STRETOSAURUS GEN. NOV., A GIANT PLIOSAUR FROM THE KIMERIDGE CLAY

by L. B. TARLO

ABSTRACT. A giant Pliosaur is described. This is the second Pliosaur from the Kimeridge Clay in which limb girdles are known associated with the axial skeleton, but it is the only giant one of any age (with the exception of *Kronosaurus* from the Lower Cretaceous) in which the post-cranial skeleton is adequately known. The pectoral girdle of this animal is so unusual that a new generic name is considered necessary for its reception; the name *Stretosaurus* gen. nov. is proposed. However, the characters of the anterior cervical vertebrae enable it to be placed in the species *S. macromerus* (Phillips). Finally, it is shown that two quite distinct giant Pliosaurs, *S. macromerus* (Phillips) and *Pliosaurus brachydeirus* Owen, must have inhabited Kimeridgian seas.

INTRODUCTION

IN 1952 a giant Pliosaur was discovered at the village of Stretham, near Ely, during excavation of Kimeridge Clay by the Great Ouse River Board, and largely due to the voluntary efforts of their employees, in particular Mr. W. W. Wolfe and Mr. B. Woolf of Stretham, this huge skeleton was preserved for the Sedgwick Museum, Cambridge. The photographs taken at the time of the discovery give a good indication of the size of the animal (see Pl. 7). The material collected by the Sedgwick Museum in 1952 is now catalogued under J. 35990 *a–z*, *aa–zz*, *A–Q*, and consists of sixty-nine bones (see Appendix 1).

The discovery of the Stretham skeleton is of considerable importance since not only is it one of the two Kimeridgian Pliosaurs in which limb girdles are known associated with the axial skeleton, but in particular it has an unusual scapula which is unlike that of any other Plesiosaurian. Besides this, it is the only giant Pliosaur of any age in which the post-cranial skeleton is adequately known (with the exception of *Kronosaurus* from the Lower Cretaceous, Romer and Lewis 1959).

The characters of the anterior cervical vertebrae show that the Stretham specimen belongs to the species *P. macromerus* Phillips, but as indicated previously (Tarlo 1959) there are two clearly defined groups of Kimeridgian Pliosaurs, one group containing *P. brachydeirus* Owen, and the other represented by *P. macromerus* Phillips. As *P. brachydeirus* is the type species the group to which it belongs must retain the name *Pliosaurus*, thus making a new generic name necessary for *P. macromerus*. The name *Stretosaurus* gen. nov. is chosen as it seems fitting that the village of Stretham where this giant skeleton was discovered should be commemorated.

All giant Pliosaur remains were previously assigned to *P. macromerus* on the basis of size alone, but it can now be demonstrated that these remains fall into the two groups previously established (Tarlo 1959). Obviously size alone is no criterion for the identification of Kimeridgian Pliosaurs. It is now possible for one group of giant remains to be assigned to *Stretosaurus macromerus* and the other to *Pliosaurus brachydeirus*.

[Palaeontology, Vol. 2, Part 1, 1959, pp. 39–55, pls. 7–9.]

SYSTEMATIC PALAEONTOLOGY

Family PLIOSAURIDAE Seeley 1874

Genus STRETOSAURUS gen. nov.

Type species *Pleiosaurus macromerus* Phillips.

Diagnosis. Teeth trithedral in cross-section, outer surface smooth and flat; mandible with short symphysis bearing five to six large caniniform teeth, total of about twenty-five teeth in each ramus; cervical vertebrae short, length less than half width or height, ventral keel absent, cervical ribs double headed; caudal vertebrae without chevron bone facets; scapula triradiate with dorsal process produced anteriorly; coracoid long with postero-lateral expansion; ischium elongated; propodials long, compressed dorso-ventrally, slightly expanded distally; epipodials short.

Stretosaurus macromerus (Phillips)

Pliosaurus grandis Owen 1849–84, pp. 152–3, pl. 18.
Pliosaurus grandis Owen 1869, pp. 3–5, pl. 1, 2.
Pliosaurus brachydeirus Owen; Seeley 1869, p. 104.
Pleiosaurus macromerus Phillips 1871, pp. 354–8, fig. 148 only.
Pliosaurus macromerus Phillips; Lydekker 1889, pp. 131–9, fig. 41 only.
Pliosaurus macromerus Phillips; Tarlo 1958*b*, pp. 193–9, figs. 1–4, pl. 36–37.

Diagnosis. As for genus.

Syntypes. Kimeridge Clay; University Museum, Oxford. J. 10437, anterior cervical centrum, Swindon, Wiltshire; J. 10438, anterior cervical centrum, Shotover Hill, Oxfordshire; J. 10439, anterior cervical centrum, Swindon; J. 10441, anterior cervical centrum, Shotover railway cutting; J. 10444, posterior cervical centrum, Sandford, Oxfordshire; J. 10445, dorsal centrum, Swindon; J. 10460, caudal centrum, St. Giles', Oxford; J. 12498, femur, Swindon. The anterior cervical centrum (J. 10441) figured Phillips 1871, fig. 148, is here chosen as the lectotype.

Description of Lectotype

Phillips (1871, p. 354) included under *P. macromerus* a large femur from Swindon and a number of vertebrae. This material was not associated and came from several different localities. Much of it is indeterminable, although three of the cervical vertebrae and the one caudal vertebra listed by him can be assigned to *P. brachydeirus* Owen (see Appendix 2 below). The first specimen figured by Phillips (fig. 148) is chosen as the lectotype (Pl. 8, figs. 1, 1*a*, 1*b*) since of those listed it is the only one exhibiting sufficient characters for it to be of use in specific diagnosis.

The length of the lectotype centrum is less than half its width (or height). Its measurements are: length 56 mm., width 138 mm., height 135 mm. This marked shortening of the cervical vertebrae is a distinguishing feature of all Pliosaurs and was noted by Conybeare as long ago as 1824.

The lateral surface of the centrum bears two rib facets which are oval in outline, their long axes being directed antero-posteriorly. In this specimen the superior facet is smaller than the inferior, the measurements of the facets (in mm.) being—superior facet: length 45, height 34; inferior facet: length 45, height 38. The lateral surface between the base of the neural arch and the superior rib facet is quite smooth, with no suggestion of a ridge.

The anterior articular surface is concave with a poorly developed mamilla at the centre; the outline of the centrum is circular with a well-marked peripheral groove, a feature noted by Phillips. The posterior articular surface is also concave and somewhat circular in outline, with its margin bevelled along the ventral edge and also between the base of the neural arch and the region of the rib facets.

The anterior and posterior margins of the ventral surface of the centrum are somewhat roughened; there is no evidence of a ventral keel, but there is a depression on each side of the ventral surface near the lower margins of the inferior rib facets, and the surface is slightly convex between the facets.

Description of Associated Skeleton from Stretham

The Stretham specimen is one of the most important Pliosaur skeletons to have come out of the Kimeridge Clay. Of the cranial skeleton only teeth and a few jaw fragments are known, but most of the post-cranial skeleton can be described.

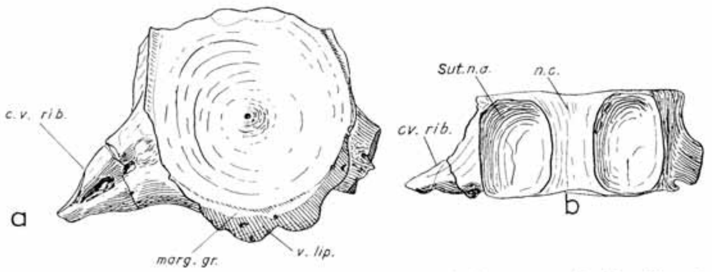
Teeth. The teeth are similar to those of *P. brachydeirus* Owen in that they are trihedral in cross-section; the enamel of the flat outer surface is smooth but the remainder of the crown is characterized by longitudinal ridges (see Pl. 9, figs. 3, 3*a*, 3*b*). This type of tooth is common to all Pliosaurs of Kimeridgian age and thus cannot be used to distinguish the different species of that age from one another (Tarlo 1958*a*).

VERTEBRAL COLUMN. Nineteen vertebrae are known from the Stretham Pliosaur. From a diagnostic point of view the most important are the anterior cervical vertebrae in which two sets of characters can be recognized: those which remain constant throughout the neck and may therefore be of diagnostic value, and those which change progressively down the neck and thus enable the relative position of the vertebrae to be established. Also of interest are the caudal vertebrae which do not bear chevron bone facets on their ventral surfaces as is the case in other reptiles.

Anterior cervical vertebrae. From the anterior part of the neck four vertebral centra are known. Their measurements are given (in mm.) in the table below:

	Length	*Width*	*Height*
J. 35990*xx* (text-fig. 1, Pl. 8, figs. 3, 3*a*) .	64	132	136
J. 35990*yy* (Pl. 8, fig. 5) . . .	64	136	132
J. 35990*A* (text-fig. 2*a*)	65	134	134
J. 35990*zz* (text-fig. 2*b*, Pl. 8, figs. 2, 2*a*) .	67	144	138

As can be seen, the length of each vertebra is less than half its width (or height). There are always double rib facets on the lateral surface of the centrum, and this feature together with the shortening of the centrum is characteristic of all Pliosaurs. There are several other characters which the four vertebrae have in common. The ventral surface is flat with no suggestion of the development of a ventral keel; the lateral surface of the centrum between the superior rib facet and the neural arch is smooth with no indication of a ridge, and in the centre of each articular surface a small mamilla is found punctured by a nutritive foramen. The constancy of these characters means that they can be used to compare this specimen with others.



TEXT-FIG. 1. *Stretosaurus macromerus* (Phillips), anterior cervical centrum. Sedgk. Mus. J. 35990*xx*. × ¼. *a*, Anterior view. *b*, Dorsal view. *cv. rib*, cervical rib; *marg. gr.*, marginal groove; *n.c.*, floor of neural canal; *Sut. n.a.*, suture of neural arch; *v. lip*, ventral lip.

The relative position of the cervical vertebrae in the neck can be ascertained in two ways: (i) by the progressive increase in the length of the vertebrae towards the back of the neck, where the rib articulation moves up from the centrum on to the neural arch, and the ribs become single headed, and (ii) by the progressive changes in the proportions of the rib facets down the neck. The latter changes are indicated by the measurements given below (in mm.).

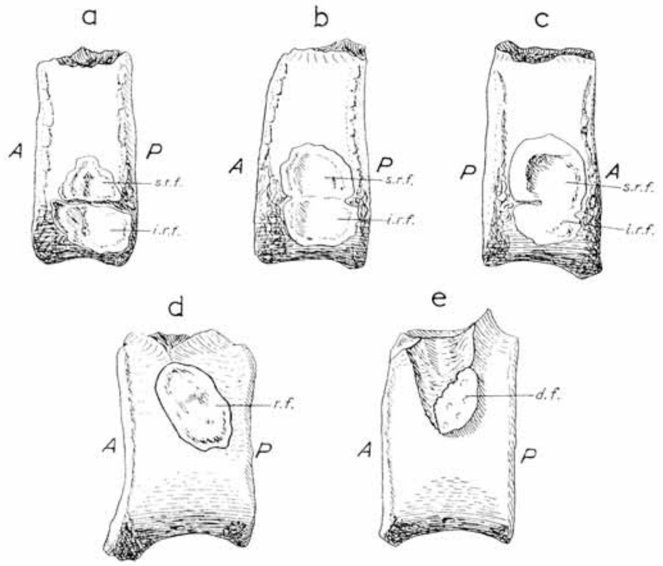
	Superior facet		*Inferior facet*	
	Length	*Height*	*Length*	*Height*
J. 35990*xx*	27	25	33	26
J. 35990*yy*	36	24	48	39
J. 35990*A*	40	34	51	36
J. 35990*zz*	47	37	49	33

The superior rib facet also changes its shape down the neck. At first it is triangular in outline, but by the time the fourth of the known centra is reached it has become oval, again confirming the order in which the vertebrae are arranged.

Once the centra are placed in order it is possible to recognize a further series of minor changes progressing down the neck. These will be given in detail, as they are relevant to the specific identification of the Stretham Pliosaur.

On the ventral margin of the anterior articular surface, a projection is developed, termed the ventral lip. This is most pronounced in the first of the four known centra, becoming reduced in the later vertebrae, so that in the last one, the only indication of it is a small roughened area on the anterior part of the ventral margin of the centrum.

There is also a well-marked marginal groove on the anterior articular surface. In the first three centra this is developed only in the ventral part, but in the fourth it runs round the periphery from the base of one neural arch to the other, and is termed a peripheral groove. The posterior articular surface of the first three vertebrae has bevelled margins; these are present on each side from the base of the neural arch to the superior rib facet, and also ventrally between the inferior rib facets. This ventral bevelling tends to produce a slight ventral lip on the posterior margin directed forwards, but both this and the bevelling disappear in the last of the four centra.



TEXT-FIG. 2. *Stretosaurus macromerus*, vertebral centra in lateral view showing progressive changes in proportions of rib facets; $\times \frac{1}{4}$. *a*, Left side, anterior cervical centrum J. 35990*A*. *b*, Left side, anterior cervical centrum J. 35990*zz*. *c*, Right side, posterior cervical centrum J. 35990*R*. *d*, Left side, posterior cervical centrum J. 35990*C*. *e*, Left side, pectoral centrum J. 35990*E*. *A*, anterior; *P*, posterior; *d.f.*, demi-facet; *i.r.f.*, inferior rib facet; *r.f.*, rib facet; *s.r.f.*, superior rib facet.

As shown from the detailed description of the lectotype centrum, it has all the constant characters outlined above. Like the fourth known vertebra of the Stretham animal it has a peripheral groove but no ventral lip and its superior rib facets are oval, and like the third the margin of its posterior articular surface is bevelled in three places and the superior rib facet is slightly smaller than the inferior facet. It thus would fit exactly into a similar series of cervical vertebrae. Agreement over such a large range of characters means that the Stretham skeleton can be placed without any hesitation into the same species as the lectotype centrum.

Posterior cervical vertebrae. Three centra are known from the posterior part of the neck. All three centra have a characteristic large rounded boss in the centre of their articular surfaces, and compared with the anterior cervical vertebrae the first two specimens show a marked reduction of the inferior rib facets, as can be seen from the following measurements (in mm.).

	Superior facet		*Inferior facet*	
	Width	*Height*	*Width*	*Height*
J. 35990*R* . .	50	43	45	29
J. 35990*D* . .	59	56	40	24

The length of the three vertebrae is proportionately greater than that of the anterior cervicals, being half or just over half the width (or height) as indicated below (in mm.).

. .	*Length*	*Width*	*Height*
J. 35990*R* (text-fig. 2*c*, Pl. 8, fig. 4) .	75	150	150
J. 35990*D*	81	155	153
J. 35990*C* (text-fig. 2*d*) . . .	84	168	145

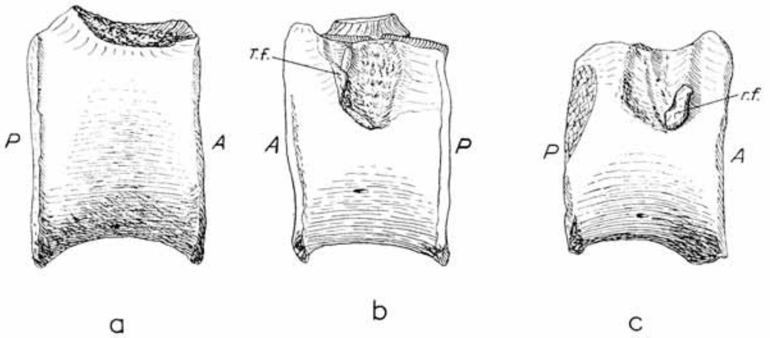
The third cervical vertebra is from the most posterior part of the neck and by the time it is reached the inferior rib facet has completely disappeared and only a single facet remains, which is borne on a pedicle situated on the upper half of the lateral surface of the centrum. A sharp ridge is developed between the dorsal edge of this pedicle and the base of the neural arch, the suture line of which extends laterally towards the rib facet.

Pectoral vertebrae. In the Stretham skeleton only one pectoral vertebra is known (J. 35990*E*, text-fig. 2*e*), measuring: length 91 mm., width 170 mm., height 150 mm. This centrum is very similar to that of the third posterior cervical vertebra just considered. The single rib facet is borne on a pedicle, but the suture line of the neural arch in this specimen extends laterally along the pedicle to reach the articular surface of the facet, the lower half only of which is present on the centrum. The upper half of the rib facet must have been borne on the neural arch, and thus this vertebra represents a stage where the rib articulates equally with the centrum and the neural arch.

Dorsal vertebrae. So far, seven dorsal centra belonging to the Stretham animal have been found. Their measurements (in mm.) are:

	Length	*Width*	*Height*
J. 35990*S* . . .	100	142	149
J. 35990*T* . . .	107	156	157
J. 35990*U* . . .	104	158	162
J. 35990*K* (text-fig. 3*a*) .	112	150	178
J. 35990*J* . . .	117	150	179
J. 35990*V* . . .	121	143	187
J. 35990*W* . . .	114	171	184

The isolated neural arch of a dorsal vertebra is also known (J. 35990*ww*). Unfortunately the dorsal vertebrae of Pliosaurs exhibit no diagnostic characters, and they can thus only be identified when found in association with other parts of the skeleton. Previously all large-sized dorsal vertebrae were considered to belong to *P. macromerus*, but with the knowledge of the existence of two different giant Pliosaurs in Kimeridgian times, the identification of isolated dorsal vertebrae becomes impossible.



TEXT-FIG. 3. *Stretosaurus macromerus*, vertebral centra in lateral view. *a*, Right side, dorsal centrum J. 35990*K*. *b*, Left side, caudal centrum J. 35990*F*. *c*, Right side, caudal centrum J. 35990*G*. × ¼. *A*, anterior; *P*, posterior; *r.f.*, rib facet.

Caudal vertebrae. Four caudal centra are known from the Stretham skeleton, and unlike those of other Pliosaurs they do not have chevron bone facets on their ventral surfaces. Normally only the two sacral vertebrae are without chevron bone facets; their absence in the caudal vertebrae is most unusual and it is difficult to find an explanation of this fact.

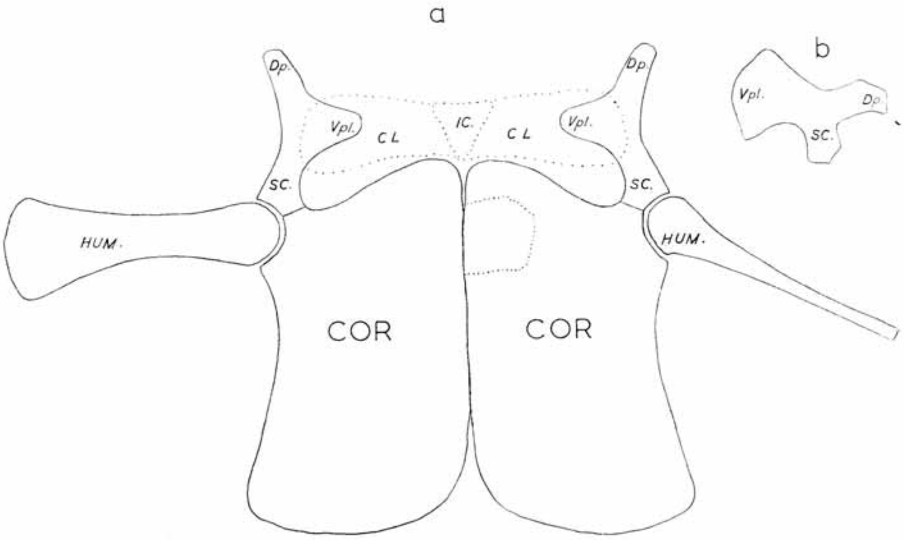
The measurements in mm. of the caudal vertebrae are as follows:

	Length	*Width*	*Height*
J. 35990*H* . . .	106	149	146
J. 35990*I* . . .	102	135	143
J. 35990*G* (text-fig. 3*c*) .	99	145	150
J. 35990*F* (text-fig. 3*b*) .	106	144	146

The caudal ribs are single headed, but the rib facets in these specimens have been somewhat crushed.

In the University Museum, Oxford, there is a series of caudal vertebrae from Cumnor, Berkshire, labelled *P. macromerus* in Phillips's handwriting; these belong to a giant Pliosaur, and as none of them have chevron bone facets developed on their posterior or anterior ventral margins I would include them in *S. macromerus*. However, the caudal vertebra from St. Giles', Oxford, which Phillips figured (1871, p. 356, fig. 151) cannot be included in *S. macromerus* as it bears four well-marked chevron bone facets, but it can be included in *Pliosaurus brachydeirus* Owen which has similar caudal vertebrae.

PECTORAL GIRDLE AND FORELIMB. The scapula is unusual since its dorsal process is produced anteriorly instead of laterally, and the ventral plate is not expanded towards the mid-line. The anterior part of the girdle thus appears extremely weak, but as the symphysial portion of the coracoids is greatly thickened and any appreciable movement of the forelimbs demands a strong pectoral girdle, it appears necessary to postulate the presence of a clavicular arch.



TEXT-FIG. 4. *a*, *Stretosaurus macromerus*. Reconstruction of pectoral girdle and humeri, $\times \frac{1}{20}$. Dorsal view, symphysial portion of right coracoid (J. 35990*X*) indicated, right humerus in posterior view. *b*, Scapula of *Pliosaurus brachydeirus* (B.M. (N.H.) R. 287) for comparison, dorsal view, $\times \frac{1}{20}$. *CL.*, Clavicle; *COR*, Coracoid; *Dp.*, Dorsal process of scapula; *HUM.*, Humerus; *IC.*, Interclavicle; *SC.*, Scapula; *Vpl.*, Ventral plate of scapula. Dotted lines indicate possible position of clavicular arch.

Scapula. The scapula has been the subject of an earlier paper (Tarlo 1958*b*). Briefly it can be described as a triradiate bone in which the whole surface is in one plane, no part being set off at an angle. The glenoid ramus is thickened and elongated, the ventral plate is not greatly expanded, and the dorsal process is produced anteriorly and does not project laterally. By the anterior production of the dorsal process of the scapula, the preglenoid length of the whole pectoral girdle is greatly increased.

A pectoral girdle containing the type of scapula described above is so different from that of any previously known Pliosaur that it clearly warrants at least generic distinction from *Pliosaurus*.

Coracoid. Unfortunately the coracoids among other bones, were broken up and pieces were removed from the site despite the efforts of the employees of the River Board to keep the skeleton intact. The actual outline of the coracoids will thus never be known with any certainty, but an attempt at reconstruction based on the photographs of the skeleton *in situ* is given in text-fig. 4.

The symphysial portion of the right coracoid is preserved. The symphysial surface itself is roughly semicircular in outline with a diameter of 225 mm. and a radius of 110 mm. Towards the glenoid cavity the bone thins out a little so that 200 mm. from the symphysis it is only 75 mm. thick. Apart from this thickened area between the glenoid cavity and the symphysis the coracoid is a very thin sheet of bone, being in parts no more than 5–10 mm. thick.

As Watson (1924) pointed out, the muscles moving the forelimbs of a Pliosaur tend to force the heads of the humeri into the glenoid cavities, thus adding to the compression of the coracoids between the cavities. Consequently, to resist this force a marked thickening of the coracoids in this region is required. The symphysial portion of these bones is generally quite thick in Upper Jurassic Pliosaurs, but the transverse section of the Stretham symphysis, with its semicircular outline, shows a proportionately greater degree of thickening. In such a large animal as the Stretham Pliosaur the compression between the glenoid cavities must have been considerable, thus explaining the need for such a strong symphysial region.

Forelimb. The complete humerus is visible in the photograph of the skeleton *in situ* (Pl. 7, fig. 2) and although it too was broken into pieces, most of these have now been collected. The head of the bone is remarkably large compared with its narrow shaft. In this it differs from the femur which, as is shown in the following table, has more normal proportions.

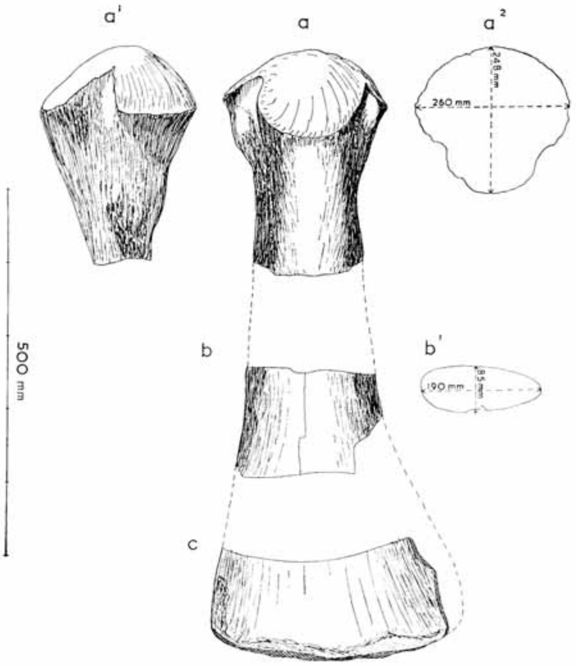
	Humerus (text-fig. 5)		*Femur (Pl. 9, fig. 1)*	
	Width mm.	*Height (thickness) mm.*	*Width mm.*	*Height (thickness) mm.*
Head	260	248	260	190
One-third-way down shaft . .	188	124	185	166
Half-way down shaft . . .	190	85	191	128
Distal end	308+	70	360	110
Total length	840 mm.		960 mm.	

The head of the humerus is more massive than that of the femur although the humerus is as a whole a smaller bone with a very slender shaft. The articular surface of its head is divided into two facets—a small dorsal facet and a large ventral one. The shaft which is expanded distally is greatly compressed dorso-ventrally.

The only other part of the forelimb that is known is the radius which is short. According to Welles (1943) short epipodials are characteristic of the Cretaceous Polycotylids and can be used to separate them from the Jurassic Pliosaurids. However, the change from long to short epipodials took place within Jurassic times, all epipodials of Oxfordian age being long and all those of Kimeridgian age, short. The length of the epipodials can therefore no longer be used as a family distinction.

Clavicular arch. An examination of the way in which the forelimb could function with the type of pectoral girdle described above, raises certain problems. In the giant *Kronosaurus* the ventral plates of the scapulae are greatly expanded and even if they did not actually meet in the mid-line there would be little difficulty in effecting some connexion which would bind them firmly together. In *Stretosaurus*, on the other hand, the ventral plates are not expanded and they could in no circumstances have met in the mid-line.

Any forward or vertical movement of the forelimb would have tended to pull the scapulae away from the mid-line, and it is therefore necessary to postulate some way in which this could have been prevented.



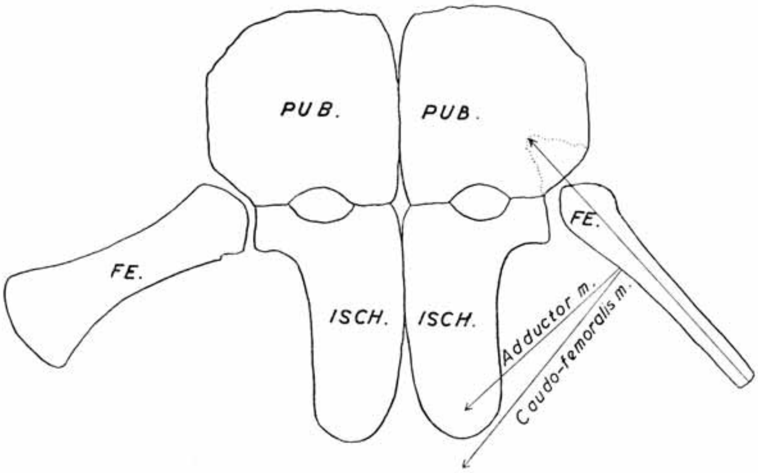
TEXT-FIG. 5. *Stretosaurus macromerus*, left humerus. *a*–*a*², Head J. 35990*Y*; *a*, dorsal view; *a*¹, lateral view; *a*², transverse section. *b*–*b*¹, Mid-part of shaft J. 35990*Z*; *b*, dorsal view; *b*¹, transverse section; *c*, Distal end J. 35990*AA*, dorsal view. ×⅕.

There is no evidence of cartilage having been present on the medial edge of the ventral plates of the scapulae, thus it would appear that no cartilaginous union of the two bones existed. What seems likely is that a clavicular arch was present to unite the two scapulae, and I shall now review the evidence for this conjecture.

In *Sthenarosaurus dawkinsi* Watson from the Upper Lias there is a triangular interclavicle in the mid-line, which is firmly attached by suture to the clavicles on either side of it. In section each clavicle somewhat resembles a boomerang, one arm of which points dorsally and covers most of the dorsal surface of the ventral plate of the scapula on which it lies. In this way, a clavicular arch binds the two scapulae together, rendering the anterior part of the pectoral girdle sufficiently firm to withstand the stresses imposed by movement of the forelimb.

In the other Plesiosaurians in which a clavicular arch is known, the clavicle also lies on the dorsal surface of the ventral plate of the scapula, and the roughening on the dorsal surface of the ventral plate of the Stretham scapula tends to suggest that such a clavicular arch may have been present.

No complete clavicular arch has as yet been found in either Oxfordian or Kimeridgian Pliosaurs, but in *Peloneustes philarchus* (Seeley) R. 2442 in the British Museum (Nat. Hist.) a small triangular interclavicle is known associated with two scapulae. The lateral



TEXT-FIG. 6. *Stretosaurus macromerus*, reconstruction of pelvic girdle and femora, $\times \frac{1}{24}$ approx. Dorsal view, acetabular portion of right pubis (J. 35990*DD–EE*) indicated; right femur in posterior view. *FE.*, Femur; *ISCH.*, Ischium; *PUB.*, Pubis. See text for explanation of swimming movement.

borders of this interclavicle are crenulated and bevelled, indicating a bone-to-bone junction. The associated scapulae bear evidence of cartilage on their medial edges, and thus it appears most unlikely that they articulated directly with the interclavicle. Indeed the outlines of the interclavicle and the ventral plates of the scapulae are such that no satisfactory junction can be envisaged between them. The scapulae do not extend sufficiently towards the mid-line for the interclavicle to have lain on top of their ventral plates and so to have been the sole element binding them together. It is evident that a further bony element, a clavicle, must have been present on either side to complete the girdle, which in fact is what Andrews (1913) suggested.

It seems reasonable to assume, therefore, that a clavicular arch somewhat similar to that found in *Sthenarosaurus* was present not only in *Peloneustes* but also in the other Upper Jurassic Pliosaurs. Both the roughening of the dorsal surface of the ventral plate of the Stretham scapula in a position where a clavicle would be attached, and the fact that, as Watson pointed out, the anterior part of the girdle must be firmly and rigidly united in the mid-line to overcome the great stress developed in this region, strongly suggest that a similar arch was present in *Stretosaurus*.

PELVIC GIRDLE AND HIND LIMBS. Apart from the acetabular portion of the pubis the pelvic girdle is known only from photographs taken of the skeleton *in situ*. The elongated ischium and the strengthened anterior part of the acetabulum provide good evidence for presuming that the main propulsive stroke was a backward adduction of the hind limbs.

Pubis. An indication of the relative size of the pubis is given in the photograph (Pl. 7, fig. 2) and as can be seen, this bone is broken into numerous fragments. I have attempted a diagrammatic reconstruction of it in text-fig. 6, but this can only give a very rough approximation of the outline of the actual bone. The acetabular portion, however, has been preserved and the shape of this fragment is indicated in the text-figure. The bone is a thin sheet but is thickened in the region of the acetabulum, the articular surface measuring 310 by 97 mm.

The force created by the backward movement of the femur is resolved into one at right angles to the bone, and a thrust along the axis of the bone which forces the head of the femur into the anterior part of the acetabulum. The strengthening of this region of the pubis is clearly due to the necessity to resist this thrust.

Ischium. The ischium is known only from photographs (Pl. 7, fig. 1, 1*b*). Unfortunately no fragment of this bone has been saved, but its relative size and outline can be ascertained (text-fig. 6).

As in other Upper Jurassic Pliosaurs, the ischium is greatly elongated posteriorly, giving the adductor muscles an increased area of attachment and a more posterior situation. This greatly increases their power, and as together with the caudo-femoralis

EXPLANATION OF PLATE 7

Figs. 1–2. *Stretosaurus macromerus* (Phillips), parts of Stretham Pliosaur *in situ*. 1, 1*a*, Left ischium, photographed by Mr. W. Martin Lane of Ely, scale in fig. 1 given by Mr. W. W. Wolfe. 2, Vertical view of post-cranial skeleton photographed by Mr. W. B. Harland, scale given by spades. *Cor.*, coracoid; *Fe.*, femur; *Hum.*, humerus; *Sc.*, scapula; *Pub.*, pubis.

EXPLANATION OF PLATE 8

Figs. 1–5. *S. macromerus*, Kimeridge Clay. 1, 1*a*, 1*b*. J. 10441, Univ. Mus., Oxford, anterior cervical centrum, lectotype, Shotover railway, Oxfordshire. 1, Anterior view; 1*a*, ventral view; 1*b*, posterior view (apparent shadow in figs. 1, 1*b*, due to discoloration). 2–5, J. 35990, Sedgk. Mus., Cambridge, cervical centra, Stretham, near Ely, Cambridgeshire. 2, 2*a*, Anterior cervical centrum, J. 35990*zz*; 2, anterior view; 2*a*, posterior view. 3, 3*a*, Anterior cervical centrum, J. 35990*xx*; 3, posterior view (lighting from bottom right); 3*a*, ventral view. 4, Posterior cervical centrum, J. 35990*R*, anterior view. 5, Anterior cervical centrum, J. 35990*yy*, anterior view. Photographs by Mr. W. Brackenbury.

EXPLANATION OF PLATE 9

Figs. 1–4. *S. macromerus*, Kimeridge Clay. 1–3, J. 35990, Sedgk. Mus., Cambridge, from Stretham, near Ely. 1, left hind limb, J. 35990*a–z*, *aa–dd*, dorsal view, photographed by Mr. A. Barlow. 2, fragment of mandible showing unerupted successional tooth, J. 35990*P*, internal view. 3, 3*a*, 3*b*, tooth, J. 35990*O*; 3, internal view; 3*a*, lateral view; 3*b*, external view. Figs. 2–3 photographed by Mr. W. Brackenbury. 4. J. 10454, Univ. Mus., Oxford, from Cumnor, Berkshire, symphysis of mandible in dorsal view, photographed by Mr. A. Veenstra.

muscles they draw the hind limbs backwards and in towards the body, a very strong propulsive force is produced which drives the animal forward.

Hind Limb. The articulated left hind limb is about 2,000 mm. in length and the femur alone measures 960 mm. Further measurements of the femur are given on p. 47 above where its proportions are contrasted with those of the humerus. The articular surface of the head of the femur is divided into two sub-equal facets—one dorsal and one ventral facet, the dorsal being slightly smaller than the ventral. The shaft and expanded distal end are dorso-ventrally compressed and as the origin of the adductor muscles is in the centre of the proximal half of the ventral surface, these muscles will pull the limb backwards into the body so that the maximum surface is presented to the water. The epipodials are both short, and the tarsals and metatarsals are all well preserved, their shapes being clearly indicated in Pl. 9, fig. 1. The intermedium is of some interest as it shows a pathological condition.

Swimming movement. The hind limbs are larger than the forelimbs and the femora are more stoutly constructed than the humeri. As Romer (1956) remarked, this suggests that the main propulsive force was from the hind limbs. The strengthening of the anterior part of the acetabulum, the elongation of the ischium, and the area of origin of the adductor muscles on the femur all indicate that the propulsive force was from the backward adduction of the hind limb.

This stroke would seem to have been initiated from a position in which the limb was directed postero-laterally with the plane of the limb held vertically (see text-fig. 6). In this position the insertions of the adductor and caudo-femoralis muscles on the femur would be almost at right angles to the shaft, and thus their mechanical efficiency would be at its maximum. Besides this, the force into the acetabulum would be directed to the thickened part of the pubis.

Description of mandible from Cumnor

In the centre aisle of the University Museum, Oxford, there is on exhibition a giant mandible (J. 10454) belonging to a Pliosaur from the Kimeridge Clay of Cumnor, Berkshire. It was first noted by Prestwich (1888, p. 227) and seems to have been acquired by the Museum some time between 1880 and 1888. In 1933 Mr. H. J. Hambidge completed the long and arduous task of renovating and reconstructing this specimen which he had first known in 1907. Professor W. J. Sollas had intended to describe the mandible in 1936, but unfortunately he died the same year. Since that time, this remarkable mandible has remained unidentified and undescribed and no recognition has been given to the skilful work of Mr. Hambidge. The following is an attempt to remedy this.

The length of the mandible as exhibited is 2,875 mm. Recently, however, the posterior part of the left ramus has come to light and it clearly shows that, with the angular and surangular bones restored, the total length would have been more than 3,000 mm. Without doubt it belongs to the largest Pliosaur ever recorded, somewhat exceeding the size of the Cretaceous *Kronosaurus* (White 1935; Romer and Lewis 1959).

The specimen is somewhat incomplete since the splenial bones are missing. In the region of the coronoids the rami are very deep and thin, but this is probably a post mortem effect due to lateral crushing. On the left side twenty-five alveoli are present in the dentary, while in the right ramus only twenty are preserved, the additional alveoli having been reconstructed. The small size of the 24th alveolus suggests that there were few teeth beyond it.

The symphysis is short, containing only six teeth on each side, its length being 470 mm. and its maximum width (at the 5th socket) 280 mm. The teeth in the expanded symphysial region were large and caniniform although the first pair were comparatively small. There is a sudden change in size from the 6th to the 7th sockets and thereafter the alveoli gradually diminish in size as is indicated by the following measurements:

	alveolus	diam. (mm.)
Right dentary (Pl. 9, fig. 4) .	1st	33
	5th	75
	7th	35
Left dentary .	24th	25

The expansion of the symphysial region is due to the presence of very large anterior teeth, for example the width of the right ramus at the 5th alveolus is 145 mm. whereas farther back (at the 10th socket) the ramus is only 75 mm. wide.

In the number of teeth and the short symphysis with its six alveoli, this specimen resembles that of the mandible B.M. (N.H.) 39362 described by Owen (1869), and as I have already shown (1959) in the discussion of *Pliosaurus brachyspondylus*, it seems reasonable to assign this type of mandible from the Kimeridge Clay to *Stretosaurus macromerus*. In the Oxfordian, the same type of mandible is also found in *P. ferox* and as previously mentioned (Tarlo 1958*a*) it seems probable that *S. macromerus* represents a continuation of the *ferox* lineage into Kimeridgian times, but with a highly specialized pectoral girdle.

DISCUSSION

Three Pliosaur skeletons of any importance are known from the Kimeridge Clay. These are the holotype of *Pliosaurus brachydeirus* Owen and the associated skeletons of *P. brachyspondylus* (Owen) and *Stretosaurus macromerus* (Phillips).

Teeth, propodials, and epipodials are known, but these have no distinguishing features. All the teeth are trihedral in cross-section; all the epipodials are short, and such differences as are present in the propodials may well be due to the relative age (and consequently size) of the individual (see Tarlo 1958*a*).

In *P. brachydeirus* the vertebral column and mandible are associated; in *S. macromerus* the scapula is known in association with the vertebral column, but *P. brachyspondylus* has both mandible and scapula associated with the axial skeleton (Tarlo 1959).

Whereas mandibles and scapulae can be used to distinguish the genera, the anterior cervical vertebrae are the only skeletal elements which are of use when comparing species. These can readily be distinguished on the characters of the ventral surface of the centra, for in *P. brachydeirus* a ventral keel is present, while in *S. macromerus* such a keel is absent. (N.B. the anterior cervical vertebrae of *P. brachyspondylus* are also without a keel, but these are easily distinguished since they possess a characteristic rugosity on the anterior and posterior margins of their ventral surface.)

All the anterior cervical vertebrae of giant size that are known from the Kimeridge Clay fall into two groups on the character of the keel. This suggests that two giant

Pliosaur species must have inhabited the Kimeridgian seas. However, it would be unwise to base such a conclusion on the evidence of cervical vertebrae alone.

Fortunately, further evidence is available from the caudal region, as here the two species can again be recognized on the character of the ventral surface of the centra. In *P. brachydeirus* chevron bone facets are present, while in *S. macromerus* these are absent. Again, there are isolated giant-sized caudal vertebrae known of both types.

Although no mandible is known from the Stretham skeleton and no scapula from *P. brachydeirus* and thus no direct comparison can be made between the two animals in these respects, the associated skeleton of *P. brachyspondylus* has shown that the isolated scapula of a giant Kimeridgian Pliosaur (R. 287) housed in the British Museum (Nat. Hist.) (text-fig. 4*b*) can be placed in the genus *Pliosaurus*. This isolated scapula is expanded medially into a broad flat ventral plate, and its dorsal process projects laterally. It thus differs greatly from the scapula of *Stretosaurus* in which the ventral plate is not greatly expanded and the dorsal process is produced anteriorly. In the present state of knowledge it seems reasonable to assign the isolated scapula R. 287 to a giant individual of *P. brachydeirus*.

Two isolated giant mandibles (39362 in the British Museum (Nat. Hist.) described by Owen (1869), and J. 10454 in the University Museum, Oxford) are known from the Kimeridge Clay. They are both very different from the mandible of *P. brachydeirus*, these mandibles having a short symphysis containing five to six large caniniform teeth in contrast to the symphysis of *P. brachydeirus* which bears ten to twelve teeth, the anterior five to six only being large and caniniform. These two forms of mandible are present in both Oxfordian and Kimeridgian times, and on this basis two possible phylogenetic lineages have been suggested (Tarlo 1958*a*). For the purpose of the present study, however, it is sufficient to establish the existence of giant mandibles different from those of *P. brachydeirus* and I therefore suggest that the two mandibles 39362 and J. 10454 be assigned to *S. macromerus*.

The remains of giant Pliosaurs from the Kimeridge Clay thus clearly fall into two groups which can be recognized on the characters of the mandibles, scapulae, and vertebral columns. Previously all giant-sized Pliosaur remains were included in *P. macromerus* on the basis of size alone but this procedure is now shown to be incorrect, since a detailed examination of these remains has demonstrated the existence of two different Pliosaur genera represented by the species *P. brachydeirus* and *S. macromerus*.

Acknowledgements. I should like to thank Professor D. M. S. Watson and Dr. W. E. Swinton for their helpful criticism of the manuscript, and Dr. P. L. Robinson for valuable discussions. I am pleased to record the generous assistance I have received from Mr. A. G. Brighton and Dr. C. L. Forbes of the Sedgwick Museum, Cambridge; Mr. J. M. Edmonds and Mr. H. J. Hambidge of the University Museum, Oxford; and Dr. W. E. Swinton and Mr. B. H. Newman of the British Museum (Natural History). I should also like to thank Professor A. S. Romer for allowing me a preview of the forthcoming paper on *Kronosaurus*. My thanks are due to the D.S.I.R., as the work embodied in this paper was carried out during the tenure of a Research Studentship.

APPENDIX I

Dispersed Parts of the Stretham Pliosaur (Stretosaurus macromerus) *recovered in 1956*

In 1952, after some of the material from the Stretham skeleton had been collected by the Sedgwick Museum, Cambridge, the Great Ouse River Board allowed local schools and private collectors to have the remainder. However, in 1956 when the importance of this skeleton was realized, a considerable part of this dispersed material was recovered with the aid of the River Board itself and the local press (*Cambridgeshire Times*, 28 April 1956). I should like to record my particular indebtedness to Miss M. A. Arber, Mr. A. A. Blackmore, Mr. W. Chapman, Mr. M. E. Delanoy, and Mr. H. R. Halls for their assistance in the search for the missing parts of the Stretham Pliosaur.

The specimens recovered are as follows (names of donors in brackets): J. 35990*R*, posterior cervical centrum (Mr. J. Chapman, Ely); J. 35990*S*, dorsal centrum (Mr. M. E. Wicksteed, Wicken); J. 35990*T*, dorsal centrum (Mr. R. A. Taylor, Soham); J. 35990*U*, dorsal centrum (Dr. B. Tilly, Ely); J. 35990*V*, dorsal centrum (Mr. Blaney, Stretham); J. 35990*W*, dorsal centrum (Mrs. J. M. Shrubbs, Lode); J. 35990*X*, symphysial portion of right coracoid (G.O.R.B., Ely); J. 35990*Y*, head of left humerus (Mr. W. E. Doran, Cambridge); J. 35990*Z*, shaft of humerus (Mr. G. W. Dobson, Witchford); J. 35990*AA*, distal end of humerus (Miss W. Foy, Cambridge); J. 35990*BB*, radius (Miss E. M. B. Martin, Littleport); J. 35990*CC*, articular portion of girdle bone in four pieces (Mr. M. E. Delanoy, Ely); J. 35990*DD*, acetabular portion of pubis adjoining *EE* (Mr. R. H. Cory, Newmarket); J. 35990*EE*, acetabular portion of pubis adjoining *DD* (Mrs. G. C. Dimock, Wilburton); J. 35990*FF*, head of right femur (Mr. W. A. Stubbings, Cambridge); J. 35990*GG*, right tibia (Mr. A. W. Gothard, Wilburton). Also numerous fragments of phalanges, girdle bones, and ribs from: Mr. D. S. Allan (Driffield), Mr. M. E. Delanoy (Ely), Miss J. Elsdon (Stretham), Mr. A. Hammond (Prickwillow), Mr. A. Murfitt (Stretham), Misses J. and B. Barber (Stretham), Mr. C. Goodge (Stretham), Miss F. Stevens (Stretham), Mrs. F. P. Horne (Ely), and Mr. D. Robinson (Sutton).

APPENDIX 2

Material now assigned to Stretosaurus macromerus (*Phillips*)

University Museum, Oxford. J. 10441, lectotype vertebra, Shotover railway, Oxfordshire, figured Phillips 1871, fig. 148. J. 10442, 10443, anterior cervical vertebrae, Horspath, Oxfordshire, probably associated with lectotype. J. 10454, mandible, Cumnor, Berks., reconstructed by Mr. H. J. Hambidge, described in this paper. J. 10459, immature scapula, Shotover, figured Tarlo 1958*b*, pl. 36, figs. 3, 3*a*. J. 12499, 1–12, twelve caudal vertebrae, Cumnor, labelled '*P. macromerus*' in Phillips's handwriting.

Not J. 10437, 10438, 10439, listed Phillips 1871, p. 354, *a*, *b*, *c*, which are now provisionally referred to *P. brachydeirus* Owen. Not J. 10460, figured Phillips 1871, fig. 151, also now referred to *P. brachydeirus*.

Sedgwick Museum, Cambridge. J. 29560–2, anterior cervical vertebrae, listed Seeley 1869, p. 97 (84e. 1–3). J. 29570, posterior cervical vertebra, Cottenham, Cambs., listed Seeley 1869, p. 97 (84.f.1) and described p. 104 under *P. brachydeirus*. J. 30057, anterior cervical vertebra, Ely, collected 1893. J. 35990, associated skeleton described in the present paper. J. 46911, immature scapula, Ely, collected 1875, figured Tarlo 1958*b*, pl. 36, figs. 2, 2*a*.

British Museum (Natural History). 39362, mandible, Kimeridge Bay, figured Owen 1869, pp. 1–2. 46466*a*, (4)6466*a*, 46466?*a*, anterior cervical vertebrae, Foxhangers, near Devizes, listed Lydekker 1889, p. 135. R. 6, anterior cervical vertebra, from drift, Stanton, Bury St. Edmunds, listed Lydekker 1889, p. 135.

Not 24684, listed Lydekker 1889, p. 134, now referred to *P. brachydeirus*.

Manchester Museum. 3174, immature scapula, Coppock's Pit, Shotover. 3175, immature scapula, same locality, figured Tarlo 1958*b*, pl. 36, fig. 4.

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L. B. TARLO
Department of Zoology,
University College, London

Manuscript received 27 November 1958

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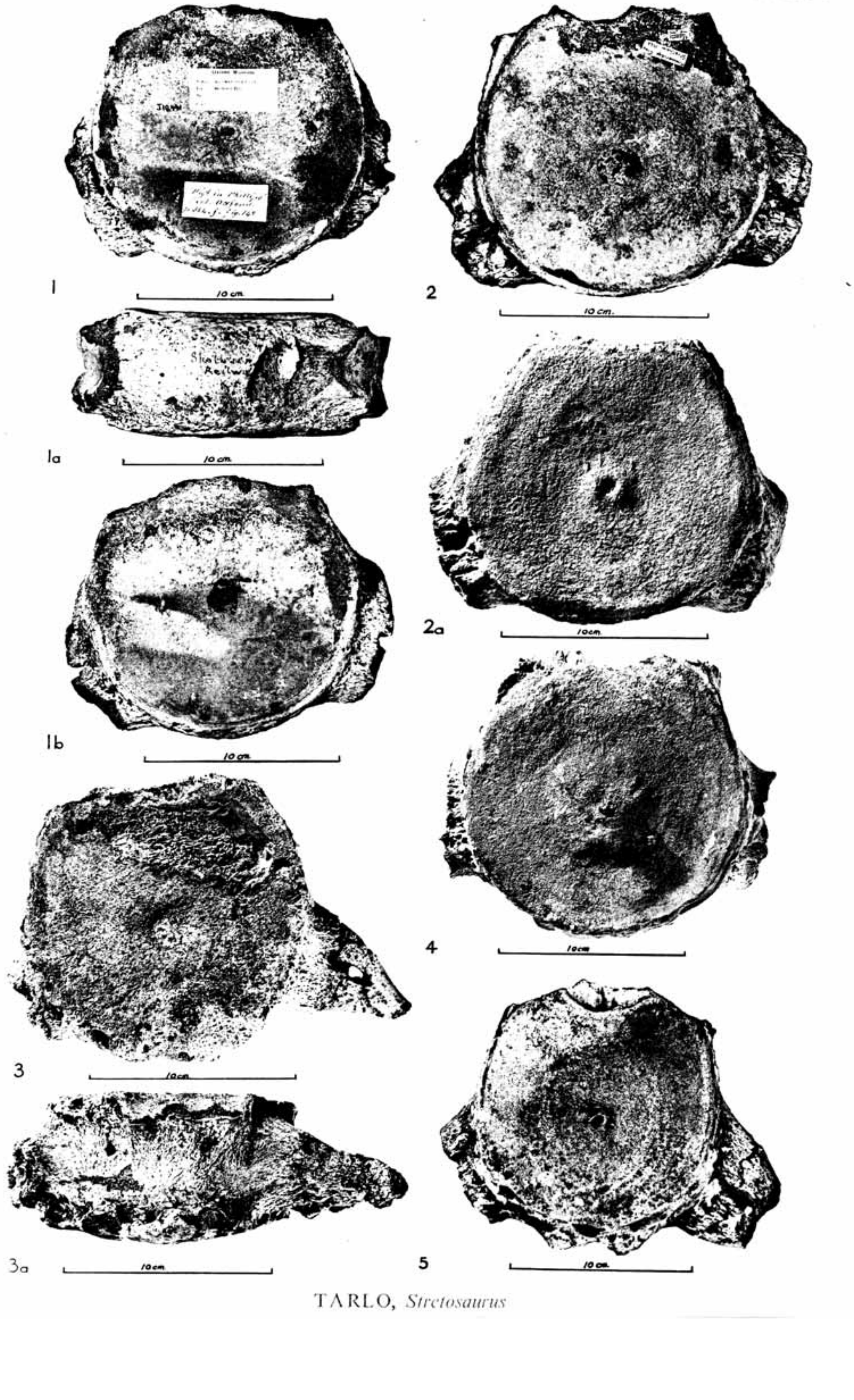
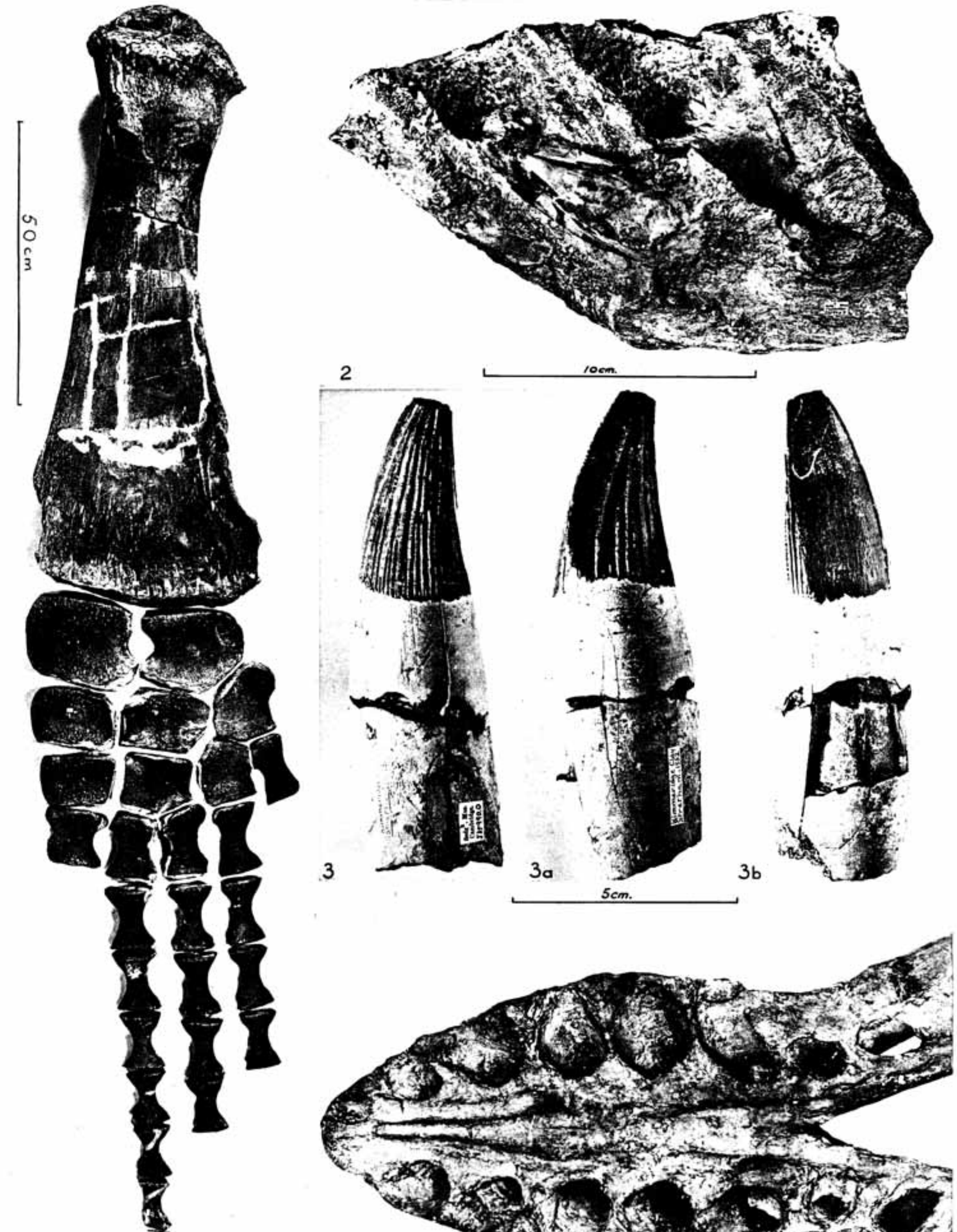
TARLO, *Stretosaurus macromerus* (Phillips), *in situ*



TARLO, *Stretosaurus*



TARLO, *Stretosaurus*