TRIASSIC REPTILES FROM THE ELGIN AREA: *STAGONOLEPIS*, *DASYGNATHUS* AND THEIR ALLIES

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The maxilla named by T. H. Huxley *Dasygnathus longidens*, from the Trias of Findrassie near Elgin, is re-described. A pterygoid from the same locality is referred to this species and described for the first time. These two bones indicate a large, carnivorous pseudosuchian apparently allied to *Erythrosuchus*.

A detailed description is given of the osteology of the pseudosuchian *Stagonolepis*, amplified by a large number of hitherto undescribed specimens. The material (considered to represent at least twenty-one individuals) shows an almost complete segregation into two size-groups, distinguished by only a few minor morphological differences of the postcranial skeleton. The larger and small individuals are considered to be males and females respectively, of the one species *S. robertsoni* Agassiz.

Study of *Stagonolepis* has demonstrated its close relationship to *Aëtosaurus* from the Stubensandstein (Keuper) of Stuttgart. The latter genus, however, was in urgent need of revision. Accordingly a brief account is included of the principal respects in which previous descriptions of this form require modification. Specimens referred by von Huene (1921) to *A. crassicauda* are shown to have been misidentified in many cases; this material is a composite of a small coelurosaur and a true aëtosaurid. Some modifications are also suggested to previous accounts of *Typothorax* and *Desmatosuchus* from the Trias of North America, and new restorations are given of the skulls of these forms.

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The extremely close relationship between *Stagonolepis* and *Aëtosaurus*, perhaps even indicating generic identity, makes unavoidable the merging of the two families previously founded on these genera. On grounds of priority the name Aëtosauridae is retained for the taxonomic unit which includes *Aëtosaurus*, *Stagonolepis*, *Typothorax* and *Desmatosuchus* as principal members. A restricted diagnosis of the family Aëtosauridae is given, based on the above four forms, and this is followed by a review of the genera which have from time to time been included in the former families Stagonolepidae and Aëtosauridae. The great majority of these genera are excluded from the group as now defined.

Possible evolutionary trends within the family are briefly outlined; the sequence of increase of specialization appears to be *Aëtosaurus, Stagonolepis, Typothorax, Desmatosuchus.* The conclusions of Dollo (1884), Adams (1919) and others concerning the function of the preorbital fossa in archosaurian reptiles are endorsed, and it is suggested that a trend towards the reduction of the anterior pterygoid muscle took place in aëtosaurids, in parallel with a similar trend in ornithischian dinosaurs. Many features of the skeleton of aëtosaurids recall the Ornithischia. These include the elongate naris, reduced dentition, vertical or forwardly inclined quadrate, slipper-shaped jaw, small skull and well-developed dermal armour. However, a direct ancestor-descendant relationship appears to be ruled out by the position of the supratemporal fossa, reduction of the infratemporal opening, probable loss of the coronoid and typically pseudosuchian pubis, although the aëtosaurids may well lie close to the root-stock of the Ornithischia.

The mode of life of the aëtosaurids is considered, and it is concluded that these animals were herbivorous, or possibly feeders upon invertebrates obtained, in the case of *Stagonolepis* at least, by digging with the peculiar expanded snout-tip and dentary rostrum. A simple muscular mechanism is postulated whereby this could be effected.

The stratigraphical implications of these studies are briefly examined and the suggestion, based primarily on the close relationship between *Stagonolepis* and *Aëtosaurus*, is put forward that the Triassic sandstone of Elgin occupies a higher horizon than has previously been considered.

I. INTRODUCTION

The first reptilian fossil discovered in the Elgin region was the impression of an articulated series of bony plates, found by a workman in a quarry at Lossiemouth in 1844. Drawings of the impressions were sent to Agassiz who named it *Stagonolepis robertsoni* after his correspondent in Elgin. Agassiz (and later Hugh Miller) believed the fossil to be part of the squamation of a large ganoid fish; at that time no other fossils had been recorded from the sandstones of Lossiemouth, Spynie and Findrassie, and there appeared no reason to doubt that these beds were of Old Red Sandstone age.

Fifteen years later, however, T. H. Huxley (1859) showed from additional material that the scales were part of the ventral armour of a reptile, thus initiating a controversy over the age of these rocks which lasted for a decade, until Huxley (1869) proved conclusively by means of the rhynchosaur *Hyperodapedon* that they were of Triassic age.

In 1875 Huxley included *Stagonolepis* and '*Belodon*' in his well-known paper on the evolution of the Crocodilia, regarding them as ancestral crocodiles. Two years afterwards his monograph of *Stagonolepis* appeared, describing in some detail the material then known.

Since that date much material has accumulated in museums in England and Scotland. Von Huene has discussed the genus on several occasions (1902, 1908*a*, 1911*a*, 1936, 1942), at first assigning it to the Phytosauria, more recently to the Pseudosuchia as a primitive member, bridging his group the Pelycosimia and the rest of the Pseudosuchia. Some skeletal elements additional to those known to Huxley were briefly described and figured by him, and a restoration of the skull was given in 1936.

However, these did not add materially to our knowledge of the animal and a revision taking into account all the new material was desirable, particularly since the genus had been made the type of a family to which many other genera had been referred from time to time. The present work was undertaken with the object of elucidating the affinities of *Stagonolepis* and preparing as complete an account as possible of its osteology.

In the course of the investigation it became clear that the nearest ally of *Stagonolepis* is *Aëtosaurus* from the Stubensandstein (Keuper) of Germany. With the aid of a grant from the Royal Society a visit was made to Stuttgart to examine the material of *Aëtosaurus*, and the more important results obtained from this study are given in this paper.

In his first paper dealing with reptilian remains from Elgin, Huxley (1859) described part of a 'dentigerous bone' as pertaining to *Stagonolepis*. This he later (1877) named *Dasygnathus longidens*, since in the meantime parts of skulls and jaws had been obtained with the characteristic 'waisted' teeth, associated with scutes of *Stagonolepis*, whereas the bone described in 1859 bears large conical teeth.

The systematic position of *Dasygnathus* remained uncertain. Huxley (1877) pointed out the resemblance of the teeth to those of 'such reptiles as *Megalosaurus*'; later suggestions included labyrinthodont (Watson 1909) and pelycosaur. The latter was due to von Huene (1913, 1925), partly because of an apparent 'precanine step' in the tooth-row which, however, is the result of the breaking away of the jaw-margin, and partly because of an incorrect reference to the locality as Cutties' Hillock quarry (Permian) instead of Findrassie (Trias). Romer & Price (1940) point out that 'it may equally well have been a therapsid, or an archosaur'.

A large pterygoid in Elgin Museum, also from Findrassie, bears Huxley's numbering in red paint, and there are reasons for believing that it came from the same skull as the 'dentigerous bone' although the two blocks do not now fit together. There can be little doubt that the pterygoid belongs to *Dasygnathus*, and the two bones indicate a large carnivorous pseudosuchian allied to *Erythrosuchus*.

This paper is the first part of a projected series which, it is hoped, will deal systematically with both the Permian and Triassic reptilian faunas from the Elgin region.

II. Material and methods

Fossils from the Elgin sandstones are frequently represented only by natural moulds, the original bone in many cases having completely disappeared. Specimens from Findrassie are of this nature; those from Lossiemouth often consist of soft, friable bone. Sometimes it is possible to prepare such specimens since the Lossiemouth matrix is usually rather incoherent and easily removed by mechanical means, but in other cases, particularly where the exposed face has been rubbed away, it is more satisfactory to remove the bone and make a cast of the cavity.

Only a few specimens were suitable for positive preparation and the methods used were entirely mechanical. The use of acetic acid proved fruitless; the cement of the sandstone resists concentrated hydrochloric acid. This fact was made use of in cleaning bone out of complicated cavities.

The sandstone varies considerably in hardness. The Findrassie matrix is invariably tough and the fossils are in the form of perfect negatives. The Lossiemouth rock is more variable, ranging from the type seen with the skull M.C.Z.D. 2, from which the sandstone parted very readily, to that of the skull B.M.N.H. R 4787, a hard rock from which the remaining bone was removed with acid and casts made of the cavities.

The complex nature of many of the impressions made necessary the use of flexible compounds as casting media; without their aid it would have been almost impossible to obtain much of the detailed information on the skull which is now available. Materials used included rubber latex, polyvinylchloride resins and hot melt compounds.

Huxley remarked on the incompleteness of many bones, but this is chiefly due to the fact that all the pieces were not collected. On the other hand the material he described certainly includes many damaged specimens; in the case of Lossiemouth it is possible that these came from a slightly different horizon from those of later finds, containing somewhat dissociated or partial skeletons. Material presumably collected later from Lossiemouth, including that presented to the British Museum by the Rev. G. Gordon, is often better preserved and includes several articulated skeletons of varying degrees of completeness.

The Findrassie material was obviously scattered, and the neural spines and processes of the vertebrae are often broken off. Gordon (1859) states that the specimens from this locality were not *in situ* but had obviously not travelled far, which explains both the curious appearance of the stone and the complete removal of the bone. Occasional pebbles in the matrix suggest that the base of the sandstone was at hand and indeed Gordon describes the specimens as 'lying on the surface of the Bishopmill silicious sandstones', i.e. on the Upper Old Red Sandstone. The identification of this locality is now uncertain; Gordon states that it was a pit opened up for road material near the east entrance to Findrassie House, and from his account and that of Murchison (1859) it may be gathered that it was only in use from 1856 to 1858, when it was filled in.

A curious feature of some of the specimens is the manner in which some bones are quite markedly distorted, whereas others associated with them are hardly affected. The right ilium R 4788 (figure 15*b*, *c*) provides a striking illustration. For some time it was doubted that this bone belonged to *Stagonolepis*. The acetabulum is abnormally deep and has a strongly overhanging lip; the lower part of the blade presents a flat surface looking downward and backward. When it became clear that the greater part of the material of *Stagonolepis* in the British Museum makes up one individual which includes both pubes and the left ilium and ischium, it was realized that the bone in question is merely a distorted element of the same (disarticulated) pelvis. This is confirmed by the proportion which it bears to the smaller ilium R 4789; a drawing of the latter can be deformed graphically to give an outline very like that of R 4788. The other pelvic bones of this large individual are apparently undistorted, whereas the right ilium seems to have behaved in a plastic manner without noticeable fracturing.

The posterior caudal vertebra (figure 10*n*) associated with the sacrum G.S.M. 90884 shows how distortion may possibly be misleading. It is unique among vertebrae of *Stagonolepis* in having widely separated postzygapophyses and a centrum in which the posterior face is nearly twice as broad as it is deep, yet it is not obviously distorted. A consideration of the attitude of this vertebra in the matrix shows that these features can be ascribed to compression in the same direction as that which is known to have affected the sacrum. The distorted vertebra is rather like those of *Stegomus arcuatus jerseyensis* (Jepsen

1948), an armoured reptile probably allied to *Stagonolepis* but differing from the latter in respect of the breadth of the caudal centra.

Examination was made of all the material of *Stagonolepis* in the collections of the following institutions, against which are set the appropriate prefixes referred to in this paper:

Inverness Museum	
Elgin Museum	E.M.
Marischal College, Aberdeen, Geology Department	M.C.G.D.
Marischal College, Aberdeen, Zoology Department	M.C.Z.D.
Royal Scottish Museum, Edinburgh	R.S.M.
Geological Survey, Edinburgh	G.S.E.
Manchester Museum	
British Museum, Natural History	R
Geological Survey Museum, London	G.S.M.

The quarries in the Triassic sandstone of the Elgin district are no longer worked and are rapidly becoming overgrown or filled in so that it is virtually impossible to collect new material. With one unimportant exception the present study has been carried out entirely on specimens belonging to the above collections; the most recent of these can hardly have been made less than fifty years ago although quarrying operations have continued until about 1947.

Most of the specimens of *Stagonolepis* in Elgin Museum bear two series of numbers. One of these, in red paint, is said to be Huxley's original numbering and is that used in his monograph of 1877. To clarify matters these numbers are used here also, with the suffix 'R'. The other series consists of black numerals on white labels, and specimens having only this type of number are here given the suffix 'W', but this does not necessarily mean that they were unknown to Huxley for E.M. 33 W was figured by him in 1877. A few specimens have no numbers, but some at least were collected a considerable time ago for certain of them are from the Findrassie pit which, as has been noted, was filled in by 1858. Where it is necessary to refer to these specimens they are denoted by the letters E.M. 'A', 'B', etc.

Establishment of approximate date of collection is important in attempting to determine the number of individuals present in the material.

Uncatalogued specimens in the collection of the Department of Zoology, Marischal College, Aberdeen, are referred to as M.C.Z.D. 1, etc. This material includes an almost complete but crushed skull succeeded by vertebrae, scutes and other bones.

Two specimens in the Geology Department of Marischal College are here called M.C.G.D. 1 and 2.

The major portion of the material of *Stagonolepis* in the British Museum can be fitted together thus proving the association of a large part of one individual, which includes a fine skull and pectoral girdle, vertebral column to the fourth caudal, some of the pelvic girdle, parts of the limbs, and dermal armour. These specimens have received some thirteen different numbers but they include many more than that number of actual blocks, some very large. The description of the skull is based largely on this specimen and on that from Marischal College.

III. DESCRIPTION OF *DASYGNATHUS*

DASYGNATHUS LONGIDENS HUXLEY

(Figure 1)

Huxley, T. H., 1877, pages 43 to 45, Pl. IV, Fig. 1, reversed.

Holotype: E.M. 1R, the impression of part of a maxilla with teeth. Trias, Findrassie, near Elgin, Scotland.

Additional material here referred to this species:

E.M. 15 R. The impression of a right pterygoid. Trias, Findrassie.

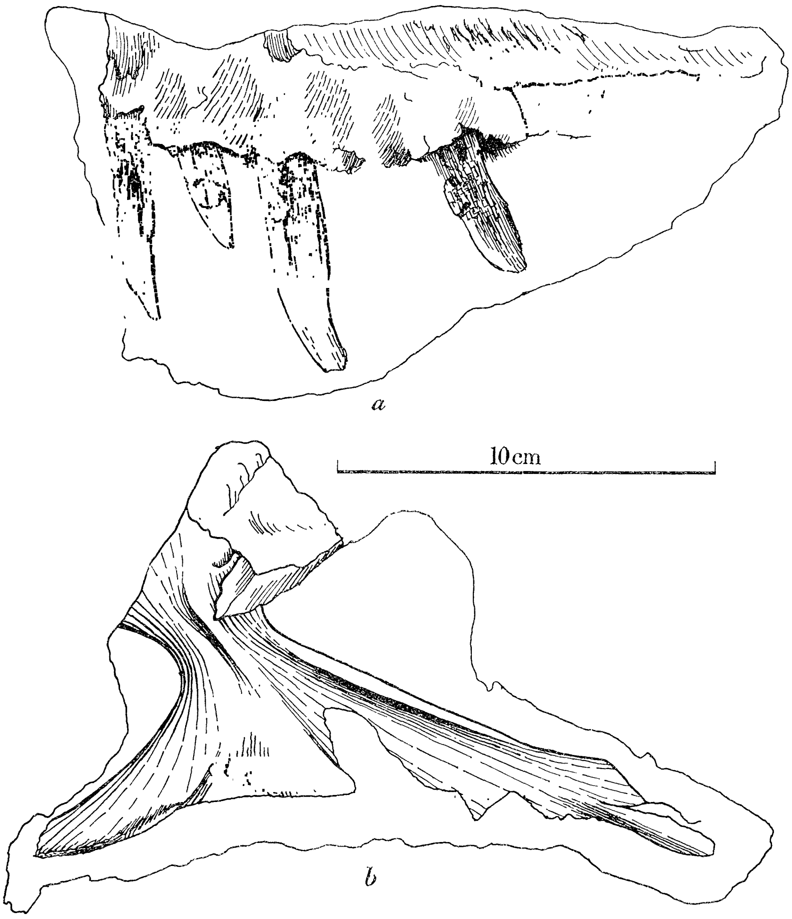

FIGURE 1. *Dasygnathus longidens* Huxley (magn. $\times \frac{1}{2}$), drawn from casts. *a*: left maxilla, E.M. 1R; *b*: right pterygoid, E.M. 15R.

E.M. 1 R and 15 R are probably derived from the same individual. Both are from the same locality and have Huxley's red painted numbers. They differ markedly from the corresponding elements of *Stagonolepis* which they greatly exceed in dimensions.

The material of *Stagonolepis* from Findrassie need be referred to only two individuals, one of which is larger than the other and now consists mainly of damaged and scattered vertebrae. The association of maxilla and pterygoid with what appear to be fragments from this individual, their concordance of size and the fact that the locality from which they were obtained yielded only a small proportion of the total material during a short space of time, suggests that they are from the same actual skull. Failing this there can be little doubt that they are from the same species.

Maxilla

The length preserved is about 17·5 cm. The bone (figure 1*a*) could perhaps be part of a dentary, but the slight convexity of the margin towards the tips of the teeth indicates that it is more likely to be a maxilla.

The margin is irregular throughout due to breakage, the whole specimen being badly crushed, accounting both for the apparent striation of the teeth and the 'peculiar vertical striation, as if the bone had possessed a coarsely fibrous structure' referred to by Huxley, and to which the generic name refers. The upward curvature of the margin near the first tooth is clearly due to breakage since the alveolar portion of the tooth is exposed.

Four teeth are preserved, to each of which corresponds a low ridge running transversely to the margin of the bone. Under oblique lighting eight of these ridges are clearly visible in a length of 14 cm with two further ill-defined areas behind them, so that there were at least eight and possibly ten teeth originally present. The third and fourth ridges are broader than the others and evidently mark the positions of the largest teeth. It is probable that the teeth were originally smooth, the apparent longitudinal striation being due to crushing. The directions of the ridges indicate that the teeth diverged slightly, although those which remain have probably been pushed a little backward.

Right pterygoid

The specimen (figure 1*b*) shows the dorsal surface of the transverse ramus and most of the palatal ramus, and the lateral surface of the constriction by which these pass to the quadrate ramus. The palatal branch is concave laterally, curving up strongly medially to a thin rounded margin. There was evidently a considerably interpterygoid vacuity.

In front of the transverse ramus there is a deep depression or embayment, now infilled by matrix. Part of this no doubt represents the postpalatine fenestra. The anterior part of the ramus shows a faint margin and obscure traces of an extensive overlap area for the transverse, marked by striae.

The dorsal region is terminated by an irregular broken edge. Anteriorly there remains a little of the root of the ascending process of the pterygoid, which in *Stagonolepis* (q.v.) marks the anterior edge of the pterygoquadrate cartilage. From just below and behind it (in the present bone) a narrow groove traverses the constriction, dying out on the palatal surface. The groove presumably received the (?cartilaginous) ventral prolongation of the epipterygoid as does a similar groove in phytosaurs and pelycosaurs (Camp 1930; Romer & Price 1940).

Although only one side of the bone is represented one gains the impression that the palatal and transverse rami are thin. The maximum preserved length is 17·7 cm.

Taken in conjunction the maxilla and pterygoid indicate a skull about 43 cm (17 in.) long. The shape of the pterygoid suggests that the skull was long and narrow, but deep. The powerful, recurved teeth clearly show that *Dasygnathus* was of carnivorous habit.

IV. RELATIONSHIPS OF *DASYGNATHUS*

Since the material referred to *Dasygnathus* is so meagre, detailed comparisons with other forms are impossible. However, the pterygoid is extremely like that of *Erythrosuchus* from the *Cynognathus* Zone of South Africa (von Huene, 1911 *b*: in these illustrations the pterygoid is inverted) and this resemblance extends also to the maxilla. The groove on the pterygoid is situated at the anterior side of the constriction, instead of centrally as in *Dasygnathus*, and taking the medial edge of the palatal ramus to be horizontal, the transverse ramus is more recurved than in the Elgin form.

Previous opinions regarding the affinities of *Dasygnathus* have already been mentioned, but these did not take into account the pterygoid described in this paper. It is clear that *Dasygnathus* was a large carnivorous pseudosuchian, whose affinities appear to lie with *Erythrosuchus* from South Africa.

V. DESCRIPTION OF *STAGONOLEPIS*

STAGONOLEPIS ROBERTSONI AGASSIZ

(Figures 2 to 23; plates 9 to 12)

Agassiz, L., 1844, p. 139, Pl. XXXI, figs. xiii, xiv.

Huxley, T. H., 1877, pp. 5 to 43, Pls. I to X.

Holotype: E.M. 27 R, the impression of a segment of the ventral armour of a small individual. Trias, Lossiemouth.

Unless otherwise stated, references to Huxley are to the monograph of 1877.

Proportions

Although no complete skeleton is available, many blocks display associations of bones from which it is possible, albeit laboriously, to determine with accuracy the proportions of the animal. This process is rendered more difficult by the incompleteness of many bones; thus many specimens consist of a part only of one surface of a particular bone, the remainder simply was not collected. The full description and illustration of many elements, particularly of the limbs, has perforce to be assembled piecemeal from several specimens of different sizes.

In only one case has there proved to be a mingling of elements of two individuals of *Stagonolepis*, but even here the 'intruding' ilium (G.S.M. 90852) is on the back of the slab displaying the other bones and some inches of matrix separate them. Acceptance of this as a true association misled Huxley in his estimate of the proportions of the pelvis.

The material shows an almost complete segregation into two size-groups, the individuals within each group being remarkably uniform in size. Because of the incompleteness of many bones this division is not always easy to demonstrate in terms of measurements. No differences of proportion have been detected between the two groups, cranial or otherwise, and such morphological differences as exist are very small and are readily explicable in terms of larger size and greater degree of ossification.

Using the proportions thus determined, and having regard to other factors such as locality, type of preservation, and approximate date of collection, most of the material can be assembled into a number of individuals, few of which even approach completeness.

Details of the specimens which are believed to make up these individuals, and the criteria employed in their assembly, are given in an Appendix to a thesis submitted to the University of Durham (Walker 1957), available in the Library of King's College, Newcastle upon Tyne. This work also contains a more extended treatment of the subject-matter of this paper and is accompanied by detailed tables of measurements of *Stagonolepis* and *Aëtosaurus ferratus*.

The overall length of an individual of the larger size-group, assuming the tail to be proportionately as in *A. ferratus*, would be about 270 cm (9 ft.); this allows about 120 cm (4 ft.) from snout to sacrum and 150 cm (5 ft.) for the tail. For an individual of the smaller size-group the corresponding figures are 210 cm (7 ft.), 93 cm (37 in.) and 117 cm (47 in.). The type-specimen is estimated to have been about 137 cm (4 ft. 6 in.) long, and the smallest individual known (represented only by a femur and two scutes) 102 cm (3 ft. 4 in.) long.

A table of main measurements of *Stagonolepis* follows (see table 1).

TABLE 1. MAIN MEASUREMENTS OF *STAGONOLEPIS*

	smaller size-group (cm)	larger size-group (cm)
skull-roof in mid-line	19·0 (M.C.Z.D. 2)	24·5 (composite)
presacral column length	—	92 (R 4793)
scapulocoracoid height	—	28·0 (E.M. 37R, 39R)
scapula height	—	20·3 (E.M. 37R, 39R)
breadth apex of scapula	10·1 (G.S.M. 90910)	12·6 (E.M. 37R, 39R)
coracoid length	—	12·2 (E.M. 37R, 39R)
coracoid breadth	—	8·0 (E.M. 37R, 39R)
interclavicle length	12·8 (G.S.M. 90848)	—
humerus length	16·0 (E.M. 26W)	19·0 (M.C.Z.D. 1)
radius length	—	12·7 (M.C.Z.D. 1)
ulna length	—	14·7 (M.C.Z.D. 1)
metacarpal IV length	—	3·2 (M.C.Z.D. 1)
ilium, crest length	15·9 (R 4789)	20·7 (E.M. 46R est.)
ilium, breadth of neck	6·2 (R 4789)	8·0 (E.M. 46R)
ilium, base diameter	10·5 (R 4789)	13·5 (E.M. 46R)
ilium, height	11·8 (R 4789)	14·6 (E.M. 46R)
pubis length	14·6 (M.C.G.D. 2)	19·5 (R 4793)
pubis, distal breadth	—	7·7 (R 4793)
ischium, ventral margin	11·7 (R 4790)	16·5 (G.S.M. 90851)
ischium, height	8·2 (R 4790)	10·8 (G.S.M. 90851)
femur length	24·2 (M.C.G.D. 1)	31·5 (E.M. 46R)
tibia length	14·4 (G.S.M. 90901)	18·7 (R 4786 est.)
fibula length	14·5 (E.M. 26R)	18·2 (E.M. 33R)
metatarsal III length	6·0 (M.C.Z.D. 3 est.)	7·8 (M.C.Z.D. 3 est.)
breadth of a large paramedian dorsal scute	12·1 (R 4790)	14·5 (E.M. 37R)
length of same scute	4·8 (R 4790)	6·5 (E.M. 37R)
breadth of a large belly-scute	5·8 (R.S.M. 1952.10.1)	7·1 (R 4793)
length of same scute	4·0 (R.S.M. 1952.10.1)	5·1 (R 4793)
estimated total length	210	270

Note: R4789 and R4790 are counterparts; E.M. 33R, 37R and 46R are probably from the same individual; R 4786 and R 4793 are from the same individual.

Number of individuals

The minimum number of individuals represented is believed to be twenty-one, of which eight are of the larger size-group and nine of the smaller. A few bones of an individual of intermediate size are known and isolated elements may indicate others. Individuals smaller than the above are as follows:

(1) E.M. 27 R, the type specimen, a segment of the ventral armour.

(2) A specimen mentioned by Huxley in the Taylor Collection at Elgin, but now untraceable. This was also a segment of ventral armour, of similar size to the type but which for various reasons cannot have been its counterpart.

(3) E.M. 34 R and counterpart B.M.N.H. 36399. A small right femur and two dorsal scutes. Femur half as long as those of the smaller size-group.

The number of individuals quoted is arrived at by making the minimum assumptions and there could possibly have been as many as thirty in the material studied. Nor is there skull material for each individual; parts of at least ten skulls, two of which are almost complete, are available.

The Lossiemouth material is considered to represent at least nineteen individuals, made up of seven of the larger size-group, eight of the smaller, one intermediate in size, and the three still smaller ones listed above.

For the Findrassie specimens it is only necessary to assume the presence of two individuals, one from each size-group.

No specimen from Spynie appears to have been recorded as such in museum lists and none has been seen which can certainly be ascribed to this locality. However, Taylor (1920) notes the occurrence of *Stagonolepis* here.

Significance of the size-groups

Apart from some details of the anterior caudal vertebrae, about which the evidence is inconclusive, differences between members of the two groups are explicable in terms of increase in size and greater degree of ossification. Since the materials are essentially from one locality and horizon, the quarries being but a few miles apart, it is not believed that more than one species is represented. A further point of importance is the approximate equality of numbers of individuals in each group, the larger exceeding the smaller in size by a factor of 25 to 30 %, varying somewhat according to the particular element chosen for comparison. In view of these facts it seems most likely that the larger and smaller individuals represent males and females, respectively.

Skull

There are now available parts of at least ten skulls, of which the following are the more important:

G.S.M. 37049 to 37051: region between middle of external naris and anterior margin of orbit, with parts of the jaws. Important for the anterior part of the palate. Preserved mainly in the form of a mould.

G.S.M. 90864 and 90865: a distorted and incomplete snout which, however, shows the anterior end of the dentary and the edentulous region.

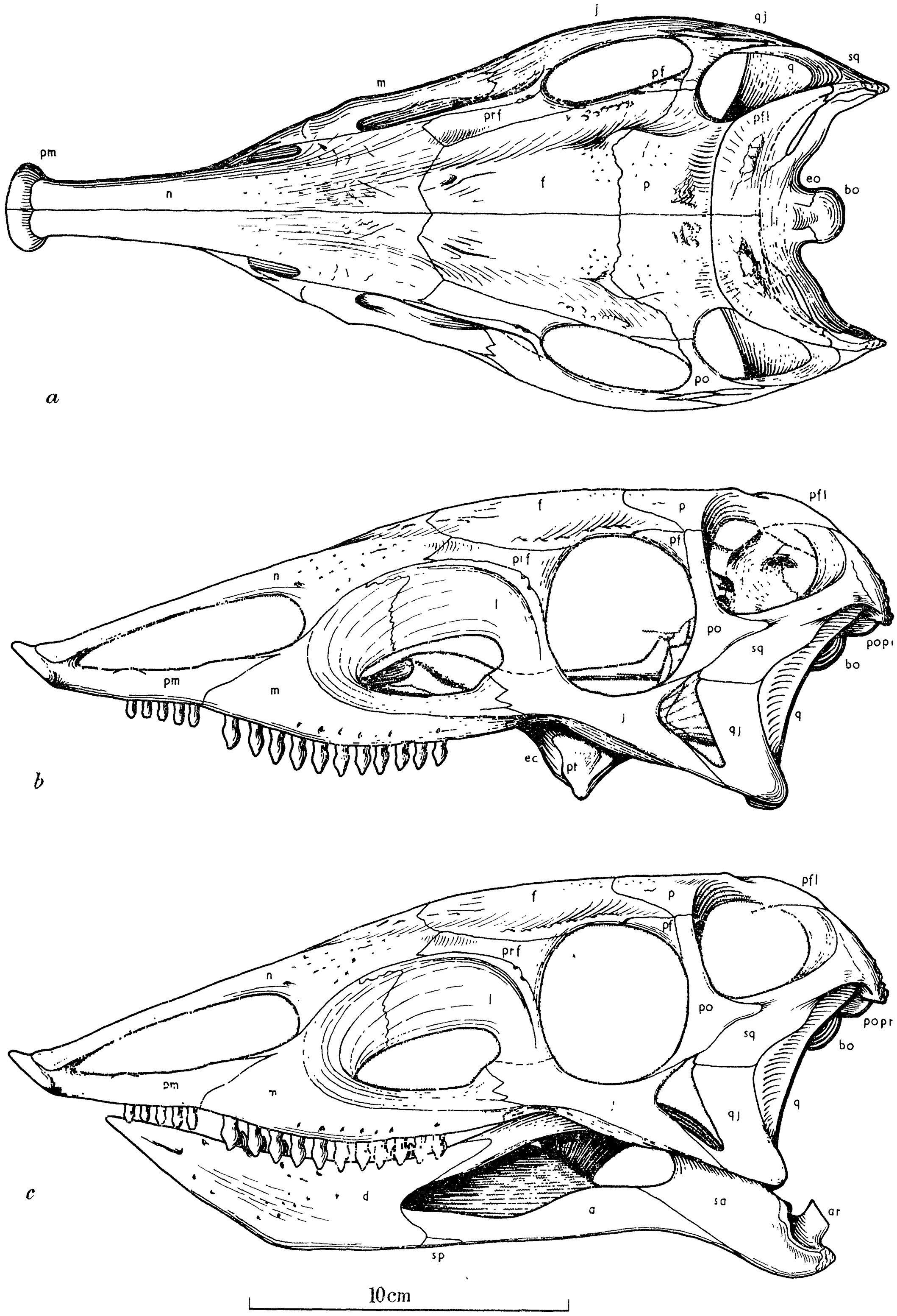

FIGURE 2. *Stagonolepis robertsoni* Ag. (magn. × $\frac{1}{2}$). Composite restoration of the skull. *a*: dorsal view; *b*: side view showing also deeper-lying structures; *c*: side view with jaw in place.

E.M. 38 R and G.S.M. 90863, 90879 to 90881: the snout region well displaying the peculiar tip of the premaxilla. The left quadrate E.M. 44 R probably belongs to this skull.

R 4784 and R 4787: the greater part of a fine (albeit partly disarticulated) skull, displaying the braincase, palate and jaws excellently, and succeeded by a good deal of the skeleton. Preserved as a series of impressions.

M.C.Z.D. 2: an almost complete but crushed skull, showing the snout, skull-roof and cheek region particularly well, and followed by parts of the skeleton. This specimen is of the smaller size-group.

E.M. 38 R (figure 34, plate 11) was wrongly interpreted by Huxley; it shows in actual fact the inner aspect of the bones which surround the left external naris. The specimen provides an important key to the understanding of the relationships of *Stagonolepis*, since when correctly identified the large naris and peculiar premaxillary tip are strikingly similar to those of *Aëtosaurus ferratus*. The 'symphysial end of a mandible' of Huxley (Pl. VI, figs. 3 to 3*c* reversed) is the compressed maxillary region of the same skull. In addition, the 'metatarsal' (Huxley, Pl. VIII, figs. 6, 6*a*, reversed) is a nearly complete right nasal from a smaller skull.

Dermal bones of the skull-roof

The nasals take up about half the length of the skull-roof. The slender anterior part forms the upper margin of the naris and ends in a small expansion overlying the premaxilla, concealing the usual backward process of the latter. The posterior part of the bone bears a sculpture of pits and shallow grooves which are most pronounced on a slightly elevated central area continuous on to the frontal.

The frontals are a little less than half as long as the nasals. Details of the junction with the parietal in the region of the postorbital bar are uncertain due to slight damage to this region, but the frontal wedges out between the postfrontal and the parietal and may gain a brief contact with the postorbital. The elevated central region of the frontal is ornamented with longitudinal grooves anteriorly and small pits posteriorly. A shallow groove dying out posteriorly separates the central region from a few irregular protuberances above the orbit.

The parietals are short, broad elements notched laterally by the supratemporal openings. They continue the elevated region on the frontals. Posteriorly they develop broad, sloping flanges for the reception of the first pair of paramedian dorsal scutes. Part of the occipital surface of the parietal is seen on R 4784. The upper part of the occiput was evidently shallowly concave and inclined somewhat forward, very much as in *Desmatosuchus* (Case 1922). The parietal forms the upper margin of the elliptical post-temporal fossa and the outer surface of its posterior portion shows a complexly grooved and tongued area for articulation with the squamosal. In the medial wall of the supratemporal fossa the parietal curves forward and outward; on R 4784 there is a strong descending process having a narrow vertical rugose outer edge which clearly received the ascending bar of the postorbital. Lower down on the inner wall of the fossa an undulating ridge indicates the junction with the lateral wall of the braincase. The ridge overhangs a little ventrally and above the outlets for the trigeminal nerve sends down a thin plate of bone separated by a few millimetres from the side wall of the braincase.

The thin, deep dorsal portion of the lachrymal meets the maxilla in an irregular suture and extends well forward appressed to its inner side. In M.C.Z.D. 2 the upper rim has been fractured (figure 27, plate 9) so that it appears at first sight to be part of the prefrontal. The bone of the outer surface is broken away on the specimens which display the region behind the antorbital vacuity and deductions as to relations with other bones are based on examination of the inner impressions and on the posterior ends of two detached maxillae (R 4790 and R 4787, figures 36 and 37, plate 11). The posterior end of the maxilla sends up two thin, somewhat divergent processes directed a little inward and backward. The foot of the lachrymal lay against the medial surface of the outer of these processes. The posterior junction of lachrymal and maxilla appears to have been partly overlapped externally by the jugal, and may have been entirely concealed as in some individuals of *Aëtosaurus ferratus.*

The lachrymal duct is prominent as a ridge slanting forward and downward on the inner impression of G.S.M. 37049, where it was mistaken by von Huene for the suture between lachrymal and prefrontal. It opens posteriorly (M.C.Z.D. 2) by two, perhaps three foramina along the suture between these two bones.

The prefrontal has three distinct portions. Dorsally it enters the skull-roof as shown, curving up anteromedially as a thin edge in contact with the outer margin of the frontal. The descending portion of the prefrontal curves inward to pass within the lachrymal. The subsequent course of the bone is best seen on the cast made of the left inner surface (R 4787) with which both sides of G.S.M. 37049 are in agreement. The lower part of the prefrontal lies against the inner surface of the posterior part of the foot of the lachrymal and continues as a tongue of bone over the anterior surface of the outer part of the transverse, concealing the junction of lachrymal and transverse and almost touching the maxilla. Immediately in front of the orbit the prefrontal sends inward a thin, vertically disposed bar which ends a short distance from the mid-line. The bar passes not far beneath the middle part of the depression on the lower surface of the frontal.

The postfrontal (figures 26 and 28, plate 9) is a thick, triangular element. A rather damaged posterior notch received the anterior edge of the ascending process of the postorbital. The lower corner of the bone is incomplete but it probably tapered out as shown.

The postorbital is a triradiate bone, all three examples of which are displaced. The ascending branch forms a long, narrow bar, almost square in section below but flattened anteroposteriorly above; its upper end lies against the postfrontal with a roughened surface of contact, and its narrow medial edge meets the descending process from the parietal. The lower branch ends above the jugal as a thin tapering strip of bone. The bluntly pointed posterior branch fits into a notch situated a little below the middle of the squamosal and lies behind in a shallow groove on the outer side of the latter. This branch is overlain by a slender tapering process from the squamosal. Reconstruction of this region of the skull is discussed later (see p. 127).

The lower end of the squamosal overlaps the quadratojugal. Dorsally it expands to continue the horn-like process of the parietal and is overlain by the outer part of the second paramedian scute. The anterior upper and medial parts of the bone are roughened and fit beneath and against corresponding surfaces on the parietal, while a broad irregular medial area was closely applied to the upper anterior surface of the tip of the paroccipital. Between these areas of contact the squamosal forms the outer corner of the post-temporal fossa and extends medially for a short distance as a wall anterior to it. The downcurving posterior tip is strongly roughened.

The underside of the squamosal bears a hemispherical smooth pit forming a continuous surface with the lower anterior face of the end of the paroccipital. This pit received the head of the quadrate, and is continued into a groove running down the posterior edge of the squamosal into which fitted the outer forward edge of the quadrate.

The jugal is incompletely preserved. The posterior branches are present on the right side of M.C.Z.D. 2 (figure 32, plate 10): the upper terminates in a laterally compressed slender point. The bottom half of the lower branch is twisted medially and is a continuation of the steeply inclined lateral area on the maxilla; it ends in a long, slender point presumably overlain by a forward process from the quadratojugal, as in *Aëtosaurus* (figure 41, plate 12).

The quadratojugal is incompletely known, but only a very small portion can be missing from the right side of M.C.Z.D. 2. Dorsally the bone forms a thin shelf with rounded upper margin, receiving the overlap of the squamosal. The shelf continues down the posterior edge of the bone but soon becomes transformed into a posterior groove into which fitted the smooth, rounded forward edge of the quadrate. The groove ceases at the quadrate foramen, below which the quadratojugal curves round posteriorly to lie over the outer part of the quadrate. There was no doubt a thin forward process making contact with the jugal, but this is not preserved.

Internal surfaces of some of the bones described above

The undersurface of the nasal is bevelled off anteriorly along its admedian edge to receive the tapering process of the premaxilla. Paired longitudinal ridges on the central parts of the nasals (figure 30, plate 10) separate a depressed median area from the smooth areas bordering on the nares. The median area broadens out behind the nares and the posterior part of the ridges then converge slightly and are produced into thin edges which partly underlie the medial margins of a pair of deep oval depressions. The latter are mainly roofed by the nasals and from each a shallow groove leads towards the upper hinder margin of the naris. The posterior part of the depression lies on the frontal, where it is bounded by a low rim. The prefrontal just enters the posterolateral margin, while most of the outer border is formed by the downturned outer edge of the nasal. The depression probably housed a large nasal gland similar to that of crocodiles.

A pair of small shallow depressions occur on the undersurfaces of the frontals close to the mid-line. These probably show the position of the olfactory bulbs since they are underlain by the medial processes of the prefrontals.

A further pocket is situated between prefrontal and lachrymal, above and behind the posterior end of the pre-orbital fossa. Imperfect preservation prevents a description of this hollow, but it appears to be homologous with the depression on the outer anterior side of the descending process of the prefrontal in crocodiles.

The groove occupied by the lachrymal duct shows up prominently as a ridge on the natural cast of the inner side of the bone; anteriorly the course of the duct is less certain, but it seems to have lain above a low ridge which extends towards the lower posterior corner of the naris. The lachrymal ends in an irregular thin edge, lying above and partly clasped by a low medial ridge on the maxilla.

A low ridge trending upward and backward departs from the inturned upper rim of the antorbital fossa close behind the middle of the opening. Behind it lies a shallow concavity, followed above and behind by rounded protuberances. Imperfect preservation of this complexly sculptured region makes full description and assessment impossible.

The frontals and parietals are extremely thick bones, the frontals of M.C.Z.D. 2, (smaller size-group) being 6 mm in thickness. The right frontal of R 4787 shows on its underside the broad smooth region bordering on the orbit, notched anteriorly for the prefrontal, and falling sharply medially to the constricted interorbital area through which ran the olfactory tracts. Only part of the lower side of the parietal and adjoining regions is visible, in the form of a natural sandstone cast (right side of M.C.Z.D. 2). A rounded longitudinal elevation, tapering gradually anteriorly and more rapidly posteriorly, seems to represent the region of the right cerebral hemisphere. It lies close to the mid-line with its hinder end a little behind the anterior margin of the supratemporal fossa. Behind it appears to be a slightly broader, lower area bounded laterally by a broad groove representing the inner wall of the fossa.

Dermal bones of the palate

The premaxillae are expanded anteriorly into a shovel-shaped structure. Faint longitudinal striations on the sloping undersurface probably entered the bone posteriorly as small foramina. The upper surface is striated in a like manner and is partly overlapped by the terminal expansions of the nasals; in a median groove beneath the latter bones lie the slender, appressed tapering processes sent upward and backward by the premaxillae.

Behind the expanded portion there is a slight notch in the side of the premaxilla, and above the first tooth occurs a small protuberance of the narial margin. The anterior half of the bone is toothless. Behind the last tooth the bone divides into two branches. The palatal branch is appressed to the lower surface of the vomer. The premaxillae are in contact as far as to the first tooth; behind this they separate to reveal a narrow vacuity, meeting again behind the last tooth. The palatal processes end behind as somewhat concave, tapering plates incompletely concealing the anterior parts of the vomers.

The lateral branch passes upward and backward as a thin tapering process in contact with the lateral surface of the maxilla. The dorsal edge of the process curves medially to fit over the anterior edge of the maxilla and the extension of this curved margin anteriorly indicates the existence of a forward process of the maxilla within the premaxilla.

A portion of a snout which has been worn down from above (G.S.M. 90865) shows the anterior tip of the vomer resting on the palatal branch of the premaxilla. The maxilla overlaps the premaxilla in front of the vomer and possibly met its fellow in the mid-line; a similar condition is shown by the British Museum specimen (R 4787).

A faintly striated, recessed area below the upper margin of the maxilla indicates the portion overlapped by the lateral branch of the premaxilla. The recessed area surrounding the antorbital vacuity is bounded by a ridge which curves posteriorly to continue on the jugal; a row of foramina below it correspond approximately in position and number to the alveoli.

The medial side (figure 37, plate 11) bears a strong shelf below the ascending process. The lower part of the latter is pierced from behind by a large foramen which apparently led into the bone. The palatine articulation is deepest opposite the anterior margin of the pre-orbital fossa, decreasing to but a few millimetres at the suborbital opening. The thin upper edge of the maxilla, continuing the medial shelf, curls over medially and slightly

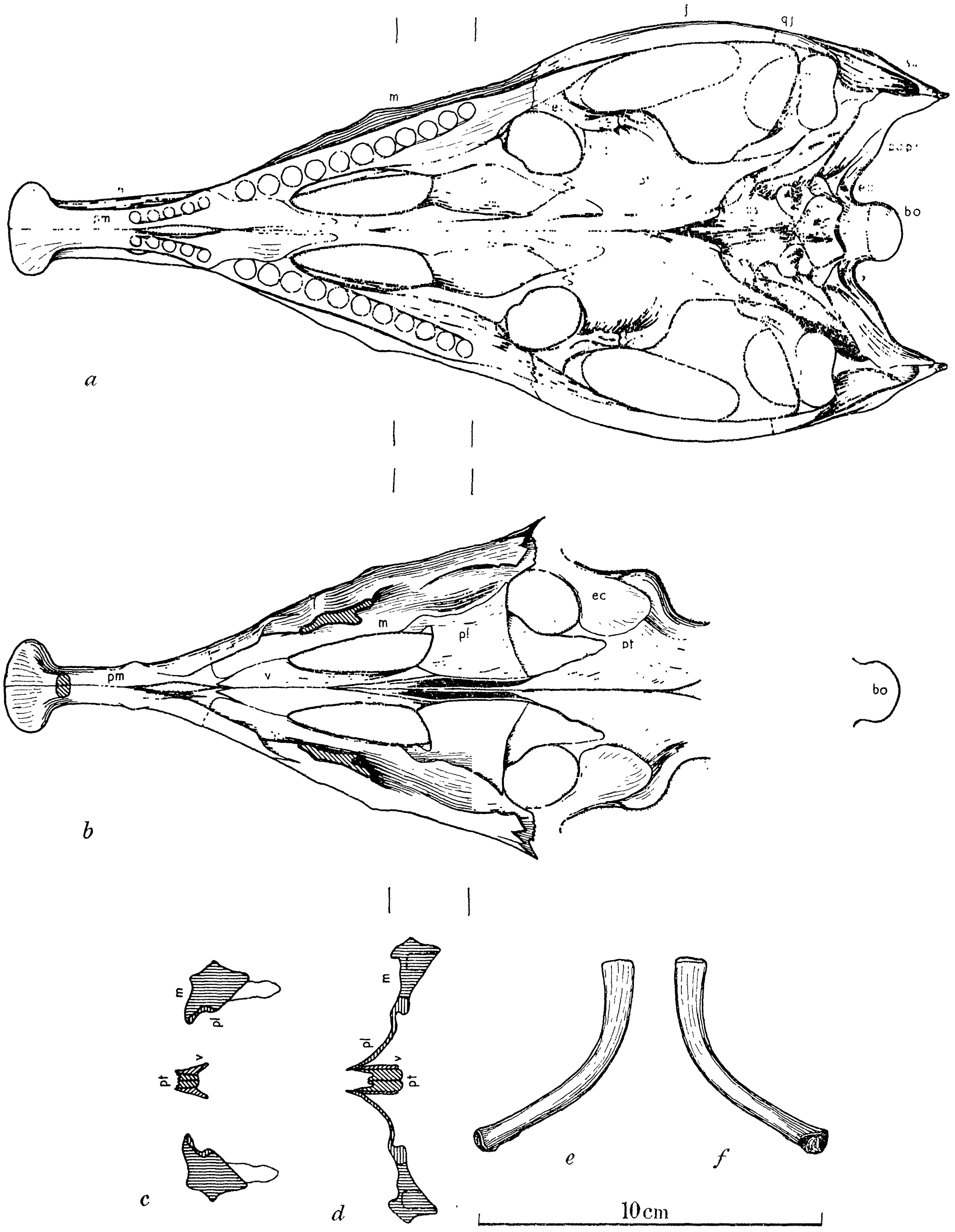

FIGURE 3. *Stagonolepis robertsoni* Ag. (magn. × $\frac{1}{2}$). Composite restoration of the palate, and hyoid bone. *a*, *b*: ventral and dorsal views (in the latter the ascending processes of the premaxillae and maxillae are sectioned horizontally); *c*, *d*: cross-sections of the palate along the lines indicated; *e*, *f*: lateral and medial views of left hyoid bone.

overlaps the palatine. From the beginning of the union with the palatine there develops on the maxilla a flattened region medial and posterior to the alveoli. This area, which is marked by faint longitudinal striations appearing in many cases to end in tiny foramina, is strongly tilted so that it faces inward as well as downward.

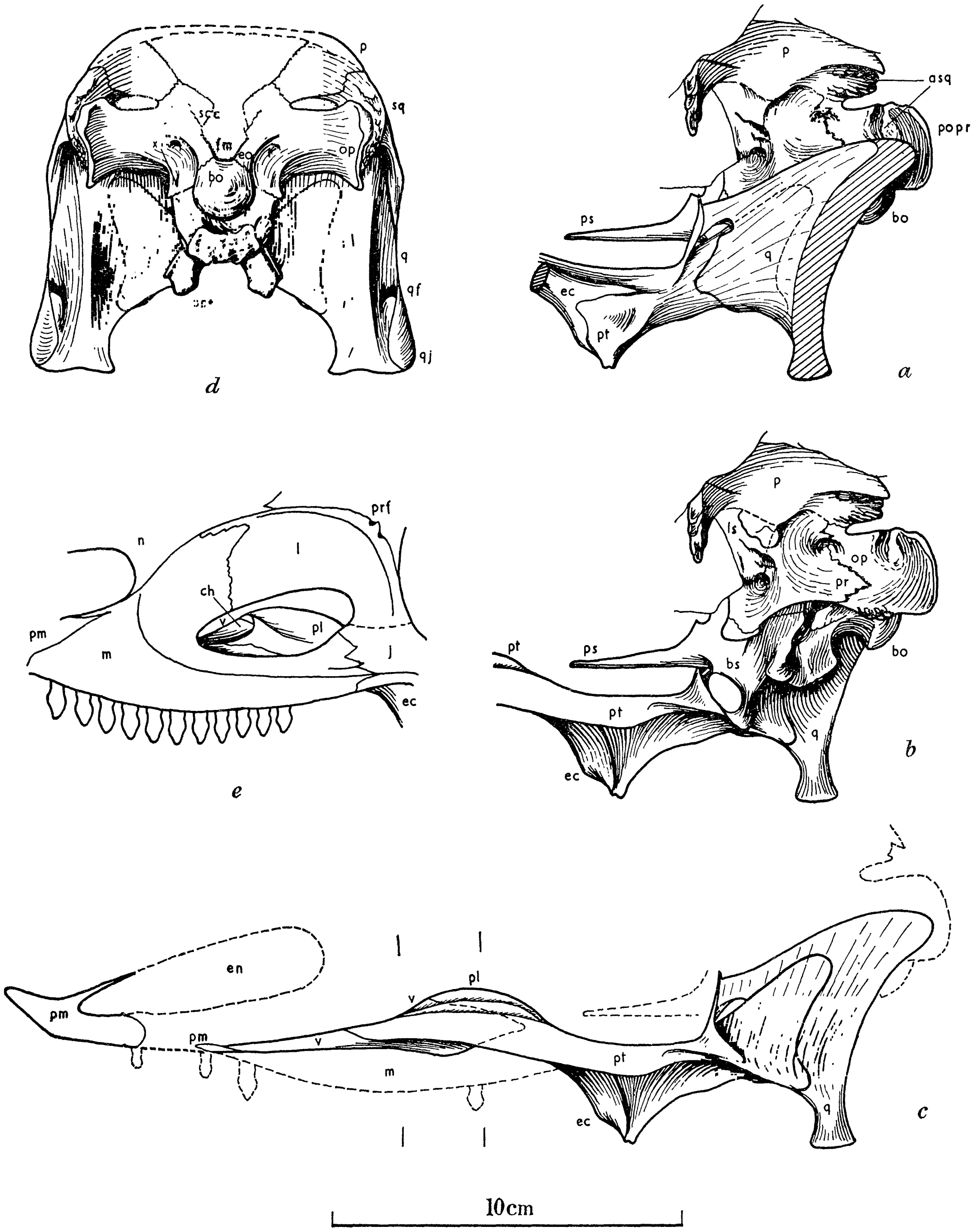

FIGURE 4. *Stagonolepis robertsoni* Ag. (magn. × $\frac{1}{2}$). The palatal complex and its relationships to the braincase. *a*: the braincase seen from the left side (descending lamina of parietal omitted) with the left pterygo-quadrate complex in place (quadrate sectioned vertically along root of lateral wing); *b*: the same with the latter removed, deeper structures now seen in medial view; *c*: medial view of right palatal complex, broken lines provide orientation with other figures ; *d*: occiput *e*: left choanal region seen through pre-orbital opening.

The posterior end of the maxilla is marked by a deep dorsal channel, on either side of which arise the thin processes which apparently clasped between them the foot of the lachrymal, and were in turn clasped between the anterior parts of the jugal. The outer of these processes probably extended some way up the outer surface of the lachrymal; it shows an irregular denticulated posterior margin and traces of the overlap of the jugal. The inner process has a short, rough, medial area of contact.

The area below the ridge on the outside of the maxilla slopes inward more steeply at its posterior end; behind the teeth its intersection with the sloping inner area produces a sharp edge.

Anteriorly the vomers are thin plates, slightly arched dorsally, overlying the premaxillae and abutting laterally against the maxillae. At the anterior margin of the choana the contact is below the medial shelf of the maxilla, but it seems that further forward the vomer rises up slightly so that it lies against the edge of the shelf. At the middle of the choanae the thin, tapering median plates of the pterygoids end between the vomers; behind this point the vomers change rapidly in shape, becoming thin, vertically disposed plates lying against the sides of the pterygoids. Because the thin ventral edge of the vomer projects below that of the pterygoid, there develops a shallow median ventral hollow at the posterior end of the choanae, ending where the lower edge of the vomer ascends and passes that of the pterygoid (opposite the last maxillary tooth).

The vomers terminate behind as slender, wing-like processes in the hollows on either side of the vertical pterygoid bars (figure 39, plate 12). The thin upper edge of the vomer (figure 38, plate 12) meets the anteromedial corner of the palatine a short distance before the hinder end of the choana; however, this contact is soon lost by the disappearance of the vomer from the upper surface of the palate and the meeting instead of the palatine and pterygoid.

The palatines form the major part of the channels which extend back from the choanae. The thick lateral edge of the bone lies against the maxilla and forms the side wall of the channel, which decreases in depth posteriorly. The palatine sends forward two slender processes along the medial side of the maxilla. The upper of these tapers out under the medial shelf of the maxilla at the middle of the choanae; the lower, which lies just above the bases of the teeth, does not reach quite so far forward. Posteriorly the palatal channel is separated from the large postpalatine opening by the thickened, elevated edge of the bone. The palatine meets the pterygoid at an indented suture (figure 31, plate 10) and also overlaps it dorsally.

The posterolateral corner of the palatine is produced into a sharp point which articulates with a shallow socket on the dorsal edge of the maxilla; this junction is a little above and behind the ending of the palatine/maxillary suture on the palatal surface. The right side of R 4787 appears to be abnormal in that the maxilla lacks an obvious area for the reception of the palatine point, while the usual ridge on the upper surface of the palatine is absent, although it occurs on the left palatine of the same skull.

The dorsal surface of the palatine curves upward as it approaches the mid-line. Anteriorly there is a brief contact with the vomer, behind which the medial portion lies against the upper edge of the pterygoid bar. Posteriorly the medial edge descends to the level of the pterygoid which it overlaps slightly, sending back a short tongue at the side of the suborbital fossa. The pointed process mentioned above is continued medially as a curving ridge on the upper surface of the bone.

The palatal channels are bordered laterally by the palatines and medially by the vertical bars of the pterygoids and the vomerine plates. The anterior margin of the palatine is convex upward and towards the outer side of the choana leads into a deeper part of the channel which shows itself also on the upper side by a convexity dying out posteriorly.

The pterygoid has three well-marked divisions, a deep vertical ramus applied to the quadrate, a lateral branch curving downward and forward, and a long palatal ramus.

The quadrate ramus is a triangular sheet of thin bone applied to the inner side of the pterygoid wing of the quadrate. The apex of the triangle lies immediately below and outside the ventral ridge from the otic bones. The lower part of the ramus is curved outward to form a groove into which fits the thickened lower edge of the quadrate. The pterygoid narrows in front of the braincase; behind this constriction the continuation of the quadrate wing curls round the anterior face of the basisphenoid (figure 33, plate 10) and extends back a short way between the basipterygoid processes. The articulation with the basisphenoid is by two facets, the basipterygoid articulation proper being situated on the inner side of the anterior part of the quadrate wing. The curving medial portion of the pterygoid has a flat inner face fitting against the smooth, flat anterior surface of the basipterygoid process. The two faces of contact are at right angles, the basipterygoid process fitting between them. The lower edge of the pterygoid is bent a little medially and partly conceals the articulation in ventral view.

Immediately behind the constriction the pterygoid sends up a slender vertical process, concave behind and incised posteriorly at its root. From below the process a shallow groove extends forward along the dorsal surface of the constriction. The ascending process is homologous with that described by Camp (1930) for *Machaeroprosopus*, where the epipterygoid is grooved behind and fits in front of a similar ascending process from the pterygoid; the foot of the epipterygoid in *Machaeroprosopus* rests on the upper margin of the pterygoid and sends a fork posteriorly and ventrally into a shallow depression on its side. However, no bone definitely answering to an epipterygoid has been found in *Stagonolepis* although its presence is inferred because of the above resemblance. A similar arrangement is figured by Romer & Price (1940) for *Dimetrodon*, where however the epipterygoid also curves over medially to provide the basal articulation.

The lateral ramus of the pterygoid curves forward and downward at its tip, which is considerably thickened. The anteroventral edge makes a broad contact with the transverse, and dorsally an extensive depressed, rough area was overlapped by the latter.

The pterygoids meet one another a short way in front of the braincase, the medial edges being thickened dorsally and ventrally into flanges so that there is an extensive contact surface between them. Anteriorly the pterygoid contracts in width and is reduced to a thick vertical bar, the continuation of the admedian ridges. The palatal channel is continued on the underside of the pterygoid as a shallow depression. The medial bars wedge out at the middle of the choanae, fitting into shallow recesses in the medial surfaces of the vomers; the thin anterior edge of the pterygoid slopes upward so that it extends a little further forward on the upper side of the palate.

On the upper surface the admedian ridges decrease in height and thickness and immediately lateral to them arise a further pair of thin ridges which exceed them in height by a few millimetres. The medial parts of the palatines are in contact with these outer ridges (figure 38, plate 12) in the anterior parts of the channels. Fusion of the two ridges on each pterygoid occurs just before the anterior end of the bone. The tip of the cultriform process of the parasphenoid is on such a level that it may have touched the pterygoids at the commencement of the dorsal ridges. Thus it seems that the cartilaginous median septum of the skull was divided ventrally in the region of the palatal channels and rested in the grooves between the pterygoid ridges.

The relations of the outer end of the transverse are incompletely known. It evidently meets the anterior end of the jugal, and presumably, the posterior end of the maxilla, and may meet the lower end of the lachrymal. The thick central part of the transverse extends downward and backward, dividing behind into two branches, a thin, expanded upper portion which overlies a large part of the lateral branch of the pterygoid and possibly touches the posterior tongue from the palatine, and a thick bar running posteroventrally along the anterior edge of the downcurving outer part of the pterygoid.

Quadrate and epipterygoid

The thickened upper end of the quadrate (figures 28 and 29, plate 9) fits into the socket provided by the squamosal and paroccipital bones. More ventrally it divides into two thin wings at an acute angle to each other. The outer wing is directed anterolaterally and its anterior edge fits into the groove on the posterior edge of the squamosal. The groove ceases in the lower part of the squamosal and almost down to the quadrate foramen the smooth, rounded anterior edge of the quadrate is seen in side view. Immediately above the foramen it rests in the groove at the back of the quadratojugal, while below the foramen the quadrate is excavated behind to receive the overlap of the quadratojugal. The lateral wing curves so that its lower part is disposed transversely and the medial wing here departs at an obtuse angle.

The complex foramen between quadrate and quadratojugal is placed a little below mid-height. The union of the two divisions of the quadrate forms a thickened, rounded pillar visible in side view. A pit medial to and slightly below the foramen has been accentuated by crushing and twisting in M.C.Z.D. 2 and E.M. 44 R.

The articular surface is not fully displayed (R 4787), but the corresponding area on the lower jaw can be seen on the right articular and surangular, which are detached from the skull and can be fitted together as casts. The articular area on the jaw is essentially horizontal. There are two shallow concavities of equal breadth separated by a low elevation. The medial part of the foot of the left quadrate is expanded and flattened; the outer condyle is not preserved.

In R 4787 the pterygoid wing of the quadrate almost reaches the 'neck' of the pterygoid, ending in front in a grooved edge indicating a former cartilaginous extension. More dorsally the quadrate extends further forward, ending at a thickened vertical edge fitting against the concave posterior edge of the ascending process of the pterygoid. Only 7 mm of this contact is preserved, but probably little is missing. The ascending process evidently formed the anterior limit of the quadrate cartilage, which, from the nature of the groove on the quadrate, appears to have lapped over the rounded upper edge of the pterygoid behind the root of the process. In an adult skull it is to be presumed that the unossified area would be filled in with a thin sheet of bone; alternatively, the unossified area may be related to motility of the quadrate relative to the palatal complex. According to Wettstein (1931) a rather similar cartilaginous remnant of the palatoquadrate cartilage at the foot of the epipterygoid of *Sphenodon* persists into old age in many individuals, but in others quadrate and epipterygoid are firmly united by suture.

There is no similar forward projection on the right quadrate of M.C.Z.D. 2, although the edge is grooved in this region, nor does it appear to be present on the left side of the same skull. This, however, is a 'small' skull, but on the other hand the isolated left quadrate E.M. 44 R (figure 35, plate 11) of the larger size-group has a very similar outline to that of M.C.Z.D. 2 although one cannot be sure that the margin is entire in this region.

The presence of an epipterygoid is inferred from the similarity of the ascending process of the pterygoid to that of phytosaurs. The only possible epipterygoid encountered was an incomplete slender bone, most of which had to be destroyed in the preparation of the basicranial region of M.C.Z.D. 2. This fragment was disposed parallel to and a little above the medial edge of the quadrate ramus of the pterygoid, and was followed as far as the base of the ascending process. It commenced posteriorly as a thin plate a few millimetres wide, soon becoming a slender rod. It is perhaps more likely to be part of the stapes than the epipterygoid.

Hyobranchial skeleton

A slender rod lying against the right side of the basioccipital of R 4784 is probably part of the right stapes; it is only a little shorter (as preserved) than the distance from the presumed position of the tympanum to the fenestra ovalis. A similar fragment on the left of the skull, near the foramen for the internal carotid artery, is possibly part of the left stapes.

Two bones representing part of the hyoid apparatus occur on the same skull. That of the left side (figure 3*e*, *f*) is complete. It is a slender rod-like bone, about 5 mm in thickness, expanded at the (now) lower end which has an irregularly rounded, rough surface. The bone is gently curved in its central portion and the upper end is slightly expanded and flattened in the plane of curvature. The lower end lay close to the left articular; it extended upward parallel to the quadrate, curving posteriorly to end 1 cm below and lateral to the occipital condyle. About half of the corresponding bone of the right side is preserved below the left articular.

These cornua doubtless represent the first ceratobranchials, which presumably articulated with a cartilaginous corpus hyoideum. No other elements were discovered, although the block was broken into small pieces. The grooved distal end of the better preserved ceratobranchial indicates the former presence of a cartilaginous tip, or of a discrete epibranchial element.

Braincase and occiput

Two specimens display portions of the braincase. The better of these (figure 5) is almost complete. The other, from a smaller individual (M.C.Z.D. 2, figure 29, plate 9), is crushed dorsoventrally but agrees perfectly with the first.

The basioccipital forms the almost hemispherical condyle, in front of which the lower surface contracts and curves strongly downward, expanding again at the tubera. The latter form a broad, chevron-shaped mass, the apex of which points forward. The hinder surface of this mass is deeply excavated; its lower side is rugose. Immediately in front of the tubera is a deep pit in the basisphenoid, which extends forward as a groove between the basipterygoid processes.

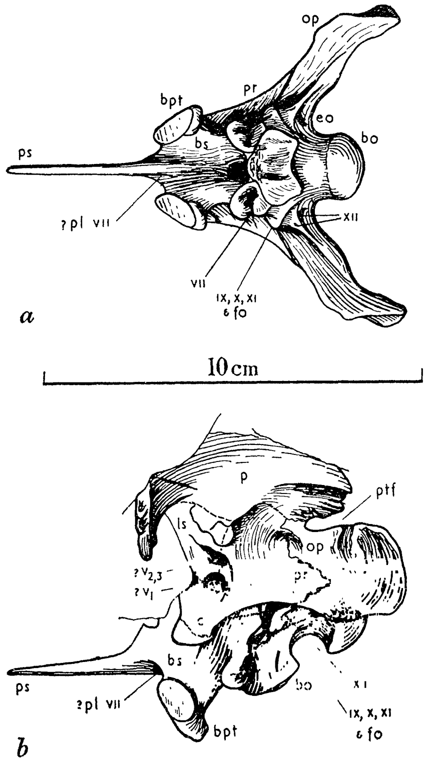

FIGURE 5. *Stagonolepis robertsoni* Ag. (magn. × $\frac{1}{2}$). The braincase. *a*: ventral view; *b*: left lateral view.

The lower surface of the basisphenoid on either side of the median groove forms strong, rounded longitudinal ridges, which expand and diverge anteriorly at the basipterygoid processes. The ridges end behind in rugose crescentic facets with flaring margins, directed somewhat outward as well as downward and backward. The suture between basioccipital and basisphenoid clearly ran along the groove at the base of each facet and can be seen to continue upward and backward following the extension of the groove on the side wall of the braincase. It disappears towards the foramen ovale in the deep cavity which that opening shares with the jugular foramen. The middle of the base of each facet is entered by a pit, which in the case of M.C.Z.D. 2 passes deeply into the bone, but ends blindly. Since R 4784+4787 is a natural mould it is not known whether the median pit actually entered the bone or not. The strongly descending basipterygoid processes are bevelled off laterally by the smooth articular facets which are almost vertical, looking a little upward as well as outward. The processes are also truncated in front by smooth plane surfaces at right angles to the articular facets; these face forward and a little downward.

The lower edge of the parasphenoid rostrum or cultriform process is at the same level as the median groove below the basisphenoid. A deep groove along the upper edge is flanked by thin vertical ridges which rise up posteriorly; a notch occurs here on the left side of R 4787 (two ridges are visible on the left side of the cast but the upper is probably the thin edge of the right side which has been pressed over). The side of the basisphenoid bears a prominent raised facet to which is closely applied the anteroventral portion of the thin descending plate of the pro-otic. Behind the facet occurs a deep depression passing antero-medially into a foramen (M.C.Z.D. 2) which emerges on a broken face close to the base of the pit for the infundibulum, and which clearly transmitted the internal carotid artery. An extensive sheath of parasphenoid ossification round the basipterygoid processes, as in lizards, appears to be indicated, but no division can be made out between basisphenoid and parasphenoid. Presumably the foramen also transmitted the palatine branch of the facial nerve, and a foramen to permit the escape of this nerve and also the palatine artery might be expected at the root of the cultriform process as in lizards. This has not been detected, but the detached right articular has obscured part of this region in R 4787.

The pro-otic projects strongly ventrally as a thin edge which in front partly overlies the lateral facet on the basisphenoid and is prolonged backward as the lower edge of the paroccipital. There is thus a long channel between this strip and the sides of the exoccipital and basisphenoid. The suture between pro-otic and basisphenoid runs more or less horizontally from behind and above the lateral facet of the basisphenoid to the jugular foramen, into which it passes. It is partly concealed in front by the ventral ridge from the pro-otic. Posteriorly the cavity is extremely deep; it is bounded behind by the thin anterior wall of the exoccipital. The deeper or medial part of the dorsal wall of the cavity is partially bridged internally by thin processes which extend towards each other from the pro- and opisthotic bones; this part of the cavity is therefore the fenestra ovalis, while the much larger pocket below it must be the jugular foramen, probably transmitting nerves IX, X, XI and the jugular vein. A groove proceeding from the posterodorsal corner of the cavity and running behind the lower part of the paroccipital process is bounded behind by a low ridge continuing from the thin anterior edge of the exoccipital. A line drawn from the fenestra ovalis through the inner, deeper part of the groove passes to the probable position of the tympanum.

In front of the fenestra ovalis a small foramen opens on the inner side of the thin wall formed by the pro-otic; it probably transmitted the facial nerve.

The side wall of the pro-otic is smooth and slightly concave, except for a low, almost vertical ridge behind the trigeminal foramina, of which there are two, placed one above the other. A narrow bridge of bone separates the foramina, which enter very obliquely from below. A suture across the middle of the bridge indicates that the anterior portion is part of the laterosphenoid, which here apparently forms a superficial bar crossing the lower branch of the trigeminal nerve. The identification of the branches of this nerve is not certain, but is based on the following considerations. In front of the foramina is a slight vertical groove on the laterosphenoid, which possibly curves round below into the lower opening. The 'bridge' has a slight notch in its upper margin, suggesting a downward course for the nerve leaving the upper opening. These points may indicate that the upper opening transmitted the maxillary and mandibular divisions of the nerve, while the lower allowed the escape of the ophthalmic root. Such an arrangement would accord better with that described by Camp (1930) for the phytosaur *Machaeroprosopus*.

The boundaries of the laterosphenoid are not clear and it is incompletely preserved in front. It seems to ascend dorsally to the root of the thin plate which the parietal sends down within the fossa, the suture probably trending upward and forward towards the descending process from the parietal between orbit and fossa. The junction with the pro-otic appears to be marked by a thin ridge running upward and a little backward from the upper trigeminal foramen. A slight ridge running anterodorsally from this opening probably indicates some small degree of telescoping of the laterosphenoid here, for some displacement has certainly occurred at the middle of the 'bridge'.

The region where the presphenoid might be expected is not preserved.

The suture between pro-otic and opisthotic emerges from the fenestra ovalis and passes round the thin edge formed by the otic bones. Its course on the side wall of the cranium is clearly visible up to the overhanging ridge which marks the lower edge of the parietal. The paroccipital process appears to be formed mainly by the opisthotic. Anteriorly the junction with the parietal is indefinite, but it appears to continue the line of the post-temporal fossa, while on the occipital surface a tongue of bone ascends medial to the fossa, between supra-occipital and parietal, overlying the latter.

The tip of the paroccipital is roughened above for reception of the squamosal and smooth below where it contributes to the socket for the quadrate. The lower edge curves outward a little and is roughened externally by a number of small, sharp, backward projections.

The occiput is incompletely preserved. The exoccipitals form prominent pillars connecting the dorsolateral portions of the condyle with the paroccipital processes. The junction between exoccipital and basioccipital runs horizontally with a finely knit suture from the constriction in front of the condyle round the posterior surface of the wall behind the jugular foramen and passes deeply into the latter. The exoccipitals form thin buttresses behind the foramen, connecting with the dorsal extensions of the tubera. On the posterior surface of the buttress near its edge a small foramen opens for a root of the hypoglossal nerve. Above and medial to this opening is a larger foramen below the exoccipital pillar for a second root of the same nerve.

Little can be said about the remainder of the occiput. No suture is apparent between exoccipital and opisthotic. A short part of the suture between paroccipital and supra-occipital, and a small area of the latter bone, are present on R 4784 medial to the post-temporal fossa. Projection of this line suggests that the supra-occipital enters the upper part of the foramen magnum. It is unknown whether or not there was an inter-parietal, but Sawin (1947) has described such a bone for *Typothorax meadei*: his account of the basicranial region of this reptile indicates that it compares closely with that of *Stagonolepis*.

Endocranial cavity

M.C.Z.D. 2 is broken near the mid-line and displays a parasagittal section of the posterior part of the skull. Unfortunately it is badly crushed and the basicranial region is pushed upward and backward so that little information of value can be got from it. Above the basipterygoid process can be seen the pocket for the infundibulum in the upper surface of the basisphenoid. Below and behind the pocket the canal emerges from the depression on the side of the basisphenoid (some of the thin, friable bone surrounding this opening was lost in course of preparation); it evidently carried the internal carotid artery into the base of the infundibular hollow.

Restoration of the skull

All the available skull-material has been used or considered in making the restoration (figures 2 to 5). The figures were prepared according to the methods of engineering drawing so that a constant check on accuracy was made throughout by means of projections. The dorsal view is based on M.C.Z.D. 2 suitably enlarged, the side view on the same specimen together with R 4784, R 4787, E.M. 23 R and E.M. 38 R. The descending process of the parietal (R 4787) which forms part of the bar between orbit and supratemporal fossa has been moved back a little to give a fossa agreeing in proportion with those of M.C.Z.D. 2. A slight forward restoration of the end of the paroccipital process has also been made since there is evidence for some lateral compression of R 4787. This compression and the crushing of M.C.Z.D. 2 explain why R 4784 is relatively narrower across the parietal 'horns' than the smaller skull.

The dissected views of the palatal complex and its relation to the braincase are mainly drawn from R 4784+R 4787 with additions from M.C.Z.D. 2. Reconstruction of the cheek region is facilitated by the fact that the left pterygoid and quadrate are in place on the left side of R 4784 and it is thus possible to build outward on these bones. The upper and outer parts of the quadrate are preserved on M.C.Z.D. 2 (both sides) and a check on the form and height of the bone is afforded by E.M. 44 R which was not identified until after the drawings had been made.

The attitude and relations of the quadratojugal and squamosal are thus accurately fixed; furthermore, a detached squamosal (R 4787) can be fitted (as a cast) on to the parietal and paroccipital of the same skull.

The postorbital is known from three displaced specimens (R 4787, M.C.Z.D. 2) which in two cases are incomplete; in the third preparation was stopped because of possible damage to adjacent bones. The only consistent explanation of the orientation of these three examples is to assume that the long, thick ramus (M.C.Z.D. 2, left side) is the ascending one. This also shows part of the area for the postfrontal in the other two examples. The slender, tapering ramus is then obviously for union with the jugal, while the blunt, pointed process meets the squamosal. This orientation also involves the least displacement of the postorbitals of M.C.Z.D. 2 from their original positions, and moreover agrees with the corresponding elements of *Aëtosaurus* and *Desmatosuchus*.

There may possibly have been a narrow fissure above the infratemporal fossa between postorbital and squamosal, but this is strictly limited by the attitude of the squamosal and the shape of the postorbital. The restoration adopted is supported by the position of a small portion of the overlap of postorbital and jugal seen on the left side of R 4787. It is, in fact, virtually impossible to restore this region otherwise than as shown.

The anterior part of the jugal and the lower edge of the quadratojugal are restored by reference to *Aëtosaurus ferratus*.

The palate is drawn from R 4787, M.C.Z.D. 2 and G.S.M. 37049, 37051, 90864 and 90865.

Lower jaw

The jaw is comprised of the usual six elements: dentary, angular, surangular, articular, prearticular and splenial. No coronoid has been observed. With the exception of the right dentary, all the bones of both sides of the jaws are present on R 4787. The left side is little disturbed and shows the general shape of the jaw well; the bones of the right side are more scattered but are more useful on that account since casts may be fitted together to yield information regarding articulations. The tip of the dentary is not preserved on this

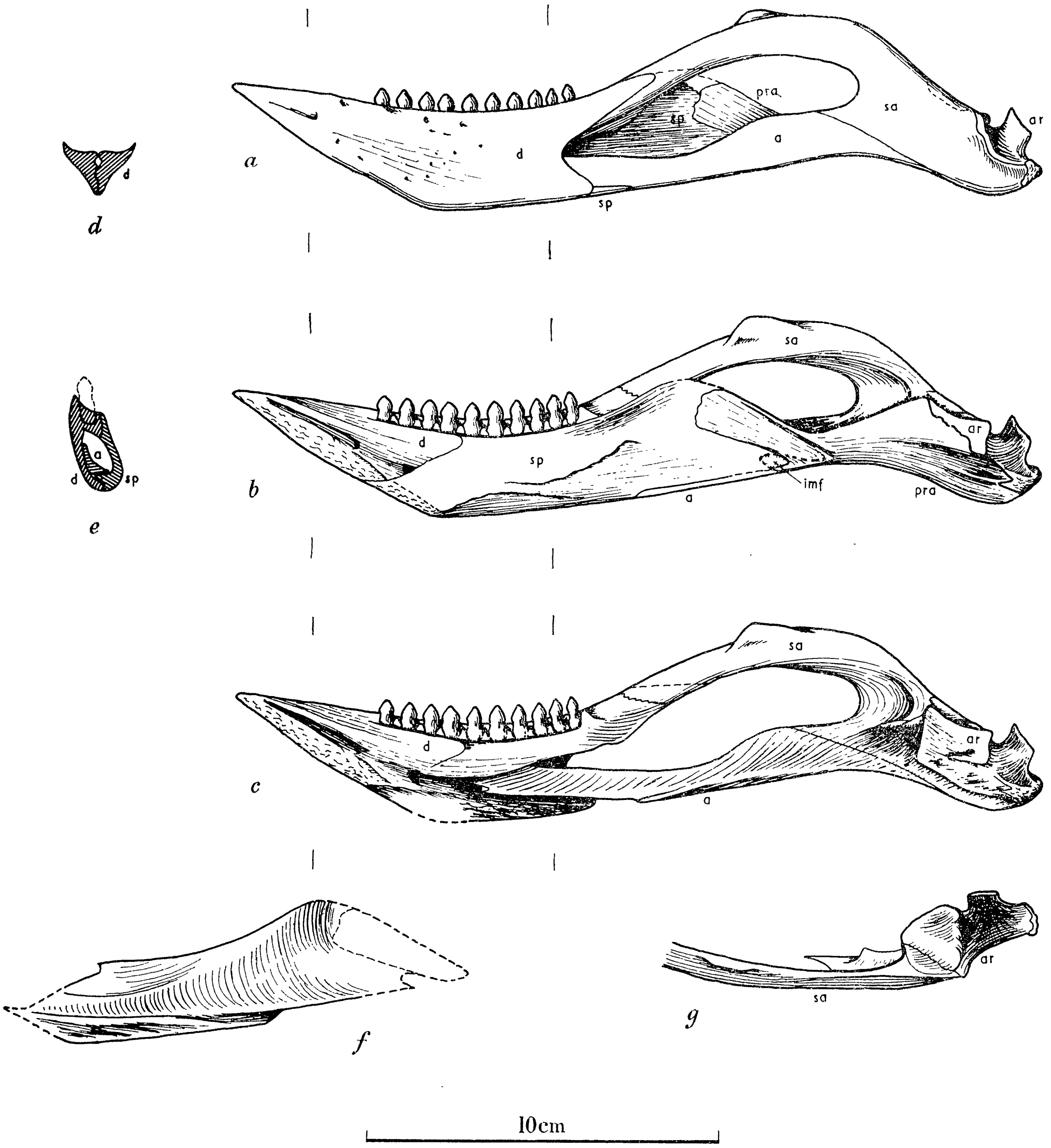

FIGURE 6. *Stagonolepis robertsoni* Ag. (magn. × ½). Composite restoration of the jaw. *a*: lateral; *b*: medial; *c*: the same with splenial and prearticular removed; *d*, *e*: cross-sections of the conjoined dentaries and of the jaw along the lines indicated; *f*: lateral view of left splenial; *g*: upper and partly posterior view of left articular and surangular.

specimen but it has been well shown, together with the edentulous region, by preparation of G.S.M. 90864 and 90865.

The dentary divides posteriorly into two branches which pass above and below the mandibular fenestra. The upper branch separates behind into two thin processes, the inner one fitting into a cleft in the anterior end of the surangular and tapering out in a groove on its underside. The relations of the outer process are inferred from the tip of the right surangular and what can be seen of the left side of R 4787. It evidently lay over the lower or more lateral of the two processes from the surangular, which then passed forward within it. The shorter lower branch of the dentary overlaps the angular.

The lateral surface slopes strongly inward and bears many small, scattered foramina. A groove on the side of the bone begins close behind the pointed tip and leads posteriorly into a foramen. The dorsal margin is concave upward; in G.S.M. 90864 the outer edge is rather irregular and it seems possible that the maxillary teeth wore against a horny sheath upon it. The rostrum of the dentary is roughly triangular in section. The inner face of the triangle forms the symphysis, and the conjoined dentaries enclose a longitudinal groove which probably diverges in front to emerge as the foramina near the tip. The smooth, toothless dorsal surface is slightly concave upward and rises laterally to form a sharp rim, the backward continuation of which conceals the tooth-bases in side view.

Opposite the first tooth the dentary symphysis is replaced by a roughened area for the attachment of the splenial extending almost to the end of the lower branch of the dentary. Below the second tooth a large foramen enters the bone from the Meckelian canal, probably supplying the small foramina on the outside. The canal is exposed for 1·5 cm before passing within the splenial. Behind the foramen there is a deep hollow below the alveolar region into which extends the angular, tapering to a thin edge below the fourth tooth. Here the Meckelian canal passes between angular and splenial with the dentary forming its upper border. The inner wall of the alveolar region is thin posteriorly; from about the fourth tooth backward it is slightly roughened for contact with the splenial.

The anterior half of the angular is roughly triangular in section; the flat outer surface lies anteriorly against the inner side of the lower branch of the dentary. Between the flat lower face of this portion and the inward-curving lower edge of the dentary is enclosed a longitudinal groove which receives a prominent ridge on the splenial. Just behind the hinder end of the dentary the medial edge of the angular develops a ridge passing obliquely backward from ventral to medial surface. The anterior end of this ridge shows where the lower edge of the splenial curves round the angular. The latter becomes thinner and deeper behind, with a flat outer side. The thin upper posterior edge is received into a deep groove in the straight lower edge of the surangular and the tip of the bone tapers to a fine point between prearticular and surangular.

The surangular is strongly arched dorsally, passing above the mandibular fossa as a long rod which forks anteriorly to meet the dentary. The inner branch overlaps the inner side of the dentary, the outer curves medially and ventrally, passing within the outer branch of the dentary and running along the groove beneath the teeth. A short ascending flange above the fossa served for muscle or tendon attachment. M.C.Z.D. 15/1, an isolated right surangular, shows that the outer surface of the bone is flattened behind the fossa; the medial side of this region is concave, rising smoothly to the thin upper margin. More posteriorly the upper half of the bone is thickened on the inner side and sends forward a short, high ridge. A blunt tubercle at the posterior end of this marks the beginning of the articular surface, and the anterodorsal corner of the articular fits against it. The articular area on the surangular is small, corresponding to about half the outer condyle of the quadrate. Above the ridge a deep concavity, probably ending in a foramen, passes back into the thickened part of the bone.

The posterior tip of the surangular is not preserved but can be reconstructed from the shape of the articular. On R 4787 (detached right surangular) the upper margin drops abruptly in level just before preservation ceases; into this notch fits a projection of the outside of the right articular. A low, broad ridge on the inner side of the surangular lies in a corresponding shallow groove on the outside of the articular and probably followed the latter to the rugose knob at its tip. The lower edge of the surangular projects below the articular and its inner side here is covered by the prearticular.

The articular is a short element, broadest at the articular surface, which is horizontal. There is a low inner rim within which is a flattened or slightly concave area, separated by a very slight convexity from an outer concave area. The medial surface slopes strongly outward and downward; below the posterior end of the articular surface is a low, rough projection. More ventrally the bone shows a slightly concave longitudinal surface bounded below by the thin ventral edge and behind by the roughened inner surface of the retroarticular process. The upper part of the posterior end of the prearticular lay along this concavity and extended a short way behind the cotylus.

The articular ends in front in a thick grooved edge inclined outward and downward. Meckel's cartilage evidently proceeded from this surface and was enclosed between the prearticular and surangular, lying below the prominent ridge on the latter, and probably not extending beyond it.

Only the medial surfaces of the prearticulars are visible. The broad posterior end is applied to the inner side of the articular, curving sharply beneath the projection below the articular surface. Posteriorly a short tongue covers the ventromedial area on the articular; this is separated by a ridge from a more ventral extension which covered the inner side of the surangular. More anteriorly it laps over the prominent ridge on the surangular. Contracting in depth it passes forward, its lower margin presumably following that of the angular. A ridge along the upper edge of the forward extension indicates the posterior limit of the splenial. A short, forward process occurs below the base of this flat anterior sheet; the notch here probably shows the position of an infra-Meckelian foramen between prearticular, splenial and angular. The prearticular formed the greater part of the inner margin of the Meckelian fossa.

The splenial is convex medially in its lower half and flattened above. The upper portion is applied as a thin sheet to the inner side of the dentary and prearticular. Posteriorly it may have met the inner process of the surangular. The lateral surface shows three ridges. The strongest of these begins at the lower edge and runs forward, rising slightly. Below it the bone is roughened. This ridge fits into the slot between the lower edge of the angular and the incurved lower edge of the dentary, and the rough surface meets a similar surface on the latter. The second ridge runs backward from above the rear end of the first, soon becoming the lower edge of the bone, after which it is in contact with the ventromedial edge of the angular. The latter passes anteriorly into the groove between the two ridges on the splenial. The lower edge of the splenial curls round the angular and passes to the medial side at the beginning of the short ridge on the inner edge of the angular; it presumably lay against the latter back to the prearticular. The splenial thus has a brief exposure on the outer side of the jaw.

Above the two ridges there is a longitudinal concavity bounding the inner side of the Meckelian canal. The third, weakest ridge runs above this area and separates it from the portion in contact with the dentary.

The lower edge of the splenial is flattened at the symphysis. The medial surfaces bear irregular but symmetrical, slightly undercut ridges. These suggest the ending of a horny sheath which curved round the lower edges of the jaws and covered the rostrum of the dentaries.

Kinetism

The palatine is fixed to the maxilla by a broad lateral surface prohibiting movement; posteriorly it overlaps the pterygoid dorsally and has a digitate suture with it ventrally such that some anteroposterior movement could conceivably have occurred: slight separation has taken place at this suture on the right side of M.C.Z.D. 2. Evidence is incomplete for the anterior end of the vomer; there is an extensive smooth overlap on the premaxilla but the union with the maxilla appears to be firm.

The anterior bars of the pterygoids were certainly free to move between the posterior wings of the vomers, and the medial edges of the palatines offer no obstruction as they seem only to rest on the pterygoids. The basipterygoid facets are smooth and lie in the anteroposterior plane, but possible movement would be limited by the truncated anterior face of the basisphenoid. The quadrate wings of the pterygoids offer little obstacle to fore-and-aft motion.

The dorsal overlap area of the transverse on the pterygoid is almost smooth, and slight displacement has occurred at this junction on the left side of R 4787. However, because of the nature of the junction between the more ventral part of the transverse and the pterygoid, and its firm union on the left side of R 4787, movement at this suture seems unlikely. Up-and-down movement is prevented anteriorly by the dorsal overlap of the palatine, and posteriorly by the ridge-and-groove arrangement between quadrate and pterygoid.

The pterygoid and palatine of G.S.M. 37049 are firmly united. Taken with the situation at the transverse and the basisphenoid this suggests that the pterygoid, and thus the palate as a whole, was immovable, or that relative movement was very limited.

The braincase is certainly firmly fixed to the skull-roof, while the squamosal, parietal and opisthotic meet at interlocking surfaces. By analogy with *Aëtosaurus ferratus* and *Desmatosuchus* (figure 24*a* and *d*), and by consideration of the detached postorbitals it is reasonable to assume that the postorbital and squamosal had a firm union below the supratemporal fossa.

There is, however, strong evidence for motility of the quadrate. The upper end of this bone could obviously pivot in the cup between squamosal and paroccipital, but from the nature of its junction with the quadratojugal it is clear that the two bones must have moved together as a unit. Movement of the quadratojugal is made possible by the overlap of the squamosal on the smooth shelf at its upper end, and by the probable nature of its overlap (by analogy with *Aëtosaurus*) on the posterior point of the jugal; the latter presumably allows sliding between jugal and quadratojugal tangential to the centre of the upper quadrate articulation.

The persistent cartilaginous area at the anterior end of the pterygoid wing of the quadrate may allow some flexibility in this region, while anterior movement would still be limited by the contact between the bony upper portion and the ascending process of the pterygoid.

The movable quadrate would permit some anteroposterior movement of the lower jaws additional to that allowed by the almost flat articular surfaces; thus a slicing action could take place between upper and lower teeth.

It is noteworthy that smooth, extensive overlapping contacts occur between many of the jaw bones. This is particularly marked where the long rod of the angular passes within the dentary and the splenial. The latter was firmly sutured to the dentary along its lower edge, but posteriorly the contact with the angular is smooth; so also is the flat area on the prearticular. It seems therefore that some degree of relative movement could take place between the anterior and posterior portions of the jaw. Details are uncertain for the dentary-surangular joint but some freedom of movement here does not seem impossible. On the other hand, although the contact between articular and surangular is a smooth one, the shape of this surface precludes relative movement and the articular was clearly fixed between surangular and prearticular. Likewise the posterior end of the angular fits firmly into its groove in the surangular and its posterior tip is held between surangular and prearticular.

Such movement as may have occurred would probably be small anteroposterior adjustments to stresses set up in the jaws during mastication or digging; extensive rotational movement would not be permitted.

Dentition

The right premaxilla of R 4787 has five alveoli, three of which still bear teeth; the left has at least four teeth. Four are present on the left premaxilla of E.M. 38 R.

The right maxilla of the same specimen (plus associated fragments) has a total of eleven teeth, but measurements of the incomplete right maxilla of R 4787 suggest twelve teeth for this bone. Both are large individuals. By combining fragmentary maxillae of different individuals counts of eleven or twelve teeth are obtained. By analogy with *Desmatosuchus* it is probable that the number of teeth could differ on opposite sides of the same skull.

The right dentary of M.C.Z.D. 2 has nine teeth, but combination of R 4787 with G.S.M. 90864 gives a total of ten dentary teeth for the larger individuals.

The formula may therefore be given as:

Premaxilla 4 or 5, maxilla 11 or 12, dentary 9 or 10.

The teeth are of the same shape throughout. Each has a long cylindrical basal portion deeply embedded in the alveolus. The exposed part of the base is faintly striated longitudinally. Between crown and base the tooth is smooth and constricted. The crown is somewhat compressed from side to side, slightly recurved, and striated toward the tip.

Well-preserved maxillary and dentary teeth show a finely denticulate anterior edge. The pulp-cavity extends to a variable amount into the crown.

The premaxillary teeth are of equal size but smaller than those borne on the other bones. The maxillary teeth increase slightly in size up to the third or fourth and thereafter gradually decrease; a similar gradation occurs in those of the dentary, which equal those of the maxilla in size.

The alveoli are very deep and are separated by very thin partitions. The teeth were but loosely implanted in their sockets as can be clearly seen from R 4787 where numerous teeth are scattered about and indeed all have been lost from the detached right maxilla. A curious feature is the medial thickening of the interalveolar septa on all the tooth-bearing bones. Since the thickened portions project upwards between the teeth and are separated by grooves from the inner margins of the jaws they bear a superficial resemblance to replacing teeth. However, there is no doubt about their true nature; they probably served to support the bases of the teeth, which have a deeper exposure on the medial side.

Little direct evidence is available concerning the replacement of the teeth, for many of the tooth-bearing elements known are isolated, and the teeth are easily lost. However, gaps in the tooth-row are infrequent in well-preserved specimens. In E.M. 38 R, for example, there are no gaps in preserved sequences which include four left premaxillary, ten left maxillary and eleven right maxillary teeth. The right dentary of M.C.Z.D. 2 has a full row of nine teeth, while there is one empty alveolus among six on the right dentary of G.S.M. 90864. No gaps occur in the preserved parts of the premaxillae and maxillae of the latter skull, but the greater part of the maxilla is wanting. Furthermore, the teeth are usually well graded in size and incompletely erupted teeth are rarely seen. Actual replacement has not been observed.

It is likely that replacement was extremely rapid rather than that it was infrequent, for reasons similar to those advanced by Romer & Price (1940) for the edaphosaurs. *Stagonolepis* is believed to have been herbivorous, the teeth performing a chopping or slicing function, so that wear would be rapid and quick replacement essential.

Functional interpretation of the dentition

The premaxillary teeth are bevelled-off obliquely on their inner sides and since they are unopposed it seems probable that they wore against a horny sheath on the sharp lateral rim of the dentary rostrum. The inclination of the bevelled surface precludes the possibility of their having bitten against the concave area within the rim. Wear facets on the maxillary teeth are observable only on the anterior end of the left maxilla of E.M. 38R (figure 34, plate 11). The first tooth shows a large, plane facet bevelling off the medial side of the crown obliquely. The second tooth has only a small facet, but this is because it has not fully descended, for the counterpart (G.S.M. 90881) shows a large facet on the third tooth, which equals the first in length. The fourth is as long as the third but shows no sign of wear. In all cases where the inner surfaces are visible the posterior maxillary teeth appear to be unworn. Only two dentary teeth show the lateral side of the crown, one (M.C.Z.D. 2) being at the anterior end, the other (G.S.M. 37051) at the posterior. Neither shows any trace of wear.

There is, in fact, little evidence upon which to arrive at a conclusion. The lack of wear on the few teeth in which the presumed occlusal surfaces are visible may merely support the hypothesis of rapid replacement; on the other hand the teeth may normally not have occluded at all. It is certain that the dentary teeth bit within those of the maxilla, and it seems most likely that the lateral faces of the crowns of the dentary teeth met the medial ones of the maxillary teeth in a slicing action: E.M. 38 R seems to show that this happened anteriorly at least. There is the further possibility that the maxillary teeth also came into contact with the high (and presumably horn-covered) lateral rim of the dentary. The

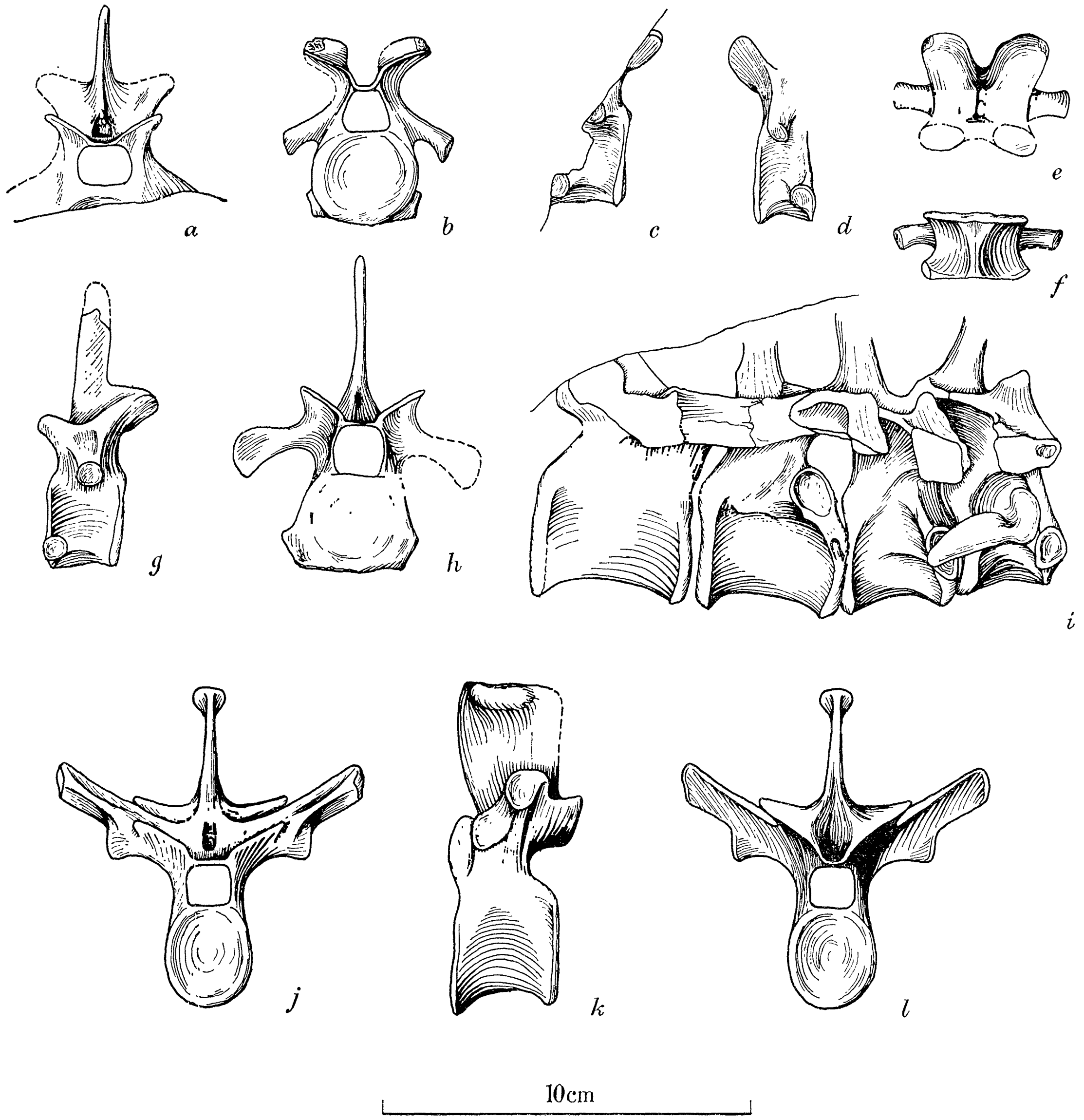

FIGURE 7. *Stagonolepis robertsoni* Ag. (magn. $\times \frac{1}{2}$). Cervical and dorsal vertebrae. *a*: front view of incomplete mid-cervical, G.S.E. 4795; *b*, *c*, *f*: back, left side and under views of incomplete (?sixth) cervical, E.M. 33W; *d*: right side of a similar vertebra, R 4790; *e*, *g*: upper and left side views of ?sixth cervical, composite of G.S.E. 4795 and E.M. 33W; *h*: front view of ?eighth cervical, E.M. 30R; *i*: right sides of last two cervicals (probably the eighth and ninth) and first two dorsals, R 4784; *j*, *k*, *l*: front, left side and back views of the fifth or sixth dorsal vertebra, R 4799 with minor additions from other specimens.

irregularity of the margin of the right dentary G.S.M. 90864 lends some support to this suggestion. In this specimen the tip of a maxillary tooth does in fact lie over the edge of the dentary, and on the left side of R 4787 the last three maxillary teeth overlap the outer margins of the dentary and surangular.

In *Aëtosaurus ferratus* the lower jaws usually lie within the upper so that wear facets are not seen. However, the posterior end of the right dentary of No. VII does show irregularities of the margin where the maxillary teeth may well have touched it.

The dentary teeth of *Stagonolepis* are more closely packed than those of the maxilla. Since the first tooth is approximately opposite the first maxillary tooth, and there are fewer dentary than maxillary teeth, the posterior two or three teeth of the maxilla are unopposed. They probably met the posterior end of the dentary and the anterior end of the surangular. The upward curvature of this part of the jaw carried it close to the oblique medial area at the back of the maxilla; as already noted, small foramina on this area suggest that it was horn-covered.

The articular area on the mandible is shallow, and since the medial part at least of the quadrate articular surface is almost flat, some anteroposterior motion seems to have been possible here. The quadrate itself was evidently moveable in a fore-and-aft direction. As well as allowing of a slicing action between maxilla and dentary, some degree of slewing may also have been permitted in order to bring the pointed dentary rostrum into more effective contact with the premaxillary teeth.

Horn-covered areas probably included the tips of the premaxillae, the oblique posterior areas on the maxillae, the greater part of the dentary (curving round below on to the splenial), and the outer sides of the maxillae up to the ridges below the antorbital openings.

It is suggested that the premaxillary teeth performed a grasping and tearing function against the rims of the dentary rostrum, while the food (probably of a vegetable nature) was chopped or sliced between the dentary and maxillary batteries. The expanded tips of the premaxillae, braced by small terminal expansions of the nasals, may have been used for digging in soft or marshy ground.

Vertebrae

There are upwards of 120 vertebrae in the material available, but many of these are incomplete and isolated or are too crushed for satisfactory preparation. The most important new material includes an articulated series of twenty-five vertebrae from the seventh cervical to the fourth caudal (R 4784, 4793 and other blocks) which derive additional importance from their association with a skull.

The vertebrae are similar throughout to those described by Case (1922) for *Desmatosuchus* and by Sawin (1947) for *Typothorax*. The number of cervicals cannot be determined directly because of imperfect preservation of the anterior parts of the columns of R 4784 and M.C.Z.D. 2, but by a consideration of the length of the section which is incompletely known, and by analogy with *Typothorax*, it seems safe to assume a total of nine cervical vertebrae. The first well-preserved vertebra of R 4784 is here described as the eighth cervical and the remainder are numbered accordingly.

The short cervicals are succeeded by sixteen more elongated dorsals; the last two of these have flattened, expanded ribs fused to short transverse processes and are in process of being incorporated in the sacrum. The two sacral vertebrae are followed by an unknown number of caudals, estimated at forty to forty-five. There is some evidence which indicates that *Stagonolepis* had a long, broad tail like that of *Aëtosaurus.*

The atlas and axis are preserved in poor condition on M.C.Z.D. 2. The atlas is represented by a short, compressed element, presumably the intercentrum, bearing laterally a pair of small foramina. The intercentrum of the axis is clearly separate and seems to be prolonged below into a median keel, which is just possibly part of a crushed cervical rib. The axis has an elongated neural spine. The side of the centrum is divided by a low ventrolateral ridge into two shallow concave areas. The upper of these is pierced by a number of irregular small foramina, which also occur on the next two vertebrae. The succeeding vertebrae are poorly preserved and preparation was not attempted. The lateral concavities become more pronounced backward. The parapophysis evidently lay at the anterior end of the ridge, the diapophysis being situated low down towards the anterior end of the neural arch, becoming centrally placed on the fourth vertebra.

The remaining cervicals are represented by isolated and incomplete specimens from Findrassie in Elgin Museum; by a small cervical R 4790, a duplicate of E.M. 33 W; and by the last two cervicals of R 4784. E.M. 33 W and R 4790 are from a position a little anterior to the first well-preserved vertebra of R 4784, say the sixth cervical. E.M. 30R is perhaps the eighth, E.M. 14R the seventh, and E.M. 35R a very incomplete mid-cervical. These vertebrae resemble those of *Desmatosuchus* closely, differing in having higher neural spines, strong ventral keels and shorter transverse processes. The sides of the centra are deeply concave and the low ventrolateral ridge leads anteriorly to the parapophysis. In the sixth cervical the diapophysis is borne on a rounded process unsupported by ridges and the posterior face of the centrum is almost circular. The eighth cervical of R 4784 shows the T-beam effect described by Case, a strong ridge connecting the posterior upper part of the centrum with the lower part of the transverse process. A blunter ridge connects the process with the anterior rim of the centrum. The parapophysis is joined to the side of the centrum by a short buttress. The ninth vertebra has a longer centrum, a less pronounced ventral keel, and has the parapophysis midway up the centrum connected by a strong ridge to the base of the transverse process, which is directed outward and a little forward.

The tenth vertebra is regarded as the first dorsal, the parapophysis having shifted to the neural arch. Here it is low down, connecting by ridges to the rim of the centrum and the transverse process. The centrum is more elongate, the keel hardly developed, the ridge from posterior rim to process has gone, and the process itself is directed slightly upward and forward. In the second dorsal the parapophysis is on the transverse process, which is incompletely cast. There are no connecting ridges to the centrum, which lacks a keel and whose faces are now equal.

The succeeding vertebrae are similar in size and shape. The neural spines are taller, and the transverse processes shorter than in *Desmatosuchus.* In the anterior dorsal vertebrae the transverse processes are inclined steeply upward and the capitular facet is situated about half-way along the anterior edge below and in front of the tubercular facet. The steeply inclined prezygapophyses are borne on the anteromedial parts of the processes. The fore part of the apex of the spine is moderately expanded to form a scute-table. The centra are strongly constricted in their middles and have flaring faces with bevelled margins.

The transverse processes become directed horizontally at about the ninth or tenth dorsal vertebra. The capitular and tubercular facets come to lie almost in the same horizontal plane (figure 8), the scute-tables increase in size and the zygapophyses become less steeply inclined until in the last two presacrals they are almost horizontal. The dorsal vertebrae have the postzygapophysis connected to the transverse process by a thin web of bone which extends out along the posterior edge of the process to its tip, separated ventrally from the body of the process by a shallow groove.

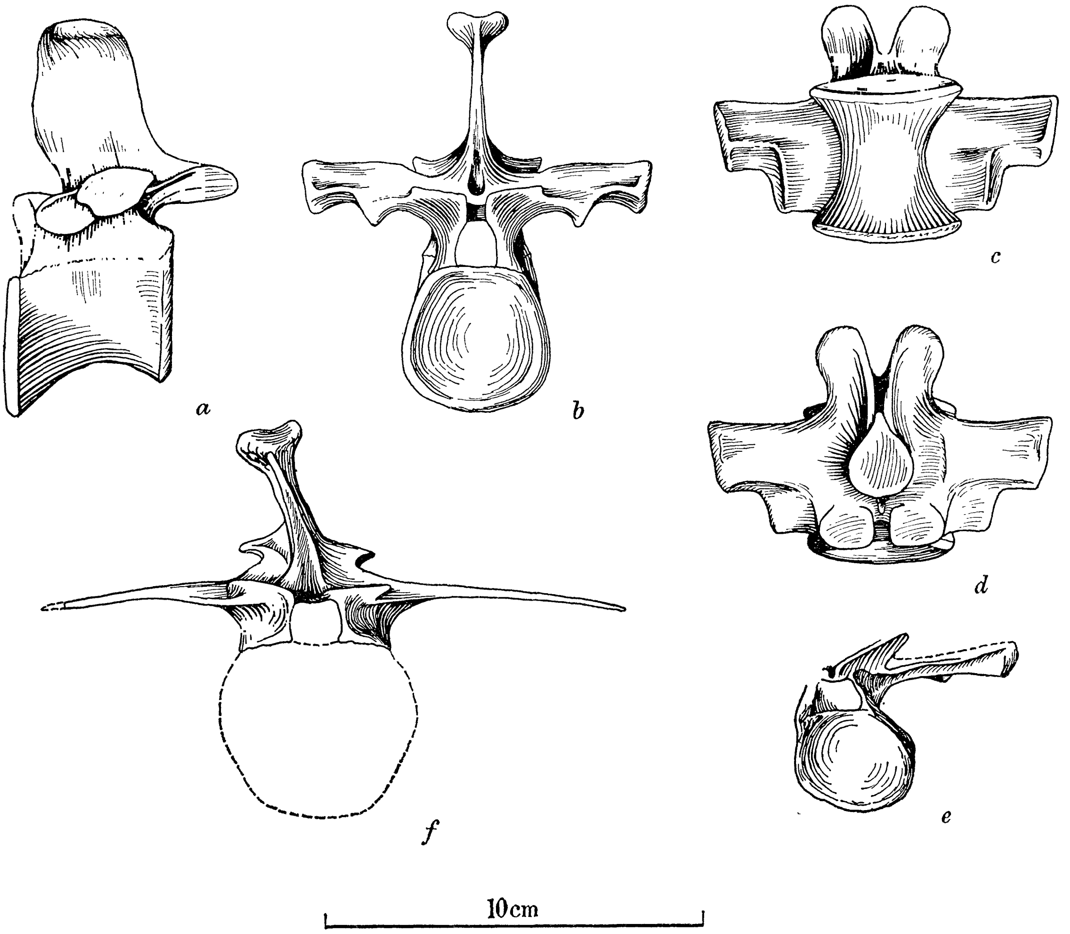

FIGURE 8. *Stagonolepis robertsoni* Ag. (magn. × ½). Dorsal vertebrae. *a*, *b*, *c*, *d*: left side, front, under and upper views of a posterior dorsal vertebra (the centrum a little distorted), based on the eleventh dorsal of R 4796 and counterpart R 4793. The neural spine completed after the thirteenth dorsal of the same series. *e*: back view of an incomplete dorsal vertebra, E.M. 46R; *f*: front view of neural arch and spine of fifteenth dorsal, G.S.M. 90884. Outline of centrum from first caudal of same.

The transverse processes maintain their length with little change and there is little difference in the position of the capitular facet. In the thirteenth and fourteenth dorsals the process is distinctly weaker and the rib-facets are smaller, the capitular facet being a little nearer the tubercular.

The two last presacrals closely resemble the sacrals. In the isolated sacrum G.S.M. 90884 (figures 8 and 9) these two vertebrae are in position in front of the sacrum proper while matrix occurs in front of them. There is also a slight displacement of the column between

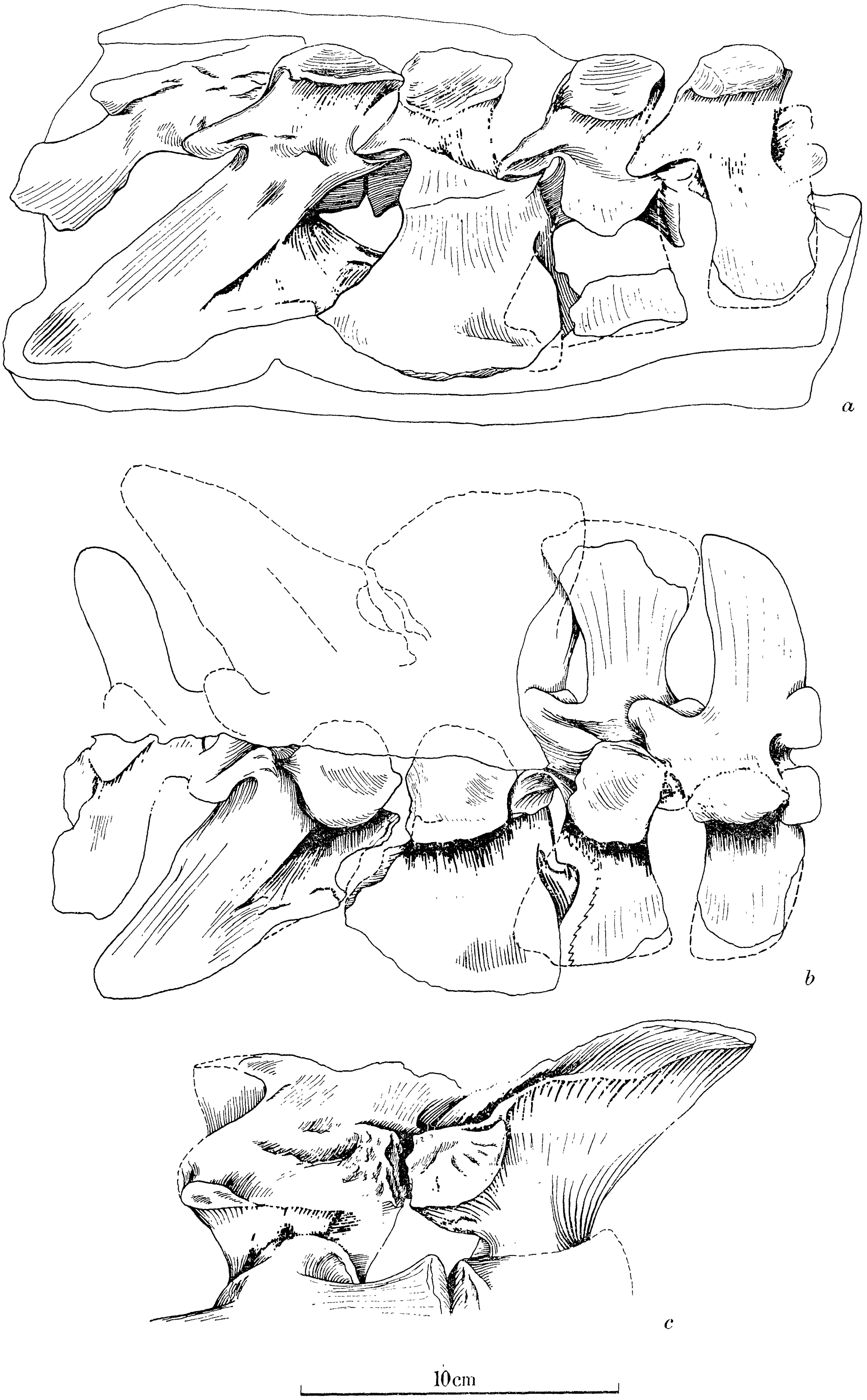

FIGURE 9. *Stagonolepis robertsoni* Ag. (magn. $\times \frac{1}{2}$). *a*, *b*: cast of parts of the last two dorsal, the two sacral and the first caudal vertebrae, with part of last dorsal rib of right side cut away to show anterior edge of first sacral rib. *a*: dorsolateral view of right side; *b*: upper view (a little reduced). *c*: distal and under surfaces of both sacral ribs of the left side, mainly drawn from casts of the counterparts of the above specimen (G.S.M. 90884), the posterior part of the second sacral rib completed from the bony original and from R 4786. The centra of the last dorsal and first sacral vertebrae are crushed together and the articular areas for the ilium have been flattened almost into the horizontal plane.

the fourteenth and fifteenth dorsal vertebrae of R 4793. These facts suggest a close association between the two last dorsals and the sacral vertebrae. The prezygapophyses of the last two presacrals are almost horizontal, but those of the sacrals and caudals have the usual steep inclination; a region of special flexibility may be indicated here.

The ribs of these two vertebrae are thin, expanded structures fused to short transverse processes which are supported below by short buttresses connecting them to the ends of the neutral arch. The outer parts of the ribs of the penultimate presacral did not touch those of the next following vertebra, but it is certain that, after allowing for telescoping of the vertebrae which has taken place (G.S.M. 90884), the distal ends of the ribs of the last presacral overlapped the first pair of sacral ribs by about 1 cm; R 4793 shows a similar condition.

The centra of the sacral vertebrae are the largest in the column. In G.S.M. 90884 the centra are badly crushed but the first caudal shows that their articular faces were essentially circular. The junctions of the sacral ribs with the transverse processes are marked by longitudinal ridges. The first sacral rib is attached by a powerful facet to the anterior end of the centrum; the second is attached to the middle of its centrum.

The first sacral rib met the ilium below and behind the anterior embayment and curved round above, attaching along the inner side of the anterior spur. The distal surface of the second rib met the posterior part of the neck of the ilium and ran right along the medial edge of the posterior process. The ribs thus afforded equally strong attachments to the ilium and interlocked with each other securely by means of rugose surfaces.

The scute-tables of the sacral vertebrae are strongly expanded, followed by a decrease in size in those of the anterior caudals, which seem to have had taller neural spines than those of the sacrum.

There is some evidence tending to suggest that differences existed between the anterior caudal vertebrae of individuals of the two size-groups, which may perhaps be explained by sexual dimorphism. Thus the first caudal of G.S.M. 90884 (a large individual) has transverse processes (fused ribs) of normal length. On the other hand R 4799 (allotted to the smaller size-group) exhibits elongated, somewhat decurved processes and lacks chevron-facets. The similarity of this vertebra to the most anterior caudals of *Aëtosaurus ferratus* and *A. crassicauda* would lead to its identification as the first caudal, since in the latter at least the chevrons begin behind the second caudal. However, R 4786 (counterpart of R 4793), also a large individual, shows an ill-defined chevron-facet at the back of the second caudal centrum and the transverse processes are of normal length at least in the first three caudals, while E.M. 47R is a larger duplicate of R 4799 with evidence of elongated processes but unfortunately it is incomplete below.

There appear to be two explanations of the above facts. The first assumes that the chevron-bones began behind the second caudal vertebra in all individuals, but that the transverse processes did not commence their elongation until about the fourth caudal in the larger animals. The second explanation is that elongation began at this point in both size-groups, but that the first chevron was situated no further forward than the fifth caudal vertebra in the smaller, presumably female, individuals. Neither of these suggestions is entirely satisfactory but little more can be said without further evidence. On the whole the first of the two is preferred.

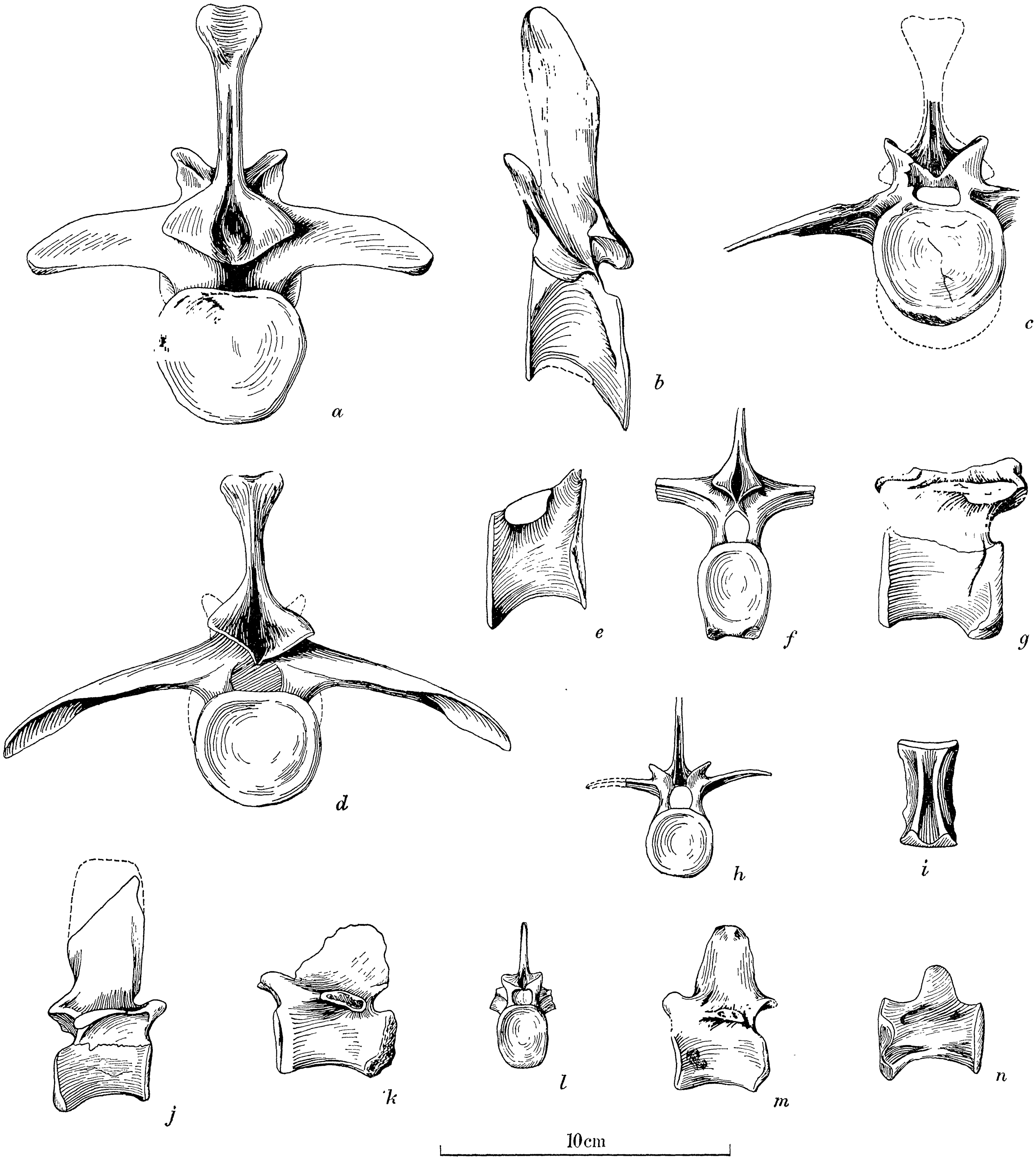

FIGURE 10. *Stagonolepis robertsoni* Ag. (magn. × $\frac{1}{2}$). Caudal vertebrae. *a*, *b*: back and left side views of distorted first caudal, G.S.M. 90884; *c*, *d*, *e*: front, back and right side views of ?first caudal, R 4799; *f*, *g*: back and left side views of anterior caudal, E.M. 27W; *h*: front view of mid-caudal, the fourth of R.S.M. 1891.92.529; *i*: under view of slightly compressed second centrum of same; *j*: right side of fifth vertebra of same, neural spine from second vertebra, broken line hypothetical; *k*, *l*: left side and front views of posterior caudal, E.M. 18R; *m*: left side of posterior caudal, E.M. 4R; *n*: oblique lower view of distorted posterior caudal, G.S.M. 90884.

The transverse processes of the first caudal (R 4793) are inclined backward, but the inclination diminishes posteriorly until in the mid-caudals it is small. Beneath the distal end of the transverse process in the first two caudals a ridge parallel to the axis of the process separates off a narrow, posterior concave area; in the second vertebra the ridge is low. In R 4799 the processes are somewhat constricted at their roots, with a broader distal part curving down and back. The zygapophyses of the anterior caudals are large and steeply inclined. At the fourth caudal vertebra the faces of the centrum have become taller than wide and the centrum is laterally compressed.

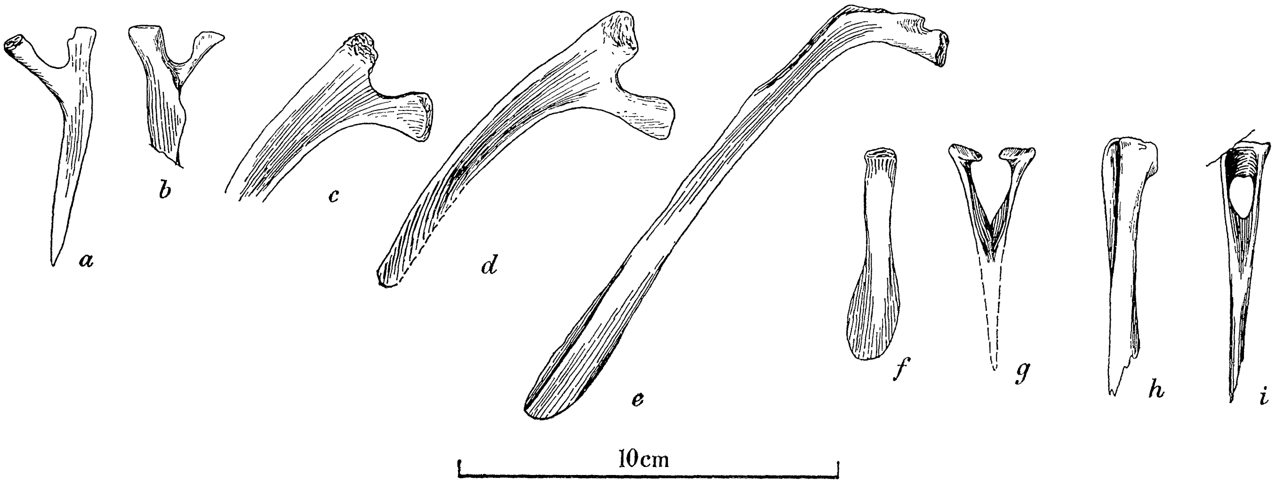

FIGURE 11. *Stagonolepis robertsoni* Ag. (magn. × $\frac{1}{2}$). Ribs and chevron-bones. *a*, *b*: upper and lower views of a cervical rib, R 4789 and R 4790; *c*, *d*: undersides of proximal ends of two posterior cervical or anterior dorsal ribs, E.M. 26R and R 4790; *e*: underside of a dorsal rib, E.M. 3R; *f*: right side of a mid-caudal chevron, E.M. 3R; *g*: back view of a similar bone, E.M. 32R; *h*, *i*: oblique left side and front views of an ?anterior chevron, E.M. 15R.

The more posterior vertebrae are represented by isolated specimens and by the articulated series of seven vertebrae described by Huxley (1877, plates III and IV). The latter are from the middle of the tail rather than from the anterior region as was thought by him. In several of these vertebrae sutures can be traced across the roots of the 'transverse processes' showing that the latter are fused ribs; some of the isolated specimens have lost their ribs (figure 10*k*, *l* and *m*).

In a typical mid-caudal vertebra the centrum is slender and elongated, expanding into oval, slightly concave faces with bevelled rims. All undistorted caudals except the most anterior have the faces higher than wide. Ventrally a deep groove is flanked by strong ridges ending behind in chevron-facets facing downward and backward. Flattened transverse processes are given off from the sides of the neural arch. The prezygapophyses are connected by short ridges to the base of the neural spine, the front edge of which is deeply grooved. There were probably small terminal expansions of the spines to receive the scutes.

In the more posterior vertebrae the neural arch is lower, the zygapophyses are close together and the transverse processes are given off almost on the neurocentral suture; they are no longer connected to the zygapophyses. E.M. 4R (figure 10*m*) still has a slight apical expansion. No true posterior caudals are known; E.M. 17R, identified by Huxley as a posterior caudal, proved on the making of a better cast to be an almost complete small thoracic vertebra, probably of the coelurosaur *Saltopus*.

Ribs

There is little to add to the account of the ribs given by Huxley. Very few ribs are well preserved, and fewer still are determinable as to position. Figure 11*a* and *b* shows a posterior cervical rib. A thin high ridge extends distally from the tubercular process on the under or medial side. Portions of other ribs are shown on figure 11; all those figured are from the smaller individuals. G.S.M. 90884 displays a dorsal rib with a proximal expansion similar to that described by Case for the ribs of *Desmatosuchus*.

Chevron-bones

The chevrons appear to have commenced, at least in some of the larger animals, behind the second caudal vertebra. Figure 11*h* and *i* shows a type in which the articular facets are united; this specimen is associated with the pterygoid attributed to *Dasygnathus* and may perhaps be of that genus. The blade is only slightly expanded. Typical mid-caudal chevrons are shown by figure 11*f* and *g*. The articular facets are separated and the distal portion forms a thin blade with rounded lower margin.

Appendicular skeleton

Shoulder girdle

Parts of thirteen scapulae, six coracoids, two clavicles and two interclavicles are now available. New material includes R 4784, a girdle almost *in situ*, and R.S.M. 1952.10.1, which is incompletely exposed but shows the relation of the girdle to the belly-armour.

The 'pubis' figured by Huxley (1877, pl. VIII, fig. 2) is an inverted scapula: the block on which it lies fits on to the block with the coracoid shown on the same plate, the two bones forming an articulated scapulocoracoid, the suture between them being clearly visible. Several other specimens labelled 'pubis' in the collection of the Geological Survey are in fact the expanded apices of scapulae. The possibility that this was the case was suggested by von Huene (1942) for the Elgin Museum specimen.

Problems are posed by distortion and abrasion of some of the specimens. Thus G.S.M. 90850 (Huxley, pl. X, figs. 1, 1*a*) is considerably damaged, the apex being partly broken away, likewise the acromial region, the supraglenoid buttress, and the anterior part of the coracoid; it now appears to be smaller than E.M. 37R plus 39R (Huxley, pl. VIII, figs. 1 and 2). This, however, is illusory, due to the degree of abrasion suffered by this bone, the glenoid lip and medial edge of the coracoid being badly worn. It should be borne in mind that the original specimen is a negative, with the limitations imposed by such a mode of preservation. Thus the apparently shallow character of the glenoid is due to the breakage and abrasion of the projecting piece of matrix which filled it; the impression surface is gone. Both of the above scapulocoracoids are considerably flattened, the true curvature of the girdle being shown by R 4784.

In smaller specimens the posterodorsal apex of the scapula ends more acutely; possibly there was a cartilaginous suprascapula which became fully ossified in the larger individuals. The rather indefinite dorsal margin of G.S.M. 90910 favours this suggestion. The straight central portion of the posterior margin is interrupted by the triceps tubercle, located about 6 cm above the glenoid in the larger examples. Above the acromion a narrow shelf on the

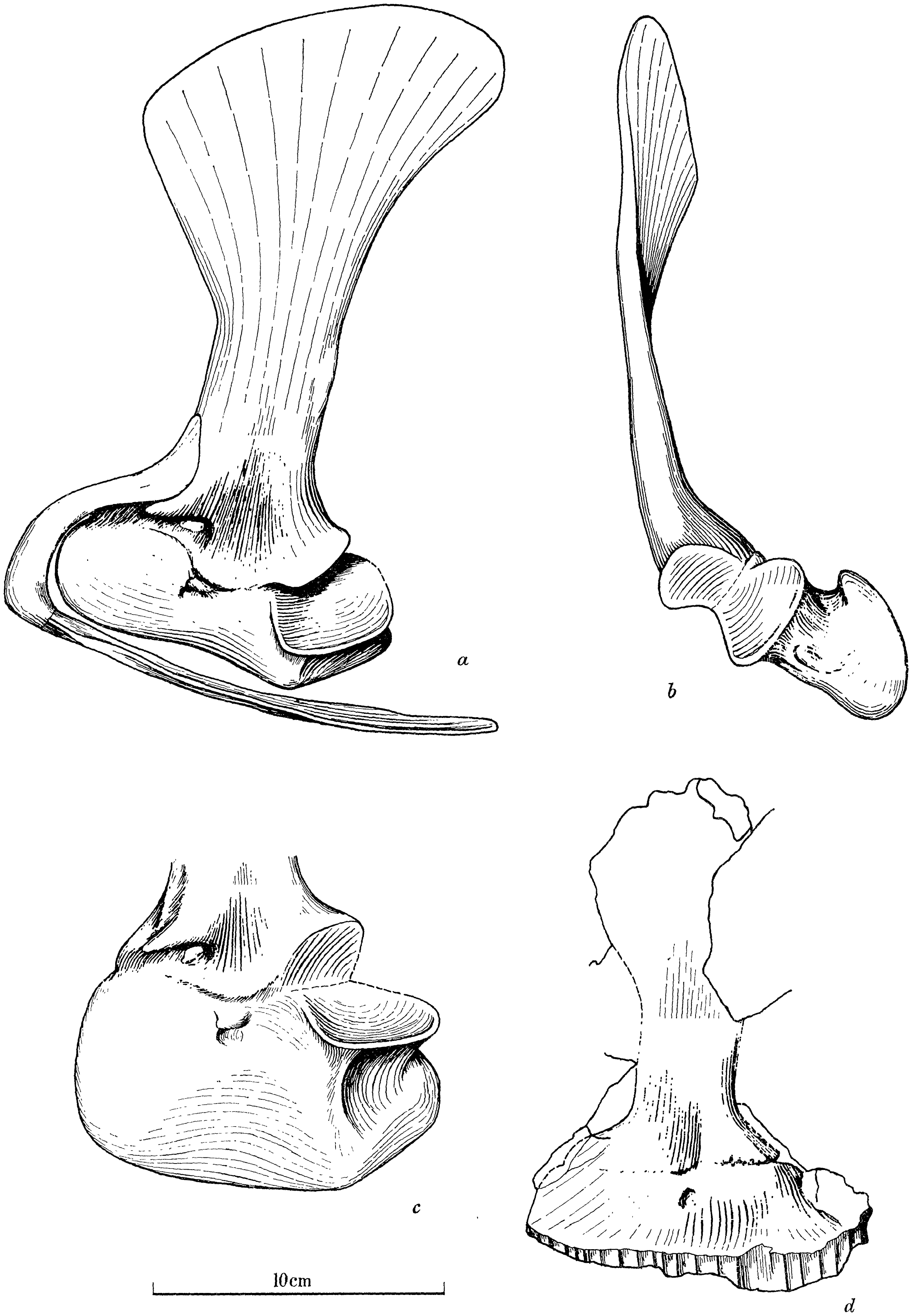

FIGURE 12. *Stagonolepis robertsoni* Ag. (magn. × ½). Shoulder girdle. *a*: restoration of girdle in left side view, mainly from R 4784, apex of scapula from G.S.M. 90853, interclavicle from G.S.M. 90848 (enlarged). *b*: rear view of scapulocoracoid, R 4784, E.M. 20R (enlarged), G.S.M. 90850 and G.S.M. 90853. *c*: outer view of coracoid and lower part of scapula, R 4784, E.M. 37R and G.S.M. 90850. *d*: inner view of incomplete cast of right scapulocoracoid, R 4784 (a little reduced).

anterior edge of the scapula received the outer part of the clavicle. The glenoid is best seen on R 4784. The coracoid contributes a large, shallow oval area forming a prominent overhanging lip. The glenoid of G.S.M. 90850 is interrupted by a slight ridge anteriorly, as noted by Case (1922) for *Desmatosuchus*; this region is not well preserved on other specimens.

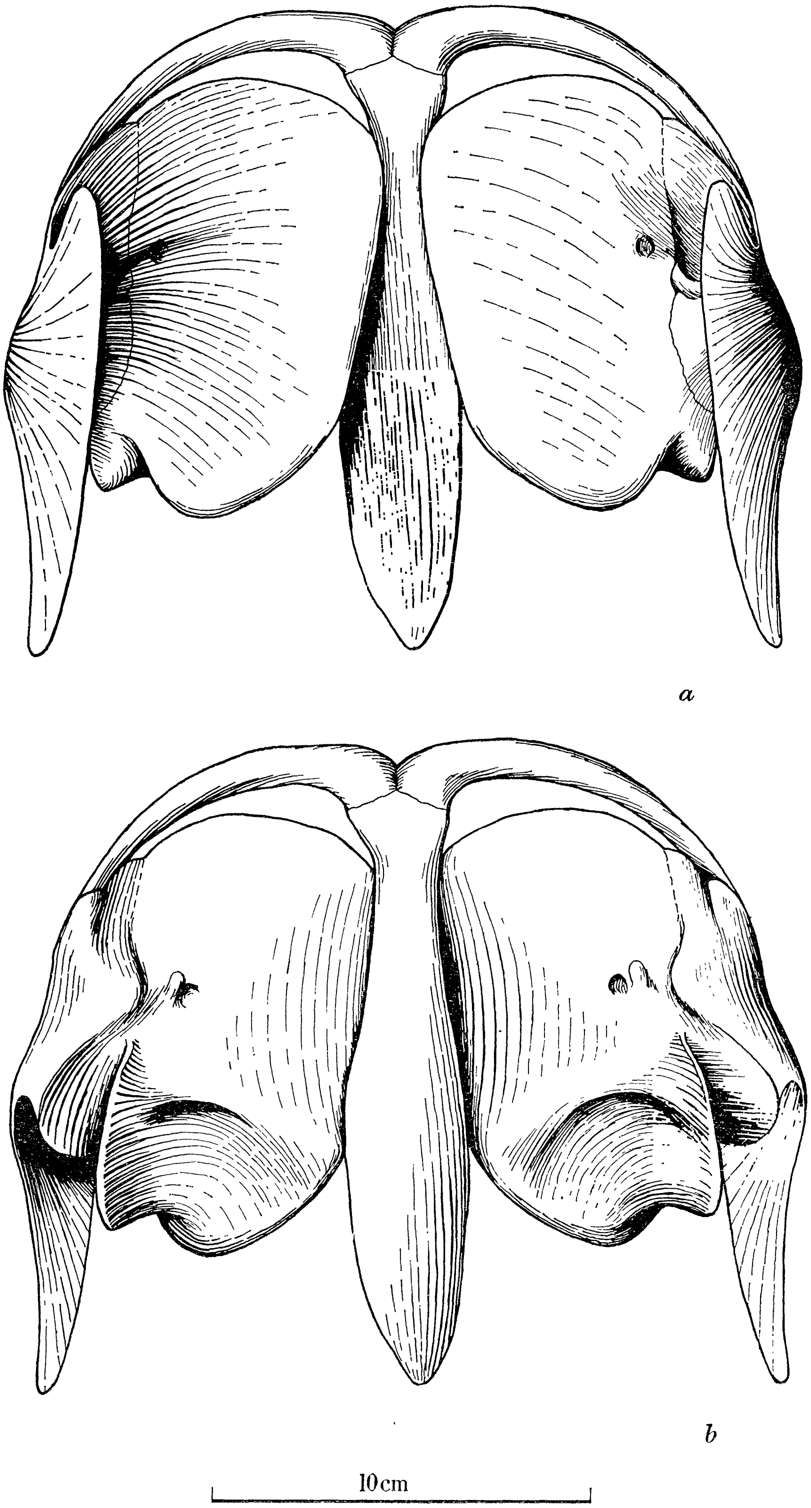

FIGURE 13. *Stagonolepis robertsoni* Ag. (magn. $\times \frac{1}{2}$). Restoration of shoulder girdle. *a*: dorsal view; *b*: ventral view. Based on same specimens as figure 12.

The coracoid as a whole is gently convex downward. It is perforated upward and inward by the foramen. Beneath the glenoid lip lies a depressed area bounded in front by a stout pillar which makes a slight projection in the medial margin and thus divides the outer surface into two areas. Posteriorly a deep incision passes obliquely beneath the glenoid lip.

About 7 cm of the medial part of the right clavicle is preserved on R 4784. It is a curved, stout bone with a thick proximal portion and a tapering shaft. A rounded, hook-like projection articulated with the interclavicle. The latter is dagger-shaped, the anterior end bearing anterolateral pits to receive the medial processes from the clavicles; the blade is thin and slightly convex downward, with a few longitudinal ridges on both surfaces. The only complete example (G.S.M. 90848) is isolated and is here assumed to be of the smaller size-group since it seems to be too short for the larger coracoids. In *Aëtosaurus ferratus* and in the pseudosuchians figured by von Huene (1942) the interclavicle is clearly longer than the coracoid.

Fore-limb

The fore-limb is much shorter than the hind, the humerus being about two-thirds the length of the femur, and when the lengths of the radius and tibia are added to these the same proportion is maintained. The manus is short and broad, the carpus poorly represented, some elements perhaps remaining cartilaginous. Portions of twelve humeri, two radii, four ulnae and four mani are known. Huxley, with some reservations, identified as the humerus of *Stagonolepis* one of the bones on the large slab E.M. 26R (his pl. VIII, fig. 7). This is the ventral surface of a femur; so also is the larger 'humerus' (G.S.M. 90855) which he mentions. The new specimens enable better figures of the humerus to be given, that figured by Huxley (pl. X, fig. 7) being somewhat worn.

The proximal end of the bone is gently convex dorsally in the anteroposterior direction and slightly concave longitudinally. The surface curves sharply down in front to the deltopectoral crest, and forms posteriorly a slightly upturned projection behind the articular region. The latter is not fully known and was tipped with cartilage.

The slender shaft is somewhat dorsoventrally compressed. The distal end of the bone is rather flat on top and strongly roughened. Anteriorly there is a deep ectepicondylar groove curving sharply round from the ventral surface and dying out on the shaft. It is bounded below by a sharp supinator process whose flat lower surface is continuous with the underside of the bone. The shaft is twisted through about 30°, so that the distal end faces backward as well as upward.

The radius is a straight-shafted bone, neither of the two examples of which is well preserved. The shaft is of oval cross-section. The ulna is widely expanded proximally with a large olecranon process, the dorsal surface of which is striated longitudinally. The ventral side of this end is deeply excavated. Part of the proximal articular area is seen on G.S.M. 90854, presenting a broad, smooth curved surface which is somewhat twisted in medial view. The distal end appears to have been finished in cartilage.

The manus is much smaller than the pes, the probable phalangeal formula being 2, 3, 4, 5, 3. Claws are present on at least the first three digits. Digits II, III and IV are of almost equal length with III perhaps the longest, I and V being considerably shorter.

Few of the carpals are identifiable. Between the distal ends of the radius and ulna and the proximal ends of the metacarpals (M.C.Z.D. 1) are two irregularly shaped bones showing rough under-surfaces. One of these is about 25 mm broad and lies opposite the proximal ends of metacarpals I and II and part of III. It evidently corresponds to the transversely elongated 'radiale' (radiale and intermedium fused?) seen in *Aëtosaurus*

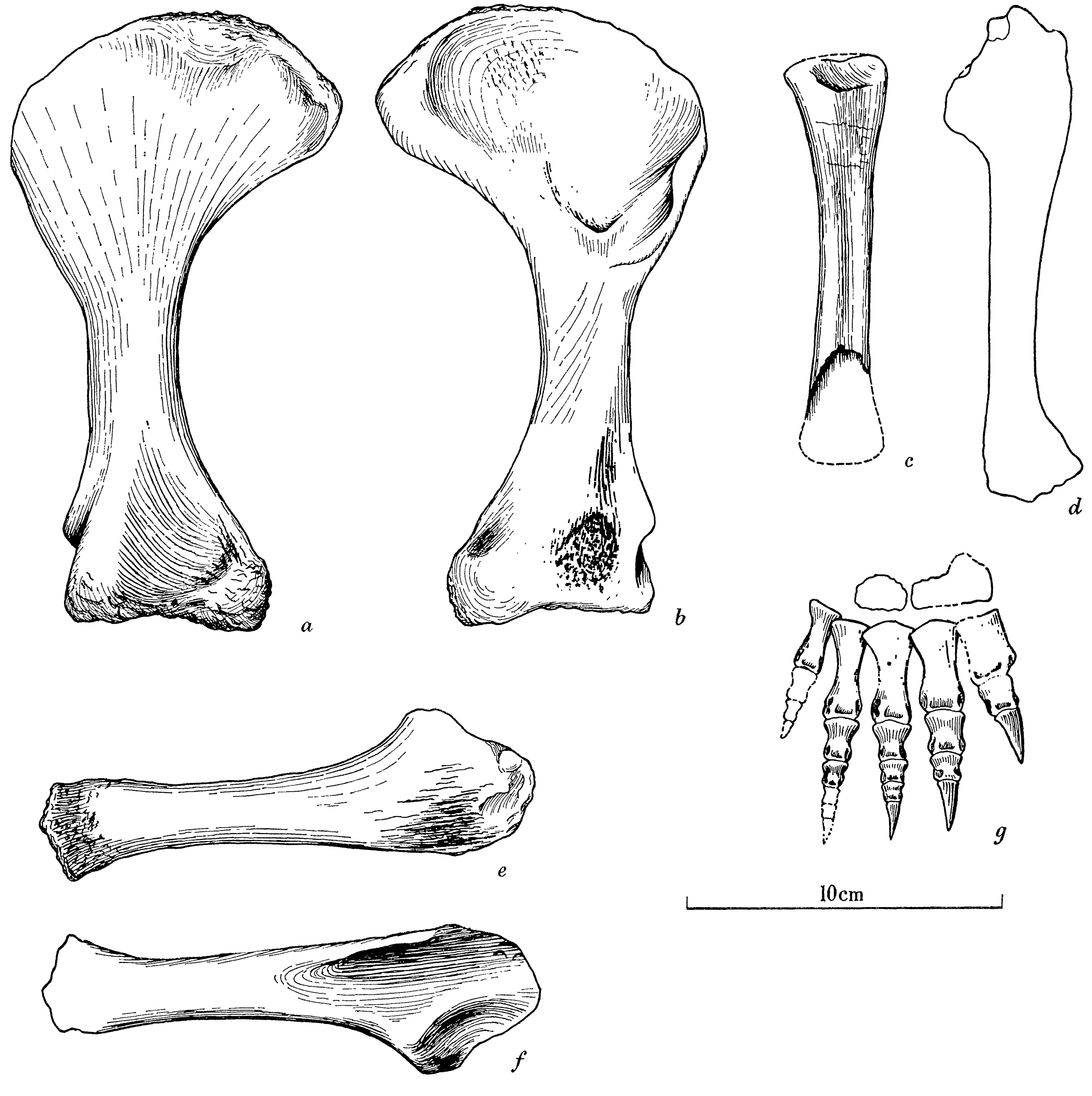

FIGURE 14. *Stagonolepis robertsoni* Ag. (magn. $\times \frac{1}{2}$). Fore-limb. *a*, *b*: dorsal and ventral views of left humerus, proximal end horizontal, mainly drawn from G.S.M. 90858 and R 4784, with minor additions from other examples. *c*: dorsal surface of crushed left radius, M.C.Z.D. 1. *d*: outline of distorted left ulna of same specimen. *e*: dorsal view of same, corrected for distortion. *f*: ventral view of same, proximal articular surface added from G.S.M. 90854. *g*: restoration of right manus, E.M. 13W, E.M. 26R and M.C.Z.D. 1.

ferratus and *Typothorax meadei* (Sawin 1947). The other element lies proximal to the outer part of the 'radiale', overlapping it a little and extending a short distance beyond it laterally, so that it is between the 'radiale' and the distal end of the ulna. It may originally have lain lateral to the 'radiale' and the subsequent folding of the manus in this specimen has perhaps displaced it. It is about 16 mm wide.

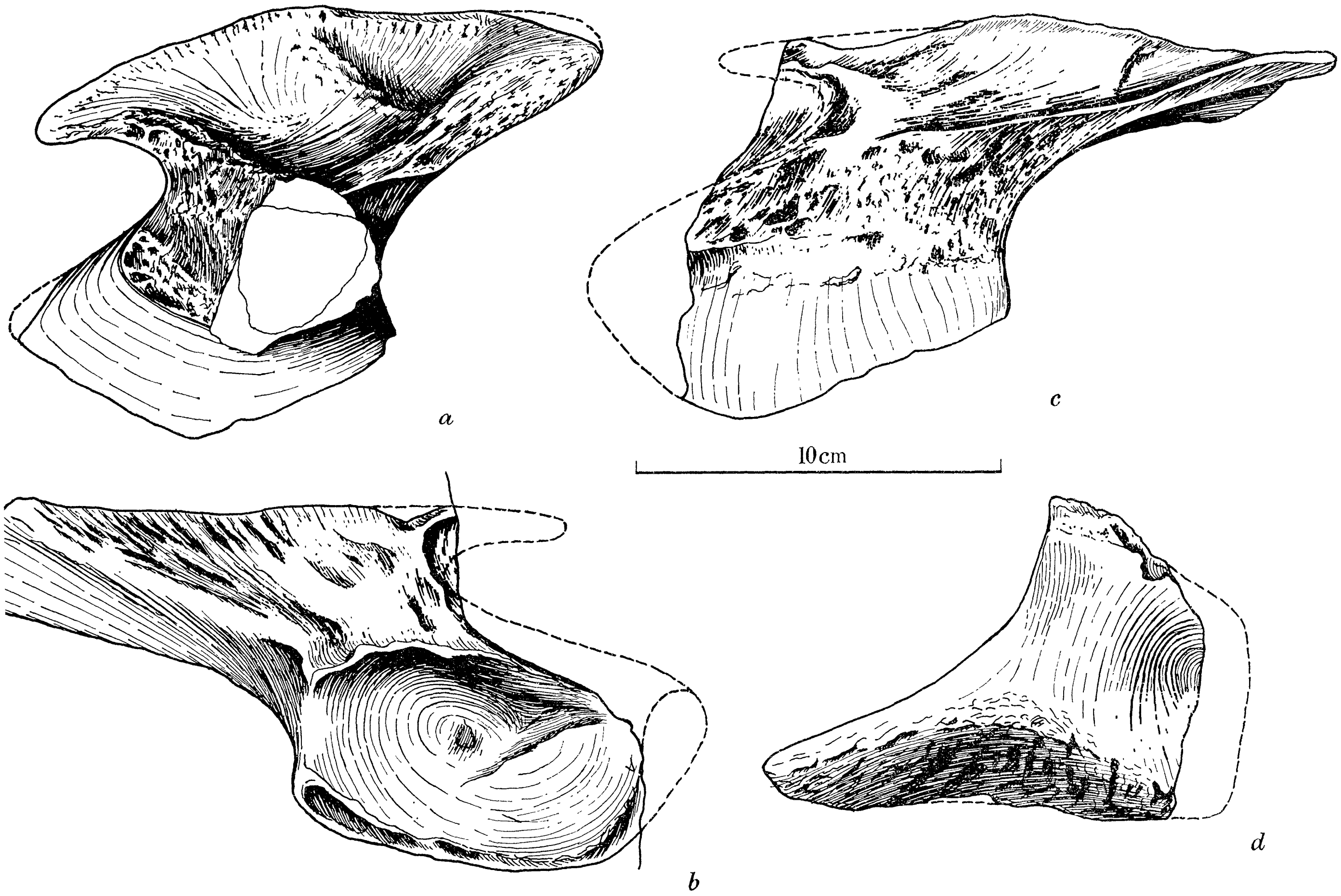

FIGURE 15. *Stagonolepis robertsoni* Ag. (magn. × $\frac{1}{2}$). Pelvic girdle. *a*: inner view of right ilium, partly obscured by scutes, R 4789; *b*, *c*: outer and inner views of distorted right ilium, R 4788; *d*: inner view of left ischium, R 4790, outline completed from R 4799.

E.M. 13W shows the distal end of the left ulna, and close to it are metacarpals II and III of the left side. The remaining bones, which at first sight appear to be the remainder of this manus, prove on closer inspection to be the five metacarpals and many of the phalanges of the right manus, together with some possible incomplete carpals, the small bones of digits II, III and IV being almost in articulation. Three ungual phalanges are preserved on this slab, the best being on the second digit. It is a large, compressed, curved claw, convex on its medial surface but flattened laterally and ventrally. From this specimen it can be seen that there were two, three and four phalanges on the first three digits, respectively, the terminal ones being ungual. Digit IV bore at least three phalanges, while those of V were not reached by the casting medium. M.C.Z.D. 1 shows that phalanges were present on digit V, but preservation is so poor that their number cannot be ascertained.

Pelvic girdle

The pelvic girdle is typically pseudosuchian in that the acetabulum is closed and the pubes descend almost vertically. The ilium exceeds the ischium in size: it has already been pointed out that the association of the small ilium G.S.M. 90852 and the larger ischium G.S.M. 90851 is anomalous. The proportion of ilium to ischium is attested by associated specimens of the smaller size-group (R 4789 and R 4790 which are counterpart slabs); by the fact that the same proportion obtains between the larger ilia and the ischium mentioned above; and by various other associations by which it is abundantly, albeit indirectly, confirmed. The proportional size of the pubis is also well authenticated and proves to be the same in both size-groups.

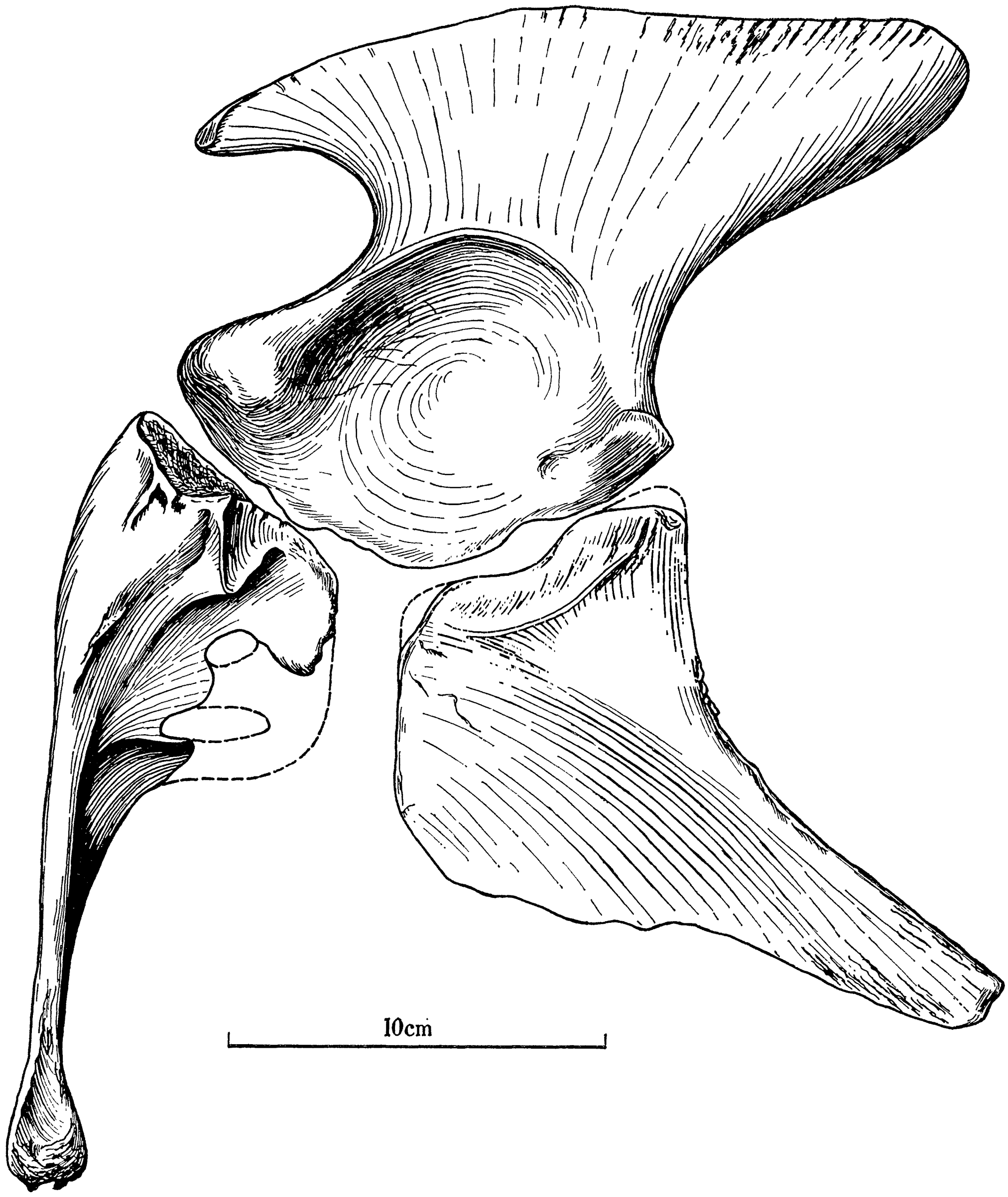

Figure 16. *Stagonolepis robertsoni* Ag. (magn. × $\frac{1}{2}$). Pelvic girdle in side view. Ilium mainly from G.S.M. 90849, posterior end of blade from E.M. 46R, anterior projection from R 4789/4790 (enlarged). Pubis from R 4793, area in broken lines from M.C.Z.D. 4 (enlarged). Ischium from G.S.M. 90851, rugosities on posterior margin from R 4804.

The pubis has the typical pseudosuchian 'twist'; an interesting feature is the presence of two foramina. The symphysis is complete, extending from the distal parts of the pubes to the tips of the ischia, with probably a small (?cartilaginous) fenestra centrally. The ischial symphysis is particularly strong: casts of a pair of ischia (R 4790) fit together well and show that the angle of junction was about 50°. The posterior parts of the pubes probably met at a similar angle, but the lateral margins of the descending portions were roughly parallel.

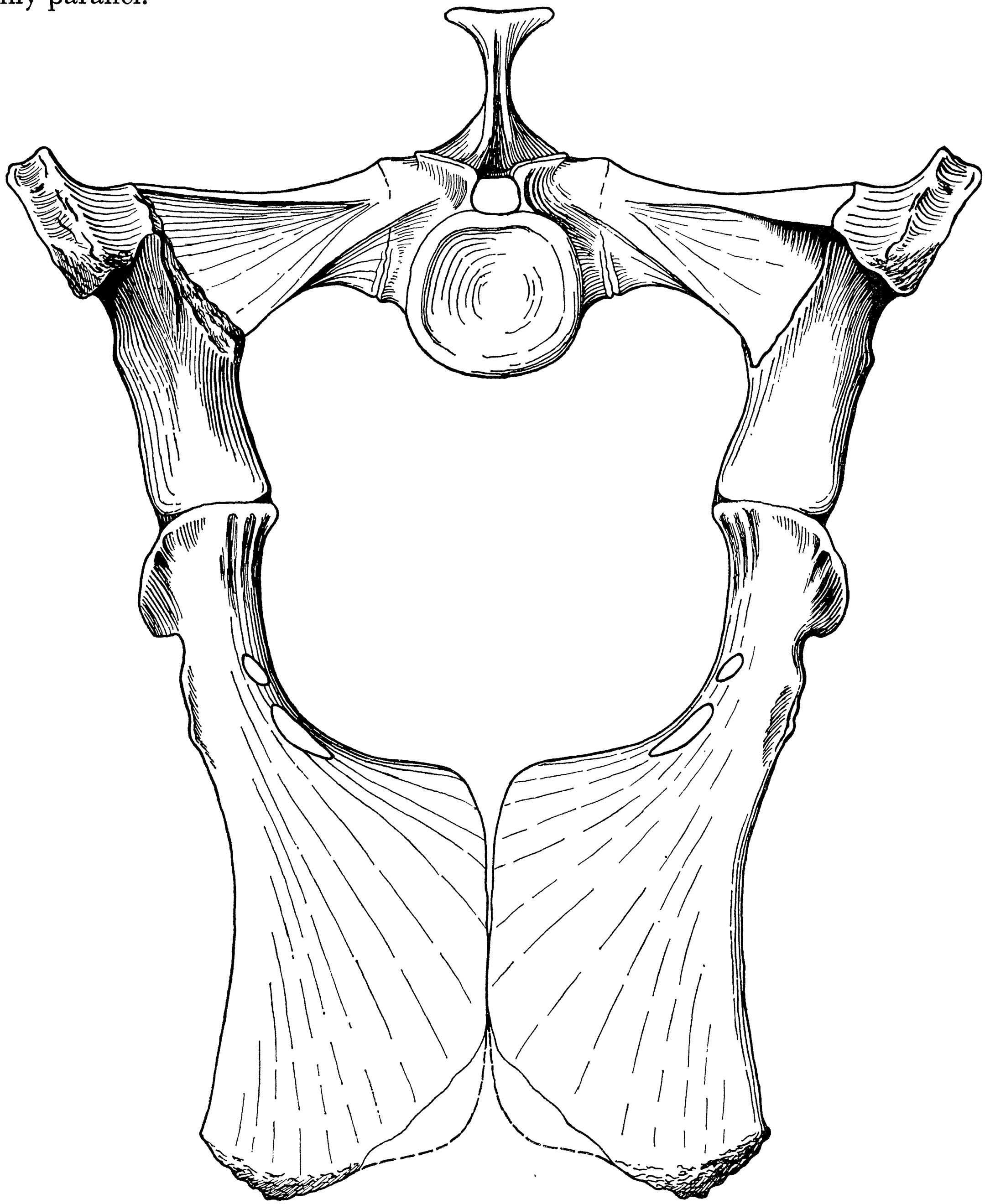

FIGURE 17. *Stagonolepis robertsoni* Ag. (magn. × $\frac{1}{2}$). Restoration of pelvic girdle and sacrum in anterior view. Ilium from R 4789/4790 (enlarged), pubis from R 4793, first sacral vertebra reconstructed from that of G.S.M. 90884. The extremity of the right sacral rib has been left incomplete anteriorly so as to reveal the inner profile of the ilium.

Ten ilia are available, of varying degrees of completeness. The most important new specimen is R 4789 plus R4790 (counterparts) (figure 15*a*), which is the only specimen to show the correct form of the anterior projection, the examples figured by Huxley being incomplete. R 4788 (figure 15*b* and *c*) is a curiously distorted bone which for various reasons is thought to belong to the R 4784 group of specimens.

The crest of the ilium is prolonged in front into a somewhat recurved process which is flattened above and below. The posterior projection curves a little outward; below it there is a broad face looking downward and outward. A large part of the medial surface is rugose, serving for the attachment of the sacral ribs in the region of the 'neck'. Above this area lies a longitudinal concavity along the inner side of the blade.

Parts of seven pubes are preserved. Of these only G.S.M. 90857 has been previously described (von Huene 1902, 1908*a*, 1911 *a*) and this unfortunately is a distorted specimen, the twist having been exaggerated. The proximal end of the pubis is roughened for cartilaginous contact with the ilium; a broad anterior area met the anterior buttress of the ilium and tapered rapidly posteriorly. The acetabulum is continued on the pubis by a strong buttress with a sharp external rim, presenting a smooth external face directed backward and somewhat outward. A sharp ridge arises from the lateral surface of the pubis in front of and below the buttress and merges distally with the margin. The upper pubic (obturator) foramen appears to be the homologue of the single one normally found. It passes outward and forward close to the buttress. The second or thyroid fenestra is larger and more ventrally placed; in this region the bone is very thin. The distal portion of the pubis forms a transversely disposed sheet which is slightly convex forward. The lateral margin is thickened, increasing distally to form a blunt terminal peduncle.

Of the eight ischia, the pair already mentioned are important as showing the symphysis. One of these is illustrated by figure 15*d*. The thin ventral margin of G.S.M. 90851 noted by Huxley (1877, pp. 31, 32) is probably due to abrasion since the associated scapulocoracoid has certainly suffered in this way. In unabraded specimens (e.g. R 4804) the acetabular lip is quite sharp. The acetabulum appears to have occupied relatively less of the ischium in the smaller animals, seeming to be absent altogether from R 4799. The dorsal margin is truncated obliquely on the inner side by a well-defined rugose area for attachment to the ilium. The posterodorsal edge is rounded off, the middle part having a rough area for muscle origin. Along the upper part of the posterior process an area inclined obliquely to the symphysis meets its fellow of the opposite side to form a flat surface facing upward and backward.

Hind-limb

The material now available includes twelve femora, four tibiae, eight fibulae and parts of nine pedes. The 'tibia' doubtfully identified by Huxley (G.S.M. 58327, pl. X, fig. 8) is the upper surface of a left femur lacking the condyles; the head of the bone is that which he described as the distal end. He also mistakenly regarded the broad end of the left femur E.M. 46R (pl. VI, figs. 2, 2*a*, reversed) as the head of the bone. The dorsal side (which he figured) of this specimen had crumbled so badly in the meantime and was in any case so crushed that it provided little information of value; accordingly the remaining bone was removed and a cast of the cavity yielded a complete but somewhat distorted ventral surface. The original of Huxley's pl. VII, fig. 8 has not been found and it seems likely that this is but a different drawing of the same bone.

The upper surface of the femur shows distally a very broad, low outer condyle, separated by a slight depression from the small inner condyle. The shaft makes a decided lateral projection opposite the fourth trochanter; proximal to it the margin is thin, with a shelf-like depression parallel to the edge. Interrupting the rough proximal surface of the head there occurs an ill-defined oblique groove. Ventrally the head is gently concave, with a thickening of the rim tending to divide it into two separate areas.

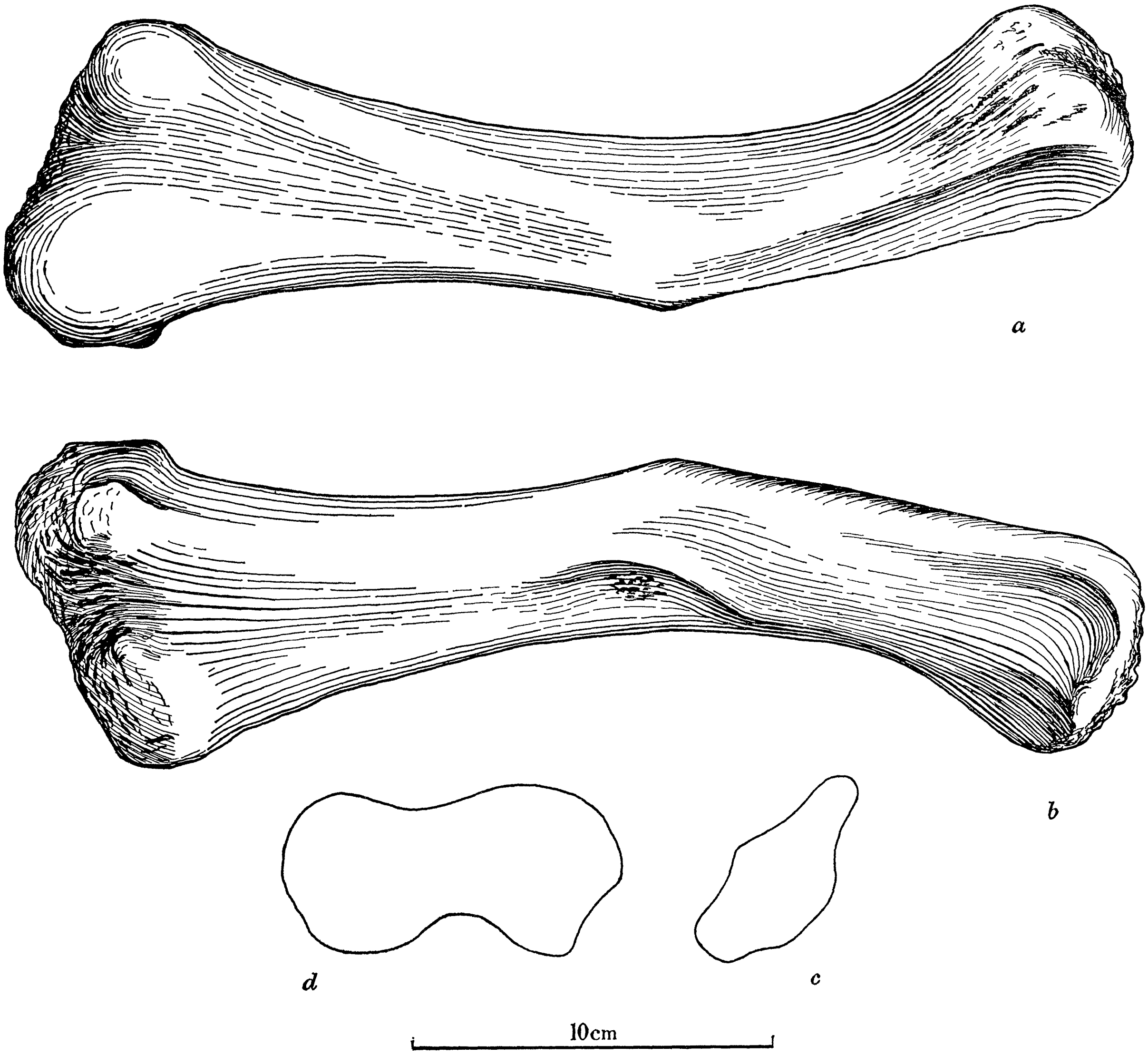

FIGURE 18. *Stagonolepis robertsoni* Ag. (magn. $\times \frac{1}{2}$). Left femur. *a*: dorsal view, G.S.M. 58327, M.C.G.D. 1 (enlarged), distal end from E.M. 34R and E.M. 'A' (both enlarged). *b*: ventral view, E.M. 46R, E.M. 26R (enlarged), and B.M.N.H. 36399 (enlarged). *c*, *d*: outlines of proximal and distal ends.

On the undersurface the inner condyle is about twice the width of the outer, the reverse of the situation on the upper side. Even in the largest examples the entire distal end is strongly roughened. Opposite the lateral condyle a distinct shelf projects distally and continues round to the lateral side of the bone where it presumably articulated with the head of the fibula.

The ridge-like fourth trochanter arises abruptly about two-thirds up the shaft, with a gradual proximal descent towards the medial margin. Measurements of the position of the fourth trochanter tend to show that it is placed a little further down the shaft in the larger individuals.

The tibia is a straight, stout bone with expanded proximal end, details of which are lacking. In G.S.M. 90901 there seems to be a groove passing obliquely downward and backward just below the proximo-medial corner, but preservation is poor. R 4786 shows the distal end with the astragalus lying close by. The distal articular surface is divided into two regions: a larger medial area with deep transverse rugae faces somewhat anteriorly as well as ventrally; about two-thirds from the medial side this face becomes smooth and curves rapidly dorsally and posteriorly so that it is inclined backward at about 45°. The distal margin on this side is thus a sharp edge formed by the intersection of this surface with the anterior face of the bone.

It is evident from the form of the distal end, and from the corresponding face of the astragalus (which fits it closely) that, even allowing for the interposition of cartilage, movement between the two must have been very limited.

Both outer and inner aspects of the fibula were figured by Huxley (1877, pl. VII, fig. 9 reversed, and pl. VIII, fig. 4 inverted and reversed). The head is oval in outline, inclined somewhat medially and overhanging a little posteriorly. The large lateral trochanter makes a decided interruption of the anterior margin a little above mid-height; it varies in form, being broad and low in most specimens (for instance G.S.E. 4794), but high, narrow and ridge-like in one (R 4792 plus R 4797). Both the examples quoted are of the larger size-group. Below the trochanter the medial surface becomes concave, terminating distally in a prominent shelf which tapers posteriorly and no doubt articulated with the astragalus. The surface for the calcaneum is a slightly concave oval area, elongated from before backward.

The only direct evidence regarding the nature of the tarsus is provided by R 4786 which has part of the left astragalus, and M.C.Z.D. 13 which shows part of a crushed tarsus and pes. In R 4786 only the anterior, medial and upper surfaces are represented. The bone appears to be an anteroposteriorly compressed hemisphere with an ascending lateral process. The front surface is irregularly rounded, the medial deeply sculptured with pits and ridges. The tibial articular surface is concave, rising laterally and to a thin, high rim behind.

R 4797 (which shows part of the pes) fits on to R 4786, the proximal end of metatarsal I being almost in contact with the astragalus with which it evidently articulated directly.

Before the bone was removed from M.C.Z.D. 13 the proximal ends of the metatarsals could be clearly distinguished; the specimen was photographed and their outlines marked on the print. The soft, indistinct bone was then cleaned off and a cast made, from which figure 19*e* is drawn. The crushed astragalus again lies immediately proximal to metatarsal I, and the hooked fifth metatarsal can be clearly seen. Between these bones and the proximal ends of the other metatarsals (which overlie one another) are two ill-defined patches of bone. The smaller, more distal of the two probably represents the medial distal tarsal, and

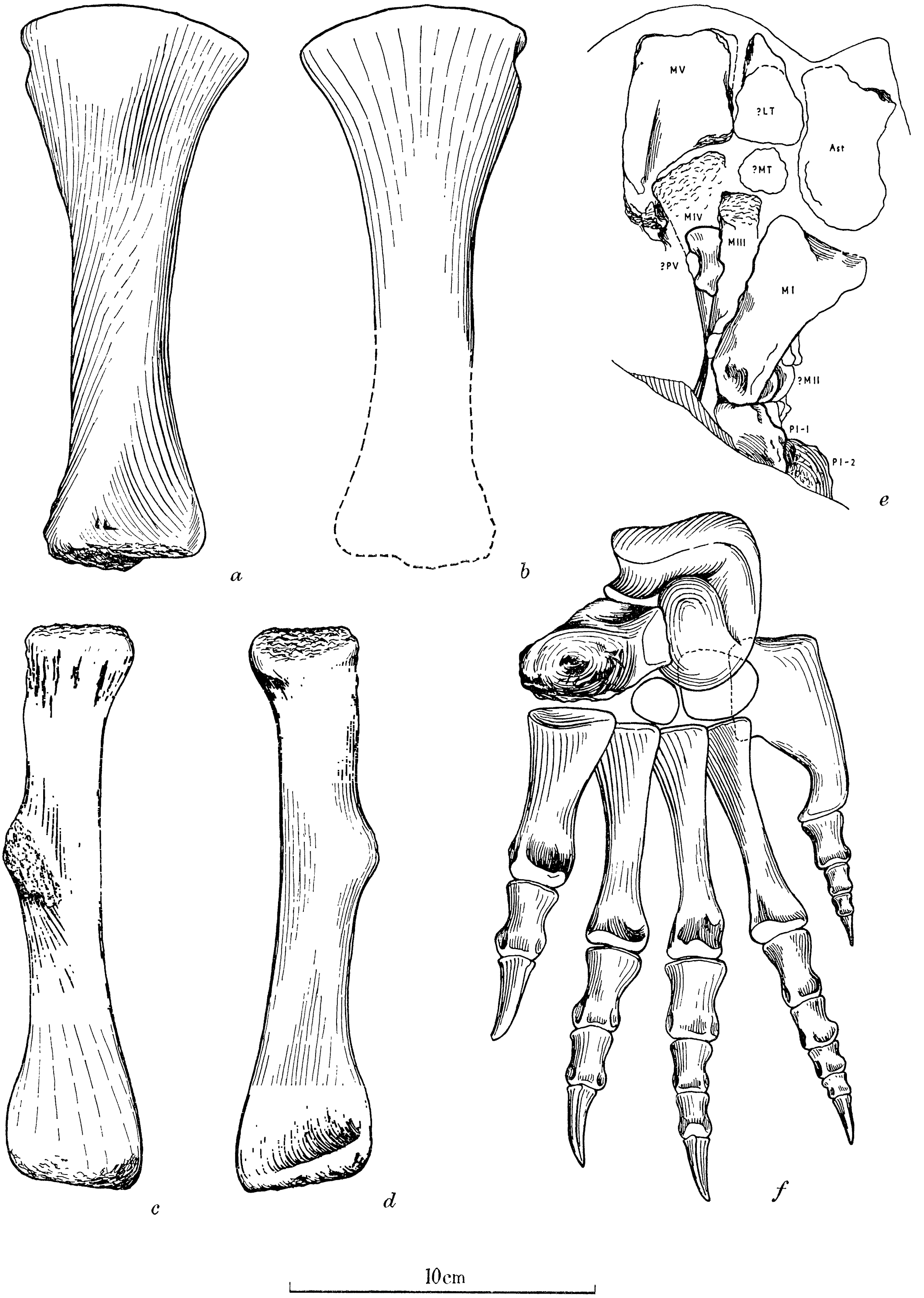

FIGURE 19. *Stagonolepis robertsoni* Ag. (magn. × $\frac{1}{2}$). Hind limb. *a*, *b*: anterior and posterior views of left tibia; *a*: G.S.M. 90901 (enlarged) and R 4786 (distal end). *b*: M.C.Z.D. 3 (slightly enlarged). *c*, *d*: lateral and medial views of left fibula; *c*: E.M. 33R, with details of proximal end from R 4797; *d*: E.M. 26R (enlarged). *e*: sketch of a cast taken from M.C.Z.D. 13, showing the underside of a crushed left pes. *f*: restoration of left pes, M.C.Z.D. 3, 10 (both slightly enlarged), M.C.Z.D. 13, R 4786, 4792, 4797, E.M. 48R. Outer part of astragalus and entire calcaneum from *Aëtosaurus ferratus*.

the larger the lateral distal tarsal. Part of the calcaneum may perhaps be included in the latter.

It is assumed, by analogy with *Aëtosaurus ferratus* and *Typothorax meadei* (Sawin 1947) that the tarsus comprised four bones, namely the astragalus, the calcaneum and two distal tarsals of which the outer was the larger. In these animals the joint is typically crocodilian, and in view of the very close relationship between these two forms and *Stagonolepis* (which will be demonstrated), there can be no doubt that the ankle-joint in the Elgin form was of the same type. Clearly, in *Stagonolepis*, movement between tibia and astragalus was strictly limited, but on the other hand the concave distal end of the fibula presumably moved freely over a convex facet on the calcaneum. This type of joint is found in crocodiles, where the tarsal joint is mesotarsal on the tibial side and crurotarsal on the fibular side. The prominent medial shelf at the distal end of the fibula of *Stagonolepis* probably met the lateral extension of the astragalus and served to hold the fibula in correct position above the calcaneum.

The first metatarsal is short and stout, with a broad proximal end tilted in the usual manner to overlap its neighbour. Metatarsals II, III and IV are progressively more slender. The proximal ends are broad and steeply inclined laterally. The usual dorsal depression behind the distal end is continuous with the lateral tendon-pit in these metatarsals. The base of metatarsal V is very wide where it presumably met the large distal tarsal.

M.C.Z.D. 10 shows all the metatarsals and phalanges of the right foot. The first three claws are very strong, decreasing in size laterally. They are convex medially and flat laterally and ventrally like those of the manus. The fourth claw is only half as long as the third, and this digit is equal in length to the second. There are four phalanges on digit V, the two distal ones being extremely small. The incomplete terminal phalanx appears to be ungual.

As they lie in the matrix, the phalanges of digit V diverge laterally, but they are not in correct articulation. The fifth metatarsal in the two known examples is not divergent and it seems unlikely that this weak fifth digit stood out very much from the others. In at least four examples of *Aëtosaurus ferratus* which has a very similar pes, digit V is approximately parallel to the others, and it has been so restored in *Stagonolepis*. It is also shown in this attitude by Sawin (1947) for *Typothorax*.

Dermal armour

The most abundant remains of *Stagonolepis* are the very numerous blocks which display scutes of various types. Unfortunately relatively few of these show segments of dorsal armour in natural articulation so that there are a few minor points concerning the arrangement of the plates which remain to be cleared up. Enough is known, however, both from articulated specimens and from comparisons with allied forms, to give a reasonably complete account of the dermal covering of the animal.

The dorsal scutes are arranged in four longitudinal rows comprising paired transversely elongated paramedian scutes flanked by quadrate lateral scutes. These rows extend from immediately behind the skull to the tip of the tail, undergoing various changes of size and shape.

Ventrally the region between the girdles was protected by thinner trapezoidal plates arranged in a definite pattern, there being a maximum of fourteen scutes in a row antero-posteriorly and eight transversely.

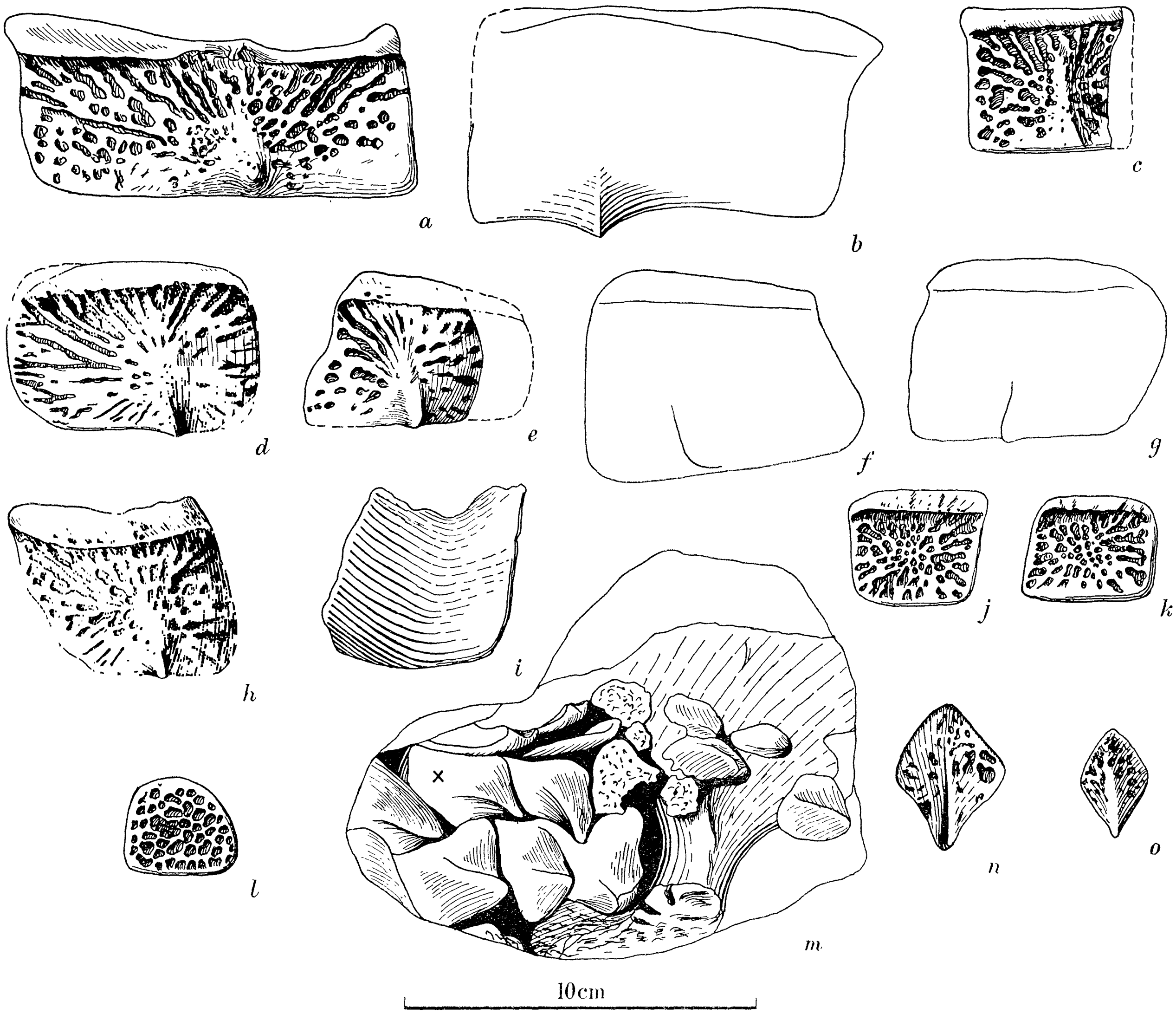

FIGURE 20. *Stagonolepis robertsoni* Ag. (magn. $\times \frac{1}{2}$). Dermal armour. *a*: left paramedian dorsal scute, R 4799; *b*: outline of right ?pelvic paramedian dorsal, E.M. 33R, boss completed from G.S.M. 90917; *c*: left caudal paramedian dorsal, R 4803; *d*, *e*: left and right lateral dorsals, E.M. 24R and 3R; *f*, *g*: outlines of left and right lateral dorsals, R 4785 and R 4789; *h*, *i*: outer and inner views of immediately prepelvic left lateral dorsals, E.M. 5R and 20R; *j*, *k*: belly scutes, E.M. 8R; *l*: anterior lateral belly scute, R 4789; *m*: segment of armour probably from thigh filling acetabulum of left ilium, R 4792; *n*: detail of scute marked '*x*' in *m*; *o*: a similar scute, R 4790.

Behind the pelvis there was probably a definite pattern of scutes in the cloacal region and behind this again four longitudinal ventral rows for a large part, if not all, of the tail.

The scutes of the dorsal and ventral series articulated with each other in the usual manner by means of a smooth anterior facet which was overlapped by the posterior edge of the preceding scute. There were no sutural unions between the scutes, nor does there seem to have been any lateral overlap between any of them. Between and behind the girdles the ventral armour probably came close to the lateral scute-rows.

The limbs were covered with an imbricating armour of small, thin, rounded plates, with a more definite organization in the thigh region.

No trace has been found of scutes bearing spikes or horns such as those described for *Typothorax* (Sawin 1947) and *Desmatosuchus* (Case 1922).

The scutes have been well described and figured by Huxley (1877) and the following remarks are confined to an amplification and correction of some points of his description.

Dorsal scutes

These correspond throughout to the vertebrae in number and position, there being no elongated cervical scutes as in the above-mentioned genera. In the paramedian dorsal scutes ('broad angulated scutes' of Huxley) the ornament radiates from an almost smooth area situated a little behind the middle of the plate on the line of angulation. The pits tend to be confined to the regions behind lines joining the radiation centre to the anterior corners; the grooves tend to occur in front of these lines. The posterior margin of the scute is usually smooth, but there is a tendency for this area to be invaded by pits in the larger individuals. The boss lies behind the centre of radiation, rarely coincident with it. In the smaller individuals the boss is low and does not reach the posterior margin. Some of the scutes from the larger animals have bosses of this type; others, almost certainly from the vicinity of the pelvis, have larger, sharper bosses which project a little posteriorly (figure 20*b*).

The lateral dorsal scutes (figure 20*d* to *i*) are similar to those of the median rows, but are never as wide. The articulatory shelf lacks the anterior concavity seen in some of the paramedian scutes, and the boss is more keel-like, falling away more steeply to the medial side. In scutes from the back region the boss trends obliquely posterolaterally and lies about one-third away from the medial margin, which has a sinuous outline corresponding to the lateral edge of the adjacent paramedian scute. The lateral edge is rounded off.

The cervical paramedian scutes have only faint ornament and lack knobs. Over the pelvis the ornament is most deeply incised and the knobs are most prominent. They disappear again in the caudal scutes (figure 20*c*) and the ornament becomes gradually fainter, while the breadth decreases so that the more posterior scutes are longer than broad.

The lateral dorsal scutes are gently arched in the cervical and dorsal regions. They become sharply angulated and keeled at the pelvis (figure 20*h* and *i*); behind this they probably revert to a condition like that of the dorsal region. In the more posterior part of the tail they become elongated and sharply angulated.

The 'narrow angulated scutes' of Huxley, which he wrongly states to have no articular surfaces, are here described as pelvic lateral dorsals.

The first two pairs of paramedian scutes lie in the embayment at the back of the skull, their anterior and outer margins overlapping the flanges formed by the parietals and squamosals. The faint ornament resembles incised lines rather than pits and grooves. The succeeding scutes broaden rapidly towards the shoulder region, the lateral row beginning at the third or fourth scute. The paramedians soon develop the projecting anterolateral corner, and the medial margin of the lateral scute becomes modified accordingly.

R 4785 shows lateral dorsal scutes in association with paramedians in the middle of the back. Some of these lateral plates (and also in isolated specimens) have the knob slanting posteromedially and are here interpreted as intermediate in position between 'normal' laterals and the pelvic laterals. Scutes of the latter type are sharply angulated about a median axis which is oblique to the articular facet, the scute being rhomboidal; this shape is acquired through the reduction of the part lateral to the keel so that at the pelvis length and breadth are equal. The assignment of these sharply angulated scutes to the pelvic or immediately prepelvic region is based on similarity to those of *Aëtosaurus ferratus*, *A. crassicauda*, and the un-named specimen described by Case (1932) in which they can be observed *in situ*.

The changes which occur in the scutes at and behind the pelvis are not well known, but it is reasonable to assume a close similarity to the forms mentioned above, particularly *A. ferratus*. In the case of this last form the paramedian dorsals contract somewhat in breadth immediately before the pelvis, afterwards regaining their former size; the lateral dorsals become sharply angulated in this narrow zone and afterwards flatten out to resume a shape like those of the back.

The four rows of scutes (of *Stagonolepis*) are maintained to at least the middle of the tail and most probably to its tip. By the middle of the tail the paramedians have become almost flat and the knob has gone leaving a smooth, slightly raised central and posterior area. These scutes (figure 20*c*) are almost perfectly rectangular and the anterolateral corner projects only slightly. They are flanked by narrow elongated lateral plates in which the keels increase in height as the scutes become narrower (R 4803; M.C.Z.D. 17, 18). Each plate has a longitudinal median keel rising up to a posterior point and falling more steeply to the medial side; at the posterior point the scute is very thick, and the inner surface only a little concave. The pattern on the lateral dorsal plates also dies out posteriorly.

The armour of the mid-caudal fragment described by Huxley (plates III and IV) does not give a true impression of the shape of the tail. The lateral dorsal scute-rows are missing, although evidence of their former presence is given by the shape of the anterolateral corners which are preserved on some of the paramedian scutes. The latter have been forced down against the ends of the transverse processes of the vertebrae, some of which are broken off, and the angulation of the scutes has been increased by cracking across their middles. The lateral edges of the paramedian plates rest on the upper surfaces of the ventral plates, and since the specimen is a negative, these junctions are lines of weakness. The missing lateral scutes and almost certainly a lateral ventral row also were in all probability in the (uncollected) counterparts.

The lower surface of the tail of *A. ferratus* bears anteriorly two rows of transversely broadened paramedian plates each flanked by a row of narrow lateral ventral plates. The paramedian plates narrow posteriorly as do the dorsals and all eight rows continue to the apex of the tail as narrow strips of bone. The close similarity of the known parts of the armour of *Stagonolepis* to that of *A. ferratus* suggests that a similar transformation occurred in the Elgin form.

Dimensions of some of the largest preserved paramedian plates are as follows (breadth first): 145 by 65 mm; 148 by 58 mm; 128 by 63 mm; 152 by 53 mm; another is 74 mm long. Associated bones show that these are of the larger size-group; scutes of the smaller size-group attain a breadth and length of about 115 and 50 mm, respectively. A lateral dorsal scute from the back region of a large animal measures 76 by 60 mm.

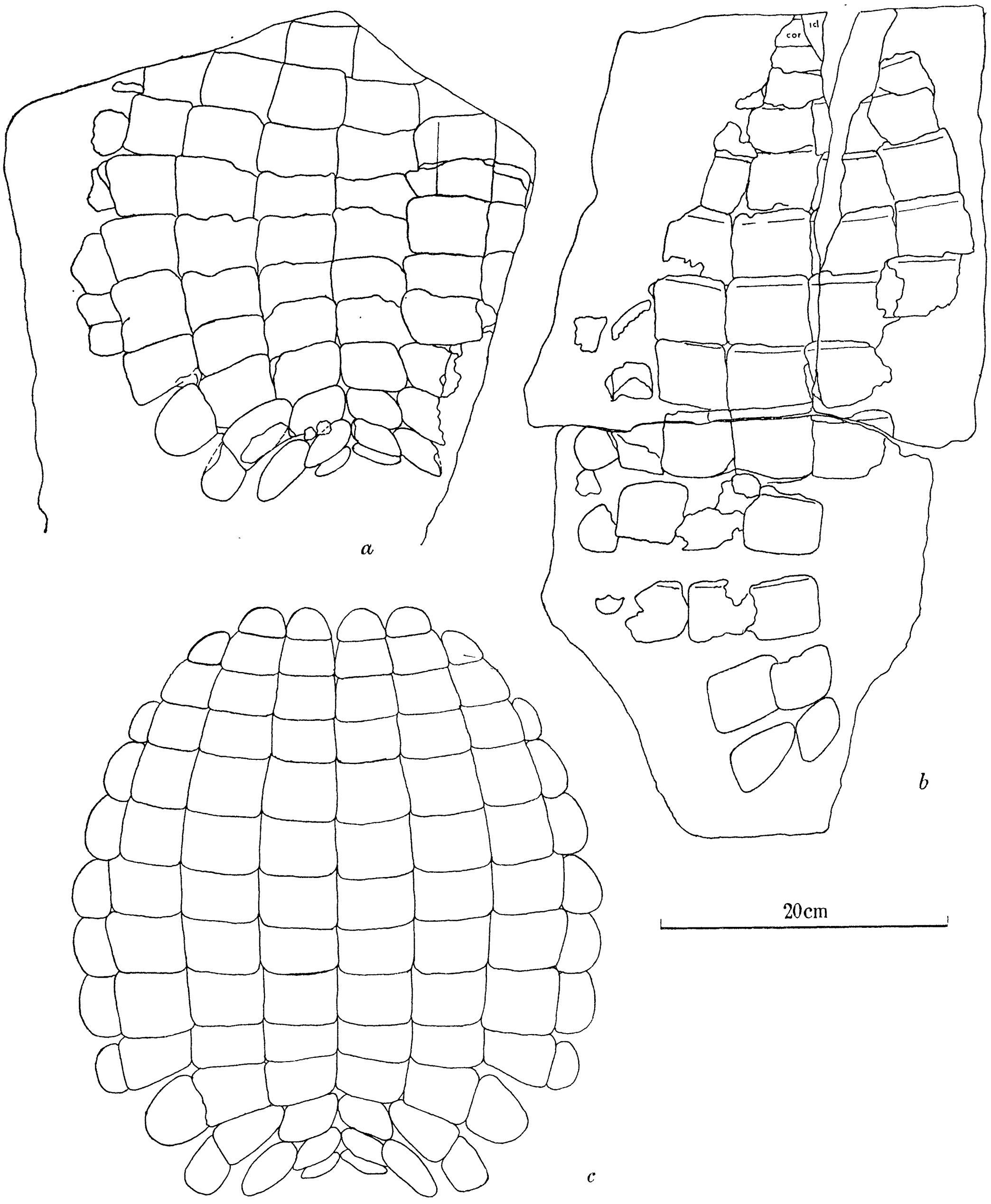

Figure 21. *Stagonolepis robertsoni* Ag. Outline drawings of the belly armour, one-fifth natural size. *a*: M.C.G.D. 2, seen from the visceral side; the most anterior (incomplete) scute probably belongs to the third transverse row. *b*: R.S.M. 1952.10.1, visceral side; additional anterior scutes are in counterpart slabs. *c*: diagram showing the arrangement of the armour between the girdles, spread out in the horizontal plane, based on the preceding specimens and M.C.Z.D. 1 and 2.

Ventral scutes

Many specimens show scattered ventral scutes, but there are in addition several blocks which display segments of armour with the scutes in articulation so that it is possible to make a full reconstruction of the armour in the region between the girdles. Evidence for the arrangement on the underside of the tail is much less complete and restoration relies to a large extent on comparison with *A. ferratus*.

The transverse rows of ventral scutes slightly outnumber the vertebrae in the belly region, whereas beneath the tail the dorsal and ventral scutes form rings corresponding to the vertebrae.

The shape and ornament of the ventral scutes has been well described by Huxley. A typical plate from the middle of the belly is broader than long, with the ornament radiating from the centre of the scute. Anteriorly in the series the ornament consists of subcircular pits centrally, becoming drop-like or elongated into grooves towards the periphery; the more posterior scutes develop a reticulate ornament with the areas between the pits reduced to dividing walls. The larger scutes, and those placed more posteriorly, show a tendency for the grooves to extend on to the margins, including the articulatory facet.

The arrangement of the scutes in the belly region (figure 21) is determined by combining several specimens. The first row consists of four small plates, rounded in front, and with the stem of the interclavicle wedging in along the mid-line almost to the second row.

Proceeding backwards the scutes increase in size and additional lateral rows are added as shown in the figure. The fourth to the tenth rows each have eight scutes, the outermost of which are longer than wide. The more posterior scutes gradually assume a rhomboidal shape and the rows become convex forward. The eleventh and twelfth rows each have six scutes, the thirteenth has four rhomboidal scutes, while the fourteenth consists of but two very small, slender rhomboidal scutes which are followed immediately (M.C.G.D. 2) by the distal ends of the pubes. There was thus a total of 90 scutes covering the belly region. Contrary to the statement of Huxley (1877, p. 15), no sutural unions have been observed between the scutes.

Behind the pelvic girdle there was probably a special arrangement of plates surrounding the cloaca, as in *Aëtosaurus*, but no specimen showing this region has survived.

Only two specimens provide evidence concerning the scutes beneath the tail. It has already been observed that one of these (R.S.M. 1891.92.529) does not give a true section through the tail; the two ventral rows shown by this specimen need not therefore be the total number. Although they are incomplete, the more anterior scutes convey the impression of being broader proportionately than those of the middle of the belly, which implies that, as in *Aëtosaurus*, there were two paramedian rows of broad scutes.

M.C.Z.D. 16 shows parts of five transverse rows of scutes. Those of the paramedian rows are almost square. Each is flanked by an almost vertical lateral row of which little is preserved. The paramedian scutes are extremely like those of the paramedian dorsal series, but the ornament is of the reticulate type never seen in dorsal scutes of *Stagonolepis*; passing backward they become a little more arched, and develop a low, smooth median keel differing from that of the dorsal scutes in that it is confined to the middle of the scute and has ornament behind it. This specimen is interpreted as showing the paramedian and lateral ventral scute-rows at about the middle of the tail.

M.C.Z.D. 17 may be the counterpart of the preceding specimen; it shows portions of a row of flat vertical scutes, perhaps the continuations of the lateral ventrals of M.C.Z.D. 16. Flanking these is a row of narrow, sharply angulated scutes interpreted as lateral dorsals, with again a very poorly preserved row of presumed paramedian dorsals alongside.

There is some evidence, therefore, which indicates that each scute-band in the middle of the tail was made up of eight plates, four being the continuation of the dorsal series and four lying ventrally, as in *Aëtosaurus ferratus*.

Abdominal ribs

It is convenient to deal with the gastralia here since they occur in close association with the belly armour. Specimens showing the smooth inner faces (or their impressions) of articulated segments of ventral armour also display abdominal ribs. They occur as forward-pointing chevrons of slender bone closely applied to the visceral surfaces of the scutes. Separation of the chevrons into smaller elements is not apparent.

In M.C.G.D. 2 the abdominal ribs appear to correspond in number to the ventral scute-rows; each passes out obliquely across three longitudinal rows. R.S.M. 1952.10.1 is unusual in that the gastralia run within the bone of the ventral scutes, appearing as ridges upon the inner surface. The ribs in this specimen are arranged irregularly, and although there seems to be a general correspondence in number to the scute-rows, many of the ribs appear to occur as parallel pairs.

Appendicular scutes

The limbs were protected by numerous small, rounded or oval plates with a faint ornament of scattered pits. These are to be seen pressed against the humerus, radius and ulna, and tibia. Some fragments near the metatarsals (M.C.Z.D. 13) indicate that part of the pes was also armoured.

The thigh region had a different type of plating. R 4792 (figure 20*m* and *n*) shows a segment of armour that has fallen into the acetabulum of the left ilium and is draped across the anterior buttress. There are at least eighteen small rhomboidal scutes closely packed in definite rows. Each scute is keeled along the long diagonal, extends at one end in a blunt process, and has an ornament of small, rounded pits. Similar scutes are scattered on other blocks.

Restoration of the skeleton

The following considerations have governed the making of the restorations (figures 22 and 23). A slight upward curvature of the neck is shown by Sawin (1947) for *Typothorax* and by Case (1922) for *Desmatosuchus*; it also occurs in the posterior cervical vertebrae of R 4784. The presacral column length is known from the same specimen, thus fixing the position of the pelvic girdle. The atlas and axis are partly restored after those of *Typothorax* and *Desmatosuchus*; the remainder of the vertebral column, with the exception of the end of the tail, can be reconstructed from available specimens. The number of caudal vertebrae has been taken as 43, the total inferred from the number of caudal scute-rings in *Aëtosaurus ferratus*. The ribs are largely hypothetical.

The ventral armour of one of the smaller individuals measures 40 cm between the girdles; this fixes the position of the shoulder girdle with respect to the pelvis, since the interclavicle ends between the first two paramedian ventral scutes and the pubes lie immediately behind the armoured region. This distance cannot be materially shortened without making the belly excessively deep.

A moderate amount of backward inclination has been given to the shoulder-girdle in order to allow the expanded blade of the scapula to lie over the first true dorsal ribs, and for the interclavicle to pass backward with a smooth curvature into the belly armour. Reconstruction indicates a body section somewhat deeper than broad in the shoulder region; it is assumed that the blade of the scapula ascended more or less vertically, curving somewhat medially at the tip. The separation at the coracoids is unknown but they probably lay not far apart, with the interclavicle a short distance below them lying on the underside of a mass of cartilage which united the coracoids. It is also assumed that the outer parts of the lateral dorsal scutes stood almost vertically; this is the case in *Typothorax* and *Desmatosuchus*, in which, however, the lateral scutes are sharply angulated throughout. Nevertheless, this assumption gives a breadth to the armour in the shoulder region of *Stagonolepis* which agrees very well with the restored girdle. The rather deep body section at the shoulder is borne out by restoration of the pelvic girdle and of the armour between the girdles.

The position and attitude of the pelvis is accurately determined by the sacral ribs and by the symphysis of the pubes and ischia.

The major limb-bones are not shown closely articulated with one another or with the girdles because of the evidence of cartilaginous terminations of unknown thickness to the principal bones.

In making the restoration of the dermal armour, data from *Aëtosaurus* has been freely drawn upon. M.C.Z.D. 2 shows that there is a region at about the fifth to the seventh paramedian dorsals where the scutes are more arched. A similar condition occurs in the former species. For the back-armour the largest-known paramedian and lateral dorsal scutes have been used for the broadest region. Enough scutes are known to make it clear that these are close to the maxima in breadth.

The variation in size and shape of the dorsal scutes is based on comparison of disarticulated plates with articulated ones of individuals of *A. ferratus*, together with information from such segments of the dorsal armour of *Stagonolepis* as are available.

The scutes surrounding the cloaca and on the underside of the tail are largely restored from Nos. XXI and XXII of the *Aëtosaurus ferratus* group.

VI. REVISION OF *AËTOSAURUS*

Two species of the genus have been described. In 1877 O. Fraas gave an account of the remarkable material discovered in the Stubensandstein (Upper Keuper) of Heslach, near Stuttgart, which he named *Aëtosaurus ferratus*. Von Huene has referred to this species on several occasions (1902, 1908*a*, 1914) and in 1920 he published a revision of the osteology which included a new restoration of the skull. Earlier, in 1907, from the same formation at Pfaffenhofen, E. Fraas had described as *A. crassicauda* part of a somewhat larger skeleton consisting of a sacrum and vertebrae with dermal armour in place. This paper also includes a restoration of the pelvis of *A. ferratus*. In 1921 von Huene gave a description of some bones and scutes which he referred to *A. crassicauda*; these are said to have come from the same quarry and horizon as the type specimen.

In order to make a valid comparison between *Stagonolepis* and *Aëtosaurus* it is first of all desirable to clear up some of the errors and deficiencies of the published accounts of both

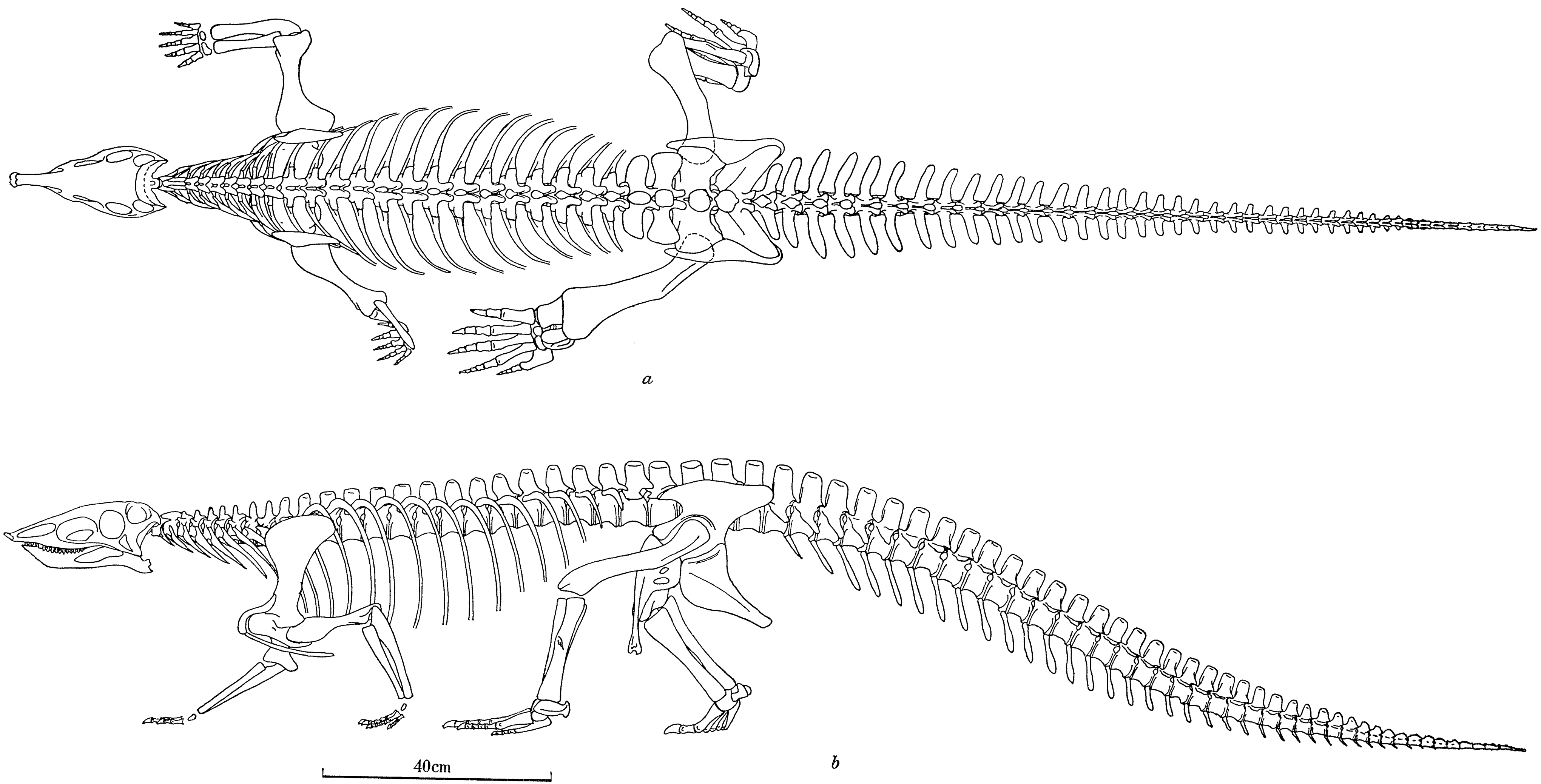

FIGURE 22. *Stagonolepis robertsoni* Ag. Restoration of the skeleton, dermal armour omitted. One-tenth natural size. *a*: dorsal view; *b*: left lateral view.

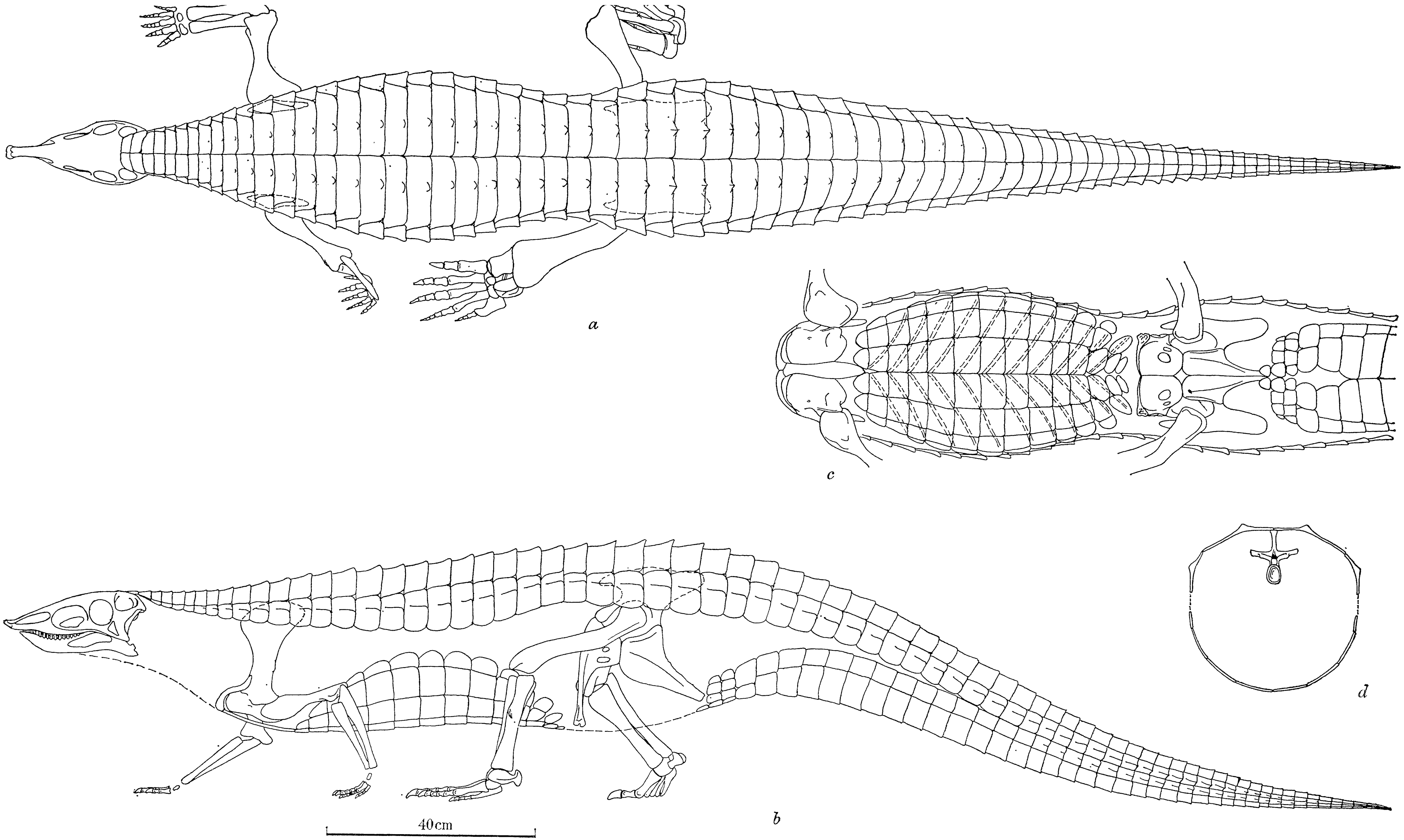

FIGURE 23. *Stagonolepis robertsoni* Ag. Restoration of the skeleton with dermal armour in place (appendicular scutes omitted). One-tenth natural size. *a*: dorsal view; *b*: left lateral view; *c*: ventral aspect from shoulder girdle to root of tail. Gastralia indicated by broken lines, cloacal region of *b* and *c* from *Aëtosaurus ferratus*. *d*: restored cross-section of the armour mid-way between the girdles.

the described species of the latter genus. The present study has shown that many important features of the skull of *Aëtosaurus* have hitherto been overlooked, and the following discussion aims at correcting these and other points rather than presenting a full description of the material.

(1) *AËTOSAURUS FERRATUS* O. FRAAS

(Figure 24*a*; plates 12 and 13)

The most important features requiring correction are as follows:

(*a*) Disposition of the bones surrounding the infratemporal fossa; the postorbital and squamosal have a long contact and the fossa is secondarily reduced in size.

(*b*) The jugal is down-turned posteriorly and the foot of the quadrate swung forward and depressed relative to the tooth-row.

(*c*) The anterior parts of both the premaxilla and dentary are toothless; the teeth are 'waisted' and have short crowns.

(*d*) The surangular is strongly upcurved in front of the cotylus.

(*e*) The dentaries are prolonged into an acute rostrum; the jaw is thus 'slipper-shaped'.

(*f*) The maximum number of scutes in a transverse row beneath the belly is twelve, not eight.

O. Fraas numbered the individuals from I to XXIV, but there is in fact no need to assume that more than twenty-two are present. Isolated elements, including the skull numbered XVIII, could be from several individuals, while 'No. XI' is but the ventral armour of No. X that has been turned out sideways. In all there are eighteen skulls of various degrees of completeness.

Most of the individuals are remarkably uniform in size, but as Fraas observed five specimens fall noticeably below the mean, which is a total length of about 86 cm. The smallest of these is estimated to have been 36 cm in length. It should be emphasized as having a possible connexion with this size-distribution that there can be no doubt that the members of the group died at the same time and in the same place.

There is no evidence that the larger individuals are still immature as suggested by Sawin (1947), many facts pointing to the opposite conclusion. Thus, the girdles and limbs are stout and well ossified, scapula and coracoid are usually firmly sutured together even though cracking may have occurred across the junction between them (No. X), and the ischial symphysis has remained firm in No. XXII although the remainder of the ischia has broken away during crushing. The incompletely ossified carpus is in contrast to the well-ossified tarsus, besides occurring also in *Stagonolepis* and *Typothorax*.

Table 2 gives a list of the principal measurements of *Aëtosaurus ferratus*, taken as far as possible from individual No. II.

Skull

In von Huene's restoration (1920) teeth are (incorrectly) shown on the upturned tip of the premaxilla. There seems no doubt of the lack of lateral expansions to the premaxillae, although they turn up to meet the nasals in similar fashion to those of *Stagonolepis*. The anterior part of the premaxilla (figure 40, plate 12) is smooth and toothless; the narial margin makes a slight protuberance above the first tooth. The maxilla usually has nine teeth but in few cases can the total be ascertained; there were probably ten on the damaged right maxilla of No. XVIII. The tooth-row ends opposite the middle of the pre-orbital fossa, and there occurs behind it a tilted area similar to, but relatively longer than, that of *Stagonolepis*.

The pointed tip of the nasal appears just to meet the premaxilla, as stated by von Huene: this region is frequently damaged. On the underside of the nasal a depression is developed in the same position as in *Stagonolepis*.

The prefrontal expands a little in front to lie against the posterolateral edge of the nasal; it does not pass forward as a long point. It extends well down within the anterior wall of the orbit, but the presence of an inwardly directed process cannot be established without further preparation.

TABLE 2. MAIN MEASUREMENTS OF *AËTOSAURUS FERRATUS*

	(cm)	
skull-roof in mid-line	9·6	(II)
presacral column length	26	(XVI est.)
scapulocoracoid height	6·35	(II est.)
scapula height	4·75	(II)
breadth apex of scapula	2·7	(XXII)
coracoid length	2·65	(II)
coracoid breadth	1·6	(II est.)
interclavicle length	5·3	(XXI magn. by 1·6)
humerus length	5·4	(II)
radius length	3·9	(II est.)
ulna length	4·4	(II)
metacarpal IV length	1·05	(II)
ilium, crest length	5·3	(XXII)
ilium, breadth of neck	2·2	(XXII)
ilium, base diameter	3·1	(XXII)
ilium, height	2·9	(XXII)
pubis length	3·9	(II)
pubis, distal breadth	2·9	(II)
ischium, ventral margin	3·6	(XXII)
ischium, height	2·4	(XXII)
femur length	8·5	(II)
tibia length	6·7	(II)
fibula length	6·7	(II)
metatarsal III length	3·15	(XXII)
breadth of a large paramedian dorsal scute	4·75	(II)
length of same scute	1·55	(II)
breadth of a large belly-scute	1·35	(V)
length of same scute	1·45	(V)
estimated total length	86	(XVI)

Note: skull of No. XVI is 9·5 cm long; femur of No. XXII is 8·8 cm long; radius and ulna of No. V measure 4·3 and 4·9 cm, respectively; femur of No. XXI is 5·3 cm long.

The postfrontal gains a brief contact with the parietal, being almost excluded by a narrow ascending bar from the postorbital.

The supra-orbitals, rather doubtfully identified by von Huene, are three in number, forming an additional arch of bones at the sides of the prefrontal, frontal and postfrontal. They are facetted medially so that they partly underlie the roofing bones. The two posterior elements (figure 43, plate 13) are subequal and together equal the first in length. The supra-orbitals are seen on several skulls, notably Nos. VII, XVI and XXIV; on the left side of No. XVIII they are curved into an arc and simulate sclerotic plates.

The postorbital has a long, narrow, ascending process lying against a rugose edge on a descending process from the parietal. A short posterior process ends bluntly in a notch below the anterior process of the squamosal. The bone descends as a broad strip which then tapers to a long point overlying the upper hinder branch of the jugal. The posterior edge of this strip is in firm contact with the squamosal. The union is best seen on the right side of No. XVIII (figure 43, plate 13), but most is visible on the right side of No. V, where however the point of the jugal has been pushed up over the lower part of the postorbital.

The squamosal ends below in an obliquely truncated edge for the quadratojugal, continuing the line of the postorbital/jugal suture so that the squamosal entered only slightly, if at all, into the lower temporal fossa. The latter is much reduced and is bordered almost exclusively by the jugal and quadratojugal.

The jugal is down-turned posteriorly, a feature often obscured by compression of the posterior end of the skull. The side of the bone has a longitudinal keel below which the surface is twisted medially, giving a flat ventrolateral face which is continued forward on the maxilla. Towards the hinder end of the jugal the lower portion faces ventrally and is at right angles to the lateral part. The jugal appears to overlap both lachrymal and maxilla where they unite in front of the orbit; in some, possibly more complete, examples (figure 41, plate 12) it conceals their junction.

As in *Stagonolepis* the quadratojugal has a curved upper margin which in the articulated skull is hidden by the overlap of the squamosal. Thus von Huene's restoration of this region of the skull is explained.

The pterygoids meet in the mid-line along vertically disposed flanges which together form median ridges. The lateral wing of the pterygoid is not recurved, but extends downward and forward to meet the transverse. On the left side of No. XXI can be seen the ending of the ventral channel from the choana. The anterior part of the palate is usually hidden, but portions of it can be seen in some specimens through the naris and pre-orbital fossa. Nos. II and XVII reveal parts of the palatines, rising medially as in *Stagonolepis*, and also the posterior rim of the choana. The left vomer and the beginning of the left choana are visible through the right naris of No. XVI.

There is a medial shelf on the maxilla at the same height and of the same extent as in *Stagonolepis*; furthermore, an isolated maxilla shows a precisely similar articular surface for the palatine.

From these facts there can be no doubt that the structure of the palate was extremely like that of the Elgin form, with the choanae in the same position.

The occipital aspect of the skull is shown only by No. V, which is compressed downward. The relations of the paroccipital, squamosal and parietal are exactly as in *Stagonolepis* and, making due allowance for compression, the occiput is in complete agreement. The supraoccipital enters the foramen magnum. The basis cranii is elongated, the tubera broad and chevron-shaped. There is a deep pit in the posterior part of the basisphenoid, passing forward as a groove flanked by ventral ridges which expand in front at the basipterygoid articulations and end behind in oblique crescentic facets. The basicranium of *Aëtosaurus* is a little larger relative to skull length than that of *Stagonolepis*, but they resemble each other closely in build and proportions.

The lower jaw is 'slipper-shaped' (cf. von Huene 1920, fig. 18; O. Fraas 1877, Taf. III, fig. 4). The lateral margin of the dentary partly conceals the teeth in side view. Whereas the restorations of both Fraas and von Huene show a full tooth-row on the dentary, it is certain that there is a considerable edentulous area at the fore-part of the bone. This is well displayed by the left dentary of No. V, but is also clearly visible on Nos. VII, XVII and an isolated dentary probably from skull No. X. Tooth-counts are difficult to obtain since the jaws are usually in position, but a total of seven teeth may be obtained by combining Nos. V and VII; the isolated example referred to above probably bore eight teeth.

The upper surface of the dentary is smooth in front of the alveolar region; within the sharp rim lies a shallow groove which in No. V bears several small, irregular pits in approximate alinement with the tooth-row. The last of these now lies opposite the first maxillary tooth.

The remainder of the jaw is so similar to that of *Stagonolepis* that further description is unnecessary. The medial aspect is best seen on Nos. IV and XIII. The sutures follow similar courses in the two animals and the mandibular fossa has the same shape and relative size.

The dentition consists of four premaxillary teeth, nine or ten maxillary teeth, and seven or eight dentary teeth. The teeth are much more like those of *Stagonolepis* in shape than is suggested by the figures of Fraas and von Huene. Crown and root are equal in diameter, being separated by a slight constriction. The crown is striated longitudinally towards the tip and is somewhat compressed and recurved. The very long alveolar portion of the tooth is cylindrical.

The premaxillary teeth are equal in size and smaller than those of the maxilla. The latter increase in size up to the third or fourth and thereafter decrease. The dentary teeth are similar in shape and size to the maxillary teeth.

Postcranial skeleton

Vertebrae

Remarkably few vertebrae are exposed, due to the blanketing effect of the dermal armour, so that it is not possible at present to give a complete description of the vertebral column. All the visible centra are slightly amphicoelous. The cervicals are short and keeled ventrally. The second sacral rib (figure 44, plate 13) is strongly expanded and attaches to almost the entire posteroventral inner margin of the ilium. The 'rückenwirbel' of von Huene (1920, fig. 21), which lies near the head of the left tibia of No. II (figure 45, plate 13) is an anterior caudal vertebra with a long transverse process; it probably belongs to the tail of No. II, since several vertebrae are missing from an exposed sequence in this specimen. Von Huene has identified as neural spines what are actually the transverse processes of the more posterior vertebrae of this series; the ends of the processes are missing, but that of the ninth caudal (of von Huene's numbering) shows the beginning of a more distal expanded portion (or anterior flange) comparable to those displayed by the anterior caudal vertebrae of *Aëtosaurus crassicauda* (E. Fraas 1907).

Immediately behind the second sacral vertebra of No. XXII are two long transverse processes which probably belong to the first two caudal vertebrae. Each has a broad central portion, tapers towards the distal end (which is concealed), and is supported below by a ridge along the longer axis in similar fashion to the anterior caudals of the type specimen of *A. crassicauda*. Like that form also, each transverse process of No. XXII shows a flange projecting forward from the anterior margin.

Shoulder girdle

The shoulder girdle differs only from that of *Stagonolepis* in the apparently greater relative length of the interclavicle, that of No. XXI (one of the smaller individuals) being twice as long as the coracoid. However, this difference seems to be mainly due to the greater relative size of the scapulocoracoid in the Elgin form, since, when compared to the length of the presacral column as a standard the interclavicles of the two have almost the same length.

Fore-limb

There is no separately ossified olecranon as indicated by von Huene (p. 480). The apparent suture at the proximal end of the ulna of No. VI is merely a groove extending partly across the bone and is probably an artifact of preparation. As shown by him (1920, fig. 39) the medial side of the ulna is excavated proximally, comparing in this respect with a similar excavation of the ulna of *Stagonolepis*.

The carpals seem to have been incompletely ossified. There is a transversely elongated element on the radial side and in No. II two smaller rounded bones lying laterally between it and the metacarpals. These have been well figured by von Huene. The large element is readily comparable to that of *Typothorax meadei* as shown by Sawin (1947).

The first metacarpal is short and roughly equal in length to the fifth, both being a little more than half as long as the fourth. Metacarpals II, III and IV are of almost equal length, increasing a little laterally. Von Huene (1920, fig. 40) included part of the first phalanx of digit I as the distal end of metacarpal I, hence his statement that metacarpals I to IV are equal.

Pelvic girdle

The pelvis has been figured by O. Fraas (1877), E. Fraas (1907) and von Huene (1920 and earlier works); it should perhaps be pointed out here that the well-known figure in Romer (1945, fig. 174A) is not of *Aëtosaurus*, but is taken from Broom's (1913) illustration of the pelvis of *Ornithosuchus*.

The pubis (figure 45, plate 13) is broader than that of *Stagonolepis* but is otherwise very similar. There is a lateral buttress continuing the acetabulum (No. II) and there are two foramina (both pubes of No. XVI). The lateral edge is thickened distally; in No. II the pseudosuchian twist of the distal or ventral portion has been exaggerated by compression. It should be noted that this is a right pubis seen in dorsal, or more correctly, anterior view, not a left as stated by von Huene (1920, p. 479 and figs. 22 and 30: these drawings include the medial part of the left pubis).

The blade of the ilium (figures 44 and 45, plate 13) has a pronounced, slightly decurved anterior projection; the posteroventral margin of the blade is curved medially; this is better displayed by No. II than No. XXII which is rather flattened. Von Huene states that the ilium of No. XX, a small individual, differs in form from that of an adult animal. However, the bone in question is a left ilium, not a right (the head of the left femur is in the acetabulum) and is in fact identical with the larger ilium of No. XXII.

The ischium has a well-developed symphysial area along the entire ventral edge, also extending some way up the central part of the medial surface. The ischia tend to remain united by this portion which breaks away when the girdle is compressed (cf. figure 44, plate 13); the lack of this portion probably accounts for the apparently slender posterior termination of the right ischium of No. II (figure 45, plate 13).

E. Fraas attempted a restoration of the pelvis in 1907. This is said to be taken from No. XVI, but it is clear that the ilium is that of No. XXII. The ventral or posterior aspects of the pubes are well shown and the second pubic foramen is portrayed as a deep embayment of the medial margin. However, the lateral margins of the pubes must have been almost parallel in life and the side view is not so successful in its depiction of the attitude of these bones which are now known to have descended vertically. The acetabulum is shown open, but it is evident from the usual obtuse angle made by the lower margin of the left ilium of No. II (figure 45, plate 13) that there could have been no extensive vacuity in this region.

Hind-limb

The femur requires little comment: in No. XXII the torsion of the head is exaggerated due to the strong lateral compression which this bone has suffered. Other femora show only a moderate amount of torsion. Furthermore, what appears to be the fourth trochanter in this femur is the projection of the lateral edge which has been forced down. As in *Stagonolepis*, this projection is opposite the fourth trochanter, and the distance from trochanter to distal end is roughly equal to the length of the tibia. However, the portion proximal to the trochanter is relatively shorter in *Aëtosaurus ferratus*.

The tibia and fibula are more slender than in *Stagonolepis*. The lateral trochanter of the fibula varies from being high and ridge-like (No. IV, right side) to low and blunt (No. IV, left side and others).

The tarsus is extremely interesting since it is so like that of a modern crocodile. It has been discussed by Schaeffer (1941), where a restoration is given based on von Huene's figures, but since the restoration is incorrect Schaeffer's conclusions concerning the type of joint present cannot be accepted; on the contrary there is some evidence which suggests that, apart from the obvious structural resemblances, the ankle-joint functioned in a typically crocodilian manner.

The astragalus has two anterior facets, for the proximal end of metatarsal I which meets it directly, and for the medial distal tarsal which interposes between it and the proximal end of metatarsal II. A strong square process (figure 44, plate 13) directed dorsolaterally articulates with the medial shelf on the end of the fibula and partly overlies the proximal surface of the calcaneum. The undersurface of the isolated right pes (Fraas 1877, plate II, fig. 4; von Huene 1920, fig. 49) shows signs of the 'hook-like, bluntly rounded process, which curves ventroanterolaterally' described by Sawin for *Typothorax* (1947, figs. 5B, 10: in the latter figure the plate is inverted with respect to the legend so that 1 and 2 are calcaneum, ventral and dorsal, 3 and 4 are astragalus, ventral and dorsal).

The medial and posterior surfaces of the astragalus (figure 45, plate 13) are rounded. Posteroventrolaterally there is a slightly convex facet which meets a corresponding concavity of the tuber calcanei, but the details of this articulation are unfortunately obscured.

In at least some examples the astragalus was firmly united with the tibia. Thus in No. II (left) a small slip of the tibia is fixed to the astragalus although the rest of the bone has parted from it, and Nos. X (right)and XXII (left) have the astragalus still united with the tibia although the metatarsals have been rotated into line with the epipodials.

The calcaneum presents a convex oval proximal surface for articulation with the fibula and the lateral process of the astragalus. Anteroventrally it meets the lateral distal tarsal. The broadest part of the calcaneum is at the tuber, which extends medially behind the astragalus. The posterior edge thickens greatly towards the medial side and is separated by a groove dorsally from the body of the bone. The inwardly projecting portion of the tuber is grooved also on the underside. The dorsal view of the calcaneum has been excellently figured by Fraas (1877, plate II, fig. 2); medial views of the tuber are shown by von Huene (1920, figs. 45 to 47). There is a remarkable resemblance between the calcaneum of *Typothorax coccinarum* [*Episcoposaurus horridus*] figured by von Huene (1915, fig. 15) and that of *Aëtosaurus ferratus*, such that von Huene's drawing would serve almost as well for either animal. The calcaneum of *T. meadei* (Sawin 1947) is also very like that of *Aëtosaurus*.

There are two distal tarsals. The small medial element articulates with the astragalus and with metatarsals II and III. A large, roughly triangular lateral tarsal meets the calcaneum proximally, metatarsals III and IV distally, the hooked fifth metatarsal laterally and the small element medially.

In No. XXII the foot has been rotated into line with the epipodials but the astragalus has remained united with the tibia while the calcaneum on the other hand has moved with the foot, so that the distal end of the fibula has slipped back to rest on the tuber calcanei. Thus the tarsus has behaved in a typically crocodilian manner for, to quote Schaeffer on the crocodilian tarsus (1941); 'as the foot is dorsiflexed on the crus the astragalus remains immobile and functionally united with the crus, while the calcaneum moves with the foot'. It cannot be stated with certainty that the articulation between astragalus and calcaneum was as well developed as in present-day crocodiles, but the appearance of the tarsus in Nos. II, VI, VII and XXII suggests that a similar arrangement was in existence.

The remainder of the pes is like that of *Stagonolepis*, but the bones are more slender. The phalangeal formula is 2, 3, 4, 5, ?4.

Dermal armour

The dorsal armour comprises four rows of scutes extending to the extreme tip of the tail. In the back region broad paramedian dorsal scutes are flanked by almost square lateral dorsal scutes. The first pair of paramedians rest on sloping posterior flanges of the parietals. The ornament is most deeply incised over the pelvis where it consists of the usual pits and grooves as in *Stagonolepis*. Anteriorly and posteriorly it becomes fainter, changing to a pattern of incised lines radiating from a smooth area behind the middle of the scute. The centre of radiation retains a constant position throughout the paramedian and lateral dorsal series. Typical paramedian dorsals are gently arched along a line nearer to the medial than the lateral edge; this becomes a low ridge in the pelvic scutes. The cervical and posterior caudal scutes are almost devoid of ornament.

Immediately in front of the pelvis there is a definite 'waist' where the paramedian (and lateral) scutes are narrower than at the pelvis itself; behind the latter the scutes again become gradually narrower so that at the tip of the tail length greatly exceeds breadth.

The paramedian scutes have the produced anterolateral corner which, however, is frequently obscured by the lateral dorsals. Thus the supposed distinction between the shape of the caudal paramedian dorsals in *Aëtosaurus ferratus* on the one hand, and *A. crassicauda* and *Stegomus arcuatus jerseyensis* on the other, mentioned by Jepsen (1948), has no existence in fact.

It is clear that any overlap by the paramedian scutes on to the laterals or vice versa is due to post-mortem telescoping. The apparent median caudal ridge of No. XVI (von Huene 1920, p. 483) seems to be due to compression of the tail, the medial edges of the scutes having been borne up by the underlying neural spines.

In the dorsal region the lateral dorsals are of quadrate shape, gently arched, the keel lying about a quarter way from the medial margin. The keel runs obliquely outward and backward across the scute, rising posteriorly and falling more steeply to the medial side. In the 'waisted' region the scutes become sharply angulated and longer than wide. The outer part of the scute is reduced so that the keel becomes central and parallel to the margins.

At the pelvis the lateral scutes resume their former shape. Proceeding posteriorly in the tail they become more and more narrow and angulated. In some individuals there appear to be two rows of this type on each side, the outer being the narrower (Nos. XVI, XVII, XXIII). The outer row in these cases is probably the continuation of the lateral ventral row.

The belly scutes begin immediately behind the interclavicle in No. XXI and end close to the pelvic girdle in No. XXII. There is no evidence of ventral ossifications anterior to the shoulder girdle. The widest part of the belly armour is between the seventh and eighth rows from the front, indicating about fourteen rows from front to back, as in *Stagonolepis*. About thirteen rows are preserved on No. III.

The maximum number of scutes in a transverse row is twelve, not eight as stated by O. Fraas, von Huene and others. A loose piece supplies the missing rows from No. XXI, but the mid-line is clearly visible on the specimen without its aid; the same total can be obtained by combining Nos. 'XI' and V. Since, however, the belly scutes are longer than wide the general shape of the armour is very much the same as in the Elgin form.

In the posterior part of the belly the scutes tend to adopt a paired arrangement. This effect is most marked in the four median rows and does not seem to affect the two outer rows on each side. The paired scutes are more obviously trapezoidal in shape than the anterior scutes; the line of contact between members of a pair is inclined outward and backward and is thus discontinuous between successive pairs, whereas the junctions between collateral pairs are continuous lines following the belly contours backward. The appearance is thereby created of an incipient reduction from twelve to eight in the number of longitudinal rows.

The underside of the pelvic region seems to have lacked dermal ossifications. The cloacal opening is preserved behind the ischia in Nos. XXI and XXII (figure 44, plate 13). In the latter there are three transverse rows of scutes between the ischia and the cloaca, the hinder two rows each consisting of eight small plates. At the beginning of the cloaca the number in a transverse row is halved but the width of the armour is maintained by the increased breadth of the scutes. The first paramedian ventral, for such it may now be called, is equidimensional, its lateral ventral a little broader than long. Succeeding paramedian ventrals increase rapidly in size until immediately behind the cloaca they equal the paramedian dorsals. The lateral ventrals increase in length correspondingly but as rapidly decrease in breadth.

The ornament is most deeply incised on the scutes anterior to the cloaca and on the medial parts of those adjacent to it. The more posterior plates have but faint ornament.

The paramedian ventral plates resemble the paramedian dorsals closely, but the following features help to distinguish between them:

(1) They lack the anterolateral projection.
(2) The angulation is along the middle of the scute.
(3) The ornament is of pits rather than grooves.
(4) The scutes bordering on the cloaca have their anteromedial corners rounded off.

However, without direct evidence of position it would be well-nigh impossible to distinguish between dorsal and ventral paramedian plates from the tail region.

The cloacal aperture extends back along two and a half scute-rows in No. XXII, whereas in No. XXI, a smaller individual, it takes up three and a half rows, reckoning in each case from the point at which the number of scutes in a row is halved. This difference may perhaps be sexual. The cloacal region of No. XXII has been inserted for the sake of completeness in the restoration of the ventral armour of *Stagonolepis* (figure 23).

No. XX, which lies across No. XXI, shows a considerable part of the underside of the tail. The paramedian ventral scutes gradually decrease in breadth to become longer than broad; they are flanked throughout by narrow lateral ventral scutes. The dorsal and ventral plates correspond, forming complete rings of eight scutes.

In the extreme posterior part of the tail the dorsal and ventral scutes lose their identity, becoming mere elongated slips of bone, but the eight rows appear to continue to the very end.

The appendages are protected by numerous small, rounded, button-like plates, while over the thigh region occur rows of small, rhomboidal scutes with downwardly projecting apices.

Having regard to their size, all the scutes are relatively as thick as their counterparts in *Stagonolepis*.

(2) *AËTOSAURUS CRASSICAUDA* E. FRAAS

(*a*) *The type specimen*

The species was founded by E. Fraas in 1907 on a single specimen consisting of a series of lumbar, sacral and caudal vertebrae with part of the pelvis and dermal armour *in situ*. The horizon is given as a hard, sandy marl band, 1 to 2 m thick, within the massive Stubensandstein of the Stromberg near Pfaffenhofen.

Fraas believed the most striking feature to be the long, powerful transverse processes of the anterior caudal vertebrae. Other differences from *A. ferratus* were stated to be:

(1) Paramedian dorsal scutes becoming broader behind the pelvis.
(2) Greater size; length of original animal estimated by Fraas at 1·5 m (i.e. about 5 ft.).
(3) Lateral dorsal scutes angulated.
(4) Ventral scutes broader than long.

However, it is clear from what has been said in the preceding section about the armour of *A. ferratus* that points 1 and 3 above apply also to the latter; the lateral dorsal plates of

A. crassicauda are angulated in the constricted region (actually this is immediately in front of the pelvis), but they become wider and flatter behind as in *A. ferratus*. A similar effect may be seen in the un-named specimen figured by Case (1932).

The ventral scutes referred to by E. Fraas are from beneath the root of the tail, and are of the same type as those occurring in the same position in *A. ferratus* which, as already noted, rapidly become broader than long. Two of these paramedian ventrals remain in the type of *A. crassicauda*, the remainder having been removed in preparation. Only a very small portion, if any, of the belly armour could have been present on the specimen and it may be safely assumed that the statement of four rows of 'bauchschilder' refers to the anterior part of the tail. This agrees with the arrangement found in *A. ferratus*.

The curious transverse processes which have an anterior flange or lamina may also be seen in the anterior caudal vertebrae of *A. ferratus*.

Thus, of the criteria given by Fraas, only that of size is valid for distinguishing between the two forms. On the other hand, the keels on the paramedian dorsal scutes are more elevated posteriorly in *A. crassicauda* and in this respect the scutes are intermediate in structure between those of *A. ferratus* and *Stagonolepis*. In other respects the dorsal armour is similar to that of the smaller species; the ornament is more deeply incised and the keels are stronger in the constricted region.

(*b*) *Referred specimens*

In 1921 von Huene described some bones from the Stubensandstein of Pfaffenhofen, referring them to *A. crassicauda*. These are said to have been obtained from the same horizon in the same quarry as the holotype, not long (1909) after the discovery of the latter.

Many of the bones referred by von Huene to *A. crassicauda* are incorrectly identified and this material is in fact a mixture of elements of two quite different animals. By kind permission of Dr K. Staesche of the Museum für Naturkunde, Stuttgart, the specimens have been lent to the writer for study. The following is a list of the revised identifications of these bones, figure references being to those of von Huene (1921).

The 'ischium' (fig. 6 and plate I, fig. 4) is a right scapula in medial view, inverted.

The 'scapula' (fig. 3) is a left pubis in side view, proximal end to the right; the 'distortion' for which the figure has been corrected is the natural distal twisting of the bone.

The single cranial fragment identified with some doubt by von Huene as the inner side of the right postfrontal and postorbital (figs. 1, 2; plate I, fig. 1) is probably the right pterygoid in ventral view.

The 'pubis' (fig. 5 and plate I, fig. 5) is a right quadrate.

The 'proximal caudal vertebra' (p. 331) is a mid-dorsal.

The cervical vertebra (plate I, fig. 2) and right ilium (fig. 5 and plate I, fig. 6) are correctly identified. There is, however, no proof that the acetabulum was closed and it is probable that the ilium is not greatly distorted.

The preceding specimens may reasonably be grouped together and indicate a small coelurosaur allied to *Procompsognathus* (described in the same paper by von Huene) but about twice as large. It would be out of place to deal in detail with this material here and re-description is therefore postponed for the present.

The remaining bones are as follows:

The 'proximal end of a right humerus' (fig. 4) is the distal end of a right femur in ventral view. The condyles have been further exposed by the use of acetic acid. The bone compares very well with femora of *A. ferratus* and *Stagonolepis*, having the same lateral and distal shelf.

The proximal end of a femur (fig. 7) is actually that of a left femur, not a right. The fourth trochanter ('trochanter major' of von Huene) is well developed on the underside.

The mid-caudal vertebra (plate I, fig. 3) agrees well with corresponding ones of *A. ferratus* and *Stagonolepis*.

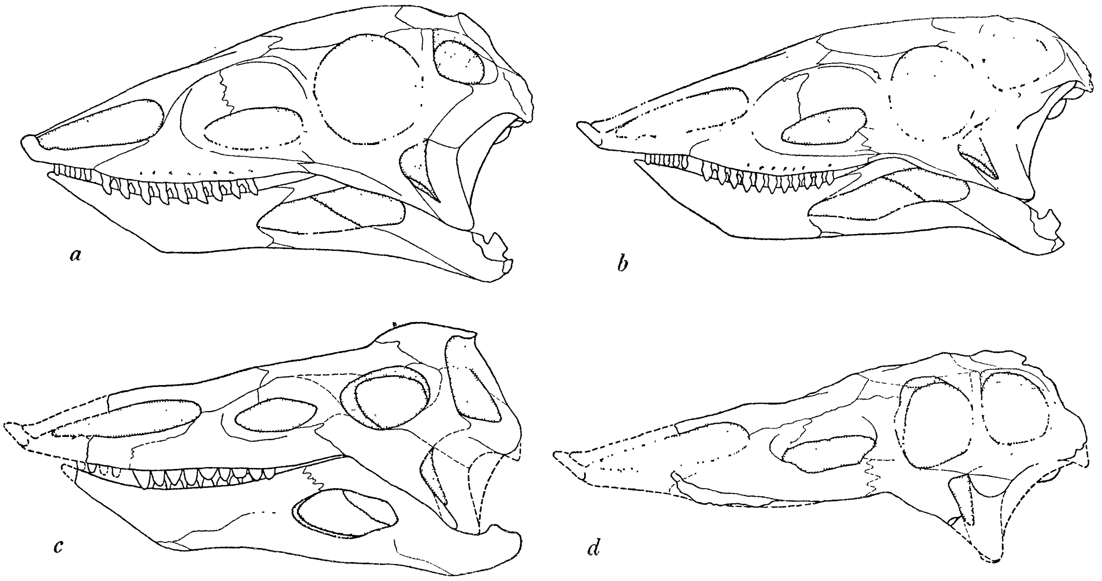

FIGURE 24. Aëtosaurid skulls in side view. *a*: *Aëtosaurus* (magn. × 0·62); *b*: *Stagonolepis* (magn. × 0·25); *c*: *Typothorax* (magn. × 0·29); *d*: *Desmatosuchus* (magn. × 0·18). (New restorations: *a*, *b*: from original material; *c*, *d*: modified from Sawin (1947), and Case (1922).)

The ornament of the scutes is of the incised line type as in *A. ferratus* and they are therefore not from the pelvic region. It is doubtful if there are any scutes other than paramedian dorsals present; the 'lateral' scute identified by von Huene appears to be a caudal paramedian and another of the same size is adjacent. The scutes are in all respects typically aëtosaurian.

The fragments of femora, mid-caudal vertebra and scutes agree in size with what might be expected from consideration of the holotype of *A. crassicauda* and they may be referred to this species with some confidence, though without absolute certainty. It is hardly likely that they formed part of the same actual individual in view of the different mode of preservation.

(3) *AËTOSAURUS FERRATUS* AND *A. CRASSICAUDA*

The original length of the holotype of *A. crassicauda* was estimated by E. Fraas at 1·5 m. However, this value is too great because the scutes of *A. ferratus* on which his comparison of size was based (No. XVI) are incompletely exposed because of lateral overlap. Direct ratios between the breadths of the largest paramedian dorsal plates of the two animals are of the order of 1·25. It is probably more accurate to compare the square roots of the areas of the largest plates; this gives a ratio of 1·4 which agrees fairly well with estimates obtained from the vertebrae.

On the above basis the length of an individual of *A. crassicauda* would be 1·2 m or about 4 ft., assuming the tail to be as elongated as in the smaller species. The two individuals of *A. crassicauda* are thus a little larger than the estimated size of the smallest known individual of *Stagonolepis*.

As far as can be determined from the materials now available, the only distinctions between the two species of *Aëtosaurus* are (i) size and (ii) the elevation of the posterior part of the keel of the pelvic paramedian dorsal scutes of the larger form. The ratio of sizes is similar to that which exists between the two size-groups of *Stagonolepis robertsoni*. It is noteworthy also that one of the few morphological differences between these two size-groups (of *Stagonolepis*) lies in the greater elevation of the boss on some of the paramedian dorsal scutes of the larger individuals. These points naturally raise the question of the validity of *A. crassicauda* as a separate species and this can hardly be answered without further material, particularly of the skull, so that it seems desirable to retain it as such for the present.

VII. *STAGONOLEPIS* AND *AËTOSAURUS*

The close relationship which exists between these two forms will have become apparent during the preceding revision of *Aëtosaurus* which had inevitably to be cast largely in terms of a comparison with *Stagonolepis*. The following discussion is therefore mainly a comparison of proportions concluding with a summary of the differences between the two animals and an assessment of their taxonomic relationship.

It would be instructive to be able to compare the two directly by expressing the various measurements in terms of some standard unit which would minimize the differences introduced by the size factor. A comparison was attempted using a unit of the type employed by Romer & Price (1940), based in the present instance on the area of the face of a sacral or immediately adjacent centrum. Expressed in such terms, the difference between the two forms appeared to lie, broadly speaking, in the greater elongation of the limbs of *Stagonolepis* rather than in the reduction of the skull. This conclusion is clearly at variance with the obviously smaller relative size of the skull of the Elgin form; as shown by the evidence of the armour, the body shape is very similar in both animals.

Instead, the length of the presacral vertebral column was used as the standard of comparison; in *Aëtosaurus* the skull is a little more than one-third the length of the presacral column, in *Stagonolepis* it is a little more than one-fourth. The bones of the fore-limb and the femur agree closely when compared in this way, divergences being shown by the girdles, crus and pes. The relatively larger girdles of *Stagonolepis* are to be expected in view of its larger size and to the same cause may be attributed the shorter and stouter crus and pes, since the greater part of the weight is borne at the pelvis in these animals.

Although the skull of *Stagonolepis* is proportionately smaller than that of *Aëtosaurus*, the two resemble each other to a remarkable degree, not only in the details of morphology but also in the relative sizes of many of the bones and fenestrae. To illustrate this similarity table 3 has been compiled from the most reliable data.

It seems likely from these figures that the nasals and external nares are a little longer, and the frontals and parietals a little shorter, in *Stagonolepis*, although the data are insufficient to establish these points with certainty. A clear difference between the two skulls lies in the expansion of the parietals of *Stagonolepis* in front of the supratemporal fossae.

In spite of the relatively larger girdles in *Stagonolepis* the proportions are very similar in both animals; however, the pubis is broader in *Aëtosaurus*. There is no doubt that this is a real difference, for when compared to other pelvic measurements, for example the depth of the ilium, the lengths of the pubes of the two animals are almost identical.

TABLE 3. SKULL PROPORTIONS OF *STAGONOLEPIS* AND *AËTOSAURUS*

	Stagonolepis		*Aëtosaurus*							
individual	M.C.Z.D. 2	R 4787	I	II	V	VII	VIII	XVI	XVII	XVIII
skull length (mid-line of roof) (mm)	190	245	—	96	—	—	—	95	94	104
nasals/skull length (%)	54	—	—	51	—	—	47	49	—	52
frontals/skull length (%)	24	—	—	—	—	—	30?	26	—	28
parietals/skull length (%)	17	—	18	20	—	—	—	21	19	20
breadth between supratemporal fossae/skull length (%)	24	—	24	25	—	—	22	—	24	21
narial length/skull length (%)	30	32*	—	24	—	28	26	28	27	29
antorbital vacuity/skull length (%)	22	—	—	22	21	22	21	21	18	19
parietal 'horns'/skull length (%)	41	34?	39	45	—	—	—	—	38	—
breadth anterior part partietals/skull length (%)	33	—	—	—	—	—	—	—	—	21
tip of dentary to mandibular fenestra/skull length (%)	—	39	36	—	—	42	—	—	37+	—
length mandibular fenestra/skull length (%)	—	35	22+	34	—	—	—	—	—	—

* E.M. 38R.

Summary of differences between Stagonolepis *and* Aëtosaurus

(1) Size.

(2) Skull of *Stagonolepis* relatively smaller.

(3) Skull differences:

(*a*) Naso-frontal suture at first inclined back from mid-line in *Aëtosaurus*, forward in *Stagonolepis*.

(*b*) Tips of premaxillae and nasals expanded laterally in *Stagonolepis*.

(*c*) Lateral grooves on frontals of *Aëtosaurus* are more pronounced and extend along the margins of the supratemporal fossae; rather variable however, and only one specimen of *Stagonolepis* shows this region.

(*d*) Parietals of *Stagonolepis* expand in front of supratemporal fossae.

(*e*) Supratemporal fossa larger in *Stagonolepis*, orbit smaller; contact of postorbital and squamosal begins lower down in consequence.

(*f*) Dental formulae

	Aëtosaurus	*Stagonolepis*
premaxilla	4	4 or 5
maxilla	9 or 10	11 or 12
dentary	7 or 8	9 or 10

(*g*) Teeth of *Aëtosaurus* somewhat more pointed and recurved, constrictions less definite.

(*h*) *Aëtosaurus* has shorter edentulous area on premaxilla, and longer oblique area at rear of maxilla.

(4) Larger girdles in *Stagonolepis* (except interclavicle), but pubis narrower.

(5) Shorter and stouter tibia, fibula and pes in *Stagonolepis*.

(6) Scute differences:

(*a*) Ridges on paramedian dorsals in *Aëtosaurus*, bosses in *Stagonolepis*.

(*b*) Keels on lateral dorsals nearer medial margin in *Aëtosaurus*.

(*c*) Maximum of twelve longitudinal rows of belly scutes in *Aëtosaurus*, eight in *Stagonolepis*; scutes of the former longer than broad.

Although some at least of the above items are merely reflexions of the larger size of the Elgin form, nevertheless, taken as a whole they are probably sufficient to show that the two are generically distinct. Also, as will be seen later, *Stagonolepis* stands morphologically between *Aëtosaurus* on one hand, and *Typothorax* and *Desmatosuchus* on the other; for this reason it seems desirable to retain separate generic status for *Aëtosaurus*.

VIII. Notes on *Typothorax* and *Desmatosuchus*

(1) *TYPOTHORAX* COPE

The following comparison is based chiefly on the species *Typothorax meadei* Sawin (1947). Another species *T. coccinarum* Cope (syn. *Episcoposaurus horridus* Cope) is less perfectly known. The nomenclature of these forms, and of *Desmatosuchus*, has been revised by Gregory (1953*a*) and need not enter into this discussion. The material of *T. meadei* is from the Dockum formation of Howard County, Texas.

It is unnecessary to dwell on the close resemblance between the skulls of *Typothorax* and *Stagonolepis*, but some modifications which might be made to Sawin's restoration are suggested by a consideration of the skulls of *Stagonolepis* and *Aëtosaurus*.

The snout of *Typothorax* was probably more acute and the external naris longer than as shown by Sawin. In making the restoration (figure 24*c*) it has been assumed that there were four premaxillary teeth and that these were preceded by an edentulous area of equal length; this gives a naris of reasonable shape and size. The skull length (measured along the mid-line of the roofing-bones) would thus be about 21 cm. The quadrate should probably be swung further forward, bringing forward the lower jaw so that the dentary teeth are within those of the maxilla, a more likely position. A tentative reconstruction of the lower cheek region has also been attempted, and this has been done with the least possible alteration of Sawin's original fig. 1. It should be noted, however, that the cheek-region is restored in what is almost certainly a distorted condition. This has been partly rectified by allowing a greater height to the quadrate, which is both reasonable and permissible since the upper end is stated by Sawin to be missing from the specimen, but it seems that the squamosal has been forced down and that the supratemporal fossa is distorted in consequence. There are also obvious discrepancies between Sawin's figs. 1 and 2 in respect of the shape of the jaw and the position of the mandibular fossa; in the new restoration the jaw has been taken from fig. 1.

The doubtfully identified 'tabulars' seem to be the elevated areas on the parietal flanges as seen in *Aëtosaurus*, *Stagonolepis* and *Desmatosuchus*. That the palate is primitive is extremely doubtful, in view of the close resemblance throughout the rest of the specialized skull to that of *Stagonolepis*: Sawin's specimen was strongly compressed and badly crushed in this region.

The 'coronoid' seems to be merely a fractured portion of the surangular.

There are seven dentary teeth as against nine or ten in *Stagonolepis*, and at least three on the premaxilla. Sawin gives varying figures for the number of maxillary teeth, but considering the low number on the dentary his statement of 'nine or ten' may be accepted provisionally. Although Sawin describes the teeth as 'bluntly conical', Professor J. A. Wilson of the University of Texas has examined the specimen on behalf of the writer and states in a personal communication that they are 'waisted'.

The vertebral column, shoulder girdle and fore-limb are in close agreement with corresponding elements of *Stagonolepis*. There is a broad carpal bone in the manus. In the humerus an ectepicondylar foramen replaces the groove of *Stagonolepis* and may indicate a late stage of ossification.

The pelvic girdle is apparently anomalous and it is difficult to believe that it can have been of the form shown in the figure. The differences are no doubt due to restoration from fragmentary material; in addition the ilium is said to be doubtfully associated.

As illustrated the femur appears to be straight, but Sawin states that the shape is sigmoid. There is a very close resemblance between the femora of *Stagonolepis* and *Typothorax coccinarum* (Cope 1887; von Huene 1915).

The fibula (shown and described in the inverted position by Sawin) is virtually identical with that of *Stagonolepis*. The tarsus compares extremely well with that of *Aëtosaurus*; in particular, the calcaneum of *Typothorax coccinarum* (von Huene 1915, fig. 15) is extraordinarily like that of the smaller animal.

Sawin states that the number of caudal vertebrae (24 or 25) was obtained by combining two specimens from different localities. While the tail of *Typothorax* may not have been as elongated as in *Aëtosaurus*, in which the caudal scute-rings indicate a total of about forty-three vertebrae, it was probably longer than as shown in the restoration.

The dorsal armour resembles that of *Stagonolepis* in its ornament and arrangement in four longitudinal rows. It is unlikely, however, that the median plates disappear in the proximal part of the tail; from a comparison with the un-named specimen figured by Case (1932, pl. I) it is considered that the 'paired angular spine-bearing plates' of the posterior part of the tail (Sawin, p. 227 and fig. 8A; 4) are the homologues of the paramedian plates of the back, while the 'thin, quadrilateral, vertically-placed plates' correspond to the spine-bearing lateral dorsal series. In Case's specimen, tentatively referred by Gregory (1953*a*) to *Typothorax*, the knobs on the paramedian plates increase in height caudally. This transformation also suggests a greater length of tail in *T. meadei*.

In addition to resembling each other closely, there is a striking agreement in actual dimensions between many of the postcranial bones of *T. meadei* and those of large individuals of *Stagonolepis*, and it is clear that the two forms have limbs and girdles of similar proportions.

From the data provided by Sawin the length of the presacral vertebral column can be estimated at 103 cm. The largest paramedian plates are also a little bigger than the largest known plates of *Stagonolepis*. On the other hand, the skull even as now estimated is somewhat smaller than skulls of the larger size-group of *Stagonolepis*, so that it is rather more than one-fifth the length of the presacral column.

As far as can be determined, the following features distinguish *Typothorax meadei* from *Stagonolepis*:

(*a*) Slightly larger overall size.

(*b*) Skull somewhat smaller; parietals shorter; jugal more down-turned; orbit smaller. Maxilla with one or two fewer teeth; dentary with two or three fewer teeth. Jaw shorter and deeper; mandibular fenestra shorter.

(*c*) First seven dorsal plates cover the cervical vertebrae. Lateral dorsal plates angulated, bearing prominent spines. Bosses on paramedian plates increase in height in the tail, those of the laterals decrease. Only two rows of ventral plates beneath the middle of the tail and one row posteriorly.

(2) *DESMATOSUCHUS* CASE

Gregory has recently shown (1953*a*) that the animal described by Case in 1922 from the Dockum formation of Crosby County, Texas, under the name of *Desmatosuchus spurensis* should properly be referred to as *D. haplocerus* (Cope), for it is conspecific with material described by Cope (1892) as *Episcoposaurus haplocerus*, while the name *Episcoposaurus* is a junior synonym of *Typothorax* and thus cannot be used.

The skull of *Desmatosuchus* was believed by Case to be so usual that, while resembling that of the Phytosauria, it should be placed in a separate suborder. Sawin's description of *Typothorax meadei* made it clear that, although highly specialized, both skulls are basically of pseudosuchian pattern. Fuller knowledge of the skulls of *Stagonolepis* and *Aëtosaurus* now makes it possible to restore the missing portions of the skull of *Desmatosuchus* with confidence (figure 24*d*).

Case laid stress on the fact that the borders of the rectangular notch lying between the bones which he regarded as the jugal and maxilla are complete and that the notches on each side are practically identical. Members of the *Aëtosaurus* group show quite clearly that this notch is the anterior part of the infratemporal fossa bounded almost entirely by the jugal (posterior end of Case's 'maxilla') and the quadratojugal (part of Case's 'jugal'). The postorbital and squamosal enter, if at all, only at the upper corner. The skull of No. VII of the *Aëtosaurus* group (figure 40, plate 12) is believed to be almost undistorted in lateral aspect (although compressed from side to side) since the orbit is circular, whereas in other individuals it has been made elliptical by vertical pressure. In No. VII the jugal takes a similar, though not so marked, downward curve to that of *Desmatosuchus*.

The supratemporal fossa of *Desmatosuchus* is very large, and because of this the secondary contact between postorbital and squamosal is much shorter than in the case of *Aëtosaurus*. On Case's photograph (1922, plate 5, fig. B) there is a line to be seen continuing the postorbital-jugal suture which almost certainly represents the junction between squamosal and quadratojugal; the lower part of the latter bone would thus be broken off. The suture between postorbital and squamosal is less obvious, but close examination of the plate suggests a similar course to that of *Aëtosaurus*.

Case's 'squamosal' is thus the parietal, his 'quadratojugal' is the squamosal, and his 'postorbital' is mainly postfrontal. He regarded the pit on the ventral surface of the posterior end of the 'quadratojugal' as being the lower articular surface of the quadrate, but there can be no possible doubt that this pit is on the squamosal and that it received the upper end of the quadrate as in *Stagonolepis* and *Aëtosaurus*.

The relations of the squamosal to the parietal and the paroccipital are the same in *Desmatosuchus* as in the allied genera, but the post-temporal fossa of the former is very small.

The quadrate and adjacent bones have been restored by reference to *Aëtosaurus*, but several aspects of the preserved parts of this area in *Desmatosuchus* suggest that the articular region was swung further forward and thus lay lower than in the former. These considerations include the downward curvature and direction of taper of the jugal, and the attitude of the lower or posterior edge of the squamosal.

The posterior part of the skull roof is much reduced when compared with that of *Stagonolepis*. Thus Case states that the nasals as preserved form a little more than the anterior half. Even with a naris of no greater relative length than that of *Stagonolepis*, the nasals must nevertheless have occupied two-thirds of the length of the skull.

Case referred to sutures on the skull roof which he considered to mark the posterior edges of the postorbitals; however, these agree closely with the positions of the fronto-parietal sutures in *Stagonolepis* and *Aëtosaurus*, and the relations of the postfrontal and upper end of the postorbital seem comparable in every way. On this interpretation the parietals of *Desmatosuchus* are much reduced.

The braincase is extremely like that of *Stagonolepis*, but shorter, indeed the entire posterior region of the skull is reduced in length. The basipterygoid processes and parts of the tubera basisphenoidales are broken off in the specimen. The basisphenoid is shorter, and there is no bridge separating the branches of the trigeminal nerve. Case described a foramen 'of unknown function' in the side of the basisphenoid which communicates with the infundibulum, and regarded the internal carotid arteries as entering near the middle of the anterior face of the basisphenoid. These latter foramina, however, evidently allowed the escape of the palatine branches of the facial nerves and the palatine arteries, while the foramen in the side of the basisphenoid clearly transmitted the internal carotid artery and the palatine branch of nerve VII.

In his account of the endocranial cast of *Desmatosuchus* Case mentioned a pair of small prominences 'which filled pits in the inner walls of the exoccipital bones', above the slender processes which he took to represent the hypoglossal nerves. These pits, which according to Case end blindly in *Desmatosuchus*, seem to be in the same positions as the large foramina below the exoccipital pillars of *Stagonolepis*, and through which in the latter animal presumably passed the posterior branches of the XIIth nerves.

The vertebrae are closely comparable with those of *Stagonolepis* but lack keels in the cervical region and have shorter neural spines. The number of presacrals shown in the restoration of *Desmatosuchus* is almost certainly too great, there being assembled eleven cervicals, one transitional dorsal, and a further sixteen dorsals. Case remarked in several places that there were some duplicate elements due to the presence of a second individual; most of the material was said to have been 'in an irregular heap'. He also regarded as the twelfth vertebra one which was found immediately behind the series identified as the fifth to the ninth, although there seems no reason why this vertebra should not actually be the tenth, since the series (Case 1922, fig. 10A) compares closely with those of *Stagonolepis* (R 4784, fig. 7*i*) which are certainly in correct order. This identification would have the effect of reducing the cervical count to nine in *Desmatosuchus*. There seems to be no evidence of elongate transverse processes in the caudal vertebrae.

The incomplete scapulocoracoid, as Case noted, is extremely like that of *Stagonolepis* figured by Huxley (1877, pl. X). Case's specimen differs from that of the type specimen of

Desmatosuchus [*Episcoposaurus*] *haplocerus* figured by Gregory (1953*a*) in much the same way as the original of Huxley's figure (G.S.M. 90850) differs from the scapulocoracoid of R 4784 (cf. figure 12). These variations must be attributed to abrasion and damage as in the case of *Stagonolepis*.

Case (1932) states that the imperfect ilium found with the material of *Desmatosuchus* which he described in 1922 is strikingly similar to that of University of Michigan No. 7470, a pelvis collected in Crosby County, Texas. The latter was illustrated by him in the earlier work (fig. 28B) and again in 1929 (fig. 21). Gregory (1953*a*) has referred this pelvis to *Desmatosuchus*. It is so like the pelvis of *Stagonolepis* that this reference is probably correct.

The skull of *Desmatosuchus* is now estimated to have been 33 cm long. Using the data given by Case, and omitting probable superfluous vertebrae (two cervical, one dorsal), the length of the presacral column is calculated to be 156 cm, so that the skull is somewhat more than one-fifth of this length.

The known differences between *Desmatosuchus* and *Stagonolepis* may be summarized thus:

(*a*) Larger size (of *Desmatosuchus*).

(*b*) Skull relatively smaller; posterior part reduced; supratemporal fossa a little larger; one or two more maxillary teeth; quadrate swung further forward and jugal more down-turned.

(*c*) First five series of dorsal plates cover the cervical vertebrae; ornament of median plates has no trace of radial arrangement; lateral dorsal plates sharply angulated with prominent spines, and in some cases, horns; plates thicker.

IX. TAXONOMY

The revised account of *Aëtosaurus* given in a preceding section demonstrates both the specialized nature of the animal and its close relationship to *Stagonolepis*; the similarity between the two forms leaves no doubt that they must be included within the same family. This unit contains *Aëtosaurus*, *Stagonolepis*, *Typothorax* and *Desmatosuchus* as principal genera, and the characters of these four provide the basis for the diagnosis given below. The question of an appropriate name for this group must now be discussed.

A survey of the literature indicates that only two family-group names are eligible for consideration, namely, Aëtosauridae and Stagonolepidae, and discussion therefore centres upon the question of priority between these two names. The earliest occurrence of a familial name based on *Aëtosaurus* appears to be that of Baur (1887), who however used the term 'Aethosauridae' as a mere passing reference without diagnosis or indication of which genera were to be included in the family. The first correctly formed family name (according to modern taxonomic usage) is apparently due to Emerson & Loomis (1904) who refer *Stegomus longipes* to the 'Aëtosauridae'. No diagnosis is given in this paper, but a footnote refers the reader to Fraas's original description (1877) of *Aëtosaurus ferratus*. Von Huene (1908*a*), in a work which includes a taxonomic review of pseudosuchian and phytosaurian genera, erected new family-group names to include certain of these forms. His proposals include 'Aëtosauria' and 'Stagonolepidae'. The latter, placed with the phytosaurs, contains only *Stagonolepis* itself. Later (1914), he emended 'Aëtosauria' to 'Aëtosauridae' and recognized Baur (1887) as the author of this name.

There can be no doubt, therefore, that the name Aëtosauridae has clear priority over Stagonolepidae, and that von Huene was correct in attributing authorship of the former name to Baur. For, even though spelled incorrectly, the formation of the name and the scope of the paper in which it was published make it quite clear that it was formed from the generic name *Aëtosaurus* and under these circumstances it must be assumed that the author had in mind a family-group unit based upon the genus *Aëtosaurus* as zoological type. Although at the time of writing there is no strict enforcement of the law of priority as regards family names, it seems likely that this rule will be more rigorously applied in the near future. It is therefore desirable, both in order to preserve strict priority, and to avoid the necessity of a future change of nomenclature, to adhere to the name Aëtosauridae. It is realized that the rejection of the name Stagonolepidae may provide a possible source of confusion, since *Aëtosaurus*, which now becomes the type genus of the family, has hitherto been misinterpreted, but it is believed that any inconvenience so caused will have only temporary effect.

X. FAMILY AËTOSAURIDAE BAUR 1887

(Family Aëtosauridae Emerson & Loomis 1904 *nom. correct.*, *pro* Aethosauridae Baur 1887 *nom. imperf.*)

(1) *Diagnosis*

Pseudosuchia of moderate to large size with relatively small skull, well-developed forelimbs and extensive dermal armour.

Skull-roof narrow, snout pointed. External naris longer than antorbital vacuity, premaxilla and nasal not meeting behind it. Jugal down-turned, quadrate swung forward and depressed, infratemporal fossa reduced in size by secondary contact of postorbital and squamosal, postorbital with long ascending process. Upper temporal opening faces laterally. Nasals at least half the length of the skull roof; parietals short, modified behind into flanges for the reception of the anterior dorsal scutes. Anterior part of premaxilla edentulous, with upturned tip; anterior part of dentary also toothless; teeth subisodont. 4 or 5 premaxillary teeth, 9 to 13 maxillary teeth, 7 to 10 dentary teeth. Palatal channels present in at least some members (*Aëtosaurus*, *Stagonolepis*).

Jaw slipper-shaped, dentaries form an acute rostrum, surangular curves up strongly in front of the cotylus, mandibular fenestra large, retro-articular process well developed.

Probably twenty-five presacral vertebrae of which nine are cervicals; two sacrals; in *Aëtosaurus* about forty-three caudals; centra shallowly amphicoelous; neural spines with expanded apices; rapid transition in position of rib-articulation from cervicals to dorsals; column tapers fore and aft of sacrum; transverse processes of anterior caudals sometimes elongated.

Scapula with strong acromion, apex broadly expanded, coracoid broad; clavicles and interclavicle retained, the latter dagger-shaped. Manus broad and short, carpus incompletely ossified and including a transversely disposed element.

Ilium with anterior process; vertically descending, apron-like pubes each with two foramina and prominent buttress below the acetabulum; ischial symphysis complete. Hind-limb markedly longer than fore; fibula with strong lateral trochanter; pes crocodilian.

Dermal armour complete where adequately known; dorsal series comprising two rows of broad paramedian scutes flanked by narrower lateral scutes which may be angulated and spinose; ornament decreases in sharpness before and behind the pelvis; belly armour of thinner, more numerous plates arranged in transverse and longitudinal bands; ventral caudal and appendicular plates also present.

(2) *Review of the Aëtosauridae*

Since its erection by von Huene in 1908 the former family Stagonolepidae became the repository of a large number of heterogeneous genera of fossil reptiles. That this occurred was largely due to inadequate knowledge of its type genus, *Stagonolepis*, but the incomplete nature of the remains of many of these forms was a contributory factor. Not until the description of *Typothorax meadei* by Sawin (1947) appeared was it possible to obtain a clear picture of what was implied by the term 'stagonolepid'. The majority of the genera formerly assigned to the family must now be excluded under the terms of the diagnosis given above; in the following paragraphs these genera, and others previously referred to the Aëtosauridae, are briefly reviewed and their qualifications for inclusion within the revised family Aëtosauridae are examined.

The small armoured reptile *Dyoplax* (O. Fraas 1867) from the Schilfsandstein of Stuttgart has sometimes been regarded as an aëtosaurid (von Huene 1908*a*, 1914; Romer 1945). The former author has also drawn attention (1920) to the close resemblance between its skull and that of *Erpetosuchus* (Newton 1894). Other points of agreement between them are the presence of but two rows of dorsal scutes, and the similarity of the 'humerus' (probably the scapula) of *Dyoplax* to the scapula of *Erpetosuchus*. The type of preservation of *Dyoplax* permits only comparisons of a general nature; the single specimen has been examined by the writer and there is little to add to Fraas's original description. It differs notably from *Aëtosaurus* in the smallness of the naris and the large size of the supratemporal fossa; indeed, practically the only feature which they have in common is the presence of scutes and even these differ in ornament and number of dorsal rows. One cannot in fact be sure that *Dyoplax* is a diapsid although it is highly probable.

Stegomus arcuatus (Marsh 1896), called by Jepsen (1948) *S. arcuatus arcuatus*, consists only of the inner impression of a segment of dorsal armour, from the New Haven Arkose, Newark Group, Connecticut Valley. Both it and *S. arcuatus jerseyensis* Jepsen (1948) from the Brunswick Shale, New Jersey, are almost certainly aëtosaurid. The latter is a fragment of the tail, which in the arrangement of the armour and in the keels on the lateral plates closely resembles *Stagonolepis* and *Aëtosaurus*. The centra of the caudal vertebrae, on the other hand, have faces which are wider than high. Examination of a cast of the type of *S. arcuatus jerseyensis*, kindly supplied by Dr Donald Baird, suggests that this feature may possibly be due to compression.

Stegomosuchus (von Huene 1914; 1922, for *Stegomus longipes* Emerson & Loomis 1904) from the Portland Arkose, Newark Group, Connecticut Valley, is a much smaller and more lightly built animal, the skull length being about 35 mm and the breadth at the occiput about 29 mm. That the skull lacks half its length, as stated by von Huene (1914) is unlikely; Lull, however (1953), believed it to have been longer and more attenuated than as restored by the original authors. He agreed with them in stating that it differs from *Aëtosaurus* in the proportions of the skull and in the position of the orbits and the size of the temporal fossae. It is not impossible that *Stegomosuchus* may be related to *Erpetosuchus* and *Dyoplax*, which it resembles in the general outline of the skull and the position of the supratemporal openings. As in those genera, the ornament of the scutes is punctate, not striate as in *Aëtosaurus* and *Stagonolepis*. A further resemblance to *Dyoplax* is the tendency for the outer margins of the scutes of *Stegomosuchus* to slant posterolaterally. However, lateral dorsal plates are present and the transverse processes of the caudal vertebrae begin to show elongation behind the pelvis, so that without further study of the specimen no definite conclusion is possible.

A pelvic girdle and fragments of centra, ribs, scutes and phalanges from Fort Wingate, New Mexico, was named *Acompsosaurus wingatensis* by Mehl (1915). The pelvis is apparently like that referred to *Desmatosuchus* (Univ. of Mich. No. 7470), according to Case (1929) and Gregory (1953*a*). The armour is said to indicate a closer alliance with *Typothorax* than with *Desmatosuchus*, and Gregory suggests that *Acompsosaurus* may be a synonym of the former.

The un-named specimen from the Dockum formation of Texas described by Case (1932, Univ. of Mich. No. 13950) has a typical aëtosaurid pelvis and vertebral column. The armour is extremely like that of *Stagonolepis* itself and the lateral plates lack spines. However, it has been pointed out earlier that the caudal armour of *Typothorax* appears to agree with Case's specimen and to differ from the European forms in that the bosses on the paramedian dorsal plates become higher behind the pelvis; it seems better therefore to follow Gregory in tentatively referring U.M. No. 13950 to *Typothorax*.

Case (1922) also figured an isolated ilium (U.M. No. 7322) from Crosby County, Texas, which may belong to *Desmatosuchus*, as suggested by Gregory (1953*a*). Since, however, the form of the ilium does not vary much throughout the group, and as this ilium differs slightly from U.M. No. 7470, which is referred with greater certainty by both Case and Gregory to *Desmatosuchus*, it may perhaps be of *Typothorax*, or of yet another aëtosaurid.

Mention must here be made of *Dolichobrachium*, from the Popo Agie Beds of Wyoming (Williston 1904; von Huene 1939) since it has been thought to have 'stagonolepid' affinities. The remains include a 'coraco-scapula' and a humerus. The former is so unusual and has such a remarkable resemblance to the pelvis of *Eubrachiosaurus* (probably a synonym of *Placerias*) illustrated by Williston (1904, fig. 4) that one can hardly doubt that it is the antimere of it, namely a right pelvis. The differences between the two can be readily explained by distortion. The humerus certainly does not appear to be of dicynodont type and is perhaps to be associated with a skull which formed part of the same collection. According to Williston (quoted in von Huene 1939) the teeth of this skull, which was too weathered to be identifiable, were of 'theropodous' nature. The affinities of the humerus do not concern the present discussion and it is sufficient to point out that it is not of aëtosaurid type.

Stagonosuchus, based by von Huene (1938*a*) on the remains of two incomplete individuals of great size from the Manda Beds of Tanganyika, must be excluded from the Aëtosauridae because of the form of the pelvis; the single cranial bone preserved, even if correctly identified (as a postfrontal) differs from the corresponding element in aëtosaurids.

For similar reasons the genera established by the same author (1938*b*; 1942) on material from the Santa Maria Beds of Brazil (*Prestosuchus*, *Procerosuchus*, *Rauisuchus*, *Rhadinosuchus*) cannot be included in the family. Two thick, pyramidal plates from the same formation were described by von Huene under the name *Hoplitosaurus* [*Hoplitosuchus*] *raui* (1942, plate 28, fig. 3) and compared by him to the lateral plates of *Desmatosuchus*. They do not appear, however, to be closely comparable, lacking the sculpture and sharp angulation of the lateral plates of the latter form, while the somewhat uncertainly associated femur differs strongly from those of *Typothorax* and *Stagonolepis*. They could conceivably be two consecutive median (i.e. mid-line) dorsal scutes and until definite evidence of their position on the body is forthcoming the systematic position of *Hoplitosaurus* remains doubtful.

The suggested classification of genera formerly included in the Stagonolepidae and Aëtosauridae is as follows:

Family Aëtosauridae

Aëtosaurus, *Stagonolepis*, *Typothorax*, *Desmatosuchus*, *Acompsosaurus*, *Stegomus*, Univ. of Mich. No. 13950.

Family Erpetosuchidae

Erpetosuchus, *Dyoplax*, ? *Stegomosuchus*.

Genera not included in the above families:

Stagonosuchus, *Hoplitosaurus*, *Prestosuchus*, *Procerosuchus*, *Rauisuchus*, *Rhadinosuchus*, *Platyognathus*, *Dolichobrachium*.

(3) *Evolutionary trends and relationships with other groups*

The four genera *Aëtosaurus*, *Stagonolepis*, *Typothorax* and *Desmatosuchus*, when arranged in that order, form a series showing apparent increase in specialization. The more important trends are as follows (data on the American forms from measurements given by Sawin (1947) and Case (1922), or from illustrations by these authors):

(1) Increase in size as shown by presacral column length, from 26 cm in *Aëtosaurus ferratus*, through 71 and 92 cm (the two size-groups of *Stagonolepis*) and 103 cm (*Typothorax meadei*) to 156 cm in the case of *Desmatosuchus*.

(2) Decrease in relative length of the skull. A little more than one-third the length of the presacral column in *A. ferratus*, this declines through about one-quarter in *Stagonolepis* to about one-fifth in *T. meadei* and *Desmatosuchus*.

(3) Decrease in relative size of orbit. This appears to be simply the result of increased skull size. The effect is most marked in *Typothorax*, but the possibility here of reduction due to crushing cannot be ruled out.

(4) Increase in snout length. A slight but definite difference between *Aëtosaurus* and *Stagonolepis* in this respect is noticeable in figure 24, but although a plausible assumption, there is at present no proof that further elongation took place in the American forms.

(5) Increase in relative length of the nasals. It is probable that *Stagonolepis* shows a slight increase over *Aëtosaurus* in this respect, but this cannot be asserted definitely in the absence of information about the range of variation of this parameter in *Stagonolepis*. The nasal of *Typothorax* is apparently similar to, or a little longer than, that of *Stagonolepis*, while a greater length is definitely indicated for *Desmatosuchus* since the suture with the frontal occurs further back than in the other forms.

(6) Decrease in relative length of the parietals. Again, it is probable, but not certain, that the parietal of *Stagonolepis* is a little shorter than that of *Aëtosaurus*. In the case of the American forms a clear reduction has taken place, perhaps to as little as 13 and 11 % of the length of the skull roof in *Typothorax* and *Desmatosuchus*, respectively.

(7) Lowering of the occipital condyle in *Typothorax* and *Desmatosuchus* compared with its position in *Aëtosaurus* and *Stagonolepis*.

(8) Increase in size of the supratemporal fossa. This can be shown by comparing the area of the supratemporal fossa with that of the orbit, expressed as a percentage: 27 % (*Aëtosaurus*), 60 % (*Stagonolepis*), ? 60 % (*Typothorax*), 80 % (*Desmatosuchus*), but is well demonstrated by figure 24. It should be noted that the supratemporal fossa of *Typothorax* is probably reduced in area as a result of distortion.

(9) Swinging forward of the quadrate. This in itself partly causes the depression of the jaw-articulation, but the pulling-down of the squamosal seen in *Desmatosuchus* has had an important contributory effect. There is little to choose between *Stagonolepis* and *Aëtosaurus* as far as the attitude of the quadrate is concerned; again, in *Typothorax*, the posterior end of the squamosal has probably been forced down and little reliance can be placed on the orientation of the quadrate shown in figure 24*c*, except that the position of the jaw-articulation is believed to be a reasonable one.

(10) Reduction in size of the pre-orbital fossa in the American forms as compared with the European genera.

(11) Changes in the jaw of *Typothorax* as compared with *Aëtosaurus* and *Stagonolepis*. In the former the jaw is deeper, the mandibular fossa is shorter, the surangular more strongly upcurved and the part of the bone above the fossa deeper, than in the European forms.

(12) Increase in spinescence of the dorsal armour.

Aëtosaurus ferratus: the scutes have longitudinal keels.

A. crassicauda: the keels on the pelvic paramedian scutes are elevated posteriorly.

Stagonolepis: the scutes have bosses, which extend forward as short keels on the lateral plates; some scutes of the larger individuals have higher, sharper bosses.

Typothorax: paramedian plates like those of *Stagonolepis*; lateral plates sharply angulated with angular spines.

Desmatosuchus: lateral spines rounded; 'horns' in the shoulder region.

(U.M. No. 13950 fits into the above series between *Stagonolepis* and *Typothorax*.)

(13) Reduction in number of dorsal scutes in the cervical region. In *Stagonolepis*, and doubtless in *Aëtosaurus* too, the dorsal scutes correspond throughout to the vertebrae, but according to Sawin and Case, the number of transverse rows covering the cervical series is reduced to seven in *Typothorax* and five in *Desmatosuchus*.

It is probable that some of the above trends could have been produced by small changes in relative growth-rates in early ontogeny. Because of this, and the lack of precise information about the time-relationships of the forms involved, the series is best regarded at present as a purely morphological one; it does, however, illustrate the position of *Stagonolepis* with respect to the other genera, and underlines the fact that it is by no means a primitive form.

It is not easy to separate the effects produced on the skull by changes in the musculature due to adaptation to digging from those due to changes in the relative importance of portions of the jaw musculature. However, it seems probable that of the above points numbers 4 to 7 and perhaps 8 are due to improvements in the use of the snout for the former purpose. The decrease in length of the parietals may be in part a product of changed growth-rates in the roofing bones, but it seems that with the pulling-down of the squamosal a greater part of the parietal passes on to the occipital surface, thus increasing the height of the occiput and the moment of the dorsal neck-musculature about the occipital condyle. A detailed comparison of the extent to which the parietal contributes to the occiput in the various genera cannot be made because of imperfect preservation and apparent absence of sutures, but the area above the post-temporal fossae is certainly greater in the American than in the European forms. The possible mechanics of digging are discussed later under 'mode of life'.

On the other hand numbers 8 to 11 are here attributed to changes in the relative importance of the temporalis and pterygoideus portions of the jaw-muscles, and these will now be considered.

Broom (1913) suggested that the pre-orbital fenestra of *Euparkeria* formerly housed a large gland. The opening had, however, earlier been held by Dollo (1884) to be correlated with the anterior extension of the anterior pterygoid muscle. This view has been adopted by later workers, notably Gregory & Adams (1915), Adams (1919), Anderson (1936) and Gregory (1951). It is important to establish the function of this opening in primitive archosaurs so that valid deductions may be made as to the significance of its reduction in size in other groups, in particular for the purposes of the present study the aëtosaurids and the ornithischian dinosaurs. The conclusions reached in this necessarily brief review amplify and extend those put forward by Lull (1908) for the Ceratopsia; a recent paper by Smith & Savage (1959) also has been particularly valuable in suggesting fruitful ideas which are applicable to groups other than those which formed the subjects of their original work.

In those pseudosuchians in which a carnivorous habit (in a broad sense) can safely be inferred, e.g. *Ornithosuchus*, *Erpetosuchus* and *Euparkeria*, the pre-orbital opening is very large. It is convenient to select from these *Ornithosuchus*, since in this form the opening (and the depressed area surrounding it) probably attains its maximum size, but the remarks which follow apply equally well to the other forms mentioned above.

In *Ornithosuchus woodwardi* (Newton 1894; Broom 1913) (figure 25*a*) the quadrate slopes backward to the cotylus. This attitude allows of a greater gape to the jaws for a given angle of opening, which in turn makes possible the employment throughout the jaws of teeth of a larger size, and for the posterior teeth to bite more effectively. Furthermore, the powerful temporal musculature, passing down from the temporal fossae to the mandibular fenestra, operates more effectively, since the posterior position of the foot of the quadrate increases the moment of this musculature about the fulcrum. However, with this position of the quadrate there is a strong tendency for the jaws to be dislocated posteriorly when closing on prey. In addition, the quadrate itself, which is rather loosely attached to the skull in pseudosuchians, tends to be rotated backwards.

The anterior pterygoideus musculature of *Ornithosuchus* is believed to have originated in large part from a membrane stretched across the depressed area on the snout surrounding the pre-orbital fenestra, and probably also from the depressed area itself. This muscle, assisted by the other components of the pterygoideus system passing back obliquely to insert on the lower posterior surfaces of the jaw, is admirably suited to resist both the above tendencies.

However, the enormous size of the pre-orbital fossa in *Ornithosuchus* suggests that the function of the anterior pterygoid muscles was not simply to bind the jaws into the skull, and the retention of the fossa in many sauropod dinosaurs and pterosaurs in which the quadrate is swung far forward leads to the conclusion that an additional purpose was fulfilled by it.

Because of their insertion close to the fulcrum the pterygoid muscles are able to give a very rapid stroke closing the jaws, the advantage of which to a carnivore needs no emphasis. There is also a tendency for the jaws to be pulled forward and upward, thus driving the powerful recurved teeth into the prey. It seems probable that in *Ornithosuchus* the very well-developed anterior pterygoid portion of this musculature was chiefly effective in securing an exceedingly rapid 'snap' when apprehending the fast-moving smaller animals which formed its food. However, because of the position of the insertion of the pterygoid muscles, their effectiveness in biting must have been considerably reduced when the teeth actually engaged, and their function was thereafter probably confined to binding the jaws and the quadrate firmly to the skull during the contraction of the more powerful temporal musculature.

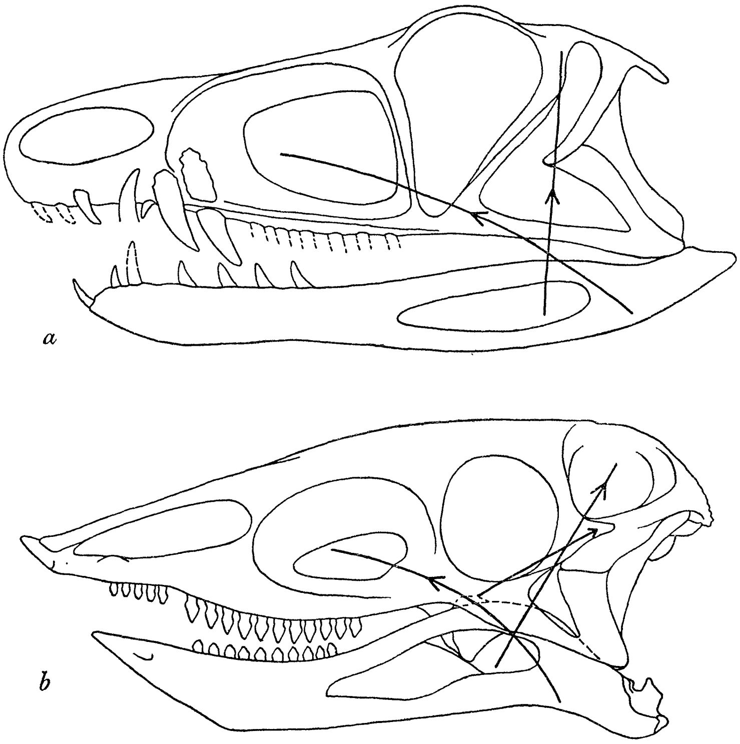

FIGURE 25. Presumed main lines of action of the jaw muscles of *a*, *Ornithosuchus* and *b*, *Stagonolepis*. For explanation see text.

The retention of the pre-orbital fossa in sauropods and pterosaurs appears to be due to this function of the anterior pterygoid muscle in providing a snapping or cropping action by the teeth which in these forms are confined to, or larger at, the front of the mouth. With the swinging forward of the quadrate the importance of these muscles as a binder is reduced. In the carnivorous dinosaurs the mechanics of the jaws were no doubt essentially as in *Ornithosuchus*.

Turning now to the ornithischian dinosaurs and bearing in mind their feeding mechanisms, it is clear that the speedy closure of the jaws is no longer essential, nor is a wide gape.

From the mechanical point of view also a shorter jaw is obviously more efficient in an animal that slices, chops up or grinds its food; indeed, considerations of inertia demand that the jaw shall be short when it is called upon to make rapidly repeated movements of any amplitude. The musculature and construction of the jaws are therefore concerned more with the treatment of the food than its apprehension. Accordingly the quadrate is vertically placed or swung forward to form a stout supporting pillar bracing the jaws on the skull. The pterygoid muscles are of less importance and in this group the pre-orbital opening is greatly reduced in size and in many forms is completely closed up. The temporal musculature plays the dominant role, passing from temporal fossae to mandible nearly parallel to the quadrate, and there is thus little tendency for the jaws to be dislocated.

A further point in ornithischians (and also in sauropods) concerns the loss of the mandibular fossa, with which is associated also the development of a coronoid process and the depression of the quadrate. Both of the latter changes increase the mechanical advantage of the temporal muscles by moving the fulcrum further from their line of action. In one case the insertion of the muscles is moved up, in the other the fulcrum is moved down; the two effects are thus additive. The result attained appears to be a compromise between the moving forward of the quadrate and the decrease in mechanical advantage which this entails.

The loss of the mandibular fenestra may be due in part to the reduction in importance of the pterygoideus musculature, although the migration of the insertion of part of the temporalis muscles to the coronoid process no doubt plays a major role. Presumably in a form such as *Ornithosuchus* or *Euparkeria* the pterygoideus muscles bulked so large at the posterior end of the jaw that additional room was required for the bulging of the temporalis muscles during contraction; this was provided by the mandibular fenestra. It does not seem likely that the pterygoid muscles inserted partly within the fossa, as implied by Gregory (1951, p. 296). In living crocodiles part of the important anterior division of the pterygoideus ('pterygoideus D' of Lakjer 1926) attaches to the intermediary tendon by which the deeper portion of the temporal musculature passes down to the jaw. This, however, is probably a secondary attachment of relatively recent origin due to the reduction of the temporal muscles which has taken place; the mechanical advantage of the pterygoideus 'D' muscle is increased by the forward movement of part of its insertion.

It is instructive now to examine the attitude of the quadrate and the relative sizes of the pre-orbital, temporal and mandibular fossae in aëtosaurids, with these generalizations in mind.

The forms which have been considered to be the more primitive in other respects, namely *Aëtosaurus* and *Stagonolepis*, have the pre-orbital fossa well developed, including here as part of it the recessed area on the side of the snout, while the supratemporal fossa is small in *Aëtosaurus* at least. It is convenient to consider *Desmatosuchus* next because it is the most specialized in other respects besides being more reliably restored than *Typothorax* in the cheek region. The pre-orbital opening (as shown by the recessed area) is smaller, and the lachrymal and maxillary bones above the fossa are shallower than in *Aëtosaurus* or *Stagonolepis*, and in this respect resemble those of *Typothorax* closely. The supratemporal fossa of *Desmatosuchus* is very much enlarged, and evidence has been presented which suggests that the quadrate was more obliquely placed than in the European forms.

Part of the enlargement of the supratemporal fossa of *Desmatosuchus* is no doubt due to the necessity of compensating for the increased snout-, and therefore presumably also jaw-length, but it does seem probable that a trend parallel to that of the ornithischian dinosaurs took place in the aëtosaurids, with the temporal portion of the jaw musculature increasing in importance at the expense of the pterygoideus anterior. The jaw of *Desmatosuchus* is unfortunately unknown, but it is interesting to note that in *Typothorax* the mandibular fenestra is shorter, the cotylus is situated lower down, the surangular curves more strongly upward, and the portion of this bone above the fossa is deeper, than in *Aëtosaurus* or *Stagonolepis*. These differences suggest that in *Typothorax* a part of the temporalis musculature which originally inserted within the fossa had been added to that already attached to the surangular, the latter forming a kind of incipient 'coronoid process'.

There are other ways in which aëtosaurids resemble ornithischian dinosaurs. Thus the skull is considerably smaller than in 'normal' pseudosuchians; the anterior parts of the jaws lack teeth and the mandible is 'slipper-shaped'. The naris is large, and in *Stagonolepis* at least there is a peculiar snout not unlike the bill of hadrosaurs. The jugal is downcurved posteriorly. In *Desmatosuchus* and *Stagonolepis* the transverse processes of the anterior dorsal vertebrae extend markedly upward and the rib-facets are comparable in position to those of ornithischians. Dermal armour is well developed in both groups.

The ilium of aëtosaurids has a forwardly projecting spine. In the pelvis referred by Case (1932) and Gregory (1953*a*) to *Desmatosuchus* the ilium has a marked thickening of the upper margin above the posterior buttress, comparable to the antitrochanter of many ornithischians; ilia of *Stagonolepis* have a notable concentration of striations in this region.

However, in view of the specialization of the armour attained by the American forms it is rather unlikely that any particularly close connexion existed between the two groups. Certain other features, such as the probable loss of the coronoid, the reduction of the lower temporal fossa, the lateral position of the upper temporal fossa, and the typically pseudosuchian pubis prevent one from regarding the known aëtosaurids as ornithischian ancestors.

Although the resemblances listed above could perhaps be due entirely to convergence, it does not seem impossible that the aëtosaurids may lie closer to the origin of ornithischians than do other pseudosuchians known at present.

Some further points touching on possible relationships within the family may perhaps be mentioned. Thus the skull of *Typothorax* displays some minor features reminiscent of that of *Aëtosaurus*; as in the latter, the smooth area at the rear of the maxilla is longer than in *Stagonolepis*, and the tooth-counts of the two are similar. In addition, the naso-frontal and fronto-parietal sutures pursue similar courses.

Desmatosuchus resembles *Stagonolepis* in having a short toothless posterior area on the maxilla (Case 1922, pl. 5C) and a relatively large number of teeth on this bone (in fact the former genus possessed the largest number of maxillary teeth known in the group). However, the ornament of the paramedian dorsal plates differs from that of the other forms, consisting of coarse, irregularly rounded pits with no trace of radial arrangement. Too much emphasis should perhaps not be laid on this difference since the armour is so specialized in other ways, and the plates are exceptionally thick. The sculpture of the lateral plates does not appear to differ much from that of corresponding plates of *Stagonolepis*.

There is thus a possibility that the aëtosaurids may be capable of further subdivision into two groups, characterized by the differences detailed above. These may reflect adaptations to small variations in habitat and diet within a narrow ecological zone. Nevertheless, *Aëtosaurus* and *Stagonolepis* are far closer to one another in the sum of morphological characters than to *Typothorax* or *Desmatosuchus*; the specializations of the American genera, particularly of *Desmatosuchus*, mark them out as near-terminal members of the family.

The disparity between the lengths of the fore- and hind-limb in aëtosaurids has been noted; von Huene (1915) was led on this account to reject part of the material of '*Episcoposaurus horridus*' as being too small to belong with the femur (*vide* Gregory 1953*a*). However, the ratio of humerus to femur is also very similar in *Euparkeria* and other small pseudosuchians (see table 4).

TABLE 4. COMPARISON OF PROPORTIONS OF AËTOSAURIDS AND OTHER PSEUDOSUCHIANS

	Euparkeria	*Hesperosuchus*	*Ornithosuchus*	*Erpetosuchus*	*Scleromochlus*	*Saltoposuchus*	*Aëtosaurus*	*Stagonolepis*	*Typothorax*
skull/presacral column (%)	—	34	46	—	60	47	37	27	21
skull/scapula	218	230	202	244	320	265	202	122	102
skull/humerus	230	154	193	203	168	—	178	119	105
skull/ilium base	460	—	460	—	—	550?	330	178	170
skull/femur	143	103	128	—	107	129	113	78	66
scapula/humerus	103	67	96	83	53	—	88	101	103
humerus/femur	62	67	66	—	64	—	64	66	64
humerus + radius/femur + tibia	*c.* 60	67	66	—	59	—	61	63	67
radius/humerus	89	92	82	74	100	—	72	67	68
metacarpal III/radius	—	—	28	37	12	—	27	25	30
tibia/femur	< 100	93	83	—	113	86	79	60	60
metatarsal III/tibia	> 40	62	50	—	50	77	45	42	50

Data and estimates from Broom (1913), Colbert (1952), Sawin (1947), Woodward (1907).

Tibia length of *Ornithosuchus* assumed equal to fibula; position of lateral trochanter on latter (Newton 1894) suggests that it is virtually complete.

The data of this table also provide some further interesting comparisons. Thus there is a tendency for the epipodials to be rather longer in the smaller pseudosuchians, *Aëtosaurus* being intermediate in this respect between the smaller animals and the larger members of its own family. The presacral lengths of most pseudosuchians are unknown, but Colbert (1952) has given estimates for some of the ornithosuchids (using this term in a broad sense) which may be taken as a working basis. Since in *Ornithosuchus* the skull length is definitely known and the estimate of presacral length is probably close to the truth this form may be selected as typical: the ratio skull length/presacral length is given by Colbert as 46 %. The ratios for the aëtosaurids are given in the table. Again *Aëtosaurus* stands midway between typical ornithosuchids exemplified by *Ornithosuchus*, and its own larger relatives. Examination of the ratios of skull length to girdle and limb measurements affords confirmation of the above conclusion.

A point of special interest in some individuals of *Euparkeria* is the occurrence of a thyroid fenestra in the pubis in addition to the normal obturator foramen (Broom 1913; Haughton

1922). This does not appear to have been recorded in other thecodonts, with the notable exception of the Aëtosauridae as evinced by *Aëtosaurus* and *Stagonolepis*, in which it is closely comparable in shape and position with that of *Euparkeria*.

The palate of *Stagonolepis* was compared to that of Recent Crocodilia by Huxley (1877), who showed convincingly that 'the arrangement of the bones which surround the posterior nares is still distinctively and characteristically crocodilian'. The present study has confirmed this conclusion, disregarding, of course, for the purposes of the comparison the secondary enclosure of the narial passages posterior to the choanae in Recent crocodiles.

On the other hand Huxley regarded *Stagonolepis* and '*Belodon*' as the oldest true crocodiles, a point of view to which later discoveries did not lend support. The specializations of the skull of *Stagonolepis* are certainly more than sufficient to remove it from consideration as a direct crocodilian ancestor, nevertheless, the palate approximates rather closely in structure to that which one might expect to find in a Triassic crocodile.

The similarity in disposition of the vomers, palatines and pterygoids to those of Crocodilia was demonstrated by Huxley. A further resemblance lies in the occurrence of a thin ridge on the lateral or dorsal surface of the palatine in crocodiles which passes obliquely backward and upward towards the highest part of the bone. The lower lateral parts of the palatines already project slightly medially in *Stagonolepis*, and the development of distinct shelves meeting in the mid-line would give rise to the mesosuchian condition. For this to be accomplished, however, it is necessary for the vomers and the anterior parts of the pterygoids to be considerably elevated in the roof of the mouth.

Differences from the crocodilian condition are shown by, first, the occurrence of two ridges on the upper anterior part of each pterygoid of *Stagonolepis* as against a single thin ridge in crocodiles, which suggests that the lower edge of the median septum was divided in this region, and secondly, by the higher position of the medial shelf of the maxilla in *Stagonolepis*, which does not seem to be homologous with the palatal shelf of the maxilla of crocodiles.

The prefrontal of Crocodilia is peculiar in that its descending portion meets the dorsal surface of the palate close to the mid-line at the junction of the palatines and pterygoids; in some forms, for example, *Alligator*, *Crocodylus* and *Gavialis*, there is a distinct process given off medially from this descending portion, but in *Osteolaemus* there is no clear division into two parts. In crocodiles the olfactory tracts lie above these medially directed processes.

The prefrontal descends to meet the outer part of the palatine in *Sphenodon* and in many lizards and turtles, while in some lizards there are rudimentary processes of the prefrontals below the olfactory tracts. Brink has recently (1955) shown that in the specimen of *Chasmatosaurus* described by Broili & Schroeder (1934) the prefrontal extends down to meet the posterior end of the maxilla. On the other hand he notes that there seems to have been no descending process in a second specimen of the same genus, but the prefrontal has instead a short segment directed inward and downward. In *Stagonolepis* the prefrontal passes down on to the transverse and almost touches the maxilla; there is also a well-developed medial process below the region of the olfactory tracts, which however does not reach the mid-line.

It is difficult to imagine the derivation of the crocodilian descending process from that which meets the palate laterally in the forms mentioned above, since in crocodiles the process lies medially to the pterygoideus musculature. It may perhaps be homologous with the medially directed process of *Stagonolepis*.

The presence of a crocodilian type of ankle-joint has been noted in the aëtosaurids, being known definitely to occur in *Aëtosaurus* and *Typothorax*. Case (1929, figs. 23 and 24) has illustrated the calcaneum of a phytosaur, and an isolated astragalus said also to be of a phytosaur, which, as he points out, are extremely crocodilian. They are, however, more compressed from side to side than the corresponding bones of crocodiles and in this respect also they differ from the proximal tarsals of aëtosaurids. (The legends to Case's figures are transposed and require emendation, which probably accounts for his incorrect reference on page 54 to the calcaneum of '*Episcoposaurus*', figured by von Huene in 1915, as an astragalus.) A similar type of tarsus has been figured also in the case of *Prestosuchus chiniquensis* (von Huene 1942) and isolated calcanei referred by him to *P. loricatus* are very like that of *Typothorax meadei*, so that the crocodilian ankle-joint appears to have been present in at least three types of thecodont.

(4) *Mode of life*

The probable method of functioning of the dentition of *Stagonolepis* has already been considered, and whether or not the interpretation given is correct, it is clear that the mechanics of the jaws were essentially similar in all the four principal members of the family. It was also suggested that *Stagonolepis* was herbivorous, and some further evidence bearing on this question may now be discussed.

Sawin (1947) thought that *Typothorax meadei* was a necrophile, but it is difficult to imagine the weak premaxillary teeth of *Stagonolepis* dealing effectively with carrion, while the terminal expansions of the premaxillae seem obviously adapted for digging, or grubbing amongst soft vegetation, perhaps in shallow water. It is reasonable to assume, having in mind the greater degree of specialization shown by the American forms, that this structure was present in them also, and possibly even further elaborated. Digging may have been accomplished in the following manner. With the jaws closed and the skull held at an angle of about 45° to the horizontal, the snout and dentary rostrum are inserted into the substratum. Assuming that the occipital condyle remains stationary, contraction of the powerful depressor mandibulae muscle (shown by the rough area on the squamosal and the well-developed retro-articular process), assisted by the neck musculature results in the elevation of the snout. The rotation of the skull on the condyle carries the quadrate down and forward, and the jaws, which are now open, are driven deeper into the substratum. Contraction of the jaw muscles, accompanied by relaxation of the depressor mandibulae, now allows of a scooping action by the dentary rostrum as the jaws are closed. It is obvious that the greater the separation between the condyle and the jaw articulation, the greater will be the distance moved by the jaws for a given angle of rotation of the skull. The fact that in *Desmatosuchus* this separation is not greater than in *Stagonolepis* or *Aëtosaurus* (unless the restoration given is seriously in error), suggests that the depression of the quadrate has little connexion with the adoption of a digging habit by aëtosaurids. On the other hand the lower position of the occipital condyle in *Desmatosuchus* and *Typothorax* gives a better mechanical advantage to the dorsal neck muscles and this may well be the result of closer adaptation to the process outlined above.

There is no need to assume that the elongated naris of the aëtosaurids accommodated any kind of sac serving as a reserve air supply when grubbing under water, as was suggested by Romer & Price (1940) for the (differently shaped) naris of caseids, although this may have been the case. The shape of the naris seems but a consequence of the elongation of the snout, and the need to fashion an efficient poking apparatus from the materials at hand. Presumably the actual narial opening lay at the rear of the bony aperture, and some backward emargination has taken place, separating the nasal from the posterior tip of the premaxilla, in order to allow the deepest penetration of the snout without fouling the naris proper.

The number of preserved individuals of *Stagonolepis* from the sandstones of Lossiemouth, Spynie and Findrassie approaches that of all the other species combined. Of the other forms *Hyperodapedon* equals *Stagonolepis* in size, *Ornithosuchus*, *Erpetosuchus* and *Saltopus* are smaller, while *Brachyrhinodon*, *Leptopleuron* and *Scleromochlus* are very much smaller. Only the rare *Dasygnathus* is likely to have exceeded *Stagonolepis* in bulk. Assuming that the preserved specimens bear some relation to the number of dead individuals in the area, and it is clear that virtually all the fossils obtained from these rocks are little disturbed, the supply of cadavers would be totally inadequate for the subsistence of such a numerous and large species as *S. robertsoni*.

Also bearing on the problem of the diet of *Stagonolepis* are the palatal channels leading back from the choanae. In life these were perhaps closed in below by a soft palate; at any rate they conduct the air passages through the region between the maxillary and dentary batteries, suggesting that the food was of a nature requiring some degree of mastication before swallowing. The slicing action postulated after consideration of the dentition of *Stagonolepis* (see p. 133) could have been performed in the following way (figure 25*b*). The pterygoideus 'D' muscle (Lakjer 1926), originating from the upper surface of the palate and from the pre-orbital fossa, possibly gave a tendon to the intermediary tendon (as in crocodiles), but its main insertion was probably on the pre-articular. This muscle had a strong tendency to protract the jaw, movement of the latter being made possible by the flat nature of the articular surfaces and the movable quadrate. Retraction appears to have been facilitated by a slip from the medial portion of the external adductor which had a tendinous insertion on the small flange arising from the surangular. This portion probably originated from the inner sides of the postorbital and squamosal below the supratemporal fossa and perhaps helps to explain the close association of these elements in aëtosaurids.

The reduction in size of the skull finds its parallel in other reptilian groups which are commonly believed to have been herbivorous, e.g. sauropod and ornithischian dinosaurs and edaphosaurid pelycosaurs. The large naris, shape of the mandible, loss of anterior teeth and attitude of the quadrate particularly recall ornithischians, while a large naris is also found in the sauropods and in *Casea* and *Cotylorhynchus* among edaphosaurs.

The postcranial skeleton of aëtosaurids gives little positive indication of the mode of life of the group, unless the short manus and the excavation below the proximal end of the ulna be taken to indicate the use of the fore-limbs for digging, as seems not unlikely. The general construction of the skeleton is that of a thorough-going terrestrial animal, and as far as the Elgin Trias is concerned there is no trace of an aquatic environment, either lithological or faunal, unless the rhynchosaurs, as has been sometimes suggested, lived on fresh-water molluscs. The known fauna, however, is entirely reptilian and neither labyrinthodonts nor phytosaurs have been recorded. The reference to *Ceratodus* from Spynie (Traquair 1896; von Huene 1908*b*) was later stated by Taylor (1920) to be due to an error, the locality being in fact New Spynie in beds of the Upper Old Red Sandstone; the whereabouts of this specimen is unknown and it does not appear to have been described or illustrated. Most probably the record refers to *Conchodus*, since Traquair (1896) notes the occurrence of this genus in the Upper Old Red Sandstone of the region.

As already pointed out, the great majority of the specimens from the Elgin sandstones show that relatively little disturbance of the skeleton took place upon fossilization. There is therefore the anomalous situation of animals which apparently subsisted on vegetable matter (the aëtosaurids) occurring with relative abundance in what is probably an aeolian sandstone. It is very doubtful whether *Stagonolepis* at least could have existed for long in the environment suggested by the rocks in which it is found. Other members of the fauna, however, may have been able to do so, for example *Scleromochlus*. The construction of the pes in this animal parallels those of several modern types of rodent and marsupial which have independently become adapted for leaping over a sandy terrain (cf. Buxton 1955); indeed, Andrews (1907) compared *Scleromochlus* to a jerboa rat, although later authors have somewhat fancifully suggested arboreal habits.

Finally, it is possible that the expanded tail of *Aëtosaurus* provided a store of fat, as does a similar expansion in certain Recent lizards which inhabit arid regions. It would also have served as a counterbalance in bipedal stance, but the construction of the shoulder girdle and fore-limb indicate that quadrupedal locomotion was the normal mode of progress. Probably rapid movement was possible for short periods in aëtosaurids as in crocodiles by holding the limbs below the body; this would be facilitated by the separation at the glenoids, which is much less than in crocodiles.

To summarize, the evidence suggests that the aëtosaurids were herbivorous and that the snout was used for grubbing in soft vegetation or for roots, or possibly for digging out invertebrates. They appear to represent the first radiation of the archosaur stock along lines later adopted with greater success by the ornithischian dinosaurs.

XI. Note on the horizon of the Triassic sandstones of Elgin

Von Huene (1908*b*, *c*) correlated the sandstones of Lossiemouth, Spynie and Findrassie with the Lettenköhle of Germany. Neaverson (1955) states that the latter, although usually taken as the basal member of the Keuper, is closely connected with the Muschelkalk because of the occurrence of a band of dolomite near the top containing marine fossils including the ammonite *Alloceratites*. Von Huene's reasons for this correlation were as follows:

(1) Remains attributed to *Hyperodapedon gordoni* Huxley, a form first described by T. H. Huxley from the Trias of Elgin, are recorded from the Lower Keuper Sandstone (Waterstones) of Bromsgrove and Warwick in the English Midlands.

(2) *Mastodonsaurus giganteus* and *Equisetum arenaceum* are said to occur at Warwick and Bromsgrove respectively in the same formation as *Hyperodapedon gordoni*, and also in the German Lettenköhle.

It seems probable also that the views of von Huene (and other authors) concerning the age of the Elgin Trias have been influenced by the supposedly primitive nature of *Stagonolepis*, earlier looked on by von Huene as a primitive phytosaur and more recently as a primitive pseudosuchian. Better knowledge of *Stagonolepis* demands that a fresh approach be made to the problem.

The material said to be of *H. gordoni* from the Midlands (and also from Devonshire) consists in the main of isolated premaxillary 'tusks' and palatomaxillary tooth-plates. The more recently described rhynchosaurs from Brazil, East African and India (von Huene 1938*c*, 1940, 1942) have very similar tooth-bearing elements, and it is not impossible that the English specimens may represent a species, if not genus, distinct from that at Elgin. Thus von Huene (1940, pp. 7, 8) remarks on the similarity of the premaxillae and maxillae of *Hyperodapedon*, *Paradapedon*, *Cephalonia* and *Scaphonyx*.

The correlation of the Lower Keuper Sandstone of the Midlands with the Lettenköhle rests on rather slender grounds. In a later paper by Wills (1910) *Equisetum* (*Equisetites*) *arenaceum* is stated to be doubtfully identified from a single poorly preserved fragment; according to Schmidt (1928) its range is from the Lettenköhle to the Stubensandstein, while the distribution table in the Nachtrag to the above work (1938) extends this down to the Middle Muschelkalk and up to the Rhaetic. The specimens referred to *Mastodonsaurus giganteus* consist of casts of fragments of two mandibles (the originals have been lost) figured by Owen (1842) as *Labyrinthodon Jaegeri*. In 1874 Miall, in the course of a revision of the Warwickshire labyrinthodonts, states (p. 433): 'The fossil cannot, I believe, be certainly identified with *Mastodonsaurus giganteus* Jager, which differs in its sculpturing'. On the other hand he shows (fig. 2) a fragment of a 'left lateral thoracic plate' (clavicle), which is referred by him to that species, though whether such elements are diagnostic of species is perhaps doubtful. At any rate, *Mastodonsaurus* as a genus is known to range in Germany from the Middle Bunter to the Schilfsandstein, with a less certain extension to the Stubensandstein (Schmidt 1938).

Von Huene's correlation of the Elgin Trias had perforce to rely upon an intermediate stage involving the Lower Keuper Sandstone of the Midlands. In view of the extremely close relationship between *Aëtosaurus* and *Stagonolepis*, which can be demonstrated in practically every feature of the osseous anatomy, it is clearly preferable to take these two forms as providing the surest indication of age yet available, in contrast to the fragmentary and uncertainly identified amphibian and plant remains from the Midlands. There is the further immeasurable advantage that the German Keuper is known to succeed marine Middle Triassic rocks containing ammonites, and is followed in turn by Rhaetic and Liassic strata whose age cannot be in doubt.

The horizon of *Aëtosaurus* is thus fixed within narrow limits, since it occurs in the upper part of the middle division of the Stubensandstein, this formation in south-west Germany being separated from the Rhaetic Beds only by the Knollenmergel (Vollrath 1928; von Bubnoff 1935). Brinkmann (1948) gives as typical thicknesses: Knollenmergel 30 m; Stubensandstein 60 m; strata between the latter and the Lettenköhle 135 m. Following Continental practice, the Rhaetic is classed as the uppermost stage of the Trias on the affinities of its ammonite faunas in the marine developments of southern Europe. The Stubensandstein itself probably lies in the upper part of the Norian (or middle) stage of the Upper Trias.

An analysis of the morphological trends within the Aëtosauridae, and a direct comparison between *Aëtosaurus* and *Stagonolepis*, shows that the latter is the more specialized. Possibly, therefore, it is slightly the younger of the two, but the danger attendant upon using degree of specialization as an indicator of geological age is underlined by the occurrence of spinose scutes similar to those of *Typothorax* (Gregory 1953 *b*) in the Stubensandstein of Stuttgart.

Following von Huene, later authors have considered the '*Stagonolepis* Sandstone' as equivalent to the Lettenköhle. Colbert, for instance (1946), placed *Hypsognathus* from the Newark Series of New Jersey in the Upper Trias because of the advances it showed over *Leptopleuron* from Elgin, supposedly Middle Trias. However, as Colbert himself points out more than once, *Leptopleuron* and *Hypsognathus* are extremely closely allied as well as being highly specialized. The dentitions of the two are virtually identical. *Hypsognathus* has more spikes on the quadratojugal than *Leptopleuron*, but the spike on the tabular is better developed in the latter genus. There is some doubt about the age of the Newark Series (reviewed in Colbert 1946), but the consensus of opinion is that an Upper, perhaps even Late, Triassic position is indicated. *Hypsognathus* may well be a little later in date than *Leptopleuron*, but the difference between them can hardly be great.

It is of interest to note that many of the forms from the Trias of Elgin are specialized members of their respective groups. *Leptopleuron* has been mentioned above, and *Scleromochlus* in the preceding section. *Stagonolepis* needs no further emphasis. *Erpetosuchus* resembles *Stagonolepis* somewhat in the structure of the palate but differs in other respects, notably in that the teeth are restricted to the anterior parts of the jaws, being followed by what appear to have been horn-covered crushing flanges. The scapulocoracoid is very like that of the coelurosaur *Procompsognathus* (von Huene 1921, fig. 24). Pseudosuchian features, according to the list given in the latter work, would include the short cervical vertebrae, presence of interclavicle, and scutes. Discussion of the affinities of *Erpetosuchus* would be out of place here, and for the present it may be regarded as a very advanced pseudosuchian which perhaps preyed upon terrestrial arthropods. The enormous development of the anterior pterygoid muscle of *Ornithosuchus*, probably an adaptation to ensure rapid closure of the jaws, may also be looked upon as a specialization for the capture of fast-moving prey.

The abundance of pseudosuchians (five genera: *Ornithosuchus*, *Erpetosuchus*, *Scleromochlus*, *Stagonolepis*, *Dasygnathus*, out of a described fauna of ten genera) contrasts with the paucity of dinosaurian remains; the coelurosaur *Saltopus* (von Huene 1910) is known only from a partial skeleton and the single vertebra mentioned on p. 141 which is now provisionally referred to the genus. The explanation may be ecological: the pseudosuchians themselves exhibit a wide range of specializations and the place of the larger carnivorous dinosaurs may have been partly filled by the large pseudosuchian *Dasygnathus*. An ecological explanation must certainly be invoked to account for the absence of phytosaurs and stereospondyl labyrinthodonts which form a prominent element of Upper Triassic vertebrate faunas elsewhere, and which must have existed also during the Middle Trias.

The close affinity between the four main genera of aëtosaurids tends to show that, in a broad sense, the Dockum and Chinle formations include the equivalents of the Triassic sandstone of Elgin and the Stubensandstein of Germany, while the slightly higher degree of specialization attained by *Typothorax* and *Desmatosuchus* favours the allocation of a somewhat younger horizon to these forms. The pseudosuchians *Ornithosuchus* and *Erpetosuchus*, and the coelurosaur *Saltopus*, resemble in a general way *Saltoposuchus* and *Procompsognathus* respectively from approximately the same horizon in the Stubensandstein as the *Aëtosaurus ferratus* Group; *Ornithosuchus* also resembles *Hesperosuchus* from the Chinle of Arizona.

The most serious obstacle to the correlation of the Elgin Trias with a horizon close to the Stubensandstein lies in the absence of described rhynchosaur remains from the German Keuper. It may be noted, however, that the specialized procolophonids, for example *Hypsognathus* which is commonly regarded as Upper Triassic in age, have no known representative in the German Upper Triassic sequence. Furthermore, rhynchosaurs were until very recently entirely unknown from the North American continent and partly on this account Romer (1956) has suggested that they were 'essentially a Middle Triassic group'. The recent discoveries of rhynchosaurian remains by Baird and Take (Baird 1960) in the Wolfville Sandstone of Nova Scotia may go a long way towards resolving this difficulty. These workers have already (1959) provisionally correlated the Wolfville Sandstone with the New Haven Arkose of the Connecticut Valley and the Lower Brunswick Formation of New Jersey.

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XII. NOTE ON THE ILLUSTRATIONS

With few exceptions, the figures of *Stagonolepis* are drawn from casts; this is an inevitable consequence of the fact that most bones are preserved as natural moulds. As so many specimens are incomplete, it has been thought desirable, both for the sake of clarity and in order to reduce the number of illustrations to manageable proportions, to give composite figures in many cases. The sources of these are given either in the legends, or, in the case of the skull, in a separate section in the text. As far as possible the elements illustrated are of the left side and many specimens have been reversed to achieve consistency in this respect. The restorations of the skull and jaw (figures 2 to 6), of the whole skeleton (figures 22 and 23), and the majority of the text-figures of postcranial bones, refer to an individual of the larger size-group.

Figures (other than of the skull) drawn from or including actual bones

Figure 12*c*:	E.M. 37 R	Figure 19*f*:	M.C.Z.D. 3
Figure 19*a*:	G.S.M. 90901	Figure 20*b*:	G.S.M. 90917
Figure 19*b*:	M.C.Z.D. 3	Figure 21*a*:	M.C.G.D. 2
Figure 19*c*:	E.M. 33 R	Figure 21*b*:	R.S.M. 1952.10.1

Figures (other than of the skull) incorporating reversed specimens

Figure 12*a*: R 4784
Figure 12*b*: R 4784 and G.S.M. 90850
Figure 12*c*: R 4784, G.S.M. 90850 and E.M. 37 R
Figure 14*a*, *b*: R 4784
Figure 16: R 4789/4790, G.S.M. 90849 and E.M. 46 R
Figure 18: E.M. 34 R and E.M. 'A'
Figure 19*a*: G.S.M. 90901
Figure 19*c*: E.M. 33 R
Figure 19*d*: E.M. 26 R
Figure 19*f*: E.M. 48 R and M.C.Z.D. 10

Figures of specimens of the smaller size-group: 7*d*, *j* to *l*; 10*c* to *e*; 11*a* to *d*; 15*a*, *d*; 20*a*, *g* to *l*, *o*; 21.

Figures of specimens not assignable to either group: 10*f* to *m*; 11*e* to *i*; 20*c* to *e*.

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EXPLANATION OF ABBREVIATIONS USED IN FIGURES

Skull and jaw (figures 2 to 6)

a	angular	op	opisthotic
ar	articular	p	parietal
asq	articular areas for squamosal	pf	postfrontal
bo	basioccipital	pfl	parietal flange
bpt	basipterygoid process	pl	palatine
bs	basisphenoid	pm	premaxilla
c	coronoid	po	postorbital
ch	choana	popr	paroccipital process
d	dentary	pr	pro-otic
ec	ectopterygoid (transverse)	pra	prearticular
en	external naris	prf	prefrontal
eo	exoccipital	ps	parasphenoid
f	frontal	pt	pterygoid
fm	foramen magnum	ptf	post-temporal fossa
fo	fenestra ovalis	q	quadrate
ic	foramen for internal carotid	qf	quadrate foramen
imf	infra-Meckelian foramen	qj	quadratojugal
j	jugal	sa	surangular
l	lachrymal	soc	supraoccipital
ls	laterosphenoid	sp	splenial
m	maxilla	sq	squamosal
n	nasal	v	vomer

Foramina for cranial nerves in Roman numerals.

?pl VII inferred position of emergence of palatine branch of nerve VII and palatine artery.

Pes (figure 19*e*)

Ast	astragalus	?MII	possible distal end of metatarsal II
?MT	possible medial distal tarsal	PI-1	first phalanx of digit I
?LT	possible lateral distal tarsal	PI-2	second (ungual) phalanx of digit I
MI to MV	metatarsals I to V	?PV	possible phalanx of digit V

Shoulder girdle (figure 21*b*)

icl	posterior tip of interclavicle
cor	part of left coracoid

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FIGURES 26 TO 29

For explanation of plates see pp. 203, 204.

(*Facing p.* 202)

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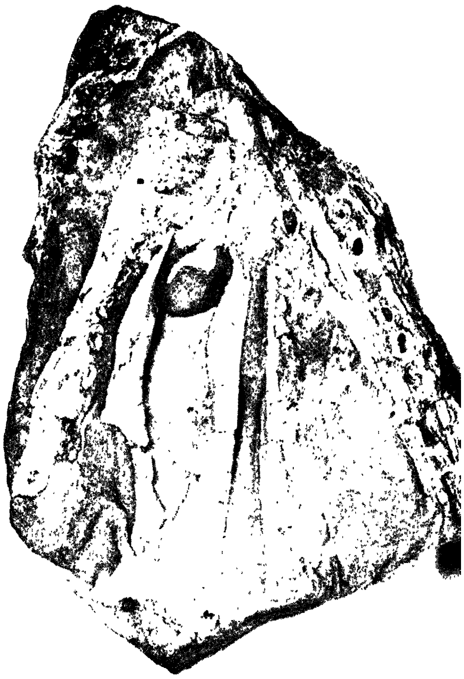

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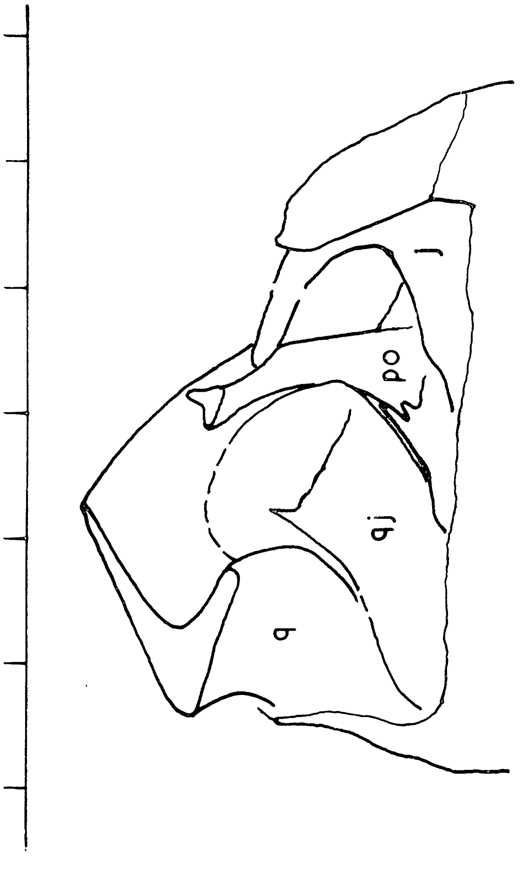

FIGURES 30 TO 33

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FIGURES 34 TO 37

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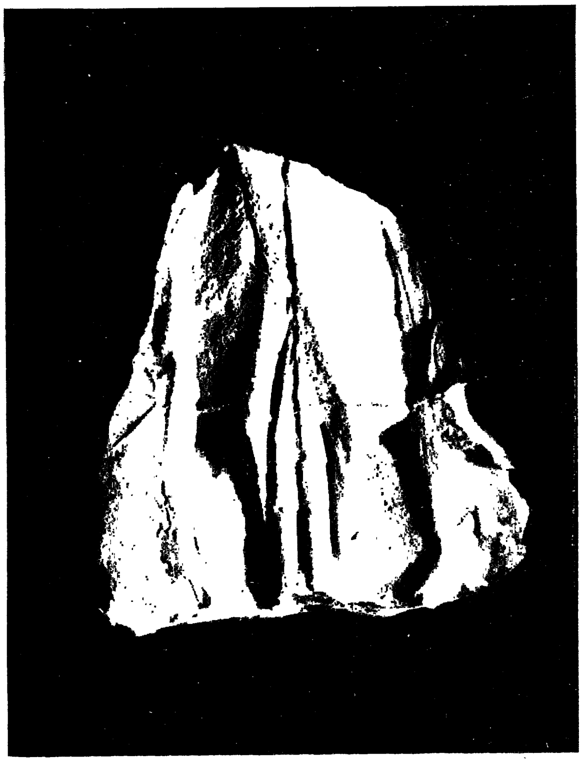

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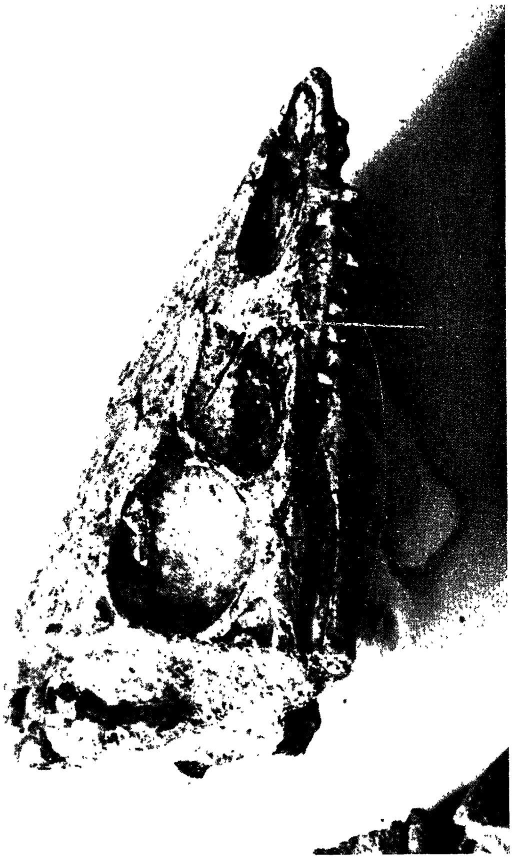

FIGURES 38 TO 41

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FIGURES 42 TO 45

EXPLANATION OF PLATES 9 TO 13

PLATE 9

Stagonolepis robertsoni Ag.

FIGURE 26. Left half of posterior portion of skull roof showing parietal flange, first two paramedian dorsal scutes of left side, and postorbital lying in supratemporal fossa. The slight excavation of the medial (morphologically anterior) edge of the anterior branch of the postorbital is an artifact of preparation. Skull compressed and upper end of squamosal displaced backward. Natural size. M.C.Z.D. 2/4.

FIGURE 27. Upper view of casts of compressed snout region showing expanded tips of premaxillae, nasals and portions of adjoining bones, parts of nares and left pre-orbital fossa. Scale in centimetres and millimetres. M.C.Z.D. 2/3 and 2/6.

FIGURE 28. Left side of specimen shown in figure 26. Upper margin of orbit, supratemporal fossa, squamosal and end of paroccipital with head of quadrate *in situ*, fragment of quadratojugal. Quadrate telescoped at mid-height and lower end missing.

FIGURE 29. Under view of same specimen, showing quadrate wing of left pterygoid, left quadrate, squamosal, paroccipital and part of left half of braincase with ventral ridge from otic bones, foramina for nerves VII and XII and left lateral pit at junction of basioccipital and basisphenoid.

PLATE 10

Stagonolepis robertsoni Ag.

FIGURE 30. Cast of undersurfaces of parts of the nasals, frontals and adjoining bones to show the paired depressions medial to the pre-orbital fossae; these have been made shallower by the compression suffered by the specimen. M.C.Z.D. 2/2.

FIGURE 31. Underside of the block from which the above cast was taken showing posterior end of right choana and right palatine and pterygoid forming palatal channel. Vomer missing. M.C.Z.D. 2/2.

FIGURE 32. Cast from M.C.Z.D. 2/5, showing parts of right quadrate (sectioned horizontally above), quadratojugal, postorbital (fractured below) and posterior rami of jugal. Key diagram to right.

FIGURE 33. Upper view of cast of left pterygoid (hole is artificial). Natural size. E.M. 20R.

PLATE 11

Stagonolepis robertsoni Ag.

FIGURE 34. Oblique medial view of left premaxilla, maxilla and nasal (with fragment of right nasal) surrounding external naris. Natural size. E.M. 38R.

FIGURE 35. Anterolateral view of left quadrate, the lateral wing broken off. Natural size. E.M. 44R.

FIGURE 36. Outer view of cast of detached right maxilla, incomplete in front. Natural size. R 4787.

FIGURE 37. Inner view of same cast. Natural size. R 4787.

PLATE 12

Stagonolepis robertsoni Ag.

FIGURE 38. Cast of upper surface of middle part of palate (magn. × 0·93). G.S.M. 37049.

FIGURE 39. Cast of lower surface of middle of palate, showing choanae and palatal channels (magn. × 0·93). Taken from the counterpart of the above, G.S.M. 37051.

Aëtosaurus ferratus O. Fraas

FIGURE 40. Right side of the skull of No. VII. Two-thirds natural size. The left premaxilla (showing alveoli) is detached and lies close to the snout-tip, the detached left maxilla is seen in medial view crossing beneath the tip of the right dentary, the left jaw ramus is also displaced and the dentary projects from beneath the right ulna. Also visible are parts of both fore-limbs, the right uppermost. The supra-orbitals form an arch across the top of the orbit but the bone has been largely stripped off.

FIGURE 41. Right side of the skull of No. XVI. Natural size. The posterior two supra-orbitals occur towards the top of the orbit.

PLATE 13

Aëtosaurus ferratus O. Fraas

FIGURE 42. Left side and roofing bones of skull of No. XVII, spread out in the same plane. Natural size. The bones of the cheek region have been stripped off, revealing part of the left transverse, pterygoid, quadrate (lateral wing missing) and, parallel to the posterior edge of the latter, the ?hyoid bone. The lachrymal canal is seen as a dark line crossing the lachrymal obliquely.

FIGURE 43. Right side of skull of No. XVIII, showing the natural contact of the postorbital and squamosal, the lower edges of which are complete. The three supra-orbitals lie across the upper part of the orbit.

FIGURE 44. Left ilium, parts of both ischia and left hind-limb of No. XXII, also second sacral and first caudal vertebrae, and ventral armour surrounding the cloaca and at the root of the tail (for a restoration of this region see figure 23*c*) (magn. × 0·6).

FIGURE 45. Pelvis and left hind-limb of No. II (magn. × 0·69). Left ilium in medial view, the blade partly hidden beneath vertebrae; both pubes and ischia seen obliquely from above right, the symphysis of the ischia not exposed and the lateral margin of the right pubis somewhat forced down across the left femur. Left crus and pes in posteromedial view.

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FIGURES 26 TO 29

For explanation of plates see pp. 203, 204.

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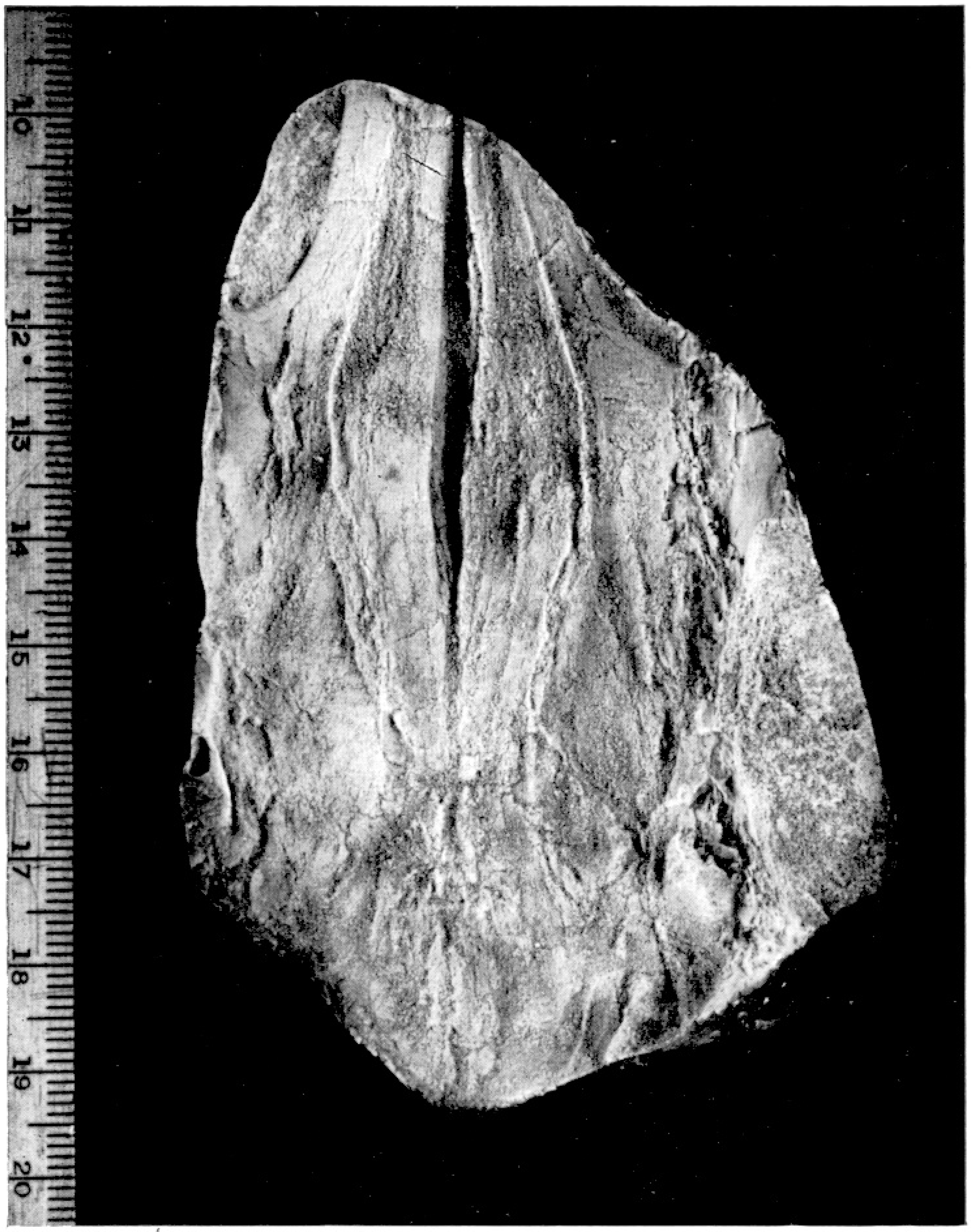

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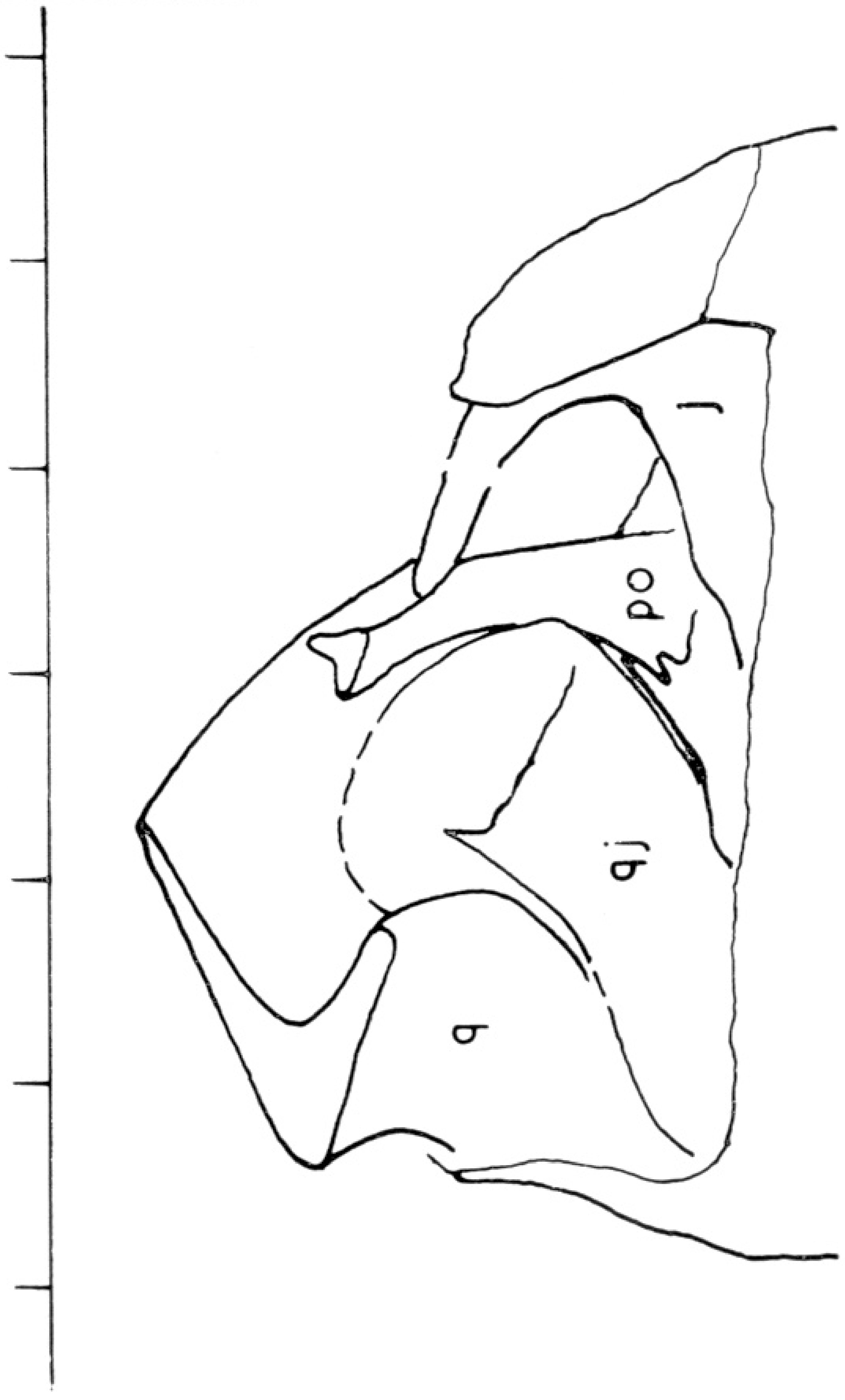

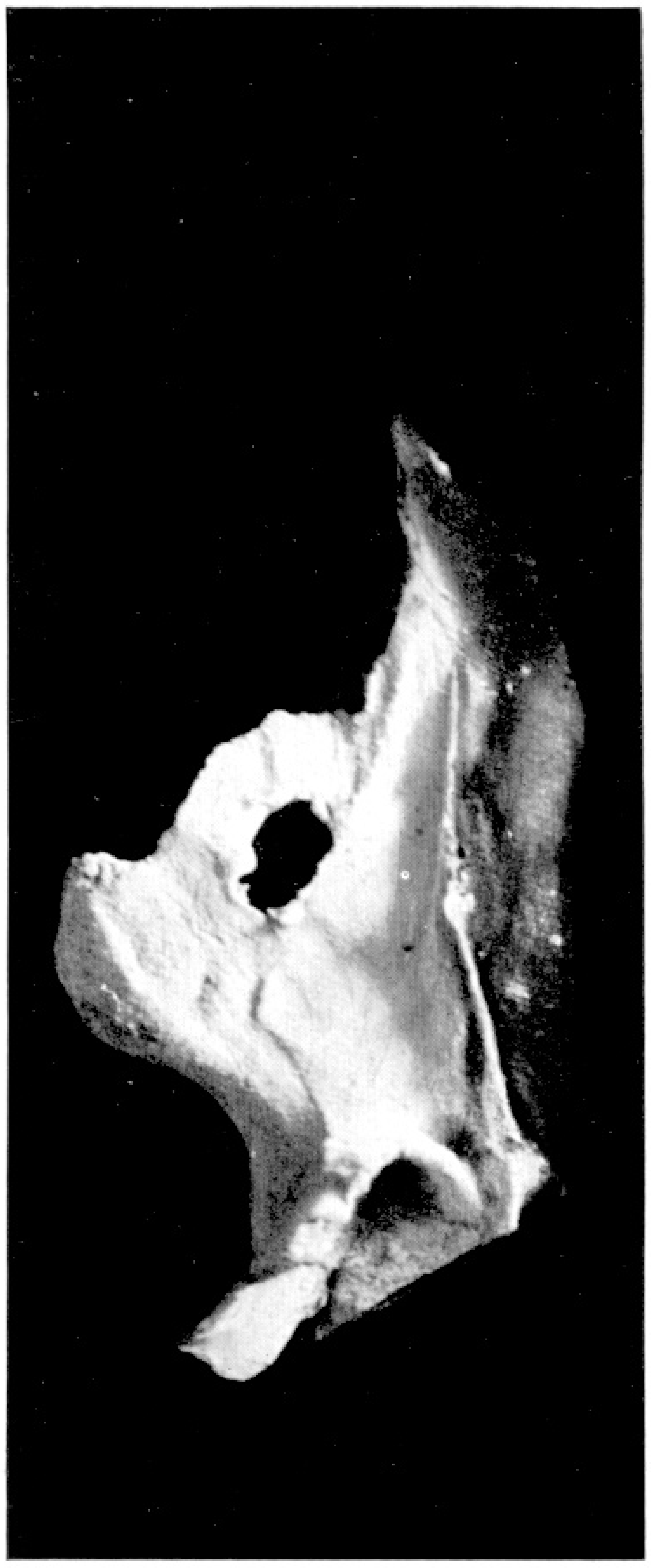

FIGURES 30 TO 33

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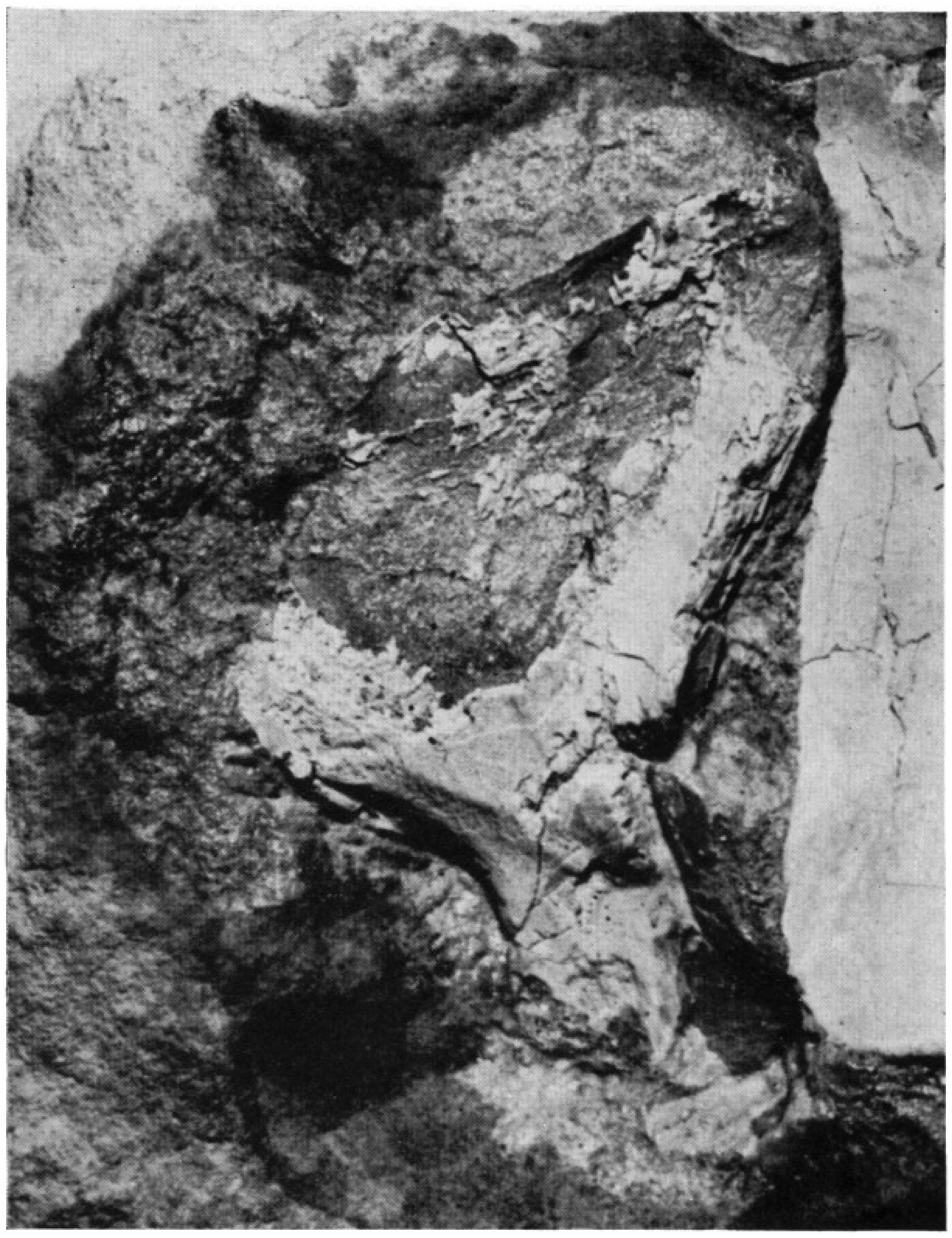

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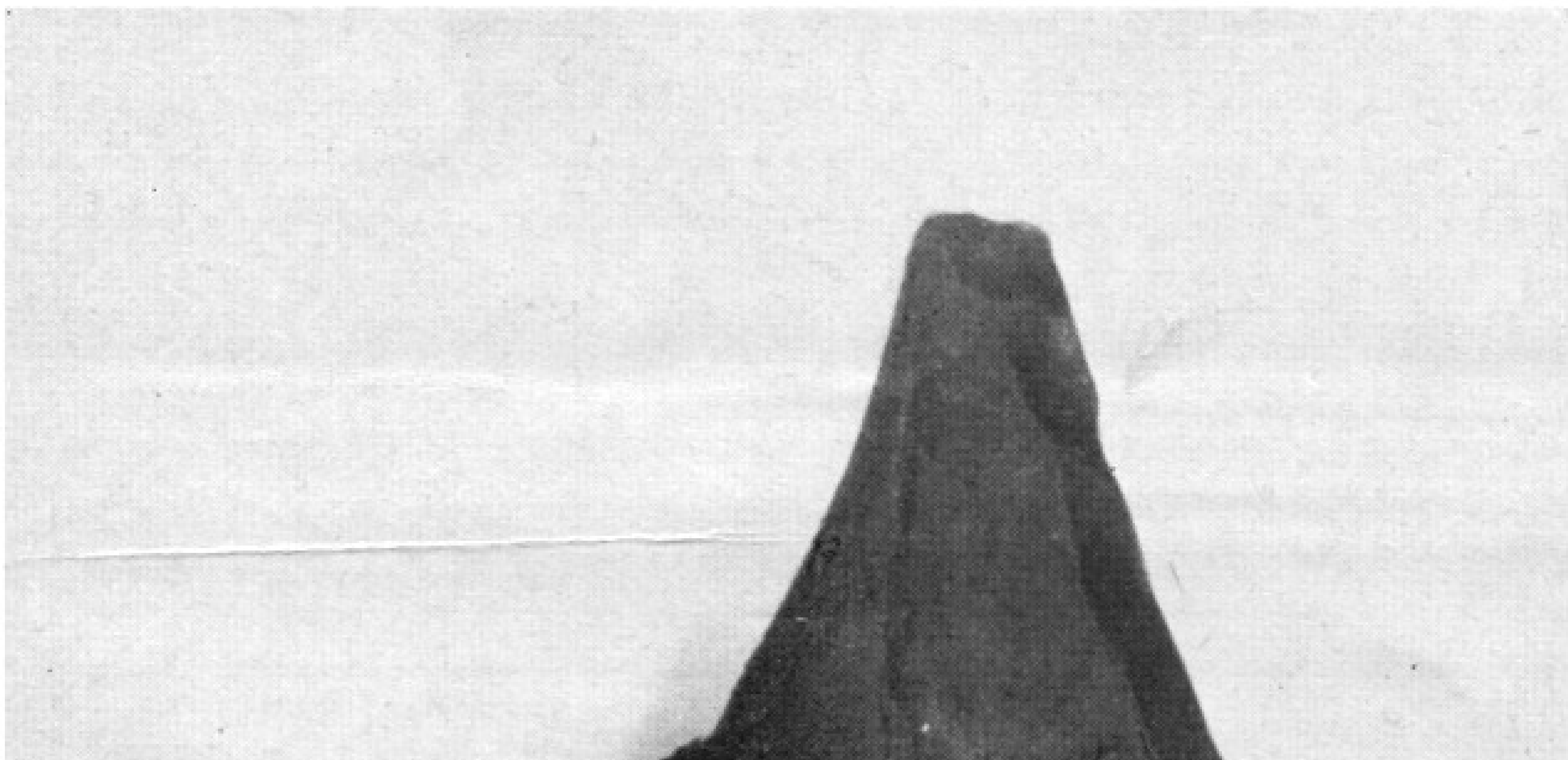

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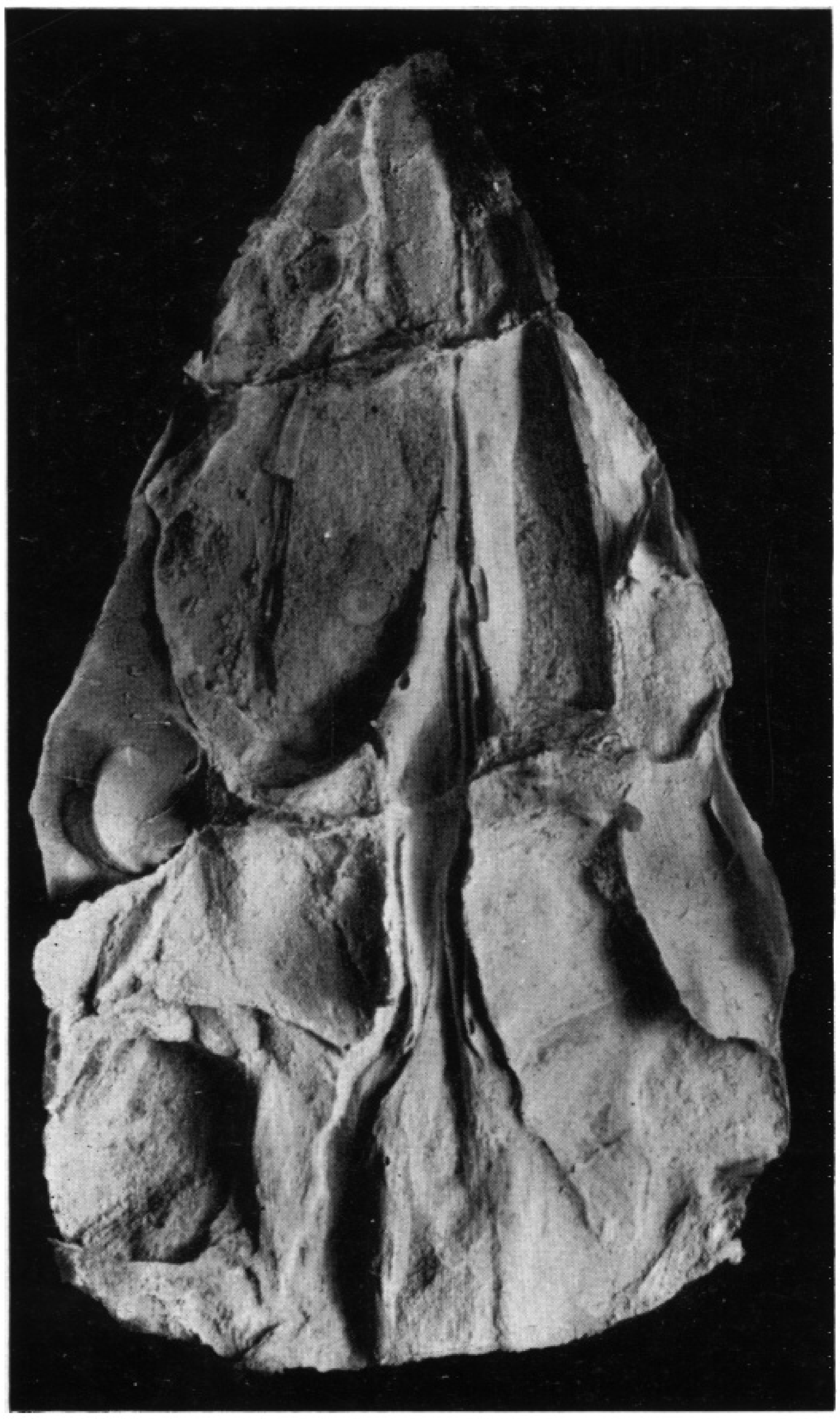
Figures 34 to 37



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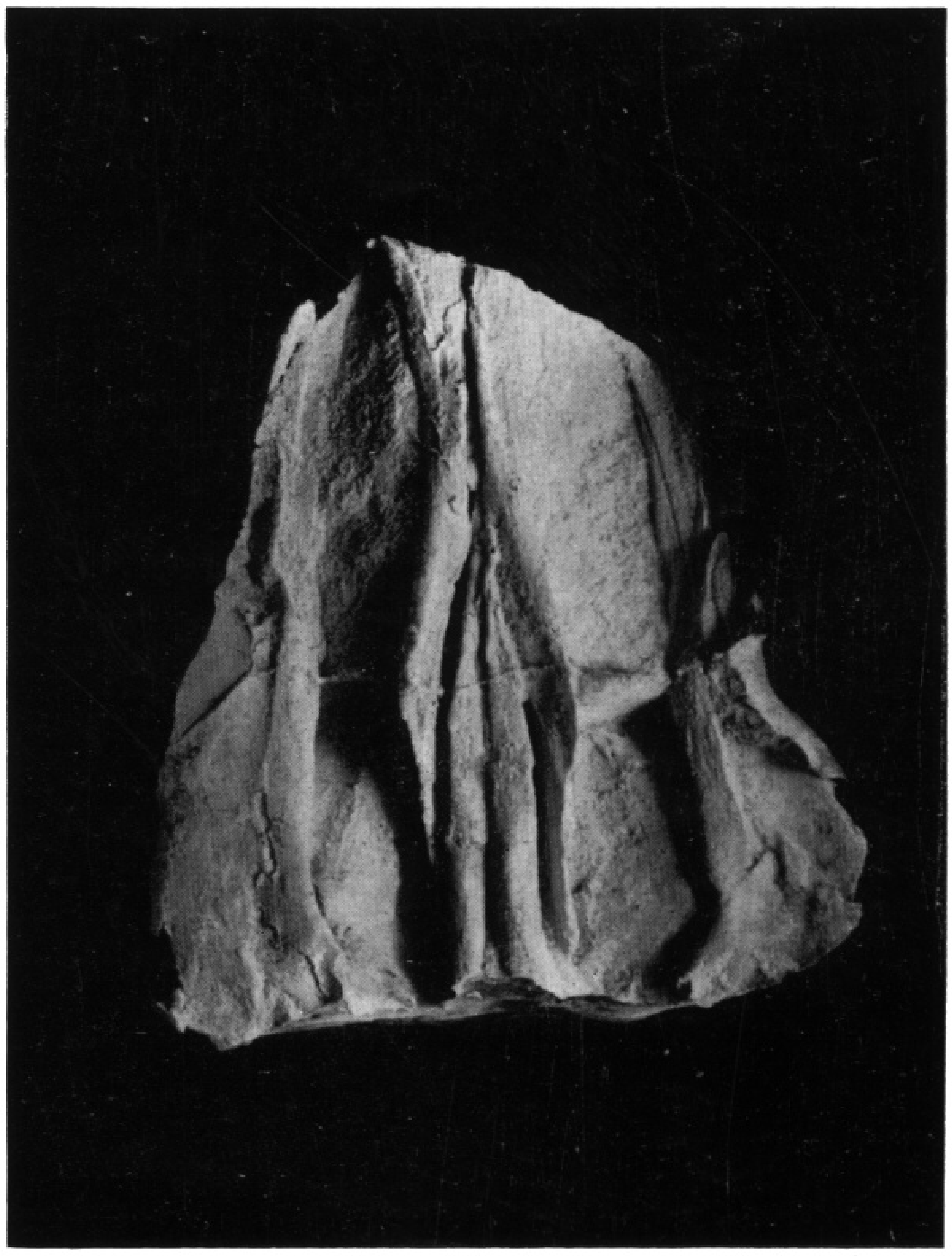

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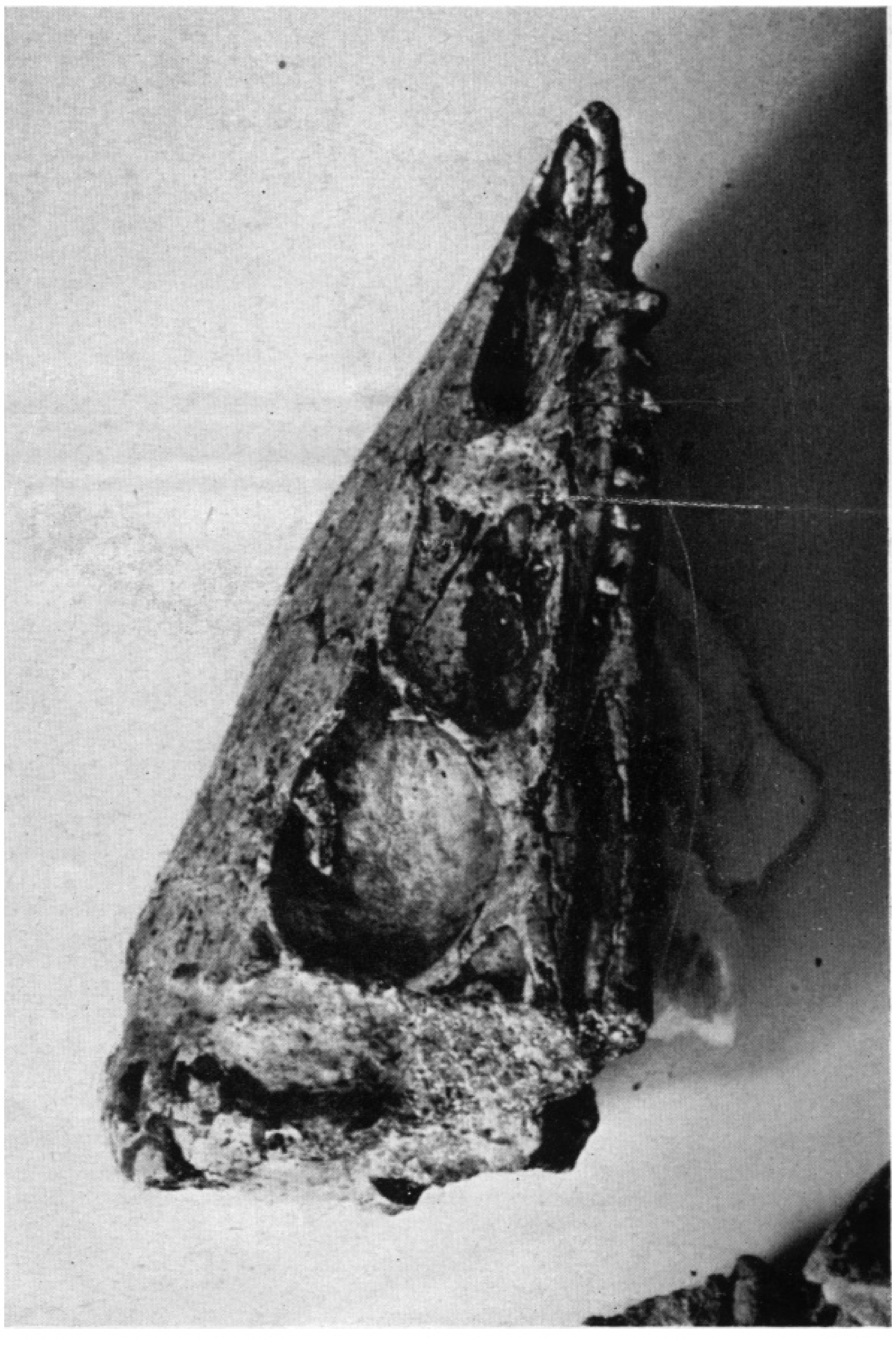

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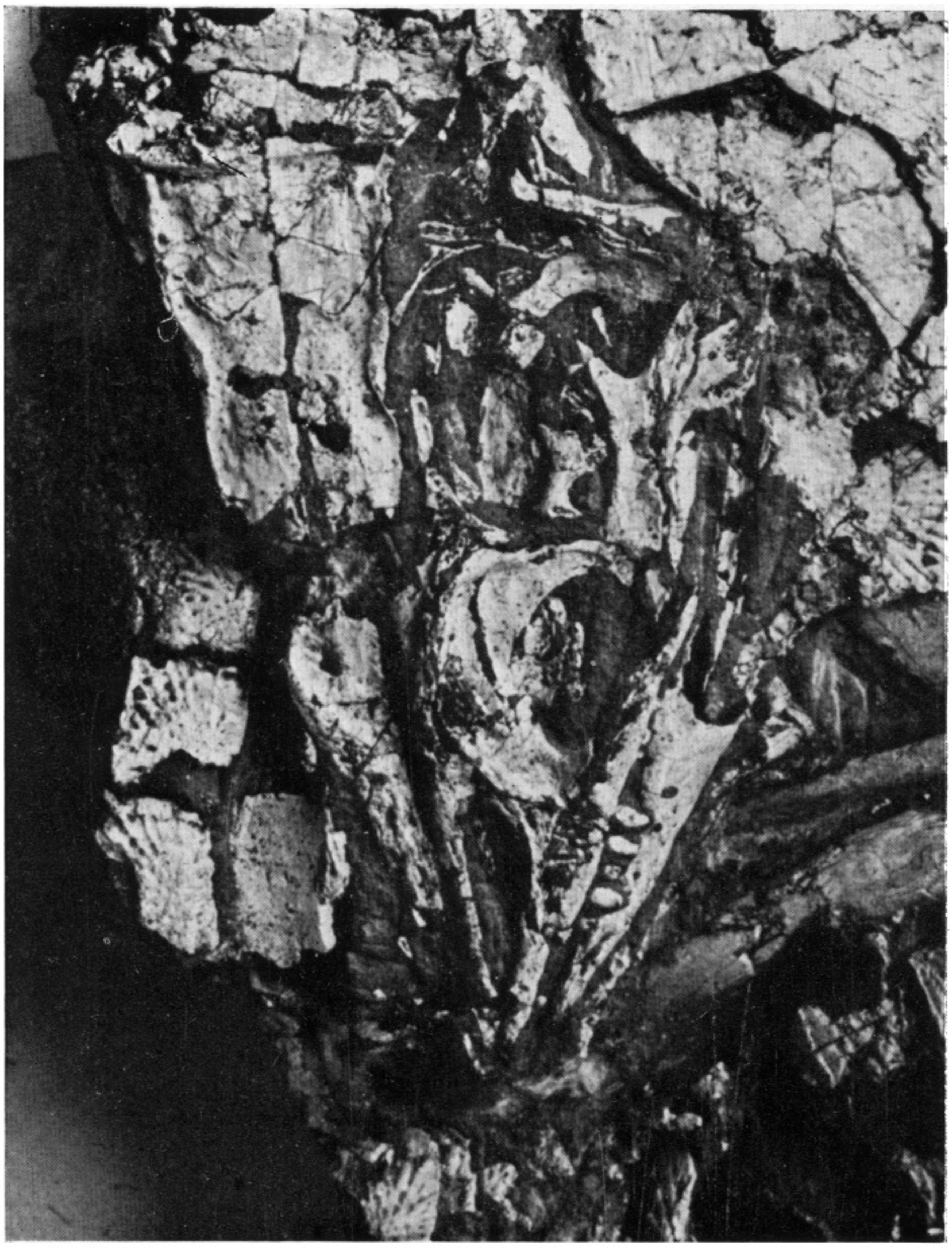

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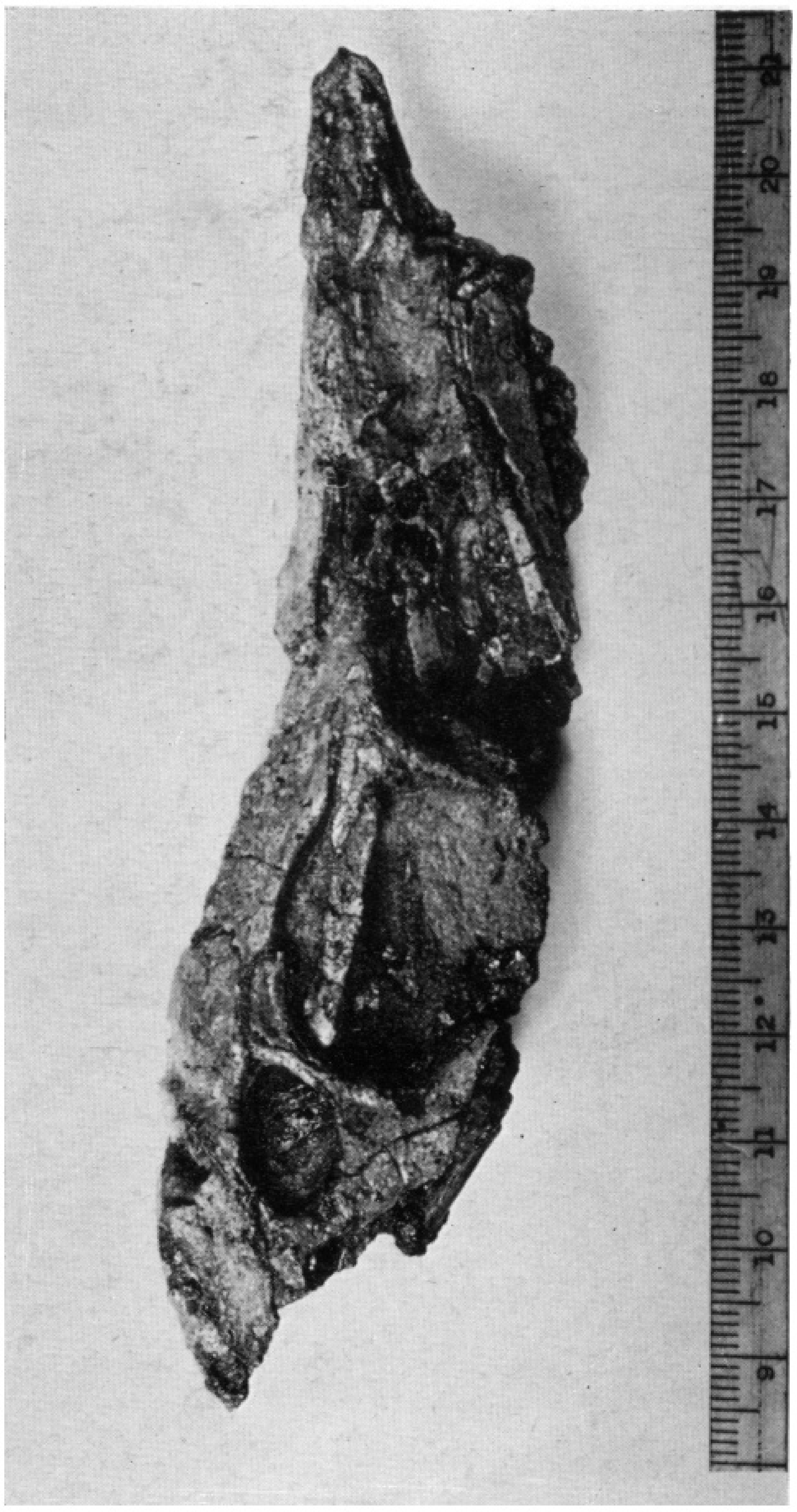

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Figures 42 to 45