventral to the transverse process. The ridge of bone joining the two is much less marked in this small specimen than in the large ones. From the 14th vertebra onwards the transverse process diminishes progressively in size but does not change position: by the 19th vertebra it is merely a rounded projection and has practically vanished on the last presacral. At the same time the parapophysis moves a trifle more dorsally, so that it comes to lie almost on a level with the diapophysis: as the latter shortens the two articulations approach each other and have become confluent on the last presacrals.

(*e*) *Sacral vertebrae* (figure 8)

The dorsal surfaces of the two sacral vertebrae are exposed in specimen 6049; in 6048, although they are damaged, a few further details may be made out, while the type shows the ventral surface of the centrum of the second sacral. Unfortunately the centra cannot be measured in 6049, but they appear to be a trifle longer than those of the posterior dorsals.

The transverse process to which the sacral ribs are attached are strong and deep, extending from about midway up the centrum to the level of the zygapophyses. In the 1st sacral the transverse process is situated anteriorly; in the 2nd it is approximately centrally placed. The junction of the rib with transverse process is clearly visible not only in 6049, the small specimen, but also in 6048. The distal ends of the ribs are widely expanded, that of the 2nd more than the 1st. They abut against the inner surface of the ilium: the 1st meets a flattened area at the anterior end, on a level with the top of the acetabulum and the 2nd meets the lower margin of the posterior spine, its anterior end being received into a slight groove just posterior to the position of the posterior margin of the acetabulum. The neural spines of the sacral vertebrae are not significantly expanded.

(*f*) *Caudal vertebrae*

The most anterior caudals are preserved in the type and in specimens 6048 and 6049. The long tail fragment preserved in the same block with an ilium and hind limb in specimen 7689 probably belongs to the same animal. As is to be expected if the tail is indeed long, the centra of the anterior caudals of the other specimens are not very strikingly smaller than those of the posterior dorsals. The first caudal has a large transverse process (fused rib); in succeeding vertebrae this becomes progressively smaller but is still present on the 5th caudal—the last preserved in the type.

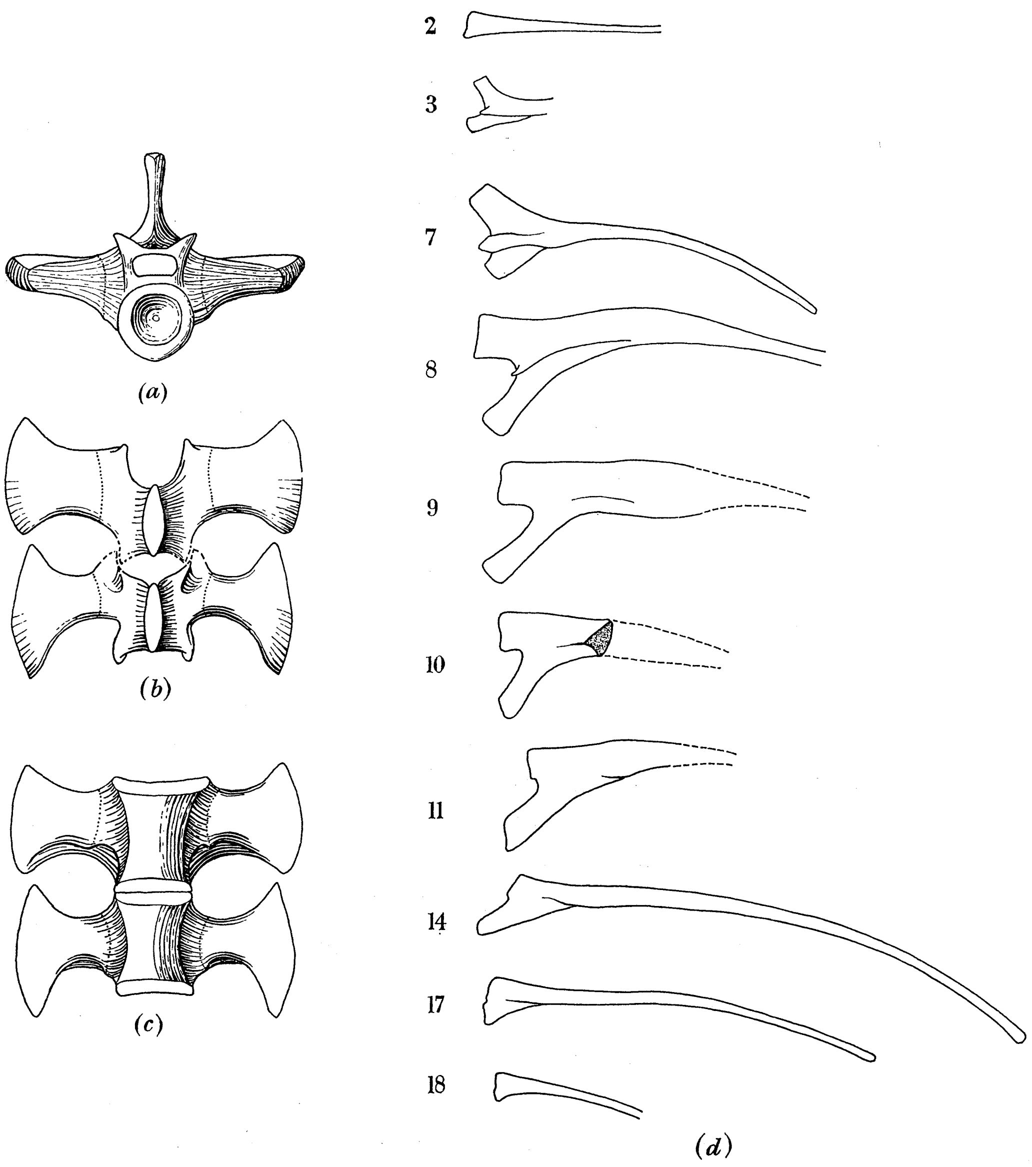

FIGURE 8. (*a*) Anterior, (*b*) dorsal and (*c*) ventral views of sacral vertebrae. In the region of the articulation of the two vertebrae with each other the bone is somewhat crushed (broken lines) and does not represent the natural condition. (*d*) Dorsal view of series of ribs from the right side. (The number of the corresponding vertebra is given on the left.) (Magn. × 1½.)

In specimen 6048 the 1st chevron bone lies between the 3rd and 4th caudals and the same is true of the much damaged series in specimen 7702. In the type no chevrons are preserved but facets for them are present between the 3rd and 4th vertebrae but not anterior to this point. There were thus 3 caudals without chevrons and there is no evidence of sexual dimorphism in this respect.

(*g*) *Intercentra and chevron bones*

Intercentra can be seen in a number of specimens. They consist of small slips of bone, a trifle over 1 mm in antero-posterior length and about 4 mm wide. They lie ventrally, forming a little collar between successive centra. Owing to their small size they are not always preserved but in 6047A they are present in the cervical region between vertebrae 5 and 6 and 6 and 7 and also in the pectoral region between vertebrae 9 and 10. Specimen 6047B has intercentra preserved in the posterior cervical and the whole of the dorsal region, including one between the last dorsal and 1st sacral. It is thus clear that intercentra were present along the whole length of the presacral column.

Intercentra are not visible in the first three caudals but may well have been present. As mentioned above, chevron bones are present from the 4th caudal onwards. Only traces of them are shown in specimen 7702, but 6048 shows the whole of the proximal end of the most anterior one. It consists of a pair of haemal arches, fused distally but separated proximally and the proximal ends are linked by a horizontal bar of bone representing the intercentrum. Unfortunately it is incomplete distally so that its total length cannot be determined.

(*h*) *Ribs* (figure 8*d*)

Although few complete ribs are preserved, the proximal ends of a considerable number are known. Watson's specimen *B* and the type each show a slim, more or less single-headed, rib in association with the axis, while 6047A has remnants of 2 very slim ribs beside the axis centrum, presumably representing an atlantal as well as an axial rib, together with the head of a rib belonging to the 3rd vertebra. The latter is double headed with a distinct keel on the external face and the shaft appears to have been only a little wider than that of the 2nd rib. The 4th rib is unknown. In the type, fragments of the proximal ends of the 5th to 7th ribs are preserved. These show that they had well developed tubercula and capitula and were keeled on the external surface, but no further details of their structure can be made out.

On the right side specimen 6047A shows an almost complete 7th rib and parts of the shafts of the 8th, 9th and 10th. On the left side of the same specimen the heads of the 8th to 11th ribs are almost complete. The 7th rib has a large tuberculum and a somewhat shorter capitulum. Between the two articulations, the external keel is enlarged and thickened, so that the rib is virtually three-headed. Distally the shaft narrows rapidly and becomes rounded. Comparing this rib (figure 8*d*) with those of *Erythrosuchus triplicostata* (v. Huene) figured by v. Huene (1960) it is clear that the extra (central) head of the posterior cervical and anterior dorsal ribs of the latter corresponds with the enlarged keel on the 7th rib of *Euparkeria*. Unfortunately it is not possible to be certain whether the 4th to 6th ribs of the latter also showed an accessory head formed from the external keel.

The 8th rib has a wide thick tuberculum and a longer and thinner capitulum. An external keel is present but it is not enlarged to form a secondary articulation. The proximal part of the shaft is rather wide and the rib only narrows and becomes rounded some 20 mm beyond the head. In the 9th rib the tuberculum is shorter than in the 8th and the external keel considerably smaller, but the widening of the proximal part of the shaft is more marked. In the 10th and 11th ribs the shortening of the tuberculum and reduction of the keel continue, but the proximal part of the shaft does not show any widening.

Specimen 6049 shows the ribs of the last 9 dorsals, i.e. the 14th to 22nd vertebrae. The most anterior of these has an extremely short tuberculum and only a trace of an external keel. Distally the shaft narrows and becomes rounded and shows no widening of the region immediately adjacent to the head. Passing backwards, as the transverse process on the vertebra becomes shorter and the parapophysis approaches it more closely, so the tuberculum and capitulum on the corresponding rib become less distinct and the last few ribs are virtually syncephalous.

(3) *The limbs and their girdles*

(*a*) *The pectoral girdle* (figure 9)

The pectoral girdle consists of coracoids, scapulae, clavicles and interclavicle. In the type the right scapula is virtually complete, the coracoid slightly damaged and portions of the right clavicle and the interclavicle are also present: all are visible from the external surface. In specimen 6047B the left coracoid is complete; the scapula is broken and the central portion is missing but the proximal and distal ends are preserved together with the posterior end of the interclavicle. It has been possible to free these bones from the matrix so that both internal and external surfaces are visible. Specimen 6049 preserves much of the interclavicle and the posterior ends of the coracoids, seen from the internal (dorsal) aspect. Specimen 7700 includes a much damaged scapula.

The coracoids are large, considerably longer than they are wide and slightly convex on the external face. The curvature is maximal in two areas about one-third and two-thirds of the way along the bone and less centrally, so that on the dorsal surface two slight basins are formed, one anterior the other posterior. These presumably represent attachment areas for the supracoracoideus and scapulo-coracoideus muscles. Postero-externally the bone is thick, but elsewhere it thins away to form a plate-like structure. The coracoid foramen lies close to the lateral margin rather less than half way back along the length of the bone. It penetrates the bone almost directly vertically with a slight outward (lateral) slope from below. The coracoid portion of the glenoid is only slightly concave, its surface facing laterally and slightly posteriorly. On either side of the glenoid there is a deep depression on the ventral surface. As a result, the thickest areas of bone form three struts radiating out from the middle of the posterior half of the bone. The central one supports the glenoid, the second runs laterally to buttress the articulation with the posterior portion of the scapular margin, while the third runs postero-ventrally and may have supported a cartilagenous extension.

The scapula is narrow and high. It is widest ventrally where it meets the coracoid, narrows above this and then expands again slightly dorsally. The main part of the blade is thin, slightly thicker towards the rounded posterior edge than anteriorly, but postero-ventrally where it forms the upper wall of the glenoid, the bone is considerably thickened. The glenoid facet itself is a slightly concave semi-lunar area at the postero-ventral corner. The postero-dorsal margin of the facet is extended to a backwardly directed point in the type, but is more rounded in specimen 6047B.

The interclavicle is a spatulate structure, slightly curved in cross-section with the concave surface facing dorsally. It lies in the midline ventral to the median border of the coracoids and extends behind them for a short distance. Its anterior end is not preserved in any of the specimens and its union with the clavicles is therefore not known.

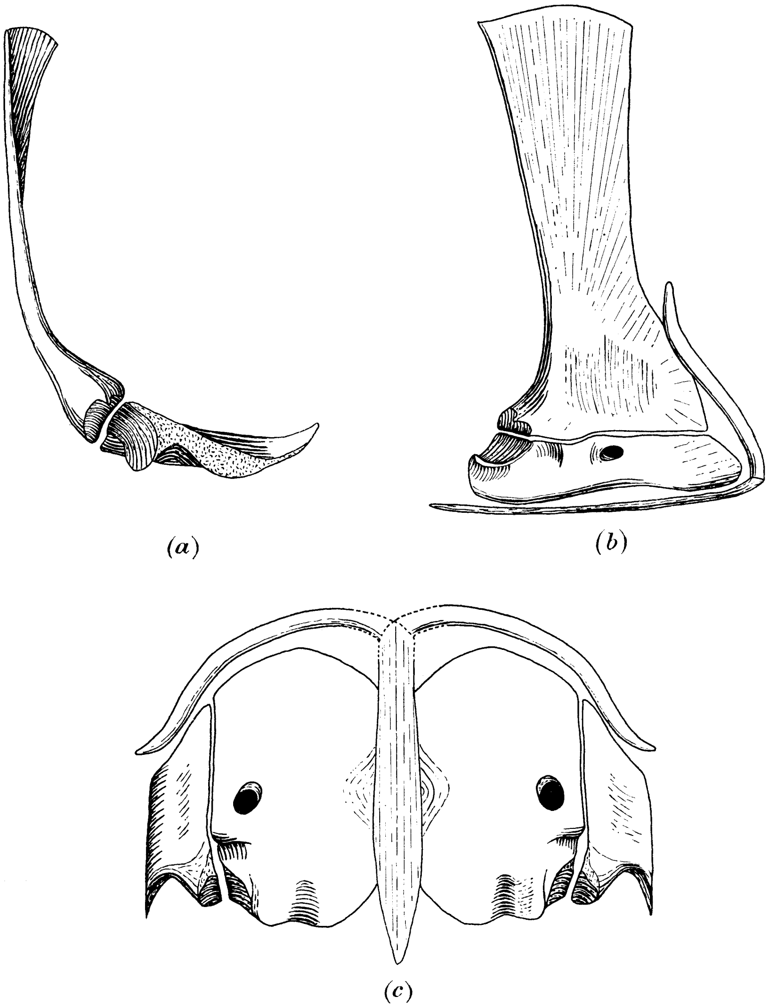

FIGURE 9. Pectoral girdle. (*a*) Posterior view of left side: the roughened posterior face of the coracoid visible in this view may have supported a cartilaginous extension. (*b*) Lateral view of right side. (*c*) Ventral view: the parts of the clavicle and interclavicle shown in broken lines are missing from the specimens and have been restored.

The scapulae and interclavicle are marked on both surfaces with a sculpturing of fine lines, approximately parallel to the long axes of the bones. The coracoids are also slightly sculptured with radiating lines.

No complete specimen of a clavicle exists. In the type only the distal end of the right clavicle is present, but an impression on the matrix extends mesially towards the midline. The proximal end is not visible, even as an impression. The dorsal extremity of the bone runs almost vertically for a short distance, then curves forward slightly.

(*b*) *The fore-limb*

The type includes the right humerus, radius and ulna and specimen 6047A the distal end of a humerus, with the proximal ends of radius and ulna. Associated with the damaged scapula, 7700, is a humerus (somewhat flattened proximally) and the proximal end of a radius. Of the carpus nothing is preserved and of the manus only a few fragments in specimens 13666 and 13667.

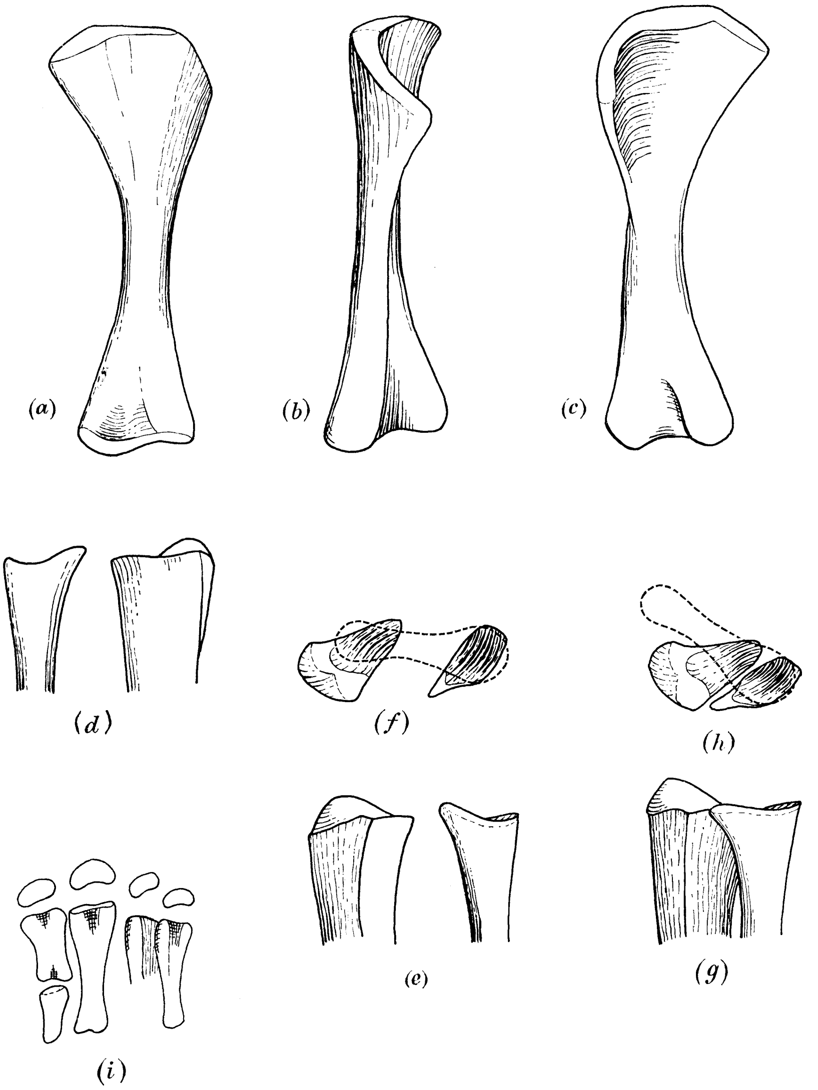

FIGURE 10. (*a*) to (*c*) Right humerus: (*a*) dorsal, (*b*) anterior and (*c*) ventral views. (*d*) and (*e*) Proximal ends of right radius and ulna in natural positions relative to each other: (*d*) internal lateral and (*e*) external lateral views, (*f*) articular surfaces with outline of distal end of humerus superposed. (*g*) Apparent natural position of proximal ends of radius and ulna in external lateral view. (*h*) Articular surfaces with outline of distal end of humerus superposed, showing that this position of radius and ulna is incorrect. (*i*) Ventral view of metacarpals with outlines of proximal ends above. (*a*), (*b*) and (*c*) mainly from the type, (*d*) to (*h*) from 6047A.

The fore-limb is distinctly shorter than the hind: in the type the humerus is 66 % of the length of the femur and the combined length of humerus + radius is 67 % of that of femur + tibia. The proximal segment is distinctly longer than the distal, the length of the radius being 84 % of that of the humerus.

The humerus (figure 10*a* to *c*) consists of flattened proximal and distal expansions, linked by a short rounded shaft. The two expansions do not lie in the same plane but are so arranged that if the bone is placed with the proximal expansion facing directly anteriorly, then the distal one will face antero-laterally. The proximal end of the humerus is gently curved from its posterior margin to the end of the articular area; from here it turns sharply downwards and forwards to the deltopectoral crest. Distally the bone is thickened along the pre- and post-axial margins, while the central area is thinner. The trochlea and capitellum lie at the margins of the bone, so that there are virtually no ect- or ent-epicondylar expansions. This wide separation of the two condyles, contrasting with their position in the Lepidosauria where they lie close together near the middle of the distal end of the humerus, is characteristic of archosaurian humeri.

The radius and ulna are straight, slender bones, slightly flattened proximally. The isolated proximal ends of specimen 6047A show the articular faces. That of the radius is oval, drawn out to a point posteriorly. The head of the ulna is roughly triangular. The apex of the triangle is slightly concave, forming the articulation with the humerus, while the base is rounded and roughened. This rounded roughened area represents a very reduced olecranon and very likely it was slightly extended by cartilage round the outer side of the elbow to provide the attachment for the tendons of the extensor muscles.

If the radius and ulna (specimen 6047A) are placed side by side as in figure 10*g* they appear to fit together and the articular areas on the proximal ends of the two bones continue each other's curvature so as to make a functionally single articulation. This, however, does not give a satisfactory union with the distal end of the humerus: radius and ulna combine to make a socket which fits the pre-axial humeral condyle but the post-axial one is left projecting antero-internally without support. In order to achieve a satisfactory elbow joint it is necessary for the proximal ends of radius and ulna to be widely separated as in figure 10*d*, *e*. Radius and ulna now articulate with trochlea and capitellum and the rounded roughened part of the ulna projects behind the joint to form a very short olecranon. The tip of the radius also projects behind the articulation and would appear to have provided a further area for the attachment of elbow extensor muscules.

No trace of the carpus is preserved but in specimen 13667 the distal end of the radius is present in association with metacarpals. The absence of any bone in the space between them suggests that the carpus may have been largely cartilagenous. In both 13666 and 13667 there are 4 metacarpals (figure 10*i*). The 2nd is elongated and moderately stout, the 3rd and 4th a trifle more slender but apparently of about the same length. The 1st metacarpal is only about half the length of the 2nd and rather stouter. Of the phalanges only the proximal one of the 1st digit is preserved (specimen 13666): it is short and stout. The proximal articulations of the metacarpals are visible in specimen 13667: they are moderately broad, suggesting a somewhat spreading type of hand. The short stout form of the 1st digit is of some interest, since many saurischians show a similar condition. A manus of *Massospondylus* in the South African Museum collection may serve as an example. The terminal articulation of the 1st metacarpal is slightly asymmetrical, with the outer condyle a trifle larger than the inner, so that the thumb projects inwards, out of line with the other digits. All the bones of the thumb are short and massive and the terminal phalanx is much larger, sharper and more recurved than those of the other digits. The contrast in the terminal phalanges is very striking and at once puts one in mind of the fore foot of a cheetah. In the latter the non-retractile claws of the digits used in locomotion are worn down so as to be rather blunt and are of no use as weapons, but the dew-claw, borne on the shortened 1st digit and slightly off-set from the main axis of the paw, is large and sharp and capable of inflicting severe wounds. In *Euparkeria* the whole of the 1st digit is not preserved but the metacarpal shows the same asymmetry as does that of *Massospondylus*, although it is less pronounced and the short stout thumb must have projected slightly inwards. There can be little doubt that in *Euparkeria*, as in *Massospondylus*, the first digit bore a large sharp claw and it seems reasonable to conclude that this type of specialization of the thumb reflects its use as a weapon, offensive or defensive according to the feeding habits of its possessor.

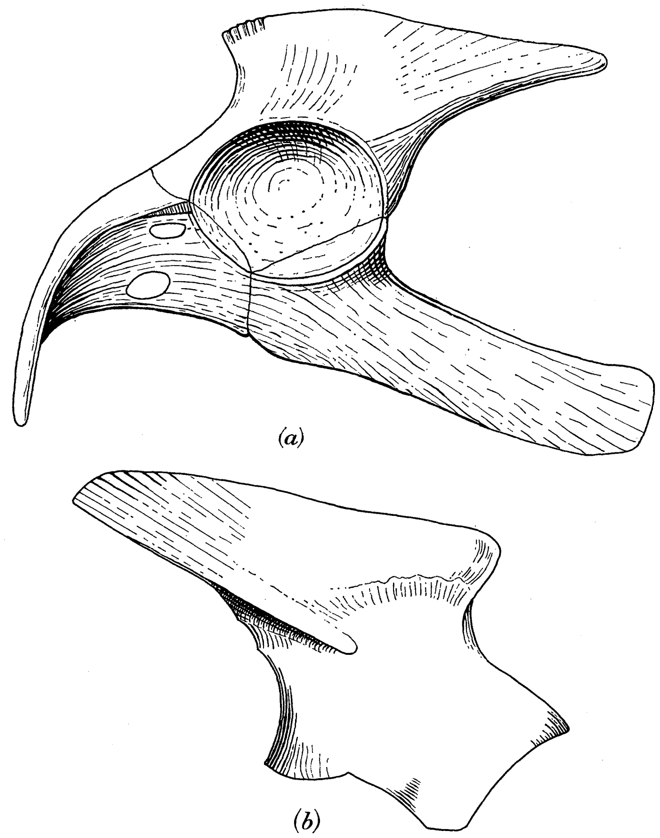

FIGURE 11. (*a*) Pelvis, from left side. (Magn. × 1½.) (*b*) Specimen S.A.M. 7698, internal surface of left ilium. (Magn. × 1½.)

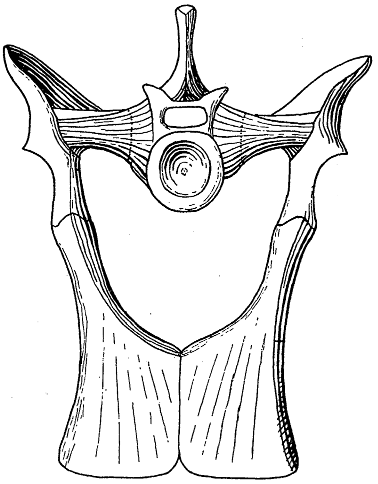

FIGURE 12. Anterior view of pelvis. (Magn. × 1½.)

(*c*) *The pelvic girdle* (figures 11 and 12)

In specimen 6049 the pelvis is almost complete, although somewhat dorso-ventrally flattened, and most of its structure can be made out. The bone forming the posterior part of the pubis in the symphyseal region is, however, very thin and is not well preserved in this specimen. Various parts of the pelvis are visible also in specimens 6047 B, 6048 and 7698.

Although the bones are slightly displaced and the anterior end of the left pubis is missing, figure 29, plate 34, gives a good general idea of the structure of the pelvis, showing the downturned pubis and elongated, backwardly directed ischium. The symphysis extends along the whole length from the anterior margin of the downturned pubic 'apron' to the posterior tips of the ischia.

The ilium forms almost the whole of the imperforate acetabulum. The upper margin of the latter is extended as a very well-marked shelf, so that the socket faces distinctly downwards as well as outwards. Above the acetabulum the iliac crest projects backwards, but is not extended anteriorly. On the inner surface a slight roughening anteriorly at the level of the upper margin of the acetabulum marks the articulation with the 1st sacral rib, while posteriorly, where the crest meets the central portion of the bone, a slight groove receives the anterior end of the 2nd sacral rib. The anterior margin of the ilium in front of the acetabulum forms a downturned rounded pillar which meets the dorsal edge of the pubis.

The pubis forms the antero-ventral rim of the acetabulum. From this point its lateral margin forms a thickened pillar passing forwards, it then thins slightly and turns more sharply downward forming the rounded lateral edge of the anterior 'apron'. The latter is probably more nearly vertical than appears in specimen 6049, where there has been some dorso-ventral compression. Towards the midline the bone becomes thinner and towards the back it is extremely fragile and rather poorly preserved: it is therefore not certain whether the symphysis is complete as an ossified structure, or whether a small portion in the posterior pubic region is cartilagenous. Broom (1913*b*) states that there are two pubic foramina, a character also found by Walker (1961) in *Stagonolepis*. The outer foramen is clearly visible in a number of specimens but the more mesial one, owing to the poor preservation of the very thin bone, is more difficult to make out. Broom seemed to be perfectly certain of its existence and although it is not now obvious in specimen 6049, it is possible that the specimen has suffered some damage since he examined it. In specimen 6048 the left pubis is crushed, but part of the ventral plate is visible. This shows the outer foramen and slightly antero-mesial to it another gap in the bone which, although its margins are a little indistinct and eroded, is difficult to interpret as an artifact due to damage: I consider it to be the 2nd foramen. The type also shows a gap in the bone in this area, but here no definite margins at all are preserved and it is thus difficult to be certain that the gap is in fact a true foramen, but it is certainly in the expected position. In view of the definiteness of Broom's opinion, the fact that the gaps in the bone occur in exactly the same position in the type and in specimen 6048 and the presence of a 2nd foramen in a related form, there seems to be no justification for rejecting Broom's statement.

The thickened antero-dorsal wall of the ischium forms the postero-ventral margin of the acetabulum. In specimen 6049 the ischia are slightly displaced and the lower border of the ilium is pushed inwards: as a result, instead of continuing the curve of the acetabulum smoothly, the ischial facet makes a sharp angle with it, but this is certainly not natural. The blade of the ischium is elongated and directed posteriorly. As in the case of the pubis, the dorso-ventral compression of the specimen has probably given this bone a slightly more horizontal direction than its natural one. The symphysis runs the whole length of the ventral surface and the union is extremely firm: the bones of the two sides meet at an angle of 68°. The compression already mentioned may have splayed the bones out slightly and it is possible that the natural angle was a little less than this.

Like the bones of the shoulder girdle, those of the pelvis are sculptured with a pattern of fine lines on all the flat surfaces.

(*d*) *The hind limb*

In the type the right femur, tibia, tarsus and proximal ends of the metatarsals are preserved. In specimen 6047 B a left femur, tibia and part of the fibula (probably the proximal end) are present and have been completely freed of matrix. In specimen 6049 it has been possible to free a right femur, tibia, distal end of fibula, astragalus and calcaneum. The distal tarsals and proximal ends of the metatarsals are also preserved but have been left *in situ* and are visible only from the dorsal aspect. There is also a 1st digit of the left foot and fragments of the 2nd digit. Associated with the type and figured with it by Broom (1913 *b*), is a right foot belonging to some other specimen but bearing no number.

As previously mentioned, the hind limb is considerably longer than the fore-limb. The ratio of proximal to distal segments is similar to that of the fore-limb, the tibia being 86 % of the length of the femur in the type, 83 % in 6047 B and 82 % in 6049.

The femur is very similar to that of a modern crocodile (figure 31, plate 34). The expanded proximal and distal ends are united by a slightly flattened shaft. The two articulations lie in different planes. If the proximal one is placed in the horizontal plane, then the distal one slopes downwards and forwards at an angle of approximately 32° to the vertical. The trochanter is relatively small, consisting of a slightly curved ridge and is placed well down the shaft.

The tibia (figure 32, plate 34) has a straight, slender shaft. The proximal end of the bone is slightly flattened antero-posteriorly and expanded to form a large, somewhat hollowed articular surface: the distal end is only slightly expanded and the articular surface is almost flat.

The tarsus is preserved complete both in specimen S.A.M. 6049 and in the un-numbered foot figured by Broom. The arrangement is identical in the two specimens and in neither is there anything to suggest than any bones are missing.

The tarsus consists of astragalus, calcaneum and 2 distal tarsals. The astragalus is considerably larger than the calcaneum. Proximally it has a flat facet for articulation with the tibia and externally a slightly curved one for the calcaneum. The distal surface bears a short almost flat facet for articulation with the innermost distal tarsal and mesially it forms a large convexity sweeping right round onto the ventral surface, with which metatarsals 1 and 2 articulate. On the ventral surface, external to this rounded metatarsal articulation there is a deep groove, presumably marking the path of the main digital flexor tendon.

In the foot figured by Broom, the astragalus is rotated, so that the facet for articulation with the calcaneum lies against the end of the fibula and the calcaneum is in contact with the distal tarsal facet (figure 30, plate 34). The calcaneum is roughly rectangular in dorsal view, with its long axis lying transversely. Towards the external margin the bone is not very thick dorso-ventrally, but mesially, where it articulates with the astragalus, it extends ventrally and forms a deeper pillar.

There are only 2 distal tarsals. From their positions it is clear that these are the 3rd and 4th, and that the 1st and 2nd have been lost in the course of evolution.

The outermost (4th) distal tarsal is roughly triangular in dorsal view; it lies between the calcaneum and the proximal ends of the 5th and 4th metatarsals. The inner (3rd) distal tarsal is a smaller bone, lying between the external corner of the astragalus and the 3rd metatarsal.

The relative sizes of the metatarsals and phalanges can be seen from figure 13. The phalangeal formula is 2, 3, 4, 5, 3: the 3rd and 4th digits are the longest and all are tipped by sharp claws. From specimen 6049 it can be seen that the proximal ends of the 1st and 2nd metatarsals are somewhat elongated and the 1st overlaps the 2nd. Watson's material includes a damaged foot which shows that the proximal ends of the 3rd and 4th are similar.

FIGURE 13. Dorsal view of right pes. (Magn. × 1½.)

The 5th metatarsal, however, is different from the rest. The shaft is relatively short and thick, it is expanded proximally and is sharply curved over on its mesial side. Proximally the bone ends in a point, where the smooth articulating surface sloping away mesiodistally meets a roughened face sloping outwards.

(4) *Dermal armour*

(*a*) *Dorsal scutes*

On either side of the backbone along the length of the body runs a row of overlapping scutes. In both the type and in specimen 6049 a few members of a smaller series of lateral scutes are preserved lying on top of the ribs. Broom (1913 *b*) noticed these and was inclined to interpret them as uncinate processes of the ribs but he also said that they might just possibly represent a lateral scute row. Further cleaning has made it perfectly clear that the latter interpretation is correct. The paramedian scutes are leaf-like in outline, drawn out to a point in front and truncated at the back. They overlap, the anterior point of each scute fitting into a groove on the lower surface of the one in front. On the dorsal surface the scutes are longitudinally keeled, so that in the central region anterior to the groove, they are triangular in transverse section. The keel is not exactly median, but lies a trifle nearer the external than the mesial edge. Apart from the most anterior pair of scutes, which are very small, there is no significant change in size along the length of the presacral column. The arrangement of the scutes is not absolutely regular. Left and right are not exactly in register, but at the same time are not exactly alternating: they are best described as being slightly out of step. There is approximately one pair of scutes per vertebra, but the correspondance is by no means accurate and the inaccuracies are not necessarily bilaterally symmetrical. For instance, in Watson's specimen *A* there are only five scutes on either side corresponding to 6 vertebrae (nos. 9 to 14) but in specimen 6049 6 vertebrae (nos. 17 to 22) have 6 scutes on the left and 7 on the right.

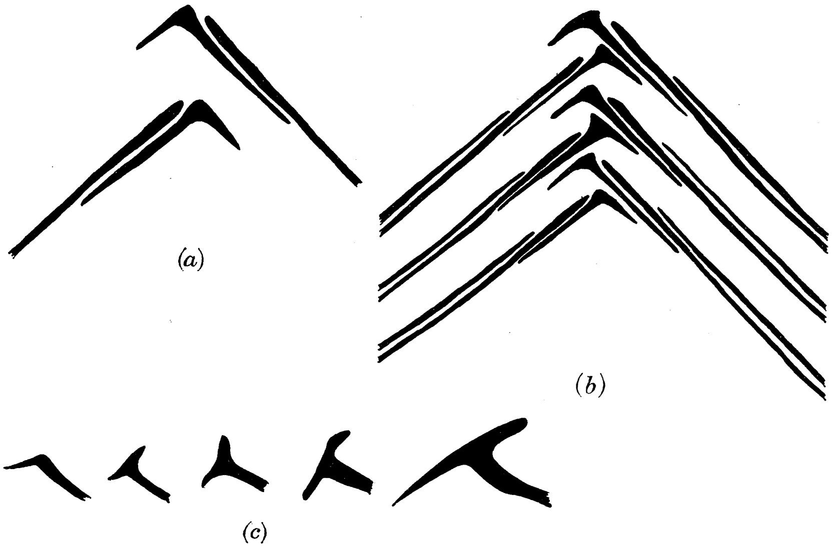

FIGURE 14. Gastralia. (*a*) The mesial ends of left and right elements. (*b*) Diagrammatic representation of the arrangement of the gastralia in the midline. (*c*) A number of 'goosenecked' gastralia elements, drawn from specimen S.A.M. 7713, to show the range of variation. (Magn. × 1½.)

The scutes of the outer row are much smaller than the paramedians and are not in contact with each other. They are elongated, slightly irregular in outline and gently pointed at either end: like the paramedians, they bear a dorsal longitudinal keel situated slightly lateral to the midline.

(*b*) *Gastralia*

The type preserves a complete series of gastralia, covering the ventral surface over the whole area between pelvic and pectoral girdles. As can be seen from (figure 20, plate 31), the gastralia are in the form of thin rods, forming a chevron-like pattern. Each set of bones comprises a number of overlapping elements, at least two, possibly three, on either side. The way in which they meet in the midline is difficult to make out in the type because the bones are broken, part remaining in the main block of matrix and part having come away with the counter-slab. Specimen 7713, however, shows the greater part of a series of gastralia of which some are split apart as in the type but for a short distance the central region was undamaged and completely covered in matrix. This area has been cleaned so as to expose the central ends of a number of sets of gastralia from the dorsal surface. From this specimen it can be seen that two elements from either side are involved in the union.

Of these the more anterior is long and has a simple slightly spatulate end; the other is short and ends in an angled 'goose neck'. The elements from the two sides fit together as shown in figure 14 to form a sort of herringbone pattern. Figure 14*b* is a highly idealized version, for in reality the goose necks are extremely variable in shape, so that the arrangement is less regular and symmetrical than is portrayed. The intermeshing herringbone pattern is of some interest, since it clearly bonds the entire gastralial complement into a unified structure giving some resistance to longitudinal compression: it is not merely a set of sloping struts which would concertina together and have no antero-posterior stability.

The sets of gastralia are more numerous than the body segments. In the type, where the whole series is present, there are approximately 32 sets. The exact number of body segments with which these correspond is not clear, but the number can hardly be more than 15 (the total number of dorsals) so that there are approximately two sets per segment.

III. FUNCTIONAL CONSIDERATIONS

(1) *The skull*

With its sharp blade-like teeth and large orbits, the skull of *Euparkeria* is clearly that of an active carnivorous animal. Its architecture must therefore be considered in relation to this mode of life.

The main desideratum is a skull which is strong, but at the same time relatively light. In general terms, the principle on which this is achieved is simple. The dermal bones of the skull table form a strong longitudinal axis and to this there is attached a relatively light system of struts forming the scaffolding of the jaws, the housing of the special sense organs and the walls of the antorbital fenestra. With such a basic design, the main mechanical problem is to provide a sufficiently firm attachment of the struts to the axis. The complex interlinking of individual bones already described in § II receives a functional explanation in terms of this requirement. Anteriorly the most important stabilizing element is the descending flange of the nasal, which bonds together the premaxilla, maxilla and lachrymal. Posteriorly the squamosal is the main link between skull table and scaffolding while below, the jugal supports the posterior end of the maxilla and is united with the pre- and postorbital bars in such a way as to prevent upward dislocation when the teeth encounter resistance.

It is next necessary to consider the action of the jaws, which entails an attempt to deduce the arrangement of the muscles responsible for opening and closing them. A predator requires powerful jaw muscles which are capable of performing two functions. Capturing large prey requires jaws which can open widely and snap shut rapidly from the fully open position: killing the prey requires the exertion of a powerful force as the jaws close, to drive the teeth home into the prey. Two sets of muscles are therefore necessary, one acting approximately at right angles to the fully open lower jaw, the other approximately at right angles to it in the all-but-closed position. These actions are carried out by the forwardly sloping pterygoideus and the vertical temporalis muscles respectively and both must have been well developed in *Euparkeria*.

It is convenient to consider first the temporalis musculature. The arrangement of the temporal adductors of *Euparkeria* was probably very much as described by Lakjer (1926) for *Sphenodon*, with the various subdivisions of the adductor externus arising from the upper temporal arch, the dorsal and posterior borders of the temporal fossa and the fascia covering the inferior temporal fossa; the adductor posterior from the pterygoid wing of the quadrate and the pseudotemporalis from the area round the anterior wall of the superior temporal fossa. The insertion on the mandible was presumably at the level of the mandibular fenestra, which lies considerably anterior to the glenoid. Although the quadrate slopes slightly backwards, the line of action of the temporal adductors makes only a small angle with the widely open jaw, so that at this stage of the bite they must be relatively ineffectual. As the jaw closes, however, their effect increases and in the final stages of the bite their line of action is almost at right angles to the mandible. A further point emphasized by Watson (1957) is that if the jaw is to open widely the muscle fibres must be long. This can be achieved only by ensuring that the origin on the skull is high above the lower jaw, that is by having a long quadrate and a skull which is high posteriorly—characteristic features of *Euparkeria* and carnivorous pseudosuchians in general.

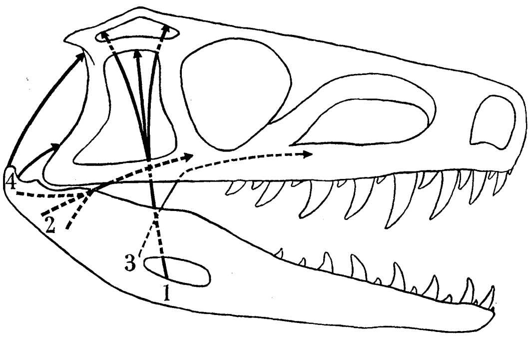

FIGURE 15. Diagrammatic representation of suggested lines of action of jaw muscles. 1, Main temporal adductors; 2, posterior part of pterygoideus; 3, pterygoideus D; 4, depressor mandibuli.

The pterygoideus musculature is a little more complex. The main bulk of this musculature in *Euparkeria* presumably originated on the broad posterior part of the large pterygoid flange and inserted on the mesial surface of the retro-articular process and of the part of the lower jaw immediately anterior to the glenoid. With the jaw widely open the force exerted by fibres inserted on the retro-articular process is almost directly through the condyle and their action is to stabilize the glenoid, rather than to accelerate the jaw upwards. Fibres inserted a little anterior to the glenoid will act almost at right angles to the open mandible and be maximally efficient in snapping the jaw closed rapidly. In *Euparkeria* one would therefore conclude that much of the pterygoideus musculature must have had its insertion in this position.

In animals that capture very large prey a strong bite is necessary with the jaws still widely open. This may be achieved by increasing the mechanical advantage of the pterygoideus musculature by shifting its insertion further forward along the mandible. This, however, will necessitate lengthening the fibres if the jaw is still to open widely. This can only be done by shifting the origin on the skull forwards along the dorsal surface of the palate, i.e. by creating an anterior subdivision of the pterygoideus, the pterygoideus D of Lakjer (1926). The functional significance of this muscle is thus to provide a strong bite with the jaws widely open: its development should therefore be maximal in species which capture very large prey and in which the temporalis musculature is relatively weak. In *Euparkeria*, probably subsisting on small or medium-sized prey and with well-developed temporalis musculature, the need for this type of specialization of the pterygoideus does not appear to be very great. Although a pterygoideus D may well have been present it is unlikely to have been very large.

The depressor mandibuli muscle presents no particular problems. It presumably originated from the posterior face of the parietal, squamosal and quadrate and inserted by a fleshy head on the smooth saddle-shaped post-glenoid depression and a more tendinous one on the dorso-mesially projecting peg on the retro-articular process. Figure 15 gives a diagrammatic representation of the suggested arrangement of the jaw muscles.

The skull probably showed very little kinetism. There is no mesokinetic hinge joint between frontal and parietal, the character of the suture making any such movement impossible. Similarly a metakinetic movement of the braincase relative to the skull roofing bones is precluded by the firm union between the supraoccipital and the interparietal and parietals. The quadrate, however, joins the squamosal in a rounded articulation which would easily permit a back-and-forth rocking movement, if the lower end of the bone were free to move. The whole palate is firmly united with the skull roofing bones and is not free to move, so that the only possibility for quadrate movement is for slip to occur between it and the posterior wing of the pterygoid. That some movement of this type did occur is quite possible. Walker (1961) has come to exactly the same conclusion with regard to kinetism in the skull of *Stagonolepis* and points out that even a relatively small movement of this type could be functionally significant, as it would permit propalinal movement of the lower jaw, with a resulting slicing action between upper and lower teeth. It has already been suggested in § II that there may have been a muscle running from the lower part of the quadrate wing of the pterygoid to the vertical ramus of the quadrate. If such a muscle did exist, its action would be to rock the lower end of the quadrate forwards and produce the type of movement envisaged by Walker.

One major feature of the skull architecture remains to be considered: in *Euparkeria*, as in other thecodonts, one of the most striking features is the importance of the pre-orbital region. In lepidosaurs, except where there is prolongation of the snout into a narrow rostrum, there is a general tendency for the distance between nostril and orbit to be reduced in later as compared with earlier forms. This is not surprising, since this region does not appear to house any structure of great importance. In thecodonts, however, there is no such tendency and the distance between eye and nostril does not undergo reduction. One can hardly avoid the conclusion that in these animals some functional importance was attached to this region and, if so, it is likely to have been associated with the antorbital fenestra, which is the main structural feature of this part of the skull. Indeed, it is the main distinguishing feature of early archosaurian skull architecture, for behind the orbits, primitive lepidosaur and early thecodont skulls are very similar. Any understanding of thecodont skull architecture therefore necessitates an understanding of the function of the fenestra.

As long ago as 1884 Dollo pointed out that in advanced archosaurs there appears to be a correlation between the size of the antorbital fenestra and the type of jaw musculature. Where the temporal muscles are important (as evidenced by a large superior temporal fossa and sagittal crest and a large coronoid apophysis on the mandible) but the pterygoideus musculature is relatively small (pterygoids not broadly expanded and no mandibular fossa) then the antorbital fenestra is reduced or absent. Where the opposite is the case and the pterygoideus musculature is more important than the temporal, the fenestra is large. He therefore inferred that a large fenestra is associated in some way with the pterygoideus D. The same conclusion was reached by Gregory & Adams (1915) and has been adopted by many later workers. It is not exactly clear from Gregory & Adams's paper or Adams's subsequent one (1919) just what relationship between the muscle and the fenestra is envisaged; one is left in some doubt as to whether it is regarded as actually providing an increased area of origin, or merely acting as a 'bulging hole', i.e. providing a space to accommodate the increased thickness of the muscle when it shortens. Walker (1961) makes it clear that he adopts the former alternative, but consideration of the situation in the Crocodilia appears to render this view untenable. The conditions making for a large pterygoideus D are that a strong bite should be required and that the temporal muscles should be relatively weak. Both these conditions are maximally fulfilled in the crocodile, but the antorbital fenestra has been lost. This would hardly have occurred had the fenestra been the main area of origin of the muscle. Had it merely acted as a bulging hole, however, its loss is understandable, since this function could have been taken over by the large palatal fenestrations which are present in Crocodilia.

One of the weaknesses of both Dollo's and Gregory & Adams's discussions of this subject is that they are based on advanced species and do not consider the problem of the evolutionary origin of the pterygoideus D, nor whether there is any evidence for its presence in early archosaurs. The fenestra may well have functioned as a bulging hole for a large pterygoideus D in later forms, but it does not necessarily follow that this was its primary function and that one may therefore assume that a well-developed fenestra *ipso facto* implies a large pterygoideus D.

As an evolutionary starting point it is reasonable to assume pterygoideus musculature of normal type, originating mainly on the dorsal surface of the broad posterior flange of the pterygoid and inserting at the back of the lower jaw, probably wrapping round to the outer surface. The functional significance of the pterygoideus D and the reasons for expecting its development to be associated with large-scale predation have already been discussed: it provides the powerful bite with the jaws widely open which is necessary for coping with large prey. As the insertion of the most anterior fibres of the pterygoideus is shifted forward on the mandible to give increased mechanical advantage their origin on the skull must also move forward. One would expect it to be taken right forward on the palate clear of the eye and that, as space to accommodate the increased thickness of the contracted muscle became necessary, palatal fenestrations would have developed beneath the belly of the muscle, of the type shown not only in Crocodilia but also in advanced thecodonts. It is difficult to believe that an antorbital fenestra would have developed to fulfil this function, since it does not seem to be very advantageously placed, at least in early thecodonts. Nevertheless, if it were already present for some other reason, it might in addition have acquired some function in this respect.

The immediate problem is to try to decide whether the antorbital fenestra in *Euparkeria* can be functionally related to the development of the pterygoideus D, or whether it requires some other explanation. Reasons have already been given for concluding that although this muscle may have been present it is unlikely to have been very large. The antorbital fenestra, however, is large; too large to be accounted for in terms of a pterygoideus D. The size of the latter is limited by the space available beneath the eye and a muscle small enough to fit into this space could not have required such a large attachment area as the walls of the fenestra offer, still less a bulging hole as extensive as its opening provides. Furthermore, if the muscle did originate in or on the walls of the fenestra, the slight insetting of the preorbital pillar is inexplicable, since it results in reducing the available space exactly where this would be maximally inconvenient.

In the earlier *Chasmatosaurus* there was almost certainly no pterygoideus D. Here the backward slope of the quadrate is so pronounced that temporal muscles inserted vertically below the superior temporal fossa act at such an angle as to make the development of a pterygoideus D quite unnecessary, while the preorbital bar is so much inset as to leave little space for such a muscle and it certainly precludes any attachment within the antorbital fenestra itself. It thus seems that although in later forms the antorbital fenestra may have been turned to account in accommodating a large pterygoideus D muscle, the fenestra was evolved before the muscle in relation to some other function.

This conclusion is supported by the details of the shape of the fenestra. In many of the thecodonts the antorbital fenestra is not simply an aperture but takes the form of a curved depression, like a basin with the bottom knocked out, the most extreme case being seen in *Sphenosuchus*, as restored by Broom (1927). This basin-like structure, with the walls sloping inwards, seems quite unsuited to act either as a bulging hole for a muscle originating on the palate or as an extra surface for muscle attachment; nor is it what one would expect were the function of the fenestra only that of lightening the skull. Broom (1913*b*) notes that in *Euparkeria* the shape is 'suggestive of the antorbital vacuity having housed a large gland'. This, indeed, is exactly what it does suggest, but Broom offered no opinions as to what the function of the gland might have been. The obvious possibility is that it might have been a nasal salt gland. In living reptiles salt glands of various types are known, those of *Caretta caretta* being extremely large and closely associated with the eye (Schmidt-Nielsen & Fange 1958). If indeed the antorbital fenestra was originally developed in relation to a salt gland, this implies that the environment of the earliest thecodonts was such as to provide excess salt in the diet and so present a salt excretory problem. There is, as yet, no evidence that this was the case and if the contrary can be shown, then the salt gland hypothesis must be abandoned and some other solution to the problem must be found. For the present the possible function of the postulated gland cannot therefore be decided.

The conclusions which have been reached may be briefly summarized as follows. The antorbital fenestra was first evolved with no relation to the pterygoideus D muscle, most probably as the housing of a gland whose function cannot yet be decided, although possibly it may have been a nasal salt gland. At this stage the backwardly sloping quadrate made any moving forward of the insertion of part of the pterygoideus musculature unnecessary. Subsequently, as an adaptation to more predacious habits, the quadrate became more vertically orientated, thus permitting a wider opening of the jaws. Concomitant with the resulting change in the angle of action of the temporal musculature, together with increasing need for strength in the early stages of the bite, came a moving forward of the insertion of some of the pterygoid musculature. This, in turn, necessitated a moving forward of the origin on the skull and thus a separate pterygoideus D ultimately developed. At some stage the importance of the antorbital gland diminished, but the fenestra was not always lost: it was retained wherever it was of value either because it was advantageous to keep the skull as light as possible or because the fenestra had come to be functionally associated with the now fully developed pterygoideus D. In this series *Chasmatosaurus* represents a stage before the development of the pterygoideus D, *Euparkeria* (clearly much more predacious) one in which it was probably present, but not yet very large, while in the later *Ornithosuchus* the presence of palatal vacuities suggests that a well developed pterygoideus D was present.

The skull of *Euparkeria* is thus at a stage where there are some adaptations to a carnivorous habit, but specialization has not proceeded very far. The skull is lightly but firmly built but the quadrate is still slightly backwardly directed and no concentration on either temporal or pterygoid musculature at the expense of the other is apparent. From such a condition the most obvious advance is further adaptation to predation, but specialization has not reached the stage where a turn to a more omnivorous, or even ultimately vegetarian habit, seems to be ruled out.

(2) *The limbs and their girdles*

Since the archosaurs are a group in which speed through bipedalism has been evolved, the first question which it is natural to ask of the limbs is: do they suggest that the animal was bipedal or not? In this connexion it is customary to consider the relative lengths of fore and hind limbs, since obviously a bipedal animal will be expected to have relatively long hind limbs. Another factor, however, ought also to be taken into account, to wit the distance between the fore and hind limbs. For efficient bipedal locomotion it is necessary for the hind limbs to be long relative to the fore limbs, but also for the trunk region to be relatively short. The ratio of leg length: trunk length may therefore be expected to be useful as an index of bipedal adaptation.

It is desirable to have as a standard of comparison a series of measurements on living species whose locomotory habits are known. For this purpose I have used *Sphenodon* and *Varanus* as normally quadrupedal forms which are not particularly speedy, a fast running quadrupedal *Agama* and lastly *Chlamydosaurus* and *Basiliscus*, both of which run bipedally, the latter more effectively than the former. Unfortunately only single specimens are available but clearly it would be interesting to know the range of variation shown in each case. I have also included figures for *Saltoposuchus*, an obligate biped, based on measurements given by Colbert & Mook (1951) and an estimate of the trunk length made from von Huene's (1921) restoration. Fore and hind limb lengths are taken as humerus + radius and femur + tibia respectively while trunk length is the distance along the vertebral column from a point directly over the glenoid to one directly above the acetabulum.

Figure 16 shows, first, the length of the fore-limb as a percentage of the length of the hind. While *Saltoposuchus* clearly has far the greatest disparity, it is the comparison of the facultatively bipedal lizards with the quadrupedal forms that is of most interest. The latter have fore-limbs at least 75 % of the length of the hind, while in the former the ratio is close to 70 % or less. With a fore limb 67 % of the length of the hind, *Euparkeria* is in the same class as *Basiliscus*. The comparison of hind limb and trunk length is more striking. Here there is a complete series from the very long bodied *Varanus* to *Basiliscus* and *Saltoposuchus* in which the hind limb is approximately the same length as the trunk. In this character, *Euparkeria* comes between the fast quadrupedal *Agama* and the facultatively bipedal *Chlamydosaurus*.

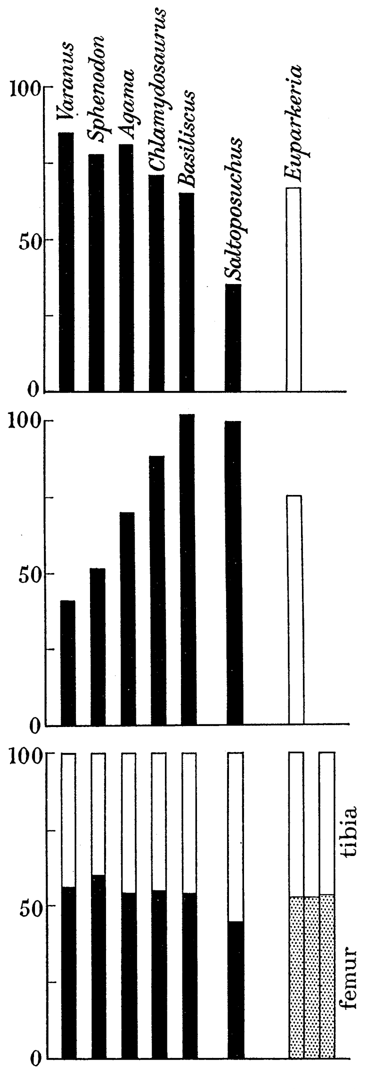

FIGURE 16. Limb proportions in various species. Top, length of radius + ulna as percentage of femur + tibia. Centre, length of femur + tibia as percentage of trunk. Bottom, relative lengths of femur and tibia, the combined length being taken as 100.

Another ratio often considered is the relative lengths of propodials and epipodials. These are also shown for the hind limb in figure 16. It will be seen that in every case except *Saltoposuchus* the femur is longer than the tibia and there is no significant difference between quadrupedal and bipedal lizards. In mammals, cursorial adaptation is characterized by relatively short proximal and long distal limb segments but clearly the same is not true of lizards. This is presumably a reflexion of limitations imposed by the horizontal carriage of the lacertilian femur: as long as the limb is angled and the animal has to rest frequently with its belly on the ground, no great disproportion in length of the two limb segments is possible. The femur can only be shortened after the mammalian type of vertical limb carriage has been achieved. One can therefore conclude that if in a fossil the femur is distinctly shorter than the tibia then the carriage of the femur was vertical, but not vice versa: a femur longer than the tibia does not prove that the femur was horizontal.

Snyder (1949) has shown that in *Basiliscus basiliscus* the counter-balance of the long tail is essential for bipedal locomotion. Although no specimen of *Euparkeria* has a complete tail there is evidence that it was indeed long and there is no reason to doubt that it could have provided the necessary counterweighting.

From the data summarized in figure 16 it seems reasonable to conclude that *Euparkeria* was capable of running bipedally about as effectively as *Chlamydosaurus*, but no opinion can be formed about the carriage of the femur. For information on this point it is necessary to consider the pelvis and its muscles and the shape of the proximal end of the femur.

A vertical limb is important in bipedal locomotion not only because it allows lengthening of the stride, but also because it minimizes side-to-side movement. The importance of this latter factor is shown by the method adopted to reduce lateral movement in bipedal lizards. Here the femur cannot be brought into a vertical position if the pelvis remains normally orientated and the solution adopted is to twist the body about the long axis at each stride so that the pelvis instead of remaining horizontal, is at an angle, the side opposite the leg in contact with the ground being thrust high in the air at each stride. This clearly is wasteful of energy and a vertical limb carriage would be much more efficient.

In considering the hip joint, it is helpful to compare *Euparkeria* with a quadrupedal form such as *Varanus*. In both, the articular head of the femur is terminal, with perhaps a trifle more curvature over on to the ventral surface in *Euparkeria*. Clearly in both animals a horizontal position of the femur is a natural posture. There are, however, two major differences between *Euparkeria* and the lizard. In *Euparkeria*, first, the acetabulum is more deeply excavated and has a very considerable overhang at the top and, secondly, the trochanter on the femur is smaller and situated further down the shaft. The importance of these two characteristics is at once apparent if the femur is placed horizontally in the acetabulum and then turned downwards into a vertical position. In *Varanus* not only is the femur easily dislocated upwards because of the absence of sufficient dorsal lip to the acetabulum, but in addition the trochanter fouls the lower margin. In *Euparkeria* neither of these things happens and the limb can be brought to a vertical position without difficulty.

If in *Euparkeria* the femur did take up this position during fast running, one would expect there to be certain changes in the muscles responsible for moving the femur. With a less horizontal carriage, adduction and abduction become less important while a long stride, coupled with the position of the trochanter, require that muscles swinging the limb fore and aft should originate well in front of and behind the acetabulum.

Apart from the caudifemoralis, the main muscles concerned in moving the femur are the retractor femoris and ischio-femoralis in the power stroke and the puboischio-femoralis internus and ambiens in the recovery stroke. Figure 17 shows the origins of these muscles in *Varanus* and their probable sites in *Euparkeria*, the latter being partly based on the arrangement found in *Alligator*. If the two drawings are superposed it is seen that the ischio-femoralis origin has been shifted considerably further back in *Euparkeria*, giving strong retraction of the femur at the end of the stride, but there appears to be much less alteration in the positions of the puboischio-femoralis internus and ambiens. This is at first sight rather puzzling, since the caudifemoralis is in a position to provide powerful retraction and one would therefore have expected that the first desideratum would have been increased protractor efficiency. Two factors may be relevant in explaining this situation. Snyder (1962) notes that in *Crotaphytus*, the fastest bipedal lizard that he studied, the caudifemoralis muscle was relatively small. This might be advantageous in giving the tail greater freedom of movement, for the balancing movements of the tail required in bipedal running are very considerable. The increased efficiency of the ischio-femoralis in *Euparkeria* may thus be compensation for a reduction in the caudifemoralis. Furthermore, protractor efficiency is not necessarily reflected in changes in the pelvis. In the Crocodilia the femur can be brought so far forward that it is almost parallel with the body axis. This is achieved not by a muscle originating on the girdle but by one (derived from the puboischio-femoralis internus) originating on the centra of the vertebrae well in front of the pelvis, closely resembling the mammalian psoas. It therefore seems reasonable to suggest that in *Euparkeria* also a muscle of this type was present.

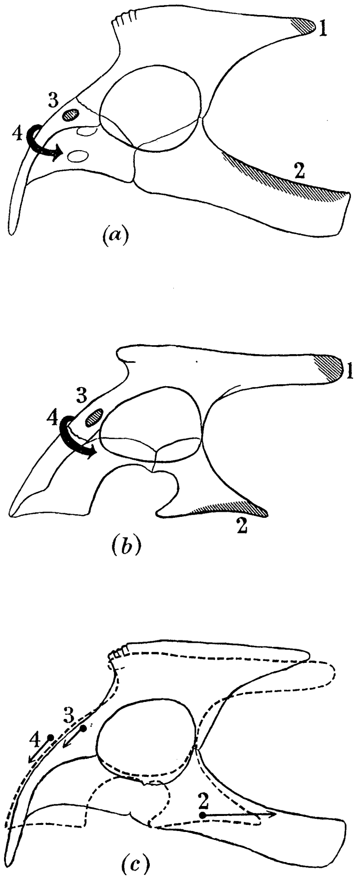

FIGURE 17. Pelvis of (*a*) *Euparkeria* and (*b*) *Varanus* showing origins of various muscles. 1, retractor femoris: 2, ischio-femoralis; 3, ambiens; 4, puboischio-femoralis internus. (*c*) The two shown with the acetabula superposed: arrows show the differences in the relative positions of muscles in the two animals.

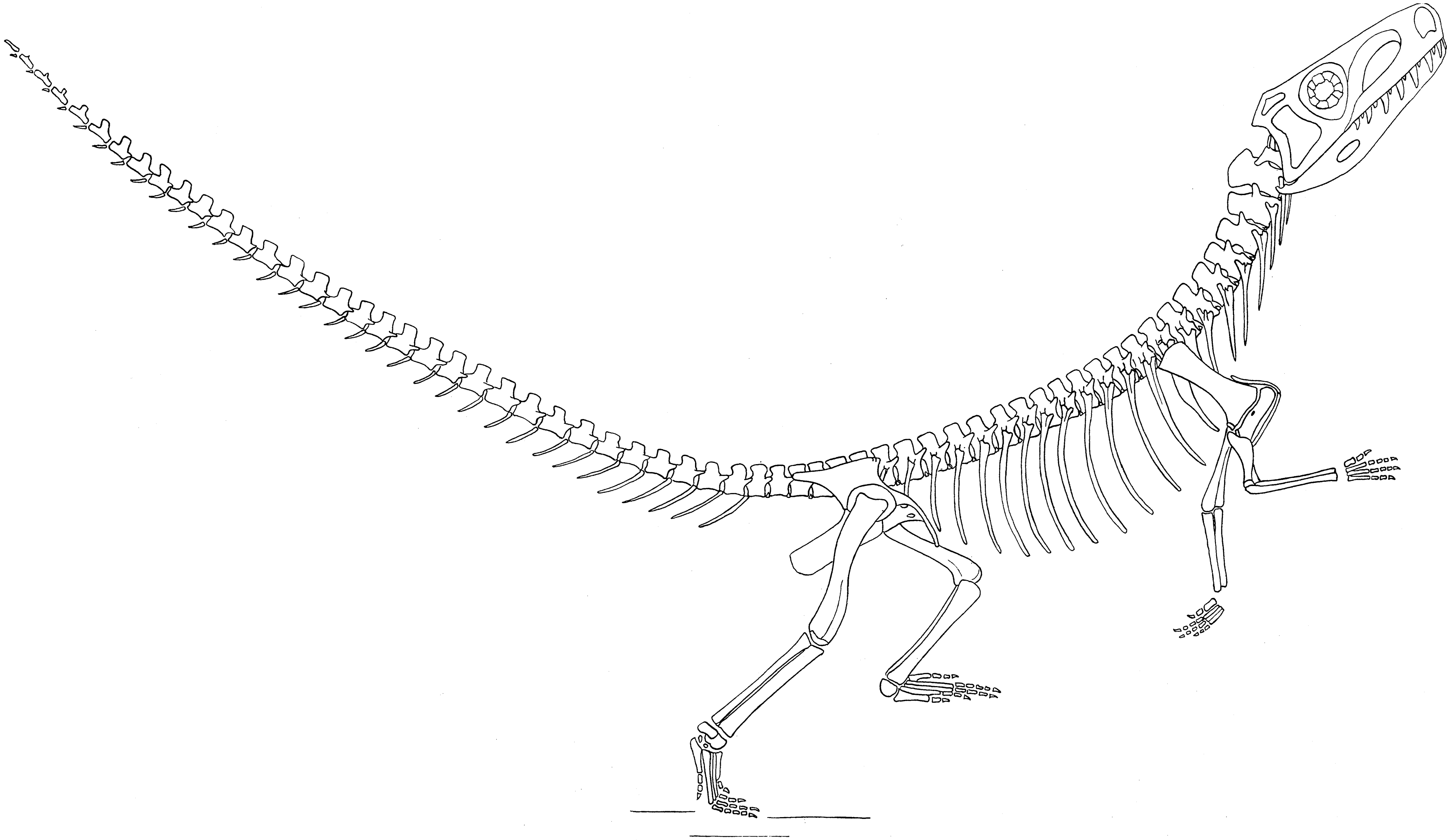

FIGURE 18. Restoration of the whole skeleton.

From the structure of the hind limb and girdle it therefore seems legitimate to conclude that *Euparkeria* rested and moved slowly quadrupedally with the femur horizontal, but that for fast running a bipedal gait with the femur nearly vertical was adopted. In bipedal running the foot was presumably set down in an approximately plantigrade manner, but lifted progressively from heel to toes as shown in Snyder's drawings (1949) of *Basiliscus*. The greater part of the weight could be transmitted down the tibia to the astragalus and hence to digits 1 and 2, which would therefore have to take most of the landing shock. This may account for the fact that they are considerably stouter than digits 3 and 4.

The ankle joint is of considerable interest. In specimen 6049, the shank had been pushed forwards so that the tibia lay in the same plane as the foot with its proximal end directed anteriorly. This movement of the tibia carried the astragalus with it, so that it lay almost upside down. The calcaneum, however, retained its position relative to the other foot bones and did not move with the fibula. Similarly, in the foot figured by Broom (1913*b*), the calcaneum is in position relative to the foot, but the tibia has been pushed round mesiad and has carried the astragalus with it, rotating it through approximately 90° in a horizontal plane. The facet which should articulate with the calcaneum now faces directly proximally and the calcaneum, as mentioned before, lies against the distal tarsal facet. The fact that in both cases the astragalus has moved with the tibia but the calcaneum has remained with the foot indicates that the union between tibia and astragalus was much firmer than that between calcaneum and fibula. In fact, the astragalus is functionally part of the shank but the calcaneum belongs to the foot. One can go further. The thin external part of the calcaneum is roughened and clearly the Achilles tendon was attached to this part of it. The external edge of the 5th metatarsal is also thin and roughened and the tendon obviously continued on and was attached here too. The outside of the calcaneum and of the 5th metatarsal are thus very firmly bound together, which, of course, is why they stay together when the ankle is broken. Furthermore, not only are they physically tied, but they form a functional unit. This implies that, unless there is a complete reversal of trend, the calcaneum is irrevocably part of the foot. It is impossible to imagine that without functional discontinuity it could give rise to a true mesotarsal articulation with both calcaneum and astragalus functionally part of the shank, although a pseudo-mesotarsal condition could be achieved by reduction and ultimate loss of the calcaneum. An alternative possibility is further elaboration of the articulation between astragalus and calcaneum to give the crocodilian type of ankle joint.

The characteristics of the fore-limb and girdle accord well with the type of locomotion that has been suggested. The relative shortness of the limb has already been mentioned: it is also much more lightly built than the hind limb, the shaft of the humerus being much slimmer than that of the femur. In addition the glenoid articulation faces so much posteriorly that the humerus can take a near vertical position only when it is somewhat retracted: during protraction the limb must have been considerably angled. The relatively large coracoid, providing attachment for a large coracobrachialis muscle, also suggests that strong adduction of the humerus was necessary, again indicating that the limb was used with the humerus approximately horizontal. The shoulder joint thus does not show modifications permitting the humerus to be used vertically. In this it contrasts sharply with the hip, where modifications permitting a vertical carriage of the femur are clearly evident. This contrast between fore and hind limbs is strongly suggestive of facultative bipedalism.

Figure 18 shows a restoration of the whole skeleton, with the animal using this suggested bipedal gait. The only parts of this which are conjectural are the digits of the manus, the lengths of some of the ribs and of the chevron bones, the length of the tail and the intercentra of the anterior caudal vertebrae.

(3) *The vertebral column and ribs*

The general characteristics of the vertebral column are such as are to be expected in a swiftly moving active animal. Although strong, the vertebrae are extremely light: there is nowhere any great thickness of compact bone, for both centra and neural arches are composed of cancellous bone almost as spongy as that of an avian vertebra. The sloping zygapophyses suggest that the column had a moderate degree of mobility in both the vertical and the horizontal plane. There are, however, three points that require further discussion: the shift in rib articulation positions along the column, the spine tables and the dorsal depressions in the centra.

(*a*) *Rib articulations*

The shift of rib articulations along the length of the vertebral column is a distinctive archosaur characteristic but although the positions of parapophyses and diapophyses are frequently described in great detail, the functional implications of the changes in position are rarely considered. They appear, however, to be related to efficiency of pulmonary ventilation. In an animal without a diaphragm and with ribs extending all the way to the sacrum, the most effective way of increasing the volume of the body cavity is to rock the ribs upward in the vertical plane. Such movement is, however, possible only in the region behind the pectoral girdle. In the region of the girdle movement of the ribs is restricted by the scapula to fore-and-aft rocking. The movement of a two-headed rib must be a rocking motion at right angles to the line joining the two heads. The archosaur pattern with the two heads almost vertically above each other at the shoulder but behind this point coming to lie more nearly in line horizontally thus reflects rib movements which give the most effective pulmonary ventilation that can be achieved without the development of a diaphragm, an upward component being introduced into the rocking movement once the obstacle of the shoulder girdle has been cleared.

In the Lepidosauria, with single-headed ribs, an analogous adaptation is shown. In *Varanus*, for instance, the articulation for the rib is an elongated oval apophysis and the movement of the rib is in a plane at right angles to the long axis of the oval. In the shoulder region the articulations are arranged with their long axes almost vertical, so that the rib must rock back and forth. Further back along the column the articulation becomes more oblique, sloping forwards and downwards, so that the movement of the rib is slightly upwards as well as forwards. Although the change in angle of the articular facets is not very great, the upward movement of the posterior ribs is easily visible in a live *Varanus*. In archosaurs the change in rib articulations is more pronounced and their pulmonary ventilation must have been correspondingly more efficient.

(*b*) *Spine tables*

If the function of the spine tables were, as has been suggested, to provide a support for overlying scutes then one would expect the development of scutes and tables to correspond. This, however, is not the case. In *Euparkeria* the paramedian scutes extend all along the vertebral column with no significant change in size, but the spine tables are developed only in the posterior cervical and anterior dorsal region (see table 2 and figure 6). Moreover, in *Stagonolepis*, where the armour extends over the whole body, Walker's (1961) illustrations show maximal development of the spine tables in the sacral region. In modern crocodiles also there are scutes, but little development of tables. It therefore seems that the tables must have some function not associated with the presence of scutes.

The most obvious possibility is that the spine tables are related to the attachments of muscles belonging to the transversospinalis system. An investigation of the muscles attached to the tips of the neural spines of the alligator was therefore made. In the mid-trunk region, two pairs of tendons are attached to the top of each neural spine, a pair at the front and another pair at the back. The tendons of the anterior series slope outwards, downwards and forwards, each overlapping its neighbour from the preceding vertebra.

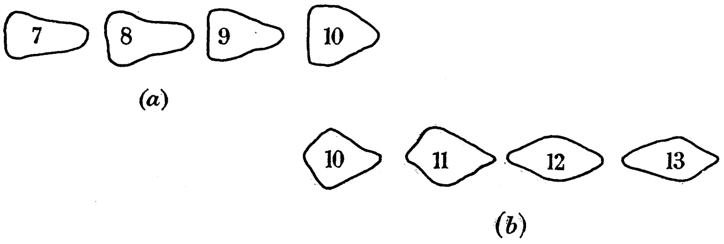

FIGURE 19. Outlines of spine tables, seen from above. (*a*) Specimen S.A.M. 6047B vertebrae 7 to 10; (*b*) specimen S.A.M. 6047A vertebrae 10 to 13. (Magn. × 1½.)

From the tendons arise forwardly sloping muscle fibres which form the outermost part of the block of muscle lying in the angle between neural spine and transverse process. The tendons of the posterior series slope downwards and backwards, each overlapping its neighbour from the succeeding vertebra and give off backwardly sloping muscle fibres forming the mesial part of the musculature between spine and transverse process. The action of the anterior series is to raise the part of the column anterior to the origin on the neural spine, while that of the posterior series is to raise the part of the column posterior to the origin.

Passing backwards along the column, the muscles of the anterior series diminish in importance and those of the posterior series become larger, reflecting the fact that the tail is raised on the body, not the body on the tail.

Passing forwards, the muscles of the posterior series diminish in importance and at the level of the posterior margin of the scapula the tendons of the anterior series are replaced by the attachments of the large dorsal neck muscles constituting the semispinalis capitis and rectus capitis posterior. There is some slight widening of the tips of the spines in this region to form incipient tables. These certainly can have nothing to do with supporting the scutes, for in the neck region the scutes are nowhere near the neural spines, being separated from them by the thick neck muscles.

If then the spine tables represent the attachment areas of these anterior and posterior muscle series, it follows that in *Euparkeria* raising of the anterior end of the column was more important than raising the tail but in *Stagonolepis* the opposite was the case. This seems to be functionally comprehensible. *Euparkeria's* head is large and in bipedal running it would be necessary to hold it well up and back to preserve balance. Enlarged attachments for the neck muscles in the posterior cervical and shoulder region are therefore to be expected. The heavily armoured *Stagonolepis* was almost certainly quadrupedal and there is no reason for large tables to be developed anteriorly. The tail is extremely heavy and if it were either raised during fast locomotion or, possibly, used as a defensive weapon as is that of *Varanus*, then the enlarged tables in the region round the sacrum are explicable.

If this interpretation is correct and the anterior spine tables of *Euparkeria* accommodated muscles attached to the front of the spines, but those of *Stagonolepis* are related to tendons originating on the back of the spines, then one would not expect the tables to be anteroposteriorly symmetrical. Those of *Euparkeria* should be wider at the front than at the back, those of *Stagonolepis* narrow in front and wider behind. Figure 19 shows that in *Euparkeria* the tables do have the predicted shape and Walker's illustration (1961, Fig. 22*a*) gives a suggestion of the converse shape in *Stagonolepis*.

(*c*) *Central excavations*

Although the depressions in the middle of the centra are dilations of the neural canal, it is impossible to believe that they could have been filled by a ganglionic expansion of nervous tissue. It seems more plausible to suggest that the spaces may have accommodated some non-nervous expansion of the cord, comparable with the sinus lumbosacralis of birds. In the latter the dilation is dorsal, not ventral and is confined to the sacral region. It consists of a mass of large cells, loaded with glycogen (Terni 1924). Unfortunately the function of this tissue in birds is quite unknown. It therefore does not throw any light on the possible significance of the central depressions in *Euparkeria* apart from showing that a dilation of the neural canal need not necessarily imply a corresponding increase in nervous tissue. In this connexion it is strange that the pelvic enlargement of the neural canal characteristic of many dinosaurs is customarily assumed to be purely ganglionic: it is sometimes even compared with the sinus lumbosacralis of birds (e.g. Colbert 1962) without mentioning that, although there is some enlargement of the ventral part of the cord in correlation with the large leg muscles, the sinus itself is non-nervous. Edinger (1960) is a notable exception, and gives a careful and accurate assessment of the limitations of our knowledge of pelvic enlargements. Clearly a physiological investigation of the avian sinus is much to be desired and might cast some light on the sacral enlargement of the dinosaur cord.

Depressions in the centra exactly like those of *Euparkeria* also occur in the vertebrae of early ornithischians from the Red Beds of Southern Africa (Compton, personal communication). Without an understanding of their functional significance it is not possible to decide whether the presence of the depressions in *Euparkeria* and in Ornithischia is indicative of any close relationship.

IV. Relationships with other groups

When he first described *Euparkeria* Broom (1913*b*) was quite clear that he was dealing with a progressive but relatively unspecialized member of a group that probably included the ancestors of all the major lineages of the later archosaurs. He stressed the dinosaurian characters of the skull of *Euparkeria* and noted that 'there is nothing in the post-cranial skeleton that is not just what we should expect to find in the Dinosaur ancestor'. In addition Broom was of the opinion that the Pseudosuchia are probably also ancestral to the birds. Heilmann (1926) later elaborated this idea, making a detailed comparison of *Archaeopteryx* and *Euparkeria*. There has been little subsequent disagreement with Broom's general assessment of *Euparkeria* as typifying a group including the ancestry of all the later archosaurs, and Watson (1957) expresses exactly the same opinion.

The problem, however, becomes more complex if we wish to push the analysis further and consider *Euparkeria* not merely as a reasonably typical example of an ancestral group, but as a potential ancestor in its own right and ask which later groups might have descended from *Euparkeria* itself. *Euparkeria* possesses a number of primitive characters such as the palatal teeth, the distinct interparietal, the presence of intercentra, the large coracoid and the retention of clavicles, which one would expect to be lost in later descendants. *Euparkeria* was an active, lightly built carnivore but, with one exception, its adaptations to this mode of life are not so extreme as to constitute specializations restricting its future evolutionary possibilities. The one exception is the structure of the ankle joint. As noted above, the fact that the astragalus is functionally part of the shank but the calcaneum belongs to the foot suggests that there are only two further evolutionary possibilities for the ankle joint: on the one hand, elaboration of the movement between astragalus and calcaneum to give the crocodilian type of joint and, on the other, reduction and ultimate loss of the calcaneum to give a pseudo-mesotarsal articulation. If this is correct, then *Euparkeria* cannot itself be ancestral to any form possessing a true mesotarsal joint with both astragalus and calcaneum fused to the shank. This at once excludes two major groups—the Ornithischia and the birds. The former typically show a separate calcaneum bound to the fibula, while in the embryonic stages of the latter a separate ossification representing the calcaneum is present. The evidence from the ankle joint is reinforced by the structure of the pelvis: while the saurischian pelvis is easily derived from that of *Euparkeria* that of the Ornithischia and the birds presents more difficulties. Lacking as we do information on the early stages of evolution of the ornithischian type of pelvis it is not possible to show how it arose from a more typically reptilian form, but to suggest that both the Ornithischia and the ancestors of the birds arose from some form other than *Euparkeria*, differing from the latter in the structure of both pelvis and ankle, does not seem unreasonable. While the ornithischian ankle joint does not seem to be derivable from that of *Euparkeria*, the same is not true of the Saurischia. In the sauropods the calcaneum fails to ossify and no calcaneum is present in the foot of the prosauropod *Melanosaurus* from the South African basal Red Beds, described by Crompton & Wepenaar (1964). This condition could easily have been derived from that of *Euparkeria*.

Apart from its potential ancestry of the prosauropods and sauropods, there appear to be at least two further evolutionary paths which might have been followed by the descendants of *Euparkeria*. The first is simply to continue as a cursorial carnivore and become more fully adapted to this mode of life. This path would lead to such forms as *Ornithosuchus* and *Hesperosuchus*. The latter (see Colbert 1952) is indeed so like a slightly 'improved' version of *Euparkeria* that it must surely have evolved, if not from *Euparkeria* itself, at least from some very closely related form.

The second possibility that must be considered is the abandonment of the carnivorous cursorial life and adoption of a vegetarian habit. This, in addition to changes in the dentition and jaws, one would expect to be characterized by reversion to quadrupedal locomotion, development of heavier armour and increase in size and could have given rise to the Aëtosauridae (*sensu* Walker 1961). *Stagonolepis* in particular is almost exactly what such an evolutionary trend would be expected to produce. In this connexion it is interesting to note the presence of a second pubic foramen in *Stagonolepis*, a characteristic not known elsewhere except in *Euparkeria*. There can be little doubt that the Aëtosauridae do represent vegetarian adaptation of a lineage closely related to *Euparkeria*, but whether this lineage is actually derived from *Euparkeria* or from some slightly less advanced form depends on whether or not the latter has already gone too far along the path of adaptation to a carnivorous life for such a change in habit to occur. The structure of the ankle joint seems to indicate that it has: although a calcaneum is present and, as suggested above, elaboration of the movement between this bone and the astragalus to give a crocodilian type of joint is formally possible, a more detailed consideration shows that the derivation is less simple than appears at first sight. The astragalus of *Euparkeria* is large and the weight of the body is mainly transmitted through it to the first and second digits. The calcaneum, by comparison, is small, smaller than is apparent in dorsal view. Although fairly wide mesiodistally, the calcaneum is not deep dorso-ventrally, except for a pillar-like extension mesially where it meets the astragulus. Its whole structure suggests that it is already being reduced and that the tarsus has in fact started on the path towards a pseudo-mesotarsal articulation involving eventual elimination of the calcaneum. The Aëtosauridae must thus have originated from a form which, while closely similar to *Euparkeria*, was still a trifle more unspecialized in limb structure. It thus appears that while *Euparkeria* could have been directly ancestral to advanced pseudosuchians such as *Ornithosuchus* and *Hesperosuchus* and possibly to the prosauropods and sauropods, it was itself a trifle more advanced than the actual ancestor of the closely related Aëtosauridae and was not directly ancestral to the Ornithischia or the birds.

As for *Euparkeria's* own ancestry, clearly the relationship with the Proterosuchia is close. Two recent papers have dealt in considerable detail with the latter group and it is therefore not necessary to review their structure in any detail. Tatarinov (1961) reviews the Russian Proterosuchia and concludes, with justification, that both *Vjushkovia*, v. Huene 1960 and *Garjainia* Otschev 1958 should be placed in the genus *Erythrosuchus*. In his opinion the Proterosuchia are a sufficiently uniform group to be united in a single family, Proterosuchidae, comprising the subfamilies Proterosuchinae and Erythrosuchinae. The former includes *Proterosuchus*, *Chasmatosaurus*, *Chasmatosuchus*, *Elaphrosaurus* and *Archosaurus* while the latter contains only the single genus *Erythrosuchus*. *Euparkeria* is not discussed, so presumably Tatarinov would not include it amongst the Proterosuchidae, although its affinities are clearly closest with the more actively predacious Erythrosuchinae.

Hughes (1963) has also reviewed the Proterosuchia and reaches conclusions basically very similar to Tatarinov's. He agrees with the latter about the synonymy of *Vjushkovia* and *Garjainia* with *Erythrosuchus* but considers the Proterosuchia sufficiently distinctive to retain the group as a sub-order, containing the two families Chasmatosauridae and Erythrosuchidae. The similarities between *Euparkeria* and *Erythrosuchus* are considered to be so great that the former must be included in the family Erythrosuchidae. Certainly there are many similarities, both in general structure and in such detailed points as the three-headed ribs. At the same time, no dermal armour has been found associated with *Erythrosuchus* and its ankle joint appears to have functioned in a different manner from that of *Euparkeria*. Although in both genera the tarsus consists of astragalus, calcaneum and two distal tarsals, Hughes considers that in *Erythrosuchus* the astragalus and calcaneum were 'securely bound together and to the crus'. In *Euparkeria*, on the other hand, the astragalus is firmly bound to the tibia but the calcaneum is functionally part of the foot and movement occurred between astragalus and calcaneum. Even should the relationship of *Euparkeria* and *Erythrosuchus* ultimately prove to be less close than Hughes envisages, a strong case can still be made for including *Euparkeria* in the Proterosuchia. The latter would then constitute a 'horizontal' grouping, including all lower Triassic archosaurs and based on their common possession of a number of primitive characteristics.

Von Huene (1962) adopts a rather different arrangement. The Proterosuchidae (identical with Tatarinov's Proterosuchinae) are regarded as the most primitive pseudosuchians. From these are derived the Sphenosuchidae, in which are included not only such primitive forms as *Euparkeria* and *Vjushkovia* (whose synonymy with *Erythrosuchus* is not accepted) but also such advanced forms as *Saltoposuchus*. The Erythrosuchidae are regarded as a separate family, related to the Sphenosuchidae, but no particular affinity with the Proterosuchidae is stressed. This arrangement in which the most primitive genera are distributed amongst three different families appears to have little to recommend it.

Whatever taxonomic arrangement is ultimately agreed upon, the relationship of *Euparkeria* to the rest of the Thecondontia seems to be reasonably clear in general terms. It is an early form, retaining many primitive features which serve to underline its relationship to the other lower Triassic forms constituting the Proterosuchia as defined by Romer (1956). These are the characters which have impressed Hughes and caused him to classify *Euparkeria* in the Erythrosuchidae. At the same time *Euparkeria* shows many progressive characteristics, reflecting adaptation to a more active terrestrial carnivorous habit than any other known form of comparable age and these serve to link the early Triassic Proterosuchia with the later Pseudosuchia of the Middle and Upper Triassic. It is the existence of these locomotor adaptations, as reflected in the characters of the limbs and their girdles, that have been responsible for v. Huene's classifying *Euparkeria* in the Sphenosuchidae. To argue at length as to whether *Euparkeria* should be classified amongst the primitive forms with which it shares many characteristics, or amongst the forms that have proceeded further along the same type of evolutionary pathway, does not seem a very profitable occupation at the present time: nor does it seems worthwhile at present to attempt any more detailed analysis of the relationship of the Thecondontia to the Ornithischia and the Saurischia. A great deal of new material is now being recovered from the South African Red Beds which it is to be hoped will be of assistance both in determining more exactly the relationships between Lower and Upper Triassic thecodonts and between the thecodonts and the other archosaurian orders. At the present time it therefore seems more important to provide detailed descriptions of such material as is available and to attempt to analyse the adaptive significance of the pecularities of each species than to attempt to erect phylogenies when further important material is likely to be forthcoming in the near future.

TABLE 3

(All measurements are given in millimetres)

	type							
	S.A.M. 5867	S.A.M. 6047A	S.A.M. 6047B	S.A.M. 7700	S.A.M. 6049	S.A.M. 7698	S.A.M. 6048	un-numbered foot
skull length, front of snout to occipital condyle	78·8	—	—	—	—	—	—	—
skull length, front of snout to back of quadrate	86·3	—	—	—	—	—	—	—
maximum horizontal diameter of external naris	—	11·5	—	—	—	—	—	—
maximum length of antorbital fenestra	22·2	—	—	—	—	—	—	—
maximum length of orbit	20·8	—	—	—	—	—	—	—
maximum length of superior temporal fossa	*ca.* 12	—	—	—	—	—	—	—
maximum length of inferior temporal fossa (lower margin)	17·7	—	—	—	—	—	—	—
maximum height of inferior temporal fossa	18·2	—	—	—	—	—	—	—
width of skull table between orbits	—	13·8	—	—	—	—	—	—
length of lower jaw	90·5	—	—	—	—	—	—	—
maximum length of coracoid	*ca.* 25	—	30·0	—	—	—	—	—
maximum height of scapula	37·4	—	—	—	—	—	—	—
length of humerus	37·8	—	—	43·2	—	—	—	—
length of radius	31·8	—	—	—	—	—	—	—
length of ulna	33·7	—	—	—	—	—	—	—
length of iliac crest	—	—	—	—	29·5	37·8	—	—
straightline distance from tip of pubic apron to suture with anterior end of ilium	29·2	—	36·0	—	22·8	—	—	—
maximum length of ischium	—	—	42·0	—	31·0	—	36·7	—
length of femur	55·8	—	61·6	—	53·8	—	—	—
length of tibia	47·8	—	51·0	—	44·1	—	—	—
length of metatarsal 1	—	—	—	—	11·8	—	—	12·3
length of metatarsal 2	—	—	—	—	17·7	—	—	18·7
length of metatarsal 3	—	—	—	—	—	—	—	21·7
length of metatarsal 4	—	—	—	—	—	—	—	20·6
length of metatarsal 5	—	—	—	—	—	—	—	12·8

During the course of this work I have received from a great many sources assistance which it is a pleasure to acknowledge. First, I owe to Dr A. W. Crompton the opportunity to study the material in the South African Museum collection and must also thank him for the interest he has shown throughout the course of the work and for a critical reading of the manuscript. To Professor D. M. S. Watson, F.R.S., and to Dr F. v. Huene I am grateful for the opportunity to study specimens in their collections and to Professor P. B. Medawar, F.R.S., for the hospitality of his department during the time I was working on Professor Watson's material. To the Royal Society and Nuffield Foundation I owe a travel grant which made it possible for me to visit London and Tübingen. I have received technical assistance and advice of much value from Mrs F. Mussett and Mr V. C. Moran took many of the photographs for me. To Dr K. Kermack and Dr P. L. Robinson I am indebted for many useful discussions and to the latter also for permission to make measurements on her specimens of *Chlamydosaurus* and *Basiliscus* and I am grateful to Mr B. Hughes for permission to read the manuscript of his paper before its publication. I should also like to thank Dr F. R. Parrington, F.R.S., for a critical reading of the manuscript. Finally, this work would not have been possible without the financial support of the South African Council for Scientific and Industrial Research to whom I am indebted for a series of research grants.

Note on the illustrations

Almost all the drawings have been made from several specimens, the numbers of which may be found in the appropriate section of § II. Wherever S.A.M. 6047B (the very large animal) or S.A.M. 6049 (the very small one) has been used, measurements have been multiplied by the factor necessary to bring the animal to the same size as the type. All the drawings may therefore be taken as representing a medium size animal, similar to the type. Table 3 gives such measurements as can be made with reasonable accuracy.

With the exception of the first, all the plates are stereo pairs.

Explanation of abbreviations used in figures

Ang.	angular	*Pa.*	parietal
Art.	articular	*Pal.*	palatine
B.O.	basioccipital	*Po.Fr.*	postfrontal
B.S.	basisphenoid	*Pr.O.*	prootic
Ect.	ectopterygoid	*Pre.Fr.*	prefrontal
E.O.	exoccipital	*Pt.*	pterygoid
f.ov.	fenestra ovalis	*Pt.Q.*	pterygoid wing of quadrate
Fr.	frontal	*Q.*	quadrate
I.P.	interparietal	*Q.J.*	quadratojugal
J.	jugal	*Q.Pt.*	quadrate wing of pterygoid
L.	lachrymal	*S.Ang.*	surangular
Mx.	maxilla	*S.O.*	supraoccipital
Na.	nasal	*Sq.*	squamosal
O.O.	opisthotic	*St.*	stapes
P.Mx.	premaxilla	*Ty.*	tympanum
P.O.	postorbital	*Vo.*	vomer
P.T.F.	posttemporal fossa		

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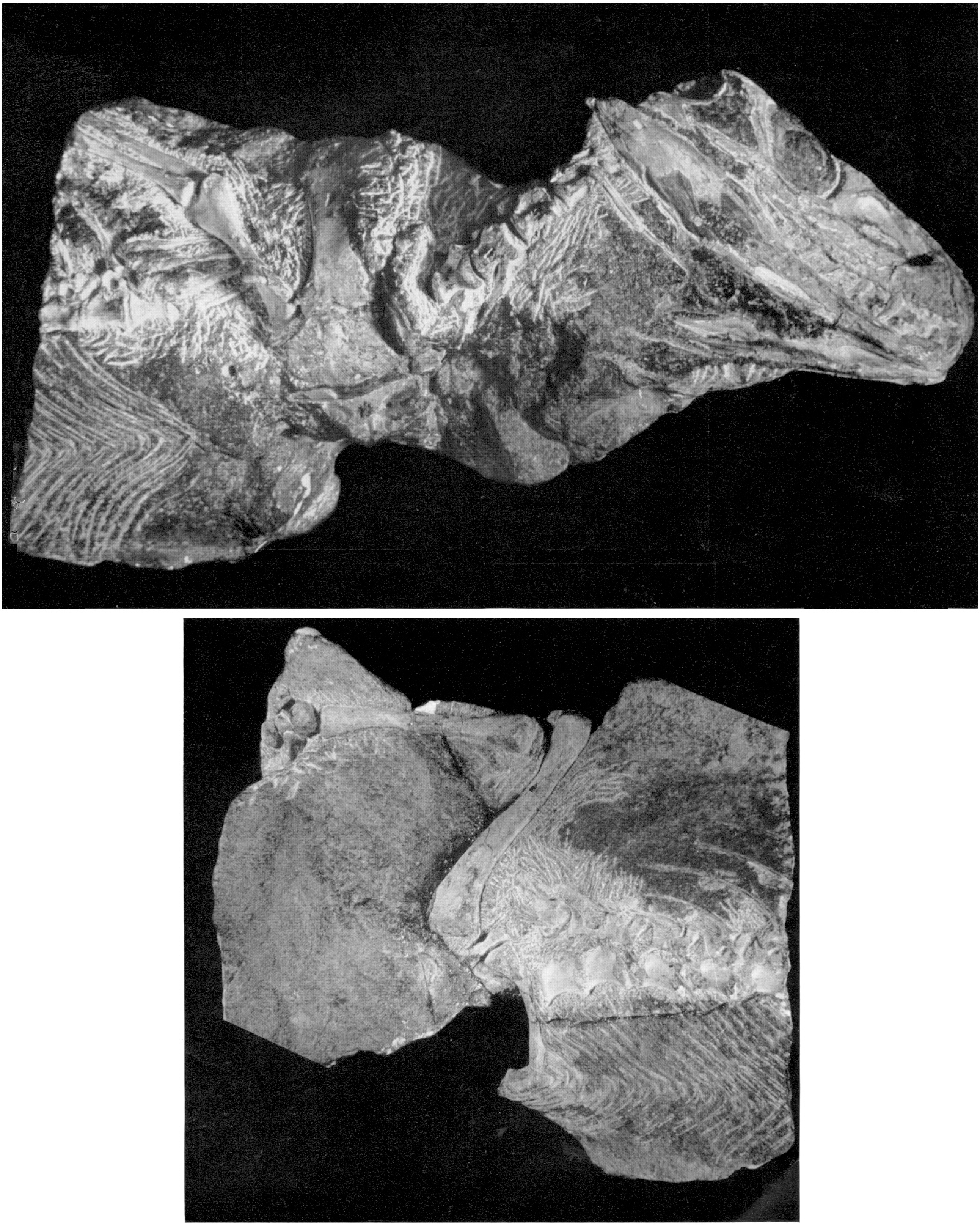

Figure 20. The type specimen (S.A.M. 5867). The counter-slab shows that there is one vertebra missing between the two pieces. (Natural size.)

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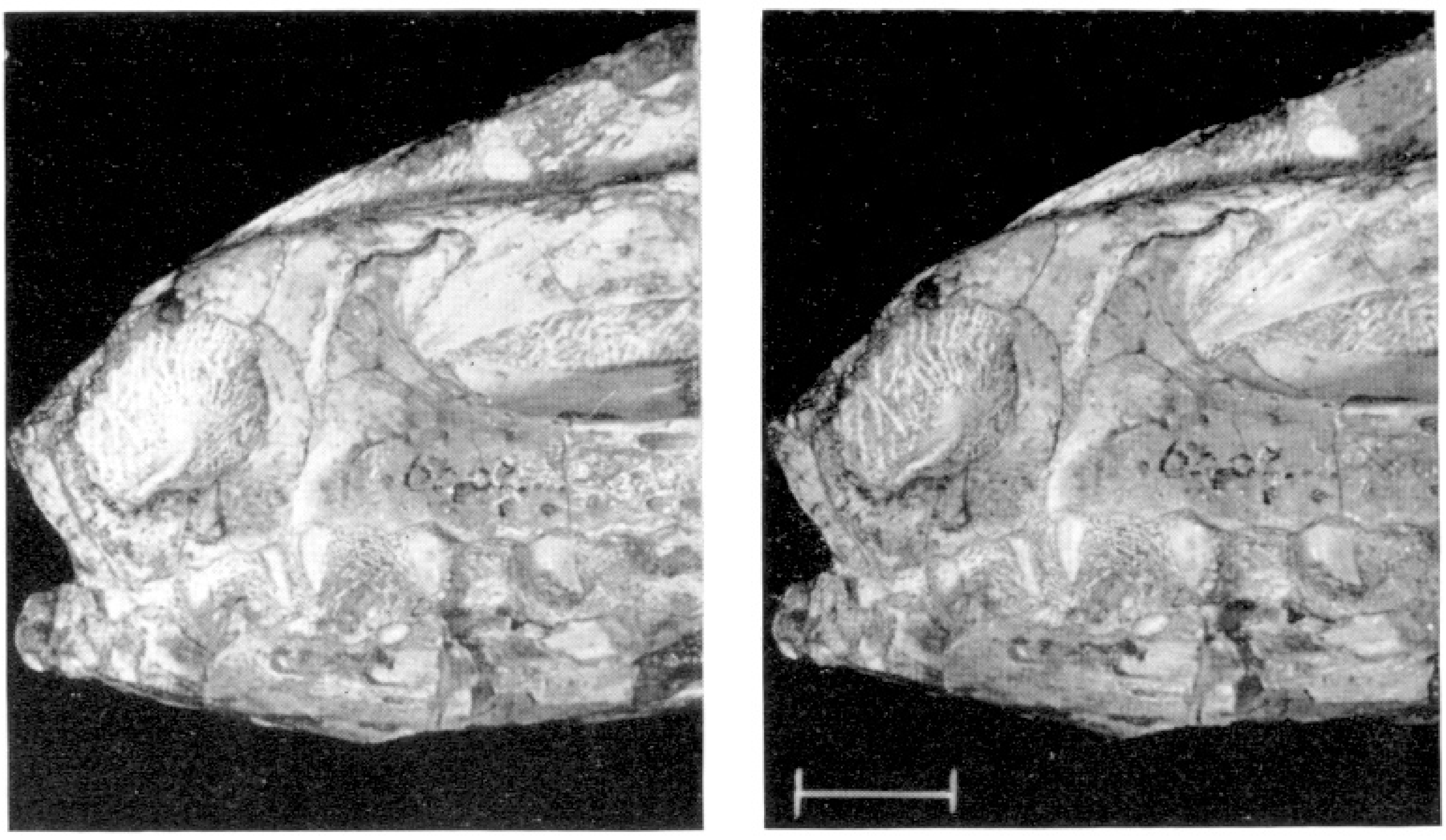

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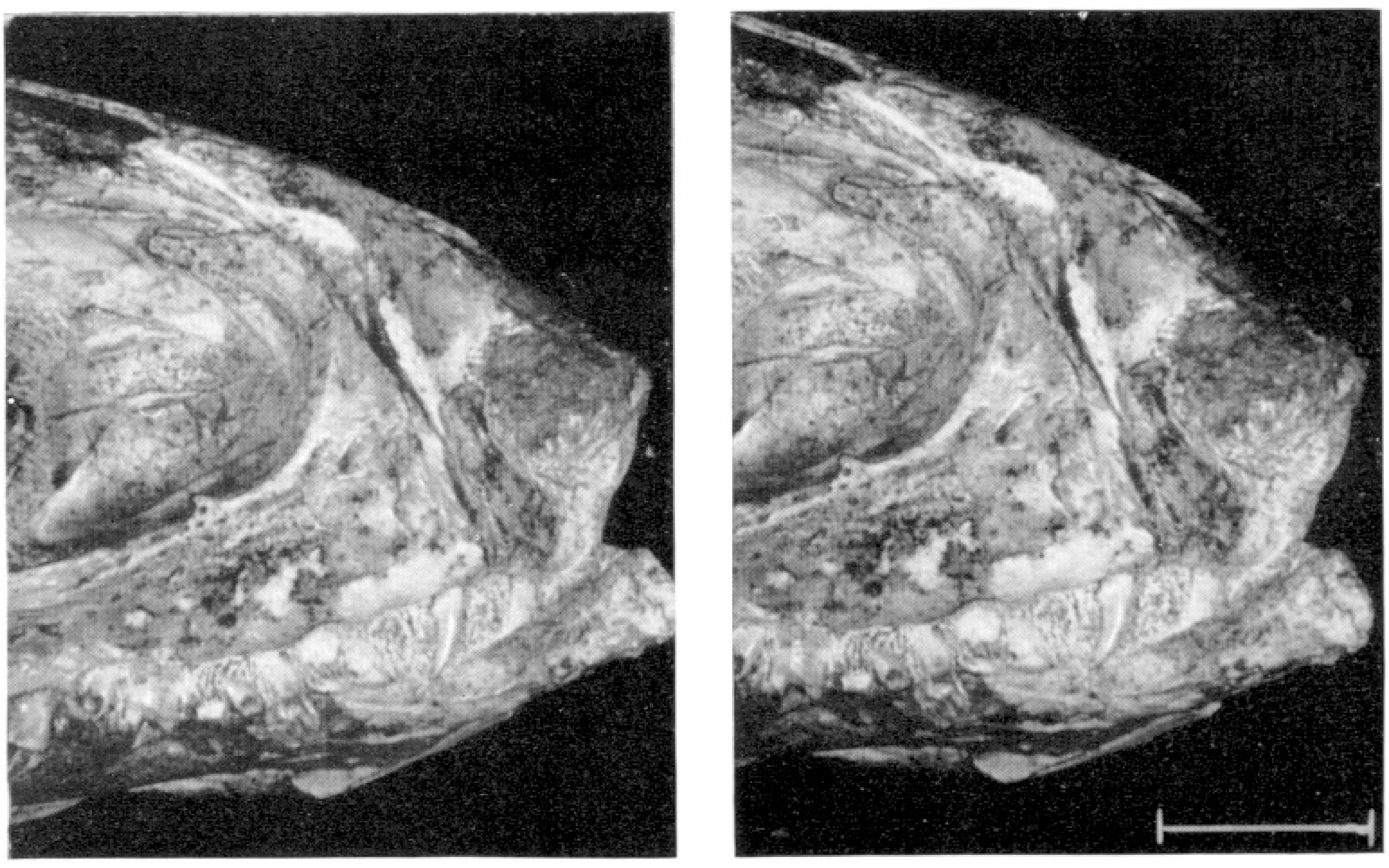

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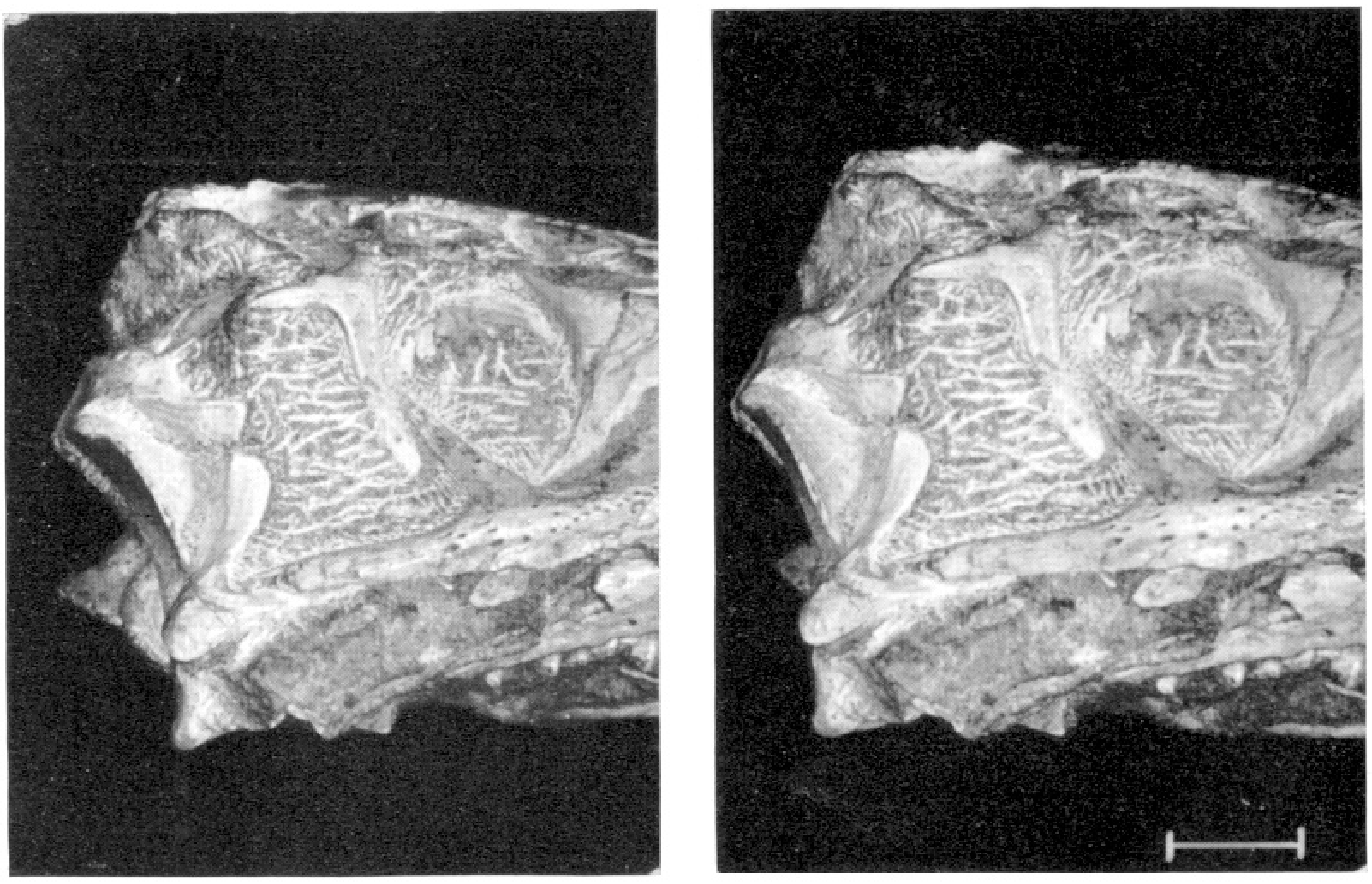

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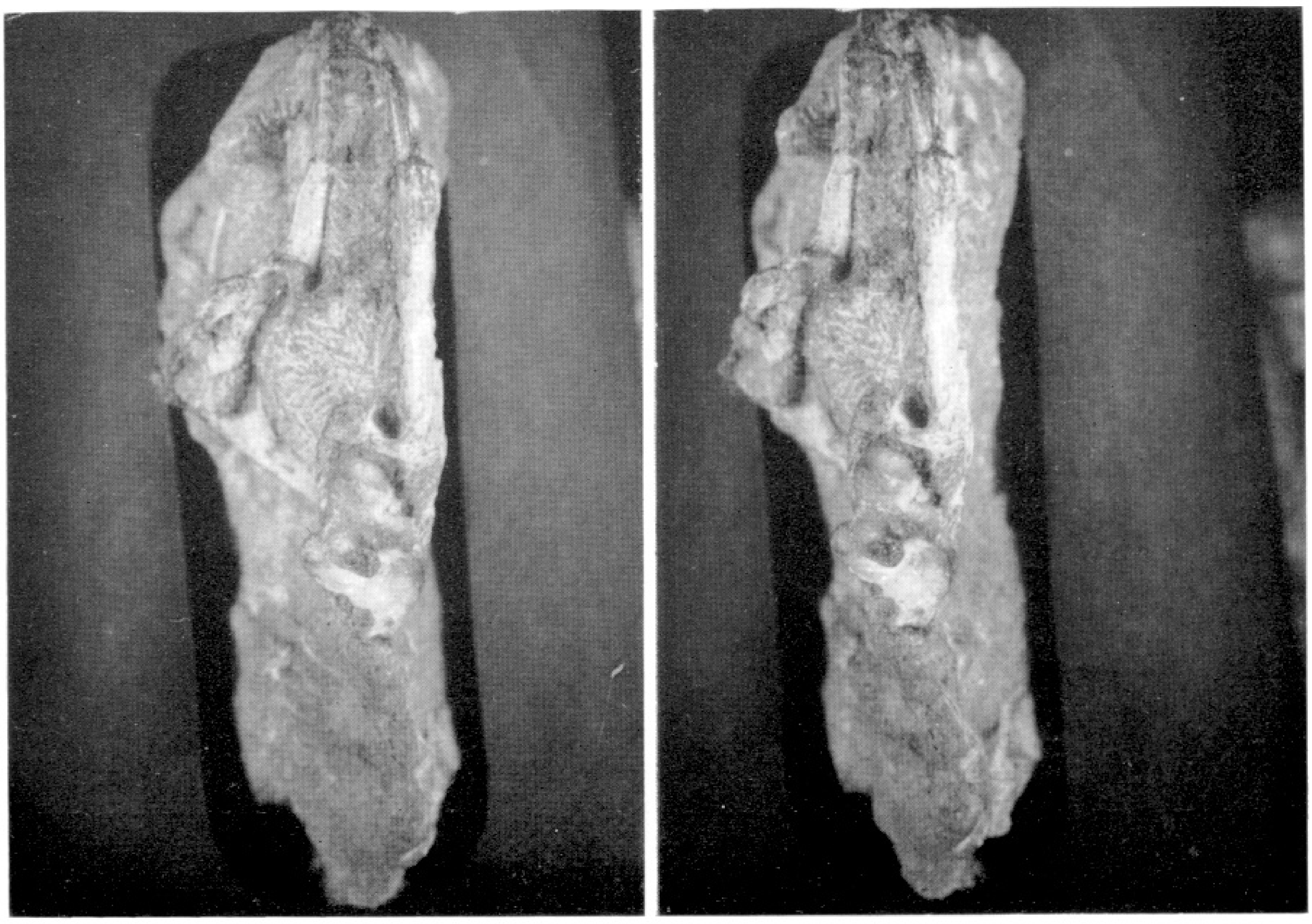

FIGURES 21–24. For description see facing page.

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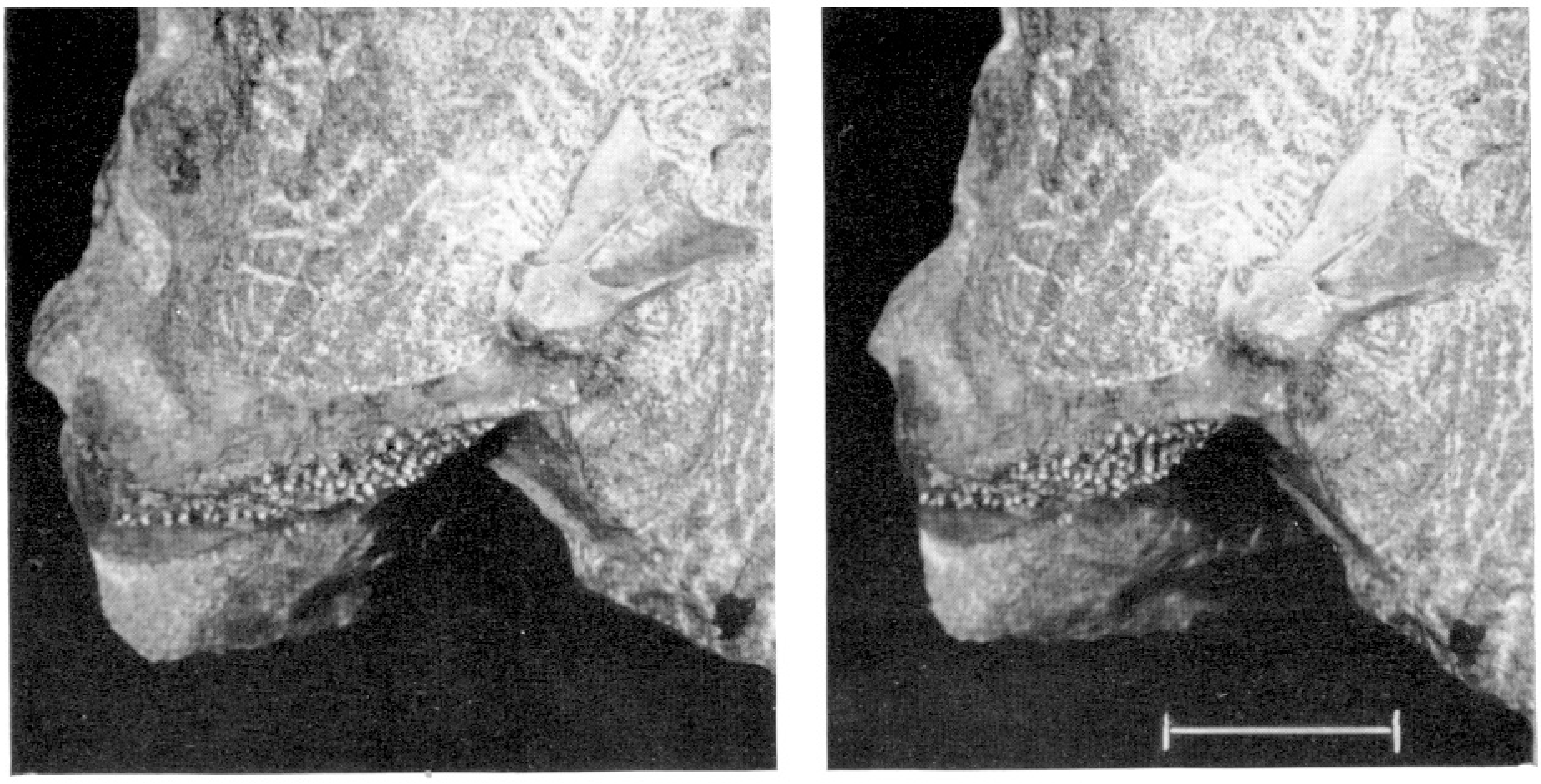

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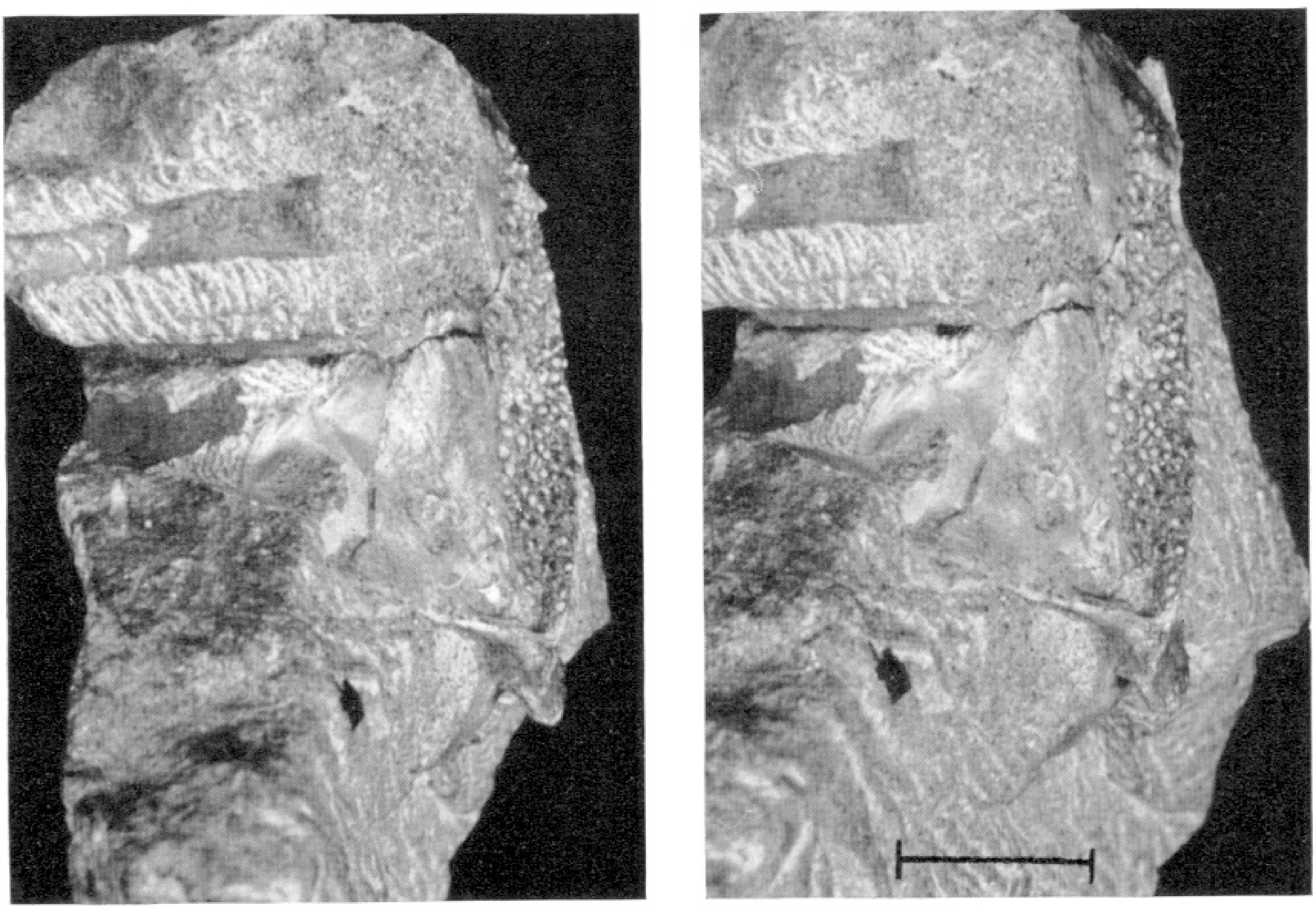

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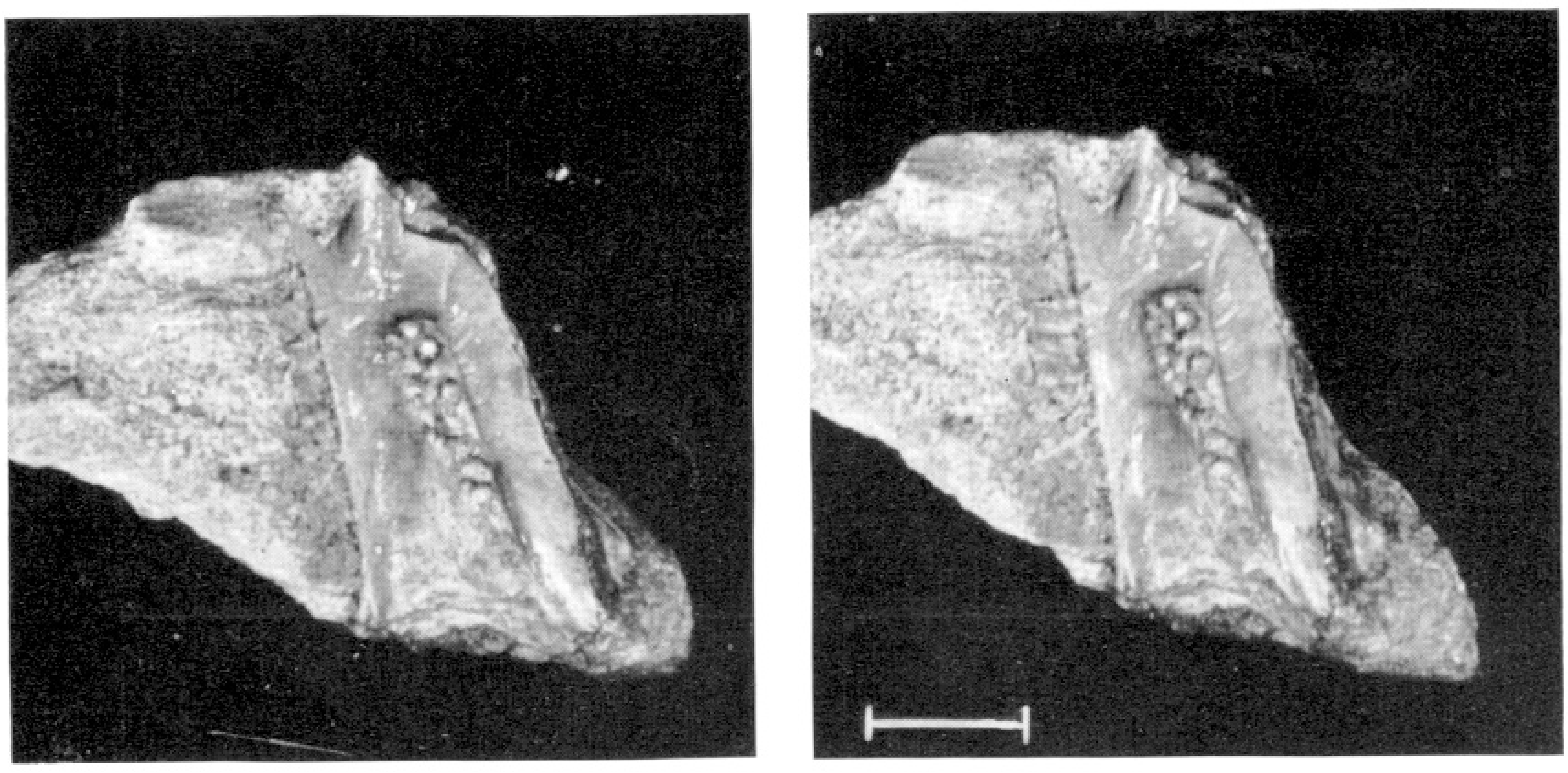

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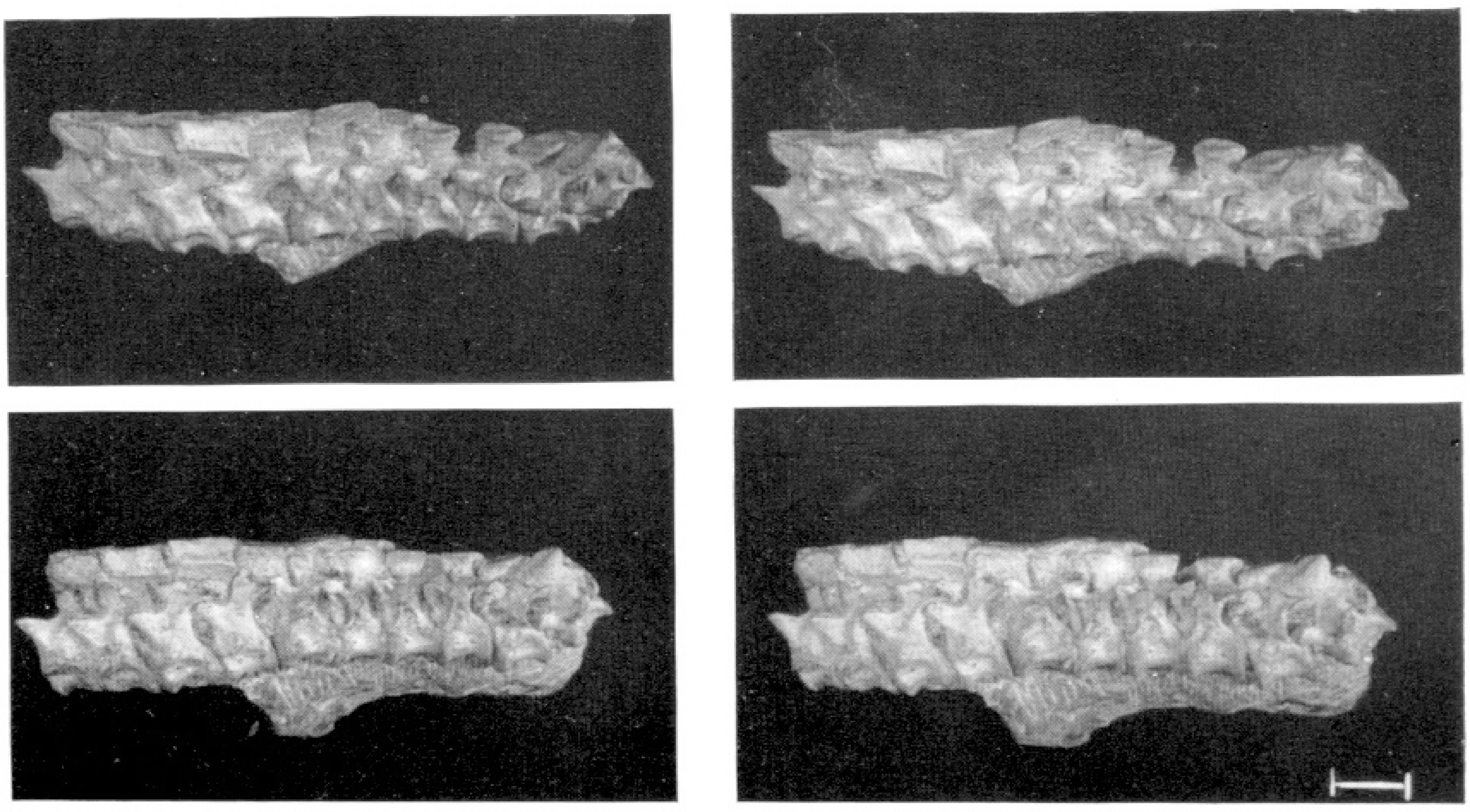

FIGURES 25–28. For description see facing page.

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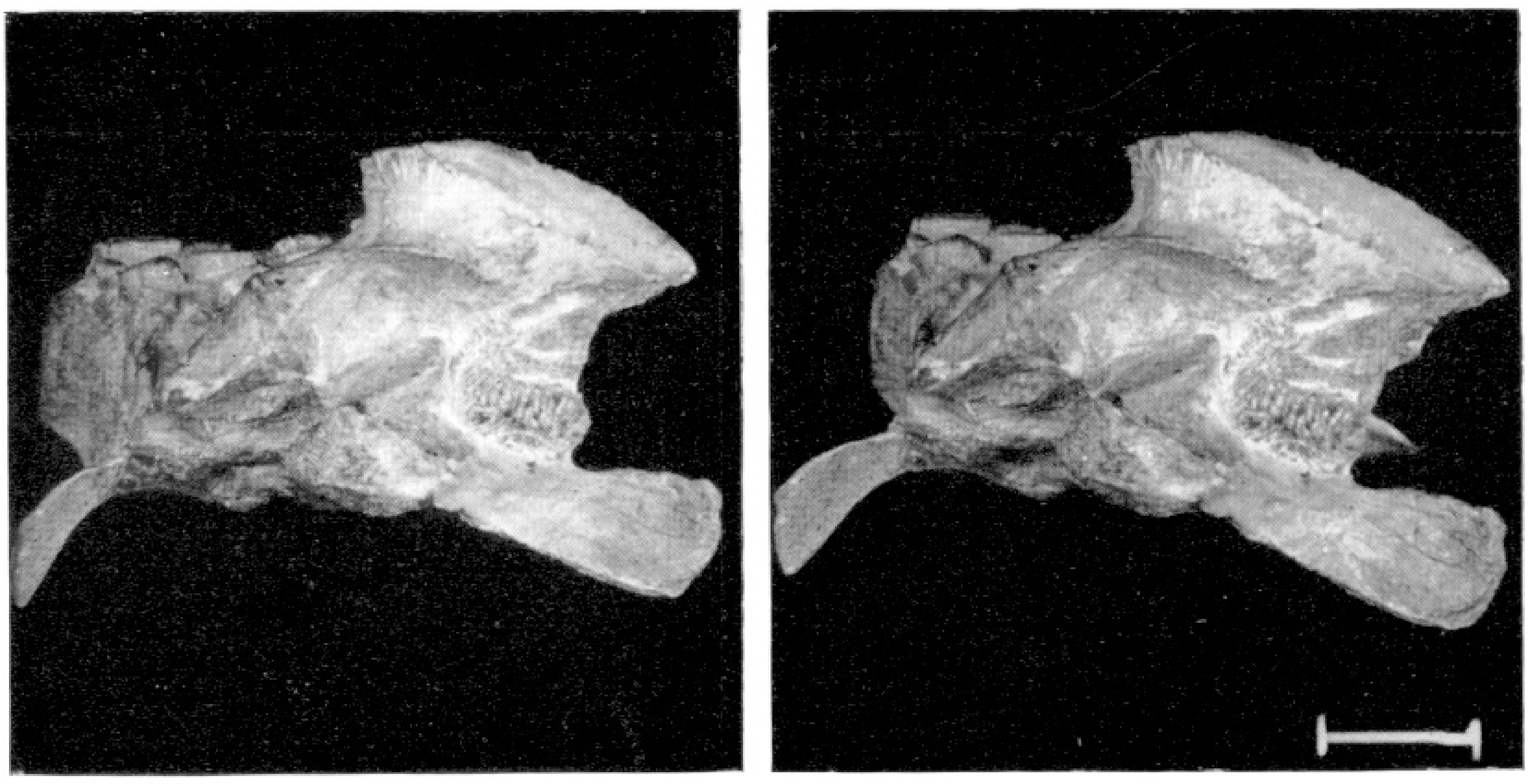

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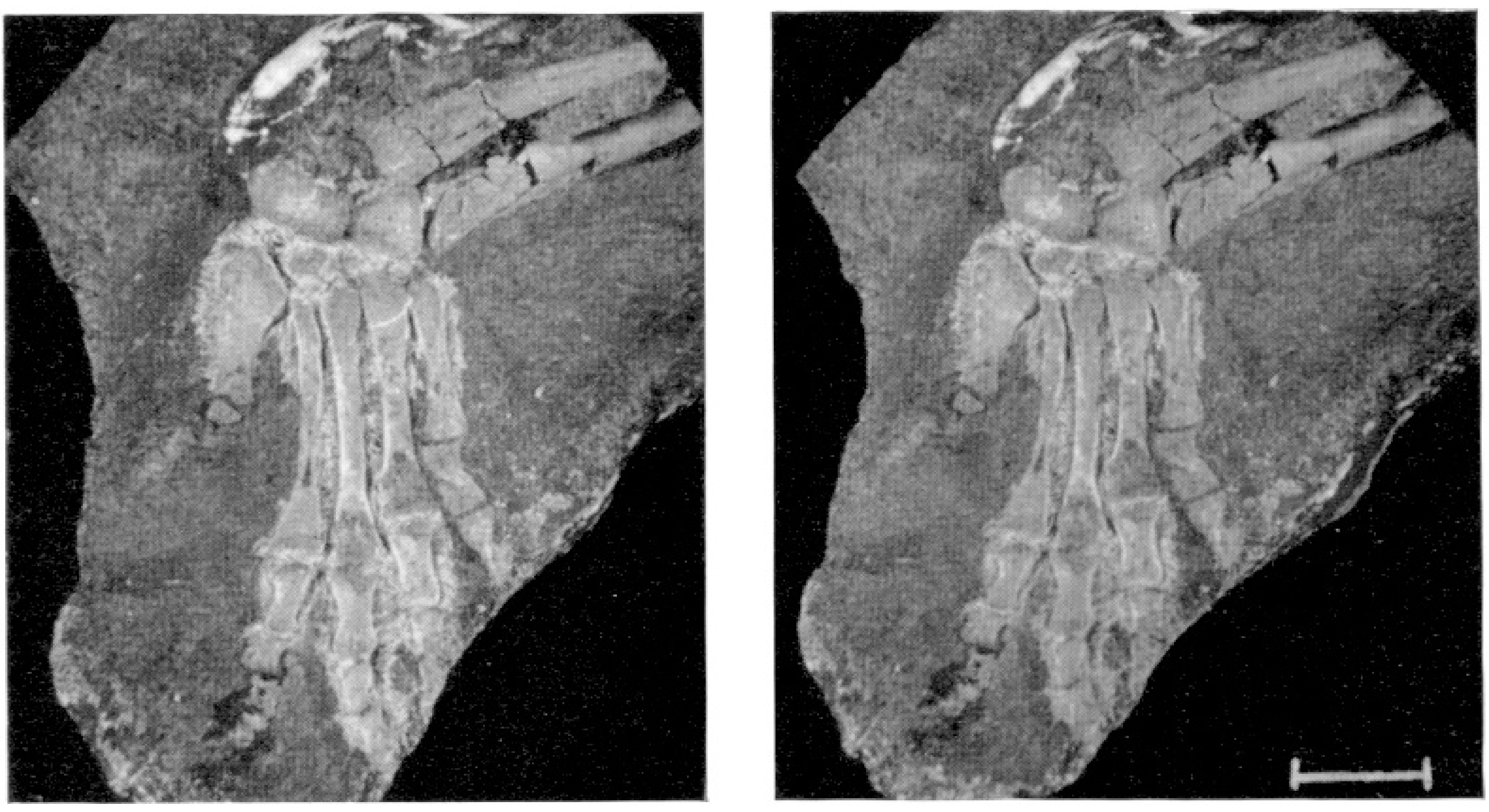

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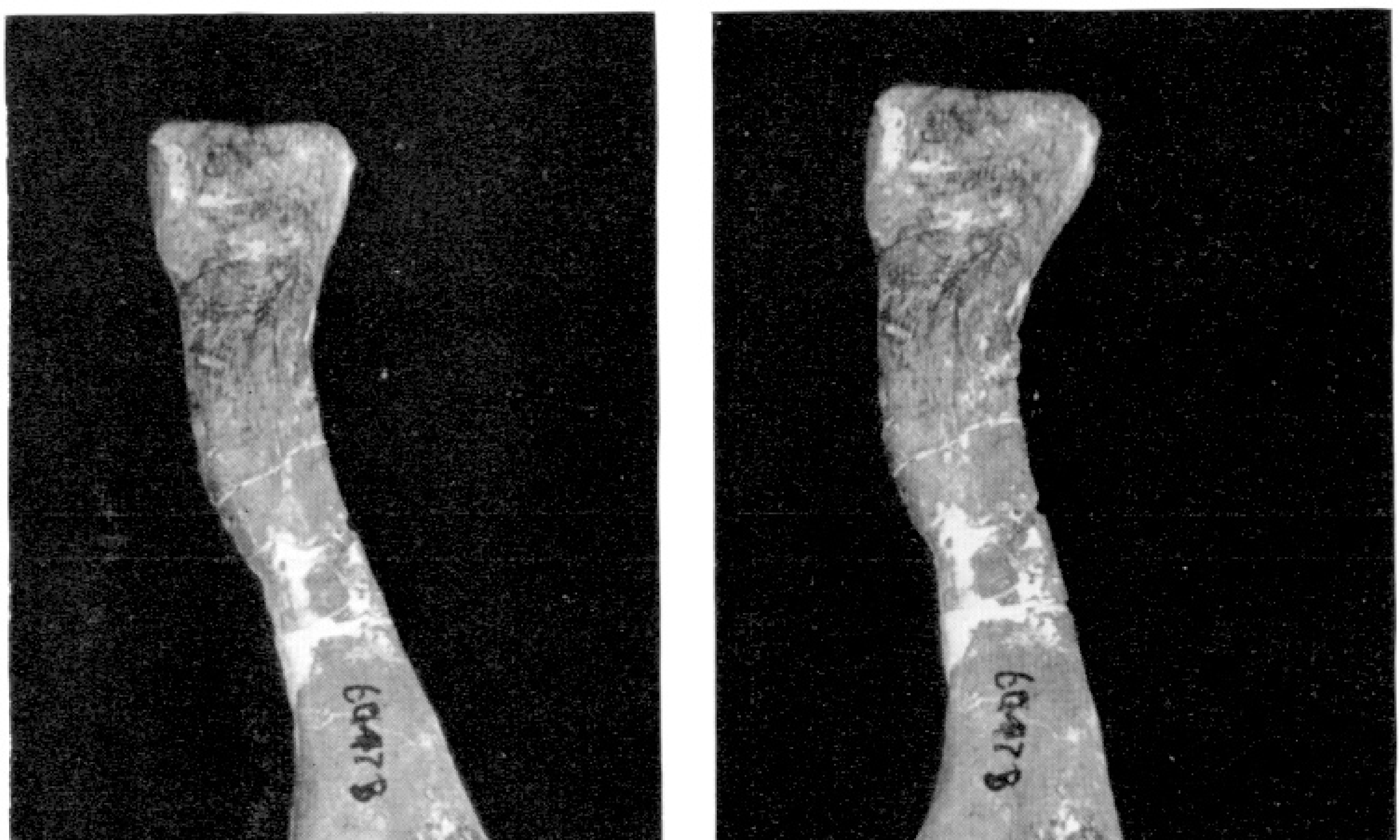

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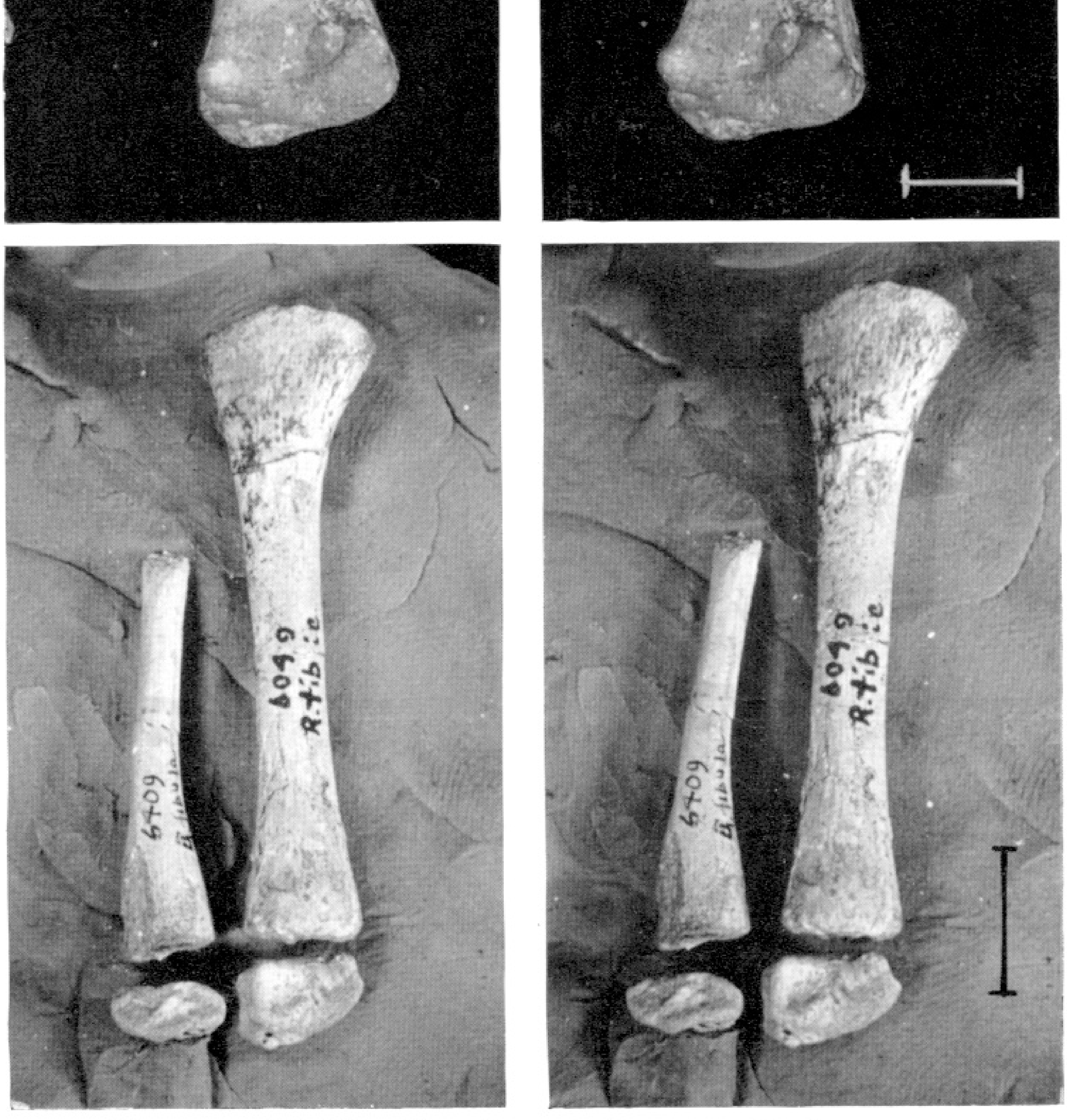

FIGURES 29–32. For description see facing page.