TRIASSIC REPTILES FROM THE ELGIN AREA: *ORNITHOSUCHUS* AND THE ORIGIN OF CARNOSAURS

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CONTENTS

The osteology of *Ornithosuchus* is described in some detail. This study is largely based on material discussed by previous workers, but also takes into account specimens hitherto undescribed. It is considered that the species *O. taylori* Broom 1913 is invalid, being based on larger individuals of the form previously named *O. woodwardi* by Newton (1894). Furthermore, evidence is presented to show that specimens previously described by Huxley (1877) and Walker (1961) as *Dasygnathus longidens* are also referable to *Ornithosuchus*. It is concluded that but one species is present in the material, the correct name for which is *Ornithosuchus longidens* (Huxley). At least eleven individuals are present with skulls ranging from about 50 to 450 mm in length. Observations on the smaller members of this series suggest that changes in the shape and proportions of the skull took place with growth in a similar manner to those seen in living crocodiles.

In the light of new information concerning the osteology of *Ornithosuchus* it is considered that this reptile is a primitive carnosaur, occupying a position very close to the ancestry of the Jurassic and Cretaceous members of this group. An examination of descriptions and figures of Triassic reptiles referred by von Huene (1932) and later authors to the Carnosauria has led to the conclusion that the great bulk of this material is more properly allocated to the Prosauropoda, and that the only Triassic carnosaurs known at the present time, apart from *Ornithosuchus*, are *Teratosaurus* and *Sinosaurus*, these two names being here used in a restricted sense.

It is suggested that *Ornithosuchus* is close to the common ancestry of both the Megalosauridae and the Tyrannosauridae, and the derivation of the skull patterns of these forms from that of *Ornithosuchus* is discussed. Additional fenestrations marginal to the preorbital fossa and in the surangular of advanced carnosaurs are held to be related to the development of the pterygoid musculature rather than to the need to lighten the skull. In the course of a brief review of the Carnosauria the view is put forward that *Acrocanthosaurus* is a Lower Cretaceous representative of the tyrannosaur group, using this term in a broad sense, and is perhaps related to the Cenomanian *Spinosaurus* and the Wealden *Altispinax*. As a result of examination of English megalosaurian material, the name *Eustreptospondylus oxoniensis* gen. et sp.nov. is proposed for the Oxford specimen previously known as '*Streptospondylus*' *cuvieri*, and *Metriacanthosaurus* gen.nov. for *Megalosaurus parkeri*. The incomplete cranium from Dives figured by Piveteau (1923) is made the type of a new species, *E. divesensis*, to which certain other carnosaurian material from Normandy is provisionally allocated. Following

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Chakravarti (1935), the endoskeletal elements included by Matley (1923) in the type material of the Indian nodosaur *Lametasaurus* are held to belong to one or other of the two carnosaurs *Indosuchus* and *Indosaurus*, but the numerous scutes are not thought to be carnosaurian and the name *Lametasaurus* is here restricted to them. It is suggested that *Indosuchus* from the ? Turonian is a tyrannosaurid. On the other hand *Ceratosaurus* and *Proceratosaurus* are regarded as coelurosaurs.

A modified classification of the Infra-order Carnosauria is given, in which two main groups are recognized; Superfamily Megalosauroidea to include the Megalosauridae, and Superfamily Tyrannosauroidea to include the Ornithosuchidae (restricted), Spinosauridae and Tyrannosauridae.

I. Introduction

The name *Ornithosuchus woodwardi* was first applied by Newton (1894) to the skeleton of a small reptile from the Triassic sandstone of Spynie quarry, near Elgin, although, as will appear later, this was not the first specimen of this genus to be discovered. Newton was able to describe most of the skeleton with the exception of the shoulder girdle and fore-limb. He concluded: 'the difficulty of separating the two groups (i.e. the Parasuchia, which then included both *Stagonolepis* and 'Belodon', and the Dinosauria) is increased by a study of this new Elgin reptile, which holds, as I think, a more intermediate position between the two series, than any form hitherto described, for although the characters of its skull and teeth find their nearest counterpart among the Dinosaurs, and the pelvis and limbs might belong to either a Theropodous Dinosaur, or a Parasuchian... it seems most in accordance with the facts to place it provisionally with the Dinosaurs'. Earlier Newton (1893) had made the interesting statement that 'the skull is, in fact, that of a miniature megalosaur'.

In 1901 remains of two much larger individuals were discovered at Lossiemouth and were described by Boulenger (1903), who considered that there were no differences between these specimens and that of Newton which might not be dependent on age, and nothing, in his opinion, would justify their reference to a distinct species. Boulenger disagreed with the conclusions of Newton concerning the systematic position of *Ornithosuchus*, preferring to regard it as a member of the Parasuchia, along with *Aetosaurus*, '*Herpetosuchus*' (i.e. *Erpetosuchus*), *Stagonolepis* and '*Belodon*'. His reasons for doing so are not clearly expressed, but apparently the presence of clavicles and abdominal ribs were the main criteria upon which he based his judgement.

Notwithstanding the remarks made by Boulenger about the larger individuals mentioned above, Broom (1913) established a new species *O. taylori* for the reception of these forms, and in addition gave figures of the skull and pelvis of *O. woodwardi* which differed somewhat from those of Newton. Broom also illustrated the shoulder girdle and fore-limb of a specimen of equal size to that described by Newton, which had been recently acquired by the British Museum. He pointed out that the views of Newton and Boulenger were not really so much at variance as appeared at first sight, and he went on to consider the Pseudosuchia as a group ancestral to dinosaurs, pterodactyls and birds.

Von Huene (1914) re-figured the shoulder girdle and fore-limb which had been dealt with by Broom; his illustrations differ considerably from those of the latter author. In the same paper he also described the scapula and fore-limb of a specimen in the Manchester Museum. In this work the idea of the Pseudosuchia as a basic stock from which may be derived the two orders of dinosaurs, the pterosaurs, birds and also the crocodiles is fully elaborated and has since gained wide acceptance. Heilmann, for example (1926), used *Ornithosuchus* extensively in his reconstruction of the 'hypothetical proavian'; his drawings were based upon plasticine models, the data being derived from previous publications. His life restoration of *Ornithosuchus* is usually accorded the place of honour at the base of the family tree of the dinosaurs. This Elgin reptile has thus become firmly established in the literature of vertebrate palaeontology as an archetypal pseudosuchian, almost, in fact, *the* archetypal pseudosuchian.

Yet the materials for a different assessment of the status of *Ornithosuchus* have existed since the early part of this century, both in the skeletons already mentioned and in other museum specimens.

The present study has shown that, although *Ornithosuchus* is fully as important an ancestor as previous workers have believed, it stands in special relationship to one group only among the dinosaurs, namely the Carnosauria, for while von Huene (1932) derived the Jurassic and Cretaceous members of this group from certain Triassic forms, this has never been wholly convincing, and now that *Ornithosuchus* is more accurately known the great majority of these Triassic 'carnosaurs' can be relegated to the vicinity of the group known as the Prosauropoda, to which they are obviously more nearly allied.

The foregoing is not intended to be a complete resumé of the history of previous work upon *Ornithosuchus*, since this is bound up with questions of a taxonomic nature which are more appropriately considered in a later section.

II. Material and methods

It is convenient at this point to give a list of the known specimens of *Ornithosuchus* in order of size together with their museum reference numbers. The latter will then be used in the taxonomic and succeeding sections of this paper in order to avoid unnecessary repetition. The prefix 'R' denotes a specimen in the collection of the British Museum (Natural History), 'G.S.M.', 'E.M.' and 'L' likewise indicate specimens in the collections of the Geological Survey and Museum, London, Elgin Museum and Manchester Museum, respectively.

1. R 8170. A series of ten small dorsal vertebrae with ribs and scutes, the left scapula, coracoid and humerus; estimated skull length 50 mm. Spynie Quarry, collected by the Rev Dr G. Gordon, *ca.* 1890. A note by Newton attached to the specimen identifies the vertebrae as ?cervicals (this is due to the misleading appearance of the natural mould) and states that it was associated with the type of *O. woodwardi*, to which, however, it could not be fitted; the occurrence of three larger scutes on the same block tends to confirm the association. (Previously numbered R 2410*a*.)

2. R 3149. A skull and most of the skeleton; skull length (snout–quadrate) estimated at 60 mm. East Quarry, Lossiemouth, collected by William Taylor in 1895.

3. G.S.M. 91072–78, 91080–81, 91085–86. A series of poorly preserved small vertebrae with paired scutes above, traces of a fore-limb, and a pair of hollow femora incomplete at both ends. Length of the latter probably between 50 and 75 mm originally. There is little definite upon which to identify this specimen, but the presence of paired dorsal scutes associated with hollow femora probably indicates an *Ornithosuchus* which would be midway in size between numbers 2 and 4 of this list. The peculiar preservation and matrix link

these eleven pieces together and many of them do in fact fit. Spynie Quarry, 'purchased by Mr Howell (of the Geological Survey), March 14th, 1893'.

4. R 2409 (skull) and R 2410 (postcranial skeleton). The type specimen of *O. woodwardi* Newton, described and figured by Newton (1894) and Broom (1913). Skull, vertebrae from the third dorsal to the middle of the tail, pelvis, parts of the hind-limbs, scutes and abdominal ribs. Skull length (snout–quadrate) 115 mm. Spynie Quarry, collected by the Rev Dr G. Gordon, *ca.* 1890.

5. R 3561. A series of vertebrae from about the ninth dorsal to the posterior region of the tail, with scutes above, an excellent pelvis, right femur, proximal ends of tibia and fibula, and left femur. Estimated skull length 115 mm (based on similarity of size to R 2410). Mentioned by Broom (1913, p. 626). Lossiemouth, purchased from W. Taylor, November 1907.

6. R 3916. Vertebrae from the fifth cervical to the 1st sacral, with scutes above, almost the entire shoulder girdle and right fore-limb, left humerus, incomplete pelvis, proximal half of right femur, abdominal ribs. The rear part of the specimen shows obvious distortion. Partly figured by Broom (1913) and von Huene (1914). Estimated skull length again 115 mm. Lossiemouth, purchased from W. Taylor, July 1911.

7. L 8271. Specimen showing part of a skull, posterior cervical and/or anterior dorsal vertebrae, scutes, right scapula and most of fore-limb. Figured by von Huene (1914), but pieces containing parts of the limb cannot now be traced. Skull length estimate (based on length of ulna) 138 mm. West Quarry, Lossiemouth, given to the Manchester Museum by D. M. S. Watson.

8. R 3562. A distorted incomplete skull and two cervical scutes. Mentioned by Broom (1913, p. 626). Estimated skull length 180 mm. Lossiemouth, purchased from W. Taylor, November 1907. (Some further parts of this skeleton are described in the Appendix.)

9. R 3142. The greater part of a somewhat distorted and crushed skull in several pieces, cervical vertebrae with scutes above, also dorsal and caudal scutes, caudal vertebrae, crushed shoulder girdle, right humerus, proximal ends of radius and ulna, proximal end of left humerus, gastralia. Many other small pieces are in a very poor state of preservation; few of these can be fitted together and most are unidentifiable. Partly figured by Boulenger (1903, 'first specimen', Plate 15); one of the syntypes of *O. taylori* Broom (1913). Estimated skull length 220 mm. Collected by W. Taylor, West Quarry, Lossiemouth, 1901, purchased November 1903.

10. R 3143. A partial skull consisting of the snout with left dentary and entire right jaw ramus in place. Behind these are the detached right quadrate, quadratojugal, pterygoid, palatine, transverse and jugal, also the left lachrymal, angular and splenial. A small fragment shows several dorsal scutes. There are also a large number of pieces with unidentifiable bones. Partly figured by Boulenger (1903, 'second specimen', Plate 14); one of the syntypes of *O. taylori* Broom. Skull length 250 mm. Collected by W. Taylor, West Quarry, Lossiemouth, 1901, purchased November 1903.

11. E.M. 1 R. A large right maxilla, type of *Dasygnathus longidens* Huxley (1877), also figured Walker (1961). Right pterygoid (E.M. 15R), figured Walker (1961). Additional bones here referred to this individual are the stapes, a partial caudal vertebra, a phalanx and chevron-bone (all on the E.M. 15R slab), right nasal (E.M. unnumbered) and left

articular (E.M. 29R). Estimated skull length 450 mm. All from Findrassie Quarry, collected *ca.* 1859.

A complete right pubis 150 mm long (R 3152) probably belongs to either number 9 or 10 of the above list since it formed part of the same purchase from W. Taylor by the British Museum, November 1903, and is of suitable size to have come from either of these individuals.

It is necessary to give an explanation of the state of preservation of the skull of R 2409, since certain facts do not emerge clearly from Newton's account of this specimen. The skull has been prepared in such a way as to leave a 'frame' of matrix about one inch thick around it, extending outwards on all sides from the lower margin of the skull. In two areas longitudinal slots have been created; one of these extends along the left side from near the snout back to the base of the orbit. The other exposes the base of the right orbit. Much bone has been lost from these and other areas of the skull. The skull roof in front of the orbits has been repaired with plaster and the sutures between the nasals, frontals, lachrymals and prefrontals are now obscure. The left postfrontal area is largely represented by the impression of its lower surface. It is suspected that a good deal of the damage was incurred during the collection and preparation of the specimen, since the bone, as usual, is extremely friable, and the greater part of the basioccipital had already been lost at the time of Newton's account.

The methods used in the study of *Ornithosuchus* have not differed in any important way from those employed during the investigation of *Stagonolepis* (Walker 1961). As before, a great deal of detailed information has been obtained from the exploitation of natural moulds or from negatively prepared specimens by the use of flexible casting compounds. Most of this work has been carried out by the writer in the Department of Geology, University of Newcastle upon Tyne. Some positive preparation has been done on the skulls of R 3149 and R 3562 in Newcastle, and in addition some further development has been undertaken by Mr A. E. Rixon in the British Museum on the skull of R 3142.

In order to illustrate the distribution of size amongst the individuals in the material studied, the estimated skull lengths are listed below:

	mm		mm
R 8170	50	L 8271	138
R 3149	60	R 3562	180
G.S.M. 91072, etc.	85	R 3142	220
R 2409	115	R 3143	250
R 3561	115	E.M. 1R, etc.	450
R 3916	115		

III. TAXONOMY

There are two matters to be considered under this heading, first, the question of the validity of the distinction made by Broom (1913) between the larger skulls R 3142 and R 3143 on the one hand and R 2409 on the other, and secondly, the status of the specimens referred to *Dasygnathus*. Only after these issues have been decided can the choice of a correct name for the material be made.

If one examines Newton's figure of the right side of the skull of *Ornithosuchus* (1894, Plate 55) the following points may be observed: (*a*) the jugal/quadratojugal bar is apparently very slender, with a relatively long overlap between these two bones; (*b*) the lower part of the postorbital/jugal bar is also slender; (*c*) the lower edge of the premaxilla is depicted as horizontal. We have seen that Boulenger did not consider that the two larger individuals represented anything other than older specimens of the same species as R 2409, but that Broom took the opposite view and created the species *O. taylori* for these forms. Broom did not in fact seem to be sure that there were two distinct individuals in this material, but of this there can be no possible doubt since the symphysis and right jaw ramus are present in both, while new casts have duplicated other bones. His restoration of the side view of the skull of R 2409 (1913, Plate LXXVII, Fig. 9) differs only in detail from that of Newton; again, the slenderness of the posterior rami of the jugal and the shape of the premaxilla may be noted.

Broom's reasons for erecting the species *O. taylori* were very briefly stated and he did not make any detailed comparison between the specimens. His criteria may be listed as follows:

(*a*) Size, that is, R 3142 and R 3143 are approximately twice as big as R 2409. Also 'the British Museum has recently acquired from Elgin two new specimens, the one exactly corresponding in size to the type of *O. woodwardi*, and the other, so far as can be made out, agreeing in size with the large form'. These two specimens are evidently R 3561 and R 3562, although the numbers are not given.

(*b*) 'The arches are seen to be massive instead of slender bars'.

(*c*) 'The snout (is) relatively much more powerful'.

The material of *Ornithosuchus* now known comprises at least ten individuals. These have a curious tendency to group themselves into a series approximately doubling in size at each interval. Thus we have R 8170 and R 3149 of about equal size, R 2409, R 3561 and R 3916 again of closely similar size with skull length about twice that of the smallest specimens, and R 3142 and R 3143 with skulls about twice as large again. On a size basis alone, therefore, it would appear equally logical to divide the material into three species. However, the Geological Survey individual probably bridges the gap between R 3149 and R 2409, L 8271 is somewhat bigger than the R 2409 group, and R 3562, cited by Broom as providing supporting evidence for the existence of a larger size-group, has not only proved upon further development to be intermediate in size between Broom's two 'species' but the skull roof now exposed is identical in pattern, contour and ornament with that of R 2409 (figure 1).

Furthermore, as will be demonstrated shortly, the very large individual previously referred to as *Dasygnathus* also belongs to *Ornithosuchus* and there is no reason, apart from its size, to suppose that it represents yet another species. The criterion of size is therefore rejected as a basis for subdividing this material. If more data were available concerning the circumstances of discovery of these specimens it might prove, for example, that the 'size-groups' comprised associated individuals representing some kind of age-stratification within the original population; it certainly seems likely that R 3142 and R 3143 were found close together, to judge from Boulenger's account (1903).

Until recently a large, square mass of matrix covered the right side of the skull of R 3142, extending forward from the front half of the orbit and reaching up to the edge of the skull roof. Even so, it could be seen that the postorbital and jugal bars were telescoped and it was obvious that Broom had not sufficiently allowed for this. At my request, and with the permission of Dr E. I. White, the block of matrix was very skilfully removed by Mr A. Rixon, revealing the structures seen in figure 2*e*. The amount of compression suffered by this skull is now fully revealed; the orbit has been reduced to about half of its original height, and there is no reason to suppose that the skull was in any way different in its general proportions from that of R 2409. It is obvious that when the orbit is restored to

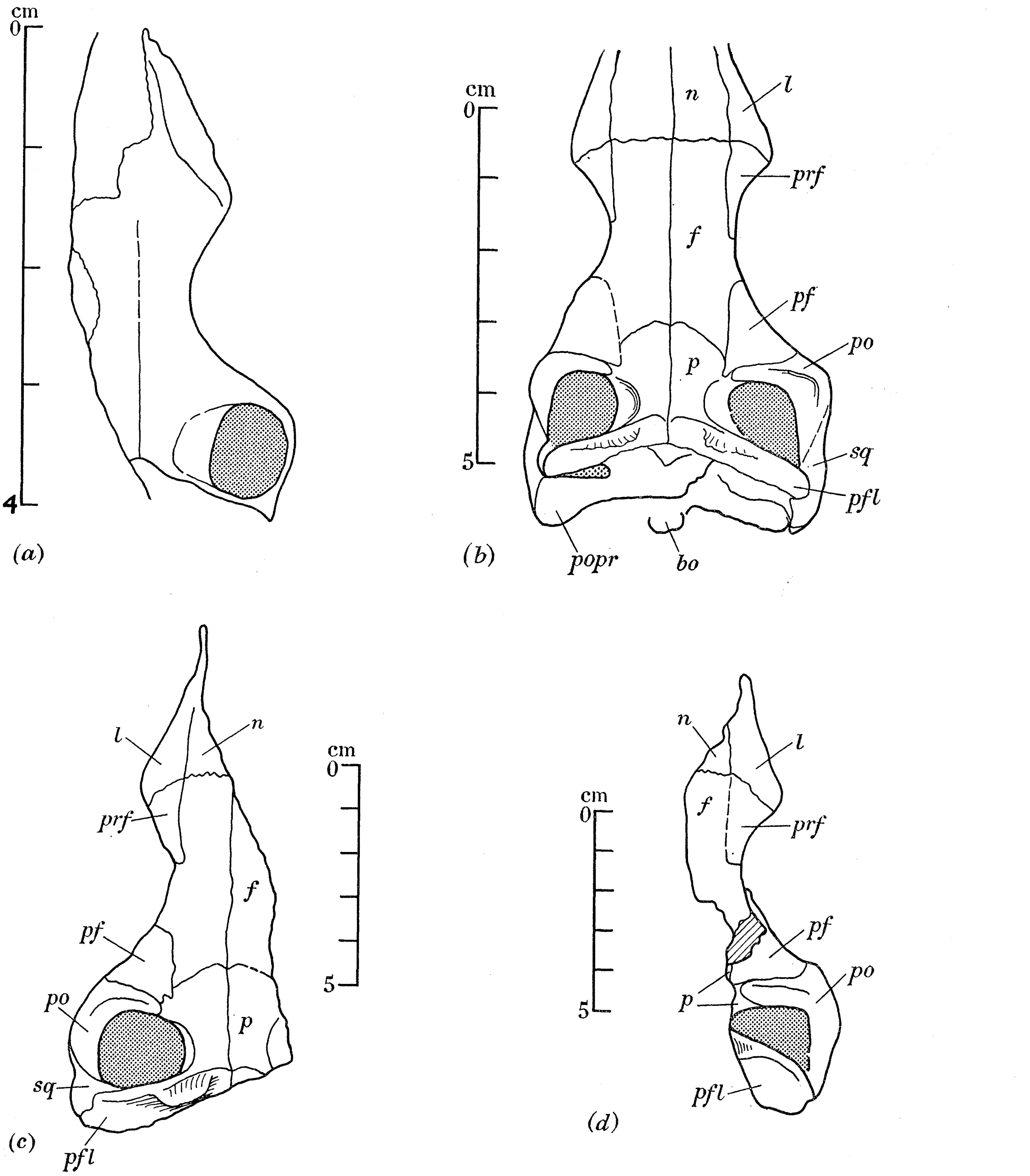

FIGURE 1. *Ornithosuchus longidens* (Huxley). Upper views of skull roofs (scales in cm). *a*: R 3149; *b*: R 2409, anterior sutures from Newton (1894); *c*: R 3562; *d*: R 3142, postfrontal partly overlapped by frontal, matrix cross-hatched. For explanation of abbreviations used in figures see facing p. 134.

its original shape, the 'arches' will appear more slender than they do now. However, comparison of the posterior branch of the jugal with the corresponding rami of R 2409 does suggest that it is relatively more massive and the reasons for this difference are discussed below.

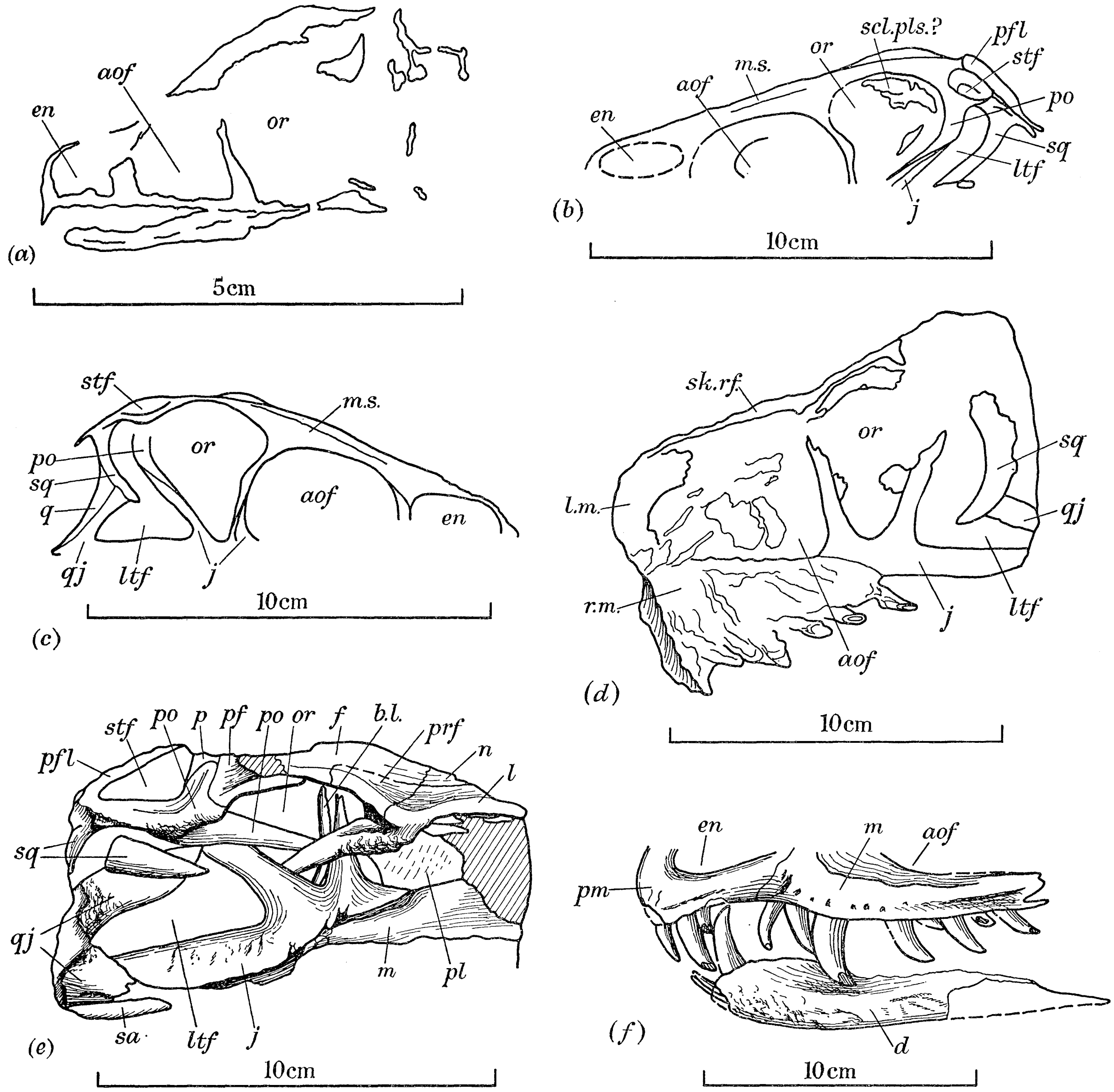

FIGURE 2. *Ornithosuchus longidens* (Huxley). Side views of skulls (various magnifications). *a*: R 3149, left side; *b*: R 2409, left side; *c*: R 2409, right side; *d*: R 3562, inner view of right side; *e*: R 3142, right side; *f*: R 3143, left side of snout and left dentary, the lower margin of the latter imperfect.

Boulenger (1903, Plate 14, figure 5 and p. 185) briefly described some bones which lie not far behind the right mandible of R 3143; these were identified by him as the right clavicle and the interclavicle. Examination of the specimen, however, convinced me that these bones are really the right quadrate and pterygoid which have been displaced backward. In order to obtain some further information about the pterygoid, the reason for which will appear shortly, the portion of the specimen containing these elements was cut off, so that the bone might be removed with acid without damaging the mandible. The excellent casts which were made by Mr Rixon not only confirmed the identification of the quadrate and pterygoid, but also revealed the presence of several other cranial and left mandibular bones, including the complete right jugal (figure 3). The latter has a well-developed lateral ridge surmounted by a longitudinal recess. On comparing this bone with the jugals of R 2409, it is clear that on the right side of the latter skull the recess was taken by both Newton and Broom for the suture between the jugal and quadratojugal, whereas this must in reality lie farther back, as in R 3142 and R 3143, and the jugal on this side has been exposed only as far down as the lateral ridge. The jugal/quadratojugal overlap is clearly seen on the left side of R 2409 where these two elements are slightly separated, but on this side the matrix has been removed only from the area *below* the ridge; however, the suture is clearly farther back than as shown in the earlier figures. In this way the misleading impression of an unusually slender bar has been created. The true thickness is probably close to 6 mm (measured immediately behind the postorbital branch) as compared with 13 mm in the case of the jugal of R 3143 and is therefore perfectly in accordance with the ratio of skull sizes.

It is thus the jugal of R 3142 which is unusual, and the reason for this is seen when that of R 3143 is placed alongside it; the originally lateral ridge of R 3142 has been crushed so that it now faces ventrally and the depth of the posterior ramus has been considerably increased thereby.

The postorbital ramus of the right jugal of R 2409 is more slender than would be expected by comparison with the other examples (this area is damaged on the left side). In this bone a line prolonging the lower margin of the lateral temporal fossa just touches the bottom of the orbit, whereas in the larger examples (R 3562, R 3142, R 3143) such a line passes somewhat below the orbit. It seems likely that the true base of the orbit lies slightly higher and deeper in R 2409, as it does in the larger jugals, but it is impossible to remove any further matrix from this region because the lower edge is already damaged and the bone itself is extremely friable.

When the anterior parts of the various jugals are compared, it is seen that R 2409 resembles R 3142 in having a relatively broad triangular area within the preorbital fossa and these areas agree in expected proportions, whereas the jugals of R 3562 and R 3143 have somewhat smaller such areas. Also the lower corner of the orbit is a little more acute in R 3142 and R 3143 than in R 2409 and R 3562. There seems no reason to ascribe these differences to anything other than normal individual variation combined with slight distortion.

The quadratojugal and squamosal of R 3142 do appear to be somewhat more massive than in R 2409 and possibly some relative thickening of these bones has taken place with increased age, nevertheless, the imperfection and strong compression of this specimen make such a supposition difficult to verify. Furthermore, sex differences of this nature are not unknown in both fossil and recent reptiles.

The third of Broom's distinctions concerned the supposedly more powerful snout of the larger individuals, and in this it is to be presumed that he included the downwardly projecting rostrum of the premaxilla of R 3143. However, this structure is also present in R 2409, albeit somewhat mutilated, and it is also found in the smallest skull, that of R 3149 (see p. 100).

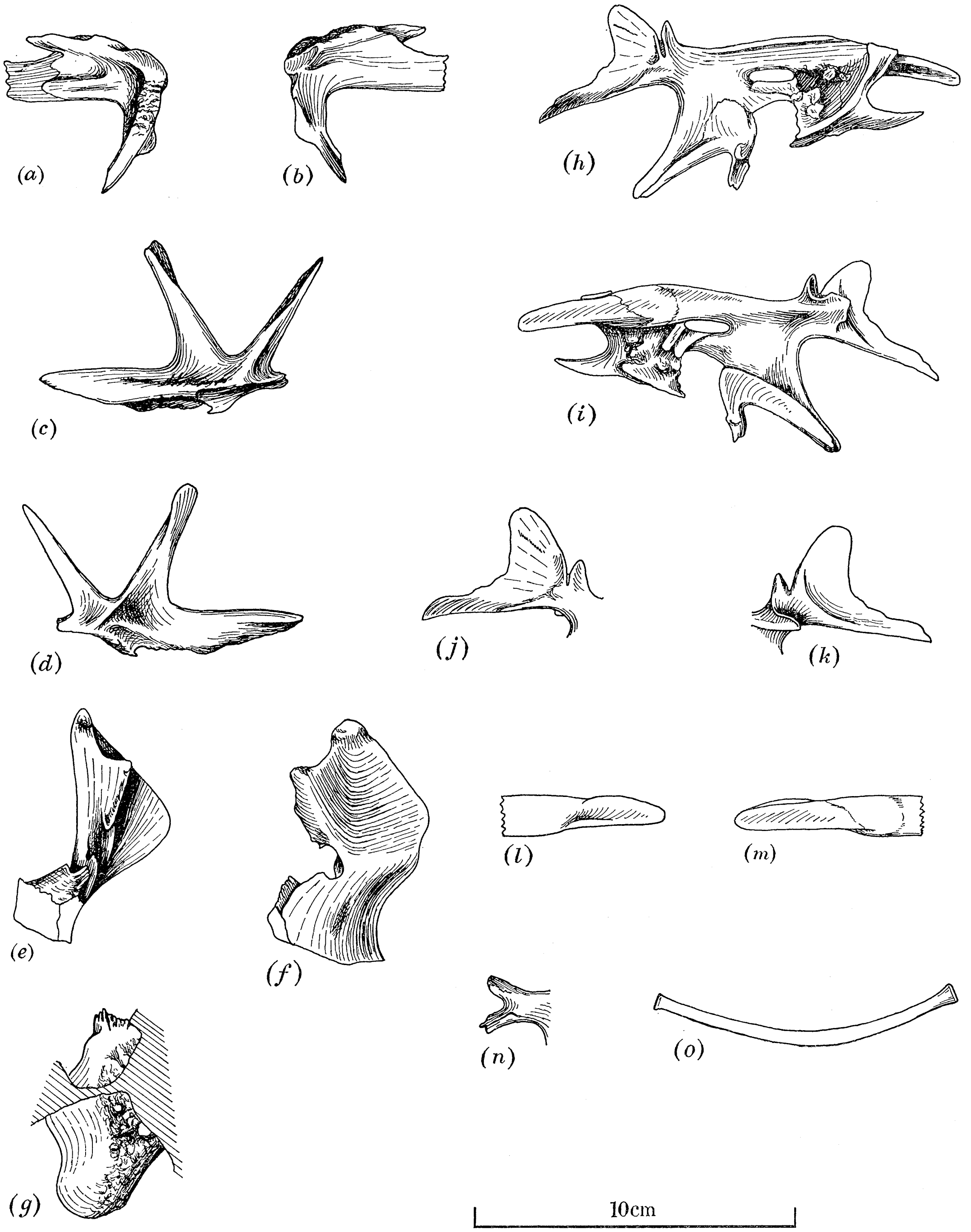

FIGURE 3. *Ornithosuchus longidens* (Huxley). Separated elements of the skull of R 3143 (half natural size). *a*, *b*: lateral and medial views of left lachrymal; *c*, *d*: lateral and medial views of right jugal; *e*, *f*: lateral and anterolateral views of right quadrate with part of displaced quadratojugal; *g*: oblique posterior view of right quadratojugal; *h*, *i*: dorsolateral and ventromedial views of right palatal complex; *j*, *k*: unforeshortened outer and inner views of rear end of right pterygoid; *l*, *m*: lateral and medial views of anterior end of right pterygoid; *n*: anterior view of outer end of right transverse; *o*: left hyoid, anterior end to right. (Drawn from casts.)

I can therefore find no support for Broom's specific distinction within this series of skulls, and all my comparisons between them have on the contrary tended to strengthen my conviction that they are from one and the same species. This view derives further support from the identical structure of the palate in R 3143 and R 2409. Unfortunately postcranial material of the larger individuals is meagre, and on the whole very poorly preserved. Where comparisons can be made they show no differences other than of size. This can be asserted of the scapula, humerus and pubis; the proportion which these bones bear to the skull of R 3142 is, as far as can be made out, the same as that which corresponding elements of R 2410, R 3916 and R 3561 bear to the skull of R 2409. Also

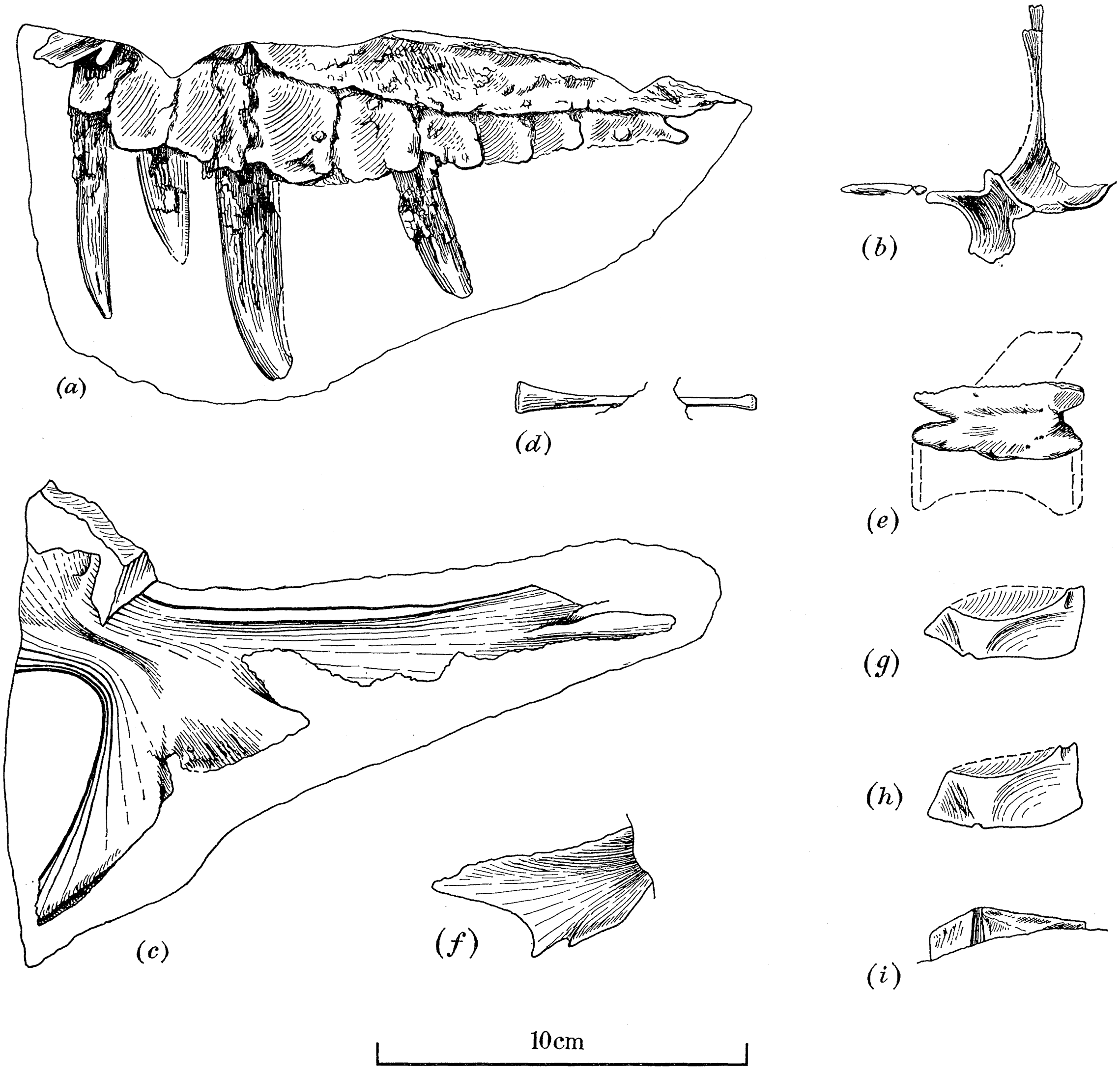

FIGURE 4. *Ornithosuchus longidens* (Huxley). Bones of the largest known individual (half natural size). *a*: inner view of right maxilla, holotype of *Dasygnathus* Huxley, E.M. 1R; *b*: incomplete neural arch and spine of an anterior caudal vertebra, anterior view, E.M. 1R; *c*: right pterygoid, lateral view, E.M. 15R; *d*: stapes, proximal end on right, E.M. 15R; *e*: left side of neural arch of a mid-caudal vertebra, E.M. 15R; *f*: inner view of right nasal, E.M. unnumbered; *g*: medial view of left articular, E.M. 29R; *h*, *i*: ventromedial and ventrolateral (under) views of same. (Drawn from casts.)

the distinctive angulated and spinose cervical scutes occur in R 8170, R 3916, L 8271, R 3562 (see Appendix) and R 3142. Finally, there is some evidence, from the incomplete ossification of the left coracoid of R 3916, the detachment of the first sacral rib of R 2410, and particularly from the unfinished anterior edge of the blade of the ilium in each case, that the three specimens of equal size (R 2409, R 3561 and R 3916) were all immature.

Thus Broom's species *Ornithosuchus taylori* is held to have been founded on larger individuals of the same species as that which had been named by Newton *O. woodwardi*. However, it would be incorrect to assume that the latter name should be applied to the material, for it has become apparent during the study of *Ornithosuchus* that the bones which I described under *Dasygnathus longidens* Huxley (Walker 1961) are indistinguishable (apart from their larger size) from the corresponding elements of *Ornithosuchus*.

The discussion of *Dasygnathus* will begin with a consideration of the maxilla, for, as this is the type specimen, the question of nomenclature ultimately hinges upon it. Huxley (1877) regarded this specimen as part of a mandible; in 1961 I described it as a left maxilla, but a re-examination of the specimen has since convinced me that what I took to be an accidental fragment of bone lying on the outer surface is in reality a medial shelf such as that which occurs in *Antrodemus* (Gilmore 1920, Fig. 12), and the presence of damaged but still recognizable interdental plates or rugosae (Osborn 1916) confirms that this bone is a right maxilla seen in medial view. A new illustration of the specimen (figure 4*a*) is given which incorporates these and other modifications. Formerly I considered that there were 'at least eight and possibly ten teeth originally present'. The large skull R 3143 has nine teeth (including empty alveoli) on the left maxilla and eight on the right, the difference being due to the omission of the smaller first tooth on the right side, and the distinctive rear forking of both maxillae shows that they are complete although the jugals are not in place. A total of nine teeth can also be counted on the left maxilla of R 2409, but the right is too poorly preserved for their number to be ascertained; probably nine teeth are present on both maxillae of the Manchester specimen (L 8271), but preservation is again unsatisfactory. The first maxillary tooth is somewhat different from the succeeding teeth, being more slender and of more cylindrical form; these features are most clearly seen on the left side of R 3143. On comparing the maxilla of *Dasygnathus* with those of R 3143 the rear forking of the bone can be recognized as a faint but distinct impression also marked by a slight staining of the matrix. Using the swellings along the margin as guides to the positions of the alveoli, the number of teeth can be definitely determined as nine. In addition, the first maxillary tooth is more slender and more cylindrical than the following teeth. These points, taken with the rather low tooth number which is in itself somewhat unusual, are held to be sufficient evidence to justify the placing of this maxilla with the *Ornithosuchus* material.

Supporting evidence for this conclusion is supplied by the pterygoid (E.M. 15R, figure 4*c*). Reasons were given in the earlier paper (Walker 1961) for the belief that this bone came from the same actual skull as the maxilla; these included the apparent association of each bone with fragments from the same individual of *Stagonolepis*. A re-examination of the specimens associated with the maxilla and pterygoid has, however, shown that there is no reason to doubt that all these bones came from the one individual of '*Dasygnathus*'. The chevron-bone (E.M. 15R) differs from those of *Stagonolepis*, as was indeed pointed out earlier, in having the articular facets united, and the partial caudal vertebra (E.M. 15R, figure 4*e*), only recently positively identified, is quite distinct from the caudal vertebrae of that genus. The incomplete neural arch (E.M. 1R, figure 4*b*) offers no diagnostic features. The occurrence in each case of a cranial element of the right side with caudal fragments is strongly suggestive of original association.

The large pterygoid (E.M. 15R, figure 4*c*) is known only from the dorsal surface and was thus difficult to compare with the palate of R 2409, the type of *Ornithosuchus woodwardi*. The identification of the quadrate and pterygoid of R 3143 ('clavicle and interclavicle' of Boulenger) unexpectedly offered an opportunity to relate the various pterygoids, since these bones were preserved in the solid; after the bone had been removed casts were obtained which showed both surfaces. The right palatine and transverse were also found attached to the pterygoid. A distinct zone of shearing across the middle of the palatine, and a less obvious one affecting the anterior bar of the pterygoid, show that a certain amount of anteroposterior compression has taken place which has also caused the arching of the anterior part of the pterygoid. Nevertheless, the palate of this larger skull is strikingly similar (figure 3*h* and *i*) to that of R 2409. The subsidiary postpalatine fenestra (mistaken by Newton for the choana in the smaller skull) is present in the same position and the details of the palatine/pterygoid suture are identical. On comparing the pterygoid and associated bones of R 3143 with the pterygoid of *Dasygnathus* (E.M. 15R, figure 4*c*), it is apparent that the latter had identical relationships with the transverse and also possesses a subsidiary postpalatine vacuity along the outer margin of which is a depression on the dorsal surface for the reception of a posterior tongue from the palatine. The earlier assumption of a 'considerable interpterygoid vacuity' has since proved to be incorrect, as the E.M. 15R bone was obviously more nearly vertically disposed in the skull than was previously thought to be the case. The anterior portion evidently formed a deep bar appressed to its antimere; the one surface preserved creates a misleading impression when this bone alone is considered, but comparison with the smaller pterygoid makes its structure clear. There is also a similar ridge-and-groove system along the anterior dorsal edge of both bones. One must allow that a thin triangular area has been broken off the anterior upper edge of the R 3143 pterygoid; this is likely in view of the compression mentioned above and the occurrence of thin cavities in the adjacent matrix.

Another small block of Findrassie sandstone in Elgin Museum displays the impression of a large right nasal (figure 4*f*) which compares well with that of *Ornithosuchus*. There is also the impression of a large detached left articular (E.M. 29R, figure 4*g* to *i*) in another small block from Findrassie; both these specimens probably come from the same skull as the maxilla and pterygoid.

In view of the reasons given earlier for rejecting Broom's assignment of the larger individuals to a distinct species, there seems no further reason to suppose that these even larger elements represent yet another species, bearing in mind the well-known fact of indeterminate growth in reptiles. It is noteworthy that the degree of distortion and disarticulation increases with size. Thus the skull of R 2409 is complete but the brain-case has been pushed slightly backward and the left orbit and lateral temporal fossa have been slightly compressed. The skull of R 3562 was apparently complete; distortion has not greatly affected the skull roof although the sides of the skull now slope away to the right at about 45°; the right orbit and lateral temporal fossa are not greatly distorted. In R 3142, again a complete skull, distortion is carried a stage further so that the palate has risen up to lie close behind the right side of the skull and the palatine is pressed against the preorbital fossa. The right orbit has been reduced to about half of its original height with concomitant telescoping of the adjoining bones. In the case of R 3143 the snout and entire right jaw are in place, but the rear half of the left jaw and the greater part of the skull are missing and several elements have been displaced backward. Finally, the largest skull ('*Dasygnathus*') is represented only by a few scattered bones.

The name *Dasygnathus longidens* was given by Huxley in 1877 to the maxilla, E.M. 1R. But *Dasygnathus* was already preoccupied (Macleay 1819, Coleoptera) and Kuhn (1961) proposed *Dasygnathoides* to replace it. However, since *Dasygnathus* Huxley is now considered to be congeneric with *Ornithosuchus* Newton, the latter name takes priority over *Dasygnathoides* Kuhn. The full synonymy may be set out as follows:

Genus *Ornithosuchus* Newton 1894:

Type species *Ornithosuchus woodwardi* Newton 1894.

Genus *Dasygnathoides* Kuhn 1961 nom.nov., for *Dasygnathus* Huxley 1877 *non* Macleay 1819:

Type species *Dasygnathoides longidens* (Huxley 1877) [*Dasygnathus*]. But *D. longidens* and *Ornithosuchus woodwardi* are considered to be conspecific. Therefore:

(*a*) *Dasygnathoides* Kuhn 1961 becomes a subjective junior synonym of *Ornithosuchus* Newton 1894, so that *Dasygnathoides longidens* (Huxley 1877) should be called *Ornithosuchus longidens* (Huxley 1877).

(*b*) *O. woodwardi* Newton 1894 becomes a subjective junior synonym of *O. longidens* (Huxley 1877).

(*c*) *O. taylori* Broom 1913 becomes a subjective junior synonym of *O. longidens* (Huxley 1877).

The type species of *Ornithosuchus*, however, is still *O. woodwardi*, and may be cited as '*O. woodwardi* Newton 1894 [= *O. longidens* (Huxley 1877)]'.

IV. DESCRIPTION OF *ORNITHOSUCHUS*

Skull

Restoration of the skull

The drawings of the skull were originally made to represent that of an individual the size of R 3143, that is, 25 cm in length. This was found to be a convenient size at which to work and also facilitated the incorporation of additional details from the skulls of about this size which are available. For the side view, the right side of R 2409, suitably enlarged, has been taken as the basis. It is believed that this side of the skull is virtually undistorted for the following reasons. The bones show no sign of compression or shearing (with the exception of the lower part of the squamosal, which may have slid downward a millimetre or two over the quadratojugal), and the right quadrate appears to be undisturbed. On the left side the postorbital has moved downward a short distance along its suture with the jugal; nevertheless, the shapes of the orbit, postorbital and upper part of the lateral temporal fossa compare very closely with the corresponding areas of the right side, also the postorbital of R 3142 has a similar curvature to those of R 2409. The casts of the slightly disarticulated elements of R 3143 can be fitted together in their original relationships, and, when this is done, the attitude of the quadrate with respect to the horizontal ramus of the jugal is found to be identical with the situation on the right side of R 2409. Finally, the skull roof of R 3562 agrees closely in contours with that of R 2409, so that it is impossible to imagine that the orbit and lateral temporal fossa of the latter have been significantly distorted.

TABLE 1. MAIN MEASUREMENTS OF A SMALL INDIVIDUAL OF *ORNITHOSUCHUS*

	mm	
skull length (snout–quadrate)	115	(R 2409)
jaw length	105	(R 2409)
estimated presacral column length	240	(composite)
scapula height	56	(R 3916)
coracoid length	31	(R 3916)
scapulocoracoid height (maximum)	67	(R 3916)
humerus length	57	(R 3916)
radius length	48	(R 3916)
ulna length	50	(R 3916)
metacarpal I length	12	(R 3916)
metacarpal II length	16	(R 3916)
metacarpal III length	? 13	(L 8271)
metacarpal IV length	7·5	(R 3916)
ilium, blade length	42	(R 3561)
ilium, across acetabulum	28	(R 3561)
ischium, maximum length	55	(R 3561)
pubis, maximum length	68	(R 3561)
femur length	87	(R 2410)
tibia length	*ca.* 73	(R 2410)
fibula length	73	(R 2410)
metatarsal I length	23	(R 2410)
metatarsal II length	32	(R 2410)
metatarsal III length	35	(R 2410)
metatarsal IV length	32	(R 2410)
metatarsal V length	22	(R 2410)
length of a paramedian dorsal scute from the middle of the back	15	(R 3916)
breadth of same scute	11	(R 3916)
estimated total length about 3 ft. or	900	(composite)

Note. In order to obtain the estimated dimensions of the largest known individual, the above figures should be multiplied by four.

The validity of using R 2409 as a basis has to be firmly established because of the emphasis laid upon the shape of the lateral temporal fossa in a later section, and also because of the slightly different angles of divergence of the various rami of the jugal in the several specimens of this bone available. To take one example, it is evident that the lachrymal ramus of the right jugal of R 3143 (figure 3*c*, *d*) is now inclined forward at a more acute angle than was originally the case. This is shown by comparing it with other examples, and also by placing it in relationship with the (left) lachrymal from the same skull (figure 3*a*, *b*); the resulting highly improbable shape for the preorbital fossa shows that both bones are distorted.

The upper view of the skull is also based on R 2409, with details of the lachrymals from the larger skulls. For the occipital view, if one excepts the quadrate region, R 2409 again provides most of the available information.

The palate is drawn from both R 2409 and R 3143, with a small amount of evidence about the anterior portion obtained from L 8271.

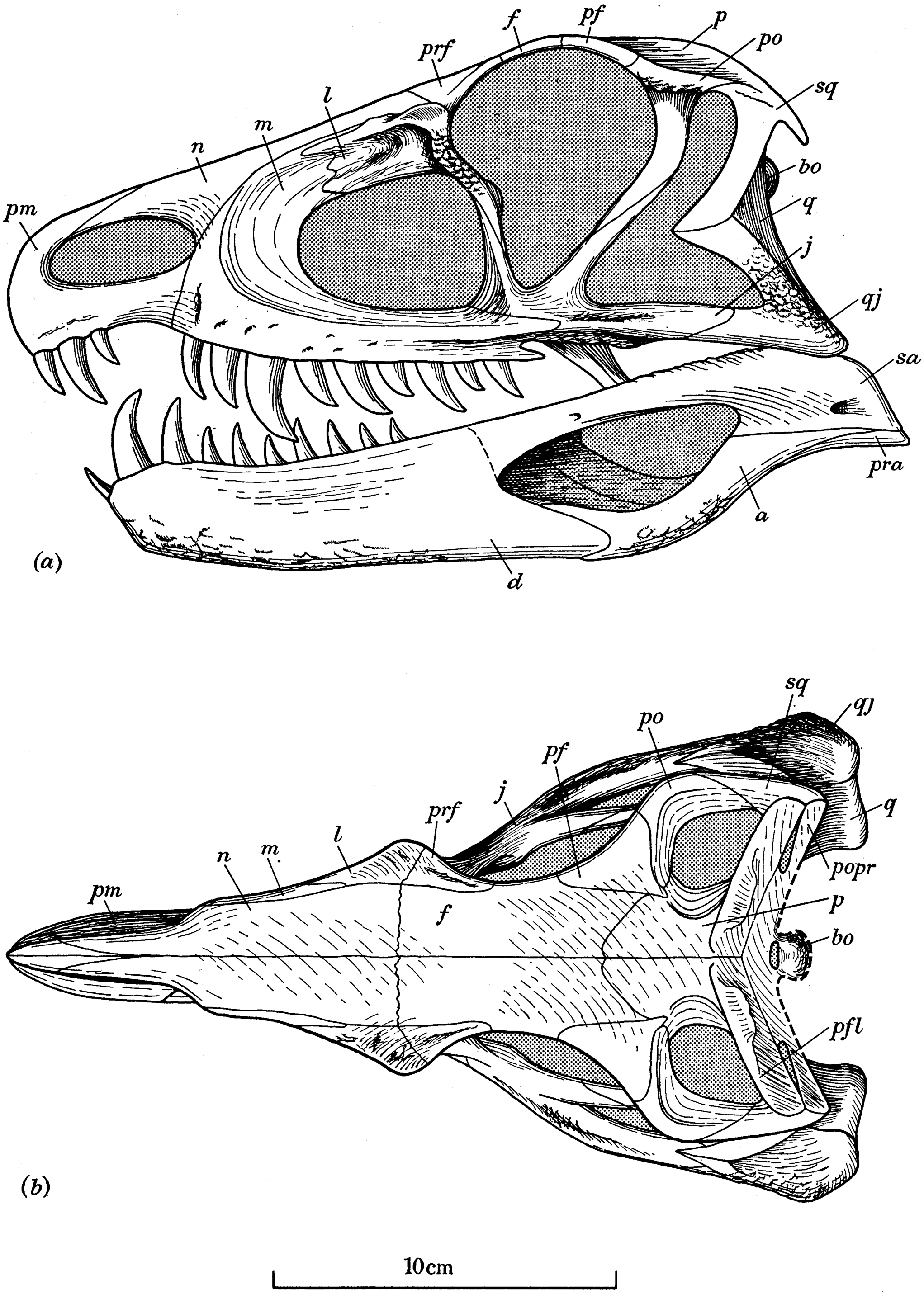

FIGURE 5. *Ornithosuchus longidens* (Huxley). Composite restoration of the skull (half natural size). *a*: lateral view; *b*: dorsal view, superficial ornament omitted.

Newton's account of the skull is, in the main, an excellent one and it is unnecessary to repeat it here; I will merely add such new information as is available and make any corrections which may be desirable.

It is worth pointing out that the snout is even more compressed than has been shown in previous figures of the skull. When the palatal outline is superimposed on the dorsal view there is seen to be a marked posterior expansion of the skull beginning at the orbits, which is significant in connexion with the evolutionary development to be outlined later.

Skull roof

With the exception of the parietal flanges and the recessed areas bordering on the supratemporal fossae, the rear part of the skull roof of R 2409 is covered by an irregular ornament of small pits. It is probable that, allowing for damage and loss of bone, this ornament also extended well forward on to the nasals; it is certainly found on the posterior parts of these bones and on the lachrymals and prefrontals of R 3562 and R 3142, and on the posterior part of the large isolated nasal. The postfrontal regions of the skull are somewhat elevated, with the frontals forming a shallow, broad trough between them. In front of this area the skull slopes fairly uniformly down to the snout; there is a slight depression between the lachrymals but this is not particularly noticeable in the profile of the skull.

A characteristic feature is that the line of the lachrymal/nasal and prefrontal/frontal suture is continued by the postfrontal/frontal suture, is approximately parallel to the midline, and passes close to the deeper edge of the inner border of the supratemporal fossa. The last point does not apply in the case of R 3562 because of the sideways distortion of the skull.

The isolated right nasal (figure 4*f*) mainly shows the lower or medial surface. The anterior embayment represents the posterior margin of the naris; passing backward the underside becomes angulated-concave corresponding to the external change of shape as the bone reaches the dorsal surface of the skull. Behind the naris the lower margin develops a strong inward flange which rested on the thickened anterior margin of the ascending process of the maxilla.

The lachrymal is chiefly notable for the occurrence of a sharp, dorsolaterally projecting ridge, which is best preserved on the left side of R 3143. The prefrontal fits against an obliquely bevelled posteromedial area on the lachrymal and sends down a short tapering process medial to the latter. The triangular postfrontal is confined to the skull roof and does not enter into the formation of the postorbital bar.

The posterior angle of the orbit is formed by the postorbital, which here strongly overhangs the descending portion of the bone, and in R 3142 at least forms a definite rugosity. The postorbital extends medially in a tongue-like process which overlies the parietal. The suture with the squamosal is clearly seen on the left side of R 2409; probably most of the upper portion of the squamosal has been broken off in the case of R 3142. The recessed areas bordering on the supratemporal fossae are largely borne upon the postorbitals with the parietals forming the inner portion. Short additional flanges on the sloping occipital surfaces of the parietals, seen in R 2409, R 3562 and R 3142, probably supported the first pair of cervical scutes.

Side view

The premaxilla curves down somewhat in front and this portion bears three teeth. Farther back its lower margin contracts in breadth to permit the enlarged dentary teeth to slide past it. The maxilla has the usual well-marked ascending process which overlaps the lachrymal with a squamous junction and also sends a thin process upward and backward to enter the skull-roof medial to the latter bone. The union with the jugal is of particular interest. The posterior end of the maxilla forks into two processes. In front of this division the upper edge is thickened to form a longitudinal ridge which fits into a corresponding groove below the jugal, the outer margin of the latter riding on a shallow recess on the lateral surface of the maxilla. Both branches of the maxilla become quite thin toward their tips, the upper being applied to a well-marked area on the outer side of the jugal, immediately below the longitudinal ridge on the latter. The lower branch of the maxilla is supported internally by a slender recurved point of the jugal, both bones ending as a free process. The jugal also bears a short, medially directed flange below the lachrymal process; this probably lay over the maxilla, but the details of the junction are unknown.

The detached jugal of R 3143 shows all the details of the bone to perfection. In this example, as apparently in R 3562, the anterior web of bone below the lachrymal process is quite small, whereas on both sides of R 2409 and on the right side of R 3142 it is more extensive; thus this variation is not size-controlled. The lachrymal process tapers uniformly to a slender point and is grooved posteriorly to fit against a correspondingly grooved surface of the descending process of the lachrymal. In a similar manner the postorbital is received into a longitudinal recess on the anterior surface of the postorbital process of the jugal. The surface which united with the quadratojugal faces downward and a little inward. The lower edge of the jugal is roughened in a manner suggestive of muscle origin; laterally it bears the strong ridge mentioned earlier which is a continuation of the lower rim of the preorbital vacuity.

The lachrymal forms a deep plate above the latter opening. The course of the lachrymal duct appears to be indicated by a low ridge which extends back into the deep recess below the dorsal crest; it probably curves down behind to emerge at a foramen in the anterior wall of the orbit. A curious feature is the presence of a distinct backwardly directed flange opposite the upper limit of the jugal. This is seen on both sides of R 2409 and also on R 3142 and R 3143. Between this flange and the dorsal crest the outer rim of the bone is strongly roughened.

One of the most distinctive features of the skull of *Ornithosuchus* is the pronounced forward projection made by the squamosal and quadratojugal into the lateral temporal fossa. There can be no doubt that this is an original feature, for reasons already explained. The squamosal overlaps and is sutured to the upper end of the lateral face of the quadratojugal, and the lateral projection of the quadrate extends into the notch behind the two bones, which however project freely in front of it. The superficial portions of the larger quadratojugals (R 3142, R 3143) are quite strongly roughened.

Towards the upper rear corner of the left orbit (of R 2409) several irregular areas of thin bone occur close together. These appear to represent the sclerotic ring, but no definite shape or arrangement of the individual elements can be made out.

Occipital view

R 2409 still provides the only information concerning the occiput proper (figures 1*b* and 7*a*). The occipital flanges of the parietals and the left paroccipital process are readily identified, and the squamosal binds the outer ends of these together in the usual way. There is a distinct post-temporal fossa preserved on the left side and this broadens somewhat inwards. Medial to this is the 'four-sided plate' referred to by Newton (1894) which he considered to be formed by the exoccipitals meeting above the foramen magnum. However, this area is too far above the basioccipital for this to be likely, and there is little doubt that it is actually the supraoccipital. What at first sight appears to be a median suture is in reality a low vertical ridge from the left side of which a thin layer of bone has flaked off. The triangular area below the parietals, which Newton thought might possibly be the supraoccipital, is fairly obviously a breakage, since it is not symmetrical and its line of separation is incomplete just to the left of the mid-line. The only other possible identification for this area would be as an interparietal, but in *Euparkeria* which is the nearest antecedent relative of *Ornithosuchus* at present known, the interparietal wedges in between the parietals, above the supraoccipital. It seems most likely that this area was originally part of the supraoccipital, but the upward and backward rotation of the braincase which has occurred has caused it to fracture. The supraoccipital is thus a wide element, but as its lower edge at present terminates in a line of breakage, its apparent shallowness may be misleading. A possible suture between the supraoccipital and the paroccipital trends obliquely downward and inward from the inner corner of the left post-temporal fossa.

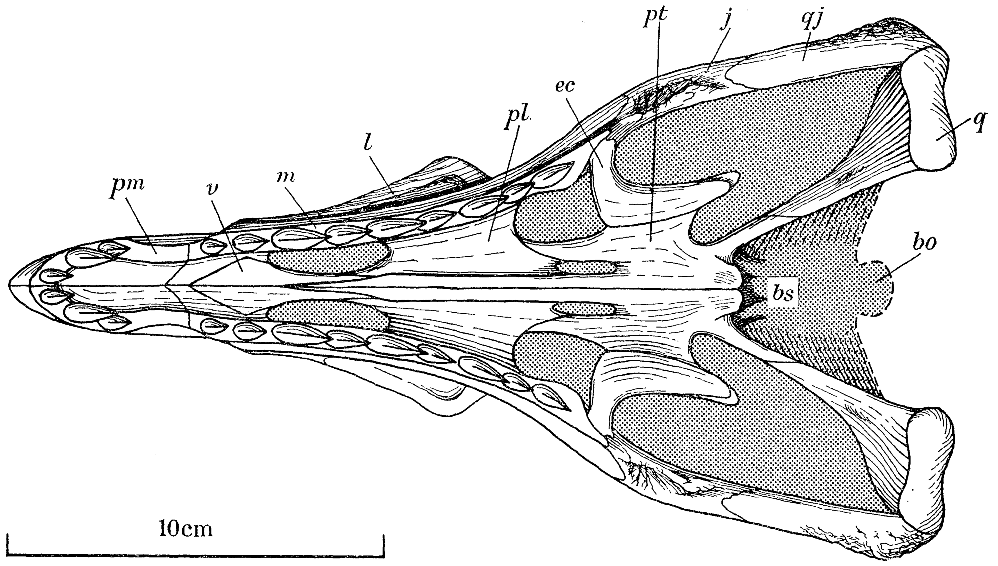

FIGURE 6. *Ornithosuchus longidens* (Huxley). Composite restoration of the palate (half natural size).

The basioccipital is largely missing, being represented by a hole passing from the posterior to the ventral surface. However, part of the bony substance of the condyle remains behind the hole.

The paroccipital process of the right side is damaged, revealing the broken otic region. A groove in the matrix on the right side of the hole mentioned above represents a ridge which ran ventromedially from below the paroccipital process to the region of the tubera; it probably joined up with the latter on the side of the braincase.

The exoccipitals appear to have been lost in the course of collection and preparation.

The quadrate and quadratojugal are well shown by the detached elements of R 3143 (figure 3). The right quadratojugal has slipped downwards and inwards and now lies obliquely across the back of the right quadrate. The latter is of the usual form, sending forwards a thin triangular wing which was covered by the posterior portion of the pterygoid. The lateral wing is somewhat thicker and its upper margin is concave, indicating the presence of an opening facing posteriorly between it and the squamosal. The quadrate foramen is of substantial size, passing vertically upward and thus intersecting the bone obliquely. Although the actual articular surface is not preserved only a millimetre or two can be missing, and the shape of the preserved part indicates that the articular surface sloped medially. The right quadratojugal is almost complete. The most dorsal portion of its medial edge is grooved to receive the edge of the quadrate, but this soon gives way ventrally to an overlapping relationship. The posterior surface of the quadratojugal is devoid of sculpture.

Structure of the palate

The anterior part of the palate is not known in detail. The Manchester specimen (L 8271) shows a diamond-shaped area bisected by a median suture between the anterior parts of the maxillae, but unfortunately provides no further information. These bones are presumed to be the vomers, since they lie farther back than the medial processes of the maxillae as shown by E.M. 1 R. It seems likely, because of the extreme narrowness of the snout, that these maxillary processes met in the mid-line for a short distance in front of the vomers, but it is possible on the other hand that they were separated by the anterior tips of the latter bones. The medial process of the maxilla (figure 4 *a*) closely resembles that of *Antrodemus* (Gilmore 1920, Fig. 12), but is imperfectly preserved and possibly somewhat damaged. It extends forward in front of the maxilla, lying 1 cm medial to it, and its inner surface (which is produced downward as a thin edge) is marked by striations which are inclined anteroventrally. Possibly this indicates an upward shift in level of the palate towards the choanae which are set high up.

The large maxilla (E.M. 1 R, figure 4 *a*) also shows the crushed interdental plates, which alternate with the teeth since they are expansions of the interalveolar septa. The plates are bounded dorsally by a longitudinal groove above which the medial surface thickens slightly. The foramina between the interdental plates along this groove are obscured except above the third tooth where the surface of a replacing tooth can be seen. The plates decrease in size posteriorly in the usual manner. Their lower edges are not well preserved, but here and there are indications that the lower margin of each plate made an obtuse angle downward as in *Teratosaurus suevicus* (von Huene 1908, Plate LXIV, Fig. 1) to which this maxilla bears a close resemblance.

The interdental plates, and the longitudinal groove above them, may be seen (largely in the negative) on the right side of L 8271, and less clearly on R 3143.

It is assumed that the vomers met the palatines towards the rear ends of the choanae and thus excluded the pterygoids from these openings in the usual way. The palatines are inclined strongly upwards towards the mid-line, abutting against the long anterior bars of the pterygoids; the mid-line of the palate thus lies about half-way up the antorbital fenestra. Laterally the palatine meets the maxilla at a broad contact. The upper edge of this surface (figure 3*h*) curves forward and inward, rising as it does so and forming a deep posterior rim to the choana. The upper surface of the palatine together with the pterygoid thus forms a bowl-shaped depression which probably gave origin to a branch of the pterygoideus anterior muscle. Posteriorly the palatine sends back a narrow tapering process along the outer side of the subsidiary postpalatine fenestra; however, this process is broader and more tongue-like on the dorsal surface where it lies in a shallow depression on the pterygoid.

The anterior bar of the pterygoid of R 3143 is 12 mm deep but only 4 mm thick ventrally. It meets its antimere at a flat surface along the mid-line. Laterally it is slightly concave, rising to a rounded dorsal edge. The beginning of the union with the vomer is shown by the anterior tapering of the pterygoid, but the vomer itself is not preserved in this specimen. Opposite the posterior end of the choana there develops a lateral thickening of the upper part of the anterior pterygoid bar (R 3143). Passing forwards this rises to a thin dorsal edge (figure 3*l*, *m*) which is higher by some 2 mm than the original upper edge of the bar. The two ridges join together at the anterior termination of the bone. This arrangement is similar to that of *Stagonolepis* (Walker 1961), where, however, the accessory dorsal ridge arises much farther back, opposite the anterior margin of the postpalatine opening. The large pterygoid (E.M. 15R) (figure 4*c*) differs from that of R 3143 in having a higher dorsal edge at the commencement of the lateral thickening, but as noted earlier, this difference is probably due to breakage of the smaller bone.

The subsidiary postpalatine fenestra has been drawn from R 3143, since in the smaller skull (R 2409) a good deal of matrix obscures the margins of these openings, making them appear larger than they really are. The fenestra was erroneously regarded by Boulenger (1903, Fig. 4, R 3142) as the choana, the 'vomer' of his figure being the broken anterior bar of the pterygoid.

In front of the triangular quadrate lamina the pterygoid sends up a short, almost vertical pointed process, comparable to, but of different shape from, that of *Stagonolepis*. Formerly I considered that, by comparison with the phytosaur *Machaeroprosopus* (Camp 1930), the epipterygoid rode over the front of this process, but I am now inclined to think that the base of the epipterygoid fitted into the notch behind it. It seems probable that the anterior extension which meets the ascending process in *Stagonolepis* (Walker 1961, Fig. 4) and which was described as part of the quadrate, is actually the lower part of the epipterygoid. The unossified area in front of the quadrate would thus represent the cartilaginous base of the epipterygoid, riding over the pterygoid and sending a narrow tongue forward into the groove on the 'neck' of the latter. This interpretation accords much better with the appearance of the specimen and the position of the groove in both *Stagonolepis* and *Ornithosuchus*.

The anterior margin of the ascending process continues medially and ventrally as a thin ridge, curving round the basipterygoid process to form the medial margin of a short, blunt backward extension which just touched its fellow of the opposite side, but without the development of a contact-surface between them. This backward process may be termed the *parabasal process*. The basipterygoid articulation lies immediately above the parabasal process and below the notch for the epipterygoid, and appears to have faced anterolaterally and a little downward. Behind it a curving ridge delimits a depressed area on the medial side of the quadrate wing of the pterygoid.

In the small skull (R 2409) the basipterygoid processes are visible diverging downward, and since the articular facets are exposed it is evident that the braincase has been displaced backwards. This confirms that the slope of the supraoccipital is less steep than should be the case.

The transverse overlaps the upper surface of the lateral wing of the pterygoid anteriorly and then runs backwards and downwards as a long tongue of bone along its outer edge and ventral surface. It forks laterally to meet the jugal in two short processes which enclose a small longitudinal foramen, although this is restricted by a swelling of the inner side of the jugal. The upper process tapers out behind a medial ridge on the jugal which runs anteroventrally from the anterior margin of the postorbital ramus. The lower process, placed vertically below the upper, makes contact with an area immediately above the short backwardly directed process at the ventral margin of the jugal, and may originally have had a very slight contact with the maxilla. The transverse thus served to brace the free backward process of the combined maxilla and jugal.

Stapes and hyoid

Curiously, the few bones which are preserved of the largest individual include the stapes, lying near the posterior end of the pterygoid (E.M. 15R). This element (figure 4*d*) is 65 mm long. The presumed proximal end is oval in outline and 4½ mm broad. The distal end, 8 mm broad, appears to be flattened with the long axis in the same plane as that of the proximal end, but only the one surface is preserved. This stapes compares closely with the figures and descriptions of the stapes of *Dromaeosaurus* and *Corythosaurus* given by Colbert & Ostrom (1958), rather than with that of *Plateosaurus* (von Huene 1926*a*), and has been oriented by reference to the stapes of the former two genera.

Both hyoids are present between the lower jaws of R 3143, lying close together with the concave sides facing one another, the anterior end of the left element being 2½ cm behind the right and almost in contact with it. The left hyoid is the more completely represented but because of a small gap between the blocks the length of 9·2 cm is more easily obtained from the bone of the right side. Figure 3*o* shows the left element from the (now) ventral aspect. The bone is slightly flattened, the ends being somewhat expanded and a little concave.

Lower jaw

The description of the lower jaw is based on the following material:

(*a*) R 3143, which shows the left dentary and complete right ramus, and includes a block showing the lower surface of the symphysis. The rear part of the right ramus has been twisted so that the external surface of the surangular is at right angles to the plane of the side of the snout and the prearticular has been rotated downwards and outwards during compression. The detached left splenial and angular are juxtaposed to the detached right quadrate and pterygoid. These elements have avoided the distortion which their

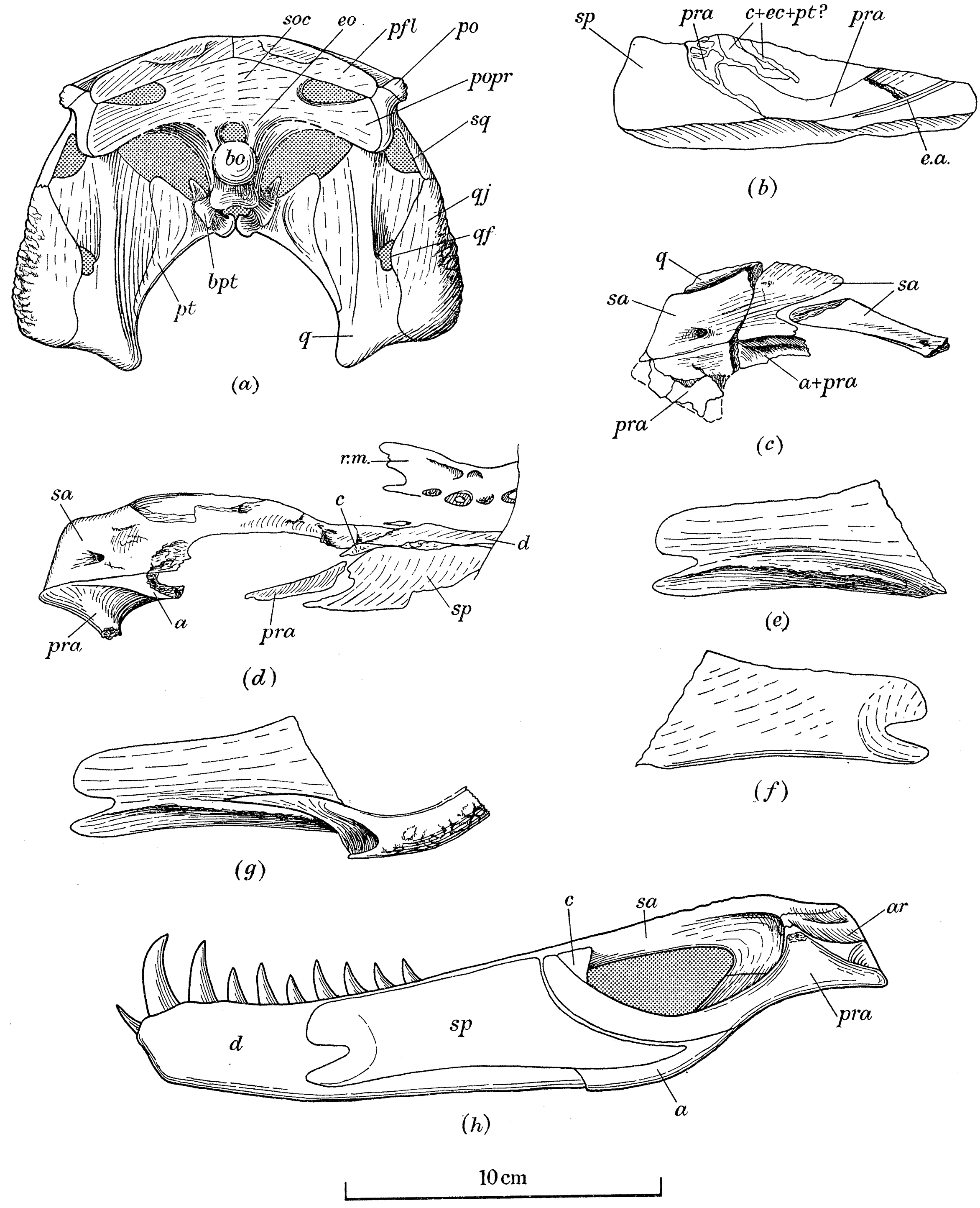

FIGURE 7. *Ornithosuchus longidens* (Huxley). (Half natural size.) *a*: Composite restoration of the occiput; *b*: part of the left jaw of R 3142, lateral view; *c*: rear end of right jaw of R 3142, lateral view; *d*: parts of right jaw and maxilla of R 3142; *e*, *f*: lateral and medial views of left splenial of R 3143; *g*: lateral view of left splenial and angular of R 3143 in articulation; *h*: composite restoration of the jaw in medial view. (*e*, *f* and *g* from casts.)

counterparts of the right jaw have suffered and have been particularly helpful in reconstructing the shape of the mid-part of the jaw.

(*b*) R 3142. This specimen shows the rear end of the right jaw, again with the prearticular rotated outwards into the same plane as the surangular. Other blocks show the damaged symphysis and part of the left ramus from above, and an outer view of the left splenial, prearticular and coronoid.

(*c*) R 2409, which has most of both rami but has lost a great deal of bone. The rear half of the left ramus is tolerably well preserved; it explains the tendency for the prearticular to rotate outward during compression, for it is evident that both surfaces of the jaw slope towards each other below the articular region and the prearticular has a prominent projection medial to the articular surface for the quadrate. Newton's figure of the jaw is inaccurate as regards the rear end, which does not differ in outline or construction from those of the larger individuals.

(*d*) E.M. 29R, a large detached left articular.

Only the outer surface and lower edge of the dentary is available for study. Behind the portion which bears the large anterior teeth its upper half curves inwards to allow the large anterior maxillary teeth to slide past it. The outer and lower surfaces are roughened and have many small vascular foramina and grooves. The dentaries meet in symphysis for some 5 cm, the details being concealed, and behind this is a short splenial symphysis about 2 cm long. The suture with the surangular is not exposed but the position of the lower rear termination of the dentary is shown by a recess on the lateral surface of the angular (figure 7*g*) and an overlap area on the anterior portion of the latter bone.

The splenial is almost completely flat medially with a bevelled-off area on either side of the forked anterior end for union with its antimere. The fork shows the point of junction of the Meckelian canals from each jaw. Ventrolaterally there is a strong longitudinal ridge below which the surface for union with the dentary slopes away medially. The anterior process of the angular passes within the splenial and dentary and tapers to a fine point between and above these bones, flooring the Meckelian canal. The smooth surface of this anterior process contrasts with the strong union of the dentary and splenial and suggests that some degree of anteroposterior movement was possible at this point.

The central portion of the angular is a stout, gently curved rod with cross-section of the form of a vertical ellipse. The details of the junction with the posterior part of the splenial are obscure but no very firm union is indicated. Posteriorly the angular tapers out between the surangular, articular and prearticular in the manner shown. The suture with the prearticular cannot be detected on the actual bony portions of R 3142 and R 3143, but is visible as a raised line on the outer impression of the latter jaw.

The prearticular is a narrow, flattened strip anteriorly, curving up to meet the splenial which probably overlapped its medial surface. A small coronoid of uncertain shape is present. Posteriorly the prearticular broadens out and it has been restored to its original position on the assumption that the rugose knob fitted against the anteromedial corner of the articular surface as it does in *Stagonolepis* and '*Dryptosaurus*' (Lambe 1904). Some degree of lateral exposure of the prearticular is also indicated.

The surangular lies above the angular with a straight suture and just above and in front of the rear tip of the latter a large pit or foramen enters the bone obliquely from behind.

The upper edge of the surangular is strongly roughened for muscle attachment above the rear end of the mandibular vacuity. More anteriorly a foramen emerges obliquely on to the outer surface. The lateral surface of the bone is concave for a short distance behind the rear end of the mandibular opening.

The left articular (E.M. 29R, figure 4*g* to *i*) is remarkable for its extreme blockiness. The cast shows the ventromedial surface and parts of the anterior and ventrolateral surfaces. Comparison with the detached articular of a Recent crocodile makes its orientation plain, for it is evident that the area below the articular surface for the inner condyle of the quadrate sloped ventrolaterally, although the articular surface is then inclined medially instead of being almost horizontal as in the crocodile. The ventromedial surface is smooth and has a vertical buttress towards the rear end. This is comparable with the strong medial projection of the articular of *Antrodemus* (Gilmore 1920), '*Dryptosaurus*' (Lambe 1904) and *Tyrannosaurus* (Osborn 1912). The anterior surface is quite smooth and flat and is at right angles to the ventromedial surface. The ventrolateral surface is almost smooth and is disposed at slightly less than a right angle to the ventromedial side. A groove tapering medially interrupts this surface below the aforementioned buttress.

This articular seems somewhat small if reduced in proportion to the maxilla and pterygoid of '*Dasygnathus*' in order to fit the jaw of R 3143, but probably the explanation is that the articular did not grow as rapidly in size as the skull as a whole. In the crocodiles the angular reaches to the rear end of the jaw and meets a narrow tapering area on the ventrolateral surface of the articular. The arrangement in *Ornithosuchus* is basically similar, for a tapering area for the angular articulation can just be made out on E.M. 29R, apparently ending at the inner termination of the foramen. It thus seems that the surangular foramen led inward, downward and forward to emerge medially as a smaller hole between the articular and angular. Since the angular apparently ended at the inner limit of the foramen in E.M. 29R, it would appear that this opening was more posteriorly placed, or that the angular was shorter, in the largest individual; possibly the inner termination varied somewhat in position (in R 3142 the outer pit is only slightly oblique). Actually it seems that this 'foramen' was a blindly ending pit, for it tapers inwards and its inner end is in a position where one would normally expect the prearticular to lap over it and in fact the relationship of the latter with the surangular demands that it should do so. Yet there is no sign of an opening on the left prearticular of R 2409. The surangular and prearticular clasped the articular between them and probably met below it posteriorly. The retroarticular process is very short. The restoration of the rear end of the jaw, and the shape of the preserved part of the quadrate combine to indicate that the articular surfaces sloped medially.

Dentition

The number of premaxillary teeth is constant at three in the four skulls in which they can be counted. These skulls range in length from 60 mm (R 3149) to 250 mm (R 3143). Boulenger's statement of four premaxillary teeth for the latter skull is apparently due to the misidentification of the tip of one of the dentary teeth. On the left side of R 3143 the middle premaxillary tooth is longest, whereas on the right side the first tooth is fully as long, and slightly exceeds the second in length. On both sides the third tooth is shorter and there is some reason to think, taking into account the appearance of the broken teeth of R 2409, that this was the normal condition.

The normal number of maxillary teeth is the unusually low total of nine (see §III), but it seems that even this number was not always attained, as for example on the right side of R 3143, where the slender first maxillary tooth is omitted. The second and third maxillary teeth are the largest, and thereafter the teeth decrease regularly in size, allowing for the usual variation due to replacement.

The exact number of dentary teeth is unknown, but is close to ten, the end of the series being opposite the fifth or sixth maxillary tooth. Possibly an additional tooth should have been inserted in the figures between the almost procumbent first dentary tooth and the two enlarged teeth which bite into the hiatus at the back of the premaxilla. Replacement of the largest teeth was thus arranged to ensure that at least one of these was functional at any given time in each of the tooth-bearing bones.

In shape the teeth are of the type generally referred to as 'megalosaurian', that is, they are compressed, recurved and provided with small serrations separated by minute grooves set at right angles to, or inclined to the edge of the tooth. The greatest thickness of the tooth is somewhat in front of its longitudinal axis proximally, so that the cross-section is more rounded anteriorly than posteriorly. This is also reflected in the distribution of the serrations, which in general occupy the distal half of the leading edge of the tooth and the entire posterior edge, for the cross-section becomes more markedly lenticular at the beginning of the anterior serrated portion.

The first maxillary tooth resembles those of the premaxilla more than those of the maxilla in having a less compressed cross-section, the proximal diameter only slightly exceeding the thickness. Contrary to the statement of Boulenger (1903) the anterior edge of this tooth is serrated over the distal sixth now, and probably originally over the distal two-fifths, some of the serrations having been removed by wear. The first dentary tooth also resembles the premaxillary teeth in shape, and it is probable that the posterior edge, and the extreme distal portion of the anterior edge are serrated, although these cannot be exposed (in R 3143) without risk of damage to the other teeth. The large second dentary tooth is well exposed on the left side; it exhibits a shape transitional between those of the premaxilla and maxilla. The succeeding dentary teeth are imperfectly preserved but were apparently like the maxillary teeth, but smaller.

An interesting feature concerns the direction of inclination of the serrations, to which attention was drawn by Boulenger (1903), who observed that these were directed obliquely to the edges of the teeth. However, not all the teeth are modified in this way, for in the premaxilla and anterior part of the maxilla the serrations are at right angles to the edges, and it is not until the third and succeeding maxillary teeth are reached that the serrations become inclined obliquely distally. This modification affects both the anterior as well as the posterior edges. Furthermore, on the second dentary tooth the serrations are perpendicular to the posterior edge in the proximal half of the tooth, but become obliquely inclined to the margin in the distal half.

The teeth of the isolated maxilla (E.M. 1R, type of *Dasygnathus* Huxley) are relatively longer than those of R 3143, although in each case the longest teeth appear to be fully erupted. In the former the lengths of the first and third maxillary teeth are estimated to be 48 and 62 mm respectively, set in a maxilla which is 165 mm long, measured to the fork at the posterior end. These compare with lengths of 18 and 26 mm for the corresponding teeth and 97 mm for the length of the left maxilla of R 3143, giving ratios of 2·7 and 2·4 for the lengths of the first and third maxillary teeth against 1·7 for the lengths of the two maxillae. Comparison with the smaller skull R 2409 is difficult owing to faulty preservation, but using Newton's estimate of the length of the third maxillary tooth ratios are obtained which suggest that this tooth is again relatively shorter than the corresponding one of R 3143. These differences might be taken to indicate that the maxilla did not increase in length at the same rate as the skull as a whole, but this is contradicted both by the evidence of the large pterygoid (E.M. 15R), whose relative size agrees closely with that of the maxilla, and by a comparison with the teeth of *Gavialis*. Two skulls of the latter genus having lengths of 452 and 763 mm respectively (snout to occipital condyle) were compared. The ratio of length of these skulls is thus 1·7, while the ratios of various breadth-parameters at the rear ends of the skulls vary from 2·0 across the postorbitals to 2·3 across the quadrates. On the other hand the ratio of the longest teeth near the front end of the maxilla is 2·8, indicating a relative increase in tooth-length with growth. This comparison is admittedly a crude one and it would be desirable to check it by a more elaborate series of measurements on other crocodilian skulls.

Mechanics of the jaws

The mechanics of the jaws of *Ornithosuchus* have already been briefly discussed by the writer (Walker 1961). Although the figures of the skull, and particularly of the jaw, which are given in the present paper differ somewhat from those of Newton, whose drawings and description provided the data for the previous analysis, they do not do so to such an extent as to call for a modification of the views previously advanced. Further consideration of these and allied problems will be undertaken in a later section.

Vertebrae

As in the case of most of the postcranial skeleton, the description of the vertebral column has been drawn up to a large extent on the evidence of the smaller specimens (but see Appendix). Taken together, the three individuals R 2410, R 3561 and R 3916 supply a continuous series of vertebrae from the fifth cervical to the twenty-fifth caudal. Probably the complete series of cervical vertebrae are present below the scutes in the case of the larger individual R 3142, but are unfortunately very poorly preserved. Other segments of vertebral columns occur with the Manchester specimen (L 8271), and with the two very small individuals (R 3149 and R 8170). It is assumed that there were twenty-four presacral vertebrae since there are three well-developed sacrals and the last of these evidently corresponds, from the shape of the sacral rib, to the original second sacral. One presacral vertebra has thus been added to the sacrum. The vertebrae have been numbered by counting forward from the sacrum and, although there is no clear distinction between the cervical and dorsal regions, for convenience of description it is also assumed that these were divided in the ratio of nine cervicals to fifteen dorsals. The number of caudal vertebrae is unknown, but an estimate of some forty-five to fifty seems not unreasonable. The vertebrae vary little in length throughout the portions of the series which are preserved; the most

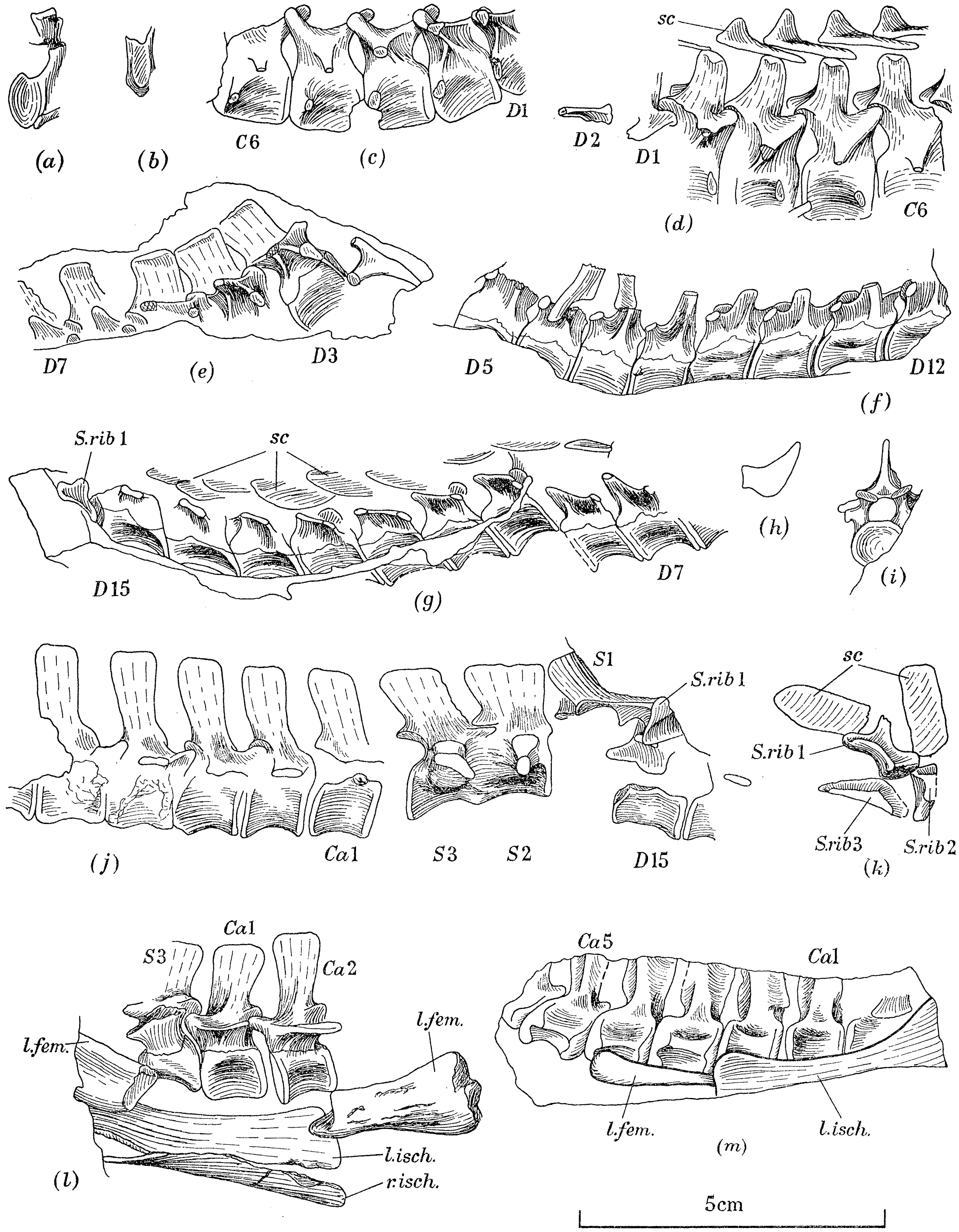

Figure 8. *Ornithosuchus longidens* (Huxley). Vertebrae (natural size). *a*: posterior view of (damaged) fifth cervical; *b*: anterior face of seventh cervical; *c*: left sides of sixth to ninth cervicals and first dorsal; *d*: right sides of same, with scutes above and diapophyses of first and second dorsals; *e*: right sides of parts of third to seventh dorsals, oblique view of an anterior dorsal rib; *f*: oblique left lower view of fifth to twelfth dorsals; *g*: right sides of (distorted) seventh to fifteenth dorsals with scutes above, oblique anterior view of first sacral rib; *h*: upper view of ?last presacral rib of right side, anterior end upward; *i*: anterior view of an incomplete posterior dorsal; *j*: right sides of parts of the last two presacrals, the three sacrals and the first six caudals (the first sacral centrum missing and the distal ends of the sacral ribs incomplete); *k*: approximate shapes of distal ends of second and third sacral ribs of left side, viewed medially; above them are the detached first left sacral rib and inner surfaces of scutes; *l*: left sides of third sacral and first two caudals, incomplete cast of left femur and ischia; *m*: oblique lower right view of third sacral and first six caudals, part of left femur and upper view of incomplete left ischium. *a* to *d*, *f* to *h*: R 3916; *e*, *j*, *k*: R 2410; *i*, *l*, *m*: R 3561. (Drawn from casts.)

anterior centrum (sixth cervical) is 11 mm in length, the posterior cervicals and anterior dorsals are slightly shorter, that is about 10 mm long. There is again a slight increase in the most posterior dorsals and sacrals to 11 mm or slightly more, followed by a decrease in the anterior caudals to 9 or 10 mm which is maintained as far as the end of the preserved series of R 3561 (twenty-fifth caudal).

The more anterior vertebrae were obtained by splitting one of the slabs of R 3916, revealing a well-preserved series of posterior cervicals. Fortunately, before this was done, casting material from a previous cast had entered the cavities, in which some scraps of bone still remained. There were thus obtained partial casts of these vertebrae which show some details of the ends of the centra which would otherwise have been lost, since the very thin sandstone partitions fell away when the block was broken. The cervical vertebrae are remarkable for the compression of the centra, the lower portions of which are reduced to thin plates of bone joining the anterior and posterior faces. The articular ends are oval in shape and vertically elongated. There is apparently some degree of opisthocoely in the anterior members of the preserved series, although this might have been overlooked but for the existence of the partial cast of the seventh cervical alluded to above. In this vertebra (figure 8*b*), and also in the one preceding it, the anterior face of the centrum is drawn out forwards, ending in a flattened oval face 3·3 mm in diameter and 6·5 mm high. The posterior face of the sixth cervical vertebra is not seen, but the posterior half of the fifth vertebra is somewhat in advance of the rest and a cast of its posterior face (figure 8*a*) shows it to be uniformly concave, the articular surface being 4·5 mm across. The more cordate form of the end of this vertebra possibly indicates a decrease in the degree of compression in the anterior cervicals. Comparison of the cast of the posterior face of the fifth cervical with that of the anterior face of the sixth suggests that, when closely articulated, the latter extended forward slightly within the former. The fifth cervical centrum is broken across at its middle and shows a Y-shaped cross-section where the narrow vertical median portion of the centrum diverges upwards towards the neural arch.

The cervical vertebrae are 25 mm high. The neural spines are rather narrow, with apices slightly expanded in the transverse direction. The zygapophyses are widely separated, those of the sixth and seventh vertebrae measuring 10 mm across; in the ninth vertebra this has decreased to 7 mm. The neural canals are very large and sag down deeply into the centra, a feature characterising all the vertebrae. The junction between the neural arch and centrum is clearly marked in the presacrals, the central part of the suture making a sharp upward projection in all members of the series. In the sixth cervical the parapophysis is situated low down at the anterior end of the centrum; the diapophysis lies on the lower portion of the neural arch and is directed downward. Passing backward, the parapophysis rises gradually until in the third dorsal it is entirely on the neural arch. The diapophysis also ascends, changing its inclination so that in the ninth cervical it is directed straight outward, and in the anterior dorsals, slightly upward. The appearance of a supporting ridge below the diapophysis to the posterior end of the centrum is first noticeable in the eighth cervical; this becomes more marked posteriorly. In this vertebra also the diapophysis is joined by a ridge to the prezygapophysis, and by a fainter ridge to the postzygapophysis. In the ninth cervical the full pattern of supporting ridges is present: the diapophysis is buttressed below by a lamina which runs out beneath it, and which forks ventrally on the side of the neural arch, sending a low ridge to the parapophysis in addition to that already mentioned towards the posterior end of the centrum. The ridges to the pre- and postzygapophyses are now well-developed, bounding hollows on either side of the supporting lamina below the diapophysis. The first dorsal vertebra shows these features in a more accentuated form; these are best seen in the partial cast of this vertebra. The ridge to the parapophysis is here well marked, and a deep cavity is formed in the angle between it and the ridge to the prezygapophysis. The second dorsal vertebra is not fully preserved but its right diapophysis with supporting lamina below is seen on one of the blocks of R 3916.

The third and fourth dorsals are well shown at the anterior end of the series of R 2410. In these vertebrae the parapophysis is a short, stout process low down at the anterior end of the neural arch, linked by a short, oblique ridge to the underside of the diapophysis which is some 7 mm long. A separate narrow ridge now runs obliquely backward towards the posterior end of the centrum. The diapophysis is still connected by ridges to the zygapophyses so that a series of three hollows in all is enclosed by this system of buttresses.

Passing backward in the series the rib articulations and the system of ridges exhibit the following changes. The diapophysis gradually decreases in length, the parapophysis approaches more and more closely to the same horizontal plane, but remains joined to the diapophysis by a thin lamina, and the two processes come to lie closer together. Finally, in the last dorsal vertebra there is only a single rib-facet, 4 mm in length, projecting about 2 mm from the side of the neural arch. The ridge to the postzygapophysis is present until the last two vertebrae, likewise the ridge running towards the posterior end of the centrum. This latter ridge, and the hollow between it and the parapophysis, are particularly marked in the seventh, eighth and ninth dorsals of R 3916. The parapophyses of the sixth and succeeding dorsal vertebrae are supported by very thin laminae extending down to the anterior ends of the neuro-central sutures; these laminae are considerably reduced in the last two vertebrae. The ridge connecting the diapophysis to the prezygapophysis, and the anterior hollow which this encloses, becomes progressively reduced until at about the tenth dorsal vertebra it may be said to be absent. A similar disappearance of this feature at about this point may be noted in figures of the vertebrae of *Plateosaurus* given by von Huene (1926*a*, 1932).

The neural spines of the dorsal vertebrae increase gradually in breadth towards the sacrum, but there is little change in the height of the vertebrae and the neural canals remain large. The centra have shallowly concave, approximately circular articular faces. From about the sixth dorsal vertebra backwards the lower parts of the centra assume a definitely spool-like aspect, the sides being considerably pinched-in a short distance below the neuro-central sutures; this character is also present to a lesser extent in the more anterior dorsals. The transition from the ventrally keeled cervicals is not seen, but the keel is certainly absent at the third dorsal vertebra.

The sacral vertebrae are best exposed on R 2410; they are also present on R 3561 but have been left largely unexposed to avoid damaging the pelvis of this specimen. The centrum of the first sacral vertebra of R 2410 has fallen out of position and now lies close to the anterior edge of the left pubis; like the centra of the hinder two sacrals it is flattened below, and its articular face is broader than high (9 by 7 mm). The neural arch and spine of this vertebra (figure 8*j*), together with the first sacral rib, have been pushed upward and to the left; the neural arch of the last dorsal vertebra is also free from its centrum and its spine is concealed by the first sacral rib. The similarity of the rib-facet of this latter vertebra to that of the last dorsal of R 3916 (figure 8*g*) confirms its identification and also verifies the correctness of Newton's original interpretation (1894) of the sacral vertebrae and their ribs. The first sacral rib attaches to a facet which was evidently shared by the centra and neural arches of the last dorsal and first sacral vertebrae; the area of attachment to the last dorsal vertebra is seen on both R 3916, where it is the last portion of the column preserved, and R 2410 (figure 8). In the case of R 2410 the sacral rib is seen to expand downwards and outwards, ending in a large articular surface whose anterior end is not preserved. R 3916 shows the anterior face of the same rib (figure 8*g*). As noted by Newton, the detached first sacral rib of the left side of R 2410 is now lying above sacral ribs 2 and 3 of the left side (figure 8*k*); comparison of this rib with that of the right side has, however, so far failed to bring out its correct orientation. The second sacral rib is attached near to the anterior end of its vertebra by a facet which, like that of the third sacral rib, is shared by the centrum and neural arch. The base of the third sacral rib is exceptionally strong and lies at about the mid-point of the vertebra. The distal ends of the ribs are not clearly exposed, but it can be determined that the second sacral rib expands downwards and is compressed from side to side, and that the third broadens distally in an oblique antero-posterior direction, although it probably does not reach as far forward as Newton has shown it.

The neural spines of the three sacral vertebrae are much expanded anteroposteriorly and, although the anterior edge of that of the third sacral vertebra is now damaged, it seems that they were originally in contact.

The centrum of the first caudal vertebra is somewhat flattened below, although not to such an extent as in the sacrals. Its sides are compressed; passing backwards the spool-like shape of the centrum again becomes more obvious. The chevron-facets commence at the rear of the third caudal vertebra in both R 2410 and R 3561; from this point backwards the lower surface of the centrum is grooved in the usual manner. The centra gradually diminish in height to an observed minimum of 4 mm at the twenty-fifth caudal but with little change of length. The transverse processes of the anterior caudals are broadly expanded, reaching a length of some 18 mm, and are supported below by a low longitudinal thickening; little is known about the more posterior processes, save that they are set well to the rear of the neural arches.

The neural spines of the caudal vertebrae increase rapidly in height behind the sacrum, so that the fifth caudal attains a total height of 29 mm. Behind this point there is a gradual decrease in the height of the spines; they become progressively more inclined backward, and are set increasingly farther back with respect to the centra, so that at the eighteenth caudal the greater part of the spine lies behind the centrum (figure 14*n*). At the eleventh caudal vertebra the scutes have already fused to form median ridge-scutes which ride on top of the apices of the neural spines of this and succeeding vertebrae.

An interesting feature of the caudal vertebrae is the development of a rectangular median vertical lamina projecting forward from the base of the neural spine, which is clearly quite distinct from the prezygapophyses. It is particularly well seen in the thirteenth to the eighteenth caudals of R 3561 (figure 14*m*, *n*). In the fifteenth, seventeenth and eighteenth caudals the anterior corner of this process is drawn upward into a short point which in the twenty-second caudal is accentuated to form a more definite separate anterior vertical projection. The development of the lamina cannot be fully traced but its first appearance may be seen (R 2410) as a slight forward sinuosity at the base of the neural spine of the fifth caudal vertebra.

Among the few postcranial elements known of the largest individual of *Ornithosuchus* (‘*Dasygnathus*’) are portions of two caudal vertebrae. These are illustrated at figure 4*b* and *e*. The latter of these was particularly difficult to identify but was ultimately determined (because of the single postzygapophysis) as the left side of the neural arch of a posterior caudal vertebra, 46 mm in length. The side of this neural arch is extraordinarily flat. Ventrally there is a slight indication of the base of the transverse process which must therefore have been given off between neural arch and centrum, and dorsally a longitudinal ridge connects the pre- and postzygapophyses, somewhat as in a caudal of *Antrodemus* figured by Gilmore (1920, Fig. 29), or as in *Dryptosaurus aquilunguis* (von Huene 1932, Pl. 3, Fig. 8), but the closest resemblance to this neural arch which I have been able to discover is in a caudal vertebra of *Gresslyosaurus ingens* (von Huene 1908, Pl. 42, Fig. 4).

Ribs

Little information of value can be gathered concerning the ribs of the cervical and dorsal series, because of their small size and slenderness which makes them particularly difficult to study in the form of negatives. Little more can, in fact, be deduced about them than is not already obvious from the form of their articular surfaces on the vertebrae. The proximal ends of two ribs from the anterior dorsal region are shown on figure 8. Of more interest is the discovery of a rib of unusual shape (figure 8*h*), the proximal end of which lies close to the transverse process of the fourteenth dorsal vertebra of R 3916, and whose distal end is close to or touching the inner sides of the right pubis and ischium at their junction. This rib has a single, slightly concave articular facet; it expands outwards and its distal end is turned strongly forward. In spite of its present position, it is considered that this rib belongs to the fifteenth or last dorsal vertebra, for the following reasons. The breadth of the proximal facet agrees very well with that of the single articular area on the last presacral vertebra and is noticeably narrower than that of the fourteenth dorsal which apparently still has two separate (but confluent) rib-facets. In this specimen the posterior vertebrae are distorted and have been pushed backward with respect to the pelvis; the amount of displacement is such that if the last dorsal rib had remained stationary in the matrix it would come to occupy approximately its present position. Finally, the posterior vertebrae are in contact with the medial sides of the pubis and ilium giving a narrow matrix-filled cavity which is bounded above by the right row of scutes. No additional rib was discovered within the matrix of this region. It must, however, be admitted that the articular areas of this unusual rib and the last transverse process do not agree in detail, since both are slightly concave longitudinally; perhaps this may be attributed to incomplete ossification at the junction (cf. the detachment of the first sacral rib of the left side of R 2410). If the above identification is correct, the rib would be in a suitable position to make contact with the outwardly curving anterior end of the blade of the ilium and its presumed cartilaginous forward continuation. Alternatively, there may have been two forwardly curving ribs as in the specimen of *Plateosaurus* described by von Huene (1926*a*, p. 25 and Pl. 2) in which a somewhat similar arrangement with respect to the ilium occurs.

Chevron-bones

These have already been briefly described and figured by Newton (1894, Plate 54) and there is nothing to add to his statement, save to point out that a single chevron of the largest individual has been illustrated in a previous publication (Walker 1961, Fig. 11*h*,*i*).

Appendicular skeleton

Shoulder girdle

The shoulder girdle is represented by four specimens. The best of these is undoubtedly R 3916 which displays the entire girdle with the exception of the blade of the right scapula. The impressions are contained within two blocks of a hard variety of the sandstone which yields excellent casts. This specimen was figured both by Broom (1913, Pl. LXXVIII) and von Huene (1914, Fig. 40), but since the greater part of the girdle was then concealed by matrix their illustrations not surprisingly contain many inaccuracies. In this individual the glenoid region of the right scapulocoracoid has been crushed, but the coracoid apparently retains its natural curvature. On the other hand the left glenoid is exceptionally well preserved but the left coracoid has been pushed against the right and has been curled up along its medial edge (figure 9), thus accentuating the lateral ridge below the glenoid. Also, the left coracoid is less fully ossified than its fellow of the opposite side; its ventral margin is thicker, as if edged with cartilage, and it is noticeably smaller, even allowing for its excessive curvature. Probably the notch at the anteroventral corner of the left scapula also indicates a residual area of cartilage, for there seems no reason to attribute this to damage.

The scapula is slender, increasing gradually in width dorsally and terminating in a somewhat expanded apex. Anteroventrally it extends forward as a shallowly concave area surmounted by a longitudinal thickening. Above the glenoid is situated an oval muscle-attachment area with a central ridge. The blade of the scapula is almost flat, but ventrally the bone curves somewhat inward. The coracoid is less than 1 mm thick in this specimen. It is crescentic, or, considered in isolation, 'battle-axe' shaped, the suture with the scapula slanting anteroventrally. Probably the right coracoid shows the true curvature; this bone is as a whole gently convex towards the ventral or outer surface. The coracoidal part of the glenoid is large and shallowly concave, surrounded by a sharp rim. A ridge descends from below the glenoid on the outer surface and curves posteriorly, running out to the sharp rear point and imparting to the latter a three-edged cross-section.

The dermal elements of the girdle are also well displayed by this specimen. The clavicles are 20 mm long and 2 mm thick and are slightly curved. The stem of the interclavicle is 4 mm broad and about 1 mm thick. The blade is extremely thin, convex ventrally from side to side, attaining its greatest breadth of 8 mm at about two-thirds of its length. The lateral margins of the rear third are slightly concave in outline. The length of the interclavicle is 37 mm and the bone is gently convex along this dimension.

The smallest individual (R 8170) shows most of a left scapulocoracoid a little less than half the size of that of R 3916 and agreeing very well with it, but otherwise showing no

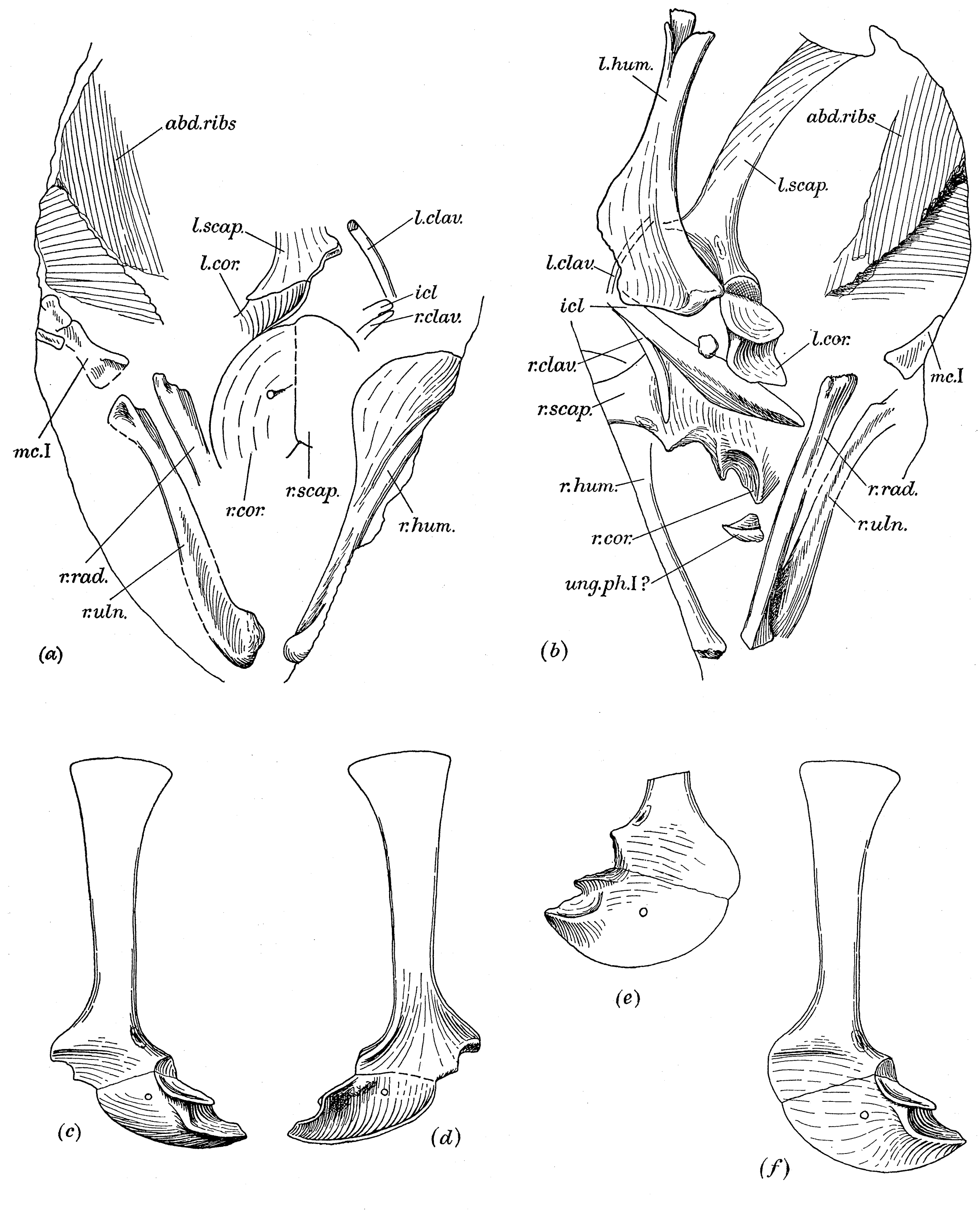

FIGURE 9. *Ornithosuchus longidens* (Huxley). Shoulder girdle and fore-limb of R 3916 (natural size). *a*, *b*: casts from counterpart slabs showing shoulder girdle, right fore-limb, left humerus and gastralia (the latter diagrammatic); in *a* the girdle is seen from above, in *b* from below. *c*, *d*: lateral and medial views of left scapula and distorted coracoid; *e*: lateral view of lower part of right scapula and coracoid, glenoid crushed; *f*: restoration of the scapulocoracoid in lateral view, based on the above two examples. In *c*, *d* and *f* the curvature of the scapula has been omitted.

distinctive features. The only shoulder girdle material of the larger individuals is that of R 3142, figured by Boulenger (1903, Plate 15, Fig. 2), since it has been mentioned previously that the supposed clavicles and interclavicle of R 3143 are the quadrate and pterygoid. This specimen (R 3142) is badly preserved and the girdle is indistinct, but it seems that the areas which Boulenger took to be the clavicles are really the crushed coracoids and possibly parts of the scapulae, merging medially and anteriorly into the interclavicle, the posterior end of which can be distinguished with difficulty. Portions of the true clavicles are present in front of the coracoids, and other blocks supply the shaft and expanded apex of the right scapula. There is no reason to suppose that this girdle differs in any way, apart from its greater size, from the smaller example already described.

Fore-limb

Both humeri are well shown by R 3916. The bone is extremely slender with a very large deltopectoral crest and a small internal tuberosity behind the head, which is curved considerably backward. The distal extremity of the left humerus is twisted slightly with respect to the plane of the deltopectoral crest so that it faces a little medially, but this may be due to the crushing of this end of the bone, since the right humerus does not show this feature. The right humerus is also somewhat less broad across the distal end (10 mm) compared with the left (12 mm). There is a deep trochlear recess anteriorly; this is better seen on the right humerus. The shaft of the latter bone has apparently been flattened somewhat from side to side, agreeing with the direction of crushing of the glenoid of the right scapulo-coracoid, and implying that the bone was hollow, as is known to be the case for the femur.

R 3142 displays parts of both humeri, the right example being the more complete. It is exactly twice as long as the humeri of R 3916 and, as far as can be told, identical with them, having a large deltopectoral crest and backwardly inclined head. This specimen also shows parts of the proximal ends of the radius and ulna, which are too imperfect to be helpful.

Two specimens are known which contain the radius, ulna and part of the hand. These are L 8271 and R 3916. Since the former was figured by von Huene (1914, Fig. 39) a piece has been lost which contained most of the right humerus, as well as the impression of the lower surface of the radius, ulna and part of the manus. Fortunately a rather indistinct gutta-percha cast of the lower arm and hand of this specimen is preserved in the British Museum (R 3622), but for the sake of completeness von Huene's Fig. 39*a*, which is evidently drawn from a cast of the missing piece, is reproduced here (figure 10*f*), although the bones are considerably more slender than the figure would suggest. Also, another fragment (L 8271 F) has the impression of the upper surface of the carpus and part of the manus of this same limb. This aspect of the manus has not previously been described and is of some considerable interest. The carpus is absent from the British Museum's cast of the undersurface of the limb and it seems likely that von Huene inserted it from the counterpart.

The radius (R 3916) is very slender, cylindrical in shape becoming flattened distally with the development of a lateral recess or shelf which appears to have been overlapped by a similar shelf developed on the ulna. The proximal end is oval in outline and concave, with the longer axis set obliquely to the plane of the distal end; it terminates dorsally (or laterally) in a sharp point. The ulna is a little stouter than the radius. There is little development of an olecranon process and the proximal articular surface is not well preserved (R 3916) and was probably still cartilaginous. Ventrally there is a longitudinal depression extending more than half-way along the shaft. The cast of the ventral surface of the ulna (R 3622) shows a similar anterior flange for the radius to that of R 3916, although this does not appear on von Huene's figure of the bone. The distal ends of the radius and ulna are not well preserved in either example; that of the ulna is curved postaxially in a curious manner in both specimens.

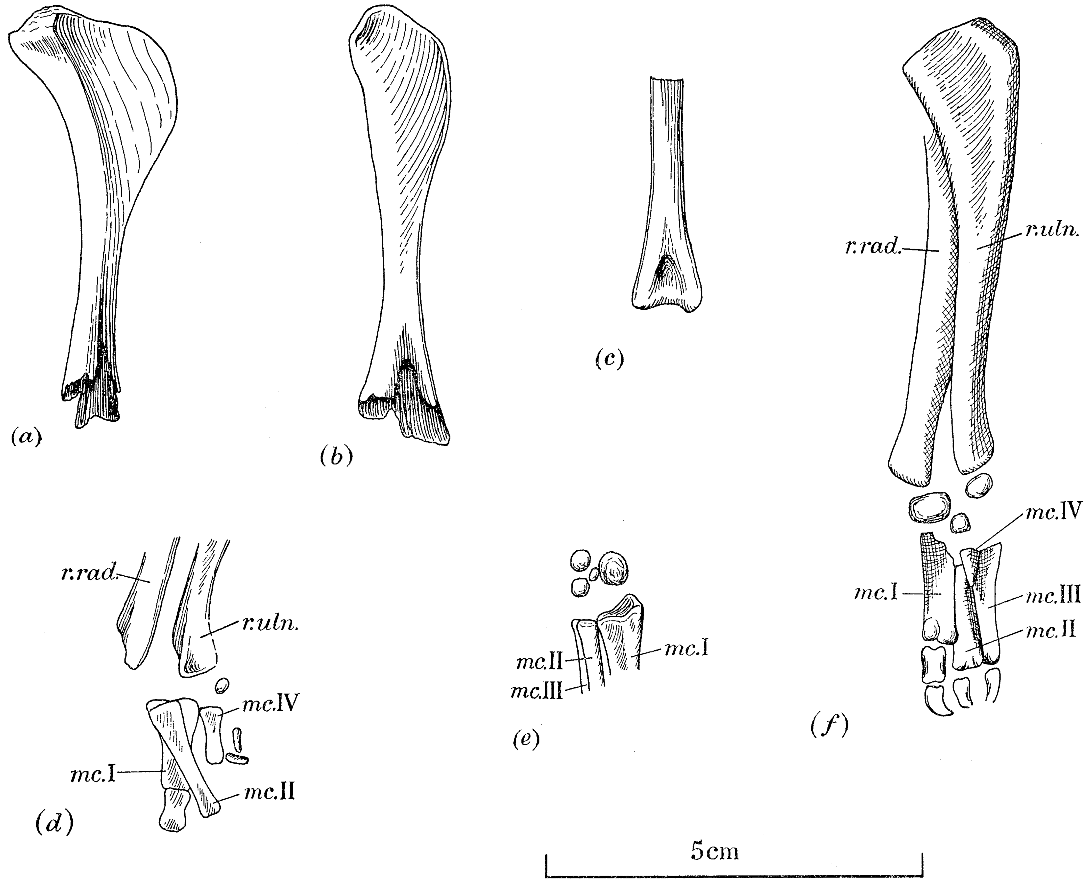

FIGURE 10. *Ornithosuchus longidens* (Huxley). Fore-limb (natural size). *a*, *b*: medial and anterior views of left humerus, R 3916; *c*: anterior view of distal end of right humerus, R 3916; *d*: lower view of distal ends of right radius and ulna and part of manus, R 3916; *e*: upper view of right carpus and proximal ends of first three metacarpals, L 8271 F; *f*: lower view of right radius, ulna, carpus and part of manus of L 8271, after von Huene (1914). (Drawn from casts.)

The carpus is best preserved on L 8271F. A large, rounded carpal is situated between the proximal end of metacarpal I and the radius, and this is flanked by two smaller, rounded elements lying lateral to it (figure 10*e*). During the cleaning of this region prior to casting a very small additional carpal was discovered between the other three. The only trace of wrist-bones on R 3916 is a single small element near the end of the ulna.

Knowledge of the manus again depends on the two specimens noted above. A cast from L 8271F, showing part of the dorsal surface, supplements the information about the ventral surface given by von Huene (figure 10*f*). Some further evidence from R 3916 than was known to him is also available. L 8271 F does not show the distal ends of the metacarpals, but these are seen on the British Museum's cast of the counterpart (R 3622). In this specimen (L 8271 F, figure 10*e*) the proximal end of metacarpal II directly overlies that of metacarpal III, but the former bone slopes downward distally so that (R 3622) the first three metacarpals come to lie almost in the same plane. There is a strong suggestion in the attitude of the metacarpals that there was some degree of opposability of the pollex; metacarpal I, which has a concave base, presumably pivoted on the large rounded medial carpal. This is to some extent borne out by the attitude of the first claw in von Huene's figure (reproduced on figure 10*f*) which is curved to oppose the two outer digits.

Metacarpal I is short and stout, 12 mm long; metacarpals II and III are much more slender, II being 16 mm long. Metacarpal III is shown by von Huene as equal in length to II, but close examination of the cast suggests that a phalanx has been included and that its length is actually 13 mm. Beneath the proximal ends of metacarpals II and III (R 3622) is the stub, 4·5 mm long, of a further metacarpal, probably the fourth, which has been incompletely cast. The gutta-percha cast is too indistinct in the case of the phalanges to be of any further value.

R 3916 (figure 10*d*) also shows a stout metacarpal I, 12 mm in length, 6·5 mm broad proximally and 4·4 mm distally. The first phalanx of this digit is also present, 6 mm in length. A more elongated, slender metacarpal (16 mm in length), lies obliquely beneath the first metacarpal. This is probably metacarpal II. It seems to the writer that von Huene has misinterpreted two small impressions on a small flake of rock which fits vertically across the junction of the two slabs which contain this right manus. According to my interpretation of these impressions, they are of the lateral side of the distal end of metacarpal I and the lateral edge of the first phalanx of the same digit. There are thus no phalanges of digit II preserved on this specimen. When a flake of matrix was removed to release the cast of metacarpal II, a further metacarpal was discovered. This is slender and but 7·5 mm in length and is presumably metacarpal IV. Lateral to this bone are two further small impressions, one of which lies on the vertical edge of the block. These may perhaps be the phalanges of digit III but preservation is not good. No other remains of the hand are preserved on this specimen, with the exception of a bone which is apparently the large claw of digit I, lying behind the right coracoid (figure 9*b*). If so, it is considerably larger (7 mm in length) than the figure given by von Huene (see figure 10*f*) of the corresponding claw of L 8271.

Presumably there was an even more reduced fifth metacarpal and this, like metacarpal III, may well lie within the matrix quite close to those at present exposed but it would be hazardous to attempt to reveal them. The lengths of metacarpals I and II are closely similar in the two specimens L 8271 and R 3916, although the ulna of the former indicates an individual some 20 % bigger and this agrees with the relative breadths of the apices of the scapulae.

Pelvic girdle

The figures which are given of the pelvic girdle also show considerable differences from those of previous workers. This is chiefly due to the study of casts which have been prepared from an almost perfect pelvis (R 3561) which has not hitherto been studied, although

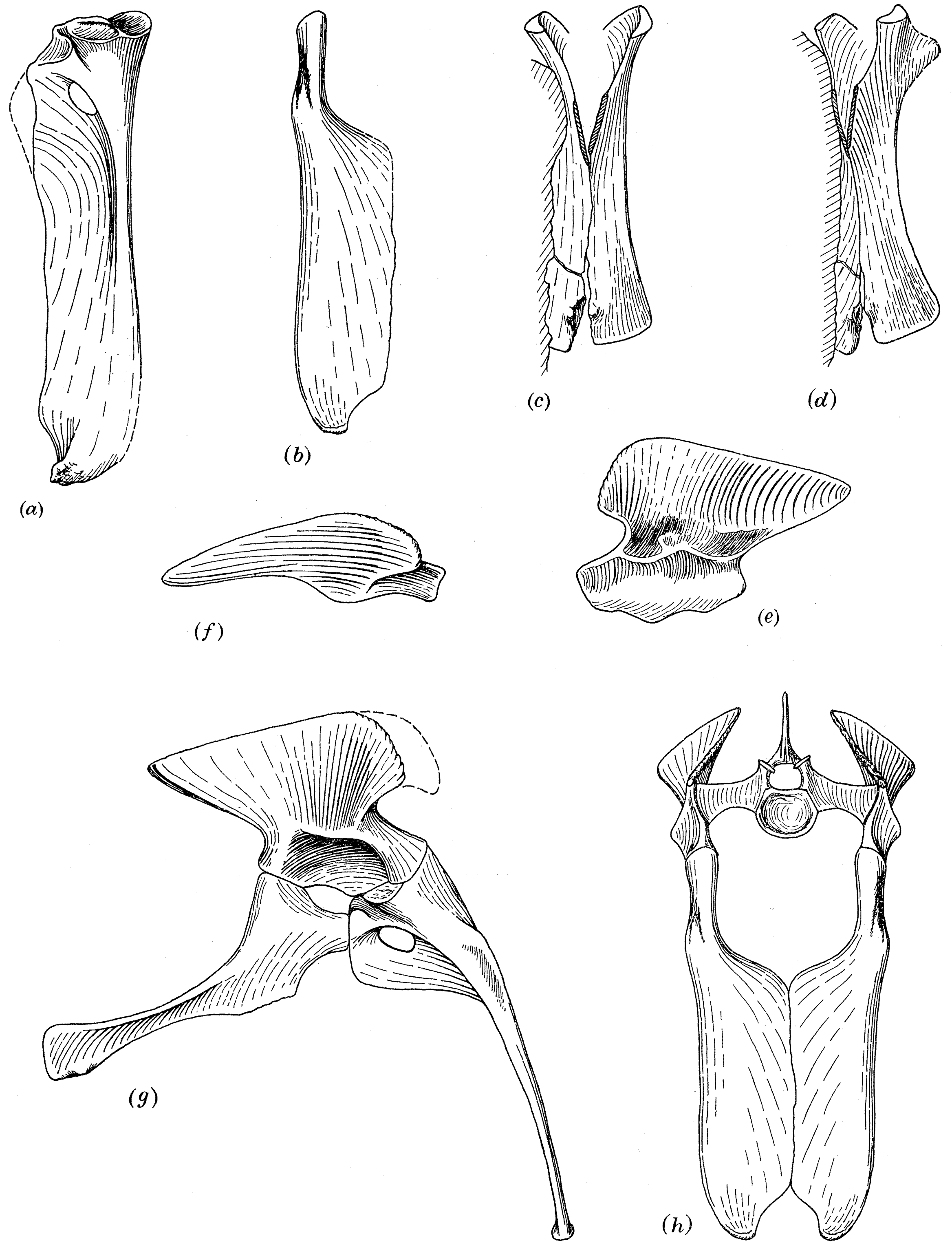

FIGURE 11. *Ornithosuchus longidens* (Huxley). Pelvic girdle (all natural size except *a*, which is half natural size). *a*: posterior view of right pubis, R 3152; *b*: anterior view of right pubis, R 3561; *c*: ventral view of ischia, R 3561; *d*: both ischia, viewed normal to distal end of left ischium, R 3561; *e*: inner view of right ilium, R 3561; *f*: upper view of same; *g*, *h*: lateral and anterior views of the pelvic girdle of R 3561, with some details from R 2410. (Drawn from casts.)

it appears to be one of the specimens referred to by Broom (1913, p. 626). There is also a somewhat distorted pelvis (R 3916), not mentioned by von Huene, which shows the ilium and ischium of the right side and both pubes. These two specimens also have portions of the femora and vertebrae associated with them. They can thus be compared in detail with R 2410 and in addition to their value in demonstrating the homogeneity of the material, they enable important corrections to be made to earlier descriptions and figures. R 3149 contains the complete pelvis of an individual about half the size of the three mentioned above, but only the pubes and ischia are exposed and the preservation is not such as to add any information to that obtained from the study of the larger specimens. Of great interest is the occurrence of an isolated large right pubis (R 3152) which probably belonged originally to one of the two individuals numbered R 3142 and R 3143.

The ilium is high anteriorly, the superior margin of the blade attaining a peak above the anterior portion of the acetabulum. Regarding the anterior and posterior buttresses of the acetabulum as lying in a horizontal line, and assuming that this line is parallel to the mid-line, the upper margin of the blade declines posteriorly, at the same time swinging markedly outwards. The anterior part of the blade is concave laterally and slopes inward dorsally towards the mid-line; the posterior half is gently convex. Due to the thin nature of the bone these curvatures are reproduced in the opposite sense by the inner surface, and the perfect symmetry of the ilia of R 3561 leaves no room to doubt that the original shapes are preserved. A deep groove extends along the distal half of the posteroventral edge of the blade, but this is hardly visible in side view. The anterior margin of the blade in both R 3561 and R 3916 is slightly thickened, roughened and minutely fissured in a manner suggestive of former cartilaginous extension; this edge is continued posteroventrally as a strong lateral ridge which merges into the well-developed supra-acetabular lip. In the case of the specimen illustrated by Newton (1894, R 2410) the plane of fracture of the block has passed through the left ilium in such a manner as to give a misleading impression of the shape of the lower half of the bone, and neither Newton nor Broom mentions the fact that the anterodorsal corner of the blade has been lost along a line of fracture.

The acetabulum is deeply cupped and strongly overhung by the supra-acetabular lip. The ventral margins of both ilia of R 3561 show a small upward deflexion in the region which lay above the ischium. This cannot be seen in the case of R 3916 due to the manner of preservation, nor can it be verified for the left ilium of R 2410, since examination of the negative shows that at some time two cavities have been made in the matrix in the relevant area and these pass through into a deeper-lying bone (probably the right ilium). There was thus a small acetabular perforation between the ilium and the ischium.

The medial side of the ilium shows quite clearly the area of attachment of the sacral ribs, which lies above an undulating ridge running across just below the 'neck' of the bone. The first sacral rib attached immediately behind the anterior embayment of the ilium and probably extended a short distance forward above it. The area for the second rib is not clearly delimited from that for the third, which runs obliquely upward and backward from the posterior part of the 'neck'. This obliquity of direction, combined with the shape of the rib, shows that it is equivalent to the second sacral rib of those forms which have only two sacral ribs. It is clear that Newton (1894) and following him, Heilmann (1926), have placed the articulation with the sacrum too high upon the ilium, and that the neural spines of the sacral vertebrae are mostly concealed by the blade in side view.

The pubis articulates with the ilium in front by means of a large, somewhat upcurving facet. Behind this the articular edge thins rapidly and lateral to it is developed an additional, freely projecting surface directed upward and a little outward. Between this and the facet for the ischium a groove passes upward and backward to the apex of the bone. The pubis meets the ischium at a short, well-defined articular area below which the margin is very thin and easily broken. The pubic foramen is a relatively large opening. A low, rounded tuberosity arises from the proximal portion of the thickened lateral edge of the bone. The pubes have a continuous symphysis, beginning at the very thin proximal portion below the foramen and curving downward abruptly at the commencement of the narrow distal part. The latter area is slightly convex anteriorly, becoming flat distally, and terminates in a medially curving, thickened tip. In R 3561 the right and left pubes are 16 and 13 mm broad respectively in their descending portions.

The isolated right pubis (R 3152), 15 cm long, is of interest as demonstrating the similarity of this larger bone to the other, smaller examples. In this specimen some of the characteristic curvature of the medial part of the proximal end has been reduced by post-mortem pressure; however, the articular areas for the ilium and ischium and the curious shape of the distal end are practically identical, except for their larger size, with the corresponding regions of the smaller specimens. This pubis is relatively narrower than the smaller examples, being only 30 mm broad across the distal portion. Another point of interest is the rather blunter posterodorsal corner, which suggests that the acetabulum was somewhat more open than in the smaller individuals.

The general form of the ischium has been described by Newton, who first noted the presence of an obturator process, although this has been omitted from the figures of later authors. However, the details of this portion of the bone are not clear in the specimen which he described (R 2410), and comparison with R 3561 shows that the ischia of R 2410 have been distorted by compression of their proximal ends. The ischia of R 3561, on the other hand, have been rotated towards each other dorsally, but have avoided distortion save that the proximodorsal tip of the left ischium has been flattened by compression against the rear end of the blade of the right ilium.

The ischium articulates with the pubis at an isolated facet. Above this the concave acetabular margin is very thin, expanding at the dorsal apex to meet the postacetabular facet of the ilium. Unlike the pubes, the symphysis of the ischia is interrupted in front of the obturator processes, their thin lower edges here curving in an arc towards the pubes. The inner surfaces of these forwardly directed processes are concave, corresponding to the adjoining inner surfaces of the pubes. The lower margins of the ischia are thickened at the obturator processes which are bevelled-off medially. The posterior ends of the ischia are also thickened ventrally and originally met in a 'peg-and-socket' type of junction which is now separated by several millimetres. In order to restore the ischia to their original attitude, it is necessary to imagine them rotated ventrally so that the obturator processes and distal extremities meet each other. The ventral margins in between these surfaces then meet along thin edges and, in side view, the lower margin is concave in outline and the portion of the bone lying distal to the obturator process is considerably foreshortened.

Hind-limb

The femur is represented by five examples from three small individuals of closely similar size. The original shape is best preserved in the right femora of R 2410 and R 3561; because of its hollow nature the bone is particularly liable to distortion by crushing. The shaft is virtually straight in anterior view, but seen from the side shows a gentle dorsal curvature. A portion of the sandstone matrix recovered from the shaft of the right femur of R 3561 is oval in cross-section, measuring 5·3 mm by 3·5 mm, in comparison with an external diameter of some 8 mm. The proximal end curves medially, with only a small development of the great trochanter; however, this area is roughened and was obviously finished in cartilage. The presence of a well-formed lesser trochanter, not hitherto recorded, is of great interest. It forms a narrow ridge which terminates proximally in a thin edge which is slightly undercut. Proximal to the lesser trochanter the lateral side of the dorsal surface is considerably excavated; probably the right femur of R 3561 (figure 12*c*) shows this area most accurately. The left femur of R 2410 (figure 12*a*) is somewhat flattened proximally and it seems that the lesser trochanter has been pushed forward, but it is well developed in the right femur of this specimen. The underside of the head of the femur is divided into two areas by a short proximal ridge.

The fourth trochanter is situated well over to the medial side of the shaft; it is an elongated ridge ending abruptly distally. Probably the depression dorsal to the trochanter seen in the right femora of R 3916 and R 3561 is due to crushing. The shaft is approximately cylindrical, slightly broader than deep in cross-section. The distal end is not well preserved in any of the examples available, due to slight crushing and the former presence of cartilaginous cappings.

The tibia and fibula are best shown by R 2410, and this specimen, figured by Newton (1894) is still the only example of the foot available. The proximal end of the right tibia and fibula are also present on R 3561, but are crushed. The identification of the foot-bones of R 2410 adopted by Newton, with one exception, is accepted here. New latex casts have provided additional details concerning this specimen, and a solid PVC cast obtained by combining silicone rubber negatives has been particularly helpful. The specimen is unfortunately marred by the occurrence of a number of small ochreous concretions; these have tended to form at the ends of bones and at points where two or more bones are in contact, and are stippled in the drawings (figure 13).

The proximal ends of the right tibia and fibula are well preserved, the fibula lying on the medial side of the tibia. The latter presents a stout triangular proximal face, with a well-developed laterally curving cnemial crest behind which is a shallow concavity for the head of the fibula. The proximal end of the latter extends somewhat backward and is slightly undercut on the medial side. The proportion of the lower segment of the hind-limb may be obtained from the left fibula, which displays its full length of 73 mm, compared with 87 mm for the length of the femur. The left tibia and fibula are considerably crushed, especially towards the proximal ends. The fibula crosses below the tibia, and at this point both bones pass directly below the thick head of the right tibia. It is therefore difficult to ascertain to what extent the expansion of the left fibula in this region represents a true trochanter, and what should be attributed to compression, especially since the surface of the negative is not well preserved. The distal ends of the tibia and fibula are partly obscured by ferruginous concretions. The lateral side of the posterior face of the tibia (figure 13*b*) shows a concave distal area rising a little laterally and proximally. The outline of the distal end of the fibula (figure 13*a*) serves only to give a general indication of the form of the bone.

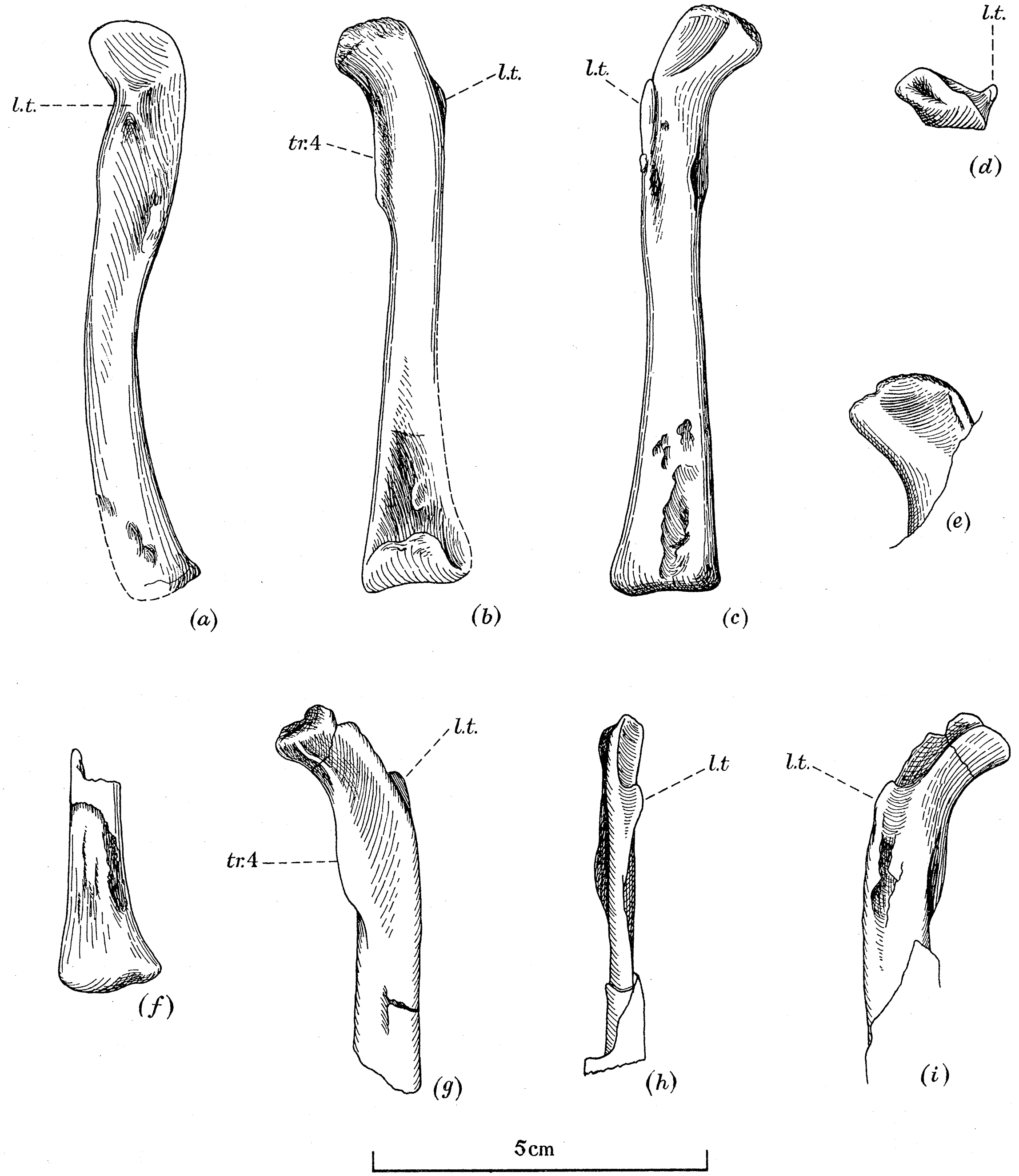

FIGURE 12. *Ornithosuchus longidens* (Huxley). Femur (natural size). *a*: lateral view of crushed left femur; *b*: posterior view of right femur; *c*: anterior view of right femur; *d*: proximal view of same; *e*: anterior view of proximal end of left femur; *f*: lateral view of distal end of same (somewhat compressed); *g*, *h*, *i*: posterior, lateral and anterior views of proximal end of crushed right femur, *a*, *b*; R 2410; *c* to *f*: R 3561; *g* to *i*: R 3916. (Drawn from casts.)

Only two elements of the tarsus are exposed. The larger of these lies close against the distal end of the tibia and was identified by Newton as the astragalus. However, in view of the disarticulation of the pes the association has no particular significance and the bone is here identified, with some reservations, as the left calcaneum. The upper surface presents an elongated convex facet for the fibula (possibly somewhat crushed), with a well-developed tuber behind this. The lower surface (figure 13*b*) has an almost straight anteromedial margin, behind which the surface is almost flat, forming a thickened, posteroventrally sloping area. Behind this again the central portion is gently concave. To avoid misunderstanding in the future, it should be stated here that some matrix was inadvertently removed from the lateral margin during the cleaning-out of the cavity; resulting casts give the appearance of an additional ventral projection in this region. This has, of course, been omitted from the figure.

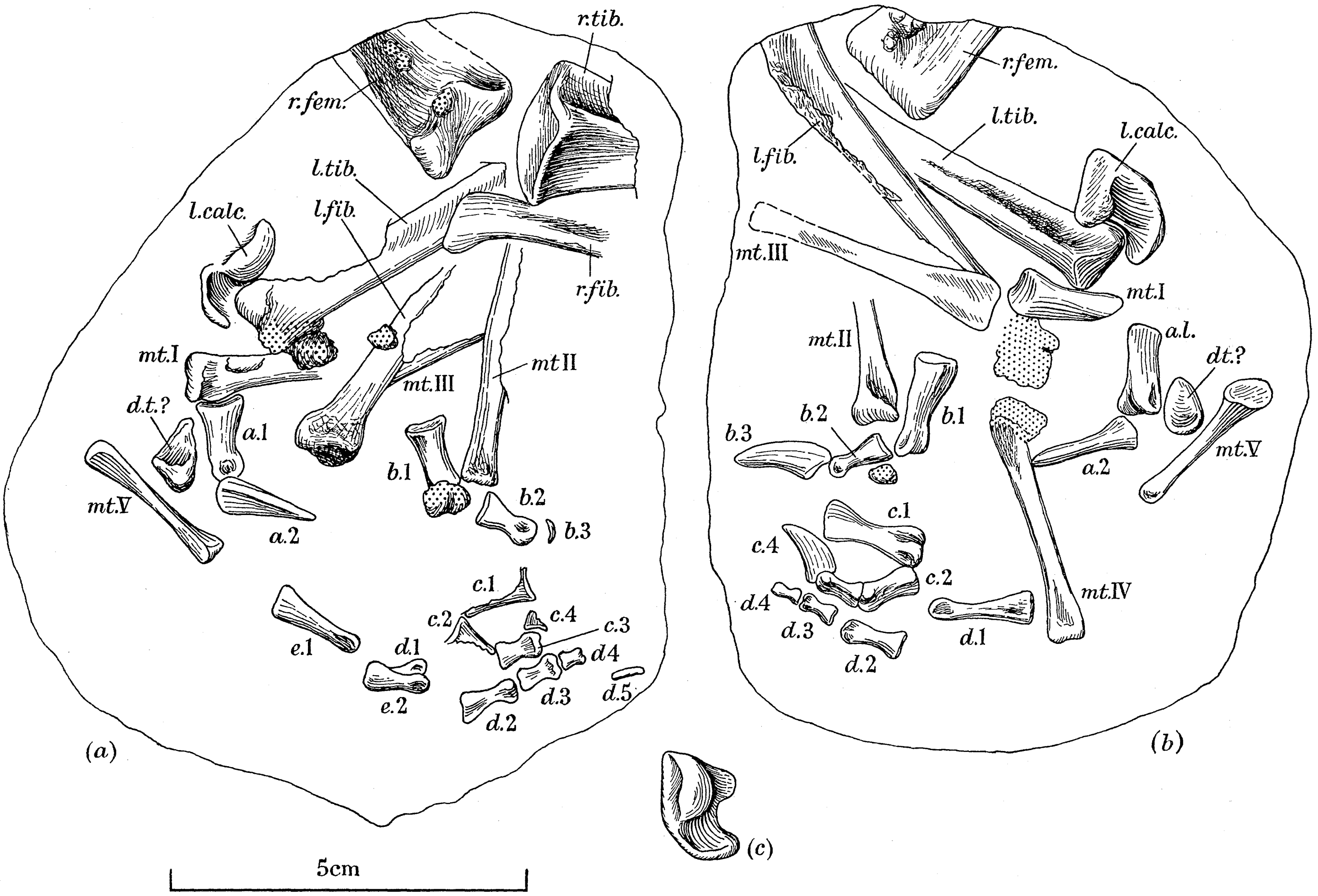

FIGURE 13. *Ornithosuchus longidens* (Huxley). Hind-limb of R 2410 (natural size). *a*: ventral view of distal end of right femur, posterolateral view of proximal ends of right tibia and fibula, anterior view of left tibia, medial view of left fibula, upper view of left calcaneum, metatarsals and phalanges of left foot; *b*: posterior view of left tibia, lateral view of left fibula, lower view of left calcaneum, bones of the left foot, metatarsal V in medial view; *c*: upper view of a 'solid' cast of the calcaneum, details of anteromedial portion unknown. (Drawn from casts of counterpart slabs; small ochreous concretions are stippled.)

The calcaneum, if correctly identified, is unusual in the inward curvature of the tuber and the anterior position of the medially projecting thin wing of bone which apparently corresponds to that portion of the crocodilian calcaneum which interlocks with the astragalus. No such interlocking relationship seems to have occurred in this calcaneum.

The other tarsal element is placed between metatarsal V and the first phalanx (*a 1*) of digit I. This is definitely a bone and not a small concretion. It is irregularly triangular in shape, flattened on one side and ridged on the other. This element is presumably one of the distal tarsals but if so is of considerable size.

The remaining bones of the pes have been well described by Newton, and the new, sharper latex casts do not provide any essentially new information, except in the case of the fifth metatarsal. Figure 13*b* shows the medial aspect of this bone, which is seen to be obliquely truncated proximally, probably a vestige of the medial expansion shown in, for example, *Euparkeria* (Broom 1913).

Scutes

The scutes of *Ornithosuchus* are arranged in a paired longitudinal series. Contrary to the statements of Newton (1894), each pair of scutes is joined together at a well-developed sutural contact along the mid-line until the anterior caudal region is reached, whereupon the scutes co-ossify to give a single median series forming a narrow ridge. No sign of scutes other than those of the dorsal series has been observed.

The cervical scutes are most completely represented on R 3142, but the details are better made out in the smaller specimen R 3916. This shows an almost continuous series of scutes from about the fifth cervical vertebra to the sacrum. The outer portions of the cervical scutes are bent down almost at right angles to the dorsal portions; at the posterior end of the angle so formed a prominent spine is developed projecting dorsolaterally. The spine is flattened towards the tip in a plane trending outward and backward. The portion of the scute medial to the spine is thickened, giving the effect of a succession of transverse bar-like ridges when the articulated paired scutes are viewed from above (figure 14*g*). Frequently also these elevated areas are traversed by one or more transverse grooves, but are otherwise devoid of ornament. The anterior and lateral parts of the scutes bear radiating ridges, and it is this ornamented portion of the scute which, contrary to the usual state of affairs, is overlapped by the scute in front. The anterior margins of these plates are concave, the anterolateral corner being drawn out anteriorly. About half of each scute is overlapped, and this corresponds to a slight change of level of the scute as a whole at the rear of the overlapped area, thus producing the elevated portion of the upper surface referred to above. In the lower aspect the anterior portion of each scute is more markedly concave, falling away to the thin anterior edge; the median portions of a pair, on the other hand, are slightly convex. The cervical scutes (of R 3916) measure 16 mm in maximum length by 10 mm in breadth.

R 3142 shows a series of thirteen paired scutes which, since they commence immediately behind the skull, probably represent the first thirteen rows, although the anterior members are poorly preserved and the seventh scute of the left side is missing.

These scutes agree extremely closely with the scutes of R 3916, which are about half as large. The bone of two of these larger scutes was removed in order to make the casts which are shown at figure 14*a* to *d*. The scutes of R 3142 also interlock securely along the mid-line by a system of more or less vertically alined ridges and grooves. The discrepancy between

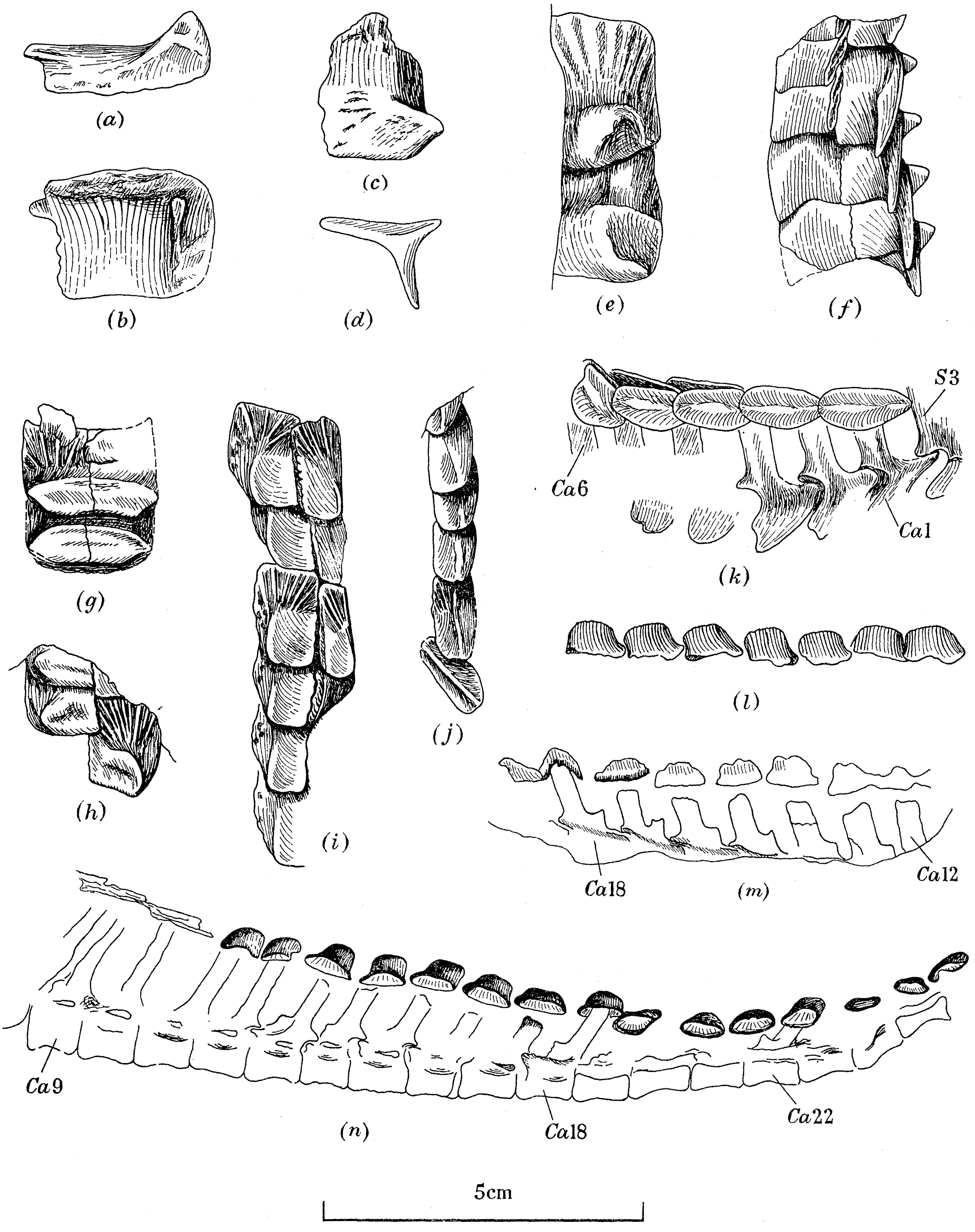

FIGURE 14. *Ornithosuchus longidens* (Huxley). Scutes and caudal vertebrae (all natural size except *n*, which is slightly reduced). *a*, *b*: left side and under views of incomplete cast of fourth left cervical scute; *c*, *d*: upper and posterior views of incomplete cast of seventh right cervical scute; *e*: upper view of two anterior dorsal scutes of the right side with broken spine-bases; *f*: lower view of portions of sixth cervical to second dorsal pairs, anterior end downward; *g*: upper view of seventh and eighth pairs of cervical scutes; *h*: upper view of ninth cervical and first dorsal pairs; *i*: upper view of portions of sixth to eleventh dorsal pairs; *j*: upper view of eleventh to fifteenth and first sacral scutes of right side; *k*: first five caudal scutes of the right side; *l*: right sides of ridge-scutes lying above eleventh to seventeenth caudal vertebrae; *m*: impression of the left sides of parts of the twelfth to the eighteenth caudal vertebrae and corresponding ridge-scutes; *n*: ninth to twenty-fifth caudal vertebrae, mainly as an impression of their right sides, with cavities representing ridge-scutes above. *a* to *d*: R 3142; *e*: R 3562; *f* to *j*: R 3916; *k* to *n*: R 3561. (Drawn from casts, except for *m* and *n*.)

Boulenger's account and figure of this specimen (1903, p. 186 and Plate 15, Fig. 4) and the description of the cervical scutes given above is due to the fact that only the more dorsal surfaces of these scutes have been exposed, and the apparent outward taper noted by Boulenger represents the elevated region leading to the spine.

Behind the thirteenth pair of scutes in R 3142 there is a break in preservation followed by two or three typical mid-dorsal scutes which have been turned upside-down and are lying about half an inch above the abdominal ribs. The best preserved of these is reversed end for end; it also shows the sutural medial edge, and measures at least 28 mm in length by 26 mm in width.

The changes in the dorsal scutes proceeding posteriorly are best shown by R 3916. The angulation of the scutes decreases gradually, until at about the fifth dorsal vertebra the inner surface is virtually flat. The spine is progressively reduced to a low longitudinal ridge; one of the anterior radiating ridges becomes more accentuated to form a linear continuation of this structure. In the mid-dorsal region the posterior half of the scute is still slightly elevated and the posterolateral portion is obliquely truncated, otherwise the scute is rectangular in shape. The part of the scute lateral to the ridge shows a tendency for pitting to develop. The posterior dorsal scutes are narrower, but there is little change of length, that which lies adjacent to the transverse process of the last dorsal vertebra measuring 15 by 6 mm. The ornament is very faint or absent and the keel is centrally placed. The last scute preserved on R 3916 just touches the upper margin of the right ilium and apparently corresponds to the first sacral vertebra.

The two scutes of R 3562 which are preserved (figure 14*e*) are apparently not strongly angulated yet they retain a well-marked elevation of the posterior portion; therefore they are assumed to come from the anterior dorsal region. The interest of these scutes lies in the fact that the spines have been broken off, but the preservation is not sufficiently good to be able to say whether this is due to pre- or post-mortem damage.

The scutes of the sacral and anterior caudal region of R 2410 are scattered and provide little useful information. However, the succession of scutes is taken up by R 3561 which is a particularly interesting specimen from this point of view. The first five caudal scutes of the right side are well preserved (figure 14*k*). These scutes are bluntly pointed in front and have rounded outer margins. The central longitudinal ridge is divided into two portions, there being a short anterior segment representing the original radiating ornament, and a longer posterior portion which is slightly domed up in the middle. There is no sign of other ornament. Before the bone was removed, the inner face of the first caudal scute showed a flat surface, with a slightly concave, gently upcurving posterior quarter which overlapped the point of the next scute. Behind the seventh caudal vertebra the tail is sharply deflected upward and to the right. In this region the neural spines and scutes are crowded together and the bone is preserved in a different manner; consequently the details of the changes in the scutes to form the median ridge cannot be observed. At the eleventh caudal vertebra the paired scutes have already fused to form a single series which is traceable as far as the twenty-fifth vertebra and presumably extended to the end of the tail. The drawings (figure 14*m*, *n*) show these scutes in the form of negatives, and a latex cast (figure 14*l*) has been made of caudal scutes 11 to 17. Each scute has a deeply hollow, elongate-oval base. Slender vertical ridges on the negative represent grooves on the inner (or lower) surface of the scute, converging a little towards the apex of the cavity. The outer surfaces of the scute converge upwards to form a blade-like keel. The sides are finely striated in a vertical direction, terminating in a minutely serrated upper edge. The anterior portion of the base of each scute is produced forward and this area was over-ridden by the scute in front, whose posteroventral margin accordingly rises up slightly. At present many of these scutes are tipped slightly backwards, but when restored to their correct attitude, the upper edges would lie along a straight line. The sixteenth scute measures $8\frac{1}{2}$ mm along the base, which is 4 mm wide, and is 5 mm high. The neural spines of the seventeenth and eighteenth caudal vertebrae can be clearly seen entering the hollow bases of the scutes; behind this point the scutes have fallen over sideways to lie against the left sides of the neural spines. Some of these ridge-scutes are also preserved alongside the caudal vertebrae of the larger individual R 3142.

The scutes of the largest individual of *Ornithosuchus* might have been expected to attain a length of 64 mm and a breadth of 44 mm; they would thus have been of comparable size to some of the scutes of *Stagonolepis*. A careful search amongst the material of the latter genus, particularly that from Findrassie in Elgin Museum, has failed to reveal any large scutes of *Ornithosuchus*, but this, although disappointing, is hardly surprising in view of the meagre amount of material of '*Dasygnathus*' which is preserved.

Abdominal ribs

These elements have been figured by Boulenger (1903, Plate 15) and by Newton (1894, Plate 54). They are also excellently preserved on R 3916 (figure 9), where they have been folded and broken longitudinally close to the mid-line. In this specimen each median chevron-shaped portion is about 3 mm broad at its forwardly projecting apex, tapering gradually outwards. Two zones of overlap of the elements may be discerned, each of which takes up about 10 mm, the medial end of the outer segment in each case passing forward in front of the section medial to it. The median elements measure about 22 mm in maximum length from the mid-line, the next lateral elements have a total length of about 24 mm; those of the outer (third) series are not fully preserved so that their length is unknown.

The juvenile individual, R 3149

This specimen is of considerable interest because of its small size, and the fact that the skull was apparently complete at first suggested the possibility of studying changes in proportion with growth. Unfortunately these hopes have remained largely unrealized. The skeleton is very lightly ossified and the bone is very friable, furthermore, the specimen is preserved in a relatively loosely cemented sandstone; as soon as the thin bones of the skull were approached with the needle they tended to flake off very easily, making preparation difficult. Nevertheless, the skull roof and right supratemporal fossa have been exposed, in addition to what was already visible, and some statements can be made concerning differences from the larger individuals, in particular R 2409.

The specimen was probably a complete skeleton when first found. The main block shows a series of presacral vertebrae, the centra of which are merely thin cylinders of bone. This block and other pieces also display both pubes (32 mm long) and ischia, cross-sections of the ilia, the crushed hollow left femur (50 mm long) and bones beneath it which are probably the tibia, fibula and foot, and a few caudal vertebrae. At the anterior ends of the blocks are portions of the shoulder girdle and fore-limbs incompletely preserved and unfavourably placed for preparation. The postcranial skeleton is too poorly preserved to yield positive information on growth changes; the femur appears to be more elongated compared with the pubes than in R 2410 but is crushed flat. The chief interest of the postcranial region lies in the occurrence of an irregular small mass of bone close to the right side of the mid-dorsal vertebrae. Careful examination of this area under strong magnification revealed the presence of a number of small teeth, recognizable by the thin amber-coloured enamel layer which contrasts with the bluish-white bone. The teeth, seen in broken cross-sections, are apparently arranged in two converging rows. The enamel layer of these teeth is thicker than those in the skull, in which the jaws are *in situ.* It seems therefore that the mass represents the last meal of this small reptile and is of interest in indicating that it was at least partially carnivorous even at this stage, perhaps including in its diet the young of its contemporaries.

The vertebrae curve dorsally in front of the shoulder girdle, and while a satisfactory fit is lacking between this piece and those which contain the skull and cervical vertebrae, it seems most likely that the neck also twists over to the left and the skull is inverted with respect to the body, although of course it is impossible to determine the attitude of the latter relative to the original bedding. The skull is contained within three small blocks. One of these (figure 2*a*) shows the left side of the snout and jaw, indications of the typical 'pear-shaped' orbit and the damaged left temporal region. This piece has been prepared to reveal most of the skull roof and right supratemporal fossa (figure 1*a*). The counterpart exposes an inner view of the snout and jaw with the large preorbital fossa of characteristic form well displayed. The tip of the premaxilla is slightly down-curved and bears three teeth; this region is a little damaged, the naris having been shortened and the rear of the premaxilla pushed upward. After a short diastema the slender first maxillary and three or four of the large maxillary teeth are also seen but no details of the jaw are available. The third piece displays the frontals and parietals seen from below, partly as bone and partly as an impression of their upper surfaces. The orbit is seen to be bordered medially by a curved ridge flanked by a smooth concave area sloping up to the orbital edge and suggesting the contour of the eyeball. In addition to the broken areas mentioned above the nasals are fractured and in view of this and the fragility of the bones it did not seem profitable to attempt to expose the right side of the skull.

The skull length of 60 mm (snout–quadrate) has been estimated from several measurements, notably the breadth across the supratemporal fossae and the length of the skull roof in the mid-line. This is based on the assumption that the proportion: snout–quadrate length/skull roof length is the same as in the larger skull R 2409, but if, as in young crocodiles, the quadrate was less inclined backward, the estimate given may well be too great. The length from the snout tip to the rear of the parietals, allowing for slight telescoping of the naris, is 48 mm, comparing with 100 mm in R 2409.

Comparison has been made with a series of skulls of *Crocodylus niloticus* ranging in length from 42·5 to 345 mm (snout–quadrate), kindly made available by the Zoology Department of the British Museum. As might be expected from the changes which are well known in the growth of the crocodile (Kälin 1933), the skull of R 3149 shows a relatively shorter preorbital region, larger orbit (although the skull roof may have risen upward a little) and narrower inter-orbital region than is the case in the larger skull R 2409. The next largest skull, R3562, is incompletely preserved but shows little difference in proportions from R 2409.

The most notable features of the smallest skull of *C. niloticus* examined are the inflated appearance of the cranium, the lack of a transverse ridge at the rear of the parietals, and the shape of the supratemporal fossae. The latter take the form of a pair of widely separated slits, diverging foward, with the fossa proper at the anterior end of each. The fossae are not delimited by ridges medially, the surfaces of the parietals sloping smoothly into them. At successively later stages the fossae become oval in shape, relatively larger, and develop well-defined parallel inner margins bordering on the deeper-lying recesses which lie within them. These changes may perhaps be ascribed to the effect of the attachment of the jaw muscles which gradually encroach upon the skull roof, in so doing producing recessed rims to the supratemporal fossae. It is of interest that in a skull of *C. niloticus* 228 mm in length the recessed area falls short of the frontoparietal suture by some $4\frac{1}{2}$ mm, whereas in a skull 345 mm long it actually reaches the suture. This change recalls the increase in size of the supratemporal fossa and its adjacent recessed areas with increase in skull size in a series of genera (not necessarily related) of large carnivorous dinosaurs.

The differences between R 3149 and R 2409 are comparable to those outlined above. In R 3149 the cranium is more inflated and lacks the posterior flanges of the parietals. The latter bones slope smoothly into the supratemporal fossae, which diverge somewhat anteriorly. Measurement of the breadth between the inner margins of the fossae is deceptive, since it appears to be equal to that of the larger skull (9 mm), but this is due to the lack of clear development of the recessed areas in R 3149. Examination of the counterpart in the case of the latter suggests that a slight medial marginal ridge is developed giving a breadth of 4 mm between the superficial portions of the openings. The small pointed process at the rear of the right supratemporal fossa, which is evidently formed by the squamosal, is more medially placed than in the larger skulls. Portions of the mid-line suture and a groove along the position of the lachrymal/nasal suture are the only other noteworthy features of the skull roof. So bird-like in appearance is this small skull that it is perhaps fortunate that it was not one of the earliest specimens to be discovered in the Elgin sandstones.

Restoration of the skeleton, appearance and habits

At least three previous restorations of *Ornithosuchus* have been published. One of these (von Huene 1914, Plate IV) shows the animal in stationary quadrupedal pose, another by Heilmann (1926, Figs. 136 and 137) depicts it in the act of running rapidly with the body almost horizontal and the fore-limbs raised well above the ground. It seems doubtful to the writer whether this latter attitude was a possible one for an animal of the body form restored by Heilmann, in which the centre of gravity is situated well forward of the pelvis. The evidence of the large size attained by *Ornithosuchus*, as witnessed by the individual previously named *Dasygnathus*, makes the assumption of habitual bipedal running, as distinct from swift walking, even less likely, although it may have been possible for short periods of time. Was *Ornithosuchus* a biped? Certain points in its osteology are in favour of

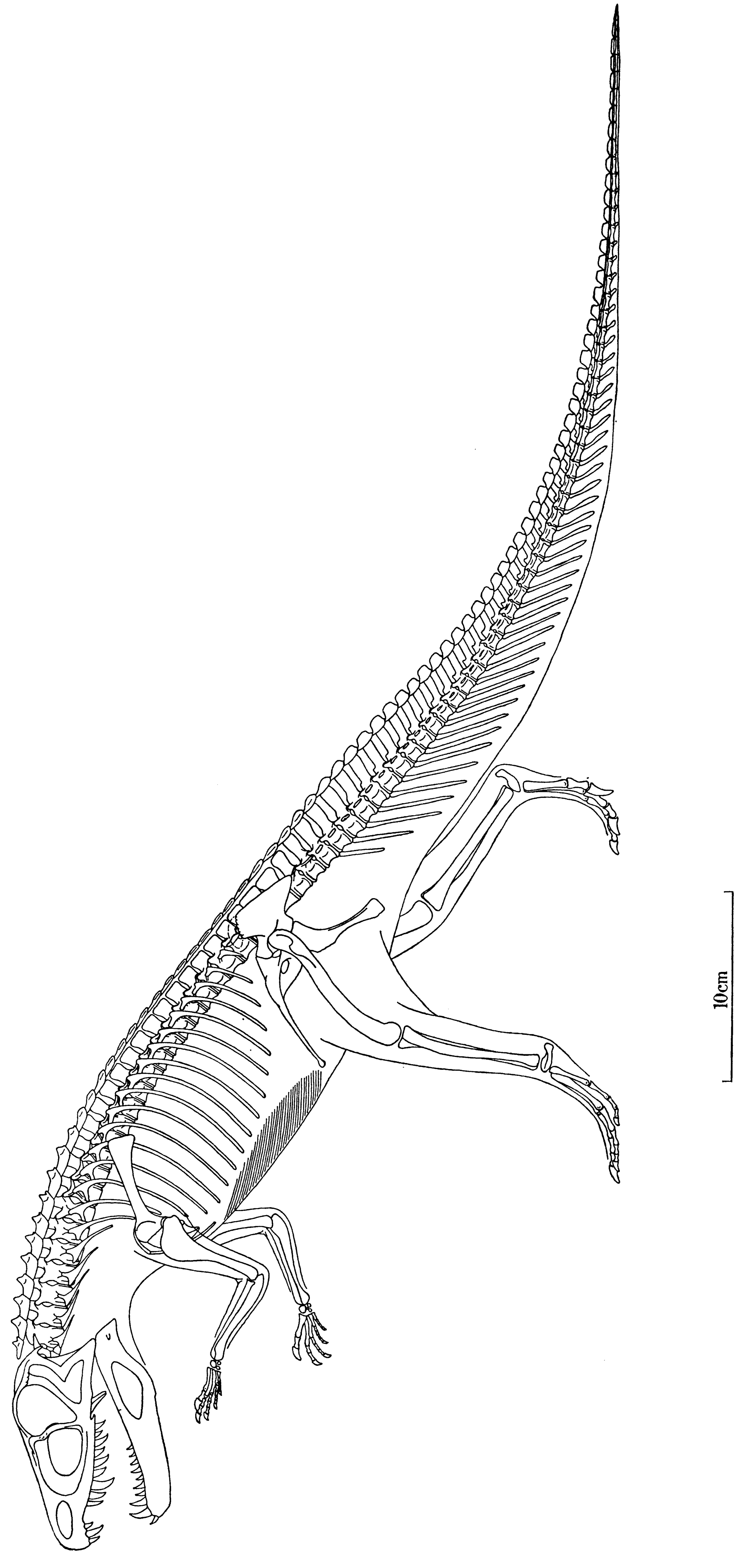

Figure 15. *Ornithosuchus longidens* (Huxley). Restoration of the skeleton of a small individual (one-third natural size). The largest known specimen is estimated to have been about 12 ft. long.

at least a partial bipedality. The fore-limb is slightly less than two-thirds as long as the hind and in addition is more slenderly constructed, the contrast in build between the humerus and femur being particularly marked. Also the outer digits of the hand are reduced and it appears to have functioned more in the nature of a grasping organ than for use in locomotion—witness the smallness of the olecranon. The construction of the pelvis and femur imply that in normal walking the hind-limb moved in a fore-and-aft plane close to the longitudinal axis of the body, and this deduction is supported by the elongation of the central three metatarsals and the symmetrical distribution of the lengths of the digits, which measure 47, 62, 69, 65 and an estimated 45 mm for I to V, respectively. The development of a lesser trochanter on the femur appears to be a consequence of a change in the attitude of the hind-limb, the iliofemoralis externus muscle assisting in retaining the head of the femur in the acetabulum, a development unnecessary when the femur is directed obliquely outward and downward. In quadrupedal locomotion, therefore, the stride of the hind-limbs would have been considerably longer than those of the fore, and even with the latter held at almost complete extension a substantial amount of arching of the backbone at the pelvis would have been required in order to allow sufficient clearance for the lower segment of the hind-limb during the recovery stroke. There are three well-developed sacral ribs, the first, although representing a modification of the last of the dorsal series, being particularly powerful. Furthermore, it seems that an additional presacral vertebra was partly incorporated in the sacrum, making an incipient fourth sacral. The rapid increase in height of the neural spines of the caudal vertebrae immediately behind the pelvis is taken to indicate the existence of powerful longitudinal dorsal components of the axial musculature in this region which in turn suggests that the animal was accustomed to adopt a semi-erect posture. It is therefore concluded that although *Ornithosuchus* was probably not an obligate biped, an upright stance may reasonably be attributed to it when in rapid movement. Heilmann's restoration shows a double flexure of the neck vertebrae which has the effect of further raising the head, and while a considerable degree of flexibility of the presacral vertebral column is suggested by the long overlaps of the scutes, a more conservative attitude has been adopted in making the present restoration. A criticism which may be made of Heilmann's life-restoration is that the muzzle appears to be depressed, thus negating the principal character upon which Newton based the name of his genus, namely the bird-like 'beak'. This criticism may also be applied to a restoration by Neave Parker (Colbert 1962, Plate 26), in which the animal is shown running rapidly in a similar attitude to that portrayed by Heilmann, but in this instance the hind-limbs are disproportionately elongated.

Considerable help in determining body form is provided by the scutes. Thus the shape of the angulated cervical scutes suggests a narrow neck. In an individual of the size of R 3916 (with a total length of about 1 m) a pair of cervical scutes measures 2·2 cm across the tips of the spines, a dimension closely similar to the breadth across the outer margins of the scutes, compared with an estimated depth of some 6 cm, although no doubt the neck broadened out somewhat below the scutes. In fact the body-section appears to have been considerably deeper than broad throughout, contrary to the appearance created by Heilmann's restorations. The breadth at the shoulder and at the pelvis, including the musculature, cannot materially have exceeded 6 cm, compared with depths of about

9 and 10 cm, respectively. Again, the rapid development of a sharp median caudal ridge above tall neural spines shows that the tail was compressed from side to side.

In figure 15 the first four cervical vertebrae and the distal half of the tail have been restored. Fifty-six caudal vertebrae have been drawn, but even this number may be on the low side. In the attitude shown the weight of the pelvis and hind-limb with their associated musculature, together with the tail, are considered to be more than adequate to counterbalance the large skull and fore part of the body including the slender fore-limbs. At maximum known size, the skull is some 18 in. long and the total length about 12 ft., standing about 5 ft. high. An individual of this size obviously constituted a formidable carnivorous animal, the jaws armed with sabre-like serrated teeth up to $2\frac{1}{2}$ in. in length and the fore-limbs adapted for grasping and holding the prey. *Ornithosuchus* thus fulfils the role of a large predatory form, a type whose presence is to be expected in a fauna in which, in number of individuals, the herbivorous or 'insectivorous' rhynchosaurs and aetosaurids are well represented. Such an animal would have been well capable of preying alike upon the unprotected rhynchosaurs (*Hyperodapedon*, about 6 ft. long) and the armoured aetosaurids (*Stagonolepis*, about 9 ft. long) although the latter would, in the nature of things, have proved more obdurate victims. A parallel may be drawn in the relationship between *Stagonolepis* and *Ornithosuchus* with that which existed in the Cretaceous between the armoured ankylosaurs and more advanced flesh-eating dinosaurs such as *Tyrannosaurus*. The less mature individuals of *Ornithosuchus* had a wider choice of forms upon which to feed. These included young individuals of the two genera already mentioned, and in addition, the small crocodilian *Erpetosuchus*, the rhynchocephalian *Brachyrhinodon* and the procolophonid *Leptopleuron*. As noted earlier, there is evidence that even one of the smallest individuals of *Ornithosuchus*, at a length of some 18 in., was at least partially carnivorous. The presence of spinose cervical scutes implies the need to protect the neck region from attack, and it is difficult to avoid the conclusion that this was necessary because of the cannibalistic habits of the larger individuals, although the coelurosaur *Saltopus* would be a likely source of danger to the smaller animals in the fauna. In duels of this nature the sharp-edged caudal ridge-scutes would probably have been capable of dealing an effective blow to an assailant, mounted as they are on the neural spines of a long and powerful tail.

V. Comparative section

(*a*) *Summary of the essential characters of* Ornithosuchus

1. Attaining large size: skull length up to 18 in. (45 cm), total length estimated at about 12 ft. (4 m).

2. Skull relatively large, orbit constricted ventrally, lachrymal with dorsolateral crest and incipient 'pneumatic cavity'. Postorbital with rugose area. Lateral temporal fossa partly divided by sharp V-shaped projection of squamosal and quadratojugal. Maxilla with interdental plates. Deep mandible with large foramen piercing the posterior part of the surangular; some evidence of intramandibular movement.

3. Short cervical vertebrae of which the anterior members appear to be opisthocoelous; dorsals with rib-articulations of theropod type with supporting buttresses below the diapophyses. Three sacrals, last dorsal vertebra probably acting as an additional sacral,

neural spines of sacrals in contact. Caudal vertebrae with median vertical anterior flange at base of neural spine.

4. Narrow scapula with anteroventral expansion, crescentic coracoid ending in a posterior point, with strong lateral ridge, scapulocoracoid suture slanting forward and downward and coracoid somewhat set back. Slender clavicles and interclavicle retained.

5. Pelvic girdle with well-developed iliac blade, the latter high anteriorly but superior margin sloping posteriorly, ilia converging dorsally with powerful supra-acetabular rims. Acetabulum slightly open. Elongated, narrow pubes with small terminal thickenings. Ischium with distinct separate facets for pubis and ilium, obturator process developed. Symphysis interrupted in front of the latter.

6. Humerus two-thirds as long as femur. Femur hollow, other major limb bones probably also hollow. Slender humerus with well-developed deltopectoral crest. First digit of manus strongly developed, digit III somewhat reduced, IV and probably V much more so, pollex probably partly opposable. Femur with well-developed lesser trochanter, fourth trochanter posteromedial in position. Tibia shorter than femur. Calcaneum with tuber. Digits of pes symmetrical about digit III which is longest, V not greatly reduced.

7. Paramedian dorsal scutes sutured together in pairs, with spikes in the cervical region. Scutes fused in pairs above caudal vertebrae to form a single row of median ridge-scutes capping the neural spines.

(*b*) *Discussion of affinities*

It will be evident from the combination of characters enumerated above that only two groups of reptiles need be seriously considered in a discussion of the affinities of *Ornithosuchus*. These are the coelurosaurs and carnosaurs of the Sub-order Theropoda. The first of these can be dismissed immediately, since their characteristics include elongated cervical vertebrae, relatively small skull, ilium with elongated blade disposed essentially horizontally and tibia longer than femur, none of which is found in *Ornithosuchus*.

Turning now to the forms usually classified under the Infra-order Carnosauria, it will be found from examination of a standard work such as Romer's (1956) *Osteology of the reptiles* that this group contains two assemblages of somewhat diverse character. These are the Triassic carnosaurs (in the sense of von Huene 1932), comprising the families Palaeosauridae and Teratosauridae (sometimes called Zanclodontidae), and the Jurassic and Cretaceous carnosaurs, conveniently for the present purpose considered to include two loosely categorized families, the Megalosauridae and the Tyrannosauridae (or Deinodontidae).

A comparison of *Ornithosuchus* has been made with as many as possible of the forms included in the above groups. No claim is made that the coverage has been exhaustive, but it is believed that no important genus has been overlooked. The chief sources of reference have been the works of Broom (1911), Buckland (1824), Cope (1870), Gilmore (1920, 1946), Haughton (1924), Hay (1908), von Huene (1908, 1915, 1926*a*, 1926*b*, 1932), von Huene & Matley (1933), Huxley (1869), Janensch (1925), Lambe (1904, 1917), Leidy (1860), Marsh (1896), Matthew & Brown (1922, 1923), von Meyer (1861), Osborn (1903, 1905, 1906, 1912, 1916, 1924), Owen (1857, 1883), Parks (1928), Phillips (1871), Piveteau (1923), Sauvage (1882), Stovall & Langston (1950), Stromer (1915, 1931, 1934), and Young (1948). The literatur epertaining to the Prosauropoda and Coelurosauria has also been examined.

From this comparison it emerges that *Ornithosuchus* shows clear affinities with the carnosaurs of the Jurassic and Cretaceous periods, and differs in important respects from the so-called carnosaurs of the Triassic. When the latter are reviewed (see, for example, Broom (1911), Haughton (1924) and von Huene (1908, 1932)) it is notable that they differ from the later carnosaurs in just those features which link *Ornithosuchus* with the post-Triassic forms. The principal characters of the Triassic 'carnosaurs' (*sensu* von Huene 1932) which prevent them from being seriously considered as an ancestral group are as follows:

1. Relatively small skull, as far as available evidence indicates. Skull material of the Triassic 'carnosaurs' is exceedingly meagre, but, leaving out of consideration for the moment the maxillae of *Teratosaurus* and *Sinosaurus*, a few cranial bones have been figured by von Huene (1932) in the case of a series of specimens which he referred to *Palaeosaurus*(?) *diagnosticus*, although it may be noted in passing that this generic name is not available.
2. Elongated cervical vertebrae (*Aetonyx*, '*Palaeosaurus*', *Gresslyosaurus*).
3. Ilium with low, pointed anterior process but large posterior development of the blade. Ilia not greatly convergent dorsally (*Gryponyx*, '*Palaeosaurus*', *Gresslyosaurus*, material referred by von Huene (1908, 1915) to *Teratosaurus*).

These features are also typical of the Prosaurus.

On the other hand, the later carnosaurs are notable for the large size of the skull, and the short, frequently opisthocoelous cervical vertebrae. The ilium differs markedly from those of the Triassic 'carnosaurs', the blade being high anteriorly and the lateral surface concave so that the ilia converge dorsally in a bird-like manner.

It is now necessary to consider the specimens referred by von Huene (1908, 1915, 1932) to *Teratosaurus*. This genus was founded upon a single maxilla, now in the collection of the British Museum, to which the name *T. suevicus* was given by von Meyer (1861). This specimen was identified both by von Meyer and von Huene (1908) as a left maxilla, but since it shows well-developed interdental plates and the presence of a medial shelf, it is evidently of the right side, figured in medial aspect by von Huene (1908, Plate 64, Fig. 1). The large, sabre-like teeth and interdental plates leave little room to doubt that this maxilla, which is from the Stubensandstein, is of a true carnosaur, but it must be emphasized that von Huene's (1932) restoration of the skull of *Teratosaurus* is based entirely on this single bone. The antorbital fenestra was not small, as some authors have supposed, for examination of the specimen shows that the lower border of the fenestra has been strongly crushed and the outer layer of the bone has been forced upwards. In 1908 and again in 1915 von Huene referred additional material to the genus, in each case on the grounds of associated but detached teeth, said to be like those of the type. Whether these teeth correctly belong to the associated material or not, this reference is extremely dubious, for the other specimens which constitute these finds, like the postcranial skeleton of Triassic 'carnosaurs' in general, resemble much more the corresponding bones of prosauropods. Thus the humerus and ilium, to name two examples, of the material referred by von Huene to *Teratosaurus suevicus*, are closely similar to those of *Plateosaurus*, and quite different from these bones in true carnosaurs. Furthermore, allocation of specimens on the basis of similarity of teeth is notoriously unreliable. I consider, therefore, that there is a strong probability that the material referred by von Huene to *Teratosaurus* is not properly so assigned, and mention of this genus in succeeding pages is to be taken to apply only to the original maxilla described by von Meyer (1861).

It is not correct to synonymize *Zanclodon* with *Teratosaurus*, as has been done by Romer (1956), for as von Huene pointed out long ago (1908, p. 187), the name *Zanclodon* should be restricted to the original jaw-fragment from the Lettenköhle of Gaildorf, figured by Plieninger (1846). The teeth of this specimen differ from those of *Teratosaurus* in lacking serrations.

Another Triassic form *triassicus Sinosaurus* (Young 1948), is probablya true carnosaur. Again, in addition to jaw fragments, the type material includes a large maxilla referred to the left side, but in this case the bone is correctly identified; the author's figures permit the recognition of damaged interdental plates, and the presence of a small replacing tooth visible high up between these (Young, Plate IIB) confirms that it is a maxilla of carnosaurian type. There is no reason to assume that the pelvic girdle and vertebrae referred by Young to *Sinosaurus* belong to this genus, since the specimens were obtained from different localities and are of prosauropodous type. A similar restriction on the name *Sinosaurus* is therefore applied as in the case of *Teratosaurus*.

Of the Triassic 'carnosaur' genera, these two appear to be the only ones which can at present be reasonably assigned to the Carnosauria proper. The remaining material of the Palaeosauridae and Teratosauridae is here provisionally placed with the Prosauropoda; Attridge, Chang & Crompton in preparation have arrived at essentially similar conclusions concerning the affinities of these forms and will shortly be publishing a more detailed treatment of their systematics.

Mention should be made at this point of a reptile from the Triassic Ischigualasto Beds of Argentina which Reig (1963) has recently described under the name of *Herrerasaurus*. This animal is in most respects similar to saurischians of the *Plateosaurus* type, but the distal end of the pubis is expanded into a well-developed 'foot' similar to that of Upper Jurassic and Cretaceous carnosaurs. I do not consider, however, that this necessarily implies any close affinity between *Herrerasaurus* and these later forms, and would suggest that there may be some connexion between *Herrerasaurus* and the peculiar pelvis described by Case (1943) from the Dockum formation of Texas, in which the pubis also has an anteroposteriorly expanded distal extremity. There may be, in turn, some affinity between the specimen described by Case and *Poposaurus*, as suggested by Colbert (1961), who concluded that the latter reptile is probably a theropod dinosaur of peculiar type, whose 'relationships are probably closest to such Triassic carnosaurs as the Paleosauridae and the Zanclodontidae'—here considered to be mainly prosauropods.

It is maintained, therefore, that von Huene's opinions as to the ancestry of Jurassic and later carnosaurs cannot be upheld, and that *Ornithosuchus* provides a much more suitable basis for the derivation of these forms. The special significance of the cranial structure of *Ornithosuchus* in relation to the origin of carnosaur skull patterns will be discussed in a later section, and the following paragraphs are accordingly limited to consideration of some aspects of the postcranial skeleton.

It is unfortunate that Lambe's restoration (1917, Fig. 31) of the shoulder-girdle of *Gorgosaurus* should have been chosen to represent the carnosaurian type in Romer's *Osteology* (1956), since the student of reptiles will naturally assume that the form of the coracoid is typical of the group. In fact this is not so. When one examines Lambe's illustration of the actual girdle (1917, Fig. 7), as distinct from his restoration of it, the coracoid is seen to be more crescentic in shape, the scapulocoracoid suture slants anteroventrally, and the coracoid extends well behind the glenoid to a blunt apex. That this is the correct shape for *Gorgosaurus* is made clear by Parks (1928), who also figures a scapulocoracoid of *Albertosaurus* (possibly a synonym of *Gorgosaurus*) which is again of this type. The coracoid of *Tyrannosaurus* has never been described and is figured by Osborn (1916) only as part of the mounted skeleton. However, Colbert has published photographs of it (1951, p. 34; 1962, Plate 38) which render a description largely unnecessary. It is of the same type as those of *Albertosaurus* and *Gorgosaurus*. Gilmore has given figures of the scapulocoracoid of *Antrodemus* (1920, Plate 5) which show that this also conforms to the same pattern, except that, as in *Megalosaurus* (von Huene 1926*b*), the suture between the two elements is at right angles to the long axis of the scapula. According to existing figures of the latter genus, the posterior apex does not appear to be developed; however, examination of the coracoids of *Megalosaurus bucklandi* from the Great Olite of Stonesfield in the collections of the British Museum and Oxford University Museum shows an abraded backwardly projecting apex in at least two examples. Since an accurate figure of the scapulocoracoid of *M. bucklandi* is not available in the literature it seems desirable to provide one here (figure 16*a*); the anterior expansion of the middle part of the blade is a typical feature.

The carnosaurian shoulder girdle therefore has an elongated scapula with slightly expanded apex, a scapulocoracoid suture in some cases inclined obliquely downward and forward (tyrannosaurs), in others at right angles to the scapular axis (megalosaurs), a crescentic coracoid with recurved posterior apex, the latter bearing a ridge or low swelling on its outer surface which descends from below the glenoid lip and curves back to the posterior tip. This definition, it will be seen, readily includes the scapulocoracoid of *Ornithosuchus*, and the latter, curiously enough, resembles the scapulocoracoids of *Gorgosaurus*, *Albertosaurus* and *Tyrannosaurus* more closely than it does the corresponding regions of *Megalosaurus* or *Antrodemus*.

On the other hand the humerus shows considerable similarity to that of *Antrodemus* (Gilmore 1920, Plate 6) and does not bear a particularly close resemblance to the humerus of *Megalosaurus bucklandi*. We have seen that some degree of opposability of the pollex of *Ornithosuchus* is suggested by the attitude of the metacarpals in L 8271; at any rate, the structure of the hand is suitable as a basis from which to derive the more specialized and reduced hands of later carnosaurs.

The pelvis of *Ornithosuchus* is most readily compared with the excellent figures of this region of *Antrodemus* provided by Gilmore (1920); although the pelvis of *Megalosaurus bucklandi* (figure 16*b* to *d*) is basically similar to that of the American form it lacks the pronounced pubic 'foot' and the ischium differs in certain particulars. The ilium and ischium, and to a lesser extent, the pubis, of *Antrodemus* can be compared in detail with those of *Ornithosuchus*, leaving little doubt of their derivation from a pelvis of the latter type. The pubic 'foot' appears to have originated as two distinct thickenings (figure 11). In more advanced forms, with the reduction in width of the pubic apron and the compression of the pelvis, these have coalesced, leaving a median foramen below the shortened symphysis. The irregular anterior margin of the iliac blade of the megalosaurs and tyrannosaurs suggests that, as in the case of the Elgin form, ossification rarely proceeded to the extent of complete replacement of the original cartilage.

The straight-shafted (in anterior view) and somewhat dorsally arched femur of *Ornithosuchus* is again precisely what one would expect to find in a primitive carnosaur (compare figure 12 with Gilmore 1920, Plate 14).

The girdles, indeed, undergo relatively little change in the long history of the group, and those transformations which do occur are clearly related to the full development of bipedality and increase of size, mainly affecting the pelvis and hind-limb.

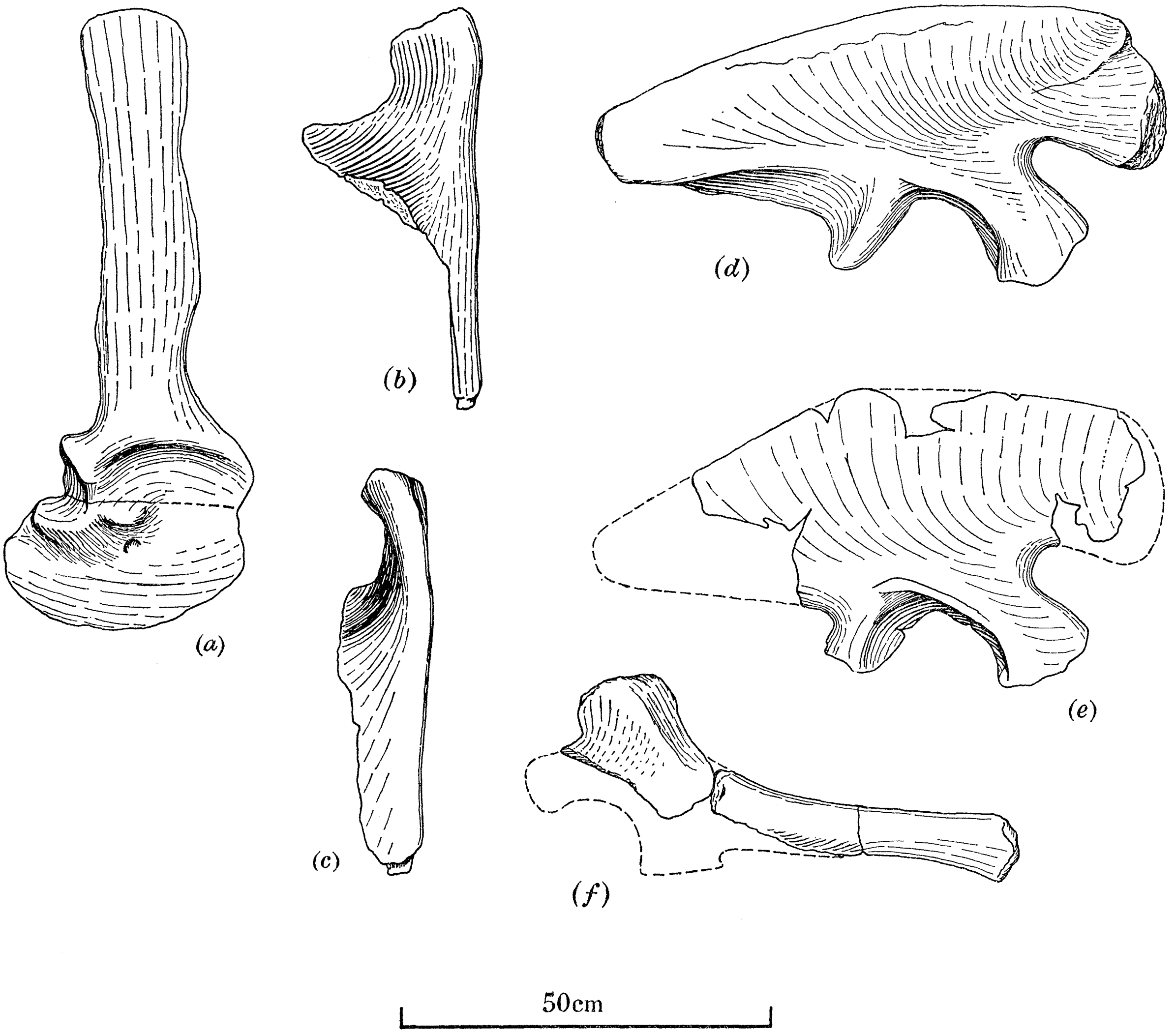

FIGURE 16. (One-tenth natural size.) *a*: lateral view of right scapulocoracoid of *Megalosaurus bucklandi*, Stonesfield Slate, Great Oolite Series (Bathonian), Stonesfield, near Oxford, O.U.M. J. 13574; *b*, *c*: medial and anterior views of left pubis of same (about 10 cm missing from distal end), B.M.N.H. 25582; *d*: lateral view of right ilium of same, O.U.M. J. 13560; *e*: lateral view of right ilium of *Metriacanthosaurus parkeri* (von Huene) gen.nov., adherent organisms and vertebrae omitted, Upper Oxford Clay (Lower Oxfordian), 1½ miles north of Weymouth, Dorset, O.U.M. J. 12144/14; *f*: lateral view of left ischium of same, O.U.M. J. 12144/18 and /23.

(*c*) *Status of* Ornithosuchus

The question of the precise status of *Ornithosuchus* must now be considered. In this connexion it is unfortunate that the postcranial skeleton is known mainly from immature individuals, and that changes during growth which might affect important diagnostic characters, for example, the degree of fenestration of the acetabulum, remain largely unknown. We have seen that Newton placed *Ornithosuchus* provisionally with the dinosaurs, while Boulenger disagreed with this judgement apparently because of the presence of clavicles and abdominal ribs. The latter are, of course, now well authenticated amongst all groups of theropods, including animals as late in time and as advanced as *Gorgosaurus* (Lambe 1917), and *Tyrannosaurus* (Osborn 1906). Vestigial clavicles have been reported by von Huene in the Triassic *Plateosaurus* (1926*a*), by Camp in the ?Lower Jurassic *Segisaurus* (1936), a T-shaped interclavicle (which may perhaps include parts of the clavicles) was described by Osborn (1924) in the Cretaceous coelurosaur *Oviraptor*, and the dermal elements are also retained in certain groups of the Ornithischia. While the loss of the dermal shoulder girdle is typical of advanced dinosaurs, its retention in primitive members of the group need occasion no surprise. Possibly of more importance is the fact that the bone identified as the calcaneum of *Ornithosuchus* apparently possesses a well-developed tuber. Nevertheless, certain coelurosaurs retain such a structure, namely *Hallopus* (Marsh 1896; von Huene & Lull 1908; von Huene 1914) from the Upper Triassic, *Saltopus* from the Upper Triassic and *Segisaurus* (Camp 1936) from the ?Lower Jurassic, although the last is of equivocal status. I have previously pointed out (Walker 1961) that a calcaneal tuber and crocodilian type of ankle-joint is found in a variety of thecodonts; to these must now be added an un-named pseudosuchian from the Anisian beds of Monte San Giorgio, whose tarsus has recently been described by Krebs (1963). It seems not impossible to the writer that, in spite of its apparent specialization, the crocodilian joint may after all represent a basic archosaurian pattern. In this case the retention of a calcaneal tuber in certain theropods is more easily explained. Certainly it is difficult, if not impossible, to derive the mesotarsal joint of post-Triassic carnosaurs from that which existed in Triassic 'carnosaurs' of the *Gresslyosaurus* type, the latter again showing affinity to the Prosauropoda in this character. Unfortunately the preservation of the only known angle-joint of *Ornithosuchus* is far from perfect and throws little light on this problem.

In dealing with a form which lies morphologically close to the boundary between two major groups, difficulty may be encountered in attempting to decide in which category to place the form in question. To a large extent this is an artificial problem, the choice depending on which criteria are thought to be most important in framing the definitions of the groups. In the present case, if one relied strictly upon the nature of the ankle-joint, it might ultimately prove necessary to retain *Ornithosuchus* within the Pseudosuchia. However, in the sum of characters, *Ornithosuchus* shows such close affinities with the larger carnivorous dinosaurs that I consider that it is better placed with them. Strong additional ground for so doing is that phylogenetic relationships are more clearly expressed.

Ornithosuchus is therefore grouped with *Teratosaurus* and *Sinosaurus* in the Triassic (true) carnosaur family Ornithosuchidae (which has priority over Teratosauridae von Huene 1932) of the Infra-order Carnosauria of the Sub-order Theropoda. Until the remaining archosaurs from the Elgin sandstone shall have been revised, and in view of work proceeding in other quarters, it is not considered desirable to make detailed proposals for the classification of other genera which have from time to time been included in the Ornithosuchidae.

VI. The evolution of carnosaurs

Of prime interest in this connexion are the characters of the skull. The preorbital vacuity of carnosaurs is of large size, and in the larger members additional fenestrations have developed (*a*) within the ascending lamina of the maxilla, (*b*) within the jugal at the postero-inferior corner of the vacuity, and (*c*) as 'pneumatic' cavities within the lachrymal. These fenestrations are often thought of as serving to lighten the bones without loss of strength. However, the function of the preorbital fossa as an important area of muscle origin, first suggested by Dollo (1884) and recently emphasized by the writer (Walker 1961), makes it likely that the additional apertures provided firmer sites of origin of important muscle slips, which thus gained a stronger attachment to the rims of these openings than would be the case when arising from solid bone. The constant three-fold localization of these areas in the depressions at the corners of the preorbital vacuity appears significant in this connexion. The appearance of two of the areas, in addition to the lamina of the maxilla, may be discerned in *Ornithosuchus*, the lachrymal being deeply recessed below the dorsal crest, and the jugal having a depressed area within the preorbital fossa. Comparison of *Ornithosuchus* should be made with the figures of *Antrodemus* and *Ceratosaurus* given by Gilmore (1920), of *Gorgosaurus* by Lambe (1917) and Gilmore (1946), and of *Tyrannosaurus* by Osborn (1912).

The development of a lachrymal crest and postorbital rugosity is variable among the larger carnivorous dinosaurs, thus *Antrodemus* has a very strong lachrymal crest but no postorbital rugosity, *Gorgosaurus* has a smaller crest and although again no rugosity is developed, the postorbital appears to overhang in *G. libratus*, while in *Tyrannosaurus* although no definite ridge occurs, both lachrymal and postorbital bear closely approximated roughened protuberances. Affinity of *Ornithosuchus* with these forms is suggested by the development of a sharp dorsolaterally projecting flange on the lachrymal, the roughening of the lateral edge of the bone, and the rugose overhanging area of the postorbital.

A striking feature of the skull of *Ornithosuchus* is the marked forward projection of the squamosal and quadratojugal into the lateral temporal opening. Although a V-shaped projection of these bones is stated by Romer (1956) to be characteristic of pseudosuchians and saurischians, in fact the projection rarely causes more than a gentle sinuosity of the posterior margin of the fossa, and a careful examination of the literature has failed to discover more than three genera in which the projection is known to be at all marked, but in these three, *Ornithosuchus*, *Gorgosaurus* (Gilmore 1946) and *Tyrannosaurus*, it is very striking. (The existence of such a projection in the Lower Triassic *Vjushkovia* (von Huene 1960) depends upon the correct identification of an isolated quadratojugal; in view of the otherwise close similarity of *Vjushkovia* to *Erythrosuchus* this identification is open to question.)

It is suggested that the skull pattern of the tyrannosaurs may be derived from that of *Ornithosuchus* by a complex series of changes involving the following transformations:

(i) Great reduction of the length of the frontals, accompanied by the enlargement and inward and backward migration of the lachrymals (figure 17*a*). It is as if the two points of junction of the four bones, lachrymals, prefrontals, nasals and frontals in *Ornithosuchus* had been seized and pulled medially nearly to the mid-line and posteriorly to a point now opposite the posterior ends of the prefrontals. The latter are thus reduced almost to vanishing point, but retain their former morphological relationships. The postfrontal is reduced and perhaps fused with the enlarged postorbital which now meets the lachrymal above the orbit so that the rugosities on these bones are continuous. Actually, relatively little change in breadth of the already narrow beaked snout of *Ornithosuchus* has occurred, rather the difference lies in the lateral expansion of the muzzle in *Tyrannosaurus*. These backward migrations of bones are presumably due in part to the great development of the anterior pterygoid muscle and a reduction in its relative length giving a slower, but more powerful action to the bite, coupled with the additional advantage of a more oblique inward pull on the jaw. An equally important factor in maintaining the narrowness of the beak may have been that in this way some degree of overlapping of the fields of vision was secured; examination of photographs and figures of the skulls of *Gorgosaurus* and more especially, *Tyrannosaurus* (e.g. Osborn 1912, Fig. 3) gives the definite impression that the eyes were capable of being turned well forward.

At the rear of the skull the effective height of the occiput has been somewhat increased over that of *Antrodemus*, for in the latter the height of the occiput above the condyle is about three-quarters of the height of the quadrate, whereas in *Tyrannosaurus* it is nearly equal to the latter dimension, although in both these forms and in *Gorgosaurus* the quadrate is approximately half of the total height of the skull. This backward migration of the parietals on to the occipital surface is analogous to the change outlined in the evolution of aetosaurids (Walker 1961), where it was attributed to the use of the snout in digging, whereas in the present instance it would seem to be in response to the enormous size and weight of the head in the Upper Cretaceous carnivores, but for the same basic reason, namely to give greater leverage to the dorsal neck musculature.

The much enlarged supratemporal fossae of *Tyrannosaurus* and *Gorgosaurus* have encroached upon the frontals, but in *Ornithosuchus* the latter bones take no part in the formation of these apertures.

(ii) In the side view, the relative reduction of the orbit, which began ventrally in *Ornithosuchus*, has progressed until in the Upper Cretaceous forms the opening is extremely small. At the same time the pre- and postorbital rugosities have come to be approximated above it. In *Tyrannosaurus* and *Gorgosaurus* the postorbital and jugal form a massive vertical bar behind the orbit, and so striking is this in side view, that it seems highly probable that this bar has come to form a supporting strut at least equal in importance to the quadrate in resisting the contraction of the enormous adductor muscle mass.

Concomitant with these changes has occurred a reduction in the ventral length of the lateral temporal fossa. This is doubtless due to the necessity for the quadrate to become vertically disposed in order to resist forces of compression and dislocation in such a large skull, but a general shortening of the jaws would also be advantageous in biting for mechanical reasons.

With the forward movement of the foot of the quadrate, the rear margin of the quadratojugal has become vertical, probably to act as a further brace, and as a result of the backward and downward migration of the paroccipital process (accompanied by a good deal of relative shortening of the quadrate) the upper end of the squamosal has, as it were, been drawn downward and backward. In this way the lower ramus of the squamosal has come to lie almost horizontally over the upper end of the quadratojugal and thus the upper part of the lateral temporal vacuity has assumed its present form. Nevertheless, the relations of the lateral process of the quadrate to the squamosal and quadratojugal are precisely as in *Ornithosuchus*, as is borne out by examination of the cast of the skull of *Tyrannosaurus* in the British Museum.

The writer has attempted to adduce reasons as to why the free forward projection of the squamosal and quadratojugal should persist in *Tyrannosaurus* and its allies and not in *Antrodemus*. That this is not an effect solely of exceptional size seems to be demonstrated by the fact that *Antrodemus* attained a skull length of 885 mm without it occurring, and it seems unlikely that the further increase of skull length to 980 mm in *Gorgosaurus libratus* (Gilmore 1946) and 1355 mm in *Tyrannosaurus* would suffice to cause such a marked change; moreover, the projection is well developed in *G. sternbergi* which has a skull 678 mm long. The reason for the projection would seem to be to afford additional area for the origin of the m. adductor externus superficialis et medialis (groups I and IIb of Lakjer 1926), since it is comparable in position to that portion of the crocodilian quadrate from which these muscles arise, and the writer can only suggest that this may have been significant in *Ornithosuchus* in assisting in the alinement of the narrow jaws upon closure, and hence was retained in the deinodonts in which the muzzle is relatively much narrower than in the antrodemids. Otherwise the mechanics of the jaws and the feeding processes seem to have been closely similar in both groups of carnosaurs.

(iii) The presence of a large foramen piercing the surangular is regarded as an important feature tending to link the tyrannosaurs with *Ornithosuchus*, although it is also found in some other forms, *Euparkeria* (Haughton 1922), *Velociraptor* (Osborn 1924), and *Dromaeosaurus* (Colbert, personal communication). It also occurs in the Lower Cretaceous (Aptian or Albian) *Acrocanthosaurus* (Stovall & Langston 1950), a form somewhat doubtfully referred to the Antrodemidae (see p. 115). If *Antrodemus* and *Ceratosaurus* are regarded as typical of the megalosaurs, and the structure of the posterior part of the jaw is only known with certainty in these members of the family, then the foramen does not occur in this group. Whatever may be the truth as regards the phylogenetic relationships of *Ornithosuchus*, the surangular foramen is here regarded as homologous throughout, since it pierces the rear part of the bone and is morphologically in a constant position with respect to the angular, which tapers out between the surangular and prearticular at the same point behind the foramen in each case (Lambe 1904: in this paper 'dentary' at rear of jaw = angular, and 'angular' = prearticular; Osborn 1912).

Possibly the surangular pit or foramen transmitted a nerve and/or blood vessel in *Euparkeria* and *Ornithosuchus*. It is here suggested that the opening was taken over as a source of muscle insertion in comparable fashion to the accessory apertures around the preorbital fossa which have already been discussed. In this case also a part of the pterygoideus musculature would seem to be involved, and support is lent to this hypothesis by the position of the foramen (or foramina, for there may be more than one) in tyrannosaurs, in which it lies in a deeply recessed area at the rear of the jaw, precisely where the pterygoideus musculature would be expected to wrap around the ventral margin to insert on the outer surface. In *Ornithosuchus* the posteroventral margin of the jaw is also concave, and the foramen lies close to the limit of possible dorsal extension of pterygoideus insertion.

(iv) A further resemblance between *Ornithosuchus* and *Tyrannosaurus* as concerns the jaw musculature lies in the curious free lower posterior fork of the maxilla of the former, which is comparable to the blunt free posterior corner of the maxilla in the later form. Presumably this afforded origin for a muscle slip passing to the upper margin of the surangular, assisting in retaining the jaw in the cotylus.

The palates of the larger carnivorous dinosaurs are, with certain exceptions, very inadequately known. Lambe (1904) illustrated parts of this region in skulls of '*Dryptosaurus*' from the Upper Cretaceous of Alberta; these specimens were later (1905) named *Albertosaurus* by Osborn, who has also (1912) given excellent figures of the palate of *Tyrannosaurus*. Hay (1908) and Gilmore (1920) have described that part of the palate of *Ceratosaurus* which can be seen through the various skull fenestrae, while Gilmore (1946) has also illustrated part of the palate of *Gorgosaurus*. The most ready comparison of the *Ornithosuchus* palate may be made with Gilmore's account of *Ceratosaurus*, which repeats the essential parts of Hay's description verbatim. The detached pterygoid of '*Dasygnathus*' was originally compared by the writer with that of *Erythrosuchus*, but I have since realized that there is an even closer resemblance to the pterygoid of *Ceratosaurus*, well shown by Gilmore (1920, Plate 17, Fig. 2). The palates of the two animals are also quite similar in the details of the articulation of the transverse and the relationships of the palatine; probably there was little original development of an interpterygoid vacuity in *Ceratosaurus* also.

However, the pterygoid of *Ornithosuchus* is fundamentally similar to that of a specimen from the Stubensandstein lent to the author by the Stuttgart Museum. This latter specimen is of a coelurosaur allied to *Procompsognathus*, if not actually of that genus, but about twice as large. It seems, therefore, that the form of the pterygoid is basically similar in animals as far separated in time as *Erythrosuchus* and *Ceratosaurus*, and is likely to represent merely a primitive condition. This is not to say that the structure of the more anterior part of the palate is the same in all these forms.

Von Huene (1926*b*) considered *Ceratosaurus* to be an offshoot of the coelurosaurian stock which had attained large size and had in consequence adopted carnosaurian specializations. I am in agreement with this conclusion and would only add the following points to those made by him:

(*a*) The 'open' build of the skull and slender lower jaw.

(*b*) The fact that the diapophyses of the mid-cervical vertebrae extend down almost to the level of the bases of the centra. This character is particularly striking in a cervical vertebra of the Triassic coelurosaur alluded to above.

(*c*) The blade of the ilium is more or less horizontally disposed.

(*d*) The form of the head and of the lesser trochanter of the femur are more coelurosaurian in type.

The palate of *Ornithosuchus*, with the pterygoids meeting in the mid-line for the greater part of their length, must therefore be considered as the primitive form in the Carnosauria, and that of *Tyrannosaurus*, in which they are separated, is specialized, and not primary, as some have believed. This is probably an adaptation for the swallowing of large masses of flesh, analogous to the specializations of snakes, and it is therefore of great interest that the symphysis of the mandibles in *Tyrannosaurus* was almost entirely membranous, according to Osborn (1912).

A review of the available descriptions of the jaws of carnosaurs, coupled with personal observation, reveals the interesting fact that the symphysis is extremely weak throughout the entire group. This is the case in *Spinosaurus* (Stromer 1915), *Albertosaurus* (Lambe 1904) and *Genyodectes* (Woodward 1901). Lack of a definite symphysial area is also shown by examination of the following forms: *Megalosaurus nethercombensis* (Middle Inferior Oolite, Nether Combe, Sherborne, Dorset); '*M. bucklandi*' (Upper Inferior Oolite, Sherborne; this is probably a distinct species, having a greater number of teeth than the true *M. bucklandi* and a lateral groove between premaxilla and maxilla); *M. bucklandi* (Stonesfield Slate, Great Oolite Series, Oxfordshire); '*M. cuvieri*' (Upper Callovian, Oxford; also generically distinct from the Stonesfield *Megalosaurus*, see p. 124); and *Gorgosaurus* (skull in the collection of the British Museum). Dr E. H. Colbert also informs me (personal communication) that the same state of affairs is displayed by a specimen of *Antrodemus* in the American Museum of Natural History. This leads to the supposition that some outward spreading of the jaws was possible to increase the dimensions of the throat during swallowing (cf. Gans 1961), a process which would be facilitated by the inward tilting of the articular surfaces of the jaws.

There is also some indication of intramandibular kinesis, first mentioned, as far as I am aware, by Romer (1956). In fact, intramandibular movement, as pointed out in the descriptive section, probably took place in *Ornithosuchus*; the similar build of the jaw in *Ceratosaurus*, *Albertosaurus* (Lambe 1904) and *Gorgosaurus* (Gilmore 1946) suggests that it was a common feature in all these forms.

The palate of *Tyrannosaurus* is readily derivable from that of *Ornithosuchus* by the extension of the medial shelves of the maxillae and premaxillae and the backward migration of the choanae, accompanied by broadening of the muzzle. This is a fairly obvious response to the shortening and broadening of the snout and the need to stiffen the anterior part of the palate in the transverse direction, while the expanded palatines would also afford additional areas for the insertion of the pterygoideus anterior muscles.

A possible link, albeit an indirect one, between *Ornithosuchus* and the Upper Cretaceous deinodonts, lies in *Acrocanthosaurus* from Oklahoma, described by Stovall & Langston (1950). This form is of Upper Aptian or Lower Albian age. Although tentatively assigned to the Antrodemidae by the authors, the following features suggest tyrannosaurian affinities:

(*a*) The acute angle made by the lower branch of the squamosal with the postorbital branch, which indicates a lateral temporal fossa of semi-divided type. In *Antrodemus*, in contrast, the squamosal is obtusely angulated at the upper rear corner of the fossa.

(*b*) The tendency for the descending ramus of the postorbital to broaden downwards and project into the orbital opening.

(*c*) The occurrence on the postorbital of a 'heavy, eave-like brow ridge' which is 'considerably roughened and tuberous above'.

(*d*) The approach to a rectangular pattern adopted by the recessed areas medial and anterior to the supratemporal fossae (figure 17*d*). This provides a type of structure from which the T-shaped arrangement of ridges formed by the frontals and parietal crest of *Gorgosaurus* and *Tyrannosaurus* could have been derived by further medial encroachment of the depressed areas.

(*e*) The development of a large foramen in the surangular.

The illustrated portions of the postcranial skeleton, on the other hand, are not especially suggestive of deinodont relationship, but one might expect at this stage a considerable degree of resemblance between the two carnosaur groups as they converge backwards in time. Stovall & Langston draw attention to the curious step-like development of the anterior edges of the neural spines of the caudal vertebrae of *Acrocanthosaurus*, which in the middle caudals becomes a definite bifurcation (in the anteroposterior sense) caused by the upward projection of the anterior portion of the 'step'. The authors state that a similar development is known only in two caudal vertebrae of a skeleton of *Antrodemus* in the Carnegie Museum, and, to a much smaller degree, in *Segisaurus* (Camp 1936). It is accordingly of great interest that an exactly comparable development occurs in the caudals of *Ornithosuchus* (figure 14*m*, *n*) as a step-like median lamella whose anterior corner sends up a short process in the more posterior vertebrae of the preserved series.

The elongated neural spines of *Acrocanthosaurus*, and the relative elongation and pronounced opisthocoely of the cervical and anterior dorsal vertebrae were considered by Stovall & Langston to indicate a parallel development to *Spinosaurus* of the Cenomanian (Stromer 1915), rather than close affinity. I am inclined to take the opposite view, and suggest that, in consideration of the resemblance between the structure of the medial side of the jaw in *Spinosaurus*, *Albertosaurus* (Lambe 1904) and *Tyrannosaurus*, coupled with the points mentioned above, *Acrocanthosaurus* and *Spinosaurus* represent a group allied to the deinodonts, which may conveniently be placed in a separate family, the Spinosauridae of Stromer. It is true that there are differences between the dorsal vertebrae of *Acrocanthosaurus* and *Spinosaurus*, but possibly the importance of these can be over-emphasized when one considers the significant resemblances between the Oxford specimen of '*Streptospondylus cuvieri*' and *Antrodemus* (to be discussed later), whose vertebrae on the other hand show many differences.

Whether the Spinosauridae may be considered to extend backward in time through the high-spined *Altispinax* of the English Wealden to the Lower Oxfordian *Megalosaurus parkeri* (von Huene 1926*b*) in which some elongation of the neural spines has taken place, is more doubtful. Stovall & Langston (1950) have discussed the possible significance of the structure of the vertebrae of these forms. According to personal observations of the writer, *Megalosaurus parkeri* is generically distinct from the Stonesfield *Megalosaurus* (*M. bucklandi*) which is the type species of the genus. A new reconstruction of the ilium (figure 16*e*), using additional pieces apparently not available to von Huene, shows that there is a marked difference from that of *M. bucklandi* (figure 16*d*) due to the abrupt change in inclination of the superior margin, at which point the blade is relatively deeper. Other distinctions between the ilia made by von Huene are less easy to assess due to imperfect preservation. The region of the pubic foramen was probably open behind, and the distal ends are expanded to form a considerable 'foot', now much corroded but possibly as much as 18 cm long originally. The distal two-thirds of the conjoined ischia are also present (figure 16*f*), which have a touch-contact with the proximal portion of the left ischium figured by von Huene (1926*b*, Fig. 51). The obturator processes proper are missing, but the general form of the bone was obviously as in *Antrodemus*, albeit more massive. There is certainly no posterior and downward curvature of the ischium as in *M. bucklandi*. The ischia are 63 cm long, the pubes probably some 80 cm originally. There is also preserved one mutilated anterior dorsal vertebra which is compressed fore-and-aft, indicating a heavy skull; the diapophyses are supported by thin laminae, the vertebra as a whole resembling very much the third dorsal of *Antrodemus* or the fourth or fifth dorsal of *Tyrannosaurus*. In the posterior dorsal vertebrae the supporting ridge from the posterior end of the centrum to the diapophysis is vertically alined and not inclined forward as shown in the figure of von Huene (1926*b*, Fig. 49); the ridge from the parapophysis dies out in the hollow between the diapophysis and the posterior vertical ridge much as in the eleventh dorsal of *Tyrannosaurus*. The neural spines of the dorsal vertebrae are inclined slightly forward.

Megalosaurus parkeri differs from *M. bucklandi* in the elevation of the neural spines of the dorsal vertebrae, the shape of the ilium and ischium, and the expansion of the pubic 'foot'. The femora are relatively more slender and the lesser trochanter is more proximally placed; the cnemial process of the tibia projects more strongly upward. The characters of the vertebrae and the ilium are sufficient also to distinguish it generically from '*Streptospondylus cuvieri*'. I suggest that this specimen (Oxford University Museum No. J. 12144) should be named *Metriacanthosaurus* gen.nov. ('moderately spined lizard'), type species *Metriacanthosaurus parkeri* (von Huene). The horizon, shown by a specimen of *Gryphaea dilatata* attached to the ilium, is Upper Oxford Clay (Lower Oxfordian), the locality, as given by von Huene (1926*b*), 1½ miles north of Weymouth, Dorset.

There is nothing definite, therefore, apart from the tall neural spines, to connect this form with *Acrocanthosaurus* and for the present it may be considered as a slightly aberrant member of the *Megalosaurus–Antrodemus* group.

At this point it is convenient to discuss the Indian carnosaurian material described by Matley (1921, 1923) and von Huene & Matley (1933), since my interpretation of certain of these specimens differs from that of these authors, and one of them in particular appears to fill a gap in the evolution of the deinodonts.

The carnosaurian remains from India were obtained from the Lameta formation (Upper Cretaceous) of Jubbulpore. Matley (1921) described the stratigraphy of these rocks. In the section dealing with the fossils from the Lameta formation, he gave an account of the discovery of a large mass of bones from a single spot, the 'Carnosaur Bed' of Bara Simla Hill, Jubbulpore, the bulk of which was obviously referable to 'two or more megalosaurians'. The collection included about 100 vertebrae, two sacra, pelvic and limb bones, parts of skulls, and about 5000 scutes of various sizes, most however being small. At this time Matley did not doubt that the scutes belonged to one or more of the 'megalosaurians', referring in a footnote to the scutes found with the type of *Tyrannosaurus* [*Dynamosaurus*] *imperiosus* from the Upper Cretaceous of Wyoming, and to the dermal ossifications of *Ceratosaurus* from the Morrison of Colorado.

However, when the material had been brought to London and part of it had been prepared, Matley selected from among it a few bones (a sacrum, a pair of ilia and a tibia) which he considered to belong to a new armoured dinosaur, describing these and the scutes under the name *Lametasaurus indicus* (Matley 1923), and referring the genus to the Stegosauria.

The dinosaur material from the Lameta formation was described by von Huene & Matley (1933). Some of the cranial fragments from the Carnosaur Bed were allocated to two 'allosaurids', *Indosuchus* and *Indosaurus*, but it was not then found possible to associate any postcranial remains with these, and the remaining cranial and postcranial material was simply described and figured as 'allosaurid'. In addition a small quantity of coelurosaurian and sauropod material was described from the Carnosaur Bed. *Lametasaurus* was the subject of a brief note by Matley in this work, again placed in the Stegosauridae, although von Huene on a later page referred to it as a nodosaurian.

In 1935 Chakravarti published a short paper in which he demonstrated that Matley's determination of the affinities of *Lametasaurus* was incorrect, and produced evidence to show that these bones were in fact all of megalosaurian type. Chakravarti also considered that the majority of the scutes were correctly associated with the carnosaurian material, again drawing attention to the scutes discovered with the American genera.

However, two distinct types of crania are represented by the specimens referred to *Indosuchus* and *Indosaurus*. One of these (K27/685, von Huene & Matley 1933, Plate IX, Fig. 2) apparently consists of the frontals of a theropod closely related to *Tyrannosaurus* or *Gorgosaurus*, having a narrow median ridge between the relatively elongated supratemporal fossae, of which the frontals form the anterior half (Osborn 1912; Gilmore 1946). The concave facet to the right of the frontals indicates the position of a crescent-shaped, reduced prefrontal as in *Tyrannosaurus*. This reptile would seem to be more primitive than *Tyrannosaurus*, because the median frontal ridge is not so narrow, and the prefrontals are more widely separated. The specimen K20/350 (von Huene & Matley 1933, Plate IX, Fig. 1), also referred to *Indosuchus*, is difficult to interpret in relation to other theropod skulls and I am inclined to suspect that it is a portion of the skull roof of an armoured dinosaur (*Lametasaurus?*).

K27/565 (von Huene & Matley, Plate X, Fig. 1) on the other hand, is a fragment of the cranium of a reptile closely allied to *Antrodemus*, as noted by von Huene. As he remarks, the supratemporal fossa in this case must have been very short and broad as in the American form. In front of the supratemporal fossae there are apparently a pair of lobed, recessed areas such as are borne upon the frontals of *Antrodemus*. The interesting point is that in this case they almost meet in the mid-line, implying a greater degree of specialization in the Indian genus.

Von Huene distinguished two types of femur and tibia in the carnosaurian material. In the stouter type of femur the lesser trochanter extends as far as the head of the bone, as in the femur of *Tyrannosaurus* (Osborn 1916) and this type probably belongs therefore to *Indosuchus*, while in the more slender femora the trochanter ends below the head and one would expect these to belong to an antrodemid, i.e. *Indosaurus*. Likewise the tibiae may be separated primarily on the basis of stoutness into the two carnosaurian types.

We may now proceed to consider the specimens referred by Matley to *Lametasaurus*. The sacrum (Matley 1923, Pl. 8) resembles that of *Antrodemus* more than *Tyrannosaurus*, but since many of the bones in the Carnosaur Bed are crushed, and this specimen is similar to the compressed sacrum of *Tyrannosaurus* figured by Osborn (1916), assignment to either of the two carnosaurian types is probably unjustified. Certainly this sacrum is not in the least nodosaurian (see, for example, Gilmore 1930). The left ilium, (Matley 1923, Pl. 9,' right ilium') is obviously very different from the ornithischian type, lacking the antitrochanter and the horizontal overhanging rim of the blade which one would expect in a nodosaur. It is also apparent from Matley's figures that in both ilia the bowl-like central part of the blade has been broken off. A shorter, deeper type than that of *Antrodemus* is indicated, with a more pronounced anterior part of the blade, and a shorter, deeper posterior part; possibly the ilia are of a more 'concentrated' type, as in *Albertosaurus* (Parks 1928). The lateral concavity of the blade is apparently more marked than in other carnosaur ilia, but this may be an effect of the curious attitudes in which Matley has chosen to illustrate them. It is also perhaps significant that no carnosaurian ilia were figured by von Huene although most other parts of the skeleton were represented.

The orientation of the tibia is not clear from the accounts of either Matley or Chakravarti. However, there cannot be the least doubt as to the carnosaurian nature of this particular bone; it is obviously a left tibia, and in Matley's figures (1923, Pl. 11) the proximal end is to the right, Figs. 1 to 3 being anterior, medial and lateral views respectively. It is an extremely stout bone, with a very powerful cnemial process, but as von Huene did not illustrate the stouter type of tibia from the Carnosaur Bed, assignment of this particular bone to either of the two types is uncertain.

The occurrence of the 5000 or so scutes with bones of tyrannosaurian and antrodemid type recalls the discovery of dermal plates with the type of *Tyrannosaurus* [*Dynamosaurus*] *imperiosus* (Osborn 1905, 1906, 1916) and I was at one time inclined to follow Chakravarti (1935) in regarding these plates as correctly associated. However, examination of the plates of '*Dynamosaurus*' (which are now in the collection of the British Museum) suggests that they are basically of the same type as those which constitute the dermal armature of nodosaurs or ankylosaurs such as *Hoplitosaurus* (Gilmore 1914, Pl. 27) and *Palaeoscincus* (Gilmore 1930, Pl. 5, Fig. 1). Scutes closely similar to those of '*Dynamosaurus*', from the Upper Cretaceous of Wyoming, have been figured by Wieland (1911, Figures 4 and 5) but unfortunately without any skeletal material in association. According to Osborn, the '*Dynamosaurus*' material also includes part of an iguanodontid jaw and fragments of a ceratopsian frill so that it is evident that little reliance can be placed upon the mere fact of the association of the scutes. In view of the lack of dermal plates in other discoveries of large carnivorous dinosaurs (with the exception of *Ceratosaurus*) it seems more reasonable to assume that the scutes of *Lametasaurus* belong to an armoured dinosaur, save that some of those figured by Matley are probably crocodilian, as noted by Chakravarti. Having regard to the fact that Matley set out to describe an armoured dinosaur, the scutes are here looked upon as constituting the type material of *Lametasaurus indicus* Matley 1923. Of the carnosaurian bones which he described in error, the ilia are probably referable to the genus *Indosuchus* von Huene 1933, while the sacrum and tibia cannot at present be definitely assigned either to *Indosuchus* or *Indosaurus*. *Orthogoniosaurus* Das-Gupta 1931, from the same formation, being founded upon an isolated tooth, is here considered to be indeterminable.

The derivation of the cranial pattern of *Antrodemus* (Gilmore 1920) from that of *Ornithosuchus* is more straightforward (figure 17), and here there is the added satisfaction of the existence of an intermediate stage in the form of the specimen in the Oxford University Museum which has previously been called *Megalosaurus* (or *Streptospondylus*) *cuvieri*. In *Antrodemus* the nasals have increased in relative length, and the frontals and parietals have been correspondingly reduced presumably due to changes in the relative height of the occiput and the backward enlargement of the preorbital vacuities for similar reasons to those already outlined for the tyrannosaurs. In the present case, however, the nasals and frontals remain relatively broad. The lachrymal crests attain an enormous size and the lachrymal has grown backward so as to leave only a very narrow notch at the top of the orbit; according to Gilmore the prefrontal and postorbital meet below this notch. The backward growth of the lachrymal has carried the prefrontal with it thus producing the U-shaped distortion of this bone, so well figured by Gilmore. Yet the anterior termination of the prefrontal has retained its original position and the bone is in consequence drawn out on the skull roof as a narrow strip between the lachrymal and the nasal and frontal.

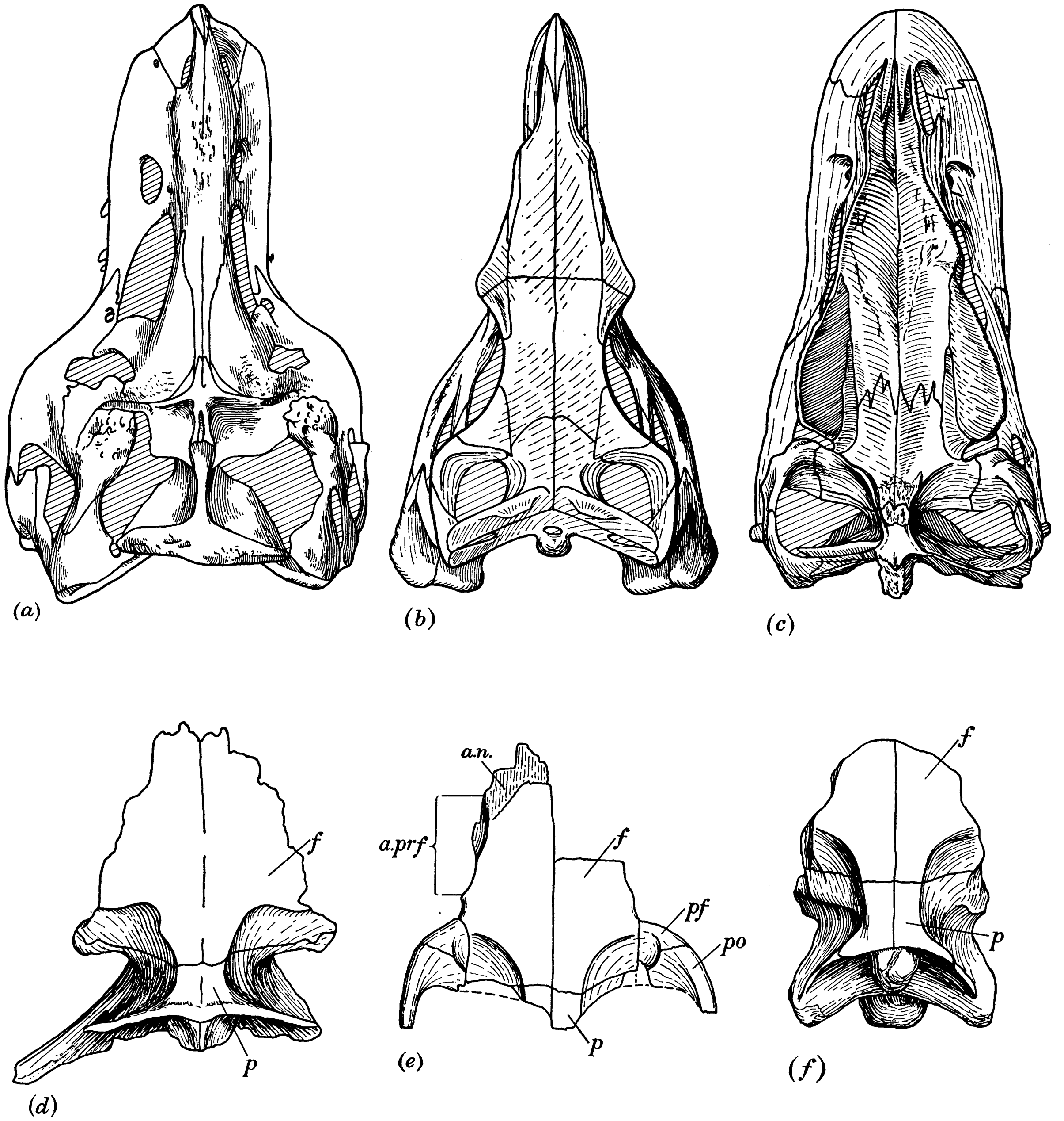

FIGURE 17. Carnosaur skulls in dorsal view for comparison with that of *Ornithosuchus*. *a*: *Tyrannosaurus rex*, after Osborn (*ca.* × 1/15); *b*: *Ornithosuchus longidens* (*ca.* × 1/5); *c*: *Antrodemus valens*, after Gilmore (*ca.* × 1/7); *d*: *Acrocanthosaurus atokensis*, after Stovall & Langston (*ca.* × 1/5); *e*: *Eustreptospondylus oxoniensis* gen. et sp.nov. (*ca.* × 1/3); Middle Oxford Clay (Upper Callovian), Oxford, O.U.M. J. 13558; *f*: *E. divesensis* sp.nov., after Piveteau (*ca.* × 1/6).

The posterior parts of the frontals are greatly expanded transversely, thus pushing the postorbitals to the outer corners of the supratemporal fossae. It is probable, as we shall see, that the postfrontal is still present in *Antrodemus*, indeed it is possible to recognize traces of it on Gilmore's plate (1920, Plate 3). Again, the backward migration of the fronto-parietal suture has allowed the recessed areas anterior to the supratemporal fossae to spread widely on to the frontals. In this case, however, the anterior margins of these areas curve smoothly and uniformly backward and inward towards the parietals.

Before considering the cranial pattern of '*Streptospondylus cuvieri*' some clarification must be attempted of the confused taxonomic situation of the various specimens which have been referred to this species. This material falls into three groups:

(*a*) The type specimens of *S. cuvieri* Owen (1841, p. 88), consisting of the 'anterior half of an anterior dorsal vertebra', part of a 'compressed, conical, hollow tooth...resembling that of *Megalosaurus*', a portion of a 'broad, flat bone...and fragments of long bones'. All these are stated to have been found associated in the 'oolite' in the vicinity of Chipping Norton, which may presumably be taken to mean the Chipping Norton Limestone, at the base of the Great Oolite Series, or early Bathonian. Owen also described a posterior dorsal vertebra from the Jet Rock (Toarcian) near Whitby, but since this was stated only to be 'referable to the present genus', it evidently cannot be regarded as forming part of the type material of the species under discussion. The specimens from Chipping Norton were never figured, and their present whereabouts are unknown.

(*b*) A series of specimens from the Upper Jurassic of Normandy described and figured, but not named, by Cuvier in the *Ossemens fossiles*, of which the fourth edition is the most accessible (1836, Vol. 9, pp. 308 to 312; Vol. 10, pp. 204 to 207; Pl. 236, Figs. 12, 13; Pl. 237, Figs. 3, 6 and 10; Pl. 249, Figs. 34 to 39). These included various vertebrae, the distal end of a tibia with the astragalus, a tarsal bone, and fragments doubtfully identified as the upper and lower ends of a fibula. It has usually been assumed, presumably because of the specific name, that Owen in 1941 referred these specimens, or at least the vertebrae, to his species *Streptospondylus cuvieri*, but in fact he did not do so; however, a footnote to the description of *S. major* (Owen 1859, p. 23) cites Cuvier's description and figures as examples of vertebrae of *S. cuvieri*. Nevertheless, it is evident that the specimens from Normandy cannot be regarded as comprising part of the type material of *S. cuvieri* Owen. Other specimens from Normandy which have also been referred to this species will be discussed below.

(*c*) An almost complete skeleton including a good deal of the skull, from the Middle Oxford Clay (Upper Callovian) of Oxford. This specimen is well known historically from the accounts of Phillips (1871), von Nopcsa (1906) and von Huene (1926*b*, 1932).

Geoffroy (1825, pp. 146 to 149) gave names to Cuvier's 'Gavials d'Honfleur', distinguishing them as 'première espèce, *Steneosaurus rostro-major*' and 'deuxième espèce, *S. rostro-minor*'. The genus *Streptospondylus*, however, was first introduced by von Meyer (1830, p. 518) along with *Metriorhynchus*, as a *nomen nudum*. A later publication by von Meyer (1832, p. 106) shows that his intention was to elevate Geoffroy's two species of *Steneosaurus* to the rank of genera, calling the former of these *Streptospondylus*, and the latter *Metriorhynchus*. Since the name *Steneosaurus* cannot be eliminated in such a procedure, and *S. rostromajor* Geoffroy 1825 is evidently the type species of *Steneosaurus*, *Streptospondylus* von Meyer 1832 is thus an objective junior synonym of *Steneosaruus* Geoffroy 1825, now recognized as a genus of Crocodilia. Furthermore, *Streptospondylus altdorfensis* von Meyer (1832, p. 106), the only species of the genus named by von Meyer and therefore presumably the type species of *Streptospondylus*, is actually equated with *Steneosaurus rostromajor* Geoffroy in this work, the same list of bibliographic references serving for both, so that the former species is also an objective junior synonym of the latter. The immense confusion of the nomenclature of the crocodilian material from Normandy, largely brought about by the juxtaposition by Cuvier of skulls and vertebrae of different types from different horizons and localities, fortunately does not concern the present discussion; suffice it to say that, consequent upon the description of the Oxford '*Streptospondylus*' by Phillips (1871), the carnosaurian nature of certain of these vertebrae was gradually realized.

Swinton (1955) has argued that the detailed description of a vertebra of '*S. cuvieri*' given by Owen (1841), and its apparent similarity to the vertebrae of the Oxford and Normandy specimens, serves to validate Owen's species. This conclusion seems hard to justify. The description given by Owen of this vertebra (which is evidently little more than half of a centrum) indicates only that it is a carnosaurian vertebra from the posterior cervical or anterior dorsal region. The presence of a deep pit behind the 'costal articular surface', upon which emphasis is laid by Swinton, is a characteristic carnosaurian feature, usually lying above the parapophysis in the cervical vertebrae and gradually shifting downward and backward to lie behind it in the anterior dorsals. Nor can the N-shaped pattern of supporting lamellae so lucidly described by Owen as distinguishing the vertebrae of the genus '*Streptospondylus*' (1841, p. 88) be taken as anything more precise than a definition of the general structure of carnosaurian presacral vertebrae. An anterior dorsal vertebra of *Spinosaurus* from the Cenomanian (Stromer 1915) or *Tyrannosaurus* from the Danian (Osborn 1916), shows similar features, with modifications due to differences in the attitude of the diapophyses. Point is added to this comparison by Owen's description of the vertebra from the Lower Toarcian of Whitby which, *pace* Swinton (1955), was probably carnosaurian and was also referred by Owen to '*Streptospondylus*'.

In view of the lack of figures and the absence of the type material, and in consideration of the points mentioned above, the species '*S. cuvieri*' Owen 1841 is here regarded as indeterminable. Even if Owen's specimens should in future come to light, it seems doubtful whether material from the Upper Callovian and higher horizons could be assigned to an early Bathonian species founded on such inadequate specimens.

Another species, *Streptospondylus major* Owen (1841, p. 91; 1859, p. 22, Pls. V, VI; 1861, Pl. VII) was listed by Lydekker (1888, p. 201) as a probable synonym of *Iquanodon bernissartensis* Boulenger.

It is thus apparent that the specimens from Normandy and the Oxford skeleton, hitherto referred to *Streptospondylus cuvieri* Owen, are without valid generic or specific names. Piveteau (1923) has given excellent new figures of most of the specimens illustrated by Cuvier, adding the distal end of a femur mentioned by von Huene (1926*b*) and, significantly, the posterior part of a skull from Dives. According to von Nopcsa (1906), von Huene (1926*b*, 1932) and Piveteau (1923), these specimens belong to one species, to which the Oxford specimen is also assigned by the first two authors. Piveteau and von Nopcsa regarded '*Streptospondylus*' as generically distinct from *Meqalosaurus*, whereas von Huene

(1932) and Swinton (1955) place '*Streptospondylus cuvieri*' as a species of the latter genus. An examination of the early literature raises doubts as to the validity of grouping together the Normandy material under one species. It is quite clear from the explicit statement made by Cuvier (1836, Vol. 9, p. 287) that he did not know whether the carnosaurian and crocodilian material which he described came from the Oxford Clay or the Kimmeridge Clay and, according to Lennier (1870, p. 42), some of the material is from the Lower Kimmeridgian of Cap de la Hève, other specimens from higher in the Kimmeridgian, and yet others from the Oxfordian of Villers, Dives, and other localities in the Calvados area. Von Huene (1926*b*) lists megalosaurian material from this region with horizons varying from Lower Callovian to Middle Kimmeridgian.

It is therefore far from certain that the carnosaurian specimens from Normandy which have been referred to '*S. cuvieri*' belong to one genus, let alone one species. As to the further question of whether these specimens belong to the same species as the Oxford individual, it is sufficient for the present to point out that the cranial fragment from Dives figured by Piveteau (1923) shows at least specific distinction from the Oxford specimen; these crania are further discussed below.

Swinton (1955, p. 132) states that the ischium of the Oxford '*Streptospondylus*' is 'almost identical with that of the Honfleur specimen'. In order to explain this remark (since no ischium from Honfleur is known) we must discuss the identification of the element figured by Cuvier (1836, Pl. 249, Fig. 39) and doubtfully identified by him as the upper end of a fibula. Piveteau (1923, Pl. IV, Fig. 1) has provided excellent photographs of this same bone, identifying it as the proximal end of an ulna, apparently following von Nopcsa (1906) in this. Von Huene (1926*b*, p. 38), on the other hand, seems to have accidentally duplicated portions of Numbers 27 and 29 of his list of material, since the distal end of the tibia with astragalus occurs twice, and the element under consideration appears both as the proximal end of an ulna and the distal end of an ischium, the latter identification being repeated in a later work (1932, p. 230). After careful examination of Piveteau's figures I am satisfied that this disputed element can only be the distal end of a left pubis; it is clearly not the proximal end of an ulna, and the direction of compression of the shaft shows that it is neither a fibula nor an ischium, nor does the shape of the termination agree with the latter possibility. Comparison with Gilmore's figures (1920) of the pubes of *Antrodemus* makes this identification quite certain.

It seems therefore that Swinton was actually comparing the distal ends of the pubes in the statement quoted above, for the distal end of one of the pubes of the Oxford skeleton was figured by von Huene (1926*b*, Fig. 31*b*) as the distal end of an ischium, and was also said by him to be identical with the element figured by Cuvier. The distal ends of the pubes are now correctly mounted in the Oxford skeleton, whereas the distal ends of the ischia are missing. Two points only need be made in respect of the comparison between the pubes of the Oxford and Normandy specimens. First, the pubic 'foot' is better developed in the 'Honfleur' specimen, thus agreeing with the more progressive features of the cranium from Dives as compared with the Oxford cranium, and providing an interesting intermediate stage in the evolution of this structure. Secondly, the 'Honfleur' pubis is only slightly larger than the Oxford specimen, and therefore much too small to belong to the same individual as the tibia and astragalus shown adjacent to it in Cuvier's figure.

For reasons given below, the Oxford '*Streptospondylus*' is considered to be generically distinct from *Meqalosaurus* as shown by the characters of its type species *M. bucklandi* from Stonesfield. Taking into account the relative completeness of the Oxford skeleton, the fact that it is known to be a single individual, and because it probably comes from a lower horizon than the material from Normandy, it seems preferable to found a new genus and species upon it rather than upon the latter specimens. The name here chosen is *Eustreptospondylus oxoniensis* gen. et sp.nov. ('well-curved vertebra'). The holotype of this species is the skeleton in the University Museum, Oxford, Number J. 13558, from the Athleta Zone, Middle Oxford Clay (Upper Callovian) of Summertown brick pit, Wolvercot, near Oxford.

The cranium from the Oxfordian of Vaches Noires, near Dives, figured by Piveteau (1923, pp. 115 to 123, Pls. I, II) differs from the corresponding region of *E. oxoniensis* by virtue of the anterior contraction of the frontals; it is therefore selected as the holotype of a new species, *Eustreptospondylus divesensis* sp.nov. (figure 17*f*). The specimen is in the collection of the Musée d'histoire naturelle, Paris. As a matter of convenience, the remaining specimens from the same region which have traditionally been regarded as part of the material of '*Streptospondylus*' *cuvieri* (Cuvier 1836; von Nopcsa 1906; Piveteau 1923; von Huehe 1926*b*, 1932) may also be referred to *Eustreptospondylus divesensis*, but the probability is again stressed that this material is not homogeneous.

E. oxoniensis differs from *Megalosaurus bucklandi* in the strongly opisthocoelous character of the cervical and anterior dorsal vertebrae, the greater elongation of the vertebrae, the smaller scapula, the more slender humerus, and the deeper posteroventral channel below the iliac blade. According to my examination and interpretation the pubis and ischium differ considerably from the figures of von Huene (1926*b*). The pubis is a straight, rod-like bone 42 cm long, much more like that of *Antrodemus* than von Huene has portrayed it. The obturator foramen was probably open behind and there is a small terminal expansion or 'foot' 8 cm in length. The ischia as now repaired curve down slightly posteriorly but a good deal of this curvature is misleading and could be corrected by re-cementation of the fractures. The left ischium, which is the better preserved, is incomplete distally and the nature of the fractured surface again implies a straighter type than in *Megalosaurus bucklandi*. The femur is more slender and the lesser trochanter is situated more proximally; the metatarsals are also more slender than in *M. bucklandi*.

The cranial bones of *Eustreptospondylus oxoniensis* were figured and described by von Huene in 1932 (as *Megalosaurus cuvieri*) and have since been mounted on a plaster core simulating the approximate form of the skull. Some corrections are necessary to von Huene's identifications of these bones. Thus the element figured as the left quadratojugal (von Huene 1932, Plate 43, Fig. 10), and now mounted in this position, is in reality the right lachrymal inverted (compare with Gilmore 1920, Fig. 8). The bone is less acutely angulated and produced backward than in *Antrodemus* and the crest is poorly developed; the orbit was therefore relatively larger than in the American form. The bone described as the left post-frontal+postorbital (von Huene 1932, Plate 43, Fig. 8) is from the right side; at some time this has been realized and it is now mounted correctly with respect to the frontal. The left squamosal (von Huene 1932, Plate 43, Fig. 9) is correctly identified but an attempt has been made to place it in symmetry with the single preserved paroccipital; in this position it actually projects into the endocranial cavity. This bone is extraordinarily like the squamosal of *Antrodemus* (Gilmore 1920, especially Figs. 1 and 6 and Plate 3). The postorbital and quadratojugal branches meet at an obtuse angle and there was obviously no marked projection into the lateral temporal fossa. Assuming that the quadrate was approximately vertical, articulation of the two bones shows that the upper surface of the squamosal sloped backwards at between 30° and 45° to the horizontal.

The remaining portion of the skull roof (figure 17*e*) consists of most of the frontals and the anterior parts of the parietals and both postfrontals and postorbitals. The frontals are longer (9·6 cm excluding the area for the overlap of the nasal) than wide (8 cm). There is a distinct orbital notch on either side, 7 mm in length. In front of this on the left side is clearly seen the lateral recess and overlap area for the prefrontal. The recessed areas on the frontals extend laterally on to the postfrontals and postorbitals, a sharp raised edge which curves posteromedially probably indicating the medial part of the suture between these two latter elements. The outer part of this suture is discernible on both sides so that the postfrontal is present here as a distinct element. The anterior lateral extensions of the parietals probably met the postorbitals as shown in the figure.

The significant point about this skull roof is that it shows obvious affinities to *Antrodemus* but is more primitive in that the frontals are still longer than wide, the prefrontals are situated considerably farther forward and farther apart, and the upper part of the orbit is not so compressed. On the other hand traces of the original cranial pattern of *Ornithosuchus* are still preserved. The prefrontal/frontal suture and the postfrontal + postorbital/frontal suture are still in line, with the orbital border of the frontal expanding slightly outward between them, and the postfrontal/postorbital relationship is essentially unchanged.

The cranial fragment from the Oxfordian of Vaches Noires near Dives, figured by Piveteau (1923) shows a stage of evolution intermediate between *Eustreptospondylus oxoniensis* and *Antrodemus valens*. By comparison with the latter two forms, it seems that the area labelled 'lachrymal' by Piveteau is more probably for the articulation with the prefrontal, and that the concavity marked 'prefrontal' is the very small orbital margin of the frontal. This cranium (figure 17*f*) shows a more definite anterior contraction of the frontals than in *Eustreptospondylus oxoniensis* but does not match *Antrodemus* in this respect nor in the broadening of the posterior parts of these bones. The precise horizon of the specimen is not stated in zonal terms and there are difficulties in interpreting the designation 'Oxfordian', the Upper Callovian of Arkell (1956) being included by Dangeard (1951) in this stage. It is only possible to say that the specimen, herein named *Eustreptospondylus divesensis*, is approximately contemporaneous with, or more likely slightly younger than, *E. oxoniensis*.

As pointed out earlier, *Indosaurus* from the Upper Cretaceous apparently manifests a greater degree of specialization than *Antrodemus* in the more medial extension of the recessed areas anterior to the supratemporal fossae.

There is some evidence which tends to show that the primitive carnosaurian maxilla bore a relatively low number of teeth, rather than that a reduction in number occurred in the later forms, as postulated by Osborn (1912) and Gilmore (1920). Thus in *Teratosaurus* there are thirteen maxillary teeth, in *Ornithosuchus* nine. The maxilla of *Megalosaurus bucklandi* from Stonesfield figured by Huxley (1869) had twelve teeth; another specimen, also in the Oxford Museum, is less well preserved along the jaw margin but the number of teeth can hardly have exceeded twelve. The maxillae of *Eustreptospondylus* are incomplete but here again a low number, approximately twelve, is indicated. An unnumbered megalosaurian maxilla in the collection of the British Museum, from the 'Inferior Oolite of Gloucestershire' probably had twelve or thirteen teeth originally; this bone is of particular interest in showing the interdental plates clearly. Against these must be set the specimen described by Owen (1883) (by implication) as *Megalosaurus bucklandi* and commonly accepted as belonging to that genus and species; thus von Huene used it as the basis for his 'construction' of the skull (1926*b*, Fig. 1). The specimen comprises portions of both premaxillae, the right maxilla, the upper end of a quadrate, and both dentaries. There are four premaxillary teeth. The maxilla, which is incomplete posteriorly, now bears twelve teeth; the original number certainly exceeded this, an estimate of the probable total being fifteen to eighteen teeth. This specimen, which comes from the Upper Inferior Oolite of Sherborne, Dorset, is somewhat older than *M. bucklandi* and is at least specifically distinct from the latter. A further point of interest lies in the occurrence of a lateral notch between the premaxilla and the maxilla, presumably for the reception of the large second or third dentary tooth, which recalls the condition in *Ornithosuchus*. The premaxilla of *Megalosaurus bucklandi* is unknown, but the third alveolus of the dentary is a little larger than those preceding and following it, and as in the case of the Sherborne specimen there is a slight lateral convexity of the jaw at the second and third dentary teeth. Possibly therefore a lateral notch was present also in *M. bucklandi*. Data on later forms have been given by Gilmore (1920) for *Antrodemus* (late Jurassic, sixteen to eighteen maxillary teeth); Stromer (1931) for *Carcharodontosaurus* (Cenomanian, twelve); Lambe (1904) for *Albertosaurus* (Danian, twelve); and (1917) for *Gorgosaurus* (Upper Senonian and Danian, thirteen); and Osborn (1912) for *Tyrannosaurus* (Danian, twelve). From this review it emerges that a maxillary tooth count of twelve to thirteen is the most common number in carnosaurs and this is in fact to be expected if an ultimate descent of the group from a form close to *Euparkeria* (twelve to thirteen maxillary teeth) is postulated.

VII. Phylogeny and classification of the Carnosauria

From the preceding discussion it will be apparent that *Ornithosuchus* is here considered to be a primitive carnosaur, a close collateral ancestor of both the Megalosauridae and the Tyrannosauridae. A direct ancestral position is *a priori* unlikely and the early reduction in tooth-number tends to rule this out also. *Teratosaurus* (*sensu stricto*) and *Sinosaurus* (*sensu stricto*) are known only from tooth-bearing bones plus some isolated teeth; these two genera, with *Ornithosuchus*, at present form the Upper Triassic carnosaur family Ornithosuchidae.

Special points of resemblance between *Ornithosuchus* and the Upper Cretaceous tyrannosaurs include the narrow, beaked premaxillae and nasals, the curious shape of the lateral temporal fossa, the presence of a large surangular foramen and the build of the scapulocoracoid. Matthew & Brown (1922) considered that the tyrannosaurs were independently descended from coelurosaurs, and while it is true that it is difficult to derive the tyrannosaurs directly from the megalosaurs, the combination in *Ornithosuchus* of resemblances to both these carnosaurian families suggests a position for the Elgin genus close to their common ancestry. The notion that the tyrannosaur line existed throughout Jurassic times, although novel, need not necessarily cause surprise. Certain ornithischian groups appeal for the first time in the Cretaceous, having sprung from primitive, but unknown ancestral stocks which must have existed since the Trias.

Some of the many described 'species' of *Megalosaurus* may in fact bridge the gap between *Ornithosuchus* and the earliest known tyrannosaur (in the broad sense) *Acrocanthosaurus*, but in default of the critical regions of the skull these will be well-nigh impossible to recognize. Carnosaur skull material is extremely rare, much more so than ornithischian skull material. Prior to the Upper Cretaceous there is the incomplete skull of *Acrocanthosaurus* (Upper Aptian or Lower Albian), several skulls of *Antrodemus* (uppermost Jurassic), the incomplete skulls of *Eustreptospondylus divesensis* (Oxfordian) and *E. oxoniensis* (Upper Callovian), but otherwise discoveries of cranial material are virtually limited to numerous teeth and parts of jaws. As noted earlier, *Ceratosaurus*, following von Huene (1926*b*), is here regarded as a coelurosaurian derivative. Similarly, the incomplete skull from the Great Oolite of Minchinhampton named *Proceratosaurus* by von Huene (1926*b*; Woodward 1910) is also thought to belong to the coelurosaur group. It differs considerably from the normal carnosaurian type in many features, notably in its small size (26 cm in length), the acute anterior triangular extension of the maxilla, the rounded orbit, the apparently small size of the lateral temporal fenestra, the low position of the jaw-articulation, the slender jaws and rather small teeth and the probably low build of the rear part of the skull. There appears to be no reason to presume any particularly close relationship between *Proceratosaurus* and *Ceratosaurus*.

The Megalosauridae (taking *Antrodemus* to be typical of this family) have a 'normal' lateral temporal fossa and lack a surangular foramen, as far as is known; they would appear, therefore, to have lost the latter feature after diverging from an immediately pre-*Ornithosuchus* stock. This assumes derivation of *Ornithosuchus* from *Euparkeria* or a close ally, for in the latter genus the surangular foramen is already present (Haughton 1922), although the lateral temporal fossa is of 'normal' shape. It is suggested that *Acrocanthosaurus* represents a Lower Cretaceous side branch of the tyrannosaur like, which may provisionally be placed with *Spinosaurus*, and possibly *Altispinax*, in the family Spinosauridae of Stromer (1915). The Tyrannosauridae are more progressive than the Megalosauridae as shown by the greater degree of deformation of the original pattern of the skull roof, the reduction of the shoulder girdle and fore-limb, the shortening of the ischium, the more proximal position of the lesser trochanter of the femur and the appression of the metatarsals, to name only some of the more obvious features. The Megalosauridae on the other hand persist through to late Cretaceous times with apparently little modification of the type of structure established in the Upper Jurassic *Antrodemus*. It is not known whether *Teratosaurus* and *Sinosaurus* are in the strict sense ornithosuchids or not, but it is convenient to classify them as such at the present time. The two carnosaurian stocks seem to have diverged from their common ancestor while still technically in the pseudosuchian stage of evolutionary development; this indicates a much greater degree of polyphyletism in the dinosaurs than has previously been anticipated.

These suggestions concerning phylogeny are summarized in the accompanying diagram (figure 18, p. 128). A revised classification of the Carnosauria is appended, listing only the more important of the many genera which have been proposed.

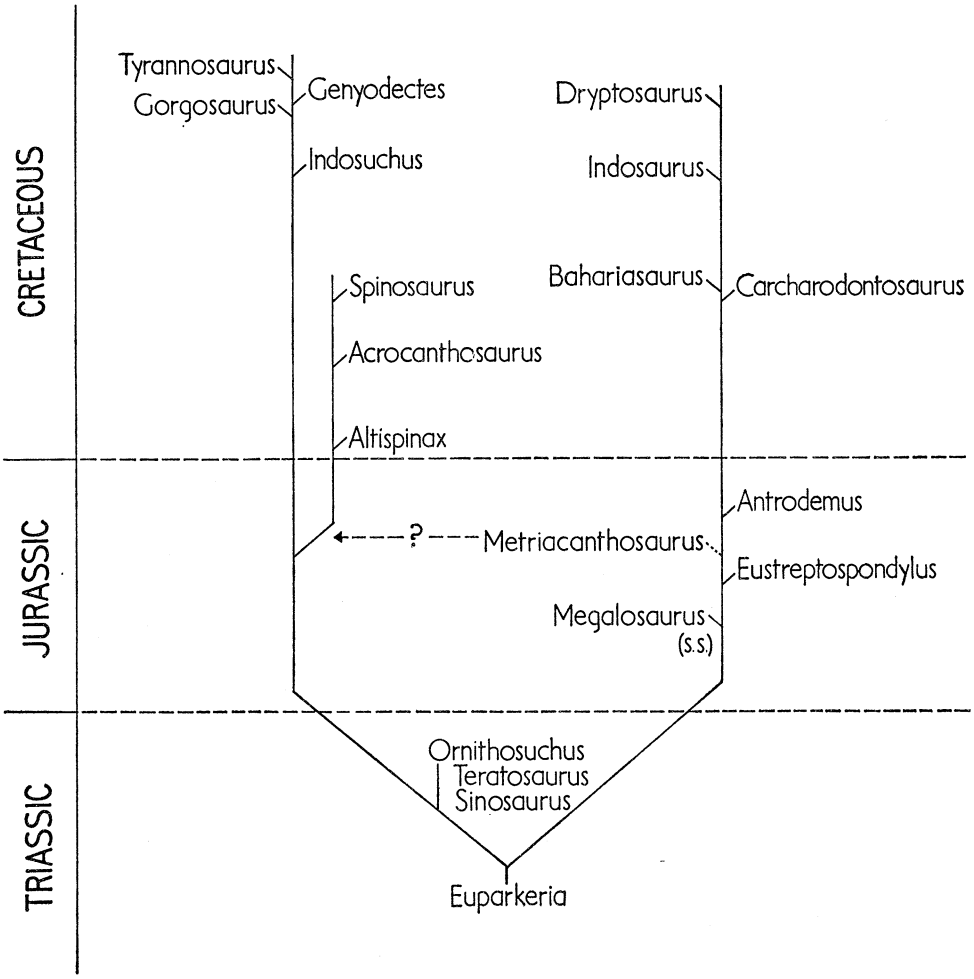

FIGURE 18. Suggested phylogeny of the Carnosauria. The significance of *Metriacanthosaurus* is discussed on p. 116.

Infra-order CARNOSAURIA

- Superfamily TYRANNOSAUROIDEA
  - Family Ornithosuchidae von Huene 1908, 1914.
    - *Ornithosuchus* Newton 1894, *Sinosaurus* Young 1948, *Teratosaurus* von Meyer 1861.
  - Family Tyrannosauridae Brown 1914.
    - *Albertosaurus* Osborn 1905, *Deinodon* Leidy 1856, *Genyodectes* Woodward 1901, *Gorgosaurus* Lambe 1914, *Indosuchus* von Huene 1933, *Tarbosaurus* Maleev 1955, *Tyrannosaurus* Osborn 1905.
  - Family Spinosauridae Stromer 1915.
    - *Acrocanthosaurus* Stovall & Langston 1950, *Altispinax* von Huene 1926, *Spinosaurus* Stromer 1915.
- Superfamily MEGALOSAUROIDEA
  - Family Megalosauridae Huxley 1870.
    - *Antrodemus* Leidy 1870, *Bahariasaurus* Stromer 1934, ?*Carcharodontosaurus* Stromer 1931, *Dryptosaurus* Marsh 1877, *Eustreptospondylus* gen.nov., *Indosaurus* von Huene 1933, *Megalosaurus* Parkinson 1822, ?*Metriacanthosaurus* gen.nov.

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Appendix

Note on additional portions of R 3562 (*added* 24 *February* 1964)

After this paper was completed my attention was drawn to some further portions of the skeleton of R 3562 which had inadvertently been placed in the wrong cabinet. In view of the scarcity of postcranial material of the larger individuals of *Ornithosuchus*, some brief comments on these specimens may be of interest. They include several small pieces with fragments of the skull and jaw which, while making the palatal region of this specimen more intelligible and confirming its close similarity to those of R 2409 and R 3143, do not add any new information. The most important portions are, however, two blocks which are counterparts, containing between them a series of twelve vertebrae surmounted by scutes, and portions of both scapulocoracoids and humeri.

Because of their long diapophyses and lack of ventral keels the anterior vertebrae are not believed to include any cervicals, and this conclusion is borne out by the similarity of the more posterior members of the series to the posterior vertebrae of R 3916, and also by the rapid narrowing of the more posterior scutes. Accordingly, the last vertebra is identified as the twelfth dorsal, and the termination of the series at this point shows that in this case at least the rear portion of the skeleton had been removed prior to fossilization. It seems likely that the cervical vertebrae had also been removed or disturbed, at any rate the neck region is only represented by several small fragments with impressions of damaged spinose scutes. Among these should now be included the two scutes shown a figure 14*e* which, from the completeness of the dorsal series, are evidently cervicals and not anterior dorsals as originally suggested.

Comparison of the vertebrae, which are each 18 mm long, with those of the smaller individuals, suggests a skull length for R 3562 of some 19 cm, which agrees well with the previous estimate. The vertebrae are crushed ventrally and the extreme pinching-in of the sides of the centra below the neural arches, which is particularly striking in all of them, is no doubt somewhat exaggerated in consequence. The neural canals are very large; as in the smaller vertebrae a narrow median ventral cavity extends well down into the centrum from the main body of the canal. In the eighth dorsal vertebra the articular face of the centrum is 15 mm broad, the breadth of the contracted central portion is 7 mm, and the walls of the centrum at this point are 2 mm thick. The diapophyses of the anterior dorsals (with the exception of the first, which is not fully preserved on either side) are very long, that of the right side of the third dorsal measuring 24 mm from the mid-line and those of the succeeding vertebrae as far as to the sixth being only slightly shorter. These vertebrae are also notable for the development of the thin lamellae buttressing the diapophysis to the zygapophyses, the parapophysis and the posterior end of the neural arch; the hollows behind the parapophyses of the fifth and sixth dorsals are particularly deep. The short parapophyses are still low down at the base of the neural arch in the fifth and sixth dorsals, with the centrum contributing a little to the articulation. Beyond this point they gradually ascend until on the twelfth vertebra they are almost on a level with the diapophyses.

The distal ends of both scapulae are broken off, and the thin coracoids, which overlap each other in the mid-line, are also incomplete. At some time in the past an attempt has been made to expose the right scapula by positive preparation, which has resulted in the loss of portions of the impressions of the scapula and humerus. Both scapulae show the anteroventral expansion, although the margins in each case are not clearly defined; however, the right scapula is obviously closely similar to that of R 3916. The area around the glenoid has in each case been eroded and filled with sand, and only on the right side can part of the recurved posterior extension of the coracoid be positively identified.

The head of the humerus is in each case close to the glenoid region. The proximal half of the right humerus and the proximal quarter of the left are all that remain of the forelimbs. The resemblance between these humeri and those of R 3916 is striking. The lower part of the deltopectoral crest of the right humerus, and the internal tuberosity, are somewhat better developed than in the smaller humeri; these are differences which one would expect to find between individuals of such disparate size. On the other hand, the details of the curvatures of the proximal portion of the bone, including the slight lateral flexure of the thin internal tuberosity, are faithfully reproduced in the larger specimen. A portion of the bone of the right humerus immediately distal to the deltoid crest shows a thin, flat cavity proximally, as might be expected in this region; distally, that is at about the narrowest part of the shaft, there is a relatively large central cavity.

A complete double row of dorsal scutes is present above the vertebrae, ending above the eleventh dorsal. These scutes are closely comparable to those of the smaller individuals, and undergo a similar series of changes. Only a few points need therefore be noted. First, the keels are more strongly developed, an effect no doubt correlated with size, since this tendency has been noted in the larger individuals of *Stagonolepis*. Secondly, the rapid attenuation of the more posterior scutes, especially the eleventh pair, which are only half as wide as the tenth, presumably indicates that in this particular specimen the formation of the median ridge occurred farther forward than in the smaller individual R 3561. Thirdly, the spines or bosses of the anterior scutes are broken off or otherwise damaged, and finally the scutes are partly replaced by fluorite which occurs as small cubes disseminated throughout the bone or concentrated at its upper and lower surfaces.

The damage sustained by this specimen is of interest, since in so few cases in material from the Elgin sandstone is it possible to prove that the incompleteness of a specimen is not due to inadequate collecting. The surfaces of the second and third dorsal scutes of the left side are damaged and the first four scutes have lost their spines. The diapophyses of the first three dorsal vertebrae of the same side are broken off short, and the anterior edge of the left scapula, which passes directly below these vertebrae, is also broken and incomplete. Only the proximal end of the blade is preserved in this scapula; both it and the humerus which lies immediately beneath it, terminate distally at the same point. The ribs of the left side are missing, whereas a full sequence is present on the right; no sign is seen of the gastralia. The loss of the distal portions of the fore-limbs and the scapulae, and possibly of the cervical vertebrae, together with the other evidence detailed above, show that considerable disturbance of the skeleton has taken place, but whether this was caused by a carnivorous animal (presumably a larger *Ornithosuchus*) which was also responsible for the death of this individual, or whether it was caused subsequently by a scavenger, cannot be stated.

The close resemblance of the vertebrae, scutes, scapulae and humeri to those of the smaller individuals, especially R 3916, when taken with the remarks made about the skull of this specimen (R 3562) in the taxonomic section, are considered to provide strong additional support for the conclusion already put forward, namely, that there is no reason to suppose that more than one species is present in this series of specimens.

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