The English Upper Jurassic Plesiosauroidea (Reptilia) and a review of the phylogeny and classification of the Plesiosauria

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Synopsis

English Upper Jurassic marine reptiles of the superfamily Plesiosauroidea are reviewed in depth. Four genera and six species are recognized and described from previously known material, these being *Cryptoclidus eurymerus* (Phillips), *C. richardsoni* (Lydekker), *Muraenosaurus leedsii* Seeley, *M.*

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beloclis Seeley, *Tricleidus seeleyi* Andrews and *Colymbosaurus trochanterius* (Owen). In addition a skull from the Kimmeridge Clay of Dorset is described as *Kimmerosaurus langhami* gen. et sp. nov. The genus *Cryptoclidus* is described first and is taken subsequently as a model for comparison with other genera. A restoration of the skeleton of *C. eurymerus* is offered, and the skulls of *Cryptoclidus*, *Tricleidus* and *Kimmerosaurus* are reconstructed for the first time. A further three generic and twenty-five specific names are listed, discussed and rejected: some are junior synonyms but most are *nomina dubia*.

Published work on the phylogeny and classification of the order Plesiosauria is reviewed critically. Differing family-level classifications have been produced through the arbitrary weighting of differing characters of the postcranial skeleton. Thirty-eight plesiosaur characters used by taxonomists are discussed in the light of the present work, and of these fifteen (seven being skull characters) are of importance in distinguishing phyletic lineages.

The evolution and phylogeny of the Plesiosauria is discussed, three main lineages are identified, and a new classification is proposed. The order is divided into two superfamilies and four families. The Pliosauroidea represent one line of evolution and contain the single family Pliosauridae. The Plesiosauroidea contain an ancestral family (Plesiosauridae) and two descendant families (Cryptoclididae and Elasmosauridae). Diagnoses of these groups are given and referred genera listed. The Cryptoclididae comprise the genera *Cryptoclidus* and *Kimmerosaurus* together with the South American Upper Cretaceous genus *Aristonectes* Cabrera, hitherto considered an aberrant pliosaur. The genera *Muraenosaurus*, *Tricleidus* and *Colymbosaurus* are primitive elasmosaurs, as also is the English Lower Jurassic genus *Microcleidus* Watson.

Introduction

The order Plesiosauria is a group of the reptilian subclass Sauropterygia, and comprises reptiles which dominated the seas throughout the Jurassic and Cretaceous periods. On the basis of features which include the form of the skull and the comparative length of the neck they are divided into two superfamilies, the Plesiosauroidea and the Pliosauroidea. The vernacular names 'plesiosaur', 'plesiosauroid' and 'pliosauroid' (also 'pliosaur') refer to members of the order and the two superfamilies respectively.

Plesiosaur material is plentiful from most stages of the Jurassic System in Europe, and in particular from England. European specimens become scarce in the Cretaceous, and the principal remains are then to be found in North America. By the Upper Cretaceous the group had achieved a world-wide distribution, but in common with most groups of large reptiles it became extinct by the close of the Mesozoic era.

Most plesiosaur material was found and described in the nineteenth century. Early collectors depleted the coastal exposures, and by about 1910 most quarries became mechanized, this severely limiting the collection of fossil material before it was destroyed. After this date finds of new material were few, and although taxonomists continued to adjust the classification, very little redescription was attempted. Excellent as was much of the original description for its time, it proved to be an inadequate basis for subsequent work, and the need arose for a complete review. In more recent years Welles (1943, 1952, 1962; Welles & Gregg 1971) has reviewed the Cretaceous plesiosaurs, and Tarlo (1960) has reviewed the Upper Jurassic pliosaurs.

Most material of Upper Jurassic plesiosauroids has been recovered from English deposits, and especially from the two great clay formations, the Oxford Clay (mainly Callovian Stage) and the Kimmeridge Clay (Kimmeridgian Stage). The nomenclature of all genera is based on English type specimens in the collections of the British Museum (Natural History) (specimens with numbers prefixed by R or without prefix); the Sedgwick Museum, Cambridge (S.M.C.; numbers prefixed by J); the University Museum, Oxford (U.M.O.; numbers prefixed by J) and the Hunterian Museum, University of Glasgow (H.M.G.; numbers prefixed by V). Additional useful material is preserved in the National Museum of Wales, Cardiff (N.M.W.), the Castle Museum, Norwich (C.M.N.) and the Manchester Museum, University of Manchester (M.M.). During the course of the present study all these museums were visited and their collections examined. Further material in the Museum of the Royal College of Surgeons of England, London (R.C.S.), which was catalogued by Owen in 1854, was destroyed in 1941 by a fire caused by enemy action.

Almost all the plesiosauroid material from the Oxford Clay was collected in the late nineteenth century by one man, Alfred N. Leeds. His collection was made from brick-pits near and to the south of Peterborough; a map indicating the geography of these pits was published in a biographical work by the collector's son (Leeds 1956). Mechanization now prevents the collection of almost all specimens from these sites, but a few good finds, including an almost entire skeleton of *Cryptoclidus eurymerus* (see Charig & Horrell 1971), have been recovered in recent years through the cooperation and good will of the London Brick Company.

The bulk of the Leeds Collection, including most of the best specimens, was sold to the British Museum (Natural History) where it was catalogued and described by Andrews (1910, 1913). His description is full and largely accurate, and now requires only to be emended and supplemented. Plesiosauroids from the Kimmeridge Clay and higher deposits, on the other hand, are known only from isolated finds which are separately described and located. The present work is the first general review of these forms.

Examples are known of plesiosauroid individuals ranging from half-grown to full-grown. Differences of osteological structure of specimens of a single species, attributable entirely to ontogeny, have in the past been misinterpreted and used to produce taxonomic divisions. This, together with misinterpretation of other characters used in taxonomy, has led to the publication of a hyperabundance of generic and specific names, and a proliferation of schemes of classification based upon these. In order to facilitate description and the study of ontogeny, specimens are here allocated to one of three categories which represent growth stages, as follows:

(i) 'Juveniles', in which the neural arches of the vertebrae are not fused to the centra;

(ii) 'Adults', in which fusion of neural arches and centra has taken place, and

(iii) 'Old adults', in which the neural arches and centra are fused, and in addition further characters of advanced ossification are found.

Throughout the present work, the use of inverted commas indicates these special meanings of the words 'juvenile', 'adult' and 'old adult'.

Systematic descriptions

In the descriptive sections which follow, English Upper Jurassic plesiosauroid genera and species are described and discussed objectively, without reference to higher classification. There then follows a discussion of the phylogeny and classification of plesiosaurs; a new classification of the Plesiosauria is subjectively proposed and the genera of plesiosaurs are assigned to family-group taxa.

Genus ***CRYPTOCLIDUS*** Seeley, 1892

1892 *Cryptoclidus* Seeley: 145 (as a subgenus).
1895*a* *Cryptoclidus* Seeley; Andrews: 333 (as a genus).
1909 *Cryptocleidus* Andrews: 418 (incorrect subsequent spelling).
1915 *Apractocleidus* Smellie: 341 (subjective-objective synonym *sensu* Blackwelder 1967).

TYPE SPECIES. *Plesiosaurus eurymerus* Phillips, 1871.

ADDITIONAL ENGLISH SPECIES. *Cryptoclidus richardsoni* (Lydekker, 1889).

DIAGNOSIS. Plesiosauroids in which tooth ornament is reduced; the dentary bears 24 to 26 teeth on each ramus; the premaxillae bear 6 teeth each, of which the first (most anterior) is small and the second to sixth are large; the parietals form a sagittal crest; the paroccipital process of the exoccipital-opisthotic is of moderate length; the occipital condyle is not ringed by a groove, and extends onto the pedicles of the exoccipitals; there are about 55 presacral vertebrae, of which usually 32 are cervical; the cervical vertebrae have relatively amphicoelous centra, the length of which very rarely exceeds the height; the clavicles are triangular and well developed, lie visceral to the ventral rami of the scapulae, and meet in the midline; the interclavicle is absent or rudimentary; the coracoids meet the scapulae in the ventral midline in 'adults'; the width across the posterior cornua of the coracoids exceeds the interglenoid width in 'adults' by up to 40%; the elements of the pectoral girdle tend to fuse in old individuals; there are normally only two epipodials in the manus; a foramen only appears between the epipodials in specimens showing advanced ossification. (Diagnostic characters of the skull are taken only from the type species.)

Cryptoclidus eurymerus (Phillips, 1871)
(Figs 1–18, 43a, 44a)

1869 *Plesiosaurus oxfordiensis* Seeley. Published as *P. oxfordiensis* Phillips, MS (*nomen nudum*).
1871 *Plesiosaurus oxoniensis* Phillips: 307, figs 113–117 (*nomen dubium*).
1871 *Plesiosaurus eurymerus* Phillips: 315, fig. 120.
1874*b* *Muraenosaurus oxoniensis* (Phillips) Seeley: 448.
1888 *Plesiosaurus oxoniensis* Phillips; Lydekker: 352.
1888 *Plesiosaurus eurymerus* Phillips; Lydekker: 352.
1889 *Cimoliosaurus eurymerus* (Phillips) Lydekker: 205, figs 66–68 (mis-spelling of *Cimoliasaurus* Leidy, 1852).
1889 *Cimoliosaurus oxoniensis* (Phillips) Lydekker: 209.
1892 *Cimoliosaurus eumerus* ('Phillips'); Seeley: 145 (*lapsus*).
1892 *Plesiosaurus durobrivensis* (Lydekker) Seeley: fig. 5.
1892 *Muraenosaurus (Cryptoclidus) platymerus* Seeley: 145, figs 13–15.
1895*a* *Cryptoclidus oxoniensis* (Phillips) Andrews: 333, figs 1–4.
1895*a* *Cryptoclidus platymerus* (Seeley) Andrews: 335.
1895*b* *Cryptoclidus oxoniensis* (Phillips); Andrews: 241, fig. 1, pl. 9.
1896 *Cryptoclidus oxoniensis* (Phillips); Andrews: 145, fig. 1.
1909 *Cryptoclidus oxoniensis* (Phillips); Bogolubov: 44.
1909 *Cryptoclidus eurymerus* (Phillips) Bogolubov: 48.
1909 *Cryptoclidus platymerus* (Seeley); Bogolubov: 50.
1909 *Cryptocleidus oxoniensis* (Phillips); Andrews: 418.
1910 *Cryptocleidus oxoniensis* (Phillips); Andrews: 164, text-figs 78–94, frontispiece, pls 9, 10.
1915 *Apractocleidus teretipes* Smellie: 341, fig. 1.
1916 *Apractocleidus teretipes* Smellie; Smellie: 609, text-figs 1–9, pl. 1.
1959 *Cryptocleidus eurymerus* (Phillips); Delair: 66.
1959 *Cryptocleidus oxoniensis* (Phillips); Delair: 67.
1962 *Cryptoclidus oxoniensis* (Phillips); Welles: 8.
1962 *Cryptocleidus oxoniensis* (Phillips); Welles: tables 1, 4.
1963 *Cryptocleidus oxoniensis* (Phillips); Persson: 24.
1963 *Cryptocleidus eurymerus* (Phillips); Persson: 24.
1964 *Cryptocleidus oxoniensis* (Phillips); Novozhilov: figs 303, 304.
1964 *Apractocleidus teretipes* Smellie; Novozhilov: 320, fig. 304.
1964 *Cryptocleidus eurymerus* (Phillips); Novozhilov: 320.

Lost holotype. A forelimb formerly in the Woodwardian (= Sedgwick) Museum, Cambridge. The specimen was described and figured by Phillips (1871) from a plaster cast then in the University Museum, Oxford. It was originally misidentified as a hindlimb, and was named *Plesiosaurus eurymerus*. Andrews (1910) states that vertebrae similar to those of *P. oxoniensis* Phillips, 1871, were associated with the limb.

The lost holotype was from Bedford, England, taken from Oxford Clay, and therefore of Callovian or, improbably, Lower Oxfordian age. (No English plesiosauroid material of certain Oxfordian age is known.)

The holotype was realized to be missing in 1958, since when repeated searches of the Sedgwick Museum have been fruitless. Furthermore, there is no documentary record relating to its existence in that museum (personal communication, Dr C. L. Forbes). The plaster cast in Oxford University Museum is also missing (personal communication, Mr H. P. Powell). I am therefore obliged to propose a neotype.

NEOTYPE. Specimen R.2860, a Leeds Collection specimen in the BM(NH). This is one of the most complete 'adult' plesiosaur skeletons known, and was described, figured extensively and reconstructed by Andrews (1910 : 164; frontispiece; text-figs 78c, 78d, 91a, 91b, 94; pl. 9 figs 1, 1a, 2, 3). The forelimbs show the same distinctive characters as Phillips' figure of the lost holotype (1871 : fig. 120); these are included in the diagnosis below.

The neotype is from an unspecified brick-pit near Peterborough, England. Its horizon is Upper Jurassic, Callovian Stage, from the lowest deposits of the Oxford Clay, which includes the zones of *Kosmoceras jason*, *Erymnoceras coronatum* and *Peltoceras athleta* (see Andrews 1910 : vii).

DIAGNOSIS. Members of the genus *Cryptoclidus* in which the teeth have a characteristic ornament of longitudinal ridges: two opposing axial ridges (mesial and distal) rise from the base of the crown and almost meet over the tip, and between these rise from 4 to 7 lingual ridges which extend from the base to approximately one-third of the height of the crown; there are usually no buccal ridges. The humerus is greatly expanded distally by an anterior expansion of the portion bearing the radial facet. The radius is enlarged by anterior expansion of the portion bearing the humeral facet, which may be up to twice as long as the facet for the radiale, so causing the anterior margin to describe a sigmoid curve. The ulna is much wider than long.

DISTRIBUTION AND RANGE. Diagnostic material is known only from the Peterborough and Bedford districts. Upper Jurassic; Callovian Stage only.

REFERRED SPECIMENS. Since remains of this species are comparatively abundant, only those specimens mentioned in the text are listed below; a fuller list is given elsewhere (Brown 1975). All specimens are from the Oxford Clay in the Peterborough area.

R.2412. Incomplete 'adult' postcranial skeleton partly figured by Seeley (1892 : figs 13–15) as the holotype of *Muraenosaurus (Cryptoclidus) platymerus*, and by Andrews (1910 : text-figs 79, 80, 83, 84, 90c) as *C. oxoniensis*.

R.2416. Incomplete 'juvenile' postcranial skeleton partly figured by Andrews (1895*a* : fig. 3b; 1910 : text-figs 89a, 90b) as *C. oxoniensis*.

R.2417. 'Juvenile' skeleton (mounted) figured by Andrews (1895*b* : pl. 9; 1910 : text-figs 78a, 78b, 90a, 92, pl. 9 figs 4, 4a, 5, 6) as *C. oxoniensis*.

R.2616. Incomplete 'adult' postcranial skeleton partly figured by Andrews (1895*a* : figs 1, 2; 1896 : fig. 1; 1910 : text-fig. 87, pl. 10) as *C. oxoniensis*.

R.2862. Postcranial skeleton of an 'old adult'. Gastralia figured by Andrews (1910 : text-fig. 86) as *C. oxoniensis*.

R.3538. Pectoral girdle of an 'adult'. Figured by Andrews (1910 : text-fig. 88) as *C. oxoniensis*.

R.3703. Incomplete 'adult' postcranial skeleton. Hindlimb figured by Andrews (1910 : text-fig. 93) as *C. oxoniensis*.

R.3730 (Figs 6, 7). Incomplete 'adult' skeleton. Jaws figured by Andrews (1910 : pl. 9 fig. 7) as *C. oxoniensis*.

R.8621 (Figs 3–5). Lower jaw, two teeth and postcranial skeleton of an 'adult'. Figured *in situ* by Charig & Horrell (1971).

H.M.G. V.1091. Postcranial skeleton of an 'old adult', lacking a tail (mounted with the tail of V.1104). Figured by Smellie (1915 : fig. 1; 1916 : figs 1–9, pl. 1) as the holotype of *Apractocleidus teretipes*.

H.M.G. V.1104 (Figs 8–9, 11–12, 14–18). Postcranial skeleton of an 'adult'.

H.M.G. V.1807. Coracoids, scapulae and humeri of an 'old adult'.

H.M.G. V.1809. Right forelimb of an 'old adult'.

H.M.G. V.1835. Right humerus of an 'old adult'.

Discussion of synonymy

Phillips (1871 : 307–312) described as *Plesiosaurus oxoniensis* various dissociated plesiosaur remains from the Oxford Clay of Long Marston, Oxfordshire. This included several vertebrae, a hindlimb and a pectoral girdle (figured upside down and described by Phillips as a pelvis). Subsequent opinions regarding the affinities of the limb and girdle differed (Seeley 1874*b*; Lydekker 1888; Andrews 1895*a*, 1910); they are in fact plesiosauroid, but generically non-diagnostic. Andrews (1910) concluded that the only parts of Phillips' material to which the name *P. oxoniensis* could be applied were the vertebrae. In the same work of 1871, Phillips (: 315–316) described and figured a forelimb from the Oxford Clay of Bedford as *Plesiosaurus eurymerus*, misidentifying it as a hindlimb.

After visiting the private collections of A. N. Leeds at Eyebury, near Peterborough, and studying several almost complete skeletons, Lydekker (1888) identified the holotype of *P. eurymerus* as a forelimb and recognized its association with vertebrae similar to those of *P. oxoniensis*. Believing Leeds' specimens to be of significantly larger size, he retained both names, *P. eurymerus* being used to refer to the larger species. In 1889 he referred both species to the genus *Cimoliasaurus* Leidy, and figured as *C. eurymerus* a cervical vertebra and associated forelimb of a partial skeleton (R.2412) acquired by the BM(NH) from Mr Leeds.

In 1892, Seeley made R.2412 the holotype of *Muraenosaurus (Cryptoclidus) platymerus*, new subgenus and species. His subgeneric distinction was based on the form of the clavicles which he described for the first time; but he did not distinguish between the forelimb and that of the holotype of *P. eurymerus*, and so his introduction of a new specific name was not justified.

During the succeeding two decades the BM(NH) received numerous specimens from the Leeds Collection which were then described and catalogued by Andrews. He believed (1895*a*, 1910) that *P. oxoniensis* and *P. eurymerus* were sexual dimorphs, differing only in size, of a single species for which he used the name *Cryptoclidus oxoniensis*.

Subsequent to Andrews' work, a second species of the genus *Cryptoclidus* (*C. richardsoni*) has been recognized. The two species differ in the structure of the forelimb but their vertebrae together with those of *Tricleidus seeleyi* are mutually indistinguishable. The type vertebrae of *P. oxoniensis* are therefore non-diagnostic, and this name is a *nomen dubium*. The valid name for the present species is *Cryptoclidus eurymerus* (Phillips, 1871).

In 1915, Smellie described a Leeds Collection plesiosauroid in the Hunterian Museum, University of Glasgow, as *Apractocleidus teretipes*. It is argued below that the holotype (V.1091) is an 'old adult' individual of *C. eurymerus*.

Description of material

The skull. Andrews (1910) described the skull of *C. eurymerus* only by comparative reference to that of *Muraenosaurus*. It is known from several rather fragmentary specimens, the most complete of which is that of R.2860 (the neotype), and it differs in several important respects from those of its contemporaries. The reconstruction which is now presented (Figs 1, 2) is based largely upon R.2860, together with details of the dentition taken from R.3730. These skulls are now described, together with additional skull material.

SKULL OF R.2860 (NEOTYPE). This skull is preserved as 12 separate fragments: (A) most of the right premaxilla, the left premaxilla and the anterior part of the left maxilla; (B) a small part of the right premaxilla and the anterior part of the right maxilla; (C) the posterior part of the right maxilla; (D) the posterior part of the left maxilla, both frontals, both parietals, the supraoccipital and a small part of the left squamosal; (E) both the fused exoccipital-opisthotic elements, the basioccipital and the basisphenoid; (F) most of the left squamosal; (G) the right squamosal and right quadrate; (H) the vomers, upon which are compressed fragments probably of the premaxillae and frontals; (I) the left ramus of the dentary and the anterior portion of the right; (J) the posterior portion of the right ramus of the dentary; (K) the left angular, surangular and articular; and (L) the right angular, surangular and articular.

The dorsal surface of the premaxillae (fragments A, B) is much roughened by an irregular ornament of pits and ridges. The right element is better preserved than the left, and includes a complete toothrow containing the sockets for six teeth. With the exception of the small first

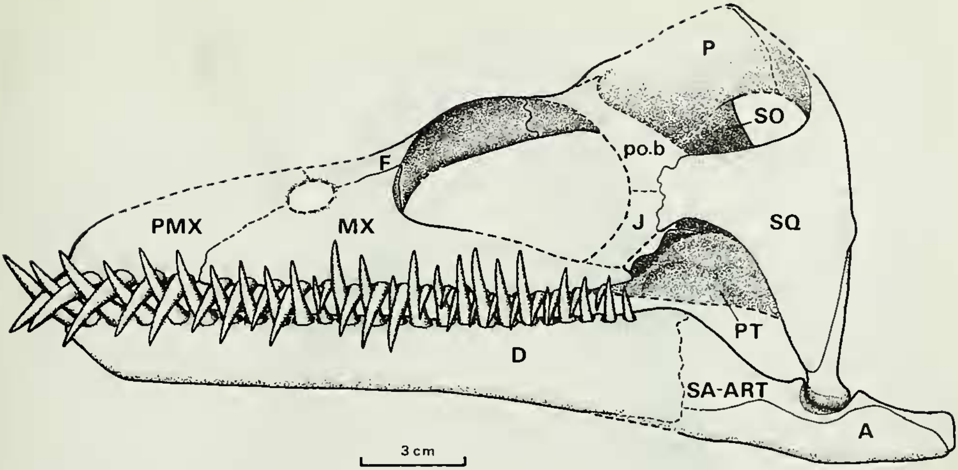


Fig. 1 *Cryptoclidus eurymerus* (Phillips). Composite reconstruction of skull in lateral view. A, angular; D, dentary; F, frontal; J, jugal; MX, maxilla; P, parietal; PMX, premaxilla; po.b, postorbital bar; PT, pterygoid; Q, quadrate; SA–ART, fused surangular-articular; SO, supra-occipital; SQ, squamosal.

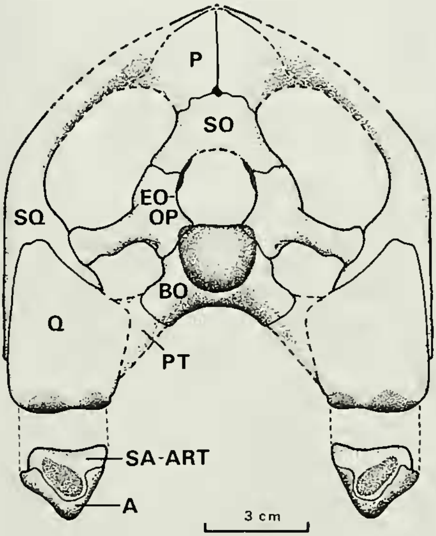


Fig. 2 *Cryptoclidus eurymerus* (Phillips). Composite reconstruction of skull in occipital view. A, angular; BO, basioccipital; EO–OP, fused exoccipital-opisthotic; P, parietal; PT, pterygoid; Q, quadrate; SO, supraoccipital; SQ, squamosal.

socket these are all of relatively large size. The third to sixth sockets remain on the left side, the fifth containing the only tooth preserved with the present specimen. The tip of this tooth is broken off; but the remaining part is ornamented with only 5 or 6 ridges which are widely spaced and confined to the lingual side. It is thus of the same characteristic type as the teeth of R.2417, R.3730 and R.8621 (see below). Both premaxillae are broken and eroded dorsally, and there is no evidence for their suture with the frontals or for the margin of the external nares. Posteriorly the sutures with the maxillae remain intact.

The maxillae (fragments A, B, C, D) have been somewhat eroded dorsally, but the alveolar regions are better preserved, and the left toothrow is complete. This contains sockets for 21 teeth, the posterior sockets appearing as grooves due to the loss of their lingual halves. The teeth evidently formed a graded series, showing a gradual reduction in diameter posteriorly.

The antorbital process of each maxilla extends dorsally to an extensively overlapping suture with the frontal, without any evidence for the existence of a discrete prefrontal or lacrimal element. From this suture the orbital margin is preserved downwards and backwards in an arc for about 3 cm on either side, but posterior to this point the edge of the bone is continuously broken back to the posterior end of the toothrow. The anterior margin of the antorbital process is also missing. There is therefore no evidence for the position of the external naris or of posterior sutures of the maxilla with other elements.

The frontals (fragment D) are relatively narrow posteriorly, where they meet the parietals and separate the dorsal margins of the orbits by only 3 cm; but more anteriorly they expand to carry the orbital margins outwards and upwards in an arc which reaches 1 cm above the median suture before continuing in descent to the sutures with the maxillae. The anterior expanded part of each frontal is thin, but ventrally it is strengthened by two thicker bony bars set at an angle of about 40°. One bar follows the median suture anteriorly towards the premaxillae; the other forms the orbital margin.

The parietals (fragment D) are fused, there being no trace of their suture on the skull table. Anteriorly they meet the frontals in a complex interlaminating suture which is split in the midline by the pineal foramen; this foramen is contained largely within the parietals, but on the dorsal aspect the frontals form a small part of its anterior margin.

Posterolateral to the pineal foramen the parietals are expanded to form the bases of the postorbital bars. These are not preserved; but the position of the squamous suture of at least the postfrontal element is indicated by ridges on the parietals and posterolateral margins of the frontals. This evidence suggests that the postorbital bar was thin, and that its plane was tilted downwards and backwards at an angle of about 30° to the plane of the skull table.

Behind the postorbital bars the parietals form a high and narrow sagittal crest, which is flanked by deep excavations for the temporal musculature. Behind these excavations each parietal is produced into a process which unites with the squamosal to form the post-temporal bar. On the left side a portion of this bar remains with the dorsal margin preserved to within 3 mm of the midline. At this point the bar is formed largely from the parietal; but above this is sutured the squamosal, which here has the form of a thin strand of bone tapering towards the midline, where it probably just met its opposite at the skull vertex.

The parietals form the uppermost 2·5 cm of the occipital surface of the skull, and in this part the median suture is still visible. Ventrally they unite with the supraoccipital.

The supraoccipital (fragment D) forms an arch over the dorsal half of the foramen magnum. In the midpoint of the suture with the parietals is a small foramen (observed in all plesiosauroid skulls studied) which may have housed the origin of a nuchal ligament. Ventrally the facets for the prootics and exoccipitals are of approximately equal size, the anterior prootic facets being grooved for the dorsal part of the posterior vertical semicircular canals.

The fused exoccipital-opisthotic elements together with the basioccipital and the basisphenoid (fragment E) were described and figured by Andrews (1910 : 166; pl. 9, figs 1, 1a, 2) in union with the supraoccipital and the posterior part of the parietals. The fusion of the exoccipital and opisthotic appears to be usual in all plesiosaurs. The opisthotic part contains half the utriculus (identified as the ampulla of the posterior vertical semicircular

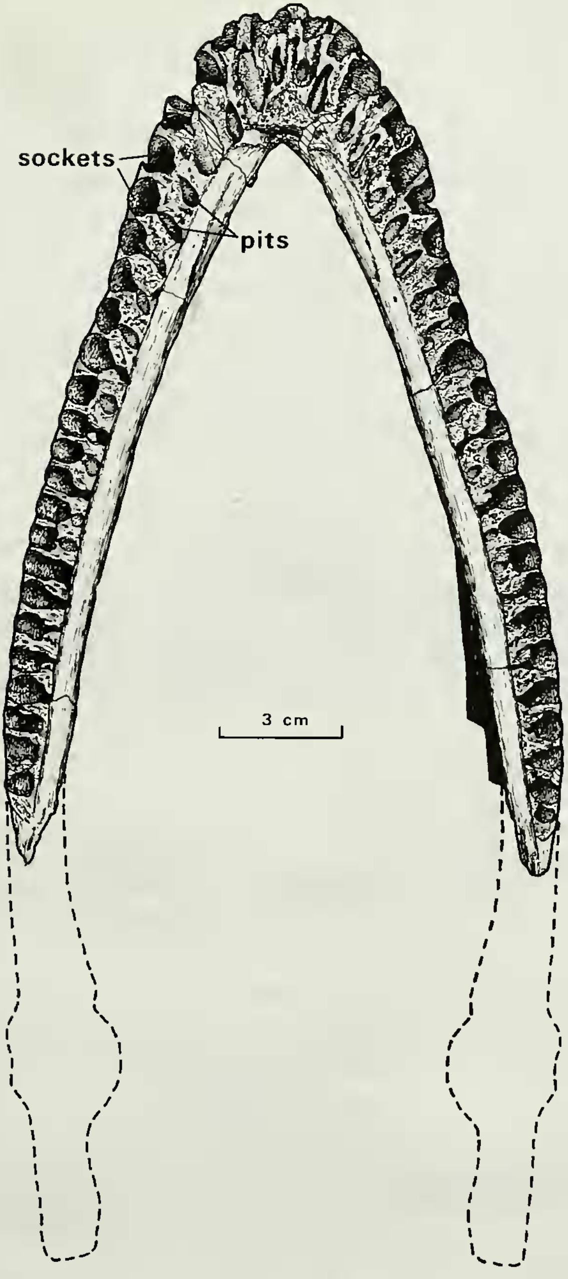


Fig. 3 *Cryptoclidus eurymerus* (Phillips), R.8621. Dentary in dorsal view. Outline of posterior elements of jaw (Fig. 4b) in dashed lines.

canal by Andrews, 1910) and parts of the posterior vertical and horizontal semicircular canals. The paroccipital process is relatively shorter than in *Muraenosaurus* and *Tricleidus*, yet longer than in *Kimmerosaurus*.

The occipital condyle of *Cryptoclidus eurymerus* differs markedly from all contemporary species. It is formed largely from the basioccipital, but includes a small part of the pedicles of the exoccipitals, whereas in the genera *Muraenosaurus* and *Tricleidus* (see below) the condyle is formed entirely from the basioccipital, and is separated from the exoccipitals by a groove.

The squamosals (fragments F, G) are triradiate in structure: the dorsal ramus forms the major part of the post-temporal bar and curves dorsomedially to meet its opposite above the parietals (these rami have been eroded heavily and cannot now be fitted to the parietals); the anterior ramus forms the zygoma and probably met the postorbital bar; the ventral ramus is a vertically-orientated plate of bone extending downwards almost to the jaw articulation and largely obscuring the quadrate in lateral view.

On the inner surface of the squamosal just beneath the base of the dorsal ramus is a flange which, together with the ventral ramus, forms a ventrally-orientated socket housing the primary head of the quadrate (Fig. 2). On the medial surface of this flange there is a large oval facet which matches in size and shape the head of the paroccipital process. It is therefore evident that the opisthotic articulated with the squamosal, and not with the quadrate as has been suggested by Andrews (1910) and Welles (1952).

The right quadrate (fragment G) is a strongly-built element and is preserved *in situ* with the right squamosal. At its ventral end it bears two ovoid condyles for articulation with the lower jaw. These are positioned at right angles to the skull axis, with the lateral condyle slightly larger than the medial. The process for suture of the quadrate with the pterygoid is broken away close to the medial condyle, and their precise arrangement cannot be determined. The combined quadrate and squamosal elements have been flattened a little in preservation, and the natural angle between them widened; this has been taken into account in the reconstruction (Figs 1, 2).

The only parts of the palate which have been preserved are the fused vomers (fragment H). Onto these have been compressed small parts of the premaxillae and frontals, and the whole fragment has been eroded heavily. The vomers were probably similar in form to those of *Muraenosaurus* and *Tricleidus*; a part of the margin of the right internal naris can be identified in the same relative position.

Small discontinuities of the toothrow are present on both rami of the dentary (fragments I, J), but the number of sockets per ramus may be estimated, 26 being the most probable figure. This compares with 24 sockets per ramus in R.8621, 24 or 25 in R.2417 and 25 in R.3730, these being the only specimens in which the dentary is preserved.

The posterior elements of the lower jaw (fragments K, L) do not differ significantly from those of R.8621 (described below).

The skull reconstructions (Figs 1, 2) were based as far as possible on the present specimen. It was necessary to restore the general outlines of the postorbital bar and jugal element from a consideration of plesiosauroid skull reconstructions by Andrews (1910) and Welles (1943, 1952, 1962). The dentition was restored by reference to specimens R.3730 and R.8621.

SKULL OF R.8621. With the exception of a small unidentifiable fragment, only the lower jaw and two isolated teeth remain of this skull. These are very well preserved, and have been prepared fully in the British Museum (Natural History).

The toothrow of the dentary (Fig. 3) has been preserved intact and without any post-mortem distortion, but all mature teeth have been lost. Each ramus bears sockets for 24 teeth, the largest (implying that these held the largest mature teeth) being the 4th, 5th and 6th. The anterior sockets are only slightly smaller than these; posteriorly they decrease regularly in size from the 6th to 22nd, then reduce abruptly to the small 24th.

The sockets are inclined outwards at a considerable angle from the vertical. This angle increases from 40° posteriorly up to 60° or more in anterior sockets. They are also inclined forwards, again this inclination increasing from behind forwards.

The present specimen exhibits the characteristic structure of the sauropterygian toothrow in which large tooth sockets, which held the functional teeth, are paired on the lingual side with small pits in which the replacement teeth developed. The pits take the form of small depressions or sometimes elevations, the surfaces of which are evenly textured, resembling the appearance of fine sandpaper. This surfacing contrasts with the surrounding bone, which is smooth and shows grain. Each pit is connected to the socket by a fine line or groove. The crowns of developing replacement teeth appear to pass from the pit outwards along this line until they occupy the socket; stages of this process are to be found in relation to the left 2nd, 4th and 7th, and the right 1st, 2nd, 4th, 9th and 14th sockets.

The pits appear on the surface of the bone lingual and posterior to their associated sockets, but owing to the inclination of the sockets, they are actually sited immediately above the socket bases. It is evident that the developing teeth move downwards into the socket; the apparent lateral movement of the crowns as seen on the surface of the bone is caused by increase in the length of the outwardly-inclined tooth crown coupled with a downward movement of the whole tooth.

The specimen shows the characteristic plesiosauroid 'short symphysis', which represents a simple unexpanded union of the left and right rami between the first alveoli. The dorsal

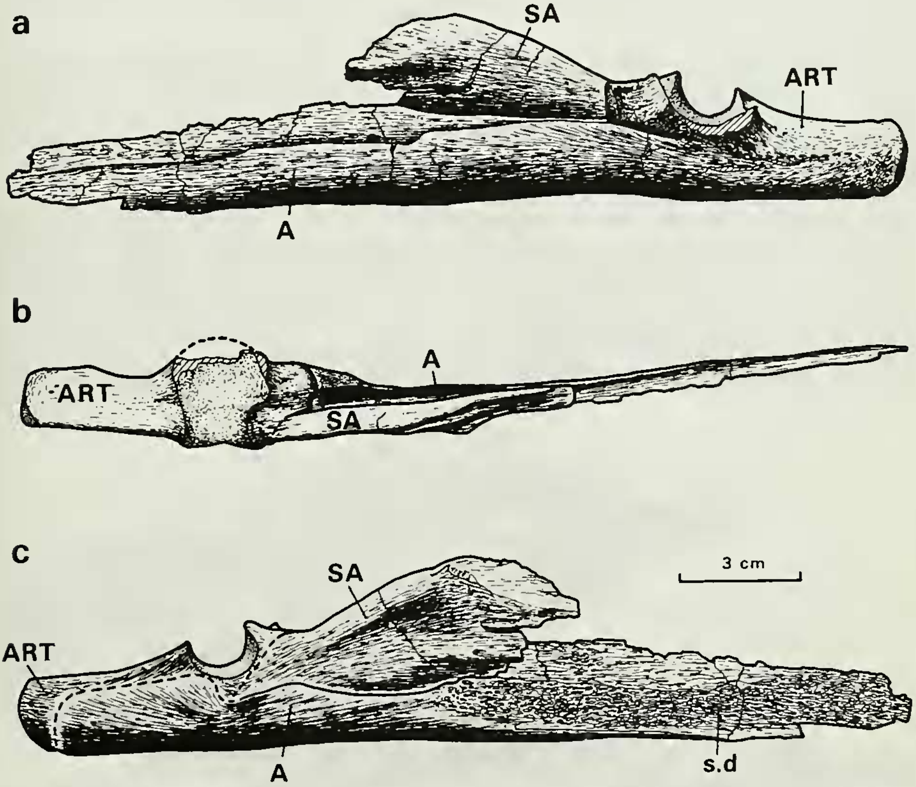


Fig. 4 *Cryptoclidus eurymerus* (Phillips), R.8621. Posterior elements of right lower jaw ramus: a, medial; b, dorsal; c, lateral aspect. A, angular; ART, articular; SA, surangular; s.d, surface for union with dentary. Sites of fusion between the articular, angular and surangular (indicated by

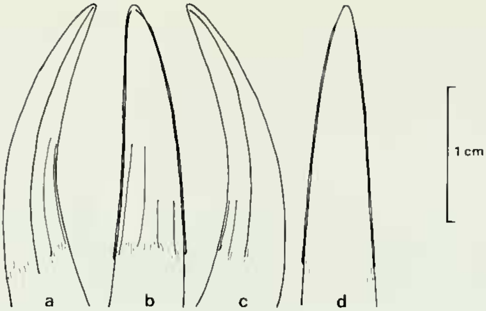


Fig. 5 *Cryptoclidus eurymerus* (Phillips), R.8621. Tooth showing ornamental ridges: a and c, axial; b, lingual; d, buccal aspect.

length of the symphysis is 3·2 cm and the length of the left ramus is 22·4 cm; the symphysis is therefore comparatively much shorter than in pliosaurs (cf. measurements given by Andrews, 1913).

The internal surface of the dentary is grooved deeply for the reception of the surangular and possibly a splenial. Thin broken fragments perhaps of this latter element remain in place anteriorly on both rami.

The posterior elements of the right lower jaw ramus are preserved united in a second piece (Fig. 4), and consist of the fused articular-surangular together with the angular. There is no separate coronoid element in this species.

Fusion of the articular and surangular appears to occur in all plesiosaurs. The combined elements form the glenoid for articulation with the skull. This is laterally expanded, and has two concavities to fit the double condyles of the quadrate.

In the present specimen the articular-surangular is in the process of fusing with the angular. Anteriorly the suture is clearly visible, but fusion has been completed posteriorly, the line of fusion being still traceable from the growth-pattern of the elements. Posteriorly the angular is a thin lamina in plesiosaurs, which is wrapped round the sides and ventral surface of the massive and cylindrical articular. Anteriorly it takes the form of a thin vertical lamina which unites externally with the inner surface of the dentary. Its medial surface is folded to produce a dorsally orientated meckelian groove for the insertion of jaw

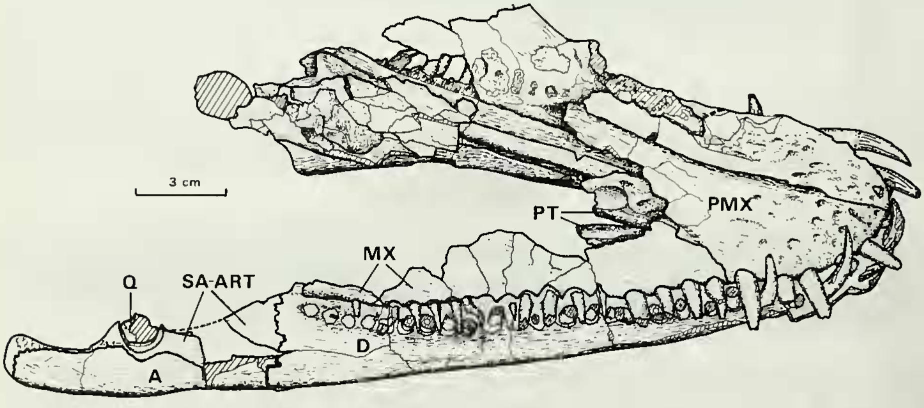


Fig. 6 *Cryptoclidus eurymerus* (Phillips), R.3730. Skull in right dorsolateral view. Broken bone hatched, clay matrix stippled. Abbreviations as in Fig. 1, p. 259.

musculature. A fragment consisting of part of the left angular and surangular is also preserved.

Two isolated teeth were found near the jaw. The smaller tooth is well preserved (Fig. 5) and shows clearly the characteristic ornament found in this species (see description in diagnosis).

SKULL OF R.3730. The preserved parts of this skull are the upper and lower jaws together with the frontals, parietals and supraoccipital. These latter elements (which comprise a separate fragment) resemble closely those of R.2860, and add nothing to the description. Despite much post-mortem flattening, however, the jaws (Figs 6, 7) retain almost the full set of teeth, and have been compressed together in such a way as to preserve their interlocking arrangement. This arrangement has been incorporated into the skull reconstruction (Fig. 1).

There are 25 teeth in each ramus of the lower jaw (cf. 26 sockets in R.2860), the largest being the anterior six. In conformity with the sockets of R.8621 they show a gradual decrease in size posteriorly, but only the most posterior tooth could be described as small. In this respect the lower and upper teeth differ. The most anterior tooth in the premaxilla is very small, and the left and right teeth are very close together. The remaining five premaxillary teeth are large, being as large as the dentary teeth with which they interlock. Each maxilla bears 18 teeth (cf. 21 sockets in R.2860) of which the anterior eight (the 7th to 14th upper teeth) are approximately equal in size to the 7th to 14th lower teeth. Posterior to these the upper teeth diminish considerably, becoming much smaller than their adjacent teeth in the dentary.

On the right side of the jaw (Fig. 6) the detailed interlock of the teeth has been very well preserved. The most anterior teeth in the combined jaws are the first upper teeth, which bite together in advance of the first lower teeth. Thereafter, upper and lower teeth interlock in a one-to-one fashion anteriorly, with the upper teeth biting in advance of the lower. Behind the 10th teeth the interlock becomes disrupted occasionally, with two upper or lower teeth biting together between their opposites. At such places invariably one or more mature teeth have been lost and their places only partly occupied by smaller developing replacement teeth. The fully detailed interlock on the left side (Fig. 7) could not be determined, but it was apparent that the sites of confused interlock did not coincide with those of the right side. All teeth show the characteristic ornamentation.

The tooth crowns curve towards the vertical (i.e. the lingual side is shorter), this curvature amounting to 40° posteriorly but reducing to about 20° in the most anterior teeth. From a consideration of the orientation of empty sockets in R.8621 it is evident that in posterior teeth the curvature fully counteracts the outward inclination of the socket such that the tooth

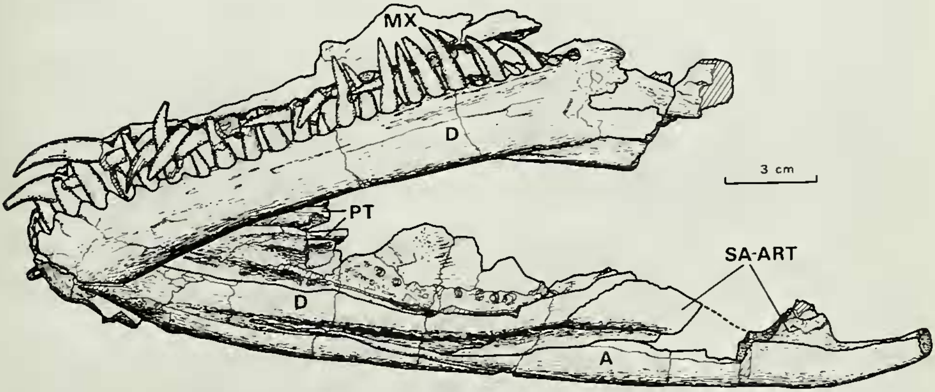


Fig. 7 *Cryptoclidus eurymerus* (Phillips), R.3730. Skull in left ventrolateral view. Abbreviations as in Fig. 1, p. 259.

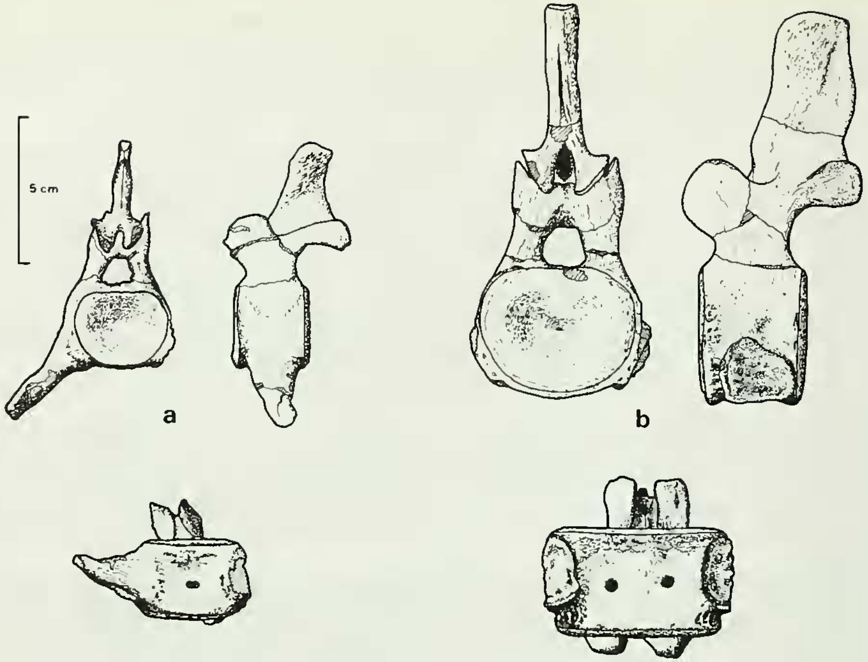


Fig. 8 *Cryptoclidus eurymerus* (Phillips), H.M.G. V.1104. a, fifth and b, twenty-fifth cervical vertebrae: posterior, left lateral and ventral views.

tip was vertical; in the most anterior teeth the tip may have had a natural orientation of as much as 40° from the perpendicular.

A scale lateral reconstruction of the appearance of the closed jaws was produced by reference to the right jaws of R.3730 and the toothless jaw of R.8621, as above. This was then reversed (so as to appear to face to the left) and reduced slightly until it fitted the toothless restoration of R.2860. In this way the composite lateral reconstruction (Fig. 1) was derived.

SKULL OF R.2417. The skull of this 'juvenile' individual is very fragmentary, and has been mounted on thin steel bars to which the fragments have been glued. It is less complete than that of R.2860, and adds little to the description.

Three teeth, preserved *in situ* on the premaxillae, show the diagnostic ornamentation. Fragments of the frontals and parietals are preserved, and the supraoccipital, exoccipital-opisthotics, basioccipital and basisphenoid were figured by Andrews (1910 : pl. 9, figs 4, 4a, 5; the 'median foramen' in the basisphenoid, figured and labelled *for.*, is actually a hole that has been drilled to facilitate mounting on a steel peg). The form of the occipital condyle, in which the exoccipitals are involved, is exactly as in R.2860. Parts of the right squamosal and both quadrates are also preserved.

The right ramus of the lower jaw (Andrews 1910 : pl. 9 fig. 6) contains 24 tooth sockets with posteriorly a small depression suggestive of a 25th socket developing. The left ramus is heavily eroded. In this 'juvenile' specimen the angular extends slightly posterior to the ossified part of the articular, which was completed posteriorly in cartilage.

The postcranial skeleton. The detailed description of the postcranial skeleton of this species which was given by Andrews (1910 : 168–202, text-figs 78–94, frontispiece, pl. 10) is largely accurate, and a complete redescription is unnecessary. In the following account several details are added concerning ageing and osteological development; some misconceptions regarding characters of taxonomic importance are clarified and Andrews' reconstruction (1910 : text-fig. 94) is modified (Fig. 10).

VERTEBRAE. Five types of vertebrae are distinguished in describing the vertebral column of plesiosaurs, these being cervical, pectoral, dorsal, sacral and caudal. Pectoral vertebrae (defined by Seeley, 1874*a*) are transitional between cervicals and dorsals; in these the rib articulates with both the centrum (as in cervicals) and the neural arch (as in dorsals). In sacral vertebrae the centrum and neural arch together form a large facet for the modified sacral rib, and in the caudals the rib articulates only with the centrum, this usually possessing additional ventral facets for the chevrons.

Pectoral vertebrae (Fig. 9) can be identified and counted easily in 'juveniles' since the neural arches and centra are free, but in 'adults' these elements fuse and the line of fusion cannot be traced. It is therefore necessary to estimate the numbers of cervical, pectoral and dorsal vertebrae in 'adults' by comparison with the appearance of these vertebrae in 'juvenile' specimens. The boundary between dorsal and sacral regions is always obvious, and in entire specimens the number of presacral vertebrae may be counted reliably.

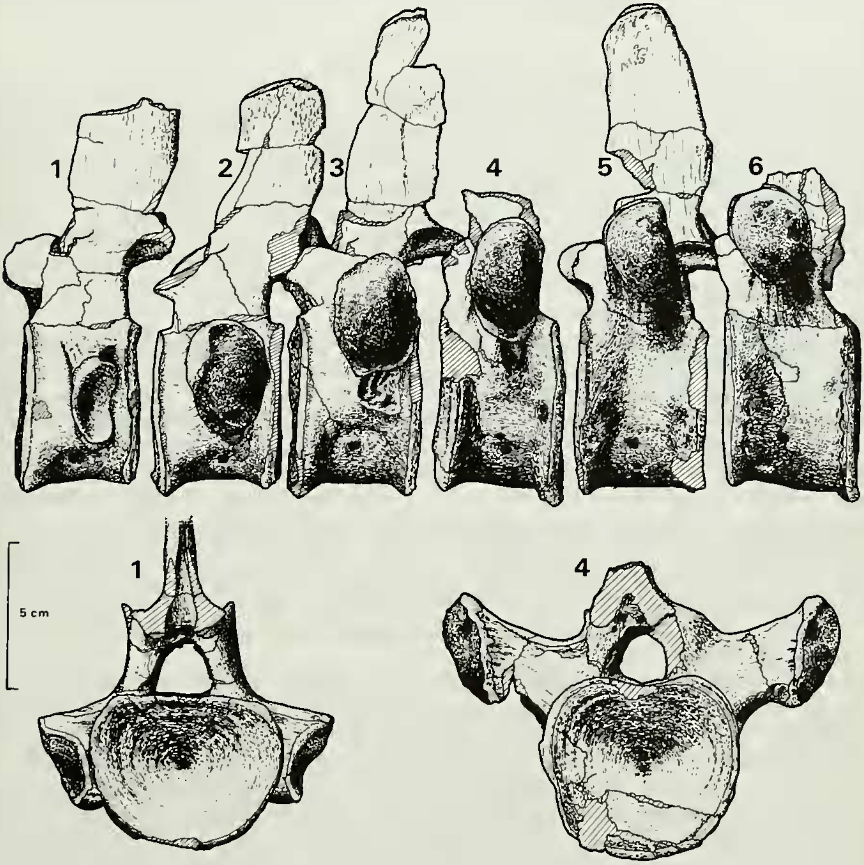


Fig. 9 *Cryptoclidus eurymerus* (Phillips), H.M.G. V.1104. 1–3, pectoral vertebrae; 4–6 anterior dorsal vertebrae (first, second and third dorsals). Left lateral view, with posterior views of two vertebrae.

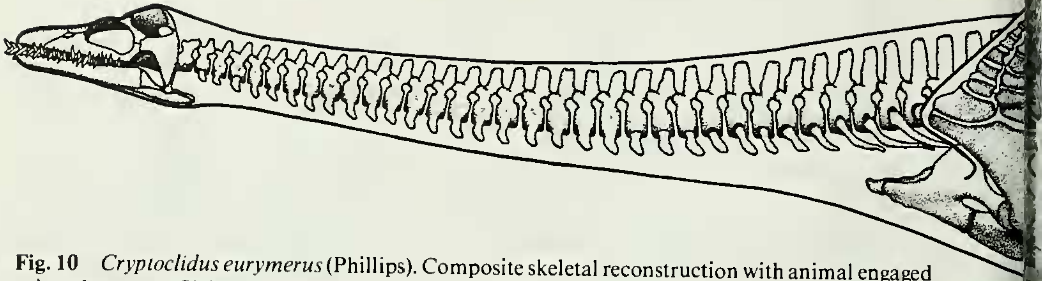


Fig. 10 *Cryptoclidus eurymerus* (Phillips). Composite skeletal reconstruction with animal engaged in subaqueous flight locomotion. Overall length of adult about four metres. See 'Note on the reconstruction', p. 280.

There are three specimens of *C. eurymerus* in which 55 presacral vertebrae are preserved. In R.2417, which is a 'juvenile', there are 32 cervicals, 3 pectorals and 20 dorsals, and this is also the estimated distribution of vertebral types in the 'adult' specimen R.2860. In the 'old adult' V.1091 the estimate of 29 cervicals, 3 pectorals and 23 dorsals suggests that the position of the transition from cervicals to dorsals is subject to variation. If a constant number of presacral vertebrae in this species is assumed from the evidence of 3 specimens with the maximum recorded number, then it must also be assumed that specimens with rather less than 55 presacrals (such as R.2862 with 53, R.2416 with 48) have been incompletely collected. Since the bones are disarticulated and entirely clear of the matrix, this cannot be checked but seems probable.

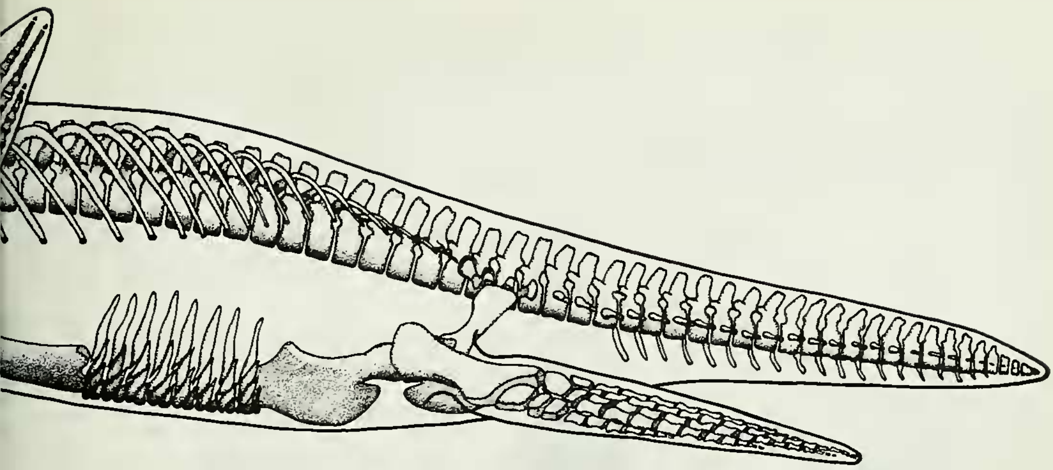
The vertebral column of plesiosaurs shows several features which do not vary significantly throughout the suborder but have sometimes been used erroneously for taxonomic purposes. These include relative size of vertebral types; proportional length of neural spines; relative diameter of the neural canal; relative development of zygapophyses and presence of nutritive foramina. In these features the present species is typical of all forms.

In any individual the largest vertebrae are the mid-dorsals, and these have proportionally (as well as actually) the longest neural spines. The diameter of the neural canal is maximal in the posterior dorsal vertebrae, and reduces both posteriorly and anteriorly.

The zygapophyses of dorsal and caudal vertebrae are small and weak, whereas those of cervical vertebrae are large and well developed. Williston (1914) thought that this indicated a relative lack of flexibility of the neck, but the reverse is more likely, since the spaces for cervical intervertebral discs are large, and the zygapophyses are constructed so as to limit only rotational movements.

Nutritive foramina are present in all vertebral centra. In the most anterior cervicals the paired foramina are very close together and are separated by a mid-ventral ridge; they may occasionally coalesce into a single median foramen as in Fig. 8a. They become progressively further apart in posterior cervicals and are laterally placed in pectorals, dorsals and sacrals. In caudals the nutritive foramina again become ventral, and tend to become subdivided.

Proportions of vertebral centra in plesiosaurs vary from species to species, and hence are of genuine taxonomic importance; however, taxonomists have frequently found difficulty in delimiting and defining taxonomic characters involving central proportions, and so their usefulness has been restricted. For example, Welles (1952, 1962) devised a 'vertebral index' system involving comparison of all three dimensions of centra (length, width and height) together with absolute measurements, but found this system to be too complicated to be of use other than for distinguishing plesiosauroid and pliosauroid material.



All plesiosauroid specimens here studied show the same pattern of variation in shape of the posterior articular facet. Maximum width always exceeds minimum central height, and their average ('average centrum diameter') is maximal in mid-dorsal vertebrae. Cervical, sacral and anterior caudal centra have oval articular facets, whereas these become rounded in dorsals and posterior caudals. If significant interspecific variation of this pattern were to occur, it would affect to only a small extent the strength and possibly the mobility of the column.

In contrast, interspecific variation of relative centrum length occurs and is of taxonomic importance since, being cumulative, it may affect considerably the overall proportions of the animal. However, proportional length of the centrum also increases with ontogeny, and shows individual variation, different regions of the column having differently proportioned centra; this must be understood before interspecific variation may be distinguished and employed as a taxonomic character. If the midventral centrum length is calculated as a percentage of the posterior average centrum diameter, the resulting index ('vertebral length index') may be plotted against vertebral number and used to analyse and distinguish these different variants.

When the graph of vertebral length index against vertebral number is plotted for one individual, this illustrates the pattern of intraindividual variation. If the graphs of conspecific individuals of different ages are plotted together (as in Fig. 13), this tests the relationship of the pattern of intraindividual variation to ontogeny and at the same time permits an analysis of the ontogenetic increase in central proportional length for each region of the vertebral column.

In *C. eurymerus* (Fig. 13) the anterior cervicals are proportionally the longest vertebrae; yet centrum length never exceeds average centrum diameter, and they cannot be described as elongated. The centra become proportionally shorter towards the pectorals; then posterior to these they increase in proportional length and reach a peak at or just before the anterior sacrals. The index then falls abruptly, the posterior sacral and anterior caudals being proportionally the shortest vertebrae. The proportional length of the centrum again increases towards the tip of the tail. This pattern of intraindividual variation is exhibited by individuals of all growth categories. In Fig. 13 the centra of the 'juvenile' individual (R.2417) have proportional lengths approximately 20% (20 index points) less than the corresponding centra of the 'old adult' specimen (V.1091). The graph also illustrates the fact that the anterior cervicals of 'juvenile' individuals may have the same central proportions as posterior cervicals of 'old adults'.

In the present species the centra are always amphicoelous, and there is sometimes a small notochordal pit. The vertebrae of 'juveniles' are smoother and neater in general appearance than those of older individuals, which generally have a rough and more wrinkled surface.

Ribs. These have been described by Andrews (1910) and Smellie (1915). All ribs are single-headed. Cervical and caudal ribs become fused to the centra in 'adults', but pectoral, dorsal and sacral ribs always remain free.

The anterior cervical ribs develop an anterior flange halfway along their length, giving

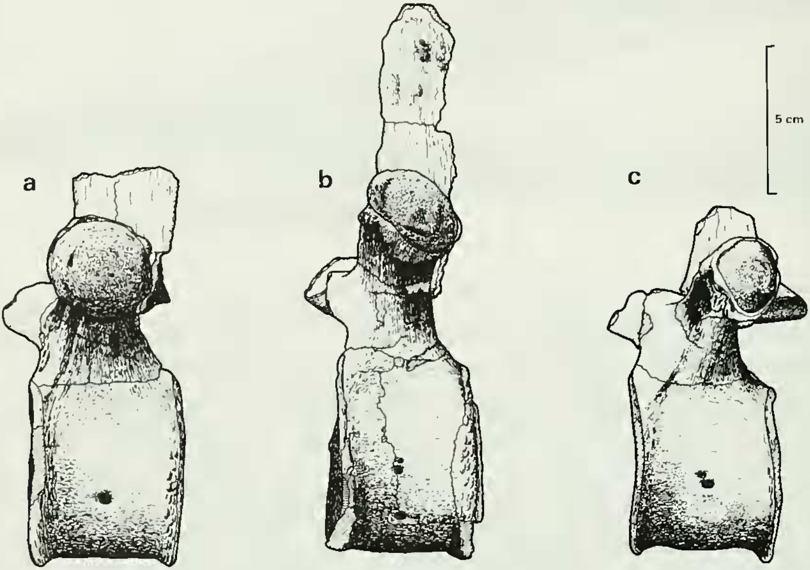


Fig. 11 *Cryptoclidus eurymerus* (Phillips), H.M.G. V.1104. a, eighth; b, fifteenth and c, twentieth dorsal vertebrae. Left lateral view.

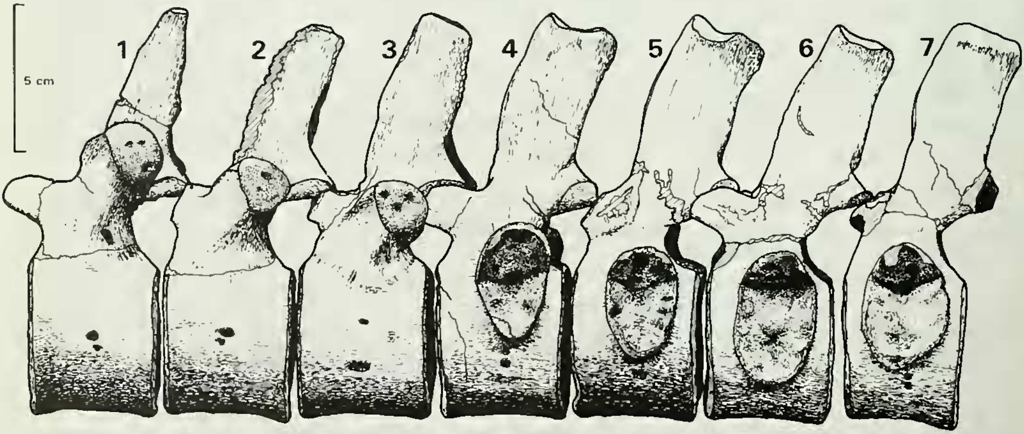


Fig. 12 *Cryptoclidus eurymerus* (Phillips), H.M.G. V.1104. 1–3, posterior dorsal vertebrae; 4–7, sacral vertebrae. Left lateral view.

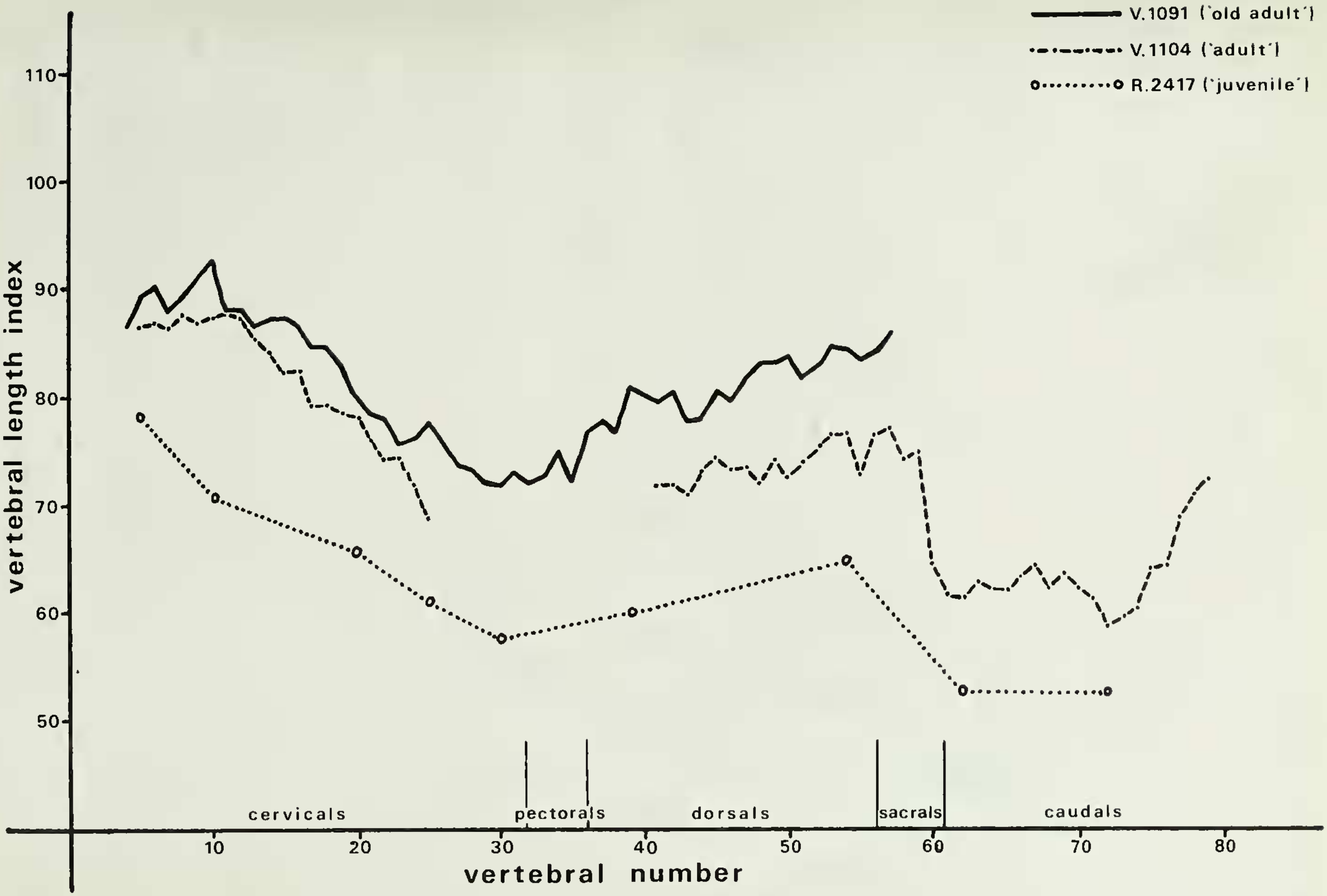


Fig. 13 *Cryptoclidus eurymerus* (Phillips). Graph of vertebral length index against vertebral number for three specimens of differing age, showing relationship of vertebral length index to topography and ontogeny. Measurements of R.2417 from Andrews (1910).

them an appearance which Andrews described as 'hatchet-shaped'. This flange is most prominent in 'old adults', but its development is irregular and may differ markedly in adjacent ribs.

Pectoral ribs are more elongated and curved than cervicals. Facets on the curved distal portions were observed in several specimens, and indicate that they overlapped one another to form a strengthened area for the attachment of the scapulae.

The anterodorsal and mid-dorsal ribs are long and curved, but posteriorly they become much shorter and straighter. The shape of the articulation with the transverse process changes with position on the column (see Fig. 11) and this enables ribs to be positioned with reasonable accuracy. When held in articulation with the respective transverse processes they can be spatially orientated; observations made using this approach have been taken into account in the drawing of the reconstructed skeleton (Fig. 10).

The sacral ribs are short and massive. On the anterior and posterior aspects of their dorsal ends they bear facets or depressions where they contacted and moved against adjacent sacral ribs. The 1st and 4th ribs are longer than the 2nd and 3rd, and they are orientated by their respective vertebrae so as to converge distally (Fig. 14). The shape of the dorsal end of the ilium matches the distal outline of the proximated sacral ribs, and it seems probable that the resulting joint was relatively mobile with respect to the vertebrae.

The caudal ribs are straight, dorsoventrally flattened, and orientated in a horizontal plane. They decrease in size posteriorly, and are absent from the terminal segments of the tail.

CHEVRONS. These paired bones are shorter than the corresponding caudal ribs, are slightly curved, and are orientated almost in a vertical plane. They are proportionally shorter in 'juveniles' and may fuse to the caudal centrum in 'old adults'. Chevrons are present from the 3rd caudal vertebra to within about four segments from the tip of the tail. Anterior to the 8th caudal vertebra their single heads articulate only with the facets on the posterior edge of the ventral aspect of the centrum; but posteriorly they articulate between vertebrae, and the 8th or 9th and subsequent caudal centra also bear anterior chevron facets.

PECTORAL GIRDLE. This has been described and figured by Andrews (1895*a*; 1910 : text-figs 87–89) and by Smellie (1915), and consists of the clavicles, scapulae and coracoids. An interclavicle is known only in specimen R.3538, in which it is a rudimentary splint of bone (Andrews 1910 : text-fig. 88).

The clavicles are comparatively large in 'juveniles', but grow at a much slower rate than the ventral rami of the scapulae, which come to meet superficial to them in 'adults' (Andrews 1895*a*). Their simplest shape is that of a right-angled triangle, with the right angle at the posteromedial corner, as in R.2616; more frequently the posterior border is concave, with the posterolateral corner drawn out into a short process as in R.2860, R.3538, R.3730 and V.1091. The two elements meet in the midline.

The 'adult' scapula is not distinctive, and has the usual triradiate structure. It consists of a strong vertically-orientated dorsal ramus, a short posterior ramus which forms the anterior half of the glenoid, and an expanded plate-like ventral ramus which meets its opposite superficial to the clavicles in the ventral midline and is prolonged posteriorly to meet the coracoids, thus forming a median keel-like scapulocoracoid bar. A rough prominence on the lateral border of the ventral ramus and prominent rugosities along the posterior margin of the dorsal ramus indicate the origin of powerful muscles at these sites.

The 'adult' coracoids are large plates which are thin in section except for the lateral margins and the anterior region between the glenoids. In the interglenoid region a horizontal bar is formed to resist the inward forces produced by the paddles in locomotion (Watson 1924, Robinson 1975). The lateral margins are thickened to form bars which curve posterolaterally and terminate as the posterior cornua. When developed fully in 'adults' and 'old adults' the distance between the tips of the two cornua is up to 40% wider than the distance across the posterior margins of the glenoids, a character which distinguishes the genus *Cryptoclidus* from its contemporaries. In 'juveniles' the coracoids cannot be distinguished since the cornua are incompletely formed.

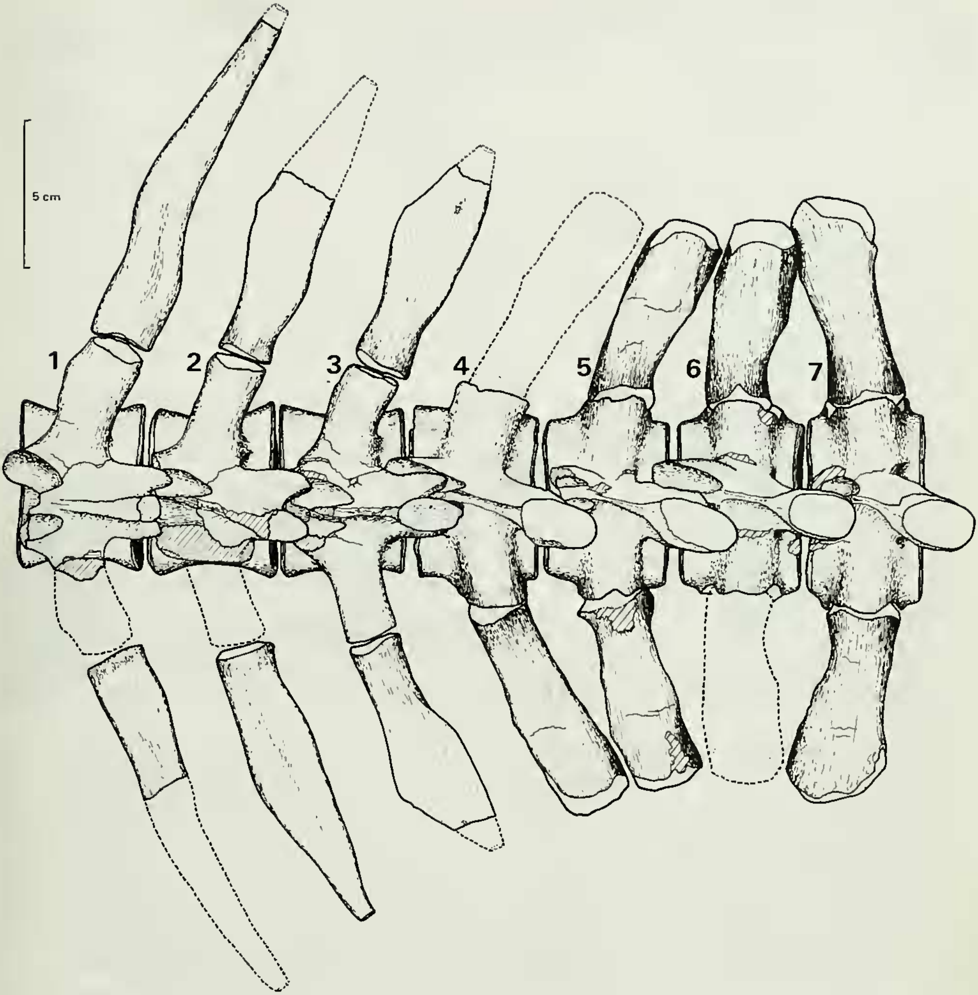


Fig. 14 *Cryptoclidus eurymerus* (Phillips), H.M.G. V.1104. 1–3, posterior dorsal vertebrae and ribs; 4–7, sacral vertebrae and ribs. Dorsal view.

The posterior margin of the coracoids does not ossify fully until the 'old adult' stage. The thin median part of the coracoids then extends backwards well behind the cornua, and on either side of this extension rounded notches are developed. The extension is best shown by specimen V.1807, but is beginning to develop in V.1091 (Smellie 1915 : text-fig. 7a) in which the position of the notches is apparent. It seems probable that the median posterior growth was visceral to the most anterior gastralia, which then curved upwards and inwards through the notches. In this way a fairly firm union between the pectoral girdle and the gastralia would be formed.

The glenoid is a large oval facet which is elongated anteroposteriorly and is only shallowly cupped. It is formed equally by the scapulae and coracoids. On the surrounding dorsal and ventral surfaces of these elements are numerous small foramina, the apertures of which face towards the glenoid. These are also found in abundance around the head of the humerus, and were associated with capsular ligaments. Comparison of the relatively small humeral head with the large glenoid indicates that the capsule was large, and the joint must have been very flexible. Elevation and depression of the humerus in the glenoid, as would occur with the sub-aqueous flight locomotion postulated by Robinson (1975), is osteologically unrestricted; whereas full rotation of the humerus to produce a rowing stroke as suggested by Watson (1924) is not possible, since the humeral tuberosity and anterior margin of the coracoid would coincide spatially.

In 'juvenile' individuals the clavicles appear relatively large and the ventral rami of the scapulae do not meet in the midline. In the 'adult' stage the ventral rami in the midline meet anterior processes of the coracoids to form the scapulocoracoid bar, but the six elements still remain separate. In 'old adults' progressive fusion of the pectoral girdle takes place, as is shown by specimens V.1091, V.1807 and R.2862. In all these specimens the coracoids are fused, and the scapulae are fused. In V.1091 the sutures between scapulae and coracoids in the scapulocoracoid bar are fusing, but those behind the glenoids remain open, and the single clavicle preserved with this specimen is quite free. In V.1807 all sutures between the scapulae and coracoids are fully fused; unfortunately the clavicles are not preserved, but their absence demonstrates that they were still free from the scapulae. Finally in R.2862 the clavicles are fused to each other and are also fused posteriorly onto the visceral surface of the ventral rami of the scapulae. Thus in this specimen the pectoral girdle is a single composite structure.

PELVIC GIRDLE. This has been described and figured adequately by Andrews (1896, 1910 : text-fig. 92), and is indistinguishable from the pelvic girdles of contemporary plesiosauroids. The pubes and ischia form expanded ventral plates which meet their opposites in the midline, and they were probably connected by a median cartilaginous bar which divided the obturator foramen; this bar is sometimes ossified in Cretaceous elasmosaurs (Welles 1962). The ischium is proportionally shorter than this element in pliosaurs. The ilium contacts the ischium only, and is reduced to a bar which ascends posteromedially from the acetabulum to the sacrum. The acetabulum has an elongated oval shape, and differs from the pectoral glenoid by facing posterolaterally rather than laterally.

GASTRALIA. In plesiosaurs the gastralia form a well-developed basket which functioned as a ventral carapace. In the present species this comprises eight complete rows of elongated cylindrical elements, each row consisting of a median element and three pairs of lateral elements (1st, 2nd and 3rd laterals). Posterior to these are a further two rows which lack the median element.

Median elements show bilateral symmetry and are the most massive. In dorsal view the left and right rami meet at an angle of about 165°, with the apex directed anteriorly. Laterally the anterior surface of each ramus forms a large concave facet into which fits the medial end of the 1st lateral element. In anterior or posterior view the median element is very slightly curved, giving the ventral surface of the animal a very gentle convex shape.

The 1st and 2nd lateral elements are closely similar. In dorsal view they appear twisted into a gentle S-shape as a result of excavations for the articulation of adjacent elements. The

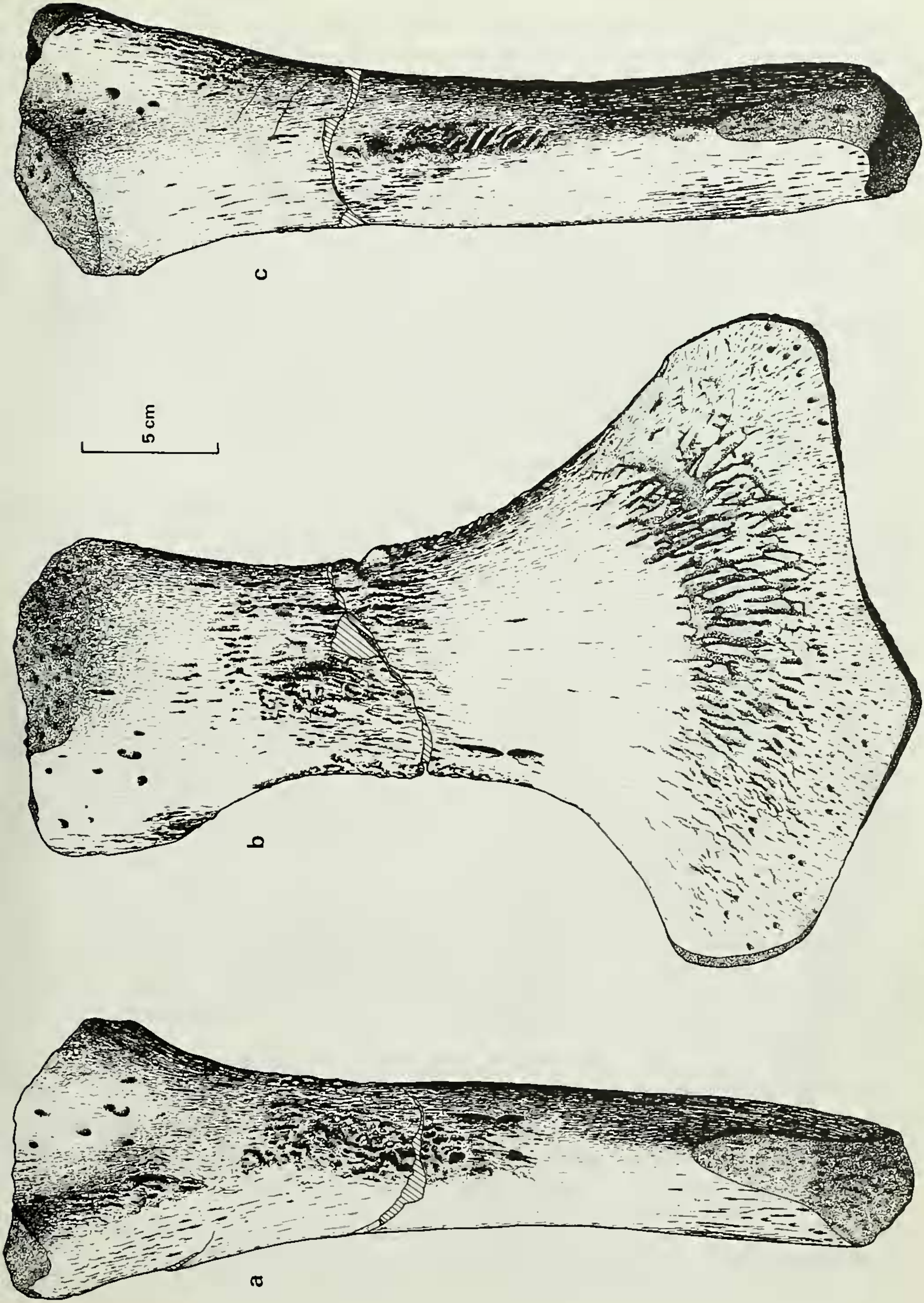


Fig. 15 *Cryptoclidus eurymerus* (Phillips), H.M.G. V.1104. Left humerus: a, posterior; b, ventral; c, anterior aspect.

1st lateral has a long posterior facet on the medial end for articulation with the median element, and the lateral end is hollowed on its anterior aspect for the reception of the 2nd lateral. Similarly, the 2nd lateral articulates posteromedially with the 1st lateral and anterolaterally with the 3rd lateral element. 1st and 2nd laterals may be orientated spatially by the form of their ends: the medial end is the most gently tapering and pointed, and the lateral end shows more curvature in the vertical plane. When 1st and 2nd laterals are compared, the 2nd laterals show more vertical curvature and their lateral ends are more tapered.

Third lateral elements show more vertical curvature than other elements, and are easily distinguished as there is only one posteromedial facet for articulation with the 2nd lateral. The outer end is somewhat flattened and bluntly terminated.

In specimen R.2862 the plastron has been preserved *in situ* because of an unusual concretion of the surrounding clay matrix (Andrews 1910 : text-fig. 86). The elements of each row are closely associated, and in addition the plastron is strengthened by the interlocking of the tips of gastralia of adjacent rows. Lying superficial to the anterior margins of the pubes are the incomplete 9th and 10th rows, the 9th lacking the median element and the 10th consisting only of a forked piece of bone representing the medial end of a lateral element. In V.1104 this forked gastralium is almost entire and was probably the only element in the row. It has a small anterior facet towards the lateral end, where it probably contacted the posterior surface of the 9th row laterals.

Forelimb. This has been described and figured by Andrews (1910 : text-figs 90, 91A) and by Smellie (1915). In the 'adult' the humerus, radius and ulna are diagnostic of the species, whereas the distal parts of the paddle are indistinguishable from those of contemporary species. The length of the entire limb may exceed 1 m, and the overall span of the outstretched paddles may be 3 m in a specimen of overall length 4 m.

The 'adult' humerus (Figs 15, 16a, 17a, 17b) is characterized by a disproportionate enlargement of the anterodistal part which forms the radial facet. In 'juveniles' this character is insufficiently developed to be diagnostic.

Rugosities on the surface of the bone indicate the positions of muscle insertions. Prominent rugosities are present running axially down both the anterior and posterior borders of the humeral shaft (Figs 15a, 15c), and between these on the ventral surface is a prominent band of rugosities which is most developed midway anteroposteriorly and at about one third of the humeral length from the proximal end (Fig. 15b). The dorsal surface of the shaft (Fig. 16a) is smooth and without evidence of muscle attachments. It is not possible from a study of rugosities to distinguish and outline all the numerous muscle insertions shown in the reconstructed figures of the humerus of *Cryptoclidus* given by Robinson (1975) or of *Muraenosaurus* given by Watson (1924).

Rugosities are present on the prominent tuberosity of the humerus, being most evident on the anterior and posterior edges and the proximal part of the dorsal surface (Figs 15a, 15c and 16a). These probably mark the insertions of the rotator cuff musculature. In the 'old adult' the tuberosity may become separated from the head by the development of a strip of finished periosteal bone surface which divides the usually single proximal cartilaginous area (Fig. 17a) into two, as in V.1835.

On the dorsal and ventral surfaces of the distal end of the humerus there are extensive areas of shallow grooves and ridges, which become more prominent distally. In addition this area, together with the surfaces of all the epipodials and mesopodials, is marked by numerous small foramina, the apertures of which face peripherally. The distal paddle bones have roughened surfaces. All these various markings indicate the presence of a tough yet thin covering of ligaments and small muscles whose function was to strengthen and slightly stiffen the paddle, making it streamlined and only slightly flexible.

Even in small 'juveniles' the radius of this species has a characteristic shape, being greatly expanded proximally and anteriorly to match the expansion of the humerus. The bone thus has a sigmoid anterior outline which is convex proximally and concave distally, and by this

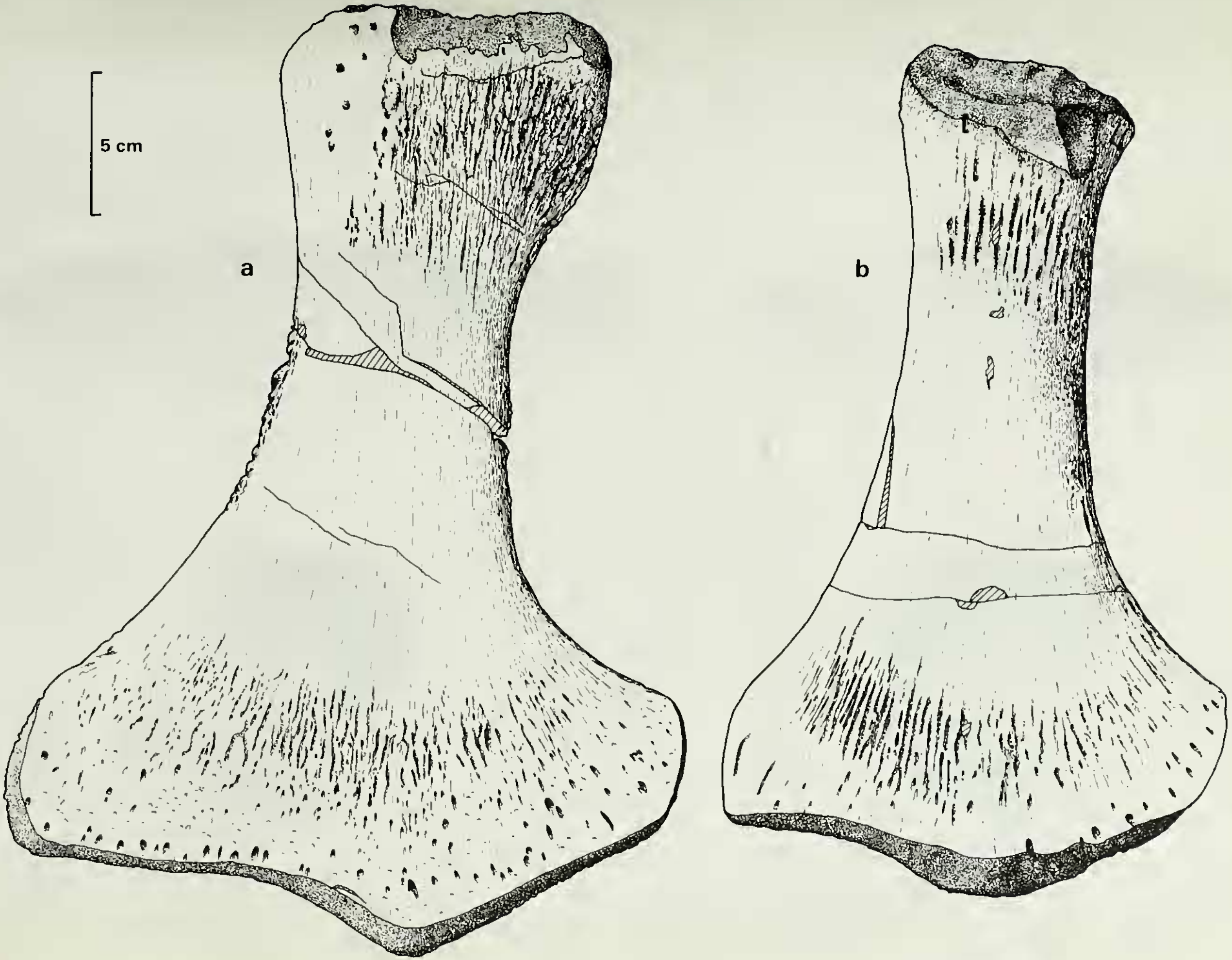


Fig. 16 *Cryptoclidus eurymerus* (Phillips), H.M.G. V.1104: a, left humerus; b, left femur: dorsal aspects.

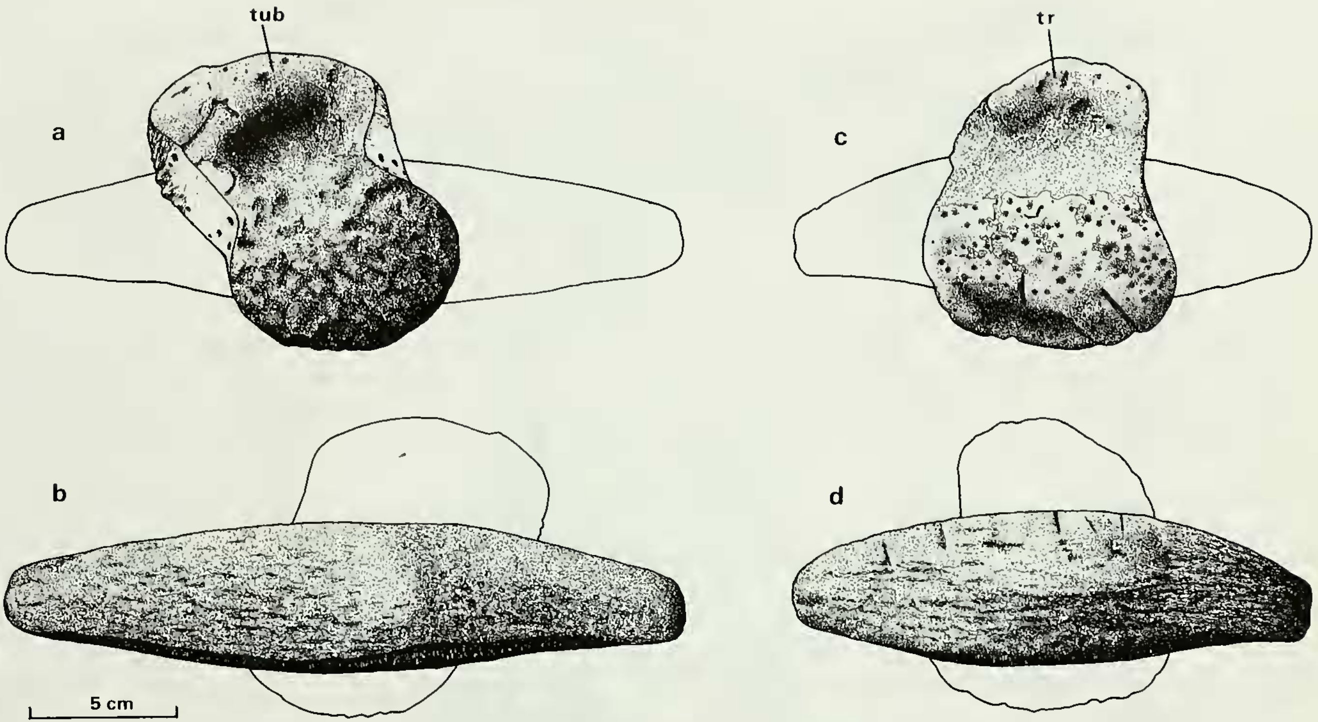


Fig. 17 *Cryptoclidus eurymerus* (Phillips), H.M.G. V.1104. Left humerus: a, proximal; b, distal aspect. Left femur: c, proximal; d, distal aspect. tub, tuberosity of humerus; tr, trochanter of femur.

character it may be distinguished from the radius of all contemporary species in which the anterior margin is concave throughout.

The ulna is generally very short and wide, its anteroposterior width being approximately twice its length. Occasionally, as in V.1091, there is evidence that it may ossify from two distinct centres.

The combined shape of the radius, ulna and distal end of the humerus results in the distal part of the paddle being orientated backwards at an angle of about 25° to the axis of the humeral shaft, with the characteristic expansions of the humerus and radius forming a prominent elbow in this species.

In all plesiosaurs the radius and ulna are separated by a gap or foramen, presumably for the passage of interosseous nerves and blood vessels. This foramen is usually evident at all stages of growth, but in the present species it is visible only when the advanced ossification of the 'old adult' stage is reached, as in V.1091, V.1809 and R.2862.

There are essentially six carpals (mesopodials), arranged in two rows of three, the proximal row consisting of the radiale, intermedium and ulnare. There is a considerable tendency to develop additional elements (accessory ossicles) which may be preaxial or postaxial, or both, and which may remain free or fuse to an adjacent epipodial or carpal. They usually result in asymmetry between left and right paddles of an individual, and are of no taxonomic significance.

The first (most anterior) metacarpal is flattened and resembles a carpal, whereas the second to fifth are cylindrical and phalangiform. The fifth metacarpal, characteristically for plesiosaurs later than the Lower Jurassic, is displaced proximally into the distal metacarpal row and articulates with the ulnare.

The exact number of phalanges in each digit cannot be stated since the paddles have usually suffered from post-mortem disturbance and in the past were generally collected without due attention being paid to their position. The longest digits (3rd and 4th) probably consist of about 15 phalanges, with the 2nd, 5th and 1st containing decreasingly fewer.

Hindlimb. This has been described and figured by Andrews (1910). It is slightly shorter and a little more slender than the forelimb, and is very similar to the hindlimbs of contemporary species. The femur and tibia differ from the humerus and radius, but the fibula, tarsals, metatarsals and phalanges are indistinguishable from the corresponding elements of the forelimb.

In 'juveniles' the femur (Figs 16b, 17c, 17d, 18) may be closely similar to the humerus, but these elements are distinguished readily in the 'adult'. The distal anterior portion of the femur is not so expanded; the trochanter is not so well developed as the tuberosity of the humerus and does not form so prominent an angle at its posterodorsal margin; and the proximal portion of the femoral shaft is circular in section, whereas that of the humerus is oval, with definite anterior and posterior margins.

The rugosities marking muscle insertions on the proximal portion of the femur have the same general appearance as in the humerus, but differ in two details. The anterior marginal area of rugosities is less prominent than in the humerus, and is surrounded by an area of smooth bone (cf. Figs 18c and 15c); the rugosities on the ventral surface of the femoral shaft tend to be aggregated around two centres, one on either side of the ventral midline of the shaft, rather than around one as in the humerus (cf. Figs 18b and 15b). It is not possible from these rugosities to delimit the insertions of a large number of individual muscle blocks in the way suggested by Robinson (1975).

Surface evidence for the presence of capsular ligaments, rotator cuff musculature and the ligaments and small muscles of the paddle are exactly as in the pectoral girdle and limb. Several deep posterior foramina at the base of the distal expansion probably held the origins of large postaxial collateral ligaments. As in the humerus, the trochanter of 'old adults' may become separated from the head by the development of a strip of finished periosteal bone surface which divides the usually single cartilaginous area into two; this is seen in specimen V.1810.

The tibia is a rectangular, almost square bone, differing from the radius in that it lacks the proximal anterior expansion. A foramen between the tibia and fibula is evident only when the 'old adult' stage is reached, as in R.2616.

The left hindlimb of R.3703 (Andrews 1910 : text-fig. 93) is believed to be complete, and has a phalangeal formula of 3 : 9 : 13 : 13 : 12.

Note on the reconstruction

Fig. 10, pp. 268–9, represents a reconstructed lateral view of a swimming 'adult' individual of *Cryptoclidus eurymerus*, and was based so far as possible on the neotype specimen R.2860. The skull is a proportional reduction of Fig. 1. The outlines of the vertebrae were drawn from the frontispiece in Andrews (1910) (a photograph of the mounted skeleton) but with spacing to allow for intervertebral discs. The ribs (which were incorrectly 'hung' in order to fit the specimen into the narrow showcase) have been reorientated after study of specimens R.2860, V.1104 and V.1091 (the latter specimen has been mounted correctly in this respect). The girdles were drawn from R.2616 in which they are mounted accurately, and the gastralia were reconstructed from R.2860, R.2862 and V.1104.

The limbs were drawn largely from R.2860, with the full complement of phalanges of the forelimb taken from R.2864 (a specimen of *Muraenosaurus leedsii*). The orientation of the active paddles conforms with the theory of subaqueous flight locomotion of plesiosaurs discussed by Robinson (1975, 1977).

The body shape of this animal is flatter and wider than in the reconstruction of Andrews, and the neck is proportionally longer. There is little if any support for the argument presented by Robinson (1977 : fig. 12) and followed by Taylor (1981) that the vertebral column and the ventral skeletal elements (girdles and gastralia) were analogous in shape to an archer's bow and taut bow-string respectively; they are of almost equal length. However, the arrangement of the pectoral ribs, the close association of the gastralia with the girdles, and the structural arrangement of the sacrum and ilia strongly support her contention that these functioned as tensional force-transmitting elements. In the present reconstruction the hydrostatic pressure of the viscera assists in tensioning the ventral skeletal elements in a gently curving configuration, and the flattened body shape provides additional dorsoventral stabilization during subaqueous flight locomotion as in marine turtles.

Cryptoclidus richardsoni (Lydekker, 1889)

(Fig. 44b)

1889 *Cimoliosaurus richardsoni* Lydekker: 240, figs 73, 74 (mis-spelling of *Cimoliasaurus* Leidy, 1852).
1889 *Cimoliosaurus richardsoni* Lydekker; Mansel-Pleydell: 171, fig. 1; pl. 1.
1909 *Cryptoclidus richardsoni* (Lydekker) Bogolubov: 48.
1959 *Crytpocleidus richardsoni* (Lydekker); Delair: 66 (lapsus).
1959 *Cryptocleidus richardsoni* (Lydekker); Delair: 67.
1963 *Cryptocleidus richardsoni* (Lydekker); Persson: 24.

HOLOTYPE. Specimen R.6696, an almost complete postcranial skeleton which was discovered and collected by Nelson M. Richardson of Dorset and identified initially as *Plesiosaurus plicatus* Phillips (a *nomen dubium*) by Mansel-Pleydell (1888). The pectoral girdle was figured by Lydekker (1889) and the whole (then mounted) skeleton was described and figured by Mansel-Pleydell (1889). No other specimen is known.

TYPE LOCALITY AND HORIZON. A label with the holotype states that it was found 'in a brick-field between Montevideo House [near Weymouth] and Chickerell, at a depth of 30 feet'. Upper Jurassic, Callovian or Oxfordian Stage. From the Oxford Clay, which includes (Arkell 1933) the six ammonite zones from the zone of *Kosmoceras jason* to the zone of *Cardioceras cordatum*.

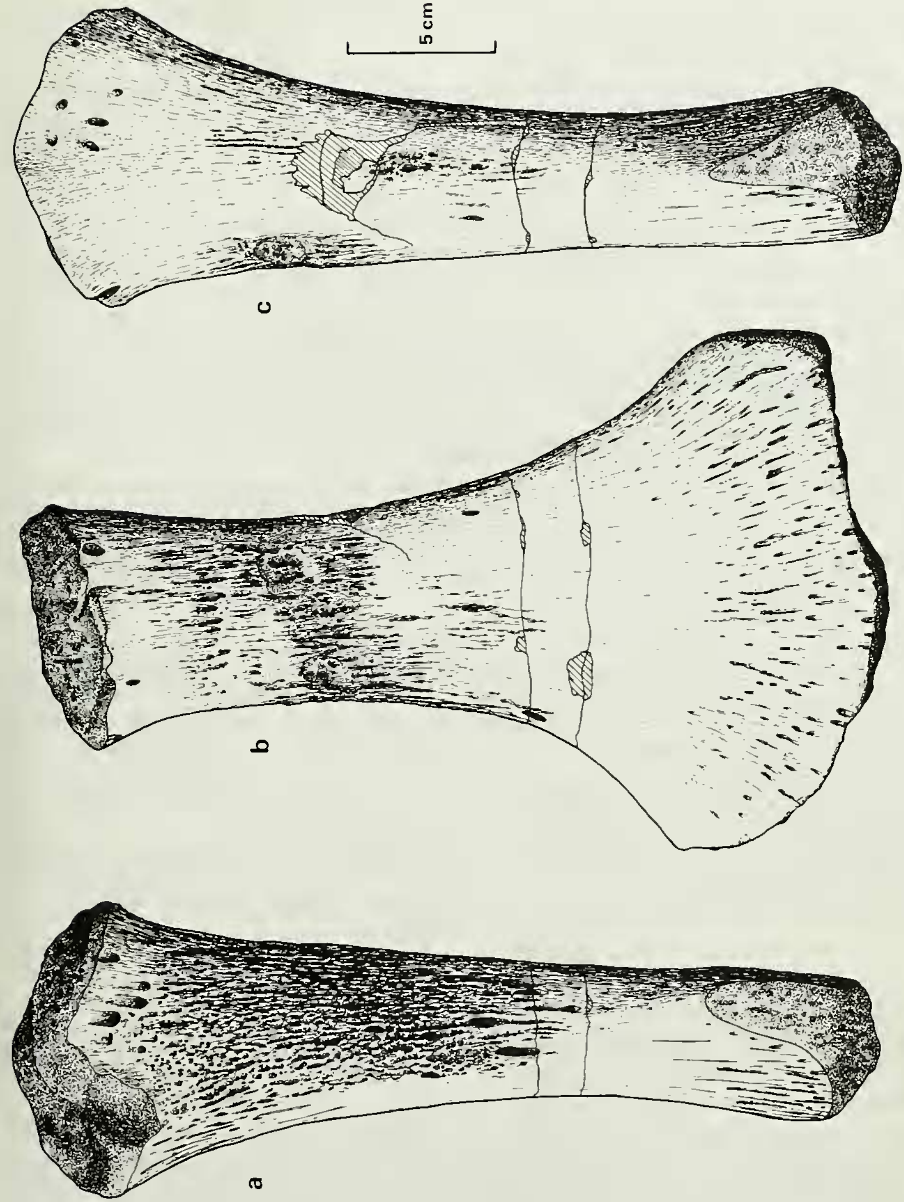


Fig. 18 *Cryptoclidus eurymerus* (Phillips), H.M.G. V.1104. Left femur: a, posterior; b, ventral; c, anterior aspect.

Diagnosis. Member of the genus *Cryptoclidus* in which the distal anterior portion of the humerus is not greatly expanded; the radius has a concave anterior border, and the humeral facet is only slightly longer than the facet for the radiale; the ulna is approximately square.

Description of material. Specimen R.6696 is an 'old adult', and resembles closely 'old adult' specimens of *C. eurymerus* in size, proportions, structure and degree of ossification. The skull and the right hindlimb are missing.

The vertebrae have been crushed, distorted and broken so that not all can be orientated or identified positively. They bear numbers in white paint in two series, but this is neither original nor reliable. Parts of 73 vertebrae are preserved and are here tentatively identified as 32 cervicals, 3 pectorals, 17 dorsals, 2 sacrals and 19 caudals. Three or four caudal centra are required to complete the tip of the tail. It is quite possible that 2 dorsals, 2 sacrals and a few caudals are missing; these would bring the vertebral count up to that of *C. eurymerus.* The neural arches and the cervical and caudal ribs are fused to the centra throughout, and an 'old adult' feature is the fusion of the chevrons to the caudal centra; all these are now largely broken away and missing.

The scapulocoracoid bar and the thin areas of the coracoids have been eroded away. The remaining parts of the pectoral girdle have been broken into several pieces which can be fitted together. Anteriorly the specimen has suffered from postmortem decay of the spongy bone such that the outer lamellar parts are separated. A piece of bone (numbered '7' in white paint) which has suffered in this way appears to be part of the right clavicle, and shows that it was large and triangular in outline as in *C. eurymerus.*

The scapulae and coracoids agree in structure with those of *C. eurymerus*, and are fused together (an 'old adult' feature). The posterior cornua of the coracoids are not quite complete to their tips, but on the right side are preserved parts of the lateral and posterior margins of this element. Extrapolation of these margins indicates that the cornua were developed to the same extent as in *C. eurymerus.*

The pubis and ischium do not differ from the corresponding elements in *C. eurymerus*, but the dorsal head of the ilium is smaller and more rounded.

The humerus lacks the anterodistal expansion characteristic of *C. eurymerus.* The distal expansion is produced very largely by posterior growth of the posterodistal part, and thus resembles closely that of *Muraenosaurus leedsii* (see Fig. 44). The radial facet is larger than that for the ulna. Both humeri have been slightly squashed so that the shaft appears a little too wide in dorsal aspect.

The femur is not quite so expanded distally as in *C. eurymerus*, and this expansion is greater posterior to the axis of the shaft.

The epipodials of both limbs resemble those of *Muraenosaurus leedsii.* A foramen is formed between each pair as in 'old adult' specimens of *C. eurymerus.* Numerous phalanges and fragments of ribs and gastralia are also preserved, and show no distinctive characters.

Genus ***MURAENOSAURUS*** Seeley, 1874

1874*a* *Muraenosaurus* Seeley: 197.
1909 *Picrocleidus* Andrews: 421 (subjective synonym).
1940 *Tremamesacleis* White: 463 (subjective-objective synonym).

Type species. *Muraenosaurus leedsii* Seeley, 1874.

Additional English species. *Muraenosaurus beloclis* Seeley, 1892.

Diagnosis. Plesiosauroids in which the teeth are ornamented by many longitudinal ridges; the dentary bears 19 to 22 teeth on each ramus; the premaxillae bear 5 teeth each, of which the 1st and 5th are small and the 2nd to 4th are large; the most anterior maxillary tooth (6th upper tooth) is small and the 8th and 9th upper teeth are large; the parietals form a sagittal crest; the quadrate overlaps the quadrate ramus of the pterygoid posteromedially; the paroccipital process of the exoccipital-opisthotic is relatively long and slender; the occipital condyle is ringed by a groove, and is formed from the basioccipital only; there are about 66 presacral vertebrae, of which usually 44 are cervical; the cervical vertebrae have relatively platycoelous centra, the length of which exceeds the height in anterior vertebrae, and exceeds or is approximately equal to the height in posterior vertebrae; the clavicles are reduced or absent; the interclavicle is developed and may be plate-like or reduced and lanceolate; the coracoids meet the scapulae in the midline in 'adults'; the width across the posterior cornua of the coracoids is about equal to or only just in excess of the interglenoid width in 'adults'; the elements of the pectoral girdle tend to fuse in old individuals; there are normally only two epipodials in the manus; a foramen is present between the epipodials even in 'juveniles'.

Muraenosaurus leedsii Seeley, 1874
(Figs 19–21, 43b, 44c)

1871 *Plesiosaurus plicatus* Phillips: 313, figs 118, 119 (*nomen dubium*).
1874*a* *Muraenosaurus leedsii* Seeley: 197; pl. 21.
1881 *Plesiosaurus leedsii* (Seeley) Whidborne: facing p. 480.
1888 *Plesiosaurus plicatus* Phillips; Lydekker: 351.
1888 *Muraenosaurus leedsi* 'Seeley'; Lydekker: 351 (incorrect subsequent spelling).
1889 *Cimoliosaurus durobrivensis* Lydekker: vii (mis-spelling of *Cimoliasaurus* Leidy, 1852).
1889 *Cimoliosaurus plicatus* (Phillips) Lydekker: 234.
1892 *Muraenosaurus platyclis* Seeley: 139, figs 6, 7.
1895*c* *Muraenosaurus plicatus* (Phillips) Andrews: 429, figs 1–3.
1909 *Muraenosaurus leedsi* 'Seeley'; Andrews: 418.
1909 *Muraenosaurus platyclis* Seeley; Andrews: 418.
1909 *Muraenosaurus durobrivensis* (Lydekker) Andrews: 418.
1910 *Muraenosaurus leedsi* 'Seeley'; Andrews: 120, text-figs 44, 59, 62, 63; pls 3, 4, 6 fig. 6.
1910 *Muraenosaurus durobrivensis* (Lydekker); Andrews: 127, text-figs 43, 45, 49–57, 60, 65, 67; pl. 5.
1910 *Muraenosaurus platyclis* Seeley; Andrews: 134, text-figs 48, 58, 68, 69; pl. 6 figs 1–5.
1940 *Muraenosaurus leedsi* 'Seeley'; White: 463.
1940 *Tremamesacleis platycleis* ('Seeley') White: 463, fig. 9d (mis-spelling).
1940 *Tremamesacleis durobrivensis* (Lydekker) White: 463.
1959 *Muraenosaurus leedsi* 'Seeley'; Delair: 60.
1959 *Muraenosaurus plicatus* (Phillips); Delair: 60.
1962 *Muraenosaurus leedsii* Seeley; Welles: 7; table 4.
1962 *Muraenosaurus leedsi* 'Seeley'; Welles: table 1.
1962 *Muraenosaurus durobrivensis* (Lydekker); Welles: tables 1, 4, 5.
1962 *Muraenosaurus platyclis* Seeley; Welles: 9; table 1.
1963 *Muraenosaurus leedsi* 'Seeley'; Persson: 24.
1963 *Muraenosaurus plicatus* (Phillips); Persson: 24.
1963 *Tremamesacleis platyclis* (Seeley); Persson: 24.
1963 *Tremamesacleis durobrivensis* (Lydekker); Persson: 24.
1964 *Muraenosaurus leedsi* 'Seeley'; Novozhilov: 321, figs 305–307.
1964 *Tremamesacleis platycleis* ('Seeley'); Novozhilov: fig. 308.

HOLOTYPE. The Leeds Collection specimen R.2421, an almost complete 'adult' postcranial skeleton. It was described initially by Seeley (1874*a*), and was described and figured extensively by Andrews (1910 : pl. 3 figs 1, 1a, 2, 2a, 3, 3a, 6; pl. 4 figs 1–10). Note that the teeth figured by Andrews (1910 : pl. 3 figs 4, 4a and 5), stated to belong with this specimen, are crocodilian and probably referable to the genus *Metriorhynchus*.

TYPE LOCALITY AND HORIZON. An unspecified brick-pit near Peterborough, England; Upper Jurassic, Callovian Stage. From the lowest deposits of the Oxford Clay, which includes the zones of *Kosmoceras jason*, *Erymnoceras coronatum* and *Peltoceras athleta* (see Andrews 1910 : vii).

DIAGNOSIS. Members of the genus *Muraenosaurus* in which the cervical ribs rarely develop a prominent anterior flange; the interclavicle is plate-like with a median anterior notch and a median posterior projection; in the manus the intermedium has a very small contact with the radius and a large articulation with the ulna; the overall length of the 'adult' is 4·5 to 5·2 metres.

DISTRIBUTION AND RANGE. Diagnostic material is known only from the Peterborough area. Upper Jurassic, Callovian Stage only.

REFERRED SPECIMENS. Since remains of this species are comparatively abundant, only those specimens mentioned in the text are listed below; a fuller list is given elsewhere (Brown 1975). All specimens are from Oxford Clay in the Peterborough area.

R.2422 (Fig. 20). Incomplete 'old adult' skeleton. Neurocranium figured by Andrews (1910 : text-fig. 44).
R.2424. Incomplete 'juvenile' postcranial skeleton. Clavicle figured by Seeley (1892 : fig. 8).
R.2426. Incomplete 'old adult' postcranial skeleton. Interclavicle figured by Seeley (1892 : fig. 9).
R.2628 (Fig. 21d). Incomplete 'juvenile' postcranial skeleton partly figured by Andrews (1895*c* : figs 1–3; 1910 : text-figs 65, 67; pl. 5 figs 1–9, 11, 12). Holotype of *M. durobrivensis.*
R.2678 (Fig. 21a). Incomplete 'adult' skeleton partly figured by Seeley (1892 : fig. 7) and by Andrews (1910 : text-figs 48, 68, 69; pl. 6 figs 1–5) as the holotype of *M. platyclis.*
R.2861. Incomplete 'adult' skeleton partly figured by Andrews (1910 : text-figs 43, 45) as *M. durobrivensis.*
R.2863. Incomplete 'juvenile' skeleton.
R.2864. 'Adult' skeleton. Limbs figured by Andrews (1910 : text-figs 59, 63).
R.3704 (Fig. 21b). Pectoral girdle of an 'old adult'. Figured by Andrews (1910 : text-fig. 62; pl. 6 figs 6, 6a).

Discussion of synonymy

In 1871, Phillips described thirteen vertebrae from the Oxford Clay of St Clements, near Oxford, under the new name *Plesiosaurus plicatus.* These he distinguished from other vertebrae (variously named) by their greater relative length and their flat articular faces. Three years later, Seeley (1874*a*) described a postcranial skeleton then in the private collection of A. N. Leeds (now specimen R.2421), naming it *Muraenosaurus leedsii.* This specimen, which is an 'adult', has relatively elongate centra and an ossified scapulocoracoid bar. The dermal elements of the pectoral girdle are missing.

Lydekker (1888) visited the Leeds Collection, taking with him the type vertebrae of *P. plicatus* Phillips. He found that these were indistinguishable from vertebrae of the holotype of *M. leedsii*, whereupon he referred Seeley's specimen to *P. plicatus.* In 1889 this species was included in the genus *Cimoliasaurus.*

In 1889, Lydekker mentioned a further Leeds Collection specimen (now R.2428, which is a 'juvenile') for which he proposed the new name *Cimoliasaurus durobrivensis*; this he distinguished from *C. plicatus* on account of its slightly shorter vertebrae and the absence of an ossified scapulocoracoid bar. Andrews (1895*c*) examined several Leeds Collection specimens including the types of *C. durobrivensis* and *M. leedsii*, and found that the only differences were variations in size and in the extent of ossification. These he correctly ascribed to age differences (and perhaps sexual dimorphism) and referred all specimens to *Muraenosaurus plicatus.*

In 1892, Seeley described under the new name *M. platyclis* a further Leeds Collection specimen (now R.2678) which he distinguished from *M. beloclis* (herein a distinct species) and *M. (Cryptoclidus) platymerus* (herein a junior synonym of *Cryptoclidus eurymerus*) on the form of the dermal elements of the pectoral girdle. He did not attempt to distinguish the specimen from the types of *M. leedsii* and *C. durobrivensis* in which at that time no dermal pectoral elements had been recognized.

In 1909, Andrews reversed his earlier opinion by recognizing *M. leedsii, M. platyclis* and *C. durobrivensis* as discrete congeneric species. In 1910 he published distinguishing diagnoses, using as his criteria comparative size, comparative proportions and superficial features of the cervical vertebrae, proportions of the humerus and the structure of the dermal elements of the pectoral girdle. It is argued below that his characters involving comparative

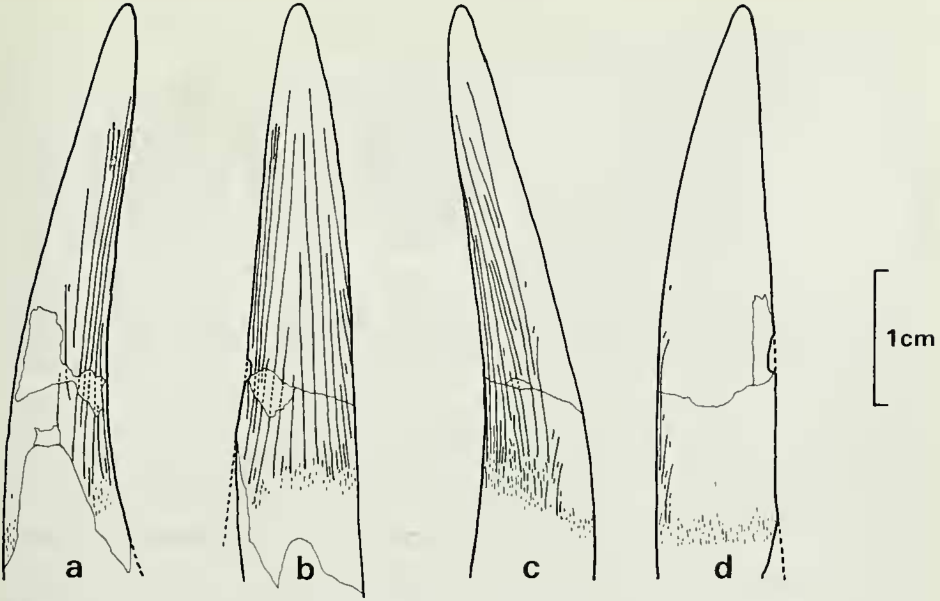


Fig. 19 *Muraenosaurus leedsii* Seeley, R.2861. Tooth showing ornamental ridges: a and c, axial; b, lingual; d, buccal aspect.

size and the proportions of vertebrae and humeri are of ontogenetic significance only. The recognition of an interclavicle associated with *M. durobrivensis* together with a reinterpretation of this element in *M. platyclis* shows the structure of the pectoral girdles to be the same.

Isolated vertebrae of the present species and of *M. beloclis* cannot be distinguished; the size differences between the species is inapplicable since posterior cervicals of *M. beloclis* (the smaller species) are considerably larger than anterior cervicals of *M. leedsii*. The type specimens of *P. plicatus* (cervical vertebrae) are therefore not diagnostic, and this name must be regarded as a *nomen dubium*. The earliest name applied to diagnostic material is *Muraenosaurus leedsii* Seeley, which is the valid name for this species.

Description of material

The description given by Andrews (1910) is extensive and largely accurate. He noted much variation in the size and ossification of individuals, interpreting this in terms of taxonomic characters by which he distinguished three species (see above). This variation is now reinterpreted as of solely ontogenetic significance.

The skull. Cranial material is preserved with several specimens, the most complete skull being that of R.2678. It was largely upon this skull that Andrews (1910 : text-figs 47, 48) based his description and reconstruction. Unfortunately this specimen has since been set in plaster for exhibition and could only be examined superficially.

JAWS AND TEETH. Parts of the jaws and teeth are preserved with specimens R.2421, R.2422, R.2427, R.2678, R.2861, R.2863 and R.2864. The teeth (Fig. 19) resemble those of Lower Jurassic plesiosauroids and Cretaceous elasmosaurs rather than those of *Cryptoclidus*. They are ornamented by numerous longitudinal ridges which are most prominent lingually, and in this aspect about 20 ridges are simultaneously visible. Several ridges may rise almost to the apex, but the prominent axial ridges characteristic of *Cryptoclidus* are lacking. The buccal aspect is ridged, though here the ridges are fewer especially in younger specimens, and may be confined largely to the basal half of the crown.

Very few whole teeth are preserved *in situ*; nevertheless, the relative sizes of teeth may be estimated from the diameter of empty sockets or the broken tooth bases. There are five premaxillary teeth, of which the 1st (most anterior) is very small; the left and right 1st sockets may be confluent, as in R.2421. The 2nd, 3rd and 4th upper teeth are large, and the 5th is usually much smaller. Behind the maxillo-premaxillary suture the 6th and 7th upper teeth (1st and 2nd maxillary teeth) are small and are of similar size to the 5th. Posterior to these the 8th and 9th upper teeth are very large, and the 10th is enlarged, but to a lesser extent. Thereafter the upper teeth decrease posteriorly forming a more or less evenly graded series. Complete maxillary toothrows are preserved in specimens R.2422 and R.2678, in both of which the maxilla bore 16 teeth, making a total of 21 teeth in the upper jaw. In the holotype (R.2421) the maxillae are less complete, the best being the right in which the most anterior 11 maxillary sockets are preserved.

The toothrow of the lower jaw is complete on at least one side in four specimens; the lower teeth number 19 in specimen R.2678, 20 in R.2422, 21 in R.2421, and in R.2861 there are 21 teeth on the left ramus and 22 on the right. In all cases the 1st (most anterior) lower tooth is of medium size, and the 2nd to 6th are very large, being equal in size to the upper 8th and 9th teeth. The lower 7th tooth is of medium size, about equalling the 1st, and the 8th is smaller. From here backwards the lower teeth form an even series, gradually decreasing in size.

The jaws of specimen R.2678 are virtually undistorted, and it is possible to superimpose them and to observe their occlusion. As in *Cryptoclidus*, the upper 1st teeth bit in advance of and between the lower 1st teeth, and from here backwards to the 7th teeth the upper and lower teeth interlocked in a one-to-one fashion. Behind the 7th teeth the width of the lower jaw decreases slightly whereas the width across the maxillae increases. This structural arrangement carries the sockets for the enlarged upper 8th and 9th teeth laterally such that they project completely clear of the lower teeth. Thus the upper 8th and 9th teeth form fangs which bit outside the smaller lower teeth, resulting in an overlapping occlusion at this point. Behind the fangs the bone outlines of the upper and lower jaws again coincide, and the more usual interlocking occlusion is resumed.

It may be noted that where Welles (1943, 1949, 1952, 1962) gives details of relative size of teeth in Cretaceous elasmosaurs, he indicates that the first one or two maxillary teeth are small and 'peg-like', and these are followed by two or three which are large and 'caniniform'; in the lower jaw the largest teeth are those beneath the premaxillae. It therefore appears that *Muraenosaurus* shows the same general pattern of dentition as that of Cretaceous elasmosaurs.

The structure of the lower jaw is essentially the same as in *Cryptoclidus*. Parts of the splenials (poorly known in that genus) are preserved in several specimens and are especially clear in R.2421, in which they fuse anteriorly in the symphysis, and extend posteriorly between the angular and surangular to reach the position of the 16th tooth socket. In specimen R.2678 the element labelled 'splenial' by Andrews (1910 : text-fig. 48) is not that element but is a part of the dentary.

NEUROCRANIUM. The general form of the braincase was described by Andrews (1910), and is very similar to that of *Cryptoclidus* except for the structure of the occipital condyle and the proportions of the paroccipital processes. The occipital condyle resembles that of *Tricleidus* and also of all Cretaceous elasmosaurs in that it is formed entirely from the basioccipital without any participation by the exoccipitals. The articular surface of the condyle is hemispherical, without a median pit, and is ringed by a constricting groove which separates it from the basioccipital-exoccipital sutures. This groove is developed to its fullest extent in 'old adults' (e.g. R.2422; see Andrews 1910 : text-fig. 44). The paroccipital process resembles *Tricleidus* closely, and is proportionally longer and slimmer than *Cryptoclidus* (Figs 2 & 23).

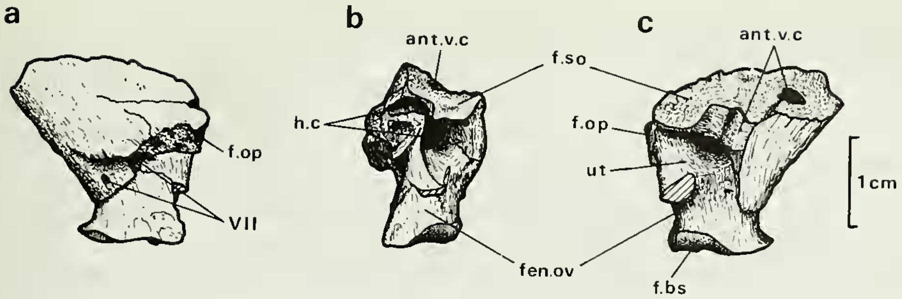


Fig. 20 *Muraenosaurus leedsii* Seeley, R.2422. Left prootic: a, lateral; b, posterior; c, medial aspect. ant.v.c, anterior vertical semicircular canal; f.bs, facet for basisphenoid; f.op, facet for opisthotic; VII, foramina for facial nerve. Other abbreviations as in Fig. 36, p 311.

In the 'old adult' specimen R.2422 the basioccipital and basisphenoid have largely fused, but a dorsal median pit, probably marking the embryonic basicranial fenestra, is present in this suture and was traced vertically downwards to a smaller median opening between these elements on the ventral surface.

The prootics (which are not known in *Cryptoclidus*) have not hitherto been described for any plesiosaur. Both are preserved with specimen R.2422, of which the left element (Fig. 20) is the most complete. This bone has been crushed and 'telescoped' somewhat, but its original shape may be perceived. It is essentially four-sided in lateral view, but with the lower posterior corner hollowed out into a short concave fifth side which forms the upper anterior margin of the fenestra ovalis. The ventral surface is a horizontal facet for union with the basisphenoid, and above the fenestra ovalis is a short and almost vertical facet for suture with the opisthotic; this is pierced by the horizontal semicircular canal. The supraoccipital facet faces upwards and backwards, and the rounded anterior margin of the prootic, the longest side, lies in the vertical plane.

The lateral surface of the prootic is convex and is marked by three small foramina, in a horizontal row, at least one of which must have been for the facial nerve. The medial surface is concave, and the posterior edge is hollowed for the utriculus which is shared equally with the opisthotic (Andrews, 1910 : text-fig. 45c, identified the opisthotic half of the utriculus cavity as the ampulla of the posterior semicircular canal). The prootic also houses the anterior half of the horizontal semicircular canal and the ventral half of the anterior vertical semicircular canal; these many be traced through the bones from the utriculus. There is no evidence of ossification around the cochlea, and so this must have been encased in cartilage.

Welles (1962), in his diagnosis of the 'suborder' Plesiosauria, stated that the fenestra ovalis and stapes are absent in the group. However, when the neurocranial elements of R.2422 are assembled the fenestra ovalis becomes at once apparent. It has the form of a short duct of circular section, its walls being formed in approximately equal thirds by the prootic, the opisthotic and the combined basioccipital and basisphenoid. There is no evidence for the existence of a stapes, but in view of the well-developed state of the fenestra ovalis its total absence may not be assumed.

SKULL ROOF AND PALATE. The remaining parts of the skull are less completely preserved in *Cryptoclidus* than in *Muraenosaurus leedsii*, but in so far as the former is known, they appear to differ only in details of the toothrow (described above). The postorbital bar, the jugal and the complete palate are known only for the present species, being preserved in R.2678. The palate was described fully and figured by Andrews (1910 : text-fig. 46a), with the postorbital bar and jugal receiving lesser notice but being included in the lateral reconstruction of the skull (1910 : text-fig. 46b).

In R.2678 the postfrontal elements are well preserved on both sides; they are orientated in an almost horizontal plane, and they sutured posterolaterally with the postorbitals. Only the left postorbital and jugal are preserved, and form part of a much crushed fragment which includes also the major part of the squamosal. The sutures of these latter elements are largely obscured by plaster or bad preservation and cannot be restored reliably. Moreover, the ventral part of the jugal, which Andrews (1910 : text-fig. 46b) united with the posterior end of the maxilla, is definitely not preserved.

In none of the plesiosauroid species here considered does the tapering posterior termination of the maxilla show any indications of a posterodorsal suture with the jugal such as was suggested by Andrews in his reconstruction of *Muraenosaurus leedsii*. Close inspection of specimen R.2678 indicates that the structural link between the jugal and the upper jaw was achieved not by direct union with the maxilla but instead through the ectopterygoid. This element is small but strongly constructed, and sutures anteriorly with the palatine, proximally with the pterygoid and distally with the posterior part of the medial margin of the maxilla. The dorsal surface of the left ectopterygoid is visible, and bore a thick and strong posterodorsal process, the broken section of which is oval with diameters of 1 cm (lateral axis) and 0·5 cm (anteroposterior axis). This process almost certainly provided the mechanical link to the temporal and postorbital bars.

Judged from the comparative length of the toothrow and the number of teeth, the snout of *M. leedsii* was proportionally shorter than in *Cryptoclidus* and slightly longer than *Tricleidus*. The jaws are distinguished further from the former and to a lesser extent from the latter genus by the great development of the upper 8th and 9th teeth. With the exception of these details, the shapes and proportions of the skull elements do not differ substantially from those of *Cryptoclidus* and *Tricleidus*, both of which are reconstructed here (Figs 1, 22). The overall length of the skull of 'adult' specimens is about 40 cm.

The postcranial skeleton. Postcranial material of this species is plentiful, and all growth stages are well represented. The description given by Andrews (1910) is extensive and largely accurate with regard to morphology, but differences in the osteological development of individuals are interpreted as of taxonomic rather than ontogenetic significance. Andrews took three individuals which differ in extent of osteological development (and which had been described previously by other authors, without cross-reference, as the type specimens of distinct species) and then attempted to group the remaining individuals around them. His diagnoses were based entirely upon characters of the postcranial skeleton, and he assigned all three species to the genus *Muraenosaurus*. The three type specimens are now interpreted as belonging to the single species *M. leedsii*, as follows:

(i) R.2428 (holotype of *Cimoliasaurus durobrivensis* Lydekker) has free neural arches and centra and an incompletely ossified pectoral girdle, and is therefore a 'juvenile'. By comparison with other 'juvenile' specimens (the most complete being R.2424 and R.2863) it is typical and representative of this growth stage, and is slightly smaller than the smallest 'adult' specimens.

(ii) R.2421 (holotype of *Muraenosaurus leedsii* Seeley) has the neural arches fused to the centra, and the elements of the pectoral girdle are fully formed yet still free. It is larger than all 'juvenile' forms but smaller than several other 'adult' specimens, and is therefore a relatively small 'adult'.

(iii) R.2678 (holotype of *M. platyclis* Seeley) is also an 'adult' and is one of the largest specimens, being about 10% larger than R.2421. By comparison with the two most complete 'old adult' specimens (in which the elements of the pectoral girdle are fused) it is slightly larger than R.3704 and is about the same size as R.2426 (misprinted R.2456 in Andrews 1910).

AXIAL SKELETON. A total of 66 presacral vertebrae are preserved in three specimens (R.2421, R.2863 and R.2864), and this appears to be the full complement for the species. As in *Cryptoclidus*, there is slight variation in the position of the pectoral vertebrae, there being 44 cervicals, 3 pectorals and 19 dorsals in R.2421 and R.2864, and 43 cervicals, 3 pectorals and 20 dorsals in R.2863. Four sacrals are preserved in specimens R.2421 and R.2863, and the tail is complete in R.2422 with a total of 24 caudal vertebrae.

In the holotype (R.2421) the vertebral column is complete from the atlas-axis to the 8th caudal, and the centra have been mounted with small intervening gaps amounting to rather less than the space required for intervertebral discs. The length of the series as mounted is 3·78 m; by comparison with R.2422 the missing portion of the tail would have measured approximately 0·5 m and the length of the skull of R.2421 is 0·37 m. Thus the total overall length of this small 'adult' specimen was at least 4·65 m. Comparative measurements of R.2678, the largest individual, indicate an approximate overall length of 5·2 m for this specimen.

As in *Cryptoclidus*, the centrum width is always greater than the height, but in *M. leedsii* the length of the cervical centra always exceeds the height and generally also the width in the most anterior cervicals, giving a vertebral length index in excess of 100%. In 'juveniles' the index reaches 105% in the anterior third of the neck, and in 'adults' an index of 110% or slightly more is commonly reached in the region of the 10th to 15th cervical vertebrae. Proportional length of the centra decreases posteriorly, the index dropping to about 80% at the pectorals. Thereafter, the dorsal vertebrae are very slightly longer and the caudals proportionally slightly shorter than in *Cryptoclidus.*

The neck is proportionally almost twice as long as in *Cryptoclidus*. This length is achieved both by development of a larger number of vertebrae and by the proportional lengthening of each centrum. Conversely, the tail of *M. leedsii* is proportionally slightly shorter since there are fewer caudal vertebrae (about 24 compared with about 30) and these are each proportionally shorter.

The articular faces of the vertebrae differ in shape from those of *Cryptoclidus*, and have been described as 'flat' rather than 'concave' (Andrews 1910). These terms are misleading, since vertebrae of *M. leedsii* become increasingly concave with age, and the real difference lies in the outline of a longitudinal section across the articular face. In *Cryptoclidus* this is a double sigmoid curve, the centre of the face being concave whilst the borders are convex and continue fairly smoothly into the sides of the centrum. In *M. leedsii*, on the other hand, the whole outline is concave or a very open V-shape, the borders of the face forming an abrupt angle with the centrum sides.

In 'adults' a longitudinal crest is developed on the sides of the cervical centra especially in the anterior half of the neck, and lies midway between the facets or sutures for the rib and the neural arch. Such a crest is absent in the shorter-necked forms *Cryptoclidus* and *Tricleidus* but is found in Cretaceous elasmosaurs (Welles 1943, 1952, 1962) and perhaps functioned to assist the neck muscles and ligaments in their role of supporting a very long neck when held out of the water. It is generally absent in 'juveniles' in which the neck is not so long.

In 'juveniles' and smaller 'adults' the centra are ornamented with small, closely-spaced longitudinal ridges, which occur in bands on the sides and ventral surface immediately adjacent to the articular faces. Andrews (1910) used the term 'plications' for this ornament, which is shown clearly in his plate 5, figs 2 and 3. In the largest 'adults' and 'old adults' the plications become further ossified into bands of irregular rugosities, losing the neat appearance which is characteristic of younger specimens. The ornament is strongly developed in the cervical vertebrae and continues backwards onto the dorsals with decreasing prominence, eventually to disappear before the sacrals. It was presumably associated with the insertion of longitudinal ligaments.

Andrews used comparative size, the proportional length of the centrum, the presence of a longitudinal ridge on cervicals and the development of plications as characters in the diagnoses of his three species. The differences which he noted relate entirely to the differences in the relative age and ossification of the three type specimens.

The ribs and chevrons do not differ in any respect from those of *Cryptoclidus*. The development of an anterior flange on the cervical ribs is irregular and is seldom strongly developed; in this respect the present species appears to differ from *M. beloclis*.

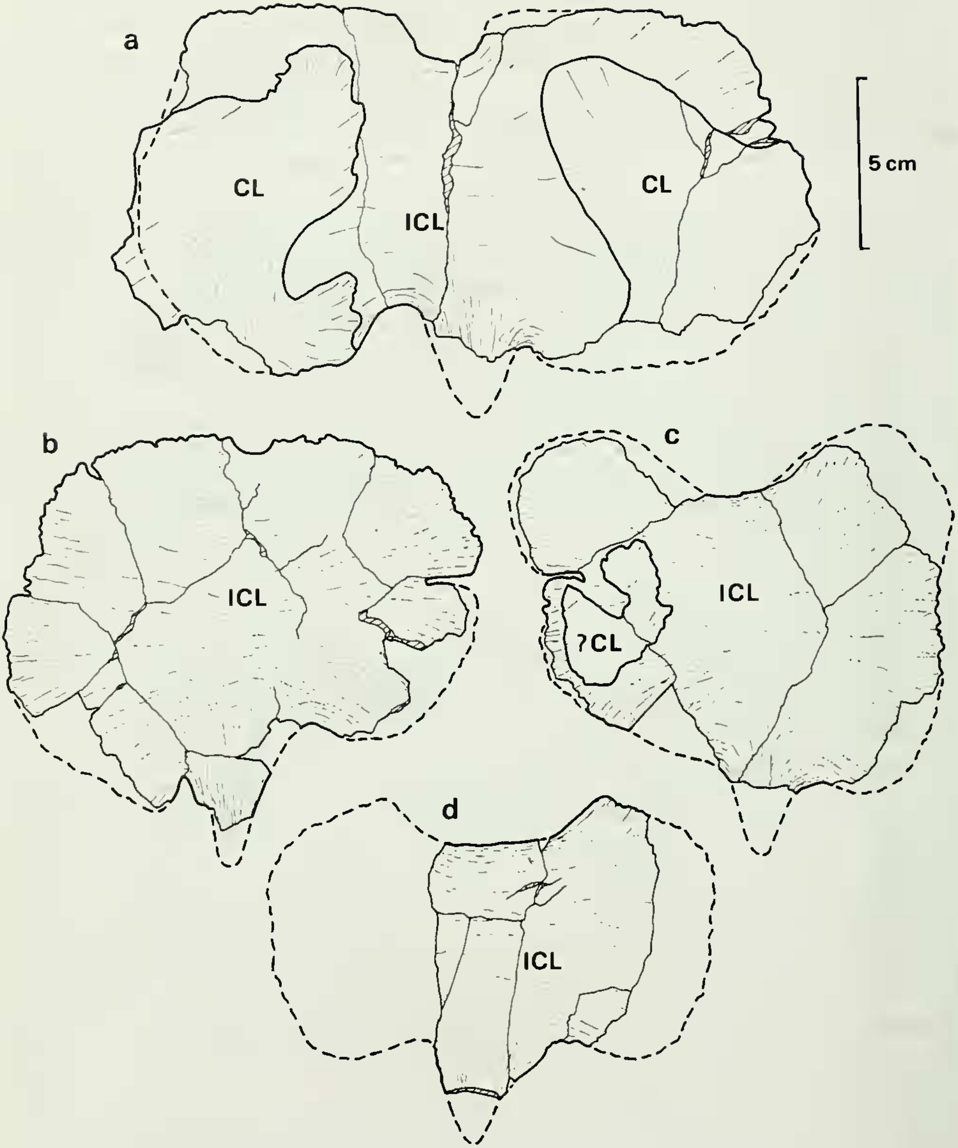


Fig. 21 *Muraenosaurus leedsii* Seeley, interclavicles and clavicles in dorsal view: a, R.2678; b, R.3704; c, R.2426; d, R.2428. Missing outlines restored with broken lines. CL, clavicle; ICL, interclavicle.

The isolated gastralial elements are identical to those of *Cryptoclidus*, suggesting a similar arrangement, but the number of rows in the complete basket is not known. Specimens of the forked posterior element which is present in *C. eurymerus* have not been seen in any other species.

APPENDICULAR SKELETON. The pelvic girdle and the distal portions of the limbs (mesopodials and phalanges) are indistinguishable from those of *Cryptoclidus*; whereas the pectoral girdle differs in several important respects, and the propodials and epipodials are also distinct.

The scapulae resemble those of *Cryptoclidus* except for the structure of the ventral rami. In 'juvenile' specimens (e.g. R.2428; see Andrews 1910 : text-fig. 67) these first contact just in advance of the developing scapulocoracoid bar, and anteriorly are separated by a V-shaped space. Ossification in a posterior direction then produces the scapulocoracoid bar typifying the 'adult' stage, as in *Cryptoclidus*; but anteriorly the ventral rami fail to contact along their entire length, being instead separated by an elongated U-shaped notch which persists in all 'adult' and 'old adult' specimens. Posteriorly this notch forms part of a foramen (interscapular foramen of Andrews) which is enclosed by the scapulae and the overlying interclavicle.

The coracoids differ from those of *Cryptoclidus* in the development of the posterior cornua. In the 'adult' and 'old adult' these are equal to or only just in excess of the interglenoid width, and they are therefore much less prominent than in that genus (cf. Figs 43a and 43b, p. 331).

The interclavicle is well developed in the present species. Andrews (1910) was confused about its structure, and used supposed differences of structure in the diagnoses of his three species. He correctly described the element in his '*M. leedsi*' from specimen R.3704 (1910 : text-fig. 62; pl. 6 figs 6, 6a), but in his description of *M. durobrivensis* he described and figured as an interclavicle a non-plesiosaurian bone accidentally associated with specimen R.2863 (1910 : pl. 5 fig. 10); this in turn led him to misinterpret the structure of the interclavicle of R.2678 (holotype of *M. platyclis*). Further to this confusion, and relying on the accuracy of Andrews' descriptions, White (1940) produced a classification of plesiosaurs based entirely on characters of the pectoral girdle, in which he made *M. platyclis* the type species of a new genus *Tremamesacleis* and founded the new family Tremamesacleididae for its reception.

The interclavicle is now known from four good specimens (see Fig. 21) and a further fragment is preserved with R.2427. These show considerable variation in size, but the basic structure is the same. The element forms an irregular oval plate, the longest axis being lateral, the ventral surface convex and the dorsal surface flat or concave. The bone is thickest in the centre, and towards the edges it becomes very thin with a ragged margin. In the anterior margin of all specimens there is a median notch, of varying size, bordering which the bone is smooth and rounded. Posteriorly there is developed a median peg-like process which is frequently triangular in section, the apex of the triangle being ventral. On either side of this process are small clefts or notches which are irregular in size and frequently asymmetrical, as in R.2678 (Andrews overlooked the broken base of the posterior process in this specimen, and interpreted the notch to its left as a median notch). The interclavicle lay dorsal to the ventral rami of the scapulae, and both elements bear rugosities marking the insertions of connecting ligaments.

The clavicles are best preserved in specimen R.2424 (see Seeley 1892 : fig. 8). They are irregularly triradiate in form, and from their shape it is evident that they did not meet in a median symphysis, but instead sutured squamously with the interclavicle (not preserved with that specimen). Parts of the clavicles are also preserved with R.2678 but here they are much thinner and have fused to the dorsal surface of the interclavicle (Fig. 21a). They are broken posterolaterally and their original outline cannot be reconstructed, but the shape of the preserved anterior portions conforms with these parts in R.2424. A fragmentary scale of bone compressed onto the left dorsal surface of the interclavicle of R.2426 (Fig. 21c) may possibly represent another clavicle.

There is a tendency towards fusion of the elements of the pectoral girdle in 'old adults', as in *Cryptoclidus*. In specimen R.2426 the left and right coracoids are fused, and in R.3704 the coracoids and scapulae are fused in the midline, and are also fused to each other at the glenoid. In both specimens this fusion involves only the ventral parts of the sutures, which remain open dorsally. In neither of these 'old adult' specimens is the interclavicle involved in fusion with the scapulae.

The humerus is indistinguishable (amongst English forms) from that of *Cryptoclidus richardsoni*, and also from that of *M. beloclis* except by superior size (Fig. 44). It thereby differs appreciably from the humerus of *C. eurymerus*. Likewise, the radius and ulna differ from these elements in *C. eurymerus* and resemble closely those of *C. richardsoni* and many Cretaceous plesiosauroids. The radius is nearly square in shape, the facet for the ulna being rather shorter than the anterior border and the facets for the humerus and radiale. Between the ulnal and radialial facets is a very small oblique facet for the intermedium; this serves to distinguish the element from the radius of *M. beloclis*, in which the intermedial facet is much larger and is equal to the intermedial facet of the ulna.

The ulna is a pentagonal bone, the longest side being the humeral facet. The thin posterior edge usually remains cartilage-covered; a small pisiform element articulates with it in the left forelimb of R.2864 (Andrews 1910 : text-fig. 63). Distally there are two facets of equal size, one facing obliquely posteriorly for articulation with the ulnare, the second facing slightly to the anterior for union with the intermedium. The anterior margin of the ulna meets the radius proximally and distally; interposed between these elements is a foramen which, unlike this structure in *Cryptoclidus*, is detectable in even the youngest individuals.

The femur of 'adults' is indistinguishable from that of *C. richardsoni* and closely similar to that of *C. eurymerus*. In 'old adults' the tibia and fibula are identical to those of *Cryptoclidus*, but in younger specimens they may be distinguished since the interposed foramen is always discernible.

The distal elements of the limbs are indistinguishable from those of *Cryptoclidus*. The left limbs of R.2864 are almost complete, and have phalangeal formulae of 6 : 12 : 14 : 13 : 8 (forelimb) and 6 : 13 : 15 : 13 : 9 (hindlimb). The hindlimb is very slightly smaller than the forelimb, as is usual in plesiosauroids. The 5th metacarpals have moved proximally only half their length into the distal carpal rows; this represents an intermediate stage between Lower Jurassic plesiosaurs (such as *Plesiosaurus dolichodeirus*) in which they are entirely level with the metacarpals, and Cretaceous forms in which these elements lie entirely in the distal carpal row.

Muraenosaurus beloclis Seeley, 1892
(Figs 43c, 44d)

1892 *Muraenosaurus beloclis* Seeley: 143, figs 10–12.
1909 *Picrocleidus beloclis* (Seeley) Andrews: 421, fig. 3.
1910 *Picrocleidus beloclis* (Seeley); Andrews: 140, fig. 70; pl. 7.
1962 *Picrocleidus beloclis* (Seeley); Welles: 9; table 1.
1963 *Picrocleidus beloclis* (Seeley); Persson: 24.
1964 *Picrocleidus beloclis* (Seeley); Novozhilov: fig. 305.

HOLOTYPE. The Leeds Collection specimen R.1965, an incomplete postcranial skeleton consisting of 6 cervical and 2 dorsal vertebrae, fragments of ribs, the pectoral girdle, both humeri and ulnae and one radius. It was described and figured by Seeley (1892 : figs 10–12) and Andrews (1910 : text-fig. 70; pl. 7 figs 2–4; note that pl. 7 fig. 1, which represents part of a lower jaw, was labelled incorrectly as associated with R.1965 but was described correctly in the text as belonging with R.3698).

TYPE LOCALITY AND HORIZON. An unspecified brick-pit near Peterborough, England; Upper

Jurassic, Callovian Stage. From the lowest deposits of the Oxford Clay, which includes the ammonite zones of *Kosmoceras jason*, *Erymnoceras coronatum* and *Peltoceras athleta* (see Andrews 1910 : vii).

DIAGNOSIS. Members of the genus *Muraenosaurus* in which the anterior cervical ribs normally develop a very prominent anterior flange; the interclavicle is small and lanceolate; in the manus the intermedium articulates equally with the radius and the ulna; the overall length of the 'adult' is about 2·5 m.

DISTRIBUTION AND RANGE. Diagnostic material is known only from the type locality. Upper Jurassic, Callovian Stage only.

REFERRED SPECIMENS. All the following are from the Oxford Clay of the Peterborough area.

R.2739. Incomplete 'adult' skeleton. Neurocranium figured by Andrews (1910 : text-fig. 71) as *Picrocleidus*, sp.

R.3698. Incomplete 'adult' skeleton. Lower jaw fragment figured by Andrews (1910 : pl. 7 fig. 1) as *Picrocleidus beloclis*.

R.2429. Incomplete postcranial skeleton of an 'old adult'.

DESCRIPTION OF MATERIAL. Andrews (1910) believed the holotype and the three referred specimens to represent two species of a distinct genus *Picrocleidus* (the second species was not named). However, similarities in the structure of the occipital condyle, tooth ornament, vertebral structure and numbers, development of the elements of the pectoral girdle and the form of the forelimb indicate that *M. beloclis* and *M. leedsii* are congeneric. They may be distinguished only by the four characters listed in the diagnosis.

The skull is very poorly known. A fragment of the right lower jaw ramus of R.3698 contains the broken stumps of several teeth, from which it is clear that their ornament consisted of many longitudinal ridges occurring all round the tooth. The basioccipital is preserved in R.3698 and R.2739 and forms the entire condyle, which is ringed by a groove. Fragments of an exoccipital-opisthotic, a quadrate and a squamosal are preserved with R.3698, and also part of the basisphenoid and parasphenoid with R.2739, these differing only in their smaller size from the corresponding elements of *M. leedsii*.

The most complete vertebral column is that of R.3698. Including the fused atlas-axis, 37 cervical vertebrae are preserved, and the most posterior of these is by no means the last as the facets for the cervical ribs have not begun to rise up the side of the centrum. It is therefore possible that the neck was of similar construction to that of *M. leedsii* in which 43 or 44 cervical vertebrae are found. In specimen R.2429 a sequence of ten vertebrae are preserved, these being 6 posterior cervicals, 3 pectorals and the most anterior dorsal. The dorsal vertebrae are inadequately known, and the largest number of sacrals preserved in a single specimen is two (in R.2739). In specimen R.3698 the tail is complete from the last sacral to the penultimate caudal, there being 22 caudal centra preserved. Posterior chevron facets begin on the 5th caudal and anterior facets on the 6th. In the posterior caudal vertebrae a sizeable projection develops ventrolaterally on each side of the centrum. These coexist with chevron facets and therefore cannot be fused chevrons. Such projections have never been noted in other plesiosaurs and may perhaps be an oddity of the specimen rather than typical of this species.

The overall length of the 'adult' (about 2·5 m) was calculated by comparing the length of the first 37 cervical vertebrae of specimen R.3698 with those of R.2421 (the holotype of *M. leedsii*, estimated overall length 4·65 m), and assuming similar vertebral numbers and proportions in the two species.

The vertebrae resemble those of *M. leedsii* in the shape of the articular facets, the development of the lateral longitudinal crest on anterior cervicals, and in the proportional length of the centra; in R.3698 the vertebral length index again rises over 100% in anterior cervicals, and reaches a maximum of 106% at the 16th cervical vertebra.

The development of a prominent flange to the anterior cervical ribs is most evident in specimen R.3698 and is seen to a lesser extent in R.2739. Lack of anterior cervical vertebrae and ribs with the holotype (R.1965) makes the taxonomic importance of this character somewhat dubious; it was used by Andrews (1910) and is included with reservations in the present diagnosis.

The scapulae and coracoids are preserved with specimens R.1965 and R.2429. The scapulae are indistinguishable (except by their smaller size) from those of *M. leedsii*, with an identical development of the interscapular foramen, and the coracoids differ only in being proportionally rather narrower midway between the glenoids and the cornua. Specimen R.2429 is an 'old adult' in which these elements are partially fused with their opposites in the midline, and fused to each other at the glenoid.

The interclavicle is preserved only in R.1965 (Fig. 43c), and at first sight it appears to differ widely from that of *M. leedsii*; it is lanceolate and triangular in section, with the apex of the triangle ventral. However, its wider anterior end is marked by a median notch with smooth edges, whereas the posterior end is developed into a stout and cylindrical process which may have terminated in cartilage; this structure could easily be derived from that of *M. leedsii* by the loss of the thin plate-like lateral sections of that species.

The humerus, femur, tibia and fibula are indistinguishable in shape from those of *M. leedsii*, but the radius is distinctive since it has a considerably larger facet for the intermedium and consequently a more elongated shape. Posteriorly it meets the ulna, enclosing between these elements the usual foramen. In R.3698 the ulna resembles closely the typical form of this element in *M. leedsii*, whereas in R.1965 it has a small facet facing obliquely posteriorly and proximally for articulation with an accessory ossicle. The distal parts of the limbs of *M. beloclis* are not known.

Genus ***TRICLEIDUS*** Andrews, 1909

TYPE SPECIES. *Tricleidus seeleyi* Andrews, 1909.

DIAGNOSIS. As for type species (monotypic genus).

Tricleidus seeleyi Andrews, 1909
(Figs 22–25, 43d, 44e)

1909 *Tricleidus seeleyi* Andrews: 419, figs 1, 2.
1910 *Tricleidus seeleyi* Andrews; Andrews: 149, text-figs 72–77; pl. 8.
1962 *Tricleidus seeleyi* Andrews; Welles: table 1.
1963 *Tricleidus seeleyi* Andrews; Persson: 24.
1964 *Tricleidus seeley* 'Andrews'; Novozhilov: fig. 305 (lapsus).

HOLOTYPE. The Leeds Collection specimen R.3539, consisting of disarticulated elements representing most of the skull together with about half the postcranial skeleton. It was described and figured by Andrews (1909 : figs 1, 2; 1910 : text-figs 72–77; pl. 8).

TYPE LOCALITY AND HORIZON. 'From the pit worked by Messrs Hicks and Gardner immediately across the lane from Woodston Lodge' (Leeds 1956), at Fletton, near Peterborough, England. Upper Jurassic, Callovian Stage. From the lowest deposits of the Oxford Clay, which includes the zones of *Kosmoceras jason, Erymnoceras coronatum* and *Peltoceras athleta* (see Andrews 1910 : vii).

DIAGNOSIS. Plesiosauroids in which the teeth are ornamented by many longitudinal ridges; the dentary bears 17 teeth on each ramus; the premaxillae bear 5 teeth each, of which the 1st and 5th are small and the 2nd to 4th are large; the most anterior maxillary tooth (6th upper tooth) is small and the 8th and 9th upper teeth are large; the parietals form a sagittal crest; the quadrate overlaps the quadrate ramus of the pterygoid posteromedially; the paroccipital process of the exoccipital-opisthotic is relatively long and slender; the pterygoid bears a process for union with the basisphenoid; the occipital condyle is ringed by a groove, and is formed from the basioccipital only; there are at least 26 and possibly slightly more cervical vertebrae with relatively amphicoelous centra, the length of which only slightly exceeds the height (but never the width) in the most anterior vertebrae; the clavicles are triangular and well developed, and lie visceral to the interclavicle which separates them in the midline; the interclavicle is well developed and plate-like; the coracoids meet the scapulae in the midline in 'adults'; the width across the posterior cornua of the coracoids exceeds the interglenoid width in 'adults'; the humerus is not greatly expanded distally, and articulates with four epipodials.

Distribution and range. Diagnostic material is known only from the Peterborough area. Upper Jurassic, Callovian Stage, type horizon only.

Referred specimens. Both from the Oxford Clay of the Peterborough area.
N.M.W. 19.96.G7 (Figs 25b, 25d). The pectoral girdle and humeri of an 'adult'.
H.M.G. V.1800. The right humerus of an 'adult'.

Description of material

The skull. Cranial material is preserved only with the holotype (R.3539). Andrews (1910) described and figured the neurocranium extensively, but the remainder of the skull received brief attention and no reconstruction was attempted.

The skull of R.3539 is disarticulated, and the separate parts are almost entirely without distortion or crushing. In consequence, the elements may be placed together and their combined shape deduced with the minimum of restoration. The skull reconstructions (Figs 22, 23) were produced by combining a large number of scale photographs of isolated or grouped elements. The dorsal midline is preserved from the parietals to the tip of the snout; a further anteroposterior line is preserved from the maxillae through the vomers and pterygoids to the right quadrate; the interlock of the teeth can be observed directly by superimposing the jaws; the lower jaw is entire, and only the absence of the supraoccipital prevents this from being linked back to the parietals.

The toothrow of the premaxillae and maxillae resembles closely that of *Muraenosaurus*: each premaxilla bears 5 tooth sockets, the 2nd to 4th being much larger than the 1st and 5th; and the maxillae bear sockets for 15 teeth each (6th to 20th upper teeth), that for the 6th upper tooth being small and those for the 8th and 9th teeth being large. The border of the external naris is fully preserved in the left premaxilla, but the posterior edge of that element is missing. Here the bone is extremely thin, and a series of ridges and grooves on the ventral surface of the premaxilla, also seen on the dorsal surface of the anterior part of the frontal, suggests an extensive area of squamous overlap. The internal surface of the premaxilla is divided by a ridge which runs from the tip of the snout to the midline of the maxillo-premaxillary suture and which indicates the line of union with the vomers.

In the left maxilla are preserved a part of the margin of the external naris and all the orbital margin of that element. As in *Cryptoclidus* and *Muraenosaurus*, there is no evidence for the presence of a lacrimal or prefrontal (a part of the frontal remains *in situ* suturing with the antorbital process), and likewise no evidence for suture of the posterior part of the maxilla with the jugal. There may therefore have been a link to the jugal through the ectopterygoid as is suggested above for *M. leedsii.*

The frontals and parietals resemble closely these elements in *Cryptoclidus* and *Muraenosaurus.* Most of the right frontal is preserved, and remains sutured posteriorly to the parietals; its broken anterior end retains a part of the border of the naris and fits exactly against a similarly broken edge on the posterior part of the right premaxilla, thus permitting the reconstruction of the dorsal midline. The pineal foramen lies almost entirely between the fused parietals, being just contacted by the frontals. The parietals form a high sagittal crest, the vertex of which is now broken away; the arrangement of the parietal-squamosal sutures shown in Fig. 22 was assumed to be as in *Cryptoclidus* and *Muraenosaurus.* The suture between the parietals, obliterated by fusion on the skull roof, is still visible on the occipital surface.

The left squamosal is almost complete, and was described and figured as two pieces by

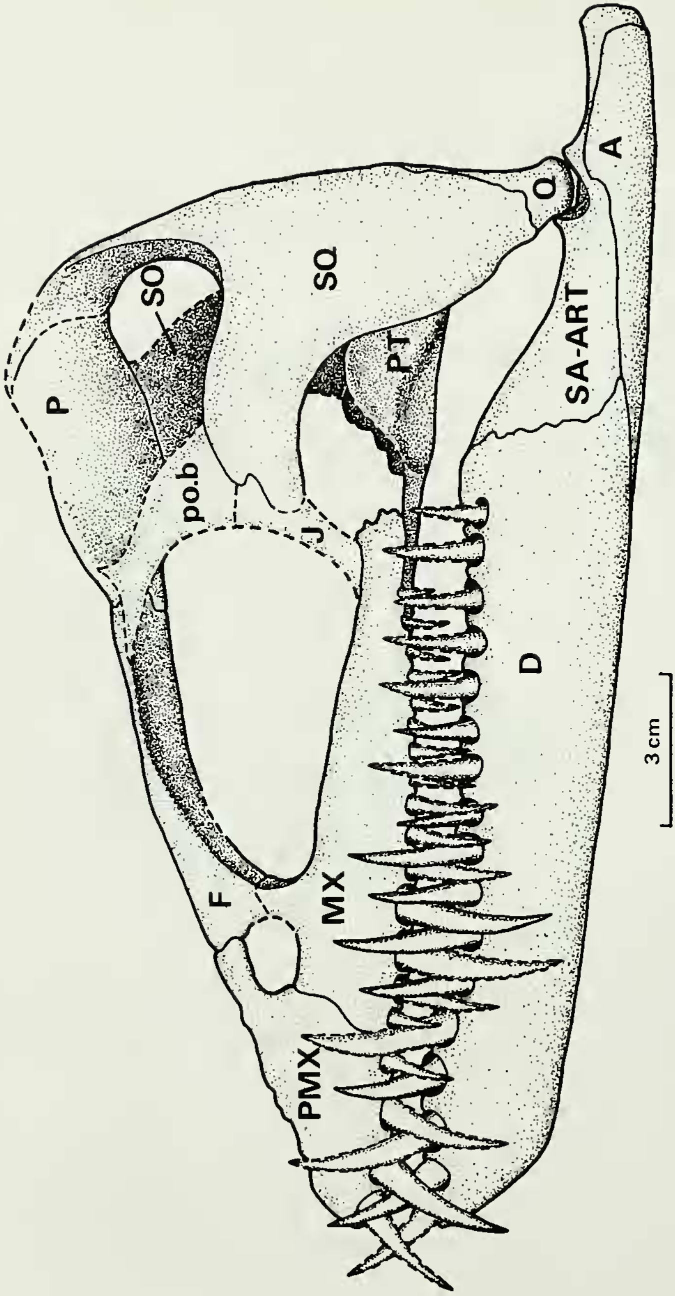


Fig. 22 *Tricleidus seeleyi* Andrews, reconstruction of skull of holotype R.3539 in lateral view. Abbreviations as in Fig. 1, p. 259.

Andrews (1910 : text-fig. 75), who labelled these sq. and sq′. The pieces, however, were separated by a natural break, not a suture, and this has now been repaired. The element is triradiate, and resembles closely that of *Cryptoclidus* and *Muraenosaurus*. No parts of the jugal or postorbital bar are preserved.

Andrews (1910) described the 'left' quadrate as consisting of two elements or fractions which he labelled q. and q′. (1910 : text-fig. 75), and the 'right' was said to be of similar construction. He suggested that either the elements were symmetrically fractured or his q. represented the quadratojugal and his q′. the true quadrate. Upon dissolving the glue binding the portions of each quadrate the adjoining surfaces were found to be covered in part with matrix. This was removed with an 'Airbrasive' machine, and the four fragments were then fitted together exactly, but with q′. belonging to the right quadrate and q. to the left.

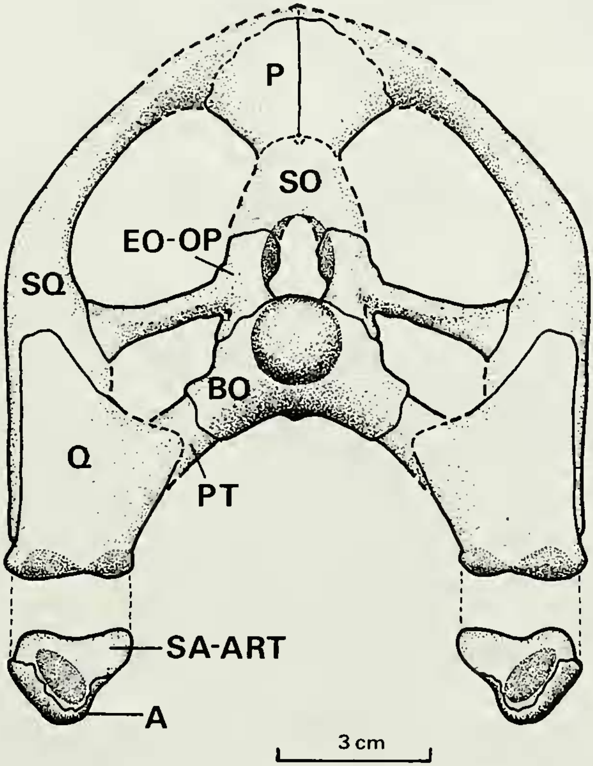


Fig. 23 *Tricleidus seeleyi* Andrews, reconstruction of skull of holotype R.3539 in occipital view. Abbreviations as in Fig. 2, p. 259.

As now assembled, the quadrates are closely similar to those of *Cryptoclidus* and *Muraenosaurus*. Pits and ridges on the anteromedial surface of the right quadrate and the posterior surface of the pterygoid show that these elements were arranged with the pterygoid in advance of the quadrate, the latter obscuring the posterior tip of the pterygoid in occipital view (Fig. 23). This arrangement is also found in *Muraenosaurus* as witnessed by the structure of the pterygoids, but differs from *Kimmerosaurus* (p. 309). The arrangement in *Cryptoclidus* is not known.

The form of the pterygoids was described accurately and figured by Andrews (1910 : text-fig. 74). They differ from all other described plesiosauroid pterygoids in the development of a

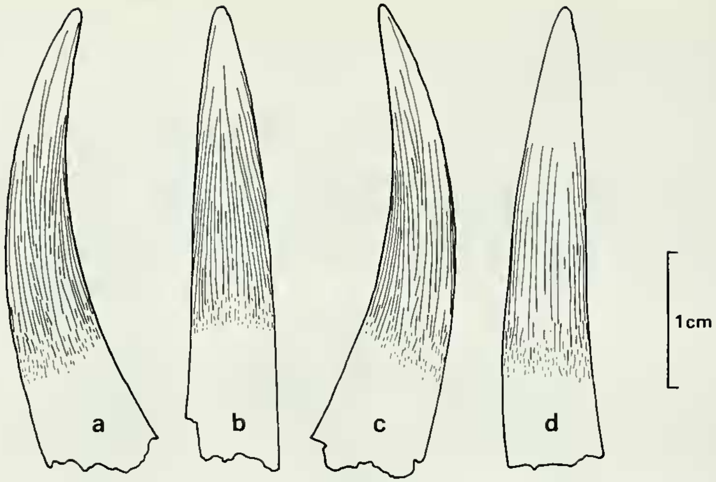


Fig. 24 *Tricleidus seeleyi* Andrews, tooth of holotype R.3539 showing ornamental ridges: a and c, axial; b, lingual; d, buccal aspect.

special process for articulation with the basisphenoid (labelled pt.f′. by Andrews). They also differ from the pterygoids of *Muraenosaurus* in that there is no prolonged process for contact with the ectopterygoid, and it must be assumed that the missing ectopterygoid in the present species was proportionally larger than in that genus.

The vomers are fused to form a single median element which has the shape of an arrowhead and resembles closely that of *Muraenosaurus.* Welles (1952 : 98) misidentified this bone as the nasals, which are not known as separate elements in Jurassic plesiosaurs.

The preserved elements of the braincase were described and figured fully by Andrews (1910). The form of the occipital condyle and the paroccipital processes are as in *Muraenosaurus*, and thereby differ from those of *Cryptoclidus* (cf. Figs 23 and 2).

The lower jaw (Andrews 1910 : pl. 8) differs from that of *Muraenosaurus* (which it otherwise resembles closely) by having only 17 tooth sockets on each ramus. Of these the 2nd to 8th are the largest, but the size does not greatly diminish posteriorly, and the most posterior may be described as of medium size. The fine state of preservation permits the orientation of the teeth to be assessed; this was just as in *C. eurymerus*, specimen R.8621 (pp. 262–3).

The right ramus of the lower jaw contains *in situ* eight complete teeth, and in addition several isolated teeth are preserved (Fig. 24). These are ornamented with many longitudinal ridges which, as in *Muraenosaurus*, are found all round the teeth and especially on their lingual sides.

By comparison with *Cryptoclidus* (Fig. 1) the skull of *Tricleidus* (Fig. 22) is relatively short in the snout region, relatively high posteriorly, and has fewer teeth. It therefore resembles more closely reconstructions by Welles (1943, 1952) of the skulls of Cretaceous elasmosaurs.

The postcranial skeleton. The axial skeleton was described and figured by Andrews (1910). It is incompletely known, and is preserved only in the holotype (R.3539). Leeds (1956) recorded that his father found this specimen disarticulated and scattered over an unusually large area, and that although he took great pains to collect as much as possible, especially of the skull, inevitably some parts were lost. It follows that the apparently complete series of 26 cervical and 3 pectoral vertebrae may in fact be incomplete, with several cervicals lost at random from the column such that no obvious gaps appear in the sequence. Five dorsals and

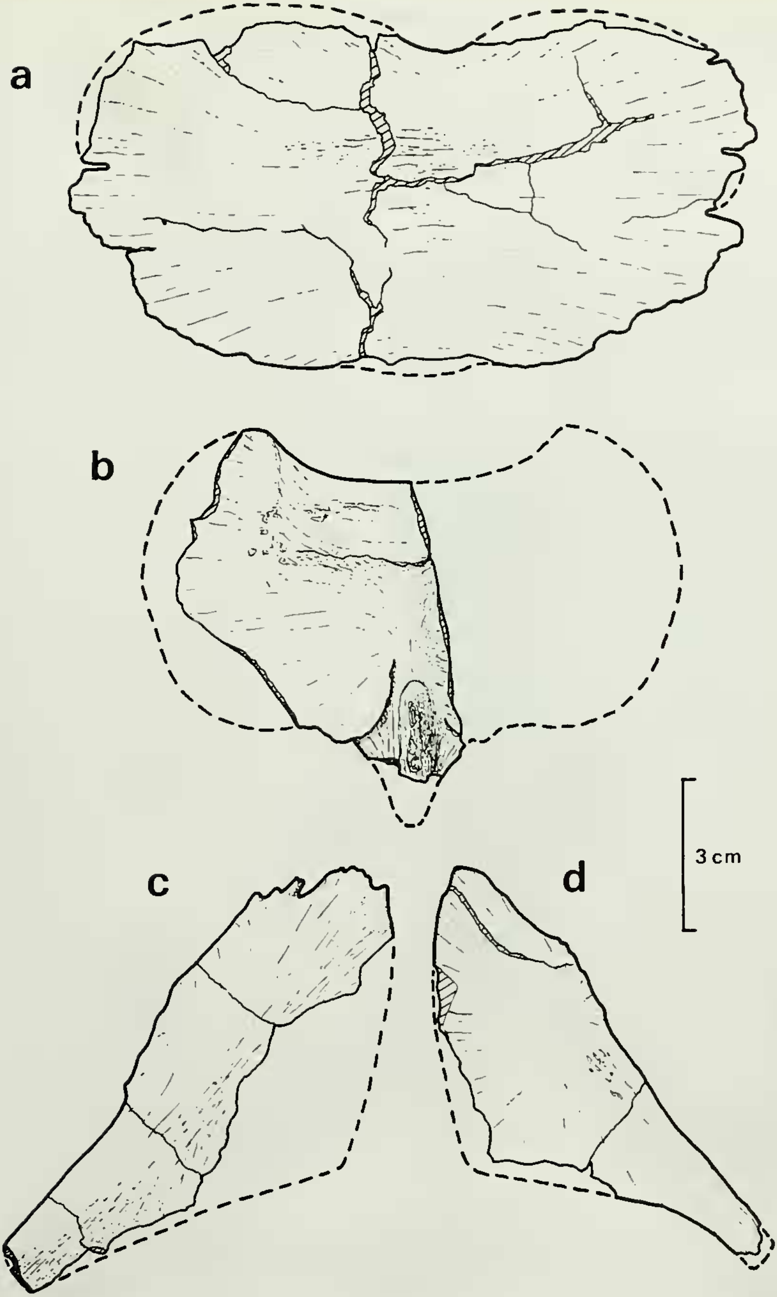


Fig. 25 *Tricleidus seeleyi* Andrews: a, interclavicle of holotype R.3539 in dorsal view; b, interclavicle of N.M.W. 19.96.G7 in ventral view; c, left clavicle of holotype R.3539 in dorsal view; d, left clavicle of N.M.W. 19.96.G7 in ventral view. Missing outlines restored with broken lines.

two caudals are also preserved, together with a few ribs and gastralia. All these parts are indistinguishable from those of 'adult' specimens of *Cryptoclidus*.

The distinctive pectoral girdle (Fig. 43d) is preserved both in R.3539 (Andrews 1909 : fig. 1; 1910 : text-fig. 76; pl. 8) and in N.M.W. 19.96.G7 (newly identified). The scapulae resemble those of *Muraenosaurus*; the ventral rami remain separated anteriorly, but the gap between them is V-shaped rather than U-shaped as in that genus. The structure of the coracoids is midway between those of *Cryptoclidus* and *Muraenosaurus*, the posterior cornua extending laterally beyond the level of the glenoids, but not to the extent seen in *Cryptoclidus*.

The dermal elements of the pectoral girdle are well developed. In R.3539 (Fig. 25a) the interclavicle is very large and plate-like, but most of its area is only thin. There is a small anterior notch as in *Muraenosaurus*, and the central part is strengthened by a T-shaped thickened area consisting of an anterior transverse bar and a median longitudinal bar. A small portion of the interclavicle of 19.96.G7 is preserved (Fig. 25b) and includes part of the anterior notch (which is wider than in R.3539) and part of the median thickening. In this specimen the interclavicle was structurally similar to that of *M. leedsii*, the median longitudinal thickening continuing posteriorly as a peg which was triangular in section. The interclavicle of 19.96.G7 was evidently smaller than that of R.3539, indicating considerable variation of the element as in *Muraenosaurus*.

The clavicles are elongated bones with a thickened anterolateral axis: the left clavicle of 19.96.G7 is almost complete and enables the form of the entire element to be restored (Fig. 25d). The posterolateral corner consists of the thickened part of the bone only, and is roughened ventrally for attachment to the scapula. The thickened axis continues anteromedially, and on the posteromedial side and to a lesser extent the anterolateral side there are developed thin expansions, such that the final shape of the bone is triangular with a concave posterior border. The ventral surface is almost flat, the dorsal surface convex. The preserved parts of the clavicles of R.3539 (Fig. 25c) agree closely in form with those of 19.96.G7.

The humerus (Fig. 44e) is relatively short and stout, and has a characteristic shape because it articulates distally with four elements. The radial facet is the largest, and faces obliquely anterodistally. The ulnal facet is distally orientated, and behind this is a small facet for the pisiform which faces obliquely posterodistally. The fourth facet, for a postaxial accessory ossicle, is about as large as the ulnal facet and faces posteriorly. The rugosities for muscle insertion are arranged as in *Cryptoclidus* and are strongly developed, this giving the bone an especially well-ossified appearance.

Distal elements of the forelimb are preserved only with R.3539, and were described and figured in articulation with the humerus by Andrews (1910 : text-fig. 77). The distal carpal row contains three small carpals together with the fifth metacarpal, which has shifted proximally for almost its entire length, as in *Cryptoclidus*. The phalanges are not known.

Of the pelvic girdle only the pubis is known, associated with R.3539. Except for its slightly smaller size, this is indistinguishable from pubes of *C. eurymerus* and *M. leedsii*.

The hind limb is represented only in R.3539 by the femur, tibia, fibula, intermedium and tibiale, which were described and figured by Andrews (1910 : pl. 8). These elements are indistinguishable from those of *Muraenosaurus* and are of the same size as in *M. beloclis*. The femur is slightly longer than the humerus and has a slimmer and less massive appearance.

Genus ***KIMMEROSAURUS*** nov.

NAME. From the stratigraphical horizon of the type species (Kimmeridgian Stage, Kimmeridge Clay).

TYPE SPECIES. *Kimmerosaurus langhami* n. sp.

DIAGNOSIS. As for the type species (monotypic genus).

Kimmerosaurus langhami sp. nov.
(Figs 26–39)

NAME. In honour of R. A. Langham, Esq., of Reading, Berkshire, who found the holotype skull in 1967 and presented it to the British Museum (Natural History) the following year.

HOLOTYPE. R.8431, a disarticulated incomplete skull consisting of the frontals, parietals, squamosals and pterygoids; the right postfrontal, postorbital and fused exoccipital-opisthotic; the left quadrate; the basioccipital; the right angular and fused surangular-articular; the dentary and 11 isolated teeth.

TYPE LOCALITY AND HORIZON. Endcombe Bay (also known as Egmont Bay), on the coast about 5 km south of Corfe Castle, Dorset, England. Upper Jurassic, Kimmeridgian Stage. From the Kimmeridge Clay; the exposed cliff section at Endcombe Bay consists lithologically of the Crushed Ammonite Shales, which are included (Arkell 1933) in the zone of *Pavlovia rotunda*.

Fig. 26 *Kimmerosaurus langhami* gen. et sp. nov. **Holotype**, R.8431. Skull roof in ventral view, *c.* × 0·8. See Fig. 32, p. 307.

Fig. 27 *Kimmerosaurus langhami* gen. et sp. nov. **Holotype**, R.8431. Dentary in dorsal view, see Fig. 37, p. 312. Skull roof in dorsal view, see Fig. 31, p. 306. Basioccipital in anterior aspect (inverted), see Fig. 35c, p. 309. All *c.* × 0·6.

Fig. 28 *Kimmerosaurus langhami* gen. et sp. nov. **Holotype**, R.8431. Posterior elements of right mandible in buccal view, see Fig. 38c, p. 313. Also four teeth. All *c*. ×0·8.

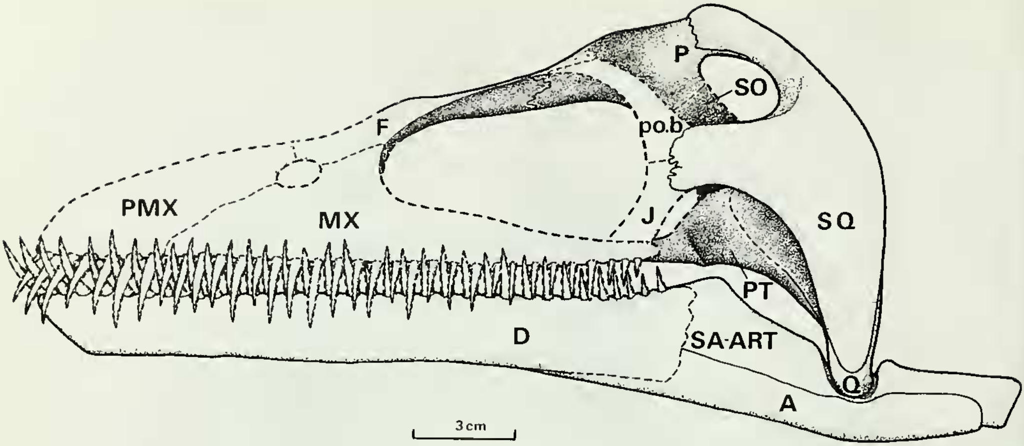


Fig. 29 *Kimmerosaurus langhami* gen. et sp. nov. R.8431, reconstruction of skull in lateral view. Abbreviations as in Fig. 1, p. 259.

Diagnosis. Plesiosauroids in which tooth ornament is absent; the teeth are greatly recurved, sharply pointed and buccolingually compressed; the premaxilla bears at least 8 teeth; the dentary bears 36 teeth on each ramus; the parietals do not form a sagittal crest; the quadrate overlaps the quadrate ramus of the pterygoid anterolaterally; the paroccipital process of the exoccipital-opisthotic is relatively short and massive; the occipital condyle is not ringed by a groove, and extends onto the pedicles of the exoccipitals. (The postcranial skeleton is not known.)

Referred specimen. In September 1978 R. A. and P. A. Langham exhibited at the 26th Symposium of Vertebrate Palaeontology and Comparative Anatomy, University of Reading, a second specimen of this species, consisting of a less complete skull (but including the basisphenoid) and some anterior cervical vertebrae. It is hoped that this specimen may receive description in subsequent work.

Description of holotype. Specimen R.8431 was presented almost clear of the Clay matrix, and the last traces were removed with an industrial 'Airbrasive' machine. This revealed the suture lines and surface ornament. The skull is remarkably well preserved, and consists of eight pieces with an additional nine isolated teeth. The frontals, parietals, postorbital bar and squamosals are associated in a single piece (Figs 26, 27, 31, 32) and the right angular and fused surangular-articular form a second piece (Figs 28, 38) onto which have been compressed two isolated teeth and an unidentifiable skull fragment. The remaining elements listed above are preserved completely disarticulated. A small sliver of bone compressed onto the left anterior part of the dentary appears to be a fragment of the left premaxilla.

The reconstruction of an occipital view of the skull (Fig. 30) necessitated restoration only of the missing supraoccipital, other elements being reproduced as mirror images of their opposites. From this occipital reconstruction can be determined the distance between the jaw articulations and the height from these to the skull vertex. The entire right ramus of the lower jaw is preserved, and thus the skull length can be restored; furthermore, the dorsal line of the skull is preserved almost to the anterior margin of the orbit. It was therefore possible to reconstruct a lateral view (Fig. 29), the missing outlines being restored from the reconstruction of *Cryptoclidus eurymerus* (Fig. 1).

The tooth number is known for the lower jaw from empty sockets, and their interlock was reconstructed on a one-to-one basis (approximately as in other forms) by assuming a similar

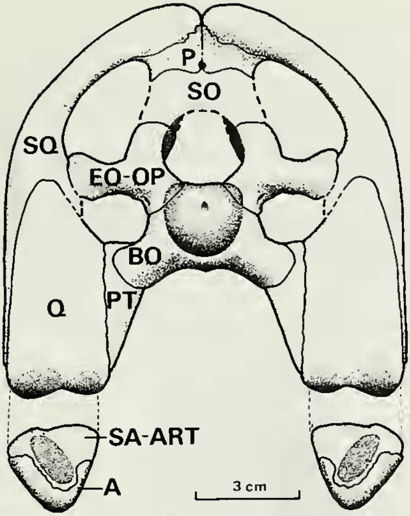


Fig. 30 *Kimmerosaurus langhami* gen. et sp. nov., R.8431. Reconstruction of skull in occipital view. Abbreviations as in Fig. 2, p. 259.

number of teeth in the upper jaw. As thus restored, the premaxilla bears 8 teeth, and this figure is upheld as a minimum number by osteological evidence (see below, p. 311).

The preserved parts of the frontals agree in general structure with those of *Cryptoclidus*. Posteriorly they unite with the parietals by complex interlaminating sutures, forming the anterior border of the pineal foramen. In advance of the foramen they suture ventrally, but dorsally they remain separated by a median groove. Judged from the shape of the orbital margins, the orbits must have been relatively large (see Fig. 29). Anteriorly the frontals are broken, and there is no evidence for the position of the nares.

A proximal portion of the postorbital bar is preserved *in situ* on the right side. It is flat and very thin, and lies in a plane which dips downwards and backwards to form an angle of about 30° with the skull table. The preserved part shows no downward curvature, and it is not possible to determine the form of its connection, if any, with elements of the cheek region. The bar is composed of the postfrontal and the postorbital; accidental breaks (now repaired with plastics soluble in chloroform) showed sections which confirmed beyond any doubt the presence of both these elements. The postfrontal is a thin lamina of bone sandwiched between a lateral flange of the parietal, upon which it rests dorsally, and the postorbital by which its posterior part is overlain. The thickest preserved part of the element is the broken anterior margin, which is 2 mm thick; when complete, the postfrontal probably met the posterolateral corner of the frontal in the region of its suture with the parietal. The postorbital is also laminate and is exceedingly thin, being only 0·5 mm in vertical section.

The parietals appear to be in the process of fusing with one another: their median suture is visible on the dorsal and occipital surfaces, but cannot be traced ventrally. Anteriorly the parietals are somewhat overlapped by the frontals, and in dorsal view the oval pineal foramen is bordered equally by both elements. Behind the foramen each parietal expands to produce a lateral flange, the plane of which curves downwards and backwards reaching a maximum angle of about 45° to the skull table. This forms the base of the postorbital bar, and together with the overlying postfrontal it forms the upper part of the orbital margin.

Behind the lateral flange, the sides of the parietals are excavated concavely for the temporal musculature. Unlike any plesiosaur described previously there is no development of a sagittal crest; instead, the temporal fossae are separated by at least 1 cm of irregularly-pitted dorsal surface, the edges of which actually overhang the excavations. In lateral view the dorsal outline of the skull is approximately linear, the parietals continuing the lines of the frontals, whereas in other plesiosaurs the sagittal crest is elevated well above this line.

Behind the smooth ventral surfaces of the lateral flanges the roof of the braincase is divided into three distinct areas (Fig. 32). In the ventral midline is a groove which widens and deepens into a roughened pit halfway along its length. The groove is surrounded by a smooth cartilage-covered area which in turn is bordered laterally by areas of roughened bone which curved ventrally to form part of the braincase walls and unite with the prootics. The posterior part of the smooth area is inclined posteroventrally at a slight angle and forms two facets, divided by a groove, for union with the supraoccipital. With the latter element in place, the groove would form a median channel leading from the occipital surface to the pit;

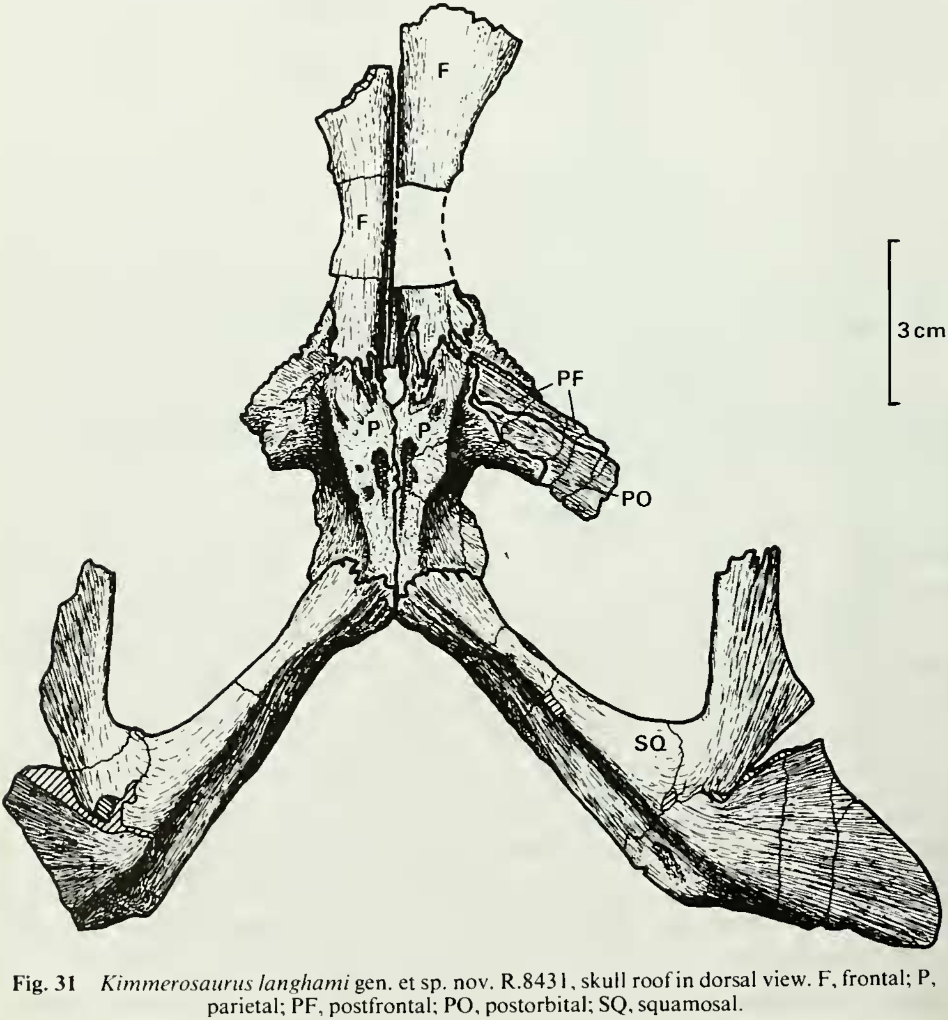


Fig. 31 *Kimmerosaurus langhami* gen. et sp. nov. R.8431, skull roof in dorsal view. F, frontal; P, parietal; PF, postfrontal; PO, postorbital; SQ, squamosal.

as was suggested with regard to a similar structure in *Cryptoclidus eurymerus*, this may have housed the origin of a nuchal ligament. The occipital surface of the parietals is proportionally small by comparison with that of the other forms described above.

Posteriorly the parietals suture with the squamosals, beneath which they are produced into posterolateral processes which play a part in the formation of the post-temporal bar.

The squamosals are relatively large; the right element is complete and has the usual triradiate structure. Post-mortem crushing has resulted in spreading apart the ventral rami and thereby somewhat straightening the dorsal rami. The elements meet in the midline above the parietals, where the dorsal rami become unusually bulbous and form the highest part of the skull profile. In consequence, the post-temporal bar is thicker and stronger than in *Cryptoclidus*, *Muraenosaurus* and *Tricleidus*, in which genera the dorsal ramus is neatly spliced into the parietal.

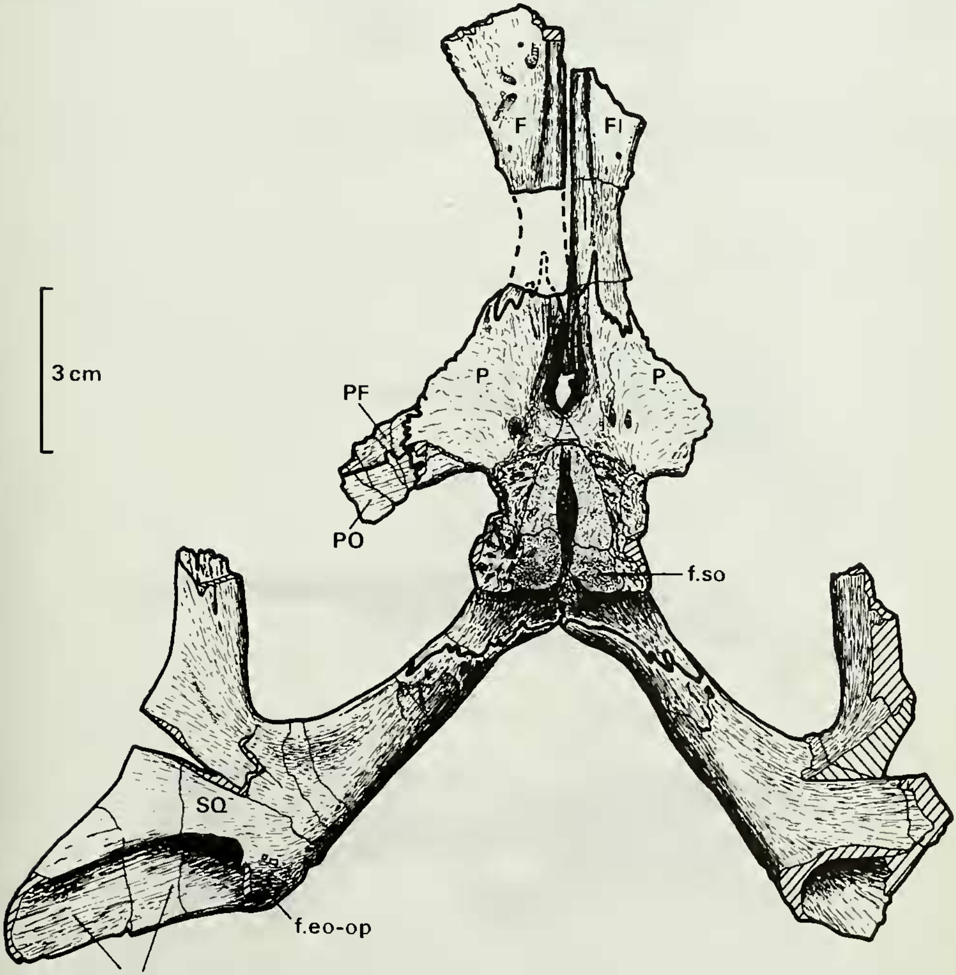


Fig. 32 *Kimmerosaurus langhami* gen. et sp. nov. R.8431, skull roof in ventral view. f.eo–op, facet for articulation with paroccipital process of the exoccipital-opisthotic; f.q, facet for quadrate; f.so, facet for supraoccipital. Other abbreviations as in Fig. 31.

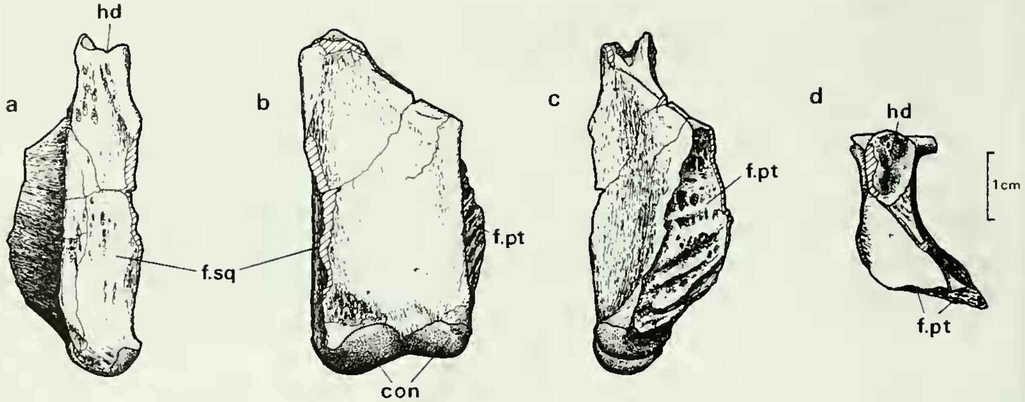


Fig. 33 *Kimmerosaurus langhami* gen. et sp. nov. R.8431, left quadrate: a, lateral; b, posterior; c, medial; d, dorsal aspect. con, condyles for jaw articulation; f.pt, facet for pterygoid; f.sq, facet for squamosal; hd, head of quadrate.

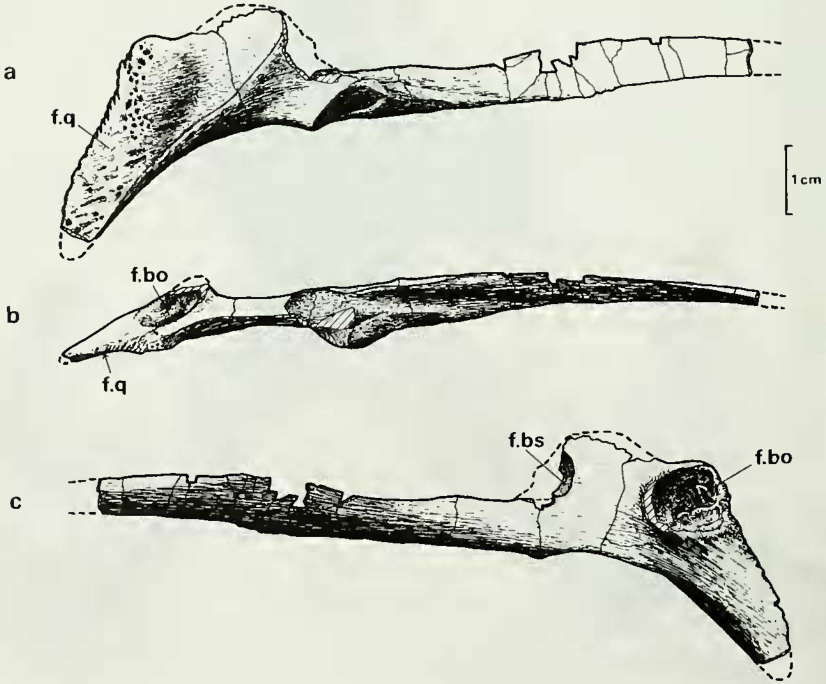


Fig. 34 *Kimmerosaurus langhami* gen. et sp. nov. R.8431, right pterygoid: a, lateral; b, dorsal; c, medial aspect. f.bo, facet for basipterygoid process of basioccipital; f.bs, facet for basicranial process of basisphenoid; f.q, facet for quadrate.

The anterior ramus of the squamosal terminates in a large sutural surface, but there is no indication of the nature and direction of the elements with which it was united. The ventral ramus has the same structure as in *C. eurymerus*: on its medial surface is a large facet for the quadrate, above which is a small facet for the paroccipital process of the exoccipital-opisthotic.

The quadrate (Fig. 33) is relatively larger and proportionally longer than in the preceding genera. Ventrally it forms two ovoid condyles for articulation with the lower jaw, the lateral condyle being slightly larger than the medial. The large lateral facet for the squamosal is 5·7 cm long; above its dorsal end is the conical primary head, which was tipped with cartilage. From this prominence the dorsal edge of the quadrate describes an inward, forward and downward arc which terminates along the upper edge of the pterygoid facet and was continued by the pterygoid. The large pterygoid facet is vertically orientated, extends for 4·8 cm from the dorsal margin to the inner angle of the medial condyle, and faces posteromedially at *c.* 20° to the long axis of the skull; the anteromedial margin is thin and broken, and may possibly have continued as a thin film of bone further anteriorly across the lateral surface of the pterygoid, its ultimate extent being indicated by a ridge on the pterygoid. The mechanism of suture of the two elements in the present specimen, where the quadrate extensively overlaps the pterygoid anterolaterally, is the reverse of that described in *Muraenosaurus* and *Tricleidus*, where the posterior end of the pterygoid fits into an anterolateral notch in the quadrate.

Parts of both pterygoids are preserved, the right being the more complete (Fig. 34). It is an elongated element consisting of a long, thin and horizontally orientated anterior part which was involved in the formation of the palate, together with a more massive posterior part which bears facets for union with the basisphenoid, basioccipital and quadrate.

The quadrate facet is large, its surface is much pitted, and its anteroventral edge is defined

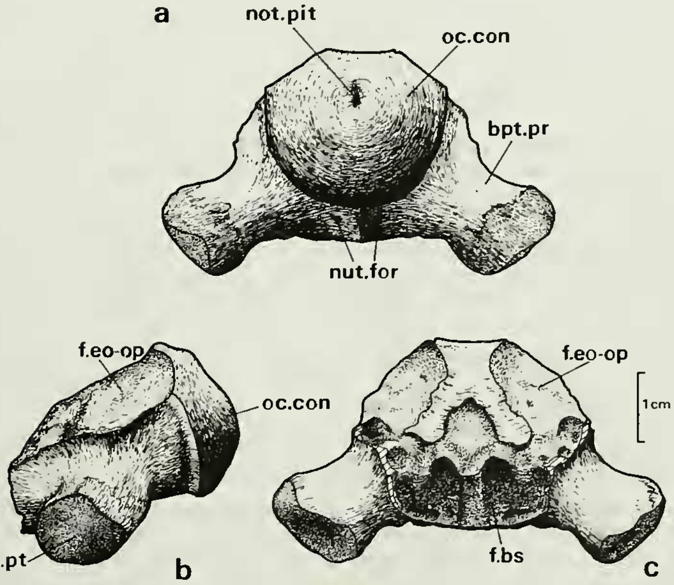


Fig. 35 *Kimmerosaurus langhami* gen. et sp. nov. R.8431, basioccipital: a, posterior; b, left lateral; c, anterior aspect. bpt.pr, basipterygoid process; f.bs, facet for basisphenoid; f.eo–op, facet for exoccipital-opisthotic; f.pt, facet for pterygoid; not.pit, notochordal pit; nut.for, nutritive foramina; oc.con, occipital condyle.

by a prominent oblique ridge. This facet is confined to the lateral surface of the bone, the pterygoid thereby differing in form from those of *Muraenosaurus* and *Tricleidus*.

The facet for articulation with the basioccipital is a deep and oval depression on the medial surface of the pterygoid. It has a much roughened floor and an elevated rim, and it faces posteromedially. Since it is situated opposite the upper end of the quadrate facet, the basioccipital and quadrate are at this point separated only by a lamina of pterygoidal bone about 2 mm thick.

Anterior to the quadrate and basioccipital facets the dorsal edge of the pterygoid rises to form a thin crest of bone, beyond which it falls to the base of the palatal ramus. The facet for union with the basisphenoid, which is a crescentic depression with a roughened floor, lies on the medial surface just posterior to this point and about 2 cm anterior to the basioccipital facet. There is no development of a process marking a second and more posterior contact with the basisphenoid such as characterizes the pterygoid of *Tricleidus*.

Immediately in front of the basisphenoid facet the pterygoid expands to twice its width, this increase being produced on the lateral side of the bone. From here the palatal ramus extends forwards as a flattened rod. At first this is orientated to face about 45° dorsolaterally, but further forward the angle is increased by spiralling until the plane of the bone is vertical. The twist may perhaps be a result of post-mortem distortion or of cumulative small errors in repairing many breaks across the very thin bone; if this be the case, then it is likely that the present flat medial surface was once ventrally orientated and played a normal role in the formation of the palate as in other plesiosaurs. It is not possible, however, to judge how this anterior part of the pterygoid might have connected with the rest of the palate. There are no facets on the preserved parts, and it is unlikely that contact was made with the parasphenoid as in *Tricleidus*.

The basioccipital (Figs 27, 35) is relatively large, and articulated with the exoccipital-opisthotics, basisphenoid, pterygoids and atlas. The dorsal surface is comprised of the large lateral facets for the exoccipital-opisthotic elements, between which lies the floor of the braincase. Posteriorly this is concave, but anteriorly it is divided by a median ridge the surface of which has not been completely ossified.

The anterior basioccipital surface is the facet for the basisphenoid. This is compressed dorsoventrally into an elliptical shape and is relatively small, barely equalling a facet for an exoccipital-opisthotic. It is marked by a median vertical groove which with the basisphenoid may have formed a small dorsoventral channel such as was noted in *Muraenosaurus*. The ventral surface of the element is marked by a gentle median ridge, on either side of which are small nutritive foramina.

On the lateral surfaces are produced the short and massive pterygoid processes. Distally these form the pterygoid facets, which are orientated anterolaterally and are isolated completely from the basisphenoid facet by finished bone surface. In the genera described previously, the pterygoid and basisphenoid facets are confluent except in fully ossified 'old adult' specimens.

The structure of the occipital condyle is unique. It is reniform in outline, being formed largely from the basioccipital with about one tenth of its area being borne on the pedicles of the exoccipitals (this character is known to be shared only with the genus *Cryptoclidus*). Furthermore, its surface is not spherical, but instead is marked by a well-developed notochordal pit which is situated a little above the centre.

The exoccipital and opisthotic are fused, as in other plesiosaurs. The right combined element is preserved (Fig. 36), in which the line of fusion of its components is indicated on the medial surface by a ridge and at the dorsal and ventral margins by notches. The exoccipital portion largely forms the facet for the basioccipital, and is pierced anteriorly by a large jugular foramen and more posteriorly by two foramina for branches of the hypoglossal nerve; it also forms a small part of the occipital condyle. The opisthotic portion largely forms the facet for the supraoccipital, and contains the posterior half of the utriculus and parts of the horizontal and posterior vertical semicircular canals. It is not clear which part formed the paroccipital process, which in this genus is comparatively shorter and more massive than in

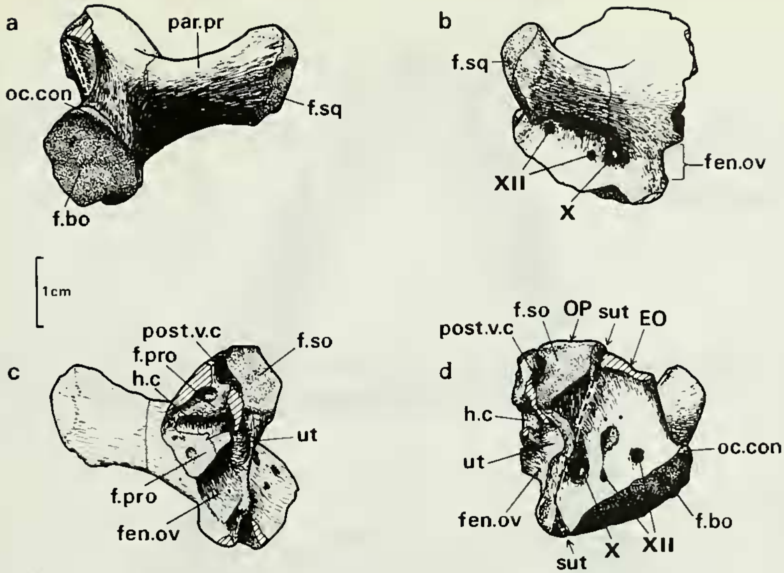


Fig. 36 *Kimmerosaurus langhami* gen. et sp. nov. R.8431, fused right exoccipital-opisthotic: a, posterior; b, lateral; c, anterior; d, medial aspect. EO, exoccipital part; f.bo, facet for basioccipital; f.pro, facet for prootic; f.so, facet for supraoccipital; f.sq, facet for squamosal; fen.ov, position of fenestra ovalis; h.c, horizontal semicircular canal; oc.con, occipital condyle; OP, opisthotic part; par.pr, paroccipital process; post.v.c, posterior vertical semicircular canal; sut, position of fused suture between component elements; ut, depression for utriculus; X, jugular foramen; XII, foramina for branches of hypoglossal nerve.

Cryptoclidus, and considerably more so than in *Muraenosaurus* and *Tricleidus*. Distally the paroccipital process bears a facet for union with the squamosal.

The dentary (Figs 27, 37) is remarkably slender and lightly built, and in dorsal view the tooth-bearing area of spongy bone is predominant whilst the solid lamellar bone which strengthens the medial margin of the jaw ramus appears deficient by comparison with other genera (e.g. *Cryptoclidus*, cf. Figs 3 and 37). The specimen has been eroded somewhat: the dorsal portions of the tooth sockets have been lost yet the ventral parts remain, and so the sockets appear as grooves which are orientated outwards and inclined slightly upwards. There are 34 well-preserved sockets on the right ramus, the most posterior of which blends into a space large enough to have held a further two sockets, thus making a total of 36; this is probably also the total for the left ramus. No remains of splenials could be identified on the medial surface.

A small fragment of bone which represents part of the left premaxilla (judged from its position and close fit with the dentary) is compressed onto the dentary over the 3rd to 7th left tooth sockets. This fragment suggests that in life the premaxilla extended posteriorly at least to the level of the lower 7th socket. As the 1st upper tooth interlocks in advance of the 1st lower tooth in all described plesiosaurs, and as the interlock of the teeth is on a one-to-one basis at least for the length of the premaxilla, it follows that there were probably at least 8 pairs of premaxillary teeth in the present species. This figure, and also the number of dentary teeth, exceeds that recorded for all plesiosauroids except one, the South American Cretaceous form *Aristonectes parvidens* Cabrera, 1941. In that genus and species (described as 'aberrant' by Welles, 1962) there are 15 pairs of premaxillary teeth and 58 pairs of teeth on the dentary.

The angular, surangular and articular are preserved on the right side (Figs 28, 38); these

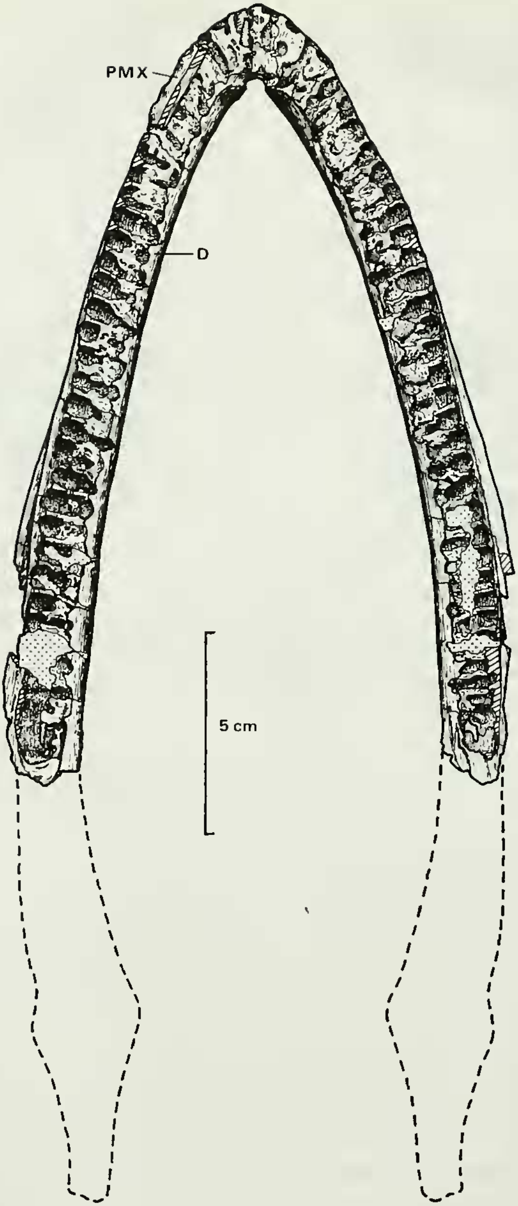


Fig. 37 *Kimmerosaurus langhami* gen. et sp. nov. R.8431, dentary in dorsal view. Outline of posterior portions of lower jaw restored with broken lines. D, dentary; PMX, a small fragment of the left premaxilla.

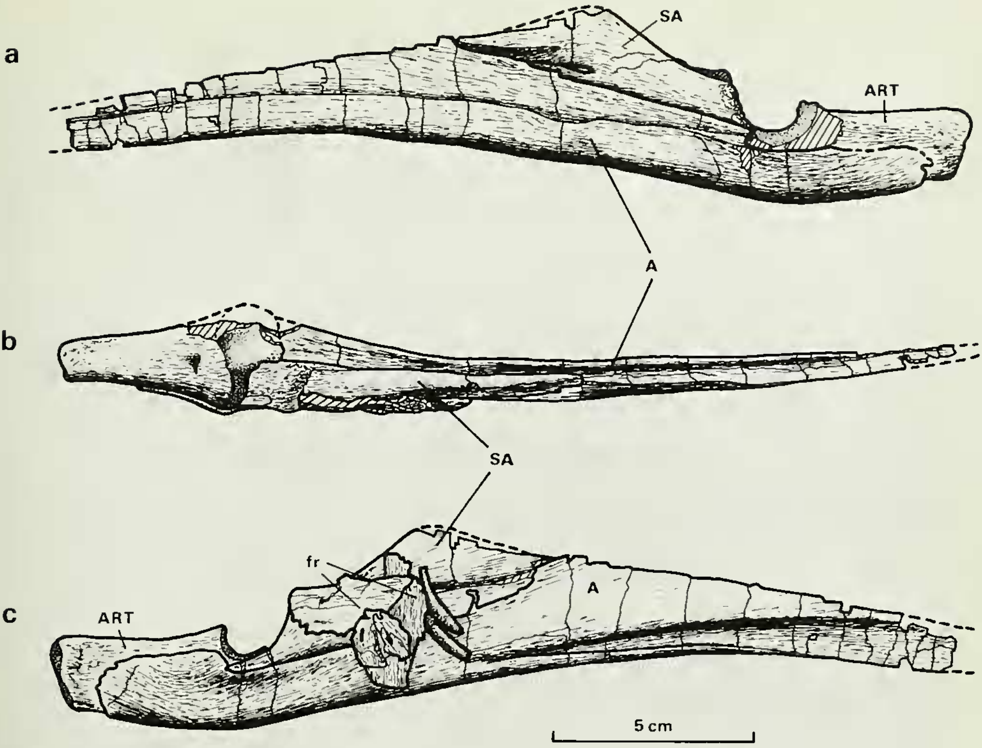


Fig. 38 *Kimmerosaurus langhami* gen. et sp. nov. R.8431, posterior elements of right lower jaw: a, medial; b, dorsal; c, lateral aspect. fr, compressed fragments of skull and two teeth. Other abbreviations as in Fig. 4, p. 263.

are very similar to the corresponding parts of *Cryptoclidus* (cf. Fig. 4). The articular and surangular appear to be fused as in other forms, but what is probably the line of fusion may be traced across the jaw articulation. In lateral view the angular shows marked curvature in the vertical plane, with the ventral edge concave. This curvature has the effect of lowering the jaw articulation with respect to the toothrow, which also occurs to a slightly lesser extent in *Cryptoclidus* but not at all in *Tricleidus* (cf. Figs 29, 1 and 22). The lateral surfaces of the angular and surangular were overlapped by the dentary, whose posterior limit is indicated on these elements by ridges which are partly overlain by compressed unidentifiable debris and two teeth. The extent of this overlap is shown in Fig. 29.

The teeth (Figs 28, 39) are unique amongst plesiosaurs in three respects: they are completely lacking in longitudinal ornamental ridges; they are greatly recurved, the crowns curving through an arc of up to 75°; and in section the distal parts of the crowns are not circular but elliptical, being buccolingually compressed. They are very sharply pointed, and it is notable that even the largest teeth show no signs of attrition. Some large specimens show facets resulting from resorbtion of the root in advance of an approaching replacement tooth.

With regard to the proportional length of the snout and the dentition, the present specimen is quite unlike any plesiosaur reconstructed previously. Several characters (including increase in numbers of teeth, reduction in dental ornament, form of the occipital condyle, reduction in length of the paroccipital process and curvature of the angular) suggest an affinity closer to *Cryptoclidus* than to *Muraenosaurus* or *Tricleidus*.

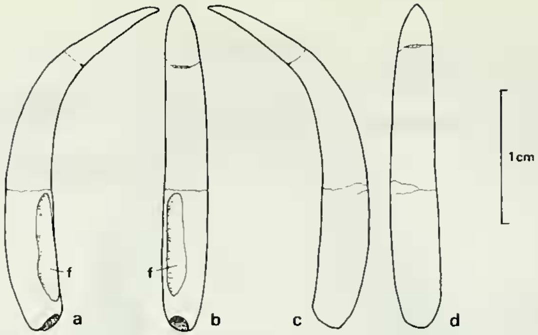


Fig. 39 *Kimmerosaurus langhami* gen. et sp. nov. R.8431, tooth: a and c, axial: b, lingual; d, buccal aspect. Note absence of ornamental ridges. f, resorbtion facet on root.

Genus *COLYMBOSAURUS* Seeley, 1874

Type species. *Plesiosaurus trochanterius* Owen, 1840.

Diagnosis. As for the type species (monotypic genus).

Colymbosaurus trochanterius (Owen, 1840)
(Figs 40, 43e, 44f)

1840 *Plesiosaurus trochanterius* Owen: 85.
1841 *Plesiosaurus (Pliosaurus) trochanterius* Owen; Owen: 64.
1869 *Pliosaurus trochanterius* (Owen) Owen: 7 (name only).
1869 *Pliosaurus portlandicus* Owen: 8; pl. 4.
1869 *Plesiosaurus megadeirus* Seeley: xx.
1869 *Plesiosaurus macrodeirus* Seeley: 143 (alternative original spelling for *P. megadeirus*, rejected Lydekker 1889 : 190).
1870 *Plesiosaurus manselii* Hulke: 612; pl. 41 figs 1–6.
1870 *Plesiosaurus megadeirus* Seeley; Hulke: 618.
1870 *Plesiosaurus trochanterius* Owen; Hulke: 620.
1870 *Pliosaurus portlandicus* Owen; Hulke: 620.
1871 *Plesiosaurus trochanterius* Owen; Phillips: 316, fig. 162.
1871 *Pliosaurus portlandicus* Owen; Seeley: 181.
1871 *Plesiosaurus megadeirus* Seeley; Seeley: 184.
1874*b* *Colymbosaurus megadeirus* (Seeley) Seeley: 445, fig. 12.
1874*b* *Muraenosaurus manselli* ('Hulke') Seeley: 448 (mis-spelling).
1879*a* *Muraenosaurus manselii* (Hulke); Sauvage: 1.
1879*a* *Muraenosaurus manselii* (Hulke); Sauvage: 1.
1883 *Plesiosaurus manseli* 'Hulke'; Hulke (mis-spelling).
1888 *Plesiosaurus trochanterius* Owen; Lydekker: 353, fig. 2.
1888 *Plesiosaurus megadirus* 'Seeley'; Lydekker: 353 (mis-spelling).
1888 *Plesiosaurus manseli* 'Hulke'; Lydekker: 354.
1889 *Cimoliosaurus trochanterius* (Owen) Lydekker: 190, figs 59, 62–65 (mis-spelling for *Cimoliasaurus* Leidy, 1852).
1889 *Muraenosaurus manseli* ('Hulke'); Lydekker: 190 (cited in synonymy).
1889 *Plesiosaurus macrodirus* 'Seeley'; Lydekker: 190 (mis-spelling cited in synonymy).
1889 *Colymbosaurus megadirus* ('Seeley'); Lydekker: 190 (cited in synonymy).
1889 *Cimoliosaurus portlandicus* (Owen) Lydekker: 227, fig. 70.
1892 *Colymbosaurus megadeirus* (Seeley); Seeley: 138.
1892 *Colymbosaurus manselli* ('Hulke') Seeley: 138.
1892 *Colymbosaurus portlandicus* (Owen) Seeley: 147.
1895*c* *Muraenosaurus manselli* ('Hulke'); Andrews: 432.

1911 *Cryptocleidus trochanterius* (Owen) Sauvage: 186–215 (mis-spelling for *Cryptoclidus* Seeley, 1892).
1924 *Colymbosaurus manselli* ('Hulke'); Watson: 902.
1959 *Colymbosaurus portlandicus* (Owen); Delair: 62.
1959 *Colymbosaurus manseli* ('Hulke'); Delair: 63.
1959 *Colymbosaurus trochanterius* (Owen) Delair: 64.
1963 *Colymbosaurus megadeirus* (Seeley); Persson: 24.
1963 *Colymbosaurus manseli* ('Hulke'); Persson: 24.
1963 *Colymbosaurus portlandicus* (Owen); Persson: 24.
1963 *Colymbosaurus trochanterius* (Owen); Persson: 24.
1964 *Colymbosaurus megadeirus* (Seeley); Novozhilov: 321, fig. 305.

HOLOTYPE. Specimen 31787, the right humerus of a large 'old adult' individual. It was collected by Viscount Cole (later 3rd Earl of Enniskillen), described by Owen (1840) and figured from a plaster cast in the Oxford Museum by Phillips (1871 : fig. 162).

TYPE LOCALITY AND HORIZON. From the Kimmeridge Clay of Shotover Hill, Oxfordshire, according to Owen (1840). Phillips (1871) recorded the dissent of the Earl of Enniskillen, who claimed that although several specimens similar to the type had been collected by him from Shotover Hill, the holotype itself was taken from the Oxford Clay of Christian Malford, Wiltshire. Lydekker (1889) cited the horizon and locality as the Kimmeridge Clay of Wiltshire; this is an unsatisfactory compromise. In view of the fact that many specimens similar to 31787 are known, all of which are from Kimmeridge Clay, it seems more reasonable to accept Owen's account rather than to trust the Earl's memory thirty years after that publication.

DIAGNOSIS. Plesiosauroids in which there are 42 cervical vertebrae with amphicoelous centra, the length of which never exceeds the height; the ventral ramus of the scapula is relatively large and plate-like, and has a convex anterior margin; the coracoids meet the scapulae in the midline in 'adults'; the width across the posterior cornua of the coracoids slightly exceeds the interglenoid width in 'adults'; the humerus and to a lesser extent the femur are expanded posterodistally, both forming three distal articular facets; there are three epipodials in both the manus and the pes; the overall length of the 'adult' is 5·0 to 6·6 m. (The skull and dermal elements of the pectoral girdle are unknown in this genus and species.)

DISTRIBUTION AND RANGE. Diagnostic material is known from several English localities ranging from Kimmeridge Bay, Dorset, through Oxfordshire and Cambridgeshire to Downham Market, Norfolk. Upper Jurassic, Kimmeridgian and Portlandian Stages. Two referred specimens may be accurately placed: 40106 is from the cliffs to the east of Clavell's Tower, Kimmeridge Bay, Dorset (Hulke 1870), and therefore from the zone of *Pectinatites pectinatus*, Upper Kimmeridgian Stage (Arkell 1933); 40640 is from the Portland Stone of Portland Island, Dorset (Owen 1869) and therefore from the zone of *Titanites giganteus*, Portlandian Stage (Arkell 1933).

REFERRED SPECIMENS. The following specimens are diagnostic: those with numbers without prefixed letters are in the collection of the British Museum (Natural History) (see p. 254).

31785. An 'adult' left femur from the Kimmeridge Clay of Shotover, Oxfordshire.

31795. An 'adult' left humerus from the Kimmeridge Clay of Shotover, Oxfordshire.

40106. Incomplete 'adult' postcranial skeleton from the Kimmeridge Clay (*Pectinatites pectinatus* Zone) of Kimmeridge Bay, Dorset. Described and partly figured by Hulke (1870) as the holotype of *Plesiosaurus manselii* Hulke. Originally catalogued (Lydekker 1889) under the numbers 40106, 40107a, 40107b, 40108a, 42496 and 42496a.

40107. An 'adult' left femur from the Kimmeridge Clay of Kimmeridge Bay, Dorset.

40640. A 'juvenile' right femur and associated epipodials, tarsals and proximal phalanges from the Portland Stone (*Titanites giganteus* Zone) of Portland Island, Dorset. Figured by Owen (1869 : pl. 4) and by Hulke (1883 : fig. 8) as the holotype of *Pliosaurus portlandicus* Owen.

46479. A 'juvenile' right humerus from the Kimmeridge Clay (locality unknown). A figure by Lydekker (1889 : fig. 62), alleged to be of this specimen, is not representative.

C.M.N. 15.72(2) (Fig. 40). An 'adult' left femur, tibia, fibula, two distal tarsals and several phalanges (on display), and a right femur. Collected from the Kimmeridge Clay of Downham Market, Norfolk, by C. B. Rose.

M.M. LL.5513–8. An incomplete 'adult' postcranial skeleton consisting of the right humerus (LL.5513), left humerus (LL.5514), left scapula (LL.5515), both coracoids (LL.5516–7) and two ulnae, one ulnare and a carpal (LL.5518a–d) from the Kimmeridge Clay of Coppock's Pit, Shotover, Oxford. Figured by Watson (1924 : figs 8, 10d).

S.M.C. J.29596 etc. Incomplete 'adult' postcranial skeleton collected from the Kimmeridge Clay of Ely by Stead Jones. Catalogued and made a syntype of *Plesiosaurus megadeirus* by Seeley (1869). Each bone is numbered separately: coracoids J.29596–7; vertebrae J.29598–653; left hindlimb J.29654–91, and the right hindlimb J.59736–43.

S.M.C. J.63919. Incomplete 'adult' vertebral column from the Kimmeridge Clay of Haddenham. Catalogued and made a syntype of *Plesiosaurus megadeirus* by Seeley (1869).

Discussion of synonymy

Owen (1840) described the holotype (31787) as a 'limb bone'. It was identified correctly by Phillips (1871) as a humerus, but was misidentified as a femur by Hulke (1870, 1883) and by Lydekker (1889). Hulke also mistook it for the type specimen of *Pliosaurus brachydeirus* Owen, apparently because it was incorrectly labelled (Lydekker 1889), and misidentified specimen 31795 as the type of the present species. Fortunately, specimen 31787 shows several distinguishing features which were described by Owen and Phillips. Much confusion exists in the literature, but happily not in the type material.

Seeley (1869) listed two specimens (now J.29596 etc. and J.63919) in the Sedgwick ('Woodwardian') Museum, Cambridge, under the new name *Plesiosaurus megadeirus*. He merely listed the bones present, this leading Lydekker (1888, 1889) to regard the name as not established. However, Seeley's listing revealed that the neck consists of 42 cervical vertebrae (in J.29596 etc.); this is still used as a distinguishing taxonomic character, and so *P. megadeirus* is an available name.

Owen (1869) described a small right femur and associated paddle bones of a 'juvenile' specimen (40640) under the new name *Pliosaurus portlandicus*. A character shown by this limb (in which the elements are preserved *in situ*) is that the distal end of the femur articulates with three epipodials.

In 1870, Hulke described and figured a large 'adult' postcranial skeleton (specimen 40106) under the new name *Plesiosaurus manselii*. This specimen includes most of the vertebral column and proximal parts of both left limbs including the humerus and the femur (which were confused by Hulke). An important observable character is the form of the humerus ('femur' of Hulke) which, like the femur ('humerus') articulates distally with three epipodials.

Hulke commented on the apparent similarity of his specimen to the syntypes of *P. megadeirus*, but was prevented from making a detailed comparison by the lack of adequate description of the latter specimens. He also noted a strong similarity between the humerus ('femur') of *P. manselii* and the type humerus ('femur') of *P. trochanterius* ('*Pliosaurus brachydeirus*'). Finally he engaged upon a comparison between them and the type specimen of *Pliosaurus portlandicus* (which is truly a hind limb) and came very close to invalidating his new name through synonymy. Lydekker (1888, 1889) formally synonymized *P. manselii* and *P. megadeirus* with *P. trochanterius* and transferred the species to the genus *Cimoliasaurus* (a *nomen dubium*, see Welles 1962).

Seeley (1874*b*) distinguished several English genera of plesiosaurs using as his principal criterion the structure of the pectoral girdle. He introduced the new generic name *Colymbosaurus*, and indicated *P. megadeirus* as the type species. He later modified the diagnosis (Seeley 1892) to enable *Colymbosaurus* to be distinguished from *Muraenosaurus*, this time using the comparative form of the vertebrae and propodials and the presence of at least three epipodials in each paddle in *Colymbosaurus*. Three species were referred to the genus (*C. megadeirus*, *C. manselii* and *C. portlandicus*), Seeley believing that these could be distinguished by the comparative form and number of epipodials (he misinterpreted *C. manselii* as having four epipodials, and separated *C. portlandicus* by characters which are typical of 'juvenile' individuals).

It is now argued that the material described under the names *Plesiosaurus trochanterius*, *P. megadeirus*, *P. manselii* and *Pliosaurus portlandicus* represents a single species, the valid name for which is *Colymbosaurus trochanterius* (Owen). The taxon is distinguished by characters of the cervical vertebrae, scapula, humerus, femur and epipodials, yet the holotype consists only of an isolated humerus and even the most complete specimens (40106 and J.29596 etc.) do not display all the characters. The diagnosis depends upon the overlap of several specimens which together show all characters. In 40106 are preserved distinctive cervical vertebrae, a humerus with epipodials and a femur. The humerus is of the same kind as the holotype (31787) and also of LL.5513–8; with the latter is preserved a pectoral girdle including the characteristic scapula. The femur of 40106 is of the same kind as those of 40640 and 15.72(2), in which epipodials are preserved, and also J.29596 etc. in which is preserved the full complement of cervical vertebrae.

Description of material

Colymbosaurus trochanterius is the largest and longest of the English Upper Jurassic plesiosauroids. The preserved vertebral columns of specimens 40106 and J.29596 etc. are incomplete but complementary, and it was possible to deduce the composition of the entire column in this species, and hence to estimate the postcranial length of each specimen. Allowing 10% for intervertebral cartilage, the postcranial length estimate for 40106 is 5·7 m. If the skull-length to postcranial-length ratio was as in *Muraenosaurus*, then the skull might have been 0·45 m long, and the total length about 6·15 m. A similar procedure with specimen J.29596 etc. gives an estimated length of 5·0 m. The holotype (31787) is the largest known humerus, with a total actual length (discounting plaster involved in a repair to the shaft) of 0·57 m. Comparative measurements of the humeri of 40106 and 31787 indicate that the total overall length of the latter individual may have been as great as 6·6 m.

The vertebral column of J.29596 etc. is apparently complete from the fused atlas-axis to the middle of the dorsal series, and comprises 42 cervical vertebrae, 3 pectorals and 11 dorsals. In 40106 is preserved the axis-atlas, behind which is a gap (large enough for 10 vertebrae) followed by a further 30 cervicals. Distortion and damage makes many of the trunk vertebrae difficult to identify; the 32 centra probably represent 3 pectorals, 25 dorsals and 4 sacrals. Posterior to these are 20 well-preserved caudal vertebrae; between two of these is a small gap for 3 vertebrae, and a further 3 or 4 are required to complete the tip of the tail. Posterior chevron facets begin on the 4th caudal, and anterior facets on the 10th.

The shape and proportions of the vertebral centra are similar to those of *Cryptoclidus*: the outline of a longitudinal section across the articular face is a double sigmoid curve (cf. *Muraenosaurus*), and the length of the cervical centra never exceeds the height. By comparison with *Cryptoclidus*, the neck of *Colymbosaurus* is lengthened by an increase only in the number of vertebrae, without the accompanying increase in proportional length which occurs in *Muraenosaurus*.

The most complete pectoral girdle is that of LL.5513–8, in which the left scapula and both coracoids are preserved (Fig. 43e). The coracoids are similar in form to those of *Tricleidus*, the width across the posterior cornua being slightly in excess of the interglenoid width. The scapula is distinctive, and differs from other scapulae in the structure of the ventral ramus. This part ('anterior ramus' of Watson 1924) is greatly expanded anteroposteriorly, and unusually so where it meets the base of the dorsal ramus. The dorsal and ventral rami thus appear confluent; their combined anterior margin is convex and thereby differs in shape from that of contemporary genera, in which the base of the ventral ramus is constricted into a bar. The dorsal ramus is broken distally, but the proximal part has the usual structure, and there is no evidence to support the statement by Watson (1924 : 903) that in this species it was 'of very small size, being thin and weak in consonance' (*sic*).

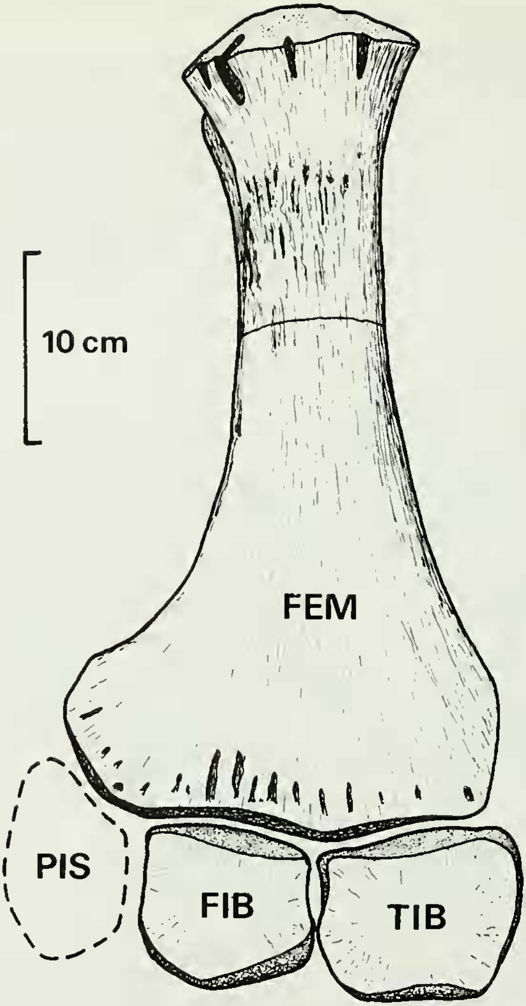


Fig. 40 *Colymbosaurus trochanterius* (Owen), left femur and epipodials of C.M.N. 15.72(2) in ventral view. FEM, femur; FIB, fibula; PIS, pisiform; TIB, tibia.

There are no indications either for or against the presence in this species of an interclavicle or clavicles. The pelvic girdle is not preserved with any specimens.

The humerus (Fig. 44f) is proportionally large and is strongly built with a cylindrical shaft. It is expanded distally, this expansion being largely posterior to the axis of the shaft as in *Muraenosaurus*. Three facets are formed for articulation with the epipodials, the anterior facet for the radius facing somewhat anterodistally and the ulnal facet somewhat posterodistally. The posterior and smaller facet for the pisiform is orientated obliquely posterodistally. The humeri of specimens LL.5513–8 and 46479 (the latter is rather small and probably 'juvenile') show the complete form of the distal facets, whereas the remaining specimens including 31787 and 40106 have the posterodistal part of the bone broken away.

Specimen 31787 was evidently part of an 'old adult': the cartilage-covered areas of the head and the tuberosity are separated by a strip of finished periosteal bone surface such as was noted above in 'old adult' specimens of *Cryptoclidus* and *Muraenosaurus*.

The three epipodials of the forelimb have been found only with specimen 40106 (a further two ulnae are preserved with LL.5513–8). Since the original description of 40106 (Hulke 1870, 1883) the specimen has suffered badly from pyritic decay, and all that now remains of the epipodials are the proximal parts of the radius and ulna. These have been fortified with cement and varnish to prevent further crumbling, but little can now be made of their structure. However, Hulke's description is detailed and the specimens were figured (Hulke 1870 : pl. 41 fig. 3; 1883 : fig. 7). Both the radius and ulna ('tibia' and 'fibula' of Hulke 1870; 'tibia' and 'intermedium' of Hulke 1883) were described as pentahedral, and the pisiform (not named by Hulke 1870; 'fibula' of Hulke 1883) was said to be five- or six-sided and approximately equal in size to the radius and ulna. The elements were evidently held *in situ* by the matrix, and from their combined shape Hulke was able to restore the original posterodistal outline of the humerus ('femur').

The femur of *C. trochanterius* is very similar to the humerus, but the propodials may be distinguished, as with all plesiosauroid propodials, by differences in the development of the humeral tuberosity and the femoral trochanter. The tuberosity is better developed than the trochanter and lies obliquely posterodistal to the head, forming a prominent posterior angle when seen in proximal view; whereas the trochanter is dorsal but never posterior to the head (see *Cryptoclidus eurymerus*, Fig. 17a and c).

Complete femora are preserved with specimens 15.72(2) (an 'adult', Fig. 40) and 40640 (a 'juvenile', figured Owen 1869 : pl. 4), and in addition the femora of 40106 and J.29596 etc. are almost entire and may be restored. The distal end is expanded only slightly less than in the humerus, and three articular facets for the epipodials are also developed and orientated as in that element.

Tibiae and fibulae are preserved with 15.72(2) (Fig. 40), with J.29596 etc. and with 40640. Both elements are five-sided, but they differ in shape, the facet on the tibia for the intermedium being less than half the length of that facet on the fibula. The fibula has a long femoral facet, short facets for the tibia and pisiform and similar distal facets for the intermedium and fibulare. The pisiform (termed 'fabella' by Owen, 1869) is known only in 40640, and there only from its external mould in the matrix. This impression is half the size of the fibula and shows that the element articulated by three almost equal facets with the femur, fibula and fibulare.

In specimen 40640 all six tarsals together with the first three metatarsals are preserved *in situ*; wide spaces for much intervening cartilage testify to the 'juvenile' nature of the individual. The fibulare bears two almost equal distal facets, one facing obliquely anterodistally and articulating with the third distal tarsal, and the second facing obliquely posterodistally, evidently for articulation with the missing fifth metatarsal, which element had therefore completed its proximal migration into the distal tarsal row in this species.

Miscellaneous additional material

Isolated teeth. Three teeth in the Sedgwick Museum, Cambridge (J.30069, J.30070 and J.30071) were collected from the Kimmeridge Clay of Ely by J. Carter. J.30070 (Fig. 41) is complete almost to the tip, and its crown is approximately 3 cm long. The crown is ornamented with numerous longitudinal ridges which are confined to the lingual side, and in this it resembles teeth of 'juveniles' of *Muraenosaurus leedsii*. Another tooth in the Sedgwick Museum (J.14270a, Fig. 42) is labelled 'from the Portland Oolite', and has a cylindrical crown approximately 4 cm long. The proximal part of the crown is ornamented by numerous longitudinal ridges which are longer and more pronounced on the lingual side, but the distal third is smooth and without ornament. This tooth resembles those of *Muraenosaurus* and/or *Tricleidus* in general form except for the lack of ornament distally.

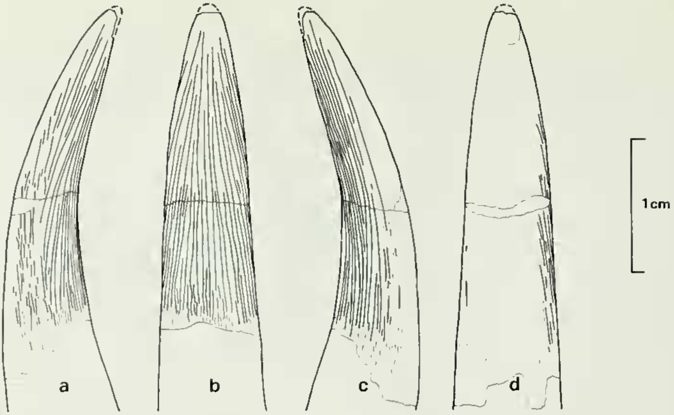


Fig. 41 S.M.C. J.30070, indeterminate tooth from Kimmeridge Clay: a and c, axial; b, lingual; d, buccal aspect.

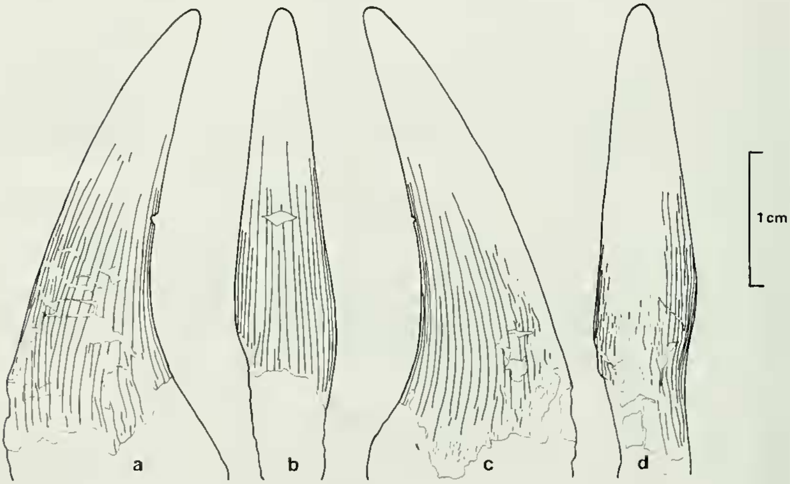


Fig. 42 S.M.C. J.14270a, indeterminate tooth from Portland Stone: a and c, axial; b, lingual; d, buccal aspect.

Both J.30070 and J.14270a may be referable to *Colymbosaurus trochanterius*, in which the teeth are unknown, or they may indicate that the ranges of the genera *Muraenosaurus* and/or *Tricleidus* extend upwards above the Callovian.

LOWER JAW SYMPHYSIS. Specimen L.9412 in the Manchester Museum is the anterior portion of a dentary collected from the Kimmeridge Clay by P. Manning. It consists of the symphysis together with eight tooth sockets on the right ramus and five on the left. Two immature teeth are present and are ornamented by longitudinal ridges. The specimen is indistinguishable from lower jaws of *Muraenosaurus leedsii* and *Tricleidus seeleyi*, and may indicate the extension of the ranges of either species into the Kimmeridgian.

VERTEBRAE. Several large vertebrae in the Castle Museum, Norwich and numbered 15.72(3)–(5) were collected from the Kimmeridge Clay of Downham Market, Norfolk, by C. B. Rose. The largest specimen, 15.72(5), is a cervical centrum of an 'adult' and has a length of 8·5 cm, a posterior height (to the neural canal) of 9·1 cm and a posterior width of 10·1 cm, and is to the best of my knowledge the largest plesiosauroid vertebra from the English Jurassic. It is distinct from the vertebrae of *Colymbosaurus trochanterius* in that it has 'flat' articular faces as in *Muraenosaurus*, and each end is ringed by an ornament of 'plications' such as are described above in 'juveniles' of *M. leedsii*. They differ from those of the latter species only in size and known geological range, but might prove to represent a distinct species were more diagnostic associated material to be found.

Several vertebrae in the Castle Museum, Norwich, and in the Sedgwick Museum, Cambridge (e.g. specimen J.29717) are recorded as from the Kimmeridge Clay, and are indistinguishable from vertebrae of the Callovian genera *Cryptoclidus* and *Tricleidus*. These may indicate that the ranges of those genera extend into the Kimmeridgian; alternatively, they may represent *Kimmerosaurus langhami*, in which species the postcranial skeleton is unknown but the skull is in several ways similar to that of *Cryptoclidus*.

Rejected names

The most frequent causes for rejection of names (below) are that they are *nomina dubia* or *nomina oblita:*

(i). A *nomen dubium* is defined (Stoll *et al.* 1964 : 151) as 'a name not certainly applicable to any known taxon', and thus covers names erected upon indeterminate type specimens. Such names were called *nomina vana* by Simpson (1945), a term which Welles (1952, 1962) used extensively with this meaning, but the term *nomen vanum* was redefined by Moore (1955) to indicate an unjustified emendation of spelling (*sensu* Stoll *et al.* 1964). Chorn & Whetstone (1978) noticed the resultant ambiguity of the *nomen vanum*, and the present work follows their recommendation that *nomen dubium* be used to indicate names erected on indeterminate type specimens or with inadequate original diagnoses.

(ii). A *nomen oblitum* is defined (Stoll *et al.* 1964 : 23, art. 23b) as a forgotten name which has 'remained unused as a senior synonym in the primary zoological literature for more than fifty years'. Such names are not to be used unless the International Commission on Zoological Nomenclature so directs. Subjective interpretation of 'the primary zoological literature' is required: in the present work the mere listing of a name in a taxonomic catalogue has been discounted, but the inclusion of any remarks indicating that the author has positive reasons for regarding that name as a senior synonym has been counted for this purpose.

For synonymies of names which are junior synonyms, see section on the senior synonym, above. Synonymies of other names are restricted to show original and subsequent combination authorship only.

Genus ***APRACTOCLEIDUS*** Smellie, 1915

TYPE SPECIES. *Apractocleidus teretipes* Smellie, 1915.

STATUS. Subjective-objective junior synonym of *Cryptoclidus* Seeley, 1892. (*Sensu* Blackwelder 1967: the synonymy of the genera is objective so long as the synonymy of their type species is subjectively maintained.)

Genus ***PICROCLEIDUS*** Andrews, 1909

TYPE SPECIES. *Muraenosaurus beloclis* Seeley, 1892

STATUS. Subjective junior synonym of *Muraenosaurus* Seeley, 1874*a*.

Genus ***TREMAMESACLEIS*** White, 1940

TYPE SPECIES. *Muraenosaurus platyclis* Seeley, 1892.

STATUS. Subjective-objective junior synonym of *Muraenosaurus* Seeley, 1874*a*.

Plesiosaurus affinis Owen, 1840

Holotype. A small propodial from the Kimmeridge Clay of Heddington pits, Oxford, and originally in the collection of Viscount Cole. Present location unknown, presumed lost.

Status. *Nomen dubium; nomen oblitum.*

Plesiosaurus brachistospondylus Hulke, 1870

1870 *Plesiosaurus brachistospondylus* Hulke: 611; pl. 41 figs 7–9.
1889 *Cimoliosaurus brachistospondylus* (Hulke) Lydekker: 200 (mis-spelling of *Cimoliasaurus* Leidy, 1852).
1912 *Colymbosaurus brachistospondylus* (Hulke); Bogolubov: 1–4.

Holotype. 45869, a phalanx, a carpal or tarsal, rib fragments and five axially-compressed dorsal vertebrae preserved in Kimmeridgian clay-stone from Kimmeridge Bay, Dorset.

Status. *Nomen dubium.*

Cimoliasaurus brevior Lydekker, 1889

1889 *Cimoliosaurus brevior* Lydekker: 243, fig. 75 (generic mis-spelling).
1911 *Muraenosaurus brevior* (Lydekker) Sauvage: 186–215.
1963 *Cimoliasaurus brevior* Lydekker; Persson: 24.

Holotype. 41955, 6 cervical centra of a 'juvenile' from the Kimmeridge Clay of Weymouth, Dorset.

Status. *Nomen dubium.*

Plesiosaurus brevis Owen, 1854

Holotype. R.C.S. 249, which was a cervical centrum from the Oxford Clay of Wiltshire. Destroyed by a fire in the Royal College of Surgeons Museum.

Status. *Nomen dubium; nomen oblitum.*

Plesiosaurus carinatus Phillips, 1871 (*non* Cuvier, 1824)

Holotype. See *Plesiosaurus phillipsi* Sauvage, 1879 (p. 323).

Status. Junior homonym, rejected and replaced by *P. phillipsi* Sauvage, 1879*a*.

Plesiosaurus doedicomus Owen, 1840

Holotype. R.273, a badly-eroded indeterminate bone, not of a plesiosaur.

Status. *Nomen dubium*. (Not plesiosaurian).

Cimoliasaurus durobrivensis Lydekker, 1889

Holotype. R.2428.

Status. Subjective junior synonym of *Muraenosaurus leedsii* Seeley, 1874*a* (see p. 284).

Plesiosaurus ellipsospondylus Phillips, 1871

Holotype. U.M.O. J.12083 and J.25942–9, nine associated cervical vertebrae from the Kimmeridge Clay of Shotover, Oxfordshire.

Status. *Nomen dubium; nomen oblitum.*

Plesiosaurus hexagonalis Phillips, 1871

HOLOTYPE. U.M.O. J.12068, a caudal centrum from the Kimmeridge Clay of Cowley Pit, Oxfordshire.

STATUS. *Nomen dubium; nomen oblitum.*

Plesiosaurus infraplanus Phillips, 1871

SYNTYPES. U.M.O. J.12069, J.12087 and J.12088, isolated single cervical centra from the Kimmeridge Clay of Stanford, Brill and Shotover (respectively), Oxfordshire.

STATUS. *Nomen dubium; nomen oblitum.*

Plesiosaurus levis Owen, 1854

SYNTYPES. R.C.S. 245 and 246, which were two dorsal vertebrae from the Kimmeridge Clay of Shotover Hill, Oxfordshire. Destroyed by fire at the Royal College of Surgeons Museum.

STATUS. *Nomen nudum; nomen oblitum.*

Plesiosaurus manselii Hulke, 1870

HOLOTYPE. 40106.

STATUS. Subjective junior synonym of *Colymbosaurus trochanterius* (Owen, 1840) (see p. 316).

Plesiosaurus megapleuron Owen, 1854

1854 *Plesiosaurus megapleuron* Owen: 60.
1959 *Colymbosaurus megapleuron* (Owen) Delair: 65.

HOLOTYPE. R.C.S. 233, which consisted of four cervical vertebrae. Destroyed by fire at the Royal College of Surgeons Museum.

STATUS. *Nomen nudum.*

Plesiosaurus oxoniensis Phillips, 1871

SYNTYPES. Phillips (1871) mentioned numerous finds of material from various Oxford Clay sites in Oxfordshire preserved in the University Museum, Oxford. These included 6 cervical vertebrae, various dorsal vertebrae, rib fragments, 8 caudal vertebrae, a pectoral girdle (described as a pelvis), a femur and several other paddle bones. These cannot now be identified amongst a mass of unlabelled plesiosauroid bones (H. P. Powell, personal communication).

STATUS. *Nomen dubium* (See discussion of synonymy of *Cryptoclidus eurymerus*, pp. 257–8).

Plesiosaurus phillipsi Sauvage, 1879(*a*)

HOLOTYPE OR SYNTYPES. U.M.O. J.12070 and J.25920–7, one cervical, two pectoral and six dorsal vertebrae from Quainton, Buckinghamshire.

STATUS. *Nomen novum* for *P. carinatus* Phillips, 1871 (*non* Cuvier, 1824); see above. *Nomen dubium; nomen oblitum.*

Plesiosaurus planispondylus Damon, 1860

SYNTYPES. 'Saurian bones' from the Oxford Clay of Dorset. These are believed to have been in the Dorset County Museum, Dorchester, but are now lost (Delair 1959).

STATUS. *Nomen nudum.*

Muraenosaurus platyclis Seeley, 1892

HOLOTYPE. R.2678.

STATUS. Subjective junior synonym of *Muraenosaurus leedsii* Seeley, 1874*a*. (see p. 284). Type species of the genus *Tremamesacleis* White, 1940.

Muraenosaurus (Cryptoclidus) platymerus Seeley, 1892

HOLOTYPE. R.2412.

STATUS. Subjective junior synonym of *Cryptoclidus eurymerus* (Phillips, 1871) (see p. 258); *nomen oblitum.*

Plesiosaurus plicatus Phillips, 1871

1871 *Plesiosaurus plicatus* Phillips: 313, figs 118, 119.
1889 *Cimoliosaurus plicatus* (Phillips) Lydekker: 234 (generic mis-spelling).
1895*c* *Muraenosaurus plicatus* (Phillips) Andrews: 429.

HOLOTYPE OR SYNTYPES. U.M.O. J.25929–41, 8 cervical and 5 dorsal vertebrae from the Oxford Clay of St Clements, Oxfordshire.

STATUS. *Nomen dubium.*

Pliosaurus portlandicus Owen, 1869

HOLOTYPE. 40640.

STATUS. Subjective junior synonym of *Colymbosaurus trochanterius* (Owen, 1840) (see p. 316).

Plesiosaurus subdepressus Owen, 1854

HOLOTYPE. R.C.S. 248, which was a cervical centrum from the Kimmeridge Clay of Nuneham, Oxfordshire. Destroyed by fire at the Royal College of Surgeons Museum.

STATUS. *Nomen nudum; nomen oblitum.*

Apractocleidus teretipes Smellie, 1915

HOLOTYPE. H.M.G. V.1091.

STATUS. Subjective junior synonym of *Cryptoclidus eurymerus* (Phillips, 1871) (see p. 258); type species of the genus *Apractocleidus* Smellie, 1915.

Plesiosaurus truncatus Owen, 1854

1854 *Plesiosaurus truncatus* Owen: 59.
1889 *Cimoliosaurus truncatus* (Owen) Lydekker: 230 (generic mis-spelling).
1911 *Muraenosaurus truncatus* (Owen) Sauvage: 186–215.

HOLOTYPE. R.C.S. 228, which was a cervical centrum of a 'juvenile' from the Kimmeridge Clay of Shotover, Oxfordshire. Destroyed by fire at the Royal College of Surgeons Museum.

STATUS. *Nomen dubium.*

Plesiosaurus validus Phillips, 1871

SYNTYPES. U.M.O. J.28542–56, 15 cervical vertebrae from the Kimmeridge Clay of Cumnor, Oxfordshire, together with cervical, dorsal and caudal vertebrae from other Kimmeridge Clay sites including Baldon, Oxford. These latter syntypes cannot now be distinguished from other unlabelled material in the Museum.

STATUS. *Nomen dubium; nomen oblitum.*

Plesiosaurus winspitensis Seeley, 1871

HOLOTYPE. S.M.C. J.5345–6, two associated cervical vertebrae from the Portland Stone of Winspit, Dorset. Seeley (1871) also mentioned a pectoral vertebra, but this cannot now be found.

STATUS. *Nomen dubium; nomen oblitum.*

Discussion of the phylogeny and classification of plesiosaurs

Historical review

In 1821, Conybeare proposed the generic name *Plesiosaurus* for an animal whose structure he considered to be intermediate between *Ichthyosaurus* and the crocodiles. In 1824 he named the type species *Plesiosaurus dolichodeirus* on account of its long neck.

The ordinal name Plesiosauria was proposed and defined by de Blainville (1835) to include only the plesiosaurs, and is now established by useage rather than by priority (Welles 1943) as the name for an order of the subclass Sauropterygia Owen, 1860 ('suborder' and 'order' of Welles; present ranking after Tarlo 1967).

Owen made the first major division of the order by introducing the name *Pliosaurus* (in 1841 as a subgenus, in 1861 as a genus) to include all plesiosaurs with large 'canine' teeth, a large head and a short neck. The genera *Plesiosaurus* and *Pliosaurus* are now the types of the two major superfamilies, but the significance of Owen's division was not appreciated until 1924, when Watson discussed the evolution of the group and distinguished divergent lines of long-necked and short-necked forms ranging from the Lower Jurassic to the Upper Cretaceous.

The years between 1861 and 1943 saw a host of attempts to produce classifications in the absence of an understanding of evolution. Most of these attempts were based upon isolated skeletal characters rather than upon a synthesis of characters taken from the whole skeleton. Characters so used include the relative length of the neck (Kiprianov, 1882; Seeley, 1892; Bogolubov, 1912; Nopcsa, 1928); the length of individual centra (Owen, 1865); the number of cervical rib-heads (Seeley, 1892; Williston, 1925; Woodward, 1932; Kuhn, 1935); the presence or absence of an interclavicle (Seeley, 1874*b*; Sauvage, 1879*a*) and the general structure of the pectoral girdle (White, 1940).

Of some historical importance was a classification proposed by Seeley (1892). He divided the Plesiosauria into Dicranopleura and Cercidopleura on the basis of double-headed or single-headed cervical ribs, and then subdivided the Dicranopleura into Brachydeira and Dolichodeira on the basis of a relatively short or long neck (a few intermediate forms being termed 'mesodeiran'). He overlooked the fact that his Cercidopleura also contained brachydeiran and dolichodeiran forms. Although his classification was little used, his names have remained widely employed as descriptive terms, and his emphasis on the number of cervical rib-heads has influenced several taxonomists including Welles.

In 1943, Welles emphasized the importance of basing the classification upon a synthesis of all observable characters, and compiled a list of 22 characters available for study. He recognized that several characters (including general increase in size, reduction of cervical rib-heads from two to one, shortening and broadening of epipodials and development of hyperphalangy) represent progressive evolutionary trends which apply to all lineages and are therefore of secondary importance in taxonomic subdivision. Of greater importance are those characters of opposing nature which occur simultaneously throughout the group, such as the tendencies to lengthen or shorten the neck, and to shorten or lengthen the head and the pelvis. These are the distinguishing features of Watson's (1924) phyletic lines, and from them Welles constructed his diagnoses of the superfamilies Plesiosauroidea and Pliosauroidea. He then subdivided the superfamilies into grades using characters of cervical ribs and epipodials.

In 1962 Welles modified his classification to include the Pistosauridae, but his criteria remained essentially unchanged. Thus the primitive families Plesiosauridae and Pliosauridae are dicranopleurous with elongate epipodials, and the advanced families Elasmosauridae and Dolichorhynchopidae[1] are cercidopleurous with short epidodials.

Welles' division of the superfamilies into grades on the basis of double or single-headed cervical ribs has the advantage of easy practical application; yet Welles did not trust the scheme fully, and placed the English Upper Jurassic plesiosauroid genera (all of which are cercidopleurous) in the primitive dicranopleurous family Plesiosauridae, this presumably on account of their moderate length of neck. It would seem that the precise position of the supposed 'mesodeiran' forms of Seeley (1892) was even here considered to be a problem.

Three classifications have been published subsequently: by Persson (1963), Novozhilov (1964) and Romer (1966, based largely on his work of 1956). Welles' division into the superfamilies Plesiosauroidea and Pliosauroidea has been followed in each classification; but by the use of criteria differing from both those of Welles and of each other these authors have distinguished additional families containing 'mesodeiran' forms. Thus, Persson and Romer have each divided the superfamilies into three (differing) families, and Novozhilov has distinguished four plesiosauroid and five pliosauroid families.

Unfortunately, Persson, Novozhilov and Romer have not listed consistently the state of every character for each family diagnosis. In consequence, the differences between families are not absolutely clear, nor can their classifications be compared. In practice, genera must be assigned to families because of a comparative similarity between the generic and family diagnoses, and not through an absolute conformity to the diagnosis of one family.

The most serious criticism of these three recent classifications is, however, the lack of supporting phylogenetic theory. Novozhilov and Romer did not attempt to relate their classifications to evolution, except in so far as Romer (1956) likened the branching of plesiosaurian phylogeny to that of a bush, with the main branches having a common stock. By means of a figure, Persson suggested that his three pliosauroidean families Rhomaleosauridae, Pliosauridae and Polycotylidae[2] represent grades of a single lineage, whereas in the Plesiosauroidea the Jurassic family Plesiosauridae was ancestral to the two Cretaceous families Cimoliasauridae[2] and Elasmosauridae. Persson did not support this suggestion on osteological grounds. On the contrary, he used as his principal taxonomic criterion the comparative proportions of cervical vertebrae; it is argued below that the extent of variation of such proportions, even intraspecifically, is such as to render them unsatisfactory as taxonomic characters.

It is generally agreed (Welles 1943, 1962; Romer 1956, 1966; Persson 1963; Novozhilov 1964) that the Triassic nothosaurs were ancestral to the Jurassic and Cretaceous plesiosaurs, and that the genus *Pistosaurus* and allied Triassic genera form a phylogenetic link (or links) between the suborders. Traditionally these genera were classified with the Nothosauria, but in the four most recent classifications at least some of the pistosaurs have been included in the Plesiosauria. Welles (1962) included the family Pistosauridae within the Plesiosauroidea; Persson (1963) ranked this group as a separate superfamily; and Novozhilov (1964) and Romer (1966) included within the Pistosauroidea a second Triassic family, the Cymatosauridae. A widely acceptable classification of these forms is unlikely to become available until both the nothosaurs and the Lower Jurassic plesiosaurs have received adequate revision, and their phylogenetic interrelationship is understood.

As a result of discussion of taxonomic characters and a revision of theories on the phylogeny of plesiosaurs (below), it is concluded that existing schemes for the classification of plesiosaurs are inappropriate. A new classification is therefore proposed.

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[1] The name Dolichorhynchopidae Welles, 1962, is a junior synonym of Leptocleididae Romer, 1956; *non* Leptocleididae White, 1940, which is itself a junior synonym of Rhomaleosauridae Nopcsa, 1923.

[2] The names of the family type genera *Polycotylus* and *Cimoliasaurus* were found by Welles, 1962, to be *nomina dubia*.

Characters employed in taxonomy

In 1943, Welles listed and discussed 22 skeletal features at that time known to be variable amongst plesiosaurs, and emphasized the importance of considering all of these together when compiling a classification. Modern classifications reflect this thinking, being based upon a synthesis of many characters; however, there is as yet no general agreement on a scheme of classification below the superfamily level. This situation would appear to stem from a general lack of understanding of evolution within each superfamily. This in turn has led to a widespread misunderstanding of the relevance of each character to ontogeny or phylogeny.

At the present time the best-known plesiosaur material is that in the United States, since this has been reviewed extensively by Welles (1943, 1952, 1962). Unfortunately the American species which he studied do not seem to be represented adequately by specimens of differing and intergrading developmental stages, and so he has not always been able to recognize and distinguish between ontogenetic variants and variants of real evolutionary (and hence taxonomic) significance. The same would apply to English material and its interpretation were it not for the preservation of representative populations of some species in the unique Leeds Collection. Study of this material has enabled the ontogeny of several skeletal features to be observed directly; and furthermore the interspecific variation of certain features of the skulls of these forms has provided additional characters for use in taxonomy.

A total of 38 variable features of the plesiosaurian skeleton are recognized here and are available for consideration as taxonomic characters. These are listed and discussed below.

1. General size. There is a trend towards increase in size with time which is shown throughout the suborder. Most early Jurassic forms have an overall length of 3–5 m, whereas late Cretaceous forms may reach a length of 8–12 m and be proportionally more massive.

2. Relative skull size. The skull may remain relatively small (with respect to the trunk), or may show a chronological trend towards increase in size. The ratio of skull-length to neck-length has been used frequently as an index of skull size, but this is misleading, as decrease of neck length is correlated with increase of skull size in many but not all forms.

3. Tooth form. Large-skulled plesiosaurs have teeth with relatively large roots and a relatively short, wide-based and slightly curving crown which may show considerable wear on its tip. Small-skulled forms have teeth with smaller roots, and with proportionally slimmer crowns which are rather more curved and show little or (usually) no wear on their tips. Crowns are usually circular in section, but may be subtriangular (in Kimmeridgian pliosaurs: Tarlo 1960), or be buccolingually compressed and show a curvature of up to 75° (in *Kimmerosaurus*).

4. Tooth ornament. The teeth of all plesiosaurs except *Kimmerosaurus* are ornamented by numerous longitudinal ridges. The pattern of these ridges is distinctive and therefore taxonomically useful in some genera (in *Cryptoclidus*, and in Oxford Clay pliosaurs reviewed by Tarlo 1960), but since little attention has been paid to it in forms outside the Upper Jurassic, the extent of its usefulness is not known. There is some ontogenetic variation, ornamental ridges being more prominent and sometimes more numerous on the teeth of older individuals.

5. Lower jaw symphysis. The symphysis is generally described as either short or long. A short symphysis is a simple unexpanded median union of the rami, relates only to the first pair of teeth and is correlated with a small skull. A long symphysis shows median antero-posterior expansion, is correlated with a relatively large skull and relates to the alveoli of several pairs of teeth (the number of pairs is variable).

6. Number of pairs of dentary teeth. The range of variation in lower tooth numbers is much less in Lower Jurassic genera (about 24–30) than in those from the Upper Cretaceous

(about 14–58), and trends to increase or decrease the toothrow are evident. The teeth of Lower Jurassic plesiosaurs have seldom been counted accurately, but from personal observations *Plesiosaurus dolichodeirus* (small-skulled, short symphysis) has about 24 teeth each side, whereas *Macroplata longirostris* and *Rhomaleosaurus zetlandicus* (large-skulled, long symphysis) have about 30 each.

The Upper Jurassic large-skulled forms have from 25 (in *Simolestes*) to 40 (in *Peloneustes*) (Tarlo 1960), and the Upper Cretaceous genus *Dolichorhynchops* has 26 pairs (*D. osborni*) or 34 pairs (*D. willistoni*) (Welles 1962). There is therefore no trend in these forms to increase or decrease the number of lower teeth, which averages consistently about 30 pairs.

The small-skulled forms, on the other hand, show a marked trend to decrease the lower teeth from 24 pairs: the Upper Jurassic genus *Muraenosaurus* has about 22 pairs (present work), and in Upper Cretaceous forms this is reduced to between about 18 (in *Styxosaurus*) and 14 (in *Thalassomedon*) (Welles 1952). Only two genera with a short symphysis do not follow this trend: the Upper Jurassic genus *Kimmerosaurus* has 36 pairs (present work), and the South American Upper Cretaceous genus *Aristonectes* has 58 pairs of lower teeth (Cabrera 1941).

There is slight ontogenetic variation in this character, 'adults' having one or two pairs of dentary teeth more than 'juveniles'.

7. Number of pairs of premaxillary teeth. There are usually 5 teeth borne by each premaxilla, and this number is probably primitive for the group. Large-skulled forms appear always to retain this number. In the Upper Jurassic small-skulled genera *Muraenosaurus* and *Tricleidus* the most anterior tooth is reduced in size (present work), as in most Cretaceous forms, and in the Cretaceous genera *Thalassomedon* and *Styxosaurus* it is lost, reducing the count to four (Welles 1952). There are only three genera in which the premaxilla bears more than 5 teeth, these being *Cryptoclidus* and *Kimmerosaurus* with 6 and at least 8 respectively (present work), and *Aristonectes* with 15 (Cabrera 1941).

8. Regularity of dentition. Large-skulled forms (all with a long symphysis) tend to develop large 'caniniform' teeth towards the tip of the snout around the symphysis and on the premaxillae. Posterior to these the teeth are smaller and form a regularly decreasing series. Early small-skulled forms (all with a short symphysis) have a regular dentition without the precocious development of 'caniniform' teeth. Later forms showing an increase in tooth number (*Cryptoclidus, Kimmerosaurus* and *Aristonectes*) retain this regularity (present work; Cabrera 1941), whereas in the remaining later genera (showing a trend towards reduction in tooth number) the regularity becomes disrupted by the reduction in size of the most anterior premaxillary tooth and by increase of all other premaxillary teeth together with one or two maxillary teeth in a position beneath the anterior margin of the orbit (present work). The lower toothrow in small-skulled forms is generally regular, and the largest teeth occur beneath the maxillo-premaxillary suture.

9. Parietal crest. When Williston (1903) stated that the parietals may form a high thin crest or be without such a crest he was almost certainly referring to ontogenetic development, the sagittal crest being the last part of the parietals to ossify. However, a crest is not developed in *Kimmerosaurus*, and in this genus only are the lateral excavations of the parietals separated by at least 1 cm of finished dorsal surface (present work).

10. Pterygoid structure. Usually the pterygoid is overlapped posterolaterally by the quadrate, which develops a rough socket for its reception; but in *Kimmerosaurus* the pterygoid overlaps the quadrate posteromedially, and the quadrate produces a large flange which extends forward along the anterolateral surface of the pterygoidal quadrate ramus. The manner of contact with the braincase is variable, and the form of the facets and processes on both the pterygoid and the braincase elements differs from genus to genus. Details of pterygoidal structure are known only for English Upper Jurassic small-skulled genera (present work), and so wide-ranging conclusions cannot be drawn.

11. PAROCCIPITAL PROCESS. The relative length and thickness of the paroccipital process is variable (present work). In *Muraenosaurus* and *Tricleidus* it is long and slender and resembles those of Cretaceous genera figured by Welles (1943, 1952, 1962). In *Cryptoclidus* it is shorter, and in *Kimmerosaurus* it may reasonably be described as short and massive by comparison with most genera. This character is inadequately described for most genera, and wide-ranging conclusions cannot be drawn.

12. OCCIPITAL CONDYLE. Welles (1962) described the occipital condyle as either 'projecting, hemispherical, marked off by a constricting groove' (in the Plesiosauroidea) or 'short and close to the skull' (in the Pliosauroidea). The constricting groove develops ontogenetically in at least the genus *Muraenosaurus* (present work), being most prominent in the oldest individuals, but its presence is indeed characteristic of small-skulled forms. The occipital condyle of almost all small-skulled genera is formed from the basioccipital only; but in *Cryptoclidus* and *Kimmerosaurus* (present work) its formation is shared by the pedicles of the exoccipitals. In these two genera the condyle is also very short, and is not ringed by a groove. A third genus with this structure might be *Aristonectes*; in this form the exoccipitals are not known, but the basioccipital part of the condyle is described as very short, without a separating groove (Cabrera 1941). The condyles of most large-skulled forms have not been described adequately, and a detailed comparison cannot be made.

13. ATLAS. Linder (1913) distinguished between two types of atlas formation: 'a. Atlas centrum forms most of the support for the condyle. b. Atlas intercentrum and arches ring the centrum and may exclude it from the condyle'. However, the atlas and axis fuse in 'adults' with complete obliteration of all sutures, and in 'juveniles' the very small atlas intercentrum and neural arch are usually lost. Although apparently variable, this character is scarcely known and therefore only of dubious taxonomic value.

14. NUMBER OF CERVICAL VERTEBRAE. The primitive number of cervical vertebrae for the suborder Plesiosauria is probably around 28 to 32 (there are 32 in *Plesiosaurus* and *Macroplata*, and 28 in *Rhomaleosaurus*; primitive Lower Jurassic genera). By the Cretaceous the number of cervical vertebrae ranges from 71 (in *Elasmosaurus*) to 13 (*Brachauchenius*). Trends to increase or decrease the number of cervical vertebrae are evident, and are correlated with small skulls and a short symphysis (increase in numbers) or with large skulls and a long symphysis (decrease in numbers). The primitive number of cervical vertebrae is apparently retained only in one Cretaceous genus, that being *Aristonectes*, with 25 preserved and an estimated 5 missing (Cabrera 1941).

15. PROPORTIONS OF VERTEBRAL CENTRA. Early writers placed much taxonomic emphasis on the variations of central proportions, probably because isolated centra are the most frequent finds of plesiosaurian material. After some statistical work, Welles (1952) demonstrated that central proportions vary intergenerically (taxonomically important variation), but also vary according to the ontogeny (centra shorter in younger individuals) and to position on the vertebral column (neither type of taxonomic consequence). In the present work it is observed that the centrum breadth is always greater than the height (or in dorsals is subequal to height), and so for all regions of the column the ratios of these parameters are of no taxonomic use, whereas the ratio of length to average diameter, especially of the neck region, shows intergeneric variation. In the neck, proportional length is correlated with number of cervical centra such that a relatively long (or short) neck is usually produced both by increasing (or decreasing) the number of vertebrae and by increasing (or decreasing) the proportional length of each. The vertebrae with the greatest proportional length (or shortness in short-necked forms) are always those in the anterior one-third of the neck.

Relative neck length has been recognized as of major taxonomic significance since the publications of Owen (1869), Lydekker (1889) and Seeley (1892), but there has been much confusion of what are here regarded as three interrelated characters. The true relative neck length (i.e. relative to the length of the trunk) is itself a function of the number of cervical vertebrae and their individual relative lengths. For example, *Plesiosaurus dolichodeirus*

(Lower Jurassic) and the genus *Cryptoclidus* (Upper Jurassic) both have 32 cervical vertebrae which are similarly proportioned; however, the former is always regarded as 'dolichodeiran' whereas the latter, having a neck which is relatively shorter than in contemporary genera such as *Muraenosaurus*, is described frequently as 'mesodeiran' (e.g. Delair 1959, Persson 1963). The term 'mesodeiran' is meaningless, and is also misleading since its use implies evolutionary change from the primitive condition.

16. LATERAL KEEL ON CERVICAL CENTRA. The 'lateral keel' (Welles 1952, 1962) or 'lateral longitudinal ridge' (Welles 1943, Persson 1963) is a small but prominent crest of bone which, if it occurs, divides the lateral surface of cervical centra longitudinally into subequal upper and lower concave areas. It is correlated with neck length, and is almost invariably present on anterior cervicals of long-necked forms of the Upper Jurassic and Cretaceous. Its development is presumably associated with the strengthening of neck muscles and ligaments which would have been required for the efficient mechanical management of the elongated neck. It is absent in all short-necked forms.

17. ARTICULAR FACES OF CENTRA. The centra of primitive forms have concave articular faces, but these tend to become flat in long-necked forms and especially in Cretaceous genera. There is also some ontogenetic variation (present work): in 'juveniles' the articular faces tend to be relatively flat and have angular edges and there may be a small central pit, whereas in 'adults' the pit may fill and the edges ossify so as to become more rounded and cause the face to be more concave.

18. SURFACE ORNAMENT OF CENTRA. Superficial surface features of centra such as 'plications', rugosities, extent of the development of a ventral keel and the position of nutritive foramina, have been variously emphasized by early writers. Such features are very variable, and also vary ontogenetically (present work); for example, 'plications' found on the centra of 'juveniles' of *Muraenosaurus* develop into less regular rugosities in the 'adult'. Nutritive foramina follow a regular pattern, being close together (with the development of a keel between them) in anterior cervicals, moving farther apart in posterior cervicals, ascending the lateral surface in dorsals and sacrals and either disappearing or returning to the ventral surface in an irregular fashion (usually multiplied in number) in caudal centra. Surface ornament cannot be relied upon as a primary character for distinguishing species, but may be of secondary use in some cases, as with the forms described by Tarlo (1960).

19. FUSION OF NEURAL ARCHES AND RIBS WITH CENTRUM. In Upper Jurassic forms the fusion of axial skeletal elements is ontogenetic: neural arches and cervical and caudal ribs are free in 'juveniles', but fuse with complete obliteration of the sutures in the 'adult' (present work). Welles (1962) regarded fusion of neural arches and centra as of minor taxonomic importance in Upper Cretaceous forms, and gave 'arches not fused to centra' as a character in his diagnosis of the Lower and Middle Jurassic family Plesiosauridae. It is most unlikely that this character can be applied taxonomically at the family level; but it is nevertheless possible that free neural arches in the 'adult' may prove to be a feature of some primitive forms.

20. HEIGHT OF NEURAL SPINE. Welles (1943) included 'neural spines high or short' in his list of characters available for taxonomic consideration; however, this variation is ontogenetic, the bony part of the neural spines being proportionally shorter in 'juveniles' since they are terminated in cartilage.

21. CERVICAL RIB HEADS. The cervical ribs of all Lower Jurassic plesiosaurs are double-headed (dicranopleurous), and in consequence the cervical centra bear paired facets for the tuberculum and capitulum. There is a trend throughout the whole group to combine the heads into a single structure (ribs cercidopleurous). In forms with a short symphysis this has occurred by the Upper Jurassic, whereas in forms with a long symphysis it is delayed until the Cretaceous. Welles (1962) based the subdivision of his superfamilies upon the number of cervical rib heads; but he did not apply his diagnoses strictly, and included the English Upper Jurassic cercidopleurous genera in his dicranopleurous family Plesiosauridae.

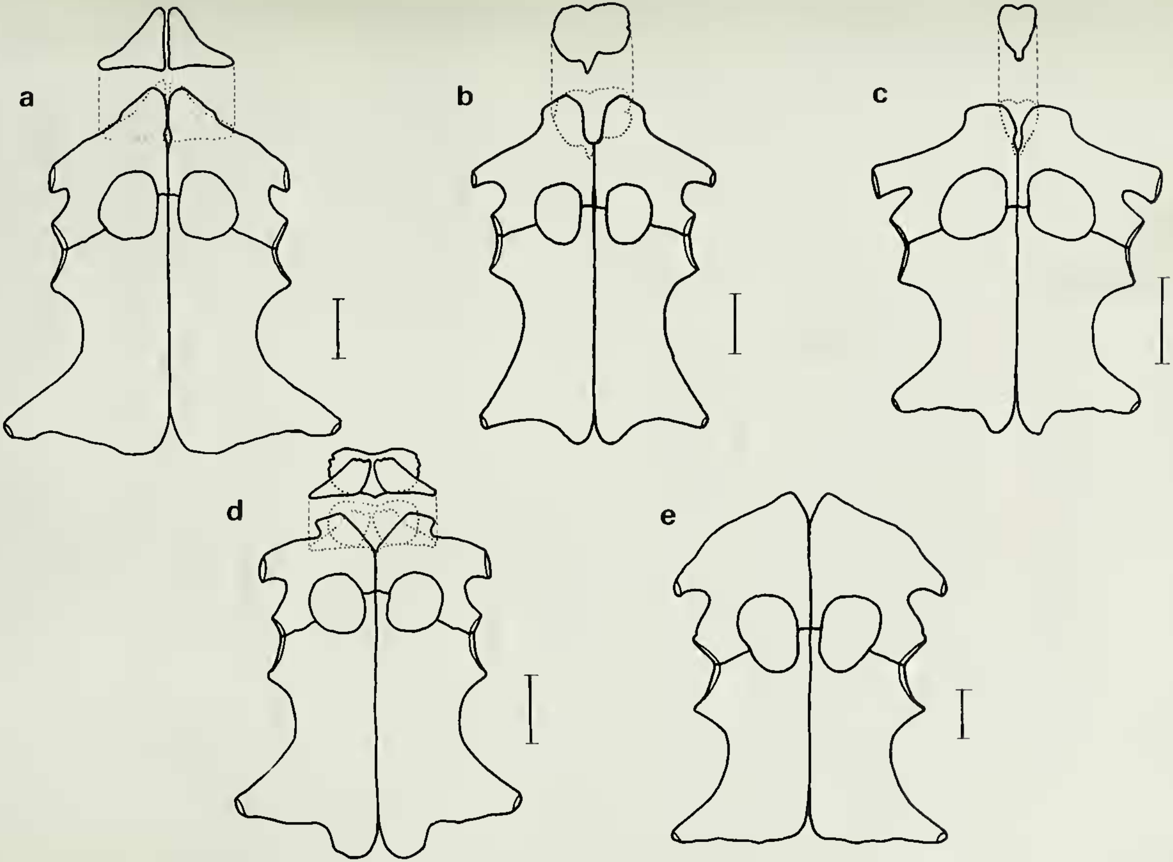

Fig. 43 Comparison of pectoral girdles of English Upper Jurassic plesiosauroids, with dermal elements moved forwards to show ventral rami of scapulae. Dorsal profiles: a, *Cryptoclidus eurymerus* R.2616; b, *Muraenosaurus leedsii* R.3704; c, *M. beloclis* R.1965; d, *Tricleidus seeleyi* R.3539; e, *Colymbosaurus trochanterius* M.M. LL.5513–8. Scale lines represent 10 cm.

22–23. CLAVICLES AND INTERCLAVICLE. Variations in the development and shape of the clavicles and the interclavicle (elements which are typically very conservative in other reptile groups) have been overemphasized frequently in taxonomic discussion, and have been taken as of primary taxonomic importance at generic and even family level (e.g. by Andrews 1910 and White 1940). It is important that this variation be put into proper perspective.

In other reptile groups the clavicles and interclavicle play important functional roles for which they are structurally adapted. Thus any change in their form reflects a change in their function, and is of importance at a relatively high taxonomic level. However, in all but the earliest plesiosaurs the ventral rami of the scapulae become greatly expanded and meet in the ventral midline superficial to the interclavicle and clavicles. Muscles which once had their origins on the ventral surfaces of the dermal girdle must therefore have transferred to the ventral rami of the scapulae, which thus replace the interclavicle and clavicles both mechanically and as sites for muscle origin.

In plesiosaurs, therefore, these elements are no longer functionally important, and cease to be structurally adapted for the lost functions. Tendencies to modify, reduce and even to lose the clavicles and interclavicle are evident, but as these changes are not of functional significance they must be regarded as of only minor taxonomic importance. Indeed, it is possible to demonstrate variation in the relative development of the dermal pectoral girdle elements within a single species, as for example in *Muraenosaurus leedsii* (see Fig. 21, p. 290).

Clavicles and the interclavicle are retained in a moderately well-developed state in several Upper Cretaceous genera (e.g. *Thalassomedon, Morenosaurus*), and so any supposition that they had been lost in earlier genera in which they are unknown (e.g. *Colymbosaurus*) must be regarded with suspicion unless the number of otherwise entire specimens is large. However, there are forms (e.g. *Muraenosaurus beloclis, Cryptoclidus eurymerus*) in which the clavicles or interclavicle or both are preserved but reduced to insignificance; this trend towards reduction could well have resulted in the loss of these elements in their descendants. The absence of clavicles or interclavicle is an unreliable negative character which should be used with much caution in taxonomic discussion.

24. VENTRAL PROCESS OF SCAPULA. In all but the earliest plesiosaurs the ventral processes of the scapulae in 'adults' met in the ventral midline superficial to the clavicles and interclavicle. In 'juveniles' they were separated to a varying degree by cartilage, as was demonstrated by Andrews (1895*a*) in *Cryptoclidus eurymerus*; such variation of length is therefore ontogenetic. The relative width of the ventral process in 'adults' is, however, of some taxonomic use. The process is relatively narrow in many early forms; it tends to remain so in short-necked large-skulled genera, and may become progressively broader in long-necked forms.

25. PECTORAL BAR. The presence or absence of a median pectoral (scapulocoracoid) bar has been overemphasized and misunderstood frequently by taxonomists. In many Lower Jurassic plesiosaurs this bar does not develop even in the 'adult'; but in Upper Jurassic genera its development is typically ontogenetic, ossification being completed in the 'adult' and frequently followed by fusion of the scapulae and coracoids in 'old adults' (present work). It is probable that many of the Upper Cretaceous forms which have been described (e.g. by Welles 1962, subfamily Alzadasaurinae) as lacking the pectoral bar are in fact based upon 'juvenile' individuals.

26. POSTERIOR CORNUA OF CORACOIDS. The development of cornua is ontogenetic, and so only 'adult' specimens should be considered. There is variation from an almost complete absence of cornua (the width across which is less than the interglenoid width) to a strong projecting development which reaches an extreme condition in *Cryptoclidus* (present work; see Fig. 43).

27. INTERCORACOID FORAMEN. The coracoids unite medially along their entire length in all Jurassic forms, and also in Cretaceous large-skulled short-necked forms, but are character-

istically separated posteriorly by a wide intercoracoid foramen in Cretaceous long-necked forms.

28. Anterior border of pubis. Welles (1943 : 199) stated that the 'pubes . . . may become convex anteriorly or concave'. This, however, appears to be an ontogenetic character. 'Juveniles' have rounded pubes which are therefore convex anteriorly; but as ossification reaches the region of the posterior gastralia, concavities in the anterior border appear which mark the places of contact and possible interlock with the plastron (present work).

29. Relative length of ischia. The ischia are relatively short anteroposteriorly in long-necked forms and relatively long in short-necked large-skulled forms (correlation first noticed by Mehl, 1912).

30. Pelvic bar. Welles (1962) divided his family Elasmosauridae into two subfamilies upon the presence or absence of a pectoral bar and a median pelvic bar. However, as with the pectoral bar, anterior growth of the ischia and posterior growth of the pubes towards each other in the midline is an ontogenetic feature. Complete ossification of the pelvic bar (as in *Elasmosaurus platyurus* and *Brancasaurus brancai*) is probably not of major taxonomic significance.

31. Ilial breadth. Welles (1943 : 199) listed 'ilia becoming narrow proximally or

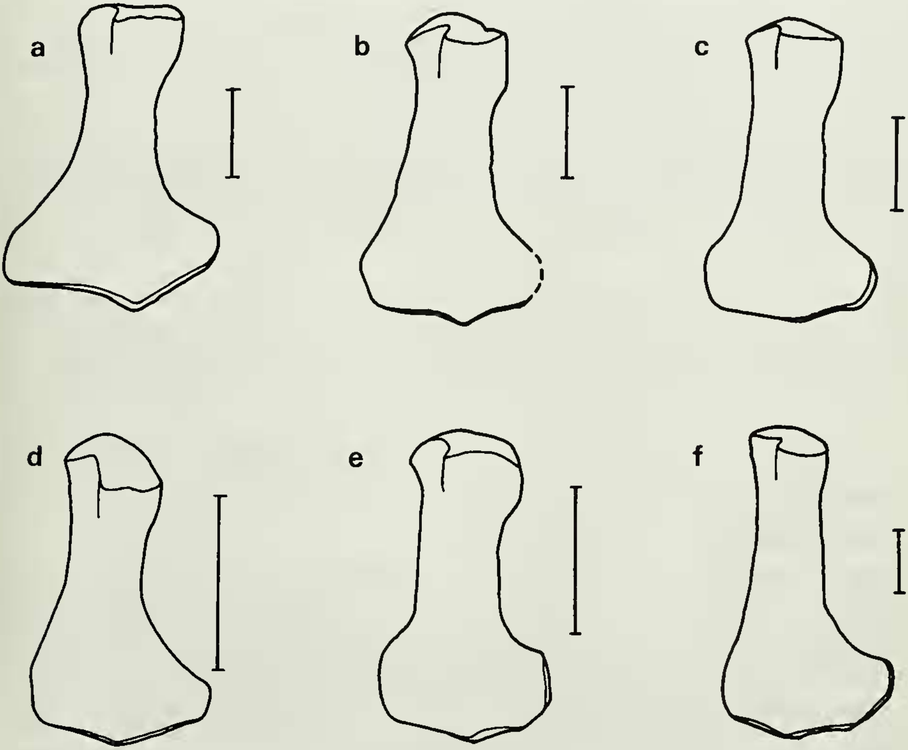

Fig. 44 Comparison of humeri of English Upper Jurassic plesiosauroids, dorsal profiles: a, *Cryptoclidus eurymerus* H.M.G. V.1104; b, *C. richardsoni* R.6696; c, *Muraenosaurus leedsii* R.2426; d, *M. beloclis* R.1965; e, *Tricleidus seeleyi* R.3539; f, *Colymbosaurus trochanterius* M.M. LL.5513–8. Scale lines represent 10 cm.

remaining broad', but without further comment. No evolutionary trends in ilial development have been demonstrated, and irregularities in the form of this element are therefore only of minor taxonomic use.

32. PROPODIAL PROPORTIONS. In short-necked large-skulled forms (which also have elongate ischia) the femur is larger than the humerus, and both propodials tend to have a slim and elongated appearance which Welles (1943, 1962) termed 'pendulous'. In all other forms the propodials are either equal in size or, more usually, the humerus is slightly larger than the femur; these propodials have a more 'massive' (short and stout) appearance.

33. CAPITULUM AND TUBEROSITY (IN HUMERI) OR TROCHANTER (IN FEMORA). Welles (1943 : 199) stated that these '... may remain connected or show changes leading up to complete separation'. These changes are entirely ontogenetic (present work). In 'juvenile' individuals the capitulum and tuberosity (or trochanter) are covered by a single sheet of cartilage, but as ossification proceeds the isthmus between them becomes reduced in width, and they may eventually become separated completely by a strip of periosteal bone in 'old adults'.

34. NUMBER OF EPIPODIALS. In early Jurassic forms there are two epipodials in each limb, and these remain the principal epipodials in all later forms. There is, however, a tendency in several genera to produce additional postaxial ossifications in the epipodial row; this is not of taxonomic importance above the generic level.

35. RELATIVE LENGTH OF EPIPODIALS. The epipodials of primitive forms are elongate and dumb-bell shaped, recalling the shape of the epipodials of a terrestrial ancestor. There is a trend throughout the entire order for the epipodials to shorten and widen until they resemble mesopodials in shape, and they may be considerably broader than long.

36. EPIPODIAL FORAMEN. Welles (1943) stated that the epipodial foramen may be retained or lost. In most forms it is evident between the epipodials in both 'juvenile' and 'adult' specimens, but in a few genera (notably in *Cryptoclidus*) it is not revealed until ossification reaches the advanced 'old adult' stage (present work). It is not possible to prove its absence in any species, since in no specimens apparently lacking the foramen are the epipodials actually fused.

37. PROXIMAL SHIFT OF FIFTH METAPODIAL. In primitive forms the five phalangiform metapodials lie distal to the distal mesapodial row. There is a trend throughout the entire order to shift the fifth (most posterior) metapodial proximally into the distal mesapodial row, and this is achieved fully in many Upper Jurassic forms and almost all Cretaceous forms.

38. EXTENT OF HYPERPHALANGY. There is a general trend to increase the number of phalanges. Early Jurassic forms show hyperphalangy up to about ten in the longest digit, and this is increased to a maximum (Welles 1962) of seventeen phalanges in the longest digit in Cretaceous forms.

Analysis of characters

It is probably true to say that constant variants of any of the above 38 variable features of plesiosaurian osteology could, in appropriate circumstances, prove sufficient for the taxonomic distinction of species, and several in combination might distinguish genera. Ranking of taxa above the generic level is more complicated since to be satisfactory the classification must reflect evolution. It is therefore necessary first to establish which variable characters are of phylogenetic significance, to assess their relative importance, and then to formulate a hypothesis of plesiosaurian phylogeny.

The 38 characters listed above may be grouped together into four categories of differing phylogenetic significance, as follows:

CATEGORY A. Eight characters (9, 18, 19, 20, 25, 28, 30 and 33) may be dismissed as of no phylogenetic significance since their variations are due largely or entirely to ontogenetic growth. Taxonomic use of these characters should be limited to specific and generic diagnoses; and even here they are likely to prove unsatisfactory.

CATEGORY B. The variation of six characters (10, 11, 13, 26, 31 and 36) is either apparently random (showing no evolutionary trends which may be correlated with those of other characters) or is inadequately known for conclusions about evolutionary trends and correlation to be drawn. A seventh character (4, tooth ornament) belongs largely in this category, except that there appears to be a trend towards reduction and ultimate loss of tooth ornament in the genera *Cryptoclidus* and *Kimmerosaurus*. These seven characters are taxonomically reliable, but as they apparently lack any phylogenetic significance (with the exception mentioned), their use should be limited at the present time to specific and generic diagnoses.

CATEGORY C. Eight characters (1, 21, 22, 23, 34, 35, 37 and 38) show progressive unidirectional evolutionary change which affects the entire order. These changes (general increase in size, reduction of the dermal elements of the pectoral girdle and improvements to the structure of the paddles) are associated largely with adaptation of a once-terrestrial body form to an aquatic mode of life, and occur irrespective of other changes which result in fragmentation of the group. Use of these characters in classification at the family-group level would produce chronologically horizontal divisions and separate all phyletic lineages into primitive and advanced grades.

CATEGORY D. The remaining fifteen characters (2, 3, 5, 6, 7, 8, 12, 14, 15, 16, 17, 24, 27, 29 and 32) exhibit variants of opposing nature which occur simultaneously. The variants frequently show divergent evolutionary trends which increase and accentuate their differences. Furthermore, the variants and trends of any one of these characters are found in association with particular variants and trends of several other characters within this category. Correlation of these associated variants and trends leads to the recognition of phyletic lineages and enables evolutionary hypotheses to be formulated. By combining the essentials of these correlated character variants into family-group diagnoses, and ranking the groups with respect to an evolutionary hypothesis, a classification may be produced which reflects evolution.

It is interesting to note that, of the fifteen characters listed in category D, the first seven occur in the skull. Emphasis in the higher classification of plesiosaurs should therefore be placed equally upon features of the skull and the postcranial skeleton, as is the case in the majority of reptile groups. That such equal emphasis has never before been given to the skull is explained by the relative lack of good skull material compared with the relative abundance of postcranial remains.

The phylogeny of plesiosaurs

In order to recognize phyletic lineages within the Plesiosauria it is necessary to undertake an analysis and correlation of the fifteen category D characters. If the genera *Cryptoclidus*, *Kimmerosaurus* and *Aristonectes* are omitted from consideration, such an analysis indicates clearly the presence of two distinct lineages which agree in essence with those recognized by Watson (1924) and Welles (1943, 1962) and classified by the latter as the superfamilies Plesiosauroidea and Pliosauroidea.

The first lineage ('plesiosauroidean' lineage of Welles 1943) includes forms which have relatively small skulls; a short mandibular symphysis; teeth with slim crowns not worn on their tips; a relatively broad scapular ventral ramus; relatively short ischia; and propodials which are 'massive' and of which the humerus is generally the larger. These forms show chronological trends to decrease the tooth number; to develop large premaxillary and maxillary teeth separated by smaller teeth around the maxillo-premaxillary suture; to increase the number of cervical vertebrae; and to increase the relative length of each cervical centrum. Advanced members of this lineage also develop platycoelous rather than amphicoelous vertebrae; a lateral keel on cervical centra; and a wide intercoracoid vacuity.

The second lineage ('pliosauroidean' lineage of Welles 1943) includes forms which have relatively large skulls; a long mandibular symphysis; teeth with relatively short, broad and strong crowns which frequently show considerable wear on their tips; a relatively narrow scapular ventral ramus; relatively long ischia; and propodials which are 'pendulous' and of which the femur is larger than the humerus. These forms show chronological trends to develop large teeth around the mandibular symphysis; to decrease the number of cervical vertebrae; and to decrease the relative length of each cervical centrum.

The known geological range of both these lineages extends from the base of the Jurassic to the Upper Cretaceous (a few indeterminate remains from Middle and Upper Triassic deposits have been recorded as plesiosaurian) and their ancestors are undoubtedly to be found amongst the nothosaurs of the Trias. Much has been suggested relating *Pistosaurus* to the 'plesiosauroidean' lineage (e.g. Edinger 1935; Welles 1943; Romer 1956), but the relationships of the 'pliosauroidean' lineage have been largely overlooked. Welles (1943) doubted that all plesiosaurs could have descended from pistosaurs, since the 'plesiosauroidean' and 'pliosauroidean' lineages do not show sufficient 'retrospective convergence'. Skull reconstructions of other nothosaurs, for example *Ceresiosaurus* (by Peyer, reproduced in Romer 1966: fig. 188) show that at least some forms had relatively large skulls and a long mandibular symphysis, and so it would seem probable that the two lineages had separate nothosaurian origins.

The English Upper Jurassic genera *Cryptoclidus* and *Kimmerosaurus* (described above), together with the South American Upper Cretaceous genus *Aristonectes* (described from an incomplete skull and partial postcranial skeleton by Cabrera 1941) show distinct characters and trends in their teeth and dentition and in the form of the occipital condyle, and at the same time lack the principal divergent trends which characterize the 'plesiosauroidean' and 'pliosauroidean' lineages. The dentition is regular, lacking regional precocious development. The number of cervical vertebrae (known in *Cryptoclidus* and reasonably estimated in *Aristonectes*) remains about thirty, which seems to have been the primitive number in all lineages; these forms therefore lack trends either to increase or decrease the cervical number. There is also no trend to lengthen or shorten the individual cervical centra, which have proportions similar to the most primitive Lower Jurassic forms. *Aristonectes* is unique among Upper Cretaceous genera in possessing the primitive neck construction.

Four features of the skull serve to unite these genera and to distinguish them from all other forms:

(i) The premaxilla of all other genera bears a total of 5 teeth (some elasmosaurs have secondarily lost the most anterior tooth), but in *Cryptoclidus*, *Kimmerosaurus* and *Aristonectes* this number is exceeded. There is a definite trend to increase the premaxillary tooth number, which is 6 in *Cryptoclidus*, at least 8 in *Kimmerosaurus* and 15 in *Aristonectes*.

(ii) There is a trend to increase the number of teeth on the lower jaw ramus from 24–26 in *Cryptoclidus* through 36 in *Kimmerosaurus* to 58 in *Aristonectes* (the latter, known from the number of sockets, being the greatest number recorded among the Sauropterygia).

(iii) The teeth (not known in *Aristonectes*) show a trend towards the reduction (in *Cryptoclidus*) and absence (in *Kimmerosaurus*) of the ornament of longitudinal ridges which characterizes the teeth of all other forms.

(iv) The occipital condyle, which in all other genera is formed entirely from the basioccipital, is formed from both the basioccipital and the exoccipitals in *Cryptoclidus* and *Kimmerosaurus*; it is possible that this may also have been the case in *Aristonectes* (see discussion of character 12, p. 329).

The evidence cited above indicates that the genera *Cryptoclidus*, *Kimmerosaurus* and *Aristonectes* are representatives of a third and distinct phyletic lineage. This lineage has a known geological range from the Upper Jurassic (Callovian) to the Upper Cretaceous

(Maastrichtian). *Cryptoclidus*, with only 6 premaxillary teeth and 24–26 pairs of dentary teeth, is a primitive representative, whereas *Aristonectes* is an advanced form.

Several characters shown by *Cryptoclidus*, *Kimmerosaurus* and *Aristonectes* (such as those of the neck) are primitive to both the 'plesiosauroidean' and 'pliosauroidean' lineages. There are, however, no characters retained which are primitive only to the 'pliosauroidean' lineage, whereas there are six characters exhibited by these genera which are found in primitive members only of the 'plesiosauroidean' lineage. These are a relatively small skull; a short mandibular symphysis; teeth with relatively slim crowns not showing wear on their tips; a relatively large ventral process of the scapula; a relatively short ischium; and propodials which are 'massive', and of which the humerus is larger than the femur. The postcranial characters are known only for *Cryptoclidus*, but as this is the most primitive representative of the newly recognized lineage it is unlikely that the similarity is due to convergence. It is therefore evident from this analysis that the *Cryptoclidus–Kimmerosaurus–Aristonectes* lineage is descended from primitive 'plesiosauroidean' stock, perhaps in the Lower or Middle Jurassic.

Plesiosaurian classification

Welles (1943) described the two principal phylogenetic lineages, and ranked them as separate superfamilies. Using the single or double-headed form of the cervical rib, he then divided each lineage into two grades which he ranked as families. In 1962 he enlarged the diagnoses of his two plesiosauroidean families (Plesiosauridae and Elasmosauridae) by reference to further characters which show progressive unidirectional evolutionary change. However, he did not adhere strictly to his diagnoses, referring the genera *Cryptoclidus*, *Muraenosaurus* and *Tricleidus* to the family Plesiosauridae rather than to the cercidopleuran family Elasmosauridae. This inconsistency was noticed by Persson (1963) who, rather than place those genera in the family Elasmosauridae, was led to produce new and less precise diagnoses of the families which then enabled him to include them in the Plesiosauridae.

The reluctance of previous authors (with the exception of Andrews 1910) to include the cercidopleuran English Upper Jurassic genera with the Cretaceous elasmosaurs results from their concept of what constitutes a 'long neck'. Undeniably, these English genera have shorter necks; even *Muraenosaurus*, with 44 cervical vertebrae, has fewer than the shortest-necked Cretaceous elasmosaurs. However, if it is accepted that the primitive number of cervical vertebrae for all the Plesiosauria is of the order of 28 to 32 (as is argued above), then it follows that any form with significantly more than that number shows a trend towards elongation of the neck, and possesses a neck which is relatively long. *Muraenosaurus* and *Colymbosaurus* must therefore be considered to be long-necked forms, whereas *Tricleidus* and *Cryptoclidus* have necks of a (primitive) moderate length.

Neck length, however, is only one of several characters which show progressive evolutionary change in the plesiosaur–elasmosaur lineage, and which may therefore be used to distinguish primitive and advanced forms. Some characters limited to this lineage, such as the development of platycoely and of lateral crests on the cervical centra, are first developed in Upper Jurassic forms (*Muraenosaurus*), whereas the evolution of a wide posterior intercoracoid foramen has occurred only in some Cretaceous forms. One such trend which shows a gradual development is the reduction in the number of teeth borne by the dentary. This decreases from about 24 teeth in each ramus (as in the Lower Jurassic species *Plesiosaurus dolichodeirus*) to 14 in the Cretaceous genus *Thalassomedon*. Of the English Upper Jurassic genera, *Muraenosaurus* has from 19 to 22 teeth on each dental ramus, whereas *Tricleidus* has only 17, this being fewer than in several Cretaceous forms. In respect to this character, therefore, *Tricleidus* is more advanced than *Muraenosaurus*; this is the opposite of their relationship when judged by the relative length of their necks.

Existing diagnoses which divide the plesiosaur–elasmosaur and the 'pliosauroidean' lineages into primitive and advanced grades rely on the heavy weighting of one character, the nature of the cervical rib head. This character has the advantage of easy practical operation; the cervical rib head can be double (primitive grade) or single (advanced grade), with no known borderline case. However, the reduction in number of cervical rib heads from two to one involves all lineages, and as a consequence the taxonomic weighting of this character serves only to cloud the real issue (that of reflecting phylogeny in classification) by drawing emphasis away from the characters which are of special adaptive significance for each individual lineage. One must therefore question the necessity or desirability of such arbitrarily-based divisions.

In the case of the Pliosauroidea, which appears to be a single major lineage, the reduction in the number of cervical rib heads coincides chronologically with the Jurassic–Cretaceous boundary. Thus the Upper Jurassic forms such as *Pliosaurus* and *Stretosaurus*, which show an advanced development of the shortened neck, enlarged head and powerful dentition, are currently grouped together with primitive Lower and Middle Jurassic forms such as *Rhomaleosaurus* and *Macroplata*, and are taxonomically separated from advanced Cretaceous forms such as *Leptocleidus* and *Dolichorhynchops* which they resemble much more closely. Any sizeable taxonomic group will contain primitive and advanced forms; these terms are well understood, and there seems little point in the creation of arbitrary and less meaningful taxonomic distinctions.

In the case of the Plesiosauroidea the issue is now changed by the recognition of a third phyletic lineage which has evolved from primitive members of the plesiosaur–elasmosaur lineage; it is desirable to recognize the elasmosaurs and the new lineage as separate families, and to distinguish these from their common stock. The descendant families are mutually distinct, and the primitive parental family may be defined objectively by ensuring that it contains only those forms which (except by generic or specific innovations) are not debarred from ancestry to both the descendant families.

The newly recognized lineage is represented by the three genera *Cryptoclidus*, *Kimmerosaurus* and *Aristonectes*; the only available family-group name is Cryptoclididae Williston, 1925 (originally mis-spelt Cryptocleididae). In addition to the progressive trends discussed above, the family is distinguished clearly from all others by two characters, namely, increase in the number of pairs of premaxillary teeth above 5, and involvement of the exoccipital in the formation of the occipital condyle. Two negative features are also of importance in distinguishing the family from the Elasmosauridae, namely the lack of any reduction in the number of pairs of lower teeth below the primitive number of about 24 (there is on the contrary a trend towards the increase of this number, evident even in the primitive genus *Cryptoclidus*), and the lack of any increase in the number of cervical vertebrae above the primitive number of about 28 to 32.

In order to be retained in the family Plesiosauridae, primitive forms must therefore have 5 pairs of premaxillary teeth; an occipital condyle formed from the basioccipital only; not less than the primitive number of pairs of lower teeth and not more than the primitive number of cervical vertebrae. Such forms would not then be debarred from ancestry to either the Elasmosauridae or the Cryptoclididae.

A consequence of this action is to reduce considerably the size and chronological range of the Plesiosauridae, and at the same time to enlarge and extend the Elasmosauridae. In particular, the English Lower Jurassic genus *Microcleidus* Watson, 1909, which has hitherto been included always with the Plesiosauridae because of the double-headed condition of the cervical ribs, must now be recognized as a primitive elasmosaur since it has increased the number of cervical vertebrae to 40 and elongated proportionally each cervical centrum. This genus also demonstrates that reduction in number of cervical rib heads evolved by convergence not only in the two superfamilies but also within the Plesiosauroidea in the families Elasmosauridae and Cryptoclididae.

Only one genus may with certainty be included within the family Plesiosauridae, that being the type genus *Plesiosaurus*. However, this genus has in the past been made a 'catch-all' group, and still remains diverse and in need of revision. It is evident that, of the better-known species, the type species *P. dolichodeirus* and also *P. guilelmiimperatoris* (pro *Guilelmi imperatoris* Dames 1895: 16, emend.) belong in the Plesiosauridae, whereas *'Plesiosaurus' hawkinsii* Owen, 1840 belongs in the Pliosauroidea.

A second Lower Jurassic genus, *Sthenarosaurus* Watson, 1909, is clearly plesiosauroidean but is known from incomplete material. The cervical centra show no definite trend towards proportional elongation, which indirectly implies that the cervical vertebrae may not have been increased in number; but as the skull is not preserved, the presence or absence of cryptoclidid trends cannot be demonstrated. This genus is therefore placed as Plesiosauroidea, *incertae sedis.* All other named plesiosaur genera may be assigned to a family.

There yet remains to be considered the taxonomic position of the genus *Pistosaurus.* Whereas it is generally assumed (e.g. by Romer 1956, Welles 1962, Persson 1963) that the pistosaurs were in some way ancestral to at least the Plesiosauroidea, the nature of this relationship and the relationship to nothosaurs is not understood. In consequence, the genus cannot as yet be classified in either order as a result of phylogenetic arguments, but only for reasons of taxonomic convenience. For the present, an arbitrary line must be drawn which separates the Nothosauria from the Plesiosauria. If the retention or loss of nasals be made the decisive criterion, then the genus *Pistosaurus* must be retained in the Nothosauria; this arrangement permits a classification of the Plesiosauria which is based entirely upon current theories of phylogeny.

The classification of the Plesiosauria which I propose may now be formalized.

A classification of the Plesiosauria

Class **REPTILIA**

Subclass **SAUROPTERYGIA** Owen, 1860

Order **PLESIOSAURIA** de Blainville, 1835

Diagnosis. Sauropterygia in which the nasals are absent; paroccipital processes usually long and slender, meeting squamosal; post-temporal fenestrae large; stapes probably absent; thecodont, with new teeth developing lingual to old and moving buccally to replace them; overall length up to 14 metres; vertebral centra with paired nutritive foramina; coracoids, pubes and ischia developing into large ventral plates; epipodials becoming broader than long; hyperphalangy reaching a maximum of 17. (Diagnosis modified from that given by Welles, 1962.)

Range of order. ? Upper Triassic; Lower Jurassic (Hettangian Stage) to Upper Cretaceous (Maastrichtian Stage).

Included superfamilies. Plesiosauroidea and Pliosauroidea.

Superfamily **PLESIOSAUROIDEA** (Gray, 1825) Welles, 1943

Diagnosis. Plesiosauria with relatively small skulls; mandibular symphysis short, being between the first pair of alveoli only, these not bearing especially enlarged teeth; teeth with slim crowns which do not usually show wear on their tips; at least 28 cervical vertebrae; cervical centra of moderate relative length or elongated; the ventral rami of the scapulae becoming broad; ischia relatively short anteroposteriorly; propodials massive, humerus generally larger than femur.

Range of superfamily. Lower Jurassic (Hettangian Stage) to Upper Cretaceous (Maastrichtian Stage).

Included families. Plesiosauridae, Elasmosauridae and Cryptoclididae. The Lower Jurassic genus *Sthenarosaurus* Watson, 1909 is *incertae sedis.*

Family **PLESIOSAURIDAE** Gray, 1825

Diagnosis. Plesiosauroidea with five pairs of premaxillary teeth; about 24 pairs of dentary teeth; teeth ornamented with numerous longitudinal ridges; occipital condyle formed from the basioccipital only; overall length not known to exceed 3 m; not more than 32 cervical vertebrae; cervical centra of moderate relative length; cervical ribs double-headed; ventral rami of the scapulae remaining relatively narrow; epipodials longer than broad; the fifth metapodial retained in the metapodial row; hyperphalangy limited to about ten phalanges in the longest digit.

Range of family. Lower Jurassic only.

Included genera[3]. The single genus *Plesiosaurus* Conybeare, 1821.

Family **ELASMOSAURIDAE** Cope, 1869

Diagnosis. Plesiosauroidea with a maximum of five pairs of premaxillary teeth; upper tooth row of advanced forms characterized by the development of enlarged premaxillary and anterior maxillary teeth separated by smaller teeth around the maxillo-premaxillary suture; dentary teeth primitively 24 pairs, reducing to a minimum of 14 pairs in advanced forms; teeth ornamented with numerous longitudinal ridges; occipital condyle formed from the basioccipital only, and usually ringed by a constricting groove; overall length from about 3 m in primitive forms to a maximum of 14 m in advanced forms; number of cervical vertebrae primitively *c*. 32 and reaching a maximum of 71 in advanced forms; except for some primitive forms, cervical centra relatively elongated; cervical ribs (primitively double-headed) are single-headed in Upper Jurassic and later forms; ventral rami of the scapulae relatively broad and meeting in the ventral midline in 'adults'; epipodials primitively longer than broad, becoming broader than long in advanced forms; the fifth metapodial shifting proximally into the distal mesapodial row in advanced forms; hyperphalangy of up to 17 phalanges in the longest digit.

Range of family. Lower Jurassic (Toarcian Stage) to Upper Cretaceous (Maastrichtian Stage).

Included genera[3]. *Microcleidus* Watson, 1909 (Lower Jurassic genus); *Colymbosaurus* Seeley, 1874; *Muraenosaurus* Seeley, 1874 and *Tricleidus* Andrews, 1909 (Upper Jurassic genera); *Alzadasaurus* Welles, 1943 and *Brancasaurus* Wegner, 1914 (Lower Cretaceous genera); *Aphrosaurus* Welles, 1943; *Elasmosaurus* Cope, 1868; *Fresnosaurus* Welles, 1943; *Hydralmosaurus* Welles, 1943; *Hydrotherosaurus* Welles, 1943; *Leurospondylus* Brown, 1913; *Mauisaurus* Hector, 1874; *Morenosaurus* Welles, 1943; *Styxosaurus* Welles, 1943 and *Thalassomedon* Welles, 1943 (Upper Cretaceous genera).

Family **CRYPTOCLIDIDAE** Williston, 1925

Diagnosis. Plesiosauroidea with from 6 to 15 pairs of premaxillary teeth; toothrows regular, teeth decreasing in size distally without any enlargement of special teeth; lower teeth, primitively 24 pairs, increasing in number to 58 pairs in advanced forms; tooth ornament reduced or absent; occipital condyle formed by the basioccipital and exoccipitals and not ringed by a constricting groove; overall length probably does not exceed 8 m; number of cervical vertebrae remains about 28 to 32; cervical centra remain of moderate relative length; cervical ribs single-headed; ventral rami of the scapulae relatively broad and meeting in the ventral midline; epipodials broader than long; the fifth metapodial has shifted proximally into the distal mesapodial row; hyperphalangy of up to 15 phalanges in the longest digit.

Range of family. Upper Jurassic (Callovian Stage) to Upper Cretaceous (Maastrichtian Stage).

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[3] Junior synonyms and *nomina dubia* have been omitted from these lists of included genera.

INCLUDED GENERA[3]. *Cryptoclidus* Seeley, 1892 and *Kimmerosaurus* nov. (Upper Jurassic genera); *Aristonectes* Cabrera, 1941 (Upper Cretaceous genus).

Superfamily **PLIOSAUROIDEA** (Seeley, 1874) Welles, 1943

DIAGNOSIS. As for the single family Pliosauridae.

Family **PLIOSAURIDAE** Seeley, 1874

DIAGNOSIS. Plesiosauria with relatively large skulls; premaxillae bear 5 pairs of teeth; mandibular symphysis long, extending back between several pairs of alveoli which bear enlarged teeth; from 25 to 40 pairs of dentary teeth; teeth broad and strong and frequently show wear on their tips; teeth ornamented with longitudinal ridges and may also be keeled; occipital condyle formed from the basioccipital only; overall length from 3 m in primitive forms to about 12 m in some advanced forms; number of cervical vertebrae primitively about 30 and reducing to a minimum of 13 in advanced forms; except for some primitive forms, cervical centra relatively short; cervical ribs double-headed in Jurassic forms, becoming single-headed in Cretaceous forms; ventral rami of the scapulae usually remaining narrow; ischia relatively long anteroposteriorly; propodials slender, the femur larger than the humerus; epipodials primitively longer than broad, becoming broader than long in advanced forms; the fifth metapodial shifting proximally from the metapodial row in primitive forms to the distal mesapodial row in advanced forms; hyperphalangy of up to 16 phalanges in the longest digit.

RANGE OF FAMILY. Lower Jurassic (Hettangian Stage) to Upper Cretaceous (Senonian Stage).

INCLUDED GENERA[3]. *Archaeonectrus* Novozhilov, 1964; *Eretmosaurus* Seeley, 1874; *Eurycleidus* Andrews, 1922; *Eurysaurus* Gaudry, 1878; *Macroplata* Swinton, 1930 and *Rhomaleosaurus* Seeley, 1874 (Lower Jurassic genera); *Liopleurodon* Sauvage, 1873; *Megalneusaurus* Knight, 1898; *Peloneustes* Lydekker, 1889; *Pliosaurus* Owen, 1841; *Simolestes* Andrews, 1909; *Stretosaurus* Tarlo, 1959 and *Strongylokrotaphus* Novozhilov, 1964 (Upper Jurassic genera); *Kronosaurus* Longman, 1924; *Leptocleidus* Andrews, 1922 and *Peyerus* Stromer, 1935 (Lower Cretaceous genera); *Brachauchenius* Williston, 1903; *Dolichorhynchops* Williston, 1902 and *Polyptychodon* Owen, 1841 (Upper Cretaceous genera).

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