THE SCAPULA OF *PLIOSAURUS MACROMERUS* PHILLIPS

by L. B. TARLO

ABSTRACT. The scapula of *Pliosaurus macromerus* from the Kimeridge Clay (Jurassic) is described for the first time. It differs in shape from the scapulae of all other Plesiosaurians by the anterior production of its dorsal process. This change in shape and the consequent increase in the pre-glenoid length of the pectoral girdle confers important functional advantages which are outlined. The locomotion of Pliosaurs is briefly considered, and it is suggested that the main propulsive force was from the hind limbs.

IN 1952 the post-cranial skeleton of a giant specimen of *Pliosaurus macromerus* Phillips was uncovered at the village of Stretham, near Ely, during excavations of Kimeridge Clay by the Great Ouse River Board. It is housed in the Sedgwick Museum, Cambridge (J. 35990). This specimen is the only Kimeridgian Pliosaur in which limb girdles are known associated with the axial skeleton, and the scapula is of particular interest as it is quite unlike that of any other type of Pliosaur, or indeed of any other reptile.

Several isolated Pliosaur scapulae of Kimeridgian age have previously been recorded, but they are similar to scapulae known from the Oxford Clay. Lydekker (1889, p. 122) figured an immature scapula from the Kimeridge Clay and listed (p. 126) an adult one which I now figure (text-fig. 1*b*; Pl. 36, figs. 1, 1*a*).

This type of scapula is a triradiate bone with a strong thickened glenoid ramus which bears a facet for the articulation of the coracoid, and another which forms the anterior part of the glenoid cavity. Medially the scapula thins out and is expanded into a broad flat sheet termed the ventral plate. Laterally there is a further extension—the dorsal process which is approximately the same width as the glenoid ramus, but again forms a thin sheet. The dorsal process projects either laterally or posterolaterally and in ventral view is set off at an angle to the plane of the bone from a ridge which extends to the anterior point of the ventral plate from the glenoid cavity (Pl. 36, fig. 1*a*).

The three scapulae *Peloneustes philarchus* from the Oxfordian, *Pliosaurus sp.* from the Kimeridgian and *Kronosaurus queenlandicus* from the Lower Cretaceous (text-fig. 1) form a reasonable morphological series in which the ventral plate is progressively expanded and the dorsal process moves forward. The scapula of *Pliosaurus macromerus* (text-fig. 1*c*) obviously cannot be included in any such morphological series. It is again a triradiate bone, but it has quite a different shape from the scapulae I have mentioned previously. Again, one process is thickened and this I take to be the glenoid ramus, although unfortunately its end is crushed and it is not possible to recognize the two facets normally present. This time the surface of the bone is in one plane, no part of it being set off at an angle.

I consider that the narrow elongated projection, rather than the broad flange, must be the dorsal process, despite its position relative to the glenoid, i.e. produced anteriorly instead of laterally. This process could not have formed the ventral plate as it would have produced a very weak connexion in the mid-line, which is unlikely in an animal

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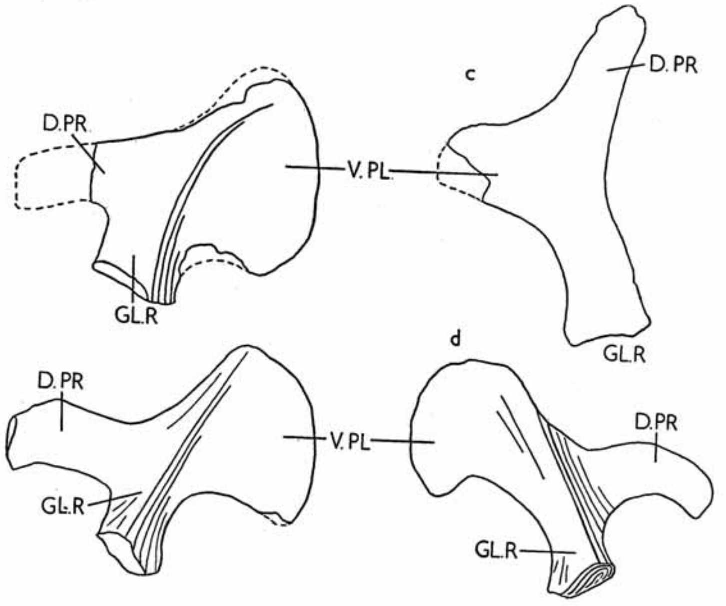
nearly 40 feet in length. This leaves the third process to be the ventral plate, although its expansion is less marked than, for example, in *Peloneustes philarchus*.

The dorsal process is increased in size, and by virtue of its elongation anteriorly, considerably increases the pre-glenoid length of the whole pectoral girdle (see text-fig. 2). Watson (1924) suggested that in Pliosaurs the dorsal process at no time moved forward,



TEXT-FIG. 1. Scapulae in ventral view. *a*, *Kronosaurus queenlandicus* Longman, right scapula, Lower Cretaceous. Mus. Comp. Zool. Harvard 1285. Figured by White 1940, fig. 11*a*. $\times\frac{1}{13}$. *b*, *Pliosaurus sp.*, right scapula, Kimeridgian. B.M. (N.H.) R. 287. Listed by Lydekker 1889, p. 126. $\times\frac{1}{10}$. *c*, *Pliosaurus macromerus* Phillips, left scapula, Kimeridgian. Sedgk. Mus. J. 35990. $\times\frac{1}{8}$. *d*, *Peloneustes philarchus* (Seeley), left scapula, Oxfordian. B.M. (N.H.) R. 3318. Figured by Andrews 1913, fig. 21. $\times\frac{1}{5}$. D. PR., dorsal process; GL. R., glenoid ramus; V. PL., ventral plate.

but here we have a striking case of its not only moving forward, but moving much farther forward than in any other Plesiosaurian.

Taking the girdle as a whole, the large flat coracoids would have met in the mid-line

EXPLANATION OF PLATE 36

Figs. 1. 1*a*. *Pliosaurus sp.*, right scapula, Kimeridge Clay, Shotover, near Oxford. 1, dorsal view. 1*a*, ventral view. Brit. Mus. (N.H.) R 287.

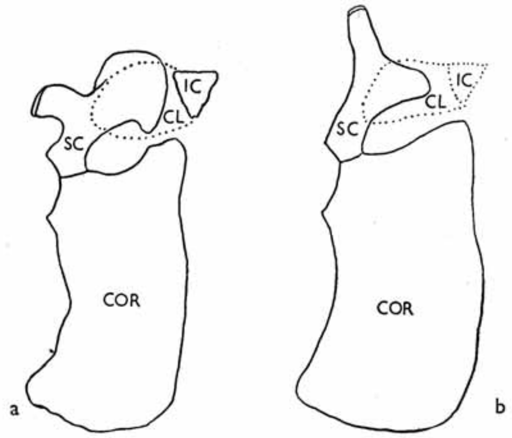
Figs. 2. 2*a*. *Pliosaurus macromerus* Phillips, left scapula, Kimeridge Clay, Ely. 2, ventral view. 2*a*, dorsal view. Sedgk. Mus. Cambridge J. 46. 911.

Figs. 3. 3*a*. *P. macromerus*, right scapula, Kimeridge Clay, Shotover. 3, dorsal view. 3*a*, ventral view. Univ. Mus. Oxford. J. 10. 459.

Fig. 4. *P. macromerus*, right scapula, Kimeridge Clay, Coppock's Pit, Shotover. Ventral view. Manchester Museum. 3175.

at an angle, as is indicated by the bevelling of their symphysial surfaces. This suggests that in the anterior part of the girdle the scapulae would also have been held at a similar angle. The ventral plates of the scapulae are not large enough to meet in the mid-line and on their medial edges there is no indication of a cartilaginous extension which might have joined them. My conjecture is that the ventral plates of the scapulae were firmly united by a clavicular arch consisting of an interclavicle and two clavicles, rather like that suggested for *Peloneustes philarchus* by Andrews (1913).

The existence of two distinct types of scapula and consequently two distinct types of pectoral girdle within the Kimeridgian Pliosaurs leads one to believe that there were at least two phylogenetic lineages present in Kimeridgian times. *Kronosaurus* from the Lower Cretaceous may represent the continuation of the more conservative type.



TEXT-FIG. 2. Pectoral girdles in dorsal view. *a*, *Peloneustes philarchus* (Seeley), $\times \frac{1}{9}$, from Andrews. *b*, *Pliosaurus macromerus* Phillips, $\times \frac{1}{18}$. CL., Clavicle; COR., Coracoid; IC., Interclavicle; SC., Scapula. Dotted lines indicate possible position of clavicular arch.

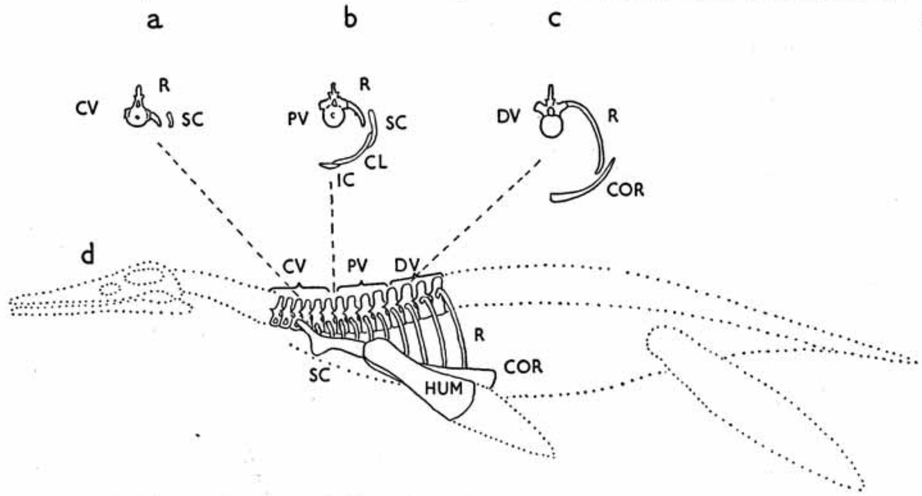
It is worth noting that the remarkable scapula from Stretham is not unique. Since seeing it I have recognized several similar scapulae. An extremely well-preserved left scapula of this type belonging to an immature animal is housed in the Sedgwick Museum, Cambridge (Pl. 36, figs. 2, 2*a*). This is from the Kimeridge Clay of Ely. An examination of this bone confirms that the thickened end of the Stretham scapula is indeed the glenoid ramus, as in this case articular facets for both coracoid and humerus are present.

The Oxford University Museum have an immature right scapula, the dorsal process of which has been broken off, but a comparison with the Ely specimen clearly establishes its identity (Pl. 36, figs. 3, 3*a*). In addition there are two specimens in the Manchester Museum—a right and a left scapula, the larger and more complete of which is shown in Pl. 36, fig. 4. This specimen is from the Kimeridge Clay of Coppock's Pit, Shotover.

These scapulae are isolated specimens, and thus it has not hitherto been possible to identify them. The discovery of the associated skeleton at Stretham in 1952 now allows them to be assigned provisionally to the species *Pliosaurus macromerus*.

As this unusual type of scapula has not previously been noted it is important to investigate the significance of its peculiar shape. In text-fig. 3 I have indicated the position of the bone in relation to the rest of the thorax, and have shown how the anterior production of its dorsal process means that the scapula extends well forward. The musculature of the pectoral girdle must therefore be examined to see in what way it has been affected by this change.

The Stretham scapula shows roughened areas which indicate the position of the insertions or origins of muscles. These are clearly visible in Pl. 37, figs. 1, 1*a*. Text-fig. 4 shows



TEXT-FIG. 3. Diagram showing probable position of scapula of Stretham Pliosaur in the body. *a*, transverse section through posterior part of neck and dorsal process of scapula. *b*, transverse section through anterior part of thorax and clavicular arch. *c*, transverse section through posterior part of thorax and coracoid. *d*, lateral view of thorax and pectoral girdle. CL., Clavicle; COR., Coracoid; HUM., Humerus; IC., Interclavicle; R., Rib; SC., Scapula; V., Vertebrae (CV., cervical; PV., pectoral; DV., dorsal).

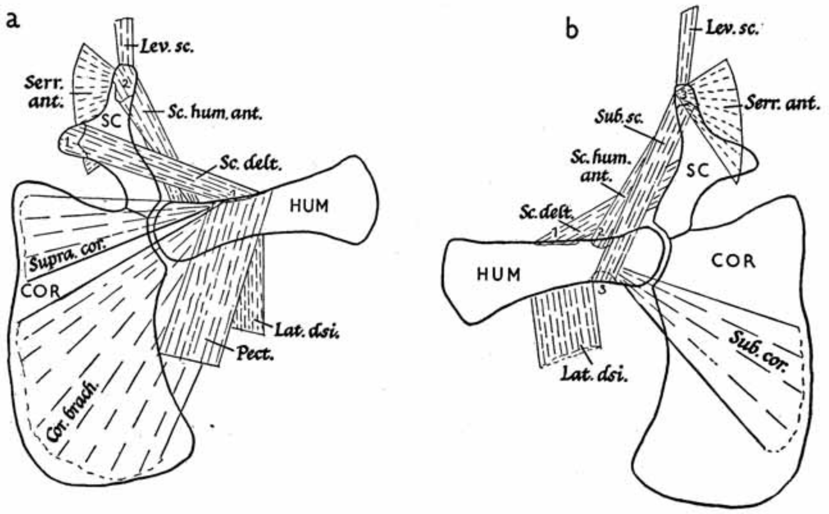
diagrammatically the important muscles of the pectoral girdle, but in this section I shall be concerned only with those related to the scapula.

On the ventral surface of the ventral plate of the scapula is a large roughened area for the origin of the scapular deltoid muscle, which is inserted on the anterior surface of the proximal end of the shaft of the humerus. At the end of a swimming stroke the anterior edge of the humerus faces downwards, and is then rotated into the horizontal plane by this muscle, which also draws the limb forward so that it offers the least resistance to the water.

The scapulohumeralis anterior muscle originates on the distal part of the ventral (external) surface of the dorsal process. It is inserted on the anterior edge of the dorsal surface of the proximal end of the humerus. This muscle also draws the humerus forwards, but at the same time lifts it and rotates its anterior edge upwards.

The origin of the subscapularis muscle is on the distal part of the dorsal (visceral) surface of the dorsal process, and its insertion is on the posterior part of the dorsal surface of the shaft of the humerus, behind the scapulohumeralis anterior. The action of this muscle is to draw the humerus forwards and lift it while rotating its anterior edge downwards.

These two muscles, the scapulohumeralis anterior and the subscapularis, act in concert and are thus able to determine at what angle the forelimb is held as it is drawn forwards. For example, if the subscapularis is contracted more than the scapulohumeralis anterior, the anterior edge of the forelimb is depressed and a backing stroke results. By



TEXT-FIG. 4. Diagrammatic reconstruction of pectoral girdle of Stretham Pliosaur. $\times\frac{1}{18}$. *a*, Ventral view; *b*, Dorsal view. COR., Coracoid; HUM., Humerus; SC., Scapula. Muscles: *cor. brach.*, coracobrachialia; *lat. dsi.*, latissimus dorsi; *lev. sc.*, levator scapulae; *pect.*, pectoralis; *sc. delt.* (1), scapular deltoid; *sc. hum. ant.* (2), scapulo-humeralis anterior; *serr. ant.*, serratus anterior; *sub. cor.*, subcoracoideus; *sub. sc.* (3), subscapularis; *supra. cor.*, supracoracoideus. Nos. 1, 2, 3 indicate insertions or origins.

backing with one forelimb and swimming with the other, the animal is able to turn rapidly.

The large roughened area extending forward from the glenoid end of the scapula probably marks the place of attachment of the capsular ligament which holds the head of the humerus in the glenoid cavity. The distal end of the dorsal process has a pitted surface indicating that it is capped by cartilage, and in all probability the levator scapulae muscle is inserted on it. This muscle originates on the back of the skull and holds the pectoral girdle firm, preventing it from slipping backwards during any forward movement of the humerus. On the visceral surface of the dorsal process is the origin of the serratus anterior muscle, which is inserted on to a number of ribs. This forms a sling which prevents any rotation of the girdle around the ribs when the forelimb is moved in a vertical direction, as occurs during swimming, diving, and rolling.

From the foregoing it can be seen that the anterior production of the dorsal process has affected two groups of muscles: (i) those concerned with holding the girdle firm (levator scapulae and serratus anterior), and (ii) those concerned with drawing the humerus forward (scapulohumeralis anterior and subscapularis). In both cases the attachments of these muscles are carried far forward. It seems reasonable to suppose that as a result the levator scapulae muscle is shortened and the girdle is more rigidly held. It also means that the dorsal process to which the serratus anterior muscle is attached now projects forward into the posterior part of the neck where the ribs are very short. In this way the 'sling musculature' is shortened and thus becomes firmer, allowing very little play—an obvious advantage to a giant animal that has to dive in pursuit of its prey.

The more anterior origin of the 'backing' muscles (scapulohumeralis anterior and subscapularis) increases their length, thereby extending the distance through which they can contract. The forelimb can thus be drawn forward through a greater arc and can also be lifted higher, allowing a longer and more powerful swimming stroke. Besides this, these muscles now pull at a greater angle to the humerus, so that less force is required to move it.

The shape of the Stretham Pliosaur scapula therefore seems to be due to the functional advantages which changes in the various muscle insertions confer. *Pliosaurus macromerus* thus appears to be a more efficient swimming and diving animal than its Oxfordian ancestors or the conservative contemporaneous forms.

NOTE ON THE LOCOMOTION OF PLIOSAURS

It has generally been considered that Pliosaurs swam by rowing themselves through the water with their limbs acting as paddles, but I have come to the conclusion that it is more likely that Pliosaurs in fact swam with their hind limbs providing the main propulsive force, while their forelimbs performed a strong forward swimming stroke or initiated a change in direction.

In his paper on the Liassic Plesiosaurian *Plesiosaurus guilelmi imperatoris* Dames (1895) figured a skeleton (part of which I reproduce as Pl. 37, fig. 2) which shows the impression of an extension of skin along the posterior edge of the right forelimb. This means that in section the limb would taper posteriorly, producing a hydrofoil and not the ellipse of an oar, and it is unlikely that the later more streamlined Pliosaurs would have lost such an important feature.

The most effective swimming stroke is one in which the forelimb is driven downwards through the water with its dorsal surface facing forwards and slightly upwards, from a position in which the limb is somewhat above the horizontal and a little forward from the glenoid. This action with a hydrofoil-shaped limb creates less turbulence than does the stroke of an oar, and consequently is more efficient.

With this swimming stroke, the pressure of water is less on the dorsal surface of the limb than on the ventral side, and there is a tendency for the limb to move forwards. However, it is prevented from doing so by strong latissimus dorsi and pectoralis muscles,

EXPLANATION OF PLATE 37

Figs. 1. 1*a*. *Pliosaurus macromerus*, left scapula, Kimeridge Clay, Stretham, near Ely. 1, dorsal view. 1*a*, ventral view. Sedgk. Mus. J. 35990.

Fig. 2. *Plesiosaurus guilelmi imperatoris* Dames. Reproduction of part of Dames's original figure of the type specimen showing impressions of skin in the forelimb and tail regions.

the insertions of which are clearly visible on the humerus. In this way the force tending to move the limb is transmitted to the body, and thus it is not just the forelimb, but the whole body, that moves forward.

At the end of this stroke the limb is adducted backwards by the coracobrachialis muscle, and drawn forward ready for the next swimming stroke by the deltoid, scapulo-humeralis anterior, and subscapularis muscles, the actions of which have already been dealt with in detail.

Also in Dames's figure, the impression of skin in the caudal region seems to indicate that his animal had a ventral fin which followed the line of the muscles, and a dorsal one which flared away from the body. In Pliosaurs too a tail of this sort may have played some part in their locomotion.

The hind limb of the Pliosaur is generally larger than the forelimb and furthermore the ischium is greatly elongated. Thus the area of attachment of the adductor muscles is greatly increased and placed more posteriorly. The large insertion for these muscles in the centre of the ventral surface of the proximal end of the femur indicate that the hind limb is drawn back strongly and pulled in to the body. This produces a powerful propulsive force and together with the hydrofoil-shaped forelimb must have made the Pliosaur a most efficient hunter of the Mesozoic seas.

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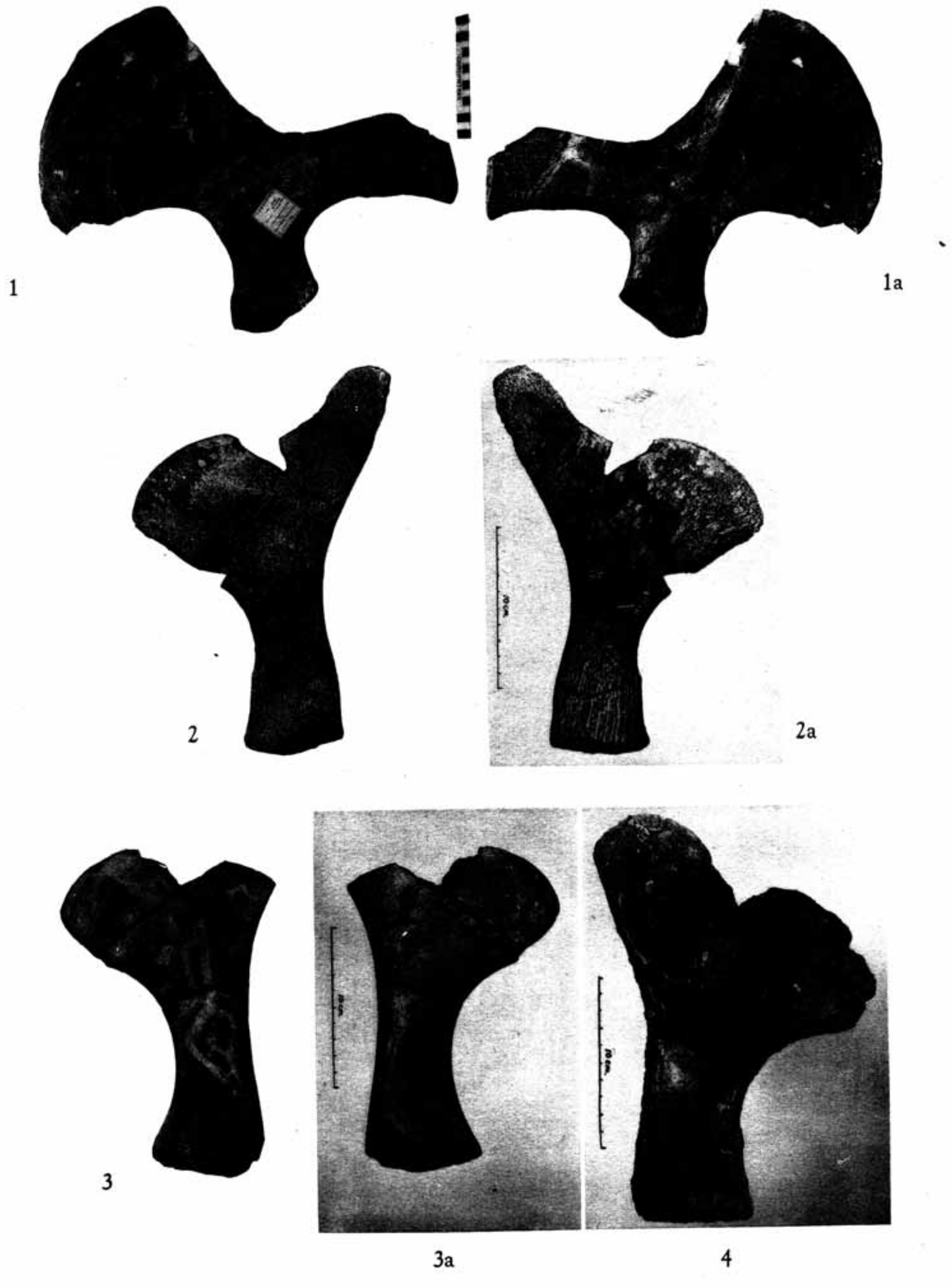
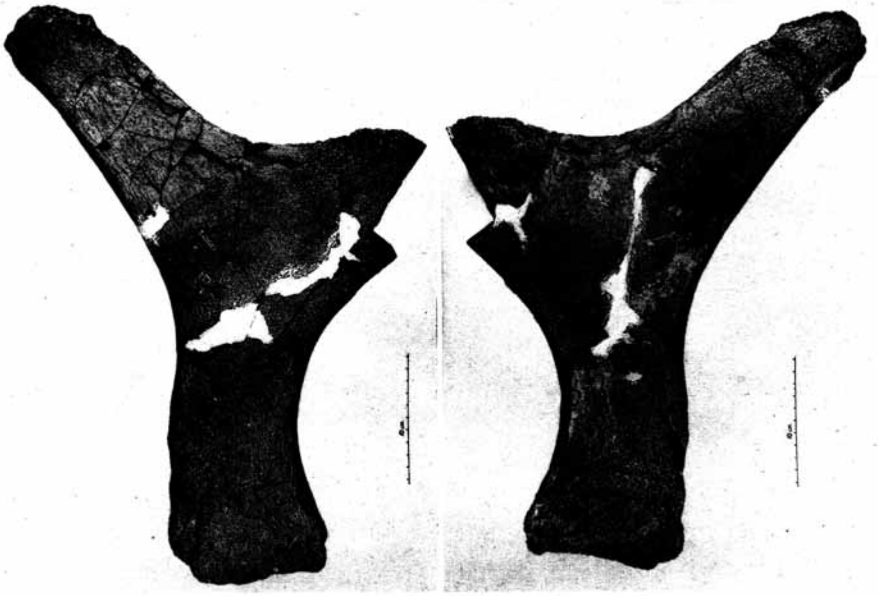


TARLO, Jurassic *Pliosaurus*



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