PLIOSAURUS BRACHYSPONDYLUS (OWEN) FROM THE KIMERIDGE CLAY

by L. B. TARLO

ABSTRACT. The associated skeleton of a Pliosaur from the Kimeridge Clay of Ely is described. Since it is the first known Pliosaur of Kimeridgian age which possesses both mandible and limb girdles associated with the vertebral column, it provides a means whereby Kimeridgian Pliosaurs can be separated into two distinct groups. On the characters of its mandible and scapula the Ely specimen is placed in the genus *Pliosaurus*, while the characters of its cervical vertebrae enable it to be included in the species *P. brachyspondylus* (Owen).

INTRODUCTION

HITHERTO it has been impossible to do more than suggest from circumstantial evidence that there were two distinct groups of Pliosaurs in Kimeridgian times. The known remains fall into two groups on the characters of the mandible, and also into two groups on those of the scapula. No associated skeleton has yet been described in which both mandible and scapula are present, and it has therefore not been possible to say with any certainty what the relationship was between the groups based on mandibles and those based on scapulae.

The two associated skeletons known, *Pliosaurus brachydeirus* and *Pliosaurus macromerus*, both lack essential parts. In *P. macromerus* the pectoral girdle, but no mandible, is known, whereas in *P. brachydeirus* the mandible is preserved but there is no pectoral girdle. A type of mandible different from that of *P. brachydeirus*, and a type of scapula different from that of *P. macromerus*, are also known, but as these are all from isolated specimens they could not be assigned to definite species.

This problem has now been resolved. In the Sedgwick Museum, Cambridge, there is a mandible and vertebral column of a Pliosaur from the Kimeridge Clay of Ely (J. 35991) which, although collected in 1889, has never been identified or described. Along the length of the ventral surface of the vertebral column are fragments of the limb girdles, forming a long narrow strip of broken and somewhat distorted bone 150 mm. wide. This mass, except for the vertebrae themselves, has been difficult to interpret, but a careful examination has now revealed the presence of the left scapula and coracoid. This scapula is of the same kind as the isolated scapulae mentioned above, which are quite different from that of *P. macromerus* (see Tarlo 1958*b*); further, the mandible agrees almost exactly with that of the type of *P. brachydeirus*.

This means that the isolated scapulae can now be linked with the mandible of the *brachydeirus* type, leaving the isolated mandibles to be assigned to *P. macromerus*.

HISTORY OF THE SPECIES

Conybeare (1824*a*) figured four Pliosaur vertebrae from the Kimeridge Clay of Weymouth which were then housed in the Collection of the Philosophical Society of Bristol. Later (1824*b*) he proposed the name *Plesiosaurus giganteus* for Plesiosaurians with shortened neck vertebrae, and included the centra from Weymouth in this species.

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Owen (1839) also described such shortened cervical vertebrae from the Kimeridge Clay of Heddington Pits, near Oxford, and he proposed the name *Plesiosaurus brachyspondylus* for them. He also used this name to cover the vertebrae from Weymouth. In his description of the cervical vertebrae from the Heddington Pits, Owen noted that the 'articular surfaces are very slightly concave, with small round depression, but no convex rising at the centre. The sides and underpart of the body are concave [i.e. from anterior to posterior, L. B. T.], the surface is tolerably smooth.'

The specimens from Heddington were in the collection of Viscount Cole (later Earl of Enniskillen), the greater part of which is in the British Museum. Unfortunately none of the vertebrae can now be traced, and Woodward and Sherborn (1890) could not locate the type material. Also I have been unable to find the Weymouth vertebrae.

The only author to discuss the species *Plesiosaurus brachyspondylus* was Seeley (1869), who correctly assigned it to *Pliosaurus*. Seeley listed and described a late cervical vertebra, with which thirty dorsal vertebrae were associated, from the Kimeridge Clay of Roswell Pit near Ely, Cambridgeshire. His description agrees with Owen's and it seems that the Heddington and Roswell specimens were conspecific. The posterior ('late') cervical centrum from Roswell (now in the Sedgwick Museum, Cambridge) is thus the only specimen of *P. brachyspondylus* (Owen) mentioned in the literature which is still extant. It should be noted that in 1871 Phillips described and figured several Plesiosaur vertebrae, incorrectly assigning them to *Plesiosaurus brachyspondylus* Owen.

In 1889 an associated Pliosaur skeleton was collected from the Kimeridge Clay of Ely and the characters of its posterior cervical vertebrae are identical to those of Seeley's Roswell cervical centrum. It appears that it is specifically identical to *P. brachyspondylus*, the types of which are now lost. In view of this I feel there is a good case for erecting a neotype, and I shall make the requisite application for the late cervical centrum described by Seeley to be so considered.

SYSTEMATIC PALAEONTOLOGY

Family PLIOSAURIDAE Seeley 1874

Genus PLIOSAURUS Owen 1841

Type species *Pliosaurus brachydeirus* Owen 1841

Diagnosis. Mandible with long symphysis bearing 10–12 teeth of which the anterior 5–6 are large and caniniform; total of 30–38 teeth in each ramus. Cervical vertebrae short, length about half width or height; cervical ribs double-headed. Scapula triradiate with dorsal process directed laterally and ventral plate expanded medially; coracoid elongated with postero-lateral expansion; ischia elongated; propodials long, compressed dorso-ventrally, expanded distally; epipodials short.

Pliosaurus brachyspondylus (Owen)

Plates 51 and 52

Plesiosaurus giganteus Conybeare 1824*b*, p. 389.
Plesiosaurus brachyspondylus Owen 1839, pp. 78–80.
Pliosaurus brachyspondylus (Owen), Seeley 1896, pp. 97, 102–4.
Pliosaurus brachyspondylus (Owen), Lydekker 1889, pp. 139–40.
Non *Plesiosaurus brachyspondylus* Phillips 1871.

Diagnosis. Teeth trihedral in cross-section, outer surface smooth and flat. Cervical vertebrae with double rugosity and without ventral keel; posterior cervical vertebrae without boss in centre of articular surfaces.

Neotype (here proposed). J. 29564, Sedgwick Museum, Cambridge, posterior cervical centrum, Kimeridge Clay, Ely, Cambridgeshire, described Seeley 1869, pp. 97, 103.

Other material. G. 102, Dorset County Museum, anterior cervical centrum, Kimeridge Clay, Osmington, Dorset; J. 47225, Sedgwick Museum, Cambridge, anterior cervical centrum, Kimeridge Clay, Chettisham, near Ely, Cambridgeshire; J. 35991, Sedgwick Museum, Cambridge, associated skeleton, Kimeridge Clay, Ely, Cambridgeshire, described in present paper.

DESCRIPTION OF NEOTYPE

The posterior cervical centrum described by Seeley (1869) and now in the Sedgwick Museum (J. 29564) is chosen as the neotype of *Pliosaurus brachyspondylus* (Owen). It is here figured for the first time (Pl. 51, figs. 1, 1*a–c*). This vertebra is very distinctive since it possesses a double rib facet on the left side and a single facet on the right.

The articular surfaces of the vertebra are transversely ovate in outline, and are slightly concave. Each has a small depression at its centre, there being no suggestion of any convexity developed such as is the case in the posterior cervical vertebrae of other Kimeridgian Pliosaur species. The margins of the articular surfaces are very sharply defined, and there is no evidence of either a marginal bevel or groove.

On the ventral surface of the centrum are two nutritive foramina, and the surface itself is convex between the rib facets. On the anterior and posterior margins of this ventral surface are two strips of finely sculptured rugose bone between which the surface is remarkably smooth. This last feature is very striking and can readily be used to distinguish the species.

	Measurements (in mm.)		
	Length	*Height*	*Width*
Centrum	36	68	79
Left superior rib facet . . .	24	27	..
Left inferior rib facet . . .	20	15	..
Right rib facet	25	33	..

DESCRIPTION OF ASSOCIATED SKELETON FROM ELY

In 1889 and 1890, Mr. H. Keeping, the collector of the Woodwardian (now Sedgwick) Museum, brought to the Museum an associated Pliosaur skeleton, now catalogued under J. 35991.

This specimen consisted of numerous teeth; the complete mandible; the greater part of the vertebral column; two limb bones, and fragments of limb girdles, many of which had been preserved in natural articulation with the vertebral column cemented on top of them.

The bulk of the vertebral column is preserved in two blocks, the larger of which (Block A) contains fragments of the skull, the posterior half of the cervical vertebrae and the anterior half of the dorsal vertebrae (see Pl. 52, figs. 1, 1*a*). Part of the left scapula and the lateral half of the left coracoid adhere to the ventral surface of these

vertebrae. The second block (Block B) consists of eight dorsal centra, with several abdominal ribs and part of the pubis preserved on their ventral surface.

The atlas, axis, and the two cervical vertebrae following them are preserved in association with the mandible. In addition, there are some isolated fragments of bone, including the symphysial regions of both coracoids, the left one of which fits on to the glenoid part of the coracoid which adheres to the ventral surface of the dorsal vertebrae. Part of an ischium is present as an isolated bone, as are also the right humerus and left femur.

TEETH. The teeth are similar to those of *Pliosaurus 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. 51, figs. 3, 3*a*). 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*).

MANDIBLE. The separate elements of the mandible are all preserved, but it is somewhat difficult to distinguish between sutures and post-mortem effects due to the process of fossilization. The total length of the mandible is 1,200 mm. The symphysis is 328 mm. in length and 128 mm. at its greatest width. It contains ten teeth on each side, of which the anterior six are large and caniniform. The fourth, fifth, and sixth teeth are the largest, and the mandible is expanded to accommodate them, but it becomes constricted at the seventh tooth which is markedly smaller than the three previous teeth. There is a total of thirty teeth in the right ramus and thirty-one in the left (see Pl. 51, fig. 2).

This specimen is similar in shape to the mandible of *P. brachydeirus* in which there is also an elongated mandibular symphysis containing ten to twelve teeth of which the anterior five to six are large and caniniform. In consequence I consider this specimen to be generically identical to *P. brachydeirus*, the type species.

VERTEBRAL COLUMN. A total of forty-five vertebrae are known, of which nineteen are cervical, two pectoral, and twenty-four dorsal. Since many of these centra are preserved in natural articulation it is an easy task to determine their serial position. The length of

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EXPLANATION OF PLATE 51

Figs. 1–5. *Pliosaurus brachyspondylus* (Owen), Kimeridge Clay, Ely, Cambridgeshire. Figs. 1, 1*a–c*, J. 29564, Sedgk. Mus., Cambridge, posterior cervical centrum here proposed as neotype. 1, Anterior view; 1*a*, Ventral view showing finely-sculptured rugose strips; 1*b*, Lateral view of right side showing single-rib facet; 1*c*, Lateral view of left side showing double-rib facet, approx. ×1. Figs. 2–5. J. 35991, Sedgk. Mus. 2, Mandible in dorsal view showing long mandibular symphysis, ×$\frac{1}{8}$. 3, 3*a*, Tooth, 3, External view; 3*a*, Lateral view, ×1. **4**, Block B in ventral view showing dorsal vertebrae, abdominal ribs, and part of pubis, ×$\frac{1}{8}$. 5, Left femur in dorsal view, ×$\frac{1}{8}$.

EXPLANATION OF PLATE 52

Figs. 1–2. *P. brachyspondylus* (Owen), Kimeridge Clay, Ely, J. 35991, Sedgk. Mus., Cambridge. 1, Block A in ventral view showing cervical vertebrae, left scapula, and lateral half of left coracoid; 1*a*, Dorsal view showing squamosal, cervical, pectoral, and dorsal vertebrae, also dorsal process of left scapula; 1*b*, Atlas and axis with 3rd and 4th cervical centra, ×$\frac{1}{8}$. 2, Fragment of limb girdle showing chitinous hooks from the tentacles of cephalopods, which must have formed a major part of the food of the animal, ×1.

the vertebrae can be used as an indication of their relative position in the body as shown in the table below.

Vertebrae in Block A	*Length (in mm.)*	*Vertebrae in Block A*	*Length (in mm.)*
Anterior Cervical 14th	37	Pectoral 1st	48
15th	38	2nd	50
Posterior Cervical 1st	40	Dorsal 1st	52
2nd	42	2nd	56
3rd	43	7th	67
4th	44	12th	71

The cervical vertebrae are the most compressed, but these gradually increase in length down the neck. However, in the region of the posterior cervicals and pectoral vertebrae there is a rapid increase, so that by the time the seventh dorsal vertebra is reached its length is almost double that of the anterior cervicals. The vertebrae reach a maximum length in the centre of the dorsal region, and from then on the trend is reversed.

Cervical vertebrae. The first two cervical vertebrae—the atlas and axis—are incomplete, the arch of the atlas and both sub-vertebral wedge bones being missing.

The third vertebra has a pronounced ventral lip directed anteriorly with a marked rugose area behind it on the ventral surface of the centrum, which tends to produce a faint ventral keel. However, in the majority of the cervical vertebrae there is no suggestion of such a ventral keel, and the rugosities on their ventral surface are limited to strips along the anterior and posterior margins.

There are double rib facets on the lateral surfaces of the centra of all the anterior cervical vertebrae except the atlas and axis. The inferior facet in each case is more or less circular in outline, while the superior facet tends to be in the form of a triangle, with a narrow ridge extending from its apex to the base of the neural arch.

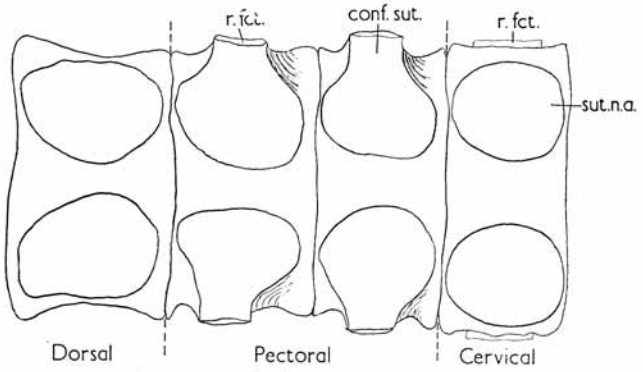
The articular surfaces of the anterior cervical vertebrae show a well-developed marginal bevel, but this disappears in the posterior cervicals. The articular surfaces are slightly concave and have a small central pit, no mamilla being developed as is the case in other Kimeridgian species.

Posterior cervical vertebrae. In Block A the four most posterior of the cervical centra can be distinguished from the anterior cervical vertebrae by the fact that they have single rib facets, and the bevelling of the margins of the articular surfaces is slight. In view of these differences these four vertebrae are designated posterior cervicals, but this distinction is clearly an arbitrary one, as the neotype itself has a single-rib facet on one side and a double one on the other side.

As in the anterior cervical vertebrae, there are two rugose strips of bone on the ventral surface of the centra—one on the anterior border and one on the posterior. The articular surfaces are slightly concave and each has a depression in the centre, no boss being present such as is found in the posterior cervical centra of other Kimeridgian species. The posterior cervical vertebrae are therefore considered conspecific with the neotype already described, as they possess the two strips of rugose bone on their ventral surface and their articular surfaces show no central convexity and virtually no marginal bevelling.

Pectoral vertebrae. Pectoral vertebrae are defined as those transitional vertebrae in which the articular facet for the rib lies partly on the centrum and partly on the neural

arch. This is the intermediate position between cervical vertebrae in which the facet is on the centrum, and dorsal vertebrae where it is on the neural arch. As can be seen from Pl. 52, fig. 1*a* and text-fig. 1, there are only two vertebrae of this type in the Ely specimen, the transition having taken place rapidly.



TEXT-FIG. 1. *Pliosaurus brachyspondylus* (Owen), vertebral centra in dorsal view, showing changes in outline of suture of neural arch as rib articulation rises from body of centrum on to neural arch itself. Sedgk. Mus. J. 35991. ×$\frac{1}{2}$. conf. sut., suture of neural arch confluent with rib facet; r.fct., rib facet; sut. n.a., suture of neural arch.

The dorsal view of Block A shows clearly how the suture of the neural arch and the rib facet become confluent during this transition. In these two pectoral centra the lower half only of the rib facet is present on the centrum, the upper half having been borne by the neural arch, which is missing.

Dorsal vertebrae. The rib facet in these vertebrae is borne wholly on the transverse process of the neural arch, and in dorsal view the suture of the neural arch on the centrum reverts to the shape it possessed in the cervical vertebrae, this change in shape being indicated in text-fig. 1.

PECTORAL GIRDLE AND FORELIMB. Sufficient of the left scapula and coracoid are preserved for a full description of them to be given. In addition, a complete right humerus is preserved.

Scapula. The major portion of the left scapula is preserved in one piece on the ventral surface of the second pectoral vertebra and the first four dorsal vertebrae, and can be seen in Pl. 52, fig. 1. The length of the part preserved is 250 mm. and its maximum width is 150 mm.

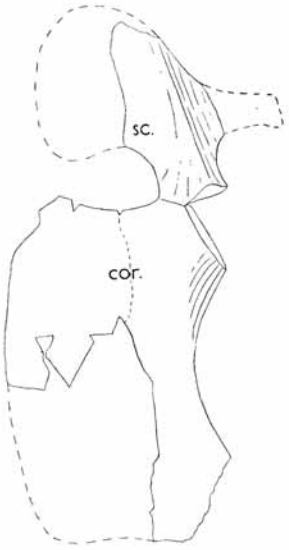
The ventral surface of the scapula is visible, and it is clear that it is a triradiate bone with a thickened glenoid ramus which bears a facet for the articulation of the coracoid, and another which forms the anterior part of the glenoid cavity. Medially the scapula thins out and is expanded into a broad flat ventral plate, part of which has been broken off. A ridge extends from the glenoid cavity towards the anterior extremity of the scapula, and from this ridge there is a lateral extension of the bone—the dorsal process

—which is set off at an angle to the plane of the bone. Again part of this process is missing, but in dorsal view the cross-section of the process is clearly visible (Pl. 52, fig. 1*a*).

From the above description and reconstruction in text-fig. 2, it is obvious that the scapula of the Ely skeleton is very similar to that of *Pliosaurus sp.* figured earlier (Tarlo 1958*b*) and is quite different from the scapula of *Pliosaurus macromerus* Phillips.

Coracoid. On the ventral surface of the fifth to the eleventh dorsal vertebrae is preserved the lateral half of the left coracoid, showing both the glenoid and the lateral border. The whole outline including the thickened glenoid portion has suffered no distortion, and although the sheet of bone is fractured it presents a smooth clean edge. The preserved lateral portion of the coracoid is visible in Pl. 52, fig. 1, and as can be seen both from the photograph and from the reconstruction of the pectoral girdle in text-fig. 2 the postero-lateral corner of the bone is somewhat expanded.

Fortunately, in addition a number of fragments of this same bone show the symphysial region of the left coracoid and fit exactly on to the anterior part of the bone which adheres to the vertebral column. It is thus possible to establish the full outline of the coracoid, the measurements of which are: length 500, width 325 mm.



TEXT-FIG. 2. *P. brachyspondylus* (Owen), reconstruction of left side of pectoral girdle in ventral view, Sedgk. Mus. J. 35991. ×$\frac{1}{8}$. COR., coracoid; SC., scapula.

Humerus. This is preserved complete and is indistinguishable from the propodials of most other Pliosaurs. Its rounded head is divided into two sub-equal facets, the dorsal one of which is slightly smaller than the ventral. The bone is dorso-ventrally compressed and expanded distally.

PELVIC GIRDLE AND HIND LIMBS. Preserved in a similar way to the pectoral girdle, part of the pelvic girdle is found adhering to the ventral surface of several vertebrae, together with a number of abdominal ribs. In addition, part of an ischium and the complete left femur are known as isolated bones.

Pelvic girdle. Fixed to the ventral surface of the last four dorsal vertebrae of Block B is part of a flat girdle bone measuring 360 mm. in length and having a maximum width of 150 mm. Just anterior to this bone are cemented a number of abdominal ribs, and as the bones seem to be lying more or less as they would in the body, it seems reasonable to assume that the flat girdle bone is part of the pubis (Pl. 51, fig. 4).

In the isolated ischium, the acetabular portion is complete and the greater part of the lateral edge is preserved, but the posterior extremity and medial aspects of this bone are missing. The length of the fragment is 344 mm. and together with the pubis a minimum length of 700 mm. can be established for the pelvic girdle. However, it seems more likely that with the completion of the ischium and also the pubis the full length would be nearer 800 mm.

Femur. The left femur (Pl. 51, fig. 5) is preserved complete, with a number of phalanges adhering to it. This bone is very similar to the humerus in its proportions although it is larger, as can be seen from the comparative table below, the measurements being given in mm.

	Humerus		*Femur*	
	width	*thickness*	*width*	*thickness*
Head	89	90	105	96
Half-way down shaft .	104	55	112	61
Distal end . . .	180	52	200	57
Total length . .	400		450	

DISCUSSION

The significance of the Ely skeleton is that it provides the means whereby the Kimeridgian Pliosaurs can be separated into two groups each with a distinct type of mandible and scapula. *Pliosaurus brachydeirus* and *P. brachyspondylus* belong to one group which has a mandible in which there is a long symphysis containing ten to twelve teeth of which the anterior five to six are large and caniniform, and a scapula in which the dorsal process is set off at an angle to the rest of the bone and is produced laterally or posterolaterally. The second group, represented by *P. macromerus*, is characterized by a mandible with a short symphysis bearing only five to six large caniniform teeth, and a scapula in which the dorsal process is in the same plane as the rest of the bone, and is produced anteriorly.

The differences between the two groups are such that it is no longer feasible to retain them both in the genus *Pliosaurus*, which name must be kept for the group containing the type species, *P. brachydeirus*. In a later paper I shall propose a new generic name for *P. macromerus*.

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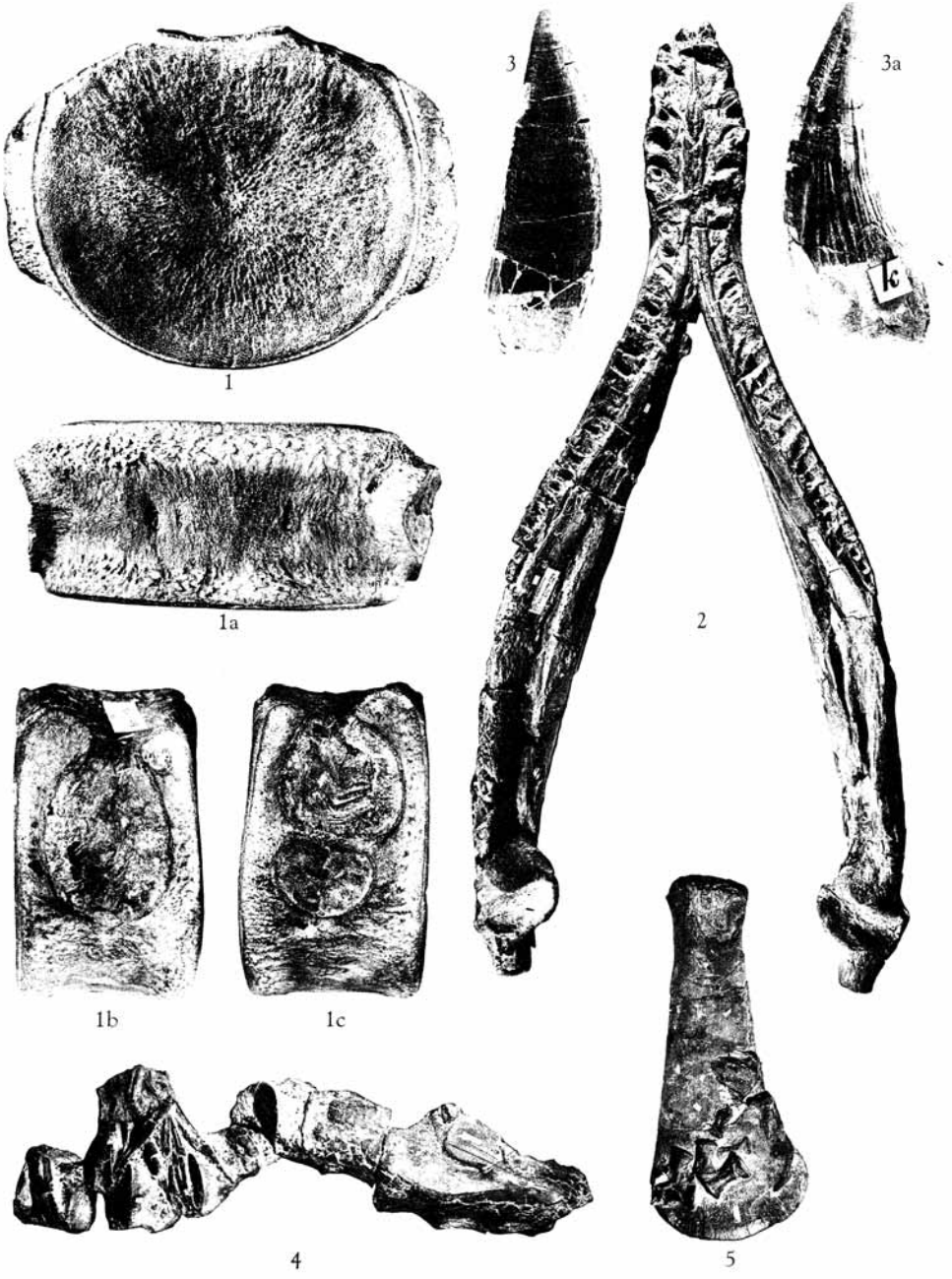
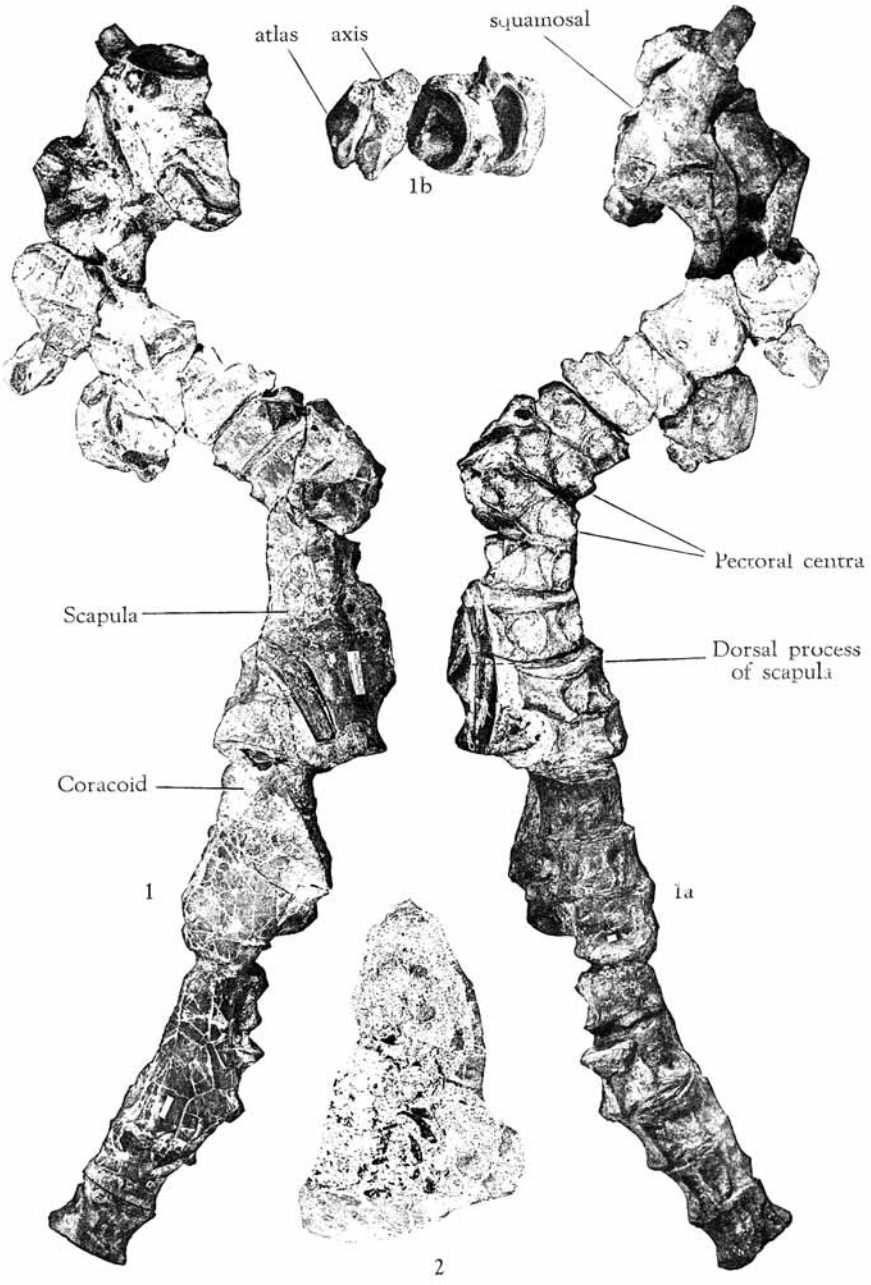


TARLO, *Pliosaurus*



TARLO, *Pliosaurus*